

SYSTEMATICS AND PHYLOGENY OF *ELAPHOGLOSSUM* SECTION
LEPIDOGLOSSA (DRYOPTERIDACEAE)

by

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ABSTRACTSYSTEMATICS AND PHYLOGENY OF *ELAPHOGLOSSUM* SECTION*LEPIDOGLOSSA* (DRYOPTERIDACEAE)

by

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Advisor: Robbin C. Moran, Ph.D.

Elaphoglossum (Dryopteridaceae) is one of the most diverse genera of ferns, yet it is noteworthy for lacking monographic studies for any of its subgroups. This study was an attempt to find clades of convenient size for monographic study within *Elaphoglossum* section *Lepidoglossa*, one of the largest sections of the genus. To do that the phylogeny of the section was investigated using three chloroplast markers. These molecular phylogenetic analyses identified 13 clades, two of which were selected for monographic revision: the *Elaphoglossum ciliatum* group and *Elaphoglossum* subsection *Muscosa*. The *Elaphoglossum ciliatum* group turned out to have nine species characterized by laminar scales reduced to minute dots, spiny perispores, and resinous rhizomes. *Elaphoglossum* subsection *Muscosa* turned out to have 15 species characterized by flat scales with acicular marginal cells, scaly laminae, and spores about twice as long as other species of *Elaphoglossum*. Besides constituting a framework from which to choose morphologically recognizable clades of convenient size for monographic study, the phylogeny provided important new insights into the systematics and taxonomy of *Elaphoglossum* section *Lepidoglossa*.

To my mother, sister, and brother

To the memory of my father

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Reading the acknowledgments of any scientific publication has been a secret obsession of mine for years. I just can't help myself from going directly to the acknowledgments of an article or thesis. I guess this is because this section is a window into a part of the story that no scientific publication will tell. This is the part of the story about the human being behind the scientific work...which really intrigues me after all these years of trying to become a researcher.

This obsession, and the fact that this is one of the few parts of my PhD thesis that will make fully sense to some of the ones I love and would like to thank, makes me feel anxious. The anxiety comes also from the fact that I do not want to forget anybody who has helped me, and after five years my memories have become blurry. So I would first like to thank those that I have forgotten. I apologize for having done so.

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INTRODUCTION

With approximately 600 species, *Elaphoglossum* (Dryopteridaceae) is one of the most species-rich genera of ferns (Mickel and Atehortúa, 1980). It has a Panropical distribution, occurring principally in wet-montane and cloud forests; however, a few species reach the temperate regions to 39° latitude north (Azores Archipelago) and to 50° south (Marion and South Sandwich Islands) (Rouhan et al., 2004; Fig 1). The center of diversity is tropical America where ca. 450 described species occur (Mickel, 1990a). Other centers of diversity are Africa and Madagascar (ca. 70 species) and Southeast Asia (ca. 50 species) (Rouhan, 2005).

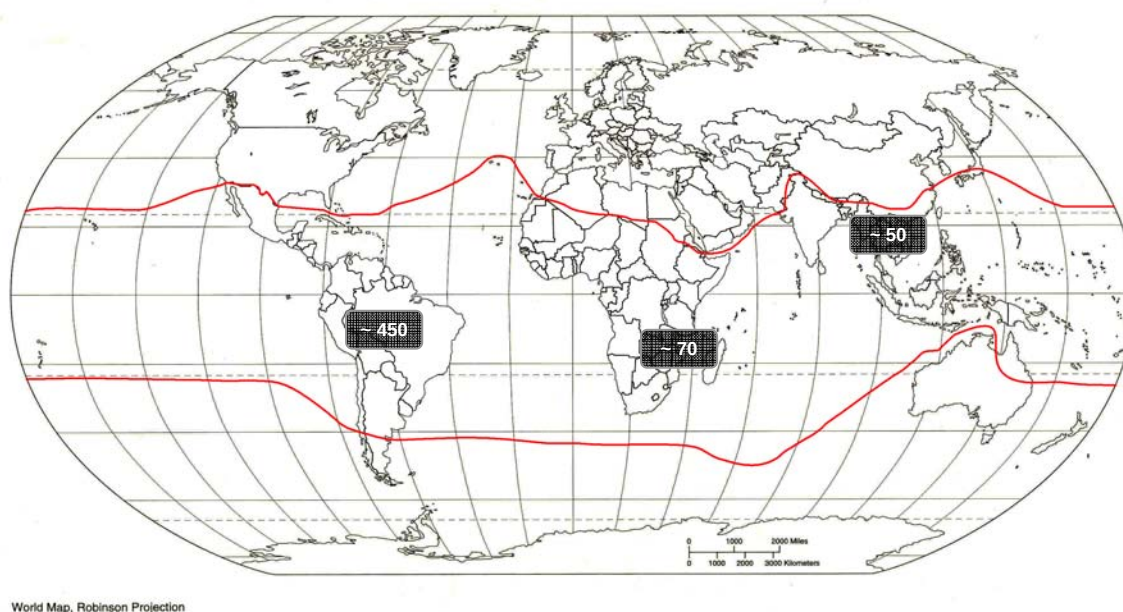


FIG. 1. Distribution of *Elaphoglossum* and centers of diversity with approximate number of species

Morphologically, *Elaphoglossum* is characterized by a mainly epiphytic habit, simple entire leaves, and phyllopodia. Other characteristics, common to *Elaphoglossum* and its most closely related genera, *Bolbitis*, *Lomogramma* and *Teratophyllum* (Schuettpelz and Pryer, 2007) are dorsiventral rhizomes, dimorphic sterile and fertile leaves, free veins, and acrostichoid sori (Fig 2).



FIG. 2. Distinctive characteristics of *Elaphoglossum*. **A.** Acrostichoid sori and dimorphic sterile and fertile leaves. **B.** Transversely elongated ventral meristele in the rhizome. **C.** Free veins.

Elaphoglossum is considered taxonomically difficult at the species level because its species are similar and their distinguishing morphological characters are often few and subtle. To make it more manageable taxonomically, several pteridologists have split *Elaphoglossum* into subgroups (Fée, 1845; Sodiro, 1893; Christ, 1899; Mickel and

Atehortúa, 1980). The most recent study (Mickel and Atehortúa, 1980) proposed a new classification, dividing the genus into nine sections and 21 subsections (Table 1). This classification was based on morphological evidence, such as scale characters, the presence or absence of hydathodes and phyllopodia, rhizome habit, blade texture and shape, and spore morphology. Mickel and Atehortúa's paper stands as the most comprehensive, precise, and extensive study on the classification of the group. Even today it serves as the framework for all taxonomic and phylogenetic studies of the genus, including the present one (Mickel, 1995b; Rouhan et al., 2004; Skog et al., 2004).

TABLE 1. Classification of *Elaphoglossum* by Mickel & Atehortúa (1980)

1. Section Elaphoglossum Subsection Pachyglossa H. Christ Subsection Tenuifolia Mickel & Atehortúa	5. Section Polytrichia H. Christ Subsection Hymenodium (Fée) H. Christ Subsection Hybrida H. Christ Subsection Apoda Mickel & Atehortúa
2. Section Squamipedia Mickel & Atehortúa Subsection Squamipedia Mickel & Atehortúa Subsection Peltapteris (Link) Mickel & Atehortúa Subsection Ovata H. Christ Subsection Feeana H. Christ	6. Section Setosa (H. Christ) Mickel & Atehortúa Subsection Setosa H. Christ Subsection Pilosella H. Christ Subsection Alpestris Mickel & Atehortúa Subsection Plumeriana Mickel & Atehortúa
3. Section Decorata Mickel & Atehortúa	7. Section Eximia Mickel & Atehortúa Subsection Eximia Mickel & Atehortúa Subsection Cardenasiana Mickel & Atehortúa
4. Section Lepidoglossa H. Christ Subsection Polylepidea H. Christ Subsection Microlepidea H. Christ Subsection Pilosa H. Christ Subsection Petiolosa H. Christ Subsection Huacsaro Mickel & Atehortúa Subsection Muscosa Mickel & Atehortúa	8. Section Undulata H. Christ 9. Section Amygdalifolia (H. Christ) Mickel & Atehortúa

More recently, phylogenetic relationships within *Elaphoglossum* have been examined by two studies using chloroplast DNA (Rouhan et al., 2004; Skog et al., 2004). These studies support five of the nine sections originally proposed by Mickel and Atehortúa (1980). The five clades are: 1) the amygdalifolia clade, sister to the rest of the genus and consisting of the

single species *E. amygdalifolium* (Mett. ex Kuhn) H. Christ, characterized by long-creeping rhizomes, hydathodes, phyllopodia, and reddish young fronds; 2) the elaphoglossum clade, consisting of two well supported subclades, platyglossa and pachyglossa, which are sister and characterized by phyllopodia and inconspicuously scaly or glabrous laminae (no known macromorphological characters separate the two subclades, but their perispores differ; Moran et al., 2007); 3) the squamipedia clade, characterized by long-creeping rhizomes, distichously arranged leaves, peg-like aerophores 1–2 mm long, leaves less than 15 cm long, and echinulate spores; 4) the subulata clade, characterized by subulate scales (enrolled at the base); and 5) the lepidoglossa clade, sister to the subulata clade and characterized by phyllopodia, scaly laminae, and scales with acicular marginal cells.

At the species level, morphological similarity continues to hinder the recognition of small natural groups within the genus. As a consequence, taxonomic revision has been slow. The only monographic treatment of *Elaphoglossum* is that by Christ (1899), who included 142 species—all those known at the time. Besides this, over the past 25 years there have been many regional or country-wide floristic studies, such as for Mexico (Mickel and Smith, 2004), Mesoamerica (Mickel, 1995b), Venezuela (Mickel, 1995a), Peru (Mickel, 1991), the Mascarene Islands (Lorence and Rouhan, 2004), and French Polynesia (Rouhan et al., 2008). Yet monographic treatments either of the entire genus or of small groups within it had not been published until the present study was carried out (Vasco et al., 2009a).

The present work constitutes an effort to find clades of convenient size for monographic study within *Elaphoglossum*. Attention was focused on *Elaphoglossum* section *Lepidoglossa*, which contains about one-third of the nearly 600 species described for the genus. The section was recognized on the basis of morphology by Mickel and Atehortúa (1980) and recovered in

the molecular phylogenetic analyses of Rouhan et al. (2004) and Skog et al. (2004).

Morphologically the section contains species with blades covered mostly or entirely by flat scales with acicular marginal teeth (all other *Elaphoglossum* species have laminar scales with marginal teeth terminated by glandular or bulbous cells or gland-tipped marginal processes), veins slender-tipped (not hydathodous), and phyllopodia present. My goal was to investigate the phylogeny of the section using data from chloroplast DNA to provide a framework from which to choose morphologically recognizable clades for monographic study.

A BRIEF SUMMARY OF THE CHAPTERS

This Ph.D. thesis compiles several articles prepared for different peer-reviewed journals. The first two chapters are molecular phylogenetic analyses, which ultimately provided the bases for the work presented in the other two chapters. The last two chapters present monographic revisions of two clades recovered by those molecular phylogenies.

In Chapter 1, molecular data from three non-coding intergenic chloroplast spacers (*atpB-rbcL*, *rps4-trnS*, and *trnL-trnF*) were used to determine what other species might belong to a clade of three species (*E. burchellii*, *E. ciliatum*, and *E. nigrescens*) recovered by previous molecular analyses. The molecular data were also used to examine the phylogeny of the species in that clade. Besides the three species, the taxon sampling included 39 other species of section *Lepidoglossa*. Maximum parsimony and maximum likelihood analyses resolved a clade of ten species (the *Elaphoglossum ciliatum* group) that included the three original species. In Chapter 2, the same three non-coding intergenic chloroplast spacers were used to reconstruct the phylogeny of the entire section *Lepidoglossa*, which contains about one-third of the species described for *Elpahoglossum*. Given the size of the section (ca. 200 species)

and the morphological similarity of its species, a strategy was developed to sample the group broadly and to choose species that represent the morphological and geographical variation of the section. The taxon sampling included 97 species of section *Lepidoglossa*, 21 of which were from the Old World. The analyses identified 13 clades, and these were discussed in terms of their morphological common characters and/or geographical distribution patterns.

Chapters 3 and 4 present taxonomic revisions of two clades recovered by the molecular phylogenetic analyses. The revisions include keys, full synonymy, descriptions, representative specimens examined, index to collectors' names and numbers, illustrations or photo plates, spore photomicrographs, and distribution maps for all species. Chapter 3 is a monograph of the *Elaphoglossum ciliatum* group, a clade that turned out to have nine species characterized by laminar scales reduced to minute dots, spiny perispores, and resinous rhizomes. Chapter 4 is a monograph of *Elaphoglossum* subsection *Muscosa*, a group previously recognized on the basis of morphology (Mickel and Atehortúa, 1980) and recovered in our phylogenetic analyses. *Elaphoglossum* subsection *Muscosa* turned out to have 15 species characterized by flat scales with acicular marginal cells, scaly laminae, and spores about twice as long as other species of *Elaphoglossum*. As part of the taxonomic revisions three new species were described, one nom. et stat. nov. was proposed, and several lectotypes were designated.

CHAPTER 1

CIRCUMSCRIPTION AND PHYLOGENY OF THE *ELAPHOGLOSSUM CILIATUM* GROUP (*E.* SECT. *LEPIDOGLOSSA*, DRYOPTERIDACEAE) BASED ON CPDNa SEQUENCES

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1.1. ABSTRACT

Elaphoglossum (Dryopteridaceae) is one of the most diverse genera of ferns, yet it is noteworthy for lacking monographic studies for any of its subgroups. This study was an attempt to find a clade within *Elaphoglossum* with a convenient size for monographic study. The main goals were to determine what other species might belong to a clade of three species (*E. burchellii*, *E. ciliatum*, and *E. nigrescens*) recovered by previous molecular analyses and to examine the phylogeny of the constituent species of that clade. Molecular data from three non-coding intergenic chloroplast spacers *atpB-rbcL*, *rps4-trnS*, and *trnL-trnF*, were used. The taxon sampling included 42 species of *Elaphoglossum* section *Lepidoglossa*. Maximum parsimony and maximum likelihood analyses resolved a ten species clade (here named the *Elaphoglossum ciliatum*-group), which included the three original species. Three of the species are endemic to the island of St. Helena in the southern Atlantic Ocean. The other seven species are all Neotropical, occurring from Mexico and the West Indies to southern Brazil. Species of the *E. ciliatum*-group are characterized by laminar scales reduced to

minute dots, cristate, echinate perispores, and resinous rhizomes. Other well supported clades within sect. *Lepidoglossa* were recovered in the analyses and are briefly discussed.

Keywords. cpDNA, Dryopteridaceae, *Elaphoglossum*, Ferns, *Lepidoglossa*, Pteridophyta.

1.2. INTRODUCTION

With approximately 600 species, *Elaphoglossum* Schott ex J. Sm. is one of the most diverse genera of ferns (Mickel, 1995a). It is pantropical in distribution and most species-rich in the Neotropics where about 450 described species occur (Mickel, 1990a).

Morphologically, *Elaphoglossum* is characterized by dorsiventral rhizomes, simple entire leaves, free veins, dimorphic sterile and fertile leaves, and acrostichoid sori (Holtum, 1978; Mickel and Atehortúa, 1980). The monophyly of the genus and its placement within the Dryopteridaceae has received strong support from two molecular phylogenetic studies (Liu et al., 2007; Schuettpelz and Pryer, 2007).

Given its diversity, *Elaphoglossum* is noteworthy for lacking monographic studies. This is because the genus presents difficulties in the identification of monophyletic groups of suitable size for monographic study. Those difficulties are mainly due to the big size and taxonomic complexity of the genus: the species are very similar and their distinguishing morphological characters often few and subtle (A. Vasco pers. obs).

Phylogenetic relationships within *Elaphoglossum* have been examined by two studies using the non-coding intergenic chloroplast spacers (IGS) *rps4-trnS*, and *trnL-trnF* (Rouhan et al., 2004; Skog et al., 2004), and the coding chloroplast region *rbcL* (Skog et al., 2004). These studies recognized several clades that largely agreed with groups previously

recognized on the basis of a non-cladistic, morphological study by Mickel and Atehortúa (1980). Of the two molecular studies, the one by Rouhan et al. (2004) included the greatest number of species (123 species, ca. 20% of the species described in *Elaphoglossum*). The study recognized six clades: 1) amygdalifolia, sister to the rest of the genus and consisting of the single species *E. amygdalifolium* (Mett. ex Kuhn) H. Christ, characterized by long-creeping rhizomes, hydathodes, phyllopodia, and reddish young fronds; 2) platyglossa and 3) pachyglossa, which are sister to each other and contain species with phyllopodia and inconspicuously scaly or glabrous laminae (no known morphological characters separate the two groups); 4) squamipedia, characterized by long-creeping rhizomes, distichously arranged leaves, 1-2 mm long peg-like aerophores, leaves less than 15 cm long, and echinulate spores; 5) subulata, characterized by subulate scales (enrolled at the base); and 6) lepidoglossa, sister to the subulata clade and characterized by phyllopodia, scaly laminae, and scales with acicular marginal cells.

The present paper concerns three species belonging to this last group, the lepidoglossa clade (hereafter referred to as sect. *Lepidoglossa*, a name used by Mickel & Atehortúa, 1980). These species, which were included in the Rouhan & al. (2004) analysis, are *Elaphoglossum burchellii* (Baker) C. Chr., *E. ciliatum* (C. Presl) T. Moore, and *E. nigrescens* (Hook.) T. Moore ex Diels (*E. palmense* H. Christ and *E. wacketii* Rosenst. from the Rouhan et al. (2004) study were placed into synonymy with *E. nigrescens* by Vasco & al.(2009a)). These species are atypical within sect. *Lepidoglossa* because their laminae are inconspicuously scaly, the scales being reduced to reddish dots (typical members of the section have conspicuously and densely scaly laminae). Also, these species have rhizomes that dry blackish and produce a shiny, lacquer-like exudate when dry, and their spores are all

echinate (Moran et al., 2007). These similarities are so striking that the above species are frequently confused in herbaria (A. Vasco pers. obs.) and often keyed close together and compared in floras (e.g. Mickel, 1991, 1995b).

In the Rouhan & al. (2004) analysis, these three species (*E. burchellii*, *E. ciliatum*, and *E. nigrescens*) formed a clade that in turn formed a trichotomy with *E. huacsaro* (Ruíz) H. Christ and a clade of eight other species. The objectives of the present study were (1) to determine what other species of sect. *Lepidoglossa* belong to the clade that includes all of the three above-mentioned species, and (2) to examine the phylogeny of the constituent species of that clade. Furthermore, would the same morphological characteristics mentioned above also characterize this clade? The reason for asking these questions was to determine whether the clade might be a convenient size for monographic study.

1.3. MATERIALS AND METHODS

Taxonomic sampling

By examining herbarium specimens, a list of all species of sect. *Lepidoglossa* that had dots (either alone or mixed with typical large scales) on their laminae, and/or blackish shiny rhizomes, and/or echinate spores was generated. Analyses were performed on all of the species on this list and from which suitable material for DNA analyses (26 species) could be gathered. Other species of sect. *Lepidoglossa* were also included that did not have these characters (16 species), but corresponded to clades retrieved in the published molecular analysis close to the clade formed by *E. burchellii*, *E. ciliatum*, and *E. nigrescens* (Rouhan et al., 2004). Multiple accessions for some species were included. As outgroups, species belonging to the other sections of *Elaphoglossum* (based on Rouhan et al., 2004) were

selected. Section *Setosa*, *E. aubertii*; sect. *Polytrichia*, *E. hybridum*; and sect. *Elaphoglossum*, *E. mitorrhizum*, and *E. sieberi*. Information on specimen vouchers and provenance are provided in the Appendix 1.

DNA extraction, amplification, and sequencing

This study utilized sequences from three non-coding intergenic chloroplast spacers (IGS): *atpB-rbcL*, *rps4-trnS* (GGA), and *trnL(UAA)-trnF(GAA)*. Genomic DNA was isolated from silica-dried or herbarium specimens' leaf tissue, using the DNeasy Plant Mini Kit (Qiagen). Dry leaf tissue (approximately 1 cm²) was sealed in a microcentrifuge tube with approximately 1 g of sterile garnet and a ceramic bead. The sealed tubes were placed in a Fastprep lysing FP-120 bead mill (MP biomedical), for 25 sec at maximum speed. Lysis buffer was added directly to the tube (beads and garnet were not removed) and the tubes were incubated at 65°C for 30 min. Extraction then proceeded following the manufacturer's protocol. With the herbarium material an additional proteinase K digestion during the lysis step was performed: 30 µL of proteinase K (20 mg/ml) plus 30 µL of β-mercaptoethanol (98%) were added per tube and tubes were incubated on a tipping plate at 42°C for 24 hr.

General laboratory protocols for amplifying the IGS were as described in Rouhan & al. (2004) for *rps4-trnS*, *trnL-trnF*, and in Rouhan & al (2007) for *atpB-rbcL*. The resulting PCR products were sent to the High-Throughput Genomics Unit (HTGU), Department of Genome Sciences, Univ. of Washington, where they were purified using ExoSap-IT (USB Corporation). Sequencing of the cleaned PCR products used the amplification primers and was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Sequencing reactions were run on an ABI Prism 3130 DNA Analyzer (Applied Biosystems). Forward and reverse sequences obtained were edited and assembled using

Sequencher 4.5 (Gene Codes Corporation). This study newly generated 205 sequences out of 277 included in the analyses presented. All sequences were deposited in GenBank (see Appendix 1 for accession numbers).

Sequence alignment and phylogenetic analyses

Sequences were aligned using ClustalX (Thompson et al., 1997) and then adjusted manually with WinClada 1.00.08 (Nixon, 2002). Ambiguously aligned regions were excluded from the data sets. The three markers' individual matrices were analyzed separately and in combination to identify potential lab errors or conflicts.

Maximum parsimony (MP) analyses were performed using NONA version 2.0 (Goloboff, 1993) running under WinClada 1.00.08 (Nixon, 2002). Indel events were coded using the simple indel coding method of Simmons and Ochoterena (2000) as implemented in 2xread (Little, 2005). Uninformative characters were deactivated, and all sequence characters were treated as non-additive (unordered) and equally weighted. One thousand replications 'mult*N', holding 10 trees per replicate 'Hold/', up to 10000 trees 'hold' were conducted. 'Mult*max*' was used as the tree search strategy. Tree length as well as ensemble Consistency (CI) and Retention (RI) indexes were calculated excluding parsimony uninformative characters. WinClada was used to generate a bootstrap procedure file. Each resampled matrix was analyzed with NONA using 1000 random sequences addition replicates and 3 trees per replicate were held. The strict consensus of the shortest trees, found for each iteration, was saved. The bootstrap values of each clade were mapped onto the strict consensus tree using WinClada.

The data were also analyzed under maximum likelihood (ML) using Garli 0.96 Beta (Zwickl, 2006). Indels were treated as missing data. The ML analyses were performed using

a GTR+I+G model of sequence evolution, as recommended by the program Modeltest 3.7 (Posada and Crandall, 1998), with parameters estimated from the data. Two single “best tree” searches were performed from different random starting trees. Runs proceeded until they met Garlii’s default termination conditions. Support was assessed with 500 bootstrap searches under Garli’s default parameters. The ML tree presented here is output from FigTree v.1.1.2 (Rambaut, 2006-2008).

1.4. RESULTS

Table 1 gives the total length of the aligned matrices after coding indels, the number of parsimony informative characters and its percentage, and the number of parsimony informative indels for each IGS. The amount of parsimony informative variation coincided with the length of the IGS sequenced *atpB-rbcL* (the longest) had the greatest while *trnL-trnF* (the shortest) had the least (Table 1). In the combined data set, coded indels contributed 11.7% of the parsimony informative characters. MP strict consensus trees from each of the three marker regions were compared to check for incongruence, and since none was found, the datasets were combined.

TABLE 1. Summary of the variation in data sets and analyses statistics

Matrix	Terminals	Total				Parsimony informative characters			
		Alignment length	Regular	Indels	% missing data	Total	Regular	Indels	% informative
<i>atpB-rbcL</i>	87	925	877	48	12.9	104	91	13	11.2
<i>rps4-trnS</i>	95	398	381	17	3	90	82	8	22.6
<i>trnL-trnF</i>	95	320	291	29	3	80	69	11	25
Combined analysis	98	1643	1549	94	8.5	274	242	32	16.7

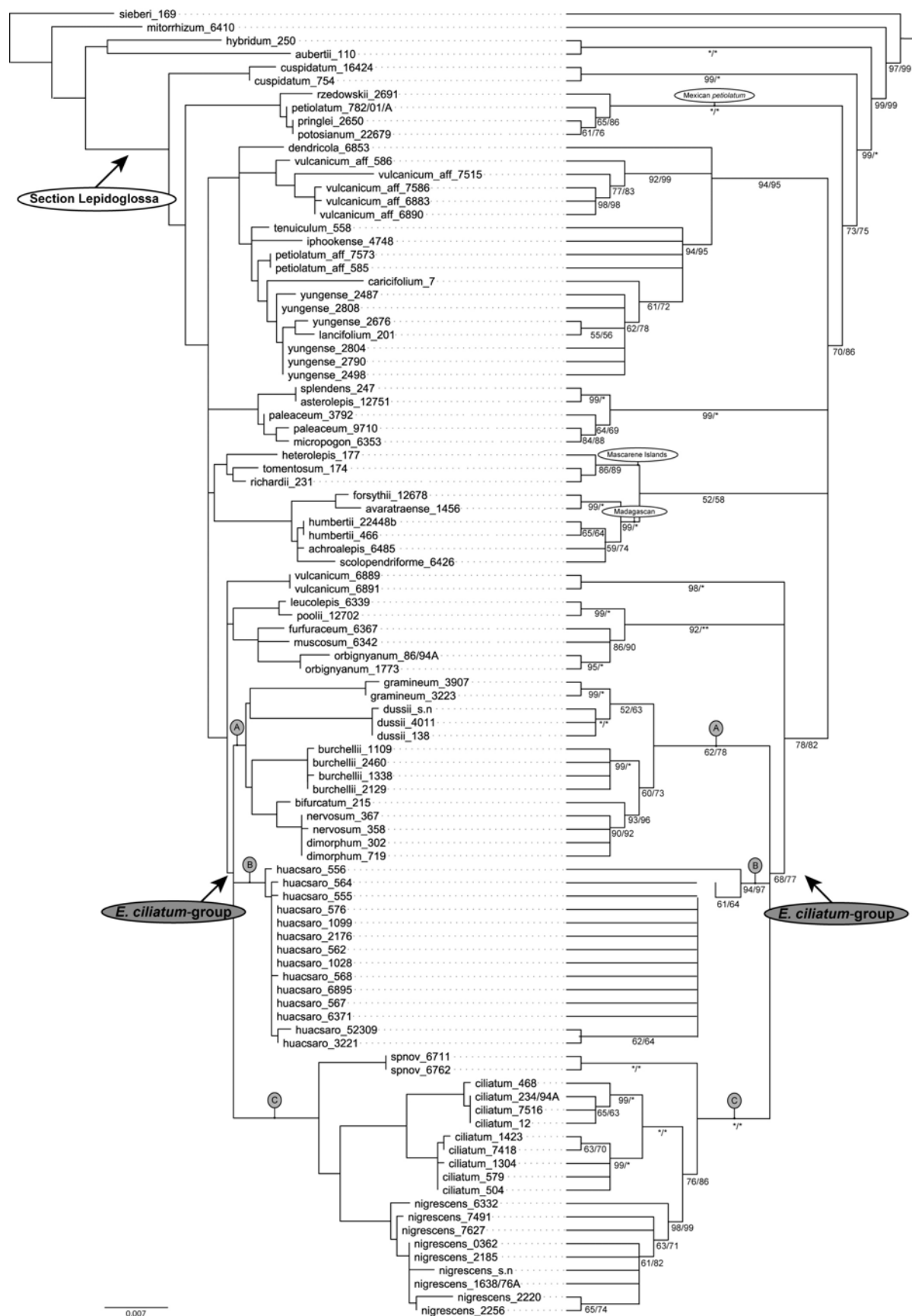
The MP analysis resulted in 72 equally parsimonious trees of 466 steps (CI=0.71, RI=0.91). In the strict consensus tree (472 steps, CI=0.70, RI=0.90), 36 nodes were collapsed. Two most likely trees ($-\ln=5844.156465$ and $-\ln=5844.156498$) with the same topology were obtained from the two “best tree” searches in the ML analysis using the GTR+I+G model.

The MP strict consensus and the ML topologies were completely congruent (Fig. 1). Both the MP strict consensus tree and the ML tree resolved a clade (bootstrap [BS] 68/77; MP/ML- the MP bootstrap value will precede the ML bootstrap value in all future presentations) that includes the three species – *E. burchellii*, *E. ciliatum*, and *E. nigrescens*– with dots on their laminae previously recovered as monophyletic. This clade, hereafter referred as the *E. ciliatum*-group, contained 10 species.

Although not the aim of these analyses, three other well supported clades were recovered in both MP and the ML analyses (Fig. 1): a Mexican-*petiolatum* clade (BS 100/100), a Mascarene Islands clade (BS 86/89), and a Madagascan clade (BS 99/100). The taxon sampling implemented in this study was not designed to evaluate these clades, and therefore it likely does not represent all of their included species.

The *E. ciliatum*-group

For this clade in particular multiple collections for the same species were sampled (referred to in the text as sequences, see Appendix 1 for details). Ten species were resolved in this clade (Appendix 2), which was part of an unsupported polytomy in the MP strict consensus and ML trees (Fig. 1). Within the *E. ciliatum*-group three clades were resolved (Fig. 1, clades A, B and C). Clade A (BS 62/78) included sequences of four species and consisted of two subclades: one containing *E. gramineum* and *E. dussii* (both endemic to the



West Indies; Appendix 2); and the other containing *E. burchellii* (from tropical America and the Dominican Republic; Appendix 2), sister to a subclade containing three species endemic to St. Helena Island. Clade B (BS 94/97) contained sequences of *E. huacsaro*. Clade C (BS 100/100) was formed by three subclades: the first, sister to the other two, consisted of sequences of an undescribed species from Pichincha, Ecuador (*E. sp nov.*); the second consisted of sequences of *E. ciliatum*, sister to a clade comprising sequences of *E. nigrescens*.

For the *E. ciliatum*-group all the sequences belonging to the same species were resolved as part of the same clade. The only exception was the clade composed of species from St. Helena, where sequences of *E. dimorphum* and *E. nervosum* formed a polytomy in the same clade.

1.5. DISCUSSION

The low branch support found here for some clades is common in *Elaphoglossum* (see the published phylogenies Rouhan et al., 2004; Skog et al., 2004) and for clades of mainly Andean distribution, as is the *E. ciliatum*-group (see for example Hughes and Eastwood, 2006 and references therein). Low levels of sequence differentiation, as revealed by the low percentage of parsimony informative characters (see Table 1), is one explanation for the low

◀ **FIG. 1.** Phylogeny obtained from the analyses of *atpB-rbcL*, *rps4-trnS* and *trnL-trnF* intergenic chloroplast spacers, presented both as a maximum likelihood phylogram (left) to reveal branch lengths and as a maximum parsimony strict consensus cladogram (right) to clarify relationships and allow for the presentation of support values. The three major clades of the *E. ciliatum*-group are indicated by lettered circles on the trees. Numbers below branches are bootstrap values (> 50%) for parsimony and maximum likelihood topologies, respectively. Bootstrap values of 100 are indicated by an asterisk (*). All taxa are from the genus *Elaphoglossum*. Numbers after the species epithets correspond to the collectors numbers (Appendix 1).

supports found in this study. Despite the relative low support, the *E. ciliatum*-group clade was recovered in the ML tree and all 72 MP trees. Morphological characteristics common to the species forming the *E. ciliatum*-group (see below) further support the existence of the clade.

Circumscription of the *E. ciliatum*-group

The *E. ciliatum*-group consists of 10 species (Appendix 2), distributed from Mexico and the West Indies to southern Brazil and the island of St. Helena in the Atlantic Ocean (Fig. 2). The regions with the most species are the mountains of Costa Rica and western Panama and the northern Andes (Appendix 2). The 10 species are characterized by abaxial laminar scales reduced to minute dots, echinate perispores, and resinous rhizomes. These are the same morphological characters common to the three species (*E. burchellii*, *E. ciliatum*, and *E. nigrescens*) that originally sparked our interest in the group.

The reddish to yellowish-brown dots on the surface of the lamina are the result from the body of the scale being highly reduced or completely lost so that only the base remains embedded in the epidermis. These stumps appear as minute dots, often resinous, and thus the laminae appear glabrous. However, close examination of the species of the *E. ciliatum*-group reveal that, except for *E. gramineum*, some of the scales maintain part of their body. The body can range from less than 0.5 mm to 1 mm, and tends to be pale. *Elaphoglossum gramineum* seems to be the only species in the group that has lost the body of the scale completely, and only dots (even on young leaves) can be found.

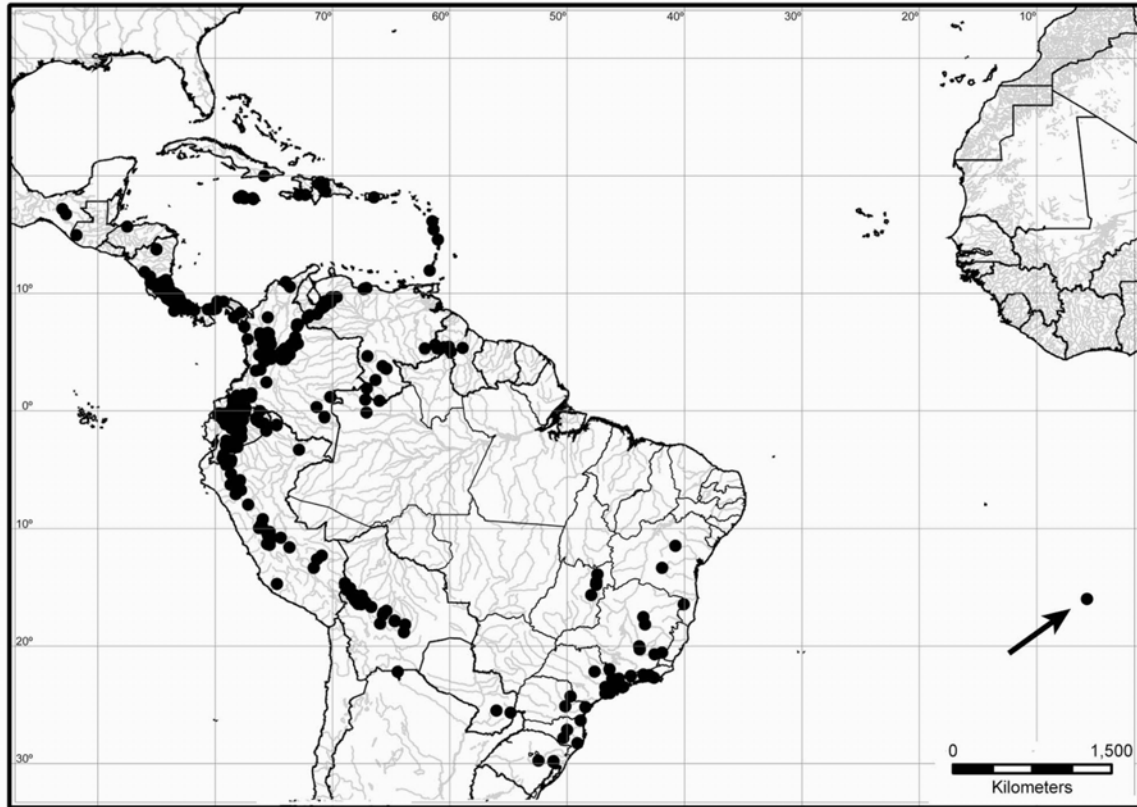


FIG. 2. Distribution of the *E. ciliatum*-group. The arrow points to St. Helena Island.

In their analyses of spore morphology, Moran & al. (2007) found that the presence of echinate perispores appears to be a synapomorphy for smaller clades within the sect. *Lepidoglossa*, whereas perispores without spines is a plesiomorphic character for the section. All the *E. ciliatum*-group species have echinate perispores, except for *E. dussii* (Fig. 3).

Resin on the rhizomes is sometimes overlooked by fern systematists. It can be obscured by scales, making it difficult to assess whether the resin is present or absent. Unfortunately little is known about the origin and composition of the resin, but it can certainly be an informative character. All the *E. ciliatum*-group species (except *E. dussii*) have resinous rhizomes that produce a reddish exudate upon drying that often stains the newspaper in which the plants are pressed.

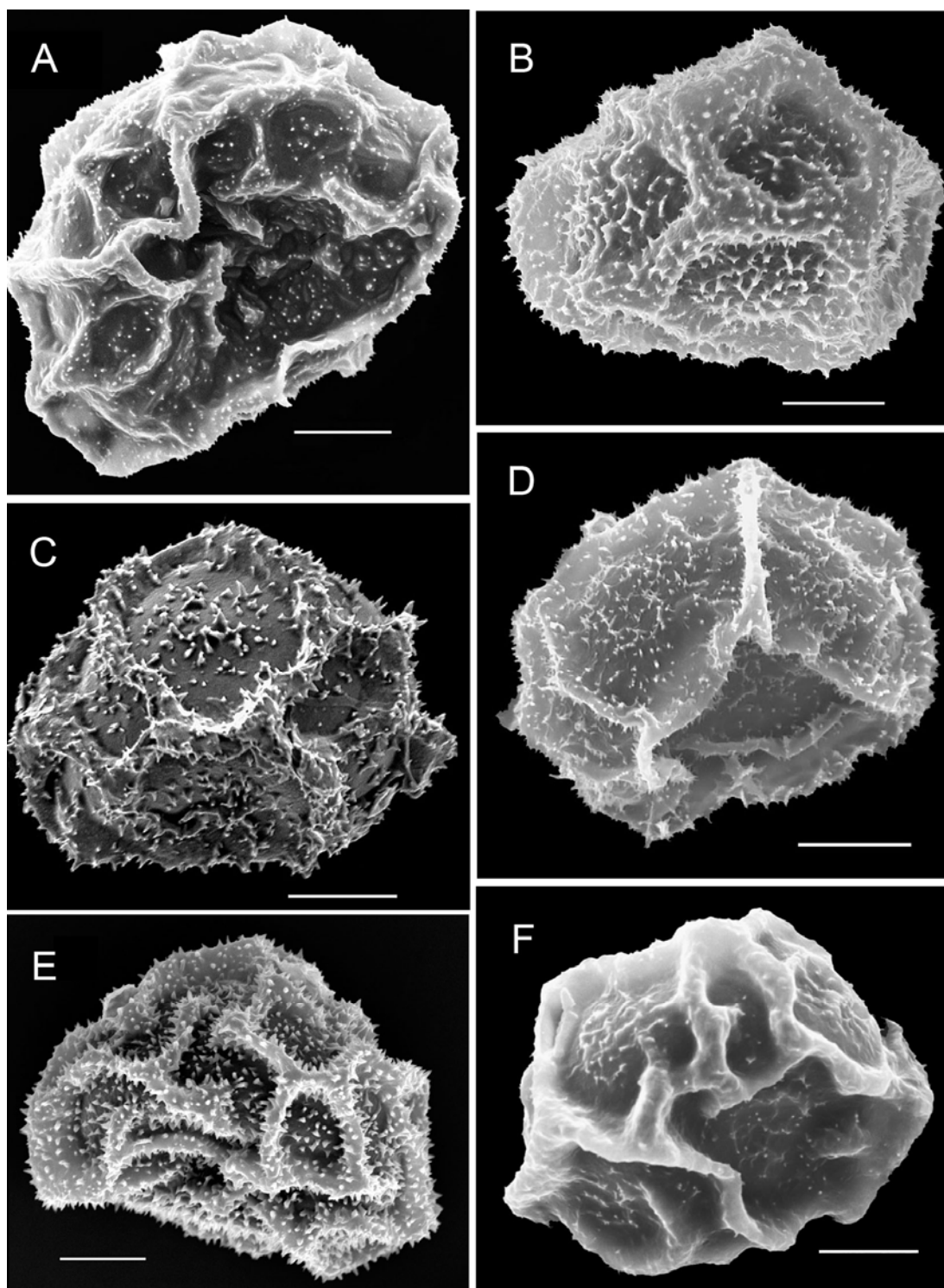


FIG. 3. Spores of the *E. ciliatum*-group. **A.** *E. nigrescens* (Ingram & Ferrell-Ingram 1308, NY). **B.** *E. huacsaro* (Ruiz-Teran 6124, NY). **C.** *E. gramineum* (Valeur 634, NY). **D.** *E. burchellii* (Dusen 7225, NY). **E.** *E. ciliatum* (Balslev & Madsen 10402, AAU). **F.** *E. dussii* (Lloyd 351, NY). Scale bars = 10 micrometers.

Although characteristic of the *E. ciliatum*-group, the three morphological characters discussed above are also found in two other species of sect. *Lepidoglossa*: *E. humbertii* C. Chr. and *E. scolopendriforme* Tardieu, both endemic to Madagascar (Fig. 1, Madagascan clade). The resemblance is so great that Moran and Smith (2001) considered *E. humbertii* a ‘species pair’ with *E. ciliatum*. Our molecular analyses and those by Rouhan & al. (2004) did not support this hypothesis and suggest that the morphological characters they share have evolved at least twice in sect. *Lepidoglossa*.

Within the *E. ciliatum*-group (Fig 1), all sequences belonging to the same species were resolved as one clade. Thus, the molecular analyses presented here supported our morphological species delimitation. The only exception was the St. Helena clade, where sequences of *E. dimorphum* and *E. nervosum* formed a polytomy within a subclade. Evidence from allozymes (Eastwood et al., 2004b; Eastwood et al., 2004a) indicates that *E. dimorphum* might be of hybrid origin between *E. nervosum* and *E. bifurcatum* (the third species in the St. Helena clade). The morphology of *E. dimorphum* is also variable and sometimes intermediate between *E. bifurcatum* (a species with pinnate leaves) and *E. nervosum* (a species with simple leaves) which would also support hybrid origin (Mickel, 1980). The hybrid condition of *E. dimorphum* and the low level of genetic diversity between this species and *E. nervosum* reported by Eastwood & al (2004a; b) explain the lack of resolution within this clade.

Phylogenetic position of *Elaphoglossum dussii*

The placement of *E. dussii* within the *E. ciliatum*-group seems surprising because it has only one of the three morphological characteristics common in the *E. ciliatum*-group; namely, it has resinous dots on the laminae. Its blades are scallier than those of other species in the group (with the exception of some specimens of *E. huacsaro* and *E. nigrescens* with

unusually persistent scales). The shape of its laminar scales also differs, being substellate instead of circular as in the other species. Moreover its long (3–6 mm), reddish brown rhizome scales are unique in the group. When it first appeared in the phylogenetic analyses as belonging to the *E. ciliatum*-group, contamination was suspected, but this idea was discarded because three different accessions of the species (one from Puerto Rico and two from Guadeloupe) were resolved in the same clade. The sister species relationship of *E. dussii* and *E. gramineum* suggests that the clade containing these two species underwent a process of morphological diversification within the West Indies.

Conflicts between morphology and molecular data have been encountered previously in studies of *Elaphoglossum* phylogeny. Either species with very similar morphologies are not recovered as part of the same clades (for example, see the relative placement of *E. humbertii* and *E. ciliatum* in this study and in Rouhan & al. (2004)); or species with no apparent morphological similarities are retrieved in, otherwise, morphologically well-defined clades (see for example the relative placements of *E. dussii* in this study, and that of *E. nidusoides* in Rouhan & al. (2007)). Structural and developmental studies of the gametophytic and sporophytic phases could provide novel morphological characters that help to understand the nature of these conflicts.

South Atlantic Ocean species

Although the *E. ciliatum*-group is primarily Neotropical, three species are endemic to the island of St. Helena in the South Atlantic Ocean. This oceanic island was formed by volcanic activity in the mid-Atlantic ridge 14.5 million years ago (Bakuh, 1973). It is approximately 1800 km from Africa and 3500 km from South America (Cronk, 1990). Despite being closer to Africa, our analyses suggest that the three species of St. Helena were the result of a single

dispersal event either from South America or from the West Indies and that diversification of this clade took place in the island. This same pattern of west to east dispersion has been reported for other ferns (Tryon, 1966; Moran and Smith, 2001; Janssen et al., 2007) and angiosperms (Renner, 2004).

Other clades of interest within section *Lepidoglossa*

The three clades discussed here (the Mexican-*petiolatum* clade, the Mascarene Islands clade and the Madagascan clade) are not part of the *E. ciliatum*-group (Fig. 1). The taxon sampling of this study was too limited to determine all the species that belong to these groups; future studies will probably identify additional member species given the size of sect. *Lepidoglossa*. A short discussion of these newly discovered clades is given here to stimulate further investigation on them.

The Mexican-*petiolatum* clade (Fig. 1) contained four Mexican species, three of which are endemic. These species belong to a group informally called the *E. petiolatum* complex (Mickel and Smith, 2004), which consists of about 12 species distributed worldwide. It is characterized by resinous dots on the abaxial blade surfaces, usually black, entire rhizome scales, and dark-tipped scales on the proximal portions of the stipes (these dark-tipped scales can also occur on the rachis). Within these species there is considerable variation in the degree of scaliness and density of resinous dots on the adaxial lamina surfaces. Paradoxically, these two characters are used to separate several species in the complex. This complex needs taxonomic and phylogenetic study not only to assess its monophyly, but also to determine its constituent species.

The Mascarene Islands clade (Fig. 1) was formed by three species, all endemic to the Islands of Mauritius and La Réunion in the Indian Ocean (Lorence and Rouhan, 2004). The results obtained in this study differ slightly from those of Rouhan & al. (2004), which found that *E. richardii* was part of a clade containing the Mexican species *E. pringlei* and *E. petiolatum* (both part of the Mexican-*petiolatum* clade here). The results presented here are more biogeographically parsimonious, suggesting a diversification of both clades within the Mascarene Islands and Mexico, respectively. The conflicting results point to the need for further studies including more species from both regions.

The Madagascan clade (Fig. 1) consisted of five species, all endemic to Madagascar. This clade in turn was sister to the Mascarene Island clade. Interestingly, *E. humbertii* and *E. scolopendriforme*, the two species that have the morphological characters common to the *E. ciliatum*-group but do not belong to it (see discussion above), formed part of this clade. There may be other species of sect. *Lepidoglossa* in Madagascar, the Mascarene Islands, and Africa that have some of the morphological characters present in the species of this clade. It will be interesting to see if further analyses, including more species from sect. *Lepidoglossa* with similar geographic distributions, still retrieve a monophyletic clade of Madagascan species sister to a Mascarene Islands clade.

1.6. CONCLUSION

This study allowed us to recognize within *Elaphoglossum* a monophyletic group of suitable size for taxonomic revision and provided insight into the evolution of sect. *Lepidoglossa*. Given the large number of species in *Elaphoglossum* and the difficulty in unraveling evolutionary relationships among its species based on morphology alone, the

approach we followed in this study seems to be the best way to pursue taxonomic studies and explore the genus phylogenetically.

1.7. APPENDIXES

APPENDIX 1.

Voucher information and GenBank accession numbers for taxa used in this study. A dash indicates the region was not sampled. The sections follow Mickel and Atehortúa (1980).

Species, section, country of origin, collector, collection number, herbarium acronym,

GenBank accession numbers: *atpB-rbcL*, *rps4-trnS*, *trnL-trnF*

Elaphoglossum achroalepis (Baker) C. Chr., *Lepidoglossa*, Madagascar, Rakotondrainibe, M. F., 6485, P, EF040636, AY540225, AY536288. ***E. asterolepis*** (Baker) C. Chr., *Lepidoglossa*, Madagascar, Kessler, M., 12751, NY, EF040642, AY540231, AY536294. ***E. aubertii*** (Desv.) T. Moore, *Eximia*, Comoros, Rouhan, G., 110, P, EF040647, EF040622, EF040608. ***E. avaratraense*** Rakotondr., *Lepidoglossa*, Madagascar, Rakotondrainibe, M. F., 1456, P, EU907660, AY540233, AY536296. ***E. bifurcatum*** (Jacq.) Mickel, *Lepidoglossa*, St. Helena, Eastwood, A., 215, --, EU907737, AY194070. ***E. burchellii*** (Baker) C. Chr., *Lepidoglossa*, Bolivia, Jimenez, I., 2129, NY, EU907662, --, EU907802; Bolivia, Jimenez, I., 2460, NY, EU907663, EU907738, EU907803; Ecuador, Lehnert, M., 1338, GOET, LPB, NY, EU907664, EU907739, EU907804; Brazil, Prado, J., 1109, NY, --, AY536150, AY534822. ***E. caricifolium*** Mickel, *Lepidoglossa*, Costa Rica, Halley, 7, NY, --, AY536143, AY534814. ***E. ciliatum*** (C. Presl) T. Moore, *Lepidoglossa*, Costa Rica, cultivated at NYBG, 234/94A, --, AY536148, AY534820; Costa Rica, Gonzalez, J., 12, CR, INB, UCR, EU907665, EU907740, EU907805; Ecuador, Lehnert, M., 1304, GOET, LPB, NY, EU907666, EU907741, EU907806; Ecuador, Lehnert, M., 1423, GOET, LPB, NY, EU907667, EU907742, EU907807; Ecuador, Moran, R. C., 7418, NY, EU907668, EU907743, EU907808; Ecuador, Moran, R. C., 7516, NY, EU907669, EU907744, EU907809; Colombia, Vasco, A., 468, HUA, MO, NY, EU907670, EU907745, EU907810; Colombia, Vasco, A., 504, HUA, NY, EU907671, EU907746, EU907811; Colombia, Vasco, A., 579, HUA, NY, EU907672, EU907747, EU907812. ***E. cuspidatum*** (Willd.) T. Moore, *Lepidoglossa*, Venezuela, Fernández, 16424, VEN, --, AY536155, AY534827; Bolivia, Jimenez, I., 754, EU907675, EU907750, EU907815. ***E. dendricola*** (Baker) C. Chr., *Lepidoglossa*, Ecuador, Moran, R. C., 6853, NY, QCA, QCNE, EU907676, EU907751, EU907816. ***E. dimorphum*** (Hook. & Grev.) T. Moore, *Lepidoglossa*, St. Helena, Eastwood, A., 302, EU907677, EU907752, AY194068; St. Helena, Eastwood, A., 719, EU907678, EU907753, EU907817. ***E. dussii*** Underw. ex Maxon, *Lepidoglossa*, Guadeloupe, Christenhusz, M., 4011, NY, EU907679, EU907754, EU907818; Guadeloupe, Jérémie, J, s.n., P, NY, EU907680, AY540229, AY536292; Puerto Rico, Sánchez, C., 138, NY, EU907681, EU907755, EU907819. ***E. forsythii-majoris*** H. Christ, *Lepidoglossa*, Madagascar, Kessler, M., 12678, NY, EF040644, EF040620, EF040606. ***E. furfuraceum*** (Mett. ex Kuhn) H. Christ, *Lepidoglossa*, Costa Rica, Moran, R. C., 6367, NY, --, AY540249, AY536312. ***E. gramineum*** (Jenm.) Urb., *Lepidoglossa*, Jamaica, Anderson, 3223, US, EU907682, EU907756, EU907820; Jamaica,

Proctor, G. R., 3907, US, --, EU907757, EU907821. ***E. heterolepis*** (Fée) T. Moore, *Lepidoglossa*, Mauritius, Rouhan, G., 177, P, EU907683, AY540251, AY536314. ***E. huacsaro*** (Ruíz) H. Christ, *Lepidoglossa*, Jamaica, Christenhusz, M., 3221, NY, EU907684, EU907758, EU907822; Bolivia, Jimenez, I., 2176, --, EU907759, --; Costa Rica, Moran, R. C., 6371, MO, EU907685, EU907760, EU907823; Ecuador, Moran, R. C., 6895, NY, QCA, QCNE, EU907686, EU907761, EU907824; Dominican Republic, Nee, M., 52309, NY, EU907687, EU907762, EU907825; Brazil, Prado, J., 1099, NY, --, AY536151, AY534823; Costa Rica, Redden, 1028A, NY, EU907688, EU907763, EU907826; Colombia, Vasco, A., 555, HUA, MO, NY, EU907689, EU907764, EU907827; Colombia, Vasco, A., 556, HUA, NY, EU907690, EU907765, EU907828; Colombia, Vasco, A., 562, COL, HUA, MO, NY, EU907691, EU907766, EU907829; Colombia, Vasco, A., 564, HUA, MO, NY, EU907692, EU907767, EU907830; Colombia, Vasco, A., 567, HUA, MO, NY, EU907693, EU907768, EU907831; Colombia, Vasco, A., 568, HUA, NY, EU907694, EU907769, EU907832; Colombia, Vasco, A., 576, HUA, MO, NY, EU907695, EU907770, EU907833. ***E. humbertii*** C. Chr., *Lepidoglossa*, Madagascar, Humbert, 22448b, P, --, AY540254, AY536317; Madagascar, Rouhan, G., 466, P, EU907696, EU907771, EU907834. ***E. hybridum*** (Bory) Brack., *Polytrichia*, La Réunion, Rouhan, G., 250, P, EU907697, EU907772, EU907835. ***E. iphookense*** Mickel, *Lepidoglossa*, Mexico, Mickel, J., 4748, NY, EU907698, EU907773, EU907836. ***E. lancifolium*** (Desv.) C.V.Morton, *Lepidoglossa*, La Réunion, Rouhan, G., 201, P, EU907699, AY540259, AY536322. ***E. leucolepis*** (Baker) Krajina ex Tardieu, *Lepidoglossa*, Madagascar, Rakotondrainibe, M. F., 6339, P, EF040638, AY540261, AY536324. ***E. micropogon*** Mickel, *Lepidoglossa*, Costa Rica, Moran, R. C., 6353, NY, EF040643, AY540268, AY536331. ***E. mitorrhizum*** Mickel, *Elaphoglossum*, Costa Rica, Boyle, B., 6410, CR, INB, NY, USJ, EF040656, AY540269, AY536332. ***E. muscosum*** (Sw.) T. Moore, *Lepidoglossa*, Costa Rica, Moran, R. C., 6342, NY, EF040637, AY540270, AY536333. ***E. nervosum*** (Bory) H. Christ, *Lepidoglossa*, St. Helena, Eastwood, A., 358, EU907700, EU907774, AY194069; St. Helena, Eastwood, A., 367, EU907701, EU907775, EU907837. ***E. nigrescens*** (Hook.) T. Moore ex Diels, *Lepidoglossa*, Brazil, Berg (cultivated at Selby), 362, NY, EU907702, EU907776, EU907838; Brazil, cultivated at NYBG, s.n., EU907703, EU907777, EU907839; Bolivia, Jimenez, I., 2185, LPB, NY, EU907704, EU907778, EU907840; Bolivia, Jimenez, I., 2220, LPB, NY, EU907705, EU907779, EU907841; Bolivia, Jimenez, I., 2256, LPB, NY, EU907706, EU907780, EU907842; Bolivia, Kuhn, 1638/76A, NY, --, AY536149, AY534821; Costa Rica, Moran, R. C., 6332, CR, INB, NY, UCR, EU907707, AY540274, AY536337; Ecuador, Moran, R. C., 7491, NY, EU907708, EU907781, EU907843; Ecuador, Moran, R. C., 7627, NY, EU907709, EU907782, EU907844. ***E. orbignyanum*** (Fée) T. Moore, *Lepidoglossa*, Bolivia, Bach, K., 1773, NY, EU907710, EU907783, EU907845; , NYBG, living collection, 386/94A, --, AY536147, AY534819. ***E. paleaceum*** (Hook. and Grev.) Sledge, *Lepidoglossa*, Hawaii, Annable, 3792, NY, --, AY536153, AY534825; Hawaii, Mickel, J., 9710, NY, EU907711, EU907784, EU907846. ***E. petiolatum*** (Sw.) Urb., *Lepidoglossa*, Mexico, Nicholson, 782-01-A, NY, EU907712, AY540275, AY536338. ***E. petiolatum* aff.**, *Lepidoglossa*, Colombia, Vasco, A., 585, HUA, MO, NY, EU907713, --, EU907847; Ecuador, Moran, R. C., 7573, NY, EU907714, EU907785, EU907848. ***E. poolii*** (Baker) H. Christ, *Lepidoglossa*, Madagascar, Kessler, M., 12702, NY, EF040639, AY540278, AY536341. ***E. potosianum*** H. Christ,

Lepidoglossa, Mexico, Hirton, 22679, NY, EU907715, EU907786, EU907849. ***E. pringlei*** (Davenp.) C. Chr., *Lepidoglossa*, Mexico, Campos, 2650, NY, EU907716, EU907787, EU907850. ***E. richardii*** (Bory ex Fée) H. Christ, *Lepidoglossa*, La Réunion, Rouhan, G., 231, P, EU907717, AY540284, AY536347. ***E. rzedowskii*** Mickel, *Lepidoglossa*, Mexico, Bartholomeus, 2691, NY, EU907718, EU907788, EU907851. ***E. scolopendriforme*** Tardieu, *Lepidoglossa*, Madagascar, Rakotondrainibe, M. F., 6426, P, EU907719, AY540288, AY536351. ***E. sieberi*** (Hook. and Grev.) T. Moore, *Elaphoglossum*, Mauritius, Rouhan, G., 169, P, EU907720, AY540290, AY536353. ***E. splendens*** (Bory ex Willd.) Brack., *Lepidoglossa*, La Réunion, Rouhan, G., 247, P, EU907721, AY540296, AY536359. ***E. tenuiculum*** (Fée) T. Moore ex Baker, *Lepidoglossa*, Colombia, Vasco, A., 558, HUA, NY, EU907722, --, EU907852. ***E. tomentosum*** (Bory ex Willd.) H. Christ, *Lepidoglossa*, Mauritius, Rouhan, G., 174, P, EU907723, AY540300, AY536363. ***E. vulcanicum aff.*** *Lepidoglossa*, Ecuador, Moran, R. C., 6883, NY, EU907724, EU907789, EU907853; Ecuador, Moran, R. C., 6890, NY, QCA, QCNE, EU907725, EU907790, EU907854; Ecuador, Moran, R. C., 7515, NY, EU907726, EU907791, --; Colombia, Vasco, A., 586, HUA, MO, NY, EU907727, EU907792, EU907855; Ecuador, Moran, R. C., 7586, NY, EU907728, EU907793, EU907856. ***E. vulcanicum*** H. Christ, *Lepidoglossa*, Ecuador, Moran, R. C., 6891, NY, EU907729, EU907794, EU907857; Ecuador, Moran, R. C., 6889, NY, QCA, QCNE, EU907730, EU907795, EU907858. ***E. yungense*** de la Sota, *Lepidoglossa*, Bolivia, Jimenez, I., 2487, NY, EU907731, EU907796, EU907859; Bolivia, Jimenez, I., 2498, NY, EU907732, EU907797, EU907860; Bolivia, Jimenez, I., 2676, NY, EU907733, EU907798, EU907861; Bolivia, Labiak, P., 2790, NY, EU907734, EU907799, EU907862; Bolivia, Labiak, P., 2804, NY, EU907735, EU907800, EU907863; Bolivia, Labiak, P., 2808, NY, EU907736, EU907801, EU907864. ***E. sp nov.***, *Lepidoglossa*, Ecuador, Moran, R. C., 6711, NY, EU907673, EU907748, EU907813; Ecuador, Moran, R. C., 6762, NY, QCA, QCNE, EU907674, EU907749, EU907814.

APPENDIX 2.

Species belonging to the *E. ciliatum*-group clade, their publication and type information, and their distribution by country

1. ***E. bifurcatum* (Jacq.) Mickel**, Brittonia 32: 116. 1980. Type: St. Helena. Locality and collector not designated (holotype: W).
St. Helena
2. ***E. burchellii* (Baker) C. Chr.**, Index filic. 304. 1905. Type: Brazil. *W. Burchell 5155* (holotype: K; isotypes B, P).
Bolivia, Brazil, Colombia, Costa Rica, Dominican Republic, Ecuador, Panama, Peru, Paraguay, Venezuela
3. ***E. ciliatum* (C. Presl) T. Moore**, Index fil. 8: 353. 1862. Type: Peru. Huánuco: near Huánuco, *T. Haenke s.n.* (holotype: PR, photo NY ex PR).
Colombia, Costa Rica, Ecuador, Panama, Peru
4. ***E. dimorphum* (Hook. & Grev.) T. Moore**, Index fil. 8: 1862. Syntypes: St. Helena. *A. Walker s.n.* (K?), Madras, *Dr. Shuter s.n.* (K?).
St. Helena
5. ***E. dussii* Underw. ex Maxon**, Sci. Surv. Porto Rico & Virgin Islands. 6: 398. 1926. Type: Martinique. Bois du Lorrain, 540-900 m, Sep 1901, *A. Duss 4688* (holotype: NY).
Dominica, Dominican Republic, Grenada, Guadeloupe, Martinique, Puerto Rico, St. Kitt's, St. Vincent
6. ***E. gramineum* (Jenm.) Urb.**, Symb. Antill. 4: 60. 1903. Type: Jamaica. 1876, *G. S. Jenman 27* (holotype: K; isotype: NY).
Cuba, Dominican Republic, Jamaica
7. ***E. huacsaro* (Ruíz) H. Christ**, Neue Denkschr. Allg. Schweiz. Ges. Gesamnten Naturwiss. [Monogr. *Elaphoglossum*] 36: 96. 1899. Type: Peru. Habitat in Andinum montibus ad Sanatolmas et Tarmac Provinciae, *H. Ruíz 54* (holotype: B; isotypes: BR, US; photos F, US ex B).
Bolivia, Brazil, Colombia, Costa Rica, Dominican Republic, Ecuador, Guatemala, Haiti, Jamaica, Mexico, Peru, Venezuela
8. ***E. nervosum* (Bory) H. Christ**, Neue Denkschr. Allg. Schweiz. Ges. Gesamnten Naturwiss. [Monogr. *Elaphoglossum*] 36: 50, fig. 13. 1899. Type: St. Helena. *D. D'Urville s.n.* (holotype: P).
St. Helena
9. ***E. nigrescens* (Hook.) T. Moore ex Diels**, Nat. Pflanzenfam. 1(4): 332. 1899. Type: Venezuela (as "British Guiana"). Bolivar: Roraima, 1842, *R. Schomburgk s.n.* (holotype: K).
Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guyana, Nicaragua, Panama, Peru, Venezuela
10. ***E. sp.* Nov.**
Ecuador

CHAPTER 2

SYSTEMATICS OF *ELAPHOGLOSSUM* SECTION *LEPIDOGLOSSA* (*DRYOPTERIDACEAE*)

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2.1. ABSTRACT

Elaphoglossum section *Lepidoglossa* is one of the largest sections of the genus *Elaphoglossum* with ca. one-third of the nearly 600 species described for the genus. The section was first recognized on the basis of morphology and later found to be monophyletic by molecular phylogenetic analyses. Chloroplast markers *atpB-rbcL*, *rps4-trnS*, and *trnL-trnF* were used here to reconstruct the phylogeny of section *Lepidoglossa*. The gene trees resulting from our analyses recovered 13 major clades, two of which broadly correspond to previously named subsections. The morphological characteristics and/or geographical distribution patterns that are particular to each of these 13 clades are discussed. This phylogeny provides important new insights into the systematics of the section *Lepidoglossa*. It also constitutes a solid framework from which to choose morphologically recognizable clades of convenient size for monographic study, and for addressing other aspects of the biology of this section.

Key Words. *atpB-rbcL*, cpDNA, Dryopteridaceae, *Elaphoglossum*, Ferns, *Lepidoglossa*, Pteridophyta, *rps4-trnS*, *trnL-trnF*.

2.2. INTRODUCTION

With approximately 600 species, *Elaphoglossum* Schott ex J. Sm. is one of the most species-rich genera of ferns (Mickel, 1995b). It is pantropical in distribution and most diverse in the Neotropics where about 450 described species occur (Mickel, 1990b).

Morphologically, *Elaphoglossum* is characterized by dorsiventral rhizomes, simple entire leaves, free veins, dimorphic sterile and fertile leaves, and acrostichoid sori (Holttum, 1978; Mickel and Atehortúa, 1980). The monophyly of the genus and its placement within the Dryopteridaceae has received strong support from two molecular phylogenetic studies that used chloroplast genes: *atpB*, *rbcL* (Liu et al., 2007), and these plus *atpA* (Schuettpelz and Pryer, 2007)

There have been several attempts to split *Elaphoglossum* into smaller groups to make it more manageable taxonomically (Fée, 1845; Sodiro, 1893; Christ, 1899; Holttum, 1966; Mickel and Atehortúa, 1980). The most recent and comprehensive of these (Mickel and Atehortúa, 1980) divides *Elaphoglossum* into nine sections and 21 subsections using morphological data, and provides keys to distinguish these groups. This non-cladistic study, has served as the main framework for subsequent taxonomic and phylogenetic studies of *Elaphoglossum* (e.g. Mickel, 1995b; Rouhan et al., 2004; Skog et al., 2004).

Phylogenetic relationships within *Elaphoglossum* have been examined by two previous studies using chloroplast DNA (Rouhan et al., 2004; Skog et al., 2004). These studies clearly support five of the nine sections originally proposed by Mickel and Atehortúa (1980). One of

these supported clades is section *Lepidoglossa* H. Christ, which was originally described by Christ (1899) and later recognized by Mickel & Atehortúa (1980). The section is pantropical and most species-rich in the Neotropics. It contains species with scaly blades covered mostly or entirely by flat (i.e., non-subulate) scales with acicular marginal cells, veins ending at or close to the margin but not hydathodous, and phyllopodia. Mickel and Atehortúa (1980) recognized six subsections within section *Lepidoglossa* based on the texture and shape of the blades, density of scales, type of scales, and spore morphology (Table 1).

We estimate that the number of species belonging to section *Lepidoglossa* is about 200 (see <http://sweetgum.nybg.org/elaphoglossum/taxonomy.php> for a complete list of the species we are recognizing in the section). This number is unevenly distributed among the subsections of section *Lepidoglossa* (Table 1). At least three of the subsections (i.e. *Petiolosa*, *Microlepidea*, and *Huacsaro*) have fewer than 10 described species, whereas two (*Pilosa* and *Polylepidea*) account for more than half (Mickel and Atehortúa, 1980; A. Vasco & R. Moran, pers. obs).

Understanding the taxonomy and diversity of section *Lepidoglossa* is difficult because of the lack of a comprehensive phylogeny for the section. To date, there are three molecular phylogenetic studies for *Elaphoglossum* based on chloroplast DNA. One study (Skog et al., 2004) included 15 species of section *Lepidoglossa* and two studies included 42 (Rouhan et al., 2004; Vasco et al., 2009b). Despite having different objectives than reconstructing the phylogeny of section *Lepidoglossa*, these studies supported the monophyly of section *Lepidoglossa*, but suggested that several of the subsections as proposed by Mickel and Atehortúa (1980) were not monophyletic.

TABLE 1. Classification of *Elaphoglossum* section *Lepidoglossa* proposed by Mickel and Atehortúa (1980), and principal characters of each subsection. Species that were not included in Mickel and Atehortúa's classification were assigned a subsection based on the key they provided (see Appendix 1 for details).

Subsection	Morphological Characteristics	Species included in Mickel and Atehortúa classification	Species included in this study
<i>Huacsaro</i> Mickel & Atehortúa	<i>Rhizomes</i> long-creeping to ascending; <i>rhizome scales</i> black, entire. <i>Sterile laminae</i> elliptic, with resinous dots, the apex obtuse; <i>laminar scales</i> stellate or lanceolate. <i>Spores</i> densely spiculate with ridges	7	11
<i>Microlepidea</i> H. Christ	<i>Rhizome scales</i> linear-lanceolate, entire. <i>laminar scales</i> stellate below, round and peltate above. <i>Spores</i> with low, smooth ridges	2	4
<i>Muscosa</i> Mickel & Atehortúa	<i>Rhizomes</i> short-creeping; <i>rhizome scales</i> linear-lanceolate. <i>Stipes</i> densely scaly. <i>Sterile laminae</i> narrowly elliptic, lanceolate or ovate-lanceolate, coriaceous, the apex obtuse, densely scaly. <i>Intersporangial scales</i> present. <i>Spores</i> with papillae	9	14
<i>Petiolosa</i> H. Christ	<i>Rhizomes</i> short-creeping; <i>rhizome scales</i> dark brown. <i>Sterile laminae</i> elliptic, the apex caudate; <i>laminar scales</i> lanceolate or lacking, occasionally with resinous dots. <i>Fertile laminae</i> conduplicate. <i>Spores</i> with low ridges	3	2
<i>Pilosa</i> H. Christ	<i>Rhizomes</i> short-creeping; <i>rhizome scales</i> usually dark, entire to long ciliate. <i>Sterile laminae</i> <i>Laminar scales</i> lanceolate denticulate or resembling stellate hairs, often punctated with resinous dots. <i>Spores</i> with low ridges or narrow crests	12	23
<i>Polylepidea</i> H. Christ	<i>Rhizomes</i> short-creeping to ascending; <i>rhizome scales</i> dark, ciliolate. <i>Sterile laminae</i> narrowly elliptic; <i>laminar scales</i> long-ciliate. <i>Spores</i> with low ridges, usually with small verrucae between the ridges	20	36

The present study investigates the phylogeny of section *Lepidoglossa* using combined analyses of three chloroplast markers (the intergenic spacers *atpB-rbcL*, *rps4-trnS*, and *trnL-trnF*) for half of the currently recognized species in the section. The usefulness of these markers to resolve relationships at the infrageneric level in *Elaphoglossum* has been demonstrated by several studies (Rouhan et al., 2004; Vasco et al., 2009b). The gene trees resulting from these analyses provide a consistent picture of the phylogeny of section *Lepidoglossa*. The implications of these trees for the taxonomy of the section are discussed, both in terms of the subsections previously recognized and the morphological and geographical characters common to the recovered clades. This phylogeny should also constitute a solid framework from which to choose morphologically recognizable clades of convenient size for monographic study, as well as the starting point to carry out morphological phylogenetic studies that address the characters mentioned as diagnostic for some of the clades, given better insights into the biology and character evolution of section *Lepidoglossa*.

2.3. MATERIALS AND METHODS

Taxonomic sampling

Given the size of section *Lepidoglossa*, the morphological similarity of its species, and the fact that diversity is not uniformly distributed within it (see Table 1), we developed a strategy to sample the group broadly. Initially we included all the species from which we had readily available material, making sure we had at least one species from all the subsections.

Subsections for all species included were assigned based on Mickel and Atehortúa's (1980) key for section *Lepidoglossa*. With that dataset (which included 42 species), we generated a

preliminary phylogeny (Vasco et al., 2009b). Based on these results we predicted the phylogenetic position of an additional 55 species, which were then sequenced and included in the present analyses. We tried to choose species that represented the morphological variation found in each clade. In total we sampled 160 accessions corresponding to 97 species, or about half of the currently recognized species in section *Lepidoglossa*. Of the species sampled, 21 are from the Old World and 76 are from the New World. All six of the traditionally recognized subsections (Mickel and Atehortúa, 1980) are represented in the species sampled. The preliminary analyses included multiple accessions for some species. The analyses and results shown here exclude some of these accessions (only the accessions included in the final analyses presented are listed in Appendix 1). Exclusion of duplicate species accessions took into account sequence similarity (the most similar ones that belong to the same species were deleted); the fact that their exclusion did not change the groupings recovered when the full dataset was analyzed; and, for species with widespread distributions, that all the geographical regions, if possible, were represented. Species belonging to the other sections of *Elaphoglossum* (based on Rouhan et al., 2004) were selected as outgroups (16 species). Because it has been demonstrated that *E. amygdalifolium* is the sister to the rest of *Elaphoglossum* (Rouhan et al., 2004; Skog et al., 2004), that species was used to root the trees. This study includes several new species that will be described elsewhere, thus they are marked as either *aff* or *spnov* in Appendix 1. Other information on specimen vouchers and provenance is also provided in Appendix 1.

DNA extraction, amplification, and sequencing

This study utilized sequences from three non-coding intergenic chloroplast spacers: *atpB-rbcl*, *rps4-trnS* (GGA), and *trnL(UAA)-trnF(GAA)*. Genomic DNA was isolated from

silica-dried or herbarium-specimen leaf tissue, using the DNeasy Plant Mini Kit (Qiagen). Dry leaf tissue (approximately 1 cm²) was sealed in a microcentrifuge tube with approximately 1 g of sterile garnet and a ceramic bead. The sealed tubes were placed in a Fastprep lysing FP-120 bead mill (MP biomedical), for 25 sec at maximum speed. Lysis buffer was added directly to the tube (beads and garnet were not removed) and the tubes were incubated at 65°C for 30 min. Extraction then proceeded following the manufacturer's protocol. With herbarium material an additional proteinase K digestion during the lysis step was performed: 30 µL of proteinase K (20 mg/ml) plus 30 µL of β-mercaptoethanol (98%) were added per tube and tubes were incubated on a tipping plate at 42°C for 24 hr.

General laboratory protocols for amplifying the markers used in this study were done as described in Rouhan et al.(2004) for *rps4-trnS* and *trnL-trnF*. Amplification of *atpB-rbcL* was carried out using the following program: 50 sec at 94°C, then 35 cycles at 94°C (1 min), 52°C (45 sec), 72°C (75 sec), followed by 72°C (7 min). The resulting PCR products were sent to the High-Throughput Genomics Unit (HTGU), Department of Genome Sciences, Univ. of Washington, where they were purified using ExoSap-IT (USB Corporation). Sequencing of the cleaned PCR products used the amplification primers and was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Sequencing reactions were run on an ABI Prism 3130 DNA Analyzer (Applied Biosystems). Forward and reverse sequences were edited and assembled using Sequencher 4.5 (Gene Codes Corporation). This study newly generated 332 sequences out of the 512 included in the analyses presented. All new sequences were deposited in GenBank (see Appendix 1 for accession numbers).

Sequence alignment and phylogenetic analyses.

Sequences were aligned using MUSCLE (Edgar, 2004) and then adjusted manually. Data editing, manual alignment, and tree viewing were performed in WinClada (Nixon, 2002). Ambiguously aligned regions were excluded from the data sets. The three markers' individual matrices were analyzed separately and in combination to identify potential lab errors or conflicts.

Indel events were coded using the simple indel coding method of Simmons and Ochoterena (2000) as implemented in 2xread (Little, 2005). Maximum parsimony (MP) analyses were performed using TNT version 1.1 (Goloboff et al., 2008). Uninformative characters were deactivated, and all sequence characters were treated as non-additive (unordered) and equally weighted. As the tree search strategy, 1000 random addition sequence replicates holding 20 trees per replicate (mu=rep1000ho20rat) were performed. Each starting tree was first exhaustively swapped with SPR followed by TBR and then a 200-iteration ratchet (Nixon, 1999). The ratchet used a probability of five for upweighting and a probability of five for downweighting, 10% of the informative characters were reweighted for each replicate (rat:iter200up5do5), other parameters were set to default. After the random addition sequences were complete, trees were swapped to 500000 trees using TBR (bbreak=tbr). Tree length as well as ensemble Consistency (CI) and Retention (RI) indexes were calculated excluding parsimony uninformative characters. TNT version 1.1 (Goloboff et al., 2008) was used to generate a jackknife procedure file. Each resample matrix was analyzed with TNT using 1000 jackknife replicates, doing 10 rachets per replicate, and holding 20 trees per ratchet. Branches were collapsed if supported ambiguously. Only the strict consensus tree was retained for each replicate (resample jak savetrees rep 100

[μ =rep10ho20rat]). The jackknife values of each clade were mapped onto the strict consensus tree using WinClada (Nixon, 2002).

The data were also analyzed under maximum likelihood (ML) using Garli 0.96 Beta (Zwickl, 2006). Indels were treated as missing data. The ML analyses were performed using a GTR+I+G model of sequence evolution, as recommended by the program Modeltest 3.7 (Posada and Crandall, 1998), with parameters estimated from the data. Two single “best tree” searches were performed from different random starting trees. Runs proceeded until they met Garli’s default termination conditions. Support was assessed with 500 bootstrap searches under Garli’s default parameters.

2.4. RESULTS

The aligned matrix contained 2043 characters (including 158 characters resulting from indel coding), of which 494 (23.8%) were parsimony informative. Table 2 gives the total length of the aligned matrices after coding indels, the number of parsimony informative characters and its percentage, and the number of parsimony informative indels for each marker. In the combined data set, coded indels contributed 12.7% of the parsimony-informative characters. MP strict consensus trees from each of the three marker regions did not provide any resolution, thus the datasets were combined.

TABLE 2. Summary of the variation in data sets and analyses statistics

Data Partition	Terminals scored	Total				Parsimony informative characters			
		Alignment length	Regular	Indels	% missing data	Total	Regular	Indels	% informative
<i>atpB-rbcL</i>	157	1002	948	54	13.7	184	164	20	18.3
<i>rps4-trnS</i>	173	589	540	49	4.9	166	145	21	28.1
<i>trnL-trnF</i>	180	452	397	55	1.1	136	115	21	29.9
Combined analysis	182	2043	1885	158	8.4	486	424	62	23.8

The MP search resulted in 483840 trees, of 1006 steps with a consistency index (CI) of 0.60 and retention index (RI) of 0.89. The strict consensus of the combined data is presented in Fig. 1. Two most likely trees ($-\ln = 10107.0686$ and $-\ln = 10107.0687$) with the same topology were obtained from the two “best tree” searches in the ML analysis using the GTR+I+G model. The most likely tree is presented in Fig. 2.

The MP strict consensus and the ML tree resolved section *Lepidoglossa* as monophyletic with very strong support (jackknife [JS] and bootstrap [BS] 99/98; MP/ML), and recovered 13 major clades within section *Lepidoglossa*. Two of these 13 major clades (Fig 1) correspond with previously recognized subsections (Mickel and Atehortúa, 1980): subsection *Petiolosa* (JS 92/BS 97) and *Muscosa* (JS 63/ BS 68). The rest of the recognized subsections were polyphyletic and were spread throughout the tree, mainly in the other 11 major clades. For discussion purposes we gave names to these 11 major clades. These names are informal and not intended to represent a new infrageneric classification. The 13 major clades recovered have generally good jackknife and bootstrap support, yet relationships among those clades and among species within them are sometimes weakly supported or not resolved.

2.5. DISCUSSION

Monophyly of Section *Lepidoglossa*

Compared to previous the present study included more species of section *Lepidoglossa* (Rouhan et al., 2004; Skog et al., 2004; Vasco et al., 2009b), and an additional marker– *atpB-rbcL* (Rouhan et al., 2004; Skog et al., 2004). As in the previous studies, section *Lepidoglossa* is strongly supported as monophyletic (JS 99/BS 98).

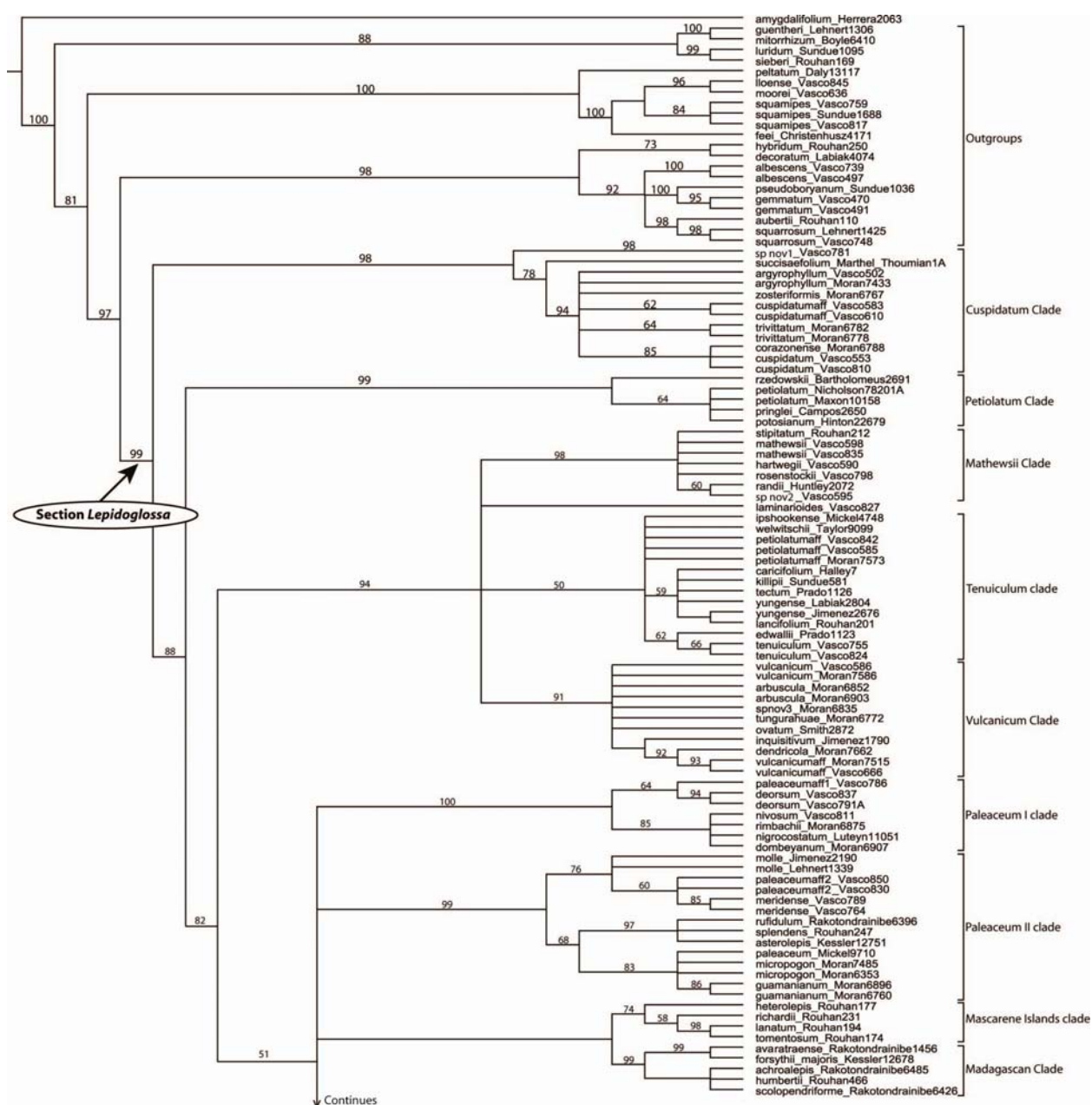


FIG. 1. Phylogeny of *Elaphoglossum* subsection *Lepidoglossa* obtained from the analyses of *atpB-rbcL*, *rps4-trnS* and *trnL-trnF* chloroplast markers, presented as a maximum parsimony strict consensus. Numbers above branches are Jackknife values. All taxa are *Elaphoglossum*. Names and numbers after the specific epithets correspond to the collectors and their numbers (Appendix 1).

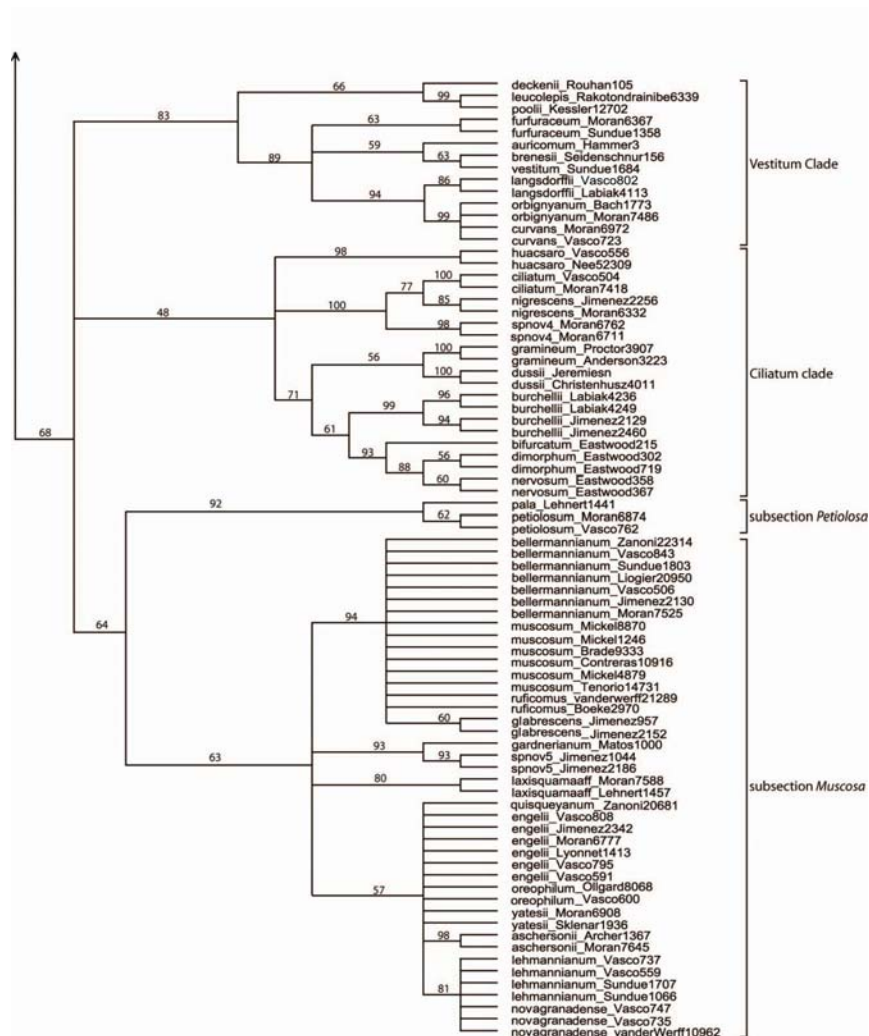


FIG. 1. continuation

Section *Lepidoglossa* is distinguished by scales with acicular marginal cells. All other *Elaphoglossum* species have laminar scales with marginal teeth consisting of glandular or bulbous marginal cells or gland-tipped marginal processes. Other characteristics help distinguish section *Lepidoglossa*, such as flat (not subulate) scales on the petioles and laminae, non-hydrathodous veins endings, and phyllopodia.

Almost all species of section *Lepidoglossa* are characterized by scaly blades covered mostly or entirely by flat scales. This character has been traditionally used to assign species

to the section. Some species of section *Lepidoglossa*, however, have scales lost or reduced so that only the base remains embedded in the epidermis. In adult specimens, these bases appear as minute, often resinous dots, and are often mixed with scales. Some species, however, have only dots present and thus the laminae appear glabrous. This appearance has resulted in some species of section *Lepidoglossa* being assigned to other sections, especially section *Elaphoglossum* (e.g., *E. burchellii*, *E. gramineum* and *E. nigrescens*). Resinous dots, either alone or with scales, are present in other clades (i.e., the petiolatum, mathewsii, tenuiculum, and ciliatum clades; Figs. 1 and 2). This suggests that reduced, dot-like laminar scales evolved several times in section *Lepidoglossa*.

Phylogeny of section *Lepidoglossa*

Parsimony (MP) and likelihood (ML) analyses recovered 13 major clades within section *Lepidoglossa*. In general the recovered clades have good jackknife and bootstrap support, the groups of species forming those clades could be defined by morphological characteristics and/or geographical distribution. Relationships among clades and among species within those clades, however, are sometimes weakly supported or not resolved, and characteristics common to the larger groups recovered are yet to be found.

Our analysis identifies a basal split into two well-supported clades. The smaller one is here called the **cuspidatum clade** (JS 98/BS 98). The other clade consists of all other species of section *Lepidoglossa* (JS 88/BS 79). The cuspidatum clade contains species belonging to subsection *Polylepidea*. Species of this group are characterized by long-creeping rhizomes, dark brown rhizome scales, and acute to cuspidate lamina apices. The

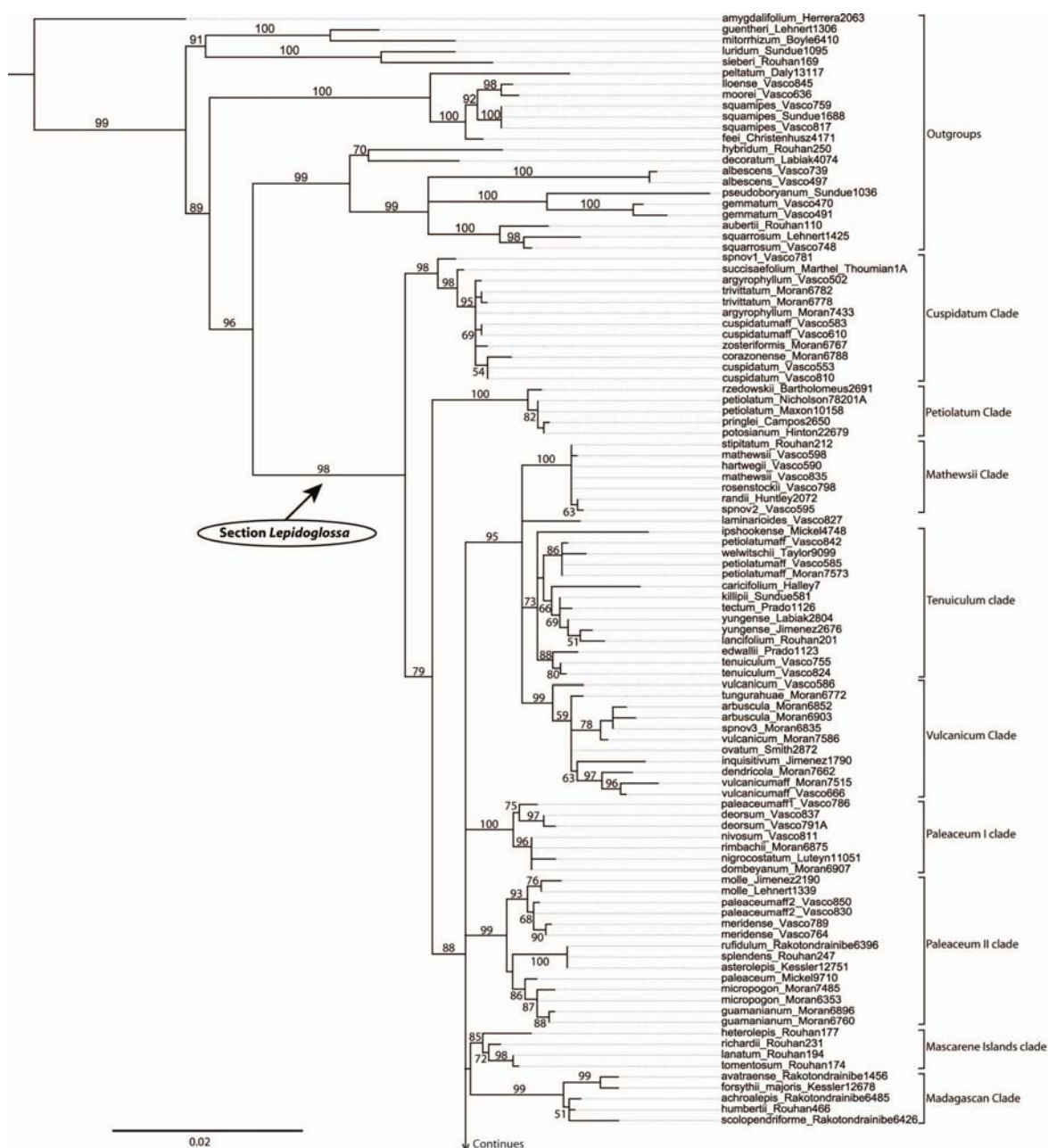


FIG. 2. Phylogeny of *Elaphoglossum* subsection *Lepidoglossa* obtained from the analyses of *atpB-rbcL*, *rps4-trnS* and *trnL-trnF* chloroplast markers, presented as a maximum likelihood phylogram. Numbers above branches are bootstrap values. All taxa are *Elaphoglossum*. Names and numbers after the specific epithets correspond to the collectors and their numbers (Appendix 1).

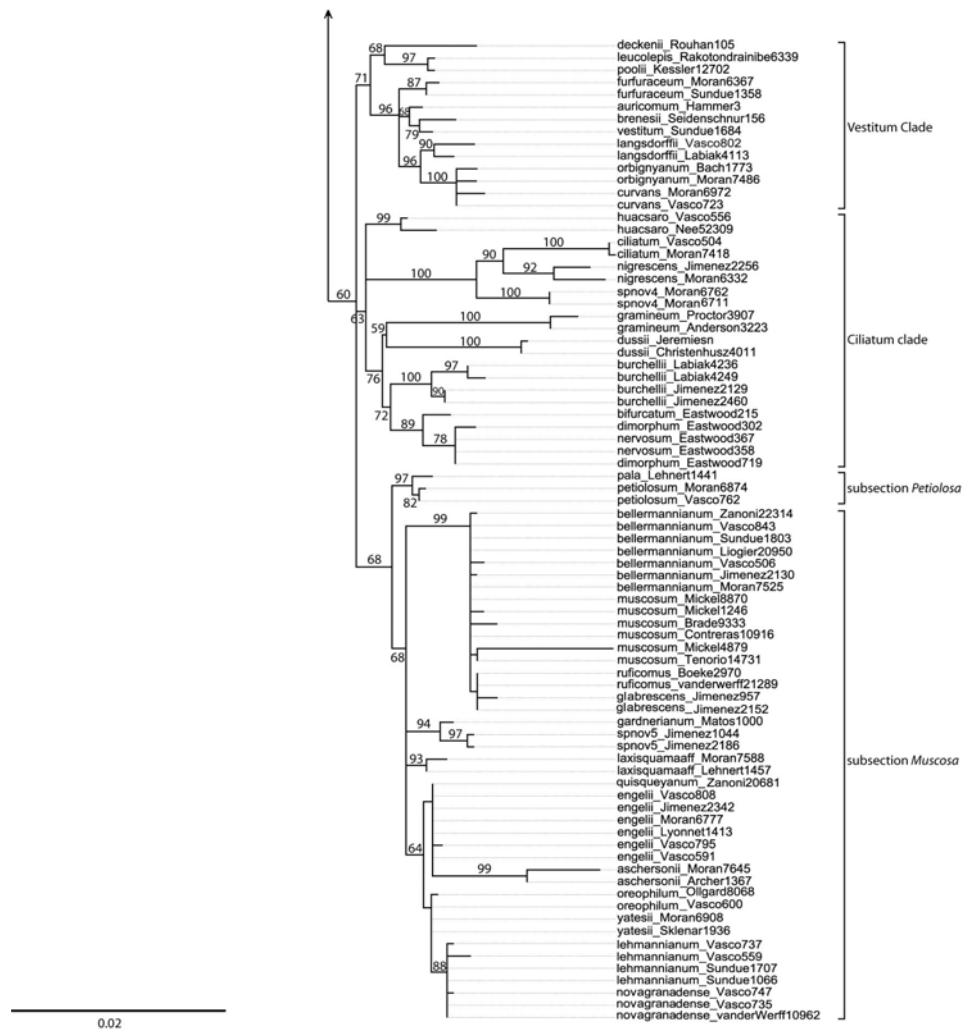


FIG. 2. continuation

scales of the laminae are also distinctive by being circular, peltate, imbricate, appressed, and darkened at the point of insertion. Typically, they obscure the surface of the lamina. The clade is mainly Neotropical, occurring from Costa Rica to Bolivia. Only *E. succisaefolium* occurs outside the Neotropics on Tristan da Cunha and Gough Islands in the South Atlantic Ocean, and on Amsterdam Island in the Indian Ocean. Rouhan et al. (2004) proposed that *E. succisaefolium* was a species pair with *E. cuspidatum*. The analyses presented here, which

included more species of this group, show that *E. succisaefolium* belongs to the *cuspidatum* clade but is not sister to *E. cuspidatum*. Instead, it is sister to an unresolved clade of Andean species (that includes *E. cuspidatum*). *Elaphoglossum succisaefolium* differs from all other species in this clade by its obtuse laminar apices and generally smaller, thicker leaves.

Rouhan et al. (2004) hypothesized that these differences could represent an adaptive character to the exposed habitat and to the temperate to subantarctic climate of the islands where this species grows. Among the Neotropical species there is considerable variation in what has been called *E. cuspidatum*. The Mesoamerican material tends to have more compact rhizomes than the material from Colombia, Ecuador, and Venezuela (the type is from northern Venezuela). Also in Ecuador and Colombia some plants have red-brown rhizome scales instead of dark brown or blackish as is found in northern Venezuela where the type of *E. cuspidatum* was collected. Taxonomic studies are needed to determine if this variation indicates different species.

The other large clade recovered has, in turn, another basal split between two well-supported clades. The smaller of these two groups is here called the **petiolatum clade** (JS 99/BS 100), which is sister to the other group that contains the remaining 11 clades (JS 82/BS 88). The petiolatum clade is composed of four species from subsection *Pilosa*. It was previously recovered by Vasco et al. (2009b) as the Mexican petiolatum clade. All the species in this clade were from Mexico, but in this study *E. petiolatum* from Jamaica (where the type of *E. petiolatum* was collected) was recovered as part of this clade. Thus, it is preferable to call this the petiolatum clade. Species of this clade are characterized by resinous dots on the abaxial blade surfaces, usually black, entire rhizome scales, and dark-tipped scales on the proximal portions of the petioles (these scales sometimes also occur on the rachis). All

species recovered as part of the petiolatum clade are from the New World (Mexico and Jamaica). Mickel & Smith (2004) informally recognized a group of about 15 species of *Elaphoglossum* as the *E. petiolatum* complex. This complex comprises species distributed worldwide and defined more or less by the same characteristics as the petiolatum clade recovered in our analysis. Our results suggest that the *E. petiolatum* complex of Mickel & Smith (2004) is not monophyletic (Figs. 1 and 2). The species of this complex were recovered in three different clades: the petiolatum (*E. rzedowskii*, *E. petiolatum*, *E. pringlei*, *E. potosianum*), the tenuiculum (*E. tenuiculum*, *E. welwitschii*, *E. killipii*, *E. yungense*, *E. lancifolium*), and the ciliatum clades (*E. bifurcatum*, *E. nervosum*, *E. dimorphum*). Furthermore, our results show that what has been called *E. petiolatum* in Central and South America (as *E. petiolatum* aff., recovered as part of the tenuiculum clade) is a different species. The considerable morphological variation that has been reported for this species in Central and South America (Mickel and Beitel, 1988; Mickel, 1995b; Mickel and Smith, 2004) suggests that more than one species exists in the region.

For the remaining 11 major clades, the MP and ML trees show a difference in the resolution of the backbone. For clarity purposes the discussion will follow the order and resolution obtained in the MP strict consensus tree (Fig.1). These 11 clades belong to two clades in the MP tree (Fig. 1). The first clade (JS 94/BS 95) consists of a four-way polytomy that includes three clades and a single species (*E. laminarioides*) standing by itself. The first of these is here called the **mathewsii clade** (JS 99/BS 100), composed of six species from subsection *Pilosa*. These species grow on rocks or terrestrially in mats of bryophytes. They are characterized by creeping rhizomes with dark brown scales, upper lamina surface generally covered by peltate scales, and lower lamina surface glabrous or with resinous dots

or reduced scales (in *E. stipitatum*). The *mathewsii* clade contains New and Old World species. The New World species occur mainly at elevations above 2800 m in the Andes. The Old World species occur either at high elevations, between 2000 and 2500 m (*E. stipitatum* in Lorence and Rouhan, 2004), or at lower elevations, below 1200 m (*E. randii* in Alston and Schelpe, 1957). Moran and Smith (2001) proposed that *E. mathewsii* from the New World and *E. subcinnamomeum* from the Old World constitute a species pair. Although the latter species was not included in this study, several authors (Mickel, 2002; Lorence and Rouhan, 2004) have suggested that it could be conspecific with the La Réunion endemic *E. stipitatum*, which was included here. This makes us suspect that *E. subcinnamomeum* belongs to the *mathewsii* clade, and that the relationship proposed on the basis of morphological similarity by Moran and Smith (2001) could eventually be supported by the molecular data.

The second clade is here called the **tenuiculum clade**. This clade, which contains ten species in our analysis, has relatively low support (JS 50/BS 73). Of the ten species, six are from subsection *Pilosa* (*E. tenuiculum*, *E. petiolatum* aff., *E. welwitschii*, *E. killipii*, *E. yungense*, *E. lancifolium*), two from subsection *Microlepidea* (*E. ipshookense*, *E. tectum*), one from subsection *Polylepidea* (*E. edwallii*), and one from subsection *Huacsaro* (*E. caricifolium*). Based on morphology, *E. laminarioides*, the species that it is standing by itself in the four-way polytomy, should belong to the tenuiculum clade. Species in the tenuiculum clade have linear-elliptic to linear laminae with resinous dots and scales that vary from round to linear with long acicular cilia. The rhizomes are long-creeping with dark scales, and the fertile leaves are slightly longer than the sterile ones. This clade contains species from both the New and the Old World, and the bulk of the species that were considered part of the *petiolatum* complex (Mickel and Smith, 2004), yet it does not include *E. petiolatum*. In the

present study, the New World species representing the petiolatum complex are *E. killipii*, *E. petiolatum*, and *E. yungense*; and the Old World ones are *E. lancifolium* and *E. welwitschii*. Two species of the tenuiculum clade, *E. yungense* and *E. lancifolium*, constitute a species pair that Moran and Smith (2001) proposed on the basis of morphology (for the latter species they used the name *E. salicifolium*, a synonym; see Rouhan, 2005). Our gene trees support the species pair hypothesis of Moran and Smith and suggest these two species are conspecific. Additional analyses that included four more accessions of *E. yungense* from Bolivia (Vasco et al., 2009b), showed *E. lancifolium* nested within an *E. yungense* clade. This result agrees with the present study. A careful revision of material from both species should be undertaken before taxonomic decisions are made.

The third clade of the polytomy is the **vulcanicum clade** (JS 91/BS 99), which consists of eight species, seven belonging to subsection *Huacsaro*. *Elaphoglossum ovatum*, is the only one that do not belong to subsection *Huacsaro*, Mickel and Atehortúa (1980) placed this species in section *Squamipedia* because of its long-creeping rhizomes and small leaves (<12 cm long). *Elaphoglossum ovatum*, however, is atypical in section *Squamipedia* because it lacks the paired peglike aerophores on the rhizomes, has dark rhizome scales (not pale tan as all the other members of section *Squamipedia*), and has phyllodia. By its scales with acicular marginal cells, it is a typical member of section *Lepidoglossa*. Species in the vulcanicum clade are mainly epiphytes with long-creeping ascending, densely scaly rhizomes, lustrous, brown-red, spreading rhizome scales with tortuous apices, obtuse to acuminate (in *E. inquisitivum*) laminae apices, and fertile leaves that tend to be erect and longer than the sterile ones (except in some plants of *E. dendricola*). The species in the vulcanicum clade are all Neotropical.

The remaining eight clades of section *Lepidoglossa* form a four-way polytomy in the MP tree, which is weakly supported (JS 51). Two of the subclades, here called the **paleaceum I** (JS 100/BS 100) and **paleaceum II** (JS 99/BS 99) clades, are strongly supported, but we know of no morphological characters that distinguish them. The 15 species of these two clades all correspond to subsection *Polylepidea* and are part of what has been informally called the paleaceum complex (Mickel and Smith, 2004). Species of the paleaceum clades are characterized by black or orange petiole scales with black margins or teeth, laminae densely scaly with attenuate to acute (never obtuse) apices, and attenuate to cuneate bases. The paleaceum I clade is composed entirely of New World species, whereas the paleaceum II clade consists of species from both the New and Old Worlds. The paleaceum clades are the most diverse and taxonomically difficult groups of section *Lepidoglossa*, mainly because of the high number of species they contain. Because the type locality of *E. paleaceum* is Madeira and no material from that island was included in this study, relationships within this species complex are not fully understood and require further study.

The third clade of the polytomy is not well supported (support values less than 50), but it is divided into two smaller, relatively well supported clades: the **Mascarene Islands clade** (JS 74/BS 85) and the **Madagascan clade** (JS 99/BS 99). In the Mascarene Islands clade, three of the four species belong to subsection *Polylepidea* (*E. heterolepis*, *E. tomentosum*, *E. lanatum*), and the remaining one to subsection *Pilosa* (*E. richardii*). All species of this clade occur in the Old World and are endemic to the islands of Mauritius and La Réunion in the Indian Ocean (Lorence and Rouhan, 2004). Our results differ slightly from those of Rouhan et al. (2004) who found that *E. richardii* was part of a clade containing the Mexican species *E. pringlei* and *E. petiolatum* (both part of the petiolatum clade in this study). Although *E.*

richardii has resinous dots typical of the petiolatum clade, the results obtained in this study make sense geographically, suggesting a diversification of this clade solely within the Mascarene Islands, and multiple origin of resinous dots.

The **Madagascan clade** was supported by previous analyses (Rouhan et al., 2004; Vasco et al., 2009b), as was its sister relationship with the Mascarene Islands clade (Vasco et al., 2009b). The species recovered as part of this clade belong to three different subsections: *Pilosa* (*E. avaratense*, *E. forsythii-majoris*) and *Polylepidea* (*E. achroalepis*) of section *Lepidoglossa*, and subsection *Tenuifolia* of section *Elaphoglossum* (*E. humbertii* and *E. scolopendriforme*). We know of no morphological characters that distinguish this clade. All of its species are endemic to Madagascar, suggesting diversification within that island. It is important to note that not all species of section *Lepidoglossa* that occur in Madagascar belong to this clade; for example, see *E. leucolepis* and *E. poolii*. Interestingly, *E. humbertii* and *E. scolopendriforme* resemble the species of the ciliatum clade in having minutely punctate laminae (which appear glabrous), resinous rhizomes, and echinulate spores.

The fourth clade of the polytomy (JS 68/BS 60) contains a trichotomy. Its first clade, here called the **vestitum clade** (JS 83/BS 71), consists of ten species, eight of which belong to subsection *Polylepidea*, and one (*E. furfuraceum*) to subsection *Microlepidea*. Species of this clade can be distinguished by compact rhizomes, concolorous rhizome scales, acute lamina apices, and abaxial laminar scales that are bicolorous, round to lanceolate, and ciliate-denticulate, with dark teeth. The vestitum clade consists of two clades, one exclusively Old World (JS 66/BS 68) and the other exclusively New World (JS 89/BS 96). The Old World clade was recovered in previous molecular analyses (Rouhan et al., 2004): it includes *E. poolii*, a species endemic to Madagascar. This species was hypothesized to be closely related

to a New World species, *E. muscosum*, because of their morphological similarities (Christensen, 1932; Moran and Smith, 2001). Rouhan et al. (2004), however, found that the two species belong to different clades within section *Lepidoglossa* and thus the relationship proposed for them is not supported. Our results agree with this statement. However what Rouhan et al. (2004) called *E. muscosum* (specimen at NY *Moran*, 6342) is actually *E. vestitum*. The vestitum clade has been recognized by Mickel (1995b, see *E. furfuraceum* discussion) as one of the most problematic groups of *Elaphoglossum* in which much work is required to define species limits and the circumscription of the complex.

The second clade in the trichotomy is the **ciliatum clade** (JS 62/BS 63), which was the subject of a phylogenetic study and monographic revision by Vasco et al. (2009a, 2009b). It consists of ten species, of which three belong to subsection *Huacsaro* (*E. ciliatum*, *E. huacsaro*, *E. sp. nov4*) and four to subsection *Pilosa* (*E. bifurcatum*, *E. nervosum*, *E. dimorphum*, *E. dusii*) of section *Lepidoglossa*. The other three were placed by Mickel and Atehörtúa (1980) in section *Elaphoglossum* subsection *Tenuifolia* (*E. burchellii*, *E. gramineum*, *E. nigrescens*). Species of the ciliatum clade are characterized by resinous rhizomes, laminar scales reduced to minute dots, and cristate, echinate perispores. Of the ten species in this group, three are endemic to the island of St. Helena in the southern Atlantic Ocean, and the other seven are New World, occurring from Mexico and the West Indies to southern Brazil. The morphological characters common to species of the ciliatum group are also found in two other species (*E. humbertii* and *E. scolopendriforme*) that were recovered in this analysis as part of the Madagascan clade (as explained above). The morphological resemblance of these last two species with species of the ciliatum clade is so great that Moran and Smith (2001) considered *E. humbertii* a species pair with *E. ciliatum*. This study and

these of Rouhan et al. (2004) and Vasco et al. (2009b) do not support this hypothesis and suggest that these morphological characters have evolved independently in section *Lepidoglossa*.

The third clade of the polytomy (JS 64/BS 68), is composed of two subclades that correspond to subsections named by Mickel and Atehortúa (1980): **subsection *Petiolosa*** (JS 92/BS 97) and **subsection *Muscosa*** (JS 64/BS68). The sister relationship between these two clades is proposed here for the first time. Both clades have species that occur primarily at high elevations in the Andes.

The clade that corresponds to **subsection *Petiolosa*** contains two of the three species mentioned as part of that subsection by Mickel and Atehortúa (1980). Species in this clade are characterized by short-creeping rhizomes; dark, shiny linear, entire rhizome scales; petioles with capitate glands (sometimes also present on the margins of the rhizome scales and on the petiole bases); blades with caudate tips and resinous dots; and conduplicate fertile blades. This is the only clade within section *Lepidoglossa* in which capitate glands have been found (A. Vasco and R. Moran pers. obs); such glands are known elsewhere in *Elaphoglossum* only in the subulate clade (sensu Rouhan et al., 2004). All species of subsection *Petiolosa* occur in the New World above 1800 m in the Andes. The monophyly of subsection *Petiolosa*, its relatively small number of species, and the fact that there are several morphological characters that define the group, make this group of species a good candidate for taxonomic revision. *Elaphoglossum murinum* M. Kessler & Mickel, a species claimed to be similar to *E. petiolosum* (Kessler and Mickel, 2006), seems more related to species of the vulcanicum clade because of its long creeping rhizomes, rhizomes scales that are maroon and curly, and flat (not conduplicate) fertile leaves.

Sister to subsection *Petiolosa* is **subsection *Muscosa***, the second of the two subsections named by Mickel and Atehortúa (1980). Our gene trees supported it as monophyletic. Originally nine species were included as part of this subsection, but the present study includes 14 species that, based on morphology, we assigned to this subsection. Species of subsection *Muscosa* are characterized by scaly rhizomes, petioles, and laminae, laminae with obtuse apices, and papillate spores about twice as long (more than 70 μm) as other species of *Elaphoglossum*. All the species of the subsection are native to the New World. Most of the species are restricted to the Andes from 1800–4000 m, primarily in cloud forests and páramos. Subsection *Muscosa* is the subject of a monographic revision by the senior author (See Chapter 4)

2.6. FURTHER PROSPECTS

The molecular analyses presented here provide the first comprehensive view of the phylogeny of *Elaphoglossum* section *Lepidoglossa*. The gene trees presented identify 13 major clades, most of which can be distinguished by one or more putative morphological synapomorphies. However there are some clades that do not have known characteristics common to their member species, thus the phylogeny does not have the predictive power one might want, in that some species of section *Lepidoglossa* that were not included in the analyses would have to be sequenced in order to definitely know their phylogenetic position.

Although these analyses confirm some aspects of the existing classification of section *Lepidoglossa* (e.g., the monophyly of subsections *Petiolosa* and *Muscosa*), they show that the current classification needs to be revised. The phylogenetic trees described here should be the basis for future phylogenetic and taxonomic studies of section *Lepidoglossa*. Besides

providing a basis for choosing clades of convenient size for monographic study, the phylogeny offers a framework to address other biological aspects of section *Lepidoglossa*, such as biogeography, ecological diversity, and the evolution of morphological characters.

Although the current phylogeny is an important step forward, further work is needed to improve both resolution and support for relationships among and within the recovered clades. It will also be important to pursue comparative studies of developmental, ecological, and distribution patterns in order to understand in more detail patterns of evolution in section *Lepidoglossa*.

2.7. APPENDIX 1.

Voucher information and GenBank accession numbers for taxa used in this study (An X indicates new sequences that will be submitted to GenBank and eventually will have an accession number). A dash indicates the region was not sampled. The sections and subsections follow Mickel & Atehortúa (1980).

Species, subsection or section (if not sect. *Lepidoglossa*), country of origin, collector, collection number, herbarium acronym, GenBank accession numbers: *atpB-rbcL*, *rps4-trnS*, *trnL-trnF*

Elaphoglossum achroalepis (Baker) C. Chr., *Polylepidea*, Madagascar, Rakotondrainibe, 6485, P, EF040636, AY540225, AY536288. ***E. albescens*** (Sodirol) H. Christ, sect. *Polytrichia*, Colombia, Vasco, 497, NY, X, X, X. Colombia, Vasco, 739, HUA, NY, X, X, X. ***E. amygdalifolium*** (Mett. ex Kuhn) H. Christ, sect. *Amygdalifolia*, Costa Rica, Herrera, 2063, CR, INB, NY, USJ, --, AY536173, AY534845. ***E. arbuscula*** (Rosenst.) stat. nov., *Huacsaro*, Ecuador, Moran, 6852, NY, X, X, X. Moran, 6903, NY, X, X, X. ***E. argyrophyllum*** (Sodirol) comb. nov., *Polylepidea*, Ecuador, Moran, 7433, NY, X, X, X. Colombia, Vasco, 502, HUA, NY, X, X, X. ***E. aschersonii*** Hieron., *Muscoca*, Colombia, Archer, 1367, MEDEL, US, X, X, X. Ecuador, Moran, 7645, NY, X, X, X. ***E. asterolepis*** (Baker) C. Chr., *Polylepidea*, Madagascar, Kessler, 12751, P, EF040642, AY540231, AY536294. ***E. aubertii*** (Desv.) T. Moore, sect. *Eximia*, Comoros, Rouhan, 110, P, EF040647, EF040622, EF040608. ***E. auricomum*** (Kunze) T. Moore, *Polylepidea*, Mexico, Hammer, 3, NY, --, AY536145, AY534817. ***E. avaratense*** Rakotondr., *Pilosa*, Madagascar, Rakotondrainibe, 1456, P, EU907660, AY540233, AY536296. ***E. bellermannianum*** (Klotzsch) T. Moore, *Muscoca*, Bolivia, Jiménez, 2130, LPB, NY, X, X, X., Dominican Republic, Liogier, 20950, NY, X, X, X. Ecuador, Moran, 7525, NY, X, X, X. Costa Rica, Sundue, 1803, NY, X, X, X. Colombia, Vasco, 506, HUA, MO, NY, X, X, X. Venezuela, Vasco, 843, MER, NY, VEN, X, X, X. Dominican Republic, Zanoni, 22314, JSBD, NY, --, X, X. ***E. bifurcatum*** (Klotzsch) T. Moore, *Pilosa*, St. Helena, Eastwood, 215, EU907661, EU907737, AY194070. ***E. brenesii*** Mickel, *Polylepidea*, Costa Rica, Seidenschur, 156, NY, X, X, X. ***E. burchellii*** (Baker) C. Chr., sect. *Elaphoglossum*, Brazil, Labiak, P., 4236, NY, --, X, X. Brazil, Labiak, P., 4249, UPGB, X, X, X. Bolivia, Jiménez, 2129, NY, EU907662, --, EU907802. Bolivia, Jiménez, 2460, NY, EU907663, EU907738, EU907803. ***E. caricifolium*** Mickel, *Huacsaro*, Costa Rica, Halley, 7, NY, --, AY536143, AY534814. ***E. ciliatum*** (C. Presl) T. Moore, *Huacsaro*, Ecuador, Moran, 7418, NY, EU907668, EU907743, EU907808. Colombia, Vasco, 504, HUA, MO, NY, EU907671, EU907746, EU907811. ***E. corazonense*** H. Christ, *Polylepidea*, Ecuador, Moran, 6788, NY, X, X, X. ***E. curvans*** (Kunze) T. Moore, *Polylepidea*, Ecuador, Moran, 6972, NY, X, X, X. Colombia, Vasco, 723, HUA, NY, X, X, X. ***E. cuspidatum*** (Willd.) T.

Moore, *Polylepidea*, Colombia, Vasco, 553, HUA, NY, X, X, X. Venezuela, Vasco, 810, HUA, MER, NY, VEN, X, X, X. ***E. cuspidatum* aff.**, *Polylepidea*, Colombia, Vasco, 583, HUA, MO, NY, X, X, X. Colombia, Vasco, 610, HUA, MO, NY, X, X, X. ***E. deckenii*** (Kuhn) C. Chr., *Polylepidea*, Comoros, Rouhan, 105, CNDRS, NY, P, PTBG, --, AY540244, AY536307. ***E. decoratum*** (Kunze) T. Moore, *Polylepidea*, Brazil, Labiak, P., 4074, UPCB, X, X, X. ***E. dendricola*** (Baker) C. Chr., *Huacsaro*, Ecuador, Moran, 7662, NY, X, X, X. ***E. deorsum*** Vareschi, *Polylepidea*, Venezuela, Vasco, 837, MER, NY, VEN, X, X, X. Venezuela, Vasco, 791A, HUA, MER, NY, VEN, --, X, X. ***E. dimorphum*** (Hook. & Grev.) T. Moore, *Pilosa*, St. Helena, Eastwood, 302, EU907677, EU907752, AY194068. St. Helena, Eastwood, 719, EU907678, EU907753, EU907817. ***E. dombeyanum*** (Kunze) T. Moore, *Polylepidea*, Ecuador, Moran, 6907, NY, X, X, X. ***E. dussii*** Underw. ex Maxon, *Pilosa*, Guadeloupe, Christenhusz, 4011, NY, EU907679, EU907754, EU907818. Guadeloupe, Jeremie, sn, NY, EU907680, X, X. ***E. edwallii*** Rosenstock, *Polylepidea*, Brazil, Prado, 1123, NY, --, AY536144, AY534816. ***E. engelii*** (H. Karst.) H. Christ, *Muscosa*, Bolivia, Jiménez, 2342, LPB, NY, X, X, X. Mexico, Lyonnet, 1413, US, X, X, X. Ecuador, Moran, 6777, NY, X, X, X. Colombia, Vasco, 591, HUA, MO, NY, X, X, X. Venezuela, Vasco, 795, MER, NY, VEN, X, --, X. Venezuela, Vasco, 808, MER, NY, VEN, X, X, X. ***E. feei*** (Bory ex Fée) T. Moore, sect. *Squamipedia*, Guadeloupe, Christenhusz, 4171, NY, X, X, X. ***E. forsythii-majoris*** H. Christ, *Pilosa*, Madagascar, Kessler, 12678, P, EF040644, EF040620, EF040606. ***E. furfuraceum*** (Mett. ex Kuhn) H. Christ, *Microlepidea*, Costa Rica, Moran, 6367, CR, INB, NY, UCR, --, AY540249, AY536312. Costa Rica, Sundue, 1358, NY, X, X, X. ***E. gardnerianum*** (Kunze ex Fée) T. Moore, *Muscosa*, Brazil, Matos, 1000, CEPEC, X, X, X. ***E. glabrescens*** A. Vasco, *Muscosa*, Bolivia, Jiménez, 957, LPB, NY, X, X, X. Bolivia, Jiménez, 2152, LPB, NY, X, X, X. ***E. gemmatum*** Vasco, sect. *Polytrichia*, Colombia, Vasco, 470, NY, X, --, X. Colombia, Vasco, 491, NY, X, --, X. ***E. gramineum*** (Jenm.) Urb., sect. *Elaphoglossum*, Jamaica, Anderson, 3223, herbarium, EU907682, EU907756, EU907820. Jamaica, Proctor, 3907, herbarium, --, EU907757, EU907821. ***E. guamanianum*** (Sodiolo) C. Chr., *Polylepidea*, Ecuador, Moran, 6760, NY, X, X, X. Ecuador, Moran, 6896, NY, X, X, X. ***E. guentheri*** Rosenst., sect. *Squamipedia*, Ecuador, Lehnert, M., 1306, NY, X, X, X. ***E. hartwegii*** (Fée) T. Moore, *Pilosa*, Colombia, Vasco, 590, HUA, MO, NY, X, X, X. ***E. heterolepis*** (Fée) T. Moore, *Polylepidea*, Mauritius, Rouhan, 177, P, EU907683, AY540251, AY536314. ***E. huacsaro*** (Ruíz) H. Christ, *Huacsaro*, Dominican Republic, Nee, 52309, NY, EU907687, EU907762, EU907825. Colombia, Vasco, 556, HUA, NY, EU907690, EU907765, EU907828. ***E. humbertii*** C. Chr., sect. *Elaphoglossum*, Madagascar, Rouhan, 466, P, EU907696, EU907771, EU907834. ***E. hybridum*** (Bory) Brack., sect. *Polytrichia*, La Réunion, Rouhan, 250, P, EU907697, EU907772, EU907835. ***E. inquisitivum*** M. Kessler & Mickel, *Huacsaro*, Bolivia, Jiménez, 1790, NY, X, X, X. ***E. ipshookense*** Mickel, *Microlepidea*, Mexico, Mickel, 4748, NY, EU907698, EU907773, EU907836. ***E. killipii*** Mickel, *Pilosa*, Bolivia, Sundue, 581, LPB, NY, USZ, --, AY540257, AY536320. ***E. laminarioides*** (Fée) T. Moore, *Microlepidea*, Venezuela, Vasco, 827, HUA, MER, NY, VEN, X, X, X. ***E. lanatum*** (Bojer ex Baker) Lorence, *Polylepidea*, Mauritius, Rouhan, 194, MAU, NY, P, PTBG, --, AY540258, AY536321. ***E. lancifolium*** (Desv.) C.V. Morton, *Pilosa*, La Réunion, Rouhan, 201, P, EU907699, AY540259, AY536322. ***E. langsdorffii*** (Hook. & Grev.) T. Moore, *Polylepidea*, Brazil, Labiak, 4113, NY, UFPR, X, X, X. Venezuela, Vasco, 802, HUA, MER, NY, VEN, X, X,

X. *E. laxisquama* **aff.**, *Muscoca*, Ecuador, Lehnert, 1457, NY, X, X, X. Ecuador, Moran, 7588, NY, X, X, X. *E. lehmannianum* H. Christ, *Muscoca*, Ecuador, Sundue, 1066, NY, QCA, X, X, X. Costa Rica, Sundue, 1707, INB, NY, X, X, X. Colombia, Vasco, 559, HUA, X, X, X. Colombia, Vasco, 737, HUA, NY, X, X, X. *E. leucolepis* (Baker) Krajina ex Tardieu, *Polylepidea*, Madagascar, Rakotondrainibe, 6339, P, EF040638, AY540261, AY536324. *E. iloense* (Hook.) T. Moore, sect. *Squamipedia*, Venezuela, Vasco, 845, HUA, MER, NY, VEN, X, X, X. *E. luridum* (Fée) H. Christ, sect. *Elaphoglossum*, Ecuador, Sundue, 1095, NY, X, X, X. *E. mathewsii* (Fée) T. Moore, *Pilosa*, Venezuela, Vasco, 835, HUA, MER, NY, VEN, X, X, X. Colombia, Vasco, 598, HUA, MO, NY, X, X, X. *E. meridense* (Klotzsch) T. Moore, *Polylepidea*, Colombia, Vasco, 764, HUA, NY, X, X, X. Colombia, Vasco, 789, HUA, NY, X, X, X. *E. micropogon* Mickel, *Polylepidea*, Costa Rica, Moran, 6353, NY, EF040643, AY540268, AY536331. Ecuador, Moran, 7485, NY, X, X, X. *E. mitorrhizum* Mickel, sect. *Elaphoglossum*, Costa Rica, Boyle, 6410, CR, INB, NY, USJ, EF040656, AY540269, AY536332. *E. molle* (Sodirol) H. Christ, *Polylepidea*, Bolivia, Jiménez, I., 2190, NY, X, X, X. Ecuador, Lehnert, 1339, GOET, QCA, NY, UC, X, X, X. *E. moorei* (E. Britton) H. Christ, sect. *Squamipedia*, Colombia, Vasco, 636, HUA, NY, X, X, X. *E. muscosum* (Sw.) T. Moore, *Muscoca*, Brazil, Brade, 9333, UC, X, X, X. Guatemala, Contreras, 10916, MO, US, --, X, X. Mexico, Mickel, 1246, NY, X, X, X. Mexico, Mickel, 4879, NY, X, X, X. Dominican Republic, Mickel, 8870, NY, X, X, X. Guatemala, Tenorio, 14731, MO, NY, X, X, X. *E. nervosum* (Bory) H. Christ, *Pilosa*, St. Helena, Eastwood, 358, EU907700, EU907774, AY194069. St. Helena, Eastwood, 367, EU907701, EU907775, EU907837. *E. nigrescens* (Hook.) T. Moore ex Diels, sect. *Elaphoglossum*, Bolivia, Jiménez, 2256, LPB, NY, EU907706, EU907780, EU907842. Costa Rica, Moran, 6332, CR, INB, NY, UCR, EU907707, X, --. *E. novogranatense* A. Vasco, *Muscoca*, Ecuador, vanderWerff, 10962, MO, X, X, X. Colombia, Vasco, 735, HUA, NY, X, X, X. Colombia, Vasco, 747, HUA, NY, X, X, X. *E. orbignyanum* (Fée) T. Moore, *Polylepidea*, Bolivia, Bach, 1773, LPB, EU907710, EU907783, EU907845. Ecuador, Moran, 7486, NY, X, X, X. *E. oreophilum* A. Vasco, *Muscoca*, Ecuador, Øllgaard, 8068, AAU, NY, X, X, X. Ecuador, Sklenar, 3077, NY, --, X, X. Ecuador, van der Werff, 13359, MO, NY, --, --, X. Colombia, Vasco, 600, HUA, MO, NY, X, X, X. *E. ovatum* (Hook. and Grev.) T. Moore, sect. *Squamipedia*, Ecuador, Smith, 2872, UC, EF040641, AY540273, AY536336. *E. pala* André ex H. Christ, *Petioloessa*, Ecuador, Lehnert, 1441, GOET, QCA, NY, UC, X, X, X. *E. paleaceum* (Hook. & Grev.) Sledge, *Polylepidea*, Mexico, Mickel, 9710, NY, EU907711, EU907784, EU907846. *E. paleaceum* **aff.1** Colombia, Vasco, 786, HUA, NY, X, X, X. . *E. paleaceum* **aff.2** Venezuela, Vasco, 830, NY, VEN, X, X, X. Venezuela, Vasco, 850, HUA, MER, NY, VEN, X, X, X. *E. peltatum* (Sw.) Urb., sect. *Squamipedia*, Mexico, Daly, 13117, NY, X, X, X. *E. petiolatum* (Sw.) Urb., *Pilosa*, Jamaica, Maxon, 10158, NY, --, X, --. Mexico, Nicholson, 78201A, NY, EU907712, AY540275, AY536338. *E. petiolatum* **aff** Ecuador, Moran, 7573, NY, EU907714, EU907785, EU907848. Colombia, Vasco, 585, HUA, MO, NY, EU907713, --, EU907847. Venezuela, Vasco, 842, MER, NY, VEN, X, X, X. Ecuador, Moran, 6874, NY, X, X, X. Colombia, Vasco, 762, HUA, NY, X, X, X. *E. poolii* (Baker) H. Christ, *Polylepidea*, Madagascar, Kessler, 12702, NY, EF040639, AY540278, AY536341. *E. potosianum* H. Christ, *Pilosa*, Mexico, Hinton, 22679, NY, EU907715, EU907786, EU907849. *E. pringlei* (Davenp.) C. Chr., *Pilosa*, Mexico, Campos, 2650, NY, EU907716, EU907787, EU907850. *E. pseudoboryanum*

Mickel, sect. *Polytrichia*, Ecuador, Sundue, 1036, NY, --, --, X. ***E. quisqueyanum*** A. Vasco, *Muscosa*, Dominican Republic, Zanoni, 20681, JBSD, --, X, X. ***E. randii*** Alston and Schelpe, *Pilosa*, Marion Island, Huntley, 2072, P, --, AY540282, AY536345. ***E. richardii*** (Bory ex Fée) H. Christ, *Pilosa*, La Réunion, Rouhan, 231, P, EU907717, AY540284, AY536347. ***E. rimbachii*** Mickel, *Polylepidea*, Venezuela, Luteyn, 11051, NY, --, AY536152, AY534824. Ecuador, Moran, 6875, NY, X, X, X. ***E. rosenstockii*** H. Christ ex Rosenst., *Pilosa*, Venezuela, Vasco, 798, MER, NY, VEN, X, X, X. ***E. ruficomum*** Mickel, *Muscosa*, Peru, Boeke, 2970, MO, NY, X, X, X. Peru, van der Werff, 21289, MO, --, --, X. ***E. rufidulum*** (Willd. ex Kuhn) C. Chr., *Polylepidea*, Madagascar, Rakotondrainibe, 6396, P, --, AY540285, AY536348. ***E. rzedowskii*** Mickel, *Pilosa*, Mexico, Bartholomeus, 2691, NY, EU907718, EU907788, EU907851. ***E. scolopendriforme*** Tardieu, *Pilosa*, Madagascar, Rakotondrainibe, 6426, P, EU907719, AY540288, AY536351. ***E. sieberi*** (Hook. and Grev.) T. Moore, sect. *Elaphoglossum*, Mauritius, Rouhan, 169, P, EU907720, AY540290, AY536353. ***E. sp nov1***, *Polylepidea*, Colombia, Vasco, 781, HUA, NY, X, X, X. ***E. sp nov2***, *Pilosa*, Colombia, Vasco, 595, HUA, MO, NY, X, X, X. ***E. sp nov3***, *Huacsaro*, Ecuador, Moran, 6835, NY, X, --, X. ***E. sp nov4***, *Huacsaro*, Ecuador, Moran, 6711, NY, EU907673, EU907748, EU907813. Ecuador, Moran, 6762, NY, QCA, QCNE, EU907674, EU907749, EU907814. ***E. sp nov5***, *Muscosa*, Bolivia, Jiménez, 1044, LPB, NY, X, X, X. Bolivia, Jiménez, 2186, LPB, NY, X, X, X. ***E. splendens*** (Bory ex Willd.) Brack., *Polylepidea*, La Réunion, Rouhan, 247, P, EU907721, AY540296, AY536359. ***E. squamipes*** (Hook.) T. Moore, sect. *Squamipedia*, Costa Rica, Sundue, 1688, INB, NY, X, X, X. Colombia, Vasco, 759, HUA, NY, X, X, X. Venezuela, Vasco, 817, HUA, MER, NY, VEN, X, X, X. ***E. squarrosus*** (Klotzsch) T. Moore, sect. *Polytrichia*, Ecuador, Lehnert, 1425, GOET, QCA, NY, UC, --, X, X. Colombia, Vasco, 748, HUA, NY, X, X, X. ***E. stipitatum*** (Bory ex Fée) T. Moore, *Pilosa*, La Réunion, Rouhan, 212, NY, P, PTBG, --, AY540297, AY536360. ***E. succisaefolium*** (Thouars) T. Moore, *Polylepidea*, Amsterdam Island, Marthel-Thoumian, 1A, P, X, AY540299, AY536362. ***E. tectum*** (Humb. & Bonpl. ex Willd.) T. Moore, *Microlepidea*, Brazil, Prado, 1126, NY, --, AY536142, AY534813. ***E. tenuiculum*** (Fée) T. Moore ex C. Chr., *Pilosa*, Colombia, Vasco, 755, HUA, NY, X, X, X. Venezuela, Vasco, 824, HUA, MER, NY, VEN, X, X, X. ***E. tomentosum*** (Bory ex Willd.) H. Christ, *Polylepidea*, Mauritius, Rouhan, 174, P, EU907723, AY540300, AY536363. ***E. trivittatum*** (Sodirol) H. Christ, *Polylepidea*, Ecuador, Moran, 6778, NY, X, X, X. Ecuador, Moran, 6782, NY, X, X, X. ***E. tungurahuae*** Sodirol, *Huacsaro*, Ecuador, Moran, 6772, NY, --, X, X. ***E. vestitum*** (Schltdl. & Cham.) T. Moore, *Polylepidea*, Costa Rica, Sundue, 1684, NY, X, X, X. ***E. vulcanicum*** H. Christ, *Huacsaro*, Ecuador, Moran, 7586, NY, EU907728, EU907793, EU907856. Colombia, Vasco, 586, HUA, MO, NY, EU907727, EU907792, EU907855. ***E. vulcanicum aff.*** *Huacsaro*, Ecuador, Moran, 7515, NY, EU907726, EU907791, X. Colombia, Vasco, 666, NY, X, X, X. ***E. welwitschii*** (Baker) C. Chr., *Pilosa*, Tanzania, Taylor, 9099, P, --, AY540303, AY536366. ***E. yatesii*** Sodirol, *Muscosa*, Ecuador, Moran, 6908, NY, X, X, X. Ecuador, Sklenar, 1936, AAU, NY, X, X, X. ***E. yungense*** de la Sota, *Pilosa*, Bolivia, Jiménez, 2676, NY, EU907733, EU907798, EU907861. Bolivia, Labiak, 2804, NY, EU907735, EU907800, EU907863. ***E. zosteriformis*** Mickel, *Polylepidea*, Ecuador, Moran, 6767, NY, X, X, X.

CHAPTER 3

MONOGRAPH OF THE *ELAPHOGLOSSUM CILIATUM* GROUP (DRYOPTERIDACEAE)

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3.1. ABSTRACT

The *Elaphoglossum ciliatum* group was supported by a previous study as monophyletic on the basis of cpDNA sequence data. The present paper provides a monograph of this group. It includes keys, full synonymy, descriptions, specimens examined, index to collectors' names and numbers, photographs, and distribution maps for all species. Morphologically, these species are characterized by abaxial laminar scales reduced to minute dots, resinous rhizomes, and (except for *E. dussii*) spiny perispores. These characteristics are not unique to the *E. ciliatum* group because they are found in other species of *Elaphoglossum* sect. *Lepidoglossa*. Nine species are here recognized in the *E. ciliatum* group, with no subspecies or varieties. Six species are neotropical and primarily montane, being largely absent from Amazonia. The remaining three species are endemic to the island of St. Helena in the South Atlantic Ocean. A lectotype is designated for ***E. calaguala***.

Key words: Dryopteridaceae, *Elaphoglossum*, fern, floristics, pteridophytes, taxonomy.

RESUMEN

Se presenta la monografía del grupo de *Elaphoglossum ciliatum*, un grupo definido como monofilético basado en análisis de secuencias de ADN del cloroplasto. La monografía incluye claves, sinonimia completa, descripciones, especímenes examinados, un índice de colectores y sus números de colección, fotografías y mapas de distribución de todas las especies del grupo. Las especies de este grupo se caracterizan por tener las escamas de la superficie abaxial de la lámina reducidas a puntos muy pequeños, rizomas resinosos y (exceptuando *E. dussii*) perisporas equinadas. Sin embargo estas características no son únicas al grupo de *E. ciliatum*, y pueden encontrarse en otras especies de *Elaphoglossum* sect. *Lepidoglossa*. Se reconocen nueve especies en el grupo de *E. ciliatum*, sin subespecies ni variedades. Seis especies son neotropicales y principalmente de regiones de montaña. El resto de las especies son endémicas de la isla de St. Helena en el sur del océano Atlántico. Se designa un lectotipo para ***E. calaguala***.

3.2. INTRODUCTION

Elaphoglossum Schott ex J. Sm. is one of the largest fern genera, with at least 600 species worldwide, about three-quarters of which are neotropical (Mickel, 1995a).

Elaphoglossum is known among fern taxonomists as being taxonomically difficult at the species level, mainly because for such a large genus its species are remarkably similar. The only monographic treatment of the genus is that by Christ (1899), which included 142 species—all those known at the time. In 1980, however, a comprehensive infrageneric classification was proposed by Mickel and Atehortúa based mainly on sporophyte and spore morphology. Over the past 25 years there have been many regional or country-wide floristic

studies, such as for Mexico (Mickel and Smith, 2004), Mesoamerica (Mickel, 1995b), Venezuela (Mickel, 1995a), Peru (Mickel, 1991), and the Mascarene Islands (Lorence and Rouhan, 2004). Yet monographic treatments either of the entire genus or of any small groups within it have not been published, mainly because of the difficulties in finding small monophyletic groups.

Molecular data were expected to be helpful in establishing relationships among the species of *Elaphoglossum* and in pointing out small monophyletic groups suitable for monographic research. Recently, two molecular phylogenetic studies examining the relationships of the *Elaphoglossum* species have been published (Rouhan et al., 2004; Skog et al., 2004). These studies resolved some of the long-standing questions in the systematics of *Elaphoglossum*. They demonstrated the monophyly of the genus and recognized several monophyletic subgroups. These subgroups largely agree with the sections proposed on the basis of morphology by Mickel and Atehortúa (1980). One of the subgroups recognized on the basis of morphology and supported by the molecular work was section *Lepidoglossa* H. Christ. Members of this section typically have phyllopodia, conspicuously scaly laminae, and scales (of both rhizome and laminae) bearing acicular marginal cells.

The present paper concerns a clade within sect. *Lepidoglossa*: the *Elaphoglossum ciliatum* group. This group of nine species was recovered as monophyletic by molecular phylogenetic analyses using three chloroplast intergenic spacers—*atpB-rbcL*, *rps4-trnS*, and *trnL-trnF* (Vasco et al., 2009b). Morphologically the species of this group are atypical within sect. *Lepidoglossa* because their laminae are inconspicuously scaly, the scales being reduced to minute dots (typical members of the section have conspicuously and densely scaly laminae). Besides that, these species have rhizomes that dry blackish and produce a shiny,

lacquer-like exudate when dry. Their spores are also similar by being spiny (Moran et al., 2007). These similarities have resulted in the species being frequently confused in herbaria and often keyed close together and compared in floras (e.g. Mickel, 1991, 1995b).

Although the three morphological characters mentioned above are common to all species of the *E. ciliatum* group, they are not unique to the group, being found in two other species of sect. *Lepidoglossa* endemic to Madagascar: *E. humbertii* C. Chr. and *E. scolopendriforme* Tardieu. In the phylogenetic analyses these two species are recovered in a different clade not even sister to the *E. ciliatum* group (Vasco et al., in press). This suggests that these three characters have evolved at least twice in sect. *Lepidoglossa*.

The *E. ciliatum* group is characterized by reddish to yellowish-brown dots on the surface of the lamina (Fig. 7F). These dots result from the body of the scale being highly reduced or completely lost so that only the base remains embedded in the epidermis. Because of this reduction, the laminae appear glabrous, but close inspection with the naked eye can reveal the stumps of the scales dotting the surface of the lamina. In the cases in which the body of the scales is not completely reduced, some scales (typically less than 0.1 mm wide) can be distinguished. The scales exude resin from their base, and they appear as shiny dots on the lamina surface. The resin is also present on the rhizomes and when dry it appears as a dark reddish brown exudate. This often stains the newspapers in which the plants are pressed in the field.

The spores of all species (except for *E. dussii*) in the *E. ciliatum* group have spiny perispores (Figs. 1, 2). Moran et al. (2007) found that the presence of spines appears to be a synapomorphy for smaller clades within the sect. *Lepidoglossa* (the *E. ciliatum* group being

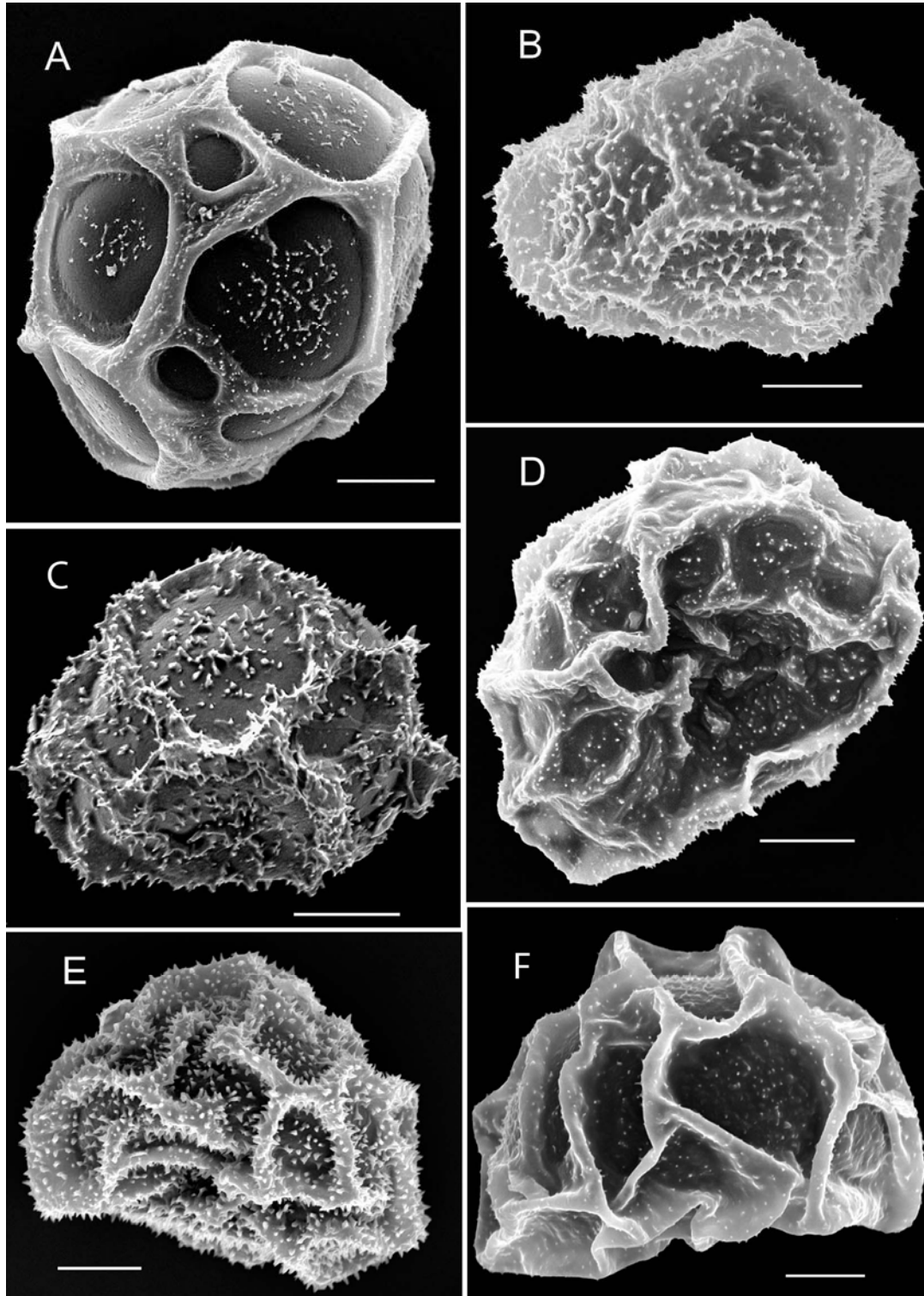


FIG. 1. Spores of the *Elaphoglossum ciliatum* group. **A.** *E. nigrescens* (Ingram & Ferrell-Ingram 1825, NY). **B.** *E. huacsaro* (Ruiz-Teran 6124, NY). **C.** *E. gramineum* (Valeur 634, NY). **D.** *E. nigrescens* (Ingram & Ferrell-Ingram 1308, NY). **E.** *E. ciliatum* (Balslev & Madsen 10402, AAU). **F.** *E. nigrescens* (Maas 6858, NY). Scale bars = 10 micrometers.

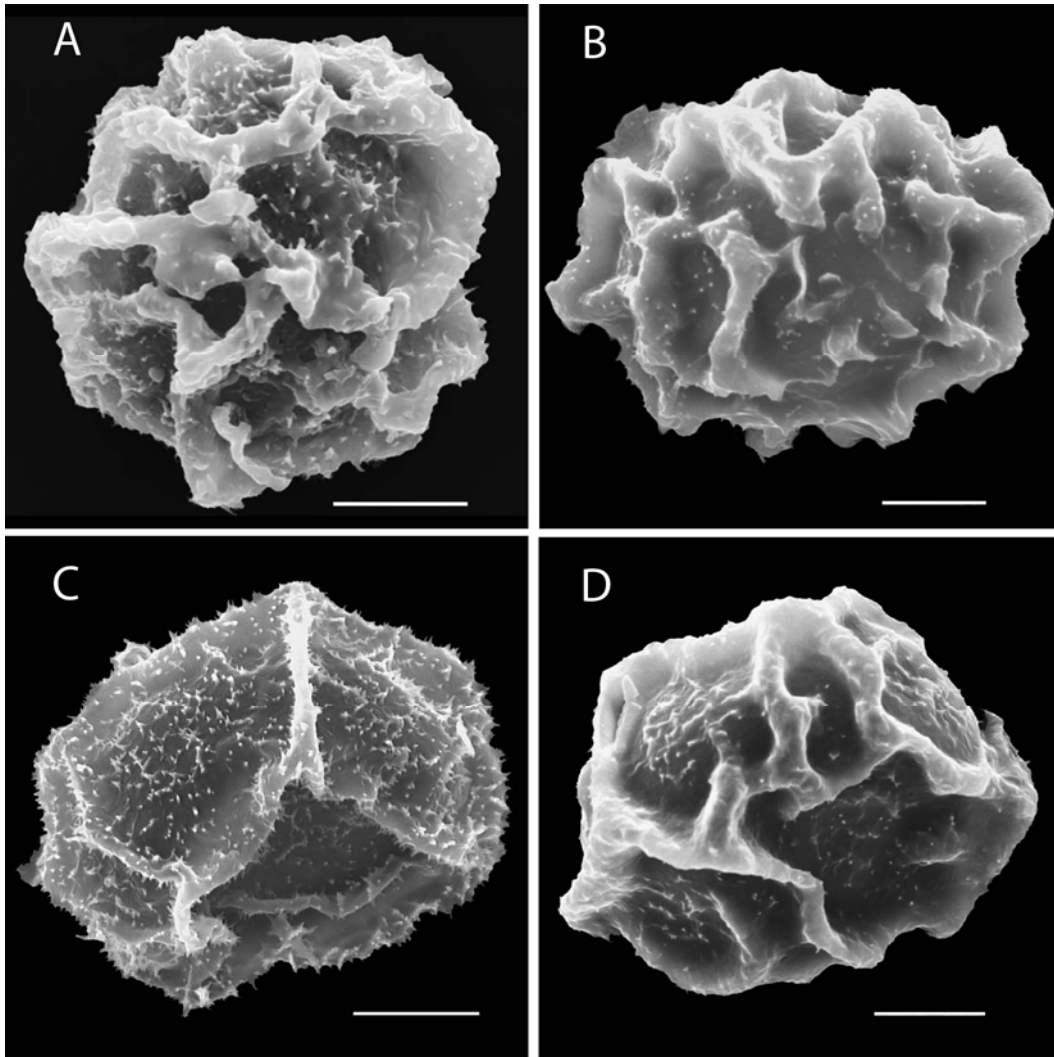


FIG. 2. Spores of the *Elaphoglossum ciliatum* group. **A.** *E. bifurcatum* (Cumming s.n, NY). **B.** *E. dimorphum* (collector unknown s.n., P). **C.** *E. burchellii* (Dusén 7225, NY). **D.** *E. dussii* (Lloyd 351, NY). Scale bars = 10 micrometers.

one of them), whereas the plesiomorphic character for the section was perispores without spines.

Mickel and Atehortúa (1980) classified eight of the nine species of this group (Appendix 1) in three subsections of *Elaphoglossum* within sections *Lepidoglossa* and *Elaphoglossum*; *E. ciliatum* and *E. huacsaro* were placed in subsect. *Huacsaro* Mickel & Atehortúa, the three species endemic to St. Helena (*E. bifurcatum*, *E. dimorphum* and *E. nervosum*) were placed

in subsect. *Pilosa* H. Christ, and the remaining three species, all neotropical (*E. burchellii*, *E. gramineum* and *E. nigrescens*), in subsect. *Tenuifolia* Mickel & Atehortúa. *Elaphoglossum dussii* was not assigned to any section.

Three species of the *E. ciliatum* group are endemic to the island of St. Helena in the southern Atlantic Ocean; however, the *E. ciliatum* group is primarily neotropical, distributed from Mexico and the West Indies to southern Brazil (Fig. 3). It is largely absent from the Amazon basin. The regions with the most species are the mountains of Costa Rica and Panama and the northern Andes (Appendix 2). The group primarily occurs in middle elevation forests, from 800 m to 2000 m.

In the Specimens Examined section, the geographic coordinates in brackets were determined using geographical gazetteers; they were not on the labels of the specimens. These coordinates were used to make the dot distribution maps. This study is based on an examination of over 1000 collections (Appendix 3).

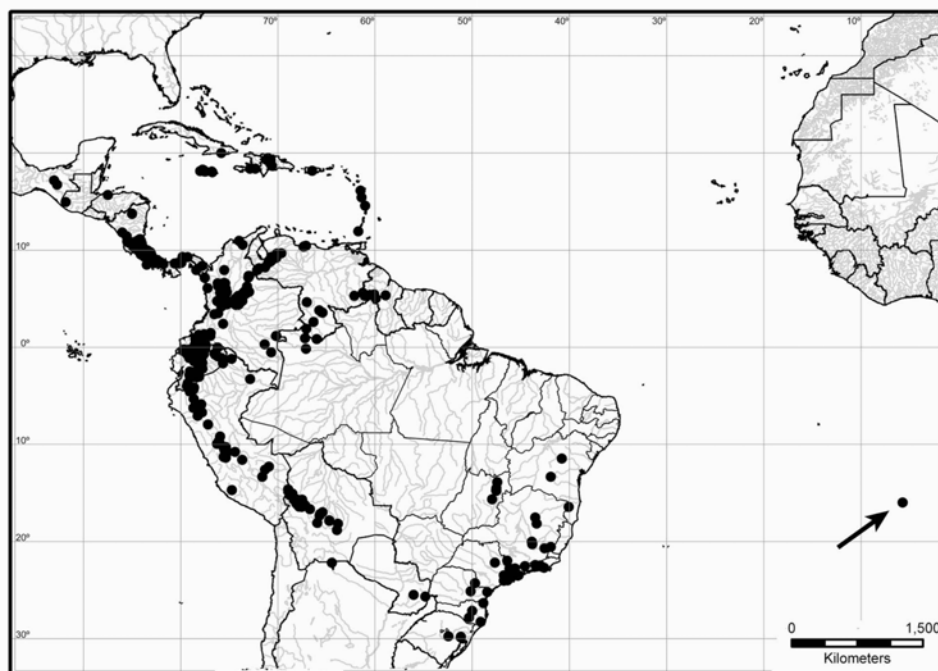


FIG. 3. General distribution of the *Elaphoglossum ciliatum* group. The arrow points to St. Helena Island.

3.3. KEY TO THE SPECIES OF THE *ELAPHOGLOSSUM CILIATUM* GROUP

1. Lamina of the sterile leaves pinnate.....1. *E. bifurcatum*
1. Lamina of the sterile leaves simple
 2. Laminae of the sterile leaves irregularly lobed; St. Helena Island.....4. *E. dimorphum*
 2. Laminae of the sterile leaves entire; St. Helena Island or elsewhere
 3. Laminae decurrent all the way to phyllopodia; scales present on the margins of the laminae, 0.3–1 mm long, dissected.....9. *E. nigrescens*
 3. Laminae tapering but ending well above phyllopodia; scales present or absent on the margins of the laminae, when present 0.1–0.3 mm long, entire or nearly so
 4. Rhizomes glabrous or glabrescent, remains of the scale bodies when present less than 1 mm long, round
 5. Laminae 5–16(–20) × 0.6–1.5 cm; scales on rhizomes and laminae completely reduced to resinous dots; Cuba, Jamaica and Dominican Republic.....6. *E. gramineum*
 5. Laminae 10–80 × 1–3 cm; some scales on rhizomes and laminae not completely reduced to resinous dots, remains of the scale bodies 0.5–1 mm; Central and South America 3. *E. ciliatum*
 4. Rhizomes scaly, the scales 1–6 mm long, lanceolate to linear-lanceolate
 6. Rhizome scales 2–6 mm long; plants epiphytic or rarely saxicolous

7. Rhizomes 2–4 mm wide, the scales 2–4.5 mm long; laminae 8–12 × 2–3 cm, the veins uniting apically into a submarginal vein; St. Helena Island 8. *E. nervosum*
7. Rhizomes 5–8 mm wide, the scales 3–6 mm long; laminae 15–45 × 1.5–3 cm, the veins free at their apices; West Indies 5. *E. dussii*
6. Rhizome scales 1–3 mm long; plants usually terrestrial
8. Rhizome scales black, rigid, flat; lamina apex obtuse to broadly acute; lamina surface adaxially sparsely scaly with thin, pale, appressed scales; rhizomes ascending to erect 7. *E. huacsaro*
8. Rhizome scales dark brown, twisted, spreading; lamina apex acute to acuminate; lamina surface adaxially lacking scales (only resinous dots present); rhizomes creeping 2. *E. burchellii*

3.4. TAXONOMIC TREATMENT

1. *Elaphoglossum bifurcatum* (Jacq.) Mickel, Brittonia 32: 116. 1980. *Osmunda bifurcata* Jacq., Collectanea 3: 282, tab. 20, fig. 4. 1789. *Acrostichum bifurcatum* (Jacq.) Sw., J. Bot. (Schrader) 3: 13. 1801 [“1800”], nom. illeg., non Cav. 1799. *Gymnogramma bifurcatum* (Jacq.) Kaulf., Wessen Farrenk. 81. 1827. *Polybotrya bifurcata* (Sw.) J. Sm., J. Bot. 4: 150. 1841. *Microstaphyla bifurcata* (Jacq.) C. Presl., Epimel. Bot. 161. 1849. Type: St. Helena. Locality and collector not designated (holotype: W-n.v.). (Fig. 4)

Adiantum furcatum L. f., Suppl. Pl. 447. 1781. *Elaphoglossum furcatum* (L.f.) H. Christ,

Neue Denkschr. Allg. Schweiz. Ges. Gesamten Naturwiss. [Monogr. Elaph.] 36: 98, fig. 50. 1899, nom. illeg., non Keyserl. 1873. *Microstaphyla furcata* (L. f.) Fée, Mém. Foug., 7. Ic. Esp. Nouv. 45, fig. 13. 1857. *Polybotrya furcata* (L. f.) Mett. ex Kuhn, Filic. Afr. 52. 1868. Syntypes: St. Helena. *C. Thunberg s.n.* (LINN?, S?); *A. Thouin s.n.* (LINN?, S?); Plukenet, Phytographia [Almagesti botanici mantissa] 83, tab. 350, fig. 4. 1700.

Darea furcans Bory in Duperrey, Voy. monde, Crypt. 269, fig. 35, 2. 1828. Type: St. Helena. 1825, *D. D'Urville s.n.* (holotype: P)

Epiphytic, terrestrial, or saxicolous. *Rhizome* 1–2 mm wide, short-creeping, scaly, black, resinous; scales 2–4 mm long, lanceolate, castaneous, entire, the apex acute. *Sterile leaves* pinnate, 4–15 cm long, 1–2 mm apart; phyllopodia present, 0.15–0.2 cm long; petioles $\frac{2}{3}$ the length of the sterile leaf, tan to brown; scales reduced to resinous dots or sometimes with a few scattered scales, 0.5–1 mm long, lanceolate, light brown; lamina 2–7 x 1–2.5 cm, lanceolate, papyraceous, the base ending well above the phyllopodia; veins inconspicuous; hydathodes absent; lamina scales reduced to resinous dots, these often on both surfaces but more pronounced on the abaxial side. *Fertile leaves* similar to the sterile but smaller and with the divisions of the pinnae more shallow; petioles $\frac{1}{2}$ the length of the fertile leaf, tan to brown; laminae 1 cm wide, lanceolate, glabrous.

Distribution.— Endemic to St. Helena Island, above 650 m (Fig. 3; elevation according to Eastwood et al., 2004a).

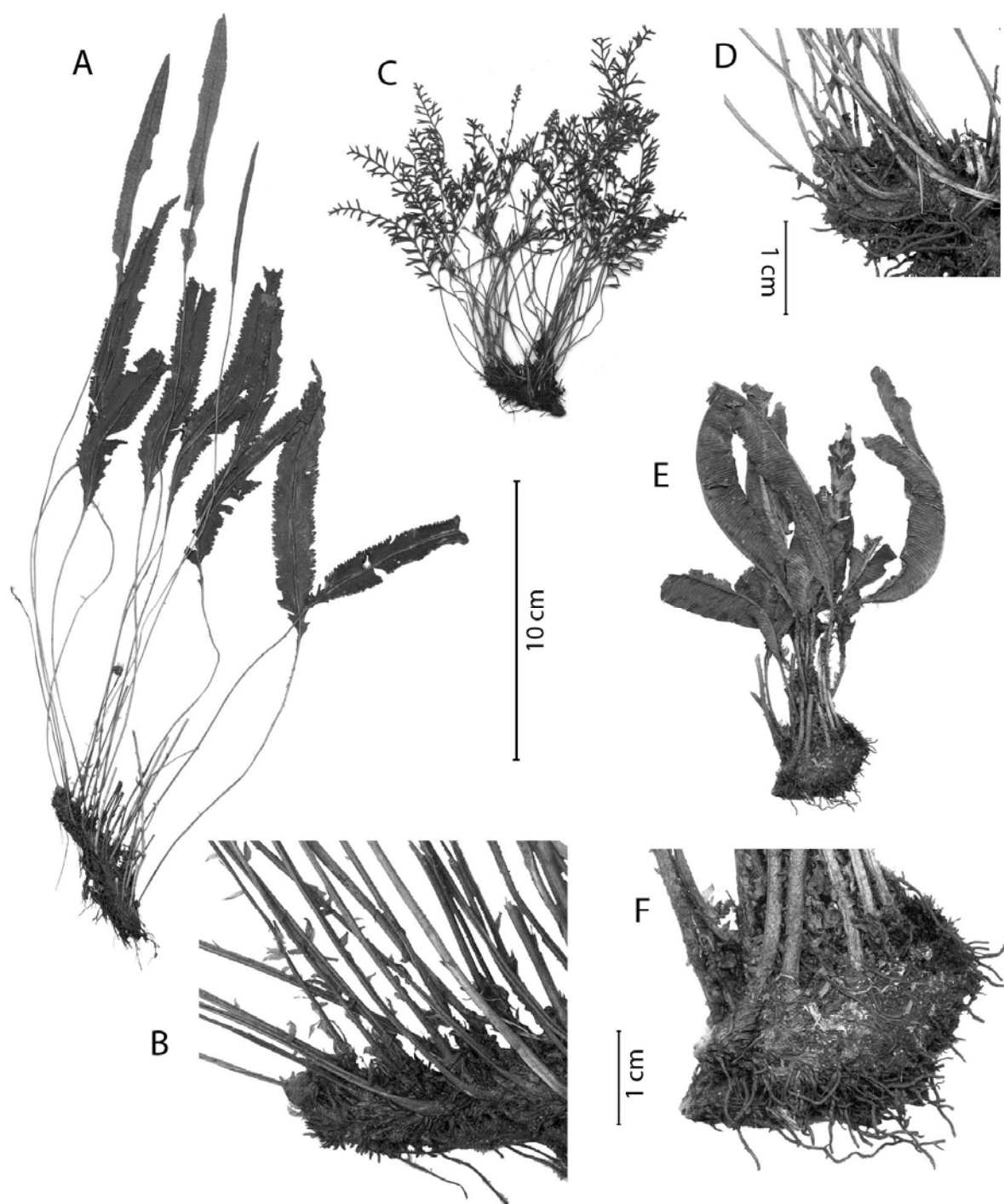


FIG. 4. The three species of *Elaphoglossum* endemic to St. Helena Island. *E. dimorphum*: **A.** Habit. **B.** Rhizome detail. *E. bifurcatum*: **C.** Habit. **D.** Rhizome detail. *E. nervosum*. **E.** Habit. **F.** Rhizome detail. (A, B from collector unknown s.n., P-herb H. Christ; C, D from Balansa s.n., 1872, P; E, F from D'Urville s.n., 1825, P)

Additional specimens examined. ST. HELENA. Sommet du Pic de Diane, 16 Aug 1872, *Balansa s.n.* (P); 16 Dec 1822, *Buchanan s.n.* (P); *Burchell 177* (P); *Burchell s.n.* (P); *Cumming 420* (P); *Cumming 2464* (P); *Cumming s.n.* (P); *Cunningham 135* (P); 1825, *D'Urville s.n.* in herb. Bory de St. Vincent 27,11 (P), 1825, *D'Urville s.n.* (P); Pic de Diane, 6 Jan 1825 *D'Urville s.n.* (P); *Harvard s.n.* (P); 1864, *Haughton 1149* (NY, P) *Houghton s.n.* (NY); *Limninghebo s.n.* (P); 1840, *Perroltet s.n.* (P); Pic Diane, 18 Mar 1879, *Savatier 1993* (P), *collector unknown s.n.* in herb. Ménager (P); at the roadside beyond Hutts gate, 6 Mar 1855, *collector unknown s.n.* (P); *collector unknown s.n.* (NY-3 sheets).

Elaphoglossum bifurcatum is endemic to St. Helena Island in the South Atlantic Ocean. Its pinnate laminae are unique within the *E. ciliatum* group. The other two species endemic to St. Helena have entire margins. *Elaphoglossum dimorphum* has a toothed margin, but it is never pinnate; *E. nervosum* has simple, entire leaves.

This species has been classified as vulnerable by the IUCN (Eastwood, 2004).

2. *Elaphoglossum burchellii* (Baker) C. Chr., Index filic. 304. 1905. *Acrostichum burchellii* Baker, Syn. Fil. 401. 1868. *Acrostichum flaccidum* var. *burchellii* (Baker) Vareschi, Fl. Venez. 1(2): 829. 1969, comb. illegit. [no basionym cited] Type: Brazil. W. *Burchell 5155* (holotype: K-n.v.; isotypes B, P). (Fig. 5)

Elaphoglossum xanthoneuron H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesamten Naturwiss. [Monogr. Elaph.] 36: 89. 1899. *Acrostichum xanthoneuron* Kunze ex Eaton, Mem. Amer. Acad. n.s. 8. 194. 1860 (*nomen nudum*). *Elaphoglossum xanthoneuron* T. Moore, Index fil. 370. 1862 (*nomen nudum*). Syntypes: Venezuela. Aragua: Colonia Tovar, A. *Fendler 280* (US), J. W. K. *Moritz s.n.* (B-n.v.); Trujillo: *Engler 62* (B-n.v.).

Elaphoglossum praelongum (Fée) C. Chr., Dansk. Bot. Ark. 9(3): 8. 1937. *Acrostichum praelongum* Fée, Crypt. Vasc. Br.1: 9, tab. 3, fig. 2. 1869. Lectotype, designated by Rouhan & Cremers (2006): Brazil. Rio de Janeiro: Serra da Estrela, 9 Apr 1867, A. F. M.

Glaziou 952 (P, NY (fragment); photo NY ex P).

Elaphoglossum tenerum (Fée ex Kuhn) Hieron., Bot. Jahrb. Syst. 34: 557. 1904, nom. Illeg., non (Baker) H. Christ 1899. *Acrostichum tenerum* Fée ex Kuhn, Linnaea 36. 52. 1869. *Elaphoglossum alpinum* F. Ballard, Bull. Misc. Inform. Kew 1937: 350. 1937. [nom. nov. for *E. tenerum* (Fée ex Kuhn) Hieron., non (Baker) H. Christ 1899]. Type: Ecuador. Pichincha: Mt. Pichincha, alpine region, W. *Jameson* s.n. (holotype: P-n.v.).

Elaphoglossum balansae C. Chr., Index filic. 303. 1905, new name for *Acrostichum tenerum* Baker, J. Bot. 303. 1878, nom. illegit., non Fée ex Kuhn 1869. *Elaphoglossum tenerum* (Baker) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesamnten Naturwiss. [Monogr. Elaph.] 36: 62. 1899. Type: Paraguay. Caaguazú, 29 Mar 1876, B. *Balansa* 390 (holotype: P-2 sheets, photo US ex P; isotype BR).

Elaphoglossum burchellii (Baker) C. Chr. var. *crenulato-dentatum* Rosenst., Hedwigia 46: 151. 1907. Type: Brazil. Rio Grande do Sul: Sta. Cruz, Sanga da Roseira, C. *Jürgens* 61.1 (holotype: S?; isotype: NY)

Elaphoglossum burchellii (Baker) C. Chr. var. *major* Rosenst., Hedwigia 46: 151. 1907. Syntypes: Brazil. Rio Grande do Sul: Sta. Cruz, Colonia Montealverne, near Castilhaninho River, C. *Jürgens* 144 (B, NY), 144.1 (S?).

Elaphoglossum dusenii H. Christ, Ark. Bot. 9(15): 2. 1910. Type: Brazil. Paraná: Vila Velha, 17 Dec 1903, P. K. H. *Dusén* 2748 (holotype: P, photo: US ex P; isotype: BM-n.v, UC).

Terrestrial or rarely epiphytic. *Rhizome* 2.5–7 mm wide, short- to long-creeping, scaly, black, often resinous; scales 1–3 mm long, lanceolate, dark brown, twisting and spreading,

entire, the apex acute. *Sterile leaves* (18–)25–53 cm long, 1–5 mm apart; phyllopodia present, 1.5–4 cm long; petioles $1/3$ – $2/5$ (– $1/2$) the length of the sterile leaf, stramineous to tan or light brown; scales reduced to resinous dots or sometimes with a few scattered scales, 1 mm long, lanceolate, light to dark brown; laminae 15–30 x 1–4 cm, narrowly elliptic, chartaceous, the base evenly or abruptly cuneate, ending well above the phyllopodia, the apex acute to acuminate; veins conspicuous, 1 mm apart, at an angle of 75° with respect to the costa, the apices free; hydathodes absent; lamina scales reduced to resinous dots, these often on both surfaces but more pronounced on the abaxial side; marginal scales caducous (most easily seen on young leaves), 0.2–0.3 mm long, lanceolate, subentire or entire. *Fertile leaves* longer than the sterile; petioles $2/3$ the length of the fertile leaf, tan to black; laminae 0.5–1 cm wide, linear, glabrous, the base narrowly cuneate, the apex acuminate.

Distribution.—Costa Rica, Panama, Dominican Republic, Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia, Paraguay (Fig. 6); elevation 950–2900 m.

Selected specimens examined. COSTA RICA. PUNTARENAS: Cantón de Buenos Aires, Río Kuyé, $9^\circ 17' 30''$ N, $83^\circ 16' 00''$ W, 1530 m, 11 Mar 1993, *Bittner 1722* (INB, NY); Cantón de Coto Brus, Zona Protectora Las Tablas, Cuenca Terraba-Sierpe, $8^\circ 54' 21''$ N, $82^\circ 45' 04''$ W, 2100 m, 20 Nov 1996, *Rojas et al. 3278* (CR, INB, NY). **SAN JOSÉ:** road from Copey de Dota to Providencia, [$9^\circ 36' 30''$ N, $83^\circ 55' 00''$ W], 1900–2050 m, 9–10 Jul 1987, *Evans & Lellinger 221* (US); Cantón de Vásquez de Coronado, cuenca del Sarapiquí, bajo La Hondura, $10^\circ 03' 15''$ N, $83^\circ 59' 10''$ W, 1500 m, 23 Apr 1999, *Rojas & Pacheco 5105* (MO).

PANAMA. PANAMÁ: Cerro Campana, [$8^\circ 43' 00''$ N, $79^\circ 54' 00''$ W], 19 Aug 1967, *Stimson 5400* (NY).

DOMINICAN REPUBLIC. SANTIAGO: Cordillera Central, La Guácara Arriba, tributary to Río Bao, [$19^\circ 20' 00''$ N, $70^\circ 47' 00''$ W], 1300–1400 m, 5–9 Nov 1968, *Liogier 13422* (NY). **PROV. UNKNOWN:** 10 Oct 1946 *Canela s.n.* (US).

COLOMBIA. ANTIOQUIA: Mun. Medellín y Guarne, Parque Ecológico Piedras Blancas, $6^\circ 18' 00''$ N, $75^\circ 29' 00''$ W, 2350 m, 20 May 1995, *Fonnegra et al. 5614* (HUA, MO). **CAUCA:** along road from Popayán, near Río Anabío, 2200 m, 26 May 1944, *Killip & Lehmann 38503* (US). **CUNDINAMARCA:** Mun. Usaquén, carretera La Cita a La Calera, [$4^\circ 42' 00''$ N, $74^\circ 02' 00''$ W], 2780 m, 23 Apr 1974, *Acosta-Arteaga 324* (COL, NY, VEN). **MAGDALENA:** vic. of Pantano, 3 km W of San Sebastián de Rabago, $10^\circ 34' 00''$ N, $73^\circ 36' 00''$ W, 2000 m, 15 May 1977, *White & Alverson 508* (NY). **NARIÑO:** Mun. Pasto, SE de la

población de Jamondino, [1°12'N, 77°16'W], 2900 m, 12 Jun 1993, *Ramirez* 5349 (COL). **SANTANDER:** Río Surata valley, above Surata, [7°22'10"N, 72°59'14"W], 2000–2300 m, 5–6 Jan 1927, *Killip & Smith* 16555 (US).

VENEZUELA. ARAGUA: La Victoria-Colonia Tovar road, 11.5 km N of Pie de Cerro, 10°22'N, 67°20'W, 1950 m, 14 Jan 1982, *Luteyn et al.* 8238 (NY, VEN). **DISTRITO FEDERAL:** between Catia and El Junquito, [10°28'N, 67°05'W], 1980 m, 25 Jun 1944, *Steyermark* 56989 (US). **LARA:** Distr. Jiménez, Parque Nacional Yacambú, 10–14 km SE of Sanare, 9°42'N, 69°37'W, 1800–2100 m, 25–27 Oct 1982, *Davidse & González* 21137 (MO, VEN). **TRUJILLO:** Mun. Boconó, Parque Nacional Guaramacal, NE slopes of Cerro Guaramacal, 9°15'N, 70°12'W, 2200 m, 21 Sep 2003, *Stergios et al.* 20609 (NY).

ECUADOR. NAPO: Cosanga, 20 km S of Baeza, 0°37'S, 77°52'W, 2000–2100 m, 26 Oct 1976, *Balslev & Madsen* 10336 (AAU, NY); Cantón Archidona, S slopes of Volcán Sumaco, along Hollín – Loreto road, 0°35'S, 77°40'W, 1200 m, 26 Jan 1991, *Moran & Rohrbach* 5179 (MO, QCNE). **PICHINCHA:** Nono-Tandayapa Km 10, 2320m, 14 May 1981, *Dodson & Clendenin* 10761 (CR, SELB). **ZAMORA-CHINCHIPE:** Miazí, junction of Río Chumbiriatza with Río Nangaritzá, [4°19'S, 78°40'W], 950–1200 m, 21–23 Oct 1991, *Øllgaard et al.* 99337 (AAU, QCA).

PERU. AMAZONAS: Bongara, 8 km above Pedro Ruíz (Jazan) on road to Pomacochas, 5°55'S, 77°53'W, 1500–1600 m, 3 Jun 1986, *Knapp & Alcorn* 7550 (MO, NY).

BRAZIL. BAHIA: Mun. Abaíra, Distrito de Catolés. Caminho para o Pico do Barbado, Mata da Forquilha, [13°18'S, 41°54'W], 14 Apr 1999, *Forzza et al.* 1219 (NY). **DISTRITO FEDERAL:** lower slopes of Chapada da Contagem, ca. 15 km NE of Brasília, [15°37'02"S, 47°56'W], 1000 m, 4 May 1966, *Irwin et al.* 15629 (NY, US). **GOIÁS:** Chapada dos Veadeiros, ca. 20 km N of Alto do Paraíso, [13°51'S, 47°25'W], 1250 m, 21 Mar 1971, *Irwin et al.* 32893B (MO, NY, US). **MINAS GERAIS:** Itabirito, Condomínio Aconchego da Serra, na rodovia BR-040, [20°15'S, 43°48'W], 13 May 1999, *Salino* 4635 (NY), *Widgren s.n.* (US). **PARANÁ:** Vila Velha, [25°05'S, 50°09'W], 11 Mar 1904, *Dusén* 4045 (NY, US). **RIO DE JANEIRO:** Serra da Estrela, 22°30'39"S, 43°11'04"W, *Glaziou* 952 (P; photo MO, NY ex P), [Syntype of *Acrostichum praelongum*]; Teresópolis, [22°26'S, 42°59'W], 24 Apr 1868, *Glaziou* 2433 (BR, P-3 sheets), [Syntype of *Acrostichum praelongum*]; Serra dos Órgãos, [22°30'S, 43°06'W], *Glaziou* 2455 [not 2855 as cited] (P), [Syntype of *Acrostichum praelongum*]; Mun. Itatiaia, Parque Nacional do Itatiaia, trilha para o Vêu da Noiva, [22°30'S, 44°34'W], 19 Jun 2000, *Prado et al.* 1109 (NY). **RIO GRANDE DO SUL:** Sta. Cruz, [29°43'S, 52°26'W], Jul 1904, *Jürgens* 61a (NY, US). **SANTA CATARINA:** Pinheiral, Major Gercino, [28°14'S, 49°07'W], 420 m, 15 Jul 1950, *Rohr* 1059 (NY, US). **SÃO PAULO:** Campos do Jordão, [22°44'S, 45°35'W], 5–20 Feb 1937, *Porto* 3014 (MO, NY); Mun. Analândia, Serra do Cusuzeiro, [22°08'S, 47°39'W], 1000 m, Jun 1993, *Salino* 1780 (NY), 1810 (NY).

BOLIVIA. COCHABAMBA: Prov. Nor Yungas, NE of Chuspipata on the road to Coroico, 16°16'S, 67°47'W, 2300 m, 21 Feb 1986, *Solomon* 14956 (NY, US). **SANTA CRUZ:** Siberia, entre El Empalme y Locotal, 17°50'38"S, 64°41'30"W, 2100–2850 m, 8 Apr 2004, *Arroyo et al.* 2743 (NY, USZ). **TARIJA:** Arce. Mun. Padcaya. Reserva Nacional de Flora y Fauna Tariquia. Saliendo de Cambarí hacia Motoví, 22°08'45"S, 64°24'67"W, 1030 m, 20 Jan 2005, *Huaylla et al.* 1714 (NY).

PARAGUAY. ALTO PARANÁ: Estancia Río Bonito, 25°37'55"S, 54°48'17"W, 30 Aug 1994, *Zardini & Vera* 40813 (MO, NY). **PROV. UNKNOWN:** *Hassler* 4612 (NY).

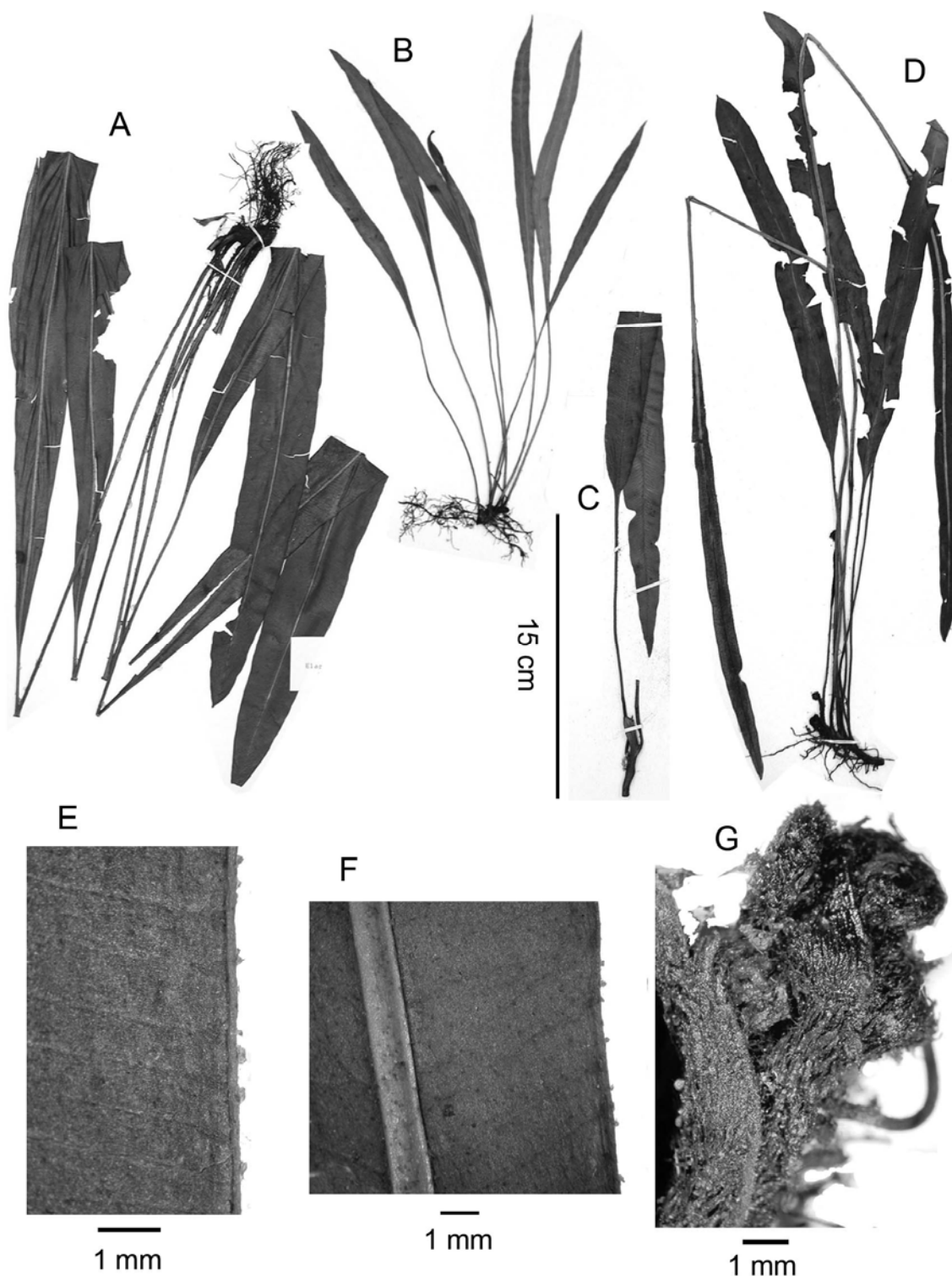


FIG. 5. *Elaphoglossum burchellii*. **A–D.** Habit. **E.** Lamina abaxial surface. **F.** Lamina adaxial surface. **G.** Rhizome and petiole bases with scales. (A, E, and F from *Luteyn* 8238, NY; B from *Irwin* 32893b, NY; C from *Balslev & Madsen* 10336, AAU; D from *Acosta-Arteaga* 324, NY; G from *Bittner* 1722, NY)

Elaphoglossum burchellii differs from *E. ciliatum* by having thicker and shorter-creeping rhizomes that have prominent scales at least around the apex, shorter phyllopodia, and a terrestrial habit, often among rocks. *Elaphoglossum ciliatum* typically has long-creeping rhizomes, rhizome scales that are highly reduced, most of them to black dots (thus apparently absent), and epiphytic habit. Both species have laminae decurrent for only a short distance along the petioles, never decurrent all the way to the base as in *E. nigrescens*. The petioles typically constitute about 1/3–1/2 the leaf length. The scales on the lamina margin (often difficult to see because they are deciduous) are whitish and entire or nearly so and 0.1–0.3 mm long. This scale characteristic is useful in distinguishing the species from *E. nigrescens*, which has dissected scales, 0.3–1 mm long



FIG. 6. Distribution of *Elaphoglossum burchellii*.

The other species in the group with scaly rhizomes is *E. huacsaro*, but the scales of *E. burchellii* tend to be dark brown, twisted, and spreading, whereas the scales of *E. huacsaro* are black, rigid, flat, and tend to be more appressed.

Elaphoglossum burchellii varies in the shape and size of the laminae. Specimens from southern Brazil and Paraguay have usually long-decurrent lamina bases and smaller leaves, whereas those from Ecuador to Bolivia have typically more abruptly narrowed, short-decurrent lamina bases and larger leaves. Several specimens from Mato Grosso, Brazil, are very small (e.g., *Macedo 3071*, US) but otherwise appear typical.

We have not seen the type at P of *E. tenerum* (Fée ex Kuhn) Hieron. from Ecuador, but the original description says it has a scaly rhizome and an acuminate apex. The only plant in the *E. ciliatum* group in Ecuador that fits this description is *E. burchellii*. Accordingly, *E. tenerum* is placed here in synonymy.

Rosenstock (1907) described *Elaphoglossum burchellii* var. *major* as twice the size typical for the species, and var. *crenulato-dentatum* as being larger than usual but with a crenate margin. Both of these characteristics are variable within the species, even in specimens from regions outside Brazil. The two varieties are placed here in synonymy.

3. *Elaphoglossum ciliatum* (C. Presl) T. Moore, Index fil. 8: 353. 1857. *Acrostichum ciliatum* C. Presl, Reliq. Haenk. 1. 15. 1825, non Desv. 1811. *Olfersia ciliata* C. Presl, Tent. Pterid. 234. 1836, nom. nov. for *Acrostichum ciliatum* C. Presl, non Desv. 1811. Type: Peru. Huánuco: near Huánuco, *T. Haenke s.n.* (holotype: PR, photo NY ex PR). (Fig. 7)

Elaphoglossum preslianum (Fée) H. Christ, Neue Denkschr. Allg. Schweiz. Ges.

Gesamnten Naturwiss. [Monogr. Elaph.] 36(1): 95. 1899. *Acrostichum preslianum* Fée, Mém. Fam. Foug. 2: 46, tab. 24, fig. 1. 1845, nom. nov. for *Acrostichum ciliatum* C. Presl, non Desv. 1811. Type: Peru. Huánuco: Huánuco and Pampayacu, E. Poeppig s.n. (holotype: P).

Epiphytic or rarely terrestrial. *Rhizome* 2.5–3 mm wide, short- to long-creeping, glabrescent, black, often resinous; scales sometimes present but minute, easily seen in older parts of the rhizome and not in the apex, scales 0.2–0.5 mm long, round, whitish to castaneous, subentire. *Sterile leaves* (18–)25–53 cm long, 5–15 mm apart; phyllopodia present, 4–8 cm long; petioles $1/3$ – $2/5$ (– $1/2$) the length of the sterile leaf, stramineous to tan or light brown; scales absent or reduced to resinous dots; laminae 15–30 x 1.1–2.6 cm, narrowly elliptic, chartaceous, the base evenly or abruptly cuneate, ending well above the phyllopodia, the apex acute to acuminate; veins conspicuous, 1 mm apart, at an angle of 75° with respect to the costa, the apices free; hydathodes absent; lamina scales reduced to resinous dots, often on both surfaces but more pronounced on the abaxial side, sometimes with scattered scales in the abaxial costa, 0.5–1 mm long, lanceolate, tan, entire; marginal scales caducous (most easily seen on young leaves), 0.1–0.3 mm long, lanceolate, subentire or entire. *Fertile leaves* longer than the sterile; petioles $2/3$ the length of the fertile leaf, tan to black; laminae 0.5–0.8 cm wide, linear, glabrous, the base narrowly cuneate, the apex acuminate.

Distribution.—Costa Rica, Panama, Colombia, Ecuador, Peru; elevation 400–3000 m (Fig. 8). Mickel (1995b) cited this species for Nicaragua.

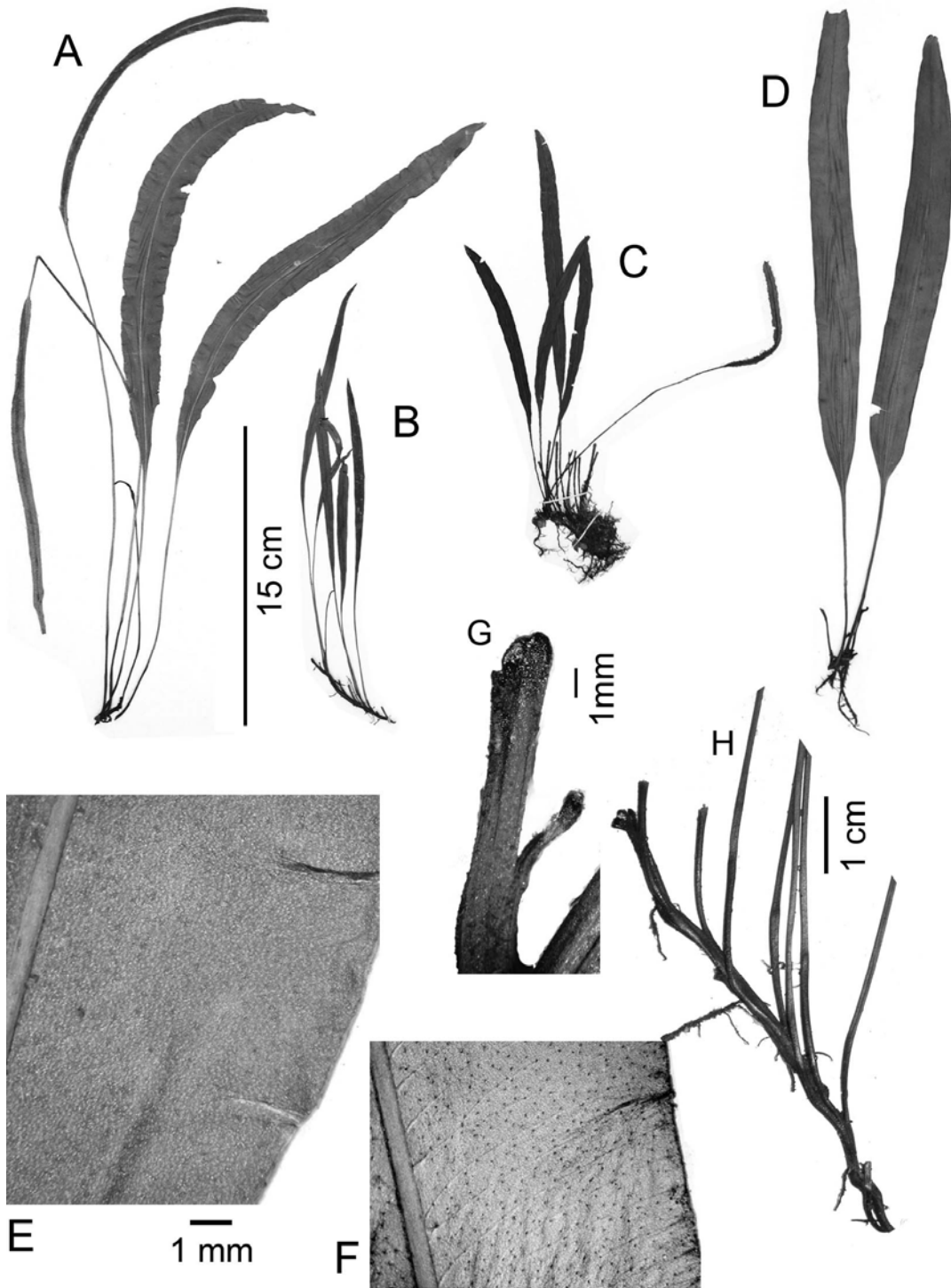


FIG. 7. *Elaphoglossum ciliatum*. **A–D.** Habit. **E.** Abaxial lamina surface with scales reduced to pale resinous dots. **F.** Abaxial lamina surface with scales reduced to dark resinous dots. **G.** Rhizome apex. **H.** Rhizome with petioles and (at left) two persistent phyllopodia. (A from Horich 1947-67, NY; B from Øllgaard & Navarrete 2456, NY; C from van der Werff & van Hardeveld 6649, NY; D, F from Porter 4939b, NY; E from Baker et al 5537, NY; G from Moran & Rohrbach 5183, NY; H from Øllgaard & Navarrete 2456, AAU).

Selected specimens examined. COSTA RICA. ALAJUELA: Cantón de San Ramón, Reserva Forestal San Ramón, Estación Río San Lorenzo, 10°13'10"N, 84°35'35"W, 800–900 m, 6 May 1996, *Angulo 602* (CR, INB, MO, NY). **CARTAGO:** Río Chis, near Juan Viñas, [9°54'N, 83°45'W], 1200 m, 30 Mar 1910, *Brade 528* (NY, US); Cantón de Paraíso, Valle del Reventazón, Estación de Biología Tropical Río Macho, 9°46'N, 83°52'W, 1580–1800 m, 1 Nov 1994, *Rojas & Mejía 1629* (CR, INB, MO). **GUANACASTE:** Cantón de La Cruz, Parque Nacional Guanacaste, Estación Pitilla, 10°59'25"N, 84°25'40"W, 700–800 m, 4 Sep 1996, *Rojas & Mata 2966* (INB, NY). **HEREDIA:** near Cariblanco, Río Sarapiquí, [10°29'N, 84°01'W], 800 m, 27 Apr 1956, *Williams 20323* (US, NY). **LIMÓN:** Braulio Carrillo, path beyond Río Sucio, [10°27'N, 83°59'W], 400–500 m, May 1984, *Gómez et al. 22794* (CR, MO, NY). **PUNTARENAS:** Cantón de Golfito, Parque Nacional Corcovado, Península de Osa, Cerro Rincón, nacientes del Río del Tigre, 8°31'N, 83°28'W, 700 m, 28 Jan 1998, *Rojas et al. 4197* (INB, MO, NY). **SAN JOSÉ:** Bajo de Hondura, Parque Nacional Braulio Carrillo, 10°04'N, 83°58'W, 1100–1200 m, 23 Jan 1983, *Davidse et al. 23226* (CR, MO, NY).

PANAMA. BOCAS DEL TORO: Cerro Colorado, 7.5 mi from Chami Camp, 8°35'N, 81°45'W, 1220–1250 m, 13 Apr 1986, *McPherson 8869* (NY, US). **CHIRIQUÍ:** Distr. Boquete, Fortuna Dam, [8°47'N, 82°26'W], 1200 m, 7 Feb 1985, *van der Werff & van Hardeveld 6649* (NY). **COCLÉ:** Cerro Pilón, above El Valle de Antón, [8°38'N, 80°08'W], 610 m, 28 Mar 1969, *Porter et al. 4665* (MO, NY), 4673 (MO, NY), 4669 (NY). **PANAMÁ:** summit of Cerro Campana, [8°43'N, 79°54'W], 31 Mar 1969, *Porter et al. 4939b* (NY), 4942 (NY), 4941a (MO). **SAN BLAS:** Cerro Brewster, 9°18'N, 79°16'W, 850 m, 21 Apr 1985, *de Nevers et al. 5401* (NY).

COLOMBIA. ANTIOQUIA: Mun. Yarumal, Vereda El Cedro, 7°10'N, 75°30'W, 1600–1900 m, 23 Jan 2004, *Vasco et al. 468* (HUA, MO, NY). **BOYACÁ:** Carretera Sogamoso-Pajarito, finca Comijoque, margen del Río Cusiana, [5°43'14"S, 72°55'47"W], 1800 m, 10 Oct 1967, *Hagemann 641* (COL). **CALDAS:** Mun. Villa María, Reserva Hidrográfica Romerales, 4°59'37"N, 75°25'54"W, 2540 m, 6 Aug 2006, *Vasco & Marín 579* (HUA, NY). **CHOCÓ:** NW side of Alto del Buey, trail along ridge from the confluence of Río Mutatá and Río Dos Bocas to the top of Alto del Buey, [6°06'N, 77°13'W], 1450–1750 m, 9 Feb 1971, *Lellinger & de la Sota 290* (US). **CUNDINAMARCA:** Mun. Junín, hacia el Río Sta. Barbara, [4°47'45"N, 73°38'20"W], 2200 m, 14 Jan 1967, *Murillo 973* (COL). **MAGDALENA:** Sierra Nevada de Sta. Marta, Quebrada Indiana, 10°59'N, 73°58'W, 1600 m, 30 Aug 1972, *Kirkbride 1991* (NY). **NARIÑO:** Carretera entre La Victoria (inspección de policía Mun. Ipiales) y Monopampa (inspección de policía Mun. Puerres), Km 32, Motilón, [1°23'N, 77°33'W], 2500 m, 10 Jan 1973, *Hagemann & Leist 1865* (COL). **PUTUMAYO:** Valle de Sibundoy, [1°11'N, 76°55'W], 2800 m, 29 Dec 1963, *collector unknown, 18* (COL). **QUINDÍO:** Mun. Génova, camino finca Las Mirlas-Servia, [4°12'39"N, 75°47'36"W], 2400–2700 m, 29 Apr 1990, *Vélez et al. 1306* (COL). **RISARALDA:** Mun. Pereira, Parque Regional Ucumarí, ca. 22 km ESE of Pereira, 4°40'N, 75°35'W, 2100–2670 m, 25 May 1989, *Lutelyn & Rangel 13161* (NY), 13170 (NY). **TOLIMA:** Mun. Sta. Isabel, Vereda de La Yuca, cerca de Las Bodegas. Finca Buenavista, alto de La Esperanza. Cordillera Central, vertiente oriental, [4°43'N, 75°06'W], 2700 m, 31 Jul 1980, *Idrobo et al. 10298* (COL). **VALLE DEL CAUCA:** at and on both sides of the principal ridge of the Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, [4°45'47"N, 76°13'35"W], 2200–2250 m, 28 Mar 1971, *Lellinger & de la Sota 825* (COL, CR, US).

ECUADOR. CARCHI: along Río Verde, 0°52'N, 78°08'W, 1890 m, 29 Nov 1987, Hoover 1958 (MO), 2060 (MO). **Esmeraldas:** Bilsa biological station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Sta. Isabel, 0°21'S, 79°44'W, 400–600 m, 15 Oct 1994, Bass *et al.* 172 (NY, QCNE); same locality, 28 Mar – 11 Apr 1995, Clark & Troya 578 (MO, NY, QCNE). **LOS RÍOS:** Bosque Protector Cerro Samama, SWW of Caluma, NE part of Hda La Clementina, above Destacamento La Pita, 0°40'S, 79°20'W, 600–730 m, 29 Feb – 1 Mar, 1996, Øllgaard 1569 (AAU). **MORONA-SANTIAGO:** road Macas – Guamote, Km 25, 2°13'S, 78°13'W, 1800 m, 16 Mar 1997, Øllgaard & Navarrete 2456 (AAU, NY, QCA); Cantón Huamboya, Shankaimi, 1°58'S, 77°49'W, 850 m, Sep 1993, Palacios 11414 (MO, NY, QCNE). **NAPO:** road Baeza – Tena, 8 km from Baeza, towards Río Cosanga, 0°31'S, 77°50'W, 1800–1900 m, 28 Oct 1976, Balslev & Madsen 10402 (AAU, NY, QCA); Cantón Archidona, S slopes of Volcán Sumaco, along Hollín – Loreto road, 0°35'S, 77°40'W, 1200 m, 26 Jan 1991, Moran & Rohrbach 5183 (MO). **PASTAZA:** Hacienda San Antonio del Barón von Humboldt, 2 km NE de Mera, 1°27'S, 78°06'W, 1100 m, 5–19 Mar 1985, Baker *et al.* 5537 (NY, QCNE); Mera, in hills above town, [1°28'S, 78°08'W], 1200 m, 22 Nov 1974, Plowman & Davis 940 (B), 4513 (S). **PICHINCHA:** Cerro Antisana, 1 mi NE of Borja, [0°31'54''S, 78°07'27''W], 1800 m, 17 Aug 1960, Grubb *et al.* 1314 (NY, US); bosques de los Colorados, [0°14'S, 79°14'W], Nov 1883, Sodiro *s.n.* (P). **SUCUMBIOS:** Río Bermejo, cofan community of Alto Bermejo, NW between Lumbaquí and Cascales, 0°14'44''N, 77°23'04''W, 450 m, 25 Jul 2001, Aguinda *et al.* 999 (NY). **TUNGURAHUA:** forest W of Río Guambí, 7 km along road and trails S of Río Negro, [1°27'S, 78°15'W], 1780 m, 31 Mar 1998, Øllgaard & Navarrete 3033 (QCA). **ZAMORA-CHINCHIPE:** Cantón Nangaritza, Río Nangaritza, Miazi, [4°18'S, 78°40'W], 10 Dec 1990, Neill 9648 (NY, QCNE).

PERU. AMAZONAS: Laguna de Pomacochas, [5°50'S, 77°52'W], 2550 m, 27 Mar 1998, van der Werff *et al.* 15821 (NY). **HUÁNUCO:** Huánuco and Pampayacu, [9°44'S, 76°00'W], Poeppig *s.n.* (P). **JUNÍN:** Prov. Satipo, Cordillera Vilcamamba, Río Poyeni watershed, 11°33'35''S, 73°38'28''W, 2050 m, 1 Jul 1997, Boyle *et al.* 4915 (F, NY, USM), 4958 (F, NY, USM). **PASCO:** Pichis Trail, Eneñas, [10°45'S, 75°14'W], 1700 m, 1 Jul 1929, Killip & Smith 25668 (NY, US); Oxapampa, La Suiza Nueva, 10°38'S, 75°27'W, 2240 m, 21 Jun 2003, van der Werff *et al.* 17612 (MO, NY).

Elaphoglossum ciliatum and *E. nigrescens* are most readily distinguished by the lamina bases and petiole lengths. In *E. nigrescens* the lamina is long-decurrent to the base of the petiole, usually ending at the phyllopodium. Therefore, it has no or almost no petiole. In contrast, *E. ciliatum* has a short-decurrent lamina that leaves a distinct petiole about 1/3–2/5(–1/2) the length of the sterile leaf.

The rhizomes of *Elaphoglossum ciliatum* are apparently glabrous, but a closer inspection reveals the presence of minute (less than 1 mm), round, appressed scales. These are easily

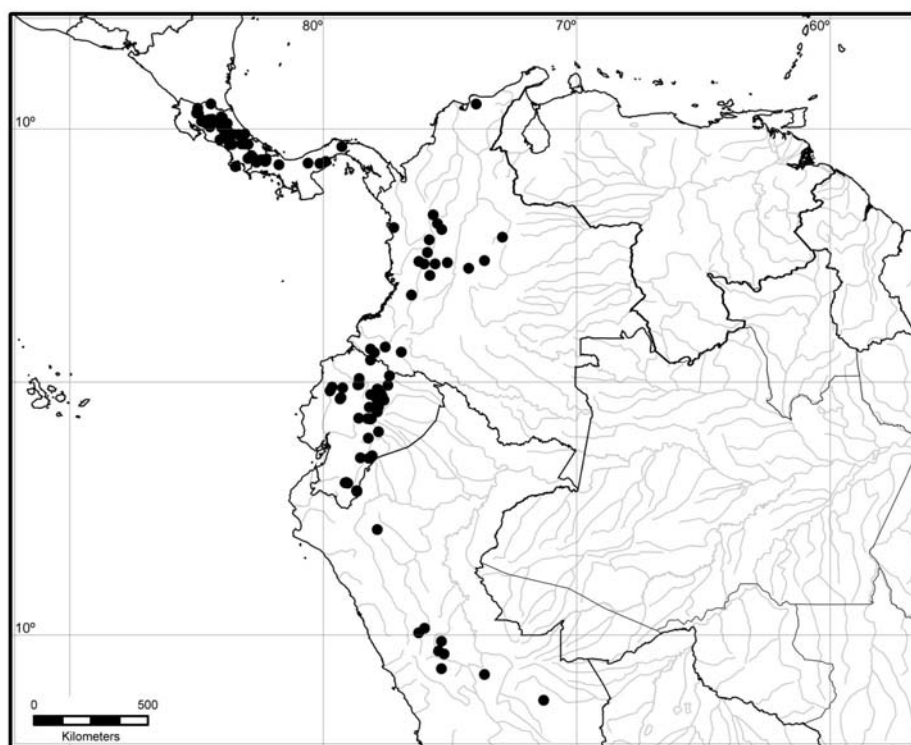


FIG. 8. Distribution of *Elaphoglossum ciliatum*.

seen in the older parts of the rhizome; at the apex they seem to be obscured by the resin. Because these rhizome scales are small and difficult to see, in the description and key they are described as glabrescent. For the distinction between *E. ciliatum* and *E. burchellii*, see the discussion of *E. burchellii*.

See *Elaphoglossum gramineum* for a comparison with that species.

4. *Elaphoglossum dimorphum* (Hook. & Grev.) T. Moore, Index fil. 8. 1857. *Acrostichum dimorphum* Hook. & Grev., Icon. Filic. 2, tab. 145. 1830. *Olfersia dimorpha* (Hook. & Grev.) C. Presl., Tent. Pterid. 235. 1836. *Microsptaphyla dimorphum* (Hook. & Grev.) J.

Sm., Hist. Fil. 131. 1875. Syntypes: St. Helena. *Alex. Walker s.n.* (K?), Madras, *Dr. Shuter s.n.* (K?). (Fig. 4)

Terrestrial. *Rhizome* 1–3 mm wide, short-creeping, ascending, scaly, brown, resinous; scales 2–4.5 mm long, lanceolate, brown, entire, the apex acute. *Sterile leaves* 10–25 cm long, 1–2 mm apart; phyllopodia present, 0.3 cm long; petioles 1/2–1/3 the length of the sterile leaf, brown; scales reduced to resinous dots or sometimes with a few scattered scales, 0.5–1 mm long, lanceolate, light brown; laminae 4–11 x 0.5–2 cm, lanceolate with the margin irregularly lobed, chartaceous, the base evenly or abruptly cuneate, ending well above the phyllopodia, the apex acute; veins conspicuous, 1 mm apart, at an angle of 45° with respect to the costa, the apices free; hydathodes absent; lamina scales usually reduced to resinous dots, the unreduced scales minute, less than 0.5 mm long, ovate, appressed, pale, translucent, membranous, entire. *Fertile leaves* variable in size; petioles 1/2 the length of the fertile leaf, tan to brown; laminae lanceolate, the base cuneate, the apex acute.

Distribution.— Endemic to St. Helena Island (Fig.3), above 750 m (elevation according to Eastwood et al., 2004b).

Additional specimens examined. ST. HELENA. 16 Feb 1882, *Buchanan s.n.*, (right specimen only, P); *Burchell 180* (P); *Burchell s.n.* (NY); 1825, *D’Urville s.n.* (right specimen only, P); *Parish s.n.* (P); *Perroltet s.n.* (P); 1840 *Perroltet s.n.* (P); *collector unknown 34* (P); *collector unknown 42* (P); by the roadside not far from Hutts gate, 6 Mar 1855, *collector unknown s.n.* (P); *collector unknown s.n.* in herb. Bory de St Vincent (P).

Elaphoglossum dimorphum can be distinguished from the other species occurring in St. Helena Island, by its lobed lamina margin. The world population of this species is less than 50 mature individuals, comprising two subpopulations in Diana’s Peak National Park

(Eastwood et al., 2004b). Evidence from allozymes indicates that *E. dimorphum* might be of hybrid origin between *E. nervosum* and *E. bifurcatum* (Eastwood et al., 2004a), which may explain its rarity. *Elaphoglossum dimorphum* has been classified as critically endangered by the IUCN (Eastwood, 2004).

5. *Elaphoglossum dussii* Underw. ex Maxon, Sci. Surv. Porto Rico & Virgin Islands. 6: 398. 1926. *Elaphoglossum petiolatum* (Sw.) Urb. var. *dussii* (Underw. ex Maxon) Proctor, Rhodora 68: 467. 1966. Type: Martinique. Bois du Lorrain, 540–900 m, Sep 1901, A. Duss 4688 (holotype: NY). (Fig. 9)

Acrostichum plumieri Desv., Mém. Soc. Linn. Paris. 6: 209. 1827, non *Elaphoglossum plumieri* T. Moore, 1857. Type: Martinique. Plumier, Traité foug. Amér. 113, tab. 129. 1705, illustration based on a specimen in the Desvaux herb., collector unknown (holotype: P)

Epiphytic. *Rhizome* 5–8 mm wide, short-creeping, scaly, brown; scales 3–6 mm long, narrowly lanceolate, reddish brown, with a few distant cilia, the apex attenuate, flexuous. *Sterile leaves* 20–65 cm long, 1–2 mm apart; phyllopodia present, 0.5–1 cm long; petioles 1/3–1/2 the length of the sterile leaf, stramineous to tan or light brown; scales reduced to resinous dots or 0.8–2 mm long, lanceolate, light brown, sometimes also with substellate scales; laminae 15–45 x 1.5–3 cm, narrowly elliptic, chartaceous to coriaceous, the base gradually tapered, ending well above the phyllopodia, the apex attenuate to acuminate; veins conspicuous, 1 mm apart, at an angle of 75° with respect to the costa, the apices free; hydathodes absent; lamina scales on the abaxial surface of the laminae reduced to resinous

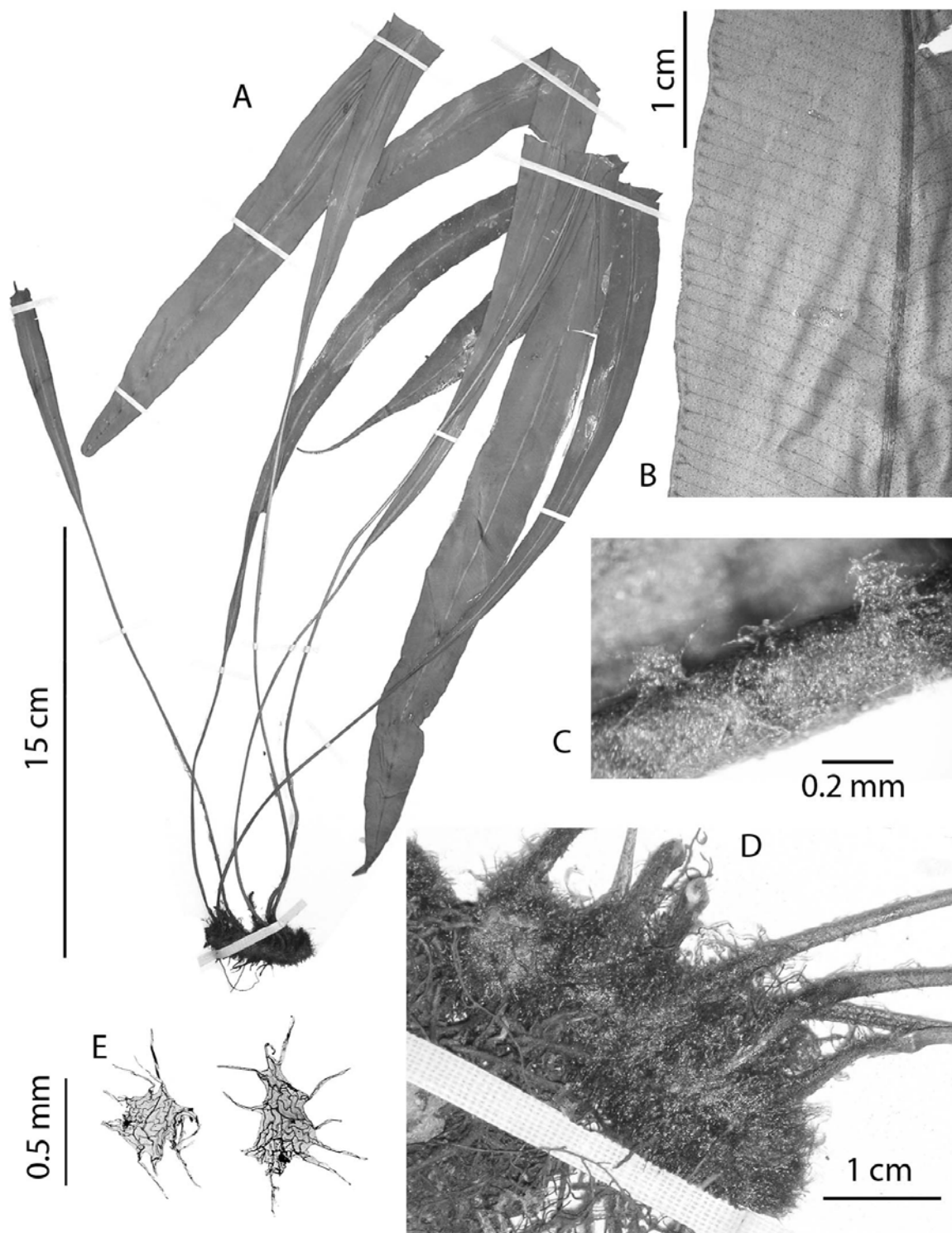


FIG. 9. *Elaphoglossum dussii*. **A.** Habit, fertile leaf at left. **B.** Detail of the abaxial surface of the lamina showing resinous dots. **C.** Substellate scales on the margin of the lamina. **D.** Detail of rhizome and petiole bases. **E.** Lamina scales. (A from Lloyd 336, NY; B–D from Duss 4688; E from Duss 4400, NY).

dots, those on the adaxial surface and the margin less than 0.5 mm long, substellate, appressed or subappressed, thin, pale, with irregular teeth; marginal scales caducous (most easily seen on young leaves), 0.2–0.3 mm long, entire or subentire. *Fertile leaves* ca. equalling the sterile; petioles 2/3 the length of the fertile leaf, tan to brown; laminae 0.4–1 cm wide, linear, adaxially scaly, the base narrowly cuneate, the apex acuminate.

Distribution.— Puerto Rico, Montserrat, St. Kitts, Guadeloupe, Dominica, Martinique, St. Vincent, Grenada (Fig. 10). According to Proctor (1977), the species also occurs on Haiti, Dominican Republic, and Nevis.

Selected specimens examined. PUERTO RICO. Luquillo, Caribbean National Forest, by the visitor information center, 28 Sep 1989, *Acevedo* 2976 (NY).

MONSERRAT. 9 Feb 1907, *Shafer* 592 (F).

ST. KITT'S. Molyreaux Estate, 8 Sep – 5 Oct 1901, *Britton & Cowell* 690 (NY).

GADELOUPE. Basse Tere, Bains Jaunes, between route D11 to La Souffrière and the path leading to Grande Chute du Gallion, 16°02'N, 61°40'W, 950–1000 m, 10 Mar 2004, *Christenhusz & Katzer* 4011 (NY); Bois des Bains-Jaunes, Vallée de Saint Louis. Camp. Jacob, cascada Vanchelet, 500–900 m, [2 sheets, "1892–1894" and "1897–1898"], *Duss* 4131 (NY); Bois des Bains, Grandmarron, 700–900 m, 1901, *Duss* 4400 (NY).

DOMINICA. Laudat, 1903, *Lloyd* 199A, 336, 357 (NY), St. Paul, Bona Vista State, S of Morne Cola Anglais, 500 m, 18 Jun 1965, *Webster* 13417 (NY).

MARTINIQUE. Bois du Louvain, 400–700 m, 1882, *Duss* 1622 (NY); Bois de Sunke, Marie du Camp Balate, 1877, *Duss* 1623 (NY); near Deux-Choux, 700–750 m, Sep 1901, *Duss* 4607 (NY); 1907, *collector unknown s.n.* (NY).

ST. VINCENT. *collector unknown s.n.* (NY).

GRENADA. Black Forest Mountains, 17 July 1906, *Broadway* 1900 (NY); 1894, *Mills s.n.* (NY); 22 Nov 1890, *Shering s.n.* (NY).

Elaphoglossum dussii is distinguished from all other species belonging to the *Elaphoglossum ciliatum* group by its longer (3–6 mm), reddish brown rhizome scales that often cover most or all of the phyllopodia. Also, the blades are scaly than those of other species in the *E. ciliatum* group (with the possible exception of some specimens of *E. huacsaro* and *E. nigrescens* with unusually persistent scales). The blade scales occur on both

surfaces and are pale, thin, substellate, and subappressed. This species seems more similar to *E. petiolatum* (Sw.) Urb. (sect. *Lepidoglossa*), and it was considered as a variety of that species by Proctor (1977). Proctor (1977) listed this species in “South America,” but his report probably refers to the various segregates of *E. petiolatum*.

Although surprising from a morphological point of view, our molecular analyses that included several species from the *E. petiolatum* complex (Vasco et al., 2009b) recovered only *E. dussii* as part of the *E. ciliatum* group. The sister relationship with the other endemic West Indian species *E. gramineum* and the presence of resinous laminar dots over the lamina make the inclusion of *E. dussii* in this group plausible despite the apparent morphological disagreement.

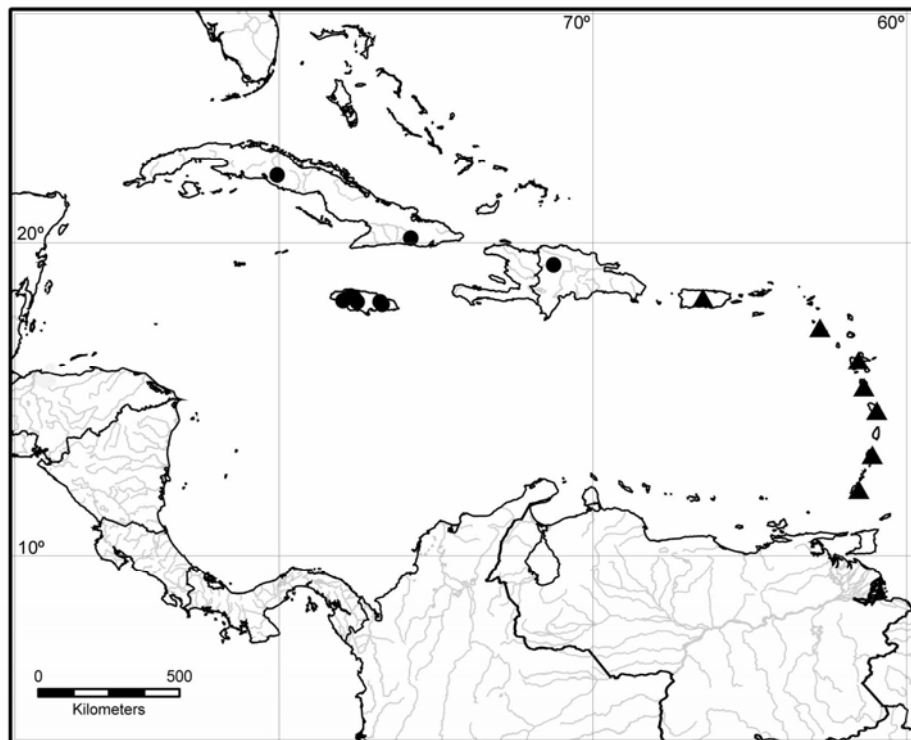


FIG. 10. Distribution of *Elaphoglossum dussii* (triangles) and *E. gramineum* (circles).

6. *Elaphoglossum gramineum* (Jenm.) Urban, Symb. Antill. 4: 60. 1902. *Acrostichum gramineum* Jenm., J. Bot. 17 (n.s. 8): 263. 1879. Type: Jamaica. 1876, G. S. Jenman 27 (holotype: K; isotype: NY). (Fig. 11)

Epiphytic or saxicolous. *Rhizome* 2–3 mm wide, short-creeping, glabrous, black, highly resinous. *Sterile leaves* 15–25 cm long, 1–4 mm apart; phyllopodia present, 0.2–0.9 cm long; petioles 1/4–1/2 the length of the sterile leaf, tan to brown; scales absent or reduced to resinous dots, rarely with a few minute (ca. 1 mm) dark scales toward the base; laminae 5–16(–20) x 0.6–1.5 cm, linear, papyraceous to chartaceous, the base narrowly cuneate, ending well above the phyllopodia, the apex gradually tapered and narrowly acute or rarely short-acuminate; veins inconspicuous, 1 mm apart, at an angle of 65° with respect to the costa, the apices free; hydathodes absent; lamina scales reduced to resinous dots, these often on both surfaces but more pronounced on the abaxial side. *Fertile leaves* usually longer than the sterile; petioles 1/3–1/2 the length of the fertile leaf, tan to brown; laminae 0.4–0.8 cm wide, linear, glabrous, the base cuneate, the apex acute.

Distribution.—Honduras, Jamaica, Cuba and Dominican Republic (Fig. 10); elevation 450–1100 m.

Selected specimens examined. CUBA. SANTIAGO DE CUBA: Mt. Liban, [20°01'S, 75°48'W], Jun 1844, *Linden 1922b* (NY). **SANCTI SPIRITUS:** Pico Potrerillo, Sierra de Trinidad, Mayo 1932, *Acuña 20323* (HAC).

JAMAICA. Tweedside, [18°07'N, 77°31'W], 22 Oct 1898, *Harris 7429* (NY); Crown lands, 4 mi W of Troy, [18°16'N, 77°40'W], 750 m, 29 Jun 1904, *Maxon 2918* (NY, US); Mt. James and Vic., St. Andrews, [18°07'N, 76°47'W], 450 m, 29 May 1926, *Maxon 8611* (NY, US); *Shering s.n.* (US); Tweedside, [18°07'N, 77°31'W], 650–1000 m, 10–13 Apr 1903, *Underwood 2120* (NY).

DOMINICAN REPUBLIC. SANTIAGO: Distr. San José de las Matas, Arroyo Juan Fino, Jicomé, [19°20'N, 71°11'W], 500–600 m, 14 May 1931, *Valeur 634* (MO, NY, US).

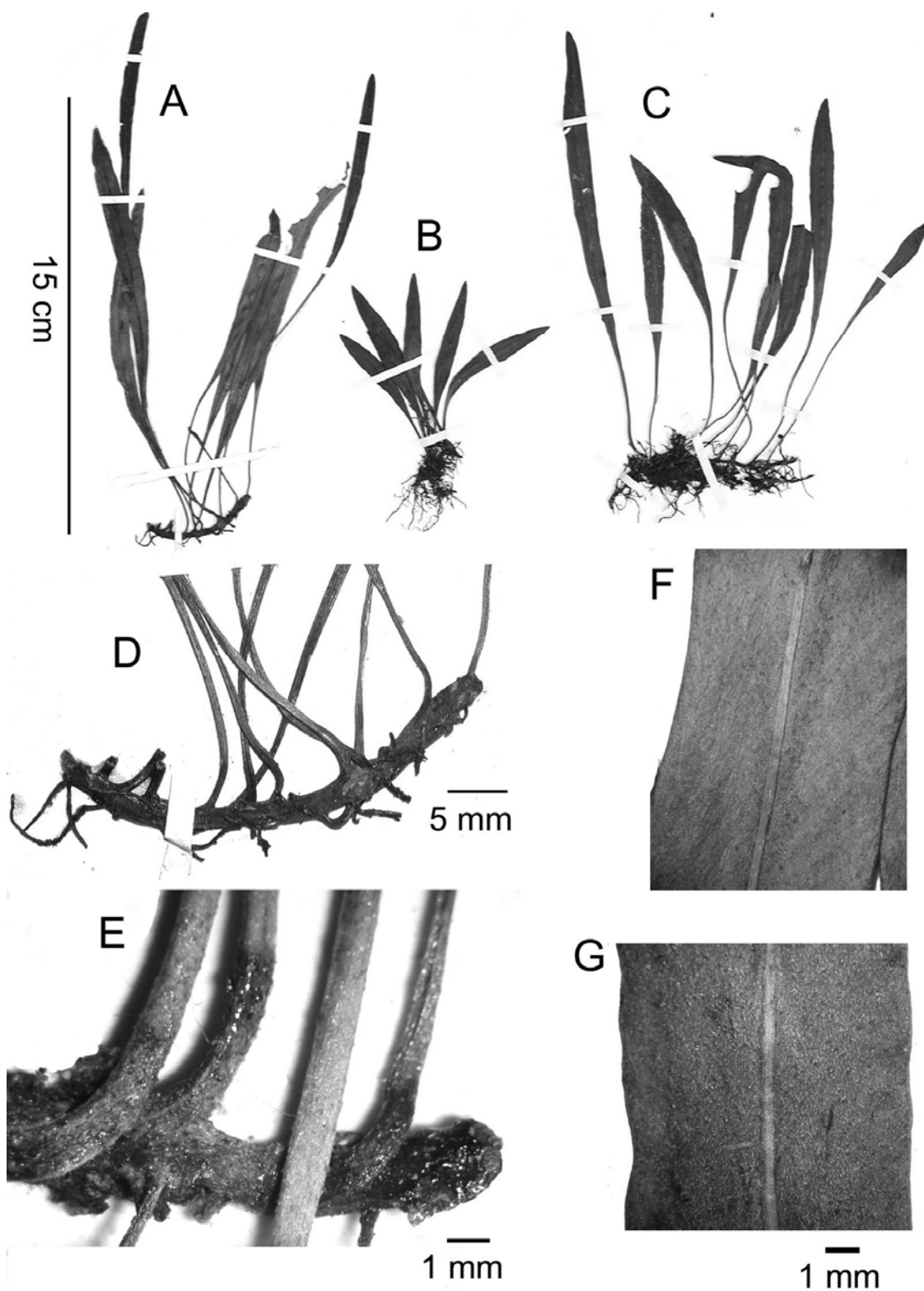


FIG. 11. *Elaphoglossum gramineum*, from Jamaica. **A–C.** Habit. **D, E.** Rhizome. **F.** Lamina adaxial surface. **G.** Lamina abaxial surface. (A, D from Harris 7429, NY; B, C from Sherring s.n., NY; D, E, F from Underwood 2120, NY).

Elaphoglossum gramineum is the smallest species in the *E. ciliatum* group. The sterile laminae are 0.6–1.5 cm wide and long-tapered at both ends. The rhizomes are glabrous, covered with a coating of resin, which tends to be thicker than that in other species with resinous rhizomes in the group. This species is very much like *E. ciliatum* but seems to be consistently distinct by its smaller size and the lack of scale remains around the resinous dots. The molecular analyses (Vasco et al., in press) recovered both species in two different non-sister clades. This further supports their distinction, although few morphological characters distinguish them.

A specimen of *E. gramineum* from Honduras (*Chockerong 116*, US) is probably mislabeled. The Honduran locality seems too far out of range for this species.

7. *Elaphoglossum huacsaro* (Ruíz) H. Christ, Mon. Neue Denkschr. Allg. Schweiz. Ges. Gesamten Naturwiss. [Monogr. Elaph.] 36(1): 96. 1899. *Acrostichum huacsaro* Ruíz, Mem. Calaguala, 57. 1805. Type: Peru. Habitat in Andinum montibus ad Sanatolmas et Tarmac Provinciae, *H. Ruíz 54* (holotype: B; isotypes: BR, US; photos F, US ex B).

(Fig. 12)

Elaphoglossum calaguala (Klotzsch) T. Moore, Index Fil. 7. 1857. *Acrostichum calaguala* Klotzsch, Linnaea 20: 421. 1847. Lectotype, **here designated**: Venezuela. Mérida: Páramo de Mucute, *J. W. K. Moritz 315* (lectotype: BM, photos MO, NY ex BM; ; duplicates: B, BR, STR); [other syntype cited: Peru, Habitat in Andinum montibus ad Sanatolmas et Tarmac Provinciae, *H. Ruíz 54* (B, BR, US; photos F, US ex B)]

Elaphoglossum ernestii Brade, Arquiv. Jard. Bot. Rio de Janeiro 18: 19. 1965. Type: Brazil. Minas Gerais: Ouro Preto, 1892, *E. Ule 265* (holotype: HB; isotype US-2 sheets)

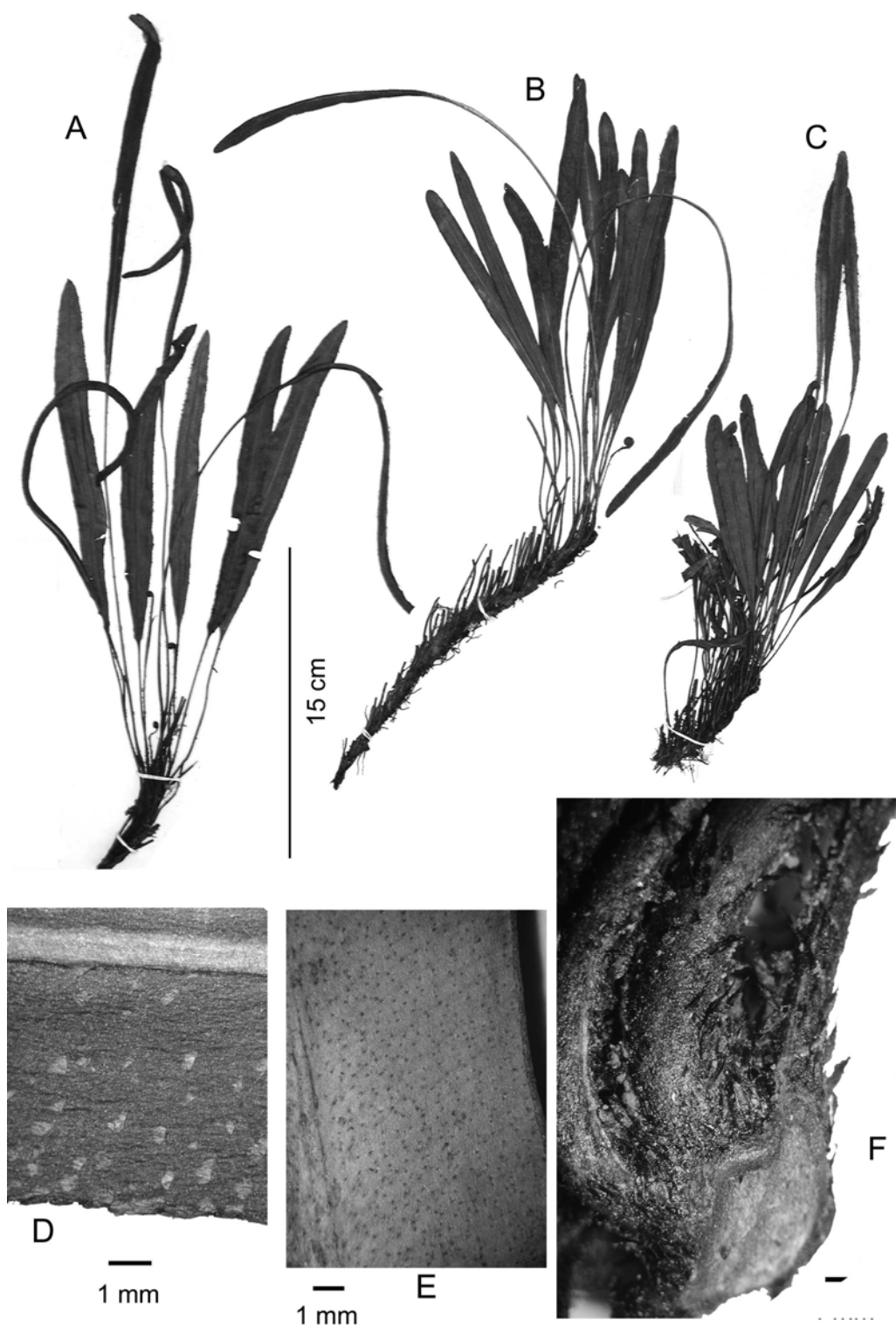


FIG. 12. *Elaphoglossum huacsaro*. **A.** Habit. **B.** Habit, note persistent phyllopodia along rhizome. **C.** Habit. **D.** Adaxial lamina surface with thin whitish scales. **E.** Abaxial lamina surface with scales reduced to resinous dots. **F.** Rhizome and petiole bases, note black scales. (A from Luteyn 5367, NY; B from Murillo & Fayad 132, NY; C from Luteyn 9831, NY; D from Killip & Hazen 8850, NY; E, F from Prado 1099, NY).

Terrestrial or saxicolous. *Rhizome* 3–7 mm wide, erect or ascending, scaly, black; scales 1–3 mm long, lanceolate, black, rigid and flat, entire, the apex often piliform, tortuous. *Sterile leaves* (10–)17–34 cm long, 1–2 mm apart; phyllopodia present but often weakly defined and hidden by the scales; petioles $1/4$ – $1/3$ the length of the sterile leaf, tan to brown; scales present, 0.5–1.5 mm long, lanceolate, dark or light brown, usually spreading, the larger ones often becoming dark first at the apex; laminae (6–)15–24 x 0.8–1.6 cm, linear, subcoriaceous, the base narrowly cuneate, ending well above the phyllopodia, the apex obtuse or broadly acute; veins inconspicuous, 1 mm apart, at an angle of 60–75° with respect to the costa, the apices free; hydathodes absent; lamina scales present on both surfaces (some of them reduced to resinous dots), those on the abaxial surface present mainly on the costa, 0.5–1 mm long, lanceolate to ovate, light brown to white, subentire; those on the adaxial surface, 0.3–0.8 mm long, round to ovate, appressed, thin, pale whitish, entire; marginal scales sparse, 0.5–1 mm long, lanceolate, subentire. *Fertile leaves* typically longer than the sterile; petioles ca. $2/3$ the length of the fertile leaf, tan to brown; laminae (6–)8–11 cm wide, linear to narrowly elliptic, scaly, the base narrowly cuneate, the apex obtuse to broadly acute.

Distribution.—Mexico, Guatemala, Costa Rica, Jamaica, Haiti, Dominican Republic, Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia (Fig. 13); elevation (150–) 900–3500 m. Also cited from Panama by Mickel (1995b).

Selected specimens examined. MEXICO. CHIAPAS: Mun. Zinacantán, Hwy. 190 in Paraje Navenchauk, [16°45'N, 92°42'W], 2200 m, 14 Nov 1971, *Breedlove & Smith* 22412 (MO, NY); Mun. Rayón, 10 km above Rayón Mezcalapa along road to Jitotol, [17°12'N, 93°00'W], 1700 m, 12 Dec 1971, *Breedlove* 23167 (NY).

GUATEMALA. SAN MARCOS: 10 miles S of San Marcos along road from San Raphael, [14°58'N, 91°48'W], 2100 m, 13 Jul 1977, *Croat* 41016 (MO).

COSTA RICA. CARTAGO: Irazu, [9°58'N, 83°51'W], 2000 m, 8 Sep 1908, *Brade* 80 (B), 81 (US); 110 km S of San José on Interamerican Hwy., 3 Aug 1965, *Croat* 82, 8241

(MO). **SAN JOSÉ:** Cantón de Dota, camino a San Gerardo de Dota, entrada por Jaboncillo, 9°36'15"N, 83°49'20"W, 2400–3000 m, 16 Jul 1996, *Rojas & Coto 2716* (CR, INB, MO, NY).

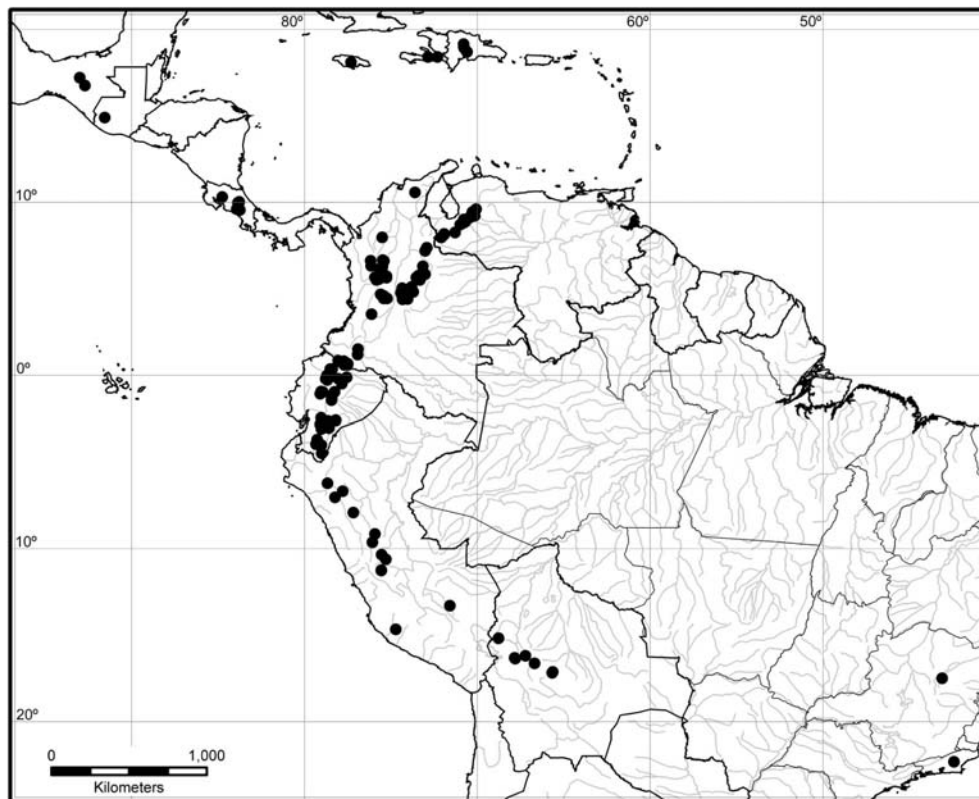


FIG. 13. Distribution of *Elaphoglossum huacsaro*.

JAMAICA. St. Thomas, summit of Blue Mountain Peak, 18°03'N, 76°35'W, 2000–2265 m, 25 Jan 2004, *Christenhusz & Tuomisto 3221* (NY); 1600 m, 1874–1879, *Jenman s.n.* (NY).

HAITI. L'OUEST: Massif de la Selles, Morne la Visite National Park, N slope of Morne La Visite, [18°24'N, 72°51'W], 2100–2250 m, 12 May 1984, *Judd & Slean 4517* (NY); Vic. Of Furcy, [18°24'N, 72°18'W], 1950 m, 26 May – 15 Jun 1920, *Leonard 4513* (NY).

DOMINICAN REPUBLIC. LA VEGA: Cordillera Central, La Nevera, 42 km N of central park of San José de Ocoa on the road to Constanza, [18°42'N, 70°36'W], 2050 m, 22 Feb 1982, *Mickel et al. 8258, 8268, 8275* (NY); 9 km SE of Constanza near Valle Nuevo, 18°50'N, 70°42'W, 1930 m, 18 Aug 1990, *Thompson & Rawlins 7872* (JBSD, NY). **OCOÁ:** on road from San José de Ocoa to Constanza, 18°41.5'N, 70°35.5'W, 2215 m, 20 Apr 2003, *Nee & Montero 52309* (NY).

COLOMBIA. ANTIOQUIA: Mun. Caramanta, Límites con el Mun. de Támesis, sector nacimiento quebrada El Conde, 5°33'27"N, 75°40'51"W, 2650 m, 16 Apr 2005, *Rodríguez*

et al. 5445 (HUA, NY); Mun. Belmira, Vereda Los Patos, camino hacia el páramo de Sta. Inés, 6°37'07''N; 75°40'43''W, 2590 m, 30 Jul 2005, *Vasco & Benavides* 562,567, 568, 576 (HUA, MO, NY). **BOYACÁ:** entre Arcabuco y Villa de Leyva, camino de Las Coloradas, [5°45'N, 73°24'W], 2750 m, 28 Aug 1967, *Jaramillo-Mejía* 2984 (COL); W slopes Páramo La Rusia, Km 7–20 along road from Duitama to San Gil, [5°49'37''N, 73°01'13''W], 2900–3375 m, 8 May 1979, *Luteyn et al.* 7572 (NY). **CALDAS:** Carretera del Quindío, vertiente occidental, 3000 m, 27 Jul 1958, *Bischler* 1318 (COL); Salento, cordillera central, [4°38'15''N, 75°34'13''W], 1600–1800 m, 25–31 Jul 1922, *Killip & Hazen* 8850 (NY, US). **CUNDINAMARCA:** Quebrada San Cristóbal at SE edge of Bogotá, [4°36'N, 74°05'W], 2850 m, 29 Jun 1944, *Little & Little* 8171 (COL, US); Guasca, páramo de Guasca, [4°30'43''N, 73°55'23''W], 23 May 1961, *Murillo & Fayad* 132 (AAU, COL, NY). **MAGDALENA:** San Sebastián, Sierra Nevada de Sta. Marta, [10°34'N, 73°36'W], 1900 m, 17 Aug 1946, *Foster & Smith* 1513 (COL). **NARIÑO:** Cerro Tablón, above Las Mesas on W slope of Volcán Doña Juana, [1°30'N, 76°54'W], 2700–2800 m, 15 Dec 1944, *Ewan* 16589 (US). **PUTUMAYO:** vertiente oriental de la Cordillera, entre Sachamates y San Francisco de Sibundoy, [1°11'N, 76°55'W], 1600–1750 m, 30 Dec 1940, *Cuatrecasas* 11469 (COL). **RISARALDA:** Mun. Pereira, Parque Regional Ucumarí, ca. 22 km ESE of Pereira, 4°40'N, 75°35'W, 2100–2670 m, 25 May 1989, *Luteyn & Rangel* 13167 (NY). **SANTANDER:** mountains E of Las Vegas, [7°11'32''N, 73°00'52''W], 3000–3300 m, 20–21 Dec 1926, *Killip & Smith* 15798 (COL, NY, US). **TOLIMA:** road to Nevado del Tolima, NW of Ibagué, ca. 17–19 km beyond Juntas to end of road, 4°35'N, 75°25'W, 2500–2750 m, 16 May 1984, *Luteyn et al.* 10620 (MO, NY). **VALLE DEL CAUCA:** Cord. Central, hoyo del Río Amayme, La Albania, [3°31'N, 76°07'W], 3000–3100 m, 2 Feb 1965, *Cuatrecasas et al.* 26800 (US). **PROV. UNKNOWN:** 1760–1808, *Mutis* 3317 (US).

VENEZUELA. LARA: Distr. Morán, carretera Humocar Alto – Buenos Aires, 9°36'N, 70°04'W, 2000 m, 19 Jul 1984, *Agostini & Rivero* 2863 (NY). **MÉRIDA:** Distr. Rangel, El Baho, arriba de Sto. Domingo, en la carretera Mérida – Barinas, [8°51'54''N, 70°41'40''W], 2750 m, 19 May 1971, *Ruiz-Terán* 6124 (NY, US). **TÁCHIRA:** below Páramo de Zumbador, Zumbador – Quenique road, 3 km SE of Zumbador, [7°58'N, 72°05'W], 2775 m, 31 Jan 1978, *Luteyn* 5367 (NY, US, VEN); Distr. Jáuregui, 1–6 km SSW of Zumbador on road to San Cristóbal, 7°58'N, 72°06'W, 2135–2350 m, 13 Apr 1984, *Luteyn & Lebron-Luteyn* 9831 (NY, VEN). **TRUJILLO:** Distr. Boconó, Montañas de Misisí, carretera vieja Trujillo – Boconó, ca. 12 km by air NW of Boconó, 9°21'N, 70°18'W, 2000–2400 m, 6 Jul 1990, *Dorr et al.* 7292 (NY, US, VEN); carretera Boconó – Trujillo, entrada a Burbusay, 9°26'N, 70°17'W, 1600 m, 23 Nov 1984, *Ortega & van der Werff* 2260 (MO, NY, VEN). **VARGAS:** Monumento Natural Pico Codazzi, carretera Arco de la Colonia Tovar - Pto. Cruz, 1.5 km desde el Arco, entre Hotel Casa de Campo Tovar y Urbanización residencial Jenjibrillar, 10°26'N, 67°14'W, 2050–2100 m, 26 Sep 1999, *Mostacero et al.* 344 (VEN).

ECUADOR. AZUAY: 1–8 km N of Sevilla de Oro, [2°48'S, 78°37'W], 2900 m, 12 Aug 1945, *Camp* 4661 (NY, US); Sevilla de Oro, old road 10–12 km N of village, 2°46'S, 78°37'W, 2750–2850 m, 11 Sep 1976, *Øllgaard & Balslev* 9361, 9378 (AAU, NY). **CAÑAR:** carretera Gualaquiza-Sigsig, Altarurco a 50 km de Gualaceo, [2°28'S, 79°02'W], 2840–2950 m, 31 Aug 1984, *Jaramillo* 7142 (AAU, MO, NY, QCA). **CARCHI:** Montufar, 3 km from Colonia Huaqueña, 0°35.5'N, 77°42'W, 3200 m, 26 Jun 1994, *Fay & Fay* 4273 (AAU, MO, QCNE), 4308 (AAU, COL, MO, NY, QCNE). **COTOPAXI:** Quevedo-Latacunga road, above Pilaló, 0°58'S, 78°58'W, 2850 m, 8 Apr 1973, *Holm-Nielsen et al.* 3264 (AAU, MO, NY).

IMBABURA: Apuela, [0°21'N, 78°30'W], 2920 m, 1 Dec 1975, *Madison & Coleman* 2260, 2261 (GH); road Cotachaci-Apuela, 33–36 km from Cotachachi (Intac Valley), 0°20'N, 78°26'W, 2900 m, 11 Aug 1976, *Øllgaard & Balslev* 8734 (AAU, NY). **LOJA:** road Loja-Cuenca, La Cofradía, near Santiago, 3°50'S, 79°13'W, 2750 m, 11 Jun 1996, *Lewis et al.* 2382 (NY, QCNE). **MORONA-SANTIAGO:** Gualaceo-Limón (General L. Plaza Gutiérrez), E of pass, 3°02'S, 78°35'W, 3000 m, 19 Aug 1987, *Jorgensen* 61898 (QCA). **NAPO:** 8–12 km ESE of Sta. Barbara, 0°40'N, 77°30'W, 2780–2880 m, 11 Jan 1985, *Luteyn & Cotton* 10995 (NY, QCA, QCNE), 10997 (NY, QCA, QCNE). **NAPO-PASTAZA:** Sta. Barbara de Sucumbios, road to El Carmelo, 2500 m, 10–15 Feb 1959, *Harling* 4166 (S). **PICHINCHA:** carretera Nono-Nanegalito, falda N de Cerro Pichincha, [0°03'S, 78°37'W], 2000–2500 m, 9 May 1982, *Balslev & Boom* 2474 (AAU, NY), 2476A (NY, QCA); Km 10 Nono – Tandayapa, [0°02'S, 78°42'W], 2320 m, 14 May 1981, *Dodson & Clendenin* 10752 (QCNE), 10756 (MO), 10757 (NY, QCNE, US). **SUCUMBIOS:** along road between La Bonita and Sta. Barbara, 0°39'01"N, 77°29'46"W, 2739 m, 22 Aug 2004, *Croat & Ferry* 93854 (MO); road to La Bonita, 37.5 km from s junction to Panamerican Hwy., 0°30'S, 77°50'W, 2550 m, 5 Dec 1991, *Øllgaard* 99968 (QCNE). **TUNGURAHUA:** road Patate – Triunfo, 1°18'S, 78°25'W, 2950 m, 5 Nov 1983, *Brandbyge & Barfod* 42517 (QCA); volcán Tunguragua, [1°27'S, 78°26'W], *Sodiño* 22 (B). **ZAMORA-CHINCHIPE:** Cantón Palanda, parroquia Valladolid, S slopes of Cordillera de Sabanilla, Tapichalca Reserve, 4°29'40"S, 79°07'56"W, 2300–2700 m, 29 May 2003, *Clark & Mendoza* 8079 (NY). **PROV. UNKNOWN:** 1898, *Stidle s.n.* (US).

PERU. AMAZONAS: Prov. Chachapoyas, Cerros Calla Calla, E side, 5 km above Leimebamba on road to Balsas, at San Miguel, [6°41'S, 77°47'W], 2400 m, 1 Apr 1964, *Hutchison & Wright* 4818 (MO, NY, US). **CAJAMARCA:** carretera entre Cajamarca y Celedín, [7°02'00"S, 78°13' 9"W], 2950–3500 m, 18 Oct 1986, *Díaz* 2171 (MO, NY). **CUSCO:** Paucartambo, [13°18'S, 71°35'W], 2800 m, 25 Jul 1961, *Woytkowski* 6740, 6741 (MO, US). **HUÁNUCO:** Prov. Huánuco, Huánuco – Tingo María road, Km 449–451, from Bandera Blanca to Carpath tunnel, [9°09'S, 75°55'W], 2700 m, 26 Feb 1978, *Luteyn & Lebron-Luteyn* 5453 (NY, US). **JUNÍN:** Carpapata, above Huacapistana, [11°15'44"S, 75°33'07"W], 2700–3200 m, 7 Jun 1929, *Killip & Smith* 24411 (NY), 24414 (US). **PASCO:** Oxapampa, Cañón de Huancabamba, Fundo La Esperanza, [10°21'S, 75°32'W], 1000–1500 m, 11 Aug 1985, *León* 618 (MO). **SAN MARTÍN:** Distr. Huallaga, valley of Río Apisoncho, 30 km above Jucusbamba, 7°55' S; 77°10' W, 1965, *Hamilton & Holligan* 901 (US).

BRAZIL. MINAS GERAIS: Serra de Ouro Preto, [20°23'S, 43°30'W], Jan 1982, *Ule* 265 (US). **RIO DE JANEIRO:** Serra dos Órgãos, 1600 m, *Brade* 9759 (US); Mun. Nova Friburgo, subida do Pico da Caledônia, 22°40'S, 42°35'W, 1706 m, 15 Jun 2000, *Prado et al.* 1099 (NY).

BOLIVIA. COCHABAMBA: Prov. José Carrasco Torrico, 101 km antigua carretera Cochabamba – Villa Tunari, 17°08'S, 65°38'W, 2550 m, 4 Jul 1996, *Kessler et al.* 6993 (NY). **LA PAZ:** Prov. Nor Yungas, Parque Nacional Cotapata, Valle de Coscapa, 16°12'S, 67°13'W, 3350 m, 10 Sep 1997, *Kessler et al.* 11784 (NY).

Elaphoglossum huacsaro can be distinguished from all other species in the *E. ciliatum* group by its erect to ascending rhizomes with dark, rigid scales, and by the sparsely scaly

abaxial lamina surfaces and costae. The scales of the lamina surfaces are thin (translucent), pale, round to ovate, and appressed. The leaves are ascending, fasciculate, and with an obtuse or broadly acute apex. The density of scales on the laminae and petioles is variable, but normally *E. huacsaro* has more scales on the laminae and petioles than *E. ciliatum* or *E. burchellii*.

Brade (1964) distinguished *Elaphoglossum ernestii* from *E. huacsaro* on the basis of longer leaves, scaly laminae on the abaxial surfaces, and dorsiventral rhizomes with two rows of leaves. The first two characteristics are well within the range of variation we have seen in *E. huacsaro*. After looking at the specimens determined by Brade as this species, we believe that the rhizome is actually polystichous and not distichous as stated by Brade (1964); therefore, we put *E. ernestii* in synonymy with *E. huacsaro*.

8. *Elaphoglossum nervosum* (Bory) H. Christ, Neue Denkschr. Allg. Schweiz. Ges.

Gesamnten Naturwiss. [Monogr. Elaph.] 36: 50, fig. 13. 1899. *Acrostichum nervosum* Bory in Duperrey, Voy. monde, Crypt. 1: 252. 1828. *Aconiopteris nervosa* (Bory) J. Sm., Ferns Brit. for. 107. 1866. Type: St. Helena. *D. D'Urville s.n.* (holotype: P, 2 sheets, one sheet a mixed collection). (Fig. 4)

Acrostichum subdiaphanum Hook. & Grev., Icon Filic. 2, fig. 205. 1830. *Aconiopteris subdiaphana* (Hook. & Grev.) C. Presl, Tent. Pterid. 236, tab. 10, fig. 17. 1836. *Olfersia subdiaphana* (Hook. & Grev.) T. Moore, Index Filic. 1857. Syntypes: St. Helena Island, *Alex. Walker s.n.* (B?, NY), "Madras" [label error] *Wright s.n.* (K?).

Epiphytic or rarely saxicolous. *Rhizome* 2–4 mm wide, short-creeping, scaly, black, often resinous; scales 2–4.5 mm long, lanceolate, light brown, subentire, apices acute. *Sterile leaves* 12–25 cm long, 1–2 mm apart; phyllopodia indistinct; petioles 1/3–1/2 the length of the sterile leaf, brown; scales reduced to resinous dots or spreading, lighter and sometimes narrower than those of the rhizomes; laminae 8–12 x 2–3 cm, lanceolate to narrowly elliptic, papyraceous to chartaceous, the base cuneate, ending well above the phyllopodia, the apex acute; veins conspicuous, prominent, with a marginal collecting vein, 1–1.5 mm apart, at an angle of 70° with respect to the costa, the apices free; hydathodes absent; lamina scales present on both surfaces (some of them reduced to resinous dots), those on the abaxial surface present only on the costa, 0.5–1 mm long, lanceolate, tan, entire; those on the adaxial surface, ca. 0.4–0.6 mm long, round to ovate, appressed, thin, pale whitish, subentire. *Fertile leaves* not seen, but in the figure in the *A. subdiaphanum* protologue they are longer and narrower than the sterile frond.

Distribution.— Endemic to St. Helena Island (Fig.3), above 750 m (elevation according to Eastwood et al., 2004b)

Additional specimens examined. ST. HELENA. 1825, *D’Urville s.n.* (2 sheets, one with left specimen only P); 1828, *Lesson s.n.* in herb. Bory de St Vincent 27,10 (P).

Elaphoglossum nervosum can be distinguished from all others in the *E. ciliatum* group by its prominent lateral veins and submarginal connecting vein. Presumably the syntype of *Acrostichum subdiaphanum* from Madras, India, represents a label mix-up.

This species has been classified as class endangered by the IUCN (Eastwood, 2004).

9. *Elaphoglossum nigrescens* (Hook.) T. Moore ex Diels, Nat. Pflanzenfam. 1(4): 332.

1899. *Acrostichum nigrescens* Hook., Sp. Fil. 5: 214. 1864. Type: Venezuela (as “British Guiana”). Bolivar: Roraima, 1842, R. Schomburgk s.n. (holotype: K). (Fig. 14)

Elaphoglossum pallidum (Mett. ex Baker) Hieron., Hedwigia 62: 36. 1921.

Acrostichum pallidum Mett. ex Baker in Hook. & Baker, Syn. Fil. 401. 1868. *Acrostichum flaccidum* var. *pallidum* Mett. ex Baker in Mart., Fl. Brazil I, 2: 569. 1870. Type: Brazil. H. K. Beyrich s.n. (holotype: LZ-herb. Kunze, destroyed).

Elaphoglossum sherringii (Baker) C. Chr., Index Filic. 315. 1906. *Acrostichum sherringii* Baker, Ann. Bot. 6: 100. 1892. Type: Grenada. On St. Catherine’s Peak, 5 May 1891, Sherring s.n. (holotype: K-n.v., isotype: NY)

Elaphoglossum wacketii Rosenst., Hedwigia 46. 151. 1907. Type: Brazil. São Paulo: Rio Grande, 19 Apr 1906, M. Wacket 114 (holotype: B; isotypes: NY, UC).

Elaphoglossum palmense H. Christ, Bull. Soc. Bot. Genève sér. 2, 1: 223. 1909. Syntypes: Costa Rica. San José: La Palma, 1500 m, 9 Nov 1905, C. Wercklé 17102 (P; photo NY ex P), westabhang des Irazu, Vista de mar, 2000 m, 8 Sep 1908, A. C. Brade 236 (P).

Elaphoglossum williamsii Vareschi, Acta Bot. Venez. 1(2): 108, fig. 11B. 1966. Type: Venezuela. Amazonas: Capihuara (Capibara), Sabanetas del Casiquiare, 118 m, 24 May 1942, R. S. Williams 15538 (holotype: VEN?; isotypes: NY, US).

Epiphytic or rarely terrestrial. *Rhizome* 1–3 mm wide, compact, glabrous, black, resinous. *Sterile leaves* 11–30 cm long, 1–2 mm apart; phyllopodia present, 0.6–1 cm long; petioles 1/30–1/5 the length of the sterile leaf, stramineous to tan or light brown; scales

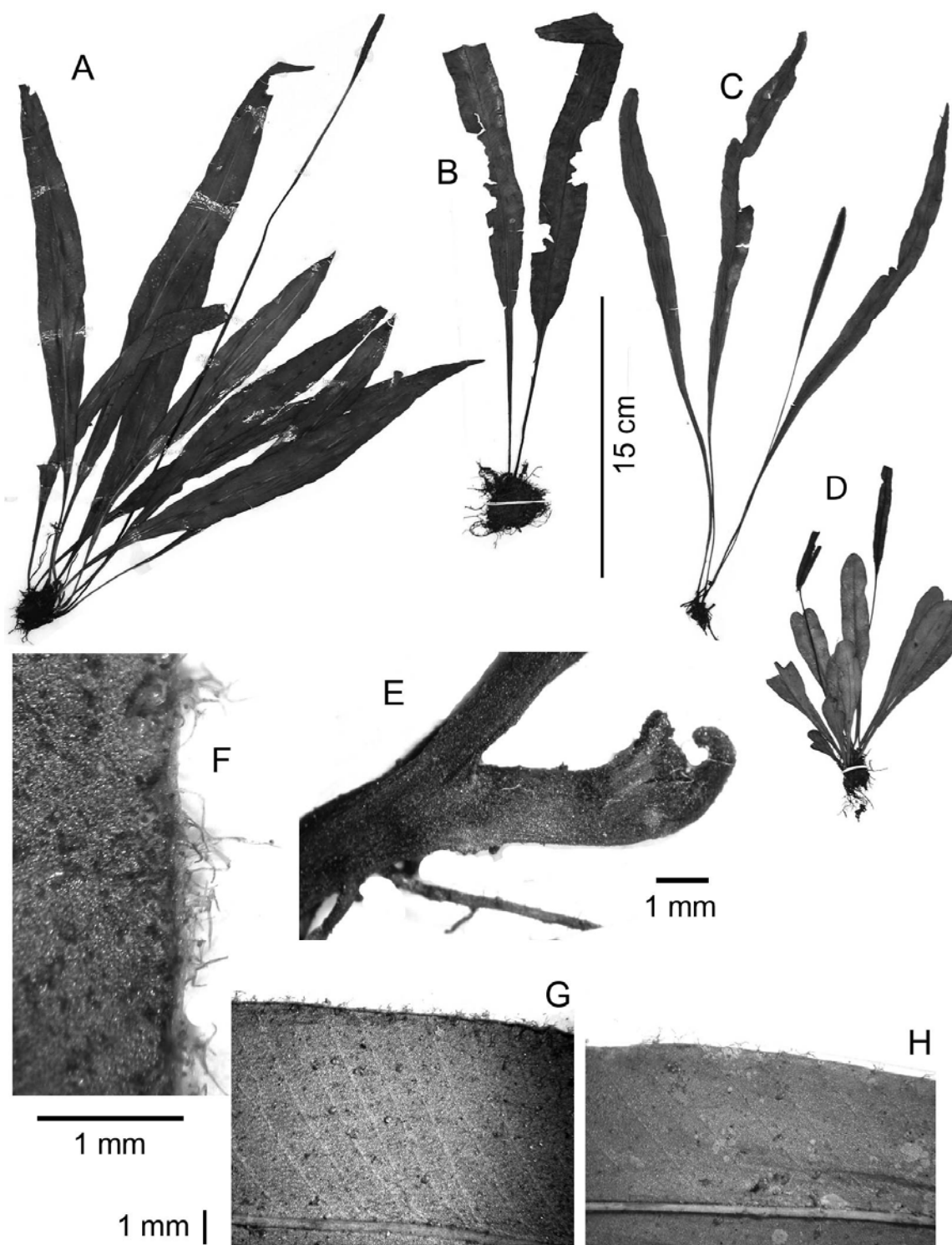


FIG. 14. *Elaphoglossum nigrescens*. **A–D.** Habit. **E.** Rhizome. **F.** Dissected marginal scales of lamina. **G.** Lamina abaxial surface. **H.** Lamina abaxial surface. (A from *Maguire* 33543, NY; B from *Liesner* 25826, NY; C from *Tuomisto* 7749, NY; D from *Grayum* 2929, NY; E from *Beitel* 85268, NY; F–G from *Øllgaard & Navarrete* 2476, AAU)

absent or reduced to resinous dots; laminae 10–30 x 1.2–2 cm, narrowly elliptic or narrowly oblanceolate, papyraceous to chartaceous, the base decurrent all the way to the phyllodia, the apex obtuse or broadly acute; veins conspicuous or inconspicuous, 1.5–2 mm apart, at an angle of 65° with respect to the costa, the apices free; hydathodes absent; lamina scales reduced to resinous dots, these often on both surfaces but more pronounced on the abaxial side; marginal scales sparse, 0.3–1 mm long, lanceolate to ovate, dissected. *Fertile leaves* longer than the sterile; petioles 2/3–3/4 the length of the fertile leaf, stramineous to black; laminae 3–5 cm wide, linear to narrowly elliptic, sometimes scaly, the base cuneate, the apex obtuse to broadly acute.

Distribution.—Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Ecuador, Peru, Brazil, Bolivia (Fig. 15); elevation 60–1800 (–2000) m. This is the only species in the *E. ciliatum* group that occurs in lowland Amazonia.



FIG. 15. Distribution of *Elaphoglossum nigrescens*.

Selected specimens examined. NICARAGUA. GRANADA: E of Volcán Mombacho, above Finca Las Delicias, [11°50'N, 85°59'W], 850 m, 16 Jul 1975, *Atwood & Neill* AN196 (MO, US). **REGIÓN AUTÓNOMA ATLÁNTICO NORTE:** Mun. Siuna, Reserva BOSAWAS, Cerro Saslaya, 13°47'N, 84°59'W, 300–1000 m, 9–14 Apr 1999, *Rueda et al.* 10552, 10692 (MO). **RIO SAN JUAN:** Mun. San Juan del Norte, reserva Indio-Maíz, río Caño Negro a 1 km abajo de la desembocadura del río Caño Blanco, 10°58'N, 84°04'W, 60 m, 17 May 2002, *Rueda & Mendoza* 17043 (MO). **RIVAS:** Isla Ometepe, Lago de Nicaragua, N slope of Volcán Maderas, [11°27'N, 85°32'W], 800–1000 m, 24 Feb 1978, *Neill & Vincelli* 3249, 3253 (CR, MO).

COSTA RICA. ALAJUELA: S of Aguas Zarcas, 10°22'N, 84°22'W, 600 m, 20 May 1968, *Burger & Stolze* 5097 (NY). **CARTAGO:** Cantón de Paraíso, Parque Nacional Tapantí, cuenca del Reventazón, 9°45'20"N, 83°47'00"W, 1300–1500 m, 22 Jan 1999, *Rojas & Soto* 4871 (CR, INB, MO, NY). **GUANACASTE:** Parque Nacional Rincón de la Vieja, SE slope of Volcán Sta. María, 10°47'N, 85°18'W, 900–1200 m, 27–28 Jan 1983, *Davidse et al.* 23424 (CR, MO, NY); Cantón de Liberia, Parque Nacional Guanacaste, Estación Cacao, 10°55'45"N, 85°28'15"W, 1100–1500 m, 5 Sep 1996, *Rojas & Mata* 3029 (INB, NY). **HEREDIA:** Finca La Selva, 27 Jun 1980, *Grayum* 2929 (NY); Cantón de Sarapiquí, Distr. La Virgen, ca. 3 mi E of La Virgen. Estación Biológica La Tirimbina, 10°24'09"N, 84°06'03"W, 220 m, 14 Jan 2001, *Moran* 6332 (NY). **LIMÓN:** Cantón de Limón, R.B. Hitoy Cerere, Cuenca del Estrella, orillas del Río Cerere, 9°39'35"N, 83°02'25"W, 100–200 m, 12 May 1998, *Rojas et al.* 4545 (CR, INB, NY). **PUNTARENAS:** Monteverde Reserve, 1 km SW station, 10°18'N, 84°48'W, 1500 m, 10 Feb 1992, *Ingram & Ferrell-Ingram* 1308 (CR, NY); same locality, 15 Apr 1993, *Ingram & Ferrell-Ingram* 1825 (NY). **SAN JOSÉ:** along Río Zurquí, downstream from Guápiles Hwy., 10°03'N, 84°01'W, 1400–1500 m, 18 Jan 1986, *Smith et al.* 1707 (CR, MO, NY).

PANAMA. BOCAS DEL TORO: Oleoducto road, 2 km NE of Continental Divide, ridge between Ríos Quabo and Quabito, 8°48'N, 82°12'W, 1000 m, 9 Feb 1984, *Churchill et al.* 4933 (MO, NY), 4935 (NY). **COCLÉ:** summit of Cerro Pilon, above El Valle de Antón, [8°38'N, 80°08'W], 820 m, 28 Mar 1969, *Dwyer et al.* 4493 (MO). **COLÓN:** Sta. Rita ridge, end of road from Trans-Isthmian Hwy., 10 miles from Hwy., [9°19'N, 79°47'W], 19 Mar 1969, *Porter et al.* 4797 (MO). **DARIÉN:** Vic. of upper gold mining camp of Tyles Kittredge on headwaters of Río Tuquesa, [8°23'N, 77°47'W], 26 Aug 1974, *Croat* 27272 (MO).

COLOMBIA. AMAZONAS: Río Miritiparaná, Caño Guacayá, 0°30'S, 70°40'W, 215 m, 28 Mar 1952, *Schultes & Cabrera* 15739 (US). **CHOCÓ:** Upper Río Truando, 2 km SSW of the confluence of Río Nercua near MADUREX Comp, [7°10'N, 77°30'W], 100 m, 4 Mar 1971, *Lellinger & de la Sota* 570 (COL, US). **VAUPÉS:** Río Pacoa, tributary of the Río Apaporis, 0°20'N, 71°20'W, 300 m, 7–12 Feb 1952, *Schultes & Cabrera* 15285 (NY, US).

VENEZUELA. AMAZONAS: Río Negro, Cerro de Neblina, 6.2 km NNE Pico Phelps, 0°51'45"N, 65°58'52"W, 1350–1450 m, 26 Feb 1985, *Beitel* 85268 (NY); Depto. Casiquiare, Río Casiquiare, 40 km después de la boca, [1°56'N, 67°03'W], 28 Jan 1991, *Colella et al.* 1602 (NY); Dpt. Atabapo, E side of Cerro Huachamacarí, 3°49'N, 65°43'W, 800–1300 m, 5 Nov 1988, *Liesner* 25826 (NY). **BOLIVAR:** Gran Sabana, ca. 10 km SW of Karaurin Tepui at junction of Río Karaurin and Río Asadon (Río Sanpa), 5°19'N, 61°03'W, 900–1000 m, 22 Apr 1988, *Liesner* 23598 (NY, US); Ilu-tepui, Gran Sabana, [5°25'N, 60°29'W], 1300 m, 23 Mar 1952, *Maquire* 33543 (NY).

GUYANA. Region Cuyuni-Mazaruni, 9 km W of Paruima, 1 km E of Ararata, 5°49'N, 61°08'W, 780 m, 6 Jul 1997, *Clarke 5453* (CAY, US); Region Potaro-Siparuni, Pakaraima Mts, Mt. Wokomung, Suruwabaru Creek, 2–3 km upstream from juncture with Yuarka River, 5°03'N, 59°54'W, 675–750 m, 11 Feb 1993, *Henkel 1287* (CAY, NY, US); Potaro River, [5°22'N, 58°54'W], 1899, *Jenman s.n.* (NY).

ECUADOR. CARCHI/Esmeraldas: Lita, [0°50'N, 78°27'W], 600 m, 20 May 1987, *van der Werff et al. 9544* (MO, QCNE). **MORONA-SANTIAGO:** ca. 7 km N of Limón, 2°54'42"S, 78°24'03"W, 960 m, 3 Mar 2005, *Moran et al. 7627* (NY); road Patuca – Santiago, Km 8.4 from Santiago, 3°01'S, 78°05'W, 480 m, 19 Mar 1997, *Øllgaard & Navarrete 2476* (AAU, NY, QCA). **NAPO:** Yasuní National Park, 5 km after crossroads at Km 42, 0°41'S, 76°24'W, 250 m, 19 Apr 1996, *Moran et al. 6243* (AAU, NY, QCA, QCNE, TUR). **PASTAZA:** Near Canelos, 1°37'S, 77°50'W, 800 m, 18 Feb 2005, *Moran et al. 7491* (NY); sector Puca Urca, 1 km NW of Canelos, 1°34'S, 77°45'W, 650 m, 3 Jul 1997, *Øllgaard & Navarrete 2384* (QCA). **SUCUMBIOS:** Reserva Faunística Cuyabeno S of Laguna Garzacocha, 0°01'S, 76°11'W, 265 m, 1 Apr 1989, *Balslev et al. 84690* (AAU, QCA, QCNE). **ZAMORA-CHINCHIPE:** Cantón Nangaritza, Río Nangaritza, Pachicutza, [4°07'S, 78°37'W], 900 m, 3 Dec 1990, *Palacios & Neill 6479* (QCNE).

PERU. AMAZONAS: Distr. Bagua, along road from Chiriaco towards Bagua, 5°16'57"S, 78°38'10"W, 800 m, 20 Mar 2001, *van der Werff et al. 16256* (NY). **JUNÍN:** Prov. Satipo, Gran Pajonal, trail to Pajonal Panquerete, S of Chequitavo, 10°45'S, 74°23'W, 1200 m, 22 Sep 1983, *Smith 5133* (NY, UC). **LORETO:** Prov. Maynas, Distr. Napo, Río Sta. María, 1°10'S, 74°44'W, 100 m, 9 May 1982, *King 452* (F, NY); Prov. Maynas, Explorama/ACEER reserve, 5–15 km E of the mouth of Quebrada Sucusari at lower Napo, 3°15'S, 72°50'W, 100–200 m, 22 Jan 1995, *Tuomisto et al. 7749* (NY). **MADRE DE DIOS:** Manú, Cerro de Pantiacolla, 12°15'S, 70°54'W, *Foster 10792* (F, GH). **PASCO:** Prov. Oxapampa, logging area at Abra Los Mellizos, 4–8 km from Eneñas, [10°45'S, 75°14'W], 1750 m, 23 May 1978, *Skog et al. 5042* (US).

BRAZIL. AMAZONAS: Rio Negro, 1 hour upstream by motorboat from mouth of Rio Xié, Indian village of Campina, 0°57'N, 67°11'W, 25 Oct 1987, *Mass et al. 6858* (NY). **BAHIA:** Arataca, topo da Serra do Peito-de-Moça, ca. 22.4 km na estrada que liga Arataca à Una, 15°10'25"S, 39°20'30"W, 1000 m, 15 Apr 2006, *Amorim et al 5812* (CEPEC, NY). **MINAS GERAIS:** Sta. Maria do Salto, Distrito Talismã, 16°24'16"S, 40°03'27"W, 750–850 m, 10 Oct 2003, *Salino et al. 9260* (NY). **PARANÁ:** Mun. Guaraqueçaba, Serra Negra, [25°10'S, 48°26'W], 100 m, 10 Dec 1970, *Hatschbach 25799* (US). **SANTA CATARINA:** Joinville, estrada Dona Francisca, [26°18'S, 48°50'W], 600 m, 18 Dec 1957, *Reitz & Klein 5714* (US). **SÃO PAULO:** Campo Grande, [23°58'S, 46°21'W], 17 Jan 1915, *Brade 7605* (NY); Mun. Mogi das Cruzes, limite com Salesópolis, Estrada Usaka, Represa Casa Grande da SABESP, 23°39'17"S, 45°57'34"W, 800 m, 24 Apr 2000, *Salino et al. 5399* (NY); Estação Biológica Alto da Serra, [23°47'S, 46°19'W], 800–900 m, 2 Feb 1929, *Smith 1855* (US); Rio Grande, [23°48'S, 46°20'W], 1906, *Wacket s.n.* (US).

BOLIVIA. COCHABAMBA: Prov. José Carrasco Torrico, Km 143 antigua carretera Cochabamba-Villa Tunari, 17°07'S, 65°34'W, 1300 m, 22 Aug 1996, *Kessler et al. 7525* (NY). **LA PAZ:** Prov. Nor-Yungas, Puerto Linares 39 km hacia Caranavi, [15°49'S, 67°33'W], 1410 m, 10 Mar 1979, *Beck 465* (NY); Prov. Caranavi, Serranía de Bella Vista, 15°40'S, 67°29'W, 1180–1590 m, 5 – 7 Apr 2004, *Jimenez 2185, 2220, 2256* (NY).

Elaphoglossum nigrescens is distinguished by laminae that taper to the phyllopodia and the presence of dissected scales along the lamina margin. The species varies with respect to the length of the fertile leaves, from shorter to much longer than the sterile. The specimens from southern Venezuela and the Guianas (where the type was collected) tend to have longer fertile leaves, whereas those from Costa Rica and Panama tend to have shorter ones. Plants from southeastern Brazil have mostly longer fertile leaves and non-black fertile petioles.

We decided to place in synonymy *Elaphoglossum palmense*, a species described from Central America. Although specimens from Central America tend to have smaller overall sizes, smaller lamina scales, sparsely spiculate spores (those of South America are densely spiculate), and a tendency toward obtuse laminae, there is a lot of variation within specimens making some of them indistinguishable from specimens of South America. Thus, what appears to be a difference at the beginning is a gradation. An example of these gradations is illustrated in the variation on the shape and size of the lamina scales (Fig. 16). Molecular analyses (Vasco et al., 2009b) support our hypothesis, showing a clade of *E. nigrescens* sequences from both Central and South America.

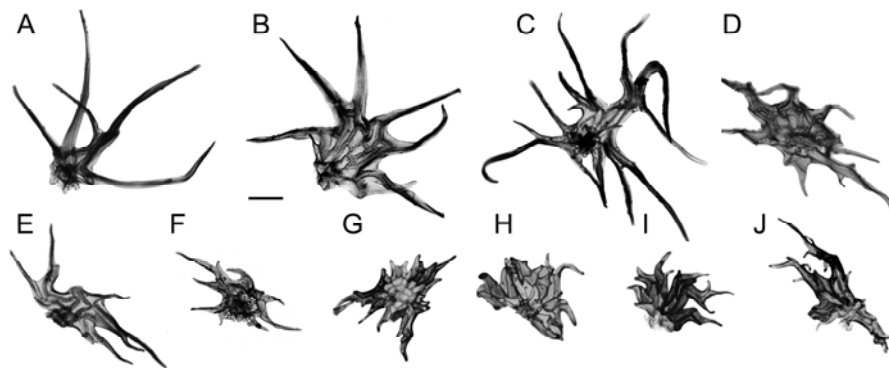


FIG. 16. Scales from the lamina margin of *Elaphoglossum nigrescens*. **A–D.** South American specimens. **E–J.** Central American specimens. (A from *Colella* 1602, NY; B from *King* 452, NY; C from *Moran* 7627, NY; D from *Beck* 465, NY; E from *Burger & Stolze* 5097, NY; F from *Moran* 6332, NY; G from *Rojas & Soto* 4871, NY; H from *Davidse* 23424, NY; I–J *Churchill* 4935, NY). Scale bar = 100 micrometers.

Vareschi stated that the type of *Elaphoglossum williamsii* has proliferous blade apices; however, this character does not occur in any species of the *E. ciliatum* group. His statement seems based on a misinterpretation of the type, which is illustrated in the protologue. This plant consists of two sterile leaves with incompletely developed, notched apices. This gives the impression of a bud in the notch, as occasionally happens in other ferns (e.g., *E. phoras* Mickel). The holotype of this species was not found at VEN, although most of Vareschi's types are there. That is why neither the NY nor the US collections is considered a holotype. We suspect that the holotype is at VEN but has been misplaced.

Nomina Dubia

The name *Anogramma paradoxa* Fée (Mem. Foug., 5. Gen. Filic. 64, 184. 1850–52) was intended to apply to both *Elaphoglossum bifurcatum* and *E. dimorphum*. Fée mentioned specimens but did not cite any, and claimed that they intergraded completely. We are therefore unable to apply this name, which for either species would be a later homonym.

Species Excludendae

Elaphoglossum huacsaro Ruíz f. *minus* Kuntze (published as *E. huscaro* Ruíz f. *minus*), Revis. Gen. Pl. 3 (3): 376. 1898. Type: Bolivia. Tunarigebirge, 1000m, Apr–May 1892, O. Kuntze s.n. (holotype: NY). This species corresponds to *Elaphoglossum tenuiculum* (Fée) T Moore ex C. Chr., a species that does not belong to the *E. ciliatum* group.

3.5. APPENDIXES

Appendix 1. List of Taxa

1. *Elaphoglossum bifurcatum* (Jacq.) Mickel
2. *E. burchellii* (Baker) C. Chr.
3. *E. ciliatum* (C. Presl) T. Moore
4. *E. dimorphum* (Hook. & Grev.) T. Moore
5. *E. dussii* Underw. ex Maxon
6. *E. gramineum* (Jenm.) Urb.
7. *E. huacsaro* (Ruíz) H. Christ
8. *E. nervosum* (Bory) H. Christ
9. *E. nigrescens* (Hook.) T. Moore ex Diels

APPENDIX 2. Distribution of *Elaphoglossum* ciliatum species group by country

BOLIVIA: 3 species. *burchellii*, *huacsaro*, *nigrescens*.

BRAZIL: 3 species. *burchellii*, *huacsaro*, *nigrescens*.

COLOMBIA: 4 species. *burchellii*, *ciliatum*, *huacsaro*, *nigrescens*.

COSTA RICA: 4 species. *burchellii*, *ciliatum*, *huacsaro*, *nigrescens*.

CUBA: 1 species. *gramineum*.

DOMINICA: 1 species. *dussii*

DOMINICAN REPUBLIC: 4 species. *burchellii*, *dussii*, *gramineum*, *huacsaro*.

ECUADOR: 4 species. *burchellii*, *ciliatum*, *huacsaro*, *nigrescens*.

GRENADA: 1 species. *dussii*

GUADELOUPE: 1 species. *dussii*.

GUATEMALA: 1 species. *huacsaro*.

GUYANA: 1 species. *nigrescens*.

HAITI: 1 species. *huacsaro*.

HONDURAS: 1 species. *gramineum*.

JAMAICA: 2 species. *gramineum*, *huacsaro*.

MARTINIQUE: 1 species. *dussii*.

MEXICO: 1 species. *huacsaro*.

NICARAGUA: 1 species. *nigrescens*.

PANAMA: 3 species. *burchellii*, *ciliatum*, *nigrescens*.

PERU: 4 species. *burchellii*, *ciliatum*, *huacsaro*, *nigrescens*.

PARAGUAY: 1 species. *burchellii*.

PUERTO RICO: 1 species. *dussii*.

ST. HELENA: 3 species. *bifurcatum*, *dimorphum*, *nervosum*.

ST. KITT'S: 1 species. *dussii*.

ST. VINCENT: 1 species. *dussii*.

VENEZUELA: 3 species. *burchellii*, *huacsaro*, *nigrescens*.

APPENDIX 3. List of Exsiccatae

The number in parentheses refers to the species number assigned in the monograph; the numbers in boldface are types.

Acebey, 176 (2)
 Acevedo, 2976 (5)
 Acosta-Arteaga, 73 (7); 165, 324, 359 (2); 493, 779 (7); 800 (2); 1071, 1082 (7); 1205 (2)
 Acuña, 20323 (6)
 Agostini, 2835 (2); 2863 (7)
 Aguinda, 999 (3)
 Allart, 374 (2)
 Albert de Escobar, 5573, 7400 (7)
 Alfaro, 1117 (3)
 Alston, 6517, 7419 (7)
 Amorim, 5812 (9)
 Anderson, 3223 (6); 7523, 8864 (2)
 André, 1961 (3)
 Angulo, 71 (9); 602 (3)
 Arbeláez, 84, 1244 (7)
 Archer, 1278 (2)
 Arroyo, 2743 (2)
 Asplund, 16945, 17135, 17412 (7)
 Atehortúa, 1004, 1014 (7)
 Atwood, AN196 (9)
 Aulestia, 1722, 1957, 2000 (9)
 Azofeifa, 108, 109 (9)
 Baker, 5537 (3)
 Balansa, **390** (2)
 Balslev, 1725, 2474, 2476A (7); 10327 (3); 10336 (2); 10402 (3); 84690, 97427 (9)
 Barclay, 4459 (7)
 Barringer, 2284 (9)
 Bass, 172 (3)
 Bayon, 98 (2)
 Beck, 465 (9)
 Beitel, 85268 (9)
 Bell, 666 (7)
 Bello, 978 (9); 2712, 4501 (3); 4578 (9)
 Bischler, 1233, 1318, 2258 (7)
 Bittner, 206 (9); 686, 709 (3); 1014, 1227 (9); 1722 (2); 2024, 2354 (3)
 Boyle, 4915, 4958 (3)
 Brade, 80, 81 (7); **236** (9); 237(7); 528 (3); 7605, 8415 (9); **9759** (7); 9764 (2)
 Brandbyge, 30808 (9); 42517 (7)
 Breedlove, 22412, 23167 (7)
 Brenes, 19274, 20531 (3)

Bridarolli, 4338, 4402 (2)
 Bristol, 456 (3)
 Britton, 690 (5)
 Broadway, 1900 (5)
 Buchtien, 8 (9); 2712 (7); 5169 (2); 5175 (9); 5927 (7)
 Bües, 2100 (7)
 Burch, 4619 (3)
 Burchell, 177 (1); 180 (4); **5155** (2)
 Burger, 5018 (3); 5097 (9); 5808 (9)
 Callejas, 3834, 3891 (7); 10504 (3); 10518 (7)
 Camp, 4661 (7)
 Campos, 3677 (2)
 Carvajal, 453 (9)
 Carvalho, 112 (2)
 Chavarría, 24 (2); 485 (9)
 Chockerong, 116 (6)
 Christenhusz & Katzer, 3221 (7); 4011 (5)
 Churchill, 4933, 4935 (9)
 Clark, 163, 578, 4875, 6441 (3); 8079 (7) ; 9059 (3)
 Clarke, 5453 (9)
 Clute, 82 (7)
 Colella, 1366 (7); 1601, 1602 (9)
 Core, 451 (7)
 Cornman, 1354 (3)
 Correa, 18A134 (7)
 Correll, E419 (7)
 Cotton, 905, 929 (9)
 Croat, 821, 824 (7); 27272 (9); 35768 (3); 36458 (9); 41016 (7); 49976 (3); 51523 (7);
 59961, 70770 (3); 72196 (7); 88085 (3); 92143, 93854 (7)
 Crosby, 2564 (3)
 Cuatrecasas, 11469 (7); 13938 (3); 26800 (7)
 Cumming, 420, 2464 (1)
 Cuninghame, 135 (1)
 Davidse, 21137 (2); 23226 (3); 23424 (9)
 Dawson, 14507, 14574 (2)
 de Garganta, 2047 (7)
 de la Sota, 5209 (3); 6206 (7)
 de Nevers, 5401 (3)
 Díaz C., 2171, 3605 (7)
 Díaz S., 1666, 3015 (7)
 Dodson, 10670, 10674, 10752, 10756, 10757 (7); 10761 (2); 10774, 10802 (3); 10895, 12088
 (7); 14673 (3); 15417 (7)
 Dorr, 7292, 7994, 8132, 8214 (7); 8623 (2); 9256 (7)
 Duncan, 2607 (7)
 Dusén, 735, 2045, **2748**, 4045, 7225, 7280 (2)
 Duss, 1622, 1623, 4130, 4130, 4131, 4150, 4400, 4607, **4688**, 4748 (5)

Dwyer, 4493 (9)
 Eberhardt, 166, 300, 421, 423, 442 (2)
 Ekman, 13878 (7)
 Engler, **62** (2)
 Evans, 221 (2)
 Ewan, 16589 (7)
 Fay, 1580, 1605, 1606 (7); 2193, 2487 (2); 2651A (3); 4273, 4308 (7)
 Fendler, 276, **280** (2)
 Fernández, 27, 223A (7)
 Feuerer, 8750A (2)
 Folsom, 3298, 3980 (3)
 Fonnegra, 2773 (7); 5614 (2)
 Forzza, 1219 (2)
 Fosberg, 43355 (9)
 Foster, 1348, 1513 (7); 10792 (3)
 Franco, 5098 (3)
 Garcia-Barriga, 12604 (2)
 Gehriger, 327 (7)
 Gentry, 19319 (7)
 Gil, 9 (3)
 Giraldo, 1581 (3)
 Glaziou, **952**, 2433, 2455, 2800, 2855 (2)
 Gómez, 247, 2171 (3); 20831 (9); 20845 (9); 22794 (3)
 González, 441 (9)
 Grant, 9086 (7); 90-00885 (2)
 Grayum, 1958, 2426, 2819, 2929 (9); 6738 (3); 7955, 9079 (9)
 Grubb, 1314 (3)
 Gutiérrez, 20 (3)
 Gutiérrez-H, 246 (7)
 Hagemann, 81 (2); 369, 641 (3); 1153, 1192 (7); 1261 (3); 1865 (3); 2025 (9)
 Hahn, 498 (9)
 Hamilton, 901, 908 (7)
 Hammel, 2003, 2092 (3)
 Handro, 1078 (9)
 Harley, 50623 (2)
 Harling, 809, 4166 (7)
 Harris, 7429 (6)
 Hassler, 4612 (2)
 Hatschbach, 9801 (2); 25799 (9); 31136, 31460 (2)
 Haught, 6133 (2); 3163 (7)
 Haughton, 1149 (1)
 Henkel, 1287 (9)
 Henrich, 211 (9)
 Herrera, 1377 (9); 1855, 2532 (3); 3221 (9); 3233a (3); 5108 (9); 5239, 5298, 6202, 7857 (3)
 Herzog, 2227 (7)
 Hinchley, 179 (6)

Hno. Daniel, 1021, 1215 (7); 3277 (2)
 Hodge, 16 (5)
 Holm-Nielsen, 1366 (7); 3264 (7); 3517 (2); 16171, 18302, 23572, 29352 (7)
 Hoover, 1958, 2060 (3)
 Huaylla, 1714 (2)
 Hutchison, 4818 (7)
 Idrobo, 4146 (7); 10298 (3)
 Ingram, 1308, 1448, 1825 (9)
 Irwin, 15629, 29118, 32893B (2)
 Ivey, 292, 327 (3)
 James, 13, 109 (9)
 Jaramillo, 5778, 7142, 7145 (7); 12234, 14163, 14319 (3)
 Jaramillo-Mejía, 2984 (7)
 Jenman, **27**, 179 (6)
 Jimenez, 1052 (2); 2185, 2220, 2256 (9)
 Jorgensen, 61898 (7)
 Judd, 4517 (7)
 Juncosa, 1018 (7)
 Jürgens, **61.1**, 61a, **144**, **144.1** (2)
 Kennedy, 3167 (3)
 Kessler, 6239, 6264 (2); 6698, 6993 (7); 7395, 7525, 7536B, 7842 (9); 9092, 9147 (2); 459
 (7); 9773 (9); 10506 (2); 10507 (7); 10528 (2); 11325 (9); 11515, 11543 (2); 11784 (7)
 Killip, 8850, 15798 (7); 16555 (2); 16732, 17190, 19304, 24411, 24414 (7); 25668 (3);
 34641 (7); 34648 (3); 38503 (2)
 King, 452 (9)
 Kirkbride, 1991, 4268 (3)
 Knapp, 2488 (3); 7550 (2)
 Kress, 91-3359 (9); 94-5110 (3)
 Lægaard, 51207 (9)
 Langenheim, 3390 (7)
 Lawesson, 43444 (9)
 Labiak, 2942 (2); 3638 (9); 4236 (2)
 Leal, 60 (7)
 Lehmann, BT1190 (2)
 Lehnert, 1338 (2); 1304, 1423 (3)
 Leite, 411, 2758, 3480 (2)
 Lellinger, 290 (3); 570 (9); 825, 1276 (3); 1834 (9)
 León, 618, 955 (7)
 Leonard, 4513 (7)
 Lewis, 2382 (7)
 Licata, 422 (7)
 Liesner, 6407, 6645, 7499 (9); 12995 (7); 14862 (3); 17646, 18597, 23561, 23598, 25826 (9)
 Linden, 1922b (6)
 Liogier, 13422 (2)
 Little, 7826, 7891, 8171, 8568, 8582a (7)
 Lloyd, 199A, 336, 351, 357, 753 (5); 4182, 4189, 4250, 4256 (3)

Løjtnant, 11927 (7)
 López, 7239 (9)
 Luederwaldt, 7844 (2)
 Luer, 4941 (2)
 Luteyn, 5367, 5453 (7); 6628 (2); 7049, 7255, 7572 (7); 8238 (2); 9731, 9831, 9935, 10620, 10995, 10997 (7); 13161 (3); 13167 (7); 13170 (3) 14191 (7)
 Macedo, 3071 (2)
 Madison, 2260, 2261, 2550 (7)
 Madsen, 7111 (2)
 Mägdefrau, 1450 (7)
 Maguire, 28489, 33543, 34927 (9)
 Martínez, 406 (3); 420 (9)
 Marulanda, 511 (7)
 Mass, 5298 (7); 6858 (9)
 Matos, 371 (9)
 Maxon, 2274, 2847, 2918, 8611 (6)
 McPherson, 8869 (3); 8687, 9655, 15387 (9)
 Mejía, 3776 (3)
 Melo, 139 (2)
 Méndez, 924 (7)
 Mexia, 7102, 7188 (3)
 Mickel, 2577 (3); 3495 (9); 8258, 8268, 8275, 8392, 8406, 8411, 8449 (7)
 Miranda, 170 (9)
 Montgomery, 8542 (3)
 Mora, 928 (9)
 Morales, 1256 (9)
 Moran, 4118, 5164 (3); 5179 (2); 5183, 5377 (3); 5836 (9); 5925 (2); 6121, 6243, 6332 (9); 6371 (7); 6711, 6762 (3); 6895 (7); 7418 (3); 7491 (9); 7516 (3) 7627 (9)
 Moritz, 122 (2); **315** (7); 316 (2)
 Mostacero, 344 (7)
 Murillo 132, 737, 927 (7); 973 (3); 2112, 2954 (7)
 Mutis, 3317 (7)
 Navarrete, 1540, 1808 (3)
 Nee, 49325 (2); 52309 (7)
 Neill, N41, 3249, 3253 (9); 9648 (3)
 Nuñez, 711 (2)
 Øllgaard, 986 (3); 1293 (7); 1569, 1637 (3); 1891, 2384 (9); 2456 (3); 2476 (9); 2639, 2725, 2892, 3033 (3); 8734, 9361, 9378 (7); 99337 (2); 99968 (7); 99985 (3)
 Ortega, 1951, 2260 (7)
 Pachón, 60 (7)
 Palacio, 66 (7)
 Palacios, 22, 4134, 5400, 5697 (3); 6479, 8739 (9); 11414 (3)
 Peñuela, 60 (7)
 Pipoly, 5128, 10915 (9)
 Pittier, 3554 (3); 7404 (2)
 Plowman, 940, 4513 (3)

Porter, 4665, 4669, 4673 (3); 4797 (9); 4939b, 4941a, 4942 (3)
 Porto, 2113, 3014 (2)
 Posada, 282 (2)
 Prado, 1099 (7); 1109 (2)
 Proctor, 3907 (6); 32242 (9)
 Ramírez, 4804 (7); 5349 (2)
 Rangel, 5583 (3)
 Ranker, 1823 (9)
 Regnell, 336 (2)
 Reitz, 110, 3972 (2); 5714 (9)
 Rieckl, 1823 (9)
 Roa, 30 (7)
 Rodríguez, 3250 (3); 3272 (2); 3464, 5064 (3); 5226, 5445 (7); 5620 (3)
 Rohr, 292, 1059 (2)
 Rojas, 406 (3); 591 (9); 616, 1022 (3); 1025 (9); 1040 (3); 1054, 1295 (9); 1629, 1777 (3);
 1802, 1827, 2096 (9); 2107, 2218, 2265, 2345, 2441, 2606 (3); 2716 (7); 2795, 2966 (3);
 3029 (9); 3278 (2); 3361 (7); 3367 (9) 3999, 4197 (3); 4230, 4545 (9); 4627 (3); 4663 (7);
 4824, 4856 (3); 4871 (9); 5105 (2); 5458 (3); 5492 (7); 6050 (2); 6051, 6310 (3)
 Romero, 8 (7)
 Romoleroux, 2070 (9)
 Rueda, 6207, 10552, 10692, 17043 (9)
 Ruiz, **54** (7)
 Ruiz-Terán, 6124 (7)
 Rusby, 298 (2)
 Saldarriaga, 27 (7)
 Salino, 1780, 1810, 4635, 5196 (2); 5399 (9); 5527 (2); 6480 (9); 6871, 7454, 9260 (2)
 Sánchez, 137, 138 (5); 1665, 6001 (7)
 Sandeman, 5841 (9)
 Santa, 1078 (7)
 Saravia, 3019A (7)
 Savatier, 1993 (1)
 Schultes, 15285, 15739 (9)
 Schunke, 136, A145 (9)
 Seidenschnur, 127, 128 (3); 137 (9); 155, 164, 168 (3); 173 (9); 175, 191a (3); 194 (9); 202
 (3); 261a (7); 280 (3); 281 (9); 381 (9)
 Shafer, 592, 3433, 3482, 3669 (5)
 Skog, 5042 (9)
 Smith, 1707, 1855 (9); 2103 (3); 5133 (9) 5525 (3)
 Sodiro, 22 (7)
 Soejarto, 3031 (7)
 Solomon, 11748, 14956 (2); 4903 (7)
 Spannagel, 10 (2)
 Sparre, 16526 (2); 16973, 17389 (7)
 Spruce, 5230 (3); 2187 (9)
 Standley, 36417, 36494, 37767, 37847, 37963 (3)
 Stergios, 4253 (9); 17340, 17341, 17474 (7); 20609 (2);

Steyermark, 144 (9); 56989 (2); 110109 (7); 129728, 130312A (9)
 Stimson, 5400 (2)
 Stones, 2041 (7)
 Stork, 9892 (7)
 Tate, 940 (2)
 Thompson, 7872 (7)
 Torres, 19 (7); 96, 2277 (3)
 Torres-Rojas, 181 (9)
 Tryon, 5309, 6020 (7)
 Tuomisto, 7749 (9)
 Ule, **265** (7)
 Underwood, 479 (7); 1337, 1388, 1619, 2057, 2120, 2144 (6); 2589 (7)
 Valeur, 634 (6)
 van Cotthem, 1523, 1588 (2); 1708, 1999 (7)
 van der Werff, 5939, 5943 (7); 6649, 6877, 7064 (3); 7670 (7); 8745 (2); 9544 (9); 13428, 15821 (3); 16256 (9); 17612 (3)
 Vareschi, 5556, 7167 (7)
 Vargas, 2365 (3); 2501 (7)
 Vasco, 468, 504 (3); 555, 556 (2); 562, 567, 568, 576 (7); 579 (3)
 Vásquez, 28869 (7)
 Velásquez, 99 (3)
 Vélez, 1306 (3)
 Vivas, 1452 (9)
 Wacket, **114** (9)
 Webster, 13417 (5)
 Wercklé, **17102** (9)
 Werling, 248 (7)
 Werner, 278 (3); 1547 (2)
 White, 508 (2)
 Wiggins, 10991 (7)
 Williams, **15338** (9); 19943, 20323 (3)
 Woytkowski, 6740, 6741 (7); 7693 (2)
 Zaroni, 19347, 20278 (7)
 Zardini, 40813 (2)
 Zarucchi, 6212 (7)

CHAPTER 4

TAXONOMIC REVISION OF *ELAPHOGLOSSUM* SUBSECTION *MUSCOSA* (*DRYOPTERIDACEAE*)

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4.1. ABSTRACT

The present paper provides a monograph of *Elaphoglossum* subsection *Muscosa*, a monophyletic group supported by molecular phylogenetic analyses. The monograph includes keys, full synonymy, descriptions, representative specimens examined, an index to collectors' names and numbers, illustrations, spore photomicrographs, and distribution maps for all species. Morphologically, the subsection is recognized by obtuse leaf apices, spores that are about twice as long as other species of *Elaphoglossum*, and scaly rhizomes, petioles, and laminae. Fifteen species of subsection *Muscosa* are here recognized, with no subspecies or varieties. All are Neotropical occurring from southern Mexico to Bolivia and southeastern Brazil, with three species in the West Indies. Most of the species occur in the Andes from 1,500–4,000 m, primarily in cloud forests and páramos. Three new species are described: ***E. novogranatense***, ***E. oreophilum***, and ***E. quisqueyanum***. The name ***E. glabrescens*** A. Vasco, nom. et stat. nov. is proposed. Lectotypes are designated for ***E. aschersonii***, ***E. bellermannianum***, ***E. blandum***, ***E. caulolepia***, ***E. corderoanum***, ***E. decipiens***, ***E. engelii***, ***E. gardnerianum***, ***E. lehmannianum***, ***E. muscosum***, ***E. yarumalense***, and ***E. yatesii***.

Keywords—ferns, floristics, pteridophytes, taxonomy.

4.2. INTRODUCTION

Elaphoglossum Schott ex J. Sm. (Dryopteridaceae) is one of the most species-rich genera of ferns with nearly 600 species (Mickel 1990). It is pantropical and most diverse in the Neotropics where about 450 described species occur (Mickel 1990). Morphologically, *Elaphoglossum* is characterized by a mainly epiphytic habit, simple entire leaves, free veins, and phyllopodia. Other characteristics, common to *Elaphoglossum* and its sister groups *Bolbitis*, *Lomogramma* and *Teratophyllum* (Schuettpelez and Pryer 2007) are dorsiventral rhizomes, simple, dimorphic sterile and fertile leaves, and acrostichoid sori. The monophyly of the genus and its placement within Dryopteridaceae have received strong support from several molecular phylogenetic studies (Rouhan et al. 2004; Liu et al. 2007; Schuettpelez and Pryer 2007).

There have been several attempts to split *Elaphoglossum* into subgroups to make it more manageable taxonomically (Fée 1845; Sodiro 1893; Christ 1899; Mickel and Atehortúa 1980). The most recent and comprehensive of these (Mickel and Atehortúa 1980) recognized nine sections and 21 subsections. More recently, phylogenetic molecular analyses have shed some light on relationships within *Elaphoglossum* (Rouhan et al. 2004; Skog et al. 2004) and supported five of the nine sections originally proposed by Mickel and Atehortúa on the basis of morphology.

At the species level, the morphological similarity of *Elaphoglossum* species continues to hinder the recognition of small natural groups within the genus. As a consequence, taxonomic revision within the genus has been slow. The only monographic treatment of the

genus is that by Christ (1899), which included 142 species—all those known at the time.

Over the past 25 years there have been many regional or country-wide floristic studies, such as for Mexico (Mickel and Smith 2004), Mesoamerica (Mickel 1995a), Venezuela (Mickel 1995b), Peru (Mickel 1991), the Mascarene Islands (Lorence and Rouhan 2004), and French Polynesia (Rouhan et al. 2008). Yet no monographic treatments either of the entire genus or of natural small groups within it were published until 2009 (Vasco et al. 2009a).

The present monograph resulted from an effort to use chloroplast-DNA data to find clades of convenient size for monographic study within *Elaphoglossum* section *Lepidoglossa* H. Christ (Vasco et al. 2009b; Vasco and Moran in prep). This section was recognized on the basis of morphology by Mickel and Atehortúa (1980) and recovered in the molecular phylogenetic analyses of Rouhan et al. (2004) and Skog et al. (2004). Section *Lepidoglossa* contains species with blades covered mostly or entirely by flat scales with acicular marginal teeth (all other *Elaphoglossum* species have laminar scales with marginal teeth consisting of glandular or bulbous marginal cells or gland-tipped marginal processes), veins ending at or close to the margin but not hydathodous, and phyllopodia. The monophyly of section *Lepidoglossa* was further supported by the molecular phylogenetic analysis of Vasco and Moran (in prep). This study recovered 13 major clades within the section, some of which with suitable sizes for monography. Two of those clades were selected for monographic revision: the *Elaphoglossum ciliatum* clade (Vasco et al. 2009a), and *Elaphoglossum* subsection *Muscosa* Mickel & Atehortúa, the subject of the present paper.

Taxonomic History of *Elaphoglossum* subsection *Muscosa*

Fée (1845) was the first to present a treatment of *Elaphoglossum* (as *Acrostichum*). He knew only two species now recognized in subsection *Muscosa*: *A. muscosum* Sw. and *A. gardnerianum* Kunze. These he placed within his scaly group, *Polylepideae*. Under the name *Acrostichum*, Sodiro (1893) cited four species currently recognized in subsection *Muscosa* from Ecuador: *A. bellermannianum* Klotzsch, *A. corderoanum* Sodiro, *A. muscosum* Sw., and *A. yatesii* Sodiro. These he placed in the group *Polylepidia*, along with all species with densely scaly blades. Christ (1899) placed most of the species that are here recognized as part of the subsection *Muscosa* in his ordo *Stenoneura* (plants lacking hydathodes), sectio *Lepidoglossa*, subsectio *Polylepidea*, divisio *Muscosa* and *Bellermanniana*. In his divisio *Muscosa* he included *E. muscosum* (Sw.) T. Moore, *E. cuspidatum* (Willd.) T. Moore, *E. lepidotum* (Willd.) J. Sm., and *E. tomentosum* (Bory) T. Moore (the three last species do not belong to subsection *Muscosa* as recognized here, but were included in the divisio by Christ because of their short-ciliate blade scales). The bulk of the species that are here recognized as part of subsection *Muscosa*, were placed by Christ within his divisio *Bellermanniana*: *E. bellermannianum* (Klotzsch) T. Moore, *E. corderoanum* (Sodiro) H. Christ, *E. engelii* (H. Karst.) H. Christ, *E. lehmannianum* H. Christ, and *E. yatesii* (Sodiro) H. Christ. Christ (1899) placed *E. gardnerianum* (Kunze ex Fée) T. Moore within the ordo *Condyloneura* (species with hydathodes), sectio *Gymnoglossa*, subsectio *Pilosa*, divisio *Gardneriana*. This placement seems strange and was probably due to the fact that Christ did not see the type of this species (although he cites some collections from Brazil that correspond to *E. gardnerianum*). Mickel and Atehortúa (1980) recognized and formally described subsection *Muscosa*, including within it nine species: *E. aschersonii* Hieron, *E. bellermannianum*, *E.*

blandum Rosenst., *E. corderoanum*, *E. decipiens* Hieron, *E. engelii*, *E. lehmannianum*, *E. muscosum*, and *E. plicatum* (Cav.) C. Chr. (this last species does not belong to subsection *Muscosa* as circumscribed by this study). They stated that some of Christ's groups, including division *Gardneriana*, were of unknown relationships with their subsections. This was again probably because they did not have access to the type of this last species and were following Christ's opinion.

4.3. METHODS

This study is based on an examination of over 2,400 herbarium sheets which represent approximately 1,200 individual collections borrowed from 35 herbaria (see Acknowledgments). For most of the specimens, geographic coordinates were estimated using geographical gazetteers because this information was often not provided on the labels. These coordinates were used to make dot distribution maps for the species and are given in brackets for the herbarium specimens cited below. Illustrations and spore microphotographs were prepared from herbarium specimens for all species. Fieldwork was carried out in Colombia, Venezuela, and Costa Rica.

Available at the "*Elaphoglossum* Pages" at <http://sweetgum.nybg.org/elaphoglossum/index.php> are the descriptions and comments for the species included in this monograph. Also given is information on all specimens examined, photographs of all the types and of selected specimens, copies of all protologues, and additional spore microphotographs.

4.4. RESULTS

Fifteen species are here recognized (Appendix 1), of which three are new (*E. novogranatense*, *E. oreophilum*, and *E. quisqueyanum*), and one is a new name and status (*E. glabrescens*). Additionally 12 lectotypes are designated. No infraspecific taxa are recognized. The 15 recognized species are provided with a key, described, discussed, and illustrated below. A synopsis of their distributions is given in Table 1. A list of collectors and their numbers for all examined specimens is given in Appendix 2.

Morphology

Elaphoglossum subsection *Muscosa* comprises small to medium-size ferns ([6–]10–55[–63] cm long), which are often covered by different types of scales. Species of the group are distinguished by a tendency to have obtuse leaf apices (never long-acuminate as in nearly all other species of section *Lepidoglossa*) and papillate spores about twice as long (more than 70 µm) as other species of *Elaphoglossum* (Figs. 1 and 2). The only exception is *E. engellii*, which has irregular deposits instead of papillate spores (Fig. 1D). Other morphological characters that distinguish subsection *Muscosa* but that also occur either in its sister group *Elaphoglossum* subsection *Petiolosa* (Vasco and Moran in prep) or in other species of section *Lepidoglossa* are broad, flat (i.e. not subulate) scales on the rhizomes and leaves, and green spores. Most species of the subsection vary greatly in size and scale density. Given this, the more consistent characteristics of morphology of scales and spores are emphasized in the keys and comparative discussions herein.

Scales in subsection *Muscosa* are important for distinguishing species. Normally the scales differ on the rhizomes, petioles, abaxial and adaxial laminae, lamina costae, and fertile laminae, but there is a continuum from scales on the rhizomes to petioles to blades. Thus the

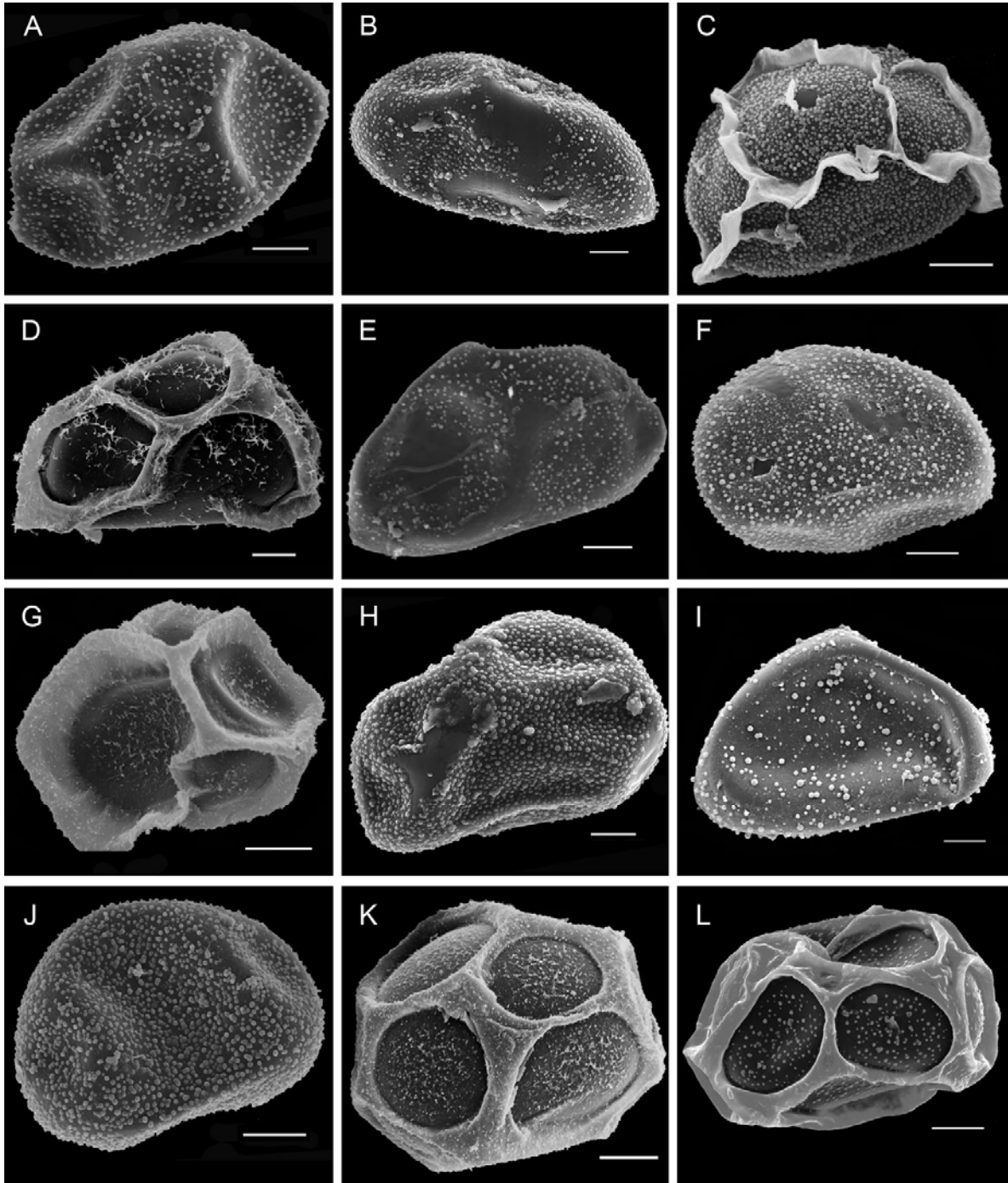


FIG. 1. Spores of *Elaphoglossum* subsect. *Muscosa*. **A.** *E. aschersonii* (Moran 7645, NY). **B.** *E. bellermannianum* (Meier 302, NY). **C.** *E. corderoanum* (Holm-Nielsen 3260, AAU). **D.** *E. engelii* (Sánchez 465, US). **E.** *E. gardnerianum* (Wacket 186, UC). **F.** *E. glabrescens* (Buchtien 2725, US). **G.** *E. laxisquma* (Vásquez 28162, NY). **H.** *E. lehmannianum* (Ruíz-Terán 976, NY). **I.** *E. muscosum* (Underwood 3212, NY). **J.** *E. novogranatense* (Vasco 746, NY). **K.** *E. oculatum* (Hutchinson 1629, UC). **L.** *E. oreophilum* (Holm-Nielsen 19071, AAU)

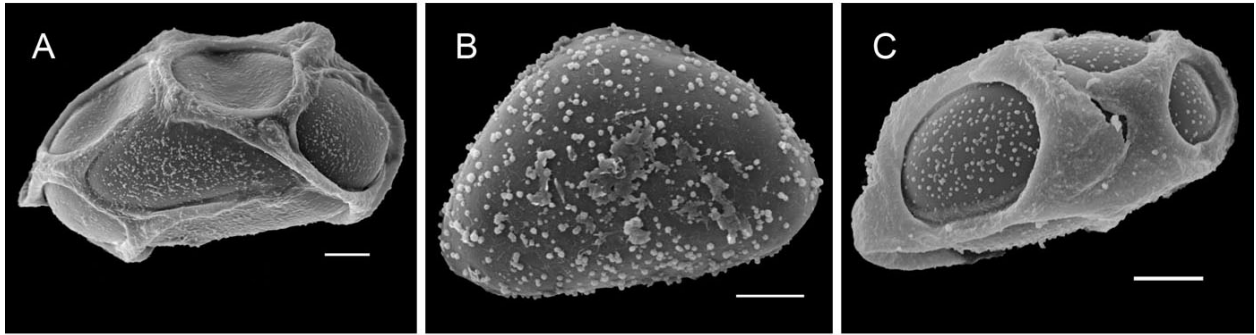


FIG. 2. Spores of *Elaphoglossum* subsect. *Muscosa*. **A.** *E. quisqueyanum* (Zanoni 20917, NY). **B.** *E. ruficomum* (Sagástegui 12091, NY). **C.** *E. yatesii* (Navarrete 1402, NY).

best place to look for the scales is in the middle of each structure. In the key, descriptions, and discussions, the petiole scales are divided into two categories: large and small. This division is artificial and was made only for the purpose of describing the two extremes of scale morphology in the petiole, which are generally different. Nevertheless, there is a continuum between these larger and smaller scales, and usually all intermediate morphologies can be found on a single plant. In the descriptions the term imbricate means that the surface of the leaf is obscured by the scales. In describing the scale margins, I followed the terminology presented by Lellinger (2002).

The perispore distinguishes species within the subsection. The presence (Fig. 1K) or absence (Fig. 1A) of perisporal ridges is easy to determine if spores are put under a light microscope, and with an experienced eye even under a good dissecting scope. The presence of irregular deposits (Fig. 1D) versus papillae (Fig. 1C) is almost impossible to distinguish without the SEM. Both spore characters are included in the key, but neither is essential to key the species. In most cases, the key can be used with specimens lacking fertile leaves. The descriptions do not repeat the characteristics that are constant for the subsection.

Geography

Elaphoglossum subsection *Muscosa* is a Neotropical group of species distributed from southern Mexico to Bolivia and southeastern Brazil, with three species in the West Indies (Fig. 3). Most species of subsection *Muscosa* occur in the Andes from Venezuela to Bolivia, from 1,500–4,000 m, primarily in cloud forests and páramos. The subsection is absent from Amazonia and the lowlands of Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela.

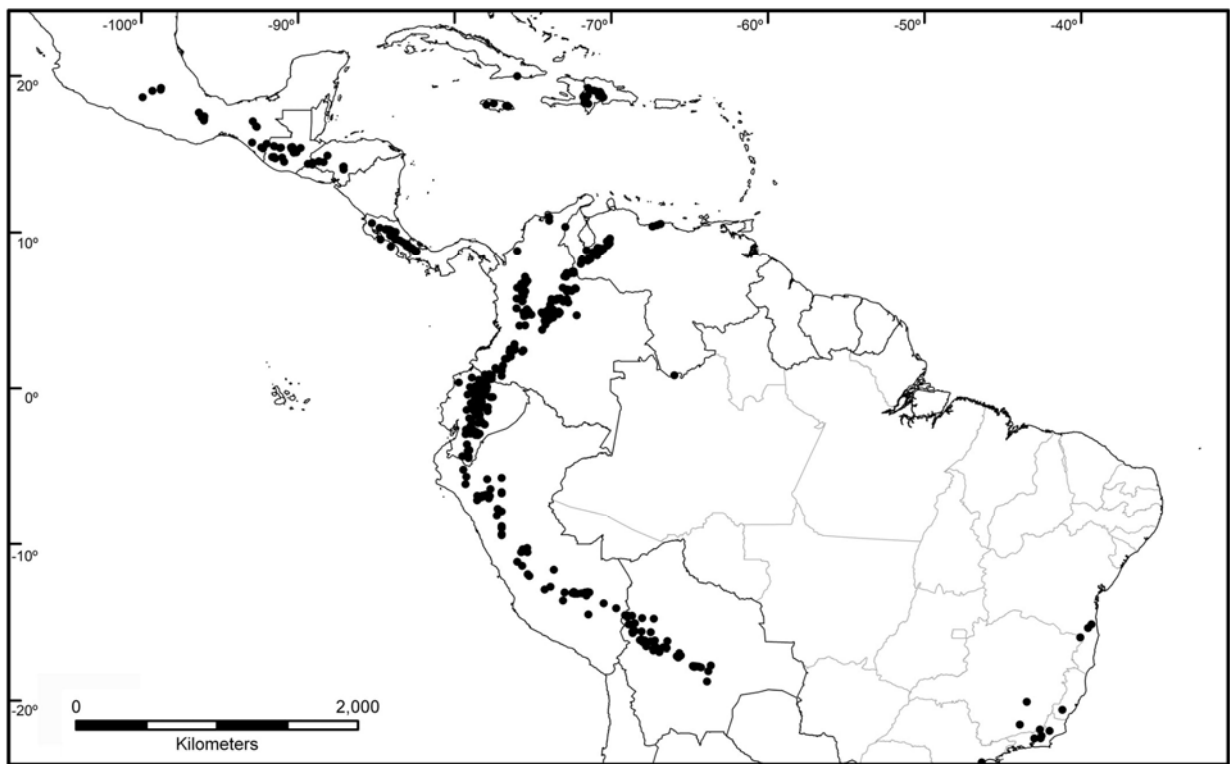


FIG. 3. General distribution of *Elaphoglossum* subsect. *Muscosa*.

4.5. TAXONOMIC TREATMENT

ELAPHOGLOSSUM SUBSECTION MUSCOSA Mickel & Atehortúa, Amer. Fern J. 70: 62.

1980. TYPE: *Acrostichum muscosum* Sw. [= *Elaphoglossum muscosum* (Sw.) T. Moore].

Plants epiphytic, terrestrial or saxicolous. *Rhizomes* short- to long-creeping, erect or compact; *rhizome scales* orange to dark brown, basally attached (sometimes appearing peltate because of the large auricles), entire to long-ciliate, the marginal teeth acicular. *Sterile leaves* (6–)10–55(–63) cm long, approximate to 2 cm apart, erect; *phyllopodia* present (sometimes obscured by the petiole bases); *petioles* scaly, the scales flat, the marginal teeth acicular; *laminae* simple, linear-lanceolate to oblanceolate, the base broadly cuneate to rounded, the apex obtuse (less frequent acute); *veins* free, simple to 2-forked; *hydathodes* absent; *laminar scales* frequently different from those of the rhizomes or the petioles, abundant to scattered, the base sessile or stalked, the marginal teeth acicular. *Fertile leaves* longer, with narrower blades, and proportionally with longer petioles than the sterile; *intersporangial scales* generally present. *Spores* (55–)70–90 µm, monolete, green, with papillae or irregular deposits.

4.6. KEY TO THE SPECIES OF *ELAPHOGLOSSUM* SUBSECTION *MUSCOSA*

1. Larger petiole scales ciliate, the teeth well differentiated from the body, often as long as or longer than the width of the scale (especially in the distal half)
 2. Petioles 1/6–1/3 the length of the sterile leaf; Brazil 5. *E. gardnerianum*
 2. Petioles 2/5–2/3 the length of the sterile leaf; Guatemala, Costa Rica, Dominican Republic, Venezuela, Colombia, Ecuador, Peru, Bolivia
3. Abaxial laminar scales present, funnellform throughout (without flattened body), patent, the base enrolled; petiole and laminar scales of the sterile and

- fertile leaves when bicolorous with dark apices (including the cilia) and lighter bases and points of attachment 7. *E. laxisquama*
3. Abaxial laminar scales present or absent, when present round, ovate, oblanceolate, or lanceolate with the body flat, slightly elevated above the surface of the lamina, the base cordate or stalked; petiole and laminar scales of the sterile and fertile leaves when bicolorous mottled or with dark centers or points of attachment, and lighter margins and cilia (those never darker than the center of the scale)
4. Abaxial laminar scales absent or present but not imbricate
5. Abaxial costal scales pointing parallel or at right angles to the costa, slightly elevated, orange to dark-brown or mottled with lighter margins or darker at the point of attachment; intersporangial scales absent ..6. *E. glabrescens*
5. Abaxial costal scales pointing parallel to the costa, not elevated, dark-brown to black, sometimes mottled with lighter margins; intersporangial scales present 10. *E. novogranatense*
4. Abaxial laminar scales present, imbricate
6. Rhizomes compact; spores without ridges 14. *E. ruficomum*
6. Rhizomes short- to long-creeping; spores with ridges
7. Rhizome scales denticulate; abaxial costal scales pointing parallel to the costa, becoming spreading towards the base, not elevated, always darker and very well differentiated from the laminar scales 12. *E. oreophilum*
7. Rhizome scales denticulate to more commonly ciliate; abaxial costal scales pointing parallel or more typically at right angles to the costa,

slightly elevated, generally the same color or slightly darker than the
laminar scales

8. Rhizome scales ciliate, cilia up to 0.4 mm long; spores with irregular
deposits; Central and South America 4. *E. engelii*

8. Rhizome scales denticulate to ciliate, cilia up to 0.6 mm long; spores
papillate; Dominican Republic 13. *E. quisqueyanum*

1. Larger petiole scales entire, denticulate, erose, or lacinate, the teeth when present
often shorter than the width of the scale (especially in the distal half)

9. Rhizome scales denticulate to ciliate, teeth numerous, 0.2–0.6 mm long
..... 13. *E. quisqueyanum*

9. Rhizome scales entire to denticulate, teeth absent to sparse, less than 0.2 mm
long

10. Rhizomes long-creeping; leaves 1–2 cm apart

11. Rhizomes 3–5 mm wide; petiole and abaxial laminar scales lacinate to
long-ciliate, with the cells of the body differentiated with the central portion
formed of irregular, isodiametric cells, and the broad border formed of
elongated cells, that have their long axis perpendicular to that of the scale (use
magnification). 12. *E. oreophilum*

11. Rhizomes 1–3 mm wide; petiole and abaxial laminar scales erose to
ciliate, with the cells isodiametric 15. *E. yatesii*

10. Rhizomes compact, erect, or short-creeping; leaves approximate to 1 cm
apart

12. Abaxial laminar scales (at least some) highly dissected, the cilia longer than the width of the scale; larger petiole scales oblanceolate to ovate; spores papillate, ridged
13. Laminar scales 0.5–2.5 mm; abaxial costal scales light-brown throughout; Ecuador 3. *E. corderoanum*
13. Laminar scales 0.2–0.5 mm; abaxial costal scales dark-brown or mottled with white margins; Peru 11. *E. oculatum*
12. Abaxial laminar scales absent or present, when present, lanceolate to round, ciliate (but never highly dissected), the cilia shorter or as long as the width of the scale; larger petiole scales linear-lanceolate to lanceolate; spores papillate, without ridges
14. Abaxial costal scales oblanceolate to round; abaxial laminar scales absent to scattered, when present never obscuring the surface of the laminae; small petiole scales not obscured by the larger ones, not imbricate; phyllopodia easily seen, not obscured by the basal petiole scales 1. *E. aschersonii*
14. Abaxial costal scales lanceolate to round; abaxial laminar scales absent to dense, when present sometimes obscuring the surface of the laminae; small petiole scales mostly obscured by the larger ones, imbricate; phyllopodia usually obscured by the petiole-base scales
15. Base of the abaxial costal scales of sterile and fertile leaves mostly sessile, thus the scale body not elevated above the surface of the lamina; rhizome scales with acuminate apices; petiole and laminar

scales usually bicolorous or mottled with white margins

.....2. *E. bellermannianum*

15. Base of abaxial costal scales of sterile and fertile leaves mostly

stalked, thus the scale body elevated above the surface of the lamina;

rhizome scales with piliform apices (these often broken); petiole and

laminar scales usually concolorous, when bicolorous only darker at the

point of attachment

16. Rhizome scales orange to dark-brown, denticulate, the teeth 0.1–0.2

mm long; Costa Rica, Panama, Venezuela, Colombia, Ecuador

.....8. *E. lehmannianum*

16. Rhizome scales reddish orange, entire or occasionally denticulate,

the teeth when present less than 0.1 mm long; Mexico, Guatemala,

Honduras, El Salvador, Cuba, Jamaica, Haiti, Dominican Republic,

Brazil 9. *E. muscosum*

1. ELAPHOGLOSSUM ASCHERSONII Hieron., Engl. Jahrb. 34. 555. 1904.—TYPE:

COLOMBIA. Cauca: auf Bäumen in parkartigen Wäldern auf dem Hochland von

Popayán, 1,600–1,800 m, s.d., *F. C. Lehmann 5074* (**lectotype, designated here**: B!;

duplicates F!, GH! US!). **Fig. 1A, 4, 5A.**

Elaphoglossum drewianum Mickel, Brittonia 39: 318, f. 3A–C. 1987.—TYPE.

VENEZUELA. Apure: A lo largo del Río Talco (Oira) y sus afluentes, en páramo entre Alto

de Cruces y Tierra Negra, Páramo de Pata de Judío, en la frontera Colombo-Venezolana, 30 km al S de San Vicente de la Revancha, 32 km al S de Alquitrana, SE del Páramo del Tamá, SW de Santa Ana, [7°23'N, 72°23'W], 3,000–3,200 m, 19 Jan 1968, *J. A. Steyermark et al.*, 101131 (holotype: NY!; isotype: VEN!)

Plants epiphytic. *Rhizomes* 4–6 mm wide, compact and erect; *rhizome scales* 4–7 mm long, linear-lanceolate, orange to brown, subentire, with small teeth, the base truncate to cordate, the apex acuminate to piliform. *Sterile leaves* 15–37 cm long, approximate; *phyllopodia* present not obscured by the petiole-base scales; *petioles* 7–18 cm long, 3/7–3/5 the length of the sterile leaf; *larger petiole scales* 3–5.5 mm long, scattered to dense, spreading, lanceolate, light brown to dark brown, or mottled, always darker at the point of attachment, the margins lighter, erose, the base cordate, the apex acute; *smaller petiole scales* 0.2–1.5 mm long, dense, not imbricate, appressed, oblanceolate to round, light brown to black, or mottled, darker at the point of attachment, the margins lighter, erose to ciliate, the base cordate, the apex acute; *laminae* 8–19 × 2.3–4 cm, oblanceolate to obovate, chartaceous, glabrescent with age, the base broadly cuneate to truncate, the apex obtuse; *veins* 1–2 mm apart, at an angle of 70° with respect to the costa; *adaxial laminar scales* 1–1.5 mm long, scattered, oblanceolate to round, white to dark brown, sometimes darker along the costa, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.2–1 mm long, absent to scattered, not elevated above the surface of the lamina, oblanceolate to round, light brown to dark brown or mottled, darker at the point of attachment, the margins lighter, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.2–1.5 mm long, dense, not imbricate, appressed, oblanceolate to round, dark brown to black or mottled, sometimes with lighter

margins, erose to ciliate, the base cordate to short-stalked, the apex acute; *marginal scales* 0.5–1 mm long, dense, imbricate, not elevated above the surface of the lamina, oblanceolate to round, light brown, erose to ciliate, the base cordate to short-stalked, the apex acute.

Fertile leaves longer than the sterile; *petioles* 3/5–5/7 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 6–16 × 0.8–1.5 cm, narrowly elliptic to elliptic, coriaceous, glabrescent with age, the base broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.5–1.5 mm long, dense, imbricate, oblanceolate to round, light brown to dark brown, sometimes darker along the costa, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, imbricate, appressed, oblanceolate to round, light brown to black or mottled, sometimes with lighter margins, erose to ciliate, the base cordate, the apex acute; *intersporangial scales* 0.5–1 mm long, scattered, oblanceolate, orange, ciliate, the base cordate, the apex acute. *Spores* papillate, without ridges.

Distribution—Colombia, Venezuela, Ecuador; 1,500–3,200 m (Fig. 5A). Epiphytic in montane forests.

Comments—*Elaphoglossum aschersonii* can be distinguished from all other species in subsection *Muscosa* by its epiphytic habit, compact, erect rhizomes, petioles with the larger scales scattered to dense, oblanceolate to obovate laminae glabrous to glabrescent, and abaxial costal scales appressed, round, dark brown to black. *Elaphoglossum bellermannianum*, a similar species, can be distinguished by petioles densely scaly, laminae oblong to oblanceolate, and scales typically obscuring the surface of the lamina. The abaxial costal scales of *E. bellermannianum* can range from oblanceolate to round and are generally brown to black or mottled with a white margin.

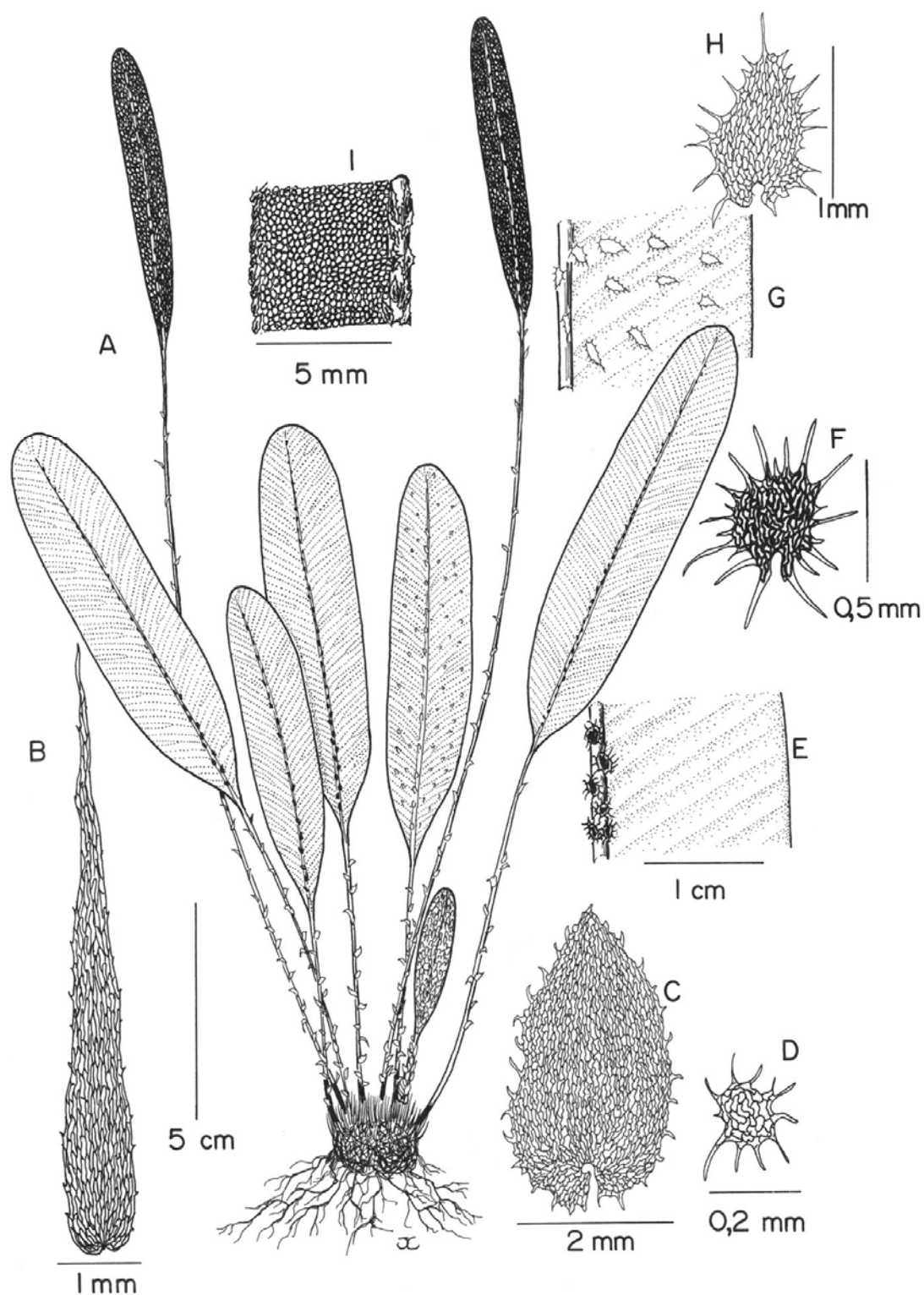


FIG. 4. *Elaphoglossum aschersonii*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial costal scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. (From *Atehortúa* 1240, HUA; A fertile frond and I from *Callejas* 6412, HUA)

Elaphoglossum aschersonii is similar to *E. novogranatense* in its epiphytic habitat, appressed dark brown abaxial costal scales, evident veins, and papillate spores; however, *E. aschersonii* differs in having compact rhizomes, easily visible phyllopodia, erose larger petiole scales, and obovate laminae. In contrast, *E. novogranatense* has short-creeping rhizomes, phyllopodia obscured by the petiole-base scales, ciliate larger petiole scales, and oblanceolate to lanceolate laminae.

Representative Specimens Examined—COLOMBIA. **Antioquia:** Mun. Urrao, carretera entre Urrao y Caicedo, sitio El Chuscal, cerca al Páramo de Frontino, paraje conocido como El 15, [6°27'N, 76°46'W], 2,900 m, 17 May 1985, *Atehortúa et al.* 1240 (HUA); An Bäumen in mäßig geschlossenen Gebirgswäldern über La Ceja und am Río de Piedras, [6°42'N, 75°45'W], 2,500 m, 20 Sep 1883, *Lehmann* 3084 (B-20 0069845, syntype of *E. aschersonii*); Mun. Betania, alrededores de la Parcela Permanente UN, 5°44'10.8"N, 76°00'11.9"W, 1,900–2,100 m, 5 Nov 2004, *Rodríguez* 4603 (HUA). **Boyacá:** Mun. Arcabuco, vereda Peñas Blancas, hacienda Las Delicias, [5°45'N, 73°26'W], 2,600 m, 11 May 1996, *Fernández-Alonso et al.* 14130 (COL, HUA); Sta. María, vereda Caño Negro, 4°51'0.9"N, 73°16'59.2"W, 1,540–1,620 m, 3 Nov 2003, *Murillo* 3372 (COL). **Caldas:** Mun. Manizales, Monteleón, Cordillera Central, 2,250 m, 8 Sep 1984, *de Fraume* 262 (HUA). **Cauca:** Bei "Los Motilones" Westgehänge des Sotará, 3,000 m, 21 Feb 1884, *Lehmann* 3676 (B-20 0069844, syntype of *E. aschersonii*); forests of Popayán, [2°26'N, 75°37'W], 1,700–2,200 m, Jun 1889, *Lehmann B.T.* 431 (NY); forests of Río Huangubio in highlands of Popayán, 1,700–2,000 m, May 1886, *Lehmann B.T.* 873 (NY, US). **Cundinamarca:** Monte Redondo, 1,700–2,000 m, 15 Jul 1953, *Idrobo* 1491 (COL, NY, US); Ubala B. vereda Campo Hermoso, escuela de Campo Hermoso, 4°45'31"N, 73°21'29"W, 1,500 m, 2 Jul 1998, *Murillo et al.* 1761, 1803 (COL). **Magdalena:** Sierra Nevada de Santa Marta, Quebrada Indiana, 10°59'N, 73°58'W, 1,600 m, 30 Aug 1972, *Kirkbride* 1990 (COL, NY); Santa Marta, top of the Sierra de Onaca, [11°11'N, 74°00'W], 1,980 m, Aug 1898–1899, *Smith* 2460 (NY). **Quindío:** Mun. Salento, carretera Salento-Cocora, [4°38'N, 75°34'W], 2,000–2,200 m, 10 Sep 1989, *Vélez et al.* 535 (COL). **Risaralda:** Mun. Pereira, Parque regional Ucumarí, vereda La Pastora, trail from El cedro to La Pastora, 4°02'N, 75°30'W, 1,900 m, 19 Feb 1990, *Croat* 70763 (COL); El Cedral, trocha a El Silento, 20 km de Pereira, 2,140 m, 15 Oct 1989, *Rangel et al.* 5837 (COL).

ECUADOR. **Morona-Santiago:** road from Limón to Azogues, 3°00'35"S, 78°30'25"W, 1,980 m, 5 Mar 2005, *Moran et al.* 7645 (NY). **Napo:** Cerro Antisana, NE Borja, [0°28'S, 78°08'W], 1,706 m, 29 Aug 1960, *Grubb et al.* 1387 (NY).

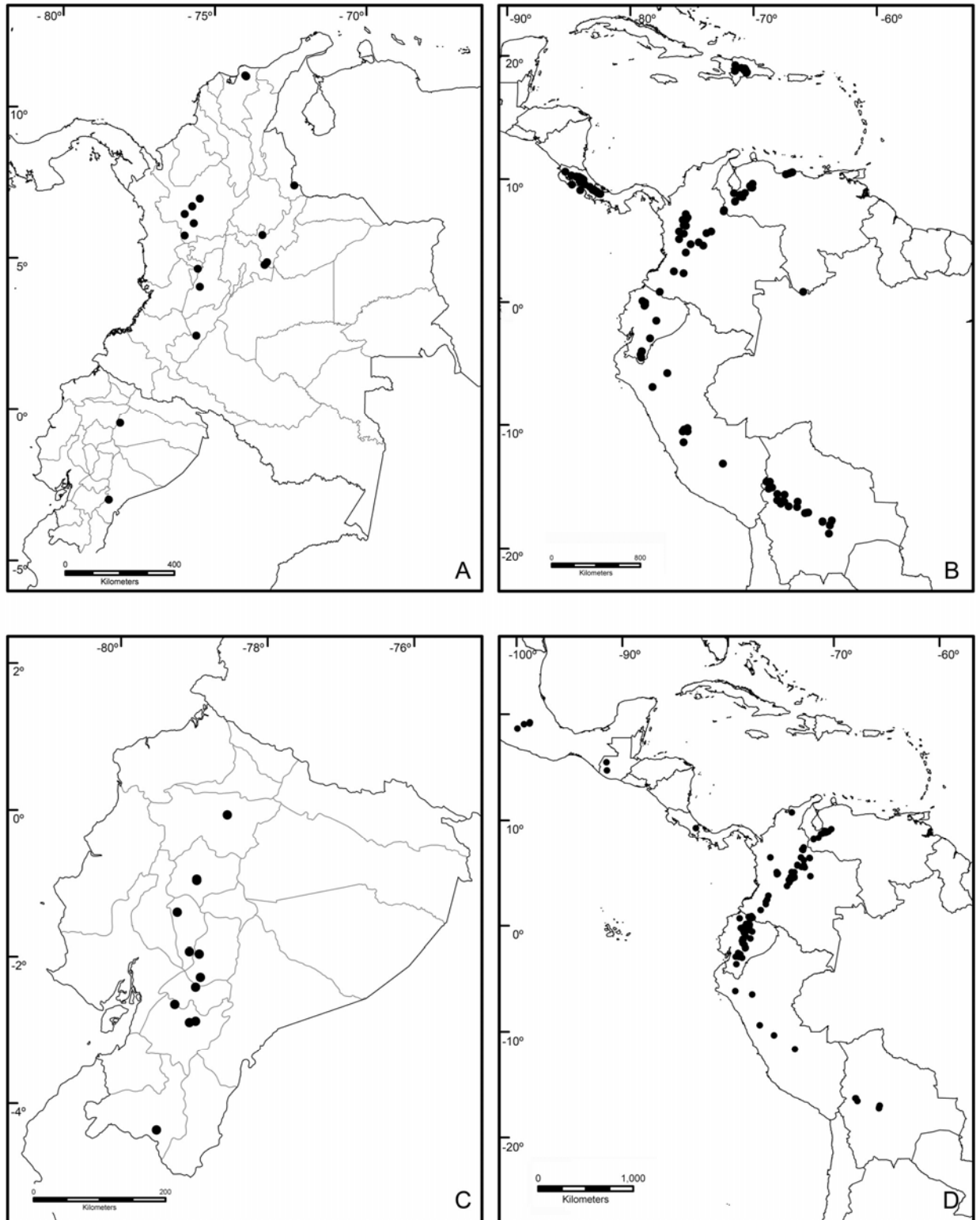


FIG. 5. Distribution of four species of *Elaphoglossum* subsect. *Muscosa*. **A.** *E. aschersonii*. **B.** *E. bellermannianum*. **C.** *E. corderoanum*. **D.** *E. engelii*.

2. ELAPHOGLOSSUM BELLERMANNIANUM (Klotzsch) T. Moore, Index fil. 7. 1857.

Acrostichum bellermannianum Klotzsch, Linnaea 20: 426. 1847.—TYPE: VENEZUELA.

Aragua: Colonia Tovar, [10°23'N, 67°21'W], s.d., *J. W. K. Moritz* 259 (**lectotype, designated here**: US!; duplicates HBG, LE; photo P! ex HBG). **Fig. 1B, 5B, 6.**

Elaphoglossum blandum Rosenst., Repert. Spec. Nov. Regni Veg. 12: 476. 1913.—

TYPE: BOLIVIA. North Yungas: Polo Polo bei Coroico, [16°24'S, 67°47'W], 1,100 m, Oct–Nov 1912, *O. Buchtien* 3456 (**lectotype, designated here**: S!; duplicates: B!, US!)

Elaphoglossum atropunctatum Mickel, Fieldiana, Bot., n.s. 27: 124. 1991.—TYPE:

PERU. Pasco: Prov. Oxapampa, 2–4 km N of Mallampampa, 10°32'S, 75°45'W, 2,200–2,400 m, 22 Jan 1984, *D. N. Smith & J. Canne* 5835 (holotype: MO!; photo NY! ex MO)

Elaphoglossum fuliginosum Mickel, Novon 2: 374. 1992.—TYPE: COSTA RICA. San

José: ca. 3 km NW of Cascajal near the union of the Cascajal and Bajo Maquina Rivers, [10°04'N, 83°57'W], 30 Jul 1972, *J. Taylor & C. Taylor* 11339 (holotype: NY!; isotype: US!)

Plants epiphytic. *Rhizomes* 4–6 mm wide, compact to short-creeping; *rhizome scales* 5–10 mm long, linear-lanceolate, brown, lustrous, subentire, with small teeth, the base truncate, the apex acuminate. *Sterile leaves* (6–)10–30(–40) cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* 5–16 cm long, 1/2–2/5 the length of the sterile leaf; *larger petiole scales* 2–5 mm long, scattered to dense, spreading, lanceolate, light brown to dark brown or mottled, darker at the point of attachment, the margins lighter, erose to almost entire, the base cordate, the apex acute; *smaller petiole scales* 0.3–1.5 mm long, scattered to dense, appressed, oftentimes hidden by the larger ones, oblanceolate to round, from light brown to black or mottled with lighter margins, darker at the point of attachment,

erose to ciliate, the base cordate, the apex acute; *laminae* 6–17 × 1.5–4 cm, oblong to oblanceolate, coriaceous, the base broadly cuneate to truncate, the apex obtuse; *veins* ca. 1 mm apart, at an angle of 75° with respect to the costa; *adaxial laminar scales* 0.5–2 mm long, scattered, lanceolate to round, white, occasionally getting dark at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–2 mm long, scattered, slightly elevated above the surface of the lamina, lanceolate to round, brown to black or mottled with lighter margins, ciliate, the base cordate, the apex acute; *abaxial costal scales* same as the laminar ones, mostly sessile, thus the scale body not elevated, pointing parallel or at right angles to the costa; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* 3/4 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* (2.5–)5–13 × 1.1–2 cm, narrowly elliptic to elliptic, coriaceous, the base broadly cuneate, the apex acute to obtuse; *adaxial laminar scales* 0.5–1.5 mm long, dense, lanceolate to round, white to light brown, darker at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.3–1 mm long, scattered, not elevated, lanceolate to round, brown to black, ciliate, the base stalked, the apex acute; *intersporangial scales* ca. 1 mm long, scattered, lanceolate, brown to black or mottled with lighter margins, ciliate, the base stalked, the apex acute. *Spores* papillate, without ridges.

Distribution—Costa Rica, Panama, Dominican Republic, Venezuela, Colombia, Ecuador, Peru, Bolivia; 1,000–3,000 m (Fig. 5B). Epiphytic in montane forests.

Comments—*Elaphoglossum bellermannianum* can be distinguished by its oblong laminae, bicolorous scales on the petioles and laminae (at least along the costae), fertile leaves twice as long as the sterile, and papillate spores. It differs from *E. muscosum* and *E.*

lehmannianum by the bicolorous petiole and/or lamina scales. These scales are bicolorous because they can be darker at the point of attachment, or mottled, or black medially with white borders. In contrast, the scales of *E. muscosum* and *E. lehmannianum* are typically concolorous, or if bicolorous they are darker only at the point of attachment. Another difference is that the costal scales of the sterile and fertile leaves of *E. bellermannianum* are mostly sessile, thus the scale body is not elevated above the surface of the lamina; whereas scales of *E. muscosum* and *E. lehmannianum* have bases typically short-stalked and thus the scale body is elevated above the surface of the lamina. The three species are epiphytes with compact to short-creeping rhizomes, linear rhizome scales with few short teeth up to 0.2 mm, erose petiole scales, and papillate spores without ridges (Fig. 1B, H, I). These characteristics distinguish them from *E. engelii*, which differs by being terrestrial with short- to long-creeping rhizomes and by having linear rhizome scales with many teeth longer than 0.2 mm, ciliate petiole scales, and spores with ridges and irregular deposits (Fig. 1D).

There is considerable variation in the color of the laminar scales of *Elaphoglossum bellermannianum*. Some plants have all the scales of the abaxial lamina either completely black or mottled; these were described as either *E. atropunctatum* (from Peru) or *E. fuliginosum* (from Costa Rica). Other plants have almost all adaxial laminar scales white and have been named *E. blandum* (type from Bolivia). Throughout the geographic distribution of *E. bellermannianum*, however, scale color varies from white to black. Because no other differences distinguish these plants, they are treated here as a single species, *E. bellermannianum*.

See *Elaphoglossum gardnerianum* for a comparison with that species

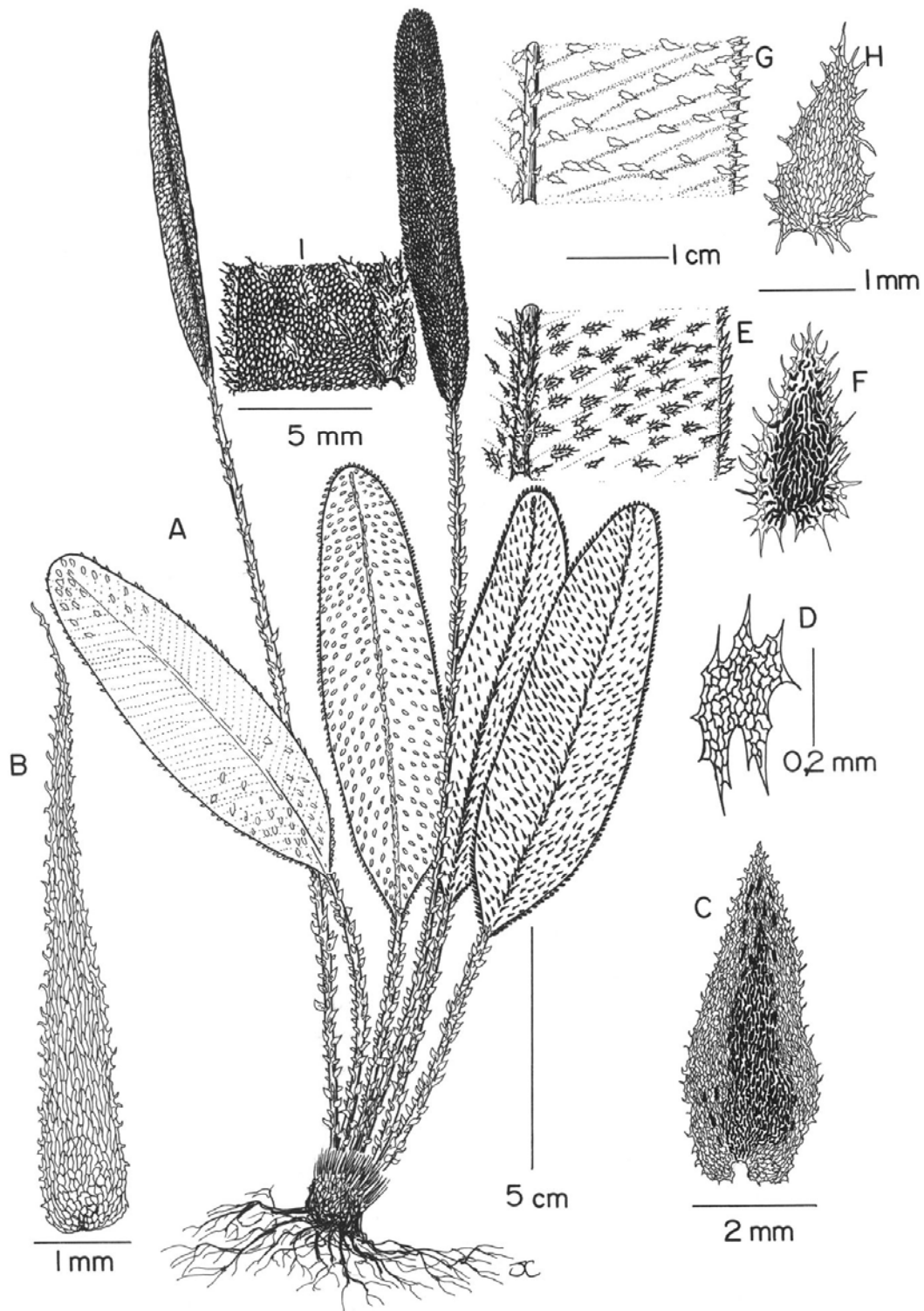


FIG. 6. *Elaphoglossum bellermannianum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. (From Rodriguez 6323, HUA).

Representative Specimens Examined—COSTA RICA. **Alajuela:** region of Zarcero, Palmira, [10°12'42"N, 84°22'51"W], 1,830 m, 13 Jan 1938, *Smith H98* (F); above Lechería on Volcán Poás, [10°11'N, 84°13'W], 2,290 m, 30 Jul 1932, *Stork 3371* (UC, US). **Cartago:** Irazú West, [9°58'48"N, 83°50'60"W], 2,000 m, 8 Sep 1908, *Brade 184* (NY, UC); vic. of Coliblanco, [9°57'N, 83°48'W], 1,950 m, 30 Apr–2 May 1906, *Maxon 281* (NY, US). **Guanacaste:** entrance to Finca Montecristo, off. rt. 113, 1,800 m, 28 Jul 1983, *Moran 3309* (CR, F, MO, NY); Cantón de Heredia, Cordillera Central, Vara Blanca, detrás del Rest. Vara Blanca, 10°09'35"N, 84°09'25"W, 1,900 m, 15 Sep 1994, *Rojas 1483* (CR, INB, MO); Cerro Chompipe, 9°5.198'N, 84°4.265'W, 2,103 m, 5 Feb 2008, *Sundue et al. 1788* (HUA, INB, NY). **Limón:** Cordillera de Talamanca, Atlantic slope, valle del Silencio along the Río Terbi, 0.5–1.5 airline km W of the Costa Rican-Panamanian border, 9°08'N, 82°57'W, 9 Sep 1984, *Davidse et al. 28772* (MO). **Puntarenas:** Cantón de Buenos Aires, cuenca Térraba-Sierpe, estación Tres Colinas, 9°07'44"N, 83°03'58"W, 1,940 m, 9 Sep 1996, *Alfaro 708* (INB, MO); Cantón de Coto Brus, Z.P. Las Tablas, cuenca Terraba-Sierpe, orillas de la quebrada Surú, 8°58'30"N, 82°46'15"W, 1,960 m, 11 Feb 1999, *Rojas et al. 4899* (CR, INB, NY). **San José:** Cantón Perez Zeledón, Savegre lodge, 9°33.2'S, 83°48.28'W, 2,212 m, 26 Jun 2006, *Moran 7756* (HUA, NY); Cantón de Desamparados, Cordillera de Talamanca, El Empalme, 9°43'20"N, 83°57'20"W, 2 Oct 1994, *Rojas 1551* (CR, INB, UC).

PANAMA. **Chiriquí:** Guadalupe, Cerro Punta, finca Santamaría No. 2, [8°51'N, 82°34'W], 2,000 m, 11 Sep 1982, *Caballero 214* (MO, US); vic. of Casita Alta, Volcán de Chiriquí, [8°48'N, 82°32'W], 28 Jun–2 Jul 1938, *Woodson et al. 823* (MO, NY, US).

DOMINICAN REPUBLIC. **Ázua:** Loma Nalga de Maco, [19°14'N, 71°29'W], 1,800 m, 9 Jun 1926, *Ekman 6301* (US); Cordillera Central, Valle del Yaque, 1,550 m, 5 Oct 1929, *Ekman 13682* (S). **La Vega:** ca. 17 km S of Constanza, vía El Convento, on road to San José de Ocoa, at Arroyo La Siberia, 18°50'N, 70°42'W, 1,600 m, 24 Jul 1980, *Mejía 7604* (MO, NY); 4.7 km S de la calle principal de Constanza y 8 km W en el camino al Pinar Parejo, 18°50'N, 70°45'W, 1,800 m, 27 Apr 1982, *Zanoni et al. 20175* (JBSD). **Peravia:** 15 km N desde el parque central y a 8–10 km desde el cruce de Los Arroyos en el camino a Carmona, zona rural denominada El Caliche o Carrao, 18°40'N, 70°32'W, 21 Jul 1982, *Zanoni et al. 21827* (JBSD); Loma Los Palos Mojados, NNW de El Bejucal, en la cabecera del Río El Canal, 18°37.5'N, 70°35'W, 1,700 m, 4 Aug 1982, *Zanoni et al. 22314* (JBSD, NY). **San Juan:** along Bao river, upper Bao valley, headwaters of Bao river, [19°01'N, 70°59'W], 1,700 m, 1–7 Oct 1968, *Liogier 12878* (NY).

COLOMBIA. **Antioquia:** Mun. Sta. Rosa, Llanos de Cuiba, 6°50'18"N, 75°29'38"W, 2,800 m, 30 Abr 2004, *Vasco 506* (HUA, MO, NY); vereda Los Patos, camino hacia el Páramo de Santa Ines, 6°37'07.8"N, 75°40'43.8"W, 2,590 m, 30 Jul 2005, *Vasco 561* (HUA, MO, NY). **Boyacá:** bosques de Arcabuco, [5°45'N, 73°26'W], 2,700 m, 7 Feb 1959, *Bischler 1887* (COL); Chiquinquirá, bosque detrás del Cuartel, [5°37'N, 73°49'W], 2,675 m, 12 Oct 1967, *Jaramillo-Mejía et al. 3474* (COL). **Caldas:** Mun. Manizales, Monte León, Cordillera Central, 2,250 m, 24 Mar 1984, *de Fraume et al. 105* (HUA). **Cauca:** 5 km E of Timbío, [2°21'N, 75°41'W], 2,050 m, 29 Dec 1944, *Grant 10663* (US); Mun. Totoró, vereda San Antonio, bosque en inmediaciones de las torres 265 y 266, costado NE de la vía que conduce de Popayán a Inza, 2°30'20.7"N, 76°28'08.7"W, 2,450 m, 16 Nov 1998, *Rivera-Díaz et al. 709pp* (COL). **Cundinamarca:** carretera Guasca a Gachetá, Km 60–61, 2,720 m, 22 Jan 1974, *Acosta-Arteaga 103* (COL); Albán, vereda Las Marías, Fundación Granjas Infantiles del Padre Luna, [4°52'N, 74°27'W], 1,900 m, 11 Nov 2001, *Triana 107* (COL). **Nariño:** entre

La Victoria, inspección de policía Mun. Apiales, y el Páramo El Consuelo, [0°50'N, 77°37'W], 2,900 m, 12 Jan 1973, *Hagemann 1928* (COL, PSO). **Risaralda**: Mun. Pereira, Parque regional Ucumari, vereda La Pastora, trail from El cedro to La Pastora, 4°02'N, 75°30'W, 1,900 m, 19 Feb 1990, *Croat 70777* (COL); Mun. Santuario, PNN Tatamá, camino que lleva al Páramo de Tatamá, subiendo hacia Morro Zancudo, 5°07'28.1"N, 76°02'30.6"W, 2,643 m, 17 Apr 2007, *Vasco et al. 734* (NY). **Tolima**: Mun. Sta. Isabel, vereda de La Yuca, cerca de Las Bodegas, Finca Buenavista, Alto La Esperanza, [4°43'N, 75°06'W], 2,700 m, 31 Jul 1980, *Idrobo 10311* (COL).

VENEZUELA. **Amazonas**: Dpto. Río Negro, Cerro de la Neblina, Camp II 2.5–3.5 km NE Pico Phelps (Neblina), 0°50'N, 65°58'28"W, 16 Feb 1984, *Funk 6313* (VEN). **Aragua**: prope Colonia Tovar, [10°23'N, 67°22'W], 1854–1855, *Fendler 270* (MO, NY, US); carretera Los Anaucos/Costa de Maya-Colonia Tovar. Monumento Natural Pico Codazzi, 10°23'18.1"N, 67°21'57.9"W, 2,127 m, 9 Jun 2008, *Vasco et al. 844* (NY, VEN). **Barinas**: Dist. Bolivar, along road from Altamira to Santo Domingo, near Feldspar mine, 8°51'N, 71°35'W, 1,700 m, 4 Aug 1983, *van der Werff 5847* (VEN); Quebrada de Barinitas, 1,100 m, 28 Jul 1960, *Vareschi 7427* (VEN). **Distrito Federal**: Cordillera de la Costa, fila del Avila, lado S, directamente debajo de la estación meteorológica, entre la estación del teleférico y el Hotel Humboldt, 10°32.6'N, 66°52.6'W, 2,100 m, 19 Aug 1991, *Meier 302* (NY, VEN); cloud forest 8 km W of junction of Colonia Tovar-Caraya road, 2,300 m, 17 Oct 1963, *Steyermark 91697* (US, VEN); Cordillera de la Costa, Cerro El Avila, bosques cerca a la carretera que desde Galipán conduce al teleférico, 10°32'29.2"N, 66°52'55.6"W, 2,078 m, 8 Jun 2008, *Vasco et al. 839* (NY, VEN). **Lara**: Mun. Morán, vía al Páramo Las Rosas en las inmediaciones de la pica, 9°37'N, 70°05'W, 2,400 m, 5 Dec 1984, *Rivero 775* (NY). **Mérida**: Mun. Rangel, along road near Santo Domingo, 8°52'N, 70°42'W, 7 Aug 1989, *van der Werff 6005* (MO, VEN); Parque Nacional La Culata, en el camino hacia el Cerro Pan de Azúcar, 8°41'52.4"N, 71°05'42.5"W, 2,400 m, 26 May 2008, *Vasco et al. 799* (NY, VEN). **Portuguesa**: Mun. Sucre, en La Divisoria de La Concepción, 9°18'N, 70°06'W, 23–26 Oct 1985, *Ortega et al. 2782* (NY). **Táchira**: faldas debajo del Páramo de Tamá, cerca de la frontera Colombo-Venezolana, arriba de Betania y Tamá, cerca de la quebrada Buena Vista, [7°24'N, 72°25'W], 22–24 May 1967, *Steyermark et al. 98662* (VEN); Quebrada La Lejia, S of Quebrada Agua Azul, along and above stream on steep slopes, 15–16 km SE of Delicias, 7°30'N, 72°24'W, 2,300 m, 25 Jul 1975, *Steyermark 118596* (MO, VEN). **Trujillo**: carretera Boconó-Trujillo, entrada a Burbusay, 9°26'N, 70°17'W, 1,600 m, 23 Nov 1984, *Ortega 2290* (MO, NY, UC); Parque Nacional Guaramacal, vertiente N, 9°18.4'N, 70°12.7'W, 2,200 m, 30 Apr 1998, *Stergios et al. 17298* (NY).

ECUADOR. **Pichincha**: ca. 2 km NW of Mindo, Hacienda San Vicente, ca. 2 km from Finca buildings, [0°02'S, 78°48'W], 10–14 Feb 1985, *Foster 85-93* (UC); old road Chiriboga to Sto. Domingo, 14 km from recinto de Las Palmeras, 0°18'S, 78°51'W, 800 m, 13 Feb 2004, *Moran et al. 6843* (NY). **Loja**: trails ca. 5 km ENE of San Pedro de Vilcabamba, from El Bosque to Quebrada Romerillos and Banderilla, 4°14'S, 79°10'W, 30 Nov 1994, *Øllgaard 105943* (AAU); Nudo de Sabanillo along road Yangana-Valladolid, [4°27'S, 79°08'W], 3 May 1987, *van der Werff 9277* (MO). **Morona-Santiago**: small ravine ca. 7 km N of Limón, disturbed forest, 2°54'42"S, 78°24'03"W, 960 m, 3 Mar 2005, *Moran et al. 7604* (NY). **Napo**: Cantón Quijos, Baeza, along road leading to radio tower behind town, 1°28'18"S, 77°53'51"W, 2,016 m, 24 Feb 2005, *Moran et al. 7525* (HUA, NY). **Zamora-Chinchipe**: road Loja-Zamora, Km 24–25, 3°59'S, 79°045W, 15 Apr 1973, *Holm-Nielsen et al. 3519*

(AAU, MO, NY, UC); Reserva Tapichalaca, 4°29'S, 79°07'W, 2,600 m, 18–19 Sep 2004, *Lehnert 1302* (NY, UC). **Sucumbios**: Km 15–18, carretera Pun-Aguarico, 13 Aug 1949, *Acosta-Solís 13281* (F).

PERU. **Amazonas**: a few km from Molina Pampa, [6°52'37"S, 78°12'18"W], 14 Mar 1998, *van der Werff et al. 14960* (MO, UC). **Cusco**: Machupichu, [13°09'S, 72°29'W], Mar 1936, *Soukup 176, 177* (F). **Junín**: Prov. Chanchamayo, Chillpez ca. 26 km S of San Ramón, 10°16'S, 75°22'W, 19 Oct 1982, *Smith 2652A* (MO); Prov. Tarma, Agua Dulce, [11°25'S, 75°41'W], 1,900 m, 9 Mar 1948, *Woytkowski 35433* (UC, US). **Pasco**: Prov. Oxapampa, Pasco, 2–4 km N of Mallapampa, 10°32'S, 75°45'W, 22 Jan 1984, *Smith 5861* (MO, USM); Prov. Oxapampa, Parque Nacional Yanachaga Chemillén, sector San Alberto, 10°32'S, 75°21'W, 2,200 m, 20 Jan 2003, *Vásquez et al. 27857* (MO, USM). **San Martín**: Rioja-Pomacochas road, below Venceremos, ca. 20 km NW of Rioja near Restaurant El Amigo, 5°45'S, 77°38'W, 1,600 m, 8 Feb 1984, *Gentry 45177* (MO).

BOLIVIA. **Cochabamba**: Prov. Franz Tamayo, Piedra Blanca, 10.4 km al S de Pata, sobre el camino a Sta. Cruz del Valle Ameno, 14°37'44"S, 68°40'19"W, 1,900 m, 12 Nov 2003, *Fuentes et al. 5999* (LPB, MO, NY, UC); Prov. Saavedra, Km 18 Charazani a Apolo, 15°10'S, 68°45'W, 2,150 m, 4 Jul 1997, *Kessler et al. 10555* (LPB, NY, UC). **Santa Cruz**: Prov. Valle Grande, Loma Larga, 4 km a Masicurí, 18°47'S, 63°53'W, 1,600 m, 3 Jun 1996, *Kessler et al. 6289* (LPB, NY, UC); Prov. Florida, Samaipata, Achira, estrada para Paredones, ca. 5 km da estrada Sta. Cruz de la Sierra-Samaipata, 18°07'26"S, 63°48'18"W, 1,750 m, 7 Dec 2002, *Labiak et al. 2799* (LPB, NY).

3. ELAPHOGLOSSUM CORDEROANUM (Sodirol) H. Christ, Neue Denkschr. Allg. Schweiz. Ges.

Gesamnten Naturwiss. [Monogr. *Elaphoglossum*] 36(1):81. 1899. *Acrostichum*

corderoanum Sodirol Crypt. Vasc. Quit. 470. 1893.—TYPE: ECUADOR. Loja: El Toldo [in the protologue: Crece en las pendientes occidentales del Pichincha, Corazón y "el Altar" en la provincia de Ríobamba, 2,000 y 3,000 m], [4°22'S, 79°31'W], 1891, *L. Sodirol 202* (**lectotype designated here** P! (sheet 00577719); photos GH!, US! ex P). **Fig. 1C, 5C, 7.**

Plants epiphytic. *Rhizomes* 3–6 mm wide, compact, erect; *rhizome scales* 6–9(–14) mm long, linear-lanceolate, orange to dark brown, entire to denticulate, the base cordate, the apex acuminate. *Sterile leaves* 15–41 cm long, approximate; *phyllopodia* present, sometimes obscured by the petiole-base scales; *petioles* (5–)10–22 cm long, 1/3–1/2 the length of the

sterile leaf; *larger petiole scales* 3–6 mm long, dense, spreading, oblanceolate to ovate, light brown to orange, erose to lacinate, the base cordate, the apex acute; *smaller petiole scales* 0.5–1.5 mm long, dense, appressed, oftentimes hidden by the larger ones, oblanceolate to round, light brown to slightly mottled, ciliate, the base cordate, short-stalked, the apex acute; *laminae* 10–22 × (1.8–)2.8–5 cm, oblong to oblanceolate, coriaceous, glabrescent with age, the base broadly cuneate to obtuse, the apex obtuse to acute; *veins* free, forked, 1–2 mm apart, at an angle of 70°–75° with respect to the costa; *adaxial laminar scales* 0.5–2.5 mm long, dense, oblanceolate to ovate, white to light brown, lacinate to ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–1 mm long, dense, not imbricate, patent, lanceolate to round, highly dissected, orange, long-ciliate, the base stalked, the apex piliform; *abaxial costal scales* 1–2 mm long, dense, pointing at right angles to the costa, not elevated, oblanceolate to round, light brown, ciliate, the base cordate, the apex acute; *marginal scales* 1–2 mm long, dense, oblanceolate, light brown, ciliate, the base cordate, short-stalked, the apex acute. *Fertile leaves* longer than the sterile; *petioles* 2/3 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 10–25 × 1.2–2.4 cm, narrowly-elliptic to linear-lanceolate, coriaceous, glabrescent with age, the base broadly cuneate to obtuse, the apex obtuse; *adaxial laminar scales* 0.5–2.5 mm long, dense, imbricate, oblanceolate to round, white to orange, lacinate to ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, oblanceolate to round, light brown to dark brown with lighter margins, lacinate to ciliate, the base cordate, the apex acute; *intersporangial scales* 0.7–1.5(–4) mm long, dense, not obscuring the sporangia, oblanceolate to round, orange to dark brown, sometimes mottled towards the apex, ciliate, the base cordate, the apex acute. *Spores* papillate, with ridges.

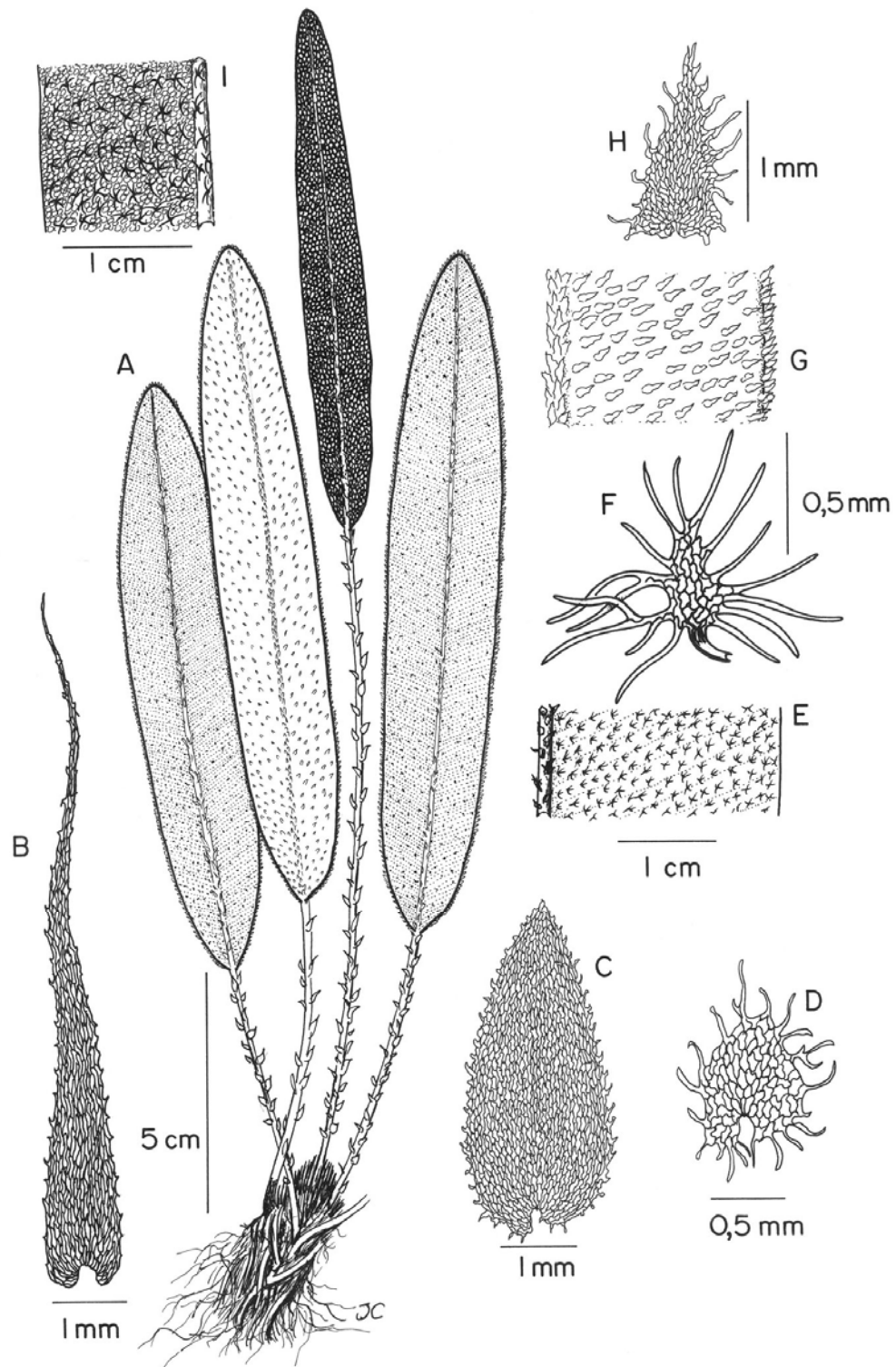


FIG. 7. *Elaphoglossum corderoanum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial laminar surface. H. Adaxial laminar scale. I. Fertile lamina. (From Holm-Nielsen 3256, NY).

Distribution—Ecuador; (600–)2,100–3,400 m (Fig. 5C). Epiphytic in montane forest and páramos.

Comments—*Elaphoglossum corderonum* can be distinguished by its larger petiole scales oblanceolate to ovate, erose to lacinate, abaxial laminar scales lanceolate to (more commonly) round, highly dissected, long-ciliate, and ridged, papillate spores. The abaxial laminar scales, although dense, do not obscure the surface of the lamina.

Some specimens collected by Sodiro and annotated by him as *E. corderoanum* correspond to *E. lehmannianum*; therefore, it might be that the original material is mixed. Sodiro designated all the specimens with large leaves and somewhat glabrous abaxial laminae as *E. corderoanum*. Examination of more material revealed that species with large leaves belong either to *E. corderoanum* or *E. lehmannianum*. To assign the lectotype I took into account the original description in which Sodiro stated that besides the larger leaves, the difference between *E. corderoanum*, *E. bellerannianum*, and *E. lehmannianum* (in the original description as *Acrostichum bellerannianum* and *A. muscosum*) is that the abaxial laminar scales of the sterile leaves and the adaxial laminar scales of the fertile leaves of *E. corderoanum*, were “round similar to stellate hairs”. Round, highly dissected, long-ciliate laminar scales (similar to stellate hairs) distinguish *E. corderoanum* from *E.*

bellerannianum and *E. lehmannianum*. Another characteristic that distinguishes these species is that *E. corderoanum* has spores with ridges and papillae (Fig. 1C), whereas *E. bellerannianum* and *E. lehmannianum* have papillate spores without ridges (Fig. 1B, H).

Because of its ridged spores and occurrence at high elevations, *E. corderoanum* can be confused with *E. engelii*. These two species are easy to distinguish by their habit, and scales of the rhizomes and laminae. Typically, *E. corderoanum* is epiphytic, has rhizome scales that

are entire to denticulate, and abaxial laminar scales round, highly dissected, long-ciliate, and spaced far enough apart that they do not obscure the lamina surface. In contrast, *E. engelii* is usually terrestrial, has rhizome scales that bear numerous cilia, and abaxial laminar scales lanceolate to oblanceolate and obscuring the lamina surface.

See *E. oculatum* comments for a comparison with that species.

Representative Specimens Examined—ECUADOR. **Azuay**: Cruz Pampa region above Baños, ca. 15 km SW of Cuenca, [2°54'S, 79°04'W], 2,750–3,050 m, 29–30 Jun 1945, *Camp* 3935 (F, MO, NY, US, VEN); Westgehang der West-Andes von Cuenca, [2°53'S, 78°59'W], 2,500–3,000 m, s.d., *Lehmann* 5703 (B, F, US). **Bolivar**: along first 15 km of road Chillanes-El Tambo, [1°56'S, 79°04'W], 2,400 m, 18 Jul 1991, *van der Werff et al.* 12448 (MO, UC). **Cañar**: N of Tipococha, [2°25'S, 78°59'W], 3,200 m, 18 Aug 1933, *Diels* 629 (B). **Chimborazo**: Pallatanga, comunidad Jesús del Gran Poder, from Panza Redonda (S Pan American Hgw.), 2 km S on colbble dirt road, ca. 4 km NE of Pallatanga, 1°58'S, 78°56'W, 2,800–3,200 m, 10–14 Jul 1995, *Clark et al.* 1236 (MO); W slope of Azuay, close to Chunchi, [2°17'S, 78°55'W], 3,000 m, s.d., *Rimbach* 696 (S). **Cotopaxi**: Quevedo-Latacunga road above Pilaló, 0°58'S, 78°58'W, 2,850 m, 8 Apr 1973, *Holm-Nielsen et al.* 3256 (AAU, MO, NY, UC), 3260 (AAU, UC). **Los Ríos**: Centinela ridge, ca. 20 km E of Patricio Pilar, [1°24'S, 79°14'W], 600 m, 16 Jul 1991, *van der Werff et al.* 12431A (MO). **Pichincha**: carretera vieja Chillogallo-San Juan, sitio de colección San Juan-Ventanillas-Las Comunas, 23 Jun 1980, *Jaramillo* 2587 (AAU); in silvis suban. Nono-Gualea, [0°04'S, 78°33'W], Sep 1899, *Sodiño* s.n. (P).

4. ELAPHOGLOSSUM ENGELII (H. Karst.) H. Christ, Neue Denkschr. Allg. Schweiz. Ges.

Gesamnten Naturwiss. [Monogr. *Elaphoglossum*] 36(1): 81. 1899. *Acrostichum engelii* H.

Karst., Fl. Columb. 1: 118, t. 59. 1860.—TYPE: VENEZUELA [In the original description

“Colombia”]. Merida: cordillera Meridensis, s.d., *H. Karsten* s.n. (first-step lectotype,

inferentially designated by Mickel in *Fieldiana, Bot.*, n.s. 27: 131. 1991: B; **second-step**

lectotype, designated here: B! (sheet 20 0070391, [specimen glued to the sheet, excluding the fertile leaf portions in the pocket]); duplicates: W! (sheet 0018475, specimen on the left, excluding the fertile leaf on the right]), LE; photos UC!, BM! ex W). **Fig. 1D, 5D, 8**

Elaphoglossum caulolepia (H. Karst.) Hieron., Bot. Jahrb. Syst. 34: 548. 1904.

Acrostichum caulolepia H. Karst., Fl. Columb. 1: 121, t. 60. 1860.—TYPE: COLOMBIA.

Cundinamarca: Bogotá, s.d., *H. Karsten s.n.* (**lectotype, designated here:** W (sheet 0018476)!; duplicates: B, LE).

Elaphoglossum atrorubens Mickel, Brittonia 39: 314, f. 3D, E. 1987.—TYPE:

VENEZUELA. Mérida: Distrito Campo Elías, Municipio Pueblo Nuevo, Páramo de Quirorá, alto de las Cruces, [8°20'N, 71°27'W], 3,200 m, 23 Apr 1971, *L. E. Ruiz-Terán & M. López-Figueiras 1754* (holotype: NY!).

Elaphoglossum cristatum E. Ballenthien, J.-H. Dudenhöffer & M. Kessler, Brittonia

61:46-49. 2009.—TYPE: BOLIVIA. Cochabamba: Prov. José Carrasco Torrico, 63 km antigua carretera Cochabamba-Villa Tunari, 17°15'S, 65°43'W, 3,700 m, 2 Jul 1999, *M. Kessler et al. 6875* (holotype: GOET; isotypes: LPB, NY!, UC!).

Plants terrestrial. *Rhizomes* 4–8 mm wide, short to long-creeping; *rhizome scales* 6–11 mm long, linear-lanceolate, light brown to dark brown, sometimes bicolorous, the margins lighter, ciliate, with abundant cilia (up to 0.4 mm long), the base cordate, the apex piliform and tortuous to acute. *Sterile leaves* 14–47(–63) cm long, approximate to up to 1 cm apart; *phyllopodia* present, sometimes obscured by the petiole-base scales; *petioles* 6–25(–41) cm long, 2/5–3/5 the length of the sterile leaf; *larger petiole scales* 4–6 mm long, dense, spreading, sometimes pointing parallel to the petiole, linear-lanceolate to oblanceolate, light brown to dark brown, or mottled, darker at the point of attachment, the margins lighter, ciliate, the base cordate to truncate, the apex acute; *smaller petiole scales* 0.5–1(–3) mm long, scattered to dense, appressed, oftentimes hidden by the larger ones, oblanceolate to

round, from light brown to black or mottled with lighter margins, darker at the point of attachment, ciliate, the base cordate, the apex acute; *laminae* 8–23 × 1.5–4.5 cm, linear-lanceolate to oblanceolate, coriaceous, glabrescent with age, the base truncate to broadly cuneate, the apex obtuse; *veins* 0.5–1.5 mm apart, at an angle of 70°–85° with respect to the costa; *adaxial laminar scales* 1–3 mm long, dense, imbricate, oftentimes pointing downwards, lanceolate, white to light brown, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 2–3 mm long, dense, imbricate, slightly elevated above the surface of the lamina to patent, lanceolate to oblanceolate, from light brown to black or mottled with lighter margins, darker at the point of attachment, ciliate, the base stalked (up to 0.4 mm), the apex acute; *abaxial costal scales* same as the laminar ones, pointing parallel or at right angles to the costa, slightly elevated, sometimes darker; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* 1/2–3/4 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* 7–22 × 1–2 cm, narrowly elliptic, coriaceous, the base truncate to broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.5–3 mm long, dense, imbricate, lanceolate to round, from light brown to black or mottled with lighter margins, darker at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2(–3) mm long, dense, pointing parallel or at right angles to the costa, lanceolate to round, from light brown to black or mottled, darker at the point of attachment, ciliate, the base cordate, the apex acute; *intersporangial scales* 1–2 mm long, absent to scattered, lanceolate, from light brown to black or mottled with lighter margins, darker at the point of attachment, ciliate, the base cordate to short-stalked, the apex acute. *Spores* with irregular deposits and ridges.

Distribution—Mexico, Guatemala, Costa Rica, Venezuela, Colombia, Ecuador, Peru, Bolivia; 1,300–4,300 m (Fig. 5D). Mainly terrestrial growing in montane forest and páramos in exposed, rocky, dry areas.

Comments—*Elaphoglossum engelii* and *E. muscosum* are two names commonly applied to species of subsection *Muscosa* in the Andes. What has been called *E. muscosum* in the Andes is actually *E. lehmannianum* (see comments under that species for a discussion on the application of this name). The Andean species *E. lehmannianum* and *E. engelii* are often confused in herbaria, but they are easy to differentiate. *Elaphoglossum engelii* is terrestrial with short- to long-creeping rhizomes, linear rhizome scales with many teeth longer than 0.2 mm, ciliate petiole scales, and spores with ridges and irregular deposits (Fig. 1D). In contrast, *E. lehmannianum* is typically epiphytic with compact to short-creeping rhizomes, linear rhizome scales with few short teeth, erose petiole scales, and papillate spores without ridges (Fig. 1H).

In *E. engelii*, density of the laminar scales varies, and there is a slight geographic component to this variation. Typically, the scales of both surfaces of the laminae are imbricate, although the adaxial ones tend to fall off when the leaf gets older. Specimens at the southern and northern limits of the distribution (Mexico, Guatemala and Peru) sometimes have abaxial laminar scales more scattered and not necessarily obscuring the surfaces of the lamina.

Some specimens of *E. engelii* from Ecuador (e.g., *Clemants 2142*, NY) have unusually black rhizome scales. These might be confused with *E. yatesii*, a species restricted to Ecuador and Colombia. *Elaphoglossum yatesii* differs by thinner and longer creeping

rhizomes, petiole scales that generally point parallel to the petiole, and papillate spores with ridges (Fig. 2C).

The type material from B and W have some fertile-frond fragments not attached to the sterile parts. These fragments do not belong to *E. engelii* or any other species of subsection *Muscosa*.

Representative Specimens Examined—MEXICO. **México:** San Rafael, [19°14'N, 98°45'W], Jan 1938, *Lyonnet 2024* (US); cerca de Amealco, camino a Amecameca Tlmacas, vertiente NW del Popocatepetl, [18°38'N, 99°55'W], 3,100 m, 9 Oct 1966, *Rzedowski 23279* (NY). **Morelos:** Zempoala, [19°03'N, 99°18'W], Dec 1936, *Lyonnet 1413* (UC, US); Lagunas de Zempoala, [19°03'N, 99°18'W], Dec 1946, *Sánchez 465* (US).

GUATEMALA. **Huehuetenango:** Sierra Chuchumatanes between Kms 136 to 150 to San Juan Ixcay, [15°30'N, 91°30'W], 3,000–3,500 m, 12–23 Jan 1966, *Molina et al. 16539* (F, NY, US). **Quezaltenango:** NW-facing forested Abies slopes of barranco of Volcán Zunil, [14°44'N, 91°27'W], 3,000 m, 22 Jan 1940, *Steyermark 34911* (F, US).

COLOMBIA. **Antioquia:** Mun. Urrao, Inspeccion Jaiperá, vereda El Chuscal, Páramos de Frontino, Sitios Pico de Aguila-La Laguna, 6°27'N, 76°46'W, 3,590–3,750 m, 6 Apr 1989, *Callejas et al. 7672* (HUA, NY); Mun. Urrao, Páramo de Frontino, sitio Llano Grande, [6°27'N, 76°46'W], 3,380 m, 10 Sep 1986, *Roldán et al. 321* (HUA). **Arauca:** Sierra Nevada del Cocuy, Quebrada El Playón, Hoya S. Luis 1.5 km al NNE de la finca El Playón., [6°23'N, 72°16'W], 3,540 m, 13 Mar 1973, *Cleef 9122* (COL, NY). **Boyacá:** Peña de Arnical, N de Vado Hondo, [5°30'N, 72°45'W], 3,580 m, 7 Apr 1973, *Cleef 9485* (COL, NY); Mun. Chisacá-San Pedro de Iguaque, SFF de Iguaque, sendero subiendo a la laguna de Iguaque, 5°41'03.2"N, 73°26'22.3"W, 3,536 m, 30 Apr 2007, *Vasco et al. 765* (HUA, NY). **Caldas:** Mun. Manizales, vereda La Esperanza, reserva Torre Cuatro, cerca del nacimiento de la quebrada El Diamante, 5°03'52"N, 75°23'20"W, 3,650–3,750 m, 6 Aug 1999, *Alvear-P 494* (COL); PNN los Nevados, Alto del Cisne, 4°51'17.1"N, 75°22'03.5"W, 4,127 m, 7 Aug 2006, *Vasco 591* (HUA, MO, NY). **Cauca:** Páramo de Puracé, [2°15'N, 76°25'W], 3,400 m, 22 Sep 1967, *Hagemann 572* (COL, PSO); Páramo de Moras, between Mozoco and Pitayó, Tierra Adentro, [2°50'N, 76°11'W], 3,000–3,500 m, Feb 1906, *Pittier 1532* (US). **Cundinamarca:** cerca a la laguna de Chisacá, Km 31 de la carretera, [4°17'N, 74°12'W], 3,670 m, 20 Apr 1074, *Acosta-Arteaga 302* (COL, NY); Boquerón de Bogotá (cordill. Or. Nov. Granat.), 2,900 m, 26 Jan 1876, *André 1296* (NY, P); Páramo de Sumapaz, páramo y bosque altoandino cerca de Lagunitas al S de San Juan. Alto de Chorreras; 2.5 km al N de la laguna Gobernador, [3°45'N, 74°25'W], 3,780 m, 27 Jan 1937, *Cleef 8359* (COL, MO, NY). **Magdalena:** Sierra Nevada de Santa Marta, S of Cerro Icachui, Mamancanaca-Camberimena, [10°45'N, 73°58'W], 3,900 m, 30 May 1905, *Waston 10384* (CR). **Meta:** Páramo de Sumapaz, hoyo de la quebrada Sitiales, [4°05'N, 74°12'W], 3,550 m, 26 Jan 1972, *Cleef 1043* (COL); Macizo del Sumapaz, alrededores de la laguna La Guitarra, [4°05'N, 74°12'W], 3,370–3,400 m, 5 Jul 1981, *Díaz 2492* (COL).

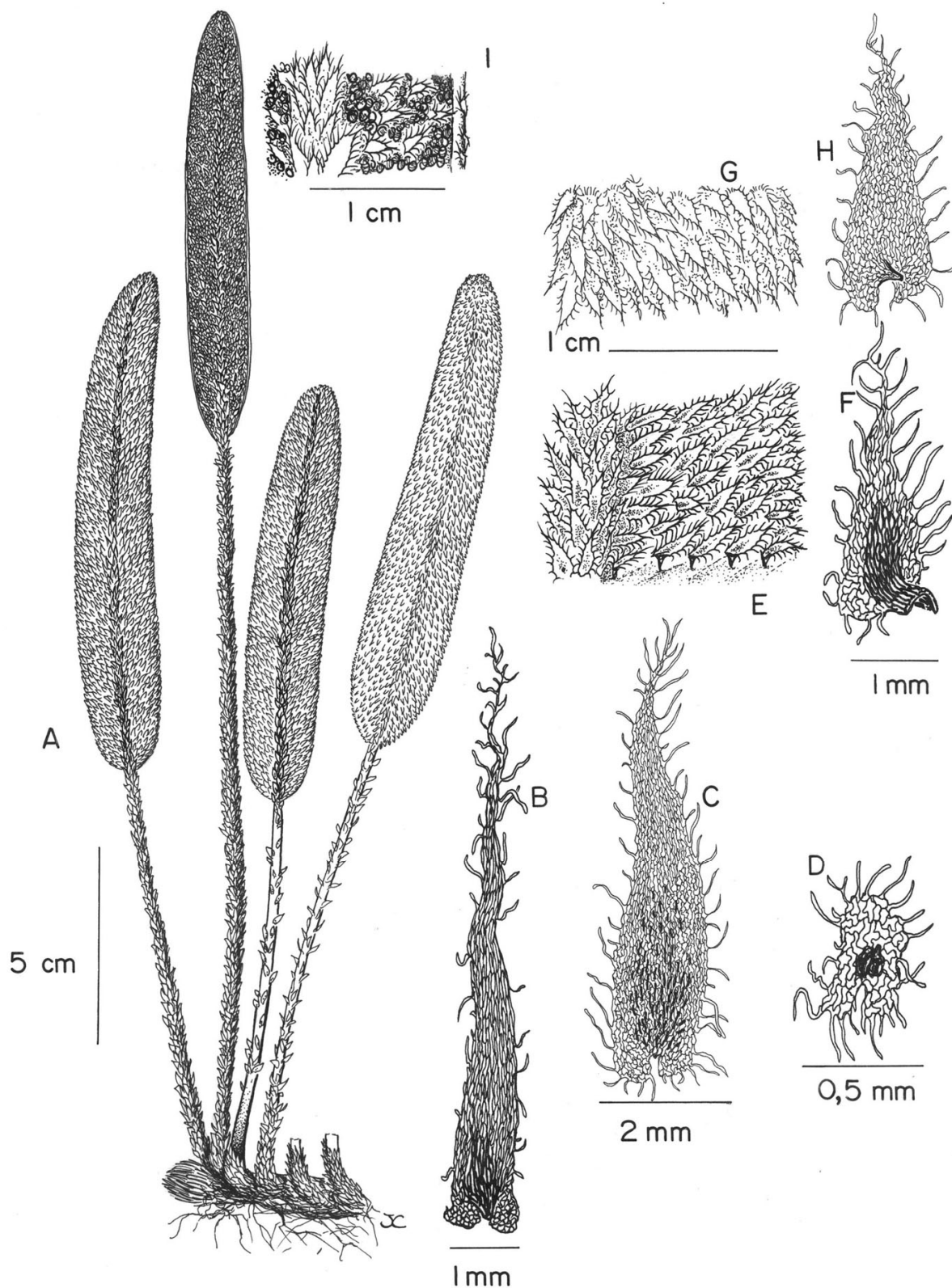


FIG. 8. *Elaphoglossum engelii*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. (From Rentería 5387 HUA).

Nariño: W slope of Volcán Doña Juana, Cerro Macha, [1°28'N, 76°55'W], 3,200 m, 16 Dec 1944, *Ewan 16605* (UC, US); Cumbal, Laguna La Bolsa, páramo, [0°54'N, 77°47'W], 3,400 m, 21 Jan 1973, *Hagemann 1956* (COL, PSO). **Norte de Santander:** Mun. Cucutilla, vereda Carrizal, Páramo El Romeral, [7°24'N, 72°51'W], 3,200–3,800 m, 1 Mar 2002, *Galván et al. 34* (COL); Páramo de Romeral, 3,800–4,200 m, 30 Jan 1927, *Killip 18672* (NY, US).

Santander: Páramo de San Turban, near Vetás, [7°12'N, 72°59'W], 3,950–4,160 m, 17 Jan 1927, *Killip 17571* (NY, US); carretera entre Bucaramanga y Pamplona, El Picacho, [6°27'N, 73°06'W], 3,400 m, 7 Nov 1969, *Murillo 1250* (COL). **Tolima:** Mun. Murillo, cerca del Nevado del Ruiz, carretera a Murillo, 4°56'N, 75°17.5'W, 3,900 m, 9 May 1991, *Churchill 17881* (COL, HUA, NY).

VENEZUELA. **Mérida:** entre Timote y Pico de Aguila, 3,000–3,500 m, 24 Nov 1984, *Ortega 2339* (MO, NY, UC); Parque Nacional La Culata, en el camino hacia el Cerro Pan de Azúcar, 8°45'21.8"N, 71°03'25.9"W, 3,169 m, 26 May 2008, *Vasco et al. 795* (NY, VEN).

Táchira: carretera Bailadores-La Grita, vía Páramo La Negra, 8°15'20"N, 71°52'46"W, 3,000 m, 29 May 2008, *Vasco et al. 808* (NY, VEN). **Trujillo:** Mun. Boconó, Laguna Larga, vía Laguna Las Parias to Laguna Eco. Páramo Motumbo, Monumento Natural Teta de Niquitao-Guirigay, [8°56'N, 70°30'W], 3,400–3,600 m, 15 Sep 2003, *Stergios et al. 20424* (NY, UC, US); cumbre del Páramo de Guaramacal, entre Boconó y Guaramacal, [9°10'N, 70°14'W], 3,000 m, 25 Feb 1971, *Steyermark 104854* (MO, VEN).

ECUADOR. **Azuay:** carretera Cuenca-Pasaje, Km 22, partidero a Patococha Hacienda Tarquí, 8 Aug 1986, *Jaramillo et al. 8962* (HUA, NY); 16 km NE of Azogues along road to Pindilíg, 2°40'S, 78°50'W, 3,340 m, 19 Jan 1985, *Luteyn 11137* (HUA, NY, UC). **Carchi:** Tulcán-El Angel road, 21 km S of Las Juntas, [0°41'N, 77°50'W], 3,350 m, 20 Nov 1980, *Balslev 875* (AAU, NY, UC); Páramo El ángel, in the pass on road El ángel-Tulcán, 0°41'N, 78°54'W, 3,450 m, 15 May 1973, *Holm-Nielsen et al. 5504* (AAU, F, MO, NY, UC).

Chimborazo: Chimborazo-Cañar border, W escarpment, near Pino, 3,100–3,200 m, 9 Jul 1945, *Camp 4146* (NY); near Riobamba, [1°40'S, 78°38'W], 3,400 m, 28 Jul 1933, *Diels 386* (B); Río Chimbo, 3,400 m, Sep 1905, *Rimbach Rosenst. Filices ecuatorianas*, No. 7 (B, P, S, US). **Cotopaxi:** Parque Nacional Cotopaxi, 3–6 km S de la Estación Ferrocarril, 0°40'S, 78°30'W, s.d., *Balslev 2655* (AAU, GH, NY); Cotopaxi National Park, ca. 14 km E along entrance road opposite Km 60 Panamerican Hwy., 0°44'S, 78°28'W, 3,540 m, 15 May 1982, *Luteyn 8398* (NY). **Imbabura:** Lago San Marcos, Cayambe, 3,413 m, 29 Nov 1961, *Cazalet 5408* (NY, UC, US); Mojanda, ca. 10 km SSW Otavalo, 0°10'N, 78°18'W, 2,900–3,150 m, 12 Dec 1966, *Sparre 13467* (S). **Loja:** Páramos de Saraguro, 10 km S of Saraguro, [3°36'S, 79°13'W], 3,050 m, 2 Jan 1979, *Luteyn et al. 6663* (NY). **Napo:** N side of Cerro Sumaco, upper part of the loma NW of camp site, 0°34'S, 77°43'W, 3,750 m, 25 Apr 1979, *Holm-Nielsen et al. 17232* (AAU, NY); Parque Nacional Llanganates, vía Salcedo-Tena, Km 45–55, cabecera del Río Anatenorio, Siete Vueltas, 0°59'S, 78°20'W, 3,600 m, 17 Sep 1998, *Vargas et al. 2586* (MO, NY, QCNE, UC). **Pichincha:** above Hacienda Monjas, Concepción, [0°28'S, 78°35'W], 3,962 m, 29 Mar 1951, *Bell 91* (S); in monte Pichincha, [0°10'S, 78°35'W], 3,400 m, 1917, *Mille s.n.* (GH, NY). **Tungurahua:** Parroquia San José de Poaló, Loma Potrerillos, 1°05'S, 78°20'W, 3,200 m, 4 Apr 1987, *Cerón 1122* (MO, UC, US); Salasaca, Telegote Sacha hillside, 1°19'S, 78°32'W, 3,000 m, 16 Mar 1983, *Franquemont 186* (F, NY).

PERU. **Amazonas:** Prov. Chachapoyas, Jalca Calla-Calla, [6°28'S, 77°43'W], 3,450 m, 29 Jul 1991, *Mostacero et al. 2634* (MO). **Ancash:** Prov. Huari, Huascarán National Park,

quebrada Pachachaca, a lateral valley of quebrada Rurichinchay, 9°23'S, 77°17'W, 3,700–3,860 m, 12 Jun 1986, *Smith et al.* 12543 (MO). **Junín**: Prov. Satipo, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 11°39'36"S, 73°40'02"W, 3,350–3,400 m, 8 Jun 1997, *Boyle et al.* 4262 (NY). **Lambayeque**: Prov. Ferreñafe, Laguna Tembladera, distrito Incahuasi, [6°09'S, 79°18'W], 3,100 m, 11 Sep 1985, *Sagástegui et al.* 12780 (GH, MO, NY, UC). **Pasco**: Prov. Oxapampa, Dist. Huancabamba, sector Santa Barbara, 10°20'55"S, 75°39'08"W, 3,379 m, 27 Jan 2005, *Mellado* 2658 (MO).

BOLIVIA. **Cochabamba**: Prov. Chapare, Corani, pasando el km 405 de la carretera Villa Tunari-Cochabamba, [17°08'S, 65°42'W], 3,350 m, 24 May 2004, *Jiménez* 2342 (LPB, NY); Prov. Carrasco, Km 84 antigua carretera Cochabamba-Villa Tunari, 17°15'S, 65°43'W, 3,750 m, 30 Jun 1996, *Kessler et al.* 6833 (LPB, NY, UC). **La Paz**: Prov. Murillo, bajando de la cumbre 16,7 km hacia Unduavi, pasando Pongo, [16°19'S, 67°57'W], 3,700 m, 28 Apr 1991, *Beck* 18754 (HUA, LPB, NY); Prov. Sud Yungas, 16.2 km E of pass between Mururata and Illimani, 16°34'S, 67°46'W, 3,650 m, 11 Dec 1983, *Solomon* 11376 (MO, UC, US).

5. ELAPHOGLOSSUM GARDNERIANUM (Kunze ex Fée) T. Moore, Index Filicum xvi. 1857.

Acrostichum gardnerianum Kunze ex Fée, Mém. Foug. [Hist. Acrostich.] 2: 55, t. 15, f. 3.

1845.—TYPE: BRAZIL. Rio de Janeiro: Montes Órgãos, [22°16'S, 42°32'W], 1837, *G.*

Gardner 93 (**lectotype designated here**: BM! (sheet 000890236); duplicates: BM (sheet 000890238)!, GCE, P! (sheets 00249739 [specimen on the left], 0249740, 0249741) W; photos BM! (sheet 000890239) ex W, GH! ex P, MO! ex BM, NY! ex CGE). **Fig. 1E, 9, 10A.**

Plants epiphytic. *Rhizomes* 2–5 mm wide, compact; *rhizome scales* 3–5 mm long, linear-lanceolate, orange to brown, entire to denticulate, the base truncate, the apex piliiform, oftentimes broken. *Sterile leaves* (4.5–)7.5–17 cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* 1.5–5 cm long, 1/6–1/3 the length of the sterile leaf; *larger petiole scales* 2–5 mm long, scattered to dense, spreading, oblanceolate, light brown to orange, ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute; *smaller*

petiole scales 0.3–0.5 mm long, scattered to dense, appressed, oblanceolate to round, light brown to orange, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute; *laminae* (3–)5.5–13.5 × (1–)1.5–3 cm, oblanceolate, coriaceous, the base broadly cuneate, the apex obtuse; *veins* ca. 1 mm apart, at an angle of 75° with respect to the costa; *adaxial laminar scales* 0.5–2.5 mm long, dense, not imbricate, oblanceolate to linear-lanceolate, light brown, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute to piliform; *abaxial laminar scales* 0.5–2.5 mm long, dense, not imbricate, slightly elevated above the surface of the lamina to patent, oblanceolate to linear-lanceolate, light brown to orange, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute to piliform; *abaxial costal scales* same as the laminar ones, pointing at right angles to the costa, slightly elevated; *marginal scales* same as the laminar ones, dense. *Fertile leaves* longer than the sterile; *petioles* 1/2–3/5 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* (2.5–)5–10 × 0.4–2 cm, narrowly elliptic, coriaceous, glabrescent with age, the base broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.5–2 mm long, dense, imbricate, lanceolate to round, light brown to orange, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute to piliform; *abaxial costal scales* 0.5–1.5 mm long, dense, pointing at right angles to the costa, oblanceolate to round, light brown to orange, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute to piliform; *intersporangial scales* 0.5–1.5 mm long, scattered, oblanceolate to round, light brown to orange, long-ciliate, the base truncate, short-stalked (ca. 0.1 mm), the apex acute to piliform. *Spores* papillate, without ridges.

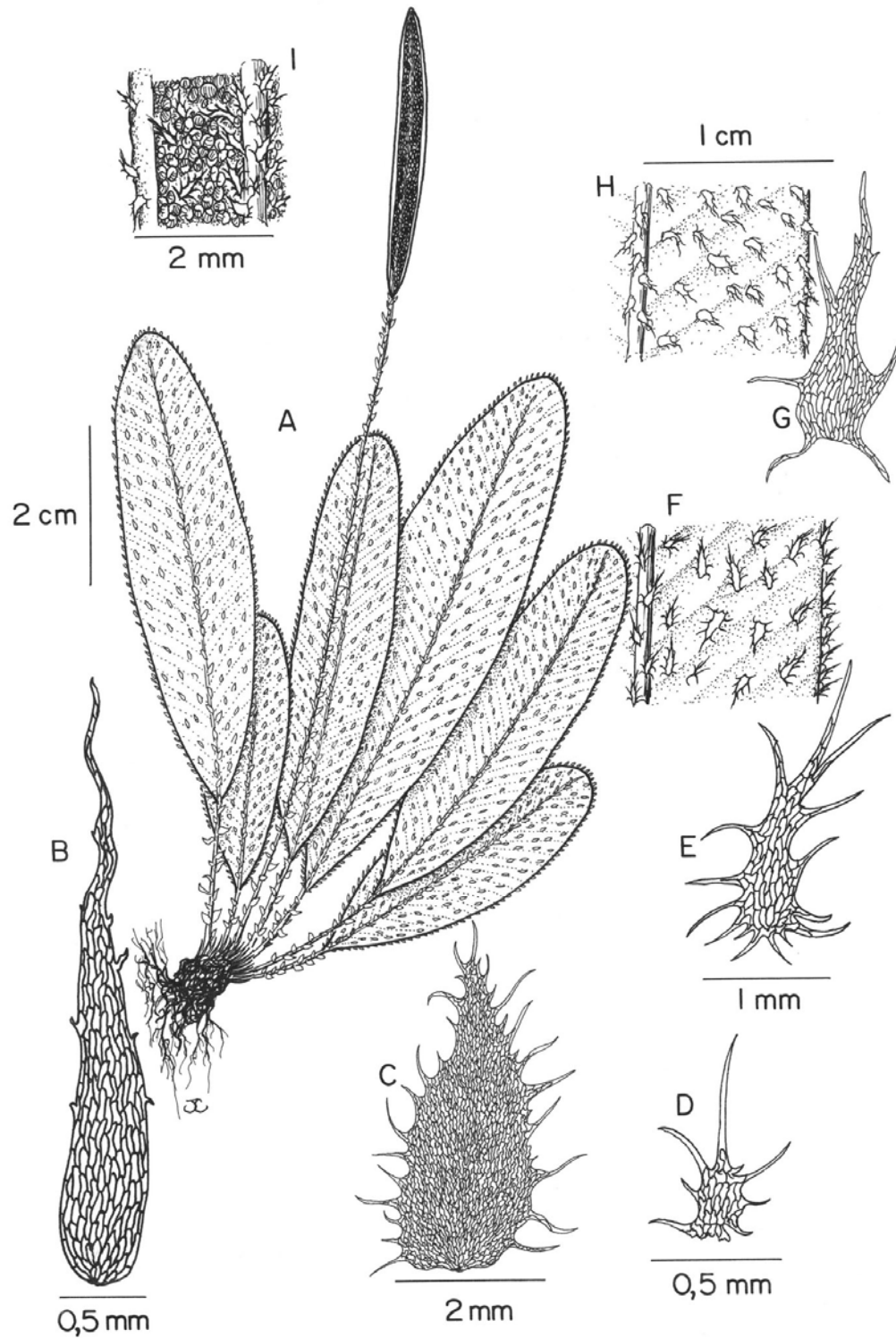


FIG. 9. *Elaphoglossum gardnerianum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar scale. F. Abaxial lamina surface. G. Adaxial laminar scale. H. Adaxial lamina surface. I. Fertile lamina. (From *Matos 939b*, CEPEC).

Distribution—Brazil, states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo; 900–1,700 m (Fig. 10A). Epiphytic, growing in montane forests. Generally the plants grow alone instead of in dense populations.

Comments—*Elaphoglossum gardnerianum* can be distinguished by its small size (sterile leaves (4.5–)7.5–17 cm long), epiphytic habit, compact rhizomes, short petioles ($1/6$ – $1/3$ of the sterile leaf), long-ciliate, concolorous petiole and laminar scales, and papillate spores. It has intersporangial scales, which sometimes are difficult to distinguish because their color is similar to that of the sporangia. *Elaphoglossum muscosum*, the other species of the group occurring in Brazil, can be distinguished from *E. gardnerianum* by longer leaves (10–35 cm long), longer petioles ($1/3$ – $2/5$ of the leaf length), erose petiole scales, and ciliate laminar scales. The cilia of the abaxial laminar scales of *E. muscosum* are never longer than the body of the scale, which is always the case in *E. gardnerianum*. Another difference between these two species is that generally *E. muscosum* has imbricate scales that obscure the abaxial surface of the laminae, whereas *E. gardnerianum* has dense to scattered scales that are never imbricate, thus the abaxial surface of the lamina is visible.

Plants from Brazil that have been identified as *E. bellermannianum* are misidentified; they represent either *E. gardnerianum* or *E. muscosum*. The main difference between *E. bellermannianum*, which does not occur in Brazil, and *E. gardnerianum* is that the former has bicolorous petiole and/or lamina scales (Fig. 6 C, F). These are darker at the point of attachment, or mottled, or black medially with white borders. In contrast, *E. gardnerianum* scales are always concolorous. Another difference is that the larger scales of the petioles and laminae of *E. gardnerianum* are always long-ciliate, whereas those of *E. bellermannianum* are erose.

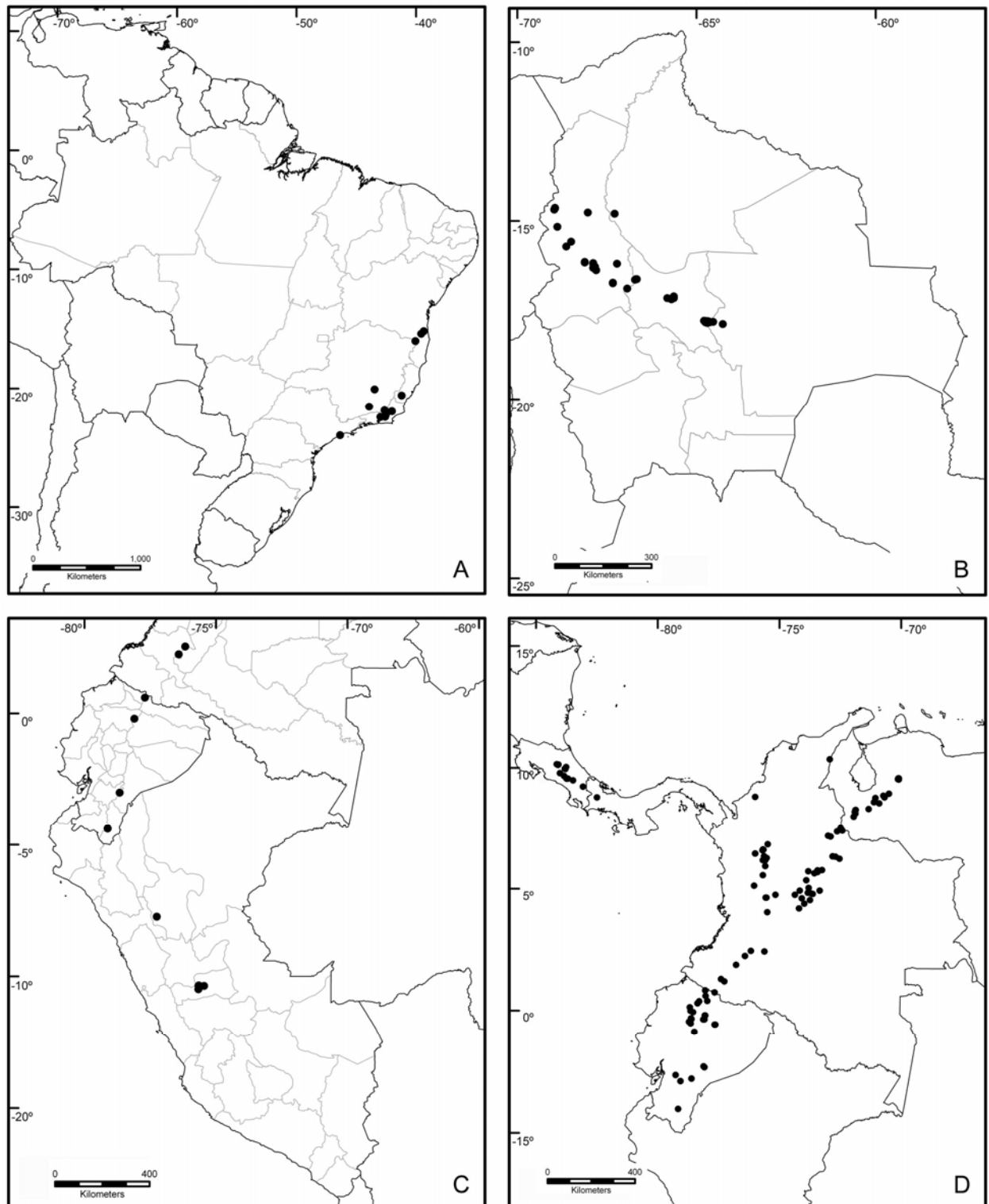


FIG. 10. Distribution of four species of *Elaphoglossum* subsect. *Muscosa*. **A.** *E. gardnerianum*. **B.** *E. glabrescens*. **C.** *E. laxisquama*. **D.** *E. lehmannianum*.

Representative Specimens Examined—BRAZIL. **Bahia:** Arataca, Serra do Peito de Moça, estrada que liga Arataca à Una, ramal ca. 22.4 km de Arataca com entrada no Assentamento Santo Antônio, 15°10'25"S, 39°20'30"W, 1,000 m, 16 Feb 2006, *Matos et al.* 1000 (CEPEC); Camacan, RPPN Serra Bonita, 15°23'30"S, 39°33'55"W, 950 m, 31 Jul 2088, *Matos* 1569 (UPCB). **Espírito Santo:** Castelo, Braço do Sul, [20°36'S, 41°12'W], 13 Aug 1948, *Brade* 19289 (BR). **Minas Gerais:** Serra do Caraça, [20°05'S, 43°28'W], s.d., *Damazio* 1803 (BR); Santa Maria do Salto, divisa entre Bahia e Minas Gerais, Fazenda Duas Barras, Reserva do Alto Cariri, 16°24'23"S, 40°03'16"W, 950 m, 9 Feb 2006, *Matos et al.* 939B (CEPEC); Serra do Ibitipoca, [21°33'S, 43°55'W], 11 Aug 1896, *Schwacke* 12331 (P). **Rio de Janeiro:** Teresópolis, [22°26'S, 42°59'W], Oct 1929, *Brade* 9726 (NY); Sta. M. Madalena, Alto da República, [21°57'S, 42°01'W], 1,700 m, Mar 1935, *Brade* 14353 (BR); Serra dos Órgãos, Rio Paquequer, [21°52'S, 42°38'W], 1,000 m, 25 Aug 1940, *Brade* 16638 (BR); Itatiaia, Maromba, [22°25'S, 42°35'W], 1050 m, May 1950, *Brade* 20301 (BR); 22 Mar 1869, *Glaziou* 2439 (P). **São Paulo:** 4 Mar 1962, *Travassos* 326 (BR); Campo Grande, [23°58'S, 46°21'W], 1907, *Wacket* 186 (UC).

6. ***Elaphoglossum glabrescens*** A. Vasco, nom. et stat. nov. *Elaphoglossum engelii* (H. Karst.) H. Christ var. *subnudum* [as “*subnuda*”] Rosenst, Repert. Spec. Nov. Regni Veg. 11: 59. 1912.—TYPE: BOLIVIA. La Paz: Prov. North Yungas, Unduavi, [16°19'S, 57°54'W], 3,300 m, Nov 1910, *O. Buchtien* 2725 (holotype: S!; isotype: US!). **Fig. 1F, 10B, 11.**

Plants epiphytic or terrestrial. *Rhizomes* 4–8 mm wide, short-creeping to erect; *rhizome scales* 4–8 mm long, linear-lanceolate, dark red to dark brown, sometimes with paler margins, denticulate to ciliate (teeth up to 0.3 mm), the base truncate to slightly cordate, the apex piliform. *Sterile leaves* 17–40(–58) cm long, approximate to up to 1 cm apart; *phyllopodia* present, not obscured by the petiole-base scales; *petioles* 9–16(–30) cm long, 2/5–3/5 the length of the sterile leaf; *larger petiole scales* 3–6 mm long, scattered to dense, spreading, lanceolate, light brown to dark brown, sometimes mottled, ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *smaller petiole scales* 0.5–3 mm long, scattered to dense, appressed, oftentimes hidden by the larger ones,

oblanceolate to round, light to dark brown, sometimes mottled with lighter margins, ciliate, the base cordate, the apex acute; *laminae* 6–17(–28) × 1.8–3.8 cm, linear-oblong to oblong, chartaceous to coriaceous, glabrescent with age, the base truncate to obtuse, the apex obtuse; *veins* 1–1.5 mm apart, at an angle of 70° with respect to the costa; *adaxial laminar scales* 0.5–2 mm long, dense, lanceolate, white to light brown, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–3 mm long, from absent to scattered, when present slightly elevated above the surface of the lamina and never imbricated, lanceolate to round, light to dark brown, sometimes mottled with lighter margins, ciliate, the base cordate to short-stalked (up to 0.2 mm), the apex acute; *abaxial costal scales* 0.5–3.5 mm long, dense, pointing parallel or at right angles to the costa, slightly elevated, lanceolate to round, orange to dark brown, sometimes mottled with lighter margins or darker at the point of attachment, ciliate, the base cordate, the apex acute; *marginal scales* 0.5–1.5 mm long, dense, lanceolate to oblanceolate, orange, ciliate, the base cordate to short-stalked (up to 0.1 mm), the apex acute. *Fertile leaves* longer than the sterile; *petioles* 2/5–3/4 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf, but the small ones tend to be darker, mottled to entirely black; *laminae* 8–19 × 1–2 cm, narrowly elliptic, chartaceous to coriaceous, glabrescent with age, the base truncate, the apex obtuse; *adaxial laminar scales* 0.5–1.2 mm long, dense, lanceolate, light brown to dark brown, sometimes mottled with lighter margins, darker along the costae, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2(–3) mm long, dense, pointing parallel or at right angles to the costa, lanceolate to round, orange to black, ciliate, the base cordate, the apex acute; *intersporangial scales* absent. *Spores* papillate, without ridges.

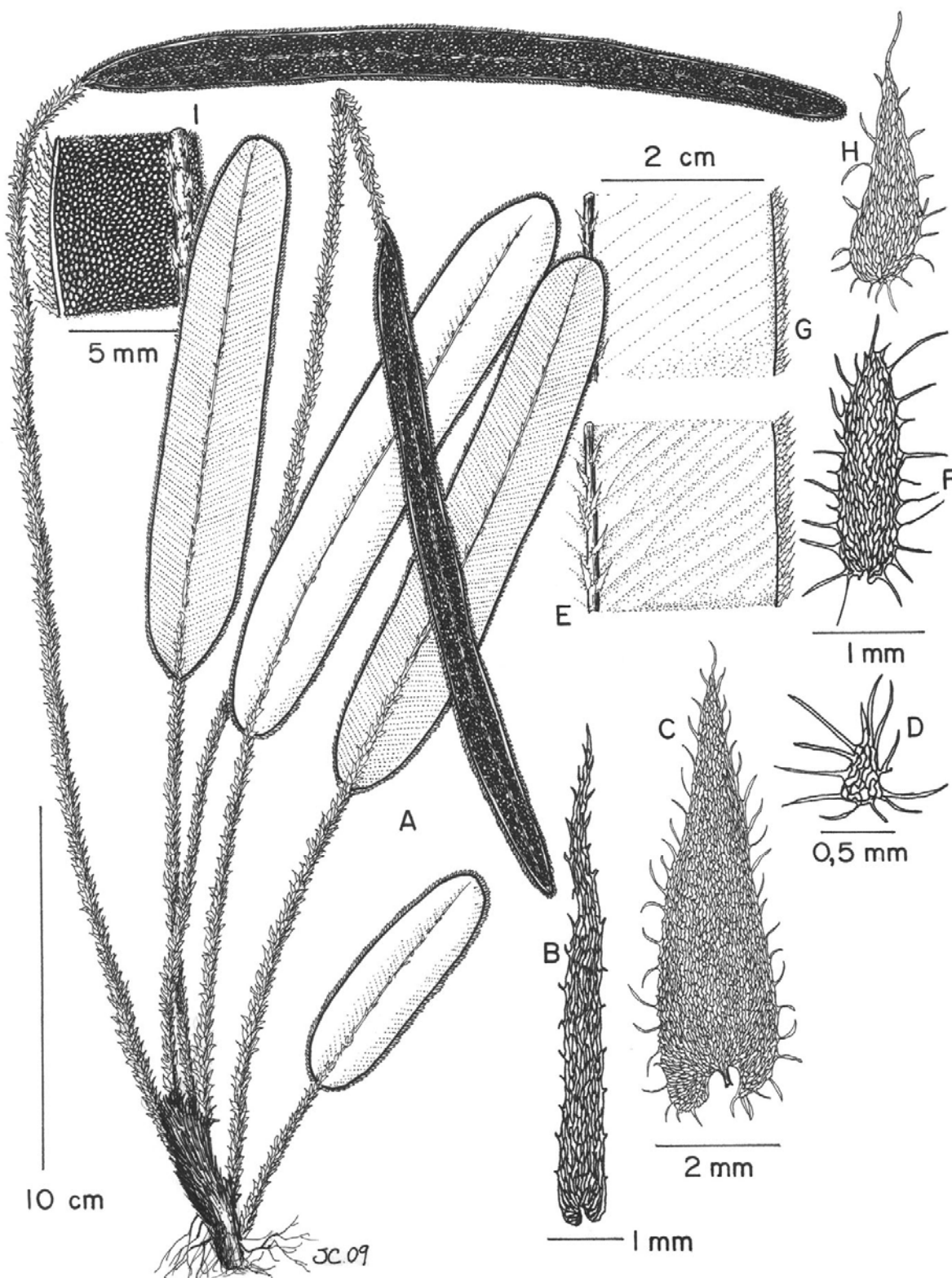


FIG.11. *Elaphoglossum glabrescens*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. (A from Nee 34051, NY; B-I from Arroyo 61, HUA).

Distribution—Bolivia, departments of Cochabamba, La Paz, Santa Cruz; 2,000–3,800 m (Fig. 10B). Epiphytic or terrestrial in montane forests.

Comments—*Elaphoglossum glabrescens* is characterized by short-creeping, ascending rhizomes, dark red to dark brown rhizome scales, and linear-oblong to oblong sterile laminae with obtuse apices and truncate to obtuse bases. The type of *E. glabrescens* (Buchtien 2725) has the lower surface of the laminae completely glabrous, with scales present only on the costae and margins. Specimens with glabrous adaxial surfaces are easy to identify; however, some specimens of *E. glabrescens* are scaly abaxially. The scales range from scattered to dense, but they are small and never obscure the surface of the laminae. Specimens with scaly abaxial surfaces can be confused with *E. laxisquama*, a species endemic to Peru. Yet *E. laxisquama* has long-creeping, usually branched rhizomes, linear-lanceolate, acuminate larger petiole scales, that when bicolorous have dark apices (including the cilia) and lighter bases and point of attachment. In contrast, *E. glabrescens* has short-creeping, ascending rhizomes that typically do not branch, larger petiole scales that are lanceolate with acute apices, and when bicolorous, it is the center of the scale, not the apex that becomes darker (the cilia are never dark). Moreover the spores of *E. laxisquama* are ridged (Fig. 1G), whereas the spores of *E. glabrescens* are not (Fig. 1F).

Elaphoglossum glabrescens was originally described by Rosenstock as a variety of *E. engelii*, from which it differs by the dark red to black rhizome scales, oblong laminae, and papillate spores. *Elaphoglossum engelii* has typically light brown to brown rhizome scales, linear lanceolate to oblanceolate laminae, and spores with ridges and irregular deposits. I gave the variety a new status and a new name. I chose a different epithet because *Elaphoglossum subnudum* C. Chr. already exists; however, to acknowledge that Rosenstock

noticed the difference and described it, I chose a similar epithet that denotes the glabrous condition of the lower laminae surface of some individuals of this species. Moreover I designated as the type of the species the specimens that Rosenstock cited in the original description of his variety.

See *E. novogranatense* comments for a comparison with that species.

Representative Specimens Examined—BOLIVIA. **Cochabamba**: Prov. Carrasco, Siberia Oeste, Monte Hotel, 17°47'19"S, 64°47'18"W, 2,700 m, 22 Sep 2003, *Fernández et al.* 2528 (BOLV, MO); Prov. Carrasco, Km 100 antigua carretera Cochabamba-Villa Tunari, 17°12'S, 65°42'W, 3,300 m, 26 Jun 1996, *Kessler et al.* 6734 (LPB, NY, UC). **La Paz**: Prov. Nor Yungas, Estación Biológica de Tunquini, senda nueva del camino de la mina (curva al lado W) al pantanón, 16°11'S, 67°53'W, 3,000 m, 14 Sep 2000, *Bach et al.* 1042 (LPB, UC); Prov. Nor Yungas, Coscapa, sobre el sendero prehispánico Sillutinkara, 16°12'S, 67°53'W, 3,100 m, 27 Apr 2004, *Jiménez* 2152 (LPB, NY, UC). **Santa Cruz**: Prov. Caballero, 28 km desde Comarapa camino a la Siberia, 17°50'S, 64°38'W, 2,600 m, 15 Aug 1991, *Arroyo et al.* 61 (HUA, LPB, NY, UC); Prov. Caballero, 50 km al N de Mataral (en la carretera Santa Cruz-Comarapa) pasando por San Juan del Potrero y bajando a la cuenca del alto Río Ichilo, [17°53'S, 64°16'W], 2,000 m, 25–26 May 1989, *Smith* 13319 (MO, UC).

7. ELAPHOGLOSSUM LAXISQUAMA Mickel, *Fieldiana, Bot.*, n.s. 27: 141. 1991.—TYPE:

PERU. San Martín: Prov. Mariscal Cáceres, Puerta del Monte, Río Abiseo Nat. Park, [7°45'S, 77°15'W], 3,400 m, 19 Nov 1985, *K. Young* 1741 (holotype: NY!; isotype: USM). **Fig. 1G, 10C, 12.**

Plants terrestrial. *Rhizomes* 3–7 mm wide, long-creeping, ascendant; *rhizome scales* 7–11 mm long, linear, maroon to dark brown, sometimes darker at the center, denticulate to ciliate (teeth up to 0.7 mm), the base cordate (appearing peltate because of the large auricles), the apex acuminate. *Sterile leaves* 15–55(–66) cm long, approximate to up to 1 cm apart;

phyllopodia present, sometimes obscured by the petiole-base scales; *petioles* 9–32(–41) cm long, 3/5–2/3 the length of the sterile leaf; *larger petiole scales* 5–8 mm long, dense, spreading, linear-lanceolate to lanceolate, orange to brown, mottled, sometimes black in the center or in the apical portion (including the cilia), long-ciliate (up to 11 mm), the base cordate (appearing peltate because of the large auricles), short-stalked (ca. 0.1 mm), the apex acuminate to piliform; *smaller petiole scales* 0.3–2.5 mm long, dense, spreading, oftentimes hidden by the larger ones, lanceolate to round, orange to brown, long-ciliate, the base cordate, the apex acuminate to piliform; *laminae* 6–25 × 2–3.5 cm, linear-oblong to oblanceolate, coriaceous, glabrescent with age, the base truncate to broadly cuneate, the apex obtuse to acute; *veins* 1–1.5 mm apart, at an angle of 70°–80° with respect to the costa; *adaxial laminar scales* 0.5–3 mm long, scattered to dense, not imbricate, oblanceolate to round, orange to brown, mottled, sometimes black in the center or in the apical portion (including the cilia), long-ciliate, the base cordate, the apex acuminate to piliform; *abaxial laminar scales* 0.2–1.5 mm long, scattered to dense, not imbricate, patent, lanceolate to oblanceolate, funnelform throughout (without flattened body), orange to brown, long-ciliate, the base enrolled; *abaxial costal scales* 0.5–3 mm long, dense, pointing at right angles to the costa, slightly elevated to patent, oblanceolate, orange to brown, mottled, sometimes black in the center or in the apical portion (including the cilia), long-ciliate, the base truncate, short-stalked (up to 0.2 mm), the apex acuminate to piliform; *marginal scales* 0.5–1 mm long, dense, patent, ovate to round, orange to brown, mottled, sometimes black in the apical portion or just the apical cilia black, long-ciliate, the base truncate, short-stalked (up to 0.1 mm), the apex acuminate to piliform. *Fertile leaves* longer than the sterile; *petioles* 3/4 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones

more spreading; *laminae* 5–16 × 1–2.5 cm, narrowly elliptic to oblong, coriaceous, the base truncate to broadly cuneate, the apex obtuse to acute; *adaxial laminar scales* 0.5–3 mm long, dense to scattered, not elevated to elevated above the surface of the lamina, oblanceolate to round, orange to brown, mottled, sometimes black in the apical portion or just the apical cilia black, long-ciliate, the base truncate, short-stalked (up to 0.1 mm), the apex acuminate to piliform; *abaxial costal scales* 1–5 mm long, dense, oblanceolate to round, orange to brown, mottled, sometimes black in the apical portion or just the apical cilia black, long-ciliate, the base cordate, short-stalked (up to 0.1 mm), the apex acuminate to piliform; *intersporangial scales* 0.5–1.5 mm long, scattered, oblanceolate to round, orange to brown, mottled, sometimes black in the apical portion or just the apical cilia black, long-ciliate, the base cordate, short-stalked (up to 0.1 mm), the apex acuminate to piliform. *Spores* papillate, with ridges.

Distribution—Colombia, Ecuador, Peru; 2,400–3,800 m (Fig. 10C). Terrestrial in montane forest and páramos.

Comments—*Elaphoglossum laxisquama* can be distinguished by its long-creeping, erect rhizomes, long-ciliate petiole and laminar scales, and papillate, ridged spores. This is the only species of subsection *Muscosa* in which some of the petiole and laminar scales have black or mottled tips (including the cilia) (Fig. 12C, H). This is a different color pattern compared to other species of the subsection which, when bicolorous, have their centers black and the margins, including the cilia, lighter. Also, the abaxial laminar scales of this species are unique within subsection *Muscosa* because they are patent and funnellform throughout their length, without a flattened body (Fig. 12F). All other scales of the subsection *Muscosa*

that have enrolled or stalked bases are never enrolled apically, thus the body of the scale remains flat and parallel (or nearly so) to the lamina surface (i.e. Fig. 8E, F).

Some specimens (e.g., *Wilson et al 2812*, UC) have rhizome scales that are lighter and more oblanceolate than the typical ones, which are maroon to dark-brown and linear lanceolate. Also, the larger petiole scales of these specimens are more oblanceolate than the typical *E. laxisquama* petiole scales, which tend to be linear-lanceolate to lanceolate. However these specimens have the typical dark-tipped, funnellform laminar scales that distinguish *E. laxisquama* from all other species of subsection *Muscosa*. For these reasons I considered the specimens as belonging to this species.

Representative Specimens Examined—COLOMBIA. **Cauca:** al frente de la Laguna San Rafael, Páramo de Puracé, [2°15'N, 76°25'W], 3,300 m, 6 May 1984, *Albert de Escobar et al. 4388* (HUA); ca. 28 km E of Totoró, 2°33'N, 76°10'W, 3,075 m, 6 May 1984, *Luteyn et al. 10179* (JAUM, NY); ca. 28 km E of Totoró, 2°33'N, 76°10'W, 3,075 m, 6 May 1984, *Luteyn et al. 10184* (JAUM, NY).

ECUADOR. **Cañar:** road from Gualeceo to Limón, 2°59'58"S, 78°39'36"W, 3,410 m, 2 Mar 2005, *Moran et al. 7588* (NY). **Carchi:** Canton Montufar, Guandera Reserve, ca. 6 km E of Fernández Salvador, 0°36'N, 77°42'W, 3,500 m, 2 Jul 1996, *Wilson et al. 2812* (UC). **Loja:** Cerro Toledo, E of Yangana, between Loja and Valladolid, 4°23'S, 79°07'W, 3,000–3,100 m, 26 Oct 2004, *Lehnert 1457, 1461* (NY, UC). **Napo:** Oyacachi, 5 km después del paso, bosques en las márgenas de la carretera, 0°12'S, 78°06'W, 3,500 m, 28 Dec 1996, *Navarrete 1373* (NY).

PERU. **Cusco:** Prov. La Convención, Huayopata, in part of the Pistipata drainage called Puncuyo, 10 km SW of Incatambo, 2,400 m, 6 Oct 1982, *Peyton 1442* (MO). **Pasco:** Prov. Oxapampa, Dist. Huancabamba, Santa Barbara, 10°21'48"S, 75°39'42"W, 3,389–3,419 m, 29 Jan 2005, *Mellado 2684* (MO, NY); Parque Nacional Yanachaga-Chemillen, Abra Yanachaga, 10°22'S, 75°27'W, 2,870–3,200 m, 12 Jun 2003, *Vásquez et al. 28162* (NY, UC). **San Martín:** Prov. Mariscal Cáceres, forest patch above timberline, Puerta del Monte, [7°45'S, 77°15'W], 3,450 m, 20 Nov 1985, *Young 1847* (NY); Prov. Mariscal Cáceres, small forest patch, above timberline, Chochos, 3,400 m, 24 Nov 1985, *Young 2536* (NY).

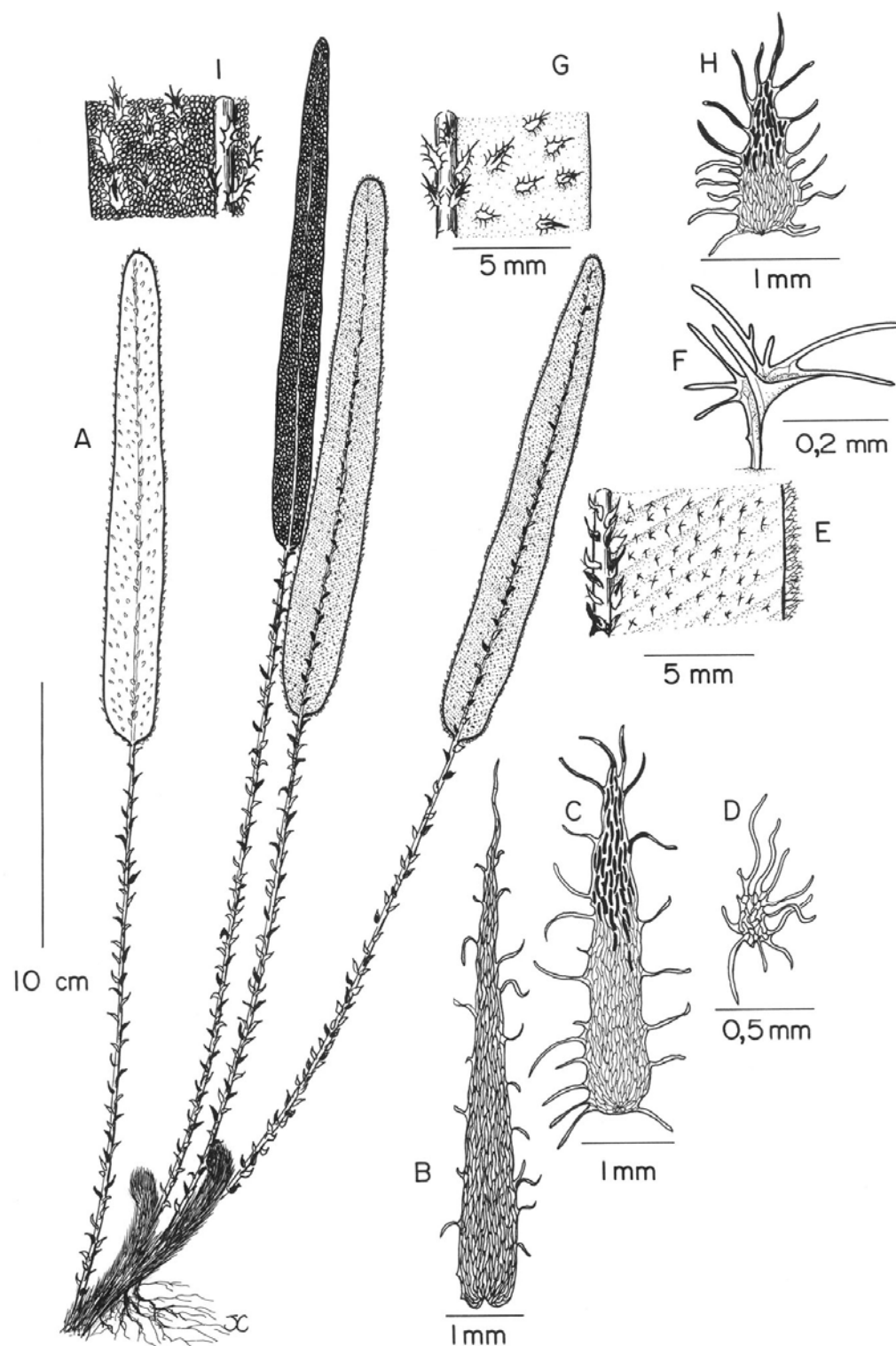


FIG. 12. *Elaphoglossum laxisquama*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial fertile lamina surface. H. Adaxial fertile laminar scale. I. Abaxial fertile lamina. (From Vásquez 28162, NY).

8. ELAPHOGLOSSUM LEHMANNIANUM H. Christ, Neue Denkschr. Allg. Schweiz. Ges.

Gesamnten Naturwiss. [Monogr. *Elaphoglossum*] 36(1): 81, f. 36. 1899.—TYPE:

COLOMBIA. Cauca: wächst an Bäumen in lichten Wäldern um Popayán, 1,750 m, s.d., *F.*

C. Lehmann 3557 (**lectotype, designated here**: US!; duplicate B!). **Fig. 1H, 10 D, 13**

Elaphoglossum decipiens Hieron., Bot. Jahrb. Syst. 34: 554. 1904.—TYPE:

COLOMBIA. Cauca: in a dense forest close to Poblazon supra urbem Popayán, 2,000–2,500 m, s.d., *F. C. Lehmann* 5075 (**lectotype, designated here**: B!; duplicates F!, US!).

Elaphoglossum yarumalense Hieron., Bot. Jahrb. Syst. 34: 556. 1904.—TYPE:

COLOMBIA. Antioquia: Yarumal, habitat ad arborum truncos silvarum pratis interruptarum prope El Yarumal in parte septentrionali provinciae Antioquia, [5°56'N, 75°35'W], 1,600–2,200 m, s.d., *F. C. Lehmann* 7675 (**lectotype designated here**: B!; duplicates: US (sheets 00067395 and 1067595 [drawing of B lectotype with a fragment in pocket])!).

Elaphoglossum squamiferum A. Rojas, Brenesia 45–46: 21, f. 11. 1996.—TYPE:

COSTA RICA. Heredia: Parque Nacional Braulio Carrillo, Volcán Barva, 10°07'20"N, 84°06'00"W, 2,600 m, 7 Aug 1989, *G. Rivera* 28 (holotype: INB!)

Plants epiphytic or terrestrial. *Rhizomes* 2–7 mm wide, short-creeping to erect; *rhizome scales* 9–12 mm long, linear, orange to dark brown, denticulate, the base truncate, the apex piliform, sometimes tortuous. *Sterile leaves* 10–40(–60) cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* 3–15(–35) cm long, 1/4–1/2 the length of the sterile leaf; *larger petiole scales* 3–7 mm long, scattered to dense, spreading, linear-lanceolate, light brown, erose to laciniate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *smaller petiole scales* 0.5–2 mm long, scattered

to dense, appressed, oftentimes hidden by the larger ones, oblanceolate, light brown, erose to ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *laminae* 6–25 × (1.5–)2–4(–5.5) cm, oblanceolate to linear-lanceolate, coriaceous, the base broadly cuneate to rounded, the apex obtuse to acute; *veins* 1–2 mm apart, at an angle of 75°–80° with respect to the costa; *adaxial laminar scales* 1–2 mm long, scattered to dense, lanceolate, white to light brown, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–2 mm long, dense to absent, not imbricate, slightly elevated above the surface of the lamina, lanceolate, light brown to brown, ciliate, the base stalked, the apex acute; *abaxial costal scales* same as the laminar ones, typically pointing at right angles to the costa, slightly elevated; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* 1/2–3/4 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* (5.5–) 8–24(–35) × 0.6–2.5 cm, narrowly elliptic, coriaceous, glabrescent with age, the base broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.5–3 mm long, dense, imbricate, lanceolate to round, light brown to brown, darker at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–3 mm long, dense to scattered, pointing at right angles to the costa, lanceolate to round, brown, ciliate, the base truncate, the apex acute; *intersporangial scales* 1.5–4 mm long, scattered to dense, sometimes almost obscuring the sporangia, lanceolate, orange to brown, ciliate, the base stalked, the apex acute. *Spores* papillate, without ridges.

Distribution—Costa Rica, Panama, Venezuela, Colombia, Ecuador; 1,150–3,500 m (Fig. 10D). Epiphytic or terrestrial, in montane forests and páramos.

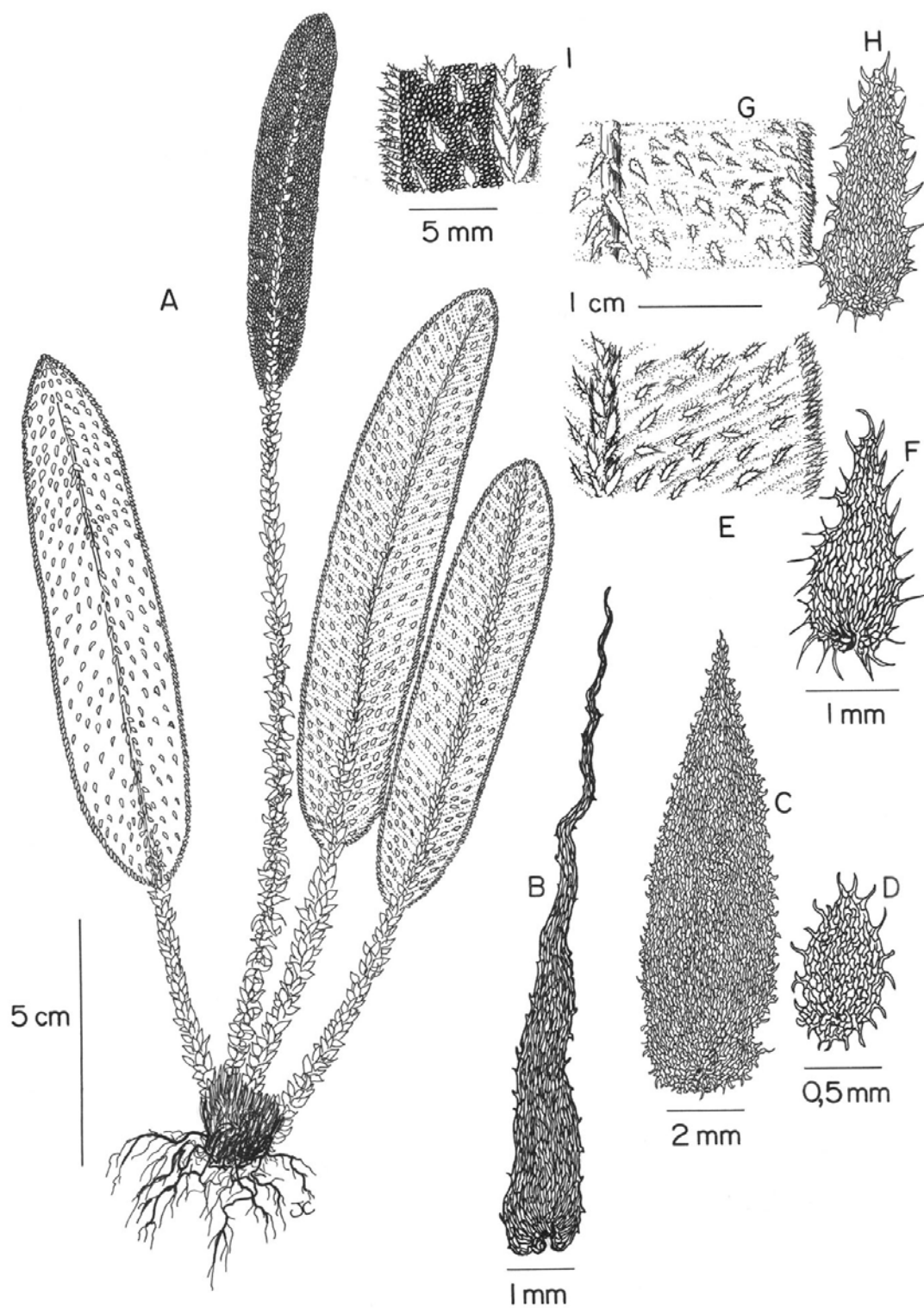


FIG. 13. *Elaphoglossum lehmannianum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. (A, F-I from *Rentería* 5165, HUA; B-D from *Rodríguez* 5449, HUA).

Comments— *Elaphoglossum lehmannianum* can be distinguished by its epiphytic habit (although it can be terrestrial above 3,000 m), short-creeping to erect rhizomes, long, linear, denticulate rhizome scales, erose to lacinate (never ciliate) larger petiole scales, and papillate spores without ridges. It exhibits considerable variation in the density of the abaxial laminar scales. Some plants have their abaxial surfaces completely obscured by the scales, whereas others are subglabrous, with the laminar scales restricted to the margins and costae. The two extremes intergrade completely. Moreover, field observations of the plants in Colombia and Venezuela reveal that scaly and glabrous laminae can be found on the same rhizome (e.g. Vasco 821, NY). The plants with glabrous laminae were described from Costa Rica as *E. squamiferum*, here considered a synonym.

Elaphoglossum lehmannianum resembles *E. muscosum*, and the latter name is the one that has been commonly applied to *E. lehmannianum* in Costa Rica, Panama, and northern South America. The differences between these two species, especially the scaly specimens of *E. lehmannianum*, are extremely subtle. Phylogenetic molecular analyses (Vasco and Moran in prep), however, recovered those two species in two different clades, thus they are recognized here as two different entities. Although similar, *E. lehmannianum* and *E. muscosum* can be distinguished by scales of the rhizomes and petioles and by geographic distribution. *Elaphoglossum lehmannianum* has orange to dark brown denticulate rhizome scales with teeth 0.1–0.2 mm long. *Elaphoglossum muscosum* has reddish orange, entire rhizome scales. Occasionally these scales have teeth, but they are less than 0.1 mm long. The larger petiole scales of *E. lehmannianum*, although erose like those of *E. muscosum*, tend to have slightly longer teeth. Those teeth are never longer than the width of the scale, as in *E. engelii*. As to geographic distribution, *E. lehmannianum* occurs in Costa Rica, Panama,

Venezuela, Colombia, and Ecuador (Fig. 10D). In contrast *E. muscosum* occurs from Mexico to El Salvador, and in Cuba, Jamaica, Haiti, Dominican Republic, and Southern Brazil (Fig. 14A). The two species do not overlap geographically. Because of the variation within each species in scale shape, scale density, and lamina shape, it is difficult to find more characters that distinguish them; however, *E. lehmannianum* has a tendency toward darker rhizome scales, acute leaf apices, and smaller abaxial laminar scales that do not obscure the abaxial surface (especially in specimens of lower elevations). The abaxial laminar scales are stalked in both species, but tend to be longer-stalked, therefore appearing more elevated above the surface, in *E. lehmannianum*.

Another species with which *E. lehmannianum* is likely to be confused is *E. ruficomum*, endemic to Peru and northwestern Bolivia. These two species can be distinguished by their rhizome and petiole scales. The rhizome scales of *E. lehmannianum* are less than 12 mm long, orange to dark brown, and dull; in contrast, those of *E. ruficomum* are typically 12–20 mm long, maroon, and lustrous. The petiole scales of *E. lehmannianum* are erose to lacinate, whereas those of *E. ruficomum* are ciliate.

Although Lehmann's main set of specimens is deposited at B, I designated the specimen at US as the lectotype. This specimen is more complete and has a rhizome and fertile leaves all belonging to a single plant. In contrast, the B specimen does not have a rhizome, and the collection consists of one fertile and three sterile leaves detached from each other.

See *Elaphoglossum bellermannianum* and *E. engelii* comments for a comparison with those species.

Representative Specimens Examined—COSTA RICA. **Cartago:** Cantón de Paraíso, investigation area of the CATIE, 9°33'30"N, 83°41'30"W, 2,600–2,700 m, 20 Dec 1990, *Bittner 180* (CR, HUA, NY); Interamerican Hwy., slope below hotel La Georgina, [9°57'N, 83°48'W], 3,093 m, 27 Jan 2008, *Sundue et al. 1693* (HUA, INB, NY). **Heredia:** Volcán Barba, on property of Finca Georgina, [10°09'N, 84°09'W], 2,560 m, 17 Jun 1982, *Lumer 1320* (NY); Cantón de Barva, Parque Nacional Braulio Carillo, cuenca del Tárcoles, estación Barva, entre la estación y Laguna del Barva, 10°07'20"N, 84°06'00"W, 2,700–2,900 m, 30 May 1997, *Rojas 3546* (CR, INB, NY). **Limón:** Cantón de Talamanca, P.N. La Amistad, Tararia, sendero a Cerro Kámuk, entre Cerro Nai y Cerro Dudu, 9°13'39"N, 83°04'23"W, 2,750–3,100 m, 9 Nov 1996, *Rojas 3227* (CR, INB, NY). **San José:** Cerro Chirripó, SW slopes, along ridge trail from Canaan to summit, [9°29'N, 83°29'W], 2,600–3,050 m, 22–27 Aug 1967, *Evans et al. 85A* (NY, US); Cerro de la Muerte, along the old oxcart trail above the interamerican Hwy., 9°33.23'N, 83°44.439'W, 2,963 m, 28 Jan 2008, *Sundue et al. 1707* (HUA, INB, NY).

PANAMA. **Chiriquí:** above camp Aguacatal, E slope of Chiriquí Volcano, [8°47'N, 82°30'W], 2,400–2,500 m, 10–13 Mar 1911, *Maxon 5297* (US).

COLOMBIA. **Antioquia:** Mun. Belmira, vereda Yermalito, 6°36'27.8"N, 75°39'29.7"W, 2,825 m, 2 Jul 2002, *Rodríguez et al. 3469* (JAUM, NY); Mun. Caramanta, límites con el Mun. de Támesis, sector nascimientos Quebrada El Cóndor, 5°33'27.5"N, 75°40'51.2"W, 2,650 m, 16 Apr 2005, *Rodríguez et al. 5449* (HUA, NY). **Boyacá:** Mun. Villa de Leyva, SFF de Iguaque, bosques secundarios de Robles, cerca al centro de visitantes, 5°41'43.8"N, 73°27'08.4"W, 2,850 m, 29 Apr 2007, *Vasco et al. 760* (HUA, NY); Mun. Chisacá-San Pedro de Iguaque, SFF de Iguaque, sendero subiendo a la laguna de Iguaque, 5°41'43.8"N, 73°27'08.4"W, 2,900 m, 30 Apr 2007, *Vasco et al. 761* (HUA, NY). **Cauca:** "Canaan", Mt. Purace, Cordillera central, [2°15'N, 76°25'W], 3,100–3,300 m, 11–16 Jun 1923, *Killip 6695* (NY, US); in parte septentrionali altiplanitie popayanensis, 1,600–1,800 m, *Lehmann 5139 pp* (B-070310, P-00577723, US-1067593, syntype of *E. decipiens*); Popayán, [2°26'N, 75°37'W], 1,500–1,800 m, s.d., *Lehmann 6945* (B, US, syntype of *E. decipiens*); forests of Popayán, [2°26'N, 75°37'W], 1,700–2,300 m, Jan 1901, *Lehmann B.T. 1299* (NY). **Cesar:** Sierra del Perijá, E of Manaure, sabana Rubia, [10°21'N, 72°56'W], 3,000–3,100 m, 7 Nov 1959, *Cuatrecasas 25092* (US). **Cundinamarca:** Bogotá, D.C. Región del Sumapaz, cerca a Santa Rosa, 4°11'21"N, 74°11'36"W, 3,160 m, 19 Feb 1997, *Betancur et al. 7026* (COL, HUA, NY); Sueva Valley, 9 km W of Junín, 45 km NE of Bogotá, [4°48'N, 73°42'W], 2,400 m, 21 Apr 1944, *Grant 9087* (HUA, NY, US); Mun. Fómeque, Río Frío, colecciones en la margen del río, 4°31'52.8"N, 73°44'54.9"W, 3,200 m, 3 May 2007, *Vasco et al. 787* (HUA, NY). **Nariño:** Mun. La Florida, Margen derecha del río Barrancos, [1°18'N, 77°24'W], 2,300 m, 3 Aug 1977, *Díaz et al. 989* (COL); Mun. Pasto, Bosque Botana, [1°12'N, 77°16'W], 3,100 m, 22 Aug 1963, *Soejarto 480* (COL). **Norte de Santander:** hoyá del Río Chitagá en Vega, 2,880 m, 28 Nov 1941, *Cuatrecasas 13462* (COL, US); Herran, Parque Natural Nacional Tama, Sector Orocué, hacia el Alto El Pesebre, [7°30'N, 72°29'W], 2,650–3,020 m, 2 Apr 1987, *Lozano et al. 5502* (COL). **Quindío:** Boquerón del Quindío in Cordillera Central, [4°38'N, 75°32'W], 3,500 m, 10 Mar 1876, *André 2089* (P); Salento to Laguneta, old Quindio trail, [4°38'N, 75°34'W], 2,400–2,700 m, 1 Aug 1922, *Killip 9125* (US); "Pinares", above Salento, [4°38'N, 75°34'W], 2,600–2,800 m, 2–10 Aug 1922, *Pennell 9252* (NY, US). **Risaralda:** Mun. Pereira, Parque regional Ucumarí, vereda La Pastora, trail from El Cedro to La Pastora, 4°02'N, 75°30'W, 1,900 m, 19 Feb 1990, *Croat 70779* (COL); Mun. Santuario,

PNN Tatamá, camino que lleva al Páramo de Tatamá, subiendo hacia Morro Zancudo, 5°07'28.1"N, 76°02'30.6"W, 2,643 m, 17 Apr 2007, *Vasco et al.* 737 (HUA, NY). **Santander**: along road between Pamplona and Chorro Colorado vía Chiquirá, at Km 128 marker, 7°22'N, 72°38'W, 2,580 m, 4 May 1983, *Croat* 56407 (JAUM, UC); carretera del Páramo de Guantiva a Onzaga, [6°20'N, 72°49'W], 3,100 m, 1 Dec 1967, *Jaramillo-Mejía* 4417, 4445, 4455 (COL). **Tolima**: Libano-Murillo road., ca. 18–24 km W of Libano, 4°45'N, 75°10'W, 2,450–2,770 m, 18 May 1984, *Luteyn et al.* 10627A (NY).

VENEZUELA. **Barinas**: Mun. Montes, vertiente lareense del Páramo de El Jabón, en dirección E a partir de la casa del Sr. Emiliano Vergara, 3,000–3,050 m, 4 Oct 1970, *Ruíz-Terán* 976 (NY); Mun. Morán, pica que va desde Buenos Aires al Páramo de Las Rosas, 9°34'N, 70°06'W, 2,300–2,600 m, 15 Nov 1984, *van der Werff* 7968 (MO, UC). **Mérida**: Páramo de La Negra, [8°16'N, 71°52'W], 2,980 m, 13 Feb 1939, *Alston* 7000A (COL, MO, VEN); Distrito Rangel, cuenca del río Los Granates, entre la Casa Grande y El Hático, Páramo de Los Granates, [8°47'N, 70°41'W], 2,940 m, 15 Sep 1971, *Ruíz-Terán* 6313 (NY, UC). **Táchira**: trail leading to summit of Páramo de Táma, [7°24'N, 72°25'W], 2,500–3,200 m, 29 Jan 1978, *Luteyn et al.* 5336 (NY); carretera Bailadores-La Grita, vía Páramo La Negra, 8°15'20"N, 71°52'46"W, 3,000 m, 29 May 2008, *Vasco et al.* 806, 807, 809, 812 (NY, VEN). **Trujillo**: Guiriguay, hacia Peña Blanca, [8°56'N, 70°30'W], 3,200 m, Aug 1958, *Aristeguieta* 3608 (NY, VEN); Mun. Carache, Páramo El Jabón, 9°31'N, 70°06'W, 2,900–3,000 m, 28 May 1988, *Rivero et al.* 1802 (NY, UC, VEN).

ECUADOR. **Azuay**: E cordillera, 1–8 km N of the village of Sevilla de Oro, [2°48'S, 78°37'W], 2,438–2,743 m, 27 Jul–12 Aug 1945, *Camp* 4590 (F, NY, US); Río Patul, path from El Cajas to Manta Real following Río Patul (2–3 day Trek), 2°39'10.2"S, 79°16'00.4"W, 2,100–2,600 m, 5 Feb 2001, *Clark et al.* 6241 (NY, QCNE). **Carchi**: Valle de Maldonado, km 53 on the road Tulcán-Maldonado, steep slopes in cloud forest, 0°50'N, 78°03'W, 3,150 m, 17–18 May 1973, *Holm-Nielsen* 5647 (AAU, MO, NY, UC); near El Pun, [0°40'N, 77°37'W], 3 Jan 1953, *Prescott* 617 (NY). **Cotopaxi**: in “pas c. m.” Corazón, [0°53'S, 78°30'W], 3,400 m, Sep 1892, *Sodiño s.n.* (P). **Imbabura**: N slope of Volcán Cotacachi, protected forest area above town of Peribuela, 0°22'50.7"N, 78°17.787'W, 2,879 m, 30 Nov 2006, *Sundue* 1066 (NY, QCA); vic. of Shanshipampa, ca. 15 km E of Pimampiro, [0°24'N, 77°58'W], 2,800 m, 5 Aug 1989, *van der Werff* 10914 (MO, UC). **Morona-Santiago**: W de la ciudad del Macas, 2°18'S, 78°07'W, 1,160 m, 28 Feb 1986, *Baker* 6689 (NY); Macas, carretera hacia Domono, frente a la granja del CREA, 2°20'S, 78°05'W, 1,255 m, 4 Nov 1991, *Gudiño et al.* 1583 (MO). **Napo**: Oyacachi, 4 km al E de Pueblo Viejo, 0°12'S, 78°03'W, 3,000 m, 4 Jun 1996, *Navarrete* 1727 (NY, QCA); Paso de Guamaní, Río Chalpi, at the bridge on road Papallacta-Baeza, [0°22'S, 78°05'W], 2,800 m, 6 May 1967, *Sparre* 15886 (S). **Loja**: about 10 km SW of Loja, along road past the University towards La Violeta, [4°02'S, 79°10'W], 2,950 m, 26 Apr 1987, *van der Werff* 9055 (MO, NY, UC). **Pichincha**: Nono-Galea, [0°04'S, 78°33'W], Sep 1899, *Sodiño s.n.* (S, US); Volcán Corazón, [0°32'S, 78°39'W], Oct 1903, *Sodiño s.n.* (B); carretera Quito-Sto. Domingo, [0°28'S, 78°43'W], 2,500 m, 24 May 1987, *van der Werff* 9581 (MO, NY, UC). **Sucumbios**: Km 15–18, carretera Pun-Aguarico, 2,800–2,900 m, 13 Aug 1949, *Acosta-Solís* 13283 (F).

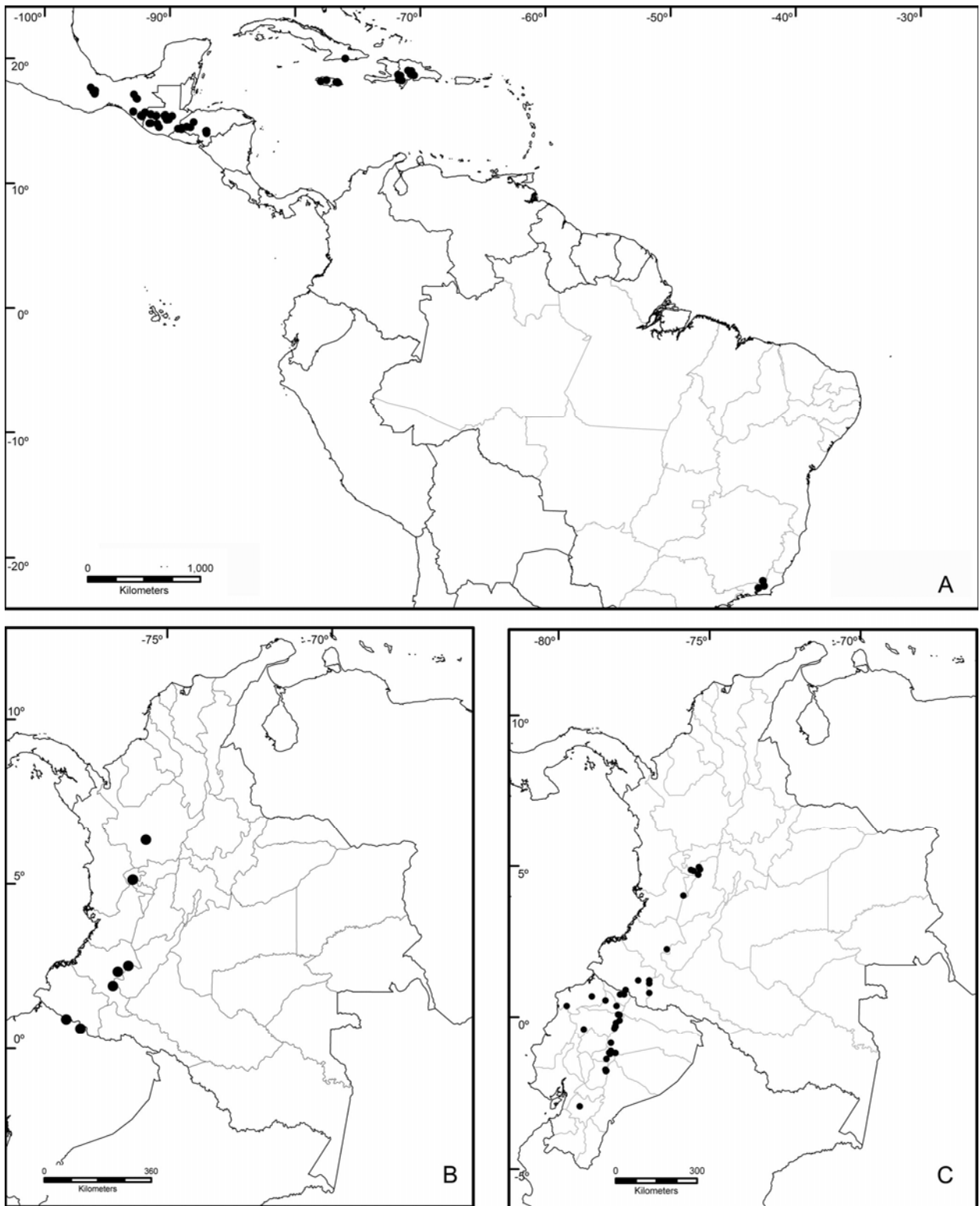


FIG. 14. Distribution of three species of *Elaphoglossum* subsect. *Muscosa*. A. *E. muscosum*. B. *E. novogranatense*. C. *E. oreophilum*.

9. ELAPHOGLOSSUM MUSCOSUM (Sw.) T. Moore, Index fil. 12. 1857. *Acrostichum muscosum* Sw., *Prodr.* 128. 1788.—TYPE: JAMAICA. O. Swartz s.n. (first-step lectotype, inferentially designated by Proctor in *Ferns of Jamaica*: 503, 1985: S, duplicate BM; **second-step lectotype, designated here**: S! (sheet P12230); duplicates B! (sheet W-19514 [frond mounted on the right]), BM! (sheet 000585005), S! (sheet R-65); photos US! ex B, BM, S).

Fig. 11, 14A, 15.

Acrostichum muscosum var. *latifolium* Hook., Sp. Fil. 5: 231. 1864.—SYNTYPES: JAMAICA. J. Macfayden s.n. (K), E. N. Bancroft s.n. (K)

Elaphoglossum hookerianum Underw. ex Maxon, Contr. U.S. Natl. Herb. 13(1): 6. 1909.—TYPE: GUATEMALA. Alta Verapaz: Cobán, 1,350 m, Aug 1907, H. von Tuerckheim II 1862 (**lectotype, designated here**: US!; duplicates: F!, NY!).

Plants epiphytic or epipetric. *Rhizomes* 2–6 mm wide, short-creeping to erect; *rhizome scales* 10–15 mm long, linear, reddish orange, entire or occasionally with small teeth (less than 0.1 mm), the base truncate, the apex piliform, oftentimes broken. *Sterile leaves* (7–)10–35(–40) cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* 3–15.5 cm long, 1/3–2/5 the length of the sterile leaf; *larger petiole scales* 2–6 mm long, scattered to dense, spreading, linear-lanceolate, light brown, erose, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *smaller petiole scales* 0.5–2 mm long, scattered to dense, appressed, oftentimes hidden by the larger ones, oblanceolate, light brown, erose to ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *laminae* 7–25 × (1.5–)2–5(–5.5) cm, oblanceolate, coriaceous, the base broadly cuneate to rounded, the apex obtuse to acute; *veins*

1–2 mm apart, at an angle of 75° with respect to the costa; *adaxial laminar scales* 1–3 mm long, scattered to dense, lanceolate, white to light brown, ciliate, the base cordate, the apex acute; *abaxial laminar scales* (0.5–)1.5–3 mm long, dense, imbricate, more dense towards the costa, slightly elevated above the surface of the lamina, lanceolate, light brown to brown, ciliate, the base cordate (sometimes appearing peltate because of the large auricles), very short-stalked (ca. 0.1 mm), the apex acute; *abaxial costal scales* same as the laminar ones, pointing at right angles to the costa, slightly elevated; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* 1/2–4/5 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* (14.5–)18–42(–52) × 0.8–2(–2.5) cm, narrowly elliptic, coriaceous, the base broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.5–2 mm long, dense, imbricate, lanceolate to round, light brown to brown, slightly darker at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, pointing at right angles to the costa, slightly elevated, lanceolate to round, reddish brown, ciliate, the base truncate, the apex acute; *intersporangial scales* 0.5–2 mm long, scattered but abundant, not obscuring the sporangia, lanceolate, brown, ciliate, the base truncate, the apex acute. *Spores* papillate, without ridges.

Distribution—Mexico, Guatemala, Honduras, El Salvador, Cuba, Jamaica, Haiti, Dominican Republic, Brazil; 1,300–3,200 m (Fig. 14A). Epiphytic or epipetric, in montane and cloud forests.

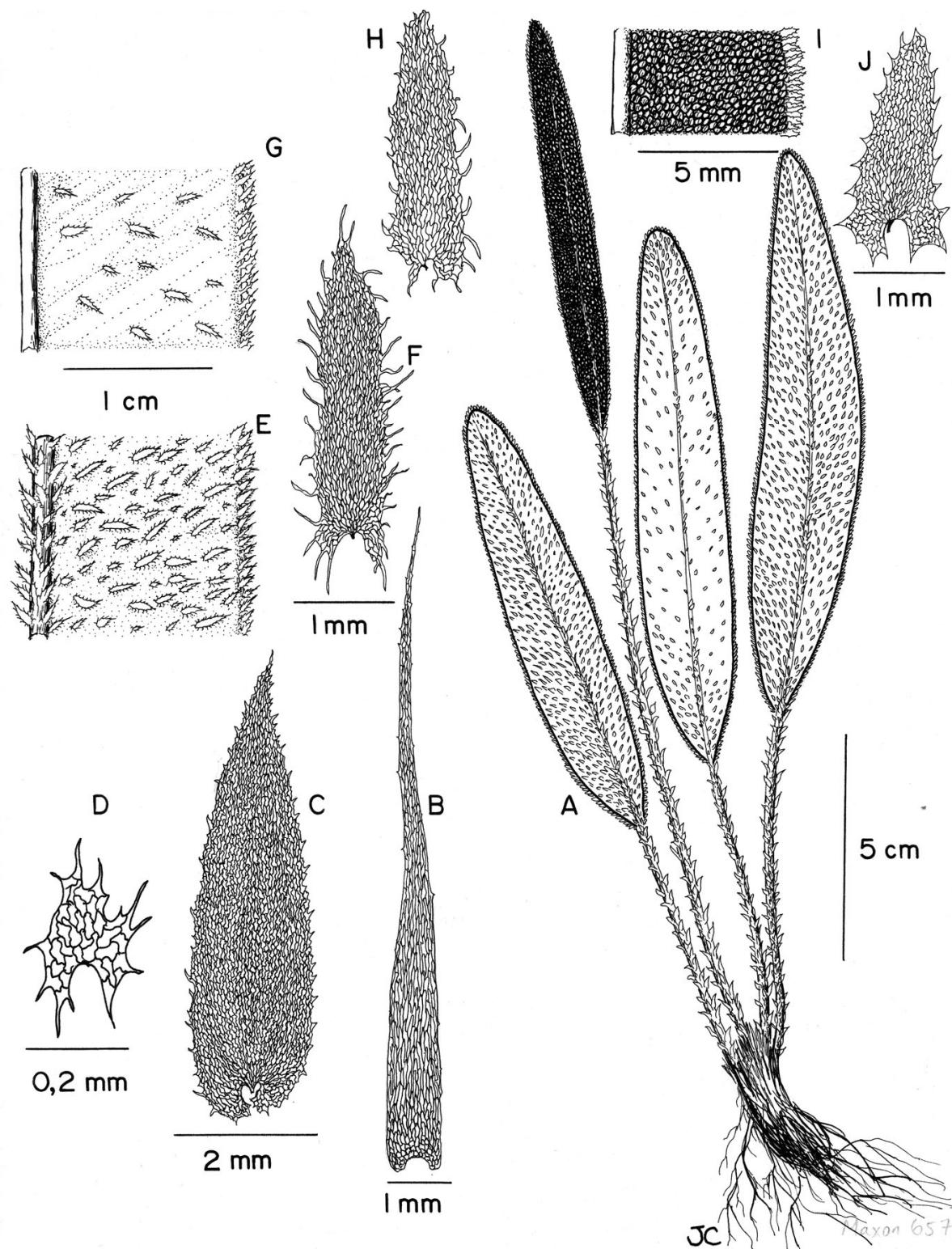


FIG. 15. *Elaphoglossum muscosum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial laminar surface. H. Adaxial laminar scale. I. Fertile lamina. J. Fertile adaxial laminar scale. (From Maxon 657, NY).

Comments — *Elaphoglossum muscosum* is characterized by compact rhizomes, rhizome scales linear with long-piliform apices, erose petiole scales, and papillate spores. The density of the laminar scales is variable. Specimens from Jamaica (where the type was collected), Cuba, Dominican Republic, and Brazil, have laminae completely covered by scales, whereas specimens from Mexico, Guatemala, El Salvador, and Honduras tend to have smaller and more dissected abaxial laminar scales that do not necessarily obscure the surface of the lamina

Elaphoglossum muscosum has been the name previously applied to specimens from Costa Rica, Panama, and northern South America that I recognize here as *E. lehmannianum*. The two species are subtly different morphologically, and their differences are further supported by molecular phylogenetic analysis (Vasco and Moran in prep). See comments under *E. lehmannianum* for a comparison of these two species. Also, see *E. bellermannianum* comments for a comparison with that species.

The application of the name *Elaphoglossum muscosum* has been confusing because, in the protologue, Swartz (1788) provided a Latin description of plants he had collected in Jamaica, but cited an illustration (tab. 139) from Plumier's *Traité des Fougères de l'Amérique* (1705). The specimens annotated by Swartz and the Latin description agree with the present use of the name, whereas the illustration probably corresponds to *E. eggersii* (Baker) H. Christ.

The lectotype duplicate of *Elaphoglossum muscosum* at B (B-W-19514) is the frond mounted on the right side of the sheet. The frond on the left is the fertile lamina of another species of *Elaphoglossum*. Apparently the frond of *E. muscosum* was mounted on this sheet by mistake, instead of in sheet B-19523. The B-19523 sheet has information about *E.*

muscosum, but it has a sterile frond that presumably should have been mounted with the fertile frond of the sheet B-19514.

Representative Specimens Examined—MEXICO. **Chiapas:** SW side of Zontehuitz, Mun. Chamula, [16°47'N, 92°41'W], 2,591 m, 30 Jul 1964, *Breedlove* 6664 (US); near residences at Yerba Buena Mission, near Pueblo Nuevo Solistahuacan, along route 195, [17°06'N, 92°53'W], 1,524–1,829 m, 18 Dec 1972, *Somers et al.* 199 (NY). **Oaxaca:** Distrito of Villa Alta, 2.3 miles S of Villa Alta on trail toward Betaza, [17°21'N, 96°09'W], 1,520 m, 5 Aug 1962, *Mickel* 1126 (NY); Santiago Comaltepec, carretera de Ixtlán a Valle Nacional, despues de Cerro Pelón, ca. de 500 m antes de Vista Hermosa, sendero Tarabundí, [17°39'47"N, 96°19'46"W], 1,450 m, 20 Mar 1998, *Rojas et al.* 4496 (INB). **Veracruz:** Cerro del San Martín, 28 Sep 1971, *Calzada* 572 (F, MEXU).

GUATEMALA. **Alta Verapaz:** Cobán, Chicusha'b 8 km al SW de Cobán, 15°26'N, 90°27'W, 22 Jul 1988, *Tenorio et al.* 14731 (MO, NY); Cobán, [15°28'N, 90°22'W], 1,310 m, Jul 1886, *von Tuerckheim II* 1001 (US). **Baja Verapaz:** Chilasco, in forest on Concepción Road, [15°07'N, 90°06'W], 28 Jul 1971, *Contreras* 10916 (MO, US); Mun. Salama, San Rafael Chilosco, [15°06'N, 90°16'W], 10 Sep 1973, *Guzmán-Váldez* 626 (F). **Chimaltenango:** Cerro de Tecpám, region of Sta. Elena, [14°47'N, 91°01'W], 2,700 m, 4 Dec 1938, *Standley* 58696 (F, US); slopes of Volcán Acatenango, above Las Calderas, [14°31'N, 90°53'W], 2,400–2,700 m, 3 Jan 1939, *Standley* 61971 (F, US). **Huehuetenango:** above San Juan Ixcay, Sierra de los Cuchumatanes, [15°31'N, 91°32'W], 2,400 m, 4 Aug 1942, *Steyermark* 50016 (F, US); La Sierra (Tuchimaj), across river from San Juan Atitán, Sierra de los Cuchumatanes, [15°31'N, 91°32'W], 2,500–2,900 m, 8 Sep 1942, *Steyermark* 51995 (US). **Quezaltenango:** El Pocito S of San Martín Chile Verde, on road to Colomba, [14°49'N, 91°39'W], 2,200 m, 27 Jan 1941, *Standley* 84988 (F). **Quiché:** Nebaj, ca. 13 km on Sacopulas Road, [15°24'N, 91°08'W], 2,440 m, 13 Jun 1964, *Contreras* 4978 (US); above Trigal Montane cloud forest, 19 Feb 1997, *Lautner* L97-2 (UC). **Totonicapán:** Pacajá, region of Desconsuelo, mountains above Totonicapán, [14°50'N, 91°32'W], 3,100–3,200 m, 23 Jan 1940, *Standley* 84561 (F). **Zacapa:** summit of Sierra de las Minas, vic. of Finca Planados, 2,500 m, 14 Oct 1939, *Steyermark* 29999 (F).

HONDURAS. **Francisco Morazán:** on Cerro La Tigra near Tegucigalpa, [14°12'N, 87°07'W], 11 Apr 1972, *Clewell s.n.* (NY); Cerro de Uyuca, [14°01'N, 87°05'W], 1,650–2,000 m, 10–20 Mar 1951, *Morton* 7170 (US); Sierra San Juancito, road to San Juancito, 27–28 Oct 1951, *Swallen* 11125 (US). **Intibucá:** cut over cloud forest of Sierra Opalaca above El Duraznillo, [14°30'N, 88°22'W], 1,800 m, 8 Aug 1971, *Molina* 26084 (F, NY). **Lempira:** Celaque National Park, trail from camp 1 to Río Naranjal, 14°33'N, 88°40'W, 2,000 m, 14 Nov 1991, *Moran* 5540 (MO); arriba del campamento de Don Tomás, parque Nacional Celaque, 14°32'N, 88°40'W, 2,000 m, 14 Nov 1991, *House* 1117 (MO). **Ocatepeque:** cloud forest of El Portillo on Cordillera Meredó, 20 kms from Nueva Ocatepeque, [14°28'N, 89°04'W], 1,800 m, 28 Aug 1968, *Molina* 22327 (F); Cordillera Meredón, vic. of El Portillo, [14°28'N, 89°04'W], 2,000 m, 2 Sep 1975, *Molina* 31010 (F). **Santa Bárbara:** 7 km N of El Mochito, on the E slopes of Mt. Santa Bárbara, 14°55'N, 88°07'W, 2,200–2,500 m, 23 Nov 1991, *Moran* 5710 (MO).

EL SALVADOR. **Chalatenango**: El Pital, [14°20'N, 89°05'W], 2,600 m, 16 Nov 1978, *Seiler* 740 (NY). **Santa Ana**: Bosque Montecristo, [14°23'N, 89°22'W], 2,200 m, 10 Oct 1978, *Seiler* 653 (F, NY, UC); same locality, 9 Apr 1979, *Seiler* 1153 (NY).

CUBA. **Santiago de Cuba**: crest of Sierra Maestra between Pico Turquino and La Bayamesa, [19°59'22"N, 76°50'09"W], 1,350 m, 27–29 Oct 1941, *Morton* 3792 (US).

JAMAICA. **Portland**: vic. of waterfall, about 1 km N of Hardwar Gap, [18°05'N, 76°43'W], 2 Feb 1980, *Fosberg* 59452 (US); Portland Gap, [18°03'N, 76°36'W], 1,667 m, 30 Mar 1898, *Harris* 7518 (US); vic. of Portland Gap, [18°03'N, 76°36'W], 1,650 m, 16 Mar 1920, *Maxon* 1094 (US). **St. Andrew**: lower western ridge of the Blue Mountain Peak, [18°03'N, 76°35'W], 1,700–1,950 m, 4–9 Jul 1926, *Maxon* 9822 (NY, US); vic. of Cinchona, summit Sir John Peak, [18°06'N, 76°38'W], 2–10 Sep 1906, *Underwood* 3212 (NY, US).

HAITI: Guimbi Galata, Morres des Commissaires, 1,800 m, 24 Oct 1943, *Holdridge* 1796 (US).

DOMINICAN REPUBLIC. **Ázua**: Sierra de Ocoa, San José de Ocoa, Loma Sucia, [18°38'N, 70°30'W], 2,300 m, 21 Mar 1929, *Ekman* 11998 (S). **Elias Piña**: Sierra de Neiba, 31–34 km by road NNW of La Descubierta, 11–14 km N of El Angel Felix, [18°38'N, 71°46'W], 1,850–1,900 m, 21 Feb 1983, *Mickel et al.* 8773 (NY). **Independencia**: Sierra de Neiba, entre cerros de Plan Ciquen and Loma El Hoyazo, 34 km de la Descubierta en la carretera de la frontera a Aniseto Martínez y Valle Hondo, 18°41'N, 71°47'W, 1,800 m, 15 Dec 1982, *Zanoni et al.* 24902 (JBSD, NY); Sierra de Baoruco, 25.5 km S de Puerto Escondido, en el camino a la caseta No. 1 de Foresta y al E en el camino a Charco Colorado, 18°13'N, 71°28'W, 1,800 m, 24 Jan 1987, *Zanoni et al.* 37869 (JBSD). **La Vega**: Cordillera Central, La Nevera, 41.7–43.7 km N of central park of San José de Ocoa on the road to Constanza, [18°59'N, 70°43'W], 2,050 m, 22 Feb 1982, *Mickel et al.* 8279pp (NY, US); Loma de Mono Mojao y arroyo Las Piedras, 36 km S de Constanza, 18°43'N, 70°47'W, 2,150 m, 10 Jun 1982, *Zanoni* 20879 (JBSD). **Pedernales**: Sierra de Baoruco, 45 km S of Jimaní-Duverge Hwy. (cruce del escondido), 8 km S of El Aguacate, 7.2 km N of the ridge top, [18°17'N, 71°43'W], 1,700 m, 22 Feb 1983, *Mickel et al.* 8870 (NY); Sierrra de Baoruco, 44 km desde Pedernales en el camino a Los Arroyos y Duvergé, 6 km N del Puesto Militar de Los Arroyos, 18°17'N, 71°43'W, 1,600 m, 6 May 1982, *Zanoni et al.* 20440 (JBSD). **Peravia**: San José de Ocoa, La Nevera, 25 km N of Los Arroyos de Ocoa, 18°36.5'N, 71°35.5'W, 2,130 m, 27 Oct 1980, *Mejía* 8746 (JBSD); Río La Nevera, arriba del Vivero La Nevera de la Dirección Nacional Forestal, 41 km N de San José de Ocoa, 18°41'N, 70°35'W, 2,200 m, 7 Feb 1984, *Zanoni et al.* 29051 (NY, US). **San Juan**: trail between Lagunita (Lagüita) and Pico Duarte, [19°01'N, 70°59'W], 2,250 m, 20 Jul 1967, *Gastony et al.* 376 (NY).

BRAZIL. **Rio de Janeiro**: Teresópolis, Brade Frade, [22°26'S, 42°59'W], Sep 1929, *Brade* 9333 (UC); Serra dos Órgãos, Picada do Rancho Frio, [21°52'S, 42°38'W], 1,400 m, 24 Jul 1940, *Brade* 16466 (BR); Alto Macaé, [22°16'S, 42°32'W], 12 Mar 1870, *Glaziou* 4364 (P).

10. ***Elaphoglossum novogranatense*** A.Vasco, sp. nov.—TYPE: COLOMBIA. Risaralda: Mun. Santuario, PNN Tatamá, camino que lleva al Páramo de Tatamá, 5°07'22.0"N, 76°02'45.2"W, 3,060 m, 17 Apr 2007, A. Vasco *et al.* 746 (holotype: HUA!; isotype: NY!).

Fig. 1J, 14B, 16

Haec species quoad habitum epiphyticum, rhizomata brevia erecta, petiolorum squamas cilatas majores, laminam abaxialiter glabram vel subglabram squamis sparsim dispersis nunquam imbricatis et sporas papillatas *Elaphoglosso glabrescenti* similis, sed ab eo squamis costalibus adaxialibus atrobrunneis, venis prominentibus et praesentia squamarum inter sporangia differt.

Plants epiphytic. *Rhizomes* 3–5 mm wide, short-creeping to erect; *rhizome scales* 5–9(–13) mm long, linear-lanceolate, orange to dark brown, denticulate to ciliate, the base truncate to slightly cordate or stalked, the apex piliform to tortuous. *Sterile leaves* 20–36(–50) cm long, approximate; *phyllopodia* present, not obscured by the petiole-base scales; *petioles* 8–15(–21) cm long, 1/3–1/2 the length of the sterile leaf; *larger petiole scales* 3–5 mm long, dense, spreading, lanceolate to oblanceolate, orange to dark brown, sometimes mottled or darker at the point of attachment, ciliate, the base truncate, sometimes short-stalked, the apex acute; *smaller petiole scales* 0.5–1 mm long, dense, oftentimes hidden by the larger ones, oblanceolate to round, orange to dark brown, or mottled, ciliate, the base truncate to stalked, the apex acute; *laminae* 11–24(–30) × 3–5 cm, oblanceolate to lanceolate, coriaceous, the base broadly cuneate to obtuse, the apex obtuse; *veins* 1–2 mm apart, at an angle of 75°–80° with respect to the costa; *adaxial laminar scales* 1–2 mm long, scattered, oblanceolate, white to light brown, ciliate, the base cordate to truncate, the apex acute; *abaxial laminar scales*

0.5–3 mm long, from absent to scattered, when present slightly elevated above the surface of the lamina and never imbricate, lanceolate to round, orange to dark brown, sometimes mottled with lighter margins, ciliate, the base truncate to short-stalked, the apex acute; *abaxial costal scales* 0.5–2.5 mm long, dense, pointing parallel to the costa, not elevated, lanceolate to round, dark brown, sometimes mottled, ciliate, the base cordate to truncate, the apex acute; *marginal scales* 0.5–1 mm long, dense, oblanceolate, orange, ciliate, the base truncate, short-stalked, the apex acute. *Fertile leaves* longer than the sterile; *petioles* $3/5$ – $5/7$ the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 9–15 × 1.5–2 cm, narrowly-elliptic to linear-lanceolate, coriaceous, the base truncate, the apex obtuse; *adaxial laminar scales* 0.5–1.5 mm long, dense, oblanceolate to round, orange to dark brown, sometimes mottled, long-ciliate, the base truncate to cordate, the apex acute; *abaxial costal scales* 0.5–1.5 mm long, dense, pointing parallel to the costa, slightly elevated, oblanceolate to round, orange to dark brown, sometimes mottled, long-ciliate, the base truncate to short-stalked, the apex acute; *intersporangial scales* 0.5–1.5 mm long, scattered, not obscuring the sporangia, lanceolate to oblanceolate, orange, sometimes mottled, long-ciliate, the base truncate, the apex acute to piliform. *Spores* papillate, without ridges.

Distribution—Colombia, Ecuador; 2,600–3,300 m (Fig. 14B). Epiphytic in montane and cloud forests.

Comments—*Elaphoglossum novogranatense* can be distinguished by its epiphytic habit, short-creeping or ascending rhizomes, appressed, dark brown abaxial costal scales, and papillate spores. The abaxial lamina surface is always visible, prominently veined, and either glabrous or sparsely scaly. It is similar to *E. glabrescens*, from which it can be distinguished by its appressed, dark brown adaxial costal scales, and the presence of intersporangial scales.

In contrast, *E. glabrescens* has appressed to spreading, orange to dark brown, sometimes mottled with lighter margins or darker at the point of attachment costal scales, and lacks intersporangial scales.

See *Elaphoglossum aschersonii* comments for a comparison with that species.

The specific epithet refers to New Granada (Nueva Granada), a former name for Colombia, after which the species is named. The name when used alone refers to the present-day country of Colombia, but it also can refer to several political entities at different historical periods that also included parts of the present-day countries of Panama, Venezuela and Ecuador, with smaller portions of Brazil, Costa Rica and Nicaragua: New Kingdom of Granada (1538—1717), Viceroyalty of New Granada (1717—1810 and 1816—1819), United Provinces of New Granada (1810—1816), Republic of the New Granada (1830—1858), and Granadine Confederation (1858—1863).

Representative Specimens Examined—COLOMBIA. **Antioquia:** Mun. Bello, Corregimiento de San Felix, Alto de Las Baldías, sector antenas de El Colombiano, 6°20'38"N, 75°38'54"W, 2,950–3,050 m, 1 Oct 2005, *Rodríguez et al.* 5500 (HUA, NY). **Cauca:** Km 55 on road from Totoró to Inzá, E of Páramo de Guanacas, [2°31'N, 76°11'W], 2 Aug 1972, *Barrington* 484 (COL); Mun. Puracé, San Rafael Km 149, vía La Plata-Popayán, margen derecha del Río Cocuy, [2°20'N, 76°30'W], 3,300 m, 16 Apr 1982, *Torres* 884 (COL). **Huila:** Macizo Colombiano, Páramo de Las Papas, cerros y alrededores de la laguna La Magdalena, [1°54'N, 76°39'W], 3,530 m, 16 Oct 1958, *Idrobo et al.* 2947pp (COL). **Risaralda:** Mun. Santuario, Parque Nacional Natural Tatamá, camino que lleva al Páramo de Tatamá, subiendo hacia Morro Zancudo, 5°07'28.1"N, 76°02'30.6"W, 2,643 m, 17 Apr 2007, *Vasco et al.* 735 (HUA, NY); Mun. Santuario, Parque Nacional Natural Tatamá, camino que lleva al Páramo de Tatamá, 5°07'22.7"N, 76°02'40.5"W, 3,060 m, 17 Apr 2007, *Vasco et al.* 742 (HUA, NY).

ECUADOR. **Carchi:** Valle de Maldonado, Km 67 on the road Tulcán-Maldonado, 0°53'N, 78°04'W, 2,600 m, 21 May 1973, *Holm-Nielsen et al.* 6246 (AAU); border area Prov. Carchi and Sucumbios, road Julio Andrade-Playón de San Francisco, [0°36'N, 77°38'W], 3,300 m, 9 Aug 1989, *van der Werff* 11067 (MO). **Chimborazo:** along road Julio Andrade-El Carmelo-Tulcán, 2,900–3,200 m, 7 Aug 1989, *van der Werff* 10962 (MO, UC).

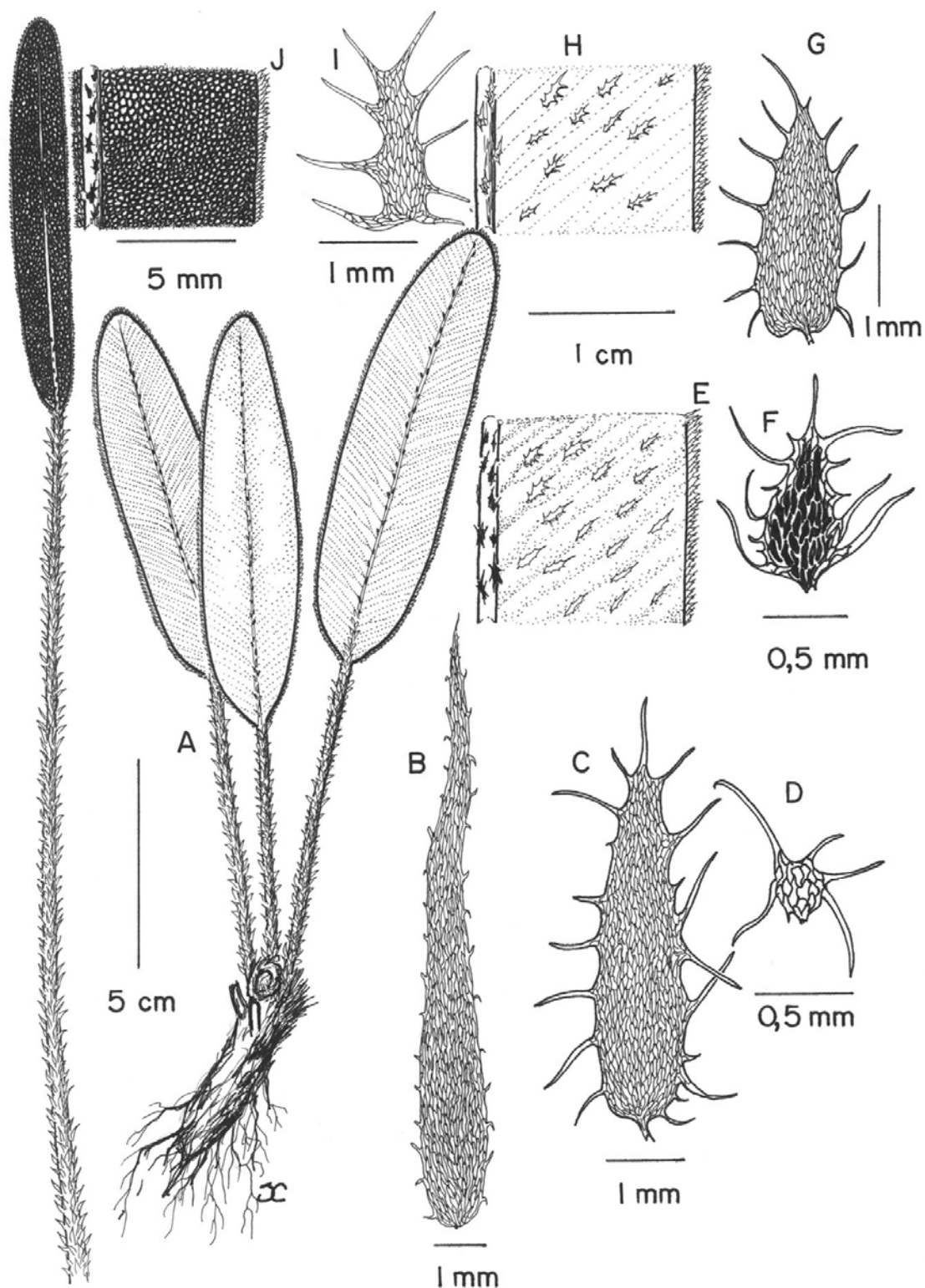


FIG. 16. *Elaphoglossum novogranatense*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial costal scale. G. Abaxial laminar scale. H. Adaxial lamina surface. I. Adaxial laminar scale. J. Fertile lamina. (From Vasco *et al.* 746, HUA).

11. *ELAPHOGLOSSUM OCULATUM* Mickel, Fieldiana, Bot., n.s. 27: 150. 1991.—TYPE: PERU. Piura: Prov. Huancabamba, above Huancabamba, road to Canchaque, [5°14'S; 79°27'W], 3,100 m, 10 Oct 1957, *P. C. Hutchison 1629* (holotype: UC!; isotype: GH!; photo NY! ex UC). **Fig. 1K, 17, 18A.**

Plants epiphytic. *Rhizomes* 3–5 mm wide, compact; *rhizome scales* 5–10 mm long, linear-lanceolate, dark brown, darker at the center, denticulate, the base truncate, the apex acuminate. *Sterile leaves* 22–35 cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* 8–13 cm long, 2/5 the length of the sterile leaf; *larger petiole scales* 3–4.5 mm long, dense, ascending, ovate, with the point of attachment dark brown, or mottled with lighter margins, erose to laciniate, the base cordate, the apex acute; *smaller petiole scales* 0.2–1 mm long, dense, ovate to round, with the point of attachment dark brown, or mottled with lighter margins, erose to laciniate, the base cordate, the apex acute; *laminae* 13–22 × 3–4 cm, oblong to oblanceolate, coriaceous, glabrescent, the base broadly cuneate to rounded, the apex obtuse; *veins* 1–1.5 mm apart, at an angle of 75°–80° with respect to the costa; *adaxial laminar scales* 0.2–0.5 mm long, scattered, round, some highly dissected, white to light brown, long-ciliate, the base cordate to truncate; *abaxial laminar scales* 0.2–0.5 mm long, scattered, round, some highly dissected, light brown, long-ciliate, the base cordate to truncate; *abaxial costal scales* 0.5–1.5 mm long, dense, pointing parallel to the costa, not elevated, ovate to round, dark brown or mottled with white margins, laciniate to ciliate, the base strongly cordate, the apex acute; *marginal scales* 0.5–1.5 mm long, dense, imbricate, obovate to oblanceolate, light brown to slightly mottled, laciniate, the base cordate to short-stalked (up to 0.1 mm), the apex acute. *Fertile leaves* longer than the

sterile; *petioles* 1/2–3/5 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 8–19 × 1–2 cm, narrowly elliptic to oblong, coriaceous, the base broadly cuneate to truncate, the apex obtuse; *adaxial laminar scales* 0.5–1.5 mm long, dense, oblanceolate to round, dark brown or mottled with lighter margins, laciniate to ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, imbricate, not elevated, oblanceolate to round, orange, laciniate to ciliate, the base cordate, the apex acute; *intersporangial scales* 0.5–1.5 mm long, dense, almost covering the sporangia, oblanceolate to round, orange, ciliate, the base cordate to truncate, the apex piliform to acute. *Spores* papillate, with ridges.

Distribution—Peru, known only from the type; 3,100 m (Fig. 18A). Epiphytic in cloud forests.

Comments—*Elaphoglossum oculatum* can be distinguished by its larger petiole scales that are ovate, have a dark point of attachment, and are mottled with white margins. Furthermore, the laminar scales are 0.2–0.5 mm long, round, highly dissected, long-ciliate, and the abaxial costal scales are dark brown or mottled with white margins. The spores are ridged and papillate. The laminar scales are more abundant on the abaxial surface, but they are so small that the surfaces appear glabrous to the naked eye.

This species is similar to *E. corderoanum* but differs by its shorter (0.2–0.5 mm long) laminar scales and dark-brown abaxial costal scales. *Elaphoglossum corderoanum* has larger (0.5–2.5 mm long) laminar scales and light-brown abaxial costal scales.

Elaphoglossum oculatum is only known from the type collected in northwestern Peru, in a cloud forest at 3,100 m. The two paratypes of *E. oculatum* (Mickel 1991), Woykowski 35433 (UC, US) and Sokup 176 (F), are *E. bellermannianum*.

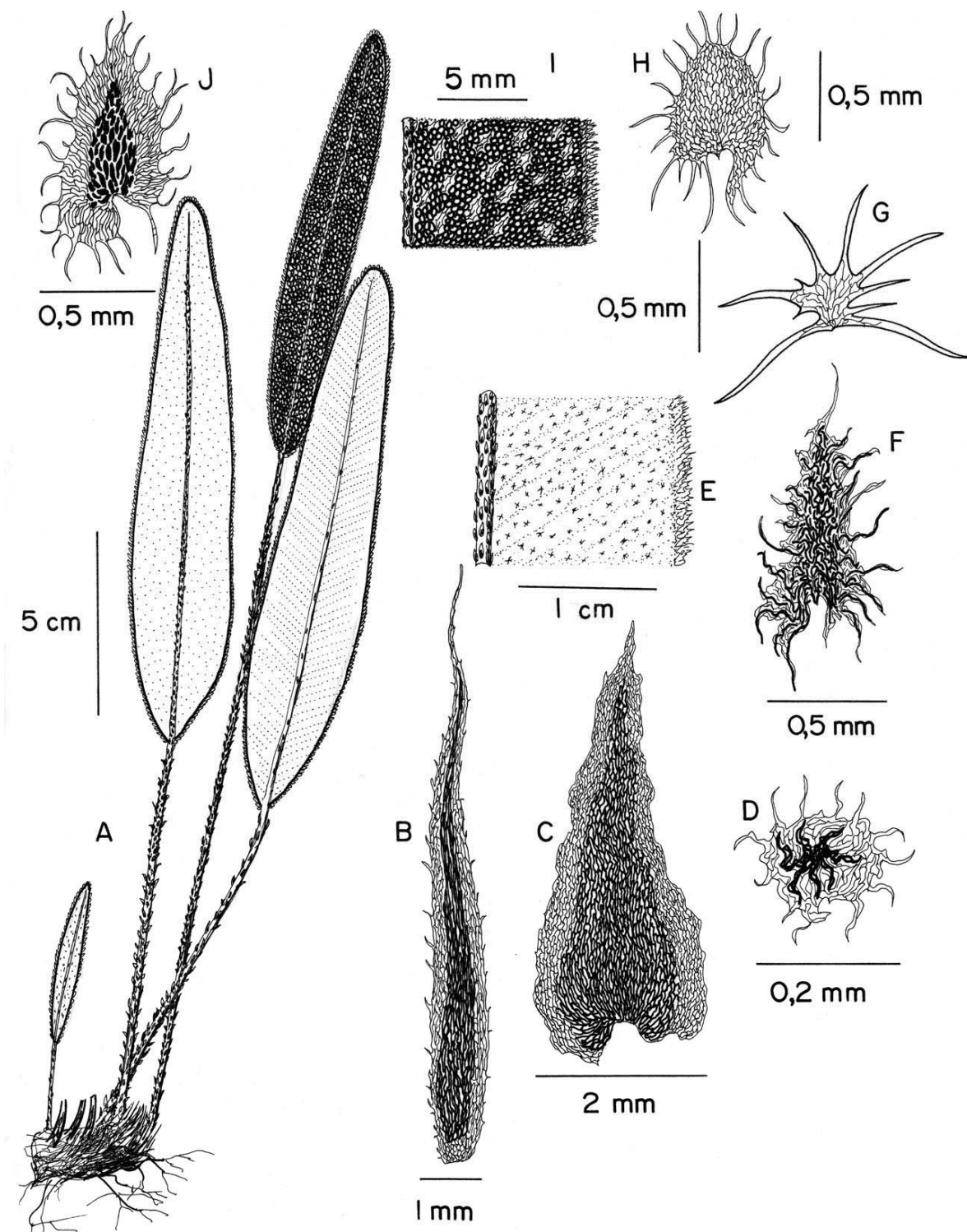


FIG. 17. *Elaphoglossum oculatum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar costal scale. G. Abaxial laminar scale. H. Marginal laminar scale. I. Fertile lamina. J. Intersporangial scale. (From Hutchison 1629, UC).

12. **Elaphoglossum oreophilum** A.Vasco, sp. nov.—TYPE: ECUADOR. Napo: road Quito-Baeza, 7–8 km NW of Laguna de Papallacta, Páramo de Guamaní, 0°19'S, 78°08'W, 3,800 m, 20 Jul 1976, B. Øllgaard & H. Balslev 8149 (holotype: NY!; isotypes: AAU!, GH!). **Fig. 1L, 14C, 19**

Haec species quoad habitum terrestrem, rhizoma longirepente, laminas foliaries oblanceolatas usque oblongas apicibus obtusis basibus truncatis et sporas papillatas porcatas *Elaphoglossum yatesii* similis, sed ab eo rhizomatis crassioris (3–5 mm) squamis fuscis vel atrofuscis saepe bicoloribus marginibus pallidioribus, petiolo marginato sicut laminae squamis abaxialibus longiciliatis et squamis costalibus abaxialibus adpressis differt.

Plants epiphytic or terrestrial. *Rhizomes* 3–5 mm wide, long-creeping; *rhizome scales* 3–9 mm long, linear-lanceolate, light brown to dark brown, bicolorous with the margins lighter or mottled, denticulate, the base cordate, the apex piliform. *Sterile leaves* 20–45 cm long, approximate to up to 1 cm apart; *phyllopodia* present, sometimes obscured by the petiole-base scales; *petioles* 9–28 cm long, ca. 1/2 the length of the sterile leaf; *larger petiole scales* 4–8 mm long, dense, spreading, sometimes pointing parallel to the petiole, linear-lanceolate to oblanceolate, light brown to dark brown, or mottled, darker at the point of attachment, the margins lighter, lacinate to long-ciliate, the base cordate, the apex acute; *smaller petiole scales* 0.2–1(–3) mm long, dense, appressed, oblanceolate to round, mottled to dark brown, always with lighter margins, long-ciliate, the base cordate, the apex acute; *laminae* 9–27 × 2–6 cm, oblanceolate to oblong, coriaceous, glabrescent with age, the base truncate to obtuse, the apex obtuse; *veins* 0.7–1.5 mm apart, at an angle of 75°–80° with respect to the costa;

adaxial laminar scales 0.5–2 mm long, dense, imbricate or not, lanceolate to round, white to brown, sometimes darker along the costa, erose to long-ciliate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–1 mm long, dense, imbricate, not elevated to slightly elevated above the surface of the lamina, oblanceolate to round, light brown to orange, ciliate to long-ciliate, the base stalked (up to 0.2 mm), the apex acute; *abaxial costal scales* 0.2–3 mm long, dense, pointing parallel to the costa, becoming spreading towards the base, not elevated, oblanceolate to round, dark brown with lighter margins or mottled, ciliate to long-ciliate, the base cordate to truncate, the apex acute; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* $3/5$ – $2/3$ the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 10–24 × 1.5–3.6 cm, narrowly elliptic to oblong, coriaceous, the base truncate to obtuse, the apex obtuse; *adaxial laminar scales* 0.4–1 mm long, dense, imbricate, lanceolate to round, white to light brown sometimes mottled, ciliate, the base cordate, the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, pointing parallel to the costa, slightly elevated, lanceolate to round, dark brown with lighter margins or mottled, erose to ciliate, the base cordate to short-stalked, the apex acute; *intersporangial scales* 0.2–2 mm long, scattered, sometimes inconspicuous, lanceolate to round, light brown to mottled, ciliate, the base cordate to truncate, the apex acute. *Spores* papillate, with ridges.

Distribution—Colombia, Ecuador; 3,000–4,200 m (Fig. 14C). Mainly terrestrial or growing in mats of bryophytes in páramos.

Comments—*Elaphoglossum oreophilum* can be distinguished from all other species of subsection *Muscosa* by its scales on the petioles and abaxial surface of the laminae. These scales have the cells of the body differentiated (Fig. 19C, F, G, K). The central portion is formed of irregular, usually darker isodiametric cells, and the broad border is formed of

usually lighter, elongated cells. The latter have their long axis perpendicular to that of the scale. This characteristic is not easily detected with the naked eye and even with a dissecting microscope can be difficult to discern. Another peculiarity is that the laminar scales tend to be round instead of oblanceolate to lanceolate as in most species in the group. The species is further characterized by long-creeping rhizomes, abaxial costal scales laying flat against the surface (not elevated), darker and differentiated from the laminar scales, and papillate, ridged spores. It is terrestrial and always occurs over 3,000 m.

Elaphoglossum oreophilum is similar to *E. yatesii*. Both species occur only above 3,000 m in Colombia and Ecuador. They share a mainly terrestrial habit, long-creeping rhizomes, oblanceolate to oblong laminae with obtuse apices and truncate bases, and papillate, ridged spores. They can be distinguished by their rhizome diameter and scales of the rhizomes, petioles, and laminae. *Elaphoglossum oreophilum* has thicker rhizomes (3–5 mm), brown to dark-brown rhizome scales often bicolorous with lighter margins, lacinate to long-ciliate petiole and abaxial laminar scales, and abaxial costal scales not elevated. In contrast, *E. yatesii* has thinner rhizomes (1–3 mm), typically dark-brown rhizome scales, erose to ciliate petiole and abaxial laminar scales, and abaxial costal scales elevated.

The specific epithet comes from the Greek *oreo*-, which means pertaining to mountains, and *-philus* meaning loving. It refers to the restricted occurrence of this species in mountains of Ecuador and Colombia.

Representative Specimens Examined—COLOMBIA. **Caldas:** PNN los Nevados, Alto del Cisne, 4°57'44.8"N, 75°21'15.1"W, 4,050 m, 8 Aug 2006, *Vasco 600* (HUA, MO, NY). **Cauca:** Parque Nacional del Puracé, camino del Pilimbalá al Volcán del Puracé, [2°15'N, 76°25'W], 3,700 m, 19 Jul 1976, *Jaramillo-Mejía 5220* (COL); en el alto del Volcán Puracé, [2°15'N, 76°25'W], 3,000 m, 7 Nov 1948, *Yepes-Agredo et al. 18 Ca. 123* (COL, MEDEL, US). **Nariño:** Mun. Pasto, Volcán Galeras, páramo al S de la cima, [1°13'N, 77°22'W], 3,700 m, 24 Dec 1972, *Hagemann 1780* (COL, PSO). **Quindío:** Mun. Salento, vereda Cocora below Nevado del Quindío, 4°40–45'N, 75°20–25'W, 3,500 m, 20–22 May 1989, *Luteyn et*

al. 13052 (COL, NY); Páramo del Quindio, [4°43'N, 75°23'W], 3,500–3,800 m, 15–20 Aug 1922, *Pennell 10079* (US). **Risaralda**: Mun. Sta. Rosa, vertiente Occidental, hacienda La Sierra, [4°50'N, 75°32'W], 3,700 m, 22 Jan 1980, *Jaramillo-Mejía et al. 5846* (COL). **Valle**: hoya del Río Bugalagrande, Bargaán, Páramo de Bavaya, [4°01'N, 75°52'W], 3,600 m, 16 Mar 1946, *Cuatrecasas 20043* (US).

ECUADOR. **Azuay**: Páramo de Soldados, at highest point of road W of Soldados, 2°57'S, 79°18'W, 3,700–4,000 m, 3 Mar 1985, *Øllgaard et al. 58524* (AAU). **Carchi**: Laguna Verde, 11 km W of Tufiño, on road to Maldonado, 0°45'N, 77°50'W, 3,910 m, 11 Nov 1988, *Dorr 6051* (NY); Páramo El Angel, in the pass on road El Angel-Tulcán, very humid Espeletia-páramo, 0°41'N, 78°54'W, 3,750–3,850 m, 15 May 1973, *Holm-Nielsen et al. 5482* (AAU, MO, NY). **Chimborazo**: Cerros Yuibug-Pailacajas, E side of the mountain ridge, 1°45'S, 78°27'W, 4,100–4,200 m, 30 Jul 1997, *Sklenar 3077* (NY). **Esmeraldas**: between Río Blanco and Río Quinindé, near the town of Qunindé, [0°22'N, 79°44'W], 1980, *de Vélez 4016* (COL). **Imbabura**: timber line vegetation on Hacienda Yura Cruz, 10 km N of Ibarra, 0°22'N, 78°05'W, 3,700–3,800 m, 25 May 1973, *Holm-Nielsen et al. 6501* (AAU, UC). **Napo**: Cerro Conga, Cordillera de Chalupas, elfin forests, 0°52'S, 78°16'W, 3,800 m, 10 Aug 1979, *Holm-Nielsen 19071* (AAU); road Quito-Baeza, 5 km NW of Laguna de Papallacta, Páramo de Guamaní, 0°19'S, 78°07'W, 3,700–3,750 m, 18 Jul 1976, *Øllgaard 8068* (AAU, NY). **Pichincha**: along road Quito-Papallacta, in páramo near Papallacta, [0°25'S, 79°10'W], 2,800–3,900 m, 27 Feb 1994, *van der Werff 13359* (MO, NY). **Tungurahua**: Santiago de Pillaro, Parque Nacional Llanganates, W of Cerro Hermoso, near saddle between headwaters of Río Topo, 1°11'40"S, 78°19'34"W, 3,950 m, 12 Nov 1999, *Neill et al. 11995* (MO, UC).

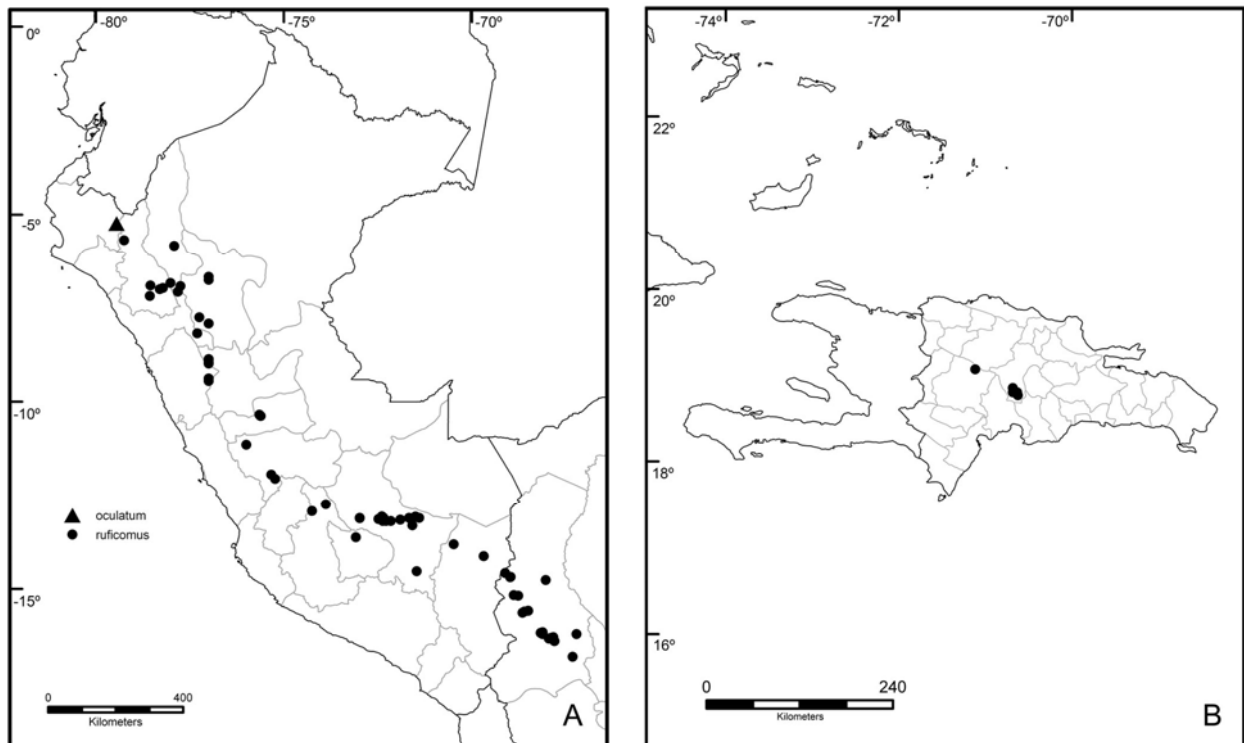


FIG. 18. Distribution of three species of *Elaphoglossum* subsect. *Muscoca*. A. *E. oculatum* and *E. ruficomum*. B. *E. quisqueyanum*.

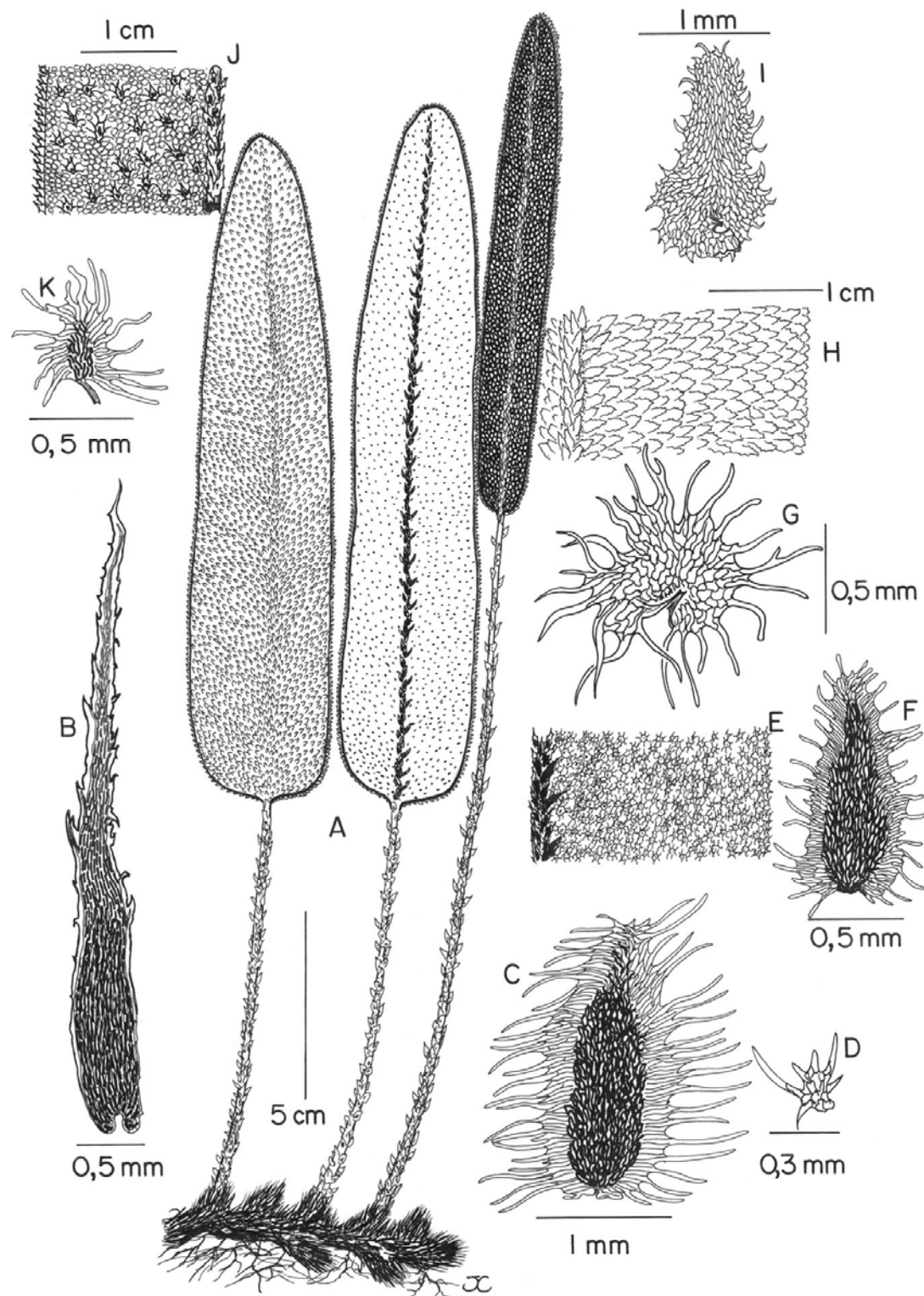


FIG. 19. *Elaphoglossum oreophilum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial lamina surface. F. Abaxial costal scale. G. Abaxial laminar scale. H. Adaxial lamina surface. I. Adaxial laminar scale. J. Fertile lamina. K. Intersporangial scale. (From Øllgaard 8149, NY).

13. ***Elaphoglossum quisqueyanum*** A.Vasco, sp. nov.—TYPE: DOMINICAN REPUBLIC.

Ázua: Cordillera Central, Loma de la Mediana, [19°04'N, 71°07'W], 2,600 m, 15 Sep 1929,

E. L. Ekman 13556 (holotype: NY!; isotypes: F!, GH!, US!). **Fig. 2A, 18B, 20.**

Haec species quoad habitum terrestrem, squamas rhizomatis ciliatas et laminae foliaris squamas abaxiales densas imbricatas leviter arcuatas *Elaphoglossum engelii* similis, sed ab eo rhizomatis crassioris ramosi squamarum ciliis paucioribus longioribus (usque ad 0.6 mm) et sporis papillois porcatis differt.

Plants terrestrial. *Rhizomes* 5–10 mm wide, long-creeping; *rhizome scales* 8–11 mm long, linear-lanceolate, maroon to dark brown, sometimes bicolorous, the margins lighter, ciliate, denticulate to ciliate (the cilia up to 0.6 mm long), the base truncate, the apex piliform. *Sterile leaves* 20–45 cm long, approximate to up to 1 cm apart; *phyllopodia* present, sometimes obscured by the petiole-base scales; *petioles* 8–25 cm long, 2/5–3/5 the length of the sterile leaf; *larger petiole scales* 4–7 mm long, dense, spreading, sometimes pointing parallel to the petiole, linear-lanceolate to oblanceolate, from orange to brown or mottled, darker at the point of attachment, erose to ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *smaller petiole scales* 0.5–2(–3) mm long, dense, appressed, oblanceolate to round, from orange to brown, darker at the point of attachment, ciliate, the base cordate, the apex acute; *laminae* 9–28 × 2.1–4.2 cm, linear-lanceolate to oblanceolate, coriaceous, glabrescent with age, the base truncate to rounded, the apex obtuse; *veins* 1–1.5 mm apart, at an angle of 75° with respect to the costa; *adaxial laminar scales* 1.5–3 mm long, dense, imbricate, oftentimes pointing downwards, lanceolate,

white to light brown, ciliate, the base cordate, the apex acute; *abaxial laminar scales* 1–3.5 mm long, dense, imbricate, slightly elevated above the surface of the lamina, lanceolate to oblanceolate, from orange to brown, darker at the point of attachment, ciliate, the base stalked (up to 0.4 mm), the apex acute; *abaxial costal scales* same as the laminar ones, longer; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* $3/5$ – $3/4$ the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* 9.5 – 20×1 – 2.1 cm, narrowly elliptic, coriaceous, the base truncate to broadly cuneate, the apex acute to obtuse; *adaxial laminar scales* 1–3 mm long, dense, imbricate, lanceolate, from orange to brown, darker at the point of attachment, ciliate, the base cordate, the apex acute; *abaxial costal scales* 1–4 mm long, dense, pointing parallel or at right angles to the costa, slightly elevated, lanceolate to round, from light to dark brown, darker at the point of attachment, ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *intersporangial scales* 1–2.5 mm long, scattered, lanceolate, from light to dark brown, ciliate, the base cordate to truncate, the apex acute. *Spores* papillate, with ridges.

Distribution— Dominican Republic, provinces of Ázua and La Vega; 2,000–2,800 m (Fig. 18B). Terrestrial in cloud forests.

Comments —*Elaphoglossum quisqueyanum* is characterized by a terrestrial habit, long-creeping rhizomes, maroon to dark brown, linear, denticulate to ciliate rhizome scales, erose to ciliate larger petiole scales, and papillate, ridged spores. It resembles *E. engelii*, a species from Central and South America, but differs by its thicker (5–10 mm wide) rhizomes, rhizome scales denticulate to ciliate, the cilia up to 0.6 mm long, and papillate, ridged spores.

In contrast, *E. engelii* has thinner (4–8 mm wide) rhizomes, scales that when ciliate, have abundant cilia that are no longer than 0.4 mm, and spores with ridges and irregular deposits.

Jones & Norris 1119 (NY) is a small form of this species, with thinner rhizomes and smaller leaves, but is otherwise typical.

The specific epithet refers to Quisqueya, the name given by the indigenous peoples, the Tainos, to the Dominican Republic, where this species is endemic. In the Taino language *quisqueya* means “mother of the earth.”

Additional Specimens Examined—DOMINICAN REPUBLIC. **Ázua:** between Valle Nuevo and Azua, [18°47'N, 70°38'W], 2,000–3,000 m, 24 Dec 1964, *Jones & Norris 1119* (NY). **La Vega:** in Loma Rosilla, 2,700 m, 6 Aug 1912, *Fuertes 1808* (NY, US); Valle Nuevo, [18°48'N, 70°41'W], 2,300 m, 5 Apr 1947, *Jiménez 1379* (NY, US); 11 km S of Constanza, vía el Convento, on road to San José de Ocoa, vic. of El Convento, 18°51'N, 70°41'W, 1,500 m, 24 Jul 1980, *Mejía 7650* (NY); Pico Alto de la Bandera, E de Valle Nuevo, 18°48'N, 70°38'W, 2,790–2,800 m, 14 May 1982, *Zanoni 20681* (JBSD); Cordillera Central, 31.9 km S de Constanza (camino vía Río Grande), 6 km N del monumento La Pirámide, 18°46'N, 70°37.5'W, 2,225 m, 11 Jun 1982, *Zanoni 20917* (JBSD, MO, NY).

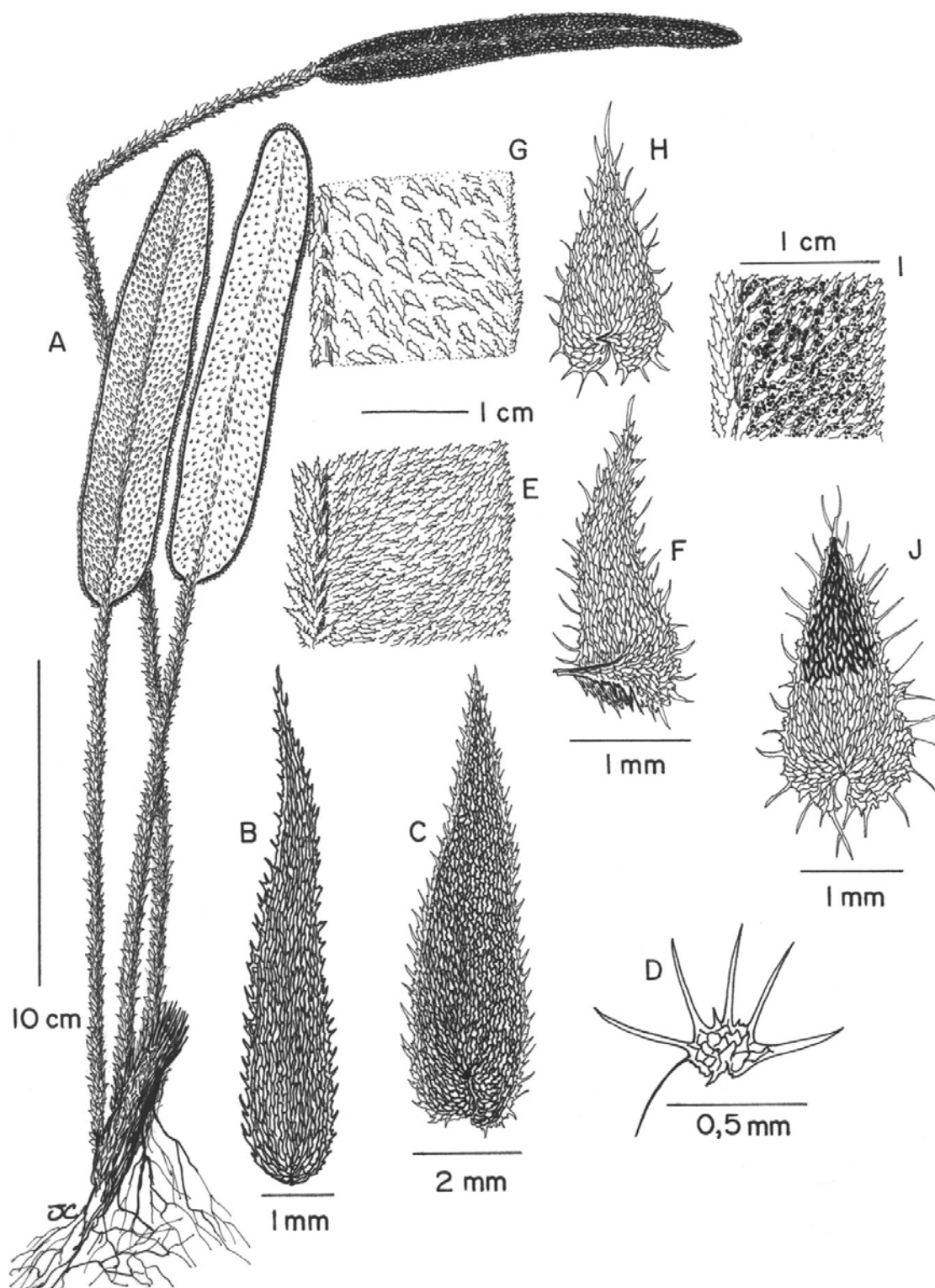


FIG. 20. *Elaphoglossum quisqueyanum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Adaxial laminar scale. I. Fertile lamina. J. Intersporangial scale (From Ekman 13556, US).

14. ELAPHOGLOSSUM RUFICOMUM Mickel [as “*ruficomus*”], Fieldiana, Bot., n.s. 27: 159.
 1991.—TYPE: PERU. Cajamarca: Celendín, Sendamal, ruta a Celendín, 3,050 m, 17 Aug
 1984, A. Sagástegui *et al.* 12091 (holotype: NY!, isotype: GH!). **Fig. 2B, 18A, 21**

Plants terrestrial. *Rhizomes* 8–11 mm wide, compact; *rhizome scales* (6–)12–16(–20) mm long, linear, red-orange, lustrous, entire to denticulate, the base truncate, the apex piliform. *Sterile leaves* (8–)16–30(–55) cm long, approximate; *phyllopodia* present, obscured by the petiole-base scales; *petioles* (3.5–)7–17(–27) cm long, 1/3–2/5 the length of the sterile leaf; *larger petiole scales* (3–)4–6 mm long, dense, spreading, linear-lanceolate, light brown, sometimes dark brown or mottled, ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *smaller petiole scales* 0.5–1(–3) mm long, dense, appressed, oftentimes hidden by the larger ones, oblanceolate to round, light brown, sometimes black or mottled with lighter margins, ciliate, the base cordate (sometimes appearing peltate because of the large auricles), the apex acute; *laminae* (5–)10–17(–27) × 1.4–3.5 cm, narrowly elliptic to oblanceolate, coriaceous, glabrescent with age, the base broadly cuneate to rounded, the apex obtuse to acute; *veins* 1–2 mm apart, at an angle of 75°–80° with respect to the costa; *adaxial laminar scales* 1–3 mm long, dense, imbricate, pointing downwards, lanceolate, white, the costal ones sometimes darker at the point of attachment to completely black, ciliate, the base cordate to short-stalked, the apex acute; *abaxial laminar scales* 1–3 mm long, dense, imbricate to scattered, slightly elevated above the surface of the lamina to patent, lanceolate to oblanceolate, light brown, sometimes darker at the point of attachment, ciliate, the base cordate to short-stalked (up to 0.2 mm), the apex acute; *abaxial costal scales* same as the laminar ones, pointing parallel or at right angles to the costa,

slightly elevated; *marginal scales* same as the laminar ones. *Fertile leaves* equal to longer than the sterile; *petioles* 2/5–3/5 the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf but the larger ones more spreading; *laminae* 8–20(–25) × 0.8–2.5 cm, narrowly elliptic, coriaceous, the base truncate to broadly cuneate, the apex obtuse; *adaxial laminar scales* 1–2.5 mm long, dense, imbricate, lanceolate, white to light orange, ciliate, the base cordate to short-stalked (less than 1 mm), the apex acute; *abaxial costal scales* 1–3 mm long, dense, pointing parallel or at right angles to the costa, slightly elevated to patent, lanceolate to round, orange to black with lighter margins, ciliate, the base cordate to short-stalked, the apex acute; *intersporangial scales* 1–2 mm long, absent to scattered, lanceolate, orange, sometimes darker at the point of attachment, ciliate, the base cordate, the apex acute. *Spores* papillate, without ridges.

Distribution—Peru, Bolivia; 1,900–4,300 m (Fig. 18A). Usually terrestrial in montane and cloud forests and in páramos.

Comments—*Elaphoglossum ruficomum* can be distinguished from all other species of subsection *Muscosa* by its long [(6–)12–20 mm], linear, bright red-orange rhizome scales. Also distinctive are its terrestrial habit and compact rhizomes. It differs from *E. engelii* by the long, entire to denticulate rhizome scales and papillate spores. *Elaphoglossum engelii* scales are typically up to 12 mm long, ciliate, with many teeth longer than 0.2 mm, and have spores with ridges and irregular deposits

See *Elaphoglossum lehmannianum* comments for a comparison with that species

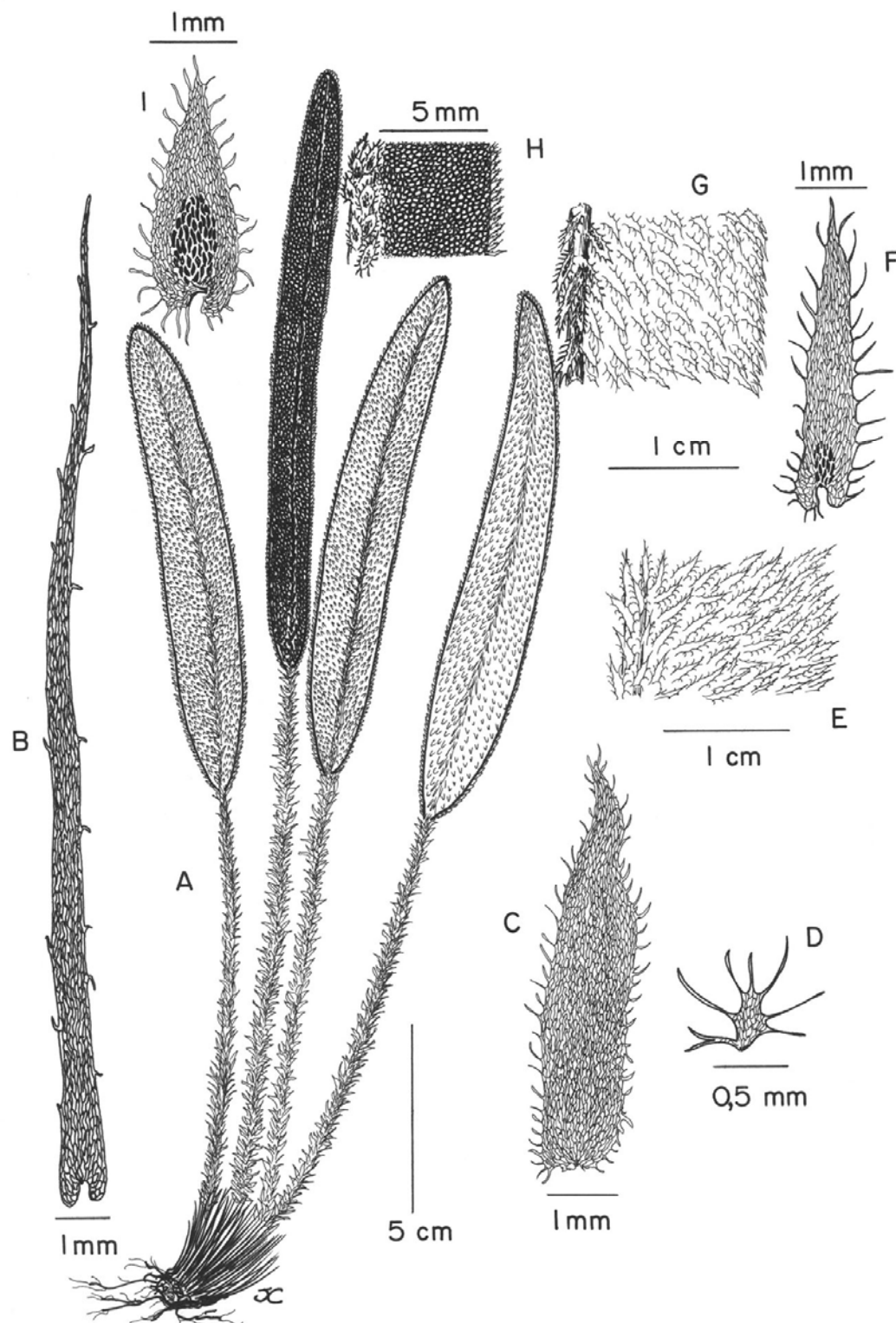


FIG. 21. *Elaphoglossum ruficomum*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial lamina surface. F. Abaxial laminar scale. G. Adaxial lamina surface. H. Fertile lamina. I. Fertile costal scale. (From Boeke 2970, HUA and NY).

Representative Specimens Examined—PERU. **Amazonas:** Prov. Chachapoyas, Balsas-Leimebamba road, Km 403, 4 Jun 1977, *Boeke 1940* (MO, NY); Prov. Chachapoyas, Cerros Calla Calla, E side, 19 km above Leimebamba on road to Balsas, [6°55'N, 77°45'W], 3,100 m, 6 Jun 1964, *Hutchison 5567* (NY, UC). **Ancash:** Prov. Yungay, Huascarán National Park, quebrada Paria, 8°57'S, 77°33'W, 4,200 m, 13 Jan 1985, *Smith et al. 9174* (MO, NY); Prov. Huari, Huascarán National Park, slopes below and valley of Laguna Ichicpotrero, 9°27'S, 77°15'W, 8 May 1986, *Smith et al. 12382* (MO, NY). **Apurímac:** 5 km N of Huancarama, [13°38'S, 73°05'W], 3,500 m, 6 Nov 1935, *West 3801* (UC). **Ayacucho:** Prov. La Mar, E mass of the Cordillera Central opposing the cordillera Vilcabamba between Tambo San Miguel, Ayna and the Hacienda Luisiana, 12°45'S, 73°53'W, 24 Aug 1968, *Dudley 12057* (MO, US); Pampalca, between Huanta and Río Apurímac, [12°56'S, 74°15'W], 3,200 m, 4–18 May 1929, *Killip 23283* (NY, US). **Cajamarca:** Prov. Jaén, Sallique, localidad La Cocha, 5°40'58'S, 79°14'53"W, 17 Jun 1998, *Campos et al. 5004* (MO, NY, UC); Prov. Cajabamba, Cajabamba-Luchubamba, 3,800 m, 17 Nov 1983, *Sagástegui et al. 11200* (GH, MO, NY). **Cusco:** Prov. La Convención, Dist. Vilcabamba, Vilcabamba La Vieja, 13°07'S, 72°59'W, 1,892 m, 20 Sep 2003, *Calatayud et al. 1873* (MO, NY, UC); Prov. Urubamba, Dist. Urubamba, Mantamay, 13°12'03"S, 72°09'20"W, 15 Sep 2002, *Farfán et al. 404* (MO, UC). **Huánuco:** Pampayacu, [11°09'07"S, 76°36'15"W], 17 Jan 1927, *Kanehira 164* (US); Prov. Huánuco, road from Huánuco to Tingo María, N of Carpish Pass, 50–52 km NE of Huánuco, 6 Dec 1981, *Plowman 11143* (F). **Junín:** Prov. Huancayo, Mito, [11°57'S, 75°20'W], 8–18 Apr 1923, *Bryan 370* (F); Prov. Huancayo, Torre-Torre, [12°04'S, 75°14'W], Feb 1948, *Soukup 3593* (F, US). **La Libertad:** Prov. Sánchez Carrión, road from Trujillo to Huamachuco, at edge of escarpment where road begins descent toward Aricapampa, 4,000 m, 22 Feb 1982, *Dimmitt 1135* (NY); Prov. Pataz, alrededores de Minera La Estrella, Huaylillas, 8°10.8'S, 77°18.2'W, 4,000 m, 23 Aug 2002, *Sagástegui 17032* (UC). **Lambayeque:** Prov. Ferreñafe, ca. 7 km NW of Incahuasi, near Cerro Punamachay on trail to laguna Ualtaco, [6°14'S, 79°19'W], 16 Nov 1984, *Dillon 4116* (F, GH). **Pasco:** Prov. Oxapampa, Dsit. Huancabamba, sector Santa Barbara-Milpo, 10°22'55"S, 75°37'19"W, 1 Feb 2005, *Mellado 2725* (MO, NY); Prov. Oxapampa, Distrito Huancabamba, localidad de Lanturachi, sector Santa Bárbara, alrededor del campamento en Milpo, 10°23'S, 75°37'W, 2,862 m, 20 Oct 2003, *Perea et al. 800* (MO). **Puno:** Prov. Carabaya, 10 km S of Ollachea, [13°49'S, 70°29'W], 13 Aug 1980, *Boeke 2970* (HUA, MO, NY); Prov. Sandia, 2–6 km S of Limbani, [14°08'S, 69°41'W], 11–12 May 1942, *Metcalf 30453* (UC, US). **San Martín:** Prov. Huallaga, Valley of Río Apisoncho, 30 km above Jucusbamba, 7°55'S, 77°10'W, 3,200 m, 9 Sep 1965, *Hamilton 906* (US); Prov. Mariscal Cáceres, Puerta del Monte valley, Río Abiseo National Park, [7°45'S, 77°15'W], 3,550 m, 11 Mar 1988, *León 1441* (NY).

BOLIVIA. **La Paz:** Prov. Murillo, Valle de Zongo, Santa Rosa, 3 km hacia La Paz, [16°09'S, 68°07'W], 3,030 m, 8 Apr 1979, *Beck 1094* (LPB, NY); Prov. Larecaja, Gran Poder, small gold mine about 40 km N of Sorata, below Tacacoma, [15°38'S, 68°39'W], 3,000 m, 7 Jun 1950, *Brooke 6447* (BM, F, NY); Prov. Nor Yungas, Unduavi, [16°19'S, 67°54'W], 3200 m, Feb 1914, *Buchtien s.n.* (F, NY); Prov. Murillo, Zongo Valley, ca. 62 km from La Paz, the Chaca, Pampa turn off, 16°11'10"S, 68°08'10"W, 3,500 m, 5–6 Aug 1990, *Fay 2868* (LPB, MO, NY, UC).

15. ELAPHOGLOSSUM YATESII (Sodirol) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesamten Naturwiss. [Monogr. *Elaphoglossum*] 36(1): 83, f. 37. 1899. *Acrostichum yatesii* Sodirol, Anales Univ. Centr. Ecuador 4: 174. 1890.—TYPE: ECUADOR. Pichincha: Crece en la pendiente occidental del Pichincha a 3,900 m en el sitio llamado "Tablahuasi", s.d., L. Sodirol s.n. (**lectotype, designated here** P! (sheet 00577720); duplicate: P! (sheet 00577721)). **Fig. 2C, 22, 23.**

Plants terrestrial or epipetric. *Rhizomes* 1–3(–4) mm wide, long-creeping; *rhizome scales* 4–5 mm long, linear-lanceolate to lanceolate, maroon to dark brown, sometimes bicolorous with lighter margins, denticulate to ciliate, the base cordate (appearing peltate because of the large auricles), the apex acuminate to piliform. *Sterile leaves* 13–33 cm long, 1–2 cm apart; *phyllopodia* present, not obscured by the petiole-base scales; *petioles* 6.5–20 cm long, 1/2–3/5 the length of the sterile leaf; *larger petiole scales* 3–5 mm long, dense, spreading, to most of the times pointing parallel to the petiole, lanceolate to oblanceolate, light brown to dark brown, or mottled, always darker at the point of attachment, the margins lighter, erose, the base cordate, the apex acute; *smaller petiole scales* 0.2–1(–3) mm long, dense, appressed, oblanceolate to round, light brown to dark brown, or mottled, darker at the point of attachment or bicolorous with the centers dark brown and the margins lighter, erose to ciliate, the base cordate, the apex acute; *laminae* 6.5–13 × 1.7–3 cm, linear-lanceolate to ovate, coriaceous, glabrescent with age, the base truncate to obtuse, the apex obtuse; *veins* ca. 1 mm apart, at an angle of 75°–80° with respect to the costa; *adaxial laminar scales* 0.5–2 mm long, dense, imbricate, oblanceolate to round, white to black or mottled, erose to lacinate, the base cordate, the apex acute; *abaxial laminar scales* 0.5–2.5 mm long, dense, imbricate, elevated

above the surface of the lamina to patent, oblanceolate to round, light brown to orange, sometimes dark brown, ciliate, the base stalked (up to 0.3 mm), the apex acute; *abaxial costal scales* 2–3 mm long, dense, pointing at right angles to the costa, elevated, linear-lanceolate to oblanceolate, dark brown to black, always with lighter margins, erose to ciliate, the base cordate to short-stalked, the apex acute; *marginal scales* same as the laminar ones. *Fertile leaves* longer than the sterile; *petioles* $2/3$ – $3/4$ the length of the fertile leaf; *petiole scales* same as the ones of the sterile leaf; *laminae* 4.5 – 13×1.2 – 2 cm, narrowly elliptic to oblong, coriaceous, glabrescent with age, the base truncate to broadly cuneate, the apex obtuse; *adaxial laminar scales* 0.3–2.5 mm long, dense, imbricate, oblanceolate to round, white to black, sometimes mottled, erose to lacinate, the base cordate (appearing peltate because of the large auricles), the apex acute; *abaxial costal scales* 0.5–2 mm long, dense, pointing at right angles to the costa, elevated, oblanceolate to round, dark brown with lighter margins or mottled, lacinate to ciliate, the base cordate, the apex acute; *intersporangial scales* 1–2.5 mm long, scattered to dense, sometimes almost obscuring the sporangia, lanceolate to oblanceolate, light brown to dark brown with lighter margins or mottled, ciliate, the base stalked (up to 0.3 mm), the apex acute. *Spores* papillate, with ridges.

Distribution—Colombia, Ecuador; 3,000–4,500 m (Fig.23). Terrestrial or epipetric in montane forest and páramos.

Comments—*Elaphoglossum yatesii* can be distinguished by its thin long-creeping rhizomes, dark brown rhizome scales, petiole scales appressed-ascending, and papillate, ridged spores. It occurs above 3,000 m.

Elaphoglossum yatesii is similar to *E. oreophilum* in its distribution (Colombia and Ecuador, over 3,000 m), habit (mainly terrestrial), rhizome type (long-creeping), and spore

micromorphology (ridges and papillae); however, the species can be easily distinguished by their petiole and laminar scales. *Elaphoglossum oreophilum* has long-ciliate petiole and laminar scales, whose cells of the body are differentiated with the central portion formed of irregular, isodiametric cells, and the broad border formed of elongated cells that have their long axis perpendicular to that of the scale). In contrast, *E. yatesii* has erose to ciliate petiole and laminar scales, whose cells are all isodiametric. Some specimens of *E. yatesii* have glabrescent abaxial laminar surfaces, whereas those of *E. oreophilum* are scaly.

See *Elaphoglossum oreophilum* comments for a further comparison

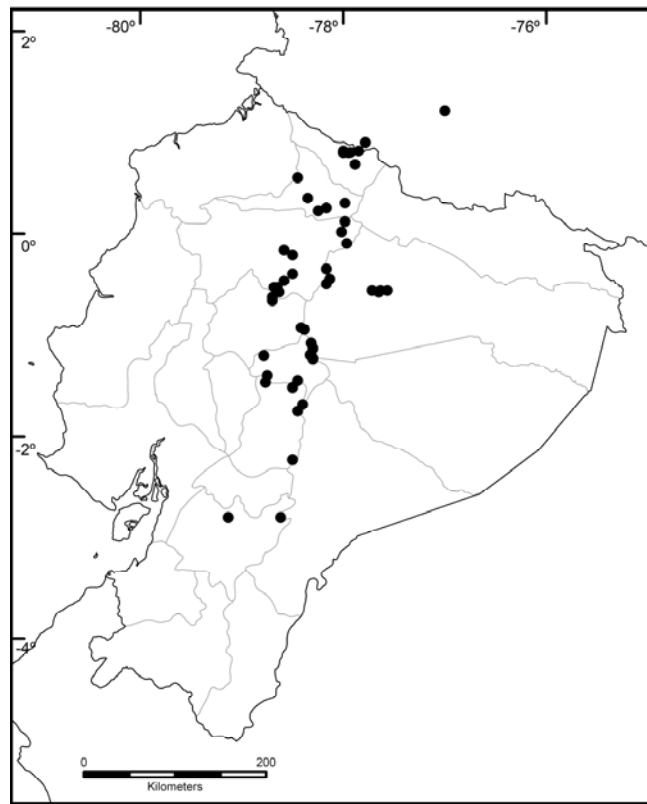


FIG. 22. Distribution of *Elaphoglossum yatesii*.

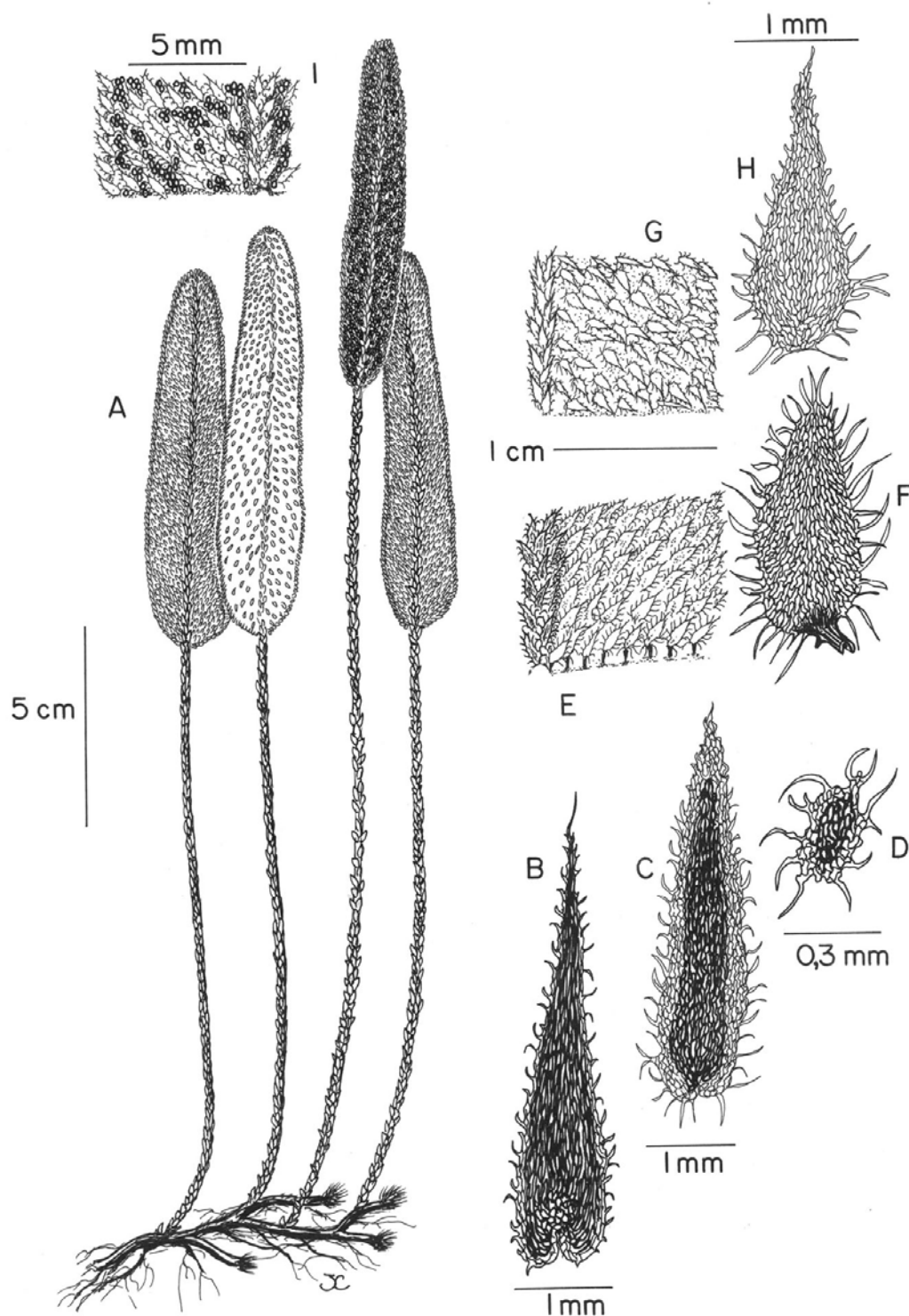


FIG. 23. *Elaphoglossum yatesii*. A. Habit. B. Rhizome scale. C. Larger petiole scale. D. Smaller petiole scale. E. Abaxial laminar surface. F. Abaxial laminar scale. G. Adaxial laminar surface. H. Adaxial laminar scale. I. Fertile lamina. (From Mille 202, US).

Representative Specimens Examined—COLOMBIA. **Nariño:** Mun. Pasto, Volcán Galeras, páramo al S de la cima, [1°13'N, 77°22'W], 3,700 m, 24 Dec 1972, *Hagemann 1782* (COL, PSO); Mun. Pasto, Volcán Galeras, [1°13'N, 77°22'W], 4,000 m, 22 Oct 1968, *Plowman 1949* (F, NY, US).

ECUADOR. **Azuay:** Cuenca, Area Nacional de Recreación Cajas, Laguna Toreadora, 2°48'S, 79°08'W, 3,800 m, 10 Oct 1995, *Alexander 31* (MO, UC); Sevilla de Oro, [2°48'S, 78°37'W], 3,700 m, 29 Jun 1947, *Harling 1256* (S). **Carchi:** Páramo del Angel, along road from El Chical to Tulcán, 68.1 km E of El Chical, 13.6 km W of Tufiño plaza, 0°48'08"N, 77°55'45"W, 3,200 m, 19 Feb 2004, *Croat 95025* (NY, UC); road Tulcán-Maldonado, W of the pass, base of Volcán Chiles, 0°49'N, 78°00'W, 3,650 m, 3 Aug 1976, *Øllgaard 8411* (AAU, NY, UC). **Chimborazo:** Cerro Altar, [1°31'S, 78°30'W], 3,700 m, 9 Aug 1935, *Heinrichs 899* (B); Carro Yanaurcu, N ridge of the mountain, 2°14'S, 78°30'W, 4,200 m, 29 Oct 1995, *Sklenar 1438* (AAU, NY). **Cotopaxi:** near origin of Río Langoa, E of Latacunga, Laguna Salayambo Cocha, 0°56'S, 78°25'W, 30 Sep 1976, *Øllgaard 9888* (AAU, NY, UC). **Imbabura:** Cerro Imbabura, E and S sides of the volcano just below the rocky escarpment, 0°15'N, 78°10'W, 5 Jun 1995, *Sklenar 568* (AAU); Nevado Cotacachi, SE ridge of the volcano, 0°21'N, 78°21'W, 9 Sep 1995, *Sklenar 1229* (NY). **Napo:** Cerro Sumaco, upper 100 m of cone, 0°34'S, 77°43'W, 1 May 1979, *Holm-Nielsen et al. 17586* (AAU, HUA, NY, QCA); Tena Canton, Parque Nacional Llanganates, vía Salcedo-Tena, de Laguna Chaloa Cocha desvío a Rayo Filo, 0°57'S, 78°23'W, 3,740 m, 20 Sep 1998, *Vargas et al. 2687* (MO, UC). **Pichincha:** NE Paschoa, en bosque a 50 m de la cúspide, [0°24'S, 78°30'W], 30 Jul 1980, *Jaramillo et al. 3181* (AAU, MO); Mount Pichincha, [0°10'S, 78°35'W], 4,000 m, 1919, *Mille 202* (COL, US). **Tungurahua:** Mocha, Parroquia Pinguili, Reserva Faunística del Chimborazo, 2 km antes de la base del lado E del Caryguayrazo, Cerro Pocacochas, Páramo de Salasaca entrando por Mocha, 1°24'S, 78°45'W, 3,860 m, 2 Jul 1992, *Cerón 19211* (MO); Santiago de Pillaro, Parque Nacional Llanganates, W of Cerro Hermoso, near saddle between headwaters of Río Topo, 1°11'40"S, 78°19'34"W, 3,950 m, 12 Nov 1999, *Neill et al. 11997* (MO, UC).

NAMES OF UNCERTAIN APPLICATION

Elaphoglossum dichrorum Mickel, Fieldiana, Bot., n.s. 27: 129. 1991.—TYPE: PERU.

San Martín: Mariscal Cáceres, Parque Nac. Río Abiseo, Puerta del Monte, 13 Mar 1988, *B.*

León & K. Young 1510 (holotype: USM; isotype: NY!; photo NY! ex USM).

I was only able to see the isotype of this species, which is sterile, and a photo of the holotype. Based on these and Mickel's (1991) description (which does not cite any

paratypes), I cannot discern if it is a distinct species or if it should be considered as a synonym of either *E. glabrescens* or *E. oculatum*. Mickel (1991) thought *E. oculatum* was the most similar species because of its concentration of scales along the margin, ciliate intersporangial scales, bicolorous petiole and costal scales, and the reduced scales of the abaxial lamina surface. However the shape and bigger size of the laminae, the lanceolate adaxial laminar scales, and the ciliate petiole scales suggest that the isotype of *E. dichroum* might correspond also to *E. glabrescens*. Until more material is available from *E. oculatum* and *E. dichroum*, I refrain from recognizing the last name as a species or from synonymizing it with either of the species mentioned above.

Acrostichum muscosum var. *macropodum* Sodiro, Crypt. Vasc. Quit. 473. 1893.—

TYPE: ECUADOR. Cerro de Puntas, sobre 3,800 m, s.d., *L. Sodiro*, s.n. (?).

I was not able to find any specimens of Sodiro that were annotated with this name, and from Sodiro's description I am uncertain to what species this name belongs.

Acrostichum lepidotum var. *engelii* (H. Karst.) Kuntze, Revis. Gen. Pl. 3 (2): 376.

1898.—TYPE: Bolivia. Tiraqui-Santa Rosa, s.d., *O. Kuntze*, s.n. (?).

I was not able to find the type of this variety. The only information the original description gives is that it is glabrescent. This characteristic and the provenance of the type suggest that the plant might be *E. glabrescens*, but I cannot be sure.

4.7. APPENDIXES

Appendix 1. List of Taxa

1. *Elaphoglossum aschersonii* Hieron.
2. *Elaphoglossum bellermannianum* (Klotzsch) T. Moore
3. *Elaphoglossum corderoanum* (Sodirol) H. Christ
4. *Elaphoglossum engelii* (H. Karst.) H. Christ
5. *Elaphoglossum gardnerianum* (Kunze ex Fée) T. Moore
6. *Elaphoglossum glabrescens* A. Vasco
7. *Elaphoglossum laxsquama* Mickel
8. *Elaphoglossum lehmannianum* H. Christ
9. *Elaphoglossum muscosum* (Sw.) T. Moore
10. *Elaphoglossum novogranatense* A. Vasco
11. *Elaphoglossum oculatum* Mickel
12. *Elaphoglossum oreophilum* A. Vasco
13. *Elaphoglossum quisqueyanum* A. Vasco
14. *Elaphoglossum ruficomum* Mickel
15. *Elaphoglossum yatesii* (Sodirol) H. Christ

APPENDIX 2. Distribution of *Elaphoglossum* subsection *Muscosa* species by country.

BOLIVIA: 4 species. *bellermandianum*, *engelii*, *glabrescens*, *ruficomum*.

BRAZIL: 2 species. *gardnerianum*, *muscosum*.

COLOMBIA: 8 species. *aschersonii*, *bellermandianum*, *engelii*, *laxisquama*,
lehmannianum, *novogranatense*, *oreophilum*, *yatesii*.

COSTA RICA: 3 species. *bellermandianum*, *engelii*, *lehmannianum*.

CUBA: 1 species. *muscosum*.

DOMINICAN REPUBLIC: 3 species. *bellermandianum*, *muscosum*, *quisqueyanum*.

ECUADOR: 9 species. *aschersonii*, *bellermandianum*, *corderoanum*, *engelii*,
laxisquama, *lehmannianum*, *novogranatense*, *oreophilum*, *yatesii*.

EL SALVADOR: 1 species. *muscosum*.

GUATEMALA: 2 species. *engelii*, *muscosum*.

HAITI: 1 species. *muscosum*.

HONDURAS: 1 species. *muscosum*.

JAMAICA: 1 species. *muscosum*.

MEXICO: 2 species. *engelii*, *muscosum*.

PANAMA: 2 species. *bellermandianum*, *lehmannianum*.

PERU: 5 species. *bellermandianum*, *engelii*, *laxisquama*, *oculatum*, *ruficomum*.

VENEZUELA: 4 species. *aschersonii*, *bellermandianum*, *engelii*, *lehmannianum*.

APPENDIX 3. Index to Collections

The number in parentheses refers to the species number assigned in the monograph (see Appendix 1); the numbers in boldface are types.

Abbott, J. R.: 17051, 17077 (6)
 Acosta, M.: 21 (4); 193 (8)
 Acosta-Arteaga, C. E.: 103 (2); 251, 302, 372 (4); 563 (8)
 Acosta-Solís, M.: 13281 (2); 13283, 14320 (8)
 Albert de Escobar, L.: 4151, 4302 (4); 4388 (7)
 Alexander, M.: 31 (15)
 Alfaro, E.: 708 (2)
 Alston, A. H. G.: 6597 (4); 7000A (8)
 Alvarez, A.: 2562 (15); 2608 (4)
 Alvear-P, M.: 494 (4)
 Anderson, W. R.: 3147, 3185 (9)
 André, B.: 1296 (4); 2089 (8); 3285 (12)
 Arbeláez, A. L.: 128 (8); 460 (4)
 Archer, W. A.: 1367 (1)
 Aristeguieta, L.: 851 (2); 3608 (8)
 Arroyo, L.: 61, 2767 (6)
 Asplund, E.: 17405 (4)
 Atehortúa, L.: 1235, 1237, 1238, 1239 (8); 1240 (1); 1310 (8); 1319 (1); 1320, 1321, 1322 (8)
 Azofeifa, A.: 110 (2)
 Bach, K.: 1042, 1430 (6); 1659 (2)
 Baker, M. A.: 6689 (8)
 Balslev, H.: 875 (4); 2636pp (8); 2636pp, 2655, 23815 (4)
 Bang, M.: 2601 (14)
 Barclay, H. G.: 6446, 8400, 9735 (4); 256 (2)
 Barrington, D.: 458 (8); 484 (10)
 Beck, S. G.: 1094 (14); 1141 (6); 1246, 3134A (2); 6825 (6); 11954 (14); 18754 (4); 25145 (14); 25147 (6); 28383 (2)
 Bejarano, M.: 190 (4)
 Bell, P. R.: 91 (4); 100 (15); 698 (4); 701 (15)
 Bello, M. A.: 82 (4)
 Bernal, C.: 15 (4)
 Besse, L.: 2208 (4); 2235 (8)
 Betancur, J.: 7026 (8)
 Bischler, H.: 1493A (12); 1887 (2); 2372 (4)
 Bittner, J.: 140 (2); 156, 180 (8)
 Black, G. A.: 46-615 (4)
 Boeke, J. D.: 1940, 2970 (14)

Boyle, B.: 4262 (4)
 Brade, A. C.: 184 (2); 9333 (9); 9726, 14353 (5); 16466 (9); 16638, 19289, 20301 (5)
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 Briceño, B.: 632 (4)
 Bro. Apollinaire: 155 (4)
 Bro. Ariste-Joseph: A552 (8)
 Brooke, W. M. A.: 6447 (14)
 Brown, C. A.: 64 (2)
 Bryan, G. S.: 370 (14)
 Buchtien, O.: 881, 2164, 2723, 2724 (14); **2725** (6); **3456**, 5188 (2); 8878 (14)
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 Cabalion, P.: 833 (14)
 Caballero, R.: 214 (2)
 Calatayud, G.: 1873 (14)
 Callejas, R.: 6269 (1); 6412pp (1); 7672 (4); 13357 (2)
 Calzada, J. I.: 572 (9)
 Camargo, L. A.: 8095 (4)
 Camp, W. H.: 3935 (3); 3938 (8); 4146 (4); 4590 (8)
 Campos, J.: 5004 (14)
 Carlos, J.: 1721 (9)
 Cazalet, P. C. D.: 5408 (4)
 Cerón, C. E.: 1122 (4); 1211, 19211 (15)
 Chacón, A.: 488 (2)
 Churchill, S. P.: 17881 (4)
 Clark, J. L.: 1236 (3); 2198 (15); 3487 (12); 6239 (3); 6241 (8); 6242 (3)
 Cleef, A. M.: 135, 983, 1043, 2916, 3390, 8359, 9122, 9485 (4)
 Clemants, S. E.: 2052 (14); 2142 (4); 2326 (8)
 Contreras, E.: 4978, 10916 (9)
 Cook, O. F.: 1290 (14)
 Correa, E.: 676 (4)
 Correa, M.: 1475 (8)
 Croat, T. B.: 10522 (2); 41225 (9); 43385 (2); 47286 (9); 56407 (8); 70763 (1); 70777 (2);
 70779 (8); 78160 (14); 95025 (15)
 Cuamacás, B.: 526 (4)
 Cuatrecasas, J.: 7906 (4); 13462 (8); 20043 (12); 25092 (8)
 Damazio, L. B.: 1803 (5)
 David, H.: 465 (2)
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 de Vélez, P.: 4016 (12)
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 Diels, L.: 386, 423 (4); 629 (3)
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 Dimmitt, M.: 1135 (14)
 Dodson, C.: 10708, 10866 (4); 10977 (2)

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 Dudley, T. R.: 12057 (14)
 Ekman, E. L.: 6301 (2); 11998 (9); **13556** (13); 13682 (2)
 Eriksen, B.: 59083 (12)
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 Ewan, J. A.: 16605 (4)
 Farfán, J.: 404 (14)
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 Fendler, A.: 270 (2)
 Fernández, E.: 2067, 2201, 2485, 2528 (6)
 Fernández-Alonso, J. L.: 7747, 8700 (4); 14130 (1)
 Fernández-Casas, J.: 6572pp (6)
 Feuerer, T.: 4543 (14)
 Figueroa, Y.: 566 (4)
 Filskov, P.: 37102 (8)
 Firmin, G.: 487 (4)
 Fosberg, F. R.: 20789 (4); 59452 (9)
 Foster, M. S.: 79-109, 79-169, 85-93, 85-1 (2)
 Franco, P.: 644 (4)
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 Gentry, A.: 45177 (2)
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 Grant, M. L.: 9087 (8); 10663 (2)
 Grant, J. R.: 0B, 0B (2)
 Grubb, P. J.: 1035 (4); 1387 (1); P.14b (4)
 Gudiño, E.: 1583 (8)
 Guzmán-Váldez, F.: 626, 1221 (9)
 Hagemann, W.: 572 (4); 1289 (4); 1780, 1781 (12); 1782 (15); 1928 (2); 1956 (4); 1993, 1994 (15); 1995 (12)
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 Harling, G.: 1256, 4561 (15); 25659 (4)
 Harris, W.: 7518 (9)
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 Murillo, J.: 1761, 1803 (1); 2946 (8); 3372 (1)

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 Narváez, E.: 668 (4)
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 Navarro, E.: 896 (2)
 Nee, M.: 34051 (6); 39131 (2)
 Neill, D.: 11919 (4); 11995 (12); 11997, 12022 (15)
 Núñez, R.: 127, 346, 627 (6)
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 Peyton, B.: 139 (14); 1442 (7)
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 Rivera-Díaz, O.: 709pp (2)
 Rivero, R.: 775 (2); 1588, 1802 (8); 2288 (2)
 Rodríguez, C. A.: 145, 155 (8)
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