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Botany

NEW SERIES NO. 34

PTERIDOPHYTA OF PERU

Part VI

22. Marsileaceae-28. Isoetaceae

Rolla M. Tryon

Robert G. Stolze

With the collaboration of:

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CLAY, E. H. 1978. *Flora of the Galapagos*. Island Studies University Press, Stanford, Calif. 943 pp.

CLAY, E. H., J. R. CLAYTON, and P. C. PHILLIPS (eds.). 1963. A comparison of marine and inland pine forest in Ecuador. I. The forest structure, phytogeography and floristic. *Journal of Ecology*, 51: 577-601.

LEWIS, E. D. 1979. Yielding the Sierra: Cultural patterns in vision, pp. 67-86. In *Intersections*, D. L. and R. A. GREGG, eds. Spiller, Gardner, and Gize, Waco, TX Publishers. The Hispanic Heritage Series.

MORSE, J. 1960. The Island of the Galapagos, pp. 185-221. In Seward, J. J., ed., *Handbook of South American Botany*, Vol. 7. Van Nostrand Reinhold, Inc., Inc. 147, Bureau of American Education, Smithsonian Institution, Washington, D.C.

SPRIG, K. G. 1963. *Forest and agriculture of Ecuador*, Vol. D, Polypodiaceae. *Fieldiana Botany*, n.s., 6: 1-122.

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PTERIDOPHYTA OF PERU

Part VI

22. Marsileaceae-28. Isoetaceae

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Table of Contents

INTRODUCTION	1
ACKNOWLEDGMENTS	1
22. MARSILEACEAE	2
<i>Marsilea</i>	2
23. SALVINIACEAE	5
<i>Salvinia</i>	6
<i>Azolla</i>	8
24. PSILOTACEAE	11
<i>Psilotum</i>	11
25. EQUISETACEAE	12
<i>Equisetum</i>	12
26. LYCOPODIACEAE	16
<i>Huperzia</i>	19
<i>Lycopodium</i>	52
<i>Lycopodiella</i>	58
27. SELAGINELLACEAE	66
<i>Selaginella</i>	66
28. ISOETACEAE	88
<i>Isoetes</i>	89
ADDENDUM	97
1. Species to Be Added to the Pteridophyte Flora, Parts I–V	97
2. Consideration of Pteridophyte Diversity in Respect to Ecology and Geography ...	98
DEPARTMENTS OF PERU	103
COMPREHENSIVE INDEX TO NAMES	104

List of Illustrations

1. <i>Marsilea</i> : <i>M. ancylopoda</i> ; <i>M. vestita</i>	3
2. <i>Salvinia</i> : <i>S. minima</i> ; <i>S. auriculata</i>	7
3. <i>Azolla</i> : <i>A. filiculoides</i> ; <i>A. microphylla</i>	9
4. <i>Psilotum</i> : <i>P. nudum</i>	13
5. <i>Equisetum</i> : <i>E. giganteum</i> ; <i>E. bogotense</i>	14
6. <i>Huperzia</i> : <i>H. eversa</i> ; <i>H. binervia</i> ; <i>H. linifolia</i> var. <i>tenuifolia</i> ; <i>H. cuneifolia</i> ...	18
7. <i>Lycopodium</i> : <i>L. clavatum</i> ; <i>L. thyoides</i>	53
8. <i>Lycopodiella</i> : <i>L. caroliniana</i> var. <i>meridionale</i> ; <i>L. cernua</i>	59
9. <i>Selaginella</i> : <i>S. peruviana</i> ; <i>S. haematodes</i> ; <i>S. exaltata</i>	67
10. <i>Isoetes</i> : <i>I. andicola</i> ; <i>I. lechleri</i> ; <i>I. discipora</i>	90

List of Tables

1. Data on the diversity of pteridophyte species in Peru	100
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List of Maps

1. The most species-rich departments in Peru	99
2. The main vegetational zones in Peru and their ferns	101

Back cover: Selaginella haematodes

PTERIDOPHYTA OF PERU

Part VI

22. Marsileaceae–28. Isoetaceae

Introduction

This sixth and final part of the “Pteridophyta of Peru” contains the aquatic fern families Marsileaceae and Salviniaceae as well as the “fern allies” Psilotaceae, Equisetaceae, Lycopodiaceae, Selaginellaceae, and Isoetaceae. A brief section on the diversity and ecology are included, written by the senior author. The comprehensive index contains not only the names in this final part but those of the other five parts as well. The general style, typography, form of citations, and so forth follow the previously published parts. These matters are adequately dealt with in Part I (*Fieldiana: Botany*, n.s., No. 20, 1989), and it is not necessary to repeat them here.

Treatment of the Lycopodiaceae has been contributed by Benjamin Øllgaard and that of Isoetaceae by R. James Hickey. Both are recognized specialists in these two families. The other genera are a joint effort of Rolla M. Tryon and Robert G. Stolze, each critically reviewing the treatments prepared by the other.

Type collections from Peru are mentioned in the nomenclature but are not repeated in the specimen citations. They are, however, included in the Peru range and ecology. The nomenclature of the genera and species is not intended to be complete. It includes all names based on Peru material and other names that are considered useful to mention.

Abbreviations of periodicals generally follow the system of *Botanico-Periodicum-Huntianum* (1968), while those of books and authors generally follow the system of *Taxonomic Literature* (TL-2, 1976 *et seq.*). The acronyms for herbaria follow *Index Herbariorum* and are also provided below.

Acknowledgments

Benjamin Øllgaard produced a recent Index to the names of Lycopodiaceae, as well as taxonomic treatments for the family in “The ferns and fern allies of Guatemala” and in the “Flora of Ecuador.” R. James Hickey contributed Isoetaceae for

“The ferns and fern allies of Guatemala” and is currently working on a monograph of the family. Consequently, both have a keen understanding of the problems in these pteridophyte families, and for their outstanding efforts in the production of this Flora the authors wish to express their deep appreciation.

We would like to extend special thanks to Blanca León (USM) for her invaluable assistance in preparing loans and arranging for their packing and shipment from this important Peruvian herbarium, as well as from the Universidad Nacional de Trujillo (HUT). Rolla M. Tryon appreciates the facilities provided by the Department of Biology, University of South Florida, Tampa, and the aid of Alice F. Tryon in the preparation of the treatment of *Selaginella*.

The illustrations were contributed by Field Museum scientific illustrator Zorica Dabich, who created the original drawings and adapted the rest from those previously used in the *Fieldiana: Botany* publication “The ferns and fern allies of Guatemala.” Her art work, which now has appeared in all six parts of this Flora, is an invaluable complement to the descriptions. We are extremely grateful to her. Thanks also go to Bent Johnsen, free-lance artist of Copenhagen, Denmark, for his drawing of *Huperzia*. We also appreciate the valuable comments presented by reviewers of the manuscript.

We are grateful to the officers of the following institutions for granting loans of their material or allowing us to examine specimens in their herbaria: Herbarium Jutlandicum, Aarhus Universitet, Denmark (AAU); Field Museum of Natural History, Chicago (F); Harvard University, Cambridge, Massachusetts—most Gray Herbarium (GH), some Arnold Arboretum (A); Herbarium Truxillense, Universidad Nacional de Trujillo, Trujillo, Peru (HUT); Missouri Botanical Garden, St. Louis (MO); Miami University, Oxford, Ohio (MU); Muséum National d’Histoire Naturelle, Paris (P); University of California, Berkeley (UC); United States National Herbarium, Smithsonian Institution, Washington, D.C. (US); and Herbario

San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (USM).

Materials, mostly types, have also been studied in the following herbaria (acronyms follow *Index Herbariorum*, ed. 8): AWH, B, BKL, BM, BONN, BR, C, CGE, CPUN, CR, DUKE, G, GB, GL, HB, HEID, K, KRA, L, LG, LIL, LINN, LP, MA, MICH, MOL, MSC, NO, NY, PR, Q, QCA, RB, S, SAPF, U, UPS, W, WIS, and Z.

This project has been supported in part by grant #BSR-85-16358 from the National Science Foundation, Systematic Biology Program. The work would not have been possible without this assistance. However, any opinions and conclusions expressed are those of the authors and do not necessarily reflect the views of the Foundation.

Family 22. MARSILEACEAE

Marsileaceae Mirb., *Hist. nat. veg.* (Lam. & Mirb.) 5: 126. 1802. TYPE: *Marsilea* L.

Stem short- to long-creeping, slender, often branched, hardly indurated, bearing trichomes. **Leaves** ca. 1–40 cm long, with 4, 2, or no leaflets at the apex of the petiole, circinate in the bud. **Sori** borne within sporocarps, indusiate, with indehiscent, short- to long-stalked, not annulate, megasporangia and microsporangia; heterosporous, spores without chlorophyll.

The Marsileaceae are a family of three genera, all in tropical America. The genera (*Marsilea*, *Regnellidium*, and *Pilularia*) are clearly distinct and not very closely allied.

There are numerous detailed studies on the Marsileaceae centering on the form and development of the elaborate reproductive structures and simplified leaves. These plants have also been useful in physiological and experimental work on factors influencing leaf form. However, some of the basic problems concerning the nature of the leaflets and the sporocarp are not resolved, and the phyletic relationships of the three genera are not wholly certain.

Pilularia L. is not known from Peru. However, *Pilularia americana* A. Br. has been collected nearby in Bolivia (as *P. mandonii*) and it probably also

grows in Peru. It is a small plant with no leaflets on the petiole; the filiform leaves (petioles) are 1–10 cm long. A single subglobose sporocarp is borne at the base of a leaf. Unless sporocarps are present, the plant can easily be taken for a species of Cyperaceae, which grows in wet habitats that are similar to those of *Marsilea*.

I. *Marsilea*

Marsilea L., *Sp. pl.* 1099. 1753; *Gen. pl.* ed. 5, 485. 1754. TYPE: *Marsilea quadrifolia* L. **Figure 1.**

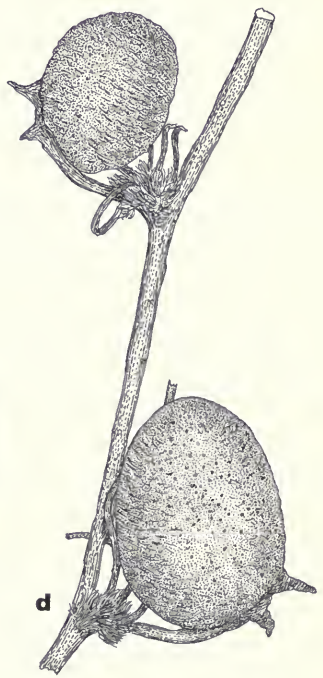
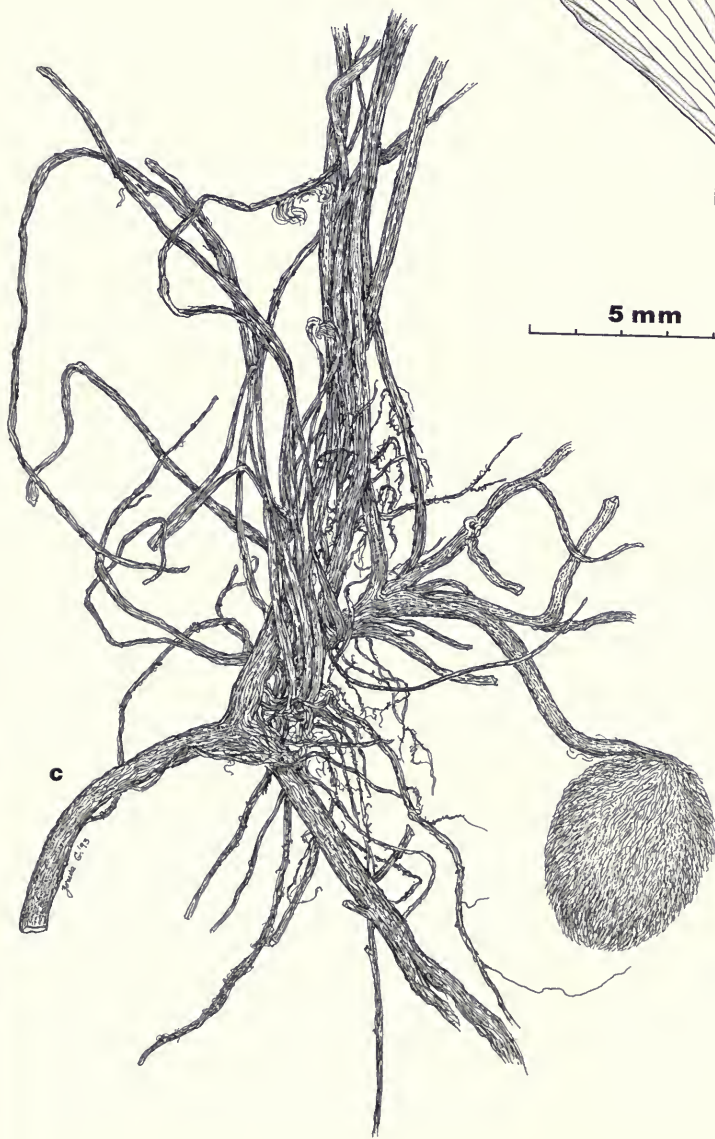
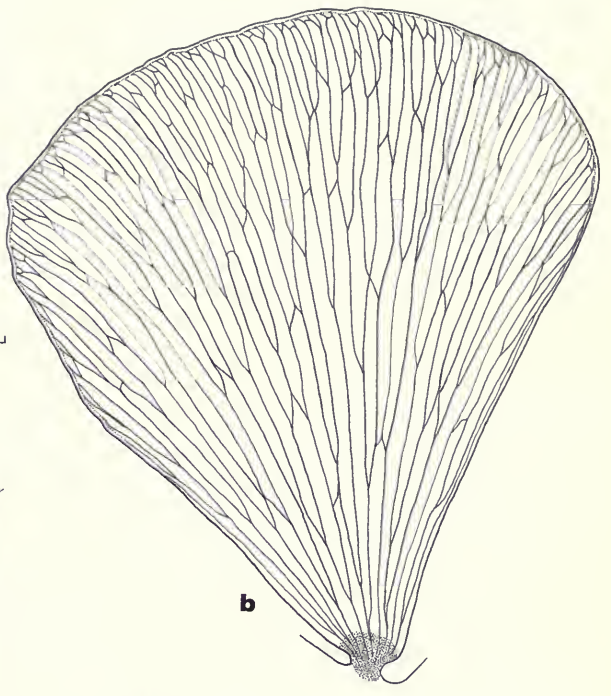
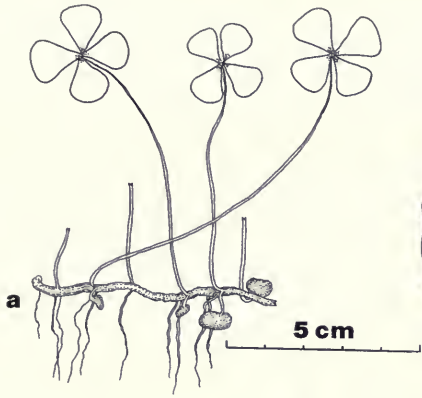
Plants palustral or aquatic. **Stem** usually long-creeping, commonly bearing long roots at the nodes of the stem or along the internodes. **Leaves** with the petiole terminated by 2 adjacent pairs of narrowly cuneate to broadly flabellate leaflets that are glabrous or pubescent. **Veins** more or less anastomosing, usually connected at the margin. **Sori** borne within 1 to several stalked, indurated sporocarps attached to the petiole or at its base, enclosed by a diaphanous indusium, with microsporangia and megasporangia. **Megaspores** somewhat ellipsoidal with an apical papillalike laesura, the surface papillate. **Microspores** spheroidal, trilete, the surface slightly rugulose.

Marsilea is a nearly worldwide genus of perhaps 50 species, with about 12 in America. The tropical American species are poorly known for there are relatively few collections and these often lack sporocarps. The species of *Marsilea* are most diverse and common in regions that support vernal pools or shallow pools that dry out, at least along the borders. Mexico is one center of diversity, Australia and Africa are others.

The following treatment is based directly on that of Johnson (1986). When necessary, specimens are indicated as cited by Johnson.

The sporocarp is borne on a stalk that is connected to the petiole. If this stalk is attached by its end to the sporocarp, there is neither raphe nor inferior tooth. If the stalk is attached along its side (the raphe), there may be an inferior tooth (the end of the stalk). The superior tooth is an extension of the sporocarp near the inferior tooth (fig. 1d).

FIG. 1. *Marsilea ancylopoda*: a, habit; b, leaflet; c, stem and roots, with sporocarp. *Marsilea vestita*: d, sporocarps. (a, b from *Alston 6354*, Venezuela, F; c from *Alston 5874*, Venezuela, F; d from *Sandberg*, United States (Idaho), F.)



The sporocarps may be very long-lived (to 100 years; Johnson, 1986) and they presumably are dispersed by waterfowl. Species also may be dispersed as a result of discarded aquaria.

JOHNSON, D. M. 1986. Systematics of the New World species of *Marsilea* (Marsileaceae). Syst. bot. monogr. 11: 1-87.

References

GUPTA, K. M. 1962. *Marsilea*, Bot. monogr. 2, pp. 1-113, Council Sci. India Res., New Delhi.

Key to Species of *Marsilea*

- a. Roots borne only at the nodes of the stem (rarely a few to 1 cm distant from a node); raphe present b
- b. Superior tooth acute 3. *M. vestita*
- b. Superior tooth blunt or absent c
- c. Sporocarps borne below the ground or stem level; leaflets essentially glabrous 2. *M. ancylopoda*
- c. Sporocarps borne above the ground or stem level; leaflets pubescent 4. *M. mollis*
- a. Roots borne at the nodes of the stem and along the internodes d
- d. Sporocarps 1-4, borne on the basal 1/4 of the petiole 1. *M. deflexa*
- d. Sporocarps 5-20, borne on the basal 2/3 of the petiole *M. crotophora* (see Comments)

1. *Marsilea deflexa* A. Br., Monatsber. königl. preuss. akad. wiss. Berlin. 1863: 421. 1864. TYPE: Piauhy, Brazil, *Gardner 2760* (holotype, G; isotypes, BM, G, K, P, all cited by Johnson).

Plants forming dense colonies. **Roots** at nodes and internodes. **Sporocarps** 1-4, on basal 1/4 of the petiole, 3.5-6 mm long with conspicuous lateral ridges.

In a pool, ca. 59 m; a single collection from San Martín.

Mexico and Central America; Venezuela and Colombia, south to Brazil; Paraguay and Peru.

San Martín: Morales, Tarapoto, *Ule 6866* (G, K, P, all cited by Johnson).

2. *Marsilea ancylopoda* A. Br., Monatsber. königl. preuss. akad. wiss. Berlin. 1863: 434. 1864. TYPE: Guayaquil, Ecuador, *Jameson 304* (holotype, G; isotypes, BM, G, K, all cited by Johnson). Originally as *James 304*, corrected later (A. Br., 1871, *op. cit.* 1870: 717). **Figure 1a-c.**

Roots borne only at the nodes (rarely a few 2-3 cm distant). **Raphe** present. **Superior tooth** absent or slightly raised. **Sporocarps** 2.5-6 mm long, borne below the ground or stem level, 1 at the base of a petiole. **Leaflets** of non-floating leaves glabrous or with a few trichomes.

Northern Peru, Tumbes to La Libertad, near sea level.

Mexico; Florida and Greater Antilles; Venezuela, Colombia to Peru; Brazil; Argentina; Uruguay.

Tumbes: Laguna de Salitoral Grande, *Coronado 235* (GH, UC). **Lambayeque:** San Nicolás, entre Lambayeque et Chiclayo, *Santos Quiroz 2401* (F, GH). Prov. Lambayeque, Yencala, *Santos Quiroz 71* (HUT). **Laguna Boro,** Chiclayo, *León 600* (USM). **La Libertad:** Prov. Trujillo, Huamán, *Angulo & López 348* (GH).

3. *Marsilea vestita* Hooker & Grev., Icon. fil. 2: t. 159. 1830. LECTOTYPE (designated by Johnson, Syst. bot. monogr. 11: 62. 1986): Columbia River, *Scouler 338* (K; isolectotypes, GH, NY). **Figure 1d.**

Marsilea uncinata A. Br., Amer. J. Sci. ser. 2, 3: 55. 1847. TYPE: Arkansas, *Englemann 33* (holotype, MO; isotypes, K, M, MO, all cited by Johnson).

Marsilea mucronata A. Br., Amer. J. Sci. ser. 2, 3: 55. 1847. TYPE: Near Devil's Lake, North Dakota, *Geyer 71* (holotype, MO; isotypes, K, NY, all cited by Johnson).

Plants in diffuse or dense colonies. **Roots** only at the nodes (rarely a few to 10 mm distant). **Raphe** present. **Superior tooth** acute, often hooked at apex. **Sporocarp** 3.0–7.6 mm long with lateral ridges. **Leaflets** of non-floating leaves covered by overlapping trichomes on both surfaces.

All of the above pertains to ssp. *vestita*; ssp. *tenuifolia* (A. Br.) Johnson is endemic to central Texas. It differs from ssp. *vestita* in having very narrow leaflets with sparse trichomes or none abaxially.

Known in Peru only from the Department of Lambayeque.

Southern British Columbia east to western Minnesota; south to Louisiana, Florida; Mexico; Peru. The Peru and Florida localities may be introductions.

Lambayeque: Chiclayo, *León* (MICH, det. Johnson). Prov. Lambayeque, *Salazar H1* (USM).

4. *Marsilea mollis* Rob. & Fern., Proc. Amer. Acad. 30: 123. 1895. TYPE: San Diego, Chihuahua, Mexico, *Hartman 604* (holotype, GH; isotypes, F, GH, MSC, NY, UC, all cited by Johnson).

Roots borne only at the nodes (occasionally to 10 mm distant). **Raphe** present. **Superior tooth** absent or to 0.2 mm long. **Sporocarps** at or near petiole base, 1.7–6.7 mm long, on recurved peduncles, borne above the ground level. **Leaflets** of non-floating leaves adaxially glabrous to sparingly pilose, abaxially densely pilose.

2000–3900 m, Cajamarca south to Puno.

Arizona and Texas south to northern South America, south to Argentina, Chile and Brazil.

The following sterile specimens are considered to represent this species. All have been seen by the present authors except the *Hill* collections from Puno. All have been placed here by Johnson except the *Núñez et al.* collection from Cuzco.

Cajamarca: Cajamarca, *Müller & Gutte 27322* (USM). **Junín:** Huancayo, *Kunkel 422* (GH). **Huancavelica:** Prov.

Angaraes, 4 km W of Huanta, *Stork & Horton 10808* (F, UC). **Cuzco:** Prov. Espinar, Yauri, *Núñez et al. 7810* (F, MO), *Vargas 13524* (GH). **Puno:** Towards Juliaca, *Hill 562* (K), *563* (K).

Comments

Marsilea crotophora D. M. Johnson, Syst. bot. monogr. 11: 46. 1986. TYPE: Mato Grosso, Brazil, *Hatschbach & Scherer 30470* (holotype, US; isotypes, C, LP, M, MICH, NY, UC, all cited by Johnson).

This species may be found in the upper Amazon or its tributaries. It may be distinguished from Peruvian species by the roots being borne on the internodes as well as the nodes, the lack of a raphe and superior tooth, and the 5–20 sporocarps borne on the basal $\frac{2}{3}$ of the petiole, the lowest one borne well above the petiole base.

Family 23. SALVINIACEAE

Salviniaceae Reichenb., Bot. damen künst. freunde pflanzenw. 255. 1828. TYPE: *Salvinia* Séguier.

Azollaceae Wettst. Handb. syst. bot. 2: 77. 1903. TYPE: *Azolla* Lam.

Plants floating in water or stranded in wet mud. **Stem** elongate, small, and slender, often branched, not indurated, usually bearing trichomes. Floating **leaves** ca. 0.5–2.5 cm long, not circinate in the bud. **Sori** borne on a lobe of a leaf or on a branched leaf, indusiate, with the sporangia stalked, not annulate, the sori either megasporangiate or microsporangiate; heterosporous, spores without chlorophyll.

The structure bearing the sporangia is considered to be a sorus, surrounded by an indusium, and accordingly the special term sporocarp is not used.

The living Salviniaceae are represented by two genera, *Salvinia* and *Azolla*, floating aquatics of wide distribution, especially in the tropics. Although *Azolla* is sometimes included in a separate family, it has many basic similarities with *Salvinia*.

Key to Genera of Salviniaceae

- a. Leaves in whorls of 3, 2 floating, ca. 5–25 mm long, with anastomosing veins and not lobed, 1 submerged, highly branched I. *Salvinia*
- a. Leaves alternate, ca. 0.5–1.5 mm long, without veins, bilobed II. *Azolla*

I. *Salvinia*

Salvinia Séguier, Fl. veron. 3: 52. 1754. TYPE: *Salvinia natans* (L.) All. (*Marsilea natans* L.) **Figure 2.**

Plants floating aquatics. Stem short or elongate, slender, bearing trichomes and no roots. Leaves borne in whorls of 3, dimorphic, 2 of them green, floating, entire, oblong to suborbicular, ca. 0.5–2.5 cm long, often pubescent, usually papillate on the upper surface, one of them submerged, pendent in the water, highly branched, bearing many trichomes. Veins anastomosing. Sporangia borne in stalked sori on the submerged leaf, enclosed by the indusium, with either megasporangia or microsporangia. Spores trilete, enclosed within a vacuolate tapetal formation, the megaspore surface perforate, the microspore surface somewhat rugose.

Salvinia is a widely distributed genus of about ten species, with seven of them in America.

Shaparenko (1956) recognized four sections, and these were adopted by de la Sota (1962); they are not recognized here because the genus is a small one.

The descriptions of the species are freely adapted from Stolze (1983).

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- SHAPARENKO, K. K. 1956. History of the *Salvinias* (in Russian). Act. Inst. Bot. Komarov. Ser. VIII Paleobotania 2: 1–44.
- SOTA, E. R. DE LA. 1962–1964. Contribución al conocimiento de las “Salviniaceae” neotropicales. I–V. Darwiniana 12: 465–520, 612–623; 13: 529–536.
- STOLZE, R. G. 1983. Ferns and fern allies of Guatemala, III. Fieldiana: Bot., n.s. 12: 11–13.

Key to Species of *Salvinia*

- a. Trichomes at the apex of the papillae, on the upper surface of the floating leaves, separate (not joined) at their tip 1. *S. minima*
- a. Trichomes at the apex of the papillae, on the upper surface of the floating leaves, joined at their tip 2. *S. auriculata*

1. *Salvinia minima* Baker, J. Bot. 24: 98. 1886. TYPE: Santa Catarina, Brazil, Müller 479 (holotype, K; isotype, BM). **Figure 2a–c.**

Stele of the stem more or less circular in cross-section. Floating leaves oblong-elliptic, the apex obtuse (rarely retuse), the larger ones 0.6–1.3 cm long, their upper surface papillate, each papilla

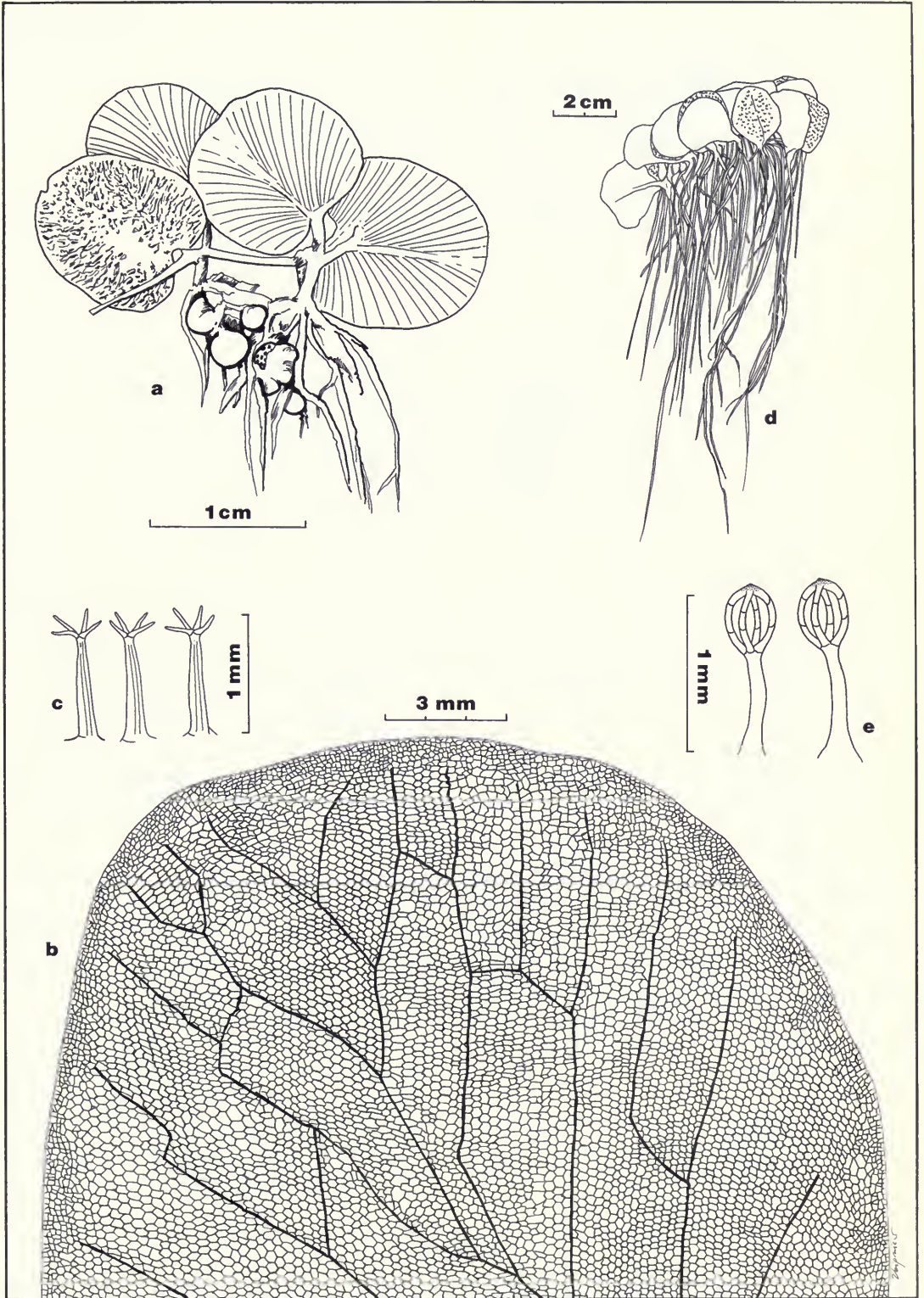
with apical trichomes, these separate (not joined) at the apex.

130–160 m, Loreto and Madre de Dios.

Southeastern United States; Mexico and Central America; South America, south to Argentina and Uruguay.

This species has often been called *S. rotundifolia* but that name = *S. auriculata*.

FIG. 2. *Salvinia minima*: a, habit; b, portion of leaf showing venation; c, papillae with free, spreading trichomes. *Salvinia auriculata*: d, habit; e, papillae with joined trichomes. (Adapted from Stolze, Ferns and fern allies of Guatemala, 1983.)



Loreto: Iquitos, *McDaniel 11776* (MO). Near Iquitos, *Ellenberg 8301* (F). Río Itaya, Iquitos, *Revilla 467* (F, MO, US, USM). Lupuna Cocha, Iquitos, *Tryon & Tryon 5188* (F, GH, US, USM). **Madre de Dios:** Prov. Tambopata, Tambopata Nature Reserve, 30 air km SSW of Puerto Maldonado, *Barbour 5373* (MO). Prov. Manú, Parque Nacional Manú, *Foster 12206* (F).

2. *Salvinia auriculata* Aublet, Hist. pl. Guiane Franc. 2: 969. 1775. TYPE: French Guiana, Terr. Caux, Aublet (P?). **Figure 2d-e.**

Salvinia rotundifolia Willd., Sp. pl. ed. 4, 5: 517. 1810. TYPE: Brazil, *Hoffmannsegg* (see Morton, Contr. U.S. Natl. Herb. 38: 75. 1967).

Stele of the stem U-shaped in cross-section. Floating leaves oblong-elliptic and nearly circular, obtuse or retuse at the apex, larger floating leaves 1.5–2.5 cm long, their upper surface papillate, each papilla with 4 apical trichomes, these joined at the apex.

At ca. 100 m, Loreto and Madre de Dios. Cuba; Mexico south to Argentina.

Loreto: Río Amazonas, SE of Iquitos, *Croat 19296* (MO). Prov. Maynas, mouth of Río Nanay, *Gentry et al. 21715* (MO, UC). Yanamono, *Gentry et al. 42574* (F, MO). **Madre de Dios:** Prov. Tambopata, Tambopata Nature Reserve, 30 air km SSW of Puerto Maldonado, *Barbour 4888* (MO).

II. *Azolla* Lam., Encycl. 1: 343. 1783. TYPE: *Azolla filiculoides* Lam. **Figure 3.**

Floating aquatics. Stem short, elongate, slender, sometimes bearing trichomes, and usually short roots. Leaves ca. 0.5–1.5 mm long, bilobed, the upper lobe usually minutely to strongly papillate, without veins. Sporangia borne in short-stalked sori enclosed by an indusium, with either 1 megasporangium or several microsporangia. Spores trilete, the megaspores irregularly marked, with a perforate surface, the microspores smooth, embedded in massulae.

The megaspore has accessory structures usually referred to as a columella bearing floats. These are partially enclosed by a band of sporoderm, the

collar, which is between the megaspore proper and the floats. In the living species the floats are either three or nine in number. The microsporangia contain a few to several massulae, within which the microspores are embedded. Projecting structures called glochidia are often on the outer surface of the massulae.

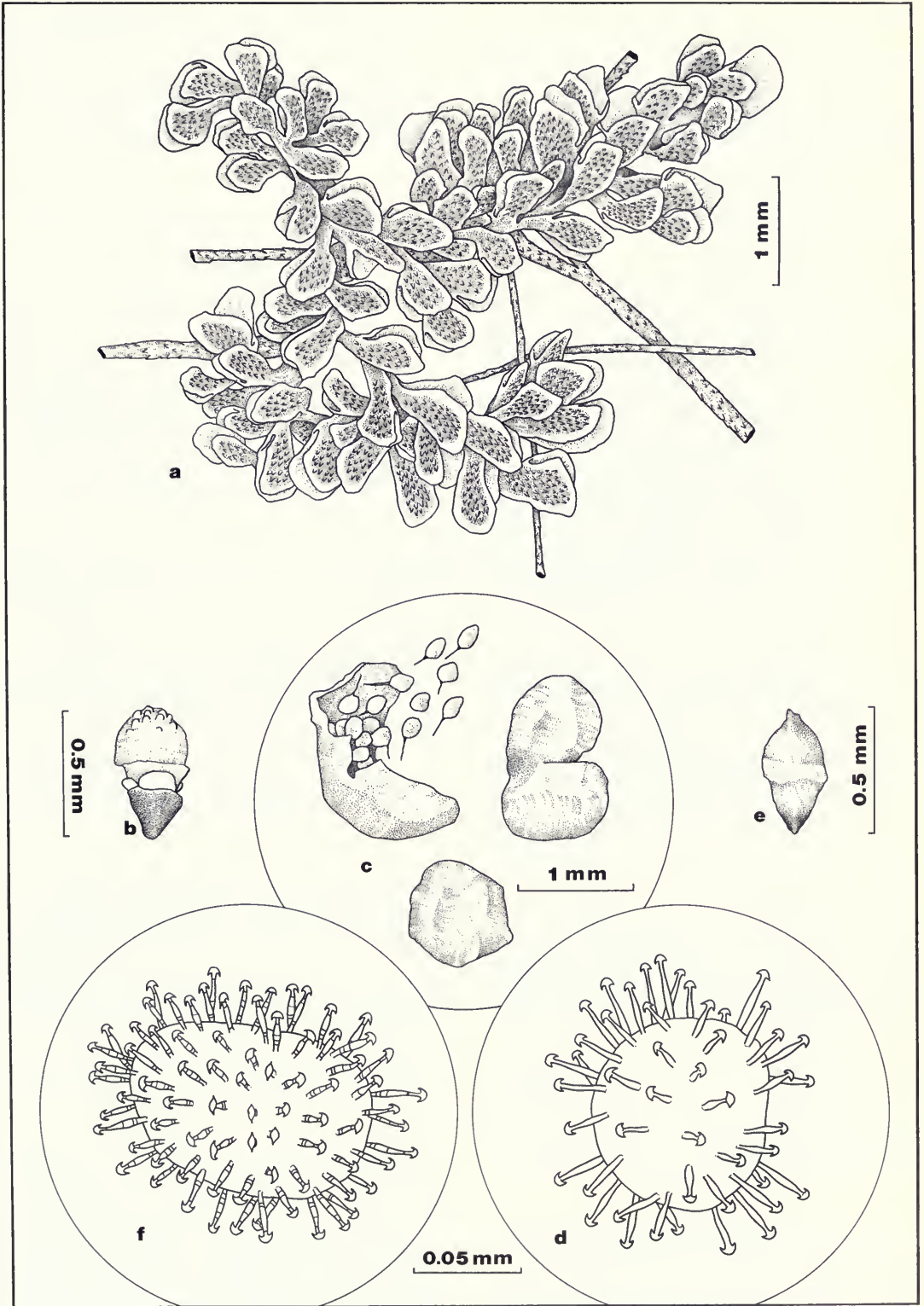
Azolla is a widely distributed genus of six species, with four of them (sect. *Azolla*) in America and in Peru. It is notable in having the most complex reproductive structures of any plant and in having a colony of *Anabaena azollae* within the lobes of each leaf. This blue-green alga has the ability to fix atmospheric nitrogen, and accordingly *Azolla* is the center of wide interest as a green-manure (Lumpkin & Plucknett, 1980), especially for the rice paddies of Southeast Asia.

Azolla is a very distinctive genus, but the species are poorly known due to the fact that sterile material is difficult to identify. Fertile material is uncommon. Accordingly, the species in Peru and their characters are only provisionally known. In spite of evidence to the contrary, the treatment of Svenson (1944) is largely followed. The key is adapted from his key to species of the Americas and the megaspore characters are taken from Perkins et al. (1985). Species names may be assigned to one of the four species adopted, although this does not mean that the material is accurately determined. The following Peru collections have not been identified to species: **Cajamarca:** *Dillon 2919*. **La Libertad:** *Killip & Smith 21511*; *D. Smith et al. 2225*. **Cuzco:** *Herrera 2616, 2618*; *Cook & Gilbert 237, 241, 1078*; *Cook 1963*; *Maldonado 17*. **Puno:** *Barclay 9273*.

Species of *Azolla*, as they are known, are not restricted to particular environments as differences in range and habitat statements might imply. Accordingly, the range, habitat, and altitude are given for the genus as a whole in Peru, rather than for each species.

In wet mud of riverbanks or stream banks, where stranded by higher water, usually floating in standing water of lakeshores, ponds, or small streams, also in ditches, in stagnant or fast-flowing water, less often in swamps or wet parts of cultivated land, near sea level to 4100 m, Cajamarca, Amazonas, and Loreto, south to Puno and Moquegua.

FIG. 3. *Azolla filiculoides*: a, habit; b, megasporangium; c, sporocarp indusia with microsporangia; d, massula with nonseptate trichomes. *Azolla microphylla*: e, megasporangium; f, massula with septate trichomes. (Adapted from Stolze, Ferns and fern allies of Guatemala, 1983.)



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- PERKINS, S. K., G. A. PETERS, T. A. LUMPKIN, AND

- H. E. CALVERT. 1985. Scanning electron microscopy of perine architecture as a taxonomic tool in the genus *Azolla* Lamarck. *Scanning Electron Microscopy* **4**: 1719–1734.
- SVENSON, H. K. 1944. The New World species of *Azolla*. *Amer. Fern J.* **34**: 69–84.

Key to Species of *Azolla*

- a. Plants dichotomously branched, 0.5–1.5 cm long; leaves less than 1 mm long; megaspore collar with or without filaments b
- b. Plants small, 0.5–1.0 cm in diameter; leaves small (0.5 mm long), nearly orbicular and nearly smooth; glochidia not septate; megaspore collar with dense filaments, the megaspore surface more or less smooth, obscured by dense filaments 1. ***A. caroliniana***
- b. Plants often larger, 1.0–1.5 cm in diameter; leaves with the upper lobe 0.7 mm long, the lower lobe much larger, more or less obovate; glochidia septate; megaspore collar lacking filaments, megaspore surface with large and small pits, but few filaments 2. ***A. mexicana***
- a. Plants pinnately branched, 1–6 cm long; leaves 1 mm long; megaspore collar lacking filaments ... c
- c. Plants often 2–6 cm long; leaves oblong to ovate; glochidia not septate (or with 1–2 septa distally); megaspore surface with raised hexagonal markings 3. ***A. filiculoides***
- c. Plants 1–2 cm long; leaves nearly orbicular; glochidia septate, some septa located below the middle; megaspore surface rugulate-verrucate 4. ***A. microphylla***

1. ***Azolla caroliniana*** in the sense of Svenson and other authors, not Willd., as usually thought.

Plants dichotomously branched, 0.5–1.0 cm in diameter. Leaves divaricate (not closely imbricate), nearly orbicular, nearly smooth, small, 0.5 mm long. Glochidia not septate. Megaspore collar with dense filaments on its surface (magnification $\times 200$ or more), rugulate-verrucate beneath filaments.

Eastern North America; Mexico and the Caribbean; introduced in Europe and South America.

The name is used in the sense of Svenson and most authors (not Willd.) until a definitive treatment is published.

Jermy (Somerfeltia 6: ix–x. 1987) has pointed out that according to the Ph.D. thesis of D. Dunham (Portsmouth Polytechnic) the type of *Azolla caroliniana* is *A. filiculoides*. This leaves *Azolla* of eastern North America presumably without a name.

Amazonas: Río Santiago, S of La Poza, *Berlin 3711* (MO, UC). **La Libertad:** Prov. Bolívar, Laguna de las Ichus, *López & Sagástegui 3238* (GH, MO). **San Martín:** Prov. Mariscal Cáceres, 2–4 km W of Tocache Nuevo, *Plowman 11437* (F). **Loreto:** Prov. Maynas, Río Itaya, *Revilla 632* (F, MO, UC). Prov. Maynas, Yanuyaca, *Gentry et al.*

32119 (GH). **Ayacucho:** 44 km N of Tambo, *Luteyn & Lebrón-Luteyn 6369* (UC, US). **Cuzco:** Prov. Cuzco, Saylla, *Fernández et al. 455* (USM). **Puno:** Santa Rosa, *Staford 495* (F). Ichu, *Soukup 354* (F).

2. ***Azolla mexicana*** Presl, *Abh. Böhm. Ges. Wiss. Ser. V*, 3: 150. 1845. TYPE: Mexico, *Schiede & Deppe* (holotype, PR).

Plants dichotomously branched, often 1.0–1.5 cm in diameter. Leaves divaricate (not closely imbricate) with the upper lobe ca. 0.7 mm long, the lower one much larger. Glochidia septate. Megaspore collar glabrous; megaspore surface (magnification $\times 200$ or more) coarsely rugose, also with pits, and with many dense filaments.

North America; Mexico; Central America; northern half of South America.

Tumbes: Casa Fernandez, *Haught 183* (US). **Loreto:** Prov. Maynas, Iquitos, *Tryon & Tryon 5213* (GH, US). **Ancash:** Lago Santa Cruz Chico, Huascarán National Park, *D. Smith et al. 9261* (F, HUT, MO). **Junín:** Huancayo, *Kunkel 421-1/2* (GH). Acopalca, *Kunkel 421* (GH). Cerca Carhuamayo, *Ferreya 5242* (USM). **Cuzco:** Pampa de Anta, *Illis & Ugent 785* (GH, UC, US, USM). 3.5 km NW of Saylla, *Illis et al. 1208* (GH, US). Prov. Paucartambo, Paucartambo, *Plowman & Davis 4920* (F). **Madre de Dios:** Prov. Manú, Parque Nacional Manú, *Foster 9872*

(MO). **Puno:** Pucará, *Hunnewell 15874* (GH). Lake Titicaca, *Shepard 1511* (GH, US). **Moquegua:** Ilo, *Stafford 926* (F).

3. ***Azolla filiculoides*** Lam., *Encycl.* 1: 343. 1783.
TYPE: "Magellan Region," *Herb. Lamarck* (P). **Figure 3a-d.**

Plants pinnately branched, often 2–6 cm long. **Leaves** closely appressed, imbricate, oblong to ovate, ca. 1 mm long. **Glochidia** not septate (rarely 1–2 "septa" toward the apex). **Megaspore** collar more or less glabrous; megaspore surface (magnification $\times 200$ or more) prominently rugose with hexagonal markings, with few filaments.

Southern South America north to western North America and to Alaska; introduced in Europe, Asia, and Australia. *Azolla filiculoides* var. *rubra* (R. Br.) Strasb., treated as a species *A. rubra* R. Br. by Perkins et al. (1985), is not considered to occur in Peru.

Cajamarca: Prov. Contumazá, Río San Benito, San Benito, *Sagástegui et al. 12509* (HUT, MO). **Amazonas:** Prov. Bongará, Laguna Pomacocha, *Wurdack 888* (F, GH, UC, US). **La Libertad:** Prov. Trujillo, Tschudi, *Shimokowa 7294* (HUT). Playa de Chan Chan, *Angulo 18* (US). **Loreto:** Paraiso, above Iquitos, Río Amazonas, *Fosberg 29076* (US). **Huánuco:** Chasqui, *Macbride 3306* (F, US); 3307 (F, US). **Lima:** Prov. Lima, Laguna de Villa, *Coronado 5* (GH, MO, UC, US); *Tryon & Tryon 5458* (GH); *Cerrate 2766* (USM). **Huancavelica:** Prov. Tayacaja, Pampas, *Stork & Horton 10243* (F, UC, US). **Cuzco:** *Cook & Gilbert 197* (US). Prov. Paucartambo, Huilabamba, *Balls B7632* (F, UC, US). **Arequipa:** Prov. Arequipa, Río Yarabamba, *Ponce 32* (USM).

4. ***Azolla microphylla*** Kaulf., *Enum. fil.* 273. 1824.
TYPE: "California," *Chamisso* (LE?). **Figure 3e-f.**

Plants pinnately branched, small, 1–2 cm long, many leaves orbicular, 1 mm long, most leaves closely imbricate. **Glochidia** septate. **Megaspore** collar glabrous; megaspore surface slightly filamentous, slightly pitted, rugulate (high magnification) to verrucate.

Western and northern South America; southern North America; West Indies.

Loreto: Yurimaguas, *Killip & Smith 27707* (US); Prov. Requena, Río Ucayali, *Encarnación E-1101* (US). **Ayacucho:** Puquio, *Gentry et al. 23296* (F, MO, US). **Cuzco:** Prov. Anta, Pampas de Anta, *Tryon & Tryon 5364* (GH, US, USM). Yauri, *Núñez et al. 7813* (F, MO).

Family 24. PSILOTACEAE

Psilotaceae Kanitz, *Növényrends. Attek.* 43. 1887.
TYPE: *Psilotum* Sw.

Stem flaccid to somewhat indurated, lacking indument and roots. **Leaves** (or pinnae) small to minute, borne alternately, with a single vein or none. Two or 3 **sporangia** joined in a sessile, thick-walled synangium. Homosporous. **Spores** without chlorophyll.

The Psilotaceae are a family of two genera, *Tmesipteris* Bernh. of western Malesia, Australia, and the Pacific, and *Psilotum*, which is pantropical in distribution.

After an extensive series of studies, D. W. Bierhorst concluded that the Psilotaceae were primitive elements in the Filicopsida. This interpretation of the position of the family provoked further interest in its phylogeny and resulted in a symposium on the taxonomic and morphological relationships of the Psilotaceae (White et al., 1977).

The Psilotaceae have a number of characters that occur in the Filicopsida, such as the details of early ontogeny of the leaf, the subterranean, cylindrical gametophytes, multiflagellate sperm, and several aspects of the rhizoids and gametangia. These and the evidence from the structure and wall formation of *Psilotum* spores are indicative of relationships with the ferns. However, Cooper-Driver (1977) has shown that the chemical evidence does not support this relationship.

References

- COOPER-DRIVER, G. 1977. Chemical evidence for separating Psilotaceae from the Filicales. *Science* **198**: 1260–1261.
WHITE, R. A., ET AL. 1977. Taxonomic and morphological relationships of the Psilotaceae. *Brittonia* **29**: 1–68.

I. *Psilotum*

Psilotum Sw., *J. Bot. (Schrader)* 1800 (2): 8, 109. 1801, *nom. nov.* for *Hoffmannia* Willd. (not Sw.) and with the same type.

Hoffmannia aphylla Willd. = *Psilotum nudum* (L.) Beauv. **Figure 4.**

Plants terrestrial, rupestral or usually epiphytic. **Stem** compactly branched in the substrate, the ae-

rial stems green, erect to pendent, with several dichotomous divisions, ca. 20 cm to 1 m long, without roots. **Leaves** minute, alternate, leafy stem glabrous. **Synangia** large, borne singly in the axil of forked fertile leaves. **Spores** elongate-ellipsoidal, monolete, the laesurae $\frac{1}{2}$ to $\frac{2}{3}$ the spore length, the surface coarsely rugose to shallowly and compactly verrucate.

Psilotum is a highly distinctive genus of wide distribution in the tropics and with some extensions to subtemperate regions. Notable characters of the genus are the dichotomously branched stem, the bifurcate sporophylls, and the large synangium. *Psilotum* has a simple morphology, probably through reduction from more complex ancestors.

1. *Psilotum nudum* (L.) Beauv., Prodr. Fam. Aethéog. 112. 1805. **Figure 4.**

Lycopodium nudum L., Sp. pl. 1100. 1753. TYPE: LINN 1257.1.

Psilotum triquetrum Sw., J. Bot. (Schrader) 1800 (2): 109. 1801, *nom. superfl.* for *Lycopodium nudum* L. and with the same type.

Plants pendent or usually erect. **Branches** 3-angled, to 1.2 mm wide, leaves distant, 2–3 mm long, triangular-subulate.

Epiphytic, especially on palms and tree ferns, 200–600 m, San Martín south to Madre de Dios.

American and Old World tropics and subtropics.

P. complanatum Sw. may be a distinct species. It has flattened branches 2 mm or more wide and is especially distinctive in the Pacific islands.

San Martín: Dist. Chazuta, *Rimachi* 7945 (MO). Dist. Tocache Nuevo, *Schunke* 4084 (F, US). Gramalote ad Saposoa, *Woytkowski* 7300 (GH, MO, US). **Loreto:** Lower Río Huallaga, *Killip & Smith* 29244 (Coll. W. J. Dennis). Padre Isla, Iquitos, *Encarnación* 26314 (MO, US). Prov. Requena, Río Ucayali, *Ayala et al.* 3753 (MO). **Huánuco:** Tingo María, *Moran* 3687 (USM). **Madre de Dios:** Prov. Tambopata, Cuzco Amazonico Lodge, 15 km NE of Puerto Maldonado, *Núñez* 12214 (MO); *Gentry et al.* 68958 (MO). Prov. Manú, Parque Nacional Manú, *Foster* 11336 (F).

Family 25. EQUISETACEAE

Equisetaceae A. P. DC., Fl. Franc. (Lam. & DC.) ed. 3, 2: 580. 1805. Type: *Equisetum* L.

Stem jointed, more or less indurated, the aerial usually green, the subterranean with numerous wiry roots. **Leaves** each with a single vein, borne in whorls, joined in a sheath. **Sporangia** thin-walled, borne on stalked, peltate sporangiophores that form a strobilus. Homosporous. **Spores** with chlorophyll and bearing elaters.

I. Equisetum

Equisetum L., Sp. pl. 1061. 1753; Gen. pl. ed. 5, 484. 1754. TYPE: *Equisetum fluviatile* L. **Figure 5.**

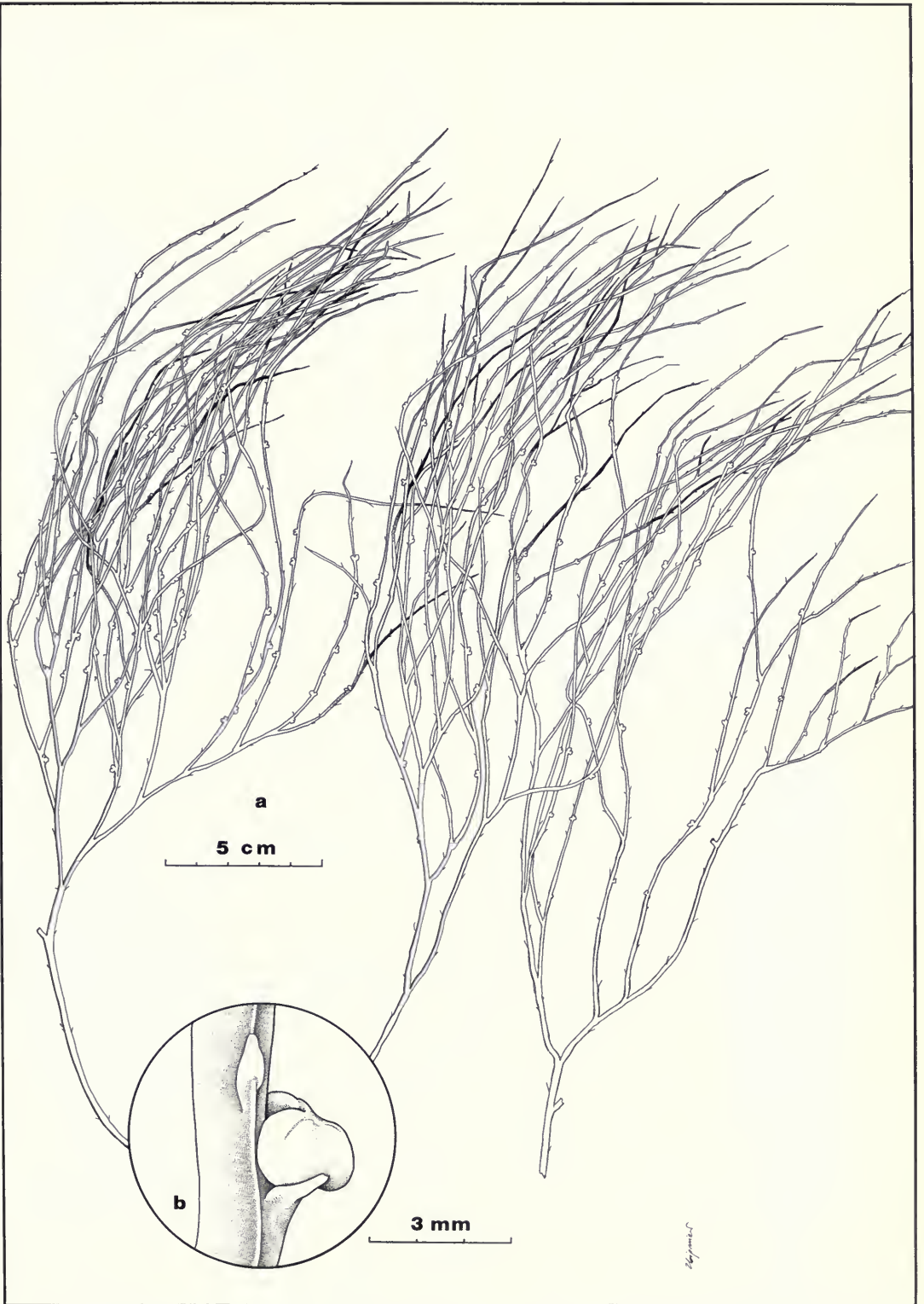
Terrestrial, palustral or aquatic. **Stem** subterranean, short- to long-creeping, freely branched, bearing erect, aerial stems that are jointed, longitudinally ridged, and usually hollow, ca. 10 cm to 8 m long, often with whorls of branches. **Leaves** small, in whorls at nodes, the lower portion laterally fused in sheaths, the upper portion in more or less prolonged teeth. **Sporangia** large, several borne on each stalked, peltate, apically flattened sporangiophore, in a condensed terminal strobilus. **Spores** spheroidal with circular aperture, and 4 paddle-shaped elaters, the surface with small granulate and large spherical deposits.

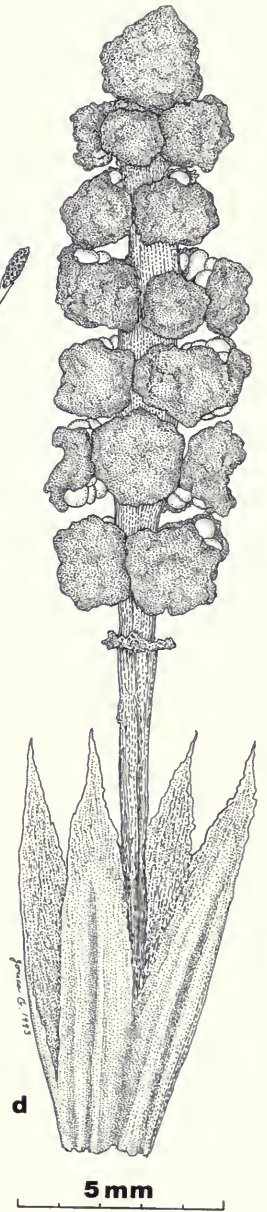
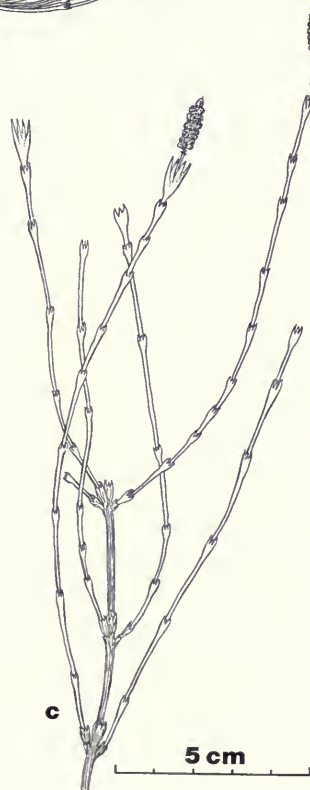
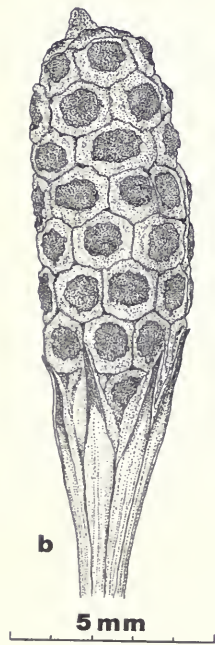
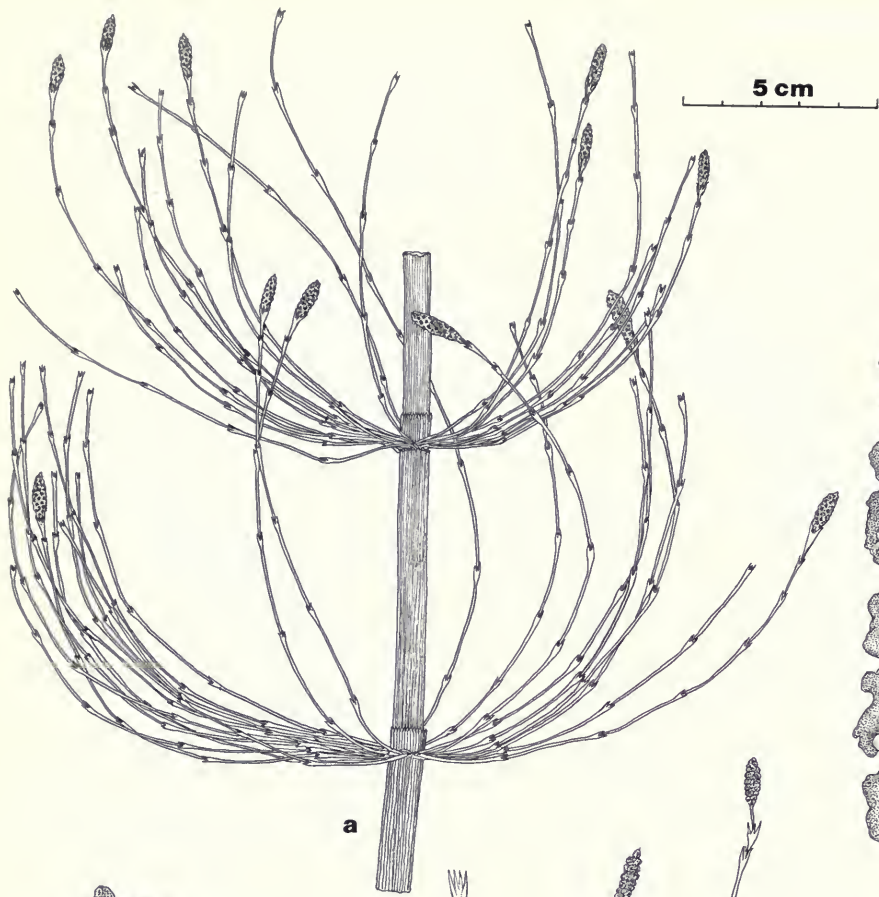
The *Equisetum* strobilus is composed of sporangiophores that are sometimes called sporophylls. A detailed study of these structures by Page (1972) shows they are partly modified from a leaf and partly from a cauline appendage; thus the term sporangiophore is more appropriate. The small leaves that surround each node are laterally fused below and form coarse teeth above.

References

HAUKE, R. L. 1961–1962. A resume of the taxonomic reorganization of *Equisetum* subgenus

FIG. 4. *Psilotum nudum*: a, habit; b, portion of fertile branch with sporangium. (Adapted from Stolze, Ferns and fern allies of Guatemala, 1983.)





Hippochaete, I-IV. Amer. Fern J. **51**: 131-137; **52**: 29-35, 57-63, 122-130.
 HAUKE, R. L. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. Beih. Nova Hedwigia **8**: 1-123.
 HAUKE, R. L. 1973. A taxonomic monograph of

Equisetum subgenus *Equisetum*. Nova Hedwigia **30**: 385-455.
 PAGE, C. N. 1972. An interpretation of the morphology and evolution of the cone and shoot of *Equisetum*. J. Linn. Soc. Bot. **65**: 359-397.

Key to Species of *Equisetum*

- a. Main aerial stem large, usually 10 mm or more wide (pressed), rarely less (to 5 mm), usually 2-5 m tall, with a hollow center; strobilus sessile or nearly so 1. ***E. giganteum***
- a. Main aerial stem small, to 2 mm wide (pressed), usually 0.5 m tall or less, with a solid center; strobilus stalked 2. ***E. bogotense***

1. ***Equisetum giganteum*** L., Syst. nat. ed. 10: 1318. 1759. TYPE: Plumier, Pl. Amér. (ed. Burman) *t. 125, f. 2* (1757 as to the plate). **Figure 5a-b.**

Equisetum myriochaetum Schlect. & Cham., Linnaea **5**: 623. 1830. TYPE: Misantla, Veracruz, Mexico, *Schiede and Deppe 833* (holotype, ♀?).

Equisetum schaffneri Milde, Verh. Zool.-Bot. Ges. Wien **11**: 345. 1861. TYPE: Orizaba, Mexico, *W. Schaffner 315* (holotype, ♀?).

Stem usually 2-4 m tall, often bearing an apical strobilus, usually 15-25 mm wide (10 mm or more, rarely 5 mm or less), with a central hollow. **Endodermis** surrounding each of the vascular bundles. **Sheaths** of the main stem usually light brown, with often deciduous, rather indurated teeth. **Branches** in regular whorls, with 8-10 ridges. **Strobilus** sessile or nearly so.

In wet, usually open areas, in sloughs, on the banks of streams, rivers, and irrigation ditches, in boggy areas, and in streambeds, 1900-3500 m, Piura, Cajamarca and Amazonas, south to Arequipa and Puno.

Greater Antilles; Mexico and Central America; Venezuela and Colombia, south to Chile, Argentina and Brazil.

Equisetum myriochaetum may be a species, as Hauke and others have it, or it may be an extreme variation of *E. giganteum*, as treated here. Most

likely it should be recognized as a subspecies, as is *E. ramosissimum* ssp. *debile*, but we do not wish to make a new combination at this time.

Equisetum giganteum has the tubercles on the ridges of the stem square or flattened in profile while the tubercles of *E. myriochaetum* appear rather similar to the teeth of a saw. The former species has two to several lines of stomates on each side of a groove of the stem, while the latter species has a single line of stomates. Characters of the strobilus (apiculate or not) and of the sheath color (different from the stem or not) are not species-specific.

Equisetum schaffneri has a variable mixture of the characters of *E. giganteum* and of *E. schaffneri*. It has a wider distribution than a sterile hybrid should have, and it occurs in regions in which only one of the putative parents is known (Venezuela and in Peru, for example). Accordingly, it may be a natural intermediate of the extremes of *E. giganteum*. The abortive spores present in some collections (not all have strobili) are also present in some other species: in *E. bogotense* and *E. variegatum* (Hauke, 1963, 1978) where hybridization is not concerned.

Hauke (Ph.D. dissertation, University of Michigan) cites the following collections of *E. myriochaetum* from Peru: Ayacucho, *Killip & Smith 22757* (us); Cuzco, *Cook & Gilbert 1372* (us). Also the following collections of *E. × schaffneri* from Peru: Lima, *Rose 18762* (NY, us); Ucayali?, *Herrera 1392* (us); Cuzco: *Cook & Gilbert 1091* (us).

FIG. 5. *Equisetum giganteum*: a, habit; b, apex of branch with strobilus. *Equisetum bogotense*: c, habit; d, apex of branch with strobilus. (a, b from *Lowell 535*, Ecuador, F; c, d from *Cuatrecasas 11807*, Colombia, F.)

Piura: Hills of Chiarnique, *Barbour 2160* (MO). **Lambayeque:** Olmos to Jaén, *Correll & Smith P792* (GH). **Cajamarca:** Prov. Cutervo, Llatun, *Mostacero et al. 1740* (HUT). Prov. Celendín, alrededores de Celendín, *Mostacero et al. 835* (MO, UC). **Amazonas:** Prov. Bagua, 3.9 km NE of Chiriaco, *Barbour 4360* (F, MO). Utcabamba, *Pennell 15586* (GH, US). **La Libertad:** Prov. Trujillo, valle de Río Chicama, *Müller & Krebs 12137* (USM). **San Martín:** Tarapoto, *Martin & Plowman 1843* (F, GH). Prov. Mariscal Cáceres, 45 km NE of Tingo María, *Tryon & Tryon 5270* (GH). **Ancash:** Prov. Santa, alrededores de Jimbe, *Mostacero et al. 1096* (F). **Huánuco:** Prov. Huánuco 6 km S of Huánuco, *Stork & Horton 9376* (F, GH, MO, UC). **Lima:** Villa Lagoon (Prov. Lima, Chorrillos), *Coronado 6* (GH, UC, US). **Pasco:** Oxapampa, *Soukup 2677* (US). **Junín:** 3 km N of La Merced, *Tryon & Tryon 5442* (GH, UC). **Ucayali:** Prov. Coronel Portillo, Arboretum von Humboldt, *Diaz et al. 687* (F, MO, US). **Huancavelica:** Prov. Tayacaja, Huari, *Saunders 1148* (F, GH, US). **Ayacucho:** Ayna, *Killip & Smith 22757* (F). **Apurímac:** Prov. Abancay, Trancapata, *Vargas 9617* (F, UC, US). **Cuzco:** Aguas Calientes, *Solomon 3180* (F, MO); 39 km E of Urohuasi on Abancay-Cuzco road, *Gentry et al. 23399* (MO, UC). **Madre de Dios:** Prov. Manú, Parque Nacional del Manú, *Foster 9796* (MO); *9856* (MO). **Arequipa:** Yura, *Solomon 2912* (F, MO, USM). **Puno:** Puno, *Angulo 1760* (HUT).

2. *Equisetum bogotense* HBK., Nov. gen. sp. pl. 1: 42. 1815. TYPE: "Prope Santa Fe de Bogota et Alto del Roble, Columbia," *Humboldt & Bonpland* (holotype, P?). **Figure 5c-d.**

Stems usually 20–50 cm tall, commonly bearing an apical strobilus, 1–2 mm wide, solid in the center. **Endodermis** single, surrounding the ring of vascular bundles. **Sheaths** with short, brown, papery teeth. **Branches** irregular, with 4 ridges. **Strobilus** stalked.

In soil or among rocks, in wet open places, including banks of creeks, rivers, and irrigation ditches in moist to wet seeps and clay road banks, 100–4200 m, most often above 2000 m, Piura south to Puno and Tacna.

Costa Rica and Panama; Galápagos Islands; the Andes of Venezuela and Colombia, south to Bolivia; to southern Argentina and Chile.

Piura: Prov. Huancabamba, Cerro Blanco, *Stork 11415* (GH, UC, US). **Cajamarca:** Prov. Contumazá, Guzmango to Santiago, *Sagástegui & López 10584* (F, MO). San Pablo, *Hutchison & Wright 5060* (F, MO, UC, US). **Amazonas:** Hills WNW of Pomacocha, *Wurdack 9445* (GH, UC, US, USM). **La Libertad:** Above Yamobamba, *Conrad 2728* (MO). **San Martín:** NW corner of Río Abiseo National Park, *Young & León 4534* (HUT, USM). **Ancash:** Prov. Recuay, *López et al. 7596* (MO, US). **Huánuco:** Prov. Huánuco, Cerro Carpish, *Luteyn & Lebron-Luteyn 5483* (F, UC, US). **Lima:** Prov. Huarochirí, *Sullivan et al. 1103* (F, MO); Prov. Canta, Dist. Huaros, *Pennell 14715* (F,

GH, US). **Pasco:** Prov. Oxapampa, Los Chacos, near Oxapampa, *Smith & Pretel 1514* (F, MO, USM). **Junín:** Above Concepción, *Correll & Smith P736* (GH). **Huancavelica:** Prov. Huancavelica, Yauli, *Stork & Horton 10863* (F, UC). **Ayacucho:** Santiago, about 67 km from Nasca on road to Puquio, *Correll & Smith P151* (GH). **Cuzco:** Prov. Urubamba, Pomatales, *Núñez 7327* (F, MO). **Arequipa:** Chacra Pachacutac, *Balls B5868* (F, UC, US). **Puno:** San Gabon (San Gabán) to Ollachea, *Dillon et al. 1239* (MO). **Tacna:** Prov. Tarata, Chuvire, *Metcalfe 30407* (MO, UC, US).

Family 26. LYCOPODIACEAE

Contributed by Benjamin Øllgaard

Lycopodiaceae Mirbel, in Lam. & Mirbel, Hist. nat. vég. 4: 293. 1802. ("Lycopodia"). TYPE: *Lycopodium* L.

Plants terrestrial or epiphytic, erect to pendulous herbs or climbers. **Stems** dichotomously branching, sometimes also with lateral branching, protostelic, with the xylem arranged radially or in parallel bands, or forming an incomplete cylinder (*Phylloglossum*). **Leaves** simple, with 1 simple vein, arranged in low alternating spirals or irregular alternating whorls, or seemingly decussate, homophyllous or heterophyllous, isophyllous or anisophyllous. **Sporophylls** like the foliage leaves, or modified, in some groups specialized and aggregated into distinct strobili. **Sporangia** solitary, axillary or on the upper side of the sporophyll base, homosporous, unilocular, reniform to subglobular, short-stalked, dehiscing by a transverse slit, which divides each sporangium into 2 nearly equal or strongly unequal valves. **Spores** without chlorophyll, tetrahedral, with a trilete scar. **Gametophytes** monoecious, tuberous, subterranean, and mycorrhizal and without chlorophyll or surface-living and green.

The family occurs in almost all humid regions of the world, both warm and cold. It is here treated as consisting of four genera including *Phylloglossum* (Australia, New Zealand). Up to 14 genera have been recognized by other authors (Holub, 1975, 1983, 1985, 1991; Wagner & Beitel, 1992), the genera of these authors generally corresponding to the infrageneric taxa of Øllgaard (1987, 1989, 1992); for a review of the classification, an index to the family, and an overview of the Neotropical species, see these publications. Most of the Peruvian species are illustrated in Øllgaard (1988).

The total number of species in the family probably exceeds 350, and approximately 185 of these are tropical American. The Andes have a particularly high diversity, and many species are conspicuous elements in the montane and alpine vegetation of these mountains.

This treatment includes 62 species for Peru, but the real number is likely to be higher. Although largely all available material has been consulted for this treatment, it is evident that much collecting needs to be done before a complete presentation can be made. Many species are represented by a single or few collections, and intensive efforts in limited areas such as those of Blanca León and Kenneth Young in the Río Abiseo National Park, of Abundio Sagástegui in the north of Peru, and of the late David N. Smith in several areas have turned up several species not formerly known from Peru and widely disjunct from other known occurrences, as well as species new to science.

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Key to Genera of Lycopodiaceae

- a. Stem dichotomies equal (isotomous) throughout, plants without elongate, indeterminate main stems, but sometimes with equally thick, somewhat heteroblastic branches; roots usually forming 1 basal tuft; sporophylls and vegetative leaves alike, or the sporophylls, if smaller, persisting, not subpeltate, not ephemeral; spores foveolate or fossulate I. **Huperzia**
- a. Stem dichotomies unequal (anisotomous) throughout, the branches differentiated into elongate, indeterminate, rhizomatous, or creeping, or trailing, main stems, and usually determinate aerial branchlet systems; sporophylls strongly modified, ephemeral, unlike vegetative leaves, usually subpeltate, aggregated in compact, terminal strobili; spores reticulate or rugate b
- b. Strobili erect, sessile or pedunculate, borne on branchlet systems that arise in a dorsolateral position on the main stem; side walls of sporangium epidermis cells sinuate, lignified throughout; spores reticulate II. **Lycopodium**
- b. Strobili pendulous and sessile, or strobili erect and terminating simple erect branches that arise dorsally on the creeping stem, side walls of sporangium epidermis cells straight, not lignified, except for nodular or semiannular thickenings; spores rugate III. **Lycopodiella**



FIG. 6. *Huperzia eversa*: a, habit; b, portion of fertile division with sporangia. *Huperzia binervia*: c, habit; d, portion of fertile division with sporangia. *Huperzia linifolia* var. *tenuifolia*: e, habit; f, leaf from basal division; g, portion of fertile division with sporangia. *Huperzia cuneifolia*: h, habit; i, expanded leaves from basal division; j, fertile shoot tip. (a from Holm-Nielsen et al. 3873, Ecuador, AAU; b from Holmgren 674, Ecuador, s; c, d from Mathews, Peru, k; e, f, g from Holm-Nielsen et al. 4422, Ecuador, AAU; h, i, j from Hutchison & Wright 6943, Peru, p.)

I. *Huperzia*

Huperzia Bernh., J. Bot. (Schrader) 1800 (2): 126. 1801. LECTOTYPE (designated by Rothmaler, Feddes Repert. Spec. Nov. Regni Veg. 54: 59. 1944): *Huperzia selago* (L.) Martius & Schrank (*Lycopodium selago* L.). **Figure 6.**

Plananthus Mirbel in Lamarck & Mirbel, Hist. nat. veg. 3: 476. 1802. TYPE: *Plananthus selago* (L.) Beauv. (*Lycopodium selago* L.).

Lycopodium subgen. *Selago* Baker, Handb. Fern-Allies 8. 1887. TYPE: *Lycopodium selago* L.

Lycopodium subgen. *Urostachya* Pritzel, Nat. Pflanzenfam. 1 (4): 592. 1901. TYPE: *Lycopodium selago* L.

Urostachys (Pritzel) Herter, Beih. Bot. Centralbl. 39: 249. 1922. TYPE: *Urostachys selago* (L.) Herter (*Lycopodium selago* L.).

Phlegmariurus Holub, Preslia 36: 21. 1964. TYPE: *Phlegmariurus phlegmaria* (L.) Sen & Sen (*Lycopodium phlegmaria* L.).

Plants epiphytic or terrestrial, pendent, recurved, erect or ascending, isotomously branched throughout (except in connection with bulbil formation in the group of *H. selago*, and sprouting from the base of old plants), the branches all similar (homoblastic), or in some terrestrial species differentiated (heteroblastic) into prostrate (sometimes subterranean) versus erect, aerial branches. **Roots** arising from the stem stele, descending through the cortex to the stem base, here emerging as 1 basal tuft, or in heteroblastic species sometimes emerging directly along the underside of prostrate shoots. **Shoots** homophyllous or heterophyllous. **Sporophylls** and vegetative leaves alike, not peltate, without mucilage cavities, persisting and green after sporangium dehiscence, the gradual or abrupt constriction of distal divisions of heterophyllous species associated or not with presence of sporangia. **Sporangia** axillary, reniform, isovalvate, with a short slender stalk; side walls of sporangium epidermis cells sinuate, thickened and lignified together with the inner walls. **Spores** foveolate or fossulate. **Gametophytes** (not known for any Peruvian species) usually subterranean (in terrestrial plants), mycorrhizal, cylindrical with radial or bilateral symmetry, with pluricellular, uniseriate trichomes among the gametangia.

The genus is virtually cosmopolitan, occurring in tropical, temperate, arctic, and alpine environments. Species diversity is highest throughout the tropics in evergreen montane forests, and in the wet Andean grass and shrublands in South America.

There are approximately 300 species worldwide, 49 in Peru. Seven species are endemic to Peru, four are shared only with Bolivia and more southerly regions, 26 occur also in Ecuador or farther north in the Andes and the Neotropics, while 12 species occur both to the north and south of Peru.

Species delimitation is problematic almost throughout the genus due to the simple morphology of the group and to plasticity of the characters (Øllgaard, 1992). Morphogenesis seems to be somewhat unstable in most species and may be modified by external factors. Most characters are plastic within a species (e.g., stem thickness, number of leaf orthostichies, leaf crowding, leaf direction, color, degree of heterophyllous differentiation). Hybridization seems to occur rather frequently, contributing to the blurring of species limits, and the putative hybrids often have normally developed spores. As a consequence, species recognition is often based on some experience and comparison with identified material, rather than a set of definite characters.

Measurements and terminology. The descriptions and key characters are based on dried material, unless otherwise indicated. Very often measurements and solid shape of organs in life deviate strongly from the dried condition.

Branching is isotomous throughout the genus, except in connection with sprouting (lateral branching) from the base of old or injured individuals. Isotomy results in the formation of equally thick branches each with an equal amount of vascular tissue. However, many species of high Andean grasslands develop heteroblastic branch pairs; i.e., the isotomous branches differentiate into distinct aspects and functions due to different leaf development, as exemplified by the sporangiate, erect, aerial shoots and the sterile, prostrate or even subterranean, basal, rejuvenating shoots of *Huperzia crassa* and *H. hypogaea*. Homoblastic branches have the same aspect and function and similar leaf development.

Phyllotaxis is poorly understood in the Lycopodiaceae. It seems to be irregularly organized morphogenetically and quite variable within one species, sometimes even within the same individual. Stevenson (Bot. J. Linn. Soc. 72: 81–100. 1976) interpreted the phyllotaxis of *Huperzia lucidula* (Michx.) Trevisan (temperate North America) as consisting of low alternating spirals, and found a definite relation between the number of orthostichies and the number of protoxylem lobes in the stele. In many species this relation is different or

possibly absent, and transitions from spiral to irregularly whorled phyllotaxis is common, although whorled arrangement is the more common. The number of longitudinal leaf ranks is readily observed in some cases but often must be estimated, or calculated, from the number of leaves in each leaf whorl, or from the number of leaves contained in one rotation of the leaf spiral. As the leaves of a whorl or a rotation of the spiral alternate with the adjacent whorls or spirals above and below, the number of leaves in two whorls or rotations makes up the number of longitudinal leaf

ranks of a shoot. For the sake of brevity, I have described leaf arrangement in terms of leaf whorls, although this is not everywhere completely accurate.

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Key to Species of *Huperzia*

- a. Plants erect, or ascending to erect, terrestrial or epiphytic and shoot apices erect; leaf margins smooth, fimbriate, denticulate or erose, or leaves papillate b
- b. Leaf margins denticulate (at least of some leaves, sometimes minutely and remotely denticulate) by pointed teeth, ciliolate, fimbriate, or leaves papillate c
- c. Leaves densely papillate abaxially, at least at the apex 12. *H. weberbaueri*
- c. Leaves not papillate d
- d. Leaves of upper, sporangiate divisions loosely to closely appressed, abaxially strongly convex throughout; leaf margins fimbriate by irregularly shaped and directed pale and soft teeth; plants bright red or tinged with red e
- e. Erect shoots predominantly quadrangular 25. *H. tetragona*
- e. Erect shoots hexagonal or terete f
- f. Leaves of upper, sporangiate branches triangular-lanceolate to triangular-ovate, with smooth abaxial epidermis, arranged in alternating whorls of 3-4 24. *H. attenuata*
- f. Leaves of upper, sporangiate branches strongly uneven abaxially by protruding, blister-like epidermal cells, arranged in alternating whorls of 5 23. *H. sagasteguiana*
- d. Leaves of upper, sporangiate divisions patent to recurved (sometimes appressed and green in *H. affinis*), abaxially flat or convex; leaf margins ciliate or denticulate; plants green ... g
- g. Leaves borne in alternating whorls of 4-5(-6), denticulate or long-ciliate, narrowly triangular-lanceolate, linear-lanceolate or nearly subulate, (2.5-)3-6 mm long, 0.5-1.5 mm wide h
- h. Sporangiate leaves usually with long-ciliate margins, 1-1.5 mm wide at the somewhat clasping base, 4-6 mm long, spreading to appressed 10. *H. affinis*
- h. Sporangiate leaves denticulate, to 1 mm wide at the base, 2.5-5 mm long, not clasping, spreading to strongly reflexed 9. *H. eversa*
- g. Leaves borne in alternating whorls of (6-)7-11, denticulate, subulate to linear-subulate, 4-10 mm long i
- i. Leaves borne in alternating whorls of (6-)7-8, ascending to spreading or sharply reflexed, straight to strongly recurved, usually evenly tapering, with very sparsely to densely and sharply denticulate to short-ciliolate margins throughout 7. *H. reflexa*
- i. Leaves borne in alternating whorls of 8-11, usually sharply bent upward from a perpendicular junction to the stem and then gently to strongly claw-like recurved, narrowed shortly above the base, with rather densely denticulate-ciliolate margins at base, usually sparsely denticulate or smooth at apex 8. *H. acifolia*
- b. Leaf margins entirely smooth, or uneven, rugose to erose-rugose, without pointed teeth or cilia, not fimbriate or papillate, or papillate only on leaf base margins j
- j. Epiphytes with spreading leaves; leaves filiform, up to 0.5 mm wide, (6-)10-17 mm long, leaf bases often red 36. *H. wilsonii*

- j. Terrestrial plants with spreading, reflexed or appressed leaves; leaves linear-filiform to nearly orbicular, not red k
- k. Leaves wide-spreading to reflexed or patent-ascending, the widest ones linear-filiform to lanceolate, without a basal swelling (air sac) l
 - l. Broadest leaves of sporangiate divisions linear-filiform to subulate, 1.5 mm wide or less m
 - m. Leaves softly herbaceous, usually straight or slightly recurved, 0.5–1.3 mm wide, usually flat abaxially n
 - n. Leaves linear to linear-subulate, 0.8–1.3 mm wide at base, slightly convex to canaliculate adaxially 1. **H. hippuridea**
 - n. Leaves linear-filiform, 0.5–0.8 mm wide at the base, canaliculate abaxially 2. **H. lechleri**
 - m. Leaves coriaceous, usually sigmoid, 1.2–1.5 mm wide, usually bisulcate abaxially 4. **H. binervia**
 - l. Leaves lanceolate, the narrowest ones 1.5 mm wide or more o
 - o. Leaves reflexed to patent-ascending, thickly coriaceous, adaxially evenly convex, or with slightly prominent vein, margins flat or involute, smooth 5. **H. weddellii**
 - o. Leaves papery to thinly subcoriaceous, folded slightly down along the vein, margins revolute, minutely rugose 6. **H. brongniartii**
- k. Leaves, at least of sporangiate divisions, appressed, the narrowest ones linear-lanceolate to broadly triangular-cordate and appressed, with or without a basal swelling, or patent to reflexed and oblong, ovate or wider p
 - p. Shoots strongly heteroblastic, with deeply subterranean, elongate, horizontal shoots bearing stiffly erect aerial branches 22. **H. hypogaea**
 - p. Shoots homoblastic to heteroblastic, above the ground or shallowly subterranean, not deeply subterranean q
 - q. Sporangiate divisions with shortest leaves 6 mm or longer, linear to widely lanceolate or widely triangular-ovate r
 - r. Aerial shoots somewhat club-shaped, compactly caespitose, narrowed and somewhat etiolated at the base and here with pale and irregularly appressed leaves; shoots strongly heteroblastic, the basal, prostrate shoots short and with much reduced leaves 21. **H. saururus**
 - r. Aerial shoots usually equally thick throughout or tapering, loosely to densely caespitose, with all leaves nearly alike; shoots homoblastic or heteroblastic; prostrate shoots (if any) with leaves the same size or larger than those of aerial shoots s
 - s. Shoots heteroblastic, with prostrate basal, rejuvenating, often rooting shoots bearing erect, fingerlike aerial shoots t
 - t. Aerial shoots often short, unbranched, appearing narrower than creeping shoots; leaves of creeping shoots larger than in aerial shoots 20. **H. andina**
 - t. Aerial shoots well developed, simple or branched, not appearing narrower than creeping shoots; leaves of creeping and aerial shoots of nearly equal size u
 - u. Leaves dull, pruinose, usually red-tinged, abaxially rugose from protruding, blisterlike epidermis cells (rarely smooth) v
 - v. Leaves 5–9 × 1–2 mm, with a prominent basal air cavity causing a perpendicular appearance of the junction to the stem in sporangiate leaves 18. **H. crassa**
 - v. Leaves 9–12 × 2–2.5 mm, without a prominent basal air cavity, appressed from the base 19. **H. nesselii**
 - u. Leaves dull to somewhat glossy, green, abaxially smooth w
 - w. Leaves of aerial shoots lanceolate to widely lanceolate, slightly long-acuminate, (1.8–)2–2.5(–3) mm wide, strongly curved upward at apex 17. **H. darwiniana**

- w. Leaves of aerial shoots lanceolate, evenly tapering, 1.5–2 mm wide, straight to slightly curved upward at apex 16. **H. macbridei**
- s. Shoots homoblastic, all essentially alike x
- x. Leaves of basal divisions linear to linear-subulate, up to 1.5 mm wide, usually bisulcate abaxially, usually somewhat sigmoid 4. **H. binervia**
- x. Leaves of basal divisions linear-lanceolate or wider, 1.5–4 mm wide, not bisulcate abaxially, sigmoid or not y
- y. Plants rather fragile and slender; stems 2–3.5 mm thick excluding leaves; leaves 5–10 × 1.5–2 mm, distal divisions ca. 5–10 mm in diameter including leaves 15. **H. capellae**
- y. Plants large, robust; stems 3–8 mm thick excluding leaves; leaves 5–12 × 2–4 mm, distal divisions ca. (7–)10–25 mm in diameter including leaves z
- z. Leaves of aerial shoots evenly tapering to short-acute, straight or curved apex aa
- aa. Leaves triangular-lanceolate to widely triangular-ovate, straight to slightly curved upward; leaf base margins in sporangiate leaves usually slightly revolute, sometimes subauriculate 11. **H. kuesteri**
- aa. Leaves lanceolate to widely lanceolate, usually strongly curved upward (rarely patent-ascending and somewhat sigmoid); leaf bases not revolute or auriculate 14. **H. polylepidetorum**
- z. Leaves of aerial shoots slightly long-acuminate, strongly curved upward at apex 17. **H. darwiniana**
- q. Sporangiate divisions with longest leaves up to 6 mm long, lanceolate or wider bb
- bb. Leaves (longest ones) up to 4 mm long, ovate, elliptic, or cordate cc
- cc. Broadest leaves ovate or elliptic, (1.8–)2–2.6(–3.5) mm long, (1.2–)1.5–2(2.4) mm wide, sporangia 1–1.5 mm wide 26. **H. sellifolia**
- cc. Broadest leaves widely ovate to widely suborbicular-cordate or triangular-cordate, 2–4 mm long, 2–4(–5) mm wide, sporangia 1.5–2.5 mm wide 28. **H. brevifolia**
- bb. Leaves, even shorter ones, 4 mm or longer, or if shorter, then lanceolate dd
- dd. Stem, excluding leaves, 1–1.5 mm thick, sporangia 2–2.5 mm wide, subglobose 27. **H. engleri**
- dd. Stem, excluding leaves, usually more than 2–4 mm thick; sporangia 1.5–2 mm wide, flattened ee
- ee. Leaves triangular-ovate to widely ovate, usually red-tinged, leaf bases with a strongly prominent air cavity 29. **H. hohenackeri**
- ee. Leaves lanceolate, green, leaf bases without or with a slightly prominent air cavity 13. **H. colanensis**
- a. Plants pendulous, or initially erect with nodding to pendulous shoot apices, epiphytic or terrestrial; leaf margins entire ff
- ff. Leaves more or less sharply dimorphic: basal divisions with long, expanded leaves, apical divisions constricted, with appressed, reduced, decussate or subdecussate leaves; or the entire plant covered by appressed, short, broad, decussate leaves gg
- gg. Plants robust, stem excluding leaves at least 2 mm thick at the base, without red coloration hh
- hh. Constricted divisions sharply quadrangular, 3–8 mm thick including leaves; sporangiate leaves 3–8 mm long, sharply carinate, often with a conduplicate apex 41. **H. molongensis**
- hh. Constricted divisions bluntly quadrangular to subterete, 2–4 mm thick; sporangiate leaves 3 mm long or less, rounded to bluntly carinate throughout abaxially, not conduplicate apically ii
- ii. Plants entirely pendulous, expanded leaves of proximal divisions in usually densely crowded, alternating whorls of 3, the whorls 2.5–5 mm apart; sporangiate leaves 2–3 mm long

- 42. *H. campiana*
- ii. Plants erect to scandent, with recurved shoot tips and constricted divisions, expanded leaves of proximal divisions in distant, alternating whorls of 4, the whorls 6–9 mm apart; sporangiate leaves 1.2–1.6 mm long 9. *H. pruinosa*
- gg. Plants slender, stem excluding leaves usually 1 mm thick or less (rarely to 1.7 mm) at the base; stem base with or without red coloration jj
- jj. Expanded leaves of basal divisions very uniform in size, shape, and position throughout, closely situated, with almost continuously overlapping leaf margins (pressed specimens), borne in alternating whorls of 3 at the base, broadly lanceolate to ovate, acute; stems not red 44. *H. ericifolia*
- jj. Expanded leaves uniform or variable in shape and position, close to distant and not continuously overlapping, decussate, subdecussate or in alternating whorls of 3 at the base, linear-subulate to ovate or oblanceolate; stems with or without red coloration kk
- kk. Expanded leaves decussate or subdecussate, lanceolate to ovate, the broadest ones 2–3.5 mm wide ll
- ll. Constricted terminal divisions usually not sharply distinct from expanded divisions, with irregularly sized and directed leaves; expanded divisions usually well developed and more extensive than constricted divisions 45. *H. myrsinites*
- ll. Constricted terminal divisions sharply distinct from expanded divisions, with regularly sized and uniformly directed leaves throughout; expanded leaves restricted to a short zone at the base (rarely lacking), and sometimes inserted in short zones of constricted divisions 43. *H. heteroclita*
- kk. Expanded leaves decussate or in whorls of 3, linear-subulate to lanceolate or oblanceolate, the broadest ones 2 mm wide or less, or if wider then less than 6.5 mm long and oblanceolate mm
- mm. Expanded leaves decussate or in whorls of 3, linear-subulate to lanceolate, the broadest ones 1–2 mm broad, the longest ones 8–15 mm long nn
- nn. Expanded leaves linear, or linear-subulate to linear-lanceolate, 0.5–1 mm broad 47. *H. subulata*
- nn. Expanded leaves linear-lanceolate to lanceolate, 1.3–2 mm broad 46. *H. phylcifolia*
- mm. Expanded leaves decussate, lanceolate to oblanceolate, the broadest ones 1.5–3 mm broad, the longest ones less than 6.5 mm long 48. *H. cuneifolia*
- ff. Leaves uniform throughout, long and expanded, or gradually smaller and more appressed, but not predominantly decussate or subdecussate toward the shoot apices oo
- oo. Plants very delicate, the longest leaves less than 6(–8) mm long, acicular, less than 0.5 mm broad; stems less than 1 mm thick at base excluding leaves pp
- pp. Non-sporangiate leaves of narrow terminal divisions closely appressed to the stem, with cuneate to rounded base; leaves of basal divisions usually strongly curved upward and inward from a patent base, or sigmoid 39. *H. curvifolia*
- pp. Non-sporangiate leaves of terminal divisions with a patent, rounded to auriculate or subhastate leaf base; leaves of basal divisions spreading to ascending, often unilaterally curved 40. *H. tenuis*
- oo. Plants slender to robust, longest leaves of basal divisions more than 8 mm long; leaves filiform or linear to lanceolate; stems 0.5–5 mm thick at base, excluding leaves qq
- qq. Leaves of basal divisions alternate or paired, or in occasional whorls of 3, more than 13 mm long, 1–4 mm broad, with a narrowed, twisted, often petiolelike and approximately perpendicular lamina base, leaves of terminal divisions alternate to whorled; stem base usually 1 mm or less thick excluding leaves 35. *H. linifolia*
- qq. Leaves of basal divisions predominantly or entirely whorled, without petiolelike lamina bases, 8–23 mm long; stem base 0.5–5 mm or more thick rr
- rr. Leaves closely appressed throughout, linear-subulate to linear-lanceolate, apically convex to conduplicate abaxially ss
- ss. Leaves borne in whorls of 7–8, linear-subulate, falcate-appressed

- 33. *H. funiformis*
 ss. Leaves borne in whorls of 4–5, linear to linear-lanceolate, straight to slightly recurved at apex 34. *H. buesii*
 rr. Leaves, at least in basal divisions, ascending to patent, filiform to lanceolate, flat, concave, or convex tt
 tt. Leaves filiform to linear, or linear-subulate from an auriculate leaf base, up to 1 mm broad; the leaves, if linear and 1 mm broad, borne in whorls of 5 or more uu
 uu. Leaf bases of non-sporangiate leaves auriculate and often somewhat overlapping neighboring leaf bases of the same whorl; lamina usually less than 0.7 mm broad above the auriculate base 38. *H. sarmentosa*
 uu. Leaf bases of non-sporangiate leaves without auricles; lamina 0.2–1 mm broad vv
 vv. Leaves filiform, 0.3–0.5 mm broad just above the base ww
 ww. Leaves not twisted at base, perpendicularly spreading to slightly upward curved, or ascending, (6–)10–17 mm long, with green or bright red bases; stems usually 1.5–2 mm thick ... 36. *H. wilsonii*
 ww. Leaves twisted at base, obliquely falcate-ascending, 6–10(–12) mm long, with green leaf bases; stems usually 1–1.5 mm thick
 37. *H. polycarpus*
 vv. Leaves linear, 0.7–1 mm broad, (10–)14–19 mm long ... 3. *H. arcuata*
 tt. Leaves linear-lanceolate to lanceolate, the broadest ones more than 1.5 mm broad; or the non-sporangiate leaves of basal divisions linear, 1 mm broad or more, and borne in whorls of 3–4 xx
 xx. Leaf margins minutely uneven by individually protruding epidermis cells, especially near the apex; leaves lanceolate, 2–4 mm broad
 32. *H. rosenstockiana*
 xx. Leaf margins smooth; leaves linear to lanceolate, 1–3.5 mm broad yy
 yy. Stem base 2.5–5 mm thick excluding leaves; leaves, at least of basal divisions, brightly shining, firmly coriaceous throughout, not twisted at base, 2.5–3.5 mm broad; sporangia 1.7–3 mm broad 30. *H. hartwegiana*
 yy. Stem base (1–)1.5–2 mm thick; leaves dull or slightly shining, firmly herbaceous to subcoriaceous, twisted or straight at base, 2–2.5 mm broad; sporangia 1–2.2 mm broad 31. *H. taxifolia*

1. *Huperzia hippuridea* (Christ) Holub, Folia Geobot. Phytotax. 20: 73. 1985.

Lycopodium hippurideum Christ in Pittier, Primit. Fl. Costar. 3 (1): 56. 1901. TYPE: Costa Rica, El Páramo, 3000 m, massif de Buena Vista, 1897, Pittier 10619 (holotype, p!; isotype, us!).

Urostachys hippurideus (Christ) Nessel, Bärlappgewächse 88. 1939.

Urostachys poseidonis Herter, Revista Sudamer. Bot. 10: 122–123. 1953. TYPE: Ecuador, Prov. Chimborazo, Penipe, 3400 m, Rose in Mille 35 (holotype, us!; isotypes, GH!, NY!).

Lycopodium poseidonis (Herter) Morton, Amer. Fern J. 54: 42. 1964.

Plants ascending to stiffly erect from a decumbent base, up to 60 cm tall, sparsely branched.

Shoots homophyllous, equally thick throughout, 10–35 mm in diameter including leaves. Stems excluding leaves 2.5–4 mm thick at the base, tapering to ca. 2–3 mm upward. Leaves borne in irregular alternating whorls of 5–8, spreading to reflexed, sometimes sharply reflexed and appressed to the stem, linear to linear-subulate, evenly tapering from the base or the middle, (10–)11–19 mm long, 0.8–1.3 mm wide, not, or rarely, twisted at base, adaxially with a slightly prominent vein, with smooth, usually slightly revolute margins, and indistinctly to prominently and widely decurrent bases. Sporangia 1.5–2 mm wide.

Upper montane forest, especially near the forest limit, usually on the forest floor, in semishade, alt.

2500–3500 m, Cajamarca, San Martín, Pasco, Cuzco.

Central America; Andes from Venezuela to Bolivia.

Huperzia hippuridea belongs to a group of closely related taxa of high montane forests throughout tropical America, including also *H. arcuata* B. Øllg. (Colombia, Ecuador), *H. lechleri*, *H. montana* (Underw. & Lloyd) Holub (Greater Antilles), *H. nuda* (Nessel) B. Øllg. & Windisch (Brazil).

Hutchison & Bismarck 6455 and *Matthews 963* (presumably from Chachapoyas) have thicker stems and more crowded and coriaceous leaves than usual for the species, thus approaching *Huperzia weddellii* (Herter) Holub and *H. loxensis* B. Øllg. *Matthews 963* is a mixed collection, sheets of the same number at BM pertaining to *H. macbridei*.

Cajamarca: Prov. Hualgayoc, Hda. Taulis, 4.6 km beyond Palmito junction on the road to La Playa, 2740 m, *Hutchison & Bismarck 6455* (UC, USM). **San Martín:** Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, Chochos, 3500 m, *Young & León 4660* (AAU). Prov. Mariscal Cáceres, Puerta del Monte, 3100–3300 m, *Young & León 4436* (AAU), 3450 m, *León & Young 1305* (USM). **Pasco:** Prov. Oxapampa, Santa Barbara, 3200–3300 m, *D. Smith 8176* (AAU, USM). **Cuzco:** Prov. Paucartambo, Cerro Macho Cruz, Parque Nacional Manú, 3400 m, *León 2303* (USM). **Department unknown:** (possibly from Chachapoyas) *Matthews 963* (G).

2. *Huperzia lechleri* (Hieron.) Holub, Folia Geobot. Phytotax. 20: 74. 1985.

Lycopodium lechleri Hieron., Bot. Jahrb. Syst. 34: 571. 1905. LECTOTYPE (designated by Rolleri, Revista Mus. La Plata (n.s.) Bot. 13 (78): 82. 1981): Peru (Dept. Puno), Tabina, *Lechler*, ed. Hohe-nacker 2012 (B!; isotypes, G!, K!, P!, UPS!).

Urostachys lechleri (Hieron.) Nessel, Bärlappgewächse 85. 1939.

Urostachys lechleri Hieron. var. *lehmannii* Nessel, Revista Sudamer. Bot. 6: 61. 1940. SYNTYPES: BONN, *Herb. Nessel 148!*, Ecuador, *Spruce*, Pallatanga 1858, marked 7; Ecuador: *unknown collector* "Aus dem Herbar Bonaparte, Paris," annotated "Ur. *lehmannii* Boge.".

Urostachys lehmannii (Nessel) Herter, Index Lycopodiorum 67. 1949.

In most features resembling *Huperzia hippuridea* closely, but differing consistently in the narrower, linear to nearly filiform leaves 10–23 mm long and 0.5–0.8 mm wide at the base, adaxially usually canaliculate, with a slightly prominent vein

at the base, and the margins not revolute, the sporangia 1–1.8 mm wide.

Upper montane forest, especially near the forest limit, usually on the forest floor, in semishade, alt. 1800–3600 m, Junín, Huancavelica, Cuzco, Puno.

Peru and Bolivia.

Closely related to *Huperzia hippuridea* (see the preceding species for discussion).

Junín: Prov. Tarma, Carpapata, *Soukup 3477* (F, GH). Huacapistana, 1800–2400 m, *Killip & Smith 24503* (F, GH, US). **Huancavelica:** Prov. Tayacaja, Marcavalle, between Huachocolpa and Tintay, 2600 m, *Tovar 4085* (USM), *Tovar 4089* (USM). **Cuzco:** Valle Occobamba [Occobamba], 1900 m, *Bües 856* (US). Prov. Paucartambo, Valle de Pilcopata, near Pillahuata, 2500 m, *Foster & Wachter 7501* (AAU). Pillahuata, 2850 m, *Fitzpatrick & Willard* (F). San Ignacio, Huadquiña, *Bües 1410* (US). **Puno:** Ollachea to San Gabán, 1000–2000 m, *Dillon et al. 1156* (AAU, F, MO). Prov. Carabaya, road San Gabán (Lanlacuni Bajo) to Macusani, near Ollachea, 2600 m, *Maas et al. 6111* (AAU, USM). **Department unknown:** *Lechler 2023a* (K). *Vargas 16767* (GH).

3. *Huperzia arcuata* B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 15, t. 1D. 1988. TYPE: Ecuador, Prov. Carchi, Road El Angel to Tulcán, 3500 m, *Holm-Nielsen et al. 5341* (holotype, AAU!; isotypes, GB!, QCA!, US!).

Plants ascending to erect from a decumbent base, with nodding shoot apices, up to 30 cm tall (terrestrial), or recurved to pendulous and up to 90 cm long (epiphytes), sparsely branched. Shoots homophyllous, equally thick throughout, 25–30 mm in diameter, or tapering to ca. 12 mm including leaves. Stem excluding leaves 2–3 mm thick at base, tapering to ca. 1.5 mm upward. Leaves borne in irregular alternating whorls of 6–7 near the base, upward of 5–6, spreading to falcately ascending, linear to subulate from a slightly widened lamina base, (10–)14–19 mm long, (0.5–)0.7–1 mm wide above the widened base, gradually tapering in the distal half or so, adaxially flat to slightly concave, or with slightly revolute margins, with abaxially slightly prominent vein and smooth margins, with slightly widened lamina base, twisting the lamina to a vertical position. Vegetative leaves of basal divisions often spreading to reflexed and not twisted. Sporangia 1.3–2 mm in diameter.

Upper montane forest, near timberline, on the forest floor, in semishade, or epiphytic, alt. 2700–3500 m, Amazonas, San Martín.

Southern Colombia to Peru.

Closely related to *Huperzia hippuridea*, from which it differs by its obliquely falcate-ascending, twisted leaves and the nodding to pendulous shoot tips. *Huperzia arcuata* also resembles *H. dichotoma* (Jacq.) Trevisan (tropical America) but is larger in all parts and restricted to timberline forest habitats. The Peruvian collections generally have short leaves, 8–15 mm long.

Amazonas: Chachapoyas, *Matthews* (E). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, Puerta del Monte, 3450 m, *Young 1627* (AAU, USM). Prov. Mariscal Cáceres, near La Playa Camp, 2700 m, *Young & León 4954* (AAU).

4. *Huperzia binervia* (Herter) B. Øllg., *Opera Bot.* 92: 169. 1987.

Lycopodium binervium Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 48. 1909. TYPE: Peru, Prov. Chachapoyas, *Matthews* (holotype, P!; isotypes, BM!, GL!, K!).

Urostachys binervius (Herter) Nessel, *Bärlappgewächse* 110. 1939.

Plants ascending to erect from a decumbent base, up to 50 cm tall. **Shoots** homophyllous, equally thick throughout, 15–30 mm in diameter including leaves or with gradually shorter leaves and tapering to 5–8 mm. **Stems** excluding leaves 3–6 mm thick at the base, sometimes tapering to 2–2.5 mm, ridged by decurrent leaf bases and margins. **Leaves** borne in very close alternating whorls of 6–9, spreading or somewhat reflexed to ascending or appressed upward, slightly recurved or sigmoid, linear to linear-subulate, 7–16 mm long, 1.2–1.5 mm wide, upwards sometimes reduced to 3–7 mm long, not twisted at base, thick, coriaceous, adaxially convex and shallowly rounded or with a slightly to sharply prominent veinal ridge, abaxially convex and shallowly rounded, when dried usually with a prominent vein and irregular longitudinal ridges or wrinkles, or sometimes the vein sunken and hence the adjacent leaf tissue appearing as 2 longitudinal veins, with smooth margins, green. **Stomates** often forming 2 irregular, slightly sunken longitudinal bands along the vein. **Sporangia** 1.5–2 mm wide.

Open shrubland and grassland (jalca), seepage areas, 2000–3100 m, Cajamarca, Amazonas.

Endemic.

Related to *Huperzia loxensis* B. Øllg. (southern Ecuador) and *H. hippuridea*.

Cajamarca: Prov. Cutervo, Llama to Huambos, 2700 m, *López et al. 6591* (AAU, GH, MO). Cutervo, *Raimondi 3126* (B, USM). Trail Socota to Tambillo, 3300 m, *Stork & Horton 10174* (F, K, UC). **Amazonas:** Prov. Chachapoyas, Cerros Calla Calla, W side, 45 km above Balsas, 3100 m, *Hutchison & Wright 5784B* (UC). Cerros Calla Calla, E side, 19 km above Leimebamba, 3100 m, *Hutchison & Wright 5559* (F, GH, M, MO, NY, P, UC). Caño Santa Lucía just E of Chachapoyas, 2000–2400 m, *Wurdack 600* (F, GH, K, UC).

5. *Huperzia weddellii* (Herter) Holub, *Folia Geobot. Phytotax.* 20: 78. 1985.

Lycopodium weddellii Herter, *Bot. Jahrb.* 43: Beibl. 98: 45. 1909. TYPE: Peru, Dept. Puno, Carabaya, 1847, *Weddell 4684* (holotype, P!; isotype frag., BONN, *Herb. Nessel 170!* in part).

Urostachys weddellii (Herter) Nessel, *Bärlappgewächse* 91. 1939.

Plants erect, or erect from a decumbent base, very robust, up to 30 cm tall, or to 50(–70) cm long, sparsely branched. **Shoots** homophyllous, almost equally thick throughout, (14–)16–23 mm in diameter including leaves. **Stems** excluding leaves 3–6 mm thick at the base, tapering to 3–4 mm in diameter. **Leaves** almost uniform throughout, borne in alternating whorls of 6–7, ascending to spreading or reflexed, straight, curved upward or recurved, lanceolate, acute to slightly acuminate or short-acute, 6–11(–12) mm long, 1.5–2.5 mm wide, thick and coriaceous, often glaucous, rarely with red tips, adaxially convex with a slightly prominent vein, usually irregularly concave abaxially (dried), with vein abaxially obscure to distinctly and widely prominent, sometimes in ascending leaves abaxially convex and rounded with obscure vein, with usually smooth to minutely unevenly rugose, narrowly sclerified, translucent margins, or rarely papillate near the base. **Leaf bases** prominently decurrent, with a small, sometimes indistinct swelling (air sac), especially in sporangiate leaves. **Sporangia** 1.5–2.2 mm in diameter.

Terrestrial in exposed habitats in timberline forest and lower shrub páramo, 2600–3900 m, Amazonas, Puno.

Ecuador to Bolivia.

Amazonas: Prov. Bagua, Cordillera Colán, NE of La Peca, ca. 3170 m, *Barbour 3446* (MO).

6. *Huperzia brongniartii* (Spring) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 248. 1874.

Lycopodium brongniartii Spring, Bull. Acad. roy. Sci. Bruxelles 8 (2): 515. 1841. TYPE: Bolivia, Yungas, D'Orbigny 227 (holotype, P!; isotypes, BONN, Herb. Nessel 169! in part, BR!).

Lycopodium taxifolium Sw. var. *brongniartii* (Spring) Baker, Handb. Fern Allies 16. 1887.

Urostachys brongniartii (Spring) Nessel, Arch. Bot. Est. S. Paulo 1: 388. 1927.

Plants erect from an ascending base, up to 50 cm tall, sparsely branched. **Shoots** homophyllous, almost equally thick throughout, 20–30 mm in diameter including leaves. **Stems** excluding leaves 2.5–4 mm thick near the base, sometimes tapering to 1.5–2 mm upward, somewhat ridged by decurrent leaf bases. **Leaves** uniform throughout, borne in alternating, rather distant whorls of 4–5, wide-spreading to somewhat reflexed, usually straight, not twisted at the base, lanceolate, with long-acute apex, papery to subcoriaceous and opaque, 9–12(–15) mm long, 2–3 mm wide, almost flat, with prominent vein adaxially, or folded slightly down along the vein, with slightly revolute, minutely rugose margins. **Sporangia** ca. 2.5 mm wide.

Terrestrial in humid montane forest, ca. 2900–3300 m, Cuzco.

Colombia to Bolivia.

Related to *Huperzia rosenstockiana* (Herter) Holub with which it shares the minutely rugose leaf margins. The specimens cited correspond to the Bolivian representatives of the species.

Cuzco: Prov. Urubamba, Machu Picchu, hillside above Río Mandor, 2920 m, *Peyton 1350* (AAU). Alturas de Río Calzada, Huadquiña, 3300 m, *Bües 756* (us). Prov. Paucartambo, Parque Nacional Manú, Road Acjanaco to Pilcopata, bridge between Pillahuata and La Esperanza, 2750 m, *León 2228* (usm); Prov. Paucartambo, Parque Nacional Manú, below Acjanaco, 2950 m, *León & Cano 2129* (usm).

7. *Huperzia reflexa* (Lam.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium reflexum Lam., Encycl. 3: 653. 1789. TYPE: Martinique, *Comm. Joseph Martin* (holotype, P, *Herb. Lam. 442!*).

Plananthus reflexus (Lam.) Beauv., Prodr. Aeth. 100. 1805.

Urostachys reflexus (Lam.) Herter, Beih. Bot. Centralbl. 39: 249. 1922.

Plants erect or ascending from a decumbent base, soft, usually loosely caespitose, 10–30(–40) cm tall. **Shoots** homophyllous, almost equally thick throughout, 7–15 mm in diameter including leaves. **Stems** excluding leaves 1.5–3(–4) mm thick at base, sometimes tapering to 1–1.5 mm in diameter, ridged by decurrent leaves or almost smooth. **Leaves** borne in alternating irregular whorls of (6–)7–8(–9), ascending to spreading or sharply reflexed, straight to strongly recurved, linear-subulate, widest just above the base, 4–8 mm long, 0.5–1(–1.2) mm wide, softly herbaceous to subcoriaceous, adaxially convex, or concave near the base, abaxially flat, or slightly concave to convex, with an obscure to somewhat prominent vein, with flat to revolute, very sparsely to densely denticulate to short-ciliolate margins. **Leaf bases** often somewhat decurrent. **Sporangia** 1–1.5 mm in diameter.

A frequent pioneer on permanently moist, disturbed ground, mainly in the montane forest zone, also in peat bogs, or rarely as a low epiphyte.

Tropical America.

Closely related to *Huperzia eversa*, *H. acifolia*, and *H. affinis*.

Huperzia reflexa is variable with respect to leaf and stem size, direction and crowding of leaves, and leaf margin characters. Part of the variation undoubtedly reflects variable growth conditions, but very often several distinct forms can be found growing intermixed in the same habitat, indicating that genetic differences exist. The variation patterns are complex and in need of a detailed study.

A variety with smaller dimensions stands somewhat apart and is recognized taxonomically. The remaining material, referred to the type variety, is polymorphic.

Key to Varieties

- a. Shoots including leaves 9–15(–20) mm in diameter, leaves (5–)6–8 mm long, 0.7–1(–1.2) mm wide, with regularly denticulate to short-ciliolate margins, sporangia ca. 1.5 mm wide . . . 7a. var. **reflexa**
- a. Shoots including leaves 7–10 mm in diameter, leaves 4–5(–6) mm long, 0.5–0.7 mm wide, with sparsely and remotely denticulate margins, sporangia ca. 1 mm in diameter 7b. var. **minor**

7a. *Huperzia reflexa* var. *reflexa*

Lycopodium bifidum Willd., Sp. pl. ed. 4, 5: 53. 1810. TYPE: Venezuela, Cuchilla de Guajana Guajana, *Humboldt & Bonpland 474* (holotype, v, *Herb. Willd. 19421!*; isotype, p, *Herb. Humb.!*).

Lycopodium reversum Presl, Reliq. haenke. 1: 82. 1825. TYPE: Ecuador, Guayaquil, *Haenke* (holotype, PRC!).

Lycopodium reflexum Lam. var. *majus* Spring, Mém. Acad. roy. Belg. 15 [Mon. Lyc. 1]: 26. 1842.

Huperzia reflexa (Lam.) Trev. var. *bifida* (Willd.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium reflexum Lam. var. *densifolium* Baker, Handb. Fern-Allies 11. 1887. SYNTYPES: *Hartweg 1480* (k!); *Moritz 2266* (= *2266b?* k!); Brazil, *Glaziov 15797* (k!).

Lycopodium densifolium (Baker) Underw. & Lloyd, Bull. Torrey Bot. Club 33: 106. 1906.

Lycopodium mexiae Copel., Univ. California Publ. Bot. 19: 294, t. 47. 1941. TYPE: Peru, Dept. Huánuco, Churubamba, trail Cotirarda to Mercedes, 1875 m, *Mexia 8193a* (holotype, ucl; isotypes, GH!, k!, MICH).

Urostachys stellae-polaris Herter, Revista Sudamer. Bot. 10: 121. 1953. TYPE: Colombia, Cundinamarca, Guayabetal to Monte Redondo, SE of Quetame, 1300–1500 m, *Pennell 1801* (holotype, us!).

Lycopodium stellae-polaris (Herter) Morton, Amer. Fern J. 54: 72. 1964.

Huperzia bifida (Willd.) Holub, Folia Geobot. Phytotax. 20: 71. 1985.

Huperzia mexiae (Copel.) Rolleri and Deferrari, Notas Mus. La Plata, Bot. 21 (100): 156. 1988.

Landslides, road banks, and other open or disturbed habitats in montane forest, alt. 900–3400 m, Cajamarca, Amazonas, San Martín, Huánuco, Pasco, Junín, Ayacucho, Cuzco.

Throughout humid mountainous regions of tropical America.

Foster & Smith 9095 (USM) is very robust and tall, with thicker stems and slightly wider leaves than usual for this variety.

Cajamarca: Prov. Cutervo, El Pajonal, San Andrés, 2200 m, *Llatas & Suarez 2828* in part (F). Prov. Cutervo, La Pucarilla, between Súcota and San Andrés, 2500 m, *Sánchez Vega et al. 5923* (AAU, F). **Amazonas:** Prov. Chachapoyas, roads to Molinopampa, 2700 m, *Sánchez Vega et al. 2218* (AAU). **San Martín:** Prov. San Martín, Dist. Tarapoto, road Tarapoto to Yurimaguas, km 9–13, ca. 700 m, *Rimachi 4102* (F, GH, NY). **Huánuco:** Prov. Huánuco, Chinchao to Puente Durán, 1900 m, *Ochoa 14597* (F, US). Carpish Pass, 2700 m, *Hodge 6294* (GH, US). **Pasco:** Manto at Yaupi, *Woytkowski 6534* (MO, US). Prov. Oxapampa, Ulcumanu SW of Oxapampa, road to María Teresa and Llaupi, 2150–2450 m, *Foster et al. 7688* (AAU). **Junín:** Tarma, Chanchamayo, above La Merced, ca. 2000 m, *Weberbauer 2006* (G, MOL). **Aya-**

cuzco: Prov. La Mar, eastern Massif of the Cord. Central opposing the Cord. Vilcabamba between Tambo, San Miguel, Ayna, and Hda. Luisiana, 1570 m, *Dudley 11826* (GH). Ayna between Huanta and Río Apurimac, 750–1000 m, *Killip & Smith 23198* (NY). **Cuzco:** Prov. Convención, Hda. Guayanay, 1800 m, *Vargas 13248* (GH). Quispicanchi, Mandor, Marcapata, 1000 m, *Vargas 5220* (US).

7b. *Huperzia reflexa* var. *minor* (Spring) B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 26. 1988.

Lycopodium reflexum Lam. var. *minus* Spring, Mém. Acad. roy. Belg. 15 [Mon. Lyc. 1]: 26. 1842. SYNTYPES: Brasil, Pr. Rio de Janeiro, *Gaudichaud* (P!); *Langsdorff* (M, *Herb. Mart.!*); Brazil, Serra dos Orgaos, fr. Majo, *Guillemín* (P!); In sylvis prov. Paraënsis, *Martius* (M!); Brazil, in prov. Minarum, *Claussen* (P!).

Lycopodium brutum Herter, Bot. Jahrb. 43: Beibl. 98: 47. 1909. TYPE: Trinidad, *Hooker* ded. 1845 (holotype, P!).

Humid montane forest, road banks, alt. 1000–2400 m, Huánuco, Cuzco, Puno. Brazil; Trinidad; Ecuador to Bolivia; probably more widespread.

This variety seems identical to *Huperzia parvifolium* (Nessel) Rolleri and Deferrari from SE Brazil. It often grows intermixed with individuals of var. *reflexa*.

Huánuco: Prov. Huánuco, Road Huánuco to Tingo María, N of Carpish Pass, 2350–2450 m, *Plowman & Rury 11146* (F, GH). **Cuzco:** Prov. Urubamba, Machu Picchu, *Soukup 167* (F). Near Machu Picchu, 2000 m, *Tryon & Tryon 5409* in part (GH, US, USM). **Puno:** Prov. Sandia, below Cuyocuyo, 2900 m, *Ferreya 16624* (USM).

8. *Huperzia acifolia* (Rolleri) Rolleri and Deferrari, Notas Mus. La Plata, Bot. 21 (100): 155. 1988.

Lycopodium acifolium Rolleri, Revista Mus. La Plata (n.s.) 14: 2, t. 1–2. 1985. TYPE: Peru, Dept. Ayacucho, Cearrapa, between Huanta and Río Apurimac, 1500 m, *Killip & Smith 22368* (holotype, us!).

Plants erect, or erect from a decumbent base, 15–30 cm tall, or up to 60 cm long. Shoots homophyllous, almost equally thick throughout, 10–20 mm in diameter including leaves. Stems excluding leaves 2–5(–6) mm thick at the base, sometimes tapering to 1–3 mm thick. Leaves uniform throughout, borne in alternating, usually densely

crowded whorls of 8–11, usually sharply bent upward from a perpendicular junction to the stem and then gently to strongly clawlike recurved, linear-subulate, widest just above the pale and soft-herbaceous base, 6–10 mm long, 0.7–1(–1.3) mm wide at the base, narrowed shortly above the base, subcoriaceous at apex, adaxially convex distally, abaxially flat to convex with obscure to somewhat prominent vein (sometimes sunken when dried), with rather densely denticulate-ciliate margins at base, usually sparsely denticulate or smooth at apex. **Sporangia** 1–1.5 mm wide.

Moist banks in montane forest at mid-altitudes, alt. 1350–2040 m, San Martín, Huánuco, Pasco, Junín, Ayacucho, Cuzco.

Venezuela to Bolivia.

Closely related to *Huperzia reflexa* and *H. unguiculata* B. Øllg. (Colombia, Ecuador). Some material earlier tentatively referred to *H. unguiculata* from Ecuador and Peru belongs here, and thus *H. unguiculata* is yet unknown from Peru.

San Martín: Prov. Rioja, Pedro Ruíz–Moyobamba road, km 390–394, Venceremos, 1910–2040 m, *D. Smith 4522* (AAU, USM). **Prov. Mariscal Cáceres,** 60 km NE of Tingo María, La Divisoria pass through Cerro Azul, 1500 m, *Tryon & Tryon 5269* (GH, US). **Huánuco:** Prov. Leoncio Prado, Dist. Daniel Alomía Robles, Road Tingo María to Pucallpa, La Divisoria, 1600 m, *J. Schunke V. 3082* (F, G, GH, NY, US); *Ferreya 1690* (USM). **Pasco:** Prov. Oxapampa, Río Boquería, ca. 26 km from Oxapampa via Río Yamaquizu, 1870 m, *D. Smith et al. 1772* (AAU, USM). **Oxapampa** [as Junín], 1600 m, *Soukup 2675* (F, GH, US). **Junín:** Prov. Tarma, road to La Mina Pichita, 9 km from the Tarma–La Merced road, ca. 13 km from San Ramón, 1600 m, *Skog et al. 5055* (US). Chanchamayo Valley, above La Merced at Cumbre Yacunay, 2000 m, *Hutchison 1194A* (F, M, NY, UC, US, USM). **Cuzco:** Prov. Paucartambo, Kosñipata, San Pedro, 1350 m, *Vargas 10219* (MO, UC).

9. *Huperzia eversa* (Poiret) B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 28. 1988.

Lycopodium reflexum Willd., Sp. pl. ed. 4, 5: 52. 1810, not Lam. 1789. TYPE: Ecuador: Tungurahua, (Humboldt) Née D. D. (holotype, v, *Herb. Willd. 19419!*).

Lycopodium eversum Poiret, in Lam., Encycl. 3: 556. 1814 [1813].

Lycopodium reflexum Lam. var. *polycarpum* Sodiro, Recens. crypt. vasc. Quit. 90. 1883. TYPE: Ecuador, valle de Nanegal, *Sodiro* (not located).

Lycopodium polycarpum (Sodiro) Underw. & Lloyd, Bull. Torrey Bot. Club 33: 105. 1906, not *L. polycarpus* Kunze 1835.

Lycopodium ecuadoricum Herter, Bot. Jahrb. 43: Beibl.

98: 48. 1909. LECTOTYPE (designated by B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 28. 1988): Ecuador, Andium nemoribus humidis, *Jameson 74* (p!).

Huperzia ecuadorica (Herter) Holub, Folia Geobot. Phytotax. 20: 72. 1985.

Plants erect or erect from a decumbent base, soft, often large, much-branched and caespitose, up to 30(–50) cm tall. **Shoots** homophyllous, equally thick throughout, (2.5–)3–6(–10) mm in diameter including leaves. **Stems** excluding leaves 1.5–2.5 mm thick at the base, sometimes tapering to 1–2 mm, prominently ridged by decurrent leaf bases (dried). **Leaves** uniform throughout, borne in irregular, alternating, subdistant to densely crowded whorls of (4–)5(–6), wide-spreading to sharply reflexed, usually strongly recurved, linear-lanceolate, widest in the basal half, (2.5–)3–5 mm long, 0.5–1 mm wide, softly herbaceous to subcoriaceous, adaxially convex with obscure vein, abaxially irregularly concave (dried), with obscure to somewhat prominent vein, with slightly revolute, denticulate-ciliate margins. **Leaf base** with prominently decurrent vein and margins. **Sporangia** 1–1.5 mm in diameter.

Terrestrial, as a pioneer on landslides, road banks, and other open, moist habitats in upper montaine forest, alt. 2400–3400 m, Piura, Amazonas, San Martín, Huánuco, Pasco, Ayacucho, Cuzco.

Costa Rica; Andes from Venezuela to Bolivia.

Huperzia eversa resembles *H. reflexa*, but has shorter and relatively wider leaves, which are usually strongly recurved, so that that shoots appear much more slender. It also differs by usually forming very densely branched individuals.

Piura: Prov. Huancabamba, Loma Redonda (Sapalache to Chinguela), 2400 m, *Sagástegui et al. 10174* (AAU, MO). **Amazonas:** Prov. Chachapoyas, middle eastern Calla-Calla slopes, 3000–3200 m, *Wurdack 1770* (F, GH, NY, UC, US, USM). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National park, NW corner, Chochos, 3400 m, *Young 3693a* (AAU). **Huánuco:** Playapampa, 2700 m, *Macbride 4486* (F). Cushi, trail to Tambo de Vaca, *Bryan 622* (F, US). **Pasco:** Prov. Oxapampa, Dist. Oxapampa, Río San Alberto, Abra Esperanza, 2400–2700 m, *Foster et al. 10300* (AAU). **Ayacucho:** Prov. La Mar, eastern Massif of the Cord. Central opposing the Cord. Vilcabamba between Tambo, San Miguel, Ayna, and Hda. Luisiana, 2920 m, *Dudley 11972* (F, GH). **Cuzco:** Prov. Paucartambo, Parque Nacional Manú, Camino Eriksson, *León & Huapalla 2387* (AAU). Michéhuañunca,

Huadquiña, 2700 m, Bües 745 (US). Department unknown: *Matthews 1082* (E).

10. *Huperzia affinis* Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium affine Grev. & Hooker, Bot. Misc. 2: 364. 1831, not Bory 1804. LECTOTYPE (designated by Nessel, *Bärlappgewächse* 97. 1939): Ecuador, Pichincha, 1824, Herb. Greville, *Jameson* (κ!; possible isotypes, E!, NY!, US!).

Lycopodium blepharodes Maxon, Contr. U.S. Natl. Herb. 17: 423. 1914.

Huperzia blepharodes (Maxon) Holub, Folia Geobot. Phytotax. 20: 71. 1985.

Plants erect from a decumbent base, at least up to 25 cm tall. **Shoots** homophyllous, equally thick throughout, 5–10 mm in diameter including leaves. **Stems** excluding leaves 1.5–3 mm thick, upward sometimes slightly tapering. **Leaves** borne in rather close alternating whorls of 5, almost covering the stem, patent to loosely appressed, narrowly triangular-lanceolate to almost subulate, with slightly widened base, (3.5–)4–6 mm long, 1–1.5 mm wide, abaxially convex and evenly rounded or with prominent veinal ridge, at least at base, somewhat clasping the sporangia, with long, flaccid marginal cilia and small teeth. **Sporangia** 1.5–2 mm in diameter.

Terrestrial on banks in upper montane forest and grassland, alt. 2700–3100 m, Amazonas, Huánuco.

Colombia to Peru.

The description above applies to the Peruvian specimens. These are generally smaller, are more compact, and have more appressed and abaxially more convex leaves than specimens from Colombia and Ecuador. *Huperzia affinis* is variable with respect to crowding and direction of the leaves. It is distinguished from *H. reflexa* var. *reflexa*, *H. eversa*, and *H. pearcei* (Baker) Holub (Bolivia) by its wider and more convex leaf bases and the slender cilia on the leaf margins.

Amazonas: Prov. Chachapoyas, Cerros Calla Calla, W side, 45 km above Balsas, 3100 m, *Hutchison & Wright 5830* (F, GH, NY, UC, USM). **Huánuco:** Mito, 2700 m, *Bryan 389a* (F). Prov. Huánuco, Punta de Pano, *Asplund 13712* (s). Pano, 2700 m, *Macbride 3602* (F).

11. *Huperzia kuesteri* (Nessel) B. Øllg., Opera Bot. 92: 169. 1987.

Urostachys kuesteri Nessel, Repert. Spec. Nov. Regni Veg. 35: 182, t. 172. 1934. LECTOTYPE (des-

ignated by Øllgaard in Harling and Andersson, Fl. Ecuador 33: 37. 1988): Ecuador, Loja to Zamora, 3500 m, 1875, "J. M. J. Mission," Quito 415 (BONN, Herb. Nessel 231!).

Plants ascending to erect, massively robust and large caespitose plants, with almost completely homoblastic divisions, up to 40 cm tall. **Shoots** homophyllous, almost equally thick throughout, or slightly tapering upward and the leaves gradually shorter and wider, 12–25 mm in diameter including leaves near the base, sometimes tapering to (7–)10–15 mm. **Stems** excluding leaves 3–8 mm thick at the base, tapering to 3–5 mm upward, almost completely concealed by leaves. **Leaves** uniform throughout or upward slightly reduced, densely crowded, borne in usually regular alternating whorls of 4–5, ascending to closely imbricate, rarely patent to recurved in basal divisions, straight to slightly upwardly curved, narrowly triangular-lanceolate near the base to widely triangular-ovate in terminal divisions, widest just above the leaf base, 8–12 mm long and 1.5–4 mm wide in basal divisions, upward (4–)5–10 mm long, 2.5–4 mm wide, evenly tapering, with acute, upward-curved apex, thick, adaxially flat or slightly concave with flush or slightly prominent vein, abaxially rounded with slightly to strongly prominent, narrow vein, with a short, flattened basal swelling (air sac), shining or pruinose, green or rarely with red-tinged margins, with smooth to uneven or rugulate, opaquely to transparently sclerified margins. **Leaf base** margins usually slightly revolute, sometimes subauriculate in apical divisions. **Sporangia** 2–2.5 mm wide.

Low, wet mossy and grassy páramos, alt. 2750–3400 m, Piura, Lambayeque. Southern Ecuador and northernmost Peru.

This species is related to *Huperzia macbridei* but can be distinguished from this by the homoblastic, evenly spreading branching habit, wider leaves, and greater size.

Plura: Purchased in the market of Huancabamba, *Friedberg 7631b* (GH). **Lambayeque:** Prov. Ferrañafe, Dist. Incahuasi, Laguna Tembladera to Cerro Negro, 3300 m, *Sagástegui et al. 12818* (AAU), *12848* (F in part).

12. *Huperzia weberbaueri* (Nessel) Holub, Folia Geobot. Phytotax. 20: 78. 1985.

Urostachys weberbaueri Nessel, Revista Sudamer. Bot. 6: 162, t. 10, f. 41. 1940. TYPE: Peru, Dept. Amazonas, Ostlich Chachapoyas, Tambo Ven-

tillas, 2400–2600 m, *Rosen 672* (holotype, BONN, *Herb. Nessel 183!*).

Lycopodium papillatum Rolleri, Amer. Fern J. 65: 3. 1975. TYPE: Peru, Dept. Amazonas, Prov. Chachapoyas, Cerro Malcabal (Cerro Tumbé), 3–6 km SW of Molinopampa, 2900 m, *Wurdack 1456* (holotype, us!; isotypes, GH!, K!, UCL, USM!).

Huperzia papillata (Rolleri) Holub, Folia Geobot. Phytotax. 20: 75. 1985.

Plants erect from an ascending base, large, caespitose, homoblastic, up to 30(–40) cm tall. **Shoots** homophyllous, 10–15(–20) mm in diameter including leaves, sometimes tapering to 7 mm in diameter, strikingly whitish papillate in life. **Stems** excluding leaves 2–4 mm thick. **Leaves** uniform throughout, or slightly smaller upward, borne in more or less regular, alternating whorls of 5, patent to ascending, upward curved, lanceolate, 7–10(–15) mm long, 2–2.5 mm wide, not or slightly decurrent, without a prominent basal swelling (air sac), abaxially convex, with an obscure veinal ridge, adaxially flat to concave (dried), densely long-papillate on margins and abaxially, smooth adaxially. **Sporangia** ca. 1.5 mm wide.

Wet grassy and boggy páramos with some shelter, and lower puna 3000–3600 m, Lambayeque, Amazonas, San Martín, Cuzco.

Southernmost Ecuador and Peru.

The densely papillate, bright whitish leaves in the living plants are unique in the genus. The whitish color is often lost after drying, especially heat drying.

Lambayeque: Prov. Ferrañafe, Dist. Incahuasi, Laguna Tembladera, 3150 m, *Sagástegui et al. 12790* (AAU). **Amazonas:** Prov. Chachapoyas, Leimebamba to Calla Calla, 3100 m, *Sánchez V. 530* (AAU); *Boeke 1809* (AAU). NE of Tambo de Ventilla, Cerro de Fraijaco (Huauil to Huni), 3450 m, *Pennell 15883* (GH). Cerros Calla Calla, 3100 m, *Hutchison & Wright 5564* (F, GH, MO, NY, UC, US). **San Martín:** Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, 3400 m, *Young & León 4768* (AAU). Prov. Mariscal Cáceres, Chochos Valley, 3300 m, *Young & León 4877* (AAU). Huallaga, valley of Apisoncho, 30 km above Jucusbamba, 3600 m, *Hamilton & Holligan 1216, 1217* (US). **Cuzco:** Prov. Paucartambo, Cord. de Tres Cruces, 3600 m, *Vargas 12195* (GH). Prov. Paucartambo, Pavayoc, 2100 m, *Woytkowski 555* (MOL, USM).

13. *Huperzia colanensis* B. Øllg., *sp. nov.*

Planta erecta vel ascendens; surculi homoblastici usque ad 30 cm alti, homophylli 6–10(–12) mm diametro foliis inclusis, omnino crassitie aequali vel parum angustati. Caulis 2–4 mm crassus foliis exclusis. Folia omnino uniformes vel sursum parum minores, 8–10-faria,

patentes usque ad ascendentes vel perpendiculares usque ad parum reflexa, recta vel incurva, lanceolata, aequate angustata vel acuminata, (3–)4–6(–7) mm longa, 1.5–2 mm lata, parum decurrentes, abaxialiter convexa, ad basin vix vel parum ventricosa, plerumque angulo mediali subacuto instructa, adaxialiter plana usque ad concava (siccata), subcoriacea, hypostomatica, plerumque polita, marginibus laevibus, scleroideis et translucidis. Sporangia ca. 1.5–2 mm lata.

Plants erect from an ascending base, loosely caespitose, homoblastic, up to 30 cm tall. **Shoots** homophyllous, 6–10(–12) mm in diameter including leaves, equally thick throughout or slightly tapering. **Stems**, excluding leaves, 2–4 mm thick. **Leaves** uniform throughout, or slightly smaller upward, borne in more or less regular, alternating whorls of 4–5, patent to ascending or perpendicular to slightly reflexed in basal divisions, straight to upward curved, lanceolate, widest ca. $\frac{1}{4}$ of the leaf length above the base, evenly tapering in the distal $\frac{3}{4}$ or slightly acuminate, straight to slightly upward curved, (3–)4–6(–7) mm long, 1.5–2 mm wide, somewhat decurrent, without or with a slightly prominent basal swelling (air sac), abaxially convex, rounded or usually with a rather sharp medial ridge, adaxially flat to concave (dried), somewhat coriaceous, usually glossy on both sides, the margins smooth, sclerified and somewhat translucent. **Sporangia** ca. 1.5–2 mm wide.

TYPE—Peru, Dept. Amazonas, Prov. Bagua, Cord. Colán NE of La Peca, 10,800 ft, 8 Sep 1978, *Barbour 3384* (holotype, MO!; isotypes, AAU!, USM!).

Andean grassland, open patches in shrub páramo, alt. 3140–3600 m, Amazonas, San Martín. Endemic.

The specimen cited from San Martín deviates from the other material by a softer texture and less glossy leaves with less sclerified margins and is included in the species with some doubt.

Huperzia colanensis appears to be intermediate in position between the *Huperzia brevifolia* and *H. saururus* groups of Øllgaard (1987, 1989). It does not appear to be intimately related to other Peruvian species.

Amazonas: Prov. Bagua, Cord. Colán NE of La Peca, 3170 m, *Barbour 3446* (MO). Prov. Bagua, Cord. Colán NE of La Peca, ridge W of peaks, 3140 m, *Barbour 3197* (MO), 3198 (AAU). **San Martín:** Dist. Huallaga, Valley of Río Apisoncho, 3600 m, *Hamilton & Holligan 1218* (US).

14. *Huperzia polylepiderum* B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 42, f. 6B. 1988.

TYPE: Ecuador, Prov. Azuay, *Laegaard 55117* (holotype, AAU!; isotype, QCA!).

Plants ascending to erect, large, robust, caespitose, nearly homoblastic, up to 35 cm tall, or more than 50 cm long. Shoots homophyllous, equally thick throughout, or slightly tapering upward and the leaves gradually shorter, 10–25 mm in diameter including leaves. Stems excluding leaves 5–7 mm thick at the base, sometimes tapering to 2 mm thick, usually not completely concealed by leaves. Leaves uniform throughout, or gradually shorter upward, well spaced to densely crowded, borne in more or less regular, alternating whorls of 5–6, patent-ascending to arcuate-appressed, strongly curved upward and inward, lanceolate to widely lanceolate, acute or short-acute, 6–12 mm long, (2–)2.5–3(–3.5) mm wide, somewhat fleshy, abaxially convex or rarely flattened, with an obscure to prominent adaxial and abaxial, long decurrent median ridge, with an indistinct air sac, adaxially concave or flat, with smooth, slightly involute margins, green throughout or with red-tinged tips. Sporangia 2.5–3.5 mm wide.

In open *Polylepis* forest among mossy rocks, 3900–4300 m, Ancash.

Ecuador and Peru.

The Peruvian collection was made in shaded *Polylepis* woods, and the specimen differs slightly from Ecuadorean plants by the more patent-ascending leaves, which tend to be abaxially flat to slightly concave in the basal divisions, while the distal, more exposed divisions have abaxially convex leaves. It thus seems close to *Huperzia weddellii*.

Ancash: Prov. Huari, Huascarán National Park, Quebrada de Yuracocha, a lateral valley of Quebrada Rurichinchay, 3900–4300 m, *D. Smith et al. 12716* (AAU, F).

15. *Huperzia capellae* (Herter) Holub, *Folia Geobot. Phytotax.* 20: 71. 1985.

Urostachys capellae Herter, *Revista Sudamer. Bot.* 10: 114–115. 1953. LECTOTYPE (designated by Rolleri, *Revista Mus. La Plata, n.s., Bot.* 13 (71): 78. 1981): Ecuador, prov. Napo [as Imbabura], E of Volcán de Cayambe, along trail between Río Boquerón and Río Arturo, 11,000 ft, *Drew E 314* (us!; isotype, MSC!).

Lycopodium capellae (Herter) Morton, *Amer. Fern J.* 54: 72. 1964.

Plants ascending to erect, sparsely to densely branched, without prostrate-ascending, rejuvenat-

ing shoots, up to ca. 35 cm tall. Shoots homoblastic, homophyllous to gradually slightly heterophyllous, 12–20 mm in diameter at the base including leaves, usually tapering to 5–10 mm. Stems excluding leaves 2–3 mm thick at the base, often brown to reddish brown, terete to prominently ridged by decurrent leaf bases. Leaves of basal divisions (and shaded shoots) borne in irregular, rather distant, alternating whorls of 5–6, usually patent to ascending, not covering the stem, linear-lanceolate, 7–10 mm long, 1.5–2 mm wide, adaxially flat, shining, abaxially flat to slightly convex, dull to shining green, usually with long-decurrent leaf bases. Leaves of distal divisions gradually shorter, closer, and more appressed, borne in alternating whorls of 4–5(–6), ascending to arcuate-appressed, straight to strongly upward or unilaterally curved or twisted, lanceolate to broadly lanceolate, often slightly cuspidate above the middle, (5–)6–8 mm long, 1.5–2 mm wide, adaxially concave (dried) or flat to shallowly rounded in life, abaxially convex, rounded and irregularly wrinkled (dried), with slightly prominent, short to long, narrowly decurrent basal swelling (air sac), with smooth to densely irregularly rugulate, slightly to distinctly, translucently sclerified margins, shining to dull green. Sporangia ca. 2 mm wide.

Grass páramos, usually growing in partial shade among grasses, 3600 m, Cajamarca, Cuzco.

Andes from Venezuela to Peru.

Known from two collections in Peru, matching the Ecuadorean plants perfectly.

Cajamarca: Prov. Chota, Laguna Yahuarcocha, above Incahuasi, 3600 m, *Sagástegui et al. 12908* (F). Cuzco: Prov. Paucartambo, Parque Nacional Manú, vicinity of El Mirador, 3600 m, *León 2270* (USM).

16. *Huperzia macbridei* (Herter) B. Øllg., *Opera Bot.* 92: 169. 1987.

Urostachys macbridei Herter, *Revista Sudamer. Bot.* 10: 115. 1953. TYPE: Peru, Dept. Huánuco, 3–6 mi NW of Mito, 11,000 ft, *Macbride & Featherstone 1922* (holotype, us!; isotypes, B!, F!, MA!, S!).

Lycopodium macbridei (Herter) Morton, *Amer. Fern J.* 54: 72. 1964.

Plants erect from a decumbent base, loosely to densely caespitose, with basal, prostrate-ascending, rejuvenating shoots at the periphery, up to 32 cm tall. Shoots homophyllous or with leaves gradually slightly reduced upward, equally thick throughout or slightly tapering upward, 15–20 mm

in diameter including leaves near the base, often tapering to 6–9 mm in diameter. **Stems** excluding leaves 2–4 mm thick at the base, upward tapering to ca. 2 mm, almost completely concealed by leaves. **Leaves** uniform throughout, or upward slightly reduced, borne in irregular, alternating whorls of 4–5(–6), densely crowded, spreading to ascending in basal divisions, upward often gradually becoming closely imbricate, straight or slightly upward curved, narrowly lanceolate to lanceolate, widest near the base, evenly tapering, 10–15 mm long and 1.5–2.5 mm wide in basal divisions, upward 6–11 mm long, 1.5–2 mm wide, without or with a slightly pronounced basal swelling (air sac), adaxially concave with flush or slightly prominent vein, abaxially rounded, with slightly prominent and often slightly darker and long decurrent vein, with smooth to slightly uneven, somewhat involute, indistinctly sclerified margins, green to yellowish green. **Sporangia** ca. 2.5 mm wide.

Terrestrial in low shrub páramos, at the edge of woods, 2500–3600 m, Amazonas, La Libertad, Huánuco, Ayacucho, Cuzco.

Southern Ecuador and Peru.

Individuals of shaded or sheltered habitats (e.g., *Macbride 3487*) tend to retain juvenile leaf morphology, being completely homophyllous with relatively wide and long, patent-ascending rather than appressed and gradually reduced leaves and often with a more loosely caespitose growth habit. *Mathews 963* is a mixed collection, sheets of the same number at G pertaining to *H. hippuridea*.

Amazonas: Chachapoyas (presumably), *Mathews 963* (BM). **La Libertad:** Prov. Bolívar, Nevado del Cajamarquilla, puna, *Ferreya 1350* (USM). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, Puerta del Monte, 3350 m, *León & Young 1500* (AAU, USM). Prov. Mariscal Cáceres, Río Abiseo National Park, Valle de Chochos, 3450 m, *León 1870* (AAU, USM). **Huánuco:** Mito, 2700 m, *Bryan 381* (F). Cani, 7 mi NE of Mito, 2500 m, *Macbride 3487* (F, US). **Ayacucho:** Prov. La Mar, eastern Massif of the Cord. Central opposing the Cord. Vilcabamba between Tambo, San Miguel, Ayna and Hda. Luisiana, 3200–3500 m, *Dudley 11989* (F, GH). **Cuzco:** Paucartambo, Tres Cruces, 3600 m, *Bües 2214* (MO). Prov. Paucartambo, Parque Nacional Manú, vicinity of El Mirador, 3600 m, *León 2269* (USM).

17. *Huperzia darwiniana* (Nessel) B. Øllg., *comb. nov.*

Urostachys darwinianus Nessel [Bärlappgewächse 80, t. 3, f. 20. 1939, *nom. nud.*], Revista Sudamer. Bot. 6: 161. 1940. TYPE: "Columbien: Andinum montibus nemoribus, Ruiz" (holotype, BONN, Herb. Nessel 133!).

Plants erect, or erect from a prostrate to ascending base, sometimes loosely caespitose, with basal, prostrate-ascending, rejuvenating shoots at the periphery, and erect, fingerlike shoots in the center, at least up to 35 cm tall. **Erect shoots** homophyllous or almost so, equally thick throughout, 10–15 mm in diameter including leaves, or sometimes tapering to ca. 8 mm upward. **Stems** excluding leaves 3–5 mm thick at the base, sometimes tapering to 2 mm, usually completely concealed by leaves. **Leaves** uniform throughout, or slightly reduced upward, borne in alternating whorls of 4–7, in distal fully sporangiate divisions usually 4–5, crowded, loosely to closely imbricate, slightly upward curved and usually with a strongly upward curved apex, lanceolate to widely lanceolate, slightly long-acuminate from a wide and somewhat rounded base, 8–12 mm long, (1.8–)2–2.5(–3) mm wide, upward sometimes reduced to 7 mm long, with an inconspicuous, narrow, long-decurrent basal swelling (air sac), adaxially concave to slightly convex at the base, abaxially convex and rounded, with a prominent, often darker colored (dried) ridge along the vein, smooth and often shining, with smooth, slightly sclerified margins, green, not or scarcely pruinose. **Sporangia** 2–3 mm wide.

Boggy páramo and jalca, humid rocks, 2700–3600 m, Huánuco, Pasco, Cuzco.

Peru and Bolivia.

The information on the type label is in Nessel's handwriting, and the geographic information is as dubious as on numerous other Nessel labels. Specimens in Geneva, "Peruvia, Herb. Pavon" (G!), are likely to be isotypes. See **Comments** under *Huperzia polyclada*.

Huánuco: Cushi, trail to Tambo de Vaca, *Bryan 677* (F, US). Playapampa, ca. 2700 m, *Macbride 4475* (F, US). **Pasco:** Prov. Oxapampa, trail to summit of Cord. Yanachaga via Río San Daniel, 3150–3300 m, *D. Smith 7710* (AAU, USM). **Cuzco:** Cerro Puncuyoc, 4500 m, *Bües 563* (US). Prov. Urubamba, near Wenner Gren ruins, 3400–3600 m, *Metcalfe 30745* in part (UC). Trail Puyupata to Sayaccmarca, 3600 m, *Vargas 2910* (US). **Department unknown:** Perou (1839–1840), *Gay* (F). Peru, *Pearce* (US 1431555).

18. *Huperzia crassa* (Willd.) Rothm., Feddes Rept. Spec. Nov. Regni Veg. 54: 60. 1944.

Lycopodium crassum Willd., Sp. pl. ed. 4, 5: 50. 1810. TYPE: Ecuador, Antisana, *Humboldt & Bonpland 2263* (holotype, B, Herb. Willd. 19417!; isotypes, BM!, P!).

Urostachys crassus (Willd.) Nessel, Bärappgewächse 75. 1939.

Urostachys pilgerianus Nessel, Revista Sudamer. Bot. 6: 161, t. 9, f. 32. 1940. TYPE: "Peru, Cordillere, Rautenstock et Mann, in 1901" (holotype, BONN, Herb. Nessel 124!).

Huperzia pilgeriana (Nessel) Holub, Folia Geobot. Phytotax. 20: 75. 1985.

Plants erect from a prostrate to ascending base, slightly to strongly heteroblastic, loosely to densely caespitose with prostrate-ascending or shallowly subterranean basal shoots, these bearing often numerous erect, fingerlike shoots in the center, at least up to 40 cm tall. **Erect shoots** homophyllous or almost so, equally thick throughout, or slightly tapering upward, 5–10 mm in diameter including leaves. **Stems** excluding leaves 2–3 mm thick, usually completely concealed by leaves. **Leaves** uniform throughout, or slightly reduced upward, borne in irregular, alternating whorls (or low spirals) of 5–7, densely crowded, usually closely imbricate, straight (or slightly upward curved in shaded divisions), linear-lanceolate to lanceolate, 5–9 mm long, (1–)1.2–2 mm wide, upward sometimes reduced to 4.5 mm long, with a prominent, short to long decurrent basal swelling (air sac) causing a perpendicular appearance of the very leaf base in sporangiate leaves, adaxially concave to slightly convex, with a raised veinal ridge near the base, abaxially convex and rounded or with a prominent veinal ridge, slightly to strongly rugose by protruding, blisterlike epidermal cells, with smooth to rugose margins, green to brick red or dark red, usually strongly pruinose. **Sporangia** 1–2 mm wide.

Terrestrial in high páramo and superpáramo, puna, 3600–4850 m, La Libertad, Ancash, Junín, Cuzco, Puno.

As here delimited, *Huperzia crassa* is a widely distributed polymorphic species, occurring from Mexico to Panama, Hispaniola, and in the Andes from Venezuela to Bolivia.

The Peruvian material represents a disjunct population, widely separated from the Ecuadorian populations, and it may be distinct at least at the variety level. Therefore, the synonyms included for the type variety in Øllgaard (1988) are not cited here.

The holotype of *Urostachys pilgerianus* most likely is a mislabeled duplicate of *Weberbauer 6626* (F, GH, MOL, US) from Dept. Junín, Nevado Runatullu, SE of Jauja, on rocks, 4400–4500 m, as this collection matches it exactly. Mislabeled (or re-labeled?) specimens abound in Nessel's herbari-

um. The type and the Weberbauer collection both have creeping basal shoots and are rather densely tufted. The leaves are twisted unilaterally, but otherwise this corresponds to most of the Peruvian material.

La Libertad: Prov. Santiago de Chuco, Jalca de Quesnada (Quirvilca to Huamachuco), 4000 m, *Sagástegui & Fabris 7574* (MO, NY). Prov. Santiago de Chuco, Dist. Calchicadan, Escalerilla–Conzuzo road near Tamboras, 3960 m, *Saunders 882* (F, GH). **Ancash:** Prov. Carhuaz, Huascarán National Park, Quebrada Ishinca, 4380–4500 m, *D. Smith 9480* (AUU). Prov. Carhuaz, Huascarán National Park, Quebrada Honda, 4300–4750 m, *D. Smith et al. 11643* (F). Cord. Blanca, above Vicos, toward Lejiacocho, 3600 m, *Hutchison & Wright 4323* (F, GH, NY, UC). Prov. Huaylas, Huascarán National Park, Quebrada Alpamayo, 4750 m, *D. Smith et al. 9715* (AUU, F). **Junín:** Mount La Juntay, near Huancayo, 4700 m, *Killip & Smith 22114* (F, NY, US). **Cuzco:** Cerro Salamanca, Valle Lucumayo, 2200 m, *Bües 569* (US). Prov. Urubamba, Abra de Málaga, 4300 m, *Chávez 2822* (MO); 4150–4230 m, *Molau & Ohman 1639* (GB). **Puno:** "Cord. jugis pr. Tabina," *Lechler 2043* (E). Cord. near Agapata and Sachapata, *Lechler 2028* (BR, G, S).

19. *Huperzia nesselii* (Nessel) Rolleri & Deferrari, Notas Mus. La Plata, Bot. 21 (100): 156. 1988.

Urostachys nesselii Nessel, Revista Sudamer. Bot. 6: 161. 1940 [Bärappgewächse 78, f. 12. 1939, *nom. inval.*]. TYPE: "Ost Peru, Cuzco, 1868, *Reinhardt*" (holotype, BONN, Herb. Nessel 132, in part!).

Plants erect from a prostrate to ascending base, slightly to strongly heteroblastic, loosely to densely caespitose with prostrate-ascending basal shoots, these bearing numerous erect, fingerlike shoots in the center, up to 20 cm tall. **Erect shoots** homophyllous or almost so, equally thick throughout, 10–15 mm in diameter including leaves. **Stems** excluding leaves 2–6 mm thick, usually completely concealed by leaves. **Leaves** uniform throughout, borne in irregular, alternating whorls (or low spirals) of 5–6, densely crowded, closely imbricate, straight to irregularly curved upward or twisted at the apex, linear-lanceolate to lanceolate or narrowly elliptic, 9–12 mm long, 2–2.5 mm wide, without a prominent basal swelling, adaxially concave to slightly convex, with a raised veinal ridge near the base, abaxially flat especially at the base to rounded especially at the apex, with a broadly prominent medial ridge especially at the base, slightly rugose because of protruding, blisterlike epidermal cells, with smooth to slightly uneven margins, pruinose. **Sporangia** 2–3 mm wide.

High Andine grassland near the timber line, 3000–3500 m, Junín.

Endemic.

The material referred to this species including the type seems to represent a single gathering, referable to Weberbauer. The information on the type label is in Nessel's handwriting, and the geographic information is dubious as are numerous other Nessel labels.

The species seems most closely related to *Huperzia saururus* with respect to size and growth habit; however, it differs by the open growth of basal portions of the plant, and the ridged leaf bases, and smooth margins. From Peruvian *H. crassa* it differs by the large, rather flat leaves without a prominent basal air sac.

Junin: Tarma, mountains W of Huacapistana, 3400–3500 m, *Weberbauer 2222* (G, MOL). "Lagasca ex herb. Swartz, ex Tarma Provincia in Peruvia, n. 2222" (BONN, *Herb. Nessel 132* in part).

20. *Huperzia andina* (Rosenst.) Holub, *Folia Geobot. Phytotax.* 20: 70. 1985.

Lycopodium andinum Rosenst., *Repert. Spec. Nov. Regni Veg.* 5: 239. 1908, not Herter 1909. TYPE: Bolivia, La Paz, Murusata, 5000 m, *Buchtien 173* (holotype, sl!).

Urostachys andinus (Rosenst.) Nessel, *Bärlappgewächse* 76. 1939.

Plants with prostrate, rooting shoots from which 1 to several, usually short, erect, fingerlike shoots arise, sometimes loosely caespitose, up to 10(–15) cm tall. **Prostrate shoots** densely covered with 8–15 mm long, unilaterally upward curved, linear, red-tinged leaves. **Erect shoots** homophyllous or almost so, equally thick throughout or slightly tapering upward, ca. 6–10 mm in diameter including leaves. **Stems** of erect shoots excluding leaves 2–3 mm thick, usually completely concealed by leaves. **Leaves** of erect shoots uniform throughout, or somewhat reduced upward, borne in close, irregular, alternating whorls of 4–5, usually closely imbricate, straight to unilaterally or irregularly twisted and often somewhat deformed, linear-lanceolate to lanceolate or triangular-lanceolate, evenly to abruptly tapering from the slightly widened base or slightly acuminate, 5–8(–11) mm long, 1–2(–2.5) mm wide, upward sometimes reduced to 4–6 mm long, with a prominent basal swelling (air sac), adaxially concave to canaliculate apically, abaxially convex and rounded, smooth without

protruding, blisterlike epidermal cells, with smooth to irregularly rugose, often strongly sclerified margins, green to reddish-tinged. **Sporangia** 2–2.5 mm wide.

In boggy grassland, open turfy puna, wet ground at lakes, alt. (3300–)4000–4700(–5000) m, Cajamarca, La Libertad, Ancash, Junín, Huancavelica, Cuzco, Puno.

Peru and Bolivia.

Some collections, especially from lower altitudes, are referred to this species with doubt. *León & Young 1566, 1621* (AAU), from San Martín, Río Abiseo National Park, alt. 3650 m, and *León & Young 1105* (USM), from La Libertad, Prov. Pataz, Río Abiseo National Park, Cueva de Manachaqui, 3600–3800 m, are smaller, more slender, and entirely green but share the growth habit with relatively large leaves on the creeping shoots and rather slender erect shoots.

Cajamarca: Prov. Contumazá, Jalca El Chuño (Pozo Chuño), 4500 m, *Sagástegui et al. 9380* (AAU, F). **La Libertad:** Prov. Santiago de Chuco, Laguna La Victoria (road to Conzuzo), 4000 m, *Sagástegui et al. 6180* (GH, MO). Huillilas, N of Cachicadan, 4000 m, *Stork & Horton 10003* (F, UC). **Ancash:** Prov. Yungay, Dist. Yungay, Lake Llanganuco, ca. 3500 m, *Saunders 503* (F). **Junin:** Prov. Huancayo, Dist. Huancayo, Huaytapallana, Huancayo-Pariahuanca road, ca. 4480 m, *Saunders 1151* (GH). Dist. Huancayo, ca. 28 km E of Huancayo, 4500 m, *Tyron & Tryon 5469* in part (F, GH, US). **Huancavelica:** Prov. Taya-caya, Millpu, puna de Tocas, between Colcabamba and Paucarbamba, 4000 m, *Tovar 1945* (USM). Marcapata, 3600 m, *Stafford 1007* (F, K). **Puno:** Carabaya, Aricomá Lake, 4400 m, *Stafford 1118* (K).

21. *Huperzia saururus* (Lam.) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 249. 1874.

Lycopodium saururus Lam., *Encycl.* 3: 653. 1789. TYPE: Ile de Bourbon (Réunion), *Commerson* (holotype, P, *Herb. Lam.*!).

Lycopodium elongatum Sw., *Syn. Fil.* 175. 1806. TYPE: Peru, Prov. Junín, Tarma, *collector unknown* (holotype, sl!).

Urostachys saururus (Lam.) Herter, *Repert. Spec. Nov. Regni Veg.* 19: 162. 1923.

Urostachys elongatus (Sw.) Herter, *Index Lyc.* 60. 1949. *Lycopodium sanctae-barbarae* Rolleri, *Darwiniana* 16: 129, f. 1 D–E, t. 1, 3B. 1970. TYPE: Argentina, Prov. Jujuy, *de la Sota 2883* (holotype, LP).

Huperzia sanctae-barbarae (Rolleri) Rolleri and De-ferrari, *Notas. Mus. La Plata, Bot.* 21 (100): 156. 1988.

Plants erect, very compactly caespitose with basal, prostrate, rejuvenating shoots from which

stiffly erect, sparsely branched, fingerlike shoots arise, at least up to 50 cm tall. **Erect shoots** homophyllous or almost so, usually narrow and somewhat etiolated at the base and gradually becoming wider and green upward, 5–10 mm in diameter including leaves at the base, upward usually 8–15 mm. **Stems** excluding leaves (2–)3–5 mm thick, usually completely concealed by leaves except at the etiolated base. **Leaves** uniform throughout or gradually shorter upward in old shoots, often smaller, narrower, pale and irregularly appressed at the etiolated base of shoots, borne in irregular, alternating whorls (or low spirals) of 6–8, densely crowded, closely appressed, the sporophylls appressed from a nearly perpendicular leaf base, straight or somewhat secund, linear to linear-lanceolate, the uppermost sometimes lanceolate to widely lanceolate, 10–12(–15) mm long, 1–2(–3) mm wide, upward sometimes reduced to 5–8 mm long, sporophylls with a prominent basal swelling (air sac), adaxially concave to slightly convex, abaxially convex and rounded throughout or at least at the apex, smooth, with minutely rugose, thickened, sclerified margins, especially in the basal leaves, green and shining to reddish-tinged or rusty-colored and sometimes strongly pruinose. **Sporangia** 2–2.5 mm wide.

Moist shrubland and grassland (jalca), often among rocks, alt. 3300–4500 m, Cajamarca, La Libertad, Ancash, Pasco, Junín, Huancavelica, Cuzco.

Peru to Argentina and Chile; Kerguelen; Tristan da Cunha; alpine regions of tropical and southern Africa; Madagascar; Reunión; Mauritius.

Contrary to the view of Rolleri (Amer. Fern J. 67: 109–120. 1977), the present author finds the Neotropical distribution of *Huperzia saururus* restricted to Peru and more southern regions in America. The Central American and north Andine material referred to *H. saururus* by Rolleri belongs to various different species.

Some plants of this species are distinctly pruinose and reddish-tinged, similar to *Huperzia crassa*, but can usually be distinguished by the leaf shape, the etiolated character of the base of the erect shoots, and the lack of blisterlike, protruding epidermis cells on the abaxial leaf surface.

Cajamarca: Contumazá, Jalca El Chuño, 4500 m, *Sagástegui et al.* 9559 (AAU, F, NY). Pozo Kuan, 3790 m, *Sagástegui et al.* 13089 (AAU, F). Pozo Kuan, Laguna el Toro, 4100 m, *Sagástegui* 9452 (F). **La Libertad:** Prov. Santiago de Chuco, Pampas de la Julia, 3600 m, *Sagástegui et al.* 11123 (AAU, GH). Jalca de Quiruvilca, 4200

m, *López* 1506 (US). **Ancash:** Prov. Huari, Huascarán National Park, Quebrada Rima Rima, a lateral valley of Quebrada Carhuazcancha, 4200–4440 m, *D. Smith et al.* 12311 (AAU, F). Prov. Yungay, Huascarán National Park, Quebrada Ranicuray, 4000–4300 m, *D. Smith et al.* 9142 (AAU, F). **Pasco:** Pasco, Huayllay, *ex herb.* *Cruckshanks* in 1830 (GH). **Junín:** San José, ca. 3960 m, *Macbride & Featherstone* 1111 (F, G, US). **Huancavelica:** Prov. Tayacaja, above Hda. Tocas, between Colcabamba and Paucarbamba, 3200 m, *Tovar* 1967 (USM). **Cuzco:** Nevado Sallcantay, 3900–4200 m, *Bües* 744 (US). Prov. Urubamba, Dist Chinchero, Cuper, Hatun Wayk'o quebrada, 3300 m, *Sallo ex Franquemont* 281 (AAU, F). Prov. Paucartambo, Pfyucalla?, Huilcacunca, 4000 m, *Vargas* 9840 in part (MO). **Madre de Dios:** Piñasnocij, Pantiacolla, Pass, 3600 m, *Cook & Gilbert* 1867 (US). **Department unknown:** Peru, *Rusby* 354A (US).

22. *Huperzia hypogaea* B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 58. 1988. TYPE: Ecuador, Prov. Carchi, *Øllgaard & Balslev* 8517 (holotype, AAU!; isotype, QCA!).

Plants with short or up to 36 cm long, horizontal, usually subterranean, isotomously branching shoots, from which stiffly erect, aerial shoot systems arise. **Subterranean divisions** with pale appressed leaves, 2–4 mm thick including leaves. **Aerial shoots** up to 40 cm tall including erect subterranean divisions, stiffly erect, homophyllous, equally thick throughout, or slightly tapering, 4–6(–8) mm thick including leaves. **Stems** of aerial shoots 1.5–3 mm thick excluding leaves, partly to completely concealed by leaves, brownish to bright red, with smooth to somewhat rugose epidermis. **Leaves** borne in alternating, irregular whorls of 4–5, arcuate-appressed to closely appressed, abaxially convex and rounded or with a prominent, long decurrent veinal ridge, with or without a slightly prominent basal swelling (air sac), adaxially concave to slightly convex, linear-lanceolate to lanceolate, 4–6(–7) mm long, 1–1.8(–2) mm wide, upward often reduced to 3.5–4 mm long, red-tinged to entirely red, with smooth to unevenly rugose and sclerified margins. **Sporangia** 1–1.3(–1.5) mm wide.

Wet and boggy páramo and jalca, alt. 3000–4300 m, Lambayeque.

Colombia to northern Peru.

Usually a very easily recognizable species of marshes and wet depressions of the lower páramos with a soft substrate where the subterranean runner-shoots are well developed. Where the species grows on more solid substrates, e.g., open soil in landslides and road cuts, supraterranean creeping shoots with well-developed, patent-ascending

leaves replace the runner shoots, and make the distinction from slender forms of *Huperzia crassa* more subtle. In such cases the difference of leaf curvature, leaf size, and the number of leaf orthostichies are helpful characters.

Lambayeque: Prov. Ferrañafe, Dist. Incahuasi, Laguna Tembladera to Cerro Negro, 3300 m, *Sagástegui et al.* 12847 (AAU, F, GH).

23. *Huperzia sagasteguiana* B. Øllg., *sp. nov.*

Species cum habitu *Huperziae hypogaeae* et *H. attenuatae*. A *H. hypogaea* differt surculis horizontalibus epigaeis vel non profunde hypogaeis, foliis brevioribus, marginibus denticulato-fimbriatis, epidermide abaxiali rugulosa cellulis protrusis pustuliformibus. A *H. attenuata* differt foliis 10-fariis, epidermide abaxiali foliorum rugulosa, basibus foliorum minus ventricosis.

Plants with up to 20 cm long, horizontal, epiterranean and creeping, or shallowly subterranean, isotomously branching shoots, rooting along the underside, bearing stiffly erect, up to 20 cm tall aerial shoot systems with short to long intervals between branches. **Creeping shoots** with loosely appressed to upward curved, secund leaves, 3–5 mm thick including leaves. **Aerial shoots** stiffly erect, homophyllous, terete, equally thick throughout, 4–6 mm thick including leaves. **Stems** of aerial shoots 1.5–3 mm thick excluding leaves, partly to completely concealed by leaves, brownish to bright red, with rugosely striate epidermis. **Leaves** borne in alternating, irregular whorls of 5, arcuate-appressed to closely appressed, abaxially strongly convex and rounded to apically indistinctly carinate, with a prominent, short to long-decurrent veinal ridge, with a somewhat prominent basal swelling (air sac), adaxially concave (dried), lanceolate to triangularly ovate-lanceolate, 3–5 mm long, 1.5–2 mm wide, red-tinged to entirely red, abaxially wrinkled (dried) and strongly uneven due to the protruding blisterlike epidermal cells, with numerous irregularly shaped and directed, soft and pale marginal processes. **Sporangia** 1–1.5 mm wide.

TYPE—Peru, Dept. La Libertad, Prov. Pataz, Paso de Alaska, carretera a Tayabamba, en ladera abierta de Gramíneas, Jalca, 3900 m, *López & Sagástegui* 8177 (holotype, MO; isotypes, AAU!, GH!, NY!).

Terrestrial in jalca vegetation, 3900–3950 m, La Libertad.

Endemic.

The growth habit resembles *Huperzia hypogaea*,

but the trailing stems are usually on or just below the surface of the ground, and the leaves are shorter, strongly pruinose, with many blisterlike cells on the abaxial leaf epidermis, and have densely denticulate-fimbriate margins. *Huperzia attenuata* is rather similar but is less distinctly heteroblastic, has a smooth abaxial leaf epidermis, and has a more sharply prominent basal abaxial air sac on the upper leaves, and the leaves are borne in whorls of three to four.

La Libertad: Prov. Pataz, between Retama and La Paz, 3950 m, *López & Sagástegui* 3590 (GH).

24. *Huperzia attenuata* (Spring) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 249. 1874.

Lycopodium attenuatum Spring, *Mém. Acad. roy. Belg.* 24 [Mon. Lyc. 2]: 8. 1849. **LECTOTYPE** (designated by Lellinger, *Proc. Biol. Soc. Wash.* 89: 717. 1977): Ecuador (Prov. Pichincha), in declivitate montis Pichincha, *Hartweg* 1470 (us!; isolecotypes, BM!, GL!, K!, NY!, P!).

Urostachys attenuatus (Spring) Nessel, *Bärlappgewächse* 101. 1939.

Plants ascending to erect, rather small, caespitose with erect shoots in the center, and prostrate-ascending, rejuvenating basal shoots in the periphery, up to 20 cm tall, or up to 30 cm long. **Shoots** homophyllous to slightly gradually heterophyllous, terete to hexagonal, equally thick throughout, 4–7 mm in diameter including leaves. **Stems** excluding leaves 1.5–2 mm thick at the base, sometimes tapering to 1–1.5 mm in diameter upward, completely concealed by leaves, tinged with red or brick-red. **Leaves** borne in alternating whorls of 3–4, forming 6 or 8 usually regular ranks, appressed to the stem throughout, in basal divisions lanceolate and convex abaxially, upward gradually changing to narrowly triangular-ovate with acute or slightly acuminate apex, abaxially strongly convex to subcarinate near the apex, with a prominent basal swelling (air sac), (4–)5–6 mm long, in basal divisions 1–1.5 mm wide, distally 1.5–2.2 mm wide, with fimbriate margins, tinged with red. **Sporangia** 1.5–2 mm wide.

Exposed cushion vegetation in páramo, pioneer vegetation on landslides, road banks, etc., in the páramo zone, alt. 3400–3500 m, Cajamarca, La Libertad, San Martín.

Costa Rica; Ecuador and Peru to Bolivia.

An easily recognizable species, characterized by fimbriate leaf margins. *Huperzia attenuata* is a

close relative of *H. tetragona* (see the following for discussion).

Cajamarca: Prov. Cajamarca, N of Canal Cumbe Mayo, 3400–3500 m, *Sánchez V. & Molau 3746* (AAU). **La Libertad:** Prov. Huamachuco, Pallar–Huaguil, road to Tayabamba, 3400 m, *López & Sagástegui 8148* (AAU, F, MO). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, NW sector, Valle de Chochos, 3450 m, *León 1872* (AAU, USM). Prov. Mariscal Cáceres, Río Abiseo National Park, Pampa de Cuy, 3450 m, *León & Young 1401A* (USM).

25. *Huperzia tetragona* (Hooker & Grev.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium tetragonum Hooker & Grev., Icon. Fil. 1: t. 109. 1829. TYPE: Ecuador (Prov. Pichincha), Prope verticem montis Pichincha, *Jameson* (E!, K!).

Lycopodium catharticum Hooker, Ann. Nat. Hist. 1: 430–431, t. 14. 1838. SYNTYPES: Ecuador (Prov. Azuay), “Asuay of the Equator,” *W. Turner* (K!); Ecuador (Prov. Cañar), from the mountains of Pillzhum, *Jameson* (K!).

Lycopodium myrsinites Lam. var. *minus* Spring, Mém. Acad. roy. Belg. 15 [Mon. Lyc. 1]: 29. 1842, based on *Lycopodium catharticum* Hooker and with the same type.

Lycopodium tetragonum Hooker & Grev. var. *patulum* Spring, Mém. Acad. roy. Belg. 24 [Mon. Lyc. 2]: 12. 1849, based on *Lycopodium catharticum* Hooker and with the same type.

Urostachys tetragonus (Hooker & Grev.) Nessel, Bärlappgewächse 135. 1939.

Urostachys catharticus (Hooker) Nessel, Bärlappgewächse 135. 1939.

Plants ascending to erect, rather small, caespitose with erect shoots in the center, and usually prostrate to ascending rejuvenating basal shoots in the periphery, up to 20(–30) cm tall. **Shoots** homophyllous, or gradually slightly heterophyllous, quadrangular and equally thick throughout, 2.5–3.5(–4) mm in diameter including leaves. **Stems** excluding leaves 1–2 mm thick. **Leaves** decussate throughout, imbricate, concealing the stem, in basal divisions widely lanceolate to triangular-ovate, abaxially rounded and evenly decurrent, upward triangular, carinate at least in the upper half, somewhat decurrent or abaxially with a prominent basal swelling (air sac), 3.5–5(–7) mm long, 2–4 mm wide at the base, evenly tapering into an acute or slightly acuminate apex, orange to bright red-tinged at the margins throughout, with fimbriate margins. An occasional branch may be hexagonal or terete, with leaves borne in alternating whorls of 3. **Sporangia** 1.3–2.5 mm in diameter.

Exposed cushion vegetation, pioneer vegetation on landslides, road banks, etc., in the lower part of páramos and jalca, 2750–3600 m, Cajamarca, La Libertad, San Martín, Huánuco, Cuzco.

Columbia to Bolivia.

The red or reddish, quadrangular, erect shoots make this species an easily recognizable one. Incomplete material of some epiphytic species with quadrangular constricted shoots have been frequently misidentified as this species. They are readily separated because of the fimbriate leaf margins in *Huperzia tetragona*.

Huperzia tetragona is closely related to *H. attenuata*. The occasional aberrant hexagonal or terete shoots in some specimens of *H. tetragona* are virtually indistinguishable from slender shoots of *H. attenuata*. The two species are also ecologically rather similar and are often found to grow intermixed. There are numerous examples of species in which the number of leaves in each whorl is variable in the same population. The difference of terete and quadrangular shoots in *Huperzia attenuata* and *H. tetragona* may be due to such simple and taxonomically overrated variation within populations of one species.

Cajamarca: Prov. Chota, Laguna Yahuarcocha, above Incahuasi, 3600 m, *Sagástegui et al. 12901* (AAU). Prov. Cajamarca, N of canal Cumbe Mayo, 3400–3500 m, *Sánchez Vega & Molau 3747* (AAU). **La Libertad:** Pataz, Puerta del Monte, ruta de Huaylillas, 3200 m, *López & Sagástegui 3450* (GH). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, Chochos valley, 3425 m, *Young 3507* (AAU); 3300 m, *Young & León 4878* (AAU). **Huánuco:** 3–6 mi NW of Mito, ca. 3350 m, *Macbride & Featherstone 1923* (F, s, US). Playapampa, ca. 2750 m, *Macbride 4890* (F, G, US). **Cuzco:** Paucartambo, Huillcacunca to Huaisampilla, 3800 m, *Vargas 9859* (MO, UC).

26. *Huperzia sellifolia* B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 68, f. 12C. 1988. TYPE: Ecuador, Prov. Carchi, *B. Øllg. & Balslev 8432* (holotype, AAU!).

Plants erect or ascending, usually forming large, caespitose, homoblastic plants, often more than 25 cm tall, with up to 45 cm long shoots. **Shoots** homophyllous, almost equally thick throughout, (5–)6–8(–10) mm in diameter including leaves. **Stems** excluding leaves (2.5–)3–4 mm thick, almost completely concealed by leaf bases, except in basal divisions. **Leaves** almost uniform throughout, usually densely crowded throughout, borne in rather regular alternating whorls of 4–5, loosely imbricate or ascending to patent or sharply

reflexed and appressed to the stem, usually distinctly sigmoid, widely lanceolate to ovate or elliptic, acute or obtuse, (1.8–)2–2.6(–3.5) mm long, (1.2–)1.5–2(–2.4) mm wide, coriaceous, usually brightly red-tinged, abaxially convex to concave with prominent vein in basal part of lamina, rounded in the apex, with prominent, short to long-decurrent basal swelling (air sac), with usually slightly involute, narrowly sclerified, darker, smooth to slightly uneven margins, adaxially with slightly to distinctly prominent vein. **Sporangia** 1–1.5 mm in diameter.

Terrestrial in exposed wet páramos, alt. 3150–3650 m, Piura, Lambayeque, Amazonas, San Martín.

Andes of southern Colombia to northern Peru.

Piura: Purchased in the market of Sullana, *Friedberg 3933c* (GH). **Lambayeque:** Prov. Ferrañafe, Dist. Incahuasi, Laguna Tembladera, 3150 m, *Sagástegui et al. 12799* (AAU, F). **Amazonas:** Prov. Bagua, Cord. Colán NE of La Peca, ca. 3300 m, *Barbour 3382* (AAU, MO, USM). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, Paredones, 3650 m, *León & Young 1564* (AAU).

27. **Huperzia engleri** (Herter) B. Øllg., *Opera Bot.* 92: 169. 1987.

Lycopodium engleri Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 45. 1909. TYPE: Peru, Dept. Huánuco, Prov. Huamalies, mountains SW of Monzón, 3200–3300 m, *Weberbauer 3359* (holotype, B!; isotype, BONN, *Herb. Nessel 173!*, MOL!).

Urostachys engleri (Herter) Nessel, *Bärlappgewächse* 94. 1939.

Plants erect or ascending, up to 10 cm tall. **Shoots** homophyllous, equally thick throughout, 8–10 mm in diameter including leaves. **Stems** excluding leaves 1–1.5 mm thick, densely papillate. **Leaves** well spaced at base, crowded upward, borne in alternating whorls of 4, patent to somewhat reflexed, widely lanceolate to oblong-lanceolate, acute to obtuse, 4–5.5 mm long, 1.5–2 mm wide, slightly convex abaxially with slightly prominent vein, with evenly decurrent base, without a basal swelling, adaxially with a shallow groove along the vein, with minutely rugose margins. **Sporangia** 2–2.5 mm wide, nearly globose.

Habitat information according to protologue: Bog at grass steppe interrupting the shrub formation.

Endemic, Huánuco.

Possibly related to *Huperzia rufescens* (Hooker)

Trev. (Ecuador) and *H. brevifolia* but apparently adapted to more sheltered habitats. The sporangia are disproportionately large, thick, and voluminous and do not open as is otherwise usual in dried specimens. This, plus the rarity of the species, suggests hybridity, but there is no other evidence of hybridity, *because the spores seem normally developed*. The collection by Jelski from the Nessel Herbarium needs to be confirmed; it was not found in Kraków.

Department unknown: “Ost-Cordilere, *Jelski*” [possibly Dept. Cajamarca, Prov. Cutervo] (BONN, *Herb. Nessel 173!*).

28. **Huperzia brevifolia** (Grev. & Hooker) Holub, *Folia Geobot. Phytotax.* 20: 71. 1985.

Lycopodium brevifolium Grev. & Hooker, *Hooker Bot. Misc.* 3: 104. 1832. TYPE: Peru, in Herb. Lambert, *Ruíz and Pavon* (BM?; possible isotypes, FI, Herb. Webb; AAU photo ex FI!, G!).

Urostachys rufescens (Hooker) Nessel var. *brevifolius* (Grev. & Hooker) Nessel, *Bärlappgewächse* 103. 1939.

Urostachys brevifolius (Grev. & Hooker) Herter, *Index Lyc.* 54. 1949.

Plants erect or ascending, stiff and robust, forming small to large, caespitose, homoblastic plants, often more than 25 cm tall. **Shoots** homophyllous, almost equally thick throughout, (5–)7–12 mm in diameter including leaves. **Stems** excluding leaves (3–)4–7 mm thick at the base, slightly tapering upward, usually concealed by leaf bases. **Leaves** almost uniform throughout, densely crowded, or sometimes more spaced in basal divisions, borne in alternating whorls of 4–5, ascending or perpendicular to sharply reflexed, with straight to upward curved apex, widely ovate or triangular-ovate to widely suborbicular-cordate or triangular-cordate, acute to almost obtuse or mucronulate, 2–4 mm long, 2–4(–5) mm wide, stiffly coriaceous, green- or red-tinged, abaxially concave, with sharply prominent vein, with sharply prominent, somewhat flattened, short-decurrent basal swelling (air sac), with slightly revolute, strongly sclerified, darker and somewhat translucent, slightly erose margins. **Sporangia** 1.5–2.5 mm wide.

Terrestrial in wet páramos, jalca, alt. 2700–4120 m, Piura, Lambayeque, Cajamarca, Amazonas, Huánuco, Pasco, Cuzco.

Costa Rica; Colombia to Peru.

The total distribution range is uncertain, as there

is considerable regionally characteristic variation in the material referred to *Huperzia brevifolia*. Populations from Colombia, southern Ecuador and Peru are slightly different and usually recognizable; perhaps they are worth taxonomic recognition.

Huperzia brevifolia differs from *H. rufescens* and *H. sellifolia* by its larger size, thick stems, and stiff and almost prickly leaves and by the frequent lack of red coloration.

Dudley 11109 deviates by its slender shoots with very short leaves.

Piura: Purchased in the market of Sullana, *Friedberg 3933e* (GH). **Lambayeque:** Prov. Ferrañafe, Dist. Incahuasi, Laguna Tembladera, 3150 m, *Sagástegui 12792* (F, GH), *12848* (GH in part). **Cajamarca:** From Chiclayo market, *León* (AAU, USM). **Amazonas:** Prov. Chachapoyas, Leimebamba–Chilchos trail, *Boeke 2130* (AAU). Prov. Bagua, Cord. Colán NE of La Peca, 3300 m, *Barbour 3381* (AAU, MO). **Huánuco:** Playapampa, 2700 m, *Macbride 4476* (F, US). Cushi, trail to Tambo de Vaca, *Bryan 678* (F, US). **Pasco:** Prov. Oxapampa, trail to summit of Cord. Yanachaga via Río San Daniel, 3350–3620 m, *D. Smith 7742* (AAU, USM). **Junín:** Prov. Tarma, mountains W of Huacapistana, 3400–3500 m, *Weberbauer 2225* (MOL). **Cuzco:** Prov. Paucartambo, Paso del Gallo, 2900 m, *Vargas 4279* in part (UC, US). Urubamba, Machu Picchu, Runcuraccay–Sayamarca pass, 4120 m, *Peyton 288* (AAU). Prov. La Convención, summit ridge of Vilcabamba, ca. km 28 along trail from Hda. Luisiana and Río Apurímac, 3330–3410 m, *Dudley 11109* (GH, US).

29. *Huperzia hohenackeri* (Herter) Holub, Folia Geobot. Phytotax. 20: 73. 1985.

Lycopodium hohenackeri Herter, Bot. Jahrb. 43: Beibl. 98: 46. 1909. TYPE: Peru, Dept. Puno, in summis Cordiller. jugis pr. Tabina, *Lechler 2043* (B!, BR!, K, NY!, P, S!).

Urostachys hohenackeri (Herter) Nessel, Bärlappgewächse 105. 1939.

Plants erect or ascending, forming small to large, caespitose, homoblastic plants, up to 40 cm tall. **Shoots** homophyllous or with gradually smaller leaves upward, equally thick throughout, 10–13(–15) mm in diameter including leaves, or tapering to (5–)7–10 mm in diameter upward. **Stems** excluding leaves 5–6 mm thick at the base, upward tapering to (2–)3–4 mm thick, partly to completely concealed by leaves. **Leaves** borne in more or less regular, alternating low spirals or whorls of 5–6, often well spaced in basal divisions, densely crowded upward, those of basal non-sporangiate divisions ascending to spreading, widely triangular-lanceolate or ovate-lanceolate, 4.5–5.5 mm long, 2.5–3 mm wide, with short to long, evenly decurrent leaf bases. **Leaves** of upper, sporangiate

divisions patent to loosely imbricate, triangular-ovate to ovate or widely ovate, acute, 3–5 mm long, 2–3.5 mm wide, softly to firmly coriaceous, green- to red-tinged, adaxially concave, or slightly convex and with a prominent veinal ridge at the base, abaxially usually slightly concave at the base, above the base convex and rounded or with a slightly to strongly prominent veinal ridge, with a strongly prominent, narrow basal swelling (air sac), with upward curved apex, with usually strongly sclerified, irregularly rugose to minutely erose margins. **Sporangia** 1.7–2 mm wide.

Terrestrial on banks, steep, mossy slopes in wet páramos, jalca, alt. 3400–4000 m, Cuzco, Puno. Colombia to Peru.

Huperzia hohenackeri resembles most the large individuals of *H. brevifolia*, with which it shares the general aspect of size and growth habit. It differs in the longer, more acute and usually appressed leaves. *Metcalf 30745* deviates by having recurved leaves throughout.

Cuzco: Prov. Urubamba, trail Pajupata to Sayacmarca, 3600 m, *Vargas 2911* (US). Near Wenner Gren ruins, 3400–3600 m, *Metcalf 30745* (UC in part). Prov. La Convención, Alturas de Río Calzada, Huadquiña, ca. 3660 m, *Bües 755* (US). **Puno:** Tabina, in summis Cordilleras, julio 1854, *Hohenacker* (BONN, *Herb. Nessel 199*). Cordillera near Tabina, *Hohenacker 4204* (BONN, *Herb. Nessel 199*). Cord. near Ayapata and Sachapata, *Lechler 2028* (E). **Department unknown:** Cordillera, 1902, *Landoni* (BONN, *Herb. Nessel 199*).

30. *Huperzia hartwegiana* (Spring) Trev., Atti. Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium hartwegianum Spring, Mém. Acad. roy. Belg. 24 [Mon. Lyc. 2]: 14. 1849. LECTOTYPE (designated by Øllgaard in Harling and Anderson, Fl. Ecuador 33: 76. 1988): Colombia, Prov. Popoyan, *Hartweg 1466* (K! annotated by Spring; isoelectotypes, BM!, G!, LG!, NY!).

Lycopodium caracasicum Herter, Hedwigia 49: 88, t. 3a. 1909. TYPE: Venezuela, Caracas, Jan. 1856, *Gollmer* (holotype, B!).

Urostachys hartwegianus (Spring) Nessel, Bärlappgewächse 90. 1939.

Urostachys caracasicus (Herter) Nessel, Bärlappgewächse 90. 1939.

Huperzia caracasica (Herter) Holub, Folia Geobot. Phytotax 20: 71. 1985.

Plants robust, recurved or pendulous, at least up to 30 cm long. **Shoots** homophyllous to gradually heterophyllous, 15–30 mm in diameter including leaves in basal divisions, sometimes tapering to 10–15 mm in diameter. **Stems** excluding

leaves 2.5–3.5(–5) mm thick at the base, tapering to 1.5–2 mm. **Leaves of basal divisions** borne in often regular alternating whorls of 4–5, falcately patent-ascending to imbricate, radially directed to somewhat secund, almost completely covering the stem and sporangia, lanceolate, coriaceous, usually shining, 14–23 mm long, 2.5–3.5 mm wide, widest below the middle to near the base, abaxially convex at the base, usually slightly concave toward the tip, with smooth, flat to somewhat involute margins, the vein slightly prominent at the base and apically obscure. **Leaves of terminal divisions** conform, or usually smaller, 7–10(–13) mm long, 1.5–3 mm wide, often somewhat clasping with the base widened, softer and less shining. **Sporangia** 1.7–3 mm in diameter.

Rupestal in montane forest, alt. 2400–3100 m, Ancash, Cuzco.

Southern Mexico; Guatemala; Andes from Venezuela to Peru.

Huperzia hartwegiana is widely distributed and variable. The species is often epiphytic outside Peru, but in Peru all records are from rocky substrates. The variation seems partly correlated with habitat type. The species frequently occurs in sites that are too dry for the other *Huperzia* species. In such exposed rupestal sites, the plants initially grow erect, then recurved, and may develop rather short and rigid shoots only. Such forms were recognized as *Lycopodium caracasicum* by Herter and others. In moist, shaded, epiphytic situations long, lax, pendulous forms are developed. *Huperzia hartwegiana* is related to *H. taxifolia*.

Ancash: Prov. Bolognesi, Quero E of Huasta, *Cerrate 2471* (USM). **Cuzco:** Prov. Cuzco, Cadena de Pactatayan, *Vargas 17044* (GH). Prov. Urubamba, Ollantaytambo, 3050 m, *Plowman & Davis 4741* (GH). Cusuchaca, 2400 m, *Vargas 22971* (GH). Valle de Urubamba, *Herrera 3423* (C). Valle de Urubamba, ca. 10 km from the village, *León 446* (USM). Quebrada Las Peñas, 3100 m, *Chávez 3493* (MO).

31. *Huperzia taxifolia* (Sw.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium taxifolium Sw., Prodr. 138. 1788. TYPE: A remounted specimen, marked as type, without original annotation, in the Regnellian type herbarium in s!, is possibly the holotype.

Lycopodium passerinoides Kunth, in HBK., Nov. gen. sp. 1: 41. 1816. TYPE: Peru, prope Olleras et Aipate, alt. 747 hexp., *Humboldt* (holotype, P, *Herb. Humb.*!; isotypes, B, *Herb. Willd.* 19410!, BONN, *Herb. Nessel* 160!).

Lycopodium nitens Schlecht. & Cham., Linnaea 5: 623. 1830. TYPE: Mexico, in arboris vetustis prope Jalapam, *Schiede & Deppe* (holotype, B!; isotype, BM!).

Huperzia passerinoides (Kunth) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Huperzia passerinoides (Kunth) Trev. var. *nitens* (Schlecht. & Cham.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium schwendeneri Herter, Bot. Jahrb. 43: Beibl. 98: 50. 1909. TYPE: Not designated. Mexico indicated as locus classicus by Herter 1923.

Urostachys taxifolius (Sw.) Herter, Repert. Spec. Nov. Regni Veg. 19: 162. 1923.

Phlegmariurus taxifolius (Sw.) Löve & Löve, Taxon 26: 324. 1977.

Plants lax and pendent, or sometimes recurved from an erect and somewhat rigid stem base, up to 50(–70) cm long. **Shoots** usually gradually tapering from ca. 20–30 mm in diameter including leaves at the base, to 4–10 mm in distal divisions of fully developed plants, sometimes not, or only slightly tapering, rarely abruptly constricted. **Stems** excluding leaves 1.5–2 mm thick at the base, tapering to 1–1.5 mm. **Leaves** usually reduced and modified upward, borne in irregular alternating whorls of 3–5. **Leaves of basal divisions** spreading to ascending or somewhat appressed, often twisted at the base, narrowly lanceolate, widest in the lower half, firmly herbaceous to subcoriaceous, 14–23 mm long, 2–3 mm wide, almost flat or somewhat concave adaxially, with flat or slightly revolute, smooth margins, with evident to somewhat prominent vein abaxially. **Leaves of middle and terminal divisions** usually gradually shorter, narrower and more appressed, abaxially more convex, with involute margins. **Leaves of fully sporangiate divisions** often distinctly 6–(10–) ranked, with widened, clasping base, partly covering the sporangia, often abruptly contracted into a short to long, narrow, involute apex, 3–8 mm long, 1–1.5(–2) mm wide. **Sporangia** 1–1.5 mm wide.

Usually epiphytic in lower to mid-altitude wet montane forest, alt. 1300–1400 m, Cajamarca, Amazonas.

Central America; West Indies; northern tropical South America.

Huperzia taxifolia is a variable species, the delimitation of which is problematic, especially outside Peru. The Peruvian specimens cited below are unusual in having the leaves arranged in alternating whorls of 5. *Hutchison & Bismarck 6379*, unusual in the nearly conform sporophylls and uniformly patent-ascending leaves throughout, is apparently juvenile.

Cajamarca: Prov. Hualgayoc, Hda. Taulis, between the Casa Hacienda and Palmito, 2000 m, *Hutchison & Bismarck 6379* (UC, USM). **Amazonas:** Prov. Bongará, vicinity of Campamento Ingenio 1–3 km up road to Pomacocha (and Rioja) from camp along the Río Ingenio, 1300–1400 m, *Hutchison & Wright 3825* (F, GH, UC).

32. *Huperzia rosenstockiana* (Herter) Holub, *Folia Geobot. Phytotax.* 20: 76. 1985.

Lycopodium rosenstockianum Herter, *Hedwigia* 49: 90. 1909. TYPE: Ecuador, Ost-Abhang des Tunurahua, 3000 m, *Rimbach 130* (holotype, *Herb. Rosenstock*, not located; isotypes, s!, UC!, us!).

Urostachys rosenstockianus (Herter) Nessel, *Bärlappgewächse* 174. 1939.

Plants lax, pendulous, rarely recurved from an ascending base, at least up to 150 cm long. **Shoots** homophyllous, or with gradually slightly smaller leaves upward, 20–25(–30) mm in diameter including the leaves in basal divisions, sometimes tapering to 10–14 mm. **Stems** excluding leaves (1.5–)2–3(–5) mm thick at the base, tapering to 1–2 mm. **Leaves of basal divisions** borne in alternating irregular whorls of 3–5, irregularly spreading to ascending, usually somewhat twisted at the base, with oblique to vertical lamina, lanceolate to narrowly oblong, widest at or below the middle, with widely cuneate to somewhat rounded base, with short to long acute apex, 10–15 mm long, 2–4 mm wide, subcoriaceous and opaque to herbaceous and translucent, almost flat, with prominent vein adaxially, or sometimes folded down along the vein, with slightly revolute, minutely rugose margins with individually protruding epidermis cells, especially at the apex. **Leaves of middle and terminal divisions** conform, or gradually smaller and more ascending to loosely appressed, more densely crowded. Leaves of densely **sporangiate divisions** usually widest just above the base, lanceolate to narrowly triangular, with a rounded base, 6–9 mm long, 1.5–2.5 mm wide, partly covering the sporangia. **Sporangia** 1.5–2 mm wide.

Usually epiphytic, rarely terrestrial, in cloud forest and elfin forest above 3000 m, San Martín.

Colombia to northern Peru.

Huperzia rosenstockiana resembles *H. taxifolia*, but details of the leaf margin, color, and ecology are quite distinct. Closely related to *H. brongniartii* with which it shares the rugulate leaf margins. *Huperzia socratis* (Herter) Rolleri & Deferrari (type from Colombia) seems to be a synonym of the present species.

San Martín: Prov. Mariscal Cáceres, Río Abiseo National Park, Puerta del Monte, 3400 m, *León & Young 1303* (AAU, USM). Prov. Mariscal Cáceres, Río Abiseo National Park, Laguna de Chochos, 3300 m, *Young & León 4855* (AAU).

33. *Huperzia funiformis* (Spring) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 248. 1874.

Lycopodium funiforme Spring, *Bull. Acad. roy. Sci. Bruxelles* 8 (2): 516. 1841. LECTOTYPE (designated by Spring, *Mon. Lyc.* 2: 49. 1949): Guadeloupe, *L'Herminier* (P!; isolectotypes, BR!, GH!, NY!, UC!).

Urostachys funiformis (Spring) Herter in Urban, *Symb. Antill.* 9: 387. 1925.

Plants robust, flaccidly pendulous, ropelike, at least up to 250 cm long. **Shoots** homophyllous, almost equally thick throughout, 5–10(–15) mm in diameter including leaves, or sometimes tapering from a thicker base with patent-ascending leaves. **Stems** excluding leaves 1.5–3(–5) mm thick at the base, ridged by decurrent leaf bases. **Leaves** almost uniform throughout, or slightly shorter upward, borne in crowded alternating whorls of 7–8, densely covering the stem, usually closely falcate-appressed throughout, not twisted, linear-subulate, widest just above the base, 6–10(–12) mm long, 1–1.5 mm wide, evenly tapering into a long pungent apex, firmly herbaceous to coriaceous, dull to shining, abaxially strongly convex, often apically conduplicate, with smooth margins. **Sporangia** 1–1.5 mm wide.

Lower montane rain forest, up to alt. ca. 1300 m, Huánuco.

West Indies; southern Mexico to Panama; Guyana; Venezuela to Peru.

Huperzia funiformis is a very distinct species, not easily confused with other species due to its smooth ropelike shoots.

Huánuco: SW slope of the Río Lllallapichis watershed, on the ascent of Cerros del Sira, 1290 m, *Wolfe 12330* (GH).

34. *Huperzia buesii* (Herter) B. Øllg., *comb. nov.*

Urostachys buesii Herter, *Revista Sudamer. Bot.* 10: 126. 1954 [as 1953]. TYPE: Peru, Tranca de Yarracuaya, 1800 m, *Bües 742* (holotype, us!).

Lycopodium buesii (Herter) Morton, *Amer. Fern J.* 54: 72. 1964.

Plants robust, pendent, up to 50 cm long. **Shoots** homophyllous, almost equally thick throughout,

ca. 10–20 mm in diameter including leaves, or tapering to 10 mm. **Stems** excluding leaves 2–3 mm thick, prominently ridged by decurrent leaf bases. **Leaves** almost uniform throughout, or slightly shorter distally, borne in close alternating whorls of 4–5, densely covering the stem, usually closely appressed throughout, slightly recurved at the apex, not twisted, linear to linear-lanceolate, widest just above the slightly rounded base, 12–19 mm long, 1–2 mm wide, evenly tapering into a long apex, firmly herbaceous to subcoriaceous, shining, abaxially convex, somewhat involute, with smooth margins. **Leaves of sporangiate divisions** sometimes reduced to 6–8 mm. **Sporangia** 1.5–2 mm wide.

A rare endemic. Epiphytic in forest, 1800 m, Cuzco.

Perhaps related to *Huperzia funiformis* and *H. aristei* (Nessel) Rolleri and Deferrari (?Colombia) with which it shares the high number of leaves in each whorl and the general leaf shape. However, the leaves are longer and more diverging. The similarity to the juvenile plants of *H. sotae* (Rolleri) Rolleri and Deferrari (NW Argentina to Bolivia, e.g., *Venturi 2955*, isotype in us!) is close.

Cuzco: Prov. La Convención, Choquellohuanca, 1800 m, *Marin 2247* (F).

35. *Huperzia linifolia* (L.) Trev., Atti Soc. Ital. Sci. Nat. 17: 248. 1874.

Lycopodium linifolium L., Sp. pl. 1100. 1753. TYPE: Plumier, *Traité foug. Amér. t. 166, f. C*, from an unspecified locality, either Martinique or Hispaniola (see Proctor, *Fl. Lesser Antilles* 2: 26. 1977).

Urostachys linifolius (L.). Herter, *Repert. Spec. Nov. Regni Veg.* 19: 154. 1923.

Plants pendulous, usually with flaccidly hanging divisions, the terminal divisions often aggregated in fasciculate clusters, up to 60(–80) cm long. **Shoots** homophyllous or gradually heterophyllous, equally thick throughout, 20–30(–45) mm in diameter including leaves, or gradually tapering to (7–)10–15 mm in diameter in terminal, densely sporangiate divisions. **Stems** excluding leaves 0.5–1 mm thick at the base, slightly tapering upward, almost straight to somewhat flexuous, pale greenish in life. **Leaves of basal divisions** spirally arranged, single, or in occasional pairs or whorls of 3, not predominantly whorled, forming about 6 indistinct longitudinal ranks, subdistant, soft-herbaceous, wide-spreading to ascending, straight to slightly falcate, usually with the lamina vertical due to a twist of the lamina base, linear-lanceolate to lanceolate, widest in the basal 1/3 or 1/4, distinctly narrowed into a petiolelike, twisted, usually perpendicular to deflexed lamina base, (10–)13–24 mm long, 1–5 mm wide, flat, or with slightly revolute, smooth margins. **Leaves of middle and terminal divisions** spirally arranged, paired or borne in irregular to regular, alternating whorls of 3, conform, or usually narrower, (5–)10–15(–20) mm long, (1–)1.5–2(–3) mm wide, often with a long narrow apex from a subauriculate, non-twisted lamina base. **Sporangia** 1–1.5 mm wide.

Southern Mexico to Panama; West Indies; northern South America.

Huperzia linifolia is a widespread and polymorphic species. Its variation is especially complex in the northern Andes. The two varieties keyed out below are fairly well characterized morphologically and are geographically well defined.

Key to Varieties

- a. Shortest sporophylls of densely sporangiate divisions with distinctly widened, usually not twisted lamina base, usually ascending to loosely appressed, opaquely green; stem usually opaque-stramineous, usually above 1000 m elevation 35a. var. *tenuifolia*
- a. Shortest sporophylls of densely sporangiate divisions usually conform to leaves of basal divisions, or shorter, usually with a twisted, narrow to slightly widened lamina base, perpendicular to spreading-ascending, pale, transparently green or brownish green; stem, at least in terminal divisions, usually transparently stramineous to reddish brown, the vascular tissue usually visible through the cortex, usually below 600 m elevation 35b. var. *jenmanii*

35a. *Huperzia linifolia* var. *tenuifolia* (Nessel) B. Øllg. in Harling and Andersson, Fl. Ecuador 33: 90. 1988.

Urostachys linifolius (L.) Herter var. *tenuifolius* Nessel, Revista Sudamer. Bot. 6: 164. 1940 [Bärlappgewächse 162, Abb. 39, f. 14. 1939, nom. nud.]. LECTOTYPE (designated by Øllgaard, in Harling and Andersson, Fl. Ecuador 33: 90. 1988): Peru, Prov. Huánuco, Pampayacu, Poeppig ["Moritz 210 und 1155"] (BONN, Herb. Nessel 381!; isotype, G!).

Wet forests of the eastern Andine slopes, alt. 100–2700 m, Cajamarca, Amazonas, San Martín, Huánuco, Pasco, Junín, Cuzco. Colombia?, Ecuador and Peru.

Cajamarca: Tabillo, *Jelski 1022* (KRA). Huancabamba, *André K1763* (F, GH, NY, US). Tambillo, *Jelski 1022* (KRA). **Amazonas:** Prov. Bongará, 5 km N of end of Lake Pomacocha, on road to Rioja, 2000 m, *Hutchison & Wright 6791* (F, GH, NY, UC). Prov. Chachapoyas, Cerros Calla Calla, 10 km above Leimebamba, 2700 m, *Hutchison & Bennett 4743* (F, GH, M, MO, NY, UC, US). **San Martín:** Tarapoto, monte Campana, *Spruce 4627* (BR). Prov. Rioja, Pedro Ruíz–Moyobamba road, km 390, Venceremos, 1750 m, *D. Smith 4372* (AAU). Prov. Rioja, Pedro Ruíz–Moyobamba road, km 291, 1850 m, *Gentry et al. 45502* (AAU). **Pasco:** Prov. Oxapampa, Quebrada San Alberto, on the borders of Parque Nacional Yanachaga–Chemillen, *León et al. 944* (F, USM). **Junín:** La Merced, Chanchamayo, *Soukup 1007* (F); 1000 m, *Esposito 11978* (USM). **Cuzco:** Prov. La Convención, Potrero, Sapan Sachayoc, 2300 m, *Vargas 13643* (GH). Valley of Santa Ana, 1000–1500 m, *Herrera 2628* (US). **Department unknown:** Peru, Ruíz & Pavon (E, G).

35b. *Huperzia linifolia* var. *jenmanii* (Underw. & Lloyd) B. Øllg. & Windisch, Bradea 5: 13. 1987.

Lycopodium jenmanii Underw. & Lloyd, Bull. Torrey Bot. Club 33: 112. 1906. TYPE: Guyana, Moruca River, *Jenman* (holotype, NY!; isotypes, BONN, Herb. Nessel 388 in part, E!).

Urostachys jenmanii (Underw. & Lloyd) Nessel, Bärlappgewächse 158. 1939.

Huperzia jenmanii (Underw. & Lloyd) Holub, Folia Geobot. Phytotax. 20: 74. 1985.

Epiphytic in lowland rain forest up to ca. 600 m, San Martín.

Throughout the Amazonian basin and the Guianas.

San Martín: Prov. Mariscal Cáceres, Palo Blanco, W of Puente, Tocache Nuevo, *J. Schunke V. 5738* (F, NY, S, US).

36. *Huperzia wilsonii* (Underw. & Lloyd) B. Øllg., Opera Bot. 92: 170. 1987.

Lycopodium wilsonii Underw. & Lloyd, Bull. Torrey Bot. Club 33: 111. 1906. TYPE: Puerto Rico, Luquillo Mountains, *Wilson 271* (holotype, NY!).

Lycopodium trichodendron Herter, Bot. Jahrb. 43: Beibl. 98: 49. 1909. SYNTYPES: Guadeloupe, *L'Herminier* (P!); *Bory 103* (P!).

Lycopodium andinum Herter, Bot. Jahrb. 43, Beibl. 98: 49. 1909, not Rosenst. LECTOTYPE (designated by Øllgaard in Harling & Andersson, Fl. Ecuador 33: 97. 1988): Ecuador, *Fraser*, in Herb. Drake (P!; isolectotype, G!).

Lycopodium lindavianum Herter, Hedwigia 49: 90. 1909, nom. nov. for *L. andinum* Herter, not Rosenst., and with the same type.

Lycopodium stamineum Maxon, Smithsonian Misc. Coll. 56 (29): 2, pl. 2. 1912. TYPE: Panama, Chiriquí, above El Boquete, ca. 1750 m, *Maxon 5636* (holotype, US!).

Urostachys wilsonii (Underw. & Lloyd) Herter, RePERT. Spec. Nov. Regni Veg. 19: 163. 1923.

Lycopodium arcanum Maxon in Yuncker, Field. Mus. Publ. Bot. 17: 310, t. 3. 1938. TYPE: Honduras, Comayagua, above El Achote, above plains of Siguatepeque, 1800 m, *Yuncker et al. 6149* (holotype, US!).

Huperzia lindaviana (Herter) Holub, Folia Geobot. Phytotax. 20: 74. 1985.

Plants erect, arcuate-spreading to pendulous, up to 20(–30) cm long. **Shoots** homophyllous, 15–25(–30) mm in diameter including leaves, equally thick throughout, or in some slender individuals gradually tapering to 1–1.5 cm. **Stems** excluding leaves (1–)1.5–2(–3) mm thick at the base, often tapering to (0.7–)1 mm, prominently ridged by decurrent leaf bases, pale green to stramineous, often with bright red spots on leaf bases. **Leaves** usually uniform throughout, borne in alternating, irregular whorls of 6–7, in basal divisions, upward often in whorls of 4–5, perpendicularly spreading to ascending, straight to upward curved, usually not twisted at the base, linear to filiform, (6–)10–17 mm long, 0.3–0.5 mm wide at the base, quickly narrowed to ca. 0.2 mm due to involution, gradually tapering, adaxially canaliculate to involute, often with a prominent vein abaxially near the base. **Leaves of terminal divisions** in old plants sometimes gradually reduced to 6(–4) mm long. Decurrent leaf bases usually not wider than the lamina base, often bright red. **Sporangia** 1–1.5 mm wide.

Epiphytic in lower montane forests, up to alt. 2750 m, San Martín.

West Indies; southern Mexico to Panama; Andean South America south to Peru.

Huperzia wilsonii is related to *H. dichotoma* and *H. mandiocana* (Raddi) Trev. (Brazil) and to *H. polycarpus*. With these it shares the bottlebrush-like growth habit, and with *H. mandiocana* the bright red coloration of the leaf bases in some individuals. The absence or presence of red color seems uncorrelated with other characters. The intensity and size of the coloration are variable.

Pendent individuals of *H. wilsonii* are rather similar to *H. polycarpus*, but the latter has shorter, more flattened leaves and uniformly falcate leaves due to a basal twist, and this species apparently is always pendulous. The direction of leaves is correlated with growth habit. In erect-growing plants the leaves are wide-spreading to almost reflexed, while in pendent plants the leaves are somewhat ascending.

San Martín: Prov. Rioja, Pedro Ruiz–Moyobamba road, km 390, Venceremos, 1750 m, *D. Smith 4372A* (MO). **Prov. Mariscal Cáceres,** Río Abiseo National Park, trail La Playa camp–Papayas, 2650–2750 m, *Young & León 4968* (AAU). **Department unknown:** *Ex herb. Pavon* (G, P). **Peru,** *M. Matthews* (G, K). **Peru,** *Matthews 1082* (G).

37. *Huperzia polycarpus* (Kunze) B. Øllg., *Opera Bot.* 92: 169. 1987.

Lycopodium polycarpus Kunze, *Linnaea* 9: 5. 1834. TYPE: Peru, ad Cassapi [Casapi?, Huánuco], *Poeppig* (w!).

Urostachys polycarpus (Kunze) Herter, *Index Lycopodium* 76. 1949.

Urostachys cuatrecasasii Herter, *Revista Sudamer. Bot.* 10: 123. 1953. TYPE: Colombia, Valle, Cord. Occidental, Vertiente Occidental, hoya del río Digua, Piedra de Moler, 900–1180 m, *Cuatrecasas 15143A* (holotype, us!).

Lycopodium cuatrecasasii (Herter) Morton, *Amer. Fern J.* 54: 72. 1964.

Plants pendulous, with flaccidly hanging divisions, up to 30 cm long. **Shoots** homophyllous, almost equally thick throughout, 10–15 mm in diameter including the leaves. **Stems** excluding leaves 1–1.5 mm thick near the base, tapering to 0.5–1 mm, somewhat ridged by decurrent leaf bases. **Leaves** almost uniform throughout, densely crowded, borne in alternating, irregular whorls of 6–7 in basal divisions, upward of (3–)4 whorls, wide-spreading to ascending, often subsecund, usually with vertical lamina due to a twist at the base, linear to filiform, 6–10(–12) mm long, 0.4–0.5 mm wide, evenly tapering, usually oblique-falcately curved, adaxially flat or shallowly canaliculate, often with an abaxially prominent vein

near the leaf base, with green decurrent leaf bases. **Sporangia** ca. 1 mm wide.

Pendulous epiphyte in montane forest, ca. 2000 m, Huánuco?, Junín.

Costa Rica to Colombia; Peru.

Huperzia polycarpus is close to *H. wilsonii*, which see for discussion. From *H. sarmentosa* it is distinguished by the lack of leaf base auricles. From *H. mollicoma* (Spring) Holub (tropical America), it differs in the more patent, twisted leaves, with much less prominent veins.

Junín: Chanchamayo Valley, 2000 m, *C. Schunke 529* (F).

38. *Huperzia sarmentosa* (Spring) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 248. 1874.

Lycopodium sarmentosum Spring, *Mém. Acad. roy. Belg.* 24 [Mon. Lyc. 2]: 13. 1849. LECTOTYPE (designated by Øllgaard in Harling and Anderson, *Fl. Ecuador* 33: 100. 1988): Ecuador, Quitonian Andes, *Jameson 41* (K!).

Urostachys sarmentosus (Spring) Herter, *Repert. Spec. Nov. Regni Veg.* 19: 165. 1923.

Plants slender, pendulous, with flaccidly hanging divisions, up to 100(–200) cm long. **Shoots** homophyllous or almost so, equally thick throughout, 15–25 mm in diameter including leaves in basal divisions, or sometimes tapering to ca. 8 mm in diameter. **Stems** excluding leaves 1–1.5 mm thick at the base, often tapering to 0.4–0.8 mm, slightly to prominently ridged by decurrent leaf bases. **Leaves** borne in alternating irregular whorls of 4–7, spreading to ascending, or rarely loosely appressed in terminal divisions, usually twisted at the lamina base, straight to slightly upward curved, linear to linear-subulate, with distinctly widened, auriculate, usually strongly revolute, often overlapping lamina bases, 7–15 mm long, 0.4–0.7 mm wide just above the auriculate base, usually ca. 0.3 mm wide in the middle, usually somewhat revolute, with obscure to prominent vein, with smooth margins, or the auricles irregularly dentate. **Leaves of terminal divisions** often densely crowded, conform, or gradually reduced to 5–7 mm long. **Decurrent leaf bases** narrower than the lamina base. **Sporangia** 1–1.3 mm in diameter.

Epiphytic or rarely hanging from banks, in upper montane forest, alt. 2100–3450 m, Amazonas, San Martín.

Ecuador and northern Peru.

Huperzia sarmentosa is quite variable with respect to leaf length. It resembles *H. polycarpus*, and pendulous forms of *H. wilsonii* but differs from these by its auriculate lamina base.

Amazonas: Chachapoyas, Leimebamba–Lajasbamba trail, *Boeke 2059* (MO, US, USM). San Martín: Prov. Mariscal Cáceres, Río Abiseo National Park, NW sector, Valle de Chochos, 3450 m, *León 2161* (AAU, USM).

39. *Huperzia curvifolia* (Kunze) Holub, *Folia Geobot. Phytotax.* 20: 72. 1985.

Lycopodium curvifolium Kunze, *Linnaea* 9: 5. 1835. TYPE: Peru (Dept. Huánuco), sylv. densarum arboribus prope Pampayaco (Pampayacu), 1829, *Poeppig* (LZ, holotype, destroyed; isotypes, AWH!, B!, BR!, E!, G!, K!, M!, NY!, W!).

Lycopodium tenue Willd. var. *tenuissimum* Spring, *Mém. Acad. roy. Belg.* 24 [Mon. Lyc. 2]: 21. 1849, based on *L. curvifolium* Kunze and with the same type.

Urostachys curvifolius (Kunze) Nessel, *Bärlappgewächse* 129. 1939.

Plants delicate to extremely delicate, flaccidly pendulous, up to 60 cm long. **Shoots** gradually (rarely abruptly) heterophyllous, 2.5–6 mm in diameter including the leaves in basal divisions, tapering to 0.3–1.5(–2) mm in diameter including leaves in terminal divisions. **Stems** excluding leaves 0.4–0.7 mm thick at the base, tapering to 0.2–0.4 mm upward, usually not concealed by leaves. **Leaves of basal divisions** borne in alternating whorls of 4–5, patently sigmoid to strongly falcately upward curved, acicular-filiform, long and widely decurrent, 2–4(–5) mm long, 0.2–0.3 mm wide at the base, extremely delicate, abaxially convex, flat or canaliculate adaxially. **Vegetative leaves of terminal constricted divisions** alternate, or borne in alternating irregular whorls of 3, closely appressed, lanceolate to linear-lanceolate, somewhat clasping with the base, 1.2–3.5 mm long, 0.2–0.6 mm wide at the base, usually strongly involute, often sharply carinate at the base, short to long decurrent. **Sporophylls** usually few and scattered, often unilateral, conform, or shorter and wider, lanceolate to widely ovate, or subcordate and short to long acuminate, usually widely spreading, 1–3 mm long, 0.3–0.8 mm wide, sometimes scarcely exceeding the sporangia, abaxially with a prominent vein, or carinate. **Sporangia** 0.6–0.8 mm wide.

Epiphytic in lower, wet montane forest, alt. 400–1750 m, San Martín, Ucayali, Huánuco.

Costa Rica to Peru.

Huperzia curvifolia is variable in size and compactness, seemingly not only as a response to environmental factors. It is easy to recognize by the strongly upward curved leaves of basal divisions and the appressed non-sporangiate leaves of the terminal divisions. The smallest forms with hair-like terminal shoots represent the most fragile and slender extreme known in the family. Only these are represented in Peru. They correspond to the type collection. Other, stronger forms to the north in the Andes and in Central America approach slender forms of *H. acerosa* and *H. filiformis*.

San Martín: Boquerón pass, 92 km from Tingo María on road to Pucallpa, 400 m, *Allard 22098* (us). Prov. Rioja, Pedro Ruíz–Moyobamba road, km 390, Vencermos, 1750 m, *D. Smith 4372A* (usm). **Ucayali** (as Loreto): Prov. Coronel Portillo, Boquerón Padre Abad, 400 m, *J. Schunke V. 3046* (F, GH, US), 480 m, *Hutchison et al. 6054* (F, GH, UC, US, USM).

40. *Huperzia tenuis* (Willd.) Trev., *Atti Soc. Ital. Sci. Nat.* 17: 248. 1874.

Lycopodium tenue Willd., *Sp. pl. ed.* 4, 5: 55. 1810. TYPE: Ecuador, Valley of Vinajacu, near Loja, *Humboldt & Bonpland 3363* (holotype, B, *Herb. Willd.* 19423!; isotypes, BM!, LG!, P!).

Urostachys tenuis (Willd.) Nessel, *Arch. Bot. Est. S. Paulo* 1: 401. 1927.

Plants delicate to extremely delicate, flaccidly pendulous, at least up to 75 cm long. **Shoots** gradually heterophyllous, 3–8 mm in diameter including the leaves in the basal divisions, tapering to 1–3 mm. **Stems** excluding leaves 0.5–0.7 mm thick at the base, tapering to ca. 0.3 mm upward. **Leaves of basal divisions** borne in irregular alternating whorls of 3–5, or spirally arranged, forming 6–10 indistinct longitudinal ranks, usually densely crowded, spreading to ascending, straight to somewhat curved, often secund, acicular, tapering from a subauriculate base, 3–5(–7) mm long, 0.3–0.5 mm wide, decurrent. **Vegetative leaves and sporophylls of constricted terminal divisions** almost conform, borne in alternating irregular whorls of 3, or irregularly alternate, patently diverging from the stem, with upward curved tips, widely ovate to subhastate, 1–3 mm long, 0.5–1.4 mm wide, clasping at base, tapering to abruptly narrowed into a short to long acuminate apex, bluntly to sharply carinate, usually unilaterally, discontinuously, but often densely sporangiate. **Sporangia** 0.8–1.2 mm wide.

Usually epiphytic, in high montane forests, alt. 1350–3300 m, Amazonas, San Martín, Cuzco.

Costa Rica; Andes from Venezuela to Peru.

Huperzia tenuis exhibits the same type of size variation as mentioned for *H. curvifolia*. Some forms are as extremely fragile and slender but differ by the spreading leaves in terminal divisions. The typical forms of the species are also ecologically distinct, being restricted to the uppermost montane forests, while the extremely thin forms (*Ll. Williams 7348* and *Spruce 4621*) appear to occur only at lower altitudes.

Amazonas: Prov. Chachapoyas, Cerros Calla Calla, 18 km above Leimebamba on road to Balsas, 3000–3100 m, *Hutchison & Wright 6932* (F, GH, MO, NY, UC, US, USM); *Wurdack 1762* (F, G, GH, K, NY, S, UC, USM). **San Martín:** Tarapoto, Monte Campana, *Spruce 4621* (BM, BR, P). Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, Puerta del Monte, 3100–3300 m, *Young & León 4458* (AAU). Prov. Mariscal Cáceres, Chochos valley, 3100 m, *Young 2667* (AAU, USM). San Roque, 1350–1500 m, *Ll. Williams 7348* (F, US). **Cuzco:** Camino a Huarcan, caqui Acobamba [Ocobamba], Valle Neapillo, 2400 m, *Bües 1376* (NY). **Department unknown:** *Poeppig* in 1829 (MO). *Lehmann 5021* (F, GH, US).

41. *Huperzia molongensis* (Herter) Holub, *Folia Geobot. Phytotax.* 20: 75. 1985.

Lycopodium molongense Herter, *Bot. Jahrb.* 43: Beibl. 98: 51. 1909. TYPE: “Molong,” *Pearce* (holotype, K!) [erroneously as “Östaustralische Provinz: Gebirgswälder Neu-Süd-Wales” in the protologue].

Urostachys molongensis (Herter) Nessel, *Bärlappgewächse* 240. 1939.

Plants robust to very robust, pendulous, at least up to 150 cm long. **Shoots** heterophyllous, usually not sharply differentiated, 20–35 mm in diameter including the expanded leaves in basal divisions, distally gradually to abruptly constricted to 3–8 mm in diameter including the shorter, imbricate leaves in the terminal divisions. **Stems** excluding leaves 2–3.5 mm thick at the base, tapering to 1–1.5 mm. **Expanded leaves of basal divisions** borne in alternating whorls of 3, patent to ascending, or slightly recurved, lanceolate to lanceolate-ovate, acute, 10–18 mm long, 3–6(–7) mm wide, flat, or with slightly revolute margins, coriaceous, often shining, usually twisted at the base. **Leaves of constricted divisions** decussate or subdecussate, imbricate, discontinuously sporangiate, ovate to subcordate, acute, sharply carinate and clasping with the base, usually conduplicate in the apex, usually

shining, (2.5–)3–10 mm long, 3–6 mm wide. **Sporangia** 1.5–2.5 mm in diameter.

Usually epiphytic, in montane, wet cloud forest on the eastern Andean slopes, 3100–3550 m, Amazonas, San Martín.

Andes of Venezuela, south to northern Peru.

This species is easily distinguished because of its large size and the sharply quadrangular terminal divisions. The expanded leaves are sometimes developed only along a very short portion of the stem base and are sometimes lacking in herbarium specimens.

Amazonas: Prov. Chachapoyas, Leimebamba, road to Balsas, 3240 m, *Luteyn 11370* (NY). Cerros Calla Calla, 3450–3550 m, *Wurdack 1707* (F, GH, NY, US); 3360 m, *Hutchison & Wright 6998* (C, E, F, G, GH, K, M, MO, NY, S, UC, US). **San Martín:** Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, trail to Mirador, 3100–3300 m, *Young & León 4457* (AAU). Prov. Mariscal Cáceres, Río Abiseo National Park, Puerta de Monte, 3400 m, *León & Young 1308* (AAU). Prov. Mariscal Cáceres, Río Abiseo National Park, Chochos Valley, 3100 m, *Young 2620* (AAU).

42. *Huperzia campiana* B. Øllg., in Harling and Andersson, *Flora of Ecuador* 33: 109. 1988. TYPE: Ecuador, Prov. Loja, E of Nudo de Cajanuma, *Øllgaard et al. 57861* (holotype, AAU!; isotype, QCA!).

Plants rather robust, pendulous, at least up to 1 m long. **Shoots** heterophyllous, the basal divisions ca. (15–)20–30 mm in diameter including the expanded leaves, the distal quadrangular divisions abruptly constricted to 2–4 mm thick including the imbricate, reduced leaves. **Stems** excluding leaves 2–4 mm thick at the base, tapering to 0.5–1.5 mm, pale greenish or brownish. **Expanded leaves of basal divisions** usually uniform throughout, borne in alternating whorls of 3, spreading to perpendicular, lanceolate to widely lanceolate-ovate, usually widest below the middle, (7.5–)10–15 mm long, 2.5–4(–4.5) mm wide, often somewhat shorter near the contraction of the shoot, twisted at the base, with flat to revolute margins, herbaceous to subcoriaceous, dull to somewhat shining. **Leaves of terminal constricted divisions** decussate, or rarely in alternating whorls of 3 near the base of constricted divisions, usually sporangiate throughout, appressed and clasping with their bases, bluntly to sharply carinate, widely ovate to triangular-ovate, short-acuminate or mucronulate, 2–3 mm long, 1.5–2 mm wide, the sporo-

phylls equalling or slightly exceeding the sporangia. **Sporangia** 1.2–2 mm in diameter.

Epiphytic in upper cloud forest and elfin forest, alt. 2400–3500 m, San Martín, Huánuco.

Ecuador; Peru.

Bryan 719 deviates from typical *Huperzia campiana* by the relatively wide expanded leaves and slightly thicker constricted divisions.

San Martín: Prov. Mariscal Cáceres, Río Abiseo National Park, NW sector, Valle de Chochos, 3450 m, *León 2179* (AAU). **Huánuco:** Cushi, trail to Tambo de Vaca, *Bryan 719A* (F, G, US).

43. *Huperzia heteroclita* (Poirot) Holub, *Folia Geobot. Phytotax.* 20: 73. 1985.

Lycopodium heteroclitum Poirot, in Lam., *Encycl.* 3: 554. 1814 [1813]. LECTOTYPE (designated by Øllgaard in Harling and Andersson, *Fl. Ecuador* 33: 112. 1988): America calidiore, *Herbier de A. N. Desvaux* (p!).

Plants pendulous, lax, at least up to 80 cm (possibly to 400 cm) long. **Shoots** heterophyllous, with expanded, perpendicular leaves, often only in the first 5–20 cm of the basal divisions, upward abruptly constricted, sharply to bluntly quadrangular, 2–3 mm thick including the small, imbricate leaves, the constricted divisions often interrupted by short zones with expanded leaves. **Stems** excluding leaves 1–1.7 mm thick at the base, tapering to 0.7–1 mm, often bright red. **Expanded leaves** decussate, or subdecussate, perpendicular to the stem, lanceolate to widely lanceolate, widest in the middle, acute, 6–9 mm long, 2–3.5 mm wide, soft-herbaceous, usually twisted at the base. **Leaves of constricted divisions** decussate, closely imbricate, usually discontinuously sporangiate, ovate-cordate, acute, bluntly to sharply carinate to conduplicate in the apex, 1.5–4 mm long, 2–2.5 mm wide, dull, sometimes with shallowly erose, or indistinctly dentate margins. **Sporangia** ca. 1.5 mm wide.

Epiphytic in upper wet montane forest, ca. 2100 m, Amazonas.

Southern Ecuador and northern Peru.

The species is usually recognizable by its long, sharply quadrangular constricted shoots with extensive non-sporangiate zones and sharply carinate, apically conduplicate leaves. However, the specimen cited below deviates from the typical in the terete rather than sharply quadrangular con-

stricted divisions and is tentatively referred to this species.

Amazonas: Leimebamba, 2100 m, *Woytkowski 7749* (F, MO, NY, USM).

44. *Huperzia ericifolia* (Presl) Holub, *Folia Geobot. Phytotax.* 20: 72. 1985.

Lycopodium ericaefolium Presl, *Reliq. haenk.* 1: 77. 1825. TYPE: "Peruvia, verosimiliter Luzon," *Haenke* (holotype, PRC!; isotype, BR!). *Urostachys phlegmaria* (L.) Herter var. *ericaefolius* (Presl) Nessel, *Bärlappgewächse* 217. 1939.

Plants slender, pendulous, at least up to 6 cm long. **Shoots** heterophyllous, in the basal divisions ca. 8–14 mm in diameter including the expanded leaves, then abruptly constricted to 1.5–2 mm including the imbricate, reduced leaves of the quadrangular, terminal divisions. **Stems** excluding leaves ca. 1 mm thick, tapering to ca. 0.5 mm, pale greenish. **Expanded leaves** usually uniform in position, shape and size throughout, borne in alternating whorls of 3, or decussate upward, almost continuously overlapping throughout (pressed specimens), widely lanceolate to oblong-lanceolate, acute to obtuse and mucronate, 7–9 mm long, 2–3 mm wide, with slightly revolute margins, the lamina usually twisted at the base to a vertical position. **Leaves of terminal, constricted divisions** decussate, discontinuously sporangiate, appressed and clasping with their bases, carinate to conduplicate in the apex, lanceolate to ovate- or triangular-ovate, short to long acuminate, 2–4 mm long, 1.5–2 mm wide, the sporangiate leaves 1.5–2.5 × longer than the sporangia. **Sporangia** 1–1.5 mm wide.

Wet lower montane forest, alt. 625–2040 m, San Martín, Huánuco.

Ecuador to Bolivia.

Huperzia ericifolia is closely related to *H. dichaeoides* (Maxon) Holub (Central America to Ecuador) and *H. aqualupiana* (West Indies, N Venezuela to NW Colombia). Its distinctness from the latter is doubtful, although *H. ericifolia* can usually be distinguished by its narrower, more acute expanded leaves in whorls of three, while *H. aqualupiana* usually has ovate, subacute to obtuse, decussate expanded leaves.

Problems of typification were discussed by Øllgaard in Harling and Andersson, *Fl. Ecuador* 33: 113. 1988.

San Martín: Prov. Rioja, Pedro Ruíz–Moyobamba road, km 390, Venceremos, 2040 m, *Smith & Vásquez 4589* (AAU, USM). Tingo María, 625–1100 m, *Allard 20935* (US). **Huánuco:** SW slope of Río Llullapichis watershed, ascent of Cerros del Sira, 1290 m, *Dudley 13029* (GH, US).

45. *Huperzia myrsinites* (Lam.) Trev., Atti Soc. Ital. Sci. Nat. 17: 249. 1874.

Lycopodium myrsinites Lam., Encycl. Méth. Bot. 3: 654. 1789. TYPE: Dominican Republic, "S. Domingue," *Comm. Joseph Martin*, (holotype, P, Herb. Lam!).

Urostachys myrsinites (Lam.) Herter, Repert. Spec. Nov. Regni Veg. 19: 166. 1923.

Lycopodium skutchii Maxon, Proc. Biol. Soc. Wash. 46: 159 (1933). TYPE: Guatemala, Chimaltenango, Chichavac, alt. 2400–2700 m, *Skutch 243* (holotype, us!).

Plants pendulous, slender, at least up to 65 cm long. **Shoots** heterophyllous, usually not all sharply differentiated, the basal divisions 10–18 mm in diameter including the expanded leaves, distal divisions gradually or abruptly constricted to 1.5–3 mm thick including the reduced, imbricate leaves. **Stem** excluding leaves ca. 1 mm thick at the base, tapering to ca. 0.5 mm, pale greenish or reddish. **Expanded leaves of basal divisions** decussate or subdecussate, often irregularly shaped, subdistant to densely crowded and somewhat overlapping, ascending to perpendicular, ovate-lanceolate or lanceolate, acute, usually the widest ones with a rounded base, 6–11 mm long, 1.5–3 mm wide, usually flat, straight to somewhat recurved. **Leaves of terminal constricted divisions** highly variable, often with complete reduction series, and with recurrent series to expanded shape, decussate or subdecussate, continuously or discontinuously sporangiate. **Transitional leaves** with widely ovate base, and short to long acuminate apex, appressed and clasping, with the wide base abaxially rounded to bluntly carinate, with straight to recurved apex, 2.5–5 mm long, 1.5–2 mm wide. **Shortest leaves** with base conform, but with straight to falcate apex, bluntly to sharply carinate, scarcely exceeding the sporangia, ca. 2 mm long. **Sporangia** 1–1.3 mm in diameter.

Epiphytic in montane forest, ca. 2500 m, Cajamarca.

Hispaniola; Central America; Trinidad; Guyana; Venezuela to Peru.

For illustration of the species, see A. R. Smith (Pteridophytes, in Breedlove: Flora of Chiapas, part 2: 347, f. 82a–b. 1981).

Huperzia myrsinites is closely related to *H. phyllicifolia*. Species of the group of *Huperzia quadrifariata* (Bory) Rothm. (SE Brazil) were erroneously placed under *H. myrsinites* by several earlier authors.

Cajamarca: Prov. Hualgayoc, Hda. Taulis, 2500 m, *Hutchison & Bismarck 6391* (F, NY, US). Prov. Contumazá, Bosque de Cachil, 2450 m, *Sagástegui 14873* (AAU).

46. *Huperzia phyllicifolia* (Poirot) Holub, Folia Geobot. Phytotax. 20: 75. 1985.

Lycopodium phyllicifolium Poirot, in Lam., Encycl. 3: 546. 1814 [1813]. LECTOTYPE (designated by Øllgaard in Harling and Andersson, Fl. Ecuador 33: 117. 1988): "Habitat in Chili," *Herbier de A. N. Desvaux*, Donnée par Mme Vve Lavallée en 1896 (p!).

Urostachys phyllicifolius (Poirot) Nessel, Bärblappgewächse 246. 1939.

Lycopodium congestifolium Spring, Mém. Acad. roy. Belg. 15 [Mon. Lyc. 1]: 70. 1842. TYPE: Peruvia, *Dombey*, H. M. P., *Herb. Deless.* (p!).

Lycopodium nubigenum Herzog, Meded. Rijks-Herb. 27: 2. 1915. TYPE: Bolivia, Comarapa, *Herzog 1967* (holotype, L!; isotypes, B!, Z!).

Urostachys nubigenus (Herzog) Nessel, Bärblappgewächse 246. 1939.

Plants slender, pendulous, up to 150 cm long. **Shoots** heterophyllous, in the basal divisions ca. 10–20(–25) mm in diameter including the expanded leaves, then abruptly (rarely gradually) constricted to (1–)1.5–2(–2.5) mm in diameter including the imbricate, reduced leaves. **Stems** excluding leaves 0.7–1.2 mm thick at the base, upward tapering to ca. 0.5 mm, greenish to bright red. **Expanded leaves of basal divisions** borne in alternating whorls of 3, or decussate, subdecussate, or alternate, usually widely spaced in alternate-leaved stem portions, perpendicular to the stem to falcately ascending, lanceolate to linear-lanceolate, widest at or below the middle, (4–)6–10(–13) mm long, (1–)1.5–2 mm wide, softly to firmly herbaceous, with flat to slightly revolute margins, the lamina twisted to a vertical position. **Expanded leaves** near the constriction often sporangiate. **Leaves of constricted terminal divisions** decussate, or subdecussate, continuously or discontinuously sporangiate, appressed and clasping with their bases, abaxially rounded to carinate, widely lanceolate to widely ovate or subcordate, acute to mucronate or cuspidate, rarely with an elongate flat apex, 1.7–2(–4) mm long (in gradually heterophyllous shoots sometimes longer), 1–1.5 mm wide,

equalling to more than twice as long as the sporangia. **Sporangia** 1.2–1.5 mm wide.

Epiphytic or rarely rupestral in upper montane and elfin forest, 2300–3700 m, Cajamarca, Amazonas, Huánuco, Huancavelica, Apurímac, Cuzco, Puno.

Due to uncertain delimitation of the species the total distribution of this species is unsettled. In an inclusive sense it is wide-ranging: from Costa Rica, along the Andes south to northern Argentina, and SE Brazil.

Huperzia phyllicifolia occurs in a wide range of epiphytic and rupestral habitats with highly variable exposure and humidity. Its growth habit (i.e., size, leaf size, texture and crowding, and stem color), responds strongly to the environmental conditions. It is closely related to *H. myrsinites*, *H. subulata*, *H. biformis* (Hooker) Holub (Brazil), and *H. erythrocaulon* (Fée) Holub (Brasil). Forms of the species corresponding to the type of *Lycopodium nubigenum*, with expanded leaves slightly longer and widest just above the base, are prevalent in the southern part of the range (Peru, Bolivia, Argentina).

Cajamarca: Prov. Cutervo, *Jelski 1013* (P). **Amazonas:** Chachapoyas, *Matthews 1081* (G, K, P). **Huánuco:** Cani, NE of Mito, 2800 m, *Macbride 3546* (F, US). Cushi, trail to Tambo de Vaca, *Bryan 719B* (F, GH, US). **Huancavelica:** Prov. Tayacaja, Marcavalle, between Huachocolpa and Tintay, 2700 m, *Tovar 4751* (GH, USM). **Apurímac:** Prov. Abancay, Ampay, 3400–3700 m, *Vargas 8388* (MO). **Cuzco:** Prov. La Convención, Dist. Vilcabamba, Yupañqui, 2700 m, *Davis et al. 1210* (AAU, F, GH). Prov. Paucartambo, Paso de Aguila, Pillawata, 2450 m, *Vargas 22995* (GH). **Puno:** Prov. Sandia, 2300 m, *Weberbauer 633* (G, MOL). Prov. Carabaya, Ayapata–Kahuallayoc, 2600–3600 m, *Vargas 10741* (GH). Tabina, *Lechler 2023* (US).

47. *Huperzia subulata* (Poiret) Holub, *Folia Geobot. Phytotax.* 20: 77. 1985.

Lycopodium subulatum Poiret, in Lam., *Encycl.* 3: 544. 1814 [1813]. LECTOTYPE (designated by Øllgaard in Harling and Andersson, *Fl. Ecuador* 33: 119. 1988): *Herbier de A. N. Desvaux*, Donnée par Mme Vve Lavallée en 1896 (P!).

Urostachys subulatus (Poiret) Nessel, *Arch. Bot. Est. S. Paulo* 1: 420. 1927.

Urostachys ewanii Herter, *Revista Sudamer. Bot.* 10: 126–127. 1953. TYPE: Colombia, drainage of upper Río Pascual, above Córdoba, 2840 m, *Ewan 16526* (holotype, US!; isotype, NO!).

Lycopodium ewanii (Herter) Morton, *Amer. Fern J.* 54: 72. 1964.

Plants slender, pendulous, up to 2 m long. **Shoots** heterophyllous, ca. 15–25 mm in diameter including the expanded leaves in the basal divisions, abruptly constricted to 1.5–2 mm in diameter including the reduced and appressed leaves of the terminal divisions. **Stems** excluding leaves ca. 1 mm thick at the base, upward tapering to less than 0.5 mm, pale greenish to bright red. **Expanded leaves of basal divisions** borne in alternating, often irregular whorls of 3, or often upward subdecussate, spreading to perpendicular to the stem, narrowly lanceolate to linear-subulate, straight to obliquely falcate-ascending, (6–)10–15 mm long, 0.5–1 mm wide, twisted at the base, flat, soft-herbaceous. **Leaves of terminal constricted divisions** subdecussate, or in alternating whorls of 3 just above the constriction of the shoots, sporangiate almost throughout, closely imbricate, widely ovate with obtuse to acute apex, abaxially rounded to carinate, 1.3–2 mm long, 1.3–1.5 mm wide, equalling or slightly exceeding the sporangia. **Sporangia** ca. 1 mm wide.

Epiphytic, in cloud forest and elfin forest, alt. 1500–3400 m, Amazonas, San Martín, Huánuco, Cuzco.

Costa Rica; Colombia to Peru.

Huperzia subulata is closely related to *H. phyllicifolia* but seems to tolerate a narrower range of growth conditions, being restricted to the most humid forests of the eastern slopes of the Andes.

Amazonas: Prov. Bagua, Serranía de Bagua, ca. 12–18 trail km E of La Peca, 1800–1950 m, *Gentry et al. 22904* (AAU, MO, USM). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, Puerta del Monte, 3400 m, *León & Young 1340* (AAU). **Huánuco:** Pampayacu, Hda. at mouth of Río Chinchao, *Bryan 725* (F, G, US). **Cuzco:** Prov. La Convención, Cord. Vilcabamba, Hda. Luisiana–Río Apurímac, 3250 m, *Dudley 11105* (F, GH, US, USM). Prov. La Convención, Chontapampa, Valle San Miguel, 1500 m, *Bües 2987* (GH).

48. *Huperzia cuneifolia* (Hieron.) Holub, *Folia Geobot. Phytotax.* 20: 72. 1985.

Lycopodium cuneifolium Hieron., *Bot. Jahrb. Syst.* 34: 572. 1905. LECTOTYPE (designated by Nessel, *Bärlappgewächse* 252. 1939): Costa Rica, Volcán Barba, *Hoffman 50* (B!).

Urostachys cuneifolius (Hieron.) Nessel, *Bärlappgewächse* 252. 1939.

Plants pendulous, delicate, up to 60 cm long. **Shoots** heterophyllous, in the basal divisions (5–)7–13 mm in diameter including the expanded leaves,

then abruptly constricted to 1–2 mm in diameter including the reduced, imbricate leaves in the terminal, constricted, quadrangular divisions. **Stems** excluding leaves 1 mm thick, or less, at the base, tapering to ca. 0.5 mm, greenish to bright red. **Expanded leaves of basal divisions** decussate, spreading to perpendicular or slightly reflexed, spatulate to lanceolate or lanceolate-obovate, usually widest above the middle, obtuse or mucronulate, 2–6.5 mm long, 1.5–3 mm wide, flat, the lamina twisted to a vertical position, softly to firmly herbaceous. **Leaves of terminal constricted divisions** decussate, often sporangiate in rather short zones of the divisions, appressed and clasping with their bases, widely ovate to subcordate, 1.5–2 mm long, 1–1.5 mm wide, carinate, with falcate to reflexed mucronulate tips, the sporophylls equalling or slightly exceeding the sporangia. **Sporangia** ca. 1 mm wide.

Epiphytic or occasionally on banks in upper montane forest and elfin forest, ca. 3000–3100 m, Amazonas and San Martín.

Costa Rica; Andean Venezuela; Colombia and Peru.

Amazonas: Prov. Chachapoyas, Cerros Calla Calla, 19 km above Leimebamba, 3100 m, *Hutchison & Wright 6943* (F, GH, K, M, P, US); *Wurdack 1744* (F, GH, NY, US, USM). **San Martín:** Prov. Mariscal Cáceres, NW sector of Río Abiseo National Park, near Mirador, 3000–3100 m, *León 2119* (AAU).

49. ***Huperzia pruinosa*** (Herter) Holub, *Folia Geobot.* Phytotax. 20: 76. 1985.

Lycopodium pruinosum Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 52. 1909. TYPE: Peru, Dept. Amazonas, Prov. Chachapoyas, Tambo Ventillas, 2400–2600 m, *Weberbauer* (err. as Ule in protologue) 4410 (holotype, B!; isotypes, BONN, *Herb. Nessel 621!*, G!).

Lycopodium durissimum Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 52. 1909. TYPE: Peru, “Voyage à l’Equateur et au Perou, 1876–77, Guayaba mars 1877” (err. “Colombia, Guayabal” in protologue), *Vidal-Sênèze* [“Senège”] (holotype, P!; isotype, BONN, *Herb. Nessel 621!*).

Urostachys pruinosus (Herter) Nessel, *Arch. Bot. São Paulo* 1: 420. 1927.

Urostachys durissimus (Herter) Nessel, *Bärlappgewächse* 240. 1939.

Huperzia durissima (Herter) Holub, *Folia Geobot. Phytotax.* 20: 72. 1985.

Plants erect and distally recurved, unbranched or sparsely branched at base, distally with densely tassel like ramification, at least up to 70 cm long.

Shoots heterophyllous, the basal divisions with expanded leaves ca. 10–18 mm in diameter including leaves, distally abruptly constricted to ca. 2–2.5 mm including the reduced, imbricate leaves. **Stems** excluding leaves up to 5 mm thick at the base, upward tapering to ca. 0.5–1.5 cm, rigid, dark brown to purplish brown. **Expanded leaves of basal divisions** borne in alternating, irregular, distant whorls of 4, the whorls 6–9 mm apart, ascending to spreading or sharply reflexed, lanceolate, straight or recurved, (6–)8–10 mm long, 2.5–3 mm wide, acute, flat, coriaceous, with smooth, revolute margins, often adaxially concave. **Leaves of recurved, constricted divisions** subdecussate, densely crowded, sporangiate almost throughout, imbricate, widely ovate with obtuse to acute apex, abaxially rounded to carinate, 1.2–1.6 mm long and wide, equalling or slightly exceeding the sporangia. **Sporangia** 1–1.3 mm wide.

Indicated as terrestrial scandent shrub, in ceja scrub (protologue) and as an epiphyte in high *Swietenia* trees (Nessel, in Hoehne, *Fl. Bras.* 11: 88. 1955).

Endemic, Amazonas and San Martín.

The two taxonomically synonymous basionyms were published simultaneously. The epithet *pruinosa* is maintained due to the quality of its type material and greater certainty of its origin.

San Martín: Mount Organero, ceja, 1900 m, *Melin 96* (s). “Tarapoto, 1908, G. *Huebner*” (BONN, *Herb Nessel 621!*).

Comments

Huperzia polyclada (Sodirol) Rolleri and Deferrari, *Notas Mus. La Plata, Bot.* 21 (100): 156. 1988.

Lycopodium polycladum Sodirol, *Crypt. vasc. Quit.* 561. 1893. TYPE: Ecuador, Mojanda, *Sodirol* (not located).

The type locality in Ecuador contains several taxa of the *Huperzia crassa* group. Due to the absence of authoritative material and the relatively scarce information of the protologue it is not possible to certify to which of these taxa the name applies. However, none of the taxa correspond to the Peruvian material that was placed in this species by Rolleri (1980). This material is here referred to *H. darwiniana*.

II. *Lycopodium*

Lycopodium L., Sp. pl. 1100. 1753. TYPE: *Lycopodium clavatum* L. **Figure 7.**

Lepidotis Mirbel, in Lam. & Mirbel, Hist. nat. veg. 3: 477. 1802. TYPE: *Lycopodium clavatum* L.

Lycopodium subgen. *Lepidotis* Baker, Handb. Fern-Allies 8. 1887. TYPE: *Lycopodium clavatum* L.

Lycopodium subgen. *Rhopalostachya* Pritzl, Nat. Pflanzenfam. 1 (4): 601. 1901. TYPE: *Lycopodium clavatum* L.

Diphasiastrum Holub, Preslia 47: 104. 1975. TYPE: *Lycopodium complanatum* L.

Diphasium Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 64. 1944. TYPE: *Diphasium jussiaei* (Poir.) Rothm. (= *Lycopodium jussiaei* Poir.).

Austrolycopodium Holub, Folia Geobot. Phytotax. 26: 87, 91. 1991. TYPE: *Lepidotis magellanica* Beauv. (= *Lycopodium magellanicum* (Beauv.) Sw.).

Plants anisotomously branched, with elongate, indeterminate, subterranean, creeping, or scandent, plectostelic main stems (rhizomes), which, in a dorsolateral position, give rise to usually determinate, ascending to erect, dendroid or spreading, repeatedly inclinate-bilaterally branched, branchlet systems. **Roots** emerging directly along the underside of main stems, with plectostelic main roots. **Branchlet leaves** uniform or anisophyllous. **Strobili** erect, simple or forked, sessile or borne on simple or forked peduncles. **Sporophylls** peltate without a basal mucilage cavity, or subpeltate with a thin basal decurrent wing and with a basal mucilage cavity. **Sporangia** attached to the sporophyll

Key to Species of *Lycopodium*

- a. Branchlets radially symmetrical, isophyllous b
- b. Branchlet leaves with a colorless hair tip, or a colorless membranous apex; sporophylls subpeltate, with a basispic, membranous wing on the stalk (sect. *Lycopodium*) c
- c. Branchlet leaves hair-tipped, or with a short membranous apex; branchlets green; strobili sessile or borne on short or long, simple or branched peduncles 1. **L. clavatum**
- c. Apical half or more of branchlet leaves colorless, membranous; branchlets grayish to silvery white; strobili sessile or borne on short, simple, indistinct peduncles 2. **L. vestitum**
- b. Branchlet leaves green throughout, without membranous or hairlike tips; sporophylls peltate, with a slender, terete, wingless stalk (sect. *Magellanica*) 3. **L. magellanicum**
- a. Branchlets dorsiventral, flattened, anisophyllous, with dimorphic or trimorphic leaves d
- d. Branchlet leaves decussate, arranged in 4 ranks, with widened lateral leaves, and 1 rank of dorsal and 1 rank of ventral, median narrow leaves (sect. *Complanata*) 5. **L. thyoides**
- d. Branchlet leaves alternate, with 2 ranks of wide, dorsolateral leaves, and ca. 3 indistinct ranks of narrow, ventral, apically membranous leaves (sect. *Diphasium*) 4. **L. jussiaei**

base, reniform, with a short thick stalk, isovalvate or slightly anisovalvate, their epidermis cells with thin, lignified, sinuate side walls, without partial thickenings. **Spores** reticulate. **Gametophytes** obconic to convoluted disc-shaped, subterranean, mycoparasitic, lacking pluricellular uniseriate trichomes among the gametangia.

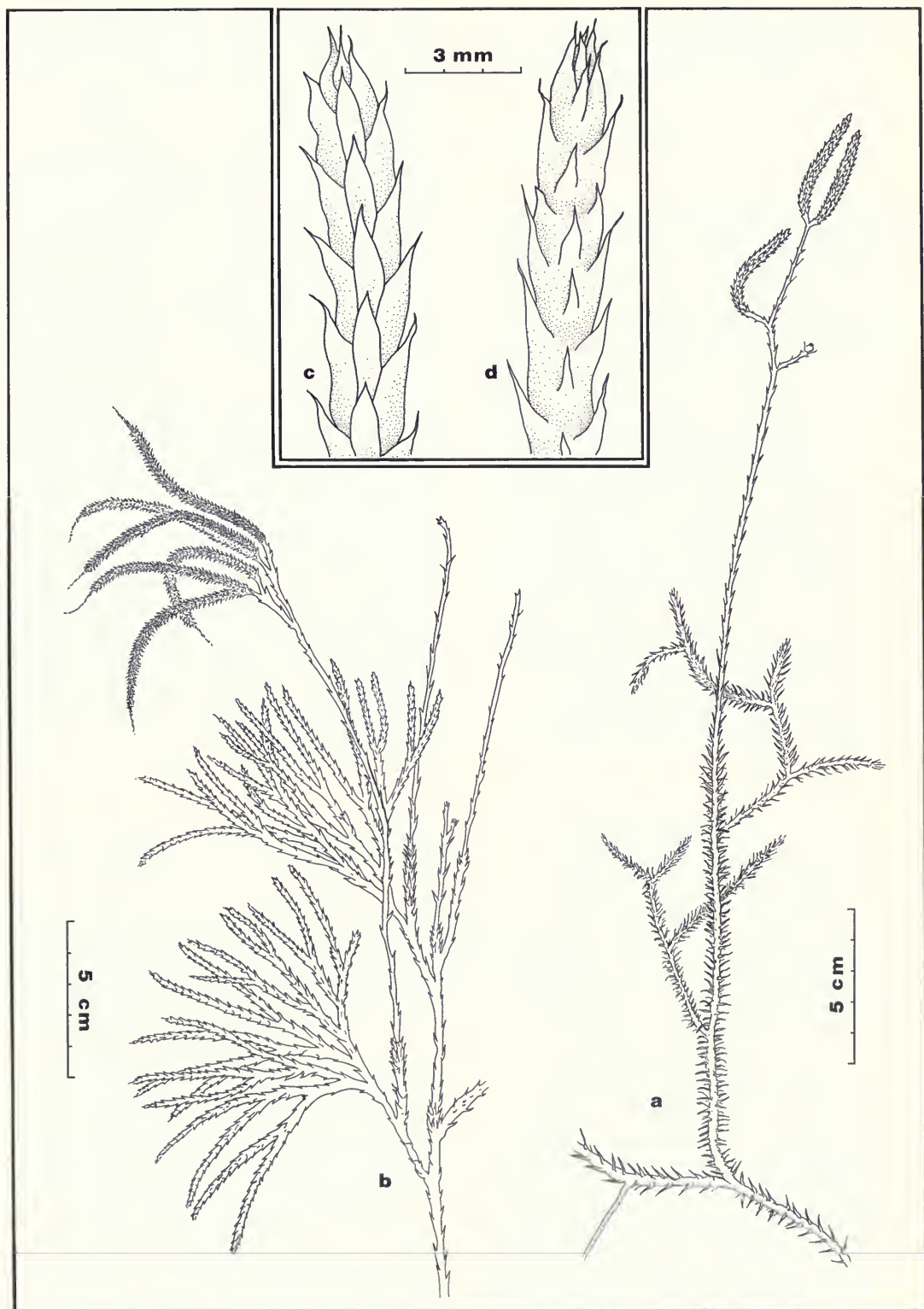
The generic description and synonymy above includes only the Neotropical representatives. For a fuller general treatment of the genus, see Øllgaard (1987).

The genus *Lycopodium* as here circumscribed has perhaps 40 species mainly in temperate regions of both the Northern and Southern Hemispheres, with eight species in the Neotropics and five in Peru, all of these, except *L. vestitum*, with wide distributions. It includes several of the genera of Holub (1975, 1983, 1985, 1991), also advocated by Wagner and Beitel (1992). These genera correspond to the sections in Øllgaard (1987, 1989). Four of the nine sections are represented in the Neotropics. These sections are very distinct groups of species. None of them are connected by intermediate species or by intersectional hybrids.

Reference

WILCE, J. H. 1965. Section *Complanata* of the genus *Lycopodium*. *Beih. Nova Hedw.* 19: I-IX, 1-233, t. 1-40.

FIG. 7. *Lycopodium clavatum*: a, aerial shoot, habit. *Lycopodium thyoides*: b, aerial shoot, habit; c, tip of branchlet, adaxial side; d, tip of branchlet, abaxial side. (Adapted from Stolze, Ferns and fern allies of Guatemala, 1983.)



1. *Lycopodium clavatum* L., Sp. pl. 1101. 1753.
LECTOTYPE: *Herb. Burser XX: 49* (UPS, designated by Jonsell & Jarvis, *Regnum Veg.* 127: 63. 1993).

Lepidotis clavata (L.) Beauv., *Prod. Aetheogamie* 108. 1805.

Plants creeping, trailing, or hanging over banks. **Main stem** usually above ground with ascending to stiffly erect, up to at least 50 cm tall, repeatedly unequally branched aerial shoots, with strongly diverging to almost parallel branchlets. **Ultimate branchlets** terete. **Leaves** borne in low alternating spirals or whorls of 6–8(–10), patent to ascending or imbricate, linear-acicular, 6–8(–10) mm long and 0.5–0.8 mm wide, terminating in a long colorless trichome or short membranous apex, with smooth to sparsely denticulate margins. **Strobili** sessile or pedunculate. **Peduncles**, if present, erect, up to 30 cm long, simple, or branched and bearing up to 6 pedicellate strobili. **Strobili** 1.5–6(–8) cm long, ca. 6 mm in diameter including sporophylls, sometimes forked. **Sporophylls** borne in alternating whorls of 5–6, subpeltate, with triangular-ovate to rhombic-ovate, acuminate exterior face, with usually widely scarious, dentate to erose-laciniate margins. **Sporangia** 1.3–1.6 mm wide, their epidermal cells with strongly sinuate side walls with pocket-like in- and evaginations. **Spores** reticulate on all faces.

Key to Subspecies of *Lycopodium clavatum*

- a. Strobili rarely forked, borne on elongate, simple or branched peduncles; aerial shoots amply branched, with more or less diverging branchlets; sporophylls short to long acuminate 1a. ssp. **clavatum**
a. Strobili sessile, or borne on short, simple, often indistinct peduncles, frequently forked; aerial shoots sparsely branched, usually stiffly erect, with parallel branchlets; sporophylls usually with a long, wide, scarious apex 1b. ssp. **contiguum**

1a. *Lycopodium clavatum* ssp. **clavatum**

Lycopodium aristatum Willd., in L., Sp. pl. ed. 4, 5: 17. 1810. TYPE: Venezuela, Silla de Caracas, *Humboldt & Bonpland* (holotype, B, *Herb. Willd.* 19351!).

Lycopodium piliferum Raddi, Pl. Bras. nov. gen. 1: 79, t. 3. 1825. Based on *L. aristatum* Willd. and with the same type.

Lycopodium trichophyllum Desv., Mém. Soc. Linn. Paris 6: 184. 1827 [as *trychophyllum*]. LECTOTYPE (designated by Øllgaard in Harling and Andersson, Fl. Ecuador 33: 125. 1988): "Habitat in

Almost cosmopolitan, in humid temperate and boreal regions of the Northern Hemisphere and on tropical mountains in the Old and New World. The species is highly variable and adaptive to external factors. The discovery of tetraploids in Japan indicates that genetic variation is also involved. There is as yet no indication of polyploidy in the Neotropical representatives of the species.

Lycopodium clavatum varies almost continuously from amply branched plants with diverging branches and spreading, soft leaves, and long-branched peduncles, growing in moist, warm, sheltered habitats, to small, compact, parallel-branched plants with more imbricate and firm leaves, and lacking, or short, simple or once forked peduncles, belonging to cold, exposed habitats. The latter forms are here recognized as ssp. *contiguum*. Corresponding monostachyous forms are found in the Arctic and high mountains of New Guinea. The two subspecies recognized here are often considered to be distinct species. However, there are many intermediate forms that cannot be placed in one or the other taxon with certainty. These intermediates form normal spores and have normal meiosis. Also there are rare examples of single individuals showing characters of one subspecies in the growth of one year and of the other the following year. As the two forms are usually recognizable and are ecologically rather distinct, I treat them as subspecies.

Brasilia, no. 41 in *herb. de A. N. Desvaux*, Donnée par Mme Vve Lavallée en 1895" (P!).

Lycopodium clavatum L. var. *aristatum* (Willd.) Spring, *Flora* 21 (1): 173. 1838.

Lycopodium eriostachys Fée, *Crypt. Vasc. Brésil* 1: 224. 1869. TYPE: Brasilia fluminensi, Serra dos Orgaos, *Glaziou 1788* (BR!, C!, P!, RB!).

Clearings exposed habitats in montane forest, 700–3200 m, Piura, Cajamarca, Amazonas, La Libertad, San Martín, Loreto, Huánuco, Pasco, Junín, Ucayali, Ayacucho, Cuzco, Puno.

Humid temperate and boreal regions of the Northern Hemisphere, montane in the tropics. Absent from Australia.

For more complete synonymy, see Øllgaard (1988).

Cajamarca: Prov. Cutervo, Cutervo–Socota, 2320 m, *López & Sagástegui 5331* (F, MO). Prov. Hualgayoc, Culquirrumi, 2448 m, *Sánchez Vega 2099* (AAU). **Amazonas:** Prov. Chachapoyas, Pipus, between Chachapoyas and Molinopampa, 2100 m, *Sánchez Vega et al. 2180* (AAU). **La Libertad:** Prov. Bolívar, above Longotea, 2800 m, *Sagástegui 14189* (F). **San Martín:** Prov. Rioja, Pedro Ruíz–Moyobamba road, km 390–394, Venceremos, 1910–2040 m, *D. Smith 4524* (AAU). Zepelacio, near Moyobamba, 1100–1600 m, *Klug 3360* (MO, S, US). Tarapoto, *Spruce 4732* (BR, E, G, P, US). **Huánuco:** Prov. Leoncio Prado, Dist. Rupa Rupa, near Tingo María, 700 m, *King 337* (F). Prov. Huánuco, Dist. Churubamba, Santo Toribio, 1500 m, *Mexia 8144* (F, MO, S, UC, US). **Pasco:** Prov. Oxapampa, Cord. San Gutardo, 2600 m, *León 512* (AAU). Cord. Yanachaga, 12 km E of Oxapampa–Villa Rica road, 2100–2200 m, *Gentry & Smith 35922* (AAU). **Junín:** Prov. Tarma, Chanchamayo Valley, above La Merced at Cumbre Yacunay, 2000 m, *Hutchison 1194* (F, M, S, UC, US). Huacapistana, *Killip & Smith 24255* (US). **Ucayali:** Prov. Coronel Portillo, La Divisoria, ca. 20 km NNE of Tingo María on road to Pucallpa, 1600 m, *Dillon 2641* (F). **Ayacucho:** Prov. La Mar, eastern Massif of Cord. Central opposing the Cord. Vilcabamba, between Tambo, San Miguel, Ayna and Hda. Luisiana, 1300 m, *Dudley 11953* (F). Cearapa, *Killip & Smith 22459* (US). **Cuzco:** Valle del Urubamba, Machu Picchu, 2400 m, *Herrera 3197* (C, F). Tres Cruces, *Gentry et al. 23458* (US). **Puno:** Below Limbani, 3100–3200 m, *Brandbyge 523* (AAU). At Lake Titicaca near Huancano, 2000 m, *Charpin AC-12704* (G).

1b. *Lycopodium clavatum* ssp. *contiguum* (Klotzsch) B. Øllg. in Harling & Andersson, *Flora of Ecuador* 33: 126. 1988.

Lycopodium contiguum Klotzsch, *Linnaea* 18: 519. 1844. LECTOTYPE (designated by Øllgaard in Harling & Andersson, *Flora of Ecuador* 33: 126. 1988): Ecuador, Páramo de Tiopullo [between Cotopaxi and Illiniza], *Hartweg 1474* (B!; isolecotypes, BM!, GL!, K!, NY!, P!).

Lycopodium vestitum Poiret, var. *herbaceum* Spring, *Mém. Acad. roy. Belg.* 24 [Mon. Lyc. 2]: 45. 1849. TYPE: Colombia, Sierra Nevada, *Moritz* (holotype, B!; isotype, LG!).

Lycopodium clavatum L. var. *pseudo-contiguum* Christ, *Primitiae Fl. Costar.* 3 (1): 55. 1901. TYPE: Costa Rica, Cerro de las Vueltas, 3000 m, versant W du massif de Buena Vista, *Pittier 10467* (holotype?, BR!; isotype?, P!).

Lycopodium herbaceum (Spring) Hieron., *Bot. Jahrb. Syst.* 34: 575. 1905.

Clearings and exposed habitats in uppermost montane forest and in grass páramo, frequent in

disturbed páramo, 2600–3800 m, Piura, Cajamarca, Amazonas, San Martín, Ancash, Pasco, Huancavelica, Apurímac, Cuzco.

Costa Rica; Andes from Venezuela to Peru.

For more complete synonymy, see Øllgaard (1988).

Piura: Prov. Huancabamba, Cuello del Indio, 2800 m, *López et al. 8883* (AAU). **Cajamarca:** Prov. San Miguel, near El Tingo (Agua Blanca), 3100 m, *Mostacero et al. 1130* (AAU). Cutervo, *Jelski 1016* (US). **Amazonas:** Prov. Chachapoyas, Saullamur–Calla Calla, 3250 m, *Sánchez Vega et al. 2136* (AAU). **San Martín:** Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, 3500 m, *Young & León 4712* (AAU). **Ancash:** Prov. Carhuaz, Huascarán National Park, Quebrada Ishinca, 3900 m, *D. Smith et al. 9588 A* (AAU). Prov. Yungay, Huascarán National Park, Quebrada Ranincuray, 3850 m, *D. Smith et al. 9067* (USM). **Pasco:** Prov. Oxapampa, Dist. Huancabamba; Sta. Barbara, above Lanturachi, 3300–3500 m, *Foster et al. 10398* (AAU). **Huancavelica:** Prov. Tayacaja, Montepungo, 5 km E of Surcubamba, 300 m, *Stork & Horton 10386* (F). Prov. Tayacaja, vicinity of Huachocolpa, 3000–3100 m, *Tovar 3950* (USM). **Apurímac:** Prov. Abancay, Cerro Turrónmocco, NW of Nevado Ampay, 3500 m, *Brandbyge 422* (AAU). **Cuzco:** Prov. Urubamba, Antakillqa, 3300 m, *Franquemont 285* (F).

2. *Lycopodium vestitum* Poiret, in Lam., *Encycl.* 3: 546. 1814. LECTOTYPE (designated by Øllgaard in Harling & Andersson, *Flora of Ecuador* 33: 128. 1988): Ecuador (Prov. Loja), prope Loxam, *Humboldt* (P-Humboldt!; isotypes, B, *Herb. Willd. 19428!*, BR!, LG!, US!).

Lycopodium scariosum Hooker, *Icon. Pl.* 1: t. 89. 1836, not Forst. TYPE: Peru, Casapi, *Matthews 1765* (holotype, K!; isotype, NY!).

Lycopodium albidum Baker, *J. Bot.* 25: 37. 1887. TYPE: Ecuador, Prov. Loja, Mataba 1883, *Hübeck* (holotype, K!).

Rhizome creeping, scrambling or hanging over banks, usually above ground, 3–5 mm in diameter including leaves. **Aerial shoot systems** stiffly erect, sparsely branched, with almost parallel branches, silvery whitish. **Branchlet leaves** appressed, linear-lanceolate, 5–9 mm long, 0.6–0.8 mm wide, herbaceous in less than half of their length, with colorless, translucent, membranous, slightly widened, coarsely erose-laciniate apex. **Strobili** sessile or borne on a short, simple, indistinct peduncle. **Sporophylls** borne in alternating whorls of 5–6, subpeltate, 5–7 mm long, 1.5–2 mm wide, narrowly triangular-ovate, with a long membranous apex, with widely membranous, erose-dentate to laciniate margins. **Sporangia** 1.2–2 mm wide, their epidermis cells with strongly sinuate

side walls with pocketlike evaginations. **Spores** reticulate on all faces.

Clearings, road banks, and exposed sites in upper montane forest, and in the lower páramos, 2400–3500 m, Piura, Cajamarca, Amazonas, San Martín.

Southern Ecuador and northern Peru.

Lycopodium vestitum is closely related to *L. clavatum*, especially to ssp. *contiguum*. In spite of the striking appearance of this species, it is only doubtfully distinct from *L. clavatum*. Individuals with intermediate characters between *L. vestitum* and both subspecies are frequent. These have normal meiosis and normal spores.

Piura: Prov. Huancabamba, Cord. Chinguela (Sapalache–El Carmen), 2900 m, *Sagástegui et al. 10223* (AAU). Above Huancabamba, 3400–3500 m, *Weberbauer 6145* (F, GH, US). **Cajamarca:** Prov. Cutervo, Fortaleza de Santa Cruz, San Andrés, 2400 m, *Llatas & Suarez 2866* (F). Cutervo, *Jelski 990* (P), *994, 1007* (KRA). **Amazonas:** Prov. Bagua, Cord. Colán E of La Peca, 3200 m, *Barbour 3261* (AAU). Prov. Chachapoyas, Cerros Calla Calla, E side, 19 km above Leimebamba on road to Balsas, 3100 m, *Hutchison & Wright 5545* (F, GH, MO, P, UC, US, USM). **San Martín:** Río Abiseo National Park, Mariscal Cáceres, NW corner of the Park, 3300 m, *Young 2754* (AAU, USM). Río Abiseo National park, Mariscal Cáceres, Laguna del Eco, Chochos, 3450 m, *Young & León 4901* (USM).

3. *Lycopodium magellanicum* (Beauv.) Sw., Syn. Fil. 180. 1806.

Lepidotis magellanica Beauv., Prod. Aetheogamie 102. 1805. TYPE: Fretum magellanicum, unknown collector (holotype presumably in G, *Herb. Lessert n.v.*; isotype, P!, *Herb. Palisot de Beauvois, comm. M. de Jussieu*).

Lycopodium spurium Willd., Sp. pl. ed. 4, 5: 28. 1810. TYPE: Ecuador (Prov. Tungurahua), Quito, in vulcano Tungurahua, *Humboldt* (holotype, B, *Herb. Willd. 19364*).

Lycopodium pichinchense Hooker, Icon. pl. 1: t. 85. 1837. LECTOTYPE (designated by B. Øllgaard, Biol. Skr. Dan. Vid. Selsk. 34: 62. 1989): Ecuador, Pichincha, 10,000 ft, *Col. Hall (38?)* (K!).

Austrolycopodium magellanicum (Beauv.) Holub, Folia Geobot. Phytotax. 26: 91. 1991.

Rhizome subterranean or occasionally above ground, 1–2 mm thick excluding leaves. **Aerial shoots** ca. 1 mm thick excluding leaves at origin, up to 25 cm long excluding peduncles and strobili, repeatedly unequally branched, with spreading to ascending branchlets. **Branchlets** 4–7 mm in diameter including leaves. **Branchlet leaves** acicular, flattened, smooth, with a long, pointed, non-piliferous apex, 3–5 mm long, 0.6–0.8 mm wide. **Strobili** sessile, or terminating somewhat indistinct, simple or up to twice-forked peduncles, 3–4 mm thick, 2–10(–15) cm long, often forked. **Sporophylls** borne in alternating whorls of 4, peltate, with a slender, terete, wingless stalk, with widely ovate, short to long acuminate exterior face attached to the stalk near the center, with narrowly scarious, almost smooth to shallowly erose-denticulate margins. **Sporangia** ca. 2 mm wide; sporangium epidermis with evenly sinuate side walls. **Spores** with unornamented proximal faces, with an irregular, fine-meshed reticulum on distal faces.

Creeping or hanging over banks in grass páramo, usually in relatively dry páramos, but also often in mossy bogs, 2750–4000 m, Lambayeque, Cajamarca, La Libertad, San Martín, Ancash, Huánuco, Cuzco.

Hispaniola; Costa Rica; Andes from Venezuela to Chile and Argentina.

The subterranean rhizomes seem to enable this species to survive in vegetation that is burned frequently.

Lycopodium magellanicum is possibly identical to certain forms included in *L. fastigiatum* R. Br. of New Zealand and Australia.

Lambayeque: Ferrañafe, Laguna Tembladera, Incahuasi, 3150 m, *Sagástegui et al. 12791* in part (F). Prov. Ferrañafe, ca. 7 km NW of Incahuasi, near Cerro Punamachay, 3300–3550 m, *Dillon & Skillman 4125* (F). **Cajamarca:** Cajabamba–Luchubamba, 3800 m, *Sagástegui et al. 11202* (AAU). San Miguel, Millan (El Tingo–Taulis), 3000 m, *Sagástegui 9526* (NY). Cutervo, *Jelski 993, 1012, 1017* (KRA). **La Libertad:** Bolívar, Laguna de los Ichus, 3600 m, *López & Sagástegui 3239* (GH). **San Martín:** Prov. Mariscal Cáceres, Parque Nacional Río Abiseo, Paredones, 3650 m, *León & Young 1606* (USM). Prov. Mariscal Cáceres, Parque Nacional Río Abiseo, Chochos, 3400 m, *Young & León 4896B* (USM). **Ancash:** Prov. Carhuaz, Huascarán National Park, Quebrada Ishinca, 3900 m, *D. Smith et al. 9588B* (AAU). Prov. Huari, Huascarán National Park, Quebrada Pachachaca, 3700–3860 m, *D. Smith et al. 12547* (USM). **Huánuco:** Yanano, 2000 m, *Macbride 4928* (F). **Cuzco:** Paucartambo, 3700 m, *Vargas 13938* (GH). Paucartambo, Parque Nacional Manú, Cerro Macho Cruz, 3200 m, *León & Aguilar 2345* (USM).

4. *Lycopodium jussiaei* Poirét, in Lam., Encycl. 3: 543. 1814. TYPE: Perou (holotype, P, *Herb. Jussieu 658!*).

Lycopodium jussiaei Poirét var. *microphyllum* Poirét, in Lam., Encycl. 3: 543. 1814. TYPE: Amérique meridionale, *Herb. Bonpland* (holotype, P!). *Lycopodium haenkei* Presl, Reliq. haenk. 1: 78. 1825.

TYPE: Peru (Dept. Huánuco), In montosis Peruviae ad Huanocco, *Haenke* (holotype, PRC!; possible isotype, K!).

Lycopodium heterophyllum Sprengel, Syst. Veg. ed. 16, 4: 13. 1827. TYPE: Peruvia, *Humboldt* (holotype, B, *Herb. Willd.* 19425!).

Lycopodium scariosum Forst. var. *jussiaei* (Poirot) Baker, Handbook Fern Allies 29. 1887.

Diplazium jussiaei (Poirot) [Presl ex] Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 65. 1944 [as *jussiaei*].

Rhizomes creeping, scrambling to scandent, rigid, 2–4 mm thick, usually above ground, with leaves radially arranged, uniform, 3–5 mm long, ca. 1 mm wide, linear-lanceolate, with widely membranous, irregularly obtuse apex. **Aerial shoot systems** 5–75 cm tall, branched almost from the base, in large individuals with a main axis almost conform to the rhizome, upward gradually changing to anisophyllous, bearing alternating, fan-shaped branchlet systems. **Branchlets** dorsiventral, anisophyllous, flattened, 4–6(–8) mm wide including leaves, with 2 dorsolateral ranks of wide leaves and 2–3 indistinct ventral ranks of narrow leaves. **Dorsolateral leaves** flattened in the plane of the branchlet system, or inclinate to it, obliquely elliptic, with the acroscopic margin 2–3 mm long, 1–1.5 mm wide, forward and ventrally curved, mucronate to short hair-tipped, short to long decurrent. **Ventral leaves** appressed, lanceolate-subulate, with membranous apices. **Peduncles** up to 50 cm long (rarely absent), simple or up to twice-forked, bearing 1–3 strobili, terete. **Strobili** (1–)3–10 cm long, 4–6 mm in diameter including sporophylls. **Sporophylls** borne in alternating whorls of 4, subpeltate, with ovate, more or less acuminate exterior face, 4–6 mm long, ca. 2 mm wide, with narrowly membranous, shallowly erose-denticulate margins. **Sporangia** 1.5–2 mm wide, the side walls of epidermis cells evenly sinuate and finely curled. **Spores** reticulate, with large, regular meshes on distal faces, and unornamented proximal faces.

Usually a vigorous scrambling to scandent plant, common in clearings and on road banks and open places in montane forest, 1700–3700 m, Piura, Cajamarca, Amazonas, San Martín, Huánuco, Pasco, Huancavelica, Ayacucho, Cuzco, Puno.

Jamaica; Dominican Republic; Costa Rica; Venezuela; Andes south to Bolivia; Brazil (Itatiaia).

A variable species, apparently due to environmental factors. *Lycopodium jussiaei* is closely related to *L. scariosum* (Indonesia to New Zealand)

and to plants from Chile and Juan Fernandez recognized as *L. gayanum* Remy. The plants referred to *Lycopodium jussiaei* are generally larger and coarser than those species. A modern revision of the group is needed. For more complete synonymy, see Øllgaard (1988).

Piura: Huancabamba, Loma Redonda (Sapalache-Chinguela), 2400 m, *Sagástegui et al.* 10203 (AAU). **Cajamarca:** Prov. Cutervo, 10 km NW of Socota, 3200 m, *Stork & Horton* 10143 (F, G, MO). Cutervo, *Jelski* 1025 (KRA). **Amazonas:** Prov. Bagua, Cord. Colán, E of La Peca, 3200 m, *Barbour* 3262 (AAU, MO, USM). Prov. Chachapoyas, Puma-urcu SE of Chachapoyas, 3100–3200 m, *Wurdack* 1158 (F, S, UC). **San Martín:** Prov. Mariscal Cáceres, NW corner of Río Abiseo National Park, 3300 m, *Young & León* 4882 (AAU). **Huánuco:** Prov. Huánuco, Carpish Pass, 3300 m, *Hodge* 6291 (AAU, F). Churubamba, Pampa Hermosa, 1400 m, *Mexia* 8146 (F, G, MO, S). **Pasco:** Cord. Yanachaga, 12 km E of main Oxapampa-Villa Rica Road, 2100–2200 m, *Gentry & Smith* 35924 (AAU, MO). Oxapampa, 1970 m, *Smith & Pretel* 1645 (AAU). **Huancavelica:** Prov. Tayacaja, Montepungo, 5 km E of Surcubamba, 3000 m, *Stork & Horton* 10384 (F). **Ayacucho:** Prov. La Mar, eastern Massif of Cord. Central opposing the Cord. Vilcabamba between Tambo San Miguel, Ayna and Hda. Luisiana, *Dudley* 11973 (F). **Cuzco:** Prov. Paucartambo, Valle de Pilcopata, Patria-Pilahuata, 2000 m, *Foster & Wachter* 7475 (AAU). **Puno:** Below Limbani, 3100–3200 m, *Brandbyge* 558 (AAU).

5. *Lycopodium thyoides* Willd., Sp. pl. ed. 4, 5: 18. 1810. TYPE: Venezuela, Silla de Caracas, *Humboldt* (holotype, B, *Herb. Willd.* 19352!).

Lycopodium complanatum L. var. *tropicum* Spring, in Mart., Flora Bras. 1 (2): 116. 1840.

Lycopodium complanatum L. var. *thyoides* (Willd.) Christ, in Schwacke, Pl. Nov. Mineiras 2: 42. 1900 [as *thujoides*].

Lycopodium complanatum L. var. *validum* Weatherby, Proc. Amer. Acad. Arts Sci. 45: 414. 1910, based on *L. thyoides* Willd. and with the same type.

Diplazium thyoides (Willd.) Holub, Preslia 47: 108. 1975.

Plants with creeping, trailing to scandent rhizomes, usually above ground, or hanging over banks. **Rhizomes** terete, 1.2–2.5 mm in diameter excluding leaves. **Rhizome leaves** relatively distant, borne in irregular spirals, or subverticillate, subulate, appressed to ascending. **Aerial shoots** ascending to erect, 10–50 cm tall, with vegetative portions up to ca. 30 cm tall. **Main upright axis** terete to somewhat flattened, bearing lateral, flattened, fan-shaped branchlet systems. **Ultimate branchlets** flattened, dorsiventral, anisophyllous, 1.5–3 mm wide including leaves, with trimorphic,

decussate leaves. **Upper, median branchlet leaves** with pointed, subulate to acicular, appressed, 1–2 mm long, free blades, and a conspicuous, ca. 0.4–0.6 mm wide, prominently decurrent base. **Lateral branchlet leaves** bilaterally compressed, long-decurrent, 2.5–7 mm long including bases, the free blades 1–3 mm long, appressed to spreading, acuminate to long-pointed, the leaf bases 0.6–1.5 mm wide, with almost parallel to distinctly diverging margins, often curved down. **Ventral leaves** inconspicuous, acicular, without decurrent base, 1–2 mm long. **Peduncles** 10–25 cm long, terete, bearing 4–9 pedicellate strobili. **Strobili** 1.5–5 cm long, 2–4 mm in diameter including sporophylls, often with protracted sterile tips. **Sporophylls** usually borne in alternating whorls of 3, subpeltate, widely deltoid-ovate, long-cuspidate, ca. 2–3 mm long, 1.5–2 mm wide, with almost entire, widely membranous margins. **Sporangia** 1.5–2 mm wide, with side walls of epidermal cells evenly sinuate. **Spores** densely reticulate on all faces.

Clearings, road banks, open habitats, and secondary scrub in upper montane forest, and in the lowest páramos, alt. 2000–3400 m, Piura, Lambayeque, Cajamarca, Amazonas, La Libertad, San Martín, Ancash, Huánuco, Pasco, Junín, Huancavelica, Ayacucho, Cuzco, Puno.

Throughout moist mountainous regions of tropical America, south to northern Argentina.

The present application of the name *Lycopodium thyooides* corresponds to the “*L. thyooides*-complex” of Wilce (1965). I have not attempted to treat the infraspecific variation. The Peruvian material referred to this species is highly variable and may belong to more than one species, but also external factors apparently greatly affect the growth habit of the individuals. *Ferreyra 15111* (USM), from Dept. Cajamarca, Prov. Celendín, Celendín, ca. 3100 m, has unusually wide branchlets with very wide lateral leaves.

For more complete synonymy, see Øllgaard (1988).

Piura: Prov. Huancabamba, Dist. Sondor, Cerro La Viuda, 2170 m, *Sagástegui et al. 8197* (AAU, MO). **Piura:** Loma Redonda, 2400 m, *Sagástegui 10175* (AAU). **Lambayeque:** Prov. Ferreñafe, Incahuasi (Sinchigual–Laguna Tembladera, 3000 m, *Sagástegui et al. 12870* (AAU, F).

Cajamarca: Prov. Chota, Chota Tacabamba road, km 14, 2800 m, *Smith & Vásquez 3549* (AAU, F). Prov. San Miguel, El Tingo, 3100 m, *Mostacero et al. 1123* (AAU, F). **Amazonas:** Prov. Chachapoyas, Leimebamba–Calla Calla road, km 12–15, 2960–3100 m, *Smith & Vásquez 4992* (AAU). Donile–Cohechan, *Soukup 4160* (F, US). **La Libertad:** Prov. Pataz, Cerro Colpar, above Yalén, 3300–3700 m, *Young 3046* (AAU, USM). Prov. Bolívar, above Longotea, 2800 m, *Sagástegui 14195* (F). **San Martín:** Río Abiseo National Park, NW corner, 2800 m, *Young 1480* (AAU); Río Abiseo National Park, Laguna del Eco, Chocho, 3450 m, *Young & León 4902* (USM). **Ancash:** Prov. Yungay, Huascarán National Park, Quebrada Ranincuray, 3650–3900 m, *D. Smith et al. 10336* (AAU, USM). **Huánuco:** Prov. Huánuco, Huánuco–La Unión road km 32, 2940–3100 m, *Huapalla 2201* (AAU). Carpish Pass, 2850 m, *Asplund 12748* (S). **Pasco:** Above Oxapampa (Cerro Corporación), ca. 2300 m, *collector unknown* (F). **Junín:** Huacapistana, 1800–2400 m, *Killip & Smith 24255* (F). **Huancavelica:** Prov. Tayacaja, Marcavalle, between Huachocolpa and Tintay, 2800 m, *Tovar 4765* (USM). **Ayacucho:** Ccarrapa, between Huanta and Río Apurímac, 2500 m, *Killip & Smith 22293* (F, US). **Cuzco:** Prov. Calca, below Kachin, 2700–3800 m, *Sallo ex Franquemont 244* (AAU, F). Prov. Paucartambo, Marcacha, Achirani, 2500–3000 m, *Vargas 11133* (F, MO, UC). Paucartambo, *Woytkowski 6744* (MO, US). **Puno:** Below Limbani, 3100–3200 m, *Brandbyge 546* (AAU). Prov. Sandía, between Sandía and Cuyo-Cuyo, 3100–3300 m, *Ferreyra 16813* (USM). Tabina, *Lechler 2034* (E, G, S).

III. *Lycopodiella*

Lycopodiella Holub, *Preslia* 36: 22. 1964. TYPE: *Lycopodiella inundata* (L.) Holub. **Figure 8.**

Lycopodium subgen. *Cernuistachys* Herter, *Bot. Jahrb.* 43: Beibl. 98: 29. 1909. TYPE: *Lycopodium cernuum* L.

Palhinhaea Vascon. & Franco, *Bol. Soc. Brot.* II, 41: 24 (1967). TYPE: *Palhinhaea cernua* (L.) Vascon. & Franco (= *Lycopodium cernuum* L.).

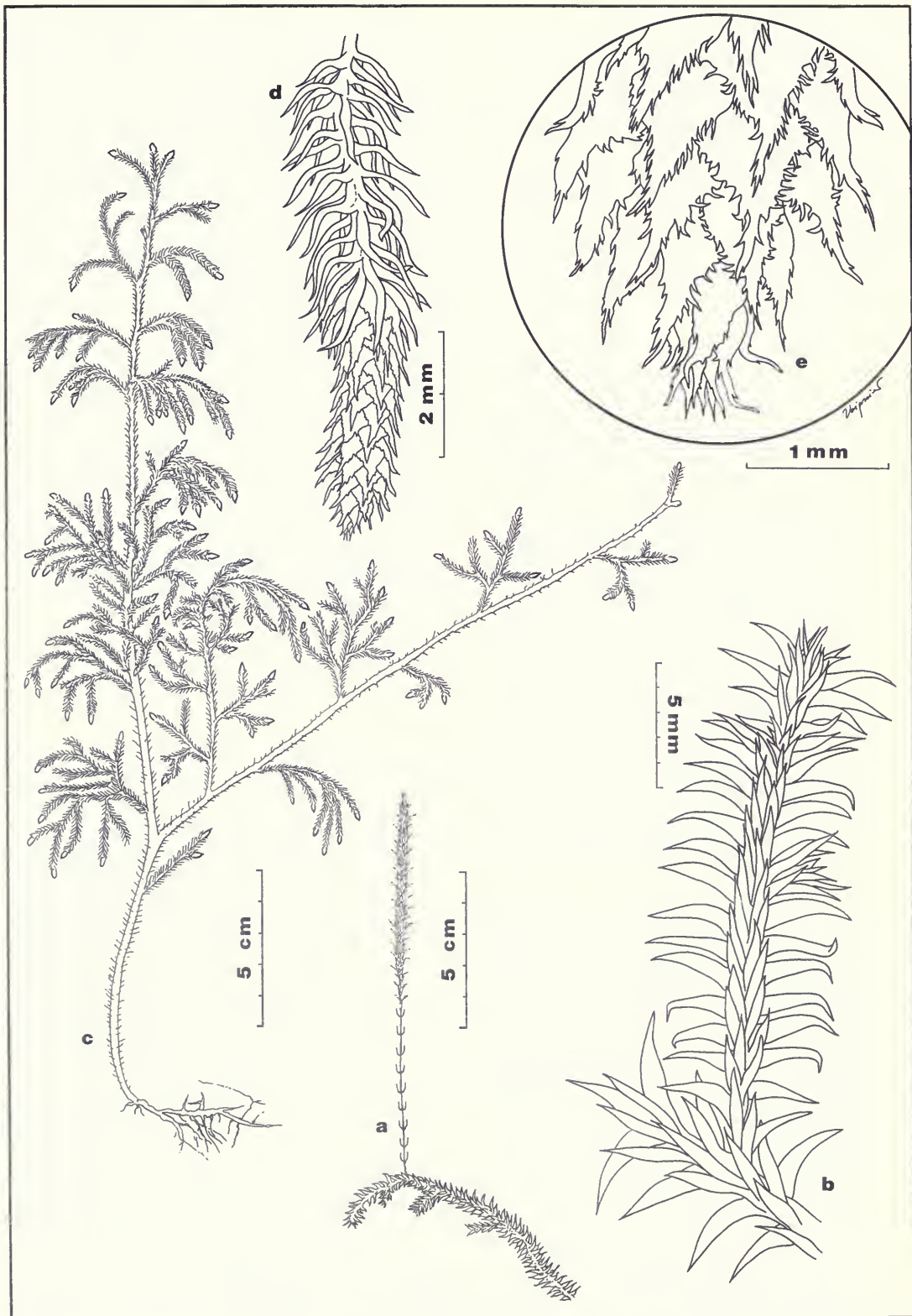
Lycopodium sect. *Caroliniana* Bruce, *Amer. Fern J.* 66: 136. 1976. TYPE: *Lycopodium carolinianum* L. *Pseudolycopodiella* Holub, *Folia Geobot. Phytotax.* 18: 441. 1983.

Lepidotis auct., not Mirbel 1802.

Lycopodium subgen. *Lepidotis* auct., not Sprengel, *Anleit.* ed. 2, 2, 1: 108. 1817, nor Baker 1887.

Plants with prostrate, rooting, indeterminate, isophyllous or anisophyllous, horizontally branching shoots, and dorsally arising, erect, simple strobiliferous branches (sect. *Lycopodiella* and sect. *Caroliniana*), or with trailing to arching or looping

FIG. 8. *Lycopodiella caroliniana* var. *meridionale*: a, habit; b, portion of stem and branch. *Lycopodiella cernua*: c, habit; d, ultimate branchlet, showing sterile leaves and strobilus; e, apex of strobilus. (Adapted from Stolze, *Ferns and fern allies of Guatemala*, 1983.)



indeterminate runner shoots that root with usually long intervals, and branch occasionally in the horizontal plane giving off horizontal branchlet systems, and usually bearing 1 vertical, dorsally arising, dendroid branch system on each loop (sect. *Campylostachys*). **Dendroid branch system** with a series of subdecussate, spreading to hanging, flabellate branchlet systems, which in turn may terminate in sessile, nodding to pendulous strobili. **Sporophylls** subpeltate, with a median basicopic wing, or with coalescent basal membranes that almost enclose the sporangia (sect. *Campylostachys*). **Sporangia** on the sporophyll base, or axillary (sect. *Lycopodiella*), strongly anisovalvate, or isovalvate (sect. *Caroliniana*), the epidermis cells with thin, straight, non-lignified side walls, but with lignified, nodular, or semiannular thickenings. **Spores** rugate. **Gametophytes** green, tuberous and lobed on the upper side, surface-living, with mycorrhiza in the base.

Almost all moist temperate and tropical regions of the world. Perhaps 40 species, the majority of these in the Americas and probably nine in Peru, all fairly widely distributed.

The generic description above covers only the

Andean representatives of the genus. Although growth habit and morphological details are quite diverse, features of branching, sporangium anatomy, spores, and gametophytes indicate that *Lycopodiella* is a natural entity.

In sect. *Campylostachys*, most species have erect, dendroid branch systems arising from the dorsal side of horizontal, looping main axes (e.g., *Lycopodiella cernua*), but in some species the corresponding dendroid branch system is scandent, hanging, or creeping. In these cases the dendroid branch system can be distinguished from the horizontal branch system by the orientation of lateral branchlet systems on the main axes. In the horizontal system they are distichous, all arranged in the horizontal plane. In the dendroid branch system the lateral branchlets are polystichous, arranged in an irregularly subdecussate manner.

Zimmer, in a review in Bot. Jahrb. Syst. 112: 414, 1991, claimed that *Lepidotis* is the correct name for this genus as lectotypified by Rothmaler (1944). However, Rothmaler's lectotypification does not refer to the protologue of *Lepidotis* and is superceded by the choice of *Lycopodium clavatum* (Pichi Sermolli, Webbia 26: 145-149. 1971).

Key to Species of *Lycopodiella*

- a. Strobili erect, terminating simple, erect branches that arise dorsally on the creeping stem b
- b. Creeping shoots isophyllous or nearly so; leaves of the erect branch crowded, borne in alternating whorls of 6 or more c
- c. Sporangia subglobose, strongly anisovalvate, ca. 1 mm wide; sporophylls and vegetative leaves with the same color and texture; leaves of erect branch with flattened, appressed base (sect. *Caroliniana*) 1. **L. alopecuroides**
- c. Sporangia reniform, isovalvate, 1-1.5 mm wide; sporophylls and vegetative leaves with different color and texture; leaves of erect. branch strongly upward curved from a subterete, diverging base (sect. *Caroliniana*) 3. **L. contexta**
- b. Creeping shoots strongly anisophyllous, with wide and long ventrolateral leaves and narrow dorsal leaves; leaves of the erect branch borne in distant, alternating whorls of 4 or 5 (sect. *Caroliniana*) 2. **L. caroliniana** var. **meridionalis**
- a. Strobili nodding to pendulous, terminating spreading to pendulous branchlets that are borne on dendroid, erect or scandent, amply branched shoot systems (sect. *Campylostachys*) d
- d. Branchlet leaves closely imbricate, flattened throughout, lanceolate, with fimbriate margins and densely hairy leaf bases 9. **L. riofrioi**
- d. Branchlet leaves spreading to ascending, subterete, angular or apically flattened, acicular to linear-lanceolate, glabrous or hairy, not fimbriate e
- e. Leaves of the main axes closely appressed, less than 4 mm long; stems usually densely hairy, dendroid shoot system flexible, usually bending to hanging from an erect base 6. **L. descendens**
- e. Leaves of main axes patent to ascending or reflexed or, if loosely appressed, more than 4 mm long; stems glabrous or hairy f
- f. Dendroid branch system usually indeterminate, up to 4 m long, scandent to creeping, or all

- axes scandent to creeping; main axes robust; leaves of main axes coriaceous, apically flattened, usually strongly upward curved and hook-shaped, with hairy leaf bases 7. *L. glaucescens*
- f. Dendroid branch system determinate, vertical, not scandent or climbing g
- g. Lateral branchlet systems of dendroid branch system recurved to long-pendulous; strobili 3–5 mm in diameter; sporophylls usually more than 3 mm long, with irregularly dentate margins 8. *L. pendulina*
- g. Lateral branchlet systems of dendroid branch system erect or spreading to horizontal and distally nodding; strobili 2.5–3 mm in diameter, sporophylls rarely more than 2 mm long, with coarsely dentate to erose-laciniate margins h
- h. Branchlet systems divaricate to somewhat aggregate, patent to horizontal, usually with gently recurved tips; strobilus-bearing branchlets softly nodding at tip 4. *L. cernua*
- h. Branchlet systems stiffly ascending or suberect, often densely aggregated, pointed upward, not recurved; strobilus-bearing branchlets usually sharply reflexed at tip, or only the strobilus reflexed 5. *L. camporum*

1. *Lycopodiella alopecuroides* (L.) Cranfill, Amer. Fern J. 71: 97. 1981.

Lycopodium alopecuroides L., Sp. pl. 1102. 1753.
TYPE: Eastern temperate North America, Virginia, *Kalm* (LINN 1257.7).

Lycopodium matthewsii Hooker, Icon. pl. 1: t. 26. 1836. TYPE: Peru, Bagasan, [Bagazán, Dept. Amazonas] *Matthews 1778* (holotype, k!; isotype, BM!).

Lepidotis alopecuroides (L.) Rothmaler, Feddes Rept. Spec. Nov. Regni Veg. 54: 66. 1944.

Lycopodiella matthewsii (Hooker) Holub, Folia Geobot. Phytotax. 18: 441. 1983.

Horizontal shoots creeping and firmly rooted throughout, up to 25 cm long, sparsely and unequally branched, densely covered on all sides by almost uniform, somewhat upwardly secund, or spreading to perpendicular leaves, 7–12 mm wide including leaves, bearing stiffly erect, dorsally arising, simple, strobiliferous branches. **Leaves** linear-lanceolate to subulate, flat, with smooth to denticulate-ciliate margins, soft, light green, 5–8 mm long, 0.5–1 mm wide. **Erect branches** ca. 5–8 mm in diameter including leaves, up to 30 cm tall including the strobilus, with radially arranged leaves borne in alternating whorls of 6 or more, like leaves of horizontal shoots, or slightly narrower, usually more ascending. **Strobili** up to 12 cm long, 10–18 mm in diameter including sporophylls. **Sporophylls** arranged as peduncle leaves, narrowly lanceolate to lanceolate from a subpetalate base, not coalescent at base, with few to many spreading to hooked teeth on margins, 6–10 mm long, 1–1.7 mm wide at base. **Sporangia** axillary, subglobular, ca. 1 mm wide, strongly anisovalvate, almost completely concealed by sporophyll bases, the epidermal cells with straight, unligified side walls with

semiannular lignified thickenings. **Spores** rugate, with a distinct equatorial rim.

On open, wet, peaty or sandy soil, in the jalca or montane forest zone, 2400–3450 m, Cajamarca, Amazonas, San Martín, Huánuco, Pasco.

Eastern temperate North America; Cuba; throughout continental tropical America.

As here delimited, in the wide sense, *Lycopodiella alopecuroides* is a polymorphic species, consisting of several elements. In the narrow sense, the species is restricted to temperate North America and Cuba, while other elements are present in South America. High altitude forms in the Andes are relatively compact, wide-leaved, and robust and perhaps deserve recognition as a species of which the correct name is *Lycopodiella matthewsii*; the material cited below belongs to this form.

Cajamarca: Prov. Cutervo, El Suro, 2400 m, *Sánchez Vega et al. 6019* (AAU, F). Cumbemayo 10 km WSW of Cajamarca, 3550 m, *Molau & Sánchez Vega 840* (GB). **Amazonas:** Prov. Chachapoyas, 1–5 km W of Molinopampa, 2400 m, *Wurdack 1381* (F, GH, UC, US). Leimbamba–Calla Calla, km 12–15, 2960–3100 m, *Smith & Vásquez 5000* (AAU). Chachapoyas, 2400–2600 m, *Weberbauer 4397* (G). Prov. Bagua, Cord. Colán E of La Peca, 3500 m, *Barbour 3197, 3200A* (AAU, MO). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, NW corner of the park, 3425 m, *Young 3475* (AAU); 3450 m, *León 1854* (AAU). **Huánuco:** Tingo María, *Morrow 11131* (GH). **Pasco:** Prov. Oxapampa, San Gotardo, 36 km W of Oxapampa, 2850 m, *D. Smith 2753* (AAU).

2. *Lycopodiella caroliniana* (L.) Pichi-Sermolli var. **meridionalis** (Underw. & Lloyd) B. Øllg. & Windisch, Bradea 5: 27. 1987.

Lycopodium meridionale Underw. & Lloyd, Bull. Torr.

Bot. Club 33: 121. 1906. TYPE: Puerto Rico, dry savannahs, Luquillo Mountains, *Wilson 94* (holotype, NY!).

Lycopodium carolinianum L. var. *meridionalis* Nessel. Arch. Bot. Est. S. Paulo 1: 431. 1927.

Pseudolycopodiella meridionalis (Underw. & Lloyd) Holub, Folia Geobot. Phytotax. 18: 442. 1983.

Horizontal stems creeping and firmly rooted throughout, to ca. 30 cm long, sparsely and unequally branched, anisophyllous, with long and wide lateral leaves, and usually shorter and narrower dorsal leaves, 7–12(–15) mm wide including leaves, bearing 1 to few, dorsally arising, stiffly erect, simple, strobilus-bearing branches. **Lateral leaves** 3–5(–7) mm long, (1–)1.5–2.5(–3) mm wide at the base, triangular-ovate to lanceolate, obliquely spreading to falcately recurved, tapering into an acute to long pointed apex. **Dorsal leaves** arranged in (1–)2–4 longitudinal ranks (often on the same individual), widely lanceolate to subulate, diverging to appressed, straight to upward curved, (1.5–)3–4(–5) mm long, 1–1.3(–2) mm wide at the base. **Erect branches** up to 30 cm tall including the strobilus, 1–1.5 mm thick excluding leaves, bearing small, 3–5 mm long, acicular leaves in remote, alternating spirals or irregular whorls of 4–5. **Strobili** up to at least 13 cm long, 3–5 mm thick with appressed sporophylls. **Sporophylls** borne in alternating whorls of 4 or 5, subpelate, rhombic or ovate-acuminate or ovate-cuspidate to triangular-lanceolate, 3.5–6 mm long, (1–)1.5–2(–2.5) mm wide, with entire to crose-denticulate, minutely fimbriate-denticulate margins. **Sporangia** reniform, isovalvate, borne on the sporophyll stalk, ca. 1.5–2 mm wide. **Spores** rugate, with a distinct equatorial rim.

Terrestrial or sometimes epilithic, usually on wet ground, on road banks, slopes, ledges, grasslands in the jalca zone, on seepages, 1350–2400 m, Amazonas, San Martín.

Widely distributed in tropical America, rare in the Andes.

The distinctness of the present taxon from the type variety (temperate North America) has been doubted (e.g., Proctor, 1977, pp. 32–33), because the distinguishing characters usually indicated for them are widely overlapping, and seem to be based entirely on features related to the size of the plants.

Amazonas: Chachapoyas, 1–5 km W of Molinopampa, 2400 m, *Wurdack 1382* (F, GH, NY, US, USM). **San Martín:** San Roque, 1350–1500 m, *Ll. Williams 7763* (F, US).

3. *Lycopodiella contexta* (Mart.) Holub, Folia Geobot. Phytotax. 18: 441. 1983.

Lycopodium contextum Mart., Icon. Crypt. Brasil. 38, t. 20, f. 1. 1834. TYPE: In campis graminosis apricis in summo monte Arara-Coára, fluvii Japura cataractae imminente, alt. ca. 1200 p., *Martius* (holotype, M!).

Lycopodium alopecuroides L. var. *contextum* (Mart.) Baker, Handb. Fern Allies 19. 1887.

Lycopodium sprucei Baker, Handb. Fern Allies 24. 1887. TYPE: Venezuela, San Carlos del Rio Negro, *Spruce 3151* (holotype, K!; isotype, BONN, frag. *Herb. Nessel 200!* in part).

Lycopodium alopecuroides L. subsp. *contextum* (Mart.) Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45: 92. 1928.

Lepidotis contexta (Mart.) Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 66. 1944.

Pseudolycopodiella contexta (Mart.) Holub, Folia Geobot. Phytotax. 26: 93. 1991.

Horizontal shoots creeping and firmly rooted throughout, up to at least 30 cm long, sparsely and unequally branched, isophyllous, with somewhat upwardly secund, ascending, acicular leaves, 3–7 mm in diameter including leaves, bearing stiffly erect, dorsally arising, simple, or sometimes 1–2 × forked, up to at least 40 cm tall, vegetative or strobiliferous aerial shoots. **Erect branches** 4–6 mm in diameter including leaves, densely foliose, isophyllous. **Leaves of erect branches** borne in alternating irregular whorls of 6–7, subterete at the base (angular when dry), sometimes apically flattened, strongly upward curved from a strongly diverging to almost perpendicular base, 4–5(–7) mm long, ca. 0.5 mm wide, with conspicuously acroscopically adnate and long decurrent leaf bases, with smooth margins. **Strobili** up to 8 cm long, 3–4 mm in diameter with appressed sporophylls. **Sporophylls** borne in alternating whorls of 4–5, subpelate, widely triangular-ovate to ovate-lanceolate at base, with a long, narrow apex, 4.5–7 mm long, 1–1.5 mm wide, with subentire to slightly crose-dentate margins at the base. **Sporangia** borne on the sporophyll base, reniform, isovalvate, 1–1.5 mm wide.

Terrestrial, humid places on white sand, grasslands, and river margins, ca. 120 m, Loreto.

Circum-Amazonian, periphery of the Amazonian lowland of Brazil, Peru, Colombia, and Venezuela.

Loreto: Manfina, on the upper Río Nanay, *Ll. Williams 1106* (F, US); Vicinity of Iquitos, ca. 120 m, *Revilla 4340* (F).

4. *Lycopodiella cernua* (L.) Pic.-Ser., *Webbia* 23: 165. 1968.

Lycopodium cernuum L., Sp. pl. 1103. 1753. TYPE: LINN 1257.13, see Proctor, *Ferns of Jamaica*, London 29. 1985.

Lepidotis cernua (L.) Beauv., *Prodr. Aethéogamie* 108. 1805.

Lycopodium cernuum var. *capillaceum* Spring, *Mém. Acad. roy. Belg.* 15 [Mon. Lyc. 1]: 80. 1842. TYPE: Venezuela, Edo. Monagas, Guanaguana, *Humboldt* 473 (holotype, v. *Herb. Willd.* 19429!).

Lycopodium capillaceum (Spring) Hieron., *Bot. Jahrb. Syst.* 34: 573. 1905.

Palhinhaea cernua (L.) Vasc. & Franco, *Bol. Soc. Brot.* 41: 25. 1967.

Plants with arching-looping runner shoots, with up to 1 m tall, erect, dendroid branch systems, these with several, subdecussate to alternate, highly compound, spreading to horizontal, 5–15(–20) cm long lateral branchlet systems. **Ultimate branchlets** nodding, 3–4(–6) mm in diameter including leaves. **Branchlet leaves** usually borne in densely crowded, alternating whorls or low spirals of 3–5, usually 3–4 mm long, ca. 0.3 mm diameter, acicular, terete to angular (dried), with often conspicuously acroscopically adnate and decurrent leaf bases, gradually changing from patent-reflexed and distant on main axes, to patent, upward curved and densely crowded in ultimate branchlets, occasionally with sparse, lax trichomes or minute spinules; leaf bases often with longer, irregularly crisped or branched trichomes, these rarely also on stem surfaces. **Strobili** usually numerous, sessile, terminating ultimate branchlets, 4–10(–20) mm long, 2.5–3 mm in diameter. **Sporophylls** usually borne in alternating whorls of 5, ovate-deltoid, short to long cuspidate, ca. 2 mm long, ca. 1 mm wide, with membranous, coarsely erose-laciniate margins. **Sporangia** globose, 0.5–0.8 mm in diameter, strongly anisovalvate. **Spores** rugate, without a distinct equatorial rim.

A common pioneer species on road cuts and moist disturbed soil, along rivers, in forest clearings, etc., from sea level up to 3000 m, Cajamarca, Amazonas, San Martín, Loreto, Huánuco, Pasco, Junín, Ayacucho, Cuzco, Puno.

Pantropic.

Where *Lycopodiella cernua* grows intermixed with *L. descendens*, intermediates may occur.

Llanos & Chimouy 61 (USM), from Dept. Cajamarca: Prov. Jaen, San Patricio, Santa Rita, Chontalí, 1600 m, with the growth habit of *L. cernua*, deviates from typical forms of the latter

by the densely crowded and strongly reflexed leaves on the main erect axis, by the somewhat flattened branchlet leaves, and by the densely hairy leaf bases and stem surfaces. It closely resembles forms from similar altitudes in Ecuador (Prov. Zamora-Chinchipec) and Bolivia and may represent a distinct element, but more field observations and material are desirable for an assessment of its status.

Cajamarca: Prov. Cutervo, La Pucarilla–San Andrés, 2400 m, *Sánchez Vega et al.* 5999 (AAU, F). San Ignacio, San José de Lourdes, Villarica, 1650 m, *Díaz* 2053 (F). **Amazonas:** Prov. Bagua, road Chiriaco–Puente Venezuela, ca. 200–300 m, *Barbour* 4326 (AAU, MO). Prov. Chachapoyas, ca. 1800 m, *Raimondi* 350 (USM). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache Nuevo, *J. Schunke* V. 3713 (F, US). La Divisoria, 59 km from Tingo María on road to Pucallpa, *Allard* 22175 (US). **Loreto:** Prov. Maynas, Dist. Iquitos, near mouth of Río Nanay, *Rimachi* 449 (F, MO, USM). Balsapuerto, 220 m, *Klug* 2970 (F, MO, S, UC, US). **Huánuco:** Prov. Huánuco, Dist. Churubamba, Hda. Mercedes, 1875 m, *Mexia* 8193 (F, GH, S, US). Vilcabamba, 2000 m, *Macbride* 5014 (F, GH, MO, US). **Pasco:** Prov. Oxapampa, Palcazú valley, 300 m, *D. Smith* 3927 (AAU). Pichis Trail, Eneñas, 1700 m, *Killip & Smith* 25688 (F, US). **Junín:** Chanchamayo Valley, 1200 m, *C. Schunke* 188 (F). La Merced, *Killip & Smith* 23755 (US). **Ayacucho:** Prov. La Mar, eastern Massif of the Cord. Central opposing the Cord. Vilcabamba between Tambo, San Miguel, Ayna and Hda. Luisiana, 1570 m, *Dudley* 11889 (GH, US). **Cuzco:** Pilcopata–Atalaya, 700 m, *Vargas* 13309 (GH). **Puno:** Ollaheca to San Gabán, 1000–2000 m, *Dillon et al.* 1166 (F, MO).

5. *Lycopodiella camporum* B. Øllg. & P. G. Windisch, *Bradea* 5: 24, t. 3. 1987. TYPE: Brasil, Est. Minas Gerais, Mun. Santana do Riacho, Serra do Cipó, *Prado et al.* 69 (holotype, HBL; isotypes, AAU!, RB!, SP!, SPF!).

Palhinhaea camporum (B. Øllg. and Windisch) Holub, *Folia Geobot. Phytotax.* 26: 93. 1991.

Plants with arching-looping runner shoots, with up to 1 m tall, stiffly erect, dendroid branch systems, these with several, subdecussate to alternate, often densely aggregated, stiffly ascending, 5–10(–20) cm long lateral branchlet systems. **Ultimate branchlets** 2.5–7 mm in diameter including leaves, stiffly ascending to erect, only the strobiliferous ones rather sharply recurved at the tip. **Branchlet leaves** usually borne in densely crowded, alternating low spirals or oblique whorls of 5–7, 2.5–4 mm long, ca. 0.3–0.5 mm in diameter, acicular, terete or angular (dried), sometimes flattened in the lower half, with often slightly acroscopically adnate and long decurrent leaf bases, patently ar-

cuate-ascending to arcuate-appressed, entirely smooth to densely hairy on leaf bases, rarely with soft trichomes on leaf margins. **Strobili** usually numerous, sessile, terminating tips of ultimate branchlets with a sharp bend, to 2.5 cm long, 2–3 mm in diameter. **Sporophylls** borne in alternating whorls of 5–7, widely ovate, short to long cuspidate, 1.5–2 mm long, 0.6–0.9 mm wide, with scarious, coarsely erose-laciniate margins. **Sporangia** globose, ca. 0.6 mm in diameter, strongly anisovalvate.

Swamps, moist campo-grasslands, on peaty or sandy soil, often in the light-open vegetation adjacent to gallery-vegetation at rivers, subject to flooding during the rainy season; alt. 120–1800 m, San Martín, Junín, Loreto.

Amazonian Colombia, Peru and Bolivia; savanna region of Venezuela and Guyana, campos vegetation in Brazil.

Lycopodiella camporum is a widespread species which has been confused with *L. pendulina* and synonyms thereof. The distinctive branching habit and characteristic ecology make *L. camporum* a rather easily recognizable and ecologically well-defined taxon, although detail characters of morphology do not seem strong.

San Martín: Tarapoto, *Ll. Williams 5960* (F). **Junín:** Prov. Satipo, Gran Pajonal, 1000–1200 m, *Peña & Oventini 915* (USM). **Loreto:** Prov. Maynas, Quisto Cocha, Iquitos, 120 m, *Sagástegui & Aldave 5821* (GH, MO).

6. *Lycopodiella descendens* B. Øllg., in Harling and Andersson, Fl. Ecuador 33: 143. 1988. TYPE: Ecuador, Prov. Pastaza, Mera, *B. Øllg. & Balslev 9076* (holotype, AAU!; isotypes, F!, QCA!).

Palhinhaea descendens (B. Øllg.) Holub, Folia Geobot. Phytotax. 26: 93. 1991.

Runner shoots arching-looping, usually densely hairy, with relatively distant, appressed, subulate leaves, with initially erect, then recurved and descending, amply branched, up to at least 75 cm long dendroid branch systems, these with several subdecussate to alternate, highly compound, spreading to hanging lateral branchlet systems, with usually densely hairy main axis with relatively distant, appressed, subulate leaves. **Ultimate branchlets** 3–4 mm in diameter including leaves. **Branchlet leaves** borne in alternating, densely crowded whorls or low spirals of 5–6, 2–4 mm long, ca. 0.3 mm thick, subterete, acicular to quadrangular, with

long-decurrent and acroscopically adnate, hairy leaf bases, ascending and upward curved, glabrous, or with few lax trichomes above the base. **Strobili** usually numerous, sessile, terminating ultimate hanging branchlets, 5–20 mm long, ca. 3 mm in diameter. **Sporophylls** usually borne in alternating whorls of 5, ovate-deltoid, cuspidate, 1.5–2 mm long, ca. 1 mm wide, with membranous, coarsely erose-laciniate margins. **Sporangia** globose, ca. 0.5 mm in diameter, strongly anisovalvate. **Spores** rugate, without a distinct equatorial rim.

Road banks, moist disturbed soil in lower, wet montane forest, alt. 1000–1500 m, Amazonas, San Martín, Loreto, Huánuco.

Lower eastern slopes of the Andes in Peru and Ecuador.

Lycopodiella descendens is closely related to *L. cernua*, and is sometimes seen growing intermixed with it. In such situations intermediate individuals may be found. In addition to the key characters mentioned, *L. descendens* very often differs from *L. cernua* by its longer strobili.

Amazonas: Prov. Bagua, Mesones–Muro highway, 286 km E of Olmos, 8 km E of Montenegro, 650 m, *Huchison & Wright 3820* (F, UC, US). **San Martín:** Prov. Lamas, Dist. Lamas, Río Curiyacu, affluent of Río Cumbasa, ca. 450 m, *Belshaw 3585* (GH, MO, NY, US, US). Prov. Mariscal Cáceres, Tocache Neuvo–Juanjui road, km 88, 850 m, *D. Smith 2152* (AAU). Prov. Moyobamba, Jepelacio, Cerro Shalcahuro, 1320 m, *Fernández & Clematis 27* (USM). **Loreto:** Pumayacu, between Balsapuerto and Moyobamba, 600–1200 m, *Klug 3232* (F, G, GH, K, MO, NY, S, US). **Huánuco:** Prov. Huánuco, Dist. Churubamba, Hda. Mercedes, 1640 m, *Mexia 8195* (F, GH, K, S, UC, US). SW slope of the Río Llullapichis watershed, on the ascent of Cerros del Sira, ca. 1000 m, *Dudley 13125* (GH).

7. *Lycopodiella glaucescens* (Presl) B. Øllg., Opera Bot. 92: 176. 1987.

Lycopodium glaucescens Presl, Reliq. haenk. 1: 81. 1825. TYPE: Peru (Huánuco), In montanis ad Huanocco, *Haenke* (holotype, PRC!). *Palhinhaea glaucescens* (Presl) Holub, Folia Geobot. Phytotax. 26: 93. 1991.

Runner shoots long, robust, arching-looping to scandent, with initially erect, amply branched, up to several meters long, bending to long-scandent dendroid branch systems, these with several spreading or nodding to long pendulous, usually alternate, up to at least 40 cm long lateral branchlet systems. **Leaves of main axes** patent to reflexed, usually strongly upward curved to hook-shaped, 3–5 mm long, up to 1 mm wide, with terete to

quadrangular, hairy leaf bases, apically flattened, usually coriaceous. **Ultimate branchlets** 3–5 mm in diameter including leaves, the sterile ones often tapering to less than 2 mm in diameter. **Leaves of ultimate branchlets** borne in densely crowded, alternating whorls or low spirals of 4–6, acicular to lanceolate, usually with flattened apex, 2.5–4 mm long, 0.3–0.8(–1.0) mm wide, usually strongly upward curved or hook-shaped from a spreading or perpendicular to reflexed base, soft herbaceous to rigidly coriaceous, hairy only on leaf base. **Strobili** variable, 5–30 mm long, 3–4.5(–5) mm in diameter. **Sporophylls** borne in alternating whorls of 5, lanceolate-ovate, apically acute-acuminate, 2–3 mm long, 0.8–1.2 mm wide, with shallowly dentate-ciliate margins, of herbaceous, pale green texture throughout. **Sporangia** globose, strongly anisovalvate, 0.7 mm in diameter. **Spores** rugate, without a distinct equatorial rim.

Clearings and open places in wet upper montane forest, alt. 1600–3700 m, Cajamarca, San Martín, Huánuco, Pasco, Cuzco.

Costa Rica; Colombia to Peru; possibly farther north and south.

A remarkable species with often very long scandent dorsally arising shoots. Under favorable conditions, these may reach a length of several meters. *Lycopodiella glaucescens* is highly variable with respect to strobilus size, size, coarseness, and direction of the branchlet systems. Plants of exposed habitats are usually relatively short and compact and with rigid, coriaceous leaves, approaching the growth habit of *L. pendulina*, while individuals from protected habitats are longer, more lax, and soft and with long pendulous branchlets.

Cajamarca: Prov. Cutervo, La Pucarilla (San Andrés-Sócota), 2420 m, *López & Sagástegui 5459* (GH). **San Martín:** Huallaga, Valley of Río Apisoncho, 30 km above Jucusbamba, *Hamilton & Holligan 1248* (K). Prov. Mariscal Cáceres, Río Abiseo National Park, hill past Las Palmas, 2650–2750 m, *Young 4000* (USM). **Huánuco:** Prov. Huánuco, Carpish, 2850 m, *Asplund 13076* (S). Playapampa, 3000 m, *Macbride 4506* (F, G, US). **Pasco:** Prov. Oxapampa, Cord. San Gutardo, 2800 m, *León 523a* (AAU, USM). **Cuzco:** Prov. La Convención, Cord. Vilcabamba, 2825 m, *Dudley 10782* (USM).

8. *Lycopodiella pendulina* (Hooker) B. Øllg., Opera Bot. 92: 176. 1987.

Lycopodium pendulinum Hooker, Icon. pl. 1: t. 90. 1837. TYPE: Peru, Casapi, *Mathews 1776* (holotype, K!).

Lycopodium cernuum L. var. *pendulinum* (Hooker) Baker, Handb. Fern Allies 23. 1887.

Palhinhaea pendulina (Hooker) Holub, Folia Geobot. Phytotax. 26: 93. 1991.

Runner shoots robust, shallowly arching, with up to ca. 40 cm tall, erect dendroid branch systems, these with several subdecussate to upward alternate, sparsely subequally branched, up to 12(–20) cm long, usually long pendulous lateral branchlet systems. **Leaves of main axes** loosely appressed, upward curved, 5–7 mm long, up to 1 mm wide. **Ultimate branchlets** (3–)5–6(–9) mm in diameter including leaves, rarely tapering to 2 mm in diameter. **Branchlet leaves** borne in densely crowded alternating whorls or low spirals of 5–7, acicular, terete to quadrangular, or sometimes apically flattened, (3–)4–6 mm long, up to 1 mm wide, patent-ascending, upward curved, softly to firmly herbaceous, glabrous, or with few marginal cilia. Leaf bases and stem surfaces usually glabrous, rarely with short crisped trichomes. **Strobili** 10–20 mm long, 5–6 mm in diameter. **Sporophylls** borne in alternating whorls of 5–6, lanceolate-ovate, short acuminate, (2.5–)3–3.5 mm long, ca. 1.5 mm wide, with irregularly dentate, narrowly membranous margins, pale greenish, of herbaceous texture throughout. **Sporangia** globose, strongly anisovalvate, ca. 1 mm in diameter. **Spores** rugate, without a distinct equatorial rim.

Wet grassland, open spaces or clearings in the upper montane forest and, 2200–3600 m, Piura, Amazonas, Huánuco, Cuzco.

Costa Rica; Andes from Venezuela to Bolivia, southeastern Brazil.

Lycopodiella pendulina is most closely related to *L. glaucescens*, and distinguished from the latter by its stiffly erect main shoots with thick, sparsely ramified, weeping branchlet systems and large strobili.

Piura: Prov. Huancabamba, Loma Redonda (Sapalache–Chinguela), 2400 m, *Sagástegui et al. 10217* (AAU). **Amazonas:** Prov. Chachapoyas, Cerros Calla Calla, E side, 18 km above Leimebamba on road to Balsas, 3100 m, *Hutchison & Wright 5663* (BR, C, E, F, G, GH, M, MO, NY, S, UC, USM). Prov. Bagua, Cord. de Colán E of La Peca, 3400 m, *Barbour 3199* (AAU, MO). **Huánuco:** Prov. Huánuco, Carpish, 2800 m, *Asplund 13105* (S). Chushi, trail to Tambo de Vaca, *Bryan 681* (F, US). **Cuzco:** Prov. La Convención, Cord. Vilcabamba, 2825 m, *Dudley 10707, 10782* (GH, MO).

9. *Lycopodiella riofrioi* (Sodirol) B. Øllg., Opera Bot. 92: 176. 1987.

Lycopodium riofrioi Sodirol, Crypt. vasc. Quit. 582. 1893. TYPE: Ecuador (Prov. Pichincha), In silv.

occid. m. Pichincha ad Gualea, 9/888, *Sodi* (holotype, si 21230!).

Lycopodium pensum Lell., Proc. Biol. Soc. Wash. 89: 717, t. 2. 1977. TYPE: Costa Rica, Prov. Heredia, 6 mi from San Rafael de Heredia on slopes of Volcán Barba [Cerro Chompipe], *McAlpin 216* (holotype, DUKE; isotype, GH!).

Palhinhaea riofrioi (Sodi) Holub, Folia Geobot. Phytotax., Praha 26: 93. 1991.

Growth habit as in *Lycopodiella pendulina*, up to 2 m tall. **Branchlet leaves** imbricate, densely crowded, borne in alternating whorls of 4–6, lanceolate to ovate-lanceolate, acuminate, 2.5–4 mm long, ca. 1 mm wide, with densely ciliate-fimbriate margins, with a very short, patent, terete-subangular base. **Stems and leaf bases** densely hairy. **Strobili** 1–2.5 cm long, 3–5 mm thick including sporophylls. **Sporophylls** borne in alternating whorls of 5, ca. 2.5 mm long, ca. 1 mm wide. **Sporangia** 0.7–1 mm in diameter.

Wet montane forest, in clearings and on road banks, 1700–2600 m. To be expected in northernmost Peru.

Costa Rica; Panama; Venezuela; Colombia to southern Ecuador.

A very distinctive species with its smooth-appearing branchlets covered by closely imbricate, scalelike leaves.

Family 27. SELAGINELLACEAE

Selaginellaceae Milde, Höher. Sporenpfl. Deutschl. Schweiz 136. 1865, as Selaginelleae. TYPE: *Selaginella* Beauv.

Stem indurated or not, branched, bearing rather few, often long roots usually at a branch of the stem. **Leaves** simple, ca. 0.5–10 mm long, with 1 (very rarely 2) vein(s). **Sporangia** short-stalked, single, near the axil of a leaf. Heterosporous, spores without chlorophyll.

The Selaginellaceae are a distinctive family including the single genus *Selaginella*, only distantly related to others such as the Lycopodiaceae and

Isoetaceae. Heterospory, and the presence of vessels in some species of subgenus *Selaginella*, indicate the family is specialized.

I. Selaginella

Selaginella Beauv., Magasin Encycl. 5: 478. 1804; and Prod. Fam. Aethéog. 101. 1805, *nom. conserv.* TYPE: *Selaginella spinosa* Beauv., *nom. nov.* for *Lycopodium selaginoides* L. = *Selaginella selaginoides* (L.) Link. **Figure 9.**

Bryodesma Sojak. Preslia 64: 154. 1992. Type: *Bryodesma rupestris* (L.) Sojak (*Lycopodium rupestre* L.) = *Selaginella rupestris* (L.) Spring.

Terrestrial, rupestral, or rarely epiphytic. **Stem** slender, branched, sometimes dichotomously, prostrate-creeping or with ascending branches, or pendent-epiphytic, or erect from a usually stoloniferous base. **Leaves** ca. 1.0–10 mm long, with usually 1 vein, borne in a close spiral or usually alternate in 4 ranks. **Sporangia** large, borne in or near the axil of a well-differentiated sporophyll, in a quadrangular or (in *S. deflexa* and *S. selaginoides*) a cylindrical strobilus. **Megasporangia** commonly basal in the strobilus, usually with 4 megaspores, larger than the microsporangia and different in size and color. **Microsporangia** usually borne above the megasporangia and with many microspores. **Megaspores** tetrahedral-globose, trilete, the laesurae $\frac{3}{4}$ to usually equaling the radius, often with a more or less prominent equatorial ridge, rugose-reticulate, rugose, papillate, tuberculate, granulate, rarely nearly smooth on the proximal face. **Microspores** tetrahedral-globose, trilete, often compressed or the proximal face more or less depressed, the laesurae $\frac{1}{2}$ to equaling the radius, usually finely to coarsely echinate, rugose, papillate, perforate-cristate, or granulate.

Selaginella is a large genus of perhaps 700 species, with about 40 of them in Peru, or expected there. The descriptions are drawn from Peruvian material and are intended to be parallel within related groups of species. The genus has not been amenable to segregation although five subgenera are

FIG. 9. *Selaginella peruviana*: a, habit; b, tip of branch with aerial root. *Selaginella haematodes*: c, habit; d, portion of branch, abaxial side, showing axillary and lateral leaves. *Selaginella exaltata*: e, habit; f, portion of secondary branch, adaxial side, showing median leaves. (a, b from *Solomon & Nee 17895*, Bolivia, F; c, d from *Taylor 5049*, Brazil, F; e, f from *Bohs 2215*, Ecuador, F.)



currently recognized (Jermy, 1986), and Sojak has recently recognized a second genus, *Bryodesma*, for the *S. rupestris* group.

The genus is probably more diverse in Peru than presently known. Species are difficult to identify, and many may appear similar to the field botanist unacquainted with special specific characters. At the same time, a better understanding of the variation within species and the morphology of juvenile plants will lead to an increase in synonyms.

The species have been placed in a sequence that, presumably, extends from primitive to advanced. Species 1–2 are homophyllous, while the remainder of the species are heterophyllous.

Species 3–10 are prostrate and not articulate (both primitive characters), while species 11–12 are prostrate and articulate. These species relate to the former group by their small leaves and often intricate stems. Species 13–15 have erect, not articulate stems that are usually short and pinnately branched. Species 16–25 are also erect and not articulate but usually have a main stem with appressed leaves toward the base and flabellate branches. Species 17 may be unbranched or with irregular branches. Species 26–30 are prostrate and articulate, as are species 11–12. However, these have large leaves and mostly separate stems. Species 31–34 are articulate and erect (both derived characters). Species 35 is a climbing species and 36 is a highly derived, xeric species.

The following treatment is based to a large extent upon the published work of A. H. G. Alston

(1934), especially the (posthumous) publication with A. C. Jermy and J. M. Rankin (1981). The Koller and Scheckler (1986) paper is among the many that could be cited, but it is selected because of the great potential of their work to the classification of the genus.

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Key to Species of *Selaginella*

- a. Leaves of branches and stems more or less uniform, spirally arranged; main stem prostrate, creeping b
 - b. Leafy stem radially symmetrical; leaves all alike; base of the lower leaves abruptly adnate, distinct from the stem 1. *S. sellowii*
 - b. Leafy stem somewhat dorsiventral; upper leaves differ from the lower leaves on the same portion of the stem; base of the lower leaves strongly decurrent on the stem 2. *S. peruviana*
- a. Leaves of the branches and often of the main stem dimorphic, in 4 ranks with 2 smaller median ranks on the upper side of the leafy stem and 2 larger lateral ranks; main stem erect, assurgent at the apex, to prostrate c
 - c. Main stem very short, erect, bearing leafy branches that form a rosette; branches strongly involute when dry 36. *S. convoluta*
 - c. Main stem long, erect, assurgent at the apex, to prostrate; branches straight or nearly so when dry d
 - d. Main stem erect, uniformly red or reddish, especially below the basal branch, not articulate e
 - e. Acroscopic edge of lateral leaves ciliate or ciliolate, at least near the base; erect stem and branched portion ca. 10–25 cm, mostly 10–15 cm long 21. *S. erythropus*

- e. Acroscopic edge of lateral leaves minutely denticulate to essentially entire; erect stem and branched portion mostly 30–65 cm long 22. *S. haematodes*
- d. Main stem erect to prostrate, brownish, greenish, or stramineous, rarely red and then articulate (with a break, a dark ring, a swollen area, or usually a constriction) f
- f. Main stem climbing or scrambling to 8 m long, articulate 35. *S. exaltata*
- f. Main stem erect to prostrate, not exceeding 1 m long, articulate or not g
- g. Strobilus with sporophylls only on the upper side of the leafy stem 10. *S. ramosissima*
- g. Strobilus tetragonous, sporophylls spirally arranged on the stem h
- h. Branches pubescent, especially on the branch axils, trichomes sometimes sparse ...
..... 30. *S. articulata*
- h. Branches glabrous i
- i. Leaves tightly clasping the stems when dry 9. *S. microphylla*
- i. Leaves spreading, ascending or appressed, not clasping the stems when dry j
- j. Plants with an erect main stem and often a flabelliform arrangement of branches; basal part of the main stem usually with appressed leaves, these dimorphic or not; rhizophores usually confined to the basal portion of the main stem, or rarely above the first branch k
- k. Ultimate leafy branches 5–20 mm broad l
- l. Axis of primary branches fractiflex, branches sometimes flagelliform; main stem articulate 31. *S. parkeri*
- l. Axis of primary branches straight or nearly so, branches not flagelliform; main stem not articulate m
- m. Median leaves more or less acute to acuminate, not or hardly aristate
..... n
- n. Median leaves inequilateral, the outer side larger, the costa acentric
..... 24. *S. praestans*
- n. Median leaves equilateral, the sides nearly equal in size, the costa central 23. *S. quadrifaria*
- m. Median leaves aristate o
- o. Primary branches usually 1-pinnate, sometimes 2-pinnate with branches nearly parallel from the first branch to the apex of the main stem 16. *S. bombycina*
- o. The main stem and branches irregularly or dichotomously divided
..... p
- p. Branches usually few, erect, of irregular lengths, not forming a flabelliform arrangement 17. *S. chrysoleuca*
- p. Branches forming a broad, flabelliform arrangement
..... 18. *S. speciosa*
- k. Ultimate leafy branches 5 mm broad or less q
- q. Axis of primary branches fractiflex r
- r. Median leaves oblong, with a basal auricle that is entire or nearly so 32. *S. geniculata*
- r. Median leaves ovate-lanceolate, with a ciliolate basal auricle
..... 34. *S. stellata*
- q. Axis of primary branches straight or nearly so s
- s. Main stem articulate 33. *S. asperula*
- s. Main stem not articulate t
- t. Base of the main stem slender, 0.25–0.50 mm broad; leaves short, the longest 2 mm long .. 13. *S. novae-hollandiae*
- t. Base of the main stem stouter, 0.75–3.5 mm broad; longest leaves 2–5 mm long u
- u. Median leaves aristate 25. *S. haenkeana*
- u. Median leaves acute to acuminate, rarely a few aristate
..... v

- v. Leaves of the main stem distal to the second branch, strongly ascending to spreading (patent); stem and leaves near the axil of the first branch usually 4–5 mm broad 19. *S. lechleri*
- v. Leaves of the main stem distal to the second branch, appressed; stem and leaves near the axil of the first branch 1–3 mm broad 20. *S. anceps*
- j. Plants with a prostrate or assurgent, sometimes intricate, or rarely erect stem; basal part of the main stem with dimorphic leaves; lateral leaves spreading; rhizophores usually borne throughout the main stem, or at least above the first branch w
- w. Main stem articulate x
 - x. Leafy branches slender, 2–4 mm broad, often intricate y
 - y. Lateral leaves with ciliolate margins at the base, without a prolonged auricle 12. *S. lingulata*
 - y. Lateral leaves with entire margins, with 1 or 2 prolonged, ciliolate auricles 11. *S. diffusa*
 - x. Leafy branches 4–20 mm broad, not intricate z
 - z. Leafy branches 8–20 mm, often 10 mm broad aa
 - aa. Base of the lateral leaves without prolonged auricles 28. *S. trisulcata*
 - aa. Base of the lateral leaves with 1 or 2 prolonged auricles, the inner sometimes an acute lobe bb
 - bb. Leafy main stem 12 mm or less broad, glabrous; branches forming an open, dichotomous arrangement 29. *S. poeppigiana*
 - bb. Leafy main stem 15–20 mm broad, often pubescent beneath, especially on the axils, trichomes sometimes sparse; branches at the apex forming a broad, compact, flabellate arrangement 30. *S. articulata*
 - z. Leafy branches 4–8 mm, usually 5 mm broad cc
 - cc. Apical portion of the main stem, and often of the primary branches, forming a somewhat rhomboid arrangement, the apex acute to acuminate 26. *S. kunzeana*
 - cc. Apical portion of the main stem, and often of the primary branches, forming a broadly ovate to obdeltate arrangement, the apex obtuse to truncate 27. *S. silvestris*
- w. Main stems not articulate dd
 - dd. Median leaves with a short, acute apex often extended in a cusp 5. *S. truncata*
 - dd. Median leaves aristate or subaristate ee
 - ee. Edges of lateral leaves entire, denticulate, or ciliolate ff
 - ff. Leafy branches, when present, 5–20 mm, mostly ca. 15 mm broad; main stem with no, or rarely few primary branches, these strongly ascending, mostly dichotomous 17. *S. chrysoleuca*
 - ff. Leafy branches, 3–12 mm, mostly ca. 5 mm broad; main stem with many, spreading branches gg
 - gg. Stems erect; rhizophores confined to the base of the main stem or not beyond the first branch hh
 - hh. Ultimate branches short, the apex acute. 15. *S. flagellata*
 - hh. Ultimate branches longer, with the apex truncate to somewhat rounded 14. *S. xiphophylla*
 - gg. Stems prostrate, creeping, sometimes intricate, forming a mat;

- rhizophores extending to the stem apex, or above the first branch to ½ the length of the stem ii
- ii. Stems usually intricate, forming a mat; penultimate leafy branches 2–4 mm broad 6. *S. tarapotensis*
- ii. Stems elongate, discrete; penultimate leafy branches 4–10 mm broad jj
- jj. Median leaves orbicular, the base truncate; lateral leaves oblong with an obtuse apex 8. *S. producta*
- jj. Median leaves ovate to oblong, the base with an extended, round lobe; lateral leaves elongate-ovate, with an acute apex 7. *S. seemannii*
- ee. Edges of lateral leaves ciliate, the cilia most abundant from the base to the mid-part of the leaf kk
- kk. Median leaves without a prolonged auricle 3. *S. revoluta*
- kk. Median leaves with a prolonged auricle 11
- 11. Main stem short, erect; rhizophores at base of the stem or mostly below the first branch ... 13. *S. novae-hollandiae*
- 11. Main stems creeping, often intricate and forming a mat; rhizophores extending above the first branches 4. *S. brevifolia*

1. *Selaginella sellowii* Hieron., Hedwigia 39: 306. 1900. LECTOTYPE (by R. Tryon, 1955): Brazil, Paria de San Diego *Sellow*, in 1821 (holotype, B; frag., NY).

Selaginella rupestris f. *amazonica* Milde, Fil. Eur. Atlant. 263. 1867. TYPE: Peru, Cajamarca, (Río) Marañón, *Bonpland* (holotype, B; isotype, BM).

Selaginella amazonica (Milde) Hieron., Hedwigia 39: 310. 1900, not *S. amazonica* Spring, 1840.

Selaginella mildei Hieron., in Engler & Prantl, Nat. Pflanzenfam. 1 (4): 671. 1902, *nom. nov.* for *S. amazonica* (Milde) Hieron.

Main stem prostrate, creeping, assurgent at the tip, not articulate, pinnately branched throughout, green to brownish, glabrous. Primary **branches** mostly simple, 1-pinnate, or often 2-pinnate, the ultimate branches as broad as the main stem or nearly so, 1–1.5 mm broad including the leaves. **Rhizophores** throughout the stems, mostly at the axils of the branches. **Leaves** similar (homophyllous), spirally arranged, subulate, long-triangular to broadly lingulate to lanceolate, the edges whitish, denticulate, the apex setate, the seta opaque, milky-white, the base abruptly adnate, ciliate or ciliolate, rarely lacking cilia, abruptly distinct from the stem in form and color, glabrous.

On exposed or wooded, rocky bluffs, or among stones, from ca. 300 to 2900 m, Lambayeque, Cajamarca, Ancash, and Cuzco.

Central Mexico, Cuba, Venezuela, and Colombia south to Argentina, and eastern Brazil.

The species belongs to the *Sartorii* series of the *Selaginella rupestris* group and appears most closely allied to *S. sartorii* Hieron. Geographically it is wide-ranging from Mexico and Cuba through South America. It is readily distinguished from the nine others of series *S. sartorii* and other Peruvian species by the glabrous leaf bases, especially by the opaque, milky-white setae on the leaves. This and *S. peruviana* have elongate stems that differ from the radially symmetrical plants of *S. convoluta*.

Lambayeque: Hacienda Valor, *Ellenberg 3613* (GH). **Cajamarca:** between Llaconora and Namora, *Correll & Smith P893* (GH, MO). Between Jaén and Quemado, *Ferreira & Sanchez 19668* (USM). **Ancash:** Mancos, Yungay, *Tryon & Tryon 6551* (GH). **Cuzco:** Bües 608 (US); *Herrera 3009a* (US).

2. *Selaginella peruviana* (Milde) Hieron., Hedwigia 39: 307. 1900. **Figure 9a–b.**

Selaginella rupestris f. *peruviana* Milde, Fil. Eur. Atlant. 263. 1891. TYPE: Peru, Huánuco, *Ruíz 98* (holotype, B; isotype, NY).

Selaginella peruviana var. *dombeyana* Hieron., Hedwigia 39: 308. 1900. PARATYPE: Peru, *Dombey 14* (B).

Selaginella sheldonii Maxon, Proc. Biol. Soc. Wash. 31: 171. 1918. TYPE: United States, Quanaah Mountains, Oklahoma, *Sheldon 233* (holotype, US).

Main stem prostrate, creeping, not articulate, pinnately branched throughout, glabrous, green to brownish. Leafy **branches** forming compact to dif-

fuse mats with discrete, simple or 1-pinnate, sometimes 2-pinnate stems. **Rhizophores** borne throughout the stems at the axils of branches. **Leaves** generally similar (homophyllous), spirally arranged, setate, the seta usually more or less lutescent, or often not well differentiated in color, the base adnate, glabrous, sometimes denticulate, the edges usually ciliate, or sometimes somewhat pubescent, leaves on the underside of the stem differ from those on the upper side, on the same part of the stem, those on the upper side linear, acuminate to long-triangular, the lower leaves subulate, acuminate, broadest at or near the base, to linear-lanceolate, gradually distinct from the stem.

Mats on bluffs, dry rocky slopes, ledges or crevices of cliffs, exposed or in light shade, igneous, calcareous, or sandstone rock, 1750–4400 m, Cajamarca south to Puno.

Southwestern United States south to Puebla, Mexico; Peru to Argentina.

The species is recognized as the least specialized and basic species within the series *Eremophila*, in the treatment of the *Selaginella rupestris* group (Tryon, 1955). Geographically it is the widest ranging species of that series. On the basis of the slender leaves bearing long setae, it is most closely related to *S. arizonica* Maxon, a species of north-west Mexico and the states of Texas and Arizona. However, it is distinguished from this as well as Peruvian selaginellas by the lower leaves that are strongly decurrent on the stem. Among the Peruvian selaginellas, it is most closely allied with *S. sellowii*, another species with homophyllous leaves.

Cajamarca: Between Cajamarca and San Juan, Müller & Gutte 8869 (USM). **Ancash:** Near Mancos, Tryon & Tryon 6550 (GH). **Huánuco:** Prov. Huánuco, Plowman & Rury 11103 (F, GH, USM), Prov. Huánuco, Stork & Horton 9388 (F, UC). **Lima:** Prov. Canta, Punte San José, López & Riccio 10080 (GH). Prov. Huarochirí, León 583 (USM). **Junín:** Above Concepción, Correll & Smith P748 (GH, MO). Prov. Tarma, Illis et al. 108 (GH, wis). **Apurímac:** Prov. Andahuaylas, Stork & Horton 10719 (F, UC). **Cuzco:** Near Pisac, McDaniel & Gorski 11402 (GH, MO). Urubamba valley, León 443 (F, USM). Prov. Urubamba, Chicon, Vargas 11058 (F, UC). **Puno:** Near Puno, Solomon 2895 (F, MO).

3. *Selaginella revoluta* Baker, J. Bot. 21: 141. 1883.

TYPE: Venezuela, Amazonas, near Mau-pures, Spruce 3621 (holotype, K; isotypes, CGE, US).

Selaginella demissa Christ, Bull. Herb. Boissier 2, 1:

75. 1883. TYPE: Peru, Cerro Canchahuaya, Huber 1421 (holotype, P).

Main stem short, creeping, often forming compact mats, not articulate, stramineous, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** short, distant, usually 1–2-pinnate, extending to the base of the main stem, 3–5 mm broad including the leaves, the terminal branches short. **Rhizophores** extending from the base of the main stem to the apex of the branches. **Lateral leaves** above the first branch not imbricate, spreading, elongate-ovate, broadest at the base, 0.5–0.2 mm long, ca. 3 × longer than broad, acute, with a round, ciliolate, scarcely prolonged basal lobe, without conspicuous whitish borders, the edges with long cilia, these denser at the base. **Median leaves** suborbicular, broadest at the center, aristate, the arista ½ as long as the lamina, cuspidate, the auricles not prolonged, often with narrow, whitish borders, the edges denticulate.

In wet, primary forests, 100–1100 m, Loreto and Huánuco.

Costa Rica and Panama; in South America from the Guianas south to Peru and Brazil.

The compact, creeping habit of the plants with short, lateral branches bearing discrete, wide-spread leaves along the main stem form a distinctive growth pattern. The species was allied with *Selaginella producta* by Alston et al. (1981), but distinguished by the strongly tapering, ciliate, more acute lateral leaves, sometimes pubescent on the upper surface near the margin. However, that species also has broader, more delicate leafy stems.

Loreto: Prov. Maynas, Mishuyacu, Klug 1220 (F, US). Prov. Maynas, below Iquitos, Moran 3651 (MO). Gamitanacocha, Schunke 322 (F, GH, US, USM). **Huánuco:** Tingo María, Allard 20485 (MO), 20846 (US).

4. *Selaginella brevifolia* Baker, J. Bot. 21: 83. 1883.

TYPE: Brazil, Janarate Cochoeira, Rio Negro, Spruce 2547 (holotype, K; isotypes, BM, CGE).

Main stem prostrate, creeping, it and its branches forming a mat of stems, sometimes elongate to 15 cm, not articulate, stramineous, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves. Primary **branches** 2–3-pinnate, alternate, distant, extending to the base of the main stem, 2–3 mm broad including the leaves. **Rhizophores** above the first branch, up to

1/3 the length of the stem. **Lateral leaves** ovate, acute, ca. 1–2 mm long, without prolonged auricles, ciliate especially on the acroscopic margin, the cilia usually long, discrete. **Median leaves** ovate-elliptic, acuminate to aristate, the arista 1/4 the lamina length, the base with a broad, long, ciliolate auricle, without conspicuous whitish borders, the edges denticulate.

On soil and among rocks, along roadsides, 400–2400 m, Cajamarca, San Martín, and Huánuco.

Venezuela, Colombia, Peru, and western Amazonas, Brazil.

Although the plants are small and mosslike in habit, growing over soil or among rocks, they are well collected and known to be wide-ranging in South America and in Peru.

The species is considered close to the Greater Antillean *Selaginella cordifolia* but with longer aristae on the median leaves (Alston et al., 1981). It also resembles *S. novae-hollandiae*, but the strongly prostrate habit with rhizophores above the median part of the main stem contrast with the erect habit and rhizophores, mainly at the base of the stem in *S. novae-hollandiae*.

Cajamarca: Prov. Contumazá, Guzmango, *Sagástegui 3932* (GH). Prov. Cajamarca, El Molino, *Sagástegui 7995* (F). Contumazá, Lledén, *Sagástegui et al. 10887* (F). **San Martín:** Boquerón Pass, between Tingo María and Pucallpa, *Allard 22124* (US). **Huánuco:** Cushi, trail to Tambo de Vaca, *Bryan 718* (F, US).

5. *Selaginella truncata* A. Braun, Index Sem, Hort. Bot. Berol. Appendix 1857: 15. SYNTYPES: Colombia, Cundinamarca, Bogotá, Andes of New Grenada, *Karsten* (B, BM); Susumuco, *Triana 696* (BM), *238* (NY).

Selaginella weberbaurei Knox, Trans. Bot. Soc. Edinburgh 35: 282. 1950. Only spores are described. "TYPE": based on a specimen collected by Weberbauer, named by Hieronymus, B?

Main stem prostrate, assurgent, not articulate, stramineous, glabrous, the basal part with spreading leaves and often smaller appressed, ascending leaves. Primary **branches** 1–2-pinnate, pinnately branched, extending to the base of the main stem, the central branches distant on the main stem, strongly ascending, forming an open, dichotomous division of the branches, the ultimate branches as broad as the main stem, 4–6 mm broad including the leaves. **Rhizophores** slender, threadlike, throughout the main stem. **Lateral leaves** uniform

in length, 2–3 mm long, oblong to broader near the base, the apex obtuse, the base truncate, with narrow, whitish borders and delicate, long cilia at the edges, especially dense at the base. **Median leaves** ovate, the apex acute, sometimes with a short cusp, the base truncate, with whitish borders, the edges regularly ciliate or ciliolate, more strongly so at the base.

Epiphytic in dense jungle, or on rotted logs, in dense forests, 365–700 m, San Martín and Cuzco.

Venezuela and Colombia south to Bolivia.

The compact, deep green leaves, imbricate on the stems, give a distinctive aspect to the plants.

Ecological information on collections indicates the plants are epiphytic on trees 15 ft above the ground. This is corroborated by the dense rhizophores on the branches and the stems that are free from soil.

Selaginella applanata A. Braun, Ann. Sci. Nat. Bot. 5, 3: 274. 1865, may be a synonym; UC has a fragment of an isotype, Peru, Puno, San Gaván, (Gabán) *Lechleri 2405*.

San Martín: Prov. Lamas, San Antonio, *Belshaw 3569* (H, GH, UC, US). Guayrapurima, Tarapoto, *Spruce 4024* (GH, US). **Pasco:** Prov. Oxapampa, Cordillera de San Matías, *D. Smith 2000* (F). **Cuzco:** Prov. Quispicanchis, entre Inombaris y Quincemil, *Vargas 11690* (GH); entre Quincemil y San Lorenzo, *Vargas 16481* (GH).

6. *Selaginella tarapotensis* Baker, J. Bot. 21: 98. 1883. TYPE: Peru, Mt. Guayrapurima, near Tarapoto, *Spruce 4625* (holotype, K; isotypes, BM, CGE, US).

Main stem prostrate or assurgent at the tip, often forming a mat of stems, not articulate, stramineous, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** 3–4-pinnate, alternate, distant, extending to the base of the main stem, 2–4 mm broad including the leaves, the ultimate branches short. **Rhizophores** filamentous, dense at the base, extending nearly to the stem apex. **Lateral leaves** oblong-lanceolate, but not imbricate on the main stem, 0.5–2.0 mm long, approximately more than 3 × longer than broad, obtuse to acute, the auricles not prolonged, without conspicuous whitish borders, the edges short-denticulate. **Median leaves** rhomboidal to ovate, aristate, the arista slender, usually whitish, 1/2 as long to nearly equal the length of the lamina, the base not or hardly prolonged, often with narrow, whitish borders that extend into the whitish arista, the edges denticulate.

Rarely epiphytic, in deep cloud forests, and on shaded banks bordering roads, 500–1200 m, Amazonas and San Martín south to Cuzco.

Costa Rica south to Bolivia.

The truncate leaf bases on both lateral and median leaves, along with the rhomboid shape and prominent aristata on the median leaves, distinguish the species. This is one of the slender-stemmed, mat-forming species most closely resembling *Selaginella revoluta*.

Selaginella calosticha Spring, *Nouv. Mém. Acad. roy Sci. Belg.* 24: 206. 1849. TYPE: Venezuela, Caracas, *Funck & Schlim 3321* (κ), may be an earlier name for this species. Two Allard collections from Peru—20821 and 21206—are cited as *S. calosticha* in Alston et al. (1981).

Amazonas: Prov. Bagua, Montenegro, *Hutchison & Wright 3822* (F, GH, UC, US). Monte Campana, near Taramoto, *Spruce cf 4625* (us). **San Martín:** Tocache Nuevo-Juanjui, *Smith et al. 2132A* (UC). **Huánuco:** Prov. Tingo María, Cueva de las Pavas, *Aldave & Fernandez 5578* (GH). **Pasco:** Oxapampa, Cordillera San Matías, *León et al. 321* (F, MO, USM). **Junín:** Satipo, Pichanaki, *León 222* (F, USM). **Cuzco:** Prov. Paucartambo, Quebrada Quita Calzón, *León et al. 2936* (USM). Achirani, *Vargas 11147* (F).

7. *Selaginella seemannii* Baker, *J. Bot.* 21: 244. 1883. TYPE: Colombia, Chocó, Cacaqual Island, *Seemann 1006* (holotype, κ ; isotype, BM).

Main stem assurgent at the tip, ca. 5–25 cm long, not articulate, stramineous, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** 2–3-pinnate, arising a short distance above the base of the main stem, sometimes gradually reduced, forming a flabelliform arrangement, the ultimate leafy branches short, unequal, 4–6 mm broad including the leaves. **Rhizophores** mostly near the base to the mid-portion of the main stem. **Lateral leaves** elongate-ovate, broadest at the base, spreading above the first branch, approximate, imbricate toward the apex, 2–3 mm long, membranous, acute, the base truncate or 1 side enlarged and rounded, with narrow, whitish, denticulate edges, or sparsely denticulate along the base. **Median leaves** elongate-ovate, the apex acuminate to subaristate, the arista less than $\frac{1}{4}$ the lamina length, the base truncate or with an enlarged, rounded outer side, with narrow, whitish, denticulate edges, dentate at the base.

On open floor of dense forest, in deep ravines,

or dense, seasonally flooded forest, 130–625 m, Loreto and Huánuco.

Costa Rica, Colombia, Suriname, Ecuador, and Peru.

The flabelliform arrangement of the branches, with rhizophores concentrated at the base of the stem, distinguishes this from other slender-stemmed species such as *S. producta* and *S. revoluta* that clearly are prostrate, creeping.

Although the species is reported to be wide-ranging from Costa Rica to Peru, we have seen collections only from Loreto, and Huánuco in Peru.

Loreto: Prov. Maynas, Calentura, *Killip & Smith 29141* (us). Prov. Maynas, Iquitos, *Tryon & Tryon 5195* (F, GH, US, USM). Prov. Maynas, Yanamono Tourist Camp, *van der Werff et al. 9959* (UC). Rio Itaya, *Ll. Williams 238* (F, US). **Huánuco:** Tingo María, La Cueva de las Pavas, *Allard 20514* (us).

8. *Selaginella producta* Baker, *J. Bot.* 21: 243. 1883. LECTOTYPE (chosen by Alston et al., 1981); Brazil, Amazonas, between Barcellos and San Gabriel, *Spruce 2043* (holotype, BM; isotype, CGE).

Main stem prostrate or assurgent, 10–20 cm long, not articulate, several stems usually arising at the base of the plants, stramineous to somewhat greenish, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves. Primary **branches** 2–3-pinnate, with distant secondary divisions spreading, sometimes forming a broad, flabelliform arrangement, or with elongate, alternatively pinnate branches as long as the main stem or nearly so, 5–10 mm broad including the leaves, the ultimate leafy branches short, unequal in length. **Rhizophores** mostly at the stem base, or extending to the central part of the main stem and branches. **Lateral leaves** oblong to ovate, spreading, approximate to somewhat imbricate above the first branch, 2–5 mm, usually 4 mm long, broader at the base, obtuse to subacute, the base truncate, or with an enlarged, round basal lobe, without conspicuous whitish borders, the edges sparsely denticulate with the teeth somewhat denser at the base. **Median leaves** suborbicular, broadest at the center, the apex acuminate to subaristate and cuspidate, the arista usually $\frac{1}{4}$ or less the lamina length, the base truncate, with or without narrow, whitish margins, the edges evenly denticulate.

Terrestrial, or a trunk epiphyte, on rotted logs, or commonly on white sand of the forest floor, 100–860 m, Loreto, Huánuco, and Pasco.

Tobago and Trinidad, French Guiana west to Colombia and south to Peru and Brazil.

The species is compared to *Selaginella revoluta* by Alston et al. (1981). However, it differs in broader lateral leaves that have a truncate base and lack cilia. The imbricate leaves covering most of the branches resemble those of *S. truncata* but are clearly broader and may have a whitish surface.

Loreto: Prov. Maynas, Iquitos, *Killip & Smith 27322* (GH, US). Iquitos, *Klug 198* (F, US). Iquitos, *Revilla 4285* (F, MO). Iquitos, *McDaniel et al. 22107* (F). Mishana, *Solomon 3595* (MO). Prov. Maynas, Alpahuayo, *van der Werff et al. 10262* (F, MO). **Huánuco:** Río Llullapichis, Cerros del Sira, *Wolfe 12264* (GH). **Pasco:** Prov. Oxapampa, Palcazú, *Foster 9532* (MO, USM).

9. *Selaginella microphylla* (HBK.) Spring, Bull. Acad. roy Sci. Bruxelles 10: 234. 1843.

Lycopodium microphyllum HBK., Nov. gen. sp. 1: 37. 1816. TYPE: Colombia, Cauca, Qulcacé, *Bonpland* (holotype, P?, photo, GH; isotype, BM).

Main stem short, creeping, usually it and its branches forming a compact mat, not articulate, stramineous or greenish, glabrous. Primary **branches** often intricate, 1–2-pinnate, short, distant, extending to the base of the main stem, slender, ca. 0.5 mm broad, including the leaves. **Rhizophores** abundant at the base, extending nearly to the apex of the main stem and branches. **Lateral leaves** extending nearly to the base of the stems, minute, inserted obliquely, 0.25–0.50 mm long, ovate or ovate-elliptical, tightly clasping the stem and enveloping the median leaves when dry, imbricate, less so on the ultimate branches, the apex acute with a more or less extended cusp, the borders whitish, ciliolate to fimbriate along the edges, especially at the base. **Median leaves** ovate, about half as long as the lateral leaves, subacute, not auriculate, the edges with regular, dense cilia, the border broad, whitish.

Terrestrial in open forest, on soil or among damp rocks, in deep shade, 800–2700 m, Cajamarca, La Libertad, Huancavelica, Apurímac, and Cuzco.

Costa Rica and Panama, Venezuela along the Andes south to Argentina, east to southern Brazil, Paraguay and Uruguay.

The abundant cilia along the borders of the leaves, and especially the lateral leaves that strongly clasp the dry stems, readily characterize the species. The slender, intricate stems have a growth

form that resembles some species in the *Selaginella rupestris* group.

The species is known from a broad geographic range through South America and has been widely collected in Peru. Specimens from southern Colombia collected by Bonpland on his travels in South America with Humboldt represent the type.

Cajamarca: Prov. Contumazá, El Túnel, *Sagástegui et al. 12565* (MO). **La Libertad:** Prov. Pataz, Vista Florida, *León & Young 1086* (USM). **Huancavelica:** Prov. Tuya- cajo, Surcubamba, *Tovar 3696* (GH). **Apurímac:** Prov. Abancay, *Vargas 16584* (GH). **Cuzco:** Prov. Convención, Sahuayaco, *Bües 834* (US). Urubamba Valley, San Miguel, *Cook & Gilbert 1782* (US).

10. *Selaginella ramosissima* Baker, J. Bot. 23: 295. TYPE: Peru, San Martín, near Tarapoto, *Spruce 4088* (holotype, K; isotypes, BM, GH, NY).

Main stem erect, or assurgent at the tip, short, less than 10 cm long, not articulate, greenish, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves. Leafy **branches** 2-pinnate, ascending, longest in the central part of the stem, the secondary branches straight, ascending, forming a short, deltate arrangement of the stems, ca. 3 mm broad. **Rhizophores** mostly at the base extending to the first branch. **Lateral leaves** slender, elongate, broadest at the center, closely placed to somewhat imbricate especially on the secondary branches, oblong, 0.5–1.0 mm long, membranous, acute, the base truncate, not prolonged, with narrow, whitish borders, the edges denticulate especially at the base. **Median leaves** slender, elongate-ovate, or somewhat broader at the center, membranaceous, acuminate to aristate, the arista $\frac{1}{4}$ or more the length of the lamina, the base more or less equal, without a prolonged auricle, the borders narrow, whitish, the edges denticulate. **Strobilus** dorsiventral with 2 ranks of sporophylls on the upper surface of the leafy stem.

Along roadside or bank of stream below the forest, 200–2700 m, Cajamarca, San Martín, Lima, and Cuzco.

Ecuador and Peru.

The strobilus is dorsiventral with two ranks of sporophylls on the upper part of the leafy stem. This readily distinguishes the species from all others in Peru. The thinner, membranaceous texture of the leaves also is a characteristic of the Peruvian plants.

Cajamarca: Prov. Hualgayoc, *Soukup 3872* (us). **Lima:** Prov. Cantua, *Acleto 758* (USM). **Cuzco:** *Bües* in Junio, 1930 (F).

11. *Selaginella diffusa* (Presl) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 143. 1843.

Lycopodium diffusum Presl, Reliq. haenk. 78. 1825. TYPE: Panama, *Haenke* (holotype, PR; isotype, B).

Selaginella eggersii Sodiro, Crypt. vasc. Quit. 605. 1893. TYPE: Ecuador, Valle Takatanga, *Sodiro* (holotype, not found; isotype, us).

Selaginella atirrensis Hieron., in Engler & Prantl, Nat. Pflanzenfam. 1 (4), 711. 1901. LECTOTYPE: (by Alston, 1955), Costa Rica, Cartago, near Atirro, *Donn. Smith 5103* (holotype, us; isotype, NY).

Main stem elongate, prostrate, assurgent at the tips, sometimes compact and matlike, articulate, stramineous, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** distant, ascending, unequally forked, 2–3-pinnate, extending to or nearly to the base of the main stem, 2–4 mm broad including the leaves, the ultimate branches short. **Rhizophores** hairlike, extending nearly to the apex of the branches. **Lateral leaves** spaced or approximate, not imbricate, 1–2 mm long, elliptical-lanceolate, acute, short, with a prolonged auricle, often densely ciliolate, sometimes with whitish borders, the edges sparsely ciliolate to nearly entire. **Median leaves** elongate-ovate, broadest near the middle, the apex long-acuminate, the base with a prolonged, lingulate auricle that is usually ciliolate, with or without a whitish border, the edges finely denticulate.

In moist places in deep forest, on steep banks, on logs or among rocks, sometimes forming large mats, 1100–2100 m. Huánuco, and Pasco south to Cuzco.

Costa Rica; Trinidad; South America east to Suriname, and in the Andes south to Bolivia.

Plants appear to have lateral leaves of more than one form. Most abundant are slender, elliptical leaves with entire margins. Other, larger leaves are broader with the base abundantly ciliolate, and the cilia sometimes extending along the margins to the mid-region of the leaf. The ciliolate base resembles that of the median leaves.

Selaginella atirrensis Hieron. is included here although it has been recognized as a distinct species on the basis of its acute median leaves. It is not easily distinguished on leaf shape and possibly intergrades with *S. diffusa*.

Huánuco: Tingo María, *Croat 21245* (MO, UC). Churubamba, *Mexia 8256* (F, GH, MO, UC, US). Tingo María, *Tryon & Tryon 5227* (F, GH, US, USM). **Junín:** near La Merced, *Killip & Smith 23949* (F, GH). Chanchamayo valley, *Schunke 197* (F). Tarma, Pan de Azúcar, *Velarde 5490* (GH). **Pasco:** Prov. Oxapampa, between Oxapampa and Paucartambo, *D. Smith 1466* (MO). Ucayali: Bquerón, *Ferreira 8128* (USM). **Cuzco:** Prov. La Convención, Río Mapitunuari, *Dudley 11352* (GH, MO). Kosñipata, Sta. Isabel, *Vargas 23011* (GH).

12. *Selaginella lingulata* Spring, Nouv. Mém. Acad. roy. Sci. Belg. 24: 224. 1849. TYPE: Ecuador, Pichincha, *Jameson* (holotype, K; isotype, BM).

Selaginella intacta Baker, J. Bot. 21: 335. 1883. TYPE: Ecuador, San Nicolás, *Sodiro* (holotype, K).

Main stem prostrate, intricate, usually compact, forming a dense mat, articulate, stramineous, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves. Leafy **branches** 1–3-pinnate, usually pinnately branched, distant, extending to the base of the main stem, the ultimate branches short, 2–4 mm broad. **Rhizophores** extending nearly to the stem apex. **Lateral leaves** closely placed to distant, 1–3 mm long, spreading on the upper part of the stems and penultimate branches, oblong, acute, the basal lobes more or less equal, not prolonged, with long, dense cilia, without whitish borders, the edges entire. **Median leaves** elongate-ovate, the apex usually long-acuminate, the base with 2 equally long auricles, ciliate at the base, without conspicuously whitish borders, the edges denticulate above.

On soil or among rocks, in shade, sometimes forming dense mats on hillsides or on steep banks, sometimes in deep forests, 1000–1300 m, Pasco and Junín.

Colombia south to Bolivia.

The long marginal cilia at the base of the leaves form a small fringe especially on the lateral leaves. The median leaves are clearly more slender than the lateral ones and have a long-acuminate apex in the material examined. However, the apex of the median leaves was considered as acute in the treatment by Alston et al. (1981).

The axillary leaves are distinctive, somewhat larger than the median and lateral leaves, and more or less ovate, acute, usually with one prolonged auricle and few long cilia.

Pasco: Pichis trail, San Nicolás (as Junín), *Killip & Smith 26056* (F, GH, US). **Junín:** Above San Ramón,

Schunke 4251 (us), Chanchamayo Valley, *Schunke 230* (us), 788 (us). Prov. Tarma, San Ramón, *Tryon & Tryon 5448* (F, GH, US).

13. *Selaginella novae-hollandiae* (Sw.) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 234. 1843.

Lycopodium novae-hollandiae Sw., Syn. fil. 184, 410. 1806. TYPE: "Nova Hollandiae," probably an error for Nova Granada, not located.

Selaginella pearcei Baker, J. Bot. 22: 246. 1884. TYPE: Peru, Huánuco, Cordilleras of Pozuzo, *Pearce 249* (holotype, K).

Selaginella chionoloma Crabbe & Jermy, Amer. Fern J. 63: 137. 1973. TYPE: Peru, Cuzco, Cuquipata, *Herrera 1636* (holotype, us; isotype, BM).

Main stem short, erect or assurgent, usually less than 20 cm long, not articulate, stramineous, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves, or the basal part with only appressed leaves. Primary **branches** 2–3-pinnate, often forming a complex system of branches broadest at the base, the penultimate branches straight or nearly so, 1–3 mm broad including the leaves. **Rhizophores** at base of the main stem, mostly below the first branch. **Lateral leaves** 0.5–2.0 mm long, elliptical to somewhat ovate, acute, not auriculate, the base ciliolate, sometimes with narrow whitish borders, the edges ciliolate, often densely so. **Median leaves** ovate, usually more or less elongate, the apex acuminate to aristate, the arista $\frac{1}{4}$ the lamina length, the base with a prolonged, lingulate, ciliolate auricle, or a somewhat enlarged, round, ciliate base, the borders narrow, whitish, the edges ciliolate or denticulate.

On damp, shaded ledges or crevices of rock faces, or moist banks along streams, wooded hillsides, open woods, dense forests, sometimes carpeting the forest floor, rarely epiphytic, 400–3600 m, Lambayeque, south to Puno.

Nicaragua south to Bolivia and Argentina.

This differs from other slender-stemmed species in lacking articulations on the stems and having generally smaller leaves. It is one of the most common species of tropical America and is wide-ranging in Peru.

Lambayeque: Along Olmos-Jaén road, *Correll & Smith P826* (GH, MO, US). **Cajamarca:** El Molino, *Sagdstegui et al. 7995* (F, MO, UC). **Amazonas:** Prov. Bagua, Chachapoyas, *Hutchison & Wright 5782* (F, GH, MO, UC, US, USM). **La Libertad:** Prov. Otuzco, road to Paranday, *López 1044* (us). **San Martín:** Río Sión, *Schunke 3494* (F, US). **Loreto:** Balsapuerto, *Killip & Smith 28488* (F, GH). **Huá-**

nuco: Tingo María (as San Martín), *Allard 21130* (MO, UC). La cueva de las Pavas, *Schunke 3257* (F, GH, US). **Lima:** Matucana, *Bryan 48* (F, MO). **Junín:** Prov. Tarma, San Ramón, *H. Iltis & C. Iltis 18* (GH, WIS). E of Quimiri Bridge, *Killip & Smith 23945* (F, GH). **Ucayali:** Boqueron Padre Abad (as Loreto), *Schunke 3065* (F, GH, US). **Huan-cavelica:** Surcubamba, *Tovar 3682* (GH). **Ayachucho:** Ccarrapa, *Killip & Smith 22331* (F, GH, US). **Apurímac:** Prov. Abancay, *Vargas 11083* (GH). **Cuzco:** Chincheros, *King et al. 293* (USM). Machu Picchu, *Léon 457* (USM). **Puno:** Prov. Carabaya, Ollachea, *Vargas 6914* (us).

14. *Selaginella xiphophylla* Baker, J. Bot. 22: 296. 1884. TYPE: Peru, San Martín, Mt. Guayrapurima, near Tarapoto, *Spruce 3990* (holotype, K; isotypes, BM, CGE, GH, NY).

Main stem erect, ascending, 10–14 cm long, not articulate, stramineous to greenish, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 1–2-pinnate, alternate, distant, extending to, or nearly to the base of the main stem, the lower branches usually longest, the penultimate leafy branches 6–12 mm broad. **Rhizophores** confined to the lower $\frac{1}{2}$ – $\frac{1}{2}$ of the main stem, rarely above. **Lateral leaves** ascending to somewhat appressed, those above the first branch approximate, 2–6 mm long, oblong-lanceolate, the apex acute, the base truncate, with denticulate edges especially at the base. **Median leaves** ovate-lanceolate, gradually attenuate, aristate, the arista as long as the lamina, the base truncate, the outer side ciliolate, with narrow, whitish denticulate margins, the teeth extending onto the arista.

Panama, Colombia, and Peru.

We have seen only a single collection, the type material from San Martín listed above. The species is also reported from Panama and Colombia by Valdespino (1993). The small size, erect habit of the plants, the rhizophores borne in the basal $\frac{1}{2}$ – $\frac{1}{2}$ of the main stem, and median leaves with an arista as long as the lamina are characteristics by which the species can be recognized.

15. *Selaginella flagellata* Spring, Bull. Acad. roy. Sci. Bruxelles 10: 228. 1843. TYPE: French Guiana, Río Inini, "source of the Río Oyapok," *Leprieur* (holotype, LG; isotype, P).

Selaginella regularis Baker, J. Bot. 22: 277. 1884. TYPE: Peru, San Martín, near Tarapoto, *Spruce 3977* (holotype, K; isotypes, BM, GCE).

Main stem erect, short, 5–20 cm long, the base 2–3 cm below the leafy branches, not articulate,

stramineous, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** 2–3-pinnate, sessile or subsessile, distant, spreading, the central ones longest, the lateral branches ascending in a broad, frondlike arrangement, the penultimate leafy branches straight, 3–5 mm broad. **Rhizophores** basal, or mostly below the lowest branches. **Lateral leaves** 1–3 mm long, elliptic, or broadest at the base, attenuate to acute, the base truncate, the borders not conspicuously whitish, the edges denticulate, **Median leaves** ovate to somewhat elongate, aristate, the arista $\frac{1}{4}$ as long as the lamina, the base not auriculate, the borders narrow, whitish or not, the edges denticulate, especially at the base.

Terrestrial, or climbing in cloud forest, among moist rocks and on cliffs, 200–2000 m, San Martín, Loreto, and Cuzco.

Mexico south to French Guiana and Brazil, and in the Andes to Bolivia.

The short, ultimate branches clearly differ from other slender, erect-stemmed species in Peru. There is a general resemblance to *Selaginella xiphophylla* in the erect habit and rhizophores confined to the basal part of the main stem.

San Martín: Juan Jui, *Klug 4230* (F, GH, US). **Loreto:** Pongo de Manseriche, *Mexia 6333A* (UC). **Cuzco:** Prov. Convención, Echarate, *Bües 787* (US).

16. *Selaginella bombycina* Spring, Nouv. Mém. Acad. roy. Sci. Belg. 24: 191. 1849. TYPE: Peru, San Martín, *Matthews* (Mathews) 1781 (holotype, K).

Main stem erect, 25–30 cm long, 1-pinnate, not articulate, stramineous, glabrous, the basal part with appressed, ascending leaves. Primary **branches** alternate, mostly 1-pinnate, extending in nearly parallel alignment from the first branch to the apex of the stem, 10–16 mm broad including the leaves, the axes straight or nearly so. **Rhizophores** largely at the base of the main stem, rarely with a few among the main branches. **Lateral leaves** imbricate on the lateral branches, oblong, slender 5–10 mm long, 4 or 5 × longer than broad, obtuse, the base with a slightly enlarged, round lobe, usually densely ciliate, without conspicuous whitish borders. **Median leaves** suborbicular, asymmetric, the outer side larger, aristate, the arista $\frac{1}{2}$ to equal the length of the lamina, with a somewhat longer basal auricle, the base ciliolate, without conspicuous

whitish borders, cilia often dense along the outer edges.

On hillsides and deep ravines of wet forests, 700–1100 m, San Martín and Huánuco. In Peru nearly restricted to the area around Tingo María.

Costa Rica south to Peru.

The plants usually have long primary branches that are 1-pinnate. This feature and the ciliate lateral leaves distinguished the species.

San Martín: Prov. Mariscal Cáceres, 4 km de Puerto Pizana, *Schunke 4893* (F, US). **Huánuco:** Tingo María, *Tryon & Tryon 5255* (GH, US). Prov. Leoncio Prado, Tingo María, *Plowman & Kennedy 5732* (F, GH, USM). Prov. Leoncio Prado, Rupa Rupa, *Schunke 10172* (F, MO).

17. *Selaginella chrysoleuca* Spring, Bull. Acad. roy. Sci. Bruxelles 10: 226. 1843. TYPE: Bolivia, *D'Orbigny*, (holotype, P).

Selaginella sprucei Hooker, Sec. cent. ferns, t. 83. 1861. TYPE: Peru, San Martín, Mt. Campana, near Tarapoto, *Spruce 4623* (holotype, K; isotypes, BM, CGE, US).

Main stem below the first branch short, usually less than 5 cm long, erect, not articulate, greenish, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves, or the basal part only with appressed, ascending leaves. Leafy **branches** dichotomously divided 1 or 2 ×, often with 1 longer branch, sometimes with tuft-like branches arising from a slender creeping runner, ultimate leafy branches 5–20 mm, mostly 15 mm broad, axes of primary branches straight. **Rhizophores** mostly at the base, sometimes extending to $\frac{1}{3}$ the length of the stem, but not among the broad, leafy branches. **Lateral leaves** spreading above the first branch, imbricate, 5–10 mm long, oblong to linear, 3–5 × longer than broad, the apex acute to obtuse, asymmetrical, with the upper (acrossopic) edge somewhat larger, round, and finely denticulate, with narrow whitish borders, the edges finely denticulate. **Median leaves** elongate-ovate to suborbicular, asymmetrical, acuminate to aristate, the arista sometimes $\frac{1}{2}$ the lamina length, the base truncate with a slightly enlarged, round lobe, the borders narrow, whitish, the edges finely denticulate.

Among mosses on rocks, in damp soil, on shaded slopes of ravines, on moist riverbanks, and in dense, dark cloud forests, 400–2000 m, Amazonas, south to Cuzco.

Panama, Venezuela to Bolivia.

Similarities in the general aspect of the broad, leafy branches, in the asymmetrical shape of the median leaves with a long arista and dentate margins, suggest an alliance with *Selaginella speciosa*.

Amazonas: Prov. Bagua, La Peca, *Barbour 2839* (MO). Prov. Bagua, near Montenegro, *Hutchison & Wright 3821* (F, GH, UC, US). Above Montenegro, *Wurdack 1879* (F, GH, UC, US). **San Martín:** Road from Tarapoto to Yurimaguas, *Kennedy 3544* (F, US). Between Tarapoto and Yurimaguas, *Knapp & Mallet 8474* (F, MO). Tarapoto–Yurimaguas road, *McDaniel 13805* (GH, MO). Near Tarapoto, *Spruce 4628* (GH). **Ucayali** (as Loreto): Between Tingo María and Pucallpa, *Ferreyra 1008* (USM). **Huánuco:** Cerros del Sira, Río Lullapichis Watershed, *Dudley 13360* (GH). **Cuzco:** Prov. La Convención, *Dudley 10355* (GH, MO).

18. *Selaginella speciosa* A. Braun, Ann. Sci. Nat. Bot. 5, 3: 274. 1865. TYPE: Colombia, Bogotá, *Triana* (holotype, B?; isotype, BM).

Selaginella huberi Christ, Bull. Herb. Boissier 2, 1: 73. 1901. TYPE: Peru, "entre Ucayali et Huallaga," *Huber 1547* (holotype, P).

Main stem erect, 30–70 cm long, not articulate, green to brownish, glabrous, the basal part with appressed, ascending leaves. Primary branches dichotomous, long, 1-pinnate, with 2 or more long divisions, the lower ones divided at short intervals forming a frondlike, somewhat flabelliform arrangement, 10–20 mm broad including the leaves, the axes straight. **Rhizophores** at the base of the main stem. **Lateral leaves** closely placed to imbricate, linear-oblong, to broader above the base, 8–10 mm long, 5–6× longer than broad, asymmetrical, the acroscopic side larger, the apex obtuse, the base truncate, the borders sometimes whitish at the base, the edges finely denticulate. **Median leaves** orbicular to somewhat ovate, asymmetric with the outer side larger, acuminate to aristate, the arista often nearly ½ as long as the lamina, the auricles not prolonged, borders narrow, whitish, the edges finely denticulate.

In deep, shady forests, in rain forests, in moist ravines, rarely epiphytic, 100–600 m, Amazonas and Loreto.

Colombia, Ecuador, and Peru.

This and *Selaginella chrysoleuca* have exceptionally broad leafy branches and asymmetrical median leaves that are long aristate. Both species occur in dense forest in the Andes, but *S. speciosa* occurs mainly in the north of Peru while *S. chrysoleuca* extends south to Cuzco.

Amazonas: Huampami, *Kayap 1311* (UC). **Loreto:** Between Yurimaguas and Balsapuerto, *Killip & Smith 28340* (F, US). Balsapuerto, *Klug 2921* (F, GH, MO, US). Prov. Maynas, Iquitos, *McDaniel & Rimachi 17473* (GH). Sierra del Pongo, *Mexia 6283* (F, GH, MO, UC, US). Gamitanacocha, Río Mazán, *Schunke 109* (F, GH, UC, US).

19. *Selaginella lechleri* Hieron., in Engler & Prantl, Nat. Pflanzenfam. 1 (4): 683. 1901. LECTOTYPE (chosen by Alston et al., 1981): Peru, Puno, near San Gaván (San Gabán), *Lechler 2159* (holotype, B?; isotype, BM).

Main stem erect, 12–40 cm long, not articulate, stramineous, glabrous, the basal part with appressed, ascending leaves. Primary branches 3-pinnate, forming an extended, flabelliform arrangement, distant, the lower stalked, those above sessile or nearly so, penultimate leafy branches straight or nearly so, ultimate leafy branches slender, 3–5 mm broad. **Rhizophores** confined to the base of the main stem. **Lateral leaves** of the main stem, above the first branch, ascending, coarse, mostly strongly imbricate, 2–5 mm long, oblong, acute, the auricles not prolonged, without conspicuous whitish borders, the edges denticulate to short ciliate, the cilia denser at the base. **Median leaves** elongate, ovate, acuminate, the base sometimes unequal, with a slightly enlarged auricle, not or sparsely ciliolate, without conspicuous whitish borders, the edges slightly denticulate or entire.

Terrestrial on clay or sandy soil, along trails or on stream banks in primary forest or rain forests, 130–1200 m, Amazonas and Loreto south to Puno. Colombia and Peru.

This taxon seems to intergrade with *Selaginella anceps* but is maintained here in its traditional sense. The broad, erect stems with appressed leaves, the primary branches forming a broad, flabelliform arrangement, and small size of the leaves on the ultimate branches are similar to those of *S. anceps*.

Amazonas: E of Cinkan, *Berlin 254* (F, MO, UC). **Loreto:** Prov. Maynas, Puca Urquillo, *Plowman et al. 6628* (F, US). La Victoria, *Ll. Williams 2919* (F, US). **Pasco:** Prov. Oxapampa, between Puerto Bermúdez and San Matías, *León et al. 333* (F, USM). Puerto Bermúdez (as Junín), *Killip & Smith 26467* (F, GH). **Cuzco:** between Mistiana and Keros, *Scolnik 868* (UC). **Madre de Dios:** Alto Madre de Dios, *Rauh & Hirsch P1570* (GH). **Puno:** Prov. Carabaya, Qllachea a Quillabamba, *Vargas 17539* (GH).

20. *Selaginella anceps* (Presl) Presl, Abh. Böhn. Ges. Wiss. 5, 3: 581. (Bot. Bemerk., 151). 1844.

Lycopodium anceps Presl, Reliq. haenk. 1: 80. 1825. TYPE: "Luzon," but probably from Peru, *Haenke* (holotype, PR, photo, GH).

Lycopodium gracile Poirlet, in Lam., Encycl. suppl. 3: 551. 1814. TYPE: Peru (Holotype, *Herb. Desvaux* P, photo GH).

Selaginella gracilis (Poirlet) Hieron., Hedwigia 58: 293. 1917, not Moore, 1886.

Main stem erect, 20–25 cm or longer, not articulate, 2–3.5 mm broad at the base, stramineous, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 3–4-pinnate, forming an elongate, flabelliform arrangement, distant, stalked, the penultimate branches straight or nearly so, the ultimate leafy branches slender, 1–2 mm broad. **Rhizophores** confined to the base of the main stem. **Lateral leaves** above the first branch, appressed, 2–3 mm long, elongate-ovate, broadest at the base, acute, with a somewhat prolonged, ciliate auricle, without conspicuous whitish borders, long ciliate at the base of the leaf. **Median leaves** ovate-elongate, acuminate with a somewhat prolonged auricle or an enlarged, ciliolate basal lobe, the borders not conspicuously whitish, the edges usually prominently ciliolate.

Disturbed forests, primary and secondary rain forests, steep hillsides in wet forests, 150–1500 m, San Martín and Loreto to Cuzco and Madre de Dios.

Costa Rica south to Venezuela and to Bolivia.

On the basis of similarities in the small, imbricate leaves densely covering the ultimate branches *Selaginella anceps* appears to be allied to *S. lechleri*. However, the usually denticulate base of the median leaves in *S. lechleri* is distinct from the usually prominently ciliolate one in *S. anceps*.

San Martín: Between Tocache Nuevo and Juanjui, *Croat* 58038 (F, MO). **Loreto:** Pongo Manseriche, *Mexia* 6371 (GH, MO, UC, US). **Huánuco:** Pampayacu, *Kanehira* 118 (GH, US). **Pasco:** Prov. Oxapampa, Palcazú, *Foster & d'Achille* 10177 (USM). **Junín:** Río Perené, *Killip & Smith* 25104 (F, GH, US). Perené, *Seibert* 2193 (F, MO, US). **Ayacucho:** Estrella, between Huanta and Río Apurímac, *Killip & Smith* 22671 (F, GH, US). **Cuzco:** Prov. Convención, *Dudley* 11381 (GH, MO). **Madre de Dios:** Prov. Manú, Atalaya, *Foster & Wachter* 7456 (MO).

21. *Selaginella erythropus* (Mart.) Spring, in Martius, Fl. bras. 1 (2): 125. 1840.

Lycopodium erythropus Martius, Icon. pl. crypt. 39. 1834. TYPE: Brazil, Piauí, *Martius* (holotype, BR).

Plants 10–25 cm, mostly 10–15 cm long. **Main**

stem erect and simple below the lowest, well-developed branch, not articulate, reddish, glabrous, the basal part with appressed, ascending leaves. Primary **branches** often irregular, mostly 2-pinnate, ultimate branches not exceeding 5 mm broad, including the leaves. **Rhizophores** usually confined to the base of the main stem, reddish. **Lateral leaves** strongly imbricate, reddish, especially the borders, the color extending into the marginal cilia, elongate-oblong, 0.25–0.5 mm long, the acroscopic side somewhat larger, acuminate (not aristate), with a rounded, denticulate basal lobe, the upper edges ciliate or ciliolate. **Median leaves** elongate-ovate, strongly imbricate, somewhat asymmetrical, acute to aristate, the base more or less truncate, the borders whitish, the edges denticulate, somewhat denser at the base.

On moist riverbanks, steep, wet road banks, thickets in dense forests, sometimes forming dark green mounds on the floor of lowland rain forests, 250–1800 m, Amazonas south to Cuzco.

Costa Rica; Colombia to Bolivia; Brazil.

Among the species with erect main stems, *Selaginella erythropus* is distinguished by the reddish color of the main stem that often extends into the branches and rhizophores, and by the small size of the plants. It also differs from *S. haematodes* by the ciliate or ciliolate lateral leaves.

Amazonas: Prov. Bagua, between Aramango and Montenegro, *López et al.* 4212 (GH, MO). **San Martín:** Juan Jui, *Klug* 4267 (GH, MO, US). Tarapoto, *Spruce* 3989 (GH, US). **Junín:** Colonia Perené, *Killip & Smith* 24918 (F, GH, US). **La Merced,** *Macbride* 5549 (F, US). **Ayacucho:** Estrella, between Huanta and Río Apurímac, *Killip & Smith* 22664 (F, US). **Cuzco:** Prov. La Convención, *Dudley* 11438 (GH).

22. *Selaginella haematodes* (Kunze) Spring, in Martius, Fl. bras. 1 (2): 126. 1840. **Figure 9c-d.**

Lycopodium haematodes Kunze, Linnaea 9: 9. 1834. TYPE: Peru, San Martín, Mission Tocache, *Poeppig*, in June 1830 (isotype, K).

Selaginella filicina Spring, Nouv. Mém. Acad. roy. Sci. Belg. 24: 189, 1849. SYNTYPE: Peru, *Mathews* (Mathews) 4036 (K). Other collections from Venezuela are also cited.

Plants 30–65 cm long. **Main stem** erect, not articulate, bright red below the branches, glabrous, the basal part with appressed, ascending leaves. Primary **branches** usually red, ultimate branches 3–8 mm broad including the leaves, the basal part

with appressed, ascending leaves. **Rhizophores** near the base of the main stem, deep red. **Lateral leaves** often reddish, oblong to elongate-ovate, broader at the base, 0.25–2.0 mm long, acute, the base truncate, without conspicuous whitish borders, the upper (acroscopic) edge finely denticulate, the teeth longer toward the apex, or nearly entire. **Median leaves** slender, elongate-ovate, acuminate to aristate, the arista $\frac{1}{4}$ or less the lamina length, the base truncate, with narrow, whitish borders, the edges denticulate especially near the apex.

Frequent along riverbanks, on steep, moist hillsides, or scattered on floor of dense forests, primary forests, rocky hillsides, or along trails, 135–900 m, San Martín and Loreto, south to Madre de Dios.

Panama, and Venezuela south to Bolivia.

The large, deep green, branches borne on long, simple, red-colored stems, readily distinguish the species. The vivid red color extends into the base of the main branches and also to the rhizophores that are confined to the basal part of the main stem.

San Martín: Tocache Nueve, *Schunke 7077* (F, US). Prov. Mariscal Cáceres, Uchiza, *Schunke 3202* (F, GH, US). Tarapoto, *Spruce 4036* (GH, US). **Loreto:** San Antonio, Río Samira, *Ayala & Arévalo 4227* (F, MO). Puerto Arturo, *Killip & Smith 27747* (F, GH, US). Cueva de las Pavas, *Fukushima 6521* (F, GH, MO). **Huanáco:** Prov. Huánuco, *Mexia 8302* (GH, MO, UC). **Pasco:** Pichis Trail, *Killip & Smith 26214* (F). **Junín:** La Merced, *Soukup 2369* (F, GH). **Madre de Dios:** Cocha Cashu, lake of Río Manú, *Foster et al. 3417* (F).

23. *Selaginella quadrifaria* Alston et al., Bull. Brit. Mus. (Nat. Hist.) Bot. 9: 261. 1981. TYPE: Peru, Prov. Loreto, Sierra del Pongo, *Mexia 6282* (holotype, BM; isotypes, GH, UC, US).

Main stem erect, 20–70 cm long, not articulate, stramineous, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 3–4-pinnate, distant, ascending, usually dichotomously divided, forming a broad, flabellate arrangement of ultimate branches, 8–20 mm broad including the leaves, the axes straight. **Rhizophores** confined to the base of the main stem. **Lateral leaves** coarse, rigid, imbricate, 4–8 mm long, oblong or broader near the base, equilateral, with a central costa, the apex acute, the base truncate, with an enlarged, rounded, ciliolate lobe, without conspicuous whitish borders, the edges denticulate. **Median leaves** ovate, equilateral, with a central costa, acute, the

base truncate, the edges sometimes narrow, whitish, finely denticulate.

In dense forest or rain forest, on slopes, on well-drained soils, 450–860 m, Amazonas to Pasco.

Colombia and Peru.

Among related species with an erect stem and appressed leaves *Selaginella quadrifaria* is generally distinguished by the median leaves that are equilateral and not or hardly aristate. Differences from *S. praestans* are noted under that species.

Amazonas: Prov. Bagua, near Montenegro, *Hutchison & Wright 3821B* (UC). Prov. Bagua, near Campamento, *Wurdack 1869* (GH, US). **Huanuco:** Cerro del Sira, Río Lullapichis, *Wolf 12263B* (F, US). **Pasco:** (as Junín) Puerto Yessup, *Killip & Smith 26372* (F, US). Prov. Oxapampa, valle del Palcazú, Iscozacín, *Foster 4556* (F). Cabeza de Mono, near Iscozacín, *D. Smith 3752* (UC).

24. *Selaginella praestans* Alston et al., Bull. Brit. Mus. (Nat. Hist.) Bot. 9: 260. 1981.

Selaginella sprucei A. Braun, Ann. Sci. Nat. Bot. 5, 3: 277. 1865, not Hooker 1861. TYPE: Peru, San Martín, near Tarapoto, Guayrapurina, *Spruce 4788* (not 4708 as originally cited) (holotype, G; isotypes, BM, NY).

Main stem erect, 20–70 cm long, not articulate, green to brownish, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 1–2-pinnate, distant, ascending, sparingly pinnate, the basal ones often longer, the axes straight, ultimate branches 10–15 mm broad including the leaves. **Rhizophores** confined to the base of the main stem. **Lateral leaves** above the first branches, ascending, imbricate, those below coarse, elongate-ovate to oblong, broadest at the base, 7–8 mm long, 3 or 4 × longer than broad, inequilateral, the acroscopic side larger, the costa acentric, acute to obtuse, the base truncate, or with a slightly enlarged, ciliolate auricle, without conspicuous whitish borders, the edges delicately ciliolate, sometimes denticulate, **Median leaves** suborbicular to somewhat ovate, asymmetric, inequilateral, the outer side larger, acute, the base truncate, without conspicuous whitish borders, the edges ciliolate or entire.

In dense shade of deep woods or rain forests, and along stream sides, 630–1500 m, San Martín, Huánuco, and Pasco.

Colombia to Peru.

The species is similar to *Selaginella quadrifaria* in the robust size of the plants and coarse leaves

appressed to the main stem. It can be distinguished from that species by the inequilateral shape and acentric costa of the lateral and median leaves in contrast to the equilateral leaves and centric costa in *S. quadrifaria*.

San Martín: Valley of Huallaga, between Tocache Nuevo and Juanjuí, *Croat 58057* (MO). **Huánuco:** Prov. Huánuco, Cotirarda, *Mexia 8196* (BM, GH, MO, UC, US). **Pasco:** Prov. Oxapampa, between Iscozacín and Villa America, *D. Smith 2840* (F).

25. *Selaginella haenkeana* Spring. Bull. Acad. roy. Sci. Bruxelles 10: 225. 1843. TYPE: probably Peru, "cordilleris chilensibus," *Häenke* (holotype, PR; photo, GH; isotypes, B, US).

Selaginella dimorpha Klotzsch, Linnaea 18: 523. 1844. TYPE: "Auf den Anden von Chile," *Häenke* (holotype, B; isotypes, PR, US). Probably the same Peru collection cited above.

Main stem erect, up to 40 cm or more long, usually unbranched $\frac{1}{3}$ or more above the base of the main stem, the base stout, 1–3 mm broad, not articulate, greenish to stramineous, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 1-pinnate, sessile or subsessile, distant, spreading, often arching upward, the central ones usually longest, slender, the axes straight, ultimate branches not more than 5 mm broad including the leaves. **Rhizophores** basal, or below the lowest branch. **Lateral leaves** 2–3 mm long, oblong, acute, without prolonged auricles, with long, discrete cilia especially dense at the leaf base. **Median leaves** ovate to somewhat elongate, aristate, the arista slender, $\frac{1}{4}$ or less the lamina length, the base not auriculate, the borders narrow, whitish or not, the edges long-ciliate, especially long and dense at the base.

Terrestrial, among rocks, or climbing, in cloud forest and dense forest, 1700–2000 m, Amazonas, and Pasco.

Colombia, south to Bolivia.

Well-developed plants often have an unusual branching system with a long, slender central stem and widely spaced, 1-pinnate lateral branches bearing short, ultimate divisions.

Amazonas: Prov. Bagua, La Peca, *Barbour 2820* (F, MO, UC), *2961* (F, MO). **Pasco:** Pichis Trail, Dos de Mayo (as Junín), *Killip & Smith 25843* (F, GH).

26. *Selaginella kunzeana* A. Braun, Ann. Sci. Nat. Bot. 5, 3: 296. 1865. LECTOTYPE (chosen

by Alston et al., 1981): Peru, Huánuco, Pampayacu, *Poeppig 195* (holotype, B; isotype, BM, P).

Main stem prostrate long-creeping to assurgent, articulate, stramineous, glabrous, the basal part with spreading leaves and often smaller, appressed, ascending leaves. Primary **branches** 2–3-pinnate, ascending, mostly widely distant, these as well as the apex of the main stem forming a rhomboid arrangement, with an acute to acuminate apex, ultimate branches 5–8 mm broad including the leaves. **Rhizophores** extending above the lowest branches, mostly in the lower half of the stem. **Lateral leaves** above the first branch distant, wide-spreading, imbricate at the stem apex, 2–3 mm long, oblong, elongate with somewhat parallel sides, acute, the base with a prolonged auricle forming a round or slender lobe, with narrow, whitish, finely denticulate edges, the teeth especially dense at the base. **Median leaves** slender, elliptic, the apex long-acuminate to aristate, the arista to $\frac{1}{4}$ the lamina length, the base prolonged with one, sometimes two, large, auricles, with narrow, whitish, finely denticulate edges.

Trailing on steep banks, in dense woods, often in disturbed areas, 500–1950 m, Huánuco, south to Cuzco.

Mexico to Panama; Venezuela, Andes of Colombia to Peru.

A widely distributed species occurring from Mexico to Peru, with a broad range in Peru, often in disturbed places. The rhomboid arrangement of the terminal, leafy branches distinguishes this from other articulate, prostrate species.

Huánuco: Prov. Huánuco (as San Martín), Tingo María, *Allard 20361* (US); *Asplund 12140* (US). Hacienda Mercedes, *Mexia 8197* (F, GH, MO, UC, USM). **Pasco:** south of Pozuzo, *Teppner 79/269* (US). **Ucayali:** Divisoria, Cerro Azul, *Tryon & Tryon 5272* (F, GH, US, USM). **Ayacucho:** Prov. La Mar, southwest of Hacienda Luisiana, *Dudley 11721* (GH). Estrella, between Huanta and Río Apurímac, *Killip & Smith 22663* (GH, US). **Cuzco:** Prov. Quispicanchis, Marcapata, *Vargas 3178* (MO, US). Kosñipata, *Velarde 7987* (GH).

27. *Selaginella silvestris* Asplund, Ark. f. Bot. 20A (7): 30. 1926. TYPE: Bolivia, Sur Yungas, El Chaco, *Asplund 1140* (holotype, UPS; frag., BM; photo, GH).

Main stem prostrate, long-creeping to decumbent, articulate, stramineous, glabrous, the basal part with spreading leaves, and often smaller, ap-

pressed, ascending leaves. Primary **branches** 2–3-pinnate, often dichotomous, forming a broadly ovate to obdelatate arrangement, the ultimate leafy branches short, with a round to truncate apex, 4–8, usually 5 mm broad including the leaves. **Rhizophores** mostly at the base of the main stem, extending above the first branch. **Lateral leaves** distant, spreading above the first branch, 3–4 mm long, oblong, somewhat broader near the base, asymmetrical, the apex obtuse to acute, the auricles not prolonged, without conspicuous whitish borders, the edges denticulate, especially at the base. **Median leaves** elongate-ovate, usually acuminate, or if aristate the arista less than $\frac{1}{4}$ the lamina length, the base unequal with 1 prolonged, curved auricle that may be up to $\frac{1}{2}$ the length of the lamina, the borders not conspicuously whitish, the edges prominently denticulate.

In humid forests, tropical rain forests, wooded ravines or thickets, also among rocks, rarely on rock walls or epiphytic, 650–3000 m, Cajamarca, and Amazonas, south to Ayacucho and Cuzco.

Mexico south to Panama; Venezuela and Colombia south to Bolivia.

The long-creeping stems with abundant rhizophores and prolonged auricles on the median leaves suggest an alliance with *Selaginella trisulcata*.

Cajamarca: Cueva San Andrés, *Velarde 6984* (GH). Prov. Cutervo, Guta de las Huacharos, San Andrés, *López & Sagástegui 5404* (GH). **Amazonas:** Prov. Chachapoyas, Quebrada Molino, *Wurdack 636* (F, GH, UC, US); Prov. Bagua, 25 km E of La Peca, *Barbour 2962* (F, MO). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo Nacional Park, *Young & León 4957* (HUT, USM). **Huánuco:** Prov. Huánuco, Carpish, *Asplund 12842* (US). **Pasco:** Oxapampa, *León et al. 913* (F). **Junín:** Yucapata, Yaupi, *Woytkowski 6627* (MO, US). **Huancavelica:** Prov. Tayacaja, Marcavalle, *Tovar 4754* (GH). **Ayacucho:** Ccarrapa, *Killip & Smith 22359* (US). **Cuzco:** Machu Picchu, *Peyton & Peyton 1320* (GH, MO); *Núñez 7516* (MO, UC).

28. *Selaginella trisulcata* Asplund, Ark. f. Bot. 20A (7): 34. 1926. TYPE: Bolivia, La Paz, El Chaco, *Asplund 1482* (holotype, UPS; photo, GH).

Selaginella poeppigiana var. *peruviana* A. Braun, Ann. Sci. Nat. Bot. 5, 3: 295. 1865. TYPE: Peru, Puno, near Tabina, *Lechler 2015* (holotype, B?).

Main stem prostrate, elongate, creeping, only rarely assurgent at the apex, articulate, pale green or sometimes light brown, glabrous, the basal part with spreading leaves, and often smaller, appressed, ascending leaves. Primary **branches** 3–4-

pinnate, distant, extending to the base of the main stem, more or less equally divided, in a flabelliform arrangement, the terminal branches nearly the same length, 8–12 mm broad including the leaves. **Rhizophores** long, coarse, stramineous, throughout the stems. **Lateral leaves** above the first branch spreading, distant, imbricate only on the ultimate leafy branches, 6–8 mm long, oblong-lanceolate, the sides more or less parallel, symmetrical, acute, the auricles not prolonged, without whitish borders, the edges denticulate, sometimes sparingly. **Median leaves** elongate-ovate, long-acuminate to subaristate, the arista less than $\frac{1}{4}$ the lamina, the base with a prolonged, lingulate auricle, the borders narrow, whitish or not, denticulate along the edges.

In moist ravines, in secondary forest, primary rain forests, in soil among rocks, 730–2700 m, Amazonas, south to Puno.

Ecuador to Bolivia.

The general aspect of the leaves and system of branches is similar to those of *Selaginella poeppigiana* and *S. articulata*, but the lateral leaves in those species have prolonged auricles that are not found in *S. trisulcata*. The stem also has two vascular bundles.

Amazonas: Prov. Bongará, N of Pedro Ruíz, *Smith & Vasquez 4896* (MO, UC, USM). **Huánuco:** Carpish Pass, *Allard 20996* (US). **Pasco:** Prov. Oxapampa, *Smith & Canne 5824* (MO). Prov. Oxapampa, Canyon de Huáncabamba, *León 670* (F, GH). **Junín:** Carpapata, above Huacapistana, *Killip & Smith 24467* (US). Yaupe, *Woytkowski 6331* (MO, US). **Ayacucho:** Between Huanta and Río Apurímac, *Killip & Smith 22751* (F, US). **Cuzco:** Ca. 5 km N of Aguas Calientes, *Solomon 3162* (MO). Portero, 8 km W of Quillabamba, *Tryon & Tryon 5394* (F, GH, US).

29. *Selaginella poeppigiana* (Spring) Splitg., Tijdschr. Naturl. Gesch. Physiol. 7: 443. 1840.

Selaginella sulcata subsp. *poeppigiana* Spring, Flora (Jena), 21: 185. 1838. TYPE: Ecuador, Pichincha, *Jameson* (holotype, K).

Main stem prostrate, long-creeping, ca. 20–40 cm long, articulate, stramineous, sometimes light brown at the apex, glabrous, the basal part with spreading leaves, and often appressed, ascending leaves. Leafy **branches** 3–4-pinnate, dichotomous, in a subflabellate arrangement, extending to the base of the main stem, the ultimate branches similar in length or nearly so, 8–10 mm broad. **Rhizophores** at the base of the main stem, extending to the upper branches nearly to the apex. **Lateral**

leaves above the first branch distant, spreading to patent, 4–6 mm, usually 5 mm long, oblong, symmetrical or nearly so, acute, the base narrowed with 1 or 2, prolonged, acute or lingulate, ciliate auricles, without conspicuous whitish borders, the edges finely denticulate. **Median leaves** elongate-ovate, long-acuminate or subaristate, the arista less than $\frac{1}{4}$ the lamina length, the base with a prolonged, lingulate, often ciliate auricle, without conspicuous borders, the edges sparsely denticulate.

Creeping, prostrate, forming dense mats on shaded floor of wet forest, trailing along banks and roadsides, or in rock crevices, 900–2800 m, Amazonas south to Puno.

Ecuador and Peru.

The long, creeping stems, with abundant rhizophores throughout and in a subflabelliform arrangement, suggest alliances with *Selaginella trisulcata* and *S. articulata*. However, the leafy branches are not as broad, and usually more open and dichotomous than in those species.

Amazonas: Prov. Bagua, La Peca, *Barbour 2493* (F, MO, UC), *2819* (F, MO). La Peca, Serrania de Bagua, *Gentry et al. 23065* (F, MO, UC). **San Martín:** Prov. Moyobamba, *Ferreira 18518* (USM). Tarapoto, *Spruce 4626* (GH, US). **Loreto:** Upper Río Macusari, below Ecuadorian border, *McDaniel 10984* (GH, MO). **Huánuco:** Pampayacu, *Kanehira 182* (GH, US). **Pasco:** Prov. Oxapampa, Río San Alberto, *León 645* (F, USM). **Junín:** Above San Ramón, *Killip & Smith 24657* (F, GH); Chanchamayo Valley, *Schunke 192* (F), *194* (F), *231* (F). **Cuzco:** Prov. Paucartambo, Suecia, *Woytkowski 175* (USM). **Puno:** Churumayo, *Soukup 434* (GH).

30. *Selaginella articulata* (Kunze) Spring, *Flora* (Jena), 21: 182. 1838.

Lycopodium articulatum Kunze, *Linnaea* 9: 10, 1834. TYPE: Peru, Tocache, *Poeppig*, in 1830 (not located).

Main stem prostrate, long-creeping, articulate, stramineous or light brown near the apex, pubescent especially at the apex and branch axils, or the main stem glabrescent. Leafy **branches** usually 3-pinnate, the apex forming a broad, compact, flabelliform arrangement, the ultimate branches 10–20 mm broad. **Rhizophores** long, coarse, numerous, extending $\frac{3}{4}$ the length of the stem, stramineous or golden-colored. **Lateral leaves** closely placed to somewhat imbricate at the apex, those on the leafy branches oblong, spreading, approximate, 8–10 mm long, oblong, somewhat broader near the base, nearly symmetrical, obtuse to acute,

with a prolonged, round auricle, the edges narrow, whitish, denticulate to entire. **Median leaves** short, ovate, the apex attenuate, the base with 2 prolonged, round auricles, the edges narrow, whitish, finely denticulate.

Plants subrepent, on floor of rain forest, along streams and roadsides, 350–2000 m, Amazonas and Loreto south to Pasco and Ucayali.

Panama; Suriname and French Guiana; Peru, Bolivia, Brazil, Paraguay, and Argentina.

The large, flabellately aligned branches with imbricate leaves on the terminal portion of the stems compose form-flattened sprays that distinguish this from other Peruvian species. The prolonged basal auricles on the outer side of the median leaves are also exceptional.

Amazonas: Prov. Bagua, Montenegro, *Hutchison & Wright 3749* (F, GH, MO, UC, US). Prov. Bagua, near Campamento, *Wurdack 1892* (F, GH, UC, USM). **San Martín:** Prov. Mariscal Cáceres, Tocache Nuevo, *Schunke 6916* (F, MO, UC). Tarapoto, *Spruce 4627* (GH, US). **Loreto:** Prov. Maynas, *Poeppig*, in 1831 (MO). **Pasco:** Prov. Oxapampa, *Smith & Salick 8366* (MO). **Ucayali:** Padre Abad, *Schunke 3074* (F, GH).

31. *Selaginella parkeri* (Hooker & Grev.) Spring, *Bull. Acad. roy. Sci. Bruxelles* 10: 146. 1843.

Lycopodium parkeri Hooker & Grev., *Bot. Misc.* 2: 388. 1831. TYPE: Guyana, Demerara, *Parker* (holotype, K).

Selaginella pedata Klotzsch, *Linnaea* 18: 521. 1844. TYPE: Guyana, *Schomburgk 118* (holotype, B?; isotype, BM).

Selaginella fragilis A. Braun, *Ann. Sci. Nat. Bot.* 5, 3: 305. 1865. TYPE: Brazil, Amazonas, Río Vaupes, *Spruce 2533* (holotype, B?; isotype, BM, CGE).

Selaginella brachylepis Christ, *Bull. Herb. Boissier* 2, 1: 74. 1901. TYPE: Peru, "entre Ucayali et Huallaga," *Huber* (holotype, P).

Main stem erect, 20–25 cm long, articulate, stramineous, or rarely red, glabrous, the basal part with appressed, ascending leaves. Primary **branches** 3–4-pinnate, sessile, the axis fractiflex, the branches forming compact, frondlike, flabelliform sprays, ultimate branches 5–12 mm broad including the leaves. **Rhizophores** at or near the base of the main stem, well below the first branch. **Lateral leaves** above the first branch, coarse, spreading to somewhat ascending, usually approximate, 4–6 mm long, oblong, broader just above the base, acute, the base usually with a prolonged, denticulate auricle, sometimes 2, 1 an acute lobe, with narrow whitish borders or not, the edges dentic-

ulate, the teeth somewhat longer and denser at the base. **Median leaves** lanceolate, the apex long-acuminate, the base with a prolonged, peltate, lingulate auricle, or sometimes 2, without conspicuous borders, the edges finely denticulate.

Primary forests, sometimes in wet or swampy forests, on sand or clay soils, usually in deep shade, 140–650 m, Amazonas and Loreto, south to Pasco.

Colombia and Peru; the Guianas, Amazonian Venezuela; Brazil.

The plants have stems with one vascular bundle, and there are short auricles on the axillary leaves similar to those on the median leaves. The long main stems bearing flagelliform branches that appear somewhat frondlike, and the fractiflex axes of the primary branches clearly suggest alliances between this and *S. geniculata*. Some specimens with unusually attenuated, flagelliform branches have been recognized as a distinct species, *Selaginella fragilis*.

Amazonas: Prov. Bagua, Montenegro, *Hutchison & Wright 3821A* (UC). **San Martín:** Alto Río Huallaga, Juan Jui, *Klug 3831* (F, GH, both mixed with *S. anceps*). **Loreto:** Prov. Requena, *van der Werff et al. 9966* (MO, UC), *10108* (MO, UC). **Huánuco:** Prov. Pachitea, Bosque Nacional de Iparia, *Schunke 2258* (F, GH, US). **Pasco:** Prov. Oxapampa, Quebrada Castilla, *León & Young 1036* (F, GH). Prov. Oxapampa, Iscozacín, *D. Smith 3735* (MO, UC).

32. *Selaginella geniculata* (Presl) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 230. 1843.

Lycopodium geniculatum Presl, Reliq. haenk. 1: 80. 1825. TYPE: "Luzon," but doubtless Peru or Ecuador, *Haenke* (holotype, PR; photo, BM, GH).

Selaginella ferruminata Spring, Bull. Acad. roy. Sci. Bruxelles 10: 231. 1843, TYPE: Peru, Pangoa, *Matthews* (Mathews) *1083* (holotype, K; isotypes, GH, US).

Selaginella elongata Klotzsch, Linnaea 18: 522. 1844. TYPE: Peru, Cuchero, *Ruiz 94* (holotype, B).

Selaginella nodosa Presl, Abh. Böhm Ges. Wiss. 5 (2): 580 (Bot. Bermerk. 50). 1844. TYPE: Peru, Casapi, *Poeppig* (not located).

Selaginella tomentosa Spring, Nouv. Mém. Acad. roy. Sci. Belg. 24: 231. 1849. TYPE: Colombia, Cauca, Gorgona Isl., *Hinds* (holotype, K).

Main stem erect, 10–50 cm or longer, articulate, stramineous, glabrous, or sometimes pubescent, the basal part with appressed, ascending leaves. **Primary branches** 3–4-pinnate, sessile above the lowest branches, forming flat, imbricate sprays in

an extended flabelliform, frondlike arrangement, axis of the primary branches fractiflex, the ultimate leafy branches 2–5 mm broad. **Rhizophores** borne at the base of the main stem, or below the first branch. **Lateral leaves** of the main stem, above the first branches, coarse, ascending or spreading, usually approximate, those below distinct, peltate, 2–5 mm long, elongate-ovate, broadest above the base, acute, the base with a short, acute lobe, without conspicuous whitish borders, the edges denticulate, especially at the base. **Median leaves** imbricate, oblong, acute to acuminate with a long, lingulate auricle, without conspicuous whitish borders, the edges entire or nearly so.

On white sand or clay soil in high forest or rain forest, usually terrestrial but sometimes on tree trunks, or on rocks, 120–1500 m, Amazonas and Loreto south to Cuzco and Madre de Dios.

Colombia, Ecuador and Peru.

The axillary leaves are truncate; there are two vascular bundles at the base of the main stem, and there are peltate leaves on the main stem, below the first branch. These characters distinguish the species from other erect, articulate species of Peru.

An alliance with *Selaginella parkeri* is indicated by the long main stem, the alignment of branches, and the fractiflex axes of the primary branches; however, the leafy branches are not as broad as in *S. parkeri*.

Amazonas: Río Cenepa, vicinity of Huampami, *Berlin 633* (F, MO, UC); *Ancuash 1042* (MO, UC). Prov. Bagua, above Cascadas de Mayasi, *Wurdack 1894* (F, GH, UC, US, USM). **San Martín:** Prov. Mariscal Cáceres, Campanilla, *Schunke 4118* (F, US). **Loreto:** Between Yurimaguas and Balsapuerto, *Killip & Smith 28250* (F, GH, US). Prov. Maynas, between Río Momon and Río Momonillo, *McDaniel 16121* (F, GH, MO). **Huánuco:** Prov. Huánuco, *Vargas 5288* (MO). **Pasco:** Prov. Oxapampa, between Puerto Bermúdez and Hito San Matías, *León et al. 327* (F, USF, USM). **Junín:** Satipo, *Ridoutt 11397* (USM). **Ucayali:** Boquerón del Padre Abad, *Skog et al. 5128* (US). **Cuzco:** Marcapata, Quispicanchis, *Vargas 3781* (MO, US). **Madre de Dios:** Prov. Manú, *Vargas 16643* (GH).

33. *Selaginella asperula* Spring, in Martius, Fl. bras. 1 (2): 127. 1840. SYNTYPES: "ad fluvium Amazonum," *Martius* (M), "et ad flumen S. Francisco," *Martius* (M).

Main stem slender, erect, sometimes arching, and rooting at the apex, usually 1-pinnate, 15–30 cm long, articulate, stramineous, glabrous, the basal part with appressed, ascending leaves. **Primary**

branches distant, often forming tufts of slender, dichotomous branches along the main stem, sometimes rebranching into uniformly slender ultimate leafy branches 1–3 mm broad, the axes straight or nearly so. **Rhizophores** mostly at or near the base of the main stem. **Lateral leaves** above the first branch ascending or wide-spreading, 0.5–3 mm long, elongate-ovate, somewhat broader just above the base, acute, with an auricle sometimes forming a small, acute tooth, the edges narrow, whitish, ciliolate, these longer at the base. **Median leaves** ovate, asymmetrical, acute, with a prolonged, ciliate auricle, the edges narrow, whitish, denticulate, the teeth longer and denser at the base.

Steep slopes and road banks, open areas, thickets and moist areas in dense forests, 680–1300 m, Amazonas and Loreto to Junín.

Amazonian Venezuela and Brazil, south to Bolivia.

The diffuse branches that form a uniformly slender, dichotomous, leafy branch system, with small, strongly imbricate leaves, are distinctive among the Peruvian species. The species has a single stele at the base of the erect stem, a character that separates it from *Selaginella geniculata*.

Amazonas: Prov. Bagua, 43 km NE of Chiriaco, *Barbour 4458* (MO, USM). **San Martín:** San Rogue, *Ll. Williams 7415* (F, US). Prov. Rioja, *Woytkowski 6036* (GH, MO, US). **Loreto:** Río Huallaga, above Lagunas, *Croat 18097* (F, GH, MO). **Huánuco:** Tingo María (as San Martín) *Allard 20823* (MO). **Pasco:** Prov. Oxapampa, Parque Nacional Yanachaga-Chemillen, *León et al. 989* (F). **Junín:** San Ramón, *Killip & Smith 24785* (F, GH, US). Prov. Chanchamayo, La Merced, *Macbride 5504* (F, US); La Merced, *D. Smith 4063* (MO, UC).

34. *Selaginella stellata* Spring, in Martius, Fl. bras. 1 (2): 129. 1840. LECTOTYPE (designated here): Brazil, Prov. Para. Obidos, *Martius* (holotype, M).

Selaginella conduplicata Spring, in Martius, Fl. bras. 1 (2): 129. 1840. TYPE: Brasil, Prov. Para, *Martius* (holotype, M).

Selaginella calcarata A. Braun, Ann. Sci. Nat. 5, 3: 305. 1865. TYPE: ?, several syntypes are cited.

Main stem erect to sometimes creeping, 10–30 cm long, articulate, stramineous, glabrous, the basal part with appressed, ascending leaves. Primary branches 3–4-pinnate, usually with an extended, flabelliform, frondlike arrangement, branches distant, the lowest often longest, or in creeping stems the branches of similar length, axes of the branches

fractiflex, ultimate leafy branches slender, 2–5 mm broad. **Rhizophores** abundant on the lower part of the stem nearly to the first branch, or in creeping stems among the upper branches. **Lateral leaves** above the first branches distant, ascending, those below distant, peltate, 1–4 mm long, lanceolate, slightly broader above the base, acute, the base with a prolonged, membranaceous auricle on the acroscopic side and usually a sharp tooth on the basiscopic side, with narrow, whitish, denticulate edges. **Median leaves** very small, usually $\frac{1}{2}$ the length of the lateral leaves, ovate-lanceolate, acuminate or subaristate, with a prolonged, lingulate, ciliate basal auricle, with narrow, whitish, denticulate edges.

In dense stands on clay or often sandy soil in lowland woods or rain forests and secondary forests. Common in humid, disturbed areas, in chacras, especially old ones, ca. 100–250 m, Loreto and Junín.

Guianas, Amazonian Brazil west to Peru.

We follow Alston (Repert. Spec. Nov. Regni Veg. 40: 309. 1936) in accepting the name *Selaginella stellata* over *S. conduplicata*, both published by Spring in the same work.

The species is readily distinguished by the unusually prolonged, ciliate auricles on axillary, median, and lateral leaves. The bright stramineous color of the fractiflex axes contrasting with the deep green leaves resembles what is seen in *Selaginella geniculata*, and there are peltate leaves on the lower part of the main stem and branches similar to that species.

Loreto: Iquitos, *Croat 18306* (MO, US), *20051* (GH, MO, UC). Iquitos, road to San Juan, *Mexia 6496* (F, GH, MO, UC). Prov. Maynas, Picuruyacu, *Revilla 123* (F, MO, UC). Gamitanacocha, *Schunke 144* (F, GH, UC, US). Iquitos, *Tryon & Tryon 5166* (F, GH, US). **Junín:** Chanchamayo Valley, La Merced, *Soukup 1117* (F), *1118* (F). La Merced, *Macbride 5503* (F).

35. *Selaginella exaltata* (Kunze) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 234. 1843. **Figure 9e–f.**

Lycopodium exaltatum Kunze, Linnaea 9: 8. 1834. TYPE: Peru, San Martín: “ab Uchiza ad Toache,” *Poeppig*, July 1830, Diar. 1953 (not located).

Selaginella strobilifera Christ, Bull. Herb. Bossier 2, 1: 72. 1901. TYPE: Peru, “entre Ríos Huallaga et Ucayali,” *Huber 1515* (holotype, P; isotype, MG).

Main stem erect, scandent up to 8 m long, articulate, 2–6 mm broad including the leaves, stra-

mineous, often pubescent. Primary **branches** widely spreading, 2–3-pinnate, often pubescent. **Rhizophores** few, borne in axils of branches. **Lateral leaves** distant, clasping on the main stem when dry, approximate, or imbricate on the ultimate branches, obtuse, elongate, 1–3 mm long, 3 or 4 × longer than broad, acute, or sometimes entire, somewhat acuminate, the base truncate, sometimes with conspicuous whitish borders. **Median leaves** acentric, the outer side larger, ovate, acuminate to aristate, the arista ¼ the lamina length, glabrous, the base entire.

In lowland forests, rain forests, secondary forests, and disturbed areas, scandent or scrambling over shrubs, often forming dense thickets, 30–760 m, Amazonas south to Madre de Dios.

Costa Rica south to Bolivia and western Brazil.

The scandent habit of these plants, often forming dense thickets, is exceptional among species of *Selaginella*. The stems are noted to be up to 8 m long, but in most collections they are indicated as 3 m. The habit of these plants, with dense branches bearing closely placed leaves, forms a compact cover over other vegetation.

Amazonas: Prov. Bagua, Montenegro, *Sagástegui et al.* 7158 (F, GH, HUT, MO, UC). Prov. Bagua, above Cascadas de Mayasi, *Wurdack* 1800 (F, GH, UC, US). **San Martín:** between Tocache Nuevo and Juanjui, *Croat* 58035 (F, MO). Lamas, Naranjal, *Knapp & Mallet* 6958 (F, MO, UC). **Loreto:** Bosque Nacional von Humboldt, *Gentry & Revilla* 20418 (F, MO). Prov. Maynas, *Plowman et al.* 6502 (F, GH, US). Nanay, *Woytkowski* 5126 (GH, MO, US). **Huánuco:** Casa de Koepke, Río Lullapichis, *Dudley* 12484 (GH). Bosque Nacional de Iparia, *Schunke* 1299 (F, GH, MO, US). **Pasco:** Prov. Oxapampa, Cabeza de Mono, *D. Smith* 3768 (MO, UC). Puerto Bermúdez (as Junín), *Killip & Smith* 26498 (US). **Madre de Dios:** Prov. Tambopata, Tambopata Nature Reserve, *Barbour* 4881 (F, MO). Manú National Park, *Gentry et al.* 27209 (F, MO).

36. *Selaginella convoluta* (Arnott) Spring, in Martius, Fl. bras. 1 (2): 131. 1840.

Lycopodium convolutum Arnott, Mem. Wernerian Nat. Hist. Soc. 5: 199. 1824 TYPE: Brasil, Rio de Janeiro, *Jameson* (holotype, E).

Main stem erect, very short, not articulate, green to brownish, glabrous. Primary **branches** forming an open rosette curling inward when dry, 1–2-pinnate, with the ultimate branches, including the leaves, 3–5 mm broad. **Rhizophores** few at the base of the main stem. **Lateral leaves** rigid, strongly imbricate, 1–2 mm long, ovate-lanceolate or somewhat elliptic, acuminate to acute, strongly

imbricate, the base with a prolonged, densely ciliate auricle, the acroscopic side with a broad, whitish border, the edges irregularly denticulate. **Median leaves** broadly ovate to somewhat elliptical, obliquely oriented, acute or short aristate, the base not prolonged, the borders not conspicuously whitish, the edges regularly dentate.

On dry desert slopes, 1250 m, Cajamarca.

Guatemala; Greater Antilles; Guyana; Peru; Brazil and Paraguay.

The habit of these plants forming a rosette of stems, with lateral branches curling inward, readily characterizes the species. The leaves are dimorphic; both lateral and median leaves are strongly imbricate and have whitish margins and dentate edges.

Selaginella convoluta is widely distributed in Central and South America, but only a single collection has been seen from Peru. The inrolled, brownish, leafy stems may be easily overlooked on the dry, desert slopes where the plants occur.

Cajamarca: Prov. Celendín, Balsas-Celendín road, Río Marañón valley, *D. Smith* 6179 (MO).

Comments

The following species are accepted by Alston et al. (1981) as growing in Peru. Adequate material of these has not been seen and a better evaluation of them is desired than is now possible.

- a. *Selaginella acanthostachys* Baker, J. Bot. 21: 99. 1883. TYPE: Peru, San Martín, *Spruce* 4328 (holotype, κ).
- b. *Selaginella asplundii* Crabbe & Jermy, Fern Gaz. 11: 257. 1976. TYPE: Peru, Huánuco, *Asplund* 12822 (holotype, s; isotype, BM).
- c. *Selaginella muscosa* Spring, in Martius, Fl. bras. 1 (2): 120. 1840. Type: Brazil, *Luschnatt* (holotype, M).
- d. *Selaginella suavis* (Spring) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 229. 1843. *Selaginella sulcata* ssp. *suavis* Spring, Flora (Jena) 21: 185. 1838. TYPE: Brazil, *Sellow* (holotype, κ; isotype, B?).
- e. *Selaginella wolfii* Sodiro, Crypt. vasc. Quit. 620. 1893. TYPE: Ecuador, “woods of the western region, 1800 m.” *Sodiro* (holotype?, ρ).

The following species was credited to Peru on the basis of the type, which is now considered to have been collected in Panama.

f. *Selaginella horizontalis* (Presl) Spring, Bull. Acad. roy. Sci. Bruxelles 10: 226. 1843. *Lycopodium horizontale* Presl, Rel. haenk. 1: 78. 1825. TYPE: Panama, *Haenke* (holotype, PR), not from Peru as originally thought.

Family 28. ISOETACEAE

Isoetaceae Reichenb., Bot. Damen Kunst. Freunde Pflanzenw. 309. 1828. TYPE: *Isoetes* L.

Stem erect, subterranean, not indurated, bearing numerous, fleshy to wiry, dichotomously branched roots. **Leaves** numerous, spirally arranged, ligulate, acicular with a single vein and 4 rows of air chambers, each transversely partitioned by multicellular septa. **Sporangia** foliar, large, single, sessile at or near the adaxial leaf base. **Megaspores** tetrahedral-globose and trilete, without chlorophyll, germinating endosporically to form a small, short-lived megagametophyte. **Microspores** ellipsoidal and monolete, germinating endosporically to form a small megagametophyte producing 4 multiflagellate spermatozoa.

An ancient genus with representatives known from the lower Cretaceous; represented today by a single, distinctive, and cosmopolitan genus exhibiting distant affinities with *Selaginella* and *Lycopodium*.

Species recognition is greatly hindered by tremendous phenotypic plasticity and active speciation, both through hybridization and polyploidy as well as through diploid divergence (Taylor & Hickey, 1992). Species identification is also hampered by these phenomena but is made even more difficult by a suite of specialized characters not found elsewhere in the plant kingdom. Unique terminology, therefore, is an historic addendum to *Isoetes* systematics. Most of these novel terms were first introduced by Alexander Braun in 1864. The use of them, although inconvenient at first, adds clarity and uniformity of understanding. Within the body of this treatment I employ them in the following contexts: **corm**—the “stem” of the plant, that part to which the leaves and roots are attached; **fossa**—the groove (or one of several) on the side of the corm (lateral fossa), or extending all the way around the corm (circumbasal fossa) and from which roots are derived; **synchronous roots/acropetal roots**—in *Isoetes*, roots are initiated with a distinctive rhizotaxy (Paolillo, 1963)

with root initiation simultaneous (synchronous) or not (acropetal); **subula**—the distal, non-laminate portion of the leaf; **ala**—the lateral, proximal laminate portion of the leaf, not including the expanded midvein or sporangial regions; **scales**—leaf primordia that have been arrested early in ontogeny and have become sclerified and blackened; these initially surround the corm apex during dormancy and, as new leaves are initiated, are displaced outward, and hence may be found surrounding the fully developed leaves on a corm; **ligule**—a multicellular, planar, and glandular tissue growing out of a small pit (foveola) in the proximal portions of the adaxial leaf surface, just distal to the sporangium; the ligule is composed of a thickened central region (the cushion) and peripheral, delicate margins; **labium**—a nonglandular, planar tissue that is apparently a modification of the proximal rim of the foveola; this tissue can be quite extensive and may be erroneously identified as the ligule (it has also been called “pseudoligule”); **velum**—a tissue of leaf derivation that completely or partially covers the sporangium, the latter in most species somewhat impressed within the leaf tissue.

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I. Isoetes

Isoetes L., Sp. pl. 2: 1100. 1753. TYPE: *I. lacustris* L.

Stylites Amstutz, Ann. Missouri Bot. Gard. 44: 121. 1957. TYPE: *S. andicola* Amstutz = *I. andicola* (Amstutz) Gómez. **Figure 10.**

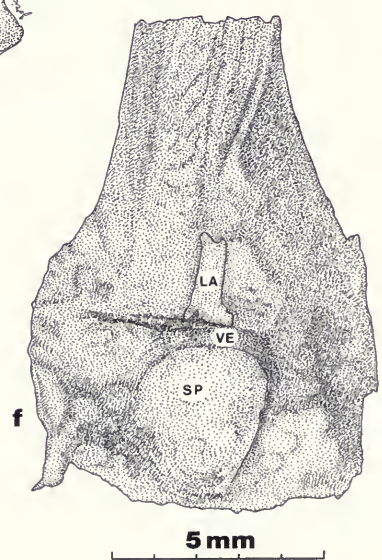
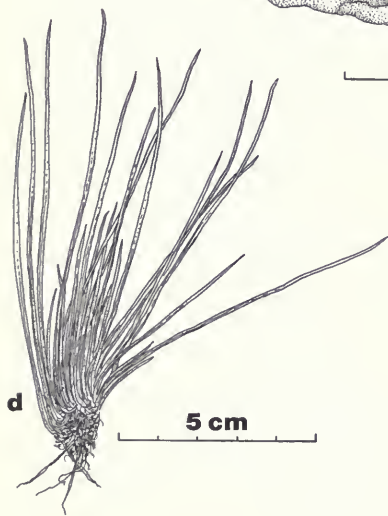
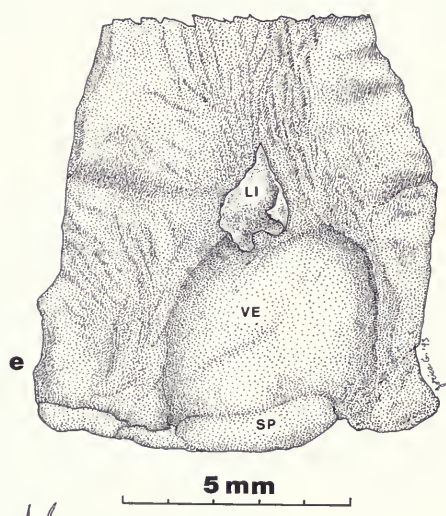
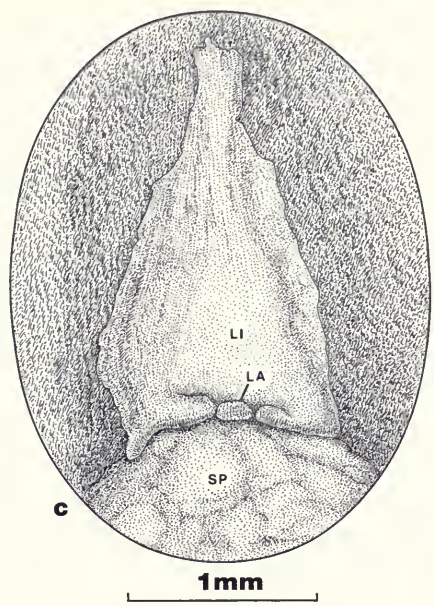
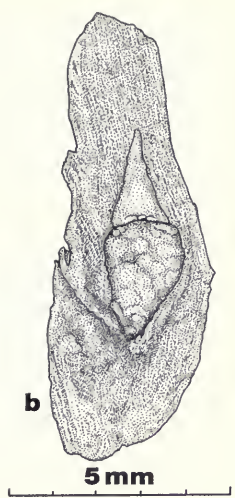
Aquatic, amphibious or terrestrial perennials. **Stem** globose, to vertically or horizontally elongate, buried in substrate. **Leaves** terete, trigonal (broadly 3-angled) or triquetrous (sharply 3-angled). **Ligule** delicate, to ca. 8 mm, glandular, auriculate. **Labium** variable in expression, minute

to completely covering the ligule, generally thick and fleshy. **Sporangium** elliptic to ovate, embedded in the leaf or partially emergent, exposed or completely covered by the velum. **Megaspores** laevigate, reticulate, echinate, tuberculate or cristate, 250–1,200 μm in diameter. **Microspores** laevigate, tuberculate, or echinate, 25–50 μm long. $2n = 22-132$.

The cosmopolitan genus *Isoetes* has been variously divided into sections based on megaspore surface morphology. Recent studies, however, suggest that spore morphology is extremely variable and highly subject to convergence.

Key to species of *Isoetes*

- a. Plants of lowland (less than 1500 m) pools; subula triquetrous; scales present; megaspores baculate 1. ***I. panamensis***
- a. Plants of high altitude (more than 3000 m) pools, streams, or moist meadows; subula terete or trigonal; scales usually absent; megaspores laevigate, tuberculate, pustulate, cristate, echinate, rugulate, or reticulate, not baculate b
- b. Megaspores reticulate 2. ***I. novo-granadensis***
- b. Megaspores not reticulate, surface ornamentation variable c
- c. Plants diminutive, the leaves of mature, fertile plants rarely longer than 30 mm in length, scale leaves around corm bases and surrounding shoot apex 3. ***I. parvula***
- c. Plants larger, only juveniles with leaves less than 30 mm, fertile adult plants larger, lacking scale leaves d
- d. Velum covering, at most, $\frac{1}{4}$ of the sporangium, the sporangium essentially exposed e
- e. Corm vertically elongate, frequently producing unbranched roots only along a lateral groove (fossa); alae extending more than 50% of the total leaf length; sporangia elevated above the leaf base; megaspores laevigate, pustulate or rugulate—often variable within a single sporangium; mature plants deeply embedded in substrate, with only the distal (+/–) quarter of the leaf tip exposed 4. ***I. andicola***
- e. Corm globose to slightly elongate vertically and producing roots along a continuous circumbasal groove (fossa); alae extending less than 50% of the leaf length; sporangia basal; megaspores laevigate or with subtle, indistinct markings; mature plants not deeply embedded in substrate, typically with at least the distal half of the leaf exposed f
- f. Leaves broad, 3.5–6 mm wide at mid-length, 6–8 mm wide at the base, subula and alae dark brown to dark green, the apex subacute to acute; labium narrowly oblong, 40–60 μm wide, 140–180 μm high; megaspores of 2 size and shape classes 5. ***I. dispora***
- f. Leaves narrow, ca. 1.5–1.6 mm wide at mid-length, 3.6–4 mm wide at the base, subula and alae light green, the apex attenuate; labium depressed-ovate, 540 μm wide, 120 μm high; megaspores similar in size and shape 6. ***I. hewitsonii***
- d. Velum covering $\frac{3}{4}$ or more of the sporangium g
- g. Plants terrestrial or amphibious; distal portions of subulae strongly trigonal; leaves often leathery or cartilaginous, the apex acute 7. ***I. saracochensis***
- g. Plants aquatic or occasionally amphibious; distal portions of subulae terete to half-round, lax to erect, flaccid or stiffly turgid, the apex attenuate to subacute h
- h. Leaves stiffly erect, extremely turgid (to the point of being brittle), dark green, most often with dark brown to nearly sclerotic pigmentation basally; corm globose to extensively elongate horizontally; megaspores laevigate 8. ***I. lechleri***



- h. Leaves flexuous to weakly erect, barely turgid, bright green and without dark pigmentation basally; corm globose to slightly elongate horizontally; megaspores laevigate to minutely tuberculate or cristate 9. ***I. boliviensis***

1. ***Isoetes panamensis*** Maxon & Morton, Ann. Missouri Bot. Gard. 26: 272–273. 1939. TYPE: Panama, Prov. Panama, vicinity of Bejuco, *Woodson et al. 1685* (holotype, US!; isotypes, GH!, NY!).

Isoetes pacifica Svenson, Amer. Fern J. 34: 123. 1944. TYPE: Ecuador, Prov. Guayas, east of Chanduy, *Svenson 11022* (holotype, BKL; isotypes, GH!, NY!).
Isoetes savannarum Gómez, Phytologia 49: 339. 1891. TYPE: Costa Rica, Prov. Guanacaste, *Gómez 17088*, as *7088* (holotype, CR!).

Corm globose, 7–34 mm in diameter, 2–3-lobed, dichotomous roots arising synchronously within the circumbasal fossa(e). **Leaves** to 100, erect, 160–540(–760) mm long, 6–16 mm wide at the base, 0.5–1.5(–2) mm wide at mid-length; alae colorless and hyaline proximally, stramineous to bright green or bluish green and chartaceous distally, 2–4 mm wide at the sporangium, 35–185(–230) mm long ([17–]22–30[–40]% of the total leaf length), apices attenuate; subula triquetrous (sharply 3-angled), stramineous to bright green to bluish green, the apex attenuate to subacute, with 3 groups of fibrous bundles forming distinct longitudinal ridges, continuing to the apex; stomates present; scale leaves present. **Sporangium** obovate, tan, unspotted, 6–12 mm long, 3.5–7 mm wide, basal. **Velum** rudimentary, 0.2–0.5 mm wide along the lateral edges of the sporangium, absent along the upper edge of the sporangium. **Ligule** delicate, ephemeral, occasionally represented by a whitish, deltate to triangular fragment, 3–4 mm long, 2.5–4.5 mm wide. **Labium** depressed-ovate, entire, lacinate or shallowly scalloped, 800–2,800 μm high, 2,500–4,500 μm wide. **Megaspores** white, not shiny, 380–580 ($x = 496$) μm in diameter, baculate, the bacula occasionally laterally confluent; equatorial and proximal ridges narrowly triangular to deltoid in cross-section, equatorial ridges often undulate. **Microspores** ash-gray, 27–40 ($x = 34$) μm long, 20–33 ($x = 26$) μm wide, sparsely echinate, to papillate, to laevigate. $2n = 44$.

In ephemeral bodies of water such as rain pools, riverbanks, and marshes, from sea level to 1500 m, Tumbes.

Western Guatemala to Panama; coastal Ecuador and Peru; Brazil and Paraguay. Rarely collected.

Throughout its range, this species exhibits considerable variation in the shape, size and distribution of the bacula on megaspores. Microspores also vary in surface morphology, but no parallel trends are evident. The single tetraploid count for this species is from Costa Rican material; it would not be surprising to find distinctive reproductively isolated elements within *I. panamensis*, with the Peruvian material presumably assigned to *I. pacifica* Svenson.

Isoetes panamensis is the only Peruvian species with either triquetrous subulae or baculate megaspores and as such is a distinctive element in the flora. Gómez's description of the ligule in *I. savannarum* refers to the condition of the labium.

Tumbes: South of Zarumilla, *Ellenberg 1380* (GH, U).

2. ***Isoetes novo-granadensis*** Fuchs, *Caldasia* 8: 314–315. 1969. TYPE: Colombia, Comisaría del Putumayo, 3250 m, *Cuatrecasas 11770* (US!).

Isoetes dichotoma Mora-Osejo & Hagemann, *Mutisia* 43: 5. 1977. TYPE: Colombia, Dept. Nariño, Volcán Galeras, 3900 m, *Hagemann & Leist 1773* (COL, HEID!).

Corm slightly elongate horizontally to globose, up to 15 mm tall and 30 mm in diameter, 2-lobed, roots arising synchronously within a continuous circumbasal fossa. **Leaves** to about 80, stiffly erect, up to 200 mm long, often with reflexed tips, 6–10 mm wide at the base, 2–7 mm wide at mid-length, dark green to brown proximally, bright to dark green distally; alae dark green to nearly black, membranaceous, 1.5–4 mm wide at the sporan-

←
FIG. 10. *Isoetes andicola*: a, habit; b, proximal portion of leaf showing elevated sporangium; c, enlargement of "b" showing ligule (LI), labium (LA), sporangium (SP). *Isoetes lechleri*: d, habit; e, proximal portion of leaf showing ligule (LI), velum (VE), sporangium (SP). *Isoetes dispersa*: f, proximal portion of leaf showing labium (LA), velum (VE), sporangium (SP). (a from *Hutchison et al. 5890*, F; b, c from *Saunders 1154*, MU; d from *Sanchez Vega 1330*, F; e from *León 2074*, MU; f from *Skillman et al. 12850*, MU.)

gium, 20–140 mm long ([44–]50–63[–70]% of the leaf length), parallel-sided, their apices attenuate; subula trigonal (broadly 3-angled in cross-section, erect to slightly reflexed, heavily cutinized, the apex sharply acute; fibrous bundles absent; stomates absent; scale leaves absent. **Sporangium** elliptic to ovate, diaphanous to light brown, concolorous, 4–9 mm long, 3.5–5 mm wide, basal. **Velum** rudimentary, represented by a narrow ridge of tissue along the lateral portions of the sporangium, absent along the upper edge of the sporangium. **Ligule** sagittate, brown, 7–9.5 mm high, 3.5–5 mm wide, delicate; the margins especially ephemeral, the cushion occasionally persistent as a widely ovate remnant, ca. 2 mm high × 2.5 mm wide. **Labium** obsolete. **Megaspores** white to light gray, not lustrous, 880–1,120 ($x = 1,015$) μm in diameter, reticulate; equatorial and proximal ridges straight, distinct, as high or slightly higher than broad, generally obscured by the dense muri. **Microspores** dark brown, 37–52 ($x = 47$) μm long, 30–43 ($x = 37$) μm wide, smooth. $2n = 132$.

Wet boggy soil, 3500–3600 m, Cuzco.

Colombia, Ecuador and Peru.

Known from Peru only by this single collection. The species is common in moist páramos throughout Ecuador and Colombia where it grows either as a submerged aquatic or, more commonly, as a terrestrial species deeply embedded in surrounding vegetation. The Peruvian material is typically terrestrial, with only the upper half to upper third of the leaves protruding above the substrate.

Cuzco: Prov. Paucartambo, camino peatonal de El Mirador a Cerro Macho Cruz, 3500–3600 m, *León 2246* (F).

3. *Isoetes parvula* Hickey, *sp. nov.*

Ab aliis speciebus altitudis celsis staturō parvulo, squamis sclerotiscis praesentibus, et megasporis subfationis differt.

Corm globose, 3–5 mm in diameter, bilobed; dichotomous roots arising synchronously within the circumbasal fossa. **Leaves** 8–15, stiffly reflexed, 20–30 mm long, 3–4 mm wide at the base, 0.3–0.5 mm wide at mid-length; alae hyaline, 0.5–1 mm wide at the sporangium, 0.5–1 mm long (25–50% of the total leaf length), each apex attenuate; subula half-terete (?), bright green, not highly cutinized, straight to slightly reflexed, the apex attenuate; fibrous bundles not evident; stomates not seen; scales present. **Sporangia** circular to elliptic,

embedded, basal, hyaline, unspotted, 1–3 mm long, 1–2 mm wide. **Velum** incomplete, extending (10–) 50–75% down the sporangium. **Ligule** quickly ephemeral, not seen. **Labium** not evident. **Megaspores** reddish brown en masse, 30–36.7 ($x = 33.2$) μm long, 25–28.4 ($x = 26.4$) μm wide, shortly echinate.

TYPE—Peru, Dept. Ayacucho, Prov. Ayacucho, Laguna Yaurihuirí, about 205 km from Nazca on the road to Abancay, rocky and stony slopes, dominant in site with seeping water, 4300 m, *Brandbyge 321* (holotype, AAU!).

High-altitude seeps, 4300 m, Ayacucho.

Known only from the type specimen.

4. *Isoetes andicola* (Amstutz) Gómez, Brenesia 18: 4. 1980. **Figure 10a–c.**

Stylites andicola Amstutz, Ann. Missouri Bot. Gard. 44: 121. 1957. **TYPE:** Peru, Dept. Lima, Prov. Huarochiri, above Casapalca, in alpine bogs, 4750 m, *Amstutz 2000* (holotype, MO).

Stylites gemmifera Rauh, in Rauh & Falk, Sitzungsber. Heidelberg Acad. Wiss. Math. Naturwiss. Kl. 1959: 11. 1959. **TYPE:** Peru, Dept. Lima, Prov. Huarochiri, above Casapalca, *von Appen* (holotype, HEID).

Isoetes andicola var. *gemmifera* (Rauh) Gómez, Brenesia 18: 4. 1980.

Corm vertically elongate, 20–67 mm tall, 11–15 mm in diameter, 1-lobed (2–3-lobed in juvenile plants), roots arising acropetally along a single (2–3) lateral fossa(e) (in juveniles arising synchronously within a continuous circumbasal fossa). **Leaves** 200 or more, stiffly erect in terrestrial individuals, weakly recurved in submerged individuals, 30–50(–75) mm long, 3.5–6 mm wide at the base, 4–7 mm wide at mid-length, dark brown to black proximally, bright to dark green distally; alae colorless and hyaline to dark brown or black, chartaceous proximally, membranaceous distally, 1–2.8 mm wide at the sporangium, 20–37 mm long (55–85% of the leaf length), each apex obtuse; subula trigonal, highly cutinized, strongly reflexed in terrestrial plants, weakly reflexed to arcuate in submerged plants, the apex attenuate to acute; fibrous bundles absent; stomates absent, scale leaves absent. **Sporangium** elliptic to obovate, superficial to emergent, chocolate-brown, concolorous, 2.5–5.5 mm long, 1.7–3 mm wide, positioned 3.5–9 mm above the leaf base. **Velum** rudimentary, represented by a narrow ridge of tissue along the lateral portions of the sporangium, absent along the upper edge of the sporangium. **Ligule** triangular, weakly

cordate, off-white, 3–4.5 mm high, 2–2.5 mm wide; the margin delicate and ephemeral, the cushion persistent, deltate, 2–3 mm high, 1.8–2.3 mm wide. **Labium** deltate to depressed-ovate, entire, dark brown, 280–320 μm high, 180–240 μm wide. **Megaspores** mottled, gray on brown, or uniformly brown, not lustrous, 460–720 ($x = 559$) μm in diameter, laevigate to obscurely pustulate, the pustules occasionally merging laterally to form short meandriform rugae; equatorial and proximal ridges straight, distinct, as high or slightly higher than broad. **Microspores** dark brown, 35–43.8 ($x = 39$) μm long, 28.8–37.5 ($x = 32$) μm wide, scabrate. $2n = 44$. Vegetative reproduction by cortical gemmae.

In wet, boggy soil or inundated plains of puna vegetation from 4100 to 4900 m, Lima, Pasco (numerous collections), Junín, Cuzco, Puno.

Peru and Bolivia.

The inclusion of *Stylites* as a generic synonym of *Isoetes* is well supported by the early development of the sporophyte and the internal anatomy of the plants (Hickey, unpubl.) as well as the confirmation of the chromosome number as $2n = 44$. Earlier reports of $2n = 48$ –52 are incorrect.

Lima: Prov. Huarochirí, Laguna Caprichosa, 4800 m, *Rauh 186* (M). Lago Aguascocha, near Mina Caprichosa, 4780 m, *Hutchison & Tovar 4244* (C, E, F, G, L, MICH, MU, S, UC, US, WIS). **Pasco:** Prov. Pasco, Cerro de Pasco, ca. 4300 m, *Asplund 11830* (S). **Junín:** Prov. Jauja, Pachayo, 3800 m, *Ameghino* (MU). Prov. Huancayo, Laguna Condoray, 4700 m, *Marshall*, 6 Sept. 1961 (BM). **Prov. Junín,** 13–14 km N of Junín, *Karrfalt & Hunter 22* (USM). **Prov. Tarma,** Lago Junín, east side near road, 13 km north of Junín, 4100 m, *Hutchison et al. 5890* (F, NY, UC, US). **Cuzco:** In high Andes above Cuzco, toward Puno, *Gómez AS2189* (CR). **Prov. Chumbivilcas,** Laguna Huarmicocha, 4600 m, *Carlier 241* (USM). **Puno:** Prov. Carabaya, pampa de Lacka Macusani, 4360 m, *Vargas 7128* (US).

5. *Isoetes dispora* Hickey, sp. nov. **Figure 10f.**

Differt ab aliis speciebus *Isoetes*, megasporis dimorphis necnon laevibus, sporangiis paene superficialibus, subulis plus minusve triquetris et labiis ligulatis.

Corm globose to slightly elongate vertically, ca. 20 mm wide, ca. 30 mm high, 2-lobed, dichotomous roots arising synchronously from a complete circumbasal fossa. **Leaves** ca. 30, stiffly erect, dark brown to dark green proximally, dark green distally, to 65 mm long, 6–8 mm wide at the base, 3.5–6 mm wide at mid-length; alae dark green, chartaceous to sub-membranaceous, 2–3 mm wide at the sporangium, 10–20 mm long (15–34% of

the total leaf length), each apex attenuate; subula trigonal, highly cutinized, straight to slightly reflexed, the apex blunt, subacute; fibrous bundles not evident; stomates absent; scales absent. **Sporangia** ovate to obovate, essentially superficial, basal, light brown, concolorous or occasionally with scattered dark spots, 2.5–4.5 mm long, 2–3.5 mm wide. **Velum** completely absent. **Ligule** ephemeral, occasionally represented by a dark auriculate fragment, 2.5 mm long by 2 mm wide. **Labium** light to dark brown, narrowly oblong, often cryptic, 140–180 μm long, 40–60 μm wide, the apex asymmetric, erose. **Megaspores** gray, not lustrous, laevigate to minutely tuberculate, dimorphic, showing Types I and II spores (sensu Marsden 1976), 750–1,125 ($x = 920$) μm wide, the proximal and distal ridges laevigate, straight, distinct. **Microspores** gray en masse, 37.5–42.5 ($x = 40.3$) μm long, 26.3–32.5 ($x = 29.9$) μm wide, laevigate to slightly papillate.

TYPE—Peru, Dept. Lambayeque, Prov. Ferreñafe, Dist. Incahuasi, Jalca, Laguna Tembladera, Cerro Negro, 3300 m, *Skillman et al. 12850* (holotype, MU!; isotypes, F!, HUT!).

High-altitude páramo (aquatic?), 3300 m, Lambayeque.

Known only from the type specimen.

Isoetes dispora is, despite being known only from the type collection, a very distinctive species. The combination of dimorphic, laevigate megaspores, nearly superficial sporangia, more or less trigonal subulae, no velum, and a strap-shaped labium differentiate it from all other known collections of *Isoetes*. The presence of dimorphic megaspores is normally taken as an indication of hybridity, often involving unbalanced genomes. The materials of *Skillman et al.*, however, have certain anomalies suggesting that alternative possibilities should be entertained. Notable among these is the absence of any other collected taxa from the Lambayeque region. Hybrids are typically found in lower numbers than the sum of their parental taxa and it seems unlikely that three individual F1 hybrids would be the sole collections from a mixed population of quillworts. Furthermore, there is no evidence of vegetative reproduction in these specimens, suggesting that all three have had separate origins from spore. In addition, there is a previously undescribed regularity to the production of the two spore types in this material. Careful dissection of individual sporangia showed that each sporangium contained 20 spores, of which 10 were large and fully formed and contained cytoplasm, whereas the other 10 were flattened in the equa-

torial plane and contained no cytoplasm. Because of space limitations within the sporangia, the spores derived from each megaspore mother cell retained their tetrad orientation, and so it was possible to observe directly the end products of all meiotic events (10 total) in two separate sporangia. In all cases tetrads consisted of two large globose spores and two smaller flattened ones. Taken together, these data are inconsistent with previous data on *Isoetes* hybrids, leading us to believe that these plants are either sexual or apogamous.

Apogamy in the genus is relatively rare, being confined to a few species in Australia and India. In virtually all known cases of apogamy in *Isoetes*, microspores are either rare or lacking and the megaspores are irregular in shape, often forming Type III spores or having single contact faces, i.e., diplospores. Such is not the case in *Isoetes dispora*. The presence of normal microspores (less than 10% abortion) and the extreme regularity of megaspore production suggest meiotic consistency, albeit irregular. The presence of two types of megaspores in this species may, therefore, reflect differential resource allocation among meiotic products in a fashion analogous to that seen during megaspore development in *Selaginella* and angiosperms and during oogenesis in mammals.

6. *Isoetes hewitsonii* Hickey, *sp. nov.*

Species nova *L. dispora* proxima, cujus megasporis laevibus, velo carenti et subulis infirme triquetris habet. Differt megasporis uniformibus et foliis angustatis habens apicibus attenuatisque minus corneis.

Corm globose, slightly elongate laterally, ca. 15 mm wide, 2-lobed, with fleshy dichotomous roots arising from a continuous circumbasal fossa. **Leaves** light green, 10–20, erect, 50–160 mm long, 3.5–6 mm wide at the base, 1.5–1.6 mm wide at mid-length; alae light green to hyaline, chartaceous, 0.9–1.5 mm wide at the sporangium, 23–27 mm long (36–46% of the total leaf length), each apex attenuate; subula weakly triquetrous, highly cutinized, straight, the apex attenuate, scales absent. **Sporangia** elliptic, embedded, although only slightly so for the megasporangia, light tan, concolorous, 2.8–4 mm long, 1.5–2 mm wide, basal. **Velum** completely absent. **Ligule** widely ovate, auriculate, ephemeral, ca. 1.1 mm high by 0.6 mm wide, the margins entire. **Labium** tan to pale green, depressed-ovate, ca. 12 μm high by 54 μm wide. **Megaspores** white, laevigate, 650–750 ($x = 715$) μm in diameter; proximal ridges straight, distinct, the equatorial ridge distinct or not. **Microspores**

gray en masse, 28–35 ($x = 31.7$) μm long, 21–28 ($x = 24.9$) μm wide, with acute to truncate echinae. Vegetative reproduction by cortical budding.

TYPE—Peru, Dept. Cajamarca, Prov. Celendín, desvío a Guagal siguiendo la ruta a Celendín, 3700 m, *Sánchez Vega et al.* 2021 (holotype, MU!; isotypes, ASU!, F!, CPUN).

High-altitude aquatic endemic, 3700 m, so far known only from Cajamarca.

This species is dedicated to Dr. Walter Hewitson, a student of the fern genus *Osmunda* and the man who first introduced me to the excitement of both botany and *Isoetes*.

A delicate and distinctive species, with the general appearance of a rigid *Isoetes boliviensis*, but with stiffer leaves and no velum. The large megaspores suggest polyploidy. Additional collections should be sought to determine the chromosome number of this species and to encompass its variation.

7. *Isoetes saracochensis* Hickey, *sp. nov.*

Species foliis latis, subulus valde trigonis, apicibus acutis corneisque, sporangiis basalibus, velis fere completis et megasporis laevibus ad leniter rugulatis a congeneribus diversa.

Corm globose, 2-lobed, 17–23 mm in diameter, with dichotomous roots arising from a continuous circumbasal fossa. **Leaves** 13–14, stiffly erect, 55–135 mm long, 6–10 mm wide basally, 5–7 mm wide at mid-length; alae chartaceous, light to dark brown, extending 1.2–3 mm wide at the sporangium, 35–75 mm long (46–73% of the leaf length), apices acute; subula highly cutinized and strongly trigonal, with 3 distinct, rounded ridges continuing to the apex; leaf apices acute, sharp, corneous; fibrous bundles absent; stomata absent; scale leaves absent. **Sporangium** elliptic to ovate, concolorous, 2.5–6 mm long, 2.5–3.5 mm wide, basal. **Velum** virtually complete, extending $(\frac{3}{4})\frac{7}{8}$ or more down from the upper edge of the sporangium. **Ligule** delicate, transparent, broadly to narrowly ovate with a weakly cordate base, 1.9–2.7 mm high, 1.7–2 mm wide, ephemeral, frequently degraded in mature leaves. **Labium** light to dark brown, a transverse ridge along the lower border of the foveola, entire, 100–150 μm high, 500–800 μm wide. **Megaspores** white to gray, 400–620 ($x = 515$) μm in diameter, laevigate or with indistinct to distinct, short, low meandriform rugae; equatorial and proximal ridges straight, distinct, with equatorial ridges as broad as high and proximal ridges fre-

quently twice as broad as high. **Microspores** dark gray to dark brown, 30–36 ($x = 33.5$) μm long, 22–28 ($x = 24.3$) μm wide, with clavate or echinate projections.

TYPE—Peru, Dept. Puno, Laguna Saracochoa, 14,000 ft, *Tutin 1424* (holotype, BM; isotype, BM).

Submerged or emergent in high-altitude lakes, 3900–4400 m, Cuzco, Puno.

Endemic.

This species is fairly well described despite the few collections available. It is distinctive but obviously belongs in an alliance close to *I. lechleri*. The extensive velum and the distinctive labium are shared characteristics that are quite unusual in the genus for this part of the world. The *I. lechleri* complex (below), however, is distinctive unto itself, having a number of unique characters (horizontally elongate corm, turgid leaf condition) that set it apart from *I. saracochoensis*.

Cuzco: Chectuyoc, near Sicuna, 3950 m, *Tutin 1406* (BM). **Prov. Cañas,** Laguna Langui y Layo, *Chávez 2313, 2321* (MO). **Puno:** Prov. Carabaya, Lake Chungara, 4400 m, *de Macedo & Enriquez* (GH). **Prov. Lampa,** Laguna Lagunilla, ca. 4300 m, *Tutin 1407a, 1420* (BM).

8. ***Isoetes lechleri*** Mett., Fil. Lechl. 2: 36. 1859.

TYPE: Peru, “in laguna cacuminis, Cordler. pr. Agapata,” *Lechler 1937* (holotype, B!; isotypes, G! [2 sheets], UPS!, frag. S!). **Figure 10d–e.**

Isoetes socia A. Br., Verh. Bot. Ver. Brandenb. 4: 332. 1862. **TYPE:** Peru, in laguna cacuminis (mixta cum plantula repente ignota), *Lechler 1937b* (holotype, B!).

Isoetes glacialis Asplund, Ark. Bot. 20A: 34–35. 1926. **TYPE:** Bolivia, Dept. La Paz, Prov. Murillo, Jainvags stationem La Cumbre, 4700 m, *Asplund 4041* (holotype, UPS!; isotypes, G!, M!, S!).

Isoetes laevis Weber, Hedwigia 63: 252. 1922. **TYPE:** Peru, Dept. Ancash, Cordillera regia uber Caraz, auf dem Grunde eines Tumpels, völlig untergetaucht, 4400 m, *Weberbauer 3111* (holotype, B!).

Isoetes peruviana Weber, Hedwigia 63: 246. 1922. **TYPE:** Peru, Dept. Junín, Prov. Tarma, Beige westl. von Huacapistana, 3500 m, *Weberbauer 2228* (holotype, B!; isotype, B!; frag., UPS!; photos, S and UPS of B).

Corm (globose) laterally elongate, distinctly bilobed [more so in damaged specimens], 15–44 mm wide, 2–5 mm high; dichotomous roots arising synchronously within the circumbasal fossa. **Leaves** to 20–40, stiffly turgid and erect, 88–160(–240) mm long, 8–19 mm wide at the base, 2–3 mm wide at mid-length; alae dark green to dark brown, nearly black, 2–3.5 mm wide at the sporangium,

20–55 mm long (46–75% of the total leaf length), each apex attenuate; subula terete, dark green, the apex attenuate to subacute, corneous; fibrous bundles absent; stomates absent; scale leaves absent. **Sporangium** obovate to elliptic, hyaline, unspotted, 4–19 mm long, 3.5–4 mm wide, basal. **Velum** complete to nearly complete, extending 75–100% down the sporangium. **Ligule** ephemeral, ovate to very widely ovate, with an auriculate base, 1.2–1.8 mm high, 0.8–2 mm wide, the more persistent cushion ovate to widely ovate, ca. 0.8–1 mm high, 0.4–0.6 mm wide. **Labium** not evident. **Megaspores** white, laevigate, typically shiny, showing variable abortion, 280–440 ($x = 340$) μm wide, the equatorial ridges indistinct in larger spores, the proximal ridges sharp, distinct. **Microspores** gray in mass, 33.8–38.8 ($x = 36.2$) μm long, 26.3–30 ($x = 28.1$) μm wide, with acute to truncate projections. $2n = 44$.

In high-altitude ponds and streams, typically submerged, 3300–4750 m, Cajamarca, San Martín, Ancash, Junín, Ayacucho, Cuzco, Puno.

Peru and Bolivia.

The high-altitude ponds, lagunas, and streams of south-central Bolivia and central Peru are replete with laevigate-megaspored plants that have the same overall form but that differ from one population to another in the extent of pigmentation, the size and rigidity of the leaf, and the amount of lateral growth in the corms. Quite a few of these variants have been formally recognized as discrete species and even more are now published (Fuchs-Eckert, 1982) as *nom. nud.* Nearly all populations show some degree of meiotic abnormality as evidenced by irregularly shaped or sized spores. To date, all of these populations have been found to be tetraploids, with $2n = 44$. The publication (Hickey, 1984) of $2n = 44$ for *I. “ticlioensis”* Fuchs *ined.*, *I. glacialis*, and *I. herzogii* (in part) are referable to this assemblage. The distinctive coloration, corm shape, velum structure, and ligule form strongly suggest a common origin for these plants. All of these plants undoubtedly have had a common hybrid origin, and it would appear that rapid speciation via reciprocal gene silencing is occurring. Each population, or perhaps even subsets within a population, is differentially silencing the tetraploid genome down to the diploid level. As this phenomenon proceeds, genetic isolation slowly builds up and functional spores become rarer and rarer. We are left, then, with a mosaic of variable morphologies, established by drift or perhaps selection, which are partially isolated from each

other and perpetuated by vegetative reproduction (corm budding). An examination of only a few populations gives a false sense of discreteness, and only after a broad survey can one observe the complete intergradation in forms. All of these populations are, therefore, best included within a single species concept, *I. lechleri*.

Sagástegui et al. 13098 and 14347, while of the general form of *I. boliviensis*, have much longer, narrower, more slenderly tapering leaves, with some pigmentation along the bases. Provisionally, it has been identified as *I. lechleri aff.* Likewise, *León & Young 2833* is provisionally assigned to *I. lechleri*. This collection has the darkened leaf bases and alae, laevigate megaspores, and extensive velum coverage typical of *I. lechleri*. It differs in having a large (up to 5 mm long), strongly auriculate ligule more typical of *I. andina* of Ecuador, Colombia, and Venezuela and in having emarginate ala apices reminiscent of those seen in *I. karstenii (s.l.)* of Colombia and Venezuela.

The species is best distinguished by its brownish (almost caramel) coloration and the distinctly tere- rete leaves that are turgid to the point of being brittle. Herbarium material is best identified by coloration, the presence of a horizontally elongate corm (in most populations), the laevigate megaspores, the more or less complete velum, and the widely ovate ligule which has a tendency toward an auriculate base.

Isoetes lechleri is a plant of high-altitude (over 3500 m) lakes, streams, and pools. It grows in both shallow and deep water, with an individual plant's form being strongly influenced by water depth. Shallow plants have short, stiffly rigid leaves. Plants of deeper water "etiolate": the leaves are a bit more lax and considerably longer. Vegetative reproduction, by corm budding, is very common and may be a primary means of reproduction. The plants often form dense mats in quiet water; in streams and shallows the plantlets are often broken off and transported by animals or wave/current action. In Bolivia one road, cutting between two lakes, was completely covered by washed-out plants and corms.

Cajamarca: Pozo Kuan, 3790 m, *Sagástegui et al. 13098 & 14011* (F, HUT, MU). Prov. Contumazá, Pozo Kuan, 3900 m, *Sagástegui et al. 14347* (F, HUT, MU). **San Martín:** Prov. Mariscal Cáceres, forest on the edge of Laguna de Chochos, NW corner of Río Abiseo National Park, 3300 m, *Young & León 4856* (MU). **Ancash:** Prov. Huari, Huascarán National Park, 4440–4490 m, *D. Smith et al. 12355* (HUT). Prov. Yungay, Laguna de Llanganuco, 4100–4200 m, *Enderlin (USM)*. **Lima:** Prov. Cajatambo, Raura, perimetro de Ada, 4800–4900 m,

Chanco & Montoya 188 (MU). **Pasco** (as Junín): Huarón, lake, 4200 m, *Asplund 11828* (c, G [2 sheets], NY, s, UPS, us.). **Junín:** Prov. Yauli, Ticlio, small lake, 4750 m, *Asplund 11669* (s). **Ayacucho:** Prov. Huanta, Mt. Razu- huilca, 4000–4100 m, *Weberbauer 7500* (F, NY, US). **Cuzco:** Prov. Cañas, Laguna de Langui y Layo, 3900 m, *Chávez 2323* (GH). Prov. Paucartambo, *León & Young 2833* (F, USM). **Puno:** Cordillera Real, Laguna Rinconada, 4680 m, *Thomasson* (s).

9. *Isoetes boliviensis* Weber, *Nova Hedwigia* 63: 247. 1922. TYPE: Bolivia, circa La Paz, via ad Coroico, Lancha, 5000 m, *Mandon 1532* (holotype, G!; isotypes, BM!, G!).

Corm globose to slightly elongate laterally, 5–16 mm in diameter, 2-lobed; dichotomous roots arising synchronously within the circumbasal fossa. **Leaves** to 40, delicate, flexuous, erect to laxly spreading, 70–120(–240) mm long, 6–16 mm wide at the base, 1–1.5 mm wide at mid-length; alae hyaline to light brown, 1–2 mm wide at the sporangium, 20–30 mm long (12–33% of the total leaf length), each apex attenuate (rarely truncate); subula terete, bright green, the apex attenuate; fibrous bundles absent; stomates absent; scale leaves absent. **Sporangium** obovate to elliptic, hyaline, unspotted, 5–8 mm long, 3–5 mm wide, basal. **Velum** incomplete to complete, extending 6–100% down the sporangium. **Ligule** ephemeral, widely ovate, with an auriculate base, ca. 2 mm high, 1.7 mm wide, the more persistent cushion narrowly depressed-ovate, often bilobed, ca. 0.2 mm high, 0.6 mm wide. **Labium** not evident. **Megaspores** white to light gray, laevigate to minutely tuberculate, shiny, 380–460 ($x = 433$) μm wide, the equatorial and proximal ridges sharp, distinct. **Microspores** gray in mass, 26.3–40 ($x = 33$) μm long, 20–30 ($x = 25.3$) μm wide, with acute to truncate projections. $2n = 22$.

In shallow water, edges of lakes, ponds, and vernal pools, 4100–5000 m, Cajamarca, San Martín, Ancash, Lima, Pasco, Junín, Ayacucho, Cuzco, Puno.

Peru and Bolivia.

A very distinctive plant due to its small and relatively delicate appearance; several collectors have even suggested that it is an annual. This is the only Peruvian species with lax, flexuous leaves. It has a partial to complete velum normally covering about 75% of the sporangium, corms that are slightly elongate horizontally, and megaspores that are laevigate to minutely tuberculate. It is found in shallow (= ephemeral?) portions of ponds and lakes. The microspores are quite distinctive

in appearance, having acute or club-shaped projections which themselves are spiny. Microspores of some *I. lechleri* collections are similar.

The only counts for this species, $2n = 22$, are from Bolivian material.

La Libertad: Prov. Huamachuco, east of Quiruvilca, 4100 m, *Hutchison et al. 6143* (F, GH, MO, NY, UC, US). **Ancash:** Prov. Yungay, Huascarán National Park, 4100–4200 m, *D. Smith et al. 10432* (F, MO, MU). Huascarán National Park, 4500 m, *D. Smith et al. 9210* (MO, MU). **Lima:** Prov. Huarochirí, Ticlio Pass, between Lima and Oroya, 4840 m, *Hutchison et al. 6081* (C, E, F, G, GH, HEID, L, LIL, M, MICH, MO, NY, S, UC, WIS). **Junín:** 5 km above Hacienda Cochás, 34 km W of la Oroya–Huanacayo Route 3 on road to Pachacayo, 4425 m, *Keeley & Keeley 11087, 11088* (MU, OCC).

Comments

Isoetes triquetra A. Braun, Verh. Bot. Vereins Prov. Brandenburg 3 (4): 332–333. 1862. TYPE: Peru, Sachapata (am ostlichen Abhang der Cordillera von Peru), in pascuis humidis, *Lechler 3337* (holotype, B!; photos, s and UPS of B).

Calamaria triquetra (A. Braun) Kuntze, Rev. gen. pl. 2: 828. 1891–1893.

Isoetes lechleri var. *triquetra* (A. Braun) Gómez, Brenesia 18: 5. 1980.

The type material for this species is very fragmentary. There are no megaspores and the microspores are of a very common form (echinate). The most distinctive features of the specimen are the trigonal subula, the moderate labium, and the large auriculate ligule. In these regards, the type of *L. triquetra* is nearly identical to *I. andina* of Ecuador, Colombia, and Venezuela but differs from all other known Peruvian collections. I have argued (Taxon 35: 243–246. 1986) for the conspecificity of these taxa. The major argument against the common identity is distribution (some 1,400 km separate the type locality of *I. triquetra* from the nearest “good” locality of *I. andina*).

Isoetes herzogii Weber, Hedwigia 63: 250. 1922. TYPE: Bolivia, Tunari, 4300 m, *Herzog 2083* (holotype, M; isotypes, L!, M!, US!; frag., UPS!).

Although not recorded from Peru, this species is geographically proximate in Bolivia and should be expected in Peru. The species has stiffly erect, narrow, subulate leaves with attenuate apices. It lacks the pigmentation typical of *I. lechleri*, has a

nearly complete velum, and has megaspores that vary from tuberculate to rugulate to nearly laevigate. *Isoetes herzogii* is a high-altitude, nearly emergent plant of streams and shallow pools.

Addendum

1. Species to Be Added to the Pteridophyte Flora, Parts I–V

The following species have come to the attention of the authors as growing in Peru, after their generic treatment had been published.

Trichomanes arbuscula Desv., Mém. Soc. Linn. Paris 6: 326. 1827. TYPE: “Crescit in Guiana,” P, *Herb. Desvaux*.

Trichomanes coriaceum Kunze, Linnaea 9: 105. 1834. TYPE: “Prope Collares, Brasiliae,” *Poeppig* in 1832 (*Diar. 2981*), not located.

This species has an alate rachis and petiole and is sometimes subdimorphic. Illustrations are Hooker & Greville, *Icones Filicum*, t. 204. 1831 (as *T. bancroftii*) and Vareschi, *Flora de Venezuela*, Vol. 1 (Helechos), t. 47. 1969.

Loreto: Prov. Maynas, Puerto Almendras, *van der Werff et al. 9845* (MO), *9798* (MO), det. K. U. Kramer.

Trichomanes crispum L., Sp. pl. 1097. 1753. TYPE: “Martinica,” Plumier, *Traité foug. Amér.*, t. 86. 1705.

This is a critical and polymorphic species (see Windisch, *Bradea* 6: 99. 1992 for discussion).

Huánuco: Prov. Pachitea, region of Pucallpa, *Wallnöfer 11-261088* (Z), det. K. U. Kramer.

Pterozonium paraphysatum (A. C. Sm.) Lell., Mem. New York Bot. Gard. 17: 13. 1967.

Syngamma paraphysata A. C. Sm., Bull. Torrey Bot. Club 58: 301. 1931. TYPE: Venezuela, Amazonas, Cerro Duida, *Tate 441* (NY; frag., US).

This species is distinguished by the scales (vs. trichomes) on the stem, the keeled lamina, and relatively distant veins.

Huánuco: Prov. Pachitea, region of Pucallpa, low, elfin forest, 1750 m, *Wallnöfer 110-13988* (z), det. K. U. Kramer.

Lindsaea phassa Kramer, Bot. Helvetica 101: 207. 1991. TYPE: Peru, Loreto, Río Ampiyaco, vicinity of Pucaurquillo, *Davis et al. 849* (holotype, UC). Paratypes: **Loreto:** Prov. Maynas, Yanamono Explorama tourist camp, *van der Werff et al. 9869* (MO, z), *1994* (MO, z).

Kramer provides a discussion of the relationship of this new species and an illustration (fig. 1, p. 228) of it.

2. Consideration of Pteridophyte Diversity in Respect to Ecology and Geography

This treatment of the pteridophytes of Peru includes 28 families, 118 genera, and 1,060 native or adventive species. The account includes all families of the Pteridophyta except for four that occur only in the Old World and the Hymenophyllopsidaceae of northern South America. It includes most of the genera in the Americas and about one-third of the Neotropical species. This indicates that Peru ranks high in pteridophyte diversity. It is not surprising that among the 24 departments of Peru, those with the greatest number of species are also those that are ecologically diverse. The six most speciose departments (map 1; table 1) are ecologically strongly diverse, and they include relatively large areas of montane rain forest and/or cloud forest. All of these have been relatively accessible to collectors since the late 18th century, and with the exception of Pasco they are all large departments. About 90% of the species and 86% of the endemics are in one or more of the six most speciose departments.

It is doubtful whether any additional families will be added to the pteridophyte flora except by segregation of those already present. A few genera may be added, such as *Microlepia* in Ecuador and Bolivia, *Pilularia*, known to occur in Bolivia, and *Maxonia*, known in Ecuador. Additional species most likely will be found in the northern departments of Amazonas and Cajamarca and the southern departments of Madre de Dios and Puno. The number also may be increased by addition to large genera such as *Selaginella* and *Thelypteris*.

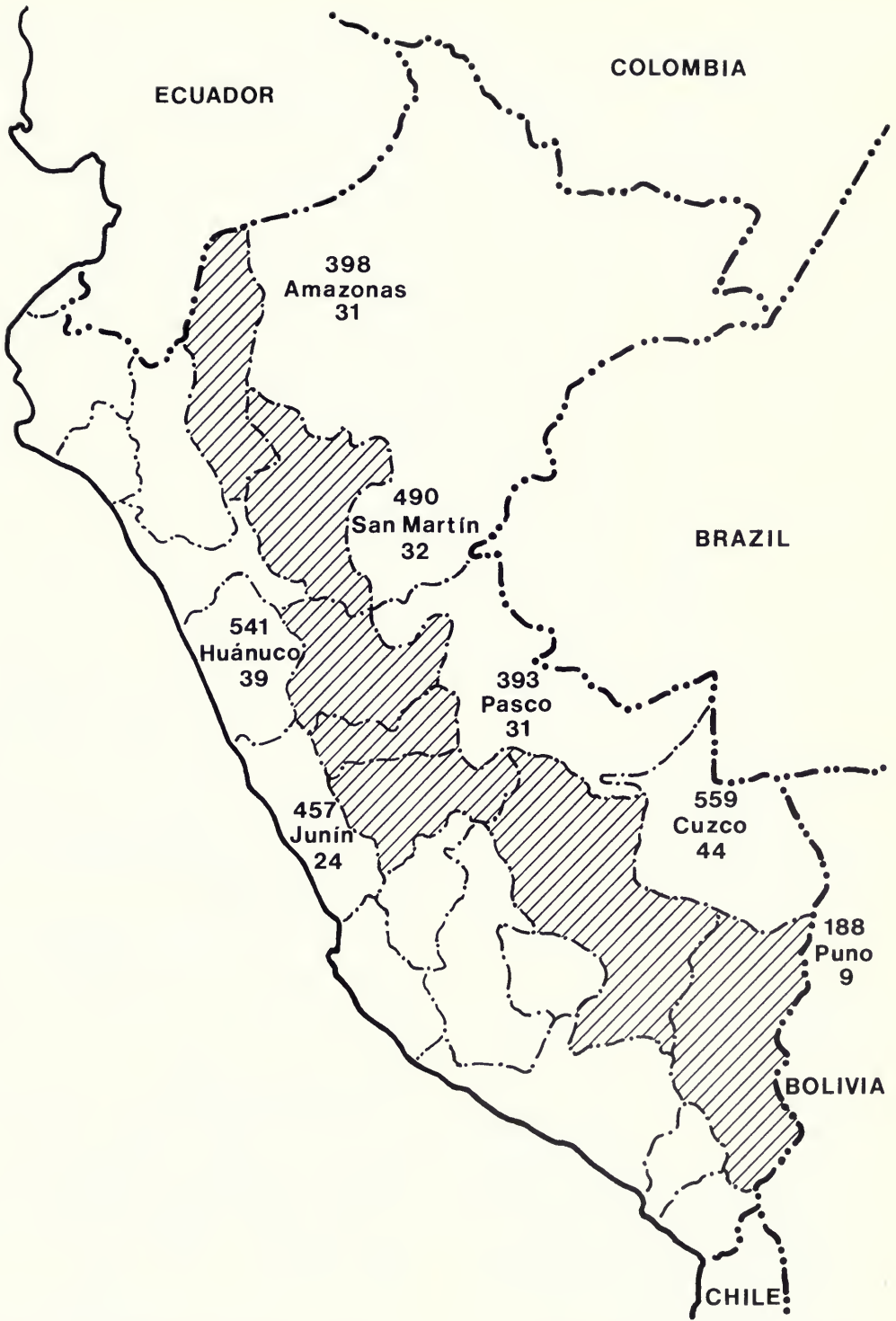
The 130 species endemic to Peru are included in Table 1 and some of them are also on Map 1. The map shows that there appears to be no clear geographic center of endemism. Rather, the de-

partments that have the most endemics are those with the most species. This suggests that disruptions of ranges during the Pleistocene may have occurred throughout the Andes of Peru. However, there is need for more detailed knowledge of the Pleistocene in the Andean region, such as that for Europe published by Lang (1992).

There are few studies of local diversity, although the ecological work of Young and León (1989, 1991) on pteridophytes of Peru supplies critical new data. Their analysis of a low elevation forested area in central Peru, including 61 species within 2 hectares, suggests that edaphic and topographic gradients affect the diversity of species. Their work on a high elevation forest, on the east slope of the Peruvian Andes, including 109 species in about 5 square km, shows greatest pteridophyte diversity in the montane rain forest. They suggest that the high and nearly constant humidity is a factor helping to account for the species richness.

The Andes are the major feature of Peru that has molded the vegetation and distribution patterns of the biota. The principle types of vegetation and species diversity are in large part based upon altitudinal zones affecting temperature and precipitation. The species of Peruvian pteridophytes are treated here in four main zones, based upon their ecology. They include Montaña Ferns, Ceja Ferns, Sierra Ferns and Loma Ferns. The ecological zones are shown on Map 2, along with a diagrammatic section showing the zones in profile.

Montaña Ferns occur in the forest region that covers the largest part of Peru. On the east flank of the Andes, this extends up to 1800 m. This region receives 1500–3500 mm of rain annually, usually between October and April. It is difficult to recognize floristic elements among several hundred species in the Montaña, but they may be characterized by their large size or by their epiphytic habit. The large ones have creeping stems, often forming large colonies with continued growth throughout the year. The leaves may be more than a meter long and are often modified for vegetative reproduction. There may be a relatively large number in a given locality, but many may be rare species. The large-leaved species include *Nephrolepis biserrata* (leaves to 3.6 m), *Lygodium volubile* (to 12 m), *Hemidictyum marginatum* (to 3 m), *Adiantum pectinatum* (to 2.5 m), and the tree ferns, mostly ca. 3 m. Some of the large-leaved species that form conspicuous colonies are *Dennstaedtia cicutaria*, *Gleichenia bifida*, *Dicranopteris pectinata*, and *Pteridium aquilinum* var. *arachnoideum*. The last is the most aggressive and may occupy



MAP 1. The most species-rich departments in Peru (Cuzco and northward) are hatched. The number of species is above the name, the number of endemics below. Puno is included to illustrate the transition to the less species-rich regions of Bolivia.

TABLE 1. Data on the diversity of pteridophyte species in Peru.

Department	Size (ca. 1,000 km ²)	Number of Pteridophyta	
		Species	Endemic to Peru
Loreto	207	252	8
Cuzco	152	559	45
Madre de Dios	144	169	8
Ucayali	106	105	6
Puno	68	188	9
Arequipa	57	32	3
Ayacucho	47	145	7
San Martín	45	490	32
Huánuco	40	541	39
Piura	39	38	2
Lima (incl. Callao)	39	72	4
Ancash	38	86	5
Amazonas	36	398	31
Cajamarca	32	225	19
Pasco	30	393	31
Junín	29	457	24
La Libertad	26	128	14
Ica	25	1	0
Apurímac	21	57	3
Huancavelica	21	73	2
Moquegua	14	4	1
Tacna	13	1	0
Lambayeque	12	51	3
Tumbes	4	20	0

whole hillsides after clearing for agriculture. Fertile leaves may be present only during a brief period as in *Bolbitis serratifolia*, *B. lindigii*, *Polypodium caudata*, and *P. osmundacea*. Some species may be more common, or confined to more tropical areas, at altitudes below 300 m. This region may be distinctive, based on distributions of flowering plants, but it is clearly a part of the Montaña Fern flora.

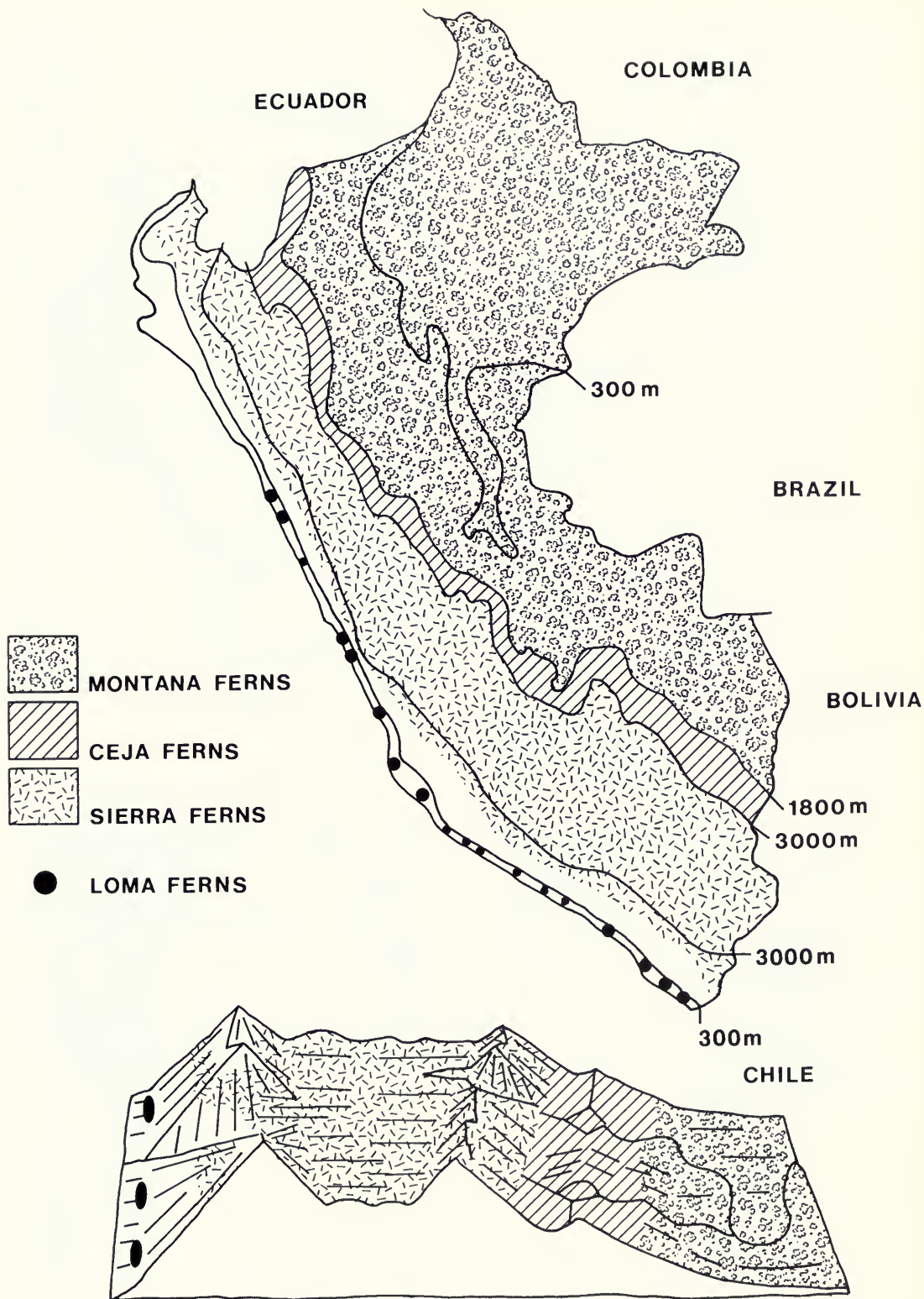
The Montaña Ferns have two main types of leaf modification for vegetative reproduction. Species that have buds toward the apex of the lamina include *Polystichum platyphyllum*, *Thelypteris macrootis*, *Bolbitis serratifolia*, and *Diplazium macrophyllum*. *Doryopteris pedata* var. *palmata* has buds at the base of the lamina, and *Tectaria incisa* has buds at the base of pinnae and along the pinna-rachises. In these species the buds are persistent and develop into plantlets, especially on old leaves, while still attached to the leaf. Deciduous buds are produced in the axils of pinnae in *Dennstaedtia arborescens*. Other species have leaves that root at the tip of the rachis. The rachis tip is elongated as in *Adiantum deflectens*, *Trichomanes diversifrons*, and *Asplenium radicans*. All or nearly all of the leaves in *Asplenium radicans* become rooted.

The epiphytic ferns that are primarily plants of the forest include *Grammitis serrulata*, *Pecluma filicula*, *Campyloneurum angustifolium*, *Polypodium polypodioides* var. *burchellii*, *Pleopeltis percussa*, *Asplenium serrulatum*, and *Ophioglossum palmatum*, as well as several species of *Elaphoglossum*. Some may grow on bare rock or may survive, for a time, on fallen branches. These species are biologically similar to the Sierra Ferns. They may become dormant during the relatively mild dry season, especially if growing on more exposed branches. Many Montaña Ferns are not sufficiently common to use in defining the zone, but the presence of numerous species of *Adiantum* with large dimidiate segments, only in the Montaña, helps to characterize this zone. These include *Adiantum petiolatum*, *A. latifolium*, *A. macrophyllum*, *A. anceps*, *A. platyphyllum*, *A. pectinatum*, *A. tetraphyllum*, *A. tomentosum*, *A. pulverulentum*, and *A. villosum*.

Ceja Ferns occur in the region extending along the higher eastern slopes or low summits of the Andes, at elevations of about 1800–3000 m. This is a moist, cool region where clouds and fog are present most of the year. It is a transitional climatic and vegetational band: the Ceja de la Montaña. Tree ferns and the bamboo *Chusquea* are the dominant elements in the Ceja Region. Under moist conditions where fog often occurs, frequent species are *Hymenophyllum ruizianum*, *Eriosorus flexuosus*, *Lycopodium clavatum*, *L. jussiaei*, and *Lycopodiella pendulina*. The absence of *Adiantum* species with large dimidiate segments, as noted above in the characterization of the Montaña, helps to define the Ceja zone.

In drier situations lacking mists, most of the ferns are terrestrial, the leaves less than 6 dm long. They are usually fertile and not modified for vegetative reproduction. In these features the plants generally resemble those of the Sierra species. They grow more or less throughout the year or at least retain leaves in fresh condition. A mixture of Sierra species such as *Pellaea ovata*, *P. sagittata*, and *Woodsia montevidensis* may occur here, as well as species more characteristic of the Montaña such as *Niphidium crassifolium* or *Nephrolepis pectinata*. The Ceja Ferns are largely a mixture of species from the Montaña and Sierra rather than species restricted to the Ceja.

Sierra Ferns center in the high central part of the Sierra, or Altiplano, between 3000 and 4300 m elevation. The land is somewhat rolling or may be rather flat. There is considerable relief where valleys penetrate the mountains. The region is bordered, except in the north, by chains of high moun-



MAP 2. The main vegetational zones in Peru and their ferns (diagrammatic).

tains, many of which rise to 5500 m or more and support snow fields and glaciers. The temperature is relatively cool and the air is dry. The vegetation largely consists of grasses, sedges, semi-desert shrubs and cacti. Locally there are small woods, especially those dominated by *Polylepis*. The puna, the land above the limits of agriculture, extends from 4000 m up to the limit of vascular plants, at about 5200 m. Here cold prevails and low cushion plants are the principal vegetational feature.

The Sierra Ferns are seasonally dormant but the dormancy may be intermittent due to infrequent rains during the dry season. The available moisture is largely in the soil or rock crevices. Many species occur where there is local seepage or where conditions are suitable for condensation of atmospheric moisture. The annual rainfall, between 500 and 1100 mm, is by no means deficient but the dry air, winds, and strong insolation at the high altitudes combine to diminish the moisture.

One of two main kinds of Sierra Ferns is the mesic type, typical of the locally moist habitats. Leaves of these plants die during the dry season unless they are in an unusually favorable place. Species characteristic of this habitat include *Adiantum poiretii*, *A. digitatum*, *Cystopteris fragilis*, *Asplenium peruvianum*, and *Woodsia montevidensis*. *Asplenium peruvianum* and the closely related *A. gilliesii* are exceptional in this group in having proliferous buds on the leaves. The petioles of these plants elongate and act as stolons. The petiole persists after the lamina withers and a plantlet develops at what appears to be the tip of the rachis.

Xeric species are the second characteristic type of Sierra Ferns. These plants retain their leaves but they become curled during the dry season, reviving during the brief moist periods. Species characteristic of this group include *Cheilanthes incarum*, *C. pruinata*, *C. bonariensis*, *C. scariosa*, *Polypodium pycnocarpum*, *Pellaea ternifolia*, and *Notholaena nivea*.

Loma Ferns occur on the Pacific side of the Andes, usually near the coast. This region becomes progressively drier toward the ocean and finally

barren, or with very sparse vegetation. In the north of Peru, these desert conditions are less pronounced. At the northernmost tip of Peru there is a small forested area. The otherwise barren coastal zone is relieved, at intervals, by green, irrigated valleys, and by the naturally verdant Lomas. The ferns of this region are part of a unique vegetation that occurs along the coast of Peru and Chile, north to about 8 degrees south latitude. This vegetation develops in response to local physiographic conditions. In winter there is more or less constant fog and "guara" (a dense mist) on certain hills and upper parts of valleys. The summer months are continuously dry. A rather lush vegetation may develop where unusual moist conditions occur. The long, continuously dry periods evidently restrict the flora. Loma Ferns include a selection of the Sierra species including *Polypodium pycnocarpum*, *Adiantum subvolubile*, and *A. digitatum* and, less commonly, *Ophioglossum reticulatum*, *Anogramma leptophylla*, *Woodsia montevidensis*, and *Cheilanthes peruviana*. It is of interest to note that while about 80% of the Loma seed plants are endemic, there are no endemic ferns. This may be due to slower evolution of the ferns but more likely reflects their superior means of dispersal. The spores undoubtedly are blown from the Sierra to the Lomas with sufficient frequency to prevent endemism.

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DEPARTMENTS OF PERU

Comprehensive Index to Names

Accepted names are in roman type, synonyms are in *italics*, and new names are in **boldface**. A page number is provided for the principal place, or the only place, where the name occurs. Prefixes (1–6) indicate the number of the volume or part, followed by a hyphen and then the page number within that part. (Thus, the prefix “6” indicates entries for the present series number of *Fieldiana*, whereas lower numbers indicate entries for previously published parts, their series numbers as follows: 1 = New Series No. 20; 2 = No. 22; 3 = No. 29; 4 = No. 27; 5 = No. 32.) Entries for Parts I through V pertain only to names of species and genera. Listings for categories above and below these taxa may be found in the indices to those particular parts.

- Acrospermum
 maxonii 5-112
- Acrostichum 2-81
 acuminatum 4-154
- adnolepis* 4-166
 albescens 4-121
 alcicorne 5-181
 alienum 4-100
 apodum 4-157
 aureonitens 2-48
 aureum 2-83
 auricomum 4-125
 bakeri 4-125
 barbatum 4-125
 bonariense 2-28
 calaguuala 4-137
 calomelanos 2-18
 calophyllum 4-166
 castaneum 4-127
 caudatum 4-64
 cervinum 4-85
 chrysoconium 2-20
 chrysolepis 4-61
 chrysophyllum 2-16
 ciliatum 4-128
 citrifolium 2-92
 cladotrichum 4-125
 curvans 4-166
 cuspidatum 4-129
 danaeifolium 2-83
 decoratum 4-129
 denticulatum 4-131
 dichotomum 1-33
 digitatum 1-33
 discolor 4-130
 dissimile 4-166
 diversifolium 4-130
 ebeneum 2-18
 elegans 1-34
 elongatum 4-162
 engelii 4-131
 erinaceum 4-132
 erythrolepis 4-132
 eximium 4-133
 fendleri 3-68
 flabellatum 4-169
 flaccidum 4-133
 fractiserialle 4-60
 furfuraceum 4-164
 glabellum 4-134
 graminioides 5-72
 guamanianum 4-135
- hackelianum* 4-61
 hartwegii 4-135
 hayesii 4-136
 haynaldii 4-136
 heterophyllum 5-63
 hickenii 4-136
 horridulum 4-137
 huacsaro 4-137
 hystrix 4-138
 ilvense 4-94
 insigne 4-61
 japurense 4-107
 juglandifolium 4-61
 laminarioides 4-139
 lanuginosum 2-32
 latifolium 4-140
 lechlerianum 4-141
 leprosum 4-142
 leptophyllum 4-146
 lindenii 4-142
 lindigii 4-103
 lingua 4-142
 litantum 4-143
 luridum 4-144
 mathewsii 4-144
 minutum 4-146
 moorei 4-167
 muscosum 4-147
 nicotianifolium 4-102
 nigrescens 4-148
 nivosum 4-148
 nodosum 1-15
 oligarchicum 4-102
 orbignyanum 4-151
 osmundaceum 4-62
 pachyphyllum 4-151
 paleaceum 4-152
 pandurifolium 4-105
 papillosum 4-152
 patinii 4-153
 peltatum 4-169
 petiolosum 4-154
 phlebodes 4-107
 piloselloides 4-154
 plumbicaule 4-60
 plumosum 4-155
 poepppianum 4-156
 polybotryoides 4-61
 polypodioides 5-137
 preslianum 4-128
 propinquum 4-156
 quitense 4-157
- raywaense* 4-157
 reptans 5-153
 rufum 2-47
 scariosum 2-32
 schomburgkii 4-144
 serratifolium 4-101
 serratum 4-101
 serrulatum 5-83
 setigerum 4-160
 sinuatum 2-34
 sorbifolium 4-105
 sphenophyllum 4-169
 squamipes 4-161
 stenophyllum 4-161
 suberectum 4-61
 tambillense 4-162
 tartareum 2-19
 tectum 4-162
 tenuiculum 4-163
 tereticaulon 2-40
 thalictroides 5-50
 thelypteris 3-6
 trifoliatum 2-21
 unitum 4-146
 villosum 4-156
- Actinostachys* 1-33
 digitata 1-33
 pennula 1-36
- Adiantopsis* 2-34
 chlorophylla 2-36
 paupercula 2-34
 radiata 2-36
 ternata 2-36
- Adiantum* 2-52
 alarconianum 2-67
 amabile 2-56
 anceps 2-68
 capillus-veneris 2-58
 cayennense 2-64
 ceciliae 2-63
 chilense 2-57
 concinnum 2-58
 crenatum 2-57
 cuneatum 2-56
 decorum 2-56
 deflectens 2-62
 delicatulum 2-62
 digitatum 2-61
 dolabriforme 2-62
 filiforme 2-62
 flagellum 2-62
 fructuosum 2-64

- fuliginosum* 2-64
guianense 2-120
henslovianum 2-59
hirtum 2-64
humile 2-66
imbricatum 2-60
incisum 2-67
kalbreyeri 2-63
kaulfussii 2-66
killipii 2-66
laetum 2-59
lancea 2-121
latifolium 2-66
lobatum 2-60
lucidum 2-69
lunulatum Burm. 2-62
lunulatum Houtt. 4-40
macrocladum 2-64
macrophyllum 2-70
mathewsianum 2-67
mexiae 2-64
microsorium 2-62
moorei 2-56
obliquum 2-57
orbignyanum 2-60
palmatum 2-61
patens 2-61
pauperculum 2-34
pectinatum 2-62
pedatum 2-61
peruvianum 2-68
petiolatum 2-66
phillipense 2-62
phyllitidis 2-70
pilosum 2-63
platyphyllum 2-68
poepigianum 2-69
poiretii 2-57
pulverulentum 2-65
raddianum 2-56
radiatum 2-36
rhizophyllum 2-62
ruizianum 2-62
scalare 2-69
serratodentatum 2-65
sessilifolium 2-59
speciosum 2-61
steerei 2-62
strictum 2-121
subaristatum 2-62
subvolubile 2-59
sulphureum 2-58
terminatum 2-65
tetraphyllum 2-64
thalictroides 2-57
tinctum 2-56
tomentosum 2-63
urophyllum 2-63
× variopinnatum 2-66
veitchianum 2-62
villosissimum 2-64
villosum 2-64
Aleuritopteris
farinosa 2-23
peruviana 2-30
- Allantodia*
asplenioides 4-75
Alsophila 1-116
armigera 1-123
aterrima 1-114
australis 1-116
blechnoides 1-111
capensis 1-118
caracasana 1-133
conjugata 1-128
contracta 1-109
cuspidata 1-120
dombeyi 1-123
elongata 1-115
engelii 1-116
erinacea 1-118
floribunda 1-123
frigida 1-126
incana 1-120
infesta 1-123
kalbreyeri 1-124
killipii 1-125
lasiosora 1-125
latevagans 1-124
lechleri 1-128
macrosora 1-115
melanopus 1-124
microdonta 1-127
nigra 1-124
nigripes 1-124
pallescens 1-131
paucifolia 1-118
peruviana 1-123
phegopteroides 1-127
pilosissima 1-125
podophylla 1-124
poepigii 1-115
procera 1-123
pruinata 1-109
pterorachis 1-123
pubescens 1-126
pyncocarpa 1-123
quadripinnata 1-109
rostrata 1-111
sprucei 1-115
swartziana 1-122
tarapotensis 1-125
tryonorum 1-128
ulei 1-128
Amauropelta 3-9
breutelii 3-9
cheilanthoides 3-34
concinna 3-29
deflexa 3-30
diplazioides 3-14
oligocarpa 3-15
opposita 3-32
pilosula 3-19
rivulorum 3-32
rudis 3-26
thomsonii 3-22
Amphineuron 3-39
opulentum 3-43
Anabaena
azollae 6-8
- Ananthacorus* 2-89
angustifolius 2-89
Aneimia 1-24
Anemia 1-24
adiantifolia 1-24
buniifolia 1-24
clinata 1-25
ferruginea 1-27
flexuosa 1-27
haenkei 1-29
hirsuta 1-28
hispidula 1-30
humilis 1-29
myriophylla 1-28
oblongifolia 1-29
pastinacaria 1-28
phyllitidis 1-29
repens 1-30
tomentosa 1-27
villosa 1-25
Anemirhiza 1-24
adiantifolia 1-24
Anetia 2-92
Anetium 2-92
citrifolium 2-92
Anisogonium 4-67
fraxinifolium 4-67
pinnatifidum 4-89
Anogramma 2-22
chaerophylla 2-23
leptophylla 2-23
Antrophyum 2-84
brasilianum 2-87
cajenense 2-87
ensiforme 2-85
guayanense 2-87
lanceolatum 2-87
lineatum 2-86
plantagineum 2-84
Arachniodes 4-35
aspidioides 4-35
denticulata 4-37
ochropteroides 4-38
Argyrochosma 2-37
nivea 2-38
stuebeliana 2-38
Aspidium 4-21
abruptum 3-46
articulatum 4-96
atrorubens 3-24
biolleyi 3-62
biserratum 5-51
braunianum 4-24
catocarpum 4-10
cheilanthoides 3-34
coarctatum 3-32
confertum 4-47
conterminum 3-32
ctenitis 4-5
dicksonioides 4-21
draconopterum 4-27
excultum 4-35
extensum 3-43
funestum 4-21
gelidum 4-54

- gongylodes* 3-40
guianense 4-48
heracleifolium 4-27
hispidulum 3-41
incanum 3-52
karstenii 4-9
kunzei 4-29
macrophyllum 4-29
macrourum 3-44
martinicensis 4-24
meniscioides 4-48
microchlaena 4-9
navarrense 3-15
nemophilum 4-10
nobile 4-38
nodosum 4-96
opulentum 3-43
orbiculatum 4-53
paleaceum 4-36
parallelogramma 4-36
patulum 4-36
pectinatum 5-53
pendulum 4-98
pilosulum 3-19
platyphyllum 4-52
poepigii 4-29
protensum 4-19
pusillum 3-17
pycnolepis 4-54
rostratum 1-111
rotundatum 4-42
rutaceum 5-17
scalare 3-15
semihastatum 3-57
sprengelii 3-31
stipulare 3-44
 trianae 4-47
truncatulum 4-40
uliginosum 3-3
Asplenium 5-2
abrotanoides 5-27
abscissum 5-41
achilleifolium 5-32
aethiopicum 5-46
alatum 5-40
alienum 4-72
amazonicum 5-13
angustum 5-12
arborescens 4-80
auriculatum 5-44
auritum 5-42
balliviani 5-21
bangii 5-38
barbaense 5-37
blechnoides 5-60
brasiliense 5-40
callipteris 4-83
canelense 5-30
caracasana 4-79
castaneum 5-17
caucense 4-85
celtidifolium 4-83
centripetale 4-87
cicutarium 5-24
cirrhatum 5-20
cladolepton 5-24
clausenii 5-39
concinnum 5-4
congestum 5-41
conquisitum 5-18
crassifolium 4-76
cristatum 5-24
cuneatum 5-44
cuspidatum 5-26
davisii 5-30
delicatulum 5-25
delitescens 5-71
dentatum 5-35
denticulosum 4-80
denudatum 5-48
desvauxii 4-77
dimidiatum 5-46
discolor 5-48
discrepan 5-36
divaricatum 5-23
drepanophyllum 5-42
eggersii 4-87
erosum 5-46
escaleroense 5-14
escragnollei 5-30
expansum 4-75
extensum 5-15
falcinellum 5-28
ferulaceum 4-90
flabellulatum 5-21
flavescens 4-85
flavidum 5-30
flexuosum 4-77
foeniculaceum 5-27
formosum 5-14
fragile 5-34
fragrans 5-27
fuscopubescens 4-72
gillesianum 5-34
gilliesii 5-33
haenkeanum 5-24
hallii 5-18
haplophyllum 5-13
harpeodes 5-39
hastatum 5-44
integerrimum 5-28
jamesonii 5-26
juglandifolium 5-28
kapplerianum 5-29
kunzei 4-87
laetum 5-31
lechleri 4-85
lindbergii 4-78
lividum 5-47
longicaudatum 5-19
lorentzii 5-33
macrophyllum 4-77
macrurum 5-19
marginatum 4-90
marinum 5-2
mathewsii 5-28
maxonii 5-18
melanopus 5-31
monanthemum 5-16
monanthes 5-16
myriophyllum 5-25
neogranatense 5-29
nidus 5-11
nigricans 5-46
ocanniense 4-85
oligophyllum 5-30
otites 5-48
partitum 5-21
parvulum 5-15
pearcei 5-13
perkinsii 5-18
peruvianum 5-34
plantagineum 4-86
plantaginifolium 4-86
poloense 5-35
praemorsum 5-46
procerum 4-77
projectum 5-33
pseudoangustum 5-12
pteropus 5-36
pulchellum 5-35
pumilum 5-14
purdieanum 5-47
purpurascens 5-32
quitense 5-35
raddianum 5-39
radicans 5-19
repandum 5-28
repens 5-21
resiliens 5-15
rhizophyllum 5-20
rhomboideum 5-22
roemerianum 4-85
rosenstockianum 5-37
ruizianum 5-43
rusbyanum 5-30
rutaceum 5-17
salicifolium 5-43
sandwichianum 4-72
scolopendrium 5-4
serra 5-45
serratum 5-11
sessilifolium 5-37
shepherdii 4-80
spruceanum 5-18
squamosum 5-26
striatum 4-79
stuebelianum 5-12
tabinense 5-38
tenue 5-22
ternatum 5-22
theciferum 5-48
tomentosum 2-46
trapezoides 5-48
tricholepis 5-30
trichomanes-dentatum 5-34
trilobatum 5-22
trilobum 5-48
triphyllum 5-22
tucumanense 5-26
tuerckheimii 5-29
tungurahuae 4-76
uniseriale 5-21
vargasii 5-17
vastum 4-73
venulosum 4-76
virens Desv. 5-31
virens Presl 5-30

- vomeriforme 5-28
wagneri 5-17
weberbaueri 5-49
- Athyrium** 4-88
achilleifolium 5-32
ambiguum 4-71
 "bradearum" 4-88
celtidifolium 4-83
dombei 4-90
dombeyi 4-90
expansum 4-75
ferulaceum 4-90
felix-femina 4-88
flexuosum 4-77
fumaroides 4-92
haenkeanum 5-24
praestans 4-87
- Austrolycopodium** 6-52
magellanicum 6-56
- Azolla** 6-8
caroliniana 6-10
filiculoides 6-11
 var. *rubra* 6-11
mexicana 6-10
microphylla 6-11
rubra 6-11
- Balantium**
karstenianum 1-105
- Blechnum** 5-56
acutum 5-64
andinum 5-61
angustifolium 5-64
arborescens 5-62
asplenioides 5-60
auratum 5-67
auriculatum 5-68
binervatum 5-63
blechnoides 5-60
brasiliense 5-61
buchtienii 5-67
caudatum 5-58
chilense 5-62
ciliatum 5-68
cognatum 5-68
columbiense 5-67
confluens 5-59
cordatum 5-62
delicatum 5-68
divergens 5-63
ensiforme 5-64
fragile 5-64
fraxineum 5-59
glandulosum 5-58
gracile 5-59
heterophyllum 5-63
kunthianum 5-64
l'herminieri 5-61
lanceola 5-60
lechleri 5-68
lehmannii 5-61
longifolium 5-59
loxense 5-65
magellanicum 5-68
malacothrix 5-68
- maxonii* 5-61
meridense 5-64
nigrosquamatum 5-61
nudum 5-56
obtusifolium 5-67
occidentale 5-58
orientale 5-58
ornifolium 5-62
pectinatum 5-58
penna-marina 5-62
peruvianum 5-62
polypodioides Raddi 5-60
polypodioides (Sw.) Kuhn 5-64
pteropus 5-63
rubicundum 5-65
scandens 5-70
schomburgkii 5-66
serrulatum 5-60
sprucei 5-66
squamulosum 5-65
stenophyllum Presl 5-65
stenophyllum (Klotzsch) Mett.
 5-65
stipitellatum 5-65
subtile 5-61
triangulare 5-59
trilobum 5-68
unilaterale 5-60
volubile 5-70
- Blotiella** 2-111
glabra 2-111
lindeniana 2-113
- Bolbitis** 4-98
aliena 4-100
bradeorum 4-103
crenata 4-101
guianensis 4-109
killipii 4-102
lindigii 4-103
macrophylla 3-68
nicotianifolia 4-102
oligarchica 4-102
pandurifolia 4-105
portoricensis 4-101
serrata 4-101
serratifolia 4-101
stuebelii 4-103
- Botrychium** 1-6
cicutarium 1-8
lunaria 1-6
mirifica 1-58
schaffner 1-6
underwoodianum 1-6
virginianum 1-8
virginicum 1-8
- Bryodisma** 6-66
Byrsopteris 4-35
aristata 4-35
- Caenopteris**
achilleifolia 5-32
myriophylla 5-25
- Calamaria**
triquetra 6-97
- Camptosorus** 5-2
- Campyloneurum** 5-158
abruptum 5-172
aglaolepis 5-167
amphostenon 5-165
angustifolium 5-168
angustipaleatum 5-169
aphanophlebium 5-161
asplundii 5-167
brevifolium 5-170
caespitosum 5-162
chlorolepis 5-168
coarctatum 5-164
decurrens 5-132
densifolium 5-166
fasciale 5-163
fendleri 5-132
fuscocosquamatum 5-163
heterolepis 5-168
inflatum 5-164
irregulare 5-166
jamesonii 5-172
lapathifolium 5-162
latum 5-170
lorentzii 5-167
magnificum 5-132
nitidissimum 5-171
nodosum 5-172
occultum 5-161
ophiocaulon 5-162
pascoense 5-171
phyllitidis 5-169
repens 5-162
serpentinum 5-163
solutum 5-172
sphenodes 5-164
taeniosum 5-169
trichiatum 5-161
vulpinum 5-167
- Ceradenia** 5-72
capillaris 5-90
curvata 5-72
dendroxa 5-88
discolor 5-86
farinosa 5-89
herrerae 5-88
longipinnata 5-85
meridensis 5-85
mirabilis 5-91
pearcei 5-87
pilipes 5-90
praeclara 5-89
terrestris 5-87
- Ceratopteris** 2-50
pteridoides 2-50
richardii 2-50
thalictroides 2-50
- Ceropteris**
adiantoides 2-19
- Ceterach**
aspidioides 3-13
- Cheilanthes** 2-23
andina 2-27
arequipensis 2-33
bonariensis 2-28
borsigniana 2-37
buchtienii 2-34

- cantangensis* 2-32
chlorophylla 2-36
concolor 2-31
crenata 4-94
elegans 2-31
farinosa 2-30
fasciculata 2-27
fractifera 2-25
fraseri 2-28
glandulosa 2-106
glauca 2-30
hostilis 2-110
hypoleuca 2-34
incarum 2-33
intramarginalis 2-23
lonchophylla 2-33
macleanii 2-27
marginata 2-30
mathewsii 2-27
micropteris 2-23
mollis 2-29
moritziana 2-25
myriophylla 2-31
notholaenoides 2-25
obducta 2-29
obtusata 2-111
orbignyana 2-29
ornatissima 2-32
parallelogramma 2-110
peruviana 2-32
pilosa 2-27
pilosa × *pruinata* 2-27
poeppigiana 2-30
pruinata 2-27
radiata 2-36
rigida 2-34
rufopunctata 2-29
saundersii 2-25
scariosa 2-32
sinuata 2-34
squamosa 2-34
tripinnata 2-32
Cheiroglossa 1-8
palmata 1-9
Christella 3-39
dentata 3-42
hispidula 3-41
parasitica 3-39
Christensenia 1-13
Chrysodium
lindigii 4-103
serratum 4-101
Cnemidaria 1-136
alatissima 1-138
cocleana 1-139
horrida 1-138
nervosa 1-139
speciosa 1-139
uleana 1-138
Cochlidium 5-72
graminioides 5-72
pumilum 5-82
serrulatum 5-82
Coptophyllum 1-24
buniifolium 1-24
Cryptosorus 5-72
blumei 5-72
Ctenitis 4-5
ampla 4-10
andicola 4-19
biserialis 4-15
catocarpa 4-10
distans 4-5
hirsuto-setosa 4-16
honesta 4-14
karsteniana 4-17
microchlaena 4-9
mollicoma 4-17
nemophila 4-10
nigrovenia 4-9
protensa 4-21
pulverulenta 4-17
refulgens 4-7
sloanei 4-10
subincisa 4-10
submarginalis 4-8
Ctenopteris 5-72
amylacea 5-87
anfractuosa 5-99
apiculata 5-94
asplenifolia 5-104
athyrioides 5-113
capillaris 5-90
congesta 5-89
contacta 5-107
crispata 5-72
cultrata 5-108
discolor 5-86
dolorensis 5-104
ecuadorensis 5-110
farinosa 5-89
firma 5-100
gracilis 5-96
herrerae 5-88
heteromorpha 5-105
lanigera 5-106
leucosticta 5-111
longipinnata 5-85
longiuscula 5-111
major 5-96
melanosticta 5-98
meridensis 5-85
moniliformis 5-98
obovata 5-95
peruviana 5-102
phlegmaria 5-97
pilosissima 5-101
pseudocapillaris 5-94
pseudonutans 5-103
pteropus 5-95
rigens 5-101
rigescens 5-102
semihirsuta 5-112
sericeo-lanata 5-106
stella 5-106
sublabelliformis 5-107
subimpressa 5-94
subsessilis 5-95
taxifolia 5-113
tunguraguae 5-95
venulosa 5-72
yungensis 5-113
Culcita 1-103
coniifolia 1-103
macrocarpa 1-103
Cuspidaria 5-145
furcata 5-145
Cyathea 1-129
andina 1-130
arborea 1-129
aterrima 1-114
bipinnatifida 1-126
caracasana 1-133
castanea 1-135
cuspidata 1-120
delgadii 1-132
divergens 1-131
dudleyi 1-135
ebermina 1-135
elongata 1-117
equestris 1-131
erinacea 1-118
frigida 1-126
fulva 1-135
incana 1-120
kalbreyeri 1-124
lasiosora 1-125
latevagans 1-124
lechleri 1-135
macrosora 1-115
meridensis 1-135
mexicana 1-133
microdonta 1-127
microphylla 1-132
multiflora 1-130
multisegmenta 1-132
nigra 1-125
nigripes 1-124
oligocarpa 1-132
oreites 1-115
pallescens 1-131
panamensis 1-131
petiolata 1-131
phegopteroides 1-127
pilosa 1-132
pilosissima 1-125
poeppigii 1-115
polystichoides 1-118
primaeva 1-125
procera 1-123
pubens 1-127
pubescens 1-127
pungens 1-123
quindiuensis 1-116
rufescens 1-114
ruiziana 1-132
schanschin 1-132
sprucei 1-115
subtropicala 1-128
ulei 1-128
vilhelmii 1-130
willdenowiana 1-123
Cyclodium 4-47
guianense 4-48
meniscioides 4-48
 trianae 4-47
Cyclopetlis 4-29
semicordata 4-29

- Cyclosorus* 3-39
dentatus 3-42
gongyloides 3-40
Cyrtomium 4-38
dubium 4-38
falcatum 4-40
nobile 4-38
Cyrtophlebium 5-158
phyllitidis 5-169
repens 5-162
Cystodium 1-103
Cystopteris 4-92
fragilis 4-92
translucens 4-92
- Danaea* 1-15
cuspidata 1-19
elliptica 1-18
grandifolia 1-17
humilis 1-20
jamaicensis 1-19
longifolia 1-17
moritziana 1-19
nodosa 1-17
oblanceolata 1-18
stenophylla 1-19
trichomanoides 1-20
wendlandii 1-20
Davallia
arborescens 2-100
concinna Presl 2-100
concinna Schrader 5-4
glauca 2-99
inaequalis 2-103
multiflora 5-52
thecifera 5-48
Davalliopsis
elegans 1-84
Dennstaedtia Bernh. 2-95
Dennstaedtia Moore 2-95
Dennstaedtia
arborescens 2-100
bipinnata 2-99
cicutaria 2-98
concinna 2-100
dissecta 2-100
distenta 2-95
erosa 2-100
flaccida 2-95
glauca 2-99
globulifera 2-99
mathewsii 2-100
obtusifolia 2-100
pearcei 1-99
punctilobula 2-95
rubiginosa 2-98
sprucei 2-101
wercklei 2-101
Deperia
mathewsii 2-100
Dicksonia 1-105
arborescens 1-105
berteriana 1-105
bipinnata 2-99
cicutaria 2-98
coniifolia 1-103
dissecta 2-100
erosa 2-100
gigantea 1-105
karsteniana 1-105
montevideensis 4-94
obtusifolia 2-100
pearcei 1-99
polypodioides 2-95
rubiginosa 2-98
sellowiana 1-105
spruceana 1-105
stuebelii 1-105
Dicranoglossum 5-49
desvauxii 5-147
furcatum 5-145
panamense 5-145
polypodioides 5-148
subnudum 5-147
Dicranopteris 1-46
affinis 1-42
bancroftii 1-39
bifida 1-41
brittonii 1-44
dichotoma 1-46
flexuosa 1-47
linearis 1-47
longipinnata 1-45
nervosa 1-47
pectinata 1-49
pennigera 1-39
peruviana 1-45
pruinosa 1-42
remota 1-44
rubiginosa 1-46
schomburgkiana 1-47
seminuda 1-47
simplex 1-39
velata 1-42
yungensis 1-44
Didymochlaena 4-40
lunulata 4-40
sinuosa 4-40
truncatula 4-40
Didymoglossum 1-76
angustifrons 1-86
hymenoides 1-86
krausii 1-87
membranaceum 1-88
muscooides 1-86
reptans 1-87
sphenoides 1-86
Diphasiastrum 6-52
thyoides 6-57
Diphasium 6-52
jussiaei 6-56
Diplazium 4-65
aberrans 4-87
alienum 4-72
altissimum 4-70
ambiguum 4-71
angelipolitanum 4-79
appolinaris 4-77
arboresum 4-80
asplenioides 4-75
bicolor 4-74
bogotense 4-70
bombonasae 4-81
bonapartii 4-75
bradeorum 4-88
brasiliense 4-79
buchtienii 4-72
callipteris 4-83
caracasanaum 4-79
celtidifolium 4-83
centripetale 4-88
chimborazense 4-87
costale 4-77
crassifolium 4-76
cristatum 4-80
cuneifolium 4-82
delitescens 5-32
denticulosum 4-80
diplazioides 4-71
divergens 4-70
drepanolobium 4-81
eggersii 4-88
expansum 4-75
ferulaceum 4-90
flavescens 4-85
flexuosum 4-76
fraxinifolium 4-67
fuscopubescens 4-72
fuscum 4-87
gracilescens 4-72
grande 4-78
grandifolium 4-82
hians 4-70
induratum 4-78
lechleri 4-85
legalloi 4-84
lehmannii 4-72
lindbergii 4-78
lonchophyllum 4-80
macrodictyon 4-87
macrophyllum 4-77
melanopus 5-31
melanosorum 4-75
moritzianum 4-73
obscurum 4-85
obtusum 4-79
oxylobum 4-77
pactile 4-87
paucijugum 4-84
pedatum 4-74
pinnatifidum 4-86
plantagineum 4-86
plantaginifolium 4-86
praestans 4-87
preslianum 4-76
remotum 4-74
riedelianum 4-85
roemerianum 4-85
rostratum 4-75
sandwichianum 4-72
shepherdii 4-80
striatum 4-79
stuebelianum 4-80
subnudum 4-79
subobtusum 4-78
tabalosense 4-79
tarapotense 4-73

- tungurahuae 4-76
 unilobum 4-81
 vastum 4-73
 venulosum 4-75
 verapax 4-85
 werckleanum 4-80
Diplopterygium 1-37
 bancroftii 1-39
Doryopteris 2-43
 concolor 2-31
 crenulans 2-44
 lomariacea 2-44
 lorentzii 2-44
 palmata 2-44
 pedata 2-44
Drynaria
 acuminata 5-156
Dryopteris 4-35
 ampla 4-10
 anceps 3-68
 ancyriothrix 3-63
 andicola 4-19
 andreana 3-76
 angustifolia 3-74
 arcana 3-76
 aristata 4-35
 aspidioides 3-13
 assurgens 3-30
 asterothrix 3-62
 atorrubens 3-24
 balbisii 3-31
 bangii 3-42
 biformata 3-60
 biserialis 4-15
 boqueronensis 3-26
 brachyodus 3-49
 brachypus 3-18
 brausei 3-28
 canadasi 3-21
 catocarpa 4-10
 caucaensis 3-28
 cheilanthoides 3-34
 christii 4-45
 chrysodioides 3-69
 clypeata 3-65
 coarctata 3-32
 columbiana 3-15
 comosa 3-49
 concinna 3-29
 consobrina 3-73
 contermina 3-32
 corazonensis 3-27
 ctenitis 4-5
 decussata 3-49
 deflexa 3-30
 deltoidea 3-46
 densa 3-34
 densiloba 3-52
 dentata 3-42
 denticulata 4-37
 desvauxii 3-71
 diplazioides 3-14
 dumetorum 3-27
 eggersii 3-59
 engelii 3-26
 ensiformis 3-75
 euchlora 3-25
 extensa 3-43
 falcata 3-75
 fibrillosa 4-13
 filix-mas 4-35
 furva 3-19
 gigantea 3-68
 glandulosa 3-49
 glandulosolanosa 3-20
 heterophlebia 4-45
 hirsuto-setosa 4-16
 honesta 4-14
 incana 3-52
 jamesonii 3-56
 jurgensenii 3-75
 juvencensis 3-61
 karsteniana 4-17
 karstenii 4-9
 killipii 4-33
 laevigata 3-24
 lechleri 3-69
 leprieurii 3-51
 leptosora 4-14
 leucothrix 3-32
 limaensis 3-20
 lindigii 3-30
 lingulata 3-75
 linkiana 3-14
 lomatosa 3-15
 longicaudata 4-44
 lugubriformis 3-58
 macbridei 3-19
 macrophylla 3-68
 macrostegia 4-38
 macrotis 3-57
 mapiriensis 3-49
 megalodus 3-64
 mercurii 3-31
 microchlaena 4-9
 microsora 4-14
 millei 3-28
 mollicoma 4-17
 mollis 3-42
 multiformis 3-35
 nemophila 4-10
 nigrovenia 4-9
 nitens 3-35
 ochropteroides 4-38
 oligocarpa 3-15
 oligophylla 3-45
 opaca 4-45
 pachyrhachis 3-31
 paleacea 4-36
 paludosa 4-48
 parallelogramma 4-36
 patens 3-44
 patula 4-36
 paucinervata 4-45
 pavoniana 3-23
 pellucido-punctata 4-44
 permollis 3-70
 peruviana 3-23
 phacelothrix 3-22
 pilosohispida 3-27
 pilosula 3-19
 platyloba 4-15
 poiteana 3-65
 prasina 4-45
 protensa 4-21
 ptarmiciformis 3-17
 pteroidea 3-25
 pubescens 3-35
 pulverulenta 4-17
 pusilla 3-17
 pyramidata 3-58
 quadrangularis 3-41
 refulgens 4-7
 resinosofoetida 3-34
 retrorsa 3-27
 rimbachii 3-19
 rivulorum 3-32
 rudis 3-26
 rufa 3-20
 ruiziana 3-35
 saffordii 4-37
 salzmannii 3-73
 scalaris 3-16
 sellensis 3-31
 semihastata 3-57
 serrata 3-71
 simplicifrons 3-68
 sprengelii 3-31
 stuebelii 3-22
 subandina 3-20
 subincisa 4-16
 submarginalis 4-8
 supina 3-26
 supralineata 3-52
 tarapotensis 4-15
 tetragona 3-64
 thelypteris 3-6
 thomsonii 3-22
 tremula 3-9
 tristis 3-61
 uliginosa 3-3
 valdepilosa 3-50
 vasta 4-17
 wallichiana 4-36
 warmingii 3-56
 yungensis 4-14
 Elaphoglossum 4-111
 affine 4-147
 albescens 4-121
 alipes 4-122
 amazonicum 4-122
 amphioxys 4-123
 amplum 4-123
 angustius 4-124
 apodum 4-123
 atropunctatum 4-124
 atrosquamatum 4-124
 auricomum 4-125
 bakeri 4-125
 bangii 4-167
 barbatum 4-125
 blepharoglossis 4-126
 calaguata 4-137
 camptolepis 4-126
 cardenasii 4-126
 castaneum 4-127

caudatum 4-154
chloödes 4-127
ciliatum 4-128
concinnum 4-128
conforme 4-111
craspedotum 4-128
crinipes 4-160
cuspidatum 4-129
decoratum 4-129
denticulatum 4-131
dichroum 4-129
discolor 4-130
diversifrons 4-130
eatonianum 4-127
elegantipes 4-131
elongatum 4-162
engelii 4-131
ensiforme 4-131
erinaceum 4-132
erythrolepis 4-132
eximium 4-133
flaccidum 4-133
fortipes 4-133
glabellum 4-134
glossophyllum 4-134
glutinosum 4-154
gracillimum 4-134
guamanianum 4-135
hartwegii 4-135
hayesii 4-136
haynaldii 4-136
hickenii 4-136
hieracioides 4-137
"hikenii" 4-137
horridulum 4-137
huacsaro 4-137
hystrix 4-138
jucundum 4-138
killipii 4-138
laminarioides 4-139
lanatum 4-139
lasioglottis 4-139
latevagans 4-140
latifolium 4-140
latum 4-123
lawyeræ 4-141
laxisquama 4-141
lechlerianum 4-141
leprosum 4-142
leptophyllum 4-146
lindbergii 4-126
lindenii 4-142
lingua 4-142
linguaeforme 4-134
litanum 4-143
lloense 4-132
longipes 4-144
longius 4-143
luridum 4-144
macilentum 4-144
mathewsii 4-144
megalurum 4-145
megarhizon 4-146
meladenium 4-145
melancholicum 4-145
metallicum 4-146

minutum 4-146
molle 4-152
moorei 4-167
moyeri 4-147
muscosum 4-147
nastukiae 4-148
nidiformis 4-148
nigriscens 4-148
nigrocostatum 4-140
nivosum 4-148
obovatum 4-149
obtusum 4-149
oculatum 4-150
odontolepis 4-150
orbignyanum 4-150
ornatum 4-149
oxyglossum 4-151
oöphyllum 4-150
pachyphyllum 4-151
pachyrrhizum 4-152
paleaceum 4-152
palorense 4-153
papillosum 4-153
pascoense 4-153
patinii 4-153
pattersoniae 4-166
peltatum 4-169
petiolosum 4-154
pichincae 4-158
piloselloides 4-154
pilosius 4-155
plicatum 4-152
plumosum 4-155
poeppigianum 4-15
potomogeton 4-166
preslianum 4-128
propinquum 4-156
pseudohirtum 4-158
pumilio 4-156
punae 4-157
quitense 4-157
raywaense 4-157
rimbachii 4-158
rosenstockii 4-158
rubellum 4-159
ruficomus 4-159
rufum 4-159
russelliae 4-160
schomburgkii 4-144
setigerum 4-160
siliquoides 4-136
simulans 4-160
spatulatum 4-155
squampipes 4-161
stenophyllum 4-161
styriacum 4-161
subciliatum 4-143
tambillense 4-162
tectum 4-162
tenuë 4-163
tenuiculum 4-163
tomentellum 4-163
velongum 4-164
vittarioides 4-164
vulcanicum 4-164
wardiae 4-165

williamsiorum 4-165
williamsii 4-123
zebrinum 4-165
Enterosora 5-72
campbellii 5-72
parietina 5-84
trichosora 5-84
trifurcata 5-83
Equisetaceae 6-12
Equisetum 6-12
bogotense 6-16
fluviatile 6-12
giganteum 6-15
myriochaetum 6-15
ramosissimum
ssp. debile 6-15
schaffneri 6-15
× schaffneri 6-15
variegatum 6-15
Eriosorus 2-3
accrescens 2-6
aureonitens 2-6
cheilanthoides 2-6
elongatus 2-8
flabellatus 2-8
flexuosus 2-7
lechleri 2-8
orbignyanus 2-7
rufescens 2-4
ruizianus 2-20
scandens 2-7
stuebelii 2-6
wurdackii 2-7
Eschatogramme 5-145
desvauxii 5-147
furcata 5-147
polypodioides 5-148
subnuda 5-147
Eupodium 1-15
kaulfussii 1-15

Feea
diversifrons 1-91
heterophylla 1-94
humboldtii 1-94
trollii 1-91

Glaphyropteris 3-48
decussata 3-49
Gleichenia 1-37
affinis 1-42
bancroftii 1-39
bifida 1-41
boliviensis 1-43
buchtienii 1-42
costaricensis 1-43
flexuosa 1-47
glauca 1-37
hypoleuca 1-43
lechleri 1-44
leucocarpa 1-44
longipinnata 1-45
mathewsii 1-41
mellifera 1-4

- nervosa* 1-47
nitidula 1-43
pectinata 1-49
pennigera 1-39
peruviana 1-45
polypodioides 1-37
pruinosa 1-42
remota 1-44
revoluta 1-42
rigida 1-47
rubiginosa 1-46
simplex 1-39
subandina 1-43
tomentosa 1-41
truncata 1-37
tuberculata 1-43
velata 1-42
yungensis 1-44
Glyphotaenium 5-72
trifurcatum 5-83
Goniophlebium 5-71
incanum 5-125
pectinatum 5-121
semipinnatum 5-140
subauriculatum 5-72
Goniopteris 3-52
biolleyi 3-62
crenata 3-52
eggersii 3-59
juvuensis 3-61
pennata 3-64
poiteana 3-65
pyramidata 3-58
tetragona 3-64
tristis 3-61
Grammitis 5-72
albidula 5-87
alsopteris 5-110
amylacea 5-87
andicola 5-103
andina 5-109
anfractuosa 5-99
apiculata 5-94
aromatica 5-100
asplenifolia 5-104
assurgens 5-99
athyrioides 5-113
basalis 5-109
bipinnata 5-92
bishopii 5-86
blepharidea 5-112
blepharolepis 5-108
bryophila 5-81
buesii 5-112
campbellii 5-72
capillaris 5-90
cheilanthoides 2-6
chrysleri 5-104
congesta 5-89
crispata 5-72
cultrata 5-108
curvata 5-72
daguensis 5-109
david-smithii 5-109
dendroxa 5-88
dependens 5-104
discolor 5-86
dudleyi 5-92
elongata 5-143
erecta 5-98
farinosa 5-88
firma 5-100
flabelliformis 5-102
flexuosa 2-7
gracilis 5-96
graminioides 5-72
herrerae 5-88
heteromorpha 5-105
immixta 5-115
jamesonii 5-82
jamesonioides 5-93
lanceolata 5-143
lanigera 5-105
laxa 5-107
lehmanniana 5-104
leucosticta 5-111
limbata 5-81
linkiana 3-14
longipinnata 5-85
major 5-96
marginella 5-72
mathewsii 5-91
melanosticta 5-97
meridensis 5-85
mirabilis 5-91
moniliformis 5-98
myosuroides 5-82
myriophylla 5-114
nigrolimbata 5-81
obliquata 5-72
paramicola 5-81
parietina 5-84
peruviana 5-102
phlegmaria 5-97
pichinchae 5-110
pichinchensis 5-110
pilipes 5-90
pilosissima 5-100
praeclara 5-89
pseudocapillaris 5-94
pseudonutans 5-103
pumila 5-82
recondita 5-95
revoluta 5-143
rigens 5-101
rigescens 5-102
ruiziana 2-7
sectifrons 5-72
semihirsuta 5-111
senilis 5-107
sericeo-lanata 5-106
serrulata 5-82
sprucei 5-84
squamulosa 5-143
subflabelliformis 5-106
subsessilis 5-95
taxifolia 5-113
terrestris 5-87
trichosora 5-83
trifurcata 5-83
truncicola 5-109
tunguraguae 5-94
variabilis 5-115
venulosa 5-72
werfii 5-92
xiphopteroides 5-101
youngii 5-97
Gymnogramma
aureonitens 2-7
diplazioides 3-14
elongata 2-8
ferruginea 2-20
flabellata 2-8
flexuosa 2-7
goudotii 2-12
jamesonii 2-20
lechleri 2-8
mathewsii 2-4
mohriaeformis 2-4
ochracea 2-19
orbignyana 2-7
pearcei 2-21
peruviana 2-19
polypodioides 3-14
pumila 2-84
reniformis 2-15
rufescens 2-4
stuebelii 2-6
Gymnopteris 2-46
aliena 4-100
nicotianifolia 4-102
pandurifolia 4-105
rufa 2-47
tomentosa 2-46
Hecistopteris 2-84
pumila 2-84
Hemidictyum 4-90
marginatum 4-90
Hemionitis 2-46
brasiliانا 2-87
cajenensis 2-87
lanceolata 2-87
lineata 2-86
palmata 2-48
pinnata 2-48
plantaginea 2-84
rufa 2-47
tomentosa 2-46
Hemiphlebium
kapplerianum 1-88
Hemitelia 1-129
andina 1-130
horrida 1-138
lechleri 1-131
multiflora 1-130
nervosa 1-139
petiolata 1-131
rufescens 1-114
speciosa 1-139
subincisa 1-139
uleana 1-138
Hicriopteris
bancroftii 1-39
Histiopteris 2-115
incisa 2-115
vespertilionis 2-115

Hoffmannia 6-11
aphylla 6-11
Holodictyum 5-2
Homoetes 1-76
heterophylla 1-94
Huperzia 6-19
acerosa 6-46
acifolia 6-28
affinis 6-30
andina 6-35
aqualupiana 6-48
arcuata 6-25
aristei 6-43
attenuata 6-37
bifida 6-28
blepharodes 6-30
binervia 6-26
brevifolia 6-39
brongniartii 6-27
buesii 6-42
campiana 6-47
capellae 6-32
caracasica 6-40
colanensis 6-31
crassa 6-33
cuneifolia 6-50
curvifolia 6-46
darwiniana 6-33
dichaeoides 6-48
dichotoma 6-26
durissima 6-51
ecuadorica 6-29
engleri 6-39
ericifolia 6-48
eversa 6-29
filiformis 6-46
funiformis 6-42
hartwegiana 6-40
heteroclita 6-48
hippuridea 6-24
hohenackeri 6-40
hypogaea 6-36
kuesteri 6-30
jenmanii 6-44
lechleri 6-25
lindaviana 6-44
linifolia 6-43
 var. *jenmanii* 6-44
 var. *tenuifolia* 6-44
loxensis 6-26
lucidula 6-19
macbridei 6-32
mandiocana 6-45
mexiae 6-28
mollicoma 6-45
molongensis 6-47
montana 6-25
myrsinites 6-49
nesselii 6-34
nuda 6-25
papillata 6-31
parvifolium 6-28
passerinoidea 6-41
 var. *nitens* 6-41
pearcei 6-30
phylicifolia 6-49

pilgeriana 6-34
polycarpus 6-37
polyclada 6-51
polylepidetorum 6-31
pruinosa 6-51
quadrifariata 6-49
reflexa 6-27
 var. *bifida* 6-28
 var. *minor* 6-28
 var. *reflexa* 6-28
rosenstockiana 6-42
sagasteguiana 6-37
sanctae-barbarae 6-35
sarmentosa 6-45
saururus 6-35
selago 6-19
sellifolia 6-38
socratis 6-42
sotae 6-43
subulata 6-50
taxifolia 6-41
tenuis 6-46
tetragona 6-38
unguiculata 6-29
weberbaueri 6-30
weddellii 6-26
wilsonii 6-44
Hydroglossum 1-33
oligostachyum 1-33
Hymenodium
kunzeanum 4-151
Hymenophyllum 1-50
adiantoides 1-66
amabile 1-70
andinum 1-62
apiculatum 1-59
axillare 1-62
beyrichianum 1-68
calodictyon 1-56
ciliatum 1-67
contortum 1-64
crispatum 1-68
crispum 1-67
cristatum 1-55
dendritis 1-59
dependens 1-72
dicranotrichum 1-50
ectocarpon 1-57
elegans 1-66
elegantulum 1-70
endiviiifolium 1-63
fendlerianum 1-64
ferax 1-61
fragile 1-69
fucoides 1-55
fusagasugense 1-73
fusagasugense 1-73
hirsutum 1-66
interruptum 1-72
karstenianum 1-71
lamellatum 1-58
latipes 1-59
lindenii 1-71
lineare 1-66
lobatoalatum 1-74
mathewsii 1-60

mexiae 1-59
microcarpum 1-68
mirificum 1-58
molle 1-65
multialatum 1-73
multiflorum 1-63
myriocarpum 1-62
nigrescens 1-63
nigricans 1-63
pedicellatum 1-57
peltatum 1-57
peruvianum 1-75
platylobum 1-68
plumieri 1-72
plumosum 1-72
poepigianum 1-76
polyanthos 1-59
polycarpum 1-64
procerum 1-65
pulchellum Hooker 1-70
pulchellum Mett. 1-65
pyramidatum 1-74
reniforme 1-64
rimbachii 1-64
ruizianum 1-69
rupestre 1-82
simplex 1-69
speciosum 1-70
spectabile 1-70
sprucei 1-76
superbum 1-72
tarapotense 1-75
tenerrimum 1-66
tomentosum 1-73
tortuosum 1-57
trapezoidale 1-69
 trianae 1-61
trichomanoides 1-61
trichophyllum 1-65
trifidum 1-76
tunbridgense 1-50
undulatum 1-63
valvatum 1-68
verecundum 1-75
Hymenostachys
diversifrons 1-91
Hypoderris
stuebelii 4-103
Hypolepis 2-106
bogotensis 2-110
flexuosa 2-110
hostilis 2-110
nigrescens 2-109
obtusata 2-110
parallelogramma 2-110
pteroides 2-111
stuebelii 2-109
tenuifolia 2-106

Isoetaceae 6-88
Isoetes 6-89
andicola 6-92
 var. *gemmifera* 6-92
andina 6-97
boliviensis 6-96

- dichotoma* 6-91
dispora 6-93
glacialis 6-95
herzogii 6-97
hewitsonii 6-94
karstenii 6-96
lacustris 6-89
laevis 6-95
lechleri 6-95
 var. *triquetra* 6-97
novo-granadensis 6-91
pacifica 6-91
panamensis 6-91
parvula 6-92
peruviana 6-95
saracochensis 6-94
savanarum 6-91
socia 6-95
 "ticliensis" 6-95
triquetra 6-97
- Jamesonia** 2-8
alstonii 2-12
blepharum 2-14
boliviensis 2-12
cinnamomea 2-14
glutinosa 2-13
goudotii 2-12
imbricata 2-13
paleacea 4-54
peruviana 2-11
pulchra 2-11
rotundifolia 2-10
scalaris 2-12
scammanae 2-11
- Lacostea**
tanaica 1-89
- Lastrea**
cheilanthoides 3-34
nitens 3-35
poepigiana 3-57
poiteana 3-65
pubescens 4-31
recedens 4-31
rudis 3-26
scabriuscula 3-44
- Lastreopsis** 4-31
amplissima 4-33
effusa 4-33
exculta 4-35
killipii 4-33
recedens 4-31
tenera 4-31
- Lecanium**
membranaceum 1-88
- Lellingeria** 5-72
apiculata 5-94
major 5-96
myosuroides 5-82
phlegmaria 5-97
pseudocapillaris 5-94
subsessilis 5-95
tunguraguae 5-95
- Lepicystis* 5-125
 incana 5-125
- Lepidotus* auct. 6-58
Lepidotus Mirbel 6-52
 alopecuroides 6-61
 cernua 6-63
 clavata 6-54
 contexta 6-62
 magellanica 6-56
- Lepisorus* 5-140
- Leptochilus**
alienus 4-100
bradeorum 4-103
crenatus 4-101
guianensis 4-109
killipii 4-102
lindigi 4-103
nicotianifolius 4-102
oligarchicus 4-103
pandurifolium 4-105
serratifolius 4-101
serratus 4-101
stuebelii 4-103
- Leptocionium** 1-50
dicanotrichum 1-50
fucoides 1-56
pedicellatum 1-57
- Leptopteris** 1-20
- Lindsaea** 2-115
arcuata 2-117
divaricata 2-118
guianensis 2-120
hemiglossa 2-122
lancea 2-121
latifrons 2-122
portoricensis 2-120
phassa 6-98
schomburgkii 2-122
spruceana 2-118
sprucei 2-118
stricta 2-121
taeniata 2-118
tarapotensis 2-118
trapeziformis 2-115
ulei 2-122
- Litobrochia**
horizontalis 2-77
- Lomagamma** 4-109
guianensis 4-109
- Lomaria** 5-56
acuta 5-64
andina 5-61
angustifolia 5-64
arborescens 5-62
aurata 5-67
caudata 5-66
chilensis 5-62
cordata 5-62
cuspidata 5-64
divergens 5-63
ensiformis 5-64
euphlebia 1-101
fragile 5-64
fraxinea 5-59
heterophylla 5-63
linariaefolia 5-68
- loxensis* 5-65
meridensis 5-64
nuda 5-56
obtusifolia 5-67
ornifolia 5-62
pteropus 5-63
schomburgkii 5-66
serrulosa 5-62
squamulosa 5-65
stenophylla 5-65
stipitellata 5-65
volubilis 5-70
- Lomaridium**
semicordatum 1-101
- Lomariopsis** 4-105
erythrodes 4-107
fendleri 4-106
japurensis 4-106
latipinna 4-107
nigropaleata 4-108
sorbifolia 4-105
vestita 4-106
- Lonchitis** 2-113
glabra 2-111
hirsuta 2-113
lindeniana 2-113
pedata 2-80
tenuifolia 2-106
- Lophidium** 1-33
elegans 1-34
flabellum 1-34
latifolium 1-33
poepigianum 1-36
- Lophosoria** 1-107
pruinata 1-109
quadripinnata 1-107
- Loxoma** 1-98
Loxoscaphe 5-4
 concinna 5-4
 thecifera 5-48
- Loxosma** 1-98
Loxosomopsis 1-99
costaricensis 1-99
lehmannii 1-99
notabilis 1-99
pearcei 1-99
- Lycopodiaceae** 6-16
- Lycopodiella** 6-58
 sect. *Campylostachys* 6-60
 sect. *Caroliniana* 6-58
 sect. *Lycopodiella* 6-60
 alopecuroides 6-61
 camporum 6-63
 caroliniana
 var. *meridionalis* 6-61
 cernua 6-63
 contexta 6-62
 descendens 6-64
 glaucescens 6-64
 inundata 6-58
 matthewsii 6-61
 pendulina 6-65
 riofrioi 6-65
- Lycopodium** 6-52
 sect. *Caroliniana* 6-60
 sect. *Complanata* 6-52

- sect. *Diphasium* 6-52
sect. *Lycopodium* 6-52
sect. *Magellanica* 6-52
subg. *Cernuistachys* 6-58
subg. *Lepidotis* auct. 6-58
subg. *Lepidotis* Baker 6-52
subg. *Rhopalostachya* 6-52
subg. *Selago* 6-19
subg. *Urostachya* 6-19
acifolium 6-28
affine 6-30
albidum 6-55
alopecuroides 6-61
 var. *contextum* 6-62
 ssp. *contextum* 6-62
anceps 6-80
andinum 6-35
arcanum 6-44
aristatum 6-54
articulatum 6-84
attenuatum 6-37
bifidum 6-28
binervium 6-26
blepharodes 6-30
brevifolium 6-39
brongniartii 6-27
brutum 6-28
buesii 6-42
capellae 6-32
capillaceum 6-63
caracasicum 6-40
carolinianum 6-58
 var. *meridionalis* 6-62
catharticum 6-38
cernuum 6-64
 var. *capillaceum* 6-64
 var. *pendulinum* 6-65
clavatum 6-54
 ssp. *clavatum* 6-54
 ssp. *contiguum* 6-55
 var. *aristatum* 6-54
 var. *pseudocontiguum* 6-55
 var. *thyoides* 6-57
 var. *validum* 6-57
congestifolium 6-49
contextum 6-62
contiguum 6-55
convolutum 6-87
crassum 6-33
cuatrecasasii 6-45
cuneifolium 6-50
curvifolium 6-46
densifolium 6-28
diffusum 6-76
durissimum 6-51
ecuadoricum 6-29
elongatum 6-35
engleri 6-39
ericaefolium 6-48
eristachys 6-54
erythropus 6-80
eversum 6-29
ewanii 6-50
exaltatum 6-86
fastigiatum 6-56
funiforme 6-42
gayanum 6-57
geniculatum 6-85
glaucescens 6-64
gracile 6-80
haematodes 6-80
haenkei 6-56
hartwegianum 6-40
herbaceum 6-55
heteroclitum 6-48
heterophyllum 6-57
hohenackeri 6-40
hypogaea 6-19
hippurideum 6-24
jenmanii 6-44
jussiaei 6-56
 var. *microphyllum* 6-56
lechleri 6-25
linifolium 6-43
lucidula 6-19
macbridei 6-32
magellanicum 6-56
mathewsii 6-61
meridionale 6-61
mexiae 6-28
microphyllum 6-75
molongense 6-47
myrsinites 6-49
 var. *minus* 6-38
nitens 6-41
nubigenum 6-49
nova-hollandiae 6-77
nudum 6-12
papillatum 6-31
parkeri 6-84
parvifolium 6-28
passerinoides 6-41
pendulinum 6-65
pensum 6-68
phlegmaria 6-19
phylicifolium 6-49
pichinchense 6-56
piliferum 6-54
polycarpus 6-45
polycarpum 6-29
polycladum 6-51
poseidonis 6-24
pruinatum 6-51
reflexum Lam. 6-27
 var. *densifolium* 6-28
 var. *majus* 6-28
 var. *minus* 6-28
 var. *polycarpum* 6-29
reflexum Willd. 6-29
reversum 6-28
riofrioi 6-65
rosenstockianum 6-42
sanctae-barbarae 6-21
sarmentosum 6-45
saururus 6-35
scariosum 6-55
 var. *jussieui* 6-57
schwendeneri 6-41
selaginoides 6-66
selago 6-19
skutchii 6-49
sprucei 6-62
spurium 6-56
stamineum 6-44
stellae-polaris 6-28
subulatum 6-50
taxifolium 6-41
 var. *brongniartii* 6-27
tenue 6-46
 var. *tenuissimum* 6-46
tetragonum 6-38
 var. *patulum* 6-38
thujoides 6-57
thyoides 6-57
trichodendron 6-44
trichophyllum 6-54
trychophyllum 6-54
unguiculata 6-29
vestitum 6-55
weddellii 6-26
wilsonii 6-44
Lygodium 1-30
digitatum 1-32
mexicanum 1-33
micans 1-32
oligostachyum 1-33
polymorphyum 1-33
radiatum 1-32
scandens 1-30
venustum 1-30
volubile 1-32
Macrothelypteris 3-3
torresiana 3-3
Marattia 1-13
alata 1-15
kaulfussii 1-15
laevis 1-15
Marginaria 5-125
angustifolia 5-169
polypodioides 5-125
Marginariopsis 5-71
Marsilea 6-2
ancylopoda 6-4
crotophora 6-5
deflexa 6-4
mollis 6-5
natans 6-6
mucronata 6-5
uncinata 6-5
vestita 6-4
 ssp. *tenuifolia* 6-5
 ssp. *vestita* 6-5
Marsileaceae 6-2
Mecodium 1-50
apiculatum 1-59
contortum 1-64
dendritis 1-59
endiviifolium 1-63
fendlerianum 1-64
ferax 1-61
mexiae 1-59
microcarpum 1-68
multiflorum 1-63
myriocarpum 1-62
polyanthos 1-59
trichomanoides 1-61

- undulatum* 1-64
Megalastrum 4-11
andicola 4-18
biseriale 4-15
hirsutosetosum 4-16
honestum 4-13
leptosorum 4-14
microsorium 4-14
mollicomum 4-17
pansamalense 4-18
platylobum 4-15
pulverulentum 4-17
spectabile 4-16
subincisum 4-16
vastum 4-17
villosum 4-11
yungense 4-14
Melpomene 5-96
Meniscium 3-66
andreanum 3-76
angustifolium 3-74
arborescens 3-70
cristatum 4-80
falcatum 3-75
giganteum 3-68
guyanense 3-68
jurgensenii 3-75
macrophyllum 3-68
opacum 4-45
salzmannii 3-73
serratum 3-71
Meringium
fucoides 1-56
Mertensia 1-46
bancroftii 1-39
bifida 1-41
dichotoma 1-46
flexuosa 1-47
laevigata 1-37
longipinnata 1-45
mathewsii 1-41
nervosa 1-47
pectinata 1-49
pennigera 1-39
pruinosa 1-42
remota 1-44
revoluta 1-42
rigida 1-47
simplex 1-37
tomentosa 1-41
velata 1-42
Metaxya 1-109
rostrata 1-111
Microgramma 5-148
acatallela 5-152
acuminata 5-157
baldwinii 5-155
bifrons 5-181
chrysolepis 5-151
ciliata 5-153
fuscopunctata 5-144
geminata 5-157
latevagans 5-151
lindbergii 5-157
lycopodioides 5-154
megalophylla 5-157
percussa 5-144
persicariifolia 5-157
piloselloides 5-152
recreense 5-157
reptans 5-163
rosmarinifolia 5-154
squamulosa 5-156
tecta 5-154
thurnii 5-156
ulei 5-156
vacciniifolia 5-152
Microlepidia 2-95
flaccida 2-95
inaequalis 2-103
polypodioides 2-95
spelunca 2-95
Micropolypodium 5-72
pseudotrichomanoides 5-72
Microstaphyla
bangii 4-167
moorei 4-167
Mildella 2-23
intramarginalis 2-23
Mohria 1-23

Nephelea 1-118
cuspidata 1-120
erinacea 1-118
incana 1-120
polystichoides 1-118
Nephrodium
antioquoianum 4-26
brachypus 3-18
canadasii 3-21
"carazanense" 3-27
caucaense 3-28
conspersum 3-42
corazonense 3-27
crassipes 3-31
deflexum 3-30
eggersii 3-59
firmifolium 4-47
funestum 4-21
gardnerianum 3-52
jamesonii 3-56
kunzeanum 3-46
lagerheimii 4-8
lechleri 3-69
leprieurii 3-51
lizarzaburui 4-25
longipilosum 3-14
macradenium 3-21
macrotris 3-57
microsorium 4-14
nemorale 3-62
nigrovenium 4-9
ochropteroides 4-38
pilosohispidium 3-27
polyphyllum 4-53
quadrangulare 3-41
resinosofoetidum 3-34
retrosum 3-27
schizotis 3-44
sodiroy 4-26
supinum 3-26
tarapotense 4-8
trapezoides 4-53
valdepilosum 3-50
villosum 4-18
Nephrolepis 5-49
biserrata 5-51
cordifolia 5-52
hirsutula 5-54
multiflora 5-52
occidentalis 5-53
pectinata 5-53
pendula 5-52
rivularis 5-52
Neuromanes
pinnatum 1-92
Neurophyllum
hostmannianum 1-93
pinnatum 1-92
Niphidium 5-173
albopunctatissimum 5-174
americanum 5-173
anocarpos 5-177
carinatum 5-176
crassifolium 5-174
longifolium 5-173
macbridei 5-176
vittaria 5-177
Notholaena 2-37
arequipensis 2-33
aurea 2-28
bonariensis 2-28
brackenridgei 2-32
buchtienii 2-34
candida 2-37
cantangensis 2-32
chrysophylla 2-40
fraseri 2-28
lonchophylla 2-33
marantae 2-37
mollis 2-29
nivea 2-38
obducta 2-29
peruviana 2-32
sinuata 2-34
stuebeliana 2-33
sulphurea 2-37
tectaria 2-34
tenera 2-40
tomentosa 2-34
trichomanoides 2-37

Odontomanes
hostmannianum 1-93
Oleandra 4-96
articulata 4-96
distenta 4-96
hirta 4-98
lehmannii 4-97
micans 4-98
neriiformis 4-96
nodosa 4-96
pilosa 4-98
Olfersia 4-55
caudata 4-64
cervina 4-57

- ciliata* 4-128
corcovadensis 4-57
Onoclea
polypodioides 1-37
Ophioglossum 1-8
coriaceum 1-12
crotalophoroides 1-12
ellipticum 1-12
lusitanicum 1-12
nudicaule 1-11
opacum 1-12
palmatum 1-9
pendulum 1-8
peruvianum 1-9
petiolatum 1-9
reticulatum 1-9
scandens 1-30
scariosum 1-11
tenerum 1-11
vulgatum 1-8
ypanemense 1-11
Osmunda 1-21
adiantifolia 1-24
cervina 4-57
cicutaria 1-8
cinnamomea 1-21
flexuosa 1-27
hirsuta 1-28
humilis 1-29
lunaria 1-6
oblongifolia 1-29
palustris 1-23
peltata 4-169
phyllitidis 1-29
polypodioides 5-64
regalis 1-23
spectabilis 1-23
virginiana 1-8

Paesia 2-106
amazonica 2-106
anfractuosa 2-106
glandulosa 2-106
viscosa 2-106
Palhinhaea 6-58
camporum 6-63
cernua 6-63
descendens 6-64
glaucescens 6-64
pendulina 6-65
rofioi 6-66
Parablechnum
ciliatum 5-68
Paraceterach
marantae 2-37
Parkeria
pteridoides 2-50
Peculuma 5-116
absidata 5-119
boliviana 5-120
camptophyllaria 5-122
choquetangensis 5-116
curvans 5-119
dispersa 5-125
divaricata 5-120

eurybasis 5-121
filicula 5-119
funicula 5-116
hygrometrica 5-124
pectinata 5-121
plumula 5-118
ptilodon 5-123
venturii 5-122
Pellaea 2-40
atropurpurea 2-40
cordifolia 2-41
crenulans 2-44
dealbata 2-38
lorentzii 2-44
nivea 2-38
ovata 2-4
peruviana 2-41
sagittata 2-41
tenera 2-40
ternifolia 2-41
weddeliana 2-41
wrightiana 2-41
Peltapteris 4-167
moorei 4-167
peltata 4-169
peruviana 4-170
Peltochlaena 4-47
Phanerophlebia 4-38
nobilis 4-38
Phegopteris
cochleata 4-55
dictyophylla 4-38
dubia 4-38
laevigata 3-24
lechleri 4-45
membranacea 3-69
mollis 3-70
pycnolepis 4-55
refulgens 4-7
Phlebodium 5-125
aureum 5-134
decumanum 5-135
Phlegmariurus 6-19
taxifolius 6-41
Phyllitis 5-4
scolopendrium 5-4
Phylloglossum 6-16
Pilularia 6-2
americana 6-2
mandonii 6-2
Pityrogramma 2-16
austroamericana 2-18
chrysoconia 2-20
chrysophylla 2-18
ebenea 2-18
ferruginea 2-20
ochracea 2-19
pearcei 2-21
perelegans 2-19
peruviana 2-19
presliana 2-20
tartarea 2-19
trifoliata 2-21
Plagiogyria 1-101
costaricensis 1-101
denticulata 1-101

euphlebia 1-101
latifolia 1-101
semicordata 1-101
Plananthus 6-19
reflexus 6-27
selago 6-19
Platycterium 5-181
alcorne 5-181
andinum 5-181
Plecosorus 4-49
mexicanus 4-49
peruvianus 2-111
speciosissimus 4-49
Pleopeltis 5-140
angusta 5-140
astrolepis 5-143
fuscopunctata 5-144
lanceolata 5-143
macrocarpa 5-142
percussa 5-144
pinnatifida 5-135
revoluta 5-143
squamulosa 5-143
Pleuridium
albopunctatissimum 5-174
Pleurosorus 5-2
Poecilopteris
crenata 4-101
Polybotrya 4-57
aequatoriana 4-64
alfredii 4-65
altescandens 4-61
andina 4-61
appressa 4-64
caudata 4-64
cervina 4-57
crassirhizoma 4-60
decorata 4-62
fractiserialis 4-60
fulvastrigosa 4-65
glandulosa 4-63
hickeyi 4-65
juglandifolia 4-61
kalbreyeri 4-61
lechleriana 4-63
lomarioides 4-65
macbridei 4-60
nutans 4-65
osmundacea 4-62
plumbicaulis 4-60
polybotryoides 4-61
pubens 4-62
puberulenta 4-63
serratifolia 4-57
sorbifolia 4-57
subelliptica 4-63
suberecta 4-61
Polypodium 5-125
abitaguae 5-86
abruptum 3-58
absidatum 5-119
acrodontium 5-101
acrosorum 5-177
adiantiforme 4-31
adnatum 5-133
aglaolepis 5-168

- albopunctatissimum* 5-174
alternifolium 5-108
americanum 5-173
amphostenon 5-166
amplum 4-10
andinum 5-109
anfractuosum 5-99
angustifolium 5-168
angustipaleatum 5-169
anocarpos 5-177
apiculatum 5-94
appressum 5-132
arborescens 1-129
aristatum 4-35
aromaticum 5-100
articulatum 5-133
asplenifolium 5-104
asplundii 5-167
astrolophus 5-143
athyrioides 5-113
aureum 5-134
azuyense 5-94
balaoense 5-138
balbisii 3-31
biauriculatum 5-131
bifrons 5-181
binervatum 5-63
biseriale 4-15
blepharideum 5-112
blepharolepis 5-108
bolivianum 5-120
bombycinum 5-138
brachyodus 3-49
brevifolium 5-170
bryophilum 5-81
bryopodium 5-135
buchtienii 5-136
buesii 5-112
caceresii 5-133
caespitosum 5-162
camptophyllum 5-123
capillare 5-90
chacapoyense 5-131
chartaceum 5-129
chnoodes 5-129
chrysolepis 5-151
ciliatum 5-153
circinatum 5-119
coarctatum 5-164
cochleatum 4-54
concinnum 3-29
cordatum 5-131
cordifolium 5-52
crassifolium 5-174
crenato-dentatum 4-54
crenatum 3-65
crispatum 5-167
crossii 3-23
crystalloneuron 5-139
cultratum 5-108
curvans 5-119
curvatum 5-72
dasypleuron 5-131
decumanum 5-135
decurrens 5-132
decussatum 3-49
dentatum 3-41
denticulatum 4-37
dependens 5-104
dichotomum 1-46
discolor 5-86
dispersum 5-125
disectum 2-100
dissimile 5-129
divaricatum 5-120
dolorensis 5-104
duale 5-83
dulce 5-140
ecostatum 5-85
ecuadorensis 5-110
effusum 4-33
euchlorum 3-25
eurybasis 5-121
exaltatum 5-49
falcatum 4-40
farinosum 5-89
fasciale 5-163
fendleri 5-132
fibrillosum 4-13
filicula 5-119
filix-femina 4-88
filix-mas 4-35
firmum 5-100
flabelliforme 5-102
flavopunctatum 4-42
fragile 4-92
fraseri 5-136
fraxinifolium 5-132
fulvescens 2-111
furfuraceum 5-136
fuscopunctatum 5-144
giganteum 5-133
gilliesii 5-130
glaucophyllum 5-134
glaucum 1-109
globuliferum 2-99
gracile 5-96
gracillimum 5-108
guianense 4-109
haynaldii 4-26
herzogii 5-100
heteromorphum 5-105
heterophlebium 4-45
hirsutulum 5-54
honestum 4-13
horridum 1-138
× huancayanum 5-139
hygrometricum 5-124
incanum 5-137
jamesonii 5-82
jamesonioides 5-93
karstenianum 4-17
kunthii 5-154
kunzeanum 5-131
lachniferum 5-123
laetum 5-130
laevigatum 5-134
lanceolatum 5-142
lanigerum 5-106
lapathifolium 5-162
lasiopus 5-130
latevagans 5-151
latipes 5-129
latum 5-170
laxum 5-107
leptophyllum 2-23
leucatomos 5-134
× leucosporum 5-139
leucosticton Fée 5-111
leucosticton Klotzsch 5-136
levigatum 5-134
limbatum 5-81
lomariiforme 5-125
lonchitis 4-49
longicaudatum 4-44
longifolium 5-132
longisetosum 5-114
longiusculum 5-111
longum 5-108
loretense 5-156
loriceum 5-129
lycopodioides 5-154
macrocarpum Presl 5-135
macrocarpum Willd. 5-143
macrophyllum 4-44
marginellum 5-72
mathewsii 5-91
medullare 1-112
megalodus 3-64
megalolepis 5-137
megalophyllum 5-157
melanostictum 5-97
meridense 5-85
microdontum 1-127
molle 3-41
mollendense 5-135
moniliforme 5-98
monosorum 5-138
montevidense 4-51
monticola 5-99
muricatum 4-55
murorum 5-139
mutabile 5-139
myosuroides 5-82
myriophyllum 5-114
nigrolimbatum 5-81
nitens 3-35
nitidissimum 5-172
nodosum 5-172
obliquatum 5-72
occultum 5-161
oligocarpum 3-15
oligophlebium 4-45
ophiocaulon 5-162
oppositum 3-32
parietinum 5-84
patens 3-44
pavonianum 3-23
pearcei 5-87
pectinatum 5-121
pedicellata 1-15
pendulum 5-95
penna-marina 5-62
pennatum 3-64
percussum 5-144
persicariifolium 5-157
peruvianum 5-102
phlegmaria 5-97

phyllitidis 5-169
pichinchae 5-110
pichinchense 5-110
pilipes 5-90
piloselloides 5-152
pilosissimum 5-100
plantagineum 4-27
platylobum 4-15
plumula 5-118
polypodioides 5-137
pozuzoense 5-90
prasinum 4-45
preslianum 5-132
procerum 1-123
pruinatum 1-109
pseudoaureum 5-134
pseudocapillare 5-94
pseudonutans 5-103
pteroideum 3-25
pteropis 5-95
ptilodon 5-124
pubescens Hooker & Grev. 5-130
pubescens L. 4-35
pulverulentum 4-17
punctatum 4-45
pungens 1-123
pyncocarpum 5-135
pyncnolepis 4-55
quadripinnatum 1-109
ratibori 5-135
remotum 5-136
repens 5-162
reticulatum 3-66
richardii 5-133
rigens 5-101
rigescens 5-102
rigidum 4-53
rivulare 5-52
rivulorum 3-32
rosmarinifolium 5-154
rostratum 1-111
rude 3-26
rufum 3-20
ruiz-lealii 5-135
ruizianum 3-35
rusbyi 5-135
salicifolium 3-74
saxatile 4-54
sectifrons 5-72
semicordatum 4-29
semihirsutum 5-111
semipinnatifidum 5-140
senile 5-107
sericeo-lanatum 5-106
serpentinum 5-163
serrulatum 5-83
sessilifolium 5-131
sloanei 4-10
solutum 5-172
sororium 5-129
speluncae 2-95
sphenodes 5-164
spixianum 5-86
sprucei 5-84
squamulosum 5-156
subandinum 5-130
subauriculatum 5-71
subflabelliforme 5-106
subincisum 4-16
submarginale 4-8
subscabrum 5-110
subsessile 5-95
subvestitum 5-135
surucuchense 5-131
taeniosum 5-168
tarapotense 4-15
taxifolium 5-113
tectum 5-154
tenuiculum 5-96
tetragonum 3-64
thomsonii 3-22
thurnii 5-156
thyssanolepis 5-137
totum 3-40
trichiatum 5-161
trichosorum 5-84
trifoliatum 4-21
trifurcatum 5-83
triseriale 5-132
triste 3-60
truncicola 5-109
tunguraguae 5-95
tweedianum 5-135
ulei 5-156
vacciniifolium 5-152
variabile 5-115
vastum 4-17
venturii 5-122
venulosum 5-72
villosum 4-11
vittaria 5-177
vulgare 5-125
vulpinum 5-167
xantholepis 5-135
xiphopteroides 5-101
yungense 5-113
Polystichopsis 4-35
ochropteroides 4-38
Polystichum 4-49
amplissimum 4-33
boboense 4-54
bonapartii 4-38
cochleatum 4-54
dubium 4-38
gelidum 4-54
haenkeanum 4-54
lehmannii 4-51
lonchitis 4-49
mexiae 4-51
montevidense 4-51
moritzianum 4-55
muricatum 4-55
nudicaule 4-52
orbiculare 4-53
orbiculatum 4-53
paleaceum 4-54
platyphyllum 4-52
polyphyllum 4-54
pyncnolepis 4-54
sodiroid 4-54
speciosissimum 4-49
torresianum 3-3
trapezoides 4-54
wolfii 4-52
yungense 4-52
Polytaenium 2-84
brasilianum 2-87
cajenense 2-87
guayanense 2-87
lanceolatum 2-86
Pronephrium 3-66
Pseudolycopodiella 6-58
contexta 6-62
meridionalis 6-62
Psilogramme 2-8
Psilotaceae 6-11
Psilotum 6-11
complanatum 6-12
nudum 6-12
Pteridanetium 2-92
citrifolium 2-92
Pteridium 2-105
aquilinum 2-105
arachnoideum 2-105
caudatum 2-105
Pteris 2-70
altissima 2-76
amazonica 2-106
ampla 2-78
angustifolia 2-90
aquilina 2-105
arachnoidea 2-105
atropurpurea 2-40
aurea 2-28
bakeri 2-80
biaurita 2-77
concolor 2-31
consanguinea 2-77
coriacea 2-74
cretica 2-81
decomposita 2-80
decurrens 2-77
deflexa 2-74
edentula 2-74
farinosa 2-30
fraseri 2-78
furcata 5-145
grandifolia 2-79
haenkeana 2-78
horizontalis 2-77
imbricata 2-13
incisa 2-115
interrupta 3-40
intramarginalis 2-23
killipii 2-78
kunzeana 2-76
lechleri 2-78
lineata 2-90
livida 2-80
lonchitoides 2-113
longifolia 2-70
lucida 2-69
muricata 2-74
nivea 2-38
notholaenoides 2-25
orbiculata 2-13
ovata 2-43
palmata 2-44

- pedata* 2-80
peruviana 2-41
petiolulata 2-79
podophylla 2-80
polita 2-74
propinqua 2-75
pungens 2-75
quadriaurita 2-75
reticulata 2-76
reticulatovenosa 2-76
rigida 2-34
ruffa 2-47
sagittata 2-41
speciosa 2-76
splendens 2-79
sulphurea 2-37
ternifolia 2-41
transparentis 2-76
trichomanoides 2-37
tripartita 2-81
vespertilionis 2-115
vestita 2-78
vittata 2-81
- Pteropsis*
vittarioides 2-91
- Pterozonium* 2-14
brevifrons 2-15
paraphysatum 6-96
reniforme 2-15
- Ptilophyllum*
bicorne 1-91
hostmannianum 1-93
lambertianum 1-95
martiusii 1-95
pellucens 1-96
- Ragatelus*
crinitus 1-94
- Regnellidium* 6-2
- Rhipidopteris* 4-167
flabellata 4-169
peltata 4-169
rusbyi 4-167
sphenophylla 4-169
- Rumohra* 4-31
adiantiformis 4-31
aspidioides 4-31
berteriana 4-31
- Saccoloma* 2-101
elegans 2-103
inaequale 2-103
wercklei 2-101
- Saffordia* 2-48
induta 2-50
- Salpichlaena* 5-68
hookeriana 5-70
lomarioidea 5-70
volubilis 5-70
- Salvinia* 6-6
auriculata 6-8
minima 6-6
natans 6-6
rotundifolia 6-8
- Salviniaceae* 6-5
- Schaffneria* 5-2
- Schizaea* 1-33
dichotoma 1-33
digitata 1-33
elegans 1-34
filistosa 1-34
flabellum 1-34
incurvata 1-36
pennula 1-36
poeppigiana 1-36
pusilla 1-34
- Selaginella* 6-66
acanthostachys 6-87
amazonica (Milde) Hieron. 6-71
amazonica Spring 6-71
anceps 6-79
applanata 6-73
arizonica 6-72
articulata 6-84
asperula 6-85
atirrensis 6-76
bombycina 6-78
brachylepis 6-84
brevifolia 6-72
calcarata 6-86
calosticha 6-74
chionoloma 6-77
chrysoleuca 6-78
conduplicata 6-86
convoluta 6-87
cordifolia 6-73
demissa 6-72
diffusa 6-76
dimorpha 6-82
eggersii 6-76
elongata 6-85
erythropus 6-80
exaltata 6-86
ferruminata 6-85
filicina 6-80
flagellata 6-77
fragilis 6-84
geniculata 6-85
gracilis Moore 6-80
gracilis (Poiret) Hieron. 6-80
haematodes 6-80
haenkeana 6-82
horizontalis 6-87
huberi 6-79
intacta 6-76
kunzeana 6-82
lechleri 6-79
lingulata 7-76
microphylla 6-75
mildei 6-71
nodosa 6-85
nova-hollandiae 6-77
parkeri 6-84
pearcei 6-77
pedata 6-84
peruviana 6-71
 var. *dombeyana* 6-71
poeppigiana 6-83
 var. *peruviana* 6-83
praestans 6-81
- producta* 6-74
quadrifaria 6-81
ramosissima 6-75
regularis 6-77
revoluta 6-72
rupestris 6-66
 f. *amazonica* 6-71
 f. *peruviana* 6-71
sartorii 6-71
seemannii 6-74
selaginoides 6-66
sellowii 6-71
sheldonii 6-71
silvestris 6-82
speciosa 6-79
spinosa 6-66
sprucei A. Br. 6-81
sprucei Hooker 6-78
stellata 6-86
strobilifera 6-86
sulcata
 ssp. *poeppigiana* 6-83
 ssp. *suavis* 6-87
tomentosa 6-85
trisulcata 6-83
truncata 6-73
wolfii 6-87
weberbaueri 6-73
xiphophylla 6-77
- Selaginellaceae* 6-66
Selaginelleae 6-66
Selodesmium
rigidum 1-85
Sitobolium 2-95
 punctilobulum 2-95
- Solanopteris* 5-179
bifrons 5-181
bismarckii 5-180
brunei 5-180
tuberosa 5-180
- Soromanes* 4-57
serratifolia 4-57
- Sphaerocionium* 1-50
adiantoides 1-66
ciliatum 1-67
crispum 1-67
elegans 1-66
elegantulum 1-70
fragile 1-69
hirsutum 1-67
interruptum 1-72
karstenianum 1-71
lindenii 1-71
lobatoalatum 1-74
microcarpum 1-68
molle 1-65
multialatum 1-73
nigricans 1-63
plumieri 1-72
plumosum 1-72
pyramidatum 1-74
ruizianum 1-69
simplex 1-69
spectabile 1-71
tenerrimum 1-66
tomentosum 1-73

- trichophyllum* 1-65
valvatum 1-68
 Sphaeropteris 1-112
 atahuallpa 1-115
 aterrima 1-114
 bradei 1-115
 elongata 1-115
 hirsuta 1-114
 horrida 1-112
 macrospora 1-114
 medullaris 1-112
 quindiensis 1-116
 rufescens 1-114
Steiropteris 3-46
 gardneriana 3-52
 incana 3-52
 valdepilosa 3-50
 Stenochlaena
 angusta 4-106
 fendleri 4-106
 japurensis 4-107
 vestita 4-106
Sticherus 1-37
 affinis 1-42
 bifidus 1-41
 buchtienii 1-42
 laevigatus 1-37
 lechleri 1-44
 longipinnatus 1-45
 mathewsii 1-41
 nitidulus 1-43
 penniger 1-39
 pruinosis 1-42
 revolutus 1-42
 rubiginosus 1-46
 simplex 1-39
 tuberculatus 1-43
 velatus 1-42
 yungensis 1-44
 Stigmatopteris 4-42
 alloeoptera 4-45
 ecuadorensis 4-45
 guianense 4-48
 heterophlebia 4-45
 ichtiosma 4-44
 lechleri 4-45
 longicaudata 4-44
 meniscioides 4-48
 opaca 4-45
 paludosa 4-48
 pellucidopunctata 4-44
 prasina 4-45
 rotundata 4-42
Struthiopteris
 maxonii 5-61
Stylites 6-89
 andicola 6-92
 gemmifera 6-92
Syngamma
 brevifrons 2-15
 paraphysata 6-97

 Taenitis
 desvauxii 5-147
 furcata 5-148

 Tectaria 4-21
 andina 4-25
 antioquiiana 4-26
 brauniana 4-24
 decurrans 4-29
 draconoptera 4-26
 fraxinea 5-51
 haynaldii 4-26
 heracleifolia 4-27
 incisa 4-24
 kunzei 4-29
 lizarzaburui 4-25
 martinicensis 4-24
 plantaginea 4-27
 poepigii 4-29
 sodiroi 4-26
 transiens 4-25
 trifoliata 4-27
 vivipara 4-25
 Thelypteris 3-5
 abrupta 3-58
 aequatorialis 3-45
 ancyrlothrix 3-63
 andicola 3-16
 andreaana 3-76
 angustifolia 3-74
 arborea 3-24
 arborescens 3-70
 arcana 3-76
 arenosa 3-33
 argentina 3-21
 arrecta 3-36
 aspidioides 3-13
 assurgens 3-30
 atrorubens 3-24
 balbisii 3-31
 biformata 3-60
 biolleyi 3-62
 brachyodous 3-50
 brachypus 3-18
 brausei 3-28
 canadasii 3-21
 caucaensis 3-28
 cheilanthoides 3-34
 chrysodioides 3-69
 clivalis 3-45
 clypeata 3-65
 coarctata 3-32
 comosa 3-49
 comptula 3-23
 concinna 3-29
 confluens 3-6
 consobrina 3-73
 conspersa 3-42
 contermina 3-32
 corazonensis 3-27
 ctenitoides 3-37
 curta 3-60
 decussata 3-48
 deflexa 3-30
 deltoidea 3-46
 demissa 3-21
 densa 3-34
 dentata 3-41
 depilata 3-45
 diplozioides 3-14
 dudleyi 3-33
 dumetorum 3-27
 eggersii 3-59
 enigmatica 3-16
 ensiformis 3-75
 erythrothrix 3-59
 euchlora 3-25
 extensa 3-43
 exuta 3-37
 falcata 3-75
 frigida 3-18
 funckii 3-18
 furfuracea 3-34
 furva 3-19
 gardneriana 3-52
 gigantea 3-68
 glandulosa 3-50
 glandulosolanosa 3-20
 gongyloides 3-40
 grandis 3-46
 guyanensis 3-68
 hispidula 3-41
 hutchisonii 3-29
 interrupta 3-40
 invisa 3-46
 jamesonii 3-56
 juruenensis 3-61
 killipii 3-60
 laevigata 3-24
 lancea 3-74
 leoniae 3-18
 leprieurii 3-51
 leucothrix 3-32
 limaensis 3-20
 limbata 3-9
 lindigii 3-30
 lingulata 3-75
 linkiana 3-14
 lomatosa 3-15
 longifolia 3-70
 loretensis 3-30
 lugubriformis 3-58
 macbridei 3-19
 macrophylla 3-68
 macrotrichis 3-57
 mapiriensis 3-49
 maxoniana 3-71
 megalodus 3-64
 membranacea 3-69
 mercurii 3-31
 micula 3-33
 millei 3-28
 multiformis 3-35
 navarrensis 3-15
 nemoralis 3-62
 nitens 3-35
 oligocarpa 3-15
 oligophlebia 3-3
 opposita 3-32
 opulenta 3-43
 pachyrhachis 3-31
 palustris 3-6
 parasitica 3-39
 patens 3-43
 pavoniana 3-23
 pennata 3-64

- pennellii 3-50
 peripae 3-60
 peruviana 3-23
 phacelothrix 3-22
 pilosohispida 3-27
 pilosula 3-19
 pinnatifida 3-56
 poiteana 3-65
proboscidea 3-36
 ptarmiciformis 3-17
 pteroidea 3-25
 pusilla 3-17
quadrangularis 3-41
resinosofoetida 3-34
 reticulata 3-66
retrorsa 3-27
 rudis 3-25
 rufa 3-20
ruiziana 3-35
salicifolia 3-74
 salzmännii 3-73
 scalaris 3-15
schunkei 3-63
 semihastata 3-17
 serrata 3-71
sodiroyi 3-62
sprengelii 3-31
subandina 3-20
 supina 3-26
 tetragona 3-64
 thomsonii 3-22
torresiana 3-3
totta 3-40
 tristis 3-60
tryonorum 3-62
 urbanii 3-64
 valdepilosa 3-50
 Tmesipteris 6-11
 Todea 1-20
 Trachypteris 2-48
aureonitens 2-48
 induta 2-50
 pinnata 2-48
 Trichipteris 1-120
 conjugata 1-128
 corcovadensis 1-120
dombeyi 1-123
excelsa 1-120
flava 1-125
 frigida 1-126
infesta 1-123
 kalbreyeri 1-124
lasiosora 1-125
 latevagans 1-124
 lechleri 1-127
 microdonta 1-127
 nigra 1-124
 nigripes 1-124
 phegopteroides 1-127
 pilosissima 1-125
 procera 1-123
 pubescens 1-126
serpens 1-126
 tryonorum 1-128
 Trichomanes 1-76
 accedens 1-98
 angustatum 1-83
 angustifrons 1-86
 ankersii 1-90
 applerianum 1-88
 arbuscula 6-97
bancroftii 6-97
 bicorne 1-91
 botryoides 1-92
brachyblastos 1-81
 capillaceum 1-84
 celluloseum 1-85
ciliatum 1-67
 collariatum 1-81
coriaceum 6-97
 crinitum 1-94
 crispum 6-97
 cristatum 1-97
 delicatum 1-98
 diaphanum 1-83
 diversifrons 1-91
ekmanii 1-88
elatum 1-96
 elegans Rich. 1-84
elegans Rudge 1-91
flaccida 2-95
 fragile 1-69
fucoides 1-56
 haenkeanum 1-98
heterophyllum 1-94
hirsutum 1-67
 hookeri 1-88
 hostmannianum 1-93
 humboldtii 1-94
 hymenoides 1-86
hymenophylloides 1-83
 krausii 1-87
kunzeanum 1-81
lambertianum 1-95
leptophyllum 1-83
 lucens 1-95
 martiusii 1-94
 membranaceum 1-88
muscoides 1-86
 opacum 1-84
 pedicellatum 1-90
 pellucens 1-96
pellucidum 1-96
peltatum 1-57
pennatum 1-92
 pilosum 1-95
 pinnatum 1-92
 plumosum 1-96
plumula 1-95
poepigii 1-89
polyanthos 1-59
 polypodioides 1-89
prieurii 1-84
 punctatum 1-86
 pyxidiferum 1-82
 radicans 1-81
 reptans 1-87
 rigidum 1-85
 rupestre 1-82
 scandens 1-76
sellowianum 1-97
sphenoides 1-86
 spruceanum 1-91
 sprucei 1-86
 subsessile 1-90
 tanaicum 1-89
tenerum 1-83
 trollii 1-91
 tuerckheimii 1-90
undulatum 1-97
vandenboschii 1-97
Trichopteris 1-122
 Triplophyllum 4-19
 acutilobum 4-21
 dicksonioides 4-21
 funestum 4-21
 protensum 4-19
Trismeria 2-16
aurea 2-16
microphylla 2-21
trifoliata 2-21
 Trogonospora 3-2

Urostachys 6-19
 andinus 6-35
 attenuatus 6-37
 bifida 6-28
 brevifolius 6-39
 capellae 6-32
 caracasicus 6-40
 catharticus 6-38
 cuatrecasasii 6-45
 binervius 6-26
 brogniarti 6-27
 buesii 6-42
 crassus 6-34
 cuneifolius 6-50
 curvifolius 6-46
 darwinianus 6-33
 durissimus 6-51
 elongatus 6-35
 engleri 6-39
 ewanii 6-50
 funiformis 6-42
 hartwegianus 6-40
 hippurideus 6-24
 hohenackeri 6-40
 jenmannii 6-44
 kuesteri 6-30
 lechleri 6-25
 var. *lehmannii* 6-25
lehmannii 6-25
 linifolius 6-43
 var. *tenuifolius* 6-44
 macbridei 6-32
 mexiae 6-28
 molongensis 6-47
 myrsinites 6-49
 nesselii 6-34
 nubigenus 6-49
 phlegmaria
 var. *ericaefolius* 6-48
 phylicifolius 6-49
 pilgerianus 6-34
 polycarpus 6-45
 poseidonis 6-24
 pruinosis 6-51

- reflexus* 6-27
rosenstockianus 6-42
rufescens 6-39
sarmentosus 6-45
saururus 6-35
selago 6-19
stellae-polaris 6-28
subulatus 6-50
taxifolius 6-41
tenuis 6-46
tetragonus 6-38
weberbaueri 6-30
weddellii 6-26
wilsonii 6-44
- Vandenboschia*
angustata 1-83
capillacea 1-84
diaphana 1-83
hymenophylloides 1-83
- pyxidifera* 1-82
radicans 1-81
tenera 1-83
- Vittaria* 2-89
angustifolia 2-90
costata 2-90
filifolia 2-90
filiformis 2-90
gardneriana 2-91
graminifolia 2-90
lanceolata 2-86
latifolia 2-91
moritziana 2-91
remota 2-91
ruiziana 2-91
stipitata 2-91
vittarioides 2-91
- Woodia* 4-94
Woodsia 4-94
- crenata* 4-94
ilvensis 4-94
montevidensis 4-94
peruviana 4-94
- Xiphopteris* 5-72
blepharidea 5-112
blepharolepis 5-108
buesii 5-112
jamesonii 5-82
myosuroides 5-82
serrulata 5-83
truncicola 5-109
- Zygophlebia* 5-72
dudleyi 5-92
mathewsii 5-91
sectifrons 5-72
werfii 5-92

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