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Botany
NEW SERIES, NO. 20

PTERIDOPHYTA OF PERU
Part I
1. Ophioglossaceae-12. Cyatheaceae

Rolla M. Tryon
Robert G. Stolze

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References should be typed in the following form:

- CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif. 943 pp.
- GRUBB, P. J., J. R. LLOYD, AND T. D. PENNINGTON. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. *Journal of Ecology*, 51: 567-601.
- LANGDON, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63-80. In Browman, D. L., and R. A. Schwarz, eds., *Spirits, Shamans, and Stars*. Mouton Publishers, The Hague, Netherlands.
- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2. The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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PTERIDOPHYTA OF PERU

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1. Ophioglossaceae-12. Cyatheaceae

Rolla M. Tryon

*Gray Herbarium
Harvard University
22 Divinity Avenue
Cambridge, Massachusetts 02138*

Robert G. Stolze

*Collection Manager, Fern Herbarium
Department of Botany
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496*

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PTERIDOPHYTA OF PERU

Part I

1. Ophioglossaceae–12. Cyatheaceae

Introduction

The pteridophytes form a large and conspicuous element of the Peruvian flora, including 96 genera and about 1,000 species. Peru, which encompasses one of the world's richest biotas, occupies a central position in the Andes, and accordingly a knowledge of its flora is basic to understanding the plant life of the Andes as a whole. The Andes form a largely tropical mountain chain with an essentially north and south orientation, which is of special significance to its biogeography and the underlying processes of speciation.

A portion of the Ferns of Peru was published by Rolla M. Tryon in 1964 (Contr. Gray Herb., vol. 194), with the encouragement and active support of Theodore K. Just of Field Museum of Natural History. A commitment was made at that time to complete the project after undertaking a major work on the genera of pteridophytes in America. The present work is a cooperative project of Harvard University Herbaria and Field Museum of Natural History to present an account of all of the Pteridophyta of Peru. This is particularly important in relation to the Flora of Peru, initiated at Field Museum over 50 years ago, and thus far encompassing some 8,500 published pages. It is the only comprehensive treatment of Pacific coastal, Andean, and Amazonian plants, and is closer to completion than any flora of the larger South American countries.

The taxonomy is based not only on Peruvian materials, but includes an assessment of the Andean species of a genus and, where appropriate, of all tropical American species. Most of the work will be accomplished by the authors, according to

their knowledge of particular genera, but several treatments will be contributed by specialists currently involved in monographic studies. The results will be published in five parts, divided as equally as practicable, beginning with the present volume on the Ophioglossaceae through Cyatheaceae.

Studies are based primarily on the collections at Field Museum, Harvard University Herbaria, and United States National Herbarium (Smithsonian Institution), but specimens at many other United States and European institutions have been examined. The extensive collections made under the current Flora of Peru project, a joint undertaking of Field Museum and Missouri Botanical Garden, are fully utilized. A close collaboration has also been established with Universidad Nacional de Trujillo, Trujillo, Peru, and Museo de Historia Natural "Javier Prado" de Universidad Nacional Mayor de San Marcos, Lima, Peru, including loans of their specimens. The type of each name has been determined when possible, and an effort has been made to see the holotype, or at least type photographs, or authentic material. Original drawings illustrate the diagnostic features of each genus and, where possible, some of the species. In addition, a number of plates published in *Fieldiana: Botany*, Ferns and fern allies of Guatemala, have been used for species occurring in Peru. Voucher specimens cited in the legends are from Peru unless otherwise indicated.

Prior to 1944 the Department of Pasco was a part of Junín, and until recently Ucayali was a part of Loreto. An attempt has been made to ac-

count for these changes. This is not difficult when labels cite towns and provinces; however, on older specimens the labels often contain only sketchy data, making it impossible to determine in which part of Loreto or Junín a plant was collected. The map of Peru at the end of the text shows the departments and indicates the sequence of the collection citations.

In the present work, Part I, the treatments of the Ophioglossaceae through the Plagiogyriaceae have been prepared by Robert G. Stolze, and those of the Dicksoniaceae through the Cyatheaceae, by Rolla M. Tryon. However, each author has reviewed and edited the manuscript of the other, to the extent that the treatments are a joint effort.

New names published here are indicated by boldface in the Index to Names. Collections have been cited from each department of Peru from which material has been seen, and further collections are sometimes cited to include other herbaria. In general, all collections seen are cited for rare species, and a selection is cited for common species. Type collections, mentioned in the synonymy, are not repeated in the specimen citations, although they are included in the Peruvian range and ecology.

The nomenclature of the genera and species is not intended to be complete. Synonyms are listed when they are considered useful and when the type of the name of a species or infraspecific taxon is from Peru.

Appended to some of the generic treatments are portions of text labeled **Comments**. Herein are included species to be expected in Peru, names based on Peruvian material but of uncertain application, excluded species (erroneous reports that may have special significance), and cultivated species that are possibly adventive.

Abbreviations of periodical publications generally follow the system of *Botanico-Periodicum-Huntianum* (1968), and abbreviations of authors' names and of books generally follow TL-2 *Taxonomic Literature* by Stafleu and Cowan (1976 et seq.).

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This project has been supported in part by grant #BSR-8516358 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.

Key to Families of PTERIDOPHYTA in Peru

The following key is restricted to the families that occur in South America and to the genera that are known from Peru or are likely to occur there. Several families are keyed out more than once in order to simplify the headings and to provide for more accurate identification.

- a. Two or more sporangia joined in a synangium b
- b. Synangium single in the axil of a bifid, bractlike leaf; aerial stem slender, green, dichotomously forked 24. **Psilotaceae**
- b. Two elongate synangia at the apex of a spike, or many synangia on the abaxial surface of a leaf; stem subterranean c
- c. Two elongate synangia at the apex of a spike; stem small 1. **Ophioglossaceae**
- c. Many synangia on the abaxial surface of a leaf; stem stout to massive 2. **Marattiaceae**
- a. Sporangia separate d
- d. Sporangia borne on the inner side of a peltate sporangiophore in an apical strobilus; leaves much reduced, forming a sheath at the apex of each elongate, ridged interode (joint) of the stem 25. **Equisetaceae**
- d. Sporangia single in or near the axil of a leaf, or on 1 lobe of a 2-lobed leaf, or several to many sporangia borne on a leaf: at the margin, on the abaxial surface, on a specialized portion, or on a specialized leaf e
- e. A single sporangium borne in or near the axil of a leaf f
- f. Plants homosporous; leaves lacking a ligule 26. **Lycopodiaceae**
- f. Plants heterosporous, with megasporangia and microsporangia; leaves with a ligule g
- g. Leaves less than 1 cm long, borne along an elongate stem, fertile leaves in an apical strobilus 27. **Selaginellaceae**
- g. Leaves 2 cm long or usually longer, clustered at the apex of a compact to slightly elongate stem; all leaves usually fertile 28. **Isoetaceae**
- e. Several to many sporangia borne on a leaf, or a single sporangium borne on 1 lobe of a 2-lobed leaf h
- h. Plants heterosporous; the leaf bearing megasporangia and/or microsporangia, these enclosed in small, specialized structures i
- i. Plant with stem rooted in wet soil or underwater; leaves filiform, or with 4 leaflets at the apex of the petiole 22. **Marsileaceae**
- i. Plant floating on water; the floating leaves entire, oblong to suborbicular, or unequally 2-lobed with 1 lobe submerged 23. **Salvinaceae**
- h. Plants homosporous, the isomorphic sporangia exposed at the margin or on the abaxial surface of a leaf, or on a specialized portion of a leaf, or on a specialized leaf, sometimes enclosed prior to maturity within an indusium j
- j. Sporangia sessile or subsessile, or with a stalk of 4 or more rows of cells, annulus absent, or if present then apical, lateral, or oblique, not interrupted by the stalk k
- k. Annulus lacking, or sporangia with a poorly differentiated annulus l
- l. Sporangia lacking an annulus, borne on a specialized fertile branch of a leaf; spores lacking chlorophyll 1. **Ophioglossaceae**
- l. Sporangia with a poorly differentiated lateral annulus, borne on fertile pinnae; spores with chlorophyll (green) 3. **Osmundaceae**
- k. Sporangia with a well-differentiated apical to oblique annulus m
- m. Sporangia on the abaxial surface of a fertile portion of a leaf, distantly attached in a cluster or single on a vein, or in wholly fertile panicles 4. **Schizaeaceae**
- m. Sporangia contiguous on the receptacle of marginal or abaxial sori n
- n. Sporangia in marginal sori o
- o. Leaf very thin, 1-few cells thick, translucent, lacking stomata; stem protostelic 6. **Hymenophyllaceae**
- o. Leaf thickened, with stomata; stem siphonostelic or dictyostelic p

- p. Stem long-creeping, with scattered, short, stiff trichomes; receptacle elongate 7. **Loxomataceae**
- p. Stem massive, short-creeping to arborescent, with a dense mass of very long, soft trichomes; receptacle short or globose ... 9. **Dicksoniaceae**
- n. Sporangia in abaxial sori q
- q. Stem and leaves lacking evident indument, a mucilaginous secretion (flaky when dry) sometimes present; leaves strongly dimorphic 8. **Plagiogyriaceae**
- q. Stem and usually the leaves with evident trichomes and/or scales; leaves monomorphic to somewhat dimorphic r
- r. Stem slender, long-creeping, subterranean, freely branched; leaf usually partly pseudodichotomously branched with axillary arrested or dormant buds 5. **Gleicheniaceae**
- r. Stem stout to massive, more or less epigeous or arborescent, sparingly if at all branched; leaves wholly pinnately branched s
- s. Stem and petiole bearing scales, trichomes may be present or absent 12. **Cyatheaceae**
- s. Stem and petiole bearing only trichomes t
- t. Lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatisect 10. **Lophosoriaceae**
- t. Lamina 1-pinnate 11. **Metaxyaceae**
- j. Sporangia with a 1- to 3-rowed stalk; the annulus vertical or nearly so, interrupted by the stalk u
- u. Petiole articulate at or very near the stem 21. **Polypodiaceae**
- u. Petiole continuous with the stem, or articulate well above the base of the petiole ... v
- v. Stem scales clathrate w
- w. Spores monolete x
- x. Lamina entire; indusium lacking 14. **Vittariaceae**
- x. Lamina pinnatifid or more complex, or entire and the sori indusiate .. y
- y. Spores with chlorophyll (green), or lamina more or less dichotomous (furcate) 21. **Polypodiaceae**
- y. Spores lacking chlorophyll (not green) and lamina entire or pinnately branched z
- z. Sori abaxial; indusia, when present, circular to reniform, with a sometimes narrow sinus 17. **Dryopteridaceae**
- z. Sori abaxial, indusiate, the indusia elongate, or sori nearly marginal 18. **Aspleniaceae**
- w. Spores trilete aa
- aa. Sori very long, near and parallel to the margin, or following the anastomosing veins, or in scattered groups 14. **Vittariaceae**
- aa. Sori roundish or united in a short line close to the costa 21. **Polypodiaceae**
- v. Stem scales not clathrate, or stem with trichomes bb
- bb. Spores trilete, or monolete and the sori marginal cc
- cc. Indusia absent dd
- dd. Stem with trichomes only 13. **Pteridaceae**
- dd. Stem with scales ee
- ee. Sori elongate along the veins, or sporangia acrostichoid 13. **Pteridaceae**
- ee. Sori roundish or united in a short line close to the costa 21. **Polypodiaceae**
- cc. Indusia present ff
- ff. Stem with trichomes, or with scales and an abaxial indusium present 15. **Denstaedtiaceae**

- ff. Stem with scales and an abaxial indusium absent gg
- gg. Spores trilete 13. **Pteridaceae**
- gg. Spores monolete 15. **Dennstaedtiaceae**
- bb. Spores monolete and the sori or sporangia abaxial hh
- hh. Sori elongate, adjacent to and parallel to the segment axis 20. **Blechnaceae**
- hh. Sori roundish, or elongate, and most or all of them neither adjacent to nor parallel to the segment axis, or sporangia acrostichoid ii
- ii. Pinna stalks, if present, continuous with the rachis jj
- jj. Spores with chlorophyll (green); lamina or main veins more or less dichotomous (furcate) 21. **Polypodiaceae**
- jj. Spores lacking chlorophyll (not green) and lamina pinnately veined or branched kk
- kk. Petiole, at least basally, with 2 vascular bundles ll
- ll. Lamina with unicellular, acicular, or variously branched trichomes, or if glabrate then indusia absent 16. **Thelypteridaceae**
- ll. Lamina lacking trichomes, or with multicellular ones, or with minute, unicellular, blunt trichomes; indusia present 17. **Dryopteridaceae**
- kk. Petiole, at least basally, with 3 or more vascular bundles 17. **Dryopteridaceae**
- ii. Pinnae articulate to the rachis mm
- mm. Sporangia acrostichoid, or in indusiate sori and the lamina 2-pinnate, or 1-pinnate and the pinnae with a large, basal, basiscopic auricle 17. **Dryopteridaceae**
- mm. Sporangia in indusiate sori, lamina 1-pinnate, the pinnae cordate, or the basal, basiscopic side less developed 19. **Davalliaceae**

Family 1: OPHIOGLOSSACEAE

Ophioglossaceae C. Agardh, Aphor. bot. 113. 1822.
TYPE: *Ophioglossum* L.

Stem erect or prostrate, fleshy, lacking indument, or pubescent-scaly at apex. **Leaves** erect or folded, not or scarcely circinate in vernation, entire to pinnate or subpalmate or dichotomous, commonly partially dimorphic, the sterile leaf with an expanded lamina, the fertile one with sporangia borne on a special branch (or branches) arising from the base of or below the sterile lamina. **Veins** free or anastomosing. **Sporangia** sessile or subsessile, separate or laterally joined in a synangium, lacking an annulus. **Spores** trilete, lacking chlorophyll, from 1,500–15,000 in each sporangium.

This is the most primitive of all living fern fam-

ilies and contains three genera and 50 to 60 species. *Botrychium* and *Ophioglossum* occur in Peru and are virtually cosmopolitan, with representatives in subarctic as well as tropical regions. The Ophioglossaceae are distinctive in the fleshy, mycorrhizal roots lacking root hairs, the erect or folded (rather than circinate) vernation, and the massive sporangia with an extremely high spore capacity. Some of the species tend to have very wide, and often disjunct, distributions.

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- CLAUSEN, R. T. 1938. A monograph of the Ophioglossaceae. Mem. Torrey Bot. Club, **19**(2): 1–177.
- UNDERWOOD, L. M., AND R. C. BENEDICT. 1909. Ophioglossaceae, in N. Amer. fl., **16**: 3–13.

Key to Genera of Ophioglossaceae

- a. Sterile lamina ternately decomposed; veins free; sporangia borne in a panicle, separate from each other and not immersed in the fertile segment I. **Botrychium**
- a. Sterile lamina entire or palmately or digitately lobed; veins anastomosing; sporangia joined laterally in a synangial spike II. **Ophioglossum**

I. Botrychium

Botrychium Sw., J. Bot. (Schrader) 1800(2): 8, 110. 1802. TYPE: *Botrychium lunaria* (L.) Sw. (*Osmunda lunaria* L.). **Figure 1.**

Plants terrestrial, very rarely epiphytic. **Stem** erect, short, lacking indument. **Leaves** solitary or few, 2–70 cm long, glabrous to pubescent, bud of the next leaf wholly or partly enclosed by the expanded stipular base of the current leaf. **Sterile lamina** sessile to long-stalked, pinnatifid to decomposed. **Veins** free. **Fertile branch** paniculate, racemose or spicate, arising at or below the base of the lamina. **Sporangia** protruding from the surface of the fertile branch, not immersed in the tissue.

The genus contains about 25 species, with distribution in temperate to tropical regions in both hemispheres, but is poorly represented in tropical

America. Within the four subgenera of *Botrychium* only four species of *Sceptridium* have been found in the Neotropics, and but a single species of subgenus *Osmundopteris* (*B. virginianum*). The paucity of species in the Neotropics may be partly a natural phenomenon, but the problem may be also attributed to poor and sparse collections, as ferns of this genus often go undetected. Increased collecting efforts in North America have produced more species, and similar results may be attained through greater efforts in the tropics. Collectors should be aware that when a single plant is found in the field there are likely to be many more of that and other species nearby.

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BUTTERS, F. K. 1917. *Botrychium virginianum* and its American varieties. *Rhodora*, **19**: 207.
 MILDE, J. 1869. *Botrychiorum monographia*. Verh. Zool. Bot. Ges. Wien, **19**: 55–190.

Key to Species of Botrychium

- a. Fertile leaf with the sterile lamina long-stalked; leaf bud completely enclosed by the sheath of the current leaf 1. **B. schaffneri**
- a. Fertile leaf with the sterile lamina sessile or nearly so; leaf bud partly exposed within the sheath of the current leaf 2. **B. virginianum**

1. **Botrychium schaffneri** Underw., Bull. Torrey Bot. Club 30: 51. 1903. TYPE: Mexico, San Luis Potosí, *Schaffner 9* (holotype, NY; isotype, K).

Fertile plants 12–30 cm tall (sometimes to 50 cm outside Peru), the common stalk to 4 cm long, the leaf bud completely enclosed by the sheath of the current leaf. **Sterile lamina** of fertile leaf long-stalked (3–8 cm), fleshy, ternate, to 3-pinnate-pinnatifid, 3–10 cm long, 6–10 cm broad. **Ultimate segments** 0.3–0.7 cm long, mostly obtuse to subacute, separated by usually narrow to broadly U-

shaped sinuses, the margins entire to crenate, very rarely serrate.

Terrestrial, in high scrub forests and open meadows, 2350–3600 m, Amazonas, Cuzco, Madre de Dios(?).

Mexico; Honduras south to Argentina.

This is often difficult to distinguish from *B. underwoodianum* (Guatemala to Venezuela), which is usually a much larger fern with stalks of sterile laminae up to 28 cm long. However, Mexican plants of *B. schaffneri* seem to rival the latter in size, and the more reliable diagnostic features appear to occur in the ultimate segments. Those of *B. underwoodianum* are 0.7–1.4 cm long with mar-

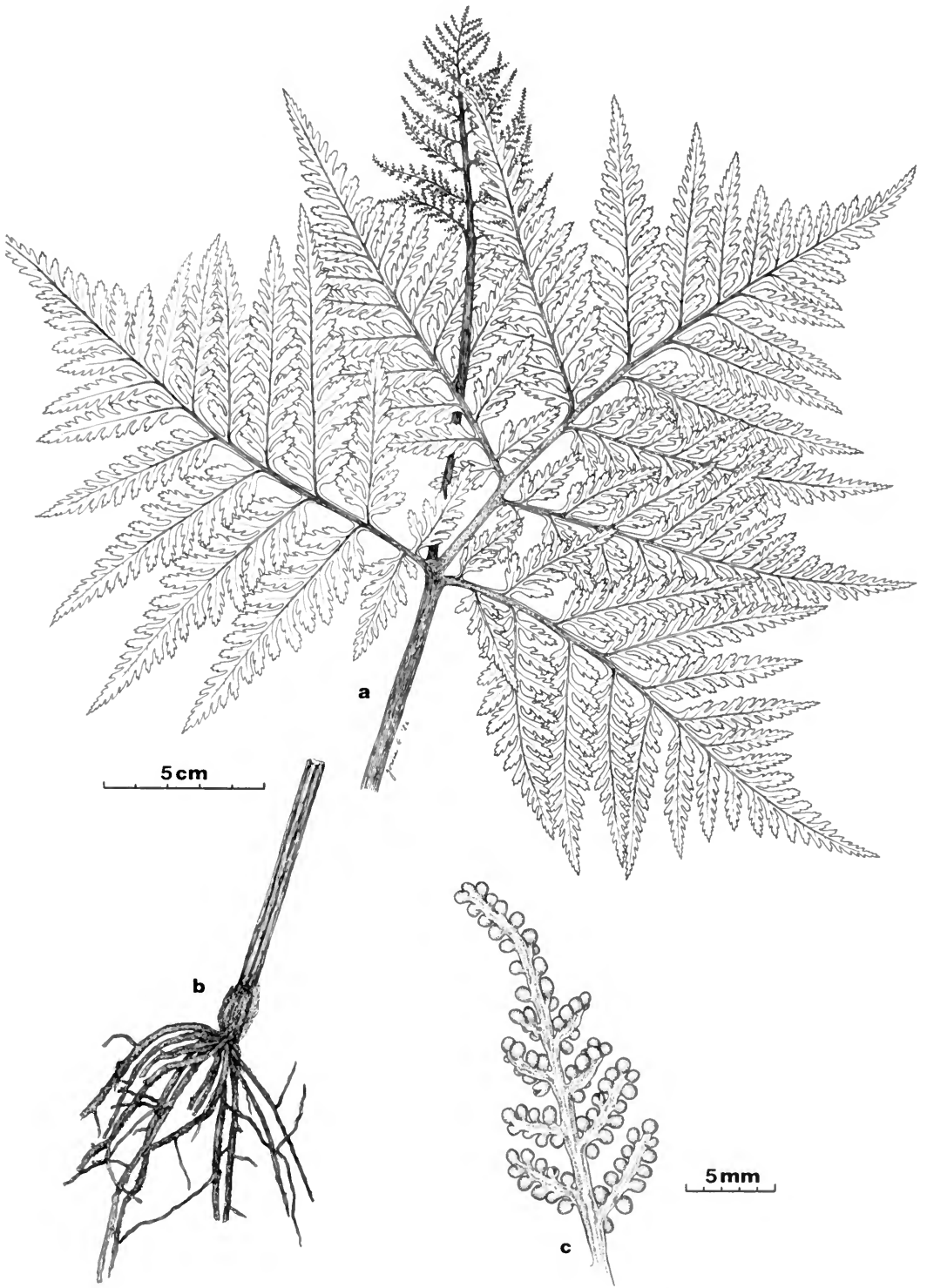


FIG. 1. *Botrychium virginianum*: a, lamina with fertile branch; b, stem and part of petiole; c, part of fertile pinna. (a from Seiler 865, El Salvador, GH; b-c from Lyonnet 896, Mexico, GH.)

gins typically serrate, whereas in *B. schaffneri* they are usually less than 0.7 cm long and entire to crenate (only rarely serrate). The taxonomy of the species complex requires detailed analysis.

Amazonas: Chachapoyas, along Río Ventilla, 1–2 km W of Molinopampa, *Wurdack 1528* (us). Middle eastern Calla Calla slopes, km 411–416 of Leimebamba-Balsas road, *Wurdack 1319* (us). **Cuzco:** Urubamba, Machu Picchu, slopes of Altillero, *Peyton & Peyton 504* (MO). **Dept. Unknown:** “Piñasniocj, Panticalla Pass,” *Cook & Gilbert 1845* (us) (this may be on Cerro de Pantiacolla, Dept. Madre de Dios, near the Cuzco border).

2. *Botrychium virginianum* (L.) Sw., J. Bot. (Schrader) 1800(2): 111. 1802. **Figure 1.**

Osmunda virginiana L., Sp. pl. 1064. 1753. TYPE: “America,” *Kalm* (LINN 1244.3).

Osmunda cicutaria Savigny in Lam., Encycl. 4: 650. 1797. TYPE: based on plants collected by Plumier in Hispaniola, *Traité foug. Amér.* 136, t. 159. 1705.

Botrychium cicutarium (Savigny) Sw., Syn. fil. 171. 1806.

Botrychium virginianum var. *mexicanum* Grev. & Hooker, Bot. Misc. 3: 223. 1833 (as *B. virginicum beta mexicanum*). SYNTYPES: Mexico, Veracruz, *Chamisso s.n.*; “Rigla,” *Veitch* (both $\epsilon?$ or $\kappa?$).

Fertile plants ca. 25–70 cm tall, the common stalk 19–40 cm long, the leaf bud partly exposed within the sheath of the current leaf. **Sterile lamina** of fertile leaf sessile or short-stalked (to 5 mm), membranous, subternate, to 3-pinnate-pinnatifid, to 20 cm long and 25 cm broad. **Ultimate segments** 0.5–0.9 cm long, joined by narrow, acute sinuses, elliptic to obovate, truncate, rounded or subacute, their apices variously dentate or lacerate.

Forests and wooded canyons, 1800–2930 m, Cajamarca, Amazonas, Huánuco, Pasco, Junín, Cuzco.

Essentially cosmopolitan. In the Neotropics from Mexico south to Bolivia and Brazil, and in the Greater Antilles.

Botrychium virginianum has been treated by earlier authors as several species or as one species with several varieties or subspecies. Variants have been distinguished primarily by relative length of the fertile branch or degree of dissection of the sterile lamina. However, closer examination of more recent and numerous collections throughout the range of the species indicates that these are variable characters and not wholly correlated with

geography. Proctor (*Ferns of Jamaica*, 1985) has observed that “... the almost complete intergradation of the alleged distinguishing characters renders even varietal recognition difficult to uphold.” We concur with this judgment.

Cajamarca: Prov. Celendín, canyon of Río Marañón above Balsas, *Hutchison & Wright 5358* (UC). **Amazonas:** Prov. Chachapoyas, Cerros Calla Calla, 5 km above Leimebamba, *Hutchison & Wright 4885* (UC). **Huánuco:** Mito, in canyon, *Bryan 387* (F). Muña, in dry woods, *Bryan 537* (F). **Pasco:** Prov. Oxapampa, 5 km SE of Oxapampa, *D. Smith 2897* (MO). **Junín:** Huacapistana, dense forest, *Killip & Smith 24308* (us). **Cuzco:** Prov. Calca, Vilcabamba, *Vargas 3907* (us).

II. *Ophioglossum*

Ophioglossum L., Sp. pl. 1062. 1753. TYPE: *Ophioglossum vulgatum* L. **Figure 2.**

Cheiroglossa Presl, Suppl. tent. pterid. 56. 1846. TYPE: *Cheiroglossa palmata* (L.) Presl = *Ophioglossum palmatum* L.

Plants terrestrial or epiphytic. **Stem** erect, globose or short-prostrate, small, lacking indument, or filiform-scaly at apex. **Leaves** solitary or several, 1–75 cm long (or to more than 1.5 m in the Old World *O. pendulum*), glabrous, the eroded stipular base of the expanded leaf not enclosing the bud of the next leaf. **Sterile lamina** sessile or short-stalked, entire, or palmately or digitately lobed. **Veins** anastomosing, often with free, included veinlets. **Fertile branch** or branches borne on or below the base of the sterile lamina. **Sporangia** joined laterally in a synangial spike.

Ophioglossum is a genus of 25–30 species scattered in temperate to tropic regions around the world. Plants are often small and inconspicuous and are commonly concealed in grassy turf or herbaceous growth; consequently, current collection records probably do not represent true distribution patterns. Although six species are recognized here from Peru, several others might be expected in the future.

Reference

WAGNER, W. H., ET AL. 1984. *Ophioglossum ellipticum* in Louisiana and the taxonomy of *O. nudicaule*. *Castanea*, 49: 99–110.

Key to Species of *Ophioglossum*

- a. Sterile lamina deeply and irregularly palmately lobed; fertile spikes several; plants epiphytic 1. ***O. palmatum***
- a. Sterile lamina entire; fertile spike solitary; plants terrestrial b
 - b. Stem globose 5. ***O. crotalophoroides***
 - b. Stem cylindrical, sometimes swollen, but never globose c
 - c. Sterile lamina stalked, the common stalk and stalks of fertile and sterile segments hypogeous and scarious 4. ***O. scariosum***
 - c. Sterile lamina sessile or nearly so, the common stalk and stalks of sterile and fertile segments mostly epigeous, not or scarcely scarious d
 - d. Primary areoles each enclosing several smaller secondary areoles and/or some free veinlets; base of sterile lamina cordate, truncate or abruptly cuneate 2. ***O. reticulatum***
 - d. Primary areoles not enclosing secondary ones or free veinlets; base of sterile lamina narrowly cuneate to attenuate e
 - e. Sterile lamina elliptic or oblong, 1.5–3 times as long as broad, cuneate at base; plants of higher elevations (over 2500 m) 3. ***O. nudicaule* var. *tenerum***
 - e. Sterile lamina linear-lanceolate to narrow-oblong, (4–)4.5–8 times as long as broad, long-attenuate at base; plants of lower elevations (under 700 m) 6. ***O. lusitanicum* ssp. *coriaceum***

1. ***Ophioglossum palmatum*** L., Sp. pl. 1063. 1753.
 TYPE: based on illustration of plant from Haiti, Plumier, *Traité foug. Amér., t. 163*, 1705. **Figure 2a.**

Cheiroglossa palmata (L.) Presl, *Suppl. tent. pterid.* 57. 1846.

Plants epiphytic. **Stem** stout, elongate, abundantly provided at apex with tawny to orange scales which are hairlike for most of their length. **Leaf** (15–)20–75 cm long, with common stalk (5–)10–40 cm long. **Sterile lamina** deeply and irregularly palmately lobed, obdeltoid, narrowly cuneate at base, lacking a distinct midvein or pale median band of tissue. **Veins** distinct, the primary areoles large, often enclosing smaller secondary areoles and occasionally a few free veinlets. **Fertile segments** (1–)3–12, borne on or below the base of the lamina, the fertile spikes 0.5–6 cm long, on stalks 0.2–2 cm long.

Suberect or pendent from trunks or branches of trees, in cloud forests, elfin forests, and shaded ravines, 1000–2450 m, Amazonas, Huánuco, Pasco, Cuzco.

Southern Florida; West Indies; southern Mexico to Peru and Brazil; scattered in Old World tropics.

Amazonas: Prov. Bagua, E of La Peca, *Barbour 2512*, 2860, 2940 (MO). Prov. Chachapoyas, along Río Ventilla 1–2 km W of Molinopampa, *Wurdack 1478* (F, GH, NY, UC, US). **Huánuco:** East of Tingo María (as San Martín)

in deep ravine, *Allard 21580* (US). **Pasco:** Prov. Oxapampa, 1800 m, *van der Werff 8352* (MO). **Cuzco:** Prov. La Convención, Tunquimayo, Idma, *Vargas 10681* (MICH, MO).

2. ***Ophioglossum reticulatum*** L., Sp. pl. 1063. 1753. LECTOTYPE (designated by Proctor, *Flora Lesser Antilles* 2: 43. 1977): Plumier, *Traité foug. Amér., t. 164*, based on specimen from Haiti. **Figure 2c-d.**

Ophioglossum petiolatum Hooker, *Exot. fl.* 1: 56. 1823.
 TYPE: based on plants from West Indies sent to Liverpool Botanic Garden and cultivated there (not located).

Ophioglossum peruvianum Presl, *Suppl. tent. pterid.* 52. 1845. TYPE: Peru, *Poeppig* (not located).

Plants terrestrial. **Stem** cylindrical, lacking indument. **Leaf** (5–)10–40 cm long, common stalk mostly epigeous, 3–20 cm long. **Sterile lamina** membranaceous, 2–12 cm long, 1.5–5 cm broad, sessile or subsessile, ovate to nearly circular, apex obtuse to acute, base cordate to truncate or (occasionally) abruptly cuneate. **Veins** distinct to indistinct, primary areoles enclosing a few smaller secondary areoles which are scarcely differentiated from the primary ones, free included veinlets several to numerous. **Fertile segment** solitary, borne at base of sterile lamina, on mature leaves somewhat to greatly exceeding the lamina, fertile spike 1.4–4 cm long, on a stalk 3.5–14.5 cm long.

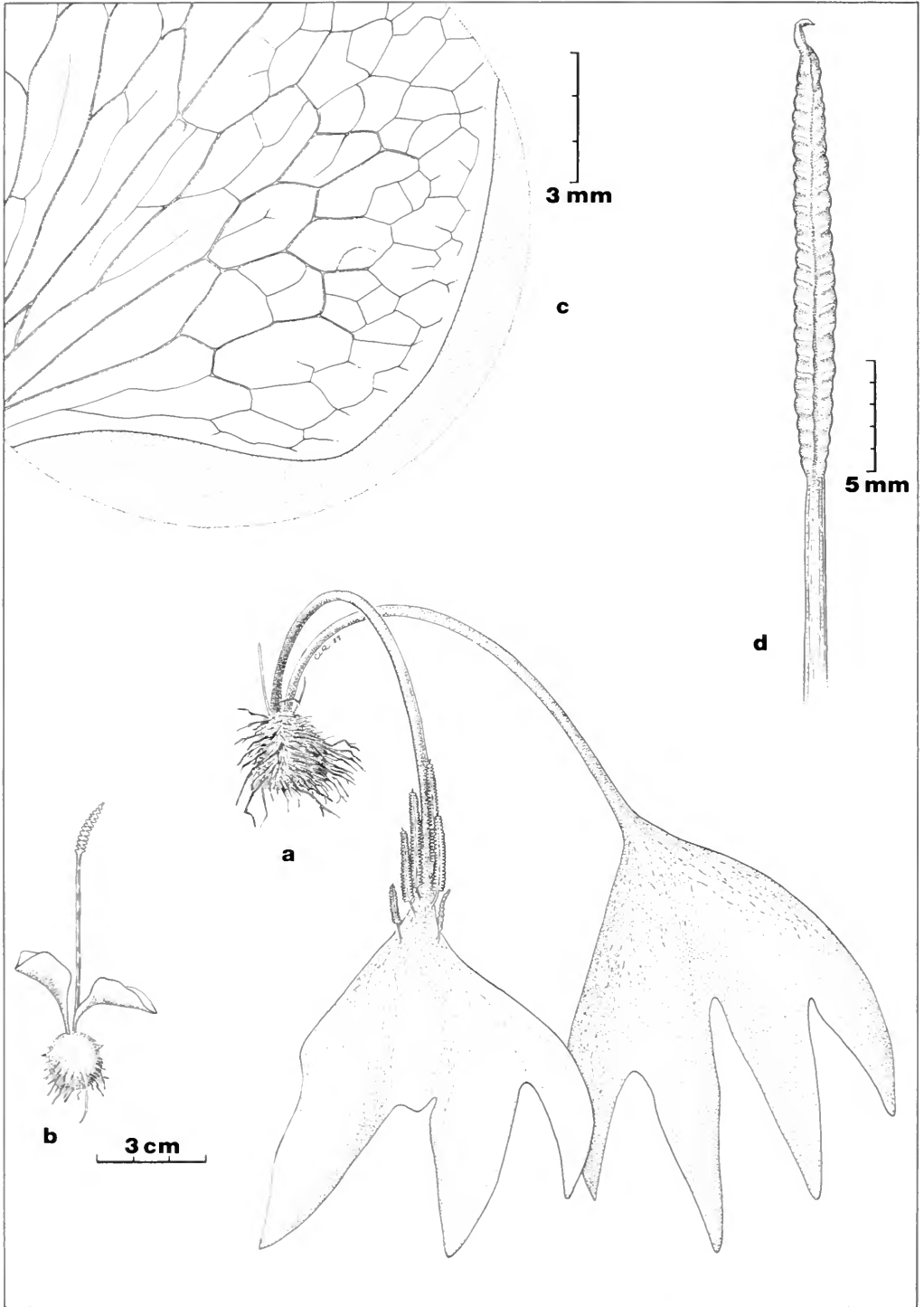


FIG. 2. *Ophioglossum palmatum*: a, habit. *Ophioglossum crotalophoroides*: b, habit. *Ophioglossum reticulatum*: c, venation of sterile leaf; d, fertile spike. (a from Allard 21580, US; b from Vargas 3978, US; c-d from Tryon & Tryon 5419, F.)

From high, rocky meadows to the open forests of middle elevations, and the grassy soil of coastal lomas, 400–3800 m, Amazonas south to Cuzco.

Widely distributed in tropical America; Old World.

Ophioglossum reticulatum is variable in the shape and base of the sterile lamina and in the frequency of secondary areoles and free, included veinlets. These characters intergrade freely with those of the often recognized *O. petiolatum*, so that it is impractical to separate the two as distinct taxa. Thus circumscribed, *O. reticulatum* is perhaps the most ubiquitous of any species in the genus.

Amazonas: Prov. Bongará, Shilla, *Young & Eisenberg 460* (MO). **La Libertad:** Prov. Patáz, Pumatambo, Puerta del Monte, *López & Sagástegui 3438* (GH). **San Martín:** Monte Campana, near Tarapoto, *Spruce 4709* (P, US). **Lima:** Lomas de Quilmaná, *Coronado 27* (US). Prov. Chancay, Lomas de Lachay, *Coronado & Velarde 15* (UC, US); *Tryon & Tryon 5419* (GH). **Pasco:** Prov. Oxapampa, Chontabamba, *D. Smith & Brack 3056* (F, MO). **Ayacucho:** Aina, between Huanta and Río Apurímac, *Killip & Smith 22809* (GH, NY, US). **Apurímac:** Prov. Abancay, Cachora, Huillcayoc, *Vargas 9096* (MICH, UC). **Cuzco:** Prov. Urubamba, Machu Picchu, *León 452* (GH, USM); *Tryon & Tryon 5400* (GH, US), *5419* (GH). **Madre de Dios:** Prov. Manú, Parque Nacional Manú, *Foster et al. 11486* (F).

3. *Ophioglossum nudicaule* L. f. var. *tenerum* (Mett.) Clausen, Mem. Torrey Bot. Club 19(2): 151. 1938.

Ophioglossum ypanemense Mart., Icon. pl. crypt. 39, 130, t. 73. 1834. TYPE: based on specimens from "Ypanema," Brazil.

Ophioglossum tenerum Mett. in Prantl, Ber. Deutsch. Bot. Ges. 1: 352. 1883. TYPE: United States, Georgia, collector undesignated (holotype, B).

Plants terrestrial. **Stem** cylindrical to somewhat swollen, lacking indument. **Leaf** 2.5–7 cm long, common stalk mostly epigeous, 0–4 cm long. **Sterile lamina** chartaceous to somewhat carnose, 0.8–2.5 cm long, 0.3–1.0 cm broad, 1.5–3 times as long as broad, sessile, elliptical to subovate, obtuse or subacute, base cuneate. **Veins** indistinct to obscure, areoles small, not enclosing secondary areoles or (except rarely) free veinlets. **Fertile segment** solitary, borne at base of sterile lamina, on mature leaves somewhat exceeding the lamina, fertile spike 0.5–1.2 cm long, on a stalk 0.8–2.5(–4) cm long.

In high rocky meadows and slopes, with grasses

and sedges, 2800–4000 m, Cajamarca, Lima, Cuzco.

Colombia; Peru; Brazil.

In spite of Clausen's work (1938), considerable study is still needed to understand the variation within *O. nudicaule*. The Peruvian plants here identified cannot be clearly placed within any of the varieties delineated by Clausen; but, aside from the fact that their fertile segments do not rise too conspicuously beyond the sterile lamina, they seem to fit best under var. *tenerum*. Diagnostic features of *O. nudicaule* are so few and variable that it is often difficult to discern which are innate differences and which are merely induced by rigorous habitat or attributed to degree of maturity of the individual plant. It is likely that this and other varieties accepted by Clausen are not supportable, as evidenced by the studies of Wagner et al. (1984), which suggest that they "all should be subsumed under the single binomial, *O. nudicaule*."

Cajamarca: Prov. Contumazá, Guzmango, *Sagástegui et al. 6412* (GH, HUT). **Lima:** Prov. Huarochiri, Dist. de Mariatana, Cueva Mortero, *Cerrate et al. 4812* (GH, USM). **Cuzco:** Prov. Acomayo, Quenco Grande, near Acomayo, *Vargas 9752* (F, GH, K, UC p.p., US). Prov. Espinar, Yauri, *Vargas 5619* (MICH). Prov. Urubamba, *Vargas 14122* (GH).

4. *Ophioglossum scariosum* Clausen, Mem. Torrey Bot. Club 19(2): 153. 1938. TYPE: Peru, Junín, vicinity of Oroya, *Kalenborn 125* (holotype, US!; isotypes, GH!, MO!, NY).

Plants terrestrial. **Stem** broadly elongate, 4–6 mm thick, lacking indument. **Leaf** 3–6 cm long, with common stalk and bases of fertile and sterile stalks hypogeous and scariosus, common stalk 0.3–0.8 cm long. **Sterile lamina** 1–1.5 cm broad, oblong-ovate to suborbicular, apex apiculate, at base truncate, reduced abruptly to an attenuate stalk 0.8–1.2 cm long. **Veins** indistinct to nearly obscure, primary areoles usually enclosing some secondary ones as well as free veinlets. **Fertile segment** solitary, borne at the base of the stalk of the sterile lamina, on mature leaves somewhat to greatly exceeding the lamina, fertile spike 0.6–1.2 cm long, on a stalk 1.3–4 cm long.

In open, grassy areas, 2840–3850 m, Junín, Cuzco, Puno.

Peru and Bolivia.

Leaves of this rare fern grow with proximal portions of leaves embedded in the soil. This is evi-

dent even in dried material, as the scarious common stalk and proximal portions of the stalks of fertile and sterile segments contrast sharply with the dark color of the rest of the leaf.

Cuzco: Prov. Urubamba, *Vargas 9165* (MICH). **Puno:** Lake Titicaca, *Bishop 1994* (US).

5. ***Ophioglossum crotalophoroides*** Walter, *Flora Caroliniana* 256. 1788. TYPE: Carolina, *Walter* (holotype, BM?). **Figure 2b.**

Plants terrestrial. **Stem** globose, 4–12 mm in diameter, lacking indument. **Leaf** 3–15 cm long, with common stalk 0.5–4 cm long. **Sterile lamina** ovate to deltoid, acute or rarely obtuse, cordate or truncate and abruptly attenuate at base, often longitudinally folded. **Veins** distinct or indistinct, primary areoles not or rarely enclosing secondary ones or free veinlets. **Fertile segment** solitary, borne at the base of the sterile lamina; in mature leaves the fertile segments somewhat to greatly exceeding the lamina, fertile spike 0.5–1.5 cm long, on a stalk to 10 cm long.

On moist, open, grassy slopes, 600–3900 m, Huánuco, Lima, Junín, Apurímac, Cuzco.

Southern United States; Mexico to Honduras; Colombia and Venezuela south to Argentina and Chile.

Among the diminutive species of *Ophioglossum*, a few plants are found with stems which are somewhat swollen. However, only in *O. crotalophoroides* is the stem so conspicuously globose. With this should probably be included *O. opacum* Carmichael, from Tristan da Cunha. It is said to differ from the former merely in the somewhat shorter fertile segment and slightly smaller globose stem.

Huánuco: Prov. Huánuco, Huánuco-Tingo María road, from Bandera Blanca to Carpisah Tunnel, *Luteyn & Luteyn 5464* (NY). **Lima:** Prov. Lima, Lomas de Luín, *Ferreya 9566 p.p.* (USM). **Junín:** Huaytapata, near Hacienda Conocancha, *Tiller 14* (USM). **Apurímac:** Prov. Abancay, Cachora, *Vargas 9054* (MICH *p.p.*, MO). **Cuzco:** Prov. Calca, Vilcabamba, *Vargas 3978* (US). Prov. Canas, slopes of San Andrés de Checca, *Vargas 11010* (F, UC).

6. ***Ophioglossum lusitanicum*** L. ssp. *coriaceum* (A. Cunn.) Clausen, *Mem. Torrey Bot. Club* 19(2): 161. 1938.

Ophioglossum coriaceum A. Cunn., *Companion Bot. Mag.* 2: 361. 1836. TYPE: based on specimens from Matauri, New Zealand (not located).

Plants terrestrial. **Stem** cylindrical to somewhat swollen, lacking indument. **Leaf** 4–8(–9) cm long, common stalk mostly epigeous, 0.5–2.5 cm long. **Sterile lamina** chartaceous to somewhat carnose, 1.5–4 cm long, 0.3–0.6 cm broad (ca. 4.5–8 times as long as broad), sessile, linear-lanceolate to narrow-ob lanceolate, apex acute or subacute, base narrowly cuneate to (typically) long-attenuate. **Veins** indistinct to obscure, areoles commonly long and narrow, not enclosing secondary areoles or free veinlets. **Fertile segment** solitary, borne at base of sterile lamina, on mature leaves somewhat to conspicuously exceeding the lamina, fertile spike 0.4–1.7 cm long, on a stalk 1–7 cm long.

In soil pockets or on thin soil over rocks, in Peru possibly confined to the coastal lomas in the vicinity of Lima, 400–650 m.

Peru; Bolivia; Chile; New Caledonia; Australia; New Zealand.

In Peru, this is typically a very delicate plant, with long, narrow, sterile leaves and a fragile, filiform, fertile stalk, and has thus far been found only at low elevations. However, we have examined some Bolivian plants of this subspecies, from elevations to 3000 m, which are more variable: sometimes more robust, with stouter fertile stalks, and with sterile laminae broader and less attenuate to base and apex. Subspecies *lusitanicum*, from Europe, Asia, and Africa, has obtuse sterile laminae with larger and fewer areoles. Subspecies *californicum* (Prantl) Clausen (California & Mexico) has laminae larger and broader, with less attenuate bases than in ssp. *coriaceum* and, according to Clausen (1938), perhaps does not merit distinction. As with the *O. nudicaule* complex (q.v.), far more study is needed to clarify the taxonomy, at both inter- and intraspecific levels.

Lima: Prov. Chancay, Lomas de Lachay, *Coronado & Velarde 16* (GH, UC, US); *Tryon & Tryon 5414* (GH *p.p.*, US). Lomas de Quilmaná, *Coronado 27* (UC, US *p.p.*). Lomas de Luín, *Ferreya 9566* (GH, USM *p.p.*). Lomas de Atocongo, *Grant 7509* (GH).

Comments

Ophioglossum ellipticum Hooker & Grev., *Icon. fil.* 1, t. 40A. 1831. TYPE: illustration, based

on specimens collected in Demerara, "British Guiana," *Parker*.

This perhaps may be expected in Peru, as its range is thus far reported from Guatemala to Costa Rica, and the Guianas southward to Brazil and (possibly) Bolivia. Although usually a smaller plant than *Ophioglossum reticulatum*, the aspect of the sterile lamina is similar in that the primary areoles contain a number of secondary areoles and usually some free veinlets. However, the secondary areoles are much more numerous in *O. ellipticum*, and the walls are thinner and far less distinct than those of the primary ones. Additionally, laminae in *O. ellipticum* have a somewhat distinct midvein and a pale, median band of tissue which persists to within a short distance of the apex. It is most closely related to *O. nudicaule*; in fact, the plants heretofore recognized as *O. ellipticum* may be merely *O. nudicaule* with larger and more fully developed leaves (see Wagner et al., 1984).

Family 2: MARATTIACEAE

Marattiaceae Bercht. & J. S. Presl, Prir. rostlin 1: 272. 1820. TYPE: *Marattia* Sw.

Danaeaceae Agardh, Aphor. bot. 117. 1822. TYPE: *Danaea* Sm.

Stem fleshy, stout to massive, creeping or erect, sometimes scaly. **Leaves** moderate in size to huge (3 m or more), circinate in vernation, 1-pinnate

Key to Genera of Marattiaceae

- a. Leaves 1-3-pinnate or more, monomorphic; synangia scattered, borne near the ends of veins I. **Marattia**
- a. Leaves 1-pinnate, somewhat dimorphic (fertile ones commonly longer and narrower and with smaller pinnae); synangia nearly covering the abaxial surface of fertile pinnae II. **Danaea**

I. *Marattia*

Marattia Sw., Prodr. 128. 1788. TYPE: *M. alata* Sw. **Figure 3.**

Plants terrestrial. **Leaves** coarse, to ca. 3(-4) m long, 2-4-pinnate, often ternate in architecture, monomorphic. **Lamina** with expanded tissue es-

to pinnately compound or rarely simple or palmate, monomorphic to somewhat dimorphic. **Petiole** with an expanded, stipular base, there swollen and sometimes subarticulate, frequently also with several swollen and darkened nodes throughout its length. **Pinnae** commonly borne in opposite pairs from swollen, darkened nodes on the rachis. **Veins** free or (in *Christensenia*) reticulate. **Sporangia** borne on the abaxial surface of leaves, with thickened walls, lacking an annulus, separate and contiguous or fused into indurated synangia and opening by terminal pores. **Spores** ellipsoidal and monolete or trilete, rugose or echinate, very numerous (1,500-1,700) in each sporangium.

Of the seven genera (about 150 species) in Marattiaceae, two are represented in Peru: *Danaea*, confined to the Neotropics, and *Marattia*, pantropical. Next to Ophioglossaceae, it is considered to be the most primitive of the living fern families and can be easily recognized by the character of the sporangia being fused into thick, elongate, double-rowed synangia.

References

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TRYON, R. M., AND A. F. TRYON. 1982. Marattiaceae, pp. 39-50, in Ferns and allied plants, Springer-Verlag, New York.

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sentially glabrous, but in some species sparsely to moderately scaly or with a few trichomes on the axes abaxially. Penultimate divisions with axes commonly broadly alate, the wings narrowing abruptly at the base of each segment. **Veins** free. **Sporangia** in two rows, opening by longitudinal slits, fused into bivalvate, ovoid synangia, which are borne near the ends of veins on a receptacle,

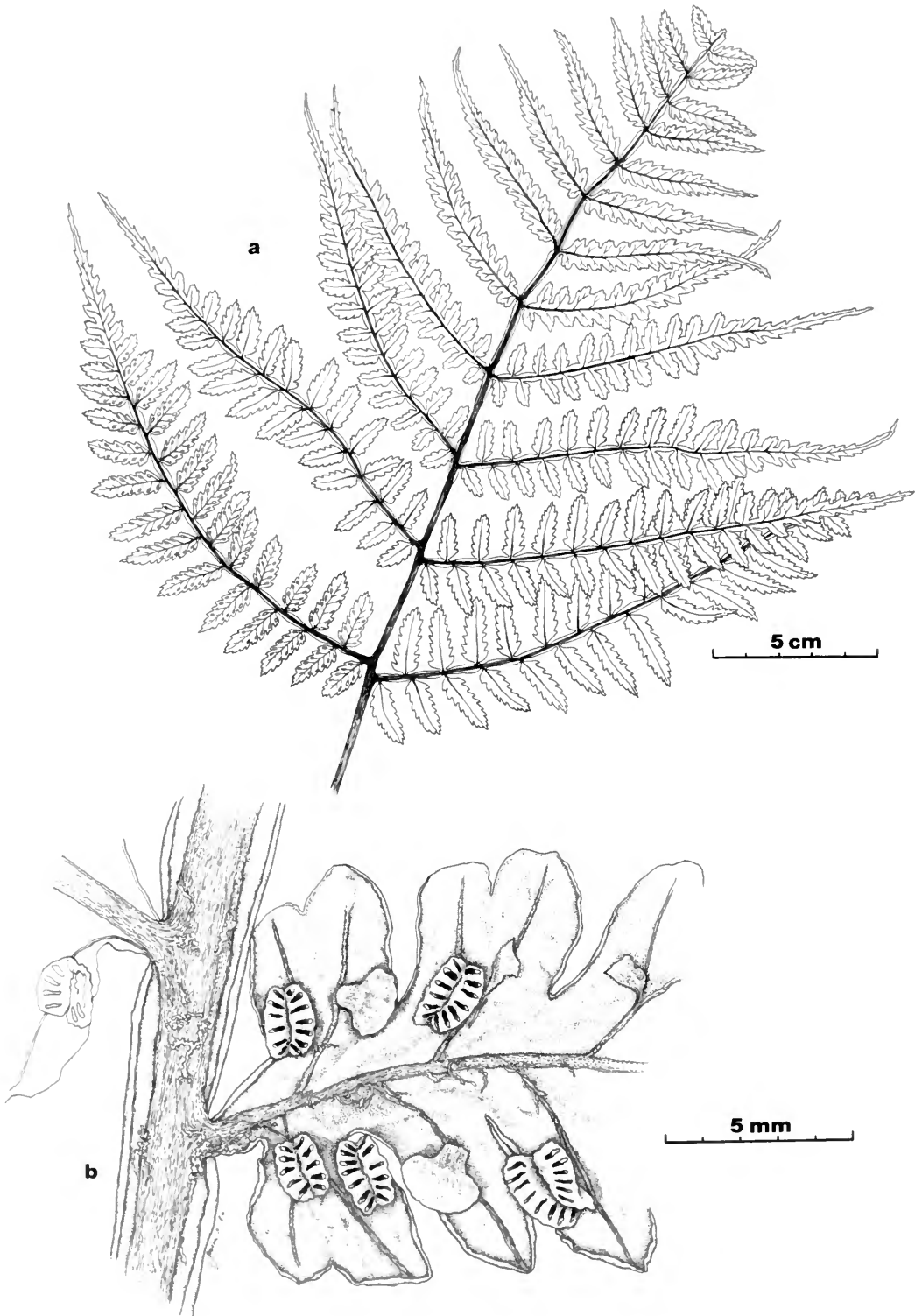


FIG. 3. *Marattia laevis*: a, portion of lamina; b, segment base, with synangia. (a from Macbride 4817, F; b from Haught 6145, Colombia, F.)

sessile or (in *M. laevis*) on short, thickened stalks. **Spores** ellipsoid, monolete.

This is a pantropical genus of about 40 species, commonly occurring in dense, wet forests. It is readily separated from other Neotropical genera by the large, decomposed, subternate leaves with stipular bases, and the distinctive ovoid synangia. A single species is known in Peru.

1. **Marattia laevis** Sm., *Plantarum Icones Ineditae ... 2: t. 47*. 1790. TYPE: as "*Polypodium pedicellata*, in argento pedunculat(o?), Ile Dominique (Dominican Republic, not Dominica), Thiery" (holotype, LINN). **Figure 3**.

Marattia alata sensu Raddi, *Pl. bras. nov. gen.* 1: 74, t. 83–84. 1825.

Marattia Kaulfussii Hooker, *Gen. fil.*, t. 26 (as to note). 1839. TYPE: Brazil, 1816, *Cunningham s.n.* (holotype, BM!; photo, F!).

Eupodium Kaulfussii (Hooker) Hooker, *Sec. cent. ferns*, t. 95. 1860.

Marattia alata Sw. var. *laevis* (Sm.) Farw., *Amer. Midl. Naturalist* 12: 308. 1931.

Leaves 2–4 m long, commonly 3-pinnate-pinnatifid, at least as to base of lamina. **Axes** (at least minor ones) sparsely to moderately provided on abaxial side with filiform to lanceolate scales, these orange to light brown, flaccid, 0.5–3 mm long, often caducous. Costae of **penultimate segments** bearing on the adaxial side 1–several well-spaced, often appressed, awns, these 0.2–1 mm long (or on older leaves sometimes withering or broken away near their bases). **Synangia** 8–16(–18)-locular, mature ones obviously stipitate, the stalks stout, to 0.7 mm long. **Spores** echinate.

Occurring in dense forests, principally along the Cordilleras Central and Oriental, in Amazonas, Huánuco, Pasco, Junín, and Cuzco, 1400–2400 m.

Costa Rica; Cuba; Hispaniola; Colombia; Venezuela; Brazil; Ecuador; Peru; Bolivia.

In various herbaria, *M. laevis* has been confused with *M. alata*, a species from the Greater Antilles. Although leaf outline is similar in each, *M. laevis* is easily distinguished by its stalked synangia and awned penultimate axes, these characters are unique in the genus, at least in New World species.

There has been some confusion as to the identity of *M. laevis*, beginning with Smith's original description, which mentioned nothing about the distinctive stalked synangia and adaxial awns. Kaulfuss (*Enum. fil.*, p. 32, 1824) mentioned seeing

some Brazilian specimens of *M. laevis* with "soros ... stipitati," upon which character Hooker (following Smith's unpublished description) partially based the new species *M. Kaulfussii* (1839). Obviously Hooker had seen the type of *M. laevis*, and supposed it lacked the stalked synangia; therefore, he surmised that the Brazilian collections of Kaulfuss represented a new species. Finally in 1936 Alston (*J. Bot.*, p. 174) combined the two names, but failed to specify reasons for doing so. In turning to the British Museum for clarification of the matter, this reply was received from Miss Josephine M. Camus: "I have examined the (type) specimen in the Linnaean Herbarium. It does indeed have synangia with very elongate receptacles. The original label bears the name *Polypodium pedicellata* in Linnaeus fil.'s hand. The 'awns' are present on the upper surface of the pinnule axes... ." Thus, there seems to be no question that the fern considered to be *M. Kaulfussii* for nearly 150 years is *M. laevis*.

Amazonas: Prov. Bagua, Cordillera Colón SE of La Peca, *Barbour 3900* (MO). **Huánuco:** Churubamba, Trail Puente Durand to Exito, Mt. Santo Toribio, *Mexia 8250* (F, GH, MICH, NY, UC, US). **Pasco:** Cushi, *Macbride 4817* (F, GH, US). **Junín:** Schunke Hacienda above San Ramón, *Killip & Smith 24540* (NY, US). Pichis Trail, Eneñas, *Killip & Smith 25738* (GH, NY, US). Chanchamayo Valley, *C. Schunke 671* (F). **Cuzco:** La Convención, above Knox's Cascade, *Dudley 10619* (GH, MO).

II. *Danaea*

Danaea Sm., *Mém. Acad. Roy. Sci.* (Turin) 5: 420. 1793, *nom. conserv.*, not Allioni, 1785. TYPE: *Danaea nodosa* (L.) Sm. (*Acrostichum nodosum* L.). **Figure 4**.

Plants terrestrial, with stems creeping to decumbent or erect. **Leaves** to 2 m long, 1-pinnate (or simple in 2 species outside Peru), monomorphic to somewhat dimorphic (fertile ones commonly longer and narrower and with smaller pinnae). **Petiole** (in most species) nodose, scaly, bearing stipules at the base. **Rachis** nodose, nonalate to conspicuously alate at least distally, glabrous or more often with appressed scales. **Lamina** with a distinct apical segment, or this replaced by a proliferous bud, provided with scales abaxially, those of the laminar tissue minute and scattered. **Sterile pinnae** opposite or subopposite, straight to subfalcate, sessile or short-stalked, entire and often undulate, or serrate near the apex. **Veins** free. **Fertile pinnae** similar to the sterile ones, but commonly reduced

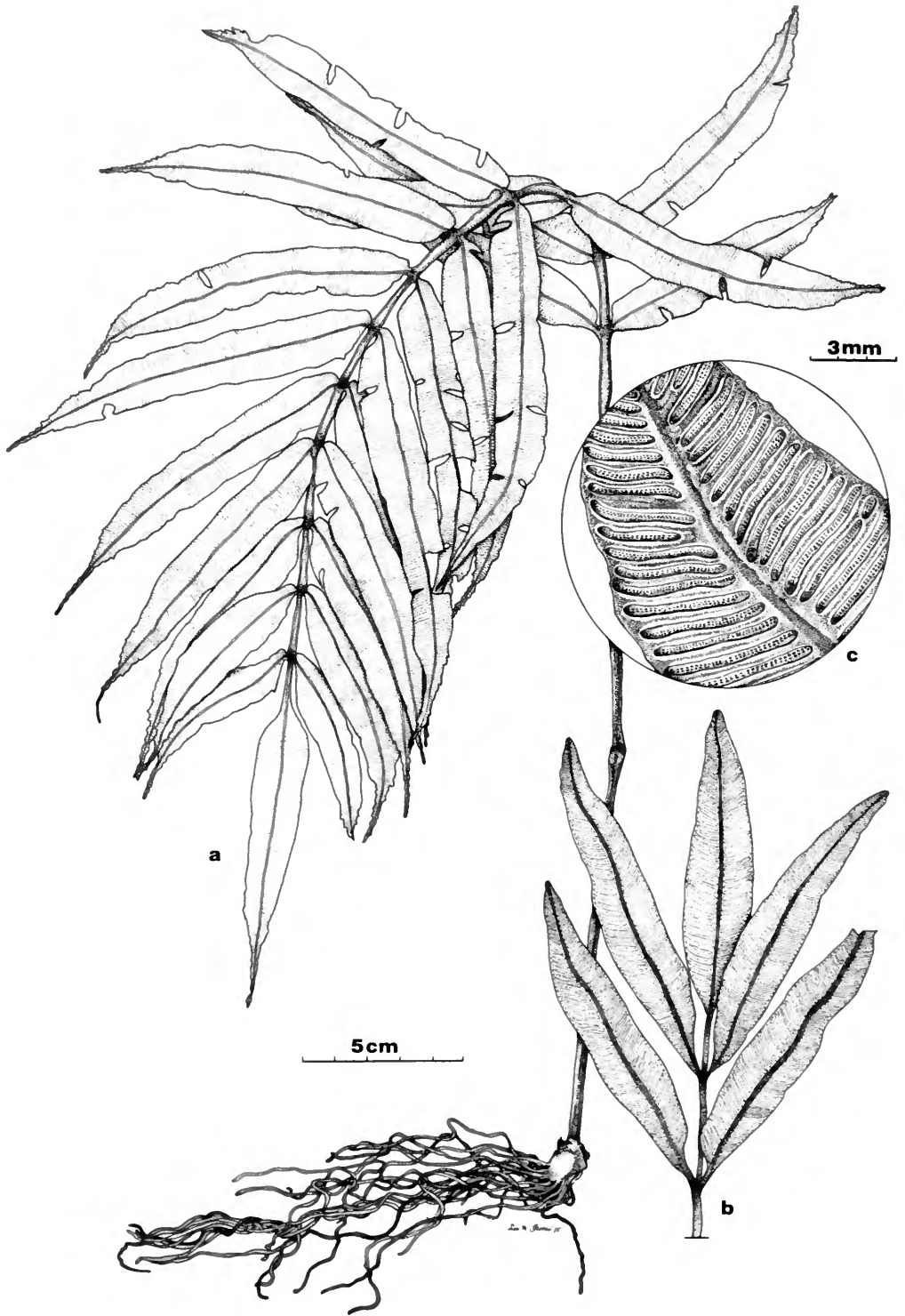


FIG. 4. *Danaea moritziana*: a, habit. *Danaea nodosa*: b, apex of sterile lamina; c, portion of fertile pinna with synangia. (a from Tryon & Tryon 5278, F; b-c from Wurdack 1934, F.)

in size, and with vegetative tissue nearly lacking. **Sporangia** nearly covering the abaxial surface, coalescing into much elongated, indurated synangia and opening by terminal pores. **Spores** monoletic, the surface prominently echinate.

Danaea is confined to the Neotropics. With its nodose leaf axes and the distinctive synangia nearly covering the abaxial surface of simple, usually opposite, pinnae, it should not be confused with other Peruvian genera. However, distinguishing species is another matter. To date there has been no comprehensive study of the genus, and many of the characters used by Underwood to separate taxa are highly suspect: e.g., length of fertile pinnae, number of veins per centimeter, veins paired in origin versus distinctly forked. Species previously thought of as distinct in Central or South

America may be synonymous with some in the West Indies. Although about 35 species have been recognized, 20–25 is a more realistic total to expect once a greatly needed revision has been undertaken. Six species from Peru are recognized in the following treatment.

References

PROCTOR, G. R. 1977. *Danaea*, pp. 45–49, in Howard, R. A., ed., *Flora of the Lesser Antilles: Leeward and Windward Islands*, Vol. 2, Pteridophyta, Arnold Arboretum, Harvard University, Jamaica Plain, Mass.
 UNDERWOOD, L. M. 1902. A review of the genus *Danaea*. *Bull. Torrey Bot. Club*, 29: 669–679.

Key to Species of Danaea

- a. Larger sterile pinnae (5–)6–40 cm long; larger fertile pinnae 4–25 cm long b
- b. Sterile pinnae 2–6 pairs; fertile pinnae 3–5 pairs 2. **D. elliptica**
- b. Sterile pinnae (7–)8–16 pairs; fertile pinnae 7–25 pairs c
- c. Petiole of mature plants lacking nodes; apices of sterile pinnae entire (very rarely serrulate); larger sterile pinnae (2.5–)3–6.5 cm broad 1. **D. nodosa**
- c. Petiole of mature plants with 1–3 nodes; apices of sterile pinnae serrate; larger sterile pinnae 1.2–2.8 cm broad d
- d. Sterile pinnae broadly oblanceolate, broadest above the middle, abruptly acuminate at the apex; veins predominantly simple, occasionally paired in origin or forked 3. **D. oblanceolata**
- d. Sterile pinnae lanceolate to oblong-lanceolate, broadest near or below the middle, tapering gradually to an acuminate or attenuate apex; veins predominantly forked, only occasionally simple or paired at the base 4. **D. moritziana**
- a. Larger sterile pinnae 1.5–3.5(–4) cm long; larger fertile pinnae 1.1–1.7 cm long e
- e. Sterile pinnae strongly inequilateral at base, narrow and rounded basiscopically, much broader and abruptly cuneate to truncate acrosopically; veins predominantly forked, some of them simple; petiole nodes 1–3; terminal segment of sterile lamina equaling or longer than the pinnae, lacking a proliferous bud 5. **D. humilis**
- e. Sterile pinnae subequilateral at the truncate base; veins simple, rarely forked; petiole nodes lacking; terminal segment of sterile lamina much shorter than larger pinnae, or replaced by a proliferous bud 6. **D. trichomanoides**

1. *Danaea nodosa* (L.) Sm., *Mém. Acad. Roy. Sci. (Turin)* 5: 420. 1793. **Figure 4b–c.**

Acrostichum nodosum L., *Sp. pl.* 1070. 1753. LECTOTYPE (designated by Proctor, *Flora Lesser Antilles* 2: 48. 1977): Plumier, *Traité foug. Amér.*, t. 108, based on specimen from Martinique or Haiti.

Danaea longifolia Desv., *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk.* 5: 307. 1811. TYPE: “in antillis” (p).

Danaea grandifolia Underw., *N. Amer. fl.* 16: 18. 1909. TYPE: Colombia, Valparaiso, Santa Marta, *H. H. Smith 992* (holotype, NY; isotypes, BM, F!, GH!, MO!, US!).

Sterile leaves to 2 m long and 60 cm broad, imparipinnate; **petiole** lacking nodes, sparsely scaly or abundantly so at base, the scales mostly appressed, dark brown, peltate, nearly circular and ca. 1 mm in diameter or to 3 mm long, margins

often fimbriate; **rachis** not or scarcely alate, sparsely scaly; **pinnae** 7–16 pairs, subsessile to short-stalked, elliptic to oblanceolate, larger ones 20–40 cm long and (2.5–)3–6.5 cm broad, base cuneate, apex long-acuminate, margins entire (very rarely serrulate along the acuminate tip), abaxial surface and veins sparsely provided with minute (ca. 0.1 mm) scales, these appressed, nearly circular, dark or reddish brown, commonly erose to stellate; **veins** mostly paired or 1-forked near the base. **Fertile pinnae** 7–14 pairs, 12–25 cm long, 1.5–2.5 cm broad, subsessile to short-stalked, the apex acute to acuminate.

Terrestrial, in dense forests, 100–2100 m, Amazonas and Loreto to Cuzco and Madre de Dios.

Southern Mexico to Panama; West Indies; Colombia; Venezuela; Surinam; Ecuador; Peru; Brazil.

Danaea grandifolia is said to differ from *D. nodosa* in the broader sterile pinnae and more broadly cuneate bases of fertile pinnae. The latter character is not consistent, and the former is hardly sufficient reason for separation even at infraspecific level. There is also some question as to the merit of separating *D. nodosa* and *D. elliptica*. While the characters of nodose or non-nodose petioles and pinnae number usually serve to distinguish the two, even these have not been reliable consistently in specimens seen from Peru. Further study is needed.

Amazonas: E of Huampami, near Pedro Alberto, *Berlin 1524* (MO). **San Martín:** Prov. Rioja, km 390, Pedro Ruíz-Moyobamba road, *D. Smith & Vásquez 4726* (F, MO). **Loreto:** Balsapuerto (lower Río Huallaga basin), *Killip & Smith 28410* (GH, US). **Huánuco:** Prov. Pachitea, Dist. Honoria, en frente a Tournavista, al este del Río Pachitea, *J. Schunke 1800* (F, GH). **Pasco:** Puerto Bermúdez (as Junín), *Killip & Smith 26511* (NY, US). **Junín:** Prov. Satipo, near Satipo, *van der Werff et al. 8644* (MO). **Cuzco:** Prov. Quispicanchi, Punkiri Río Arriba, *Vargas 16121* (GH). **Madre de Dios:** Prov. Tambopata, SSW of Puerto Maldonado, *Barbour 5178* (F, GH, MO).

2. *Danaea elliptica* Sm. in Rees, Cycl. 11: Danaea No. 2. 1808. LECTOTYPE (designated by Proctor, Flora Lesser Antilles 2: 48. 1977): Sloane Herb. 1: 85, based on plant from Mt. Diablo, Jamaica (BM).

Danaea elliptica var. *crispula* Rosenst., Repert. Spec. Nov. Regni Veg. 7: 310. 1909. TYPE: Peru, San Martín, "In montibus secus flumen Mayo, prope Tarapoto," *Spruce 4770* (holotype, K; isotypes, GH!, L, P!, UC!, US!; photo, F of L!).

Sterile leaves to 1 m long and 30 cm broad, imparipinnate; **petiole** with 1–5 nodes, sparsely scaly, the scales appressed, dark brown, amorphous, peltate, often fimbriate, commonly less than 2 mm long; **rachis** nonalate to narrowly so distally (or alate throughout in juvenile leaves), sparsely scaly; **pinnae** 2–6 pairs, subsessile to short-stalked, more or less elliptic, 8–18 cm long, (2.5–)3–4.5 cm broad, base cuneate, apex acute to acuminate, margins entire and plane to somewhat undulate, abaxial surface and veins very sparsely provided with minute (ca. 0.1 mm) scales, these appressed, nearly circular, dark or reddish brown, commonly erose to stellate; **veins** mostly paired or 1-forked near the base. **Fertile pinnae** 3–5 pairs, 5–14 cm long, (1–)1.7–2.8(–3) cm broad, short-stalked, the apex acute to acuminate.

In dense forests, principally along the Cordillera Oriental, Amazonas to Junín, 125–1600 m.

Southern Mexico to Panama; West Indies; the Guianas to Colombia and south to Brazil and Peru.

There is no justification in recognizing Rosenstock's var. *crispula* as a separate entity; supposedly it differed from the typical in having one less pair of pinnae, these broadest at or above the middle, with margins more crisped. All fall within the natural variation of this species.

Amazonas: Prov. de Bagua, valley of Río Marañón near Cascadas de Mayasi, *Wurdack 1934* (GH, US). **San Martín:** On ridge in jungle E of Tingo María, *Allard 21381* (GH, US). **Loreto:** Fierro Cano a km 4 del Centro Forestal Jenaro Herrera, *Spichiger et al. 1439* (MO). **Huánuco:** Dist. Churubamba, Hacienda Mercedes, trail to Balsa-playa, *Mexia 8170a* (UC). **Pasco:** Prov. Oxapampa, Palcazú Valley, Iscozacín, *Foster 9502* (MO). **Junín:** Pichis Trail, Yapas, *Killip & Smith 25507* (GH, NY, US).

3. *Danaea oblanceolata* Stolze, Amer. Fern J. 77: 33. 1987. TYPE: Peru, Dept. Pasco (as Junín), Cahuapanas, on Río Pichis, *Killip & Smith 26777* (holotype, US!; frag., F!).

Sterile leaves 40–50 cm long, 13–18 cm broad, apical segment (on mature leaves) replaced by a proliferous bud; **petiole** with 1–2 nodes, moderately to abundantly scaly; **rachis** narrowly alate; **pinnae** 10–12 pairs, mostly short-stalked, oblong to (more commonly) broadly oblanceolate, larger ones 7–11 cm long and 2–2.8 cm broad, inequilateral at base, narrow and rounded to cordate basiscopically, broader and cuneate acroscopically, terminating abruptly in an acuminate and ser-

rate apex, abaxial surface amply provided with minute, dark brown scales; veins commonly simple, but sometimes paired at origin or forked. Fertile pinnae 12–14 pairs, larger ones 7–8 cm long and 0.8–1 cm broad, short-stalked, the apex obtuse.

Terrestrial in dense forests, 0–500 m, thus far known only from Peru: Pasco and Ucayali.

This is perhaps most closely related to *D. alata* Sm., of the West Indies and Venezuela, especially in that both species have predominantly simple veins. However, in *D. oblanceolata* pinnae are fewer and relatively shorter and broader, and most are broadest well above the middle, where the margins then bend abruptly to a short-acuminate apex. In *D. alata*, as in all members of the *D. moritziana* complex, pinnae are broadest at or near the middle, from whence they taper gradually to a moderately acuminate or attenuate apex.

Pasco: Oxapampa, Palcazú Valley, Iscozacán, *R. Foster* 9466 (MO), 10049 (F). **Ucayali:** Vicinity of Aguaytía, *Croat* 20938 (MO).

4. *Danaea moritziana* Presl, Abh. Königl. Böhm Ges. Wiss. 5(4): 35. 1845. TYPE: Venezuela, Colonia Tovar, *Moritz* 257 (holotype, PR?; isotype, L; frag., US!; photo, US). **Figure 4a.**

Sterile leaves to 1.2 m long and 35 cm broad (somewhat broader than fertile ones), imparipinnate, or sometimes with the apical segment replaced by a proliferous bud; **petiole** with 1–3 nodes, sparsely scaly; **rachis** scarcely alate, or slightly so in younger plants; **pinnae** 8–16 pairs, subsessile to short-stalked, elliptic to oblong-lanceolate, larger ones (5–)6–20 cm long and 1.2–2.2 cm broad, inequilateral at base, narrow and rounded to cordate basiscopically, broader and cuneate to subtruncate acroscopically, gradually tapering to an acuminate or long-attenuate apex, margin subentire but conspicuously serrate at apex, veins (and often the tissue between the veins) amply provided with minute scales; veins predominantly forked at or near the base, occasionally simple, or paired at origin. **Fertile pinnae** 8–15 pairs, larger ones 4–11 cm long, 0.6–0.8 cm broad, subsessile or short-stalked, the apex acute to apiculate.

Terrestrial, in dense forests, often along streams or in ravines, 300–2300 m, Cajamarca to Loreto, south to Cuzco and Madre de Dios.

Colombia; Venezuela; Peru.

Except for *Danaea nodosa*, this is the most widely distributed representative of *Danaea* in Peru. Moreover it is likely that the Central American *D. cuspidata* Liebm. also belongs here, along with one or two West Indian species. A number of taxa with pinnae under 2.5 cm broad were separated by Underwood (1902), merely on the degree of forking and spacing of veins, an inconsistent character correlated rarely or not at all by other features, hence a comprehensive revision of the genus should prove many of these to be synonymous. Peruvian specimens of *D. moritziana* apparently are more variable than in other areas, sometimes having smaller and fewer pinnae as in Venezuela, sometimes with more and larger pinnae as in "*D. cuspidata*" of Costa Rica. A few very large specimens from Tingo María have pinnae with rather glossy undersurfaces and extremely attenuate apices. Very closely related to this is *D. alata* Sm. of the Lesser Antilles, Trinidad, and Venezuela. Although *D. alata* tends to have more numerous pinnae than *D. moritziana*, the only consistent difference between the two is that of simple versus forked veins. To further add to the confusion, some specimens of *D. moritziana* in Peru have been incorrectly determined as *D. stenophylla* Kunze, which is merely a synonym for *D. alata*.

Underwood (1902) described both of the latter as having unforked veins and distinguished them principally by the degree of crowding of veins, and that *D. stenophylla* was a "small" plant. Later (1909) he reversed himself by describing *D. stenophylla* as a "rather tall plant" and as having mostly forked veins. Obviously he had not seen the type collection, for the isotype (2 sheets) at Kew contains leaves to nearly a meter long, with veins obviously simple (only rarely forked), differing from *D. alata* in no way that we can perceive. We cannot be certain which West Indian plants with forked veins were seen by Underwood, and later by Proctor (1977), but perhaps they are *D. jamaicensis*.

Cajamarca: Tambillo, *Jelski* 1073 (P). **Amazonas:** Bagua, ca. 25 km E of La Peca, *Barbour* 2969 (MO). **San Martín:** Monte Campana, Tarapoto, *Spruce* 4711 (P). **Loreto:** Río Corrientes, Cachuela, *McDaniel* 11198 (F, GH, MO). **Huánuco:** Tingo María, *Tryon & Tryon* 5278 (F, GH, UC, US). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al.* 8434 (MO). **Junín:** Chanchamayo Valley, *C. Schunke* 156 (F, US). **Cuzco:** Prov. La Convención, ca. 10 km from Hacienda Luisiana, *Dudley* 10412 (GH). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, Río Palotoa 10–15 km NNW of Shintuya, *Foster* 10750 (F).

5. *Danaea humilis* Moore, Index fil. 286. 1861. LECTOTYPE (designated by Lellinger in Proc. Biol. Soc. Wash. 89: 710. 1987): Peru, Dept. San Martín, Tarapoto, *Spruce 4769* (lectotype, K; isoelectotypes, BM!, GH!, L!, P!, US!).

Sterile leaves 20–34 cm long, 3.5–7 cm broad, larger than the fertile ones, imparipinnate, the terminal segment equaling or longer than the largest pinnae, with or without a proliferous bud; **petiole** with 1–3 nodes, amply to abundantly scaly; **lamina** slightly shorter than the petiole, the tissue between the veins abundantly provided with minute scales; **rachis** conspicuously alate, the margins of wings sometimes revolute, but not crispate; **pinnae** 14–24 pairs, oblong-elliptic, subfalcate, 2.2–3.5(–4) cm long, 0.6–1(–1.4) cm broad, strongly inequilateral at base, narrow and rounded basiscopically, much broader and abruptly cuneate to truncate acropically, apex acute to subacuminate and usually serrulate, margin subentire, essentially plane; **veins** predominantly forked above the base, yet many of them simple. **Fertile lamina** scarcely alate along rachis; **pinnae** 12–25 pairs, 1.1–1.4 cm long, 0.2–0.3 cm broad, subsessile to short-stalked, mostly acute to subapiculate.

In Peru known only from the type collection: San Martín.

Rare, terrestrial, in rain forests, 1000–1400 m, Venezuela; Colombia; Ecuador; Peru; Bolivia.

This and *Danaea trichomanoides* are among the smallest species of the genus, with even the larger sterile pinnae commonly less than 3 cm long. Other than size, however, they share few other similar features, as evidenced by the characters listed in the key.

6. *Danaea trichomanoides* Moore, Index fil. 288. 1861. TYPE: Peru, “in monte Guayrapurima, prope Tarapoto” (San Martín), Aug. 1856, *Spruce 4710* (holotype, K!; frag., NY!; photos, F, GH; isotypes, BM!, P!).

Sterile leaves 10–12 cm long, 3–4 cm broad, shorter than the fertile ones, with a terminal segment much shorter than the larger pinnae, or replaced by a proliferous bud; **petiole** lacking nodes, abundantly scaly; **lamina** 2–4 times longer than the petiole, the tissue between veins essentially lacking scales; **rachis** broadly crispate-alate; **pinnae** 11–15 pairs, oblong, 1.5–2.2 cm long, 0.5–0.9 cm broad, subequilateral at the truncate base, apex

rounded to subacute, margin slightly crispate; **veins** predominantly simple, rarely forked. **Fertile lamina** with rachis scarcely alate; **pinnae** 1.4–1.7 cm long, 0.3–0.4 cm broad, obviously stalked, apex rounded.

Thus far known only from the type collection.

When Moore published the description of the species, taken from a Spruce manuscript, he noted that pinnae were “unequal at the base.” Perhaps this conclusion was drawn from observing the crispate margins of some of the pinnae which were partially folded on drying. However, study of the two type specimens reveals that the bases of most pinnae are subequally truncate and approximately as broad on either side of the costa. This is in marked contrast with most species of *Danaea*, whose bases are commonly broader and less abruptly tapered on the acropical side.

Danaea trichomanoides is comparable to *D. wendlandii* Reichb. f., from Costa Rica, for the two are similar in size, and have nodeless petioles and crispate pinnae, with the presence (usually) of a terminal bud. However, the latter has pinnae with inequilateral bases, veins predominantly forking, and rachis wing plane or revolute (not crispate).

Family 3: OSMUNDACEAE

Osmundaceae Bercht. & J. S. Presl, Prir. rostlin 1: 272. 1820. TYPE: *Osmunda* L.

Stem massive, woody, decumbent to erect, lacking indument, with hard, fibrous roots. **Leaves** circinate in vernation, densely caespitose, pinnate to pinnately compound, monomorphic to (in *Osmunda*) partly or fully dimorphic. **Petiole** with an expanded, stipular base, not articulate to the stem. **Veins** free. **Sporangia** not in definite sori, borne abaxially along the segments or (in *Osmunda*) completely replacing the vegetative tissue of the lamina or of only some of the pinnae, exindusiate, short-stalked, with walls 1 cell thick, the annulus lacking or of only a few thickened cells near the distal end. **Spores** uniform, green, 120–512 in each sporangium.

The three genera of the Osmundaceae are represented by 15–20 species. *Osmunda* is nearly cosmopolitan, while *Leptopteris* and *Todea* are con-

fined to the Old World. This is a very old fern family; only Ophioglossaceae and Marattiaceae are considered to be more primitive. Like the other leptosporangiate members of the Filicales, Osmundaceae have sporangial walls only one cell thick, yet the family is similar to the Eusporangiatae in that the annulus is lacking or is composed of only a few thickened cells.

References

- BENEDICT, R. C. 1909. Osmundaceae, in N. Amer. fl., **16**: 27–28.
 TRYON, R. M., AND A. F. TRYON. 1982. Osmundaceae, pp. 50–57, in Ferns and allied plants, Springer-Verlag, New York.

Key to Species of *Osmunda*

- a. Sterile lamina 1-pinnate-pinnatisect; ultimate segments entire, the veins commonly 1-forked; fertile lamina nonfoliaceous throughout 1. ***O. cinnamomea***
 a. Sterile lamina 2-pinnate; ultimate segments serrulate, the veins commonly 2-forked; fertile lamina nonfoliaceous and fertile only in the distal portion 2. ***O. regalis* var. *spectabilis***

1. ***Osmunda cinnamomea* L.**, Sp. pl. 1066. 1753. TYPE: United States, Maryland, *Kalm* (holotype, LINN 1244.12; photo, F). **Figure 5c–d.**

Leaves completely dimorphic, vegetative tissue essentially lacking in fertile ones. **Petiole** glabrous or moderately provided with tortuous, filiform or pluricellular, reddish brown trichomes, sheathed at the base. **Sterile lamina** 1-pinnate-pinnatifid, tissue glabrous, but with filiform trichomes as on the petiole appearing especially at bases of pinnae, rachis narrowly alate adaxially; **pinnae** to 10 cm long, spreading to strongly ascending, subopposite, articulate with age at the rachis, deeply incised to form broad, subfalcate, obtuse or subacute segments, the segment margins subtentire and bearing short, filiform trichomes; **veins** 1-forked. **Fertile lamina** nearly 2-pinnate, the pinnae more strongly ascending than the sterile ones, with dark, filiform

I. *Osmunda*

***Osmunda* L.**, Sp. pl. 1063. 1753. TYPE: *O. regalis* L. **Figure 5.**

Plants terrestrial. **Leaves** coarse, 1–2 m or longer, 1–2-pinnate, completely or partially dimorphic, the fertile ones (or portions of them) lacking green leaf tissue. **Sterile lamina** commonly glabrous at maturity, but the axes often sparsely to moderately provided with trichomes. **Veins** free, at least 1-forked. **Sporangia** relatively large, developing simultaneously, commonly borne in clusters on the segments of the fertile leaves. **Spores** tetrahedral-globose, trilete, rugose or crested with slender echinate processes.

This is a genus of about 10 species which generally grow in swampy areas in temperate and tropical regions of both hemispheres. Two species occur in Peru.

trichomes abundantly interspersed among the crowded sporangia.

In wet places, usually in sphagnum swamps, 1700–2800 m, Cajamarca, Amazonas, and Pasco.

Eastern and central United States and Canada; West Indies; southern Mexico to Honduras; Costa Rica; Colombia; Venezuela; Brazil; Peru; Paraguay; southeast Asia.

Some earlier authors recognized this in the Neotropics as var. *imbricata* (Kunze) Milde, distinguishing it from North American plants on the basis of darker-colored tomentum and thicker lamina. We find little justification for the separation.

Cajamarca: Jaén, Quebrada de Pajonal, above Tabaconas, 19 km ESE Huancabamba, *Fosberg 27795* (MICH, NY). **Amazonas:** Chachapoyas, Jalca zone, 3–6 km W of Molinopampa, *Wurdack 1404* (US). **Pasco:** (as Junín) Pichis trail, Eneñas, *Killip & Smith 25708* (NY, US).



FIG. 5. *Osmunda regalis* var. *spectabilis*: a, habit; b, sterile ultimate segment. *Osmunda cinnamomea*: c, habit; d, sterile ultimate segment. (From Stolze, Ferns and fern allies of Guatemala, 1976.)

2. *Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray, Manual ed. 2: 600. 1856. **Figure 5a-b.**

Osmunda spectabilis Willd., Sp. pl. 5: 98. 1810. TYPE: United States, Pennsylvania, *Mühlenberg* (holotype, v, *Herb. Willd. 19504*; photo, GH).
Osmunda palustris Schrader, Gött. Gel. Anz. 866. 1824. TYPE: not located.
Osmunda regalis ssp. *palustris* (Schrader) Löve & Löve, Taxon 26: 324. 1977.

Leaves partly dimorphic, fertile ones with fertile and sterile portions combined on the same lamina, the fertile pinnae commonly distal and essentially lacking vegetative tissue. **Petiole** glabrous at maturity, sheathed at the base. **Sterile lamina** 2-pinnate, chartaceous to subcoriaceous, tissue glabrous, but a few tortuous, pluricellular, reddish brown trichomes often clustered at the base of pinnules, the rachis nonalate; **pinnae** to 20 cm long, strongly ascending, subopposite, short-stalked, articulate with age at the rachis, costae very narrowly alate (at least distally) on adaxial side; **pinnules** distant, subopposite, short-stalked, articulate with age at the costa, oblong to narrow-elliptic, obtuse to subacute, margins serrulate. **Veins** mostly 2-forked. **Fertile pinnae** 2(-3)-pinnate, more strongly ascending than the sterile ones, the crowded sporangia almost completely replacing the leaf tissue.

In damp places near lakes or streams, occasionally among rocks, 1300–2200 m, Amazonas, Pasco, Cuzco.

Eastern and central United States and Canada; West Indies; southern Mexico; Guatemala; Honduras; Costa Rica; Colombia; Venezuela; Brazil; Ecuador; Peru; Paraguay; Uruguay.

Variety *regalis*, which occurs in the Old World, is said to differ in its broader leaves, narrower panicles, and more numerous blackish to castaneous trichomes persistent along the rachis. Although specimens we have seen from both the New and Old World do not seem to differ strongly or consistently enough to warrant separation, we maintain the traditional varietal distinction for purposes of this treatment. Earlier workers proposed yet another variant, ssp. *palustris*, for South American plants, based on size of segments and

length of their stalks. The characters are too insignificant and inconsistent to merit such a distinction.

Amazonas: Mendoza, on rocky wall of ravine, *Woytkowski 8253* (GH, MO, US). Prov. Bongará, W & S margins of Laguna Pomacocha, *Wurdack 896* (US). **Pasco:** Prov. Oxapampa, Canyon de Huancabamba, *León 612* (GH). **Cuzco:** Empalizada, *Bües 1705* (US).

Family 4: SCHIZAEACEAE

Schizaeaceae Kaulf., Wesen farrenkr. 119. 1827.
 TYPE: *Schizaea* Sm.

Stem erect to decumbent, usually small and sometimes branched, or long-creeping, slender and freely branched, provided with trichomes or (in *Mohria* of Africa) with scales. **Leaves** circinate in vernation, entire or filiform, or dichotomous, or pinnate, glabrous to pubescent or (in *Mohria*) with scales, partially or wholly dimorphic. **Sporangia** borne abaxially on slightly to strongly modified portions of the leaf, separate, or crowded on each side of a vein, or in loose clusters on wholly fertile panicles, sessile, or with a short, many-rowed stalk, and an apical annulus. **Spores** tetrahedral-globose and trilete, or ellipsoidal and monolete, lacking chlorophyll.

This is an old family, with the four extant genera so highly diverse in habit and form that some authors prefer to segregate them into distinct families. *Mohria* is confined to Africa and Madagascar; *Anemia* is in America, Africa, and southern India; the other two genera are pantropic. All except *Mohria* occur throughout tropical America and are all well represented in Peru.

References

- LELLINGER, D. B. 1969. Schizaeaceae, in The botany of the Guayana Highland—Part VIII. Mem. New York Bot. Gard., 18: 1–11.
 MAXON, W. R. 1909. Schizaeaceae, in N. Amer. fl., 16: 31–52.

Key to Genera of Schizaeaceae

- a. Leaves erect or suberect; pinnae lacking arrested buds in branch axils; sporangia not covered by a laminar flange b

- b. Leaf pinnate or pinnately decomposed, rarely pinnatifid I. **Anemia**
- b. Leaf filiform or with dichotomous veins or branches III. **Schizaea**
- a. Leaves vinelike, spreading and scandent; pinnae short-stalked, with an arrested bud in the axil of the first, pseudodichotomous branch; sporangia each covered by a laminar flange . . II. **Lygodium**

I. Anemia

Anemia Sw., Syn. fil. 6, 155. 1806, *nom. conserv.* (sometimes as “*Aneimia*”). TYPE: *Anemia phyllitidis* (L.) Sw. (*Osmunda phyllitidis* L.). **Figure 6.**

Coptophyllum Gardn., London J. Bot. 1: 133. 1842. TYPE: *Coptophyllum buniifolium* Gardn. = *Anemia buniifolia* (Gardn.) Moore.
Anemirhiza J. Sm., Seemann, Bot. Voy. Herald 243. 1854. TYPE: *Anemirhiza adiantifolia* (L.) J. Sm. (*Osmunda adiantifolia* L.) = *Anemia adiantifolia* (L.) Sw.

Plants terrestrial. **Stem** decumbent to creeping, rarely erect, bearing short to long trichomes and fibrous roots. **Leaves** ca. 1–75 cm long, erect, partially (as in Peruvian species) dimorphic, with a pair of fertile pinnae at the base of or below the sterile lamina, or with similar leaves longer and more erect than the wholly sterile leaves, or wholly dimorphic, the whole leaf either sterile or fertile. **Sterile lamina** 1–2-pinnate (rarely pinnatifid); **veins** free, or rarely anastomosing without included free veinlets. **Sporangia** borne on fertile segments which are reduced to mere axes or have narrow borders of laminar tissue along the axes. **Spores** tetrahedral-globose, trilete.

The genus contains about 80 species, which occur in tropical to subtropical regions of both hemispheres, predominantly in the Neotropics. Species limits are not always clearly drawn, as diagnostic features are often quite variable, such as: relative length of fertile pinnae and sterile portion of lamina; color of rhizome indument; degree of dissection of pinnae. Color of trichomes is particularly difficult to assess, inasmuch as each observer sees colors in different ways, and definitions of color terms are usually difficult to interpret. Rhizome indument in *Anemia* generally grades from orange to reddish orange to red to brownish red; in many specimens the distinctions are clear, but in others they are somewhat inconstant. Hybridization is not uncommon in the genus and must be taken into consideration when attempting identification of collections. The following key will be more effective if attention is given to *combinations* of characters, whenever possible.

Reference

MICKEL, J. T. 1962. A monographic study of the fern genus *Anemia*, subgenus *Coptophyllum*. Iowa State Coll. J. Sci., 36: 349–482.

Key to Species of *Anemia*

- a. Fertile pinnae borne 3 mm or more below the base of the sterile lamina; ultimate fertile segments with narrow (but distinct) borders of laminar tissue along the axes b
- b. Sterile pinnae crenate to pinnatisect, not cut entirely to the costa (except rarely as to proximal lobes of basal pinnae) 2. **A. villosa**
- b. Sterile pinnae 1–2-pinnate c
- c. Apex of stem ascending or erect, covered with petiole bases; fertile pinnae commonly shorter than the sterile portion of the lamina d
- d. Petiole slender (less than 1 mm thick), dark brown; fertile pinnae suberect, with stalk 0.3–0.8 cm long 1. **A. clinata**
- d. Petiole stout (1–2 mm thick), commonly yellow; fertile pinnae erect, with stalk 1.5–5 cm long 3. **A. flexuosa**
- c. Apex of stem horizontal, exposed beyond the most recent petiole bases; fertile pinnae commonly longer than sterile portion of the lamina e
- e. Lamina hirsute to glabrate, petiole commonly glabrate and atropurpureous (rarely light brown to yellow) 4. **A. ferruginea**

- e. Lamina and petiole conspicuously lanate, petiole yellow 5. **A. myriophylla**
- a. Fertile pinnae borne at base of sterile lamina, or less than 1 mm below it; ultimate fertile segments with laminar tissue lacking or essentially so f
- f. Veins free; stalk of fertile pinnae usually 2–4 times the length of the panicle; sterile pinnae less than 4 cm long g
- g. Petiole (at least the fertile) 8–25 cm long; lamina gradually reduced to a pinnatifid apex (or rarely terminating in a subconform lanceolate segment); apex of sterile pinnae acute or subacute h
- h. Sterile pinnae mostly deeply incised, the segments commonly narrow and cuneate 6. **A. hirsuta**
- h. Sterile pinnae crenulate or denticulate, or rarely with a few deep lobes on several proximal pinnae 7. **A. pastinacaria**
- g. Petiole less than 6 cm long; lamina abruptly terminating in a broadly obovate or obdeltoid apical segment; apex of sterile pinnae broadly rounded 8. **A. oblongifolia**
- f. Veins anastomosing; stalk of fertile pinnae usually equaling or shorter than the panicle; sterile pinnae (larger ones) 5–14 cm long 9. **A. phyllitidis**

1. **Anemia clinata** Mickel, Amer. Fern J. 56: 58. 1966. TYPE: Peru, Junín, along Río Perené, Killip & Smith 21594 (holotype, US!; isotypes, F!, NY!).

Stem with apex ascending and thickly covered with petiole bases, densely provided with orange trichomes. **Leaves** 10–25 cm long, 4–9 cm broad, pilose to hirsute, the suberect fertile pinnae borne 8–16 mm below the sterile portion of the lamina; **petiole** dark brown, less than 1 mm thick. **Sterile lamina** 1-pinnate-pinnatisect to 2-pinnate, with 5–11 pairs of pinnae; **pinnae** dissected nearly or quite to the costa, the ultimate segments joined at the base or discrete, but broadly adnate, not stalked; **veins** free. **Fertile pinnae** suberect, usually shorter than the sterile portion of the lamina, short-petiolulate (stalk 0.3–0.8 cm long), the ultimate fertile segments with narrow bands of laminar tissue on each side of the axes.

In thickets and deep forests, 600–1300 m, Junín. Panama; Colombia and Venezuela to Bolivia and western Brazil.

One of the distinguishing features of *A. clinata* is the suberect or slightly spreading position of the fertile pinnae, which are rigidly erect in most species of *Anemia*. It is also one of the smaller and more delicate species, with slender, wiry petioles less than 1 mm thick.

Junín: Near La Merced, E of Quimiri Bridge, Killip & Smith 23591 (NY, US). Colonia Perené, Killip & Smith 25036 (F, NY, US). La Merced, Kunkel 564 (GH). Chanchamayo Valley, C. Schunke 78 (F, US).

2. **Anemia villosa** Willd., Sp. pl. ed. 4, 5: 92. 1810. TYPE: “America meridionale,” Humboldt & Bonpland (holotype, B, Herb. Willd. 19496; photos, GH, US). Venezuela, Prov. Cumaná, “Between Catuaro and Cariaco”: fide HBK., Nov. gen. sp. fol. ed. 1: 26. 1815.

Stem with apex ascending and thickly covered with petiole bases, or the apex horizontal and exposed beyond the most recent petioles, densely provided with orange to brownish red trichomes. **Leaves** 10–55 cm long, villous to hirsute, the erect fertile pinnae borne 3–18 mm below the base of the sterile portion of the lamina; **petiole** yellow to light brown, 1–2 mm thick. **Sterile lamina** 1-pinnate to pinnate-pinnatisect, with 7–19 pairs of pinnae; **pinnae** with rounded lobes, not cut entirely to the costa (except rarely as to proximal lobes of basal pinnae); **veins** free. **Fertile pinnae** erect, slightly shorter than to (more typically) somewhat longer than the sterile portion of the lamina, their stalks 1–5 cm long, the ultimate fertile segments with narrow bands of laminar tissue on each side of the axes.

On rocky, open slopes, 900–2000 m, Cajamarca, Amazonas, San Martín, Ayacucho, Cuzco.

Surinam to Colombia, south to Peru; east coast of Brazil.

This appears to differ only quantitatively from *Anemia flexuosa*, the latter with sterile pinnae more strongly dissected and, typically, with fertile pinnae shorter than the sterile portion of the lamina. Fertile pinnae of *A. villosa* are commonly longer

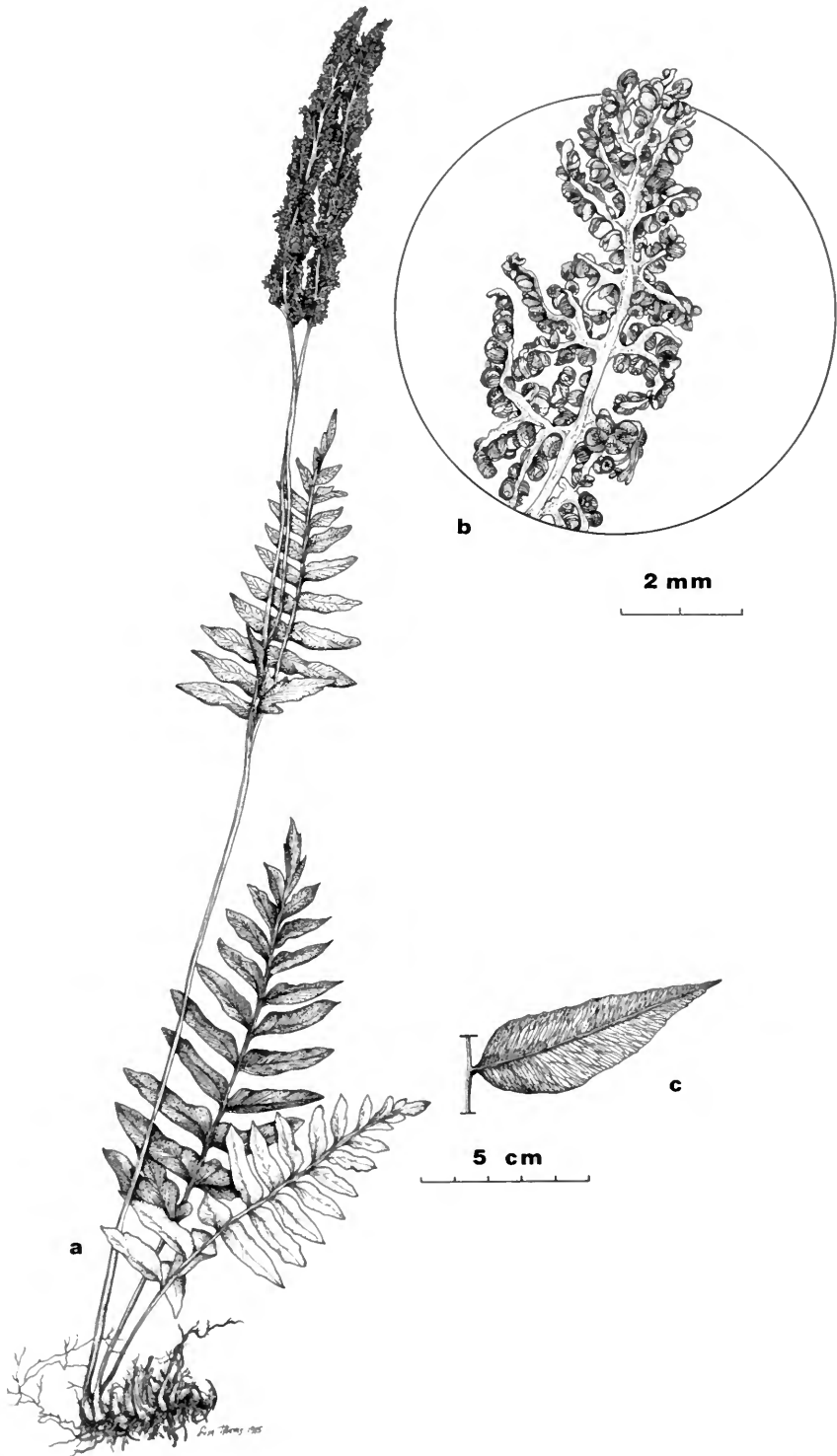


FIG. 6. *Anemia pastinacaria*: a, habit; b, apex of fertile pinna. *Anemia phyllitidis*: c, sterile pinna. (a–b from Irwin et al. 24260, Brazil, F; c from Stork & Horton 9432, F.)

than the lamina, but occasionally equal or exceed it. Evidently these are the reasons why Prantl considered it merely a variety of *A. flexuosa*. See Mickel (1962) for more detailed discussion.

Cajamarca: Prov. Jaén, San Patricio, Chontali, *Chimoy* 65 (USM). **Amazonas:** Prov. Chachapoyas, Caño Santa Lucia, *Wurdack* 599 (F, GH, NY, UC, US). **San Martín:** Tarapoto, in monte Campana, *Spruce* 4708 (GH, NY, P, US). **Ayacucho:** Prov. La Mar, Aina, *López & Soukup* 15.088 (GH). **Cuzco:** Prov. La Convención, Urusaiwa, *Vargas* 22349 (GH).

3. *Anemia flexuosa* (Savigny) Sw., Syn. fil. 156. 1806.

Osmunda flexuosa Savigny in Lam., Encycl. 4: 652. 1797. TYPE: based on undesignated specimen in Jussieu herbarium (not located).

Anemia flexuosa var. *setosa* Prantl, Unters. Morph. Gefässkrypt. 2: 95. 1881. SYNTYPES: Brazil, Lagoa Santa, *Warming* (not located); Peru, Cuchero, *Poeppig* (not located). ISOSYNTYPE: *Poeppig* (L; photos, GH, US).

Stem with apex ascending and thickly covered with petiole bases, densely provided with orange or reddish orange trichomes. **Leaves** 18–65 cm long, hirsute or glabrate, the erect fertile pinnae borne 5–25 mm below the base of the sterile portion of the lamina; **petiole** yellow to light brown, 1–2 mm thick. **Sterile lamina** 2-pinnate (sometimes 2-pinnate-pinnatifid), with 6–12 pairs of pinnae; **pinnae** (many of them) divided to the costa into broadly adnate, obtuse pinnules; **veins** free. **Fertile pinnae** erect, commonly shorter than the sterile portion of the lamina (rarely equal to it or slightly longer), their stalks 1.5–5 cm long, the ultimate fertile segments with narrow bands of laminar tissue on each side of the axes.

In thickets and open woods or on moist rocky slopes or clay banks, 900–3000 m, Amazonas, Huánuco, Junín, Ayacucho, Cuzco.

Surinam to Colombia, south to Bolivia.

Many Peruvian specimens of *Anemia flexuosa* are to be found in various herbaria; especially abundant are collections from Huánuco, Junín, and Cuzco. This is a highly variable species, particularly in the dissection of sterile laminae, sometimes 2-pinnate-pinnatifid, typically 2-pinnate, occasionally approaching the 1-pinnate-pinnatifid condition of *A. villosa* (q.v.) and thus is often confused with it. As in some other species of *Anemia*, this tends to hybridize; in fact there was a hybrid found in Cuzco: *A. flexuosa* × *A. phyllitidis*, *Var-*

gas 19836, Prov. La Convención, alt. 1650 m (GH). Leaves are much thinner in texture than typical *A. flexuosa*, with some anastomosing veins, and fertile pinnules are long-petiolulate.

Amazonas: Rodríguez de Mendoza, *Soukup* 5023 (US). **Huánuco:** Vilcabamba, on Río Chinchao, *Macbride* 4985 (F, NY, US), *Stork & Horton* 9876 (F, UC, US). **Junín:** Huacapistana, *Killip & Smith* 24152, 24324 (F, NY, US). **Ayacucho:** Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith* 22319 (F, GH, NY, US). **Cuzco:** Prov. La Convención, Valley of the Sambray, *Mexia* 8038 (F, GH, MO, UC).

4. *Anemia ferruginea* HBK., Nov. gen. sp. 1: 32. 1815, var. *ferruginea*. TYPE: Venezuela, Prov. Cumaná, “prope Guardia de San Augustin,” *Humboldt & Bonpland* (holotype, ♀?).

Stem with apex horizontal, and exposed beyond the most recent petioles, densely provided with red or brownish red trichomes. **Leaves** 10–55 cm long, the erect fertile pinnae borne 3–7 mm below the base of the sterile portion of the lamina; **petiole** commonly atropurpureous (rarely yellowish), glabrate, 1–2 mm thick. **Sterile lamina** 2-pinnate, hirsute to subglabrous, with 8–12 pairs of pinnae; **pinnae** dissected to the costa, the pinnules mostly discrete, adnate at base, acute or subacute at apex, sometimes those of proximal pinnae shallowly pinnatifid; **veins** free. **Fertile pinnae** erect, commonly longer than the sterile portion of the lamina, their stalks 1.5–6 cm long, the ultimate **fertile segments** with narrow bands of laminar tissue on each side of the axes.

In sunny places, open woods and clearings, on rocky slopes and clay banks, 850–2200 m, San Martín, Huancavelica, Cuzco.

Honduras; Guyana to Colombia, south along the Andes to Bolivia and Brazil.

The variety *ahenobarba* (Christ) Mickel, from Brazil, differs in its more deeply dissected pinnules with acute to acuminate tips. Both are difficult to distinguish from *Anemia tomentosa* (Savigny) Sw., especially var. *anthriscifolia* (Schrader) Mickel, from northern Argentina, Bolivia, Paraguay, and southeastern Brazil. See Mickel (1962) for further comments.

San Martín: Tarapoto, *Spruce* 4044 (GH, NY, P, US). **Huancavelica:** Prov. Tayacaja, Dist. Huachocolpa, near Quintabamba, *Tovar* 4157, 4693 (GH). **Cuzco:** Prov. Convención, Valley of the Sambray, *Mexia* 8038 (NY, US). Prov. Convención, Hacienda Sahuayaco, *Vargas* 1656 (GH, MO).

5. *Anemia myriophylla* Christ, Bull. Herb. Boissier 2(7): 793. 1907. TYPE: Bolivia, Padcaya, *Fiebrig 2541* (isotype, p).

Stem with apex horizontal and exposed beyond the most recent petioles, densely provided with reddish to orange trichomes. **Leaves** 20–50 cm long, the erect fertile pinnae borne 3–8 mm below the base of the sterile portion of the lamina; **petiole** yellow, conspicuously lanate, 1–2 mm thick. **Sterile lamina** 2- to nearly 3-pinnate, conspicuously lanate, with 7–12 pairs of pinnae; **pinnae** with pinules cut deeply or quite to the costule, the tips of ultimate segments commonly broadly rounded; **veins** free. **Fertile pinnae** erect, commonly longer than the sterile portion of the lamina, their stalks 1.5–5 cm long, the ultimate fertile segments with narrow bands of marginal tissue on each side of the axes.

On open slopes and rocky banks, 2000–2200 m, Cajamarca, Amazonas.

Peru; Bolivia; Argentina.

Anemia myriophylla has a more highly divided leaf than any *Anemia* in Peru. This and the densely lanate lamina and petiole make it rather easy to recognize.

Cajamarca: Between San Marcos and Cajabamba, *Correll & Smith P911* (GH, US). Prov. Celendín, *Sagástegui et al. 8457* (F, HUT, MO, UC). **Amazonas:** W of Chachapoyas on road to Caclic, *Hutchison & Bennett 4519* (F, GH, MO, NY, UC, US).

6. *Anemia hirsuta* (L.) Sw., Syn. fil. 155. 1806.

Osmunda hirsuta L., Sp. pl. 1064. 1753. LECTOTYPE (designated by Lellinger in Proc. Biol. Soc. Wash. 98: 387. 1985): Plumier, *Traité foug. Amér., t. 162*, based on a Plumier collection from Hispaniola.

Anemia hirsuta var. *humboldtiana* Hieron., Bot. Jahrb. Syst. 34: 566. 1905. LECTOTYPE (designated by Lellinger in Proc. Biol. Soc. Wash. 98: 366. 1985): Venezuela, border Edo. Sucre-Monagas, *Humboldt 459* (b, *Herb. Willd. 19495-2*; photos, GH, US).

Stem short-creeping, densely provided with orange trichomes. **Leaves** to 35 cm long and 5 cm broad, glabrate or somewhat villous on axes and lamina, the erect, fertile pinnae borne at the base of the sterile portion of the lamina; **petiole** (at least on fertile leaves) 8–18 cm long. **Sterile lamina** pinnate-pinnatifid to nearly 2-pinnate, with 7–12 pairs of pinnae, gradually tapering to a pinnatifid apex;

pinnae to 2.5 cm long and 0.8 cm broad, commonly inequilateral at base, truncate acroscopically and cuneate basiscopically, obliquely incised into linear or narrowly cuneate segments, obtuse to subacute at apex; **veins** free. **Fertile pinnae** to 18 cm long, the stalk (1.5–)2–3 times the length of the panicle, the ultimate fertile segments essentially lacking laminar tissue.

In dry, grassy areas, on slopes or mesas, 1200–2150 m, Huánuco, Cuzco.

Mexico to Panama; Greater Antilles; Trinidad & Tobago; Venezuela and Colombia south to Bolivia and Brazil.

This is scarcely distinct from *Anemia pastinacaria*, essentially differing only by the characters noted in the key. More detailed studies are needed to clarify relationships of the several variable taxa of the *A. hirsuta* group which, furthermore, appear to hybridize readily with a number of other species of *Anemia* throughout the entire range. For example, there is a specimen of *A. pastinacaria* at Paris (San Martín, Tarapoto, *Spruce 4134*) which also contains a very large, highly dissected leaf with abortive spores—possibly a hybrid between *A. hirsuta* and *A. phyllitidis*.

Huánuco: Muña, *Bryan 427* (F, GH). In grass steppe, *Woytkowski 219* (UC). **Cuzco:** Quillabamba, *Coronado 124* (UC). **Dept. Unknown:** *Mathews 3299* (US).

7. *Anemia pastinacaria* Prantl, Unters. Morph. Gefässkrypt. 2: 110. 1881. LECTOTYPE (designated by Lellinger in Proc. Biol. Soc. Wash. 98: 367. 1985): Venezuela, “in convalli del Tigre,” *Moritz 26* (b; probable isolectotype, GH!). **Figure 6a-b.**

This differs from *Anemia hirsuta* essentially only in the following characters: **Leaves** to 45 cm long and 7 cm broad. **Sterile lamina** gradually tapering to a pinnatifid apex, but occasionally with a distinct, nonconform apical segment; **pinnae** to 3.5(–5) cm long and 1.5(–2) cm broad, margins denticulate or crenate, or rarely with a few deep lobes on several proximal pinnae.

On dry, rocky slopes or in forest clearings, 750–2000 m, San Martín, Loreto, Huánuco, Junín, Ayacucho, Cuzco.

Mexico to Panama; Cuba; Jamaica; Trinidad; Surinam to Colombia, south to Bolivia and Brazil.

This and *Anemia hirsuta* differ only in their relative size and depth of dissection of pinnae, and

a few specimens in Peru tend to be intermediate even in these characters. See *A. hirsuta* for further discussion.

San Martín: Tarapoto, *Spruce 4134* (P in part). **Loreto:** Yanayacu, *Bües 1037* (US). **Huánuco:** Yanano, *Macbride 3816* (F, US). **Junín:** Prov. Huancayo, Pariahuanca, *Tovar 7948a* (USM). **Ayacucho:** Aina, between Huanta and Río Apurímac, *Killip & Smith 22614* (F, NY, US). **Cuzco:** Prov. Convención, Hacienda Sahuayaco, *Vargas 1655* (GH), *1657* (GH, MO).

8. *Anemia oblongifolia* (Cav.) Sw., Syn. fil. 156. 1806.

Osmunda oblongifolia Cav., Icon. 6: 69, t. 592, f. 2. 1801. TYPE: Panama, *Née* (holotype, MA), verified by C. Christensen [Dansk. Bot. Ark. 9(3): 31. 1937].

Osmunda humilis Cav., Icon. 6: 69, t. 592, f. 3. 1801. TYPE: Panama, Taboga Island, *Née* (not located); earlier presumed at MA, but not seen by C. Chr. [Dansk. Bot. Ark. 9(3): 31. 1937].

Anemia humilis (Cav.) Sw., Syn. fil. 156. 1806.

Anemia oblongifolia var. *humilis* (Cav.) Hooker & Baker, Syn. fil. 431. 1868.

Stem decumbent, rather densely provided with orange trichomes. **Leaves** to 30 cm long and 3.5 cm broad, sparsely to densely villous on axes and lamina, the erect fertile pinnae borne at the base of the sterile portion of the lamina; **petiole** commonly less than 6 cm long. **Sterile lamina** 1-pinnate, with 2–9 pairs of pinnae, abruptly terminating in an obovate or obdeltoid apical segment which is often as broad as long; **pinnae** to 1.8 cm long and 0.7 cm broad, strongly inequilateral at base, truncate or rounded acroscopically and cuneate basiscopically, broadly rounded at apex, the margins crenulate or subentire; **veins** free. **Fertile pinnae** to 18 cm long, the stalk 2–4 times the length of the panicle, the ultimate **fertile segments** essentially lacking laminar tissue.

In forests, on rocky slopes, 1000–1100 m, Cuzco.

Mexico to Panama; Venezuela to Brazil and Bolivia.

Anemia oblongifolia is rather distinctive in its coarse pinnae which are broadly rounded at their tips and often nearly as broad as long. Sterile leaves are commonly very short-petiolate (often subsessile), and typically are so densely caespitose that they give the appearance of a rosette. Some authors have separated *A. humilis* on the strength of its villous sterile pinnae with crenulate margins; but

these characters are too variable and inconsistent to be of real value. We tentatively maintain it here as a synonym, although we have not seen the type to fully substantiate this.

Cuzco: Echarate, Camino de Sahuayacu, *Bües 845* (US). Cochayoc, *Bües 1712, 1719* (US). Prov. Convención, Valle de Lucumayo–Pistipata, *Vargas 4176* (MO, UC, US).

9. *Anemia phyllitidis* (L.) Sw., Syn. fil. 155. 1806. **Figure 6c.**

Osmunda phyllitidis L., Sp. pl. 1064. 1753. TYPE: based on illustration of Hispaniola plant in Plummer, *Traité foug. Amér.*, t. 156. 1705.

Anemia haenkei Presl, Reliq. haenk. 1: 74. 1825. TYPE: Peru, "in vallibus Cordillerarum Peruviae," *Haenke* (holotype, PRC?).

Stem decumbent (rarely short-creeping), rather densely clothed with orange or brownish trichomes. **Leaves** to 80 cm long and 20 cm broad, the erect fertile pinnae borne at the base of the sterile portion of the lamina or less than 1 mm below it; **petiole** (at least on fertile leaves) ca. 10–35 cm long. **Sterile lamina** 1-pinnate, with 3–7 pairs of pinnae and a conform apical one; **pinnae** (larger ones) 5–14 cm long and 1.3–3 cm broad, subequilateral, ovate to lanceolate, acute to acuminate, the margins crenulate to dentate (or rarely the basal pair lobed); **veins** copiously anastomosing. **Fertile pinnae** to 40 cm long, the stalk equaling or (commonly) shorter than the panicle; the ultimate **fertile segments** essentially lacking laminar tissue.

Moist, often rocky slopes and ravine banks, in and at edges of forests, 700–1700 m, Amazonas to Loreto, south to Huancavelica and Cuzco.

Mexico to Panama; Greater Antilles; Trinidad; Venezuela and Colombia to Argentina and Uruguay.

This is one of the most common species of *Anemia* in Peru and, with its large, subentire pinnae and reticulate venation, is the easiest to recognize.

Amazonas: Prov. Bagua, S of Bagua Grande on Río Utcubamba, *Hutchison 1479* (UC, US). **San Martín:** Zepelacio, near Moyobamba, *Klug 3440* (F, MO, NY, UC, US). **Loreto:** Yanayacu, *Bües 2005* (US). **Huánuco:** Prov. Huánuco, Puente Durand, *Stork & Horton 9432* (F, GH, MO, UC, US). **Pasco:** Oxapampa, *Soukup 2361* (F, GH). **Junín:** Yucapata, *Woytkowski 6642* (GH, MO, US). **Huancavelica:** Prov. Tayacaja, SE of Tintay, *Tovar 4611* (GH). **Ayacucho:** Aina, between Huanta and Río Apurímac, *Killip & Smith 22719* (NY, US). **Cuzco:** Prov. La Con-

vención, upper valley of Río Sanbray, *Mexia 8056a*, (F, GH, UC, US).

Comments

Anemia hispida Kunze, *Linnaea* 9: 20. 1834.

TYPE: "In fruticetis ad Chibangata fl. Peruv.," 1829, *Poeppig diar.* 1165 (LZ? destroyed, B?, w?).

Apparently known thus far only from the type collection.

Kunze's plant was described as having: creeping rhizome; pinnate, hispid leaves; fertile pinnae twice as long as the sterile lamina; pinnae remote, patent, sessile, dimidiate, oblong, obtuse, with margins crenate or subincised. He likened it to *Anemia repens* Raddi (= *A. hirsuta?*), but having pinnae less incised. Assuming it belongs to subg. *Anemia* (unsubstantiated by the description), it could be *A. pastinacaria*, but we cannot be certain without examining the type.

II. Lygodium

Lygodium Sw., *J. Bot. (Schrader)* 1800(2): 106. 1802, *nom. conserv.* TYPE: *Lygodium scandens* (L.) Sw. (*Ophioglossum scandens* L.). **Figure 7.**

Plants terrestrial. **Stem** slender, short- to long-creeping, provided with short trichomes. **Leaves**

Key to Species of Lygodium

- a. Primary pinna-branch pinnate, the pinnules stalked, except sometimes near the apex of the primary branch b
- b. Pinnules (at least fertile ones) diminishing in size toward the apex of the primary branch, mostly expanded at base into lobes, the lobes often discrete or even stalked 1. **L. venustum**
- b. Pinnules subequal, not expanded at base, subentire, very rarely some basal ones lobed at the base 2. **L. volubile**
- a. Primary pinna-branch radiate, the ultimate segments deeply lobed, joined at the base 3. **L. radiatum**

1. *Lygodium venustum* Sw., *J. Bot. (Schrader)* 1801(2): 303. 1803. TYPE: Jakob Breyne, *Cent. I, t. 96.* 1678, not "Brazil, *Breynius*" (designated by Proctor, *Flora Lesser Antilles* 2: 51. 1977), a specimen which probably does not exist. **Figure 7a.**

Pinna-stalks 2–10 mm long, moderately to densely pubescent with tawny to orange pluricel-

l–10 m long, vinelike, indeterminate, spreading and scandent, partially dimorphic, the fertile portions somewhat contracted with marginal fertile lobes, pinnate, glabrous to somewhat pubescent. **Pinnae** short-stalked, pseudodichotomously branched with an arrested bud in the axil, each primary pinna-branch radiately lobed or branched or pinnate. **Veins** reticulate or (in Peruvian species) free. **Sporangia** borne separately on marginal lobes of a pinna segment or on a wholly fertile segment, each covered by a laminar outgrowth (flange). **Spores** tetrahedral-globose, trilete.

Lygodium is a natural group, easily distinguished within the family by its long leaves and vinelike and scrambling habit, often climbing to considerable heights by twining around the smaller branches of shrubs and trees. It is widely distributed, primarily pantropic, with several extratropical species both in the New and Old World. There are 30–35 species, but the number could be somewhat reduced by further study, as some appear to intergrade rather freely. Three species are recognized in Peru.

References

DUEK, J. J. 1978. *Feddes Repert.*, **89**: 411–423.
TRYON, R. M., AND A. F. TRYON. 1982. *Lygodium*, pp. 69–76, in *Ferns and allied plants*, Springer-Verlag, New York.

lular trichomes. Primary **pinna-branches** pinnate to (rarely) 2-pinnate, sessile to short-stalked, broadly to narrowly deltoid. **Fertile pinnules** 9–21, alternate and commonly widely spaced, all but the distal ones stalked, stalk often nodose at its juncture with pinnule base, sparsely to abundantly pilose on axes, veins and (occasionally) the leaf tissue, larger ones 2.5–5 cm long, gradually diminishing in size toward the apex of the primary

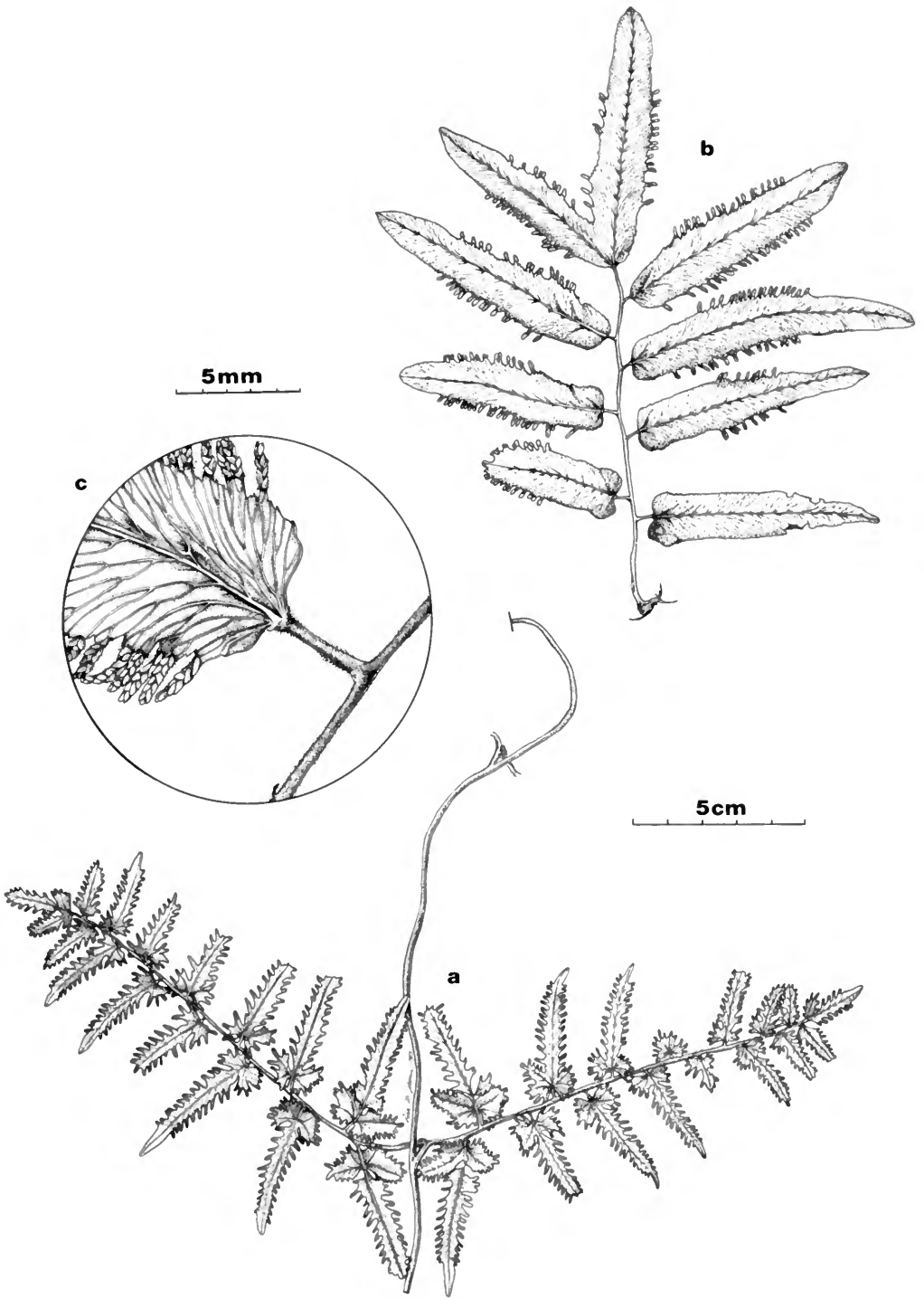


FIG. 7. *Lygodium venustum*: a, primary axis and pair of pinnae. *Lygodium volubile*: b, pinna; c, base of pinnule. (a from Irwin *et al.* 21469, Brazil, F; b from Jeanpert *s.n.*, Brazil, F; c from L. B. Smith 1352, Brazil, F.)

branch, most of them expanded at base into lobes, the lobes rounded to cordate or subpalmate. **Sterile pinnules** similar to the fertile, but often larger and not much reduced toward the apex of the primary branch. **Veins** free, 1–several times-forked, prominulous.

Along roadsides and stream banks, in fields or in thickets and open forests, usually twining over low shrubs, 100–1000 m, San Martín, Loreto, Huánuco, Junín, Ucayali, Cuzco.

Tropical America.

This species is widely distributed throughout the Neotropics. A number of other species have been confused with it or should be included within it. For detailed discussions see Smith, *Flora of Chiapas: Pteridophytes*, Calif. Acad. Sci. p. 145. 1981, and Stolze, *Ferns & Fern Allies of Guatemala: Part I*, Fieldiana, Bot. 39: 38. 1976. The closely related *Lygodium volubile* readily can be distinguished by the fewer, larger, and subequal pinnules on each pinna-branch; i.e., the distal ones are nearly or quite as large as the proximal ones. Pinnules (at least fertile ones) of *L. venustum* gradually diminish in size and shape so that subapical ones are often one-third to one-half the size of those near the pinna base. The Breyne plate was cited by Swartz and is clearly this species.

San Martín: Dist. San Martín, 2 km NW of Tarapoto, *Belshaw 3353* (F, GH, MO, NY, UC, US). Juan Jui, Alto Río Huallaga, *Klug 4218* (F, GH, MO, NY, UC, US). **Loreto:** Puerto Arturo, lower Río Huallaga below Yurimaguas, *Killip & Smith 27847* (NY, US). **Huánuco:** Prov. Leoncio Prado, Huachipa, *Plowman 5957* (F, GH). **Junín:** La Merced, *Killip & Smith 23379* (F, NY, US). **Ucayali:** Pucallpa (as Loreto), *Soukup 3049* (F). **Cuzco:** Santa Ana, *Cook & Gilbert 1614* (US).

2. *Lygodium volubile* Sw., J. Bot. (Schrader) 1801(2): 304. 1803. TYPE: Jamaica, Swartz (holotype, s-PA; photo, US). **Figure 7b-c.**

Lygodium micans J. W. Sturm in Mart., Fl. bras. 1(2): 178. 1859. TYPE: "British Guiana," *Schomburgk 399* (holotype, B).

Pinna-stalks 0.5–3 mm long, essentially glabrous. Primary **pinna-branches** pinnate or (very rarely) 2-pinnate at base, the pinnae stalked (1.5–5 cm), broadly oblong. **Fertile pinnules** 4–10, alternate and widely spaced, conspicuously stalked, nodose and often articulate at juncture with the pinnule base, glabrous to sparsely pilose on axes and veins (especially at bases of sporangia), 6–14

cm long, proximal and distal ones subequal, broadly cuneate to truncate at base, only rarely lobed at base. **Sterile pinnules** similar to the fertile, but often somewhat larger. **Veins** free, several times-forked, prominulous.

In wet, often inundated, lowland forests and open fields, scandent on shrubs and low trees, often along stream and river banks, sea level to 250 m, Amazonas, San Martín, Loreto, Madre de Dios.

Southern Mexico; Guatemala; Belize; Panama; Greater Antilles; Trinidad; Venezuela to the Guianas, south to Argentina and Brazil.

This and *Lygodium micans* have been separated on the basis of several, variable, quantitative characters, although these may appear more distinct in certain regions outside South America: relative size and shape of ultimate segments and their bases; degree of pubescence on abaxial surface; angle of veins. None of these are consistently correlated in the many Peruvian specimens examined.

Amazonas: Quebrada Huampami, *Kayap 1066* (MO). **San Martín:** Prov. San Martín, Laguna Sauce, *Ramírez & Sotero 092-85* (F, GH, HUT). **Loreto:** Río Tacsha Curaray, *Croat 20394* (F, GH, MO, NY). Gamitanacocho, Río Mazán, *J. Schunke 234* (F, GH, NY, UC, US). **Madre de Dios:** El Pilar, *López & Soukup 4601* (GH).

3. *Lygodium radiatum* Prantl, Unters. Morph. Gefässkrypt. 2: 66. 1881. TYPE: based on *L. digitatum* D. C. Eaton.

Lygodium digitatum D. C. Eaton, Mem. Amer. Acad. Arts n.s. 2, 8: 217. 1860 (not Presl, 1825). LECTOTYPE (inferentially designated by Dück, Feddes Repert. 89: 417. 1978): Panama, Gatun, *Hayes 25* (YU; isolectotype, US!).

Pinna-stalks reduced to short (0.5 mm) projections along the primary axis (or sometimes obsolete). Primary **pinna-branches** long-stalked (1.5–4 cm), the pinnae radiate (subpalmate), divided nearly to the base into (2)3–7 ultimate segments. **Fertile ultimate segments** linear-lanceolate to narrowly oblanceolate, 5–15 cm long and 1.5–2 cm broad, the margins serrate, glabrous, or sparsely pubescent along the midrib. **Sterile segments** similar to the fertile, but often somewhat longer (to 25 cm). **Veins** free, mostly 1- or 2-forked, prominulous.

Rare, in wet forests, often along stream and river banks, scandent on shrubs and small trees, 135–850 m, Amazonas, Loreto, Pasco, Ucayali.

Panama; Colombia; Ecuador; Peru.

Amazonas: Al lado de Huampami, *Kayap 1217* (MO, US). **Loreto:** Santa Rosa, lower Río Huallaga below Yurimaguas, *Killip & Smith 28937* (F, GH, NY, US). Puerto Meléndez, below Pongo de Manseriche, *Tessmann 4735* (NY). **Pasco:** Prov. Oxapampa, west side of Cordillera de San Matías, *D. Smith 2011* (F, MO). **Ucayali:** Prov. Coronel Portillo, km 89 Carretera Federico Basadre, *C. Vásquez 1* (USM).

Comments

Lygodium oligostachyum (Willd.) Desv., *Mém. Soc. Linn. Paris* 6: 205. 1827.

Hydroglossum oligostachyum Willd., *Sp. pl. ed. 4*, 5: 81. 1810. TYPE: Plumier, *Traité foug. Amér.*, t. 92. 1705 (based on specimens from Haiti, near Lake Miragoan).

This is similar in general aspect to *Lygodium venustum*, but differs in the conspicuously 2-pinnate pinnae and the strongly flexuous (zigzag) and more delicate primary and secondary pinna rachises. Although *L. oligostachyum* has been considered by most authors to be confined to Hispaniola, Duek (1978) assigned to it a broad distribution (West Indies; parts of Central and South America) and cited two specimens at Prague from Peru: *Poeppig* and *Cuming*, neither of which he had examined. Under *L. oligostachyum* he also placed *L. mexicanum* Presl and two varieties of *L. polymorphum* (Cav.) HBK. (*illeg.*); however, plants usually identified under either name have usually turned out to be *L. venustum*. We have not seen the *Poeppig* and *Cuming* collections in question, but they are probably *L. venustum* and not *L. oligostachyum* as suggested. All specimens of the latter which we have examined in various herbaria have been collected in Hispaniola, so it is unlikely to be found in Peru.

III. Schizaea

Schizaea Sm., *Mém. Acad. Roy. Sci. (Turin)* 5: 419. 1793, *nom. conserv.* TYPE: *Schizaea*

Key to Species of Schizaea

- a. Leaves with lamina obviously foliaceous, flabelliform in general outline, the divisions linear-oblong to obovate l. *S. elegans*
- a. Leaves not or scarcely foliaceous, but filiform and grasslike or, if flabelliform in outline, then the divisions filiform b
- b. Sporangiphore pinnatifid, its segments bearing sporangia in a single row on each side of the vein c

dichotoma (L.) Sm. (*Acrostichum dichotomum* L.). **Figure 8.**

Lophidium Rich., *Actes Soc. Hist. Nat. Paris* 1: 114. 1792. TYPE: *Lophidium latifolium* Rich. = *Schizaea elegans* (Vahl.) Sw.

Actinostachys Wall., Numerical list of plants in East Indies Company Museum, 1. 1829, description from R. Br., *Prod.* 162. 1810. TYPE: *Actinostachys digitata* (L.) Wall. (*Acrostichum digitatum* L.) = *Schizaea digitata* (L.) Sw.

Plants terrestrial. **Stem** erect or ascending, rather densely provided with septate trichomes and with slender, fibrous roots. **Leaves** ca. 5–50 cm long, caespitose, long-petiolate, glabrous or with scattered, small trichomes, slightly to partially or wholly dimorphic, fertile ones with elongate fertile segments borne pinnately or subdigitately at the apex of laminar axes which are simple or dichotomously branched. **Lamina** filiform, grasslike and scarcely or not at all foliaceous, or fusiform to flabelliform (in general outline) and foliaceous. **Veins** free. **Sporangia** crowded in 1 or more rows on the scarcely foliaceous segments (sporangio-phores). **Spores** ellipsoidal, monolete.

Schizaea sometimes has been divided into several genera or subgenera on the basis of the more expanded, foliaceous lamina (*Lophidium*) or the subdigitate (*Actinostachys*) versus pinnate (*Schizaea*) fertile branches, as well as some differences in the gametophytes. Nevertheless, the groups are quite closely allied and are here treated as a single genus. About 30 species occur in tropical or extratropical regions of both hemispheres, five of which are found in Peru.

Reference

TRYON, R. M., AND A. F. TRYON. 1982. *Schizaea*, pp. 76–83, in *Ferns and allied plants*, Springer-Verlag, New York.

- c. Leaves 0–2 times dichotomous, monomorphic; axis of the sporangiophore straight to slightly curved at maturity d
- d. Leaves 7–10 cm long, unbranched; sporangiophores with 5–7 pairs of ultimate segments 2. *S. pusilla*
- d. Leaves (12–)15–50 cm long, simple to once or twice acutely and dichotomously branched; sporangiophores with (10–)12–25 pairs of ultimate segments 3. *S. incurvata*
- c. Leaves 3–6 times dichotomous, dimorphic; axis of the sporangiophore strongly curved at maturity 4. *S. poeppigiana*
- b. Sporangiophore subdigitate, its segments bearing sporangia in 2 or more (sometimes indistinct) rows on each side of the vein 5. *S. pennula*

1. *Schizaea elegans* (Vahl) Sw., J. Bot. (Schrader) 1800(2): 103. 1801. **Figure 8.**

Acrostichum elegans Vahl, Symb. bot. 2: 104, t. 50. 1791. TYPE: Trinidad, von Rohr (c).
Schizaea flabellum Mart., Icon. pl. crypt. 115, t. 55. 1834. TYPE: Brazil, Prov. Rio Negro, Martius (holotype, BR; isotype, B; photo, US of B).
Lophidium elegans (Vahl) Presl, Suppl. tent. pterid. 77. 1845.
Lophidium flabellum (Mart.) Presl, Suppl. tent. pterid. 77. 1845.

Leaves 20–80 cm long, petiole 15–65 cm long, 1–2.5 mm in diameter, subterete, obtusely angled abaxially. **Lamina** subcoriaceous, essentially glabrous, flabelliform (in general outline), 1–several times-dichotomously forked or cleft, the divisions oblong to obovate, lateral margins entire, distal ones strongly and sharply lacerate. **Veins** dichotomously forked within the ultimate divisions. **Sporangiophores** borne along the distal margins of the lamina, pinnately branched at the tips of the marginal lacerations. **Sporangia** in a single row on each side of the vein.

In humus on forest floor, or in sandy or rocky soil on wooded slopes and ridges, 130–2200 m, Amazonas, San Martín, Loreto, Huánuco, Pasco, Junín, Cuzco.

Southern Mexico to Panama; Trinidad to Colombia, and south to Bolivia and Brazil.

Several varieties have been recognized, based upon number and shape of laminar divisions, characters which do not appear to merit distinction.

Amazonas: Mendoza, *Woytkowski 8211* (GH, MO). **San Martín:** Zepelacio, near Moyobamba, *Klug 3415* (F, GH, MO, NY, US). **Loreto:** Balsapuerto, *Klug 2885* (F, GH, MO, NY, US). **Huánuco:** Prov. Huánuco, Tingo María, *Tryon & Tryon 5292* (BM, GH, NY, U, UC, US, USM). **Pasco:** Prov. Oxapampa, Cordillera San Matías, *León 324* (F, GH). **Junín:** La Merced, Hacienda Schunke, *Macbride 5601* (F, US). **Cuzco:** Valle de Urubamba, Machu Picchu, *Herrera 3299* (US).

2. *Schizaea pusilla* Pursh, Fl. Amer. sept. 2: 657. 1814. TYPE: United States, New Jersey, Burlington Co., Quaker Bridge, *Pursh?* (not located).

Leaves unbranched, 7–10 cm long, linear, grass-like, with expanded lamina essentially lacking, petiole 0.4–0.5 mm broad, rather flattened, or subterete at base, sterile and fertile leaves erect and straight or slightly flexuous, fertile ones apically bearing a pinnatifid, conduplicate, scarcely foliaceous sporangiophore. **Sporangiophore** 0.5–0.7 cm long, with 5–7 pairs of linear segments, abundantly provided on the margins and among the sporangia with deep orange to reddish brown, flexuous trichomes. **Sporangia** in a single row of 5–7 on each side of the vein.

Thus far known only from Pasco, “plant colonizing sandy, wet landslide; shrubland on white sandstone, 2700–2800 m.”

United States (New Jersey, New York); Canada (Newfoundland, Nova Scotia).

Heretofore, *Schizaea pusilla* has been known to occur only in a few scattered locations in north-eastern North America. The recent collection in Pasco duplicates the northern plants in every feature (including spores) except that the sterile leaves are straight to slightly flexuous instead of conspicuously curling. The great disjunction in distribution is at first startling until one understands the problems of encountering this very inconspicuous fern. This and the other diminutive species of *Schizaea* (like those of Ophioglossaceae and Hymenophyllaceae) are very difficult to detect. Hence true distribution patterns may never come to light. It is most closely allied to *S. incurvata*, under which see further discussion. Less closely related is the Old World *S. fistulosa* Labill. and its variety *australis* (Gaud.) Fosb. from Chile and Argentina, which differ in the lack of pubescence on



FIG. 8. *Schizaea elegans*: a, habit; b, sporangiophore; c, sporangiophore segment, abaxial side; d, sporangiophore segment, adaxial side. (From Stolze, Ferns and fern allies of Guatemala, 1976.)

the sporangiophore and in the erose-lacerate margins of the fertile ultimate segments.

Pasco: Oxapampa, Cordillera de Yanachaga, Cerro Pajonál, *Foster 9065* (F, GH, MO, US).

3. ***Schizaea incurvata*** Schkuhr, 24 Kl. Linn. Pfl.-Syst. 1: 138, *t. 137*. 1809. TYPE: "British Guiana, habitat in India Occidentali circa Essequibum," *Gärtner* (not located).

Leaves simple to 1- or 2-forked at an acute angle (branches subparallel), mature ones (12–)15–50 cm long, linear, grasslike, with an expanded **lamina** essentially lacking, petiole 0.6–0.8 mm in diameter, convex abaxially, shallowly sulcate adaxially, somewhat flattened, or terete at base, sterile and fertile leaves straight or slightly flexuous, fertile ones apically bearing a pinnatifid, conduplicate, scarcely foliaceous sporangiophore. **Sporangiophore** 1.2–3 cm long, with (10–)12–25 pairs of linear segments, abundantly provided on the margins and among the sporangia with pale to light brown, flexuous trichomes. **Sporangia** in a single row of (8–)10–18 on each side of the vein.

Thus far known from a single collection (dept. unknown) in Peru; elsewhere in open woods or clearings and savannas, in sand or sandy or rocky soil, sea level to 400 m.

Surinam to Venezuela and northern Brazil; Peru.

Of the many specimens seen by us in various herbaria, only one was (possibly) collected in Peru: *Poeppig* (NY). The label is worded simply "In Peruvia, diar. Kunze, 1834." However, Kunze (*Linnaea* 9: 19. 1834) lists only one species of *Schizaea* from Peru (41. *S. dichotoma*), which is *S. poeppigiana*. Since there is no "Diar." number on the label of the New York sheet, the data are suspect. That the collecting site is correctly designated is also problematical, for the known range of the species is somewhat remote from Peru. However, as noted in the discussion of *S. pusilla* (q.v.), the grasslike appearance of several species of *Schizaea* masks them well in any savanna-type vegetation, so that more specimens may yet be discovered throughout the Neotropics after diligent search, especially in Peruvian Amazonia in sandy areas. *Schizaea pusilla* is similar to *S. incurvata*, both in general habit and pubescence of the sporangiophore, but the two are easily separated by the characters noted in the key.

4. ***Schizaea poeppigiana*** J. W. Sturm in Mart., Fl. bras. 1(2): 181. 1859. SYNTYPES: Peru, "ad Ventanilla de Cassapillo, 1829," *Poeppig* (w?); "British Guiana, in montibus Canuku," *Rich. Schomburgk 1189* (B).

Lophidium poeppigianum (J. W. Sturm) Underw., N. Amer. fl. 16: 38. 1909.

Leaves dichotomous, 12–40 cm long, dimorphic; petiole 10–30 cm long, ca. 1 mm broad, convex abaxially, flattened to concave adaxially, sparsely to amply pilose. **Sterile lamina** circular in outline (often appearing conduplicate and flabelliform after pressing), 5–8 times dichotomously forked, the divisions linear, scarcely or slightly foliaceous. **Fertile lamina** on somewhat longer petioles than the sterile, 3 or 4 times dichotomous, the divisions linear, nonfoliaceous, bearing sporangiophores at their apices. **Sporangiophores** 1.5–2 cm long, with 12–25 pairs of linear segments, amply provided on the segment margins and among the sporangia with pale to light brown, flexuous trichomes. **Sporangia** in a single row of 15–25 on each side of the vein.

Thus far known in Peru only from one of the syntypes.

Greater Antilles; Mexico (Chiapas); Costa Rica to Venezuela and Guyana; Peru; Bolivia.

5. ***Schizaea pennula*** Sw., Syn. fil. 150, 379. 1806. TYPE: "America meridionalis ... habitat in America calidiore" (holotype, S-PA).

Actinostachys pennula (Sw.) Hooker, Gen. fil., *t. 111a*. 1842.

Leaves ca. 12–50 cm long, unbranched, linear, grasslike, with expanded **lamina** essentially lacking; petiole 1–1.8 mm broad, triquetrous and the faces sulcate, often flattened apically and subterete at base, sterile and fertile leaves erect and straight or slightly flexuous, fertile ones apically bearing a subdigitate, scarcely foliaceous sporangiophore. **Sporangiophore** 1–4 cm long, with 6–14 linear, strongly ascending segments, these essentially with entire and glabrous margins, and with abundant, flexuous, reddish brown trichomes interspersed among the sporangia. **Sporangia** in 2 or more (sometimes indistinct) crowded rows on each side of the vein.

In sand and sandy soil of open forests and clearing, sea level to 260 m, San Martín, Loreto.

Costa Rica; Puerto Rico; Guadeloupe; Trinidad; Surinam to Colombia, south to Bolivia and Brazil.

San Martín: Chazuta, Río Huallaga, *Klug 3986* (F, GH, MO, NY, UC, US). **Loreto:** San Juan, vicinity of Iquitos, *Asplund 14414* (F, P, NY, US). Dist. Iquitos, Maynas, Quebrada Shushuna, *Rimachi 3995* (F, NY), *4870* (NY).

Family 5: GLEICHENIACEAE

Gleicheniaceae (R. Br.) Presl, Reliq. haenk. 1: 70. 1825, as Order *Gleicheniae* R. Br., Prod. 160. 1811, as Tribe of Filices. TYPE: *Gleichenia* Sm.

Terrestrial. **Stem** long-creeping, bearing trichomes and/or scales. **Leaves** 20 cm long, erect, to over 5 m long and scandent or trailing, often forming dense thickets, circinate in vernation, monomorphic, once or several times pseudodichotomously branched (rarely simple or with several 2-pinnate pinnae), indeterminate, with a permanently arrested bud at the fork of its branches, or the lamina partially pinnately branched, the rachis (and sometimes pinna-rachis) with a periodically dormant bud between the last developed branches, a pair of accessory foliaceous segments sometimes present at the base of otherwise usually naked axes, in addition to stipule-like segments borne *within* the forks. **Lamina** bearing scales and/or trichomes. **Veins** free. **Penultimate segments**

pinnatisect (rarely pinnate) pectinate. **Sporangia** borne in exindusiate sori on the abaxial surface of ultimate segments, with a short many-rowed stalk of cells and a central to oblique or nearly apical annulus not interrupted by the stalk. **Spores** monolete or trilete, lacking chlorophyll, 120 to ca. 800 in each sporangium.

The pseudodichotomous branching of leaves and the usually pectinate penultimate segments make this one of the most distinctive of fern families. These ferns frequently are found in dry, open areas and species with larger leaves sometimes spread over low shrubs to form dense thickets. Approximately 120 species have been recognized by various authors in as many as eight genera. The following treatment is based generally on the classification of Holttum (1957). Two genera are recognized in Peru.

References

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- MAXON, W. R. 1909. Gleicheniaceae, in *N. Amer. fl.*, **16**: 53–63.
- NAKAI, T. 1950. A new classification of Gleicheniales. *Bull. Natl. Sci. Mus.*, **29**: 1–71.
- UNDERWOOD, L. M. 1907. American ferns VIII. A preliminary review of the North American Gleicheniaceae. *Bull. Torrey Bot. Club*, **34**: 243–262.

Key to Genera of Gleicheniaceae

- a. Axils and axillary buds with scales; veins simple to 1-forked; sporangia 2–4(–5) per sorus I. **Gleichenia**
- a. Axils and axillary buds with trichomes; veins 2–4-forked; sporangia ca. 8–15 per sorus II. **Dicranopteris**

I. *Gleichenia*

Gleichenia Sm., *Mém. Acad. Roy. Sci. (Turin)* 5: 419. 1793. TYPE: *G. polypodioides* (L.) Sm. (*Onoclea polypodioides* L.). **Figure 9.**

Sticherus Presl, *Tent. pterid.* 51. 1836. TYPE: *S. laevigatus* (Willd.) Presl (*Mertensia laevigata* Willd.) = *Gleichenia truncata* (Willd.) Sprengel.
Diplopterygium (Diels) Nakai, *Bull. Natl. Sci. Mus.*

29: 47. 1950. *Gleichenia* section *Diplopterygium* Diels, *Nat. Pflanz.* 1(4): 353. 1900. TYPE: *Gleichenia glauca* (Houtt.) Hooker (*Polypodium glaucum* Houtt.).

Stem provided with setose or short-ciliate scales, and sometimes stellate trichomes. **Leaves** once or several times pseudodichotomously branched (but simple in *G. simplex*, or with several 2-pinnate pinnae in *G. bancroftii*), with the penultimate seg-

ments in diverging, subequal, usually pectinate pairs. **Axils** of forks bearing a dense tuft of setose to ciliate (very rarely entire) scales, these often flanked by reduced, stipule-like appendages. **Lamina**, at least abaxially, provided with setose to ciliate scales or stellate trichomes. **Veins** simple to 1-forked. **Sori** commonly paraphysate. **Sporangia** 2–4(–5) per sorus.

Gleichenia is a pantropical genus of more than

100 species. The three subgenera, *Gleichenia*, *Diplopterygium*, and *Mertensia*, are treated as genera by some authors.

Reference

CHING, R. C. 1940. On the genus *Gleichenia* Smith. *Sunyatsenia*, 5(4): 269–288.

Key to Species of *Gleichenia*

- a. Leaves simple (or very rarely with a single fork), deeply pinnatisect to pinnate; lamina linear 2. ***G. simplex***
- a. Leaves pseudodichotomously forked, or with 1–3 pairs of 2-pinnate pinnae; lamina broad, never linear b
- b. Pinnae 2-pinnate, not forked; axillary scales with margins entire 1. ***G. bancroftii***
- b. Pinnae once to several times pseudodichotomous; axillary scales conspicuously ciliate or setose (or entire in *G. nitidula*) c
- c. Ultimate segments moderately to densely tomentose on midrib and/or veins abaxially, the whitish to orange tomentum often obscuring the segment tissue (sometimes thinning in age) d
- d. Larger penultimate segments 1.4–2.2 cm broad; larger ultimate segments 1.2 cm long or less; pinnae usually 3–4 times-forked; branches strongly ascending, usually tightly crowded and subparallel with adjacent ones 3. ***G. pennigera***
- d. Larger penultimate segments 2.5–8 cm broad; larger ultimate segments 1.5–4.5 cm long; pinnae 1- or 2-forked; branches spreading to moderately ascending, not crowded e
- e. Sori inframedial, crowding or touching the segment midrib; ultimate segments (larger ones) 1.8–3 mm broad beyond the dilated base, usually strongly revolute 4. ***G. bifida***
- e. Sori medial, rarely crowding the midrib; ultimate segments (larger ones) (3–)3.5–4.5 mm broad, plane to moderately revolute 5. ***G. tomentosa***
- c. Ultimate segments naked to scaly abaxially, never tomentose (if trichomes present, these scattered, short, or rigid) f
- f. Penultimate segments less than 2 cm broad; ultimate segments 2–3.5(–4) times longer than broad g
- g. Scales ample to abundant on costae and veins abaxially 6. ***G. revoluta***
- g. Scales essentially lacking on lamina h
- h. Axillary scales broad, ciliate; primary axis conspicuously tuberculate to muricate 7. ***G. tuberculata***
- h. Axillary scales narrow and rigid, entire or (rarely) sparingly dentate or short-setose; primary axis smooth 8. ***G. nitidula***
- f. Penultimate segments (at least larger ones) 2.2–8 cm broad; ultimate segments (4–)5–12 times longer than broad i
- i. Midribs of ultimate segments naked 9. ***G. lechleri***
- i. Midribs of ultimate segments conspicuously scaly, at least abaxially j
- j. Ultimate segments (most of them) remote, separated by a space once or twice their width; sori medial to supramedial 10. ***G. remota***
- j. Ultimate segments approximate, contiguous at their bases; sori commonly inframedial (or some of them medial) k
- k. Costa scales commonly less than 1 mm long; midrib scales deltoid, the scale body 5 or more cells wide; axillary scales 0.5–1.5 mm long, with whitish or pale orange, lax cilia 11. ***G. peruviana***

- k. Costa scales 1.5–3 mm long; midrib scales filiform, the scale body 1–3 cells wide; axillary scales 2–3 mm long, with dark, rigid setae 1
 l. Penultimate segments 4–9 cm broad; margins of ultimate segments plane to slightly revolute; veins not or slightly raised 12. **G. longipinnata**
 1. Penultimate segments 2.2–3.2 cm broad; margins of ultimate segments moderately to strongly revolute; veins strongly raised abaxially .. 13. **G. rubiginosa**

1. **Gleichenia bancroftii** Hooker, Sp. fil. 1: 5. 1844.
 TYPE: Jamaica, *Bancroft* (holotype, K).

Mertensia bancroftii (Hooker) Kunze, Linnaea 18: 307. 1844.
Dicranopteris bancroftii (Hooker) Underw., Bull. Torrey Bot. Club 34: 252. 1907.
Hicriopteris bancroftii (Hooker) Ching, Sunyatsenia 5: 278. 1940.
Diplopterygium bancroftii (Hooker) A. R. Smith, Amer. Fern J. 70: 26. 1980.

Leaves with 1–3 pairs of 2-pinnate pinnae, these to 1.5 m long and 40 cm broad, the axes naked or with scattered, linear, or filiform scales. **Axillary scales** lanceolate to ovate, long-acuminate to attenuate, yellowish to light brown, with entire margins. **Penultimate segments** (pinnules) very numerous, crowded, at nearly right angles to the costa, pectinate, cut nearly or quite to the costa. **Ultimate segments** strongly revolute, midribs abaxially often provided with scattered, filiform scales. **Sori** inframedial.

In open forests, commonly on slopes or ravine banks, 2400–2800 m, infrequent in Peru: Huánuco, Pasco, Cuzco.
 Mexico to Panama; West Indies; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Huánuco: Huánuco, within 5 km of Carpish, *Tryon & Tryon 5316* (F, GH, UC, US). **Pasco:** Border Prov. Oxapampa and Pasco, *van der Werff et al. 8604* (MO). **Cuzco:** La Convención, Valle de San Miguel, *Bües 2126* (US).

2. **Gleichenia simplex** (Desv.) Hooker, Icon. pl., t. 92. 1837.

Mertensia simplex Desv., Dictionnaire sciences naturelles 62(2), t. 91. 1827; Mém. Soc. Linn. Paris 6: 200. 1827. TYPE: Peru, *collector unknown* (holotype, P; photo, US).
Dicranopteris simplex (Desv.) Maxon, Contr. U.S. Natl. Herb. 24: 50. 1922.
Sticherus simplex (Desv.) Ching, Sunyatsenia 5: 285. 1940.

Leaves simple (very rarely with a single fork), deeply pinnatisect to pinnate, linear, 20–50 cm

long and less than 3 cm broad. **Scales** of the petiole essentially lacking, but abundant on the rachis abaxially, these lanceolate, attenuate, orange to reddish brown, the margins long-ciliate. **Ultimate segments** contiguous at the very base or (especially proximal ones) discrete and almost their own width apart, strongly revolute, on the abaxial side slightly to conspicuously pruinose and scaly, scales along the midrib similar to those of the rachis, but toward the segment apex grading to pluricellular, stellate trichomes. **Sori** medial to inframedial.

Road cuts, banks and open rocky slopes, (1900–)2700–3800 m, Piura to Cajamarca, south to Huancavelica and Cuzco.
 Colombia to Bolivia.

There has been some confusion as to publication of the name *Mertensia simplex*. In the Dict. Sci. Nat. 1827 there is no text, but the plate with analysis constitutes a valid publication. A description was given at approximately the same time by Desvaux in Mém. Soc. Linn. Paris 6: 200. 1827.

Piura: Prov. Huancabamba, road to Canchaque, *Hutchison 1617* (F, GH, NY, UC). **Lambayeque:** Dist. Incahuasi, Laguna Tembladera, *Sagástegui et al. 12774* (F, HUT, MO). **Cajamarca:** Prov. San Miguel, El Tingo, *Sagástegui et al. 9517* (F, MO, NY). **Amazonas:** Prov. Chachapoyas, banks above swamp on summit of Cerros de Calla-Calla, *Wurdack 1212* (F, GH, NY, US). **La Libertad:** Prov. Patáz, Huaylillas, Puerta del Monte, *López & Sagástegui 3457* (GH). **San Martín:** Dist. Huallaga, Valley of Rio Apisoncho, *Hamilton & Holligan 540* (US). **Ancash:** Prov. Huari, Huascarán National Park, Quebrada Pachachaca, *D. Smith et al. 12564* (F, MO). **Huánuco:** Yanano, stony clay bank, *Macbride 4925* (F, GH, US). **Huancavelica:** Prov. Tayacaja, Chuspi-Tocas, between Colcabamba and Paucarbamba, *Tovar 2066* (GH, USM). **Cuzco:** La Convención, *Bües 2078* (GH, US).

3. **Gleichenia pennigera** (Mart.) Moore, Index fil. 381. 1862.

Mertensia pennigera Mart., Icon. pl. crypt. 130, t. 59, f. 1. 1834. TYPE: Brazil, "Prov. Minarum, in Serra de S. Geraldo," *Martius* (M; photo, US).
Dicranopteris pennigera (Mart.) Maxon, Contr. U.S. Natl. Herb. 24: 48. 1922.
Sticherus penniger (Mart.) Copel., Gen. fil. 27. 1947.

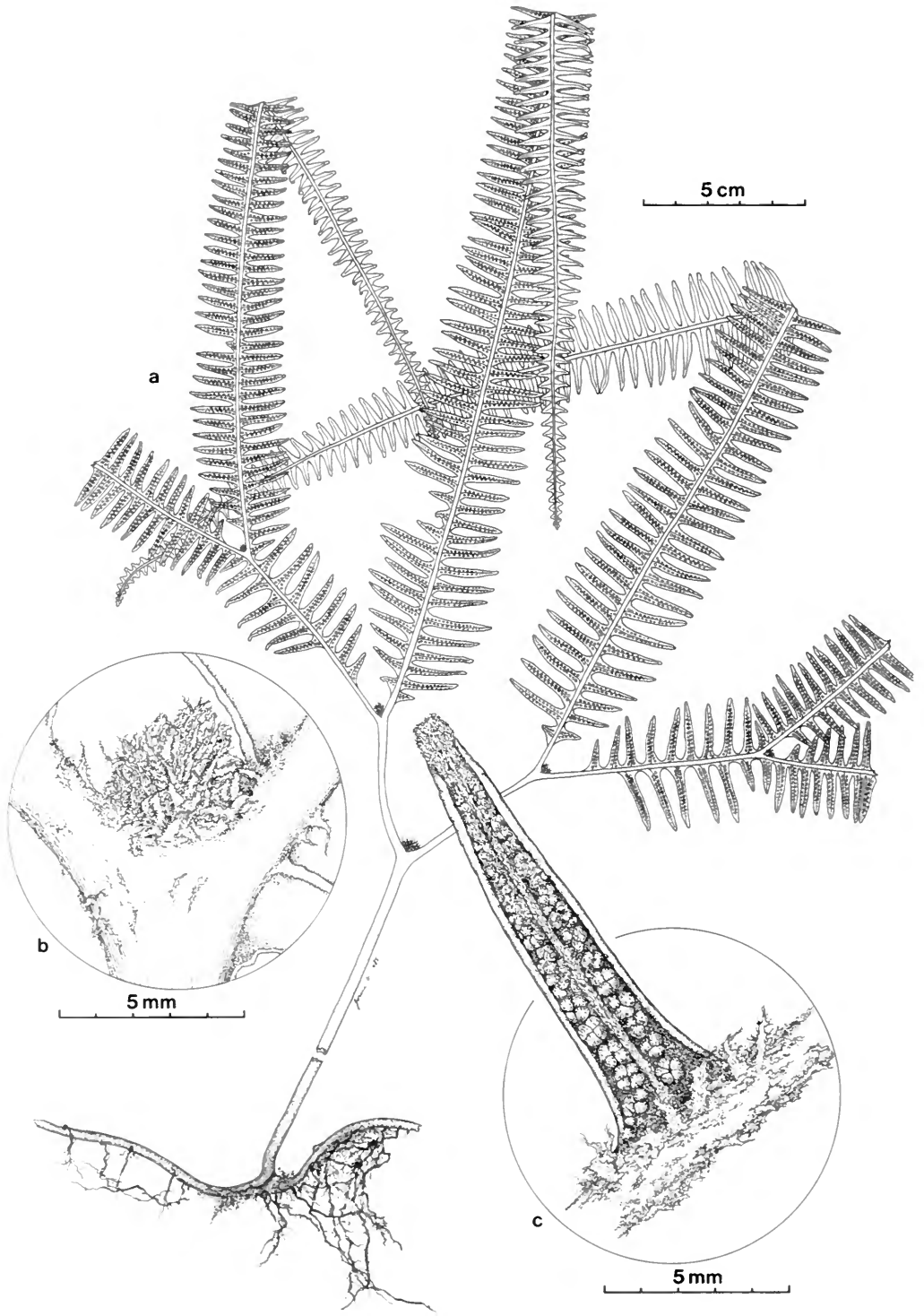


FIG. 9. *Gleichenia bifida*: a, habit; b, leaf axil with bud; c, ultimate segment. (a from Schunke V. 5976, F; b from Tryon & Tryon 6605, Brazil, F; c from Luteyn & Luteyn 6735, Ecuador, F.)

Leaves pseudodichotomously forked. **Pinnae** (2–)3–4-forked, the branches (at least in Peruvian specimens) strongly ascending, often tightly crowded and subparallel with adjacent ones. **Axillary scales** lanceolate, orange, the margins copiously beset with long, tortuous pale or whitish cilia. Larger **penultimate segments** 1.4–2.2 cm broad, the costae abaxially provided with a mixture of orange or whitish long-ciliate scales and a scattered whitish tomentum, adaxially naked or sparsely to amply white-tomentose. **Ultimate segments** slightly to strongly revolute, larger ones to 1.2 cm long, densely covered abaxially with whitish tomentum (often thinning in age). **Sori** infra-medial, mostly crowding or touching the midrib.

Open places in forests, on slopes or stream banks, 1000–2100 m, Loreto?, Huánuco, Pasco, Junín, Cuzco.

Colombia; Venezuela; Peru; Bolivia; Brazil.

Special note should be made of the branching pattern throughout the range of this species. Branches may be very strongly ascending, thus quite crowded and even subparallel with each other; or they may diverge at broader angles, as seen in the type. Thus far, all specimens examined from Peru exhibit the crowded pattern, which might tempt one to consider separation at subspecific level. However, this difference appears uncorrelated with other characters, and specimens, at least outside Peru, seem to grade freely from one pattern to the other.

Loreto?: “Altura de Salarayacu” (Sarayacu?), *Bües* 847 (US). **Huánuco**: Between Huánuco and Pampayacu, *Kanehira* 153 (GH, US). **Pasco**: Prov. Oxapampa, Gran Pajónal, *D. Smith* 5073 (F, MO). **Junín**: Concepción, *Herera* 142 (US). **Cuzco**: Valle de Lares, Hda. Huy-huy, *Bües* 1826 (US). Prov. Convención, Lucumayo, *Vargas* 4221 (US).

4. *Gleichenia bifida* (Willd.) Sprengel, Syst. veg. 4: 27. 1827. **Figure 9.**

Mertensia bifida Willd., Kongl. Vetensk. Acad. Nya Handl. 25: 168. 1804. TYPE: Venezuela, Caracas, *Bredemeyer* (holotype, v, *Herb. Willd.* 19468; photo, GH).

Dicranopteris bifida (Willd.) Maxon, N. Amer. fl. 16: 60. 1909.

Gleichenia mathewsii Hooker, Sp. fil. 1: 9. 1844. TYPE: Peru, *Mathews* 1092, in part (holotype, k; photo, us).

Mertensia mathewsii (Hooker) Fée, Mém. Foug. 11: 122. 1866.

Sticherus bifidus (Willd.) Ching, Sunyatsenia 5: 282. 1940.

Sticherus mathewsii (Hooker) Nakai, Bull. Nat. Sci. Mus. 29: 22. 1950.

Leaves pseudodichotomously forked. **Pinnae** 1- or 2-forked, the branches spreading to moderately ascending. **Axillary scales** lanceolate to ovate, attenuate, light brown to pale orange, the margins amply ciliate. Larger **penultimate segments** (2.5–)3–7 cm broad, the costa on the abaxial side amply to abundantly provided with orange, long-ciliate scales, on the adaxial naked or sometimes with sparse whitish tomentum. **Ultimate segments** moderately to (typically) strongly revolute, larger ones 1.5–3.5 mm long and 1.8–3 mm broad (beyond the dilated base), densely covered abaxially with orange to whitish tomentum (sometimes thinning in age), the midribs also sparsely provided with tawny to whitish, filiform, ciliate scales. **Sori** infra-medial, mostly crowding or touching the midrib.

In forests, thickets and clearings, often on banks and slopes, 150–1800 m (very rarely to 2200 m) Piura to Loreto, south to Madre de Dios and Puno.

Mexico to Panama; West Indies; Colombia and Venezuela south to Bolivia and Paraguay.

Piura: Prov. Huancabamba, slopes of Cerro La Viuda, *Sagástegui et al.* 8209 p.p. (NY). **Amazonas**: Prov. Bagua, along roadside, 37 km NE of Chiriaco, *Barbour* 4486 (MO). **San Martín**: Zepelacio, near Moyobamba, *Klug* 3458 (F, GH, MO, NY, US). **Loreto**: Pumayacu, between Balsapuerto and Moyobamba, *Klug* 3242 (F, GH, MO, NY, US). **Huánuco**: Dist. Churubamba, trail Cotirarda to Mercedes, *Mexia* 8191 (F, GH, MICH, MO, NY, UC, US). **Pasco**: Prov. Oxapampa; Palcazú, Río Alto Iscozacín, *Foster & d’Achille* 10098 (F). **Junín**: Huacapistana, between Tarma & San Ramón, *Ferreyra* 286 (GH, USM). **Ucayali**: Vicinity of Aguaytía, on steep slopes along Río Aguaytía, *Croat* 21003 (F, MO, UC). **Ayacucho**: Ca. 25 km SW from Hacienda Luisiana and Río Apurímac, ca. 25 km from Tambo, *Dudley* 11887 (GH). **Cuzco**: Prov. Paucartambo, near Asunción, *West* 7122 (MICH, UC). **Madre de Dios**: Prov. Manú, Río Inambari, *Chávez* 1057 (MO). **Puno**: San Gabán to Ollachea, *Dillon et al.* 1243 (F, MO, NY).

5. *Gleichenia tomentosa* (Sw.) Sprengel, Syst. veg. 4: 27. 1827.

Mertensia tomentosa Sw., Kongl. Vetensk. Acad. Nya Handl. 25: 177, t. 5, f. 4. 1804. TYPE: Peru, *Herb. Cavanilles* (holotype, s; isotype, p?; photos, us of s & p).

Mertensia velata Kunze, *Linnaea* 9: 15. 1834. TYPE: Peru, Huánuco, Pampayacu, July 1829, *Poeppig (diar. 1117)* (holotype, B?; isotype, M!; probable isotype, P!; frag., US!; photos, US of M & P).
Gleichenia velata (Kunze) Mett., *Fil. hort. bot. Lips.* 113. 1856.
Gleichenia buchtienii Christ & Rosenst., *Repert. Spec. Nov. Regni Veg.* 5: 229. 1908. TYPE: Bolivia, "Yungas australis, Sirupaya prope Yanacachi," *Buchtien 496* (holotype, P!; isotypes, F!, P!, S).
Dicranopteris velata (Kunze) Maxon, *Contr. U.S. Natl. Herb.* 24: 50. 1922.
Sticherus buchtienii (Christ & Rosenst.) Copel., *Gen. fil.* 28. 1947.
Sticherus velatus (Kunze) Copel., *Gen. fil.* 28. 1947.

Leaves pseudodichotomously forked. **Pinnae** 1- or 2-forked, the branches spreading to moderately ascending. **Axillary scales** lanceolate to ovate, attenuate, deep to pale orange, or castaneous at base, the margins amply long-ciliate. Larger **penultimate segments** 4–7 cm broad, the costa abundantly provided abaxially with orange, long-ciliate scales, and adaxially with orange to whitish filiform scales which often grade into a pale tomentum (this sometimes caducous). **Ultimate segments** plane to moderately revolute, larger ones 20–45 mm long and (3–)3.5–4.5 mm broad above the dilated base, densely covered abaxially with orange to whitish tomentum (this sometimes thinning in age), the midribs provided also with orange, ciliate scales. **Sori** mostly medial, rarely, if ever, crowding the midrib.

In cloud or elfin forests, usually in open sites on ridges, slopes or ravine banks, 1500–2700 m, Cajamarca, Amazonas, San Martín, Huánuco, Pasco, Cuzco.

Colombia; Venezuela; Ecuador; Peru; Bolivia.

Much confusion has attended circumscription of the densely tomentose species of *Gleichenia*, which include *G. bifida* as well as those combined here under *G. tomentosa*. We have been unable to obtain the type specimens of the latter, but type photos (US) indicate clearly enough that ultimate segments are too broad and soral lines appear too far from midribs to be *G. bifida*. The photos, along with Swartz's original description (1804) of *Mertensia tomentosa* and his subsequent Latin description (*Syn. fil.* 164, p. 392, 1806) make it evident that *G. tomentosa* and *G. velata* are the same. All this confusion within the species complex is warranted, for *G. bifida* and *G. tomentosa* do not differ strongly. As seen in the key, the former has narrower, more strongly revolute ultimate segments, and soral lines usually are closer to the

midrib; also the plants seem to occur at lower elevations in Peru: 150–1800 m (rarely to 2200 m) as compared with 1500–2700 m in *G. tomentosa*. Color of scales on the buds and major axes affords another, but less consistent, diagnostic feature; in both species these are pale to deep orange, but in *G. tomentosa* they are often liberally intermixed with castaneous ones. A few specimens have been seen which are intermediate, thus emphasizing the close relationship of the two species. For example, the only collection of *G. tomentosa* (cited below) from Cajamarca has segments strongly revolute and 3 mm broad or less, but sori are medial and scales frequently are castaneous at base.

Cajamarca: Prov. Cutervo, La Achira (San Andrés-Sócota), growing over bushes, *López & Sagástegui 5464* (GH, HUT). **Amazonas:** Prov. Bagua, Cordillera Colán SE of La Peca, *Barbour 3980* (MO). **San Martín:** "In monte Campana prope Tarapoto," *Spruce 4707* (P, US). **Huánuco:** Playapampa, steep banks, *Macbride 4509* (F, US). **Pasco:** Cushi, trail to Tambo de Vaca, *Bryan 687* (F). **Cuzco:** La Convención, ca. 12 km NE from Hacienda Luisiana and Río Apurímac, *Dudley 10545* (GH, US).

6. *Gleichenia revoluta* HBK., *Nov. gen. sp.* 1: 29. 1815. TYPE: Ecuador, Saraguru, *Humboldt & Bonpland* (holotype, P; isotype, B!; frag., US of B; photos, US of B & P).

Mertensia revoluta (HBK.) Desv., *Mém. Soc. Linn. Paris* 6: 200. 1827.

Mertensia pruinosa Mart., *Icon. pl. crypt.* 109. 1834. TYPE: Brazil, Minas Gerais, *Freyreiss* (probable holotype, M!; isotype, S; photos, F & US of M).

Gleichenia pruinosa (Mart.) Mett., *Ann. Mus. Bot. Lugduno-Batavum* 1: 49. 1863.

Gleichenia affinis Kuhn, *Linnaea* 36: 167. 1869. TYPE: Peru, Dept. Puno, San Gabán, *Lechler 2265* (holotype, B!; photo, US).

Dicranopteris affinis (Kuhn) Maxon, *Contr. U.S. Natl. Herb.* 24: 47. 1922.

Dicranopteris pruinosa (Mart.) Maxon, *Contr. U.S. Natl. Herb.* 24: 49. 1922.

Sticherus pruinosis (Mart.) Ching, *Sunyatsenia* 5: 284. 1940.

Sticherus revolutus (HBK.) Ching, *Sunyatsenia* 5: 285. 1940.

Sticherus affinis (Kuhn) Nakai, *Bull. Natl. Sci. Mus.* 29: 13. 1950.

Leaves pseudodichotomously forked. **Pinnae** 2- or 4-forked. **Axillary scales** lanceolate to ovate, ±lax, thin-textured, orange to reddish brown, the margins amply ciliate. Larger **penultimate segments** 1–1.8(–2) cm broad, the costa on the abaxial side amply to copiously provided with orange to reddish brown, long-ciliate scales, on the adaxial side

the costa naked or filiform-scaly. **Ultimate segments** moderately to strongly revolute, larger ones 2–3.5(–4) times longer than broad, the midrib and veins scaly as on the costa, those of the veins often filiform or grading to tortuous, stellate trichomes, the veins not or scarcely raised. **Sori** medial to supramedial.

In elfin forests, clearings, and along roadsides, 1770–3400 m, Piura to Amazonas, south to Cuzco and Puno.

Costa Rica & Panama; Colombia; Venezuela; Ecuador; Peru; Brazil; Bolivia.

This species is locally abundant in middle to upper elevations and is sometimes confused with *Gleichenia bifida*, probably because of the often copious indument borne on the abaxial surfaces. These scales, especially on the veins, often become filiform and even grade into stellate trichomes; however, the surfaces are never truly tomentose, as in *G. bifida*. Also, penultimate segments of the latter are much broader, with linear ultimate segments, and the sori crowd the midrib, whereas in *G. revoluta* sori are medial to supramedial, most of them quite remote from the midrib. Furthermore, *G. bifida* grows at lower elevations. It is likely that *G. revoluta* occurs also in Costa Rica and Panama [as *G. costaricensis* (Underw.) C. Chr.] and in Bolivia [as *G. boliviensis* (Maxon & Morton) Lell.]. Probably *G. subandina* Sodiro and *G. hypoleuca* Sodiro of Ecuador are also synonymous with *G. revoluta*.

Piura: Prov. Huancabamba, above Huancabamba, road to Canchaque, *Hutchinson 1618* (F, GH, UC, US). **Cajamarca:** Prov. Cutervo, alrededores de Cutervo, *López & Sagástegui 5314* (GH, MO). **Amazonas:** Prov. Chachapoyas, slopes of Puma-urcu SE of Chachapoyas, *Wurdack 552* (F, GH, NY). **La Libertad:** Prov. Patáz, Puerta del Monte, Paso La Sábana, *López & Sagástegui 3463* (GH). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al. 8477* (MO). **Huánuco:** Playapampa, in sphagnum montaña, *Macbride 4508* (F, GH, NY, US). **Cuzco:** Cordillera Vilcabamba, 23 km NE from Hacienda Luisiana, *Dudley 11133* (GH, US). **Puno:** Prov. Sandia, near Limbani, *Metcalf 30539* (MO, US; atypical in narrower segments and darker, narrower scales).

7. *Gleichenia tuberculata* Kuhn, *Linnaea* 36: 166. 1869. TYPE: Peru, Dept. Puno, Tatanara, *Lechler 2572* (holotype, B!; isotype, B!; photos, F & MICH of B).

Sticherus tuberculatus (Kuhn) Nakai, *Bull. Natl. Sci. Mus.* 29: 30. 1950.

Leaves pseudodichotomously forked, petiole and rachis conspicuously tuberculate to muriculate. **Pinnae** 2–3-forked. **Axillary scales** closely imbricate, ovate to lanceolate, castaneous to reddish brown, the margins amply ciliate. Larger **penultimate segments** 1.3–1.5 cm broad, pruinose abaxially, scales essentially lacking. **Ultimate segments** moderately revolute, larger ones ca. 3 times longer than broad. **Sori** supramedial.

Thus far represented only by the type collection, from Puno. This species appears to differ from *Gleichenia revoluta* only in the lack of scales on the laminar surface and in the tuberculate to muriculate primary axis. However, the specimens were taken from a plant apparently quite advanced in age, for few sporangia remain on the segments, and it is possible that any scales once borne on the axes may have fallen away as well. Density of indument varies within some species of *Gleichenia*, depending upon maturity. Furthermore, tuberculate primary axes are not uncommon in the genus, although never so conspicuously so as in *G. tuberculata*. The species is maintained as distinct here, but with reservations.

8. *Gleichenia nitidula* Rosenst., *Repert. Spec. Nov. Regni Veg.* 10: 275. 1912. TYPE: Costa Rica, San Carlos, *Brade & Brade 503* (holotype, not located; isotypes, NY, S).

Sticherus nitidulus (Rosenst.) Copel., *Gen. fil.* 28. 1947.

Leaves pseudodichotomously forked, petiole and rachis not or scarcely tuberculate. **Pinnae** 1–3-forked. **Axillary scales** not or slightly imbricate, linear or linear-lanceolate, with subcaudate tips, deep reddish brown, the margins entire or (rarely) sparingly dentate or short-setose. Larger **penultimate segments** 1.4–1.8 cm broad, not or scarcely pruinose abaxially, scales lacking. **Ultimate segments** slightly revolute, larger ones ca. 3 times longer than broad.

Scandent on wet, shady banks, in forests, 1600–1900 m, San Martín, Pasco.

Costa Rica; Panama; Ecuador; Peru.

The species is notable for its disjunct distribution, and has rarely been collected in South America. Distinctive characteristics are the lack of scales on the narrow penultimate segments, and the sparse, rigid axillary scales with entire margins.

Apparently represented thus far in Peru by the following two collections: **San Martín**: "Prope Tarapoto, in monte Guayrapurima." *Spruce 4018* (K). **Pasco**: (as Junín) Pichis Trail, Eneñas, dense forest, *Killip & Smith 25777* (F).

9. **Gleichenia lechleri** Kuhn, *Linnaea* 36: 167. 1869. TYPE: Peru, "Tabina," *Lechler 2040* (holotype, B!; isotypes, K, L; frag., US!; photos, F, GH, US of B).

Gleichenia yungensis Rosenst., *Repert. Spec. Nov. Regni Veg.* 5: 228. 1908. TYPE: Bolivia, Yungas, Unduavi, 3300 m, *Buchtien 902* (holotype, s; isotypes, ucl, us!).

Dicranopteris yungensis (Rosenst.) Maxon, *Contr. U.S. Natl. Herb.* 24: 50. 1922.

Sticherus yungensis (Rosenst.) Copel., *Gen. fil.* 28. 1947.

Sticherus lechleri (Kuhn) Nakai, *Bull. Natl. Sci. Mus.* 29: 21. 1950.

Leaves pseudodichotomously forked, with foliaceous, often pinnatifid, appendages borne within each axil (especially proximally). **Pinnae** 1–3-forked. **Axillary scales** ovate to linear-lanceolate, orange to reddish brown, attenuate, the margins short-ciliate. **Penultimate segments** (larger ones) 2.5–6 cm broad, costae sparsely to amply scaly abaxially, the scales orange, linear or linear-lanceolate, long-attenuate, the margins somewhat short-ciliate. **Ultimate segments** plane or slightly revolute, commonly pruinose abaxially, larger ones 12–28 mm long and 2.5–4.5 mm broad, the midribs lacking scales. **Sori** commonly supramedial.

In mountain forests, commonly on exposed ridges, (1100–)1800–3000 m, Huánuco, Cuzco.

Trinidad; Colombia; Ecuador; Peru; Bolivia.

This species is characterized by lack of midrib scales, commonly pruinose lamina, plane or slightly revolute ultimate segments, and the supramedial sori. With it should be included *Dicranopteris brittonii* Maxon of Trinidad, and probably also *G. leucocarpa* Sod. of Ecuador. Although we have not seen the type of the latter, a type fragment and photo (US) reveal no significant differences between the two species.

Huánuco: Carpish, *Coronado 78* (US). **Cuzco**: Machu Picchu, Valle del Urubamba, *Herrera 3286* (US). Cerro de Cusilluyoc, forest along Río Pilahuata, *Pennell 13940* (F, US). Prov. Paucartambo, "Pillawata," Yanamayo-Tambomayo, *Vargas 16702, 16705* (GH).

10. **Gleichenia remota** (Kaulf.) Sprengel, *Syst. veg.* 4: 27. 1927.

Mertensia remota Kaulf., *Enum. fil.* 39. 1824. TYPE: Brazil, Ilha de Sta. Catarina, *Chamisso* (holotype, LZ destroyed; isotype, LE?).

Dicranopteris remota (Kaulf.) Maxon, *Contr. U.S. Natl. Herb.* 24: 50. 1922.

Leaves pseudodichotomously forked, with foliaceous appendages usually borne within each axil (especially proximally). **Pinnae** 1- or 2-forked. **Axillary scales** lanceolate to ovate, attenuate, rigid, 1–1.5 mm long, often somewhat convex, castaneous to reddish brown, lustrous, not or slightly imbricate, their margins short-setose, or rarely entire or with a few short cilia at base. **Penultimate segments** (larger ones) 4–9 cm broad, costae abaxially provided with scattered castaneous or dark reddish brown scales less than 1 mm long, these ovate to lanceolate, with setose to short-ciliate margins, adaxially virtually naked (or occasionally with scattered patches of arachnoid scurf). **Ultimate segments** remote, most of them separated by a space once or twice their width, slightly strongly revolute, not or slightly pruinose abaxially, larger ones 20–50 mm long and 1.7–2.5 mm broad, the midribs amply to copiously scaly on abaxial side, the scales deltoid, orange to tawny, with long, pale cilia on the margins, or toward segment tips sometimes becoming substellate. **Veins** often raised. **Sori** medial to supramedial.

At edges of forests, roadsides, and on rocky banks, 350–2000 m, Amazonas, San Martín, Huánuco.

Costa Rica; Panama; Cuba; Trinidad; Colombia to the Guianas; Ecuador; Peru; Bolivia; Brazil (Amazonas, Ilha Sta. Catarina).

This and *Gleichenia longipinnata* are superficially similar in the great size of their penultimate segments (sometimes to 50 cm long and 9 cm broad) and the extremely long and narrow ultimate segments. However, besides the characters noted in the key, *G. remota* can also be sharply distinguished by the laminar scales. Those within the axils are relatively short (1–1.5 mm) and broad, while the costal scales are even shorter (less than 1 mm) and broader. In *G. longipinnata*, both the axillary scales and costal scales are linear to filiform, the former 2–3 mm long and the latter 1.5–2 mm long.

Amazonas: Prov. Bagua, roadside, 37 km NE of Chiraco, *Barbour 4485* (MO), *4486* (USM). **San Martin:** Tarapoto-Yurimaguas Hwy., km 39, *McDaniel 14209* (GH, MO). Tarapoto, Carretera Tarapoto-Yurimaguas, *Rimachi 5163, 5251* (MO, NY). **Huánuco:** Monzón, confluencia con Huallaga, cerca de Tingo María, *Ferreyra 10047* (GH).

11. *Gleichenia peruviana* (Maxon) Lell., Amer. Fern J. 74: 57. 1984.

Dicranopteris peruviana Maxon, Amer. Fern J. 33: 133. 1943. TYPE: Peru, Huánuco, Playapampa, ca. 2700 m, *Macbride 4510* (holotype, ♀; isotype, us!).

Leaves pseudodichotomously forked, with foliaceous appendages often borne within some of the more proximal axils. **Pinnae** 1–3-forked. **Axillary scales** ovate or lance-ovate, attenuate, 0.5–1.5 mm long, castaneous to reddish brown, closely imbricate, their margins amply ciliate, the cilia lax, short and whitish to pale orange. **Penultimate segments** (larger ones) 2.5–4(–5) cm broad, costae on abaxial side amply to copiously scaly, the scales lustrous castaneous to reddish brown, ovate to lanceolate, acuminate or attenuate, commonly less than 1 mm long, their margins short-ciliate, costae on adaxial side sparsely to amply provided with tortuous trichomes or filiform scales. **Ultimate segments** crowded, contiguous at their bases, slightly to moderately revolute, not or slightly pruinose, larger ones 12–24 mm long and 1.5–2.5 mm broad (beyond the dilated base), abaxially the midribs and (usually) veins minutely scaly, ciliate- or setose-scaly, the scales often becoming filiform or grading into stellate, whitish trichomes. **Veins** often raised. **Sori** mostly inframedial.

In thickets, open forests and ravines, often on exposed rocky ridges, 2000–3400 m, La Libertad, Huánuco, Pasco, Cuzco.

Apparently confined to Peru, Cordilleras Central and Oriental.

La Libertad: Prov. Pataz, Pampa de Huayno-huincho, Huaylillas, *López & Sagástegui 3517* (GH, HUT). **Huánuco:** Wet, dense jungle, 12 mi S of Panao, *Macbride & Featherstone 2217* (F). **Pasco:** Prov. Oxapampa, Dist. Oxapampa, Río San Alberto, *Foster et al. 10306* (F); *León 641* (F, GH); *D. Smith & Pretel 7594* (F, MO). **Cuzco:** Prov. La Convención, on open exposed ridge, *Dudley 10710* (GH, MO).

12. *Gleichenia longipinnata* Hooker, Sp. fil. 1: 9. 1844. TYPE: Surinam, *Hostmann 238* (ho-

lotype, K; isotypes, BM, K; frag., US!; photo, US of K).

Mertensia longipinnata (Hooker) Klotzsch, Linnaea 18: 537. 1844.

Dicranopteris longipinnata (Hooker) Maxon, Contr. U.S. Natl. Herb. 24: 48. 1922.

Sticherus longipinnatus (Hooker) Nakai, Bull. Nat. Sci. Mus. 29: 21. 1950.

Leaves pseudodichotomously forked, occasionally bearing foliaceous appendages within the axils. **Pinnae** commonly 1-forked. **Axillary scales** linear to filiform, 2–3 mm long, lustrous reddish brown to deep orange, not or rarely tightly imbricate, the margins with dark, rigid, ascending setae. **Penultimate segments** (larger ones) 4–9 cm broad, costae on abaxial side amply to abundantly scaly, the scales 1.5–2 mm long, lustrous reddish brown, setose and filiform or substellate, on adaxial side often appressed filiform-scaly. **Ultimate segments** approximate, contiguous at their bases (very rarely some proximal ones discrete and somewhat apart), plane to slightly revolute, not or slightly pruinose, larger ones 25–45 mm long and 2.5–3.5 mm broad, abaxially bearing filiform or substellate scales on midrib and veins and often some pale, delicate trichomes at the very margin. **Veins** not or slightly prominulous. **Sori** mostly raised.

In forests, on slopes and ridges, 300–1600 m (reported on *Dudley 10448* label as also seen at 3300 m, but probably mistaken for *G. peruviana*), Amazonas, Loreto, Pasco, Huánuco, Cuzco.

Surinam; Peru; Brazil.

Despite obvious differences, this and *Gleichenia rubiginosa* share a distinctive type of laminar scale not found in other species in Peru. The scales along the costae of penultimate divisions, abaxially, are typically long and narrow, the marginal cell walls deep reddish brown and bearing rigid dark setae. Along midrib and veins, these grade into filiform scales often only two to three cells wide (the setae then much longer than the width of the scale body) and thence into delicate, pluricellular trichomes. The Costa Rican *G. mellifera* Christ also bears this kind of laminar scale, and although we have not seen the type, it probably belongs here.

Amazonas: Prov. Bagua, valley of Río Marañón above Cascadas de Mayasi, *Wurdack 2049* (F, NY, UC, US). **Huánuco:** SW slope of Río Lullapichis watershed, *Dudley 13193* (GH). **Ucayali:** Prov. Coronel Portillo, Padre Abad, Chacra de Cesar Vela, *J. Schunke 5465*, (F, GH, MO, NY, US). **Pasco:** Prov. Oxapampa, Valle de Palcazú,

Foster 4504 (F). Cuzco: Prov. Convención, Cordillera Vilcabamba, *Dudley 10448* (GH).

- 13. **Gleichenia rubiginosa** Mett., Ann. Sci. Nat. Bot. 5, 2: 267. 1864. TYPE: Colombia, Puente Nacional, 1650 m, *Lindig 71* (holotype, B!; isotype, P; frag., US!).

Gleichenia rubiginosa f. *virescens* Hieron., Bot. Jahrb. Syst. 34: 561. 1905. SYNTYPE: Peru, *Matthews 1092* (us).

Dicranopteris rubiginosa (Mett.) Maxon, Contr. U.S. Natl. Herb. 24: 50. 1922.

Sticherus rubiginosus (Mett.) Nakai, Bull. Nat. Sci. Mus. 29: 28. 1950.

Leaves pseudodichotomously forked, rarely bearing foliaceous appendages in the axils. **Pinnae** 1- or 2-forked. **Axillary scales** linear or linear-lanceolate, attenuate, 2–3 mm long, sublustrous, reddish brown, not or loosely imbricate, the margins with dark, rigid, ascending setae. **Penultimate segments** (larger ones) 2.2–3.2 cm broad, costae on abaxial side copiously scaly, the scales 2–3 mm long, deep orange, sublustrous, lanceolate or linear-lanceolate and attenuate, with setose margins, on adaxial side naked or occasionally sparsely arachnoid-scaly. **Ultimate segments** approximate, contiguous at their bases, moderately to strongly revolute, pruinose or not, larger ones 12–18 mm long, (2–)2.5–3 mm broad, abaxially bearing fili-form and setose to substellate scales on midrib and veins, and sometimes some delicate trichomes at the very margin. **Veins** raised abaxially. **Sori** inframedial or occasionally medial.

In wet forests and thickets, 1100–2850 m, Piura, Huánuco, Pasco, Ucayali, Cuzco, Puno.

Colombia; Venezuela; Ecuador; Peru.

Although easily distinguished from *G. longipinnata* (q.v.), this is apparently closely related to the latter by virtue of the distinctive laminar scales.

Piura: Prov. Huancabamba, Dist. Sondor, subiendo al Cerro La Viuda, *Sagástegui et al. 8209 p.p.* (NY). **Huánuco**: Prov. Huánuco, Carpish, between Huánuco and Tingo María, *Ferreyra 10009* (GH, USM). **Huánuco-Tingo María** road, S of Chinchayo, *Gentry et al. 19322* (F, MO). **Pasco**: Prov. Oxapampa, road between Oxapampa and Paucartambo, *D. Smith 1592* (F, MO). **Ucayali**: Prov. Coronel Portillo, Cordillera Azul, km 43 Tingo María-Pucallpa Road, *Young & Sullivan 737* (F, MO). **Cuzco**: Valle San Miguel, La Convención, *Bües 2061* (us). **Puno**: Prov. Carabaya, San Gabán Carretera, *Vargas 18877* (GH).

II. Dicranopteris

Dicranopteris Bernh., Neues J. Bot. 1(2): 38. ("1806") 1805, *nom. nov.* for *Mertensia* Willd. (not Roth), and with same type. **Figure 10.**

Mertensia Willd., Kongl. Vetensk. Acad. Nya Handl. 25: 165. 1804, illeg. (not Roth 1790). TYPE: *Mertensia dichotoma* (Murray) Willd. (*Polypodium dichotomum* Murray), *Dicranopteris dichotoma* (Murray) Bernh. = *Dicranopteris linearis* (Burm. f.) Underw.

Stem provided with pluricellular trichomes, scales lacking. **Leaves** 1–4 (rarely to 20) m long, pseudodichotomously branched, with 1–several pairs of opposite pinnae which again typically branch 1 or more times in opposite pairs, or with several pinnae which branch unequally. **Axils** of forks each bearing a dense tuft of trichomes and often a pair of reduced, stipule-like appendages. **Lamina** glabrous, or pubescent with simple or stellate trichomes, scales lacking. **Veins** 2–4-forked. **Sori** lacking paraphyses. **Sporangia** ca. 8–15 per sorus.

This, like *Gleichenia*, is an essentially pantropical genus. The two are readily distinguished by the character of their indument: that of *Gleichenia* being scales and trichomes, while scales are completely lacking in *Dicranopteris*. Three species of the latter are recognized in Peru.

Key to Species of *Dicranopteris*

- a. Leaves with 1–several opposite pairs of stalked pinnae, which again branch 1 or more times; ultimate segments contiguous at base; lamina abaxially glabrous or moderately pubescent with orange, stellate trichomes (rarely tomentose) b
- b. Pinna-forks branching in subequal pairs; accessory, mostly reduced, leafy segments usually borne in pairs at the base of each fork (these in addition to stipule-like segments borne *within* the forks); spores trilete 1. **D. flexuosa**
- b. Pinna-forks obviously branching unequally; accessory leafy segments lacking at the base of each

fork (not to be confused with stipule-like segments often borne *within* the forks); spores monoletate

- 3. **D. pectinata**
a. Leaves 1-forked, each branch consisting of a single, sessile, pinnate (to distally pinnatisect) pinna; ultimate segments mostly well-spaced, not contiguous; lamina abaxially with dense, reddish brown tomentum 2. **D. nervosa**

1. **Dicranopteris flexuosa** (Schrader) Underw., Bull. Torrey Bot. Club 34: 254. 1907. **Figure 10b-c.**

Mertensia flexuosa Schrader, Gött. Gel. Anz. 863. 1824. TYPE: Brazil, Maximilian Prinz Neuwied s.n. (holotype, LZ? destroyed; isotype, M?).

Mertensia rigida Kunze, Linnaea 9: 16. 1834. TYPE: Peru, "Chibangata," Poeppig 1153 (holotype, LZ destroyed; isotype, P).

Gleichenia flexuosa (Schrader) Mett., Ann. Mus. Bot. Lugduno-Batavum 1: 50. 1863.

Gleichenia rigida (Kunze) Bommer & Christ, Bull. Soc. Roy. Bot. Belgique 35: 174. 1896, not *G. rigida* J. Sm.

Leaves with 1–several opposite pairs of stalked pinnae, these repeatedly pseudodichotomous, with all subsequent branches forking in subequal pairs (i.e., each of the stalks subequal in length and diverging at about the same angle), and a pair of reduced, accessory, pectinate segments commonly produced at the base of each (but rarely the ultimate) fork. **Axils** bearing a tuft of stout, rigid, castaneous trichomes and a pair of reduced stipule-like segments. **Pinnae** and their branches long-stalked, the axes and laminar surfaces glabrous, the forked, penultimate segments sessile, to 30 cm long and 6 cm broad. **Ultimate segments** contiguous at base, to 30 mm long and 4 mm broad, coriaceous, glaucous abaxially, the margins strongly revolute. **Spores** trilete.

On ridges and open slopes, at edges of forests, 750–2750 m, San Martín, Huánuco, Ucayali, Cuzco, Puno.

West Indies; southern Mexico to Panama, S to Brazil, Bolivia, and Paraguay (some isolated collections in the United States from coastal Alabama).

This species is very closely related to *Dicranopteris linearis* (Burm.) Underw. of the Paletropics. Suzanne Roth, who is working on a revision of the Neotropical Gleicheniaceae, has suggested (in litt.) that the two are probably conspecific. If so, *D. linearis* has priority.

San Martín: NW of San Martín, Rioja, Río Negro, Soukup 5156 (GH). **Huánuco:** Vilcabamba, hacienda on

Río Chinchao, Macbride 5010 (F, NY, US). **Ucayali:** Prov. Coronel Portillo, Obeteni, E ridge of basin, Chrostowski 66-13 (UC). **Cuzco:** Prov. Convención, Choqallo, Vargas 8153 (MO, UC). **Puno:** Prov. Sandia, Asalaya, Vargas 14835 (GH).

2. **Dicranopteris nervosa** (Kaulf.) Maxon, Contr. U.S. Natl. Herb. 24: 49. 1922.

Mertensia nervosa Kaulf., Enum. fil. 37. 1824. TYPE: Brazil, Sta. Catarina Is., Chamisso (holotype, not located, LZ? destroyed; isotype, LE?, S?).

Gleichenia nervosa (Kaulf.) Sprengel, Syst. veg. 4: 25. 1827.

Leaves 1-forked, each branch consisting of a single, sessile, pinnate (to distally pinnatisect) pinna. **Axils** bearing a dense tuft of long, lax, reddish brown trichomes and usually a pair of reduced stipule-like appendages. **Pinnae** (larger ones) 15–40 cm long, 5–12 cm broad, the axes and laminar surfaces abaxially covered with a dense reddish brown tomentum (this sometimes gray to whitish in age). **Ultimate segments** well-spaced, not contiguous at base, to 60 mm long and 3.5 mm broad, coriaceous, glaucous abaxially, the margins strongly revolute. **Spores** trilete.

Thus far represented in Peru by a single collection: **Puno:** Region of Río Inambari, trail from Aricoma Pass to Santo Domingo, 1800 m, McCarroll 125 (MICH).

Venezuela?; Peru; Bolivia; Brazil.

This is linked to *Dicranopteris schomburgkiana* (Sturm) Morton and *D. seminuda* (Klotzsch) Maxon by the tomentose abaxial surfaces. The three are usually separated by size of segments, color of tomentum, and other quantitative features; however, *D. nervosa* appears to be further distinguished by the delicate, somewhat flexuous axillary trichomes and the single pair of sessile pinnae. The related species have either stout, rigid axillary trichomes, or stalked, branching pinnae, or both. Whether these characters are sufficient to constitute specific or subspecific distinction is open to question. Further study of the species complex is needed.

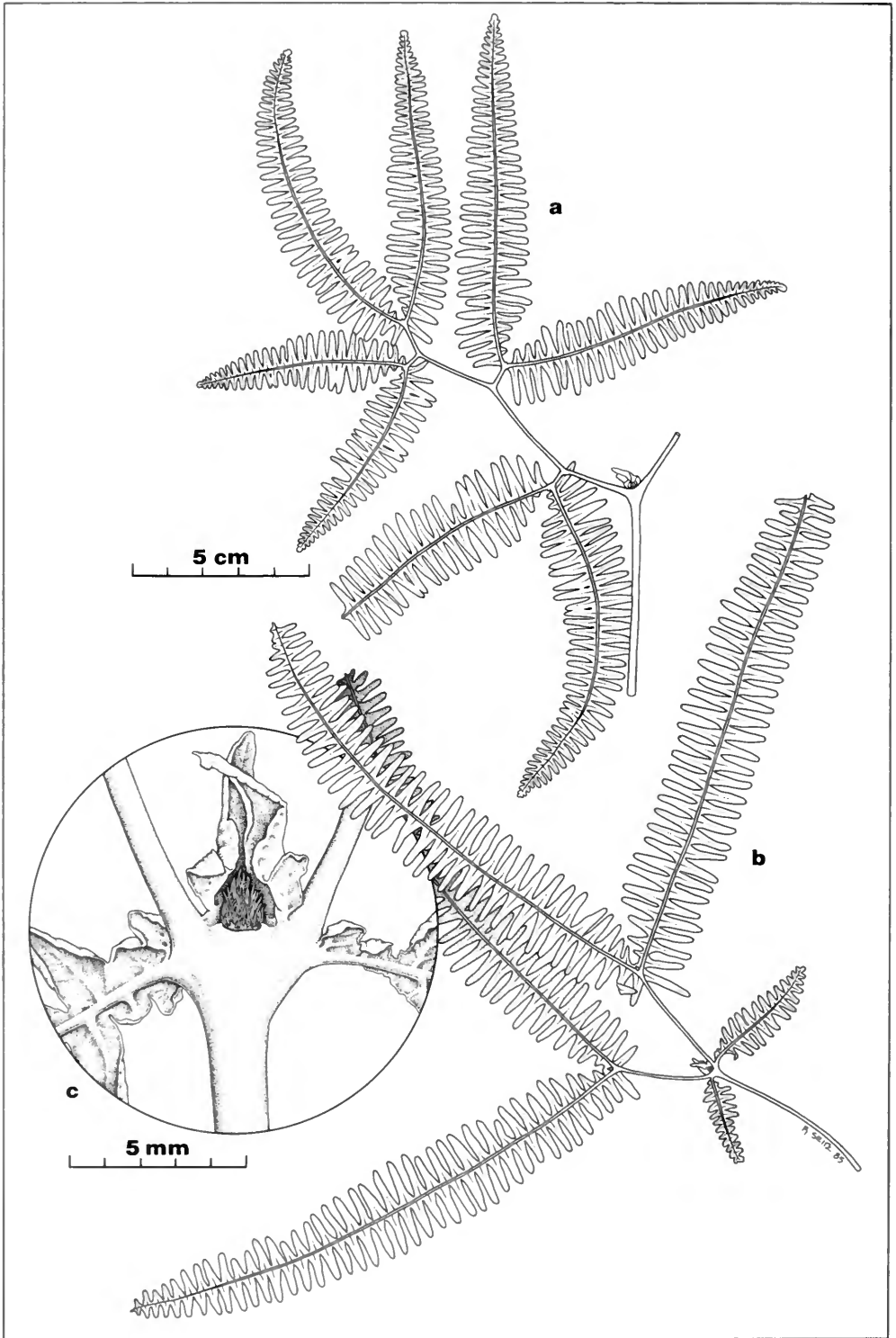


FIG. 10. *Dicranopteris pectinata*: a, primary axis and one pinna. *Dicranopteris flexuosa*: b, lamina, habit; c, axil of primary fork. (a from Belshaw 3435, F; b-c from Britton 7186, Cuba, F.)

3. **Dicranopteris pectinata** (Willd.) Underw., Bull. Torrey Bot. Club 34: 260. 1907. **Figure 10a.**

Mertensia pectinata Willd., Kongl. Vetensk. Acad. Nya. Handl. 25: 168. 1804. TYPE: Venezuela, Caracas, *Bredemeyer* (holotype, v, *Herb. Willd. 19465*; photo, GH).

Gleichenia pectinata (Willd.) Presl, Reliq. haenk. 1: 71. 1825.

Leaves with 1–several opposite pairs of stalked pinnae, these each bearing several to many unequal branches which are again unequally branched or which terminate in a pair of penultimate segments (i.e., each of the stalks unequal in length and diverging at much different angles), lacking accessory leafy segments at the base of the forks. **Axils** bearing a tuft of orange to reddish brown, curved to flexuous trichomes and often a pair of reduced stipule-like segments (at least within the proximal fork). **Pinnae** and their branches long-stalked, the axes commonly glabrous, the midribs and veins glabrous or, more often, sparsely to amply provided on the abaxial side with orange, stellate trichomes, the forked, penultimate segments sessile, to 23 cm long and 5 cm broad. **Ultimate segments** contiguous at base, to 25 mm long and 5 mm broad, chartaceous, glaucous abaxially, the margins scarcely to moderately revolute. **Spores** monolete.

Forest clearings and thickets, along roadsides and on open banks, 100–2000 m, Amazonas to Loreto, south to Cuzco and Puno.

Degree of pubescence on abaxial surfaces varies greatly in this species. In Central America and the West Indies the lamina is commonly glabrous, or with a few orange, stellate trichomes scattered along the veins; but in South America, especially in Peru, some pubescence is to be expected—varying from sparse to copious—and on a few specimens we have examined it is so dense as to nearly obscure the sori. It was perhaps one of these tomentose plants on which Hieronymus based his *Gleichenia* (*Dicranopteris*) *flexuosa* f. *monstrosa* (see discussion below under **Comments**).

Amazonas: Prov. Bagua, along roadside from Chiriaco to Puente Venezuela, *Barbour 4488* (MO). **San Martín:** Prov. Lamas, Dist. Lamas, *Belshaw 3435* (F, GH, MICH, MO, NY, UC, US). **Loreto:** Mishuyacu, near Iquitos, *Klug 850* (F, NY, US). **Huánuco:** Prov. Huánuco, Dist. Churubamba, Pampa Hermosa, *Mexia 8147* (F, GH, MICH, MO, NY, UC, US). **Pasco:** Prov. Oxapampa, road between Puente Paucartambo and Oxapampa, *D. Smith 1472* (F, MO). **Junín:** La Merced, thickets, *Killip & Smith 23804* (F, GH, NY, US). **Ucayali:** Prov. Coronel Portillo, road

Tingo María to Pucallpa, *Ridoutt s.n.* (GH). **Cuzco:** Prov. Paucartambo, near Asunción, *West 7121* (MICH *p.p.*, MO, UC *p.p.*).

Comments

Dicranopteris flexuosa f. **monstrosa** (Hieron.) Nakai, Bull. Natl. Sci. Mus. 29: 60. 1950.

Gleichenia flexuosa f. *monstrosa* Hieron. Hedwigia 48: 289. 1909. TYPE: Peru, Amazonas, Quebrada de Santa Lucía near Chachapoyas, *Stübel 1070* (holotype, not located).

This supposed form of *Dicranopteris flexuosa* was described from a plant which was rusty-tomentose on the juvenile segments of more distal pinnae. We have not seen evidence of tomentum on *D. flexuosa*, either on mature or juvenile plants, but it is possible this *could* represent a form of the species, or perhaps a hybrid. It is more likely that it belongs to the complex of tomentose species which are discussed above in the treatment of *D. nervosa*, particularly *D. seminuda* of Venezuela, which has the general aspect of *D. flexuosa*. Another likely possibility is that it may be a densely pubescent variant of *D. pectinata* (q.v.), although Hieronymus certainly should have mentioned the distinctive branching pattern of the latter if this were the case. Pending examination of the type, it is fruitless to conjecture further.

Family 6: HYMENOPHYLLACEAE

Hymenophyllaceae Link, Handbuch 3: 36. 1833.
TYPE: *Hymenophyllum* Sm.

Stem erect to decumbent, often slender and long-creeping, usually bearing scattered, short trichomes. **Leaves** commonly circinate in vernation, entire or pinnatifid to decompound, typically monomorphic, or rarely dimorphic in *Trichomanes*, glabrous or pubescent, lamina very thin (often 1 cell thick), lacking stomates. **Veins** free, or in a few species reticulate. **Sporangia** borne on marginal sori on a short to elongate receptacle, enclosed within a bivalvate or tubular indusium, with a short stalk and an oblique annulus not interrupted by the stalk. **Spores** trilete, tetrahedral-globose to spheroidal, commonly with chlorophyll.

The Hymenophyllaceae are a natural and distinctive family, with representatives found in tropical to wet temperate regions nearly throughout the world. Most of the nearly 600 species have the lamina only one cell thick, which has earned them the common name "filmy fern." The filmy leaves and the marginal sori shaped like a cup or pouch make them readily recognizable as a family, but through the years there have been great differences of opinion as to its subdivision. Various authors have split it into as many as 42 genera, whereas but two are recognized here.

The term *marginate* is used in this family to describe an axis of the leaf that has a very narrow band of green tissue on each side. Frequently this band is scarcely raised beyond the surface of the axis and is hardly discernible except for the color contrast with the axis. It is a rudimentary wing and represents the ultimate reduction of the conditions elsewhere described in the text as "broadly alate" or "narrowly alate."

The publications of Presl on the family have been cited according to the first publication, with the date and page number of the separately issued publication. Later publication with different pagination in the *Abh. Königl. Böhm. Ges. Wiss.* is not mentioned.

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Key to Genera of Hymenophyllaceae

- a. Indusium bivalvate, the valves $\frac{1}{2}$ or more the length of the indusium (rarely less); receptacle not or rarely and slightly exerted; venation anadromous; ultimate segments sometimes serrate, lacking false veins I. **Hymenophyllum**
- a. Indusium tubular and entire, or bilabiate, rarely bivalvate (and then the valves not more than $\frac{1}{3}$ the length of the indusium; receptacle commonly exerted at maturity, often strongly so; venation anadromous or catadromous; ultimate segments not serrate, with false veins sometimes present II. **Trichomanes**

I. Hymenophyllum

Hymenophyllum Sm., *Mém. Acad. Roy. Sci. (Turin)* **5**: 418. 1793. LECTOTYPE (designated by Presl, Hymenophyllaceae **31**. 1843): *Hymenophyllum tunbridgense* (L.) Sm. **Figure 11**.

Leptocionium Presl, Hymenophyllaceae **26**. 1843.

TYPE: *Leptocionium dicranotrichum* Presl = *Hymenophyllum dicranotrichum* (Presl) Sadeb.

Hymenophyllum subg. *Leptocionium* (Presl) Christ, *Farnkr. Erde* **20**. 1897.

Sphaerocionium Presl, Hymenophyllaceae **33**. 1843.

TYPE: *Sphaerocionium hirsutum* (L.) Presl (*Trichomanes hirsutum* L.) = *Hymenophyllum hirsutum* (L.) Sw.

Hymenophyllum subg. *Sphaerocionium* (Presl) C. Chr., *Index fil. Suppl.* **3**: 5. 1934.

Mecodium (Copel.) Copel., Philipp. J. Sci. **67**: 17. 1938.

Hymenophyllum subg. *Mecodium* Copel., Philipp. J. Sci. **64**: 93. 1937. TYPE: *Hymenophyllum polyanthos* (Sw.) Sw.

Plants epiphytic, occasionally epipetric or terrestrial. **Stem** filamentous, long-creeping, usually bearing scattered trichomes and small, delicate roots. **Leaves** monomorphic, petiolate, commonly 1-20(-50) cm long or, in *H. speciosum*, to nearly 2 m long. **Lamina** simple and entire (outside Peru) or pinnatifid to decompose, glabrous or sparsely to densely pubescent. **Ultimate segments** entire to

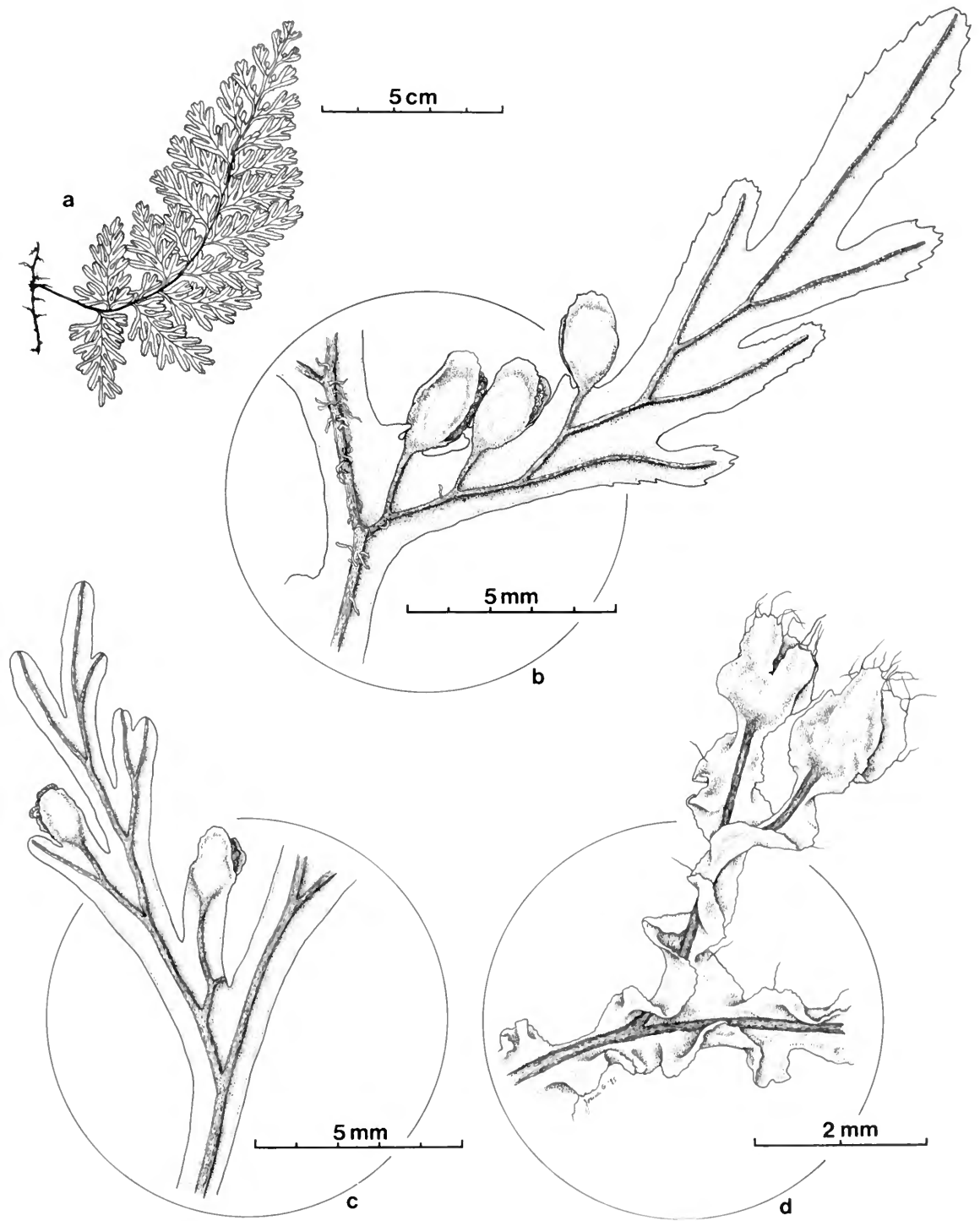


FIG. 11. *Hymenophyllum fucoides* var. *fucoides*: **a**, habit; **b**, pinna with sori. *Hymenophyllum polyanthos*: **c**, pinna with sori. *Hymenophyllum crispum*: **d**, pinna with sori. (a from Seiler 295, El Salvador, F; b from Plowman 6074, F; c from Schunke 462, F; d from Wurdack 1510, F.)

serrate, bearing usually a single vein. **Veins** free (reticulate in a few Old World species), anadromous, false veins absent. **Sori** terminal on the veins. **Indusium** bivalvate, the valves 1/2 or more the length of the indusium (rarely less), the sporangia borne on an elongate, sometimes subglobose, receptacle. **Receptacle** not or rarely exerted beyond the mouth of the indusium.

Nearly 300 species of *Hymenophyllum* are found throughout tropical regions of the world, although a few occur in wet subtropical and temperate areas. While most are epiphytes, several species have been reported from wet clay or rocky banks in dense forests. A number of genera and/or subgenera have been segregated by various authors, but in the following treatment Peruvian species are aligned into three well-defined subgenera: *Hymenophyllum*, *Mecodium*, and *Leptocionium*. A good revision of the latter was done by Morton (1947) under the name *Sphaerocionium*, but this and others still require careful study, and some of the species concepts are only provisionally treated below. Although there is no attempt here at a formal subgeneric classification, the species are so designated in the key and their descriptions follow in natural order.

To facilitate use of the key to species, some explanation of the diagnostic characters may be helpful here, especially in subg. *Leptocionium*. Caution is recommended when using the couplets that separate those species having trichomes borne only on veins and margins of segments (Morton's sub-

section *Ciliata*) from those in which trichomes are borne also on the segment surface *between* the veins and margins (his subsection *Lanata*). In a few species trichomes between the veins may be sparse—present only in areas toward the base of segments. Care must be exercised that these are not overlooked. Conversely, there are several species with stellate trichomes so dense on veins and margins, and with stalks so long, that they may at first *appear* to spring from the intervening tissue.

Furthermore, certain groups of species in subg. *Hymenophyllum* and *Leptocionium* are distinguished by the presence of lamellae: accessory green wings or crests of tissue that emerge from the veins or costae, but not on the same plane as the lamina. Typically these lamellae are made conspicuous by their size, shape, or abundance, but in *H. lobatolatum* they are small and scattered, and in *H. plumosum* they are not at all foliose, but instead are low and inconspicuous, and usually obscured by the dense, matted tomentum covering the entire lamina. In *H. mirificum* they could be mistaken for trichomes, since many of them, although four to six cells wide at the base, abruptly become uniseriate and grade to a filiform tip.

Reference

MORTON, C. V. 1947. The American species of *Hymenophyllum* sect. *Sphaerocionium*. Contr. U.S. Natl. Herb., 29: 139–201.

Key to Species of *Hymenophyllum*

- a. Ultimate segments conspicuously serrate, glabrous, or rarely the serrations tipped by a short, pluricellular trichome [subg. *Hymenophyllum*] b
- b. Costae and veins lacking lamellae c
- c. Pinnae subequilateral at least beyond the base; sori (most of them) borne in the same plane as the lamina, only occasionally arcuate; petiole usually more than 0.3 mm in diameter 1. ***H. fucoides***
- c. Pinnae dimidiate (i.e., secondary segments all borne on acroscopic side); sori (most of them) strongly arcuate, thus arranged nearly perpendicular to the plane of the lamina; petiole less than 0.3 mm in diameter 2. ***H. peltatum***
- b. Costae or veins (at least adaxially) bearing few to many lamellae not in the plane of the lamina, these several to many cells wide at base, becoming uniseriate toward apex d
- d. Petiole nonalate; rachis flexuous, nonalate, or slightly so to marginate distally; lamellae scattered and inconspicuous 3. ***H. mirificum***
- d. Petiole broadly alate, often nearly to base; rachis straight, broadly alate throughout; lamellae frequent and conspicuous 4. ***H. lamellatum***
- a. Ultimate segments entire, sometimes undulate to crispate, but never serrate, or rarely minutely denticulate and then the teeth tipped by unicellular or stellate trichomes e

- e. Lamina glabrous; ultimate segments with margins entire (although often crispate) [subg. *Mecodium*] f
- f. Leaves 1.5–4(–5) cm long; pinnae 3–6 pairs; rachis strongly flexuous to fractiflex 5. **H. apiculatum**
- f. Leaves (mature ones) 6–30 cm long; pinnae 8–30 pairs; rachis straight or slightly (rarely strongly) flexuous g
- g. Mature indusia ovoid, elliptical, or rhomboid, most of them somewhat to markedly longer than broad, apex obtuse to acute, base narrowly to broadly cuneate (occasionally rounded) and slightly to deeply immersed in the segment tissue; soriferous segment tips not or slightly constricted, as broad as (or slightly narrower than) mature indusia h
- h. Mature indusia broad- or narrow-ovoid, broadest toward the rounded or broadly cuneate base, slightly immersed in the segment tissue; receptacle filiform to narrow-cylindrical, short, not or rarely exerted i
- i. Petiole marginate or alate near apex or throughout (wings sometimes partly deciduous); rachis alate throughout; leaves commonly less than 15 cm long; growing at 100–2000(–2400) m 6. **H. polyanthos**
- i. Petiole neither alate nor marginate; rachis commonly nonalate at base, at least on one side; leaves (mature ones) commonly 14–30 cm long; growing at 2100–3150 m 7. **H. mathewsii**
- h. Mature indusia rhomboid, elliptic, or conical, broadest at or beyond the middle, the base narrow-cuneate, deeply (often halfway) immersed in the segment tissue; receptacle filiform, long, often exerted 8. **H. trichomanoides**
- g. Mature indusia subglobose, circular in outline to broader than long, the apex rounded, the base rounded or subtruncate, not or scarcely immersed in the segment tissue; soriferous segment tips somewhat to greatly constricted, narrower than the mature indusia (usually so much so that indusia appear pedicellate) j
- j. Sporangia (5–)6–20 per sorus; petiole marginate or alate, at least distally (wing sometimes deciduous); rachis alate throughout k
- k. Indusium apex erose; 1–several elongated pinnae intermixed among normal ones 9. **H. ferax**
- k. Indusium apex entire; elongated pinnae rare or lacking among normal ones 10. **H. myriocarpum**
- j. Sporangia 1–4(–5) per sorus; petiole neither marginate nor alate; rachis commonly nonalate toward base (or discontinuously alate on either side due to decurrent pinna bases) 11. **H. undulatum**
- e. Lamina pubescent (at least on margins or veins), often densely so; ultimate segments entire or rarely minutely denticulate [subg. *Leptocionium*] l
- l. Trichomes lacking on tissue between the veins m
- m. Petiole slender, 0.2–0.3 mm in diameter n
- n. Rachis nonalate at least in the proximal portion, or weakly and irregularly alate due to the decurrent pinna bases; petiole nonalate, or weakly alate on one side due to the decurrent pinna base o
- o. Pinnae (at least proximal ones) short-stalked, abundantly to densely pubescent on veins and margins p
- p. Costae regularly and conspicuously alate throughout on both sides; pinnae regularly diminishing in length toward lamina apex, larger ones with 4–9 pairs of segments 12. **H. molle**
- p. Costae partially nonalate, or discontinuously alate due to the decurrent bases of segments; pinnae often irregular in length, some of them greatly elongate, normal ones with 2–3(–4) pairs of segments 13. **H. trichophyllum**
- o. Pinnae sessile or adnate, sparsely to moderately pubescent on veins and margins q
- q. Marginal trichomes mostly forked at base or 2-forked (a few simple or stellate), petiole trichomes simple or forked; leaves determinate 14. **H. elegans**

- q. Marginal and petiole trichomes mostly stellate; leaves indeterminate 15. **H. adiantoides**
- n. Rachis regularly and conspicuously alate throughout; petiole alate on both sides, at least at its apex r
- r. Segments essentially plane; trichomes of segment margins mostly stellate or 2-forked 16. **H. hirsutum**
- r. Segments undulate-crispate; trichomes of segment margins simple or forked from base 17. **H. crispum**
- m. Petiole (of mature leaves) stout, 0.4–1.5 mm in diameter s
- s. Rachis conspicuously alate throughout; petiole usually alate just below lamina; trichomes lacking on adaxial side of lamina t
- t. Ultimate segments and rachis wing slightly to strongly undulate; stellate trichomes lacking on petiole 18. **H. valvatum**
- t. Ultimate segments and rachis wing not or scarcely undulate; stellate trichomes frequent on petiole among the simple and forked ones 19. **H. microcarpum**
- s. Rachis nonalate, at least in the proximal portion; petiole nonalate; trichomes present on axes and veins both abaxially and adaxially 20. **H. ruizianum**
- l. Trichomes (few to many) borne on the segment surface between the veins as well as on the veins and margins u
- u. Veins lacking lamellae v
- v. Petiole slender, 0.2–0.3 mm in diameter (or sometimes to 0.4 mm in *H. amabile*) ... w
- w. Pinnae or primary segments simple, entire; leaves to 7 cm long ... 21. **H. simplex**
- w. Pinnae or primary segments lobed to pinnatisect; leaves over 12 cm long (except sometimes less in *H. fragile*) x
- x. Lamina moderately to abundantly pubescent, but veins and tissue always clearly visible y
- y. Rachis broadly alate throughout; leaves determinate; petiole trichomes simple to forked and often stellate 22. **H. fragile**
- y. Rachis nonalate (sometimes alate distally); leaves indeterminate; petiole trichomes simple or forked, not or rarely stellate 23. **H. elegantulum**
- x. Lamina densely tomentose, the veins and tissue often obscured 24. **H. amabile**
- v. Petiole (of mature leaves) stout, 0.4–1.0 mm in diameter z
- z. Lamina densely tomentose, the veins and tissue mostly obscured by the tomentum; rachis nonalate throughout aa
- aa. Trichomes on rachis sessile or short-stalked, very tightly appressed; larger pinnae (2.5–)3–8 cm long, with 6–14 pairs of segments 25. **H. speciosum**
- aa. Trichomes on rachis short- to long-stalked, spreading; larger pinnae 1–2.3 cm long, with 4–7 pairs of segments 26. **H. karstenianum**
- z. Lamina moderately to abundantly pilose, but surfaces not obscured by the trichomes; rachis commonly alate, at least distally, only occasionally nonalate bb
- bb. Petiole (8–)10–15 cm long, 0.7–1.2 mm in diameter; lamina ovate to ovate-lanceolate, 8–15 cm broad, not or slightly reduced at base 27. **H. lindenii**
- bb. Petiole 2–7 cm long, 0.4–0.6(–0.7) mm in diameter; lamina linear, 3–8 cm broad, often strongly and gradually reduced toward base 28. **H. plumieri**
- u. Veins bearing conspicuous lamellae (or, in *H. plumosum*, the outgrowths low and inconspicuous, these and the veins obscured by dense tomentum) cc
- cc. Rachis nonalate nearly or wholly throughout dd
- dd. Lamellae minute and inconspicuous, these and the veins obscured by dense tomentum 29. **H. plumosum**
- dd. Lamellae broad and conspicuous, especially abaxially (if surface densely tomentose, most lamellae still usually visible among the trichomes) ee
- ee. Trichomes frequent, but not forming a dense cover; lamellae conspicuous abaxially, sometimes less so adaxially 30. **H. multialatum**

- ee. Trichomes densely covering (sometimes obscuring) tissue and veins; lamellae sometimes lacking adaxially 31. **H. tomentosum**
- cc. Rachis alate nearly or wholly throughout ff
- ff. Petiole rather stout, 0.4–0.7 mm in diameter; rachis strongly and regularly alate, at least above the base; leaves 9–60 cm long; pinnae (larger ones) with 6–24 segments gg
- gg. Pinnae mostly narrow-triangular, narrowly acute to attenuate, larger ones 20–45 mm long, with (6–)7–12 pairs of segments hh
- hh. Lamellae on abaxial side mostly consisting of scattered flanges, about as broad as long, lacking adaxially 32. **H. lobatoalatum**
- hh. Lamellae on abaxial side abundant, conspicuous, elongate, often nearly the length of the vein, sometimes less abundant and conspicuous adaxially 33. **H. pyramidatum**
- gg. Pinnae oblong to broadly triangular, obtuse or subacute, larger ones 6–20 mm long, with 3–6(–8) pairs of segments 34. **H. verecundum**
- ff. Petiole slender, 0.10–0.15 mm in diameter; rachis weakly and irregularly alate due to the decurrent pinna bases; leaves less than 7 cm long; pinnae with 2–4 segments 35. **H. tarapotense**

1. **Hymenophyllum fucoides** (Sw.) Sw., J. Bot. (Schrader) 1800(2): 99. 1802.

Leaves 4–25(–30) cm long, 1.5–8 cm broad. **Petiole** 0.3–0.8 mm in diameter, nonalate or marginate to alate distally, glabrous to sparsely or moderately pubescent with catenate trichomes. **Lamina** broadly or narrowly oblong, not or rather abruptly reduced at base, 3–4-pinnatisect. **Rachis** broadly to narrowly alate throughout, or nonalate just at the base, sparsely to moderately provided with flexuous, catenate trichomes. **Pinnae** 3–20(–25) pairs, adnate, or proximal 1–2 pairs short-stalked, subequilateral except at base, there truncate acroscopically, cuneate basiscopically, with 2–8 pairs of pinnatisect to 2-pinnatisect segments. **Sori** 1–8 per pinna, not or scarcely immersed in the segment tissue, most of them borne in the same plane as the lamina, not or only occasionally arcuate. **Indusia** narrowly to broadly oblong or elliptic, the apex obtuse to subacute and entire to lacinate, receptacle narrow-cylindrical or fusiform to ovoid, not exerted or occasionally slightly so.

The species occurs in the West Indies; southern Mexico to Panama; Venezuela and Colombia to Brazil and Bolivia.

This species has been misunderstood, both in its nomenclature and taxonomy, since it was first recognized by Swartz in 1788. The source of the greatest confusion is a supposed type collection

(BM) of *Hymenophyllum cristatum* Hooker & Grev. This sheet contains two specimens of *H. fucoides*, while pinned to it is an exact copy of *t. 148*, Icon. fil. 1829, the illustration of *H. cristatum*, complete with globose receptacle and conspicuous lamellae on the veins, which is an Ecuadorean species of a different section, *Buesia* (Morton) Morton. This led to another error, for the subsequent illustration *H. fucoides* in Hooker's "Century of Ferns" (1854) was evidently produced from this mixed sheet, thus misleading later investigators about some of the principal diagnostic features (for a full discussion see Stolze, Amer. Fern J. 77: 137–140. 1987).

A second source of confusion has been the highly variable nature of the species, which has prompted the recognition of a number of related taxa at various levels over the years. Morphological features are rather constant in the West Indian specimens, where leaves are quite small and compact; but variability increases in Central America, where some leaves are larger and more elongate, and apices of indusia are deeply dentate. Even greater differences are found in South American plants, especially in Peru, where variability is at its peak. It is likely that part of this may be due to the effects of ecological niches and altitudinal levels, but this kind of analysis must wait for a much-needed revision of this part of the genus.

For purposes of this treatment *H. fucoides* has been segregated into four varieties, a key to which is provided here.

Key to Varieties

- a. Rachis marginate to narrow-alate, or if broadly alate then alae essentially plane, ultimate segments plane b
- b. Apex of indusium entire, erose or denticulate c
- c. Rachis narrow-alate, or sometimes nonalate at base; petiole nonalate, or occasionally marginate near lamina base; basal pinnae often short-stalked; sori rarely more than 3 to a pinna la. var. **fucooides**
- c. Rachis broadly alate throughout, each wing broader than the rachis; petiole usually alate distally, at least near lamina base; basal and other pinnae adnate; sori often 5-8 to a pinna lb. var. **calodictyon**
- b. Apex of indusium spinulose-dentate to laciniate lc. var. **pedicellatum**
- a. Rachis broadly alate its entire length, alae and/or ultimate segments often undulate and their margins discontinuously conduplicate ld. var. **chachapoyense**

1a. *Hymenophyllum fucooides* var. **fucooides**. Figure 11a-b.

Trichomanes fucooides Sw., Prodr. 136. 1788. TYPE: Jamaica, Swartz (holotype, s; isotypes, B, BM; photos, F & GH of B, US of BM).

Leptocionium fucooides (Sw.) Presl, Hymenophyllaceae 27. 1843.

Meringium fucooides (Sw.) Copel., Philipp. J. Sci. 67: 45. 1938.

Petiole (0.3-)0.4-0.8 mm in diameter, nonalate, occasionally marginate near apex. **Rachis** narrow-alate or marginate, at least distally, alae plane. **Pinnae** adnate, or 1-2 proximal pairs short-stalked, ultimate segments plane. **Sori** 1-3(-4) pairs to a pinna, apex of indusia entire to denticulate, rarely dentate.

On trunks and branches of trees in wet forest, rarely on wet rock walls, 1700-3300 m, Amazonas, San Martín, Huánuco to Puno.

West Indies; southern Mexico to Panama; Venezuela and Colombia to Brazil and Bolivia.

The most diminutive of these ferns scarcely differ from *H. tunbridgense* (L.) J. Sm., the type of the genus, which is said to differ in its smaller leaves and in its strongly arched sori. The latter species supposedly occurs in the West Indies and in Europe and Africa, but it may be only another component in this complex. Some authors place it, with *H. peltatum* and a few others, in sect. *Hymenophyllum*, distinguished principally by the strongly arched sori, which are borne nearly perpendicular to the plane of the lamina. In Old World specimens especially, this character is inconstant and is but one of the problems which needs closer scrutiny when the group is revised.

Amazonas: Trail east of La Peca in Serranía de Bagua, Gentry et al. 23034 (F, MO, US). **San Martín:** Venceremos, near Amazonas border, Gentry et al. 45402 (MO). **Huánuco:** Cani, NE of Mito, Bryan 206, 384 (F); Macbride 3397 (B, F, US). **Cuzco:** Cerro Chuyapí, Bues 455 (GH, US), 456 (US). **Puno:** Sandía, Weberbauer 713 (B).

1b. *Hymenophyllum fucooides* var. **calodictyon** (Bosch) Stolze, *comb. & stat. nov.*

Hymenophyllum calodictyon Bosch, Ned. Kruidk. Arch. 5(3): 172. 1863. TYPE: Peru, Ruíz 84 (holotype, B!).

Petiole 0.5-0.8 mm in diameter, conspicuously alate to marginate distally. **Rachis** broadly alate throughout, each of the alae plane and much wider than the rachis. **Pinnae** all adnate, with ultimate segments plane. **Sori** (1-)2-8 pairs to a pinna, apex of indusia entire.

On trees in wet forests, Cajamarca and Amazonas south to Cuzco, 2100-3300 m.

Ecuador; Peru.

In addition to the characters mentioned in the key, var. *calodictyon* commonly may be distinguished from the other varieties by the broader segments, membranaceous tissue, and the lighter, yellow-green color.

Cajamarca: Prov. Cutervo, Dist. San Andrés, Agua Fría, A. Diaz et al. 5340 (USM). **Amazonas:** Prov. Bagua, Cordillera Colán SE of La Peca, Barbour 3586 (F, MO, USM). Prov. Bongará, near Pomacocha, Wurdack 865 (F, GH, UC, US). **Huánuco:** Prov. Huánuco, Carpish, Plowman 6074 (F, GH, US). **Pasco:** Prov. Oxapampa, E of Abra Cantarizú, Skog et al. 5108 (US). **Cuzco:** Prov. Paucartambo, Dist. Marcacocha, near Achirani, Vargas 11142 (F, UC, US).

1c. *Hymenophyllum fucoides* var. *pedicellatum* (Klotzsch) Hieron., Bot. Jahrb. Syst. 34: 435. 1904.

Hymenophyllum pedicellatum Klotzsch, Linnæa 20: 439. 1847. TYPE: Venezuela, Mérida, *Moritz 346* (holotype, B; isotypes, BR, US in part!).

Leptocionium pedicellatum (Klotzsch) Fourn., Bull. Soc. Bot. France 19: 249. 1872.

Petiole 0.3–0.5 mm in diameter, nonalate. **Rachis** broadly to narrowly alate, alae plane. **Pinnae** adnate, or basal pair short-stalked, ultimate segments plane. **Sori** 1–3 pairs to a pinna, apex of indusia lacinate to spinulose-dentate.

On trees in wet forests, 500–2400 m, Amazonas. Venezuela; Colombia; Ecuador; Peru.

This may be synonymous with *H. peruvianum*, which see under **Comments**. It is likely that *H. ectocarpon* Fée, of Central America and the Lesser Antilles, should be included here also.

Amazonas: Prov. Bagua, Cordillera Colán, SE of La Peca, *Barbour 3598* (F, MO, USM), *3976* (F, MO). Prov. Bagua, Montenegro-Chiriaco, *Sagástegui 5931* (GH).

1d. *Hymenophyllum fucoides* var. *chachapoyense* Stolze, var. nov.

Differt a var. *fucoides* characteribus sequentibus: alae rhachidis latae et saepe undulatae; segmenta ultima saepe undulata.

Petiole 0.5–0.9 mm in diameter, commonly alate distally, at least at the apex. **Rachis** broadly alate throughout, the alae often undulate. **Pinnae** adnate, the ultimate segments often undulate and their margins discontinuously conduplicate. **Sori** commonly 3–10 to a pinna, apex of indusia entire.

TYPE—Peru, Dept. Amazonas, Prov. Chachapoyas, Cerros de Calla Calla, 18 km above Leimebamba on road to Balsas, 3100 m, *Hutchison & Wright 5659* (holotype, GH!; isotype, UC!).

On trunks and branches of trees, in wet forests and moist, wooded ravines, 2900–3700 m, Amazonas, Huánuco.

Colombia (Dept. del Valle); Ecuador (Prov. Carchi & Napo); Peru.

This is a robust variety of higher elevations, similar to var. *calodictyon* in its stout petioles and larger leaves (to 25 cm long, occasionally longer).

In its undulate to crispate rachis wings and ultimate segments, var. *chachapoyense* resembles *Hymenophyllum tortuosum* Hooker & Grev. of Chile; however, alae and segments of the latter are much more strongly crispate and are setose-serrate as well.

Amazonas: Prov. Chachapoyas, Cerros de Calla Calla, 26 km above Leimebamba on road to Balsas, *Hutchison & Wright 6987* in part (F, GH, UC). **Huánuco:** Tambo de Vaca, *Macbride 4460* (F, US).

2. *Hymenophyllum peltatum* (Poir.) Desv., Mém. Soc. Linn. Paris 6: 333. 1827.

Trichomanes peltatum Poir. in Lam., Encycl. 8: 76. 1808. TYPE: Mauritius, "Ile-de-France, Bory de Saint-Vincent (V.s. in Herb. du Petit-Thouars)" (not located).

Leaves 2.5–8 cm long, 1–2 cm broad. **Petiole** 0.15–0.3 mm in diameter, nonalate, glabrous. **Lamina** narrowly oblong to lanceolate, slightly reduced at base, 2–3-pinnatisect. **Rachis** nonalate, occasionally marginate distally, essentially glabrous. **Pinnae** 4–10 pairs, adnate, or 1–2 proximal pairs short-stalked, dimidiate (i.e., the 1–4 secondary segments all borne on acroscopic side). **Sori** 1 or 2 per pinna, not immersed in the segment tissue, most of them strongly arcuate, thus arranged nearly perpendicular to the plane of the lamina. **Indusia** subspheroid to ovoid, the apex obtuse, entire, receptacle narrow-cylindrical, not or rarely exerted.

On rocky slopes and cliffs, 2800–4700 m, Junín, Cuzco, Madre de Dios, Puno.

Peru; Bolivia; Argentina; Chile; Europe; Africa.

Diem and Lichtenstein (1959) reported that *H. peltatum* is highly variable in southern South America. They recognized six varieties in Argentina and/or Chile and also consider that it is also present in one form or another in areas of the Old World. Apparently only var. *peltatum* occurs in Peru. It is a much more delicate fern than *H. fucoides* and can be easily distinguished from the latter by the strongly dimidiate pinnae. Most sori are rather conspicuously arched out of the plane of the lamina, a character which Morton (1968) used to separate sect. *Hymenophyllum* from others in subg. *Hymenophyllum*. This feature is not constant in some other species, notably *H. tunbridg-*

ense (L.) Sm., and its value is questionable as a diagnostic character above the level of species.

Junin: Prov. Huancayo, Dist. Huancayo, Huaytapallana, *Saunders 1167* (GH). **Cuzco:** "Ccarcco" (Ccorca?), *Bües 1395* (US). **?Madre de Dios:** Piñasniocj, "Panticalla Pass" (Pantiacolla?), *Cook & Gilbert 1868, 1870* (US). **Puno:** Prov. Carabaya, Ayapata, *Vargas 10705* (GH).

3. **Hymenophyllum mirificum** Morton, Bot. Gaz. (Crawfordsville) 93: 338. 1932. TYPE: Peru, Cuzco, Prov. La Convención, Vilcabamba, *Bües 1600* (holotype, us!; photo, F).

Buesia mirifica (Morton) Copel., Philipp. J. Sci. 67: 48. 1938.

Leaves 16–38 cm long, (5–)7–14 cm broad. **Petiole** 4.5–7 cm long, (0.4–)0.5–0.8 mm in diameter, nonalate or, rarely, very narrowly so or marginate at apex, sparsely provided with brownish, flexuous, catenate trichomes. **Lamina** broadly or narrowly oblong, not or abruptly reduced at base, deeply 3–4-pinnatisect, sparsely and inconspicuously lamellate adaxially. **Rachis** strongly flexuous, nonalate, or weakly alate toward the apex, sparsely provided with flexuous, catenate trichomes and (adaxially) also with widely scattered lamellae, these usually 4–6 cells wide at base, abruptly becoming uniseriate and often grading to a sharp, filiform tip. **Pinnae** 10–20 pairs, proximal ones subdistant and short-stalked, distal ones approximate and adnate, costae flexuous and narrowly alate, with 6–10 pairs of 2-pinnatisect secondary segments, ultimate segments long and narrow, glabrous, plane, the margins serrate, lamellae inconspicuous and often widely scattered along veins adaxially. **Sori** several to many, especially on distal pinnae, not or scarcely immersed in the segment tissue, lying essentially in the plane of the lamina. **Indusia** subspherical to ovoid, the margins subentire, receptacle subglobose, not exerted.

Endemic. In damp ravines and on trees, in wet forests, 2800–3650 m, Cuzco.

This is closely related to *Hymenophyllum cristatum* Hooker & Grev. of Ecuador, which has the same general aspect and habit. Both species have elongate, pendent leaves with flexuous rachises, subspherical to ovoid indusia, subglobose receptacles, and lamellae on axes and veins. But *H. mirificum* has larger pinnae, rachis wings essentially lacking, lamellae sparse and inconspicuous,

and apices of indusia entire to denticulate. Rachises in *H. cristatum* are obviously alate throughout, lamellae are numerous and conspicuous, and indusia are deeply dentate to lacinate at apex. For further discussion about the confused identity of *H. cristatum*, see *H. fucooides*.

Cuzco: Prov. La Convención, Vilcabamba, *Bües 1592, 1593, 2104* (US). Prov. Paucartambo, Acanacu, *Vargas 29* (GH); *West 7144* (UC, US). Prov. Urubamba, Puyupata-Yuncapata, *Vargas 2922* (MO, US).

4. **Hymenophyllum lamellatum** Stolze, *sp. nov.*

Folia 7–15 cm longa, 2.5–4.5(–6) cm lata. Petiolus 1.5–5 cm longus, 0.35–0.7 mm diametro, conspicue alatus. Lamina 2-pinnatisecta vel 3-pinnatisecta, conspicue lamellata. Rhachis recta, late alata, lamellis conspicuis instructa. Pinnae 9–13-jugatae, confertae vel imbricatae, adnatae, 1–2.5(–3) cm longae, costis et venis lamellatis praeditae. Segmenta saepe ultima undulata, marginibus serratis. Indusia sphaeroidea vel ovoidea, brevipedicellata, marginibus integris, receptaculis subglobois vel ovoideis.

Leaves 7–15 cm long, 2.5–4.5(–6) cm broad. **Petiole** 1.5–5 cm long, 0.37–0.7 mm in diameter, conspicuously alate well toward, or quite to, base, sparsely provided with brownish, flexuous, catenate trichomes. **Lamina** oblong-lanceolate, not or scarcely reduced at base, 2–3-pinnatisect, conspicuously lamellate adaxially. **Rachis** straight, broadly alate throughout, sparsely to amply pubescent with flexuous, catenate trichomes and also provided with conspicuous scalelike lamellae, these several to many cells wide at base, long-acuminate and often grading to a sharp, filiform tip. **Pinnae** 9–13 pairs, crowded to imbricate, adnate at base, 1–2.5(–3) cm long, adaxially lamellate on costae and veins as on the rachis, with 3–6 pairs of 2-pinnatisect or (distally) pinnatisect segments, ultimate segments glabrous, usually slightly to strongly undulate, the margins serrate, often conduplicate. **Sori** few, commonly 1 per pinna on the basal acroscopic segment, not immersed in the segment tissue, lying essentially in the plane of the lamina. **Indusia** subspherical to ovoid, the margins entire, receptacle subglobose or ovoid, not or slightly exerted.

TYPE—Peru, Huánuco, Prov. Huánuco, trail from S entrance of Carpath tunnel to crest of ridge, *Luteyn & Luteyn 5474* (holotype, us!; isotype, NY!).

Endemic. In wet forests, on tree trunks and branches, 2750–3000 m, Huánuco, Cuzco, Puno.

Some of the specimens cited below were earlier suspected of being new species. On the sheets of *Bües A17 & A20* (US) are Morton's penciled remarks, "sect. *Buesia*, n. sp.?"; and *Lechler 2568* (B) is annotated by Mettenius, "*H. latipes* Mett." Apparently Mettenius intended to publish, but a search of the literature has revealed nothing under this name. In its small size, compact lamina, and conspicuously alate axes, this is the most distinctive species in sect. *Buesia*.

Cuzco: Alturas de Sicre, *Bües 1562* (US). Valley of Río Urubamba, *Bües A-17, A-20* (US). Prov. La Convención, at Klaus' Folly, above Camp 5, *Dudley 11000* (GH). **Puno:** Tatanara, *Lechler 2568* (B).

5. *Hymenophyllum apiculatum* Kuhn, *Linnaea* 35: 391. 1868. TYPE: Venezuela, Edo. Aragua, Colonia Tovar, *Fendler 32* (holotype, B; isotype, US).

Hymenophyllum dendritis Rosenst., *Repert. Spec. Nov. Regni Veg.* 6: 308. 1909. TYPE: Bolivia, San Carlos near Mapiiri, *Buchtien 1093* (holotype, B?; isotype, US!).

Mecodium dendritis (Rosenst.) Copel., *Philipp. J. Sci.* 67: 26. 1938.

Mecodium apiculatum (Kuhn) Vareschi, *Flora Venezuela*, Caracas 1: 198. 1969.

Leaves 1.5–4(–5) cm long, 0.8–1.8 cm broad. **Petiole** 0.3–1.5 cm long, 0.1–0.25 mm in diameter, marginate to narrow-alate, glabrous or with a few scattered trichomes, especially at very base. **Lamina** ovate or deltoid-ovate, not or scarcely reduced at base, 2–3-pinnatifid, glabrous. **Rachis** glabrous, strongly flexuous to fractiflex, alate throughout. **Pinnae** 3–6 pairs, adnate, larger ones 0.5–1.2 cm long, bearing 1–4 pairs of secondary segments. **Ultimate segments** entire, plane, or occasionally the margins involute or conduplicate. **Sori** 1–4 to a pinna, usually confined to apical portion of lamina. **Indusia** rhomboid or ovoid, apex entire and obtuse to subacute, with broadly cuneate base, about halfway immersed in the segment tissue, receptacle filiform, not exserted, bearing 6–12 sporangia.

In dense forests on branches and trunks of trees and on fallen logs, 100–1500(–2000) m, San Martín, Loreto, Huánuco, Pasco, Cuzco.

Venezuela; Colombia; Peru; Bolivia.

This would appear to be simply a reduced form of *Hymenophyllum polyanthos*; however, it not only has smaller leaves, more delicate petioles, and

fewer pinnae, but the character of its sori is different. The narrowly cuneate base of the indusium is deeply immersed in the segment tip, whereas in *H. polyanthos* the indusium base is broadly cuneate to obtuse and only slightly immersed in the tissue.

San Martín: Prov. Mariscal Cáceres, Dist. Tocache Nuevo, Cerro Sinsín, *Plowman & Schunke 11478* (F). **Loreto:** Mishuyacu, near Iquitos, *Klug 1518* (F, NY, US). **Huánuco:** Environs of Tingo María, *Aguilar 304* (UC). Tingo María (as San Martín), *Allard 20741, 21485* (GH, US). **Pasco:** Puerto Bermúdez (as Junín), *Killip & Smith 26415* (F, US). **Cuzco:** Valle de Lares, alturas del Río Lachac, *Bües 1813a* (US).

6. *Hymenophyllum polyanthos* (Sw.) Sw., *J. Bot. (Schrader)* 1800(2): 102. 1802. **Figure 11c.**

Trichomanes polyanthos Sw., *Prodr.* 137. 1788. TYPE: Jamaica, *Swartz* (holotype, S; isotypes, B, BM; photos, US of S, F & GH of B).

Mecodium polyanthos (Sw.) Copel., *Philipp. J. Sci.* 67: 19. 1938.

Mecodium mexiae Copel., *Univ. Calif. Publ. Bot.* 19: 294, t. 48. 1941. TYPE: Peru, Huánuco, near confluence of Río Huallaga, *Mexia 8282* (holotype, UC!; isotypes, B!, F!, MO!).

Hymenophyllum mexiae (Copel.) Morton, *Contr. U.S. Natl. Herb.* 38: 173. 1968.

Leaves (6–)8–15 cm long, 2–5(–6) cm broad. **Petiole** 0.5–5 cm long, 0.3–0.6 mm in diameter, alate near the apex or throughout, glabrous. **Lamina** ovate or elliptic, scarcely reduced at base (or proximal 1–2 pairs of pinnae slightly reduced), 3–4-pinnatisect, glabrous. **Rachis** glabrous, straight or slightly flexuous, alate throughout. **Pinnae** 8–14 pairs, essentially adnate, but not strongly overlapping the rachis, larger ones 1–4 cm long, bearing 2–many secondary segments. **Ultimate segments** entire, plane or occasionally a few with conduplicate segment margins, larger ones commonly more than 1 mm broad, the free portion relatively short, usually about twice as long as broad. **Sori** 2–many per pinna. **Indusia** relatively small, usually about as broad as the segment apex, ovoid, elliptic, or lanceolate, broadest toward the base, apex obtuse or subacute, the broadly cuneate base slightly immersed in the segment tissue, margins entire, receptacle filiform to narrowly cylindrical or fusiform, not exserted, bearing 6–15 sporangia.

In dense forests, on fallen logs, and on trunks of trees and tree ferns, 100–2000(–2400) m, Amazonas, Loreto, San Martín south to Puno.

Pantropical.

This is one of the most widely distributed ferns of tropical regions around the world and with its many close relatives represents one of the more taxonomically difficult species complexes. Components of the group each have only a few distinguishing characters and these are often inconstant. Some of the features seem to vary more or less in different geographic areas, so that species concepts in each of these regions vary proportionately. The group has long been misunderstood; consequently, in most herbaria, a number of specimens may be filed incorrectly under *Hymenophyllum polyanthos*.

For purposes of this treatment, *H. polyanthos* includes *H. mexiae*, which differs only in its smaller leaves. Leaves of *H. apiculatum* are also very small, but this species (q.v.) is characterized by other, quantitative, features, and so should be considered distinct. *Hymenophyllum mathewsii* may be merely a more luxuriant, higher elevation form of *H. polyanthos*, with larger leaves and sori, and the axes less distinctly alate. Another species of the subgenus occurring in Peru is *H. myriocarpum*, which differs principally in shape and character of the indusia: in most specimens sori appear to be pedicellate, for the apices of ultimate segments are strongly constricted; furthermore, mature indusia are subglobose, or often noticeably broader than long. This contrasts with the essentially ovoid indusia of *H. polyanthos* et al., commonly somewhat longer than broad and slightly to strongly immersed in the segment tips, which are not or scarcely constricted. While this character is probably the most reliable one in subg. *Mecodium* in Peru, unfortunately even it is not 100% constant, for on occasional specimens indusia may vary somewhat from one shape to another. Consequently, most species in the subgenus must be separated by suites of characters. Ultimately, taxonomic problems will be solved only by thorough study of species groups throughout their entire range.

Two other characters are often helpful in separating *H. polyanthos* (at least in Peru) from *H. myriocarpum*—particularly useful where sterile specimens are involved. Pinnae of *H. myriocarpum* commonly have basal segments strongly overlapping the rachis. In *H. polyanthos* pinnae are adnate and basal segments often crowd or touch the rachis, but rarely do some of them overlap. Also, *H. polyanthos* occurs at lower elevations in Peru, 100–2000(–2400) m; whereas *H. myriocarpum* is found at (1700–)2000–4200 m.

Amazonas: Prov. Bagua, 12 mi E of La Peca, *Barbour 2466* (UC in part). **San Martín:** Ravine E of Tingo María, *Allard 21446* (GH, US). Prov. Mariscal Cáceres, Tocache Nuevo, *J. Schunke 5693* (F). **Loreto:** Sierra del Pongo, *Mexia 6291a* (GH, UC). **Huánuco:** Prov. Huánuco, Cerro Cucharas, *Woytkowski 1152* (GH). Prov. Huamaliaes, Río Monzón, 20 km W of Tingo María, *Tryon & Tryon 5299* (GH). **Pasco:** Prov. Oxapampa, Cordillera San Matías, *León 317* (F, GH, USM). Pichis Trail, Eneñas (as Junín), *Killip & Smith 25651* (F, NY, US). **Junín:** La Merced, E of Quimiri Bridge, *Killip & Smith 24022* (F, NY, US). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, Río Palotoa, *Foster et al. 10683* (F). **Cuzco:** Prov. Paucartambo, Kosñipata, *Vargas 17860* (GH). **Puno:** San Gabán, *Lechler 3327* (B).

7. ***Hymenophyllum mathewsii*** Bosch, Ned. Kruidk. Arch. 5: 162. 1863. SYNTYPES: "Peruvia," *Mathews* (B!; isosyntype, P; probable isosyntype, B!; photos, F, GH, & US of P). Ecuador, Quito, *Cuming* (B).

Leaves (6–)14–30 cm long, 1.5–4 cm broad. **Petiole** 2.5–6(–8) cm long, 0.35–0.5 mm in diameter, nonalate, glabrous. **Lamina** linear-lanceolate to oblanceolate, rather abruptly reduced or strongly and gradually reduced at base, 2–3-pinnatisect, glabrous. **Rachis** glabrous, alate throughout except usually nonalate at base, or there narrow-alate on only one side. **Pinnae** 14–18 pairs, adnate and often overlapping the rachis, or basal ones short-stalked, larger ones (1.5–)2–3.5 cm long, bearing 4–8 pairs of secondary segments. **Ultimate segments** entire, plane or occasionally undulate, or a few with margins conduplicate. **Sori** 4—many per pinna. **Indusia** relatively large, usually slightly broader than the segment apex, ovoid, apex obtuse to subacute, the broadly cuneate base slightly immersed in the segment tissue, margins entire, receptacle short and filiform, bearing 6–12 sporangia.

Cloud forests, commonly on trunks and branches of trees, 2100–3150 m, Huánuco, Pasco, Cuzco. Ecuador; Peru.

Hutchison 1751 (cited below) has delicate, diminutive leaves only 6–8 cm long; this depauperate condition probably results from the unusual habitat, "in cave." This species is very closely related to *Hymenophyllum polyanthos* (q.v.) and may not merit distinction at the species level. Normal specimens of *H. mathewsii* tend to have larger sori, in relation to the segment apex, and longer, pendent leaves, with no trace of tissue along the petiole and, commonly, none between the proximal two pinnae. Leaves of *H. polyanthos* are smaller and

more compact, erect or arching, with rachis distinctly alate. The petiole is marginate or alate throughout, or at least distally. Often the wing is deciduous upon drying, but traces can usually be found by close scrutiny.

Huánuco: Prov. Huánuco, Carpish, *Plowman 6074A* (F). **Pasco:** Prov. Oxapampa, San Alberto, Yanachaga, *van der Werff et al. 8437* (MO). **Cuzco:** Huadquiña, *Bües 1346* (US). Prov. La Convención, Cochapata, Valle de San Miguel, *Bües 2176* (US). Prov. Urubamba, summit of Huayna Picchu, *Hutchison 1751* (atypical) (F, UC).

8. **Hymenophyllum trichomanoides** Bosch, Ned. Kruidk. Arch. 5(3): 158. 1863. SYNTYPES: Peru, San Martín, Tarapoto, *Spruce 4696* (isosyntypes, GH!, NY!, P!, US!). Colombia, *Moritz* (BM?), *Schomburgk* (BM?). Ecuador, Pichincha, Quito, *Cuming* (not located). "British Guiana," *Schomburgk* (BM?).

Mecodium trichomanoides (Bosch) Pic.-Ser., *Webbia* 28: 469. 1973.

Leaves (9–)11–26 cm long, 4–6(–8) cm broad. **Petiole** 5–12 cm long, 0.4–0.8 cm in diameter, marginate to alate distally (rarely nonalate), with a few scattered trichomes. **Lamina** broadly or narrowly ovate (1 or 2 pairs of proximal pinnae commonly somewhat reduced), 2–3-pinnatisect, glabrous. **Rachis** glabrous, slightly flexuous, narrowly to broadly alate throughout, the wing margin sometimes conduplicate. **Pinnae** 7–14 pairs, adnate and overlapping the rachis, or 1–2 proximal pairs short-stalked, larger ones 2.2–4 cm long, bearing 4–8 pairs of secondary segments. **Ultimate segments** entire, plane, or some of them with involute margins, larger ones commonly less than 1 mm broad, the free portion linear, usually 2.5–4 times as long as broad. **Sori** 6–12 per pinna. **Indusia** relatively small, usually about as broad as the segment apex, rhomboid, elliptical or conical, broadest at or beyond the middle, apex acute to obtuse, the sharply cuneate base deeply (often halfway) immersed in the segment tissue, margins entire, receptacle long, filiform, often exserted, bearing 6–10 sporangia.

In dense, wet forests, on trunks of trees, 300–3000 m, San Martín to Cuzco.

Surinam to Colombia, south to Bolivia.

Besides the characters used in the key, *Hymenophyllum trichomanoides* can often be distin-

guished by the narrower ultimate segments. Larger ones are commonly 0.6–0.9 mm broad and linear. Other species of subg. *Mecodium* have relatively broader ultimate segments, most of them over 1 mm broad, or if not, then only about twice as long as broad. This is a rather reliable way to identify sterile specimens.

Hymenophyllum trichomanoides differs sharply from all other species of subg. *Mecodium* in Peru by the narrowly cuneate sori which are deeply immersed in the segment tissue. Indusia are broadest at or beyond the middle and, at least in Peru, are long and narrow: either narrowly elliptic with subacute apices, or conical, with rounded apices. All specimens seen from Peru clearly match the Spruce syntype. Some specimens examined from Colombia and Venezuela have shorter and broader indusia and much shorter petioles, and it is possible that these represent a variant. However, this has not been substantiated by comparison with the other syntypes from northern South America, which we have not seen. With *H. trichomanoides* probably should be included *H. trianae* Hieron. of Colombia. A syntype of the latter, *Lehmann 7410* (US), matches *Spruce 4696*, except that receptacles are not exserted.

Huánuco: Cerros del Sira, SW slope of Río Lullapichis watershed, *Dudley 13375* (GH). **Pasco:** Prov. Oxapampa, Palcazú Valley, Cabeza de Mono, *D. Smith 3756* (F, MO). **Junin:** Schunke Hacienda, above San Ramón, *Killip & Smith 24844* (F, GH, NY, US). **Cuzco:** Sahuayacu, *Bües 804, 817* (US).

9. **Hymenophyllum ferax** Bosch, Ned. Kruidk. Arch 4: 392. 1859. TYPE: Venezuela, Mérida, *Funck & Schlim 1578* (holotype, L?; isotype, P; photo, US of P).

Mecodium ferax (Bosch) Copel., *Philipp. J. Sci.* 67: 25. 1938.

Leaves 16–38 cm long, 4–8 cm broad. **Petiole** 2–9 cm long, 0.4–0.9 cm in diameter, alate toward apex (wings sometimes deciduous), essentially glabrous. **Lamina** ovate to narrow-elliptic, scarcely to somewhat reduced at base (1–several proximal pairs of pinnae reduced), 3-pinnatisect, glabrous. **Rachis** glabrous, straight or slightly flexuous, alate throughout, rachis wings and those of other axes sometimes conduplicate. **Pinnae** 12–24 pairs, adnate, and basal segments overlapping the rachis, larger ones 2.5–5 cm long, bearing 7–10 pairs of

secondary segments, some elongate pinnae intermixed with normal ones. **Ultimate segments** entire, plane to slightly undulate. **Sori** 8—many per pinna. **Indusia** relatively large, subrotund, circular in outline or broader than long, apex erose, base rounded, not immersed in the greatly constricted segment apex, receptacle short, filiform, bearing 7–12 sporangia.

On trees in wet forests, 2400–3300 m, Cuzco. Venezuela; Colombia to Peru.

This is most closely related to *Hymenophyllum myriocarpum* var. *endiviifolium*, from which it differs in the erose indusia tips and the presence of one to several unusually elongate pinnae which are scattered among the normal ones—the latter a condition similar to that of *H. undulatum*. A remarkably huge specimen, *Lechler 2420* (B; not other 2420 at B, F, K; *H. elegans*), was collected in Peru at an undesigned site. This is apparently a monstrous form of *H. ferax*. It matches this species in every way, including the erose indusia, but the leaf is 85 cm long and the petiole nearly 2 mm in diameter. It is by far the stoutest specimen of Hymenophyllaceae we have seen and belies the appellation “filmy fern.”

Cuzco: Vilcabamba, *Bües 1601* (us). Prov. Paucartambo, Pilahuata, *Vargas 4912* (us). **Dept. Unknown:** *Lechler 2420* (B in part).

10. *Hymenophyllum myriocarpum* Hooker, Sp. fil. 1: 106, t. 37d. 1844. TYPE: Colombia, Hart-

weg 1530 (holotype, K!; isotypes, BM, P; photo, F of P).

Leaves 7–28 cm long, 2.5–5(–6) cm broad. **Petiole** 1.5–8(–10) cm long, 0.3–0.7 mm in diameter, marginate to alate throughout or at least distally (wings sometimes deciduous), essentially glabrous. **Lamina** lanceolate to ovate, elliptic, or oblanceolate, scarcely to strongly reduced at base, 2–3-pinnatisect, glabrous. **Rachis** glabrous, straight or slightly flexuous, alate throughout, rachis wings and those of other axes often conduplicate. **Pinnae** 8–30 pairs, adnate and basal segments strongly overlapping the rachis, larger ones 1–4 cm long, bearing 5–10 pairs of secondary segments. **Ultimate segments** entire, plane to undulate, often with conduplicate margins. **Sori** 5—many per pinna. **Indusia** subglobose or broader than long, much broader than (and not at all immersed in) the strongly constricted segment apex, rounded at base, rounded and entire at apex, receptacle short to nearly obsolete, filiform, bearing 8–20 sporangia.

This, like *H. polyanthos* (q.v.), is a widespread and greatly misunderstood species which is sorely in need of detailed study. It seems to consist of several, not highly distinctive components which are recognized as varieties. With var. *myriocarpum* might possibly be included *H. axillare* Sw. of the West Indies and *H. andinum* Bosch of Ecuador. Of all the names, *H. axillare* has priority.

The species occurs in Mexico and Central America and in South America from Venezuela and Colombia to Bolivia.

Key to Varieties

- a. Lamina elliptic to oblanceolate, broadest at or beyond the middle; several or many proximal pinnae somewhat to greatly reduced 10a. var. **myriocarpum**
- a. Lamina ovate to lanceolate, broadest near the base; 1 or 2 proximal pinnae (if any) slightly reduced b
- b. Larger leaves 7–15 cm long; pinnae commonly patent and strongly imbricate 10b. var. **nigrescens**
- b. Larger leaves (12–)15–28 cm long; pinnae (most of them) ascending and contiguous or only slightly imbricate 10c. var. **endiviifolium**

10a. *Hymenophyllum myriocarpum* Hooker, var. **myriocarpum**.

Mecodium myriocarpum (Hooker) Copel., Philipp. J. Sci. 67: 25. 1938.

Leaves (9–)12–28 cm long. **Lamina** elliptic, oblong or oblanceolate, broadest at or beyond the middle, several proximal pinnae somewhat to greatly reduced. **Rachis** and **ultimate segments** plane, some of their margins occasional conduplicate. **Sori** 10–20 per pinna.

In wet forests, usually pendent from tree trunks and branches, or on wet, mossy rocks, rarely on the forest floor, (1700–)2000–3200 m, Cajamarca, Amazonas, Huánuco to Cuzco.

Mexico to Costa Rica; Venezuela; Colombia to Bolivia.

Cajamarca: Prov. Hualgayoc, Hacienda Taulis, *Hutchison & Bismarck 6415* (F, GH [as Lambayeque], MO, UC, US). **Amazonas:** Prov. Bongará, WSW of Pomacocha, *Wurdack 866* (GH, US). **Huánuco:** Mito, *Bryan 206a* (F). **Pasco:** Eneñas (as Junín), Pichis Trail, *Killip & Smith 25700* (F, NY, US). **Cuzco:** Prov. Urubamba, along Río Urubamba near town of Machu Picchu, *Tryon & Tryon 5410* (F, GH, US).

10b. *Hymenophyllum myriocarpum* var. *nigrescens* (Liebm.) Stolze, *stat. & comb. nov.*

Hymenophyllum nigrescens Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. 5, 1: 292. 1849. LECTOTYPE (designated by A. R. Smith, Flora of Chiapas 2: 133. 1981): Mexico, Puebla, Chinantla, *Liebmann 537* (lectotype, c; isolecotypes, BM, K, P).

Sphaerocionium nigricans Klotzsch, Linnaea 18: 536. 1844, not *Hymenophyllum nigricans* Colla, 1836. SYNTYPES: Peru, *Dombey 87* (syntype, b!; isosyntype, b); Venezuela, Aragua, Colonia Tovar, *Moritz 268* (syntype, b; isosyntype, in part, k!); 268b (syntype, b; isosyntype, BM).

Hymenophyllum nigricans (Klotzsch) Kunze, Bot. Zeit. (Berlin) 244. 1847.

Hymenophyllum nigricans (Klotzsch) Copel., Phillip. J. Sci. 67: 25. 1938.

Leaves 7–15 cm long. **Lamina** ovate. **Rachis** and **ultimate segments** plane, their margins frequently conduplicate. **Sori** 3–15 per pinna.

Erect or arching from tree trunks or branches, rarely from wet rocks, in thickets and wet forests, 1750–3400 m, Amazonas to Cuzco.

Southern Mexico to Costa Rica; Venezuela; Colombia to Bolivia.

Sterile specimens can easily be confused with *H. polyanthos*, but the latter occurs at lower elevations, and laminae are less compact. See discussion of *H. polyanthos* for further comments.

Amazonas: Prov. Chachapoyas, Cerros de Calla Calla above Leimebamba, *Hutchison & Wright 6987* (in part: F, GH, UC). **San Martín:** Prov. Rioja, Pedro Ruíz-Moyobamba Road, *D. Smith 4376* (F, MO). **Pasco:** Prov. Oxapampa, Abra los Mellizos, 4–8 km from Eneñas, *Skog et al. 5038* (US). **Junín:** Huacapistana, *Killip & Smith 24164* (US). **Ucayali:** Plantación Azul, *Ridoutt* (USM). Prov. Coronel Portillo (as Loreto), NE of pass at La Divisoria,

Skog et al. 5157 (US). **Cuzco:** Valley of Urubamba, *Bües 418, 419* (US).

10c. *Hymenophyllum myriocarpum* var. *endiviifolium* (Desv.) Stolze, *stat. & comb. nov.*

Hymenophyllum endiviifolium Desv., Mém. Soc. Linn. Paris 6: 334. 1827. TYPE: "Peruvia" (holotype, P; photos, GH, UC, US).

Hymenophyllum multiflorum Rosenst., Meded. Rijks-Herb. 19: 5. 1913. TYPE: Bolivia, Comarapa, *Herzog 1951* (holotype, b; isotype, us!).

Mecodium multiflorum (Rosenst.) Copel., Philipp. J. Sci. 67: 25. 1938.

Mecodium endiviifolium (Desv.) Pic.-Ser., Webbia 28: 469. 1973.

Leaves (12–)15–28 cm long. **Lamina** ovate or ovate-lanceolate. **Rachis** and **ultimate segments** slightly to strongly undulate, their margins often conduplicate. **Sori** 16—many per pinna.

On trees and wet banks in deep forest, 2400–4200 m, Amazonas, Huánuco, Huancavelica, Cuzco.

Colombia; Ecuador; Peru; Bolivia.

Amazonas: Prov. Chachapoyas, Calla Calla slopes near km 415–418 of Leimebamba-Balsas road, *Wurdack 1750* (US, USM). **Huánuco:** Prov. Huánuco, Mirador, road Acomayo to Chanchao, *Mexia 7761* (F, GH, K, MO, UC, US). **Huancavelica:** Prov. Tayacaja, Chuspi-Tocas, between Colcabamba and Paucarbamba, *Tovar 2050* (GH, USM). **Cuzco:** Prov. Paucartambo, Dist. Marcacocha, near Achirani, *Vargas 11143* (F, K in part, UC).

11. *Hymenophyllum undulatum* (Sw.) Sw., J. Bot. (Schrader) 1800(2): 101. 1802.

Leaves 6–35(–40) cm long, 0.7–2.5 cm broad. **Petiole** 0.5–3(–5) cm long, 0.15–0.3 mm in diameter, nonalate, essentially glabrous. **Lamina** linear to narrow-elliptic, often strongly and gradually reduced at base, 2–3-pinnatisect, glabrous. **Rachis** glabrous, marginate to crispate-alate, commonly nonalate toward base, or discontinuously alate on alternate sides due to the long-decurrent pinna bases. **Pinnae** 16—many pairs, adnate, commonly less than 2 cm long, but often a few of them greatly elongate and lamina-like, normal ones bearing 3–8(–10) pairs of secondary segments. **Ultimate segments** entire, plane, or the margins conduplicate in drying, to undulate or markedly crispate. **Sori** 3—many per pinna. **Indusia** nearly circular, but on mature sori most of them broader than long, not

or scarcely immersed in the segment tissue, commonly truncate at base, the margins entire and plane to crispate, receptacle very short, filiform, bearing 1–4(–5) sporangia.

This species varies greatly as to length and shape of lamina and margins of rachis wings and ultimate segments. In rocky habitats leaves usually tend to be less than 10 cm long and narrowly elliptic, whereas the flaccid, linear leaves pendent

from tree branches sometimes reach 40 cm in length. Several species have been described based on whether the tissue is plane or undulate or strongly crispate. However, comparison of individuals throughout the entire range seems to indicate that few of these characters are very consistent. Only the conspicuously crispate variants seem to merit recognition, as indicated in the following key.

Key to Varieties

- a. Ultimate segments and rachis wings plane to undulate, margins often discontinuously conduplicate in drying; rachis nonalate in the proximal 1/3 to 1/2 or nearly throughout 11a. var. **undulatum**
- a. Ultimate segments and rachis wings markedly crispate, often so strongly as to appear dentate; rachis commonly alate except near lamina base, or wings sometimes lacking in the proximal 1/4 or 1/6 of the rachis 11b. var. **fendlerianum**

11a. *Hymenophyllum undulatum* var. *undulatum*.

Trichomanes undulatum Sw., Prodr. 137. 1788. TYPE: Jamaica, Swartz (holotype, s; isotypes, b, *Herb. Willd.* 20238, BM!, p; photos, F & US of s).

Hymenophyllum reniforme Hooker, Sp. fil. 1: 110, t. 38c. 1844. TYPE: Peru, Mathews 1783 (holotype, κ!; isotypes, β!, F!, κ!, P!; photos, F & US of P).

Hymenophyllum rimbachii Sodiro, Anal. Univ. Quito 13: 47 (Crypt. vasc. quit. 33). 1893. TYPE: Ecuador, Prov. Azuay, Rimbach (holotype, not located; isotype, US!).

Mecodium undulatum (Sw.) Copel., Philipp. J. Sci. 67: 26. 1938.

In wet forests on rock cliffs or pendent from tree trunks and branches, 1500–4100 m, Huánuco to Puno.

Greater Antilles; Guadeloupe; southern Mexico to Panama; Surinam to Colombia, south to Bolivia; southeast Brazil.

Hymenophyllum reniforme and *H. rimbachii* were based on depauperate specimens in which ultimate segments are mostly plane but with their margins conduplicate. Thus the segments appear to be much narrower than typical *H. undulatum*. Some of this folding of the margins appears to be a product of drying and some of it merely part of the natural variation of the species.

Huánuco: Tambo de Vaca, Bryan 624 (F, US). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, van der Werff et al. 8482 (MO, UC). **Junin:** Prov. Tarma, Yanango Mountains, Weberbauer 2135 (B). **Cuzco:** Pau-

cartambo, slopes of Pilahuata, Vargas 4909 (MO, US). **Puno:** Sandia, Weberbauer 1293 (B).

11b. *Hymenophyllum undulatum* var. *fendlerianum* (J. W. Sturm) Stolze, comb. & stat. nov.

Hymenophyllum fendlerianum J. W. Sturm in Mart., Fl. bras. 1(2): 291. 1859. LECTOTYPE (designated by Lellinger, Mem. New York Bot. Gard. 38: 12. 1984): Venezuela, Edo. Aragua, Colonia Tovar, Fendler 35 (US; isolectotype, BR; photo, US of BR).

Hymenophyllum contortum Bosch, Ned. Kruidk. Arch. 5(3): 170. 1863. TYPE: Costa Rica, Aguacate, Hoffman (B).

Hymenophyllum polycarpum Kuhn, Linnaea 35: 391. 1868. TYPE: “Peruvia” (holotype, B!; photo, F).

Mecodium fendlerianum (J. W. Sturm) Copel., Philipp. J. Sci. 67: 26. 1938.

Mecodium contortum (Bosch) Copel., Philipp. J. Sci. 67: 26. 1938.

In forests on wet, rocky cliffs, or pendent from tree trunks and branches, 1250–2900 m, Amazonas, Huánuco, Junín, Puno.

Hispaniola; southern Mexico; Guatemala; Costa Rica; Surinam to Colombia, south to Bolivia; southeastern Brazil.

Amazonas: Prov. Bagua, Cordillera Colán SE of La Peca, Barbour 3539, 3738 p.p. (MO). **Huánuco:** Cushi, trail to Tambo de Vaca, Bryan 684 (F, US). Playapampa, Macbride 4498 (F, US). **Junin:** Schunke Hacienda, above San Ramón, Killip & Smith 24843 (NY, US). **Puno:** Prov.

Carabaya, road from San Gabán to Macusani, *Maas et al.* 6109 (MO). **Dept. Unknown:** Without location, *Dom-bey* (P).

12. **Hymenophyllum molle** Morton, Contr. U.S. Natl. Herb. 29: 149. 1947. TYPE: Peru, Cuzco, Vilcabamba, Achiyayoc Inca ruins, *Bües* 2102 (holotype, US!; isotype, GH!).

Sphaerocionium molle (Morton) Pic.-Ser., *Webbia* 28: 471. 1973.

Leaves indeterminate, to 35 cm long and 3.5 cm broad. **Petiole** 3–6 cm long, 0.2–0.3 mm in diameter, nonalate, sparsely pubescent with simple to (rarely) forked trichomes, or glabrate. **Lamina** 2-pinnatisect or nearly 2-pinnate, abundantly pubescent, the rachis commonly nonalate throughout. **Pinnae** short-stalked (at least proximal ones), cut deeply or nearly to costa, costae regularly and conspicuously alate on both sides, the 4–9 pairs of segments simple or bifid, entire, plane, veins and margins abundantly or densely pubescent with stellate trichomes, but trichomes lacking between veins and margins. **Indusia** slightly broader than long, often broader than the segment tips.

Endemic. In forests, 2200–3600 m, Cuzco.

Cuzco: Huadquiña, *Bües* 708 (US). Prov. La Convención, *Bües* 2072, 2115 (US). Prov. Paucartambo, *Vargas* 3636 (GH).

Key to Varieties

- a. Ultimate segments plane to slightly undulate 13a. var. **trichophyllum**
a. Ultimate segments conspicuously undulate to crispate 13b. var. **buesii**

- 13a. **Hymenophyllum trichophyllum** var. **trichophyllum**. TYPE: Venezuela, Cumaná, between Cocollar and Guardia de San Agustín, *Humboldt* (holotype, P).

Hymenophyllum procerum Bosch, Ned. Kruidk. Arch. 4: 409. 1859, *nom. nud.*

Sphaerocionium trichophyllum (HBK.) Copel., *Philipp. J. Sci.* 67: 32. 1938.

In Peru, thus far known only from one collection: on shaded rocks, Puno.

13. **Hymenophyllum trichophyllum** HBK., Nov. gen. sp. 1: 27. 1815.

Leaves indeterminate, to 25 cm long and 3 cm broad. **Petiole** 0.5–4 cm long, 0.2–0.25 mm in diameter, nonalate, sparsely pubescent with simple to stellate trichomes, or glabrate. **Lamina** 2-pinnate-pinnatisect, abundantly pubescent, the rachis commonly nonalate throughout. **Pinnae** short-stalked (at least proximal ones), cut deeply or quite to costa, costae partially nonalate or discontinuously alate by the decurrent bases of segments, normal pinnae with 2–3(–4) pairs of segments (but often a few of them greatly elongate and equaling the lamina in size and shape), the segments (or pinnules) simple or bifid, plane to undulate or crispate, veins and margins abundantly to densely pubescent with stellate trichomes, but trichomes lacking between veins and margins. **Indusia** about as broad as long and nearly as broad as the segment tips.

The species occurs in Guatemala; Costa Rica; Panama; Guyana to Venezuela and south to Bolivia.

The leaves of this delicate fern sometimes intertwine to form mats on the trunks of trees. A singular feature is the irregular character of the pinnae: often, but not always, one to several pinnae become greatly elongate and once again pinnate-pinnatisect, each of these sometimes equaling the length of the leaf on which it is borne. Of the several varieties of *Hymenophyllum trichophyllum*, two are recognized in Peru.

Elsewhere, in wet forests, on rocks, clay banks or trees, 2000–3800 m; range the same as the species.

The name *H. procerum* was based on *H. pulchellum* sensu Mett., for which there was no description. The specimen probably intended as the type is the only collection of var. *trichophyllum* thus far known from Peru. It closely matches other specimens of var. *trichophyllum* and is cited here.

Puno: San Gabán, *Lechler* 2250 (B, BR, F, P).

13b. *Hymenophyllum trichophyllum* var. *buesii* Morton, Contr. U.S. Natl. Herb. 29: 152. 1947. TYPE: Peru, Cuzco, Prov. La Convención, Abra Mirador, *Bües 2076* (holotype, us!; isotype, GH!).

Thus far known only from the type collection, 3150 m.

Although Morton distinguished his var. *buesii* from var. *trichophyllum* solely on the obviously undulate segments, it also appears that the former has less densely pubescent laminae. However, until more specimens are collected it remains to be seen if either of the differences are sufficiently significant to merit even varietal separation.

14. *Hymenophyllum elegans* Sprengel, Syst. veg. 4: 133. 1827. TYPE: Brazil, *Sellow* (holotype, LZ destroyed; isotype, B!).

Hymenophyllum tenerrimum Bosch, Ned. Kruidk. Arch. 5: 185. 1863. TYPE: Peru, San Martín, Tarapoto, "in monte Campana," *Spruce 4702* (holotype, K!; isotype, BM!).

Sphaerocionium tenerrimum (Bosch) Pic.-Ser., Webbia 28: 472. 1973.

Sphaerocionium elegans (Sprengel) Copel., Philipp. J. Sci. 67: 32. 1938.

Leaves determinate, to 20 cm long and 2 cm broad. **Petiole** 0.5–2 cm long, 0.15–0.2 mm in diameter, nonalate, sparsely pubescent with simple or forked trichomes. **Lamina** pinnate-pinnatisect, sparsely to moderately pubescent, the rachis nonalate, or narrowly and irregularly alate distally or throughout due to the decurrent bases of pinnae. **Pinnae** sessile or adnate, pinnatifid or pinnatisect, the 1–2(–3) pairs of segments, simple or (basal ones) bifid, entire, plane to slightly undulate, margins sparsely to moderately pubescent, with trichomes highly variable: simple to 2–3-forked at base, or the branches again forked; trichomes rare on veins and lacking between veins and margins. **Indusia** slightly broader than long, about as broad as the segment tips.

On shaded rocks, San Martín, Puno, and from two other collections, localities unspecified, 3000 m.

Elsewhere, in wet forests, on rocks, clay banks or tree trunks, 800–2400 m; Guatemala; Costa Rica; Panama; West Indies; Venezuela; Colombia; Peru; Bolivia; Brazil.

Hymenophyllum tenerrimum was said to differ

only by lack of trichomes on the veins, and by having marginal trichomes mostly three-forked at the base. However, in *H. elegans*, trichomes are only occasional to rare or lacking on the veins, and marginal trichomes are highly variable, often including many which are three-forked at base. The isotype of *H. tenerrimum* has occasional trichomes on the veins, and a number of marginal ones that are simple or one-forked. In fact, both taxa may be only a variant of *H. lineare* (Sw.) Sw., of Central America and the West Indies, which also lacks trichomes on veins, but which appears to have more pinna segments and simpler and less variable marginal trichomes. Further study is needed.

San Martín: Tarapoto, "in monte Campana," *Spruce 4700, 4701* (K). **Puno:** San Gabán, *Lechler* (B). **Dept. Unknown:** *Lechler* (NY, US), *Lechler 2420* (B, F, K; another 2420 at B is *H. ferax*).

15. *Hymenophyllum adiantoides* Bosch, Ned. Kruidk. Arch. 5: 184. 1863. TYPE: Peru, San Martín, Tarapoto, *Spruce* (holotype, L; probable isotypes, B!, GH!, K!, L!, NY, US; photos, GH & US of L).

Sphaerocionium adiantoides (Bosch) Pic.-Ser., Webbia 28: 470. 1973.

Leaves indeterminate, to 12 cm long and 2 cm broad. **Petiole** 1–2 cm long, 0.2–0.25 mm in diameter, nonalate, sparsely pubescent with (mostly) stellate trichomes. **Lamina** pinnate-pinnatisect, sparsely to moderately pubescent, the rachis nonalate near the base, narrowly alate distally or irregularly alate due to the decurrent bases of pinnae. **Pinnae** adnate, pinnatifid, or pinnatisect, the 3–4 pairs of segments simple or bifid, entire, slightly undulate, veins and margins sparsely to moderately pubescent with (mostly) stellate trichomes, but trichomes lacking between veins and margins. **Indusia** as long as or slightly longer than broad, about as broad as the segment tips.

Apparently known only from the type collection. With this probably should be included *Hymenophyllum sprucei* Baker, under which see **Comments**.

16. *Hymenophyllum hirsutum* (L.) Sw., J. Bot. (Schrader) 1800(2): 99. 1802.

Trichomanes hirsutum L., Sp. pl. 2: 1098. 1753. TYPE: based on *t. 50b* of Plumier, *Traité foug. Amér.*, apparently representing a plant from the West Indies.

Trichomanes ciliatum Sw., Prodr. 136. 1788. TYPE: Jamaica, Swartz (holotype, s; isotype, b; photo, us of s).

Hymenophyllum ciliatum (Sw.) Sw., J. Bot. (Schrader) 1800(2): 100. 1802.

Sphaerocionium ciliatum (Sw.) Presl, Hymenophyllaceae 34. 1843.

Sphaerocionium hirsutum (Sw.) Presl, Hymenophyllaceae 34. 1843.

Leaves determinate, to 12 cm long and 4 cm broad. **Petiole** 0.3–2.3 cm long, 0.2–0.3 mm in diameter, strongly alate (often nearly to base), sparsely provided with stellate trichomes. **Lamina** 2-pinnatisect, sparsely to moderately pubescent, the rachis regularly and conspicuously alate throughout. **Pinnae** 6–15 pairs, ovate or oblong-ovate, deeply incised, the 2–5 pairs of segments plane, simple to bifid, the veins and margins pubescent with stellate or (on the margins) 2-forked trichomes, but trichomes lacking between veins and margins. **Indusia** as long as or (usually) longer than broad, somewhat broader than the segment tips.

In dense, wet forests, on branches and trunks of trees, 500–2000 m, Loreto, Amazonas to Puno.

Mexico to Panama; West Indies; Guianas to Venezuela, south to Bolivia and Brazil.

Amazonas: Prov. Bagua, E of La Peca, *Barbour 2753* (MO). **San Martín:** Tarapoto, Monte Campana, *Spruce 4698* (K). **Loreto:** Balsapuerto, lower Río Huallaga basin, *Killip & Smith 28539* (F, GH, NY, US). **Huánuco:** Prov. Huánuco, Dist. Churubamba, crest of Santo Toribio, *Mexia 8145* (B, F *p.p.*, GH, US). **Pasco:** Prov. Oxapampa,

Key to Varieties

- a. Pinnae simple (distally) to trifid or, if pinnatisect, the secondary segments 1–2 pairs, simple to bifid 17a. var. **crispum**
a. Pinnae (larger ones) 2-pinnatisect, the secondary segments 4–8 pairs, pinnatisect 17b. var. **bipinnatisectum**

17a. *Hymenophyllum crispum* var. **crispum**. **Figure 11d.**

In forests, on trees or wet banks or cliffs, 2150–3000 m, Amazonas, Cuzco, Puno.

Range the same as the species.

Amazonas: Prov. Chachapoyas, along Río Ventilla, W of Molinopampa, *Wurdack 1510* (F, GH, UC, US). **Cuzco:**

W side of Cordillera de San Matías, *D. Smith 2054* (MO). **Cuzco:** Prov. La Convención, Valle San Miguel, San Jacinto, *Bües 2139* (US). **Puno:** San Gabán, *Lechler 2296* (B).

17. ***Hymenophyllum crispum*** HBK., Nov. gen. sp. 1: 26. 1815. TYPE: Venezuela, Silla de Caracas, *Humboldt & Bonpland* (holotype, P; photos, GH & US of P). **Figure 11d.**

Sphaerocionium crispum (HBK.) Klotzsch, *Linnaea* 1: 537. 1844.

Leaves determinate, to 20 cm long and 4 cm broad. **Petiole** 0.5–5 cm long, 0.1–0.3 mm in diameter, alate near apex, sparsely provided with delicate, simple or 1-forked trichomes. **Lamina** pinnate to nearly 3-pinnate, sparsely pubescent, the rachis regularly and conspicuously alate throughout, the wing strongly undulate or undulate-crispate. **Pinnae** 8–20 pairs, simple (distally) or bifid to nearly 2-pinnate, the 1–8 pairs of segments undulate or crispate, the veins and margins sparsely pubescent, marginal trichomes simple or 1-forked, but trichomes lacking between veins and margins. **Indusia** as long as or (usually) longer than broad, often broader than the segment tips.

The species occurs in Jamaica, Mexico, Guatemala, Costa Rica, Venezuela, Colombia, Peru, Bolivia, and Brazil.

Hymenophyllum crispum might be confused with *H. valvatum*, another species in the subgenus with undulate segments. However, the latter is larger and coarser with a much thicker petiole, and the rachis wing and segments are not as strongly undulate. Two varieties are recognized here.

Río Lachac, *Bües 1813* (GH, US). Prov. Urubamba, Machu Picchu, *Illits et al. 1061* (GH, UC, US). **Puno:** Sandia, *Weberbauer 797* (B).

- 17b. ***Hymenophyllum crispum* var. bipinnatisectum** Morton, *Contr. U.S. Natl. Herb.* 29: 161. 1947. TYPE: Peru, Cuzco, Alturas de Sieve,

Bües 1580 (holotype, us!; isotype, GH!; photo, us).

Endemic.

Thus far known only from the type and one other collection from Peru: **Cuzco**: Alturas de Sieve, *Bües 1528* (us).

18. **Hymenophyllum valvatum** Hooker & Grev., *Icon. fil. 2, t. 219*. 1831. TYPE: Ecuador, forests of Esmeraldas, on trunks of trees, *Jameston* (holotype, κ; possible isotype, κ!).

Hymenophyllum crispatum Bosch, *Ned. Kruidk. Arch. 4: 412*. 1859. TYPE: Peru, Tatanara (Puno), *Lechler 2530* (holotype, L!; isotypes, B!, P!; photos, GH & US of P).

Hymenophyllum platylobum Bosch, *Ned. Kruidk. Arch. 5: 189*. 1863. TYPE: Peru, Dept. Puno, San Gabán, *Lechler 2489* (apparently cited in error originally as *2498*) (holotype, P; isotype, F!; photo, US! of P).

Sphaerocionium valvatum (Hooker & Grev.) Copel., *Philipp. J. Sci. 67: 31*. 1938.

Leaves determinate, to 20 cm long, and 6 cm broad. **Petiole** of mature leaves (2–)3–10 cm long, 0.4–1.0 mm in diameter, commonly alate just below lamina base, pubescent with simple or forked trichomes or glabrate. **Lamina** pinnate-pinnatisect to nearly 2-pinnate-pinnatifid, sparsely to moderately pubescent, the rachis alate throughout, the wing somewhat undulate. **Pinnae** 8–15 pairs, ovate to elliptic-lanceolate, incised deeply to the costa into bifid or pinnatifid pinnules, ultimate segments slightly to strongly undulate, the veins (abaxially) and margins sparsely to amply pubescent, but trichomes lacking on tissue between veins and margins. **Indusia** commonly longer than broad, and slightly longer than the segment tips.

On tree trunks in wet forests, 900–1800 m, Huánuco, Junín, Puno.

Lesser Antilles; Guyana to Colombia, south to Bolivia.

It is with some reluctance that this is maintained as distinct from *Hymenophyllum microcarpum*, from which it seems to differ only in the undulate ultimate segments and (sometimes) rachis wings, and the character of the petiole trichomes. Even these features are variable, as only in a few specimens examined are the segments and rachis wings *markedly* undulate to crispate—most are only moderately so. Conversely, in a number of spec-

imens determined to be *H. microcarpum*, the ultimate segments are only slightly undulate. A perfect intermediate is the isotype of *H. platylobum*, which is placed here in synonymy with *H. valvatum*. The petiole trichomes of this specimen match those of *H. microcarpum*, but the segments and rachis wings are scarcely or only slightly undulate. Other features considered by Morton and subsequent workers seem not to be significant, at least in specimens from Peru. Furthermore, both species may be only robust forms of *H. hirsutum*, which seems to differ chiefly in its smaller lamina and more delicate petiole. The entire complex is in need of detailed study.

Huánuco: Río Llullapichis watershed, Cerros del Sira, *Dudley 13339* (GH). **Junín**: Chanchamayo Valley, *C. Schunke 1491, 1559* (F, US). **Puno**: “St. Gavan” (San Gabán), *Lechler* (κ). Prov. Sandia, Chunchusmayo, *Webbauer 1237* (B).

19. **Hymenophyllum microcarpum** Desv., *Mém. Soc. Linn. Paris 6: 333*. 1827. TYPE: Hispaniola (holotype, P; photo, UC).

Hymenophyllum beyrichianum Kunze, *Linnaea 9: 108*. 1834. TYPE: Peru, Huánuco, Pampayacu, *Poepig* (holotype, LZ destroyed).

Mecodium microcarpum (Desv.) Copel., *Philipp. J. Sci. 67: 25*. 1938.

Sphaerocionium microcarpum (Desv.) Copel., *Philipp. J. Sci. 67: 34*. 1938.

Leaves determinate, to 30 cm long and 10 cm broad. **Petiole** of mature leaves (3–)5–15 cm long, 0.6–1.0 mm in diameter, broadly alate just below lamina base, pubescent with simple, forked, and stellate trichomes or glabrate. **Lamina** pinnate-pinnatisect to nearly 2-pinnate-pinnatifid, sparsely to moderately pubescent, the rachis conspicuously alate throughout. **Pinnae** 10–16 pairs, ovate to elliptic-lanceolate, incised deeply or nearly to the costa into bifid or pinnatifid pinnules, the ultimate segments entire or deeply bifid, the veins (abaxially) and margins sparsely to moderately pubescent, but trichomes lacking on tissue between the veins and margins. **Indusia** commonly longer than broad, and slightly broader than the segment tips.

On tree trunks and clay banks in wet forests, 1500–2700 m, Amazonas, Huánuco to Cuzco.

Greater Antilles; Guatemala to Panama; Guyana to Colombia, south to Bolivia and Brazil.

With this probably might be included *H. valvatum*, under which see for further discussion.

Amazonas: Prov. Bagua, E of La Peca, *Barbour 2547* (MO). **Huánuco:** Río Lullapichis watershed, ascent of Cerros del Sira, *Dudley 13290B* (MO). **Pasco:** Prov. Oxapampa, Palmazú, *van der Werff et al. 8410* (MO, UC). **Junín:** Chanchamayo Valley, *C. Schunke 463* (F, US). **Cuzco:** Prov. La Convención, *Bües 2018, 2035* (US), *2034* (GH). Prov. La Convención, Alturas de Pintobamba, *Vargas 3294* (MO, US).

20. *Hymenophyllum ruizianum* (Klotzsch) Kunze, Bot. Zeit. (Berlin) 1847: 199. 1847.

Sphaerocionium ruizianum Klotzsch, Linnaea 18: 535. 1844. TYPE: Peru, *Ruiz 85* (holotype, B!; isotype, MA?, P; photos, GH & US of P).

Leaves determinate, to 45 cm long and 12 cm broad. **Petiole** of mature leaves (7–)10–20 cm long, 0.7–1.5 mm in diameter, nonalate, densely pubescent with mostly simple or forked trichomes. **Lamina** 2–3-pinnatifid, sparsely to amply pubescent on both sides of the lamina, the rachis alate distally. **Pinnae** commonly patent or their tips drooping, 10–18 pairs, ovate-lanceolate, incised nearly to the costa into pinnatifid or 2-pinnatifid pinnules, the ultimate segments entire or bifid, the veins and margins sparsely to moderately pubescent, but trichomes lacking on tissue between veins and margins. **Indusia** varying from broader than long to longer than broad, commonly slightly broader than the segment tips.

In wet forests, on tree trunks and banks of ravines, and in sphagnum on forest floor, 1000–3300 m, Amazonas, Huánuco, Pasco, Cuzco, Puno.

Colombia; Ecuador; Peru; Bolivia.

A singular feature of this species is the tendency for the long, flexible pinnae to droop gracefully at their tips, a character which is usually preserved in dried specimens. Perhaps its nearest relative is *H. trapezoidale* Lieb., from Mexico and northern South America, which is a much smaller fern with less dissected pinnae which are rather strongly ascending (never drooping) and with more delicate, merely sparsely pubescent, petioles.

Amazonas: Prov. Chachapoyas, above Leimebamba, *Hutchison & Wright 5553* (F, GH, MO, UC, US). **Huánuco:** Playapampa, *Macbride 4516* (F, US). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al. 8423* (MO), *8439, 8491* (MO, UC). **Cuzco:** Prov. La Convención, *Dudley 10790* (F, GH, MO). **Puno:** San Gabán, *Lechler 2260* (B).

21. *Hymenophyllum simplex* Morton, Contr. U.S. Natl. Herb. 29: 171. 1947. TYPE: Peru, Huánuco, Tambillo, *Jelski 897* (US!).

Sphaerocionium simplex (Morton) Pic.-Ser., Webbia 28: 472. 1973.

Leaves determinate, fragile and small, 5–7 cm long. **Petiole** slender, 0.1–0.15 mm in diameter, nonalate, glabrate or sparsely pubescent with simple to stellate trichomes. **Lamina** simply pinnate or pinnatisect, moderately pubescent, the rachis narrowly alate distally, nonalate at base or in the proximal half. **Pinnae** few, ascending, simple, linear, entire, the tissue and veins amply provided with orange, stellate trichomes. **Veins** lacking accessory wings. **Indusia** about as broad as long, usually narrower than the pinna tips.

Endemic. Besides the type (Huánuco) thus far known only from two other collections: Cajamarca and San Martín. Habitat and elevation not recorded.

This delicate little fern is distinctive among the species of subg. *Leptocionium* in its few, ascending, linear, entire pinnae. Although we now know it only from two Peruvian collections, its small, inconspicuous leaves make it difficult to detect. It is hoped that more diligent search will uncover additional specimens throughout Peru and, perhaps, in other areas of South America as well.

Cajamarca: Cutervo, *Jelski 914* (P, US). **San Martín:** Tarapoto, *Spruce* (K), collection is without number, but with notation “conf. 4048”; #4048 is type number of *H. tarapotense*.

22. *Hymenophyllum fragile* (Hedwig) Morton, Contr. U.S. Natl. Herb. 29: 172. 1947.

Trichomanes fragile Hedwig, Fil. gen. sp., t. 18. 1802. TYPE: based on illustration from plant collected in “America meridionalis.”

Sphaerocionium fragile (Hedwig) Pic.-Ser., Webbia 28: 471. 1973.

Leaves determinate, (3–)6–18 cm long, 1.5–2.5 cm broad. **Petiole** ca. 0.2 mm in diameter, sparsely to moderately pubescent with simple, forked, or often stellate trichomes. **Lamina** pinnate-pinnatisect, moderately pubescent, the rachis broadly and consistently alate throughout. **Pinnae** (3–)5–12 pairs, deeply 1-forked (distally) to pinnatisect, the 1–2 pairs of segments entire, the tissue and

veins moderately provided with orange, short-stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** about as broad as long, usually narrower than the ultimate segments, the receptacle not exerted.

In dense forests, on tree trunks or mossy banks, 800–2700 m, Pasco, Junín, Ucayali, Cuzco.

Mexico to Panama; Greater Antilles; Venezuela and Colombia to Bolivia and Brazil.

This may be confused with *Hymenophyllum elegantulum*, under which see for further discussion.

Pasco: Oxapampa, *Soukup 2650* (GH). **Junín:** East of Quimiri Bridge, near La Merced, *Killip & Smith 23834* (NY, US). **Ucayali** (as Loreto): Prov. Coronel Portillo, NE of pass at La Divisoria, *Skog et al. 5156* (us). **Cuzco:** Prov. La Convención, Pintobamba, *Vargas 3262* (MO, US).

23. *Hymenophyllum elegantulum* Bosch, Ned. Kruidk. Arch. 4: 408. 1859. LECTOTYPE (designated as type by Morton, Contr. U.S. Natl. Herb. 29: 170. 1947): based on *t. 33a* (Hooker, Sp. fil. 1. 1844), which in turn, according to Morton, was based on Ecuador, Pillzhum, *Jameson 366* (κ?; probable isolecotype, NY!).

Hymenophyllum pulchellum sensu Hooker, Sp. fil. 1, *t. 33a*. 1844, not Schlecht. & Cham. 1830.
Sphaerocionium elegantulum (Bosch) Copel., Philipp. J. Sci. 67: 32. 1938.

Leaves indeterminate, 12–35 cm long, 2–4 cm broad. **Petiole** ca. 0.2 mm in diameter, glabrate or sparsely pubescent with simple or forked trichomes. **Lamina** pinnate-pinnatisect, amply pubescent, the rachis flexuous, nonalate, or sometimes alate in the distal portion. **Pinnae** subdistant to remote, ascending, 8–24 pairs, deeply pinnatisect, the 4–6 pairs of segments 1–2-forked or bifid, the tissue and veins moderately provided with orange, sessile to short-stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** about as broad as long, and usually as broad as the ultimate segments.

On tree trunks, in forests and wet clearings, 3000–3600 m, Amazonas, Cuzco, Puno.

Mexico to Panama; Greater Antilles; Venezuela and Colombia south to Peru and Bolivia.

Some leaves of *Hymenophyllum elegantulum* vary somewhat in the character of the rachis wing, as in the case of *Bües 720*, cited below. Some of

the laminae have the rachis narrowly winged well into the proximal half, and these specimens might be confused with *H. fragile*. However, the alate condition in these atypical leaves is irregular and mostly due to the decurrent bases of pinnae, whereas in *H. fragile* the wings are very conspicuous and of nearly consistent width throughout.

Amazonas: Prov. Bagua, Cordillera Colán NE of La Peca, *Barbour 3415* (F, MO). **Cuzco:** Michihuañunca, *Bües 720* (us). **Puno:** Prov. Carabaya, Ayapata, *Vargas 10717* (GH).

24. *Hymenophyllum amabile* Morton, J. Wash. Acad. Sci. 22: 63. 1932. TYPE: Peru, Cuzco, Prov. La Convención, Huadquiña, *Bües 715* (holotype, US!; isotype, GH!; photo, F of US).

Leaves indeterminate, to 40 cm long and 4 cm broad. **Petiole** 0.2–0.3(–0.4) cm in diameter, nonalate, sparsely pubescent with mostly stellate trichomes. **Lamina** pinnate-pinnatisect, densely tomentose, the rachis nonalate throughout, or rarely slightly alate due to decurrent bases of pinnae. **Pinnae** numerous, oblong or ovate-oblong, obtuse, often incised nearly to the costa, the 4–8 pairs of segments entire to forked, ultimate divisions entire, the tissue and veins often obscured by a dense tomentum of orange, stalked, stellate or bistellate trichomes. **Veins** lacking accessory wings. **Indusia** broader than long, about as broad as the segment tips, the receptacle very short, not exerted.

Pendent from tree trunks and branches in wet forests, 2600–4200 m, Huánuco, Cuzco, Puno. Ecuador and Peru.

Huánuco: Tambo de Vaca, *Bryan 628* (F, US). **Cuzco:** Prov. La Convención, Vilcabamba, *Bües 2108, 2109, 2110* (us). Prov. La Convención, Loma Grande, *Bües 2148* (F, GH, UC, US). Urubamba, Machu Picchu, *Peyton & Peyton 1104* (MO). **Puno:** Sandia, *Weberbauer 796* (B).

25. *Hymenophyllum speciosum* Bosch, Ned. Kruidk. Arch. 5: 181. 1863. LECTOTYPE (designated as type by Morton, Contr. U.S. Natl. Herb. 29: 175. 1947): Peru, Puno, San Gabán, on tree trunks, *Lechler 2246* (L?; isolecotypes, B!, F!, P; probable isolecotype, NY!; photos, GH, US of P).

Hymenophyllum spectabile Kuhn, Linnaea 35: 392. 1868. TYPE: Bolivia, Yungas, *D'Orbigny 175* (holotype, B?; isotype, P; photo, US of P).

Sphaerocionium spectabile (Kuhn) Copel., Philipp. J. Sci. 67: 31. 1938.

Leaves indeterminate, mature ones 30–180 cm long, 4–9 cm broad. **Petiole** (of mature leaves) 0.5–0.7 mm in diameter, nonalate, glabrate or sparsely pubescent with simple to stellate trichomes. **Lamina** pinnate-pinnatifid or pinnate-pinnatisect, densely tomentose, the rachis nonalate throughout, commonly flexuous, with a tightly appressed covering of sessile or short-stalked, stellate trichomes. **Pinnae** numerous, larger ones (2.5–)3–8 cm long, lanceolate or linear-lanceolate, often attenuate, incised deeply or nearly to the costa, the 6–14 pairs of segments shallowly to deeply bifid, the ultimate divisions entire, the tissue and veins mostly obscured by a dense tomentum of orange (aging whitish), short-stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** about as broad as long and often broader than the segment tips, the receptacle not exerted.

Pendent from trees or clay banks in wet forests, 1800–3350 m, Amazonas, Pasco, Cuzco, Puno.

Peru and Bolivia.

This might better be treated as a variety of *Hymenophyllum karstenianum*, as the two differ only quantitatively, e.g., appressed versus spreading tomentum, strongly versus slightly flexuous rachis, relative size and number of segments of pinnae.

Amazonas: Prov. Chachapoyas, *Hutchison & Wright 5569* (F, GH, MO, UC, US); *Sagástegui 7453* (F, HUT). **Pasco:** Prov. Oxapampa, Cordillera San Gutardo, *León et al. 534* (USM). **Cuzco:** Valle de Lares, *Bües 1808, 1817, 1821, 1931* (US). Valle de San Miguel, La Convención, *Bües 2178* (GH, MO, US).

26. *Hymenophyllum karstenianum* J. W. Sturm, Bot. Zeit. (Berlin) 17: 298. 1859. LECTO-TYPE (designated as type by Morton, Contr. U.S. Natl. Herb. 29: 176. 1947): Venezuela, Mérida, *Moritz 381 p.p.* (BR).

Sphaerocionium karstenianum (J. W. Sturm) Pic.-Ser., Webbia 28: 471. 1973.

Leaves indeterminate, mature ones 15–50 cm long, 2–3.5(–4) cm broad. **Petiole** 0.4–0.5 mm in diameter, nonalate, glabrate or sparsely pubescent with simple to stellate trichomes. **Lamina** pinnate-pinnatifid to -pinnatisect, densely tomentose, the rachis nonalate throughout, straight or slightly flexuous, abundantly to densely covered with short-

to long-stalked stellate trichomes, these mostly spreading, not tightly appressed. **Pinnae** numerous, larger ones 1–2.3 cm long, lanceolate or linear-lanceolate, acute to subattenuate, shallowly or deeply incised, the 4–7 pairs of segments entire to bifid, the tissue and veins mostly obscured by a dense tomentum or orange to tawny, short-stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** commonly as broad as long, and as broad as the segment tips, the receptacle not exerted.

Pendent from trees or clay banks in wet forests, 700–1900 m throughout the range, but thus far apparently known in Peru only from one collection cited below.

Venezuela; Colombia; Peru.

This and *Hymenophyllum speciosum* are very closely related. See discussion of the latter for additional comments.

San Martín: Near Tarapoto, in Monte Campana, *Spruce 4694* (BR, US).

27. *Hymenophyllum lindenii* Hooker, Sp. fil. 1: 94, t. 34c. 1844. TYPE: Venezuela, Caracas, *Linden 173* (holotype, K!; isotype, P; photos, F of K, US of P).

Sphaerocionium lindenii (Hooker) Vareschi, Flora Venezuela 1: 217. 1969.

Leaves indeterminate, to 35 cm long and 8–15 cm broad. **Petiole** (8–)10–15 cm long, 0.7–1.2 mm in diameter, commonly nonalate, pubescent with simple to stellate trichomes. **Lamina** ovate-lanceolate, not or slightly reduced at base, nearly 2-pinnate-pinnatisect, moderately pilose, the rachis abundantly stellate-pubescent, scarcely alate, or alate distally (or sometimes to base). **Pinnae** patent to ascending, 14–20 pairs, 4–9 cm long, acuminate to subattenuate, incised nearly to the costa into 8–14 deeply pinnatifid pinnules, the ultimate segments entire to deeply bifid, rarely undulate or crispate, tissue between the veins sparsely provided with scattered, sessile or stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** broader than long, and about as broad as the segment tips, receptacle not exerted.

Pendent from tree trunks in wet forests, 2300–2450 m, Amazonas, Puno.

Venezuela; Colombia; Ecuador(?); Peru.

Hymenophyllum lindenii is one of the most ro-

bust species in the subgenus, the long, stout petiole often measuring a full millimeter in diameter. The presence of a rachis wing, usually a good diagnostic feature in most species of subg. *Leptocionium*, is not consistent in this or in the closely related *H. plumieri*. The rachis in *H. lindenii* is occasionally alate to the base of the lamina; more commonly the wing is present in the distal half but sometimes it is nearly lacking throughout. The two Lechler specimens cited below are most atypical, being broadly alate even well down the petiole, and with the wings very strongly crispate. The latter feature apparently was what prompted Mettenius's original annotation on this sheet as "*H. valvatum*." *Lechler 2489* is a mixed collection, as the other four specimens of *2489* at Berlin are isotypes of *H. platylobum* (= *H. valvatum*).

Amazonas: Prov. Bagua, Cordillera Colán, *Barbour 3554* (MO, USM), *3602, 3751* (MO). **Puno:** near San Gabán, *Lechler 2489* (B). Tatanara, *Lechler 2563* (B, K).

28. *Hymenophyllum plumieri* Hooker & Grev., Icon. fil. 2, t. 123. 1829. TYPE: Ecuador, western side of Pichincha, *Jameson* (holotype, K!; photo, F).

Hymenophyllum interruptum Kunze, Linnaea 9: 107. 1834. TYPE: Peru, Huánuco, Pampayacu, *Poepig 1104* (holotype, w?; isotype, HBG).

Sphaerocionium plumieri (Hooker & Grev.) Presl, Hymenophyllaceae 34. 1843.

Sphaerocionium interruptum (Kunze) Presl, Hymenophyllaceae 34. 1843.

Leaves indeterminate, to 50 cm long and 3–8 cm broad. **Petiole** 2–7 cm long, 0.4–0.6(–0.7) mm in diameter, nonalate (or sometimes alate just at the apex), pubescent with mostly forked to stellate trichomes. **Lamina** linear, usually strongly and gradually reduced at base, often interruptedly fertile (e.g., groups of fertile pinnae separated by some sterile ones), pinnate-pinnatifid to -pinnatisect, moderately pilose, the rachis alate throughout, or occasionally alate only distally or not at all. **Pinnae** patent to ascending, 15–many pairs, 1.5–6 cm long, acute to subattenuate, the 5–12 pairs of segments simple and entire to deeply bifid, the tissue between the veins sparsely to moderately provided with sessile or stalked, stellate trichomes. **Veins** lacking accessory wings. **Indusia** about as long or usually broader, as broad as the segment tips.

Pendent from tree trunks and clay banks in wet forests, 600–2200 m, San Martín to Puno.

Venezuela and Colombia to Peru and Bolivia.

It is not possible to separate this satisfactorily from *Hymenophyllum interruptum*, which was said to differ in its groups of fertile pinnae interrupted by a few sterile ones, by its rachis not alate toward the base, and by variations in lamina base and in marginal trichomes. In a number of specimens examined during this study (identified as *H. interruptum*) fertile pinnae are continuous, and rachises are fully to partially alate or (occasionally) nonalate throughout. The entire species complex, which also involves *H. dependens* Morton and *H. superbum* Morton from northern South America, needs closer examination. All may be conspecific.

San Martín: In monte Guayrapurima, prope Tarpoto, *Spruce 4025* (K, P). **Huánuco:** Río Llullapichis watershed, ascent of Cerros del Sira, *Dudley 13014* (GH, US), *13204, 13377* (GH). **Junín:** Colonia del Perené, *Killip & Smith 24955* (F, GH, NY, US). **Cuzco:** Prov. Paucartambo, Pilahuata, *Vargas 4914* (MO, US), *16756, 16761* (GH). **Madre de Dios:** Prov. Manú, Shintuya, *Chávez 861* (MO). **Puno:** Prov. Carabaya, *Vargas 17562* (GH).

29. *Hymenophyllum plumosum* Kaulf., Enum. fil. 267. 1824. TYPE: Brazil, *Chamisso* (holotype, LZ destroyed; isotype, LE?).

Sphaerocionium plumosum (Kaulf.) Copel., Philipp. J. Sci. 67: 30. 1938.

Leaves indeterminate, to 75 cm long and 6 cm broad. **Petiole** 0.3–0.7 mm in diameter, nonalate, pubescent with simple to stellate trichomes or glabrate. **Lamina** pinnate-pinnatifid to rarely nearly 2-pinnate, densely appressed-tomentose, the rachis nonalate throughout. **Pinnae** numerous, lanceolate, pinnatifid to pinnatisect, or rarely incised to the costa, the ultimate segments entire (some proximal ones bifid), the tissue and veins completely obscured by a tomentum of sessile to short-stalked, stellate trichomes. **Veins** (especially abaxially) with low, inconspicuous lamellae. **Indusia** about as broad as long, usually slightly broader than the segment tips.

Epiphyte on trunks or branches in dense, wet forests, or occasionally pendent from wet, clay banks, 550–3100 m, Huánuco, Junín, Cuzco, Madre de Dios, Puno.

Costa Rica to Colombia; Peru; Bolivia; Brazil.

The lamellae along the veins in this species are scarcely "wings" in the sense of being broad and thin flanges of tissue. Instead, they are commonly long, low outgrowths borne along the abaxial or (sometimes) adaxial sides of the veins contiguous to, but not in the same plane with, the segment tissue. They are often difficult to discern, since the veins and laminar surface are so densely tomentose. The best way to observe them is on the older (proximal) pinnae where some of the indument may have fallen away. For further discussion see also *Hymenophyllum tomentosum*.

Easily confused with *Hymenophyllum plumosum* are *H. karstenianum* and *H. speciosum*, which have no lamellae on the veins, but are similar to the former in most other features, including the dense matting of tomentum obscuring the laminar surface. Extreme care and patience must be exercised to determine whether the low outgrowths are present or lacking. In fact, the real importance of the presence or absence of lamellae bears more careful analysis in the future. During this study of Peruvian species of *Hymenophyllum*, it has been noted that size and frequency of these outgrowths, on one or both surfaces, may be more variable than earlier assumed, and thus may be of much less taxonomic significance.

Huánuco: Vilcabamba, Hacienda on Río Chinchao, *Macbride 5146* (F, US). **Junín:** Schunke Hacienda above San Ramón, *Killip & Smith 24840* (F, GH, US). **Cuzco:** Prov. Paucartambo, above Tambomayo, *West 7108* (MO, UC). **Madre de Dios:** Prov. Manú, Shintuya, *Chávez 860* (MO). **Puno:** San Gabán, *Lechler 2264* (B).

30. *Hymenophyllum multialatum* Morton, Contr. U.S. Natl. Herb. 29: 185. 1947. TYPE: Peru, Cuzco, Prov. La Convención, Alturas de Sieve, *Bües 1575* (holotype, us!; frag., GH!).

Sphaerocionium multialatum (Morton) Pic.-Ser., Webbia 28: 471. 1973.

Leaves indeterminate, to 50 cm long, 3–8(–15) cm broad. **Petiole** 0.4–0.7 mm in diameter, nonalate, sparsely hirsute with mostly simple trichomes. **Lamina** pinnate-pinnatisect, hirsute, the rachis nonalate throughout. **Pinnae** numerous, narrow-oblong or -deltoid, pinnatisect, sometimes irregularly and greatly elongate, the ultimate segments commonly bifid, the tissue and veins moderately provided with sessile to short-stalked sessile trichomes. **Veins** bearing (especially abaxially)

irregularly interrupted, conspicuous lamellae. **Indusia** about as broad as long, equaling or slightly broader than the segment tips.

Epiphyte in dense, wet forests, 2000–3200 m, Amazonas, Huánuco, Pasco, Cuzco.

Colombia; Ecuador; Peru.

Shape of lamina and pinnae can be variable and irregular in this species. Typically the leaves are linear, with numerous pinnae 3 or 4 cm long, yet at times, scattered along the rachis, there may be a few greatly elongated, attenuate pinnae, occasionally reaching 15 cm in length. Although *Hymenophyllum multialatum* has been thus far reported from four departments in Peru, the great majority are represented by Bües's collections in Cuzco. For further discussion see *H. tomentosum*.

Amazonas: Prov. Bagua, Cordillera Colán, *Barbour 3740* (F, MO). **Huánuco:** Prov. Huánuco, 5 km from Cerpish, *Tryon & Tryon 5318-B* (GH). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al. 8495* (MO). **Cuzco:** Valley of Río Urubamba, *Bües A-16* (F, GH, US). Montaña de Calca, *Bües 1916* (GH, US), 1919, 1923, 1932 (US). Prov. La Convención, Cordillera Vilcabamba, *Dudley 11137* (GH, US).

31. *Hymenophyllum tomentosum* Kunze, Linnaea 9: 107. 1834. TYPE: Peru, Huánuco, Pampayacu, 1829, *Poeppig Diar. 1134* (holotype, w?; isotype, BM?; frag., B!; probable isotype, MO!; photo, US of MO).

Sphaerocionium tomentosum (Kunze) Presl, Hymenophyllaceae 34. 1843.

Hymenophyllum fusagasugense J. W. Sturm, Bot. Zeit. (Berlin) 1859: 297. 1859 (as "*fusugasugense*"). TYPE: Colombia, Cundinamarca, "*Fusugasugá*" (*Fusagazugá*) *Karsten* (not located).

Hymenophyllum fusagasugense var. *aberrans* Morton, Contr. U.S. Natl. Herb. 29: 187. 1947 (as "*fusugasugense*"). TYPE: Venezuela, Mérida, Tabay, *Gehriger 584* (holotype, us!; isotypes, F!, GH!).

Leaves indeterminate, to 50 cm long and 2.5 cm broad. **Petiole** 0.5–0.6 mm in diameter, nonalate, sparsely pubescent with mostly simple trichomes. **Lamina** pinnate-pinnatifid, densely hirsute, the rachis nonalate throughout. **Pinnae** numerous, oblong or narrow-deltoid, pinnatifid (sometimes deeply so), the ultimate segments simple or (occasionally) bifid, the tissue and veins densely covered with (and often obscured by) sessile to short-stalked trichomes. **Veins** abaxially bearing irregularly interrupted, conspicuous winglike lamellae,

these wings much smaller or sometimes lacking adaxially. **Indusia** about as broad as long, equaling or slightly broader than the segment tips.

On steep banks and tree trunks, 2750–3100 m, Amazonas, Huánuco.

Colombia; Venezuela; Peru.

This is distinguished from *Hymenophyllum multialatum* and *H. plumosum* only by the characters used in the key. All three appear to be alike, except for the size and frequency of the lamellae along the veins and by the relative density of pubescence. Of these, *H. plumosum* (q.v.) is the most distinct, in that the lamellae are merely low and inconspicuous outgrowths and the trichomes are so densely matted as to completely obscure the veins and tissue. In *H. tomentosum* the indument is also densely matted, but the lamellae are so large and conspicuous that many of them emerge through the tomentum. Morton (1947) chose to separate *H. fusagasugense* and var. *aberrans* on the presence or absence of these processes adaxially. However, the size or lack of lamellae on the adaxial side varies considerably in the species, and the character is difficult to observe due to the dense surface tomentum. To prove that the lamellae are completely absent on a given specimen would require scraping away all the tomentum of each leaf. A thorough study of the species complex through-out its range is needed.

Amazonas: Prov. Chachapoyas, Cerros de Calla Calla, 19 km above Leimebamba, *Hutchison & Wright 5570* (UC). Prov. Chachapoyas, near km 422, Balsas-Leimebamba road, *Wurdack 1249* (F, GH, UC, US).

32. ***Hymenophyllum lobatoalatum*** Klotzsch, *Linnaea* 20: 438. 1847. TYPE: Peru, Panatahua, *Ruiz 83* (holotype, B!; isotype, MA?).

Sphaerocionium lobatoalatum (Klotzsch) Pic.-Ser., *Webbia* 28: 471. 1973.

Leaves indeterminate, to 60 cm long and 8 cm broad. **Petiole** 0.4–0.7 mm in diameter, alate, if at all, only near base of lamina, pubescent with simple to stellate trichomes or glabrate. **Lamina** pinnate-pinnatifid, pubescent with stellate trichomes, the rachis strongly alate throughout. **Pinnae** numerous, larger ones 20–45 mm long, 7–11 mm broad at base, most of them narrow-triangular, the apex narrowly acute to subattenuate, deeply pinnatifid, the 7–12 pairs of ultimate segments bifid, the tissue and veins moderately pro-

vided with light or dark brown, short-stalked, stellate trichomes. **Veins** abaxially bearing small, scattered lamellae, these about as broad as long, but lacking adaxially. **Indusia** slightly longer than broad, usually as broad as the segment tips, receptacle not exerted.

In wet forests, pendent from trunks and branches of trees, 600–1300 m, Loreto and Huánuco.

Colombia; Ecuador; Peru.

There is little, beyond the key characters, to distinguish this from *Hymenophyllum pyramidatum*. Leaves of the latter are perhaps more robust, with relatively narrower pinnae and much denser pubescence. Both also share nearly the same range, and more study may prove them to be conspecific. Also very closely related is *H. verecundum*, which is more easily separated by its much lighter colored trichomes and shorter, relatively broader and more crowded pinnae. But even these characters sometimes tend to be intermediate.

Loreto: Pumayucu, between Balsapuerto and Moyobamba, *Klug 3248* (B, F, GH, MO, US). **Huánuco:** Prov. Huánuco, Dist. Churubamba, Mt. Santo Toribio, *Mexia 8258* (B, F, GH, UC, US).

33. ***Hymenophyllum pyramidatum*** Desv., *Mém. Soc. Linn. Paris* 6: 332. 1827. TYPE: “habitat in America” (possibly a Dombey collection from Peru) (holotype, P; photos, GH, US).

Sphaerocionium pyramidatum (Desv.) Copel., *Philipp. J. Sci.* 67: 30. 1938.

Leaves indeterminate, to 65 cm long and 6 cm broad. **Petiole** 0.5–0.7 mm in diameter, often alate 1–2 cm near the apex, pubescent with simple to stellate trichomes. **Lamina** pinnate-pinnatifid, densely pubescent with simple to stellate trichomes, the rachis alate throughout. **Pinnae** numerous, larger ones 20–45 mm long, 6–11 mm broad at base, most of them narrow-triangular, the apex narrowly acute to attenuate, deeply lobed to pinnatifid, the 6–12 pairs of ultimate segments simple to bifid, the tissue and veins usually copiously provided with orange to dark brown (rarely tawny), subsessile to short-stalked, stellate trichomes. **Veins** abaxially with numerous, conspicuous, elongate, winglike lamellae (often nearly the length of the vein), these sometimes less conspicuous and abundant on the adaxial surface. **Indusia** slightly longer than broad, usually as broad as the segment tips, receptacle not exerted.

In dense, wet forests, pendent from stumps, tree trunks, and branches, and on wet banks, 600–1800 m, along Cordillera Central from San Martín to Cuzco.

Colombia; Peru; Bolivia.

This belongs to a close-knit complex of species involving *Hymenophyllum verecundum* and *H. lobatoalatum*. See discussion of the latter for further comments.

San Martín: Tingo María, *Allard 20818* (us). **Huánuco:** Pampayacu, *Kanehira 123* (F, GH, K, US). **Pasco:** Prov. Oxapampa, 4–8 km from Eneñas, *Skog et al. 5077* (us). **Junín:** Chanchamayo Valley, *C. Schunke 466, 926* (F, US), *1058* (F). **Cuzco:** Prov. Paucartambo, between Mistiana and Keros, *Vargas 7380 p.p.* (MO).

34. *Hymenophyllum verecundum* Morton, Contr. U.S. Natl. Herb. 29: 183. 1947. TYPE: Peru, Huánuco, Churubamba, *Mexia 8143-A* (holotype, US!; isotypes, GH!, MO!, UC!).

Leaves indeterminate, to 50 cm long and 4 cm broad. **Petiole** 0.4–0.6 mm in diameter, alate, if at all, just below the lamina, glabrate or slightly pubescent with simple to stellate trichomes. **Lamina** pinnate-pinnatifid, densely pubescent with stellate trichomes, the rachis alate throughout, or sometimes nonalate at base. **Pinnae** numerous, larger ones 6–20 mm long, 3–7 mm broad at base, oblong to very broadly triangular, the apex obtuse to subacute, pinnatifid, the 3–6(–8) pairs of ultimate segments simple to retuse or occasionally bifid, the tissue and veins copiously provided with whitish to tawny, sessile or short-stalked, stellate trichomes. **Veins** abaxially with numerous conspicuous, elongate, winglike lamellae, these less conspicuous and abundant on the adaxial surface. **Indusia** about as long as broad and usually as broad as the segment tips, receptacle not exerted.

In dense, wet forests, pendent from tree trunks, branches, and wet banks, (550–)1500–2700 m, Amazonas, Huánuco, Junín, Cuzco, Madre de Dios, Puno.

Colombia; Peru; Bolivia.

This is closely related to *Hymenophyllum pyramidatum* and *H. lobatoalatum*. See discussion of the latter for further comments.

Amazonas: Prov. Bagua, Cordillera Colán, *Barbour 3740* (MO in part). **Huánuco:** Río Lullapichis watershed, ascent of Cerros del Sira, *Dudley 13370* (GH, US). **Junín:** Pichis Trail, Porvenir, *Killip & Smith 25948* (F, GH, US). **Cuzco:** Hacienda Pintobamba, Chaupimayo, *Bües 1943*

(us). **Madre de Dios:** Prov. Manú, Shintuya, *Chávez 833 p.p.* (MO). **Puno:** Prov. Sandía, E of Oconeque, *Hodge 6090* (F, GH, US).

35. *Hymenophyllum tarapotense* Stolze, *sp. nov.*

Folia usque ad 6 cm longa et 1.6 cm lata. Petiolus 1–2 cm longus, 0.1–0.15 mm diametro. Lamina pinnato-pinnatifida. Rhachis versus basin non alata. Pinnae 6–12-jugatae, bifidae vel pinnatifidae, usque ad 1 cm longae, pinnae basales admodum reductae, marginibus, venis et interveniis trichomatibus stellatis instructis. Venae lamellis cristiformibus numerosis praeditae.

Leaves indeterminate, to 6 cm long and 1.6 cm broad. **Petiole** 1–2 cm long, 0.1–0.15 mm in diameter, nonalate, sparsely provided with simple trichomes. **Lamina** pinnate-pinnatifid, pubescent with stellate trichomes, the rachis weakly alate distally, nonalate toward the base. **Pinnae** 6–12 pairs, bifid, or distal ones pinnatifid with 3–4 segments, larger ones 1 cm long, basal ones often reduced to mere auricles, the margins, veins, and intervening tissue moderately to amply provided with tawny trichomes. **Veins** bearing numerous, conspicuous accessory foliar crests not in the plane of the lamina, these less frequent on the adaxial surface. **Indusia** about as long as broad, as broad as the segment tips, receptacle minute, not exerted.

TYPE—Peru, Tarapoto (Dept. San Martín) in monte Guayrapurima, Aug. 1856, *Spruce 4048* (holotype, K!; photo, F). Another Spruce specimen at K, with notation “conf. 4048,” is *H. simplex*.

Known only from the type.

This tiny fern is unquestionably the smallest of the species in subg. *Leptocionium* which bear accessory tissue on their veins. These foliar processes are not long, low wings as seen in *Hymenophyllum pyramidatum*, but are separate, crestlike flanges of tissue similar to those frequently seen in more delicate specimens of *H. verecundum*. Superficially *H. tarapotense* closely resembles *H. fragile*, in its small size, delicate petiole, and reduced, often bifid, pinnae. It may seem strange that this distinctive species has not been described before, nor collected again in over 100 years. However, many of these diminutive members of the genus are very easily overlooked by collectors.

Comments

Hymenophyllum peruvianum Hooker & Grev., Icon. fil. 2, t. 208. 1831. TYPE: Ecuador (as

Peru), Prov. Esmeraldas, *Jameson* (holotype, K).

The original drawing seems to illustrate most of the features characteristic of *Hymenophyllum fucoides* var. *pedicellatum*, except that the apex of the indusium is deeply dentate rather than lacinate. It is likely that the two taxa are synonymous, but we have not seen the type to verify this. The problem is but one of many in the *H. fucoides* complex begging solution through a complete revision of the group.

Hymenophyllum poeppigianum Presl, Hymenophyllaceae 54. 1843. TYPE: Peru, Huánuco, Pampayacu, *Poeppig* (holotype, PR; probable isotype, P; photos, GH & US of P).

Some authors have placed this with *Hymenophyllum polyanthos*. The type has not been seen, but judging from the protologue and photos of a probable isotype (P) the species is more likely to be *H. myriocarpum*. The protologue refers to: the indusia "ovate-subrotund"; the rachis alate throughout; the petiole alate toward the apex; the lamina linear-lanceolate with the base acute. The description of the indusia could conceivably fit either *H. polyanthos* or *H. myriocarpum*, but that of the lamina (as well as the photo of the possible isotype) more closely match *H. myriocarpum* or *H. undulatum*. However, the petiole and (usually) the rachis base of *H. undulatum* are nonalate.

Hymenophyllum sprucei Baker in Hooker & Baker, Syn. fil. 65. 1867. TYPE: Peru, San Martín, Tarapoto, *Spruce* (not located).

Morton (p. 155, 1947) considered that this is the same as *Hymenophyllum adiantoides*, and there is nothing in the description to argue otherwise. It is possible that Baker was unaware of the publication of the latter species, and even that he based his new species on the same specimen cited earlier by van den Bosch. Specimens (B, GH, K, L, NY, US) thought to be probable isotypes of *H. adiantoides* are those of Spruce from Tarapoto. They bear the notation "conf. 4700" and are conceivably the ones on which Baker based his "*H. sprucei*."

Hymenophyllum trifidum Hooker & Grev., Icon. fil. 2, t. 196. 1831. TYPE: Ecuador (as "Peru"), Esmeraldas, *Jameson* (E?).

In the original description the type was cited as having come from Peru, but Esmeraldas is an Ecuadorean province in which Jameson did much of his collecting. Yet *Hymenophyllum trifidum* still might be expected in Peru, as it could be merely a form of *H. elegans*. From the description and plate it appears to be very similar to the latter, but until the type is located the question must remain unanswered.

II. Trichomanes

Trichomanes L., Sp. pl. 1097. 1753. TYPE: *Trichomanes scandens* L. **Figure 12.**

Didymoglossum Desv., Mém. Soc. Linn. Paris 6: 330. 1827. TYPE: *Didymoglossum muscoides* (Sw.) Desv. (*Trichomanes muscoides* Sw.) = *Trichomanes hymenoides* Hedwig.

Trichomanes subg. *Didymoglossum* (Desv.) C. Chr., Index fil. xiv. 1906.

Trichomanes subg. *Achomanes* Presl, Hymenophyllaceae 15. 1843. TYPE: *Trichomanes crispum* L.

Trichomanes subg. *Pachychaetum* Presl, Hymenophyllaceae 16. 1843. TYPE: *Trichomanes rigidum* Sw.

Homoeotes Presl, Gefässbündel Farn, 23. 1847. TYPE: *Homoeotes heterophylla* Presl = *Trichomanes humboldtii* Lell.

Plants epiphytic, occasionally epipetric or terrestrial. **Stem** stout and erect or decumbent to long-creeping and filiform, bearing scattered to abundant trichomes and delicate to large, fibrous roots or (especially in subg. *Didymoglossum*) lacking roots. **Leaves** monomorphic or (less commonly) dimorphic, 0.5–40 cm or longer. **Lamina** entire to nearly 5-pinnate, subsessile to petiolate, with petiole commonly shorter than the lamina, glabrous or with trichomes borne mostly on costae and margins. **Veins** free or, in *Trichomanes diversifrons*, reticulate near the lamina margin, pinnate (anadromous or catadromous) or sometimes flabellate, false veins also present in some species, these mostly parallel, but in a few species perpendicular to the true veins. **Sori** terminal on the veins. **Indusium** mostly tubular, the mouth bilabiate or entire and often flaring, or very rarely nearly bilvalved, the sporangia borne on an elongate receptacle. **Receptacle** commonly exerted beyond the mouth of the indusium, often greatly so.

There are about 300 species in the genus, occurring in tropical to subtropical regions of both hemispheres. As in *Hymenophyllum*, most are

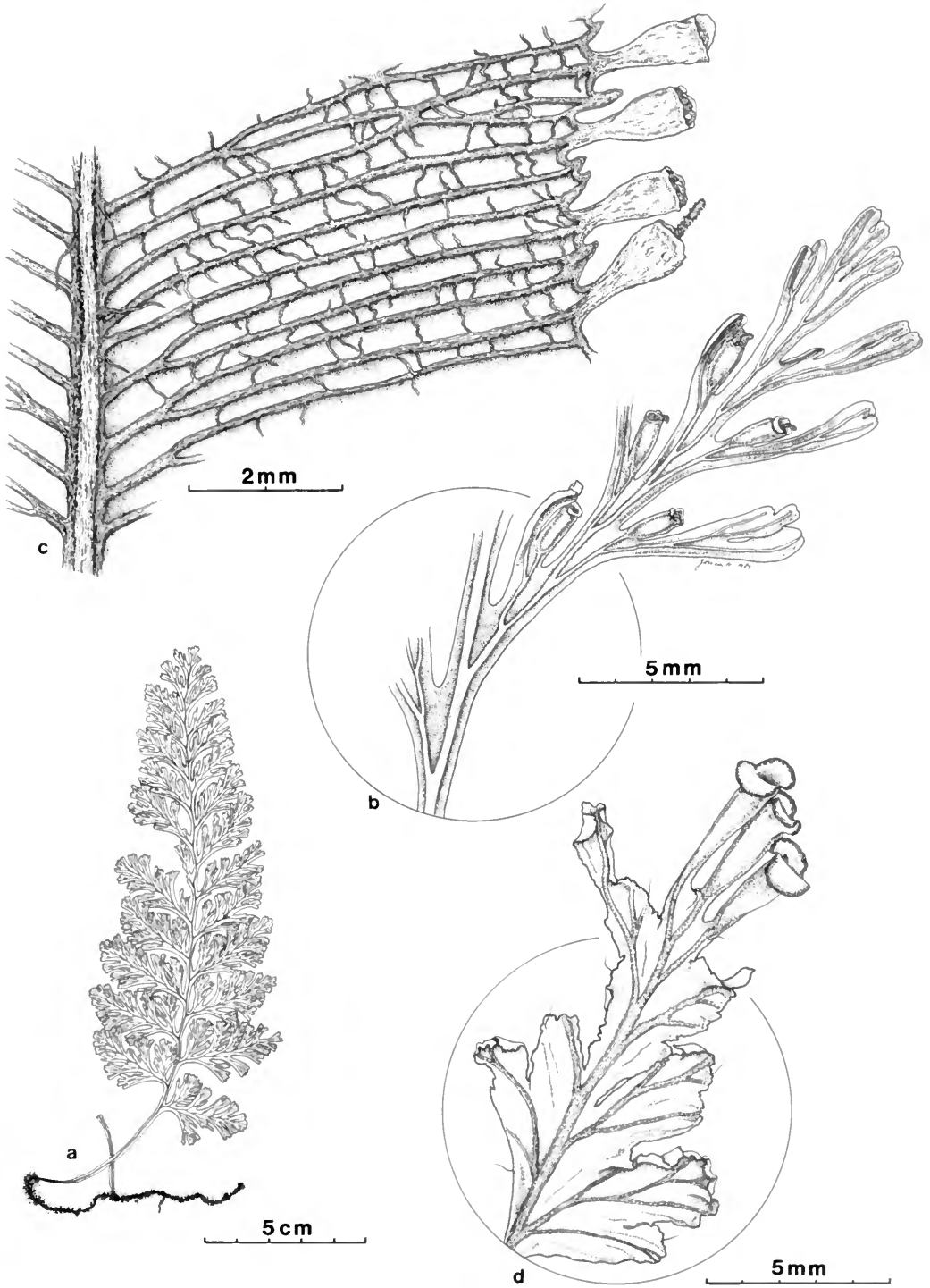


FIG. 12. *Trichomanes radicans*: a, habit; b, pinna with sori. *Trichomanes pinnatum*: c, portion of pinna with false veins and sori. *Trichomanes hymenoides*: d, apical portion of leaf. (a from Acosta-Solis 13782, Ecuador, F; b from Mathias & Taylor 5075, F; c from Barbour 5194, F; d from Wurdack 1513, F.)

found as epiphytes in dark, wet forests, but a number of species may be found on wet, rocky cliffs or occasionally on clay banks. Also as in *Hymenophyllum*, *Trichomanes* has been divided by previous authors into a number of genera and/or subgenera. Only one genus is recognized here, with the key and species order reflecting as nearly as possible four of the subgenera. The monotypic subg. *Cardiomanes* (Presl) Christ occurs in New Zealand.

“False veins” may be found on laminae in two of the subgenera. These are long sclerenchymatous strands which can be observed as faint to rather distinct lines, parallel or perpendicular to the true veins. They may be connected to the true veins but are much more commonly free from them. Their position and frequency are important characters in recognizing some of the species. As in *Hymenophyllum*, veins of several species of *Trichomanes* bear crestlike lamellae, perpendicular

to the plane of the lamina. One of these, *T. martiusii*, occurs in Peru.

The group of *Trichomanes crispum* L. in subg. *Achomanes* is the most taxonomically difficult in the genus, and a few of these species occurring in Peru may eventually be found to merit only infraspecific status. Some of the difficulties are very likely the result of yet unsolved questions involving hybridization.

References

- BOER, J. G. W. 1962. The new world species of *Trichomanes* sect. *Didymoglossum* and *Microgonium*. Acta Bot. Neerl., **11**: 277–330.
 WINDISCH, P. G. 1977. Synopsis of the genus *Trichomanes*, subgenus *Achomanes*. Ph.D. thesis, Department of Biology, Harvard University, Cambridge, Mass., 198 pages.

Key to Species of *Trichomanes*

- a. Venation anadromous, never flabellate; false veins lacking b
- b. Stem long-creeping; leaves well-spaced to remote [subg. *Trichomanes*] c
- c. Stems relatively stout, 0.7–2.2 mm in diameter; mature leaves 15–50 cm long d
- d. Pinnae 2–3-pinnatisect; stem amply to densely provided with castaneous trichomes; ultimate segments narrow, commonly linear e
- e. Indusium narrow-cylindrical or -elliptic, often subfusiform, the apex not or scarcely expanded; petiole (1–)4–15 cm long; elevation 0–500 m 1. **T. radicans**
- e. Indusium conical, apex expanded into a wide-flaring mouth; petiole 0.3–3 cm long; elevation (400–)700–3200 m 2. **T. collariatum**
- d. Pinnae pinnatifid or pinnatisect (sometimes 2-pinnatifid as to basal segments); stem with trichomes sparse to widely scattered; ultimate segments relatively short and broad, not linear 3. **T. rupestre**
- c. Stems filiform, 0.2–0.5 mm in diameter; leaves 3–15(–18) cm long f
- f. Rachis alate throughout; pinnae commonly adnate, the costae alate to base (rarely nonalate just at base) g
- g. Tube of indusium broadly conical, 1–1.5 times as long as broad, mouth not or slightly flaring; tissue of most ultimate segments with elongate, narrow folds parallel to the veins 4. **T. pyxidiferum**
- g. Tube of indusium narrowly cylindrical; 2–4 times as long as broad, mouth abruptly and widely flaring; tissue of segments essentially plane (margin sometimes undulate) 5. **T. diaphanum**
- f. Rachis nonalate nearly to the apex; pinnae stalked, the costae not alate at base h
- h. Costae alate, except not below the basal pinnule; ultimate segments 0.5–0.8 mm broad; sori 1–5 per pinna; indusia commonly alate, the wings several cells wide 6. **T. angustatum**
- h. Costae nonalate except near the apex; ultimate segments 0.1–0.4 mm broad; sori rarely more than 1 per pinna; indusia not or scarcely alate, wings (if any) 1 cell wide 7. **T. capillaceum**
- b. Stem erect, or occasionally short-creeping; leaves caespitose to (occasionally) approximate [subg. *Pachychaetum*] i

- i. Tissue of segments opaque, the cells small and occluded, not evident when observed with magnification of 8–12×; leaves (mature ones) 15–90 cm long; petiole (0.6–)0.7–3.5 mm in diameter j
- j. Rachis obtusely quadrangular, alate (often broadly so) at least in the distal half; pinnae adnate, the costae alate; lamina usually more than 1 cell thick, at least away from margins 8. **T. elegans**
- j. Rachis terete, nonalate, or marginate to slightly alate near apex; pinnae (at least proximal ones) short-stalked, costae not alate at base; lamina essentially 1 cell thick throughout 9. **T. rigidum**
- i. Tissue of segments translucent, the cells large and clear, quite evident with magnification of 8–12×; leaves commonly less than 15 cm long; petiole 0.3–0.6 mm in diameter 10. **T. cellulosum**
- a. Venation at least partly catadromous (or sometimes flabellate); false veins present or lacking . . . k
- k. False veins present, these submarginal or borne between and parallel with the true veins [subg. *Didymoglossum*] l
- l. Leaves with simple to stellate, commonly dark, trichomes along the margins; indusia distinctly bilabiate and the lips commonly dark-margined m
- m. Venation flabellate, a percurrent costa lacking 11. **T. punctatum** ssp. **sphenoides**
- m. Venation pinnate, or if subflabellate, the costa essentially percurrent n
- n. Mature leaves entire, or distally lobed; stellate trichomes borne all along the margin 12. **T. angustifrons**
- n. Mature leaves 1–2-pinnatifid; stellate trichomes confined to segment sinuses, with simple or bifid trichomes borne on outer margin o
- o. Sori protruding from the leaf tissue, or slightly immersed at base; false veinlets extending toward the lamina margin, but rarely running parallel to it p
- p. False veinlets sparse, scattered; lips of indusium mostly broader than long; cells of lamina mostly isodiametric 13. **T. hymenoides**
- p. False veinlets commonly abundant; lips of indusium mostly as long as or longer than broad; cells of lamina mostly elongate 14. **T. reptans**
- o. Sori partly to deeply immersed in the leaf tissue, or at least broadly alate; false veinlets (many of them) parallel to and very near the margin 15. **T. krausii**
- l. Leaves with margins glabrous or provided with circular scalelike processes (these sometimes deciduous in age); indusia not or scarcely bilabiate, the mouth not dark-margined q
- q. Lamina lacking paired, circular scalelike processes, but bearing a peripheral, submarginal false vein; venation essentially pinnate 16. **T. kapplerianum**
- q. Lamina bearing numerous paired, circular, scalelike processes all along the margin (these sometimes deciduous in age), but lacking a submarginal false vein; venation flabellate 17. **T. membranaceum**
- k. False veins lacking or, in *T. pinnatum*, perpendicular to the true veins (some short, veinlike lines in sect. *Lacostea*); [subg. *Achomanes*] r
- r. Lamina trichomes stellate or forked from the base; stem filiform, 0.3–0.4 mm in diameter 18. **T. polypodioides**
- r. Lamina trichomes simple or lacking; stem relatively stout and wiry, 0.5–1.2 mm in diameter s
- s. Stem long-creeping up tree trunks, leaves subdistant to remote; lamina appressed to tree trunks by means of rhizoids on axes t
- t. Lamina linear, subentire to lobed, 1–1.5 cm broad; indusia mouth rather widely flaring 19. **T. tanaicum**
- t. Lamina oblong, pinnatisect or nearly pinnate, mature ones (1.8–)2–9 cm broad; indusium mouth not or slightly flaring u
- u. Segments of sterile laminae entire or shallowly crenate; veins simple, not forked; indusium mouth not expanded; rare in Peru 20. **T. tuerckheimii**
- u. Segments of sterile laminae deeply crenate or crenate-serrate; veins (some or many) 1-forked; indusium mouth slightly flaring; locally common 21. **T. ankersii**

- s. Stem erect to decumbent and the leaves crowded to caespitose, or if in some species long-creeping and the leaves subdistant, then the lamina not appressed to tree trunks by rhizoids on leaf axes v
- v. Leaves dimorphic w
 - w. Stem erect or decumbent; leaves crowded to caespitose; fertile leaves simple and essentially entire, or without laminar tissue and the sori completely free x
 - x. Fertile leaves with lamina entire to pinnatisect; sori fully immersed in tissue . . . y
 - y. Sterile lamina with 4–8 veins issuing from the rachis between adjacent costae; mouths of indusia neither flaring nor recurved, strongly indented between the vein branches 23. **T. diversifrons**
 - y. Sterile lamina with 2(–3) veins issuing from the rachis between adjacent costae; mouths of indusia slightly flaring and recurved, but not indented between the vein branches 24. **T. trollii**
 - x. Fertile leaves without laminar tissue; sori completely free . . . 25. **T. botryoides**
 - w. Stem wiry, long- or short-creeping; leaves subdistant to remote; fertile leaves with lamina foliose and deeply pinnatisect to nearly pinnate 28. **T. humboldtii**
- v. Leaves monomorphic z
 - z. Lamina 3–4-pinnatisect; petiole conspicuously alate throughout, the alae broader than the petiole quite or nearly to base 22. **T. bicorne**
 - z. Lamina not more than 1-pinnate-pinnatisect; petiole nonalate in the proximal half or throughout, or very narrowly alate in the proximal portion aa
 - aa. Lamina abruptly terminating in a conform apical segment or the rachis prolonged, flagellate, and proliferous at tip; indusia fully exerted from segment margin, often stalked bb
 - bb. False veins copious and perpendicular to the true veins; marginal vein strong, continuous; pinna margins sharply serrate to spinulose . . 26. **T. pinnatum**
 - bb. False veins rare or lacking; marginal vein lacking or faint and discontinuous, pinna margins commonly obtusely serrate 27. **T. hostmannianum**
 - aa. Lamina gradually reduced to a pinnatifid apex, the rachis not prolonged and flagellate; indusia at least partially immersed in the laminar tissue, wholly or partially alate on each side cc
 - cc. Pinnae regularly and deeply lobed to pinnatisect dd
 - dd. Pinnae lobed to pinnatifid; lamina 1–2(–2.5) cm broad, not at all obscured by the moderate pubescence 29. **T. crinitum**
 - dd. Pinnae pinnatisect (rarely the segments again lobed); lamina (2.5–)3–12 cm broad, partially to completely obscured by the dense covering of trichomes 31. **T. lucens**
 - cc. Pinnae entire to serrate or crenate (or rarely a few with some irregularly scattered lobes) ee
 - ee. Veins bearing crestlike lamellae on abaxial side; pinnae in proximal portion of lamina deflexed 30. **T. martiusii**
 - ee. Veins lacking lamellae; pinnae patent or a few basal ones deflexed . . ff
 - ff. Petiole conspicuously alate halfway or more to the stem; stem erect to decumbent, leaves contiguous to caespitose 32. **T. pellucens**
 - ff. Petiole not alate, or scarcely so near apex due to decurrent lamina base; stem short-creeping or decumbent, the leaves subdistant to contiguous (rarely caespitose) gg
 - gg. Rachis trichomes on abaxial side predominantly dark brown, stout, rigid, most of them terete toward their base . . 33. **T. plumosum**
 - gg. Rachis trichomes tawny to orange, delicate, tortuous, the cells flattened hh
 - hh. Lamina linear or linear-lanceolate, mature ones commonly 5–12 times as long as broad; mature leaves (10–)15–50 cm

long; rachis abaxially provided with trichomes predominantly unicellular beyond the basal one, occasionally with 2–3 cells 34. **T. cristatum**
 hh. Lamina oblong- to ovate-lanceolate, 3–4 times as long as broad; mature leaves 5–15 cm long; rachis abaxially provided with trichomes of 2–8 cells beyond basal one, as well as with many unicellular ones 35. **T. vandenboschii**

1. **Trichomanes radicans** Sw., J. Bot. (Schrader) 1800(2): 97. 1802. TYPE: Jamaica, *Swartz* (holotype, s; photo, us). **Figure 12a–b.**

Trichomanes kunzeanum Hooker, Sp. fil. 1: 127. 1844. SYNTYPES: Peru, Huánuco, Pampayacu, *Poeppig 1132* (κ!; photo, us); Peru, Junín, Pangoa, *Mathews 1088* (κ!; photos, a, us); Venezuela, Mérida, *Linden 176* (κ!; isosyntypes, BM, FI).

Trichomanes brachyblastos Kuhn, Linnaea 35: 388. 1868. TYPE: Peru, San Martín, Tarapoto, Monte Guayrapurima, *Spruce 4703* (holotype, b?; isotypes, BM!, BR!, GH!, K!, w!).

Vandenboschia radicans (Sw.) Copel., Philipp. J. Sci. 67: 54. 1938.

Trichomanes radicans var. *kunzeanum* (Hooker) Duek & Lell., Amer. Fern J. 68: 120. 1978.

Stem long-creeping, relatively stout, 1–2.2 mm in diameter, amply to densely covered with castaneous trichomes. **Leaves** remote, 20–50 cm long, axes often provided with scattered septate trichomes abaxially. **Petiole** (1–)4–15 cm long, 0.8–2 mm in diameter, nonalate to marginate or alate (often the wings deciduous). **Lamina** 2–3-pinnatisect, ovate or deltoid-ovate and scarcely reduced at base, or occasionally elliptic and somewhat strongly reduced toward base. **Rachis** narrowly to broadly alate. **Pinnae** mostly 2-pinnatisect, slightly to strongly adnate to the rachis. **Ultimate segments** commonly narrow, often linear, with simple or 1-forked veins, false veinlets lacking. **Venation** anadromous. **Indusia** very slender, cylindrical or elliptic, rarely subconical, often subfusiform, not or scarcely alate, the wings of tissue (if any) 1–2(–3) cells wide, apex truncate, not expanded, receptacle short- or long-exserted.

Hemiepiphytic on tree trunks in dense, wet forests, (400–)700–3200 m, San Martín to Puno.

Mexico to Panama; West Indies; Guianas to Colombia and southward to Brazil and Paraguay; Old World.

Trichomanes radicans, *T. collariatum*, and *T.*

rupestre form a close-knit species complex which is in need of closer study. The three are only provisionally maintained here at the species level. In Central America *T. radicans* and *T. collariatum* are more distinct, e.g., leaves of the latter are consistently reduced to a very short and broadly alate petiole; whereas in *T. radicans* leaves are not or scarcely reduced at base, and petioles are much longer and not or very narrowly alate or marginate. These characters are also somewhat diagnostic in South America, but are much more variable, and are therefore not thoroughly reliable. In Peru, often the two species can be positively separated only by the soral features.

San Martín: Prov. Mariscal Cáceres, Dist. Tocache Nuevo, *J. Schunke 4361* (F, us). **Huánuco:** Near Tingo María, confluence of Monzón and Huallaga Rivers, *Stork & Horton 9501* (F, GH, MO, UC, us). **Pasco:** Paujil near Puerto Bermúdez, *León 288* (GH, USM). **Junín:** Chanchamayo Valley, *C. Schunke 459* (F, us). **Ucayali:** Prov. Coronel Portillo, Sinchono, between Tingo María and Pucallpa, *Aguilar 883* (GH). **Ayacucho:** Prov. La Mar, between Tambo San Miguel, Ayna and Hacienda Luisiana, *Dudley 11904* (GH). **Cuzco:** Prov. Paucartambo, bosques de Keros, *Vargas 7382* (UC). **Puno:** Prov. Carabaya, Hacienda Palmera, *Vargas 16137* (GH).

2. **Trichomanes collariatum** Bosch, Ned. Kruidk. Arch 4: 368. 1859. TYPE: Mexico, Tabasco, *Linden* (holotype, L?; probable isotype, κ; photo, us of κ).

Stem long-creeping, relatively stout, 1–1.7 mm in diameter, amply to densely covered with castaneous trichomes. **Leaves** remote, 15–38(–45) cm long, axes often provided with scattered, septate trichomes abaxially. **Petiole** 0.3–3 cm long, 0.7–1.5 mm in diameter, broadly alate nearly or quite throughout. **Lamina** 2–3-pinnatisect, oblong or oblong-lanceolate, often abruptly reduced at base. **Rachis** commonly broad-alate throughout. **Pinnae** mostly 2-pinnatisect, slightly to strongly adnate to

rachis. **Ultimate segments** commonly narrow, often linear, with simple or forked veins, false veinlets lacking. **Venation** anadromous. **Indusia** conical, gradually widening from base to a conspicuously flaring mouth, alate, the wings of tissue on each side 4–6 cells wide, receptacle long-exserted.

Hemiepiphyte on tree trunks in wet forests, sea level to 500 m, San Martín, Loreto, Madre de Dios.

Southern Mexico to Panama; British Guiana to Colombia, south to Peru; Brazil.

This is not greatly distinct from *T. radicans*, under which see further discussion.

San Martín: Prov. Mariscal Cáceres, Dist. Campanilla, left margin of Río Huallaga, *J. Schunke 4120* (F, GH, US). **Loreto:** Soledad, on Río Itaya, *Killip & Smith 29739* (US). **Madre de Dios:** Prov. Tambopata, Lago Tres Chimbas, *Barbour 5669* (MO). Parque Nacional del Manú, Cocha Cashu Biological Station, *M. S. Foster P-84-4* (UC), *P-84-67* (MO); *R. Foster 6868* (F).

3. *Trichomanes rupestre* (Raddi) Bosch, Ned. Kruidk. Arch. 4: 370. 1859.

Hymenophyllum rupestre Raddi, Pl. Bras. nov. gen. 1: 67, t. 80. 1825. TYPE: Brazil, *Raddi* (holotype, FI?; isotype, K; photos, A & US of K).

Stem long-creeping, stout, 0.7–1.2 mm in diameter, provided with a few scattered to sparse castaneous trichomes. **Leaves** remote, mature ones 15–30 cm long, axes sometimes provided with scattered, septate trichomes on abaxial side. **Petiole** 0.2–2 cm long, 0.6–0.8 mm in diameter, partially alate. **Lamina** commonly 1-pinnate-pinnatifid, oblong or elliptic-oblong. **Rachis** broadly alate throughout. **Pinnae** pinnatifid or pinnatisect, or rarely 2-pinnatifid as to basal segments, strongly adnate to rachis. **Ultimate segments** relatively short and broad, not linear, with simple or forked veins, false veinlets lacking. **Venation** anadromous. **Indusia** conical, gradually widening from base to a slightly flaring mouth, narrowly alate on each side, receptacle short- to long-exserted.

Creeping on tree trunks or wet banks in dense, wet forests, 1100–1600 m, Huánuco and Ucayali.

Venezuela and Colombia; Peru; Bolivia; Brazil (also reported from Costa Rica by Alan Smith, in litt.).

This is not as common as *Trichomanes radicans* or *T. collariatum* and is midway between them in

shape of indusia. The indusium in the latter is conical, with a conspicuous and widely flaring mouth; in *T. rupestre* it is narrower, with mouth only slightly flaring, and in *T. radicans* the indusium is even more slender, often narrowing slightly, with the apex truncate, not or scarcely spreading. See *T. radicans* for further discussion.

Huánuco: Prov. Huánuco, Dist. Churubamba, Cotirarda, *Mexia 8221* (F, GH, MO, UC, US). Tingo María, Selva Real, *Morrow 11132* (GH). **Ucayali:** Prov. Coronel Portillo (as Loreto), Aguaytía, *Ridoutt 13082* (USM).

4. *Trichomanes pyxidiferum* L., Sp. pl. 1098. 1753.

TYPE: based on Plumier, *Traité foug. Amér.*, t. 50E, 1705, illustrating a plant from Haiti.

Vandenboschia pyxidifera (L.) Copel., Philipp. J. Sci. 67: 53. 1938.

Stem long-creeping, filiform, 0.4–0.5 mm in diameter (excluding indument), densely covered with blackish trichomes. **Leaves** well-spaced to remote, 3–12 cm long, axes sometimes provided abaxially with scattered, minute trichomes. **Petiole** 1–3 cm long, 0.3–0.6 mm in diameter, flattened, or terete at base, narrowly to broadly alate distally or throughout, the wings plane to somewhat crispate. **Lamina** 2–3-pinnatifid. **Rachis** alate throughout, the wings commonly undulate to crispate. **Pinnae** 4–10 pairs, strongly adnate to the rachis (the costae alate). **Ultimate segments** linear, margins plane to undulate, tissue commonly with elongate, narrow folds parallel to the veins, false veinlets lacking. **Venation** anadromous. **Sori** 1–several per pinna. **Indusia** broadly conical, the tube 1–1.5 times as long as broad, not or scarcely bilabiate, the mouth not or slightly flaring, receptacle commonly long-exserted.

On trees in wet forests, 900–1200 m, Amazonas, San Martín.

Pantropical.

A distinctive feature of *Trichomanes pyxidiferum* is the rather sharp, longitudinal folding of segment tissue parallel to the veins. Other related species have plane segments, or some with the margins undulate, but none exhibit this unique character. Perhaps it was this which prompted Morton's incorrect observation (1968) of false veins in the species, since the sharper folds of tissue sometimes cause dark shadow lines in the segments. However, in careful study of specimens throughout the range, no leaves were seen with the

sclerenchymatous strands which produce these "false veins." The species thus far is represented in Peru by only two collections, even though its full range extends throughout tropical regions of the world.

Amazonas: Prov. Chachapoyas, Jazán (Ingenio-Chachapoyas), *López et al.* 4264 (GH, HUT). **San Martín:** Tarapoto, *Spruce* 4761 (BR, GH, K, L, US).

5. ***Trichomanes diaphanum*** HBK., Nov. gen. sp. 1: 25 (fol. 16). 1816. TYPE: Venezuela, *Humboldt & Bonpland* (holotype, P; isotype, B!).

Trichomanes leptophyllum Bosch, Ned. Kruidk. Arch. 4: 363. 1859 (not A. Cunn., 1836), *nom. illeg.*

TYPE: based on *T. pyxidiferum* Hooker & Grev. *Trichomanes hymenophylloides* Bosch, Ned. Kruidk. Arch. 5: 209. 1863, *nom. nov.* for *T. leptophyllum* Bosch and type based on that name.

Vandenboschia diaphana (HBK.) Copel., Philipp. J. Sci. 67: 53. 1938.

Vandenboschia hymenophylloides (Bosch) Copel., Philipp. J. Sci. 67: 53. 1938.

Stem long-creeping, filiform, 0.2–0.5 mm in diameter (excluding indument), sparsely to abundantly provided with castaneous trichomes. **Leaves** well-spaced to remote, 5–15(–18) cm long, axes glabrous, or the rachis sometimes abaxially provided with scattered, minute trichomes. **Petiole** 0.5–6 cm long, 0.3–0.8 mm in diameter, flattened, or terete at base, nonalate, or narrowly to broadly alate for most of its length, the wings plane or occasionally undulate. **Lamina** essentially 3-pinnatifid. **Rachis** alate throughout, the wings narrow to broad, plane to undulate or occasionally crispate. **Pinnae** 4–12 pairs, adnate to the rachis, the costae alate (rarely nonalate at base). **Ultimate segments** linear, 0.6–0.9 mm broad, plane, not folded, false veinlets lacking. **Venation** anadromous. **Sori** 1–10 per pinna. **Indusia** salverform, the alate tube narrowly cylindrical, 2–4 times as long as broad, abruptly expanding into a broad-flaring mouth, receptacle commonly long-exserted.

On trees, moist banks and (rarely) wet rocks, in deep forests 700–2900 m, Amazonas and Loreto to Puno.

Southern Mexico to Panama; West Indies; Trinidad; the Guianas to Colombia, south to Peru and Brazil.

Previous authors have separated *Trichomanes hymenophylloides* on characters such as number of sori per pinna, width of tissue wings flanking

axes and indusia, crowding of pinnae and dissection of lamina. Each of these may appear to be important in individual specimens, but when many collections are examined throughout the range of distribution, it becomes evident that they are quite variable and uncorrelated.

Amazonas: Prov. Bagua, Cordillera Colán SE of La Peca, *Barbour* 3904 (MO). **Loreto:** Sierra del Pongo, *Mexia* 6288B (GH, UC, US). **Pasco:** Prov. Oxapampa, Dist. Oxapampa, road Oxapampa to Villa Rica, *B. León* 660 (USM in part). **Junín:** La Merced, E of Quimiri Bridge, *Killip & Smith* 24006 (F), 24023 (GH, US). **Cuzco:** Prov. La Convención, "El Dorado," *Vargas* 3518 (GH). **Puno:** San Gabán, *Lechler* (L).

6. ***Trichomanes angustatum*** Carm., Trans. Linn. Soc. London 12: 513. 1818. TYPE: Tristan da Cunha, *Carmichael* (holotype, K!; isotype, BM!).

Trichomanes tenerum Sprengel, Syst. veg. 4: 129. 1827. TYPE: Brazil, collector not stated (holotype, LZ destroyed).

Vandenboschia tenera (Sprengel) Copel., Philipp. J. Sci. 67: 53. 1941.

Vandenboschia angustata (Carm.) Copel., Philipp. J. Sci. 73: 466. 1941.

Stem long-creeping, filiform, 0.2–0.3 mm in diameter, amply provided with castaneous trichomes. **Leaves** well-spaced to remote, 4–14(–18) cm long, glabrous. **Petiole** 0.5–5 cm long, 0.2–0.4 mm in diameter, terete, nonalate. **Lamina** 2-pinnate-pinnatifid to 4-pinnate, linear-lanceolate to ovate-lanceolate, abruptly or gradually reduced at base. **Rachis** nonalate, or scarcely alate near the apex. **Pinnae** 6–many pairs, short-stalked, the costae alate except below the basal pinnule. **Ultimate segments** linear, 0.5–0.8 mm broad, each bearing a single vein, false veinlets lacking. **Venation** anadromous. **Sori** 1–5 per pinna. **Indusia** narrowly funnelform to salverform, the tube 2–4 times as long as broad, the mouth flaring, margins commonly alate, with wings several cells wide, receptacle long-exserted.

In deep forests, on trees, wet cliffs and banks, and on decaying logs, 600–2800 m, Cajamarca and San Martín to Ayacucho and Cuzco.

Southern Mexico to Honduras; Greater Antilles; Venezuela and Colombia to NW Argentina and Brazil.

This is very closely related to *Trichomanes capillaceum*, under which see further discussion.

Cajamarca: Colasay, *Woytkowski 7002* (US). **San Martín:** Monte Campana, near Tarapoto, *Spruce 4705* (BR, K, NY). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al. 8428* (MO, UC). **Junín:** Carpapata, above Huacapistana, *Killip & Smith 24492* (F, UC, US). **Ayacucho:** Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith 22406* (F, GH, US). **Cuzco:** Valley of Urubamba, Machu-Picchu, base of Huayna Picchu, *Illis et al. 1064* (GH, MO, UC, US).

7. ***Trichomanes capillaceum*** L., Sp. pl. 1099. 1753. LECTOTYPE (designated by Proctor, Ferns of Jamaica, British Museum, London, p. 109. 1985): Plumier, *Traité foug. Amér., t. 99D*, based on a Plumier collection from Haiti.

Vandenboschia capillacea (L.) Copel., *Philipp. J. Sci.* 67: 53. 1938.

This differs from *Trichomanes angustatum* only in the characters used in the key.

In deep forests, on tree trunks, 800–1100 m, Pasco and Cuzco.

Southern Mexico to Panama; Greater Antilles; Venezuela and Colombia to Peru.

With this might possibly be included *Trichomanes angustatum*, but the two are separated here provisionally, pending much needed monographic revision. Typically, *T. capillaceum* has very little expanded tissue along the axes, and even the ultimate segments are rarely more than 0.3 mm broad. Indusia are not or scarcely alate, and sori are solitary on each fertile pinna. Conversely, beyond the first pinnule in *T. angustatum*, the costae and costules are obviously alate throughout, and ultimate segments are often nearly 1 mm broad. The tissue also forms wings on each side of the indusia, and sori are frequently four or five per pinna.

Even some of the characters listed in the key are subject to variation in certain geographic regions, and intermediates are found frequently. Nevertheless there are areas in which only one or the other occur. Only *Trichomanes angustatum* occurs in Bolivia and southern Brazil, whereas in Central America it has not been found south of Guatemala, a region where *T. capillaceum* is rather common. In Peru, the latter is rare, and even the few specimens located are not typically skeletal in their appearance, whereas *Trichomanes angustatum* is rather widespread and the specimens rather typical. One specimen from Cuzco, *Vargas 8653* (MO), is exactly intermediate between the two; significantly, Cuzco is one of the two de-

partments in which both species are known to occur. Therefore, based only on collections from Peru, one would be tempted to combine the two species, but a thorough study of the characters of both taxa throughout their range is necessary before further classification is attempted.

Pasco: Pichis Trail, San Nicolás (as Junín), *Killip & Smith 25990* (F, GH, US). **Cuzco:** Prov. Paucartambo, Cosñipata Valley, Río Tono, *Wachter et al. 199* (F).

8. ***Trichomanes elegans*** Rich., *Actes Soc. Hist. Nat. Paris* 1: 114. 1792. TYPE: French Guiana, *Le Blond* (P) (not *T. elegans* Rudge, 1805).

Trichomanes prieurii Kunze, *Analecta Pteridogr.* 48. 1837. SYNTYPES: French Guiana, *Leprieur* (LZ destroyed; isosyntype, F!); Brazil, Amazonas, Río Japurá, *Martius* (M); British Guiana, *Rudge* (K). *Trichomanes opacum* Bosch, *Ned. Kruidk. Arch.* 5(2): 175. 1861. TYPE: Peru, Puno, San Gabán, *Lechler 2175* (holotype, L?; isotype, P!; photo, F, frag., L!).

Davalliopsis elegans (Rich.) Copel., *Philipp. J. Sci.* 67: 82. 1938.

Terrestrial, rarely epiphytic or epipetric. **Stem** erect or rarely short-creeping. **Leaves** caespitose to occasionally approximate, 20–90 cm long, rachis, costae, and often costules amply to abundantly provided with castaneous, pluricellular trichomes on abaxial side. **Petiole** 10–40 cm long, 1–3.5 mm in diameter, usually alate distally. **Lamina** 2–3-pinnate-pinnatifid, deltoid, opaque, usually more than 1 cell thick, at least away from the margins, the cells small and occluded, not evident even when magnified at 10–15 \times . **Rachis** obtusely quadrangular, alate (often broadly so) at least in distal half. **Pinnae** adnate, the costae alate to base. **Ultimate segments** lacinate, with linear lobes, each of these bearing a single vein, false veins lacking. **Venation** anadromous. **Sori** usually bent down away from the plane of the lamina. **Indusia** subconical to somewhat urceolate, not bilabiate, the mouth truncate or slightly (rarely strongly) flaring, receptacle short- to long-exserted.

In dense, wet forests or wet, wooded ravines, on ground, or rarely on tree trunks or wet rocks, sea level to 1300 m, Amazonas and Loreto south to Madre de Dios and Puno.

Lesser Antilles and Trinidad; Nicaragua to Panama; Guianas to Colombia and south to Bolivia and Brazil.

With its large, blue green leaves and lacinate pinnae, this is one of the most beautiful species in the family. Its most distinctive features are the usually strongly arching sori (bent downward out of the plane of the lamina) and the relatively thick tissue. Although the lamina in Hymenophyllaceae is typically only one cell thick, the tissue in *Trichomanes elegans* is often several cells thick, especially away from the segment margins. The broadly alate rachis traditionally has been used to separate this from *T. rigidum* (with which it often grows), and although usually it is a good diagnostic feature, occasional specimens of *T. elegans* can be found throughout the range in which rachis alae are very narrow or lacking in the proximal portion. Consequently, supporting key characters should be employed for accurate identification.

Amazonas: Prov. Bagua, left bank of Río Marañón opposite Quebrada Miraná, *Wurdack 2031* (F, GH, US). **San Martín:** Prov. Mariscal Cáceres, Tocache Nuevo, *J. Schunke 4855* (F, GH, US), *6958* (F, MO in part, US). **Loreto:** Sierra del Pongo, *Mexia 1195* (F, GH, MO, US). **Huánuco:** Prov. Pachitea, Dist. Honoria, *J. Schunke 2259* (F, GH). **Pasco:** Prov. Oxapampa, Valle del Palcazú, Iscozacín, *León 692* (F, GH). **Junín:** Puerto Bermúdez, *Killip & Smith 26537* (GH, US). **Ucayali:** Prov. Coronel Portillo (as Loreto), Padre Abad, *J. Schunke 5393* (F, US). **Cuzco:** Bajada de Tocate, *Bües 1748* (US). **Madre de Dios:** Prov. Tambopata, Río Tambopata Nature Reserve, *Barbour 5165* (MO). **Puno:** Prov. Carabaya, San Gabán, *Vargas 18864* (GH).

9. *Trichomanes rigidum* Swartz, Prodr. 137. 1788.

TYPE: Jamaica, Swartz (holotype, s; isotype, b, *Herb. Willd. 20202-1*; photos, us of s, GH & US of b).

Selenodesmium rigidum (Sw.) Copel., Philipp. J. Sci. 67: 81. 1938.

Terrestrial, rarely epiphytic or epipetric. **Stem** erect or occasionally short-creeping. **Leaves** caespitose to sometimes approximate, 15–35 cm long, lamina glabrous, the axes glabrous, or rarely the rachis or petiole base with a few, scattered trichomes. **Petiole** 5–16 cm long, 0.6–1.6 mm in diameter, nonalate. **Lamina** 3–4-pinnate-pinnatifid, deltoid, opaque, 1 cell thick, but cells small and occluded, not evident even when magnified at 10–15 \times . **Rachis** terete, nonalate, or marginate to slightly alate toward apex. **Pinnae** (at least proximal ones) short-stalked and the costae not alate at base. **Ultimate segments** with linear lobes, each of these bearing a single vein, false veins lacking. **Venation** anadromous. **Sori** (most of them) borne

essentially in the plane of the lamina. **Indusia** subconical, not bilabiate, the mouth truncate, not or scarcely flaring, receptacle commonly long-exserted.

On slopes and ridges of dense forests and in wooded ravines, occasionally on wet rocks or cliffs, rarely on bases of tree trunks, 350–2500 m, Cajamarca and San Martín, south to Cuzco and Madre de Dios.

Southern Mexico to Panama; West Indies; South America, to Bolivia and Brazil; probably Old World tropics.

This is sometimes confused with *Trichomanes elegans*, with which it often grows. For comparison, see discussion under the latter species.

Cajamarca: Tambillo, *Jelski 891* (us). **San Martín:** Tarapoto, in monte Guayrapurima, *Spruce 4047* (BR, K). **Huánuco:** East of Tingo María (as San Martín), *Allard 22356* (GH, US). **Pasco:** Oxapampa, Cordillera San Matías, *León 326a* (USM). **Junín:** La Merced, Hacienda Schunke, *Macbride 5633* (F, US). **Ucayali:** Vicinity of Aguaytía, along Río Aguaytía (as Loreto), *Croat 20927* (MO). **Cuzco:** Prov. Urubamba, base of Huayna Picchu, *Illis et al. 1062* (GH). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, *Foster 10903* (F).

10. *Trichomanes cellulolum* Klotzsch, Linnaea 18: 531. 1844. TYPE: “British Guiana,” (Guyana). Kanuku Mountains, *Rich. Schomburgk 1186* (holotype, b!; photo, F; isotypes, b! 2 sheets, BM!).

Epiphytic, terrestrial, or sometimes epipetric. **Stem** erect to short-creeping. **Leaves** caespitose to (occasionally) approximate, 6–15 cm long, glabrous. **Petiole** 1–7 cm long, 0.3–0.6 mm in diameter, narrowly alate at least distally. **Lamina** 4–5-pinnate, lanceolate to ovate, translucent, the cells large and clear and quite evident when magnified at 8–12 \times . **Rachis** terete, alate throughout. **Pinna** divisions skeleton-like, the costae, costules, and ultimate segments with bands of tissue only 1–several rows wide. **Ultimate segments** linear, 0.3–0.7 mm broad, each bearing a single vein, false veins lacking. **Venation** anadromous. **Indusia** subconical to somewhat urceolate, not bilabiate, the mouth truncate or slightly flaring, receptacle short- to long-exserted.

In wet forests, on trees or on the forest floor, sometimes on wet rocks, 300–1300 m, Amazonas, Loreto, Huánuco.

Surinam to Colombia; Peru; Brazil.

With this perhaps should be included *Trichom-*

anes sprucei Baker of northern South America, which is probably only a more robust form, with broader segments and broader bands of tissue along the axes.

Amazonas: Prov. Bagua, roadside from Chiriaco to Puente Venezuela, *Barbour 4455* (MO, USM). **Loreto:** Pucallpa, between Balsapuerto and Moyobamba, *Klug 3192* (F, GH, MO, US). Tierra Doble on Río Nanay, *Ll. Williams 1057* (F, US). **Huánuco:** Río Lullapichis watershed, ascent of Cerros del Sira, *Dudley 13032* (GH), *Wolfe 12352* (GH, US).

11. ***Trichomanes punctatum* Poir. ssp. *sphenoides* (Kunze) Boer, Acta Bot. Neerl. 11: 301. 1962.**

Trichomanes sphenoides Kunze, Farnkräuter 216, t. 88, f. 2. 1840. TYPE: Peru, Cuchero (Dept. Huánuco), *Poeppig* (holotype, w!; isotype, MO!).

Didymoglossum sphenoides (Kunze) Presl, Hymenophyllaceae 23. 1843.

Stem long-creeping, filiform. **Leaves** approximate or widely spaced, to 1.5 cm long and 1 cm broad, subsessile or short-petiolate. **Lamina** circular to obovate or spatulate, margin entire to irregularly lobed, a costa lacking or, in some fertile laminae, distinct only in the proximal portion, glabrous except for the dark, stellate, marginal trichomes. **Venation** flabellate, the veins crowded, with false veinlets parallel to them. **Sori** several, or sometimes solitary, partially immersed in the lamina tissue, commonly borne between lobes, thus rarely extending beyond the outline circumscribed by the lobe apices. **Indusia** narrow-cylindrical, bilabiate, the lips mostly wide-flaring and narrowly dark-margined, receptacle not or scarcely exerted.

In dense, wet forests and wooded ravines, on tree trunks, 100–1100 m, Loreto to Pasco.

Guatemala; Costa Rica; Panama; Greater Antilles; Venezuela; Colombia to Bolivia.

Boer (1962) recognized four subspecies of *Trichomanes punctatum*, and only this one occurs in Peru. Others differ from ssp. *sphenoides* in having more distinctly lobed laminae and/or larger and more broadly dark-margined indusium lips.

Loreto: Maynas, Iquitos, Ushpa-Caña across from Río Itaya, *McDaniel 11381* (GH, MO). **Huánuco:** Prov. Huánuco, near confluence of Río Cayumba with Huallaga, *Mexia 8275* (F, MO, US). **Pasco:** Prov. Oxapampa, Valle de Palcazú, Cacazú, *León 681* (F). Puerto Bermúdez (as Junín), *Killip & Smith 26592* (US).

12. ***Trichomanes angustifrons* (Fée) Boer, Fl. Neth. Antill. I (Pterid.): 17. 1962.**

Didymoglossum angustifrons Fée, Mém. foug. 11: 113, t. 28, f. 5. 1866. TYPE: Guadeloupe, *l'Herminier* (holotype, P!).

Stem long-creeping, filiform. **Leaves** approximate or well-spaced, 0.5–1.5 cm long, to 0.6 cm broad, subsessile or short-petiolate. **Lamina** narrowly or broadly oblong, entire, or distally lobed, costa percurrent, glabrous except for the dark, stellate trichomes borne along the margin. **Venation** catadromous, pinnate, with false veinlets sparsely to amply distributed between the true veins. **Sori** solitary at lamina apex, or few and terminating each distal lobe, somewhat to deeply immersed in the tissue. **Indusia** narrow-conical, bilabiate, the lips mostly wide-flaring and narrowly dark-margined, receptacle commonly exerted.

Thus far represented in Peru by a single specimen from Huánuco, on ridge in jungle, 850 m; elsewhere apparently always epiphytic.

Costa Rica and Cocos Island; West Indies; Trinidad and Tobago; the Guianas to Brazil; Peru; Paraguay (reported from Chiapas, Mexico by Alan Smith, in litt.).

Collections of this species are rather sparse, except from Brazil and the West Indies; yet it is surely a much more common plant than the specimens would indicate. Since it is such a tiny and inconspicuous fern, it certainly has been overlooked and probably is not accurately represented in herbaria.

Huánuco (as San Martín): E of Tingo María, *Allard 21383a* (US).

13. ***Trichomanes hymenoides* Hedwig, Fil. gen. sp., t. 3, f. 3. 1799. LECTOTYPE (designated by Boer, Acta Bot. Neerl. 11: 306. 1962): Hedwig, t. 3, f. 3, probably based on a Swartz specimen from Jamaica. Figure 12d.**

Trichomanes muscoides Sw., J. Bot. (Schrader) 1800(2): 95. 1802. TYPE: Jamaica, *Swartz* (holotype, S-PA).

Didymoglossum hymenoides (Hedwig) Desv., Mém. Soc. Linn. Paris 6: 330. 1827.

Didymoglossum muscoides (Sw.) Desv. Mém. Soc. Linn. Paris 6: 330. 1827.

Stem long-creeping, densely covered with dark trichomes that extend onto the petioles. **Leaves**

well-spaced, (0.5–)1–3.5 cm long, to 1.5 cm broad, subsessile or short-petiolate. **Lamina** obovate to elliptic, 1-pinnatifid or rarely 2-pinnatifid, the costa percurrent (but juvenile laminae often subreniform and merely lobed and the costa indistinct distally), glabrous except for the dark, marginal trichomes which are stellate in sinuses and simple to bifid on outer margin, laminar cells commonly isodiametric. **Venation** catadromous, commonly pinnate (occasionally subflabellate in juvenile leaves), false veinlets sparse, scattered between true veins, extending toward lamina margin but not parallel to it. **Sori** 1–several borne near lamina apex, conspicuously exserted, or only slightly immersed at base, not or very narrowly alate. **Indusia** narrow-funnelform, bilabiate, but the lips quite short, commonly broader than long, and usually (not always) dark-margined, receptacle long-exserted.

In forests on trees, or rarely on rocky or sandy soil, 700–2400 m, Amazonas, Loreto.

Southern Mexico to Panama; West Indies; Trinidad; Venezuela and Colombia, south to Argentina and Uruguay.

Juvenile leaves are often nearly reniform and shallowly lobed, with veins subflabellate and the costae sometimes indistinct toward the apex. Hence they can be confused with *Trichomanes punctatum*. However, fertile leaves are pinnatifid, with stellate trichomes borne only in the sinuses, and sori strongly protrude from the leaf tissue. In *T. punctatum* ssp. *sphenoides* sori are partially immersed, and marginal trichomes are consistently stellate.

Amazonas: Prov. Chachapoyas, Río Ventilla W of Molinopampa, *Wurdack 1513* (F, GH, US). **Loreto:** Sierra del Pongo, *Mexia 6289B* (GH, US).

14. **Trichomanes reptans** Sw., Prodr. 136. 1788. TYPE: Jamaica, Swartz (holotype, s-PA).

Didymoglossum reptans (Sw.) Presl, Hymenophyllaceae 23. 1843.

Stem long-creeping, densely covered with dark trichomes that extend onto the petioles. **Leaves** well-spaced, 2–9 cm long, 1–4 cm broad, subsessile to short-petiolate. **Lamina** lanceolate to ovate or elliptic, 1-pinnatifid or rarely 2-pinnatifid, the rachis distinct throughout, glabrous except for the dark, marginal trichomes which are stellate in si-

nuses and simple to bifid on outer margins, laminar cells mostly elongate. **Venation** catadromous, pinnate, false veinlets commonly abundant, extending toward lamina margin but not (or very rarely) parallel to it. **Sori** 1 or a few, borne near lamina apex, conspicuously protruding from the leaf tissue, or only slightly immersed at base, not or scarcely alate. **Indusia** narrow-funnelform, bilabiate, the lips dark-margined, and sometimes flaring, most of them as long as or longer than broad, receptacle short- to long-exserted.

On wet rocks in forests, 1900–2750 m, Amazonas, Huánuco.

Southern Mexico to Panama; Greater Antilles; Venezuela; Colombia; Ecuador; Peru; Brazil; Argentina.

Although found thus far in Peru only on wet rocks, *Trichomanes reptans* may be expected also on trees, since it frequently has been reported as an epiphyte throughout much of its range.

Amazonas: Prov. Bagua, Cordillera Colán SE of La Peca, *Barbour 3903* (MO, USM). **Huánuco:** Mito, *Bryan 392* (F).

15. **Trichomanes krausii** Hooker & Grev., Icon. fil. 2, t. 149. 1831. TYPE: Dominica, Kraus (holotype, E).

Didymoglossum krausii (Hooker & Grev.) Presl, Hymenophyllaceae 23. 1843.

Stem long-creeping, densely covered with dark trichomes which extend onto the petioles. **Leaves** well-spaced, 2–8 cm long, 1–3 cm broad, subsessile to short-petiolate. **Lamina** narrow-ovate to elliptic or obovate, 1-pinnatisect to 2-pinnatifid, the rachis distinct throughout and often abaxially dark-pubescent at least near the base, the lamina provided with simple to bifid trichomes, but with stellate ones in the segment sinuses. **Venation** catadromous, pinnate, false veinlets seldom numerous, many of them parallel to and very near the lamina margin. **Sori** 1 or a few, terminating the segments, partly to deeply immersed in the segment tissue, the protruding portion narrowly or broadly alate. **Indusia** salverform, bilabiate, the lips commonly dark-margined and flaring, receptacle short- to long-exserted.

Found near 800 m, San Martín, Huánuco. There are no other label data on the only two collections

found thus far in Peru, but *Trichomanes krausii* occurs in forests on trees or wet rocks elsewhere throughout its range.

United States (Florida); Mexico to Panama; West Indies; Trinidad; the Guianas to Colombia, south to Paraguay and Argentina.

Besides the characters used in the key, *Trichomanes krausii* often can be distinguished from closely related species by the dark trichomes that frequently extend up the petiole onto the abaxial side of the lower rachis. Rachises of the other species are essentially glabrous.

San Martín: Tarapoto, *Spruce 3991* (BR, w). **Huánuco:** Fundo Chela, Sinchono, Río Chino, *Aguilar 912* (USM).

16. *Trichomanes kapplerianum* J. W. Sturm, Fl. bras. 1(2): 276. 1859. TYPE: Surinam, near Station Victoria, *Kappler 1760* (holotype, w!).

Hemiphlebiium kapplerianum (J. W. Sturm) Prantl, Hymenophyllaceae 46. 1875.

Trichomanes ekmanii Boer, Acta Bot. Neerl. 11: 319. 1962. TYPE: Dominican Republic, La Cumbre, Cordillera Central, *Ekman H-14342* (holotype, u; isotypes, f!, G, GH!, MO!, S, UC, US!).

Stem long-creeping, filiform, sparsely to abundantly provided with brown trichomes which extend onto the petioles. **Leaves** well-spaced, to 3 cm long and 1.5 cm broad, subsessile or short-petiolate. **Lamina** obovate or oblong (or in juvenile ones often circular), base rounded, cordate or cuneate, entire or distally lobed, with a distinct costa at least in the proximal portion, glabrous, or sparsely pubescent basally along the costa. **Venation** catadromous, essentially pinnate (but sometimes subflabellate distally), false veins ample to abundant, parallel to the true veins and with a submarginal, continuous or sometimes interrupted false vein around the perimeter of the lamina. **Sori** several to ample near lamina apex or on the lobes, fully immersed in the tissue. **Indusia** funnelform, not bilabiate, the mouth expanded, but not dark-margined, receptacle short- or long-exserted.

In dense forests and wooded ravines, on tree trunks (also on rocks, outside Peru), sea level to 1000 m, San Martín, Loreto, Huánuco, Puno.

Guatemala to Panama; West Indies; the Guianas to Venezuela; Peru; Brazil; Bolivia.

Detailed study of many specimens throughout the Neotropics indicates that *Trichomanes ekmanii* is not distinct. The latter was said by Boer (1962) to differ in the uninterrupted submarginal false vein, bordered on the outside by cubical cells, whereas the submarginal vein of *T. kapplerianum* was said to be sometimes interrupted and bordered by tangentially lengthened cells. These features prove to be minor ones that are quite variable. In careful study of many specimens, including types, one can nearly always find some interruptions in submarginal false veins; furthermore, shape of the border cells is seldom constant. Many leaves on the type specimen of *T. kapplerianum*, for example, have nearly as many cubical cells as tangentially lengthened ones, and some cells are even radially lengthened (supposedly a distinguishing feature of *T. hookeri* Presl, of the Greater Antilles). Additionally, most of the type specimens of *T. ekmanii* have at least a few leaves with somewhat interrupted submarginal veins. There is probably no justification for separating either species from *T. hookeri*, which Boer distinguished on similar characters. However, the type of the latter has not been examined and *T. kapplerianum* is provisionally maintained here as distinct.

San Martín: Near Tarapoto, *Spruce 4762* (BR, w). **Loreto:** San Antonio, on Río Ataya, *Killip & Smith 29522* (F, GH). Prov. Maynas, on the Amazon, 50 miles downriver from Iquitos, *Moran 3661* (F). **Huánuco:** E of Tingo María (as San Martín), *Allard 20912* (US). **Puno:** Near San "Gavan" (Gabán), *Lechler 2297* (BR).

17. *Trichomanes membranaceum* L., Sp. pl. 1097. 1753. TYPE: "America," without specific locality (holotype, LINN 1253.1).

Lecanium membranaceum (L.) Presl, Hymenophyllaceae 12. 1843.

Didymoglossum membranaceum (L.) Vareschi, Flora Venezuela 1: 222. 1969.

Stem long-creeping, slender, densely covered with dark brown trichomes which extend onto the short petioles. **Leaves** well-spaced, 2–6 cm long and often nearly as broad, subsessile. **Lamina** nearly circular and entire, or spatulate and incised into regular lobes, lacking a distinct midrib, glabrous, but bearing along the margin numerous, paired, circular, scalelike processes (these sometimes deciduous in age). **Venation** flabellate, the veins repeatedly dichotomous, false veinlets abundant and parallel with the true veins, but a con-

tinuous submarginal false vein lacking. **Sori** several to many on vein tips toward the lamina apex, partially to fully immersed in the tissue. **Indusia** narrow-funnelform, not or scarcely bilabiate, the mouth neither flaring nor dark-margined, receptacle short- or long-exserted.

In deep forests or wooded ravines, on tree trunks or wet rocks or cliffs, sea level to 850 m, Amazonas, Loreto, Huánuco.

Southern Mexico to Panama; West Indies; the Guianas to Colombia, south to Bolivia.

Amazonas: Prov. Bagua, Río Marañón opposite Quebrada Miraná, *Wurdack 2040* (F, US). **Loreto:** Dist. Tigre, Río Tigre near Tigre, *McDaniel & Rimachi 18531* (GH). Pongo de Manseriche, *Mexia 6198* (F, GH, MO, US). **Huánuco:** E of Tingo María (as San Martín), *Allard 21549* (GH, US).

18. **Trichomanes polypodioides** L., Sp. pl. 1098. 1753. NEOTYPE (designated by Proctor, Flora Lesser Antilles 92. 1977): Montserrat, Proctor 19068 (A).

Trichomanes poeppigii Presl, Hymenophyllaceae 41. 1843. TYPE: "Habitat in Peruvia," *Poeppig* (holotype, w?).

Stem long-creeping, filiform, sparsely provided with scattered brown trichomes. **Leaves** well-spaced, 4–12(–18) cm long, 1–3 cm broad, sessile or short-petiolate. **Lamina** linear- or oblong-lanceolate, deeply lobed to pinnatifid, the axes, veins and margin provided with dark brown trichomes that are stellate or forked from the base. **Venation** catadromous, lacking false veins. **Sori** 1–few at or near segment apex, fully immersed in the segment tissue. **Indusia** salverform, neither bilabiate nor dark-margined, the mouth flaring, receptacle long-exserted.

In deep forests, on tree trunks, very rarely on wet clay banks, 350–2300 m, Loreto and Huánuco to Cuzco and Madre de Dios.

Southern Mexico to Panama; West Indies; Trinidad; South America, to Brazil and Uruguay.

Smaller specimens could be mistaken for *Trichomanes reptans* or other related species of subg. *Didymoglossum*, which are similar in their delicate, long-creeping stems, small, pinnatifid leaves, marginal stellate trichomes, and general aspect. However *T. polypodioides* lacks the false veinlets common in that subgenus, and trichomes are

sparsely scattered along the stem, unlike the dense, blackish indument found on stems of *T. reptans* and its relatives.

Loreto: Sierra del Pongo, *Mexia 6228* (GH, MO, UC, US). **Huánuco:** E of Tingo María (as San Martín), *Allard 21391* (GH, US). **Pasco:** Pichis Trail, Yapas (as Junín), *Killip & Smith 25543* (F, GH), *25555* (F). **Junin:** Schunke Hacienda above San Ramón, *C. Schunke A240* (GH, US). **Cuzco:** Altura del Río Tocate, *Bües 1744* (US). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, *Foster et al. 10713* (F).

19. **Trichomanes tanaicum** J. W. Sturm in Mart., Fl. bras. 1(2): 260. 1859. TYPE: Brazil, Pará, Rio Acará, *Spruce 410* (holotype, B; possible isotypes ["*Spruce 44*"], K!, US; photo, A of K).

Lacostea tanaica (J. W. Sturm) Prantl, Unters. Morph. Gefässkrypt. 1: 50. 1875.

Trichomanes ankersii Hooker & Grev. var. *tanaicum* (Sturm) Sadebeck in Engler & Prantl, Nat. Pflanzenfam. 1(4): 105. 1899.

Stem long-creeping, stout and wiry, 0.5–0.8 mm in diameter, amply provided with brown rhizoids which extend onto the rachis and adhere to tree trunks. **Leaves** subdistant to remote, mature ones 3–15 cm long, 0.7–1.5 cm broad, sessile or scarcely petiolate. **Lamina** linear, subentire or lobed (at base occasionally incised nearly to the rachis), the rachis abaxially often provided with rhizoids, otherwise glabrous. **Venation** catadromous, veins free, 1–several times-forked in the lobes, false veins lacking. **Sori** 1 or a few, terminating the lobes, not or scarcely immersed in the segment tissue. **Indusia** salverform, not or scarcely bilabiate, the mouth rather widely flaring, not dark-margined, receptacle scarcely to long-exserted.

In deep forests, commonly hemiepiphytic on tree trunks, 100–130 m, Loreto, Ucayali.

Venezuela; Colombia; Brazil; Amazonian Peru.

The lamina in *Trichomanes tanaicum* is commonly lobed less than one-third to the rachis, but rarely (as in *Klug 92*) some of the leaves are deeply pinnatifid. Nevertheless, the narrow laminae with their linear outline distinguish them from other species in section *Lacostea*.

Loreto: Mishuyacu, near Iquitos, *Klug 92* (F, US). Prov. Maynas, Dist. Nanay, Santa María de Nanay, *J. Schunke V. 2449* (F, GH). **Ucayali:** Prov. Coronel Portillo (as Loreto), Río Mazán, *J. Schunke 300* (F, GH, UC, US, USM).

20. *Trichomanes tuerckheimii* Christ, Hedwigia 44: 361. 1905. LECTOTYPE (designated here): Guatemala, Alta Verapaz, Cubilquitz, *von Tuerckheim 8348* (lectotype, P!; isolecotypes, K, P!). LECTOPARATYPE: Peru, Loreto, near Leticia, *Ule 6228* (K!, P!).

Stem long-creeping, relatively stout and wiry, 0.5–1.2 mm in diameter, sparsely to abundantly provided with brown rhizoids that extend onto the leaf axes and adhere to tree trunks. **Leaves** subdistant to remote, larger ones (9–)12–20(–30) cm long, 2–9 cm broad, subsessile. **Lamina** broadly oblong, pinnatisect, the rachis, costae and (sometimes) veins and margins abaxially provided with simple, reddish brown trichomes that adhere to tree trunks, free portion of larger segments 2.8–4.5 cm long and 0.8–1.2 cm broad, entire to shallowly crenate. **Venation** catadromous, veins free, simple, false veins lacking, but often some very short, darkened lines scattered between the veins. **Sori** few to several on the pinna-lobes, not or scarcely immersed in the segment tissue. **Indusia** tubular, neither bilabiate nor dark-margined, mouth not expanded, receptacle commonly long-exserted.

Thus far known in Peru only from the lectoparatype, cited above, on tree trunks; elsewhere hemiepiphytic, in forests on tree trunks, sea level to 500 m.

Southern Mexico to Panama; Surinam to Colombia; Amazonian Peru.

Included on the sheet with the syntype at Paris is a fragment of a 2-pinnatifid leaf with nearly lacinate lobes, which might have been mounted here by mistake. It resembles the more highly divided specimens which have been described as *Trichomanes pedicellatum* and *T. subsessile*. Relationships with these are discussed under *T. ankersii*. (Also described there are the dark lines in the lamina which might be mistaken for the false veins of sect. *Didymoglossum*.)

21. *Trichomanes ankersii* Hooker & Grev., Icon. fil. 2, t. 201. 1831. TYPE: Guyana, Demerara, *Ankers* (holotype, K; photo, US).

Stem long-creeping, relatively stout and wiry, 0.5–1.2 mm in diameter, sparsely to abundantly provided with brown rhizoids that extend onto the leaf axes and adhere to tree trunks. **Leaves** subdistant to remote, larger ones 5–18 cm long,

(1.8–)2–6 cm broad, subsessile. **Lamina** oblong, pinnatisect, or pinnate to a broadly winged rachis, the rachis, costae, and (sometimes) veins abaxially provided with simple, reddish brown trichomes that adhere to tree trunks, free portion of larger segments 1.5–2.8(–3) cm long and 0.5–0.8 cm broad, deeply crenate or crenate-serrate. **Venation** at least partly catadromous, veins free, commonly simple, but some- to many-forked, false veins lacking, but often some very short, darkened lines scattered between the veins. **Sori** few to several on the pinna lobes, not or scarcely immersed in the segment tissue. **Indusia** tubular, neither bilabiate nor dark-margined, mouth scarcely to slightly expanded, receptacle commonly long-exserted.

In forests, commonly hemiepiphytic, tightly appressed to tree trunks, sea level to 1000 m, Loreto, Huánuco, Pasco, Cuzco.

The Guianas to Colombia, south to Brazil and Bolivia.

This, *Trichomanes tuerckheimii*, and *T. tanaicum*, all members of sect. *Lacostea*, are commonly hemiepiphytic. Their leaves usually have the distinctive habit of being tightly appressed to tree trunks. They cling to the bark by means of rust-colored, prehensile trichomes that are abundant along the stems, rachises, and in *T. ankersii* and *T. tuerckheimii*, on midribs and veins. Some collectors' labels describe them as "plastered to the bark of trees." Another character peculiar to the three species (though very rare in *T. tanaicum*) is the presence of very short, dark lines seen scattered between and parallel with the veins. They somewhat resemble the false veins of sect. *Didymoglossum*, except that they are not lengthy sclerenchymatous strands. Rather, they merely appear to be a series of (usually) two or three constricted and occluded cells that are mostly found toward the segment margin.

Very closely related to *Trichomanes ankersii* are *T. pedicellatum* Desv. and *T. subsessile* Splitg., of northern South America and the West Indies. These appear to differ only in their more highly divided sterile lamina, which is 2- to 3-pinnatifid. Further study may prove them all to be conspecific.

Loreto: Mishuyacu, near Iquitos, *Klug 149, 1135* (F, US). Sierra del Pongo, *Mexia 6289* (GH, MO, UC, US). **Huánuco:** 5 km NE of Tingo María, *Stork & Horton 9518* (F, GH, UC, US). **Pasco:** Prov. Oxapampa, Valle del Palcazú, *León 706* (F, GH). **Cuzco:** Prov. Quispicanchi, near Inambari, *Vargas 16460* (GH).

22. *Trichomanes bicornes* Hooker, *Icon. pl.*, t. 892. 1854. LECTOTYPE (designated here): Brazil, Amazonas, Barra do Rio Negro, *Spruce 1178* (lectotype, κ!; isolectotype, us!). LECTOPARATYPE: Brazil, Amazonas, São Gabriel, *Spruce 2334* (κ!, us).

Ptilophyllum bicornes (Hooker) Prantl, *Unters. Morph. Gefässkrypt.* 1: 48. 1875.

Stem stout, decumbent or erect, abundantly provided with lustrous, castaneous, pluricellular trichomes. **Leaves** monomorphic, crowded or caespitose, 3–10 cm long, 3–4-pinnatisect, the axes (and sometimes veins) sparsely provided on the abaxial side with simple, castaneous, pluricellular trichomes. **Petiole** 0.5–4 cm long, conspicuously alate throughout, the alae broader than the petiole quite or nearly to base. **Lamina** ovate, the axes broadly alate, alae and segments often undulate. **Venation** catadromous, veins free, false veins lacking. **Sori** immersed in the segment tissue. **Indusia** short-tubular, borne in the forks of veins, each of which extend well beyond the indusial mouth, the mouth not dark-margined, receptacle long-exserted.

In dense forests, epiphytic, or on wet humus or decaying logs, sea level to 150 m, Loreto.

A lectoparatype (*Spruce 2334*) is mounted on the same sheet with the lectotype at Kew. However, there are other specimens bearing this *Spruce* number that represent the type collection of *Trichomanes spruceanum* Hooker, a closely related species with dimorphic leaves which occurs in northern South America. One sheet (BM) is the isotype of *T. spruceanum*. Another, presumably the holotype, is at Kew.

The species is aptly named for its sori, which are borne at segment apices in the forks of veins. The veinlets, bordered on the outside with narrow wings of tissue, each extend well beyond the mouths of indusia and are often curved, thus appearing like two “horns.”

Loreto: Vicinity of Lago Llanchara near Río Nanay, *Croat 18705* (F, MO). Mishuyacu, near Iquitos, *Killip & Smith 29988* (F, US). Maynas, Dist. Iquitos, Cacerío Mishana, *Rimachi 1256* (GH, MO).

23. *Trichomanes diversifrons* (Bory) Sadebeck in Engler & Prantl, *Nat. Pflanzenfam.* 1(4): 108. 1899.

Trichomanes elegans Rudge, *Pl. Guian.* 24, t. 35. 1805, *nom. illeg.* (not L. C. Rich., 1792, or Poirlet, 1808). *Hymenostachys diversifrons* Bory, *Dict. class. hist. nat.* 8: 462. 1825. TYPE: “Guianc.,” *Poitteau* (holotype, P?; isotype, L; photos, GH & US of L). *Feea diversifrons* (Bory) Copel., *Phillip. J. Sci.* 67: 74. 1938.

Stem stout, erect. **Leaves** crowded to caespitose, 10–35 cm long, strongly dimorphic, sterile ones elliptic or lanceolate, deeply pinnatisect, short-petiolate, fertile ones commonly longer, linear, subentire, long-petiolate. **Sterile lamina** (2–)3–8 cm broad, deeply divided into subfalcate segments 4–7 mm broad, the rachis abaxially provided with dark, simple trichomes and often flagellate and proliferous at the tip. **Venation** catadromous, a few to many veins anastomosing toward the segment margin, 4–8 of them issuing from the rachis between adjacent costae, false veins lacking. **Fertile lamina** simple, essentially entire, with sori arranged in a nearly continuous line along each margin, fully immersed in tissue in the forks of veins. **Indusia** subconical, not bilabiate, the mouth neither flaring nor recurved, strongly indented between the vein tips, receptacle short- to long-exserted at maturity.

Terrestrial in wet forests, in wooded ravines and on ridges and banks, 150–1300 m, Amazonas and Loreto to Junín, Madre de Dios.

Southern Mexico to Panama; the Guianas to Colombia, south to Brazil and Bolivia.

This is often confused with *Trichomanes trollii*, under which see further discussion.

Amazonas: Prov. Bagua, Quebrada Tambillo, valley of Río Marañón above Cascadas de Mayasi, *Wurdack 2057* (GH, US). **San Martín:** Prov. Mariscal Caceres, Dist. Tocache Nuevo, Santa Rosa de Mishollo, *J. Schunke V. 6815* (F, MO, UC). **Loreto:** Prov. Maynas, Brillo Nuevo and vicinity, *Plowman et al. 6829* (GH). **Huánuco:** Tingo María, *Tryon & Tryon 5277* (F, GH, US). **Pasco:** Prov. Oxapampa, Cordillera San Matías, *León 320* (F, USM). **Junín:** Cahuapanas, on Río Pichis, *Killip & Smith 26762* (F, GH, US). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla NNW of Shintuya, *Foster et al. 10948* (F).

24. *Trichomanes trollii* Bergdolt, *Flora* 127: 256, 264, t. 3. 1933. TYPE: Bolivia, Dept. La Paz, San Carlos (Mapiri), *Troll 2531* (holotype, B; frag., us!).

Feea trollii (Bergdolt) Vareschi, *Flora Venezuela* 1: 247. 1969.

Stem decumbent or erect. **Leaves** crowded to caespitose, 10–25 cm long, strongly dimorphic, sterile ones elliptic, pectinate, short-petiolate, fertile ones commonly longer, linear, subentire, long-petiolate. **Sterile lamina** 1.5–4.5 cm broad, cut nearly to the rachis into subfalcate segments 1.5–3(–4) mm broad, the rachis abaxially provided with simple, dark brown trichomes and often flagellate and proliferous at the tip. **Venation** catadromous, a few to many veins anastomosing toward the segment margin, 2(–3) of them issuing from the rachis between adjacent costae, false veins lacking. **Fertile lamina** simple, essentially entire, with sori arranged in a nearly continuous line along each margin, fully immersed in tissue in the forks of veins. **Indusia** subconical, not bilabiate, the mouth very slightly flaring and recurved, but not indented between the vein tips, receptacle strongly exerted at maturity.

Terrestrial in dense, wet forests, often in wet ravines or along stream banks, 350–850 m, Amazonas to Pasco.

Surinam to Colombia; Peru; Bolivia.

This is closely related to the more robust *Trichomanes diversifrons*. Besides the characters in the key the latter can usually be recognized by its broader lamina (to 8 cm) and segments (4–7 mm), these being separated from the rachis by a conspicuous wing ca. 2 mm broad on each side. The lamina of *T. trollii* is rarely more than 4 cm broad and are cut nearly to the rachis into segments which are commonly 3 cm broad or less. Additionally, the fertile lamina of *T. diversifrons* has dentate margins, due to the apices of the indusia which are deeply indented between the vein forks. Indusial mouths of *T. trollii* are typically flush with the vein tips, so that the leaf margins are essentially entire throughout.

Amazonas: Prov. Bagua, along roadside from Chiriaco to Puente Venezuela, *Barbour 4461* (MO in part). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache Nuevo, Palo Blanco, *Plowman & Schunke 7431* (F). **Huánuco:** Ascent of Cerros del Sira, *Wolfe 12263A* (GH, MO, US). **Pasco:** Prov. Oxapampa, W side of Cordillera de San Matías, *D. Smith 2001* (MO).

25. *Trichomanes botryoides* Kaulf., Enum. fil. 263. 1824. TYPE: French Guiana, *Poiteau* (holotype?, P).

Stem erect. **Leaves** crowded to caespitose, 4–12 cm long, strongly dimorphic, sterile ones 1-pin-

nate, elliptic-lanceolate, short-petiolate, fertile ones commonly longer and long-petiolate, sori subdistichous on the nonfoliaceous axis. **Sterile lamina** 1.2–3 cm broad, the pinnae oblong-lanceolate, subentire to serrate, 3–4 mm broad, the petiole and rachis with scattered, brown, pluricellular trichomes, the rachis often flagellate and proliferous at the tip. **Venation** catadromous, the veins free, commonly 1-forked, false veins lacking. **Fertile leaves** bearing numerous, stalked or sessile, ascending sori on each side of the primary axis. **Indusia** urceolate, scarcely or not bilabiate, the mouth not flaring, receptacle strongly exerted at maturity.

Thus far known in Peru from a single collection, roadside along a sandy, rocky stream bank, 350–700 m, Amazonas.

Elsewhere terrestrial or epipetric, commonly near banks of streams or rivers, 250–800 m; Panama; the Guianas and Colombia.

The small size, strongly dimorphic leaves, and nonfoliaceous fertile leaves easily distinguish this from others in the genus.

Amazonas: Prov. Bagua, ca. 40–43 km NE of Chiriaco, *Barbour 4524* (MO, USM).

26. *Trichomanes pinnatum* Hedwig, Fil. gen. sp., t. 4, f. 1. 1799. LECTOTYPE (designated by Proctor, Flora Lesser Antilles. 89. 1977): Hedwig, t. 4, f. 1, based on specimen allegedly from Jamaica. **Figure 12c.**

Trichomanes pennatum Kaulf., Enum. fil. 264. 1824.

TYPE: French Guiana, *without collector* (holotype, LZ destroyed).

Neurophyllum pinnatum (Hedwig) Presl, Hymenophyllaceae 19. 1843.

Stem short-creeping to decumbent, provided with dark brown or blackish pluricellular trichomes. **Leaves** essentially monomorphic (but fertile ones often somewhat larger, with longer petioles), approximate or subcaespitose, to 70 cm long, 1-pinnate, the axes sparsely to amply provided on the abaxial side with castaneous trichomes. **Petiole** about as long as the lamina, nonalate (sometimes marginate toward the lamina). **Lamina** ovate or subdeltoïd, terminating in a conform apical segment, or the rachis prolonged, flagellate and proliferous at the tip, the tissue thin and translucent, glabrous. **Venation** catadromous, the veins free,

except connected at the tips by a continuous marginal vein, false veins copious and perpendicular to true veins. **Sori** arranged in a nearly uninterrupted line along pinna margins at the tips of veins, not immersed in the tissue, often stalked. **Indusia** narrowly tubular, not or scarcely bilabiate nor dark margined, mouth not flaring, receptacle long-exserted.

Terrestrial, in deep forests or wooded ravines, in humus or clay banks of streams, 150–1000 m, Amazonas and Loreto to Junín and Madre de Dios.

West Indies and Trinidad; Mexico to Panama and south to Brazil and Bolivia.

Further differences between this and *Trichomanes hostmannianum* are reviewed below in discussion of that species.

Amazonas: Prov. Bagua, valley of Río Marañón near Cascadas de Mayasi, *Wurdack 1939* (GH, US). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache Nuevo, Granja Santa Inés, *J. Schunke V. 3654* (F, GH). **Loreto:** 17 km SW of Iquitos on road to Puerto Almendra, *Croat 18475* (F, MO, UC). **Huánuco:** Prov. Pachitea, Dist. Honoria, Bosque Nacional de Iparia, *J. Schunke V. 1333* (F, GH, US). **Pasco:** Prov. Oxapampa, Palcazú Valley, Cabeza de Mono, *D. Smith 3741* (F, MO). **Junín:** E of Quimiri Bridge, near La Merced, *Killip & Smith 23924* (F, US). **Ucayali:** Along trail to Arboretum of Bosque von Humboldt Experimental Station, km 86 of Pucallpa-Tingo María road, *D. Smith 1226* (F, MO). **Madre de Dios:** Prov. Tambopata, *Vargas 18625, 18711* (GH).

27. *Trichomanes hostmannianum* (Klotzsch) Kunze, Bot. Zeit. (Berlin) 5: 352. 1847.

Neurophyllum hostmannianum Klotzsch, Linnaea 18: 532. 1844. TYPE: Surinam, *Hostmann 75* (holotype, B; isotypes, K, NY, U, US!; photos, GH & US of K).

Odontomanes hostmannianum (Klotzsch) Presl, Epimel. bot. 21. 1849.

Ptilophyllum hostmannianum (Klotzsch) Prantl, Unters. Morph. Gefässkrypt. 1: 49. 1875.

Stem decumbent to erect, provided with dark brown pluricellular trichomes. **Leaves** essentially monomorphic (but fertile ones often larger, with longer petioles), caespitose, to 30 cm long, 1-pinnate, the axes sparsely provided on the abaxial side with brown trichomes. **Petiole** commonly as long as or longer than the lamina, not alate, or narrowly so toward the lamina. **Lamina** ovate or subdeltoïd, terminating in a subconform apical segment, or the rachis prolonged, flagellate and

proliferous at the tip, the tissue relatively thick, commonly obscure, glabrous, pinna margins serrate, the serrations obtuse to subacute. **Venation** catadromous, the veins free, a lateral marginal vein faint and discontinuous or (more commonly) lacking, false veins lacking or a few very rare and faint ones perpendicular to true veins. **Sori** arranged in a nearly uninterrupted line along pinna margins at tips of veins, not immersed in the tissue, frequently stalked. **Indusia** conical to tubular, neither bilabiate nor dark-margined, mouth not flaring, receptacle exserted.

Terrestrial in dark, wet forests and wooded ravines, often in frequently inundated areas along streams, sea level to 450 m, Amazonas, San Martín, Loreto.

Surinam to Colombia; Amazonian Brazil and Peru.

This and the closely related *Trichomanes pinnatum* are sometimes confused in herbaria. Besides the differences noted in the key they also differ in size and in leaf texture. Leaves of *T. hostmannianum* do not exceed 30 cm, pinnae are rarely more than 6 cm long and 1 cm broad, and tissue of mature leaves is commonly dull green and obscure. Leaves of *T. pinnatum* often are 70 cm long, with pinnae to 15 cm long and 2 cm broad, and tissue is typically thin and translucent, so that the false veins are easily visible with little magnification.

Contrary to previous reports, false veins do occur in *T. hostmannianum*. They are infrequent and scattered and so faint as to be overlooked, or undetectable, in the thick leaf tissue. However, in immature leaves or in the rare thin-textured ones, high magnification sometimes reveals a few or several of them, perpendicular to the true veins as in *T. pinnatum*. As this character is so difficult to observe, it is rather ineffective in delineating *T. hostmannianum* from species in other sections of the subgenus; yet it serves to further establish its position in sect. *Neurophyllum* (Presl) Moore, along with *T. pinnatum*. Morton (1968) placed it outside the section because of the supposed lack of false veinlets.

Amazonas: Nazareth, *Osgood 25* (F, US). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache Nuevo, near Granja San Ysabel, *J. Schunke V. 10313* (F, MO). **Loreto:** Río Taesha Curaray, *Croat 20403* (F, MO, UC). Dist. Iquitos, trail through Versailles, *Mexia 6500* (GH, MO, UC, US).

28. *Trichomanes humboldtii* Lell., Mem. New York Bot. Gard. 38: 35. 1984, *nom. nov.* for *Trichomanes heterophyllum* Willd. and with the same type.

Trichomanes heterophyllum Willd., Sp. pl. ed. 4, 5: 503. 1810, *nom. illeg.*, not *T. heterophyllum* (Sm.) Poir. 1808. TYPE: Brazil, Amazonas, Javita, *Humboldt* (holotype, b, *Herb. Willd.* 20210; photos, F, GH).

Homoeotes heterophylla Presl, Gefässbündel Farm 24. 1847, *nom. nov.*, based on *Trichomanes heterophyllum* Willd. and with the same type.

Feea humboldtii Bosch, Ned. Kruidk. Arch. 4: 347. 1859, *nom. nov.*, based on *Trichomanes heterophyllum* Willd. and with the same type.

Feea heterophylla Copel., Philipp. J. Sci. 67: 73. 1938, *nom. nov.*, based on *Trichomanes heterophyllum* Willd. and with the same type.

Stem wiry, long- to short-creeping. **Leaves** deeply pinnatisect to nearly pinnate, subdistant or remote, to 22 cm long, dimorphic, sterile ones short-petiolate, to 3 cm broad, fertile ones long-petiolate, far exceeding the sterile ones and 1 cm broad or less, the petiole essentially nonalate, sparsely or amply provided with castaneous, pluricellular trichomes. **Sterile lamina** oblong or oblong-elliptic, commonly equaling or longer than the petiole, the apex pinnatifid. **Venation** catadromous, veins free and dichotomously branched, false veins lacking. **Fertile lamina** linear, much shorter than the petiole, with a few sori terminal on each pinna and fully immersed in the tissue. **Indusia** subconical or broadly tubular, not bilabiate, the mouth not (or scarcely) flaring nor dark-margined, the receptacle long-exserted.

Terrestrial, in open to dense forests, commonly in wet, sandy places, sea level to 1400 m, San Martín, Loreto.

Venezuela; Colombia; Amazonian Peru and Brazil.

There has been some confusion with nomenclature of this species. Lellinger's (1984) citing of *Trichomanes humboldtii* "Bosch" (1858) was in error, since there was no such name; instead, it was "*Feea humboldtii*" that Bosch had published. However, Lellinger's use of "*T. humboldtii*" is legitimate, as a *nom. nov.* (Art. 72); therefore this name is correct for the species, with Lellinger as the author.

San Martín: Rioja, *Soukup* 5055 (us). Río Negro, *Woytkowski* 6211 (GH, MO, US). **Loreto:** Prov. Maynas, Río Nanay, *Mishana, Foster & Foster* 4103 (GH);

McDaniel et al. 22121 (F). Mishuyacu, near Iquitos, *Klug* 1246 (F, US).

29. *Trichomanes crinitum* Sw., Prodr. 136. 1788. TYPE: Jamaica, *Swartz* (holotype, SBT; isotypes, BM!, s; photos, US of BM & s).

Ragatelus crinitus (Sw.) Presl, Hymenophyllaceae 16. 1843.

Stem erect. **Leaves** monomorphic, caespitose, 5–25 cm long, 1–2(–2.5) cm broad, moderately to amply pubescent, the trichomes delicate, unbranched, unicellular (or rarely pluricellular) beyond a short, enlarged, basal cell. **Petiole** nonalate, or narrowly so toward the lamina. **Lamina** linear, cut nearly or quite to the rachis into deeply lobed to pinnatifid, patent, pinnae, gradually reduced to a pinnatifid apex, lamellae lacking on veins. **Venation** catadromous, the veins free, false veins lacking. **Sori** terminating the veins on the apical part of the pinnae. **Indusia** tubular, deeply immersed in the segment tissue or, if partially immersed, broadly alate on each side, the mouth bilabiate and somewhat flaring, the lips not dark-margined, receptacle exserted.

Apparently known thus far from two collections in Peru, in damp elfin forest, on tree trunks, ca. 1850 m, Huánuco. Elsewhere epiphytic or epipetric, 700–2300 m.

West Indies; Costa Rica; Venezuela; Colombia; Ecuador; Peru.

Trichomes in many species of subg. *Achomanes* are pluricellular, with two to several greatly elongate cells, these often springing from a very short, widened basal cell. In species most closely related to *Trichomanes crinitum*, these are often mixed with a number of unicellular (above the basal cell) trichomes. However, *T. crinitum* differs from its Peruvian relatives in having all, or nearly all, of its laminar trichomes unicellular above the basal cell.

Huánuco: SW slope of Río Llullapichis watershed, on the ascent of Cerros del Sira, *Dudley* 13525 (GH), 13545 (GH, US).

30. *Trichomanes martusii* Presl, Hymenophyllaceae 36. 1843. TYPE: a renaming of *T. pilosum* (sensu Martius in part, Icon. pl. crypt. 104, t. 68 right) presumably based on "Brazil,

Arara-coara" (Araracuara, on Río Caquetá, now Colombia), *Martius* (holotype, M; isotypes, BR, L; photo, US of L).

Trichomanes plumula Presl, Hymenophyllaceae 15, 36. 1843. TYPE: based on *Martius* in part, Icon. pl. crypt. 104, t. 68 left, specimens probably as for *T. martiusii*.

Ptilophyllum martiusii (Presl) Prantl, Unters. Morph. Gefässkrypt. 1: 48. 1875.

Stem erect to decumbent. **Leaves** monomorphic, crowded to caespitose, 10–40 cm long, (2–)3–8 cm broad, densely (on axes) to amply pubescent, the trichomes unbranched, unicellular beyond the short basal cell, or pluricellular on petiole and rachis. **Petiole** nonalate. **Lamina** narrowly elliptic or lanceolate, gradually reduced to a pinnatifid apex, cut nearly or quite to the rachis into linear pinnae, the proximal ones commonly deflexed, subentire to crenulate or serrate, or rarely with a few, scattered lobes, with numerous, crestlike lamellae borne on the veins abaxially. **Venation catadromous**, the veins free, false veins lacking. **Sori** terminating the veins on the apical part of segments. **Indusia** tubular or narrow-conical, deeply immersed in the segment tissue, the mouth truncate, not dark-margined, sometimes apparently bilabiate due to narrow wings of tissue extending beyond the mouth on two sides, receptacle commonly exserted.

On tree trunks in forests, or on clay banks along roads and streams, sea level to 150 m, thus far found only in Loreto, but locally common there.

Surinam to Colombia; Peru; Amazonian Brazil.

The shape of the indusium is somewhat variable. The mouth is commonly truncate and not at all bilabiate, but frequently the wings of tissue along the sides extend beyond the mouth, giving it a "horned" appearance, much like *Trichomanes bicorne*. This is a distinctive species in Peru, because of the crestlike lamellae borne on many of the veins on the abaxial side, perpendicular to the plane of the lamina. These processes are similar to those occurring in several species of *Hymenophyllum*. On some of the more densely hirsute specimens of *T. martiusii*, the lamellae are partially obscured by the indument and thus they have been mistaken for other species in subg. *Achomanes*, particularly *T. pilosum* Raddi, of Bolivia and southern South America.

Loreto: Prov. Maynas, Río Nanay, behind Mishana, *Gentry & Revilla 20704* (MO, UC, USM). Mishayucu, near

Iquitos, *Klug 196, 511* (F, US). Prov. Maynas, 10 km S of Iquitos, *Tryon & Tryon 5179* (GH, US). Timbuchi on Río Nanay, *Ll. Williams 957* (F, US).

31. *Trichomanes lucens* Sw., Prodr. 136. 1788. TYPE: Jamaica, *Swartz* (holotype, SBT; isotype, BM; frag., B; photos, US of SBT & BM), not *T. lucens* Hooker & Grev., 1827.

Trichomanes lambertianum Hooker, Sp. fil. 1: 139, t. 41B. 1846. TYPE: Peru, Huánuco, Pillao, *Ruiz & Pavón* (holotype, K; isotype, V; photos, GH & US of K).

Ptilophyllum lambertianum (Hooker) Prantl, Unters. Morph. Gefässkrypt. 1: 48. 1875.

Stem erect to decumbent. **Leaves** monomorphic, crowded to caespitose, 10–60 cm long, (2.5–)3–12 cm broad, amply to densely pubescent (indument often obscuring the laminar surface), the trichomes unbranched, unicellular and pluricellular beyond the scarcely evident basal cell. **Petiole** nonalate. **Lamina** linear to lanceolate, pinnate-pinnatifid (occasionally 2-pinnate-pinnatifid toward base), gradually reduced to a pinnatifid apex, pinnae narrow-deltoid, mostly ascending, lacking lamellae. **Venation** catadromous, the veins free, false veins lacking. **Sori** commonly terminal on ultimate segments near apex of pinnae. **Indusia** tubular, deeply immersed in the segment tissue, the mouth scarcely or slightly flaring, not dark-margined, sometimes apparently bilabiate due to the narrow wings of tissue extending beyond the mouth on two sides, receptacle commonly exserted.

In forests and wooded ravines, pendent from trees or wet rock crevices, or in sphagnum on sandy banks, 2150–3500 m, Cajamarca, Amazonas, Huánuco, Pasco, Cuzco.

Jamaica; Costa Rica; Venezuela and Colombia, south to Bolivia; Brazil.

With its 1-(2)-pinnate-pinnatifid leaves and the copious, long trichomes that often obscure the lamina surface, this should not be mistaken for any other species of subg. *Achomanes*.

Cajamarca: Prov. Jaén, Paso de Huascarai, 15 km SE of Huancabamba, *Fosberg 27842* (US). **Amazonas:** Prov. Chachapoyas, Cerros de Calla Calla above Leimebamba, *Hutchison & Wright 5568* (F, GH, MO, UC, US). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, *Young & León 4471* (F). **Huánuco:** Playapampa, *Macbride 4499* (F, GH, US). **Pasco:** Prov. Oxapampa, Cordillera Yanachaga, Cerro Pajónal, *Foster 9047* (F, MO).

Cuzco: Prov. La Convención, Cordillera Vilcabamba, *Dudley 10789* (F, GH, MO).

32. **Trichomanes pellucens** Kunze, *Linnaea* 9: 104. 1834. TYPE: Peru, Tocache, upper Río Hualaga, *Poeppig* (holotype, LZ destroyed; isotypes, BR!, w; possible isotype, L!; photos, GH, HB & US of BR). The epithet *T. pellucidum* was used by Presl (*Hymenophyllaceae* 15. 1843), but later he indicated this was an error for *T. pellucens* Kunze (*Epimel. bot.* 16. 1851).

Ptilophyllum pellucens (Kunze) Prantl, *Unters. Morph. Gefässkrypt.* 48. 1875.

Stem erect to decumbent. **Leaves** monomorphic, close, contiguous or caespitose, 8–30 cm long, 3–7 cm broad, sparsely to moderately pubescent, the trichomes unbranched, light to dark brown, those of the veins and margins unicellular beyond a very short basal cell, those of primary axes 1–3-celled beyond the basal cell. **Petiole** rather conspicuously alate halfway or more to the stem. **Lamina** narrowly or broadly lanceolate, gradually reduced to a pinnatifid apex, cut nearly or quite to the rachis into adnate, linear or linear-oblong, patent pinnae (or basal ones deflexed), their margins subentire to crenate, lacking lamellae. **Venation** catadromous, the veins free, false veins lacking. **Sori** borne at tips of veins in the forks, near and at segment apices. **Indusia** tubular, deeply immersed in the segment tissue, the mouth not bilabiate, flaring, or dark-margined, receptacle commonly exserted.

Epiphytic in forests, or terrestrial, most commonly in sandy soil in ravines or on stream banks, 150–800 m, Amazonas, San Martín, Cuzco, Madre de Dios.

Venezuela; Colombia; Ecuador; Peru; Brazil.

Amazonas: Prov. Bagua, NE of Chiriaco, *Barbour 4461* (MO in part), *4462* (USM), *4515*, *4518* (MO). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache Nuevo, Palo Blanco, *Plowman & J. Schunke V. 7434* (F); *J. Schunke V. 5722* (F, MO). **Cuzco:** Prov. Paucartambo, Cosñipata Valley, Río Tono, *Wachter et al. 134* (F).

33. **Trichomanes plumosum** Kunze, *Linnaea* 9: 104. 1834. TYPE: Peru, “in sylvis montanis ad Pampayaco” (Pampayacu, Dept. Huánuco), *Poeppig diar. 1107* (holotype, B; isotypes, BR!, K; photo, BM of BR).

Trichomanes elatum Desv., *Mém. Soc. Linn. Paris* 6(3): 327. 1827 (not Forst., 1786, or Bosch, 1861). TYPE: “habitat in America calidiori,” without collector (holotype, P; photo, GH).

Stem short-creeping to decumbent. **Leaves** monomorphic, subdistant to contiguous, (rarely caespitose), mature ones 15–50 cm long, 3–8 cm broad, moderately to amply pubescent, the trichomes unbranched, those of the veins and margins unicellular beyond a very short basal cell, those of the rachis (especially abaxially) predominantly dark brown, 1–5-celled above basal cell, stout, rigid and spreading, most of them terete toward their base. **Petiole** essentially nonalate, amply provided with dark brown trichomes. **Lamina** lanceolate, often broadly so, gradually reduced to a pinnatifid apex, cut nearly to the rachis into linear to narrow-deltoid or -oblong segments, these patent (or the basal ones deflexed), lacking lamellae, the margins subentire to crenate or serrate, often undulate. **Venation** catadromous, the veins free, false ones lacking. **Sori** borne near and at segment apices, at tips of veins, sometimes flanked by vein forks. **Indusia** tubular or narrow-conical, deeply to fully immersed in the segment tissue, the mouth neither bilabiate nor dark-margined, not or scarcely flaring, receptacle exserted.

In dense, wet forests, occasionally epiphytic, but commonly on wet sandy or mossy soil, 550–2100 m, San Martín to Puno.

Ecuador; Peru; Bolivia; Brazil.

This and *Trichomanes cristatum* are easily confused. Some collections from Peru are intermediate between the two, and there is evidence of hybridization involving these and other closely related species. The indument on the abaxial side of the rachis seems to be the best character for distinction, as indicated in the key. In *T. cristatum* most of these trichomes are tawny to orange, rather long, delicate and tortuous, with their usually four to six cells greatly flattened. Those of *T. plumosum* are predominantly dark brown (some blackish), shorter, stout and rigid, and terete at least toward the base. Careful examination of specimens is necessary to view these trichomes, as those on the adaxial side of the rachis differ little, being primarily light brown, even tawny, on both species. Curiously (and unfortunately) most of the specimens examined for this study had been mounted with abaxial side down, so that it was very difficult to determine the character of trichomes on the other side. Besides differences in indument, *T. plu-*

mosum can usually be distinguished from *T. cristatum* (at least in Peru) by lamina shape: that of the latter is commonly linear, rarely more than 4 cm broad, whereas the lamina of *T. plumosum* is typically broadly lanceolate, usually more than 4 cm broad.

San Martín: Tarapoto, *Spruce 4766* (BR, W). **Huánuco:** SW slope of Río Llullapichis watershed, ascent of Cerros del Sira, *Dudley 13051* (GH), *13128* (GH, US), *13512* (GH). **Pasco:** Prov. Oxapampa, 19 km W of Oxapampa, *D. Smith 2209* (MO). **Junín:** La Merced, *Macbride 5634* (F, GH). **Cuzco:** La Convención, *Bües 2028, 2140* (US). **Madre de Dios:** Prov. Manú, Shintuya, *Chávez 804* (MO). **Puno:** Prov. Carabaya, San Gabán, *Vargas 18875* (GH). **Dept. Unknown:** "ad saxa humida prope Sangari," *Lechler 2548* (BR, K, W 3 sheets); although this is the type number of *T. undulatum* (= *T. vandenboschii*), these specimens represent part of a mixed collection).

34. **Trichomanes cristatum** Kaulf., Enum. fil. 265. 1824. TYPE: Brazil, collector undesignated (holotype, LZ destroyed).

Trichomanes sellowianum Presl, Hymenophyllaceae 15, 37. 1843. TYPE: "Brasilia," *Sellow 197* (holotype, PR?; possible isotypes, 2 unnumbered Sellow sheets from "Brasilia," B, K!).

Stem short-creeping to decumbent, rarely erect. **Leaves** monomorphic, subdistant to contiguous, mature ones 15–50 cm long, 2–4(–5) cm broad, moderately to rather densely pubescent, the trichomes unbranched, those of the veins and margins unicellular beyond a very short basal cell, those of the rachis abaxially tawny to orange, delicate, most of them long and tortuous and with the cells flattened, predominantly unicellular beyond the basal one (occasionally with 2–3 cells). **Petiole** essentially nonalate, amply provided with long, orange to tawny trichomes, or these dark brown toward the stem. **Lamina** linear to linear-lanceolate, commonly 5–12 times as long as broad, gradually reduced to a pinnatifid apex, cut nearly to the rachis into linear or narrowly oblong segments, these patent (or basal ones deflexed), lacking lamellae, the margins subentire to crenulate, often undulate. **Venation** catadromous, the veins free, false veins lacking. **Sori** borne near and at segment apices, at tips of veins, often flanked by the vein forks. **Indusia** tubular or narrow-conical, deeply to fully immersed in the segment tissue, the mouth not dark-margined, not or slightly flaring, not bilabiate but sometimes appearing as due

to slight projections of tissue along the flanking vein forks, receptacle exerted.

Terrestrial, or occasionally on tree trunks, commonly in wet forests on sandy soil or in open sphagnum bogs, sea level to 2000 m, San Martín and Loreto to Puno.

Venezuela and Colombia, south to Brazil and Argentina.

This species is very easily confused with *Trichomanes plumosum*; characters are discussed above in the treatment of the latter. *Trichomanes cristatum* and *T. plumosum* share nearly the same distribution and are often found growing together. In Peru, at least, there are frequent intermediates, which indicates a strong probability of hybridization. These problems are not confined to species of Peru but also occur in other taxa of the group of *T. crispum* L. throughout the Neotropics, as pointed out by Windisch (1988). Obviously there is a great need for careful analysis of plants *in situ* as well as further caryological study before accurate relationships are understood.

San Martín: Río Negro, *Woytkowski 6210* (GH, MO, UC, US). **Loreto:** Prov. Maynas, Dist. Iquitos, Río Nanay, *McDaniel & Rimachi 18924* (F, MO). **Huánuco:** Tingo María (as San Martín), *Allard 21585* (GH, US), *21589* (US). **Pasco:** Prov. Oxapampa, Palcazú, *van der Werff et al. 8376* (MO, UC). **Junín:** E of Quimiri Bridge near La Merced, *Killip & Smith 23952* (F, US). **Cuzco:** Prov. La Convención, Valle de Santa Ana, *Herrera 3008* (US). **Puno:** Prov. Sandia, *Vargas 11832* (GH).

35. **Trichomanes vandenboschii** Windisch, Bradea 5(4): 57. 1988, *nom. nov.* for *T. undulatum* Bosch.

Trichomanes undulatum Bosch, Ned. Kruidk. Arch. 5(2): 147. 1861, *nom. illeg.* (not Swartz, 1788). LECTOTYPE (designated by Windisch, Bradea 5(4): 57. 1988): "Peruvia, prope Sangari" (Dept. Puno, Prov. Carabaya, Dist. Ayapata) *Lechler 2548* (L: isolecotypes, BR!, P; photos, HB of L, GH of BR, GH & US of P). Specimens of *Lechler 2548*, a mixed collection at BR, K, and W (3 sheets), are *not* type material, but are instead *T. plumosum*. LECTOPARATYPES: "Peruvia, Tatanara" (Dept. Puno, Prov. Carabaya, Dist. Ayapata), *Lechler 2503, 2571* (L?, P?).

Stem short-creeping. **Leaves** monomorphic, approximate to subdistant, 5–15 cm long, 1.8–3 cm broad, moderately to densely pubescent, the trichomes unbranched, those of the veins and margins unicellular beyond a very short basal cell,

those of the rachis tawny to orange, delicate, many of them long and tortuous and with the cells flattened, frequently with 2–8 cells beyond basal one, as well as with many unicellular ones. **Petiole** essentially nonalate, sparsely provided with short, light to dark brown trichomes. **Lamina** oblong- to ovate-lanceolate, 3–4 times as long as broad, gradually reduced to a pinnatifid apex, cut nearly or quite to the rachis into narrowly oblong segments, these patent (or basal ones deflexed), lacking lamellae, the margins entire to crenulate, often undulate. **Venation** catadromous, the veins free, false veins lacking. **Sori** commonly borne at segment apices, at tips of veins, often flanked by the vein forks. **Indusia** urceolate, fully immersed in the segment tissue, the mouth somewhat flaring, not dark-margined, not or scarcely bilabiate, receptacle exerted at maturity.

In deep, wet forests, on tree trunks or in wet, boggy places, rarely in crevices of wet rocks, 750–1800 m, Cuzco.

Venezuela; Colombia; Ecuador; Peru; Bolivia; northern Brazil.

This is closely related to *Trichomanes cristatum*, from which it is distinguished primarily by its smaller size and relatively broader lamina. Besides the key characters, it can usually be separated from both *T. cristatum* and *T. plumosum* by its somewhat flaring indusium mouth. That of the other two species is scarcely or not at all expanded. The confused identities of species within this complex is illustrated by the fact that the number of the type collection is shared with specimens of *T. plumosum*, as noted above in the citation of types.

Cuzco: Maranura, Beatriz, *Bües 895* (US). Prov. La Convención, Sahuayaco, *Vargas 6288* (GH). Prov. La Convención, Choquello, *Vargas 8184* (UC). Prov. Paucartambo, Atalaya, Valle Kosñipata, *Vargas 23155* (GH).

Comments

Trichomanes accedens Presl, *Epimel. bot.* 14: 1851. SYNTYPES: Guyana, *Rich. Schomburgk 271* (B; photos, GH, US); Hooker & Grev., *Icon. fil.*, t. 12, based on a Guilding collection from St. Vincent (specimen not seen by Presl).

This belongs to the *Trichomanes crispum* complex and is allied to *T. cristatum*. It differs from the latter primarily in its predominantly erect stem with contiguous leaves, much longer rachis tri-

chomes (to 4 mm), reflexed pinnae in the proximal portion of the lamina, and the petiole very narrowly alate halfway to the stem. Windisch (in litt.) stated that he had seen one specimen (AAU) from Peru (Loreto, Prov. Maynas, *Plowman et al. 6633*). Although this specimen has not been examined, duplicates (F, GH) are scarcely distinct from *T. cristatum*, as rachis trichomes are less than 2 mm long and proximal pinnae are patent or just a few of them reflexed. Only a few petioles are obscurely alate to marginate. The species is found in Trinidad, the Guianas, Venezuela, Colombia, and Brazil, and future collections of this species complex from Peru need to be examined carefully to determine if *T. accedens* truly occurs in Peru.

Trichomanes delicatum Bosch, *Ned. Kruidk. Arch.* 5(2): 145. 1861. TYPE: Ecuador, Quito, *Cuming 21* (holotype, B; frag., L).

This is closely related to *T. crinitum* in that the trichomes are unicellular above the short basal cell. It differs from that species in the alate petiole, the more shallowly lobed pinnae, and the glabrous margins of the indusia. It is to be expected in Peru, since it has been found in Colombia, Ecuador, and Bolivia.

Trichomanes haenkeanum Presl, *Hymenophyllaceae* 15, 36, 65. 1843. TYPE: Peru, mountains of Huánuco, *Haenke* (holotype, PR?).

Trichomanes crispum var. *haenkeanum* C. Chr., *Index fil.* 641. 1905.

In the protologue, Presl indicated a close relationship with *Trichomanes crispum*. Characters used in the description certainly align *T. haenkeanum* with this group of species but are insufficient to place it precisely. Until the type is located and compared with other species in the complex, nothing more can be determined.

Family 7: LOXOMATACEAE

Loxomataceae Presl, *Gefässbündel Farn* 31. 1847, as *Loxosomaceae*. TYPE: *Loxoma* Cunn. (often altered to *Loxosoma*).

Stem long-creeping, slender to rather stout, branched, densely pubescent with stiff trichomes enlarged at base. **Leaves** to 5 m long, pinnate, commonly pubescent abaxially, circinate in vernation. **Petiole** lacking stipules. **Sporangia** borne in marginal sori on an elongate receptacle, within

a more or less urceolate indusium, short-stalked (ca. 6 rows of cells), with an oblique annulus not interrupted by the stalk.

This small family contains two genera: *Loxoma* of New Zealand, and the Neotropical *Loxomopsis*.

1. *Loxomopsis*

Loxomopsis Christ, Bull. Herb. Boissier II. 4: 399. 1904. TYPE: *Loxomopsis costaricensis* Christ. **Figure 13.**

Terrestrial. Stem bearing scattered fibrous roots and abundant, rigid, lustrous, dark trichomes which are enlarged at the base. **Leaves** monomorphic, well-spaced on the stem, 2-pinnate-pinnatifid to nearly 3-pinnate. **Lamina** subcoriaceous, glabrous adaxially, glabrous to pubescent abaxially. **Veins** free. **Sorus** marginal, paraphysate, the indusium narrow-cyathiform to urceolate, the rim entire, the elongate receptacle exerted. **Spores** trilete, globose-tetrahedral, the surface coarsely tuberculate.

The genus is probably represented by a single species. However, two very closely related species have been described (from Costa Rica and Bolivia, respectively), based on supposed differences in size of leaf, color of petiole, and shape of pinnae and indusia. Two others have been separated on the basis of other variable and doubtfully significant characters. Observations of a number of specimens throughout the range suggest that such characters vary with age of the plant and maturity of sori, and they demonstrate no significant correlation.

1. *Loxomopsis pearcei* (Baker) Maxon, Proc. Biol. Soc. Wash. 46: 105. 1933. **Figure 13.**

Dicksonia pearcei Baker, Ann. Bot. (London) 5: 197. 1891. TYPE: Ecuador, "Eastern Andes, 8000–9000 ft.," *Pearce 251* (holotype, k!; photo, us).
Loxomopsis lehmannii Hieron., Bot. Jahrb. Syst. 34: 435. 1904. TYPE: Ecuador, prope Chinguinda, Cordillera Oriental de Sigsig, 1800–2500 m, *Lehmann 5061* (holotype, LZ destroyed; isotype, us!).
Dennstaedtia pearcei (Baker) C. Chr., Index fil. 218. 1905.

Leaves 0.4–5 m long, 2-pinnate-pinnatifid to nearly 3-pinnate, sometimes inconspicuously

glaucescent abaxially. **Petiole** dark brown to atropurpureous, sublustrous. **Lamina** subdeltoide, sparsely to amply provided on surface, veins and costules with light to dark brown, tortuous, septate trichomes, glabrous adaxially. **Pinnae** commonly well-spaced, subdeltoide, somewhat or slightly reduced at base, with pinnules strongly ascending, segments and venation catadromous. **Veins** pinnately branched, prominulous. **Indusia** urceolate to (especially at maturity) narrow-cyathiform.

Scandent or trailing, or arching to pendent from clay banks, in elfin forests, often on exposed ridges, 2200–3400 m, Huánuco, Pasco, Cuzco.

Ecuador and Peru.

Range of the species perhaps should be extended to include Costa Rica and Bolivia. Specimens described as *Loxomopsis costaricensis* Christ differ little, if at all, from *L. pearcei*. The type (*Wercklé & Brune 279*, Costa Rica) has not been seen, but the original description and illustrations suggest the two species are synonymous. *Loxomopsis notabilis* Slosson (type from Bolivia, *R. S. Williams 1303*) is supposedly distinguished by its glaucescent abaxial surface and by the larger pinnae being greatly reduced at base. Two sheets of isotype (us) seem to illustrate this clearly, and yet another isotype (p) is only slightly glaucescent and pinnae are not very strongly reduced at base. Lack of consistency in all these features suggests that there is but one species of *Loxomopsis*.

Huánuco: SW slope of Río Llullapichis watershed, ascent of Cerros del Sira, *Dudley 13420* (GH). **Playapampa,** *Macbride 4521* (f, GH, us). **Pasco:** Prov. Oxapampa, Cord. San Gutardo, *León 532* (USM). **Cuzco:** Valle San Miguel, La Convención, *Bües 2119* (us). Prov. La Convención, Cordillera de Vilcabamba, *Dudley 10713* (GH, MO).

Family 8: PLAGIOGYRIACEAE

Plagiogyriaceae Bower, Ann. Bot. (London) 40: 484. 1926. TYPE: *Plagiogyria* (Kunze) Mett.

Stem stout, erect to decumbent, indurated, bearing stiff, fibrous roots, essentially lacking indusium. **Leaves** pinnate, circinate in veneration, dimorphic. **Petiole** expanded basally into indurated stipules, commonly with a double row of aerophores at base (these rarely discernible in dried plants). **Sporangia** exindusiate, not paraphysate, commonly covering the abaxial surface of fertile

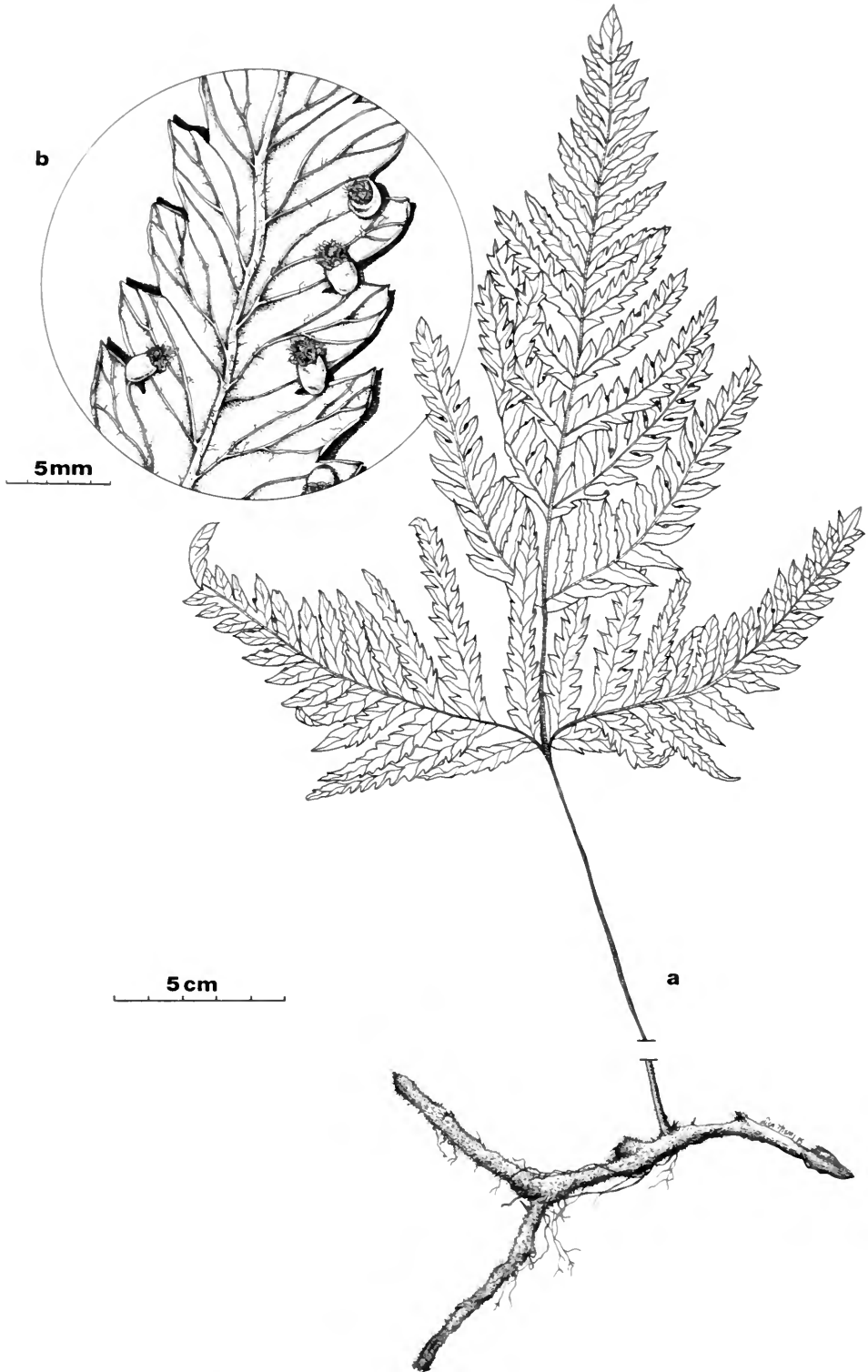


FIG. 13. *Loxsomopsis pearcei*: a, habit; b, portion of fertile pinna. (From Prieto P-259, Ecuador, F.)

pinnae, long-stalked (4–6 rows of cells), with an oblique annulus not interrupted by the stalk. **Spores** trilete, tetrahedral-globose, the surface irregularly tuberculate.

The family consists of a single genus essentially confined to wet, montane areas in Asia, Australasia, and tropical America. These ferns resemble some species of *Blechnum* because the sterile leaves arise obliquely from the thick rhizome in a circular pattern, from the center of which spring several dimorphic, fertile leaves. Stems in *Plagiogyria*, however, lack indument whereas those of *Blechnum* are scaly, an easily observed character which immediately distinguishes the former from similar-appearing *Blechnum* species.

I. *Plagiogyria*

***Plagiogyria* (Kunze) Mett.**, Abh. Senckenberg Naturf. Ges. 2: 265. 1858. TYPE: *Lomaria euphlebia* Kunze = *Plagiogyria euphlebia* (Kunze) Mett. **Figure 14.**

Terrestrial. Leaves to 2 m long, pinnatisect to 1-pinnate, dimorphic (fertile ones erect, commonly with longer petioles and narrower, constricted pinnae). **Sterile pinnae** subentire to serrulate or biserrate. **Veins** free, simple, paired at or near the base, or forked. **Fertile pinnae** subentire to erose, the margins at first slightly to strongly reflexed to protect developing sporangia, later spreading, or sometimes so strongly retroflexed that both edges touch on the adaxial side.

The most recent studies on *Plagiogyria* have recognized about 50 species in the genus; however, these have been based on a number of mostly overlapping or quantitative characters, e.g., degree of serration on pinna margins, relative length of basal pinnae, degree of branching of veins, none of which seem to be consistent or significant. Therefore, we believe the actual number of species in *Plagiogyria* is more likely to be nearer 15. Based on study of type collections and on Peruvian specimens attributed to various species, we have concluded that there is only one somewhat variable species in Peru.

References

COPELAND, E. B. 1929. The fern genus *Plagiogyria*. Philipp. J. Sci., 38: 377–417.

LELLINGER, D. B. 1971. The American species of *Plagiogyria* sect. *Carinatae*. Amer. Fern J., 61: 110–118.

1. ***Plagiogyria semicordata* (Presl) Christ, Farnkr.** Erdc. 176. 1897. **Figure 14.**

Lomaridium semicordatum Presl, Epimel. bot. 155. 1849. TYPE: "In sylvis Columbia," without collector (holotype, PRC!).

Plagiogyria costaricensis Kuhn, Linnaca 36: 149. 1869. TYPE: Costa Rica, Volcán Barba, *Wendland 1066* (holotype, c?; drawing, v!).

Plagiogyria latifolia Copel., Philipp. J. Sci. 38: 411. 1929. TYPE: Peru, Huánuco, Cani, 7 mi NE of Mito, ca. 2600 m, *Macbride 3432* (holotype, us!; isotypes, fl, GH!).

Plagiogyria denticulata Copel., Philipp. J. Sci. 38: 412. TYPE: Bolivia, Dept. Santa Cruz, alt. 2600 m, *Herzog 1954* (holotype, us!).

Petiole and rachis stramineous, the former brown at base, 8–30 cm long. **Sterile lamina** to 60 cm long and 18 cm broad, 1-pinnate to deeply pinnatisect, lanceolate-elliptic, tapering to a pinnatifid apex, gradually reduced to base, where pinnae are $\frac{1}{2}$ – $\frac{2}{3}$ as long as central ones; **pinnae** contiguous at base with adjacent ones, or widely spaced, 3–10 cm long, 0.5–1.0 cm broad, margins serrulate to biserrate, apex acute to short-attenuate; **veins** commonly 1–2-forked, or a few simple or paired at the costa. **Fertile lamina** slightly longer and narrower than the sterile; **pinnae** very widely spaced, commonly 3–4 mm broad, margins strongly retroflexed at maturity.

At edges of forests, ravines, on shaded clay and rocks banks, 1800–3600 m, Cajamarca, Amazonas, San Martín, Huánuco.

Cuba; Jamaica; Mexico; Guatemala; Costa Rica to Peru and Bolivia.

Cajamarca: Hualgayoc, *Soukup & Carmona Fa.5008* (US). **Amazonas:** Prov. Chachapoyas, Summit of Puma-Urcu SE of Chachapoyas, *Wurdack 1159* (F, GH, NY, UC, US). **San Martín:** Prov. Mariscal Cáceres, Puerta del Monte, *Young 1980* (USM). **Huánuco:** Yanano, *Macbride 3830* (F, GH, US).

Family 9: DICKSONIACEAE

Dicksoniaceae Bower, Origin land fl. 591. 1908, as Dicksonieae. TYPE: *Dicksonia* L'Hér.

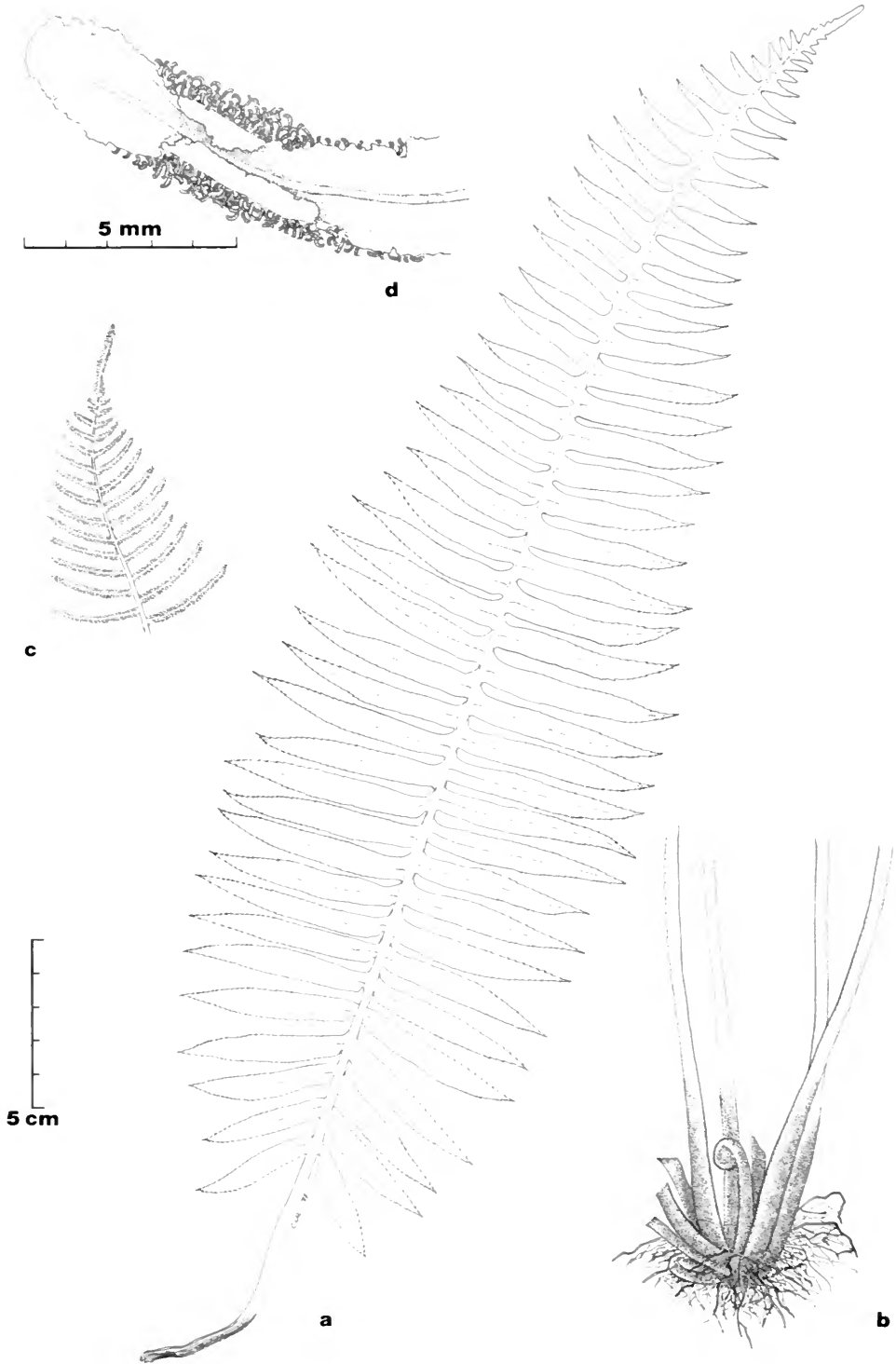


FIG. 14. *Plagiogyria semicordata*: a-b, habit; c, apex of fertile leaf; d, apex of fertile pinna. (a from Cuatrecasas 5465, Colombia, F; b from Wurdack 1159, F; c-d from Little 9184, Colombia, F.)

Stem stout to massive, usually not branched, prostrate to decumbent to erect and then often arborescent, indurated, densely covered with usually long trichomes. **Leaves** usually large, ca. 1–3 m long, circinate in veneration, monomorphic to dimorphic (the fertile nearly lacking green tissue and more complex than the sterile), pinnate, glabrous to pubescent. **Petiole** lacking stipules, not articulate to the stem. **Veins** free. **Sori** marginal, usually paraphysate with slender trichomes, enclosed within a usually firm and partly green adaxial indusium and a thinner, light brown abaxial indusium, these separate or basally or fully joined. **Sporangia** with a 4–6-rowed stalk and a complete, oblique annulus.

The Dicksoniaceae are a family of five genera and 35–40 species. Two genera are in Peru.

The family, with the possible exception of *Cystodium* of Malaysia, is natural and distinctive. It has been united with the Cyatheaceae, but that family differs in having scales on the stem and an abaxial sorus and the two are of uncertain affinity.

Reference

TRYON, R. M., AND A. F. TRYON. 1982. Dicksoniaceae, pp. 138–155, in *Ferns and allied plants*, Springer-Verlag, New York.

Key to Genera of Dicksoniaceae

- a. Lamina 4–5-pinnate-pinnatifid, broadest at the base, its tertiary axes grooved on the adaxial side I. **Culcita**
- a. Lamina 2–3-pinnate-pinnatifid (in America), reduced at the base, its tertiary axes ridged (not grooved) on the adaxial side II. **Dicksonia**

I. Culcita

Culcita Presl, Tent. pterid. 135. 1836. TYPE: *Culcita macrocarpa* Presl. **Figure 15.**

Terrestrial. **Stem** prostrate, decumbent or rarely erect and to 3 m tall, stout. **Leaves** monomorphic, to ca. 3 m long. **Lamina** 4–5-pinnate or slightly more complex, the tertiary axes grooved adaxially, veins free. **Sori** marginal, the adaxial indusium joined basally to the thinner abaxial indusium, or the two separate. **Spores** tetrahedral-globose, trilete, nearly smooth, rugulose, or tuberculate.

Culcita coniiifolia of tropical America and *C. macrocarpa* of the Canary Islands, Azores, and Spain form subg. *Culcita*. The other five species, of Malaysia to Samoa and Australia, comprise the subgenus (or, better, the genus) *Calochlaena* Maxon.

- 1. **Culcita coniiifolia** (Hooker) Maxon, Annual Rep. Smithsonian 1911: 488. 1912; J. Wash. Acad. Sci. 12: 456. 1922. **Figure 15.**

Dicksonia coniiifolia Hooker, Sp. fil. 1: 70, t. 24A. 1844. TYPE: Venezuela, (Dist. Federal), Caracas, *Linden 538* (holotype, K; isotype, BR; photo, GH).

Stem prostrate to 1 m tall, the apex with few leaves. **Leaves** to 3 m long, the petiole with a dense covering of trichomes at the base, often longer than the lamina. **Lamina** deltoid, to 4- or 5-pinnate-pinnatifid at the base, the major segments stalked, thinly pubescent, or glabrous with age, sterile ultimate segments with bluntly acute lobes. **Sorus** single on each ultimate lobe.

In wet elfin forests at ca. 2400–3100 m, Amazonas south to Cuzco.

Southern Mexico, Central America, Greater Antilles, Venezuela and Colombia south to Peru; Mt. Itatiaia, Brazil.

Culcita coniiifolia is a distinctive species and should be mistaken for no others. Although of wide distribution, it has been rarely collected in Peru.

Amazonas: Prov. Chachapoyas, 18 km above Leimebamba on road to Balsas, Cerros de Calla Calla, *Hutchison & Wright 5687* (F, GH). Along Río Ventilla, 1–2 km W of Molinopampa, *Wurdack 1468* (GH, USM).

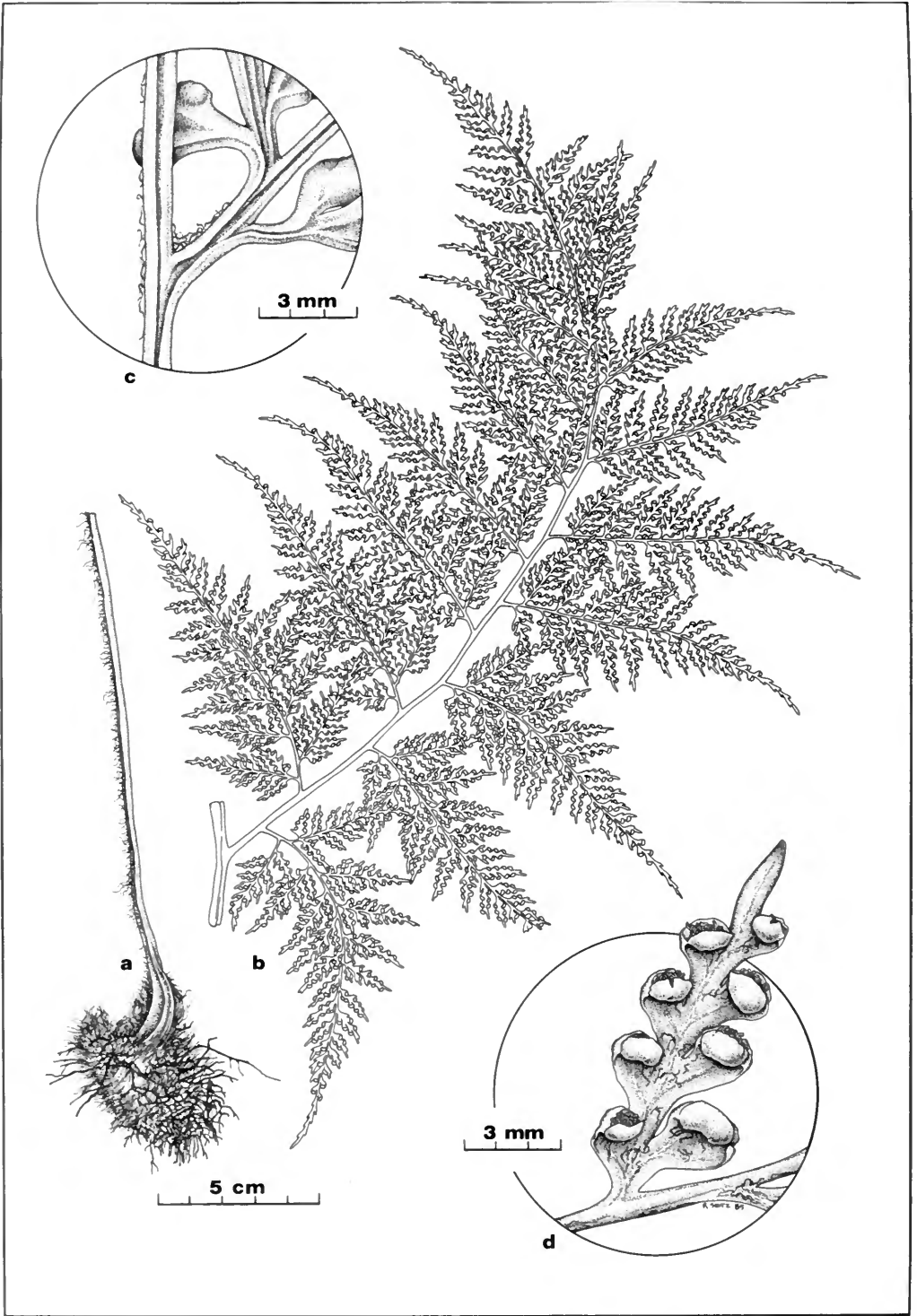


FIG. 15. *Culcita conifolia*: a, stem and part of petiole; b, pinna; c, rachis and base of pinna, adaxial side; d, fertile ultimate segment. (a from Macbride 4519, F; b-d from Lent 732, Costa Rica, F.)

Huánuco: Playapampa, *Macbride 4519* (F). **Pasco:** Prov. Oxapampa, San Alberto, Cordillera de Yanachaga, *van der Werff et al. 8436* (MO). **Cuzco:** El Dorado, Río Urubamba valley, Aug. 12, 1941, *Bües* (GH). Prov. La Convención, *Dudley 10712* (GH).

II. *Dicksonia*

***Dicksonia* L'Hér.**, Sert. angl. 30. 1788. TYPE: *Dicksonia arborescens* L'Hér. **Figure 16.**

Terrestrial. Stem erect, to 10 m tall, or decumbent at the base, usually massive. Leaves monomorphic to dimorphic (the fertile nearly lacking green tissue and more complex than the sterile), to ca. 3.5 m long. Lamina 2-pinnate-pinnatifid to

4-pinnate, reduced at the base, tertiary axes adaxially ridged (not grooved), veins free. Sori marginal, the adaxial indusium joined basally to the thinner abaxial indusium. Spores tetrahedral-globose, trilete, granulate or reticulate.

Dicksonia is a genus of about 20 species, from Malaysia to Samoa, St. Helena, tropical America, and the Juan Fernández Islands.

Reference

STOLZE, R. G. 1976. *Dicksonia*, in Ferns and fern allies of Guatemala. Part I. Fieldiana, Bot., 39: 99–102.

Key to Species of *Dicksonia*

- a. Tertiary segments of the larger fertile pinnae each with few to several sori 1. ***D. sellowiana***
a. Tertiary (ultimate) segments of the larger fertile pinnae each with a single sorus . . . 2. ***D. stuebelii***

1. ***Dicksonia sellowiana*** Hooker, Sp. fil. 1: 67. 1844. TYPE: Brazil, *Sellow* (lectotype designated here, κ ; isolectotype, HBG; photos, GH, US of HBG; lectoparatype, Brazil, *Miers*, κ). **Figure 16.**

Balanium karstenianum Klotzsch, Linnaea 20: 444. 1847. TYPE: "Columbia," *Karsten*, no. 9 (*Coll. II*) (holotype, B?; isotype, HBG; photo, GH of HBG).

Dicksonia gigantea Karsten, Fl. columb. 2: 177, t. 193. 1869. TYPE: Colombia, (Cundinamarca), Andes of Bogotá, Guadeloupe, *Karsten* (not located) (*Karsten*, HBG; photo, GH, may be authentic).

Dicksonia karsteniana (Klotzsch) Moore, Index fil. 190 (1860), 313 (1861).

Dicksonia spruceana Kuhn, Linnaea 36: 153. 1869. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4728* (holotype, B; isotypes, A!, BM, GH!; photos, GH, MO, UC of BM).

Stem to 10 m tall, enclosed, at least basally in dense fibrous roots, with persistent leaf bases, to ca. 25 cm in diameter, bearing many leaves in a crown. **Leaves** to 3 m long, the petiole very short, densely covered with long trichomes. **Lamina** 2–3-pinnate-pinnatifid, the secondary and tertiary segments nearly sessile, glabrous to thinly pubescent abaxially, sterile lobes bluntly acute to acute, the margin flat or curved. **Sori** few to several on the tertiary segments of the larger fertile pinnae.

In wet woods or cloud forests, at 1550–2400 m, Cajamarca and Amazonas, south to Cuzco.

Southern Mexico, Central America, Venezuela, and Colombia south to Bolivia, Paraguay, Uruguay and southeastern Brazil.

Dicksonia sellowiana is a widespread and variable species. Several segregates are sometimes recognized but these evidently represent minor variations. The other American species are *D. stuebelii* of Peru and *D. berteriana* (Colla) C. Chr. of the Juan Fernández Islands.

Cajamarca: Prov. Cutervo, La Pucarilla, *López & Ságastegui 5457* (GH, HUT). **Amazonas:** Prov. Bagua, ca. 20 km E of La Peca, *Barbour 2870* (MO). **Huánuco:** Cerros del Sira, Río Lullapichis watershed, *Dudley 13254* (F, GH, MO), *13259, 13373* (GH). **Pasco:** Oxapampa (as Junín), *Soukup 2334* (F, GH). Prov. Oxapampa, Canyon de Huancabamba, *León 614* (F). **Cuzco:** Prov. La Convención, Cordillera Vilcabamba, *Dudley 10439, 10603, 11308* (GH).

2. ***Dicksonia stuebelii*** Hieron., Hedwigia 45: 228, t. 12, f. 1. 1906. TYPE: Peru, (Amazonas), Tambo Ventilla, Pascomayo to Moyobamba, *Stübel 1076* (holotype, B).

Similar to *Dicksonia sellowiana*, but the lamina is 2-pinnate-pinnatifid to 2-pinnate-pinnatisect,

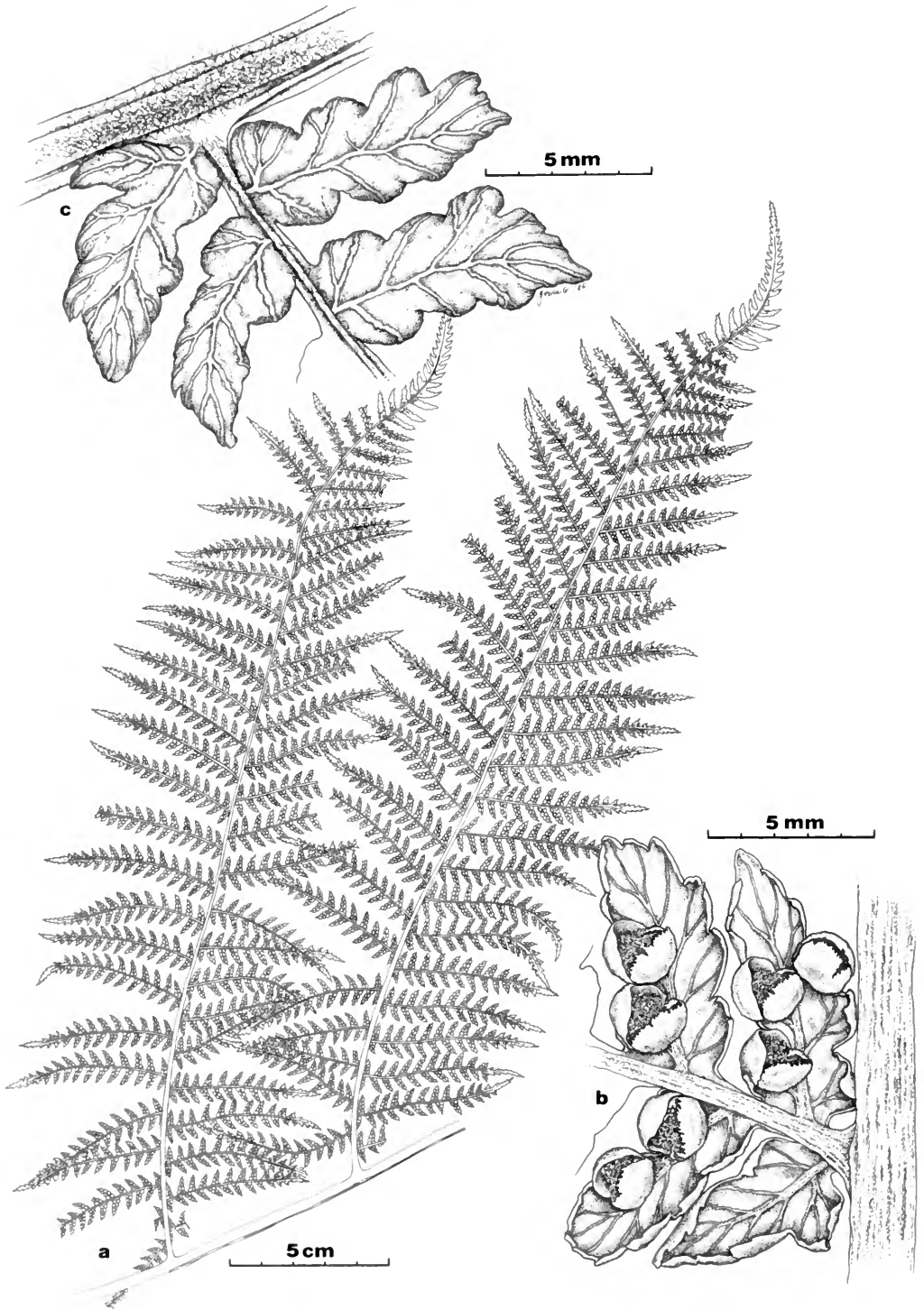


FIG. 16. *Dicksonia sellowiana*: a, 2 pinnae; b, fertile ultimate segments, abaxial side; c, secondary axis, adaxial side, with ultimate segments. (a from Reiss 61, Brazil, F; b from Killip & Smith 18095, Colombia, F; c from Holm-Nielsen et al. 5645, Ecuador, F.)

the larger fertile pinnae have the tertiary (ultimate) segments bearing a single sorus, and the sterile margins are recurved.

In the Jalca zone and in wet sandy soil, ca. 2200–3400 m, Amazonas.

Endemic in northern Peru.

This is evidently a rare and local species. It is unusual in growing within the range of the related *Dicksonia sellowiana*.

Amazonas: Cerro de Fraijaco (Huaui-Huni), NE of Tambo de Ventilla, *Pennell 15855* (GH). Prov. Chachapoyas, 3–6 km W of Molinopampa, *Wurdack 1410* (GH). Cerro Yama-uma, above Taulia, 12–15 km SE of Molinopampa, *Wurdack 1679* (F, GH, UC, US, USM).

Family 10: LOPHOSORIACEAE

Lophosoriaceae Pic.-Ser., *Webbia* 24: 700. 1970.

TYPE: *Lophosoria* Presl.

Stem sometimes branched, massive, decumbent to erect and arborescent, indurated, densely covered by long trichomes. **Leaves** usually large, ca. 1–5 m long, circinate in veneration, monomorphic, pinnate, more or less pubescent. **Petiole** lacking stipules, not articulate to the stem. **Veins** free. **Sori** exindusiate, on the abaxial surface of the segments, paraphysate with slender trichomes. **Sporangia** with a short, 6-rowed stalk and a complete, oblique annulus.

The family Lophosoriaceae contains a single, American genus.

Reference

TRYON, R. M., AND A. F. TRYON. 1982. Lophosoriaceae, pp. 156–161, in *Ferns and allied plants*, Springer-Verlag, New York.

Key to Varieties

- a. Leaf ca. 2–4 m long, pinnae spaced, patent, the central ones ca. 0.5–1.0 m long 1a. var. **quadripinnata**
- a. Leaf ca. 0.25–1 m long, pinnae imbricate, ascending, the central ones ca. 0.05–0.20 m long 1b. var. **contracta**

I. Lophosoria

Lophosoria Presl, *Gefäßbündel Farn* 36. 1847.

TYPE: *Lophosoria pruinata* (Sw.) Presl = *Lophosoria quadripinnata* (Gmelin) C. Chr. **Figure 17.**

Terrestrial. Leaves rarely 0.25 m, usually 2–3 m, sometimes to 5 m long. Lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatisect, segments often glaucous abaxially and slightly to densely pubescent. **Sori** round, borne on the veins, the receptacle hardly elevated. **Spores** trilete, tetrahedral-globose, with a large equatorial flange, coarsely tuberculate to rugose.

A monotypic genus, ranging from Mexico and the Greater Antilles, south to Bolivia and Brazil, also in southern Argentina and Chile, and the Juan Fernández Islands.

Lophosoria quadripinnata is a widely distributed and distinctive species of the cloud forest zone. One high altitude variety that is local in Ecuador and Peru may be recognized.

1. **Lophosoria quadripinnata** (Gmelin) C. Chr., *Skottsbo. Nat. hist. Juan Fernánd.* 2: 16. 1920.

Stem apex with few leaves. **Petiole** about as long as the lamina or somewhat shorter, with 3 convoluted vascular bundles. **Lamina** very narrowly lanceolate to usually broadly ovate, to 3-pinnate-pinnatisect, with sessile or short-stalked segments, very sparsely to densely pubescent and often glaucous abaxially, ultimate segments obtuse to subacute. **Sori** single on a fertile vein.

Range of the genus.

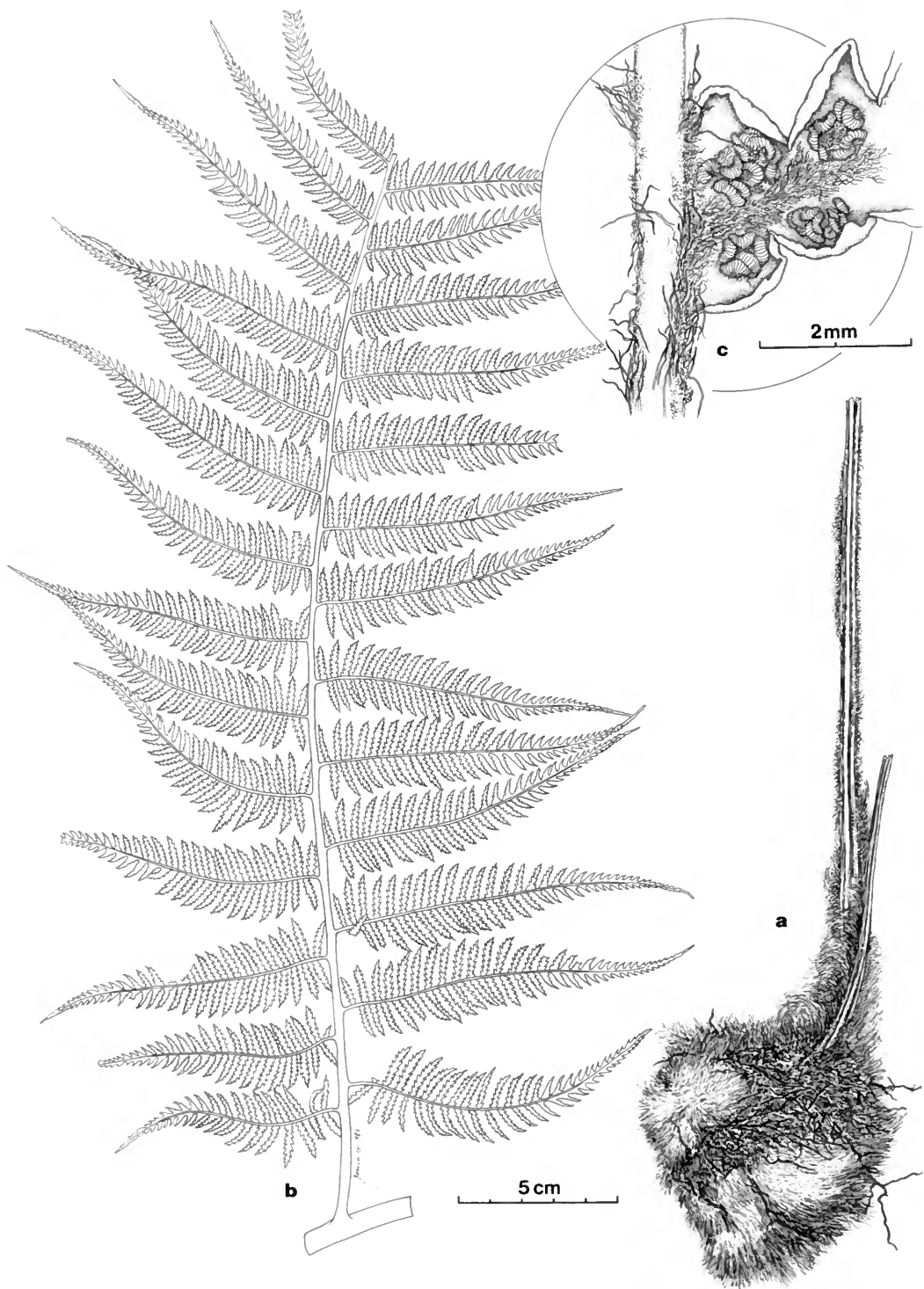


FIG. 17. *Lophosoria quadripinnata* var. *quadripinnata*: a, stem and portion of petiole; b, pinna; c, base of fertile segment. (a from Wurdack 1752, F; b-c from Stork & Horton 10348, F.)

1a. **Lophosoria quadripinnata** var. **quadripinnata**.
Figure 17.

Polypodium glaucum Sw., Prodr. 134. 1788, not Houtt. 1783. TYPE: Jamaica, Swartz (holotype, b!, *Herb. Willd.* 19723; photo, GH, designated as type by Hieronymus, it may be the holotype or an isotype).

Polypodium quadripinnatum Gmelin, Syst. nat. 2(2): 1314. 1791, *nom. nov.* for *Polypodium glaucum* Sw. (not Houtt.) and with the same type.

Polypodium pruinatum Sw., J. Bot. (Schrad.) 1800(2): 29. 1802, *nom. nov.* for *Polypodium glaucum* Sw. (not Houtt.) and with the same type.

Alsophila pruinata (Sw.) Kunze, Linnaea 9: 99. 1834. *Lophosoria pruinata* (Sw.) Presl, Gefäßbündel Farn 37. 1847.

Alsophila quadripinnata (Gmelin) C. Chr., Index fil. 44. 1905.

In wet forests, forest borders, on brushy slopes, in cloud forests and elfin forests, 700–3100 m, Cajamarca and Amazonas, south to Puno.

Range of the genus.

Throughout most of mountainous tropical America, this variety is a typical element of the cloud forest zone.

Cajamarca: Prov. Celendín, Agua Colorado, *Sánchez 206* (GH). **Amazonas:** Cerros de Calla Calla, above Leimebamba, *Hutchison & Wright 5686* (F, GH, UC, US). Cerro Puma Urco, Chachapoyas, *Soukup 4086* (F, US). **San Martín:** Monte Campana, Tarapoto, *Spruce 4248* (GH, US). **Huánuco:** Panao, *Bryan 407* (F, GH). Playapampa, *Macbride 4860* (F, US). **Pasco:** Quillasú, *Soukup 3290* (F, GH, UC, US). Yapas, Pichis Trail (as Junín), *Killip & Smith 25456* (F, GH, US). **Junín:** Huacapistana, *Ferreya 3654* (USM). **Ucayali:** La Divisoria, *Aguilar 849* (GH). **Huancavelica:** Prov. Tayacaja, Surcubamba, *Stork & Horton 10348* (F, GH, UC, US). **Cuzco:** Prov. La Convención, *Dudley 10883* (F, GH). Pilahuata, Cerro de Cusiluyoc, *Pennell 13938* (GH, US). **Puno:** Prov. Sandía, Sandía to Chunchusmayo, *Weberbauer 1333* (USM).

1b. **Lophosoria quadripinnata** var. **contracta** (Hieron.) R. & A. Tryon, *Rhodora* 84: 126. 1982.

Alsophila contracta Hieron., *Hedwigia* 45: 236, t. 15, f. 8. 1906. SYNTYPES: Peru, (Amazonas), near Inez and Calle-calle, *Stübel 1067* (b!; frag., GH!); (Amazonas), near Challuayacu and Tambo Centamala, *Stübel 1066* (b!).

Wet, shrubby areas, 2800–3500 m, in Amazonas and La Libertad.

Ecuador and Peru.

The var. *contracta* is evidently a high-altitude ecotype. The following collection is intermediate between the two varieties: Peru, Amazonas, Puma-Urcu, SE of Chachapoyas, *Wurdack 791* (US).

Amazonas: Prov. Chachapoyas, Pomacocha, *López et al. 4392* (GH). Prov. Chachapoyas. Cerros de Calla Calla slopes, *Wurdack 1752* (GH, US, USM). Prov. Chachapoyas, between Leimebamba and Calla-Calla, *Smith & Vásquez 4978* (GH). **La Libertad:** Prov. Bolívar, cerca Nevado de Cajamarquilla, *Ferreya 1349* (GH, USM).

Family 11: METAXYACEAE

Metaxyaceae Pic.-Ser., *Webbia* 24: 701. 1970.
TYPE: *Metaxya* Presl.

Stem rather stout, sometimes branched, prostrate to nearly erect, indurated, with dense, long trichomes, especially toward the apex. **Leaves** usually large, to 2 m long, circinate in veneration, monomorphic, pinnate, glabrate. **Petiole** lacking stipules, not articulate to the stem. **Veins** free. **Sori** exindusiate, on the abaxial surface of the pinnae, paraphysate with slender trichomes. **Sporangia** with a 4-rowed stalk and a complete, slightly oblique annulus.

The family Metaxyaceae contains a single, American genus.

Reference

TRYON, R. M., AND A. F. TRYON. 1982. Metaxyaceae, pp. 162–165, in *Ferns and allied plants*, Springer-Verlag, New York.

I. *Metaxya*

Metaxya Presl, Tent. pterid. 59. 1836. TYPE: *Metaxya rostrata* (HBK.) Presl (*Aspidium rostratum* HBK.). **Figure 18.**

Terrestrial or rarely on tree bases. **Leaves** to ca. 2 m long. **Petiole** usually with short trichomes at the very base. **Lamina** 1-pinnate, with simple pinnae, veins free. **Sori** roundish to elongate, the receptacle nearly flat. **Spores** globose, trilete, granulate.

A monotypic genus ranging from southern Mexico and Central America; Guadeloupe; Trinidad; and French Guiana west to Colombia and south to Bolivia; Amazonian Brazil.

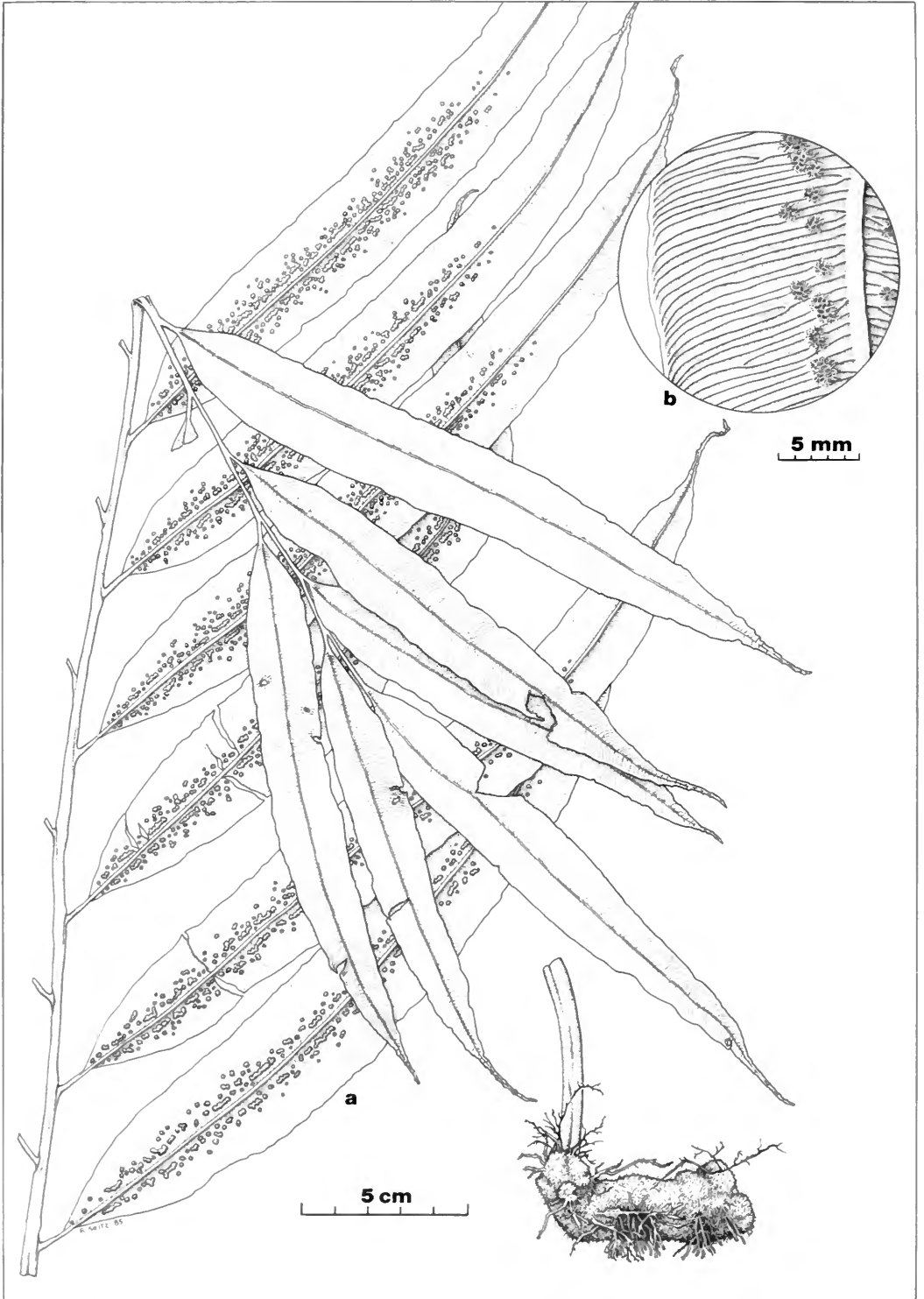


FIG. 18. *Metaxya rostrata*: a, habit; b, portion of fertile pinna, abaxial side. (From Wurdack 1872, F.)

1. **Metaxya rostrata** (HBK.) Presl, Tent. pterid. 60. 1836. **Figure 18.**

Polypodium rostratum Willd., Sp. pl. ed. 4, 5: 193. 1810, not Burm. 1768. TYPE: Venezuela, Javita, *Humboldt 966* (holotype, v!, *Herb. Willd. 19691*; photo, GH).

Aspidium rostratum HBK., Nov. gen. sp. 1: 12. 1815, *nom. nov.* for *Polypodium rostratum* Willd. (not Burm.) and with the same type.

Alsophila blechnoides Hooker, Sp. fil. 1: 35. 1844, *nom. superfl.* for *Alsophila rostrata* (HBK.) Mart. and with the same type.

Stem prostrate, the apex with few leaves. **Petiole** about as long as the lamina, with 1 convoluted vascular bundle. **Lamina** narrowly lanceolate to ovate, 1-pinnate, with a conform terminal pinna, the pinnae stalked, glabrous or nearly so abaxially, entire to finely serrate, the serrate apex acuminate to caudate. **Sori** 1–3 on each fertile vein.

Woods and dense forests, usually in sandy, moist, well-drained soil, 100–800 m, Amazonas to Cuzco and Madre de Dios.

Range of the genus.

Metaxya is unusual in having the 1-pinnate-pinnatifid leaves of juvenile plants more complex than the 1-pinnate leaves of adult plants.

Amazonas: Prov. Bagua, Río Marañón, above Cascadas de Mayasi, *Wurdack 1872* (US, USM). **San Martín:** Prov. Mariscal Cáceres, Isla de Pucunuchu, *J. Schunke 4783* (F, GH). **Prov. Mariscal Cáceres,** Río Sión, *J. Schunke 3524* (F, GH, US). **Loreto:** Iquitos, *Killip & Smith 27489* (GH, US). **Huánuco:** Prov. Pachitea, Bosque Nacional de Iparia, *J. Schunke 1620, 1833* (F, GH, US). **Pasco:** Prov. Oxapampa, Cordillera San Matías, *León 332* (USM). **Ucayali:** vicinity of Aguaytía, *Croat 20966* (US). **Prov. Coronel Portillo,** Bosque Nacional Humboldt, *Vásquez 3910* (F, MO). **Cuzco:** Prov. Quispicanchi, *Vargas 16462* (GH). **Prov. Paucartambo,** *Vargas 11245* (GH). **Madre de Dios:** Prov. Tambopata, Tambopata Nature Reserve, *Barbour 5191* (F).

Family 12: CYATHEACEAE

Cyatheaceae Kaulf., Wesen Farrenkr. 119. 1827.
TYPE: *Cyathea* Smith.

Stem usually massive, erect, arborescent, unbranched, very rarely slender and scandent, to small, decumbent and short-creeping, indurated, bearing scales and sometimes spines. **Leaves** usually large, ca. 1–4 m long, circinate in veneration, monomorphic to rarely dimorphic, pinnate or very

rarely entire, glabrous, pubescent and (or) scaly abaxially. **Petiole** lacking stipules, not articulate to the stem. **Veins** free or rarely reticulate. **Sori** ex-indusiate or indusiate, on the abaxial surface of the segments, usually paraphysate with slender trichomes or rarely with enlarged ones. **Sporangia** with a 4-rowed stalk and a complete, oblique annulus.

The Cyatheaceae are a family of six genera and a few hundred species. All of the genera occur in Peru.

This treatment has been adapted from the literature cited under the family and the genera. There are at least 19 species, especially of Ecuador but also of Bolivia, that may well also occur in Peru, but these are too numerous to mention.

Characters of all parts of the leaf are useful and often necessary for the accurate identification of the genera and species of Cyatheaceae. Of special importance are characters of the petiole scales. However, the scales may be abraded on the petiole of a mature leaf and their characters are best seen on the croziers. The height and diameter of the arborescent stem vary in a species depending upon the age of the plant and the growing conditions. Accordingly, these characters as well as other quantitative ones are usually not included in the species descriptions.

Several special terms that are used in the Cyatheaceae are the following.

PETIOLE SPINES—Corticate: The spine is an extension of the cortex of the petiole; each bears, at least when young, a scale at its apex which is rather blunt when the scale falls off. **Squaminate:** The spine is not an extension of the petiole; it breaks, or can be broken, from the petiole at its base. It has a sharp apex that does not bear a scale. These spines have evidently evolved from petiole scales.

PETIOLE SCALES—Conform: All cells, except those that may be borne on the edge, are similar in orientation, shape, and usually in size and color. **Marginate:** With a narrow to broad margin of cells different from those in the central portion of the scale in orientation, size, and usually in shape and color. **Body:** All of the scale except for cilia, teeth, or setae borne on the edge. **Margins:** The cellularly differentiated areas on each side of the central portion of marginate scales. **Concolorous:** All of the scale of one color or nearly so. **Bicolorous:** The margins definitely of lighter color than the central portion. **Concordantly bicolorous:** The lighter color confined to the differentiated margins and the darker color to the central portion of elongate cells.

Discordantly bicolorous: The lighter color of the margins extends into part of the central portion of elongate cells.

PETIOLE SCURF—Large scales: The scales are small, but definitely larger than most of the scurf which is composed of minute scales and trichomes.

INDUSIA—Hemitelioid: Attached at the base and often at the sides of the receptacle, but not completely surrounding it. **Meniscoid:** Completely surrounding the receptacle, nearly flat or with slightly upturned edges. **Cyathiform:** Cup-shaped. **Urceolate:** Urn-shaped. **Subsphaeropteroid:** Enclosing

the sporangia except for a rather small opening at the apex. **Sphaeropteroid:** Completely enclosing the sporangia and with an apical umbo.

References

- TRYON, R. 1970. The classification of the Cyatheaceae. *Contr. Gray Herb.*, **200**: 2–53.
 ———. 1986. Cyatheaceae, in Harling, G., and L. Anderson, eds., *Flora of Ecuador*, **27**: 17–56.
 TRYON, R. M., AND A. F. TRYON. 1982. Cyatheaceae, pp. 166–212, in *Ferns and allied plants*, Springer-Verlag, New York.

Key to Genera of Cyatheaceae

- a. Petiole scales conform I. **Sphaopteris**
- a. Petiole scales marginate b
- b. Petiole scales with a dark, opaque apical seta c
- c. Petiole lacking spines, or with corticinate spines that bear, at least when young, a scale at the apex, other petiole scales almost appressed to the surface and attached at a usually pseudopeltate base; croziers lacking spines II. **Alsophila**
- c. Petiole with squaminate spines, many of these large, black, with a sharp apex; petiole scales patent, attached at a usually narrowed base; croziers with large, black, sharp spines III. **Nephelea**
- b. Petiole scales lacking a differentiated apical seta, the apex rounded to filamentous d
- d. Indusium absent IV. **Trichipteris**
- d. Indusium present e
- e. Spores lacking large pores, sometimes with variously distributed small pits or pores; veins free, the basal ones of adjacent segments extending to the margin above the sinus, rarely a few costal areolae present V. **Cyathea**
- e. Spores with three large equatorial pores, often also with smaller pits or pores; veins anastomosing to form costal areolae, or if free then the basal veins of adjacent segments connivent to the sinus VI. **Cnemidaria**

I. **Sphaopteris**

Sphaopteris Bernh., *J. Bot. (Schrader)* 1800(2): 122. 1802. TYPE: *Sphaopteris medullaris* (Forster) Bernh. (*Polypodium medullare* Forster). **Figure 19.**

Terrestrial. **Stem** stout, erect and arborescent or rarely short-decumbent, lacking spines. **Leaves** monomorphic to slightly dimorphic, with scales, especially on the croziers and the base of the petiole, that are conform and with or without a dark apical seta. **Petiole** lacking spines or with corticinate spines. **Lamina** 1-pinnate to 3-pinnate-pinnatifid, veins free or rarely partially anastomosing without included free veinlets. **Sori** round, often

borne at the fork of a vein, exindusiate or with a hemitelioid or sphaeropteroid indusium. **Spores** tetrahedral-globose, trilete, echinate, porate, verrucate or nearly smooth.

Sphaopteris occurs in tropical America, India and southeastern Asia to New Zealand and Pitcairn Island. Among the 120 species, there are 23 in America and seven in Peru.

References

- TRYON, R. 1971. The American tree ferns allied to *Sphaopteris horrida*. *Rhodora*, **73**: 1–19.
 WINDISCH, P. G. 1977. Synopsis of the Genus

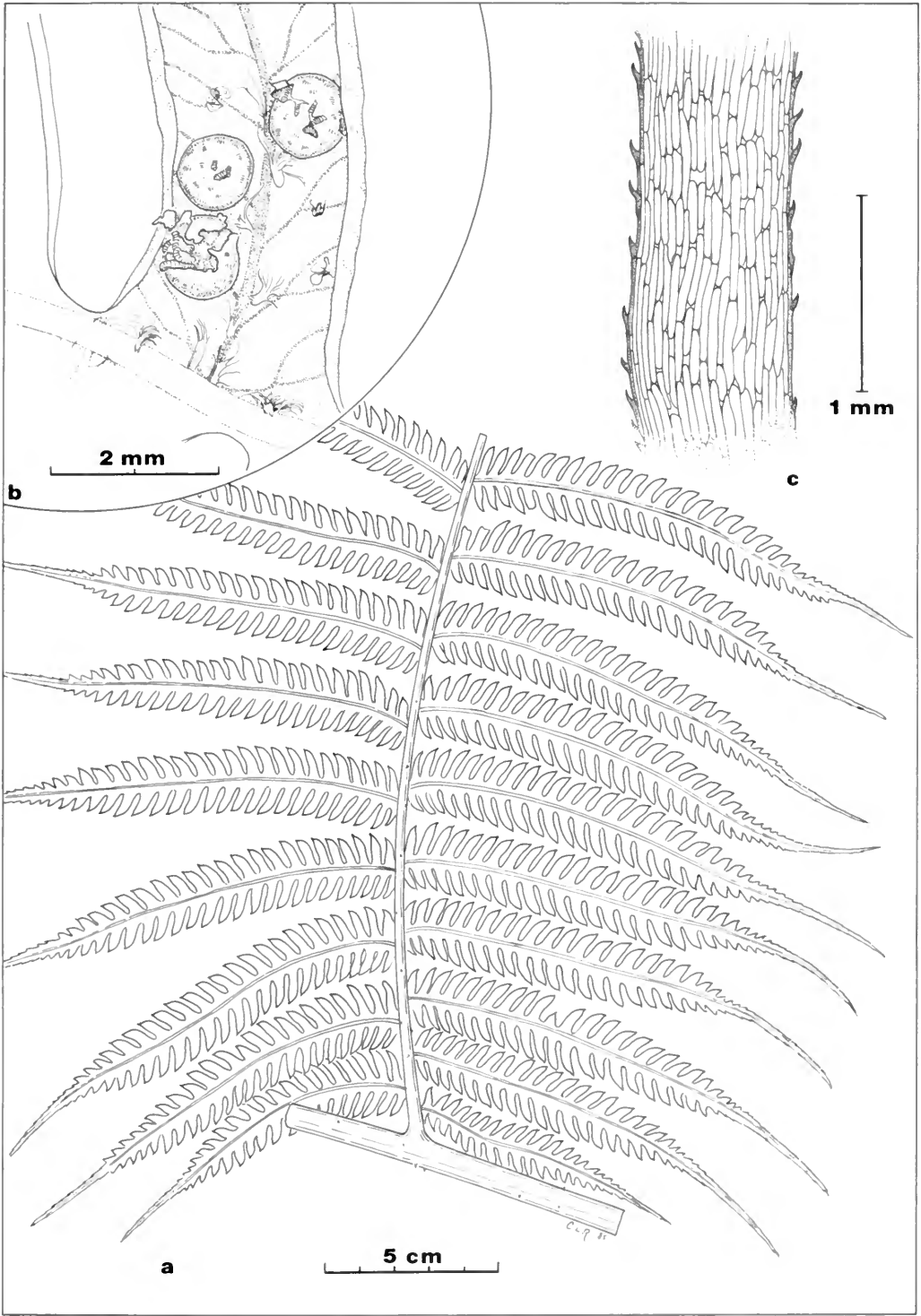


FIG. 19. *Sphaeropteris elongata*: a, portion of pinna. *Sphaeropteris quindiuensis*: b, portion of fertile segment; c, portion of petiole scale. (a from Soukup 1651, F; b from Soukup 2336, F; c from Plowman 6062, F.)

Sphaeropteris (Cyatheaceae) with a revision of the neotropical exindusiate species. Bot. Jahrb. Syst., 98: 176–198.

———. 1978. *Sphaeropteris* (Cyatheaceae), the systematics of the group of *Sphaeropteris hirsuta*. Mem. New York Bot. Gard., 29: 2–22.

Key to Species of *Sphaeropteris*

- a. Petiole scales without a dark apical seta and without dark marginal setae, rarely the margins ciliate toward the apex [subg. *Sclephropteris* Windisch] b
- b. Veins free c
- c. Sori exindusiate 1. *S. aterrima*
- c. Sori indusiate, the indusium sometimes inconspicuous d
- d. Sori with a small, hemitelioid (flabellate) indusium e
- e. Costa and costules with whitish, fimbriate or highly dissected scales abaxially 2. *S. rufescens*
- e. Costa and costules lacking scales or with scales various, but not whitish, fimbriate, or highly dissected 3. *S. macrosora*
- d. Sori with a sphaeropteroid indusium 5. *S. atahuallpa*
- b. Veins regularly anastomosing, especially along the costa, sori with a hemitelioid indusium 4. *S. bradei*
- a. Petiole scales with a dark apical seta and dark marginal setae [subg. *Sphaeropteris*] f
- f. Sori exindusiate 6. *S. elongata*
- f. Sori with a sphaeropteroid indusium 7. *S. quindiuensis*

1. ***Sphaeropteris aterrima*** (Hooker) Tryon, Contr. Gray Herb. 200: 20. 1970.

Alsophila aterrima Hooker, Syn. fil. 38. 1866. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4713* (holotype, K!; isotypes, P!, US!).
Cyathea aterrima (Hooker) Domin, Pterid. 262. 1929.

Petiole without spines or sparingly short-aculeate, with very narrow scales intergrading to trichomes, these rather dense, especially toward the base of the petiole, straw-colored to light brown, lacking a dark apical seta and dark marginal setae, sometimes ciliate. **Lamina** 1–2-pinnate-pinnatifid, pinnules long-pubescent and sometimes with a few flattish scales abaxially, veins free. **Sori** with paraphyses about as long as the sporangia, exindusiate.

This species has been collected only in San Martín at mid-elevations.

Colombia and Peru.

Sphaeropteris aterrima is notable for its petiole indument which consists of scales intergrading to trichomes.

San Martin: Monte Morro de Moyobamba, *Stübel 1113* (B, NY).

2. ***Sphaeropteris rufescens*** (Kuhn) Windisch, *Bradea* 1: 372. 1973.

Hemitelia rufescens Kuhn, Linnaea 36: 159. 1869.
TYPE: Peru, (San Martín), Monte Guairapurima, Tarapoto, *Spruce 4727* (holotype, B!; isotype, K; photo, GH of K).
Cyathea rufescens (Kuhn) Domin, Pterid. 264. 1929.

Petiole muricate, pubescent, scales brown with lighter margins to wholly light colored, the edges toothed. **Lamina** 2-pinnate-pinnatifid, with trichomes, bullate scales, and long whitish, fimbriate or highly dissected scales abaxially, veins free. **Sori** usually at the fork of a vein, paraphyses longer than the sporangia, indusium hemitelioid (flabellate).

Known only from the type collection from San Martín.

Endemic to Peru.

The whitish fimbriate scales beneath and the small indusium make this a distinctive species.

3. ***Sphaeropteris macrosora*** (Baker) Windisch, *Bradea* 1: 372. 1973.

Alsophila macrosora Baker, Timehri 5: 211. 1886.

TYPE: Venezuela, (Bolívar), Mt. Roraima, *Im Thurn* 87 (holotype, κ!; isotype, us!).

Cyathea macrosora (Baker) Domin, Pterid. 263. 1929.

Petiole glabrous to sparingly pubescent, nearly smooth to muricate with the scales whitish to brownish and with lighter margins, these sometimes broad, or most of the scales wholly whitish, lacking a dark apical seta and dark marginal setae, sometimes ciliolate, especially apically. **Lamina** 2-pinnate-pinnatifid, the pinnules glabrous, pubescent and (or) slightly scaly abaxially, the scales various, but not whitish, fimbriate, or highly dissected. **Sori** with paraphyses longer than the sporangia, indusium hemitelioid (broadly flabellate to reduced).

At 400–500 m, Pasco.

Guyana and Brazil, west to Colombia and Peru.

Sphaeropteris macrosora is represented in Peru by var. *reginae* Windisch which occurs throughout the range of the species. Variety *macrosora* is in British Guiana and Venezuela and var. *vaupensis* Windisch is in Colombia and Venezuela.

Pasco: Prov. Oxapampa, Palcazú, *Foster & d'Achille* 10168 (F).

4. ***Sphaeropteris bradei*** Windisch, *Bradea* 1: 372. 1973. TYPE: Colombia, Vaupés, Cerro Mitu, *Schultes, Raffauf & Soejarto* 24229 (holotype, GH!).

Petiole sparingly aculeate, with rather broad scales, these usually dense, especially toward the base of the petiole, shining, dark brown, lacking a dark apical seta and dark marginal setae, usually finely short-ciliate. **Lamina** 2-pinnate-pinnatifid, pinnules with scattered, short, often crispate trichomes and sometimes a few bullate scales abaxially, veins regularly anastomosing, especially along the costa. **Sori** with paraphyses shorter than the sporangia, indusium hemitelioid, usually 2-lobed.

Primary forests, 130–200 m, San Martín and Loreto.

Colombia, Ecuador, and Peru.

The regularly anastomosing veins of *Sphaeropteris bradei* are unique among the American Cyatheaceae, except for species of the genus *Cnemidaria*.

San Martín: Prov. Lamas, Caserío Bonilla, km. 75 of Tarapoto-Yurimaguas road, *Knapp & Mallet* 7141 (MO).

Loreto: Mishuyacu, near Iquitos, *Klug* 1546 (F, NY, US). Estación Biológica Callicebus, Río Nanay, 2 horas río arriba de Iquitos, *Vásquez et al.* 649 (GH). Near mouth of Río Napo, *Croat* 20194 (F, UC).

5. ***Sphaeropteris atahuallpa*** Tryon, *Rhodora* 74: 442. 1972. TYPE: Peru, Amazonas, Prov. Chachapoyas, Cerros de Calla Calla, above Balsas on road to Leimebamba, *Hutchison & Wright* 6922 (holotype, GH!; isotypes, MO, UC).

Petiole sparingly very short-aculeate, with large, broad scales to 6 cm long, these dense well above the base of the petiole, brownish white, lacking a dark apical seta and dark marginal setae, sparsely and finely ciliate, especially toward the apex. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules with prominent whitish, flattish scales abaxially, veins free. **Sori** with paraphyses about as long as the sporangia, indusia sphaeropteroid.

This species has been collected in Peru only at ca. 3000–3300 m in the Department of Amazonas.

Ecuador and Peru.

Sphaeropteris atahuallpa is a distinctive and attractive species. The croziers are completely enveloped by large, whitish scales and these form a dense covering to the petiole. Some of the scales are up to 6 cm long and several cells thick at their base.

Amazonas: Summit of Puma-Urcu, SE of Chachapoyas, *Wurdack* 1153 (GH, US). Prov. Chachapoyas, Calla-Calla, *Smith & Vásquez* 5012 (GH).

6. ***Sphaeropteris elongata*** (Hooker) Tryon, *Contr. Gray Herb.* 200: 20. 1970. **Figure 19a.**

Alsophila elongata Hooker, *Sp. fil.* 1: 43. 1844. TYPE: Colombia, *Hartweg* 1528 (holotype, κ!; isotype, LD), not *Cyathea elongata* Karsten.

Alsophila poeppigii Hooker, *Sp. fil.* 1: 43. 1844. TYPE: Peru, 1829, *Poeppig* (holotype, κ!), a synonym of *Sphaeropteris elongata* by Windisch, *Bot. Jahrb. Syst.* 98: 189. 1977.

Cyathea poeppigii (Hooker) Domin, Pterid. 263. 1929.

Petiole aculeate, with rather narrow scales, these usually sparingly persistent, whitish to light brown or with a darker base, with a dark apical seta and dark marginal setae. **Lamina** 2-pinnate-pinnatifid

to 2-pinnate-pinnatisect, pinnules sparingly to definitely pubescent and sometimes with a few flattish scales abaxially, veins free. **Sori** with persistent paraphyses mostly longer than the sporangia, exindusiate.

In primary forests, rain forests, and on open hillsides, at 450–2000 m, Amazonas and Loreto, south to Puno.

Costa Rica south to Bolivia; also in southeastern Brazil.

Sphaeropteris elongata is the most widely distributed species of the genus in America and consequently is a variable species. *Alsophila poeppigii* was described on the basis of a plant with unusually coriaceous leaves. Specimens without petiole scales may be similar to those of *Trichipteris conjugata*, but that species has sessile rather than stalked pinnae.

Amazonas: Prov. Bagua, Chiriaco to Puente Venezuela, *Barbour 4385* (MO, USM). **San Martín:** Prope Tarapoto, *Spruce 4722* (GH). **Loreto:** Cerca a Pongo, entre Yurimaguas y Tarapoto, *Ferreyra 17474* (GH, USM). **Huánuco:** Huamalíes, Valle de Monzón, *Weberbauer 3471* (USM). Chinchao, *Ferreyra 16950* (GH, USM). **Junín:** La Merced, *Soukup 1061* (F). Cerca a San Ramón, *Cerate 2870* (GH, USM). 10 km SW of San Ramón, *Tryon & Tryon 5445* (F, GH). **Ucayali:** 10 km NE of Aguaytia, *Gentry et al. 41422* (F, MO, USM). **Ayacucho:** Prov. La Mar, Hacienda Santa Rosa, *Dudley 11697* (GH). Ayña, between Huanta and Río Apurímac, *Killip & Smith 22716* (NY, US). **Puno:** Prov. Carabaya, Puente Inambari, *Vargas 18431* (GH).

7. *Sphaeropteris quindiuensis* (Karsten) Tryon, *Contr. Gray Herb.* 200: 20. 1970. **Figure 19b-c.**

Cyathea quindiuensis Karsten, *Linnaea* 28: 454. 1857. TYPE: Colombia, (Tolima), between Ríos Magdalena and Cauca, *Karsten* (not located). (Tolima), Páramo Quindío, *Karsten* (Herb. Mett. b! is authentic).

Petiole without spines, with long, narrow scales, these dense, usually well above the base of the petiole, whitish to shining brown, with a dark apical seta and dark marginal setae. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules with a few to many bullate scales, especially on the costules of fertile segments, and often some trichomes abaxially. **Sori** with paraphyses about as long as the sporangia, indusium sphaeropteroid.

On steep mountain slopes, in rain forests and cloud forests, 1700–2500 m, Amazonas south to Cuzco.

Colombia south to Bolivia.

This species is unique among those of Peru in having some of the scales at the top of the crozier with the marginal teeth retrorse at the scale apex but changing to antrorse below.

Amazonas: Prov. Bagua, Cordillera Colán, SE of La Peca, *Barbour 3749* (MO). **Huánuco:** Prov. Leoncio Prado, Cordillera Azul, *Gentry et al. 29573* (GH). Playapampa, *Macbride 4856* (F). **Pasco:** Oxapampa (as Junín), *Soukup 2336* (F, GH). Prov. Oxapampa, road Oxapampa-Paucartambo, *Smith & Pretel 1643* (F, MO). **Junín:** Prov. Chanchamayo, ca. 26 km S of San Ramón, *Smith & Palacios 2649* (F, MO). **Cuzco:** Prov. La Convención, Cordillera Vilcabamba, *Dudley 11313* (GH).

II. *Alsophila*

Alsophila R. Br., *Prodr.* 158. 1810. TYPE: *Alsophila australis* R. Br. **Figure 20.**

Terrestrial. Stem stout, erect and arborescent or very rarely short and decumbent or climbing, lacking spines or these rarely present. **Leaves** monomorphic or sometimes dimorphic, with scales, especially on the crozier and petiole base, that are marginate and with a usually dark apical seta. **Petiole** lacking spines or with corticinate spines. **Lamina** entire to 4-pinnate, veins free. **Sori** round, often at the fork of a vein, exindusiate or with a hemiteloid to sphaeropteroid indusium. **Spores** tetrahedral-globose, trilete, prominently ridged.

Alsophila is a pantropical genus of ca. 230 species with 13 of them in America, mostly in the Greater Antilles, and a single one in Peru.

In the treatment of Conant (1983), the first 13 species are *Alsophila* and the others are treated here in the next genus, *Nephelea*.

Reference

CONANT, D. S. 1983. A revision of the genus *Alsophila* (Cyatheaaceae) in the Americas. *J. Arnold Arbor.*, 64: 333–382.

1. *Alsophila engelii* Tryon, *Contr. Gray Herb.* 200: 29. 1970, *nom. nov.* for *Cyathea elongata*

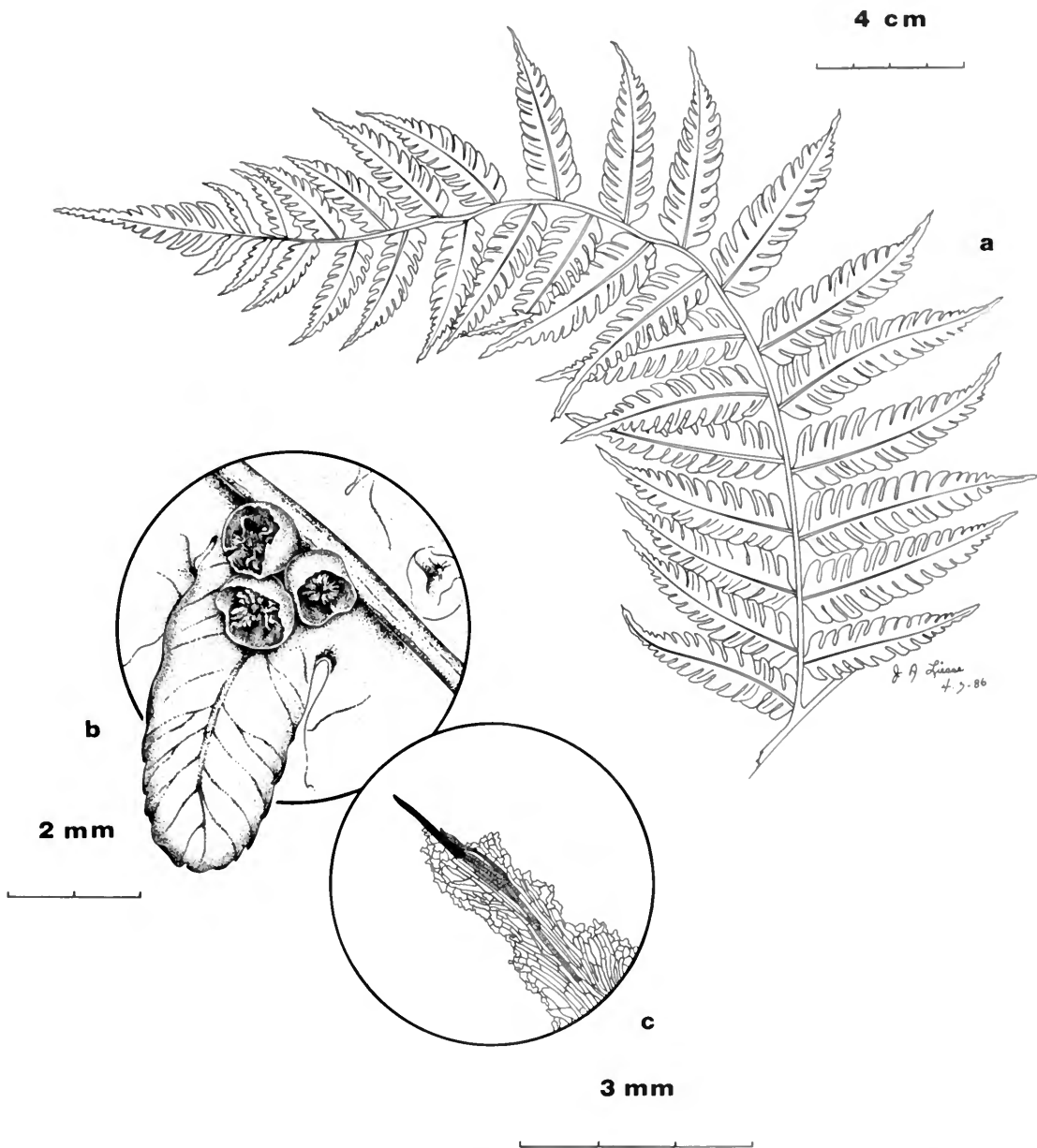


FIG. 20. *Alsophila engelii*: a, pinna; b, ultimate segment and sori; c, apex of petiole scale. (From Dudley 11944, GH.)

Karsten, not *Alsophila elongata* Hooker. Figure 20.

Cyathea elongata Karsten, Fl. Columb. 2: 159. 1869.
 TYPE: Venezuela, (Mérida), Mérida, Engel 138 (holotype, v!).

Petiole smooth to tuberculate, brown, bearing mostly blackish to light brown scales with 1 apical seta. Lamina 2-pinnate-pinnatifid, gradually tapering to the apex, rachis light brown to brown, with usually numerous, small dissected scales, pinnae sessile or nearly so. Indusia deeply cyathiform to sphaeropteroid, glabrous.

Montane rain forests, 1700–1900 m, Amazonas, San Martín, and Ayacucho.

Venezuela and Colombia, south to Peru.

Amazonas: Prov. Bongará, Shilla, *Young & Eisenberg 442* (UC). **San Martín:** Prov. Rioja, Pedro Ruíz-Moyobamba, *D. Smith 4454* (GH). **Ayacucho:** Prov. La Mar, along Inca trail between Huanhuachayo and Puncu, Cordillera Central, *Dudley 11944* (GH).

Comments

Alsophila paucifolia Baker of Colombia and Ecuador may be found in Peru. It differs from *A. engelii* in having a l-pinnate-pinnatifid lamina. *Alsophila capensis* (L. f.) John Sm. ssp. *polypodioides* (Sw.) Conant of southeastern Brazil may also occur in Peru. It is characterized by the highly dissected aplebiae at the base of the petiole.

III. Nephelea

Nephelea Tryon, *Contr. Gray Herb.* 200: 37. 1970.
TYPE: *Nephelea polystichoides* (Christ) Tryon = (*Cyathea polystichoides* Christ). **Figure 21.**

Key to Species of Nephelea

- a. Veins with stellate trichomes or squamules abaxially b
- b. Indusium glabrous; pinna-rachises not green-alate between the more distal, sessile pinnules; petiole scales on the abaxial side lacking lateral setae 1. **N. erinacea**
- b. Indusium with whitish trichomes; pinna-rachises usually (sometimes narrowly) green-alate between the more distal, sessile pinnules; petiole scales on the abaxial side with dark lateral setae 2. **N. cuspidata**
- a. Veins lacking indument abaxially, or present and not stellate; pinna-rachises green-alate between the more distal, sessile pinnules; petiole scales lacking lateral setae, indusium with trichomes 3. **N. incana**

1. **Nephelea erinacea** (Karsten) Tryon, *Contr. Gray Herb.* 200: 40. 1970.

Cyathea erinacea Karsten, *Linnaea* 28: 453. 1857.
TYPE: Venezuela, (Mérida), Mérida, 2000 m, Karsten (holotype, not located; isotype, !).
Alsophila erinacea (Karsten) Conant, *J. Arnold Arbor.* 64: 371. 1983.

Scales on the abaxial side of the petiole with a dark apical seta and without lateral setae. **Lamina** usually coriaceous, predominantly 2-pinnate-pin-

Terrestrial. **Stem** stout, erect and arborescent, sometimes branched, with spines. **Leaves** monomorphic, with scales, especially on the croziers and petiole base, that are marginate and with a dark apical seta. **Petiole** with squaminate spines. **Lamina** 1–3-pinnate-pinnatifid, veins free. **Sori** round, usually at the fork of a vein, exindusiate or with a hemitelioid to sphaeropteroid indusium. **Spores** tetrahedral-globose, trilete, with prominent short to long ridges.

Nephelea is a tropical American genus of 17 species, with three in Peru. It ranges from southern Mexico and the West Indies, south to northern Argentina and southern Brazil, centering in the Greater Antilles where nine species occur.

The squaminate spines on the petiole are distinctive of *Nephelea*. They are blackish, have a very sharp tip, and at least on old leaves they may be broken off at their base.

Reference

GASTONY, G. J. 1973. A revision of the fern genus *Nephelea*. *Contr. Gray Herb.*, 203: 81–148.

natifid, usually abruptly reduced to a pinna-like apex, pinna-rachises not green-alate between the more distal sessile pinnules, veins with minute, whitish, stellate squamules abaxially. **Indusia** cyathiform to urceolate or rarely subsphaeropteroid, glabrous to densely scaly.

In forests at ca. 1200–2000 m, Amazonas to Huánuco and Pasco.

Costa Rica south to Venezuela, Colombia, and Bolivia.

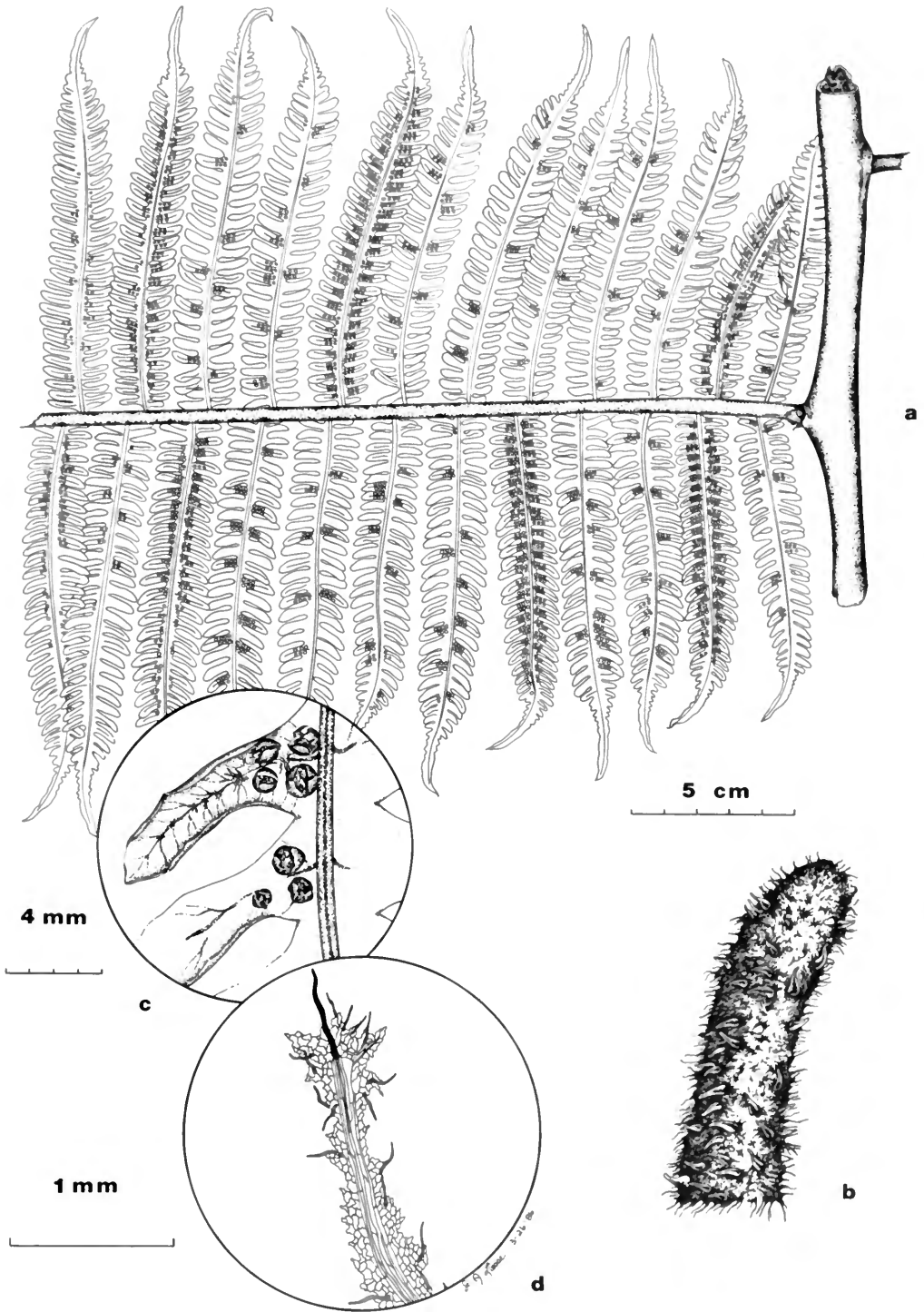


FIG. 21. *Nephelea cuspidata*: a, basal portion of pinna; b, expanding crozier; c, ultimate segments and sori; d, apex of petiole scale. (a from Cuatrecasas 14843, Colombia, F; b, d from Davis 1109, Bolivia, F; c from Rimachi 481, F.)

Nephelea erinacea var. *purpurascens* (Sodiolo) Gastony has the indusium densely and persistently scaly, rather than glabrous to sparsely scaly as in var. *erinacea*. It is presently known only from a few volcanoes in Ecuador.

Amazonas: Prov. Bongará, 5 km N of N end of lake Pomacocha, on road to Rioja, *Hutchison & Wright 6803* (GH, UC, USM). **Río Cenepa,** 10 km E of Huampami, *Berlin 219* (F, MO). **Huánuco:** *Macbride 4843* (F, US). **Pasco:** Prov. Oxapampa, trail to summit of Cordillera Yanachaga, *D. Smith et al. 7817, 7851* (F, MO). Prov. Oxapampa, Río San Alberto, *Smith & Pretel 7942* (USM).

2. *Nephelea cuspidata* (Kunze) Tryon, Contr. Gray Herb. 200: 40. 1970. **Figure 21.**

Cyathea cuspidata Kunze, *Linnaea* 9: 101. 1834. TYPE: Peru, (Loreto), Prov. Maynas, Feb. 1831, *Poeppig diar. 2286* (holotype, LZ destroyed; isotypes, B, P; photo, GH of P).

Alsophila cuspidata (Kunze) Conant, J. Arnold Arbor. 64: 371. 1983.

Scales on the abaxial side of the petiole with a dark apical seta and usually with numerous, smaller apical and lateral setae. **Lamina** usually papyraceous, predominantly 2-pinnate-pinnatifid, reduced to a pinna-like apex, pinna-rachises green-alate between the more distal sessile pinnules, veins with stellate trichomes or stellate squamules abaxially. **Indusia** rarely cyathiform, to urceolate to sphaeropteroid, glabrous or with stellate indument.

In low-elevation rain forests and less often in cloud forests, usually at 150–900 m, rarely to 2200 m. Amazonas and Loreto south to Puno.

Nicaragua to Panama, northern South America, south to Bolivia and Paraguay.

Nephelea cuspidata is the most widely distributed species of the genus. Among Peruvian species it is distinctive in having the scales of the petiole, especially on the abaxial side, with several dark apical setae and dark marginal setae.

Amazonas: Río Cenepa, ca. 5 km E of Chávez Valdivia, *Berlin 2066* (F, MO, UC). **Loreto:** Near mouth of Río Santiago, above Pongo de Manseriche, *Mexia 6197* (F, GH, MO, NY, UC, US). Alto Río Itaya, *Ll. Williams 3288* (F, GH, NY, US). **Huánuco:** Tingo María (as San Martín), *Allard 20618* (GH). **Junín:** E of Quimiri Bridge, near La Merced, *Killip & Smith 23986* (F, NY, US). **Ucayali:** Prov. Coronel Portillo, Cordillera Azul, *Young & Sullivan 705* (F, MO). **Ayacucho:** Estrella, between Huanta and Río Apurímac, *Killip & Smith 22654* (GH). **Cuzco:**

Prov. La Convención, Río Apurímac, above Boca del Tigre rapids, *Davis et al. 1304* (F, GH). **Madre de Dios:** Prov. Tambopata, SSW of Puerto Maldonado, *Barbour 5297* (F, MO). **Puno:** Prov. Carabaya, San Gabán, Puente Arica, *Vargas 18919* (GH).

3. *Nephelea incana* (Karsten) Gastony, Contr. Gray Herb. 203: 137. 1973.

Cyathea incana Karsten, Fl. Columb. 1: 75, t. 37. 1860. TYPE: Colombia, (Cundinamarca), Andes of Bogotá, 2500 m, *Lindig* (not located).

Alsophila incana (Karsten) Conant, J. Arnold Arbor. 64: 371. 1983.

Scales on the abaxial side of the petiole with a dark apical seta and without lateral setae, or rarely with an additional apical seta and lateral setae. **Lamina** rigidly papyraceous, 2-pinnate-pinnatifid, abruptly reduced to a pinna-like apex, pinna-rachises green-alate between the more distal sessile pinnules, veins glabrous abaxially, or with occasional trichomes. **Indusia** meniscoid to subsphaeropteroid, pubescent with rather soft and often crispate trichomes or trichomoid processes.

In primary forests at ca. 800–2400 m, Cajamarca and Amazonas south to Junín and Ucayali.

Colombia south to northwestern Argentina.

Cajamarca: Prov. Hualgayoc, *Soukup 3810* (F). Prov. Cutervo, San Andrés, *López et al. 6684* (GH, HUT). **Amazonas:** Laguna Pomacocha, NW of Jumbilla, *Soukup 2560a* (GH). **Pasco:** Prov. Oxapampa, Oxapampa, *León 502* (USM). **Junín:** *Esposito 670* (USM). Prov. Tarma, ca. 3 km SE of San Ramón, *Iltis & Iltis 249* (GH, USM). **Ucayali:** Prov. Coronel Portillo, Cordillera Azul, *Young & Sullivan 668* (F, MO).

IV. *Trichipteris*

Trichipteris Presl, Delic. prag. 1: 172. 1822. TYPE: *Trichipteris excelsa* Presl = *Trichipteris covadensis* (Raddi) Copel. **Figure 22.**

Terrestrial. Stem stout, erect and arborescent or rarely decumbent, lacking spines. **Leaves** monomorphic, with scales especially on the croziers and petiole base that are marginate and lack a dark, apical seta. **Petiole** lacking spines or with corticinate spines. **Lamina** 1-pinnate to 3-pinnate-pinnatifid, veins free. **Sori** round, often at the fork of a vein, exindusiate. **Spores** tetrahedral-globose, trilete, porate, verrucate, or finely echinate.

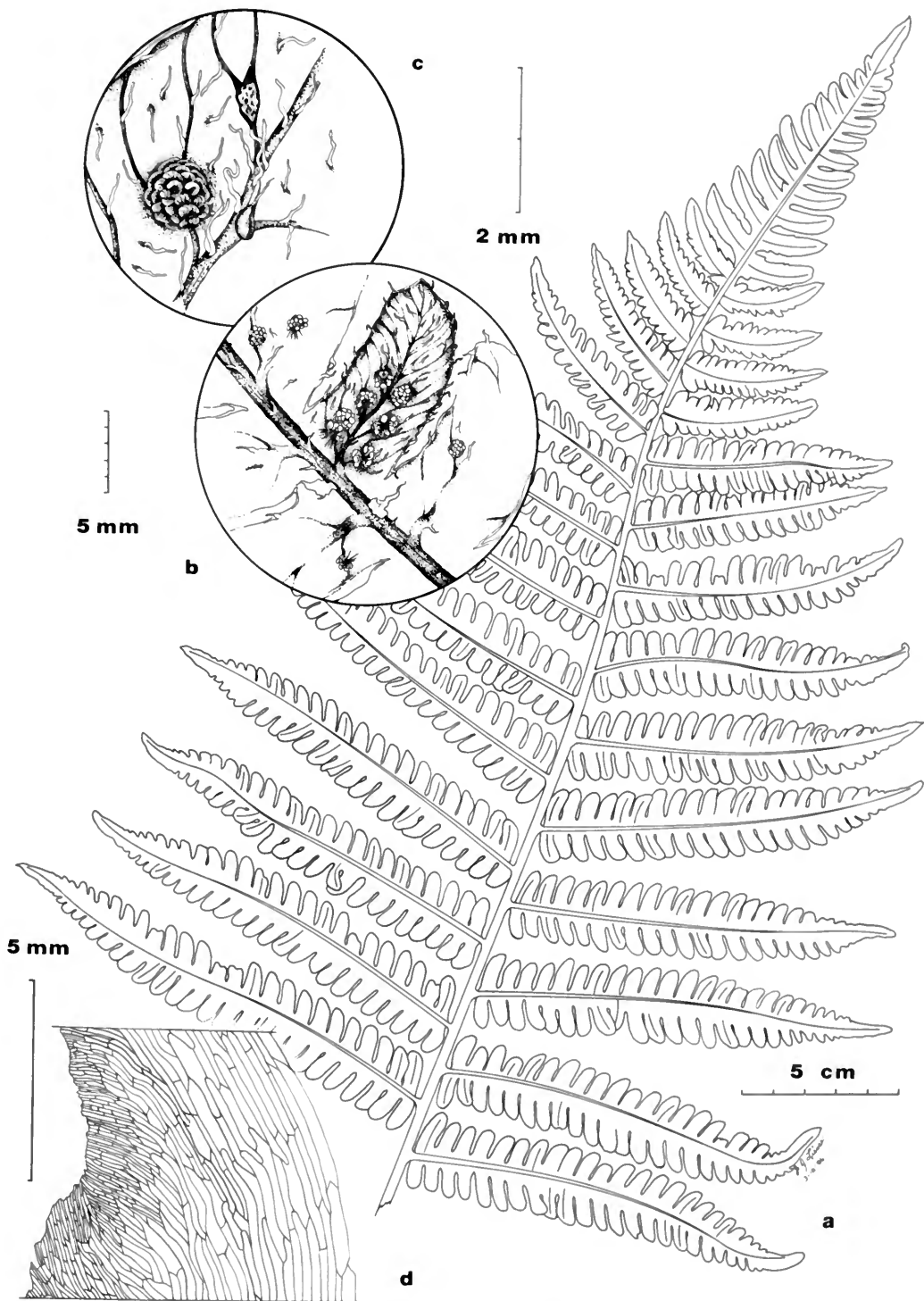


FIG. 22. *Trichipteris pubescens*: a, apical portion of lamina; b, fertile ultimate segments; c, portion of segment, showing a sorus and a receptacle; d, portion of petiole scale. (a from Buchtien 5304, Bolivia, F; b-c from Killip & Smith 24871, F; d from Ollgaard et al. 9106, Ecuador, F.)

An American genus of 55 species, from Mexico and the West Indies south to northern Argentina and southern Brazil. Fifteen species are in Peru, many formerly treated in the genus *Alsophila* because of the exindusiate sori.

The name is sometimes incorrectly spelled as *Trichopteris*. The International Code of Botanical Nomenclature, Art. 73.8 confines the use of an incorrect compounding form to epithets, thus excluding generic names. The original spelling *Trichopteris* should be maintained.

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- BARRINGTON, D. S. 1978. A revision of the genus *Trichopteris*. Contr. Gray Herb., 208: 3–91.
 RIBA, R. 1969 (1967). Revisión monográfica del complejo *Alsophila Swartziana* Mart. (Cyathea-ceae). Ann. Inst. Biol. Univ. Nac. Auton. México, ser. bot., 38(1): 61–100.

Key to Species of *Trichopteris*

- a. Lamina 1-pinnate-pinnatifid b
 - b. Pinnae sessile to short-stalked c
 - c. Petiole 15–30 cm long; lamina not or not much reduced at the base 10. **T. pubescens**
 - c. Petiole 3–6 cm long; lamina much reduced at the base 11. **T. phegopteroides**
 - b. Pinnae, especially below the lamina apex, very long-stalked 4. **T. latevagans**
- a. Lamina 2-pinnate or more complex d
 - d. Lamina mostly 3-pinnate-pinnatifid; pinnules abundantly short-pubescent adaxially, or petiole scales with a narrow, dark center stripe and broad white margins e
 - e. Leaf ca. 1.5 m long, pinnules with many small, bullate scales abaxially, abundantly short-pubescent adaxially; petiole scales nearly concolorous, brown with very narrow, lighter margins 7. **T. flava**
 - e. Leaf ca. 4 m long or more, pinnules with a few flattish scales abaxially, glabrate or with a few long trichomes adaxially; petiole scales with a narrow dark center stripe and broad whitish margins 9. **T. serpens**
 - d. Lamina 2-pinnate-shallowly lobed to 2-pinnate-pinnatisect; if rarely partly 3-pinnate-pinnatifid then sparingly long-pubescent adaxially and the petiole scales with narrow, lighter margins ... f
 - f. Lamina abruptly reduced at the apex g
 - g. Abaxial and lateral sides of the pinna-rachises lacking trichomes to (usually) sparingly pubescent with usually brown trichomes to 1 mm long h
 - h. Fertile and sterile veins simple; or if rarely forked (*T. procera*) then the ultimate lobes entire and the paraphyses much shorter than the sporangia i
 - i. Petiole aculeate, pinnules usually sessile, basal veins end above a sinus, paraphyses much shorter than the sporangia 1. **T. procera**
 - i. Petiole muricate to tuberculate, pinnules stalked, basal veins connivent to a sinus, paraphyses longer than the sporangia 13. **T. lechleri**
 - h. Fertile and sterile veins forked; ultimate lobes usually crenulate; paraphyses longer than the sporangia 5. **T. nigra**
 - g. Abaxial and lateral sides of the pinna-rachises usually densely pubescent with usually whitish trichomes mostly 1.5–2 mm long 6. **T. pilosissima**
 - f. Lamina gradually reduced at the apex j
 - j. Pinna-rachises with few to several sharp spines 12. **T. microdonta**
 - j. Pinna-rachises lacking spines k
 - k. Pinnae and pinnules mostly long-stalked; ultimate segments subobtusate to acuminate or apiculate 3. **T. kalbreyeri**
 - k. Pinnae mostly sessile to short-stalked; pinnules sessile to short-stalked or rarely long-stalked and then the ultimate segments obtuse l
 - l. Pinnules with prominent, large, flattish scales abaxially; páramo and subpáramo (elfin forest) 8. **T. frigida**

- l. Pinnules glabrate or pubescent abaxially or somewhat scaly with bullate or small flattish scales; montane forest and rain forest m
- m. Paraphyses shorter than the sporangia; petiole scales brown to dark brown, nearly concolorous; central and basal pinnae short- to long-stalked 2. **T. nigripes**
- m. Paraphyses longer than the sporangia n
- n. Petiole scales light brown to dark brown, with lighter margins; tertiary (ultimate) segments apically entire to coarsely toothed; central and basal pinnae short- to long-stalked (rarely sessile) 6. **T. pilosissima**
- n. Petiole scales dark brown to atropurpureous, usually with broad lighter margins, or whitish to light brown and concolorous; tertiary (usually ultimate) segments apically crenulate or denticulate; central and basal pinnae sessile o
- o. Petiole with long trichomes, soon glabrous, the caducous trichomes leaving a smooth petiole surface 14. **T. conjugata**
- o. Petiole with long trichomes, these more or less persistent, when deciduous leaving a hard base and a scabrous petiole surface 15. **T. tryonorum**

1. **Trichipteris procera** (Willd.) Tryon, Contr. Gray Herb. 200: 46. 1970.

- Polypodium procerum* Willd., Sp. pl. ed. 4, 5: 206. 1810. TYPE: Brazil, *Hoffmannsegg* (holotype, v!), Herb. Willd. 19717).
- Polypodium pungens* Willd., Sp. pl. ed. 4, 5: 206. 1810, a synonym of *Trichipteris procera* (Willd.) Tryon by Barrington, Contr. Gray Herb. 208: 23. 1978.
- Alsophila procera* (Willd.) Desv., Mém. Soc. Linn. Paris 6: 319. 1827.
- Alsophila dombeyi* Desv., Mém. Soc. Linn. Paris 6: 320. 1827. TYPE: Peru, (Huánuco), Cochero, *Dombey* (holotype, Herb. Desv. P!; isotype, P!).
- Alsophila infesta* Kunze, Linnaea 9: 98. 1834. TYPE: Peru, (San Martín), Tocache, Río Huallaga, *Poeppig* (holotype, LZ destroyed; isotype, v!).
- Alsophila armigera* Kunze, Linnaea 9: 98. 1834. TYPE: Peru, (Huánuco), Ventanilla de Cassapi, Jul. 1829, *Poeppig* (holotype, LZ destroyed; isotypes, MO!, P!; photos, GH, US of P).
- Alsophila pycnocarpa* Kunze, Linnaea 9: 97. 1834. TYPE: Peru, (Huánuco), Pampayacu, Jul. 1829, *Poeppig* (holotype, LZ destroyed; isotype, *Poeppig* 201, v!).
- Alsophila peruviana* Klotzsch, Linnaea 20: 441. 1847. TYPE: Peru, (Junín), Tarma, *Ruiz Herb.* 66 (holotype, v!).
- Alsophila pterorachis* Baker, Syn. fil., ed. 2, 456. 1874. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4717* (holotype, k!).
- Alsophila floribunda* Baker, Syn. fil., ed. 2, 458. 1874. TYPE: Peru, (San Martín), Cerro Campana, *Spruce 4715* (holotype, k; isotype, P!).
- Cyathea pungens* (Willd.) Domin, Pterid. 263. 1929.
- Cyathea willdenowiana* Domin, Acta Bot. Bohemica 9: 171. 1930, nom. nov. for *Polypodium procerum* Willd., not *Cyathea procera* Brause.
- Trichipteris infesta* (Kunze) Tryon, Contr. Gray Herb. 200: 45. 1970.
- Trichipteris dombeyi* (Desv.) Barr., Contr. Gray Herb. 208: 27. 1978.

Petiole lacking trichomes, the scales dark brown or with whitish margins. **Lamina** 2-pinnate-pinnatifid, abruptly reduced at the apex, central and basal pinnae short- to long-stalked, their pinnules sessile to short-stalked, abaxial and lateral sides of the pinna-rachises sparingly short-aculeate or lacking spines, glabrate or with scattered to rather numerous brownish trichomes. **Pinnules** obtuse to acuminate, glabrate or with some small scales and (or) trichomes abaxially, ultimate segments obtuse to subacute, fertile veins simple or rarely forked. **Paraphyses** much shorter than the sporangia.

In original rain forests or cloud forests, often in secondary forests or in other partly disturbed vegetation, 100–1500 m, Amazonas and San Martín south to Puno.

West Indies; South America south to northern Brazil, Peru and Bolivia.

Trichipteris dombeyi, although recognized by Barrington, is very close to *T. procera* and is here included within it. *Trichipteris procera* has an extensive distribution and is quite variable as the many synonyms described from Peru imply.

Amazonas: Prov. Bagua, Río Marañón, above Cascadas de Mayasi, *Wurdack 1825* (GH). **San Martín:** Campana, near Tarapoto, *Spruce 4323bis* (GH). Prov. Rioja, Rioja, *Ferreya 18455* (USM). **Loreto:** Gamitanacocha, Río Mazán, *J. Schunke 269* (F, GH, NY, UC). Iquitos, *Mexia 6497* (F, GH, MO, UC, US). **Huánuco:** Tingo María, *Tryon & Tryon 5256* (F, GH). Prov. Huánuco, near confluence of Río Cayumba with Huallaga, *Mexia 8293* (F, GH, MO, NY, UC, US). **Pasco:** Prov. Oxapampa, Eneñas, *Soukup 6706* (GH). Prov. Oxapampa, Río Palcazú, *León 702* (F). **Junín:** Above San Ramón, *Killip & Smith 24541* (F, GH, NY, US). **Ucayali:** Prov. Coronel Portillo, Dist. Padre Abad (as Loreto), *J. Schunke 9852* (MO). **Cuzco:**

Prov. Paucartambo, Kosñipata-Santa Ines, *Vargas 11318* (GH). **Madre de Dios:** Pantiacolla, *Gentry et al. 27351* (UC). **Puno:** Prov. Carabaya, Hacienda Palmares, *Vargas 16145* (GH).

2. *Trichipteris nigripes* (C. Chr.) Barr., *Rhodora* 78: 4. 1976.

Alsophila nigripes C. Chr., *Index fil.* 45. 1905, *nom. nov.* for *Alsophila melanopus* Hooker (not Hassk.) and with the same type.

Alsophila melanopus Hooker, *Syn. fil.* 37. 1866 (not Hassk., 1855). TYPE: Ecuador, Chimborazo, *Spruce 5742* (holotype, k!; isotype, p!).

Cyathea nigripes (C. Chr.) Domin, *Pterid.* 263. 1929.

Petiole lacking trichomes, the scales brown to dark brown, nearly concolorous. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, gradually reduced at the apex, central and basal pinnae short- to long-stalked, their pinnules sessile to nearly short-stalked, pinna-rachises lacking spines, the abaxial and lateral sides glabrous or with a few to sometimes many light brown to brown, rarely whitish trichomes. **Pinnules** obtuse to attenuate, glabrous or with short to rather long, mostly scattered trichomes abaxially, ultimate segments obtuse to acute, fertile veins simple or usually forked. **Paraphyses** shorter than the sporangia.

In primary forests and somewhat disturbed forests, wet ravines, 200–800 m, Amazonas, San Martín and Loreto south to Madre de Dios.

Costa Rica south to Peru.

Recent collections have shown that *Trichipteris nigripes* var. *brunnescens* of Colombia and Ecuador, with well-developed petiole spines, pubescent pinna-rachises, and sessile pinnules, is only one extreme within a spectrum of variation.

Amazonas: Prov. Bagua, Dist. Senepa, *Tillet 672-115* (GH). **San Martín:** Prov. Mariscal Cáceres, Puente Palo Blanco, Río Tocache, *Plowman et al. 11354* (GH). **Loreto:** Above Pongo de Manseriche, *Mexia 6191* (F, GH). **Huánuco:** Hills E of Tingo María, *Croat 21153* (MO). **Ucayali:** Km 86 on Pucallpa-Tingo María road, *Smith et al. 1179* (GH). **Cuzco:** Prov. Paucartambo, Cosñipata valley, *Wachter et al. 221* (F, GH). **Madre de Dios:** Prov. Tumbopata, SSW of Puerto Maldonado, *Barbour 4934* (MO).

3. *Trichipteris kalbreyeri* (Baker) Tryon, *Contr. Gray Herb.* 200: 45. 1970.

Alsophila kalbreyeri Baker, *Summary new ferns* 9. 1892, *nom. nov.* for *Alsophila podophylla* Baker (not Hooker) and with the same type.

Alsophila podophylla Baker, *J. Bot.* 19: 202. 1881.

TYPE: Colombia, Antioquia, *Kalbreyer 1375* (holotype, k; isotype, b!).

Cyathea kalbreyeri (Baker) Domin, *Pterid.* 262. 1929.

Petiole lacking trichomes, the scales atropurpureous or with lighter margins. **Lamina** 2-pinnate-pinnatifid, rather gradually reduced at the apex, pinnae and most of the pinnules long-stalked, pinna-rachises lacking spines, the abaxial and lateral sides glabrous or with some short, brownish trichomes. **Pinnules** acute to acuminate, glabrate abaxially, ultimate segments subobtuse, acute, acuminate or subapiculate, fertile veins simple or forked. **Paraphyses** shorter than the sporangia.

In forests, 1200–1600 m, San Martín.

Colombia south to Bolivia.

San Martín: Zepelacio, near Moyobamba, *Klug 3256* (F, GH). Monte Campana, near Tarapoto, *Spruce 4330* (GH, NY).

4. *Trichipteris latevagans* (Baker) Tryon, *Contr. Gray Herb.* 200: 45. 1970.

Alsophila latevagans Baker, *J. Bot.* 19: 203. 1881.

TYPE: Colombia, Antioquia, *Kalbreyer 1327* (holotype, k).

Cyathea latevagans (Baker) Domin, *Pterid.* 262. 1929.

Petiole lacking trichomes, the scales at the base brown, nearly concolorous. **Lamina** 1-pinnate-pinnatifid, gradually reduced at the apex, pinnae very long-stalked, especially the central and lower ones, their apex acute. **Pinnules** glabrous or somewhat pubescent on the margins, obtuse to subacute, fertile veins forked. **Paraphyses** shorter than to longer than the sporangia.

In pajonal vegetation, 2200 m, San Martín.

Colombia and Peru.

The very long-stalked pinnatifid pinnae and the atropurpureous petiole and rachis are distinctive features of this species.

San Martín: Prov. Rioja, Pedro Ruíz-Moyobamba, *D. Smith 4799* (GH).

5. *Trichipteris nigra* (Mart.) Tryon, *Contr. Gray Herb.* 200: 46. 1970.

Alsophila nigra Mart., *Icon. pl. crypt.* 71. 1834. TYPE: Brazil, Prov. Rio Negro, Rio Japurá, *Martius* (holotype, not located; isotypes, b!, k).

- Alsophila lasiosora* Kuhn, *Linnaea* 36: 157. 1869. TYPE: Peru, *Spruce 4349* (holotype, v; isotypes, GH!, P!, US!).
- Alsophila tarapotensis* Rosenst., *Repert. Spec. Nov. Regni Veg.* 7: 291. 1909. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4349* (holotype, P!; isotypes, GH!, US!).
- Cyathea lasiosora* (Kuhn) Domin, *Pterid.* 262. 1929.
- Cyathea primaeva* Domin, *Pterid.* 263. 1929, *nom. nov.* for *Alsophila nigra* Mart., not *Cyathea nigra* Fourm.
- Alsophila killipii* Maxon, *Amer. Fern J.* 32: 58. 1942. TYPE: Peru, Loreto, between Yurimaguas and Balsapuerto, *Killip & Smith 28133* (holotype, us!; isotype, F!; numerous paratypes cited).
- Trichipteris lasiosora* (Kuhn) Tryon, *Contr. Gray Herb.* 200: 45. 1970.

Petiole lacking trichomes, the scales brown or dark brown with lighter margins. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, abruptly reduced at the apex, pinnae short- to long-stalked, pinna-rachises lacking spines, the abaxial and lateral sides glabrate to somewhat pubescent, sometimes with rather numerous, long, mostly brown to light brown trichomes. **Pinnules** acuminate to attenuate, with usually scattered, short to moderately long trichomes and some small scales abaxially, ultimate segments obtuse to acute, fertile veins forked. **Paraphyses** longer than the sporangia.

In wet primary forests, 100–1100 m, Amazonas south to Madre de Dios. *Dudley 13532*, from Huánuco, is a juvenile plant, probably of *Trichipteris nigra*; it was collected in elfin forest at 1850 m.

Venezuela and northern Brazil, Colombia south to Bolivia.

The few collections with long trichomes on the abaxial and lateral sides of the pinna-rachises and the abaxial side of the segments suggest that this species may not be wholly distinct from *Trichipteris pilosissima*.

Amazonas: Prov. Bagua, Chiriaco to Puente Venezuela, *Barbour 4465* (MO). **San Martín:** Prov. Mariscal Cáceres, Tocache Nuevo, *J. Schunke V. 4781* (F, MO, US), *5644* (GH). **Loreto:** Sierra del Pongo, *Mexia 6270* (GH, UC). Prov. Maynas, Mishana, Río Nanay, *Gentry et al. 21109* (F, MO). **Huánuco:** Tingo María (as San Martín), *Allard 20607* (GH, US). **Pasco:** Prov. Oxapampa, Valle del Palcazú, *León 703* (GH). Prov. Oxapampa, Río Iscozacín, *Gentry et al. 41911* (USM). **Junín:** Santa Rosa, Pichis Trail, *Killip & Smith 26169* (GH, NY). **Ucayali:** La Divisoria (as Huánuco), *Gentry et al. 18874* (USM). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, *Foster et al. 10703* (F, GH).

6. *Trichipteris pilosissima* (Baker) Barr., *Contr. Gray Herb.* 208: 76. 1978.

Alsophila pilosissima Baker, *Syn. fil.*, ed. 2, 457. 1874. TYPE: Peru, (San Martín), Mt. Campana, *Spruce 4322* (holotype, K!; isotype, BR; photos, GH of K, GH, US of BR).

Cyathea pilosissima (Baker) Domin, *Pterid.* 262. 1929.

Petiole sometimes with abundant short to moderately long trichomes, the scales light brown to dark brown with lighter, sometimes nearly whitish, margins. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, gradually to abruptly reduced at the apex, central and basal pinnae short- to long-stalked, rarely sessile, their pinnules, especially toward the base, sessile to usually short-stalked, pinna-rachises lacking spines, the abaxial and lateral sides with abundant long, mostly whitish trichomes. **Pinnules** obtuse to attenuate, with long, mostly whitish trichomes abaxially, ultimate segments obtuse to subacute, the apex entire to coarsely toothed, fertile veins simple or usually forked. **Paraphyses** longer than the sporangia.

In primary and secondary forests, rarely in seasonally inundated forests, 50–800 m, Tumbes, Amazonas, and Loreto, south to Cuzco and Madre de Dios.

Panama south to Peru.

This species is close to *Trichipteris nigra*, and their relationship requires further study. At the present time it is maintained as a distinct species, although there seems to be intergradation with *T. nigra*.

Tumbes: Cerro Alegría, *Canchaya 5169* (GH). **Amazonas:** Prov. Bagua, Quebrada Chuiivi, *Wurdack 1927* (GH). **San Martín:** Prov. Mariscal Cáceres, Tocache, *Plowman & Kennedy 5790* (F, GH). **Loreto:** Prov. Maynas, Mishana, *López et al. 8677* (HUT). Prov. Maynas, Río Ampiyacu, *Plowman et al. 6601* (F, GH, US). **Huánuco:** E of Tingo María, *Croat 21153* (MO, UC). **Pasco:** Prov. Oxapampa, near confluence of Río Palcazú and Río Iscozacín, *Smith & Franzen 1921* (F, MO). **Junín:** Near La Merced, *Killip & Smith 23922* (F). **Ucayali:** Vicinity of Aguaytía (as Loreto), *Croat 20952* (F, MO, UC). **Cuzco:** Prov. Paucartambo, Cosñipata valley, *Wachter et al. 156* (F, GH). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, *Foster et al. 10701* (F, GH).

7. *Trichipteris flava* Tryon, *sp. nov.*

Petiolus squamis brunneis vel atrobrunneis. Lamina ca. 1 m longa tripinnata vel tripinnato-pinnatifida. Pinnulae acutae supra breviter pubescentes subter squamulis multis pallide brunneis. Soris deest.

Petiole lacking trichomes, the scales brown, concolorous or with very narrow lighter margins. **Lamina** 3-pinnate-pinnatifid nearly throughout, gradually reduced at the apex, pinnae moderately long-stalked, pinna-rachises lacking spines, the abaxial and lateral sides with scattered, short to long trichomes. **Pinnules** short-stalked, acute, with many small, light brown, bullate scales abaxially, ultimate segments mostly acute, many falcate. **Sori** absent.

HOLOTYPE—Peru, Dept. Huánuco, above Chinchao, Tingo María to Chinchao, 1 Aug. 1965, *D. Soejarto 1432* (GH 2 sheets).

Only known from the type collection from an exposed hillside at 2500 m in Huánuco.

Endemic to Peru.

The stem is reported on the label as slender and ca. 75 cm tall, the leaves ca. 1.5 m long, and the cut stem exuding yellow sap. Although the collection is sterile, it very probably represents a species of *Trichipteris*. The lamina complexity and the abundant short-pubescent on the upper surface of the segments amply distinguish the species.

8. *Trichipteris frigida* (Karsten) Tryon, Contr. Gray Herb. 200: 45. 1970.

Alsophila frigida Karsten, Fl. Columb. 1: 61, t. 30. 1859. **TYPE**: Colombia, (Cundinamarca), Andes of Bogotá, 2600 m, *Karsten* (holotype, not located; isotype, B!).

Cyathea frigida (Karsten) Domin, Pterid. 262. 1929.

Petiole lacking trichomes, the scales light to dark brown usually with rather narrow lighter margins. **Lamina** 2-pinnate-pinnatifid, rarely partly 3-pinnate-pinnatifid, gradually reduced at the apex, pinnae sessile to long-stalked, pinna-rachises lacking spines, the abaxial and lateral sides with large flattish scales or their hard bases, with scattered brown to light brown trichomes or often with dense, caducous, slender, matted, whitish trichomes or strongly dissected scales. **Pinnules** sessile to short-stalked, obtuse to rarely attenuate, with prominent, large flattish scales abaxially, ultimate segments obtuse to subacute, fertile veins forked. **Paraphyses** shorter than the sporangia or of the same length.

Growing in moist scrub forests, 2500–3500 m, Amazonas south to Junín.

Venezuela and Colombia south to Peru.

Trichipteris frigida typically grows at higher altitudes than other species of the genus.

Amazonas: Prov. Chachapoyas, Molinopampa-Diosan pass, *Wurdack 1654* (F, GH, US). **Huánuco**: Cerros al sudoeste de Monzón, *Weberbauer 3389* (USM). Huánuco-Tingo María road, near Carpish, *Gentry & Smith 44863* (F, MO). **Pasco**: Prov. Oxapampa, Santa Bárbara, *D. Smith 8172* (F, MO). San Gotardo, *van der Werff et al. 8562* (MO, UC). **Junín**: Huacapistana, *Weberbauer 2272* (P, USM).

9. *Trichipteris serpens* Tryon, *sp. nov.*

Petiolus deest. **Pedum** circinatum sine trichomata, squamis centralibus fuscatis angustis marginatis late niveis. **Lamina** ca. 3–4 m longa tripinnato-pinnatifida pinnis pinnulisque longe petiolulatis. **Pinnulae** acuminatae subter squamis paucis brunneis complanatis. **Venae** fertiles furcatae. **Paraphyses** longiores quam sporangia.

Petiole lacking trichomes, the scales with a dark, narrow central stripe and broad whitish margins (characters from croziers). **Lamina** 3-pinnate-pinnatifid nearly throughout, apex absent, pinnae long- to very long-stalked, pinna-rachises lacking spines, the abaxial and lateral sides somewhat appressed pubescent and scaly. **Pinnules** short- to long-stalked, acuminate, glabrate or with a few large, flattish, brown scales abaxially, fertile veins forked. **Paraphyses** longer than the sporangia.

TYPE—Peru, Dept. Cuzco, Prov. La Convención, Cordillera Vilcabamba, 10 July 1968, *T. R. Dudley 10949* (holotype, NA 2 sheets; isotype, GH 2 sheets).

Known only from the type collection in elfin forest at 2900 m in Cuzco.

Endemic to Peru.

The leaves of this new species are unusual: they are 4–6 m long, or more, and trail or are scandent over low vegetation. The scales of the croziers, which will in part become petiole scales, are quite different from those of the related *Trichipteris frigida*.

10. *Trichipteris pubescens* (Baker) Tryon, Contr. Gray Herb. 200: 46. 1970. **Figure 22.**

Alsophila pubescens Baker, Syn. fil. 449. 1868. **TYPE**: Peru, (San Martín), Mt. Guayrapurima, Tarpoto, *Spruce 4712* (holotype, K; isotypes, GH!, NY!, P!).

Cyathea bipinnatifida (Baker) Domin, Pterid. 262. 1929.

Cyathea pubens Domin, Pterid. 263. 1929, *nom. nov.* for *Alsophila pubescens* Baker, not *Cyathea pubescens* Kuhn.

Petiole lacking spines, the scales light brown with lighter margins. **Lamina** 1-pinnate-pinnatifid, gradually reduced at the apex, pinnae sessile to short-stalked, with abundant, short to moderately long trichomes abaxially or rarely these few, ultimate segments obtuse, fertile veins simple or forked. **Paraphyses** as long as the sporangia.

In montane rain forests, cloud forests, or ceja de la montaña, 850–2200 m, Amazonas south to Puno.

Guyana, Venezuela, and Colombia south to Bolivia.

This species and the next are the only ones in Peru with a 1-pinnate-pinnatifid lamina. *Trichipteris pubescens* is widely distributed and, although variable, is characterized by the features mentioned in the key.

Amazonas: Prov. Bagua, La Peca, *Barbour 2764* (MO, UC), 3987 (F, MO). **San Martín:** Prov. Rioja, Pedro Ruíz-Moyobamba, *D. Smith 4798* (GH). **Huánuco:** Cerros del Sira, Río Lllallapichis watershed, *Dudley 13371, 13413, 13538* (GH). **Pasco:** Prov. Oxapampa, Palcazú, *D. Smith 8553* (F, MO). **Junín:** Above San Ramón, *Killip & Smith 24871* (F, US). **Ucayali:** Cerca a La Divisoria (as Loreto), *Ferreyra 1071* (GH, USM). **Ayacucho:** Prov. La Mar, between Huanhuachayo and Puncu, Cordillera Central, *Dudley 11941* (GH). **Cuzco:** Prov. La Convención, Río Mapiitunuari, *Dudley 10159B* (GH). **Puno:** San Gabán, *Lechler 2190* (K). Prov. Sandía, San Juan del Oro, *Ferreyra 16678, 16701* (GH, USM), *16704* (GH).

11. *Trichipteris phegopteroides* (Hooker) Tryon, Contr. Gray Herb. 200: 46. 1970.

Alsophila phegopteroides Hooker, Syn. fil. 32. 1865. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4020* (holotype, K; isotypes, P!, US!). *Cyathea phegopteroides* (Hooker) Domin, Pterid. 263. 1929.

Petiole pubescent, also bearing dark brown scales with lighter brown margins. **Lamina** 1-pinnate-pinnatifid, gradually reduced at the apex, pinnae sessile, rachis scaly and densely pubescent with long trichomes. **Pinnule-segments** obtuse, pubescent adaxially and abaxially, fertile veins forked. **Paraphyses** shorter than the sporangia.

Growing at 350–1750 m, in San Martín and (probably) Puno.

Endemic to Peru.

This species has a small leaf less than 1 m long and a very short petiole ca. 3–6 cm long; the basal pinnae are much reduced.

San Martín: Mt. Guayrapurima, near Tarapoto, *Spruce 4028* (GH, NY). Prov. Rioja, Pedro Ruíz-Moyobamba, *D. Smith 4452* (GH). **Puno(?):** *Lechler* (F).

12. *Trichipteris microdonta* (Desv.) Tryon, Contr. Gray Herb. 200: 46. 1970.

Polypodium microdontum Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 5: 319. 1811. TYPE: "America australis" (holotype, Herb. Desv. P!; photos, GH, US).

Alsophila microdonta (Desv.) Desv., Mém. Soc. Linn. Paris 6: 319. 1827.

Cyathea microdonta (Desv.) Domin, Pterid. 263. 1929.

Petiole lacking trichomes, the scales light brown to dark brown, concolorous. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, gradually reduced at the apex central and basal pinnae short to long-stalked, their pinnules sessile to short-stalked, pinna-rachises with few to several sharp spines, their abaxial and lateral sides glabrate or with usually numerous short to moderately long trichomes. **Pinnules** acute to attenuate, with few to usually many, short to usually long trichomes abaxially, ultimate segments obtuse to acute, fertile veins forked. **Paraphyses** longer than the sporangia or the same length.

In primary forests or disturbed forests, 100–750 m, San Martín, Loreto, and Cuzco.

Mexico and the Greater Antilles, south to Peru and Brazil.

The sharp spines on the pinna-rachises are a distinctive feature of *Trichipteris microdonta*. Rarely, they may be few and rather short, as in *Luna 895*.

San Martín: Near Tarapoto, *Spruce 4726* (NY). **Loreto:** Mishuyacu, near Iquitos, *Killip & Smith 29876* (F, GH, NY). Quistococha, 12 km from Iquitos, *Luna 895* (F). Río Itaya, Iquitos, *Tryon & Tryon 5172* (F, GH). **Cuzco:** Prov. Quispicanchi, Quince Mil, *Vargas 15340* (GH).

13. *Trichipteris lechleri* (Mett.) Tryon, Contr. Gray Herb. 200: 45. 1970.

- Alsophila lechleri* Mett., Fil. lechl. 2: 28. 1859. TYPE: Peru, (Puno), Tatanara, *Lechler 2532* (holotype, Herb. Mett. B!; photo, GH).
- Alsophila ulei* Christ, Hedwigia 44: 367. 1905. TYPE: Peru, (Amazonas), Cerro Ponasa, *Ule 6901* (holotype, P?; isotypes, B!, L; photos, GH of B, US of L).
- Cyathea subtropica* Domin, Pterid. 263. 1929, *nom. nov.* for *Alsophila lechleri* Mett., not *Cyathea lechleri* Mett.
- Cyathea ulei* (Christ) Domin, Acta Bot. Bohemica 9: 168. 1930.

Petiole lacking trichomes, the scales dark brown to atropurpureous with rather broad, lighter margins. **Lamina** 2-pinnate-shallowly lobed to 2-pinnate-pinnatifid, abruptly reduced at the apex, central and basal pinnae long-stalked, their pinnules, especially toward the base, long-stalked, pinna-rachises lacking spines, abaxial and lateral sides glabrate. **Pinnules** acuminate to attenuate, glabrate abaxially, lobes or ultimate segments more or less obtuse, fertile veins simple. **Paraphyses** longer than the sporangia.

Wet forests and cloud forests, 500–1300 m, Amazonas, Huánuco, Junín, and Puno.

Venezuela and Colombia south to Bolivia.

Trichipteris lechleri usually has the pinnules rather shallowly pinnatifid or lobed and the basal veins on an ultimate segment are connivent to a sinus.

Huánuco: Cerros del Sira, Río Lullapichis watershed, *Dudley 13047, 13214, 13220* (GH). **Junín:** Prov. Satipo, S of Chequitavo, *D. Smith 5130* (F).

14. *Trichipteris conjugata* (Hooker) Tryon, Contr. Gray Herb. 200: 45. 1970.

Alsophila conjugata Hooker, Syn. fil. 37. 1866. TYPE: Ecuador, Chimborazo, *Spruce 4745* as published, *5745* is correct (holotype, K; frag., US!).

Petiole with long trichomes, soon glabrous, the caducous trichomes leaving a smooth surface, the scales dark brown to atropurpureous with usually rather broad, light brown to whitish margins, or light brown to whitish and concolorous, the margins slightly or not dark-denticulate apically. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, gradually reduced at the apex, pinnae sessile, pinna-rachises lacking spines, the abaxial and lateral sides with usually abundant, long, whitish to brownish trichomes. **Pinnules** sessile, acuminate to mostly attenuate, with rather sparse to usually

abundant long trichomes abaxially, ultimate segments obtuse to acute, the apex denticulate, fertile veins forked. **Paraphyses** longer than the sporangia.

In montane forests, 700–2000 m, Huánuco south to Cuzco.

Venezuela and Colombia south to Bolivia.

Trichipteris conjugata and the next species, *T. tryonorum*, are members of a group of some 13 species with dark denticulate margins on the petiole scales. The dark denticulate margins, however, are often absent in the two Peruvian species.

Huánuco: Prov. Leoncio Prado, *Young & Sullivan 867* (F, MO). Prov. Huánuco, Yuracyaca, *Ridoutt* in 1943 (GH, US, USM). **Junín:** Above San Ramón, *Killip & Smith 24643* (F, GH, US). **Ucayali:** Prov. Coronel Portillo, La Divisoria, *Aguilar 848* (F, GH). **Ayacucho:** Prov. La Mar, between Huanhuachayo and Punccu, *Dudley 11943* (F, GH). **Cuzco:** Prov. Urubamba, near town of Machu Picchu, Río Urubamba, *Tryon & Tryon 5411* (GH, USM). Machu Picchu, *Iltis et al. 1024* (GH, UC).

15. *Trichipteris tryonorum* (Riba) Tryon, Contr. Gray Herb. 200: 46. 1970.

Alsophila tryonorum Riba, Rhodora 69: 66. 1967. TYPE: Colombia, Cundinamarca, Cuesta "Fusugasugá," (Fusagasugá), *Cuatrecasas 8036* (holotype, US!).

Petiole with long trichomes, these persistent or deciduous and then leaving a hard base and a scabrous petiole surface, the scales dark brown to atropurpureous, usually with broad, lighter margins, or whitish to light brown and concolorous, the margins slightly or not dark denticulate. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, gradually reduced at the apex, pinnae sessile, pinna-rachises lacking spines, the abaxial and lateral sides with usually abundant long, whitish to brownish trichomes. **Pinnules** sessile, acute to usually acuminate or attenuate, with usually abundant long trichomes and often some whitish bullate scales abaxially, ultimate segments acute to obtuse, the apex crenulate to coarsely denticulate, fertile veins forked. **Paraphyses** longer than the sporangia.

Growing at 200–2400 m, Amazonas and Pasco. Venezuela, Colombia, south to northern Peru.

This species is especially distinguished from *Trichipteris conjugata* by the persistent trichomes on the petiole, or their hard bases that provide a sca-

brous surface when they fall off. *Trichipteris conjugata* has caducous trichomes on the petiole that leave a smooth surface.

Amazonas: Prov. Bagua, Cordillera de Colán, SE of La Peca, *Barbour 3750* (MO). **Pasco:** Prov. Oxapampa, Río Yamaquizu valley, *D. Smith 4207* (GH).

V. *Cyathea*

Cyathea Sm., *Mém. Acad. Roy. Sci. Turin* 5: 416. 1793. TYPE: *Cyathea arborea* (L.) Sm. (*Polypodium arboreum* L.). **Figure 23.**

Hemitelia R. Br., *Prodr.* 158. 1810. TYPE: *Hemitelia multiflora* (Sm.) Sprengel = *Cyathea multiflora* Sm.

Terrestrial. Stem stout, erect and arborescent, rarely very slender and scandent or short, lacking spines. Leaves monomorphic to somewhat di-

morphic, with scales, especially on the croziers and the petiole base, that are marginate and lack a dark apical seta. **Petiole** lacking spines or with corticin-ate spines. **Lamina** 1–4-pinnate, veins free or rarely anastomosing without included veinlets. **Sori** round, often at the fork of a vein, with a hemiteloid to sphaeropteroid indusium. **Spores** tetrahedral-globose, trilete, nearly smooth, porate, verrucate or minutely echinate.

Cyathea is a tropical American genus of ca. 40 species, with 14 of them in Peru. The genus is sometimes treated in a broad sense to include nearly all of the family Cyatheaceae. Here it is restricted to a natural American group.

Reference

TRYON, R. 1976. A revision of the genus *Cyathea*. *Contr. Gray Herb.*, 206: 19–98.

Key to Species of *Cyathea*

- a. Indusia hemiteloid b
- b. Sori costal 3. *C. vilhelmii*
- b. Sori medial to submarginal c
- c. Basal veins straight or nearly so, ending above a sinus d
- d. Ultimate segments with simple fertile veins and usually entire (rarely coarsely dentate), or with forked fertile veins and coarsely dentate 1. *C. multiflora*
- d. Ultimate segments with forked fertile veins, entire or finely dentate to strongly crenate 2. *C. andina*
- c. Basal veins curved, connivent to a sinus, sometimes forming costal areolae ... 4. *C. petiolata*
- a. Indusia sphaeropteroid, sometimes evanescent and then the apical umbo or a basal remnant is usually present e
- e. Petiole scales either whitish to light brownish and concolorous or nearly so, or discordantly bicolorous with whitish to brownish margins; petiole scurf whitish to light brown, or rarely brown at the base of the petiole f
- f. Lamina 2-pinnate-pinnatifid or 3-pinnate only at the base of the pinnae g
- g. Large scales of the petiole scurf flattish h
- h. Pinnae and pinnules mostly long-stalked 5. *C. divergens*
- h. Pinnae and pinnules sessile or nearly so 7. *C. ruiziana*
- g. Large scales of the petiole scurf mostly, or many of them, crested 6. *C. pallescens*
- f. Lamina 3–4-pinnate nearly throughout i
- i. Tertiary segments entire or basally 2-lobed; bullate scales on the abaxial side of the pinnule-rachis dark brown 8. *C. microphylla*
- i. Tertiary segments with up to usually 5 or more segments or lobes; bullate scales on the abaxial side of the pinnule-rachis light brown 9. *C. multisegmenta*
- e. Petiole scales either brown and nearly concolorous, or (sometimes narrowly) concordantly bicolorous with light brown to brown margins; petiole scurf brown or absent j
- j. Lamina 2-pinnate-pinnatifid or 3-pinnate only at the base of central and basal pinnae; larger ultimate segments usually ca. 10 mm long k
- k. Petiole scales light brown to brown, concolorous to narrowly bicolorous; pinnules usually

with few or no scales abaxially, abundantly to moderately long-pubescent 10. *C. delgadii*

k. Petiole scales with a reddish brown to usually dark reddish brown or atropurpureous body, or with dark areas or streaks, bicolorous with sometimes narrow margins 11. *C. caracasana*

l. Petiole aculeate to abundantly, rarely sparsely, muricate, with abundant, sometimes caducous scurf 11. *C. caracasana*

l. Petiole nearly or quite smooth, or with some scattered tubercles, scurf absent or sparse m

m. Pinnules sessile to short-stalked 12. *C. lechleri*

m. Pinnules long-stalked 13. *C. ebenina*

j. Lamina 3-pinnate nearly throughout; larger ultimate segments ca. 5 mm long 14. *C. dudleyi*

1. *Cyathea multiflora* Sm., Mém. Acad. Roy. Sci. (Turin) 5: 416. 1793. TYPE: "Amer. merid.," *R. Shakespeare* (holotype, Herb. Banks BM; photos, GH, NY, US).

Hemitelia multiflora (Sm.) Sprengel, Syst. veg. 4: 126. 1827.

Petiole aculeate or less often sparingly aculeate, the scales light brown to dark brown, nearly concolorous to usually, sometimes narrowly, concordantly bicolorous, scurf dense, often caducous, the large scales flattish. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules sessile to short-stalked, glabrate to usually slightly to prominently long-pubescent abaxially and usually with a few scales, ultimate segments entire or coarsely dentate, fertile veins simple or forked. **Sori** medial to nearly submarginal, indusia hemitelioid.

In dense forests, 100–800 m, Amazonas south to Cuzco and Madre de Dios.

Belize south to Bolivia; northern Brazil.

Although close to the next species, *Cyathea multiflora* is evidently distinct. In addition to the characters mentioned in the key, the small indusium is entire.

Amazonas: Laguna Pomacocha, NW of Jumbilla, *Soukup 5260B* (GH). **Loreto:** Gamitanacochoa, Río Mazán, *J. Schunke 117* (GH, MO, NY, UC, USM). San Antonio, Río Itaya, *Killip & Smith 29379* (F, NY, US). **Junín:** E of Quimiri Bridge, near La Merced, *Killip & Smith 23979* (F, NY, US). **Cuzco:** Cerca de Atalaya, *Vargas 16274* (GH). Entre Quince Mil y San Lorenzo, *Vargas 11754* (GH). **Madre de Dios:** Prov. Manú, Cerro de Pantiacolla, *Foster et al. 10721* (F).

2. *Cyathea andina* (Karsten) Domin, Pterid. 263. 1929.

Hemitelia andina Karsten, Linnaea 28: 452. 1856. TYPE: Colombia, "Santa Martha," 2500 m, *Karsten* (not located; authentic specimen, *Karsten*, Herb. Mett. B; photo, GH!).

Petiole slightly muricate to usually sparingly aculeate, the scales light brown, or partly whitish, to dark brown and concolorous, or usually narrowly concordantly or discordantly bicolorous, scurf dense, often caducous, the large scales flattish. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules nearly sessile to rather long-stalked, glabrate, slightly scaly or pubescent abaxially, fertile veins forked, rarely simple. **Sori** medial to submarginal, indusia hemitelioid.

In dense forests and forest borders 20–1300 m, Loreto south to Puno.

Greater Antilles, French Guiana west to Colombia and south to Bolivia.

Cyathea andina is close to *C. multiflora*, and the two species have a similar range in the Andes. The indusium of *C. andina* is usually larger than in *C. multiflora* and it commonly splits at maturity into two segments.

Loreto: Yanamona, Río Amazonas above mouth of Río Napo, *Gentry et al. 36580* (MO). **Pasco:** Prov. Oxapampa, Gran Pajonal, N of Chequitavo, *D. Smith 5088* (GH). **Junín:** E of Quimiri Bridge, near La Merced, *Killip & Smith 23995* (GH, NY, US). Prov. Tarma, *Esposito 659* (USM). **Ucayali:** La Divisoria, *Ferreyra 1694* (US). Prov. Coronel Portillo, Obeteni, *Chrostowski 66–14* (UC). **Madre de Dios:** Prov. Tambopata, Río Tambopata, *Barbour 4775* (F, MO). **Puno:** Prov. Carabaya, *Vargas 17536* (GH).

3. *Cyathea vilhelmii* Domin, Pterid. 264. 1929, *nom. nov.* for *Hemitelia lechleri* Mett., not *Cyathea lechleri* Mett.

Hemitelia lechleri Mett., Fil. lechl. 2: 28. 1859. LECTOTYPE (designated by Tryon, Contr. Gray Herb. 206: 41. 1976): Peru, (Puno), Tatanara, *Lechler 2654* (holotype, Herb. Mett. v!; frag., GH!; lectoparatype, Peru, Tatanara, *Lechler 2650*, Herb. Mett. v!).

Petiole lacking, scales and scurf unknown. **Lamina** 3-pinnate-pinnatifid, pinnules long-stalked, glabrate abaxially, ultimate segments subentire to slightly toothed, fertile veins forked. **Sori** costal, indusia hemitelioid, small, nearly concealed by the sporangia.

Only known from the two Lechler collections from Puno.

Endemic to Peru.

4. *Cyathea petiolata* (Hooker) Tryon, Contr. Gray Herb. 206: 42. 1976.

Hemitelia petiolata Hooker, Sp. fil. 1: 31, t. 26. 1844. TYPE: Isthmus of Panama, *Dr. Sinclair* (holotype, K).

Cyathea panamensis Domin, Pterid. 264. 1929, *nom. superfl.* Intended as a *nom. nov.* for *Hemitelia petiolata* Hooker, not John Sm., 1841, but the latter is invalid.

Petiole nearly smooth, the scales brown to dark brown, uniformly so or in patches, discordantly bicolorous, with whitish to light brown margins, scurf rather sparse and caducous, large scales flattish when present. **Lamina** 2-pinnate-pinnatifid, pinnules long-stalked, glabrate abaxially, ultimate segments toothed toward the apex, fertile veins simple or forked. **Sori** submarginal, indusia hemitelioid.

Montane forests and cloud forests, to 1750 m, Huánuco and Cuzco.

Panama south to Peru.

Unusual features of this species are the basal veins that are connivent to a sinus where they sometimes form costal areolae.

Huánuco: Tingo María (as San Martín), *Allard 22360* (GH) is probably a juvenile plant. **Cuzco:** Prov. La Convención, Cordillera de Vilcabamba, *Dudley 10616* (GH).

5. *Cyathea divergens* var. *divergens*

Cyathea divergens Kunze, Linnaea 9: 100. 1834. TYPE: Peru, (Huánuco), Pampayacu, Jul. 1829, *Poeppig*

(*Diar. 1163*) (holotype, LZ destroyed; authentic specimen, *Poeppig 219* (*Diar. 1152*), v!, P!; photo, GH of P).

Cyathea equestris Kunze, Linnaea 9: 100. 1834. TYPE: Peru, (Huánuco), Cerro de Cristóbal, Pampayacu, 1829, *Poeppig* (holotype, LZ destroyed; frag., K).

Petiole short-aculeate to aculeate, the scales very light brown to dark brown, predominantly discordantly bicolorous with lighter margins, scurf dense, usually persistent, the large scales flattish. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules short- to long-stalked, glabrous, slightly pubescent or with a few scales abaxially, ultimate segments subentire, slightly denticulate or shallowly crenate, fertile veins forked. **Sori** costal or nearly so, or rarely medial, indusia sphaeropteroid.

Montane forests and cloud forests, 1200–2000 m, San Martín south to Cuzco.

The var. *divergens* occurs from Costa Rica and Panama; Guyana west to Colombia and south to Peru.

Two varieties are recognized by Tryon (1976). Only var. *divergens* occurs in South America; the other, var. *tuerckheimii*, is confined to Mexico and Guatemala. In Ecuador and Peru, var. *divergens* usually has very long pinnule stalks.

San Martín: Prov. Rioja, Pedro Ruíz-Moyobamba, *Smith & Vásquez 4637* (GH). **Huánuco:** Pampayacu, *Kanehira 120* (GH). Cushi, *Macbride 4819* (F). **Junin:** Prov. Satipo, Gran Pajonal, S of Chequitavo, *D. Smith 5123* (GH). **Cuzco:** Sahuayaco, Chaupiorcco, *Bües 840* (US).

6. *Cyathea pallescens* (Sodirol) Domin, Pterid. 263. 1929.

Alsophila pallescens Sodirol, Recens. crypt. vasc. Quit. 20. 1883. TYPE: Ecuador, Bosques de Nanegal, *Sodirol* (holotype, not located; authentic specimen, *Sodirol*, P!; photo, GH).

Petiole muricate to aculeate, the scales whitish and concolorous to brown or rarely dark brown and discordantly bicolorous, with lighter margins, scurf dense, mostly persistent, the large scales crested or rarely absent. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules sessile or nearly so, glabrate to pubescent and (or) scaly abaxially, ultimate segments subentire to crenate or rarely lobed, fertile veins simple or forked. **Sori** costal to nearly medial, indusia sphaeropteroid.

On steep slopes of ceja de la montaña, in cloud forests and in grasslands, less often in secondary growth, 1500–3300 m, Amazonas, Pasco, Ucayali, and Cuzco.

Colombia south to Bolivia.

Although this is a variable species, it is characterized by the crested large scales of the petiole scurf. These are expanded into two or more planes and usually dissected at the apex. The indusium is rarely subsphaeropteroid or less developed.

Amazonas: Prov. Bagua, Cordillera Colán, SE of La Peca, *Barbour 3590* (F, MO), *3722* (MO). **Pasco:** Prov. Oxapampa, Río San Alberto, *Foster et al. 10285* (F, GH). **Ucayali:** Prov. Coronel Portillo, Cordillera Azul, *Young & Sullivan 762* (F, MO). **Cuzco:** Prov. La Convención, antes de San Luis, *Vargas 22780* (GH). Prov. La Convención, *Dudley 10950B, 11030* (GH), *11149* (GH, US).

7. *Cyathea ruiziana* Klotzsch, *Linnaea* 20: 439. 1847. TYPE: "In peruviae andium nemoribus," *Ruíz 72* (holotype, B!; isotype, US!).

Petiole aculeate, the scales with a dark center, discordantly bicolorous with whitish margins, scurf dense, rather persistent, the large scales flattish. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules sessile or nearly so, rather scaly abaxially, ultimate segments subentire, fertile veins forked. **Sori** medial, indusia sphaeropteroid.

In montane forests, ca. 2000 m, Huánuco.

Endemic to Peru.

Cyathea ruiziana has the large scales of the petiole scurf unusually well-developed and 3–4 mm long: they are whitish and mostly concolorous.

Huánuco: Huacachi, near Muña, *Macbride 4135* (F, US). The Ruíz collection also bears the name of Panatahuas, formerly a province west of Huánuco.

8. *Cyathea microphylla* Mett., *Fil. lechl.* 1: 23, t. 3, f. 1–6. 1856. TYPE: Peru, (Puno), St. Gabán (Río San Gabán), *Lechler 2160* (LZ destroyed; authentic specimen, *Lechler 2569*, Herb. Mett. B!; duplicate, F! (frag.), P!; photo, GH of P).

Petiole smooth, the scales whitish to light brown, broad, concolorous, scurf rather dense, small, more or less persistent. **Lamina** 3-pinnate to 3-pinnate-pinnatifid, pinnules sessile, scaly abaxially, ulti-

mate segments entire, fertile veins simple. **Sori** subcostal, indusia sphaeropteroid.

In thickets and forests, 2100–2800 m, Cuzco and Puno.

Endemic to Peru.

The type collection, *Lechler 2160*, is clearly a mixture. It is cited by Mettenius under *Cyathea microphylla* and also under *Cyathea schanschin* (= *C. delgadii*). There is a specimen at Paris of the collection correctly identified as the latter species. *Cyathea microphylla* is a rare species with small leaves to ca. 75 cm long.

Cuzco: Prov. La Convención, *Dudley 10943* (GH). **Puno:** Valle Grande, Sandia, *Vargas 11858* (GH).

9. *Cyathea multisegmenta* Tryon, *Contr. Gray Herb.* 206: 65. 1976. TYPE: Peru, Cuzco, Prov. La Convención, *Dudley 11326* (holotype, NA!; isotypes, GH!, US!).

Petiole nearly smooth, the scales whitish to light brown, broad, concolorous, scurf dense, persistent, the large scales flattish. **Lamina** 3-pinnate-pinnatifid to 4-pinnate, pinnules sessile, pubescent, and scaly abaxially, ultimate segments entire to lobed, fertile veins simple or forked. **Sori** subcostal, indusia sphaeropteroid.

In dense cloud forest, 1800 m, Cuzco.

Endemic to Peru.

Known only from the type collection. The leaves are noted as 4 m or more long.

10. *Cyathea delgadii* Sternb., *Vers. Fl. Vorwelt* 1: 47, t. B. 1820. TYPE: Brazil, Goiás, Gancho General Delgado, via ad Caldas Novas, *Pohl* (holotype, PRC; frag., GH!).

Cyathea schanschin Mart., *Icon. pl. crypt.* 77, t. 54. 1834. TYPE: Brazil, São Paulo, *Martius* (holotype, M?; isotype, BM!; photo, GH).

Cyathea oligocarpa Kunze, *Linnaea* 9: 101. 1834. TYPE: Peru, (Huánuco), Pampayacu, Jul. 1829, *Poeppig Diar. 1101* (holotype, LZ destroyed; isotypes, *Poeppig 218*, B!, MO!, P!).

Cyathea pilosa Baker, *Syn. fil.*, ed. 2, 19. 1874. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4729* (holotype, K; isotypes, BM!, GH!, P!; photos, GH, UC, US of K, GH of P).

Petiole slightly muricate to aculeate, the scales light brown to brown, nearly concolorous or nar-

rowly concordantly bicolorous, scurf sometimes dense, usually caducous, large scales flattish. **Lamina** 2-pinnate-pinnatifid to 3-pinnate at the base of the central and basal pinnae, pinnules sessile to short-stalked, abundantly to moderately long-pubescent abaxially, sometimes with few long trichomes or few to several concolorous scales, ultimate segments entire to partly lobed, fertile veins forked or rarely simple. **Sori** costal or nearly so, indusia sphaeropteroid.

In montane forests, primary or open forests, or cloud forests, 850–2880 m, Amazonas, San Martín, Huánuco, Pasco, and Cuzco.

Costa Rica and Panama; northern South America south to Bolivia and southeastern Brazil.

Cyathea delgadii is characterized by the long trichomes abaxially, which are usually abundant and the rather few, if any, scales. It is one of the most widely distributed species of *Cyathea*.

Amazonas: Prov. Bagua, Cordillera Colán, SE of La Peca, *Barbour 3612* (F, MO, USM). **San Martín:** Rioja, *Soukup 5223* (GH). **Huánuco:** Tingo María, *Tryon & Tryon 5219* (F, GH, US). Cerros del Sira, Río Lullapichis watershed, *Dudley 13070* (GH). **Pasco:** Prov. Oxapampa, Yanachaga National Park, *León 1014* (GH). **Cuzco:** Prov. La Convención, *Dudley 10058, 10268* (GH). Prov. Uribambamba, camino a Huñayhuayna, *Chávez 3442* (MO).

Key to Varieties

- a. Pinnules usually tapering to the apex from beyond the middle, abaxially usually with abundant scales and trichomes 11a. var. **boliviensis**
- a. Pinnules, especially toward the base of the central and basal pinnae, tapering to the apex from the base, indument abaxially sparse or absent 11b. var. **meridensis**

11a. *Cyathea caracasana* var. **boliviensis** (Rosenst.) Tryon, *Contr. Gray Herb.* 206: 77. 1976. **Figure 23.**

Cyathea mexicana var. **boliviensis** Rosenst., *Repert. Spec. Nov. Regni Veg.* 25: 56. 1928. TYPE: Bolivia, Hacienda Simaco, above Tipuani, *Buchtien 5140* (holotype, not located; isotypes, F!, GH!, NY!, US!).

In wooded ravines, mountain forests, and especially in cloud forests, 1300–2800 m, Amazonas south to Puno.

Venezuela and Colombia south to Bolivia.

11. *Cyathea caracasana* (Klotzsch) Domin, *Pterid.* 262. 1929.

Alsophila caracasana Klotzsch, *Linnaea* 18: 541. 1844.
TYPE: Venezuela, (Dist. Federal), Caracas, *Moritz 117* (holotype, not located; isotypes, GH!, F!).

Petiole muricate to aculeate, the scales predominantly dark reddish brown to atropurpureous, concordantly, sometimes narrowly, bicolorous with lighter margins, scurf dense, persistent or caducous, the large scales flattish. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules sessile to short-stalked or rarely long-stalked, glabrous, pubescent and (or) scaly abaxially, sometimes densely so, ultimate segments subentire to crenate, fertile veins forked, rarely simple. **Sori** costal to medial, indusia sphaeropteroid.

The species occurs in the Greater Antilles; Costa Rica; and Venezuela and Colombia south to Bolivia.

Cyathea caracasana is the most variable species among the American Cyatheaceae. Five varieties were recognized by Tryon (1976) in order to facilitate the study of this complex. In addition to the two varieties in Peru, var. *maxonii* is endemic to Costa Rica, var. *caracasana* is in the Greater Antilles and northern South America, and var. *chimboraensis* is in Venezuela, Colombia, and Ecuador.

Amazonas: Prov. Chachapoyas, entre Ingenio y Pomacocha, *López et al. 4312* (GH, HUT). Prov. Chachapoyas, Molinopampa-Diosan pass, *Wurdack 1653* (F, GH, US). **Huánuco:** Within 5 km of Carpish, *Tryon & Tryon 5326* (F, GH, NY, UC, US). **Pasco:** Prov. Oxapampa, Río San Alberto valley, *Smith & Pretel 8003* (F, MO). Oxapampa (as Junín), *Soukup 2335* (F, GH). **Ucayali:** Prov. Coronel Portillo, La Divisoria, (as Loreto), *Ferreyra 1074* (GH, US), *1696* (US, USM). **Huancavelica:** Prov. Tayacaja, entre Huachocolpa y Tintay, *Tovar 4201* (GH). **Cuzco:** Prov. Paucartambo, near Santa Isabel, Pilahuata to Patria, *Plowman & Davis 4988* (GH, USM). Prov. Uribambamba, Puente Ruinas, Machu Picchu, *Iltis et al. 1025* (GH, UC, US). **Puno:** Cerca a San Juan del Oro, Valle del Alto Tambopata, *Ferreyra 16684* (GH, USM).

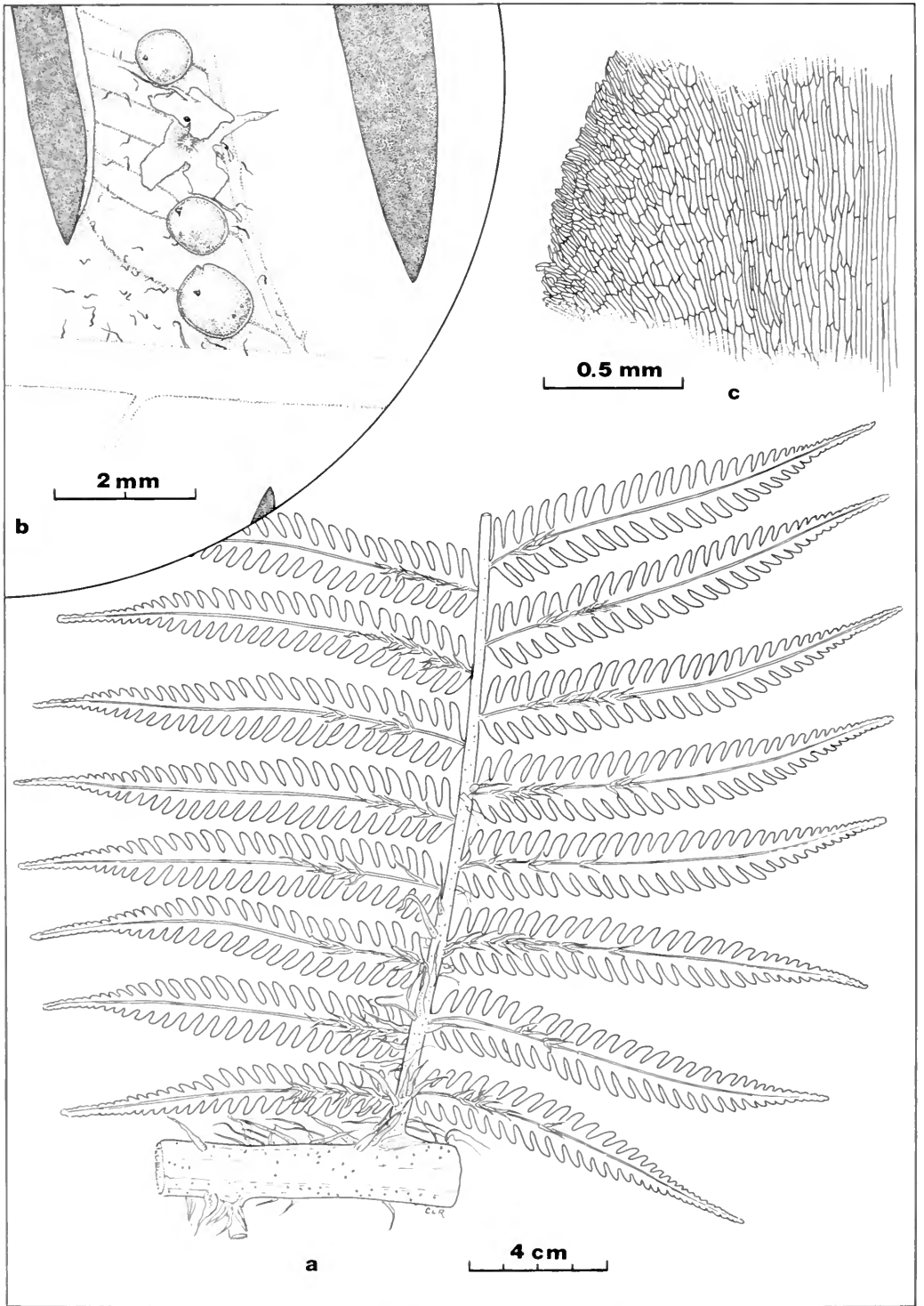


FIG. 23. *Cyathea caracasana* var. *boliviensis*: a, rachis and base of pinna; b, sori (one opened); c, portion of petiole scale. (From Wurdack 1953, F.)

11b. *Cyathea caracasana* var. *meridensis* (Karsten) Tryon, Contr. Gray Herb. 206: 79. 1976.

Cyathea meridensis Karsten, Fl. Columb. 2: 161, t. 184. 1869. TYPE: Venezuela, (Mérida), Mérida, 2000 m, *Karsten* (holotype, not located; *Karsten's* illustration is probably taken from the type collection).

In forests, 1800–2300 m, Amazonas, south to Junín.

Venezuela, Colombia, Ecuador, and Peru.

Amazonas: Prov. Bongará, Pomacocha a Yambrasbamba, *Ferreya 15243* (GH). Serranía de Bagua, E of La Peca, *Gentry et al. 22897* (MO). **San Martín:** Prov. Rioja, Pedro Ruíz-Moyobamba, *D. Smith 4401* (GH). **Huánuco:** Prov. Leoncio Prado, *Sullivan & Young 1178* (USM). **Pasco:** Prov. Oxapampa, Río San Alberto valley, *Smith & Pretel 7999* (F, MO). **Junín:** Prov. Chanchamayo, Chilpez, S of San Ramón, *Smith & Palacios 2641* (F, MO).

12. *Cyathea lechleri* Mett., Fil. lechl. 2: 32. 1859. TYPE: Peru, (Puno), St. Gabán (Río San Gabán) *Lechler* (holotype, LZ destroyed; authentic specimen, *Lechler 2309*, Herb. Mett. B!).

Cyathea castanea Baker, Syn. fil. ed. 2, 451. 1874. TYPE: Peru, (San Martín), Tarapoto, *Spruce 4723* (holotype, K; isotypes, GH!, MO!, P!, US!; photos, GH, US of P).

Petiole nearly smooth, the scales reddish brown to atropurpureous, concordantly bicolorous with lighter margins, scurf essentially absent. **Lamina** 2-pinnate-pinnatifid to 2-pinnate-pinnatisect, pinnules sessile to short-stalked, glabrate abaxially, ultimate segments subentire to slightly crenate, fertile veins forked. **Sori** medial, indusia sphaeropteroid.

In wet forests and cloud forests, ca. 600–1500 m, San Martín, Huánuco, Pasco, and Puno.

Venezuela, Peru, and Bolivia.

San Martín: 36 km NE of Tarapoto, Río Cainarache, *Gentry et al. 37928* (GH, MO). **Huánuco:** Cerros del Sira, Río Lullapichis watershed, *Dudley 13007, 13213, 13262* (GH). **Pasco:** Prov. Oxapampa, W side of Cordillera de San Matías, *D. Smith 2046* (F, MO).

13. *Cyathea ebenina* Karsten, Linnaea 28: 461. 1856. TYPE: Venezuela (Aragua), between Caracas and Puerto Cabello, *Karsten* (holotype, not located; isotype, Caracas, *Karsten*, B!).

Petiole smooth or with a few scattered tubercles, the scales reddish brown to atropurpureous, concordantly bicolorous with lighter margins, scurf absent. **Lamina** 2-pinnate-pinnatifid, pinnules long-stalked, glabrous to slightly pubescent abaxially, ultimate segments subentire to shallowly crenate, fertile veins simple or forked. **Sori** more or less medial, indusia sphaeropteroid.

Growing at 2100 m, Amazonas.

Venezuela and Colombia, south to Peru.

This species is unique in the genus in the characters of the basal segments of the pinnules being decurrent onto the pinnule-stalk which is of a strongly contrasting lighter color than the dark pinna-rachis.

Amazonas: Prov. Bongará, N end of lake Pomacocha, *Hutchison & Wright 6814* (GH, NY, US).

14. *Cyathea dudleyi* Tryon, Contr. Gray Herb. 206: 85. 1976. TYPE: Peru, Cuzco, Prov. La Convención, Cordillera Vilcabamba, *Dudley 10867B* (holotype, GH!; paratypes, same locality, *Dudley 10738, 10867* GH!).

Petiole nearly smooth, the scales brown to dark brown, nearly concolorous, scurf absent. **Lamina** 3-pinnate nearly throughout, pinnules sessile to short-stalked, somewhat scaly and pubescent abaxially, ultimate segments entire, fertile veins simple. **Sori** subcostal, indusia sphaeropteroid.

Known only from five collections, in dwarf forests or wet, dense cloud forests, 2100–2700 m, Pasco and Cuzco.

Endemic to Peru.

Cyathea dudleyi has a more complex lamina than the related *C. lechleri* and the concolorous petiole scales distinguish it from the somewhat smaller *C. microphylla* with bicolorous scales.

Pasco: San Gotardo, border of Prov. Oxapampa and Pasco, *van der Werff et al. 8589* (MO, UC). **Prov. Oxapampa,** 20 km W of Oxapampa, *D. Smith 5375* (GH).

Comments

Two collections from Dept. Amazonas, Prov. Bagua, Cordillera Colán, *Barbour 3748* and *3920* (MO), may be *Cyathea fulva* (Mart. & Gal.) Fée. The materials are not wholly adequate for certain

identification and the species is not treated under *Cyathea*. It is known in Ecuador and may well occur in northern Peru.

Specimens of *Cyathea fulva* will key out near *C. delgadii*, from which it differs in having few or no scales or trichomes on the segments abaxially, or with some trichomes and also some scales. *Cyathea delgadii* has few or no scales on the abaxial side of the segments, and the abaxial side is moderately to usually abundantly long-pubescent. In addition, *Cyathea fulva* has some to many of the large scales of the petiole scurf crested, while in *C. delgadii* they are flattish.

VI. *Cnemidaria*

Cnemidaria Presl, Tent. pterid. 56. 1836. TYPE: *Cnemidaria speciosa* Presl. Figure 24.

Terrestrial. Stem rather small to stout, ascending to erect, usually hardly arborescent, rarely to 3 m tall. Leaves monomorphic, with scales, especially on the croziers and petiole base, that are marginate and lack a dark apical seta. Petiole smooth, muricate, or with corticinate spines. Lam-

ina 1-pinnate to 1-pinnate-pinnatisect, veins free and the basal ones connivent to a sinus, or usually regularly anastomosing without included free veinlets, especially along the costa. Sori round, borne on the veins, rarely at a fork, with a hemitelioid or meniscoid indusium. Spores tetrahedral-globose, trilete, nearly smooth, with three large equatorial pores and often smaller ones.

A tropical American genus of 25 species, with five of them in Peru.

Species of *Cnemidaria* were formerly placed in *Hemitelia* because of the small indusia. The genus is characterized by a lack of trichomes on the adaxial side of the costae and costules and by the spores with three large equatorial pores. All of the Peruvian species have regularly anastomosing veins, except for *C. uleana*, which sometimes has free veins.

Reference

STOLZE, R. 1974. A taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). Fieldiana, Bot., 37: 1-98.

Key to Species of *Cnemidaria*

- a. Pinnae (excluding the basal pair and reduced apical ones) deeply pinnatifid or pinnatisect; the segment sinuses extending $\frac{2}{3}$ or more to the costa b
 - b. Lamina gradually reduced to a nonconform pinnatifid apex; rachis not alate; petiole scales bicolorous, dark brown with broad to narrow whitish margins C
 - c. Basal basicopic veins commonly arising from the costule or from its junction with the costa; rachis and petiole muricate to spiny; scales of costae and costules, if present, deep brown ... 1. *C. horrida*
 - c. Basal basicopic veins, especially toward the basal and apical portions of pinnae, commonly arising from the costa; rachis smooth, petiole smooth or tuberculate; scales of costae and costules whitish 2. *C. uleana*
 - b. Lamina abruptly reduced to a conform or subconform apical segment similar to the lateral pinnae; rachis conspicuously alate, especially distally; petiole scales predominantly whitish 3. *C. alatissima*
- a. Pinnae (excluding the basal pair and reduced apical ones) subentire to shallowly pinnatifid; the segment sinuses, if present, extending less than halfway to the costa d
 - d. Pinnae shallowly and obtusely lobed to shallowly pinnatifid; indusia more or less semicircular, attached on the costular side of the receptacle 4. *C. speciosa*
 - d. Pinnae subentire to broadly and coarsely serrate; indusia circular, completely surrounding the receptacle 5. *C. nervosa*

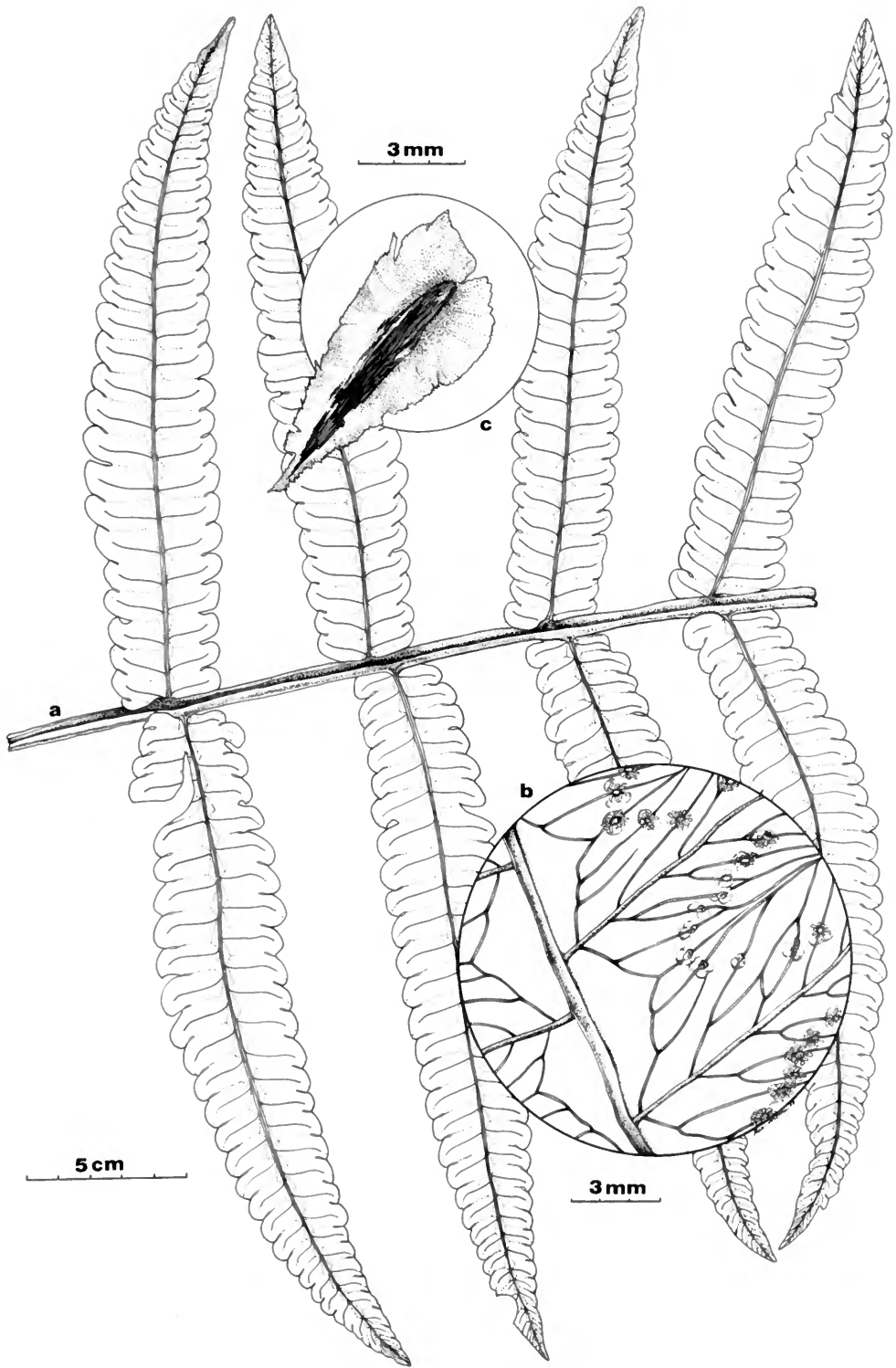


FIG. 24. *Cnemidaria speciosa*: a, part of rachis, with pinnae; b, pinna midrib, venation pattern, and sori; c, petiole scale. (a from Tryon & Tryon 5260, F; b-c from Buchtien 5224, Bolivia, F.)

1. *Cnemidaria horrida* (L.) Presl, Tent. pterid. 57. 1836.

Polypodium horridum L., Sp. pl. 1092. 1753. TYPE: Plumier descript. pl. Amer., t. 4. 1693 (Traité foug. Amér., t. 8. 1705).

Hemitelia horrida (L.) R. Br., Prodr. 158. 1810.

Petiole muricate, or more often with stout spines to 5 mm long, the scales, usually only at the base of the petiole, bicolorous, dark brown with narrow whitish margins. **Lamina** gradually reduced to a nonconform pinnatifid apex, rachis not alate, muricate or often spiny. **Pinnae** incised $\frac{7}{8}$ or more to the costa, the costa and costules rarely with dull brown scales abaxially, basal basisopic veins usually arising from the costule. **Soral** lines supra-medial to submarginal between the costule and segment margin, indusia more or less semicircular, subentire to erose.

In forest, on stream banks, and mountain slopes, 300–1500 m, Amazonas and Loreto, south to Cuzco.

Greater Antilles; Costa Rica; Venezuela and Colombia south to Peru.

Cnemidaria horrida is the most widely distributed species of the genus and has the greatest range of altitude. It is also the largest species with trunks sometimes to 3 m tall and 7 cm in diameter.

Amazonas: Prov. Bagua, Río Marañón, above Cascadas de Mayasi, *Wurdack* 1991 (us). **San Martín:** Near Tarapoto, *Spruce* 3943 (GH, US). **San Roque, Ll. Williams** 7156 (F, NY, US). **Loreto:** Pumayacu, between Balsapuerto and Moyobamba, *Klug* 3182 (F, GH, MO, NY, US). **Pasco:** Prov. Oxapampa, Río Palcazú, *Smith & Salick* 8377 (MO). **Cuzco:** Prov. Paucartambo, Villa Carmen, Kosñipata-Pilcopata, *Vargas* 11269 (GH).

2. *Cnemidaria uleana* (Samp.) Tryon var. *uleana*.

Cnemidaria uleana (Samp.) Tryon, Contr. Gray Herb. 200: 52. 1970.

Hemitelia uleana Samp., Bol. Mus. Nac. Rio de Janeiro 1: 65. 1923. TYPE: Brazil, (Rio de Janeiro), Perto de Nova Friburgo, Alta da Serra, *Ule* (holotype, R!; photos, F, GH).

Petiole smooth to slightly muricate, the scales bicolorous, dark brown with broad whitish margins. **Lamina** gradually reduced to a nonconform pinnatifid apex, rachis not alate, essentially smooth. **Pinnae** incised $\frac{2}{3}$ – $\frac{7}{8}$ to the costa, the costa and costules usually with broad, pale yellowish to whit-

ish scales abaxially, basal basisopic veins, especially toward the basal and apical portions of the pinnae, commonly arising from the costa. **Soral** lines medial to supramedial between the costule and segment margin, indusia semicircular, subentire to several-lobed.

In cloud forests, 1700–2200 m, Cuzco.

Southern Peru and southeastern Brazil.

Cnemidaria uleana is unique in the genus in that anastomosing of the basal veins may be present or absent. All other Peruvian species have costal areolae. Specimens of var. *uleana* with anastomosing veins can be separated from *Cnemidaria horrida* by the characters in the key.

The species ranges from Colombia to Peru, and in southeastern Brazil. The collections from Peru are var. *uleana* (also in Brazil), with a gradually reduced pinnatifid lamina apex and usually with costal areolae. The var. *abitaguensis* (Domin) Stolze occurs in Colombia and Ecuador, with a conform or subconform apical segment and free veins.

Cuzco: Prov. La Convención, Cordillera Vilcabamba, *Dudley* 10459 (GH, NA), 10611 (GH), 11312 (GH, NA).

3. *Cnemidaria alatissima* Stolze, Fieldiana, Bot. 37: 55. 1974. TYPE: Peru, Huánuco, Río Llullapichis watershed, *Dudley* 13282 (holotype, GH! 2 sheets; photo, F; isotype, NA!).

Petiole with minute spines, thickly covered near the base by large, ovate, whitish scales. **Lamina** abruptly reduced to a subconform apical segment, rachis with a green wing 1–2 mm wide on each side, smooth. **Pinnae** incised $\frac{2}{3}$ – $\frac{3}{4}$ to the costa, the costa and costules lacking scales abaxially, basal basisopic veins usually arising from the costule. **Soral** lines about medial between the costule and segment margin, indusia often rudimentary, usually less than semicircular, subentire.

In dense cloud forests, ca. 1500 m, Huánuco.

Endemic to Peru.

This species is characterized by the abundant white petiole scales and the broad green alate rachis, the wings extending down onto the petiole. It is known only from the type collection and one juvenile plant.

Huánuco: Río Llullapichis watershed, *Dudley* 13281 (GH, US), a juvenile plant.

4. *Cnemidaria speciosa* Presl, Tent. pterid. t. 1, f. 16–17. 1836. TYPE: Peru, (Huánuco), Pampayacu, Jul. 1829, *Poeppig 221 (Diar. 1144)* (holotype, PR or PRC; frag., NY!, US!; isotypes, B!, BR, P!). **Figure 24.**

Hemitelia subincisa Kunze, Bot. Zeit. (Berlin) 2: 296. 1844, nom. nov. for *Cnemidaria speciosa* Presl, not *Hemitelia speciosa* (Willd.) Kaulf.

Petiole smooth or rarely tuberculate at the base, the scales lanceolate to ovate, bicolorous, whitish with a brown central stripe. **Lamina** abruptly reduced to a conform or subconform apical segment, rachis not alate, essentially smooth. **Pinnae** very deeply crenate to lobed less than $\frac{1}{2}$ to the costa, the costa and costules rarely with dull, brown scales abaxially, basal basicopic veins mostly arising from the costule or its base. **Soral lines** supra-medial between the costule and segment margin, indusia more or less semicircular, rather large.

In forests and at forest borders, along stream banks, and on mountain slopes, 115–1900 m, San Martín and Loreto south to Puno.

Peru and Bolivia.

Three collections from Loreto, Varadero de Mazán, (Río Amazonas to Río Napo), *Croat 19500* (MO, UC), *19514* (F, MO) and *20791* (MO, UC) have a few broad whitish scales on the costae abaxially, rather than few small brown ones or none. These may represent a distinct variety of the species.

San Martín: Prov. Mariscal Cáceres, Palo Blanco, Tocache Nuevo, *J. Schunke V. 5682* (F, GH, NY). **Loreto:** Prov. Maynas, Varadero, *Vásquez 721* (MO). **Huánuco:** Prov. Huánuco, Tingo María, *Tryon & Tryon 5260* (F, GH, U, US). **Pasco:** Yapas, Pichis Trail, *Killip & Smith 25563* (GH, NY, US). Prov. Oxapampa, Palcazú, Cerro de

Pantiacolla, *Foster 10907* (F). **Junin:** Near La Merced, *Killip & Smith 23889* (NY, US). Chanchamayo valley, *C. Schunke 52* (F). **Ucayali:** Prov. Coronel Portillo, Padre Abad, *J. Schunke V. 5477* (F, GH, US). Aguaytía, *Huapalla 2470* (USM). **Cuzco:** Prov. Quispicanchi, entre Inambari y Quince Mil, *Vargas 16502* (GH). **Madre de Dios:** Prov. Manú, *Vargas 17738* (GH). **Puno:** Prov. Carabaya, San Gabán, *Vargas 18863* (GH).

5. *Cnemidaria nervosa* (Maxon) Tryon, Contr. Gray Herb. 200: 52. 1970.

Hemitelia nervosa Maxon, J. Wash. Acad. Sci. 34: 309. 1944. TYPE: Peru, Loreto, mouth of Río Santiago, *Mexia 6291* (holotype, US! 3 sheets; isotypes, F!, GH!, NY!, UCL).

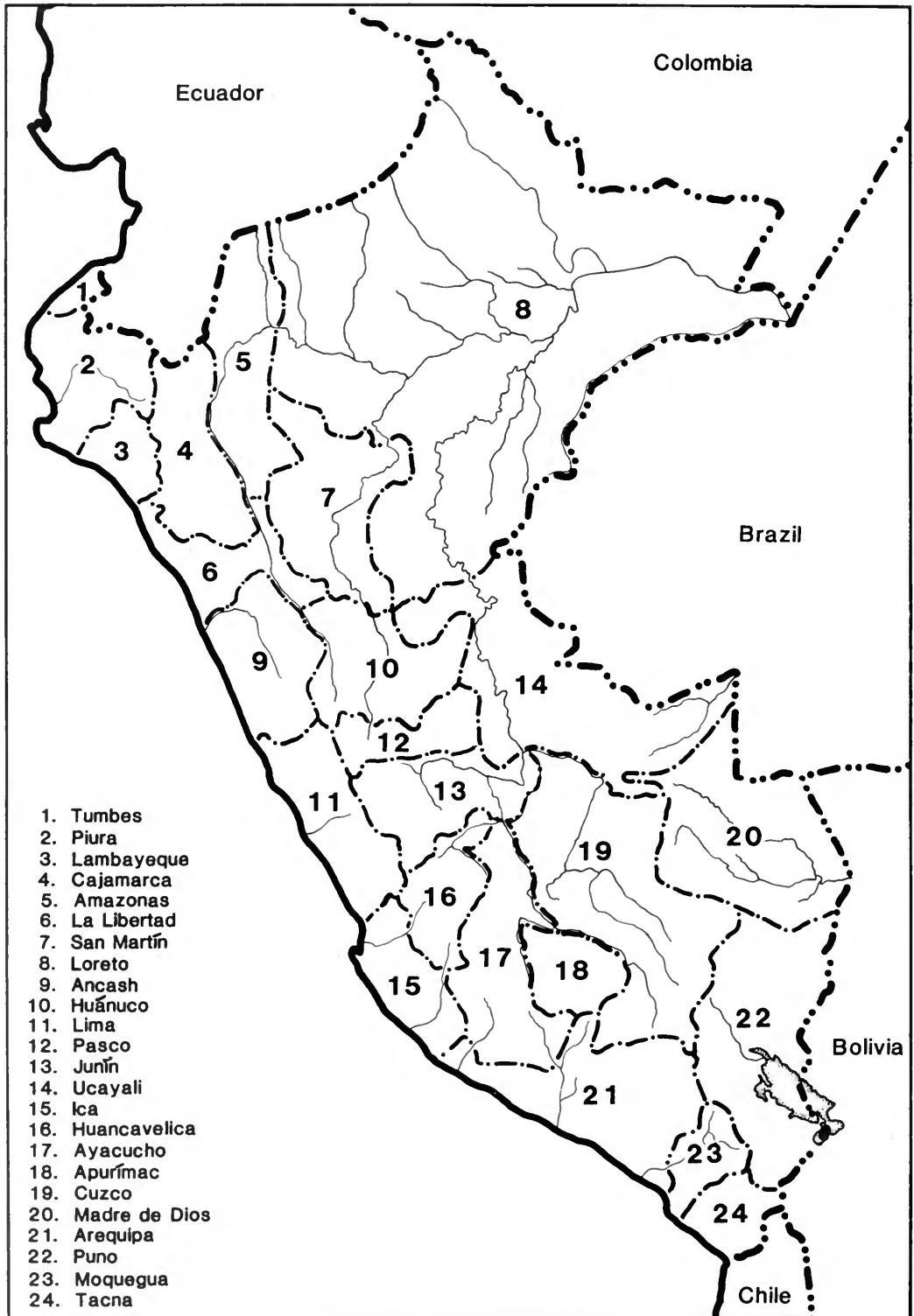
Petiole smooth to muricate, the scales, mostly near the base, lanceolate or linear-lanceolate, bicolorous, brown with narrow whitish margins. **Lamina** abruptly reduced to a conform or subconform apical segment, rachis not alate, smooth. **Pinnae** subtentire to broadly serrate, the costa and primary veins lacking scales abaxially, basal basicopic vein arising from a primary vein. **Soral lines** between the primary veins, indusia commonly circular, completely surrounding the receptacle, entire to lobed.

Rain forests, 300–450 m, Amazonas and Loreto.

Ecuador and Peru.

The circular indusium is a character in the genus shared only by *Cnemidaria cocleana* of Panama. *Cnemidaria nervosa* is a rare fern, represented by one collection from Ecuador and two from Peru.

Amazonas: Prov. Bagua, valley of the Río Marañón, *Wurdack 2059* (NY, US).



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