AMERICAN
FERN
JOURNAL

Volume 104

Number 1

January–March 2014

QUARTERLY JOURNAL OF THE AMERICAN FERN SOCIETY

The American Fern Society

Council for 2014

American Fern Journal

EDITOR

MANAGING EDITOR

ASSOCIATE EDITORS

The "American Fern Journal" (ISSN 0002-8444) is an illustrated quarterly devoted to the general study of ferns. It is owned by the American Fern Society, and published at The American Fern Society, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711. Periodicals postage paid at Austin, TX, and additional entry.

Claims for missing issues, made 6 months (domestic) to 12 months (foreign) after the date of issue, and orders for back issues should be addressed to Dr. George Yatskievych, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.

Changes of address, dues, and applications for membership should be sent to the Membership Secretary.

General inquiries concerning ferns should be addressed to the Secretary.

Back volumes are avalible for most years as printed issues or on microfiche. Please contact the Back Issues Curator for prices and availability.

Subscriptions:

Society Membership – USA, Canada, Mexico (includes Journal and Fiddlehead Forum)	$30
Society Membership – All other countries (includes Journal and Fiddlehead Forum)	$40
Society Life Membership – $360 (add $120 mailing surcharge for outside USA, Canada, Mexico)	
Regular Membership – USA, Canada, Mexico (includes Fiddlehead Forum)	$15
Regular Membership – All other countries (includes Fiddlehead Forum)	$22
Institutional Membership – $40 to USA, Canada, Mexico; $50 elsewhere (-$3 agency fee)	

POSTMASTER: Send address changes to American Fern Journal, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711.

American Fern Journal 104(1):1–6 (2014)

A Pluviometric Fern Spore, Fungal Spore, and Pollen Trap

FELIPE GÓMEZ-NOGUEZ
Área de Botánica Estructural y Sistemática Vegetal, Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Avenida San Rafael Atlixco 186, Colonia Vicentina, Delegación Iztapalapa, 09340 México, D. F., México, e-mail: tindalo@xanum.uam.mx

BLANCA PÉREZ-GARCÍA
Área de Botánica Estructural y Sistemática Vegetal, Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Avenida San Rafael Atlixco 186, Colonia Vicentina, Delegación Iztapalapa, 09340 México, D. F., México, e-mail: bpg@xanum.uam.mx

ANICETO MENDOZA-RUIZ
Área de Botánica Estructural y Sistemática Vegetal, Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Avenida San Rafael Atlixco 186, Colonia Vicentina, Delegación Iztapalapa, 09340 México, D. F., México, e-mail: amr@xanum.uam.mx

ALMA OROZCO-SEGOVIA
Departamento de Ecología Funcional, Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, Circuito Exterior, Ciudad Universitaria, México, D. F., México, e-mail: aorozco@ecologia.unam.mx

ABSTRACT.—Although rain is the most important agent in airborne biological particle deposition most of the current sampling traps retain palynomorphs (fern spore, fungal spore, pollen, among others) but are unable to measure precipitation. The objectives of this study are to present a new simple pluviometric/gravimetric spore/pollen trap and propose a spore/pollen-density rain method, based on the particle frequency and sampling area, which would facilitate ecological inferences about rainfall and Biological Airborne Particle (BAP) deposition, so as to avoid the overrepresentation of the percentage and diverse aerobiological methods. Relative to other spore traps, our proposed trap is simple to build, easy to mount in the field, easy to carry, maintenance free, and requires no energy source. In addition, our trap records rainfall volume, and the quantity of spores captured can be expressed in terms of area-density (particle m^{-2}). The rainfall measured with the trap had no significant differences with the precipitation volume obtained from the pluviometer of the Automatic Meteorological Station at Zacualtipán, Hidalgo, Mexico.

KEY WORDS.—Airborne spore, biological airborne particle, biological particle deposition, efficient spore trap

Aerobiology is a recent scientific discipline that studies the diversity and concentration of biological particles (e.g., pollen, fungal spores, and fern spores) that are transported passively by the atmosphere (Latorre and Caccavari, 2010). Most aerobiological studies focus on the variation of pollen and fungal spore concentrations because of the allergenic effect of these particles (i.e., pollinosis) on humans, and in order to assess the potential for the spread of fungal disease on economic crops (De Benito and Soto, 2001; Lacey and West, 2006). Research has resulted in the development of specialized palynomorph traps, such as the Tauber trap (Tauber, 1974), which is used to analyze pollen deposition (Levetin *et al.*, 2000), and the Burkard volumetric trap (Hirst, 1952), which was designed to study airborne pollen. Both of these devices are commonly used in many types of research (e.g., Caulton *et al.*, 2000; Hicks, 1999; Kasprzyk, 2004; Yang and Chen, 1998), as are specialized traps, such as the rotorod trap (Murray *et al.*, 2007), the cyclone spore trap (Tate *et al.*, 1980), and others reviewed by Gregory (1961) and Lacey and West (2006).

Although these types of traps can be programmed to survey the air for different periods of time, they are expensive and require energy sources unavailable in some tropical environments (Gupta and Chanda, 1991; Potter and Rowley, 1960). Furthermore, they can be lost or stolen during prolonged field surveys. For these reasons, these traps are mostly used in urban areas, on the rooftops of available buildings (Estrella *et al.*, 2006; Latorre and Caccavari, 2010; Ong *et al.*, 2011; Ting *et al.*, 2010). The use of simpler traps has been reported, such as moss clusters on trees (Limón, 1980), soil samplers (Anupama *et al.*, 2002; Tovar-González, 1987), and exposed petri dishes containing different nutritional media (Brown, 1971). However, simpler traps cannot be used to determine the palynomorph influx, and have low local flora representation (Tejero-Díez *et al.*, 1988). Other traps, such as adhesive slices, have low uptake efficiency in prolonged surveys because of sampling area saturation and particle loss due to rain-washing (Melhem and Makino, 1978). Bush (1992) proposed an inexpensive, phenologically accurate gravimetric palynomorph trap composed of a funnel (sampling area) and a carafe; this trap was later improved by Gosling *et al.* (2003), but both of these traps have the disadvantage of not being able to record pluviometric values. Rainfall is the most important meteorological factor in particle deposition (Ramírez-Trejo, 2002; Ramírez-Trejo *et al.*, 2004; Simabukuro *et al.*, 1998, 2000), yet samplers are unable to measure rainfall.

To preserve the pluviometric values associated with a spore-rain survey and to obtain more ecological inferences about rainfall and palynomorph depositions, we modified and simplified the Bush-Gosling trap.

Our trap consisted of a funnel 9 cm in diameter attached to a two-liter carafe (Fig. 1 A and B). To prevent the evaporation of the rainfall deposited in the trap, a segment of PVC tube 15.5 cm (6.5 in) in diameter was added, surrounding the trap and serving as a base. A mosquito net or another type of mesh could be used to cover the funnel and thus prevent major detritus buildup. Moreover, the cylinder–base top edge should be beveled to avoid over representation of rainfall by splashing.

The uptake area (top of the funnel) can be calculated as $A=\pi r^2$; 63.61725124 cm^2 thus, the total rainfall can be expressed in millimeters by the following equation: mm = V/A, where V is the final volume of rain collected expressed in mm^3 and A is the uptake area expressed in mm^2. In addition, the particles may be expressed in density (particles/sampling area), which facilitates analysis and avoids the problems related in the percentage method used by Simabukuro *et al.* (2000).

The advantage of this trap is that it allows better aeropalynological interpretations with the best airborne particle deposition factor (rain). To test

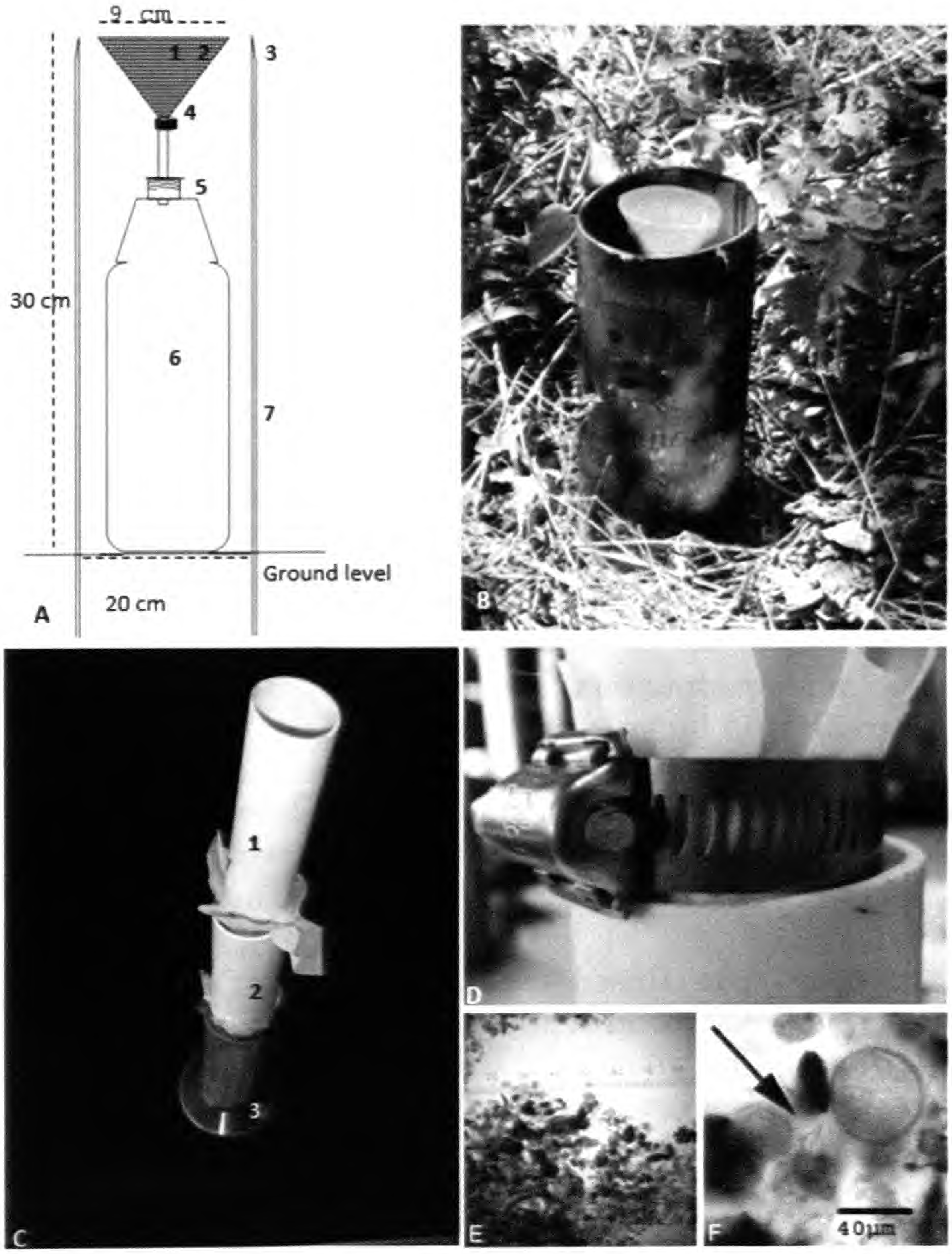

FIG. 1. Pluviometric spore/pollen trap. A. Pluviometric spore/pollen trap diagram: 1) funnel, 2) screen mesh, 3) beveled top edge PVC tube, 4) security seal to secure the mesh, 5) recapping with a hole for the funnel tube, 6) carafe with a 2 L capacity, 7) wall of the PVC tube. B. Trap mounted at an experiment site. C. Measuring and filtering of the trap content with different sized mesh: 1) 100 µm mesh, 2) 20 µm mesh, 3) graduated cylinder. D. Details of simple filter build up by a PVC tube segment, with a 100 µm mesh attached with a clamp. E. Particles captures with the device at 10 × magnification. F. Striate trilete fern spore aff. *Alsophila firma* (Baker) D. S. Conant (arrow), surrounded by diverse pollen grains at 100 × magnification.

durability and efficiency of the trap, we used it to determine the spore rain in an area near the Malila River in the state of Hidalgo, Mexico. The trap was left in the field in its cylinder-base with monthly trap changes, which did not result in damage from environmental conditions.

To vary the sampling period, one can change the carafe capacity and funnel size according to the total rainfall observed in previous years. Because we

TABLE 1. Total number of fern spores captured by six traps, mean precipitation, and spore density in a monthly one-year survey (March 2009 to February 2010). PST =Pluviometric Spore Trap.

Period	Total fern spore counted	PSTM mean precipitation (mm)	Fern spore density (spore m^{-2})
March 2009	621	10.58	16269.2
April 2009	335	10.27	8776.4
May 2009	228	73.09	5973.2
June 2009	274	115.66	7178.3
July 2009	123	7.86	3222.4
August 2009	224	226.33	5868.4
September 2009	129	204.61	3379.5
October 2009	83	154.31	2174.4
November 2009	66	55.80	1729.1
December 2009	101	47.42	2646.0
January 2010	149	98.50	3903.5
February 2010	129	24.49	3379.5

knew the maximum precipitation rates in our study site, we selected a volume capacity of two liters in order to avoid overflow.

With this trap, the palynomorphs and rain remained in the carafe and were later separated by filtration with different size mesh in the laboratory (Fig. 1 C and D). One hundred μm mesh was used to remove medium detritus and 20 μm mesh was used to collect the particles of interest. In addition, rainfall volume was measured.

The 20 μm mesh was rinsed with 70% ethanol, and the ethanol was collected in a 15 ml vial. The liquid was then centrifuged at 1500 rpm for 3 minutes. The resulting precipitate was then suspended with 5 ml of 70% ethanol from which semi-permanent preparations were made.

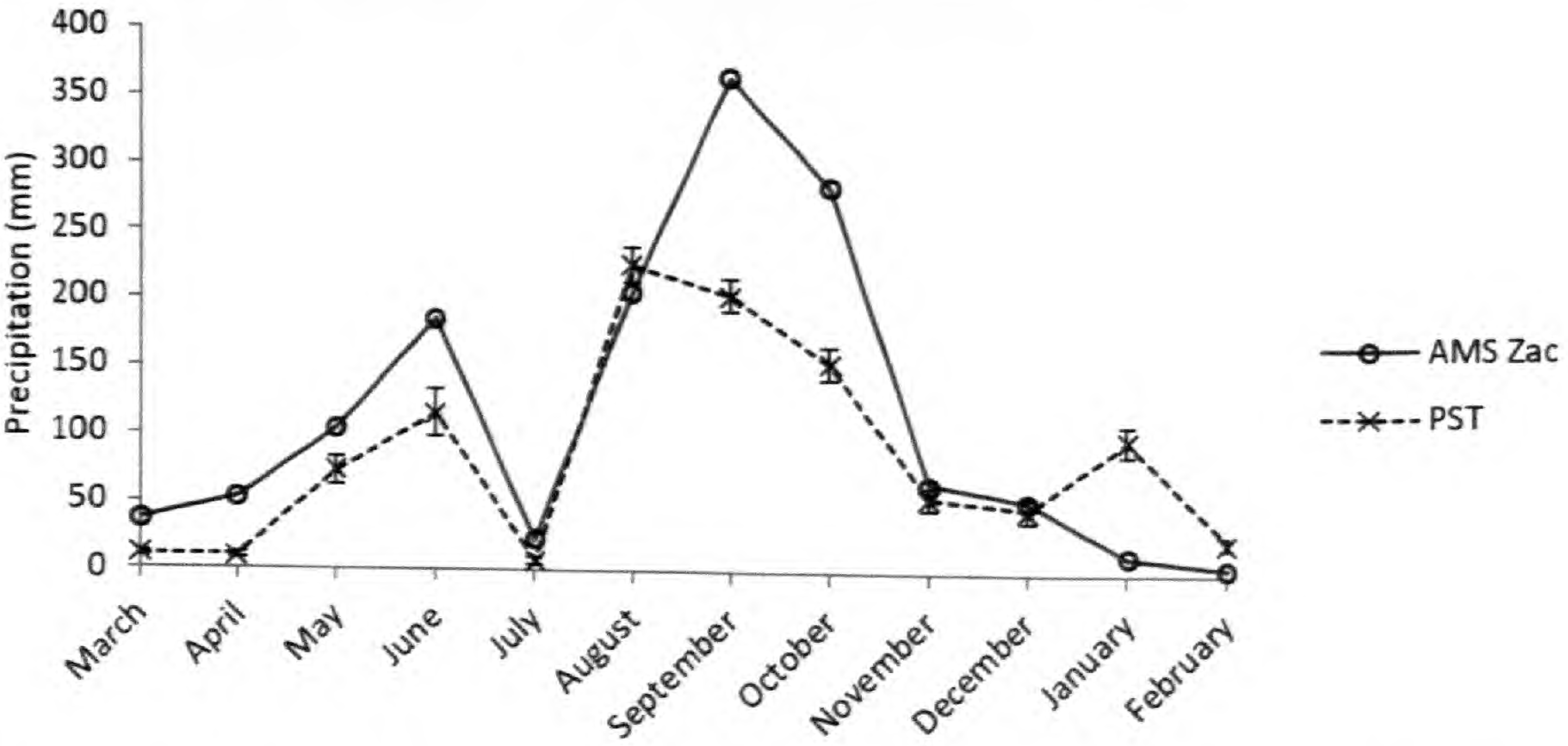

FIG. 2. Monthly precipitation values (mm) of the Automatic Meteorological station at Zacualtipán, Hidalgo, México (AMS Zac) and the mean values of six pluviometric spore/pollen traps (PST) localized at 14 km of AMS Zac, from March 2009 to February 2010.

After a one-year test, the trap showed the ability to capture diverse biological particles such as pollen, fungal spores, and fern spores (Fig. 1 E, F), the latter of which are shown in Table 1. Also the comparison between the precipitation values obtained with six trap devices and those obtained by the pluviometer of the nearest weather station, using a Mann-Whitney U-test, showed no significant differences ($W=52$, $P=0.51$, $\alpha=0.05$, Fig. 2).

Spore perine characters offer more accuracy in the identification of fern taxa and therefore we recommend using a fresh mount rather than the common Erdtman (1960) acetolysis method, in order to preserve the fragile perine of some taxa (Devi, 1980).

This simple trap could help with the determination of phenological processes in tropical environments and thus address future challenges, including understanding the possible consequences of global warming on ferns and their spore dispersal (Mehltreter, 2008).

ACKNOWLEDGMENTS

This paper is part of the thesis project of the first author, who is enrolled in the Biological Sciences Master Program at the Universidad Autónoma Metropolitana. We appreciate the support offered by the university for this study, especially from Alejandro Zavala, Ph. D. We also thank the Consejo Nacional de Ciencia y Tecnología (CONACyT) for the scholarship provided (224680), the National Meteorological Service and the valuable comments and suggestions of the Victor Steinmann, Ph. D., who helped with revision of the manuscript as well as two anonymous reviewers for their contribution.

LITERATURE CITED

ANUPAMA, K., S. ARAVAJY and S. PRASAD. 2002. Pollen and ecological studies in the Southern Eastern Ghats: a new methodological approach. http://www.ifpindia.org/IMG/pdf/anupama_papers/Anupama_et_al_2002.pdf (accessed 12 Sep 2008).

BROWN, R. M. 1971. Studies on Hawaiian fresh-water and soil algae I. the atmospheric dispersal of algae and fern spores across the island of Oahu, Hawaii, Pp. 175–188 *in* Parker, B. C. and R. M. Brown, eds. *Contributions in Phycology*. University of Virginia, USA.

BUSH, M. B. 1992. A simple yet efficient pollen trap to use in vegetational studies. J. Veg. Sci. 3:275–276.

CAULTON, E., S. KEDDIE, R. CARMICHAEL and J. SALES. 2000. A ten year study of the incidence of spores of bracken, (*Pteridium aquilinum* (L.) Kuhn.) in an urban rooftop airstream in south east Scotland. Aerobiologia 16:29–33.

DE BENITO, R. V. and T. R. SOTO. 2001. Polinosis y aerobiología del polen en la atmósfera de Santander. Alergol. Inmunol. Clin. 16:84–90.

DEVI, S. 1980. The concept of perispore—an assessment. Grana 19:159–172.

ERDTMAN, G. 1960. The acetolisis method, a revised descriptions. Svensk Bot. Tidskr. 54:561–564.

ESTRELLA, N., A. MENZEL, U. KRÄMER and H. BEHRENDT. 2006. Integration of flowering dates in phenology and pollen counts in aerobiology: analysis of their spatial and temporal coherence in Germany (1992–1999). Int. J. Biometeorol. 51:49–59.

GREGORY, P. H. 1961. The Microbiology of the atmosphere. (2nd ed.) Leonard Hill Books Limited and Interscience Publishers Inc., London.

GOSLING, W. D., F. E. MAYLE, T. J. KILLEEN, M. SILES, L. SÁNCHEZ and S. BOREHAM. 2003. A simple and effective methodology for sampling modern pollen rain in tropical environments. Holocene 13:613–618.

GUPTA, S. and S. CHANDA. 1991. Aerobiology of subtropical Eastern Himalayas (Kuseong), India. Aerobiologia 7:118–128.

HICKS, S. 1999. The relationship between climate and annual pollen deposition at northern treelines. Chemosphere Global Change Sci. 1:403–416.

HIRST, J. M. 1952. An automatic volumetric spore trap. Ann. Appl. Biol. 39:257–265.

KASPRZYK, I. 2004. Airborne pollen of entomophilous plants and spores of pteridophytes in Rzeszów and its environs (SE Poland). Aerobiologia 20:217–222.

LACEY, M. E. and J. S. WEST. 2006. The air spora, a manual for catching and identifying airborne biological particles. Springer, Dordrecht, Netherland.

LATORRE, F. and M. A. CACCAVARI. 2010. Pollen diversity in the air of Diamante (Entre Ríos, Argentina). Scientia Interfluvius 1:7–17.

LEVETIN, E., C. A. ROGERS and S. A. HALL. 2000. Comparison of pollen sampling with a Burkard spore trap and a Tauber trap in a warm temperate climate. Grana 39:294–302.

LIMÓN, B. A. 1980. Vegetación y lluvia de polen en el cerro Tetepetl, Estado de México. Tesis de Licenciatura., Facultad de Ciencias Universidad Nacional Autónoma de México, México.

MELHEM, A. and H. MAKINO. 1978. Precipitação polínica na ciudad de São Paulo (Brasil). Hoehnea 7:1–10.

MEHLTRETER, K. 2008. Phenology and habitat specificity of tropical ferns. Pp. 201–221 *in* T. A. Ranker and C. H. Haufler (eds.), *Biology and Evolution of Ferns and Lycophytes*. Cambridge University Press, New York.

MURRAY, M. G., R. L. SCOFFIELD, C. GALAN and C. B. VILLAMIL. 2007. Airborne pollen sampling in a wildlife reserve in the south of Buenos Aires province, Argentina. Aerobiologia 23:107–117.

ONG, T. C., S. H. LIM, X. CHEN, S. D. MOHD DALI, H. T. W. TAN, B. W. LEE and T. CHEW. Fern spore and pollen airspora profile of Singapore. Aerobiologia (2012), http://link.springer.com/content/pdf/10.1007%2Fs10453-011-9217-z.pdf. (accessed 10 Sep 2010)

POTTER, L. D. and J. ROWLEY. 1960. Pollen rain and vegetation, San Agustin plains, New Mexico. Bot. Gaz. 122:1–25.

RAMÍREZ-TREJO, M. R. 2002. Los Bancos de esporas de helechos en diferentes suelos y tipos de vegetación del estado de Hidalgo. Tesis de Maestría, Facultad de Ciencias Universidad Nacional Autónoma de México, México.

RAMÍREZ-TREJO, M. R., B. PÉREZ-GARCÍA and A. OROZCO-SEGOVIA. 2004. Analysis of fern spore banks from the soil of three vegetation types in the central region of Mexico. Amer. J. Bot. 91:682–688.

SIMABUKURO, E. A., L. M. ESTEVES and G. M. FELIPPE. 1998. Fern spore rain at Itirapina (Sp, Brazil): preliminary results. Ínsula (Florianópolis) 27:39–57.

SIMABUKURO, E. A., L. M. ESTEVES and G. M. FELIPPE. 2000. Fern spore rain collected at two different heights at Moji Guacu (Sao Paulo, Brazil). Fern Gaz. 16:147–166.

TATE, K. G., J. M. OGAWA, W. E. YATES and G. STUGERON. 1980. Performance of a cyclone spore trap. Phytopathology 70:285–290.

TAUBER, H. 1974. A static non-overload pollen collector. New Phytol. 73:359–369.

TEJERO-DÍEZ, D., M. REYES-SALAS and E. MARTÍNEZ-HERNÁNDEZ. 1988. Lluvia de polen moderno en un gradiente altitudinal con vegetación templada en el Municipio de Ocuilán, Edo. Mex. (Mex.). Palynol. Paleobot. 1:61–80.

TING, D. Y. P., F. HOPF, S. G. HABERLE and D. M. J. S. BOWMAN. 2010. Seasonal pollen distribution in the atmospheric of Hobart, Tasmania: preliminary observations and congruence with flowering phenology. Austral. J. Bot. 58:440–452.

TOVAR-GONZÁLEZ, R. C. 1987. Lluvia de polen en el volcán Popocatépetl: un estudio a lo largo de un transecto altitudinal. Tesis de licenciatura., Facultad de Ciencias Universidad Nacional Autónoma de México, México.

YANG, Y-L. and S-H. CHEN. 1998. An investigation of airborne pollen in Taipei city, Taiwan, 1993–1994. J. Pl. Res. 111:501–508.

American Fern Journal 104(1):7–15 (2014)

Isoëtes viridimontana: A Previously Unrecognized Quillwort from Vermont, USA

Michael A. Rosenthal and Sharon R. Rosenthal
845 Wilcox Road, Arlington, Vermont 05250
Gabriel Johnson, W. Carl Taylor[1], and Elizabeth A. Zimmer
Department of Botany, National Museum of Natural History, Smithsonian Institution Museum Support Center, 4210 Silver Hill Road, Suitland, Maryland 20746

Abstract.—*Isoëtes viridimontana* is described and illustrated. Plants of this species are currently known only from Haystack Pond, a small, acidic, oligotrophic lake in south central Vermont. *Isoëtes viridimontana* is distinguished from other *Isoëtes* species in northeastern North America by its size (less than 5 cm high) and granulate to rugulate megaspore texture.

Key Words.—Isoëtaceae, *Isoëtes viridimontana, new species*

Although plants in the genus *Isoëtes* (Isoëtaceae) are easily overlooked among other vegetation, members of this group have long had the attention of botanists in North America (Engelmann, 1882). This is especially true for several botanists working in New England in the late 1800's (Dodge, 1897; Eaton, 1898; Underwood, 1888). By the 20th century, Eaton (1900) was able to account for five species and at least five interspecific hybrids occurring in New England (although the hybrids were not originally recognized as such). New England is one of the best-botanized regions in North America and even though searches have been extensive, since 1900 only two additional *Isoëtes* species have been found in this region (Britton and Goltz, 1991; Kott, 1981). Also, most of the possible interspecific hybrid combinations appear to have been reported, so it seems that *Isoëtes* are fairly well documented in New England. Therefore, it is surprising that we are able to report the discovery of a previously unrecognized species of *Isoëtes* from New England.

While tracking historic occurrences of *Isoëtes* in Vermont, one of us (M. A. Rosenthal) visited Haystack Pond in the summer of 2010 to verify a previously recorded occurrence of *I. tuckermanii* A. Br. Rosenthal collected the *Isoëtes* in Haystack Pond, but when his specimens did not fit descriptions of *I. tuckermanii*, he asked one of us (Taylor) to examine the material.

The small size of the mature plants and the granulate to rugulate texture of the megaspores clearly distinguished Rosenthal's collections from all other known species in northeastern North America. Analyses of recently collected voucher specimens from Haystack Pond confirm that that these specimens represent a previously unrecognized species.

---

[1] Author for correspondence. Email: taylorwc@si.edu

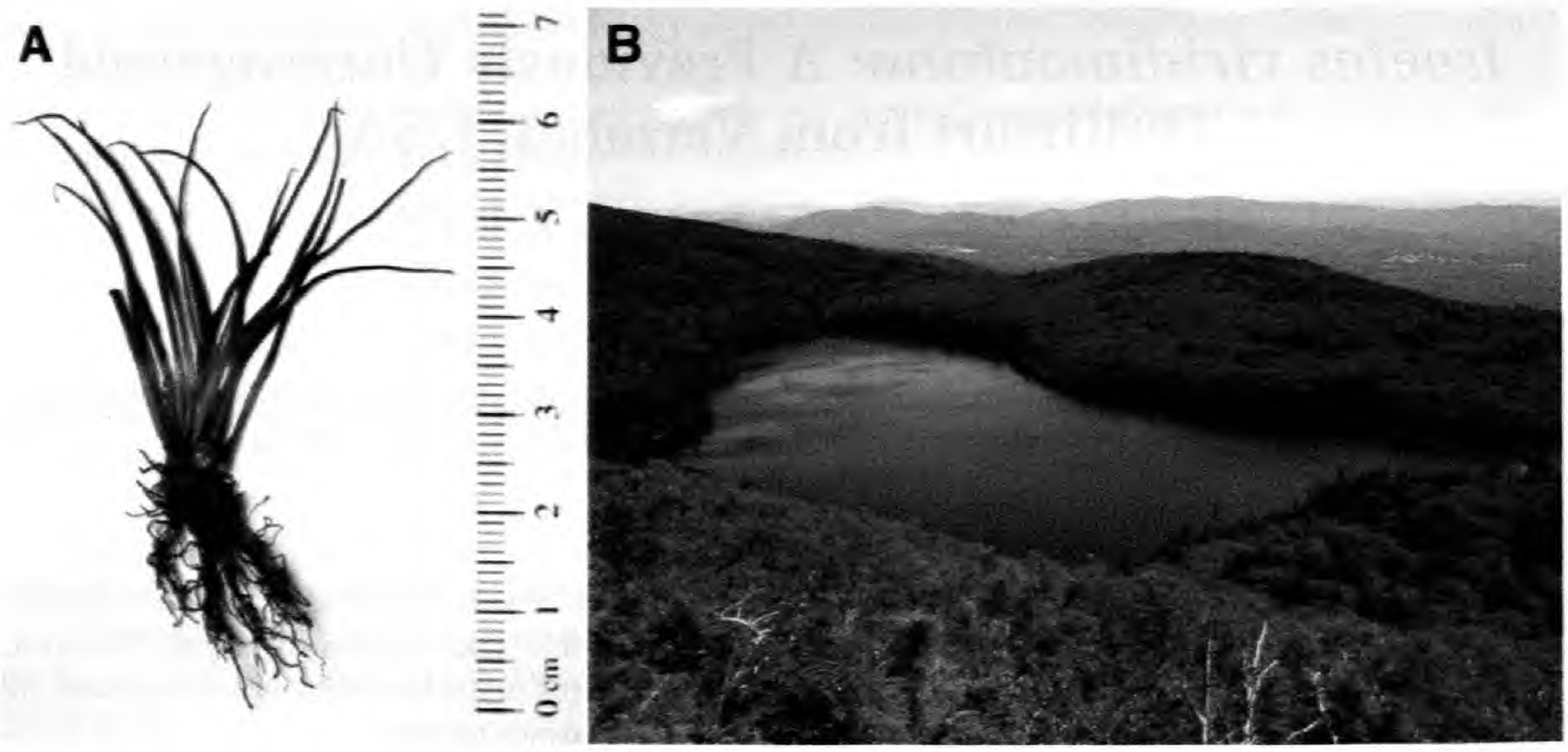

FIG. 1. *Isoëtes viridimontana* and Haystack Pond. A. *I. viridimontana*. Mature, fertile plant from the holotype collection made at Haystack Pond, *Taylor 6743*, 20 August 2012. B. Haystack Pond, northeastern slope of Haystack Mountain, Windham Co., Vermont, 24 June 2012.

Isoëtes viridimontana M. Rosenthal and W. C. Taylor **sp. nov**. TYPE: U.S.A. Vermont: Haystack Pond (42.9170°N, 72.9170°W, elevation 2979 feet), 20 August 2012, *C. Taylor 6743 with M. Rosenthal, S. Rosenthal, A. Gilman, and J. Taylor* (holotype: US; isotypes: MO, NY, VT). Fig. 1A

Plants aquatic, submerged, not emergent, weakly rooted. *Rootstock* bilobed, less than 1 cm across. *Leaves* linear, light green toward apex, brownish to white toward base, gradually tapering to apex, spirally arranged, stiff, spreading, up to ca. 5 cm long, ca. 1 mm wide at mid-length, in tufts of ca. 5–17, semi-terete, with the adaxial surface flattened, abruptly dilated and spatulate at the base, with brownish membranous alae ca. 0.5 mm wide extending along lateral edges from base to ± one-third leaf length. *Ligule* triangular–cordate, ca. 1 mm long. *Velum* incomplete, covering ca. 50% of the adaxial surface of the sporangium. *Sporangia* basal, subglobose–reniform, ca. 2 mm across, adaxial walls spotted by small scattered patches of cells that are pigmented brown. *Megasporangia* containing up to ca. 40 megaspores. *Megaspores* globose, white, trilete, ca. 335–402 μm in diameter, averaging 364 μm in diameter, with granulate to rugulate texture. *Microsporangia* containing thousands of microspores. *Microspores* elliptic–reniform, echinate, light gray in mass, ca. 22.4–27.0 μm in length, averaging 25.0 μm in length.

CHROMOSOMES.—$2n = 22$.

PARATYPE.—**U.S.A. Vermont:** North end Haystack Pond, 11 September 2011, *Michael Rosenthal 0021* (US); 27 June 2013, *Taylor 6808* (US).

Etymology.—The specific epithet for this species *viridimontana* commemorates the state of Vermont. Vermont translates from the French '*vert mont*', or Green Mountain and is often referred to as the Green Mountain State. Vermont includes the majority of the Green Mountains, some of the oldest mountains in New England, which are cloaked by evergreen forests that give them their name. Haystack Mountain and Haystack Pond, where *I. viridimontana* grows, are in the Green Mountains of Vermont.

Distribution.—Isoëtes viridimontana is currently known only from Haystack Pond located on the northeastern slope of Haystack Mountain, Manchester Ranger District (Fig. 1B). Plants grow submerged in ca. 30–70 cm of water scattered in several areas around the lake margin especially near the outflow. Plants are shallowly and weakly rooted in a silt soil containing biotite mica and albite feldspars. The pH of the water is ca. 5. Associated plants include *Lobelia dortmanna* L., *Eriocaulon aquaticum* (Hill) Druce, and *Vallisneria americana* Michx.

MATERIALS AND METHODS

Spore Size and Texture.—Spores were obtained from the type collections made on 20 August 2012. Megaspore size was determined by measuring the diameters of 51 air-dried, mature megaspores taken from several sporiferous plants using a Swift M10LB-P digital microscope (Carlsbad, California) fitted with Motic Images Plus 2 software (Hong Kong, PRC). Measurements were made following the manufacturers' protocols. All magnifications were standardized using a calibration slide. Microspore size was determined in the same manner as for the megaspores except that microspores were hydrated in a wet mount and measured across the long axes of 51 elliptic–reniform microspores.

Air-dried spore samples were prepared for scanning electron microscopy by mounting them on 13 mm stubs that were covered with Temp Fix thermoplastic adhesive (Electron Microscopy Sciences, Hatfield, Pennsylvania) and sputter coated with 30 nm gold-palladium. Spores were imaged with a Philips XL30E Scanning Electron Microscope (Amsterdam, Netherlands). SEM photomicrographs of megaspores were imaged at 200X and microspores were imaged at 2000X.

Chromosome counts.—To obtain chromosome counts, 5–10 mm lengths of roots with actively growing apices were harvested in the field at ca. 11:30 AM from plants collected on 27 June 2013. Roots were pretreated in a saturated solution of paradichlorobenzene for 3 hrs., fixed in Farmer's solution (3:1, 96% EtOH : glacial HAc), and stored at -20°C.

Several days later, root tips were removed from fixative and hydrolyzed in 1N HCl at 60°C for 10 min., washed in 95% EtOH at 21°C, stained with Whittman's hematoxylin for 1 hr., destained in glacial acetic acid for 5 min. A ca. 1 mm length of the root apex was severed and placed on a glass slide in a drop of Hoyer's medium diluted 50% by volume with distilled H_2O. Root tips were macerated and the cells spread on the slide with a brass rod. Preparation were covered with a glass cover slip, inverted on bibulous paper, and pressed on the slide with thumb to blot out excess mounting medium and flatten the preparation. The slide was warmed to 45°C for 30 sec., inverted again, and

TABLE 1. Specimens sampled for phylogenetic analysis.

Species	Voucher collection
Isoëtes bolanderi Englm.	Pond between Star Lake and Trial Lake, Summit Co., Utah, USA; 6 August 2004; *W. C. Taylor 6465 with Michael Windham & Warren Hauk* (MIL). Genbank number KJ135629.
Isoëtes echinospora Durieu	Copps Bay; Ontario, Canada; 4 September 2003; *D. F. Brunton 15765* (MIL). Genbank number KJ135630.
Isoëtes engelmannii A. Braun	Rowanty Creek intersection with Road 703; ca. 3 mi. WNW of Carson; Dinwiddie Co., Virginia, USA; 4 April 2003; *W. C. Taylor 6389 with Lytton Musselman* (MIL). Genbank number KJ135631.
Isoëtes mattaponica Musselman & W. C. Taylor	Along tidal shore of Mattaponi River; ca. ¼ mi. S of public boat dock at Aylett; King William Co., Virginia, USA; 7 August 1998; *W. C. Taylor 6052 with Lytton Musselman* (MIL). Genbank number KJ135632.
Isoëtes prototypus D. M. Britton	Bubble Pond; Acadia National Park; Hancock Co, Maine, USA; 19 August 2004; *W. C. Taylor 6475 with Arthur Haines & Thomas Vining* (MIL). Genbank number KJ135633.
Isoëtes valida (Englm.) Clute	Pond ca. 100 yards NE of Murder Creek and Road 22 intersection; Conecuh Co., Georgia; 2 October 1999; *W. C. Taylor 6115 with Lytton Musselman* (MIL). Genbank number KJ135634.
Isoëtes viridimontana M. Rosenthal and W. C. Taylor	Haystack Pond; ca. ¼ mi. NE of Haystack Mountain summit; Windham Co., Vermont, USA; 20 August 2012; *W. C. Taylor 6743 with Michael & Sharon Rosenthal, Arthur Gilman & Jerry Taylor* (US). Genbank number KJ135635.

squashed by pressing hard several times on the slide above the cover slip with a pencil eraser to further flatten the cells and spread the chromosomes.

Phylogeny.—To determine the relationship of *I. viridimontana* with the other five, aquatic, basic diploid species of *Isoëtes* known to occur in northeastern North America, a phylogenetic analysis was conducted using LEAFY intron 2 sequences from *Isoëtes echinospora* Dur., *I. engelmannii* A. Br., *I. mattaponica* Musselman, Taylor & Bray, *I. prototypus* D. M Britton, *I. valida* (Engelm.) Clute and *I. viridimontana* (Table 1). The LEAFY intron 2 sequence has been found to be variable enough to define *Isoëtes* species (Hoot et al., 2004).

DNA was isolated from 20 mg of silica-dried leaves from each sample by grinding the leaf tissue in a screw cap 1.5 ml microfuge tube containing 100 or more 1.0 mm glass beads and 5 2.3 mm zirconia/silica beads. Tissue samples were disrupted using a FastPrep® 120 tissue grinder (GMI, Ramsey, Minnesota) set at a speed of 6.5 for 30 sec. DNA was isolated from each sample using a DNeasy® Plant Mini Kit (Qiagen, Alameda, California) following the manufacturer's protocol. The LEAFY intron 2 region for all samples was amplified with the primers 30F (5′-GATCTTTATGAACAATGTGG-3′ and 1190R (5′-GAAATACCTGATTTGTAACC-3′) designed by Nancy Napier (Taylor et al. 2004). Each 25 μl PCR reaction mixture contained 2.5 μl 10X ammonium buffer (Bioline, London, UK.), 2 μl 10X dNTPs, 1.25 μl 25 mM $MgCl_2$, 1 μl of 10μM 30F primer, 1μl of 10μM 1190R primer, 0.5 μl BSA solution 10mg/ml (New England Biolabs, Ipswich, Massachusetts), 14.05 μl DNase free

H_2O, 0.2 µl Biolase® Taq enzyme (Bioline) 5 µg/µl, and 2.5 µl of sample DNA. PCR amplification of the LEAFY intron used the following thermal cycler program steps: Step 1 94°C 5 min., step 2 94°C 1 min., step 3 58°C 1 min., step 4 72°C 1min 10 sec., steps 2–4 for 9 cycles, step 5 94° 1 min., step 6 50° 1 min., step 7 72° 1 min., steps 5–7 for 31 cycles, step 8 72° 5 min. The LEAFY intron 2 region PCR products were size confirmed by electrophoresis for 30 min. at 100 volts in a 2% agarose gel in comparison with Hi-Lo® DNA Marker, (Minnesota Molecular, Minneapolis, Minnesota).

PCR products were purified and concentrated by polyethylene glycol precipitation and then ligated into plasmid vector using the TOPO-TA® cloning kit (Life Technologies, Invitrogen, Grand Island, New York). Competent *E. coli* were heat-shocked, transformed with the vector and cultured on selective medium. Vector insert was PCR amplified for 16 colonies and cycle sequenced according to standard protocols; the sequencing products were analyzed with the ABI 3730xl automated capillary sequencer (Life Technologies).

Sequences were edited and a consensus produced for the clones of each species in Geneious 5.6 (Biomatters, Auckland, New Zealand). The consensus sequences were aligned in Geneious using the program MAFFT 7.0 and the alignment exported as a Nexus file for subsequent analyses. Parsimony analyses were carried out in PAUP* v.4.0b10 (Swofford, 2003) using the Branch-and-Bound option; that option also was used for 1000 bootstrap replicates. Likelihood analyses were performed with the program GARLI 2.0 (Zwickl, 2006), using the HKY model produced via jModelTest v2.3 (Nylander, 2004). One hundred bootstrap replicates were run in GARLI. Posterior probabilities were produced in MrBayes 3.0 (Ronquist and Huelsenbeck, 2003) after running 10,000,000 generations with a burn-in of 25%.

RESULTS

Spore size and texture.—Megaspore diameters ranged from 336 µm to 402 µm. The average megaspore diameter was 364 µm. Microspore lengths ranged from 22.4 µm to 27.0 µm. The average microspore length was 25.0 µm. The granulate to rugulate megaspore texture of *I. viridimontana* is distinct from the megaspore textures of all other known, aquatic, basic diploid species in northeastern North America (Fig. 2A–C). The proximal surfaces of the megaspore are generally granulate to slightly verruculate whereas the distal surface is more verruculate to rugulate with the molded ridges occasionally anastomosing. A broad, granulate band or girdle is usually apparent along the distal side of the equatorial ridge. The microspores are echinate on all surfaces (Fig. 2D–F).

Chromosome counts.—Isoëtes viridimontana appears to be a basic diploid with a chromosome number of $2n=22$ (Fig. 3).

Further evidence that *I. viridimontana* is a basic diploid comes from the cloned sequences used in the phylogenetic analysis. Eight cloned sequences of *I. viridimontana* yielded only a single haplotype. If *I. viridimontana* were an

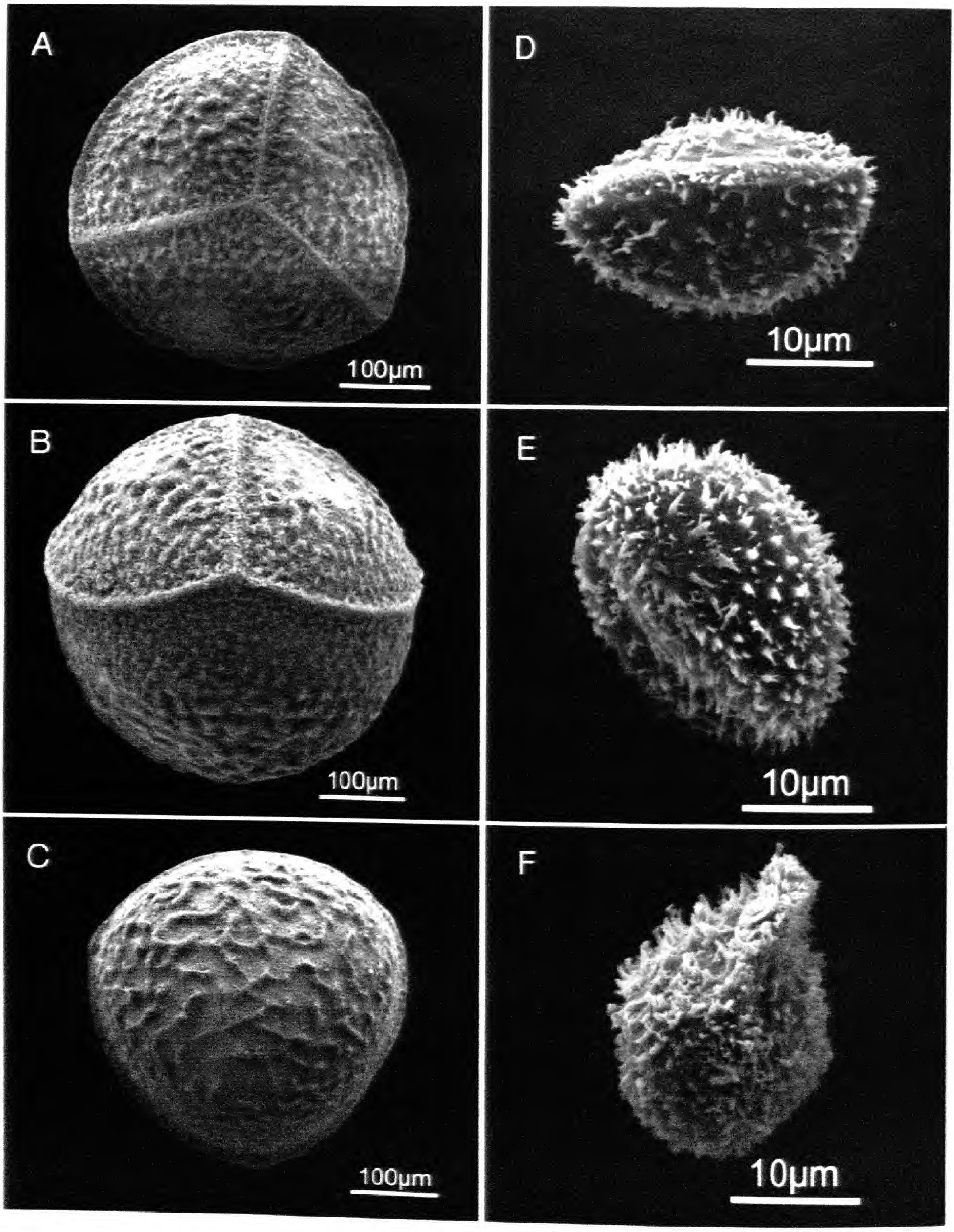

FIG. 2. SEM images *I. viridimontana* spores (*Taylor 6743*, US). A–C. Megaspores. A. Proximal view. B. Equatorial view. C. Distal view. D–F. Microspores. D. Proximal view. E. Lateral view. F. End view.

interspecific hybrid or an allopolyploid more than one haplotype sequence would be obtained.

Phylogeny.—Figure 4 depicts the relationship of *I. viridimontana* to the six aquatic basic diploid species of *Isoëtes* known to occur in northeastern North

FIG. 3. Chromosome figure of *I. viridimontana* from root tip squash (*Taylor* 6808 US) showing 2n=22.

America. Maximum parsimony, maximum likelihood, and Bayesian analyses of LEAFY intron 2 nucleotide sequences all produced a tree with strong support for *I. engelmannii* as sister to *I. viridimontana*. Although LEAFY intron 2 sequences indicate a close relationship between *I. engelmannii* and *I. viridimontana*, these species are morphologically and ecologically distinct. For example, the megaspores of *I. engelmannii* have a reticulate texture formed of regularly anastomosing, lamellate ridges and the microspores have a smooth to papillose surface (Taylor et al., 1993). In contrast, the megaspores of *I. viridimontana* have a granulate to regulate texture and the microspores have an echinate surface. In addition, *Isoëtes engelmannii* is generally a much larger plant with leaves up to 60 cm or more in length, whereas the leaves on mature plants of *I. viridimontana* are less than 6 cm long. Furthermore, *I. engelmannii* grows as an emergent along the margins of ponds and intermittent streams, whereas *I. viridimontana* is a completely submerged aquatic.

DISCUSSION

Isoëtes viridimontana appears to be a rare, localized species that was overlooked by generations of field botanists exploring New England. Its small size, distinct spore surface ornamentation pattern, and unique LEAFY intron 2 nucleotide sequence indicate that *I. viridimontana* should to be recognized as a species of *Isoëtes*. It would be interesting to know if *I. viridimontana* has been involved in the reticulate evolutionary history of *Isoëtes* as a parent in one or more of the many allopolyploid species in North America.

ACKNOWLEDGMENTS

Arthur Gilman furnished thoughtful observations on the habitat and plants of *I. viridimontana*. Lytton Musselman helped us to acquire specimens of *I. mattaponica* and *I. valida* and provided encouragement and insight. Scott Whittaker and Caitlin Baker at the Smithsonian Institution SEM Lab produced the SEM images of *I. viridimontana* megaspores and microspores. Jake White captured the image of Haystack Pond. Jerry Taylor located and imaged the chromosome figure with assistance from Stan Yankowski. Our reviewers and AFJ Associate Editor, Michael Sundue, offered

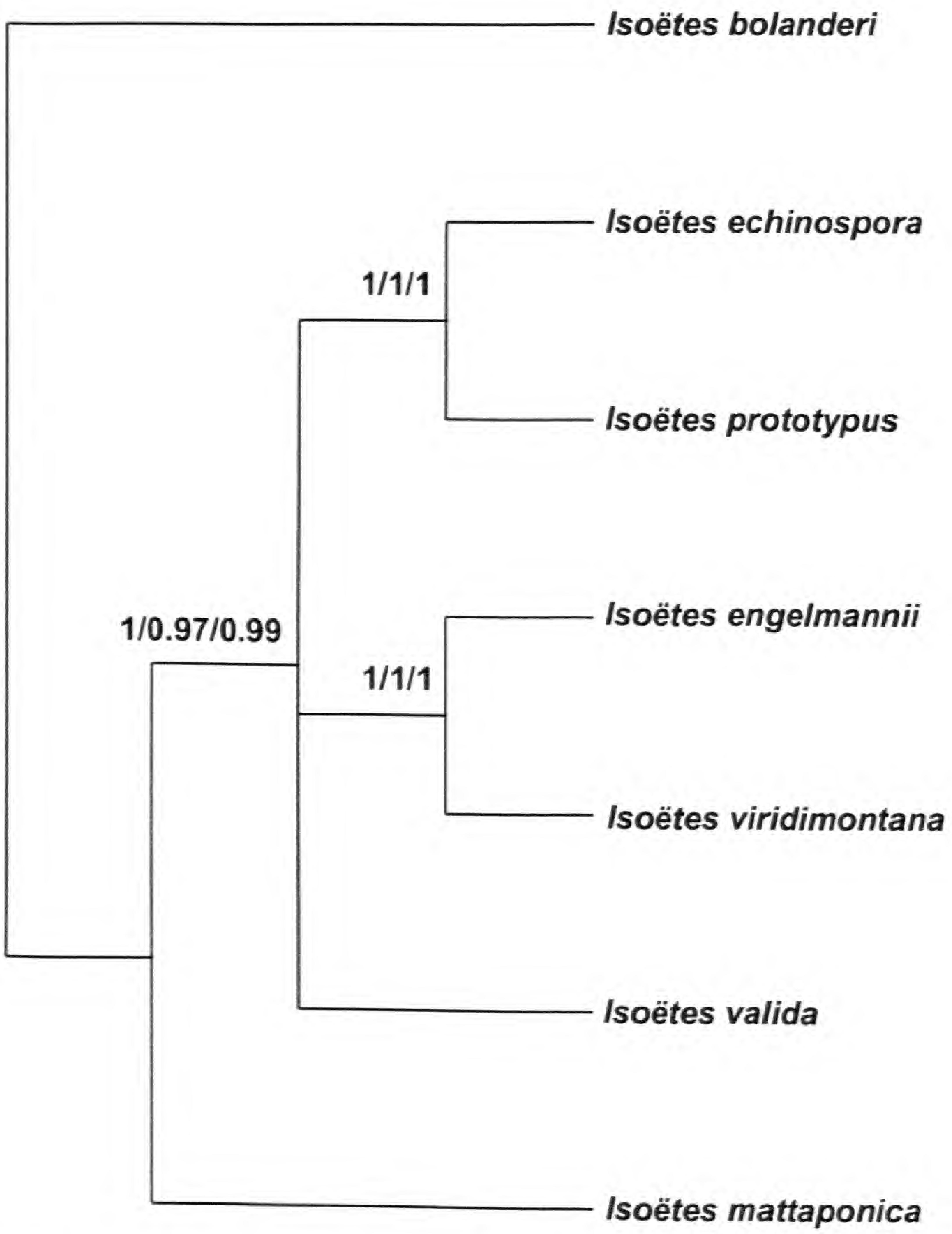

FIG. 4. Phylogenetic tree based on LEAFY intron 2 nucleotide sequences of the six known aquatic, basic diploid species of *Isoëtes* occurring in northeastern North America. The tree is rooted with *I. bolanderi*, a western North American species. Values for analyses based on maximum parsimony bootstraps (1000 reps, exhaustive search option), maximum likelihood bootstraps (1000 reps, HKY model) and Bayesian posterior probabilities (10 million generations, HKY model) are listed above the nodes.

many useful changes that greatly improved this manuscript. The authors are indebted to these individuals for their valuable assistance.

LITERATURE CITED

BRITTON, D. M. and J. P. GOLTZ. 1991. *Isoëtes prototypus*, a new diploid species from eastern Canada. Can. J. Bot. 69:277–281.

DODGE, R. 1897. A new quillwort. Bot. Gaz. 23:32–39.

EATON, A. A. 1898. A new *Isoëtes*. Fern Bull. 6:5–7.

EATON, A. A. 1900. The genus *Isoëtes* in New England. Fernwort Papers 2:1–16.

ENGELMANN, G. 1882. The genus *Isoëtes* in North America. Trans. Acad. Sci. St. Louis 4:358–390.

Geneious 5.6 created by Biomatters, Auckland, New Zealand.

Hoot, S. B., N. S. Napier and W. C. Taylor. 2004. Revealing unknown or extinct lineages within *Isoëtes* (Isoëtaceae) using DNA sequences from hybrids. Amer. J. Bot. 91:899–904.

Kott, L. S. 1981. *Isoëtes acadiensis*, a new species from eastern North America Can. J. Bot. 59:2592–2594.

Nylander, J. A. A. 2004. MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Center, Uppsala University.

Ronquist, F. and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Swofford, D. I. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods, version 4.0b10. Sinauer, Sunderland.

Taylor, W. C., N. T. Luebke, D. M. Britton, R. J. Hickey, D. F. Brunton. 1993. Isoëtaceae H. G. L. Reichenbach-Quillwort Family. Pp. 64–75, *in* Flora of North America Editorial Committee (eds.), *Flora of North America North of Mexico, Vol. 2.* Oxford Univ. Press, New York.

Taylor, W. C., A. R. Lekschas, Q. F. Wang, X. Liu, N. S. Napier and S. B. Hoot. 2004. Phylogenetic relationships of *Isoëtes* (Isoëtaceae) in China as revealed by nucleotide sequences of the nuclear ribosomal ITS region and the second intron of a LEAFY homolog. Amer. Fern J. 94:196–205.

Underwood, L. M. 1888. The distribution of *Isoëtes.* Bot. Gaz. 13:89–94.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD. dissertation, The University of Texas at Austin.

American Fern Journal 104(1):16–21 (2014)

The Identity of *Polypodium gyroflexum* (= *Pleopeltis gyroflexa, Comb. Nov.* – Polypodiaceae)

Pedro B. Schwartsburd
Dept. Biologia Vegetal, Universidade Federal de Viçosa, Av. P.H. Rolfs s.n., Viçosa, MG, Brazil, 36.570-900, email: pedro.schw@ufv.br

Abstract.—*Polypodium gyroflexum* has been a forgotten name since 1940. It is, in fact, an earlier name to a fern recently known as *Pleopeltis repanda.* Here, I provide the new combination, lectotypification, a detailed characterization, and illustrations for *Pleopeltis gyroflexa, comb. nov.*, plus the synonymization of *Pleopeltis repanda. Pleopeltis gyroflexa* is known from two populations located ca. 2500–3000 km from each other, and they show some slight morphological differences. The gap between them comprises Amazon forest, the Amazon River, croplands, disturbed areas, and semi-desert vegetation (Caatinga). A vegetation map with their distribution data is also provided.

Key Words.—Disjunct distribution, Ceará, north-eastern Brazil, *Pleopeltis repanda,* Venezuelan Guayana

Among the first plants collected in the State of Ceará, northeastern Brazil, were those by J. Huber in 1897. Based on this, Christ (1898) published one of the first accounts of ferns and lycophytes from Ceará, citing 28 taxa, two of which he recognized as new: *Pteris pedata* var. *huberi* Christ and *Polypodium gyroflexum* Christ. A more comprehensive account for Ceará was published by Brade (1940), based on Huber's collections and also on a more complete collection made by J. Eugenio in 1937. Brade (1940) recognized 67 taxa (including five new taxa), and regarded *Pol. gyroflexum* as endemic to Ceará. After Brade's publication, *Pol. gyroflexum* has been forgotten, not listed in further accounts of Brazilian ferns (e.g., Barros, Lira, and Silva, 1988; Barros *et al.*, 2004; Labiak and Hirai, 2010), nor in any synonymy.

Smith (1990, 1995), when working on the ferns from Venezuela Guayana, noticed an undescribed *Pleopeltis,* that was unique in having repand lamina margins and lacking scaly paraphyses, and he described it as *Pl. repanda* A.R. Sm. Later, Labiak and Prado (2007) expanded the known distribution of *Pl. repanda* into northwestern Brazil and Guyana.

After analyzing types and recent collections, and performing field expeditions in northeastern Brazil, I have concluded that *Polypodium gyroflexum* and *Pleopeltis repanda* are conspecific. *Polypodium gyroflexum* has priority over *Pl. repanda* by almost 100 years; thus, the new combination for *Pleopeltis gyroflexa* in *Pleopeltis* is here provided, along with the synonymization of *Pl. repanda.*

Materials and Methods

Images of the type collections were analyzed through the websites of JStor Plant Science, and University of California and Jepson Herbaria. Materials from ALCB, HRB, and HUEFS herbaria were personally analyzed. Other herbaria from northeastern Brazil were visited, but they did not have specimens of *Pleopeltis gyroflexa*.

The map was drawn using the software DIVA-GIS (Hijmans, 2013). For collections with no coordinate data, I estimated locations through searches in Google^{TM} Earth. Since the record for Guyana is based on an informal communication (see Labiak and Prado, 2007: 119), I added it near the border between Venezuela and Brazil.

Several localities in northeastern Brazil were visited during March–May 2011, especially in the States of Bahia, Pernambuco, and Ceará. Only one population of *Pleopeltis gyroflexa* was found, in Serra do Baturité, Ceará.

RESULTS

Pleopeltis gyroflexa (Christ) Schwartsb., ***comb. nov.*** for *Polypodium gyroflexum* Christ, Bull. Herb. Boissier 4:994. 1898. TYPE: BRAZIL. Ceará: Serra de Baturité, Guaramiranga, epiphyte sur les caféiers, [auf cafestrauchern hinfig], Sep 1897, *J. Huber s.n.* [*g120*] (lectotype, here designated: P-00633206, image seen; isolectotype: MG-*n.v.*). Figs. 1A–E.

Pleopletis repanda A.R. Sm., Ann. Missouri Bot. Gard. 77:259, Figs. 3A–D. 1990. TYPE: VENEZUELA. Bolívar: Altiplanicie Nuria, upper part of west-facing wooded slopes, E. of Miamo, 300–500 m, 8 Jan 1961, *J.A. Steyermark 88177* (holotype: UC, image seen; isotype: US, image seen).

Plants epiphytic. *Stems* creeping, 3–4 mm diam., scaly; *scales* peltate, lanceolate, 1.5–2.5 × 0.4–0.8 mm, centrally black, margins clathrate and erose-denticulate, commonly comose. *Fronds* subdimorphic, the *fertile* 25–40 cm long, with margins strongly repand, the *sterile* 20–25 cm long, with margins sinuous; *petioles* abaxially terete, adaxially grooved, 3–5 cm × 1–1.5 mm, light brown, glabrous; *fertile laminae* coriaceous, 20–35 × 1.3–2.8 cm, linear-elliptic, broadest in the proximal 1/4 or in middle, the *bases* attenuate to cuneate, the *apexes* attenuate, the *margins* entire in the lower half, strongly repand in the distal half, abaxially with sparse lanceolate peltate *scales*, 0.3–1 mm long, brown to blackish, with light brown margins, adaxially glabrous; *sterile laminae* coriaceous, 15–20 × 1.2–1.8 cm, linear-elliptic, broadest in the middle, the *bases* attenuate, the *apexes* cuneate to acute, the *margins* irregularly sinuate, the *indument* similar to fertile laminae; *rachises* abaxially and adaxially terete, stramineous with dark dots, essentially glabrous but with a few scales abaxially; *veins* irregularly anastomosing, adaxially some ending in dark hydatodes; *sori* submarginal, oblong to reniform, 3–5 × 2–3 mm, in one row on each side of midrib, not sunken, without scaly paraphyses; *sporangia* with long pedicels, 0.5–0.7 mm long, persistent on receptacle after capsule fallen; *spores* reniform, monolete, whitish or yellowish.

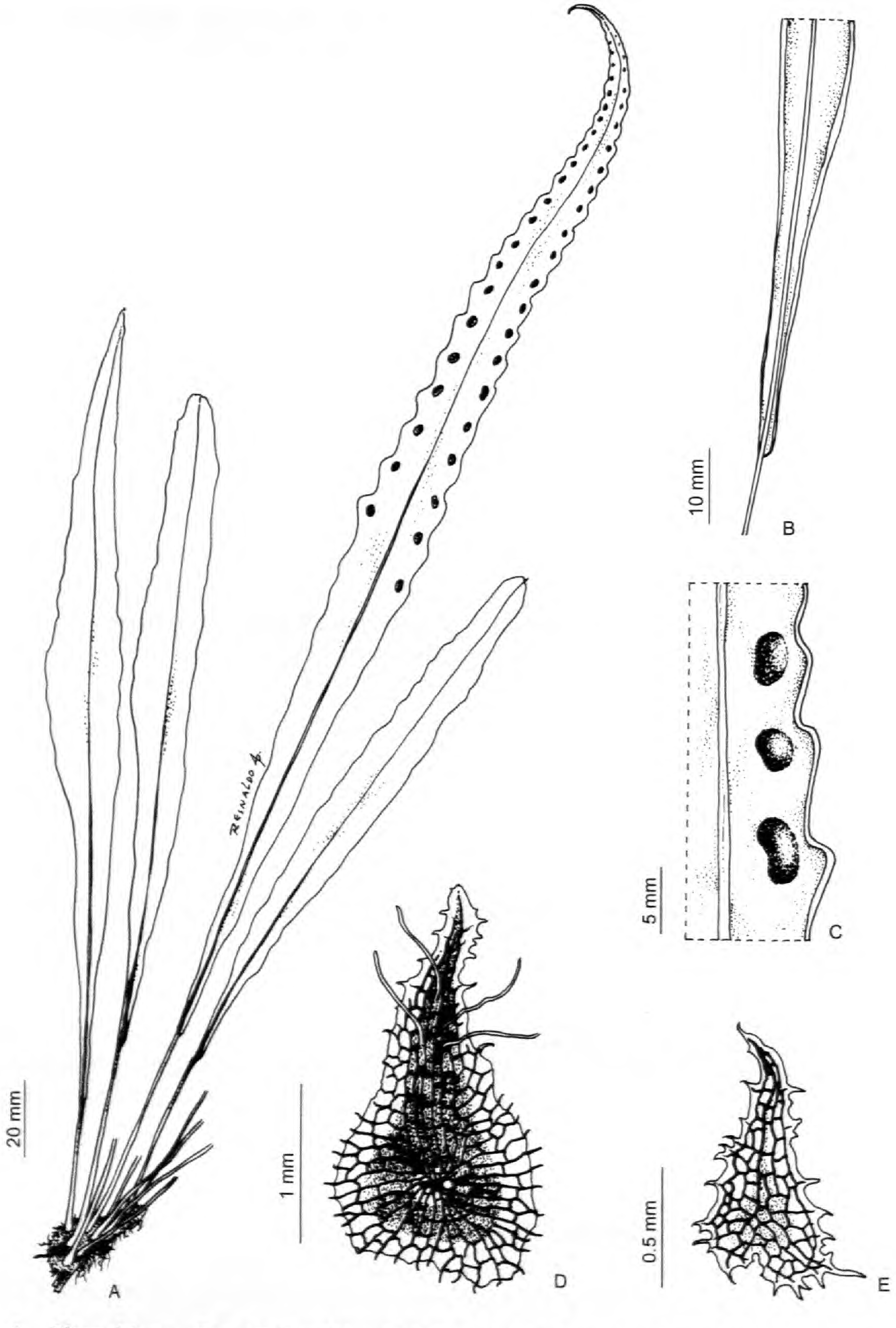

FIG. 1. *Pleopeltis gyroflexa* (*Schwartsburd 2492*): A. habit; B. proximal part of abaxial lamina; C. detail of sori and abaxial laminar margins; D. stem scale; E. laminar scale. Drawn by R. Pinto.

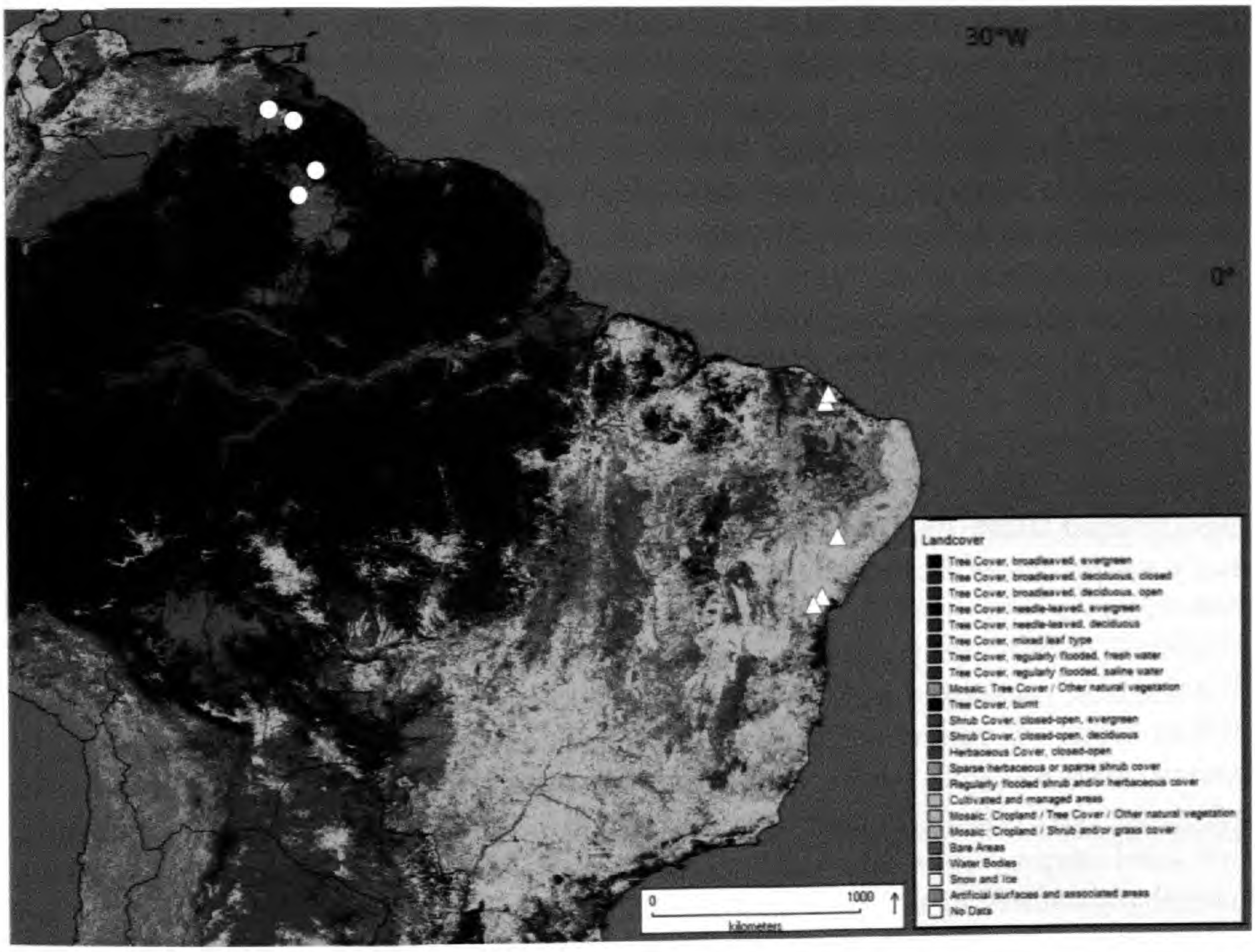

FIG. 2. Distribution of *Pleopeltis gyroflexa* and its two disjunct populations, plotted on a vegetation map. White circles: western population; white triangles: eastern population. Drawn using the software DIVA-GIS.

Distribution and ecology.—Two segregated populations. Western population: eastern Venezuela (in the State of Bolívar), Guyana, and northwestern Brazil (in the State of Roraima), where it occurs as epiphyte in the herbaceous-bushy vegetation at the edges of the Amazon Forest; 300–1050 m elev. Eastern population: northeastern Brazil, in the States of Ceará and Bahia (possibly also in other north-eastern States), where it occurs as epiphyte in wet *inselberg* forests and riparian forests; 400–850 m (Fig. 2).

Additional specimens examined.—BRAZIL. Ceará: Baturité, Serra do Baturité, 700–800 m, 9 Apr 2011, *P.B. Schwartsburd & M.F. Moro 2492* (SP, UPCB, VIC); Pacatuba, Serra de Pacatuba, ca. 03°58′S, 38°47′W, ca. 450 m, 22 July 1997, *M. Almeida Neto & C.A. Meirelles 206* (HUEFS, SJRP-*n.v.*). Bahia: Cachoeira, Bananeiras, s.d., *C. Torrend s.n.* (ALCB-00311); Cachoeira, Morro Belo, Pedra do Cavalo, ca. 12°32′S, 39°05′W, 40–120 m, Dec 1980, *Scardino et al. 979* (ALCB, HRB); Jeremoabo, 10°00′14″S, 38°26′02″W, 427 m, 12 Aug 2005, *E.B. Miranda et al. 901* (HUEFS); Santa Terezinha, 12°51′13″S, 39°28′32″W, 822 m, 25 Oct 2010, *M.L. Guedes et al. 17847* (ALCB).

Pleopeltis gyroflexa is easily recognized by its relatively large fertile fronds (25–40 cm long), repand laminar margins, and lack of scaly paraphyses (even in young fronds). Although the presence of scaly paraphyses has historically been a key feature for the circumscription of *Pleopeltis,* soral scales are not present in all species, as recently pointed out (Otto *et al.*, 2009; Smith and Tejero-Díez, *in press*). In many other aspects (e.g., stem scales blackish, clathrate, peltate, and comose, laminae abaxially with peltate scales, veins irregularly anastomosing, sori roundish and submarginal to marginal), *Pl. gyroflexa* perfectly fits within the concept of *Pleopeltis* (*sensu* Mickel and Smith, 2004; Otto *et al.*, 2009; Smith, 1995; Smith and Tejero-Díez, *in press*). Due to the coriaceous undivided laminae and blackish comose stem scales, *Pl. gyroflexa* presumably fits within the "*Pleopeltis macrocarpa* group" (*sensu* Hooper, 1995). But, Smith and Tejero-Díez (*in press*) suggested *Pl. repanda* may not be an element of this clade.

Pleopeltis gyroflexa is somewhat similar to some specimens of *Pl. macrocarpa* (Bory ex Willd.) Kaulf. with sinuous laminar margins. *Pleopeltis macrocarpa* is widespread in the Neotropics (also in some parts of the Paleotropics — *e.g.*, Smith, 1995; Smith and Tejero-Díez, *in press*), and might possibly occur sympatrically with *Pl. gyroflexa,* or at least nearby (see distribution presented by Barros *et al.*, 2004; Smith, 1995). *Pleopeltis gyroflexa* differs from *Pl. macrocarpa* by sparse, lanceolate laminar scales with light brown margins (*vs.* scales numerous, rounded to lanceolate, with whitish margins), sori oblong to reniform and not sunken (*vs.* sori round and sunken; the soral impressions adaxially visible), and lack of scaly paraphyses (scaly paraphyses present and numerous) — Figs. 1A–E.

Pleopeltis gyroflexa is known from two markedly disjunct populations, which are distant ca. 2500–3000 km from each other. Within this gap are the Amazon Forest, the Amazon River, croplands, disturbed areas, and the Brazilian semi-desert vegetation (*Caatinga*; Fig. 2). The western population occurs in eastern Venezuela (Bolívar), Guyana, and northwestern Brazil (Roraima); and the eastern population occurs in northeastern Brazil (Ceará and Bahia). In both areas, collections are few, indicating this species might be locally rare and not very successful in spreading — see examined material above, and material cited by Smith (1990, 1995) and Labiak and Prado (2007).

Some slight morphological differences exist between these two populations: in the western, the laminae are 1.7–2.8 cm wide, proximally cuneate, and broadest in the proximal 1/4 (see Smith, 1990: Fig. 3A); in the eastern, the laminae are 1.3–2 cm wide, proximally attenuate, and broadest in the middle (Figs. 1A, B). In addition, the sori in the western population are present in the distal 2/3 of laminae (Smith, 1990: Fig. 3A), while in the eastern, they are confined to the distal 1/3 of laminae, or rarely in the distal 1/2 (Fig. 1A).

These two populations may represent two different taxa at an infra-specific rank, but further collections and studies are needed. For now, several hypotheses can be made to explain this uncommon distribution, and these may be tested in the future by genotyping populations and performing biogeographical analyses: 1. *Pleopeltis gyroflexa* was once widespread in northern South America (in areas not occupied by Amazon forest), and the two populations now represent relictual populations generated by vicariance; 2. *Pleopeltis gyroflexa* is an element of the *Pl. macrocarpa* group (originated in

Mexico/Mesoamerica, with further radiation into South America – Otto *el al.*, 2009; Smith and Tejero-Díez, *in press*), with an established population in the Guyana region and a further long-distance dispersal to northeastern Brazil; 3. *Pleopeltis gyroflexa* is derived from a Brazilian Atlantic Forest element, with a further long-distance dispersal into the Guyana region. The main question that remains unanswered is: does gene flow remain between the two populations, or are they totally isolated from each other?

Acknowledgments

This work was partially funded by CNPq-Brazil during my Doctorate (Revision of South-American *Hypolepis*, 2008–2012 – trip to northeastern Brazil in 2010), and partially funded by FUNARBE/UFV/Floresta-Escola and SECTES/HidroEx/FAPEMIG (illustrations). I thank Paulo Labiak, Jefferson Prado, and Alan Smith for discussing ideas on the ms., the editors, and the anonymous reviewers for suggestions, Marcelo Moro for helping in the field, Renato Rodrigues and Laura Lima for their hospitality during my trip to northeastern Brazil, the Curators and staff of ALCB, EAC, HRB, HUEFS, and HVASF herbaria, Reynaldo Pinto for the illustrations, and Simone F. Silva for support.

Literature Cited

Barros, I. C. L., O. C. Lira and A. J. Silva. 1988. Distribuição geográfica das pteridófitas ocorremntes no Estado de Pernambuco, Brasil. Acta Bot. Bras. 2:47–84.

Barros, I. C. L., M. R. Pietrobom da Silva, A. C. P. Santiago and S. R. S. Xavier. 2004. Os gêneros *Campyloneurum, Dicranoglossum, Niphidium, Pecluma* e *Pleopeltis* (Polypodiaceae - Pteridophyta) para a região Nordeste Setentrional brasileira. Bradea 10:35–64.

Brade, A. C. 1940. Contribuição para o estudo da flora Pteridophyta da Serra de Baturité, Estado do Ceará. Rodriguesia 4:289–302.

Christ, H. 1898. Fougères recueillies dans le bassin inférieur de l'Amazone par le Dr. J. Huber à Para. Bull. Herb. Boissier 4:991–994.

Hijmans, R. J. 2013. DIVA-GIS, a geographic information system for the analysis of biodiversity data. Version 7.5. Available at: *http://www.diva.gis.org*

Hooper, E. A. 1995. New combinations in the *Pleopeltis macrocarpa* group (Polypodiaceae: Polypodieae). Amer. Fern. J. 85:75–82.

Labiak, P. H. and J. Prado. 2007. New records of pteridophytes from Bolivia and Brazil. Amer. Fern J. 97:113–123.

Labiak, P. H. and R. Y. Hirai. 2010. Polypodiaceae. Pp. 547–552, *in* R. C. Forzza et al. (orgs.). 2010. *Catálogo de plantas e fungos do Brasil.* Rio de Janeiro: Andrea Jakobsson Estúdio, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro.vol. 1.

Mickel, J. T. and A. R. Smith. 2004. The Pteridophytes of Mexico. Mem. New York Bot. Gard. 88:1–1055.

Otto, E. M., T. Janssen, H.-P. Kreier and H. Schneider. 2009. New insights into the phylogeny of *Pleopeltis* and related Neotropical genera (Polypodiaceae, Polypodiopsida). Molec. Phylogen. Evol. 53:190–201.

Smith, A. R. 1990. Pteridophytes of the Venezuelan Guyana: new species. Ann. Missouri Bot. Gard. 77:249–273.

Smith, A. R. 1995. Polypodiaceae. Pp. 219–249, *in* P. E. Berry, B. K. Holst, and K. Yatskievych (vol. eds.) 1995. Pteridophytes, Spermatophytes: Acanthaceae-Araceae *in* J. A. Steyermark, P. E. Berry, and B. K. Holst (gen. eds.). *Flora of the Venezuelan Guayana.* Missouri Botanical Garden Press, St. Louis.vol. 2.

Smith, A. R. and J. D. Tejero-Díez. *In press. Pleopeltis* (Polypodiaceae), a redefinition of the genus and nomenclatural novelties. Bot. Sci.

American Fern Journal 104(1):22–23 (2014)

SHORTER NOTES

A First Record of *Polypodium saximontanum* for the Flora of Montana.— Recent fieldwork in western Montana has yielded a new locality for *Polypodium saximontanum* Windham, a species previously known only from scattered populations in northern New Mexico, Colorado, eastern Wyoming, and western South Dakota. *Polypodium saximontanum* is an allotetraploid member of the *Polypodium vulgare* reticulate complex, derived originally through hybridization between the diploid species *Polypodium amorphum* Suksd. and *Polypodium sibiricum* Sipliv. (Windham, Contr. Univ. Michigan Herb. 19:31–61. 1993; Haufler et al., *Polypodium*. Pp. 315–323 *in* Flora of North America North of Mexico, vol. 2. Oxford University Press, New York. 1993). The collection of *P. saximontanum* from the Bitterroot Mountains in Ravalli County, Montana, greatly expands the geographic range for this species, occurring approximately 800 kilometers to the northwest of the closest known population in the Laramie Range of Wyoming. As is characteristic of *P. saximontanum,* the new specimen was obtained from a population growing on granitic rock, but at elevations lower than previously reported (1237 m versus 1800–3000 m; Windham 1993; Haufler et al. 1993).

Initially, the Montana collection was identified as *Polypodium hesperium* Maxon, a relatively common species in the mountains of western Montana (pers. obs.) and the only *Polypodium* species reported in the Checklist of Montana Vascular Plants (S. Mincemoyer, Checklist of Montana Vascular Plants. Montana Natural Heritage Program, Helena, Montana. 2012). Morphologically similar to *P. saximontanum*, *P. hesperium* is an allotetraploid derived from the diploids *P. amorphum* and *Polypodium glycyrrhiza* D.C. Eaton. Microscopic inspection of the sori (10–40× magnification) revealed the presence of glandular sporangiasters among the sporangia, a character diagnostic of *P. saximontanum*, but absent from *P. hesperium* (Windham 1993; Haufler et al. 1993). Spores removed from the sporangia were well formed, with an average length of 67 μm, consistent with the size class of other tetraploids in the complex. Analysis of biparentally inherited *gapCp* nuclear sequence data revealed that the Montana collection contains alleles inherited from both *P. amorphum* and *P. sibiricum* (Sigel et al., unpubl.), further supporting its identification as *P. saximontanum*.

Polypodium saximontanum Windham. U.S.A. Montana, Ravalli County, Bitterroot National Forest, Sweathouse Creek, on the north side of Sweathouse Creek trail, 46°25′5.3″N, 114°13′44.4″W, locally common with several large colonies on granite cliffs in *Pseudotsuga menziesii* var. *glauca* forest, southwestern aspect, with *Cystopteris fragilis* and *Rubus*, elevation 1237 meters, 14 Aug 2011, *Erin M. Sigel 2011-41a & b*, with Anne K. Johnson (DUKE, MONTU). Determined by Christopher Haufler, 20 Nov

2013. Collected under National Forest Service Forest Products Free Use Permit for Region 1, permit number 2011-7 to E. M. Sigel.

The authors thank A. R. Smith and G. Yatskievych for their helpful comments and suggestions.—Erin M. Sigel and Anne K. Johnson, Department of Biology, Duke University, Box 90338, Durham, North Carolina, 27708, U.S.A., and Christopher H. Haufler, Department of Ecology and Evolutionary Biology, University of Kansas, 1200 Sunnyside Avenue, Haworth Hall, Lawrence, Kansas, 66045, U.S.A.

INFORMATION FOR AUTHORS

Authors are encouraged to submit manuscripts pertinent to the study of ferns and lycophytes for publication in the *American Fern Journal*. Manuscripts should be sent to the editor at **hauk@denison.edu.** Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication. Mandatory fees will be charged for color figures in print and/or in electronic versions of published papers.

Information for authors, including detailed requirements for formatting manuscripts can be found online at: http://www.amerfernsoc.org/journal.html.

PTERIDOLOGIA ISSUES IN PRINT

The following issues of *Pteridologia*, the memoir series of the American Fern Society, are available for purchase:

1. Wagner, David H. 1979. Systematics of *Polystichum* in Western North America North of Mexico. 64 pp. $10.00 plus postage and handling.

2A. Lellinger, David B. 1989. The Ferns and Fern-allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). 364 pp. $32.00 plus postage and handling.

3. Lellinger, David B. 2002. A Modern Multilingual Glossary for Taxonomic Pteridology. 263 pp. $28.00 plus postage and handling.

4. Hirai, Regina Y., and Jefferson Prado. 2012. Monograph of *Moranopteris* (Polypodiaceae). 113 pp. $28.00 plus postage and handling.

For orders and more information, please contact our authorized agent for sales at: Missouri Botanical Garden Press, P.O. Box 299, St. Louis, MO 63166-0299, tel. 314-577-9534 or 877-271-1930 (toll free). For online orders, visit: http://www.mbgpress.org.

FIDDLEHEAD FORUM

The editor of the Bulletin of the American Fern Society welcomes contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns.

SPORE EXCHANGE

Mr. Brian S. Aikin, 3523 Federal Ave, Everett, WA 98201-4647 (spores.afs@comcast.net), is Director. Spores exchanged and lists of available spores sent on request. http://amerfernsoc.org/sporexy.html

GIFTS AND BEQUESTS

Gifts and bequests to the Society enable it to expand its services to members and to others interested in ferns. Back issues of the Journal and cash or other gifts are always welcomed and are tax-deductible. Inquiries should be addressed to the Membership Secretary.

VISIT THE AMERICAN FERN SOCIETY'S WORLD WIDE WEB HOMEPAGE:

http://amerfernsoc.org/

AMERICAN FERN JOURNAL

Volume 104

Number 2

April–June 2014

QUARTERLY JOURNAL OF THE AMERICAN FERN SOCIETY

SHORTER NOTES

The American Fern Society

Council for 2014

American Fern Journal

EDITOR

MANAGING EDITOR

ASSOCIATE EDITORS

The "American Fern Journal" (ISSN 0002-8444) is an illustrated quarterly devoted to the general study of ferns. It is owned by the American Fern Society, and published at The American Fern Society, ℅ Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711. Periodicals postage paid at Austin, TX, and additional entry.

Claims for missing issues, made 6 months (domestic) to 12 months (foreign) after the date of issue, and orders for back issues should be addressed to Dr. George Yatskievych, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.

Changes of address, dues, and applications for membership should be sent to the Membership Secretary.

General inquiries concerning ferns should be addressed to the Secretary.

Back volumes are avalible for most years as printed issues or on microfiche. Please contact the Back Issues Curator for prices and availability.

Subscriptions:

Society Membership – USA, Canada, Mexico (includes Journal and Fiddlehead Forum)	$30
Society Membership – All other countries (includes Journal and Fiddlehead Forum)	$40
Society Life Membership – $360 (add $120 mailing surcharge for outside USA, Canada, Mexico)	
Regular Membership – USA, Canada, Mexico (includes Fiddlehead Forum)	$15
Regular Membership – All other countries (includes Fiddlehead Forum)	$22
Institutional Membership – $40 to USA, Canada, Mexico; $50 elsewhere (-$3 agency fee)	

POSTMASTER: Send address changes to American Fern Journal, ℅ Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711.

American Fern Journal 104(2):25–48 (2014)

Cultivation Techniques for Terrestrial Clubmosses (Lycopodiaceae): Conservation, Research, and Horticultural Opportunities for an Early-Diverging Plant Lineage

JEFFREY P. BENCA[1]
Department of Biology, University of Washington, Seattle, Washington 98195-1800 USA

ABSTRACT.—Clubmosses (Lycopodiaceae) represent the closest living counterparts to early vascular plants, but inability to culture terrestrial taxa has made much of the clade inaccessible to *ex-situ* conservation, experimental research, and horticulture. In an attempt to identify conditions conducive to repeatable *ex vitro* culture, the utility of clayey and sandy loams amended with pumice as a medium was observed for 20 terrestrial species spanning all three subfamilies of Lycopodiaceae. Using this media class, a series of effective sporophyte cultivation and propagation techniques were developed for all 9 North American genera. Strategies are described for selection of appropriate propagules, establishment, propagation, and long-term maintenance for each genus. Sporophytes of all taxa established readily in oligotrophic, largely inorganic media under high humidity. Large clonal colonies were maintained with frequent application of weak fertilizer solution under bright light, high humidity, and year-round moderate temperatures in two greenhouses, a growth chamber, and laboratory.

KEY WORDS.—Cultivation, Lycopodiaceae, lycophytes, *Lycopodium*, propagation

Lycopodiaceae, commonly referred to as clubmosses, are extant representatives of an ancient lycophyte clade, retaining striking morphological similarities to Late Silurian-Early Devonian lycopsids and their putative allies (Hueber, 1992; Xue, 2011; Kerp *et al.*, 2013). As the only homosporous plants with meristems reminiscent of seed plants (Philipson, 1990; Imaichi and Hiratsuka, 2000), members of this group provide the closest plausible functional and developmental counterparts to basal eutracheophytes (Imaichi and Hiratsuka, 2000: Fig. 6). Aside from their importance phylogenetically, a number of clubmosses (*Huperzia* and *Phlegmariurus* spp.) have medicinal properties, and have yielded huperzine A used to treat neurodegenerative disorders such as Alzheimer's Disease (for review, see Cheng *et al.*, 1996; Tang and Han, 1999). Biologically active and structurally complex '*Lycopodium*' alkaloids have also been isolated from members of other genera (e.g. Ma and Gang, 2004; Mandal *et al.*, 2010).

While several paleotropical epiphytic *Phlegmariurus* spp. are widely grown, the rest of the family consists of terrestrial genera virtually absent from

---

[1] Current address: Department of Integrative Biology and Museum of Paleontology, University of California, 3060 Valley Life Sciences Building, Berkeley, California 94720-2465, USA, e-mail: jbenca@berkeley.edu. This is UCMP publication no. 2052.

cultivation. These terrestrial lineages are not only morphologically diverse but also encompass growth habits more similar to early vascular plants than the few epiphytic taxa accessible to researchers (Kerp *et al.*, 2013). Despite their importance and diversity, little has been published on successful cultivation of terrestrial Lycopodiaceae since Barrows, (1935) aside from slow and difficult pharmaceutical *in vitro* tissue culture and gemma establishment for *Huperzia* (Szyputa *et al.*, 2005; Wang *et al.*, 2011) and *in vitro* sporophyte generation from nodular callus tissue in *Lycopodiella* (Atmane *et al.*, 2000). This dearth of published work stems from a long history of failed to partially successful *ex vitro* culture attempts for terrestrial clubmosses (Jones, 1987; Mickel, 1994; Hoshizaki and Moran, 2001; Byfield and Stewart, 2007; Ma *et al.*, 2007; Cullina, 2008). What literature that does exist on the subject (e.g. Barrows, 1935; Jones, 1987; Heim, 1988; Mickel, 1994; Hoshizaki and Moran, 2001; Cullina, 2008; McAuliff, 2008; Copeland, 2010) is either limited in detail or describes results difficult to replicate in other facilities (Benca, *pers. obs.*).

Several obstacles impeding conservation efforts for terrestrial clubmosses could be overcome if reliable cultivation techniques were made available. Among these are dependence on largely unsuccessful site-to-site transplantation practices of regionally imperiled populations (Byfield and Stewart, 2007) as well as unsustainable wild harvest for pharmaceutical, homeopathic, and floral industries (Matula, 1995; Nauertz and Zasada, 1999; Ma *et al.*, 2006; Ma *et al.*, 2007).

Unlike many ferns, relying upon spore banks and *in vitro* germination are not the most effective means for short-term *ex-situ* conservation of clubmosses, particularly for those with subterranean (non-photosynthetic) gametophytes. Spores of these taxa have a low germination percentage (Whittier, 1977, 1981; Whittier and Webster, 1986; Whittier, 1998) and are slow to germinate (Whittier, 1998). Fortunately, most terrestrial clubmosses are excellent candidates for asexual sporophyte propagation due to their largely clonal growth habit.

Described here are sporophyte *ex-vitro* cultivation techniques and strategies developed across different facility types over several years. Using these techniques while controlling several environmental parameters, cultivation success was replicated for all North American genera of Lycopodiaceae, including several species of conservation concern (Table 1).

Classification.—Lycopodiaceae is divided into 16 morphologically-distinct genera (Vasconcellos and Franco, 1967; Holub, 1975; 1983; 1991; Øllgaard, 1979a; 1987; Haines, 2003; Field and Bostock, 2013) encompassing three subfamilies: Lycopodioideae, Lycopodiellioideae, and Huperzioideae (Wagner and Beitel, 1992; Øllgaard, 2012b). Fossil records indicate an Early Jurassic minimum divergence time for these subfamilies (Wikström, 2001) and their genera represent monophyletic groupings not known to hybridize (see cladograms of Wikström and Kenrick, 2000; 2001; Øllgaard, 2012b).

For simplification, the two subfamilies Lycopodioideae and Lycopodiellioideae are termed ‘strobilate’ clubmosses herein, similarly to Wikström and Kenrick, (2001). Members of these two subfamilies display shoots with

TABLE 1. Sources of material and success in establishment under greenhouse cultivation: UWBG = University of Washington Botany Greenhouse, UCBG = University of California Botanical Garden; UCB Lab = UC Berkeley laboratory; (+) = Cultivation success at the facility; (−) = cultivation failure at facility; (N/A) = Not applicable [i.e., *not tested at facility*]. * denotes *threatened species* or *exploitably vulnerable* (at state level); ** denotes *endangered species* (at state and/or national level); and *$^{(?)}$ denotes possibly new species whose known distribution is highly restricted (Larson, *per. comm.*) *State and national conservation status available on USDA website.* http://plants.usda.gov/threat.html *.

Species	Collector	Locality	UWBG	UCBG	UCB Lab
Dendrolycopodium hickeyi (Wagner, Beitel, Moran) Haines	D. Foglia	Rensselaer Co., NY	+	+	+
*Diphasiastrum digitatum** (Dill. ex Braun) Holub	D. Foglia	Rensselaer Co., NY	+	+	N/A
*Diphasiastrum sitchense*** (Ruprecht) Holub	J. Benca	Snohomish Co., WA	+	−	N/A
Huperzia haleakalae (Brack.) Holub	J. Benca	Snohomish Co., WA	+	N/A	N/A
*Huperzia lucidula** (Michx.) Trevis.	H. Bicher	NC	+	+	+
Huperzia miyoshiana (Makino) Ching	J. Benca	Snohomish Co.,WA	+	+	+
Huperzia occidentalis (Clute) Beitel	J. Benca	Snohomish Co., WA	+	+	+
Lycopodiella alopecuroides ** (L.) Cranfill	P. Sheridan	VA	+	+	+
Lycopodiella appressa ** (Chapm.) Cranfill	P. Sheridan	VA	+	−	+
Lycopodiella inundata 'robust form' (L.) Holub	J. Larson	Muskegon Co., MI	+	−	+
*Lycopodiella margueritae*** Bruce, Wagner, Beitel	J. Larson	Muskegon Co., MI	+	−	N/A
Lycopodiella prostrata (Harper) Cranfill	R. Carter	Camden Co., GA	+	+	+
*Lycopodiella subappressa*** Bruce, Wagner, Beitel	J. Larson	Muskegon Co., MI	+	−	N/A
*Lycopodiella sp. 2**$^{(?)}$	J. Larson	Muskegon Co., MI	+	+	+
Lycopodiella sp. 3 (or hybrid) *$^{(?)}$	J. Larson	Muskegon Co., MI	+	+	+
*Lycopodium clavatum*** L.	J. Benca	Thurston Co., WA	+	+	N/A
*Lycopodium clavatum*** L.	J. Benca	Snohomish Co., WA	+	−	N/A
*Lycopodium cf. clavatum*** L.	C. Husby	Dominican Republic	N/A	+	N/A
*Lycopodium venustulum**$^{(?)}$ Gaudich	K. Kowelo	Oahu, HI	+	+	N/A
Lycopodium cf. venustulum *$^{(?)}$	J. Benca	Hawaii, HI	N/A	N/A	N/A
Palhinhaea cernua (L.) Franco & Vasc.	K. Kowelo	Oahu, HI	+	+	N/A
Palhinhaea cernua (L.) Franco & Vasc.	C. Husby	Hawaii, HI	N/A	+	+
*Palhinhaea cernua** (L.) Franco & Vasc.	C. Alford	Indian River Co., FL	+	−	+
Palhinhaea cernua (L.) Franco & Vasc.	M. Grantham	South Africa	+	+	+
Phlegmariurus reflexus (Lam.) Øllg.	C. Wunderlich	Peru	+	+	+

TABLE 1. Continued.

Species	Collector	Locality	UWBG	UCBG	UCB Lab
Pseudolycopodiella cf. *caroliniana*	P. Sheridan	Surry Co., VA	+	–	+
*Pseudolycopodiella caroliniana*** (L.) Pic. Serm.	P. Sheridan	Surry Co., VA	–	N/A	N/A
*Pseudolycopodiella caroliniana*** (L.) Pic. Serm.	T. Matthews	Broxton Co., GA	N/A	N/A	+
*Spinulum annotinum*** (L.) Haines	E. Duffield	Snohomish Co., WA	+	N/A	N/A
*Spinulum annotinum*** (L.) Haines	C. Carmichael	Antrim Co., MI	N/A	–	N/A

*All specimens (unless noted in acknowledgements) were collected as cuttings from exposed road embankments outside city, county, or state parks. Cuttings were collected from private property only with prior permission of landowners. Only several cuttings were sampled from any wild specimens to ensure minimal impact on natural populations.

anisotomous dichotomous branching, giving rise to determinate, orthotropic aerial branches bearing strobili and indeterminate prostrate to arching trailing stems (referred to colloquially here as "runners") with which they spread vegetatively. While in many cases, runners grow above-ground (e.g. *Lycopodium*), in several genera they are obligately, facultatively, or seasonally subterranean (Fig. 1C,E,F). Collectively, the two subfamilies encompass seven recognizable genera in North America (Lycopodioideae: *Dendrolycopodium, Diphasiastrum, Lycopodium,* and *Spinulum*; Lycopodiellioideae: *Lycopodiella, Palhinhaea,* and *Pseudolycopodiella*) (Fig. 1C–I; Haines, 2003; Øllgaard, 2012a; Øllgaard, 2012b).

In contrast, North American members of subfamily Huperzioideae do not spread via indeterminate runners, and instead shoots undergo isotomous dichotomous branching. The huperzioid growth habit consists of tight clusters of erect to recumbent/pendant shoots. Two genera represent this group in North America (*Huperzia* and *Phlegmariurus*). *Huperzia* sensu stricto have erect shoots that are gemmiferous, while those of *Phlegmariurus* are erect to pendulous but not gemmiferous (Fig. 1A,B) (Øllgaard, 2012b; Field and Bostock, 2013). *Phlegmariurus* is ancestrally epiphytic (Wikström and Kenrick, 1997; Wikström *et al.*, 1999) and its members readily form adventitious shoots from the stem base while *Huperzia* is ancestrally terrestrial, (Wikström *et al.*, 1999) lacks adventitious branching, and instead forms clonal "fairy-rings" as older portions of the dichotomizing shoot system are buried in leaf litter and subsequently degrade (Reutter, 1987).

Materials and Methods

Cultivation techniques are divided into nine chronologic sections for clarity: I) Plant Materials: Selection of Appropriate Propagules, II) Preparation of Cuttings and Root Initiation, III) Greenhouse, Laboratory, and Growth Chamber Conditions, IV) Medium, V) Pot assembly, VI) Planting and Establishment, VII) Greenhouse Acclimation and Specimen Culture, VIII) Propagation and Exceeding Colony Climax Stage, and IX) *Huperzia* Gemmae Propagation.

I. Plant Materials: Selection of Appropriate Propagules.—All taxa were originally obtained as wild-collected cuttings or divisions (Table 1), then established at the University of Washington to supply culture attempts at facilities in California. For *Lycopodium, Lycopodiella,* and *Pseudolycopodiella,* actively growing shoots with one or more undamaged, newly-emerged roots and/or root primordia near their shoot apices were separated from the parent plant using pruning shears (Fig. 2A,E; 7A,B). *Lycopodium* cuttings ranged in length from 20 to 40 cm while *Lycopodiella* and *Pseudolycopodiella* cuttings were 14 to 20 cm.

In *Palhinhaea,* a single dichotomizing root initiates at each point the arching runner establishes contact with the ground (Figs. 1H; 2C,D; 7C). Arching runner apices that had recently developed root primordia (indicated by abaxial swelling at the shoot apex) were separated from the parent colony using

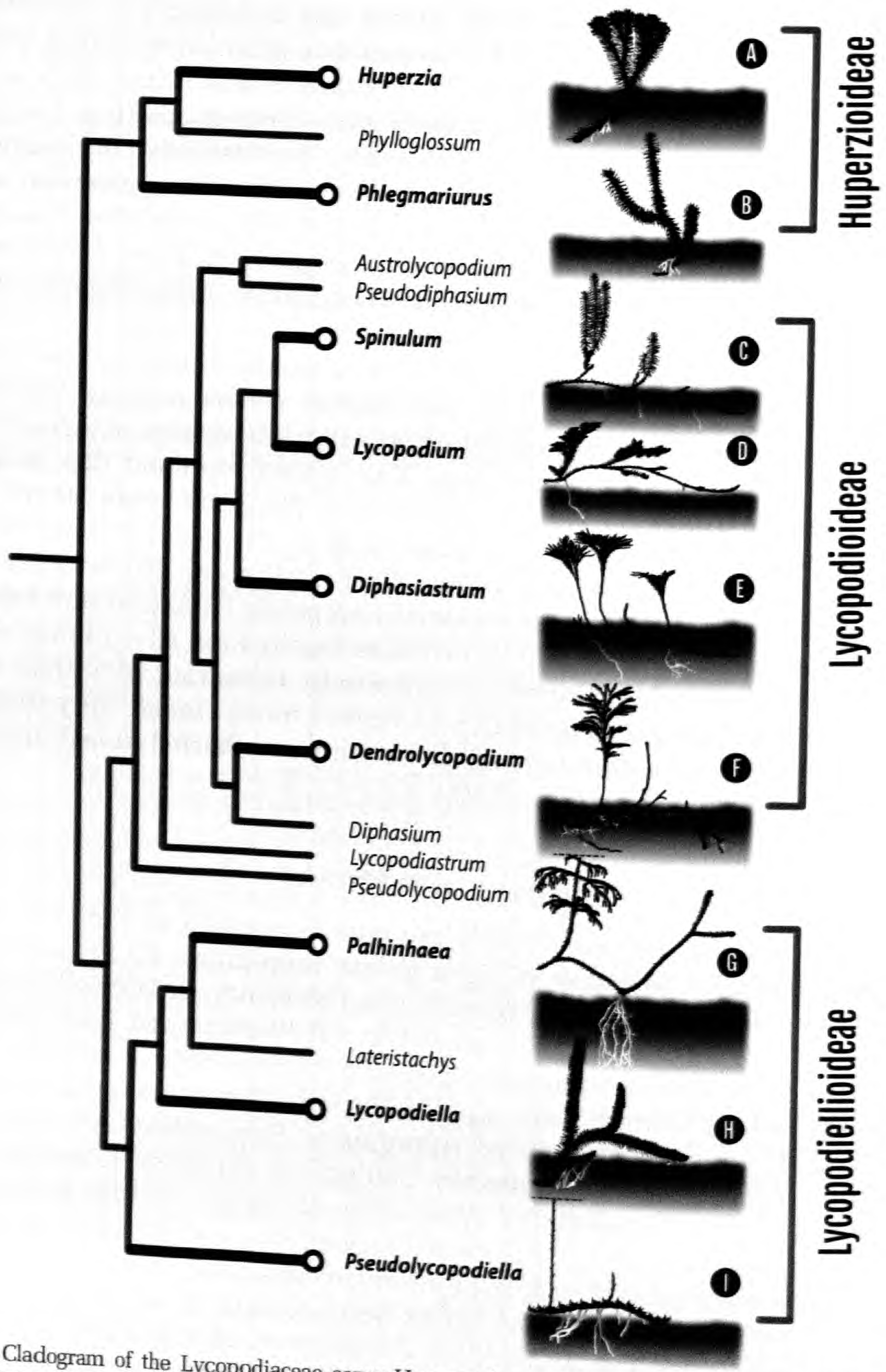

FIG. 1. Cladogram of the Lycopodiaceae *sensu* Vasconcellos and Franco, (1967), Holub, (1975; 1983; 1991), Haines, (2003), and Øllgaard, (2012a,b). Tree based on Fig. 4 of Wikström (2001). Subfamilies designated *sensu* Wagner and Beitel, (1992) and Øllgaard, (2012b). A–I: Aerial and subterranean profiles of growth habits for representatives of the nine North American genera cultivated at UWBG and UCBG (names bolded): A) *Huperzia*– *H. miyoshiana*. B) *Phlegmariurus* – *P. reflexus*. C) *Spinulum* – *S. annotinum*. D) *Lycopodium* – *L. venustulum*. E) *Diphasiastrum* – *D. digitatum*. F) *Dendrolycopodium* – *D. hickeyi*. G) *Palhinhaea* – *P. cernua*. H) *Lycopodiella* – *L. alopecuroides*. I) *Pseudolycopodiella* – *P. caroliniana*.

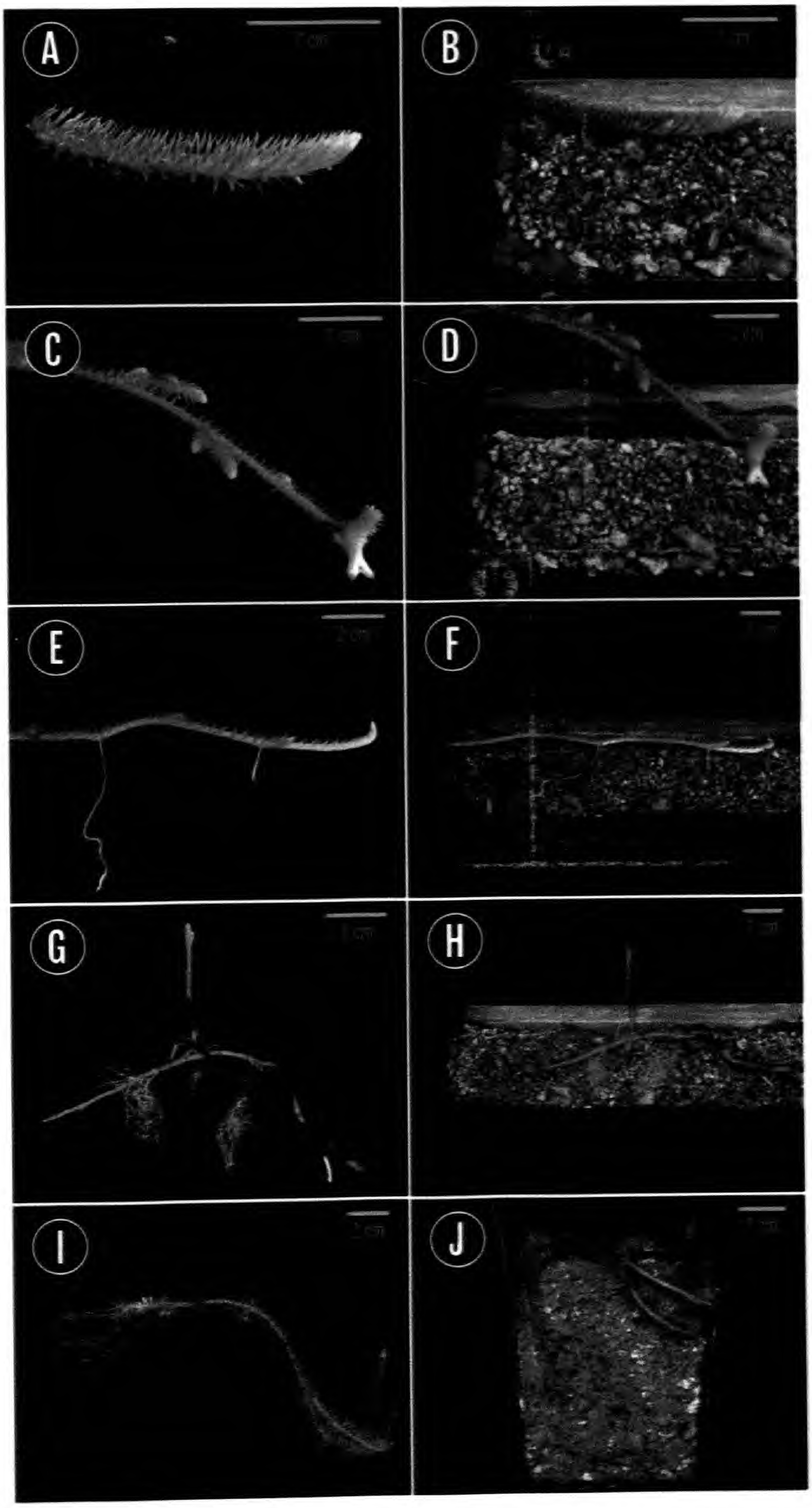

FIG. 2. A,C,E,G,I: cutting material used for establishing clubmosses with contrasting growth habits. B,D,F,H,J: Cross sectional views of pot and substrate column demonstrating orientation of planted propagules for each growth habit. A–B) *Lycopodiella alopecuroides*. C–D) *Palhinhaea cernua*. E–F) *Lycopodium clavatum*. G–H) *Dendrolycopodium hickeyi*. I–J) *Huperzia lucidula*.

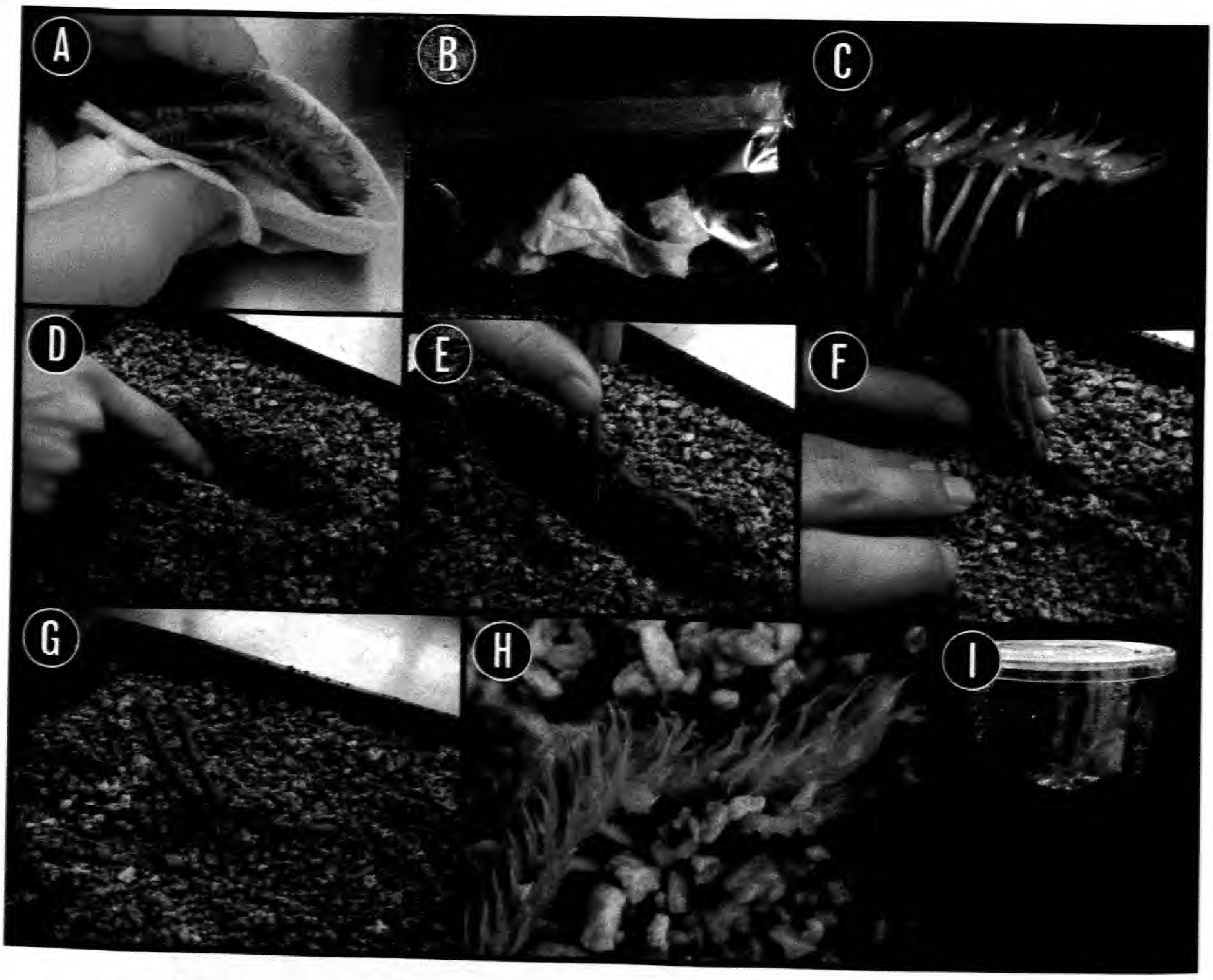

FIG. 3. A–C: Preparation of cuttings and root initiation. A) *Lycopodiella alopecuroides* cuttings wrapped in a 'funnel' of moistened paper towel. B) Wrapped cuttings [A] placed in 1-gallon Ziploc® freezer bag and misted. C) *Lycopodiella appressa* cutting ready for planting: showing root elongation, root hair production, and formation of mucilage sheaths at the root apices. D–G: Planting procedure for a strobilate clubmoss with above-ground runners (*Lycopodiella prostrata*). H) Rooting/establishment of *Lycopodiella prostrata* on medium one week after planting (note production of root hairs on extending root below shoot apex). I) Planted *Palhinhaea cernua* cutting inside sealed clear plastic cup with lid.

pruning shears and measured 10 to 20 cm in length (Fig. 2C). Collection of firmly-rooted apices in the field was avoided as root systems were difficult to extract undamaged. Cuttings collected with damaged dominant root apices seldom established and were susceptible to rot.

For *Dendrolycopodium, Diphasiastrum,* and *Spinulum,* actively growing subterranean runners were excavated using a trowel and clipped from the parent plant. Divisions included one or more aerial branches, newly-produced roots/root primordia, and branching of the subterranean runner system. Cuttings ranged between 20 to 30 cm in length (Fig. 2G).

For *Huperzia* and terrestrial *Phlegmariurus,* entire plants were collected if possible. When not feasible, stems were clipped from the parent plant towards the shoot base so that each retained at least one or more adventitious roots (Fig. 2I). In *Huperzia,* whenever present, gemmae were collected and

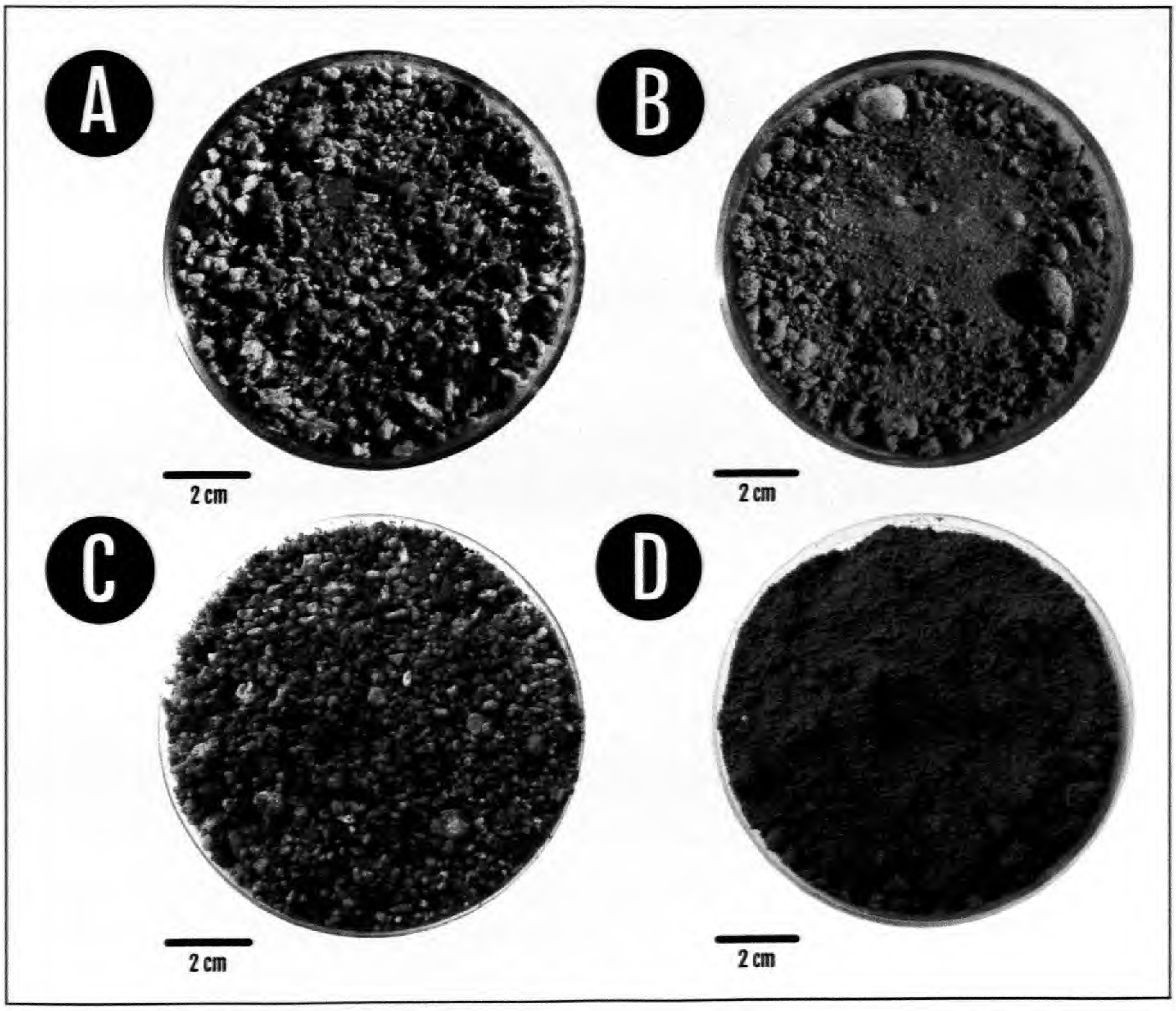

FIG. 4. A) Clayey loam/pumice mix used for growing terrestrial clubmosses at UWBG and in growth chambers. B) Clayey loam used in medium at UWBG and in growth chambers. C) Sandy loam: pumice mixture used at UCBG and in the laboratory. D) Sandy loam used in medium at UCBG and in the laboratory.

established using the protocol outlined in the "*Huperzia* Gemmae Propagation" section (Fig. 7E).

II. Preparation of Cuttings and Root Initiation.—After collection, cuttings were rinsed with cool soft tap water to remove adhered sediments and senescent tissues. Once cleaned, a moist paper towel was wrapped in a loose spiral around each individual cutting, ensuring that roots and root primordia (but not shoot apices) were placed in contact with the towel (Fig. 3A). For taxa with 'fleshy' turgor-supported stems (e.g. *Lycopodiella*, *Pseudolycopodiella*, *Huperzia*, and *Phlegmariurus*) the paper towel used was nearly saturated with water (Table 2). For taxa with more structurally-reinforced, rigid or wiry stems (e.g. *Dendrolycopodium*, *Diphasiastrum*, *Lycopodium*, *Palhinhaea*, and *Spinulum*) the towel was only lightly misted (Table 2). Lower moisture levels were necessary for the latter taxa due to their susceptibility to rot under damp conditions.

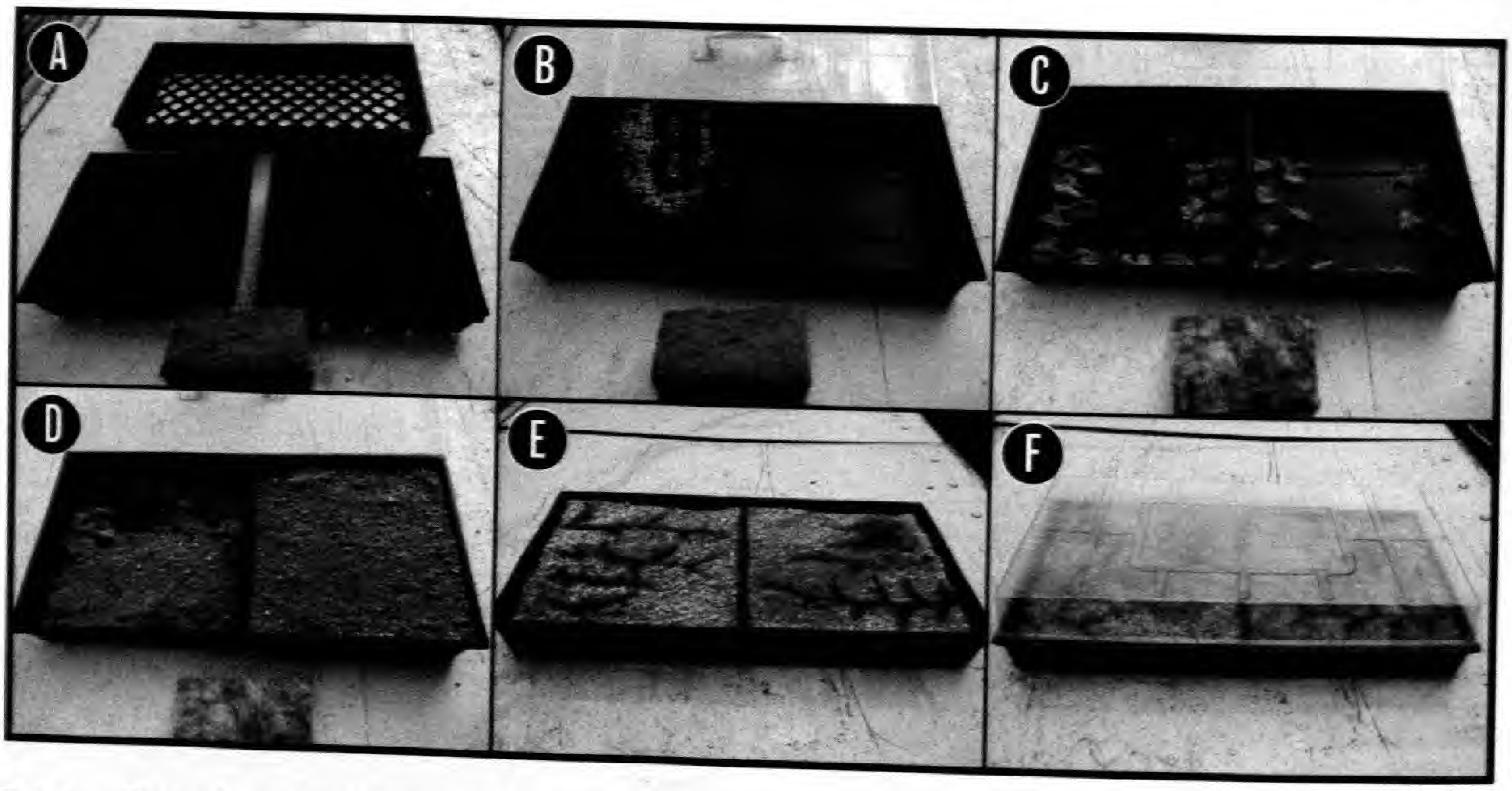

FIG. 5. Procedure for tray assembly and planting cuttings. A) Materials: two 11×11″ half-trays [used in place of one 1020 greenhouse tray], a web flat, and pre-soaked hydrophilic rockwool block (clear propagation dome not shown). B) Both half-trays placed into the web flat. C) Plugging drainage holes at the bottom of half trays with hydrophilic rockwool. D) Filling trays with pre-mixed loam/pumice medium. E) *Lycopodium clavatum* cuttings planted in medium and watered with soft tap water. F) Clear propagation dome placed on top of flat.

Wrapped cuttings were then placed in sealed clear plastic bags (1 to 2 gallon Ziploc® freezer bags) on shelves under T-5 grow lights in a laboratory for two to three weeks at 20° to 22°C (Fig. 3B). Rooting in 'fleshy' taxa occurred within 3 to 14 days, and 7 to 20 days in those with wiry stems. During the establishment phase, any regions of cuttings that began senescing were promptly disposed. Cuttings were removed from bags following root elongation, production of root hairs, and exudation of mucilage sheaths (Fig. 3C).

III. Greenhouse, Laboratory, and Growth Chamber Conditions.—Observations were made in greenhouse and growth chamber facilities at the University of Washington (UW), three greenhouses at the University of California Botanical Garden (UCBG), and a laboratory at the University of California, Berkeley (UCB). The source of tap water at the UWBG was naturally neutral to slightly basic; pH ranging from 7.5 to 7.8 without fertilizer solution and slightly acidic (6.8) with fertilizer solution. At the UCBG, the source of tap water was basic (pH: 9); while at UW and UCB, departmental tapwater used to water plants was usually neutral (pH: 6.5–7.5).

At UWBG, observations lasted from 2007 to 2013. Plants were grown on open greenhouse benches in two research rooms constructed of clear-glazed glass. Temperatures in the greenhouse rooms annually ranged from 16.5° to 27°C but were maintained at 22° to 24°C for much of the year. The research rooms both had overhead misting systems that were activated by increasing temperature. This meant that during warmer (~23° to 27°C) summer days, the misting systems operated continuously from 6:00 am to 9:00 pm whereas in October through March, they did not operate at all throughout the day due

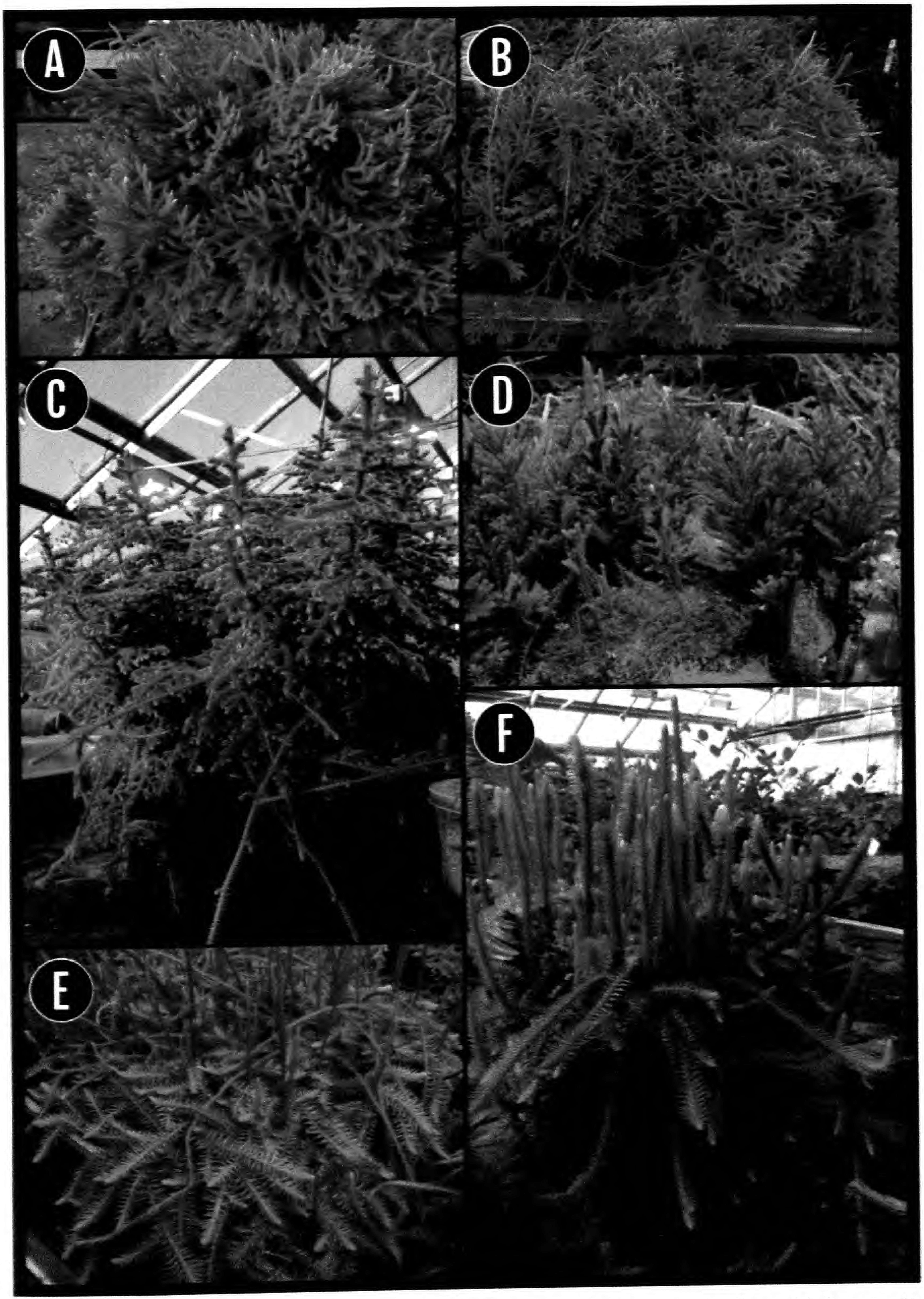

FIG. 6. Terrestrial clubmoss colonies at climax stage: ready for propagation. A) *Lycopodium venustulum* covering greenhouse tray. B) *Lycopodium* cf. *venustulum* in greenhouse trays. C) *Palhinhaea cernua* (South African form) in greenhouse tray elevated upon four perennial pots. D) *Dendrolycopodium hickeyi* in greenhouse tray. E) *Lycopodiella prostrata* clonal mat covering raised greenhouse tray. F) *Lycopodiella alopecuroides* producing strobili while extending beyond confines of a raised greenhouse tray.

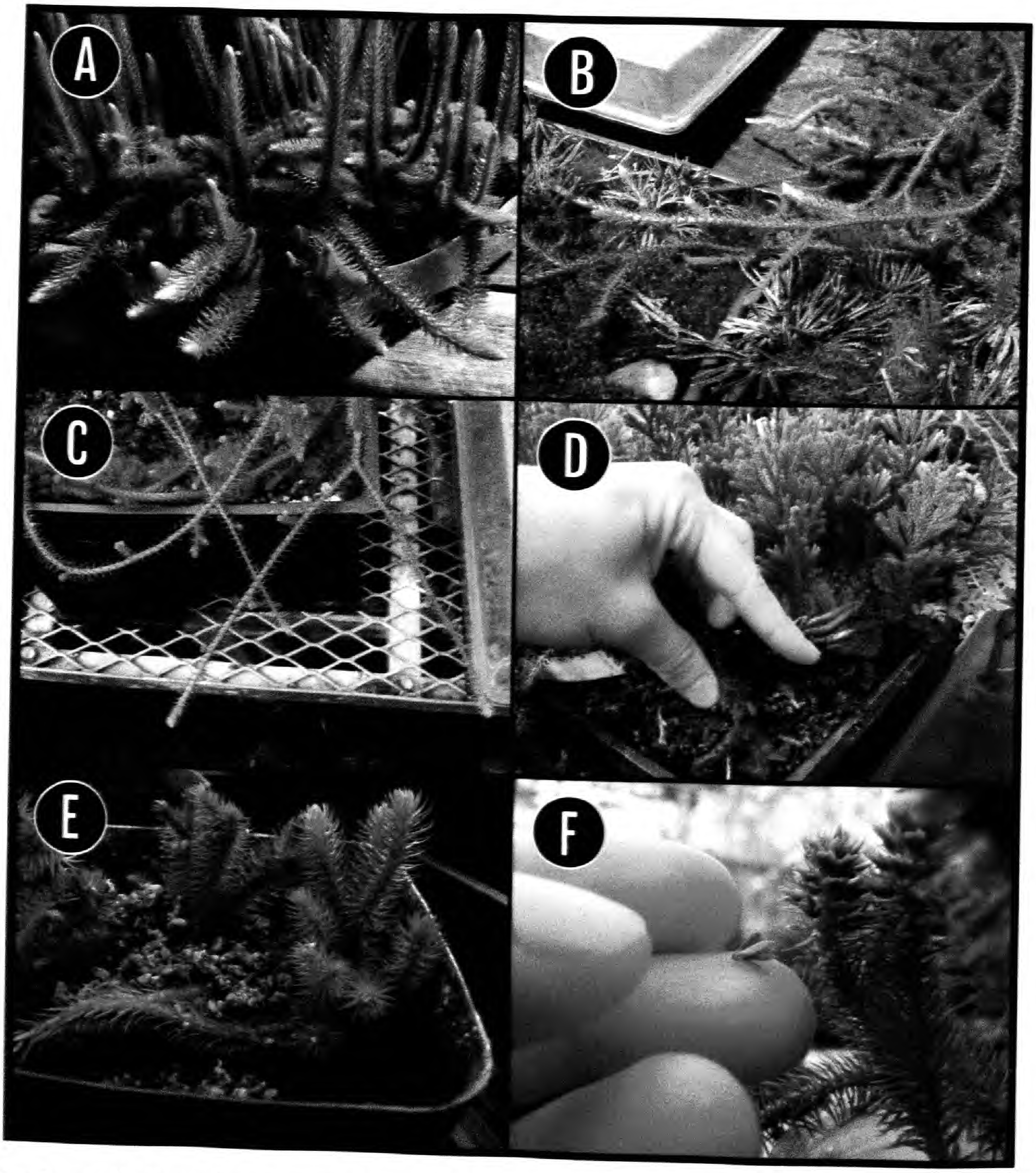

FIG. 7. A–D): Examples of regions of several clubmosses selected for cutting-based propagation. A) Runners of *Lycopodiella alopecuroides* extending beyond pot rim with root primordia. B) *Lycopodium clavatum* runner growing over greenhouse bench initiating roots. C) Shoot region of *Palhinhaea cernua* (South African form) used for cuttings or layering. D) Subterranean shoot system of *Dendrolycopodium hickeyi*. E–F: Huperzioid maintenance and propagation: E) Repotted *Huperzia miyoshiana* in the process of burial for layering (note medium partially covering lower portion of stem), roots initiating towards base. F) *Huperzia miyoshiana* gemma on finger adjacent to branch with intact gemmaphore-gemma complexes.

TABLE 2. Media and preparation phase moisture level by genus.

Subfamily	Genus	Medium	Paper towel moisture level (rooting stage)
Huperzioideae	*Huperzia*	3:1:1 pumice/peat/sandy or clayey loam	nearly saturated
	Phlegmariurus	3:1 pumice/sandy or clayey loam	nearly saturated
Lycopodioideae	*Dendrolycopodium*	3:1 pumice/sandy or clayey loam	lightly misted
	Diphasiastrum	3:1 pumice/sandy or clayey loam	lightly misted
	Lycopodium	3:1 pumice/sandy or clayey loam	lightly misted
	Spinulum	3:1 pumice/sandy or clayey loam	lightly misted
Lycopodiellioideae	*Lycopodiella*	3:1:1 pumice/peat/sandy or clayey loam	nearly saturated
	Palhinhaea	3:1 pumice/sandy or clayey loam	lightly misted
	Pseudolycopodiella	3:1:1 pumice/peat/sandy or clayey loam	nearly saturated

to cool weather. Fertilizer solution was applied every other day via hose systems, alternating weekly between 17:5:17 N-P-K and 20:10:20 N-P-K solution.

At UCBG, observations lasted from 2012 to 2014. Divisions were obtained from specimens cultivated at the UWBG and grown on open benches in three different greenhouses at UCBG. The first greenhouse, House 1, ranged from 11° to 32°C and had an overhead misting system operating for one minute every two hours in summer and one minute every three hours the rest of the year. House 1 was built of opaque fiberglass and cooled via two swamp coolers. The second greenhouse, Research House, was built of white-washed glass panes and ranged from 26° to 29°C with no overhead misting system. The third greenhouse, Propagation House, was also constructed of white-washed glass panes and ranged from 15° to 25°C with no overhead misting system. In each house, 18-18-18 N-P-K soluble fertilizer [Romeo Packing Company, Half Moon Bay, CA] was applied bimonthly via hose systems at 1/4th strength.

Growth chamber observations at UW occurred in 2011. Greenhouse trays of established *Lycopodiella alopecuroides*, *L. appressa*, and *Lycopodium clavatum* propagated from UWBG specimens were placed in a walk-in Conviron growth chamber for two 5-month temperature treatments: 15°C and 25°C. During this time, cuttings were watered every other day alternating between pure soft tap water from UW departmental facilities and dilute fertilizer solution provided by the UWBG.

Laboratory culture conducted at UCB occurred from spring 2013 through winter, 2014. Taxa listed in Table 1 were obtained as cuttings from cultivated specimens at the UWBG and UCBG and planted in a variety of shallow Glad® and Ziploc® clear plastic food storage containers half-filled (2 to 3 cm deep) with peat-ammended medium (Table 2). Planted containers were placed without lids into sealed gallon Ziploc® freezer bags and housed under T-5 growlights set to a 12-hour photoperiod (Fig. 8C). During establishment, cuttings were misted weekly with pure soft tap water. Following establishment

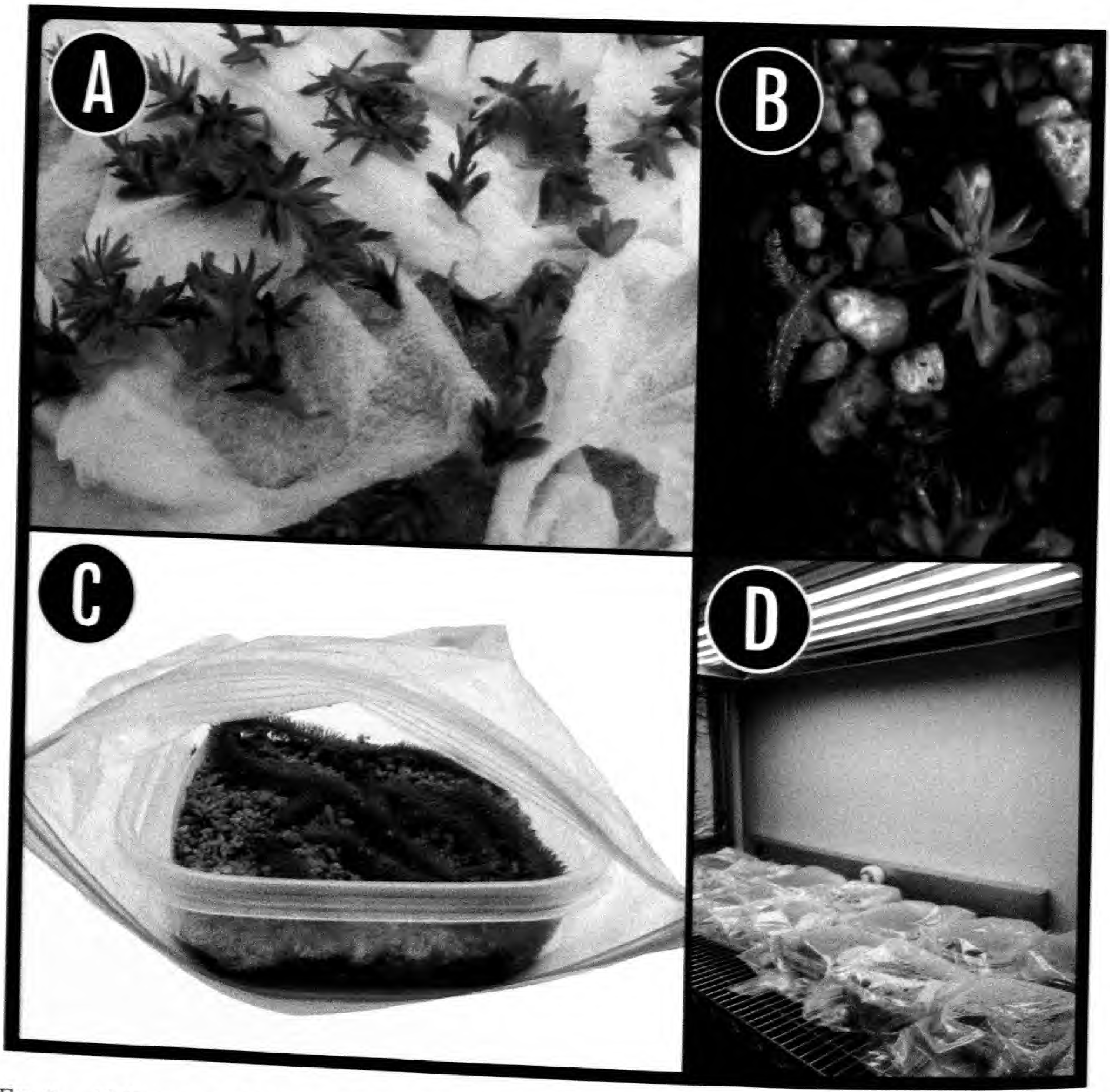

FIG. 8. A) Gemmae of *Huperzia occidentalis* rooting onto damp paper towel several weeks after removal from the parent plant. B) Established gemmling of *H. occidentalis* showing signs of establishment: shoot and root growth. C) *Lycopodiella prostrata* growing in open Glad® food storage container containing medium sealed about to be sealed in a freezer bag. D) Bagged food storage containers containing terrestrial clubmosses on wire shelving unit under a T-5 light bank in the laboratory.

[4 months after planting], containers were watered weekly alternating between one week tap water and one week diluted 7-8-6 N-P-K liquid fertilizer solution (Orchid-Pro; Dyna-Gro, Richmond, CA). Any excess water pooled at the bottom of containers was drained prior to resealing cultures in bags.

IV. Medium.—For a condensed genus-by-genus listing of media, see Table 2. For strobilate members and terrestrial *Phlegmariurus*, a mix of 3:1 fine-grained (~2–5 mm diameter) pumice to a heavy sandy or clayey loam was used (Fig. 4A,C). *Huperzia*, *Lycopodiella*, and *Pseudolycopodiella* were grown in a 3:1:1 mix of fine-grained pumice, heavy sandy or clay loam, and *Sphagnum* peat. At UWBG/UW facilities, clayey loam (Fig. 4B) was collected from an exposed hillside adjacent to the greenhouse facilities. At UCBG/UCB facilities, the sandy loam used (Fig. 4D) was pre-mixed by American Soil and Stone, Richmond, CA using sand from San Francisco and sandy clay loam from San Rafael with no organic amendments. Specifically, this sandy loam was 78.4% sand, 10.4% silt, and 11.1% clay (pH: 7.4, no lime present, ECe: 1.6 dS/m, 0.26 ppm boron, Sodium Absorption Ratio: 1.4). The sand consisted of the following grain sizes and ratios when sieved through a 2 mm screen: 2.4% 1–2 mm diameter, 6.2% 0.5–1 mm diameter, and 69.8% 0.05–0.5 mm diameter.

V. Pot Assembly.—For strobilate taxa, containers were prepared by placing standard 1020 greenhouse trays [11″ W × 21.37″ L × 2.44″ D; #11-3000-1, T.O. Plastics; Clearwater, MN] into heavy-weight web flats [10.75″ W, 21.26″ L, 2.40″ D; #15-9340-1, Belden Plastics; St. Paul, MN] (Fig. 5A–B). Web flats were used to increase structural integrity of greenhouse trays. Drainage holes within trays were then plugged with pre-soaked hydrophilic rockwool (Fig. 5C) to prevent fine-grained sediment loss while still permitting drainage. Trays were subsequently filled with medium, watered with pure soft tap water, then manually patted to a firm state (Fig. 5D–E).

For *Huperzia* gemmae and *Palhinhaea* cuttings, square rose pots [2¼″ W × 3¼″ D; #1680: Anderson Die and Manufacturing; Portland, OR] were prepared in a similar manner to greenhouse trays. For larger specimens of *Huperzia* and terrestrial *Phlegmariurus*, the same procedure was used with respective media (Table 2) in plastic perennial pots [4.25″ W × 4.87″ D; #SQL0450, Kordlok™; Brantford, Ontario].

VI. Planting and Establishment.—For *Lycopodium*, *Lycopodiella*, *Palhinhaea*, and *Pseudolycopodiella*, cuttings were planted so that the entire shoot system remained above ground while roots/root primordia were either buried or directly contacting the medium (Fig. 2B,F; 3D–G). For taxa with subterranean runners, (*Dendrolycopodium*, *Diphasiastrum*, and *Spinulum*), cuttings were planted so that only aerial branches remained aboveground (Fig. 2H). For all taxa, a depression the size and shape of the respective cutting was made in the new medium, the cutting was then lowered into this depression and 'pinched' with substrate when at a desired height (Fig. 3D–G). For wiry cuttings, stones were used to weigh down rooting portions of runners. Once planted, greenhouse trays were covered by clear vinyl propagation domes [2.5″ H × 11″ L × 21.25″ W; #11-3348-1, Hummert International™; Earth City, MO] (Fig. 5F), then placed upon four inverted perennial pots on an unshaded greenhouse bench. *Palhinhaea* cuttings planted in rose pots were misted with pure tap water then placed in clear plastic cups [24 oz.; #SCC PXT24, SOLO® brand; USA]. These cups were then filled to 1.0 cm deep with tap water, sealed, and placed on greenhouse benches in full to partial sun or under growlights (Fig. 3I). Greenhouse trays remained covered by propagation domes and *Palhinhaea* cuttings maintained in cups for 6 to 8 months after planting. Covered trays for all taxa were watered with unfertilized soft tap water on alternating days and capillary pools at the bottom of *Palhinhaea* cups were maintained as necessary to ensure constant elevated substrate moisture and humidity. After this stage *Palhinhaea* cuttings were transferred into greenhouse trays covered by tall propagation domes [6″ H × 21″ L × 11″ W; #6HD, Hummert International^{TM}; Earth City, MO] and treated similarly to the above taxa for an additional month.

For *Huperzia* and terrestrial *Phlegmariurus* cuttings/specimens, only basal regions of shoots (along with any intact roots) were buried under medium (Figs. 2J; 7E). Once planted, pots containing cuttings were placed in clear plastic tote containers with clamping lids [22.75 gallon; #292020; Container Store®] filled to 1.0 cm deep with pure soft tap water for subirrigation and elevated humidity. Totes were placed on greenhouse benches under bright light to partial shade for 6 months.

VII. Greenhouse Acclimation and Specimen Culture (UWBG).—For strobilate clubmosses, establishment was indicated by noticeable shoot elongation and/or branching, generation of new roots, and resistance to uprooting. Once established, propagation domes were removed from trays, which from then on were watered daily, alternating between one day tap water and one day dilute fertilizer solution. Whenever stray runners grew beyond the confines a tray, they were manually flexed and reoriented to colonize regions with open medium. In repositioned arching or wiry runners, rooting portions were pinned to the medium surface using stones or bent skewers to encourage establishment.

In huperzioids, establishment was indicated by terminal shoot growth and division, production of gemmae (in *Huperzia*), and resistance of the plant to uprooting attempts. Once established, specimens were removed from plastic tote containers and placed in partial shade on a greenhouse bench. Plants were watered and fertilized in the same manner as strobilate taxa.

VIII. Propagation and Exceeding Colony Climax Stage.—Two to three years following establishment, most strobilate taxa formed thick, clonal mats covering the entire tray surface (Fig. 6). Despite appearing robust and vigorous in growth, colonies at this ‘climax stage’ consistently began senescing within 6 to 8 months of covering the tray surface. Senescence (indicated by loss of turgor, discoloration, and rotting or drying of actively growing shoots) was abrupt but often followed degradation of older, underlying regions of the clonal network. Colony die-off therefore may have been influenced by a combination of factors such as media degradation/eutrophication and physical obstruction to rooting of younger runners by thickets of older branches.

To prevent colony loss at climax stage, three techniques were employed (one technique per colony). The first involved splitting colonies into several actively growing divisions, removing senescent portions and aged media, and establishment using protocols outlined for cuttings (sections VI–VII). The second involved taking and establishing cuttings from actively growing runners (Fig. 7) using the above protocols. The third technique was to encourage stray runners growing beyond tray confines to root into adjacent trays filled with fresh medium. In such cases, stones or skewers were used to pin rooting portions of runners against the medium surface. Once rooted into and spreading across the new tray, the stray runner was severed from the parent colony and maintained similarly.

When older portions of huperzioid shoots began showing signs of aging or senescence (slight yellowing or browning towards the branch base) plants were unpotted and basal senescent tissues removed, leaving one or more adventitious roots intact towards the shoot base. In a pot containing fresh medium, the oldest (basal) portions of the shoot were laid prostrate in a shallow depression, then buried under 0.5 to 1.5 cm of medium (Fig. 7E). Within 2 to 3 months of layering, adventitious roots emerged from the cortex of newly buried regions. Through time, vegetative propagation resulted from layering of progressively degrading dichotomizing axes.

IX. Huperzia *Gemma Propagation.*—In *Huperzia*, gemmae are either produced throughout the year (e.g. *H. miyoshiana, H. occidentalis, H. haleakalae*) or annually (*H. lucidula*; Reutter, 1987). For collection, gemmae were detached from gemmaphores by gently brushing shoots from the apex to base (Fig. 7F). Detached gemmae were then scattered onto moist, crumpled paper towels placed inside sealable plastic sandwich bags and misted with pure tap water (Fig. 8A). Bags containing gemmae were sealed and placed under T-5 grow lights set to a 12-hour photoperiod at 20° to 22°C in laboratory facilities. Root initiation occurred proximal to the basal abscission region of gemmae within 3 to 14 days, followed closely by shoot elongation and leaf production (Fig. 8A; Reutter, 1987; Wang *et al.* 2011). Rooting gemmlings were transplanted to rose pots containing *Huperzia* medium (Section IV; Table 2) ensuring that both root and abscission zone were buried while the shoot apex remained aboveground. Planted rose pots were then placed in clear 1 gallon Ziploc® freezer bags, sealed, and kept for 6 to 8 months on shaded greenhouse benches or under grow lights at 20° to 22°C. Weekly dilute fertilizer application began one month after planting. After 4 months, pots containing well-established gemmlings (those that rooted and displayed noticeable shoot growth (Fig. 8B)) were then placed on open greenhouse benches either in shallow troughs filled to 0.5 cm of water or on capillary mats to ensure constant moisture of the medium.

Gemmae of annual producers (*H. lucidula*) were treated in the same manner as other *Huperzia*, but provided a cool stratification treatment in a refrigerated storage room under T-5 growlights at 15°C for two months prior. For additional considerations on establishing gemmae, see Wang *et al.*, (2011).

DISCUSSION

The most challenging aspects of growing terrestrial Lycopodiaceae are initial establishment, acclimation to greenhouse conditions, and long-term maintenance of colonies. Success in all three of these stages requires six environmental conditions to be provided: I) constant high humidity and substrate moisture, II) a year-round source of bright light, III) year-round moderate temperatures, IV) fertilizer following establishment, V) well-aerated, largely inorganic substrates with a heavy loam component, and VI) reduced competition, herbivory, and pathogen exposure. Here, each of these six conditions will be discussed.

HUMIDITY AND WATERING.—Most lycophytes are highly susceptible to desiccation due to their passive stomatal control and reduced capacity to respond to atmospheric and soil water deficits, endogenous abscisic acid, and epidermal cell turgor pressure (Brodribb and McAdam, 2011; McAdam and Brodribb, 2012; 2013). Due to these ancestral physiological constraints, high humidity and constant substrate moisture together are requirements for sporophyte survival and growth in contained pots. These conditions are particularly important to maintain during cutting preparation and establishment stages, though the medium should not be kept water-logged nor shoot apices remain overly damp. Although established colonies are less susceptible to humidity fluctuations, they can succumb to dehydration quickly (sometimes within a day) during periods of hot, dry weather if watering regimes are not adjusted accordingly. Susceptibility to drying is most pronounced in root-bound specimens with large volumes of foliage at climax stage (e.g. *Palhinhaea*; D. Ewing, *pers. comm.*). At UWBG and UCBG, few plants showing symptoms of turgor loss (limp or brittle stems and shriveled leaves) recovered when subsequently hydrated. Clubmosses therefore do not appear capable of recovering from dehydration and cannot be permitted to dry at any stage.

Substrate water pH may also impose challenges on clubmoss culture in regions with naturally hard ($pH > 7.0$) tap water. Under such situations, using sodium-softened or distilled water may be necessary to provide neutral to acidic conditions ($pH \leq 7.0$) (Husby, *pers. comm.*).

LIGHT.—Contrary to prior suggestions of Barrows, (1935), bright light is an important component of successful terrestrial clubmoss culture. Many terrestrial taxa are considered stress-tolerating pioneers, forming robust colonies in frequently disturbed open habitats such as erosional scars, bunch grass páramo, forest margins, talus slopes, road embankments, heaths, and peatlands (e.g. Øllgaard, 1979b; Rasmussen and Lawesson, 2002; Muller *et al.*, 2003; Gilman and Marshfield, 2004; Wilfried Bennert *et al.*, 2007; Horn *et al.*, 2013). In Ecuador; where Lycopodiaceae has especially diverse representation, few, if any terrestrial species grow in shaded forest understories while all (more than 50 spp.) occur in cool, open, upland habitats (Øllgaard, 1979b). In evergreen conifer forest understories of western North America, specimens of numerous species are noticeably more diminutive in stature than their conspecifics growing at well-lit forest margins (Benca, *pers. obs.*). Most commonly-encountered hardwood forest understory taxa in the northern hemisphere have orthotropic aerial branches that provide ample light-harvesting opportunities when deciduous canopies are absent (Nauertz and Zasada, 1999). Similarly, Svensson *et al.*, (1994) observed that high latitude *Spinulum annotinum* cuttings produced significantly longer horizontal runners and more aerial branches when grown under deciduous rather than evergreen *Vaccinium* canopies. These observations coupled with presence of such taxa in open habitats at high latitudes and elevations suggest understory clubmosses are more likely seasonally shade-tolerant than shade-dependent. Additionally, maintaining open habitats via frequent disturbance regimes (e.g.

grazing, mowing, or controlled burning) has been a foundational practice in conservation efforts for dwindling populations of prostrate genera in Europe and North America (Byfield and Stewart, 2001; Rasmussen and Lawesson, 2002; Muller *et al.*, 2003; Gilman and Marshfield, 2004; Shackleford, 2004).

TEMPERATURE.—Clubmosses are difficult to establish and maintain if the facility itself is not capable of providing moderate temperatures in conjunction with bright light and high humidity throughout the year. For example, at UCBG, high mortality rates occurred during the establishment phase in many taxa due to prolonged dormancy induced by persistently cold temperatures, low light availability, and short photoperiod in winter (House 1), and high temperatures/drying in summer (Propagation and Research houses). Such losses did not occur during the establishment phase in temperature and humidity-controlled research rooms of the UWBG or in growth chamber and laboratory facilities.

FERTILIZER.—In *S. annotinum*, extended periods of root growth and phosphate uptake along with efficient phosphorous utilization suggest adaptations for growing in oligotrophic substrates (Headley *et al.*, 1985). This condition is likely widespread across the strobilate clades considering the habitats they associate with and the observation that *Diphasiastrum digitatum* cutting establishment is impaired by fertilizer application in the field (Railing and McCarty, 2000). In addition, premature rot of newly planted cuttings treated with fertilizer was observed across several genera at UWBG. However, cutting growth rate of most clubmosses observed at UWBG diminished if fertilizer solution was not provided within several months following establishment. Thus, previous accounts suggesting fertilizer has little (or even detrimental) effects on terrestrial clubmosses (Jones, 1987; Railing and McCarty, 2000) apply only to the rooting/establishment stage. Moreover, increased productivity in established cuttings of all taxa following weak fertilizer application indicates that fertilizer is necessary for culture success following establishment. This response also suggests clubmoss sporophytes do not require mycorrhizal or cyanobacterial associates for successful culture, contrary to prior speculation (e.g. Mickel, 1994; Byfield and Stewart, 2007; McAuliffe, 2008).

MEDIUM.—Well-aerated inorganic substrates amended with mineral loams promote establishment in terrestrial clubmosses more readily than organic-based mixes possibly because these components take longer to degrade while increasing water use efficiency and nutrient buffering capacity (Owen *et al.*, 2008). Mineral loams may also provide trace minerals necessary for growth. Furthermore, decomposing organic soil components can impede plant growth by decreasing aeration capacity of the medium through increased water retention and compaction (Bilderback *et al.*, 2005; Calonje *et al.*, 2010), while releasing harmful concentrations of CO_2 in the rhizosphere (Whitcomb, 2003). Fermenting organic media components also release organic acids that can reduce root growth, increase root oxygen loss, and induce die-back in wetland plants (Nichols, 1981; Armstrong and Armstrong, 1999, 2001).

Prior accounts emphasizing the importance of using acidic peat- and sand-based substrates for clubmoss culture (Heim, 1988; Cullina, 2008) acknowledge such mixes are less productive for strobilate taxa than substrates obtained from their natural habitats. Transplantation and greenhouse cultivation success have also been noted for several understory taxa of the Northeastern United States using well-aerated "native soils" (Barrows, 1935). Since nutrient-poor, heavy mineral substrates are prevalent across many productive habitats (Page, 1979; Øllgaard, 1979b; Jones, 1987; Matula, 1995; Page, 1997, 2004; Gilman and Marshfield, 2004; Rusea *et al.* 2009), clayey and sandy loams are likely an important contributor to the enhanced performance of clubmosses grown in 'native soils.' Establishment of all North American genera in two different types of mineral loam (clayey in Washington and sandy in California) indicates that terrestrial Lycopodiaceae can readily acclimate to a variety of loams in culture. Regardless of type, loam-amended inorganic media consistently sustain more productive colonies than fired clay products (e.g. Turface®).

COMPETITION, PESTS, AND PATHOGENS.—Being slow-growing and generally low in stature, terrestrial clubmosses are especially vulnerable to over-shading from competing vegetation (Øllgaard, 1979b; Page, 1997; Rasmussen and Lawesson, 2002). Once fertilizer application begins, competition from encroaching algal mats and bryophyte colonies becomes a persistent threat, particularly for taxa with prostrate runners such as *Lycopodiella* and *Pseudolycopodiella*. Competition can be reduced by frequent weeding followed by adding new medium, 'mowing' mosses with scissors, or discontinuing fertilizer solution application for several-week increments while flushing the substrate daily with pure soft tap water.

Slugs and snails are the most prevalent pests of terrestrial clubmosses in greenhouses, but can be hampered by elevating trays/web flats above the greenhouse bench upon inverted perennial pots (e.g. Figs. 6C,E,F; 7C) along with monthly slug bait application. Alternatively, a strip of copper wrapped around each tray may eliminate snail and slug ingress altogether (C. Husby, *pers. comm.*).

Under shaded, humid conditions with limited air circulation, colonies of some clubmosses can succumb to fungal infection and rot. Symptoms of infection include loss of turgor in hydrated plants accompanied by discoloration (orange, yellow, graying, or blackening coloration) followed by fungal fruiting body emergence and rotting shoot apices. Such symptoms did not occur in plants grown under bright light, high humidity, and ample air circulation. Infected specimens should be disposed of quickly to prevent spread of pathogens to neighboring plants.

Conclusion.—Providing the environmental conditions, media, and suggested maintenance herein, cultivation success can be achieved for members of all three subfamilies of clubmosses in greenhouse, laboratory, and growth chamber facilities. Given the success observed across much of the phylogenetic span of Lycopodiaceae, these techniques can be used to increase accessibility of the entire clade to *ex-situ* conservation, experimental research, and horticulture.

ACKNOWLEDGMENTS

I thank Alan Smith, Chad Husby, Benjamin Øllgaard, George Yatskievych, Nathalie Nagalingum, and an anonymous reviewer for their feedback on drafts of the manuscript. Thanks also go to Doug Ewing, Holly Forbes, the staff of the University of Washington Botany Greenhouse, and the University of California Botanical Garden for generously providing facilities, equipment, care, and support for plants established during this work. I also thank Ellie Duffield, Phil Sheridan, Jason Larson, Chad Husby, Kapua Kawelo, Dawn Foglia, Richard Carter, Chris Carmichael, Martin Grantham, Charles Alford, Chad Wunderlich, and Tony Matthews for providing source material for many of the species covered in this work. Collection of plant material from Hakalau Forest National Wildlife Refuge, HI was conducted under a permit with Creighton Litton during fieldwork funded by National Geographic Young Explorer's Grant #8985-11.

LITERATURE CITED

ARMSTRONG, J. and W. ARMSTRONG. 1999. *Phragmites* die-back: toxic effects of propionic, butyric and caproic acids in relation to pH. New Phytol. 142:201–217.

ARMSTRONG, J. and W. ARMSTRONG. 2001. Rice and *Phragmites*: Effects of organic acids on growth, root permeability, and radial oxygen loss to the rhizosphere. Am. J. Bot. 88:1359–1370.

ATMANE, N., A. S. BLERVACQ, N. MICHAUX-FERRIERE and J. VASSEUR. 2000. Histological analysis of indirect somatic embryogenesis in the marsh clubmoss *Lycopodiella inundata* (L.) Holub (Pteridophytes). Plant Sci. 156:159–167.

BARROWS, F. L. 1935. Propagation of *Lycopodium*; I. Spores, cuttings, and bulbils. Contr. Boyce Thompson Inst. Pl. Res. 7:267–294.

BILDERBACK, T. E., S. L. WARREN, J. S. OWEN JR. and J. P. ALBANO. 2005. Healthy substrates need physicals too. HortTechnology 15:747–751.

BRODRIBB, T. J. and S. A. MCADAM. 2011. Passive origins of stomatal control in vascular plants. Science 331:582–585.

BYFIELD, A. and N. STEWART. 2007. *Lycopodiella inundata* (L.) Holub: Marsh Clubmoss, Lycopodiaceae. UK Biodiversity Action Plan: Plant Life. http://www.plantlife.org.uk/uploads/documents/Lycopodiella_inundata_dossier.pdf

CALONJE, C., C. HUSBY and M. CALONJE. 2010. Germination and early seedling growth of rare *Zamia* spp. in organic and inorganic substrates: Advancing ex-situ conservation horticulture. HortScience 45:679–683.

CHENG, D. H., H. REN and X. C. TANG. 1996. Huperzine A, a novel promising acetylcholinesterase inhibitor. NeuroReport 8:97–101.

COPELAND, J. 2010. "Experiments in growing *Lycopodium* in pots." American Fern Society, Fern Discussions. http://amerfernsoc.org/discus/messages/14/2719.html?1289861660

CULLINA, W. 2008. Native Ferns, Moss, and Grasses. New England Wildflower Society. Houghton Mifflin Company; New York.

FIELD, A. R. and P. D. BOSTOCK. 2013. New and existing combinations in Paleotropical *Phlegmariurus* (Lycopodiaceae) and lectotypification of the type species *Phlegmariurus phlegmaria* (L.) T. Sen & U. Sen. Phytokeys 20:33–51.

GILMAN, A. V. and V. MARSHFIELD. 2004. *Lycopodiella alopecuroides* (L.) Cranfill Foxtail bog clubmoss. New England Plant Conservation Program; Conservation and Research Plan for New England. New England Wildflower Society.

HAINES, A. 2003. The families Huperziaceae and Lycopodiaceae in New England. VF Thomas Co. Bowdoin.

HEADLEY, A. D., T. V. CALLAGHAN and J. A. LEE. 1985. The phosphorous economy of the evergreen tundra plant, *Lycopodium annotinum*. Oikos 45:235–245.

HEIM, M. 1988. The cultivation of our native clubmosses. Minnesota Hort. 116:24–27.

HOLUB, J. 1975. *Diphasiastrum*, a new genus in Lycopodiaceae. Preslia 47:97–110.

HOLUB, J. 1983. Validation of generic names in Lycopodiaceae: With a description of a new genus *Pseudolycopodiella*. Folia Geobot. Phytotaxon 18:439–442.

HOLUB, J. 1991. Some taxonomic changes within Lycopodiales. Folia Geobot. Phytotaxon 26:81–94.

HORN, K., T. FRANKE, M. UNTERSEHER, M. SCHNITTLER and L. BEENKEN. 2013. Morphological and molecular analyses of fungal endophytes of achlorophyllous gametophytes of *Diphasiastrum alpinum* (Lycopodiaceae). Am. J. Bot. 100:2158–2174.

HOSHIZAKI, B. J. and R. C. MORAN. 2001. Fern Grower's Manual, Revised and Expanded Edition. Timber Press, Portland.

HUEBER, F. M. 1992. Thoughts on the early lycopsids and zosterophylls. Ann. Mo. Bot. Gard. 79:474–499.

IMAICHI, R. and R. HIRATSUKA. 2007. Evolution of shoot apical meristem structures in vascular plants with respect to plasmodesmatal network. Am. J. Bot. 94:1911–1921.

JONES, D. L. 1987. Encyclopaedia of Ferns: An Introduction to Ferns, their Structure, Biology, Economic Importance, Cultivation, and Propagation. Timber Press, Portland.

KERP, H., C. H. WELLMAN, M. KRINGS, P. KEARNEY and H. HASS. 2013. Reproductive organs and *in situ* spores of *Asteroxylon mackiei* Kidston and Lang, the most complex plant from the Lower Devonian Rhynie Chert. Int. J. Plant Sci. 174:293–308.

MA, Y. and D. R. GANG. 2004. The Lycopodium alkaloids. Nat. Prod. Rep. 21:752–772.

MA, X. Q., C. H. TAN, D. Y. ZHU and D. R. GANG. 2006. A survey of potential huperzine A natural resources in China: The Huperziaceae. J. Ethnopharmacol. 104:54–67.

MA, X., C. TAN, D. ZHU, D. R. GANG and P. XIAO. 2007. Huperzine A from *Huperzia* species—An ethnopharmacological review. J. Ethnopharmacol. 113:15–34.

MANDAL, S. K., R. BISWAS, S. S. BHATTACHARYYA, S. PAUL, S. DUTTA, S. PATHAK and A. R. KHUDA-BUKHSH. 2010. Lycopodine from *Lycopodium clavatum* extract inhibits proliferation of HeLa cells through induction of apoptosis via caspase-3 activation. Eur. J. Pharmacol. 626: 115–122.

MATULA, C. F. 1995. Growth rate, growth pattern and the effects of harvest of the Lycopodium obscurum complex in the Lake Superior region. Thesis, University of Wisconsin-Eau Claire.

MCADAM, A. M. and T. J. BROADRIBB. 2012. Fern and lycophyte guard cells do not respond to endogenous abscisic acid. Plant Cell 24:1510–1521.

MCADAM, A. M. and T. J. BROADRIBB. 2013. Ancestral stomatal control results in a canalization of fern and lycophyte adaptation to drought. New Phytol. 198:429–441.

MCAULIFFE, J. 2008. "Family Lycopodiaceae: Culturesheet.org." http://culturesheet.org/lycopodiaceae:start

MICKEL, J. T. 1994. Ferns for American Gardens. MacMillan Publishing Co., New York.

MULLER, S., C. JÉRÔME and K. HORN. 2003. Importance of secondary habitats and need for ecological management for the conservation of (Lycopodiaceae, Pteridophyta) in the Vosges Mountains (France). Biol. Cons. 12:321–332.

NAUERTZ, E. A. and J. C. ZASADA. 1999. *Lycopodium* growth form, morphology, and sustainability of a non-timber forest product. Pp. 110–115 *in* Duchesne, L. C., ed. *Forest Communities in the Third Millennium: Linking Research, Business, and Policy Toward a* Sustainable *Non-timber Forest Product Sector.* USDA Forest Service Central Research Station General Technical Report NC-217.

ØLLGAARD, B. 2012a. Nomenclatural changes in Brazilian Lycopodiaceae. Rodriguésia 63:479–482.

ØLLGAARD, B. 2012b. New combinations in neotropical Lycopodiaceae. Phytotaxa 57:10–22.

ØLLGAARD, B. 1987. A revised classification of the Lycopodiaceae s. lat. Opera Botanica 92:153–178.

ØLLGAARD, B. 1979a. Studies in Lycopodiaceae, II. The branching patterns and infrageneric groups of *Lycopodium sensu lato.* Amer. Fern J. 69:49–61.

ØLLGAARD, B. 1979b. *Lycopodium* in Ecuador—Habits and habitats. Pp. 381–395 *in* Larsen, K. and L. B. Holm-Nielsen, eds. *Tropical Botany.* Academic Press, New York.

OWEN, J. S., S. L. WARREN, T. E. BILDERBACK and J. P. ALBANO. 2008. Phosphorus rate, leaching fraction and substrate influence on influent quality, effluent nutrient content, and response of a containerized woody ornamental crop. HortScience 43:906–912.

PAGE, C. N. 1979. The diversity of ferns: an ecological perspective. Pp. 9–56 *in* Dyer, A. F., ed. *The Experimental Biology of Ferns.* Academic Press, New York.

PAGE, C. N. 1997. *The Ferns of Britain and Ireland.* Second Edition. Cambridge University Press, Cambridge.

PAGE, C. N. 2004. Adaptive ancientness of vascular plants to exploitation of low-nutrient substrates- a neobotanical overview. Pp. 447–466 *in* Hemsley, A. R. and I. Poole, eds. *The Evolution of Plant Physiology: From Whole Plants to Ecosystems.* Linnean Society Symposium Series No. 21. Elsevier Academic Press, London.

PHILIPSON, W. R. 1990. The significance of apical meristems in the phylogeny of land plants. Plant Syst. Evol. 173:17–38.

RAILING, C. A. and B. C. MCCARTHY. 2000. The effects of rhizome severing and nutrient addition on growth and biomass allocation in *Diphasiastrum digitatum.* Amer. Fern J. 90:77–86.

RASMUSSEN, K. K. and J. E. LAWESSON. 2002. *Lycopodiella inundata* in British plant communities and reasons for its decline. Watsonia 24:45–56.

REUTTER, U. 1987. Growth patterns and gemmlings of *Lycopodium lucidulum.* Amer. Fern J. 77:50–57.

RUSEA, G., K. CLAYSIUS, S. RUNI, U. JOANES, K. M. HAJA MAIDEEN and A. LATIFF. 2009. Ecology and distribution of Lycopodiaceae Mirbel in Malaysia. Blumea 54:296–271.

SHACKLEFORD, R. 2004. Conservation assessment for Northern Appressed Clubmoss (*Lycopodiella subappressa* J. G. Bruce, W. H. Wagner, & Beitel) and Northern Prostrate Clubmoss (*Lycopodiella margueritae* J.G. Bruce, W.H. Wagner, & Beitel). Schultz, J. and B. Braden, eds, USDA Forest Service, Eastern Region, Hiawatha National Forest.

SVENSSON, B. M., B. FLODERUS and T. V. CALLAGHAN. 1994. *Lycopodium annotinum* and light quality: Growth responses under canopies of two *Vaccinium* species. Folia Geobot. Phylotax. Praha 29:159–166.

SYZPULA, W., A. PIETROSIUK, O. OLSZOWSKA, M. FURMANOWA and O. KAXIMIERSKA. 2005. Somatic embryogenesis and in vitro culture of *Huperzia selago* shoots as a potential source of huperzine A. Plant Sci. 168:1443–1452.

TANG, X. C. and Y. F. HAN. 1999. Pharmacological profile of Huperzine A, a novel acetylcholinesterase inhibitor from Chinese herb. CNS Drug Rev. 5:281–300.

VASCONCELLOS, J. and J. FRANCO. 1967. Breves notas sobre Licopodiáceas. Bol. Soc. Broteriana Bol. 41:23–25.

WAGNER, W. H. and J. M. BEITEL. 1992. Generic classification of modern North American Lycopodiaceae. Ann. Mo. Bot. Gard. 79:676–686.

WANG, D-L., Y-D. QI, J-D. FENG and J-H. WEI. 2011. An efficient regeneration pattern via gemmae for *Huperzia serrata* (Thunb. ex Murray) Trev. in Hainan Province, China. Amer. Fern J. 101:182–192.

WHITCOMB, C. E. 2003. Plant Production in Containers II. Lacebark, Inc., Stillwater.

WHITTIER, D. P. 1977. Gametophytes of *Lycopodium obscurum* as grown in axenic culture. Can. J. Botany. 55:563–567.

WHITTIER, D. P. 1981. Gametophytes of *Lycopodium digitatum* (formerly *L. complanatum* var. *flabelliforme*) as grown in axenic culture. Bot. Gaz. (Crawfordsville) 142:519–524.

WHITTIER, D. P. and T. R. WEBSTER. 1986. Gametophytes of *Lycopodium lucidulum* from axenic culture. Amer. Fern J. 76:48–55.

WHITTIER, D. P. 1998. Germination of spores of the Lycopodiaceae in axenic culture. Amer. Fern J. 88:106–113.

WIKSTRÖM, N. 2001. Diversification and relationships of extant homosporous lycopods. Amer. Fern J. 92:150–165.

WIKSTRÖM, N. and P. KENRICK. 2001. Evolution of Lycopodiaceae (Lycopsida): Estimating divergence times from *rbcL* gene sequences by use of nonparametric rate smoothing. Mol. Phylogenet. Evol. 19:177–186.

WIKSTRÖM, N. and P. KENRICK. 2000. Relationships of *Lycopodium* and *Lycopodiella* based on combined plastid *rbcL* gene and *trnL* intron sequence data. Syst. Bot. 25:495–510.

WIKSTRÖM, N. and P. KENRICK. 1997. Phylogeny of Lycopodiaceae (Lycopsida) and the relationships of *Phylloglossum drummondii* Kunze based on rbcL sequences. Int. J. Plant. Sci. 158:862–871.

WIKSTRÖM, N., P. KENRICK and M. CHASE. 1999. Epiphytism and terrestrialization in tropical *Huperzia*. Plant Syst. Evol. 218:221–243.

WILFRIED BENNERT, H., P. SUKSATHAN and K. HORN. 2007. *Diphasiastrum multispicatum* (J.H. Wilce) Holub (Lycopodiaceae) in Thailand. Amer. Fern J. 97:155–165.

XUE, J. 2011. Phylogeny of Devonian lycopsids inferred from Bayesian phylogenetic analyses. Acta Geol Sin-Engl. 85:569–580.

American Fern Journal 104(2):49–57 (2014)

The Gametophytes and Young Sporophytes of *Elaphoglossum decursivum* (Dryopteridaceae) in Costa Rica

THEREIS Y. S. CHOO
Cornell University, Department of Plant Biology, 412 Mann Library Building, Ithaca, New York 14853, USA, e-mail: ytc4@cornell.edu
FERNANDO B. MATOS
The New York Botanical Garden, 2900 Southern Blvd., Bronx, New York 10458-5126 USA, e-mail: fbtms@yahoo.com.br
ROBBIN C. MORAN
The New York Botanical Garden, 2900 Southern Blvd., Bronx, New York 10458-5126 USA, e-mail: rmoran@nybg.org

ABSTRACT.—Most studies on ferns focus on the adult sporophytes, overlooking the gametophyte as a potential source of biological information. Herein, field-collected gametophytes and young sporophytes of *Elaphoglossum decursivum* are described with the aims of providing a more complete understanding on the morphology of this species and additional morphological characteristics for its sectional classification. Gametophytes share the general morphology of most other *Elaphoglossum* species, but one unusual observation was the presence of minute scales (proscales) on the thallus. Young leaves differ from the glabrous adult leaves by having papillate glandular hairs. These are the first observations of hairs in the glabrous sect. *Elaphoglossum*. Our study shows that the gametophytes and young sporophytes of *E. decursivum* have indument characters that are not present in the adult sporophytes, and studying these life stages could potentially be useful in a phylogenetic context.

KEY WORDS.—Morphology, indument, infrageneric classification

Elaphoglossum Schott ex J. Sm. is composed of over 600 species that are morphologically similar and hence difficult to treat taxonomically (Mickel and Atehortúa, 1980; Vasco *et al.*, 2013). To provide a useful framework for future monographic treatments, Mickel and Atehortúa (1980) proposed an infrageneric classification based on morphological characters of the sporophytes and spores, including such characters as rhizome habit, phyllopodia, blade scales, presence versus absence of hydathodes, and perispore morphology. Later, Rouhan *et al.* (2004) and Skog *et al.* (2004) conducted molecular phylogenetic studies using cpDNA on subsets of the genus (123 and 48 species, respectively). Their studies recovered six major clades, most of which were recognized at the rank of section (i.e., sects. *Amygdalifolia, Elaphoglossum, Lepidoglossa, Squamipedia* and *Subulata*), or at the rank of subsection (i.e., *Pachyglossa, Platyglossa, Polytrichia* and *Setosa*). They recovered *E. amygdalifolium* (Mett.) Christ, the sole species of sect. *Amygdalifolia*, as sister to all other species of *Elaphoglossum*. Recently, a new section of the genus (*E.* sect. *Wrightiana*) was erected to accommodate the early diverging Cuban endemic *E. wrightii* (Mett. ex D. C. Eaton) T. Moore (Lóriga *et al.*, 2014). These molecular phylogenies largely agree with Mickel and Atehortúa's (1980) classification system and have been useful in resolving major clades within the genus. However, some of these clades are still lacking obvious, non-molecular synapomorphies, for example, the glabrous *Pachyglossa* and *Platyglossa* clades of sect. *Elaphoglossum*.

One potential source of morphological characters that is often overlooked is the gametophytic stage. Comparative studies have found that fern gametophytes can have distinctive morphological and developmental characters useful in distinguishing genera and higher taxa (Atkinson and Stokey, 1964; Farrar *et al.*, 2008; Gabriel y Galán and Prada, 2012; Johnson *et al.*, 2012; Nayar and Kaur, 1971). Gametophyte morphology, however, has yet to be proven useful at the infrageneric level, in part due to the paucity of data. *Elaphoglossum* is no exception. To date, the gametophytes of only about 30 of the 600 *Elaphoglossum* species have been described (Atkinson and Stokey, 1964; Chiou *et al.*, 1998; Lagomarsino *et al.*, 2012; Momose, 1967; Nayar and Kaur, 1971; Perez-Garcia and Jaramillo, 1990; Sánchez-Montiel *et al.*, 2008; Stokey and Atkinson, 1957). Moreover, apart from the Lagomarsino *et al.* (2012) study of *E. amygdalifolium*, none of the other studies discussed *Elaphoglossum* gametophyte morphology in a cladistic framework.

In general, the mature gametophytes of most *Elaphoglossum* species are elongate-cordate, with nearly parallel sides, crisped wings, and shallowly notched apices (Chiou *et al.*, 1998; Nayar and Kaur, 1971; Stokey and Atkinson, 1957). Many of the examined species also show lateral branching in the older gametophytes (Chiou *et al.*, 1998; Nayar and Kaur, 1971; Stokey and Atkinson, 1957). Rhizoids are typically borne on the margins, both sides of the midrib, and on the wings (Nayar and Kaur, 1971; Stokey and Atkinson, 1957), but they are usually most abundant on the ventral side of the midrib (Stokey and Atkinson, 1957). In addition, unicellular glandular hairs are found on the margins and on both surfaces of the thallus (Chiou *et al.*, 1998; Nayar and Kaur, 1971; Stokey and Atkinson, 1957). These hairs contain chloroplasts when young and are often covered by a whitish waxy cap (Chiou *et al.*, 1998; Stokey and Atkinson, 1957). A few notable exceptions to this general gametophyte form have been described. Stokey and Atkinson (1957) found the gametophytes of two species from sect. *Squamipedia* to be hairless throughout development. This observation was recently confirmed by Vasco *et al.* (2013), suggesting that the absence of papillate hairs might be a synapomorphy for sect. *Squamipedia*. *Elaphoglossum amygdalifolium* also differs from the general form of the genus by lacking both marginal rhizoids on the thallus and waxy caps on the hairs. By these characters, it resembles the sister genus *Mickelia* and other bolbitidoid outgroups (Lagomarsino *et al.*, 2012).

Elaphoglossum decursivum Mickel occurs in the wet montane forests of Mexico, Belize, Honduras, Costa Rica and Panama, from 450–850 m (Mickel and Smith, 2004). It is one of the most abundant low-trunk fern epiphytes at Las Cruces Biological Station in Costa Rica, and is most commonly found growing on the trunks of the tree fern *Alsophila firma* (Baker) D. S. Conant (Moran *et al.*, 2003). *Elaphoglossum decursivum* was not included in the molecular phylogenetic study of Rouhan *et al.* (2004); however, it appears to belong to sect. *Elaphoglossum* of Mickel and Atehortúa (1980) based on its nearly glabrous leaves and presence of phyllopodia. Section *Elaphoglossum* consists of two subsections: subsects. *Pachyglossa* and *Platyglossa, sensu* Rouhan *et al.* (2004). These are indistinguishable morphologically except on the basis of perispore morphology: subsect. *Pachyglossa* has cristate, spinose, and perforate perispores, whereas those of subsect. *Platyglossa* are non-cristate, non-spinose, and non-perforate (Moran *et al.*, 2007).

The aim of the present study was to determine whether there was anything distinctive about the morphology of the gametophytes of *Elaphoglossum decursivum* that could potentially be useful in a phylogenetic context. Unlike nearly all previous studies of *Elaphoglossum* gametophytes, this one was carried out on gametophytes growing in nature, not in culture.

MATERIALS AND METHODS

This study was conducted during January 2013 at the Las Cruces Biological Station located near the town of San Vito, in Putarenas Province, Costa Rica (8°47′10″N, 82°57′40″W ca. 1200 m). Two populations of *E. decursivum* were sampled: one from the Wilson Botanical Garden and the other from a nearby secondary forest along the Río Java trail. The populations were photographed in the field and vouchers were made of the mature *E. decursivum* sporophytes (*Matos et al. 2075*, CR, NY, UPCB) and the host *Alsophila firma* (*Matos et al. 2084*, UPCB). Between 10–15 gametophytes were collected from each population. To reduce damage to the gametophytes during sampling, pieces of the underlying substrate surrounding one or more gametophytes were collected in the field. The gameophytes were then carefully separated from the *A. firma* root mantle in a laboratory setting and were washed in water when necessary. Many gametophytes had young sporophytes attached. All individuals were examined and measured using stereoscopes and light microscopes. Photographs were cropped and improved for colour balance using Adobe Photoshop © CS5 Extended, v. 12.0.4 ×64.

RESULTS

Gametophyte morphology.—The gametophytes of *Elaphoglossum decursivum* were most abundant on the trunks of *Alsophila firma* growing in partially shaded to relatively open areas (Fig. 1A–B). A few individuals were found on the trunks of angiosperms. Gametophytes were most frequently found 0.5–2 m from the ground, although it was not uncommon to see young sporophytes growing higher up the trunks. Gametophytes were strap-shaped, had crisped margins and terminated in an apical notch that measured 2–4 mm in width at the apex (Figs. 1D, 2A). Often the proximal part of the gametophytes had degraded leaving only the apical meristematic portion, giving the gametophyte a cordate appearance. A thickened midrib was absent, and none of the gametophytes branched. Reddish brown rhizoids extended from the ventral

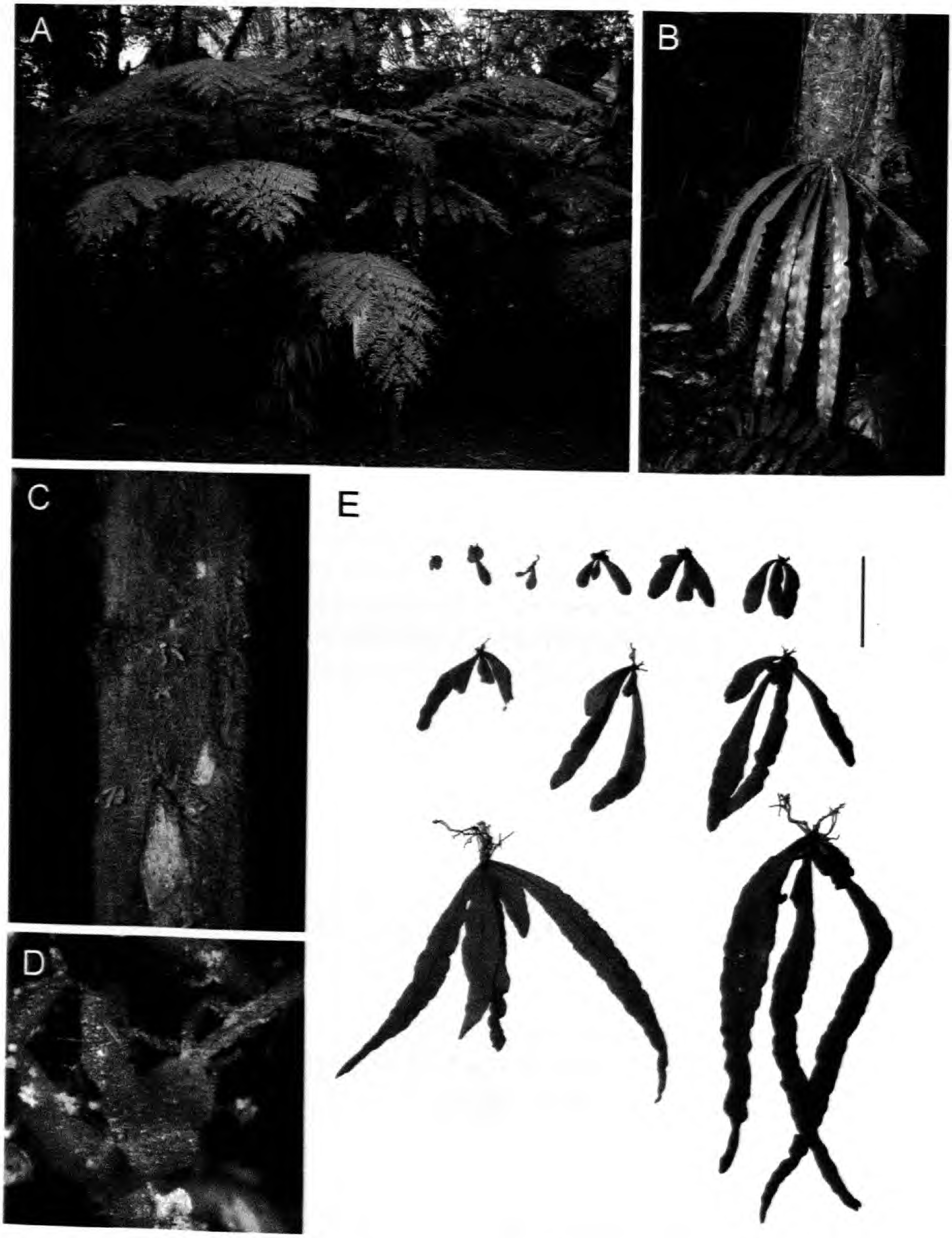

FIG. 1. A–E. Gametophytes, sporophytes, and habitat of *Elaphoglossum decursivum* at the Las Cruces Biological Station, Costa Rica. A. Habitat, showing large numbers of sporophytes growing on the lower trunks of *Alsophila firma*. B. Solitary sporophyte growing on an angiosperm. C. Gametophytes and young sporophytes on a trunk of *A. firma*. D. Mature gametophyte in the root mantle of *A. firma*. E. Developmental series from a gametophyte [upper left] to a young sporophyte [lower right]; scale bar = 2.5 cm.

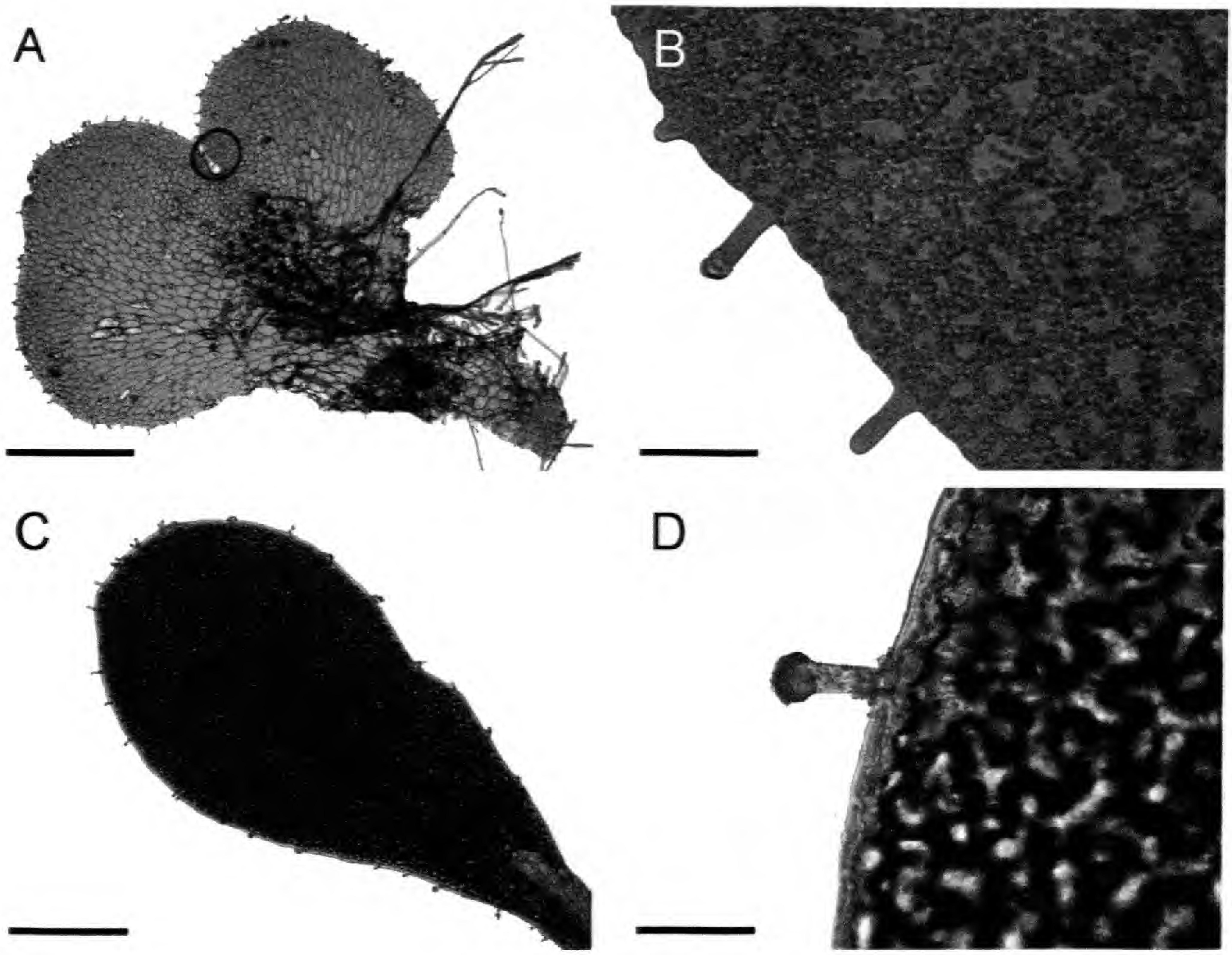

FIG. 2. Gametophyte (A–B) and first sporophyte leaf (C–D) of *Elaphoglossum decursivum*. A. Ventral view of a mature gametophyte, with a cluster of archegonia at the center, long castaneous rhizoids, and tiny unicellular marginal hairs. Black circle indicates apical notch. B. Margin of the gametophyte showing secretory, papillate-glandular hairs at different stages of development, from a tiny bulge on the surface of the cell to a fully extended secretory hair with waxy cap. C. First leaf of the sporophyte showing numerous unicellular hairs along its margin. D. Detail of a papillate-glandular hair with waxy cap on the margin of sporophyte lamina. Scale bar for A and C = 0.3 mm; scale bar for B and D = 75 μm.

surface of the thallus. Unicellular glandular hairs, often with a whitish waxy tip, were found on the thallus surface and margins. These glandular hairs often contained chloroplasts, especially when young, and measured about 50 μm long (Fig. 2B). We also observed minute, branched multicellular proscales (i.e., highly reduced, uniseriate scales; sensu Moran, 1986) on the surface of some of the gametophytes. These proscales often had swollen apical cells, as is typical of scales in many species of *Elaphoglossum* (Figs. 3A–B). Archegonia were located on the ventral surface near the apical notch (Fig. 3C). No antheridia were observed.

Young sporophyte morphology.—The surface and margins of the first few sporophyte leaves were covered with minute papillate-glandular hairs like those found on the gametophytes (Fig. 2C–D). With each successive new leaf, the glandular hairs decreased in abundance and became increasingly restricted to the margins. Glandular hairs were absent by time the young sporophyte produced leaves that were about 2 cm long. This corresponded to the fourth or

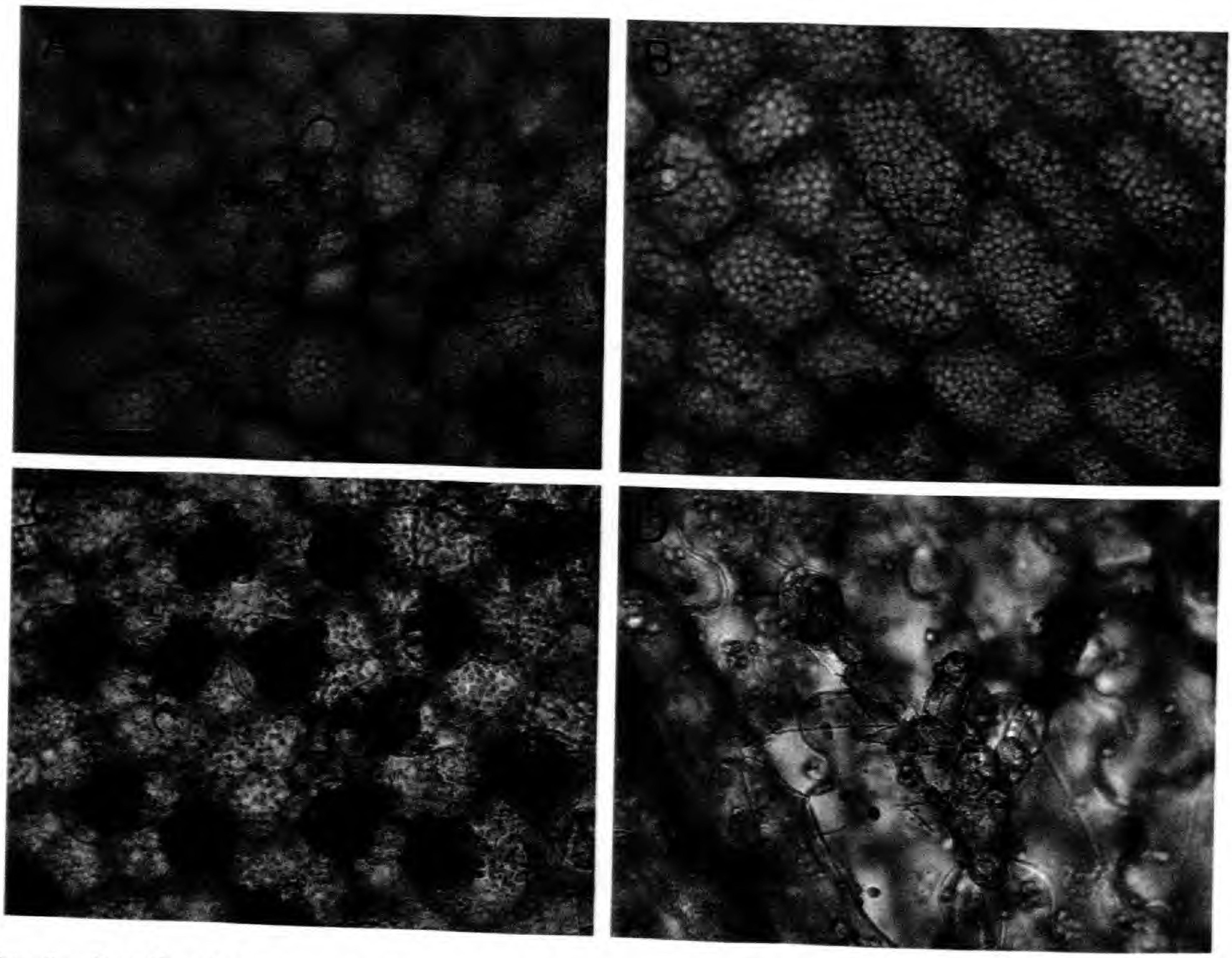

FIG. 3. Details of the gametophytes (A–C) and early sporophyte leaves (D) of *Elaphoglossum decursivum*. Scale bar = 75 µm. A. Forked proscale on ventral surface of the gametophyte. B. Proscale on the ventral surface of the gametophyte. C. Dark neck cells of the archegonia, as seen from above. D. Proscale on the abaxial side of first sporophyte leaf. Note slightly swollen dark apical cells. Scale bar = 75 µm.

fifth leaf (Fig. 1E). We also observed proscales on the abaxial surfaces of some of the young sporophyte leaf blades (Fig. 3D). These were difficult to observe because of their small size and were only seen on a few individuals.

DISCUSSION AND CONCLUSIONS

The gametophytes of *Elaphoglossum decursivum* share the same general morphology of most other species of the genus, the most prominent characters being the elongate, strap-shaped thallus and presence of papillate, glandular hairs on the margins and surface (Chiou *et al.*, 1998; Nayar and Kaur, 1971; Stokey and Atkinson, 1957). Unlike the gametophytes of many other *Elaphoglossum* species grown in culture, the field-collected gametophytes of *E. decursivum* lacked a prominent midrib, marginal rhizoids, and branched thalli. While there have been very few studies addressing the differences between field collected and culture-grown gametophytes, the work by Ranker and Houston (2002) and Skelton (2007) show that some differences are to be expected, especially with regard to the expression of sexual systems and the dorsiventral presence of archegonia and rhizoids. The fact that several of the *E. decursivum* gametophytes were at least partially degraded seems to reflect the challenges of growing in a natural environment with limited resources. The continuous growth of these elongated thalli may also be an adaptation to growing in the dense root mantle of *Alsophila firma*, which is a highly heterogenous environment.

Chiou *et al.* (1998) found that gametophytes grown in culture from spores of five other *Elaphoglossum* species only produced archegonia after 8–24 months of growth. Taking this study as a guide, the presence of archegonia and the elongated thallus both suggest that the gametophytes observed were at least several months old, if not older. Perhaps spore germination and subsequent gametophyte growth started at the beginning of the wet season in early May. This observation is consistent with the idea that many fern epiphytes employ the strategy of having long-lived gametophytes (Chiou and Farrar, 1997; Farrar *et al.*, 2008; Watkins *et al.*, 2007). Chiou *et al.* (1998) did not find any evidence of an antheridiogen system in their study on *Elaphoglossum* gametophytes and hypothesized that intergametophytic mating was most likely for this group. As we did not find hermaphrodites or antheridia-producing gametophytes, our observations support this idea. However, locating the tiny, antheridia-producing gametophytes typical in a species with an antheridiogen system would be difficult in a field setting, so it is also possible that these individuals were present in our samples but were merely overlooked.

One interesting observation from this study was the finding of proscales (*sensu* Moran, 1986) on the surface of the *E. decursivum* gametophytes. As is typical of larger "normal" scales in most species of *Elaphoglossum* (Moran, personal observation), the apical cells of these proscales were slightly swollen with darkened contents. Most important, the proscales are exactly like those found on the leaves, where complete serial homology can be demonstrated between these minute proscales and larger "typical" scales. This finding of proscales is the first observation of scales on an *Elaphoglossum* gametophyte.

Without a comprehensive survey on the morphological characteristics of gametophytes from the various sections of *Elaphoglossum*, it is not possible to confirm the position of *E. decursivum* within sect. *Elaphoglossum* based on gametophyte morphology alone. Nevertheless, the characters observed in our study do not present any compelling evidence to the contrary. For instance, the presence of glandular hairs with waxy tips in *E. decursivum* is consistent with its position outside sects. *Squamipedia* and *Amygdalifolia*, as these two sections have been reported as having no hairs or hairs without waxy tips on their gametophytes, respectively. *Elaphoglossum decursivum* differs from sect. *Lepidoglossa* by lacking scales bearing many marginal teeth, each consisting of a single, acicular cell, which is diagnostic for sect. *Lepidoglossa* (Vasco *et al.*, 2009).

The two types of indument (i.e., papillate hairs and proscales) found on the very young leaves of *Elaphoglossum decursivum* represent the first observation of such indument in sect. *Elaphoglossum*. This observation raises questions on the evolution and development of glabrousness in this clade and it would be interesting to see if the young sporophytes of other members of this clade have similar patterns of development.

Our study has shown that the gametophytes and young sporophytes of *Elaphoglossum decursivum* have additional morphological characters (i.e., papillate-glandular hairs) that are absent in the adult sporophytes. Studying these important stages in the fern life cycle not only provides a more complete picture of the biology of such organisms, but could also potentially be useful in a phylogenetic context, complementing the more traditional molecular and morphological studies.

Acknowledgments

This study was conducted in January 2013 during the *Tropical Ferns and Lycophytes* specialty course sponsored by the Organization for Tropical Studies (OTS). The course was taught by Robbin Moran (The New York Botanical Garden) and James Eddie Watkins (Colgate University). We thank Miguel Cháves from OTS for his help with plant identification. We also thank two anonymous reviewers for their helpful comments and suggestions. This research was partially funded by grants to Matos by the Fulbright Scholarship Program and The CAPES Foundation, Ministry of Education of Brazil, to Choo by the Department of Plant Biology, Cornell University, and to Moran from the U.S. National Science Foundation (DEB1020443).

Literature Cited

Atkinson, L. R. and A. G. Stokey. 1964. Comparative morphology of the gametophyte of homosporous ferns. Phytomorphology 14:51–70.

Chiou, W. L. and D. R. Farrar. 1997. Comparative gametophyte morphology of selected species of the family Polypodiaceae. Amer. Fern J. 87:77–86.

Chiou, W. L., D. R. Farrar and T. A. Ranker. 1998. Gametophyte morphology and reproductive biology in *Elaphoglossum*. Canad. J. Bot. 76:1967–1977.

Farrar, D. R., C. Dassler, J. E. Watkins, Jr. and C. Skelton. 2008. Gametophyte ecology. Pp. 222–256, *in* T. A. Ranker and C. H. Haufler, eds. *Biology and Evolution of Ferns and Lycophytes.* Cambridge University Press, Cambridge.

Gabriel y Galán, J. M. and C. Prada. 2012. Farina production by gametophytes of *Argyrochosma nivea* (Poir.) Windham (Pteridaceae) and its implication for Cheilanthoid phylogeny. Amer. Fern J. 102:191–197.

Johnson, A. K., C. J. Rothfels, M. D. Windham and K. M. Pryer. 2012. Unique expression of a sporophytic character on the gametophytes of notholaenid ferns (Pteridaceae). Amer. J. Bot. 99:1118–1124.

Lagomarsino, L. P., A. L. Grusz and R. C. Moran. 2012. Primary hemiepiphytism and gametophyte morphology in *Elaphoglossum amygdalifolium* (Dryopteridaceae). Brittonia 64:226–235.

Lóriga, J., A. Vasco, L. Regalado, J. Heinrichs and R. C. Moran. 2014. Phylogeny and classification of the Cuban species of *Elaphoglossum* (Dryopteridaceae), with description of *Elaphoglossum* sect. *Wrightiana* sect. nov. Pl. Syst. Evol. 300:937–951.

Mickel, J. T. and A. R. Smith. 2004. *The Pteridophytes of Mexico.* Mem. New York Bot. Gard. 88:1–1055.

Mickel, J. T. and L. G. Atehortúa. 1980. Subdivision of the genus *Elaphoglossum*. Amer. Fern J. 70:47–68.

Momose, S. 1967. Prothallia of Japanese ferns. Univ. Tokyo Press, Tokyo.

Moran, R. C. 1986. The neotropical fern genus *Olfersia*. Amer. Fern J. 76:161–178.

Moran, R. C., S. Klimas and M. Carlsen. 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica 35:48–56.

MORAN, R. C., J. GARRISON HANKS and G. ROUHAN. 2007. Spore morphology in relation to phylogeny in the fern genus *Elaphoglossum* (Dryopteridaceae). Int. J. Pl. Sci. 168:905–929.

NAYAR, B. K. and S. KAUR. 1971. Gametophytes of homosporous ferns. Bot. Rev. (Lancaster). 37:295–396.

PEREZ-GARCIA, B. and I. R. JARAMILLO. 1990. Desarrollo del gametófito de *Elaphoglossum petiolatum* (Sw.) Urban (Lomariopsidaceae). Acta Bot. Mex. 10:23–30.

RANKER, T. A. and H. A. HOUSTON. 2002. Is gametophyte sexuality in the laboratory a good predictor of sexuality in nature? Amer. Fern J. 92:112–118.

ROUHAN, G., J. Y. DUBUISSON, F. RAKOTONDRAINIBE, T. J. MOTLEY, J. T. MICKEL, J. N. LABAT and R. C. MORAN. 2004. Molecular phylogeny of the fern genus *Elaphoglossum* (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area. Molec. Phylogen. Evol. 33:745–763.

SKELTON, C. L. 2007. Investigations into gametophyte morphology and population sex ratios through direct comparisons between laboratory-grown and field-grown fern gametophytes. MS Thesis, Iowa State University, Ames, IA. UMI Microform: 1446061.

SKOG, J. E., J. T. MICKEL, R. C. MORAN, M. VOLOVSEK and E. A. ZIMMER. 2004. Molecular studies of representative species in the fern genus *Elaphoglossum* (Dryopteridaceae) based on cpDNA sequences *rbcL, trnL–F,* and *rps4–trnS.* Int. J. Pl. Sci. 165:1063–1075.

STOKEY, A. G. and L. R. ATKINSON. 1957. The gametophyte of some American species of *Elaphoglossum* and *Rhipidopteris.* Phytomorphology 7:275–292.

SÁNCHEZ-MONTIEL, L., M. L. ARREGUIN-SÁNCHEZ and R. FERNÁNDEZ-NAVA. 2008. Gametofitos y esporofitos jóvenes de dos pteridofitas: *Asplenium monanthes* L. (Aspleniaceae-Pteridophyta) y *Elaphoglossum minutum* (Pohl ex Fée) T. Moore (Lomariopsidaceae-Pteridophyta). Polibotánica 25:29–43.

VASCO, A., R. C. MORAN and G. ROUHAN. 2009. Monograph of the *Elaphoglossum ciliatum* group (Dryopteridaceae). Brittonia 61:241–272.

VASCO, A., J. T. MICKEL and R. C. MORAN. 2013. Taxonomic revision of the Neotropical species of *Elaphoglossum* sect. *Squamipedia* (Dryopteridaceae). Ann. Missouri Bot. Gard. 99:244–286.

WATKINS, J. E., M. K. MACK and S. S. MULKEY. 2007. Gametophyte ecology and demography of epiphytic and terrestrial tropical ferns. Amer. J. Bot. 94:701–708.

American Fern Journal 104(2):58–66 (2014)

Effects of Seasonal Changes on Pigment Composition of *Azolla filiculoides* Lam.

TAYLAN KÖSESAKAL
Istanbul University, Faculty of Science, Department of Biology, Botany Division, 34134
Süleymaniye, Istanbul, Turkey, e-mail: taylank@istanbul.edu.tr

ABSTRACT.—*Azolla* is a floating fern, which contains the nitrogen-fixing cyanobacterium *Anabaena azollae* in the dorsal lobe cavity of the leaves. This study investigated the effects of seasonal changes on the pigment composition of *Azolla filiculoides* in a small pond located in Istanbul, Turkey. Sampling was conducted in March, April, May, October, November, December 2007. The average total chlorophyll and carotenoid content of the leaves was almost a half fold lower in March-April-May than in October-November-December. For late winter–spring, while the average chlorophyll a/b ratio of the leaves was 2.6, for autumn - early winter it was 5.5. In March, leaf dimensions reduced, whereas the anthocyanin accumulation in the leaves increased. In May, together with the increasing temperature values, while the leaf dimensions and biomass increased, the leaves returned to green. From October to November, both leaf dimensions and amount of anthocyanin in the leaves reduced. Results showed that the probable growth season of the *A. filiculoides* began between April and May.

KEY WORDS.—*Azolla*, chlorophyll, anthocyanin, carotenoids, seasonal variations

Azolla is a genus of floating ferns that contains a permanent endosymbiotic community of a heterosist-forming, filamentous, nitrogen-fixing cyanobacteria *Anabaena azollae* Strasb. living in the dorsal lobe cavity of the leaves (Peters and Mayne, 1974). *Azolla* has a worldwide distribution, ranging from temperate to tropical climates. Seven species of *Azolla* in two taxonomic sections are known: the section *Euazolla* includes the species *A. filiculoides* Lam., *A. rubra* R. Br., *A. mexicana* C. Presl, *A. caroliniana* Willd and *A. microphylla* Kaulf., while the section *Rhizosperma* includes the species *A. pinnata* R. Br. and *A. nilotica* Mett. (Van Hove and Lejeune, 2002).

Plant phenology is affected by internal factors or by environmental factors (Lee *et al.*, 2009). It is well known that seasonal changes affect plant growth and physiology. Ferns are sensitive components of ecosystems and display a seasonal acclimation of some physiological changes to changing environmental conditions (Volkova *et al.*, 2011). Stress conditions may lead to different physiological responses during a plant's different growth stages (Gratani *et al.*, 1998). Green *Azolla* leaves turn red under high light intensity, low temperature, and adverse environmental conditions (Pabby *et al.*, 2004). Photosynthetic pigments (chlorophylls and carotenoids), are responsible for the absorption of light (Lichtenthaler, 2009). The changes of the photosynthetic pigments and the photosynthetic performance affected by seasonal variations has been observed in many fern species (Volkova *et al.*, 2011; Paoli and Landi, 2013). Anthocyanins are partly responsible for the colors of plant tissues. Anthocyanins are produced in the cytoplasm, and then transported into the vacuole (Shirley, 1996). The synthesis of anthocyanins is induced by UV-B (Warren *et al.*, 2003), nutrient deficiency (Pinto *et al.*, 1999), low temperatures (Rabino and Mancinelli, 1986), water deficit (Nogués *et al.*, 1998), and heavy metal stress (Ling-Peng *et al.*, 2006). The content of the most common plant pigments—chlorophylls, carotenoids, and anthocyanins—as well as their relative proportion determines both the color and appearance of plants (Abbott, 1999).

In Turkey *Azolla filiculoides* is found naturally only in the Thrace region (Unal and Uzen, 1996) and has been grown in Istanbul University Alfred Heilbronn Botany Garden for many years. The purpose of this study was to monitor and investigate the effects of seasonal changes on *Azolla filiculoides* Lam. For this reason, changes in the pigment content of *A. filiculoides* were investigated in 2007.

MATERIALS AND METHODS

Plant material and sampling.—The *Azolla filiculoides* that is grown in Istanbul University Alfred Heilbronn Botany Garden thrives in a small pond (N 41°01′06″, E 28°57′51″) with *Lemna* spp. Pigment analysis of *A. filiculoides* is based particularly on the months of previous years where there were significant temperature increases and decreases. For this reason *A. filiculoides* was collected from the botany garden in March, April, May, October, November and December of 2007. Five replicates of plants were collected from the different parts of the pond for each month sampled. After washing three times with distilled water, plant fresh weight was measured and pigment contents of the leaves determined.

Seasonal temperature.—To investigate the seasonal temperature changes in Istanbul, maximum, minimum, and mean daily temperature, data provided by the National Meteorology Service from the Florya meteorological station in Turkey was analyzed.

Chlorophyll and carotenoid levels.—To determine the chlorophyll and carotenoid contents of the leaves in March, April and May, 2–4 *A. filiculoides* plants totaling 700 mg leaves were used, and for October, November and December 4–6 plants totaling 500 mg leaves were used. Leaves were extracted in 80% acetone and the samples were centrifuged (Heraeus Labofuge 400 R) at 3000 g (4°C) for 15 minutes. The pigment contents (chlorophyll a and b, total chlorophyll, and carotenoid) were measured (Shimadzu 1601 UV-Visible Spectrophotometer) and determined in $\mu g\ g^{-1}$ fresh weight (Lichtenthaler and Welburn, 1983).

Anthocyanin determination.—The Mancinelli (1990) method was employed for the determination of the anthocyanin content in the leaves. According to this method, plant samples of 500 mg of fresh weight were extracted in 10 ml methanol-HCl (1% HCl, v/v) and kept under refrigeration at 3–5° C for 2 days with occasional shakings. Then, the extract was filtered and the anthocyanin content in the filtrate was measured (Shimadzu 1601 UV-Visible Spectrophotometer). The anthocyanin content was expressed as $\mu g\ g^{-1}$ fresh weight.

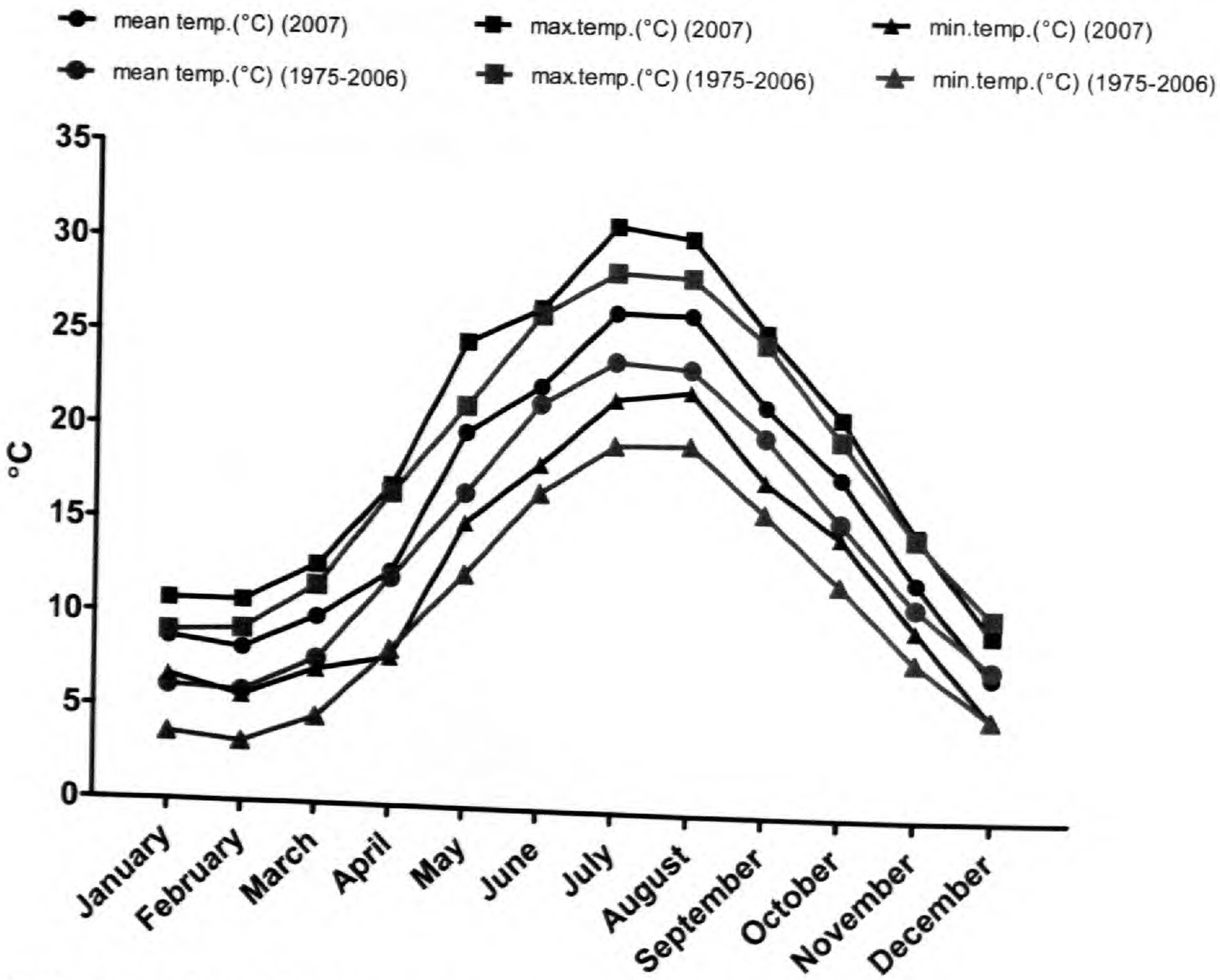

FIG. 1. Comparison of the maximum, minimum, and mean temperatures of Istanbul the years 2007 and 1975 to 2006 (data was provided by the National Meteorology Service, from Florya meteorological station in Turkey).

Statistical analysis.—Means of the five replicates of the chlorophyll, carotenoid, and anthocyanin content data were calculated. Statistical analysis was performed using GraphPad Prism version 5.2 for windows (GraphPad Software, San Diego, CA). The significance of differences between the mean values of samples were statistically evaluated by one way ANOVA followed *post hoc* analysis with the Tukey's Multiple Comparison test, $p<0.05$.

RESULTS

The mean and maximum temperatures of 2007 were high compared to the mean and maximum temperatures of those between 1975–2006; not including December. On the other hand the minimum temperatures in April and December of 2007 were lower than those of previous years (Fig. 1).

In Fig. 2, plant color, size and morphology during March-April-May and October-November-December 2007 are shown. In March (under the lowest spring temperature) the plants were small, a dark red color, and the growth of plants was very slow. At the beginning of April, the plants' color changed from red to green, plant growth increased, and vegetative multiplication accelerated.

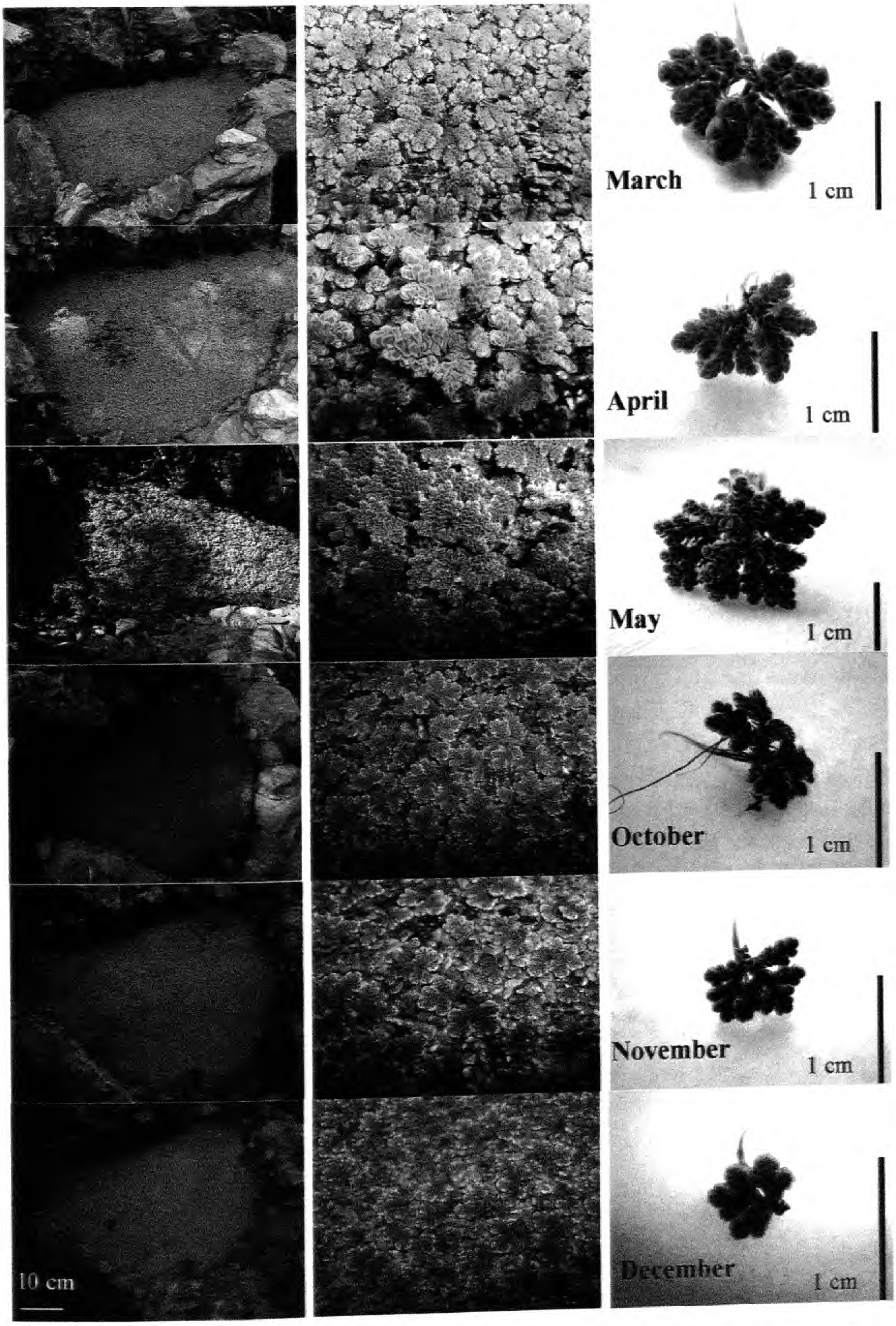

FIG. 2. Photographs of *A. filiculoides* in a small pond located in the Istanbul University Alfred Heilbronn Botany Garden in March, April, May, October, November, December 2007.

TABLE 1. Chlorophyll a, b (μg/gFW) and chl a and chl b ratio of *A. filiculoides* in March, April, May, October, November, December 2007. Chlorophyll a, b contents and chl a/chl b ratios results are means of 5 replicates in March-April-May and October-November-December, "±" indicates standard deviation. Significant differences determined by the Tukey's Multiple Comparison test ($p<0.05$) are indicated by different letters (a–e).

Months	Chlorophyll a	Chlorophyll b	Chl a/Chl b
March	197.2 ± 8.5 c	66.8 ± 2.0 a	2.9 ± 0.12 c
April	110.0 ± 12.2 e	47.1 ± 3.5 b	2.3 ± 0.14 e
May	170.6 ± 10.8 d	66.9 ± 1.4 a	2.6 ± 0.12 d
October	323.5 ± 23.8 a	63.4 ± 5.5 a	5.1 ± 0.14 b
November	269.1 ± 20.7 b	47.4 ± 4.1 b	5.7 ± 0.07 a
December	246.5 ± 10.4 b	43.7 ± 3.0 b	5.6 ± 0.15 a

In May, the plants had become fully green, were growing faster, and had completely covered the surface of the pond. During the October-November-December period, the color of the *Azolla* leaves changed from green to red, plant size decreased and plant growth also slowed down. In addition during the October-November-December period the *Lemna* spp. population density was higher than the *A. filiculoides* (Fig. 2). Although *A. filiculoides* was present in the small pond throughout the year 2007, it only reproduced vegetatively.

While the average chlorophyll a/b ratio of the leaves was 2.6 for the March-April-May period, it was 5.5 for the October-November-December period. In April the chlorophyll a/b ratio (Table 1) and total chlorophyll (Fig. 3) were significantly ($p<0.05$) lower than in the other months, while total chlorophyll was significantly highest in October. The total chlorophyll amounts were 264, 157, and 237 $\mu g\ g^{-1}$ during March, April, and May, respectively (Fig. 3). The carotenoid amount of the *A. filiculoides* leaves was lower in the March-April-May period when compared to the October-November-December period. The highest carotenoid content was determined in October ($p<0.05$), but values for November and December were not statistically different from each other (Fig. 3).

While the highest level of anthocyanins was measured in March, the lowest was found in May, and these values are significantly different statistically from all other anthocyanin values measured. The anthocyanin content of the leaves was 0.6, 0.47, and 0.33 $\mu g\ g^{-1}FW$ throughout October, November, and December respectively (Fig. 3).

DISCUSSION

Plants in their natural environment are exposed to different kinds of environmental stresses, and these conditions lead to both a reduction in growth and metabolism (Abraham, 2010). *Azolla* grows under different environmental conditions. Temperature is the most important factor affecting the growth and distribution of *Azolla* (Pabby *et al.*, 2004). The optimum growth

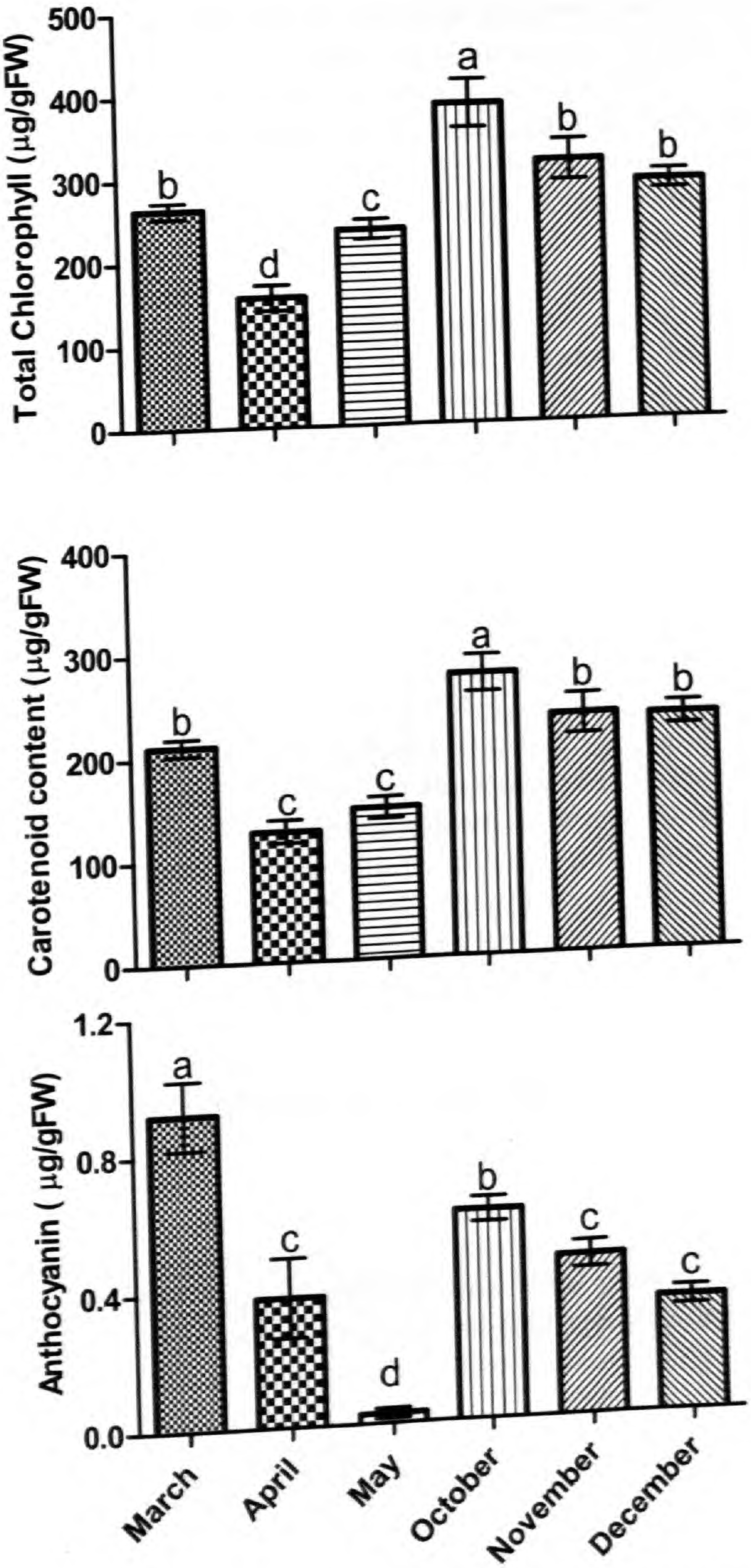

FIG. 3. Total chlorophyll, carotenoid and anthocyanin contents of *A. filiculoides* in March, April, May, October, November, December 2007. Bars represent the standard deviation. Significant differences determined by the Tukey's Multiple Comparison test ($p<0.05$) are indicated by different letters (a–d).

air temperature ranges from 18–28°C for *Azolla* spp. However, some species of *Azolla* are capable of tolerating a wide range of air temperatures from −5–35°C (Wagner, 1997). Janes (1998a), determined that under the most adverse winter conditions (January–March), *Azolla filiculoides* were very small and dark red, and in the spring/early summer, the plants' color changed from red to green. This color change was also observed in reverse in the autumn in an outdoor culture. In our study, the color and morphological results obtained from *A. filiculoides* in March-April-May, and October-November-December showed a parallelism with the Janes (1998a) results. Bocchi and Malgioglio (2010) stated that the *Azolla* (Milan strain) biomass increased from March to April (under the range from 10.4 to 18°C mean temperature/day). In the present study, the *A. filiculoides* leaf dimensions and the biomass increased and leaves returned to green from April to May (under the range from 12.4 to 19.9°C mean temperature/day; Fig. 2). Thus, the growth season of *A. filiculoides* likely began between April and May. This study also showed that under natural conditions, while *A. filiculoides* reproduced vegetatively, it did not reproduce sexually during 2007.

The photosynthetic apparatus is quite crucial for communication between the plant and the environment (Mattoo *et al.*, 1999). Chlorophyll concentration is regulated by plants in order to balance their capacity to both absorb and utilize light energy. This regulation is considered as an adaptation of plants to seasonal fluctuations under environmental stress (Close *et al.*, 2006). In May (providing the optimum growth temperature of plant), the amount of chlorophyll in leaves was higher than in April. On the other hand, the chlorophyll/carotenoid ratio was 1.6 in May and 1.2 in April. In addition, it was quite striking that the chl a/b ratio of the October-November-December months was almost twofold compared to the ratio in the months of March-April-May. Thus, in addition to its traditional role in energy transduction, the photosynthetic apparatus might also be an environmental sensor (Huner *et al.*, 1998).

With the synthesis of anthocyanins under high light intensity, low temperature, and in adverse environmental conditions, *Azolla* leaves generally have a reddish appearance. While the *A. filiculoides* population density was higher than the *Lemna* spp. during March-April-May, the opposite was observed in October-November-December. On the other hand, it was quite surprising that, while the amount of anthocyanins in March (mean temperature, 9.9°C) was 0.92 $\mu g g^{-1}$FW it was 0.33 $\mu g g^{-1}$FW in December (mean temperature, 7.6°C). Thus, anthocyanins may increase the antioxidant response of the plants against biotic and abiotic stress conditions.

Pigment synthesis in plants may be a consequence of exogenic stress or senescence, and of an ecological adaption to changing environments, respectively (Gould *et al.*, 1995). Thus, chlorophylls, carotenoids and flavonoids may contribute to maintaining a balanced physiological state in the plant tissues (Stintzing and Carle, 2004). With the amounts of chlorophyll, carotenoid and antocyanin evaluated together, the growth season of *A. filiculodies* likely began between April and May.

It is not yet known which environmental conditions induce *Azolla* to reproduce sexually. However, increased plant density, enhanced phosphate concentrations, and adverse winter conditions are factors believed to be involved in stimulating sexual reproduction in *Azolla* (Janes 1998a, 1998b). In conclusion, it is well established that changes in climate will affect the distribution of plant species (Malchair *et al.*, 2010; Rajkumar *et al.*, 2013) and agricultural productivity (Howden *et al.*, 2003). Thus the knowledge of the effect of seasonal changes on the photosynthetic pigment composition of *A. filiculoides* could help us in agriculture—especially in rice cultivation. In addition, it is important to investigate the effect of environmental conditions changing with global warming on the sexual reproduction and the formation of spores of *Azolla*, and encourage research regarding the preservation and germination of spores.

LITERATURE CITED

ABBOTT, J. A. 1999. Quality measurement of fruit and vegetables. Postharvest Biol. Tec. 15:207–225.

ABRAHAM, G. 2010. Antioxidant enzyme status in *Azolla microphylla* in relation to salinity and possibilities of environmental monitoring. Thin Solid Films 519:1240–1243.

BOCCHI, S. and A. MALGIOGLIO. 2010. *Azolla-Anabaena* as a biofertilizer for rice paddy fields in the Po Valley, a temperate rice area in Northern Italy. Int. J. Agron. 2010:1–5.

CLOSE, D. C., N. J. DAVIDSON and N. W. DAVIES. 2006. Seasonal fluctuations in pigment chemistry of co-occurring plant hemi-parasites of distinct form and function. Environ. Exp. Bot. 58:41–46.

GOULD, K. S., D. M. KUHN, D. W. LEE and S. F. OBERBAUER. 1995. Why leaves are sometimes red. Nature 378:241–242.

GRATANI, L., M. F. CRESCENTE and G. ROSSI. 1998. Photosynthetic performance and water use efficiency of the fern *Cheilanthes persica*. Photosynthetica 35:507–516.

HOWDEN, M., L. HUGHES, M. DUNLOP, I. ZETHOVEN, D. HILBERT and C. CHILCOTT. 2003. Climate change impacts on biodiversity in Australia, outcomes of a workshop sponsored by the Biological Diversity Advisory Committee, 1–2 October 2002, Commonwealth of Australia, Canberra.

HUNER, N. P. A., G. ÖQUIST and F. SARHAN. 1998. Energy balance and acclimation to light and cold. Trends Plant Sci. 3:224–230.

JANES, R. 1998a. Growth and survival of *Azolla filiculoides* in Britain I. Vegetative reproduction, New Phytol. 138:367–375.

JANES, R. 1998b. Growth and survival of *Azolla filiculoides* in Britain II. Sexual reproduction, New Phytol. 138:377–384.

LEE, P.-H., T.-T. LIN and W.-L. CHIOU. 2009. Phenology of 16 species of ferns in a subtropical forest of northeastern Taiwan. J. Plant Res. 122:61–67.

LICHENTHALER, H. K. 2009. Biosynthesis and accumulation of isoprenoid carotenoids and chlorophylls and emission of isoprene by leaf chloroplasts. Bull. Geor. Natl. Acad. Sci. 3:91–94.

LICHTENTHALER, H. K. and A. R. WELLBURN. 1983. Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. Biochem. Soc. Trans. 11:591–592.

LING-PENG, D., X. ZHI-TING, H. YU and L. MIN-JING. 2006. Cadmium-induced changes in pigments, total phenolics, and phenylalanine ammonia-lyase activity in fronds of *Azolla imbricata*. Environ. Toxicol. 21:505–512.

MALCHAIR, S., H. J. DE BOECK, C. M. H. M. LEMMENS, R. MERCKX, I. NUSB, R. CEULEMANS and M. CARNOL. 2010. Do climate warming and plant species richness affect potential nitrification, basal respiration and ammonia-oxidizing bacteria in experimental grasslands? Soil Biol. Biochem. 42:1944–1951.

MANCINELLI, A. L. 1990. Interaction between light quality and light quantity in the photoregulation of anthocyanin production. Plant Physiol. 92:1191–1195.

Matto, A. K., M.-T. Giardi, A. Raskind and M. Edelman. 1999. Dynamic metabolism of photosystem II reaction center proteins and pigments. Physiol. Plantarum. 107:454–461.

Nogués, S., D. J. Allen, J. I. L. Morison and N. R. Baker. 1998. Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. Plant Physiol. 117:173–181.

Pabby, A., R. Prasanna and P. K. Singh. 2004. Biological significance of *Azolla* and its utilization in agriculture. Proc. Indian Natl. Sci. Acad. B70:299–333.

Paoli, L. and M. Landi. 2013. The photosynthetic performance of sterile and fertile sporophytes in a natural population of the fern *Dryopteris affinis*. Photosynthetica 51:312–316.

Peters, G. A. and B. C. Mayne. 1974. The *Azolla, Anabaena azollae* relationship. I. Initial characterization of the association. Plant Physiol. 53:813–19.

Pinto, M. E., P. Casati, T. P. Hsu, M. S. B. Ku and G. E. Edwards. 1999. Effects of UV-B radiation on growth, photosynthesis, UV-B absorbing compounds and NADP-malicenzyme in bean (*Phaseolus vulgaris* L.) grown under different nitrogen conditions. J. Photoch. Photobio. 48:200–209.

Rabino, I. and A. L. Mancinelli. 1986. Light, temperature and anthocyanin production. Plant Physiol. 81:922–924.

Rajkumar, M., M. N. V. Prasad, S. Swaminathan and H. Freitas. 2013. Climate change driven plant–metal–microbe interactions. Environ. Int. 53:74–86.

Shirley, B. W. 1996. Flavonoid biosynthesis: New functions for an old pathway. Trends Plant Sci. 1:377–382.

Stintzing, F. C. and R. Carle. 2004. Functional properties of anthocyanins and betalains in plants, food, and in human nutrition. Trends Food Sci. Tech. 15:19–38.

Unal, M. and E. Uzen. 1996. A New aquatic fern record for the flora of Turkey: *Azolla filiculoides* Lam. Turk. J. Bot. 20:379–381.

Van Hove, C. and A. Lejeune. 2002. The *Azolla–Anabaena* symbiosis. Biology and Environment. Proc. Roy. Irish Acad. 102B:23–26.

Volkova, L., L. T. Bennett and M. Tausz. 2011. Diurnal and seasonal variations in photosynthetic and morphological traits of the tree ferns *Dicksonia antarctica* (Dicksoniaceae) and *Cyathea australis* (Cyatheaceae) in wet sclerophyll forests of Australia. Environ. Exp. Bot. 70:11–19.

Wagner, G. M. 1997. *Azolla*: a review of its biology and utilization. Bot. Rev. 63:1–26.

Warren, J. M., J. H. Bassman, J. K. Fellman, D. S. Mattinson and S. Eigenbrode. 2003. Ultraviolet-B radiation alters phenolic salicylate and flavonoid composition of *Populus trichocarpa* leaves. Tree Physiol. 23:527–535.

American Fern Journal 104(2):67–102 (2014)

Arbuscular Mycorrhizal (AM) and Dark Septate Endophyte (DSE) Fungal Association in Lycophytes and Ferns of the Kolli Hills, Eastern Ghats, Southern India

Raji Muthuraja, Thangavelu Muthukumar*, Kullaiyan Sathiyadash,
Eswaranpillai Uma, and Perumalsamy Priyadharsini
Root and Soil Biology Laboratory, Department of Botany, Bharathiar University,
Coimbatore 641046, Tamilnadu, India

Abstract.—We examined the extent and type of arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal associations in three lycophyte and 44 fern species collected from three different sites in the Kolli Hills, Eastern Ghats, southern India. Of the 47 plant taxa (belonging to 21 families and 33 genera) examined, 46 had AM fungal and 33 had DSE fungal associations. But, fungal structures were absent in the aquatic fern *Azolla pinnata* (Azollaceae). This is the first report of AM and DSE fungal status for 16 and 28 species, respectively. Among terrestrial lycophytes and ferns, 26 species had dual association of both AM and DSE fungi, whereas 11 species had only AM fungal association. *Vittaria elongata* from epiphytic habitats had dual association of AM and DSE fungi. Likewise, *Cheilanthes tenuifolia* (saxicolous or terrestrial), *Cheilanthes opposita, Lepisorus nudus, Pyrrosia lanceolata* (terrestrial or epiphytic), and *Asplenium lanceolatum* (saxicolous or epiphytic) examined from different sites or habitats also had dual association of AM and DSE fungi. Seventy two percent of the mycorrhizal lycophytes and ferns had intermediate-type AM and 15 percent had both *Paris*- and intermediate-types at different sites. Significant variations in AM fungal structures were evident in 16 ferns occurring in two or more sites. Nine AM fungal spore morphotypes belonging to *Acaulospora, Funneliformis, Glomus, Gigaspora,* and *Sclerocystis* were found to be associated with lycophytes and ferns.

Key Words.—arbuscular mycorrhiza, dark septate endophytic fungi, lycophytes, ferns, *Paris*-type, intermediate-type, Kolli Hills, Eastern Ghats

A wide range of soil fungi colonize plant roots, of which the most common and widespread are the arbuscular mycorrhizal (AM) fungi belonging to the phylum Glomeromycota. These fungi facilitate the uptake of nutrients, especially phosphorus (P) from nutrient deficient soils in exchange for host photosynthates (Smith and Read, 2008). Other benefits for plants from the fungal association include improved water relations, and tolerance to various abiotic and biotic stresses. Surveys of AM associations in vascular plants for over a century have established their wide spread occurrence (Brundrett, 2009 and references therein). Nevertheless, many plant taxa from natural ecosystems world-wide are yet to be examined for their mycorrhizal status. Despite their global distribution, the mycorrhizal status of lycophytes and ferns are scant. Kessler *et al.* (2010a) indicated that the 971 taxa of lycophytes and ferns whose mycorrhizal status was known to represent less than 10% of the global

---

[*] Corresponding author; e-mail: tmkum@yahoo.com, tel.091 0422 2428306

lycophyte and fern diversity. Since 2010, gametophytes and sporophytes of several lycophytes and ferns from Malaysia and Indonesia (Kessler *et al.*, 2010a), island of La Réunion (Kessler *et al.*, 2010b), Argentina (Fernandez *et al.*, 2010; 2012; Martinez *et al.*, 2012), India (Muthukumar and Prabha, 2012, 2013; Sarwade *et al.*, 2012), Honduras (Zubek *et al.*, 2010) and Japan (Ogura-Tsujita *et al.*, 2013) have been examined for their mycorrhizal status.

The AM colonization patterns encountered within plant roots have been designated as *Arum*-, *Paris*- or intermediate-types based on the distribution of AM fungal structures. In *Arum*-type, the fungal hyphae spreads in the root cortex intercellulary forming arbuscules on the lateral intracellular hyphal branches (Dickson, 2004). In *Paris*-type, the spread of the fungus within the cortex is intracellular forming hyphal coils within cells. Sometimes these hyphal coils bear rudimentary arbuscules. *Arum*-type is presumed to be formed in roots with high growth rates, and when the root cortex possesses abundant intercellular spaces. In contrast, *Paris*-type is presumed to occur in slow growing roots with limited or no intercellular spaces (Brundrett and Kendrick, 1990). A range of intermediate types exist between typical *Arum*- and *Paris*-types exhibiting the characters of both the types (Dickson, 2004). Determining the morphological structures produced by AM fungi is important because, the AM fungal structures like hyphae (inter-and intra-cellular), vesicles, arbuscules or arbusculate coils, and hyphal coils, have different roles in the symbiosis (Dickson *et al.*, 2007). It has been adequately demonstrated that fungal structures such as arbuscules, hyphal as well as arbusculate coils are involved in nutrient transfers thereby indicating a functional association (Smith and Smith, 2011). In contrast, abundance of intercellular or intracellular linear hyphae and vesicles indicate a carbon cost to the host (Sanders and Fitter, 1992). The AM morphology reported for a sample of limited lycophytes and ferns (10%), indicates the wide spread occurrence of *Paris*-type AM morphology (69%) compared to intermediate-type (28%) (Dickson *et al.*, 2007). In a recent study, Zubek *et al.* (2010) demonstrated the wide spread occurrence of *Paris*-type AM in ferns and lycophytes from Honduras. However, intermediate-type AM morphology was reported in roots of *Lycopodium paniculatum* and *Equisetum bogotense* from temperate forests of Patagonia, Argentina (Fernandez *et al.*, 2008). Muthukumar and Prabha (2013) showed that 93% of the lycophytes and ferns they examined from different habitats in the Eastern and Western Ghats, south India, had intermediate-type AM morphology.

Plant roots including those of lycophytes and ferns are also colonized by fungi with melanised or hyaline, regularly septate hyphae, with or without microsclerotia or moniliform cells (Haselwandter and Read, 1982; Newsham, 1999). These fungi, commonly known as dark septate endophytes, appear to be non-host specific, as they are known to colonize over 600 plant species (Fernandez *et al.*, 2010). Earlier studies have shown the presence of dark septate endophyte (DSE) fungal associations in lycophytes and ferns (Berch and Kendrick, 1982; Cooper, 1976; Fernandez *et al.*, 2008, 2010; Hodson *et al.*, 2009; Iqbal *et al.*, 1981; Kessler *et al.*, 2010a, 2010b; Lehnert *et al.*, 2009;

Muthukumar and Prabha, 2012; 2013). Recent studies suggest that DSE fungi could enhance plant growth and health under controlled conditions (Newsham, 2011). It has been speculated that DSE fungi could aid plants in the use of organic nutrients (Cladwell and Jumpponen, 2003). Further, it has also been proposed that DSE-plant association need not be limited to nutrient acquisition, but could be multifunctional (Mandyam and Jumpponen, 2005). For example, DSE fungi could protect plants against pathogens and herbivores through minimizing the carbon availability in the rhizosphere or through the production of secondary metabolites (Mandyam and Jumpponen, 2005). It is therefore essential to assess plants for DSE fungal associations.

Approximately 900–1000 species of lycophytes and ferns are distributed in the Indian Himalayas and the Eastern and Western Ghats. Of these around 270 species of lycophytes and ferns occur in south India (Dixit, 1984). In general, reports of AM fungal status and morphology in Indian lycophytes and ferns are very limited (see Muthukumar and Prabha, 2013 and references therein). The Eastern Ghats are isolated hill ranges occurring in peninsular India that spread over the three Indian states of Orissa, Andhra Pradesh, and Tamil Nadu. The Kolli Hills are among the eight that occur in the southern region of the Eastern Ghats. Assessments of the floristic diversity of the Kolli Hills suggest this hill range has a high degree of endemism and is one of the major reservoirs of medicinal plants in south India (Arun *et al.*, 2002; Gowrisankar *et al.*, 2011; Jayakumar *et al.*, 2002). The Kolli Hills have been subject to anthropogenic pressure ever since humans started to settle on these hills ranges over 600 years ago (Arun *et al.*, 2002). However, the magnitude of disturbance has increased several fold over the years, and includes disturbance from mining, establishment of farm lands and exotic plantations, shifting cultivation, over grazing, fire wood collection and tourism development (Mohanraj *et al.*, 2010; Sundaram and Parthasarathy, 2002). These human activities have resulted in large scale habitat destruction and substantially altered the vegetation and carbon stock (Jayakumar *et al.*, 2002; Mohanraj *et al.*, 2010).

Floristic analyses of Kolli Hills are mostly concerned with the ethnobotanical or medicinal uses of angiosperms, and information is meager for other plant groups (Arokiyaraj *et al.*, 2007; Francis Xavier *et al.*, 2011). Although, Gowrishankar *et al.* (2011) reported the presence of around 80 species of lycophytes and ferns in their floristic survey of the Kolli hills, there is no report on the root fungal associations of plants from this region. This prompted us to assess the AM and DSE fungal status of lycophytes and ferns of the Kolli Hills. Further, we also analysed AM colonization patterns and AM fungal diversity associated with these plant taxa. This information will improve our knowledge and understanding on the distribution and abundance of root fungal associations in lycophytes and ferns in this fragile ecosystem.

MATERIALS AND METHODS

Study sites and sampling.—The Kolli Hills lies at a longitude of 78° 20′ to 78° 30′E and a latitude of 11° 10′ to 11° 30′N with elevations ranging from 200

TABLE 1. Arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal association and AM morphology along with the previous reports for lycophytes and ferns examined from the Kolli Hills.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Adiantaceae							
Adiantum hispidulum Sw.		A	TE	AM,DSE*	I	AM[3,13], NM[7]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Adiantum capillus Junonis Rupr.	M	A	TE	AM*	I*	NR	NR
		B	TE	AM	I		
		C	TE	AM	I		
Adiantum incisum C.Presl	M	A	TE	AM,DSE*	I	AM[8,13]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Adiantum raddianum C.Presl		A	TE	AM,DSE*	I	AM[13]	I[13]
		B	TE	AM,DSE	P		
		C	TE	AM,DSE	I		
Cheilanthes farinosa (Forssk.) Kaulf.		A	SX	AM,DSE*	I*	AM[8]	NR
		B	SX	AM,DSE	I		
		C	SX	AM,DSE	P		
Cheilanthes tenuifolia (Burm.) Sw.	M	A	SX	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Cheilanthes opposita Kaulf.		A	TE	AM*,DSE*	P*	NR	NR
		B	EP	AM,DSE	I		
		C	EP	AM,DSE	I		
Doryopteris concolor (Langsd. & Fisch.) Kuhn		A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM	I		
Hemionitis arifolia (Burm.) T. Moore.	M	A	TE	AM,DSE*	I*	AM[14,18]	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		

TABLE 1. Continued.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Pityrogramma calomelanos (L.) Link	M	A	TE	AM,DSE	I	AM[10,13,14,18], DSE[13]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Angiopteridaceae							
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Aspleniaceae							
Asplenium indicum Sledge	NT	A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Asplenium lanceolatum Peter		A	SX	AM*,DSE*	I*	NR	NR
		B	EP	AM,DSE	I		
		C	SX	AM,DSE	P		
Asplenium tenuifolium D.Don		A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Azollaceae							
Azolla pinnata R.Br.		A	AQ	NM	—	NM[14]	NR
		C	AQ	NM	—		
Blechnaceae							
Blechnum occidentale L.		A	TE	AM	I*	AM[7]	NR
		B	TE	AM	I		
		C	TE	AM	I		
Cyatheaceae							
Cyathea gigantea (Wall. ex Hook.) Holttum		A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		

TABLE 1. Continued.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Dennstaedtiaceae							
Microlepia platyphylla (Don) J.Sm.		A	TE	AM	I*	AM[14], NM[22]	NR
		B	TE	AM	I		
Pteridium aquilinum (L.) Kuhn	M	B	TE	AM	I	AM[1,3,4,12,13,14,18,20,21], DSE[9]	I[13], P[4]
		C	TE	AM	I		
Dryopteridaceae							
Arachniodes amabilis (Blume) Tind.		A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM	I		
		C	TE	AM	I		
Tectaria coadunata (Wall.ex Hainas) Raiz. & Chowd.	M	A	TE	AM,DSE*	I*	AM[18], NM[22]	NR
		B	TE	AM,DSE	I		
Gleicheniaceae							
Dicranopteris linearis (Burm.f.) Underw.	ATR/M	A	TE	AM	I	AM[7,13,14,20], DSE[13]	I[13]
		B	TE	AM	I		
		C	TE	AM	I		
Lindsaeaceae							
Sphenomeris chinensis (L.) J.Sm.		A	TE	AM,DSE	I	AM[7,13], DSE[13]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM	I		
Lycopodiaceae							
Lycopodium cernuum L.	R/M	A	TE	AM	P*	AM[5,7], DSE[9]	NR
		B	TE	AM	P		
Marattiaceae							
Angiopteris evecta (G.Forst.) Hoffm.	M/ATR	A	TE	AM,DSE	I	AM[7,13,18,20], DSE[13]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		

TABLE 1. Continued.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Marsileaceae							
Marsilea minuta L.	M	A	MS	AM,DSE	P*	AM[7,13,18,20], NM[13]	NR
		B	MS	AM,DSE	P		
		C	MS	AM,DSE	P		
Marsilea quadrifolia L.	M	A	MS	AM,DSE	P*	AM[16], NM[13,17]	NR
		B	MS	AM,DSE	P		
Oleandraceae							
Nephrolepis auriculata (L.) Trimen	R/M	A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
Nephrolepis multiflora (Roxb). Jarrett ex Mort.		A	TE	AM,DSE*	P*	AM[7]	NR
		B	TE	AM	I		
		C	TE	AM,DSE	I		
Parkeriaceae							
Ceratopteris thalictroides (L.) Brongn.		A	TE	AM	I*	AM[7,11]	NR
		B	TE	AM,DSE*	I		
		C	TE	AM	I		
Polypodiaceae							
Drynaria quercifolia (L.) J.Sm.	ATR	B	TE	AM,DSE*	P	AM[13,18], NM[14]	I[13]
		C	TE	AM,DSE	I		
Lepisorus nudus Ching		A	TE	AM,DSE*	P*	AM[18]	NR
		B	EP	AM,DSE	P		
		C	EP	AM,DSE	P		
Leptochilus decurrens Blume	ATR	A	TE	AM*,DSE*	P*	NR	NR
		C	TE	AM,DSE	P		
Pyrrosia lanceolata (L.) Farw.	M	A	EP	AM*,DSE*	I*	NR	NR
		B	EP	AM,DSE	I		
		C	TE	AM,DSE	I		

TABLE 1. Continued.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Pteridaceae							
Pteris biaurita L.	M	A	TE	AM,DSE*	I*	AM[12]	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Pteris pellucida Baher	ATR/M	A	TE	AM,DSE	I	AM[13], DSE[13]	I[13]
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Schizaeaceae							
Lygodium microphyllum Link	M	A	TE	AM*	I*	NR	NR
		B	TE	AM,DSE*	I		
		C	TE	AM	I		
Selaginellaceae							
Selaginella sp.		A	TE	AM	I	NR	NR
		C	TE	AM	I		
Selaginella wightii Hieron.		A	TE	AM*	I*	NR	NR
		B	TE	AM	I		
		C	TE	AM	I		
Thelypteridaceae							
Christella dentata (Forssk.) Brown. & Jermy		A	TE	AM	P	AM[10,13,14,15]	I[13]
		B	TE	AM	I		
		C	TE	AM	I		
Christella parasitica (L.) H. Lev.	M	A	TE	AM,DSE*	I	AM[13,19]	I[13]
		B	TE	AM	I		
		C	TE	AM,DSE	I		
Macrothelypteris torresiana (Gaudich.) Ching		A	TE	AM,DSE*	I*	AM[22]	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		

TABLE 1. Continued.

Family/Plant species	ST/EI[a]	Site[b]	Habitat[c]	AM status[d]	AM type[e]	Previous reports[f]	
						AM status	AM type
Pseudocyclosorus xylodes (Kunze) Ching	EN	A	TE	AM*	I*	NR	NR
		B	TE	AM	I		
		C	TE	AM	I		
Pseudocyclosorus ochthodes (Kunze) Holttum		A	TE	AM,DSE*	I*	AM[14,18]	NR
		B	TE	AM,DSE	I		
		C	TE	AM	I		
Sphaerostephanos arbuscula (Willd.) Holttum		A	TE	AM*	I*	NR	NR
		B	TE	AM	I		
		C	TE	AM	I		
Vittariaceae							
Vittaria elongata Sw.	M	A	EP	AM,DSE*	I*	AM[6,7,14]	NR
		B	EP	AM,DSE	I		
Woodsiaceae							
Diplazium sylvaticum (Bory) Sw.	R	A	TE	AM*,DSE*	I*	NR	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		
Diplazium polypodioides Blume		A	TE	AM,DSE	I*	AM[8], DSE[9]	NR
		B	TE	AM,DSE	I		
		C	TE	AM,DSE	I		

* First report of AM-type, AM and DSE association.

[a] ST/EI, Status/economic importance. ATR, at risk; EN, endemic; NT, near threatened; R, rare. M, medicinal.

[b] A, Solakkadu; B, Kuzhivalavu shola; C, Nachiyarkovil.

[c] TE, Terricolous; SX, Saxicolous; EP, epiphyte; AQ, Aquatic; MS, Marshy habitat.

[d] AM, Arbuscular mycorrhizal; DSE, Dark septate endophytic fungi; NM, non-mycorrhizal.

[e] P, *Paris*-type; I, Intermediate- type.

[f] NR no report, [1] Berch and Kendrick (1982), [2] Bhat and Kaveriappa (2003), [3] Cooper (1976), [4] Dickson *et al.* (2007), [5] Duckett and Lignore (1992), [6] Gemma and Koske (1995), [7] Gemma *et al.* (1992), [8] Iqbal et al. (1981), [9] Jumpponen and Trappe (1998), [10] Khade and Rodrigues (2002), [11] Lee *et al.* (2001), [12] Mishra *et al.* (1980), [13] Muthukumar and Prabha (2012), [14] Muthukumar and Udaiyan (2000), [15] Prashar *et al.* (2005), [16] Radhika and Rodrigues (2007), [17] Raghupathy and Mahadevan (1993), [18] Raja *et al.* (1995), [19] Suseela and Devi (1998), [20] Wang and Qiu (2006), [21] Zhang *et al.* (2004), [22] Zhao (2000).

to 1415 m a.s.l. (Mohanraj *et al.*, 2010). Annual rainfall ranges between 300 and 2000 mm, and soil type varies from black to red clay. The vegetation types in the Kolli Hills include evergreen forests, shola forests, deciduous forests, mixed open forest, open scrub and plantation forests (Chittibabu and Parthasarathy, 2000; Mohanraj *et al.*, 2010; Sundaram and Parthasarathy, 2002).

Root and substrate samples of 390, lycophyte and fern sporophytes were collected between December 2011 and March 2012 from Sollakadu (longitude, 78° 20′51.0″ E; latitude, 11°18′11°30″ N, 1197 m a.s. l.) (hereafter referred to as Site-A), Kuzhilivalavu (longitude, 78°21′39.3″ E, latitude of 11°19′51.9″ N, 1237 m a.s.l.)(hereafter referred to as Site-B) and Nachiyar kovil (longitude, 78°20′53.5″ E, latitude of 11°19′4.0″ N) (hereafter referred to as Site-C) in the Kolli Hills of Eastern Ghats. The vegetation type was evergreen forest at Site-A and shola forests at Sites-B and -C. The samples collected represented 47 taxa from 33 genera in 21 families (Table 1). Three sporophytes were sampled for each species. Among the 47 taxa, one could not be identified to species level. The majority of the lycophytes and ferns (79%, 37 of 47 species) sampled were terrestrial, whereas, three species (*Cheilanthes opposita*, Adiantaceae; *Lepisorus nudus* and *Pyrrosia lanceolata*, Polypodiaceae) were found as both terrestrial and epiphytic at different sites. Similarly, *Cheilanthes tenuifolia* (Adiantaceae) was terrestrial or saxicolous, and *Asplenium lanceolatum* (Aspleniaceae) was saxicolous or epiphytic at different sites. The two *Marsilea* species existed in marshy habitat, and *Azolla pinnata* (Azollaceae) occurred as a free floating hydrophyte. *Vittaria elongata* (Vittariaceae) and *Chelianthes farinosa* (Adiantaceae) were epiphytic and saxicolous, respectively. In all, 6 aquatic, 15 marshy, 27 epiphytic, 18 saxicolous and 324 terrestrial individuals were examined from the three sites (Table 1). Plants were carefully removed and the roots were rinsed with water to remove the adhering litter and soil particles. The roots were preserved in FAA (formaldehyde/acetic acid/70% ethanol, 5V:5V:90V) until processing. Substrates shaken from the roots and adjacent to the roots were collected. Substrate associated with fern roots was very limited, even for terrestrial species, due to the superficial presence of roots and the very shallow soil profile. For epiphytic and saxicolous taxa, the substrate was a very thin layer over the tree trunk or rock surface. Therefore, soil and substrate samples of all the individuals collected from a site were bulked to form a composite substrate sample. The composite substrate samples were air dried, packed in polythene bags and stored at 4°C for AM fungal spore isolation. This composite sample was used for determining soil chemistry and the isolation of AM fungal spores.

Determination of soil characteristics.—The pH and electrical conductivity (EC) of the soil samples was determined electrometrically by using digital electronic meters (ELICO, India) in a 1:1 (soil: deionised water) suspension. Total N and available P were determined according to Jackson (1971) and exchangeable potassium (K) was determined after extraction with ammonium acetate (Jackson, 1971).

Root-fungal assessment.—The fixed roots were cut into 1-cm sections, cleared in 2.5% KOH at 90 °C (Koske and Gemma, 1989), acidified with 5N HCl and stained with trypan blue or chlorazol Black E (0.05% in lacto glycerol). Generally, fern roots remained dark after clearing and were bleached in alkaline H_2O_2 prior to acidification. The roots were stained overnight in the staining solution. The stained roots were examined with an Olympus BX51 compound microscope (×400) for the presence of AM fungal structures and the percentage of root length colonization was estimated according to the magnified intersection method (McGonigle *et al.*, 1990). In addition, the number of AM fungal structure intersections was also individually noted. It was thus possible to quantify both the root length colonized by AM fungal structures and the total root length colonized. Only root specimens possessing arbuscules or arbusculated coils were considered to be AM. The roots were also scored for total root length colonized by DSE fungal structures and total root length colonized as described above based on the presence of characteristic hyaline or melanised regularly-septate hyphae and when present, microsclerotia or moniliform cells (Peterson *et al.*, 2008). Sometimes the microsclerotia or moniliform cells were associated with a limited amount of intracellular hyphae.

The AM morphology was classified as *Paris*- or intermediate-types based on whether the fungal hyphae were linear and inter- or intracellular within the cells as coils. In this study, absence of inter or intracellular linear hyphae and limited arbuscular development on hyphal coils were used to designate *Paris*-type AM. Images of colonization and fungal structures were captured with a ProgRes®C3 digital camera.

Isolation and identification of AM fungal spores.—The substrate samples were screened for the presence of AM fungal spores according to Muthukumar and Udaiyan (2000). As AM fungal spores were either absent in most of the substrate samples or were present as spore cases, we did not enumerate them. When intact AM fungal spores or sporocarps (non-collapsed spores with cytoplasmic contents and free from parasitic attack) were present, they were transferred using a wet needle and mounted in polyvinyl alcohol-lactoglycerol with or without Melzer's reagent on a glass slide for identification (Schenck and Perez, 1990). Spores were identified from spore morphology and sub-cellular characters and compared to the original descriptions at Schüßlers lab web page (www.Irz-muenchen.de/-schuessler/amphylo/amphylo_species.html) and the culture database established by INVAM (http://www.invam.caf.wvu.edu). The spellings of scientific names are as suggested by Schüßler and Walker (2010).

Plant nomenclature, life-forms, status and economic importance.—Nomenclature and authorities for lycophytes and ferns are as used by Manickam (1996) and Irudayaraj and Manickam (2003). Life-forms were assigned as per field observation. The status (Chandra *et al.*, 2008; Maridass and Raju, 2010) and economic importance (Britto *et al.*, 2012; Mannar Mannan *et al.*, 2008; Maridass and Raju, 2010; Pathak *et al.*, 2011; Perumal, 2010) of the lycophytes and ferns were determined from the literature.

Statistical analysis.—Data on soil factors were subjected to analysis of variance (ANOVA) to assess if any significant variations occurred in the soil characteristics of different sites. The influence of plant species and sites on the extent of AM and DSE colonization and root length with different structures were analysed using Kruskal-Wallis non-parametric test as the data of fungal variables failed to satisfy normality even after transformation (Zar, 1984). Post-hoc comparisons were made using Mann-Whitney *U*-test. As both AM and DSE fungi occupy the same niche, the relation between these fungal variables was examined using Pearson's correlation to determine the nature of interaction.

RESULTS

Soil characteristics.—The sandy loam (Site-A) and clay loam (Sites-B and C) soils were slightly alkaline with pH ranging from 7.9 to 8.1. Electrical conductivity ranged from 0.06 to 0.07 mS cm^{-1}. Total N ranged from 10.3 mg kg^{-1} (Site-A and -C) to 10.4 mg kg^{-1} (Site-B). Total P ranged between 0.6 mg kg^{-1} (Site-A) and 0.7 mg kg^{-1} (Sites-B and -C), and exchangeable K ranged from 17.4 (Site-A) to 18.2 mg kg^{-1} (Site-C). The variations in soil characters among sites (pH-$F_{2,8}$=0.826; EC-$F_{2,8}$=0.273; N-$F_{2,8}$=0.125; P-$F_{2,8}$=0.500; K-$F_{2,8}$=0.164) were not significant (p>0.05).

Occurrence of AM fungal associations.—Among the 47 lycophytes and fern species (belonging to 21 families and 33 genera from the three different sites) examined, 46 had AM fungal associations (Table 1). The aquatic fern *A. pinnata* lacked AM fungal structures. The entry of fungi into roots was either directly though the rhizodermis after the formation of a swollen appressorium at the entry point, or through the root hairs (Fig. 1 a,b). Intraradical hyphae were broad, aseptate, intracellular, smooth or with knob-like projections (Fig. 1 h) or had inflated areas with a beaded appearance (Fig. 1 g), and were linear or coiled (Fig. 1 c,d). Arbuscules borne on intracellular hyphae or hyphal coils (Fig. 1 c,d,f) were very limited to elaborate, sometimes lamp brush-like (Fig. 1 i). Vesicles were intracellular (Fig. 1 e), but were absent in mycorrhizal roots of *P. lanceolata*.

Distribution of AM morphological types.—The majority (72%, 34/47) of the mycorrhizal lycophytes and ferns had features that were typical of intermediate-type morphology (Table 1). However, seven plant species (15%) exhibited both *Paris*- and intermediate-type AM morphologies. Typical *Paris*-type was characterized by the absence of inter- or intracellular linear hyphae and the presence of intracellular hyphal coils or arbusculate coils with reduced arbuscular proliferation and intracellular vesicles. Such typical *Paris*-type AM was observed in one lycophyte (*Lycopodium cernuum*, Lycopodiaceae) and four fern species (*L. nudus*, *Leptochilus decurrens*, Polypodiaceae; *Marsilea minuta* and *Marsilea quadrifolia*, Marsileaceae) (Table 1, Fig. 1. a).

Extent of AM fungal colonization.—The extent of AM fungal colonization and root length colonized by AM fungal structures varied significantly with plant species. The average percentage of root length with total AM colonization

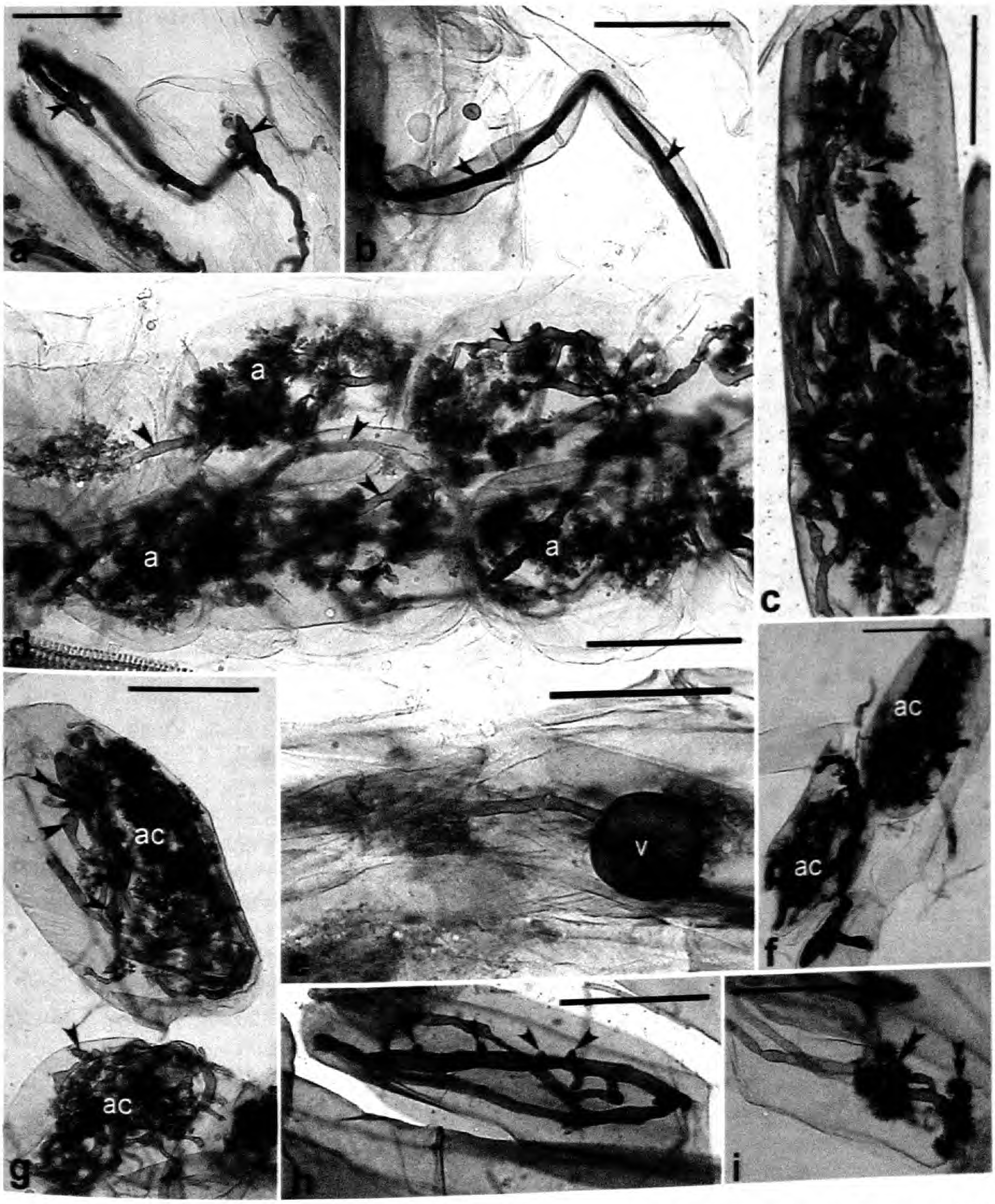

FIG. 1. a–c: Arbuscular mycorrhizal colonization in ferns of the Kolli Hills. a. Appressorium (arrow heads) and hyphal entry into roots though the rhizodermis in *Pyrrosia lanceolata*. b. Hyphal entry (arrow heads) through root hair in *Doryopteris concolor*. c. Arbusculate coil in root cells of *Lepisorus nudus* with reduced arbuscules (arrow heads). d. Intracellular hyphae (arrow heads) and arbuscules in *Adiantum incisum* e. Intracellular vesicle (v) in *Pseudocyclosorus xylodes*. f. Arbusculate coils (ac) in *Blechnum occidentale*. g. Arbusculate coils (ac) with beaded hyphae (arrow heads) in *Leptochilus decurrens*. h. Intracellular hyphal coil in *Drynaria quercifolia* with knob-like hyphal projections (arrow heads); i. Lamp-brush like arbuscules (double arrow heads) in *Diplazium sylvaticum*. Scale bars=50 μm.

TABLE 2. Average arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal colonization in lycophytes and ferns of the Kolli Hills.

	AM colonization#			
Plant species	%RLH	%RLV	%RLAC	%RLHC
Adiantum capillus	20.53 ± 1.32d–k☆	23.03 ± 2.39a–e	14.92 ± 3.29i–n	22.76 ± 2.45g–n
Adiantum hispidulum	20.21 ± 3.24d–k	11.23 ± 1.69h–o	28.30 ± 3.06a–d	20.57 ± 2.89i–p
Adiantum incisum	31.02 ± 2.16abc	9.44 ± 1.85i–q	28.51 ± 3.08a–d	7.97 ± 1.29q–t
Adiantum raddianum	15.81 ± 4.11i–l	12.00 ± 2.44h–n	2.71 ± 1.36qr	51.65 ± 4.56a
Angiopteris evecta	26.14 ± 2.25a–h	18.00 ± 1.99b–i	28.66 ± 2.36a–d	10.38 ± 1.72o–t
Arachniodes amabilis	28.60 ± 3.21a–e	10.80 ± 2.75h–p	13.59 ± 2.05j–o	25.62 ± 5.13g–l
Asplenium indicum	23.78 ± 2.04a–j	7.49 ± 0.94k–r	36.18 ± 2.54a	15.40 ± 1.87l–s
Asplenium lanceolatum	20.30 ± 5.22d–k	11.86 ± 2.41h–n	16.18 ± 3.23h–m	28.41 ± 4.15f–k
Asplenium tenuifolium	31.85 ± 2.58ab	15.22 ± 4.49e–l	5.92 ± 3.05o–r	21.39 ± 1.35h–o
Azolla pinnata	0.00 ± 0.00m	0.00 ± 0.00r	0.00 ± 0.00r	0.00 ± 0.00t
Blechnum occidentale	27.83 ± 1.53a–f	14.15 ± 3.57f–l	31.30 ± 4.34a–c	3.99 ± 1.13st
Ceratopteris thalictroides	18.83 ± 1.81e–k	11.48 ± 1.74h–n	34.80 ± 3.58ab	14.59 ± 4.64l–s
Cheilanthes farinosa	15.98 ± 5.85i–l	16.34 ± 2.79d–k	8.80 ± 3.44m–q	22.99 ± 5.28g–m
Cheilanthes opposita	15.47 ± 4.13j–l	24.90 ± 2.23a–d	8.84 ± 0.94m–q	31.95 ± 5.18d–i
Cheilanthes tenuifolia	16.51 ± 3.06h–k	16.68 ± 1.74d–j	17.14 ± 1.84h–m	29.68 ± 2.39d–j
Christella dentata	13.88 ± 3.57kl	21.36 ± 2.61b–g	15.21 ± 1.63h–n	29.23 ± 3.76e–k
Christella parasitica	23.20 ± 2.71a–k	8.03 ± 1.86j–r	22.97 ± 2.91c–i	21.27 ± 3.91h–o
Cyathea gigantea	29.16 ± 2.11a–d	10.50 ± 2.98i–p	26.32 ± 1.87b–f	16.39 ± 2.01l–r
Dicranopteris linearis	27.57 ± 1.50a–f	2.15 ± 0.94pqr	36.16 ± 2.53a	16.06 ± 2.02l–r
Diplazium polypodioides	27.14 ± 1.98a–g	17.97 ± 1.31b–i	27.83 ± 2.24a–e	8.10 ± 2.23q–t
Diplazium sylvaticum	28.46 ± 3.43a–e	25.60 ± 2.15a–c	19.33 ± 3.22e–k	6.36 ± 1.74r–t
Doryopteris concolor	30.76 ± 1.33abc	15.53 ± 3.44e–k	30.40 ± 2.78a–c	6.86 ± 1.18r–t
Drynaria quercifolia	22.17 ± 7.08b–k	2.56 ± 2.01o–r	0.23 ± 0.23r	37.42 ± 12.44c–f
Hemionitis arifolia	22.10 ± 1.89b–k	23.19 ± 1.71a–e	26.64 ± 2.86b–f	9.20 ± 3.05p–t
Lepisorus nudus	0.67 ± 0.33m	3.23 ± 1.49n–r	8.97 ± 0.53m–q	45.02 ± 4.03a–c
Leptochilus decurrens	2.36 ± 1.09m	24.97 ± 2.17a–d	13.12 ± 4.89j–o	40.20 ± 5.09b–e
Lycodium microphyllum	21.50 ± 1.99c–k	8.71 ± 1.94j–r	36.05 ± 3.20a	16.26 ± 3.55l–r
Lycopodium cernuum	1.98 ± 0.92m	6.23 ± 1.71l–r	6.91 ± 1.01n–r	51.66 ± 3.57a
Macrothelypteris torresiana	25.45 ± 2.88a–i	13.62 ± 3.20f–l	18.92 ± 2.74f–l	25.29 ± 3.73g–l
Marsilea minuta	0.00 ± 0.00m	22.38 ± 5.92a–f	5.31 ± 1.39o–r	29.70 ± 5.52d–j
Marsilea quadrifolia	0.00 ± 0.00m	1.38 ± 0.71qr	5.35 ± 0.71o–r	12.50 ± 2.06m–s
Microlepia platyphylla	15.50 ± 3.21a–k	9.10 ± 1.02g–m	20.98 ± 0.41a–d	14.24 ± 1.87l–r
Nephrolepis auriculata	26.10 ± 0.91a–h	14.04 ± 3.97f–l	30.68 ± 3.19a–c	8.82 ± 1.15p–t
Nephrolepis multiflora	5.29 ± 1.40m	3.72 ± 2.61m–r	16.33 ± 3.57h–m	50.59 ± 2.64ab
Pityrogramma calomelanos	21.31 ± 3.24c–k	19.87 ± 2.50b–h	25.94 ± 0.72c–g	10.79 ± 2.76n–t
Pseudocyclosorus ochthodes	7.53 ± 0.79lm	30.61 ± 2.70a	3.33 ± 2.21p–r	40.94 ± 2.96a–d
Pseudocyclosorus xylodes	24.23 ± 3.41a–j	26.02 ± 3.46a–c	2.60 ± 1.04qr	17.57 ± 3.18k–r
Pteridium aquilinum	25.26 ± 2.21a–i	10.92 ± 0.94h–p	11.57 ± 1.75k–p	33.83 ± 1.61d–g
Pteris biaurita	22.83 ± 1.49a–k	18.07 ± 2.47b–i	20.23 ± 2.10d–k	21.19 ± 1.59h–o
Pteris pellucida	22.51 ± 1.64a–k	17.92 ± 2.18b–i	21.27 ± 2.19d–j	19.04 ± 2.32j–q
Pyrrosia lanceolata	27.82 ± 3.32a–f	0.00 ± 0.00r	0.00 ± 0.00r	32.98 ± 2.40d–h
Selaginella sp.	18.36 ± 3.00f–k	0.17 ± 0.17r	10.59 ± 0.81l–q	46.88 ± 3.42a–c
Selaginella wightii	27.01 ± 1.99a–g	10.48 ± 2.59i–p	20.00 ± 0.88d–k	14.91 ± 4.55l–s
Sphaerostephanos arbuscula	21.28 ± 1.72c–k	26.09 ± 3.00ab	18.24 ± 2.25f–l	17.65 ± 2.40k–r
Sphenomeris chinensis	29.35 ± 2.44a–d	14.09 ± 2.32f–l	18.08 ± 1.71f–l	22.65 ± 1.94g–n
Tectaria coadunata	17.41 ± 1.52g–k	17.16 ± 3.49c–j	23.74 ± 4.20c–h	21.78 ± 1.03h–o
Vittaria elongata	32.25 ± 2.09a	13.50 ± 2.03f–l	17.68 ± 4.10g–l	7.13 ± 1.69q–t

TABLE 2. Extended.

AM colonization$^{\#}$	DSE colonization$^{\#\#}$			
%RLTC	%RLDSH	%RLMO	%RLMS	%RLDTC
81.24 ± 1.00a–c	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
80.32 ± 2.84a–c	0.31 ± 0.21fg	4.53 ± 2.56a	0.00 ± 0.00f	4.84 ± 2.52e–h
76.94 ± 2.01a–d	0.14 ± 0.14g	0.00 ± 0.00d	3.26 ± 1.15d–f	3.40 ± 1.26f–h
82.17 ± 1.19ab	0.34 ± 0.23fg	0.30 ± 0.30cd	0.00 ± 0.00f	0.64 ± 0.34gh
83.18 ± 1.05ab	1.34 ± 0.50d–g	0.22 ± 0.22cd	0.00 ± 0.00f	1.56 ± 0.66f–h
78.62 ± 2.97a–d	0.44 ± 0.29fg	0.00 ± 0.00d	0.00 ± 0.00f	0.44 ± 0.29gh
82.85 ± 1.35ab	1.99 ± 0.83d–g	0.00 ± 0.00d	0.00 ± 0.00f	1.99 ± 0.83f–h
76.75 ± 2.80a–d	5.60 ± 1.04bc	0.22 ± 0.22cd	6.13 ± 1.90cd	11.96 ± 1.76cd
74.38 ± 3.90b–e	4.00 ± 1.36b–e	1.20 ± 0.98b–d	5.13 ± 2.15c–e	10.34 ± 3.57c–e
0.00 ± 0.00k	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
77.27 ± 2.79a–d	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
79.69 ± 1.61a–c	0.96 ± 0.66e–g	0.36 ± 0.36b–d	0.00 ± 0.00f	1.33 ± 0.88f–h
64.11 ± 4.61f–h	2.47 ± 0.73d–g	0.00 ± 0.00d	5.00 ± 1.41c–e	7.47 ± 1.85d–f
81.15 ± 1.39a–c	1.91 ± 0.66d–g	0.00 ± 0.00d	0.00 ± 0.00f	1.91 ± 0.66f–h
80.02 ± 0.92a–c	2.12 ± 0.44d–g	0.97 ± 0.34b–d	3.45 ± 0.99d–f	6.63 ± 0.96d–g
79.68 ± 1.56a–c	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
75.48 ± 4.12a–d	11.95 ± 4.46a	0.00 ± 0.00d	2.06 ± 1.31ef	14.01 ± 5.15c
82.37 ± 1.27ab	5.78 ± 1.19b	0.40 ± 0.27b–d	0.00 ± 0.00f	6.20 ± 1.23e–h
81.95 ± 1.49ab	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
81.03 ± 1.09a–c	0.64 ± 0.44fg	0.00 ± 0.00d	2.19 ± 0.85d–f	2.83 ± 1.22f–h
79.75 ± 2.59a–c	0.00 ± 0.00g	0.31 ± 0.21cd	0.75 ± 0.53f	1.05 ± 0.64gh
83.55 ± 0.78ab	1.49 ± 1.27d–g	0.00 ± 0.00d	0.00 ± 0.00f	1.49 ± 1.27f–h
62.37 ± 6.55g–i	2.72 ± 0.59c–g	1.95 ± 1.24b	22.73 ± 7.04a	27.40 ± 7.81a
81.13 ± 1.20a–c	0.52 ± 0.27fg	0.00 ± 0.00d	0.00 ± 0.00f	0.52 ± 0.27gh
57.88 ± 4.17hi	4.48 ± 0.93b–d	0.00 ± 0.00d	19.07 ± 1.97b	23.49 ± 2.75ab
80.65 ± 1.01a–c	0.43 ± 0.28fg	3.82 ± 0.63a	0.00 ± 0.00f	4.24 ± 0.86f–h
82.52 ± 0.57ab	0.00 ± 0.00g	0.00 ± 0.00d	0.14 ± 0.14f	0.14 ± 0.14h
66.78 ± 3.86e–g	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
83.28 ± 0.61ab	0.60 ± 0.60fg	0.82 ± 0.58b–d	0.00 ± 0.00f	1.42 ± 0.76f–h
55.73 ± 5.63i	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
19.24 ± 2.66j	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
59.81 ± 0.94a–c	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
79.63 ± 1.33a–c	2.32 ± 0.59d–g	0.00 ± 0.00d	0.00 ± 0.00f	2.32 ± 0.59f–h
75.93 ± 2.20a–d	0.00 ± 0.00g	0.00 ± 0.00d	2.50 ± 0.93d–f	2.51 ± 0.94f–h
77.91 ± 2.11a–d	0.22 ± 0.22g	0.28 ± 0.28cd	0.91 ± 0.43f	1.41 ± 0.42f–h
82.40 ± 0.91ab	0.13 ± 0.13g	0.14 ± 0.14d	0.00 ± 0.00f	0.27 ± 0.18h
70.42 ± 2.71d–f	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
81.58 ± 2.31ab	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
82.32 ± 0.86ab	2.10 ± 0.64d–g	0.13 ± 0.13d	2.01 ± 0.54ef	4.24 ± 1.09f–h
80.73 ± 1.08a–c	0.54 ± 0.31fg	0.11 ± 0.11d	0.00 ± 0.00f	0.64 ± 0.34gh
60.80 ± 2.80g–i	0.79 ± 0.79fg	0.00 ± 0.00d	19.36 ± 3.12ab	20.15 ± 3.06b
75.99 ± 2.21a–d	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
72.40 ± 4.93c–e	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
83.26 ± 1.09ab	0.00 ± 0.00g	0.00 ± 0.00d	0.00 ± 0.00f	0.00 ± 0.00h
84.17 ± 0.86a	2.26 ± 1.37d–g	0.00 ± 0.00d	0.00 ± 0.00f	2.26 ± 1.37f–h
80.08 ± 1.92a–c	2.99 ± 1.35b–g	0.00 ± 0.00d	4.41 ± 1.25d–f	7.40 ± 2.49d–f
70.55 ± 3.02d–f	3.61 ± 1.27b–f	1.85 ± 0.51bc	8.69 ± 4.19c	14.14 ± 5.29c

TABLE 2. Continued.

Plant species	AM colonization# %RLH	%RLV	%RLAC	%RLHC
H statistics				
Plant species (PS) (df, 46)	2014.974***	2144.24***	2741.20***	2494.130***
Site (S) (df, 2)	0.5942ns	45.289***	8.4848*	33.192***
PS × S (df, 81)	924.14***	863.58***	500.64***	758.89***

RLH, Root length with hyphae; RLA/AC, Root length with arbuscules/arbusculate coils; RLV, Root length with vesicles; RLC, Root length with hyphal coils; RLTC, Root length with total colonization.

RLDSH, Root length with dark septate fungal hyphae; RLMI/MO, Root length with microsclerotia/ moniliform hyphae; RLDTC, Root length with total colonization.

☆ Means ± S.E in a column followed by same letter(s) are not significantly different.

*,**,***,ns: Significant at $p<0.05$, $p<0.01$, $p<0.001$ and not significant respectively.

ranged from 19.24% (*M. quadrifolia*) to 84.17% (*Sphenomeris chinensis*, Lindsaeaceae) (Table 2). Average percentage root length with total AM colonization for families ranged from 19.74% (Marsileaceae) to 83.18% (Angiopteridaceae). Average percentage root length with total AM colonization of lycophytes in the present study (77.41 ± 4.09%) was slightly higher compared to those of ferns (74.24 ± 2.39%). However, this variation in average percentage root length with total AM colonization between lycophytes and ferns was not significant ($U_{30,360} = 4933$; $p>0.05$). Life-forms differed significantly in average percentage root length with total AM colonization ($H_4 = 78.261$, $p<0.001$). The maximum average percentage root length with total AM colonization occurred in terrestrial taxa (78.81%) and the minimum occurred in ferns from marshy habitats (49.74%) (Fig. 2a). Although the variations in percentage root length with total AM colonization between species was significantly different, the differences between sites were not significant (Table 2, 3). The percentage root length with hyphae varied among taxa and ranged from 0.67% (*L. nudus*) and 32.25% (*Vittaria elongata*, Vittariaceae). The variations in percentage root length with hyphae among sites were significant among species but not among sites (Table 2, 3). There were differences in percentage of root length with hyphal coils both among species and sites. The percentage of root length with hyphal coils ranged from 3.99% (*Blechnum occidentale*, Blechnaceae) to 51.66% (*L. cernuum*, Lycopodiaceae). The variation in percentage root length with hyphal coils among species, sites and species × site interactions were highly significant ($p<0.001$). Percentage of root length with arbusculate coils ranged between <1 (*Drynaria quercifolia*, Polypodiaceae) and 36.18% (*Asplenium indicum*, Aspleniaceae). The differences in percentage root length with hyphal coils among species, sites and species × site interactions were significant ($p<0.001$). The percentage root length with vesicles ranged from <1% (*Selaginella* sp., Selaginellaceae) to 30.61% (*Pseudocyclosorus xylodes*, Thelypteridaceae) and the differences among species, sites and their interactions were highly ($p<0.001$) (Table 2).

TABLE 2. Continued. Extended.

AM colonization[#]	DSE colonization[##]			
%RLTC	%RLDSH	%RLMO	%RLMS	%RLDTC
1708.60***	1576.76***	461.25***	1635.94***	2178.27***
0.2155ns	0.295ns	11.566**	17.319***	6.804*
722.722***	443.756***	162.694***	216.875***	381.759***

Among the two marshy ferns, the percentage root length with total AM fungal colonization of *M. minuta* with more than 55% of its average root length colonized was significantly higher ($U_{6,9}$ = 54.00; $p<0.001$) than that of *M. quadrifolia* (19%).

AM fungal species diversity.—The majority of spores isolated from the substrate samples were devoid of contents, parasitized, or consisted of only spore cases. Nevertheless, nine AM fungal spore morphotypes were distinguished on the basis of spore morphology from the substrate samples examined (Table 4; Fig. 3). These included *Acaulospora foveata* Trappe & Janos, *Acaulospora rehmii* Sieverd & Toro, *Acaulospora scrobiculata* Trappe, *Funneliformis constrictum* (Trappe) C. Walker & Schüßler, *Funneliformis geosporum* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler, *Glomus microcarpum* Tul. & Tul., *Glomus invermaium* Hall, *Gigaspora decipiens* Hall & Abbott and *Sclerocystis rubiformis* Gerd. & Trappe.

Species richness was maximum in Site-A (8 spore morphotypes) followed by Site-C (7) and Site B (3). *Acaulospora scrobiculata*, *G. microcarpum* and *F. geosporum* occurred in all sites (Table 4).

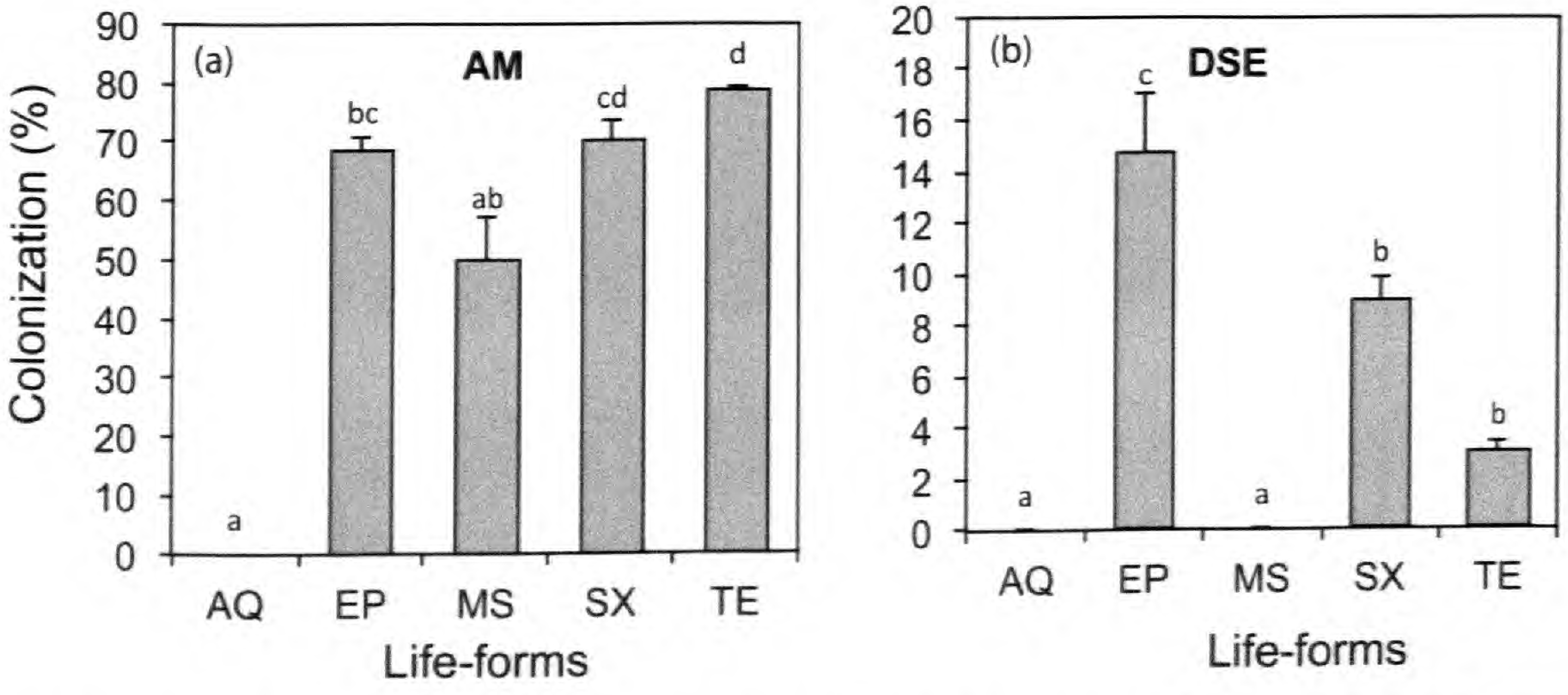

FIG. 2. Average arbuscular mycorrhizal (AM) (a) and dark septate endophyte (DSE) (b) fungal colonization in lycophytes and ferns of aquatic (AQ), epiphytic (EP), marshy (MS), saxicolous (SX) and terrestrial (TE) life-forms. Bars bearing same letter(s) are not significantly different according to DMRT (p>0.05).

TABLE 3. Extent of arbuscular mycorrhizal (AM) colonization in lycophytes and ferns at different sites of the Kolli Hills.

Plant species	Site[a]	AM colonization[b]				
		%RLH	%RLV	%RLAC	%RLHC	%RLTC
Adiantum hispidulum	A	18.86 ± 8.49a*	8.80 ± 0.96a	22.75 ± 2.83b	24.09 ± 7.54a	74.50 ± 7.39b
	B	25.98 ± 4.68a	13.18 ± 3.15a	27.01 ± 7.03ab	14.87 ± 4.15a	81.03 ± 3.49ab
	C	15.78 ± 2.21a	11.72 ± 4.27a	35.15 ± 3.89a	22.76 ± 1.13a	85.42 ± 0.36a
Adiantum capillus	A	19.03 ± 1.63a	19.50 ± 4.97a	14.32 ± 5.32a	28.50 ± 2.09a	81.35 ± 2.79a
	B	20.87 ± 1.12a	25.20 ± 5.25a	18.29 ± 9.50a	18.41 ± 5.34a	82.77 ± 0.41a
	C	21.71 ± 3.90a	24.38 ± 2.58a	12.15 ± 1.30a	21.36 ± 3.50a	79.60 ± 1.19a
Adiantum incisum	A	33.24 ± 5.09a	8.20 ± 3.48ab	25.99 ± 6.33ab	6.01 ± 2.48a	73.44 ± 3.27a
	B	30.30 ± 3.87a	13.59 ± 2.00b	23.23 ± 4.74a	7.28 ± 0.57a	74.39 ± 3.08ab
	C	29.52 ± 3.38a	6.52 ± 3.36a	36.32 ± 1.88b	10.62 ± 2.77a	82.98 ± 0.89b
Adiantum raddianum	A	26.47 ± 2.39a	12.40 ± 3.93a	0.00 ± 0.00b	43.13 ± 6.83a	82.00 ± 1.14a
	B	0.00 ± 0.00 b	5.63 ± 1.25a	8.14 ± 1.61a	66.99 ± 5.01a	80.76 ± 3.14a
	C	20.95 ± 1.27a	17.96 ± 4.01a	0.00 ± 0.00b	44.83 ± 3.83a	83.74 ± 1.88a
Angiopteris evecta	A	26.24 ± 1.88b	19.50 ± 4.12ab	26.18 ± 5.18a	10.05 ± 1.58b	81.98 ± 1.88a
	B	19.13 ± 1.92c	21.95 ± 1.27a	27.18 ± 3.96a	16.06 ± 1.19a	84.31 ± 1.97a
	C	33.05 ± 2.24a	12.55 ± 2.27b	32.63 ± 3.53a	5.04 ± 1.14b	83.26 ± 2.13a
Azolla pinnata	A	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
	C	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
Arachniodes amabilis	A	27.97 ± 6.40a	2.23 ± 1.38b	12.84 ± 5.23a	39.59 ± 6.34a	82.62 ± 5.31a
	B	24.51 ± 7.56a	12.27 ± 4.63a	10.93 ± 2.57a	21.93 ± 10.43ab	69.63 ± 3.32b
	C	33.33 ± 2.35a	17.91 ± 2.05a	17.02 ± 2.63a	15.34 ± 3.03b	83.60 ± 2.45a
Asplenium indicum	A	23.67 ± 3.31a	7.25 ± 1.69a	31.62 ± 4.41a	17.39 ± 5.31a	79.93 ± 2.77a
	B	21.62 ± 3.32a	7.79 ± 2.45a	39.81 ± 5.51a	16.74 ± 1.29a	85.96 ± 1.15a
	C	26.05 ± 4.78a	7.41 ± 1.27a	37.12 ± 3.19a	12.08 ± 1.89a	82.66 ± 1.90a
Asplenium lanceolatum	A	31.44 ± 1.10a	11.55 ± 3.40a	18.16 ± 4.18a	20.04 ± 2.05a	81.19 ± 3.23a
	B	29.47 ± 3.96a	15.95 ± 6.15a	15.11 ± 8.88a	21.48 ± 5.06a	82.01 ± 1.01a
	C	0.00 ± 0.00b	8.07 ± 2.17a	15.26 ± 2.77a	43.72 ± 1.74a	67.05 ± 3.39a
Asplenium tenuifolium	A	40.46 ± 1.27a	0.00 ± 0.00b	0.00 ± 0.00b	19.46 ± 3.81a	59.92 ± 4.49b
	B	24.36 ± 3.42b	18.30 ± 6.34a	17.76 ± 2.53a	21.78 ± 1.89a	82.20 ± 1.66a
	C	30.74 ± 0.83ab	27.37 ± 2.74a	0.00 ± 0.00b	22.92 ± 0.87a	81.02 ± 1.45a
Blechnum occidentale	A	26.82 ± 2.59a	13.30 ± 1.18b	34.29 ± 3.18a	5.94 ± 2.96a	80.36 ± 4.91a
	B	25.80 ± 3.65a	26.56 ± 0.70a	17.26 ± 6.82b	4.47 ± 0.97a	74.09 ± 7.54a
	C	30.86 ± 1.01a	2.59 ± 2.59c	42.35 ± 2.24a	1.57 ± 0.83a	77.36 ± 1.67a

TABLE 3. Continued.

Plant species	Site[a]	AM colonization[b]				
		%RLH	%RLV	%RLAC	%RLHC	%RLTC
Ceratopteris thalictroides	A	18.02 ± 3.01a	11.36 ± 2.05a	39.70 ± 4.08a	8.79 ± 2.08b	77.87 ± 1.55a
	B	17.54 ± 3.30a	9.14 ± 4.65a	25.79 ± 8.06a	32.04 ± 4.00a	84.51 ± 1.37a
	C	20.93 ± 4.01a	13.93 ± 2.17a	38.91 ± 3.35a	2.93 ± 0.86c	76.71 ± 3.02a
Cheilanthes farinosa	A	10.08 ± 4.04b	9.15 ± 3.29a	22.00 ± 2.25a	30.72 ± 0.72a	71.96 ± 6.65a
	B	37.86 ± 5.15a	20.32 ± 6.35a	0.00 ± 0.00c	3.51 ± 0.96b	61.69 ± 11.69ab
	C	0.00 ± 0.00c	19.55 ± 1.88a	4.40 ± 0.25b	34.74 ± 3.54a	58.68 ± 5.03b
Cheilanthes opposita	A	0.00 ± 0.00b	23.62 ± 7.04a	6.40 ± 0.50a	51.15 ± 3.47a	81.17 ± 3.70a
	B	25.06 ± 3.04a	25.80 ± 1.65a	11.50 ± 1.28a	18.56 ± 3.46a	80.93 ± 1.22a
	C	21.34 ± 3.60a	25.27 ± 2.50a	8.62 ± 1.59a	26.14 ± 2.70a	81.37 ± 2.82a
Cheilanthes tenuifolia	A	14.69 ± 4.05a	20.65 ± 1.18a	14.06 ± 1.92a	31.95 ± 3.66a	81.34 ± 1.75a
	B	22.18 ± 7.77a	13.37 ± 2.65a	21.23 ± 3.74a	23.03 ± 4.26a	79.81 ± 2.35a
	C	12.67 ± 3.28a	16.03 ± 3.80a	16.14 ± 3.04a	34.06 ± 1.57a	78.90 ± 0.13a
Christella dentata	A	0.00 ± 0.00b	25.86 ± 3.39a	13.9 ± 4.29a	38.92 ± 6.30a	78.68 ± 2.25a
	B	18.86 ± 1.61a	16.28 ± 6.61a	17.30 ± 3.42a	29.45 ± 4.34ab	81.89 ± 2.52a
	C	22.79 ± 1.27a	21.95 ± 1.89a	14.42 ± 3.64a	19.31 ± 6.29b	78.48 ± 3.78a
Christella parasitica	A	29.33 ± 4.86a	13.18 ± 1.69a	20.30 ± 8.98a	22.71 ± 1.66a	85.53 ± 1.04a
	B	21.77 ± 2.88a	8.93 ± 2.26ab	23.88 ± 3.56a	25.36 ± 2.35a	79.95 ± 3.93a
	C	18.51 ± 5.05a	1.98 ± 1.21b	24.74 ± 1.70a	15.75 ± 4.19a	60.97 ± 4.60b
Cyathea gigantea	A	35.21 ± 2.13a	1.80 ± 1.56c	31.18 ± 0.29a	14.47 ± 0.50a	82.67 ± 1.76a
	B	29.55 ± 1.14a	8.71 ± 2.56b	24.37 ± 4.39a	17.02 ± 5.53a	79.64 ± 1.54a
	C	22.73 ± 2.95b	20.99 ± 1.48a	23.40 ± 2.18a	17.67 ± 3.86a	84.79 ± 2.69a
Dicranopteris linearis	A	30.01 ± 0.97a	0.00 ± 0.00c	37.95 ± 1.95a	14.84 ± 2.09a	82.80 ± 1.22a
	B	30.22 ± 2.46a	0.89 ± 0.44b	31.66 ± 6.55a	16.53 ± 5.21a	79.29 ± 4.38a
	C	22.49 ± 0.73a	5.57 ± 1.25a	38.89 ± 3.83a	16.82 ± 4.04a	83.76 ± 0.72a
Diplazium sylvaticum	A	23.17 ± 6.74a	23.97 ± 4.49	21.01 ± 4.52a	7.40 ± 3.80a	75.56 ± 6.17a
	B	35.92 ± 1.71a	30.58 ± 1.54	9.81 ± 2.69b	6.98 ± 3.10a	83.30 ± 1.20a
	C	26.28 ± 6.95a	22.24 ± 3.70	27.17 ± 4.36a	4.70 ± 3.18a	80.39 ± 5.05a
Diplazium polypodioides	A	25.92 ± 3.04a	16.39 ± 2.17a	31.58 ± 1.72a	5.14 ± 3.13a	79.03 ± 1.93a
	B	30.33 ± 1.38a	18.01 ± 2.20a	25.92 ± 2.02a	8.37 ± 1.57a	82.64 ± 1.31a
	C	25.15 ± 5.30a	19.50 ± 2.92a	25.98 ± 6.52a	10.80 ± 6.25a	81.44 ± 2.32a

TABLE 3. Continued.

Plant species	Site[a]	AM colonization[b]				
		%RLH	%RLV	%RLAC	%RLHC	%RLTC
Doryopteris concolor	A	29.60 ± 1.52a	12.52 ± 4.42b	33.26 ± 0.86a	7.32 ± 1.58a	82.71 ± 1.64a
	B	34.31 ± 0.44a	8.16 ± 5.13b	36.19 ± 5.66a	4.26 ± 2.17a	82.93 ± 1.46a
	C	28.37 ± 2.97a	25.90 ± 3.31a	21.76 ± 1.39a	9.00 ± 1.90a	85.03 ± 0.90a
Drynaria quercifolia	B	6.56 ± 3.81b	5.12 ± 3.69a	0.00 ± 0.00a	64.66 ± 6.67a	76.34 ± 1.16a
	C	37.77 ± 2.46a	0.00 ± 0.00b	0.46 ± 0.16a	10.18 ± 3.65b	48.40 ± 4.59b
Hemionitis arifolia	A	19.70 ± 1.46a	27.53 ± 3.40a	27.26 ± 0.58a	7.58 ± 2.85b	82.07 ± 1.44a
	B	25.82 ± 3.04a	19.76 ± 0.91a	34.27 ± 5.05a	0.75 ± 0.75c	80.59 ± 1.83a
	C	20.79 ± 4.58a	22.29 ± 2.63a	18.38 ± 2.99a	19.27 ± 3.93a	80.73 ± 3.36a
Lepisorus nudus	A	2.00 ± 2.89a	0.00 ± 0.00b	7.32 ± 0.25a	54.60 ± 2.80a	63.92 ± 4.59a
	B	0.00 ± 0.00b	3.25 ± 3.25a	10.82 ± 1.26a	31.24 ± 1.05b	45.31 ± 5.29b
	C	0.00 ± 0.00b	6.44 ± 2.37a	8.76 ± 1.12a	49.21 ± 4.91a	64.41 ± 6.41a
Leptochilus decurrens	A	0.00 ± 0.00b	26.06 ± 3.43a	2.24 ± 0.05b	50.41 ± 0.41a	78.71 ± 1.63a
	C	4.72 ± 1.53a	23.87 ± 6.86a	24.00 ± 3.34a	30.00 ± 2.25a	82.59 ± 8.37a
Lycodium microphyllum	A	16.90 ± 4.09a	7.65 ± 2.17a	36.86 ± 8.23a	20.61 ± 8.19a	82.02 ± 0.63a
	B	22.10 ± 1.48a	11.21 ± 5.85a	33.70 ± 3.41a	16.78 ± 7.58a	83.79 ± 1.06a
	C	25.50 ± 3.12a	7.27 ± 1.26a	37.59 ± 6.27a	11.38 ± 2.27a	81.75 ± 1.05a
Lycopodium cernuum	A	0.00 ± 0.00b	10.01 ± 2.36a	8.82 ± 1.03a	50.17 ± 4.79a	69.00 ± 3.52a
	B	3.96 ± 0.25a	2.44 ± 1.25b	5.00 ± 1.20a	53.15 ± 3.53a	64.55 ± 1.62a
Macrothelypteris torresiana	A	24.09 ± 5.92a	11.39 ± 3.25a	16.41 ± 5.47a	30.11 ± 9.95a	82.00 ± 1.37a
	B	20.98 ± 4.13a	14.78 ± 8.96a	18.47 ± 7.14a	29.05 ± 1.72a	83.27 ± 0.88a
	C	31.29 ± 4.39a	14.69 ± 5.32a	21.89 ± 1.10a	16.71 ± 3.04a	84.57 ± 0.32a
Marsilea minuta	A	0.00 ± 0.00a	0.00 ± 0.00b	8.94 ± 1.15a	42.80 ± 4.88a	51.74 ± 3.16c
	B	0.00 ± 0.00a	35.31 ± 1.84a	8.59 ± 1.02a	38.89 ± 1.54b	82.79 ± 1.49a
	C	0.00 ± 0.00a	31.83 ± 6.24a	7.00 ± 1.25a	37.73 ± 1.77ab	76.56 ± 1.73b
Marsilea quadrifolia	A	0.00 ± 0.00a	0.67 ± 0.17a	5.09 ± 0.50a	15.00 ± 1.15a	20.76 ± 4.54a
	B	0.00 ± 0.00a	2.10 ± 1.24a	5.62 ± 0.25a	10.00 ± 1.25a	17.72 ± 4.04a
Microlepia platyphylla	A	27.02 ± 4.00a	11.69 ± 1.61a	28.49 ± 2.82a	13.88 ± 2.49a	81.08 ± 1.32a
	B	19.48 ± 4.72a	13.51 ± 0.68a	28.82 ± 0.47a	18.83 ± 2.35a	80.65 ± 1.88a
Nephrolepis auriculata	A	27.36 ± 2.52a	8.03 ± 2.81b	33.84 ± 4.07a	9.70 ± 1.91a	78.93 ± 2.07a
	B	24.85 ± 1.14a	20.04 ± 6.40a	27.52 ± 6.07a	7.93 ± 0.26a	80.33 ± 2.38a

TABLE 3. Continued.

Plant species	Site[a]	AM colonization[b]				
		%RLH	%RLV	%RLAC	%RLHC	%RLTC
Nephrolepis multiflora	A	0.00 ± 0.00b	11.16 ± 6.35a	19.81 ± 4.90a	46.58 ± 3.51a	77.55 ± 4.08a
	B	8.75 ± 0.97a	0.00 ± 0.00b	7.14 ± 1.14a	57.91 ± 3.29b	73.81 ± 5.93a
	C	7.11 ± 1.53a	0.00 ± 0.00b	22.04 ± 2.25a	47.28 ± 4.17c	76.43 ± 1.66a
Pityrogramma calomelanos	A	12.00 ± 4.46a	18.01 ± 6.53a	26.47 ± 0.71a	14.81 ± 7.33a	71.28 ± 1.98a
	B	27.77 ± 2.95a	20.89 ± 0.61a	25.35 ± 2.23a	7.50 ± 3.67a	81.51 ± 2.54a
	C	24.17 ± 5.42a	20.71 ± 5.45a	26.00 ± 0.61a	10.07 ± 3.20a	80.95 ± 3.17a
Pseudocyclosorus xylodes	A	26.85 ± 3.75a	17.41 ± 5.13a	1.98 ± 1.40ab	25.62 ± 4.16a	71.86 ± 6.65a
	B	20.48 ± 4.57a	36.10 ± 3.35a	4.89 ± 2.46a	9.37 ± 4.20b	70.84 ± 4.48a
	C	25.36 ± 4.81a	24.55 ± 4.11a	0.92 ± 0.12b	17.71 ± 4.52ab	68.55 ± 4.57a
Pseudocyclosorus ochthodes	A	7.00 ± 3.55b	33.27 ± 4.88a	10.00 ± 1.50a	34.16 ± 4.03a	84.44 ± 0.27a
	B	5.73 ± 1.88c	32.66 ± 5.44a	0.00 ± 0.00b	42.17 ± 4.66a	80.55 ± 1.31a
	C	9.85 ± 0.33a	25.89 ± 4.15a	0.00 ± 0.00b	46.48 ± 5.21a	82.22 ± 2.08a
Pteridium aquilinum	B	27.68 ± 3.11a	10.78 ± 1.55a	10.14 ± 2.19a	33.18 ± 3.21a	81.79 ± 4.47a
	C	22.84 ± 3.65a	11.05 ± 2.07a	13.00 ± 2.22a	34.47 ± 2.63a	81.36 ± 2.14a
Pteris biaurita	A	25.53 ± 2.18a	21.61 ± 1.11a	18.23 ± 1.35a	18.55 ± 0.72a	83.93 ± 0.66a
	B	18.82 ± 1.55a	19.88 ± 2.65a	17.59 ± 2.13a	24.36 ± 2.53a	80.64 ± 2.28a
	C	24.13 ± 2.62a	12.72 ± 6.54a	24.86 ± 5.53a	20.68 ± 3.85a	82.38 ± 0.79a
Pteris pellucida	A	24.09 ± 1.97a	11.43 ± 2.42a	22.80 ± 2.93a	22.62 ± 0.73a	80.94 ± 2.13a
	B	19.35 ± 1.69a	23.39 ± 2.50a	17.35 ± 5.34a	19.07 ± 3.56a	79.17 ± 2.54a
	C	24.07 ± 4.26a	18.93 ± 2.93a	23.65 ± 2.96a	15.43 ± 6.19a	82.09 ± 0.92a
Pyrrosia lanceolata	A	24.74 ± 8.61a	0.00 ± 0.00a	0.00 ± 0.00a	38.87 ± 4.30a	63.61 ± 5.99a
	B	31.55 ± 2.92a	0.00 ± 0.00a	0.00 ± 0.00a	27.08 ± 3.87a	58.63 ± 4.49a
	C	27.16 ± 6.13a	0.00 ± 0.00a	0.00 ± 0.00a	33.00 ± 0.89a	60.16 ± 5.63a
Selaginella sp.	C	12.19 ± 5.20b	0.35 ± 0.35a	11.55 ± 0.74a	50.81 ± 4.75a	74.90 ± 4.22a
	A	24.53 ± 2.02a	0.00 ± 0.00b	9.62 ± 1.30a	42.94 ± 2.55a	77.09 ± 3.16a
Selaginella wightii	A	27.49 ± 5.24a	12.27 ± 6.14a	20.00 ± 2.25a	23.25 ± 0.53a	83.01 ± 1.34a
	B	23.93 ± 3.90a	6.70 ± 3.38a	21.00 ± 1.75a	14.93 ± 1.62a	66.56 ± 2.61a
	C	29.62 ± 3.27a	12.46 ± 4.57a	19.00 ± 1.25a	6.53 ± 6.53a	67.62 ± 7.84a
Sphaerostephanos arbuscula	A	22.02 ± 0.84a	21.44 ± 4.36a	20.70 ± 1.62a	21.74 ± 1.67a	65.96 ± 0.60b
	B	20.61 ± 2.52a	26.20 ± 8.11a	13.55 ± 6.30a	21.98 ± 3.18a	82.33 ± 1.43a
	C	21.21 ± 3.74a	30.64 ± 1.53a	20.48 ± 1.32a	9.22 ± 1.68b	81.56 ± 2.53a

TABLE 3. Continued.

Plant species	Site[a]	AM colonization[b] %RLH	%RLV	%RLAC	%RLHC	%RLTC
Sphenomeris chinensis	A	32.14 ± 4.45a	12.43 ± 5.02a	18.81 ± 1.57a	20.36 ± 0.99a	83.74 ± 2.83a
	B	31.71 ± 5.31a	12.27 ± 5.02a	20.41 ± 4.71a	20.30 ± 4.59a	84.69 ± 0.59a
	C	24.21 ± 1.95a	17.57 ± 2.26a	15.02 ± 1.70a	27.28 ± 2.63a	84.08 ± 0.57a
Tectaria coadunata	A	17.96 ± 3.62a	24.31 ± 3.56a	16.72 ± 6.07b	19.90 ± 2.74b	78.88 ± 3.23a
	B	16.85 ± 1.21a	10.02 ± 2.31b	30.75 ± 1.20a	23.66 ± 0.87a	81.28 ± 2.96a
Vittaria elongata	A	33.13 ± 3.73a	17.47 ± 2.78a	9.26 ± 1.77b	5.47 ± 2.16a	65.32 ± 8.40b
	B	31.37 ± 0.67a	9.52 ± 1.98b	26.09 ± 2.50a	8.79 ± 2.39a	75.77 ± 1.41a

[a] A, Solakkadu; B, Kuzhivalavu shola; C, Nachiyar kovil.

[b] RLH, Root length with hyphae; RLA/AC, Root length with arbuscules/arbusculate coils; RLV, Root length with vesicles; RLC, Root length with hyphal coils; RLTC, Root length with total colonization.

* Mean ± S.E in a column for a species followed by the same letter(s) are not significantly different.

TABLE 4. Distribution of arbuscular mycorrhizal fungal species in different study sites in the Kolli Hills (+, presence; −, absence)

AM fungal species	Site A[a]	Site B	Site C
Acaulospora foveata	+	−	−
Acaulospora rehmii	+	−	+
Acaulospora scrobiculata	+	+	+
Funneliformis constrictum	+	−	−
Funneliformis geosporum	+	+	+
Gigaspora decipiens	−	−	+
Glomus invermaium	+	−	+
Glomus microcarpum	+	+	+
Sclerocystis rubiformis	+	−	+
	8	3	7

[a] A, Solakkadu; B, Kuzhivalavu shola; C, Nachiyar kovil.

Occurrence of DSE fungal association.—Dark septate endophyte fungal colonization, characterized by melanized or hyaline septate hyphae, microsclerotia and moniliform cells in root cortex was observed in 33 ferns (Table 1, Fig. 4a–h). However, DSE fungal structures were absent in the three lycophytes and 11 fern taxa belonging to nine families. These included *Adiantum capillus*

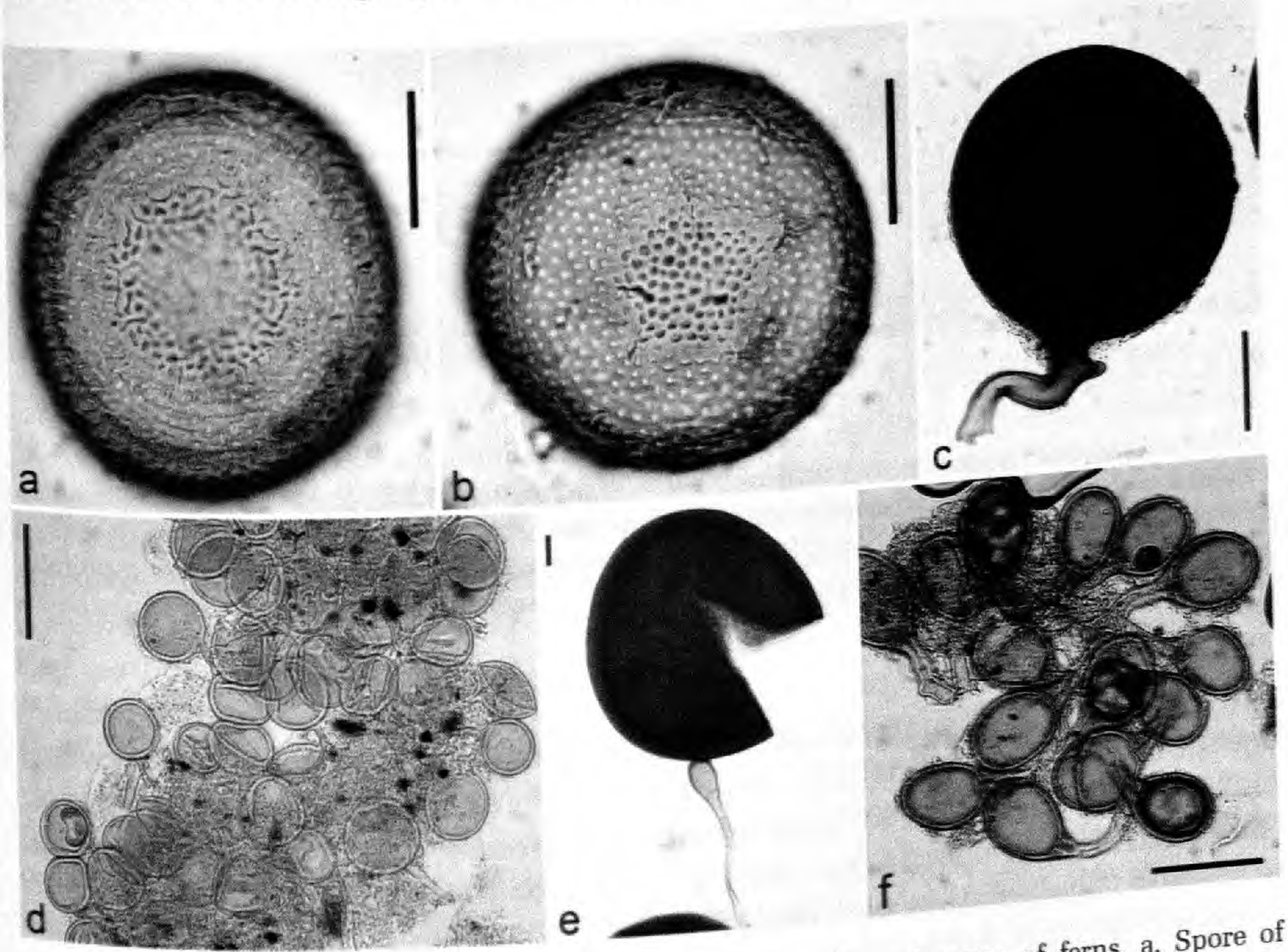

FIG. 3. a–h. Arbuscular mycorrhizal spores isolated from the substrates of ferns. a. Spore of *Acaulospora rehmii*, b. Spore of *Acaulospora foveata*, c. Spore of *Funneliformis geosporum*, d. Spores of *Glomus microcarpum*; g. Fractured spore of *Gigaspora decipens*; h. Spores of *Sclerocystis rubiformis*. Scale bars=50 µm.

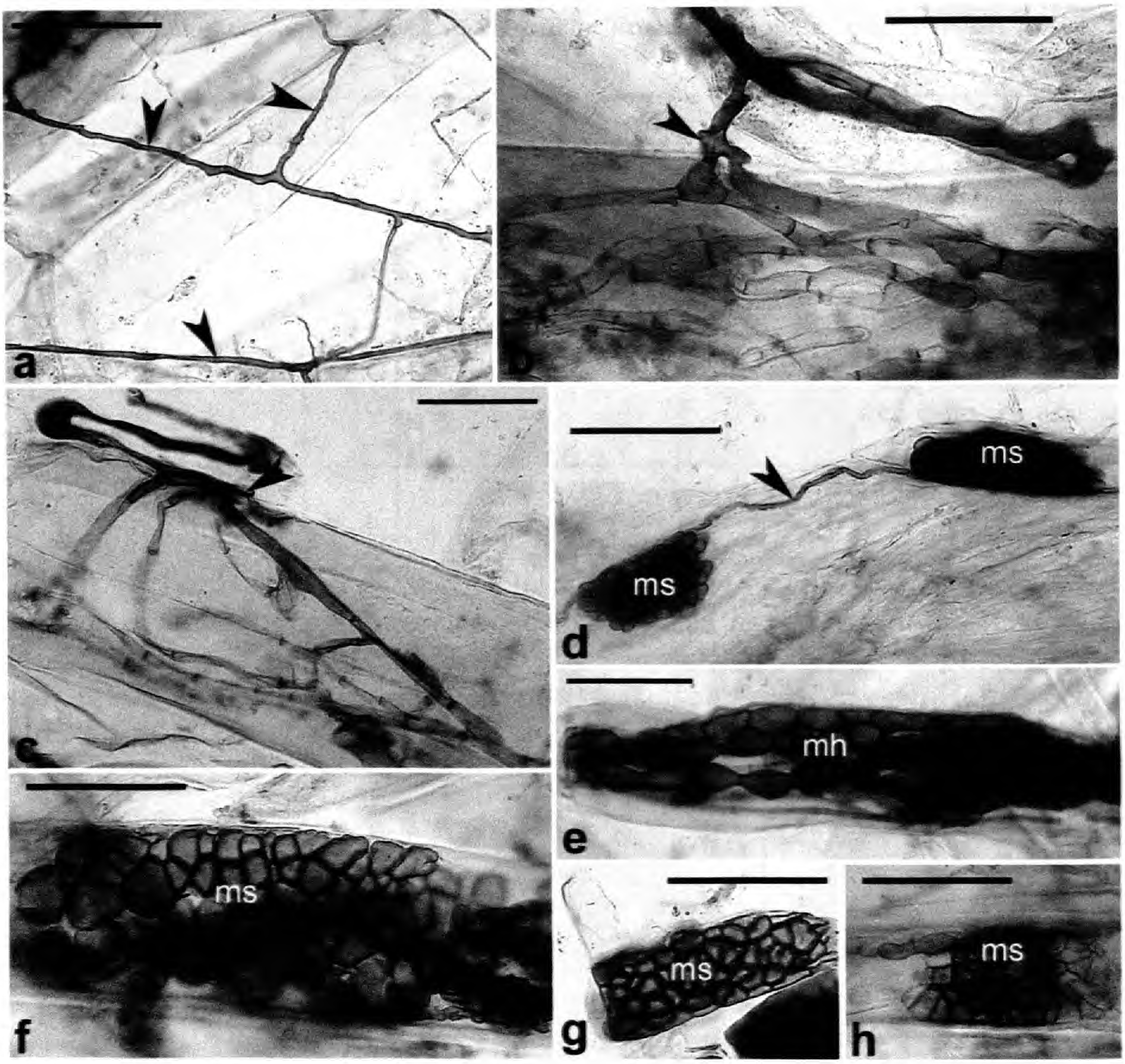

FIG. 4. a–h. Dark septate endophyte (DSE) fungal association in ferns. (a) Surface runner hyphae (arrow heads) on roots of *Adiantum incisum*; (b) Appresorium-like structure (arrow head) on root surface and septate hyphae in root cells of *Christella parasitica*; (c) Hyphal entry (arrow head) in *Chilanthes oppositia*; (d) Microsclerotia (ms) and the connecting hyphae (arrow head) in *Pityrogramma calomelanos*; (e) Moniliform cells in the root cortical cell of *Cheilanthes tenuifolia*. f–h. Microsclerotia (ms) in *Asplenium indicum* (f), *Adiantum hispidulum* (g), and *Lepisorus nudus* (h). Scale bars=50 µm.

(Adiantaceae), *A. pinnata*, *B. occidentale*, *Microlepia platyphylla*, *Pteridium aquilinum* (Dennstaediaceae), *Dicranopteris linearis* (Gleicheniaceae), *L. cernuum*, *M. minuta*, *M. quadrifolia*, *Selaginella* sp., *Selaginella wightii* (Selaginellaceae), *Christella dentata*, *P. xylodes* and *Sphaerostephanos arbuscula* (Thelypteridaceae) (Table 1).

Extent of DSE fungal colonization.—The root length colonized by DSE fungal hyphae ranged from 0.13% (*Pseudocyclosorus ochthodes*, Thelypteridaceae) to 11.95% (*Christella parasitica*, Thelypteridaceae) (Table 2). The percentage root length with moniliform cells ranged from 0.11% (*Pteris* *pellucida*, Pteridaceae) to 4.53% (*Adiantum hispidulum*, Adiantaceae). The percentage root length with microsclerotia ranged from 0.14% (*Lygodium microphyllum*, Schizaeaceae) to 22.73% (*D. quercifolia*). The percentage and root length with total DSE colonization ranged from 0.14% (*L. microphyllum*) to 27.40% (*D. quercifolia*) (Table 2). The percentage root length with total DSE fungal colonization and root length with DSE fungal structures in *Asplenium tenuifolium* (Aspleniaceae), *C. tenuifolia*, *C. parasitica* and *V. elongata* varied significantly among sites. Significant differences existed in average percentage root length with total DSE colonization ($H_4=73.16$, $P<0.001$) among various life-forms (Fig. 2b), with epiphytic ferns (14.74%) possessing maximum average percentage root length with total DSE fungal colonization and terrestrial species (3.05%) recording the minimum percentage root length with total DSE fungal colonization. Ferns examined from the marshy and aquatic habitats lacked DSE fungal colonization. However, percentage root length with total DSE colonization and root length with DSE fungal structures varied significantly among plant species and sites except for percent root length with DSE fungal hyphae (Table 2, 5). The species × site interactions were also significant for all the DSE fungal variables examined. Although a significant negative correlation existed between percentage root length with total DSE and AM fungal colonization ($r = -0.269$, $p<0.01$, $n=130$), the linear association accounted only for 7.2% of the variance in the two variables.

DISCUSSION

Our results showed the frequent occurrence of AM association in lycophytes and ferns of the Kolli Hills. This is in agreement with an earlier study (Muthukumar and Prabha, 2013) where 24 of 26 species of ferns examined from the Yercaud hills of the Eastern Ghats, south India were found to be colonized by AM fungi. Surveys from many habitats worldwide indicate both high (>75%) and low (<50%) incidence of AM in lycophytes and ferns (see Muthukumar and Prabha, 2013, and references therein). To our knowledge, AM association has been reported in 15 ferns and two lycophyte species for the first time here. The lack of AM association in the aquatic fern *A. pinnata* is consistent with previous observations of the aquatic ferns *Azolla* and *Salvinia* (Gemma *et al.*, 1992; Lee *et al.*, 2001; Muthukumar and Udaiyan, 2000; Ragupathy and Mahadevan, 1993). The non-mycotrophic nature of the free floating aquatic fern *A. pinnata* could be due to two causes. First, as the fern floats freely in water throughout the year, it has no chance of contacting mycorrhizal inocula of any type unless it drifts to the shores. Second, hydrophytes generally have a poorly developed root system as the necessary nutrients could be absorbed directly by roots and shoot surfaces that are in contact with water (Radhika and Rodrigues, 2007).

In contrast to *A. pinnata*, *M. quadrifolia* and *M. minuta* examined from marshy habitats in the present study were colonized by AM fungi, which corroborates previous findings (Bajwa *et al.*, 2001; Bareen, 1990; Iqbal *et al.*, 1988; Radhika and Rodrigues, 2007). As soil moisture levels in marshy habitats

TABLE 5. Extent of dark septate entophyte (DSE) fungal colonization in lycophytes and ferns at different sites of the Kolli Hills.

		DSE Colonization##			
Plant species	Site#	%RLDSH	%RLMO	%RLMI	%RLDTC
Adiantum hispidulum	A	0.49 ± 0.19a*	4.09 ± 0.09a	—	4.58 ± 1.87a
	B	0.00 ± 0.00b	7.41 ± 0.41a	—	7.41 ± 0.41a
	C	0.44 ± 0.14a	2.08 ± 0.30a	—	2.52 ± 0.74a
Adiantum capillus	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Adiantum incisum	A	0.43 ± 0.13a	—	4.65 ± 3.04a	5.08 ± 3.45a
	B	0.00 ± 0.00b	—	1.69 ± 0.90a	1.69 ± 0.90a
	C	0.00 ± 0.00b	—	3.43 ± 0.89a	3.43 ± 0.89a
Adiantum raddianum	A	0.50 ± 0.05a	0.89 ± 0.19a	—	1.39 ± 0.77a
	B	0.00 ± 0.00b	0.00 ± 0.00b	—	0.00 ± 0.00b
	C	0.53 ± 0.03a	0.00 ± 0.00b	—	0.53 ± 0.03a
Angiopteris evecta	A	0.31 ± 0.11a	0.00 ± 0.00b	—	0.31 ± 0.11a
	B	2.94 ± 0.87a	0.65 ± 0.15a	—	3.59 ± 1.35a
	C	0.77 ± 0.39a	0.00 ± 0.00b	—	0.77 ± 0.39a
Azolla pinnata	A	—	—	—	—
	C	—	—	—	—
Arachniodes amabilis	A	1.32 ± 0.66a	—	—	1.32 ± 0.66a
	B	0.00 ± 0.00b	—	—	0.00 ± 0.00b
	C	0.00 ± 0.00b	—	—	0.00 ± 0.00b
Asplenium indicum	A	1.34 ± 0.75a	—	—	1.34 ± 0.75a
	B	2.31 ± 1.36a	—	—	2.31 ± 1.36a
	C	2.33 ± 0.33a	—	—	2.33 ± 0.33a
Asplenium lanceolatum	C	4.14 ± 0.97a	0.67 ± 0.17a	12.46 ± 1.80ab	17.27 ± 2.94a
	A	3.81 ± 0.19a	0.00 ± 0.00b	5.54 ± 1.78b	9.35 ± 1.85a
	B	8.86 ± 2.01a	0.00 ± 0.00b	0.40 ± 0.20a	9.26 ± 2.02a
Asplenium tenuifolium	A	7.99 ± 2.93a	3.61 ± 0.69a	12.05 ± 4.00a	23.66 ± 4.06a
	B	1.09 ± 0.55b	0.00 ± 0.00b	1.02 ± 0.02a	2.11 ± 0.49b
	C	2.92 ± 0.62ab	0.00 ± 0.00b	2.33 ± 1.38a	5.25 ± 0.95b
Blechnum occidentale	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Ceratopteris thalictroides	A	0.00 ± 0.00b	0.00 ± 0.00b	—	0.00 ± 0.00b
	B	2.89 ± 0.57a	1.09 ± 0.09a	—	3.98 ± 2.02a
	C	0.00 ± 0.00b	0.00 ± 0.00b	—	0.00 ± 0.00b
Cheilanthes farinosa	A	2.76 ± 0.70a	—	6.31 ± 4.32a	9.07 ± 5.01a
	B	2.83 ± 1.50a	—	4.38 ± 1.76a	7.22 ± 2.82a
	C	1.80 ± 0.80a	—	4.32 ± 0.89a	6.12 ± 2.44a
Cheilanthes opposita	A	0.48 ± 0.18a	—	—	0.48 ± 0.18a
	B	2.92 ± 0.89a	—	—	2.92 ± 0.90a
	C	2.34 ± 1.62a	—	—	2.34 ± 1.62a
Cheilanthes tenuifolia	A	0.71 ± 0.36c	1.95 ± 0.46a	2.28 ± 0.57a	4.94 ± 0.77a
	B	3.53 ± 0.23a	0.42 ± 0.42a	1.34 ± 0.73a	5.29 ± 0.98a
	C	2.10 ± 0.41b	0.54 ± 0.14a	6.71 ± 1.65a	9.35 ± 1.50a
Christella dentata	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—

TABLE 5. Continued.

		DSE Colonization$^{\#\#}$			
Plant species	Site$^{\#}$	%RLDSH	%RLMO	%RLMI	%RLDTC
Christella parasitica	A	7.14 ± 2.14b	—	1.78 ± 0.78a	8.92 ± 3.74b
	B	0.00 ± 0.00c	—	0.00 ± 0.00 b	0.00 ± 0.00c
	C	28.71 ± 3.36a	—	4.40 ± 0.55a	33.11 ± 3.20a
Cyathea gigantea	A	7.99 ± 1.91a	0.49 ± 0.19a	—	8.48 ± 2.08a
	B	3.90 ± 1.85a	0.00 ± 0.00b	—	3.90 ± 1.85a
	C	5.45 ± 0.93a	0.72 ± 0.22a	—	6.17 ± 0.76a
Dicranopteris linearis	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Diplazium sylvaticum	A	—	0.37 ± 0.07a	1.50 ± 0.50a	1.87 ± 0.87a
	B	—	0.00 ± 0.00b	0.74 ± 0.04a	0.74 ± 0.04a
	C	—	0.55 ± 0.15a	0.00 ± 0.00b	0.55 ± 0.15a
Diplazium polypodioides	A	0.00 ± 0.00b	—	1.34 ± 0.80a	1.34 ± 0.80a
	B	0.00 ± 0.00b	—	1.11 ± 0.56a	1.11 ± 0.56a
	C	1.92 ± 1.05a	—	4.11 ± 2.20a	6.03 ± 3.04a
Doryopteris concolor	A	0.65 ± 0.15a	—	—	0.65 ± 0.15a
	B	3.82 ± 1.82a	—	—	3.82 ± 1.82a
	C	0.00 ± 0.00b	—	—	0.00 ± 0.00b
Drynaria quercifolia	B	2.86 ± 0.58a	0.00 ± 0.00b	15.07 ± 9.27a	17.93 ± 9.63a
	C	2.59 ± 1.57a	3.89 ± 2.49a	30.39 ± 6.60a	36.87 ± 8.20a
Hemionitis arifolia	A	0.40 ± 0.02a	—	—	0.40 ± 0.02a
	B	0.00 ± 0.00b	—	—	0.00 ± 0.00b
	C	1.15 ± 0.59a	—	—	1.15 ± 0.59
Lepisorus nudus	A	3.41 ± 0.68a	—	19.81 ± 2.19a	23.22 ± 2.65a
	B	6.61 ± 2.09a	—	22.28 ± 3.84a	28.89 ± 5.42a
	C	3.41 ± 1.49a	—	15.12 ± 3.74a	18.37 ± 5.16a
Leptochilus decurrens	A	0.85 ± 0.57a	4.47 ± 0.89a	—	5.32 ± 1.10a
	C	0.00 ± 0.00b	3.17 ± 0.77a	—	3.17 ± 0.77a
Lygodium microphyllum	A	—	—	0.00 ± 0.00b	0.00 ± 0.00b
	B	—	—	0.42 ± 0.12a	0.42 ± 0.12a
	C	—	—	0.00 ± 0.00b	0.00 ± 0.00b
Lycopodium cernuum	A	—	—	—	—
	B	—	—	—	—
Macrothelypteris torresiana	A	0.00 ± 0.00b	1.67 ± 0.67a	—	1.67 ± 0.67a
	B	1.80 ± 0.80a	0.00 ± 0.00b	—	1.80 ± 0.80a
	C	0.00 ± 0.00b	0.79 ± 0.19a	—	0.79 ± 0.19a
Marsilea minuta	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Marsilea quadrifolia	A	—	—	—	—
	B	—	—	—	—
Microlepia platyphylla	A	—	—	—	—
	B	—	—	—	—
Nephrolepis auriculata	A	1.40 ± 0.63b	—	—	1.40 ± 0.63b
	B	3.24 ± 0.94a	—	—	3.24 ± 0.94a
Nephrolepis multiflora	A	—	—	3.87 ± 0.39a	3.87 ± 0.39a
	B	—	—	0.00 ± 0.00b	0.00 ± 0.00b
	C	—	—	3.67 ± 1.95a	3.67 ± 1.95a

TABLE 5. Continued.

		DSE Colonization##			
Plant species	Site#	%RLDSH	%RLMO	%RLMI	%RLDTC
Pityrogramma calomelanos	A	0.00 ± 0.00b	0.84 ± 0.14a	0.00 ± 0.00b	0.84 ± 0.14a
	B	0.00 ± 0.00b	0.00 ± 0.00b	0.77 ± 0.39a	0.77 ± 0.39a
	C	0.67 ± 0.17a	0.00 ± 0.00b	1.95 ± 1.03a	2.61 ± 0.46a
Pseudocyclosorus xylodes	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Pseudocyclosorus ochthodes	A	0.00 ± 0.00b	0.42 ± 0.12a	—	0.42 ± 0.12a
	B	0.39 ± 0.09a	0.00 ± 0.00b	—	0.39 ± 0.09a
	C	0.00 ± 0.00b	0.00 ± 0.00b	—	0.00 ± 0.00b
Pteridium aquilinum	B	—	—	—	—
	C	—	—	—	—
Pteris biaurita	A	1.61 ± 1.09a	0.38 ± 0.18a	1.59 ± 0.35a	3.58 ± 1.16a
	B	2.71 ± 1.51a	0.00 ± 0.00b	2.02 ± 1.01a	4.73 ± 2.47a
	C	1.99 ± 1.10a	0.00 ± 0.00b	2.41 ± 1.47a	4.40 ± 2.56a
Pteris pellucida	A	0.41 ± 0.11a	0.00 ± 0.00b	—	0.41 ± 0.11a
	B	0.32 ± 0.02a	0.32 ± 0.02a	—	0.64 ± 0.03a
	C	0.89 ± 0.19a	0.00 ± 0.00b	—	0.89 ± 0.19a
Pyrrosia lanceolata	A	0.00 ± 0.00b	—	14.91 ± 0.60a	14.91 ± 0.60a
	B	0.00 ± 0.00b	—	27.69 ± 8.00a	27.69 ± 8.00a
	C	2.38 ± 0.38a	—	15.49 ± 0.79a	17.87 ± 1.85a
Selaginella sp.	A	—	—	—	—
	C	—	—	—	—
Selaginella wightii	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Sphaerostephanos arbuscula	A	—	—	—	—
	B	—	—	—	—
	C	—	—	—	—
Sphenomeris chinensis	A	1.16 ± 0.68ab	—	—	1.16 ± 0.68ab
	B	5.62 ± 1.62a	—	—	5.62 ± 1.62a
	C	0.00 ± 0.00b	—	—	0.00 ± 0.00b
Tectaria coadunata	A	2.31 ± 0.48a	—	4.21 ± 1.06a	6.52 ± 1.09a
	B	3.68 ± 2.92a	—	4.60 ± 2.49a	8.28 ± 5.41a
Vittaria elongata	A	6.09 ± 1.16a	1.93 ± 0.70a	17.37 ± 8.40a	25.39 ± 9.66a
	B	1.13 ± 0.58a	1.77 ± 1.12a	0.00 ± 0.00b	2.90 ± 1.66b

A, Solakkadu; B, Kuzhivalavu shola; C, Nachiyar kovil.

RLDSH, Root length with dark septate fungal hyphae; RLMI/MO, Root length with microsclerotia/ moniliform hyphae; RLDTC, Root length with total colonization.

* Means ± SE followed by same alphabet(s) for a species are not significantly different.

vary with environmental conditions, plants can acquire AM colonization during drier seasons and subsequent flooding may not affect the colonization levels within roots (Miller and Sharitz, 2000). This may be the reason for the prevalence of AM fungal colonization in both the *Marsilea* species observed from marshy habitats. The significant variation in the percentage root length among the two marshy ferns is consistent with the findings of Bajwa *et al.* (2001) who reported intense colonization in *M. minuta* during spring and summer.

Plant life-forms significantly affected the intensity of AM colonization. The average percentage root length with total AM fungal colonization of different life-forms was in the order of terrestrial > saxicolous > epiphytes > marshy plants. These results are in agreement with those of Fernández *et al.* (2012) and Gemma and Koske (1995) where the incidence and intensity of AM was reported to be higher for terrestrial species compared to other life-forms. All epiphytic and saxicolous taxa observed in the present study were mycorrhizal as previously observed (Gemma and Koske, 1995; Muthukumar and Prabha, 2013; Muthukumar and Udaiyan, 2000). Nevertheless, epiphytic or saxicolous pteridophytes are often reported to be non-mycorrhizal or facultatively mycorrhizal in other studies (Berch and Kendrick, 1982; Fernandez *et al.*, 2010, Zubek *et al.*, 2010). Lycophytes and ferns growing on bare branches or rocks are frequently exposed to changes in water supply, as water holding capacities of these surfaces are very low (Hietz, 2010). Furthermore, in these extreme environments, high temperature along with strong wind currents may dry these surfaces quite rapidly resulting in vegetative desiccation (Oliver *et al.*, 2000). Therefore, lycophytes and ferns existing on these habitats could depend more on AM fungi for water and nutrients under these stressful conditions as the association has been shown to ameliorate water stress (Smith and Smith, 2011). The lack of AM propagules has often been cited as a cause for the low incidence of AM in epiphytic and lithophytic habitats. Nevertheless, birds and animals could easily bring in the AM fungal propagules to these extreme environments (Gemma *et al.*, 1992; Gemma and Koske, 1995). In addition, AM fungal propagules could reach rock surfaces and rock crevices through the movement of overhead dry soil, dispersal of mycorrhizal root fragments by wind activity, and surface runoffs carrying eroded soil (Berch and Kendrick, 1982).

Root colonization directly through the rhizodermis and the presence of AM fungal hyphae within root hairs supports earlier observations (Berch and Kendrick, 1982; Cooper, 1976; Fernández *et al.*, 2012) where this phenomenon has been documented in lycophytes and ferns. Likewise, the morphologically distinct types of intraradical AM fungal hyphae seen in roots have been reported in vascular plants including ferns (Bentivenga and Morton, 1995; Fernández *et al.*, 2012; Merryweather and Fitter, 1998). Arbuscule formation on the intraradical hyphae or hyphal coils varied from very limited (e.g., *L. nudus*, *Diplazium sylvaticum*, Woodsiaceae) to more elaborate (e.g., *A. incisum*, *B. occidentale*) forms. These observations suggests the colonization of pteridophyte roots by different AM fungal taxa as previously shown by both conventional (root squash) and molecular studies (Muthukumar *et al.*, 2009; West *et al.*, 2009).

The consistent presence of mycorrhizae as evidenced by the presence of fungal structures in all the individuals of leptosporangiate ferns similar to the observations of Lee *et al.* (2001) and Fernandez *et al.* (2012), fails to support Boullard's (1979) hypothesis that mycotrophy was inconsistent in the advanced leptosporangiate ferns and Zhao's (2000) suggestion that the most recent common ancestor of pteridophytes was non-mycotrophic. In the present study, the extent of AM fungal colonization and root length with different AM fungal structures showed significant variations among species which is in line with the results from earlier studies (Khade and Rodrigues, 2002; Muthukumar and Prabha, 2013; Muthukumar and Udaiyan, 2000; Prashar *et al.*, 2005). As AM fungal colonization and formation of AM fungal structures are an interaction of host, fungal and environmental factors, the observed variations in colonization and AM fungal structures among species is reasonable. The higher average percentage total AM colonization in lycophytes compared to ferns is comparable to some of the previous reports for these taxa (Gemma *et al.*, 1992; Kessler *et al.*, 2010a; Muthukumar and Prabha, 2013). The high average percentage root length with total AM colonization in leptosporangiate ferns (74.03%) do not support Boullard's (1979) view that leptosporangiate ferns with fine roots are less colonized compared to eusporangiate pteridophytes with relatively thick roots.

Arbuscular mycorrhizal fungal morphology has been reported for the first time in 33 lycophytes and ferns examined in the study. The intermediate- and *Paris*-type colonization patterns found in lycophytes and ferns of the Kolli Hills are in agreement with observations for pteridophytes in general (Dickson *et al.*, 2007; Muthukumar and Prabha, 2013). This is not surprising because ferns and lycophytes are generally perennial, slow-growing, and often occur in stressful habitats (low light, highly fluctuating moisture and nutrients), where possessing *Paris*- or intermediate-type AMs may be beneficial in reducing the host's energy cost (Dickson *et al.*, 2007). The frequent (72%, 34/47) occurrence of intermediate-type AM morphology in lycophytes and ferns of the Kolli Hills contradicts many studies where AM colonization patterns in lycophytes and ferns were dominated by *Arum*- or *Paris*-type AM morphology (Kessler *et al.*, 2010a; Zubek *et al.*, 2010). The intermediate-type AM morphology observed in *Pityrogramma calomelanos* (Adiantaceae), *P. aquilinum*, *Sphenomeris chinensis* (Lindsaeaceae), *D. linearis*, *P. pellucida* and *C. parasitica* is consistent with earlier observations (Muthukumar and Prabha, 2013). However, Zhang *et al.* (2004) reported *Paris*-type AM morphology in *P. aquilinum*, from Dujiangyan, southwest China. The two *Selaginella* species examined from different sites intermediate-type AM morphology. However, AM morphological patterns tend to differ among species in *Selaginella* as shown by Zhang *et al.* (2004) and Muthukumar and Prabha (2013). Regardless of habitat, 15% of the ferns had both *Paris*- and intermediate-type AM morphologies at different sites similar to the observations of Muthukumar and Prabha (2013). It must be emphasized that the factors controlling AM colonization patterns in roots are not well resolved. It has been proposed that the presence or absence of intercellular spaces in the root cortex are determinants of AM colonization patterns (Brundrett and Kendrick, 1990). Studies (Cavagnaro *et al.*, 2001a,b; Smith *et al.*, 2004) have shown that fungal identity can also influence AM fungal morphological patterns. Further, environmental factors like temperature, light intensity and soil moisture that affect plant growth, especially root growth, are presumed to influence AM colonization patterns within roots (Becerra *et al.*, 2007; Yamato, 2004; Yamato and Iwasaki, 2002). Hence, a more detailed study on the various factors influencing AM colonization in roots is needed to understand the factors that determine colonization patterns in roots.

Diversity of AM fungi associated with lycophytes and ferns is very limited compared to the information on the prevalence of the association (Gosh *et al.*, 2012; Muthukumar *et al.*, 2009; Muthukumar and Prabha, 2013; Muthukumar and Udaiyan, 2000; Zhang *et al.*, 2004). The presence of nine AM fungal spore morphotypes of five genera is comparable to the results of previous studies where low AM fungal spore diversity has been reported for lycophytes and ferns (Ghosh *et al.*, 2012; Muthukumar and Prabha, 2013). In contrast, Zhang *et al.* (2004) reported the presence of 40 AM fungal spore morphotypes belonging to five genera from the rhizosphere of ferns and lycophytes of Dujiangyan, South west China. In the present study, spore numbers were very low (data not presented) with spores being absent in many of the substrate samples. Even among the recovered spores, most were devoid of spore contents and/or were parasitized by soil organisms. The infrequent presence of AM fungal spores did not affect the AM status or colonization rate as evidenced by moderate to high levels of colonization in all the mycorrhizal lycophytes and ferns. This clearly suggests that AM fungi perennate in the studied habitats through propagules other than spores (Smith and Read, 2008). Contrary to the general observations in tropical soils, species diversity was higher in *Acaulospora* than in *Glomus*.

Colonization of roots by DSE fungi has been reported in several plant species, including ferns and lycophytes (Fernandez *et al.*, 2012; Jumpponen and Trappe, 1998; Muthukumar and Prabha, 2013). Roots of 75% (33 of 44 species) of ferns belonging to 15 families were colonized by DSE fungi which corroborate the observations of Rains *et al.* (2003), where most of the 18 plant taxa, consisting of epiphytes and terrestrial species, in a neotropical rain forest in Costa Rica had DSE fungal associations. The DSE fungal associations have been reported for the first time in 28 ferns and corroborated for *Angiopteris evecta* (Marattiaceae), *O. chinensis*, *Diplazium polypodioides* (Woodsiaceae) and *P. pellucida* examined in this study (Jumpponen and Trappe, 1998; Muthukumar and Prabha, 2013). *Lycopodium cernuum* and *P. aquilinum* reported to possess DSE fungal association by Muthukumar and Prabha (2013) lacked the association in the present study. Co-occurrence of AM and DSE fungi within roots was observed in 33 ferns. Such dual association of AM and DSE fungi has been reported in a wide range of higher vascular plant species as well as for ferns (Chaudhry *et al.*, 2009; Fernández *et al.*, 2012; Muthukumar *et al.*, 2006; Muthukumar and Prabha, 2013). In contrast to AM fungal colonization, average percentage root length with total DSE fungal colonization was significantly higher in epiphytes compared to saxicolous and terrestrial taxa. Christie and Kilpatrick (1992) suggested that the DSE fungal association in lycophytes and ferns tend to take over the functions of AM fungi during conditions unfavourable for AM fungi. This suggestion could be realized from the observations of a recent study (Muthukumar and Prabha, 2012) where gametophytes and young sporophytes of *Nephrolepis exaltata* growing on soilless substrates like coir or bricks were predominantly colonized by DSE fungi. In the present study, all the ferns examined from the epiphytic habitats had dual association of AM and DSE, which is almost similar to the findings of Lehnert *et al.* (2009) in ferns from southern Ecuador. The existence of a weak negative correlation between the percentage total root length colonized by AM and DSE fungi suggests competition by the two endophytic fungal types (Wu *et al.*, 2009). Although, the role of DSE fungi on lycophyte and fern growth is yet to be examined, a recent meta-analysis of plant responses to DSE fungal association suggests that the DSE fungi could improve plants performance under controlled conditions (Newsham, 2011).

In conclusion, the present study clearly shows the wide-spread occurrence of AM and DSE fungal associations in lycophytes and ferns of the Eastern Ghats. Many ferns examined in this study are routinely used for medicinal purposes and some are listed as threatened species. All these taxa were associated with AM and/or DSE fungi in the present study. Although, *A. evecta*, *Cyathea gigantea* (Cyatheaceae), *Ceratopteris thalictroides* (Pakeriaceae), *D. quericifolia* and *M. minuta* were reported in IUCN's Red List as threatened or rare taxa (Walter and Gillett, 2008), a recent reassessment of these taxa indicates that they are neither threatened nor rare (Chandra *et al.*, 2008). As Bothe *et al.* (2010) suggested, a potential exists for the use of AM and/or DSE fungi to promote the growth and fitness of threatened plant taxa. Therefore, conservation management techniques for ferns such as micropropagation could involve these fungi during an acclimatization phase as AM and DSE fungi are shown to be very efficient bio hardening agents for successful acclimatization (Kapoor *et al.*, 2008). Further research is needed to focus on the utilization of AM and DSE fungi in conservation of fern diversity in the Eastern Ghats.

Acknowledgements

We are grateful to Dr. V.S. Ramachandran, Department of Botany, Bharathiar University, Coimbatore and Dr. V. Irudayaraj, Department of Plant Biology and Biotechnology, Centre for Biodiversity and Biotechnology, St. Xavier's College (Autonomous), Palayamkottai for their help in identification of the plant specimens. We thank Dr. K. Pradeepa Veerakumari, Department of Statistics, Bharathiar University, Coimbatore for her help in the statistical analysis of the data. We also thank the two anonymous reviewers for their helpful comments and suggestions on an earlier version of the manuscript.

Literature Cited

Arokiyaraj, S., K. Perinbam, P. Agastian and K. Balaraju. 2007. Immunosuppressive effect of medicinal plants of Kolli Hills on mitogen-stimulated proliferation of the human peripheral blood mononuclear cells *in vitro*. Indian J. Pharmacol. 39:180–183.

Arun, P. R., A. Rajacekaran, P. A. Aee and S. Bhupathy. 2002. Impact of anthropogenic on the biodiversity of Kolli Hills, Eastern Ghats. Pp. 175–178, *in* National Seminar on Conservation of Eastern Ghats, Tirupathi, Andhra Pradesh, India.

Bajwa, R., A. Yaqoob and A. Javaid. 2001. Seasonal variation in VAM in wetland plants. Pak. J. Biol. Sci. 4:464–470.

Bareen, F. E. 1990. Vesicular arbuscular mycorrhiza in aquatics. Pp. 1–3, *in* B. L. Jalali and H. Chand. 1990. Current Trends in Mycorrhizal Research. Proceedings of National Conference in Mycorrhiza. Haryana Agricultural University, Hisar, India.

BECERRA, A., M. CABELLO and F. CHIARINI. 2007. Arbuscular mycorrhizal colonization of vascular plants from the Yungas forests, Argentina. Ann. For. Sci. 64:765–772.

BENTIVENGA, S. P. and J. B. MORTON. 1995. A monograph of the genus *Gigaspora*, incorporating developmental patterns of morphological characters. Mycologia 87:719–731.

BERCH, S. M. and B. KENDRICK. 1982. Vesicular arbuscular mycorrhizae of southern Ontario ferns and fern allies. Mycologia 74:769–776.

BHAT, P. R. and K. M. KAVERIAPPA. 2003. Occurrence of vesicular arbuscular mycorrhizal fungi in *Marsilea minuta* L. Mycorrhiza News 15:11–13.

BOTHE, H., K. TURANAU and M. REGVAR. 2010. The potential role of arbuscular mycorrhizal fungi in protecting endangered plants and habitats. Mycorrhiza 20:445–457.

BOULLARD, B. 1979. Considerations Sur les symbioses fongiques chez less pteridophytes. National Museum of Natural Science, Syllogenus No. 19, Ottawa. Pp 1–58.

BRITTO, A. J. D., D. H. S. GARCELIN and P. B. J. R KUMAR. 2012. Phytochemical studies of five medicinal ferns collected from southern Western Ghats, Tamil Nadu. Asian Pac. J. Trop. Biomed. 12:536–538.

BRUNDRETT, M. C. 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77.

BRUNDRETT, M. C. and B. KENDRICK. 1990. The roots and mycorrhizas of herbaceous woodlands plants. II. Structural aspects of morphology. New Phytol. 114:469–479.

CAVAGNARO, T. R., F. A. SMITH, M. F. LORIMER, K. A. HASKARD, S. M. AYLING and S. E. SMITH. 2001a. Quantitative development of *Paris*-type arbuscular mycorrhizas formed between *Asphodelus fistulosus* and *Glomus coronatum*. New Phytol. 149:105–113.

CAVAGNARO, T. R., L. -L. GAO, F. A. SMITH and S. E. SMITH. 2001b. Morphology of arbuscular mycorrhizas as influenced by fungal identity. New Phytol. 151:469–475.

CHANDRA, S., C. R. FRASER-JENKINS, A. KUMARI and A. SRIVASTAVA. 2008. A summary of the status of threatened pteridophytes of India. Taiwania 53:170–209.

CHAUDHRY, M. S., S. U. RAHMAN, M. S. ISMAIEL, G. SARWAR, B. SAEED and F. H. NASIM. 2009. Coexistence of arbuscular mycorrhizae and dark septate endophytic fungi in an undisturbed and a disturbed site of an arid ecosystem. Symbiosis 47:19–28.

CHITTIBABU, C. V. and N. PARTHASARATHY. 2000. Attenuated tree species diversity in human-impacted tropical evergreen forest sites at Kolli hills, Eastern Ghats, India. Biodivers. Conserv. 9:1493–1519.

CHRISTIE, P. and D. J. KILPATRICK. 1992. Vesicular-arbuscular mycorrhizal infection in cut grassland following long-term slurry application. Soil Biol. Biochem. 24:325–330.

CLADWELL, B. A. and A. JUMPPONEN. 2003. Utilization of heterocyclic organic nitrogen by mycorrhizal fungi. P 311 *in* Fourth International Conference on Mycorrhizae, Montreal, Canada. 10–15th August 2003.

COOPER, K. M. 1976. A field survey of mycorrhizas in New Zealand ferns. New Zeal. J. Bot. 14:169–181.

DICKSON, S. 2004. The *Arum- Paris* continuum of mycorrhizal symbioses. New Phytol. 163:187–200.

DICKSON, S. and P. KOLESIK. 1999. Visualisation of mycorrhizal fungal structure and quantification of their surface area and volume using laser scanning confocal microscopy. Mycorrhiza 9:205–213.

DICKSON, S., F. A. SMITH and S. E. SMITH. 2007. Structural differences in arbuscular mycorrhizal symbioses: more than 100 years after Gallaud, where next? Mycorrhiza 17:375–393.

DIXIT, R. D. 1984. A census of the Indian pteridophytes. Flora of India, Series- 4, Botanical Survey of India, Howrah (Calcutta). India.

DUCKETT, J. G. and R. LIGNORE. 1992. A light and electron microscope study of the fungal endophytes in the sporophyte and gametophyte of *Lycopodium cernuum* with observations on the gametophyte-sporophyte junction. Can. J. Bot. 70:58–72.

FERNÁNDEZ, N., M. I. MESSUTI and S. B. FONTENLA. 2008. Arbuscular mycorrhizae and dark septate fungi in *Lycopodium paniculatum* (Lycopodiaceae) and *Equisetum bogotense* (Equisetaceae) in a Valdivian temperate forest of Patagonia, Argentina. Amer. Fern J. 98:117–127.

FERNÁNDEZ, N., M. I. MESSUTI and S. B. FONTENLA. 2012. Occurrence of arbuscular mycorrhizas and dark septate endophytes in pteridophytes from a Patagonian rainforest, Argentina. J. Basic Microbiol. 52:1–11.

FERNÁNDEZ, N., S. B. FONTENLA and M. I. MESSUTI. 2010. Mycorrhizal status of obligate and facultative epiphytic ferns in Valdivian temperate forest of Patagonia, Argentina. Amer. Fern. J. 100:16–26.

FRANCIS XAVIER, T., A. FREEDA ROSE and M. DHIVYAA. 2011. Ethnomedicinal survey of malayali tribes in Kolli Hills of Eastern Ghats of Tamil Nadu, India. IJTK 10:559–562.

GEMMA, J. N. and R. E. KOSKE. 1995. Mycorrhizae in Hawaiian epiphytes. Pac. Sci. 49:175–180.

GEMMA, J. N., R. E. KOSKE and T. FLYNN. 1992. Mycorrhizae in Hawaiian pteridophytes: occurrence and evolutionary significance. Amer. J. Bot. 79:843–852.

GHOSH, R., S. SENGUPTA and S. BHATTACHARYYA. 2012. Arbuscular mycorrhizal fungi associated with some fern species collected from Kumaon region of western Himalayas. Indian Phytopathol. 65:282–285.

GOWRISANKAR, K., R. CHANDRASEKARAN and K. NANDAKUMAR. 2011. Survey of ferns and fern allies from Kolli Hills, Eastern Ghates, Tamil Nadu. J. Sci. Trans. Environ. Technov. 5:52–55.

HASELWANDTLER, K. and D. J. READ. 1982. The significance of a root-fungus association in two *Carex* species of high-alpine plant communities. Oecologia 53:352–354.

HIETZ, P. 2010. Fern adaptations to xeric environment. Pp. 140–176, *in* K. Mehltreter, L. R. Walker and J. M. Shape. 2010. Fern ecology. Cambridge University Press, UK.

HODSON, E., F. SHAHID, J. BASINGER and S. KAMINSKYJ. 2009. Fungal endorhizal associates of *Equisetum* species from Western and Arctic Canada. Mycol. Prog. 8:19–27.

IQBAL, S. H., M. YOUSAF and M. YOUNUS. 1981. A field survey of mycorrhizal association in ferns of Pakistan. New Phytol. 87:69–79.

IQBAL, S., H. SHAHJAHAN and G. NASIM. 1988. Vesicular arbuscular mycorrhiza in an alga: *Chara* sp. Biologia 34:279–281.

IRUDAYARAJ, V. and V. S. MANICKAM. 2003. Pteridophyte flora of Nilgiris, South India. Dinesh Singh, Mahendra Pal Singh, Dehra Dun, India.

JACKSON, M. L. 1971. Soil chemical analysis. Prentice Hall, New Delhi.

JAYAKUMAR, S., D. I. AROKIASAMY and S. JOHN BRITTO. 2002. Forest type mapping and vegetation analysis in part of Kolli Hills, Eastern Ghats of Tamil Nadu. Trop. Ecol. 43:345–349.

JUMPPONEN, A. and J. M. TRAPPE. 1998. Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol. 140:295–310.

KAPOOR, R., D. SHARMA and A. K. BHATNAGAR. 2008. Arbuscular mycorrhizae in micropropagation systems and their potential applications. Sci. Hortic. 116:227–239.

KESSLER, M., R. JONAS, D. CICUZZA, J. KLUGE, K. PIATEK, P. NAKS and M. LEHNERT. 2010a. A survey of the mycorrhization of Southeast Asian ferns and lycophytes. Plant Biol. 12:788–793.

KESSLER, M., R. JONAS, D. STRASBERG and M. LEHNERT. 2010b. Mycorrhizal colonization of ferns and lycophytes on the island of La Rèunion in relation to nutrient availability. Basic Appl. Ecol. 11:329–336.

KHADE, S. W. and B. F. RODRIGUES. 2002. Arbuscular mycorrhizal fungi associated with some pteridophytes from Western Ghat region of Goa. Trop. Ecol. 43:251–256.

KOSKE, R. E. and J. N. GEMMA. 1989. A modified procedure for staining roots to detect VA mycorrhizas. Mycol. Res. 92:486–488.

LEE, J. K., A. H. EORN, S. S. LEE and C. H. LEE. 2001. Mycorrhizal symbiosis found in roots of ferns and its relatives in Korea. J. Plant Biol. 44:81–86.

LEHNERT, M., I. KOTTKE, S. SETARO, L. F. PAZMINO, J. P. SUAREZ and M. KESSLER. 2009. Mycorrhizal association in ferns from Southern Ecuador. Amer. Fern J. 99:293–306.

MADYAM, K. and A. JUMPPONEN. 2005. Seeking the elusive function of root-colonising dark septate endophyte fungi. Stud. Mycol. 53:173–189.

MANICKAM, V. S. 1996. Studies on intraspecific variations in South Indian ferns (III Pteridophyta). Taxon 46:265–269.

MANNAR MANNAN, M., M. MARIDASS and B. VICTOR. 2008. A review on the potential uses of ferns. Ethnobotanical Leaflets 12:281–285.

MARIDASS, M. and G. RAJU. 2010. Conservation status of pteridophytes, Western Ghats, south India. I. J. B. T. 1:42–57.

Martinez, A. E., V. Chiocchio, L. T. Em, M. A. Rodriguez and A. M. Godeas. 2012. Mycorrhizal association in gametophytes and sporophytes of fern *Pteris vittata* (Pteridaceae) with *Glomus intraradices*. Revista Biol. Trop. 60:857–865.

McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild and J. A. Swan. 1990. A method which gives an objective measure of colonization of roots by vesicular- arbuscular mycorrhizal fungi. New Phytol. 115:495–501.

Merryweather, J. and A. Fitter. 1998. The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta*. I. Diversity of fungal taxa. New Phytol. 138:117–129.

Miller, S. P. and R. R. Sharitz. 2000. Manipulation of flooding and arbuscular mycorrhiza formation influences growth and nutrition of two semiaquatic grass species. Funct. Ecol. 14:738–748.

Mishra, R. R., G. D. Sharma and A. R. Gathpon. 1980. Mycorrhizas in the ferns of North Eastern India. Proc. Indian Nat. Sci. Acad. 1346:546–551.

Mohanraj, R., J. Saravanan and S. Dhanakumar. 2010. Carbon stock in Kolli forests, Eastern Ghats (India) with emphasis on aboveground biomass, litter, woody debris and soils. iForest 4:61–65.

Muthukumar, T. and K. Prabha. 2013. Arbuscular mycorrhizal and septate endophyte fungal associations in lycophytes and ferns of South India. Symbiosis 59:15–33.

Muthukumar, T. and K. Udaiyan. 2000. Vesicular arbuscular mycorrhizae in pteridophytes of Western Ghats, South India. Phytomorphology 50:132–142.

Muthukumar, T. and K. Prabha. 2012. Fungal associations in gametophytes and young sporophytic roots of the fern *Nephrolepis exaltata*. Acta Bot. Croat. 71:139–146.

Muthukumar, T., K. Sathiyadash, E. Uma and V. Muniappan. 2009. Arbuscular mycorrhizal morphology in sporophyte of *Psilotum nudum*. Phytomorphology 59:141–146.

Muthukumar, T., M. Senthilkumar, M. Rajangam and K. Udaiyan. 2006. Arbuscular mycorrhizal morphology and dark septate fungal association in medicinal and aromatic plants of Western Ghats, Southern India. Mycorrhiza 17:11–24.

Newsham, K. K. 1999. *Phialophora graminicola*, a dark septate fungus, is a beneficial associate of the grass *Vulpia ciliata* spp. *ambigua*. New Phytol. 144:517–524.

Newsham, K. K. 2011. A meta-analysis of plant responses to dark septate root endophytes. New Phytol. 190:783–793.

Ogura-Tsujita, Y., A. Sakoda, A. Ebihara, T. Yukawa and R. Imaichi. 2013. Arbuscular mycorrhiza formation in cordate gametophytes of two ferns, *Angiopteris lygodifolia* and *Osmunda japonica*. J. Plant Res. 126:41–50.

Oliver, M. J., Z. Tuba and B. D. Mishler. 2000. The evolution of vegetative tolerance in land plants. Plant Ecol. 151:85–100.

Pathak, A., A. Singh and A. P. Singh. 2011. Ethnomedicinal uses of pteridophytes of Vindhyan region (M.P.). Int. J. Pharm. Life Sci. 2:496–498.

Perumal, G. 2010. Ethnomedicinal use of pteridophyte from Kolli Hills, Namakkal district, Tamil Nadu, India. Ethnobotanical Leaflets 14:161–172.

Peterson, R. L., C. Wagg and M. Pautler. 2008. Associations between microfungal endophytes and roots: do structural features indicate function? Botany 86:445–456.

Prashar, I. B., S. Sharma and S. P. Khullar. 2005. Mycorrhizal associates of some ferns from Kangra district (Himachal Pradesh). Indian Fern J. 22:81–86.

Radhika, K. P. and B. F. Rodrigues. 2007. Arbuscular mycorrhizae in association with aquatic and marshy plant species in Goa, India. Aquatic Bot. 86:291–294.

Ragupathy, S. and A. Mahadevan. 1993. Distribution of vesicular arbuscular mycorrhizae in the plants and rhizosphere soils of the tropical plant, Tamil Nadu, India. Mycorrhiza 3:123–136.

Rains, K. C., N. M. Nadkarni and C. S. Bledose. 2003. Epiphytic and terrestrial mycorrhizas in a lower montane Costa Rica cloud forest. Mycorrhiza 13:257–264.

Raja, P., S. Ragupathy and A. Mahadevan. 1995. A mycorrhizal association of pteridophytes of Nilgiris and Kodaikanal hills, South India. Acta Bot. Indica 23:181–186.

Sanders, I. R. and A. H. Fitter. 1992. The ecology and functioning of vesicular arbuscular mycorrhizas in coexisting grassland species. I. Seasonal patterns of mycorrhizal occurrence and morphology. New Phytol. 120:517–524.

SARWADE, P. P., R. U. SHAIKH, S. S. CHANDANSHIVE and U. N. BHALE. 2012. Association of AM fungi in important Pteridophytic plants of Maharashtra, India. Int. Multidiscipl. Res. J. 2:8–9.

SCHENCK, N. C. and Y. PEREZ. 1990. Manual for the identification of VA mycorrhizal fungi. Synergistic, Gainesville.

SCHÜBLER, A. and C. WALKER. 2010. The Glomeromycota. A species list with new families and new genera. Arthur Schüβler and Christopher Walker, Gloucester, England.

SMITH, S. E. and D. J. READ. 2008. Mycorrhizal symbiosis. Academic Press, London.

SMITH, S. E., F. A. SMITH and I. JAKOBSEN. 2004. Functional diversity in arbuscular mycorrhizal (AM) symbioses: the continuation of the mycorrhizal P uptake pathway is not correlated with mycorrhizal response in growth or total P uptake. New Phytol. 162:511–524.

SMITH, S. E. and F. A. SMITH. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: New paradigms from cellular to ecosystem scales. Ann. Rev. Plant Biol. 62:227–250.

SUNDARAM, B. and N. PARTHASARATHY. 2002. Tree growth, mortality and recruitment in four tropical wet evergreen forest sites of Kolli hills, Eastern Ghats, India. Trop. Ecol. 43:275–286.

SUSEELA, M. R. and S. DEVI. 1998. Scanning electron microscopic studies on the associations of vesicular arbuscular mycorrhizae in some Indian ferns. Arch. Phytopath. Pflanz. 31:423–428.

WALTER, K. S. and H. J. GILLETT. 1998. 1997 IUCN Red List of Threatened Plants. Compiled by the World Conservation Monitoring Centre. IUCN - The World Conservation Union, Gland, Switzerland and Cambridge, UK.

WANG, B. and Y. L. QIU. 2006. Phylogentic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 96:299–363.

WEST, B., J. BRANDT, K. HOLSTIEN, A. HILL and M. HILL. 2009. Fern-associated arbuscular mycorrhizal fungi are represented by multiple *Glomus* spp.: do environmental factors influence partner identity? Mycorrhiza 19:295–304.

WU, Y., T. LIU and X. HE. 2009. Mycorrhizal and dark septate endophytic fungi under the canopies of desert plants in Mu Us sandy land of China. Front. Agric. China 3:164–170.

YAMATO, M. 2004. Morphological types of arbuscular mycorrhizal fungi in roots of weeds on vacant land. Mycorrhiza 14:127–131.

YAMATO, M. and M. IWASAKI. 2002. Morphological types of arbuscular mycorrhizal fungi in roots of understory plants in Japanese deciduous broadleaved forests. Mycorrhiza 12:291–296.

ZAR, J. H. 1984. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, NJ.

ZHANG, Y., L. D. GUO and R. J. LIU. 2004. Arbuscular mycorrhizal fungi associated with common pteridophytes in Dujiangyan, Southwest China. Mycorrhiza 14:25–30.

ZHAO, Z. W. 2000. The arbuscular mycorrhizas of pteridophytes in Yunnan, Southwest China: evolutionary interpretations. Mycorrhiza 10:145–149.

ZUBEK, S., K. PIATEK, P. NAKS, W. HEISE, M. WAYDA and P. MLECZKO. 2010. Fungal root endophyte colonization of fern and lycophytes species from the Celaque National Park in Honduras. Amer. Fern. J. 100:126–136.

American Fern Journal 104(2):103–107 (2014)

SHORTER NOTES

Rediscovery, Ecology, and Habitat of *Deparia kaalaana* (Copel.) M.Kato (Athyriaceae).—Hillebrand (*Flora of the Hawaiian* Islands, Hafner reprint, New York and London, 1965) first described *Deparia kaalaana* as *Asplenium marginale* Hillebr., var. *depauperata* Hillebr. He cited observations by Baldwin in Hilo and Lydgate at Laupahoehoe on the windward side of Hawai'i Island (Mauna Loa and Mauna Kea respectively), along rocky streams. Between 1880 and 1890 Miss Frances Lack collected this fern on "O'ahu or Hawai'i (Kona or Kilauea)". In 1891 it was collected on East Maui by F.L. Clarke in Kipahulu Valley in what is now Haleakala National Park, seemingly unknowingly as it was a specimen mixed with material of the rheophytic *Cyclosorus boydiae* (D.C. Eaton) W.H.Wagner (syn. *Thelypteris boydiae* D.C. Eaton). It was not until 1992 that Herb and Florence Wagner noticed the mixed collection and annotated the specimen as *D. kaalaana*. In November of 1909 Abbé Urbain Jean Faurie, a French Catholic missionary, collected specimens on Kaua'i in the Ka'ala region east of Waimea. Copeland (Philipp. J. Sci. vol. IX, Manila. 1914) used Faurie's collection as the type (*Faurie 294* MICH; isotypes KYO, TI, UC) and named the species for the area as *Athyrium kaalaanum* Copel. (Fig. 1). Kato (J. Fac. Sci., Univ. Tokyo, Sect 3, 13, 375–400. 1984) placed the species in the genus *Deparia* as *D. kaalaana* (Copel.) M.Kato in section *Deparia* Kato. Subsequent workers (e.g., Palmer, *Hawai'i's Ferns and Fern Allies*, University of Hawai'i Press, Honolulu. 2003) have accepted this placement. It has been placed in the families Aspleniaceae (Hillebrand, 1888), Athyriaceae (Palmer 2003; pers. comm. 2013) as well as Woodsiaceae (Kato, Acta Phytotaxon. Geobot. 52:1–9. 2001).

Habitat and Ecology.—There is no information available on the few specimen labels that exist as to what elevation the historic collections were made, the plant communities in which they occurred, or any associated vegetation other than assuming Clarke gathered both his ferns at the same time. Hilo and Laupahoehoe are on the windward, wet side of Hawai'i Island, and both areas are characterized in part by deep gorges and perennial streams. Kona is on leeward Hawai'i Island on the western side of Mauna Loa while Kilauea is a separate and newer volcano further south of Hilo on the eastern flank of Mauna Loa. The Kona area is generally dry, and, coupled with its recent geological formation, does not have any perennial streams (Smith, Wilcox, & Edmunds, *Hawai'i Stream Assessment*. Hawai'i Cooperative Park Service Unit, Honolulu. 1990). Kilauea is much wetter but even younger in age, and also does not provide riparian habitat (Smith *et al.*, 1990). Kipahulu Valley on Maui is a large and wet region and has at least three perennial stream systems where *C. boydiae* still occurs (Medeiros, Hobdy, & Wagner, Am. Fern J. 83:86–89. 1993). Ka'ala, Kaua'i is approximately 300 m ASL in elevation, and is flanked by two perennial streams: Olokele to the east, and Kahana to the west. The two join at approximately 130 m ASL and are part of the Makaweli

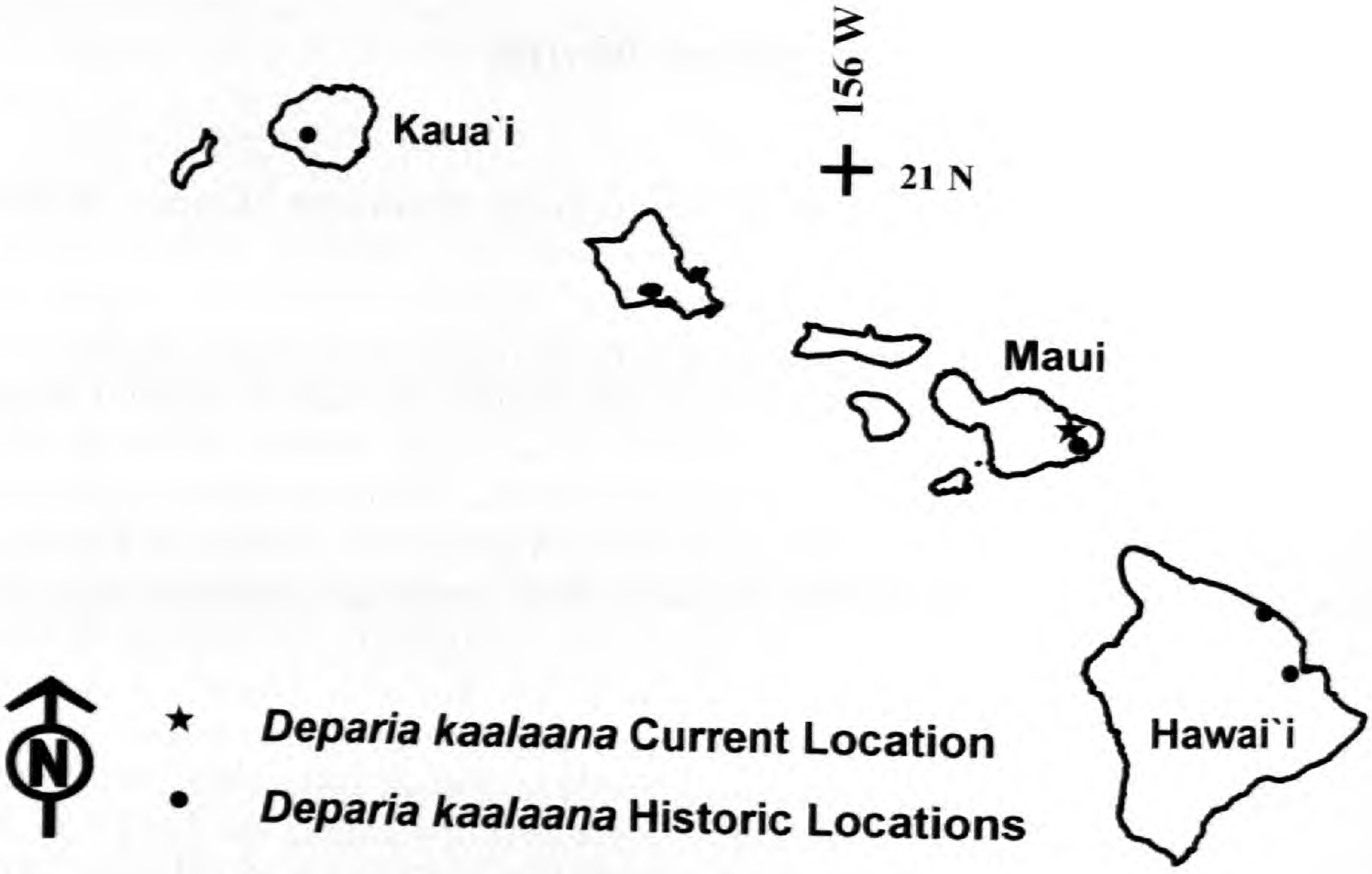

FIG. 1. Distribution of *Deparia kaalaana*, Hawaiian Islands.

River watershed. The recent rediscovery was made in a riparian site in *Metrosideros/Dicranopteris* Lowland Wet Forest (Gagne & Cuddihy in Wagner, Herbst, & Sohmer, *Manual of the Flowering Plants of Hawai‘i*. Univ. of Hawai‘i Press & Bishop Museum Press. 1990). It was growing along a perennial stream on a vertical wall, under an overhanging ledge on the western side of a small pool. Observations of debris along the banks as well as in adjacent vegetation exhibit definitive evidence that this fern is capable of surviving submergence in strong floods. Taxa immediately adjacent are *Asplenium excisum* C. Presl (Aspleniaceae), *Vandenboschia cyrtotheca* (Hillebr.) Copel. (Hymenophyllaceae), *Adiantum raddianum* C. Presl (Pteridaceae), *Dryopteris wallichiana* (Spreng.) Hyl. (Dryopteridaceae), and the herbaceous *Peperomia ligustrina* Hillebr. (Piperaceae) (Fig. 2).

The substrate is composed of relatively recent basalt lava flows from the late stage, post shield building Hana Volcanic Series (Stearns and MacDonald, *Geology and Ground-Water Resources of the Island of Maui, Hawai‘i*. Advertiser Publishing LTD, Honolulu. 1942). Rainfall at the Kuhiwa site averages approximately 6500 mm of annual rainfall. Other estimates at approximate locations are as low as 1500 mm of average annual rainfall (type location, Kaala, Kaua‘i) to 4000 mm at 550 m ASL in Kipahulu Valley. Hillebrand's and Kato's reports, as well as the Clarke specimen, suggest that *D. kaalaana* is a rheophyte. Kato also stated that morphology (well-developed roots and oblique pinnae) supported this assumption. With such scant and contrasting historical information and only a single recent observation it would be premature to state *D. kaalaana* is an obligate rheophyte. Hillebrand reported a single gemma on the tip of one frond of *Deparia kaalaana*, however,

FIG. 2. Photo of *Deparia kaalaana.*

this voucher could not be located. The holotype at MICH (*Faurie 294*) has one gemma near the apex of one of the five fronds on the specimen, which is an entire plant. An isotype at UC is a complete plant with five fronds plus two separate fronds on one sheet (UC397924). One of these loose fronds has a single gemma with several long roots near the apex. Proliferations are not unusual in three of the other four endemic Hawaiian species in the genus, namely *D. cataracticola* M. Kato (Kato 2001), *D. marginalis* (Hillebr.) M. Kato, and *D. prolifera* (Kaulf.) Hook. & Grev. Only *D. fenzliana* (Luerss.) M. Kato is not proliferous. Gemmae are a potential means of vegetative reproduction and it is possible that floodwaters could disperse gemmae to new locations downstream.

Conservation Status.—No spores could be harvested from the plant recently located as the sori were too old with all the sporangia dehisced. No gemmae were present on the fronds. There is no material *ex situ*. Much survey work has been conducted in the region without success until now, and more work has been conducted and is planned in adjacent areas in the hopes of finding additional individuals and populations. Optimistically, spores can be collected in the near future and propagated in tissue culture at the Lyon Arboretum Micropropagation Laboratory on O'ahu, or conventionally sown at the Olinda Rare Plant Facility, Maui. The low elevation riparian habitat is directly threatened by invasive plants such as *Adiantum raddianum, Blechnum appendiculatum* Willd., *Clidemia hirta* (L.) D.Don, *Hedychium gardnerianum* Sheppard ex Ker Gawl., *Prunella vulgaris* L., *Rubus argutus* Link, and *Tibouchina herbacea* (DC) Cogn., all of which occur in the immediate vicinity and are capable of displacing all of the riparian habitat elements. Additionally, the area in general has been impacted by habitat-modifying non-indigenous plants such as *Axonopus fissifolius* (Raddi) Kuhlm., *Hedychium coronarianum* J. König, *Paspalum conjugatum* P.J.Bergius, *Psidium cattleianum* Sabine, *Rubus rosifolius* Sm., and *Sphaeropteris cooperi* (Hook. ex F. Muell.) R.M.Tryon. The Maui Invasive Species Committee works to control nearby (and island-wide) populations of *Cortaderia jubata* (Lemoine ex Carrière) Stapf and *Miconia calvescens* DC, two of the world's worst habitat-modifying weeds. Feral pigs (*Sus scrofa*) are common in this region, which is below exclusion fencing constructed by Natural Area Reserve staff as well as the East Maui Watershed Partnership. The pigs facilitate invasion by weeds (Stone & Scott, *Hawai'i's Terrestrial Ecosystems: Preservation and Management*, Cooperative National Park Studies Unit, University of Hawai'i, Honolulu. 1985) and degradation of the habitat but it is doubtful they forage directly on *D. kaalaana* or are able to trample it.

Introduced non-native slugs such as *Derocerus laevis* and *Limax maximus* are common throughout the windward east Maui watershed. These herbivores have detrimental effects on the Hawaiian flora (Joe & Daehler, Biol. Invasions 10:245–255, Springer, Netherlands. 2007). Global climate change may induce more frequent and severe drought, as well as more intense flooding events, changes that may impact the habitat (Chu, P.-S., R. C. Ying, and T. A. Schroeder, J. Clim. 23:4881–4900. 2010). When evaluated using IUCN Red List criteria (IUCN, *Guidelines for Using the IUCN Red List Categories and Criteria*. Version 10. Gland and Cambridge. 2013), *D. kaalaana* falls into the Critically Endangered (CR) category, which designates species facing the highest risk of extinction in the wild: A2c+ B2(a, biii) +D. *Deparia kaalaana* meets the IUCN criteria in A2, having its population reduction observed, estimated, inferred or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible, + (c) a decline its area of occupancy (AOO), extent of occurrence (EOO), and/or habitat quality; B2- AOO of <10 km^2 +(a) severely fragmented or number of locations (=1)+ (b)-continuing decline observed, estimated, inferred or projected in (iii) quality of habitat; D <50 mature individuals.

We recommend that the U. S. Fish & Wildlife Service list this species as Endangered under the Endangered Species Act, and that a recovery plan be written, funded, and implemented. *Deparia kaalaana* is a target species for the Plant Extinction Prevention Program, easily meeting the threshold of less than 50 wild individuals.

Material Examined.—U.S.A. Hawai'i. Kaua'i, Kaala, November 1909, *Faurie 294* (Holotype MICH 1190117; Isotypes KYO, TI, UC images seen); Hawai'i. Miss Frances Lack, *s.n.* 1880–1890 BISH 04929!; Maui, Kipahulu, F.L. Clarke, *s.n.*, 24 May 1881, BISH! 62319 (originally from BISH 3761, as *Thelypteris* *boydiae*); Hana District, Hanawi Natural Area Reserve, Kuhiwa Valley, 10 April 2013, *Oppenheimer, Bustamente & Perlman H41305* (BISH!, PTBG!, portion KYO!).

We gratefully acknowledge the support and cooperation of the Maui Invasive Species Committee, especially Adam Radford, and Jeremy Gooding of the National Park Service Biological Resource Management Division, for accommodating us in their helicopter operations which led to the rediscovery of *D. kaalaana*; Windward Aviation, especially their skilled pilots who were able to land in a remote, unimproved area; State of Hawai‘i Dept. of Land and Natural Resources, Division of Forestry and Wildlife, Natural Area Reserve System for allowing access, especially Bryon Stevens who reviewed aerial imagery and potential landing zones; National Tropical Botanical Garden field biologist Steve Perlman for working with us in the field; and Dan Palmer for the confirmation of the identification of the specimen. Masahiro Kato at KYO and Tetsuo Ohi-Toma at TI quickly provided images of the isotypes at their herbaria; and Briggitte Zimmer at the Dahlem Botanical Garden & Museum for searching for Hillebrand's collections of *D. kaalaana*. This paper was much improved by a review by Dan Palmer, and two anonymous reviewers. The Plant Extinction Prevention Program is funded by the U. S. Fish & Wildlife Service and the Hawai‘i Dept. of Land and Natural Resources Division of Forestry and Wildlife.—HANK L. OPPENHEIMER and KEAHI M. BUSTAMENTE, Plant Extinction Prevention Program, Pacific Cooperative Studies Unit, University of Hawai‘i/Mānoa, Dept. of Botany, P. O. Box 909, Makawao, HI 96768, USA, e-mail: HenryO@Hawaii.edu.

INFORMATION FOR AUTHO

Authors are encouraged to submit manuscripts pertinent to the study of ferns and lycophytes for publication in the *American Fern Journal*. Manuscripts should be sent to the editor at **hauk@denison.edu.** Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication. Mandatory fees will be charged for color figures in print and/or in electronic versions of published papers.

Information for authors, including detailed requirements for formatting manuscripts can be found online at: http://www.amerfernsoc.org/journal.html.

PTERIDOLOGIA ISSUES IN PRINT

The following issues of *Pteridologia*, the memoir series of the American Fern Society, are available for purchase:

1. Wagner, David H. 1979. Systematics of *Polystichum* in Western North America North of Mexico. 64 pp. $10.00 plus postage and handling.

2A. Lellinger, David B. 1989. The Ferns and Fern-allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). 364 pp. $32.00 plus postage and handling.

3. Lellinger, David B. 2002. A Modern Multilingual Glossary for Taxonomic Pteridology. 263 pp. $28.00 plus postage and handling.

4. Hirai, Regina Y., and Jefferson Prado. 2012. Monograph of *Moranopteris* (Polypodiaceae). 113 pp. $28.00 plus postage and handling.

For orders and more information, please contact our authorized agent for sales at: Missouri Botanical Garden Press, P.O. Box 299, St. Louis, MO 63166-0299, tel. 314-577-9534 or 877-271-1930 (toll free). For online orders, visit: http://www.mbgpress.org.

FIDDLEHEAD FORUM

The editor of the Bulletin of the American Fern Society welcomes contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns.

SPORE EXCHANGE

Mr. Brian S. Aikin, 3523 Federal Ave, Everett, WA 98201-4647 (spores.afs@comcast.net), is Director. Spores exchanged and lists of available spores sent on request. http://amerfernsoc.org/sporexy.html

GIFTS AND BEQUESTS

Gifts and bequests to the Society enable it to expand its services to members and to others interested in ferns. Back issues of the Journal and cash or other gifts are always welcomed and are tax-deductible. Inquiries should be addressed to the Membership Secretary.

VISIT THE AMERICAN FERN SOCIETY'S WORLD WIDE WEB HOMEPAGE:

http://amerfernsoc.org/

AMERICAN FERN JOURNAL

Volume 104

Number 3

July–September 2014

QUARTERLY JOURNAL OF THE AMERICAN FERN SOCIETY

The American Fern Society

Council for 2014

American Fern Journal

EDITOR

MANAGING EDITOR

ASSOCIATE EDITORS

The "American Fern Journal" (ISSN 0002-8444) is an illustrated quarterly devoted to the general study of ferns. It is owned by the American Fern Society, and published at The American Fern Society, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711. Periodicals postage paid at Austin, TX, and additional entry.

Claims for missing issues, made 6 months (domestic) to 12 months (foreign) after the date of issue, and orders for back issues should be addressed to Dr. George Yatskievych, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.

Changes of address, dues, and applications for membership should be sent to the Membership Secretary.

General inquiries concerning ferns should be addressed to the Secretary.

Back volumes are avalible for most years as printed issues or on microfiche. Please contact the Back Issues Curator for prices and availability.

Subscriptions:

Society Membership – USA, Canada, Mexico (includes Journal and Fiddlehead Forum)	$30
Society Membership – All other countries (includes Journal and Fiddlehead Forum)	$40
Society Life Membership – $360 (add $120 mailing surcharge for outside USA, Canada, Mexico)	
Regular Membership – USA, Canada, Mexico (includes Fiddlehead Forum)	$15
Regular Membership – All other countries (includes Fiddlehead Forum)	$22
Institutional Membership – $40 to USA, Canada, Mexico; $50 elsewhere (-$3 agency fee)	

POSTMASTER: Send address changes to American Fern Journal, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711.

American Fern Journal 104(3):109–178 (2014)
Published on 17 October 2014

Megalastrum (Dryopteridaceae) in Andean South America, Part I

Robbin C. Moran
The New York Botanical Garden, Bronx, NY 10458-5126, USA, e-mail: rmoran@nybg.org
Jefferson Prado
Instituto de Botânica, C.P. 68041, CEP 04045-972, São Paulo, SP, Brazil,
e-mail: jprado.01@uol.com.br
Michael A. Sundue
The Pringle Herbarium, Department of Plant Biology, The University of Vermont, 27 Colchester Ave., Burlington, Vermont 05405, USA, e-mail: sundue@gmail.com

Abstract.—We recognize 46 species of *Megalastrum* in the Andean region of South America. This is the highest diversity of any region for the genus. Of these species, 38(83%) are endemic to the region. Keys, descriptions, illustrations, distribution maps, nomenclatural information, specimens examined, index to collectors' names, and number are provided. Nineteen new species are described: *M. clathratum, M. decompositum, M. fimbriatum, M. fugaceum, M. galapagense, M. insigne, M. miscellum, M. nanum, M. nigromarginatum, M. obtusum, M. oellgaardii, M. oreophilum, M. peruvianum, M. polybotryoides, M. praetermissum, M. pubirhachis, M. rhachisquamatum, M. subtile,* and *M. tepuiense.* A new combination is made for *M. fibrillosum*, and lectotypes are designated for *Aspidium araguata, Dryopteris villosula, D. villosula* var. *inaequalis, D. wolfii, D. subincisa* var. *bogotensis, Megalastrum acrosorum, M. mollicoma, M. squamosissimum,* and *Nephrodium subglabrum.* The elevation range for the genus is 250–3500 m, with most species occurring at middle elevations from roughly 800–2000 m. Only four species occur in the Tepui region of southern Venezuela and northern Brazil: *M. biseriale, M. crenulans, M. oreophilum,* and *M. tepuiense* (endemic).

Key Words.—diversity, ferns, taxonomy, new species.

Resumen.—Reconocimos 46 especies de *Megalastrum* en la región Andina del América del Sur. Esto es la diversidad más alta de cualquier región del género. De estas especies, 38(83%) son endémicas a la región. Se suministran claves, descripciones, ilustraciones, mapas de distribución, datos nomenclaturales, ejemplares examinados, indice a los nombres y números de los colectores. Diez y nueve especies nuevas son descritas: *M. clathratum, M. decompositum, M. fimbriatum, M. fugaceum, M. galapagense, M. insigne, M. miscellum, M. nanum, M. nigromarginatum, M. obtusum, M. oellgaardii, M. oreophilum, M. peruvianum, M. polybotryoides, M. praetermissum, M. pubirhachis, M. rhachisquamatum, M. subtile,* and *M. tepuiense.* Una combinación nueva se hace para *M. fibrillosum*, y se designan lectotipos para *Aspidium araguata, Dryopteris villosula, D. villosula* var. *inaequalis, D. wolfii, D. subincisa* var. *bogotensis, Megalastrum acrosorum, M. mollicoma, M. squamosissimum* y *Nephrodium subglabrum.* El rango elevacional para el género es 250–3500 m, con la mayoría de especies encontrandose desde 800–2000 m. Solamente cuatro especies existen en la región de los Tepuis en el sur de Venezuela y el norte de Brasil: *M. biseriale, M. crenulans, M. oreophilum* y *M. tepuiense* (endémica).

This work represents the sixth and last in a series of papers dealing with the worldwide diversity and taxonomy of *Megalastrum* Holttum. The first dealt with the 18 species occurring in Brazil, Paraguay, and Uruguay (Moran *et al.* 2009a); the second with seven species in the West Indies (Moran *et al.* 2009b);

the third with 21 species in Central America (Moran and Prado 2010); the fourth with the seven species in circumaustral regions in Chile, Argentina, and southern islands of the Atlantic, Pacific, and Indian Oceans (Sundue *et al.* 2010); and the fifth with three in the African-Madagascan region (Rouhan and Moran 2011). The total number of species recognized in these previous works is 53. Accounting for species that occur in two or more regions, the number of species in these previous papers plus the 46 species recognized herein for the Andes, result in a total of 91 for the genus worldwide.

Megalastrum is a member of Eupolypods I (Schuettpelz and Pryer 2007), a clade characterized by petioles containing several vascular bundles with the two adaxial ones enlarged (pers. obs. of the authors). Within the Eupolypods I, the genus belongs to the Dryopteridaceae (Christenhusz *et al.* 2011; Smith *et al.* 2006, 2008), a family for which there are no known morphological synapomorphies (pers. obs. of the authors). Within Eupolypods I, the genus can almost always be distinguished by a character of its venation: in the proximal portions of the pinna, the veinlet that supplies the basal basiscopic lobe or segment of a pinnule springs from the costule; however, distally along the pinna rachis, the segments or lobes become successively more adnate and decurrent on the pinna rachis, and the veinlet supplying the lobe or segment springs from the pinna rachis, not the costule (Christensen 1920, Holttum 1986, Smith and Moran 1987). In other words, the veinlet "migrates" from the costule onto the pinna rachis as one moves distally along the pinna. Among other Dryopteridaceae this character occurs only in a few species of *Ctenitis* (C. Chr.) C. Chr. and *Stigmatopteris* C. Chr. Other characters found in nearly all species of *Megalastrum* are erect or decumbent rhizomes, basal pinnae prolonged on the basiscopic side, pinna rachises and costules adaxially pubescent, and vein tips enlarged (hydathodous). Most species of *Megalastrum* are non-indusiate or have a minute, hair like, and fugacious indusium; in the Andean countries, only four species have a well-developed circular indusium (*M. acrosorum, M. andicola, M. crenulans,* and *M. insigne*). All species of the genus grow terrestrially, or rarely on rocks, in wet shaded forests. A more detailed treatment of the characters and taxonomic history of the genus can be found in Moran and Smith (2004) and the papers cited in the above paragraph.

Within the Dryopteridaceae, *Megalastrum* is sister to *Rumohra* Raddi, and the two genera are in turn sister to a paraphyletic *Lastreopsis* (Schuettpelz and Pryer 2007; Labiak et al., 2014). These related genera are readily distinguished from *Megalastrum*. Both differ from *Megalastrum* by creeping rhizomes, green lamina margins thickened and decurrent onto the axis of the next lowest order. *Rumohra* further differs by dorsiventral rhizomes with an elongated ventral meristele (as seen in cross section), leaf axes glabrous adaxially, and peltate indusia (Kato 1974). *Lastreopsis* further differs by colored glands on the sporangial stalks (Tindale 1965).

What follows is a taxonomic treatment of *Megalastrum* in the Andean countries of Venezuela, Colombia, Ecuador, Peru, Bolivia, and Argentina (the species in Chile were treated by Sundue *et al.*, 2010). More species of *Megalastrum* occur in these countries than in any other area. About 83% of the species are endemic to the region, and about 40% are described as new. Further collecting in the Andes will almost certainly uncover more new species.

MATERIALS AND METHODS

This treatment is based on a study of about 800 gatherings from 27 herbaria (see Acknowledgments). Species recognition was based on morphological characters such as scales, hairs, glands, lamina dissection, and peripsore. We have illustrated these characters with silhouettes for lamina dissection and line drawings for details of the indument.

Spore images of nearly all species were taken with a Scanning Electron microscope at the Pfizer Lab at the New York Botanical Garden. The spores were transferred with dissecting needles from herbarium specimens to aluminum SEM stubs and coated with an asphalt adhesive. The stubs were then coated with gold-platinum in a sputter-coater for 2.5 min, and spores were imaged digitally using a JEOL JSM-5410LV SEM equipped with a JEOL Orion 5410 software interface. The accelerating voltage was 15 kV. All images were adjusted for contrast, provided with a black background, and uploaded to a public website: http://www.plantsystematics.org/

Notes on format.—In the nomenclature section for the species, we cite barcode numbers or, if these are absent, accession numbers. For some herbaria (e.g., AAU, GOET, MICH) both numbers were absent, and therefore are not cited.

In the Selected Specimens Examined, only one or two specimens per Department or Province are listed. We tried to select those specimens that were most widely distributed in herbaria. When geographic coordinates are given in brackets, it means that we located this information on-line because the coordinates were not given on the specimen label. All specimens examined, which include those not cited in the Selected Specimens Examined section, are listed in the Index to Collectors' Names and Numbers (Appendix III). The dot-distribution maps are based on all the specimens studied for a given species. In the figures with line drawings depicting indument characters, the letter "I" has been omitted to avoid confusion with it representing a small scale bar.

RESULTS

Species diversity.—We recognize 46 species of *Megalastrum* in the Andean countries of South America. Of these species, 38(83%) are endemic to that region. This is the highest diversity of species for any region in the genus. Ecuador has the highest *Megalastrum* species diversity and endemism of any country (Appendix 4; 30 species, 7 endemics). Only four species occur in the Tepui region of southern Venezuela and northern Brazil: *M. biseriale, M. crenulans, M. oreophilum,* and *M. tepuiense* (endemic). Two species are endemic to the Galapagos Islands: *M. galapagense* and *M. pleiosoros.* Within the

Andean region, the species are distributed from northern Venezuela to northern Argentina (Fig. 1). The genus is conspicuously absent from Amazonia.

The Andes have been a barrier to species ranges, with restriction of certain species of ferns to either the eastern or western sides (Moran 1995, 1996). The following four species occur only on the western side: *M. ctenitoides, M. decompositum, M. obtusum,* and *M. reductum.* In contrast, the following nine occur only on the eastern side: *M. bolivianum, M. falcatum, M. fibrillosum, M. hirsutosetosum, M. molle, M. polybotryoides, M. praetermissum, M. pubirhachis,* and *M. subtile.*

Ecology.—All species of *Megalastrum* occur terrestrially on the floors of wet, shaded forests. Occasionally, a species may be found on rocks or boulders, but all species are primarily of forest floors. The elevation range for the genus is 250–3500 m, with most species occurring at middle elevations from roughly 800–2000 m.

Spores.—Our SEM images of the spores of nearly all Andean species of *Megalastrum* can be viewed on-line at www.plantsystematics.org. The spores of the Andean species fall neatly into two groups. The first group consists of a clade (unpublished molecular results; in prep.) defined by cristate spores with parallel ridges (Fig. 2A–C). This character defines a large clade that occurs only in the Andes, Central America, and the West Indies. This clade is nested with the second group (unpublished molecular results; in prep.), which consists of those species with echinulate spores (Fig. 2D–F). The species in this group are *M. crenulans* and seven species belonging to a clade informally called the "pulverulentum group" (unpublished molecular results; in prep.). Those seven species are *M. adenopteris, M. clathratum, M. fugaceum, M. nanum, M. oellgaardii, M. pulverulentum,* and *M. sparsipilosum* R. C. Moran & Prado (this last species occurs only in Central America; Moran & Prado 2010).

TAXONOMIC TREATMENT

Megalastrum Holttum, Gard. Bull. Singapore 39: 161. 1986. TYPE: *Megalastrum villosum* (L.) Holttum. [≡*Polypodium villosum* L.]

Dryopteris subg. *Ctenitis* C. Chr. "restricted to the species group of *D. subincisa* C. Chr.," Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd. ser. 8, 6: 32, 59. 1919 [1920].

Dryopteris sect. *Subincisae* C. Chr., Index Filic., Suppl. 3: 7. 1934. *Ctenitis* C. Chr. sect. *Subincisae* (C. Chr.) Tindale, Contr. New South Wales Natl. Herb. 3: 252. 1965. TYPE: *Dryopteris subincisa* (Willd.) Urb., 1903. [≡*Polypodium subincisum* Willd., 1810]

Plants terrestrial; *rhizomes* erect to decumbent; petioles scaly toward the base, with 4–10 vascular bundles, the two adaxial bundles enlarged; *laminae* 1-pinnate-pinnatifid ranging to 4-pinnate-pinnatifid, catadromic above the basal pinnae; basal pinnae inequilateral and enlarged on the basiscopic side or (less commonly) equilateral; *rachises, pinna rachises, and costules* not

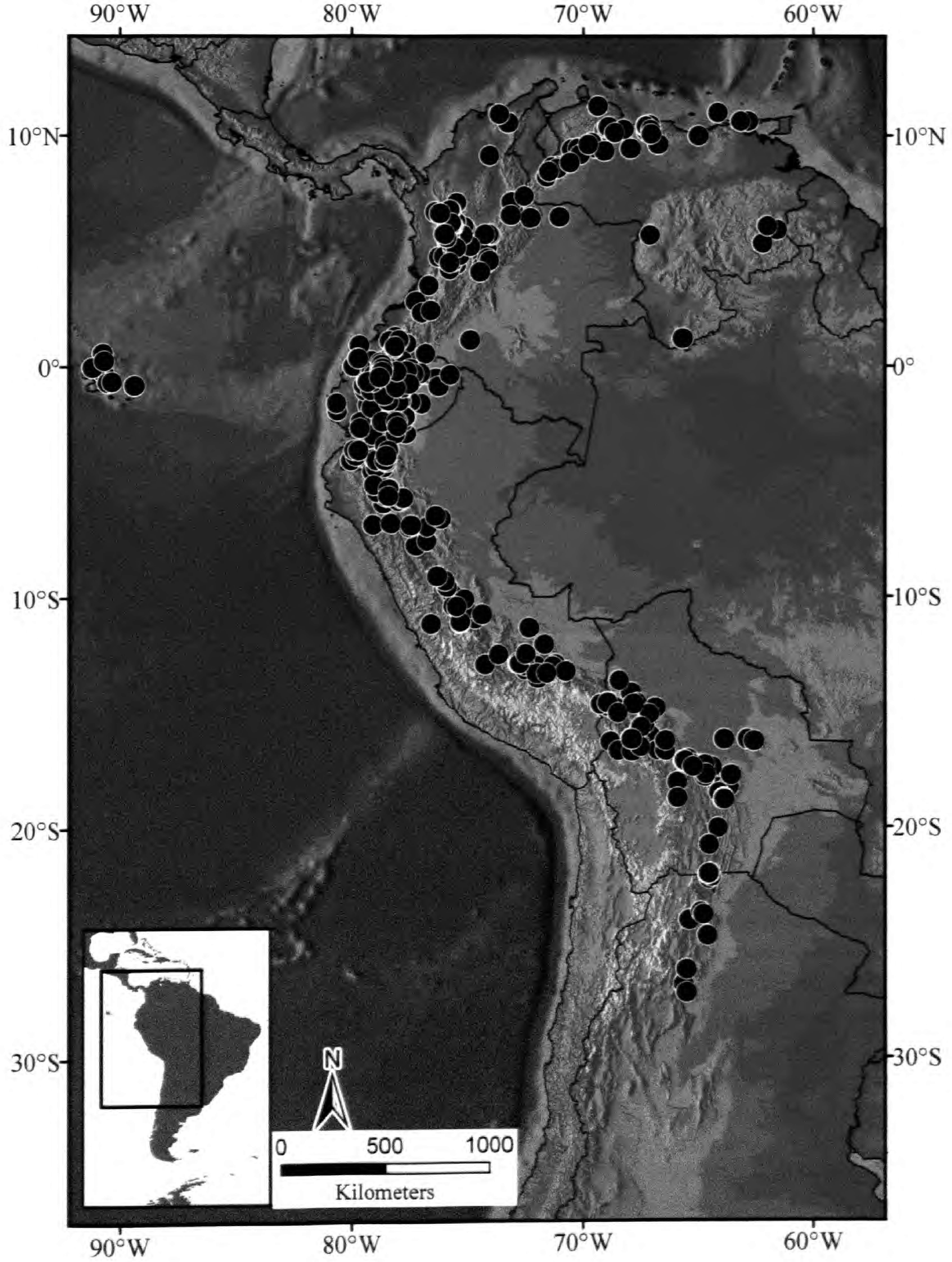

FIG. 1. Distribution of *Megalastrum* in the Andean countries.

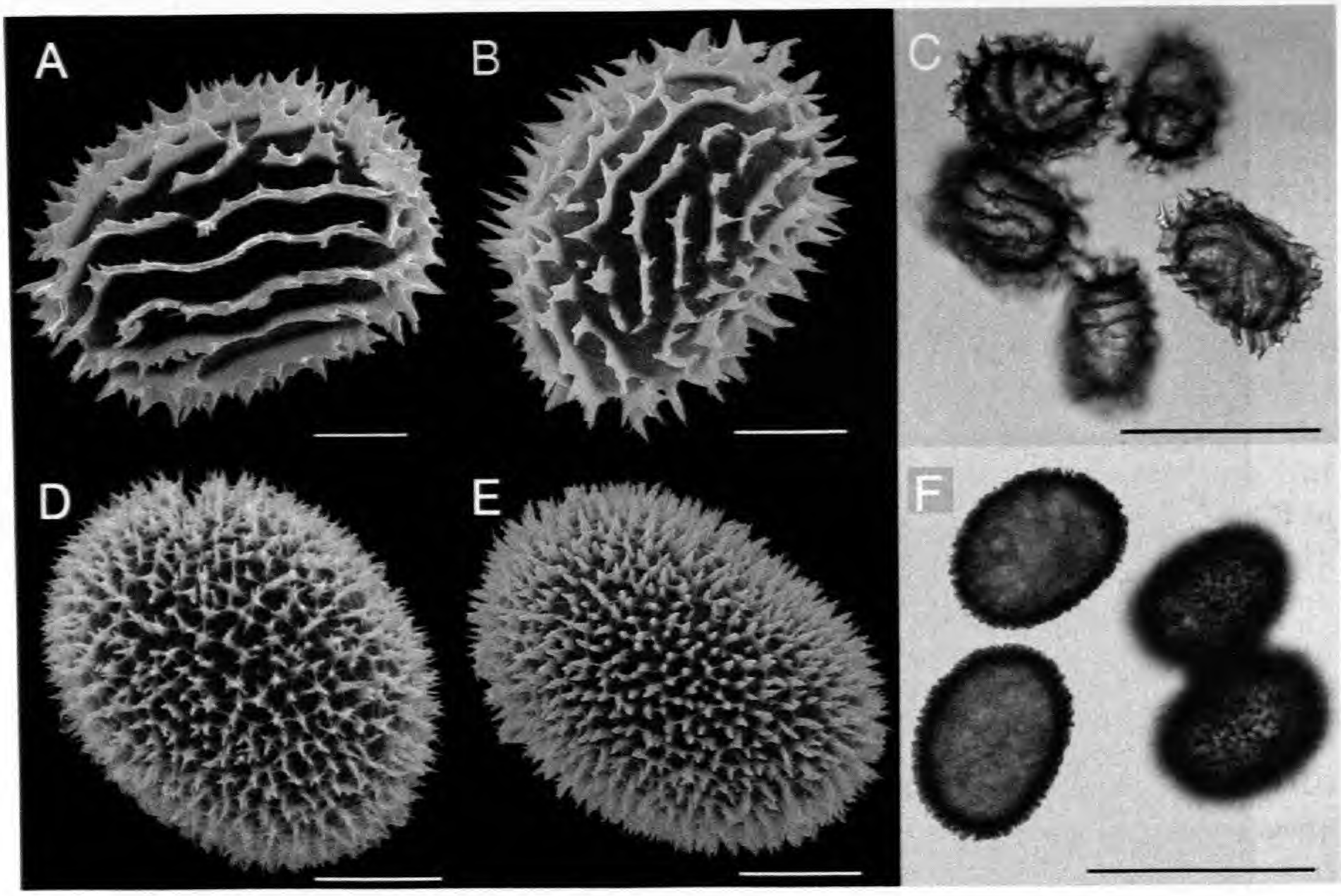

FIG. 2. Spores of Andean *Megalastrum*, showing cristate (A–C) and echinulate (D–F) perispores. A, B, D, and E were taken with the SEM; C and F with the light microscope. A. *M. falcatum*. B. *M. insigne*. C. *M. biseriale*. D. *M. fugaceum*. E. *M. nanum*. F. *M. fugaceum*. A: *Cerón 1483* (MO). B: *Grubb et al. 1195* (NY). C: *Navarrete & Øllgaard 3047* (AAU). D: *Serrano et al. 5225* (GOET). E: *Moran & Rohrbach 5380* (MO). F: *Huaylla et al. 1554* (NY). In A, B, D, and E, scale bars = 10 micrometers. In C and F, scale bars = 50 micrometers.

grooved or only shallowly so, scaly and pubescent abaxially, densely pubescent on the adaxial surfaces, the hairs whitish, spreading to antrorsely strigose, multicellular, if glands present, these ca. 0.1 mm wide, spherical, shiny, yellowish to orangish clear, sessile to stalked; *basal basiscopic segment of pinnules* becoming decurrent and adnate to the pinna rachises, the vein supplying the segment springing from the pinna rachis instead of the costule; *hydathodes* present or (more rarely) absent; *indusia* absent or (less commonly) present, circular, brown, firm, attached at the base of a sinus, in some species minute and fugacious; *spores* monolete, nongreen, the perispores cristate or spiny, non-fenestrate or rarely so (2 species); x=41 (Kramer and Green 1990).

Etymology.—The name *Megalastrum* is taken from the Greek *mega–* for large, and *–Lastrea*, which refers to the genus *Lastrea* Bory named after Charles Jean Louis Delastre (1792–1859), a French botanist. When *Ctenitis* was first published (as a subgenus of *Dryopteris*), it included species now placed in *Ctenitis* (C. Chr.) C. Chr., *Megalastrum*, and *Triplophyllum* Holttum. Christensen later (1919 [1920]) recognized four informal species groups within the subgenus, one of which he called the "Group of *D. subincisa*." This group is the same as what we are calling *Megalastrum*.

The following key relies heavily on characteristics of the hairs and scales, some of which are shown in Fig. 3, and the distribution of these structures on various parts of the leaf. Magnification of 30× and a strong light source are extremely helpful in the identification of the species. The perispore character used in couplet 5 (whether the spores are spiny or cristate) can be seen with 100× magnification.

KEY TO THE SPECIES OF *MEGALASTRUM* IN THE ANDEAN COUNTRIES

1\. Indusia present, conspicuous, circular

  2\. Pinna rachis scales bullate; laminae basally 4-pinnate; spores echinulate; s. Venezuela . . . . **10. M. crenulans**

  2\. Pinna rachis scales flat (non-bullate); laminae basally 3-pinnate-pinnatisect; spores cristate; Colombia to Bolivia

    3\. Pinna rachises abaxially with hairs 1.0–1.5 mm long; indusia pubescent with hairs 0.3–1.0 mm long . . . . **19. M. insigne**

    3\. Pinna rachises abaxially with hairs 0.2–0.5 mm long; indusia without hairs or with a few hairs 0.1–0.2 mm long

      4\. Pinna rachis scales thin and flaccid, entire, dull; hairs on the veins adaxially 0.5–0.7 mm long, 4–7-celled . . . . **1. M. acrosorum**

      4\. Pinna rachis scales firm, denticulate apically, lustrous; hairs on the veins adaxially 0.3–0.5 mm long, 2–4-celled . . . . **4. M. andicola**

1\. Indusia absent or (1 species) inconspicuous and appearing as tuft of whitish hairs in center of sorus

  5\. Spores echinulate (Fig. 2D–F)

    6\. Laminae 0.3–0.4 m long, medially 2-pinnate-pinnatisect . . . . **26. M. nanum**

    6\. Laminae 0.8–3.0 m long, medially 3-pinnate-pinnatisect

      7\. Laminae densely pubescent between the veins on both surfaces, the hairs often gland-tipped; indusia present, minute (< 0.2 mm long), fugacious and often apparently absent, usually evident as a tuft of whitish hairs in the center of the sorus . . . . **2. M. adenopteris**

      7\. Laminae glabrous between the veins on both surfaces or, if pubescent, the hairs not gland-tipped; indusia absent

        8\. Pinna rachis scales clathrate; pinna rachises and costules abaxially evenly and densely pubescent by reddish hairs 0.2–0.6 mm long. . . **9. M. clathratum**

        8\. Pinna rachis scales not clathrate; pinna rachises and costules abaxially glabrous to densely pubescent by whitish hairs ca. 1 mm long

          9\. Laminae densely and conspicuously pubescent, the hairs 1.0–2.0 mm long . . . . **38. M. pulverulentum**

          9\. Laminae sparsely and inconspicuously pubescent, the hairs 0.4–0.8 mm long . . . . **16. M. fugaceum**

  5\. Spores cristate (Fig. 2A–C)

    10\. Laminae medially 1- to 2-pinnate, most or all of the proximal pinnules adnate to the pinna rachis

      11\. Pinna rachises and costules glabrous to sparsely and inconspicuously pubescent abaxially or (in *M. polybotryoides*) minutely glandular

        12\. Basal basiscopic pinnules enlarged and more deeply lobed than the suprabasal ones, often (especially on large leaves) overlapping the lamina rachis; rhizome scales entire to sparsely denticulate. . . . . . **14. M. fibrillosum**

        12\. Basal basiscopic pinnules the same size and shape as the suprabasal ones, not overlapping the lamina rachis; rhizome scales strongly denticulate

          13\. Pinna rachises and costules minutely glandular on both surfaces, adaxially with hairs absent . . . . **34. M. polybotryoides**

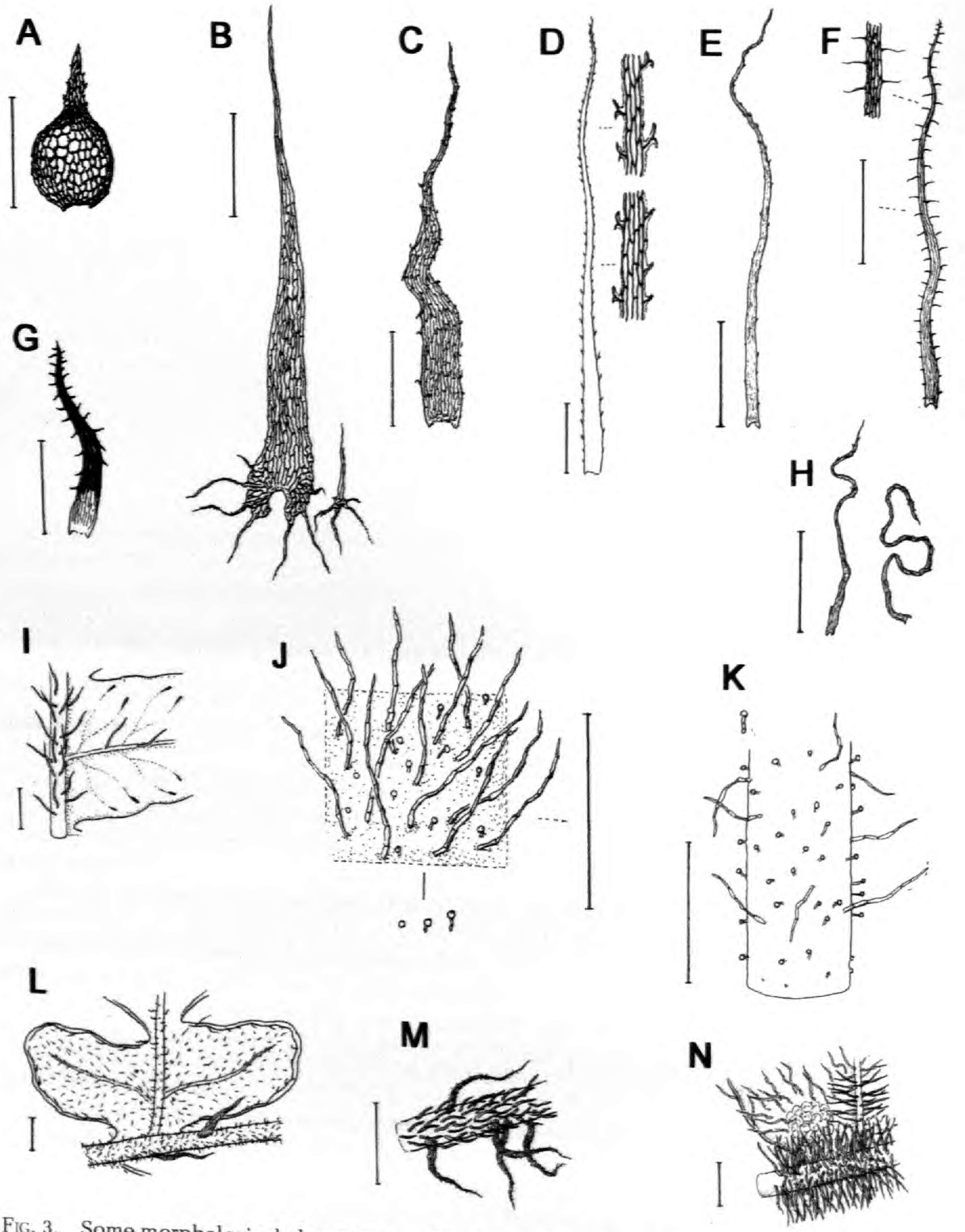

FIG. 3. Some morphological characters used in the key to species of *Megalastrum* from the Andes. A. Bullate scale from pinna rachis, *M. crenulans*. B. Lanceolate scale with ciliate base from pinna rachis, *M. decompositum*. C. Lanceolate scale, sparsely denticulate, from pinna rachis. D. Linear denticulate scale with bifid teeth, from lamina rachis, *M. galapagense*. E. Linear entire scale, from lamina rachis, *M. fibrillosum*. F. Linear denticulate scale from pinna rachis, *M. pulverulentum*. G. Lanceolate scale darkened toward apex, denticulate, from pinna rachis, *M. fugaceum*. H. Linear tortuous scales from pinna rachis, *M. reductum*. I. Hydathodes at the apices of the ultimate veins, *M. ciliatum*. J. Spreading hairs with sessile to stalked glands beneath, *M. insigne*. K. Spreading hairs with stalked glands, pinna rachis, *M. crenulans*. L. Short, even pubescence of erect acicular hairs, pinnule base and costule, *M. vastum*. M. Spreading scales and antrorsely strigose hairs, from

13. Pinna rachises and costules eglandular on both surfaces, adaxially with hairs usually present
14. Pinna rachis scales filiform, tortuous . . . . **22. M. microsorum**
14. Pinna rachis scales lanceolate, not tortuous
15. Rhizome scales 2.5–6.5 mm long; pinnules or segments entire . . . . **11. M. ctenitoides**
15. Rhizome scales 10–20 mm long; pinnules or segments crenate to lobed . . . . **6. M. biseriale**
11. Pinna rachises and costules conspicuously densely to moderately pubescent abaxially
16. Ultimate veins pubescent on the adaxial surfaces, often conspicuously so
17. Veins adaxially with hairs ca. 0.5 mm long; Galapagos Islands . . . . **33. M. pleiosoros**
17. Veins adaxially with hairs 0.5–2.0 mm long; Colombia to Bolivia
18. Pinna rachises abaxially glandular, the glands stalked, ca. 0.1 mm long, 2-celled . . . . **24. M. molle**
18. Pinna rachises abaxially eglandular
19. Laminae glabrous between the veins on both surfaces; hairs of the lamina margin ca. 0.3 mm long; pinna rachises abaxially moderately scaly, the scales 0.2–0.3 mm wide, narrowly lanceolate . . . . **7. M. bolivianum**
19. Laminae pubescent between the veins on both surfaces; hairs of the lamina margin ca. 1 mm long; pinna rachises abaxially sparsely scaly, the scales 0.1 mm wide, filiform. . . . . **18. M. hirsutosetosum**
16. Ultimate veins glabrous or subglabrous on the adaxial surfaces
20. Lamina tissue between the veins abaxially pubescent
21. Basal pinnae equilateral . . . . **22. M. microsorum**
21. Basal pinnae inequilateral (prolonged basiscopically) . . . . **32. M. platylobum**
20. Lamina tissue between the veins abaxially glabrous.
22. Pinnules or segments entire; basal pinnae equilateral . . . . **11. M. ctenitoides**
22. Pinnules or segments (at least proximal ones) crenate to lobed; basal pinnae usually inequilateral . . . . **6. M. biseriale**
10. Laminae medially 2-pinnate-pinnatifid to 4-pinnate-pinnatisect, most or all of the proximal pinnules sessile but not adnate to the pinna rachis (except *M. fimbriatum*).
23. Laminae between the veins *on both* surfaces glabrous (sometimes a few hairs present adaxially near the margins).
24. Pinna rachises abaxially pubescent.
25. Ultimate veins with hairs 0.7–1.5 mm long on the adaxial surfaces
26. Hairs of the lamina margins 0.5–1.2 mm long, 5–9-celled, lax; hairs on the ultimate veins adaxially lax, slightly tortuous; northern Peru . . . . **15. M. fimbriatum**

←

pinna rachis, *M. biseriale*. N. Dense, long straightish hairs, from pinna rachis, *M. ciliatum*. Scale bars = 1 mm. A: Brazil, *Jürgens 206* (UC). B, C: Isotype, *van der Werff et al. 12482* (MO). D: Isotype, *van der Werff 2244*, U. E: *Jiménez I. 2547* (UC). F: *Fay & Fay 3845* (NY). G: *Serrano et al. 5225* (MO). H: Isotype, *Camp 3786* (K). I: *Fuentes et al. 9013* (MO). J: *Øllgaard et al. 99554* (AAU). K: from Brazil, *Jürgens s.n.* [Rosenstock Filices Austrobrasiliensis no 206] (UC). L: *Balslev et al. 1693* (NY). M: *Stübel 770* (B). N: *Fuentes et al. 9013* (MO).

26. Hairs of the lamina margins 0.3–0.5 mm long, 2- or 3-celled, straightish; hairs on the ultimate veins adaxially whitish and straight; northwestern Ecuador, Bolivia

27. Pinna rachis scales linear; northwestern Ecuador . . .**28. M. obtusum**

27. Pinna rachis scales lanceolate; Bolivia . . . . **20. M. marginatum**

25. Ultimate veins glabrous or with hairs 0.2–0.5 mm long on the adaxial surfaces

28. Pinna rachis scales ca. 0.2–0.5 mm wide, lanceolate to linear-lanceolate, not tortuous

29. Basal pinnae 30–50 cm long, inequilateral; laminae medially 3-pinnate-pinnatisect . . . . **3. M. alticola**

29. Basal pinnae 10–25 cm long, equilateral or subequilateral; laminae medially 2-pinnate-pinnatisect. . . . . **13. M. falcatum**

28. Pinna rachis scales ca. 0.1–0.2 mm wide, filiform and slightly tortuous to linear and flat

30. Laminae basally 3-pinnate-pinnatisect; pinnules acuminate; pinna rachis scales denticulate . . . .**35. M. praetermissum**

30. Laminae basally 2-pinnate-pinnatisect; pinnules obtuse to acute; pinna rachis scales entire

31. Hairs on the pinna rachises abaxially uniformly 0.1–0.2 mm long . . . .**39. M. reductum**

31. Hairs on the pinna rachises abaxially of mixed sizes, 0.2–1.0 mm long. . . . . **32. M. platylobum**

24. Pinna rachises abaxially without hairs.

32. Ultimate veins adaxially pubescent with hairs 0.5–1.5 mm long.

33. Sori with tuft of acicular whitish hairs 0.2–0.5 mm long; costules abaxially sparsely pubescent; southern Venezuela . . . . **45. M. tepuiense**

33. Sori without tuft of hairs; costules abaxially moderately to densely pubescent; northern Venezuela, Colombia, Ecuador, Bolivia

34. Pinna rachis scales filiform (2 or 3 cells wide), dark brown; veins adaxially moderately and conspicuously pubescent . . . .**35. M. praetermissum**

34. Pinna rachis scales lanceolate to linear-lanceolate (more than 3 cells wide), golden brown; veins adaxially sparsely and inconspicuously pubescent. . . . . **5. M. aureisquama**

32. Ultimate veins adaxially glabrous

35. Lamina rachises and pinna rachises abaxially with sessile brownish glands. . . . . **34. M. polybotryoides**

35. Lamina rachises and pinna rachises abaxially eglandular

36. Pinna rachis scales 0.1–0.2 mm wide, filiform

37. Laminae 2-pinnate-pinnatisect; basal pinnae ca. 22 cm long; pinna rachis scales entire; Ecuador, Peru . . . . **44. M. subtile**

37. Laminae 3-pinnate-pinnatisect; basal pinnae ca. 50 cm long; pinna rachis scales denticulate; northern Colombia and Venezuela . . . . **21. M. martinicense**

36. Pinna rachis scales 0.2–1.5 mm wide, lanceolate to linear-lanceolate

38. Basal pinnae 15–30 cm long; Bolivia. . . . .**41. M. rupicola**

38. Basal pinnae 30–60 cm long; Venezuela to Bolivia

39. Pinna rachis scales strongly denticulate, dark brown, sometimes darker distally . . . .**29. M. oellgaardii**

39. Pinna rachis scales entire to subentire, golden brown to light pale brown throughout

40. Lamina rachises conspicuously scaly, the scales 0.5–2.0 mm wide . . . . **42. M. squamosissimum**

40. Lamina rachises inconspicuously scaly, the scales ca. 0.2–0.5 mm wide

41. Rhizome scales 5–15 mm long, dark brown; Bolivia .... **5. M. aureisquama**

41. Rhizome scales 20–25 mm long, golden brown; northern Venezuela and Colombia .... **43. M. subincisum**

23. Laminae between the veins on *one or both* surfaces pubescent

42. Laminae pubescent between the veins on only one surface

43. Lamina tissue between the veins abaxially glabrous .... **35. M. praetermissum**

43. Lamina tissue between the veins abaxially pubescent

44. Basal pinnae 15–30 cm long; leaves up to 1 m long (often folded once and mounted on a single sheet)

45. Lamina rachises pubescent; hairs on the abaxial surface of the laminae gland-tipped; pinna rachis scales entire; rhizome scales concolorous (not black-margined). .... **36. M. pubescens**

45. Lamina rachises without hairs; hairs on the abaxial surface of the laminae not gland-tipped; pinna rachis scales denticulate; rhizome scales black-margined, at least intermittently

46. Hairs present on the ultimate veins adaxially; hairs on the abaxial surfaces of the laminae 0.8–1.0 mm long; hairs on the abaxial surfaces of the costules 0.7–1.0 mm long .... **8. M. ciliatum**

46. Hairs absent on the adaxial surfaces of the ultimate veins or only 1 or 2 present distally; hairs on the abaxial surfaces of the laminae 0.1–0.2 mm long; hairs on the abaxial surfaces of the costules 0.2–0.5 mm long

47. Pinna rachises abaxially without hairs; Bolivia .... **41. M. rupicola**

47. Pinna rachises abaxially pubescent; Colombia .... **27. M. nigromarginatum**

44. Basal pinnae 30–150 cm long; leaves 1.5–4.0 m long

48. Basal pinnae equilateral; laminae 2-pinnate-pinnatifid basally; Galapagos Islands .... **17. M. galapagense**

48. Basal pinnae inequilateral; laminae 3-pinnate-pinnatifid to 4-pinnate-pinnatifid basally; Andes

49. Pinna rachis scales 5–12 × 0.5–2 mm, entire to subentire except at sometimes ciliate bases ..... **42. M. squamosissimum**

49. Pinna rachis scales 2–5 × 0.1–4 mm, strongly denticulate

50. Pinna rachises abaxially without hairs .... **35. M. praetermissum**

50. Pinna rachises abaxially pubescent

51. Hairs of the pinna rachises abaxially ca. 0.1 mm long, retrorsely strigose; Ecuador, Peru .... **37. M. pubirhachis**

51. Hairs of the pinna rachises abaxially 0.2–0.3 mm long, spreading to erect; northern Colombia, southern Venezuela...................... **30. M. oreophilum**

42. Laminae pubescent between the veins on both surfaces

52. Laminae basally 4-pinnate-pinnatisect, medially 3-pinnate-pinnatifid .... **12. M. decompositum**

52. Laminae basally 2- or 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect

53. Rachises and pinna rachises densely scaly, the scales 1.0–2.0 mm wide .... **40. M. rhachisquamatum**

53. Rachises and pinna rachises sparsely to moderately scaly, the scales 0.1–1.0 mm wide
  54. Hairs on the abaxial surfaces of the costules of mixed sizes, the smaller ones 0.1–0.3 mm long, the longer ones 0.7–1.0 mm long
    55. Laminae basally 3-pinnate-pinnatisect; basal pinnae 25–40 cm long, inequilateral (prolonged basiscopically); pinnules sessile to short-stalked but not adnate; Colombia to Bolivia . . . . **23. M. miscellum**
    55. Laminae basally 2-pinnate-pinnatifid; basal pinnae 8–15 cm long, equilateral; pinnules adnate; Galapagos Islands . . . . **33. M. pleiosoros**
  54. Hairs on the abaxial surfaces of the costules about the same size, 0.2–0.4 mm long
    56. Hairs of the lamina margins and tissue adaxially ca. 0.1 mm long; pinna rachis scales flaccid, dull, brown
      57. Petiole and rachis scales dark brown, entire to sparsely denticulate; Colombia to Bolivia. . . . . **46. M. vastum**
      57. Petiole and rachis scales golden brown, densely denticulate; northern Colombia, southern Venezuela . . . . **30. M. oreophilum**
    56. Hairs of the lamina margins and tissue adaxially 0.4–0.8 mm long; pinna rachis scales firm, shiny, yellowish brown
      58. Hairs on the ultimate veins adaxially 0.2–0.5 mm long; Colombia, Ecuador . . . . **25. M. mollicoma**
      58. Hairs on the ultimate veins adaxially 0.5–1.5 mm long; Peru, Bolivia. . . . . **31. M. peruvianum**

SPECIES TREATMENTS

1. ***Megalastrum acrosorum*** (Hieron.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [published 3 May 1988]. *Nephrodium acrosorum* Hieron., Bot. Jahrb. Syst. 34:446. 1904. *Dryopteris acrosora* (Hieron.) C. Chr., Index Filic. 250. 1905. *Ctenitis acrosora* (Hieron.) Copel., Gen. Fil. 5:124. 1947. TYPE.—COLOMBIA. Depto. unknown: Cerro Pelado, 2000–2200 m, *M. A. Stübel s.n.* (lectotype, here designated: B! [barcode 200051888]; isolectotype: BM! (frag.) [barcode 000907703). **Figs. 4A–L, 5A, 6D.**

Rhizomes erect, up to 35 cm tall, the scales ca. 10.0 × 2 mm, appressed, lanceolate, brown, lustrous, flat, entire to sparsely denticulate; **leaves** 1.2–2.5 m long; **petiole base scales** like those of the rhizomes; **laminae** up to ca. 1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 25–45 cm long, strongly inequilateral; **pinna rachises** abaxially very sparsely glandular, densely pubescent, densely to sparsely scaly, the glands ca. 0.1 mm long, sessile, yellowish, the hairs 0.2–0.3 mm long, 2- or 3(4)-celled, acicular, tortuous, appressed to spreading, the scales 1.0–2.0 × 0.3–0.8 mm, broadly lanceolate, appressed, non-bullate, whitish to pale brown, thin and flaccid, entire, dull, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.5–0.8 mm long, 5–7-celled, appressed to spreading, tortuous, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially very sparsely provided with sessile glands, sparsely puberulent and sparsely scaly, the hairs like those of the pinna rachises, the scales ca. 1.5 × 0.3 mm, otherwise like those of the pinna rachises, adaxially eglandular, pubescent, scales absent, the hairs ca. 1 mm long, 5–7-celled, acicular, ascending, appressed; **laminar tissue between veins** abaxially sparsely provided with 0.1 mm long yellowish sessile glands, sparsely puberulent, the hairs 0.1–0.2(–3.0) mm long, 1- or 2-celled, erect, acicular, whitish, adaxially eglandular, densely pubescent, the hairs 0.3–0.5 mm long, 2–3-celled, erect to appressed, acicular; **ultimate veins** visible on both surfaces, abaxially sparsely glandular and puberulent, the glands and hairs like those of the laminar tissue between the veins, adaxially eglandular, sparsely pubescent, the hairs 0.5–0.7 mm long, 4–7-celled, acicular, erect to ascending; **lamina margins** eglandular, densely ciliate, the hairs 0.2–0.3 mm long, 2- or 3-celled, acicular, ascending; **indusia** present, conspicuous, circular, 0.5–0.7 mm wide, glandular, concolorous, brown, the margin and surface of the indusia glandular, pubescent to sparsely pubescent or sub-glabrous, the glands sessile, spherical, yellow to orange, the hairs 0.1–0.2 mm long, acicular, spreading; **spores** cristate.

Distribution and ecology.—Colombia, Ecuador, Peru; 1280–2150 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Huila**: Cordillera Oriental, SE of Garzón, 1950 m, [9°8′7″N, 74°3′38″W], 7 Feb 1945, *Little 9415* (US).

ECUADOR. **Napo**: Road Baeza-Tena, 2 km N of Cosanga, 1900–2000 m, 0°34′S, 77°53′W, 19 Jan 1992, *Øllgaard et al. 99562* (AAU, QCA). **Pichincha**: Cordillera Occidental, casi 40 km por el camino oeste de Quito a Nono, 2150 m, 0°02′S, 78°38′W, 21 Jan 1984, *Moran 3567* (NY).

PERU. **Junín**: Chancamayo, Río Rondayacu, 45 km from San Ramón, 1880–1950 m, 11°20′S, 72°20′W, 15 Oct 1982, *Smith et al. 2615 p.p.* (AAU, F, MO, NY). **San Martín**: Huallaga, Saposoa, al sur de Añazco Pueblo, 2000 m, [6°56′S, 76°46′W], 3 Sep 2000, *Quipuscoa et al. 2340* (F, NY, UC).

Megalastrum acrosorum is distinguished by indusiate sori and rachises and costules abaxially with pale flaccid appressed scales. The other indusiate species of *Megalastrum* have pinna rachis scales firmer, spreading, denticulate (at least apically). The almost complete absence of glands on the pinna rachises and costules abaxially also helps to distinguish *M. acrosorum* from the other species. Most similar morphologically is *M. andicola,* which differs by the scale and pubescence characters given in the key.

Megalastrum acrosorum was originally described as having sori restricted toward the apex of the pinnules (thus the specific epithet). Although this is true for the original material, more recent specimens show that the sori may occur throughout the length of the pinnules. The restriction of sori toward the apex is diagnostic for *M. apicale* R. C. Moran & J. Prado, a species from Costa Rica and Panama long thought to be conspecific with *M. acrosorum* (e.g., by Smith and Moran 1995). *Megalastrum apicale* differs by pinna rachises abaxially with dark brown scales and hairs 0.5–0.7 mm long (Moran and Prado 2010).

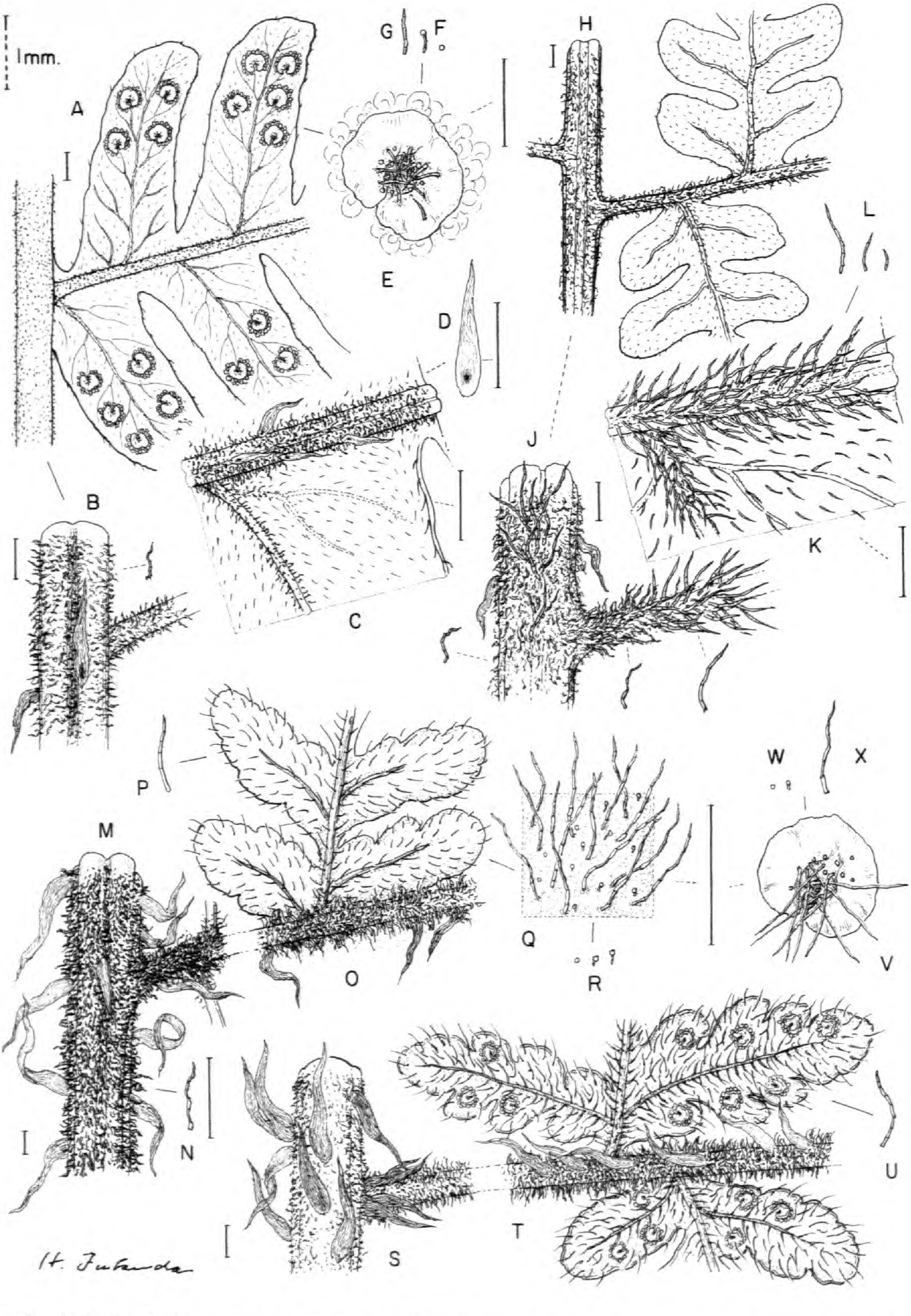

FIG. 4. Indument of two Andean species of *Megalastrum*. A–L. *M. acrosorum*. A. Abaxial surface of pinna rachis and costule. B. Adaxial surface of pinna rachis. C. Abaxial surface, detail of indument. D. Scale from costule. E. Sorus, note hairs and glands on indusium. F. Stalked gland at left, sessile gland at right. G. Non-glandular hair. H. Adaxial surface of pinna rachis and pinnules. J. Detail of hairs and scales. K. Ascending hairs on adaxial surface of the lamina. L. Hairs from

2. **Megalastrum adenopteris** (C. Chr.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [published 3 May 1988]. *Dryopteris adenopteris* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 8, 6:85. 1920. *Ctenitis adenopteris* (C. Chr.) Ching, Sunyatsenia 5:250. 1940. TYPE.—BRAZIL. Rio Grande do Sul: Silveira Martins, Val Veneta, ad terram silvae primaevae, [29°39′S, 53°35′], 1893, *C. A. M. Lindman s.n.* (Regnell A 1313) (lectotype, designated by Moran *et al.*, 2009a: BM! [barcode 000907710], photo MICH!; isolectotypes: BM! [barcode 000907710], C-n.v., L-n.v., S-n.v.; U-n.v., UPS!, US! [barcode 00067050]; fragm. MO!). **Figs. 5B, 7A–G, 8B.**

Dryopteris villosa (L.) Kuntze var. *tomentosa* Rosenst., Hedwigia 46:130. 1916. TYPE.—BRAZIL. Rio Grande do Sul: Mun. Rio Pardo, Fazenda Soledade, [29°59′23″S, 52°22′41″W], 1906, *L. C. Jürgens s.n.* (Rosenstock Filices Austrobrasilienses no. 207) (lectotpe, designated by Moran *et al.*, 2009a: MICH!; isolectotype: S! [accession 06-547]).

Dryopteris oreocharis Sehnem var. *canescens* Sehnem, Fl. Ilustr. Catarinense ASPI 1:177. 1979. TYPE.—BRAZIL. Santa Catarina: Lauro Müller, Novo Horizonte, [28°23′34″S, 49°23′49″W], 400 m, 24 Oct 1958, *R. Reitz & R. M. Klein 7516* (lectotype, designated by Moran *et al.*, 2009a: PACA! [barcode 68744]; isolectotype: HBR!).

Rhizomes erect, up to 50 cm tall, the scales 10.0–20.0 × 1.0–2.0 mm, appressed to ascending, linear-lanceolate, orange, dull or shiny, twisted, slightly tortuous apically, sparsely denticulate; **leaves** up to 4 m long; **petiole base scales** like those of the rhizomes but more spreading; **laminae** 1.0–2.0 m long, basally 4-pinnate-pinnatifid, medially 3-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** up to 1.0 m long, inequilateral; **pinna rachises** on both surfaces glandular, puberulent, sparsely scaly, the glands ca. 0.1 mm long, stalked or sessile, yellowish, the stalked 2-celled, the sessile ca. 0.1 mm long, the hairs 0.1–0.3 mm long, 1–3-celled, acicular, erect, the scales denticulate, 0.5–2.5 × 0.2–0.5 mm, appressed, ovate to lanceolate, brown, lustrous, not clathrate, not bullate; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially glandular, puberulent, and sparsely scaly, the hairs, scales, and glands like those of the pinna rachises, adaxially with similar indument but the hairs 0.3–0.4 mm, 3- or 4-celled; **laminar tissue between veins** on both surfaces densely puberulent, the hairs ca. 0.1 mm long, 1- or 2-celled, spreading, often gland-tipped, the apical cell swollen or globose, yellowish to orangish; **ultimate veins** visible on both surfaces, both surfaces glandular, puberulent, the hairs and glands like those on the laminar tissue between the veins but the hairs ca.

←

costule. M–X. *M. insigne*. M. Adaxial surface of rachis. N. Rachis hair. O. Adaxial surface of pinna rachis and pinnule. P. Hair. Q. Hairs and glands, adaxial surface of the lamina. R. Glands. S. Abaxial surface of rachis. T. Abaxial surface of pinna rachis and pinnules. U. Hair. V. Indusium with hairs and glands. W. Glands. X. Hair. All scale bars = 1 mm. A–L: *Moran 3567* (NY). M–X: *Øllgaard et al. 99554* (AAU).

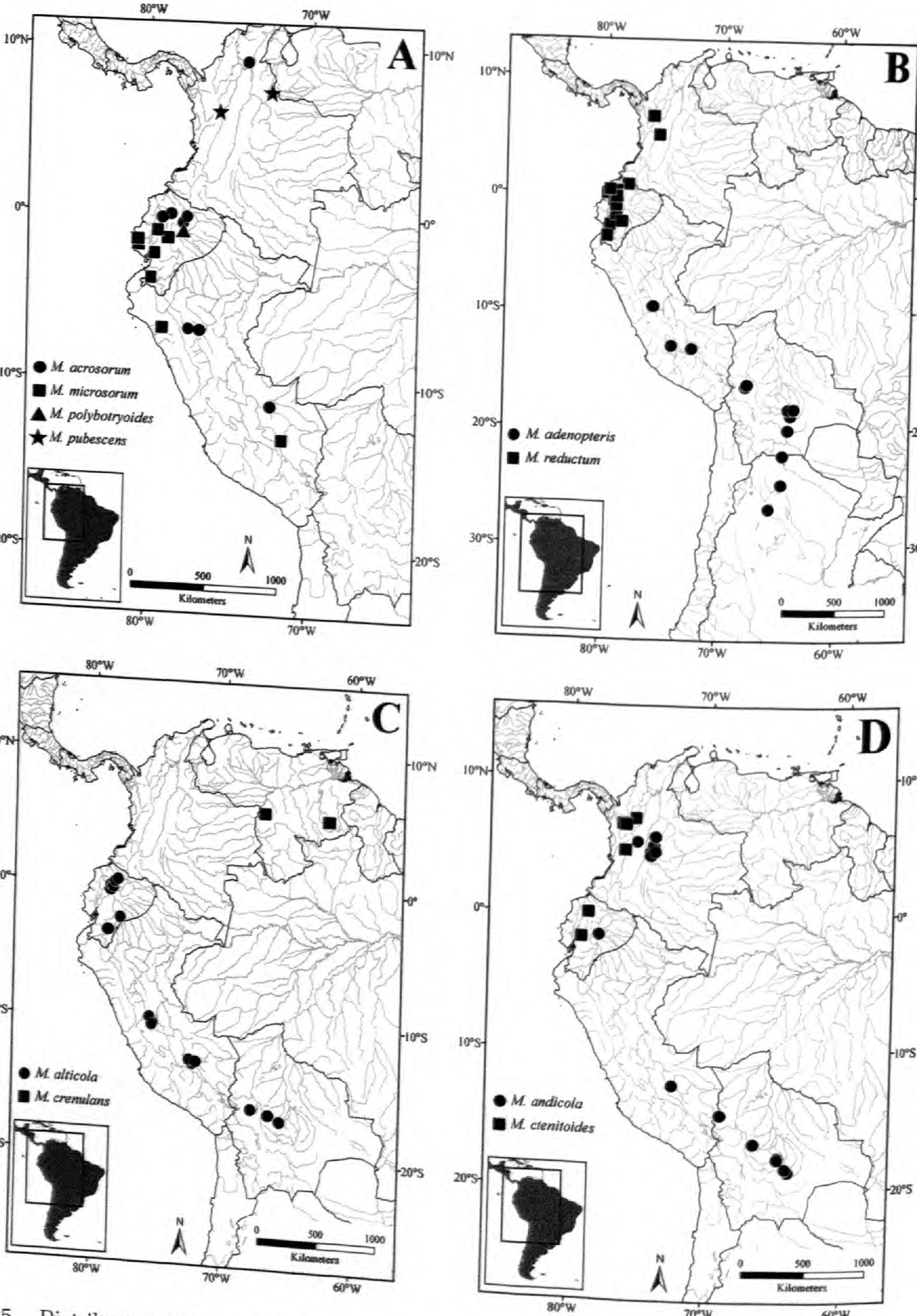

FIG. 5. Distribution of ten species of *Megalastrum* in the Andes. Some species are also known from areas outside the Andean region as here defined; for the worldwide distribution of a species, see under each species description.

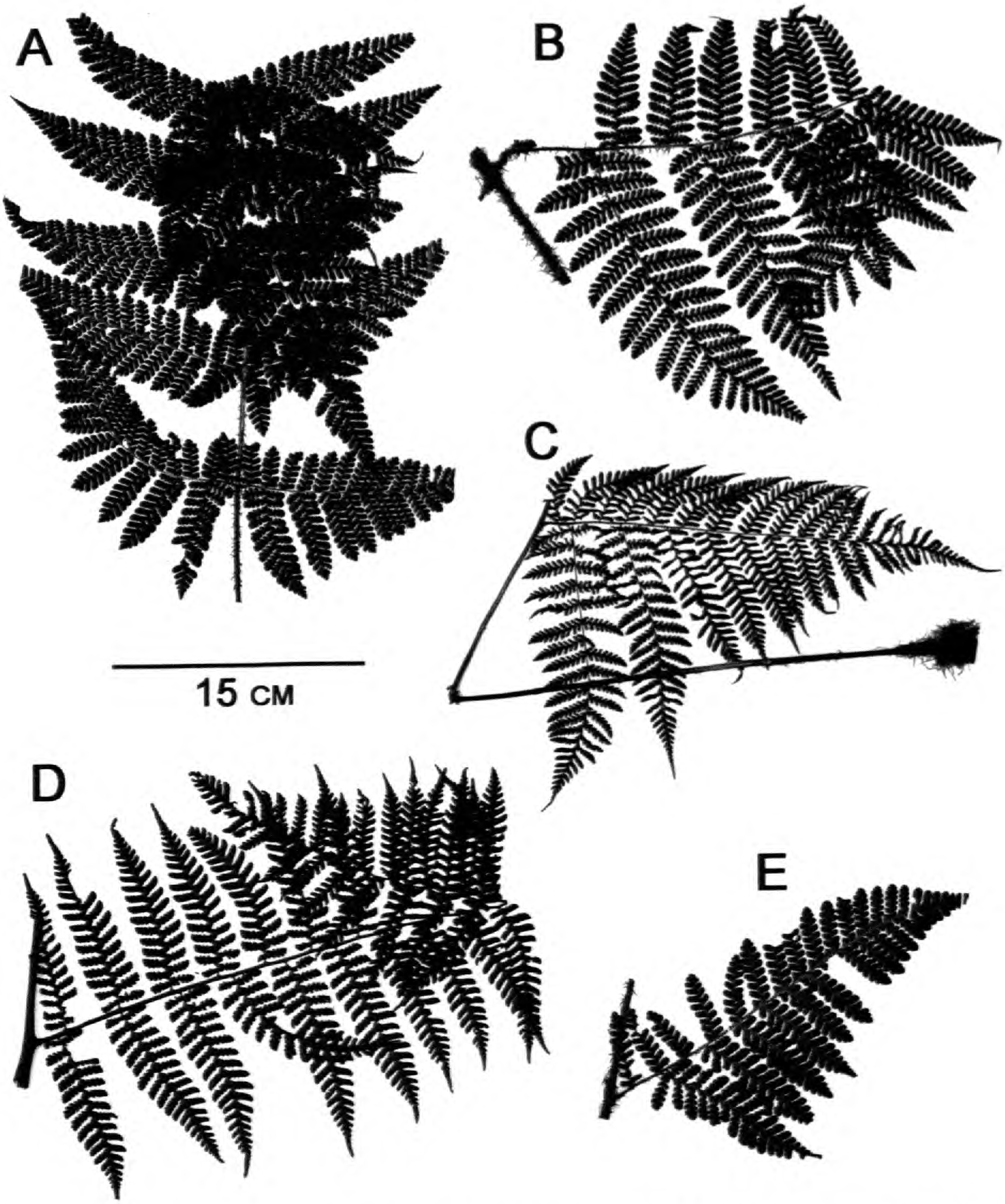

FIG. 6. Lamina dissection in the four indusiate species of Andean *Megalastrum*. A. Leaf, *M. andicola*. B. Basal pinna, *M. andicola*. C. Basal pinna, *M. crenulans*. D. Medial pinna, *M. acrosorum*. E. Basal pinna, *M. insigne*. A: *Linden 243* (K). B: *Núñez & Huaylla 279* (MO). C: Brazil, *Handro 2224* (US). D: *Moran 3567* (NY). E: *Øllgaard & Navarrete 1630* (AAU).

0.3 mm long, 2- or 3-celled, adaxially the hairs 0.3–0.5 mm long, 2–4-celled; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1–3-celled, ascending to spreading; **indusia** < 0.2 mm wide, circular, fugacious and usually seemingly absent, eglandular, pubescent by whitsh acicular hairs ca. 0.1 mm long; **spores** echinulate.

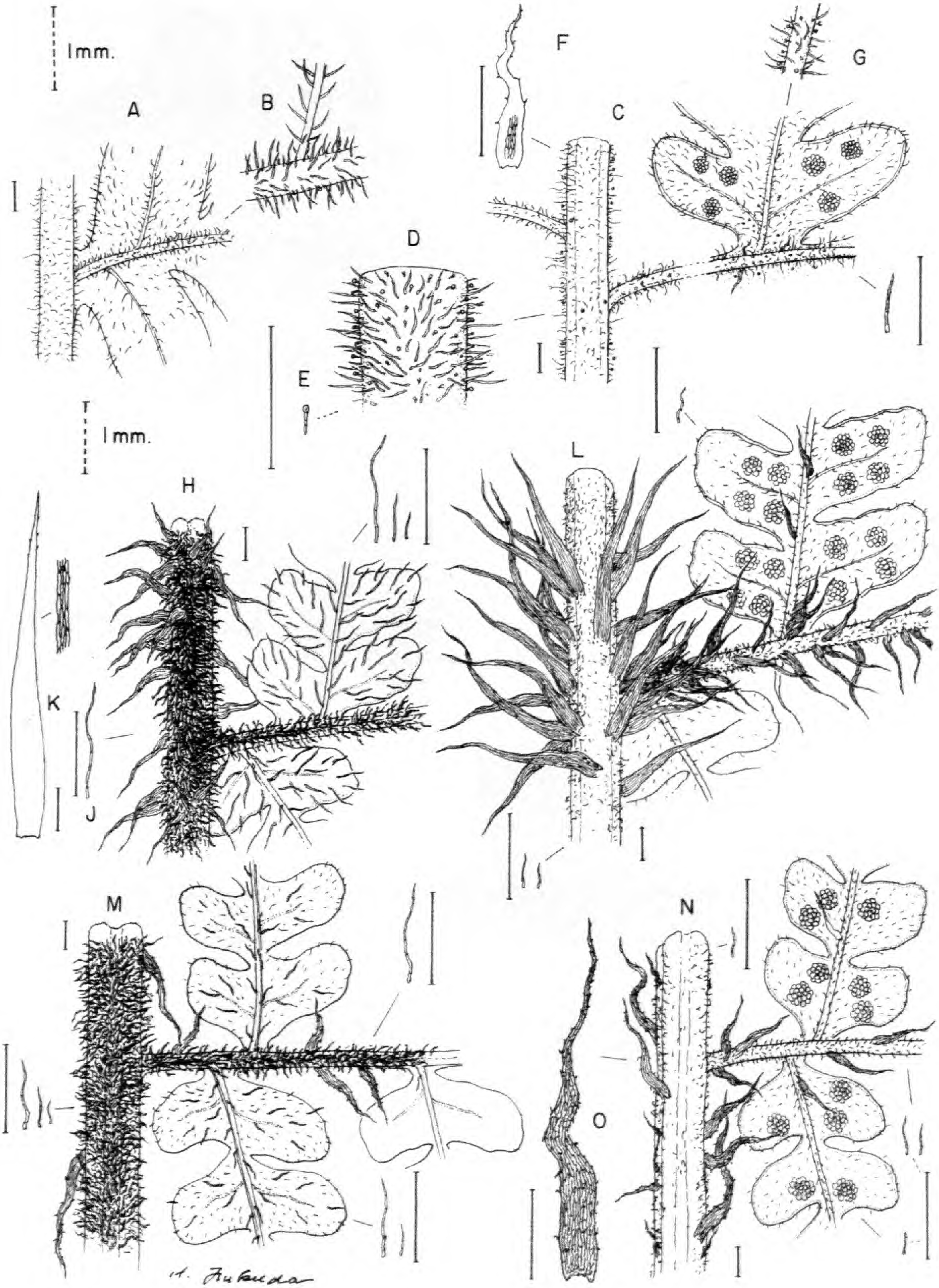

FIG. 7. Indument of three species of Andean *Megalastrum*. A–G. *M. adenopteris*. A. Adaxial surface of pinna rachis and pinnule. B. Detail of costular hairs. C. Abaxial surface of pinna rachis, costule, and pinnule. D. Pinna rachis. E. Glandular hair. F. Scale from pinna rachis. G. Details of hairs on costule. H–L. *M. rhachisquamatum*. H. Adaxial surface of pinna rachis, costule, and pinnule. J. Pinna rachis hair. K. Scale detail. L. Abaxial surface of pinna rachis, costule, and

Distribution.—Peru, Bolivia, northern Argentina, southeastern Brazil; 750–2100 m.

Selected Specimens Examined.—PERU. **Ayacucho**: Aina, between Huanta and Río Apurimac, 750–1000 m, [12°56′S, 74°15′W], 7–17 May 1929, *Killip & Smith 22779* (US). **Cusco**: Distr. Urubamba, en el camino del proyecto arqueológico Mando-Paturusi, ca. 115 km de Cusco, en Machupicchu, 2100 m, 13°09′S, 72°31′W, 4–6 Apr 1988, *Núñez V. 8929* (AAU, F, MO, NY, UC). **Huánuco**: Cochero, [9°35′S, 75°51′W], s.d., *Dombey s.n.* (P).

BOLIVIA. **Chuquisaca**: Herando Siles, 1575 m, 20°20′16″S, 62°02′42″W, 23 Dec 2005, *Serrano et al. 6873* (MO). **La Paz**: Prov. Nordyungas, Polo-Polo bei Coroico, [16°10′S, 67°43′W], Jun–Jul 1912, *Buchtien 3598* (BM, F, S, US). **Santa Cruz**: Valle Grande, 12 km de Loma Larga a Masicurí, 1250 m, 18°47′S, 63°57′W, 21 May 1996, *Kessler et al. 5971* (GOET, UC). **Tarija**: Aniseto Arce Ruíz, Campamento de guardaparques Sidras, senda La Cascada, 890 m, 22°14′S, 64°32′W, 19 Jun 2004, *Jiménez et al. 2468* (UC).

ARGENTINA. **Salta**: Parque Nacional El Rey, [24°41′S, 64°36′W], 21 Mar 1981, *Brown 1339* (MO, NY). **Tucumán**: Depto. Tafí, Quebrada de Cainzo, 900 m, [26°49′S, 65°37′W], 18 Nov 1951, *Sleumer 2097* (BM).

Megalastrum adenopteris has several distinctive characters that, in combination, make it easy to identify. The species is characterized by large, highly divided leaves and laminae on both surfaces between the veins densely and evenly pubescent. The hairs are often gland-tipped with the terminal cell enlarged or globose, yellowish or orangish. The veins tips are slender, not enlarged and hydathodous as is typical in the genus. The indusia are distinctive by being minute (< 0.2 mm wide) and pubescent. After drying and contracting, they often appear as a tuft of whitish acicular hairs in the center of the sorus. This species is a member of the *M. pulverulentum* group.

3. Megalastrum alticola M. Kessler & A. R. Sm., Amer. Fern J. 96:36. 2006. Type.—BOLIVIA. **La Paz**: Prov. Nor Yungas, 2 km de Chuspipata hacia Coroico, 16°22′S, 67°49′W, 2900 m, 17 Sep 1997, *M. Kessler 11945* (holotype: UC! [barcode 1621224, 1621225]; isotypes: GOET!, LPB-n.v.). **Figs. 5C, 9F–K, 10D.**

Rhizomes erect, the scales 6.0–10.0 × 1.0–2.0 mm, ascending, linear-lanceolate, brown, dull, flat, sparsely denticulate; **leaves** 1.0–2.5 m long; **petiole base scales** 10.0–15.0 × 1.0–1.5 mm, spreading to ascending, linear-lanceolate, brown, dull, lustrous, flat, not tortuous, denticulate, the teeth simple or sometimes bifid; **laminae** up to ca. 1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs

---

←

pinnule. M–O. *M. decompositum*. M. Adaxial surface of pinna rachis, costule, and pinnules. N. Abaxial surface of pinna rachis, costule, and pinnules. O. Detail of rachis scale. Scale bars = 1 mm. A–G: from Brazil, isolectotype, *Jürgens s.n.* [Rosenstock Filices Austrobrasilienses no. 207] (S). H–L: Isotype, *Palacios 5844* (MO). M–O: Isotype, *van der Werff et al. 12482* (MO).

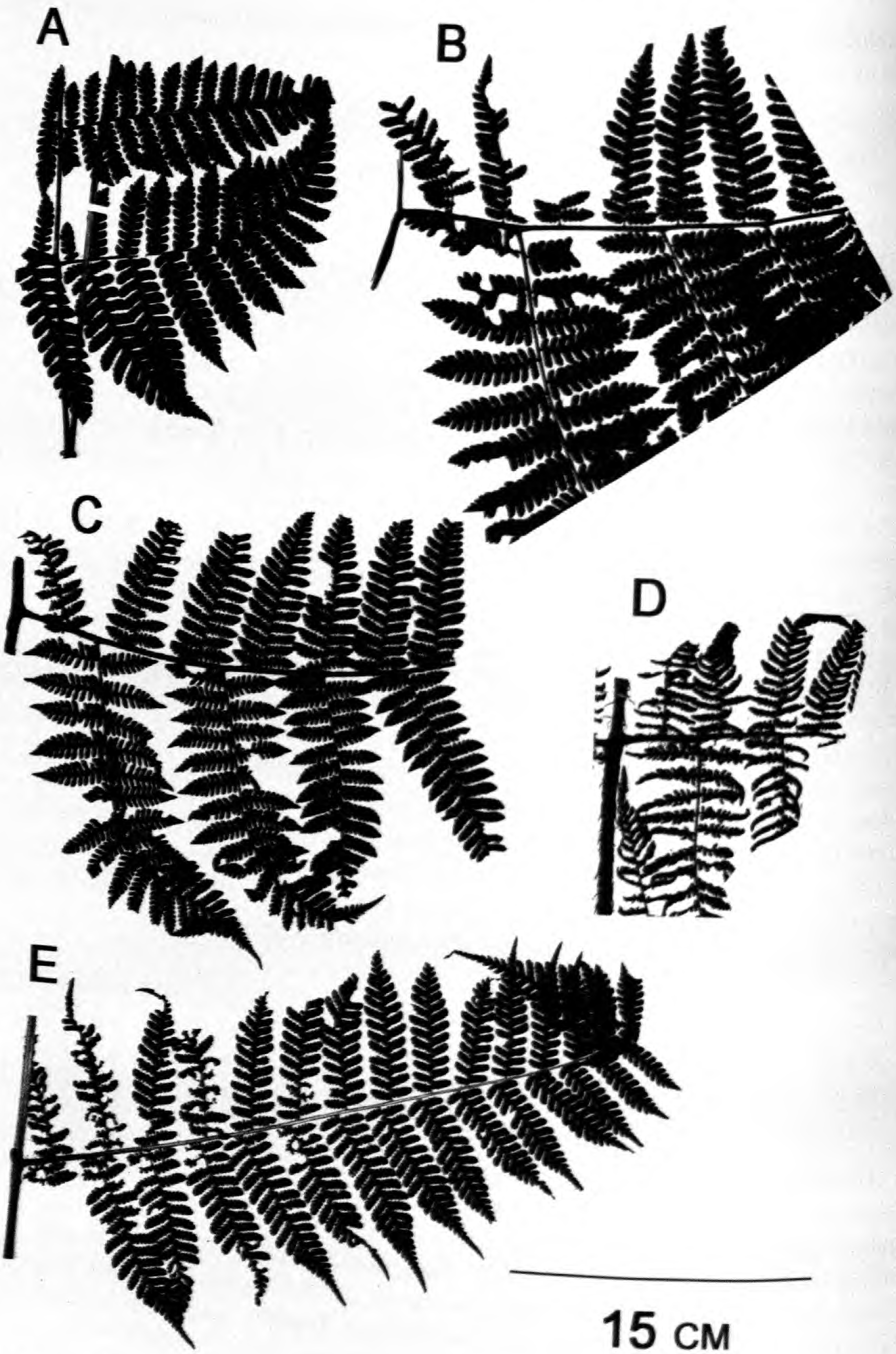

FIG. 8. Lamina dissection in the four Andean species of the *Megalastrum* "pulverulentum" group. A. Proximal pinnae, *M. nanum*. B. Proximal part of basal pinna, *M. adenopteris*. C. Proximal part of basal pinna, *M. pulverulentum*. D. Proximal part of basal pinna, *M. clathratum*. E. Basal pinna, *M. pulverulentum*. A: Holotype, *Moran 5917* (AAU). B: Brazil, *Venturi 886* (US). C: West Indies, *Ekman 5747* (NY). D: Holotype, *van der Werff et al. 23175* (MO). E: *Spruce 5257A* (K).

abaxially; **basal pinnae** 20–30 cm long, inequilateral, longer basiscopically; **pinna rachises** abaxially eglandular, pubescent, scaly, the hairs 0.2–0.4 mm long, 3–5-celled, spreading to slightly ascending and tortuous, the scales denticulate, sometimes with bifid teeth, spreading to ascending or appressed, 2.5–7.0 × 0.5–1.0 mm, lanceolate to linear-lanceolate, brown to light brown, lustrous, not clathrate, not bullate, adaxially very sparsely glandular, densely pubescent, sparsely scaly, the glands ca. 0.1 mm long, sessile, brownish, the hairs 0.6–1.0 mm long, 4–7-celled, spreading to antrorsely strigose, scales like those on the abaxial surfaces; **costules** abaxially rarely glandular, pubescent, scaly, the glands ca. 0.1 mm, sessile, globose, yellowish, the hairs 0.2–0.4 mm long, 2- or 3-celled, spreading, scales 0.5–1.0 × 0.2–0.3 mm, spreading to loosely appressed, lanceolate, entire to denticulate, adaxially eglandular, sparsely to moderately pubescent, scales absent, the hairs 0.4–0.7 mm long, 2–5-celled, antrorsely strigose; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** surfaces abaxially visible, obscure adaxially, eglandular, abaxially pubescent, the hairs 0.1–0.2 mm long, 1- or 2-celled, spreading to ascending, adaxially the hairs absent or 0.2–0.5 mm long, 3–5-celled, spreading; **lamina margins** eglandular, ciliate, the hairs 0.1–0.3 mm long, 1- or 2-celled, ascending; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru, Bolivia; 1600–3400 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Cotopaxi**: Cantón Sigchos, bosque en sucesión, dosel ca. 8 m, por fuente de agua, 3400 m, 0°35′40″S, 78°49′54″W, 21 Jul 2003, *Ramos et al. 6371* (MO, QCNE). **Imbabura**: Carretera Otavalo-Selva Alegre, 2800–3200 m, [0°14′N, 78°16′W], 13 Feb 1989, *van der Werff & Palacios 10570* (MO, MICH, QCNE). **Morona-Santiago**: road Plan de Milagro-Gualaceo, Km 10.8, 2200–2250 m, 3°00′S, 78°32′W, 24–25 Nov 1997, *Øllgaard & Navarrete 2755* (AAU, QCA). **Pichincha**: Valle de Lloa, 2800 m, [0°15′S, 78°34′W], 1919, *Mille s.n.* (GH, NY, P, S).

PERU. **Cusco**: Prov. La Convención, Distr. Huayopata, Huyro, Calquiña, 1750 m, 12°58′51″S, 72°03′31″W, 27 Jun 2003, *Bonino et al. 746* (MO, NY, UC). **Huánuco**: Cushi, 1600 m, [9°51′0″S, 75°41′0″W], 19–23 Jun 1923, *MacBride 4855* (F, US). **Junín**: Chanchamayo, Chilpez ca. 26 km of San Ramón, 1720–1850 m, 10°16′S, 75°22′W, 19 Oct 1982, *Smith & Palacios 2639* (F, MO). **Pasco**: Oxapampa, Distr. Huancabamba, Sector Quebrada Yanachaga (Parque Nacional Yanachaga-Chemillen), 2260 m, 10°23′45″S, 75°28′55″W, 18 Sep 2004, *Mellado & Becerra 1803* (MO); idem, 2410 m, 10°23′20″S, 75°28′26″W, 20 Sep 2004, *Mellado & Becerra 1835* (MO).

BOLIVIA. **Cochabamba**: Prov. Tiraque, El Limbo, 2180 m, 17°09′39.4″S, 65°37′18″W, 21 Aug 2003, *Zabalaga 1282* (NY). **La Paz**: Coroico, Nor Yungas, estrada de Coroico para Caranavi, Próximo a Chuspipata, 3000 m, 16°17′48″S, 67°48′46″W, 27 Feb 2008, *Labiak 4730* (NY, UPCB).

Among the large decompound species of the genus, *Megalastrum alticola* is characterized by pinna rachises abaxially pubescent and with lanceolate brown scales, the scales relatively large (2.5–7.0 × 0.5–1.0 mm), and the laminar tissue between the veins glabrous on both surfaces. The species most

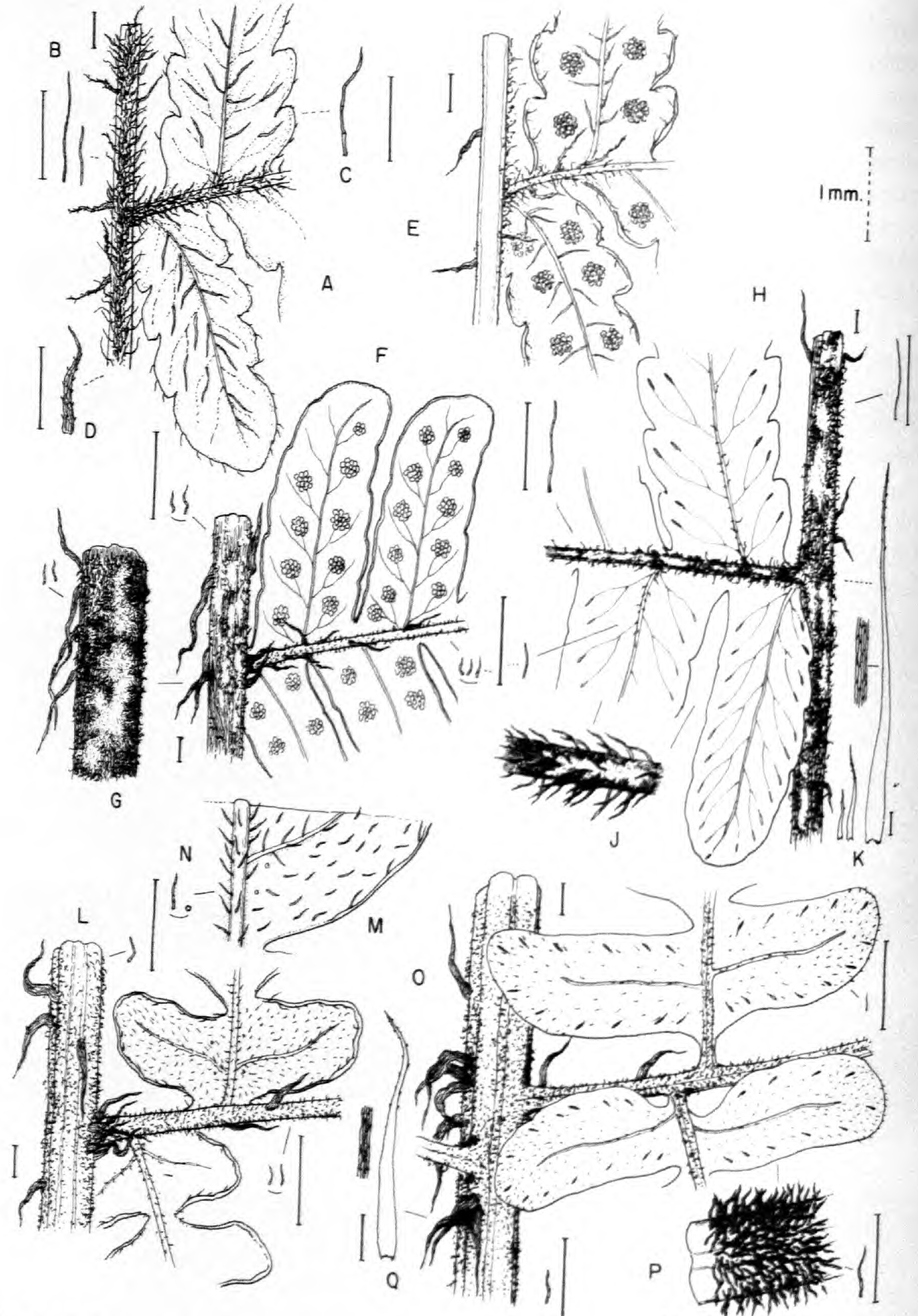

FIG. 9. Indument of three species of Andean *Megalastrum*. A–E. *M. marginatum*. A. Adaxial surface of pinna rachis, costules, and pinnules. B. Rachis hairs. C. Hair from vein. D. Rachis scale. E. Adaxial surface of pinna rachis, costules, and pinnules. F–K. *M. alticola*. F. Adaxial surface of pinna rachis, costules, and pinnules. G. Detail of lamina rachis. H. Adaxial surface of pinna rachis, costules, and pinnules. J. Pinna rachis with hairs. K. Abaxial surface of pinna rachis, costule, and

resembles *M. squamosissimum,* which differs by pinna rachises glabrous abaxially. *Megalastrum alticola* is less scaly than *M. squamosissimum*, and this is evident on the rachis of the leaf, which has widely spreading conspicuous scales in *M. squamosissimum*, but only a few scattered appressed scales in *M. alticola.*

4. **Megalastrum andicola** (C. Chr.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [published 3 May 1988]. *Nephrodium villosum* var. *opacum* Mett. ex Hieron. f. *opacum* Hieron., Bot. Jahrb. Syst. 34:446. 1904, "var. *opaca*", "f. *spruceanum*". *Dryopteris andicola* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math Afd., ser. 8, 6:88. 1920. *Dryopteris andicola* C. Chr. f. *spruceana* (Hieron.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math Afd., ser. 8, 6:89. 1920. *Ctenitis andicola* (C. Chr.) Ching, Sunyatsenia 5:250. 1940. TYPE.—ECUADOR. Pastaza: Canelos [1°30′S, 78°03′W], s.d., *R. Spruce 5295 pro parte* [mixed with *M. insigne*] (lectotype, designated by Christensen, 1920: B! [barcode 20 0052340], B! [barcode 20 0052341]; isolectotype: P! [barcode 000610853]). **Figs. 5D, 6A,B, 11M–T, U–D′.**

Dryopteris villosula C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math Afd., ser. 8, 6:89. 1920, stat. nov. for *D. villosa* var. *inaequalis*. *Dryopteris villosa* (L.) Kuntze var. *inaequalis* Gilbert, Bull. Torr. Bot. Club 24:259. 1897. *Ctenitis villosula* (C. Chr.) Ching, Sunyatsenia 5:250. 1940. *Megalastrum villosulum* (C. Chr.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:129. 1987 [published 3 May 1988]. TYPE.—BOLIVIA. La Paz: Prov. Nor Yungas: Uchumachi [coordinates unknown], 22 Aug 1894, *M. Bang 2394* (lectotype, here designated: NY! [barcode 579283]; isolectotypes: B! (fragm.) [barcode 20 0069338] BM! [barcode 000907834], *pro parte* (mounted with *M. adenopteris*), GH!, MICH!, MO! [accession 1872834], NY! [barcode 00579283, 00579284], US! [accession 32988]).

Nephrodium villosum L. var. *opacum* Mett. ex Hieron. f. *lehmannianum* Hieron, Bot. Jahrb. Syst. 34:446. 1904. *Dryopteris andicola* C. Chr. f. *lehmanniana* (Hieron.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math Afd., ser. 8, 6:89. 1920. *Megalastrum andicola* (C. Chr.) A. R. Sm. & R. C. Moran f. *lehmannianum* (Hieron.) Stolze, Fieldiana, Bot., n.s. 27:19. 1991. TYPE.—COLOMBIA. Cundinamarca: Fusagasuga [4°20′N, 74°21′W], 1800–2400 m, Jan 1892, *F. C. Lehmann 7369* (lectotype, designated by Tryon and Stolze, 1991: B! [barcode 20 0052347]; isolectotypes K!, US! [accession 1424842]).

Rhizomes erect to decumbent, scales 10.0–15.0 × 0.6–1.0 mm, appressed to ascending, lanceolate, brown, dull, flat, sparsely denticulate; **leaves** 0.9–2.5 m

---

←

pinnules. L–Q. *M. vastum*. L. Detail of hairs on costule and segments. M. Adaxial surface of pinna rachis, costule, and pinnules. N. Rachis scale. Scale bars = 1 mm. A–E: *Krömer et al. 100* (UC). F–K: *MacBride 4855* (F). K–O: *Balslev et al. 1693* (NY).

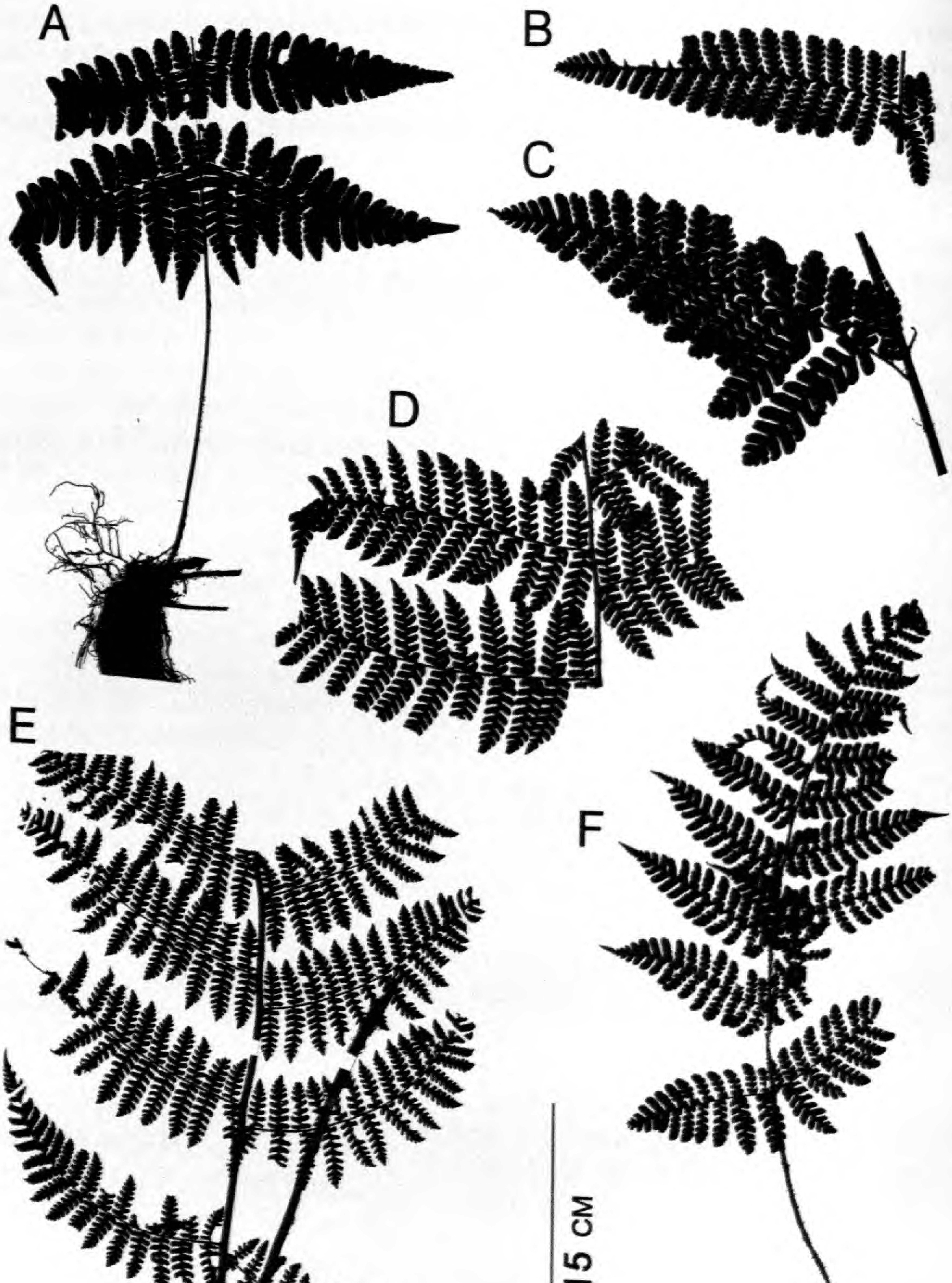

FIG. 10. Leaf dissection in three species of *Megalastrum*. A. Proximal pinnae, *M. marginatum*. B, C. Medial pinna and basal pinna, *M. obtusum*. D. Medial pinnae, *M. alticola*. E. Proximal half of lamina, *M. falcatum*. F. Leaf, *M. fimbriatum*. A: *Bach 1234* (UC). B, C: Isotype, *Ankersen & Kragelund 211* (AAU). D: *Mellado & Beccera 1835* (MO). E: *Øllgaard & Navarette 105854* (AAU). F: Isotype, *Young & León 4958* (AAU).

long; **petiole base scales** like those of the rhizomes but more spreading; **laminae** 0.5–0.8 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** abaxially pubescent by glandular hairs 0.1 mm long; **basal pinnae** 15.0–40.0 cm long, strongly inequilateral; **pinna rachises** abaxially glandular, densely pubescent, sparsely scaly, the glands ca. 0.1 mm long, spherical, sessile and stipitate, yellowish, the hairs 0.1–0.5 mm long, 2–4-celled, acicular, erect to spreading, the scales ca. 4.0–7.0 × 0.5–0.8 mm, light brown to golden brown, denticulate apically, lanceolate, firm, lustrous, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.5–1.2 mm long, 5–8-celled, spreading to ascending, acicular, the scales like those of the pinna rachises abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially sparsely glandular, sparsely to moderately pubescent, the glands 0.1 mm, sessile, spherical, yellowish, the hairs 0.1–0.5 mm long, 1–4-celled, acicular, ascending to erect, adaxially sparsely glandular, sparsely pubescent, the glands similar to those abaxially, the hairs 0.3–1.0 mm long, 3–6-celled, acicular, ascending to erect; **laminar tissue between veins** abaxially densely to sparsely glandular, sparsely to densely puberulent, the glands ca. 0.1 mm, stalked to sessile, yellowish, the hairs ca. 0.1 mm long, 1- or 2-celled, erect, acicular, more common near the axes, adaxially eglandular, sparsely to densely pubescent, the hairs similar to those abaxially; **ultimate veins** visible on both surfaces, abaxially with sessile glands, sparsely puberulent, the glands and hairs like those of the costules, adaxially sparsely pubescent, the hairs 0.3–0.5 mm long, 2–4-celled, spreading to ascending; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1–3-celled, acicular, ascending; **indusia** present, 0.5–1.0 mm wide, conspicuous, circular, glandular, sparsely pubescent, the glands 0.1 mm long, spherical, sessile to stalked, the hairs 0.1–0.2 mm long, 2-celled, acicular, erect, hyaline; **spores** cristate.

Distribution and ecology.—Colombia, Ecuador, Peru, Bolivia; 1400–2400 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Aguadita, [5°21′N, 75°21′W], 14 Jul 1934, *Guevara 75* (US). **Boyacá**: Carretera Chiquinquirá a Pauna, Puente de Piedra, 2050 m, [5°41′N, 74°01′W], 13 Oct 1967, *Jaramillo et al. 3517* (NY). **Cundinamarca**: Bosques de El Ermitaño, al S del Salto del Tequendama, 2200–2300 m, [4°37′N, 74°21′W], 18 May 1959, *Uribe 3286* (US). **Province Unknown**, 1842, *Linden 843* (BM, K, P).

PERU. **Cusco**: La Convención, above Qillouno, 2300 m, 12°28′35″S, 72°29′15″W, 29 Apr 2006, *van der Werff et al. 21118* (MO, NY).

BOLIVIA. **Carrasco**: Cochabamba, Localidad Dianpampa, 2160 m, 17°40′53″S, 64°40′55″W, 4 Sep 2003, *Fernández et al. 2362* (MO). **Cochabamba**: Prov. Ayopaya, comunidad Pampa Grande, subiendo por el sendero río arriba, pasando la primera área de cultivo, 2150 m, 16°40′S, 66°28′W, 7 Sep 2002, *Jiménez & Moguel 1428* (UC). **La Paz**: Prov. Franz Tamayo, Parque Nacional Madidi, senda Keara-Mojos, abajo de Fuertecillos, 2020 m, 14°35′S, 68°56′W, 6 Nov 2001, *Jiménez & Gallegos 877* (GOET, UC). **Santa Cruz**: Manuel M. Caballero, El Cocotal sobre el camino a San Mateo a 8.5 km del

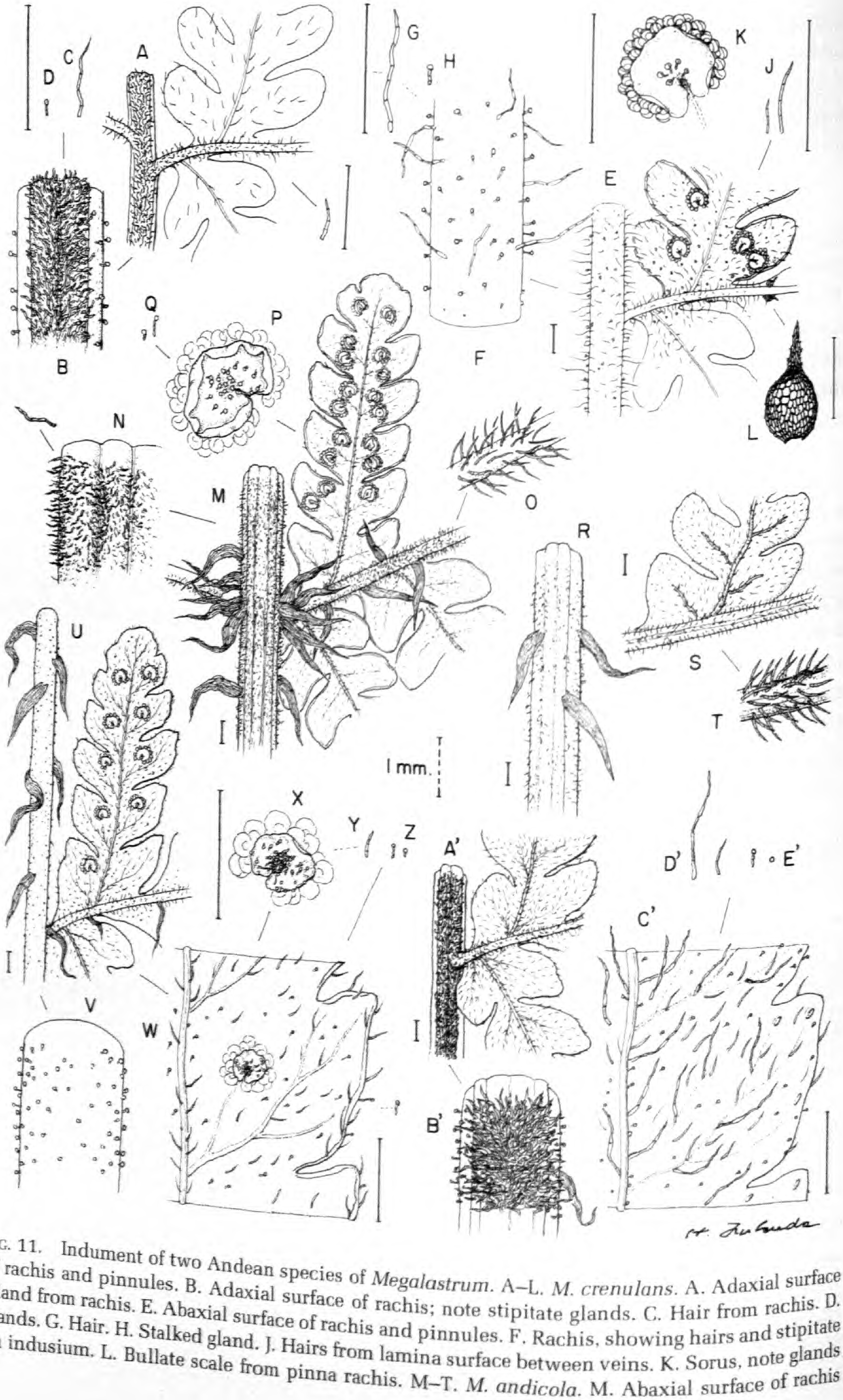

FIG. 11. Indument of two Andean species of *Megalastrum*. A–L. *M. crenulans*. A. Adaxial surface of rachis and pinnules. B. Adaxial surface of rachis; note stipitate glands. C. Hair from rachis. D. Gland from rachis. E. Abaxial surface of rachis and pinnules. F. Rachis, showing hairs and stipitate glands. G. Hair. H. Stalked gland. J. Hairs from lamina surface between veins. K. Sorus, note glands on indusium. L. Bullate scale from pinna rachis. M–T. *M. andicola*. M. Abaxial surface of rachis

cruce El Empalme, 2285 m, 17°48′15″S, 64°42′12″W, 21 Jun 2003, *Núñez & Huaylla 279* (MO, NY); Valle Grande, 5 km de Loma Larga a Valle Grande, 2100 m, 18°43′S, 63°54′W, 8 Jun 1996, *Kessler et al. 6379* (UC). **Yungas**, Uchimachi, 22 Aug 1894, *Bang 2394* (B, GH, MICH, MO, NY, US).

Megalastrum andicola is distinguished by indusia present and pinna rachis scales firm, denticulate apically, and lustrous. This species most resembles *M. acrosorum*, which differs by pinna rachises thin, flaccid, entire, and dull. Specimens from Bolivia tend to have laminae on both surfaces more glandular with gland-tipped hairs intergrading with sessile spherical ones. Such specimens have been segregated as *M. villosulum*; however, *M. andicola* s.s. is also glandular between the veins. The difference is only a matter of degree, and therefore *M. villosulum* is here placed in synonymy.

Lindig 159 and *Spruce 5295 pro parte* (B) have conspicuously bicolorous indusia with pale, thin outer edges, but this character does not appear in the remainder of the material and is not a diagnostic. *Øllgaard 99562* (AAU) from Napo, Ecuador, differs from other collections by having spreading scales on the petioles and pinna rachises. *Spruce 5295* is a mixed collection including *Megalastrum andicola* as well as *M. insigne*. Duplicates of *Spruce 5295* at BM, K, NY, and P are referable to *M. insigne*; only the specimens at B are *M. andicola*.

For *Dryopteris villosula* var. *inaequalis*, here listed in synonymy, we designate a lectotype here because Gilbert (1897) did not cite a herbarium and Christensen cited only syntypes (B, US). Kessler and Smith (2006) reported a holotype and isotypes: but these designations are not effective lectotypification because they did not say "here designated," nor are they inferential lectotypification according to Article 7.10 of the *Code* (McNeill *et al.* 2012) because the publication appeared after 2001.

The lectotype designated by Stolze (1991) for *Nephrodium villosum* var. *opaca* Hieron. is superfluous because of the earlier designation by Christensen (1920).

5. **Megalastrum aureisquama** M. Kessler & A. R. Sm., Amer. Fern J. 96:37, fig. 1H–K. 2006. Type.—BOLIVIA. Cochabamba: Prov. Carrasco, 137 Km antigua carretera Cochabamba-Villa Tunari, 17°06′S, 65°35′W, 1600 m, 18 Jul 1996, *M. Kessler, T. Krömer, J. Gonzales, B. Hibbits & I. Jiménez 7379* (holotype: UC! [barcode 1614951, 1614952]; isotypes: GOET!, LPB-n.v.). **Figs. 12G–K, 13C, 14A.**

←

and pinnules. N. Abaxial surface of rachis showing puberulence. O. Hairs on abaxial surface of pinna rachis. P. Sorus, note glands on indusium. Q. Stipitate glands. R. Abaxial surface of rachis. S. Abaxial surface of pinnule. T. Hairs on pinna rachis. U–D′. *M. andicola*. U. Abaxial surface of rachis and pinnule. V. Stipitate glands on rachis. W. Detail of indument. X. Sorus, note glandular indusium. Y. Hair from indusium. Z. Stipitate glands from abaxial surface between veins. A′. Adaxial surface of rachis and pinnules. B′. Adaxial surface of rachis. C′. Indument detail. D′. Hairs. E′. Glands. All scale bars = 1 mm. A–L: from Brazil, *Jürgens s.n.* [Rosenstock Filices Austrobrasilienses no. *206*] (UC). M–T: *Mejia et al. 3517* (NY). U–D′: *Kessler et al. 6379* (UC).

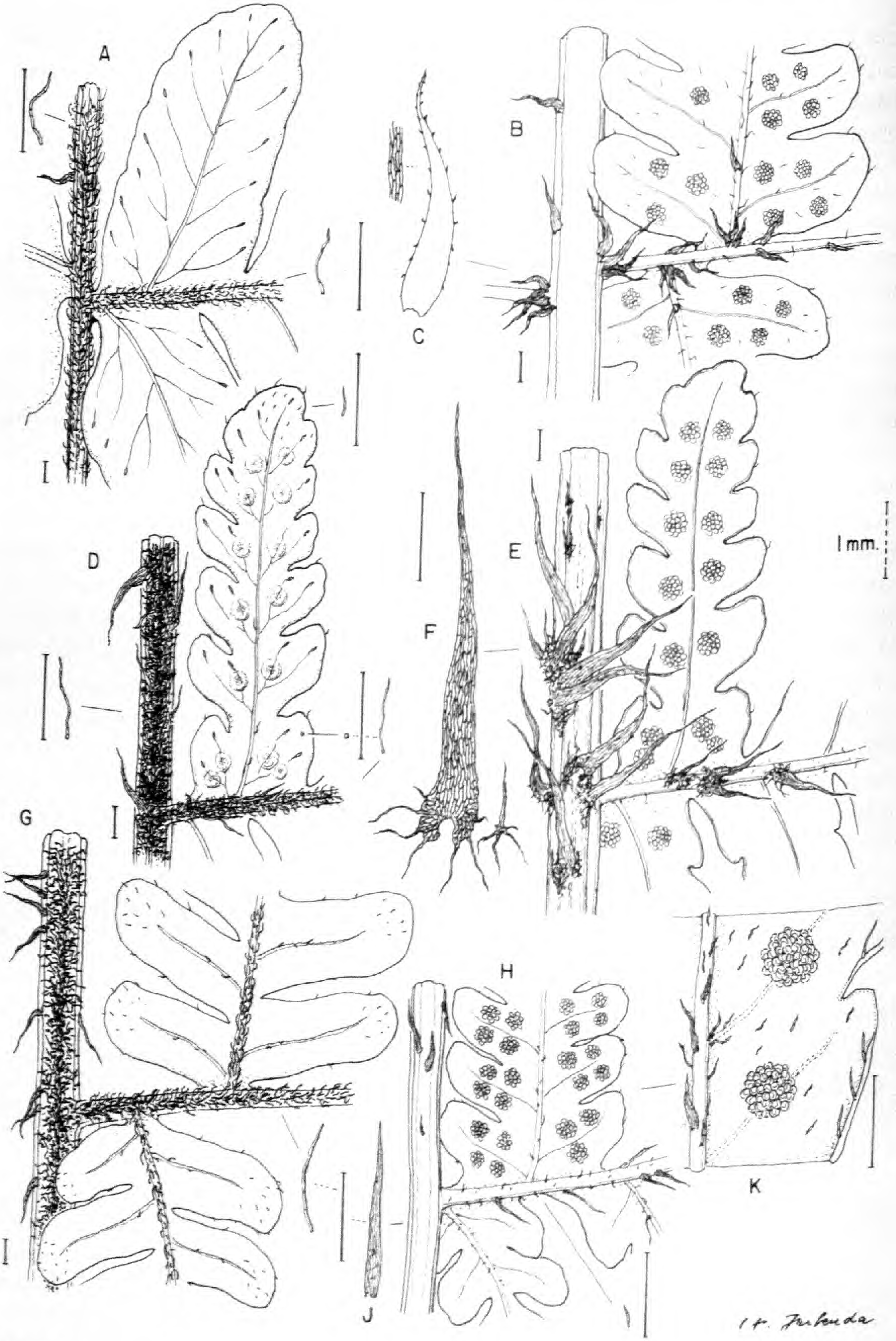

FIG. 12. Indument of three species of Andean *Megalastrum*. A–C. *M. rupicola*. A. Adaxial surface of pinna rachis, costule, pinnules. B. Abaxial surface of pinna rachis, costule, pinnules. C. Rachis scale. D–F. *M. squamosissimum*. D. Adaxial surface of pinna rachis, costule, and pinnule. E. Abaxial surface of pinna rachis, costule, and pinnules. F. Rachis scale. G–K. *M. aureisquama*. G.

Rhizomes erect, scales 5.0–15.0 × 0.5–1.2 mm, ascending to appressed, lanceolate, dark brown, lustrous to dull, flat to twisted, denticulate; **leaves** 1.0–2.0 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.4–1.0 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 30.0–50.0 cm long, inequilateral, elongated basiscopically; **pinna rachises** abaxially eglandular, without hairs or rarely pubescent distally, scaly, the hairs (when present) 0.2–0.8 mm long, 2- or 3(–6)-celled, appressed to erect, acicular, the scales 3.0–5.0 × 0.3–0.5 mm, entire or nearly so, golden brown, flat, lax, not clathrate, not bullate, adaxially densely pubescent, sparsely scaly, the hairs 0.8–1.5 mm long, 5–8-celled, the scales like those of the pinna rachises abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, glabrous to sparsely pubescent, scaly, the hairs like those of the pinna rachises, the scales 0.8–2.0 × ca. 0.3 mm, like those of the pinna rachises, adaxially pubescent, scales absent, the hairs 0.8–1.5 mm long, 5–8-celled abaxially; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, glabrous to rarely sparsely pubescent, the hairs 0.2–0.3 mm long, 1- or 2-celled, like those on the pinna rachises abaxially, adaxially eglandular, sparsely pubescent mostly on the distal veins, the hairs 0.3–0.5 mm long, 1–3-celled; **lamina margins** eglandular, sparsely ciliate, the hairs 0.1–0.3 mm long, 2- or 3-celled, acicular, substrigose, ascending; **indusia** absent; **spores** cristate.

Distribution and ecology.—Peru, Bolivia; 1300–2900 m.

SELECTED SPECIMENS EXAMINED.—PERU. **Cusco**: Distr. Sta. Ana, Tunquimayo, 2200 m, 12°54′31″S, 72°48′45″W, 27 Sep 2004, *Calatayud et al. 2911* (MO, NY); La Convención, above Qillouno, 2300 m, 12°28′35″S, 72°29′15″W, 29 Apr 2006, *van der Werff et al. 21125* (MO); idem, Distr. Sta. Ana, Poromate, 2118 m, 12°55′S, 72°47′W, 13 Jun 2003, *Calatayud et al. 1401* (MO). **Junín**: Chancamayo, Río Rondayacu, 45 km from San Ramón, 1880–1950 m, 11°20′S, 72°20′W, 15 Oct 1982, *Smith et al. 2615 p.p.* (MO).

BOLIVIA. **Cochabamba**: José Carrasco Torrico, 113 km antigua carretera a Cochabamba-Villa Tunari, 2900 m, 17°07′S, 65°38′W, 3 Jul 1996, *Kessler et al. 6908* (UC).

Among the large decompound species of the genus, *Megalastrum aureisquama* is distinctive by its pinna rachises abaxially without hairs and pinna rachis scales that are linear, straightish, ascending, golden brown, and entire or nearly so. This species resembles *M. subincisum* from northern Venezuela and Colombia and can be distinguished morphologically by dark brown, shorter

---

←

Adaxial surface of pinna rachis, costule, pinnules. H. Abaxial surface of pinna rachis, costule, pinnules. J. Rachis scale. K. Detail of costule and pinnule lobes. Scale bars = 1 mm. A–C: Holotype, *Quintana et al. 41* (UC). D–F: Isotype *Spruce 5262* (NY). G–K: *Calatayud et al. 1401* (MO).

FIG. 13. Leaf dissection in seven species of Andean *Megalastrum*. A. Proximal part of basal pinna, *M. praetermissum*. B. Proximal part of basal pinna, *M. tepuiense*. C. Basal pinnae, *M. aureisquama*. D. Basal pinna, *M. subtile*. E. Basal pinnae, *M. rupicola*. F. Basal pinna, *M. martinicense*. G. Basal pinna, *M. oellgaardii*. A: *Fay & Fay 4232* (MO). B: Holotype, *Steyermark 85913* (VEN). C: *van der Werff et al. 21125* (MO). D: *Moran 7608* (NY). E: *Kessler et al. 9900* (UC). F: West Indies, *Morton 6000* (NY). G: Holotype, *Øllgaard et al. 2219* (AAU).

(5.0–15.0 mm long) rhizome scales (vs. 20–25 mm long, golden brown in *M. subincisum*) and ultimate veins sparsely pubescent, especially distally (vs. glabrous in *M. subincisum*). In Bolivia, similar is *M. marginatum*, but that species differs by the pinna rachis scales shorter (2–4 mm long), darker, and more denticulate.

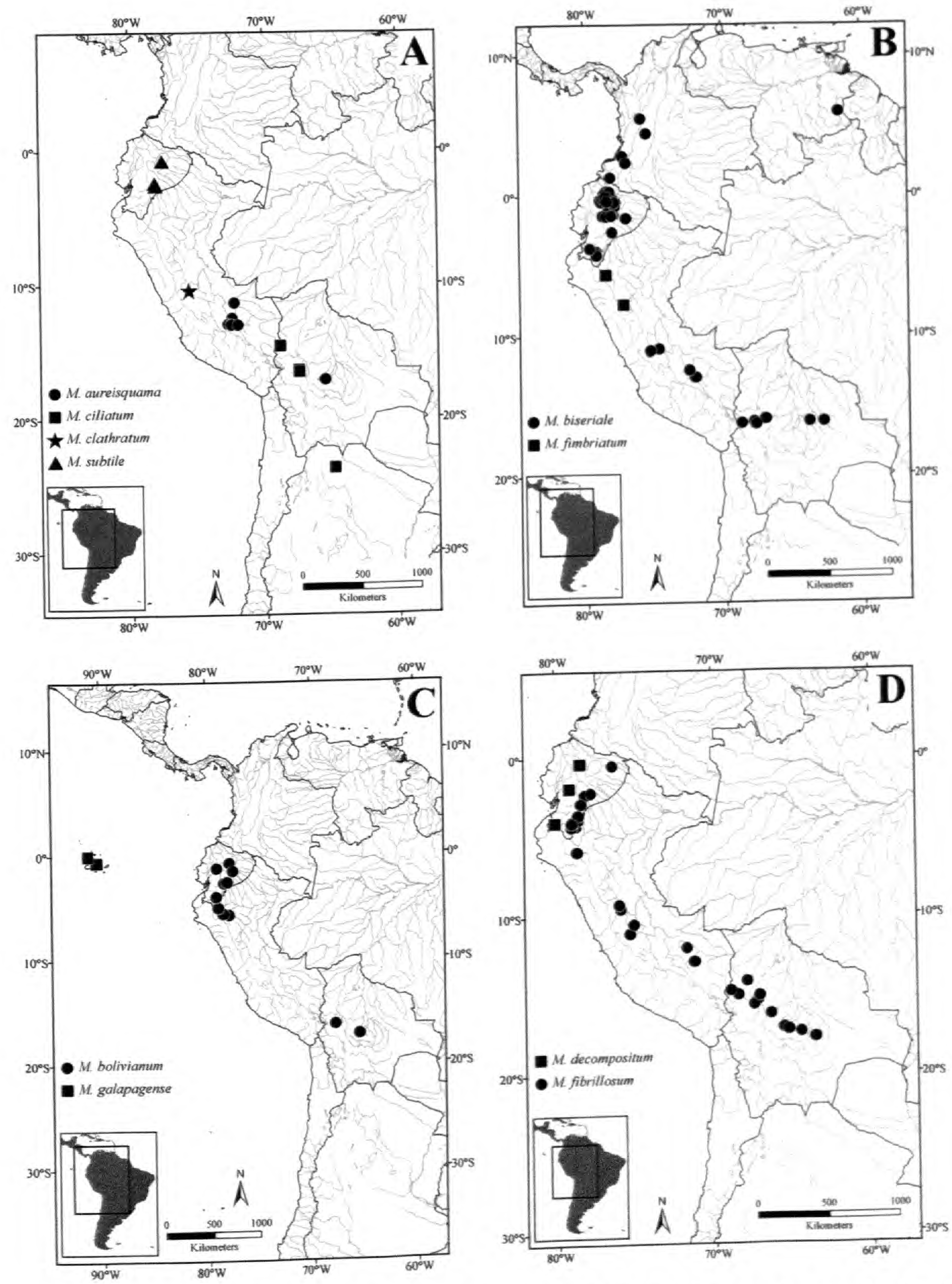

FIG. 14. Distribution of ten species of *Megalastrum* in the Andes. Some species are also known from areas outside the Andean region as here defined; for the worldwide distribution of a species, see under each species description.

6. **Megalastrum biseriale** (Baker) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [published 3 May 1988]. *Polypodium biseriale* Baker, Syn. Fil. 309. 1867. *Nephrodium biseriale* (Baker) Diels, Nat. Pflanzenfam. 1(4):170. 1899. *Dryopteris biserialis* (Baker) C. Chr., Index Filic. 254. 1905. *Ctenitis biserialis* (Baker) Lellinger, Fern Gaz. 11:108. 1975. Type.—ECUADOR. Tungurahua. Mt. Tungurahua, s.d., *R. Spruce s.n.* (lectotype, designated by Moran and Prado, 2010: K! [barcode 000200146]; isolectotypes, K! [barcode 000200146, 000227603]). **Figs. 2C, 14B, 15F–K, 16B–D.**

Ctenitis bidecorata Lellinger, Proc. Biol. Soc. Wash. 98:373, fig. 5. 1985. *Megalastrum bidecoratum* (Lellinger) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [1988]. Type.—COSTA RICA. Cartago: Estrella-Sta. María road, [9°47′N 83°58′W], 230 m, 21 Apr 1928, *H. Stork 1518* (holotype: US-n.v.; photo CR! ex US).

Dryopteris wolfii Hieron., Hedwigia 46:344, tab. 7, fig. 17. 1907. Type.—ECUADOR. Tungurahua: Baños-Pintuc, [1°23′S, 78°25′W], s.d., *M. A. Stübel 998* (lectotype, here designated: B! [barcode 20 0052936] ; isolectotype: BM! [barcode 000907720]).

Dryopteris yungensis Christ & Rosenst., Repert. Spec. Nov. Regni Veg. 5:234. 1908. *Megalastrum yungense* (Christ & Rosenst.) A. R. Sm., Amer. Fern J. 77:129. 1987 [published 3 May 1988]. Type.—BOLIVIA. La Paz: Prov. Sud Yungas, Sirupaya near Yanacachi, [16°00′S, 65°05′W], 2000 m, 16 Nov 1906, *O. Buchtien 419* (lectotype, designated by Tryon and Stolze (1991): P! [barcode 000600636]; isolectotype: US-n.v.).

Megalastrum aequatoriense A. Rojas, Mét. Ecol. Sist. 3(Supl. 1):41, fig. 1A, B. 2008. Type.—ECUADOR. Carchi: Trail to Pailon encampment, Gualpi Chico area of Awá Reserve, 0°58′N, 78°16′W, 1350–1400 m, 21 Jan 1988, *W. S. Hoover, A. Arquello, P. Gelpi & R. A. Lorentzen 3609* (holotype: MO! [barcode 3710680]; isotype: UC! [barcode 1564580]).

Nephrodium subglabrum Sodiro, Crypt. Vasc. Quit. 259. 1893. Type.—ECUADOR. Pichincha: "in silva prope San Nicolás," [0°19′S, 78°27′W], 1200 m, Oct 1891, *A. Sodiro s.n.* (lectotype, here designated: P! [barcode 000568196]; isolectotypes: P! [barcode 000600391], QPLS?-n.v., Q?-n.v.).

Rhizomes erect, scales 7.0–17.0 × ca. 1 mm long, appressed to ascending, linear-lanceolate, brown, lustrous, twisted, sparsely denticulate, the teeth simple or bifid; **leaves** 0.6–1.2 m long; **petiole base scales** ca. 10.0 × 1.0 mm, like those of the rhizomes but often spreading and more sparsely denticulate; **laminae** 0.5–0.9 m long, basally 2-pinnate to 2-pinnate-pinnatifid, medially 1- to 2-pinnate-pinnatifid; **lamina rachises** pubescent abaxially; **basal pinnae** 10.0–15.0(–23.0) cm long, equilateral to subequilateral; **pinna rachises** abaxially eglandular, pubescent, scaly, the hairs 0.2–0.3(–0.4) mm long, 2- or 3-celled, strigose or appressed to ascending, the scales 2.0–5.0 × 0.2–0.5 mm, brown, lanceolate, lustrous, appressed to spreading, twisted (but not tortuous), sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, non-scaly, the hairs 0.4–0.6 mm long, 4- or 5-celled, acicular, ascending to strigose, light brown; **basal basiscopic pinnules of medial pinnae**

not enlarged or overlapping the lamina rachis, crenate to lobate; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the scales ca. 0.8–1.0 × ca. 0.1 mm, adaxially sparsely pubescent, the hairs like those of the pinna rachises adaxially; **laminar tissue between veins** eglandular, abaxially with a few appressed proscales, without hairs on both sides of the lamina; **ultimate veins** evident and glabrous on both surfaces; **lamina margins** eglandular, very sparsely ciliate, the hairs 0.1–0.2 mm long, 1- or 2-celled, acicular, appressed; **indusia** absent; **spores** cristate.

Distribution and ecology.—Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia; 1000–2300(–3050) m.

SELECTED SPECIMENS EXAMINED.—VENEZUELA. **Bolívar**: Cerro Uananapan, S of Uei-tepui, kms from campamento 132, between Luepa and Cerro Venamo, 1450 m, [5°55′N, 61°25′W], 25 Apr 1960, *Steyermark & Nilsson 762* (NY).

COLOMBIA. **Antioquia**: Mpio. Jardín, vereda La Mesenia, sector Paramillo, 2280–2560 m, 5°29″13″N, 75°53′52″W, 9 Jan 2005, *Rodríguez et al. 4934* (NY). **Cauca**: La Gallera, Micay Valley, 1400–1500 m, 3°02′N, 77°32′W, 29–30 Jun 1922, *Killip 7758* (AAU). **Nariño**: Municipalidad Barbacoas, Corregimeinto Altaquer, Vereda El Barrio, Reserva Natural El Ñambí, vertiente occidental andina, 1325 m, 1°18′N, 78°08′W, 6 Dec 1993, *Betancur et al. 4663* (COL). **Tolima**: Along Quindio Highway, between Cajamarca and summit of Divide, 3275 m, [4°25′N, 75°30′W], 27–28 Mar 1939, *Killip & Varela 34671* (BM).

ECUADOR. **Carchi**: Mira Cantón, camino a Chical, 2000–2200 m, 0°17′N, 78°13′W, 10 Feb 1992, *Palacios et al. 9724* (AAU, MO, QCNE). **El Oro**: Río Palma, a tributary to Río Amarillo, near Pampa de los Cedros S of Cerro Chivo-Turco, 2135–2285 m, 3°45′S, 79°40′W, 11 Aug 1943, *Steyermark 53768* (F). **Loja**: Parque Nacional Podocarpus, E of Nudo de Cajanuma, trail E of Centro de Información to crest on trail to Lagunas de Compadre, 2850–3050 m, 4°05′S, 79°10′W, 7 Jun 1988, *Øllgaard 74637* (AAU, QCA, QCNE). **Morona-Santiago**: road Plan de Milagro-Gualaceo, Km 3, 1900 m, 3°00′S, 78°30′W, 16 Nov 1998, *Navarrete & Øllgaard 3047* (AAU, QCA). **Napo**: camino Oyachachi-el Chaco, sector Río Chalpi, 2500 m, 0°13′S, 77°58′W, 23 May 1996, *Navarrete 1684* (AAU); near Cosanga, Yanayacu Biological Station, 2100 m, 0°35′57″S, 77°53′26″W, 12 Feb 2005, *Moran 7443* (NY, QCA, QCNE). **Pastaza**: Fundo chela, Sinchono, 1100 m, 1°27′S, 78°06′W, 5–19 Mar 1985, *Baker et al. 5772* (MO, NY, QCNE). **Pichincha**: Maquipucuna Biological Field Station, ca. 5 km E of Nanegalito and ca. 25 km N of Quito, 1400–1700 m, 0°08′N, 78°35′W, 2 Feb 1991, *Moran & Rohrbach 5229* (AAU, MO); Mindo, San Toledo, 1300 m, [0°10′S, 78°38′W], s.d., *Stübel 770* (B); road Chillogallo-Santo Domingo, below Chrigoga, 14 km from the new road, 1500 m, 0°19′S, 78°52′W, 13 Aug 1980, *Holm-Nielsen et al. 24853* (AAU, NY). **Tungurahua**: Palmera, Río Pastaza, between Baños and Mera, 1300 m, [1°23′S, 78°03′W], 1924, *Tate 653* (NY). **Zamora-Chinchipe**: Parque Nacional Podocarpus, around pass on road Loja-Zamora, on old mule track toward Zamora, 2800–3000 m, 3°59′S, 79°07′W, 8 Mar 1990, *Madsen 87002* (AAU, QCA).

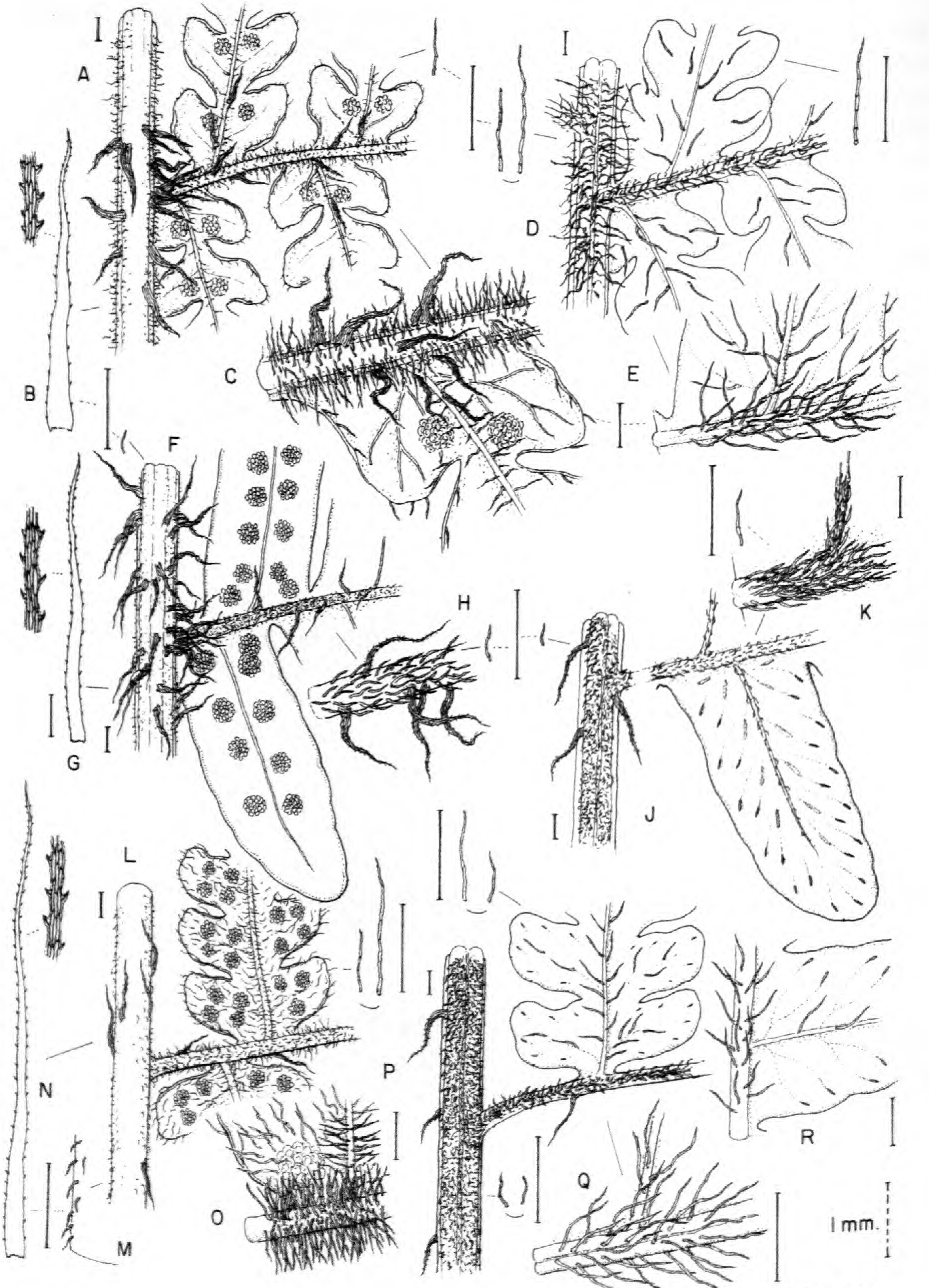

FIG. 15. Indument of three species of Andean *Megalastrum*. A–E. *M. fimbriatum*. A. Abaxial surface of leaf rachis, pinna rachis, and pinnules. B. Rachis scale, with enlarged detail of scale tip. C. Detail of abaxial surface of costule and segments. D. Adaxial surface of pinna rachis, costule, and segments. E. Detail of hairs on costule and segments. F–K. *M. biseriale*. F. Abaxial of leaf rachis, pinna rachis, and pinnules. G. Rachis scale, with enlarged detail of scale tip. H. Detail of costule. J.

PERU. **Cusco**: Distr. Huayopata, Huyro, Calquiña, 1750 m, 12°58′51″S, 72°03′31″W, 27 Jun 2003, *Bonino et al. 751* (MO). **Junín**: Pichis Trail, San Nicolas, 1100 m, 4–5 Jul 1929, *Killip & Smith 26021* (NY, US).

BOLIVIA. **La Paz**: Prov. Nor Yungas, carretera Chuspipata-Yolosa, sobre el tramo puente Loza y Sacramento, 2850 m, 16°17′S, 68°48′W, 28 Apr 2004, *Jiménez 2177* (NY, UC); idem, 19.8 km from Yolosa toward Chuspipata, 2280 m, 16°15′S, 67°45′W, 27 Jun 1989, *Fay & Fay 2205* (MO, UC, US).

Megalastrum biseriale is characterized by laminae 2-pinnate to 2-pinnate-pinnatisect, tissue between the veins on both surfaces glabrous, and pinna rachises abaxially pubescent. A specimen from Sucre, Venezuela (*Steyermark 62438 p.p.*) is atypical by the much longer hairs (0.6–1.4 mm long) on both surfaces of the laminae. In other characters, such as size and cutting of the laminae, it resembles *M. biseriale.* We have annotated the specimen as "aff. *biseriale.*" Further research might show it to be a new species.

We previously placed *Megalastrum biseriale* in synonymy with *M. macrotheca,* which has a type from Guadeloupe (Moran *et al.* 2009b; Moran and Prado 2010). After examining the larger number of South American specimens available to us since then, we believe that *M. biseriale* is distinct—a conclusion also supported by our unpublished plastid DNA sequence results (in preparation). Although similar, *M. macrotheca* differs by pinna rachises abaxially usually less pubescent with longer hairs (0.3–1.2 mm) composed of more cells (3–5-celled). The specimens from the Antilles tend to have more numerous and wider scales along the rachises of the laminae and costae.

The lectotype of this species was previously cited incorrectly as *Spruce 4656* (Moran & Prado, 2010), a specimen that is the type of *Megalastrum platylobum* (see below). In fact, the K barcodes cited as the lectotype are for a collection without a number and should be cited as *Spruce s.n.*

7. **Megalastrum bolivianum** M. Kessler & A. R. Sm., Amer. Fern. J. 96:33, fig. 1D–F. 2006. TYPE.—BOLIVIA. Cochabamba: Prov. Carrasco, 143 Km antigua carretera Cochabamba-Villa Tunari, 17°07′S, 65°34′W, 1300 m, 23 Aug 1996, *M. Kessler 7630a* (holotype: UC! [barcode 1616953]; isotypes: GOET!, LPB-n.v.). **Figs. 14C, 16E, 17A–D.**

Rhizomes erect, scales 6.0–10.0 × 0.5–1.0 mm, appressed to ascending, linear-lanceolate, brown to light brown, lustrous, denticulate, the surfaces smooth (not setulose); **leaves** up to ca. 0.8 m long; **petiole base scales** like those

---

←

Adaxial of leaf rachis, pinna rachis, and pinnules. K. Adaxial surface of pinna rachis and costule. L–R. *M. ciliatum*. L. Abaxial surface of leaf rachis, pinna rachis, and pinnules. M. Rachis hairs. N. Rachis scale, with enlarged detail of scale tip. O. Detail of abaxial surface. P. Adaxial surface of leaf rachis, pinna rachis, and pinnules. Q. Hairs along pinna rachis and costule. R. Adaxial surface of costule and segment. Scale bars = 1 mm. A–E: Holotype, *Young & León 4958* (F). F–K: *Stübel 770* (B). L–R: *Fuentes et al. 9013* (MO).

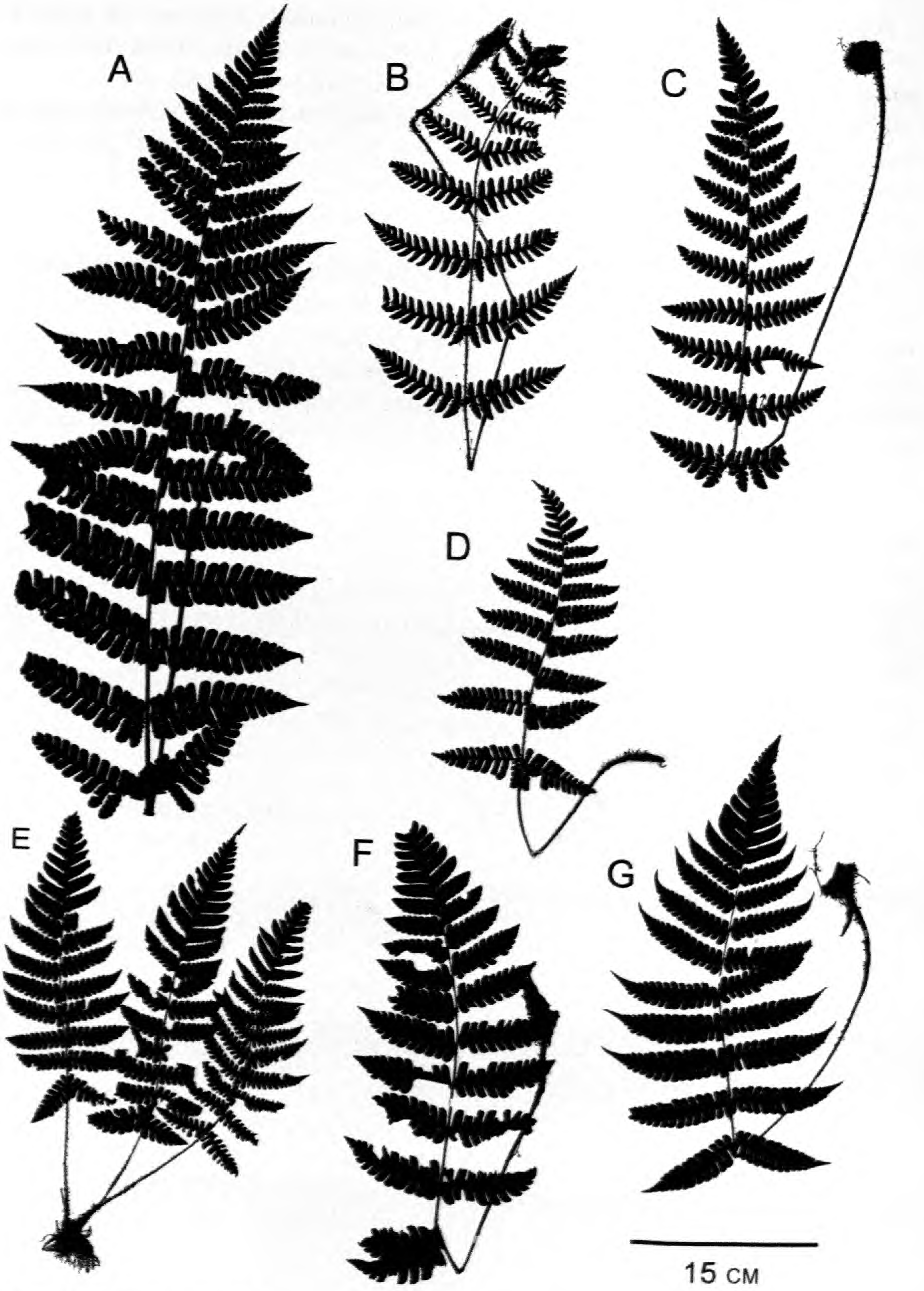

FIG. 16. Leaf dissection of five 1-pinnate-pinnatifid species of Andean *Megalastrum*. A. *M. platylobum*. B. *M. biseriale*. C. *M. biseriale*. D. *M. biseriale*. E. *M. bolivianum*. F. *M. ctenitoides*. G. *M. fibrillosum*. A: Lectotype, *Spruce 4656* (K). B: *Moran & Rohrbach 5229* (MO). C: *Navarrete 1684* (AAU). D: *Fay & Fay 2205* (MO). E: Holotype, *Kessler 7630a* (UC). F: *Øllgaard et al. 2205* (AAU). G: *Øllgaard 2859* (AAU).

of the rhizomes; **laminae** 0.25–0.5 m long, basally 2-pinnate-pinnatifid, medially 1-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 3.5–12.0 cm long, equilateral or subequilateral; **pinna rachises** abaxially eglandular, sparsely pubescent, scaly, the hairs 0.5–1.2 mm long, 4- or 5-celled, spreading, lax, the scales 0.5–1.0 × 0.2–0.3 mm, dark brown, spreading, narrowly lanceolate, sparsely denticulate, not clathrate, not bullate, adaxially eglandular, sparsely pubescent, scales absent, the hairs 1.0–1.5 mm long, 5–9-celled, ascending, light brown to whitish; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** on both surfaces with indument like that of the pinna rachises; **laminar tissue between veins** abaxially eglandular, glabrous, adaxially glabrous; **veins** visible on both surfaces, abaxially subglabrous, with few hairs towards the apex, adaxially sparsely puberulent, the hairs like those on the costules; **lamina margins** eglandular, ciliate, the hairs ca. 0.3 mm long, 2- or 1-celled, substrigose; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru, Bolivia; eastern side of the Andes, on soil or rarely on rocks; 600–2800 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Bolívar**: Carretera Salinas-Facundo Vela, 2800 m, 1°15′S, 79°02′W, Sep 1994, *Navarrete 725* (AAU). **Morona-Santiago**: along new road Mendez-Morona, Km 55–62, 800 m, [2°40′S, 78°19′W], 23 Aug 1989, *van der Werff & Gudiño 11369* (F, MO, NY). **Napo**: camino entre Baeza y Tena, 15 km al N de Tena, 1100 m, [0°59′S, 77°49′W], 24 Jan 1984, *Moran 3583* (AAU). **Pastaza**: Km 17 del propuesto oleoducto ARCO-Villano-El Triunfo, 600 m, 01°31′S, 77°30′W, 25 Feb 1994, *Palacios 12113* (MO, QCNE). **Zamora-Chinchipe**: new road Loja to Zamora, 13 km E of the Pass, 2000 m, 4°00′S, 79°02′W, 14 Feb 1991, *Moran & Rohrbach 5382* (AAU, MO, QCNE).

PERU. **Amazonas**: Bagua, 12 km E of La Peca, 1700 m, [5°36′S, 78°26′W], 23 Jun 1978, *Barbour 2499* (MO). **Cajamarca**: San Ignacio, San José de Lourdes, Buenos Aires, Cerro El Paco, 1900 m, 5°42′04″S, 77°53′06″W, Feb 2002, *Bonino 143* (MO).

BOLIVIA. **La Paz**: Nor Yungas, Canton Pacollo a 500 m de la Estación Biológica Tunquini, subiendo el Río Santa Catalina, 1690 m, 16°11′15″S, 67°52′3″, 23 Aug 1998, *Portugal et al. 246* (UC).

Megalastrum bolivianum is distinguished by short leaves (to 0.8 m long), laminae medially 1-pinnate-pinnatisect, and pinnae rachises abaxially with long (0.5–1.2 mm) whitish hairs. Similar is *M. molle*, which differs by minute glandular pubescence between the veins on both surfaces of the laminae (vs. eglandular). Also similar because of their laminae 1-pinnate-pinnatisect medially are *M. fibrillosum* and *M. platylobum*. The first differs from *M. bolivianum* by filiform scales of the pinna rachises abaxially and lacking hairs adaxially along the veins. The second species differs from *M. bolivianum* by shorter hairs (0.1–0.4 vs. 0.5–1.2 mm long) along the pinna rachises abaxially and veins adaxially glabrous (vs. pubescent).

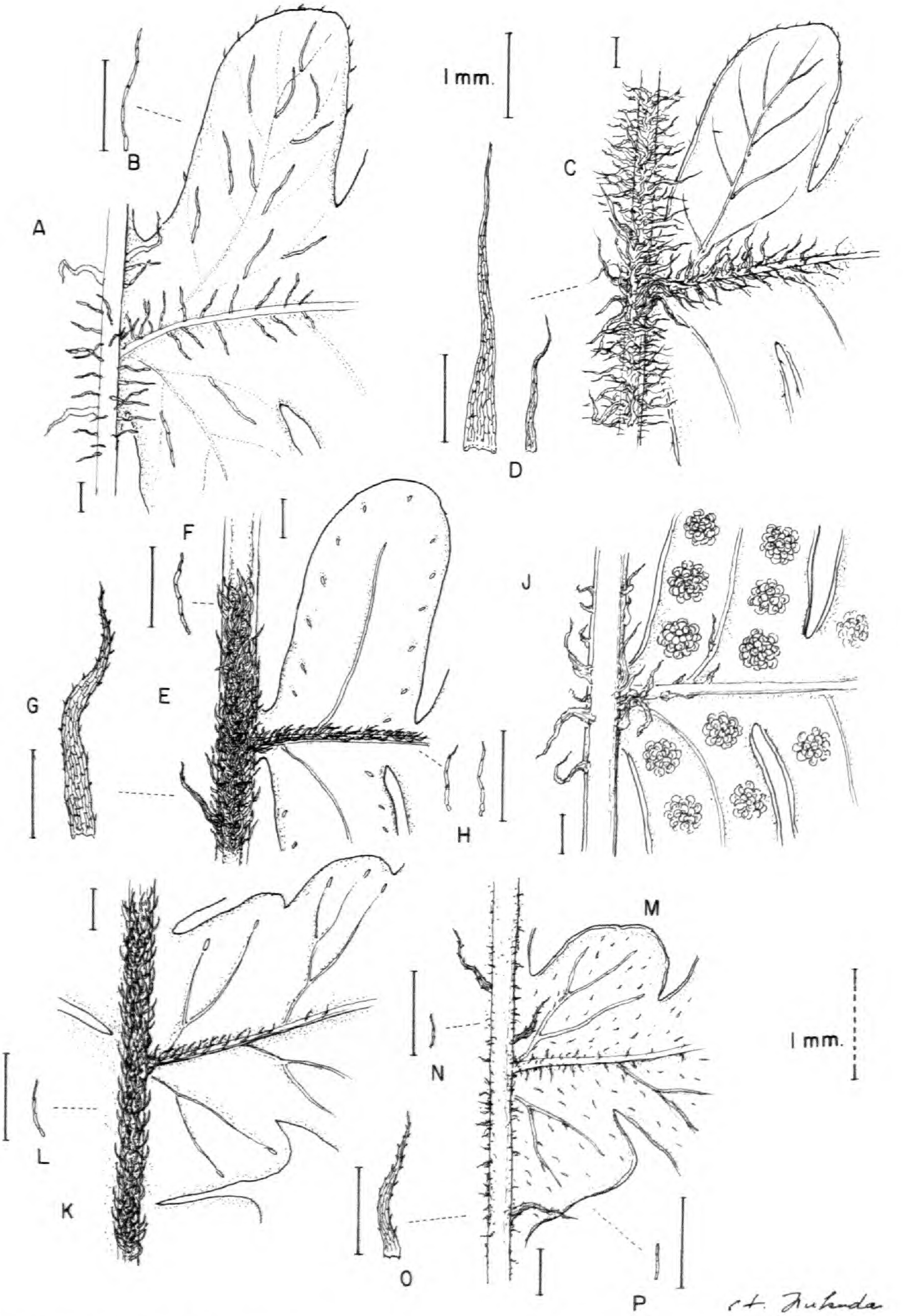

FIG. 17. Indument of three species of Andean *Megalastrum*. A–D. *M. bolivianum*. A. Adaxial surface of lamina rachis and segments. B. Hair detail. C. Abaxial surface of lamina rachis and segments. D. Scale detail. E–J. *M. oellgaardii*. E. Adaxial surface of pinna rachis and segments. F. Hair detail. G. Scale detail. H. Hair detail. J. Abaxial surface of pinna rachis and segments. K–P. *M. oreophilum*. K. Adaxial surface of pinna rachis and segments. L. Hair detail. M. Abaxial surface of

One specimen we have identified as *Megalastrum bolivianum* (*Øllgaard et al. 90906*, AAU) is atypical by subdimorphic sterile and fertile leaves, veins glabrous adaxially, and pinna rachises abaxially with ovate scales. It might be new, but we refrain from describing it on the basis of this one specimen.

8. **Megalastrum ciliatum** M. Kessler & A. R. Sm., Amer. Fern J. 96:38. 2006. TYPE.—BOLIVIA. La Paz: Prov. Sud Yungas, camino Chulumani–Ocobaya, 2.5 km después de Chulumani, 16°23′S, 67°31′W, 1600 m, 6 Jan 1992, *J. P. Schmit, T. Mione & W. Zuazo 422* (holotype: UC! [barcode 1616956]; isotype: LPB-n.v.). **Figs. 14A, 15L–R, 18B.**

Rhizomes erect, scales 6.0–10.0 × 1.0–1.5 mm, spreading to ascending, linear-lanceolate, brown with margins black-bordered (at least intermittently), lustrous, twisted, strongly denticulate; **leaves** 0.5–0.8 m long; **petiole base scales** like those of the rhizomes but more spreading to loosely ascending; **laminae** 0.4–0.7 m long, basally 3-pinnate-pinnatifid, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 10.0–30.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, pubescent, sparsely scaly, hairs 0.8–1.5 mm long, 4–7-celled, spreading, acicular, the scales 1.0–2.0 × 0.2–0.3 mm long, light to dark brown, sometimes darker distally, linear-lanceolate, strongly denticulate, not clathrate, not bullate, adaxially sparsely glandular, densely pubescent, scales absent, the glands ca. 0.1 mm long, spherical, sessile, orange to yellowish, the hairs 1.0–1.5 mm long, 6–8-celled, appressed to spreading; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** one both surfaces eglandular, densely pubescent, sparsely scaly, the hairs 0.7–1.0 mm long, 3–6-celled, spreading, the scales to 1.5 × 0.2 mm, loosely ascending, brown, linear-lanceolate, lustrous, strongly denticulate; **laminar tissue between veins** abaxially sparsely glandular, moderately to densely puberulent, the glands ca. 0.1 mm long, spherical, sessile, orange to yellowish, the hairs 0.8–1.0 mm long, 4–6-celled, appressed to erect, acicular, adaxially glabrous; **veins** on both surfaces visible or sometimes obscure adaxially, pubescent, abaxially with hairs like that between the veins, adaxially with hairs 0.5–1.0 mm long, 3–6-celled, straightish or somewhat tortuous; **lamina margins** eglandular, ciliate, the hairs 0.4–1.0 mm long, 2–6-celled, ascending to spreading; **indusia** absent; **spores** cristate.

Distribution.—Bolivia, northern Argentina; 1600–1830 m.

SELECTED SPECIMENS EXAMINED.—BOLIVIA. **La Paz**: Parque Nacional Madidi, entre Carjata y Río Yana Lomas, 1700 m, 14°34′12″S, 68°54′00″W, 28 Jun 2005, *Fuentes et al. 9013* (MO, UC).

←

pinna rachis and segment. N. Hair detail. O. Scale detail. P. Hair detail. Scale bars = 1 mm. A–D: Holotype, *Kessler et al. 7630a* (UC). E–J: Holotype, *Øllgaard et al. 2219* (AAU). K–P: Isotype, *Maguire et al. 36871* (US).

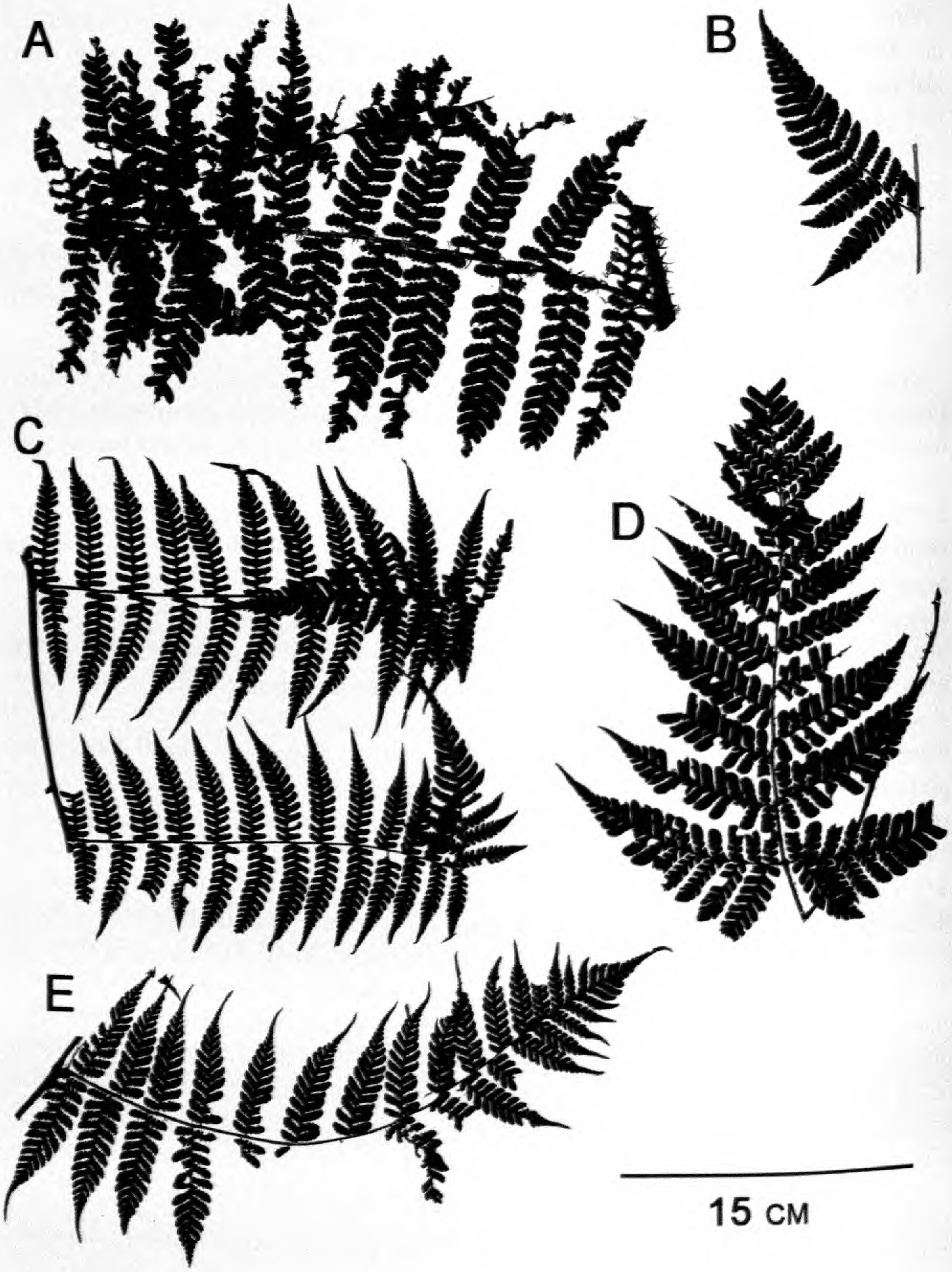

FIG. 18. Leaf dissection in five species of Andean *Megalastrum*. A. Medial pinna, *M. squamosissimum*. B. Basal pinna, *M. ciliatum*. C. Medial pinnae, *M. subincisum*. D. Leaf, *M. pubescens*. E. Medial pinna, *M. pubirhachis*. A: *Barrington 461* (GH). B: *Fuentes et al. 9013* (UC). C: *Rodríguez et al. 5629* (NY). D: *Rodríguez et al. 5559* (COL). E: Isotype, *Fay & Fay 3919* (NY).

ARGENTINA. **Jujuy**: Depto. Ledesma, Parque Nacional Calilegua, Aguada del Tigre, 1600 m, 23°41′S, 64°53′W, 7 Apr 2010, *Martínez & Prado 1893* (MCSN, NY, SP).

Megalastrum ciliatum is characterized by relatively small leaves (up to 0.8 m long). Besides size, the species is further distinctive by veins adaxially with straightish hairs 0.5–1.0 mm long, laminar tissue abaxially pubescent with hairs 0.8–1.0 mm long, and pinna rachises and costules abaxially with strongly denticulate scales.

This species most resembles *Megalastrum nigromarginatum* from Colombia. Both have similar lamina size and cutting, and the rhizome scales are intermittently black-margined—a rare character in the genus. The two species can be distinguished by characters given in the key. *Megalastrum ciliatum* also resembles *M. marginatum* and *M. rupicola* by lamina size and cutting but differs by the laminae between the veins abaxially pubescent. The densely pubescent laminae may resemble that of *M. pulverulentum*, but that species differs by much larger leaves (to 4 m long), the presence of glands, pinna rachis scales more strongly denticulate and often darkened apically, and echinulate spores.

See *Megalastrum nanum* for comparison to that species.

9. *Megalastrum clathratum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** Type.—PERU. Pasco: Prov. Oxapampa, along trail Milpo to Sta. Barbara, cloud forest and puna vegetation, on rich soil, 10°22′53S, 75°38′15″W, 3100–3500 m, 3 Nov 2009, *H. van der Werff, R. Vásquez M., A. Peña, L. Mateo & R. Rivera 23175* (holotype: HOXA! [accession 043231]; isotype: MO! [barcode 6315956, 6315957). **Figs. 8D, 14A, 19A–F.**

Rhizomes unknown; **leaves** up to 1.5 m long; **petiole base scales** 15.0–20.0 × ca. 0.1 mm, spreading to loosely ascending, linear-lanceolate, brown, twisted, dull, denticulate; **laminae** 0.8–1.0 m long, basally 4-pinnate-pinnatisect, medially 3-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** ca. 0.8 m long, strongly inequilateral; **pinna rachises** on both surfaces sparsely glandular, densely and evenly pubescent, scaly, the glands ca. 0.1 mm long, spherical, sessile, brownish or orangish, the hairs 0.2–0.6 mm long, 3–5-celled, reddish, spreading, the scales clathrate, denticulate to ciliate, sometimes darker apically, non-bullate, reddish, not bullate, of two types, small ones ca. 0.2–0.6 × ca. 0.2 mm long, narrowly lanceolate, spreading, the larger 5.0–10.0 × 0.2–0.5 mm long, linear to linear-lanceolate, spreading, adaxially with indument like that abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially sparsely glandular, the indument like that on the pinna rachises but more sparsely scaly, the scales smaller, 3.0–5.0 × 0.2–0.3 mm long, adaxially sparsely pubescent, the hairs 0.3–0.5 mm long, 3–5-celled, spreading, reddish; **laminar tissue between veins** on both surfaces sparsely glandular, glabrous, the glands ca. 0.1 mm, sessile and spherical, brownish to orangish; **ultimate veins** on both surfaces obscure, abaxially sparsely glandular and sparsely pubescent, non-scaly, the hairs 0.3–0.5 mm long, 3–5-celled, adaxially eglandular, sparsely pubescent, the hairs 1.0–1.8 mm long, 4–9-celled, spreading; **lamina margins** not glandular, ciliate, the hairs 0.2–0.3 mm long, 2- or 3-celled, spreading; **indusia** absent; **spores** echinulate.

Distribution.—Peru; 3100–3500 m.

SELECTED SPECIMENS EXAMINED.—PERU. **Pasco**: Oxapampa, along tail Milpo to Sta. Barbara, 3100–3500 m, 10°22′53″S, 75°38′15″W, 3 Nov 2009, *van der Werff et al. 23179* (MO).

Megalastrum clathratum is distinguished by pinna rachis scales clathrate and reddish, and the pinna rachises and costules evenly and densely pubescent by reddish hairs 0.2–0.6 mm long. The species has echinulate spores, a character that will separate it from all other species in the Andes except those in the "pulverulentum clade" (unpublished molecular results). The Andean members of this clade are *M. adenopteris, M. fugaceum, M. pulverulentum,* and *M. nanum*. The elevational range for this species is the highest in the genus.

10. Megalastrum crenulans (Fée) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:127. 1987 [published 3 May 1988]. *Aspidium crenulans* Fée, Crypt. Vasc. Brésil 1:139, t. 47, fig. 1. 1869. *Ctenitis crenulata* (Fée) Ching, Sunyatsenia 5:250. 1940. *Dryopteris crenulans* (Fée) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 8, 6:90. 1920. TYPE.—BRAZIL. Rio de Janiero: Rio de Janeiro, [22°56′S, 43°17′W], s.d., *A. Glaziou 1781* (lectotype, designated by Christensen, 1920: C!, photos MICH!, MO!; isolectotypes: K! [barcode 000512192, 000512193], P! [barcode 00610618], P! [barcode 00610619], RB!-n.v.). **Figs. 5C, 6C, 11A–L.**

Dryopteris villosa (L.) Kuntze var. *glandulosa* Rosenst., Hedwigia 46:129. 1907. *Dryopteris crenulans* (Fée) C. Chr. f. *glandulosa* (Rosenst.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 8, 6:91. 1920. TYPE.—BRAZIL. Rio Grande do Sul: Mun. Rio Pardo, banks of Rio Cyriaco [29°59′22″S, 52°52′41″W], 1906, *L. C. Jürgens s.n.* [Rosenstock Filices Austrobrasilienses no. 206] (lectotype, designated by Moran *et al.*, 2009a: BM!-000907729; S-n.v.; isolectotypes: B! [barcode 200053756], BM! [barcode 000907728], GH!, HB!, K!, MICH!, MO! [accession 1636088], NY! [barcode 00678829], NY! [barcode 00678938], NY! [barcode 00678937], P! [barcode 00610623], P! [barcode 00610624], P! [barcode 00610625], UC! [barcode 441613], VT! [barcode 001519]).

Rhizomes not seen; **leaves** up to 2.5 m long; **petiole base scales** 10.0–20.0 × 0.2–1.0 mm, en masse forming a dense woolly tuft, linear, light brown, twisted, tortuous, sparsely denticulate; **laminae** ca. 1 m long, basally 4-pinnate, medially 3-pinnate-pinnatifid; **lamina rachises** without hairs abaxially; **basal pinnae** 30.0–57.0 cm long, strongly inequilateral; **pinna rachises** abaxially glandular, pubescent, scaly, the glands ca. 0.1 mm long, 2-celled, stalked, yellowish, the hairs 0.8–1.2 mm long, 4- or 5-celled, acicular, spreading, the scales ca. 1.0–1.5 mm long, brown, lanceolate, subentire, not clathrate, bullate, adaxially densely pubescent, sparsely glandular, the hairs and glands similar to those of the abaxial side; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially glandular, pubescent, sparsely scaly, the glands ca. 0.1 mm, stalked, 2-celled, yellowish, the hairs 0.2–0.5 mm long, 1–3(4)-celled, acicular, spreading, hyaline, the scales ca. 1 mm long, brown, lanceolate, bullate, shiny, subentire, adaxially sparsely glandular, pubescent, without scales, the glands similar to those abaxially, the hairs 0.4–0.8 mm long, 1–4-celled, erect, acicular; **laminar tissue between veins** abaxially densely glandular and pubescent, the glands stalked, 0.1 mm long, erect, yellowish, the hairs ca. 0.1 mm long, 1-celled, erect, hyaline, acicular, adaxially moderately glandular, sparsely pubescent, indument more dense towards the segment apex, the hairs ca. 0.2 mm long, 2-celled, erect, acicular, the glands similar to those abaxially; **ultimate veins** visible on both surfaces, abaxially very sparsely glandular, pubescent, the hairs 0.2–0.3 mm long, 1- or 2-celled, adaxially sparsely pubescent, the hairs ca. 0.4–0.5 mm long, 1–3-celled; **lamina margins** eglandular, densely ciliate, the hairs ca. 0.3–0.4 mm long, 1- or 2(3)-celled; **indusia** present, 0.8–1.0 mm wide, circular, brown, glandular, the margins with a few 0.1 mm long scattered acicular hairs, sometimes laminar hairs emerging through the sinus of the indusium appear to be part of the indusium proper; **spores** echinulate.

Distribution and ecology.—Venezuela, Brazil, and Paraguay; 1500–1760 m in Venezuela, but to 725 m in Brazil and Paraguay (Moran *et al.*, 2009).

SELECTED SPECIMENS EXAMINED.—VENEZUELA. **Amazonas**: E. Slope of unnamed peak, 8 km NW of settlement of Yutaje, 4 km of Río Corocoro, W of Serranía de Yutaje, ranging from slope below wet bluff to wet bluff to unstable slope to dry bluff summit, 1500–1760 m, 5°41′S, 66°66′W, 4 Mar 1987, *Liesner & Holst 21585* (MO, NY). **Bolívar**: Faldas del Cerro Apacara, Río Caroni, 1600 m, [5°20′N, 62°12′W], 1 Jul 1946, *Cardona 1590* (US).

Megalastrum crenulans is characterized by indusiate sori and bullate scales on the pinna rachises and costules. The latter character distinguishes the species from the other indusiate ones in South America (i.e., *M. acrosorum*, *M. andicola*, and *M. insigne*). According to our unpublished phylogenetic results, it forms a clade with the Brazilian *M. abundans* and the African-Madagascan *M. lanuginosum* (Willd. ex Kaulf.) Holttum. The clade is defined by blades abaxially with minute yellowish spherical glands, and costae and costules abaxially with bullate scales. *Megalastrum crenulans* differs from *M. abundans* by the presence of an indusium (vs. absent; Moran *et al.* 2009). It differs from *M. lanuginosum* by petiole base scales 0.2–1.0 mm wide (vs. 2.0–3.0), costules abaxially with hairs 0.2–0.5 mm long and 1–3(4)-celled (vs. 0.5–0.7 mm long and 6–8-celled), and indusia 0.8–1.0 mm wide (vs. 1.0–1.5 mm; Rouhan and Moran 2011).

11. Megalastrum ctenitoides A. Rojas, Revista Biol. Trop. 49:470, fig. 2. 2001. TYPE.—COSTA RICA: Limón: Cantón Limón, El Progreso, Fila Matama, Valle de La Estrella, cabeceras del Río Cariei, 9°47′20″ N, 83°08′18″ W, 1400 m, 26 Apr 1989, *G. Herrera & A. Chacón 2794* (holotype: INB!; isotypes: CR!, K-n.v., MO-n.v.). **Figs. 5D, 16F, 20A–G, 21E–H.**

Rhizomes erect to decumbent, scales 2.5–6.5 × ca. 0.5 mm, appressed, lanceolate to filiform, dull brown, firm, not twisted, denticulate, the teeth occasionally bifid and or black; **leaves** 0.8–1.0 m long; **petiole base scales** like those of the rhizomes but more spreading; **laminae** 0.5–0.6 m long, basally and medially 1-pinnate-pinnatifid; **lamina rachises** eglandular, pubescent or without hairs abaxially, scaly, the hairs ca. 0.5 mm long, 4- or 5-celled, the scales 2–4 × 0.3–0.4 mm, lanceolate, brown, firm, dull, spreading, denticulate to entire, not clathrate, not bullate, adaxially eglandular, pubescent, the hairs ca. 1 mm long, 6–8-celled, strongly jointed (twisted at the septae); **basal pinnae** 0.10–0.15 m long, equilateral, cut ca. half way to the pinna rachises; **pinna rachises** abaxially eglandular, pubescent to subglabrous, scaly, the hairs 0.3–0.5 mm long, 2–4-celled, ascending-appressed, the scales like those of the rachises, adaxially eglandular, without hairs or sometimes with a few hairs at the base, the hairs like those abaxially; **basal basiscopic pinnules of medial pinnae** often (especially in large leaves) enlarged and overlapping the lamina rachis, entire; **costules** abaxially glabrous, scales absent; **laminar tissue between veins** on both surfaces eglandular, glabrous; **veins** abaxially obscure, sparsely pubescent, hairs 0.2–0.3 mm long, 1–3-celled, ascending, adaxially not visible, glabrous; **lamina margins** eglandular, sparsely ciliate, the hairs 0.1–0.3 mm long, 2- or 3-celled, ascending; **indusia** absent; **spores** cristate.

Distribution.—Costa Rica, western Colombia, western Ecuador; 700–2300 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Frontino, Corregimiento Carauta, Parque Nacional Natural Las Orquídeas, sector Tres Bocas, bosques a la orilla del Río Santiago, minas del Río Santiago, "Mina La Salada," Finca La Pradera, 1700–1740 m, 6°37′32″N, 76°12′54″W, 8 Sep 2012, *Sundue et al. 3265* (NY); idem, region of Murri, road between Nutibara and La Blanquita, 22.6 km from centro of Nutibara, 1340 m, 6°42′N, 76°25′W, 10 Feb 1989, *MacDougal et al. 3886* (MO). **Boyacá**: Prov. Briceno, desvío a Vereda Manzanares, 4 km W de la Troncal del Caribe sobre la vía Ventanas-Briceño, 1800–2000 m, 7°05′N, 75°30′W, 21 Mar 1988, *Callejas et al. 311* (MO). **Valle**: Mpio. El Cairo, Cordillera Occidental, Serranía de los Paraguas, Cerro del Inglés, vertiente sur, 2260–2300 m, [4°45′N, 76°15′W], 3 Jan 1987, *Silverstone-Sopkin et al. 2933* (MO).

ECUADOR. **Los Ríos**: summit of Cerro Samama, Hacienda Clementina, S of road Caluma-Catarama, 700–730 m, 1°40′S, 79°19′W, 13–14 Nov 1996, *Øllgaard & Navarrete 2046* (AAU). **Pichincha**: Km 2.2 along road to Mashpi from km 14 on road Pacto-La Delicia-La Esperanza, 1330 m, 0°8′N, 78°51′W, 1 Dec 1996, *Øllgaard et al. 2233* (AAU); Road Pacto-La Delicia-La Esperanza, Km 19, 1350 m, 0°10′N, 78°51′W, 30 Nov 1996, *Øllgaard et al. 2205* (AAU).

Megalastrum ctenitoides is characterized by laminae 1-pinnate-pinnatifid and all pinnae, even the basal ones, equilateral. All of the segments or lobes are adnate for their entire width to the pinna rachises, and their apices are obtuse to truncate. The segment margins are entire, never lobed or serrulate. The lamina rachises are pubescent and scaly, but the pinna rachises abaxially vary from glabrous to pubescent. Adaxially, the veins and midribs of the ultimate segments are glabrous. The lamina margins are glabrous to sparsely and remotely pubescent with minute hairs.

Megalastrum ctenitoides most resembles the less divided forms of *M. biseriale,* but that species differs by basal pinnae inequilateral and generally more divided laminae. Also similar by their laminae medially 1-pinnate-pinnatifisect are *M. bolivianum* and *M. fibrillosum*. The former differs by costules and veins on both surfaces pubescent with whitish, straight hairs ca. 1 mm long (vs. glabrous). The latter differs by basal pinnae inequilateral, and pinnae with the basal basiscopic segment enlarged, more lobed, and slightly overlapping the lamina rachis. Also, its scales along the pinna rachises are 3.0–4.0 mm long and fibrillose (vs 2.0–3.0 mm long). Both *M. bolivianum* and *M. fibrillosum* occur on the eastern side of the Andes, whereas *M. ctenitoides* is known only from the western side.

12. ***Megalastrum decompositum*** R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Bolívar: along road Chillanes–El Tambo, [2°10′S, 79°06′W], 1700–2300 m, 19 Jul 1991, *H. van der Werff, B. Gray & G. Tipas 12482* (holotype, QCNE!; isotypes, MO! [barcode 04930696, 04930697], QCA-n.v., UC! [barcode 1593666]). **Figs. 7M–O, 14D, 22B.**

Rhizomes erect; **leaves** up to 2.5 m long; **petiole bases scales** 25.0–30.0 × 1.0–2.0 mm, spreading, linear to linear lanceolate, brown, flat, dull, denticulate; **laminae** up to 1.5 m long, 4-pinnate-pinnatifid basally, 3-pinnate-pinnatisect medially; **lamina rachises** pubescent abaxially; **basal pinnae** ca. 75 cm long, strongly inequilateral, elongated basiscopically; **pinna rachises** abaxially eglandular, densely puberulent, densely scaly, the hairs 0.1–0.3 mm long, 2–4-celled, slightly ferruginous, curved-spreading, the scales 1.5–3.0 × 0.3–0.5 mm, brown, lanceolate, spreading, denticulate, not clathrate, not bullate, adaxially densely pubescent, scaly, the hairs 0.6–1.0 mm long, 4–8-celled, spreading, the scales ca. 0.5–1.0 × 0.2–0.3 mm, lanceolate, subclathrate, brown, appressed, denticulate; **costules** abaxially sparsely glandular, pubescent, scaly, the glands ca. 0.1 mm, sessile, spherical, yellowish, the hairs 0.1–0.4 mm long, 2–4-celled, erect, scales 1.0–2.0 × 0.2–0.3 mm, linear-lanceolate to linear, subclathrate, brown, spreading, denticulate; **laminar tissue between veins abaxially** eglandular, densely puberulent, the hairs ca. 0.2 mm long, 2-celled, erect, adaxially puberulent or (1 specimen, *Harling & Andersson 22459*) glabrous, the hairs 0.1–0.2 mm long 2- or 3-celled, lax, tortuous, ascending; **ultimate veins** on both surfaces visible, abaxially eglandular, densely pubescent, non-scaly, the hairs ca. 0.2–0.4 mm long, 3-celled, ascending to erect, adaxially eglandular, pubescent, the hairs 0.5–0.8 mm long, 5–7-celled, ascending; **lamina margins** eglandular, ciliate, the hairs 0.1–0.3 mm long, 2- or 3-celled, spreading; **indusia** fugacious, minute, consisting of a few hair-like scales, often covered by sporangia and apparently absent; **spores** cristate.

Distribution.—Central and southern Ecuador, on the western side of the Andes; 1700–2300 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Bolívar**: along road Chillanes-El Tambo, 1700–2300 m, [1°55′S, 79°06′W], 19 Jul 1991, *van der Werff et al. 12506* (MO, QCNE, UC). **Loja**: Celica-Zapotillo road, ca. Km 5, 2100–2200 m, [4°04′S, 80°03′W], 23 Feb 1985, *Harling & Andersson 22459* (NY). **Tunguragua**: Baños, [0°23′S, 78°25′W], Jan 1892, *Sodiro s.n.* (NY).

Megalastrum decompositum has large leaves up to 2.5 m long that are 4-pinnate-pinnatifid basally. It is one of the most dissected species in the genus, thus the specific epithet *decompositum*. The scales on the axes are distinctive by being thin, subclathrate, and denticulate. Both surfaces of the laminae between the veins are pubescent, except in one specimen (*Harling & Andersson 22459*). The hairs on the adaxial surfaces between the veins are slightly tortuous and ascending, whereas those on the abaxial surfaces are straighter and mostly erect. This pubescence resembles that of *M. mollicoma*, a species differing by pinna rachis scales entire, firmer, and opaque (vs. denticulate, thin, and subclathrate) and lamina margins with longer hairs (0.3–0.8 vs. 0.1–0.3 mm long).

13. **Megalastrum falcatum** A. Rojas, Mét. Ecol. Sist. 3(Supl. 1):43–44, fig. 3A, B. 2008. TYPE.—ECUADOR. Zamora-Chinchipe: along road between Zumbi on Río Zamora and summit of cordillera del Condor beyond Paquisha, 10.1 km beyond Río Nangaritza bridge, 29.1 km E of Zumbi, 3°56′13″S, 78°37′27″W, 1352 m, 16 Jul 2004, *T. Croat, L. P. Hannon, G. Walhert & T. Katan 91165* (holotype: MO! [barcode 04833356]; isotype: UC! [barcode 1793475]). **Figs. 2A, 10E, 23A–E, 24A.**

Rhizomes erect, scales 7.0–17.0 × ca. 1 mm long, appressed to ascending, linear-lanceolate, brown, lustrous, twisted, sparsely denticulate, the teeth simple or bifid; **leaves** 0.6–1.2 m long; **petiole base scales** ca. 10.0 × 1.0 mm, like those of the rhizomes but often spreading and more sparsely denticulate; **laminae** 0.5–0.9 m long, basally 2-pinnate to 2-pinnate-pinnatifid, medially 2-pinnate-pinnatifid; **lamina rachises** pubescent abaxially; **basal pinnae** 10.0–25.0 cm long, equilateral or subequilateral; **pinna rachises** abaxially eglandular, pubescent, scaly, the hairs 0.2–0.3(–0.4) mm long, 2- or 3-celled, strigose or appressed to ascending, the scales 2–5 × 0.2–0.5 mm, lanceolate, brown, appressed to widely spreading, lustrous, twisted (but not tortuous), entire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, scales absent, the hairs 0.4–0.6 mm long, 4- or 5-celled, acicular, ascending to strigose, light brown; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis, crenate to lobate, the proximal ones soon becoming adnate to the pinna rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs like those of the pinna rachises adaxially, the scales ca. 0.8–1.0 × ca. 0.1 mm, adaxially sparsely pubescent; **laminar tissue between veins** eglandular, without hairs on both surfaces; **lamina ultimate veins** obscure or not visible, glabrous on both surfaces; **lamina margins** eglandular, very sparsely ciliate, the hairs 0.1–0.2 mm long, 1- or 2-celled, acicular, appressed; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru, eastern side of the Andes; (250–)1000–2950 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Loja**: ca. 5 km ENE of San Pedro de Vilcabamba, from "El Bosque" to Quebrada Romerillos, 2100–2200 m, 4°14′S, 79°10′W, 29 Nov 1994, *Øllgaard & Navarrete 105893* (AAU, QCA). **Morona-Santiago**: along road into Cordillera del Condor departing from Chuchumbleza, then 6.8 km S of Chuchumbleza to Quime ferry on Río Zamora, then SW via Numbaime into Cordillera del Condor, 24 km SW of Río Zamora, 1562 m, 3°38′11″S, 78°25′49″W, 14 Jul 2004, *Croat et al. 91009* (MO, UC). **Napo**: camino entre Baeza y Tena, 15 km al N de Tena, 1100 m, [0°59′S, 77°49′W], 24 Jan 1984, *Moran 3583* (NY, UC). **Pichincha**: one hectare plot, Lloa Valley, Hacienda Las Palmas of Lcdo, Fernando Sotomayor, Lloa-Mindo, Km 14, 2900 m, 0°10′S, 78°38′W, 8 May 1988, *Jørgensen et al. 65337* (AAU, QCA, QCNE); Parroquia Calacalí, Reserva Geobotánica Palulahua, camino hacia los tanques de captación, 1800–3356 m, 0°05′N, 78°30′W, 1 Jun 1987, *Cerón 1483* (MO). **Zamora-Chinchipe**: road Zamora-Romerillo, 1–1.5 km N of Romerillo, 1450–1500 m, 4°13′S, 78°56′W, 27 Nov 1994, *Øllgaard & Navarrete 105854* (AAU); vic. of the mining camp at the Río Tundaime, 1000–1200 m, 3°34′44″S, 78°24′11″W, 12 Nov 2004, *van der Werff et al. 19532* (MO, QCNE, UC).

PERU. **Huánuco**: La Divisoria, ca. 25 km NE of Tingo María on the road to Pucallpa, 1700 m, [9°17′S, 76°00′W], 4 Jul 1984, *Moran 3689* (MO, NY, US).

Megalastrum falcatum resembles *M. biseriale* as to hairs and scales but differs by more divided laminae that are medially 2-pinnate-pinnatisect (vs. 1-pinnate-pinnatisect). Unlike many *Megalastrum* species with laminae 2-pinnate-pinnatisect medially, *M. falcatum* has basal pinnae equilateral or nearly so, not inequilateral by being greatly prolonged basiscopically. The pinnules are sessile proximally and soon become adnate distally along the rachis. The veins are glabrous both surfaces. Similar is *M. alticola*, which differs by laminae more divided medially (3-pinnate-pinnatisect), basal pinnae inequilateral (prolonged basiscopically), wider scales on the pinna rachises abaxially (0.5–1.0 mm vs. 0.2–0.5 mm wide), and veins adaxially pubescent.

14. *Megalastrum fibrillosum* (Baker) R. C. Moran, J. Prado & Sundue, ***comb. nov.*** *Polypodium fibrillosum* Baker, Syn. Fil. 307. 1867. *Dryopteris fibrillosa* (Baker) C. Chr., Index Fil. 264. 1905. TYPE.—PERU. San Martín: near Tarapoto, along Mayo River, [2°11′S, 74°6′W], Jul–Aug 1856, *R. Spruce 4742* (lectotype, designated by Tryon and Stolze, 1991: K [barcode 000200225]; isolectotypes: BM! [barcode 000777148], BM! [barcode 000777147], BM!

(fragm.) [barcode 000907753], BR-n.v., P! [barcode 00630757]). **Figs. 14D, 16G, 25F–K.**

Rhizomes decumbent to erect, scales 15.0–20.0 × ca. 1 mm, appressed to ascending, linear-lanceolate, brown or golden, lustrous, flat to twisted, entire to sparsely denticulate; **leaves** up to 1.2 m long; **petiole base scales** ca. 10.0 × 0.5 mm, spreading to loosely ascending, linear-lanceolate, brown, lustrous, twisted, entire to sparsely denticulate; **laminae** to 0.8 m long, basally 1-pinnate-pinnatisect or rarely 2-pinnate, medially 1-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 10.0–20.0 cm long, equilateral, the segments adnate, often with the basal basiscopic pinnule enlarged and slightly more lobed on the basiscopic side; **pinna rachises** abaxially eglandular, sparsely pubescent (sometimes apparently without hairs), scaly, the hairs 0.1–0.2 mm long, 1- or 2-celled, spreading, the scales 3.0–5.0 × 0.2–0.3 mm, reddish-brown, linear-lanceolate, brown, lustrous, flat to twisted, spreading, entire to sparsely denticulate, not clathrate, not bullate, adaxially pubescent to glabrous, lacking scales, the hairs 0.3–1.0 mm long, 5–7-celled, antrorsely curved; **basal basiscopic pinnules of medial pinnae** often (especially in large leaves) enlarged and overlapping the lamina rachis; **costules** abaxially eglandular, without hairs, sparsely scaly, the scales 1.0–1.5 × ca. 0.1 mm, otherwise like those of the pinna rachises, adaxially glabrous or sparsely pubescent, the hairs similar to those of the pinna rachises; **laminar tissue between veins** abaxially eglandular, glabrous, often with numerous appressed proscales, adaxially eglandular, glabrous; **ultimate veins** abaxially glabrous, usually obscure, adaxially obscure or glabrous partially visible; **lamina margins** eglandular, sparsely ciliate, the hairs ca. 0.2 mm long, 1- or 2-celled, acicular, ascending or sometimes appressed; **indusia** absent; **spores** cristate.

Distribution and ecology.—Ecuador, Peru, Bolivia, eastern side of Andes; 260–1700 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Morona-Santiago**: Morona Cantón, near the city of Macas, 1000 m, 2°20′S, 78°08′W, 7 Aug 1993, *Fay & Fay 4014* (AAU, F, MO). **Napo**: Añangu, Río Napo, 260–350 m, 0°31′S, 76°23′W, 8 Mar 1983, *Holm-Nielsen et al. 26896* (AAU). **Zamora-Chinchipe**: Nangaritza Cantón, Shaimi, SE de Campamento Militar, márgen derecha de Río Nangaritza, 930 m, 4°18′S, 78°43′W, 27 Oct 1991, *Palacios et al. 8764* (COL, MO, NY, QCNE).

PERU. **Huánuco**: La Divisoria, ca. 25 km NE of Tingo María on the road to Pucallpa, 1700 m, [9°17′S, 76°00′W], 4 Jul 1984, *Moran 3707* (BM, NY). **Junín**: Schunke Hacienda, above San Ramón, 1400–1700 m, 11°07′S, 75°19′W, 8–12 Jun 1929, *Killip & Smith 24659* (NY, US). **Loreto**: Fundo chela, Sinchono, 3 Aug 1948, *Aguilar s.n.* (GH). **Madre de Dios**: Prov. Manu, Parque Nacional Manu, Río Manu, Río Sotileja, 400–450 m, 11°40′S, 71°55′W, 2 Oct 1986, *Foster et al. 11598* (F, MO, US). **Pasco**: Oxapampa, along road Chatarra-Cacazu, forest on steep, rocky slopes, 890 m, 10°32′S, 075°04′W, 1 Jul 2003, *van der Werff et al. 18275* (MO, NY).

BOLIVIA. **Beni**: Prov. Ballivian, 138 km N of Caranavi, 700 m, 15°20′S, 67°12′W, 20 Jun 1989, *Fay & Fay 2051* (MO). **Cochabamba**: Chapare, El Palmar, 700 m, 17°05′S, 65°32′W, 4 Sep 1996, *Kessler et al. 8126* (GOET, NY). **La Paz**: Prov. Abel Iturralde, Parque Nacional Madidi, campamento de guardaparques Sadiri, camino Sadiri-Tumupasa, 900 m, 14°10′S, 67°55′W, 3 Jul 2004, *Jiménez & Huaylla 2547* (NY). **Santa Cruz**: Prov. Ichilo, 4 km SW del Campamento Macuñucu, 17°44′S, 63°35′W, 27 Sep 1996, *Kessler et al. 8680* (GOET).

Megalastrum fibrillosum is characterized by laminae medially 1-pinnate-pinnatisect or 2-pinnate, pinnae equilateral, and (at least in large laminae) the basal basiscopic segments often slightly enlarged and overlapping the lamina rachis. The overlapping segments are somewhat wider and more lobed on the basiscopic side. The species is further distinct by pinnae rachises abaxially with conspicuous dark spreading scales. The indument on the pinna rachises adaxially varies from glabrous to pubescent. Many specimens of *M. fibrillosum* were identified previously as *M. honestum* (Baker) A. R. Sm. & R. C. Moran (e.g., by Tryon and Stolze 1991), a name here considered of uncertain application.

Several species resemble *Megalastrum fibrillosum* in lamina dissection. One is *M. platylobum,* which differs by pinna rachis hairs longer (up to 0.5 mm) and the scales sparse, inconspicuous, and appressed. *Megalastrum bolivianum* differs by costules and veins adaxially with long (ca. 1 mm) straightish hairs (vs. glabrous), and by the lamina and pinna rachises abaxially scaly by wider lanceolate (not fibrillose) scales. *Megalastrum ctenitoides* differs by rhizome scales smaller, 2.5–4.5 mm long (vs. 15–20 mm), lamina and pinnae rachises with lanceolate scales (vs. fibrillose), and lamina margins glabrous or nearly so (vs. ciliate). See *M. molle* for comparison with that species.

15. *Megalastrum fimbriatum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—PERU. San Martín: Prov. Mariscal Cáceres, trail between La Playa camp and Papayas camp, Río Abiseo National Park, 7°45′S, 77°15′W, 25 Jul 1987, *K. Young & B. León 4958* (holotype, F! [barcode 1999770]; isotypes, AAU!, GH-n.v., USM-n.v.). **Figs. 10F, 14B, 15A–E.**

Rhizomes erect, scales 1.5–1.8 × ca. 0.3–0.8 mm, appressed to ascending, linear-lanceolate, light brown, lustrous, flat to twisted, sparsely denticulate; **leaves** up to 0.5 m long; **petiole base scales** up to ca. 1.5 × 2 mm, spreading to ascending, lanceolate to linear-lanceolate, brown, lustrous, flat, denticulate; **laminae** 20–30 cm long, basally 2-pinnate-pinnatifid or 3-pinnate, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** up to 15 cm long, equilateral to subequilateral; **pinna rachises** abaxially eglandular, densely pubescent, scaly, the hairs 0.5–0.8 mm long, 4–6-celled, spreading, the scales up to 3 × 0.5 mm long, lanceolate, brown, lustrous, flat, spreading, entire to subentire, not clathrate, not bullate, adaxially eglandular, moderately to sparsely pubescent, very sparsely scaly, hairs up to 2.5 mm long, 5–8-celled, spreading, the scales like those abaxially; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs like those abaxially, the scales like those of pinna rachises but shorter up to 2 mm long, adaxially sparsely pubescent, the hairs like those of the pinna rachises abaxially, scales absent; **laminar tissue between veins** abaxially glabrous, adaxially with scattered hairs toward the margins, the hairs 0.5–1.0 mm long, 6–8-celled, appressed; **ultimate veins** on both surfaces visible, abaxially very sparsely glandular (often apparently eglandular), sparsely pubescent, the glands ca. 0.1 mm long, sessile, reddish, the hairs 0.2–0.5 mm long, 2–4-celled, adaxially sparsely glandular, pubescent, scales absent, the glands ca. 0.1 mm long, sessile, reddish, the hairs ca. 1.0–1.5 mm long, 5–8-celled, whitish, lax, slightly tortuous; **laminar margins** ciliate, eglandular, the hairs 0.5–1.2 mm long, 5–9-celled, lax, spreading to ascending; **indusia** absent; **spores** cristate.

Distribution.—Peru; 2280–2750 m.

SPECIMENS EXAMINED.—PERU. **Bagua**: Amazonas, Third camp, Cordillera Colan SE of La Peca, 2280–2400 m, [5°38′S, 78°31′W], 30 Sep 1978, *Barbour 3682* (MO).

Megalastrum fimbriatum is distinctive by small laminae (20–30 cm long), pinnules mostly adnate for their entire width to the pinna rachises, pinna rachises abaxially densely pubescent and scaly, lamina margins fimbriate with long (0.8–1.2 mm), lax cilia (thus the specific epithet *fimbriata*). It resembles *M. peruvianum* but differs by longer (0.5–1.5 vs. 0.2–0.5 mm) hairs on the veins adaxially and the tissue between the veins glabrous on both surfaces (vs. pubescent). Tryon and Stolze (1991) thought that the holotype represented a "depauperate specimen of high elevation variant" of *M. pulverulentum*; however, this species does not have cristate spores and does not belong to the *M. pulverulentum* clade. It is amply distinct from *M. pulverulentum* by its small leaves (up to 0.5 m vs. up to 4 m long), less divided laminae (medially 2-pinnate-pinnatisect vs. medially 3-pinnate-pinnatisect), and pinna rachis scales not darkened distally.

16. *Megalastrum fugaceum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—BOLIVIA. Santa Cruz: Prov. Florida, Cantón Mairna, Parque Nacional Amboró, 7 km NNE by air from Mairana, 18°03′S, 65°55′W, 1900–2200 m, 23 Jul 1994, *R. C. Moran 5911* (holotype: LPB!; isotypes: AAU!, NY! [barcode 00870951], UC! [barcode 1604363, 1604364]). **Figs. 2D,F, 3G, 24B, 26A–D, E–G.**

Rhizomes erect, scales 20.0–35.0 × 0.5–1.5 mm, linear, ascending, castaneous, slightly lustrous, flat or twisted, not tortuous, sparsely to retrorsely denticulate, apically with spreading or retrorse teeth; **leaves** up to 4 m long; **petiole base scales** like those of the rhizomes, sometimes forming a wool-like tuft; **laminae** 1–3 m long, basally 3-pinnate-pinnatisect to 4-pinnate, medially 3-pinnate-pinnatisect; **lamina rachises** glabrous to sparsely pubescent abaxially; **basal pinnae** ca. 1.4 m long, strongly inequilateral; **pinna rachises** abaxially eglandular, glabrous or pubescent, sparsely scaly, the hairs (when present) 0.4–0.8 mm, 3–5-celled, spreading, the scales 0.1–1.8 × 0.1–0.5 mm, ovate to lanceolate, appressed or spreading, light to dark brown, often darker distally, strongly denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.3–0.5 mm long, 3–6-celled, spreading, scales 0.5–3.0 × 0.1–0.4 mm, linear-lanceolate, darkened toward the apex, strongly denticulate; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially with indument like that of the pinna rachises but scales larger, to 0.5–2.5 × 0.2–0.3 mm, ovate (smaller scales) to linear (longer scales), strongly darkened toward the tip denticulate, adaxially like the pinna rachises but hairs 0.3–2.0 mm long, 3–5-celled, spreading; **laminar tissue between ultimate veins** on both surfaces eglandular, glabrous or pubescent, the hairs (when present) 0.2–0.4 mm long, 3- or 4-celled, erect; **ultimate veins** visible on both lamina surfaces, eglandular, abaxially subglabrous to moderately pubescent, the hairs (when present) 0.2–0.4 mm long, ca. 3-celled, spreading, adaxially similar but when pubescent the hairs 0.5–0.7 mm long, 3–6-celled, strigose to laxly spreading; **lamina margins** eglandular, ciliate, the hairs 0.1–1.2 mm long, 2–4-celled, spreading to ascending; **indusia** minute, fugacious, apparently consisting of a cluster of reddish proscales, ca. 0.1 mm long, protruding from the center of the sorus, not easily observed in mature sori; **spores** echinulate.

Distribution.—Ecuador, Peru, Bolivia, Argentina; 1060–2300(–3500) m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Carchi**: Espejo, El Gualtal, faldas de Cerro Golondrina Hembra, 2450 m, 0°51′N, 78°07′W, 21 Aug 1994, *Palacios 12645* (MO, QCNE). **Chimborazo**: in valle Pallatango, [1°59′S, 78°57′W], s.d., *Sodiro 113* (P). **Loja**: trails ca. 5 km ENE San Pedro de Vilcabamba, from "El Bosque" to Quebrada Romerillos and Banderilla, open trail banks in pastures and deep wet stream ravines, 2000–2200 m, 4°14′S, 79°10′W, 30 Nov 1994, *Øllgaard & Navarrete 105941* (AAU). **Napo**: Quijos Cantón, swampy forest on NE side of Quijos, go N on the road E of the Colegio, toward the river, 1850 m, 0°27′30″S, 77°53′W, 6–8 Aug 1992, *Fay & Fay 3870* (MO, NY); road Baeza-Tena, 2 km N of Consaga, 2000–1900 m, 0°34′S, 77°53′W, 19 Jan 1992, *Øllgaard et al. 99556* (AAU). **Pichincha**: camino Calacalí-Nanegalito, 18 km from Mitad del Mundo, inclination steep, orientation 280, few disturbances, 2040–2090 m, 0°01′N, 78°37′W, 20–25 Apr 1995, *Ankersen & Kragelund 140* (AAU, QCA). **Zamora-Chinchipe**: New road Loja to Zamora, 13 km E of the Pass, Wet forest along creek that crosses the road, 2000 m, 4°00′S, 79°02′W, 14 Feb 1991, *Moran & Rohrbach 5380 p.p.* (MO, QCNE, UC).

PERU. **Cusco**: Distr. Huayopata, Huyro, Calquiña, 1600 m, 12°52″01″S, 72°32′46″W, 26 Jun 2003, *Bonino et al. 734* (MO, NY). **Urubamba**: Machu Picchu, on a slope, 5 km N of the union of the Sayacmarca and Aobamba Rivers, 2160 m, [13°09′S, 72°32′W], 14 Oct 1982, *Peyton 1497* (MO).

BOLIVIA. **Chuquisaca**: Sud Cinti, cercanías de una quebrada con aguas que desembocan al Río Alborniyoj, 2300 m, 20°45′23″S, 64°31′46″W, 11 Oct 2000, *Lliully et al. 101* (MO). **Cochabamba**: 130 km antigua carretera Cochabamba-Villa Tunari, 2000 m, 17°08′S, 65°38′W, 11 Jul 1996, *Kessler et al. 7189* (GOET, UC). **La Paz**: Prov. Franz Tamayo, Area Natural de Manejo Integrado

Apolobamba, 2372 m, [14°39′S, 69°14′W], 10 Jun 2008, *Huaylla et al. 2655* (MO). **Santa Cruz**: Manuel M. Caballero, bosque hiperhumedo de Ceja de Monte, Colecta en la comunidad El Locotal sobre el camino a San Mateo a 10 km del cruce El Empalme, 2364 m, 17°47′43″S, 64°43′15″W, 17 Jun 2003, *Núñez & Huaylla 178* (NY, UC). **Tarija**: Arce, Mpio. Padyaca, Reserva Nacional de Flora y Fauna Tariquia, 1660 m, 22°00′S, 64°29′W, 14 Nov 2004, *Serrano et al. 5225* (GOET, MO); idem, bajando de La Cumbre hacia Potreros, una sola planta, ladera con Río permanente, 1706 m, 22°00′20.5″S, 64°31′59″W, 13 Dec 2004, *Huaylla et al. 1554* (MO, NY).

ARGENTINA. **Jujuy**: Depto. Ledesma, Parque Nacional Calilegua, RP 83, Aguada del Tigre, 1600 m, 23°41′S, 64°53′W, 7 Apr 2010, *Martínez & Prado 1894* (MCSN, NY, SP). **Tucumán**: Monteros, Quebrada Pueblo Viejo, [27°10′S, 65°30′W], Jan 1965, *de la Sota 4069* (US).

Megalastrum fugaceum resembles *M. pulverulentum* by its large leaves (up to 4 m long) and scales of the pinna rachises and costules usually darkened apically and strongly denticulate. *Megalastrum pulverulentum* differs by laminae with longer (1.0–2.0 mm) and denser hairs; its lamina and pinna rachises are conspicuously pubescent to naked eye. In contrast, *M. fugaceum* is a less pubescent version. Its hairs are only 0.4–0.8 mm long and relatively sparse, not conspicuously pubescent to the naked eye. Whereas *M. pulverulentum* is pubescent between the veins abaxially, *M. fugaceum* is glabrous except in a few instances. In those instances, the hairs are much shorter (0.2–0.4 mm long) than those in *M. pulverulentum*. There is considerable variation in the occurrence of hairs in *M. fugaceum*. The type has sparse whitish hairs on both surfaces of the veins, whereas other plants are glabrous.

17. ***Megalastrum galapagense*** R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Galapagos Islands: Isla Isabela, SW slope of Volcano Cerro Azul, [0°38′S, 90°22′W], 800 m, Aug 1975, *H. H. van der Werff 2244* (holotype: NY! [barcode 01093322]; isotypes: MO-n.v., U! [barcode 0249530]). **Figs. 14C, 20O–P, 27C.**

Rhizomes erect, the scales 20.0–30.0 × 0.6–1.1 mm, appressed to ascending, linear-lanceolate, golden brown, lustous or dull, flat to tortuous, the surfaces smooth (not setulose), denticulate, the teeth simple or bifid; **leaves** up to 2.5 m long; **petiole base scales** like those of the rhizomes but to 15.0 × 0.7 mm, spreading to loosely ascending; **laminae** up to 1.5 m long, basally and medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 0.35 m long, equilateral; **pinna rachises** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs 0.4–0.5 mm long, 3–4-celled, spreading, acicular, the scales 1.5–3.5 × 0.1–0.3 mm, filiform to linear-lanceolate, brown, lustrous, conspicuously denticulate, not clathrate, not bullate, adaxially eglandular, pubescent, scales absent, the hairs 0.7–1.0 mm long, 4–6-celled, acicular, tortuous, catenate; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs 0.3–0.5 mm long, 3- or 4-celled, erect, acicular, hyaline, the scales ca. 0.5–1.0 × 0.1 mm, otherwise like those of the pinna rachis, adaxially eglandular, glabrous to sparsely pubescent, scales absent, the hairs 0.3–0.5 mm long, 3- or 4-celled, acicular, hyaline, catenate, ascending, tortuous; **laminar tissue between veins** abaxially eglandular, sparsely pubescent, the hairs 0.2–0.3 mm long, 2- or 3-celled, acicular, erect, hyaline, adaxially eglandular, glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, sparsely pubescent, the hairs similar to those of the abaxial pinna costae; adaxially eglandular, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.3 mm long, 2- or 3-celled, erect, acicular, ascending; **indusia** absent; **spores** cristate.

Distribution and ecology.—Isabella Island in the Galapagos Archipelago; *Miconia* belt vegetation; 800 m.

SPECIMENS EXAMINED.—ECUADOR. **Galápagos**: Isabella Island, SW slope of Volcano Cerro Azul, 800 m, [0°01′S, 91°12′W], Aug 1975, *van der Werff 2256, 2257* (U).

Megalastrum galapagense and *M. pleiosoros* are the only *Megalastrum* in the Galapagos Islands. They are similar in lamina shape, but *M. galapagense* differs by longer leaves, up to 2.5 m long (vs. 1.0 m), laminae more divided (2-pinnate-pinnatisect medially vs. 1-pinnate-pinnatisect to (one specimen) 2-pinnate-pinnatifid medially), and pinna rachises and costules abaxially sparsely pubescent (vs. densely pubescent). In *M. galapagense* the hairs on the abaxial surfaces of the laminae are shorter than in *M. pleiosoros* (0.4–0.5 mm long, 3–4-celled, vs. 0.6–1.0 mm long, 6–8-celled).

The specific epithet *galapagense* refers to the Galapagos Islands. *Megalastrum galapagense* occurs only on Isabella Island, whereas *M. pleiosoros* occurs on Isabella and others.

18. Megalastrum hirsutosetosum (Hieron.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:128. 1987 [published 3 May 1988]. *Dryopteris hirsutosetosa* Hieron., Hedwigia 46:343, tab. 6, 16. 1907. *Ctenitis hirsutosetosa* (Hieron.) Lellinger, Proc. Biol. Soc. Wash. 89:709. 1977. TYPE.—ECUADOR. Tungurahua?: plateau above Allpayacu between Baños and Jivaría de Píntuc, s.d., *M. A. Stübel 903* (lectotype, designated by Christensen, 1920: B! [barcode 20 0057934], photo BM; isolectotype: BM! (fragm.) [barcode 000907751]). **Figs. 24C, 28K–P, 29A.**

Rhizomes erect, scales ca. 10.0 × ca. 1.5 mm, lanceolate, golden brown, lustrous, tortuous, denticulate; **leaves** up to 1 m long; **petiole base scales** ca. 10.0 × ca. 1 mm, lanceolate, spreading, brown, lustrous, flat to twisted, denticulate; **laminae** 0.5–0.8 m long, basally 2-pinnate to 2-pinnate-pinnatisect, medially 1-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 8.0–15.0 cm long, usually slightly inequilateral, sometimes equilateral; **pinna rachises** abaxially eglandular, pubescent, sparsely scaly, the hairs ca. 1.5 mm long, 6–8-celled, acicular, spreading to erect, whitish, the scales ca. 1 × 0.1 mm, appressed to spreading, filiform, brown, tortuous, denticulate, not clathrate, not bullate, adaxially eglandular, densely pilose, without scales, the hairs similar to those of the pinna rachises abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, pubescent, without scales, the hairs ca. 1.5 mm long, 7–10-celled, appressed to spreading, acicular, hyaline, adaxially eglandular, sparsely pilose, scales absent, the hairs like those of the adaxial pinna rachises; **laminar tissue between veins** both surfaces eglandular, pubescent, the hairs similar to those of the abaxial pinna rachises and costules; **ultimate veins** obscure and pilose on both surfaces, the hairs similar to those of the laminar tissue; **lamina margins** eglandular, ciliate, the hairs ca. 1.0 mm long, 5–7-celled, acicular, spreading; **indusia** absent; **spores** cristate.

Distribution and ecology.—Colombia, Ecuador, and Peru, eastern slopes of the Andes; 450–1200(–2250) m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Chocó-El Valle**: at and on both sides of the principal ridge of the Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, 2200–2250 m, 4°12′S, 75°48′W, 20 March 1971, *Lellinger & de la Sota 840* (US).

ECUADOR. **Carchi**: Border area between Prov. Carchi and Esmeraldas, about 7 km past Lita on road Lita-Alto Tambo, 550 m, [0°50′N, 78°28′W], 27 Jun 1991, *van der Werff et al. 12094* (MO, QCA, QCNE). **Esmeraldas**: Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", Km 140 on road Loja-Gualaquiza, Tropical rain forest with cleared areas Río Zamora and along the road, 900–1000 m, 3°37′S, 78°34′W, 26–27 Apr 1973, *Holm-Nielsen et al. 4502* (AAU, MO, NY). **Napo**: Hollin-Loreto road, 32 Km mark, 3–4 km S of road, path to permanent sampling plot, 1200 m, 0°35′S, 77°25′W, 25 Jan 1991, *Moran & Rohrbach 5160* (AAU, MO, NY). **Pastaza**: Río Pastaza, between Baños and Mera, 1219 m, [1°23′S, 78°03′W], 4 Jul 1905, *Tate 650* (US). **Zamora-Chinchipe**: Cordillera del Condor, Río Wawaime watershed, tributary of Río Quimi, along road above EcuaCorriente mine camp, 1300 m, 3°34′43″S, 78°26′07″W, 26 Oct 2006, *van der Werff et al. 21715* (MO, NY); Miazi, at junction of Río Chumbiriatza with Río Nangaritza, 1200–950 m, 4°19′S, 78°40′W, 21–23 Oct 1991, *Øllgaard et al. 99268* (AAU, QCA).

PERU. **Cajamarca**: Prov. San Ignacio, Distr. San José de Lourdes, localidad de Buenos Aires, Cerro El Parco, 1900 m, 5°42′04″S, 77°53′06″W, Feb 2002, *Bonino 178* (MO). **Junín**: Pichis trail, San Nicolas, 1100 m, 4–5 Jul 1929, *Killip & Smith 26037* (NY, US). **Pampayacu**: Pampayacu, [11°09′S, 76°36′W], 28 Jan 1927, *Kanehira 184* (GH).

Megalastrum hirsutosetosum has laminae with both surfaces densely and conspicuously pubescent to the naked eye. The hairs are 1.0–1.5 mm long, 5–7-celled, and present on and between the veins of both surfaces. It is further distinguished by laminae medially 2-pinnate to 2-pinate-pinnatisect and by rachis scales filiform, ca. 1 × 0.1 mm. *Megalastrum platylobum* is similar in lamina dissection and size but differs by pinna rachises abaxially densely pubescent by hairs of mixed lengths, all of which are shorter than those found in *M. hirsutosetosum*.

19. *Megalastrum insigne* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Napo: Cantón Quijos, south of Quijos, just east of Baeza, trail through pastures and up into the jungle, now being logged, terrestrial, 0°28.5′S, 77°53.5′W, 2100 m, 4 Aug 1992, *A. Fay & L. Fay 3827* (holotype: NY! [barcode 01053865]; isotypes: AAU! 3-sheets; MO [barcode 05083493, 05083493], QCA-n.v., QCNE-n.v.). **Figs. 2B, 4M–X, 6E, 24D.**

Rhizomes erect, the scales 10.0–20.0 × 1.0–2.0 mm, appressed to ascending, lanceolate, brown to dark brown, lustrous, flat, densely denticulate; **leaves** up to 1.5 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.5–0.7 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 15.0–25.0 cm long, strongly inequilateral; **pinna rachises** abaxially glandular, densely pilose, sparsely scaly, with 0.1 mm long, short-stipitate and sessile glands, the hairs 1.0–1.5 mm long, 5–8-celled, acicular, spreading, hyaline, whitish to ferrugineous or tan, the scales 1–3 × 0.4–0.8 mm, lanceolate, spreading, brown, not flaccid, shiny, entire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, without scales, densely pilose, the hairs 0.7–1.5 mm long, 5–12-celled, spreading to ascending, acicular; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially sparsely glandular, pilose, sparsely scaly, the glands and hairs like those of the pinna rachises, the scales ca. 2.0 × 0.3 mm, like those of the pinna rachises, adaxially sparsely glandular, densely pilose, the glands and hairs like those of the pinna rachises abaxially; **laminar tissue between veins** on both surfaces glandular, moderately to densely pubescent, the hairs 0.8–1.2 mm long, 5–8-celled, acicular, erect to appressed, some of the hairs gland-tipped, 0.2–0.4 mm long, 3- or 4-celled, the sessile glands ca. 0.1 mm long, spherical, yellowish; **ultimate veins** with hairs and glands the same as those on the laminar tissue between the veins, abaxially the veins partially visible, adaxially obscure; **lamina margins** eglandular, ciliate, the hairs 0.4–0.8 mm long, 3–7-celled, acicular, spreading to ascending; **indusia** present, ca. 1 mm wide, conspicuous, circular, concolorous, brown, glandular, pubescent, the glands sessile or short-stalked, the sessile glands 0.1 mm long, the stalked glands 0.2 mm long, the hairs 0.3–1.0 mm long, 3–7-celled, acicular, erect, hyaline; **spores** cristate.

Distribution and ecology.—Colombia, Ecuador, Peru, both sides of the Andes; 1300–2400 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Río Calderas, cerca de Cocorná, [5°58′N, 75°06′W], Jan 1953, *Daniel Bro. 4473* (US). **Caldas**: Pueblo Rico [Neira], Cordillera Occidental, vertiente Occidental, 1700–1900 m, [5°08′S, 75°31′W], 17 Feb 1946, *von Sneidern 5236 p.p.* (US). **Cauca**: Montaña del Oro, [5°08′N, 75°31′W], s.d., *Lehmann 7416* (K). **Valle**: Finca la Pradera, 6 km SW of El Cairo on the trail to Río Blanco, between El Brillante and Boquerón, 2150–2200 m, [4°12′N, 75°48′W], 27 Mar 1971, *Lellinger & de la Sota 815* (US).

ECUADOR. **Loja**: trails ca 5 km ENE of San Pedro de Vilcabamba, from "El Bosque" to Quebrada Romerillos and Banderilla, 2000–2200 m, 4°14′S, 79°10′W, 30 Nov 1994, *Øllgaard & Navarrete 105938* (AAU). **Napo**: forest ridge just S of Baeza, 1950–2100 m, 0°28′S, 77°53′W, 31 Mar 1992, *Øllgaard 99904* (AAU, QCA, QCNE); road Baeza-Tena, 2 km of Cosaga, 1900–2000 m, 0°34′S, 77°53′W, 17 Jan 1992, *Øllgaard et al. 99554* (AAU); Valley of Río Oyacachi, ca 10 km along road W of El Chaco, trail along river to Río San Juan Grande, 1760–1800 m, 0°17′S, 77°51′W, 12 Mar 1996, *Øllgaard & Navarrete 1630* (AAU). **Pastaza**: Montaña de Canelos, 1600 m, [1°30′S, 78°03′W], Aug 1860, *Spruce 5295 p.p.* (BM, K, NY, P). **Pichincha**: Cantón Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old road Quito-Santo Domingo, 1900 m, 0°14′S, 78°48′W, 10 Jul 1991, *Fay & Fay 3370* (AAU, MO, NY, QCA, QCNE); Cerro Antisana, primary montane forest 2 mi. SE of Borja, 1737 m, 0°30′S, 78°W, 3 Aug 1960, *Grubb et al. 1195* (BM, NY, US). **Santiago-Zamora**: high wooded slopes, on W side of Río Valladolid, above Valladolid, 2100–2400 m, [4°33′S, 79°03′W], 15 Oct 1943, *Steyermark 54713* (F, US). **Tungurahua**: San Antonio, eastern slope of Tungurahua Volcano, 1737 m, [1°28′1″S, 78°26′30″W], 1924, *Tate 573* (US). **Zamora-Chinchipe**: Parque Nacional Podocarpus, Quebrada Río San Francisco, at new road Loja-Zamora, 2040–2250 m, 3°58′S, 79°05′W, 23 Jun 1988, *Øllgaard 74966* (AAU, QCA).

PERU. **Amazonas**: Bongara, Hills 1–5 km. S-SE (150°) of Yambrasbamba, 2100–2400 m, [5°45′S, 77°54′W], 25 Jun 1962, *Wurdack 1030* (GH, NY, US). **Cajamarca**: San Ignacio, San José de Lourdes, Camaná, 2000–2200 m, 5°00′00″S, 78°55′00″W, 20 Mar 1997, *Campos & Corrales 3593* (GH, MO, NY). **Cusco**: La Convención, Dist. Huayopata, Amaybamba, Quinsapunkuyoq, 2050 m, 12°59′18″S, 72°30′06″W, 22 Nov 2003, *Bonino et al. 1104 p.p.* (MO). **Pasco**: Oxapampa, 1768 m, [10°06′S, 75°09′W], Aug 1947, *Soukup 3354* (GH, US). **San Martín**: Prov. Mariscal Caceres, alrededores de la Morada, 2200–2300 m, [7°33′S, 76°47′W], 25 Jun 1995, *Quipuscoa et al. 11* (AAU, F). **San Martín-Huallaga**: Abajo de La Morada, cerca del Río Guabayacu, 1900–2200 m, 6°57′S, 77°32′W, 10 Aug 1997, *Quipuscoa & Bardales 958* (AAU, F).

Megalastrum insigne is characterized by the presence of conspicuous circular indusia pubescent by hairs 0.3–1.0 mm long, and laminae with both surfaces densely and conspicuously pubescent. The specific epithet *insigne* (remarkable, outstanding) refers to the dense, conspicuous indument of the leaves. *Megalastrum insigne* has been confused with *M. andicola* but differs by laminae and indusia with longer hairs (for laminae, 0.8–1.2 mm long, 5–7-celled; for indusia, 0.3–1.0 mm long, 3–7-celled). To the naked eye, the denser, more conspicuous pubescence distinguishes *M. insigne* from the similar *M. acrosorum* and *M. andicola*.

20. Megalastrum marginatum M. Kessler & A. R. Sm., Amer. Fern J. 96:40, fig. 2G–J. 2006. TYPE.—BOLIVIA. La Paz: Prov. Nor Yungas, Cerro Hornuni, 16°01′S, 67°52′W, 27 Nov 1998, *A. Portugal 538* (holotype: UC! [barcode 1736806]; isotype: LPB-n.v.). **Figs. 9A–E, 10A, 24A.**

Rhizomes erect, scales 5.0–12.0 × 0.2–0.6 mm, linear-lanceolate, spreading to ascending, brown to golden brown, lustrous, twisted, denticulate, the teeth simple or sometimes bifid, sometimes retrorse; **leaves** 0.6–0.7 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.4–0.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatifid; **lamina rachises** pubescent abaxially; **basal pinnae** 15.0–18.0 cm long, strongly inequilateral; **pinna rachises** abaxially eglandular, pubescent, scaly, the hairs (0.5–)1.0–1.7 mm long, 4–7-celled, straightish, spreading, white, the scales 1.5–3.0 × 0.2–0.8 mm, lanceolate, brown, lustrous, denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.5–1.8 mm long, 4–7-celled, spreading, straightish, white, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs like those of the pinna rachises, the scales like those of the pinna rachises but smaller 0.5–0.8 × 0.2–0.3 mm, adaxially eglandular, sparsely pubescent, without scales, the hairs 0.5–1.0 mm long, 4–6-celled; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, glabrous to sparsely pubescent, the hairs 0.2–0.4 mm long, 2- or 3-celled, spreading, straightish, white, adaxially pubescent, the hairs 0.7–1.0 mm long, 3- or 4-celled, appressed, ascending, straightish, whitish; **lamina margins** eglandular, ciliate, the hairs 0.3–0.5 mm long, 2- or 3-celled, straightish, whitish, ascending; **indusia** absent; **spores** cristate.

Distribution.—Bolivia; 400–1900 m.

SELECTED SPECIMENS EXAMINED.—BOLIVIA. **Carrasco**: Cochabamba, 400 m, 17°17′35″S, 64°52′87″W, 19 Jan 2000, *Jiménez 226* (UC). **Cochabamba**: Prov. Tiraque, Km 18 al Palmar, 900 m, 17°05′35″S, 65°29′35″W, 2 Sep 2003, *Zabalaga 16* (NY). **La Paz**: Abel Iturralde, Parque Nacional Madidi, campamento de guardaparques Sadiri (entre Tumupasa y San Juan de Uchupiamonas), 950 m, 16°10′S, 67°54′W, 2 Jul 2004, *Jiménez & Huaylla 2518* (NY, UC); Prov. Nor Yungas, Cantón Pacollo, Estación Biológica Tunquiri, Hornuni Bajo, 1900 m, 16°42′S, 67°52′W, 24 Jul 2001, *Bach 1234* (UC); Prov. Sud Yungas, Sapecho, Colonia Tupiza, 735 m, 15°32′S, 67°18′W, 29 Oct 1997, *Krömer et al. 100* (GOET, UC).

Megalastrum marginatum is characterized by 0.5–1.7 mm long, straight, whitish hairs on both surfaces of the pinna rachises, costules, and veins. The density of the hairs varies, but at least a few long straight hairs are always present. The species most resembles *M. rupicola,* which differs by the lack of hairs. In both species the lamina cutting is similar, and the pinna rachis scales are similar by being lanceolate and shiny brown.

Moran and Prado (2010) cited *Megalastrum longipilosum* A. Rojas from Ecuador and Bolivia. The Bolivian report was based on a misidentified specimen of *M. marginatum*. The Ecuadorian report was based on two specimens (*Øllgaard et al. 2247, Ankersen & Kragelund 211*, both AAU, QCA) that represent a new species, *M. obtusum*, described below. *Megalastrum longipilosum* is endemic to Costa Rica and Panama.

21. **Megalastrum martinicense** (Spreng.) R. C. Moran, J. Prado & Labiak, Brittonia 61:284. 2009. *Alsophila martinicensis* Spreng., Neue Entdeck. Pflanzenk. 3:7. 1822. *Phegopteris martinicensis* (Spreng.) Fourn., Mex. Pl. 1:90. 1872. TYPE.—MARTINIQUE. s.d., *F. Kohaut s.n.* (Sieber Syn. Fil. no. 162) (lectotype, designated by Proctor, 1989: L-n.v., photos MICH!, NY!, US!; isolectotypes: K!, P! [barcode 00600601]). **Figs. 13F, 24A, 30A–D.**

Phegopteris epierioides Fée, Mém. Foug., 5. Gen. Filic.:248. 1850–52. TYPE.—CUBA. s.d., *J. J. Linden "282* or *412"* (holotype: P! [barcode 00610891]).

Aspidium araguata Moritz ex Reichardt, Denkschr. Ak. Wien 17(2):38, tab. 2, figs. 28–31. 1859. TYPE.—VENEZUELA. Aragua: Colonia Tovar, [10°25′N, 67°16′W], 1844, *J. W. K. Moritz 202, pro parte* [mixed with *M. subincisum*] (lectotype, here designated: P! [barcode 610894], P! [barcode 610895]; isolectotypes: F!, GH!, P! [barcode 00600403, 00600404], US [barcode 00067054]).

Rhizomes erect, scales 15.0–22.0 × 0.3–0.5 cm, linear-lanceolate, light brown, lustrous, denticulate; **leaves** 1.0–3.0 m long; **petiole base scales** like those of the rhizomes but more spreading to loosely ascending; **laminae** up to 2 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnisect; **lamina rachises** without hairs abaxially; **basal pinnae** ca. 0.5 m long, inequilateral; **pinna rachises** abaxially eglandular, without hairs, scaly, the scales 1.5–3.0 × 0.1–0.2 mm long, linear-filiform, tortuous, brown, denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 1.0–1.2 mm long 4–6-celled, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs 0.3–0.8 mm long, 2–5-celled, acicular, erect to spreading, the scales like those on the pinna rachises abaxially but smaller, 1.5–2.5 × 0.1–0.2 mm, linear to linear-lanceolate, parallel sided, scarcely enlarged basally, adaxially densely pubescent, scales absent, the hairs 0.5–1.0 mm long, 4- or 5-celled, substrigose; **laminar tissue between veins** on both surfaces glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, sparsely pubescent, scales absent, the hairs ca. 0.3–0.5 mm long, 2– or 3-celled, adaxially eglandular, glabrous to subglabrous; **lamina margins** eglandular, ciliate, the hairs 0.2–0.5 mm long, 2–4-celled, spreading to substrigose; **indusia** absent.

Distribution and ecology.—Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Martinique, St. Vincent, St. Lucia, Dominica, Saba, Trinidad, northern Venezuela, Colombia; 1200–1860 m in Colombia and Venezuela; in the West Indies, 0–1600 m (Moran *et al.* 2009b).

Selected Specimens Examined.—VENEZUELA. **Aragua**: Cordillera interior, faldas que miran al norte, a lo largo del camino entre El Pauji y El Socorro, hacia la represa, al sur de El Consejo, 1350–1400 m, 10°11′N, 67°15′W, 16 Jul 1979, *Steyermark & Stoddar 118183* (GH, VEN). **Distrito Federal**: without locality, [10°35′N, 66°54′W], 1845–1846, *Funcke & Schlim 282* (B, P). **Yaracuy**: Border area between Edo. Lara-Yaracuy, Sierra de Aroa, 10–13 min NW of Urachiche (Edo. Yaracuy) along dirt road leading NW from Urachiche to Duaca (Edo. Lara), 1400 m, 10°14′N, 69°04′W, 16 Nov 1982, *Smith et al. 1342* (MO, UC).

COLOMBIA. **Antioquia**: Antioquia, 1500 m, [6°33′N, 75°49′W], 26 Jan 1988, *Arbeláez et al. 287* (NY). **Quindio**: without locality, [4°32′N, 75°40′W], Feb 1852, *Triana 615* (BM). **Tolima**: Mariquita, Combaima, 1200 m, [5°12′N, 74°54′W], Jan 1843, *Linden 1020 p.p.* (B, P).

Megalastrum martinicense is characterized by pinna rachises abaxially without hairs and with dark, tortuous, filiform scales. The scales, at least apically, are usually only 1–3 cells wide. The species greatly resembles *M. subincisum,* which differs by scales of the pinna rachises and costules golden brown, lanceolate to linear-lanceolate, and more than 3 cells wide.

The type number of the synonym *Aspidium araguatum* (*Moritz 202*) is mixed. Specimens of this number at K and P (P-00600401, P-00600402) represent *M. subincisum.*

22. **Megalastrum microsorum** (Kuntze) Stolze, Fieldiana, Bot., n. s. 27:14. 1991. *Nephrodium microsorum* Hook., Sp. Fil. 4:106. 1862. *nom. illeg.*, non Endl. 1833. *Dryopteris microsora* Kuntze, Revis. Gen Pl. 2:813. 1891, *nom. nov.* for *Nephrodium microsorum* Hook. *Dryopteris leptosora* C. Chr., Index Fil. 274. 1905, *nom. superfl.* for *Nephrodium microsorum* Hook. *Megalastrum leptosorum* (C. Chr.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:128. 1987 [published 3 May 1988]. Type.—ECUADOR. [Tungurahua?]: at the foot of Mt. Chimborazo, [1°28′S, 78°49′W] s.d., *R. Spruce s.n.* (lectotype, designated by Tryon and Stolze, 1991: K! [barcode 000200224], photos F!, GH!; isolectotype: BM! (fragm), [barcode 000921537]). **Figs. 5A, 25A–D, 27B, 28Q–X.**

Rhizomes erect, scales 10.0–20.0 × 0.5–1.0 mm, appressed, linear-lanceolate, gold-brown, flat to tortuous, the margins densely denticulate, the teeth bifid; **leaves** 0.8–1.2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.3–0.6 m long, basally 2-pinnate, medially 1-pinnate-pinnatisect to 2-pinnate; **lamina rachises** pubescent abaxially; **basal pinnae** 10.0–20.0 cm long, equilateral; **pinna rachises** abaxially eglandular, glabrous to densely and evenly puberulent, scaly, the hairs (when present) 0.2–0.5 mm long, 2- or 3-celled, erect to spreading, acicular, hyaline, the scales ca. 3 × ca. 0.1 mm, filiform, brown, tortuous, ascending, lustrous, denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, without scales, the hairs 0.5–0.8 mm long, 4–6-celled, light brown, ascending, antrorsely strigose, acicular; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, glabrous or sparsely pubescent, scales absent, the hairs (when present) 0.1–0.5 mm long, 1–3-celled, like those of the pinna rachises, adaxially eglandular, glabrous to pubescent, scales absent, the hairs similar to those abaxially; **laminar tissue between veins** abaxially eglandular, glabrous or puberulent, the hairs (when present) 0.1–0.2 mm long, 1- or 2-celled, acicular, erect, hyaline, adaxially eglandular, glabrous; **ultimate veins** on both surfaces visible, eglandular, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.1–0.2 mm long, 1- or 2-celled, acicular, appressed to ascending; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru; humid secondary forests, fog forests; 600–1300(–2800) m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Cotopaxi**: Tenefuerste, Río Pilalo, km 52–53, Quevado, Latacunga, 750–1300 m, [1°02′S, 79°27′W], 7 Feb 1982, *Dodson & Gentry 12280* (MO, QCNE). **Guayas**: Cordillera Chongón-Colonche, Bosque Protector Loma Alta, 600 m, 0°48′S, 80°47′W, 21 Dec 1996, *Cornejo & Bonifaz 5459* (AAU). **Loja**: Vic. of Orianga, 1100 m, 3°52′S, 79°51′W, 5 Mar 1990, *Madsen 86916* (AAU). **Manabi**: Cordillera de Congón, Parque Nacional Machalilla, S of San Sebastian, 500–600 m, [01°35′S, 80°41′W], 24 Mar 1993, *Øllgaard et al. 100773* (QCA).

PERU. **Cajamarca**: Prov. Santa Cruz, ruta Chorro Blanco-Monteseco, 1750 m, [6°51′S, 79°06′W], 21 Jan 1996, *Leiva et al. 1759* (F). **Junín**: Paucartambo, 2800 m, [13°18′S, 71°35′W], 24 July 1961, *Woytkowski 6742* (US).

Megalastrum microsorum is characterized by laminae medially 1-pinnate-pinnatisect to 2-pinnate, basal pinnae equilateral, and pinna rachises with filiform tortuous scales. It is extremely variable as to the pubescence of the laminae abaxially, varying from subglabrous (e.g., *Cornejo & Bonifaz 5459*) to densely and evenly pubescent (type).

Two species greatly resemble *Megalastrum microsorum* in division of the laminae. The first, *M. platylobum*, differs only by basal pinnae inequilateral (i.e., prolonged basiscopically). The second, *M. pleiosoros*, is endemic to the Galapagos Islands. *Megalastrum microsorum* has similar filiform rachis scales as in *M. pleiosoros*, but differs by longer hairs (0.6–1.5 mm) on all parts of the leaf.

23. ***Megalastrum miscellum*** R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Zamora-Chinchipe: Cantón Zamora, within 3 km of the town of Zamora, 4°03′5′S, 78°57′5″W, 1000 m, 7 Sep 1994, *A. Fay & L. Fay 4382* (holotype: QCNE!; isotypes: AAU!, MO! [barcode 05034342], NY! [barcode 01053912], QCA?-n.v.). **Figs. 22E, 31R–Z, 32A.**

Rhizomes unknown; **leaves** up to 2 m long; **petiole base scales** 15.0–25.0 × 1.0–1.2 mm, spreading to ascending, linear-lanceolate, brown, lustrous, twisted or flat, sparsely denticulate; **laminae** 0.7–1.2 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 25.0–40.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, pubescent, sparsely scaly, the hairs 0.2–1.1 mm long, 2–6-celled, spreading, the scales 3.0–5.0 × 0.3–0.5 mm long, loosely ascending to spreading, linear-lanceolate, light brown, entire to sparsely denticulate apically, not clathrate, not bullate, adaxially eglandular, densely pubescent, the hairs 0.2–0.8 mm long, 2–5-celled; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.1–1.1 mm long, 1–6-celled, the scales 0.6–0.7 × 0.1–0.2 mm, linear-lanceolate, brown, entire, adaxially with hairs like those of the pinna rachises, scales absent; **laminar tissue between veins** abaxially sparsely to moderately glandular, puberulent, the glands ca. 0.1 mm long, sessile, yellowish, spherical, grading into gland-tipped hairs, the hairs ca. 0.1 mm long, 1-celled, appressed to erect, acicular, adaxially sparsely puberulent, the hairs like those on the abaxial surfaces; **ultimate veins** on both surfaces visible, abaxially sparsely glandular and pubescent, the glands spherical, yellowish, intergrading with gland-tipped hairs, the hairs ca. 0.2 mm long, 1- or 2-celled, adaxially sparsely glandular to eglandular, pubescent, the glands spherical, yellowish, the hairs 0.5–1.0 mm long, 4–6-celled, appressed to erect; **lamina margins** eglandular, densely ciliate, the hairs 0.2–0.3 mm long, 3- or 4-celled, ascending; **indusia** minute, fugacious, apparently consisting of a cluster of reddish proscales, ca. 0.1 mm long, protruding from the center of the sorus, not easily observed in mature sori; **spores** cristate.

Distribution.—Colombia, Ecuador, Peru, Bolivia, on both sides of the Andes; 550–2300 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Mpio. Caldas, Vereda La Cara, Finca La Oculta, 1950 m, [6°05′N, 75°38′W], 17 May 1984, *Albert de Escobar et al. 4476* (NY); Mpio. Salgar, 12 km NE de Salgar, cerca de la finca Regada, costado izquierdo de la quebrada Liboriana, 2200 m, [5°54′N, 75°55′W], 16 Jan 1988, *Arbeláez et al. 276* (NY). **Valle**: Ansermanuevo-San José del Palmar rd., ca. 30–37 km W of Ansermanuevo, 1850–1875 m, [4°47′N, 76°02′W], 13 May 1984, *Luteyn et al. 10394* (NY).

ECUADOR. **Morona-Santiago**: Morona, near city of Macas, 1100 m, 2°20′S, 78°08′W, 7 Nov 1993, *Fay & Fay 4046 p.p.* (AAU,MO, NY, UC). **Zamora-Chinchipe**: Zamora, Parque Nacional Podocarpus, Guarderia en Río Bombuscaro, 970 m, [03°46′S, 78°37′W], 23 Jan 1995, *Palacios & Tirado 13214* (MO, QCNE).

PERU. **San Martín**: Mt. Campana, near Tarapoto, [6°27′S, 76°24′W], Aug 1856, *Spruce 4718* (P).

BOLIVIA. **Cochabamba**: Prov. Chapare, Parque Nacional Carrasco, cavernas del Repechón, 550 m, 17°02′S, 65°26′W, 8 Sep 1996, *Kessler et al. 8256* (UC). **La Paz**: Prov. Nordyungas, Polo-Polo bei Coroico, 1100 m, [16°10′S, 67°43′W], Oct or Nov 1912, *Buchtien 3609* (S). **Santa Cruz**: Manuel M. Caballero, 2200 m, 17°47′41″S, 64°43′09″W, 18 Jun 2003, *Núñez & Huaylla 199* (NY).

Megalastrum miscellum is characterized by pinna rachises and costules abaxially with linear-lanceolate mostly entire scales and hairs of decidedly mixed sizes (thus the specific epithet), lamina tissue between the veins pubescent, and veins adaxially with hairs 0.5–1.0 mm long. *Megalastrum praetermissum* is similar by narrow scales, minutely pubescent abaxial surfaces, and (often) long conspicuous hairs adaxially, but it differs from *M. miscellum* by pinna rachises abaxially without hairs and more strongly denticulate scales.

24. Megalastrum molle A. R. Sm., Novon 16:426, fig. 18. 2006, as "*mollis*." TYPE.—PERU. Amazonas: Distr. Bagua, along road from Chiriaco toward Bagua, [5°38′S, 78°32′W], 750 m, 21 Mar 2001, *H. van der Werff, R. Vasquez & B. Gray 16300* (holotype: MO! [barcode 5675669]; isotypes: F! [accession 2251280], NY! [barcode 01093321], UC! [barcode 1777976]). **Figs. 23M–Q, 24B, 29D.**

Rhizomes erect, scales 10.0–15.0 × ca. 0.5 mm, spreading to ascending, linear-lanceolate, brown, lustrous, twisted, subentire to sparsely denticulate; **leaves** 0.5–0.7 m long; **petiole base scales** like those of the rhizomes but smaller, 5.0–10.0 × ca. 0.5 mm, more spreading; **laminae** 25–50 cm long, basally 2-pinnate to 2-pinnate-pinnatifid, medially 1-pinnate-pinnatisect; **lamina rachises** glabrous abaxially; **basal pinnae** 7.0–9.0 cm long, slightly inequilateral; **pinna rachises** abaxially glandular, conspicuously pubescent, sparsely scaly, the glands short-stalked, ca. 0.1 mm long, 2-celled, yellowish, the hairs 1.0–2.0 mm long, 5–7-celled, acicular, spreading, tortuous, whitish, the scales ca. 2.5–3.0 × ca. 0.2 mm, appressed to spreading, linear-lanceolate, brown, lustrous, tortuous, entire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pilose, scales absent, the hairs similar to those of the pinna rachises abaxially; **basal basiscopic pinnules of medial pinnae** often (especially in large leaves) enlarged and overlapping the lamina rachis; **costules** abaxially sparsely glandular, sparsely pubescent, the glands and hairs similar to those of the pinna rachises, adaxially eglandular, densely to sparsely pilose, scales absent, the hairs similar to those of the pinna rachis adaxially; **laminar tissue between veins** on both surfaces sparsely glandular, the glands ca. 0.1 mm long, stalked, 2-celled, yellowish, abaxially glabrous to sparsely puberulent, the hairs ca. 0.1 mm long, 1-celled, erect, acicular, adaxially sparsely pilose near the lamina margins, the hairs ca. 0.5 mm long, 3- or 4-celled; **ultimate veins** visible on both surfaces, sparsely glandular on both surfaces, the glands similar to those of the lamina tissue, abaxially sparsely pilose, the hairs similar to those of the pinna rachises, adaxially pilose, the hairs 1.0–2.0 mm long, 5–7-celled, whitish; **lamina margins** eglandular, ciliate, the hairs 0.3–1.0 mm long, 2–6-celled, acicular, spreading; **indusia** absent; **spores** cristate.

Distribution and ecology.—Ecuador, Peru; eastern side of Andes, on rocks or trail banks, premontane forest, 200–1200 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Napo**: Km 86.4 along the road traversing Yasuni National Park, 200–300 m, 0°51′S, 76°16′W, 8 Mar 1998, *Tuomisto & Ruokalainen 11724* (UC). **Zamora-Chinchipe**: immediately N of Zamora, 1000–1200 m, 4°04′S, 78°57′W, 13 Jun 1988, *Øllgaard et al. 74815* (AAU).

PERU. **Cusco**: Quispicanchis, Hills around Río Araza between Pande Azucar and Quince Mil Airport, forest 292 km from Cusco, 643 m, 13°13′S, 70°45′W, 10 Aug 1991, *Nuñez 13973* (MO). **San Martín**: 5–15 km E of Shapaja on road to Chazuta, 200–300 m, 6°36′S, 76°10′W, 9 Apr 1986, *Knapp & Mallet 7022* (MO).

Megalastrum molle is characterized by lamina tissue between the veins on both surfaces glandular, pinna rachises and veins on both surfaces with hairs 1.0–2.0 mm long, 5–7-celled, and lamina margins ciliate by hairs 0.3–1.0 mm long. On the type, which has relatively large leaves, the basal basiscopic pinnules are enlarged and overlap the lamina rachis. In the paratypes, the basal basiscopic pinnules crowd or slightly overlap the lamina rachis, but they are not enlarged.

Megalastrum molle resembles *M. fibrillosum* by laminae medially 1-pinnate-pinnatisect and pinna rachises with linear-lanceolate scales. It differs by pinna rachises and laminae between the veins abaxially glandular (vs. glabrous) and pinnae rachises conspicuously pubescent with hairs 1.0–1.3 mm long (vs. 0.1–0.2 mm). *Megalastrum bolivianum* is similar by the basal basiscopic pinnules often enlarged and laminae adaxially with long hairs, but *M. molle* differs by lamina tissue between the veins abaxially glandular and rachises of the lamina and pinnae with linear-lanceolate, tortuous scales (vs. lanceolate and non-tortuous).

25. Megalastrum mollicoma (C. Chr.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:128. 1987 [published 3 May 1988]. *Dryopteris mollicoma* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 8, 6:75. 1920. *Ctenitis mollicoma* (C. Chr.) Ching, Sunyatsenia 5:250. 1940. TYPE.—ECUADOR. Napo: "in silv. suband. orient.," Oyacachi, Feb 1901, *L. Sodiro s.n.* (lectotype, first-step designated by Tryon and Stolze, (1991) and second step here designated:P! [barcode 00610850]; isolectotypes: BM! [barcode 000907824], photos F!, MICH!, S!; isolectotypes: GH!, P! [barcode 00610849, 00610851], US!). **Figs. 20H–M, 31J–Q, 32B, 33B.**

Megalastrum laxipilosum A. Rojas, Mét. Ecol. Sist. 3(Supl. 1):44, fig. 6A–C. 2008. TYPE.—COLOMBIA. **Nariño**: Reserva Natural La Planada, 7 km above Chuncunés, along road between Tuquerres and Ricauarte, along trail to El Hondón, beginning at Quebrada el Tejón and for 0.5 km beyond, 1°08′N, 77°54′W, 780–800 m, 15 Mar 1990, *T. Croat 71469* (holotype: MO! [barcode 3912989]).

Rhizomes erect, the scales 10.0–30.0 × 0.5–2.0 mm, appressed, lanceolate to linear-lanceolate, brown, entire to sparsely denticulate, flat to twisted; **leaves** 0.5–2.5 m long; **petiole base scales** like those of the rhizomes but spreading to ascending; **laminae** 0.5–1.5 m long, basally 3- to 4-pinnate-pinnatifid, medially 2- to 3-pinnate-pinnatiset; **lamina rachises** pubescent abaxially; **basal**

pinnae up to 30.0 cm long, inequilateral; **pinna rachises** abaxially sparsely to densely glandular, pubescent, scaly, the glands ca. 0.1 mm wide, short-stipitate to sessile and spherical, yellowish to orangish, the hairs 0.2–0.8 mm long, 3–6-celled, lax, spreading, the scales 2.0–7.0 × 0.3–1.0 mm, dark brown to golden brown, lanceolate, flat (not twisted or tortuous), ascending to spreading, firm to thin and, lustrous, entire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, scaly, the hairs 0.6–2.0 mm long, 4–8-celled, spreading to ascending, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** with indument like that of the pinna rachises but with scales ca. 2.0 × 0.5 mm, adaxially like the pinna rachises but scales absent; **laminar tissue between veins** abaxially pubescent, sparsely glandular, the hairs 0.1–0.2 mm long, 1- or 2-celled, erect, lax to acicular, the glands ca. 0.1 mm long, 2-celled, short-stipitate, yellowish, erect, adaxially pubescent (sometimes only so toward the margins), sparsely glandular, the hairs 0.1–1.0 mm long, 2–8-celled, lax, slightly tortuous, ascending, appressed, the glands like those abaxially; **ultimate veins** on both surfaces visible to obscure, abaxially pubescent, the hairs 0.2–0.6 mm long, 2–5-celled, spreading or appressed-ascending, lax, adaxially the hairs 0.2–0.5 mm long, 2–4-celled, slightly tortuous, spreading to ascending; **lamina margins** eglandular, ciliate, the hairs 0.3–0.8 mm long, 3–6-celled, lax, spreading; **indusia** absent; **spores** cristate.

Distribution.—Colombia, Ecuador; (750–)1800–2450 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Mpio. Fredonia, vereda Erbe, microcuenca La Chaparrala, 2150–2250 m, 5°59′01″N, 75°38′28.3″W, 20 Dec 2004, *Rodríguez et al. 4805* (HUA, NY). **Nariño**: Reserva Natural La Planada, sendero del Rondón, ca. 2 km de centro de investigación, 1900 m, 1°09′55″N, 77°58′44″W, 19 Jan 1997, *Herrera 9130* (UC); trail to El Hondón, 5–12 km SW of La Planada, 1750–1800 m, 01°04′N, 78°02′W, 6 Jan 1988, *Gentry et al. 60492* (MO).

ECUADOR. **Carchi**: El Gualtal, faldas de Cerro Golondrina Hembra, 2450 m, 0°51′N, 78°07′W, 21 Aug 1994, *Palacios & Clark 12644A* (MO, QCNE, UC). **Pichincha**: rd from Lloa to the West, Km 20.6, 2450 m, 0°13′S, 78°38′W, 1 May 1991, *Øllgaard 98891* (AAU). **Tunguragua**: without locality, [0°23′S, 78°25′W], ca. 1857, *Spruce 5257* (P).

Megalastrum mollicoma is distinctive by the pubescence on the adaxial surface of the laminae: the hairs are dense, slightly tortuous, appressed, and ascending. No other species of *Megalastrum* has pubescence like this. The abaxial surface is also pubescent but the hairs tend to be straighter and more erect. Besides these hairs, also distinctive are the pinna rachis scales conspicuous, shiny brown, and spreading, and the veins adaxially pubescent. The lamina margins are typically fimbriate by lax hairs 0.3–0.8 mm long.

Megalastrum mollicoma might be confused with *M. vastum,* which has similar lamina dissection and is pubescent between the veins on both surfaces. *Megalastrum vastum* differs by hairs between the veins on both surfaces only

0.1(–0.2) mm long, and scales of the lamina and pinna rachises usually dull brown. In *M. vastum* the scales of the lamina and pinna rachises are often inconspicuous to the naked eye, whereas in *M. mollicoma* they are conspicuous.

26. *Megalastrum nanum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—BOLIVIA. Santa Cruz: Florida, Cantón Mairana, Parque Nacional Amboró, 7 km NNE by air from Mairana, 18°03′S, 65°55′W, 1900–2100 m, 23 Jul 1994, *R. C. Moran 5917* (holotype, LPB!; isotypes, AAU!, NY! [barcode 00870945]). **Figs. 2E, 8A, 32B, 24A–E.**

Rhizomes erect; **leaves** up to 1 m long; **petiole base scales** 10.0–20.0 × 0.5–2.0 mm, linear-lanceolate, spreading to ascending, yellowish brown, twisted, lustrous, the margins denticulate; **laminae** 0.3–0.4 m long, 3-pinnate-pinnatisect basally, 2-pinnate-pinnatisect medially; **lamina rachises** pubescent abaxially; **basal pinnae** 15.0–20.0 cm long, strongly inequilateral (elongated basiscopically), the basal basiscopic pinnule 2.5–4.0 cm wide; **pinna rachises** abaxially densely pilose, sparsely scaly, sparsely glandular, the hairs 1.0–1.5 mm long, 4–7-celled, spreading, the scales light to dark brown, often darker distally, denticulate, the teeth often darker than the body of the scale, especially towards the apex, not clathrate, not bullate, of two sizes, small ones ca. 0.3–0.6 × ca. 0.2 mm long, ovate to lanceolate, mostly appressed, the larger 1.4–2.0 × 0.2–0.3 mm long, linear to linear-lanceolate, spreading, the glands ca. 0.1 mm long, spherical, sessile, orange to yellowish, adaxially with similar indument but with denser hairs; **costules** on both surfaces with indument similar to the pinna rachises; **laminar tissue between veins abaxially** pilose, glandular, the hairs ca. 1.0 mm long, 4–6-celled, spreading to erect, the glands both sessile and stalked, the sessile ones like those on the pinna rachis, the stalked glands ca. 0.2 mm, 2-celled, adaxially glabrous, eglandular; **ultimate veins** visible abaxially, obscure adaxially, abaxially glandular, pilose, the glands sessile, globose, yellowish, the hairs like those on the laminar tissue, adaxially pilose, sparsely glandular, the hairs and glands like those on the abaxial surface; **lamina margins** ciliate, eglandular, the hairs 0.4–1.0 mm long, 4–6-celled, spreading; **indusia** absent; **spores** echinulate.

Distribution.—Ecuador, Peru, Bolivia; 1900–2100 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Zamora-Chinchipe**: New road Loja to Zamora, 13 km E of the Pass, wet forest along creek that crosses the road, 2000 m, 4°00′S, 79°02′W, 14 Feb 1991, *Moran & Rohrbach 5380 p.p.* (AAU, MO).

PERU. **Amazonas**: San Martín, 1950 m, 5°41′S, 77°48′W, 4 Mar 2001, *van der Werff et al. 16720* (MO).

BOLIVIA. **Santa Cruz**: Valle Grande, 5 km de Loma Larga a Valle Grande, 2100 m, 18°43′S, 63°54′W, 8 Jun 1996, *Kessler et al. 6370* (UC). **Tarija**: Prov. Aniceto Arce Ruíz, Reserva Natural de Flora y Fauna Tariquía, Río Nogal, campamento Alisos, 1700 m, 22°00′S, 64°33′W, 6 Oct 2004, *Jiménez & Serrano 2398* (GOET, NY, UC).

Megalastrum nanum is characterized by small leaves (thus the specific epithet), densely pilose pinna rachises abaxially with hairs 1.0–1.5 mm long, 4–7-celled, laminar tissue between the veins abaxially pilose and glandular (both sessile and stalked glands present) but adaxially glabrous, and echinulate spores. The species resembles *M. fugaceum* and *M. pulverulentum* by the scales on the pinna rachises and costules abaxially strongly denticulate and often darkened toward the apex. It further resembles *M. pulverulentum* by petiole base scales 10.0–20.0 mm long (vs. 20–40 mm), laminae with pilose hairs and stipitate and stalked glands abaxially but differs by leaves up to 1 m long (vs. 4 m) and laminar tissue between the veins glabrous adaxially.

Megalastrum nanum superficially resembles *M. ciliatum*, a species that does not belong to the "pulverulentum clade." The two species are similar by leaf size, cutting, and indument, but there are several differences. First are those characters placing *M. nanum* in the "pulverulentum clade"; that is, the echinulate spores and pinna rachis scales darkened toward the tips (not all scales are darkened apically, but usually several can be found with that character). The two can be distinguished by lamina dissection of the basal basiscopic pinnule of the basal pinna: that of *M. nanum* is 2.5–4.0 cm wide with most of the segments pinnatifid; in contrast, *M. ciliatum* is 1.5–2.0 cm wide with only one or two basal pairs of ultimate segments pinnatifid, the rest being entire. Other differences are the rhizome scales of *M. nanum* that are 0.5–2.0 mm wide and yellowish brown, whereas those of *M. ciliatum* are 0.2–0.5 mm wide and dark brown. The hairs of the pinna rachises abaxially are 1.0–1.5 mm long in *M. nanum* versus 0.3–0.8 mm long in *M. ciliatum*.

27. *Megalastrum nigromarginatum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—COLOMBIA. Cundinamarca: 8 km NW of Sibate, 19 Oct 1961, *R. M. Tryon & A. F. Tryon 6103* (holotype: GH!). **Fig. 22A, 32B, 34M–Q.**

Rhizomes erect, the scales 15.0–25.0 × 0.1–0.2 mm, appressed to strongly ascending, linear, golden brown with margins black-bordered (at least intermittently), flat to twisted, sparsely denticulate; **leaves** 0.8–1.0 m long; **petiole base scales** like those of the rhizomes but loosely spreading to ascending; **laminae** 0.4–0.6 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatifid; **lamina rachises** abaxially glabrous; **basal pinnae** ca. 20 cm long, strongly inequilateral; **pinna rachises** abaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.3–0.5 mm long, 2–4-celled, acicular, spreading, the scales 2.5–4.5 × 0.3–0.5 mm, narrowly lanceolate, brown, flat, subentire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, scales absent, the hairs 0.5–0.8 mm long, 3–5-celled, ascending to spreading, acicular; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, puberulent, sparsely scaly, the hairs 0.2–0.5 mm long, 2–4-celled, acicular, spreading, the scales 1.0–4.5 × 0.1–0.2 mm, linear-lanceolate, brown, lustrous, subentire, adaxially with indument similar to those of the abaxial surfaces; **laminar tissue between veins** abaxially eglandular, densely pubescent, the hairs 0.1–0.2 mm long, 1–3-celled, erect, acicular, adaxially glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, puberulent, the hairs like those on the lamina tissue, adaxially glabrous or only 1 or 2 hairs present distally, the hairs like those on the costules; **lamina margins** eglandular, ciliate, the hairs 0.1–0.2 mm long, 1–3-celled, ascending to spreading, acicular; **indusia** absent; **spores** cristate.

Distribution.—Colombia; 2000–2700 m.

SPECIMENS EXAMINED.—COLOMBIA. **Cundinamarca**: Cordillera Oriental, 2438 m, 3 Sep 1994, *Little & Little 8597* (GH). **Santander**: between Piedecuesta and Las Vegas, 2000–2500 m, [6°50′N, 73°02′W], 19–24 Dec 1926, *Killip & Smith 15555* (NY).

Megalastrum nigromarginatum is distinctive by its black-bordered rhizome scales (thus the specific epithet). This border is often interrupted, not continuous. Also distinctive are the small laminae (0.4–0.6 m long). The indument is also distinctive. The laminae are pubescent between the veins abaxially by erect acicular hairs. *Killipp & Smith 15555* is slightly atypical by more glabrous axes, flaccid scales, and shorter pubescence between the veins abaxially.

This species resembles *Megalastrum ciliatum* from Bolivia and northern Argentina. Both have small laminae and similar cutting, and their rhizome scales are intermittently black-margined—a rare character in the genus. The two species can be distinguished by characters given in the key.

Also similar is *Megalastrum pubescens*, which also has small leaves and is pubescent abaxially between the veins. That species differs by ascending pinnules, laminae abaxially with some of the hairs gland-tipped, and concolorous rhizome scales. Also, its lamina tissue between the veins abaxially has slightly longer hairs (0.2–0.3 vs. 0.1–0.2 mm long) and longer marginal cilia (0.3–0.5 vs. 0.1–0.2 mm long).

28. *Megalastrum obtusum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Pichincha: Reserva Biológica La Perla, 2 km from La Concordia, [0°0′N, 79°23′W], 400 m, s.d., *H. Ankersen & C. Kragelund 211* (holotype: QCA!; isotype: AAU! 2 sheets). **Figs. 10B,C, 32C, 35A–E.**

Rhizomes erect, scales 5–15 × 0.3–0.5 mm, linear-lanceolate, spreading to ascending, brown to golden brown, lustrous, twisted, denticulate, the teeth simple or sometimes bifid; **leaves** 0.4–1.0 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.3–0.6 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatifid, the segments or lobes obtuse; **lamina rachises** pubescent abaxially; **basal pinnae** 6.0–23.0 cm long, strongly inequilateral; **pinna rachises** abaxially eglandular, pubescent, scaly, the hairs (0.5–)0.8–1.5 mm long, 4–7-celled, straightish, spreading, white, the scales 0.5–1.7 × 0.1–0.2 mm, linear, lustrous, brown, subentire to sparsely denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.5–2.0 mm long, 4–7-celled, spreading, straightish, white, the scales like those abaxially; **basal basiscopic pinnules of**

medial pinnae not enlarged or overlapping the lamina rachis, obtuse; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs like those of the pinna rachises but smaller 0.2–0.5 mm long, 2–4-celled, the scales like those of the pinna rachises but smaller 0.5–0.8 × 0.2–0.3 mm, adaxially eglandular, sparsely pubescent, the hairs like those on the pinna rachises, without scales, the hairs 0.5–1.0 mm long, 4–6-celled; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, pubescent, the hairs 0.5–1.5 mm long, 2- or 3-celled, spreading, straightish, white, adaxially pubescent, the hairs 0.7–1.0 mm long, 3- or 4-celled, appressed, ascending, straightish, whitish; **lamina margins** eglandular, ciliate, the hairs 0.3–0.5 mm long, 2- or 3-celled, straightish, whitish, ascending; **indusia** absent; **spores** cristate.

Distribution.—Northwestern Ecuador; 250–700 m.

SPECIMENS EXAMINED.—ECUADOR. **Cotopaxi**: Cotopaxi, Río Guapara, ca. 20 km NW El Corazón, 250 m, [0°14′S, 78°20″W], 19–24 Jun 1967, *Sparre 17168* (MO, QCA, S). **Pichincha**: Reserva Forestal Endesa, along Rio Silanche NE of Pedro Vicente Malonado, 700 m, 00°08′N, 79°03′W, 2 Dec 1996, *Øllgaard et al. 2247* (AAU).

Megalastrum obtusum is distinctive by obtuse pinnules and pinna rachises with linear scales and long straightish white hairs. The hairs are also conspicuous on the ultimate veins adaxially. This species has one of the lowest elevation ranges in the genus. Similar by lamina cutting and the presence of long whitish hairs is *M. marginatum*, a species that differs by lanceolate scales on the pinna rachises abaxially and occurrence only in Bolivia. A previous report by Moran & Prado (2010) of *M. longipilosum* A. Rojas from Ecuador was based on two specimens of *M. obtusum*. See note under *M. marginatum*

29. *Megalastrum oellgaardii* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Pichincha: road Pacto-La Delicia-La Esperanza, Km 11, wet forested ravine, 0°10′N, 78°50′W, 1600 m, 1 Dec 1996, *B. Øllgaard, H. Navarrete, E. Terneus & V. Quipuscoa 2219* (holotype: AAU! 5 sheets; isotypes: QCA-n.v., QCNE-n.v.). **Figs. 13G, 17E–J, 32A.**

Rhizomes not seen; **leaves** up to 1.5 m long; **petiole base scales** 30.0–40.0 × 0.4–0.6 mm, spreading to loosely ascending, linear, dark brown, lustrous, twisted and tortuous, strongly denticulate; **laminae** up to 0.6 m long, basally 3-pinnate-pinnatifid, medially 2-pinnate-pinnatifid; **lamina rachises** without hairs abaxially but with many scattered minute scales; **basal pinnae** 40.0–50.0 cm long, strongly inequilateral (elongated basiscopically); **pinna rachises** abaxially eglandular, glabrous, sparsely scaly, the scales 2.0–3.0 × 0.2–0.5 mm, narrowly lanceolate, spreading, ascending, dark brown, sometimes darker distally, strongly denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.5–1.2 mm long, 4–6-celled, ascending, the scales 3.0–5.0 × 0.2–0.5 mm, linear-lanceolate, dark brown, strongly denticulate; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, glabrous, sparsely scaly, scales like those of pinna rachises but smaller, 0.8–1.5 × 0.3–0.4 mm, adaxially sparsely pubescent, the hairs like the pinna rachises; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** abaxially visible, eglandular, glabrous, adaxially obscure, glabrous, eglandular; **lamina margins** eglandular, inconspicuously ciliate (often apparently eciliate), the hairs ca. 0.05 mm long, 1-celled, ascending; **indusia** absent; **spores** cristate.

Distribution.—Ecuador; 1600–1750 m.

SPECIMENS EXAMINED.—ECUADOR. **Napo**: road Baeza-Lago Agrio, ca. 114 km from Lago Agrio, 1750 m, 0°16′S, 77°46′W, 8 Aug 1980, *Øllgaard et al. 35806* (AAU).

Megalastrum oellgaardii is characterized by laminae on both surfaces between the veins glabrous, costular scales dark brown (often more so apically) and strongly denticulate, and lamina margins inconspicuously ciliate, the cilia ca. 0.05 mm long and often apparently absent. It resembles *M. squamosissimum,* a species that differs by pinna rachis scales larger (2–10 × 0.5–1.5 mm), sparsely denticulate, golden to pale brown, these often conspicuously spreading on the lamina rachises. Also similar is *M. praetermissum,* which differs by pinna rachises abaxially without hairs and with dark, denticulate, narrow scales, and minute (ca. 0.1 mm long) erect acicular hairs between the veins abaxially. Furthermore, *M. praetermissium* is often pubescent adaxially along the veins.

The specific epithet honors Benjamin Øllgaard, Danish pteridologist who collected the type and who has made many contributions to the knowledge of Ecuadorian ferns and lycophytes.

30. *Megalastrum oreophilum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—VENEZUELA. Amazonas: Cerro de Neblina, Río Yatua, S of Camp 3, [0°48′N, 66°02′W], 1200–1600 m, 24 Dec 1953, *B. Maguire, J. J. Wurdack & G. Bunting 36871* (holotype: VEN! [barcode 64080, 3 sheets of same number]; isotypes: NY! [barcode 01053916, 01053917], US! [barcode 00798652, 00798653, 00798654, 00798655]). **Figs. 17K–P, 22C, 24C.**

Rhizomes not seen; **leaves** ca. 1.5 m long; **petiole base scales** up to 20.0 × 0.4–0.7 mm, spreading to ascending, linear, lanceolate, golden brown, lustrous, slightly twisted, densely denticulate, the teeth sometimes bifid; **laminae** ca. 1.2 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 35.0–41.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.2–0.3 mm long, 2- or 3-celled, acicular, spreading to erect, the scales 2.0–3.0 × 0.1–0.4 mm, ascending to loosely spreading, linear-lanceolate, golden brown, strongly denticulate, not clathrate, not bullate, adaxially eglandular, densely pubescent, without scales, the hairs 0.4–0.7 mm long, 3- or 4-celled, substrigose; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs 0.1–0.4 mm long, 2- or 3-celled, erect, acicular, the scales ca. 1 × 0.1 mm, linear, denticulate, slightly flexuous, adaxially with indument like the pinna rachises; **laminar tissue between veins** abaxially puberulent, eglandular, the hairs ca. 0.1–0.2 mm long, 1- or 2-celled, erect, acicular, adaxially glabrous or subglabrous with only 1 or 2 hairs near the margins, the hairs ca. 0. 1 mm long, acicular, erect; **ultimate veins** visible on both surfaces, abaxially sparsely pubescent, eglandular, the hairs 0.2–0.3 mm long, 2- or 3-celled, acicular, erect, adaxially sparsely pubescent, the hairs like those of the costules; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 2- or 3-celled, substrigose; **indusia** absent; **spores** cristate.

Distribution.—Southern Venezuela, northern Colombia; 1200–2000 m.

SPECIMENS EXAMINED.—COLOMBIA. **Magdalena**: Santa Marta, 2000 m, [10°55′N, 73°38′W], 1898, *Smith 1023* (BM, F, MO, NY, S, U); idem, 1898–1899, *Smith 1024* (K).

Megalastrum oreophilum is characterized by laminae 2-pinnate-pinnatifid medially, laminae pubescent abaxially with erect acicular hairs and glabrous to subglabrous adaxially (sometimes with a few hairs near the segment margins), and pinna rachis and costule scales linear, yellowish brown, shiny, and denticulate. The species most resembles *M. vastum* but differs by petiole scales golden brown (vs. dark brown) en mass, laminae between the veins adaxially glabrous to subglabrous (vs. puberulent), and pinna rachis scales golden brown and shiny (vs. darker brown and dull). The species is known only from two isolated mountains, thus the specific epithet *oreophilum.*

For figures 19–35, descriptions of species 31–46, Names of Uncertain Application, Unusual Specimens, Acknowledgements, Literature Cited, and Appendices 1–4, see "*Megalastrum* (Dryopteridaceae) in Andean South America, Part II." American Fern Journal 104(4): 109–178.

American Fern Journal 104(3):179 (2014)
Published on 17 October 2014

ERRATUM

AFJ volume 104 issue 2, pp. 25–48 (April–June 2014)

On page 42 of the *American Fern Journal* article entitled **Cultivation Techniques for Terrestrial Clubmosses (Lycopodiaceae): Conservation, Research, and Horticultural Opportunities for an Early-Diverging Plant Lineage** by Jeffrey P. Benca the statement "Under such situations, using sodium-softened or distilled water may be necessary to provide neutral to acidic conditions ($pH \leq 7.0$) (Husby, pers. comm.)." is incorrect and should state "Under such situations, using uncontaminated rain-, steam-distilled, deionized, or reverse osmosis water may be necessary to provide neutral to acidic conditions ($pH \leq 7.0$), but sodium-softened water is not suitable due to buildup of excess salts (Husby, pers. comm.)."

INFORMATION FOR AUTHORS

Authors are encouraged to submit manuscripts pertinent to the study of ferns and lycophytes for publication in the *American Fern Journal.* Manuscripts should be sent to the editor at **hauk@denison.edu.** Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication. Mandatory fees will be charged for color figures in print and/or in electronic versions of published papers.

Information for authors, including detailed requirements for formatting manuscripts can be found online at: http://www.amerfernsoc.org/journal.html.

PTERIDOLOGIA ISSUES IN PRINT

The following issues of *Pteridologia*, the memoir series of the American Fern Society, are available for purchase:

1. Wagner, David H. 1979. Systematics of *Polystichum* in Western North America North of Mexico. 64 pp. $10.00 plus postage and handling.

2A. Lellinger, David B. 1989. The Ferns and Fern-allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). 364 pp. $32.00 plus postage and handling.

3. Lellinger, David B. 2002. A Modern Multilingual Glossary for Taxonomic Pteridology. 263 pp. $28.00 plus postage and handling.

4. Hirai, Regina Y. and Jefferson Prado. 2012. Monograph of *Moranopteris* (Polypodiaceae). 113 pp. $28.00 plus postage and handling.

For orders and more information, please contact our authorized agent for sales at: Missouri Botanical Garden Press, P.O. Box 299, St. Louis, MO 63166-0299, tel. 314-577-9534 or 877-271-1930 (toll free). For online orders, visit: http://www.mbgpress.org.

FIDDLEHEAD FORUM

The editor of the Bulletin of the American Fern Society welcomes contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns.

SPORE EXCHANGE

Mr. Brian S. Aikin, 3523 Federal Ave, Everett, WA 98201-4647 (spores.afs@comcast.net), is Director. Spores exchanged and lists of available spores sent on request. http://amerfernsoc.org/sporexy.html

GIFTS AND BEQUESTS

Gifts and bequests to the Society enable it to expand its services to members and to others interested in ferns. Back issues of the Journal and cash or other gifts are always welcomed and are tax-deductible. Inquiries should be addressed to the Membership Secretary.

VISIT THE AMERICAN FERN SOCIETY'S WORLD WIDE WEB HOMEPAGE:

http://amerfernsoc.org/

AMERICAN
FERN
JOURNAL

Volume 104

Number 4

October–December 2014

QUARTERLY JOURNAL OF THE AMERICAN FERN SOCIETY

The American Fern Society

Council for 2014

American Fern Journal

EDITOR

MANAGING EDITOR

ASSOCIATE EDITORS

The "American Fern Journal" (ISSN 0002-8444) is an illustrated quarterly devoted to the general study of ferns. It is owned by the American Fern Society, and published at The American Fern Society, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711. Periodicals postage paid at Austin, TX, and additional entry.

Claims for missing issues, made 6 months (domestic) to 12 months (foreign) after the date of issue, and orders for back issues should be addressed to Dr. George Yatskievych, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.

Changes of address, dues, and applications for membership should be sent to the Membership Secretary.

General inquiries concerning ferns should be addressed to the Secretary.

Back volumes are avalible for most years as printed issues or on microfiche. Please contact the Back Issues Curator for prices and availability.

Subscriptions:

Society Membership – USA, Canada, Mexico (includes Journal and Fiddlehead Forum)	$30
Society Membership – All other countries (includes Journal and Fiddlehead Forum)	$40
Society Life Membership – $360 (add $120 mailing surcharge for outside USA, Canada, Mexico)	
Regular Membership – USA, Canada, Mexico (includes Fiddlehead Forum)	$15
Regular Membership – All other countries (includes Fiddlehead Forum)	$22
Institutional Membership – $40 to USA, Canada, Mexico; $50 elsewhere (-$3 agency fee)	

POSTMASTER: Send address changes to American Fern Journal, % Plant Resources Center, University of Texas at Austin, Main Bldg., Rm 127, 110 Inner Campus Dr. Stop F0404, Austin, TX 78712-1711.

American Fern Journal 104(4):181–236 (2014)
Published on 24 October 2014

Megalastrum (Dryopteridaceae) in Andean South America, Part II

Robbin C. Moran
The New York Botanical Garden, Bronx, NY 10458-5126, USA, e-mail: rmoran@nybg.org
Jefferson Prado
Instituto de Botânica, C.P. 68041, CEP 04045-972, São Paulo, SP, Brazil,
e-mail: jprado.01@uol.com.br
Michael A. Sundue
The Pringle Herbarium, Department of Plant Biology, The University of Vermont, 27 Colchester Ave., Burlington, Vermont 05405, USA, e-mail: sundue@gmail.com

This is a continuation of "*Megalastrum* (Dryopteridaceae) in Andean South America, Part I." American Fern Journal 104(3): 181–236.

31. *Megalastrum peruvianum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** Type.—PERU. **Cusco**: Distr. Maranure, Mesa Pelado, disturbed cloud forest, 12°54′46″S, 72°37′24″W, 2500 m, 5 may 2006, *H. van der Werff, L. Valenzuela, E. Suclli & J. Farfan 21371* (holotype: LPB!; isotypes: MO! [barcode 6032073, 6032074, 6032075]). **Figs. 31A–H, 32C, 33C.**

Rhizomes erect, scales 15.0–30.0 × 0.5–2.0 mm, appressed, lanceolate to linear-lanceolate, brown, dull, flat to twisted, entire to sparsely denticulate; **leaves** 1.5–2.0 m long; **petiole base scales** like those of the rhizomes but spreading to ascending; **laminae** 0.5–1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** up to 30 cm long, inequilateral; **pinna rachises** abaxially sparsely glandular, pubescent, scaly, the glands ca. 0.1 mm wide, sessile, spherical, yellowish to orangish, the hairs 0.2–0.4 mm long, 3–5-celled, lax, spreading, the scales 2.0–7.0 × 0.3–1.0 mm, ascending to spreading, lanceolate, dark brown to golden brown, firm to thin and subclathrate, lustrous, flat (not twisted or tortuous), entire to sparsely denticulate, adaxially eglandular, densely pubescent, scaly, the hairs 0.6–2.0 mm long, 4–8-celled, spreading to ascending, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** with indument like that of the pinna rachises but with smaller scales ca. 2 × 0.5 mm, adaxially like that of the pinna rachises but scales absent; **laminar tissue between veins** abaxially eglandular, pubescent, the hairs 0.1–0.2 mm long, 1- or 2-celled, erect, lax to acicular, adaxially glabrous or pubescent only toward the margins, eglandular, the hairs 0.1–1.0 mm long, 2–8-celled, lax, ascending, appressed; **ultimate veins** on both surfaces visible to obscure, abaxially pubescent, the hairs 0.2–0.6 mm long, 2–5-celled, spreading or appressed-ascending, lax, adaxially the hairs 0.5–1.5 mm long, 2–5-celled, slightly tortuous, spreading to ascending; **lamina margins** eglandular, ciliate, the hairs 0.3–0.8 mm long, 3–6-

celled, acicular, lax, spreading; **indusia** fugacious, minute, consisting of a few hair-like scales, often covered by sporangia and apparently absent; **spores** cristate.

Distribution.—southern Peru, Bolivia; 1200–2500 m.

SELECTED SPECIMENS EXAMINED.—PERU. **Cusco**: Prov. La Convención, Dist. Huayopata, Amaybamba, 2050 m, 12°59′18″S, 72°30′06″W, 22 Nov 2003, *Bonino et al. 1116* (NY).

BOLIVIA. **Cochabamba**: José Carrasco Torrico, 116 km antigua carretera a Cochabamba-Villa Tunari, 2400 m, 17°08′S, 65°38′W, 6 Jul 1996, *Kessler et al. 7033* (UC). **La Paz**: Yungas, 1829 m, [16°30′S, 67°30′W], 1885, *Rusby 425 p.p.* (MICH, NY, US).

Megalastrum peruvianum resembles *M. mollicoma* but differs most conspicuously by the lamina pubescence adaxially: the hairs on the ultimate veins adaxially are longer (0.5–1.5 vs. 0.2–0.5 mm), and the lamina tissue between the veins adaxially is glabrous or only sparsely pubescent near the margins (vs. conspicuously pubescent with tortuous, appressed hairs).

32. Megalastrum platylobum (Baker) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:128. 1987 [published 3 May 1988]. *Polypodium platylobum* Baker, Syn. Fil. 307. 1867. *Polypodium tarapotense* Baker, Syn. Fil. 2:505. 1874. *Dryopteris tarapotense* (Baker) C. Chr., Ind. Fil. 297. 1905. *Dryopteris platyloba* (Baker) C. Chr., Ind. Fil. 285. 1905. TYPE.—PERU. San Martín: Mt. Guayrapurima, near Tarapoto, [5°59′S, 79°18′W], [elevation unknown], Aug 1856, *R. Spruce 4656* (lectotype, designated by Tryon and Stolze, 1991: K! [barcode 000200140, 000200141; isolectotypes: BM! [barcode 000777145, 000777146], BR-n.v. [barcode 6978211], K! [barcode 000200142, 000200143, 000200144]). **Figs. 16A, 25L–O, 32C.**

Rhizomes erect, scales ca. 15.0 × 1.0 mm, appressed to ascending, linear-lanceolate, golden brown, lustrous, strongly denticulate, the teeth often bifid; **leaves** 0.8–1.2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** to 0.8 m long, basally 2-pinnate-pinnatisect, medially 1-pinnate-pinnatisect to 2-pinnate-pinnatifid; **lamina rachises** pubescent abaxially; **basal pinnae** 10–20 cm long, inequilateral, the segments adnate; **pinna rachises** abaxially eglandular, densely pubescent, sparsely scaly (sometimes apparently absent), the hairs 0.1–0.5 mm long, of distinctly mixed sizes, 1–4-celled, acicular, straightish, erect to spreading, the scales 0.5–3.0 × 0.1–0.3 mm, filiform (2–4 cells wide), appressed, dark brown, denticulate, adaxially eglandular, pubescent, scales absent, the hairs 0.5–0.8 mm long, 4–6-celled, appressed-ascending to antrorsely strigose, light brown; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, subglabrous to pubescent, scales absent, the hairs like those on the pinna rachises abaxially, adaxially sparsely pubescent with hairs like those on the pinna rachises; **laminar tissue between veins** abaxially eglandular, subglabrous to pubescent,

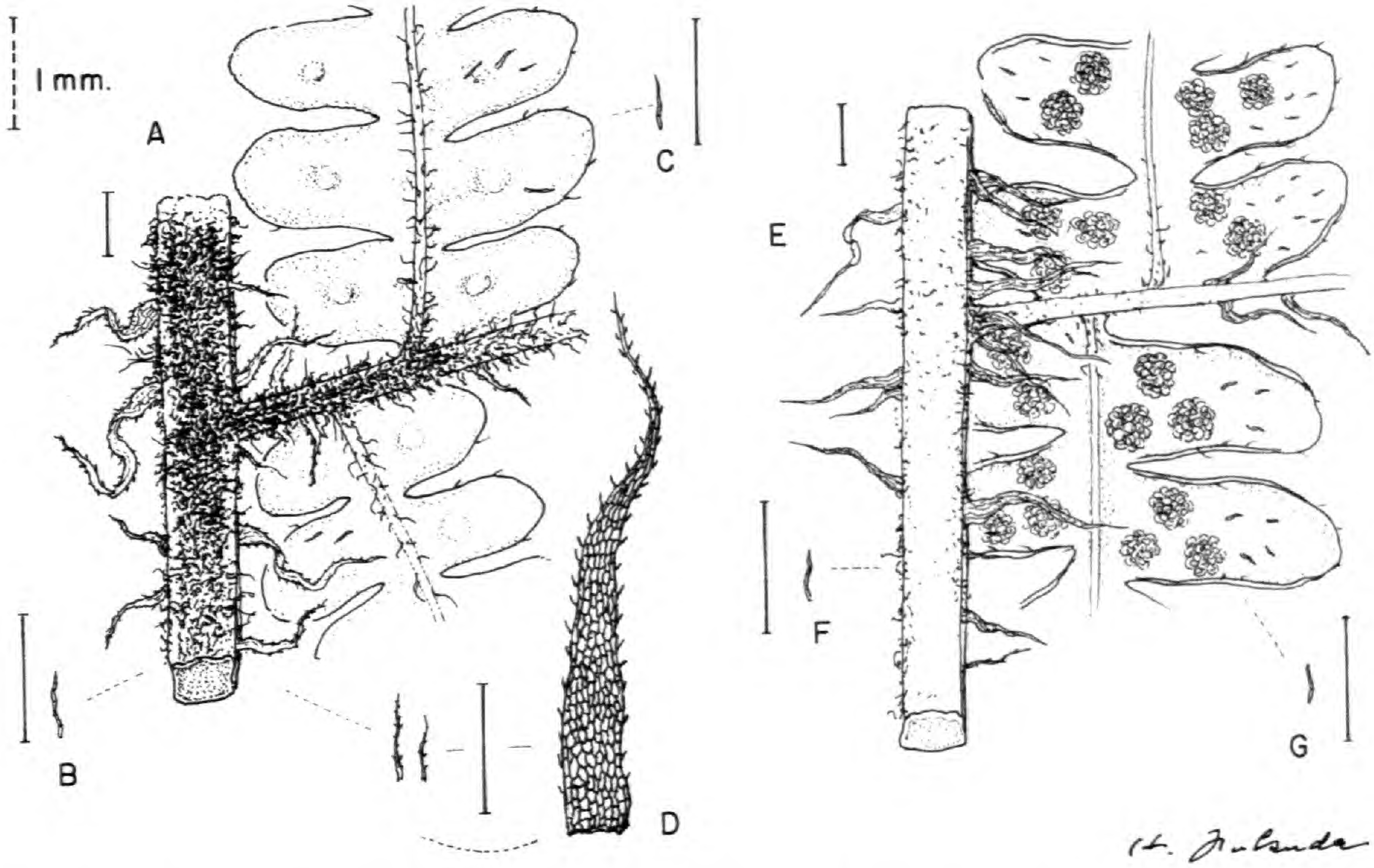

FIG. 19. Indument detail of *Megalastrum clathratum*. A. Adaxial surface of lamina rachis, pinna rachis, and pinnules. B. Hair detail. C. Marginal hair. D. Clathrate scale. E. Abaxial surface of lamina rachis, pinna rachis, and pinnules. F. Hair detail. Scale bars = 1 mm. A–F: *van der Werff et al. 23179* (MO).

the hairs 0.1–0.4 mm long, 1-celled, erect, hyaline, acicular, adaxially glabrous; **ultimate veins** visible on both surfaces or sometimes obscure adaxially, abaxially glabrous to sparsely pubescent, eglandular, the hairs like those on the laminar tissue, adaxially glabrous; **lamina margins** eglandular, ciliate, the hairs 0.1–0.3 mm long, 1–3-celled, acicular, ascending or appressed; **indusia** absent; **spores** cristate.

Distribution.—Peru; known only from the type; exact elevation unknown.

Megalastrum platylobum is distinctive by hairs of mixed lengths along the pinna rachises abaxially. The smallest hairs are 0.1 mm long, and these intergrade with sparser hairs up to 0.5 mm long. Both types of hairs are erect and whitish. Also distinctive of this species are laminae medially 1-pinnate-pinnatisect to 2-pinnate-pinnatifid and basal pinnae inequilateral (i.e., prolonged basiscopically). The pinna rachis scales are sparse or seemingly absent.

Megalastrum platylobum greatly resembles several other Andean species in size and cutting of the laminae, but none of these have the hairs of mixed lengths. The common and widespread *M. biseriale* differs by pinna rachises abaxially either glabrous or, if pubescent, the hairs sparser and more equal-sized. *Megalastrum fibrillosum* differs by pinna rachis scales more numerous, firmer, spreading, and if pubescent on the lamina rachises, then the hairs shorter (ca. 0.1–0.2 mm long). *Megalastrum reductum* is similar but differs by

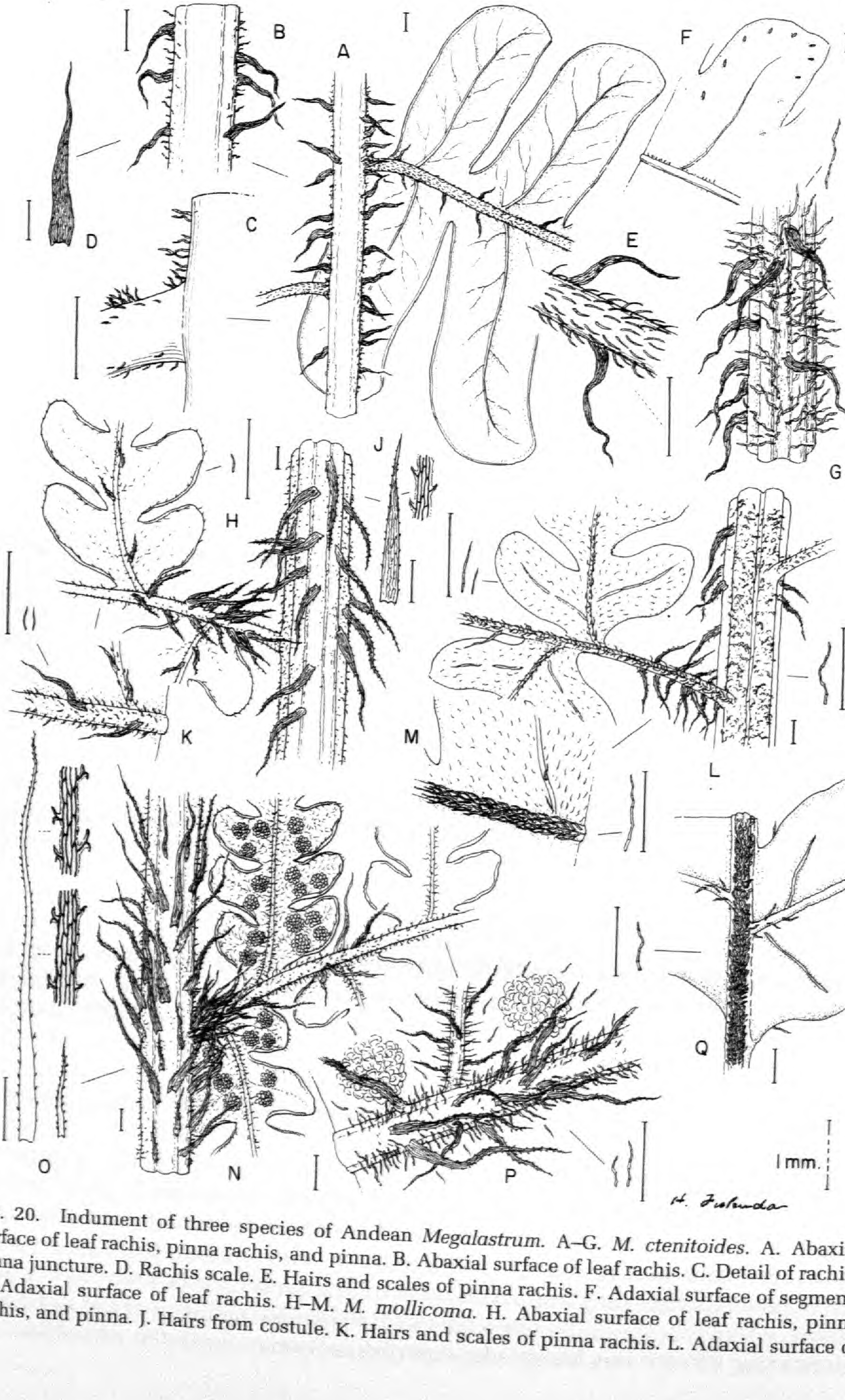

FIG. 20. Indument of three species of Andean *Megalastrum*. A–G. *M. ctenitoides*. A. Abaxial surface of leaf rachis, pinna rachis, and pinna. B. Abaxial surface of leaf rachis. C. Detail of rachis-pinna juncture. D. Rachis scale. E. Hairs and scales of pinna rachis. F. Adaxial surface of segment. G. Adaxial surface of leaf rachis. H–M. *M. mollicoma*. H. Abaxial surface of leaf rachis, pinna rachis, and pinna. J. Hairs from costule. K. Hairs and scales of pinna rachis. L. Adaxial surface of

pinna rachises abaxially with smaller, evenly lengthened (0.1–0.2 mm long), strigose hairs. *Megalastrum bolivianum* differs by long hairs on the veins adaxially. See Christensen (1912) for discussion of the synonymy and nomenclature of this species and the names proposed by Baker.

33. Megalastrum pleiosoros (Hook. f.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:129. 1987 [published 3 May 1988]. *Polypodium pleiosoros* Hook. f., Trans. Linn. Soc. London Botany 20:166. 1847. *Dryopteris pleiosoros* Svens., Bull. Torrey Bot. Club 65:316. 1938, as "*pleiosora*". *Ctenitis pleiosoros* (Hook. f.) C. V. Morton, Leafl. W. Bot. 8:190. 1957, as "pleiosora". TYPE.—ECUADOR. Galapagos Islands: James Island [San Salvador], [0°17′N, 90°42′W], without precise date, *C. R. Darwin s.n.* (holotype: CGE!). **Figs. 24D, 27A, 28A–J.**

Rhizomes erect, scales 18.0–25.0 × 0.7–1.3 mm, appressed, linear-lanceolate, gold-brown, lustrous, tortuous, the margins denticulate, the teeth simple or bifid; **leaves** up to 1 m long; **petiole base scales** like those of the rhizomes but shorter, to 12.0 mm long, and spreading; **laminae** to 0.8 m long, basally 2-pinnate, medially 1-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 8.0–15.0 cm long, equilateral, the segments adnate; **pinna rachises** abaxially eglandular, pubescent, and scaly, the hairs 0.6–1.0 mm long, 6–8-celled, spreading, acicular, hyaline, the scales 2.0–3.0 × 0.05–0.20 mm, spreading to loosely ascending, linear-lanceolate, tortuous, brown, lustrous, denticulate, the teeth simple or sometimes bifid, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 1.0–1.5 mm long, 7–9-celled, tan, acicular, spreading, the scales similar to those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, the hairs like those of the pinna rachises, adaxially eglandular, pubescent, lacking scales, the hairs similar to those abaxially; **laminar tissue between veins** abaxially sparsely glandular, sparsely to densely pilose, the glands stalked, 0.3 mm long, the hairs 0.3 mm long, 2- or 3-celled, acicular, erect, hyaline, adaxially eglandular, subglabrous to sparsely pubescent, the hairs ca. 0.5 mm long, 3- or 4-celled, ascending, acicular; **ultimate veins** visible on both surfaces, abaxially eglandular, sparsely pubescent, hairs 0.3–0.5 mm long, 3- or 4-celled, spreading or erect, acicular, hyaline; adaxially eglandular, sparsely pubescent, the hairs 0.1 mm long, 4–7-celled, ascending to appressed, acicular, hyaline; **lamina margins** eglandular, ciliate, the hairs 0.5–0.7 mm long, 4–8-celled, erect, acicular, ascending; **indusia** absent; **spores** cristate.

←

rachis, pinna rachis, and pinnule. M. Adaxial surface. N–Q. *M. galapagense*. N. Abaxial surface of rachis lamina, pinna rachis, and pinnules. O. Rachis scales; note bifid teeth. P. Abaxial surface of leaf rachis, pinna rachis, and pinnules. Q. Adaxial surface of pinna. Scale bars = 1 mm. A–G: *MacDougal et al. 3886* (MO); H–N: *Herrera 9130* (UC). N–Q: Isotype, *van der Werff 2244* (U).

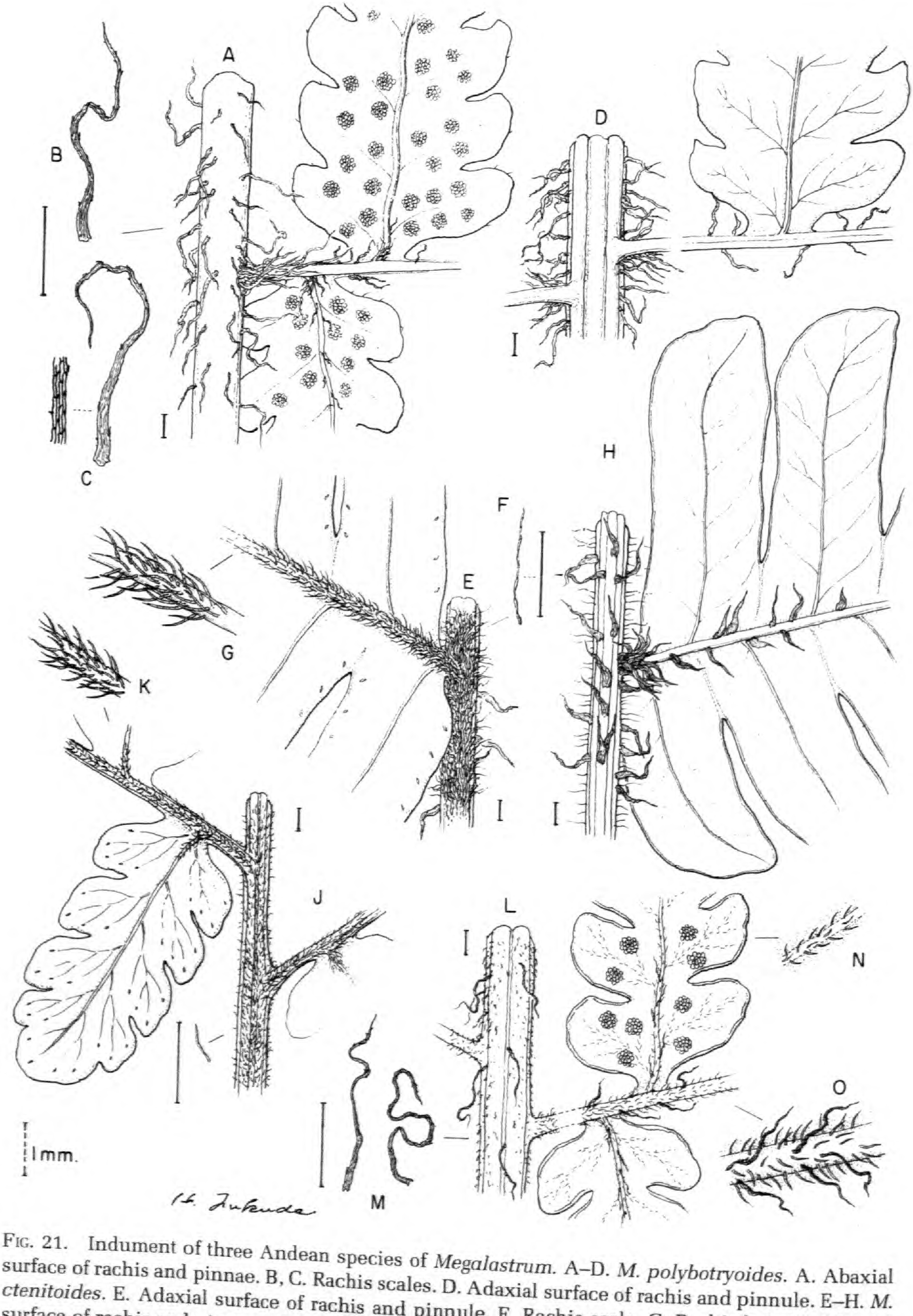

FIG. 21. Indument of three Andean species of *Megalastrum*. A–D. *M. polybotryoides*. A. Abaxial surface of rachis and pinnae. B, C. Rachis scales. D. Adaxial surface of rachis and pinnule. E–H. *M. ctenitoides*. E. Adaxial surface of rachis and pinnule. F. Rachis scale. G. Rachis hair. H. Abaxial surface of rachis and pinna. J–O. *M. reductum*. J. Adaxial surface of rachis, costa, and pinnule. K. Costal hairs. L. Abaxial surface of rachis and pinnules. M. Rachis scales. N. Hairs from costule. O.

Distribution.—Galapagos Islands; shaded moist gullies and potholes in lava (Wiggins and Porter, 1971); 400–800 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Galápagos**: Fernandina Island, Green Crater, 600 m, [0°40′S, 90°33′W], 17 Sep 1977, *Adsersen 887* (C); Idefatigable Island, Mt. Crocker, 9 May 1932, *Howell 9230* (GH); Isabella Island, SW slope of Volcano Cerro Azul, 800 m, [0°01′S, 91°12′W], Aug 1975, *van der Werff 2267* (NY, QCA, U); Pinta Island, in the old crater, central part of island, 590 m, [0°36′N, 90°45′W], 25 Mar 1972, *Hamann 915* (C); Santa Cruz Island, between Cerro Colorado II and Puntudo, 700 m, [0°38′S, 90°22′W], 18 Apr 1977, *Adsersen 84* (C, QCA); idem, Miconia belt near Media Lunz, 800 m, [0°38′S, 90°22′W], May 1974, *van der Werff 966* (NY, U); San Cristóbal Island, Wrick Bay, 800 m, [0°48′S, 89°24′W], 6 Jul 1905–1906, *Stewart 914* (GH, MO, US); San Salvador Island, El Campamento Central, 570 m, [0°15′S, 90°42′W], 16 Aug 1972, *Hamann 1985* (C).

Megalastrum pleiosoros is characterized by laminae medially 1-pinnate-pinnatisect, pinnae equilateral, and pinna rachises and costules abaxially pubescent by hairs 0.6–1.0 mm long. This species and *M. galapagense* are the only *Megalastrum* in the Galapagos Islands. See *M. galapagense* for comparison. These two species greatly resemble *M. microsorum* from mainland Ecuador and Peru. That latter species differs by laminae abaxially either glabrous or shorter-pubescent with fewer-celled hairs (0.2–0.5 mm long, 2- or 3-celled).

34. *Megalastrum polybotryoides* R. C. Moran, J. Prado & Sundue, *sp. nov.*

TYPE.—ECUADOR. Napo: proyecto de carretera Salcedo - Tena, 5 km desde donde termina el carretero desde Tena, camino a Verde-Yacu, 1°02′S, 77°52′W, 10 Aug 1994, *H. Navarrete 538* (holotype: QCA! 2-sheets; isotypes: AAU! 3-sheets, QCNE-n.v.). **Figs. 5A, 21A–D, 29C.**

Rhizomes not seen; **leaves** 1.0–1.5 m long; **petiole base scales** ca. 10.0 × 1.0 mm, appressed to spreading, linear-lanceolate, light brown, lustrous, twisted, sparsely denticulate; **laminae** ca. 0.8 m long, basally 2-pinnate-pinnatifid, medially 2-pinnate; **lamina rachises** abaxially without hairs, glandular, the glands 0.1 mm long, globose, sessile; **basal pinnae** up to 22.0 cm long, equilateral, segments adnate; **pinna rachises** abaxially densely glandular, without hairs, scaly, the glands ca. 0.1 mm wide, sessile, spherical, brown, the scales 2.0–5.0 × 0.5 mm, appressed to loosely spreading, linear-lanceolate, brown, lustrous, tortuous, sparsely denticulate, adaxially densely glandular, sparsely pubescent, scaly, the glands and scales similar to those

---

←

Costal hairs and scales. All scale bars = 1 mm. A–D: Isotype, *Navarrete 538* (AAU). E–H: *Øllgaard et al. 2233* (AAU). J–O: Isotype, *Camp 3786* (K).

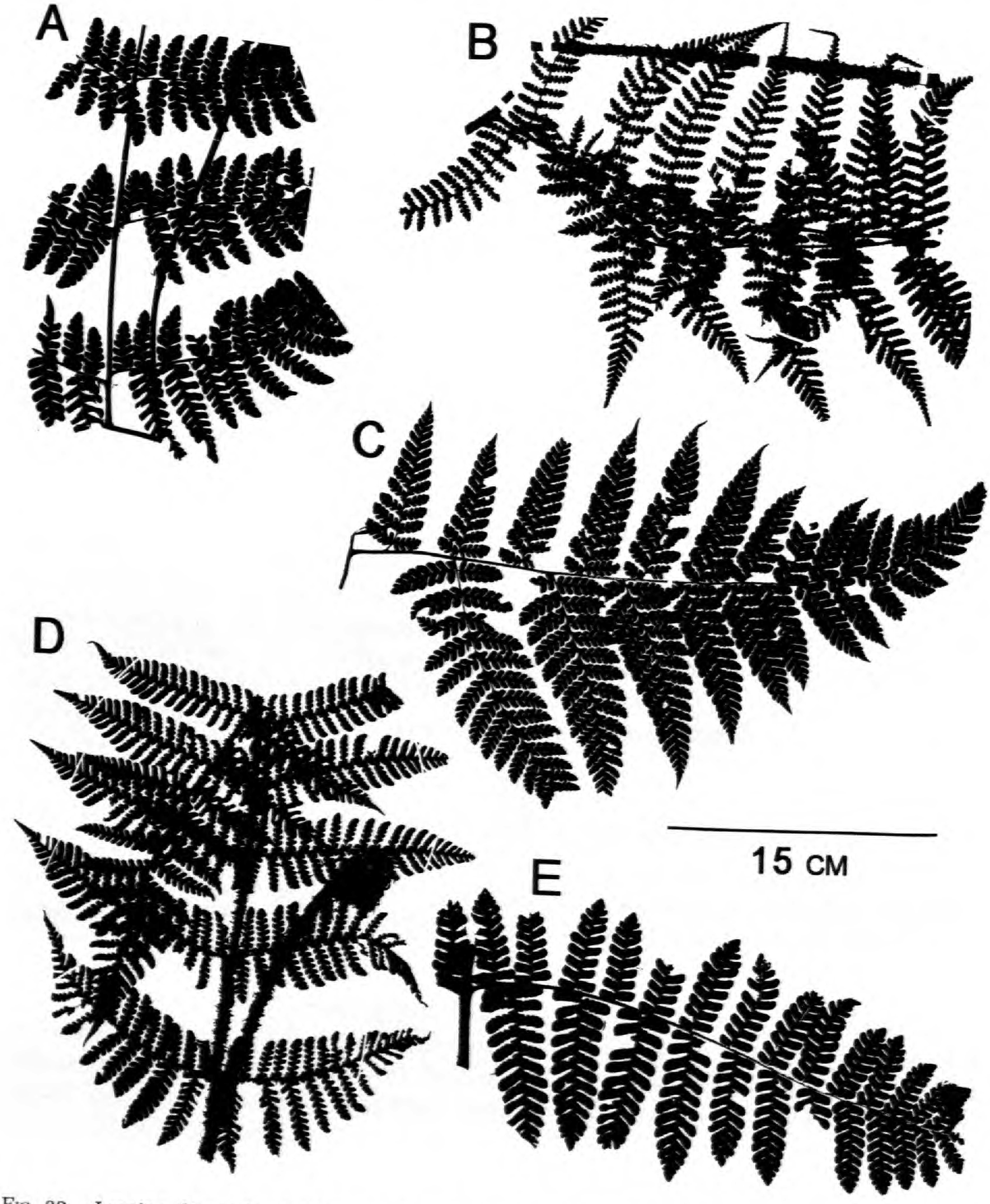

FIG. 22. Lamina dissection in five species of Andean *Megalastrum*. A. Proximal half of leaf, *M. nigromarginatum*. B. Medial pinna, *M. decompositum*. C. Basal pinna, *M. oreophilum*. D. Leaf, *M. rhachisquamatum*. E. Basal pinna, *M. miscellum*. A: Holotype, *Tryon & Tryon 6103* (GH). B: *van der Werff et al. 12506* (UC). C: *Smith 1023* (NY). D: *Øllgaard 98413* (AAU). E: *Killip et al. 10394* (NY).

abaxially, the hairs 0.2–0.4 mm long, 2–5-celled, appressed to spreading, acicular, light brown, ascending; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially sparsely glandular and sparsely scaly, without hairs, the glands like those of the pinna rachises, the scales ca. 1.0 × 0.3 mm, light brown, lanceolate, appressed to loosely ascending, lustrous, sparsely denticulate, adaxially sparsely glandular, without hairs, without scales; **laminar tissue between veins** on both surfaces sparsely glandular, without hairs, the glands like those of the pinna rachises, the glands like those of the pinna rachises; **ultimate veins** sparsely glandular and without hairs on both surfaces, the glands similar to those on the lamina tissue; **lamina margins** eglandular, sparsely ciliate, the hairs ca. 0.1 mm long, 1- or 2-celled, acicular, ascending; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, eastern side of Andes; 650 m.

SPECIMENS EXAMINED.—ECUADOR. **Napo**: Proyecto de carretera Salcedo-Tena, 5 km desde donde termina el carretero desde Tena, camino a Verde-Yacu, 650 m, 1°02′S, 77°52′W, 10 Aug 1994, *Navarrete 539, 540* (AAU, QCA!).

Megalastrum polybotryoides is distinctive by the leaf axes on both surfaces glandular and pinna rachises adaxially hairless. The glands are sessile, spherical, numerous, and brown. They are sometimes easily overlooked. The specific epithet refers to the lamina division, which resembles that of *Polybotrya caudata* Kunze and *P. pubens* Mart.

35. *Megalastrum praetermissum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Morona-Santiago: Gualaquiza Cantón, within 3 km of town of Gualaquiza, E of town and of Río Gualaquiza, 3°24′S, 78°34′W, 1000 m, 08 May 1993, *A. Fay & L. Fay 4250* (holotype: QCNE!; isotypes: AAU!, MO! [barcode 04911841, 04911842, 049118433], NY! [barcode 871000], UC! [barcode 1616316]). **Figs. 13A, 32D, 35F–M.**

Rhizomes erect, to 15 cm long, scaly, the scales 20.0–30.0 × 0.5–1.0 mm, ascending to appressed, linear to linear-lanceolate, castaneous, lustrous, flat or slightly twisted, denticulate, the teeth often bifid; **leaves** 1.0–3.5 m long; **petiole base scales** 0.8–15.0 × 0.4–0.7 mm, spreading, filiform, golden brown to castaneous, lustrous, twisted, not only slightly tortuous, strongly denticulate; **laminae** 0.7–1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 0.3–0.7 m long, strongly inequilateral; **pinna rachises** abaxially eglandular, without hairs, sparsely to moderately scaly, the scales up to 5 × 0.2–0.3 mm, linear, brown, concolorous (not darker distally), strongly denticulate, the teeth often bifid, linear, appressed to spreading, adaxially pubescent, eglandular, scaly, the hairs up to 0.5 mm long, 3–5-celled, spreading, the scales like those on the abaxial surfaces; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, pubescent, scaly, the hairs 0.4–0.7 mm long, 3- or 4-celled, the scales like those of the pinna rachises but shorter, 1.0–2.0 mm long, linear, adaxially pubescent, eglandular, sparsely scaly, the hairs 0.5–1.5 mm long, 4- or 5-celled, the scales ca. 0.5 mm long; **laminar tissue between veins** abaxially eglandular, puberulent to glabrous, the hairs (when present) ca. 0.1 mm long, fine and easily overlooked, acicular, erect, hyaline, adaxially glabrous; **ultimate veins**

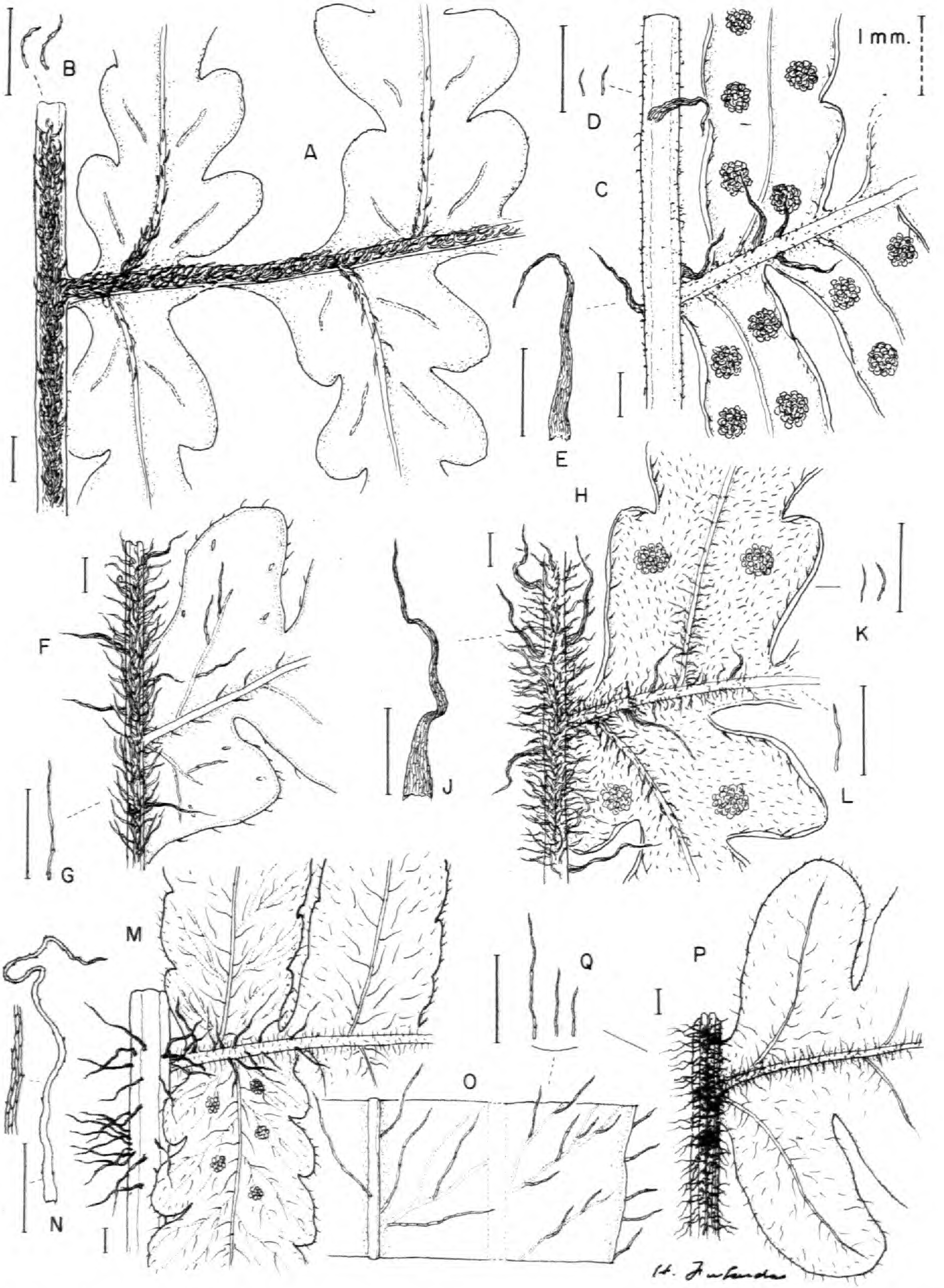

FIG. 23. Indument detail of three Andean species of *Megalastrum*. A–E. *M. falcatum*. A. Adaxial surface of pinnules, lamina and pinna rachises. B. Lamina rachis hairs. C. Abaxial surface of lamina rachis, pinna rachis, and segments. D. Detail of hairs. E. Scale from lamina rachis. F–L. *M. pubescens*. F. Adaxial surface of pinna rachis and segment. G. Hair detail. H. Abaxial surface of lamina rachis, pinna rachis, and pinnules. J. Scale detail. K, L. Hair details. M–Q. *M. molle*. M.

abaxially eglandular, sparsely and finely pubescent, the hairs 0.1–0.3 mm long, 1- or 2-celled, acicular, erect, hyaline, adaxially glabrous to pubescent, the hairs (when present) 0.3–2.0 mm long, 4–6-celled, ascending to spreading and slightly tortuous; **lamina margins** eglandular, ciliate, the hairs 0.1–0.4 mm long, 2- or 3-celled, ascending to spreading; **indusia** absent; **spores** cristate.

Distribution.—Colombia, Ecuador, Peru, Bolivia, eastern side of Andes; 280–2170 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Putumayo**: márgenes del Río Güamues, San Antonio de Güamues, 310 m, [0°34′N, 76°50′W], 19 Dec 1940, *Cuatrecasas 11185* (F).

ECUADOR. **Azuay**: Baños-Pintuc, [2°57′S, 79°06′W], s.d., *Stubel 943* (B). **Morona-Santiago**: Morona Cantón, near city of Macas, 1100 m, 02°20′S, 78°08′W, 22 Jul 1993, *Fay & Fay 4097* (AAU, MO, NY, QCNE); within 3 km of the town of Gualaquiza, 1000 m, 03°24′S, 78°34′W, 8 Mar 1993, *Fay & Fay 4232* (AAU, MO, NY, QCNE). **Napo**: Santa Rosa at Río Napo, [0°49′S, 75°30′W], 30 Apr 1972, *Lugo 2064* (AAU, GH, MO, U). **Pastaza**: East of Puyo, along the road to Macas, and wet forest around the Municipal, 950 m, 01°30′S, 77°59′W, 14 Jul 1992, *Fay & Fay 3662* (MO, NY, QCNE). **Zamora-Chinchipe**: Zamora, within 3 km of the town of Zamora, 1000 m, 4°03.5′S, 78°57.5′W, 7 Dec 1994, *Fay & Fay 4403* (AAU, MO, QCNE).

PERU. **Bagua**: valley of Río Marañon above Cascadas de Mayasi near Campamento Stte. Montenegro, Kms 280–284 of Marañon road, 450–600 m, [5°18′S, 78°25′W], 5 Sep 1962, *Wurdack 1851* (US). **Cajamarca**: San Ignacio, Ricardo Palma, 1720 m, 5°07′29″S, 79°03′16″W, 19 May 1998, *Campos & Lopez 4911* (MO, NY). **Cusco**: Paucartambo, Hacienda Villa Carmen, 540 m, [13°18′S, 71°35′W], 19 Jul 1963, *Vargas 14685* (GH). **Pasco**: Oxapampa, Gran Pajonal, vicinity of Chequitavo, 1200 m, 10°45′S, 74°23′W, 26 Sep 1983, *Smith 5260* (F, MO).

BOLIVIA. **Beni**: Prov. Gral. Ballivián, 16 km por el camino maderero, 12 km de Yucumo a Rurrenabaque, 450 m, 15°05′S, 67°07′W, 23 Jul 1997, *Kessler et al. 10774* (GOET, UC). **Carrasco**: Cochabamba, Localidad Dianpampa, 2160 m, 17°40′53″S, 64°40′55″W, 4 Sep 2003, *Fernández et al. 2366* (MO). **Cochabamba**: Prov. José Carrasco Torrico, 143 km antigua carretera Cochabamba-Villa Tunari, 1300 m, 17°07′S, 65°34′W, 23 Aug 1996, *Kessler et al. 7631* (GOET, UC). **La Paz**: Prov. Abel Iturralde, Río San Antonio, 46 km de Ixiamas a Alsto Madidi, 300 m, 13°38′S, 68°26′W, 13 Aug 1997, *Kessler et al. 11131* (GOET, UC). **Santa Cruz**: Nuflo de Chavez, Serranía de San Lorenzo, 2 km E of Est. Las Maras, 500–900 m, 16°15′S, 62°35′W, 3 Nov 1985, *Killeen 1383* (F, MO, NY, UC).

←

Abaxial surface of lamina and pinna rachises and pinnules. N. Rachis scale. O. Hairs on abaxial surface of lamina. P. Adaxial surface of pinnule. Q. Detail of hairs. Scale bars = 1 mm. A–E: holotype, *Croat et al. 91165* (MO). F–L: Isotype, *Killip & Smith 20453* (NY). M–Q: Isotype, *van der Werff et al. 16300* (NY).

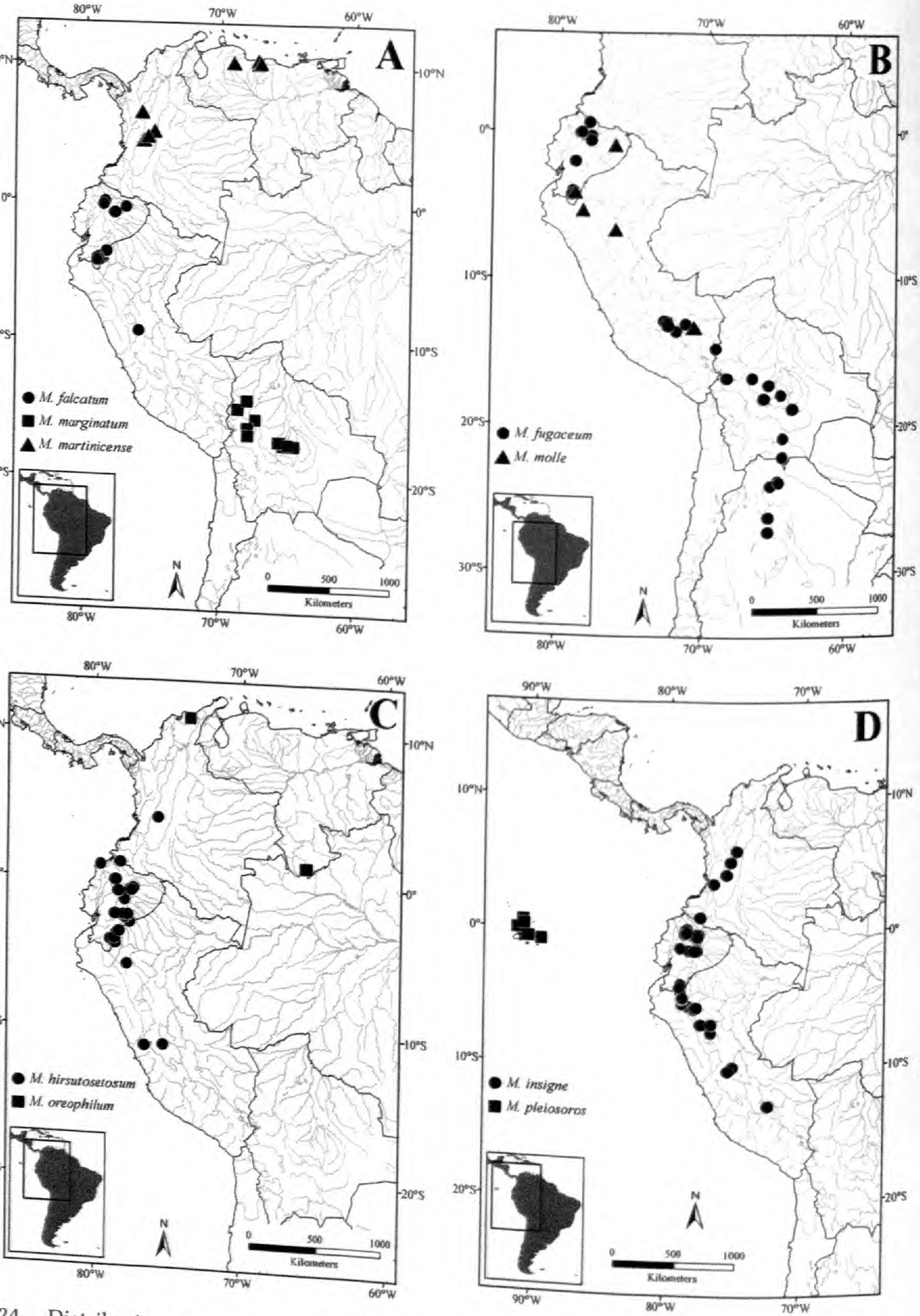

FIG. 24. Distribution of nine species of *Megalastrum* in the Andes. Some species are also known from areas outside the Andean region as here defined; for the worldwide distribution of a species, see under each species description.

Megalastrum praetermissum is distinctive by the linear, brown denticulate scales along the pinna rachises. It varies considerably in pubescence on both surfaces of the lamina. In most specimens there are at least a few ca. 0.1 mm long, erect, acicular hairs between the veins abaxially. These hairs are easily overlooked, especially when viewed from above, and thus the specific epithet *praetermissum* meaning "overlooked," or "passed by." These minute hairs are best seen in profile on folded portions of the lamina. Adaxially, the pubescence (when present) is quite different, with the veins and midribs of the ultimate segments bearing conspicuous whitish hairs 0.3–2.0 mm long. These hairs vary from sparse and inconspicuous to dense and conspicuous.

Megalastrum praetermissum resembles *M. marginatum* in lamina division, presence of filiform scales on the petiole bases and pinna rachises, and long hairs on the veins adaxially; however, *M. praetermissum* differs by pinna rachises abaxially glabrous and laminae between the veins minutely and inconspicuously pubescent.

36. Megalastrum pubescens A. Rojas, Métodos en Ecología y Sistemática (MES) 3(Supl. 1):44, fig. 5. 2008. TYPE.—COLOMBIA. Norte de Santander: Eastern Cordillera, N of Toledo, Loso and vicinity, [7°02′N, 72°05′W], 2200–2400 m, 6–7 Mar 1927, *E. P. Killip & A. C. Smith 20453* (holotype: NY! [barcode 0871575]; isotype: US-n.v.). **Figs. 5A, 18D, 23F–L.**

Rhizomes erect, scales 5.0–13.0 × 0.3–0.7 mm, appressed to strongly ascending, linear, concolorous, flat, sparsely denticulate; **leaves** to 0.8–1.0 m long; **petiole base scales** like those of the rhizomes but loosely spreading to ascending; **laminae** 0.4–0.6 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatifid; **lamina rachises** pubescent abaxially; **lamina rachises** pubescent abaxially; **basal pinnae** ca. 30.0 cm long, strongly inequilateral; **pinna rachises** abaxially eglandular, glabrous to sparsely pubescent, sparsely scaly, the hairs 0.3–0.5 mm long, 2–4-celled, acicular, spreading, the scales 3.0–4.5 × 0.2–0.3 mm, linear-lanceolate, brown, flat, subentire to denticulate, the teeth not bifid, adaxially eglandular, densely pubescent, scales absent, the hairs 0.4–1.0 mm long, 4–7-celled, ascending to spreading, acicular; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, puberulent, sparsely scaly, hairs 0.3–0.5 mm long, 2–4-celled, acicular, spreading, the scales up to 7.0 × 0.2 mm, linear-lanceolate, brown, lustrous, subentire, adaxially with indument similar to those of the abaxial surfaces; **laminar tissue between veins** abaxially glandular, densely pubescent, the hairs sometimes glandular-tipped, 0.2–0.3 mm long, 1–3-celled, erect, acicular, adaxially glabrous; **ultimate veins** visible on both surfaces, abaxially eglandular, puberulent, the hairs like those on the lamina tissue, adaxially very sparsely pubescent, the hairs like those on the costules; **lamina margins** eglandular, ciliate, the hairs 0.3–0.5 mm long, 1- or 3-celled, ascending to spreading, acicular; **indusia** absent; **spores** cristate.

Distribution.—Colombia; 2000–2400 m.

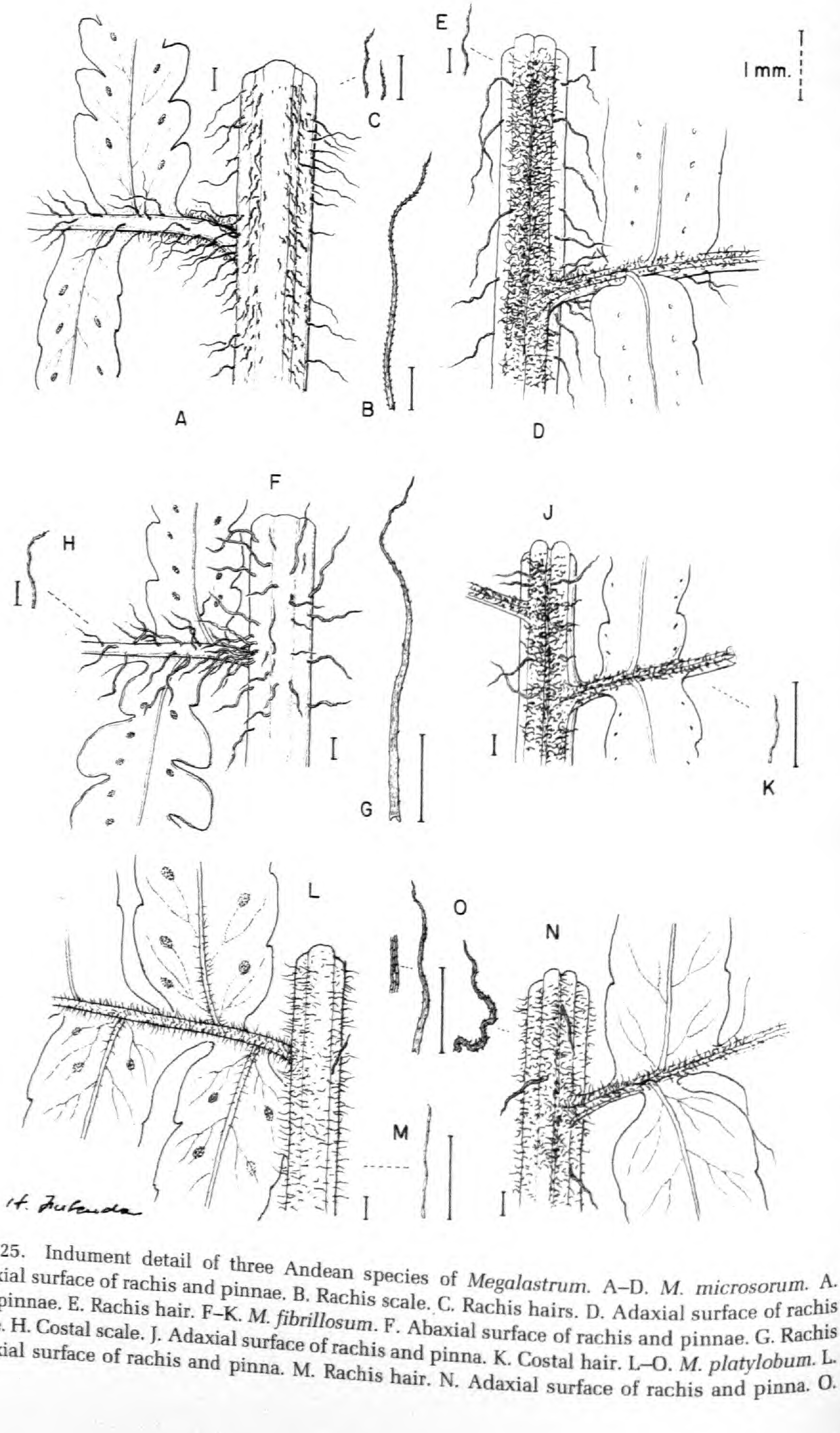

FIG. 25. Indument detail of three Andean species of *Megalastrum*. A–D. *M. microsorum*. A. Abaxial surface of rachis and pinnae. B. Rachis scale. C. Rachis hairs. D. Adaxial surface of rachis and pinnae. E. Rachis hair. F–K. *M. fibrillosum*. F. Abaxial surface of rachis and pinnae. G. Rachis scale. H. Costal scale. J. Adaxial surface of rachis and pinna. K. Costal hair. L–O. *M. platylobum*. L. Abaxial surface of rachis and pinna. M. Rachis hair. N. Adaxial surface of rachis and pinna. O.

SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Mpio. Angelópolis, Vereda Romeral, sector Bocatoma, acueducto multiveredal, Quebrada Las Animas, 2100–2200 m, 6°09′29″N, 75°42′05″W, 29 Oct 2005, *Rodríguez et al. 5559* (HUA).

Megalastrum pubescens is distinctive by laminae only 0.4–0.6 m long, abaxially densely and conspicuously pubescent, and adaxially between the veins glabrous. The pinnules tend to be slightly ascending.

Megalastrum pubescens resembles *M. vastum* but differs by laminae adaxially glabrous between the veins and longer hairs abaxially on the pinna rachises and costules (hairs 0.3–0.5 mm long, 2–4-celled vs. 0.1(–0.2) mm long, 1(–2)-celled). Also their scales on the pinna rachises abaxially differ subtly, with those of *M. pubescens* being brown, linear-lanceolate, and firmer, whereas those of *M. vastum* are golden brown, lanceolate, and flaccid.

37. *Megalastrum pubirhachis* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Napo: El Chaco Cantón, just above N side of Río Oyachachi, where the Lago Agrio Road crosses the river, 00°18′S, 77°21′W, 1500 m, 9 Aug 1992, *A. Fay & L. Fay 3919* (holotype: QCNE; isotypes: AAU!, MO! [04670566, 04670570, 04670656,], NY! [barcode 00870997], QCA?-n.v.). **Fig. 18E, 34F–L, 36A.**

Rhizomes unknown; **leaves** up to 2.0 m long; **petiole base scales** 10.0–15.0 mm long, linear, brown, shiny, smooth on both surfaces, spreading to loosely ascending, denticulate; **laminae** 0.4–1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **basal pinnae** 30.0–45.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, densely pubescent, scaly, the hairs (when present) 0.1–0.2 mm long, 2 or 3-celled, mostly retrorsely strigose, the scales 3.0–4.0 × ca. 0.1–0.2 mm, dull brown, appressed (mostly) to loosely spreading and ascending, filiform to linear, slightly tortuous, denticulate, adaxially pubescent, sparsely scaly or lacking scales, hairs like those abaxially, the scales like those abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, pubescent, without scales or only sparsely scaly, the hairs ca. 0.1 mm long, 1- or 2-celled, acicular, ascending to strigose, the scales (when present) like those of the pinna rachises, adaxially pubescent, the hairs like those on the pinnae rachises adaxially; **laminar tissue between veins** abaxially eglandular, glabrous to sparsely puberulent, the hairs ca. 0.1 mm long, easily overlooked, erect, adaxially eglandular, glabrous; **ultimate veins** abaxially visible, glabrous to sparsely puberulent, the hairs ca. 0.1 mm long,

---

←

Rachis scale. Scale bars = 1 mm. A–D: *Cornejo & Bonifaz 5459* (AAU). F–K: *Jiménez & Huaylla 2547* (UC). L–O: Lectotype, *Spruce 4656* (K).

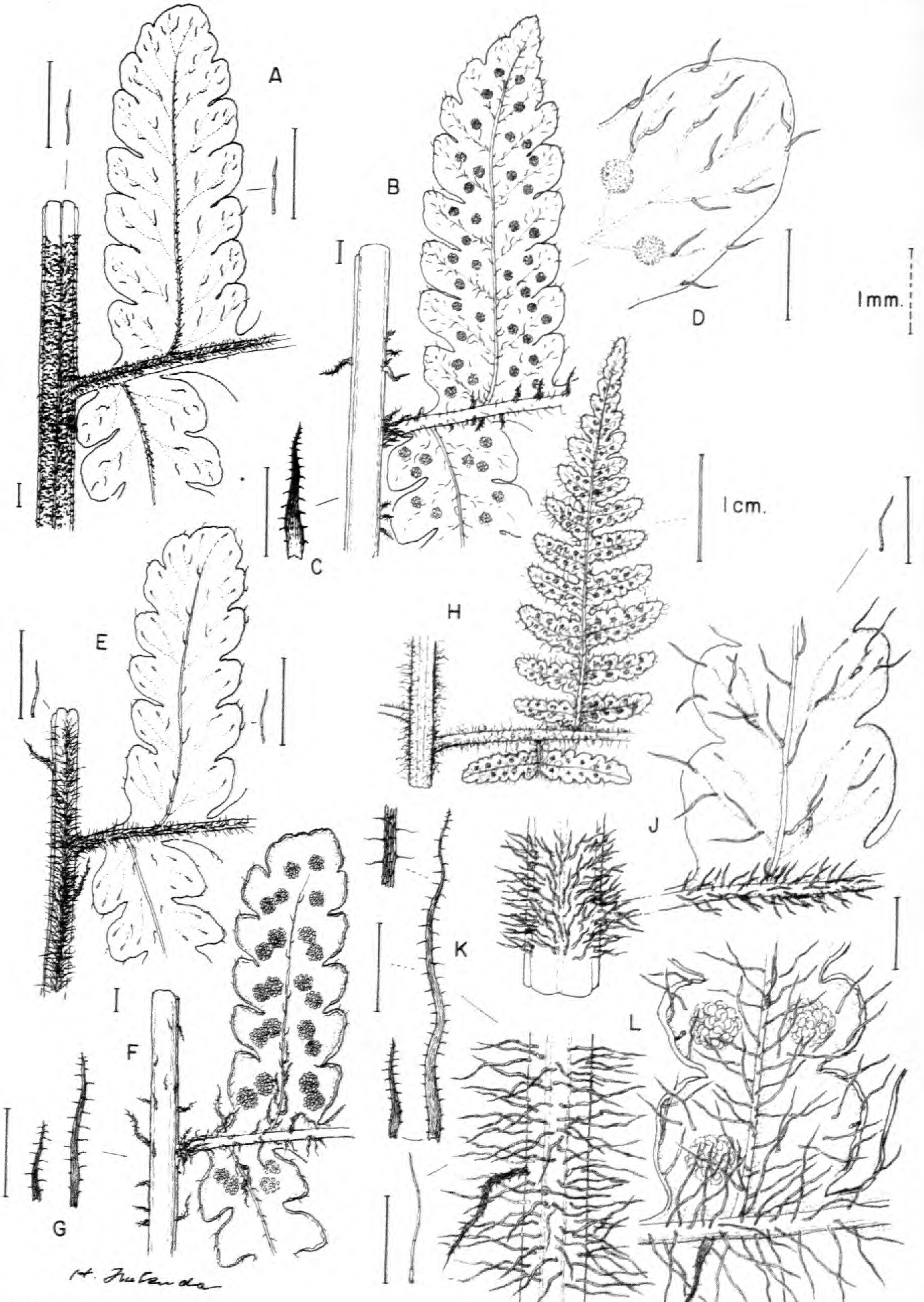

FIG. 26. Indument of two species of Andean *Megalastrum*. A–D. *M. fugaceum*. A. Adaxial surface of pinnule. B. Abaxial surface of pinnules. C. Scale from costule, note darkened apex. D. Abaxial surface of lobe. E–G. *M. fugaceum*. E. Adaxial surface of pinnules. F. Abaxial surface of pinnules. G. Scales from costule. H–L. *M. pulverulentum*. H. Abaxial surface of pinnules. J. Adaxial surface of costule and segment. K. Scales from pinna rachis. L. Abaxial surface of costule and segment.

acicular, adaxially obscure, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.1–0.2 mm long, 1- or 2-celled, acicular, ascending to appressed; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru, eastern side of the Andes; 1300–2100 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Napo**: 65 km along rd. NE of Baeza, Cordillera Oriental, 1300 m, [0°05′S, 77°30′W], 26 Jan 1984, *Moran 3594* (B, MO, NY).

PERU. **Amazonas**: Bagua, 12 km E of La Peca, 1700 m, [5°36′S, 78°26′W], 20 Jun 1978, *Barbour 2394* (MO, NY).

Megalastrum pubirhachis is distinctive by pinna rachises abaxially with linear denticulate scales and dense, even, retrorsely strigose hairs. By these characters it resembles *M. reductum*, a species that differs by filiform scales and smaller (0.4–0.8 m long vs. 0.4–1.5 m in *M. pubirhachis*), less divided laminae (basally 2-pinnate-pinnatisect, medially 1-pinnate-pinnatisect to 2-pinnate-pinnatifid vs. basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect in *M. pubirhachis*). *Megalastrum pubirhachis* occurs only on the eastern side of the Andes, whereas *M. reductum* is only on the western side. The specific epithet refers to the dense hairs on the abaxial surfaces of the pinna rachises.

38. Megalastrum pulverulentum (Poir.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:129. 1987 [published 3 May 1988]. *Polypodium pulverulentum* Poir., Encycl. Méth. Bot. 5:555. 1804. *Aspidium lutescens* Willd., Sp. Pl. 5:272. 1810, *nomen superfl. Dryopteris pulverulenta* (Poir.) C. Chr. in Urb., Symb. Antill. 9:305. 1925. *Ctenitis pulverulenta* (Poir.) Copel., Gen. Fil. 124. 1947. LECTOTYPE.—designated by Proctor (1985): Plumier, Traité Foug. Amér. 27, pl. 34, 1707, illustrating a plant from Hispaniola. **Fig. 8C,E, 26H–L, 36B.**

Polypodium barbatum Desv., Mém. Soc. Linn. Paris 6:242. 1827. TYPE.—HISPANIOLA. Without exact locality, s.d., *A. N. Desvaux s.n.* (holotype: P! [barcode 00600637], photo US!).

Polypodium karstenianum Klotzsch, Linnaea 20:390. 1847. *Phegopteris karsteniana* (Klotzsch) Mett., Abh. Senck. Nat. Ges. Frankfurt 2:314. 1858. *Nephrodium villosum* (L.) Kuntze var. *karstenianum* (Klotzsch) Jenman, Bull. Bot. Dept. Jamaica n.s. 3:114. 1896. *Dryopteris subincisa* (Willd.) Urb. var. *karsteniana* (Klotzsch) C. Chr., Index Filic. 295. 1905. *Dryopteris karsteniana* (Klotzsch) Hieron., Hedwigia 46:348. 1907. *Ctenitis karsteniana* (Poir.) Vareschi, Fl. Venez. 1(1):405. 1969.

←

Scale bars = 1 mm. A–D: Isotype, *Moran 5911* (UC); E–G: Isotype, *Øllgaard et al. 99556* (AAU). H–L: *Fay & Fay 3845* (NY).

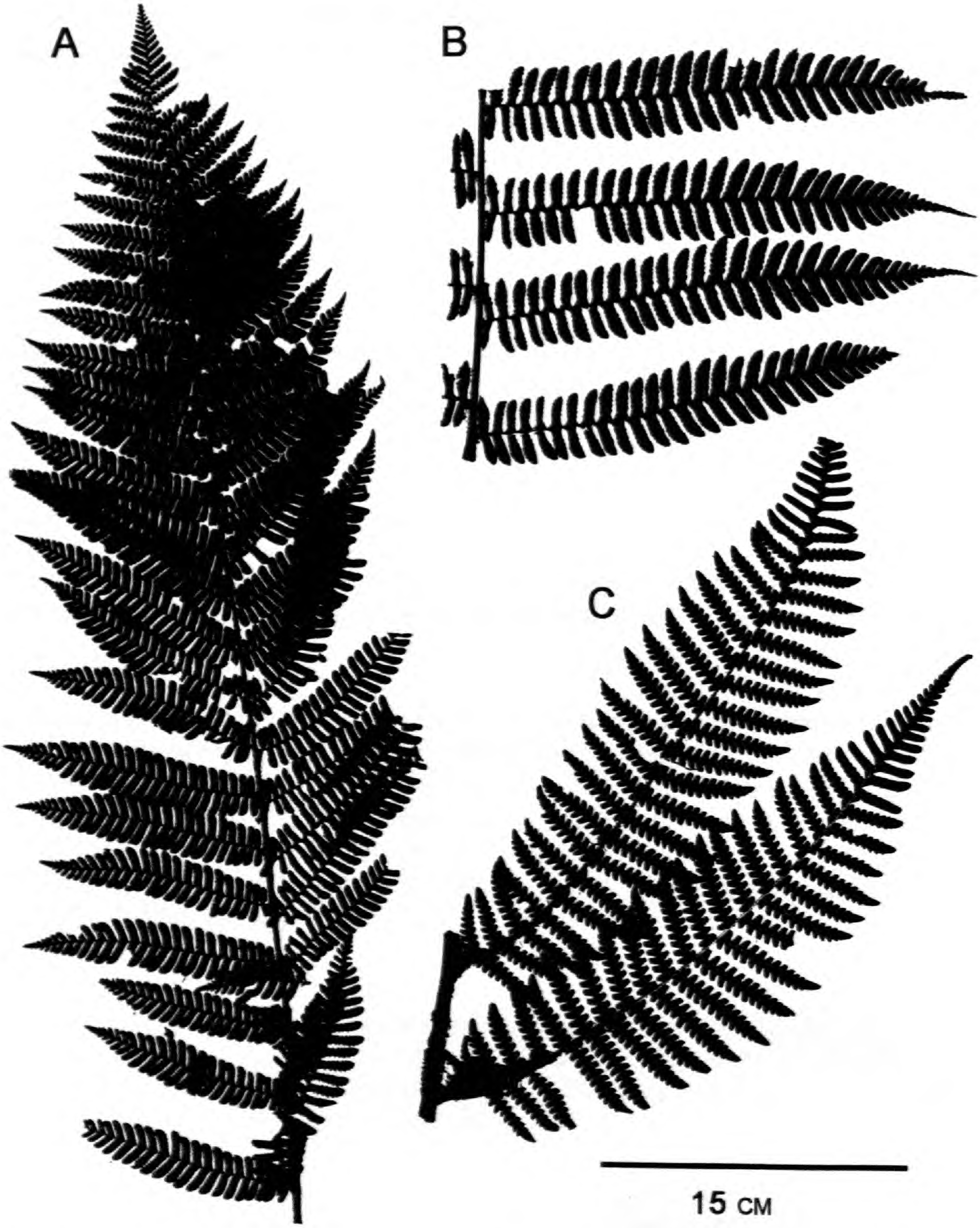

FIG. 27. Leaf dissection in three species of *Megalastrum*. A. Lamina, *M. pleiosoros*. B. Proximal pinnae, *M. microsorum*. C. Proximal pinnae, *M. galapagense*. A: *van der Werff 966* (S). B: *Cornejo & Bonifaz 5459* (AAU). C: *van der Werff 2256* (U).

Megalastrum karstenianum (Klotzsch) A. Rojas, Rev. Biol. Trop. 49:483. 2001. TYPE.—VENEZUELA ["as Colombien"]. Dec 1848, *H. Karsten II, 3* (lectotype, designated by Moran and Prado, 2010: B! [barcode 200058400], photos B!, US!; isolectotypes: H-n.v.).

Phegopteris hirsuta Fée, Mém. Foug. 5:248. 1852. TYPE.—VENEZUELA ["Mexico"]. Mérida: Aug 1846, *H. Funck & L. J. Schlim 975* (lectotype, designated by Moran and Prado, 2010: P [barcode 00600642]; isolecto types, BM! [barcode 000907809], P! [barcode 00600643, 00600644), P [barcode 583962, 00583963]).

Aspidium erythrostemma Christ, Bull. Herb. Boiss., sér. 2, 4:961. 1904. *Dryopteris erythrostemma* (Christ) C. Chr., Index Filic. 263. 1905. TYPE.—COSTA RICA: in 1903, *C. Wercklé s.n.* (lectotype, designated by Moran and Prado, 2010: P! [barcode 00600398]).

Rhizomes erect, scales 20.0–40.0 × 0.3–0.5 cm, appressed to strongly ascending, linear-lanceolate, light brown to golden, twisted, lustrous, the margins denticulate; **leaves** up to 4.0 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 1.2–3.0 m long, basally 4-pinnate-pinnatisect, medially 3-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** to 1.4 m long, strongly inequilateral; **pinna rachises** on both surfaces densely pubescent, scaly, glandular, the hairs 1.0–2.0 mm long, 5–12-celled, spreading, the scales denticulate to ciliate (the cilia often darker than the body of the scale, especially towards the apex), non-bullate, of two types, small ones ca. 0.2–0.6 × ca. 0.2 mm long, ovate to lanceolate, mostly appressed, the larger 3.0–8.0 × 0.2–0.5 mm long, linear to linear-lanceolate, spreading, the glands ca. 0.1 mm long, spherical, sessile, yellowish, adaxially with indument like that abaxially; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially glandular, densely pubescent, sparsely scaly, the indument like that on the pinna rachises but more sparsely scaly adaxially; **laminar tissue between veins** glandular and pubescent on both surfaces or only abaxially, the glands short-stalked to sessile and spherical, yellowish, the hairs 1.0–2.0 mm long, 5–8-celled, spreading to erect; **ultimate veins** on both surfaces visible to obscure, abaxially glandular, sparsely pubescent, non-scaly, the hairs ca. 0.5–2.0 mm long, 4–8-celled, adaxially eglandular, sparsely pubescent, the hairs 1.0–1.8 mm long, 4–9-celled, spreading; **lamina margins** glandular, ciliate, the hairs 0.4–1.0 mm long, 4- or 5-celled, spreading, the glands few, stalked, yellowish; **indusia** absent; **spores** echinulate.

Distribution.—Mexico, Guatemala, Honduras (Stolze, 1981), Costa Rica, Panama, Jamaica, Haiti, Dominican Republic, Guadeloupe, Martinique, St. Vincent, Dominica, Saba; Venezuela, Colombia, Ecuador, Peru; 1200–2500 (–3200) m (in West Indies from 0–1600 m; Moran *et al.*, 2009b).

SELECTED SPECIMENS EXAMINED.—VENEZUELA. **Aragua**: Colonia Tovar and vicinity, 2000–2100 m, [10°22′S, 67°16′W], 28 Dec 1921, *Pittier 10029* (GH, NY, US). **Distrito Federal**: Carretera El Junquito-Colonia Tovar, [10°28′N, 67°05′W], 24 Oct 1963, *Agostini 207* (NY). **Lara**: Morán, 8.7 mi SE of Sanare, in Parque Nacional Yacambu, 1500 m, 9°41′N, 69°35′W, 13 Nov 1982, *Smith et al. 1249* (MO). **Mérida**: Dpto. Sucre, en las Selvas Nubladas situadas al norte de la localidad conocida como La Trampa, 2000 m, 9°34′ N, 71°26′ W, 2 Feb 1987, *Ortega et al. 3030* (MO). **Trujillo**: Mpio. Boconó, entre las antenas de relevo en

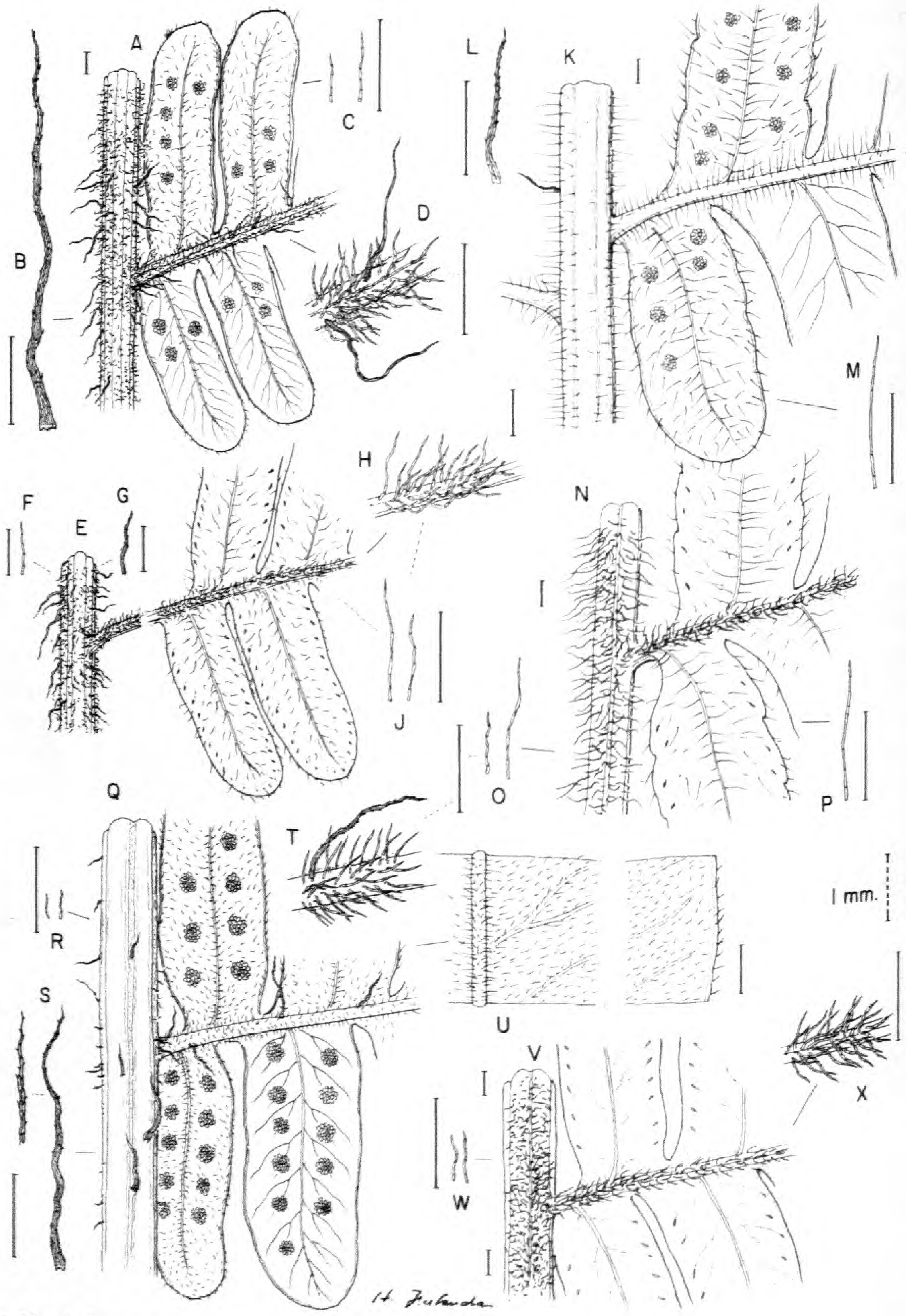

FIG. 28. Indument detail of three Andean species of *Megalastrum*. A–J. *M. pleiosoros*. A. Abaxial surface of rachis and pinna. B. Rachis scale. C. Detail of hairs. D. Costal hairs and scales. E. Adaxial surface of rachis and pinna. F. Rachis hair. G. Rachis scale. H. Hairs along costa. J. Detail of hairs. K–P. *M. hirsutosetosum*. K. Abaxial surface of rachis and pinna. L. Rachis scale. M.Hair from abaxial surface of lamina. N. Adaxial surface of rachis and pinna. O. Rachis hair. P. Hair from

el Páramo de Guaramacal y la Vega de Guaramacal, 1200–3200 m, [9°11′N, 70°12′W], 23–24 Jul 1984, *Ortega et al. 2013* (MO, NY).

COLOMBIA. **Antioquia**: Jardín, Vereda Quebrada Bonita, sector Bocatoma, quebrada La Mendoza, 2110–2150 m, 5°35′04.3″N, 75°46′36.1′″W, 7 Jan 2005, *Rodríguez et al. 4915* (HUA, NY). **Cauca**: near Popayan, 1800 m, [2°26′N, 76°37′W], 14 Apr 1939, *Alston 8026* (MO). **Cundinamarca**: Fusagasugá, m, [4°20′N, 74°22′W], s.d., *André 91* (K, NY). **Magdalena**: Cordillera Oriental, Sierra de Perijá, 10 km ENE of Manaure, 46 km E of Valledupar, 3 km from Venezuela border, 2300 m, [10°28′N, 73°15′W], 4 Feb 1945, *Grant 10810* (NY, US). **Norte de Santander**: Eastern Cordillera, Loso and vicinity, N of Toledo, 2200–2400 m, [7°17′N, 72°25′W], 6–7 Mar 1927, *Killip & Smith 20411* (GH, NY, US). **Santander**: Río Suratá valley, above Suratá, 2000–2300 m, [7°30′N, 72°58′W], 5–6 Jan 1927, *Smith 16659* (GR, NY, P, S, US).

ECUADOR. **Napo**: Quijos Cantón, within 5 km of the town of Baeza, 1900 m, 0°27′5″S, 77°53′00″W, 20 Jun 1992, *Fay & Fay 3845* (AAU, MO, NY, QCNE). **Pichincha**: camino Santo Domingo de los Colorados a Alagoa, 2.5 km E of Cornejo Astorga, bosque primario por un río, Cordillera Central, 1200 m, [0°26′S, 78°47′W], 8 Jan 1984, *Moran 3546* (F, MO, NY). **Without locality**: 1857–1859, *Spruce 5257A* (GH, K, NY, P, S).

PERU. **Cusco**: La Convención, Distr. Santa Ana, Madre Selva, 2100 m, 12°53′49″S, 72°45′02″W, 19 Mar 2004, *Valenzuela et al. 3019* (MO).

Megalastrum pulverulentum is one of the largest species in the genus, with leaves to 4 m long and basal pinnae to 1.4 m long. Its laminae are densely pubescent on both surfaces by long (1–2 mm) whitish hairs. The pinna rachis scales are prominently toothed and darker apically. Yellowish glands are present on both surfaces and may be either sessile or short-stalked. It greatly resembles *M. fugaceum* (see discussion of *M. fugaceum* for comparison).

39. **Megalastrum reductum** A. Rojas, Mét. Ecol. Sist. 3(Supl. 1):45, fig. 6A–C. 2008. TYPE.—ECUADOR. Guayas/Cañar/Chimborazo/Bolívar: foothills of the W cordillera near the village of Bucay, [2°40′S, 79°40′W], 305–365 m, 8–15 Jun 1945, *W. H. Camp 3786* (holotype: US-n.v.; isotypes: F! [accession 1409933], K!, MO! [barcode 1634138], NY! [barcode 0871594], P! [barcode 00568190]). **Fig. 5B, 21J–O, 29B.**

Megalastrum dorsiglabrum A. Rojas, Mét. Ecol. Sist. 3(Supl. 1):45, fig. 6A–C. 2008, as "*dorsoglabrum*". TYPE.—PANAMA. **Coclé**: El Valle de Antón, [8°37′N, 80°07′W], 1000 m, 4 Jun 1934, *A. H. G. Alston 8730* (holotype: CR!; isotypes: BM-n.v., US-n.v.).

←

costule. Q–X. *M. microsorum*. Q. Abaxial surface of rachis and pinna. R. Rachis hairs. S. Rachis scale. T. Costule abaxially, hairs and scale. U. Detail of abaxial surface of lamina. V. Adaxial surface of rachis and pinna. W. Rachis hairs. X. Hairs along costa. Scale bars = 1 mm. A–J: *Adsersen 84* (C). K–P: *Moran & Rohrbach 5160* (MO). Q–X: *Leiva et al. 1759* (F).

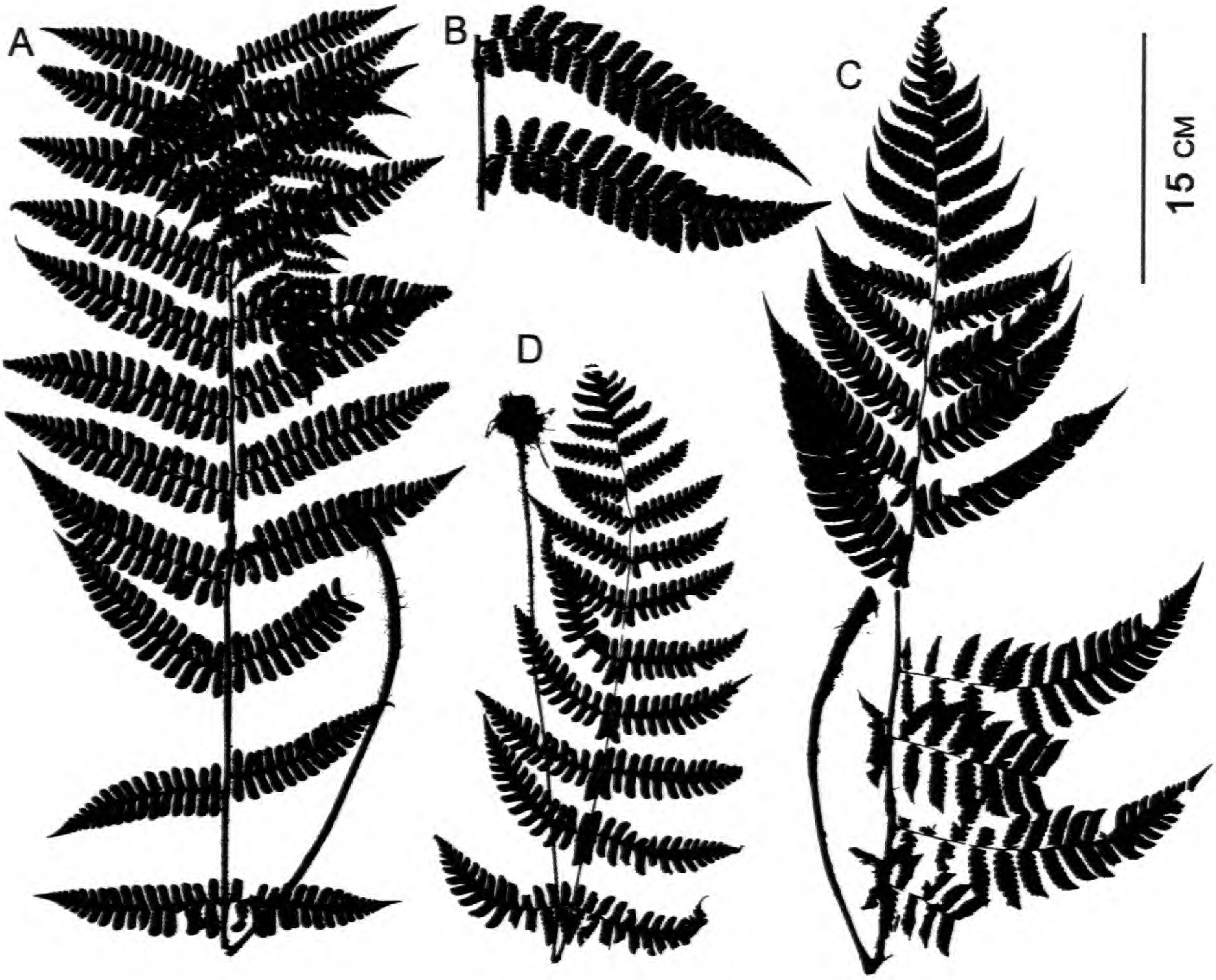

FIG. 29. Leaf dissection in four species of Andean *Megalastrum*. **A.** *M. hirsutosetosum*. **B.** *M. reductum*. **C.** *M. polybotryoides*. **D.** *M. molle*. A: *Øllgaard et al. 99268* (AAU). B: Panama, *Moran 5060* (MO); C: *Navarrete 539* (AAU). D: Isotype, *van der Werff et al. 16300* (F).

Rhizomes erect to decumbent, up to 10.0 cm long, scales 10.0–20.0 × 1.0–2.0 mm, ascending, linear, golden brown, dull, firm, setulose on both the margins and surfaces; **leaves** up to 1.2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.4–0.8 m long, basally 2-pinnate-pinnatisect, medially 1-pinnate-pinnatisect to 2-pinnate-pinnatifid; **lamina rachises** glabrous abaxially; **basal pinnae** 12.0–30.0(–40.0) cm long, equilateral or nearly so; **pinna rachises** abaxially eglandular, densely puberulent, scaly, the hairs (when present) 0.1–0.2 mm long, 1–3-celled, spreading to retrorsely strigose, the scales 3.0–4.0 × ca. 0.1 mm, dull brown, loosely spreading to ascending, filiform to linear, tortuous, entire, adaxially glabrous or pubescent, sparsely scaly or lacking scales, hairs like those abaxially, the scales ca. 1.0 × 0.1 mm, dull, brown, filiform, entire, appressed; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely puberulent or rarely glabrous, sparsely scaly or scales absent, the hairs ca. 0.1 mm long, 1- or 2-celled, acicular, ascending to strigose, the scales ca. 0.5 mm long, filiform, dull brown, entire, adaxially glabrous or subglabrous to sparsely pubescent, the hairs like those on the pinnae rachises adaxially; **laminar tissue between veins** abaxially eglandular, glabrous to puberulent, the hairs ca. 0.1 mm long, 1- or 2-celled, acicular, erect, adaxially eglandular, glabrous; **ultimate veins** abaxially visible, sparsely puberulent with hairs like those on the costules, adaxially obscure, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.1–0.2 mm long, 1- or 2-celled, acicular, ascending to substrigose; **indusia** absent; **spores** cristate.

Distribution.—Eastern Panama, Colombia and Ecuador, western side of Andes; 300–1000 m.

SELECTED SPECIMENS EXAMINED.—COLOMBIA. **Antioquia**: Mpio. Frontino, Parque Nacional Natural Las Orquídeas, vereda Venados Abajo, camino de la cabaña de Venados a la vereda Alto Bonito, 900–920 m, 6°32′10″N, 76°19′15″W, 24 Jul 2011, *Sanín et al. 5176* (NY). **Caldas**: Santa Cecilia, Cordillera Occidental, Fatamá, vertiente occidental, 800 m, 5°03′S, 75°39′W, 25 Nov 1945, *von Sneidern 5024* (F).

ECUADOR. **Bolívar**: San Miguel, within 3 km of Balzapamba, 800 m, 1°47′S, 79°10′W, 10 Jul 1995, *Fay & Fay 4626* (MO, QCNE). **Cotopaxi**: Cacaoal, 300 m, [1°01′S, 79°12′W], 6 May 1951, *Bell 920* (BM, S). **El Oro**: 10.6 millas E de Saracay hacia Piñas, 700 m, [3°37′S, 79°55′W], 23 Nov–18 Dec 1978, *Albert de Escobar 943* (NY). **Esmeraldas**: Quininde, Bilsa Biological Station, Montañas de Mache, 35 km W of Quininde, 5 km W of Santa Isabela, 400–600 m, 0°21′N, 79°44′W, 10 Dec 1994, *Pitman & Bass 1073* (MO, QCNE). **Los Ríos**: Río Palenque Estacion Biológica, Km 56 al norte de Quevado, 150–220 m, [1°22′S, 79°42′W], 29 Jan 1984, *Moran 3609* (F, NY, QCA, US). **Manabi**: Cantón Pedernales, Cerro Pata de Pájaro a 10 km al este de Pedernales, a 5 km del rancho de la familia Arroyo, 800 m, 00°01′N, 079°57′W, 10 Mar 1997, *Vargas 1295* (MO, QCNE). **Pichincha**: Hotel Tinalandia, casi 25 km al este desde Sto. Domingo de los Colorados, Cordillera Occidental, 1000 m, [0°17′23″S, 79°04′06″W], 8 Jan 1984, *Moran 3543* (MO, NY, QCA).

Megalastrum reductum is distinctive by the combination of leaf dissection and indument. The leaves are medium-sized, up to only 1.2 m long, with the basal pinnae equilateral or nearly so, not prolonged on the basiscopic side as in many other species of *Megalastrum*. The first two proximal pinnules are often slightly reduced (thus the specific epithet), and apices of the pinnules are typically obtuse or broadly acute. The pinnules are mostly adnate and appear short and stubby. The abaxial surfaces of the pinna rachises are evenly puberulent with hairs 0.1–0.2 mm long, 1- or 2-celled, and spreading to retrorsely strigose. The scales on the pinna rachises abaxially are scattered, dark, filiform to linear, and slightly tortuous. Shorter hairs (ca. 0.1 mm long) occur abaxially on the costules and sometimes along the veins, and in some specimens short erect acicular hairs (these easily overlooked) occur on the lamina tissue between the veins. The rhizome scales appear setulose on both surfaces, this apparently from the upturned and projecting ends of the cells.

Some specimens have pinna rachises adaxially glabrous, and these have been named *Megalastrum dorsiglabrum* A. Rojas (Rojas 2008). We place *M.*

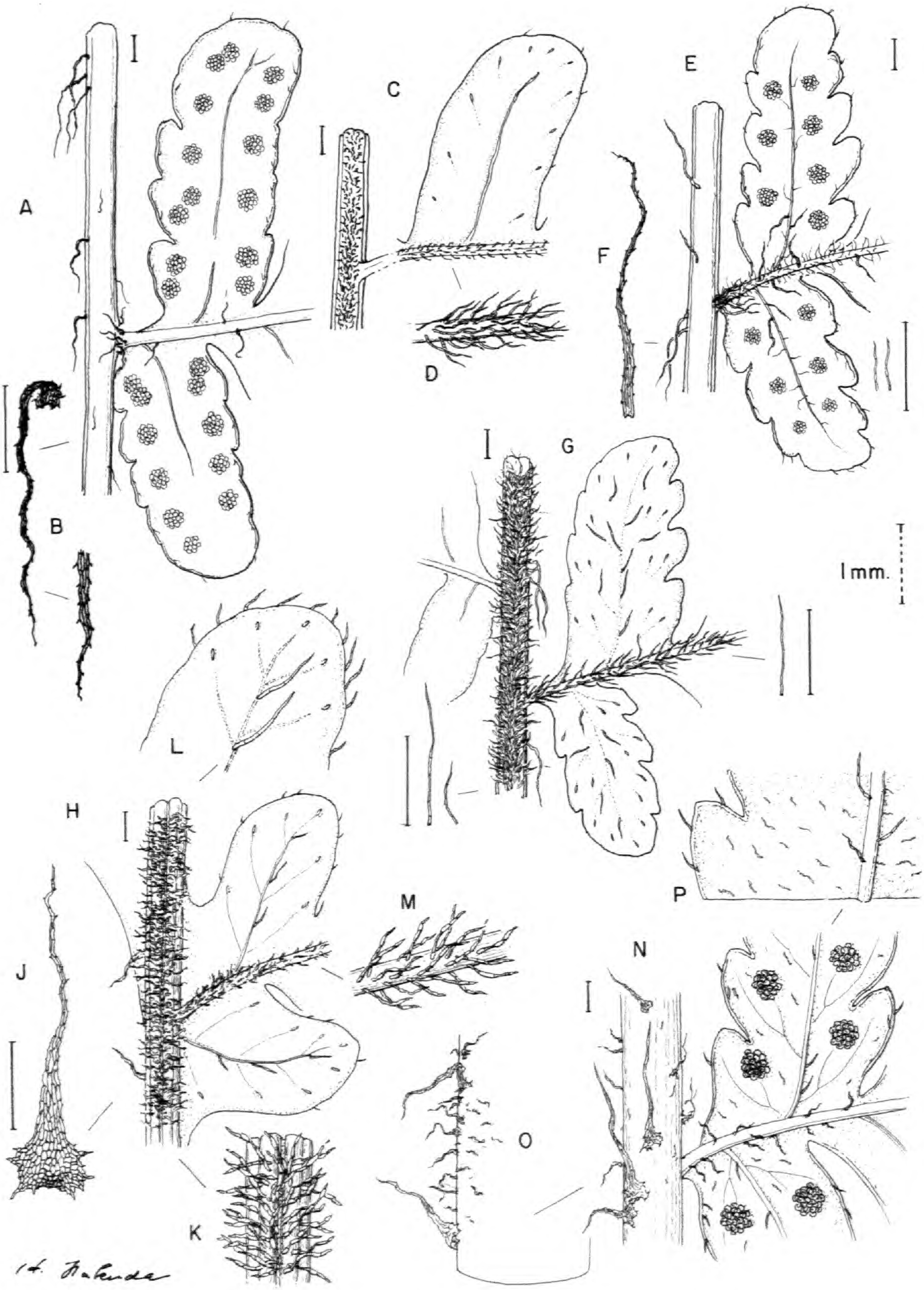

FIG. 30. Indument detail of three Andean species of *Megalastrum*. A–D. *M. martinicense*. A. Abaxial surface of rachis and pinna. B. Rachis scales. C. Adaxial surface of lamina rachis and pinna. D. Detail of pinna rachis. E–G. *M. tepuiense*. E. Abaxial surface of lamina rachis and pinnules. F. Rachis scale. G. Adaxial surface of lamina rachis and pinnules. H–P. *M. subincisum* H. Adaxial surface of pinna rachis and pinnule. J. Scale from pinna rachis. K. Detail of pinna rachis. L.

dorsiglabrum in synonymy because no other character appears to correlate with the lack of hairs adaxially on the pinna rachises.

Megalastrum vastum is similar by its short even pubescence on the laminae abaxially; however, it differs by larger, more divided laminae (up to 3-pinnate-pinnatisect), linear lanceolate (vs. filiform) scales on the pinna rachises abaxially, and laminar tissue between the veins pubescent adaxially especially toward the margins.

Megalastrum biseriale is similar but differs by inequilateral basal pinnae (at least in large leaves), scalier leaf axes abaxially, and pinna rachises abaxially with longer hairs (0.4–0.6 mm long, 3- or 4-celled) and wider, more lanceolate scales.

See *Megalastrum pubirhachis* for comparison with that species.

40. *Megalastrum rhachisquamatum* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Napo: Cantón El Chaco, Proyecto Hidroeléctrico Coca, Punto ST3, margen derecha del Río Quijos, ca. 10 km S de Reventador, 00°39′S, 77°39′W, 1500 m, 3–5 Oct 1990, *W. Palacios 5844* (holotype: QCNE!; isotypes: MO! [barcode 4062147, 4062148], NY! [barcode 0871596], QCA?-n.v., UC! [barcode 1593127]). **Figs. 7H–L, 22D, 36C.**

Rhizomes erect; **leaves** 1.0–1.2 m long; **petiole base scales** ca. 15.0 × 2.0 mm, brown, flat, ascending to spreading, sparsely denticulate, sometimes with denticulae on the surface; **laminae** 0.7–0.8 m long, 3-pinnate-pinnatisect at base, 2-pinnate-pinnatisect medially; **lamina rachises** pubescent abaxially, densely and conspicuously scaly; **basal pinnae** up to 27.0 cm long, inequilateral, longer basiscopically; **pinna rachises** on both surfaces very sparsely glandular, densely pubescent, densely and conspicuously scaly, the hairs 0.4–0.5 mm long, 4–6-celled, lax, spreading, the scales 5.0–7.0 × 1.0–2.0 mm, brown, lanceolate with conspicuously narrowed base (the point of attachment thickened), spreading, flat, lustrous, denticulate, adaxially eglandular, densely pubescent, scaly, the hairs 1.0–1.5 mm long, 5–8-celled, spreading, lax, scales like those on the abaxial surfaces; **costules** abaxially glandular, pubescent, scaly, the glands stalked, orangish, the hairs and scales like those of the pinna rachises abaxially, adaxially eglandular, pubescent, sparsely scaly, the hairs 1.0–1.5 mm long, 5–8-celled, spreading, lax, the scales like those abaxially; **laminar tissue between veins** abaxially glandular, pubescent, the glands 0.1–0.2 mm long, 2-celled, stipitate, yellowish, erect, the hairs ca. 0.1 mm long, 1- or 2-celled, erect, acicular, adaxially sparsely glandular, pubescent, the glands like those abaxially, the hairs 0.3–0.4 mm long, 2- or 3-celled, lax, spreading to appressed; **ultimate veins** not visible on

---

←

Segment apex. M. Hairs along costule. N. Abaxial surface of pinna rachis and pinnule. O. Detail of hairs and scales on pinna rachis. P. Detail of adaxial surface. Scale bars = 1 mm. A–D: Isolectotype, *Moritz 202* p.p. (F). E–G: Isotype, *Steyermark 85913* (US). H–P: from Jamaica, *Clute 132* (US).

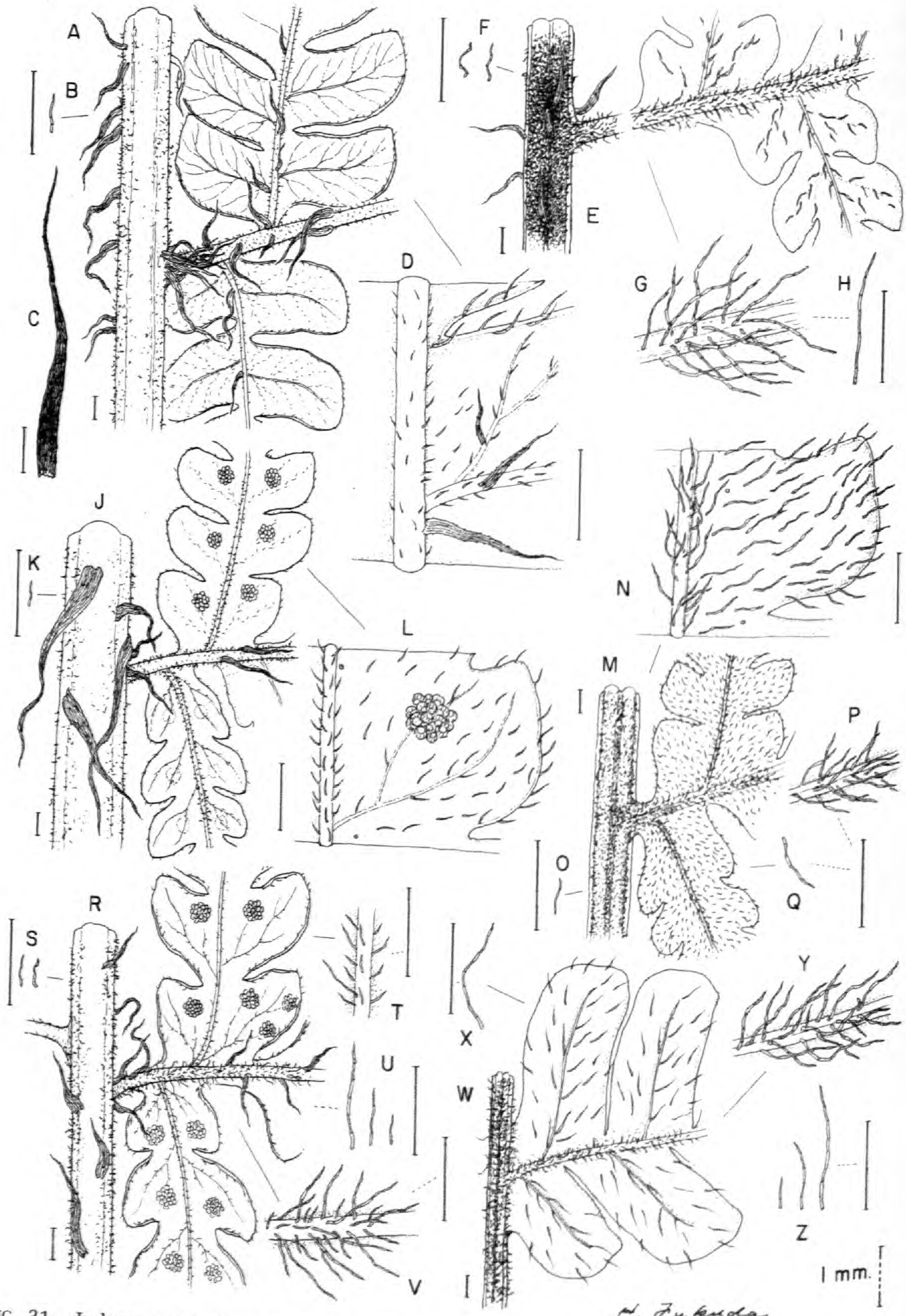

FIG. 31. Indument detail of three Andean species of *Megalastrum*. A–H. *M. peruvianum*. A. Abaxial surface of rachis and pinna. B. Rachis hairs. C. Rachis scale. D. Abaxial surface of costules and veins. E. Adaxial surface of rachis and pinnule. F. Rachis hair. G. Adaxial surface of pinna rachis. H. Hair. J–Q. *M. mollicoma*. J. Abaxial surface of rachis and pinna. K. Rachis hair. L. Abaxial surface of costule, veins, and lamina tissue. M. Adaxial surface of rachis and pinna. O. Rachis hair.

both surfaces, abaxially sparsely glandular, pubescent, the glands like those from the laminar tissue, the hairs 0.2–0.1 mm long, 2- or 3-celled, lax, spreading, adaxially like the abaxial side but hairs 0.7–1.2 mm long, 3–7-celled, spreading to appressed; **lamina margins** eglandular, densely ciliate, the hairs 0.3–0.5 mm long, 3–5-celled, ascending to spreading; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, Peru; 1350–2300 m.

SELECTED SPECIMENS EXAMINED.—ECUADOR. **Zamora-Chinchipe**: Cordillera del Condor, Chinapintza, trail leading to Destacamento Mayaycu Alto, 1350–1480 m, 4°03′S, 78°35′W, 6 Dec 1990, *Øllgaard 98413* (AAU); vic. of the mining camp at the Río Tundaime, along road to military base El Condor, 1500 m, 3°38′02″S, 78°25′32″W, 6 Nov 2004, *van der Werff 19383* (QCNE, UC).

PERU. **Cusco**: La Convención, above Qillouno, 2300 m, 12°28′35″S, 72°29′15″W, 29 Apr 2006, *van der Werff 21116* (MO, NY).

Megalastrum rhachisquamatum has petioles and rachises densely and conspicuously scaly (thus the specific epithet), the scales 1–2 mm wide and spreading. Also helpful in identification are the laminae 3-pinnate-pinnatisect at base and tissue between the veins pubescent on both surfaces. The pubescence adaxially is distinctive by the hairs between the veins being shorter (0.3–0.4 mm long) than those along the veins and midribs of the ultimate segments (0.7–1.2 mm long). This species resembles *M. mollicoma*, a species that differs by shorter, slightly tortuous, and appressed-ascending hairs adaxially on and between the veins.

41. Megalastrum rupicola M. Kessler & A. R. Sm., Amer. Fern J. 96:41, fig. 2D–F. 2006. TYPE.—BOLIVIA. La Paz: Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 16°12′S, 67°53′W, 21 Jul 2000, *D. Quintana 41* (holotype: UC! [barcode 1749582]; isotypes: GOET!, LPB-n.v.). **Figs. 12A–C, 13E, 36B.**

Rhizomes erect, scales 5.0–10.0 × 0.5–0.8 mm, ascending to appressed, linear-lanceolate, golden brown, lustrous, twisted, denticulate; **leaves** 0.6–1.2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.4–0.5 m long, basally 2-pinnate-pinnatisect or rarely 3-pinnate-pinnatisect, medially 1-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 15.0–30.0 cm long, inequilateral, elongated basiscopically; **pinna rachises** abaxially eglandular, without hairs or (more rarely) pubescent basally, scaly, the hairs (when present) 0.2–0.3 mm

---

←

P. Hairs on costule. Q. Hair from costule. R–Z. *M. miscellum*. R. Abaxial surface of rachis and pinna. S. Rachis hairs. T. Hairs on costule. U. Hairs from pinna rachis. V. Hairs on pinna rachis. W. Adaxial surface of pinna rachis, costules, and segments. X. Hair from adaxial surface of vein. Y. Hairs along costule. Z. Hairs from costule. Scale bars = 1 mm. A–H: *Kessler et al. 7033* (UC). J–Q: *Rodríguez et al. 4805* (NY). R–Z: *Arbeláez et al. 276* (NY).

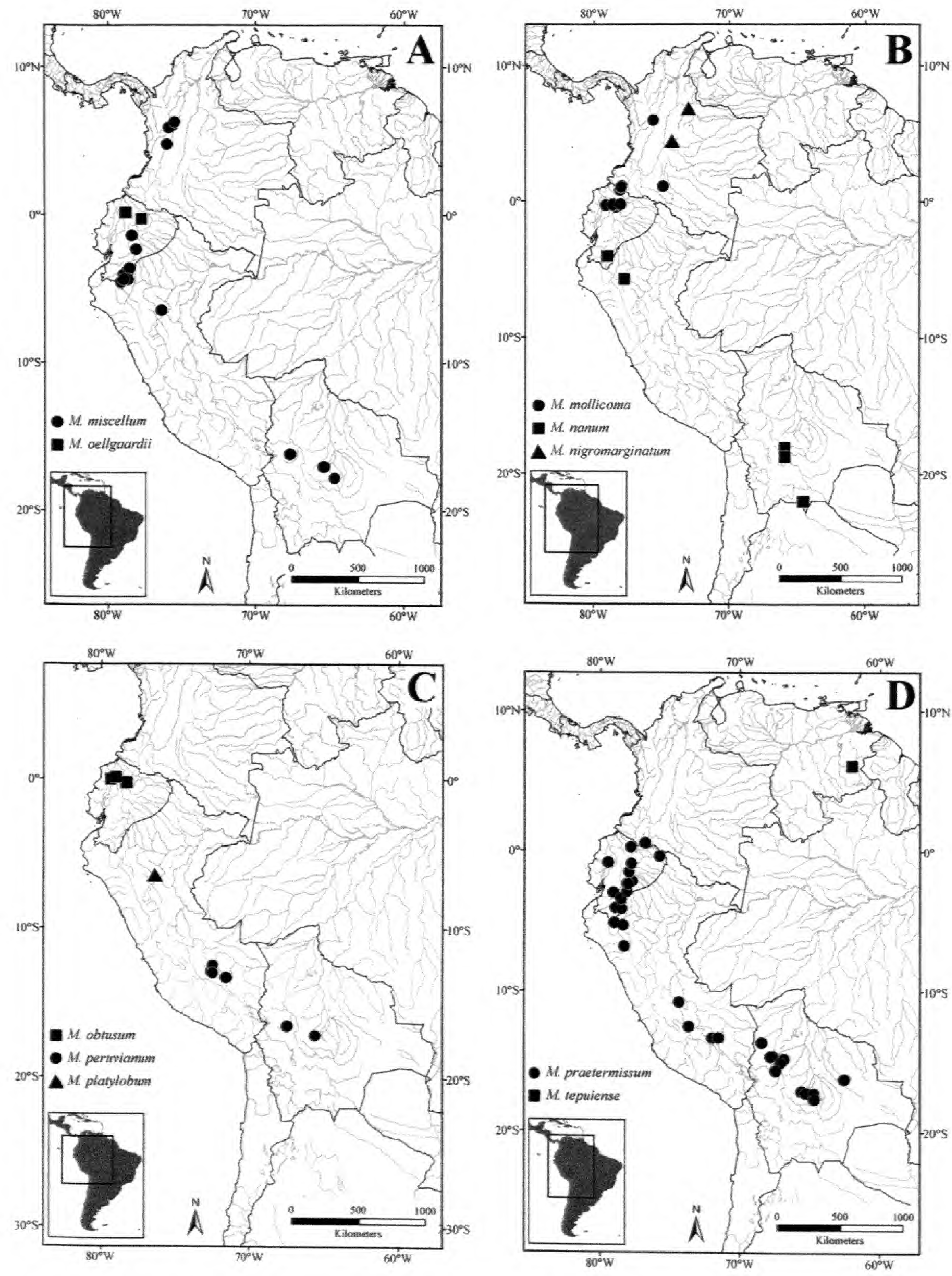

FIG. 32. Distribution of ten species of *Megalastrum* in the Andes. Some species are also known from areas outside the Andean region as here defined; for the worldwide distribution of a species, see under each species description.

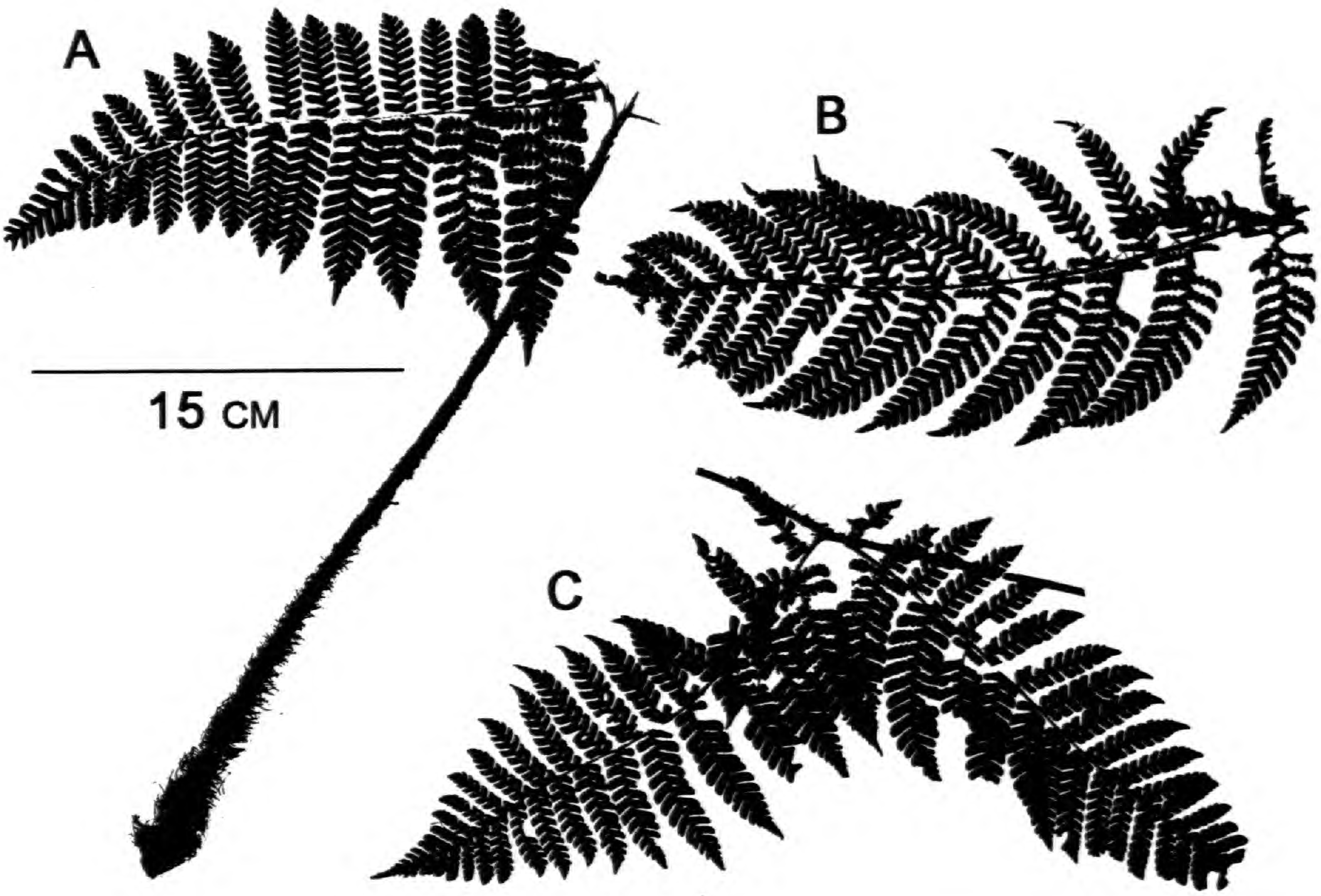

FIG. 33. Lamina cutting of three species of Andean *Megalastrum*. A. *M. vastum*. B. *M. mollicoma*. C. *M. peruvianum*. A: *Cuatrecasas 13021* (GH). B: Isolectotype, *Sodiro s.n.* (B). C: *Kessler et al. 7033* (UC).

long, 1- or 2-celled, erect, acicular, the scales 2.0–4.0 × ca. 0.5 mm, like those of the petioles, adaxially eglandular, pubescent, the hairs 0.8–1.2 mm long, 5–7-celled; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, sparsely scaly, the hairs like those of the pinna rachises, the scales 1.0–2.5 × ca. 0.3 mm, like those of the pinna rachises, adaxially like the pinna rachises abaxially but scales absent; **laminar tissue between veins** on both surfaces eglandular, glabrous or pubescent with minute hairs ca. 0.1 mm long; **ultimate veins** visible on both surfaces, abaxially eglandular, glabrous to sparsely pubescent, the hairs 0.3–0.4 mm long, 2- or 3-celled, like those on the pinna rachises abaxially, adaxially eglandular, glabrous or pubescent, the hairs (when present) 0.8–1.2 mm long, 3–6-celled; **lamina margins** eglandular, sparsely ciliate, the hairs 0.1–0.3 mm long, 2- or 3-celled, acicular, substrigose, ascending; **indusia** absent; **spores** cristate.

Distribution.—Bolivia; 100–1900 m.

SELECTED SPECIMENS EXAMINED.—BOLIVIA. **Carrasco**: Cochabamba, Parque Nacional Carrasco, Arepucho, 1050 m, 17°22′09″S, 65°14′01″W, 23 Oct 2000, *Zarate & Muriel 779* (NY). **Cochabamba**: Prov. Chapare, Territorio Indígena Parque Nacional Islboro-Secure, Cordiller de Mosetenez, Laguna Carachupa, 1300 m, 16°14′S, 66°25′W, 29 Aug 2003, *Kessler et al. 12950* (GOET, UC). **La Paz**: Parque Nacional Madidi, Fuertecillo, entre Tokoake y Carjata, 1739 m,

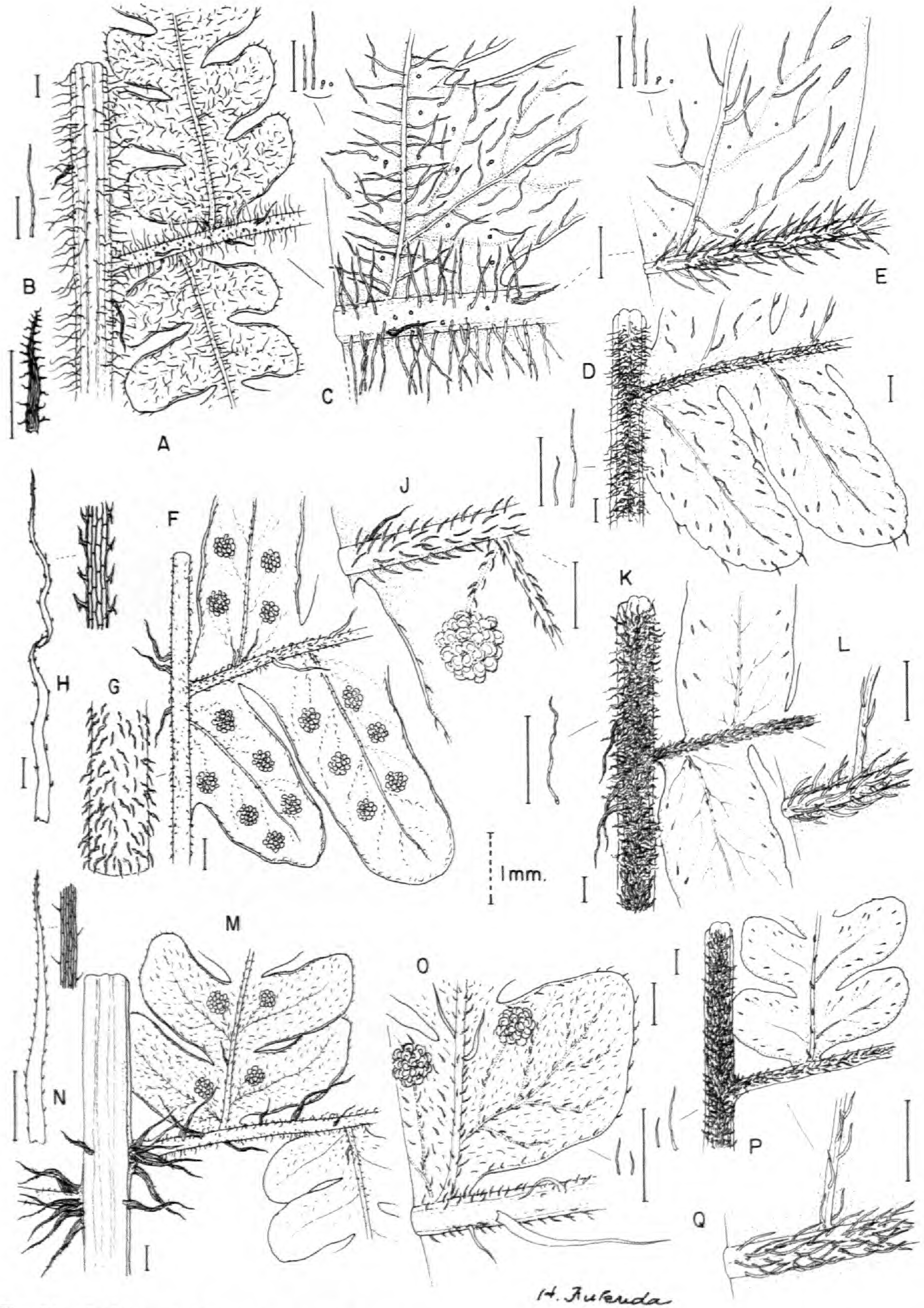

FIG. 34. Indument of three species of Andean *Megalastrum*. A–E. *M. nanum*. A. Abaxial surface of pinna rachis and pinnules. B. Rachis scale. C. Abaxial surface showing hairs and glands. D. Adaxial surface of pinna rachis and pinnule. E. Adaxial surface of segment. F–L. *M. pubirhachis*. F. Abaxial surface of pinna rachis and pinnules. G. Pinna rachis. H. Rachis scale and detail of bifid teeth. J. Hairs on costule and vein. K. Adaxial surface of pinna rachis and pinnules. L. Hair from

14°35′52″S, 68°55′46″W, 29 Jun 2005, *Fuentes et al. 9034* (MO, NY); Prov. J. Bautista Saavedra M., Pauji-Yuyo, entre Apolo y Charazani, 1450 m, 15°02′S, 68°29′W, 8 Jun 1997, *Kessler 9900* (UC).

Megalastrum rupicola is characterized by pinna rachises abaxially without hairs, pinna rachis scales lanceolate, brown to golden brown, shiny, and veins adaxially glabrous or subglabrous. The species most resembles *M. marginatum*, which differs by laminae pubescent with long, straightish, white hairs.

42. **Megalastrum squamosissimum** (Sodiro) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:129. 1987 [published 3 May 1988]. *Nephrodium squamosissimum* Sodiro, Crypt. Vasc. Quit. 256. 1893. *Dryopteris squamosissima* (Sodiro) C. Chr., Index Filic. 294. 1905. *Ctenitis squamosissima* (Sodiro) Copel., Gen. Fil. 125. 1947. TYPE.—ECUADOR. Chimborazo: Mt. Tungurahua, [1°28′S, 78°26′W], Dec. 1857, *R. Spruce 5262* (neotype, here designated: BM! [barcode 000907806]; isoneotypes: BM! [barcode 000777142, (fragm.) 000890191], GH!, K! [barcode 000200216], NY! [barcode 00871582], P! [barcode 00600375, 00610642]). **Figs. 12 D–F, 18A, 36C.**

Dryopteris subincisa (Willd.) Urb. var. *bogotensis* Hieron., Hedwigia 46:349. 1907. *Dryopteris squamosissima* (Sodiro) C. Chr. var. *bogotensis* (Hieron.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math Afd., ser. 8, 6:75. 1920. *Megalastrum squamosissimum* (Sodiro) A. R. Sm. & R. C. Moran var. *bogotense* (Hieron.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77:129. 1987 [published 3 May 1988]. TYPE.—COLOMBIA. Cundinamarca: near the city of Bogotá, [4°35′S, 74°04′W], s.d., *M. A. Stübel 418* (lectotype, here designated: BM!, fragm. [barcode 000907805]).

Rhizomes erect, sometimes forming a trunk up to 0.5 m tall, scales 15.0–20.0 × 0.5–2.0 mm, brown, ascending to appressed, lanceolate, lustrous, flat, not tortuous, denticulate, the teeth not bifid; **leaves** 1.5–3.0 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 1.2–2.1 m long, basally 3-pinnate-pinnatifisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 30.0–50.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, without hairs (often with highly reduced scales that resemble hairs, or hair-like cilia from large scales), scaly, the scales 5.0–12.0 × 0.5–2.0 mm, spreading to ascending or appressed, lanceolate to linear-lanceolate, golden to pale light brown, lustrous, often ciliate basally but otherwise entire or subentire for most of the length, adaxially eglandular, densely pubescent, sparsely scaly, the hairs 0.8–1.0 mm

←

costule. M–Q. *M. nigromarginatum*. M. Abaxial surface of pinna rachis, costule, and pinnules. N. Rachis scale. O. Abaxial surface of costule and segment. P. Adaxial surface of pinna rachis, costule, and segments. Q. Adaxial surface of costule. Scale bars = 1 mm. A–E: Isotype, *Moran 5917* (AAU). F–L: *Moran 3594* (MO). M–Q: Holotype, *Tryon & Tryon 6103* (GH).

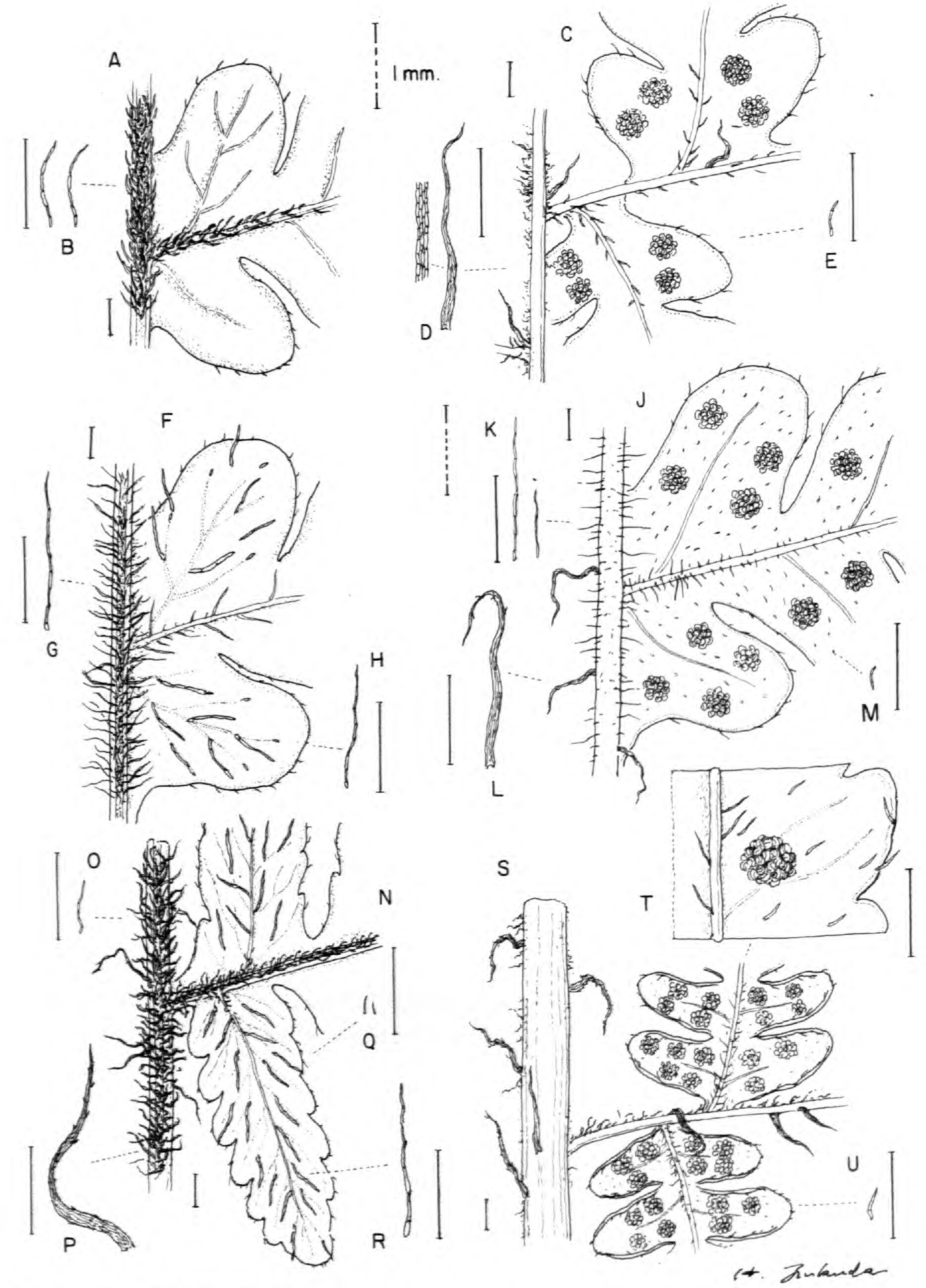

FIG. 35. Indument detail of three Andean species of *Megalastrum*. A–E. *M. obtusum*. A. Adaxial surface of pinna rachis, costule, and segments. B. Hair detail. C. Abaxial surface of lamina rachis, pinna rachis, and pinnules. D. Scale detail. E. Hair detail. F–M. *M. praetermissum*. F. Adaxial surface of pinna rachis, costule, and veins. G, H. Hair details. J. Abaxial surface of pinna rachis and pinnule base. K. Hair detail. L. Scale detail. M. Hair detail. O–U. *M. subtile*. N. Adaxial surface of

long, 4–6-celled, antrorsely strigose, scales like those on the abaxial surfaces; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, glabrous or pubescent, sparsely scaly, hairs (when present) ca. 0.2 mm long, 2-celled, acicular, scales 0.6–3.5 × 0.3–0.5, appressed, ascending, lanceolate, entire, adaxially eglandular, sparsely to moderately pubescent, scales generally absent, the hairs 0.4–1.0 mm long, 4–6-celled, antrorsely strigose; **laminar tissue between veins** on both surfaces eglandular, glabrous, or rarely with scattered erect acicular hairs ca. 0.1 mm long; **ultimate veins** on both surfaces visible or sometimes obscure adaxially, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1- or 2-celled, ascending to spreading; **indusia** absent; **spores** cristate.

Distribution.—Venezuela, Colombia, Ecuador; 1400–2800 m.

SELECTED SPECIMENS EXAMINED.—VENEZUELA. **Yaracuy**: Distr. Bolívar, entire Las Parchitas, Tierra Fria y Ojo de Agua, 1500–1600 m, 10°20′N, 68°57′W, 18 Feb 1985, *Ortega & Smith 2476* (UC).

COLOMBIA. **Antioquia**: Cocorná, [6°03′N, 75°11′W], Dec 1937, *Daniel 1898* (GH). **Boyaca**: Sierra Nevada del Cocuy, Near trail between Bocota and Bachira, in primary forest, in soil of forest floor, 2250 m, [6°26′N, 72°17′W], 25 Sep 1957, *Grubb & Guymer 94* (BM). **Cundinamarca**: Manyanos, 2700 m, [4°41′N, 74°09′W], s.d., *Lindig 331* (NY, P, US); road from Bogotá to Sylvania, 20 km S of Bogotá, [4°35′N, 74°04′W], 22 Jul 1972, *Barrington 461* (GH, MO, US). **Magdalena**: Mpio. de Ciénaga, Sierra Nevada de Santa Marta, subiendo por San Pedro de la Sierra, entrada a San Javier, [10°52′N, 73°43′W], 10 May 1983, *Santa & Escobar 642* (HUA). **Santander**: Mpio. Tona, Corregimiento Corcova, Vereda Las Mariana, along highway between Pamplona and Bucaramanga, 2220 m, 7°07′N, 73°06′W, 5 May 1983, *Croat 56541* (MO, UC).

ECUADOR. **Tungurahua**: vic. of Ambato, [1°14′S, 78°37′W], 24–26 Aug 1918, *Rose 22379* (NY, US).

Among the large decompound species of *Megalastrum, M. squamosissimum* is characterized by pinna rachises abaxially without hairs but with abundant large (5–12 mm long) lanceolate scales. The scales are conspicuous to the naked eye, especially along the rachises of the laminae and pinnae. Sometimes smaller scales resembling scurf-like hairs are present along the rachises. The long cilia from the bases of large scales accentuate this scurf-like appearance. Two specimens (*Daniel 1898, Ortega & Smith 2476*) are atypical by having acicular, erect, 0.1 mm long hairs between the veins abaxially.

Similar is *Megalastrum alticola*, which differs by pinna rachises abaxially pubescent and smaller scales along the pinna rachises abaxially.

←

pinna rachis, costule, and veins. O. Hair detail. P. Scale detail. Q, R. Hair details. S. Abaxial surface of pinna rachis, costule, and veins. T. Detail of abaxial surface of pinnule. U. Hair detail. Scale bars = 1 mm. A–E: *Sparre 17168* (MO). F–M: Isotype, *Fay & Fay 4250* (UC). O–U: Isotype, *Moran et al. 7608* (NY).

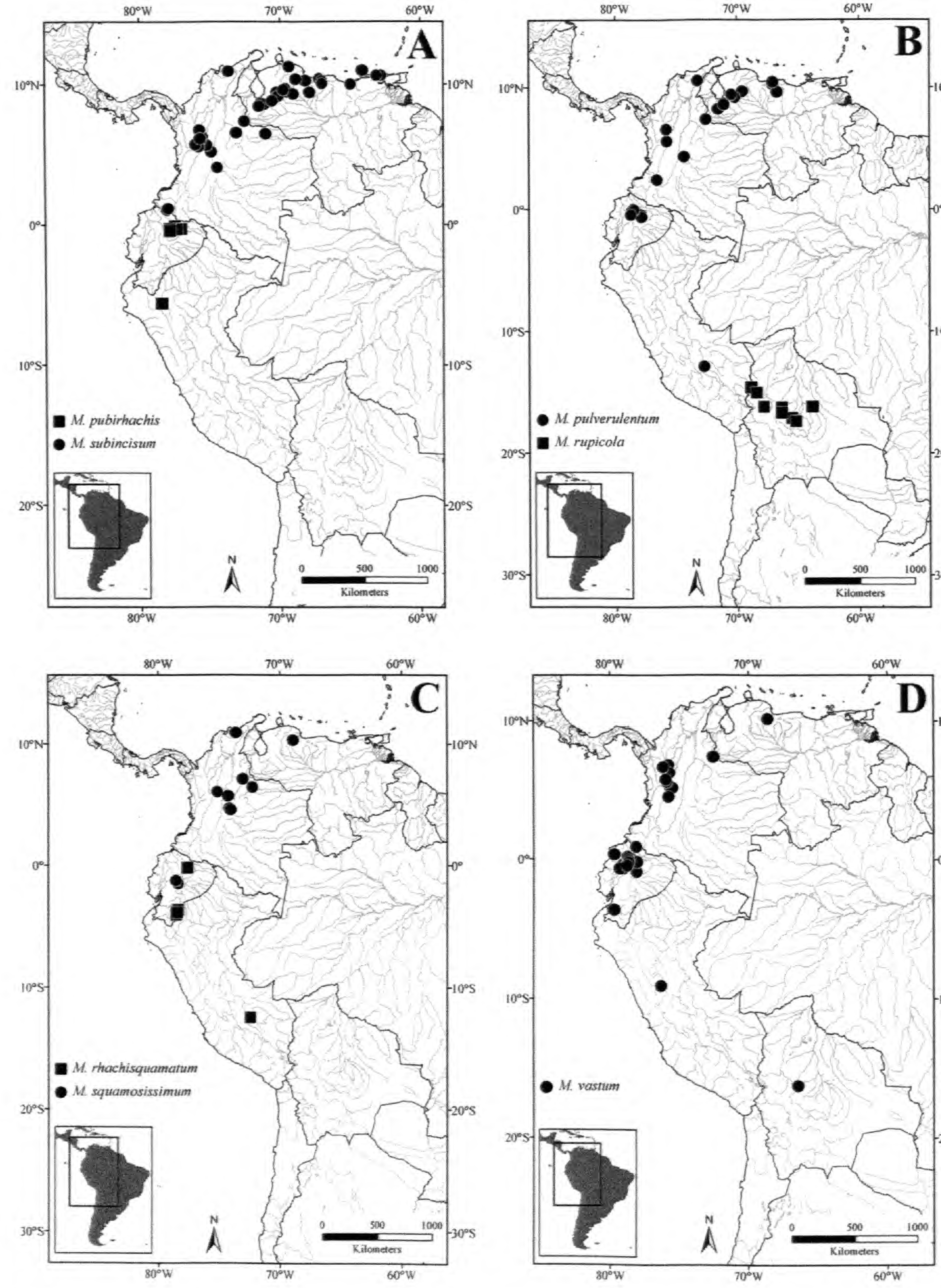

FIG. 36. Distribution of seven species of *Megalastrum* in the Andes. Some species are also known from areas outside the Andean region as here defined; for the worldwide distribution of a species, see under each species description.

Sodiro's original material (Ecuador, Prov. Chimborazo, at the foot of Mt. "El Altar," s.d., *L. Sodiro s.n.*) was not found among the specimens examined by us or by Christensen (1920), and no specimens exist in Sodiro's herbarium at QPLS (María Burbano, pers. comm., 29 Sep 2011). We neotypified the name using the specimen that Christensen cited for his concept of the species, thus preserving the established use of the name.

43. Megalastrum subincisum (Willd.) A. R. Sm. & R. C. Moran, Amer. Fern J. 77: 129. 1987 [published 3 May 1988]. *Polypodium subincisum* Willd., Sp. Pl., ed. 4, 5:202. 1810. *Phegopteris subincisa* (Willd.) Fée, Mém. Foug. [Gen. Fil.] 5:243. 1852. *Nephrodium villosum* (L.) Kuntze var. *subincisum* (Willd.) Hook. ex Sodiro, Rescensio Crypt. Vasc. Quit. 54. 1883. *Nephrodium villosum* (L.) Kuntze var. *subincisum* (Willd.) Jenman, *comb. superfl.*, Bull. Bot. Dept. Jamaica n.s. 3:114. 1896. *Dryopteris subincisa* (Willd.) Urb., Symb. Antill. 4: 19. 1903. *Aspidium subincisum* (Willd.) Christ, Bull. Herb. Boiss. sér. 2, 6(1): 56. 1906. *Ctenitis subincisa* (Willd.) Ching, Sunyatsenia 5:250. 1940. TYPE.—VENEZUELA. Distrito Federal: Caracas, [10°30′N, 66°55′W], s.d., *F. Bredemeyer s.n.* (holotype: B-W!-19701). **Figs. 18C, 30H–P, 36A.**

Rhizomes erect, scales 20.0–25.0 × 1–2 mm, ascending to appressed, linear-lanceolate, golden brown, shiny or dull, flat to twisted, denticulate; **leaves** up to 2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** up to 1.5 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 40.0–60.0 cm long, inequilateral, elongated basiscopically; **pinna rachises** abaxially eglandular, without hairs, scaly, the scales 4.0–6.0 × 0.2–0.3 mm long, golden brown, appressed to loosely ascending, linear-lanceolate, non-bullate, not tortuous, rachises adaxially eglandular, densely pubescent, the hairs 0.5–0.8 mm long, 4- or 5-celled, the scales like those on the abaxial surface; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent (especially distally), scaly, the hairs 0.2–0.3(–0.5) mm long, 2–4-celled, erect to spreading or substrigose, acicular, the scales like those on the pinna rachises abaxially but smaller, 3.0–5.0 × 0.3–0.7 mm, lanceolate, enlarged basally, the adaxial surface pubescent, the hairs 0.5–1.0 mm long, 4- or 5-celled, substrigose; **laminar tissue between veins** glabrous on both surfaces, or near the costules and sinuses very sparsely puberulent abaxially, the hairs ca. 0.1 mm long, erect, acicular; **ultimate veins** visible on both surfaces, abaxially eglandular, sparsely pubescent, non-scaly, the hairs ca. 0.5–0.8 mm long, 2- or 3-celled, spreading, adaxially eglandular, glabrous; **laminar margins** eglandular, ciliate, the hairs 0.1–0.3 mm long, 1- or 2-celled, spreading to substrigose; **indusia** absent; **spores** cristate.

Distribution.—Mexico, Honduras, Cuba, Jamaica, Haiti, Dominican Republic, Guadeloupe, Dominica, northern Venezuela, and Colombia; 450–2300 (–3200) m.

Selected Specimens Examined.—VENEZUELA. **Aragua**: Colonia Tovar, [10°22′N, 67°16′W], 1846, *Funck & Schlim 412* (BM, NY, P). **Barinas**: Distr. Bolívar, San Isidro, ca. 5 mi NW of La Soledad along Barinas-Sto. Domingo (Edo. Mérida) road, 1000 m, 8°50′N, 70°35′W, 19 Nov 1982, *Smith et al. 1398* (MO). **Carabobo**: Limite Distr. Bejuma Distr. Montalban, Cordillera de la Costa, vertiente norte, al este de la carretera Bejuma-Canoabo, al este de Las Rosas, faldas superiores y fila de la montaña, bosque secundario y cafetales, 950–1100 m, 10°16′N, 68°15′W, 26 Dec 2001, *Meier 8768* (NY). **Distrito Federal**: Upper Catuche wood (above 1400 meters), near Caracas, above 1400 m, [10°30′N, 66°55′W], 8 Jun 1921, *Pittier 9595* (GH, NY). **Miranda**: Distr. Guaicaipuro, Cordillera de la Costa, Serranía del Interior, vertiente norte, 6 km distancia aérea al S del pueblo Altagracia de la Montaña, cuenca de la Quebrada Agua Fría, 800 m, 10°04′30″N, 67°03′W, 3 Mar 2002, *Meier & Nehlin 8939* (NY). **Falcón**: Sierra San Luis, cerca del Hotel Parador, 1500 m, [11°12′N, 69°43′W], 25 Aug 1978, *Wingfield & van der Werff 6562* (U, UC). **Lara**: Morán, carretera Villanueva y Ojo de Agua, SE de Guarico, 1500 m, [9°37′N, 69°47′W], 6 Mar 1983, *Ortega et al. 1635* (NY). **Mérida**: Dpto. Sucre, Estanquez-Páramo, Las Coloradas, 1600–1200 m, [8°27′N, 71°30′W], 16 Sep 1984, *Ortega & Berti 2120* (NY). **Nueva Esparta**: Isla de Magarita, Juan Griego trail, 450 m, [11°00′N, 64°10′W], 29 Jul 1903, *Johnston 187* (NY, S). **Portuguesa**: Guanare, 2300 m, 8°39′N, 71°21′W, 24 Nov 1985, *Ortega & van der Werff 2938* (MO, NY, UC). **Sucre**: Distr. Arismendi, Península de Paria, SE de Carúpano, NE de Maturincito, Cerro La Cerbatana a lo largo del camino de La Sierra al caserío Guárico y subiendo la fila, 650–850 m, 10°38′N, 63°10′W, 9 Jan 2005, *Meier et al. 11193* (NY). **Trujillo**: entre las antenas de relevo en el Páramo de Guaramacal y la Vega de Guaramacal, 9°13′N, 70°10′W, 23–24 Jul 1984, *Ortega et al. 2025* (MO). **Vargas**: Monumento Natural Pico Codazzi, Carretera Colonia Tovar-La Victoria, Sector Matapalo, 1950 m, 10°26′N, 67°17′W, 23 Jun 1999, *Mostacero & Howorth 209* (VEN). **Yaracuy**: Distr. Bolívar, Cordillera de la Costa, Serranía de Aroa, S del pueblo Aroa, 1300–1400 m, 10°23′N, 68°54′W, 25 Aug 2002, *Meier & Flauger 9107* (VEN).

COLOMBIA. **Antioquia**: Mpio. Angelópolis, vereda Romeral, Hacienda La Argentina, quebrada Las Animas, 2050–2130 m, 6°08′22.9″N, 75°41′58″W, 20 Nov 2005, *Rodríguez 5629* (HUA, NY); Mpio. Betania, alrededores de parcela permanente (UN), 1900–2100 m, 5°44′10″N, 76°00′11″W, 5 Nov 2004, *Rodríguez et al. 4589* (HUA, NY). **Arauca**: Sarare, Santa Librada, 1300–1600 m, [6°29′N, 71°02′W], 24–25 Mar 1959, *Bischler 1951* (BM, MICH). **Choco-Antioquia**, 2100–2200 m, 4 Apr 1971, *Lellinger & de la Sota 917* (US). **Cundinamarca**: Mpio. de Venecia, Vereda Las Mercedes, alrededores de la Quebrada La Chorrera, 2200–2300 m, [4°22′N, 78°28′W], 24 Jul 1981, *Díaz 3130* (MO). **Magdalena**: Santa Marta, 1219 m, [10°55′N, 73°38′W], Mar 1898–1901, *Smith 1047* (B, BM, F, GH, K, MICH, MO, NY, P, S, U, US, VT). **Nariño**: Ricaurte, sendero hacia Hondón, 1800 m, [1°07′N, 70°14′W], 25 Jun 1995, *Sánchez-Baracaldo 64* (MO, UC). **Norte de Santander**: road from Pamplona to Toledo, crossing the divide between Río La Teja and Río Mesme, 2800–3000 m, [7°22′N, 72°39′W], 27–28 Feb 1927, *Killip & Smith 19998* (NY). **Santander**: vic.

of Las Vegas, 2600–3000 m, [6°33′N, 73°08′W], 21–23 Dec 1926, *Killip & Smith 16136* (NY). **Tolima**: Mariquita, Combaima, 1200 m, [5°12′N, 74°54′W], Jan 1843, *Linden 1020 p.p.* (B, P).

Megalastrum subincisum is characterized by pinna rachises abaxially without hairs but with linear-lanceolate, golden brown scales. The veins adaxially are glabrous to subglabrous (only one or two hairs present), and sparse hairs are often present on the costules abaxially, especially distally. In South America this species greatly resembles *M. aureisquamum* from Peru and Bolivia. They can be distinguished morphologically only by the characters of the rhizome scales as given in the key.

Christensen (1920) construed *Megalastrum subincisum* in the wide sense, occurring from Mexico to Bolivia. He admitted much variation in the type of laminar scales and the presence versus absence of hairs and glands. We find, however, that indument characteristics can be used to divide *M. subincisum* into smaller, less variable species. In this restricted sense, *M. subincisum* is more narrowly distributed than conceived by Christensen, occurring only in the Mexico and Honduras, the West Indies, and Colombia and northern Venezuela. Most of the Central American specimens identified by Christensen as *M. subincisum* are referable to *M. galeottii* (M. Martens) R. C. Moran & J. Prado (Moran & Prado, 2010).

44. *Megalastrum subtile* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** TYPE.—ECUADOR. Morona-Santiago: small ravine ca. 7 km N of Limón, 2°54′42″N, 78°24′03″W, 960 m, 3 Mar 2005, *R. C. Moran, D. Trujillo, L. Salazar & D. Aviles 7608* (holotype: QCA!; isotypes: NY! [barcode 1053900], QCNE!). **Figs. 13D, 14A, 35O–U.**

Rhizomes erect, scales 10.0–20.0 × 1–2 mm, ascending, linear, brown, dull, firm, the margins denticulate, the surfaces smooth (not setulose); **leaves** up to 1.0 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 0.5–0.6 m long, basally 2-pinnate-pinnatisect, medially 2-pinnate-pinnatifid; **lamina rachises** without hairs abaxially; **basal pinnae** ca. 20 cm long, equilateral or nearly so; **pinna rachises** abaxially eglandular, without hairs, sparsely scaly, the scales 3.0–4.0 × ca. 0.1 mm, dull brown, appressed to loosely spreading and ascending, filiform to linear, slightly tortuous, entire, adaxially pubescent, sparsely scaly or lacking scales, hairs ca. 0.3 mm long, antrorsely strigose, the scales ca. 1.0 × 0.1 mm, filiform, entire, appressed, dull, brown; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent and scaly, hairs ca. 0.2–0.4 mm long, 2- or 3-celled, ascending to strigose, the scales filiform, dull brown, entire, adaxially pubescent, the hairs like those on the pinnae rachises adaxially; **laminar tissue between veins** abaxially and adaxially eglandular, glabrous; **ultimate veins** abaxially visible, glabrous, adaxially obscure, glabrous; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1- or 2-celled, acicular, ascending to substrigose; **indusia** absent; **spores** cristate.

Distribution.—Ecuador, eastern side of the Andes; 900–1180 m.

Specimens Examined.—ECUADOR. **Morona-Santiago**: trail along Río Inimkis, ca 3 km NE of village of Inimkis (San Luis) toward foothills of Cord. Cucutú, 900–1000 m, 02°23′S, 78°06′W, 14 Nov 1995, *Øllgaard & Navarrete 1426* (AAU). **Napo**: Archidona, Reserva de Biósfera Sumaco, cordilla de Galeras, bosque protector de la comunidad de Mushullacta, 1180 m, 0°45′50″S, 77°33′28″W, 27 Mar 2003, *Huaylla 831* (MO, QCNE, UC).

Among the decompound species of *Megalastrum, M. subtile* is distinctive by relatively small leaves (up to 1 m long) and the pinna rachises abaxially hairless with filiform to linear entire scales. It resembles *M. martinicense* by lack of hairs and filiform scales, but that species differs by large leaves, strongly denticulate scales, and occurrence in northern Venezuela and Colombia. Also similar is *M. reductum*, which differs most conspicuously by pinna rachises abaxially densely and uniformly pubescent by minute hairs. The specific epithet refers to subtile differences between this species and *M. reductum*.

45. *Megalastrum tepuiense* R. C. Moran, J. Prado & Sundue, ***sp. nov.*** Type.—VENEZUELA. Bolívar: Sierra de Lema, Cabeceras del Río Chicanan, 80 km (en línea recta) al SW de El Dorado, at base of high NNE-facing sandstone bluffs, 6°05′N, 62°W[sic], 500 m, 27 Aug 1961, *J. A. Steyermark 89513* (holotype: VEN! [barcode 52682]; isotypes: NY! [barcode 000870956], US! [barcode 00798656, 00798657, 00798658]). **Figs. 13B, 30E–G, 32D.**

Rhizomes not seen; **leaves** up to ca. 1.1 m long; **petiole base scales** 12.0–20.0 × 0.3–0.5 mm, ascending to spreading, filiform, golden brown, lustrous, flat or twisted, denticulate; **laminae** 0.4–0.7 m long, basally 3-pinnate-pinnatisect, medially 2-pinnate-pinnatisect; **lamina rachises** without hairs abaxially; **basal pinnae** 25.0–35.0 cm long, inequilateral; **pinna rachises** abaxially eglandular, glabrous, sparsely scaly, scales up to 3.0 × 0.2 mm, light brown, linear-lanceolate, lustrous, spreading to slightly appressed, flat or twisted, subentire to sparsely denticulate, adaxially eglandular, densely pubescent, scaly, the hairs 0.5–1.0 mm long, 3–6-celled (the contents of the cells brown), spreading, scales like those on the abaxial surfaces but sometimes with bifid teeth; **basal basiscopic pinnules of medial pinnae** not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular, sparsely pubescent, scaly, the hairs 0.5–1.0 mm long, 3–6-celled, spreading, acicular, scales like those of the pinna rachises abaxially but shorter, up to 2 mm long, adaxially eglandular, densely pubescent with hairs like those of the pinna rachises, scales absent; **laminar tissue between veins** on both surfaces eglandular, glabrous; **ultimate veins** on both surfaces visible, abaxially eglandular, sparsely pubescent, the hairs like those of the costules, adaxially pubescent, the hairs 0.5–1.0 mm long, spreading, whitish; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1- or 2-celled, spreading; **indusia** absent, but a tuft of acicular hairs 0.2–0.5 mm long often visible in the center of the sorus; **spores** cristate.

Distribution.—Venezuela, known only from the type; 500 m.

Megalastrum tepuiense is characterized by decompound laminae, petiole bases with linear-lanceolate scales, pinna rachises abaxially without hairs but with long, linear-lanceolate scales, and costules and veins on both surfaces pubescent by whitish hairs 0.5–1.0 mm long, 3–6-celled. This species and *M. adenopteris* are the only species of *Megalastrum* with acicular hairs on fugacious indusia (the indusia often apparently absent in mature sori). Only two other species of *Megalastrum* occur in the tepuis region of southern Venezuela: *M. biseriale* and *M. crenulans.* The first species can be readily distinguished by 1-pinnate-pinnatifid laminae, and the second by large, persistent indusia.

Similar is *Megalastrum praetermissum,* which differs by the laminae abaxially between the veins minutely and finely pubescent, rachis scales strongly denticulate, and sori without acicular hairs.

Megalastrum tepuiense resembles *M. subincisum* by lamina dissection and pinna rachises abaxially glabrous. It differs by costules and midribs of the ultimate segments abaxially pubescent by long (0.5–1.0 mm) straight whitish hairs (vs. glabrous to sparsely and inconspicuously pubescent with hairs only 0.2–0.5 mm long). *Megalastrum tepuiense* occurs only in southern Venezuela and does not overlap geographically with *M. subincisum,* which occurs in northern Venezuela, Colombia, and the Antilles.

46. Megalastrum vastum (Kunze) A. R. Sm. & R. C. Moran, Amer. Fern J. 77: 129. 1987 [published 3 May 1988]. *Polypodium vastum* Kunze, Linnaea 9:50. 1834. *Phegopteris vasta* (Kunze) Mett., Fil. Lechl. 2:27. 1859. *Nephrodium vastum* (Kunze) Hieron., Bot. Jarb. Syst. 34:446. 1904, *nom. illeg.,* non Baker (1867). *Dryopteris vasta* (Kunze) Hieron., Hedwigia 46:347. 1907. TYPE.—PERU. Huánuco: "inter Pampayaco et Cocheros et ad Ventanilla de Cassapi," 1829, *E. Poeppig 217* (lectotype, designated by Tryon and Stolze, 1991: B! [barcode 200069274, 200069276, 200069277]). **Figs. 9L–Q, 33A, 36D.**

Polypodium extensum C. Presl, Rel. Haenk. 1:26. 1825, *nom. illeg.,* non Forster (1786). TYPE.—PERU. s.d., *Haenke s.n.* (holotype: PR-n.v., fotos BM!, NY!).

Rhizomes erect, scales 10.0–20.0 × 0.7–1.0 mm, appressed to spreading, linear-lanceolate, brown, dull or lustrous, twisted, sparsely denticulate; **leaves** 1.0–2.2 m long; **petiole base scales** like those of the rhizomes but spreading to loosely ascending; **laminae** 1.0–1.5 m long, basally 3-pinnate-pinnatifid, medially 2-pinnate-pinnatisect; **lamina rachises** pubescent abaxially; **basal pinnae** 20–25 cm long, inequilateral; **pinna rachises** abaxially eglandular or rarely sparsely glandular, densely and evenly puberulent, sparsely scaly, the glands (when present) sessile, spherical, yellowish, the hairs 0.1–0.2 mm long, 1–3-celled, acicular or lax, erect to strigose, the scales up to 3.5 × 0.5 mm, entire or with a few teeth distally, flaccid, pale brown, adaxially densely pubescent, eglandular, the hairs 0.6–1.0 mm long, 5–7-celled; **basal basiscopic**

pinnules of medial pinnae not enlarged or overlapping the lamina rachis; **costules** abaxially eglandular or nearly so, densely pubescent, sparsely scaly, the hairs like those of the pinna rachises, the scales ca. 1 × 0.2 mm, like those of the pinna rachises, adaxially with indument like that of the pinna rachises but scales absent; **laminar tissue between veins** abaxially eglandular or rarely glandular, densely pubescent, the hairs ca. 0.1 mm long, 1(–2)-celled, erect to curved-ascending or appressed, acicular, glands ca. 0.1 mm long, 2-celled, stalked or sessile, yellowish to orangish; adaxially puberulent, the hairs like those on the abaxial surfaces, often more abundant toward the segment margins; **ultimate veins** visible on both surfaces, pubescent on both surfaces or sometimes glabrous adaxially, eglandular or very sparsely glandular, the hairs and glands like those on the laminar tissue between the veins, or hairs sometimes longer, being 0.5–1.0 mm long, 3–5-celled; **lamina margins** eglandular, ciliate, the hairs 0.2–0.3 mm long, 1–3-celled, acicular, substrigose, ascending; **indusia** consisting of a tuft of minute reddish fugaceous hairs (often apparently absent); **spores** cristate.

Distribution.—Venezuela, Colombia, Ecuador, Peru, Bolivia; 400–2200 m.

SELECTED SPECIMENS EXAMINED.—VENEZUELA. **Yaracuy**: Distr. Nirgua, Cordillera de la Costa, Macizo de Nirgua, SW de Nigua, entre el Picacho de Nirgua y San Antonio-Buenos Aires, 1200–1400 m, 10°08′N, 68°38′W, 5 Mar 2004, *Meier & Nehlin 10084* (UC).

COLOMBIA. **Antioquia**: Mpio. Liborina, Vereda Barrio Nuevo, quebrada La Honda, límites con el municipio de Sabanalarga, 1910 m, 6°46′54.3″N, 75°47′34.2″W, 26 Sep 2002, *Rodríguez et al. 3636* (HUA, NY). **Caldas**: Pueblo Rico [Neira], Cordillera Occidental, Vertiente Occidental, 1700–1900 m, [5°08′N, 75°31′W], 17 Feb 1946, *von Sneidern 5236 p.p.* (F, US). **Norte de Santander**: Cordillera Oriental, region del Sarare, Hoya del Río Cubugon entre El Caraño y El Indio, 600–470 m, [7°01′N, 72°11′W], 12 Nov 1941, *Cuatrecasas 13021* (GH). **Risaralda**: El Cedral, trocha a El Silento, 20 km de Pereira, 2140 m, [5°18′N, 75°42′W], 15 Oct 1989, *Rangel et al. 5762* (MO).

ECUADOR. **Bolívar**: Chazo Juan, 600 m, [0°23′S, 79°05′W], 1943, *Acosta 6517* (F). **Carchi**: near Maldonado, 1400 m, [0°54′N, 78°06′W], 29 Jul 1989, *van der Werff & Gudiño 10711* (AAU, MO, NY). **Chimborazo**: El Limón, Mt. Chimborazo, 1000 m, [0°28′S, 78°49′W], Jul 1860, *Spruce s.n.* (K). **Cotopaxi**: Cantón La Mana, Reserva Ecológica Los Ilinizas, sector del Brasil, acceso desde La Carmela, Cordillera Occidental, 1480 m, 0°40′37″S, 79°05′09″W, 13 Jul 2003, *Silverstone-Sopkin 9088* (MO, QCNE). **El Oro**: Road from Pinas to Sta. Rosa, Km 12.5, 860 m, [3°38″S, 79°44′W], 7 Oct 1979, *Dodson et al. 8958* (US). **Esmeraldas**: Quininde, Bilsa Biologica Station, Mache mountains, 35 km W of Quininde, 5 km W of Santa Isabel, 400–600 m, 0°21′N, 79°44′W, 14 May 1995, *Clark & Watt 862* (MO, QCNE). **Los Ríos**: Bosque protector Cerro Samana, SWW of caluma, NE part of Hda La Clementina, 600–730 m, 0°40′S, 79°20′W, 29 Feb–1 Mar 1996, *Øllgaard 1559* (AAU). **Napo**: Oyachachi, [0°12′S, 78°04′W], Feb 1901, *Sodiro s.n.* (BM, P). **Pichincha**: Cantón Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old road Quito-Santo

Domingo, 1900 m, 0°14′S, 78°48′W, 10 Jul 1991, *Fay & Fay 3352* (AAU, MO, QCA, QCNE); New road Sto. Domingo-Quito 6–8 km E of Tandajapa, 1150 m, [0°10′S, 78°46′W], 23 Jan 1981, *Balslev et al. 1693* (AAU, MO, NY).

PERU. **Huánuco**: Leoncio Prado, km 478 on Lima-Tigo Maria road, Thicket along road , following stream to waterfall, 1400 m, [9°05′S, 76°20′W], 6 Jun 1981, *Young & Sullivan 852* (MO).

BOLIVIA. **Cochabamba**: Chapare, Territorio Indigena Parque Nacional Islboro-Secure, Cordillera de Mosetenez, Laguna Carachupa, 1300 m, 16°14′S, 66°25′W, 29 Aug 2003, *Kessler & Jiménez 12995* (UC).

Among the large decompound species of the genus, *Megalastrum vastum* is characterized by pinna rachises evenly pubescent abaxially by hairs 0.1–0.2 mm long, pinna rachis scales entire or nearly so, the tissue between the veins on both surfaces pubescent by short hairs ca. 0.1 mm long, and indusia absent. In many specimens, the hairs on the adaxial surface of the laminae are more frequent toward the margins. Glands are often lacking on the laminar tissue and veins abaxially, except for *Øllgaard 1559* and *Balslev 1693* which have spherical, sessile, orange glands abaxially along the veins.

Megalastrum vastum resembles *M. aureisquama* and *M. mollicoma* in lamina size and cutting but differs from by the laminae between the veins adaxially with hairs ca. 0.1 mm long, acicular, hyaline, appressed, ascending (vs. longer and lax). Also, its scales differ, being thinner, more flaccid, dull, and often brown; in contrast, those of *M. aureisquama* and *M. mollicoma* are firmer, shiny, and yellowish brown. The scales of the lamina rachises are inconspicuous in *M. vastum*, but conspicuous in *M. aureisquama* and *M. mollicoma*. *Megalastrum vastum* also greatly resembles *M. oreophilum*, a species that differs by petiole and rachis scales golden brown and denticulate (vs. dark brown and entire or nearly so).

Christensen (1920) had a mixed concept of this species. Some of the specimens he cited are considered by us to represent different species. The specimens he cited of *Megalastrum vastum* from Costa Rica represent either *M. skutchii* or *M. palmense* (Moran and Prado 2010); one from Colombia (*Lehmann 8924*) represents *M. reductum*; the specimen he cited from Paraguay (*Hassler 10421*) represents *M. umbrinum* (C. Chr.) A. R. Sm. & R. C. Moran (Moran *et al.* 2009a); and the specimen from Peru (*Spruce 4718*) represents *M. miscellum*.

Photos distributed by US (Morton negative 1320) at F, MICH and MO state on their labels that the plant depicted is an isotype of *Polypodium vastum*; however, there is no locality information with the specimen and therefore it is uncertain whether it is a type.

NAMES OF UNCERTAIN APPLICATION

Dryopteris fusca C. Chr., Index Filicum 267. 1905, *nom. nov.* for *Nephrodium polylepis* Sodiro, non Baker (1891). TYPE.— ECUADOR. Pichincha: "Crece en los bosques de los Colorados entre 400–500 m," s.d., *A. Sodiro s.n.* (P?-n.v.).

We did not find a type of this name. Sodiro did not designate types, and a specimen of his with sufficient locality information and date was not found by either us or Christensen (1920). A specimen at S (seen on-line) was annotated as the type of *Nephrodium polylepis* Sodiro, but its collection information does not agree with the protologue. The specimen was collected by Sodiro near Oyacachi in January 1901, but has the wrong locality, and the annotation was made after the name *Nephrodium polylepis* Sodiro had been published. The specimen was annotated by Christensen as "*D. vasta*" (=*Megalastrum vastum*).

Polypodium honestum Kunze, Linnaea 9:49. 1834. *Phegopteris honesta* (Kunze) Mett., Pheg. u Aspid. Nr. 59. 1858. *Dryopteris honesta* (Kunze) C. Chr., Index Fil. 271. 1905. *Ctenitis honesta* (Kunze) R. Tryon & A. Tryon, Rhodora 84:127. 1982. *Megalastrum honestum* (Kunze) A. R. Sm. & R. C. Moran, Amer. Fern. J. 77:128. 1987 [published 3 May 1988]. Type.—PERU. Huánuco: Pampayacu, 1829, *E. Poeppig 22* (LZ, destroyed).

The type was destroyed during WWII, and apparently no duplicates exist. The description is inadequate to apply the name. Morton negative 5268 (MICH, UC, US) shows a photo of a Poeppig collection at H identified as this species, but it is doubtful that this specimen is the type. The photo depicts a plant that is 2-pinnate-pinnatisect, whereas according to the original descriptions the lamina was only 1-pinnate-pinnatifid.

Unusual Specimens

We have not been able to identify the specimens cited below with any of the species recognized above. These specimens might represent new species, but more material is needed to confirm this.

Bonino et al. 1186 (MO). Bolivia. This specimen resembles *Megalastrum aureisquama* but differs by dark appressed scales along the lamina rachises (not golden brown scales). The cutting of the laminae also differs, being only 2-pinnate pinnatifid basally (vs. 3-pinnate-pinnatifid) and with the proximal pinnae soon becoming adnate the pinna rachises distally. The pinnules are obtuse to acute (vs attenuate or acuminate).

Mellado et al. 2390 (MO). Peru. This specimen resembles *Megalastrum subtile* by filiform to linear scales on the pinna rachises abaxially, but it differs by somewhat larger leaves and costules glabrous abaxially. It occurs at slightly higher elevation (2700 m).

Monteagudo et al. 11879 (MO). Peru. This specimen resembles *Megalastrum ciliatum* by the pubescence between the veins abaxially; however, it differs by laminae less deeply divided, basal pinnae not strongly equilateral, and pinnules obtuse more widely adnate to the pinna rachis.

Steyermark 62438 p.p. (F, VEN). Venezuela. This specimen, from Cerro Trumuquire in the state of Sucre, resembles *Megalastrum biseriale* by small lamina size and by lamina cutting; however, it differs by basal pinnae equilateral, smaller scales on the lamina rachises (2.0–3.0 mm long), and hairs on the abaxial surfaces of the pinna rachises 0.8–1 mm long, whitish, straight. More material is needed before this species can be fully described.

ACKNOWLEDGMENTS

This research was funded by a grant to the senior author from the United States National Science Foundation (DEB 0717056). A grant to the second author was made by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) for fieldwork and travel to NY (Grant nos. 303867/2004-3, 302732/2007-1). We thank the curators of AAU, B, BM, BR, CGE, COL, F, GH, GOET, HB, HBR, HOXA, K, MBM, MICH, MO, NY, P, PACA, QCA, QCNE, R, RB, S, SP, SPF, U, UC, UPCB, US, and VEN for sending us loans and/or images of specimens. We thank Regina Hirai for help generating the lists of specimens examined and index to collectors' names and numbers, and Fausto Barbo for help with the distribution maps. We thank J. G. Murrell for sending us an image of the type of *Polypodium pleiosorum* at CGE. Regina Hirai, Michael Kessler, Fernando Matos, Alan Smith, and Alejandra Vasco provided helpful comments and discussions. We greatly appreciate the encouraging and helpful efforts of George Yatskievych in editing this manuscript. The drawings of indument characteristics were made by Mr. Haruto Fukuda.

LITERATURE CITED

CHRISTENHUSZ, M. J. M., X.-C. ZHANG and H. SCHNEIDER. 2011. A linear sequence for extant families and genera of ferns and lycophytes. Phytotaxa 19:7–54.

CHRISTENSEN, C. 1919 [published 1920]. A monograph of the genus *Dryopteris*, Part II. The tropical American bipinnate-decompound species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 8, 6:3–132.

HOLTTUM, R. E. 1986 [published 1987]. Studies in the fern-genera allied to *Tectaria* Cav. VI. A conspectus of genera in the Old World regarded as related to *Tectaria* with descriptions of two genera. Gard. Bull. Straits Settlem., ser. 3, 39:153–167.

KATO, M. 1974. A note on the systematic position of *Rumohra adiantiformis*. Acta Phytotax. Geobot. 26:52–57.

LABIAK, P. H., M. SUNDUE, G. ROUHAN, J. GARRISON HANKS, J. T. MICKEL and R. C. MORAN. 2014. Phylogeny and historical biogeography of the lastreopsid ferns (Dryopteridaceae). Amer. J. Bot. 101:1207–1228.

MCNEILL, J., F. R. BARRIE, W. R. BUCK, V. DEMOULIN, W. GREUTER, D. L. HAWKSWORTH, P. S. HERENDEEN, S. KNAPP, K. MARHOLD, J. PRADO, W. F. PRUD'HOMME VAN REINE, G. F. SMITH, N. J. TURLAND and J. H. WIERSEMA. 2012. International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code). Regnum Veg. 154: i–xxx, 1–208.

MICKEL, J. T. and A. R. SMITH. 2004. The pteridophytes of Mexico. Mem. New York Bot. Gard. 88:1–1054.

MORAN, R. C. 1995. The importance of mountains to pteridophytes, with emphasis on neotropical montane forests. Pp. 359–363 *in* S. P. Churchill, H. Balslev, E. Forero and J. L. Luteyn (eds.), *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden Press, Bronx.

MORAN, R. C. 1996. The importance of the Andes as a barrier to migration, as illustrated by the pteridophytes of the Chocó phytogeographic region. p. 75 *in* J. M. Camus, M. Gibby and R. J. Johns (eds.), *Pteridology in Perspective*. Royal Botanic Gardens, Kew.

Moran, R. C. and J. Prado. 2010. *Megalastrum* (Dryopteridaceae) in Central America. Kew Bull. 65:137–188.

Moran, R. C., J. Prado and P. H. Labiak. 2009a. *Megalastrum* (Dryopteridaceae) in Brazil, Paraguay, and Uruguay. Amer. Fern J. 99:1–44.

Moran, R. C., J. Prado and P. H. Labiak. 2009b. *Megalastrum* (Dryopteridaceae) in the West Indies. Brittonia 61:273–292.

Proctor, G. R. 1985. *Ferns of Jamaica*. British Museum (Natural History), London.

Rojas, A. F. 2007. New species in *Megalastrum subincisum* complex (Dryopteridaceae) from Costa Rica. Brenesia 68:17–24.

Rojas, A. F. 2009. Novelties in the *Megalastrum biseriale* complex (Dryopteridaceae) from the Neotropics. Métodos en Ecología y Sistemática 3(Suppl. 1):41–53.

Rouhan, G. and R. C. Moran. 2011. Monograph of Paleotropical *Megalastrum* (Dryopteridaceae). Ann. Missouri Bot. Gard. 98:90–100.

Schuettpelz, E. H. and K. M. Pryer. 2007. Phylogeny of ferns inferred from 400 leptosporangiate species and three plastid genes. Taxon 56:1037–1050.

Smith, A. R. 1981. Pteridophytes. *In*: D. E. Breedlove, editor, Flora of Chiapas 2:1–370. California Academy of Science, San Francisco.

Smith, A. R. and R. C. Moran. 1987 [published 3 May 1988]. New combinations in *Megalastrum* (Dryopteridaceae). Amer. Fern J. 77:124–130.

Smith, A. R. and R. C. Moran. 1995. *Megalastrum*. Pp. 202–204 *in* G. Davidse, M. Sousa S. & S. Knapp (gen. eds.), R. C. Moran & R. Riba (eds. en pteridofitas). Flora Mesoamericana. Vol. 1. Psilotaceae a Salviniaceae. Univ. Nacional Autónoma de México. Ciudad Universitaria.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider and P. G. Wolf. 2008. Fern classification. Pp. 417–467 *in* T. A. Ranker & C. H. Haufler (eds.), Biology and Evolution of Ferns and Lycophytes. Cambridge Univ. Press.

Stolze, R. G. 1981. Ferns and fern allies of Guatemala. Part II, Polypodiaceae. Fieldiana, Bot., new series 6:1–522.

Sundue, M. A., G. Rouhan and R. C. Moran. 2010. *Megalastrum* (Dryopteridaceae) of the circumaustral region: Chile, Argentina, and southern islands of the Atlantic, Pacific, and Indian Oceans. Syst. Bot. 35:461–475.

Tindale, M. 1965. A monograph of the genus *Lastreopsis* Ching. Contr. New South Wales Natl. Herb. 211:59–78.

Tryon, R. M. and R. G. Stolze. 1991. Pteridophyta of Peru, Part IV. 17. Dryopteridaceae. Fieldiana, Bot., new series, 27:1–176.

Wiggins, I. L. and D. M. Porter. 1971. Flora of the Galápagos Islands. Stanford University Press, California.

Appendix 1: List of Accepted Names

1- *Megalastrum acrosorum* (Hieron.) A. R. Sm. & R. C. Moran
2- *Megalastrum adenopteris* (C. Chr.) A. R. Sm. & R. C. Moran
3- *Megalastrum alticola* M. Kessler & A. R. Sm.
4- *Megalastrum andicola* (C. Chr.) A. R. Sm. & R. C. Moran
5- *Megalastrum aureisquama* M. Kessler & A. R. Sm.
6- *Megalastrum biseriale* (Baker) A. R. Sm. & R. C. Moran
7- *Megalastrum bolivianum* M. Kessler & A. R. Sm.
8- *Megalastrum ciliatum* M. Kessler & A. R. Sm.
9- *Megalastrum clathratum* R. C. Moran, J. Prado & Sundue
10- *Megalastrum crenulans* (Fée) A. R. Sm. & R. C. Moran
11- *Megalastrum ctenitoides* A. Rojas
12- *Megalastrum decompositum* R. C. Moran, J. Prado & Sundue
13- *Megalastrum falcatum* A. Rojas
14- *Megalastrum fibrillosum* (Baker) R. C. Moran, J. Prado & Sundue

15- *Megalastrum fimbriatum* R. C. Moran, J. Prado & Sundue
16- *Megalastrum fugaceum* R. C. Moran, J. Prado & Sundue
17- *Megalastrum galapagense* R. C. Moran, J. Prado & Sundue
18- *Megalastrum hirsutosetosum* (Hieron.) A. R. Sm. & R. C. Moran
19- *Megalastrum insigne* R. C. Moran, J. Prado & Sundue
20- *Megalastrum marginatum* M. Kessler & A. R. Sm.
21- *Megalastrum martinicense* (Spreng.) R. C. Moran, J. Prado & Labiak
22- *Megalastrum microsorum* (Kuntze) Stolze
23- *Megalastrum miscellum* R. C. Moran, J. Prado & Sundue
24- *Megalastrum molle* A. R. Sm.
25- *Megalastrum mollicoma* (C. Chr.) A. R. Sm. & R. C. Moran
26- *Megalastrum nanum* R. C. Moran, J. Prado & Sundue
27- *Megalastrum nigromarginatum* R. C. Moran, J. Prado & Sundue
28- *Megalastrum obtusum* R. C. Moran, J. Prado & Sundue
29- *Megalastrum oellgaardii* R. C. Moran, J. Prado & Sundue
30- *Megalastrum oreophilum* R. C. Moran, J. Prado & Sundue
31- *Megalastrum peruvianum* R. C. Moran, J. Prado & Sundue
32- *Megalastrum platylobum* (Baker) A. R. Sm. & R. C. Moran
33- *Megalastrum pleiosoros* (Hook. f.) A. R. Sm. & R. C. Moran
34- *Megalastrum polybotryoides* R. C. Moran, J. Prado & Sundue
35- *Megalastrum praetermissum* R. C. Moran, J. Prado & Sundue
36- *Megalastrum pubescens* A. Rojas
37- *Megalastrum pubirhachis* R. C. Moran, J. Prado & Sundue
38- *Megalastrum pulverulentum* (Poir.) A. R. Sm. & R. C. Moran
39- *Megalastrum reductum* A. Rojas
40- *Megalastrum rhachisquamatum* R. C. Moran, J. Prado & Sundue
41- *Megalastrum rupicola* M. Kessler & A. R. Sm.
42- *Megalastrum squamosissimum* (Sodiro) A. R. Sm. & R. C. Moran
43- *Megalastrum subincisum* (Willd.) A. R. Sm. & R. C. Moran
44- *Megalastrum subtile* R. C. Moran, J. Prado & Sundue
45- *Megalastrum tepuiense* R. C. Moran, J. Prado & Sundue
46- *Megalastrum vastum* (Kunze) A. R. Sm. & R. C. Moran

APPENDIX 2: LIST OF ALL NAMES THAT APPLY TO ANDEAN MEGALASTRUM

The numbers in parentheses refer to the species numbers assigned in the taxonomic treatment (see above). Accepted names appear in bold.

Alsophila martinicensis Spreng. (21)
Aspidium araguata Moritz ex Reichardt (21)
Aspidium crenulans Fée (10)
Aspidium erythrostemma Christ (38)
Aspidium lutescens Willd. (38)
Aspidium subincisum (Willd.) Christ (43)
Ctenitis acrosora (Hieron.) Copel. (1)
Ctenitis adenopteris (C. Chr.) Ching (2)
Ctenitis andicola (C. Chr.) Ching (4)
Ctenitis bidecorata Lellinger (6)
Ctenitis biserialis (Baker) Lellinger (6)
Ctenitis crenulata (Fée) Ching (10)

Ctenitis hirsutosetosa (Hieron.) Lellinger (18)
Ctenitis honesta (Kunze) R. M. Tryon & A. F. Tryon (see Uncertain Application section)
Ctenitis karsteniana (Poir.) Vareschi (38)
Ctenitis mollicoma (C. Chr.) Ching (25)
Ctenitis pleiosoros (Hook. f.) C. V. Morton (33)
Ctenitis pulverulenta (Poir.) Copel. (38)
Ctenitis squamosissima (Sodiro) Copel. (42)
Ctenitis subincisa (Willd.) Ching (43)
Ctenitis villosula (C. Chr.) Ching (4)
Dryopteris acrosora (Hieron.) C. Chr. (1)
Dryopteris adenopteris C. Chr. (2)
Dryopteris andicola C. Chr. (4)
Dryopteris andicola C. Chr. f. *lehmanniana* (Hieron.) C. Chr. (4)
Dryopteris andicola C. Chr. f. *spruceana* (Hieron.) C. Chr. (4)
Dryopteris biserialis (Baker) C. Chr. (6)
Dryopteris crenulans (Fée) C. Chr. (10)
Dryopteris crenulans (Fée) C. Chr. f. *glandulosa* (Rosenst.) C. Chr. (10)
Dryopteris erythrostemma (Christ) C. Chr. (38)
Dryopteris fusca C. Chr. (see Uncertain Application section)
Dryopteris hirsutosetosa Hieron. (18)
Dryopteris karsteniana (Klotzsch) Hieron. (38)
Dryopteris leptosora C. Chr. (22)
Dryopteris macrotheca (Fée) C. Chr. (6)
Dryopteris microsora Kuntze (22)
Dryopteris mollicoma C. Chr. (25)
Dryopteris oreocharis Sehnem var. *canescens* Sehnem (2)
Dryopteris platyloba (Baker) C. Chr. (32)
Dryopteris pleiosoros Svens. (33)
Dryopteris pulverulenta (Poir.) C. Chr. (38)
Dryopteris squamosissima (Sodiro) C. Chr. (42)
Dryopteris squamosissima (Sodiro) C. Chr. var. *bogotensis* (Hieron.) C. Chr. (42)
Dryopteris subincisa (Willd.) Urb. (43)
Dryopteris subincisa (Willd.) Urb. var. *bogotensis* Hieron. (42)
Dryopteris subincisa (Willd.) Urb. var. *karsteniana* (Klotzsch) C. Chr. (38)
Dryopteris tarapotense (Baker) C. Chr. (32)
Dryopteris vasta (Kunze) Hieron. (46)
Dryopteris villosa (L.) Kuntze var. *tomentosa* Rosenst. (2)
Dryopteris villosa (L.) Kuntze var. *glandulosa* Rosenst. (10)
Dryopteris villosa (L.) Kuntze var. *inaequalis* Gilbert (4)
Dryopteris yungensis Christ & Rosenst. (6)
Megalastrum acrosorum (Hieron.) A. R. Sm. & R. C. Moran (1)
Megalastrum adenopteris (C. Chr.) A. R. Sm. & R. C. Moran (2)
Megalastrum aequatoriense A. Rojas (6)
Megalastrum alticola M. Kessler & A. R. Sm. (3)
Megalastrum andicola (C. Chr.) A. R. Sm. & R. C. Moran (4)
Megalastrum andicola (C. Chr.) A. R. Sm. & R. C. Moran f. *lehmannianum* (Hieron.) Stolze (4)

Megalastrum aureisquama M. Kessler & A. R. Sm. (5)
Megalastrum bidecoratum (Lellinger) A. R. Sm. & R. C. Moran (6)
Megalastrum biseriale (Baker) A. R. Sm. & R. C. Moran (6)
Megalastrum bolivianum M. Kessler & A. R. Sm. (7)
Megalastrum ciliatum M. Kessler & A. R. Sm. (8)
Megalastrum clathratum R. C. Moran, J. Prado & Sundue (9)
Megalastrum crenulans (Fée) A. R. Sm. & R. C. Moran (10)
Megalastrum ctenitoides A. Rojas (11)
Megalastrum decompositum R. C. Moran, J. Prado & Sundue (12)
Megalastrum dorsiglabrum A. Rojas (30)
Megalastrum falcatum A. Rojas (13)
Megalastrum fibrillosum (Baker) R. C. Moran, J. Prado & Sundue (14)
Megalastrum fimbriatum R. C. Moran, J. Prado & Sundue (15)
Megalastrum fugaceum R. C. Moran, J. Prado & Sundue (16)
Megalastrum galapagense R. C. Moran, J. Prado & Sundue (17)
Megalastrum hirsutosetosum (Hieron.) A. R. Sm. & R. C. Moran (18)
Megalastrum honestum (Kunze) A. R. Sm. & R. C. Moran (see Uncertain Application section)
Megalastrum insigne R. C. Moran, J. Prado & Sundue (19)
Megalastrum karstenianum (Klotzsch) A. Rojas (38)
Megalastrum laxipilosum A. Rojas (25)
Megalastrum leptosorum (C. Chr.) A. R. Sm. & R. C. Moran (22)
Megalastrum marginatum M. Kessler & A. R. Sm. (20)
Megalastrum martinicense (Spreng.) R. C. Moran, J. Prado & Labiak (21)
Megalastrum microsorum (Kuntze) Stolze (22)
Megalastrum miscellum R. C. Moran, J. Prado & Sundue (23)
Megalastrum molle A. R. Sm. (24)
Megalastrum mollicoma (C. Chr.) A. R. Sm. & R. C. Moran (25)
Megalastrum nanum R. C. Moran, J. Prado & Sundue (26)
Megalastrum nigromarginatum R. C. Moran, J. Prado & Sundue (27)
Megalastrum obtusum R. C. Moran, J. Prado & Sundue (28)
Megalastrum oellgaardii R. C. Moran, J. Prado & Sundue (29)
Megalastrum oreophilum R. C. Moran, J. Prado & Sundue (30)
Megalastrum peruvianum R. C. Moran, J. Prado & Sundue (31)
Megalastrum platylobum (Baker) A. R. Sm. & R. C. Moran (32)
Megalastrum pleiosoros (Hook. f.) A. R. Sm. & R. C. Moran (33)
Megalastrum polybotryoides R. C. Moran, J. Prado & Sundue (34)
Megalastrum praetermissum R. C. Moran, J. Prado & Sundue (35)
Megalastrum pubescens A. Rojas (36)
Megalastrum pubirhachis R. C. Moran, J. Prado & Sundue (37)
Megalastrum pulverulentum (Poir.) A. R. Sm. & R. C. Moran (38)
Megalastrum reductum A. Rojas (39)
Megalastrum rhachisquamatum R. C. Moran, J. Prado & Sundue (40)
Megalastrum rupicola M. Kessler & A. R. Sm. (41)
Megalastrum squamosissimum (Sodiro) A. R. Sm. & R. C. Moran (42)
Megalastrum squamosissimum (Sodiro) A. R. Sm. & R. C. Moran var. *bogotense* (Hieron.) A. R. Sm. & R. C. Moran

Megalastrum subincisum (Willd.) A. R. Sm. & R. C. Moran (43)
Megalastrum subtile R. C. Moran, J. Prado & Sundue (44)
Megalastrum tepuiense R. C. Moran, J. Prado & Sundue (45)
Megalastrum vastum (Kunze) A. R. Sm. & R. C. Moran (46)
Megalastrum villosulum (C. Chr.) A. R. Sm. & R. C. Moran (4)
Megalastrum yungense (Christ & Rosenst.) A. R. Sm. (6)
Nephrodium acrosorum Hieron. (1)
Nephrodium biseriale (Baker) Diels (6)
Nephrodium microsorum Hook. (22)
Nephrodium polylepis Sodiro (see Uncertain Application section)
Nephrodium squamosissimum Sodiro (42)
Nephrodium subglabrum Sodiro (32)
Nephrodium vastum (Kunze) Hieron. (46)
Nephrodium villosum L. var. *karstenianum* (Klotzsch) Jenman (38)
Nephrodium villosum L. var. *opacum* Mett. ex Hieron. f. *opacum* Hieron. (4)
Nephrodium villosum L. var. *opacum* Mett. ex Hieron. f. *lehmannianum* Hieron. (4)
Nephrodium villosum L. var. *subincisum* (Willd.) Hook. ex Sodiro (43)
Nephrodium villosum L. var. *subincisum* (Willd.) Jenman (43)
Phegopteris epierioides Fée (21)
Phegopteris hirsuta Fée (38)
Phegopteris honesta (Kunze) Mett. (see Uncertain Application section)
Phegopteris karsteniana (Klotzsch) Mett. (38)
Phegopteris martinicensis (Spreng.) Fourn. (21)
Phegopteris subincisa (Willd.) Fée (43)
Phegopteris vasta (Kunze) Mett. (46)
Polypodium barbatum Desv. (38)
Polypodium biseriale Baker (6)
Polypodium extensum C. Presl (46)
Polypodium honestum Kunze (see Uncertain Application section)
Polypodium karstenianum Klotzsch (38)
Polypodium platylobum Baker (32)
Polypodium pleiosoros Hook. f. (33)
Polypodium pulverulentum Poir. (38)
Polypodium subincisum Willd. (43)
Polypodium tarapotense Baker (32)
Polypodium vastum Kunze (46)

APPENDIX 3: LIST OF EXSICCATAE

The number in parentheses refers to the species numbers assigned in the taxonomic treatment and listed in Appendix 1. Collection numbers in boldface are types.

Abbott, J. R.: 15112 (39)
Acebey, A.: 595 (14); 730 (20)
Acosta, S. M.: 6517 (46)
Adsersen, A.: 9, 84, 774, 887, 1248, 1659, 1819 (33)

Castillón, L.: 40958 (16)
Cerón, E. C.: 1483, 1489 (13)
Clark, J. L. & Watt, C.: 862 (46)
Cook, F. O. & Gilbert, G. B.: 1128 (16)
Cornejo, X.: 8165 (46)
Cornejo, X. & Bonifaz, C.: 5459 (22)
Croat, T. B.: 56541 (42); **71469** (25); 72158 (46)
Croat, T. B. & Menke, M.: 89543 (14)
Croat, T. B. et al.: 91009, 91135A, **91165** (13)
Cuatrecasas, J.: 11185 (35); 13021 (46); 23889 (19)
Daniel, Bro.: 2013 (23); 4473 (19)
Daniel, H.: 1898 (42)
Darwin, C.: **s.n.** (33)
de la Sota, R. E.: 4069, 4298 (16)
Díaz, S.: 3130 (43)
Dodson, C. H. et al.: 7215 (46); 7844 (39); 8958 (46)
Dodson, C. H. & Gentry, A.: 10088 (39); 12280 (22)
Dombey, J.: s.n. (2)
Dorr, L. J. & Stergios, B: 8720 (38)
Dudley, R. T.: 11512 (35)
Eberhardt, D. et al.: 137, 142 (41); 204 (6); 402 (20); 513 (6)
Eliasson, U.: 379, 382, 1354, 1851 (33)
Escobar, L. et al.: 3854 (43)
Evoy, J.: 78 (39)
Fagerlind, F.: 3036 (33)
Fay, A. & Fay, L.: 2051 (14); 2205 (6); 3287 (19); 3316, 3335, 3349, 3350, 3351, 3352 (46); 3370, 3391 (19); 3662, 3663 (35); **3827** (19); 3845 (38); 3870, 3876 (16); 3910, **3919** (37); 4014 (14); 4043, 4046, p.p. (23); 4046, p.p., 4097, 4232, **4250** (35); 4381 (14); **4382** (23); 4403 (35); 4595, 4626 (39)
Fendler, A.: 156, 202 (43); 447 (38)
Fernández, E. et al.: 2362 (4); 2366 (35)
Foster, M. S.: 85–144 (1)
Foster, R. & Wachter, T: 7423 (14)
Foster, R. et al.: 11598 (14)
Franco, P. et al.: 5095 (6)
Freire, E. et al.: 1480 (16)
Fuentes, A. et al.: 9013 (8); 9034 (41); 11098 (20); 14359 (14)
Funck, H. & Schlim, L. J.: 282 (21); 407, 412 (43); **975** (38); 1575 (43)
Gentry, A. et al.: 22867 (19); 60443 (25); 60492 (25)
Giraldo, F. & Mejía, I: 2098 (46)
Gonzales, N. et al.: 7 (43)
Grant, M. L.: 10810 (38)
Grubb, P. J. & Guymer, D. A.: 94 (42)
Grubb, P. J. et al.: 1195, 1239 (19)
Guevara, V.: 75 (4)
Hamann, M.: 516, 582, 586, 886, 915, 1216, 1985 (33)
Harling, G.: 5089 (33)

Harling, G. & Andersson, N. J.: 22459 (12)
Harling, G. et al.: 7396 (35)
Herrera, G.: 9130 (25)
Herrera, G. & Chacón, A. **2794** (11)
Holdridge, L. R.: 1622 (39)
Holm-Nielsen, L. & Jeppesen, S.: 1053 (35)
Holm-Nielsen, L. et al.: 4502 (18); 4507 (35); 4547 (23); 4618 (14); 6999 (16); 7065 (39); 24760 (19); 24853 (6); 26458 (37); 26896 (14); 26904 (6)
Hoover, S. W. & Wormley, S.: 1620 (46)
Hoover, S. W. et al.: **3609** (6)
Howell, J. T.: 9230 (33)
Huamantupa, I. & Quispe, W: 3836, 3837 (16)
Huaylla, H.: 792 (18); 831 (44)
Huaylla, H.: et al.: 1554, 1720, 1853, 2655 (16)
Idrobo, J. M. et al.: 10659 (21)
Jaramillo, J. & Grijalva, R: 13607 (46)
Jiménez, I.: 226 (20); 1203, 1207, 1344 (16); 2177 (6); 2269 (14)
Jiménez, I. & Gallegos, S.: 844 (41); 877 (4)
Jiménez, I. & Huaylla, H.: 2518 (20); 2547 (14); 2551, 2583 (20); 2589, 2589 (14); 2590 (20)
Jiménez, I. & Moguel, A.: 1428 (4); 1489 (16); 1641 (3)
Jiménez, I. & Serrano, M.: 2398 (26)
Jiménez, I. et al.: 2468 (2)
Johnston, J. R.: 187 (43)
Jørgensen, P. et al.: 65337 (13)
Kalbreyer, W: 1561 (38); 1564 (19)
Kanehira, R.: 179 (14); 184 (18)
Karsten II, H.: **3** (38)
Kessler, M & Jiménez, I.: 12995 (46); 12999 (41)
Kessler, M et al.: 630 (20); 5971 (2); 6167 (16); 6171, 6180 (16); 6285 (2); 6370 (26); 6379 (4); 6381 (16); 6539 (3); 6908 (5); 6964, 7014 (3); 7033 (31); 7185 (3); 7188, 7189 (16); **7379** (5); 7426 (41); 7522 (5); 7554 (14); 7630 (20); **7630a** (7); 7631 (35); 7644 (5); 7751 (41); 7789 (5); 7907 (41); 7970, 8126 (14); 8256 (23); 8680 (14); 9088, 9105, 9488 (16); 9900 (41); 10019B (14); 10774, 10897 (35); 10982 (14); 11131 (35); 11604 (14); 11621 (35); 11944 (6); **11945** (3); 12948 (14); 12950 (41); 13393 (14)
Killeen, T.: 1383 (35)
Killip, E. P.: 7758 (6); 16659 (38)
Killip, E. P. & Hazen, T. E.: 8800 (46)
Killip, E. P. & Smith, A. C.: 15555 (27); 16136, 19998 (43); 20411 (38); **20453** (36); 22779 (2); 24550 (6); 24659 (14); 26021 (6); 26037 (18)
Killip, E. P. & Varela, J. D.: 34671 (6)
Killip, E. P. et al.: 10394 (23)
Knapp, S. & Mallet, J.: 7022 (24)
Krömer, T. et al.: 100 (20)
Labiak, P. H.: 4730 (3); 4731 (6)
Lehmann, F. C.: 101 (19); **7369** (4); 7416 (19); 8924, 8925 (39)
Leiva, S. et al.: 1759 (22)

Lellinger, D. B. & de la Sota, E. R.: 815 (19); 840 (18); 917 (43)
León, B. et al.: 3047 (31)
Liesner, R. & Holst, B.: 21585 (10)
Liesner, R. et al.: 12829 (43)
Limminghe, A. M. A.: s.n. (38)
Linden, M.: 184 (21); 243, 843 (4); 844 (38); 1020, p.p. (21); 1020, p.p. (43); 1033 (46); s.n. (21)
Lindig, A.: 159 (4); 331 (42)
Little, E. L. & Little, R. R.: 8597 (27); 9415 (1)
Lliully, A. et al.: 101 (16)
Lugo, H.: 2064 (35)
Luteyn, L. J. et al.: 6590 (13)
MacBride, F.: 4846, 4855 (3)
MacDougal, J. M. et al.: 3886 (11)
Madriñan, S. & Barbosa, C. E.: 187 (43)
Madsen, J.: 86916 (22); 87002 (6)
Madsen, J. & Rosales, C.: 8162 (23)
Maguire, B. et al.: **36871** (30)
Martínez, O. & Prado, J.: 1893 (8); 1894 (16)
Meier, W.: 2862, 8768 (43)
Meier, W. & Flauger, N.: 9107 (43)
Meier, W. & Gutiérrez, R.: 12333 (38)
Meier, W. & Molina, [?]: 9226 (43)
Meier, W. & Nehlin, S.: 8939 (43); 10084 (46)
Meier, W. et al.: 11193 (43)
Mejia, R. J. et al.: 3312, 3517 (4)
Mellado, L. F.: 1686 (19)
Mellado, L. F. & Becerra, E.: 1754, 1803, 1835 (3)
Mellado, L. F. et al.: 2390 (unusual specimen)
Mille, A.: 114 (16)
Mille, L.: s.n. (6); s.n. (19)
Mille, L. J.: s.n. (3)
Monteagudo, A. et al.: 11879 (unusual specimen)
Moran, R. C.: 3510 (6); 3522 (16); 3531 (6); 3543 (39); 3546 (6); 3546B (38); 3546A (46); 3567 (1); 3583A, p.p. (7); 3583, p.p. (13); 3591 (6); 3594 (37); 3609 (39); 3689 (13); 3707 (14); **5911** (16); **5917** (26)
Moran, R. C. & Rohrbach, C.: 5133, 5160 (18); 5200, 5220 (19); 5229 (6); 5380, p.p. (16); 5380, p.p. (26); 5382 (7)
Moran, R. C. et al.: 5949 (46); 6925 (39); 7443 (6); 7542 (19); 7545 (6); 7608 (44); 7634 (14)
Moritz, J. W. K.: **202**, p.p. (21); 202, p.p., 385, p.p., 389, 435 (43); 459 (38); s.n. (43)
Morrone, O. et al.: 2863 (16)
Mostacero, J. & Howorth, R.: 209 (43)
Navarrete, H.: **538**, 539, 540 (34); 725 (7); 789 (6); 798, 847, 896 (19); 1684 (6)
Navarrete, H. & Asimbaya, P.: 1646 (6)
Navarrete, H. & Øllgaard, B.: 3047 (6)
Neill, D. et al.: 5956 (6)

Núñez, R.: 760 (35)

Núñez, R. & Huaylla, H.: 178 (16); 199 (23); 279 (4)

Núñez, V. P.: 8929 (2); 13973 (24)

Øllgaard, B.: 1559 (46); 74637 (6); 74966 (19); 98257 (6); 98379(35); 98410 (13); 98413 (40); 98471 (23); 98888 (6); 98891 (25); 98919 (3); 98930 (16); 98942, 99593 (6); 99738 (37); 99754, 99756 (46); 99763 (13); 99890 (37); 99904 (19); 99993 (6); 100629 (46); 100631 (19); 100743 (14)

Øllgaard, B. & Borchsenius, F: 100674 (39)

Øllgaard, B. & Larrea, M.; 98857 (39)

Øllgaard, B. & Navarrete, H.: 859 (46); 1418 (18); 1426 (44); 1629 (37); 1630 (19); 1635 (35); 1713 (16); 1971 (35); 1992 (14); 2026 (35); 2046 (11); 2755 (3); 2859 (14); 99803 (23); 105622, 105657 (6); 105819 (14); 105853, 105854, 105893 (13); 105912 (6); 105938 (19); 105941, 105947 (16)

Øllgaard, B. et al.: 2205 (11); **2219** (29); 2233 (11); 2247 (28); 2900 (7); 35799 (19); 35806 (29); 37745, 37844 (46); 57852 (13); 74815 (24); 90906 (7); 90909 (16); 99268 (18); 99554 (19); 99556 (16); 99562 (1); 98468, 98694, 99792 (18); 99923 (14); 100773 (22)

Ortega, F.: 2934 (43)

Ortega, F. & Berti, L.: 2120 (43)

Ortega, F. & Smith, A. R.: 2476 (42)

Ortega, F. & Stergios, B: 1502 (43)

Ortega, F. & van der Werff, H.: 2938, 2951 (43)

Ortega, F. et al.: 1635, 1825 (43); 2013 (38); 2025 (43); 3030 (38)

Otto, E.: 603, 867 (43)

Palacios, W.: 4036, 4070 (18); **5844** (40); 10986 (18); 12113 (7); 12645 (16)

Palacios, W. & Cen, [?]: 13883 (22)

Palacios, W. & Clark, J.: 12644A (25)

Palacios, W. & Tirado, M.: 13214 (23)

Palacios, W. & van der Werff, H.: 3600 (19)

Palacios, W. et al.: 8764 (14); 8766 (18); 9569 (37); 9724 (6)

Paniagua C. N. et al.: 4216 (35)

Pedersen, H. B. et al.: 104322 (35)

Peyton, B.: 1497 (16)

Peyton, B. & Peyton, S: 1225 (16)

Pitman, N. & Bass, M.: 1073 (39)

Pitman, N. et al.: 762 (39)

Pittier, H.: 9498, 9595 (43); 10029 (38)

Plowman, T. et al.: 3942 (37)

Poeppig, E.: **34** (46)

Portugal, A. & Jiménez, I.: 452 (41)

Portugal, A. et al.: 223 (41); 246 (7); 250, 364 (6); 366, 370, 401 (41); **538** (20)

Quijada, C.: 25 (43)

Quintana, D. et al.: **41** (41)

Quipuscoa S. V. et al.: 11 (19)

Quipuscoa, V. & Bardales, J.: 958 (19)

Quipuscoa, V. et al.: 1083 (1); 1088 (probably an undescribed species); 2340 (1); 2404 (19)

Quizhpe, W.: 1746 (40)

Ramos, J. et al.: 6371, 7057 (3)

Rangel, O. et al.: 5762 (46)

Rodríguez, W. et al.: 3209, 3598 (43); 3636 (46); 4589 (43); 4591 (46); 4805 (25); 4905 (43); 4915 (38); 4934 (6); 5559 (36); 5575 (43); 5578 (46); 5594, 5629 (43)

Rose, J. N.: 22379 (42)

Rothfels, C. J. et al.: 3714 (19)

Rusby, H. H.: 425, p.p. (8); 425, p.p. (31); 426, p.p. (31); 426, p.p. (8)

Sánchez-Baracaldo, P.: 42, 60 (25); 64 (43)

Sanín, D. et al.: 5176 (39)

Santa, J. & Escobar, R: 642 (42)

Schmit, P. A. et al.: **422** (8)

Schunke, C.: 45, 46, 47, 66, 87, 225A, 453, 510, 704, 841, 862, 1555 (6); s.n. (18)

Seidel, R. et al.: 9035 (35)

Serrano, M. et al.: 5225 (16); 6873 (2)

Silverstone-Sopkin, P.: 9088 (46)

Silverstone-Sopkin, P. et al.: 2933 (11)

Sleumer, H.: 2097 (2)

Smith, A. R. et al.: 906 (43); 1180 (43); 1249 (38); 1342 (21); 1398 (43)

Smith, D.: 5260 (35)

Smith, D. et al.: 2615, p.p. (1); 2615, p.p. (5)

Smith, D. & Palacios, W.: 2639 (3)

Smith, D. N. & Vásquez, R.: 4884 (19)

Smith, H. H.: 1023, 1024 (30); 1047 (43)

Sodiro, L.: 112 (25); 113 (16); 23827, 23/36 (19); 23/36 (46); 44/145a (25); s.n. (1); s.n. (3); s.n. (6); s.n. (12); s.n. (16); s.n. (19); **s.n.** (25); s.n. (38); s.n. (39); s.n. (42); s.n. (46)

Soukup, J.: 296 (26); 1032 (6)

Soukup, S. S.: 3354, 5261 (19)

Sparre, B.: 13840, 14759 (39); 14898 (46); 16754, 16761 (38); 17168 (28)

Spruce, R.: 4340 (35); **4656** (32); 4718 (23); **4742** (14); 5257 (25); 5257A (38); **5262** (42); **5295**, p.p. (4); 5295, p.p. (19); **s.n.** (6); **s.n.** (22); s.n. (46)

Stewart, A.: 914 (33)

Steyermark, J. A. & Nilsson, S.: 762 (6)

Steyermark, J. A. & Stoddard, A.: 118183 (21)

Steyermark, J. A.: 53768 (6); 54713 (19); 62438, p.p. (unusual specimen); **85913** (45); 98970 (43)

Steyermark, J. A. et al.: 121505 (43)

Stolze, R. G. & Stolze, S: 1667 (38)

Stübel, M. A.: 896 (23); 142 (1); **903** (18); 943 (35); 852 (19); **998** (6); **418** (42); 770 (6); **s.n.** (1)

Suárez, O. et al.: 4887 (6)

Suin, L.: et al.: 1271 (35)

Sundue, M. A. & Vasco, A.: 1260 (46)

Sundue, M. A. et al.: 3155 (46); 3265 (11); 3265 (46)

Tate, G. H. H.: 573 (19); 627 (4); 650 (18); 653 (6)

Triana, J. J.: s.n. (42); s.n. (4); 615 (21); 639 (42)

Trujillo, D. et al.: **7608** (44)

Tryon, M. R. & Tryon, A. F.: 5412 (16); **6103** (27)

Tuomisto, H. & Ruokalainen, K.: 11724 (24)

APPENDIX 4: Distribution of *Megalastrum* species by country in Andean South America. The number in parentheses is the total number of species for each country. Endemics in italic and bold.

Argentina (3): M. adenopteris, M. ciliatum, M. fugaceum.

Bolivia (16): M. adenopteris, M. alticola, M. andicola, M. aureisquama, M. biseriale, M. bolivianum, M. ciliatum, M. fibrillosum, M. fugaceum, ***M. marginatum***, M. miscellum, M. nanum, M. peruvianum, M. praetermissum, ***M. rupicola***, M. vastum.

Colombia (18): M. acrosorum, M. andicola, M. biseriale, M. ctenitoides, M. hirsutosetosum, M. insigne, M. martinicense, M. miscellum, M. mollicoma, ***M. nigromarginatum***, M. oreophilum, M. praetermissum, ***M. pubescens***, M. pulverulentum, M. reductum, M. squamosissimum, M. subincisum, M. vastum.

Ecuador (30): M. acrosorum, M. alticola, M. andicola, M. biseriale, M. bolivianum, M. ctenitoides, **M. decompositum**, M. falcatum, M. fibrillosum, M. fugaceum, ***M. galapagense***, M. hirsutosetosum, M. insigne, M. microsorum, M. miscellum, M. molle, M. mollicoma, M. nanum, ***M. obtusum***, ***M. oellgaardii***, ***M. pleiosoros***, ***M. polybotryoides***, M. praetermissum, M. pubirhachis, M. pulverulentum, M. rhachisquamatum, M. reductum, M. squamosissimum, ***M. subtile***, M. vastum.

Peru (25): M. acrosorum, M. adenopteris, M. alticola, M. andicola, M. aureisquama, M. biseriale, M. bolivianum, M. clathratum, M. falcatum, M. fibrillosum, ***M. fimbriatum***, M. fugaceum, M. hirsutosetosum, M. insigne, M. microsorum, M. miscellum, M. molle, M. nanum, M. peruvianum, ***M. platylobum***, M. praetermissum, M. pubirhachis, M. pulverulentum, M. rhachisquamatum, M. vastum.

Venezuela (8): M. crenulans, M. martinicense, M. oreophilum, M. pulverulentum, M. squamosissimum, M. subincisum, ***M. tepuiense***, M. vastum.

American Fern Journal 104(4):237 (2014)
Published on 24 October 2014

Referees for 2014

All manuscripts submitted to the journal are peer reviewed. Members of the editorial board and the American Fern Society, as well as additional scientists in cognate areas do these reviews on a voluntary basis. It is their work that contributes to the high quality of articles in the *American Fern Journal* and to its continued success. The American Fern Society extends our thanks to the following reviewers for the assistance, diligence, and patience in the year 2011 (We apologize if we inadvertently omitted anyone from this list). We also sincerely thank Surjit Kaur for excellent volunteer editing of manuscripts.

NAOMI ARCAND
NAN CRYSTAL ARENS
MICHAEL BARKER
W. L. CHIOU
JOSH DER
LIBOR EKRT
HELENA FERNÁNDEZ
AURTHUR GILMAN
CHRISTOPHER HAUFLER
ANDREW MACDONALD
KLAUS MEHLTRETER
ROBBIN MORAN
NATHALIE NAGALINGUM
CARRIE OLSON-MANNING
S. PAJARON
EMILIA PANGUA
S. PAJARON
CARMEN PRADA
MARCELLA REGINATA
KAREN RENZAGLIA
ADEEB SHEHZAD
AARON SHIELS
W. CARL TAYLOR
TERESA TERRAZAS
WESTON TESTO
LESLIE TOWILL
CHRISTINE WEINGART
GEORGE YATSKIEVYCH

American Fern Journal 104(4):238 (2014)
Published on 24 October 2014

Statement of Ownership, Management, and Circulation

Publication title and number: *American Fern Journal* (0002-8444). Date of filing: 15 August 2014. Frequency of issue: quarterly. Annual subscription price 2013: $30.00. Office of Publisher: c/o Plant Resources Center, University of Texas at Austin, 1 University Station, F0404, Austin, TX 78712-0471. Editor: Warren Hauk. Managing Editor: Tom Ranker. The *American Fern Journal* is wholly owned by the American Fern Society, Inc., with no bond holders. Physical address of the Society: c/o Plant Resources Center, University of Texas at Austin, 1 University Station, F0404, Austin, TX 78712-0471. The purpose, function, and nonprofit status of the Society and its tax exempt status for Federal income tax purposes remains the same as in past years. The average press run for the past four issues is 603, and was 600 for the issue appearing immediately prior to the filing date, for which 538 copies were mailed as paid circulation and 1 copy was mailed as free distribution, leaving 61 copies for office use and back-issues sales. I certify that these statements are correct and complete. Blanca León, Membership Secretary of AFS.

INFORMATION FOR AUTHORS

Authors are encouraged to submit manuscripts pertinent to the study of ferns and lycophytes for publication in the *American Fern Journal*. Manuscripts should be sent to the editor at **hauk@denison.edu.** Acceptance of papers for publication depends on merit as judged by two or more referees. Authors are encouraged to contribute toward publishing costs; however, the payment or non-payment of page charges will affect neither the acceptability of manuscripts nor the date of publication. Mandatory fees will be charged for color figures in print and/or in electronic versions of published papers.

Information for authors, including detailed requirements for formatting manuscripts can be found online at: http://www.amerfernsoc.org/journal.html.

PTERIDOLOGIA ISSUES IN PRINT

The following issues of *Pteridologia*, the memoir series of the American Fern Society, are available for purchase:

1. Wagner, David H. 1979. Systematics of *Polystichum* in Western North America North of Mexico. 64 pp. $10.00 plus postage and handling.

2A. Lellinger, David B. 1989. The Ferns and Fern-allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). 364 pp. $32.00 plus postage and handling.

3. Lellinger, David B. 2002. A Modern Multilingual Glossary for Taxonomic Pteridology. 263 pp. $28.00 plus postage and handling.

4. Hirai, Regina Y., and Jefferson Prado. 2012. Monograph of *Moranopteris* (Polypodiaceae). 113 pp. $28.00 plus postage and handling.

For orders and more information, please contact our authorized agent for sales at: Missouri Botanical Garden Press, P.O. Box 299, St. Louis, MO 63166-0299, tel. 314-577-9534 or 877-271-1930 (toll free). For online orders, visit: http://www.mbgpress.org.

FIDDLEHEAD FORUM

The editor of the Bulletin of the American Fern Society welcomes contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns.

SPORE EXCHANGE

Mr. Brian S. Aikin, 3523 Federal Ave, Everett, WA 98201-4647 (spores.afs@comcast.net), is Director. Spores exchanged and lists of available spores sent on request. http://amerfernsoc.org/sporexy.html

GIFTS AND BEQUESTS

Gifts and bequests to the Society enable it to expand its services to members and to others interested in ferns. Back issues of the Journal and cash or other gifts are always welcomed and are tax-deductible. Inquiries should be addressed to the Membership Secretary.

VISIT THE AMERICAN FERN SOCIETY'S WORLD WIDE WEB HOMEPAGE:

http://amerfernsoc.org/