

Revision of the Genus *Salpichlaena* J. Sm. (Blechnaceae, Pteridophyta)

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ABSTRACT.—*Salpichlaena* J. Sm. (Blechnaceae) is a genus of climbing fern that grows in Central and South America. The number of species recognized for this genus varies according to different authors from one to four. The goal of this work was to provide a systematic revision of the genus *Salpichlaena* in order to contribute to the knowledge of the fern biodiversity in America. For this purpose morphological, anatomical and palynological characters were analyzed in material from the geographical distribution of *Salpichlaena*. Herbarium specimens were treated according to the standard techniques for LM and SEM studies. The type specimens and the original descriptions were consulted to determine the applications of names. Two species are recognized, *S. volubilis* (Kaulf.) J. Sm. and *S. hookeriana* (Kuntze) Alston. *Salpichlaena hookeriana* differs from *S. volubilis* by pronounced foliar dimorphism (the fertile pinnules are much reduced), the presence of foliar buds on sterile basal pinnules, ovate costular scales and the presence of glandular hairs on the abaxial surface of the costa. The spores are monoletate in both taxa, with rugulate-granulate perispore and superficial spherules. *Salpichlaena volubilis* is widely distributed in Central and South America, from Guatemala and Caribbean Islands, up to southern Brazil and Bolivia, across a wide altitudinal range of 200 to 1900 m. *Salpichlaena hookeriana* grows from Colombia, Venezuelan Guyana, Suriname, British Guiana, North Brazil to Peru and Bolivia, at altitudes up to 800 m. The diagnostic characters, illustrations and distribution maps of both species are given.

KEY WORDS.—*Salpichlaena*, America, systematics, morphology, spores

The genus *Salpichlaena* (Blechnaceae) is an American endemic and differs from other representatives of the family by its high climbing leaves, which has a counterpart only in the leaves of *Lygodium* (Schizaceae) (Tryon and Tryon, 1982). According to these authors the leaves of *Salpichlaena* are scandent to at least 15 m into the top of trees by means of the twining rachis. Other distinguishing features of this genus include: the presence of a long-creeping stem, the leaves monomorphic or dimorphic (the fertile pinnae with narrower segments than the sterile pinnae), and sori on a long vascular commissure parallel and close to the costa that are covered by an indusium that envelops the sporangia. *Salpichlaena* is most closely related to *Blechnum*, but differs in its twining habit, chromosome number and fronds with laminae bipinnate (Smith, 1995).

The number of taxa included in the genus *Salpichlaena* varies according to different authors. Until the present three species have been recognized: *S.*

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hookeriana (Kuntze) Alston, *S. thalassica* Grayum & R.C. Moran and *S. volubilis* (Kaulf.) Hook. (Moran, 1995; Jorgensen and Leon, 1999; Prado, 2005).

The species *S. thalassica* was described by Moran (1990) on the basis of a type from Costa Rica, characterized by the presence of longer stalks of the basal fertile pinnules when compared with those of *S. volubilis*, and by the higher altitude at which *S. thalassica* grows. Conversely, Smith (1990) proposed the combination *S. lomarioidea* (Baker) A.R. Smith (= *Blechnum volubile* Kaulf. var. *lomarioidea* Baker) which was distributed from Venezuelan Guayana to Perú. Later the author synonymized *S. lomarioidea* to *S. hookeriana* (Smith 1995). The existence of two geotypes of *S. volubilis* in Venezuela: *euvolubilis* and *maegdefrauiana* was established by Vareschi (1969). According to him, the former has monomorphic fronds and is distributed in the Coastal Cordillera (900–1500 m) whereas the latter has dimorphic fronds and occurs in the state of Amazonas (100 m).

Other studies focused on cytological and palynological aspects of *Salpichlaena*. Walker (1973) determined a chromosome number $X=40$ for this genus, the highest recorded in Blechnaceae. The structure of the spore wall of *S. volubilis* was described by Tryon and Lugardon (1991) as papillate-rugulate, with scattered spherules on the surface and in section with a plain exospore and a laminate perispore. They considered the spore wall characteristics to be useful in distinguishing *Salpichlaena* from other Blechnaceae.

A comprehensive work including the analyses of morphological, anatomical and palynological aspects of *Salpichlaena* across its range is lacking. Thus the aim of this study is to provide a systematic revision of *Salpichlaena* in order to contribute to the knowledge of the fern biodiversity in the Americas.

MATERIALS AND METHODS

Nearly 500 specimens from F, GH, LP, NY, P, SI and SP were analyzed during this study. Type specimens and the original descriptions were consulted to determine application of names. Vegetative as well as reproductive characters were analyzed and included: rhizomes, fronds, rachis, petiolules, pinnules, indument, indusia and spores.

For light microscopy observations (LM) the herbarium material was rehydrated with soft cold water-detergent then dehydrated through an ethanol series and embedded in Paraplast. Sections 8–12 μm thick were stained with safranin-fast green. Material was also cut employing a cryotome at 20 μm thickness and stained with safranin.

For scanning electron microscope (SEM) analysis of the spores, material was treated with hot 3% sodium carbonate for two minutes to preserve the perispore, then cleaned with distilled water and transferred to ethanol (Morbelli, 1980). Specimens were placed on acetate plates and sputter coated with gold-palladium. Observations were made using a JEOL, JSM-35 CF, SEM of "Servicio de Microscopía Electrónica de Barrido", Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

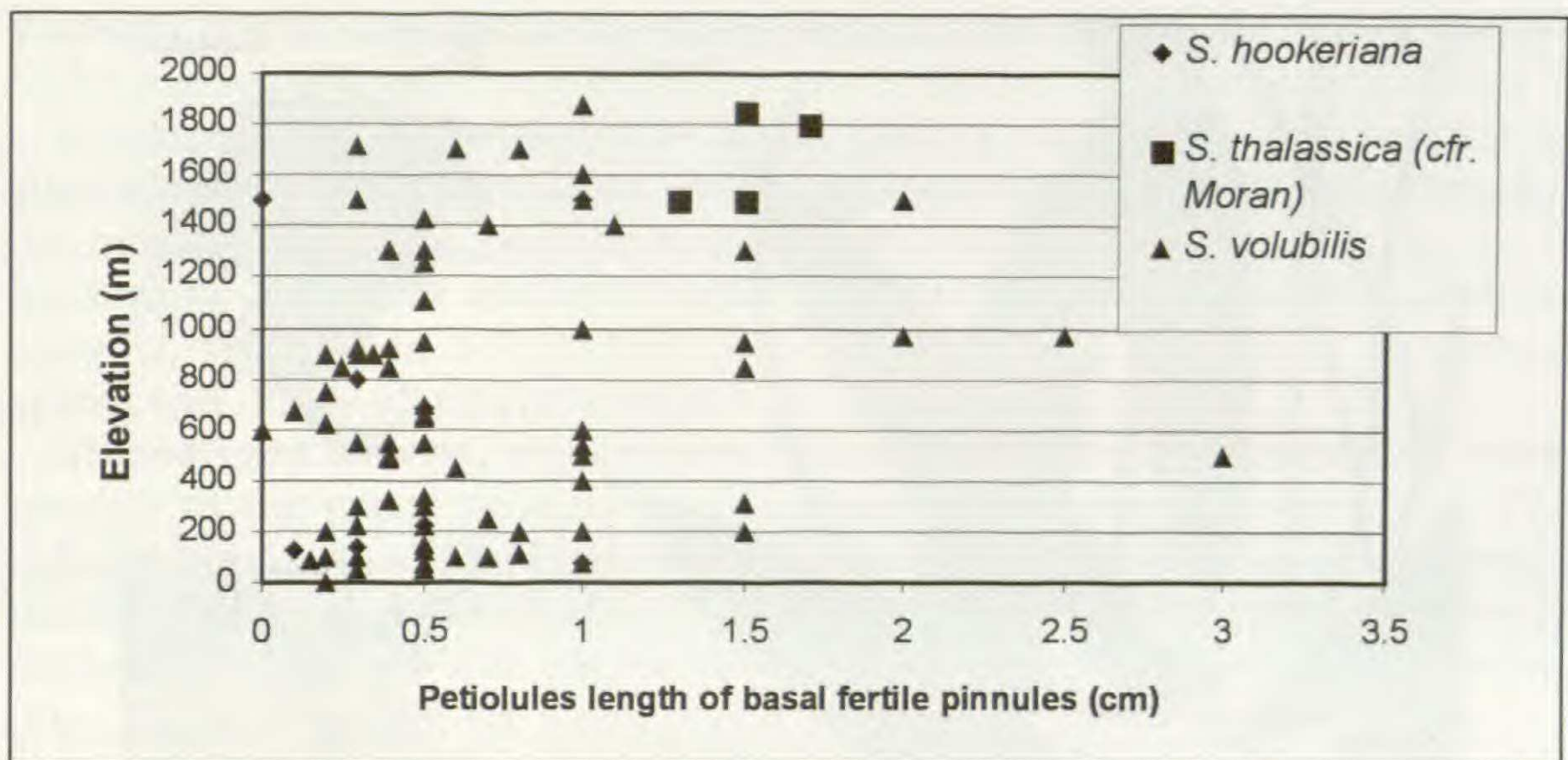


FIG. 1. Two-dimensional plot of length of the petiolules of the basal fertile pinnules related with the altitude at which the plants grow.

A distribution map based on herbarium specimens and the bibliographic data was produced.

RESULTS AND DISCUSSION

Analyzing specimens from Costa Rica and Panama, Moran (1990) described *Salpichlaena thalassica* as a new species on the basis of the correlation between the stalk length of the basal fertile pinnule and the elevation at which the plant grew. In the present work, we expanded the scope of the study and found a complete overlap of these features with those of *S. volubilis* (Fig. 1). For this reason we do not consider the ratio of altitude to stalk length a diagnostic character to distinguish *S. thalassica* from *S. volubilis*. In the same work, Moran (1990) mentioned that *S. thalassica* has blue-green colored pinnules whereas *S. volubilis* possesses dark-green ones. However, Murillo (2001) stated that the color of the fronds varied in *Salpichlaena* based on the area in which it grows, thus rejecting this characteristic as diagnostic. As our study was based on herbarium material we were not able to make definitive color observations.

We recognize the presence of foliar buds and the reduction of the fertile pinnules in *Salpichlaena hookeriana* as diagnostic characters to differentiate this species from *S. volubilis*, which has not foliar buds and their fertile pinnules are wider than the sterile pinnules. These characters were also observed by Alston (1932) and Smith (1995). Based on our observations, we are in disagreement with Murillo (2001) who considered these features as variations in the phenotypic expression due to changes in the environmental conditions. According to our observations the “geotypes” proposed by

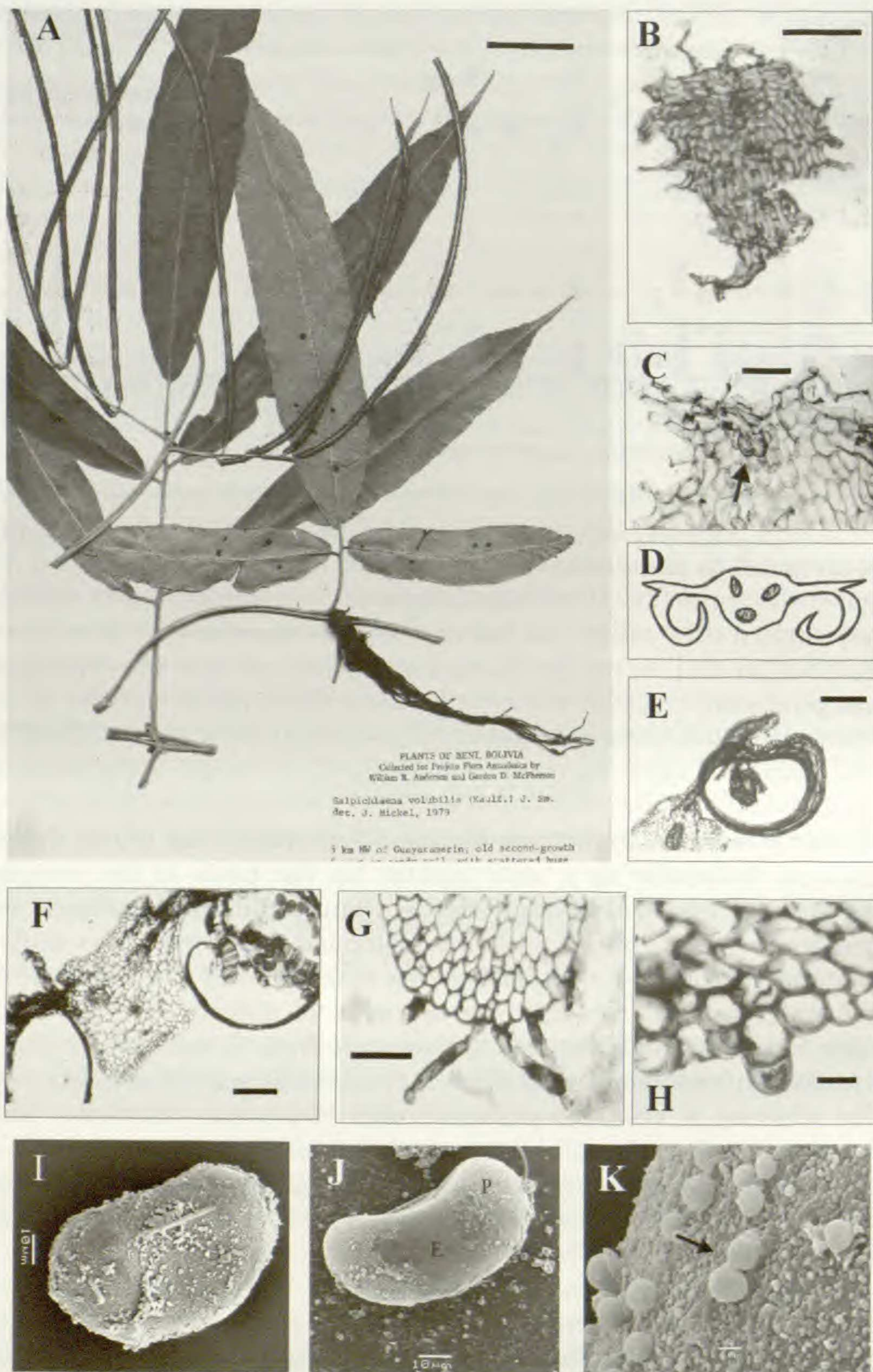


FIG. 2. *Salpichlaena hookeriana*. A. Representative herbarium sample. B. An ovate costular scale with attenuated apex and dentate-glandular margin. C. Portion of scale base that shows the foot cells (arrow). D–H: fertile pinnule. D. Outline of transverse section showing extremely reduced laminae. E. Margin in detail with sporangia and indusium. F. Transverse section with a marked costa. G and H. Details of the abaxial surfaces that show glandular, 2–3 cellular hairs. I–K: SEM

Vareschi (1969) concerning the foliar dimorphism correspond to the species *Salpichlaena volubilis* ("euvolubilis") and *S. hookeriana* ("maegdefrauiana").

Salpichlaena hookeriana also differs from *S. volubilis* by the presence of glandular hairs on the pinnules, which are absent in *S. volubilis*. Additionally, the morphology of the costular scales differs between the two species. In *S. hookeriana* the scales are ovate, with attenuate apices and dentate-glandular margins, whereas in *S. volubilis* they are lanceolate, with long attenuated apices and ciliate-glandular margin.

All analyzed material showed two linear coenosori on the comisural veins parallel to the costa, protected by elongate indusia open to the costa. The indusia were 1–4-cellular layers thick. The number of layers decreased toward the distal portion of the indusia. The cells of the outermost layer had unevenly thickened walls and take part in the indusial fragmentation at the maturity. (Fig. 2, E, F; Fig. 3, E, G).

We consider spore characteristics insufficient to differentiate among species within this genus. However, they are useful in distinguishing *Salpichlaena* from other Blechnaceae genera because species of *Salpichlaena* have a poorly developed perispore (apparently one-layered in section) and a granulate-papillate-rugulated surface, whereas other Blechnaceae have a complex perispore that is psilate and generally folded. The spherical bodies observed on the spore surface are "spherules" composed of perispore material (cf. Tryon and Lugardon, 1991, p. 9).

According to our observations two taxa of *Salpichlaena* are distinguishable based on foliar dimorphism, the morphology of the costular scales, the presence/absence of glandular hairs on the pinnules and the presence/absence of foliar buds on the sterile basal pinnules.

SYSTEMATIC TREATMENT

***Salpichlaena* J. Sm.** in Hook. Gen. Fil. T.93.1841

Salpichlaena volubilis (Kaulf.) J. Sm., in Hook., Gen. Fil., t.93.1841

Blechnum volubile Kaulf., Enum. Fil. 159. 1824

Rhizomes long-creeping and scaly, scales dark-brown to blackish, basipeltate, margins entire. *Fronde*s bi-pinnate, to ca. 15 m, pinnae dimorphic, the fertile pinnules narrower than the sterile ones. *Rachis* climbing to 15 m in

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micrographs of spores. I. Monoletic spore in proximal view. J. Spore in equatorial view. Smooth exospore (E) below abraded perispore (P). K. Surface details with granulate-papillae-rugulate sculpture and spherules (arrow). Scale bars: A: 3 cm. B, E and F: 200 μ m. C, G and H: 50 μ m. I and J: 10 μ m. K: 1 μ m.

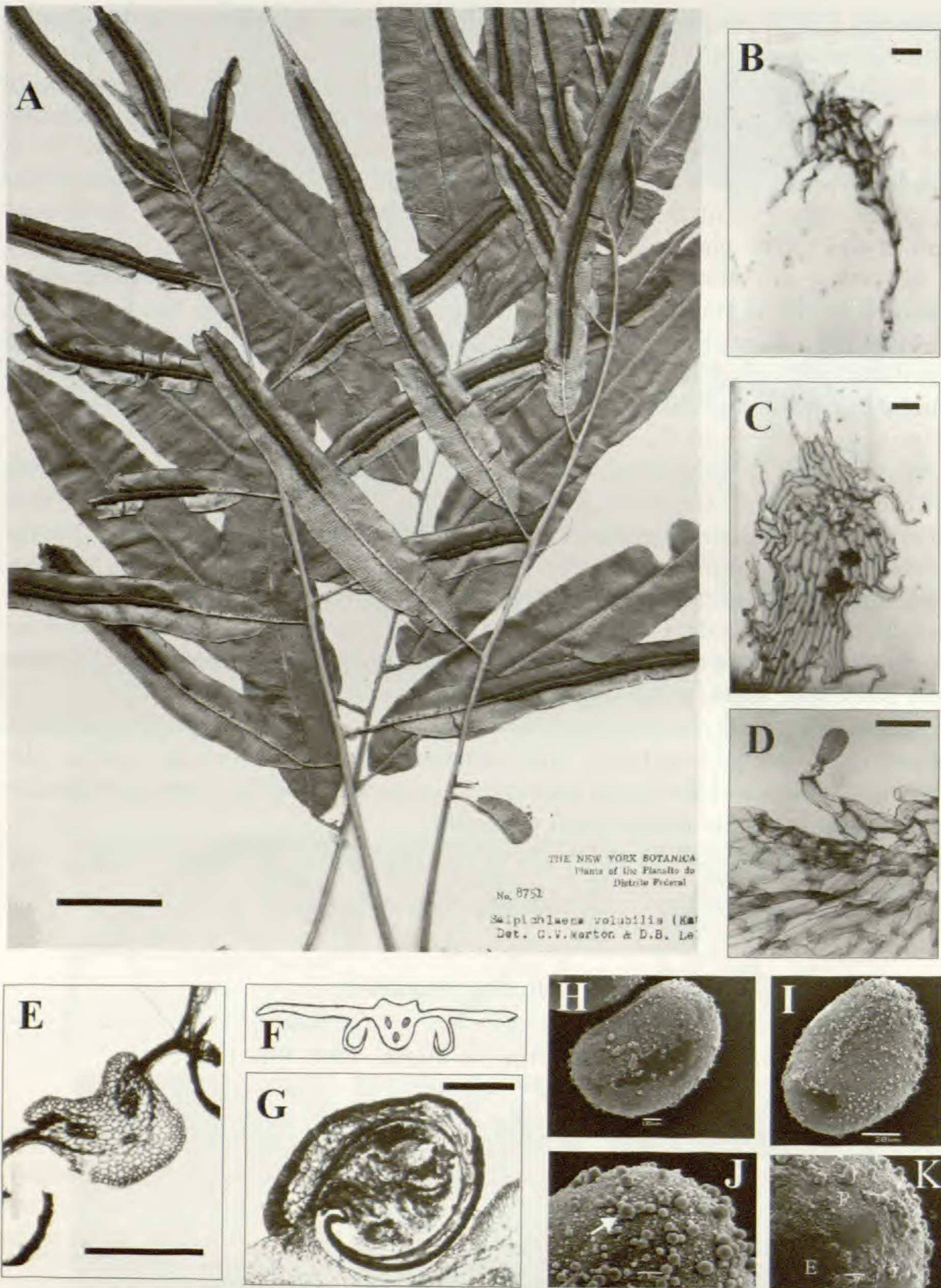


FIG. 3. *Salpichlaena volubilis*. A. Representative herbarium sample. B–D. LM micrographs of scales. Lanceolate costular scales with largely attenuated apex and ciliate-glandular margin. C. Scale base and margins in detail. D. Scale margins that show a glandular hair. E–G: fertile pinnulae in transverse section. E. Detail of pinnulae at the costa. F. Outline showing laminae expansion. G. Detail of multilayered indusium, the outermost layer shows cells with thicker walls. H–K. SEM



FIG. 4. Distribution map of *Salpichlaena hookeriana* and *Salpichlaena volubilis*.

micrographs of spores. H. Monolete spore in equatorial view. I. Spore in proximal view. J and K. Spore surface details that show a granulate-papillae-rugulate sculpture and spherules (arrow). K. A smooth exospore (E) below abraded perispore (P) is evident. Scale bars: A: 3 cm. B and C: 100 μ m. D, E and G: 0.5 cm. H: 10 μ m, I: 20 μ m. J and K: 5 μ m.

trees, twining with occasional scales similar to those of the lamina. *Pinnules* linear-elliptic to linear-lanceolate, bases asymmetric, cordate to roundish, apex acuminate to attenuate. *Veins* simple or proximally once forked. *Lamina scales* present on the costa abaxially, light brown to yellowish, deciduous, basipeltate; glandular, 2–3-celled hairs, present along the costa abaxially. *Foliar buds* absent or present at the bases of basal pinnules of trophophylls. *Cenosori* linear, positioned on the comisural veins parallel to the costa, covered by elongate indusia open to the costa; paraphyses absent. *Spores* monolet, plane-concave in equatorial view and elliptic in polar view; equatorial diameter 67.5 (78.9) 97.2 μm and polar diameter 48.6 (55.43) 70.2 μm ; laesura 25–43 μm long, tenuimarginate, scarcely evident; exospore 2–3.5 μm thick, to 5.5 μm along the proximal face, smooth, apparently two-layered, inner: outer exospore ratio, 1:2; perispore 1–1.4 μm thick, apparently one-layered in section, easily detached from the exospore, granulate-papillae-rugulate sculpture and with superficial spherules isolated or grouped.

KEY TO THE SPECIES OF *SALPICHLAENA*

- Fertile pinnules reduced, 14–40 cm long, 0.2–1.5 cm wide; foliar buds in axils of sterile basal pinnules; costal hairs abaxial, glandular, 2–3 celled; costal scales ovate, with attenuate apices and dentate-glandular margins. ***S. hookeriana***
 Fertile pinnules not reduced, 11–35 cm long, 0.5–3 cm wide; foliar buds absent; costal hairs absent; costal scales lanceolate, with long attenuated apices and ciliate-glandular margin. . . ***S. volubilis***

***S. hookeriana* (Fig. 2)**

Spicanta hookeriana Kuntze, Rev. Gen. Pl. 2: 821. 1891. ***Salpichlaena hookeriana* (Kuntze) Alston**, Bull. Misc. Inform. 1932: 312. 1932.

Lomaria volubilis Hook. Sp. Fil 399, t. 150. 1860. Isotype: Brasil, Barra by Igarapé dos Manaõs, *Spruce 1263* (P 347482). Feb. 1857!

Blechnum volubile var. *lomarioide* Baker in Mart. Fl. Bras. 1 (2): 428. 1870.
Salpichlaena lomarioidea (Baker) A. R. Smith, Ann. Missouri Bot. Gard. 77: 250. 1990

Rhizomes long-creeping, scales dark-brown to blackish, basipeltate, margins entire. *Fronde* bi-pinnate, ca. 15 m. *Fronde* dimorphic, fertile pinnules extremely reduced, 14–40 cm long, 0.2–1.5 cm wide. *Foliar buds* on sterile basal pinnules; *hairs* along abaxial surface of the costa, glandular 2–3 celled; scales along costa abaxially, light brown to yellowish, basipeltate, ovate, apex attenuate, margin dentate-glandular. *Coenosori* paired on the comisural veins parallel to the costa, covered by elongated indusia open to the costa. *Spores* monolet, granulate-papillae-rugulate sculpture.

Salpichlaena hookeriana grows from Colombia, Venezuelan Guyana, Suriname, British Guiana and northern Brazil to Peru and Bolivia, at altitudes up to 800 m (Fig. 4).

Note: *Salpichlaena hookeriana* is a combination proposed by Alston in 1932, taking into account the species *Spicanta hookeriana* as a basionym. *Spicanta hookeriana* was cited for the first time in 1891 by Kuntze as synonymus of *Lomaria volubilis*. The type specimen of *Spicanta hookeriana* was never established. Thus we consider that the type of *Salpichlaena hookeriana* correspond to the type specimen of *Lomaria volubilis*: Isotype: Brasil, Barra by Igarapé dos Manaões, Spruce 1263 (P 347482), Feb. 1857.

***S. volubilis* (Fig. 3)**

Blechnum volubile Kaulf., Enum Filic. 159. 1824. ***Salpichlaena volubilis* (Kaulf.) J.Sm.** in Hook., Gen. Fil. t. 93. 1841. TYPE.—BRAZIL, Chamisso s.n. (HT, LZ—destroyed).

Blechnum scandens Bory, Dup. Voy. Bot. 1. 272 t. 36. 1828. *Salpichlaena scandens* (Bory) C. Presl, Epim. bot. 122. 1849. TYPE.—ST. CATHERINE DU BRASIL, Durville s/n, 1827 (Coquille n° 92, P 347471!).

Salpichlaena thalassica Grayum & R.C. Moran, Ann. Missouri Bot. Gard. 77:591. 1990. TYPE.—COSTA RICA: Heredia: forest between Río Peje and Sardinalito, Atlantic slope of Volcán Barba, 10° 17' N, 84° 4.5' W. 800–1000 m, Grayum & Chazdon 6833 (MO).

Rhizomes long-creeping, scales dark-brown to blackish, basipeltate, margins entire. *Fronde* bi-pinnate, ca. 15 m. *Fronde* dimorphic, fertile pinnules 11–35 cm long, 0.5–3 cm wide. *Foliar buds* and glandular *hairs* absent, scales along costa abaxially, lanceolate, largely attenuated apex, margin ciliate-glandular. *Coenosori* paired on the comisural veins parallel to the costa, covered by elongated indusia open to the costa. Spores monoletate with granulate-papillae-rugulate sculpture.

Salpichlaena volubilis is widely distributed in Central and South America, from Guatemala and the Caribbean Islands, to southern Brazil and Bolivia, across a wide elevation range, 200 m to 1900 m (Fig. 4).

Salpichlaena hookeriana

SPECIMENS EXAMINED.—VENEZUELA: Depto Amazonas, Alto Río Orinoco, 125 m s. m., Maguire, Wurdack & Keith 41477 (F); Cerro Paráque Sipapo, Maguire & Politi 28776 (F); Depto Atures, 9 km por arriba del Raudal Remo. 04° 34' N, 67° 18' W. 120 m. Foldats & Velazco 9542 (NY). BRITISH GUIANA: Región Potaro-Siparuni, Pakaraima Mts., Mutchnick, Henkel & Williams 240 (NY), Tumatumari, Potaro River, 5° 20' N. A.S. Hitchcock 17374 (NY). COLOMBIA: Depto

Amazonas, Vaupes, Río Apaporis, 800 feet m, 0° 5' S, 70° 30' W, *Schultes & Cabrera 15410* (NY), Vaupes, Río Piraparaná, 0°15'S, 70° 30' W, *Schultes & Cabrera 17449* (GH); Depto Vichada, alrededores de "Gaviotas", Caño Urimaca, 130–160 m, *Murillo 1582* (P). PERU: Depto Loreto, Río Nanay, Shiriara, *Plowman 2550* (GH, F). BOLIVIA: Depto Beni, 5 km NW of Guayaramerin, *Anderson 11824* (F). BRAZIL: Edo Amazonas, Río Xié, 0° 55' N, 67° 15' W, *Stevenson, Daly & Guede 815* (NY); Municipio de Humaitá, Porto Velho km 60, 8° S, 63° W, *Teixeira, Fife, Mc Farland, Mota, dos Santos, Gomes & Nelson 208* (NY); Manaus, Reserva Forestal Ducke, 26. 02° 53' S, 59° 58' W, *Assunção 385* (NY), San Antonio, *de la Sota 2458 A* (LIL); Reserva Forestal Ducke, Manaus-Itacoatiara, 02° 53'S, 59° 58'W, *Ribeiro 1025 et al.* (SP), Alto Amazonas, Ex. Herb. *Schwacke 4110* (P 347479), Igarapé, *Drake 1263* (P 347482).

Salpichlaena volubilis

SPECIMENS EXAMINED.—HONDURAS: Depto Yoro, Río Guán Guán, 300–380 m, 15° 30' 00" N, 87° 27' 20" W, *Hawkins & Merello 820* (NY). NICARAGUA: Depto Zelaya, Bluefields, *Nichols 893* (GH); Cano Costa Riquita, 11° 43' N, 84° 18' W, 150–180 m, *Stevens & Krukoff 4959* (LP). COSTA RICA: Pcia Alajuela, 20 km NW of San Ramón, 10° 13' N, 84° 32' W, 850 msm, *Smith, Béliz, Grayum, Dickie & Carvajal 2239* (NY); San Ramón, 1000 m, *Mickel 2927* (LP); Idem, *de la Sota 5155* (LP); Pcia Cartago, Cantón de Paraíso, Valle del Reventazón, 09° 44' 40" N, 83° 50' 00" W, 1700–2000 m, *Rojas, Jiménez & Aguilar 2462* (NY); Mountains 5 miles S of Cartago, 1800 m s. m. *Maxon 512* (NY); 9° 42' N, 83° 47' W, 1500 m, *Burger & Liesner 6807* (NY); Refugio Nacional de Fauna Silvestre Tapanti, 1500–1620 m, *Almeda, Anderson & Zamora 5736* (NY); Valle of Río Grande del Oro, *Tryon & Tryon 7028* (GH); Pcia Heredia: Finca La Selva, *Grayum 1822* (NY); E de Puerto Viejo, *R.K. Godfrey 67300* (GH); Pcia Limón, Lomas de Sierpe, 10° 22' N, 83° 31' W, *Robles 2198* (NY); Pcia Puntarenas, San Vito, 1500 m *de la Sota 5217* (LP); Pcia San José, Vicinity of El General, 915 m, *A.F. Skutch 2166* (GH); Los Angeles de Siquirres, 1000 m, *Gómez, Liesner & Judziewicz 20541* (LP). PANAMA: Pcia Chiriqui, 8° 43' N, 82° 14' W, 1300 m., *Hampshire & Whitefoord 370* (NY); Pcia Coclé, 600 m, 8° 45' N, 80° 30' W, *Hamilton & Davidse 2806* (LP); Pcia Colón, 10 m SW of Puertobelo, 10–200 m., *Liesner 1106* (P); Pcia Panama, Cerro Campana, *Croat 14755* (NY); Idem, 900 m, *Madison 768* (GH); Pcia Veraguas, Distrito de Montijo, Isla Coiba, Playa Hermosa, *Aráuz 455 et al.* (NY). GUADALUPE: Base-Terre, forêt de Choisy, *Barrier 2356* (NY); Moscou district, south of La Citerne, 650–660 m, *Proctor 20130* (GH); trace Víctor Hugues au départ de Montebello, *Barrier 2885* (P); Forêt de Sofaïa, *Rodriguez 4257* (P). DOMINICAN REPUBLIC: Concorde Valley, moist forests bordering Pegoua River in vicinity of Deux Branches, *Hodge 3482* (GH); Rainforest bordering Imperial Road, Sylvania to Mahaut River, 459 m., *Hodge 98* (GH). MARTINICA: St. Joseph, 450–660 m, *Duss 1901* (NY). SANTA LUCIA : Barre de L' Isle Ridge, 800–1400 feet, *Webster, Ellis & Miller 9285* (GH); Forest between Quillesse and head of Muray Hill Road,

Howard 11691 (GH, P). TRINIDAD: Arima Valley, North Range, Forestry Trail, 600 m, *Cowan & Simmonds 1202* (P); Crest of Northern Range, between Arima-Blanchisseuse Road and Morne Bleu. 600–750 m, *Smith 10043* (LP); Morne Bleu ridge, from Textel station to Morne Bleu peak, 2400–2700 feet, *Mickel 9500* (NY); Tobago, Roxborough Road, West Indies, *Andrews 821* (NY); Tacarigua Ward, Las Lapas Road, *Walker 10831* (NY); West Indies, Banks of Marianne River, ca. 20 ¼ mile post on Arima – Blanchisseuse road, *Kennedy & Cope 1716* (NY). VENEZUELA: Edo Aragua, Cordillera Interior. 10° 11' N, 67° 15' W. 1400–1500 m, *Steyermark & Stoddart 118072* (GH); Edo Bolívar, Selvas ribereñas del Río Caura, 4° 44' N, 64° 01' W. *B. Stergios 12098* (NY). Edo. Mérida, Guayana Venezolana. En selva pluvial al SE de Santa Elena, 900 m, *Bernardi 6759* (NY). COLOMBIA: Depto Antioquia, Municipio San Carlos, 6° 05' N, 74° 52' W. 880–920 m, *Callejas, Roldán & Castaño 8571* (NY); Depto Chocó, Carretera Quibdó-Guayabal, orillas del Río Duatá, *Forero, Jaramillo & Mc Elroy 1227* (NY); Hoya del Río San Juan, Quebrada Taparal, 4° 12' N, 77° 10' W, *Forero, Jaramillo, Forero & Hernández 4271* (GH); Baudó, *Fuchs & Zanella 21894* (F); Valle Río Calima, *Cuatrecasas 16579* (F); Depto Magdalena, Sierra Nevada d Alto Río Buritaca, 11° 05' N, 73° 48' W, 1100–1500 m, *Madriñán & Barbosa 303* (GH); Sierra Nevada de Santa Marta. 1500 m, *Jaramill, van der Haumen, Cleef & Rangel 5204* (P); Depto Meta, Cordillera La Macarena. 1300–1900 m, *Idrobo & Schultes 971* (GH); La Serranía. 320 m, *Cuatrecasas 7871* (F); Depto Nariño, Ricaurte, 1300 m, *von Sneidern 603* (GH); Depto Santander, km 16 between Puerto Wilches and Puerto Santos, 110–115 m, *Killip & Smith 14831* (NY). ECUADOR: Pcia Carchi, Awá Indigenous Territory, Community of Baboso, 00° 55' N, 78° 25' W. 990 m s. m., *Ortiz et al. 535* (NY); Maldonado, 1500 m, *Werling & Leth-Nissen 428 A* (F); Pcia Esmeraldas, Parroquia de Concepción, Playa Rica. 105 m, *Mexia 8426* (GH, LIL); Idem, *Sodiro s/n* (SI 23160); Pcia Imbabura, Río Verde, 1700–1740 m, 0° 46' N, 78° 28' W, *Sperling & Bleiweiss 5068* (GH); Pcia Napo, Reserva Biológica Jatun Sacha, Río Napo, 04° S, 77° 36' W. 450 m, *Cerón 580* (NY); Cantón Archidona, Reserva Ecológica Antisana, 00° 44' S, 77° 48' W. 1700 m, *Clark, Narvaez & Mamallacta 5288* (NY); Río Payamino, 350 m, 0° 29' S, 77° 12' W, *Holm-Nielsen & Jeppsen 798* (GH); Cantón Napo. 400 m, *Mexía 7175* (F); Pcia Pastaza, Shell-Mera rainforest, 1° 29' S, 78° 3' W. 1050 m s m., *Holm-Nielsen & Jeppsen 445* (GH); Pcia Pichincha, Reserva Forestal ENDESA, Río Silanche, 00° 05' N, 79° 02' W. 650–700 m, *Jaramillo 7016* (NY), Pcia Santiago-Zamora, Gualaquiza, 03° 24' S, 78° 34' W. 1100 m, *Fay 4149* (NY). BRITISH GUIANA: Región Essequibo, Takutu 240 m, 01° 21' 33" N, 58° 46' 22" W, *Clarke 2795* (NY); Mazaruni. 1300 m, 05° 49' 30" N, 61° 11' 40" W, *Clarke, Hollowell, David, Chin & Perry 5530* (NY). FRENCH GUIANA: Basin du Sinnamary, Camp. Eugène, 70 m s. m. 4° 51' N, 53° 4' W, *Cremers & De Granville 13622* (P); Idem, Herb. *Leprieur 120* (GH); Saül, 4° 38' N, 52° 55' W, *Hoff 6897* (NY). PERU: Depto Loreto, Sierra del Pongo, 700 m, *Mexia 6276* (GH); Pcia Maynas, Río Nanay near Iquitos, *Tryon & Tryon 5178* (GH). BOLIVIA: Depto Cochabamba, Pcia Chapare, San Onofre. 1700 m, *Steinbach 9411* (GH). BRAZIL: Distrito Federal. 950 m, *Irwin, Souza & Reis dos Santos 8751* (F, P). Edo Amazonas, Río Amazonas, 1 km

below mouth of Río Negro, *Conant 930* (GH). Edo Bahía, Municipio Ilhéus, *Thomas, Mattos Silva, dos Santos, Amorim, Jardim & Sant' Ana 10717* (NY); Edo Goiás, Serra dos Pirineus. 975 m, *Irwin, Souza & Reis dos Santos 10803* (SP); Edo Maranhão, Isla São Luiz, *Froes 11922* (LIL); Edo. Mato Grosso, c. 270 km N of Xavantina, *R. de Santos, Andrelinho & Ratter 1508* (NY); Serra Ricardo Franco. 800–900 m, *Windisch 1391* (GH); Expedition Base Camp: 12° 49'S, 51° 46'W, *Harley & Souza 10051* (P); Edo Minas Gerais, Hermilo Alves, Corrego do Caetano, 1100 m, *Duarte 2413* (GH); Edo Pará, Municipio de Itaituba, Serra do Cachimbo, *Amaral, Silva, Monteiro, Lima, Brako, Reese & Dibben 1083* (NY). Edo Paraná, Municipio de Guaraqueçaba, Morro do Río das Pacas, *Prado 479* (NY); Serra do Mar, Porto de Cima, c. 200 m., *Dusén 14134* (GH); Antonina. 50 m, *Kramer & Hatschbach 10811* (F); Edo Santa Catarina, Nova Trento, *Sehnem 795* (GH); Azambuja, Brusque, *Reitz 3722* (SI); Idem, *Durville 1827* (Coquille N° 92, P 347471); Edo São Paulo, parque estadual das Fontes do Ipiranga, *Rosa & Pires 3988* (NY); Edo São Paulo, Río Grande, *Rosenstock 192* (SI); Municipio de Cananéia, Ilha do Cardoso, *Tosta Silva 56* (SP).

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