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Novelties and notes in *Lindsaea* (Lindsaeaceae) from Mexico and Central America

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Abstract

Three new species of *Lindsaea* are described and illustrated from Mesoamerica: *L. angustipinna*, *L. fuscopetiolata* and *L. mesoamericana*. Additionally, the status of *L. quadrangularis* subsp. *subalata* is modified to *L. subalata* and *Lindsaea horizontalis* and *L. moritziana* Klotzsch are reinstated as valid species. New records of *L. cubensis*, *L. divaricata*, *L. horizontalis* and *L. leprieurii* are reported from several countries in the area. A key to the species of *Lindsaea* in Mexico and Central America is provided.

Key words: Mesoamerica, new species, new combinations, new records, Polypodiopsida

Resumen

Se describen e ilustran tres especies nuevas de *Lindsaea* para Mesoamérica: *Lindsaea angustipinna*, *L. fuscopetiolata* y *L. mesoamericana*. También *Lindsaea horizontalis* y *L. moritziana* son aquí reconocidas como especies válidas y *L. quadrangularis* subsp. *subalata* es elevada de rango como especie. Además, *L. cubensis*, *L. divaricata*, *L. horizontalis* y *L. leprieurii* son registradas para algunos países en la región, generalmente a partir de nuevas recolectas. Finalmente, se ofrece una clave para separar las especies del género presentes en el área de estudio.

Palabras clave: Mesoamérica, nuevas especies, nuevas combinaciones, nuevos registros, clave taxonómica, Polypodiopsida

Introduction

The species now known as *Lindsaea* (*Lindsay*) Dryander ex Smith (1793: 413) were previously included with *Adiantum* Linnaeus (1753: 1094) or *Pteris* Linnaeus (1753: 1073), but they were segregated by Dryander (1797: 39) based on its peculiar sori, that are elongate, continuous and parallel to the margin, and the indusia opening toward the outside margin. Although classification of the genus has been somewhat contentious in the past (Kramer, 1957b; Lehtonen et al., 2010), most modern classifications place it in the Lindsaeaceae (Smith et al., 2006 and Christenhusz et al., 2011). This new concept includes seven genera (*Lindsaea*, *Nesolindsaea* Lehtonen & Christenhusz (in Lehtonen et al. 2010: 336–337), *Odontosoria* Fée (1852: 325), *Osmolindsaea* (Kramer 1967: 560) Lehtonen & Christenhusz (in Lehtonen et al. 2010: 336–337), *Sphenomeris* Maxon (1913: 144), *Tapeinidium* (Presl 1851.) Christensen (1906: 631) and *Xyropteris* Kramer (1957b: 599)). Just three of these genera have Neotropical representatives (*Lindsaea*, *Odontosoria* and *Sphenomeris*) (Kramer, 1957a). Dryander (1797) included ten species in his description of *Lindsaea*. More species were added by several authors (e.g. Klotzsch 1844, Fée 1852), but Kramer (1957a, 1967, 1970, 1972a, 1972b, 1976) wrote a series of regional revisions of the Old and New World Lindsaeoid ferns centering around of the *Lindsaea* genus and putting taxonomic order. The American species (found principally in clade XIII of Lehtonen et al., 2010) are genetically similar and apparently recently diverged. However, morphological characteristics such as leaf architecture are usually sufficient to allow good diagnosis (Kramer 1957a, Moran 1995). Kramer (1957a) monographed *Lindsaea* for the Neotropics and resolved several taxonomic and nomenclatural problems, but some inconsistencies

remain, especially among the Mesoamerican species. For example, Kramer (1957a) considered *Lindsaea moritziana* Klotzsch (1844: 548) to be a form of *L. stricta* (Swartz (1788: 135)) Dryander (1797: 42) var. *stricta*, whereas Moran (1995) included it as a synonym of *L. stricta* var. *stricta* and Mickel & Smith (2004) treated it as *L. quadrangularis* subsp. *mexiae* Mickel (*in* Mickel & Smith 2004: 367). Kramer (1957a: 240) recognized some infra-specific taxa in *Lindsaea lancea* (Linnaeus (1763: 1557)) Beddome (1876: 6), that molecular data resolved as polyphyletic (Lehtonen *et al.* 2010); this aspect indicates that these infra-specific taxa may actually be distinct species.

Lindsaea is a pantropical genus with ca. 200 species (Lehtonen *et al.*, 2010). In tropical America, Kramer (1957a) noted the presence of 17 taxa, seven of which are in the northern part of South America. In turn Moran (1995) indicated that in Mesoamerica (from Chiapas, Mexico to Panama) ten taxa are present. Unlike Kramer (1957), recognizes the presence of *Lindsaea taeniata* Kramer (1957a: 208) in Costa Rica and Panama (= *L. venustissima* Gómez (1982: 475)) and indicates that *L. portoricensis* is a synonym for *L. stricta*. Mickel & Smith (2004) recognized four species in Mexico and described a new subspecies (*L. quadrangularis* subsp. *mexiae*).

The aim of this study is to present new taxa, resolve names and note new distributions in *Lindsaea* for Mesoamerica (tropics of Mexico to Panama). This taxonomic improvement is the result of regional revisions for the families Dennstaedtiaceae, Lindsaeaceae and Saccolomataceae (e. g. Flora de Costa Rica, Flora del Bajío and Flora de Jalisco, Mexico).

Materials and methods

The new taxa and new records here are the result of comparisons with specimens of other Mexican and Central American species, and a review of related species and keys from the Neotropics by Kramer (1957a), Gómez & Arbeláez (2009), Moran (1995), Mickel & Smith (2004), Murillo *et al.* (2008), Smith (1989) and Tryon & Stolze (1989). The examined specimens are deposited in the following herbaria CHAPA, CR, EAP, ENCB, FCMEX, IEB, K, MEXU, MO, UAMIZ, USJ, XAL (acronyms following Thiers 2016). To ensure the correct application names, we examined original type material or digital type images as available (Jstor Global Plants (<http://plants.jstor.org/>)). It is important to consider that species of *Lindsaea* are somewhat difficult to define, especially by the uniformity of rhizome scales, the absence of indumenta in the blade surfaces and the more or less similar form of the last laminar segments. Thus, we took great care to consider all morphological characters in distinguishing species. Most of these morphological features were considered by Kramer (1957a) and Lehtonen *et al.* (2010), such as the coloring and cross-sectional geometry of stipe, the architecture of blade or, the geometric shape and size correlation between segments, and the type of laminar reduction in the apical part of the blade. In making our decisions, we also considered recent molecular phylogenetic data available for *Lindsaea* (Lehtonen *et al.* 2010).

Results

We recognize 17 species of *Lindsaea* in the tropical region of Mexico and Central America (Mesoamerica), including three new species (*Lindsaea angustipinna*, *L. fuscopetiolata*, and *L. mesoamericana*), four range extension (*Lindsaea cubensis*, *L. divaricata*, *L. horizontalis* and *L. leprieurii*) and three reinstated or elevated species (*Lindsaea horizontalis*, *L. moritziana* and *L. subalata*), and finally, two species are excluded from Mesoamerica (*L. falcata* and *L. quadrangularis*).

These are nine taxa more than Kramer (1957a) and seven more than Moran (1995) recognized for the study area. Of these, only *Lindsaea mesoamericana* can be considered as distributed throughout the region. In Mexico, we count eight species with *L. moritziana* having the northernmost (Jalisco) distribution and *L. mesoamericana* being the most common. In Central America, all Mesoamerican species can be found, but only three are endemic (*Lindsaea angustipinna*, *L. fuscopetiolata*, and *L. pratensis*), and one is a disjunct in the Antilles (*Lindsaea cubensis*). The rest of the other species also occur in northern South America (Venezuela and/or Colombia) or extend to south to Brazil.

As defined here, each taxon is more homogeneous regarding architectural characters of the fronds (e.g. petiole and rachises color, presence or absence of larger pinnate pinnae, shape of apical section, etc.) traditionally used *Lindsaea* taxonomy.

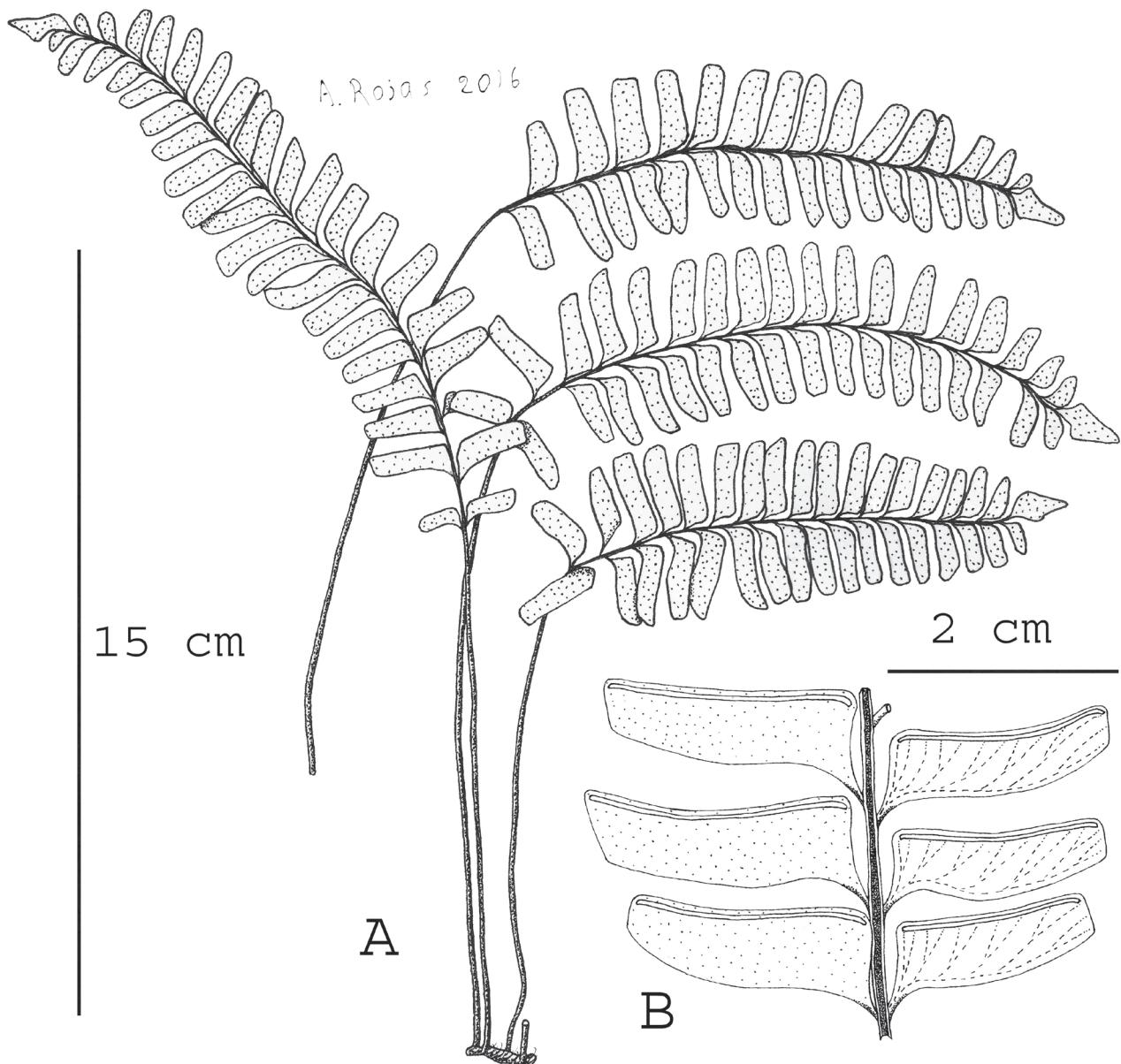


FIGURE 1. *Lindsaea angustipinna* (A. Rojas & G. Araya 7752, CR). A. General aspect of type specimen. B. Abaxial blade detail.

Taxonomic treatment

Lindsaea angustipinna A. Rojas & Tejero, sp. nov. (Fig. 1)

Lindsaea angustipinna is similar to *Lindsaea falcata* but differs in having trapezoidal (vs. falcate) pinnae with apices that are perpendicular to the rachis in the middle and ending portion (vs. arching down to apex). Additionally, the terminal pinnae are lanceolate (vs. ovate) and 2–3 times longer than wide (vs. 1–1.8 times in *L. falcata*).

Type:—COSTA RICA. Guanacaste: Liberia, Parque Nacional Guanacaste, sendero al volcán Cacao, parte alta, 10°55'58"N, 85°27'41"W, 350–1300m, 7 August 2007, A. Rojas & G. Araya 7752 (holotype CR!, isotypes MO!, USJ!).

Perennial terrestrial herb, rhizomes short-creeping, 1–2 mm in diameter, with fronds 1–3 (5) mm between them; rhizome scales 1–1.5 × 0.2–0.3 mm, dark brown to reddish-brown, entire, crisped in the middle portion; fronds 17–30 cm long, with vertical stipes, arching or inclined in the blades; stipes 9–21 cm long, at least the basal half atropurpleous; blades 9–19 × 2.5–4.3 cm, 1-pinnate, lanceolate-oblong to oblong; rachises stramineous or sometimes basally dark,

quadrangular, with stramineous wings; pinnae $1.2\text{--}2.1 \times 0.6\text{--}0.9$ cm, commonly 2.5–3.5 times longer than wide, (5–)13–20 pairs, trapezoidal, perpendicular to rachis, continuous to distant a half of pinna broad (rarely more distant at blade base), the apical segments 2–3 times longer than wide, hastate and lanceolate; sori continuous along acroscopic and distal sides of pinnules, indusia 0.2–0.3 mm broad, dark brown, entire to lobulate.

Distribution:—Mesoamerican endemic, actually known from Volcán Maderas in Nicaragua and Guanacaste and Tilarán mountains in Costa Rica at 1000–1350 m elevation.

Etymology:—The name refers to the characteristic narrow pinnae.

Additional specimens examined (paratypes):—NICARAGUA. Rivas: Isla de Ometepe, NW slope of volcán Maderas, to rim somewhat E of highest point, ca. $11^{\circ}26\text{--}27'N$, $85^{\circ}30\text{--}31'W$, 1000–1350 m, 24 February 1978, *W. Stevens & B. Krukoff* 6515 (CR!, MO).

COSTA RICA. Alajuela: San Ramón, Alto de La Palma, 1300 m, 30 November 1922, *A. Brenes* 3823 (129) (CR!), *ibidem*, *A. Brenes* 7147 (161) (CR!); *ibidem*, 10 October 1924, *A. Brenes* 7377 (4107) (CR!). Guanacaste: La Cruz, Santa Cecilia, ca. 5 km de la Estación Pitilla, fila Orosilito, camino del campamento a los nacientes del río Mena, $10^{\circ}58'35''N$, $85^{\circ}27'00''W$, 1100–1200 m, 7 April 2008, *A. Rojas* 8338 (CR!, USJ). Heredia: Barva, Transect Trail between Volcán Barva and Finca La Selva, $10^{\circ}16'34''N$, $84^{\circ}04'56''W$, 900 m, 2003, *J. Kluge* 3063 (CR).

Notes:—Specimens of this species have been previously identified as *Lindsaea lancea* or *L. arcuata*. *Lindsaea angustipinna* differs from *L. lancea* by stipes being at least in lower half atropurpureous (vs. completely stramineous), 1-pinnate (vs. 2-pinnate) blades and segments 2.5–3.5 times longer than wide (vs. 1.8–2.5 times). *Lindsaea angustipinna* is easy to separate from *L. arcuata*, besides the colour of the stipe, by the presence of an apical subconform segment in the blade (vs. apex gradually reduced). Furthermore, *L. angustipinna* differs from *L. mesoamericana* (here described) and *L. leprieurii* Hooker (1846: 208), by pinnae (= ultimate segments) that have straight basiscopic sides (vs. falcate or arching).

***Lindsaea fuscopetiolata* A.Rojas & Tejero, sp. nov.** (Fig. 2)

Lindsaea fuscopetiolata is similar to *L. divaricata* but differs in having an anadromic basal pinnule close to the primary rachis and the pinnae are therefore sessile (vs. petiolulate), blade apices that are pinnatifid with a very small terminal segment (vs. subconform, with a lanceolate, undulate, terminal segment), and more pinnules ((14–)20–32 pairs vs. 12–18(–26 pairs per pinna) that are sub-quadrangular (vs. rectangular) and 1.2–1.5 (vs. 2.0–2.6) times longer than wide.

Type:—COSTA RICA. Puntarenas: Buenos Aires, Parque Internacional La Amistad, cuenca Térraba-Sierpe, sabanas Esperanza y bosques aledaños, $09^{\circ}04'33''N$, $83^{\circ}01'45''W$, 1600–1700 m, 30 May 2006, *D. Santamaría et al.* 4411 (holotype CR!; isotype MO!).

Perennial terrestrial herbs, rhizomes short creeping, 1.5–2.5 mm in diameter, with fronds every 1–3 mm distant between them; rhizome scales 1–3 × 0.2–0.4 mm, linear, brown-yellowish to brown, entire; fronds (15–) 28–90 cm long, erect; stipes (3–)12–57 cm long, brown to atropurpureous, lustrous, not angulate and not winged abaxially; blade 2-pinnate, deltate to ovate; pinnae (4–)8–15 × 1.2–1.7 cm, (1)2–8 pairs, linear, oblique, sessile, broadly at base, apically pinnatifid or with a small attenuate segment, uniformly spaced and alternates along the rachis, the apical pinnae longer; pinnules 0.5–0.8 × 0.4–0.6 cm, 1.2–1.5 times longer than wide, (14–)20–32 pairs, ascending, dimidiate except the basal ones; sori continuous along acroscopic margin and distal sides of segments; indusia ca. 0.5 mm broad, stramineous, slightly crenate.

Distribution:—Endemic to Pacific side of cordilleras in Mesoamerica at 1000–2000 m.

Etymology:—The name of the new species refers to the brown stipes.

Additional specimens examined (paratypes):—MEXICO. Chiapas: Mpio. Ángel Albino Corzo, cerro El Triunfo, $15^{\circ}37'N$, $92^{\circ}48'W$, 2000 m, 18 February 1997, *M. Pérez* 1579 (MEXU!).

HONDURAS. Santa Barbara: above Lake Yojoa, El Sauce, 1000 m, 9 April 1951, *L. Williams & A. Molina* 17692 (EAP!).

COSTA RICA. Guanacaste: Bagaces, Guayabal, Zona Protectora Miravalles, mirador Los Sitios y orillas de quebrada en sabanas naturales, 1000–1100 m, 6 October 2012, *A. Rojas & J. Jiménez* 10358 (CR!, K!, MO!, USJ!). Puntarenas: Coto Brus, Cuenca Térraba-Sierpe, El Progreso, Finca Cafrosa, $8^{\circ}53'29''N$, $82^{\circ}45'53''W$, 1300 m, 15 September 1996, *E. Navarro* 458 (CR!).

PANAMA. Panamá: Cerro Azul, 14 July 1960, *J. Ebinger* 417 (EAP!, US!).

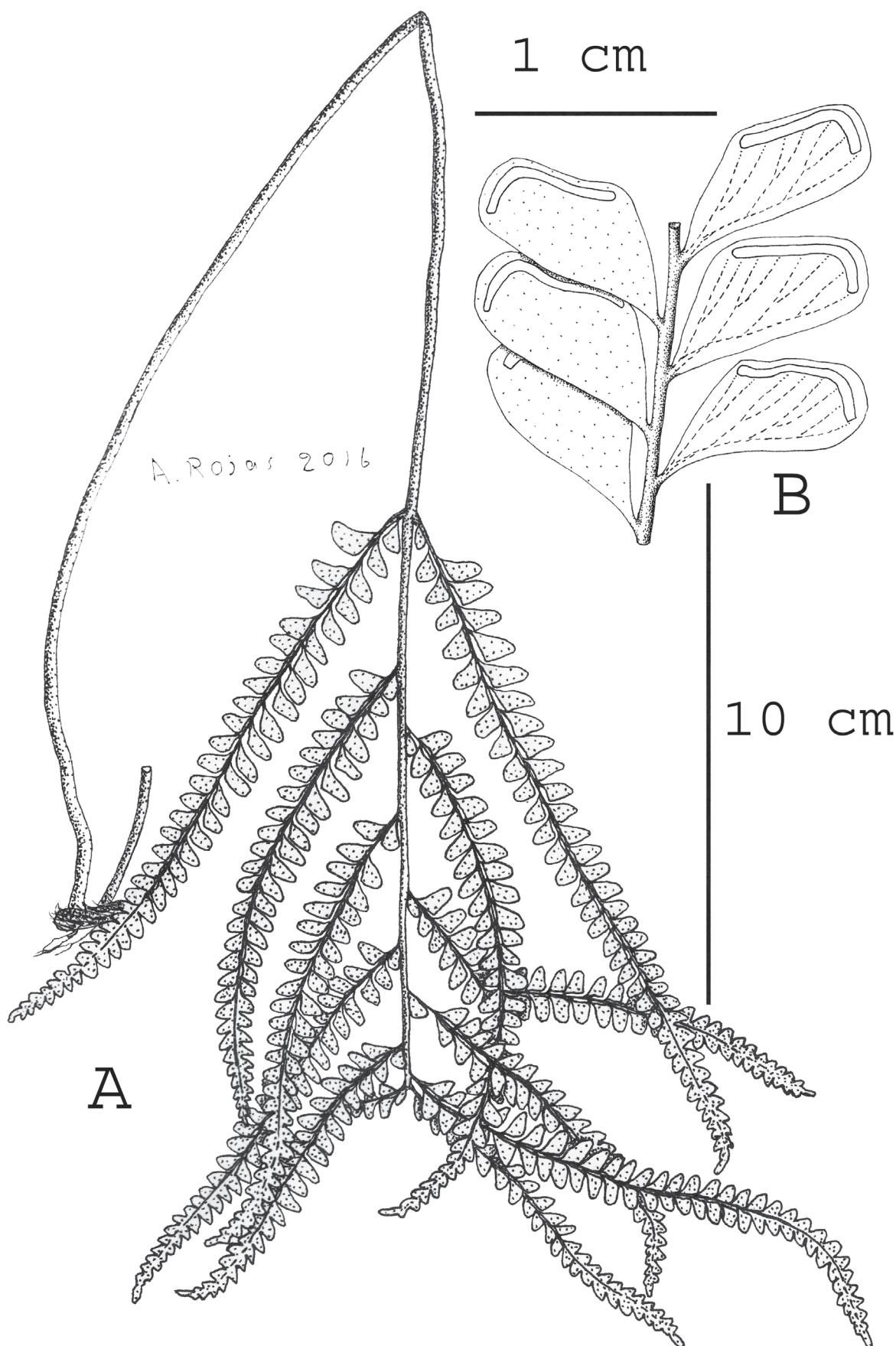


FIGURE 2. *Lindsaea fuscopetiolata* (D. Santamaría et al. 4411, CR). A. General aspect of type specimen. B. Abaxial blade detail.

Notes:—*Lindsaea fuscopetiolata* is similar to *L. divaricata* in having brown to reddish brown stipes and rachises and ascending pinnae and pinnules, but it differs in the characters mentioned in the diagnosis. The pinnatifid apex of *L. fuscopetiolata* is similar to *L. quadrangularis* subsp. *subalata* Kramer (1957a: 190–191) (= *L. subalata* (Kramer) A. Rojas & Tejero, here combined), but *L. fuscopetiolata* differs in having brown to reddish brown and lustrous stipes and rachises (vs. brown and opaque), and shorter pinnules (5–8 mm vs. 8–18 mm long) that are 1.2–1.5 times longer than wide (vs. 2.0–2.7 times). Also *L. fuscopetiolata* has been confused with *L. feei* Christensen (1906: 393) by its short, sessile pinnae, but it differs in having brown to reddish brown and lustrous stipes and rachises (vs. stramineous and matte), more graduate pinnatifid blade apices (vs. subconform), more pinnule pairs ((14–) 20–32 pairs vs. 12–18 pairs), and pinnules with entire margins (vs. lobulated).

***Lindsaea mesoamericana* A.Rojas & Tejero, sp. nov.** (Fig. 3)

Lindsaea mesoamericana is similar to *L. falcata* Dryand. and *L. leprieurii* Hooker (1846: 208) but it differs in having 1 or 2-pinnate blade (vs. only 1-pinnate in *L. falcata* and *L. leprieurii*), more segments per pinna (20–28 vs. 4–15 pairs per pinnae), blades (or distal pinnae in 2-pinnate specimens) that are narrowly triangular (vs. suboblong), with distal part of blade reduced up to 65–75% from baseline (vs. 10–15%), apical segments reduced and lobate (vs. the largest and hastate).

Type:—MEXICO. Oaxaca: Mpio. Santa María Chimalapa, cabecera del río Escolapa, ca. 15 km S de Santa María, 16°50'N, 94°41'W, 400 m, 22 October 1985, H. Hernández & C. González 1718 (holotype: MEXU!; isotypes: CHAPA!, IEB!, NY!).

Perennial terrestrial herbs, rhizomes long creeping, 2–3 mm in diameter, with fronds every 5–8 mm; rhizome scales 1–3 × 0.3–0.5 mm, cordate-ovate with aristate apices on the stipe bases to lineate-deltate with short hair-like apices on the rhizome tips, orange-reddish to reddish-brown or dark reddish, lustrous, clathrate or occluded; fronds 40–50 cm long, ascending to arching; stipes 13–25 cm long, 1/3–1/2 the length of fronds, dark brown to grayish in the rachis, sharply angular, winged abaxially in distal part; blades 1 or 2-pinnate (then with 2–5 conform pinnae: 1–4 lateral ones plus terminal one); the 1-pinnate frond parts (entire blade or apical pinna in 2-pinnate plants), linear-deltate, 16–30 × 4–6 cm, the apical ones with presence of a petiolule 2–3 cm long, with (15–)20–28 pairs of segments, that are contiguous but not overlapping, gradually reduced towards apex (the distal reduced 60–75 % with respect to proximal ones); segments dimidiate, dark green, glabrescent with scattered 2–3 celled subcapitate hairs on the abaxial surfaces (0.15 mm); basal segments 2–3 × 0.8–1 cm, falcate-trapezoid, short-petiolulate (1–1.5 mm), decurrently on the rachis and form an adaxial wing; distal segments rectangular-trapezoidal with acroscopic side perpendicular to rachis, proximal segments short divergent and distally round-truncate, subsessile; apical segment subconform, stretch tringle, equal to or larger than adjacent lateral segment; lateral pinnae in 2-pinnate plants ascending 35–45°, narrowly lanceolate, anadromic, with a small basal acroscopical pinnule, subaxillar, flabellate (cuneate), 2–3 proximal segments reduced, quadrangular, subsequent segments rectangular-arched; pinnules with a thickened strand of elongate cells runs along the margin, highlighted veins, the primary forked sympodially 3–4 times; sori continuous, parallel and close to acroscopic margin; indusium 0.5 mm wide, entire, green.

Etymology:—The name of the new species refer to its known distribution.

Distribution:—Known from Mexico to Panama at (0–)300–600(–1050) m, in the understory of tropical rain forest.

Additional revised specimens (paratypes):—MEXICO. Chiapas: Mpio. Ocosingo, 20 km arriba del arroyo Miranda (por Canoa), entrando por el río Chajul, 150 m, 19 February 1985, G. Castillo et al. 3973 (XAL!); Mpio. Ocosingo, Nvo. Veracruz, a 33 km al W del vértice del río Chixoy camino a Chanjul, en zona 1 Marqués de Comillas, 130 m, 10 January 1986, E. Martínez 15962 (IEB!, MEXU!); ibidem, E. Martínez 16002 (MEXU!), ibidem, E. Martínez 16038 (MEXU!); Mpio. Ocosingo, en vértice del río Chixoy, sobre el camino Boca Lacantum Chajul, 130 m, 12 January 1986, E. Martínez 16159 (MEXU!); Mpio. Ocosingo, en ejido Roberto Barrios, a 60 km al S de Boca Lacantum, camino a Chajul, 200 m, 18 April 1986, E. Martínez 18349 (MEXU!); ejido Loma Bonita, 150 m, 24 January 1992, E. Martínez & R. Lombra 26076 (IEB!, XAL!); Mpio. Benemérito de Las Américas, 2.8 km después de Loma Linda, rumbo a Benemérito de Las Américas, 16°04'55"N, 90°34'06"W, 179 m, 30 July 2011, A. Mendoza et al. 1784 (IEB!, UAMIZ!). Oaxaca: Mpio. Santa María Chimalapa, río Verde, 7 km en línea recta al NNE de Santa María Chimalapa, 360–430 m, 16°58'17"N, 94°39'45"W, 4 August 1985, P. Caletti et al. 75 (CHAPA!); cañada del río Negro, en la embocadura del arroyo Huapontl, ca. 15 km al S de Santa María, 16°56'N, 94°39'30"W, 300 m, 14 October 1985, H. Hernández & C. González 1628 (CHAPA, MEXU!); El Callejón, vieja vereda a Lázaro Cárdenas, cerca del camino actual que sale a arroyo Chocolate, subiendo la falda NE de cerro Azul-Escolapa, ca. 8 km al SW de Santa María, 16°52'N, 94°44'W, 350 m, 27 February 1986, H. Hernández 2109 (CHAPA!, MEXU!); ca. 10 km S de Santa María Chimalapa, por la vereda a la cabecera del Río Escolapa, 16°50'N, 94°41'W, 500 m, 24 June 1987, H. Hernández

2535 (CHAPA!); filo del cerro entre el río Blanco (al E) y el río Los Milagros (al O), ca. 25 km al SE de Santa María Chimalapa, 16°51'N, 94°35'W, 600 m, 21 August 1987, *H. Hernández* 2674 (CHAPA!); Mpio. San Juan Lalana, senda de Santiago Jalahuai al río Cuñeta, 210 m, 23 June 1991, *J. Calzada & M. Aranda* 17039 (MEXU!); Mpio. Ayotzinpec, Sierra de Juárez, entre Puerto Eligio y Comaltepec, km 150 entre Tuxtepec y Oaxaca, 29 October 1965, *G. Martínez* 440 (UAMIZ!, MEXU!); 6 km antes de Puerto Eligio, rumbo a La Esperanza, km 56 de la carretera Tuxtepec-Ixtlán-Oaxaca, 17°43'31"N, 96°19'37"W, 600 m, 8 September 2006, *A. Mendoza et al.* 1029 (UAMIZ!, XAL!); District of Villa Alta, valley of the Yelagago River, ca. 20 millas NE of Villa Alta, 17°25'N, 96°05'W, 762–1158 m [2500–3800 ft], 28 July 1962, *J. Mickel* 1048 (MEXU!, NY).

GUATEMALA. Chimaltenango: 1937–1941, *J. Johnston s. n.* (EAP!). Izabal: El Estor, March 1972, *E. Contreras* 11396 (MEXU!); vicinity Exmibal, Camp 2 (La Gloria), NW of Lake Isabal, 15°15–35'N, 89°0–25'W, 400–500 m, 9 May 1966, *G. Jones & L. Facey* 3338 (EAP!); entre caseríos Cienega y Ceja, 15°40'N, 89°W, 13 March 1972, *R. Tún* 2383 (EAP!).

BELIZE. N boundary of the BFREE reserve, in the NE Bladen watershed, 16°34'33"N, 88°42'11"W, 65 m, 7 June 2008, *S. Brewer* 4367 (MEXU!); upper Mare's Nest Branch in the Cockscomb Basin Wildlife Sanctuary, 16°44'4"N, 88°41'49"W, 250 m, 21 May 2008, *S. Brewer & Z. Goodwin* 4262 (MEXU!). Cayo District: Maya Mountains, Smokey Branch, 16.33°N, 89.02°W, 450 m, 17 March 1994, *A. Monro & T. Helgason* 219 (MEXU). Stann Creek District: 28 mi section, Humming Bird Hwy, 28 January 1957, *P. Gentle* 9305 (MEXU!); helicopter landing site 500 (HLS 500), 3.5 km E of Union Camp, 16°24'02"N, 89°06'40"W, 940 m, 19 February 1997, *T. Hawkins* 1474 (MEXU!, MO!, SEL!). Toledo: Columbia River Forest Reserve, ca. 2 km SW of SW end of Little Quartz Ridge, 16°22'58"N, 89°07'10"W, 700 m, 11 February 1997, *B. Holst* 5675 (MEXU!, MO!, SEL!).

HONDURAS. Atlántida: Mpio. Esparta, 41.5 km E of Tela on the Tela-Ceiba Hwy, then 2.7 km N along old timber road, 15°39'N, 87°16'W, 100 m, 17 April 1994, *A. Brant & D. Hazlett* 2859 (EAP!, MO!); campamento Quebrada Grande, ca. 10 km SW of Pa Ceiba, at base of N slope of Pico Bonito, from camp to 2 km E of camp, 15°42'N, 86°51'W, 80–180 m, 10 May 1993, *R. Liesner* 26151 (EAP!, TEFH!); montaña La Manga, 30 km SE de La Ceiba, 1050 m, 13–18 April 1976, *C. Nelson et al.* 3279 (EAP!). Gracias a Dios: cuenca del río Plátano, crique Sulawala, 12–14 May 1977, *M. Erazo* 338 (TEFH!); NE Honduras, near the río Patuca, under 175 m, 30 August–3 September 1973, *A. Clewell* 4576 (EAP, TEFH); orilla del río Dursuna, 70 m, 14–21 February 1979, *C. Nelson & E. Vargas* 4946 (TEFH!); ibidem, *C. Nelson & E. Vargas* 4947 (EAP!); near road crossing of río Dursuna, SW of Dursuna forest camp, 150 m, 5 February 1981, *G. Proctor* 38898 (TEFH!).

NICARAGUA. San Juan del Norte: en las lomas El Encanto, a 30 km al W de San Juan del Norte sobre el río Indio, 11°05'30"N, 83°53'W, 7 September 1982, *E. Martínez & R. Riviere* 2015 (MEXU!).

COSTA RICA. Cartago: carretera a Paraíso en junta con la de Buenos Aires, November 1979, *L. Gómez* 7209 (CR!); Turrialba, Reserva Forestal Río Pacuare, cuenca del Matina, sendero principal hasta río Barbilla, 9°58'24"N, 83°27'02"W, 500 m, 18 September 1999, *E. Mora & A. Rojas* 482 (CR). Heredia: Sarapiquí, Puerto Viejo, estación biológica La Selva, lindero sur, ca. 10°26'N, 84°01'W, 110 m, 10 September 2000, *M. Blanco & J. Horn* 1575 (USJ!); Sarapiquí, La Selva Biological Station, 10°26'N, 84°01'W, 50–150 m, 20 June 2002, *M. Jones & P. Olivas* 492 (CR!, USJ!); cerros Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí (finca La Martita), 10°28'N, 84°04'W, ca. 80–160 m, 21 January 1986, *A. Smith et al.* 1805 (CR!). Limón: 7 km SW of Bribrí, 100–250 m, 4 May 1983, *L. Gómez et al.* 20420 (CR!, MEXU!); Talamanca, Sixaola, Gandoca, El Lano, Bosque de Orey, 9°37'10"N, 82°38'00"W, 10 m, 3 April 1995, *G. Herrera* 7686 (CR); Talamanca, Cahuita, Gandoca, El Llano, humedales de Manzanillo, 9°37'00"N, 82°38'00"W, 0–5 m, 17 October 2010, *A. Rojas* 9055 (CR!). PANAMA. Coclé: along trail from caño Sucio to cerro Tife at base of waterfall, caño Sucio is a 5 hr walk from the sawmill at El Cope on the Atlantic slope, 366–427 m [1200–1400 ft], 3 February 1980, *T. Antonio* 3699 (CR).

Notes:—In the herbarium, most specimens of this species have been determinated previously as *Lindsaea lancea*. Linnaeus (1753) described this latter species, based on a specimen from Suriname, as: “*pinnate fronds: pinnae opposite, lanceolate-oblong, with triangular hastate termination.... Pinnulae recurved, oblong, obtuse: the terminals [apical segment] cordate or hastate-triangular shaped, oblong, acute*”. This description does not correspond to *L. mesoamericana* here described, because it is primarily one-pinnate or 2-pinnate with one (two) pair of pinnae at the base, the blade is gradually reduced, and the apical segment varies between lanceolate to flabellate but not hastate and large. While medial segments of *Lindsaea mesoamericana* are recurved, the two or three basal pairs are distinctively arched. The Linnaean description is also not consistent with the type of *L. falcata* (BM-000937670!: *N. Funck & L.J. Schlim* 592, Venezuela), a name used in infraspecific combination of *L. lancea*, since it is 1-pinnate, the blade is sub-oblong with few leaflets, and the basal ones are strongly falcate (the apical segment are similar to that described by Linnaeus). *Lindsaea mesoamericana* differs from *L. lancea* by its 1 or 2-pinnate (vs. full 2-pinnate) blades, pinnules

that are up to three times longer than wide (vs. ca. 2–2.5 times longer than wide), the basal and medial segments that are commonly falcate and curved down at apex (vs. pinnae with basiscopic side perpendicular to ascending with respect to rachis), the distal segments that are slightly or not reduced (vs. distal ones about 1/2 the size of the lower ones) and strongly asymmetric (vs. symmetric) terminal segment. For differences with *L. leprieurii* see the notes under that species.

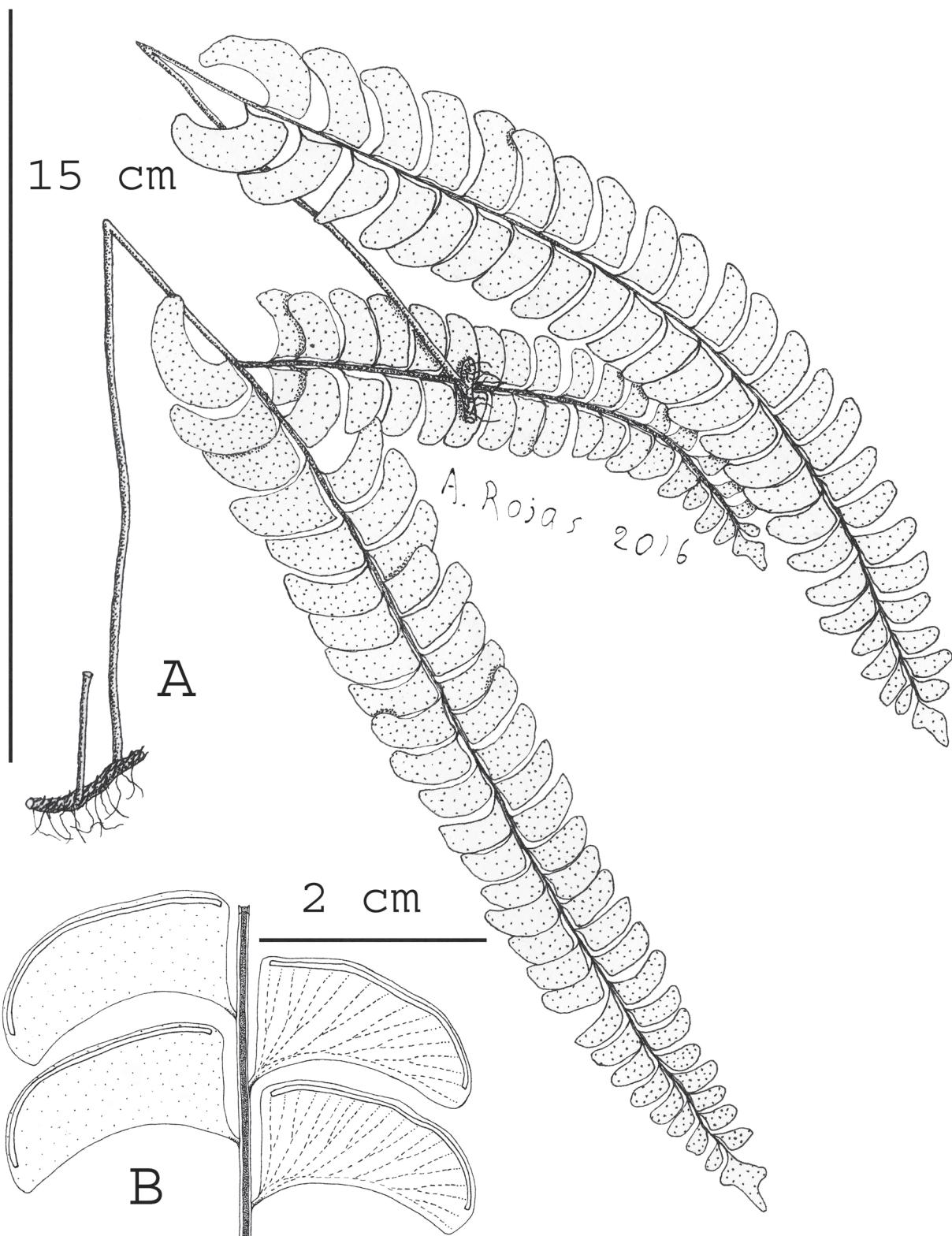


FIGURE 3. *Lindsaea mesoamericana* (H. Hernández & C. González 1718, MEXU). A. General aspect of type specimen. B. Abaxial blade detail.

Lindsaea mesoamericana is the most common species in Mesoamerica and is easily distinguished from other species in this area by the following combination of characters: blades (or terminal pinna in 2-pinnate specimens) with larger basal segments strongly recurved (falcate), towards the apex reduced in size and less recurved, ending in a sub-conform apical segment; lamina olive (dark green); stipe and rachis brown. The green wings along the rachis facilitate the recognition.

Lindsaea subalata* (Kramer) A.Rojas & Tejero, *stat. nov. Basionym: *Lindsaea quadrangularis* subsp. *subalata* Kramer (1957a: 190). Type:—COSTA RICA. San José: from the vicinity of El General, Skutch 2241 (holotype US; isotypes K, MO, NY, S-PA)

Distribution:—Southern Mexico to Panama.

Note:—According to Kramer (1957a), this taxon is easily distinguishable from the other sub-species of *Lindsaea quadrangularis* by blades being gradually reduced (vs. slightly reduced in *L. quadrangularis* subsp. *terminalis* Kramer (1957a: 192)), spores trilete (vs. monolete in *L. quadrangularis* subsp. *quadrangularis*) and stipe reddish brown to dark (vs. stramineous in *L. quadrangularis* subsp. *antillensis* Kramer [1957a: 194]. Also, the status change considered here is based on the geographical distribution, as this taxon is typically Mesoamerican (vs. West Indies *L. quadrangularis* subsp. *antillensis*, and southeast Brazil and Paraguay in *L. quadrangularis* subsp. *terminalis* and *L. quadrangularis* subsp. *quadrangularis*).

The other subspecies need to be raised to species status.

***Lindsaea horizontalis* Hooker** (1844: 214). Type:—BRAZIL. Rio de Janeiro: Organ Mountains, 1838, G. Gardner 157 (lectotype BM!; isolectotypes E!, K!)

Distribution:—Costa Rica, Panama, Colombia, Venezuela and Brazil.

Notes:—Kramer (1957a) treated this taxon as a synonym of *Lindsaea arcuata*. However, analysis of the types and other specimens demonstrates that it is distinct in having triangular pinnules, commonly 1-pinnate (vs. 2-pinnate) blades, when *L. horizontalis* is 2-pinnate have an irregular 1–2 couples of pinnae (vs. 3–8 pairs).

***Lindsaea moritziana* Klotzsch** (1844[1845]: 548). *Lindsaea stricta* var. *stricta* fo. *moritziana* (Klotzsch) Kramer (1957a: 228). Type:—Venezuela. Monagas: “Caripe, ad rivul. i. pasc. mont.”, J. Moritz 164 (lectotype B!, lectotype designed by Kramer 1957a: 228; isolectotype BM!). The duplicate in MPU! is from Colonia Tovar and belongs to *Lindsaea feei* C. Chr.

Lindsaea quadrangularis Raddi subsp. *mexiae* Mickel (in Mickel & Smith, 2004: 367).—Type: Mexico. Jalisco: West of San Sebastian, Hacienda del Ototal, Arroyo de Los Hornos, Y. Mexia 1837 (holotype: NY!; isotypes: F, G, GH, IEB!, MICH, MO, UC, US).

Distribution:—Mexico, Guatemala, Honduras, Greater Antilles and South America.

Notes:—Kramer (1957a) and Moran (1995) considered this taxon as a form of *Lindsaea stricta* (*L. stricta* var. *stricta* fo. *moritziana*). Mickel (in Mickel & Smith 2004) indicates that it is closest to *L. quadrangularis* (and form a new subsp.= *L. quadrangularis* subsp. *mexiae*). However, it is obvious that the characters of *L. moritziana* are sufficiently divergent from both *L. stricta* and *L. subalata* (= *L. quadrangularis* subsp. *subalata*) (see key). *Lindsaea moritziana* has fewer pinnae pairs (2–3 pairs vs. (2–)4–7 pairs), and fewer pinnules (12–18 pairs vs. 20–30(–40) pairs), that are shorter (5–6 mm long vs. 8–17 mm long), proportionally (1.2–1.5 times longer than wide vs. 2–3 times), and ending in an ovate to deltate segment (vs. pinnatifid). This species is likely more closely related to *L. brasiliensis* Desvaux (1811: 330) (= *L. stricta* var. *parvula* Kramer, 1957a: 230) based on its stramineous axes and small number of pinnae pairs, but it differs in having fewer (12–18 vs. (15–)25–50) pinnule pairs with an ovate to deltate terminal segment (vs. pinnatifid).

The presence in Jalisco, Mexico of this species (*Mexia* 1837 IEB!, NY!, etc.) is the northernmost distribution of the genus.

New distributional records:

***Lindsaea cubensis* Underwood & Maxon** (1907: 336). Type:—CUBA. Villa Clara: Cuba Occ., Loma Pelado, 1859–1860, C. Wright 3947 (holotype: NY-00127167!; isotypes: B-20 0141631!, GH-00021502!, GH-00359569!,

K-000644030!, NY-00127168!, P-00539202!, P-00539203!, P-00539204!, S-R3260!, U-0007333!, US-00066449!, US-01100897!)

Distribution:—Cuba, Nicaragua (first record).

Specimen examined:—NICARAGUA. Zelaya: Puerto Cabezas, 0–100 m, 12 March 1971, *J. Atwood* 4516 (MEXU!).

Notes:—*Lindsaea cubensis* is close to *L. stricta* in having strongly vertical fronds and similar habitat preferences (open areas near seasonal water bodies), but it differs in having subdimorphic fronds (vs. monomorphic), 1-pinnate (vs. 1–2-pinnate, but more commonly 2-pinnate) blades, fewer pinnate pairs ((5–) 12–22 pairs vs. 25–70 pairs), and pinnae with ascending basiscopic sides in respect to the costae (vs. perpendicular to reflexed).

Lindsaea divaricata Klotzsch (1844: 547). Type:—GUYANA. “Guiana angl.”, *M.R. Schomburgk* 368 (holotype B-200079709!).

Distribution:—Costa Rica (first record), Panama, Guadeloupe, Venezuela, Guyana, French Guiana, Suriname, Ecuador, Peru, Brazil, Bolivia and Paraguay.

Specimens examined:—COSTA RICA. Limón: Talamanca, Sixaola, Gandoca, El Llano, bosque de Orey, 9°37'10"N, 82°32'04"W, 10 m, 3 April 1995, *G. Herrera* 7694 (CR!); Talamanca, Sixaola, Gandoca, El Llano, entre filas Manzanillo y río Mile Creek, 9°37'00"N, 82°41'00"W, 50–100 m, 27 March 1995, *G. Herrera & E. Sandoval* 7597 (CR!, MO!); Parque Nacional Tortuguero, 600 m SW de Tortuguero sobre el río Tortuguero, se toma al W en zona cenagosa, 10°31'N, 83°30'W, 1 December 1987, *R. Robles* 1408 (CR!, MO!); Talamanca, Cahuita, Gandoca, El Llano, humedales de Manzanillo, 9°37'00"N, 82°38'00"W, 0–5 m, 17 October 2010, *A. Rojas* 9054 (CR!). Heredia: Sarapiquí, La Selva Biological Station, 10°26'N, 84°01'W, 50–150 m, 29 May 2007, *M. Jones & M. Putkonen* 616 (USJ!); Sarapiquí, Estación Biológica La Selva, 10°25'49"N, 84°00'25"W, 18 January 2008, *M. Sundue et al.* 1514 (USJ!).

Notes:—The mentioned specimens of *Lindsaea divaricata* from Costa Rica were previously determinated as *L. quadrangularis* based on their narrow terminal segment, but they differ in having brown to reddish-brown (vs. stramineous) stipes and rachises that are not angulate (vs. angulate) abaxially. *Lindsaea divaricata* is also similar to *Lindsaea quadrangularis* subsp. *terminalis* because both have strongly ascending pinnae and pinnules, but the later species has blackish stipes and rachises, fewer pinnae (commonly 2–3 vs. commonly 4–6 pairs), fewer pinnules ((5–)10–15 vs. (13–)20–25) pairs, and a deltate to hastate terminal segment (vs. narrowly lanceolate).

Lindsaea horizontalis Hooker (1844: 214). Type:—BRAZIL. Rio de Janeiro: Organ Mountains, 1838, *G. Gardner* 157 (holotype BM!; isotypes E!, K!).

Distribution:—Costa Rica (first record), Panama (first record), Colombia, Venezuela and Brazil.

Specimens examined:—COSTA RICA. Cartago: Paraíso, Parque Nacional Tapantí, sendero Dos Quebradas, 9 April 1986, *J. Berrocal & J. Sánchez* 140 (CR!); cerro entre cerro Chimú y cerro Matama, 1200 m, 30 April 1985, *L. Gómez* 23569 (CR!); Paraízo, Parque Nacional Tapantí-Macizo de La Muerte, cuenca del reventazón, sendero Árboles Caídos, 9°45'00"N, 83°47'00"W, 1200–1300 m, 9 July 1997, *R. Guzmán* 113 (CR, MO); Turrialba, Moravia de Chirripó, 1400 m, 1 January 1976, *R. Ocampo* 1184 (CR!); Turrialba, valle del Reventazón, Jicotea, finca La Pradera, Jicotea, 9.7875°N, 83.5472°W, 1000 m, 22 June 1995, *G. Rivera & A. Rojas* 2472 (CR!); Paraíso, Cordillera de Talamanca, Estación Biológica Río Macho, 300 m SW del embalse, 9°45'11"N, 83°51'48"W, 1700 m, 30 May 1994, *A. Rojas* 1047 (CR); Turrialba, Cordillera de Talamanca, Tayutic, Jicotea, 9°47'15"N, 83°32'50"W, 1100–1600 m, 22 June 1995, *A. Rojas et al.* 2006 (CR!); Paraíso, Parque Nacional Tapantí, cuenca del río Reventazón, sendero Árboles Caídos y Oropéndula, 9°45'20"N, 83°47'00"W, 1300–1500 m, 7 April 1999, *A. Rojas & A. Soto* 5020 (CR!, MO); *ibidem*, 19 November 1997, *A. Rojas et al.* 3971 (CR!, MO, USJ); Cartago, Agua Caliente, Muñeco, 9°46'N, 83°54'W, 1700 m, 2 April 2004, *A. Rojas et al.* 5570 (CR!, MO); Paraíso, Parque Nacional Tapantí-Macizo de La Muerte, sendero Árboles Caídos, cerca de 200 m antes de la salida del sendero, 9°45'05"N, 83°46'55"W, 1300–1350 m, 22 April 2012, *A. Rojas et al.* 9730 (CR!, MO, USJ); Orosi, Parque Nacional Tapantí-Macizo de La Muerte, sector Tapantí, sendero Árboles Caídos, en la última parte del circuito, 9°46'00" N, 83° 47'20" W, 1220–1300 m, 5 June 2012, *A. Rojas et al.* 9830 (CR!, MO, USJ); 5.6 km of San José, side of road leading to Palmichal, steep new dirt road up hill from Pan American Hwy, 1700–1800 m, *K. Walter* 79490 (CR). Limón: Talamanca, trail ca. 5 km up Alto Lari, 9.4042°N, 83.0847°W, 1300 m, 27 February 1992, *J. Bittner* 1335 (CR!); Talamanca, camp by Kivut, trail between Kivut and Alto Lari, 1 km up to

Alto Lari, 9.4042°N, 83.0847°W, 1200–1300 m, 6 March 1992, *J. Bittner* 1450 (CR!); Talamanca, Alto Urén, cerro Laúbeta, entre río Lorni y quebrada Chacho, 9.3861°N, 83.0069°W, 1190 m, 27 July 1989, *G. Herrera* 3381 (CR!); Limón, Almirante, cuenca superior del río Xichiari, 9.7639°N, 83.3292°W, 1300 m, 14 August 1995, *G. Herrera* 8480 (CR!); near Moravia de Chirripó, 1300 m, 7 April 1949, *L. Williams* 16186 (EAP!). Puntarenas: Las Cruces, ridge 6 km S of San Vito de Java, 4500 ft, February 1974, *McAlpin* 2421 (CR); Buenos Aires, Parque Internacional La Amistad, Cuenca Térraba-Sierpe, Potrero Grande, La Lucha, cabeceras del río Guineal, 9°06'38.36"N, 83°05'21.84"W, 1600–1700 m, 22 February 2008, *A. Rodríguez et al.* 11850 (CR, PMA). San José: Tarrazú, camino entre cerro Pito y cerro Toro, 9°34'50"N, 84°04'10"W, 1200–1400 m, 26 January 1998, *A. Estrada* 1430 (CR); El Guarco, Cerros de Escazú-La Carpintera, La Cangreja, 9°48'00"N, 83°57'50"W, 1900 m, 26 June 1993, *A. Rojas* 303 (CR).

PANAMA. Chiriquí: along road from Gualaca to Fortuna dam site, 5.9 mi NW of Los Planes de Hornito, 8.7167°N, 82.2833°W, 1370 m, 9 April 1980, *T. Croat* 49868 (CR!, MO!).

Notes:—*Lindsaea horizontalis* has been included as synonym of *L. arcuata*, for differences see up in the validation of this species.

Lindsaea leprieurii Hooker (1846: 208). Type:—FRENCH GUIANA. “Guyana”, *F. Leprieur* s.n. (holotype: K!)

Distribution:—Costa Rica (first record), Colombia, Venezuela, Guyana, French Guiana and Suriname.

Specimens examined:—COSTA RICA. **Puntarenas:** Golfito, Parque Nacional Corcovado, Península de Osa, cerro Rincón, 08°31'16.55"N, 83°28'07.19"W, 700–800 m, 30 January 1998, *A. Azofeifa* 621 (CR!, MO!, USJ!); *ibidem*, 8°31'N, 83°28'W, 700–745 m, 29 January 1998, *A. Rojas et al.* 4204 (CR!, MO!) (mixed with *L. lancea*).

Notes:—*Lindsaea leprieurii* is similar to *L. falcata* in having 1-pinnate blades with entire apical pinnae, but it differs in its blackish (vs. reddish-brown) stipes, dark green (vs. pale green to green) blades, and hastate apical pinnae (vs. deltate to deltate-lanceolate). similar habitat preferences. *Lindsaea leprieurii* also differs from *Lindsaea lancea* in having 1-pinnate blades (vs. commonly 2-pinnate), pinnules to 3 times as long as wide (ca. 2–2.5 times as long as wide), distal pinnae that are slightly or not reduced (vs. distal ones about 1/2 the size of the lower pinnae), and strongly asymmetric terminal pinnae (vs. symmetric).

Species excluded from the study area

Lindsaea falcata Dryander (1797: 41). Type:—FRENCH GUIANA. “Guyana”, *Aublet* s.n. (BM! [photo US])

Notes:—Rosenstock (1906) and Kramer (1957a) regarded this taxon as a variety of *Lindsaea lancea* (*L. lancea* var. *falcata* (Dryander) Rosenstock, 1906: 79). Tuomisto (1998) argued that the morphological and ecological differences between them are sufficient to recognize both taxa at the species level (*L. falcata* and *L. lancea*). Kramer (1957a) reported the specimen *Seemann* s.n. (BM-000586167) from Panama, but the specimen was collected in Chocó, what is today Colombia due to a historic change of political limits.

Lindsaea quadrangularis Raddi (1819: 294). Type:—BRAZIL. Rio de Janeiro: Vicinity of Rio de Janeiro, *G. Raddi* s.n. (FI-005046!)

Notes:—*Lindsaea quadrangularis* ssp. *subalata* Kramer is here recognized at the species level. The remaining varieties of *L. quadrangularis* considered by Kramer (1957a) are distributed in South-America and Antilles.

Key to Mexican and Central American species of *Lindsaea*

- | | | |
|----|---|---------------------|
| 1. | Acroscopic margins of segments undulate and with some short clefts; sori irregularly interrupted, at least in the more developed segments | 2 |
| - | Acroscopic margins of segments entire or repand; sori typically continuous | 4 |
| 2. | Blades 2-pinnate (Neotropics) | <i>L. feei</i> |
| - | Blades 1-pinnate | 3 |
| 3. | Blades lanceolate with 5–15 pinnae pairs, pinnae 3–6 times longer than wide, subequilateral, with primary vein centered; spores trilete (Costa Rica, Panama, Greater Antilles, South America) | <i>L. imrayana</i> |
| - | Blades linear-elliptic, with 30–50 pinnae pairs, pinnae as long as wide, dimidiate, with primary vein sympodial basiscopic; spores monolete (Panama, Colombia) | <i>L. seemannii</i> |

4. Sori present along both sides of segments (acrosticopic and basiscopic); segments long-triangular, at least 5 times longer than wide; first vein dimidiate at base and centered at the apex (Costa Rica, Panamá, Ecuador)..... *L. taeniata*
- Sori present only along acrosticopic side of segments; segments triangular to rectangular or similar, less than 4 times as long as wide; first vein full dimidiate 5
5. Longer segments less than 2-times longer than wide 6
- Longer segments more than 2-times longer than wide 10
6. The largest blades or longest pinnae with 35–75 segment pairs; if blade with two basal pinnae then these held vertically 7
- The largest blade or pinnae with less than 30 segments pairs; if 2-pinnate, the pinnae not held vertically 8
7. Blades 1 or 2-pinnate; segments rectangular with acrosticopic side convex; spores trilete (Neotropical) *L. stricta*
- Blades 1-pinnate; segments triangular with acrosticopic sides concave; spores monolete (Costa Rica, Panama) *L. pratensis*
8. Stipes (at least distally) and rachises dark brown to grayish *L. fuscopetiolata*
- Stipes (at less distally) and rachises stramineous (yellowish to green-yellow) or with dark shadows 9
9. Blades 1-pinnate (or sometimes 2-pinnate at the base); basal segments distant (>1 cm apart) and ascending; fronds 5–20 cm long (Nicaragua, Cuba)..... *L. cubensis*
- Blade fully 2-pinnate (to 3-pinnate in base); basal segments close (~0.9 cm), and perpendicular or descending (reflexed); fronds (15–) 25–70 cm long (Neotropics) *L. moritziana*
10. Distal segments (of blades or pinnae) only weakly reduced at least 75 % the size of proximal segments), apical segments subconform (0.8–2.0 cm broad at base); rachises angular abaxially, sometimes winged 11
- Distal segments strongly reduced less than 75% the size of proximal segments, apical segments reduced to less than 0.7 cm broad; rachises terete abaxially, never winged 14
11. Stipes (at least distally) and rachises stramineous (yellowish to green-yellow); blades fully 2-pinnate (Neotropics)..... *L. lancea*
- Stipes (full) and rachises (at least proximally in *L. angustipinna*) atropurpureous to brawn or blackish; blades 1- pinnate, or basally 2-pinnate 12
12. Basiscopic side of segments straight and commonly perpendicular to rachis, the apex curved up to truncate; laminar tissue pale green; indusia brown (Nicaragua, Costa Rica)..... *L. angustipinna*
- Basiscopic side of segments curved down, the apex acute; laminar tissue dark green (blackish when dry); indusia stramineous 13
13. Fronds 10–25 cm long in adult plants; blade 1-pinnate, with 10-17 (-22) pinnae pairs (Costa Rica, South America).... *L. leprieurii*
- Fronds 40–50 cm long in adult plants; blade 1 or more commonly 2-pinnate, if 1-pinnate then with more than 25 pinnae pairs (Mexico to Costa Rica)..... *L. mesoamericana*
14. Stipes and rachises (at least proximally) brown to blackish; blades 2-pinnate 15
- Stipes (at least distally) and rachises stramineous (yellowish to green-yellow; blades 1 or 2-pinnate) 16
15. Pinnae short-petiolulate, with a deltate acrosticopic subaxillary segment, lateral segments broader at the base than the apex (Mexico, Mesoamerica, Greater Antilles, N. South America)..... *L. subalata*
- Pinnae long-petiolulate, without an acrosticopic subaxillary segment; lateral segments as broad at base than the apex (Guatemala, Costa Rica, Panama, South America)..... *L. divaricata*
16. Blades 1-pinnate (or 2-pinnate at the base); segments triangular with acute apices (Costa Rica, Panama, northern South America) *L. horizontalis*
- Blades fully 2-pinnate; segments trapezoidal-rectangular with rounded to truncate apices (Neotropical)..... *L. arcuata*

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