Eight New Species of Tree Ferns (*Cyathea*, Cyatheaceae) from the American Tropics and Three New Combinations

Robbin C. Moran
Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

The new species described herein are a result of my work on the pteridophyte volume for *Flora Mesoamericana* and on general fern identifications at MO. In the descriptions, all mention of indument refers to that found on the abaxial surface of the leaf unless otherwise stated.

Cyathea albomarginata R. C. Moran, sp. nov. TYPE: Costa Rica. Heredia: NW slope of Volcán Barva, between Laguna del Barva and base of Cerros Las Marías, 2,450–2,800 m, *Grayum 7469* (holotype, MO; isotypes, CR not seen, UC). Figure 1.

Petiolus brunneus sine spinis, squamellis albis minutis, squamis ex late ovato lanceolatis, bicoloribus, atropurpureis marginibus latis albis; pinnulae 10–12 × 1.2–1.5 cm; costulae squamosae, squamis ex circulari ovatis; venae semel furcatae; sori inframediani, secus costulam dispositi, paraphysibus inconspicuis; indusia inconspicua squamiformia.

Trunk ca. 0.5 m tall; petiole brown, not spiny; petiole scales 7–12 × 4–6 mm, ovate to lanceolate, sharply bicolorous, purplish brown with wide white borders; petiole scurf consisting of dense white squamellae; lamina 2-pinnate-pinnatifid, tapered to the apex; pinnae stalked, the stalk 2.5–4 cm long; pinnules 10–12 × 1.2–1.5 cm, short-stalked, the stalk 1–5 mm long; ultimate segments ca. 3 mm wide, entire or serrulate apically; rachis, costae, and costules lacking hairs but with whitish scurf, sparsely scaly, the scales circular to ovate, golden brown, flat or subbullate; veins 1-forked, 5 or 6 pairs per segment, with appressed inconspicuous scurf; laminar tissue between the veins glabrous; sori inframedial, crowding the midribs; paraphyses shorter than the sporangia, inconspicuous; indusium hemitelioid.

Paratype. PANAMA. BOCAS DEL TORO: headwaters of Río Colubre, Colubre Camp, 2,400–2,550 m, *Gómez et al. 22370* (CR, MO, UC).

This species grows in wet forests from 2,400 to 2,800 m, which is a higher elevational range than most species of *Cyathea*. It differs from all other *Cyathea* in Mesoamerica by the broad, white-margined petiole scales (Fig. 1c) and white scurf. The aerophores at the bases of the pinnae and pinnules are frequently elongated and darkened, resembling an abscission layer, but the pinnae and pinnules do not appear to disarticulate. The minute, scalelike indusium is easily overlooked. This species is quite distinct, and I am not sure to which species it is most closely related.

Cyathea nodulifera R. C. Moran, sp. nov. TYPE: Panama. Veraguas: Cerro Tute, ca. 2 km N of Santa Fé, along ridge trail to summit, N of Escuela Primaria Alto de Piedra, 900–1,000 m, *Moran 4030* (holotype, MO; isotypes, PMA, UC, US). Figure 2.

Petiolus atropurpureus spinosus, squamis lanceolatis, brunneis centro fusciore ornatis; petioluli pinnarum 3–5 cm longi; pinnulae 15–23 × 2.5–3.5 cm, petiolulatae, petiolulis 6–10 mm longis, basi tuberculatis; rhachis et costae atropurpureae; venae semel furcatae, utrinque glabratae; sori inframediani, paraphysibus inconspicuis; indusia nulla.

Trunk to ca. 0.5 m tall; petiole atropurpureous, spiny, the spines 1–5 mm long, slender; petiole scales 10–20 × 2–3 mm, dark brown medially with lighter brown borders, narrowly lanceolate; petiole scurf consisting of dense brown squamellae; lamina 2-pinnate-pinnatisect, the apex abruptly or gradually reduced, pinnatifid; pinnae ca. 12 pairs, stalked, the stalk 3–5 cm long; pinnules 15–23 × 2.5–3.5 cm, stalked, the stalk 6–10 mm long, with a raised tubercle(s) at the juncture with the costa (Fig. 2d); ultimate segments 5–6 mm wide, 15–20 pairs per pinnule, serrate to crenate-serrate; rachis, costae, and costules lacking spines, atropurpureous, lacking hairs and scales, scurf present; costules and midribs of the ultimate segments scaly, the scales flat to subbullate, circular to ovate-acuminate, golden, finely erose-denticulate; veins 1-forked, 6–9 pairs per segment, glabrous; laminar tissue between the veins glabrous; sori inframedial; paraphyses shorter than

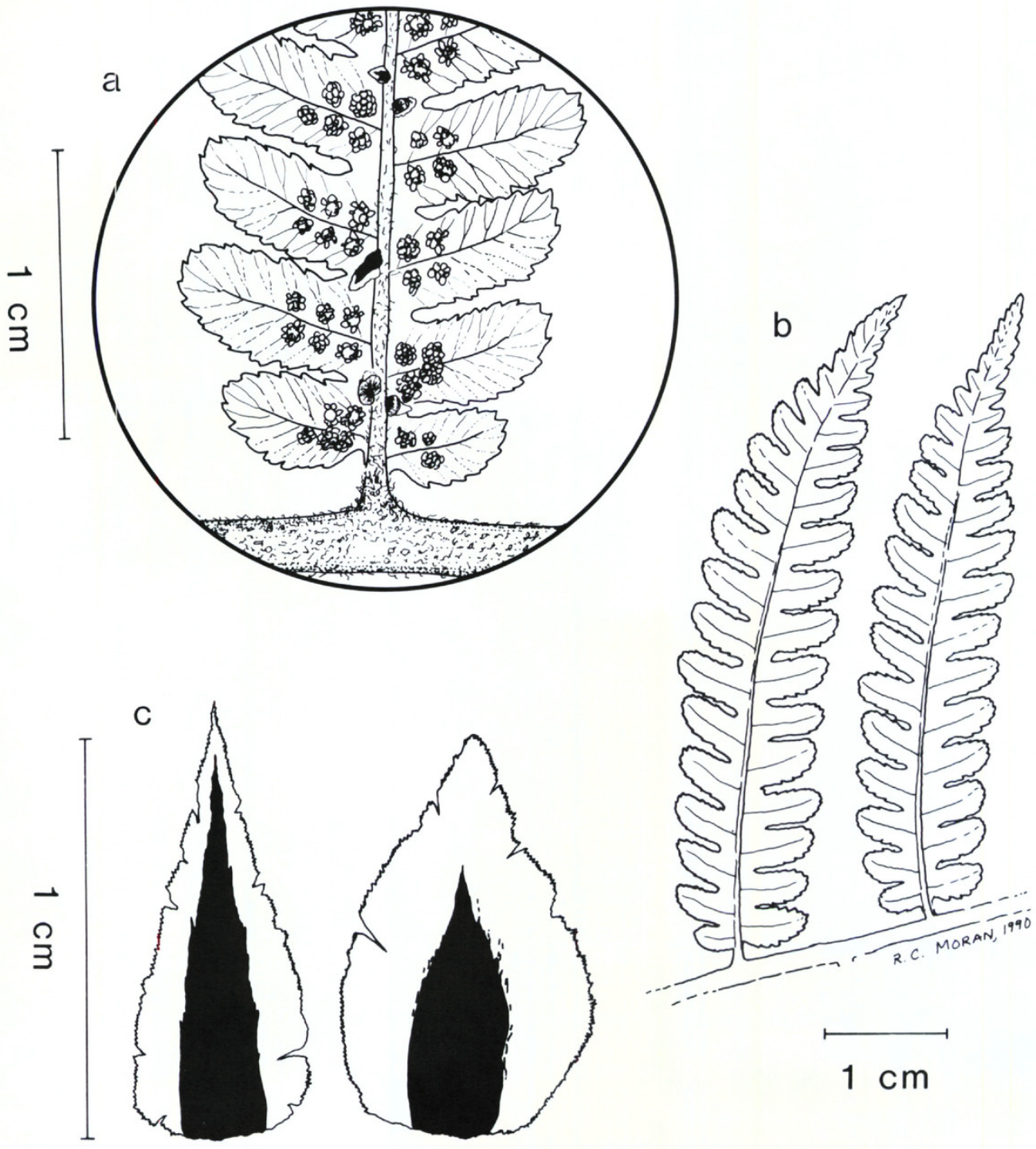


Figure 1. *Cyathea albomarginata.* —a. Pinnule base. —b. Medial pinnules from medial pinna. —c. Petiole scales showing characteristic wide white borders. a–c, *Grayum 7469*, MO.

the sporangia, few, dark red, inconspicuous; indusium absent.

Paratypes. COSTA RICA. HEREDIA: forest between Río Peje and upper Río Guácimo, Atlantic slope of Volcán Barva, 950–1,150, *Grayum et al. 7800* (CR, MO). PANAMA. DARIÉN: Cerro de Garagará, Sambú basin, 500–974 m, *Pittier 5641* (US).

Cyathea nodulifera is endemic to the mountains of Costa Rica and Panama, where it grows in wet forests from 500 to 1,150 m. It resembles *C. kalbreyeri* (Baker) Domin in having long-stalked, deeply lobed pinnules (Fig. 2c) and nonindusiate sori; it differs by having atropurpureous axes, short reddish paraphyses, more abundant costal scales, and nodules at the bases of the pinnae and pinnules. The nodules are 1–2 mm high, light brown (rather than atropurpureous like the axes), and often two or more occur at a given juncture (Fig. 2d). Many species

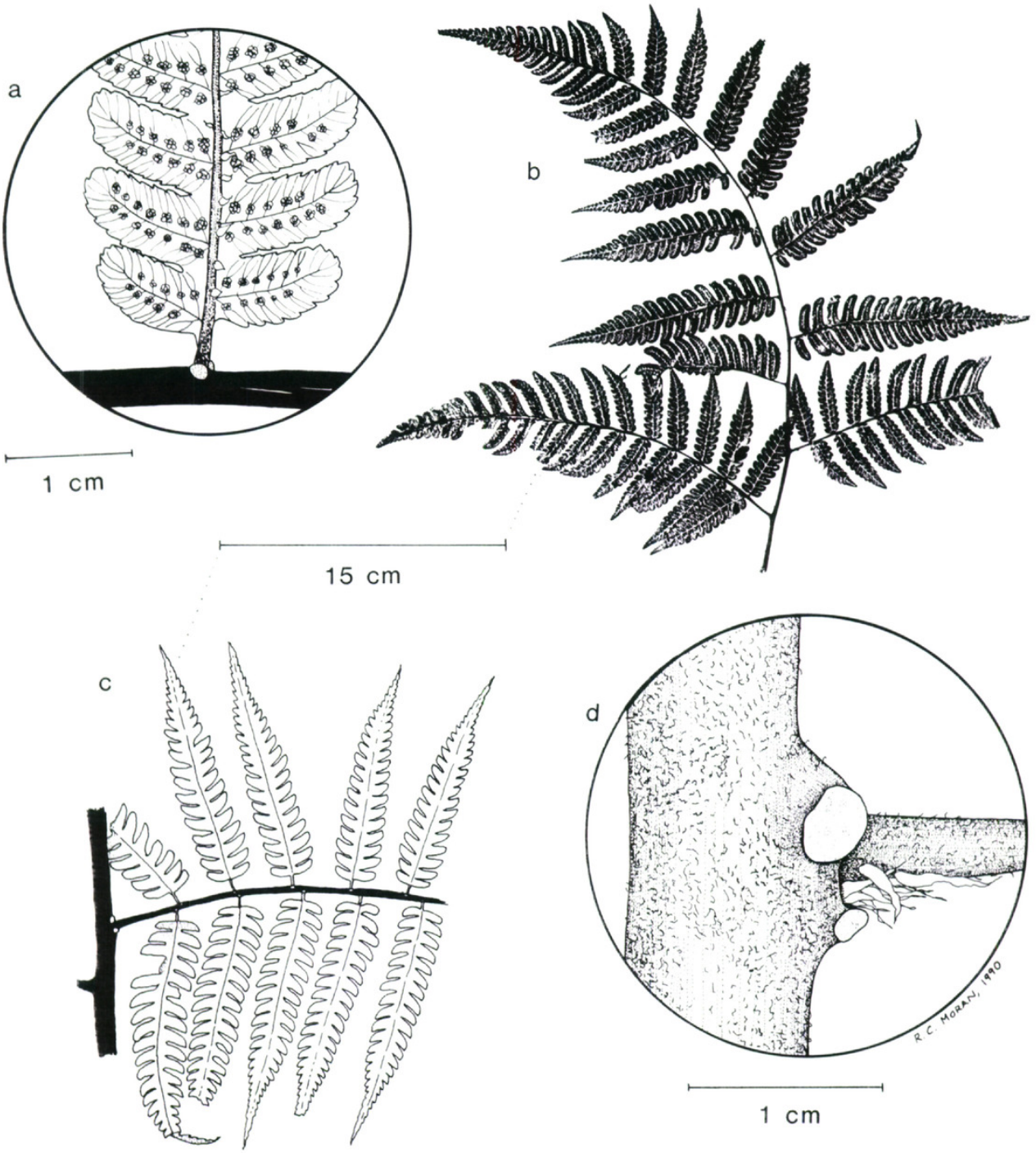


Figure 2. *Cyathea nodulifera.* —a. Pinnule base. —b. Leaf apex. —c. Base of medial pinna. —d. Juncture of rachis and costa showing nodular aerophores. a–d, *Moran 4030,* MO.

of *Cyathea* have dark, circular to oblong patches at the pinna or pinnule bases, but they are never tuberculate or nodular as in this new species.

The paratype from Panama was cited by Barrington (1978) as *Trichipteris nigripes* var. *nigripes* (= *Cyathea nigripes*), which the new species resembles in leaf cutting, number of ultimate segments per pinnule, number of vein pairs per ultimate segment, inframedial sori, and stalked pinnules. The two differ, however, by the width of the pinnules and ultimate segments, color of the axes and costular scales, presence versus absence of nodules, and margins of the ultimate segments.

Cyathea pinnula (Christ) R. C. Moran, comb. nov. Basionym: *Alsophila pinnula* Christ, Prim. Flor. Costaric. 3: 43. 1901. TYPE: Costa Rica. Limón: Río La Matina, *Pittier 10267* (holotype, P—Herb. Christ not seen, photo MICH; fragments NY, US ex P). Figure 3.

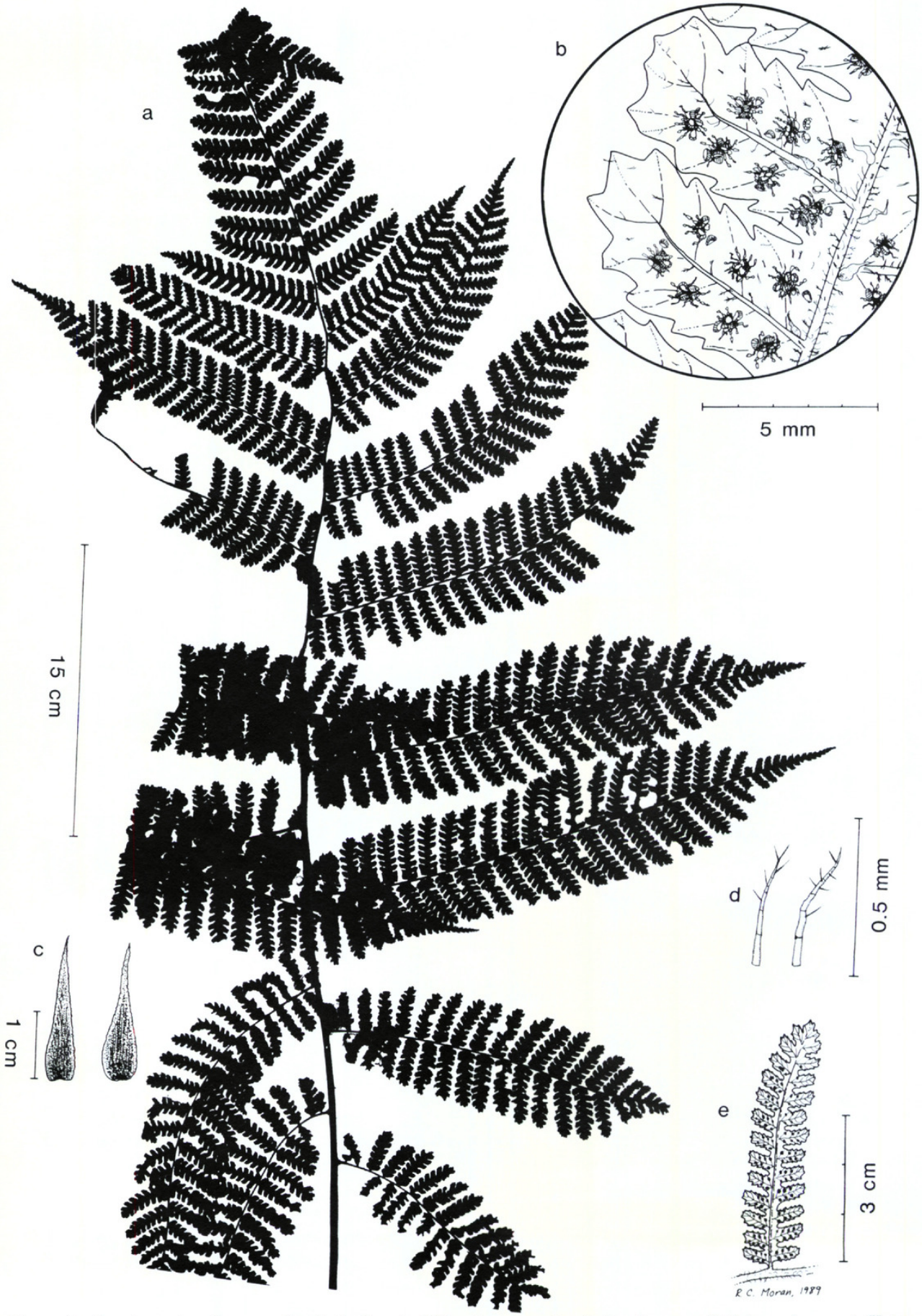


Figure 3. *Cyathea pinnula.* —a. Fertile leaf. —b. Ultimate segments of pinnule. —c. Petiole scales. —d. Hairs from abaxial surface of costa infected with black, acicular fungus. —e. Fertile pinnule. a, *Moran 4133*, MO. b–e, *Liesner & Judziewicz 14701*, MO.

Trunk 0.4–2 m tall, 4–7 cm wide; petiole light brown, spiny or not spiny, the spines 2–5 mm long; petiole scales 10–20 × 3–5 mm, lanceolate, shiny, brown with narrow brownish white borders; petiole scurf consisting of minute light brown trichomidia and squamellae, deciduous and often apparently absent; lamina 2-pinnate-pinnatifid, elliptic, sparsely pubescent between the veins; pinnae 8–14 pairs, narrowly alate between the distal pinnules, stalked, the stalk 4–15 mm long; pinnules 3–7.5 × 1–1.5 cm, sessile or nearly so; ultimate segments 2–3 mm wide, 9–16 pairs per pinnule, obtuse, serrate; rachis glabrous; costae pubescent with trichomes similar to those on the costules, lacking scales; costules pubescent and scaly, the trichomes 0.3–0.4 mm long, subulate, hyaline, erect to spreading, almost always infected by a black acicular fungus (Fig. 3b, d), the scales shiny, golden, ovate with acuminate apices to lanceolate, flat to (especially on distal portions of the lamina) bullate; veins simple, unbranched, pubescent with hairs like those on the axes; laminar tissue between the veins sparsely pubescent with hairs like those of the axes; sori ca. medial; paraphyses conspicuous, equaling or slightly longer than the sporangia, hyaline, jointed; indusia absent.

Additional specimens examined. COSTA RICA. ALAJUELA: Reserva Forestal, San Ramón, 1,350–1,500 m, *Carvajal 334* (MO, UC); 17–20 km NNW of San Ramón by road on way to San Lorenzo, 4–7 km N of Balsa, 750 m, *Liesner & Judziewicz 14701* (MO, UC); Univ. of San Ramón's Biological Field Station, ca. 20 km N of San Ramón, along Río San Lorencito, cloud forest, 10°15′N, 84°30′W, 800–900 m, *Moran 4133* (CR, MO, UC). CARTAGO: SE of Turrialba, ca. 3 km NE of La Suiza, 1,200 m, *Lellinger 1401* (MICH, MO, US). GUANACASTE: Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Hacienda Santa María, 900–1,200 m, *Davidse et al. 23401* (MO, UC). HEREDIA: between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 700–750 m, *Grayum & Jermy 6778* (MO, UC). SAN JOSÉ: Parque Nacional Braulio Carrillo, from La Montura to Los Chorritos, 1,200 m, *Gómez et al. 20926* (MO, UC). PANAMA. CHIRIQUÍ: Fortuna Dam area, N fork of the Quebrada de Arena, 1,100 m, *Churchill et al. 4674* (MO, UC); vic. of Fortuna Dam, in valley of Río Chiriquí, along aqueduct trail for water supply for IRHE facilities, 1,100–1,200 m, *Croat 66590* (MO, UC); E of main camp at Fortuna Dam site, 1,400–1,500 m, *Folsom et al. 5450* (MO, UC). VERAGUAS: Cerro Tute, ca. 2 km N of Santa Fé, along ridge trail to summit, 900–1,000 m, *Moran 4032* (MO). COLOMBIA. CHOCÓ: W of Tutunendo, Quibdó–Medellín road, 100 m, *Gentry & Brand M. 36866* (MO); banks of Quebrada Togoromá, dense tidal forest, *Killip & Cuatrecasas 39084* (US).

This species was treated by Barrington (1978) in his *Nomina Incertae Sedis* because he lacked sufficient material to make a certain assignment. Although Christ did not cite a type in his original publication, the above specimen is probably the one he used to describe the species because it is the only specimen in his herbarium labeled in his hand as "*Alsophila pinnula*, sp. nov."

Cyathea pinnula grows in wet forests, cloud forests, and (rarely) tidal forests from (0 to)700 to 1,500 m. It can be distinguished from other species of *Cyathea* in Mesoamerica by the following combination of characteristics: costal scales golden and erose-margined, lamina pubescent between the veins, fertile veins unbranched, sori nonindusiate, and paraphyses conspicuous. A peculiar characteristic is that all specimens examined were infected by a black, acicular fungus. Although the fungus occurs on the laminar tissue and axes, it is most conspicuous when it grows through and out of the hairs (Fig. 3b, d) and scales.

Cyathea pinnula is common in Costa Rica and Panama and has previously been identified (often tentatively with a "?" or "cf.") as *C. wendlandii* (Kuhn) Domin or *C. nigripes* (C. Chr.) Domin. *Cyathea wendlandii* differs from *C. pinnula* by its petiole scales that are smaller (10–15 × 1–1.5 mm) and linear, denser petiole scurf, once-forked fertile veins, entire to crenulate ultimate segments, inframedial sori, minute (ca. 0.1 mm long) appressed hairs on the costules, and tangled mass of paraphyses that are conspicuous after all the sporangia have fallen. In contrast, *C. pinnula* has larger (10–20 × 3–5 mm) lanceolate petiole scales, sparse or absent petiole scurf, simple fertile veins, serrate lobes and segments, medial sori, longer (0.3–0.4 mm) spreading to erect hairs on the costules, and untangled paraphyses that do not appear as a dense mass after the sporangia have fallen (Fig. 3b, e).

Cyathea nigripes differs from *C. pinnula* by its forked fertile veins, entire to crenulate lobes or segments, absence of hairs on the costules, presence of numerous minute squamellae on the costules, brownish costular scales, few short paraphyses, and inframedial sori (Fig. 9c, d).

Cyathea pinnula resembles *C. pilosissima* (Baker) Domin (in Panama and the Chocó) by having the laminar tissue pubescent between the veins; however, *C. pilosissima* differs by having more dense, even pubescence between the veins, pubescent rachises, white costular scales, and entire or crenulate ultimate segments.

Cyathea mucilagina R. C. Moran, sp. nov. TYPE: Costa Rica. Heredia: between Quebrada Tigre and E fork of Río Sardinal, ca. 9 km SW of Las Horquetas, 10°17′N, 84°02′W, 600 m, *Grayum et al. 5042* (holotype, MO; isotypes, CR not seen, US, UC). Figure 4.

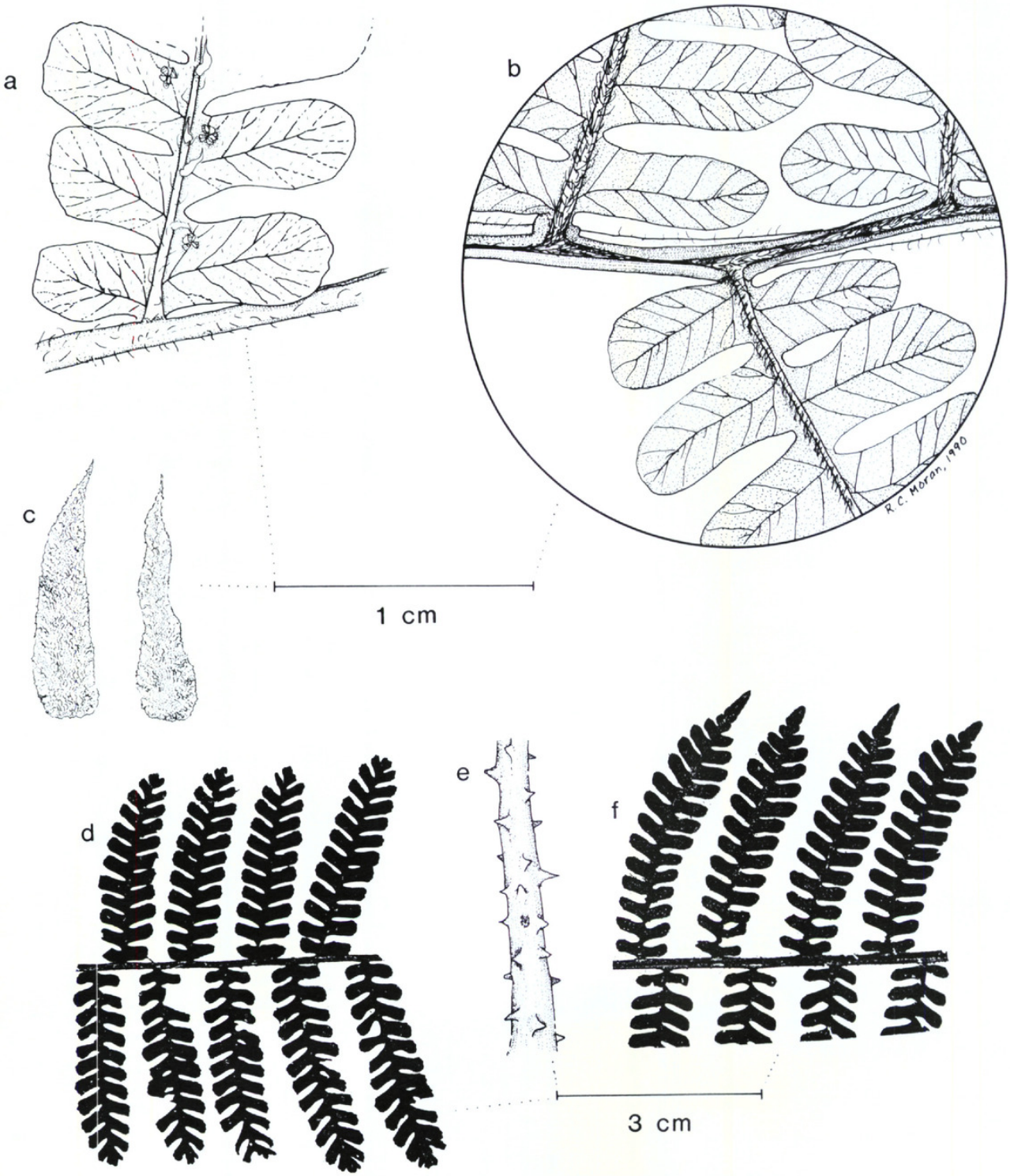


Figure 4. *Cyathea mucilagina.* —a. Pinnule base. —b. Adaxial surface of costa showing wing. —c. Petiole scales. —d. Medial pinnules. —e. Petiole base. —f. Medial pinnules. a, c, d, e, *Grayum et al. 5042*, MO. b, f, *Grayum & Chazdon 6832*, MO.

Folia juvenilia mucilagina; petiolus pallide brunneus, spinosus, puberulus, squamis 15–20 × 4–5 mm, penitus albide brunneis vel parte centrali pallide brunnea, lanceolatis vel elongate oblongis, flaccidis; pinnulae 3.5–5.5 × 1–1.5 cm, sessiles, lobis 2–3 mm latis, obtusis; rhachis costaeque pallide brunneae, spinis destitutae, adaxaliter alatae, alis viridibus, erectis; lamina inter venas pubescens; venae simplices vel semel furcatae; sori ex inframediano ad supramediani, paraphysibus conspicuis; indusia nulla.

Trunk 0.3–2 m tall; petiole tan or light brown, puberulent, spiny, the spines usually 2–3 mm long; petiole scales 15–20 × 4–5 mm, flaccid, matted, whitish brown or light brown medially, lanceolate to long-oblong; petiole scurf present, whitish; lamina 2-pinnate-pinnatifid, ovate to elliptic, gradually tapered to the apex; pinnae 3.5–5.5 × 1–1.5 cm,

sessile; ultimate segments 2–3 mm wide, 10–12 per pinnule, obtuse, entire or denticulate at the apex; rachis and costae tan to light brown, not spiny, with an erect, membranaceous, green wing adaxially, pubescent abaxially, the hairs 0.4–2 mm long, 3–6-celled, spreading, hyaline to whitish, subulate, scales rare or absent; costules pubescent with hairs like those on the costa, scaly, the scales whitish, lanceolate to oblong, flat or bullate at the base, entire; fertile veins simple or 1-forked, 4 or 5 per lobe, pubescent with hairs like those on the costules; laminar tissue between the veins pubescent, the hairs ca. 0.2 mm long, erect to spreading; sori inframedial to supramedial, nonindusiate, without delicate, irregular scales; paraphyses longer than the sporangia, conspicuous, tawny.

Paratypes. COSTA RICA. HEREDIA: forest between the Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17′N, 84°4.5′W, 800–1,000 m, *Grayum & Chazdon 6832* (MO, UC). PERU. HUÁNUCO: hills E of Tingo María, *Croat 21153* (MO, UC).

Cyathea mucilagina grows in wet forests from 600 to 1,000 m. It resembles *Cyathea pilosissima* (Baker) Domin by its laminar tissue pubescent between the veins and whitish costular scales; however, *C. pilosissima* (in Panama and the Chocó) has shiny, rigid, dark brown petiole scales with narrow white or light brown borders, nonalate rachises and costae, pinnules 5–9 cm long, and nonmucilaginous croziers. In contrast, *C. mucilagina* has dull, matted, brownish white petiole scales, adaxially alate rachises and costae (Fig. 4), pinnules 3.5–5.5 cm long, and mucilaginous croziers.

Cyathea werffii R. C. Moran, sp. nov. TYPE: Ecuador. Morona-Santiago: along new road Mendez–Morona, km 55–62, bosque húmedo, 800 m, *van der Werff & Gudiño 11386* (holotype, MO; isotypes, AAU, QCNE, UC). Figure 5.

Petiolus obscure flavidobrunneus, spinis destitutus, squamis 3–7 × 1–2 mm, lanceolatis, atrobrunnea parte centrali marginibus albis et interdum atrodenticulatis; lamina 35–50 cm longa, 1-pinnato-pinnatifida vel 2-pinnata, ex angusto lanceolato anguste elliptica; pinnulae ca. 2.3 × 1 cm, obtusae; lobi pinnularum 4–6 mm lati; rhachis pubescens trichomatibus 0.2–0.4 mm longis; squamae costularum 0.5–1 mm longae, brunneae, bullatae; sori mediani, paraphysibus inconspicuis; indusia nulla.

Trunk height unknown, width ca. 2 cm; petiole dull yellow-brown, not spiny, scurf absent; petiole scales 3–7 × 1–2 mm, lanceolate, bicolorous, dark brown medially with white borders (the proportions of brown and white varying considerably), the margins erose with occasional dark brown cells; lamina 35–50 cm long, 1-pinnate-pinnatifid to 2-pinnate, narrowly lanceolate to narrowly elliptic, tapering to the apex; pinnae 15–20 pairs, alternate; pinnules (of 2-pinnate leaves) to 2.3 × 1 cm, obtuse, crenate or shallowly lobed; lobes or ultimate segments (of 1-pinnate-pinnatifid leaves) 4–6 mm wide, obtuse to slightly truncate, ca. 12 pairs per pinna, entire; rachis light yellowish brown, lacking scales or nearly so, pubescent, the hairs 0.2–0.4 mm long, subulate, light brown, erect to spreading; costae sparsely pubescent with hairs like those on the rachis, scaly, the scales 0.5–1 mm long, brown, bullate with abruptly acuminate and often whitish apices; veins simple or forked, glabrous on both surfaces; laminar tissue between the veins glabrous on both surfaces; sori medial; paraphyses inconspicuous, shorter than the sporangia, brown; indusia absent.

Paratype. PERU. AMAZONAS: Puerto Nazareth, 540 m, *Ellenberg 3489* (UC).

Cyathea werffii grows in wet forests in Ecuador and Peru from 540 to 800 m. This species resembles *Cyathea phalaenolepis* (C. Chr.) Domin in leaf cutting and outline. *Cyathea phalaenolepis* differs, however, by its pilose petiole and rachis (the hairs 2–3 mm long), larger petiole scales (9–15 × 4–6 mm), and restricted occurrence in the Chocó region from 0 to 300 m. This new species is named for Henk van der Werff, Missouri Botanical Garden, who has made hundreds of superb fern collections and has given me much help and encouragement in pteridology.

Cyathea brevistipes R. C. Moran, sp. nov. TYPE: Ecuador. Loja: Parque Nacional *Podocarpus*, along road from Yanaga to radio towers on Cerro Toledo, mostly collected in shrubby páramo, 2,900–3,200 m, *van der Werff & Palacios 9185* (holotype, MO; isotype, UC). Figure 6.

Petiolus 2–11 cm longus, spinis carens, trichomidiis adpressis, ex albido pallide brunneis, squamis 15–30 × 2–3 mm, ex lanceolato linearibus; lamina 40–100 cm longa, elliptica; pinnulae 2.5–6.5 × 0.6–1.8 cm, fere sessiles, lobulis 2–6 mm latis, ex integro crenulatis; squamae costularum integrae, aureobrunneae, ex lanceolato ovatae, complanatae vel bullatae; venae semel furcatae, adaxialiter pubescentes, abaxaliter glabrae; sori inframediani, paraphysibus inconspicuis; indusia globosa.

Trunk 1.5–3 m tall, ca. 3 cm wide; petiole 2–11 cm long, brown to yellowish brown, not spiny, scurf consisting of whitish to light brown, appressed trichomidia; petiole scales 15–30 × 2–3 mm, lanceolate to linear, shiny dark brown medially (with occasional blackish areas) with lighter brown mar-

Figure 5. *Cyathea werffii.* —a. 2-pinnate leaf. —b. 1-pinnate-pinnatifid leaf. —c. Petiole scales. —d. Pinna base with mostly bullate scales. a–d, *van der Werff & Gudiño 11386*, MO.

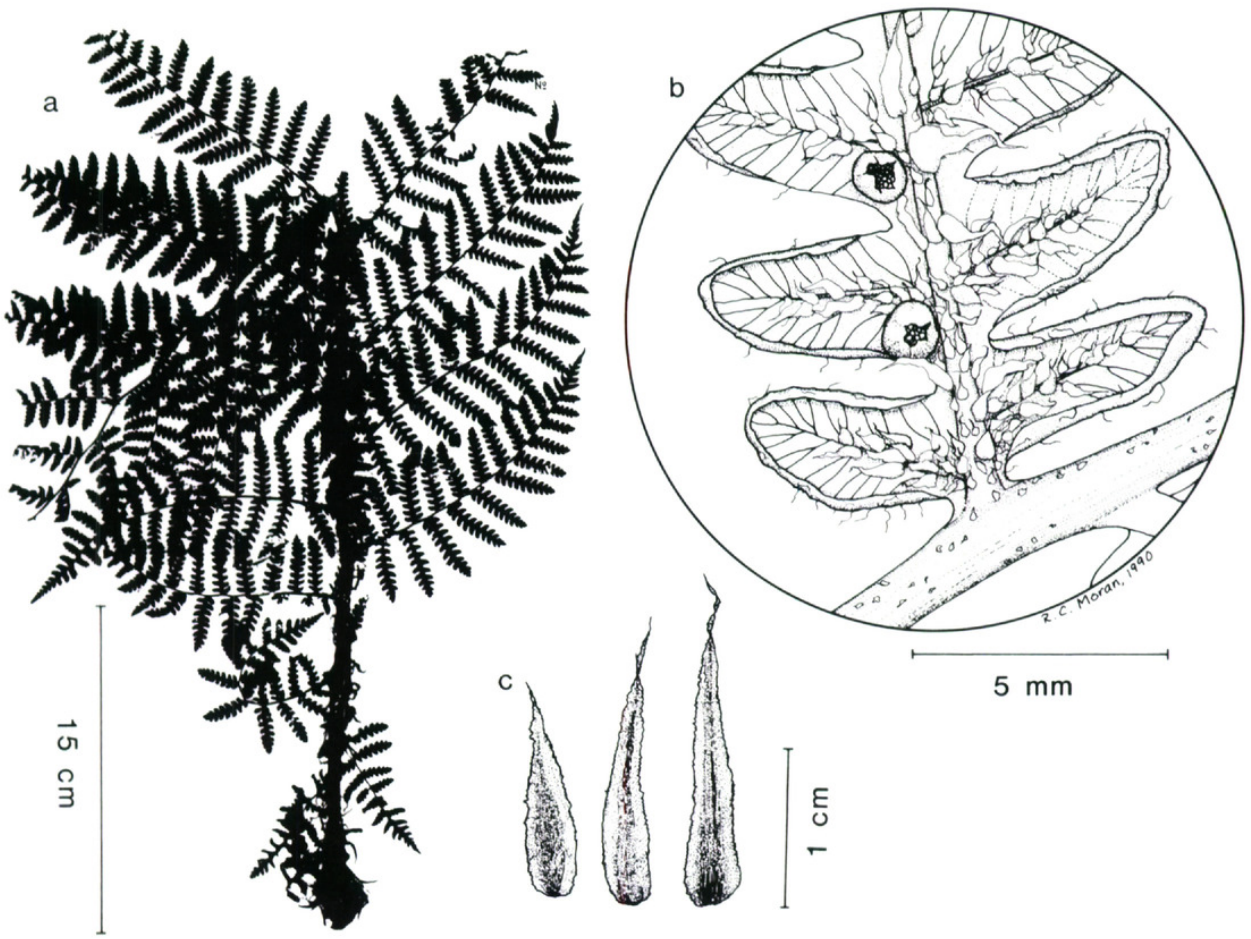


Figure 6. *Cyathea brevistipes.* —a. Fertile leaf. —b. Pinnule base. —c. Petiole scales. a–c, *van der Werff & Palacios 9185*, MO.

gins (these easily abraded or yellowish brown and nearly concolorous); lamina 40–100 cm long, elliptic with the basal pinnae strongly reduced and remote from the next distal pair, the apex gradually tapered; pinnae (exclusive of the distal pinnatifid ones) 11–14 pairs, alternate; pinnules 2.5–6.5 × 0.6–1.8 cm, sessile or nearly so; ultimate segments 2–6 mm wide, entire to crenulate, 10–12 pairs per pinnule, obtuse to acute; rachis, costae, costules, and midribs of the ultimate segments scaly and lacking hairs or puberulent, the scales golden brown, entire, ovate to lanceolate and becoming (on the distal portions of the leaf) orbicular-bullate with abruptly acuminate apices; veins 1(–2)-forked, 5–7 per ultimate segment, dark, glabrous abaxially, pubescent adaxially; laminar tissue between the veins glabrous abaxially, pubescent adaxially, the hairs 0.2–0.4 mm long, appressed, jointed, tortuous, whitish; sori subcostular, borne at the vein fork, indusiate, the indusium sphaeropteroid, with a darkened, indistinct apical umbo; paraphyses inconspicuous, shorter than the sporangia, dark reddish brown.

Paratypes. ECUADOR. LOJA: Cordillera del Loro, 50 km N of Loja, just before descending towards Saraguro, along road to radar station, 3,000–3,200 m, *van der Werff & Palacios 9429* (MO, QCNE, UC); Parque Nacional *Podocarpus*, along road from Yangana to radio towers on Cerro Toledo, 2,900–3,200 m, *van der Werff & Palacios 9187* (MO, QCNE, UC). BOLIVIA. LA PAZ: Dtto. Nor Yungas, 1.4 km E de Cotopata, por el camino entre Unduavi y Chuspipata, bosque nuboso, 3,200 m, *Solomon 18682* (MO, UC); Nor Yungas, La Paz–Yolosa road, ca. 1 km past Cotopata, 3,200 m, *Fay & Fay 2952* (MO).

Cyathea brevistipes grows in shrubby windswept páramos and cloud forests from 2,900 to 3,200 m. It can be distinguished from other Andean species of *Cyathea* by the combination of short (2–11 cm long) petioles, brown, nearly concolorous petiole scales, small (40–100 cm long), elliptical laminae, pubescence of the adaxial surface, subcostular sori, and globose indusia. The basal pinnae are often remote from the suprabasal ones, leaving a gap along the petiole. They occupy a position like the aphlebioid pinnae in *Alsophila*.

I am not sure which species of *Cyathea* is most closely related to *C. brevistipes*, but Rolla Tryon (then at GH, now at USF) annotated the holotype as "C. sp. nov., *straminea* aff." *Cyathea brevistipes*

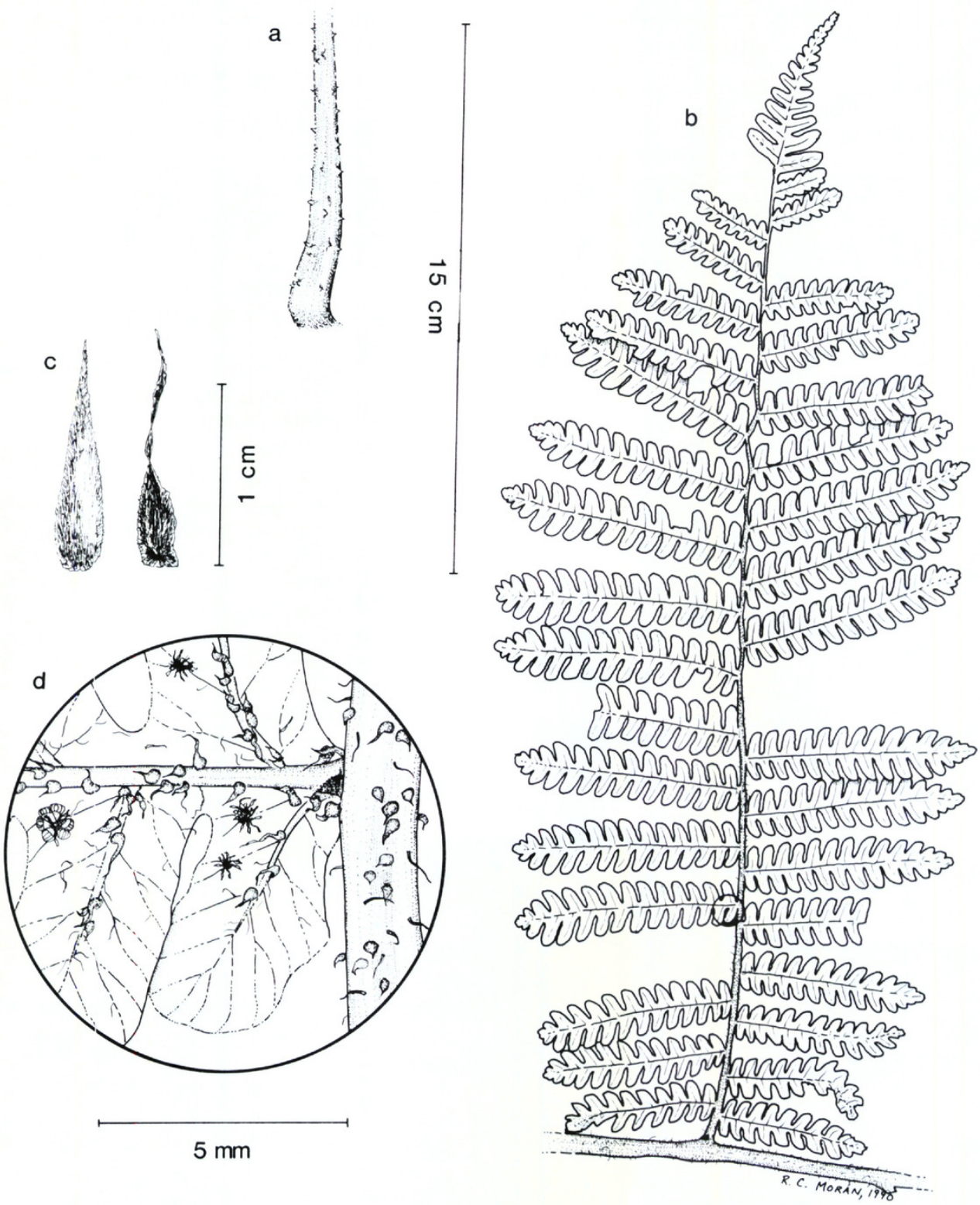


Figure 7. *Cyathea darienensis.* —a. Petiole base. —b. Medial pinna. —c. Petiole scales. —d. Pinnule base, enlargement of circular area shown in b. a, c, *Gentry & Clewell 6957*, MO. b, d. *Hartman 12350*, MO.

differs from *C. straminea* Karsten by its nonspiny petioles, dark brown scales, narrower (0.6–1 cm wide) pinnules, lack of dark peripheral or apical processes on the scales of the axes, entire to crenulate ultimate segments, and inframedial sori. In contrast, *C. straminea* has (according to Tryon, 1986) muricate to aculeate petioles, whitish to pale brown petiole scales, wider (1–2 cm) pinnules, presence of dark peripheral or apical processes on the scales of the axes, slightly to deeply crenate ultimate segments, and nearly medial sori.

Cyathea darienensis R. C. Moran, sp. nov. TYPE: Panama. Darién: summit of Cerro Pirre, 1,000–

1,400 m, 29 Dec. 1972, *Gentry & Clewell 6957* (holotype, MO). Figure 7.

Petiolus atrobrunneus, muricatus, squamis 10–12 × 2–3 mm, concoloribus, lanceolatis, brunneis vel flavide brunneis; pinnulae 5–7 × 1.1–1.7 cm, sessiles, lobulis 3–4.5 mm latis, integris vel crenulatis; costulae squamatae et pubescentes, squamis aureobrunneis, ex ovato lanceolatis vel orbicularibus et bullatis apicibus abrupte acuminatis, trichomatibus erectis subulatis; venae semel furcatae vel raro simplices; sori ex mediano supramediani, paraphysibus inconspicuis; indusia nulla.

Trunk 2–3 m tall, 2–3 cm wide; petiole dark brown, sparsely muricate, the spines less than 1 mm long, scurf present, light brown, easily abraded; petiole scales 10–12 × 2–3 mm, brown to yellow-brown, concolorous or nearly so, entire to denticulate; lamina 0.6–1 m long, 2-pinnate-pinnatifid, ovate, gradually tapered to the apex (always?); pinnae 7–10 pairs (exclusive of apical pinnatifid pinnae), alternate; pinnules 5–7 × 1.1–1.7 cm, sessile, sides parallel for most of their length, apices obtuse to broadly acute; lobes 3–4.5 mm wide, obtuse, 10–13 pairs per pinnule, entire; rachis and costae brown to purplish brown, pubescent, the hairs 1–1.5 mm long, 5–8-celled, hyaline to light brown, spreading; costules and midribs of the ultimate segments pubescent and scaly, the hairs resembling those of the rachis and costae, the scales golden brown, flat and ovate to lanceolate, grading into bullate-orbicular with abruptly acuminate, uniseriate apices; veins 1-forked or rarely (on the same leaf) simple, 4–7 pairs per lobe, dark, sparsely pubescent, the hairs resembling those on the axes; laminar tissue between the veins glabrous; sori medial to supramedial, borne at the vein fork, nonindusiate, without delicate, irregular scales; paraphyses shorter than the sporangia, brownish.

Paratypes. PANAMA. DARIÉN: Cerro Pirre, ridge top near Rancho Plastico, 1,200 m, *Folsom 4245* (MO), *Duke & Elias 13699* (MO); Cerro Sapo, 1,085 m, *Hammel 1174* (MO); SW ridge leading to Alturas de Nique on the Colombian border, 800–900 m, *Hartman 12350* (MO); Parque Nacional del Darién, Panama/Colombia border, near gold mine at headwaters of N branch of Río Pucuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, *Hammel et al. 16560* (MO); Parque Nacional Darién, camino de la Estación de Pirre hacia Rancho Frio, entre el mirador y El Real y la Estación de Pirre, *Polanco 505* (PMA); Serranía de Pirre, NW slope of mountain range, ca. 10 km SSE of El Real, elfin cloud forest, 1,400 m, *Reveal & Duke 4934* (US). PANAMA/COLOMBIA: top of Serranía del Darién, exactly on the frontier with Panama, NE of Cerro Mali, lower montane wet forest, 1,400–1,500 m, *Gentry et al. 17007* (MO).

Cyathea darienensis grows in rainforests and cloud forests from 800 to 1,500 m and is endemic to the Serranía del Darién along the Panamanian–Colombian border. *Cyathea darienensis* is most closely related to *C. brunnescens*. Although Barrington (1978) did not see specimens of *C. darienensis*, this species would key in his monograph to *C. brunnescens* (as *Trichipteris nigripes* var. *brunnescens*). Lellinger (1989) treated *C. darienensis* under *Cyathea nigripes* var. *brunnescens* (Barrington) Lellinger, thus accounting for his citation of "summit of Cerro Pirre" and the elevational extreme of 1,400 m given in parenthesis. In addition to the two characteristics given in the key at the end of this paper, *C. darienensis* differs from *C. brunnescens* by its lack of a delicate, irregular scales attached to the receptacle, darker brown axes, and more numerous bullate scales along the costules.

Cyathea darienensis might be confused with *C. schiedeana* (C. Presl) Domin because both have bullate scales on the costules. *Cyathea darienensis*, however, has concolorous petiole scales, muricate or slightly spiny petioles, nonmuricate rachises, dark brown axes, and pubescent laminar tissue, veins, and axes. In contrast, *C. schiedeana* has (in Costa Rica and Panama) bicolorous petiole scales with narrow white margins, well-developed spines on the petioles, sparsely muricate rachises, tan or light brown axes, and hairs absent on the axes, veins, and laminar tissue between the veins.

Cyathea darienensis also resembles *C. tortulosa* (described herein) by having the axes pubescent with subulate hairs 1–1.5 mm long and concolorous petiole scales. The two differ, however, in geography, elevational range, and the five morphological characters given in the key at the end of this paper.

Two collections from El Valle (*Cuatrecasas 15037*, US; *Killip 11534*, US) and one from Chocó (*Killip 35132*, US), Colombia, greatly resemble *C. darienensis* in cutting and pubescence and may eventually prove to be conspecific. They differ by having larger laminae, lighter axes, and much fewer bullate scales on the costae and costules.

Cyathea squamulosa (Losch) R. C. Moran, comb. nov. Basionym: *Hemitelia squamulosa* Losch, Mitt. Bot. Staatssml. München 1: 20. 1950. TYPE: Costa Rica. Cartago: Orosi, 1,100 m, 14 Mar. 1932, *Kupper 798* (holotype, M not seen, photo BM not seen).

Stem 1–1.5 m; petiole brown, spiny present, brownish, the scales 15–25 × 0.4–0.8 mm, lanceolate, nearly concolorous, brown to yellowish brown; lamina 2-pinnate-pinnatifid, with an evenly tapered, pinnatifid apex; pinnae stalked up to 8 cm; pinnules 8–12 × 1.5–2 cm, stalked 1–3 mm; ultimate segments ca. 4 mm wide, 12–16 pairs per

pinnule, entire or nearly so, obtuse; rachis puberulent, brown or tan, the hairs ca. 0.1 mm; costae pubescent and scaly, the hairs 0.1–0.3 mm, whitish, terete basally, antrorsely strigose, the scales 0.3–0.4 mm, shiny, brown, bullate with apiculate apices pointing toward the rachis; costules pubescent and scaly, the hairs ca. 0.1 mm, appressed, pale reddish, the scales like those on the costae but mixed with a few larger ovate ones; veins simple or 1-forked, 6–8 per segment, puberulent, the hairs ca. 0.1 mm, appressed, pale reddish; sori medial; paraphyses shorter than the sporangia, inconspicuous; indusium scalelike, partly arched over the sorus.

Additional specimens examined. COSTA RICA. CARTAGO: ca. 10 km S of Tapantí along the new road on the E slope above the Río Grande de Orosi, 1,600 m, *Burger & Burger 7578* (MO); Tapantí Reserve, 1,300–1,800 m, *Gómez 19213* (MO, UC), *Pérez-García 227* (MO), *Smith 2191* (MO, UC); new road from Tapantí, ca. 7 km S of bridge, 1,500 m, *Hauke 413* (UC); SE of Orosi, 1,800–2,300 m, *Lellinger 1517* (MO, UC); Taucito de Orosi, 1,400 m, *Pérez-García 176* (MO). PANAMA. CHIRIQUÍ: along road to Fortuna Dam site N of Gualaca on Río Chiriquí, 17.8 mi. beyond the bridge over Río Esti, 7.7 mi. beyond Los Planes de Hornito, 6.6 mi. beyond jct. of road to tunnel, 1,400 m, *Croat 48775* (MO).

Cyathea squamulosa is known only from the Orosi–Tapantí region in Costa Rica and near Fortuna Dam in Panama. It grows in wet forests at middle elevations (1,300–2,300 m).

In his revision of *Cyathea* in the New World, Tryon (1976) placed *C. squamulosa* in synonymy with *C. multiflora* J. E. Smith based on comparison of the original description of the former with specimens of the latter. Tryon apparently did not see any collections of *C. squamulosa* except for a photograph of the holotype. Although I have not seen the holotype, I feel confident that the name is applied here correctly because the original description clearly states that the species has numerous brown bullate scales and hemitelioid indusia. I have examined several collections of *C. squamulosa* and find that it can be distinguished from *C. multiflora* by its numerous, shiny, brown, bullate scales on the axes, stalked pinnae and pinnules, larger and paler petiole scales, and occurrence at higher elevations (*C. multiflora* occurs from 0 to 1,100 m). Although *C. multiflora* is variable in hair type, *C. squamulosa* has only one type of hair along the costules and veins abaxially. These hairs are minute (ca. 0.1 mm long), pale reddish, and appressed.

Cyathea squamulosa, however, is more closely related to *C. schiedeana* (C. Presl) Domin (formerly placed in *Trichipteris*) than *C. multiflora*. *Cyathea squamulosa* differs from *C. shiedeana* only by its stalked pinnae and pinnules, larger and paler petiole scales, and presence of indusia. Otherwise, the hairs and scales on the abaxial surface of the lamina are the same in the two species, and the cutting of the lamina is also similar. These two species, which are very closely related, provide the best example of the artificiality of maintaining *Trichipteris* distinct from *Cyathea*.

Cyathea tortuosa R. C. Moran, sp. nov. TYPE: Ecuador. Napo: Reserva Biológica Jatun Satcha, ca. 8 km ESE de Misahualli, 1°04′S, 77°36′W, 450 m, *Moran & Rohrbach 5187* (holotype, MO; isotypes, F, QCNE, UC, US). Figure 8.

Petiolus ex pallido atrobrunneus, muricatus vel spinosus, squamis 15–20 × 2.5–4 mm, lanceolatis, concoloribus, brunneis; pinnulae 7–10 × 1.5–2 cm, sessiles, lobulis 3–5 mm latis; costulae pubescentes, trichomatibus duorum modorum, altero pilis subulatis et erectis, altero pilis tortuosis et adpressis; venae semel furcatae; sori ex mediano supramediani, paraphysibus inconspicuis; indusia nulla.

Trunks 1–5 m tall, 4–6 cm wide; petiole light to dark brown, muricate to spiny, the spines up to 2 mm long, scurf present, brown to light brown, easily abraded; petiole scales 15–20 × 2.5–4 mm, lanceolate, concolorous, brown, with or without a 1- or 2-cell-wide border of divergent, irregular cells, the margins ciliate, the cilia hyaline, 1–2-celled, easily abraded; lamina 1–1.5 m long, 2-pinnate-pinnatifid, broadly elliptic, abruptly reduced to a pinnalike apex; pinnae 9–11 pairs (exclusive of the pinnalike apical portion), alternate; pinnules 7–10 × 1.5–2 cm, sessile or (in large pinnae) short-stalked to 1 mm, the sides parallel for ca. ¾ of their length, the apex obtuse to acuminate; ultimate segments 3–5 mm wide, 12–17 pairs per pinnule, entire to crenulate, obtuse; rachis and costae tan to brown, pubescent, the hairs 0.8–1.5 mm long, subulate, hyaline to brownish, 4–7-celled, spreading; costules pubescent with 2 kinds of hairs and sparsely scaly, the first type of hair subulate and resembling those on the rachis and costae, the second type of hair 0.1–0.3 mm long, whitish to hyaline, mostly appressed, tortuous, the scales few, ovate-lanceolate to linear-lanceolate, flat to bullate, golden brown; midribs of the lobes pubescent and sparsely scaly, the hairs 0.1–0.3 mm long, whitish to hyaline, mostly appressed, tortuous, the scales 0.2–0.3 mm long, bullate, golden brown; veins 1-forked, dark, 5–7 pairs per ultimate segment, glabrous; laminar tissue between the veins glabrous; sori medial to supramedial, borne at the vein fork, nonindusiate, often with a delicate, hyaline, irregular scale(s) attached to the receptacle (Fig. 8b), these easily detached

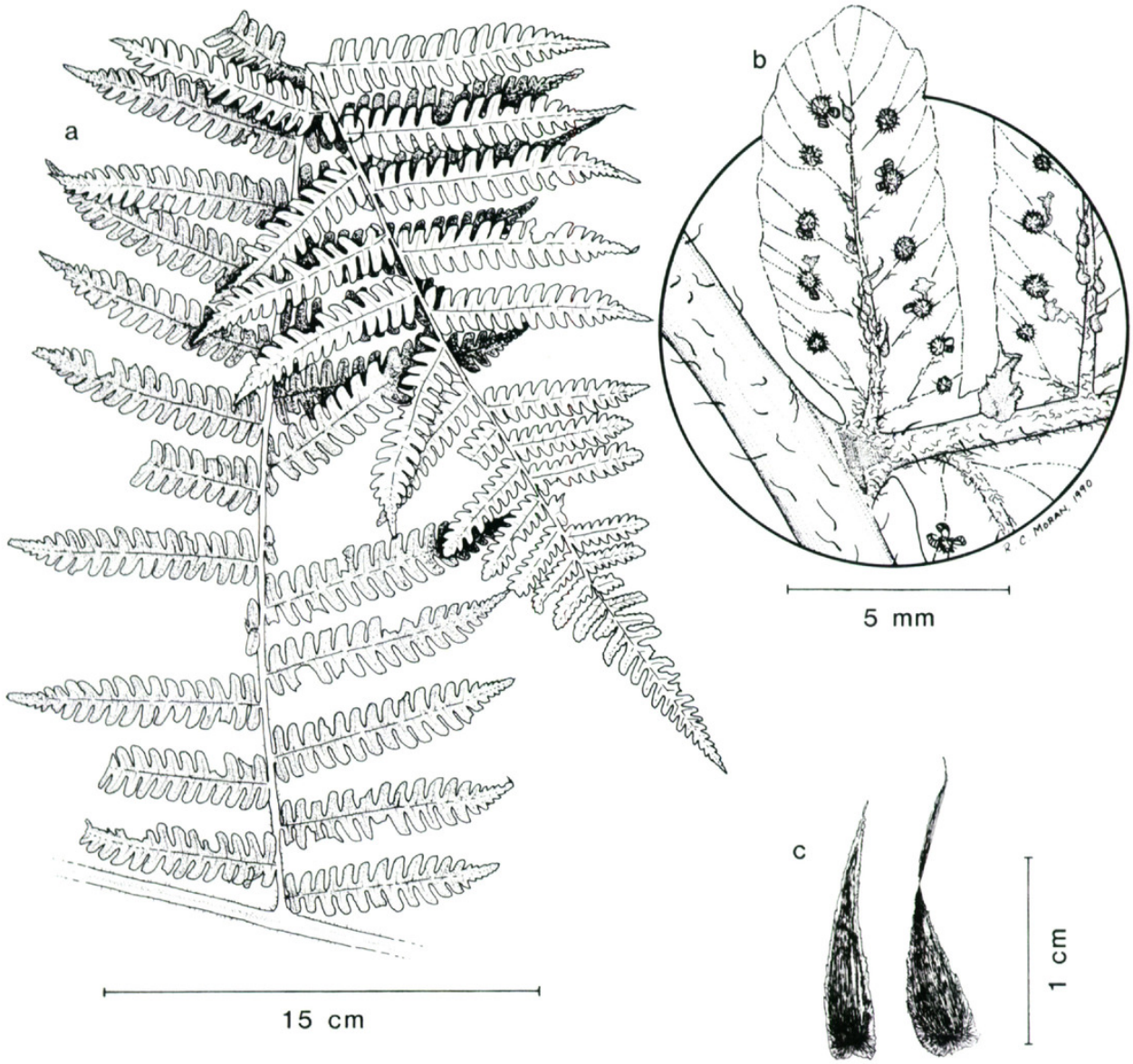


Figure 8. *Cyathea tortuosa*. —a. Medial pinna. —b. Close-up of circle shown in a. Note tortuous hairs and irregular scales attached to some of the receptacles. —c. Petiole scales. a–c, *Miller et al. 2417*, MO.

and often not present; paraphyses shorter than the sporangia, inconspicuous.

Paratypes. COLOMBIA. PUTUMAYO: Mocoa, Quebrada del Río Mulato, 570–600 m, *Cuatrecasas 11299* (US); Uchupayaco, en la planada entre Urcusique y Umbria, en las orillas del Río Uchupayaco, 300 m, *Schultes 3299* (US), *3365* (US). ECUADOR. MORONA-SANTIAGO: along new road Mendez–Morona, 800 m, *van der Werff & Gudiño 11344* (MO, QCNE). NAPO: Cantón Tena, Río Blanco Community, 6 km NNW of Ahuano, 440 m, *Kohn 1209* (QCNE); Cantón El Chaco, valle de Río Quijos, 650 m, *Palacios 5748* (MO, QCNE); Jatun Sacha Biological Station, 8 km E of Misahuali, permanent tree plot no. 1, 450 m, *Gentry et al. 59839* (MO, QCNE), *59898* (MO), *60036* (MO, QCNE, UC), *60231* (MO, QCNE, UC), *Cerón 743* (MO, QCNE), *Miller et al. 2417* (MO, UC); Hacienda Cotapino (Concepción), ca. 550 m, *Harling et al. 7107* (MO, US). PASTAZA: along newly constructed portion of road to Canelos, departing from main Puyo–Macas road at ca. 32 km from Puyo, 22.5 km S of Veracruz, 3.8 km from turn-off, near maintenence camp, ca. 1°37′S, 77°51′W, ca. 850 m, *Croat 58982* (MO, UC). SANTIAGO–ZAMORA: Taisha, ca. 500 m, *Cazalet & Pennington 7665* (UC). PERU. LORETO: above Pongo de Manseriche, streamlet near mouth of Río Santiago, 210 m, *Mexia 6191* (MICH, MO). PASCO: Prov. Oxapampa, near Shiringamazu, up Río Mamuriz, 1–2 km from Río Palcazu, 75°12′W, 10°14′S, 350 m, *Smith & Salick 8370* (MO).

Cyathea tortuosa grows in wet forests of Amazonian Colombia, Ecuador, and Peru, from 200 to 550(to 850) m. The specific epithet *tortuosa* refers to the whitish to hyaline, mostly appressed-tortuous hairs, which occur on the abaxial surface of the costules and midribs of the ultimate segments (Fig.

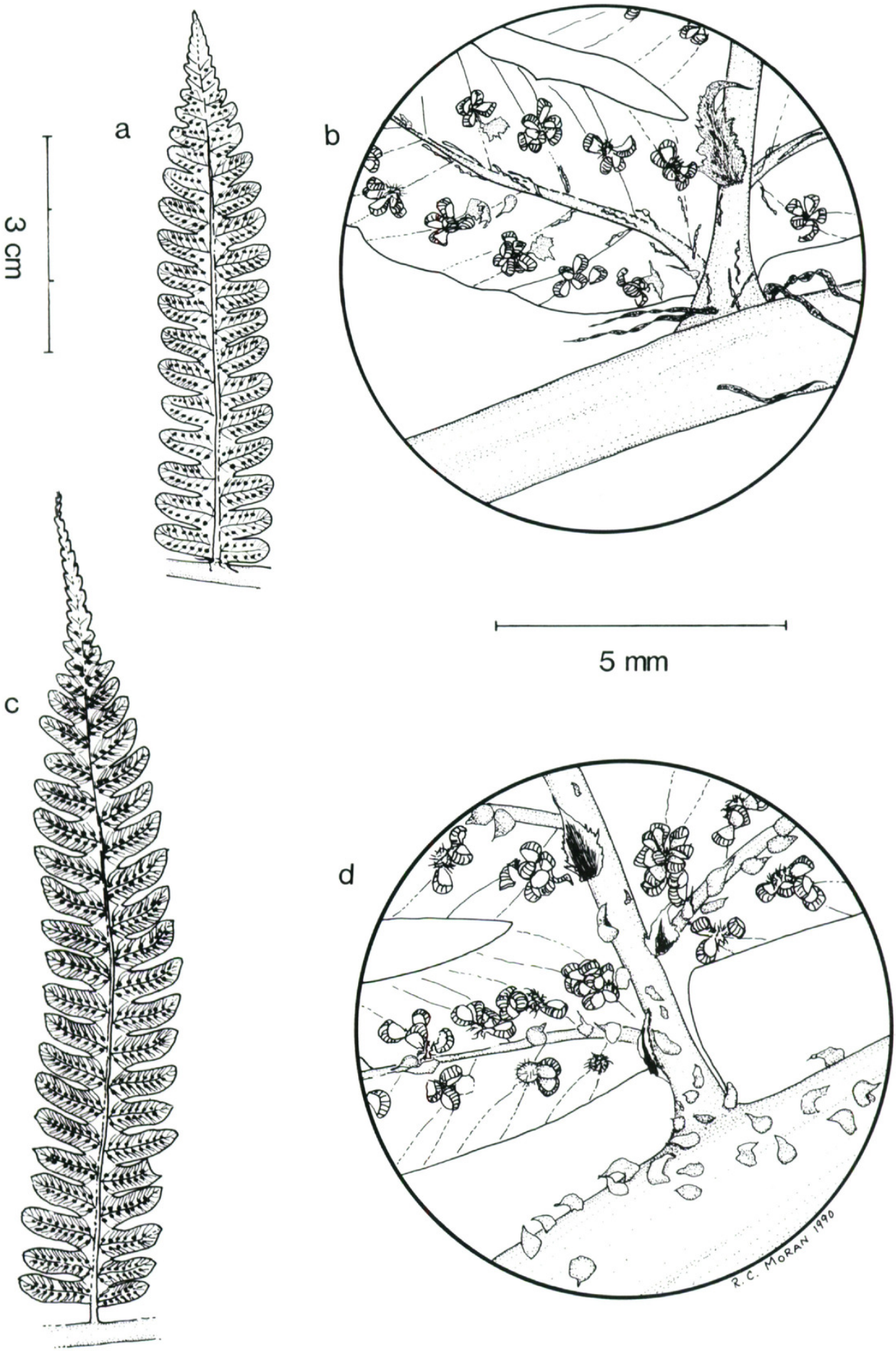
8b). *Cyathea bradei* (Windish) Lellinger has similar hairs but differs most notably by its anastomosing basal veins and presence of a hemitelioid indusium. *Cyathea cyatheoides* (Desv.) Kramer, from the Guianas, Venezuela, and northern Amazonian Brazil, also has similar hairs but differs by possessing a true indusium, longer stalked and wider (2–3 cm) pinnules, setate costular scales, longer and more numerous spines on the petiole, and absence of long, hyaline, subulate hairs on the axes.

Specimens of *C. tortuosa* were cited by Barrington (1978) as *Trichipteris nigripes* (C. Chr.) Barrington var. *brunnescens* Barrington (= *C. brunnescens* (Barrington) R. C. Moran), and by Tryon (1986) as *T. nigripes* (s.l.). *Cyathea tortuosa* differs from *C. brunnescens* by the numerous subulate hairs on the axes, the minute, whitish to hyaline, tortuous hairs on the costules and midribs of the ultimate segments (Fig. 8b), the lack of linear-filiform brown scales, and its occurrence in eastern Amazonia from Colombia to Peru. In contrast, *C. brunnescens* lacks both types of hairs on the axes and has brown, linear-filiform scales on all the axes (these being particularly abundant along the veins and midribs of the lobes; Fig. 9b), and occurs in the Chocó region in western Colombia to northwestern Ecuador. I have not seen any intermediate specimens, i.e., ones that have various combinations of the above characters. This absence of intermediates, plus the fact that each taxon has several correlating characteristics and distinct ranges, leads me to conclude that both should be treated as species. The two species, however, are closer to each other than to any other species of *Cyathea* and should be considered as sister taxa because they agree in all characteristics (other than those given above) including the presence of a delicate hyaline scale associated with the sorus—a character that is apparently unique in the genus (Fig. 8b).

Cyathea brunnescens (Barrington) R. C. Moran, comb. et stat. nov. Basionym: *Trichipteris nigripes* var. *brunnescens* Barrington, Rhodora 78: 4, t. 1, fig. 6. 1976. *Cyathea nigripes* var. *brunnescens* (Barrington) Lellinger, Amer. Fern J. 77: 101. 1988. TYPE: Colombia. Valle: Río Yurumangui, Veneral, 5–50 m, *Cuatrecasas 16155-C* (holotype, US; isotype, GH not seen). Figure 9a, b.

Trunk 1.5–5 m tall, 3–4 cm wide; petiole brown, spiny to tuberculate, the scales 20–30 × 3–5 mm, lanceolate with long-acuminate apices, concolorous, brown, scurf consisting of numerous brown squamellae; lamina 2-pinnate-pinnatifid, the apex abruptly contracted and pinnalike; pinnae stalked, the stalk 1–3 cm; pinnules 6–10 × 1.5–2.3 cm, sessile; ultimate segments 2–4 mm wide, 12–16 pairs per pinnule, entire to crenulate, obtuse; rachis and costae light brown to tan, not spiny, lacking hairs, scaly, the scales flat or becoming bullate on the distal portions of the lamina, brown, varying from large and ovate-lanceolate to minute and linear-filiform; veins 1-forked or rarely simple, 5–7 pairs per ultimate segment, sparsely scaly with filiform scales; laminar tissue between the veins glabrous; sori medial to supramedial, the paraphyses shorter than the sporangia, brown; indusium absent but scales often attached to the receptacle, the scales very delicate, hyaline, irregular, evanescent.

Additional specimens examined. COLOMBIA. CAUCA: Río Naya near El Pastico, 20–100 m, *Gentry & Juncosa 40624* (MO); Córdoba, Dagua Valley, 30–100 m, *Pittier 513* (US), *519* (US). CHOCÓ: La Concepción, 15 km E of Quibdó, *Archer 2090* (US); Mun. de Quibdó, sector puente de Cabí, carretera a Istmina, *Arias et al. 128* (MO); Mun. de Quibdó, Quebrada La Platina, carretera a Medellín, *Arias et al. 157* (MO); along road between Quibdó and Istmina, 6.6 km S of Quibdó, ca. 100 m, *Croat 52146* (MO); Río Negro, between Quibdó and Tutunendo, 80 m, *Cuatrecasas & Llano 24215* (US); Río Serrano, afluente del Río Atrato, *Forero et al. 1389* (MO); Hoya del Río San Juan, Quebrada Taparal, afluente del Río San Juan, alrededores de la comunidad indígena Waunaná de Taparalito, 5–10 m, *Forero et al. 4310* (MO, US); Mun. de Quibdó, Carretera Quibdó–Tutenendo, 15 km de Quibdó, 45 m, *Forero & Jaramillo 2553* (MO); Mun. de Quibdó, corregimiento de Guayabal, Río Hugón, 80 m, *Forero & Jaramillo 2789* (MO); Hoya del Río San Juan, Palestina, cerro al frente de la población, 30–40 m, *Forero & Jaramillo 4492* (MO, US); Mun. de Itsmina, Quebrada Raspadura, entre Raspadura y Quiadó, divorcio de aguas de las Hoyas del Río Atrato y del Río San Juan, *Forero & Jaramillo 5315* (MO, US); carretera Quibdó–Guayabal, 4 km de Quibdó, 40 m, *Forero et al. 1420* (MO); Mun. de Nóvita, vereda Llanadas, ladera N del Cerro Torrá, filo al Oeste del Río Surama, 600–900 m, *Forero et al. 3094* (MO); Carretera Tutunendo–El Carmen, margen del Río Atrato, 600 m, *Forero et al. 5969* (MO, US); area of Baudó, left bank of Río Baudó, 11.5 km upstream from the estuary, near Quebrada Anguerado, *Fuchs & Zanella 22158* (US); Istmina, carretera a Cértegui, 75 m, *García-Barriga 11180* (US); trail to Tubadó, Quibdó–Tutenendo road 14 km NE of Quibdó, 90 m, *Gentry & Renteria A. 24301* (MO); hills near highest point of Bagado–Certegui trail, 130–180 m, *Juncosa 1546* (MO); S of Río Condoto, between Quebrada Guarapo and Mandinga, 120–180 m, *Killip 35132* (US); NW side of Alto del Buey, 950–1,450 m, *Lellinger & de la Sota 212* (US); 1.5–2.5 km W of Istmina along the road to Pie de Pepé, 75–100 m, *Lellinger & de la Sota 428* (US); Mojarras de Tadó, 8.5 km E of Istmina, 150–250 m, *Lellinger & de la Sota 415* (US); low hills behind the beach, 1–1.5 km NW of El Valle N of the lagoon, 25–75 m, *Lellinger & de la Sota 361* (US). EL VALLE: Río Naya, Puerto Merizalde, 5–20 m, *Cuatrecasas 14072* (US); La Trojita, Río Calima, 5–50 m, *Cuatrecasas 16313* (US); Barco, Río Ca-


a
3 cm
b
5 mm
c
d
R.C. MORAN 1990

jambre, 5–80 m, *Cuatrecasas 16989* (US); San Isidro, Río Cajambre, 5–100 m, *Cuatrecasas 17297* (US); Río Cajambre, Silva, 5–80 m, *Cuatrecasas 17478* (US); Bajo Calima Concesión, ca. 16 km NW of Buenaventura, at end of Gasolina road, Juanchaco area, 50 m, *Faber-Langendoen et al. 750* (MO, UC); Córdoba, Dagua Valley, *Killip 11815* (US); Agua Clara, along hwy. from Buenaventura to Cali, ca. 100 m, *Killip & Cuatrecasas 38884* (UC, US); Córdoba, 50–100 m, *Killip & García 33421* (US); foothills of mountains near Buenaventura, ca. 2 hr. by bus from Cali, 100 m, *van der Werff & Brown 9750* (MO, UC). NARIÑO: Quebrada La Toma, on Río Telembi, between Río Pimbi and Río Cuembí, above Barbacoas, 70 m, *Ewan 16860* (UC, US). ECUADOR. PICHINCHA: Tinalandia, property of Hotel Tinalandia, 9.6 km E of Santo Domingo de los Colorados, S of hwy. to Aloag and Quito, above Río Toachi, 700 m, *Croat 55708* (MO, UC).

I consider *C. brunnescens* to be a species (rather than a variety of *C. nigripes* as it has previously been treated) because its distinguishing characteristics do not intergrade with those of other species and there are several that correlate: lack of hyaline subulate hairs on the axes, presence of linear-filiform brownish scales on the axes, medial sori, and sessile pinnules. In addition to these characteristics, *C. brunnescens* differs from *C. nigripes* (Fig. 9) by having 5–7 veins per lobe (vs. 8–10) and occurring at lower elevations.

Cyathea brunnescens is most closely related to *C. schiedeana*, which is another reason for not treating it as a variety of *C. nigripes*. Although *C. brunnescens* and *C. schiedeana* differ in the kinds of scales found on the axes (bullate vs. linear-filiform), they share several characteristics that distinguish them from *C. nigripes* (as well as many other species of *Cyathea*): well-developed petiole spines, sessile pinnules, fewer pairs of ultimate segments (10–14) per pinnule, fewer pairs of veins (4–7) pairs per ultimate segment, and medial sori. The lamina of *C. brunnescens* typically dries dark brownish green.

This species is endemic to the Chocó floristic region from 0 to 300(to 1,000) m. Lellinger's (1989) citation of this species (as *C. nigripes* var. *brunnescens*) from 1,500 m, Cerro Pirre, Panama, actually represents a specimen of *C. darienensis*. (See the discussion under *C. darienensis*.)

New circumscription of *Cyathea nigripes*

Cyathea nigripes has been poorly characterized in the past because not enough attention was paid to features of the hairs and scales on the abaxial surface of the lamina. The removal herein of the three species necessitates a new description of *C. nigripes* in the strict sense. After the following description is a key to *C. nigripes* and the three species previously included in it.

Cyathea nigripes (C. Chr.) Domin, Pteridophyta 263. 1929. *Alsophila nigripes* C. Chr., Index Filic. 45. 1905, nom. nov. for *Alsophila melanopus* Hook., Syn. Fil. ed. 1. 37. 1866, non Hassk. (1855). *Trichipteris nigripes* (C. Chr.) Barrington, Rhodora 78: 4. 1976. Lectotype (designated by Barrington, 1978): Ecuador. Chimborazo: Mt. Chimborazo, *Spruce 5742* (K not seen; isolectotype, P not seen).

Trunk 2–8 m tall, ca. 10 cm wide; petiole brown, muricate to spiny, the spines up to 5 mm long, scales (in the Andes) 20–30 × 2–4 mm, narrowly lanceolate to linear, brown with a very narrow white margin, thin but with a slightly thickened base, or (in Costa Rica and Panama) 10–20 × 2–3 mm, narrowly lanceolate, blackish or dark brown with very narrow white borders, thick (especially at the base); scurf consisting of numerous brown squamellae; lamina 1.5–2 m long, 2-pinnate-pinnatisect, ovate (?), gradually tapered to the apex; pinnae alternate, number of pairs unknown; pinnules 8–15 × 1.5–2 cm, stalked to 3 mm, with the sides parallel for most of their length or gradually tapered, the apex acuminate; ultimate segments 3–4 mm wide, 18–22 pairs per pinnule, entire to crenulate, obtuse to acute; rachis and costae brown, pubescent (in the Andes), the hairs ca. 0.2 mm long, antrorse, or (in Costa Rica) lacking hairs or nearly so and moderately squamellate, the squamellae 0.2–0.5 mm long, brown, ovate and occasionally subbullate, erect (Fig. 9d); costules scaly, the scales ca. 1 mm long, ovate to lanceolate, shiny blackish brown with white erose margins, scurf present, minute, hairlike; midribs of the ultimate segments with minute hairlike scurf; veins 1-forked, 8–10 pairs per ultimate segment, with minute scurf; laminar tissue between the veins glabrous; sori inframedial, borne at the vein fork, nonindusiate, lacking delicate scales; paraphyses shorter than the sporangia, inconspicuous, light brown.

Specimens examined. COSTA RICA. ALAJUELA: 18 km N of San Ramón, 1,200 m, *Armond 147* (F, MO);

←

Figure 9. *Cyathea brunnescens* (a, b) and *C. nigripes* (c, d). —a. Pinnule. —b. Basal basiscopic segment of pinnule. Note irregular scales attached to some of the receptacles. —c. Pinnule. —d. Basal segments of pinnule. a, b, *Forero & Jaramillo 4492*, MO. c, d, *Lellinger & White 1229* (MO).

N of San Ramón, ca. 4 km N of Balsa along road to Colonia Palmareña, 1,300 m, *Lellinger 1251* (UC), *1229* (MO). CARTAGO: valley of the Río Grande del Orosi, Tapantí to 7 km S, ca. 20 km SW of Cartago, 1,500 m, *Tryon & Tryon 7024* (F); slopes 4.5 km from bridge at Tapantí, ca. 1,500 m, *White & Lucansky 1968120* (US). SAN JOSÉ: 17 km N of San Isidro del General toward Cerro de la Muerte, 1,160 m, *Gastony & Gastony 754* (F); La Palma and vicinity, ca. 17 km NE of San José, above La Hondura, 1,450 m, *Gastony & Gastony 769* (F); La Ventana, adelante de La Palma, Parque Nacional Braulio Carrillo, 1,200–1,300 m, *Pérez-García 199* (MO). COLOMBIA. CALDAS: Río Santa Rita, Salento, 1,600–1,800 m, *Killip & Hazen 9013* (US). CAUCA: Km 19 on road from Cali to Buenaventura, *Barrington 501* (US). EL VALLE: Hoya del Río Dígua, Quebrada del San Juan, subiendo a Paragüita desde Queremal, 1,570–1,740 m, *Cuatrecasas 23813* (US); Santa Helena, above Topacio, edge of Los Farallones de Cali National Park, 1,940 m, *Gentry & Monsalve 53153* (MO, UC); Mpio. Calima, valle Sevilla–Barragán, 1 km de Sevilla, 1,600 m, *Silverstone 692* (MO, UC). VALLE DEL CAUCA: hoya del Río Calima, El Cairo, entre Darién y Mediacanoa, 1,650–1,750 m, *Cuatrecasas 13930* (US); hoya del Río Cali, Pichindé, Alto de las Brisas, 2,160 m, *Cuatrecasas 18240* (US); native forest of Finca Kyburz, E slope above the Bitaco River, Bitaco Valley 1 km above and E of Bitaco, Pacific slope of the western cordillera, ca. 1,500 m, *Hutchison & Idrobo 3003* (MO, UC, US). ECUADOR. COTOPAXI: Cacaoal, *Bell 918* (UC). PICHINCHA: Corazón, in Aug. 1892, *Sodiro s.n.* (UC); prope Sta. Domingo, 10/884, *Sodiro s.n.* (MO). DEPT. UNKNOWN: San Florentino, *Sodiro s.n.* (UC); near Angaurura, 12/906, *Sodiro s.n.* (MO).

Cyathea nigripes grows in wet forests from Costa Rica to Ecuador from 1,200 to 1,940 m. The Costa Rican and Panamanian specimens differ from the Andean ones by their conspicuously squamellate and nearly hairless rachises and costae, and smaller, darker, thicker petiole scales. Further study may reveal that they represent a distinct species.

Although Tryon & Stolze (1989) treated *Cyathea nigripes* in Peru, I have not seen a bona fide specimen of *C. nigripes* from that country, and the specimens they cited are probably referable to other species. For example, *Mexia 6191* is referable to *C. tortuosa*, and it is likely that the other specimens cited from the departments of Amazonas and Madre de Dios also represent that species. Two other specimens that they cited (*Croat 21153* and *Smith et al. 1179*) are certainly not *C. nigripes*, but I am not sure to what species they belong and perhaps they represent an undescribed species. These specimens differ from *C. nigripes* by lacking hairs on the axes, having brown or whitish bullate scales with filiform apices along the costules, strongly ascending veins, medial sori, and petiole scales without narrow whitish margins.

Key to the species formerly included in *Cyathea nigripes*

1a. Sori inframedial; largest pinnules 10–15 cm long, stalked 1–3 mm; lobes 15–20 per pinnule; veins 8–10 pairs per ultimate segment; (300–)1,000–1,600 m; Costa Rica to Ecuador ..... *C. nigripes*

1b. Sori medial to supramedial; pinnules 5–10 cm long, sessile or rarely short-stalked to 1 mm; lobes 10–17 per pinnule; veins 4–7 pairs per ultimate segment.

2a. Axes lacking hairs; at least some of the scales on the costae and costules linear-filiform; 0–300(–1,000) m; Chocó region of western Colombia and northwestern Ecuador ..... *C. brunnescens*

2b. Axes pubescent with hairs 1–1.5 mm long; none of the scales on the costae and costules linear-filiform.

3a. Costules and midribs of the ultimate segments pubescent with sublate, spreading, 4–7-celled hairs 0.8–1.5 mm long *and* tortuous, whitish to hyaline, mostly appressed hairs; largest pinnules 7–10 cm long; lobes 12–17 pairs per pinnule; veins glabrous or nearly so; sori with delicate, hyaline, irregular scales (these easily detached and often not present on a given sorus); 200–550(–800) m; Amazonian Colombia, Ecuador and Peru ..... *C. tortuosa*

3b. Costules and midribs of the lobes pubescent with subulate hairs as in the above species, but lacking tortuous, white to hyaline, mostly appressed hairs; largest pinnules 5–7 cm long; lobes 10–13 pairs per pinnule; veins sparsely pubescent; sori lacking delicate, hyaline, irregular scales; 800–1,500 m; Panama/Colombia border ..... *C. darienensis*

Acknowledgments. I thank Alan R. Smith for commenting on the manuscript, and Henk van der Werff and Bruno Manara for checking the Latin descriptions. I thank the curators at F, UC, and US for making loans available to me for study.

Literature Cited

Barrington, D. S. 1978. A revision of the genus *Trichipteris*. Contr. Gray Herb. 208: 3–93.

Lellinger, D. B. 1989. The ferns and fern-allies of Costa Rica, Panama, and the Chocó (Part 1: Psilotaceae through Dicksoniaceae). Pteridologia 2A: 1–364.

Tryon, R. M. 1986. 13. Cyatheaceae. *In:* G. Harling & L. Andersson (editors), Flora of Ecuador 27: 19–58.

——— & R. G. Stolze. 1989. Pteridophyta of Peru, Part I. 1. Ophioglossaceae—12. Cyatheaeceae. Fieldiana, Bot. n.s. 20: 1–145.