# Resolving the *Cyathea caracasana* complex (Polypodiopsida: Cyatheaceae)

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Abstract

In the course of studies on Neotropical tree ferns, several changes in the circumscription of species in the *Cyathea caracasana* complex have to be made. Focusing on the petiolar indument and field observations as distinguishing characters, the following groups of species are separated: *Cyathea caracasana* (Klotzsch) Domin and *C. crenata* Sodiro from mid elevations from the northern Andes and the Caribbean; *Cyathea carolihenrici* Lehnert, *C. plicata* Lehnert, and *C. meridensis* H. Karst. from the northern and central Andes at mid elevations, the latter species in three geographically and ecologically separated varieties (two of them, var. *nana* and var. *obtecta*, are newly described); *Cyathea squamipes* H. Karst., *C. catacampta* Alston, and *C. lindeniana* H. Karst. occurring in the Andes at mid to high elevations. Species allied to *Cyathea patens* H. Karst. are restricted to high elevations and show a tendency towards forming local morphospecies. This group includes *C. patens* H. Karst., *C. brachypoda* Sodiro, *C. frondosa* H. Karst., and *C. parvifolia* Sodiro (syn. *C. brevistipes* R. C. Moran). *Cyathea maxonii* Underw. ex Maxon from Central America and *C. dissoluta* Baker ex Jenm. from Jamaica are of uncertain affinity. *Cyathea herzogii* Rosenst., formerly treated as synonym of *C. caracasana* s. l. by R. M. Tryon, represents a valid species belonging to the *C. fulva* group. Putative relationships are discussed, but more studies on the ecological and molecular level are needed in order to elucidate the relationships among and between the recognized groups.

Keywords: Andes, *Cyathea*, *C. caracasana* var. *boliviensis*, hybrids, Neotropics, scaly tree ferns, scurf, South America.

Zusammenfassung

Im Zuge von Studien an neotropischen Baumfarnen werden die Arten des *Cyathea caracasana*-Komplexes neu definiert. Basierend auf dem Wedelstielindument und Feldbeobachtungen als Unterscheidungsmerkmalen werden folgende Artengruppen unterschieden: *Cyathea caracasana* (Klotzsch) Domin und *C. crenata* Sodiro aus mittleren Höhenlagen der nördlichen Anden und der Karibik; *Cyathea carolihenrici* Lehnert, *C. plicata* Lehnert und *C. meridensis* H. Karst. aus mittleren Höhenlagen der Anden, letztere Art in drei geografisch und ökologisch getrennten Varietäten (zwei davon, var. *nana* und var. *obtecta*, werden als neu beschrieben); *Cyathea squamipes* H. Karst., *C. catacampta* Alston und *C. lindeniana* H. Karst. in mittleren und höheren Lagen der nördlichen und zentralen Anden weit verbreitet. Die Arten aus der Verwandtschaft von *Cyathea patens* H. Karst. sind auf hohe Lagen beschränkt und zeigen eine Tendenz zur Bildung lokaler Morphospezies. Diese Gruppe umfasst *C. patens* H. Karst., *C. brachypoda* Sodiro, *C. frondosa* H. Karst. und *C. parvifolia* Sodiro (syn. *C. brevistipes* R. C. Moran). Die verwandtschaftlichen Beziehungen von *Cyathea maxonii* Underw. ex Maxon aus Zentralamerika und *C. dissoluta* Baker ex Jenm. aus Jamaica sind unklar. *Cyathea herzogii* Rosenst., nach R. M. Tryons Konzept aus der Synonymie von *C. caracasana* s. l., repräsentiert eine eigenständige Art aus der *C. fulva*-Gruppe. Mögliche Verwandtschaftverhältnisse werden diskutiert, aber weitere Studien auf ökologischer und molekularer Ebene sind notwendig, um die wahren Beziehungen zwischen und innerhalb der hier anerkannten Gruppen zu ergründen.

Contents

## 1 Introduction

The scaly tree ferns (Cyatheaceae) comprise ca. 600 species with a pantropical and southern temperate distribution (Kramer & Green 1990). Centers of diversity are Malesia, especially New Guinea (Holttum 1963), Madagascar (Janssen et al. 2008), Southeastern Brazil, the Caribbean, and the Andes (Tryon & Gastony 1975). In the Neotropics, the family is represented by ca. 200 species, the majority of them belonging to the genus *Cyathea* sensu Korall et al. (2007). With most of its members being large, showy plants, the scaly tree ferns have often catched the attention of plant collectors and researchers since the beginning of tropical botany. The number of collections and applied names is ample whereas the amount of material of most historic collections is lamentably pauper. During the 20th century, attempts were undertaken to resolve the hitherto confusing systematics of scaly tree ferns in comprehensive floral works (e. g., Stolze 1976, Kramer 1978, Smith 1985, Tryon 1986, Tryon & Stolze 1989) and revisions (Tryon 1970, 1971, 1976; Gastony, 1973; Stolze 1974; Windisch 1977, 1978; Barrington 1978; Conant 1983). Unfortunatley, Holttum (1963) and Holttum & Sen (1961) recognized only one genus *Cyathea* with several subgenera and sections based on his studies in the Old World, while Tryon (1970) focused on the New World and concluded that there are six distinguishable genera in the Cyatheaceae. A considerable number of species had to carry a different name in each of two rivaling generic systems.

Recent phylogentic studies on the tree fern alliance redefined the generic boundaries within the Cyatheaceae (Korall et al. 2006, 2007). Although this will help to settle the long-time conflict in the nomenclature, crucial problems in the delimitation of natural species remain. Some wide-ranging species are apparently quite variable in their morphology, which might reflect their ability to respond to different ecological conditions. There is also the possibility of active hybridization between species, which produces swarms of intermediate hybrids or may give rise to new sexually reproducing species (Conant 1975, 1990; Tryon 1976; Conant & Cooper-Driver 1980). This hampers establishing clear and comprehensible species concepts. The *C. caracasana* group as defined by Tryon (1976) is a paradigm for confusing taxa. Tryon (1976) united all Southamerican *Cyathea* with sphaeropteroid indusia, strongly bicolorous petiole scales with dark centers, and dark, long lasting scurf under this name and provided a system of varieties to structurize the intraspecific variability. However, increasing amounts of specimens and field observations in the years that followed showed that some of these varieties differ more strongly from each other than from species belonging to other of Tryon's (1976) groups. In the present account, I summarize my experiences with the *C. caracasana* complex that I gained during the past years. The circumscriptions of the species are based on field observations and extensive herbarium work. However, some species remain unresolved regarding variability of morphology, taxonomic status, and natural relationship. Therefore, this account should be considered as a preliminary guide and an encouragement for future studies.

### Abbreviations

| | |
|---|---|
| agg. | aggregat = species group |
| ex descr. | ex descriptione, based on text sources alone |
| n. l. | not located |
| n. v. | non vidi = not seen |
| n. var. | nova varietas = new variety |
| nom. nov. | nomen novum = new name (as a substitute) |
| nom. nud. | nomen nudum = bare name without taxonomic value |
| nom. superfl. | nomen superfluum = superfluous name |
| s. l. | sensu lato = in the wide sense |
| s. n. | sine numero = without number |

Extracted from Wagenitz (1996) and Stearn (2004). Herbarium acronyms follow Holmgren et al. (1990).

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## 2 Material and methods

I collected 330 fern specimens in Ecuador, Peru, and Bolivia, and documented their growth habit in word and photograph. Vouchers are mainly deposited at GOET, LPB, QCA, UC, and USM. A total of 720 numbers from tree fern collections were studied under the light microscope.

Terminology largely follows LELLINGER (2002), except for some special terms for tree fern characters that were coined by TRYON (1970, 1976). These are explained shortly here.

The petiole scales of all species treated here have a structurally differentated margin (i. e., the marginal cells are smaller and of a different orientation than those of the scale center; TRYON 1970, 1976). The scales may be of one color (concolorous) or two contrasting colors (bicolorous). In the latter case, the marginal color may be restricted to the differentiated margin (concordantly bicolorous) or may extend into the scale body (discordantly bicolorous).

The different types of indusia are used in keys to separate the tree ferns into manageable subsets. The common terms for character states are exindusiate (indusia lacking), hemitelioid (indusia not enclosing the receptacle completely; in *Cyathea* always scale-like), discoid (indusia disc-shaped), cyatheoid (indusia cup-shaped), and sphaeropteroid (indusia globose, completely closed). An umbo is an apical papilla where the indusial walls have joined in a sphaeropteroid indusium. The terms urceolate (urn-shaped) and subsphaeropteroid (closed except for a small apical orifice) describe conditions between cyatheoid and sphaeropteroid and are often exchangeable.

The variation of measurements given in the species descriptions refers to the maxima observed in the majority of specimens. Significant deviations based on single or few specimens are given in brackets.

The geographic sequence in the citation of specimens follows "A Guide for Contributors to Flora Neotropica, Appendix I" (http://www.nybg.org/files/fnai2.pdf).

## 3 Systematic treatment

### 3.1 General

Principally, the neotropical *Cyathea* species with globose (sphaeropteroid) indusia can be divided into two major groups based upon the type of petiolar and laminar indument. The first group contains the *Cyathea pallescens* (see LEHNERT 2008), *Cyathea divergens*, and *C. straminea* groups as well as *Cyathea caracasana* var. *chimborazensis* (Hook.) R. M. Tryon as defined by TRYON (1976). All species correspond in having generally long-lanceolate petiole scales that have dark colored (brown to blackish) bodies and white opaque margins, which may have dark teeth; *Cyathea atahuallpa* (R. M. Tryon) Lellinger, which has entirely white scales that lack dark teeth, is interpreted as the end of an evolutionary lineage, following the almost completely white, dark-toothed scales of *C. straminea* H. Karst. Its inclusion within this group (LEHNERT in press) is strongly supported by other characters like indusium type and laminar dissection.

The second group includes TRYON's *Cyathea fulva* group and the rest of the varieties of *C. caracasana*. These species are characterized by concolorous or bicolorous petiole scales with brown to yellow margins without marginal teeth. If the peripheral cells of the margins are truly white, then this portion is very narrow and does not account to the general color of the scale. Strongly contrasted scales can intergrade into weakly contrasted ones within one population or even on one plant. For example, the trunk scales of *C. carolihenrici* are concolorous orange-brown while the lower petiole scales are dark castaneous to atropurpureous with sharply delineated orange margins; more distally on the petiole, the scales assume a lighter hue with the marginal color changing gradually into the central color, i. e., from orange to brown. The petiole scurf is uniformly colored, tan, brown or castaneous and consists of smaller squamules than in the previous group.

Most of the species covered here are large plants with trunks mostly more than 8 cm diameter and to 15 m or more in height. A cover of old petiole bases on the trunk is only present in small plants; after reaching a trunk height that surpasses the length of the leaves, these are shed completely due to their own weight. A clean shedding of fronds when the trunk is still shorter than the frond length is rare and specific, as in *C. carolihenrici* and *C. plicata*. With the exception of *C. dissoluta*, adventitious buds and lateral shoots are not produced by the species treated here. Only after injuries of the apex, buds may be produced to create substitute apices. In *Cyathea squamipes* H. Karst., this can result in multiple crowned plants (pers. obs.). Similar conditions are known from Paleotropical Cyatheaeceae (HOLTTUM 1963).

### 3.2 *Cyathea caracasana* (Fig. 16)

*Cyathea caracasana* (Klotzsch) Domin: DOMIN 1929a: 262. – *Alsophila caracasana* Klotzsch: KLOTZSCH 1844: 541. – *Trichipteris caracasana* (Klotzsch) R. M. Tryon: TRYON


**Figs. 1–7.** *Cyathea* spp. in the field. – **1–2**. *C. meridensis* var. *nana*. **3**. *C. meridensis* var. *obtecta*. **4–5**. *C. carolihenrici*. **6**. *C. squamipes*. **7**. *C. catacampta*.


**Figs. 8–15.** *Cyathea* spp. in the field. – **8**. *C. squamipes*. **9–10**. *C. catacampta*. **11–12**. *C. lindeniana*. **13–14**. *C. frondosa*. **15**. *C. parvifolia*.

1970: 45. – Type: Venezuela. Caracas, »Moritz 117« (lectotype, B-fragm. US [designated herein]; isolectotypes, GH, P).

*Hemitelia sherringii* Jenm.: Jenman 1886: 266. – *Cyathea sherringii* (Jenm.) Domin.: Domin 1929a: 264. – Type: Jamaica. Rose Hill, XI.1886, »Sherring s. n.« (holotype, K-photo B; isotype, US).

*Cyathea ocanensis* Baker: Baker 1891: 184. – Type: Colombia. [Norte de Santander], Ocaña, »Kalbreyer 608« (holotype, K; isotypes, B [label "Dept. Santander, Nuga"], COL, US).

*Alsophila caracasana* var. *petiolularis* Domin: Domin 1929b: 95, ex descr. – Syntypes: Venezuela. Caracas, »Buschel s. n.« (n. l.); [Aragua], Colonia Tovar, »Pittier 10011« (n. l.).

*Cyathea subindusiata* Domin: Domin 1929b: 67. – Type: Venezuela. "Habitat in Columbia ad Caracas", »Buschel s. n.« (holotype, n. l.; isotypes, B [label "Venezuela"], BM-photo GH [label "Venezuela, 1855"], K).

*Cyathea producta* Maxon: Maxon 1922: 438. – Type: Cuba. Palma Mocha Peak, Sierra Maestra, Oriente, »Léon 11181« (holotype, US; isotype, NY).

Selected specimens examined

C o l o m b i a . **Antioquia**. Alto de Cueras, 10 km E of La Blanquita, 12 km W of Nutibara, 6°40'N, 76°30'W, 1670 m, 3.III.1996, »Gentry et al. 75986« (MO, UC). **Cundinamarca**. Bojaca, Vereda de San Antonio, "La Merced" en faja de robledales proximo a la carretera que conduce de Mosquera a La Mesa, 2600–2700 m, VII.1964, »Torres & Lozano 95« (COL). **Guajira**. Cerro Pintado, región del Espejo, 2300 m, 12.XI.1989, »Cuadros-V. 2336« (COL). **Nariño**. Ricaurte, Reserva Natural La Planada, Cerro León, 1°09'37"N, 77°59'13"W, 2145 m, 29.II.1997, »Guzmán 12« (UC). **Norte de Santander**. Cordillera Oriental, región del Sarare, Quebrada del Sararito, 1930–1950 m, 23.X.1945, »Cuatrecasas et al. 12584, 12584A« (COL).

V e n e z u e l a . **Trujillo**. Boconó, P. N. Guaramacal, vertiente sur, parcela de estudio fitosociológico nº 7, 9°12'28"N, 70°09'41"W, 1950 m, 19.–22.XII.1995, »Cuello et al. 1276« (UC).

Description

Trunks to 4.5–5.0(10.0) m tall, to 7–10 cm diameter. Petioles to 30–35 cm long or more, muricate to sparsely aculeate with spines to 3 mm long, stramineous to yellowish, basally darker, often plumbeous but never blackish; scurf dark brown to castaneous, consisting of scattered branched hairs and erect dissected squamellae (similar to Fig. 17B). Petiole scales to 15.0–25.0 × 3.0–4.5 mm, broadly lanceolate to ovate-lanceolate (similar to Fig. 17A), variable, dark brown to blackish with narrow golden brown to yellowish margins, or nearly concolorous brown, with straight to falcate tips.

Laminae to 150 × 100–150 cm, firmly chartaceous; bipinnate-pinnatifid, apices gradually reduced. Leaf axes smooth or rhachises with scattered small corticinate spines, stramineous to yellowish brown on both sides, scurf absent or rarely with some small pale brown to whitish squamules to 0.5 mm long, usually clumped and appearing amorphous; costules, costae, and distal parts of rhachises adaxially with hairs 1.0–1.5 mm long, tan to white; junctions of costae and rhachises abaxially swollen, each with a flat, elliptic pneumathode to 3.0–4.5 × 1.5–2.0 mm, inconspicuous, of color of the leaf axes or darker brown. Pinnae to 50–75 cm long, alternate, 8–10 pairs per frond, stalked to 2.0–3.0 cm. Pinnules to 100–130 × 20–26 mm (Fig. 16); largest ones linear-oblong to lanceolate, tapering from the middle to long-acute to attenuate tips, basally cuneate to weakly cordate, stalked 1–3(5) mm, 1.5–2.5 cm between the stalks; segments patent to weakly ascending, their tips obtuse to rounded, margins flat, weakly crenulate to subentire (Fig. 16); basal segments opposite to subopposite, rarely remote and free; pinnules weakly dimorphic, sterile ones with sinuses closed or to 3 mm wide, obtuse, fertile ones with sinuses 2–3 mm wide, acute to obtuse; segments glabrous adaxially, abaxially glabrous or with few appressed white trichomidia on the veins, rarely with small (ca. 0.4 mm long), white, multicellular hairs on veins and below the sinuses, also between them, or with single white, subbullate squamules distally on the midveins. Veins yellowish and weakly to strongly protruding adaxially, planar to weakly protruding abaxially, in the color of the laminar tissue, yellowish, or rarely brown; sterile veins forked or simple, fertile veins forked.

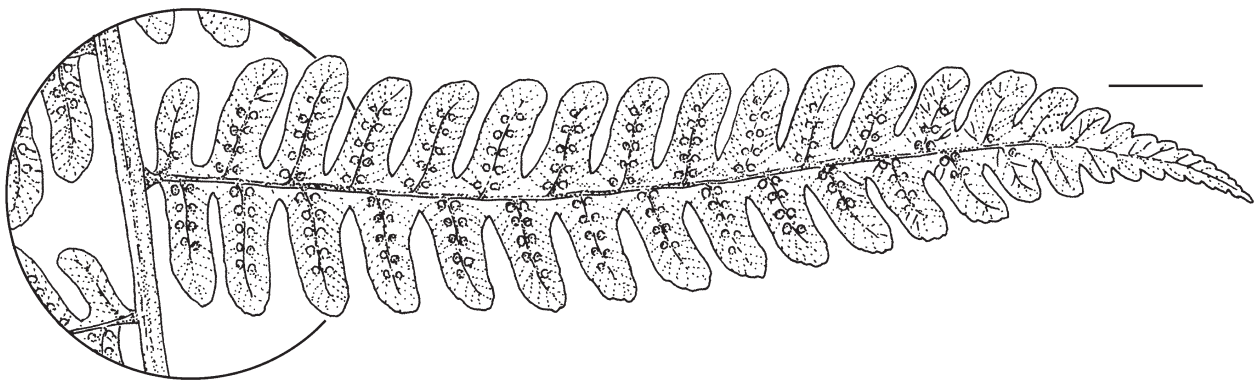

**Fig. 16**. *Cyathea caracasana*, fertile pinnule (»Moritz 394« B). – Scale: 1 cm.

Sori 1.0 mm diameter, costal, at vein forks; indusia ephemeral, very thin, colorless to whitish, opaque, potentially sphaeropteroid, with a brown umbo, but often fragmented and shed before the sporangia open, completely gone at maturity or remaining as clear, colorless fragments at the receptacles; receptacles globose, 0.5 mm diameter; paraphyses numerous, hyaline, 0.2–0.3 mm long, shorter than the sporangia. Spores pale yellow, perispore not examined.

### Distribution and habitat

In moist montane forests at 1200–2700 m in Cuba, Jamaica, Colombia, and Venezuela.

### Remarks

The original material of *Cyathea caracasana* at B is quite ample. There are six sheets containing two frond apices, several fertile pinnae, two petioles, one crosier, and even fragments of trunk cross sections that belong all to one species. Three sheets bear the number »117« of the type collection, the other ones are numbered with »117/394« or »117 et 394«. The latter do not appear to be a mixed collection of different plants so I suspect that the double numbers reflect a peculiarity in the record keeping of the collector. The double-numbered specimens are good complementary reference material to the lectotype »Moritz 117« and may be regarded as paratypes.

The main character of *Cyathea caracasana* is the fragile and fugacious indusia. In fact, it is hardly notable in one of the sheets of »Moritz 117/394« (B). Another sheet bearing the number 394 (B, GH n. v.), a collection cited to be nearly identical by Tryon (1976), shows indusia that are pulverized to a white granular layer on intact sori. Only the brown umbos on top make them recognizable as indusia. The laminar indument is limited to some small (ca. 0.4 mm long), white, multicellular hairs distributed abaxially on the veins (below the sinuses also between the veins) and small white, lanceolate to subbullate squamules. At first sight, the firmly herbaceous to chartaceous laminae appear glabrous. The pinnules are broadly linear or weakly oblong as pictured by Vareschi (1969), with their apices attenuate to long-acuminate. The petioles are muricate to shortly aculeate, yellowish to stramineous, with scattered, castaneous scurf that appears amorphous but consists of oblong to lanceolate squamules with weakly erose margins. This separates *C. caracasana* from the similar *C. meridensis*, where the scurf is usually dense and persistent on dark brown to castaneous, mostly inermous petioles.

Cuban plants of *Cyathea caracasana* are aberrant from the Andean and Jamaican populations in having many long multicellular hairs abaxially on the veins (Caluff 2003). This may be a distinct variety, represented by the synonym *C. producta* Maxon.

## 3.3 *Cyathea crenata*
(Fig. 17)

*Cyathea crenata* (Sodiro) H. Christ: Christ 1897: 323. – *Hemitelia crenata* Sodiro: Sodiro 1893: 522. – Type: Ecuador. Pichincha, "Crece en los declives del Volcán Atacatzo (Canzacoto, Boloña, 1500–2000 m)", »Sodiro s. n.« (n. l.). – Lectotype (designated by Tryon 1976): Ecuador. Pichincha, "Hacienda Boloña, 1550 m, 1882", »Sodiro s. n.« (P).

#### Selected specimens examined

E c u a d o r . **Morona-Santiago**. Area of Huamboya, región oriental, [ca. 1°48'S, ca. 78°15'W], 1500 m, 15.II.1944, »Acosta-Solis 7496« (MO, UC); Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", km 140 on road Loja–Gualaquiza, 3°37'S, 78°34'W, 900–1000 m, 26.–27.IV.1973, »Holm-Nielsen et al. 4548« (AAU). **Napo**. Cantón Quijos, road between Cuyuja and Baeza, 0°27'S, 77°56'W, 2100 m, 8.V.1990, »Palacios & Freire 4971« (MO). **Pichincha**. Ca. 2 km NW of Mindo, Hacienda San Vicente, ca. 2 km from finca buildings, 1450–1600 m, 10.–14. II.1985, »Foster 85-34« (UC); Quito, Parroquia Nanegal, Reserva Maquipucuna, trail El Pacchal to Cerro Campana, 0°08'N, 78°38'W, 1270 m, 6.VI.2000, »Wilson 2758« (UC).

P e r u . **Cajamarca**. San Ignacio, Dist. San José de Lourdes, Buenos Aires (Cerro El Parco), 5°42'04"S, 77°53'06"W, 1900 m, II.2006, »Bonino 307, 309« (MO, UC).

### Description

Trunks erect, straight, to 7–12 m tall, to 12–15 cm diameter, without old petiole bases, cortex dark brown, apices hidden in fascicles of petioles; adventitious buds lacking. Fronds to 150–280(300) cm long, patent, weakly arching. Petioles to 35–50 cm long, muricate to sparsely aculeate with spines to 3–5 mm long, dull brown, basally darker, often plumbeous but never blackish, distally stramineous to yellowish; scurf pulverulent, not matted, mostly dark brown, sometimes partially paler brown to tan, consisting of erect dissected squamellae, 0.2–0.6(1.0) mm long (Fig. 17C). Petiole scales to 20.0–37.0 × (2.5)3.0–4.5(5.0) mm, broadly lanceolate to ovate-lanceolate, always dark, matte to rarely shiny, black to dark atropurpureous, with narrow atropurpureous to yellowish white margins, these often abraded (Fig. 17A), centers in back light with darker streaks; tips straight to falcate, weakly undulate to twisted.

Laminae to 150–250 × 110–155 cm, ovate-elliptic, firmly chartaceous to subcoriaceous, brittle, bipinnate-pinnatifid, apices gradually reduced. Pinnae to 67–88 cm long, alternate, ca. 15 pairs per frond, sessile to subsessile, stalked to 0.5 cm. Leaf axes stramineous to yellowish brown abaxially, brown to yellowish brown adaxially, inermous (or rhachises with scattered small spines), costules densely hairy adaxially, distal parts of the costae and rhachises with tan to brown, antrorsely curved hairs to 0.6 mm long, otherwise leaf axes sparsely hairy with white, curved hairs 0.2–0.5 mm long; brown petiole scurf sometimes reaching up to the lower half of rhachises and adjacent bases of costae, in plants with short petioles here also with

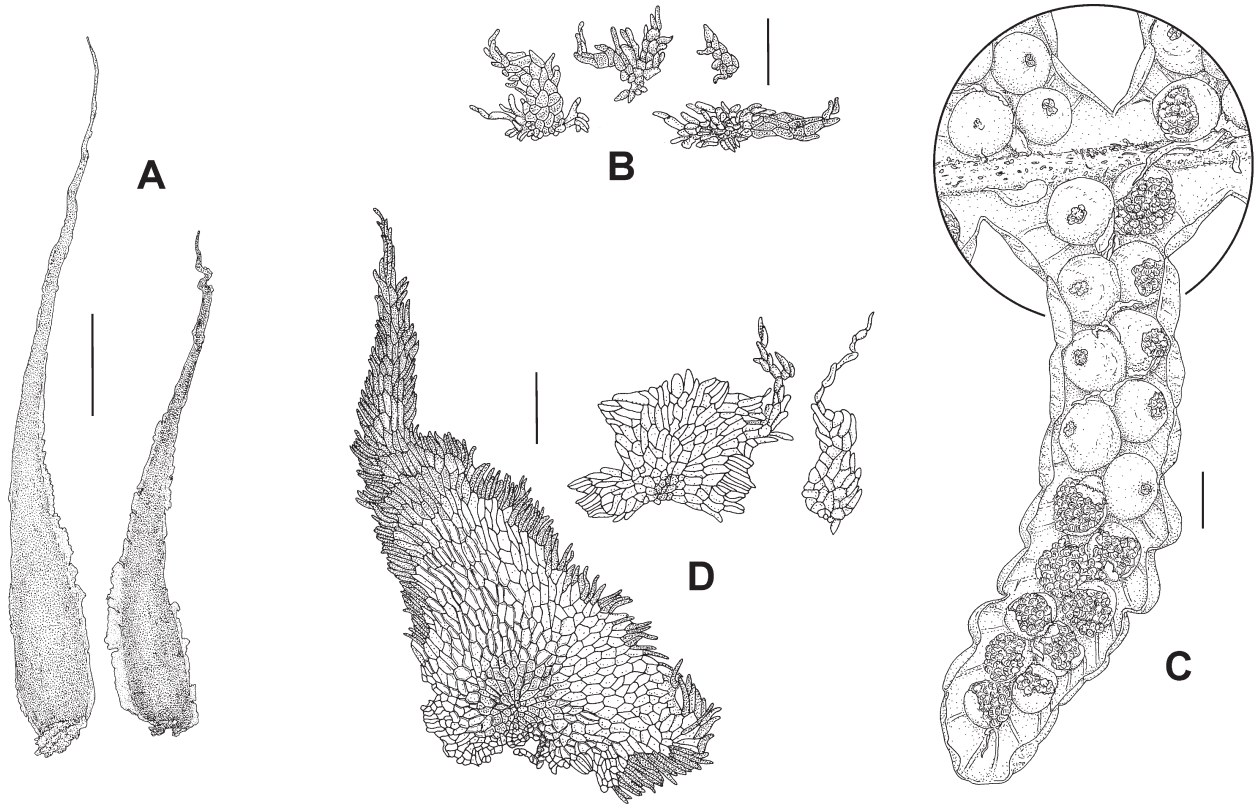


**Fig. 17.** *Cyathea crenata* (all from »Lehnert 1212« UC). – **A**. Petiole scales. **B**. Squamules of petiole scurf. **C**. Fertile segment abaxially. **D**. Laminar scales/squamules. – Scales: 5 mm (A), 1 mm (C), 0.2 mm (B, D).

persistent crosier/petiole scales; some small, pale brown to whitish squamules to 0.5 mm long on costae and costules (Fig. 17D), especially in the axils, usually clumped and appearing amorphous; costules sometimes with white, lanceolate scales to 5 mm long with dark marginal teeth (Fig. 17D); junctions of costae and rhachises abaxially swollen, each with a grayish brown, flat, elliptic pneumathode to 3.0–4.5 × 1.5–2.0 mm. Pinnules to 9.5–13.0 × 2.4–2.6 cm, sessile to subsessile (stalked to 0.5 mm), (15)20–29 mm apart; largest pinnules linear-oblong, tapering from well beyond the middle to long-acute to short-attenuate tips, rarely long-triangular, basally truncate or weakly cordate, with the basal segments slightly covering the costae; pinnules weakly dimorphic, sterile ones with obtuse to acute sinuses 1–2 mm wide, fertile ones with obtuse to polygonal sinuses 3–4 mm wide; segments patent to weakly ascending, distally falcate, their tips obtuse to round, margins weakly revolute, crenulate to crenate (Fig. 17C), rarely subentire, basal segments alternate to subopposite, not remote; segments adaxially glabrous, abaxially glabrous or with few appressed white trichomidia on the veins and with white multicellular hairs to 0.6 mm long on and between veins in proximity to costules and midveins, with white, flat to subbullate squamules on midveins. Veins yellowish and weakly to strongly protruding adaxially, planar to weakly protruding abaxially, in the color of the laminar tissue, or yellowish to rarely brown; sterile veins forked or simple, fertile veins forked once or twice (= bifurcate, three tips).

Sori 1.0 mm diameter, costal (Fig. 17C), at vein forks or on the back of bifurcate veins; indusia fragile, very thin, papery, matte white, opaque, deeply urceolate to subsphaeropteroid, rarely sphaeropteroid with weak umbo, developed as a mucose film in fresh material, ephemeral to persisting as a shallow cup or as fragments on the receptacle, the indusial tissue often crinkly and flattened to the lamina; receptacles globose, 0.5 mm diameter; paraphyses numerous, hyaline, 0.4–0.5 mm long, of the same length as the sporangia. Spores pale yellow, perispore not examined.

Distribution and habitat

In moist montane forests at 900–2100 m, scattered from Ecuador to northern Peru.

### Remarks

The sheet labelled "Corazon", »Sodiro s. n.« at SI [nº 22862] represents this species. The sheet filed under *Hemitelia crenata* at Q ("Crescit in silv. subtr. prop. San Florencio", V.1883, »Sodiro s. n.«) is *Cyathea corallifera* Sodiro.

*Hemitelia crenata* Sodiro was included in *Cyathea caracasana* (Klotzsch) Domin var. *caracasana* by TRYON (1976). SODIRO (1893) reported that the indusia of this species appear like a mucose film in fresh material. In dried material, such indusia are easily fragmented and may disintegrate without leaving a trace. This is observed in the type material of both *C. caracasana* and *C. crenata*. Additional collections showed that the indusia of *C. crenata* are more often persistent as a flattened cup of papery texture while those of *C. caracasana* are typically gone in mature sori. These differences in the indusia correlate with distinct features of the laminae: in *C. caracasana*, there are 8–10 pairs of definitely stalked pinnae per frond; in *C. crenata*, 12–15 pairs of sessile to subsessile pinnae are present. *Cyathea crenata* differs from *Cyathea caracasana* in being short-pubescent on the costules abaxially. If hairs are present on the laminae abaxially in *C. caracasana*, they are mainly on and between the lateral veins and rarely on the costules. *Cyathea crenata* has also white, fimbriate to lacerate squamules and small flattish scales with dark marginal teeth and sometimes dark, central stripes. The latter features resemble more *Cyathea corallifera* Sodiro, but that species has dense, white petiole scurf consisting of relatively large squamules and dark brown petiole scales with broad white margins.

*Cyathea crenata* may be confused with *C. squamipes* H. Karst. and *C. catacampta* Alston. Plants of these species may have pubescent costules like *C. crenata*, but have also flat to bullate, orange-brown squamules associated with this pubescence; laminar squamules of *C. crenata* are always whitish. Furthermore, the indusia are tan to brown, lustrous, translucent, and usually persisting in *C. squamipes* and *C. catacampta*, while they are whitish, matte, opaque, and ephemeral in *C. crenata*.

*Cyathea carolihenrici* Lehnert and *C. meridensis* H. Karst. have similar fine, dark brown to dark castaneous scurf similar to that of *C. crenata* and *C. caracasana*, but differ in the dark brown to atropurpureous color of their axes and the broader margins of their more bicolorous petiole scales.

## 3.4 *Cyathea carolihenrici* (Figs. 4–5, 18)

*Cyathea carolihenrici* Lehnert: LEHNERT 2003: 180. – Type: Bolivia. La Paz, Prov. Nor Yungas, Cotapata-Santa Barbara, 16°18'S, 67°52'W, 3150 m, 6.VIII.2000, »Lehnert 11« (holotype, GOET; isotypes, LPB, UC).

### Selected specimens examined

P e r u . **Cuzco**. Urubamba, 2050 m, »Bonino 1127« (CUZ).

B o l i v i a . **La Paz**. Muñecas, Camata, Alturas de Quiñuaña, 3.7 km SW of the village, 15°15'24"S, 68°46'35"W, 2820 m, 15.V.2006, »Fuentes et al. 10595« (UC, MO); 5–6 km de Chuspipata a Yolosa, 16°18'S, 67°48'W, 2750 m, 2.VIII.2000, »Lehnert 2« (GOET, LPB, UC).

### Description

Trunks to 7 m tall, to (10)15–20 cm diameter, without old petiole bases, apices hidden in fascicles of petioles (Fig. 4). Fronds to 300 cm long, arching to drooping from the middle. Petioles to 100 cm long, inermous to verrucate, rarely near the base short-aculeate, dark castaneous to blackish; scurf dark brown to castaneous, a dense tomentum of trichomidia and lanceolate squamelae with lacerate margins to 0.5 mm long, beneath the petiole scales also some larger squamellae, squamellar insertion characteristically asymmetrical (Fig. 18B), squamellar margins in backlight not lighter than the centers. Petiole scales to 15–20 × 3.5–4.0(8.0) mm, lanceolate to ovate-lanceolate (Fig. 18A), discordantly bicolorous, centers dark brown to blackish, margins orange to golden brown, tips long-attenuate, often twisted.

Laminae to 150 × 130–140 cm, coriaceous, bipinnate-pinnatifid to tripinnate (Fig. 5), apices gradually reduced. Leaf axes dark brown adaxially, in strong contrast to the lamina, brown to stramineous abaxially, smooth or rhachises with scattered small corticinate spines, with persisting scurf of minute fringed brown squamellae; costules, costae, and distal parts of rhachises with hairs 1.0–1.5 mm long adaxially; junctions of costae and rhachises swollen. Pinnae to 55–65 cm long, alternate, 12–15 pairs per frond, stalked to 1.5–3.0 cm (Fig. 5). Pinnules to 130 × 40 mm, largest ones triangular to lanceolate, tips long-acute to attenuate, bases truncate to cuneate or weakly cordate, short to long-stalked, the stalks to 3–5 mm; segments weakly ascending, their tips obtuse to rounded, margins flat to revolute, slightly crenulate to entire; basal segments sometimes remote; segments glabrous adaxially, abaxially glabrous or with few short erect white multicellular hairs 0.5–1.0 mm long on the veins, near the costules also between them, with some scurf like that of the petioles.

Sori subcostal, at vein forks; indusia subsphaeropteroid, without umbo, sometimes with scale on top. Spores pale yellow, with verrucate exospore, perispore baculate.

### Distribution and habitat

In moist tropical montane forests at 2050–3150 m in southern Peru and western Bolivia.

### Remarks

*Cyathea carolihenrici* replaces *C. meridensis* in the Central Andes. Given the strong resemblence and the vi-

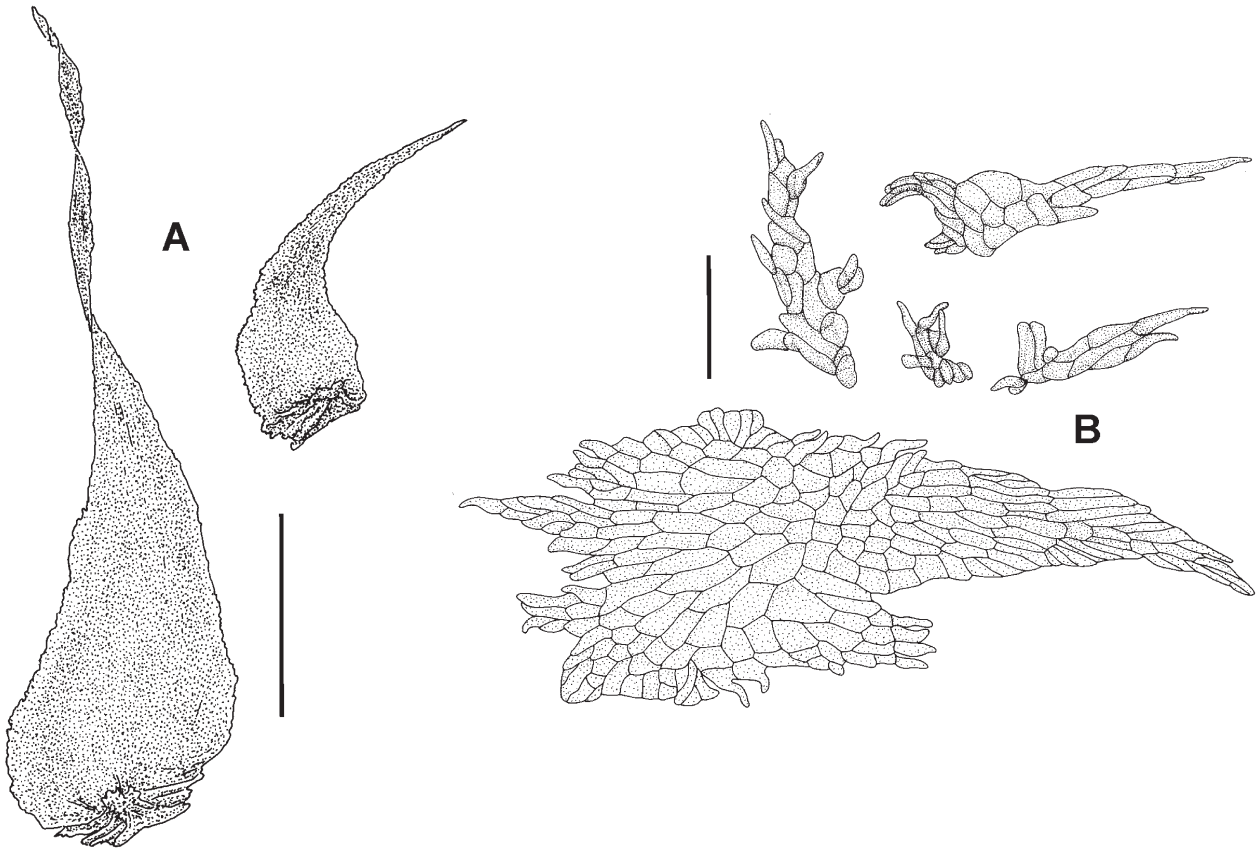


**Fig. 18.** *Cyathea carolihenrici* (all from »Lehnert 619« GOET). – **A**. Petiole scales. **B**. Squamules of petiole scurf. – Scales: 5 mm (A), 0.2 mm (B).

cariant distribution of both species, a close relationship between them is undoubted. They can be distinguished by the different trunk diameter [to (10)15–20 cm in *C. carolihenrici* vs. to 5–12 cm in *C. meridensis*] and the details of the petiole scurf (squamellae lanceolate, asymmetrically inserted, and not lighter margined in backlight vs. squamellae oblanceolate, symmetrically inserted, and lighter margined in backlight).

### 3.5 *Cyathea meridensis*
(Figs. 1–3, 19)

#### 3.5.1 General

*Cyathea meridensis* H. Karst.: Karsten 1869: 141, ex descr. – Type: Venezuela. Mérida, "Habitat in silvis montanis Meridensibus altitudine 2000 m", »Karsten s. n.« (n. l.).

#### Description

Trunks to 0.3–10 m tall, to 5–12 cm diameter, with (Figs. 1–3) or without old petiole bases, cortex dark brown to black, apical parts with lanceolate scales, concolorous dark orange-brown to bicolorous with a dark to black central stripe, colors transitional to sharply contrasting; apices hidden in fascicles of petioles. Fronds to 50–360 cm long, arching to drooping from the middle (Fig. 1), sometimes scrambling. Petioles to 17–200 cm long, inermous to verrucate or shortly aculeate, brown to castaneous; scurf dark brown to castaneous, a dense matted tomentum of trichomidia and oblanceolate squamellae with fimbriate to dissected margins, the latter appressed, rarely some larger ones erect, squamellar insertion characteristically symmetrical (Fig. 19B, C), squamellar margins in backlight lighter than the centers. Petiole scales 15–25 × 2.5–5.0 mm, lanceolate to ovate-lanceolate (Fig. 19A), concordantly to discordantly bicolorous, variable, with dark brown to blackish centers and narrow orange to golden brown margins.

Laminae to 55–240 × 27–150 cm, bipinnate-pinnatifid to tripinnate, coriaceous, apices gradually reduced. Leaf axes smooth, dark brown adaxially, in strong contrast to the lamina, brown to stramineous abaxially, with persisting scurf of minute fringed brown squamellae, sometimes

with flat, lanceolate, concolorous brown scales in the axils, hairs lacking abaxially, costules, costae, and distal parts of rhachises adaxially with hairs 1.0–1.5 mm long, tan to brown on rhachises, white to tan on costules and costae; junctions of costae and rhachises swollen, abaxially with a flat to sunken, elliptic pneumathode to 3.0–4.5 × 1.0–1.5 mm. Pinnae to 16–75 cm long, alternate, 8–15 pairs per frond, stalked to (0.3)0.5–3.4 cm. Pinnules to 65–120(130) × (6)11–45 mm, triangular to oblong, tapering from the base or beyond the middle to acute or attenuate tips, subsessile to long-stalked; segments weakly ascending, their tips obtuse to round, margins flat to revolute, crenate to entire. Veins yellowish and weakly protruding adaxially, planar to weakly protruding abaxially; sterile veins forked or simple, fertile veins forked.

Sori to 1.0–1.4 mm diameter, subcostal, in forks of veins; indusia subsphaeropteroid to sphaeropteroid, dark brown, persistent, with or without umbo, sometimes with scale on top; receptacles globose, 0.4–0.3 mm diameter; paraphyses few, thin, hyaline, of the same length as the sporangia (0.5 mm). Spores pale yellow, perispore not examined.

### Distribution and habitat

In moist montane forests at 1200–2500(2870) m in Venezuela, Colombia, Ecuador, and northern Peru.

### Remarks

The typification of *Cyathea meridensis* remains unclear (Tryon 1976). One sheet annotated as *C. meridensis* is at B, with an old label probably handwritten by Karsten, but the specimen does not match the original description (Karsten 1869). The species is maintained here because there are many collections from Colombia that sufficiently match the diagnosis and form the basis for the present description. These plants have trunks to 6 m tall but only 5–6 cm diameter and in this regard match the original description well (Karsten 1869). They are also characterized by long-triangular pinnules and by fine, dark brown scurf on the leaf axes and veins, which is not mentioned in the description but it is likely to have been overlooked. I postpone the choice of a neotype until I have seen material from the type locality, which should be preferred for this purpose.

The petiole scurf of *C. meridensis* is identical to that of *C. plicata* and superficially similar to that of *C. carolihenrici*. The three species are also similar in the coriaceous laminar texture and the general color pattern of the larger scales (i. e., strongly contrasted on the outer parts of the petioles, transitional to concolorous orange-brown nearest the trunk). The differences between *C. plicata* and *C. meridensis* are in the size and orientation of the largest pinnules, which are usually less than 2 cm broad, sessile, and pointed upwards in the former species, and more than

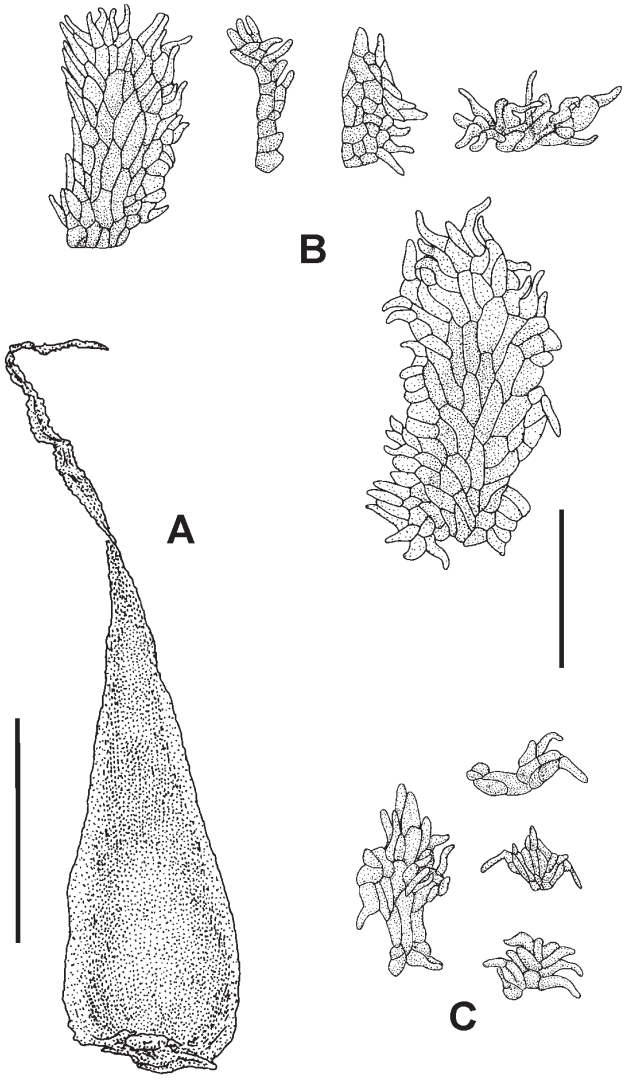


**Fig. 19.** *Cyathea meridensis* (A, B from »Lehnert 991« GOET; C from »Lehnert 1079« GOET). – **A**. var. *nana*, petiole scale. **B**. var. *nana*, squamules of petiole scurf. **C**. var. *obtecta*, squamules of petiole scurf. – Scales: 5 mm (A), 0.2 mm (B, C).

2 cm broad, short-stalked, and in plane with the leaf axes in the latter. *Cyathea carolihenrici*, which strongly resembles *C. meridensis* in the frond architecture, usually has thicker trunks [to (10)15–20 cm in diameter vs. 5–12 cm in *C. meridensis*], asymmetrical petiole scurf squamules (vs. ± symmetrical), and dark brown to castaneous laminar squamules (vs. brown to yellowish).

Petiole scales in Colombian *C. meridensis* are more strongly contrasted than in the plants from farther south, which have nearly black centers and narrow, orange-brown margins, sometimes appearing concolorous black. Ecuadorian and northern Peruvian populations also retain a sheath of old petiole bases on their trunks, reaching

8–10 cm in diameter. They grow either on open ridges as diminutive tree ferns to 1.5 m tall, with small fronds and often sessile pinnules, or they grow in the dense understory with large fronds to 3 m long draped over adjacent vegetation or being supported by nearby branches. These divergent phenotypes are most likely adaptations to unfavorable environmental conditions. Their ranges coincide with the Huancabamba-Amotape-region, a climatical and geological enclave in the Andes that forms both frontiers and sole home for a plethora of plant and animal species. I chose to present separate descriptions for the two divergent forms and to name them at varietal rank in order to facilitate the delimitation from similar, unrelated species.

### 3.5.2 *Cyathea meridensis* var. *meridensis*

Selected specimens examined

C o l o m b i a . **Antioquia**. Betania, Vereda Aguas Lindas, finca Agua Linda, río El Pedral, 1700 m, 19.VIII.2004, »Giraldo & Mejia 2077« (COL). **Cauca**. Parque Nacional Munchique, El Tambo, vereda La Romelia, La Gallera, 2000 m, 27.VII.1997, »Acevedo et al. 308« (COL). **Chocó**. La Mansa, Carretera Medellin–Quibdó km 105+500, en bosque circunadando antena Telecom, 2300 m, 3.VI.1987, »Mejia 106« (COL). **Cundinamarca**. Road from Bogotá to Fusagasugá, just S of the crest of the Cordillera, 25 km from Bogota, 19.VII.1976, »Barrington 455« (COL); Cabrera, Vereda Nuñez, en alrededores de la Quebrada Negra, 2300–2400 m, 14.VII.1992, »Linares & Morales 2346« (NY). **Huila**. La Plata, vereda Agua Bonita, Finca Merenberg, 1200–1300 m, 13.VII.1979, »Díaz-Piedrahita 450« (COL). **Risaralda**. Santuario, Vereda Las Colonias, margen derecha del Río San Rafael, 2500 m, 26.II.1987, »Torres et al. 2314« (COL). **Santander**. Piedecuesta, Vereda Cristales, trocha que conduce al NE de la Estación, 2200 m, 11.II.2001, »Bustos-P. et al. 40« (COL).

Description

Trunks to 10 m tall, to 5–12 cm diameter, erect, old petiole bases soon caducous, petiole scars conspicuous; apices hidden in fascicles of petiole bases. Fronds to 120–360 cm long, patent to arching, distally drooping. Petioles to 120 cm long, inermous, or rarely with few spines at the base in large plants, dark brown to castaneous, basally darker, distally often paler, stramineous to yellowish, on each side with a line of narrow, brown to rusty brown, inconspicuous pneumathodes; scurf dark brown to castaneous, a dense matted tomentum of trichomidia, dissected squamellae, and oblanceolate squamules with fimbriate margins. Petiole scales lanceolate to ovate-lanceolate, concordantly to discordantly bicolorous, variable, with dark brown to blackish centers and narrow orange to golden brown margins.

Laminae to 240 × 110–150 cm, bipinnate-pinnatifid to tripinnate. Pinnae to 55–75 cm long, 15–18 pairs per frond, alternate, stalked to (1.8)2.0–3.4 cm, distally narrowly green-alate, distal segments simply adnate to weakly decurrent. Costae to 3 mm broad. Pinnules long-triangular, to 120 × 22–45 mm, short to long-stalked 2–5 mm, basally truncate to weakly cordate; basal segments sometimes remote, connected by laminar tissue or free, then sometimes segments weakly auriculate; segments ascending, distally weakly falcate, with obtuse to round tips, with obtuse to rectangular sinuses 1–3 mm wide, margins crenulate to strongly crenate, sometimes revolute and appearing entire, segments weakly hairy adaxially near the margins, the hairs multicellular, white, to 1 mm long, abaxially without hairs but veins with small appressed trichomidia, scurf remnants, and some flat, lanceolate to ovate, yellowish to brown scales with fimbriate margins, to 2 mm long.

Sori to 1.0–1.4 mm diameter, costal to subcostal, in vein forks; indusia subsphaeropteroid to sphaeropteroid, dark brown, persistent, with or without umbo, sometimes with scale on top.

Distribution and habitat

Found sporadically in montane forests at 1200–2500(2870) m in Venezuela and Colombia, to be expected in adjacent Ecuador.

Remarks

*Cyathea meridensis* var. *meridensis* is characterized by the tall, thin stems and the dark appearance of its dried fronds. It may be mistaken for *C. lindeniana*, but the latter species has larger, erect scurf squamules and dark, but not blackish petiole scales, whose margins are often not contrasting with the centers.

### 3.5.3 *Cyathea meridensis* var. *nana* **n. var.**

(Figs. 1–2, 19A, B)

T y p e : E c u a d o r . **Zamora-Chinchipe**. Estación Cientifica San Francisco, T1, entre refugio y camino a las antenas, 3°59'33.6"S, 79°04'14.5"W, 2550 m, 24.X.2003, »Lehnert 970« (holotype, GOET; isotype, QCA).

P a r a t y p e s : E c u a d o r . **Zamora-Chinchipe**. Reserva Tapichalaca, study plot B1, nearby Ventanillas, 4°29'S, 79°07'W, 2600 m, 27.X.2003, »Lehnert 991« (GOET, QCA); Reserva Tapichalaca; Ventanillas, trail to study plots B2 and B3, 4°29'S, 79°07'W, 2550–2600 m, 3.XI.2003, »Lehnert 1077« (GOET, QCA); Reserva Tapichalaca, 2600–2650 m, 18.–19.IX.2004, »Lehnert & Kessler 1301« (GOET, QCA, UC); Podocarpus National Park, near the Yangana–Valladolid road, 4°28'S, 79°09'W, 2700 m, 8.VII.2000, »Pedersen et al. 104397« (AAU, LOJA); along road Yangana–Valladolid, just past the Nudo de Sabanilla towards Valladolid, 2500 m, 7.V.1991, »van der Werff & Palacios 9354« (MO, UC). – P e r u . **Cajamarca**. San Ignacio, San José de Lourdes, Cerro Picorana, 4°58'S, 78°53'W, 2830 m, 17.VIII.1998, »Campos et al. 5550« (MO, UC); ibid., Cordillera between Bajo Picorana and El Picorana, 4°58'S, 78°53'W, 2420–2470 m, 19.VIII.1998, »Campos et al. 5616« (MO).

Description

A var. *meridensi* truncis humilioribus petiolis obtectis frondibusque cum pinnis paucioribus (8–10 pares vs. 12–15 pares) pinnulisque minoribus (usque 65(80) mm vs. 65–120 mm longis) differt.

Trunks to 1.0–1.5 m tall, erect, to 12 cm diameter including persistent old petiole bases; apices hidden in fascicles of petioles (Figs. 1, 2), unfolding one to three fronds at a time. Fronds to 50–150 cm long, arching-patent. Petioles to 17–28 cm long, inermous, dark brown to castaneous (Fig. 2), on each side with a line of well spaced, rusty brown, inconspicuous, narrow elliptic pneumathodes; scurf consisting of small trichomidia and oblanceolate, strongly dissected squamules (Fig. 19B). Petiole scales 15–25 × 2.5–3.5 mm, dark brown to blackish with pale brown to yellowish white margins 0.2–0.4 mm broad (Fig. 19A), marginal color transitional to central color in backlight.

Laminae to 55–140 × 27–90 cm, bipinnate-pinnatifid to tripinnate. Pinnae to 16–47 cm long, 8–10 pairs per frond, stalked to (0.3)0.5–1.6 cm, distally narrowly green-alate, distal segments simply adnate. Costae to 2.0–2.5 mm broad. Pinnules oblong-lanceolate, (20)47–65(80) × (6)11–17 mm, subsessile to short-stalked 1–3 mm, basally truncate to weakly cordate; basal segments never remote, sometimes weakly auriculate, segments ascending, distally straight, with rounded tips, margins crenulate to subentire, sometimes revolute and appearing entire, sinuses obtuse to acute, 0–2 mm wide; segments weakly hairy adaxially near the margins, the hairs multicellular, white, to 1 mm long, abaxially without hairs, with small appressed trichomidia on the veins abaxially, also with scurf remnants and some flat lanceolate to ovate, dark brown scales with fimbriate margins, to 2 mm long, distally with small subbullate squamules to 1 mm long. Sterile veins forked or simple, fertile veins forked.

Sori to 1.0 mm diameter, costal, in vein forks; indusia sphaeropteroid with umbo, pale brown and persistent, without small scale on top.

Distribution and habitat

Found on ridges and in long-lived clearings in montane forests at 2420–2830 m in southern Ecuador and northern Peru.

Differential diagnosis

*Cyathea meridensis* var. *nana* has quite a distinct appearance compared to var. *meridensis* and var. *obtecta*, because var. *nana* has smaller fronds and lacks the characteristic large triangular, stalked pinnules. However, the scales and fine indument of the petioles and laminae are congruent with the other two varieties. The small size of the plant with the subsequent reduction of pinna pairs (to 8–10 in var. *nana* vs. to 15–18 in var. *meridensis* and var. *obtecta*) is likely an adaptation to the ridge tops to which this variety is restricted. Its habit resembles that of a small *C. plicata*, a species that is common within the geographical range of *C. meridensis* var. *nana* and most probably closely related. *Cyathea plicata* can be separated from *C. meridensis* var. *nana* by its longer, narrowly lanceolate petiole scales and adaxially flat to weakly concave pinnules (vs. pinnules adaxially convex).

3.5.4 *Cyathea meridensis* var. *obtecta* **n. var.** (Figs. 3, 19C)

Type: Ecuador. **Zamora-Chinchipe**. Reserva Tapichalaca, Ventanillas, trail to study plots B2 and B3, 4°29'S, 79°07'W, 2550–2600 m, 3.II.2003, »Lehnert 1079« (holotype, GOET; isotypes, QCA, UC).

Paratypes: Ecuador. **Zamora-Chinchipe**. Nangaritza, Cordillera de Naguipa, Cerro Colorado, ridge 8 km SSE of Nambija, 20 km ESE of Zamora, 4°07'51"S, 78°46'36"W, 2630 m, 21.II.2006, »Cole et al. 261« MO, QCNE, UC); new road Loja–Zamora, ca. 4 km E of pass "El Tiro", ridge from white cross on left road side (towards the valley), 3°59'S, 79°08'W, 2500–2600 m, 11.X.2004, »Lehnert 1430« (GOET, QCA, UC). – Peru. **Amazonas**. Laguna de Pomacochas, 2550 m, 27.III.1998, »van der Werff et al. 15835« (MO, UC).

Description

A var. *meridensi* truncis humilioribus petiolis obtectis frondibusque supra vegetationem vecinam reptantibus differt.

Trunks to 0.3–2.0 m tall, to 11 cm diameter, erect, with persistent old petiole bases (Fig. 3); apices hidden in fascicles of petioles, unfolding only one frond at a time. Fronds to 190–340 cm long, supported by or draped on surrounding vegetation. Petioles to 50–200 cm long, inermous, dark brown to castaneous (Fig. 3), basally darker, distally often paler, stramineous to yellowish, on each side with a line of narrow, brown to rusty brown, inconspicuous pneumathodes. Petiole scales to 25 × 5 mm, lanceolate to ovate-lanceolate, concordantly to discordantly bicolorous (Fig. 3), variable, with dark brown to blackish centers and narrow orange to golden-brown margins; scurf dark brown to castaneous, a dense tomentum of trichomidia and oblanceolate squamellae with fimbriate margins, the margins appearing paler than the centers in backlight (Fig. 19C).

Laminae to 140 × 110–150 cm, bipinnate-pinnatifid to tripinnate. Pinnae to 55–75 cm long, stalked to (1.8)2.0–3.4 cm, distally narrowly green-alate, distal segments simply adnate to weakly decurrent. Pinnules long-triangular, to 120(130) × 22–38 mm, short to long-stalked 2–5 mm, basally truncate to weakly cordate; basal segments sometimes remote, connected by laminar tissue or free, margins crenulate to strongly crenate, sometimes revolute and

appearing entire, in basal segments sometimes weakly auriculate; segments ascending, distally weakly falcate, with obtuse to rounded tips, with obtuse to rectangular sinuses 1–3 mm wide, weakly hairy adaxially near the margins, the hairs multicellular, white, to 1 mm long, abaxially without hairs, with small appressed trichomidia on the veins abaxially, also with scurf remnants and some flat, lanceolate to ovate, yellowish to dark brown, fimbriate scales to 2 mm long. Sterile veins forked or simple, fertile veins forked.

Sori 1.2–1.4 mm diameter, subcostal, in vein forks; indusia sphaeropteroid with umbo, pale brown and persistent, without small scale on top.

#### Distribution and habitat

In dense shrub and understory of wet montane forests in Ecuador and northern Peru at 2500–2630 m.

#### Differential diagnosis

*Cyathea meridensis* var. *obtecta* matches the typical variety in the dissection and size of the fronds but has smaller trunks that retain the old petiole bases and remain in the understory of the forests. It is restricted to southern Ecuador and northern Peru, and presumably represents a regional growth form adapted to the special climatic conditions of this area (Killeen et al. 2007). This variety of *C. meridensis* is superficially similar to *C. gracilis* Griseb., which can be found in the same area. The latter species grows mainly epiphytically and therefore also develops a small trunk with relatively long, drooping fronds, like those of *C. meridensis* var. *obtecta*. Both species differ mainly in the petiole scales (bicolorous blackish with orange margins in *C. meridensis* var. *obtecta* vs. concolorous dull brown in *C. gracilis*), color and abundance of petiole scurf (persistent, dense, and dark brown to castaneous vs. absent or ephemeral, pale brown to whitish), and soral position (subcostal to costal vs. submedial). *Cyathea ebenina* H. Karst. is another similar species with thin trunks; it has bicolorous scales like *C. meridensis* but agrees with *C. gracilis* in the soral position. It can be distinguished from both *C. meridensis* and *C. gracilis* by the black rhachises and costae that strongly contrast with the green costules (vs. not contrasting in the other two species). *Cyathea ebenina* also has more linear-lanceolate pinnules and never has the basal pinnule segments free or remote (vs. often triangular and with remote basal segments).

#### 3.5.5 Key to the varieties of *Cyathea meridensis*

**1** Fertile fronds to 1.5 m long, with 8–10 pinna pairs; all pinnules sessile, to 65(–80) mm long; trunks to 1.5 m tall, covered with persistent petiole bases. . . . . var. ***nana***

– Fertile fronds more than 1.5 m long, with 12–15 pinna pairs; largest pinnules notably stalked, to 120–130 mm long; trunks to 3–10 m tall, petiole bases persistent or not. . . . . **2**

**2** Fertile fronds leaning and draped over adjacent vegetation; trunks relatively small compared to the frond length, 0.3–2.0 m tall, petiole bases persistent, rotting off only in older plants. . . . . var. ***obtecta***

– Fertile fronds hanging free, arching to distally drooping; trunks to 10 m tall, without persistent petiole bases, petioles cleanly falling off at an early age. . . . . var. ***meridensis***

### 3.6 *Cyathea plicata*

*Cyathea plicata* Lehnert: Lehnert 2006a: 6. – Type: Ecuador. Zamora-Chinchipe, Estación Cientifica San Francisco, disturbed areas (pastures, fields remnants of forests) above the station, 3°57'48"S, 79°04'12"W, 2290 m, 14.IX.2003, »Lehnert 844« (holotype, GOET; isotypes, LOJA, QCA, UC).

#### Selected specimens examined

E c u a d o r . **Loja**. New road Loja–Saraguro, km 17, 3°55'S, 79°15'W, 2600–2650 m, 20.III.1993, »Øllgaard & Feil 91113« (AAU, QCA, QCNE). **Napo**. Oyacachi, E of village, 0°13'N, 78°02'W, 2900 m, 29.X.1999, »Øllgaard & Navarrete 1296« (QCNE). **Sucumbios**. Cartagena, km 25 from El Carmelo on road towards La Bonita, 0°37'N, 77°30'W, 2800 m, 14.IV.1983, »Løjtnant et al. 12330« (AAU). **Zamora-Chinchipe**. Chinchipe, La Esmeralda, cooperativa San Francisco de Numbala Alto, 4°22'S, 79°03'W, 2300 m, 2.II.1999, »Palacios & Tirado 13120« (UC).

P e r u . **Amazonas**. Chachapoyas, Carretera Chachapoyas–Mendoza, km 52 de Chachapoyas, 10 km detrás de Molinopampa, 6°14.26'S, 77°35.96'W, 2700 m, 4.VIII.2002, »Lehnert 240« (GOET, UC, USM). **Cajamarca**. San Miguel, Tongo Alto, following the route to Tongod, 2650 m, 16.IX.1995, »Sanchez-Vega & Briones 5807« (UC).

#### Description

Trunks to 3 m tall, to 12–16 cm diameter, erect and straight, not covered by old petiole bases. Petioles to 25 cm long, scabrous to finely muricate at bases, with caducous scurf of brown squamellae with strongly crispate margins. Petiole scales long-lanceolate with elongated tips, to 50 × 3.6 mm, nearly concolorous orange-brown to bicolorous with orange-brown to castaneous centers and orange to whitish narrow margins.

Laminae to 105–165 × 60–70 cm. Pinnae alternate, to 40 cm long, sessile to short-stalked (2 cm), acute to short-attenuate at tips. Pinnules linear-lanceolate, 1.0–1.5 × 3.0–7.0(8.0) cm, sessile or rarely short-stalked, the bases truncate to weakly cordate, tips short-acute; pinnules turned upwards with respect to the costae and often twisted towards the rhachis, especially in the proximal half of the pinnae.

Sori inframedial to costal, at vein forks; indusia sphaeropteroid, without umbo.

For full description see Lehnert (2006a).

### Distribution and habitat

Wet montane forests at 2050–2900 m in Ecuador and northern Peru. Preferentially in dwarfed vegetation and forest clearings, fertile only in full sun.

### Remarks

This distinctive species is recognized by the furrowed pinnae and relatively short fronds. The upward pointing pinnules can be detected in herbarium specimens because the pinnae are impossible to flatten without breaking off the pinnules, so they are normally folded in dried specimens. This species probably belongs to the *C. meridensis* group, whose members have similar scurf and laminar texture. However, the pinnules are held horizontally in the species of the *C. meridensis* group and they also have more strongly bicolorous and shorter scales than in *C. plicata*. The circularly swollen junctions of rhachises and costae in *C. meridensis*, *C. carolihenrici*, and *C. plicata* are shared with some other *Cyathea* species with sphaeropteroid indusia, such as *C. cystolepis* Sodiro and *C. divergens* Kunze, but the significance of this character considering relationships is still uncertain.

## 3.7 *Cyathea squamipes*
(Figs. 6, 8, 20)

*Cyathea squamipes* H. Karst.: Karsten 1860: 199. – Type: Venezuela. Mérida, 1000–1500 m, »Karsten s. n.« (holotype, W, n. v., W-photo, -fragm. BM; isotype B).

*Cyathea lepidopoda* C. Chr.: Christensen 1905: 193, nom. superfl.

*Cyathea mexicana* Schldtl. & Cham. var. *boliviensis* Rosenst.: Rosenstock 1928: 56. – *Cyathea caracasana* (Klotzsch) Domin var. *boliviensis* (Rosenst.) R. M. Tryon: Tryon 1976: 77. – Type: Bolivia. La Paz, "Hacienda Sumaco supra Tipuani", »Buchtien 5140« (holotype, n. l.; isotypes, F, GH, NY, US).

### Selected specimens examined

C o l o m b i a . **Antioquia**. Campamento, km 10–15 de la via Campamento-Las Brisas, 1570–1800 m, 20.VIII.1986, »Callejas et al. 2516« (GH, NY); Jardin, carretera hacia la selva, Alto de la Cruz, 2040 m, 12.VI.2004, »Giraldo & Mejia 2140« (COL). **Cundinamarca**. San Bernardo, Cordillera Oriental, Vereda Santa Rita, Hacienda El Placer, 2180 m, 28.VII.1985, » Jaramillo Mejia et al. 7181« (COL). **Risaralda**. Mistrato, Corregimiento de Jueguadas, 5°26'N, 76°02'W, 1500 m, 28.III.–2.IV.1992, »Betancur et al. 3256« (COL). **Santander**. Mesa de los Santos, 1500 m, 11.–15.XII.1926, »Killip et al. 15088« (US). **Valle de Cauca**. Above Finca La Mesita, W of Villa Colombia, E slope of Cordillera Occidental, 3°08'N, 76°40'W, 1900–2100 m, 28.III.1987, »Gentry et al. 40904« (COL).

V e n e z u e l a . **Mérida**. Between Antimano and Agua Negras, 900–1500 m, »Pittier 6016« (B). **Prov. unknown**. 1889, »Engel 137« (B).

E c u a d o r . **Cañar**. Vicinity of Huigra, mostly on the Hacienda de Licay, 8.IX.1918, »Rose & Rose 22605« (US). **Carchi**. Ca. 6 km above Maldonado, just below Puente de Palo, 0°54'N, 78°06'W, 2275 m, 23.V.1993, »Boyle & Bradford 1892« (MO). **Morona-Santiago**. Limón Indanza, region of Cordillera del Cóndor, Santa Susana de Chiviaza, W of Río Zamora, Cerro Chiviaza, 2°55'22"S, 78°22'18"W, 1150 m, 24.III.–3.IV.2006, »Reyes & Morales 1092« (MO, UC). **Pichincha**. Mindo Biological Station, 0°04.7'S, 78°43.9'W, 1550 m, 13.X.2006, »Lehnert 966« (GOET, QCA, UC). **Sucumbios**. Río Bermejo to Cerro Sur Pax, Cofan community of Alto Bermejo, access from Bermejo oil filed road to Pozo 2, NW between Lumbaqui and Cascales, vicinity of Oso Ridge Camp, 0°19'17.7"N, 77°25'10.0"W, 1700–1920 m, 3.VIII.2005, »Aguinda et al. 1239« (UC). **Tungurahua**. Baños, expanded area of Llanganatis National Park, Machay, Río Verde, Colina San Augustin, 1°22'S, 78°17'W, 2090 m, 1.–3.VIII.1999, »Vargas et al. 3751« (UC). **Zamora-Chinchipe**. Estación Cientifica San Francisco, areas intervenidas (pastizales, campos y remnantes del bosque) arriba de la estación, 3°57'48"S, 79°04'12"W, 2420 m, 15.IX.2007, »Lehnert 845« (GOET, QCA, UC); in the vicinity of the mining camp at the Río Tundaime, along road to military base El Condor, 3°38'S, 78°25'32"W, 1500 m, 7.XI.2008, »van der Werff et al. 19368« (UC).

P e r u . **Amazonas**. Bagua, third camp, Cordillera Colán SE of la Peca, 2100–2300 m, 11.X.1982, »Barbour 3921« (US); around Laguna Pomacochas, 5°50'11"S, 77°57'47"W, 2250 m, 21.III.2002, »van der Werff et al. 15256« (UC). **Cajamarca**. San Ignacio, Dist. San José de Lourdes, Picorana, 4°58'00"S, 78°53'01"W, 2350–2450 m, 4.XII.2002, »Campos et al. 5907« (UC). **Cuzco**. Calca, Dist. Lares, Suyo, 10°28'S, 72°00'W, 2831 m, 17.VI.2005, »Valenzuela et al. 5717« (MO); Urubamba, Dist. Machu Picchu, Cedropata (Collpani), 13°06'S, 72°38'W, 2550 m, 8.XI.1997, »Chávez Huamán 1008« (AAU). **Huanuco**. Southwestern slope of the Río Llulla Pichis watershed, on the ascent of Cerros del Sira, in a valley beyond Camp 4, 9°25'S, 74°44'W, 1540 m, 25.VII.1969, »Dudley 13276« (GH). **Pasco**. Oxapampa, Abra Villa Rica, 10°40'36"S, 75°18'55"W, 2400 m, 25.VIII.2004, »Mellado 1573« (MO). **San Martin**. Huallaga, al norte de La Morada, 2400–2500 m, 14.VIII.2001, »Quipuscoa et al. 1032« (UC).

B o l i v i a . **Cochabamba**. Carrasco, 136 km antigua carretera Cochabamba–Villa Tunari, 17°07'S, 65°35'W, 1550 m, 29.VIII.2000, »Kessler et al. 7871« (GOET, LPB, UC). **La Paz**. Serrania Bella Vista, entre Caranavi y Palos Blancos, ca. km 40.1, 15°40'S, 67°24'W, 1550 m, 15.VIII.2004, »Lehnert 25« (GOET, LPB, UC).

### Description

Trunks to 15 m tall, perhaps taller, to 10–16 cm diameter, without old petiole bases when crown exposed or trunk taller than frond length, trunk apices hidden in fascicles of petioles (Figs. 6, 8), frond scars gray or light brown, oval and well spaced in lower parts, tightly packed and rhomboid in upper parts (normally from 3–4 m height), adventitious buds absent although trunk may be forked with 2–5 separate crowns after injuries. Petioles to 110 cm long, young ones green but usually covered with a dense brown scurf, becoming brown to dark brown with age, verrucate-muricate to aculeate with corticinate spines to 4 mm long, spines with a scale on top in crosiers and young fronds; scurf persistent, consisting of crested, erect, brown to dark brown squamules 0.1–0.6 mm long (Fig. 20B), not cleanly abraded. Petiole scales to 15 × 4 mm, atropurpureus to blackish on the sides and the bases of the

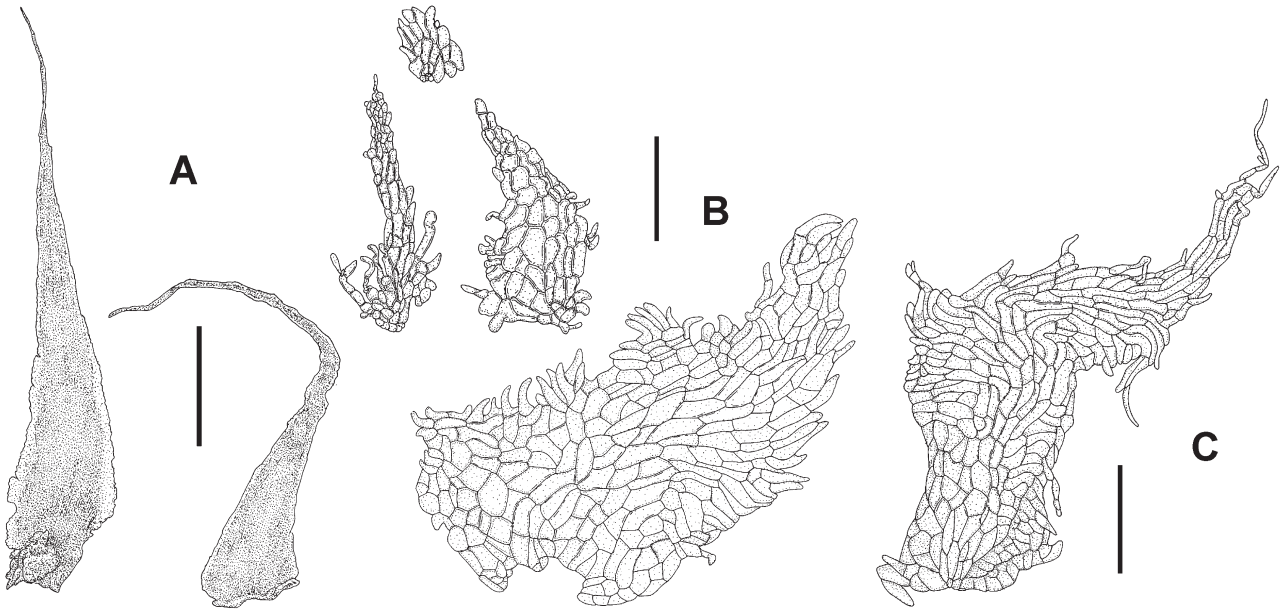


**Fig. 20.** *Cyathea squamipes* (all from »Jiménez 1014« UC). – **A**. Petiole scales. **B**. Squamules of petiole scurf. **C**. Laminar squamule. – Scales: 5 mm (A), 0.2 mm (B, C).

petioles, dark brown on distal petiole parts and the undercover, always with distinct lighter margins (Fig. 20A), brown to orange, rarely yellowish or cream-white.

Laminae to 270 × 90 cm, bipinnate-pinnatifid, lustrous dark green above, paler below, when dried characteristically black adaxially, grayish abaxially, apices gradually reduced. Rhachises brown to castaneous, becoming stramineous or grayish apically, often pruinose adaxially. Costae and costules shortly hairy with antrorse multicellular hairs to 1 mm long adaxially, glabrescent abaxially, with crested brown squamules abaxially (Fig. 20C), especially long-lasting in the axils of the costae. Pinnae short-stalked, acuminate, distally green-alate, the wings arcuate. Pinnules sessile to short-stalked (1–2 mm in the basal ones), linear, acuminate from ¾ of the total length, fertile and sterile segments planar, segment margins subentire, crenulate at the tips, with short hairs on the veins abaxially, sometimes also between them below the sinuses, glabrous adaxially or sometimes with one or two white hairs on the midveins distally, with few to many orange to tan, flattish and bullate scales abaxially on the costules and midveins (rarely abundant or lacking). Sterile veins simple or forked; fertile veins forked.

Sori costal, at vein forks; indusia sphaeropteroid, glabrous, tan and lustrous, with dark apical or slightly lateral umbo, rupturing irregularly at maturity, but persisting as deep cups or urns, usually including the umbo; paraphyses of same length as the sporangia, hyaline. Spores deep yellow, trilete, exospore verrucate, perispore baculate.

Distribution and habitat

Colombia, western Venezuela, Ecuador, Peru, and Bolivia at (900)1400–2800(3000) in moist montane forests, often persisting in cleared areas.

Remarks

*Cyathea squamipes* is represented mainly by specimens previously recognized as *C. caracasana* var. *boliviensis* (Rosenst.) R. M. Tryon. Distinguishing characters of *C. squamipes* are its dark brown to blackish petiole scales with narrow margins, the persisting petiole scurf, and its orange-brown, bullate squamules on the laminae. The similar *C. delgadii* Sternb. and *C. herzogii* share bullate squamules but have concolorous brown to orange-brown petiole scales, and have evanescent scurf or no scurf at all.

*Cyathea squamipes* differs significantly from *C. caracasana* in the type of scurf squamules found on the whole fronds. While *C. caracasana* and allies (i. e., *C. crenata*, *C. meridensis*, *C. carolihenrici*, and *C. plicata*) have dark brown to castaneous, pulverulent scurf, *C. squamipes* has round to ovate, often orange-brown squamules with crispate margins, which are erect on the petiole and often bullate on the laminae abaxially. This type of squamule, together with more abundant multicellular hairs than in the *C. caracasana* group, relates *C. squamipes* to the *C. fulva* group. The *C. fulva* group sensu Tryon (1976) is probably a natural group of species characterized by dull brown to

orange-brown petiole scales and scant to ephemeral petiole scurf; the abundance and distribution of hairs, as well as the presence of bullate squamules on the laminae, are the most important characters in distinguishing species but apparently they may also vary greatly within a species.

The widespread and common *Cyathea delgadii* of the *C. fulva* group is very close to *C. squamipes* in every aspect. In the central Andes, they often grow close together in large numbers, they have the same appearance and stature, and their spores are indistinguishable. Their laminar dissection is also similar; however, *C. delgadii* never has the basal segments of the largest pinnules separated as much as *C. squamipes*. The veins are abaxially hairy in both species, but only *C. delgadii* regularly has many hairs between the veins abaxially, or on the veins adaxially. The adaxial laminar surface of *C. squamipes* is nearly glabrous except for the densely hairy costules and costae, and sometimes single hairs on the segments' midveins. Also, the hairs are longer in *C. delgadii* (ca. 1 mm) than in *C. squamipes* (0.4–0.6 mm). Plants in the field or specimens with petioles can be readily distinguished: because of long persisting scurf and mainly castaneous scales on the petiole, the trunk apices of *C. squamipes* appear ruddy and dusky. The brighter, concolorous orange-brown scales of *C. delgadii* persist only at the sides of the petiole; the normally weakly developed scurf is soon caducous, revealing the brown to blackish, shiny cortex of the petiole bases. Thus *C. delgadii* appears more colorful and contrasting in the field than *C. squamipes*.

Two species are morphologically much closer to *C. squamipes* than to the other species in the *C. caracasana* complex (Tryon 1976), namely *C. catacampta* and *C. lindeniana*. *Cyathea squamipes* is intermediate between the two in many characters, e. g., scale size, width of differently colored scale margins, and hairiness of laminae. Some specimens of *C. squamipes* tend more to *C. catacampta*, having larger petiole scurf squamules than typical *C. squamipes* but having the typical dark, broad petiole scales (»Lehnert & Lopez 483«, »Lehnert 845, 1469«, »Jiménez 1537«). »Lehnert 1469« resembles more *C. lindeniana*, with remote segments and dark laminar color, but scurfiness and scale color fit better in *C. squamipes*. The three morphospecies may represent stabilized hybrids between members of the *C. caracasana* group and the *C. fulva* group. Typical characters of the *C. caracasana* group found in *C. squamipes* and allies are the persistent, dark brown scurf, tendency towards glabrousness, and relatively short hairs. Furthermore, *C. squamipes* and *C. lindeniana* often have triangular, notably stalked pinnae and dark green laminae, and in this point especially resemble *C. meridensis* and *C. carolihenrici* of the *C. caracasana* group. Traits that relate to the *C. fulva* group (among these species especially to *C. delgadii*) are sessile pinnules, reddish to orange-brown color in the indument and variability in the hairiness, which are evident in *C. catacampta*, and the tendency to weakly developed scurf and concolorous petiole scales, which are more pronounced in *C. lindeniana*. Future molecular work and phenological field studies should focus on this group in order to evaluate the possible existence of hybrid complexes.

### 3.8 *Cyathea lindeniana*
(Figs. 11–12)

*Cyathea lindeniana* C. Presl: Presl 1849: 30. – Type: Colombia. "Nova Granada, Prov. Maraquita", »Linden 1022« (holotype, n. l.; isotypes, B [fragm. ex Herb. Mett.], BM?, BR n. v., K, US).

*Cyathea grenadensis* Trevis.: Trevisan 1851: 164, nom. nud. (fide Tryon 1976), »Linden 1022« was cited.

Selected specimens examined

Colombia. **Antioquia**. Belmira, Páramo Sabanayo, Estación Ecológica "El Refugio", 3100 m, 15.V.1996, » Gómez R. F. et al. 5997« (F). **Chocó**. Cerro del Torre, vertiente NE, 1900–1940 m, 11.VIII.1982, »Silverstone-Sopkin 1294« (AAU, MO). **Cundinamarca**. Tabio, Cordillera Oriental, Vereda La Juaica, 3000 m, 25.III.1965, »Huertas & Camargo 4472« (COL). **Huila**. At camp of Gaucho, Cordillera Oriental, N of Palacio, about 20 km NE of Santa Ana, ca. 2530 m, 24.II.1948, »Little 7332« (COL). **Santander**. Sarare, Alto del Mirador, 1800–2100 m, 19.III.1963, »Bishler 2111« (COL, NY). **Valle de Cauca**. Km 19 on road from Cali to Buenaventura, 4.VIII.1976, »Barrington 498« (COL).

Venezuela. **Mérida**. La Cuchilla, 20 km W of Mérida on road to La Azulita, 2300 m, 16.IX.1965, »Tryon & Tryon 5773« (UC). **Tachira**. Junín, S slopes of Cerro San Isidro, directly N of El Reposa, above Hacienda Bella Vista, Quebrada Agua Caliente and tributaries, 7°34'N, 72°25'W, 2200–2450 m, 13.–14.XI.1982, »Davidse & González 22174« (UC). **Lara**. Morán, road Humacaro Alto to Guaito, 1800 m, 30.I.1991, »van der Werff & Rivero 8761« (UC).

Ecuador. **Carchi**. Río San Juan Valley, 4 h walk below Chical, at Ortiz ranch between Peñas Blancas and El Pailán, known locally as Goaltal, 1°02'N, 78°15'W, 1230–1250 m, 10.VI.1993, »Boyle et al. 1998« (MO). **Napo**. Cordillera de los Guacamayos, ca. 6 km SE of Cosanga, 0°38'S, 77°50'W, 1940 m, 5.X.2006, »Homeier 2370« (GOET, QCA). **Zamora-Chinchipe**. Estación Cientifica San Francisco, trail "antajo", 3°58'S, 79°04'W, 1800 m, 9.XI.2007, »Lehnert 1091« (GOET, QCA, UC).

Peru. **Cajamarca**. Lower edge of Cutervo National Park, 10–15 km N of San Andres de Cutervo, 6°10'S, 78°40'W, 2200 m, 13.II.1992, »Gentry et al. 61560« (UC). **San Martin**. Rioja, entre Pedro Ruiz y Rioja, 5°47.17'S, 77°58.20'W, 2000 m, 21.VII.2002, »Lehnert 198« (GOET, UC, USM).

#### Description

Trunks to 7(–10) m tall, to (7.5)9.0–12.0 cm diameter, without old petiole bases; upper parts covered in concolorous scales, similar to petiole scales; frond scars elliptic, in upper parts of taller trunks circular, not rhomboid, inconspicuously gray, with small, round, vermillion lenticels

below them; trunk apices hidden in fascicles of petioles (Fig. 12); adventitious buds lacking. Fronds to 200–350 cm long, arching, distally drooping, but not to the ground (Fig. 11). Petioles to 100 cm long, dark brown to atropurpureous, rarely basally blackish, verrucate to muricate, rarely with short spines to 2 mm long; adventitious (aphlebioid) pinnae lacking; petiole scurf weakly developed, persistent, concolorous orange-brown to dark reddish brown, consisting of erect, lanceolate, ovate, and round squamules 0.5–1.0 mm long, with fimbriate to crested margins but without dark marginal teeth, usually leaving cortex visible, long-lasting, abraded only in inermous petiole parts, basal parts of squamules persisting. Petiole scales narrowly lanceolate to lanceolate, (15.0)20.0–33.0 × 3.5–4.5 mm, tips straight to falcate, weakly undulate, the brown to dark brown centers not sharply delimited against the brown to orange margins, often appearing concolorous, usually lustrous (Fig. 12).

Laminae to 250 × 160 cm, bipinnate-pinnatifid to tripinnate, firmly herbaceous to chartaceous, brodest in the middle, apices gradually reduced and long drooping (Fig. 11); dark green adaxially, usually blackish when dried, bright green abaxially. Pinnae to 60–75 cm long, 12–15 pairs per frond, stalked to (0.6)1.4–3.0(5.0) cm, distally narrowly green-alate, the distal segments simply adnate. Leaf axes brown to atropurpureous, rarely abaxially stramineous with brownish tinges and streaks, hairs only adaxially on costules, costae, and distal parts of rhachises, hairs 0.5–1.0 mm long, whitish to tan, abaxially glabrescent with sparse tan to brown scurf consisting of small squamules 0.2–0.6 mm long, similar to those on the petioles, shortly fimbriate to entire, persisting at junctions of costae with costules and rhachises, costae inermous, rarely more than 3 mm broad, junctions of costae and rhachises abaxially swollen, each with one planar pneumathode to 3 × 2 mm, brown to dark brown, inconspicuous. Pinnules to (10.0)11.0–12.5 × 1.6–3.2 cm, subsessile to stalked 1.0–4.0(6.0) mm, alternate, (0.5)1.0–2.5 cm between the stalks, long-triangular to lanceolate, truncate at base, tapering from below the middle (rarely in large pinnules from the base) to acute to attenuate tips, segments ascending, weakly falcate in large pinnules, with crenulate to crenate margins and round or obtuse tips, basal segments alternately placed, sometimes remote from each other, sinuses (1)2–4 mm wide, acute to rectangular; sterile and fertile pinnules not different. Veins glabrous abaxially except for few occasional white to tan, erect multicellular hairs on the midveins distally, with variously developed scurf, white unicellular trichomidia, small flattish, brown, ovate squamules with elongated tips and finely dissected margins, midveins sometimes with brown bullate squamules; sterile veins forked or simple, fertile veins forked.

Sori to 1.0(–1.5) mm diameter, subcostal to costal, at vein forks, indusia sphaeropteroid, with umbo, tan, translucent, fragments persisting; receptacles globose, 0.2–0.3 mm diameter, paraphyses few, hyaline, tan, shorter than sporangia (0.3 mm). Spores pale yellow, perispore not examined.

Distribution and habitat

Colombia, western Venezuela, Ecuador, and Peru; along rivers and creeks, in moist montane forests at 1250–3100 m.

Remarks

*Cyathea lindeniana* is one of the three species recognized here that fall into Tryon's (1976) concept of *C. caracasana* var. *boliviensis*. *Cyathea lindeniana* differs from *C. squamipes* and *C. catacampta* in the weak development of laminar indument and the regular presence of petiolulate triangular pinnules, which are less common in the other two species. Among these three, it also has the most delicate appearance, with erect, slender trunks 9–12 cm in diameter and long-arching to drooping fronds. *Cyathea catacampta* and *C. squamipes* have stouter trunks to 15–20 cm in diameter and more patent fronds. The slimmer appearance of *C. lindeniana* may be an adaptation to its preferred habitat, with plants growing mainly in shaded understory near rivers and in gorges. The fact that the plants retain this habit even with increased exposure to sun after clearing (observed in southern Ecuador and northern Peru) indicates that *C. lindeniana* is not a mere ecotype of *C. squamipes*, which is common within the geographical range of *C. lindeniana*. The petiole scales of *C. lindeniana* are less contrastingly colored than in *C. squamipes* or *C. catacampta* and are almost concolorous in some parts of the petioles. When only concolorous petiole scales are preserved in specimens, *C. lindeniana* may be mistaken for *C. delgadii* or one of its allies that have concolorous orange-brown scales. These species are, however, commonly much hairier than *C. lindeniana*, having many hairs abaxially on the veins and often also between them.

### 3.9 *Cyathea catacampta*
(Figs. 7, 9–10)

*Cyathea catacampta* Alston: Alston 1958: 231. – Type: Colombia. Nariño, between Río Miraflores and Río San Martin, Volcán de Cumbal region, 2680 m, 12.–13.VII.1944, »Ewan 16153« (holotype, BM; isotype, US).

Selected specimens examined

Colombia. **Antioquia**. Bello, 4.7 km above Medellin–San Pedro road, on road to radio tower at summit, 6°22'N, 75°39'W, 2760 m, 12.XI.1992, »McPherson 13038« (COL). **Cauca**. Cerro Munchique, south slopes, 40 km W of Popayan, 2700 m, 17.X.1965, »Tryon & Tryon 6009« (COL, UC); El Tambo, 2900 m, VII.1948, »Yepes-Agredo 431« (COL). **Cundina-**

**marca**. Manta, portrero Cielo Roto, 5°00'45"N, 73°32'35"W, 2400–2600 m, 9.VI.1999, »Sánchez-Baracaldo 3, 4« (UC). **Nariño**. Camino to Mayasquer below "Tambo" NW slope of Volcán Chiles, 2740 m, 31.VIII.–1.IX.1944, »Ewan 16012« (UC). **Risaralda**. Santuario, Vereda Las Colonias, 200 m arriba del campamento, 2740 m, 2.II.1987, »Torres et al. 1409« (COL). **Santander**. Charalá, Inspección Viroin, Vereda el Volcán, 1900 m, 1.VII.1987, »Torres 2579« (COL).

Ecuador. **Loja**. Trails ca. 5 km ENE of San Pedro de Vilcabamba, from "El Bosque" to Quebrada Romerillos and Banderilla, 4°14'S, 79°10'W, 2000–2200 m, 1.XII.1998, »Øllgaard & Navarrete 105965« (AAU, QCA). **Morona-Santiago**. Road Plan de Milagro-Gualaceo, km 34.3, 3°01'S, 78°39'W, 3000 m, 21.III.2001, »Øllgaard & Navarrete 2542« (AAU, QCA). **Zamora-Chinchipe**. Reserva Tapichalaca, garden area of the station "Casa Simpson", 4°29'S, 79°07'W, 2450 m, 4.XI.2007, »Lehnert 1082« (GOET, QCA, UC).

Peru. **Amazonas**. Chachapoyas, carretera Chachapoyas-Mendoza, km 51 de Chachapoyas, 9 km detrás de Molinopampa, 6°14.26'S, 77°35.96'W, 2700 m, 4.VII.2002, »Lehnert 227« (GOET, UC, USM). **Cuzco**. Urubamba, bottom of Río Urubamba Canyon at Puente Ruinas (Machu Picchu) railrad station, 2000 m, 4.I.1967, »Iltis et al. 1025« (UC); entre San Luis y Abra Malaga, 3050 m, 16.X.2002, »Lehnert 427« (GOET, UC, USM).

Bolivia. **La Paz**. Franz Tamayo, ANMI Apolobamba, sector Laitiki crossing the bridge between Pelechuco and Apolo, 14°36'53"S, 69°00'49"W, 2600 m, 20.IV.2006, »Fuentes et al. 10397« (LPB, UC); Nor Yungas, 8.5 km NE (below) Chuspipata, 16°16'S, 67°47'W, 2400 m, 20.X.1986, »Solomon 8492« (AAU, LPB, MO, NY, UC).

## Description

Trunks straight, erect, to 14(–21) m tall, to 15–20 cm diameter, without old petiole bases, upper parts covered in concolorous to bicolorous scales, similar to petiole scales, frond scars elliptic, in upper parts of larger plants rhomboid, not circular, pale brown to gray, with small round vermillion lenticels below them; trunk apices hidden in fascicles of petioles (Fig. 10); adventitious buds lacking. Fronds to (150)200–295 cm long, arching (Fig. 7). Petioles to 50–75(100) cm long, muricate to strongly aculeate, spines to 5 mm long, dark brown to atropurpureous, basally darker but rarely blackish, distally paler, sometimes stramineous, without adventitious (aphlebioid) pinnae at the petiole bases, petiole scurf well developed, concolorous orange-brown to dark reddish brown, consisting of erect lanceolate, ovate to round squamules 0.5–1.5 mm long, with fimbriate to crested margins but without dark marginal teeth, usually leaving cortex visible, long-lasting, abraded only in inermous petiole parts, basal parts of squamules usually persisting. Petiole scales narrowly lanceolate to lanceolate, 20.0–35.0 × (1.5)3.4–4.5 mm, usually lustrous, their tips straight, undulate or twisted, varying from nearly concolorous dark brown to concordantly bicolorous with the brown to blackish centers sharply set against the reddish brown to orange margins, the aristate tips similarly lighter.

Laminae to 150–230 × 110–130 cm, broadest in the middle, bipinnate-pinnatifid, firmly herbaceous to chartaceous, dark green adaxially, blackish to plumbeous when dried, bright green abaxially, apices gradually reduced, rather short and not drooping. Pinnae to 65 cm long, 15–20(25) pairs per frond, stalked to 0.6–1.0(2.0) cm (Fig. 7), distally narrowly green-alate, the distal segments simply adnate. Leaf axes stramineous to brown, rarely darker, costules, costae, and distal parts of rhachises adaxially hairy, hairs 0.5–1.0 mm long, whitish to tan, abaxially sparsely hairy with white erect hairs to 0.6 mm or glabrous, with sparse to dense orange-brown to brown scurf consisting of small squamules 0.2–0.6 mm long, similar to those on the petioles; rhachises often with long-persisting scales adaxially and at the junctions with the costae, often with the scale margins cretaceous white (Fig. 9), junctions of costae and rhachises abaxially swollen, each with a dark brown to blackish spot and with planar, pale brown pneumathodes, either one to 6 × 3 mm, or two, each 2–3 × 2 mm. Pinnules to 9.0–13.0 × 1.4–2.2(2.8) cm, the largest ones sessile to subsessile (0.5–1.0 mm), alternate to opposite (Fig. 9), 1.5–2.0 cm between the stalks, linear-oblong, truncate at base, tapering from beyond the middle to acute or attenuate tips, segments ascending, weakly falcate distally, with crenulate to crenate margins and rounded to obtuse tips; basal segments opposite, never remote from each other, sinuses 1–2(3) mm wide, obtuse to acute, scurf variously developed abaxially on costules, midveins and lateral veins, consisting of white to tan, unicellular trichomidia and small, flat to bullate, orange-brown, ovate squamules with elongate tips and finely dissected margins; sterile and fertile pinnules not different. Veins glabrous adaxially except for an occasional white to tan, erect multicellular hairs on the midveins distally, sparsely to densely hairy abaxially, glabrous to sparsely hairy between them; hairs white, erect, multicellular, to 0.6(–1.0) mm long; sterile veins forked or simple, fertile veins forked.

Sori 1.0(–1.5) mm diameter, subcostal to costal, at vein forks, indusia sphaeropteroid, with umbo, tan, translucent, fragments persisting; receptacles globose, 0.3–0.4 mm diameter, paraphyses few, hyaline, tan, shorter than sporangia (0.3–0.5 mm). Spores yellow, perispore not examined.

## Distribution and habitat

Colombia, Ecuador, Peru, and Bolivia at 1900–3050 m in moist montane forests and humid localities in semideciduous forests, with a preference for open sites, sometimes in pastures.

## Remarks

*Cyathea catacampta* is characterized by its broad, sessile pinnules, the scaly rhachises, and the relatively narrow basal petiole scales with reddish brown to orange margins. The scales on the abaxial sides of the petioles are smaller

but more strongly bicolorous than those in the other parts of the petioles. Populations in the northern Andes have more colorful scales than those of the central Andes; plants from Bolivia have mostly concolorous scales. In all their variability, the petiole scales of *C. catacampta* are distinguished from those of *C. squamipes* by having the marginal color continued into the tips, which leads to a dominance of reddish brown in the indument; in *C. squamipes*, the scale tips are concolorous dark brown to blackish like the centers of the scales. Another distinguishing feature of *C. catacampta* are the sparser but larger (to 1 mm long), more reddish brown squamules of the petiole scurf; the scurf of *C. squamipes* appears as a dense, pale brown to castaneous cover (depending on humidity) consisting of smaller squamules (on average 0.5 mm long).

*Cyathea frondosa* from the northern Andes is similar to *C. catacampta* in its habit and may be mistaken for this species from some distance, but is easily distinguished by its scurf (grayish white to whitish brown, highly dissected appressed squamules vs. reddish brown, erect squamules with crested margins in *C. catacampta*) and the presence of adventitious pinnae near the petiole bases (vs. always absent).

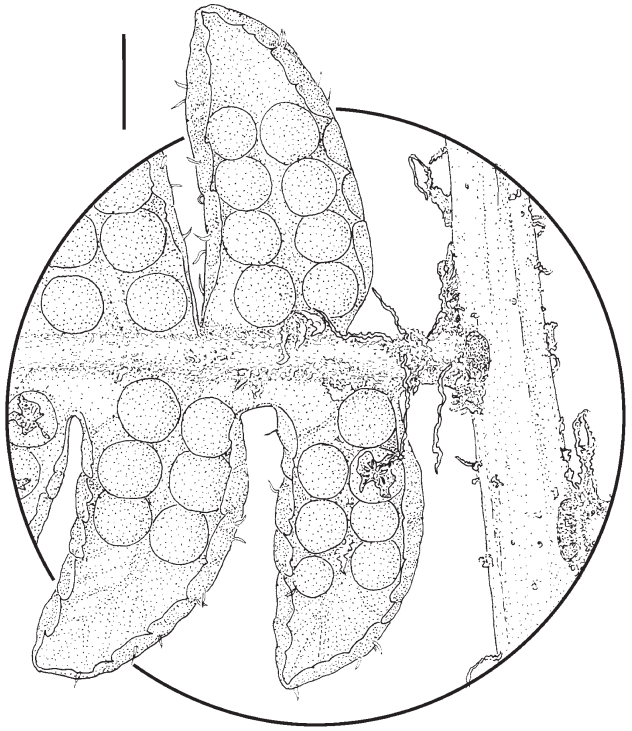

**Fig. 21.** *Cyathea maxonii*, fertile segments (»Bittner 1194« B). – Scale: 1 mm.

### 3.10 *Cyathea maxonii*
(Fig. 21)

*Cyathea maxonii* Underw. ex Maxon: Maxon 1909: 82. – *Cyathea caracasana* var. *maxonii* (Maxon) R. M. Tryon: Tryon 1976: 83. – Type: Costa Rica. Cartago, 5 miles S of Cartago, »Maxon 524« (holotype, NY; isotypes, B, US).

Selected specimens examined

C o s t a R i c a . **Alajuela**. San Ramón, Cerro Azar, 1600 m, 14.V.1983, »Pérez-García et al. 452« (UC). **Cartago**. Cantón Paraiso, investigation area of the CATIE, 9°33'30"N, 83°41'30"W, 2630 m, »Bittner 1194« (B). **Heredia**. Headwaters of Río Santo Domingo, ca. 3 km E of San Rafael de Vara Blanca, N slope of Volcán Barva, 10°11'N, 84°07'W, 2060–2080 m, 15.IV.1986, »Grayum et al. 7126« (UC). **Limón**. National Park Braulio Carrillo, transect trail between OTS-Station La Selva and Volcán Barva, 1200 m, 4.X.2006, »Kluge 3502« (GOET). **Puntarenas**. Upper Río Burú, 2010 m, 20.VIII.1987, »Gómez L. D. et al. 21771« (AAU). **San José**. 10 km N of San Rafael de Heredia on Volcán Barva, 1950 m, 20.VII.1967, »Mickel 3008« (UC).

P a n a m a . **Chiriqui**. Canal Zone, between Alto de las Palmas and top of Cerro de Horqueta, 2100–2268 m, 18.III.1911, »Maxon 5508« (BM).

Description

Trunks to 10–12 m tall, to 10 cm diameter, without old petiole bases, frond scars oval to round, 2.5–3.0 cm long, well spaced in lower parts (to ca. 2 m height), crowded in upper parts, trunk apices hidden in fascicles of petioles, with glossy, dark castaneous, bicolorous lanceolate scales with pale margins, similar to petiole scales, adventitious buds lacking. Petioles to 35–45(100) cm long, inermous to weakly aculeate, pale brown to dark brown, rarely stramineous, without adventitious (aphlebioid) pinnae at the bases, petiole scurf dense but soon caducous, concolorous brown to dark orange-brown, consisting of erect to appressed, lanceolate, ovate, and round squamules 0.2–0.5 mm long, with crested to fimbriate margins but without dark marginal teeth. Petiole scales lanceolate to ovate-lanceolate, (18.0)20.0–35.0 × 2.5–3.5 mm, tips straight to falcate, weakly twisted, lustrous, concolorous to weakly concordantly bicolorous, the dark brown to castaneous centers usually with a black base from where blackish streaks extend into the distal portions, centers either not sharply set against the brown to yellowish orange margins or transition between the centers and the margins marked by a black line. Fronds to 150–250 cm long, patent to arching, only distally weakly drooping.

Laminae to 125–150 × 90–130 cm, bipinnate-pinnatifid, firm-chartaceous, broadest at the middle, dark green adaxially, blackish when dried, dull to dark olive-green abaxially, apices gradually reduced. Pinnae to 35–45 cm long, 15–17 pairs per frond, alternate, sessile to subsessile, stalked to 0.5 cm, distally narrowly green-alate, the distal segments free to adnate, but not decurrent into the costae. Leaf axes stramineous to brown, usually darker adaxially, inermous, costules, costae and distal parts of rhachises densely hairy adaxially, hairs 0.5–1.0 mm long, whitish to

tan, antrorsely arching, abaxially glabrous to glabrescent, with a matted tomentum of orange-brown tortuous hairs and highly dissected lanceolate squamules to 1 mm long, costae 2–3 mm broad, junctions of costae and rhachises abaxially weakly swollen, each with a dark brown, inconspicuous, planar, elliptic pneumathode to 3 × 1–2 mm. Pinnules to 7.0–9.5 × 1.5–1.9(2.3) cm, alternate, articulate, long-triangular to lanceolate, basally notably cordate (Fig. 21) to truncate, tapering from the middle to acute or short-attenuate tips, the largest ones short-stalked to 2–3 mm, basally often with long persisting squamules, orange-brown to brown, segments weakly ascending, straight to distally weakly falcate, with crenulate to subentire margins and rounded to short-obtuse tips, basal segments alternately placed, often with small auricles, if remote from each other then connected by laminar tissue, sinuses 0.5–1.0(2.0) mm wide, acute to obtuse; sterile and fertile pinnules not different. Veins adaxially glabrous except for the hairy midveins to weakly hairy towards the margins, with white to tan, erect, straight to curved, multicellular hairs 0.5–1.0 mm long, the longest ones on the midveins, abaxially with many small appressed, tan to reddish brown trichomidia to 0.2 mm long, sometimes replaced by tortuous multicellular hairs 0.5–0.7 mm long, more common on the midveins than on and between the lateral veins; costules and midveins abaxially with few orange-brown to brown, flat squamules to 1.0 mm long with elongate tips and fimbriate to dissected margins, and orange-brown bullate squamules to 2 mm long with entire margins and elongate tips distally on the midveins; sterile veins forked or simple, fertile veins forked.

Sori 0.8–1.0 mm diameter, subcostal to costal, at vein forks, indusia sphaeropteroid, with umbo, tan, translucent, fragmenting to a shallow cup or disc (Fig. 21); receptacles globose, 0.2–0.4 mm diameter, paraphyses many, hyaline, tan to brown, of the same length as the sporangia (0.4–0.5 mm). Spores yellow, perispore not examined.

### Distribution and habitat

Endemic to Costa Rica and Panama, in tall cloud forests at 1200–2630 m.

### Remarks

Notably cordate bases on at least the largest pinnules characterize *Cyathea maxonii*. At first sight, the laminae appear glabrous, but usually some short hairs can be found on the veins adaxially near the margins. This and the scurf, which can persist by various degrees in the leaf axils, indicate an affinity to *C. patens* H. Karst. In both species, the laminar scurf is orange-brown and contains squamules with characteristic ciliate margins and/or ribbon-like shape. From the *C. patens* alliance, to which the sympatric *C. suprastrigosa* (H. Christ) Maxon belongs, *C. maxonii* is separated by lacking both adventitious pinnae on the petioles (present in *C. suprastrigosa* and most other species in the *C. patens* group) and arachnoid petiole scurf (present in *C. patens* and *C. suprastrigosa*). The color of the scales and the morphology of the petiole scurf squamellae of *C. maxonii* are more reminiscent of *C. squamipes* and *C. lindeniana*.

At least a part of the petiole scales in *C. maxonii* have a characteristic tinge from solid black at the scale base over a streaked center to a completely brown tip. The transition between the center and the margins is usually marked by black lines. Many petiole scales are also plain brown, especially on the adaxial side of the petioles. These brown petiole scales resemble the scales of *C. fulva* (M. Martens & Galeotii) Fée, a species which can be distinguished by its sparse, plain brown scurf on petioles. Its laminae also lack the finely dissected and ribbon-shaped squamules that are typical of *C. maxonii*. *Cyathea fulva* in a strict sense does not occur within the range of *C. maxonii*; it can be found from Mexico to Honduras (Rojas 2005), while *C. maxonii* is restricted to Costa Rica and northern Panama. Previous records of *C. fulva* from southern Central America are largely based on *C. onusta* H. Christ (Rojas 2001), which is a generally smaller species than the other two species and which can be distinguished by its whitish to tan laminar squamules (vs. brown in *C. fulva* and orange-brown in *C. maxonii*).

## 3.11 *Cyathea dissoluta*

*Cyathea dissoluta* Baker ex Jenm.: Jenman 1881: 52. – Type: Jamaica. 1879, »Jenman 1« (holotype, K-fragm. US; isotypes, NY-photo, -fragm. US, P-photo, -fragm. BM).

### Selected specimens examined

Jamaica. 1853–1855, »Barkly & Barkly s.n.« (BM); St. Anne-St. Catherine, summit area of Mount Diablo, 18°12'N, 77°07'W, 900–1000 m, 30.I.2004, »Christenhusz & Tuomisto 3312« (TUR); Trelawny-St. Elizabeth, Cockpit Country, Cook's Bottom, valley E of Eldersley, 18°14'N, 77°47'W, 450–700 m, 1.II.2004, »Christenhusz & Tuomisto 3353« (TUR).

### Description

Trunks erect, to 2–3 m tall, slender, to 5–7 cm diameter, upper parts covered with glossy, dark castaneous scales, trunk apices hidden in fascicles of the youngest petioles, adventitious buds present, growing out to short geotropic, leafy branches that eventually fall off and grow into new plants (Maxon 1909). Fronds to 150–200 cm long, arching to erect. Petioles to 30 cm long, muricate to strongly spiny, brown to dark brown, without adventitious (aphlebioid) pinnae at the petiole bases, petiole scales lanceolate to ovate-lanceolate, to 12.0 × 3.0 mm, their tips straight to falcate, weakly twisted, lustrous, concordantly bicolorous, the brown to auburn centers not sharply delineated from the brown to yellowish margins, petiole scurf

absent (in material seen; possibly weakly developed and evanescent).

Laminae to 125–150 × 75–80 cm, bipinnate-pinnatifid, firmly chartaceous, broadest at the middle, dark green adaxially, blackish to dark plumbeous when dried, dull olive-green abaxially apices gradually reduced. Pinnae to 20–40 cm long, presumably 10 pairs or fewer per frond, alternate, stalked to 1–2 cm, the distal segments simply adnate. Leaf axes stramineous to brown, rhachises also castaneous, usually darker adaxially, costules, costae and distal parts of rhachises inermous, densely hairy adaxially, hairs 0.5–1.0 mm long, tan to orange-brown, antrorsely curved, costae 2–3 mm broad, junctions of costae and rhachises only weakly swollen abaxially, bearing a dark, lunulate pneumathode. Pinnules to 5.0(–8.0) × 1.5 cm, short-lanceolate, cuneate to rounded at bases, tapering from the middle to acute to short attenuate tips, alternate, the largest ones short-stalked to 3 mm, 1.0(–1.5) cm between the stalks, the segments weakly ascending, weakly falcate distally, with crenulate margins and obtuse to short acute tips, basal segments alternately placed, rarely remote from each other, sinuses 0.2–1.0(2.0) mm wide, acute to polygonal; sterile and fertile pinnules similar. Veins adaxially glabrous except for few white to tan, erect, straight to curved, multicellular hairs 0.5–1.0 mm long on the midveins, abaxially with few scattered white, curved multicellular hairs 0.5–1.2 mm long distally, with few, often ephemeral trichomidia, orange-brown to brown, 0.2–0.4 mm long; costules and midveins abaxially brown to blackish, planar to weakly raised, with orange-brown to brown, flat, ovate-lanceolate and bullate squamules to 1.0–2.0 mm long with elongate tips and fimbriate to entire margins, lateral veins flat, dark green to blackish; sterile veins forked or simple, fertile veins forked.

Sori 0.8–1.0 mm diameter, subcostal to costal, at vein forks; indusia subsphaeropteroid to sphaeropteroid, with umbo, tan, opaque, fragmenting into persisting pieces; receptacles globose, 0.3–0.4 mm diameter, paraphyses many, tufted, atropurpureus, of the same length as the sporangia (0.4–0.5 mm). Spores not examined.

### Distribution and habitat

Endemic to Jamaica, growing at 450–1500 m in humid sheltered places; substrates include wet karsted limestone.

### Remarks

*Cyathea dissoluta* is remarkable among species with sphaeropteroid indusia because it reproduces by aerial lateral shoots of the trunk (Maxon 1909). A similar strategy occurs in *C. parvula* (Jenm.) Domin, another species from the Greater Antilles. This and the overall morphological similarity suggest that the two species are related. The shape of the indusia, historically used to subdivide the tree fern alliance, has been found to differ among closely related species. A change of indusial shape from hemitelioid (as in *C. parvula*) to sphaeropteroid (as in *C. dissoluta*) can be observed in the species pair *C. holdridgeana* Nisman & L. D. Gómez (hemitelioid) and *C. moranii* Lehnert (sphaeropteroid). Tryon (1976) described *C. dissoluta* as "a rare, variable species" and suspected it to be "a hybrid, or a series of hybrids". Judging from the variation in the fine indument of the laminae, *C. dissoluta* could indeed represent a hybrid between the sympatric *C. parvula* and *C. furfuracea* Baker, but this is still speculative. The few fertile collections of *C. dissoluta* that I have examined showed no irregularities in the formation of indusia or sporangia, which are indicators of hybrids, and thus I maintain it as a species.

Morphologically, *Cyathea dissoluta* comes closest to the Central American *C. maxonii*, which shares the fine orange laminar squamellae, cordate pinnule bases, and firm, dark brown, papery indusia. However, *C. maxonii* has larger, much stouter trunks (10–12 m tall, to 10 cm diameter vs. 2–3 m tall, to 5–7 cm diameter) that lack the lateral shoots typical of *C. dissoluta*, and also has darker petiole scales than that species.

Weakly developed or absent scurf, as found in *C. dissoluta*, is a character of the *C. lechleri* group, which is further defined by having pale brown spores. The investigated specimens of *C. dissoluta* were either sterile or had shed all their spores, and the possibility remains that the absence of the petiole scurf may be an artefact. Without confirmation of these characters, *C. dissoluta* cannot be linked confidently with any recognized *Cyathea* group with sphaeropteroid indusia.

## 3.12 *Cyathea patens*
(Fig. 22)

*Cyathea patens* H. Karst.: Karsten 1869: 173, not *Cyathea patens* hort.: Houlston & Moore 1851: 164, nom. nud. – Type: Colombia. Cundinamarca, "habitat montem Bogotensem 'Guadelupe' altitudine 2900 m", »Karsten s. n.« (holotype, n. l.; isotype, B [label "Colombia"]).

### Selected specimens examined

C o l o m b i a . **Cauca**. Macizo Columbiano, Páramo Las Papas, entre El Boqueron y La Hoyola, 3200–3510 m, 7.–27. IX.1958, »Idrobo et al. 3452« (COL). **Cundinamarca**. San Bernardo, Cordillera Oriental, Quebrada Aguas Claras, arriba de La Soledad, 3100 m, 23.VII.1981, »Jaramillo Mejia et al. 6963« (COL); carretera Bogotá–Choachi, vertiente hacia Choachi, adelante de Divorsium Acuarum, 3.III.1967, »Lozano et al. 667A« (COL). **Huila/Cauca**. Macizo Columbiano, Páramo Las Papas, Cerros y alrededores de la Laguna Magdalena, 3530 m, 16.X.1958, »Idrobo et al. 3006« (COL). **Meta**. Macizo de Sumapáz, vertiente oriental de la cordillera, quebrada El Buque, 3100 m, 9.VII.1981, »Díaz-Piedrahita 2690« (COL). **Quindio**. Salento, Estación de Navarco, bosque frente a la estación, 3000 m, 24.IX.1992, »Franco et al. 3974« (COL). **Risaralda**.

Santuario, al SO del cerro Ventanas, Macizo del Tamaná, 3820 m, 11.II.1983, »Torres et al. 1892« (COL). **Santander**. Valle del Río Susa, en el camino de hato Viejo a la laguna la Friquera o Jiquera, arriba del sitio Santa Barbara, 3600 m, 30.XI.1967, »Jaramillo Mejia 4401« (COL). **Tolima**. Above Anaime on road S of Cajamarca, 4200 m, 30.VII.1972, »Barrington 474« (COL).

Venezuela. **Tachira**. Headwaters of Río Quinimarí, slopes of El Banco, below Cerro Las Copas (below Páramo Los Judios), 20 km S of San Vicente de La Revancha, 35 km S of Alquitrana, 2500–2700 m, 16.I.1972, »Steyermark et al. 100967« (NY, UC). **Trujillo**. Carache, Páramo Las Palmas, 9°42'N, 70°08'W, 2200 m, 22.V.1991, »Rivero 1242« (UC).

Ecuador. **Bolivar**. Along first 15 km of road Chillanes–El Tambo, 2400 m, 19.VII.1995, »van der Werff et al. 12434« (AAU, MO, UC). **Carchi**. Valle de Maldonado, km 53 on road Tulcán–Maldonado, 0°50'N, 78°03'W, 3150–3250 m, 17.–18.V.1973, »Holm-Nielsen et al. 5659« (AAU). **Loja**. Pass "El Tiro" between Loja and Zamora, trail from province border sign up to the cerro, 3°59'S, 79°08'W, 2750 m, 11.XI.2003, »Lehnert 1102, 1103« (AAU, GOET, LOJA, QCA, UC). **Morona-Santiago**. Road Gualaceo–Limón, 19 km E of the pass, 3°01'S, 78°37'W, 2900–2950 m, 20.XI.1990, »Navarrete & Øllgaard 3097« (QCA, MO). **Napo**. Oyacachi, ca. 2 km below the village, opposite abandoned village, 0°13'S, 78°03'W, 3150 m, 24.XII.1998, »Øllgaard & Navarrete 1229« (AAU, QCA). **Tungurahua**. Ca. 1 km S of Patate–El Triunfo road, km 14.6, 1°21'S, 78°27'W, 2850–2975 m, 24.XI.1998, »Øllgaard & Navarrete 3103« (AAU, QCA). **Zamora-Chinchipe**. Road Loja–Zamora, km 14, 4°00'S, 79°09'W, 2770 m, 19.–20.IV.1973, »Holm-Nielsen et al. 3867« (AAU).

Peru. **Amazonas**. Bagua, 2700–3000 m, 5°36'S, 78°26'W, 25.IX.1978, »Barbour 3590« (MO). **Cajamarca**. San Ignacio, 1900 m, 5°42'S, 77°53'W, II.2002, »Bonino 243« (MO). **Cuzco**. 3300 m, 13°03'S, 73°04'W, 15.X.2003, »Suclli et al. 1330« (CUZ, MO). **Pasco**. Oxapampa, 2910 m, 10°22'S, 75°27'W, 14.II.2004, »Mellado & Monteagudo 0464« (MO, USM); Oxapampa, 3000 m, 10°22'S, 75°27'W, 15.X.2004, »Mellado & Becerra 1926« (HUT, MO, USM).

## Description

Trunks to 10 m tall, but generally smaller, with or without persistent petiole bases, to 8–14 cm diameter, often decumbent with age, pneumathodes present below frond scars, but inconspicuous, small, and of the same color as the cortex, apices hidden in fascicles of petioles, adventitious buds lacking. Fronds to 100–200(250) cm long, patent or erect, not or only weakly arching from the middle. Petioles to 35–55(110) cm long, dull brown to blackish, rarely plumbeous or yellow, aculeate to muricate, spines with scales on their tips in young petioles, with long-elliptic, gray pneumathodes on the sides basally, petiole scurf dense to diffuse, consisting of erect squamules to 0.5 mm long with white, ciliate margins (Fig. 22C), persistent, but often abraded to the indurated squamule bases. Petiole scales to 38 × 4–5 mm, long-lanceolate, persistent only on the sides of the petioles, with flat to weakly twisted apices, brown, concolorous (Fig. 22B) or weakly discordantly bicolorous (Fig. 22A), with the centers dark brown and the margins paler brown, yellowish or cream-white.

Laminae 70–140 × 70–90 cm, elliptic to narrow-ovate, bipinnate-pinnatifid, green to dark green adaxially, often becoming blackish when dried, pale gray-green abaxially, apices gradually reduced. Rhachises inermous or weakly muricate basally, with short whitish to yellowish, antrorse hairs distally, otherwise glabrous adaxially, or glabrescent with many trichomidia and squamellae on both sides, the squamellae orange-brown to brown, in glabrous forms rhachises castaneous to plumbeous-brown, in scaly forms predominantly yellowish to stramineous. Costae and costules tan, stramineous or dull brown, inermous, short-hairy adaxially, hairs to 1 mm long, multicellular, white, antrorsely curved, indument variable abaxially, ranging from a dense cover of white to tan arachnoid scurf or nearly glabrous except for white hairs and trichomidia to 0.4 mm long; bright orange-brown flattish scales with undulate fimbriate margins abundant to scarce abaxially, most frequent in axils. Pinnules to 5.0–7.5(9.7) × 0.8–1.5(1.7) cm, narrowly triangular (Figs. 22D, E), rarely linear (Fig. 22F), sessile to subsessile (stalked to 1 mm), truncate to weakly cuneate, rarely weakly cordate at base, tips acute to short-attenuate, pinnatifid to pinnatisect, basal segments rarely free and then with margins deeply crenate (Fig. 22D); segment margins serrate or sharply crenate, often still planar when dried. Veins adaxially with few to many short hairs on and sometimes between them, abaxially glabrous or glabrescent with few to many hairs restricted to the veins, hairs to 0.4 mm long, whitish to yellowish, stout and erect to thin and curved or appressed, veins with few to many small scales abaxially, ranging from broadly ovate and flat to small and bullate (Fig. 22H–J), orange-brown to brown, margins thin, paler brown to whitish, fimbriate to lacerate with long processes; sterile veins forked or simple, fertile veins forked.

Sori to 1.0 mm diameter, costal to subcostal, at vein forks (Fig. 22G); indusia sphaeropteroid, with umbo (often weakly developed), brown to yellowish, transparent, fragile, irregularly fragmenting (Fig. 22K), persistent as shallow cups or discs, receptacles globose, paraphyses of the same length as or shorter than sporangia, thin and hyaline. Spores pale yellow, perispore not examined.

## Distribution and habitat

Colombia, western Venezuela, Ecuador to central Peru, to be expected farther south. *Cyathea patens* occurs in montane forests and subparamo scrub at 2200–4200 m, which is among the highest elevations recorded for the family.

## Remarks

The typification of *Cyathea patens* is well supported by type material and the illustrations in Karsten's Florae Columbiae (1869). The earlier publication of this name by Houlston & Moore (1851) describes a cultivated species in English, but fails to deliver a comparative diagnosis and was thus considered as nomen nudum by Tryon (1976).

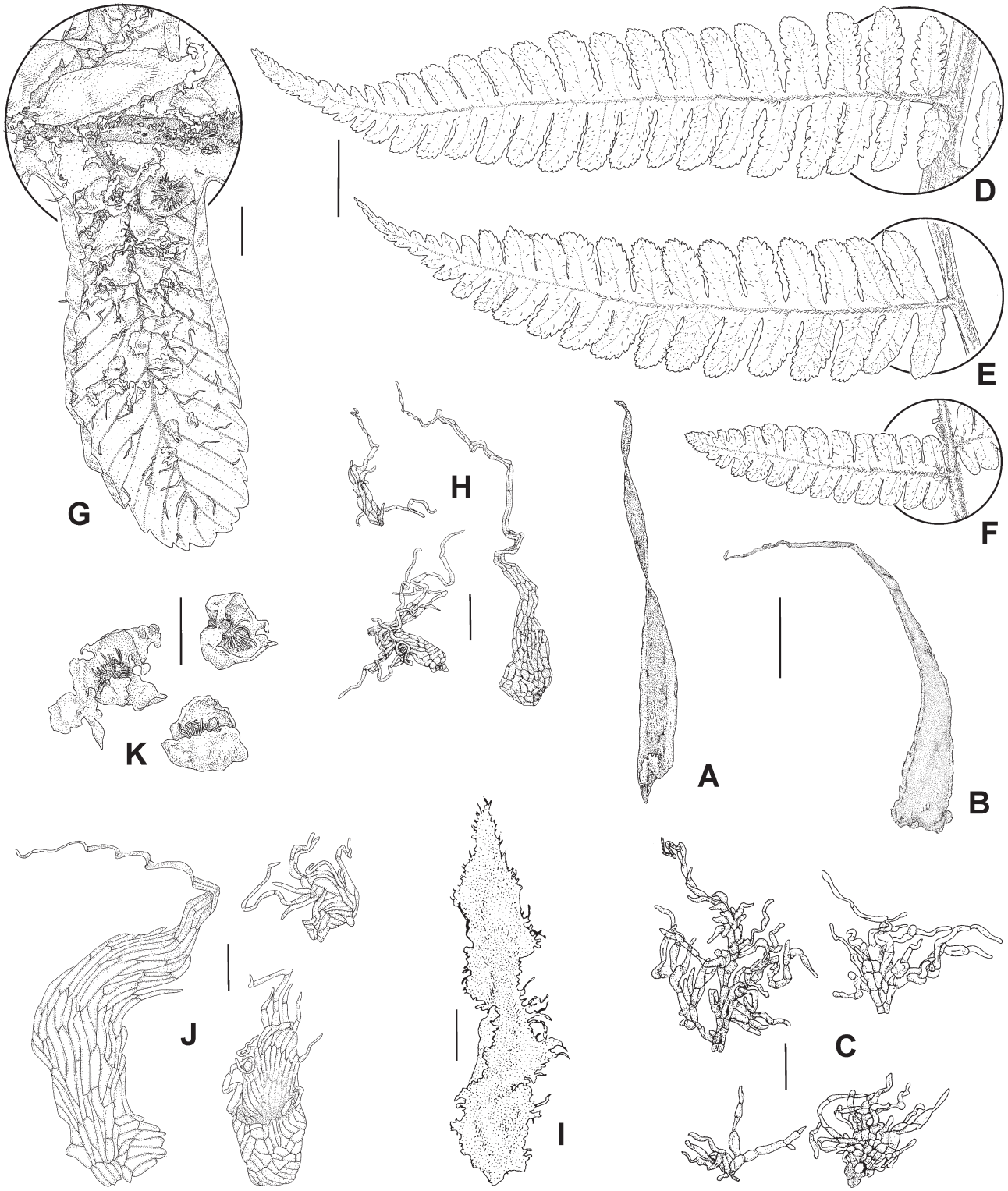


**Fig. 22.** *Cyathea patens* (A, C upper row, D, H, I from »Lehnert 950« GOET; B, E, G, K from »Lehnert 815« GOET; C lower row from »van der Werff & Palacios 10604« UC; F, J from »Lehnert 797« GOET). – **A**. Petiole scale, weakly bicolorous. **B**. Petiole scale, almost concolorous. **C**. Squamules of petiole scurf. **D**. Large pinnule, basal segments free. **E**. Large pinnule. **F**. Largest pinnule of a small frond. **G**. Fertile segment, abaxially. **H**. Laminar squamules. **I**. Small scale from costa. **J**. Laminar squamules, shortly fimbriate. **K**. Mature indusia, in different stages of fragmentation. – Scales: 1 cm (D–F, K), 5 mm (A, B), 1 mm (G, I), 0.2 mm (C, J, H).

HOULSTON & MOORE (1851) also failed to designate a type or make references to collections or illustrations. For these reasons, the name *C. patens* hort., Houlston & Moore is considered as invalid, which legitimates KARSTEN's (1869) later homonym.

*Cyathea patens* is a variable species. The indument varies with exposure to sun and wind, which in turn is correlated with elevation. In open habitats most of the orange-white, fimbriate scales, which constitute the fine indument of the crosiers, are retained especially in the axils of the rhachises and on the costae. The bullate squamules distally on the costules, which regularly have entire margins, then have fimbriate margins, too. Hairs are more abundant on the veins adaxially, but are often present and well developed on both sides. All parts of the indument are less developed if the plants grow inside the forest or at lower elevations. A nearly constant feature is the general outline of the pinnules, which is long-triangular with serrate segment margins. The variation can be observed throughout the range of the species. Very scaly forms are frequent in Ecuador, Prov. Loja/Zamora-Chinchipe.

Small plants of *C. patens* are similar to *C. bettinae* Lehnert (LEHNERT 2004) in the distribution of laminar hairs, but that species has thin trunks to 3 cm diameter (vs. to 8–14 cm in *C. patens*) and paler petiole scales (opaque white to light brown, sometimes with darker apical streak vs. concolorous brown or with paler margins).

The trunkless *C. sylvatica* Lehnert may be mistaken for precociously fertile *C. patens*, but differs in having more ovate, more concolorous petiole scales (LEHNERT 2006c).

*Cyathea suprastrigosa* (H. Christ) Maxon differs from *C. patens* by its aphleboid pinnae at the petiole bases (these are absent in *C. patens*) and the different color of the petiole scales (orange-brown to brown vs. concolorous to weakly bicolorous brown with paler margins in *C. patens*).

*Cyathea maxonii* Underw. ex Maxon is endemic to Costa Rica and Panama; previous reports from Colombia and Ecuador are based on misidentified *C. patens* and *C. fulva* agg. In both *C. patens* and *C. maxonii*, the veins are normally hairier adaxially than abaxially with the hairs relatively short (0.4–0.6 mm); indusia, laminar shape and texture, and color of scurf, petioles, and leaf axes underly the same variations. In *C. maxonii*, however, the largest pinnules are mostly subcordate to weakly auriculate at base and short-stalked to 3 mm (vs. truncate to weakly cuneate and sessile to subsessile in *C. patens*), and the scurf remnants in the axils of the leaf axes are composed of much finer dissected orange-brown squamellae.

*Cyathea squamipes* can be distinguished from *C. patens* by the more strongly bicolorous petiole scales (castaneous to blackish centers vs. brown to dark brown centers in *C. patens*), more hairs abaxially than adaxially on the veins (vice-versa in *C. patens*), and concolorous orange-brown squamellae with subentire to crested margins on the laminae (vs. mainly bicolorous with paler to whitish, crested to lacerate margins in *C. patens*).

The sympatric *C. cystolepis* Sodiro (LEHNERT in press) often grows in the same habitat as *C. patens*; both species are hairier on the veins adaxially than abaxially, and vary in the indument on the lamina abaxially from almost glabrous to densely scaly. In contrast, *C. cystolepis* has distinctly bicolorous petiole scales with brown centers and white margins (vs. concolorous brown or weakly bicolorous petiole scales in *C. patens*). »Lehnert 818« has strongly bicolorous petiole scales that match better *C. cystolepis*, but the characters of the lamina are typical of *C. patens*.

*Cyathea parvifolia* Sodiro can be distinguished by the basal aphlebioid pinnae at the petiole base, which are remote from the triangular to broadly ovate laminae; such basal pinnae are not present in *C. patens*. The petiole scales of *C. parvifolia* tend to be longer and more strongly bicolorous, often with whitish margins, although they can be simply brown as in *C. patens*. Without petiole, the discrimination of these species is difficult as both can be almost identical in laminar dissection and indument. However, the hairs in *C. parvifolia* tend to be longer (to 1.0 mm) than in *C. patens*, and its squamellae on the laminae are mostly flat, concolorous brown and not or only weakly crested marginally.

### 3.13 *Cyathea frondosa*
(Figs. 13–14, 23)

*Cyathea frondosa* H. Karst.: KARSTEN 1860: 149. – Type: Colombia. Cundinamarca, "habitat silvas humidas, umbrosas Andium Bogotensium altitudine 2700 m", »Karsten s. n.« (holotype, n. l.; isotype, B [label »Karsten 196«]).

Selected specimens examined

C o l o m b i a . **Caldas**. Manizales, Vereda La Esperanza, Reserva Torre Cuatro, 5°02'47"N, 75°22'47"W, 3000–3300 m, 26.II.2004, »Alvear-P. et al. 795« (COL). **Chocó**. Macizo del Tamaná, bajando 200 m del Valle de San Francisco, 3130 m, 16.II.1987, »Torres et al. 1957, 1963« (COL). **Cundinamarca**. La Vega, un poco mas arriba del pueblo (LaVega), 22.VIII.1980, »Acosta-Arteaga 1088« (COL). **Nariño**. Ricaurte, Reserva Natural La Planada, Cerro León, 1°09'37"N, 77°59'W, 2145 m, 29.II.1997, »Guzmán 4468« (UC). **Norte de Santander**. Cordillera Oriental, Páramo de Tamá, vertiente de Samaria, 2600–2900 m, 30.X.1945, »Cuatrecasas et al. 12728« (COL). **Valle de Cauca**. Santa Helena, above Topacio, edge of Los Farallones de Cali NP, 3°30'N, 76°35'W, 1940 m, 12.XII.1989, »Gentry et al. 53069« (UC).

E c u a d o r . **Carchi**. Reserva Guanderas, ca. 3 km E of Mariscal Sucre, 0°36'N, 77°41'W, 3400–3700 m, 13.XI.2002, »Navarrete & Øllgaard 3039« (AAU, QCA); El Ajún, along road N of El Playon de San Francisco, towards El Carmelo, 0°42'N, 77°36'W, 3050–3150 m, 11.VII.1994, »Øllgaard et al. 98143« (AAU, QCA); about half an hour E of Huaca, past Colonia Huaceña, 3100–3200 m, 20.II.1993, »van der Werff & Palacios

10603« (MO, AAU). **Imbabura**. Cerro Blanco, ca. 8 km (by air) WSW of Otavalo (road towards antennas from road toward San José de Minas), south of Otavalo-Selva, 0°13'N, 78°20'W, 3400–3460 m, 24.IX.1994, »Øllgaard 98214« (AAU, QCA). **Loja**. Reserva Huashapamba, 6 km S of Saraguro along Panamericana, 3°39'43.0"S, 79°16'09.9"W, 2850 m, 4.X.2007, »Lehnert 949« (GOET, QCA, UC). **Morona-Santiago**. E of pass on Gualaceo-Limon road, 3°00.27'S, 78°39.10'W, 3000–3200 m, 16.XI.2008, »Lehnert 1564« (GOET, QCA, UC). **Napo**. Oyacachi, ca. 2 km E of village, opposite Maucallacta, forest transect at Cuytoclla, 0°13'S, 78°04'W, 3100–3140 m, 7.III.2000, »Øllgaard & Navarrete 1605, 1608« (AAU, QCA). **Pichincha**. Camino Calicali–Nanegalito, 18 km from Mitad del Mundo, 0°01'N, 78°37'W, 2040–2090 m, 20.–25.IV.1995, »Ankersen & Kragelund 158« (AAU, QCA); faldas sur del Pichincha, antigua carretera a Chiriboga, 2800 m, 6.–7.VI.1987, »Mena-V. 734« (AAU, QCA). **Zamora-Chinchipe**. New road Loja–Zamora, ca. 5 km E of pass "El Tiro", above old landslide along road, 3°59'S, 79°08'W, 2500 m, 19.XI.2008, »Lehnert 1572« (GOET, QCA, UC).

P e r u . **San Martin**. Huallaga, arriba de La Ribera/La Meseta, 6°52'S, 77°28'W, 2060–2100 m, 17.VIII.1997, »Quipuscoa et al. 1085« (AAU).

## Description

Trunks to 10 m tall, to 12–16 cm diameter, without old petiole bases in large plants, variously persistent in smaller ones, then to 20 cm diameter (Fig. 14), trunk apices hidden in fascicles of petioles, sometimes with skirts of dead fronds if growing in dense understory; adventitious buds absent. Fronds to 280 cm long, weakly arching, patent in large plants, ascending in small ones. Petioles to 50–80 cm long, short-aculeate, brown to dark brown, densely covered with persistent but cleanly removable arachnoid scurf of branched hairs or narrow, ciliate squamules (Fig. 23A), the color varying from gray-white to tan (light brown), adventitious (aphlebioid) basal pinnae occurring regularly in 1–2 pairs, 15–40 cm long, reflexed, with strong costae (Fig. 13), the basal pinnules often pinnate with the basal segments remote and crenate, thus more strongly dissected than the laminae. Petiole scales narrowly lanceolate, 25–36(40) × 2–3 mm, with elongate, strongly twisted tips (3–4 times, especially when dried), brown to dark brown with somewhat paler margins, sometimes with diffuse darker areas in the centers, but never strongly bicolorous.

Laminae to 200 × 110 cm, bipinnate-pinnatifid to tripinnate, broadly ovate, deep green and lustrous adaxially, paler and matte abaxially, apices gradually reduced. Pinnae to 55 cm long, alternate, distally not or weakly greenalate, the distal segments adnate to weakly decurrent into the costae, basal pinnae not or weakly reflexed. Rhachises with scurf like on the petiole but not as dense and persistent, short-aculeate at base and in the middle, abaxially and laterally with persistent scales similar to the petiole scales, but generally paler than these, often with white margins when older (bleaching), hairs absent except for distal parts adaxially. Costae inermous to sparsely verrucate, 3–4 mm broad, costules inermous, light brown to brown, with scurf of gray-white to light brown branched hairs or long-ciliate squamules abaxially, with unbranched multicellular hairs 0.5–1.0 mm long adaxially, sometimes densely scaly with lanceolate to linear squamules (Fig. 23C) with sparsely fimbriate or short-ciliate margins. Pinnules to 10.0–12.0 × 1.8–2.5 cm, linear-oblong to long-triangular, sessile or subsessile (stalked 1 mm), bases truncate to weakly cuneate, never with auricles, tips long-acuminate to attenuate, segments weakly ascending, weakly falcate distally, with crenulate to crenate margins and obtuse tips; larger pinnules sometimes pinnate, their basal segments not remote, with crenate margins. Veins sparsely hairy to glabrous adaxially, densely to sparsely hairy abaxially, hairs 0.2–0.4 mm long, veins abaxially with some pale brown, bullate squamules (Fig. 23B) and ephemeral, whitish to tan scurf, similar to petiole scurf (Fig. 23A).

Sori 0.7–1.0 mm diameter, costal to subcostal, at vein forks; indusia sphaeropteroid, with umbo, tan to brown,

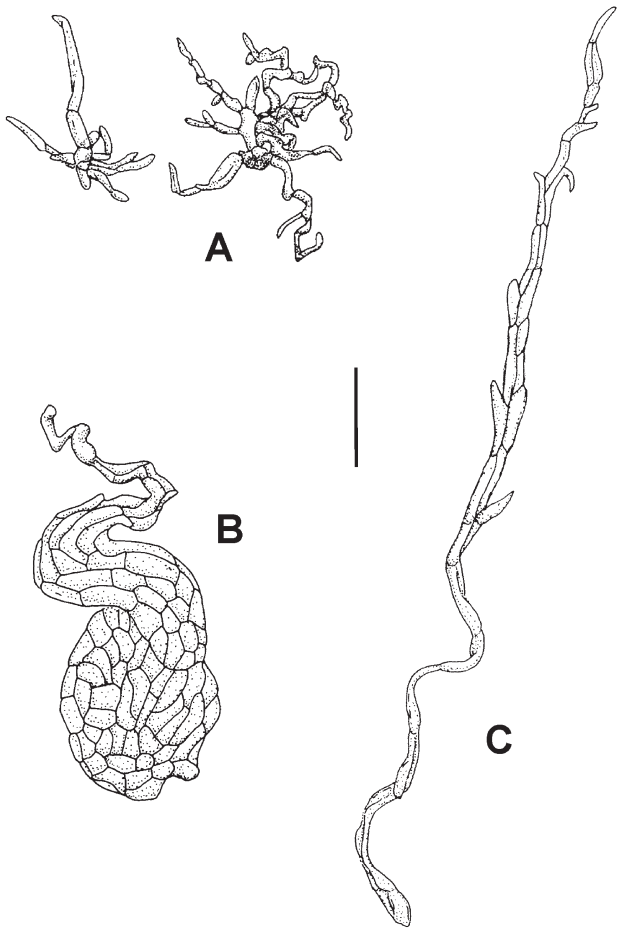


**Fig. 23.** *Cyathea frondosa* (all from »Lehnert 1572« GOET). – **A**. Squamules from petiole scurf. **B**. Bullate squamule from lamina. **C**. Ribbon-shaped squamule from costule. – Scale: 0.2 mm.

translucent, fragile, usually umbo missing, but cup-shaped part remaining, receptacles globose, 0.2–0.3 mm diameter, paraphyses few, hyaline, tan to white, of the same length as or shorter than the sporangia (0.4–0.5 mm). Spores pale yellow, perispore not examined.

Distribution and habitat

In moist montane forests at (1940)2040–3460 m in Colombia, Ecuador, and northern Peru, to be expected in western Venezuela.

Remarks

This species can be recognized by the dense, matted, whitish scurf and the aphlebioid pinnae at the petiole bases. *Cyathea brachypoda* is very similar in having adventitious pinnae and white scurf on the laminar axes, but the petiole scurf consists of browner distinct squamules and is less persistent, the largest pinnules are narrower (12–15 mm vs. 16–25 mm broad in *C. frondosa*), the indusia are less colorful and more fugacious, normally persisting only as a small disc. In both species the aphlebioid pinnae may be absent, and then they resemble *C. squamipes* H. Karst., *C. meridensis* H. Karst., or *C. aurea* H. Karst. These species, however, have darker petiole scurf consisting of distinct squamellae, and either broader or white-margined petiole scales.

*Cyathea frondosa* and *C. brachypoda* might represent only one variable species, but so far the distinguishing characters between them, which may appear feeble, seem to be constant.

*Cyathea catacampta* Alston is identical to *C. frondosa* in size and laminar dissection. Both species often have persistent crosier scales on the rhachises. The differences in the petiole scurf (whitish, arachnoid squamules in *C. frondosa* vs. orange-brown to dark reddish brown, erect lanceolate squamules in *C. catacampta*) and petiole scales (concolorous brown to weakly bicolorous with whitish margins vs. strongly bicolorous blackish with orange margins) separate both species well. *Cyathea catacampta* also lacks adventitious pinnae.

*Cyathea suprastrigosa* (H. Christ) Maxon from Costa Rica and Panama, another species with adventitious basal pinnae, is distinguished from *C. frondosa* by its broader petiole scales, stronger laminar pubescence, and more bicolorous laminar squamules. The auricles at the base of the sessile pinnules that are characteristic of *C. suprastrigosa* are absent in *C. frondosa*.

### 3.14 *Cyathea brachypoda*

*Cyathea brachypoda* Sodiro: Sodiro 1908: 8. – Type: Ecuador. Pichincha, “Sylv. suband. vulc. Atacatzo”, »Sodiro s. n.« (lectotype, Q, designated by Lehnert 2008; isolectotypes, SI [nº 22795, 22707], US).

*Cyathea asperata* Sodiro: Sodiro 1908: 9. – Type: Ecuador. Pichincha, “In silvis suband. m. Pichincha, III.1903”, »Sodiro s. n.« (lectotype, SI [nº 22801], designated by Lehnert 2008; isolectotypes, NY, US).

*Cyathea asperata* var. *brevipes* Sodiro: Sodiro 1908: 10, ex descr. No specimen cited.

*Cyathea muricatula* Sodiro: Sodiro 1908: 10. – Type: Ecuador. Pichincha, “In silvis suband. vulc. Corazón, XII.1907”, »Sodiro s. n.« (holotype, n. l.; isotypes, NY, P, US).

Selected specimens examined

E c u a d o r . **Napo**. Valley of Río Oyacachi, 10 km W of El Chaco, ridge SE of Río San Juán Grande, 0°17'S, 77°52'W, 1950–2020 m, 13.–14.III.1996, »Øllgaard & Navarrete 1690« (AAU, QCA); Baeza, 12 ha de bosque poco disturbado y disturbado, 2 km antes de Baeza (carretera Papallacta–Baeza, parte alta de “Y”), 0°28'S, 77°54'W, 2000 m, 19.–20.III.1993, »Valencia et al. 2896, 2897, 2911, 2914, 2917« (AAU, QCA). **Pichincha**. Lloa valley, one-hectare plot, Hacienda Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 0°50'N, 78°38'W, 2900 m, 13.–14.X.1990, »Jørgensen & Yepez 92576« (AAU, QCA); Reserva Maquipucuna, ca. 5 km (airline) ESE of Nanegal, Hacienda El Carmen, trail along Río Umachca, just W of research station, 0°07'N, 78°38'W, 1250–1350 m, 28.II.–4.III.1995, »Øllgaard et al. 904« (AAU, QCA).

Description

Trunks to 4(–5) m tall, to 8–12 cm diameter, without old petiole bases. Petioles with sparse scurf of pale brown, round squamellae with crested margins, usually with basal adventitious (aphlebioid) pinnae. Petiole scales dark brown, sometimes blackish, concolorous or weakly concordantly bicolorous with paler brown, rarely whitish margins. Laminar indument with small flattish to weakly bullate, whitish to brown squamules abaxially; veins glabrous or midveins adaxially with 1–3 hairs, shortly pubescent abaxially, with atrorsely curved hairs 0.2 mm long or less, sometimes replaced by appressed white trichomidia, rarely almost glabrous, hairs absent between veins or only few below the sinuses abaxially. Indusia sphaeropteroid, membranaceous, spores yellow.

For full description see Lehnert (2008).

Distribution and habitat

Restricted to northern Ecuador, to be expected in southern Colombia. Upper montane forests at 1200–2300(2900) m, preferentially along creeks in semi-shade.

Remarks

*Cyathea brachypoda* may be confused with other species having aphlebioid pinnae on the petiole bases, but differs among these from *C. suprastrigosa* and *C. frondosa* in the petiole scurf (rather sparse and brown in *C. brachypoda* vs. dense, whitish to gray in the other two species) and from *C. parvifolia* in the laminar indument (more hairs abaxially than adaxially in *C. brachypoda* vs. more hairs adaxially than abaxially in *C. parvifolia*) and the larger fronds (to 320 cm long vs. to 150 cm long). The

petiole scales of *C. brachypoda* are generally darker than in *C. parvifolia* but there is a certain overlap in the variation of this character.

### 3.15 *Cyathea parvifolia*
(Figs. 15, 24)

*Cyathea parvifolia* Sodiro: Sodiro 1908: 7. – Type: Ecuador. Pichincha, "in silvis subandinis occidentalibus montis Pichinchae", III.1901, »Sodiro s. n.« (holotype, n. l.; isotypes, A, n. v., K, P, UC, US).

*Cyathea brevistipes* R. C. Moran: Moran 1991: 94. – Type: Ecuador. Loja, Parque Nacional Podocarpus, along road from Yanaga to radio towers on Cerro Toledo, 2900–3200 m, 29.IV.1987, »van der Werff & Palacios 9185« (holotype, MO; isotype, UC).

Selected specimens examined

Colombia. **Putumayo**. Nariño, on road from Pasto to Mocoa, 9.VIII.1972, »Barrington 520« (GH).

Ecuador. **Azuay**. Road Gima–Gualaquiza (under construction), km 17.4, 3°16'S, 78°56'W, 3300 m, 28.XII.1994, »Øllgaard et al. 98608« (AAU, QCA). **Carchi**. Montufar, 0°35.5'N, 77°42'W, 3400 m, 26.VI.1994, »Fay & Fay 4295« (MO, QCNE). **Loja**. Cerro Toledo, E of Yangana, between Loja and Valladolid, 4°23'S, 79°07'W, 3000–3100 m, 27.X.2008, »Lehnert 1450« (GOET, QCA, UC); Cordillera del Loro, 50 km N of Loja, just before descending towards Saraguro, along road to radar station, 3000–3200 m, 9.V.1991, »van der Werff & Palacios 9429« (AAU, QCA). **Pichincha**. Cayambe, 0°07'N, 77°57'W, 3420 m, 27.XII. 1999, »Cuamacás & Gudiño 456« (MO, QCNE).

Peru. **Pasco**. Prov. Oxapampa, Dist. Huancabamba, Lanturachi, sector Santa Barbara, road to Milpo, 10°22'S, 75°36'W, 2824 m, 10.X.2003, »Perea et al. 721« (MO).

Bolivia. **La Paz**. Prov. Franz Tamayo, Madidi, Kalla-Tokuaque, Ichocorpa, 14°39'44"S, 68°57'54"W, 3476 m, 25.VI.2005, »Fuentes et al. 8689« (GOET, LPB).

#### Description

Trunks to 5–6 m tall, but generally smaller, fertile when still trunkless, with persistent petiole bases (Fig. 15), rotting to a fibrous mass, to 10–15(30) cm diameter, often decumbent with age, inconspicuous lenticels present below frond scars, small and in color of cortex, apices hidden in fascicles of petioles; adventitious buds lacking. Fronds to 55–150 cm long, patent, only weakly arching. Petioles to 5–35 cm long, dull brown when dried, yellowish green to greenish brown when fresh, inermous to muricate, basally often with 1–2 pairs of small adventitious pinnae (Fig. 15) of the same dissection as the main laminae, long-elliptic gray pneumathodes present on the sides of petioles and proximal rhachises; petiole scurf inconspicuous, consisting of persistent, appressed squamules to 0.5 mm long (Fig. 24A), translucent, tan to brown with opaque white marginal processes, visible as appressed hairs and trichomidia, often abraded, scurf also with few white, dissected squamules and sometimes some erect brown lanceolate squamules between the petiole scales. Petiole scales to 15.0–28.0 × 2.5–4.0 mm, narrowly to broadly lanceolate, the tips straight to falcate, weakly to strongly twisted, brown to dark brown (Fig. 15), rarely auburn to orange-brown (shade plants), concolorous or weakly discordantly bicolorous, with the centers dark brown and the margins paler, sometimes appearing yellowish or cream-white.

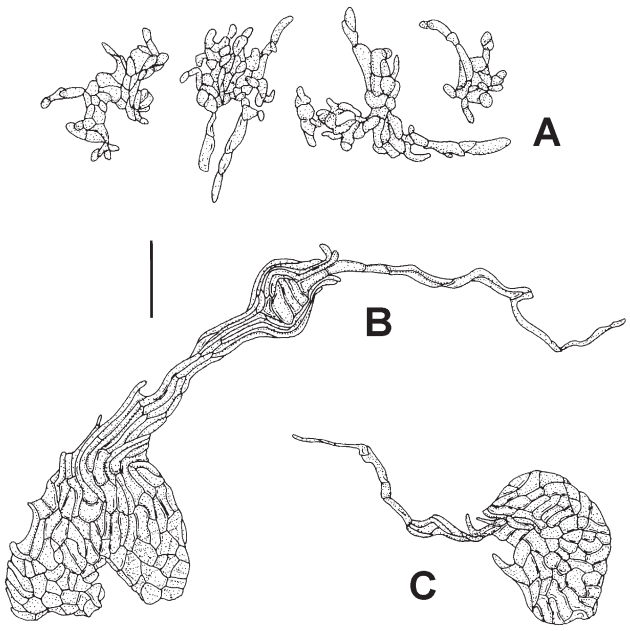


**Fig. 24.** *Cyathea parvifolia* (all from »Lehnert 1450« GOET). – **A**. Squamules from petiole scurf. **B**. Squamule from costa. **C**. Bullate squamule from lamina. – Scale: 0.2 mm.

Laminae to 70–100 × 30–70 cm, broadly ovate to triangular, bipinnate-pinnatifid, apices gradually reduced, basally truncate to cuneate, green to dark green adaxially, often turning blackish when dried, pale green abaxially. Pinnae to 20–35 cm long, sessile, distally narrowly greenalate. Leaf axes inermous to sparsely verrucate; rhachises adaxially sometimes with larger, spreading scales along the sides, densely hairy adaxially with whitish to yellowish, antrorsely curved hairs 1–2 mm long, longer ones twisted, indument abaxially varying from almost glabrous except for scattered white hairs and trichomidia to 0.4 mm long to a dense cover of white to tan scurf, also with bright orange-brown, flattish scales with undulate-fimbriate margins (Fig. 24B), most frequent in axils; costae and costules tan, stramineous or dull brown, junctions of costae and rhachises not swollen, each with a circular, planar to protruding pneumathode of 1.0–1.5 mm diameter, with a basally adjoining, glabrous, flat area, which may blacken and depress when dried. Pinnules narrowly triangular to lanceolate, rarely in small forms oblong, largest ones 3.5–6.5 × 0.8–1.5(1.8) cm, sessile to subsessile (stalked to

2 mm), bases truncate to weakly cuneate, rarely weakly cordate, tips acute to short-attenuate, basal segments rarely free and then with margins strongly crenate, sinuses to 1.0–2.0 mm wide, acute to obtuse or rectangular, segment margins serrate or sharply crenate, often still planar when dried; sterile and fertile pinnules not different. Veins adaxially with few to many multicellular hairs on and sometimes between the veins near the margins, also with tortuous, white hairs, these caducous and often completely absent in older fronds, abaxially without hairs, mainly with few to many, bullate, auburn to brown squamules to 1.0 mm long (Fig. 24C) with long, whitish tips, midveins also with flat lanceolate scales to 2–3 mm long with thin, paler brown to whitish margins; sterile veins forked or simple, fertile veins forked.

Sori costal to subcostal, at vein forks; indusia sphaeropteroid, with umbo, brown to yellowish, slightly transparent, fragile, fragmenting irregularly, a shallow cup or disc remaining, receptacles globose, 0.3–0.4 mm diameter, paraphyses thin and hyaline, shorter than sporangia (0.2–0.3 mm). Spores pale yellow, perispore not examined.

### Distribution and habitat

In elfin forests and scrub, close to and above the tree line at (2800)3000–3500 m from southern Colombia to central Bolivia.

### Remarks

*Cyathea parvifolia* occurs very locally but usually in sizeable populations. This name has been treated as a synonym of *Cyathea caracasana* var. *meridensis* (H. Karst.) R. M. Tryon (= *Cyathea meridensis* H. Karst.; Tryon 1976). The true *C. parvifolia* was recognized as distinct and newly described as *Cyathea brevistipes* by Moran (1991). Moran's error is understandable since *C. parvifolia* resembles the real *C. meridensis* only superficially in the pinnule shape. The latter species has petiole scales with almost black centers and dark castaneous, easily abraded scurf consisting of small, strongly fimbriate squamules on petioles and leaf axes. In contrast, *C. parvifolia* has dull brown to orange-brown petiole scales and scurf that consists of translucent pale brown squamules with short-ciliate margins, which are usually plastered tightly to the petiole's cortex and are detectible only if actively scraped off.

Adventitious pinnae at the petiole bases are rare in the genus *Cyathea* and were previously known only from *C. suprastrigosa* H. Christ, with which *C. parvifolia* had been compared (as *C. brevistipes*; Moran 1991). Other Neotropical species of *Cyathea* with adventitious pinnae are *C. frondosa* H. Karst., *C. brachypoda* Sodiro, and *C. pallescens* Sodiro (Lehnert 2008). In most of these species, the adventitious pinnae may sometimes be missing. A characteristic variation of this character was observed in two populations from paratype localities of *C. brevistipes* in Ecuador and Bolivia. Generally, the gap between the aphlebioid pinnae and the subsequent pinna pairs diminishes with increasing size of the trunk. The characteristic basal pinnae are generally present but may be missing in some plants of a population. Trunkless plants growing in the shade have usually triangular blades and rather long petioles that lack adventitious pinnae; despite their small size they are usually fertile. Bolivian plants have pinnules generally twice the size of most Ecuadorian plants, and have also more colorful orange-brown scales. This is probably a response to the more sheltered conditions in which they grow. Most collections from Ecuador come from wind-swept paramos, while the known Bolivian populations grow in low elfin forests.

## 3.16 *Cyathea herzogii*

*Cyathea herzogii* Rosenst.: Rosenstock 1913: 7. – Type: Bolivia. Santa Cruz, Yungas de San Mateo, [ca. 17°53'S, ca. 64°30'W,] 2400 m, IV.1911, »Herzog 1990« (holotype, L-photo GH; isotypes, S, NY, UC, US, Z).

### Selected specimens examined

P e r u . **Cuzco**. Prov. Paucartambo, Manu National Park, 2750 m, VI.2003, »García et al. 147« (CUZ, USM); Prov. La Convención, Dist. Santa Ana, Tunquimayo, 12°54'37"S, 72°50'13"W, 2675 m, 22.IX.2004, »Calatayud et al. 2820« (MO); La Convención, ca. halfway between Camp 4 & Camp 5, 12°37'S, 73°32'W, 2600–2750 m, 4.VII.1968, »Dudley 10792« (GH). **Junín**. Prov. Satipo, northern Cordillera Vilcabamba, eastern slope, upper Río Puyeni watershed, 11°33'35"S, 73°38'W, 2090 m, 26.VI.1997, »Boyle et al. 4749« (USM). **Pasco**. Prov. Oxapampa, Dist. Huancabamba, sector quebrada Yanachaga (P. N. Yanachaga-Chemillén), 10°23'31"S, 75°28'30"W, 2400–2500 m, 12.II.2004, »Mellado 286« (MO); Dist. Oxapampa, Abra Villa Rica, 10°40'36"S, 75°18'55"W, 2400 m, 28.VIII.2004, »Mellado 1652« (MO).

B o l i v i a . **Cochabamba**. Prov. Carrasco, a ca. 3 km desde el campamento Locotal, en dirección NO, a lo largo de la antigua senda de Kara Huasi a Pojo, 17°46'12"S, 64°45'62"W, 2200 m, 2.II.2000, »Jiménez 305« (GOET, LPB, UC). **La Paz**. Prov. Nor Yungas, Estación Biológica de Tunquini, senda nueva del camino de la mina (curva al lado oeste) al pantanón, 16°12'S, 67°53'W, 2800 m, 13.IX.2000, »Bach et al. 1019« (GOET, LPB, UC); Prov. Sur Yungas, 9 km de Huancané en la carretera hacia San Isidro, 16°21'S, 67°31'W, 2400 m, 2.V.1989, »Smith D. N. & Smith J. F. 13101« (AAU, LPB, MO, NY).

### Description

Trunks to 4 m tall, to 10–15(20) cm diameter, with persistent petiole bases in small plants, balding when older and larger. Petioles to 25–60 cm long, brown to stramineous, aculeate to verrucate, with inconspicuous brown scurf of appressed lacerate squamules, and sometimes with small appressed hairs. Petiole scales lanceolate to broadly lanceolate, (7)20–26(36) × (1.6)3–5(8.2) mm, concolorous brown or concordantly bicolorous with margins tan or rarely whitish.

Laminae to 80–160 × 60–110 cm. Rhachises with dense pubescence of whitish to tan multicellular hairs to 1.2 mm long. Pinnae sessile to short-stalked to 4 mm, acuminate, distally green-alate, the wings at least slightly arcuate. Pinnules to 50–75(90) × 10–15(17) mm, truncate to round basally, sessile to subsessile (stalked to 1 mm), linear-oblong to linear-obovate, acuminate apically; white multicellular hairs (0.4–0.6 mm) on and between the veins abaxially and adaxially, abundant and equally distributed on both sides to nearly glabrous with more multicellular hairs adaxially than abaxially (here substituted by short appressed trichomidia); few to many bullate squamules, 0.6–1.0 mm long, shiny auburn to orange-brown, rarely paler to whitish, on costules and larger veins abaxially.

Sori costal, indusia sphaeropteroid, with apical umbo.

For full description see Lehnert (2006b).

Distribution and habitat

Bolivia and Peru, growing in elfin forests and upper montane forests at 2000–3000 m.

Remarks

This species is characterized by the relatively short, linear to weakly oblanceolate pinnules with acute or only weakly attenuate tips. It was included in *Cyathea caracasana* var. *boliviensis* (Rosenst.) R. M. Tryon, but most specimens were erroneously identified as *C. delgadii*. Like *C. delgadii* and *C. squamipes*, *C. herzogii* has small auburn to orange-brown squamules abaxially on veins and costules, but differs in having hairs between the veins abaxially and adaxially. *Cyathea delgadii* is equally hairy on both surfaces of the veins, but not or only weakly hairy between the veins adaxially, with hairs notably longer (1 mm vs. 0.4–0.6 mm in *C. herzogii*); *Cyathea squamipes* generally has no hairs between the veins except for occasional few short hairs below the sinuses abaxially. The spore morphology supports the separation of *C. herzogii* from these two species because the exospore of *C. herzogii* is not verrucate but smooth, and resemble those of *C. austropallescens* Lehnert (Lehnert 2006b, 2008).

### 3.17 Dubious and excluded species

*Cyathea boconensis*

*Cyathea boconensis* H. Karst.: Karsten 1856: 458. – Type (cited in Karsten 1869: 171): Venezuela. Mérida, "Habitat ad pedem australis montis glacialis Meridensis altitudine 1000 m", »Karsten s. n.« (holotype, n. l.).

Listed as a synonym of *Cyathea caracasana* var. *boliviensis* by Tryon (1976). During my studies, I have not seen any material I could relate to the diagnosis, although the name has been applied to some specimens. Without any material at hand, this species is impossible to define. The depicted laminar indument (Karsten 1869), with bullate squamules on small pedicels and with caudate apices as well as the narrow, ribbon-like scales resembles that of *C. patens*. However, the described pneumathodes at the costa bases, the medial position of the sori, and the distribution of hairs of *C. boconensis* are quite different.

*Cyathea chimborazensis*

*Cyathea chimborazensis* (Hook.) Hieron.: Hieronymus 1906: 230. – *Alsophila chimborazensis* Hook.: Hooker 1866: 37. – *Cyathea caracasana* (Klotzsch) Domin var. *chimborazensis* (Hook.) R. M. Tryon: Tryon 1976: 81. – Type: Ecuador. Chimborazo, "Chimborazo, Ecuador", 914–1219 m, Spruce 5743 (holotype, K-fragm. B; isotypes, BM, P, US [fragm.]).

Treated as a variety of *Cyathea caracasana* by Tryon (1976), but the type material represents a species of uncertain status from a different group (Lehnert 2008). The laminar indument in the type material of *C. chimborazensis* varies in amount but generally agrees well morphologically with that of *C. cystolepis* Sodiro (Lehnert 2008). The pinnules, however, are much broader and more widely placed along the costae than in *C. cystolepis*.

*Cyathea fulva*

*Cyathea fulva* Sodiro: Sodiro 1883: 13, not Fée 1857: 34. – Lectotype (chosen by Tryon 1976): Ecuador. Riobamba, Tambo-Ioma [= Tamboloma], X.1882, »Sodiro s. n.« (lectotype, P-photo GH; isolectotypes, B?-fragm. NY, K-fragm. NY).
*Cyathea sodiroi* C. Chr.: Christensen 1905: 195, nom. nov. for *Cyathea fulva* Sodiro, not (M. Martens & Gal.) Fée.
= *Cyathea tungurahuae* Sodiro (Lehnert 2008).

Listed as a synonym of *Cyathea caracasana* var. *caracasana* by Tryon (1976), but the type material represents *C. tungurahuae* Sodiro.

*Cyathea membranulosa*

*Cyathea membranulosa* H. Christ: Christ 1907: 271. – Syntypes: Costa Rica. San Pascon, 1500 m, »Wercklé s. n.« (P [Herb. Inst. Nat. Costaric. 17024]); La Palma, 1500 m, »Wercklé s. n.« (P [Herb. Inst. Nat. Costaric. 17082], n. v.).

Listed as a synonym of *Cyathea caracasana* var. *maxonii* by Tryon (1976). The name has priority over *C. maxonii* but I have not seen the type material at P. Discrepancies in the descriptions, e. g., the type of indusia (membranaceous, fugacious in *C. membranulosa* [Christ 1907] vs. rather firm and persistent in *C. maxonii*) allow the possibility that both names represent different species.

### *Cyathea mettenii*

*Cyathea mettenii* H. Karst.: Karsten 1860: 113. – Type: Colombia. Cundinamarca, "habitat silvas humidas umbrosas Andium Bogotensium altitudine 2700 m", »Karsten s. n.« (holotype, n. l.; isotypes, B [label "Bogotá, 9000 ft., Karsten 195"], US [label "Bogotá, Karsten 195"]).

*Cyathea mettenii* var. *caucana* Hieron.: Hieronymus 1905: 437. – Type: Colombia. Cauca, über Palatará, 3000 m, 5.II.1884, »Lehmann 3482« (holotype, B, n. v.; isotypes, K, US).

Two specimens at B cited as isotypes by Tryon (1976) agree well with the description of *C. patens* but do not match the description of the paraphyses of *C. mettenii* given by Karsten (1860). These are described and illustrated in the Flora Columbiae as being longer than the sporangia. The Berlin specimens have much shorter paraphyses and comply in this regard with the circumscription given here. In my experience, it is unlikely that the paraphyses would have these larger proportions because sphaeropteroid indusia, as occurring in *C. patens*, are molded around the sporangia and leave limited space for the paraphyses. The illustration of the paraphyses of *C. mettenii* must be based either on a misinterpretation of the material or on a confusion of species. Another difference is the scale color, which was stated by Karsten as brown; in *C. patens*, it is mostly weakly bicolorous (Karsten 1860) and rarely almost concolorous. Otherwise the descriptions and illustrations are matching, especially the habit of the plant and the distribution of scales.

### 3.18 Partial key to *Cyathea*

Preliminary key to the genus *Cyathea* with bipinnate-pinnatifid or more complex laminae from the Neotropics. Species that have been treated as synonymous by Tryon (1976) with *C. caracasana* are spaced.

**1** Sori exindusiate, sometimes with one or few small scales attached to the receptacles, scales with narrow insertions, entire margins, and acute tips, easily detached and not present in all sori. . . . . **2**

– Sori indusiate, indusia sometimes fragmented and missing except for lacerate rings around the receptacle bases (remove receptacles for secure identification), indusial fragments sometimes scale-like but with broad insertions and with irregularly formed margins and apices. . . . . **3**

**2** Petioles with adventitious pinnae near their bases. . . . . ***C. pallescens***

– Petioles without adventitious pinnae. . . . . Various species (see Lellinger 1984, 1987 and references therein)

**3** Indusia hemitelioid to cyatheoid, not or only weakly fragmenting with maturity of the sporangia, fragments remaining attached to receptacles, mode of damage to the indusia homogenic in most sori. . . . . Various species (see Tryon 1976, Lellinger 1984 and references therein)

– Indusia sphaeropteroid to subsphaeropteroid, sometimes very fragile and fugacious with maturity of the sporangia, mode of damage to the indusia heterogenic. . . . . **4**

**4** Petiole scurf mostly lacking in mature fronds, either weakly developed or ephemeral, consisting of a matted tomentum of branched hairs and small squamules, appearing amorphous; petiole scales almost concolorous dark brown to castaneous to strongly bicolorous with bright orange margins (in latter case sometimes together with almost concolorous orange scales); petioles usually inermous, never with adventitious pinnae; mature spores pale brown. . . . . ***C. lechleri*** (Mett.) Domin group, ***C. dissoluta***

– Petiole scurf well developed, components visible as clearly separated squamules or as matted tomentum, but not appearing amorphous – if weakly developed to ephemeral then not matted but with distinct squamules, and then also petiole scales either concolorous orange-brown or with distinct white margins; petioles often strongly aculeate, sometimes with adventitious pinnae; mature spores pale to dark yellow. . . . . **5**

**5** Petiole scurf a dense matted tomentum of grayish to white, branched tortuous hairs and strongly dissected squamules, only removable in clusters or larger flakes. . . . . **6**

– Petiole scurf not matted, removable as single squamules, branched tortuous hairs absent (although long, tortuous marginal cilia may be present on squamules); if squamules dissected then dark brown to castaneous. . . . . **8**

**6** Petioles inermous, without adventitious pinnae; petiole scales ovate to broadly lanceolate, bicolorous dark brown with broad grayish margins. . . . . ***C. moranii***

– Petioles weakly to strongly aculeate, regularly with 1–2 pairs of adventitious pinnae; petiole scales with elongate, strongly twisted tips (3–4 times, especially when dried), concolorous to bicolorous dark brown with narrow paler brown margins. . . . . **7**

**7** Pinnules (at least in part) with auriculate bases; petiole scales 2.0–6.5 mm broad, concolorous to weakly concordantly bicolorous, auburn to dark brown, with slightly paler margins; laminae adaxially with white to tan, erect multicellular hairs to 1 mm long on the midveins, hairs abundant to sparse on the lateral veins 0.6 mm long, laminae abaxially with hairs 0.5–1.0 mm long to various degrees on costules, midveins, and lateral veins, rarely between the veins. – Central America. . . . . ***C. suprastrigosa***

– Pinnules with cuneate to truncate bases, never auriculate; petiole scales 2–3 mm broad, brown to dark brown with somewhat paler margins, sometimes with diffuse darker areas in the centers, but never strongly bicolorous; laminae adaxially sparsely hairy on midveins and practically no hairs on the lateral veins, variously developed abaxially, hairs only 0.2–0.4 mm long. – Andes. . . . . ***C. frondosa***

**8** Petiole scurf brown, orange-brown, atropurpureous, or castaneous, never white or bicolorous with whitish margins, either pulverulent or consisting of erect squamules of various sizes, never with long marginal cilia or short darkened cilia/teeth; petiole scales concolorous brown to dark brown, orange-brown or castaneous – if bicolorous then margins pale brown, orange-brown or yellowish, never pure white. **9**

– Petiole scurf pale brown, tan, stramineous, cream, ivory, or white, consisting of distinct erect, round to lanceolate squamules, sometimes with short darkened teeth – if squamules bicolorous then with long, often contorted, fragile whitish cilia and with pale brown (to brown) centers appressed to the petiole; petiole scales concolorous white or bicolorous with tan to white (never orange-brown) margins. . . . . **30**

**9** Petiole scurf pulverulent, consisting of fine, oblong to narrowly lanceolate squamules rarely more than 0.5 mm long, either dissected or with fimbriate margins, dark brown to castaneous; laminae glabrous to sparsely hairy with multicellular hairs less than 1 mm long. . . . . **10**

– Petiole scurf consisting of erect squamules of various sizes, usually cristate, brown to dark orange-brown or atropur-

pureous; laminae glabrous to densely hairy with multicellular hairs to 2 mm long. . . . . **16**

**10** Petiole scales very scarce and fugacious; laminae firm-herbaceous, the segment margins inciso-serrate and flat; lateral buds, stolons, or aerial roots in upper trunk parts common. . . . . .(*C. xenoxyla* group) **11**

– Petiole scales abundant and persistent at least in lower parts; laminae firm-chartaceous to coriaceous, the segment margins entire to mostly shallowly (rarely strongly) crenate and then margins weakly convolute; stolons lacking, lateral buds only forming after injury of the apex, aerial roots restricted to lower trunk parts.. . . . . (*C. caracasana* group) **12**

**11** Trunks to 5 cm diameter, forming clonal groups with basal lateral shoots; laminae spade-shaped, with truncate bases; strongly raised, pad-like pneumathodes at the junctions of rhachises and costae presumably secretive, functioning as nectaries.. . . . . ***C. planadae*** N. C. Arens & A. R. Sm.

– Trunks to 8–10 cm diameter, usually single but small adventious buds and roots occur all along the trunks; laminae ovate-elliptic, with round bases; pneumathodes at the junctions of rhachises and costae without secretive function.. . . . . ***C. xenoxyla*** Lehnert

**12** Indusia very thin, hyaline to white, sometimes a mucous layer in fresh material, evanescent when dried; petioles yellowish, stramineous to plumbeous, near the bases sometimes darker brown, usually strongly muricate to aculeate; laminar indument with pale brown to whitish, sometimes contrastingly bicolorous, lanceolate squamules; junctions of costae and rhachises swollen only abaxially. . . . . **13**

– Indusia rather firm, tan to brown, fragmenting at maturity to irregular cups or discs; petioles inermous, smooth or sparsely verrucate (exceptionally with few strong spines near the very base), usually dark brown to castaneous, not constrasting with the castaneous scurf; laminar indument with yellowish to dark brown, never contrastingly bicolorous squamules; insertions between costae and rhachises circularly swollen abaxially and adaxially. . . . . **14**

**13** Pinnae in 8–10 pairs, stalked to 2–3 cm; costules abaxially not hairy, or if single short hairs present abaxially then also with short hairs below the sinuses and scattered on lateral veins; laminar indument lacking bicolorous squamules; segment margins of larger pinnules subentire to shallowly (but never deeply) crenate.. . . . . ***C. caracasana***

– Pinnae in 12–15 pairs, stalked to 0.5 cm; costules abaxially sparsely to moderately hairy with short white erect multicellular hairs to 0.5 mm long; laminar indument including whitish, broadly lanceolate squamules with dark brown marginal teeth and basal spots; segment margins of larger pinnules shallowly to deeply crenate.. . . . . ***C. crenata***

**14** Largest pinnules less than 2 cm broad, all sessile to subsessile (exceptionally short-stalked to 3 mm), usually held upright with respect to the costae; trunks shedding old petiole bases and reaching diameter of 12–16 cm when less than 2 m tall; scales on lower parts of petioles narrowly lanceolate, to 5 cm long. . . . . ***C. plicata***

– Largest pinnules more than 2 cm broad and notably stalked, all held in one plane with the costae; if pinnules smaller and sessile then the whole plants diminuitive with trunks less than 2 m tall and to 5–12 cm diameter including the persistent old petiole bases. . . . . **15**

**15** Larger squamellae of petiole scurf oblong to oblanceolate, squamellar margins appearing paler in backlight; laminar indument brown to yellowish brown, paler than the petiole scurf; trunks with persistent petiole bases at least when smaller than 2 m, reaching 5–12 cm diameter; sizes and proportions of plants variable but habit always gracile. . . . . ***C. meridensis***

– Larger squamellae of petiole scurf asymmetrically lanceolate, squamellar margins not appearing paler in backlight; laminar indument dark brown to castaneous, of same color as the petiole scurf; trunks shedding petioles when smaller than 2 m, reaching 15–20 cm diameter; stout, massive plants. . . . . ***C. carolihenrici***

**16** Fertile plants diminuitive, trunkless; petioles inermous; laminae less than 50 cm long, shallowly but fully bipinnate-pinnatifid. . . . . ***C. sylvatica***

– Fertile plants with trunks; petioles muricate to aculeate; laminae more than 50 cm long, if shorter then pinnate-pinnatifid to bipinnate (precociously fertile juveniles). . . . . **17**

**17** Petioles usually with aphlebioid pinnae; laminar indument with whitish to pale brown, dissected squamules and pale brown to brown, bullate squamules with entire margins and attenuate tips. . . . . ***C. brachypoda***

– Petioles without aphlebioid pinnae; laminar indument with orange-brown to brown, flat ovate-lanceolate and bullate squamules to 1.0–2.0 mm long with elongate tips and fimbriate to entire margins. . . . . **18**

**18** Fronds with 10 pinna pairs or fewer; trunks small and decumbent, to 3 m tall and 7 cm in diameter, with lateral aerial shoots. – Jamaica.. . . . . ***C. dissoluta***

– Fronds with 12–15 pinna pairs, rarely fewer; trunks stout and erect, to 12 m tall and 10 cm in diameter, without lateral shoots (branching may occur after injury of apex). . . . . **19**

**19** Petiole scales concolorous or nearly so, rather dull brown to lustrous orange-brown with somewhat paler margins; scurf either scarce or ephemeral, missing in fully expanded fronds, sometimes scurf replaced by dense pubescence of muticellular hairs to 2 mm long. . . . . **20**

– Petiole scales bicolorous with dark brown to blackish centers at least in basal petiole parts, if concolorous then dark brown to atropurpureus and petiole scurf long persisting.. . . . . **27**

**20** Petiole scales lustrous orange-brown, contrasting with the blackish cortex of the lower petiole parts, scurf soon caducous; hairs often present between the veins abaxially but not adaxially. . . . . ***C. delgadii***

– Petiole scales dull brown, petiole cortex dull brown to stramineous or yellow, if scales lustrous then sparse scurf persisting or replaced by hairs; hairs absent between the veins, or if hairs present then more abundant adaxially.. . **21**

**21** Squamellae on costules (and midveins) whitish to tan, appearing pale "en masse". . . . . **22**

– Squamellae on costules (and midveins) auburn to dark brown, appearing dark "en masse". . . . . **23**

**22** Costules and midveins abaxially with predominantly flat, rarely subbullate squamules with short tips and entire margins. – Central America. . . . . ***C. onusta***

– Costules and midveins abaxially with many subbullate to bullate squamules 1–3 mm long, tan to yellowish white, concolorous or weakly bicolorous with darker brown bases, with elongate tips and entire to weakly fimbriate margins. – Jamaica, Cuba, Haiti.. . . . . ***C. furfuracea***

**23** Laminae usually sparsely hairy on both sides, or if pubescence evident then hairs more abundant abaxially and never between the veins. . . . . **24**

– Laminae usually evidently hairy on and between the veins on both sides, or if pubescence sparse then hairs more abundant adaxially. . . . . **25**

**24** Petiole scales 14–20 × 4.5–5.0 mm, concolorous orange-brown to reddish brown; costules with flat, lanceolate squamules with weakly fimbriate margins; laminae to 90–150 × 35–80 cm. – Caribbean. . . . . .***C. tenera*** (Hook.) T. Moore agg.

– Petiole scales 20–30 × 2.0–4.5 mm, concolorous to weakly concordantly bicolorous, the brown to dark brown centers

not sharply contrasting with the brown to yellowish orange margins; costules and midveins abaxially with flat squamules missing or rarely few with subentire margins; laminae to 250 × 100–130 cm. – Mesoamerica, northern Andes. . . . . ***C. fulva*** agg. (see Rojas 2001, 2005)

**25** Squamules on costules and midveins flat, with elongated tips and fimbriate to dissected margins, bullate squamules lacking; veins abaxially with many white, tortuous multicellular hairs 0.5–0.7 mm long on and between the veins. – Caribbean. . . . . ***C. harrisii*** Underw.

– Squamules on costules and midveins deeply bullate to sacculate; tortuous hairs lacking. – Andes. . . . . **26**

**26** Petioles aculeate to verrucate, with scarce scurf of brown squamellae and trichomidia; proximal segments of pinnules not covering the costules; pinnae mainly alternate. . . . . ***C. herzogii***

– Petioles inermous, scurf replaced by indument of white multicellular hairs to 2 mm long; proximal segments of pinnules partially covering the costules; central and lower pinnae opposite or nearly so. . . . . ***C. obnoxia*** Lehnert

**27** Laminar hairs more frequent adaxially than abaxially; pinnule bases notably cordate to auriculate. . . . ***C. maxonii***

– Laminar hairs more frequent abaxially than adaxially, but generally sparse; pinnule bases truncate to cuneate, not auriculate. . . . . **28**

**28** Scales of lower parts of petioles with relatively narrow blackish centers and broad ferrugineous to orange-brown margins that are confluent towards the tips; squamules of petiole scurf to 1.0 mm; rhachises with long-persistent bicolorous scales whose marginal color fades with age; largest pinnules sessile or nearly so (stalks 1 mm or less). . . . . ***C. catacampta***

– Scales of lower parts with relatively broad, dark brown to blackish centers, the marginal color not confluent towards the tips; squamules of petiole scurf to 0.5 mm; rhachises without scales or with ephemeral concolorous scales; largest pinnules often notably short-stalked to 3 mm. . . . . **29**

**29** Petiole scales narrowly lanceolate to lanceolate, 15–33 × 3.5–4.5 mm, the brown to dark brown centers not sharply set against the brown to orange margins, often appearing concolorous; laminar indument with mainly flat (rarely subbullate) squamules. . . . . ***C. lindeniana***

– Petiole scales relatively broadly lanceolate, to 15 × 4 mm, atropurpureus to blackish on the sides and the bases of the petioles, dark brown on upper petiole parts and towards the trunks, always with distinct lighter margins, brown to orange, rarely in parts yellowish or cream-white; laminar indument with flat and bullate squamules. . . . . ***C. squamipes***

**30** Trunks to 4 cm diameter, fertile plants less than 2 m tall, unfolding only one frond at a time, lacking stolons or lateral buds. . . . . **31**

– Trunks 5–25 cm diameter, fertile plants usually 2 m or taller; if smaller then trunk unfolding more than one frond at a time, lateral buds or stolons possible. . . . . **32**

**31** Petiole scurf scant, easily abraded and often absent in mature material; petiole scales broadly lanceolate to ovate, opaque white to very light brown, sometimes with a dark brown streak at tip. – Central Andes. . . . . ***C. bettinae***

– Petiole scurf well developed, persisting in mature material; petiole scales narrowly lanceolate to ovate-lanceolate, discordantly to concordantly bicolorous brown to dark brown with tan to whitish margins, distal scales broader and lighter in color than the basal ones. – Guyana Highlands. . . . . ***C. simplex*** R. M. Tryon

**32** Petiole scales very scarce and fugacious; lateral buds, stolons, or aerial roots in upper trunk parts common. . . . . (*C. xenoxyla* group) **11**

– Petiole scales numerous and long-persisting; lateral buds formed only after injury of the apex, stolons or aerial roots in upper trunk parts absent. . . . . **33**

**33** Petiole scales concolorous white, cream, stramineous, or tan, without continuous central streak. . . . . **34**

– Petiole scales at least at petiole bases bicolorous with continuous central streak, sometimes almost concolorous brown to dark brown or blackish. . . . . **35**

**34** Petiole scales relatively thick, firm, elastic; petiole scales and scurf squamules lacking long marginal cilia, but often with brown to dark brown marginal teeth. . . . ***C. straminea***

– Petiole scales thin, papyraceous, flexuous; petiole scales and scurf squamules without brown marginal teeth but with long marginal cilia not differently colored than the rest of the scale. . . . . ***C. atahuallpa***

**35** Laminar indument with linear-lanceolate squamules and small scales, both with fimbriate to ciliate margins and often transitional to branched hairs, small scales of the laminar indument concolorous and golden brown to orange-brown, or if not so then petioles with aphlebioid pinnae. . . . . **36**

– Laminar indument without linear-lanceolate squamules that are transitional to branched hairs (which may be present), usually with white, tan, or dark brown, ovate to lanceolate squamules and small scales, flat squamules of the laminar indument often bicolorous or with dark marginal teeth, squamules never golden brown to orange-brown and petioles always lacking aphlebioid pinnae. . . . . **37**

**36** Petioles without basal aphlebioid pinnae, clearly set apart from the elliptic laminae; bullate squamules with fimbriate margins present in the laminar indument; petiole scurf usually dense (but easily worn off), the squamules with marginal cilia longer than their bodies. . . . . ***C. patens***

– Petioles with pairs of basal aphlebioid pinnae, or if these absent then laminae either ± triangular or basally decurrent into a very short petiole; bullate squamules with entire margins; petiole scurf scarce and appressed, squamules with short hyaline cilia. . . . . ***C. parvifolia***

**37** Petiole scurf consisting of pale brown to tan, appressed to ascending, small squamules with fimbriate to ciliate margins, relatively sparse, never with dark marginal teeth nor transitional to larger petiole scales. . . . . **38**

– Petiole scurf consisting of erect, stramineous, cream, or white, lanceolate squamules, often transitional to larger petiole scales and/or with dark marginal teeth. . . . . **41**

**38** Petiole scurf consisting of small, isodiametric squamules with spreading marginal cilia (appearing like snowflakes or cottonballs). . . . . **39**

– Petiole scurf consisting of small flat, round to ovate-lanceolate squamules with paler marginal cilia, these not spreading. . . . . **40**

**39** Laminar indument without bullate squamules; petiole scurf squamules of more or less the same size; segments without hairs adaxially on the veins; leaf axes abaxially glabrous or glabrescent with sparse scurf; indusia very fragile and often ephemeral. . . . . ***C. tungurahuae***

– Laminar indument with bullate squamules; petiole scurf squamules of different sizes; segments with few to many hairs adaxially on the veins; leaf axes abaxially often densely covered with easily abraded white scurf; indusia fragile but usually persistent as fragments. . . . . ***C. cystolepis***

**40** Petiole scales dark brown, margins usually very narrow; hairs, if present, more abundant abaxially than adaxially; laminar indument with bullate squamules and white tortu-

ous hairs; petiole bases often with adventitious pinnae. . . . . ***C. brachypoda***

– Petiole scales brown to pale brown with broad white margins; hairs, if present, more abundant adaxially or equally frequent on both laminar surfaces; laminar indument without bullate squamules or white tortuous hairs; petiole bases never with adventitious pinnae. . . . . ***C. austropallescens***

**41** Petiole scurf diffuse, petiolar cortex visible between scurf and petiole scales; petiole scales with relatively firm, persistent margins; fronds sometimes with dark fungal infection visible as black spot between veins. . . . . **42**

– Petiole scurf dense, obscuring petiolar cortex between petiole scales; petiole scales with brittle, fragmenting margins; laminae without black spots between the veins. . . . . **43**

**42** Scurf squamules without dark marginal teeth but usually with cropped tips; petiole scales concordantly bicolorous to almost concolorous dark brown to blackish with white to pale brown margins; laminae usually with fungal infection visible as black spots between the veins. . . . . ***C. dintelmannii*** Lehnert

– Scurf squamules often with dark marginal teeth; petiole scales only pale brown to brown, discordantly bicolorous with white to tan margins; laminae without black spots between the veins. . . . . ***C. straminea***

**43** Largest pinnules notably stalked, stalk usually longer than width of basal segment; laminar indument absent to sparse (rarely strongly developed on leaf axes), appearing ± concolorous brown, consisting mainly of hyaline branched hairs with brown tips and thin concolorous brown squamellae; indusia brown, firm, persisting. . . . . ***C. divergens***

– Largest pinnules sessile to subsessile, stalk length not reaching width of basal segment; laminar indument not appearing concolorous brown, either white or bicolorous; indusia light brown to colorless, persistent to ephemeral. . . . . **44**

**44** Pinnules to 9.5–12 × 0.8–2.0 cm, mostly linear with acute tips; laminar indument consisting of strongly bicolorous dark brown squamules with white margins, smaller ones also with dark brown marginal teeth or concolorous dark brown; white bullate squamules mainly distally on the segments; indusia lustrous, tan to light brown, fragments usually persistent at maturity. . . . . ***C. ruiziana*** Klotzsch

– Pinnules to 12–16 × 1.2–4.5 cm, mostly triangular with attenuate tips; laminar indument consisting of white dissected squamules and trichomidia, sometimes with small brown scales to 4 mm long with tan to white margins and dark brown marginal teeth scattered on costules; bullate squamules absent; indusia opaque to vaguely shiny, tan to white, transparent, fragile, often ephemeral. . . . . ***C. corallifera***

## 4 List of exsiccatae

List to the exsiccatae consulted for this study (including type specimens and collections mentioned in the text). Collectors are arranged in alphabetical order; in the case of two or more co-collectors, these are abbreviated with "et al.". Reference to species in brackets; for consecutive collection numbers pertaining to the same species, the number is given only after the last collection. Collections without numbers are omitted if there are several collections belonging to different taxa (Karsten s. n., Wercklé s. n., Sodiro s. n.).

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## 5 References


Alston, A. H. G. (1958): New or noteworthy ferns from Colombia and Ecuador. – Journal of the Washington Academy of Science **48**: 230–234.

Baker, J. G. (1891): A summary of the new ferns which have been discovered or described since 1874. – Annals of Botany, Oxford **5**: 118–222, 301–332.

Barrington, D. S. (1978): A revision of *Trichipteris* (Cyatheaceae). – Contributions from the Gray Herbarium of Harvard University **208**: 3–93.

Caluff, M. G. (2003): Cyatheaceae. – Flora de la República de Cuba **8** (2): 1–63.

Christ, H. (1897): Die Farnkräuter der Erde, 404 pp.; Jena (Gustav Fischer).

Christ, H. (1907): Primitiae Florae Costaricensis. Filices V. – Bulletin de l'Herbier Boissier (2) **7**: 165–277.

Christensen, C. (1905): Index Filicum, sive enumeratio omnium generum specierumque Filicum et Hydropteridum ab anno 1753 ad finem anni 1905 descriptorum, 744 pp.; Hafniae [= Copenhagen] (Hagerup).

Conant, D. S. (1975): Hybrids in American Cyatheaceae. – Rhodora **77**: 441–455.

Conant, D. S. (1983): A revision of *Alsophila* (Cyatheaceae) in the Americas. – Journal of the Arnold Arboretum **64**: 333–382.

Conant, D. S. (1990): Observations on the reproductive biology of *Alsophila* species and hybrids (Cyatheaceae). – Annals of the Missouri botanical Garden **77**: 290–296.

Conant, D. S. & Cooper-Driver, G. (1980): Autogamous allohomoploidy in *Alsophila* and *Nephelea* (Cyatheaceae): A new hypothesis for speciation in homoploid homosporous ferns. – American Journal of Botany **67**: 1269–1288.

Domin, C. (1929a): Pteridophyta, 276 pp.; Prague (Česká Akademie Věd a Umění).

Domin, C. (1929b): The Pteridophyta of the Island of Dominica with notes on various ferns from tropical America. – Memoirs of the royal Czech Society of Sciences, Division of natural History and Science, new series **2**: 259 pp., 40 pls.

Fée, A. L. A (1857): Catalogue méthodique des Fougères et des Lycopodiacées du Mexique. – Mémoires sur la Famille des Fougères **9**: 1–38.

Gastony, G. J. (1973): A revision of the fern genus *Nephelea*. – Contributions from the Gray Herbarium of Harvard University **203**: 83–148.

Hieronymus, G. (1905): Plantae Lehmannianae in Guatemala, Columbia et Ecuador regionibusque finitimis collectae, additis quibusdam ab aliis collectoribus ex iisdem regionibus allatis determinatae et descriptae. Pteridophyta. – Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie **34**: 417–560.

Hieronymus, G. (1906): Plantae Stübelianae. Pteridophyta. – Hedwigia **45**: 215–238.

Holttum, R. E. (1963): Cyatheaceae. – Flora Malesiana (2) **1**: 1–176.

Holttum, R. E. & Sen, U. (1961): Morphology and classification of the tree ferns. – Phytomorphology **11**: 406–420.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. (1990): Index Herbariorum. Part 1: The Herbaria of the World, 693 pp.; New York (New York Botanical Garden).

Hooker, W. J. (1866): Synopsis Filicum; or, a synopsis of all known ferns, including the Osmundaceae, Schizaeaceae, Marattiaceae, and Ophioglossaceae, part 2, pp. 33–64; London (Robert Hardwicke).

Houlston, J. & Moore, T. (1851): Genera and species of cultivated ferns. – Gardeners' Magazine of Botany, Horticulture, Floriculture, and natural Science **3**: 17–149, 151–332.

Janssen, T., Bystriakova, N., Rakotondrainibe, F., Coomes, D., Labat, J.-N. & Schneider, H. (2008): Neoendemism in Madagascan scaly tree ferns results from recent, coincident diversification bursts. – Evolution **62**: 1876–1889.

Jenman, G. S. (1881): Third supplement to the ferns recorded in Grisebach's "Flora of the British West Indies"– Journal of Botany, British and Foreign (new series 10) **19**: 51–54.

Jenman, G. S. (1886): Some additional Jamaica ferns. – Journal of Botany, British and Foreign (new series 15) **24**: 265–274.

Karsten, H. (1856): Plantae Columbianae. – Linnaea **28**: 387–462.

Karsten, H. (1860): Florae Columbiae terrarumque adiacentium specimina selecta in peregrinatione duodecim annorum observata **1**, 200 pp.; Berolini [= Berlin] (Dümmler).

Karsten, H. (1869): Florae Columbiae terrarumque adiacentium specimina selecta in peregrinatione duodecim annorum observata **2**, 188 pp.; Berolini [= Berlin] (Dümmler).

Killeen, T. J., Douglas, M., Consiglio, T., Jørgensen, P. M. & Mejia, J. (2007): Dry spots and wet spots in the Andean hotspot. – Journal of Biogeography **34**: 1357–1373.

Klotzsch, J. F. (1844): Beiträge zu einer Flora der Aequinoctial-Gegenden der neuen Welt. – Linnaea **18**: 515–556.

Korall, P., Pryer, K. M., Metzgar, J., Schneider, H. & Conant, D. S. (2006): Tree ferns: monophyletic groups and their relationships as revealed by four protein-coding plastic loci. – Molecular Phylogeny and Evolution **39**: 830–845.

Korall, P., Conant, D. S., Metzgar, J., Schneider, H. & Pryer, K. M. (2007): A molecular phylogeny of scaly tree ferns (Cyatheaceae). – American Journal of Botany **94**: 873–886.

Kramer, K. U. (1978): The Pteridophytes of Suriname. – Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen (Netherlands) **93**: 1–98.

Kramer, K. U. & Green, P. S. (eds.) (1990): Pteridophytes and Gymnospermes. – In: Kubitzki, K. (ed.): The families and genera of vascular plants **1**: XIV + 410 pp.; Berlin (Springer).

Lehnert, M. (2003): Six new species of tree ferns from the Andes. – American Fern Journal **93**: 169–183.

Lehnert, M. (2004): *Cyathea bettinae* (Cyatheaceae), a new tree fern from Bolivia. – Brittonia **56**: 210–212.

Lehnert, M. (2006a): Two new tree ferns (Cyatheaceae) from southern Ecuador. – Brittonia **58**: 4–9.

Lehnert, M. (2006b): The Cyatheaceae and Dicksoniaceae (Pteridophyta) of Bolivia. – Brittonia **58**: 229–244.

Lehnert, M. (2006c): New species and records of tree ferns (Cyatheaceae, Pteridophyta) in the northern Andes. – Organisms, Diversity & Evolution **6**: 321–322, electronic supplement. http://www.senckenberg.de/odes/06-13.htm.

LEHNERT, M. (2008): On the identification of *Cyathea pallescens* (Sodiro) Domin (Cyatheaceae): typifications, reinstatements and new descriptions of common Neotropical tree ferns. – Botanical Journal of the Linnean Society **158**: 621–649.

LELLINGER, D. B. (1984): New combinations and some new names in ferns. – American Fern Journal **74**: 56–60.

LELLINGER, D. B. (1987): The disposition of *Trichopteris* (Cyatheaceae). – American Fern Journal **77**: 90–94.

LELLINGER, D. B. (2002): A modern multilingual glossary for taxonomic pteridology. – Pteridologia **3**: 263 pp.; St. Louis (American Fern Society).

MAXON, W. R. (1909): Cyatheaceae. – North American Flora **16**: 65–89.

MAXON, W. R. (1922): Ferns new to the Cuban Flora. – Journal of the Washington Academy of Science **12**: 437–442.

MORAN, R. C. (1991): Eight new species of tree ferns (*Cyathea*, Cyatheaceae) from the American Tropics and three new combinations. – Novon **1**: 88–104.

PRESL, C. (1849): Epimeliae Botanicae, 264 pp.; Prague (Haase).

ROJAS, A. F. (2001): Nuevas especies, nombres nuevamente utilizados y nuevas distribuciones en los helechos arborescentes (Filicales: Cyatheaceae) para el neotrópico. – Revista de Biología tropical **49**: 453–466.

ROJAS, A. F. (2005): Nuevos taxa de helechos arborescentes (Filicales: Cyatheaceae) en Costa Rica. – Lankesteria **5**: 191–200.

ROSENSTOCK, E. (1913): Die von Dr. TH. HERZOG auf seiner zweiten Reise durch Bolivien in den Jahren 1910 und 1911 gesammelten Pflanzen. I. – Mededeelingen van's Rijks Herbarium, Leiden **19**: 1–25.

ROSENSTOCK, E. (1928): Filices novae a cl. Dr. O. BUCHTIEN in Bolivia collectae. VI. – Feddes Repertorium Specierum novarum Regni vegetabilis **15**: 56–64.

SMITH, A. R. (1985): Pteridophytes. – In: STEYERMARK, J. A., BARRY, P. E. & HOLST, B. K. (eds.): Flora of the Venezuelan Guayana **2**, pp. 1–334; St. Louis (Missouri Botanical Garden).

SODIRO, L. (1883): Recensio cryptogamae vasculares quitenses, 112 pp.; Quito (Typis universitatis).

SODIRO, L. (1893): Cryptogamae vasculares quitensis adiectis speciebus in aliis provinciis ditionis ecuadoriensis hactenus detectis, 656 pp.; Quito (Typis universitatis).

SODIRO, L. (1908): Sertula florae ecuadoriensis. Pteridophyta, part 2, 82 pp.; Quito (Typis Universitatis) [Reprint in Anales de la Universidad Central del Ecuador, Quito **22**: 21–30, 89–104, 161–176].

STEARN, W. T. (2004): Botanical Latin, 4th edition, 546 pp.; Portland, Oregon (Timber Press, Inc.).

STOLZE, R. G. (1974): A taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). – Fieldiana Botany **37**: 98 pp.

STOLZE, R. G. (1976): Ferns and fern allies of Guatemala. Part I: Ophioglossaceae through Cyatheaceae. – Fieldiana Botany **39**: 130 pp.

TREVISAN, V. B. A. (1851): Sopra alcuni nuovi generi, e trentadue nuove specie di Felci. – Atti del reale Istituto Veneto di Scienze, Lettere ed Arti (2) **2**: 161–168.

TRYON, R. M. (1970): The classification of the Cyatheaceae. – Contributions of the Gray Herbarium **200**: 3–50.

TRYON, R. M. (1971): The American tree ferns allied to *Sphaeropteris horrida*. – Rhodora **73**: 1–19.

TRYON, R. M. (1976): A revision of the genus *Cyathea*. – Contributions of the Gray Herbarium **206**: 19–98.

TRYON, R. M. (1986): Cyatheaceae. – In: HARLING, G. & ANDERSON, L. (eds.): Flora of Ecuador **27**: 17–56.

TRYON, R. M. & GASTONY, G. J. (1975): The biogeography of endemism in the Cyatheaceae. – Fern Gazette **11**: 73–79.

TRYON, R. M. & STOLZE, R. G. (1989): Pteridophyta of Peru. I. – Fieldiana Botany, new series **20**: 111–138.

VARESCHI, V. (1969): Helechos. – In: LASSER, T. (ed.): Flora de Venezuela I, 2 vols., 1039 pp.; Caracas (Instituto Botánico).

WAGENITZ, G. (1996): Wörterbuch der Botanik; Morphologie, Anatomie, Taxonomie; die Termini in ihrem historischen Zusammenhang, 532 pp.; Jena (Gustav Fischer).

WINDISCH, P. G. (1977): Synopsis of the genus *Sphaeropteris* with a revision of the neotropical exindusiate species. – Botanische Jahrbücher für Systematik **92**: 176–198.

WINDISCH, P. G. (1978): The systematics of the group of *Sphaeropteris hirsuta* (Cyatheaceae). – In: MAGUIRE, B. (ed.): The Botany of the Guayana Highland. – Memoirs of the New York botanical Garden **29**: 2–22.

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