



Three new species of scaly tree ferns (*Cyathea*-Cyatheaceae) from the northern Andes

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Abstract

Three species of the genus *Cyathea* (Cyatheaceae-Polypodiopsida) are described as new to science from the northern Andes: *Cyathea aemula* from southern Colombia and northern Ecuador, *C. ars* from southeastern Ecuador, and *C. guentheriana* from northeastern Ecuador. All species are illustrated and compared to their putative closest relatives.

Key words: Andean cordillera, biodiversity, Colombia, *Cyathea*, Ecuador, ferns, pteridophytes

Introduction

The small Andean republic of Ecuador holds an outstanding position in the global species count, with 15,306 native species and an estimated endemism of 27.3 % in vascular plants (Jørgensen & León-Yáñez 1999). The exceptionally high number of species compared to the small size of the country is due to its varied relief and the contact of several biogeographic units (Valencia *et al.* 1994), which are mainly caused by different precipitation regimes along the Andes (Killeen *et al.* 2007). The Andean cordillera effectively separates a western and an eastern lowland rainforest biome (Gentry 1982). Despite the relatively short distance, an exchange of species between the western and eastern Andean slopes is restricted, e.g. about 25% of the pteridophyte species found on the western side do not occur on the eastern side (Moran 1995a).

The botanical explorations of this country still yield new discoveries of unknown species, including sizeable and conspicuous plants like the scaly tree ferns of the genus *Cyathea* (Moran 1991, 1995b, León & Moran 1996, Moran & Øllgaard 1998). The checklist of Ecuador lists 51 native species of *Cyathea* (Jørgensen & León-Yáñez 1999) but several new discoveries increased the total count to 64 species in the meantime (Lehnert 2003, 2006a, 2006b, 2008, 2009).

The family Cyatheaceae contains ca. 600 species with a pantropical-southern temperate distribution (Smith *et al.* 2006). Its members differ from other families of the tree fern alliance by having not only the common pluricellular hairs, but also various types of scales in their indument (Kramer & Green 1990). The family includes the tallest living ferns, whose erect trunk-like rhizomes can reach over 20 m tall. Due to their size they are less frequently and more fragmentarily collected than other fern groups (Janssen 2006). The taxonomic status, geographical range and ecological potential of many poorly understood species are just beginning to clarify (e.g. Lehnert 2005, 2008, Moran *et al.* 2008) thanks to an increased number of long-term field explorations.

The generic subdivision of the family was long disputed (Holtum & Tryon 1977). Holtum (1963) recognized only one universal genus *Cyathea* with the two subgenera *Cyathea* and *Sphaopteris*, including several sections. Tryon (1970) recognized six genera (*Cyathea*, *Cnemidaria*, *Trichipteris*, *Alsophila*, *Nephelea*, *Sphaopteris*) based on studies focused on Neotropical species. Two of these genera, *Trichipteris*

and *Nephelea*, were based on feeble morphological characters and were soon merged in *Cyathea* (Lellinger 1987) and *Alsophila* (Conant 1983), respectively. Holttum & Edwards (1983) acknowledged the remaining four genera of Tryon's classification and treated *Cyathea*, *Cnemidaria*, and *Alsophila* as subsections of the section *Cyathea* within the subgenus *Cyathea*, which further included section *Gymnosphaera*. Phylogenetic investigations (Conant *et al.* 1995, 1996, Korall *et al.* 2006, 2007, Janssen *et al.* 2008, Moran *et al.* 2008) have helped with the interpretation of the importance of various characters that are used in the definition of genera and species. Most anatomy-based changes of the generic concepts (e.g. Lellinger 1987) were corroborated by the molecular data but some supported clades remain problematic in their taxonomic definition, e.g. the separation of the monophyletic genera *Gymnosphaera* and *Alsophila* (Korall *et al.* 2007).

The genus *Cyathea* in its strict sense (Conant & Stein 2001) includes the genera *Cnemidaria* (Stolze 1974), *Trichipteris* (Barrington 1978, Lellinger 1987) and parts of the genus *Sphaeropteris sensu* Tryon (1970; Windisch 1977, 1978, Kramer 1978, Lellinger 1984). Evidently a small group of nine paleotropical species (Holttum 1982) stands basal to the rest of the genus *Cyathea*, which further contains 184 species currently recognized in the Neotropics. This number does not yet include the eight species of the genus *Hymenophyllopsis*, which apparently are just highly specialised species of *Cyathea* (Korall *et al.* 2006, 2007). This concept of *Cyathea* includes all species of Cyatheaceae that have a differentiated petiole scale margins consisting of cells smaller and of different orientation than those of the scale body and simultaneously lack dark marginal setae. The latter can be found in the other genera in combination with (*Alsophila*, *Gymnosphaera*) or without (*Sphaeropteris*) a differentiated scale margin.

Besides their conspicuous cell wall thickening, setae can be distinguished from marginal teeth by their insertion into the supporting cell layers. Setae originate from the scale body and are each supported by one to many cells, which can be best seen in the enlarged apical setae of the genus *Alsophila* (Conant 1983). In the genus *Sphaeropteris*, the marginal setae sit directly on the scale body and can be recognized as the end points of simple parallel cell rows originating from the scale base. Opposed to this, marginal teeth, which may occur in *Cyathea*, are the end points of branching rows of cells that decrease in size. Consequently, several marginal teeth may sit on one supporting cell. This concept allows the true classification of species of *Cyathea* that previously had been erroneously placed in *Sphaeropteris*. Such species like *Cyathea poeppigii* (Hooker 1844: 43) Domin (1929: 263) have the petiole scale margins in most parts reduced to only one row of conspicuous marginal teeth that may be mistaken for setae.

The new species described here were discovered during ongoing efforts towards a complete revision of the whole genus on the morphological and molecular level. Material studied for this part came mainly from the collections of GOET, MO, QCA and UC (following: Holmgren *et al.* 1990).

The terminology in this article follows principally Lellinger (2002). However, for some special tree fern characters established terms are preferably used. These include terms for the coloration of the petiole scales and shape of the indusia. "Discordantly bicolorous" refers to petiole scales with a differentiated margin of smaller cells in which the marginal color extends into the scale body, which has a different (usually darker) color. "Concordantly bicolorous" means that the structural border between scale margin and body is iterated by the coloration. The indusia may be absent (exindusiate) or cover the sori completely (sphaeropteroid, i.e. globose) or partially, and this by covering all sides of the receptacle equally (in descending order of extension: subsphaeropteroid, urceolate, cyatheoid, meniscoid, discoid) or from only one side (hemitelioid). For the relative position of the sori between the segment margins and the midveins, the terms "marginal", "medial", and "costal" are usually used. The term "costa" means midvein but in the pteridological terminology, it is generally applied to the main axis of the pinnae. Since the traditional term "costal" is not self-explaining, it is here replaced by the general term "proximal."

Systematic treatment

Cyathea aemula Lehnert, *sp. nov.* (Figs. 1A, 2)

Species generis Cyathea exindusiata apicibus frondorum abrupte vel gradualiter terminantibus, squamis discordanter bicoloratis, paraphysisibusque longis; a Cyathea ulei paraphysisibus longioribus, furfure petiolorum albicante densiore plusque persistentiore (vs. Cyathea ulei furfure brunneo, fugaci vel absente), pinnulis fertilibus incisus plusquam medio spatio usque ad costulis (vs. non plusquam medio spatio) praestans; in pinnulis longe petiolatis similis Cyathea kalbreyeri vel Cyathea divergentem, sed ab hac in paraphysisibus longis squamisque petiolorum bicoloratis (vs. paraphysisibus brevibus squamisque concoloratis Cyathea kalbreyeri), ab illa in absentia indusiorum (vs. Cyathea divergens cum indusiis sphaeropteroideis instructa) differt.

Type:—ECUADOR: Pastaza: Mera Cantón, 2 km NW of Mera, Campamento Vacacional Evangelico Mangayacu, up the ridge behind the Campamento, 01°26'00"S, 78°07'30"W, 1350–1500 m, 29 Jul 1992, Fay & Fay 3781 (holotype UC, isotype MO).

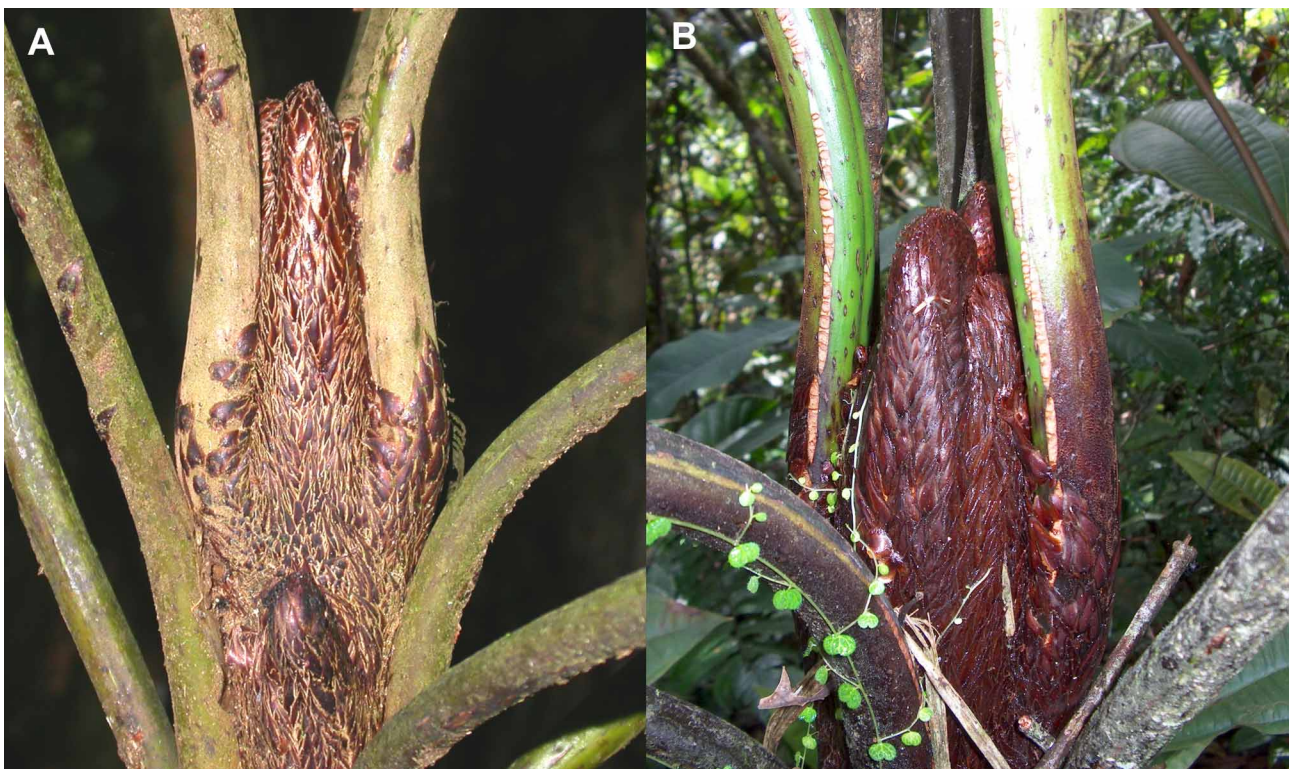


FIGURE 1. Habit of *Cyathea* species in the field. **A.** *Cyathea aemula*, trunk apex, Ecuador, Prov. Napo (Photo J. Homeier). **B.** *Cyathea ulei*, trunk apex, Ecuador, Prov. Loja (Photo M. Lehnert).

Trunks slender, to 7 m tall (but commonly smaller), straight or only basally ascending, without adventitious buds or old petioles, fronds shed cleanly; trunk apices hidden in fascicles of petioles of green fronds, consisting of two to four pseudowhorls so that the fascicles appear stretched (Fig. 1A). Fronds to 235 cm long, arching to drooping, appearing spirally arranged along the trunk (Fig. 1A). Petioles to 95 cm long, inermous to weakly muricate, stramineous to pale brown, with a line of distant, narrow whitish pneumathodes on each side, hardly seen in dried material, without adventitious pinnae at the bases; petiole scurf long persistent, a matted tomentum of small branched hairs and dissected squamules 0.2–0.4 mm long (Fig. 2C), yellowish white with brown parts, greyish white in general aspect. Petiole scales broadly lanceolate to long-ovate (Fig. 2A), 14.0–20.0 × 4.5–5.0 mm, with round to weakly cordate bases, pseudopeltately attached, tips straight, shiny auburn to dark brown, concordantly bicolorous with broad, pale brown to golden-brown,

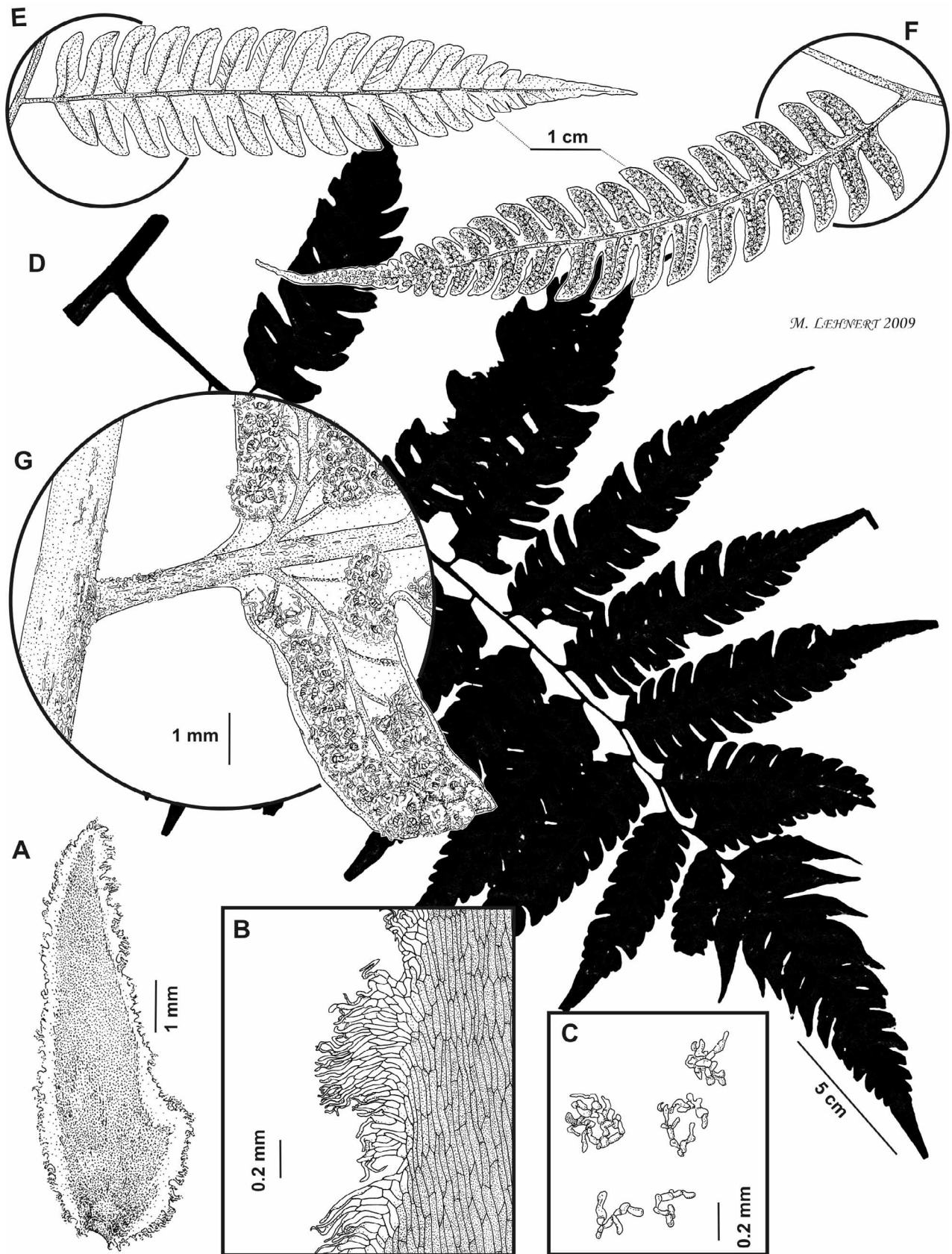


FIGURE 2. *Cyathea aemula*. **A.** Petiole scale. **B.** Detail of petiole scale margin. **C.** Petiole scurf squamules. **D.** Medial pinna. **E.** Sterile pinnule, adaxially. **F.** Fertile pinnule, abaxially. **G.** Base of fertile pinnule, abaxially. **A-E.** *Homeier et al.* 2693 (Herb. M. Lehnert); **F-G.** *Homeier et al.* 3653 (GOET).

fringed margins (Fig. 2B). Laminae 90–140 × 80–90 cm, bipinnate-pinnatifid, chartaceous, lustrous dark olive-green adaxially, not blackish when dried, olive green abaxially; apices abruptly reduced and conform or gradually reduced. Pinnae to 45 cm long, 4–5 pairs per frond, stalked to 6 cm (Fig. 2D), distally very narrowly green-alate, the distal segments decurrently adnate. Leaf axes brown on both sides, completely glabrous abaxially except for scurf remnants, hairy only adaxially on costules, costae and distal parts of rachises, hairs 1.0–1.5 mm long, tan to brown; costae smooth, 2–3 mm wide, insertions of costae into rachises swollen, each abaxially with one inconspicuous pneumathode acropically, orange-brown, elliptic, to 2 × 1 mm, and with a diffuse black spot basiscopically, at least when dried. Largest pinnules 12.0–14.0 × 2.8–3.2 cm, stalked to 14 mm, alternate, (0.6–)1.5–2.6 cm between adjacent stalks, pinnules linear-oblong to lanceolate, incised 1/2 or more towards the costules, sterile pinnules basally truncate to cuneate (Fig. 2E), fertile ones truncate to weakly cordate, tapering from beyond the middle to long-acuminate to short-attenuate tips (Fig. 2F); the brown stalks inarticulate, their bases with an orange-brown to blackish, elliptic pneumathode to 1.0 × 0.4 mm (Fig. 2G); segments to 25 × 8 mm, long-deltate to linear deltate, patent to ascending, with entire margins, tips falcate, obtuse to acute (Fig. 2G); basal segments usually opposite, the lowest ones not remote from each other, sinuses acute and narrow (1.0–1.5 mm) in sterile pinnules (Fig. 2E), wide (2.0–3.0 mm) and obtuse to acute in fertile pinnules (Fig. 2F). Veins prominent abaxially (Fig. 2G) and adaxially, ending in segment margins, basal veins connivent to sinuses; veins glabrous adaxially, abaxially glabrous except for scurfy grey-brown to brown trichomoidia and catenate hairs, these on and between the veins, also along the segment margins; sterile and fertile veins simple or forked. Sori 1.2–1.6 mm diam., inframedial to subproximal, forming a triangle pattern on each segment (Fig. 2F), on the back of simple veins or at vein forks, indusia absent, receptacles globose to ellipsoid, 0.4–0.5 mm diam.; paraphyses numerous, hyaline, white, longer than sporangia (0.8–1.0 mm) (Fig. 2G). Spores pale yellow to whitish, exospore smooth, finely porate, perispore absent.

Distribution and habitat:—Moist tropical montane forests at 1000–1560 m on the eastern Andean slopes of southern Colombia and northern Ecuador.

Etymology:—Refers to the strong similarity to several other *Cyathea* species (Latin, *aemulus* = mimicker).

Additional specimens examined (paratypes):—COLOMBIA: Putumayo: Mocoa, Corregimiento de San Antonio, Vereda Alto Campucana, finca La Mariposa, 1400 m, *Mocoa Fernández et al. 11120* (COL). ECUADOR: Napo: Hakuna-Matata private lodge, ca. 5 km W of Archidona, 1000 m, 05 Oct 2007, *Homeier et al. 2693* (QCA); Parque Nacional Sumaco-Galeras, Cordillera Galeras, 00°49.7'S, 77°32.2'W, 1560 m, 03 Apr 2008, *Homeier et al. 3653* (GOET, MO, QCA, QCNE).

Cyathea aemula has a tendency towards leaf dimorphism, which is characteristic of *Gymnosphaera* (Holtum 1963) but exceptional in *Cyathea*. The pinnule shape and the petiole indument (i.e. scurf, scales) of *Cyathea aemula* are similar to *Cyathea divergens* Kunze (1834: 100), which can be distinguished by the presence of indusia (*C. aemula* is exindusiate) and the short paraphyses (vs. long paraphyses).

The whitish to greyish scurf on leaf axes and lamina and the long paraphyses of *Cyathea aemula* are shared by *C. gibbosa* (Klotzsch 1844: 542) Domin (1929: 262) from Venezuela and Colombia. That species has more shortly stalked and generally narrower pinnules than *C. aemula* as well as concolorous shiny auburn petiole scales and laminar squamules (vs. petiole scales bicolorous and laminar squamules absent in *C. aemula*).

Cyathea kalbreyeri (Baker 1894: 129) Domin (1929: 262) has similarly strongly incised pinnules but differs from *C. aemula* in having almost concolorous auburn to orange-brown petiole scales (vs. bicolorous auburn to dark brown with broad, paler margins in *C. aemula*), none or very little scurf (vs. relatively dense and long lasting), and scandent fronds to 7 m long with 12–16 pinna pairs on average (vs. fronds to 2.35 m long with 4–5 pinna pairs).

Cyathea aemula was previously mistaken for *C. ulei* (Christ 1905: 367) Domin (1930: 108), to which it bears a striking resemblance in its habit (Figs. 1A, B). Both species grow in the understory of humid forests, and as it is often observed in *Cyathea* species growing under such conditions, they have relatively slender

trunks and fronds arranged more spirally than in pseudowhorls. This leads to a stretched appearance of the fascicle of petioles around the trunk apex compared to this condition observed in tree ferns with thicker trunks. Both species have also veins that are connivent to the sinuses between adjacent segments, relatively few, widely spaced pinnae, and a laminar dissection that appears rather coarse. *Cyathea aemula* differs from *C. ulei* in having longer paraphyses (to almost twice the length of the sporangia in *C. aemula* vs. of the same length as or weakly longer than the sporangia in *C. ulei*), more persistent and abundant, whitish petiole scurf (vs. brownish and ephemeral, usually absent), smaller, inconspicuous pneumathodes on the side of the petioles (vs. conspicuously white pneumathodes at least in fresh material) and more strongly incised fertile pinnules with obtuse to acute segments (incised more than half towards the costules vs. up to half to the costules with rounded to truncate segments). Furthermore, the veins in *C. ulei* are always simple while they may be forked in *C. aemula*. Despite the morphological similarity, preliminary analyses of chloroplast DNA sequences do not support a close affinity of both species (unpublished data).

***Cyathea ars* Lehnert, sp. nov.** (Fig. 3)

Species ex grege Cyathea platylepis, a Cyathea heliophila et Cyathea wilhelmii in squamis petiolorum valde bicoloribus (vs. squamis pallide concoloribus), a Cyathea platylepe paraphysibus longioribus indusiisque minoribus, a Cyathea serpente truncis erectis frondibusque non prostratis (vs. truncis absentibus, frondis supra vegetationem prostratis) differt.

Type—ECUADOR. Zamora-Chinchipec: Nangaritza, Cordillera de Naguipa, Cerro Colorado, ridge 8 km SSE of Nambija, 20 km ESE of Zamora, 04°07'51"S, 78°46'36"W, 2630 m, 20 Feb 2002, *Cole, Delinks & Neill* 258 (holotype UC, isotype MO).

Trunks to 1.5 m tall, otherwise unknown. Fronds to ca. 1 m long. Petioles to 20 cm long, probably more, dull brown to orange-brown, inermous, scurf persistent, white to tan, consisting of many tortuous white hairs to 2 mm long, grading into brown, subbullate squamules with few white, long, apical cilia, persistently densely scaly throughout; pneumathodes absent or not evident. Petiole scales to 16 × 5 mm, lanceolate-ovate, shiny, strongly bicolorous, discordantly so in lower parts, concordantly in upper parts of the petiole (Fig. 3A), dark castaneous with yellowish to cream-white margins; differentiated margins to 1 mm wide, fragile, lacerate to erose, with cells strongly exerted, without setae or cilia. Laminae to ca. 80 × 100 cm, bipinnate-pinnatifid to tripinnate, chartaceous, matte, dark green adaxially, blackish when dried, pale grey-green abaxially, apices gradually reduced. Rachises inermous, with many spreading ovate scales similar to petiole scales but with narrower margins; adaxially with many appressed, brown, pluricellular, uniseriate hairs 1.0(–1.5) mm long, abaxially glabrescent with white scurf like on the petioles, but whitish to brown squamules more numerous and with more white marginal cilia than those on the petioles; junctures of rachises and costae not swollen, abaxially each with one planar, brown, elliptic pneumathode to 2 × 1 mm. Pinnae to 50 cm long, stalked to 2.5 cm, inarticulate, patent to ascending (Fig. 3B), basal pinnae only half the size of medial pinnae, weakly to strongly reflexed. Costae inermous, 1.5–2.0 mm wide, dull dark brown to carnosely, short-hairy adaxially, hairs to 1 mm long, pluricellular, tan to brown, antrorsely curved, abaxially glabrescent with scurf and few dark-brown, flattish scales with undulate margins. Largest pinnules 5.0–6.5 × 1.1–1.7 cm, lanceolate to long-triangular, pinnatifid to pinnate, sessile to stalked (Fig. 3C), stalks to 5 mm, decurrently green-alate, 1.0–1.5 cm between adjacent stalks; pinnule bases truncate to weakly cordate, tips long-acute to attenuate, basal segments sometimes remote and rarely free; costules dark brown to dark carnosely, strongly prominent and ridged adaxially, with tan to brown, antrorsely curved hairs to 1 mm long, abaxially weakly prominent, with tortuous hairs to 2 mm long, tan to dark brown squamules attenuate to caudate tips and with white marginal cilia, and some ovate to almost round, pseudopeltately attached, shiny brown scales to 4 × 3 mm; costules basally without pneumathodes; segments to 9 × 3 mm, oblong, basal ones sometimes free and remote, patent to weakly ascending, straight or distally falcate, the tips obtuse to rounded, segment margins crenulate to

incisocrenate (Fig. 3C), in proximal segments usually basiscopically more strongly dissected, sinuses acute to obtuse, to 1(–1.5) mm wide, margins often still planar when dried; midveins adaxially ridged, lateral veins planar, veins adaxially glabrous or with few erect, pluricellular, uniseriate hairs and ephemeral tortuous hairs, none between the veins, abaxially with tortuous white hairs, midveins also with few brown bullate squamules to 3 mm long with white apical cilia (Fig. 3D); sterile veins forked or simple, fertile veins forked. Sori to 1.0 mm diam., subproximal, at vein forks; indusia hemitelioid (Fig. 3D), dark brown, shiny, firm, ascending, with emarginate margins, sometimes weakly bicuspidate, reaching 1/3 to 1/2 around the receptacles, covered entirely by intact sori; receptacles globose, 0.3–0.4 mm diam. (Fig. 3D), paraphyses thin, hyaline, tan, shorter than sporangia (0.2–0.3 mm). Spores not examined.

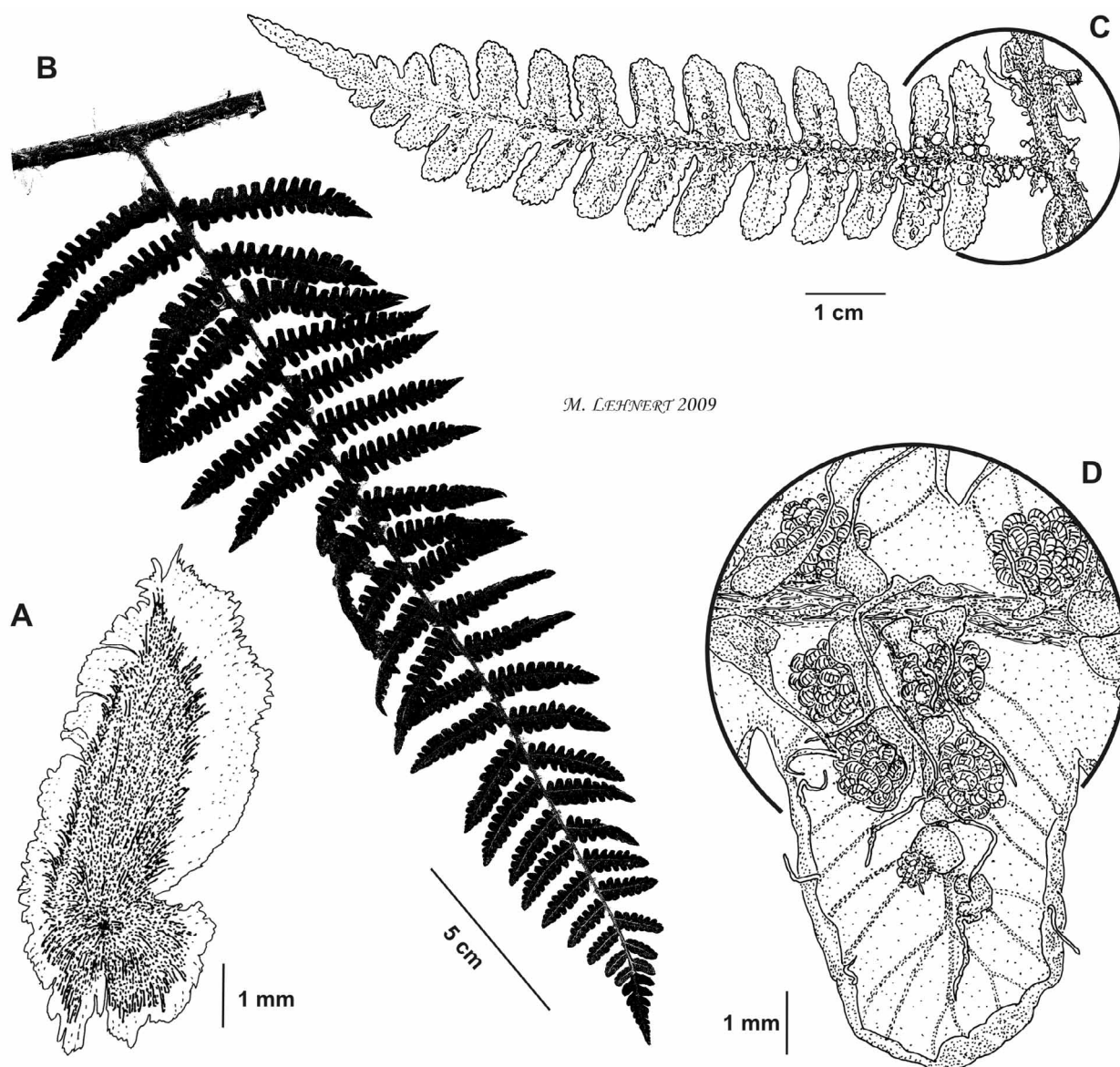


FIGURE 3. *Cyathea ars*. **A.** Petiole scale from petiole base. **B.** Medial pinna. **C.** Fertile pinnule. **D.** Fertile segment abaxially. All from *Cole et al.* 258 (**A, C–D:** UC; **B:** MO).

Distribution and habitat:—Known only from the type locality in Ecuador, Prov. Zamora-Chinchipec, where it grew open heath forest on sandstone derived soils.

Etymology:—The name refers to the artful pattern the scales create on trunks and petioles. The name is a noun in apposition.

Cyathea ars is superficially similar to *C. heliophila* Tryon (1986: 43), from which it differs in distinctly bicolorous petiole scales (vs. mainly concolorous white or with small brown basal spot in *C. heliophila*) and many concolorous brown, ovate to round scales on the leaf axes (vs. white to bicolorous, ovate-lanceolate scales).

Cyathea serpens (Tryon 1989: 126) Lehnert, *comb. nov.* (basionym: *Trichipteris serpens* Tryon), from central and southern Peru differs from *C. ars* by lacking trunks and having much longer fronds (to 7 m vs. ca. 1 m long) that scramble over adjoining vegetation or hang freely from cliffs.

Cyathea platylepis can be distinguished from *C. ars* by its concolorous brown petiole scales (margins only slightly paler than centres vs. margins white in *C. ars*) and the large indusia that arch over the sori (vs. indusia small and hidden by intact sori).

Cyathea ars is characterized by tortuous white hairs and brown scales on the leaf axes, which are also found in *C. frigida* (Karsten 1859: 61) Domin (1929: 262); that species is exindusiate and has dark brown, only weakly bicolorous petiole scales with brown margins (vs. hemitelioid indusiate and strongly bicolorous petiole scales with white margins in *C. ars*).



FIGURE 4. *Cyathea ars*, detail of upper petiole abaxially (Cole *et al.* 258, UC).

Cyathea ars occurs sympatrically with *C. heliophila* and *C. frigida*. There are several fertile specimens of putative hybrids between *C. heliophila* and *C. frigida*, coincidentally all of them from trunkless plants. Fertility in trunkless plants is known from *C. frigida* but not from *C. heliophila*. The plants in question have the appearance of a small *C. heliophila* with strongly bicolorous petiole scales that appear intermediate between the two putative parents (with the white margins inherited from one parent and the dark brown centre of the other). The main indicator for hybrid origin is, apart from intermediate morphology, the irregularly developed sporangia and the malformed spores. The single collection of *C. ars* has immature sporangia, so an investigation of aborted or malformed spores as indicator of hybrid origin is not possible. However, the abundant laminar squamules of *C. ars* with their attenuate to caudate tips and white marginal cilia are quite unique in the genus and not interpretable as an intermediate or inherited character from either putative parent. *Cyathea ars* belongs to the neotropical species referred to as the *C. multiflora* Smith (1793: 416) group (Tryon 1976). The group is held together only by the presence of hemitelioid indusia. Like all indusial characters, it is a homoplastic character that does not necessarily include all descendents of one common ancestor. A gross distinction among the species of the *C. multiflora* group can be made between those species with \pm medial to inframarginal sori and those with proximal sori. *Cyathea ars* belongs to the latter group, together with *C. platylepis* (Hooker 1861: 100) Domin (1929: 264), *C. arnecornelii* Lehnert (2003: 178), *C. heliophila*, *C.*

holdridgeana Nisman & L.D.Gómez (Gómez 1971: 168), *C. praeceps* Smith (1990: 253) and *C. wilhelmii* Domin (1929: 263). These species further agree in having inermous petioles, the clean shedding of the old petioles, lacking fascicles of petioles around the trunk apex, and having relatively broad, ovate lanceolate scales with short-acute apices on the trunk and petioles. The collectors did not describe the habit of *Cyathea ars* (a picture of the plant was taken but was not available for this study) but it is presumably concordant with its supposed closest relatives. The group with medial to inframarginal sori, to which *C. multiflora* and *C. andina* (Karsten 1856: 452) Domin (1929: 263) belong, has muricate to aculeate petioles, do not shed the old petioles cleanly (bases persist), trunk apices hidden in a fascicle of petioles, and petiole scales with long acuminate to attenuate apices (breadth of scale body varies from narrowly to broadly lanceolate).

***Cyathea guentheriana* Lehnert, sp. nov.** (Figs. 5, 6)

Species affinitate Cyathea crenatae sed in colore atrociore petiolorum (atropurpureis vs. brunneis) indusiorumque (pallide brunneis vs. albidis), pinnis ascendentibus (vs. pinnis patentibus), absentia squamarum bicolorium indumento laminarum praestans; ab Cyathea squamipede et Cyathea meridensi in pinnis pinnulisque sessilibus (vs. pinnis pinnulisque maximis quidem paulo petiolulatis), marginibus segmentorum valde crenatis vel incisoserratis (vs. marginis crenulatis subintegribusque) differt; dissectione laminarum simile Cyathea xenoxyla sed ab ea soris majoribus (1.0–1.2 mm vs. 0.8–1.0 mm in Cyathea xenoxyla), squamis persistentioribus nigribus (vs. squamis brunneis deciduis), petiolis purpureis parce nitentibus (vs. petiolis viridibus vel stramineis usque brunneis opacis), fasciculo petiolorum apice truncorum (vs. fasciculo absente), truncisque crassioribus gemmis adventitiis carentibus (usque 12 cm vs. promedio 5–8 cm diametro, gemmis presentibus) differt.

Type:—ECUADOR. Napo: Quijos Cantón, Reserva Ecológica Antisana, Río Aliso, 8 km SW of Cosanga, 00°35'S, 77°57'W, 2530 m, 12 Nov 1998, Vargas H. *et al.* 2949 (holotype UC, isotype MO)



FIGURE 5. *Cyathea guentheriana*, trunk apex, Ecuador, Prov. Napo (Photo J. Homeier).

Trunks to 6 m tall, to 12 cm diam., without persisting old petiole bases, cortex dark brown to blackish, apices hidden in fascicles of petioles (Fig. 5); without adventitious buds. Fronds to 300 cm long, patent to arching. Petioles 35–100 cm long, proximal parts weakly to strongly spiny, with spines 3–5 mm long, dark brown to atropurpureous, weakly shiny, without adventitious pinnae at the petiole bases, with a discontinuous row of narrowly elliptic pneumathodes to $9 \times 1\text{--}2$ mm, dark orange-brown in dried material; petiole scurf dense, long-lasting, concolorous whitish to tan or pale brown, consisting of small, erect to appressed, ovate to round squamules 0.2–0.5(–1.0) mm long, with strongly crested to fimbriate margins, without dark marginal teeth, only abraded in inermous petiole parts (Fig. 6A). Petiole scales lanceolate, $20.0\text{--}32.0 \times (3.0\text{--})4.5\text{--}5.5$ mm, tips straight to falcate, undulate, concordantly bicolorous, bases cordate, pseudopeltately attached (Fig. 6B), very shiny, concordantly bicolorous but differentiated margins very narrow and thus at first appearing concolorous, the black (deeply atropurpureous in backlight) centre sharply set against the golden brown

margins. Laminae to 200 × 100 cm, bipinnate-pinnatifid, chartaceous, broadest at the middle, dark green adaxially, matte, blackish to plumbeous when dried, dull greyish green abaxially, apices gradually reduced. Rachises dark-purpureous to brown, usually darker adaxially, glabrous or weakly hairy in distal parts; sometimes with remnants of tan to brown scurf, especially in the axils to the costae, consisting of squamules similar to those on the petioles. Pinnae to 55 cm long, 12–15 pairs per frond, inarticulate, ascending, sessile or short-stalked to 0.5 cm, distally not green-alate, the distal segments not decurrently adnate. Costae inermous to muricate, 3–4 mm wide, dark stramineous to purpureous, adaxially often darker, adaxially densely hairy, hairs 0.5–1.0 mm long, tan to brown, antrorsely curved to appressed, abaxially glabrous; junctures of costae and rachises abaxially weakly swollen, each with a planar pneumathode to 4 × 1–2 mm, brown, inconspicuous. Largest pinnules 8.0–9.5 × 1.7–2.0 cm, sessile or stalked to 1 mm, alternate, inarticulate, 2.0–2.2 cm between adjacent stalks, linear-oblong, cuneate to rounded at bases, tapering from beyond the middle to attenuate tips with serrate to crenulate margins (Fig. 6C); costules dark stramineous to dark brown, adaxially moderately hairy with appressed tan to brown hairs 0.5–1.0 mm long, abaxially glabrous, rarely with remnants of whitish to tan scurf or with some single erect white hairs to 1 mm long in distal parts; costules basally without pneumathodes; segments to 12.0 × 2.5 mm, linear-oblong, ascending, distally straight to weakly falcate, tips rounded to obtuse, margins deeply crenate to inciso-serrate; basal segments alternate, rarely remote from each other, if so then connected by laminar tissue, sinuses 1–2 mm wide, obtuse; sterile and fertile pinnules not different. Veins glabrous adaxially except for some white to tan, erect pluricellular hairs to 1 mm long on the midveins; abaxially glabrous except for single hairs to 1 mm long sometimes on the midveins; sterile veins forked or simple, fertile veins forked. Sori 1.0–1.2 mm diam., proximal, indusia subsphaeropteroid to sphaeropteroid, without umbo, tan, translucent, fragmenting to a shallow cup or disc (Fig. 6D); receptacles globose, 0.3–0.5 mm diam., paraphyses many, hyaline, tan, shorter than sporangia (0.3–0.4 mm). Spores pale yellow.

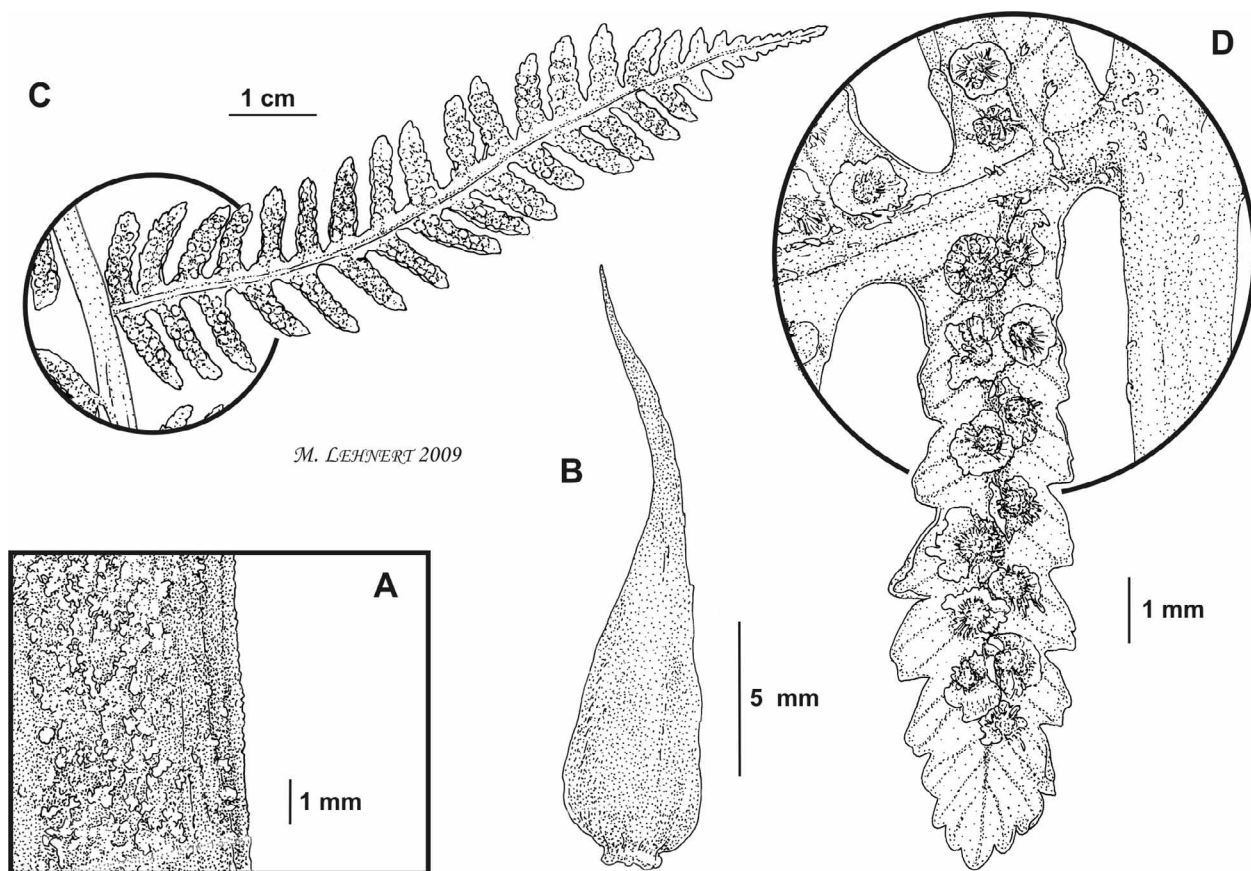


FIGURE 6. *Cyathea guentheriana*. A. Petiole scurf. B. Petiole scale. C. Pinnule, abaxially. D. Fertile segment, abaxially. All from Vargas H. et al. 2949 (UC).

Distribution and habitat:—Known only from eastern Ecuador, Prov. Napo, growing at 1920–2530 m in perhumid montane rainforest.

Etymology:—Named after Rebecca Guenther, UC Berkeley, in acknowledgement of her support to tree fern studies.

Additional specimens examined (paratypes):—ECUADOR. Napo: Parque Nacional Sumaco-Galeras, southern slope of Sumaco volcano, 00°35'S, 77°35'W, 1920 m, 06 Apr 2006, *Homeier et al.* 2243 (GOET); area of the Yanayacu Biological Station, 5 km SW of Cosanga, 00°36'S, 77°53'W, 2080 m, 21 Oct 2007, *Homeier et al.* 3093 (GOET, QCA); Quijos Canton, Reserva Ecologica Antisana, Cordillera de Guacamayos, proposed ARCO oil pipeline route, 00°38'N, 77°51'W, 2000 m, 1 Oct 1997, *Neill et al.* 10790 (MO, UC); Tena Cantón, P.N. Llanganates, trail Salcedo-Tena, Km 74, shore of Río Mulatos, 01°01'S, 78°12'W, 2020 m, 10 Sep 1998, *Vargas H. et al.* 2179 (MO, UC).

With its dark coloration, *Cyathea guentheriana* resembles other species of *Cyathea* with sphaeropteroid indusia, like the common *C. squamipes* Karsten (1869: 184) and *C. meridensis* Karsten (1861: 199). These can be easily distinguished by their dark brown to castaneous petiole scurf (in *C. guentheriana* whitish to pale brown). They further differ from *C. guentheriana* in the shape of the pinnules and segment margins: In *C. squamipes* and *C. meridensis*, the largest pinnules are lanceolate to long-triangular with truncate to weakly cordate bases and the segment margins are crenulate; they are linear-oblong with cuneate to rounded bases and have deeply crenate to incisoserrate margins in *C. guentheriana*. The pinnae and pinnules of *C. guentheriana* are usually sessile or very short-stalked; in *C. squamipes*, the largest pinnules may be stalked to 0.5 cm, in *C. meridensis* even more than 1 cm. The whole fronds of *C. guentheriana* seem to be planar and held more or less patent to weakly arching due to the stiff leaf axes, with markedly straight, ascending costae. In *C. squamipes* and *C. meridensis*, the fronds are arching to drooping with mostly perpendicular pinnae.

Regarding the fronds, *C. guentheriana* is best described as *C. xenoxyla* Lehnert (2003: 175) but with a darker hue. The laminar dissection and the spatial orientation of the pinnae are identical but the petiole scales of *C. guentheriana* are very shiny, almost concolorous black (vs. weakly shiny dark brown to castaneous with usually paler margins in *C. xenoxyla*) and the leaf axes are dark brown to purpureous and weakly shiny (vs. green in fresh material, stramineous to brown in dried material). *Cyathea xenoxyla* differs significantly from *C. guentheriana* by having almost no persistent petiole scales (only present in crosiers, rarely on young petioles vs. many persistent scales on the petiole bases in *C. guentheriana*), lacking a fascicle of petioles at the trunk apex (vs. fascicle present), having smaller sori (0.8–1.0 mm vs. 1.0–1.2 mm diameter), and having thinner trunks with adventitious buds (mostly 5–8 cm vs. to 12 cm diam., lacking adventitious buds).

The deeply crenate segment margins, the kind of scurf squamules, the fragile indusia, and the colour and shape of the petiole scales of *C. guentheriana* agree well with the condition of these characters found in *C. crenata* (Sodiño 1883: 18) Christ (1897: 323) (see: Lehnert 2009). The most obvious differences to that species are the darker colour of petioles, rachises, and laminar tissue and the stiffer, notably ascending pinnae. Due to the divergent colour of the petiolar cortex (atropurpureous in *C. guentheriana* vs. dull brown in *C. crenata*), the petiole scurf appears to be lighter coloured in *C. guentheriana*, but actually has the same colour variation in both species. Furthermore, *C. guentheriana* has no or only scattered hairs to 1 mm long on the costules abaxially while *C. crenata* is here often short-pubescent with hairs to 0.6 mm long. The laminar indument of *C. crenata* includes larger bicolorous flat scales to 5 mm long with dark centres besides smaller, concolorous whitish to pale brown squamules, whereas *C. guentheriana* lacks bicolorous scales on the laminae. The indusia of both species are very fragile but differ in colour (matte white in *C. crenata* vs. tan in *C. guentheriana*) and consistency (opaque, sometimes developed as mucose film vs. translucent, never a mucose film). Differences in colour and indument are often dependent on growing conditions, especially the exposure to direct sunlight. However, the colour of petioles and leaf axes of *C. crenata* remains comparatively pale no matter if the species grows in either sun or shade. *Cyathea guentheriana* has been found only in the shaded understory so far, thus growing under conditions unlikely to add a reddish tone to a relatively pale coloration as it is found in sun-exposed *C. crenata*.

Despite the apparent mixture of characters typical of several common species in *Cyathea guentheriana*, there are no indications of a hybrid origin of this species. Sporangia and spores are well formed and of equal size, indicating a regular development involving matching chromosome pairs.

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