

On the identification of *Cyathea pallescens* (Sodirot) Domin (Cyatheaceae): typifications, reinstatements and new descriptions of common Neotropical tree ferns

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Based on studies of type material collected by Sodiro, several Andean tree fern species formerly united in *Cyathea pallescens* (Sodirot) Domin are here distinguished: *C. pallescens* s.s. is an exindusiate species synonymous with *C. halonata* R.C.Moran & B.Øllgaard and is restricted to the western slopes of the Cordillera Occidental in southern Colombia and northern Ecuador. Reinstated species are *C. brachypoda* Sodiro, *C. tungurahuae* Sodiro and *C. cystolepis* Sodiro with var. *cystolepis*, var. ***boreopallescens*** Lehnert var. nov. and var. ***leonis*** Lehnert var. nov. from the northern Andes; ***Cyathea austropallescens*** Lehnert is newly described from the central Andes. New descriptions of all species and illustrations of important characters are given and several lectotypifications are made. Added in shorter descriptions for comparison are *C. atahuallpa* (R.M.Tryon) D.B.Lellinger, *C. bettiniae* Lehnert, *C. corallifera* Sodiro, *C. dintelmannii* Lehnert, *C. divergens* (Baker) Domin, *C. simplex* R.M.Tryon, *C. straminea* H.Karst. and *C. ruiziana* Klotzsch (= *C. boliviana* R.M.Tryon). © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 621–649.

ADDITIONAL KEYWORDS: Andes – *Cyathea austropallescens* – *C. brachypoda* – *C. cystolepis* – *C. halonata* – *C. ruiziana* – *C. tungurahuae* – exindusiate.

INTRODUCTION

Among the most important Neotropical pteridophyte specimens are those collected by the Italian born Padre Luis (alias Luigi, Aloysio) Sodiro (1836–1909). He was the first Ecuadorian botanist who took a special interest in cryptogams; numerous diligent descriptions are based on his extensive collections. A drawback of his work is the maintenance of his collection. He did not use collection numbers, so the alignment of description and corresponding specimen has to rely on the citation of the locality in his publications on the Ecuadorian cryptogams (Sodiro, 1883, 1893, 1908). This information has not necessarily been transferred exactly when a label was copied; a perfect match of book and label is rare.

Also, the Sodiro collection is dispersed around the world today, from Berkeley to Budapest. After

Sodiro's death, major parts were sold to the Instituto Darwinion, Argentina (SI). The rest is divided among several herbaria in Quito, namely the Herbario Universidad Central (Q), Herbario Padre Luis Sodiro (QPLS) and Herbario Nacional del Ecuador (QCNE), as well as the Muséum National d'Histoire Naturelle in Paris (P) and other European herbaria. Because of the easier access to European and North American researchers, the Parisian samples have often been chosen as type material or as authentic material for reference.

In the following I correct the typification of *Cyathea pallescens* (Sodirot) Domin based on the results of my studies of Sodiro's collections from the above-mentioned herbaria. Much of the material was not included in the previous studies on the genus *Cyathea* (Tryon, 1976). An increased number of original specimens allows me to designate several lectotypes. In the course of my investigations, it became clear that many of the sphaeropteroid indusiate *Cyathea* species

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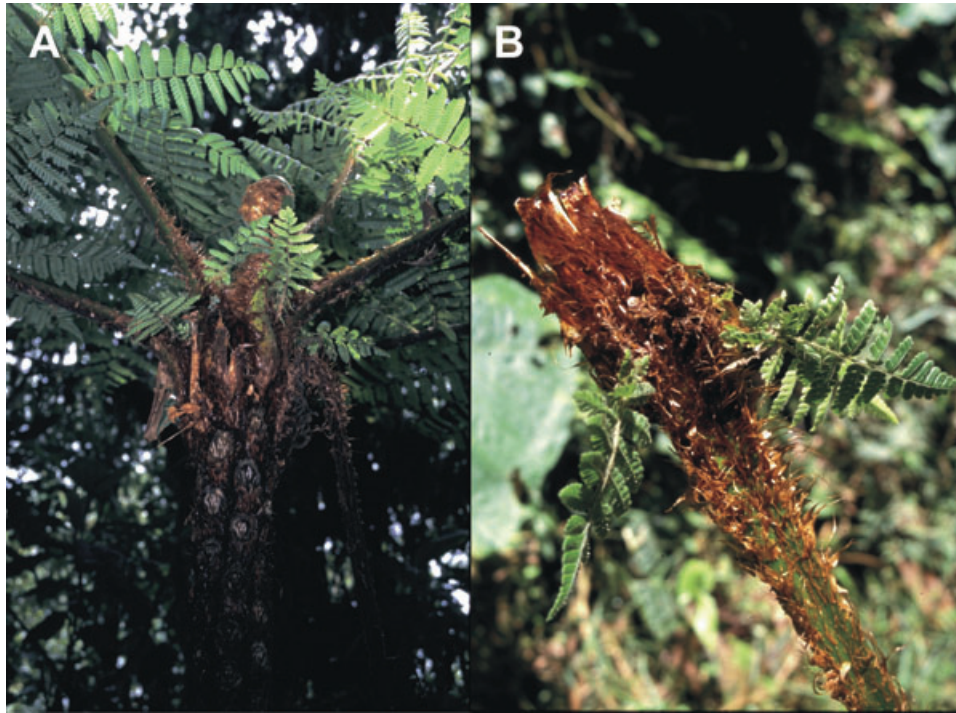


Figure 1. *Cyathea pallescens*. A, trunk apex. B, petiole base with adventitious pinnae. Photo M. Lehnert (*Lehnert 963*, Ecuador, Prov. Pichincha).

treated by Tryon (1976, 1986; Tryon & Stolze, 1989) need to be circumscribed differently in order to separate the species properly. This is especially the case between the groups of *C. pallescens*, *C. divergens* Kunze, *C. caracasana* (Klotzsch) Domin and *C. fulva* (M. Mart. & Galeotti) Fée sensu Tryon (Tryon, 1976). In this treatment, the number of taxa has been restricted to the synonyms of *C. pallescens* as given by Tryon (1976) as well as the true allies of what has previously been recognized as that species, i.e. all sphaeropteroid indusiate *Cyathea* with whitish petiole scurf and with white marginate to completely white petiole scales. The other groups will be dealt with in forthcoming publications. However, I had to include them in the provided preliminary key because of the heterogeneity of the taxa treated here in detail.

The collections of the herbaria AAU, B, BP, COL, K, LPB, MO, NY, P, Q, QCA, QCNE, QPLS, S, SI, UC and US were searched for types of Cyatheaceae and matching specimens. Many collections were made personally in Ecuador, Peru and Bolivia during my PhD thesis; specimens are mainly deposited in the herbaria GOET, LOJA, LPB, QCA, UC and USM. The original works of Sodiro were kindly provided by Hugo Navarrete (QCA), Dave Barrington (VT) and David S. Conant (LSC). The generic system used here is that of Lellinger (1987); the morphological terms

follow Tryon (1970, 1976). Herbarium acronyms follow Holmgren, Holmgren & Barnett (1990).

TAXONOMIC TREATMENT

1. *CYATHEA PALLESCENS* (SODIRO) DOMIN (FIG. 1)

Pteridophyta 263 (1929). *Alsophila pallescens* Sodiro, Rec. Crypt. Vasc. Quit. 20 (1883). *Type*: Ecuador. Pichincha: 'Bosques de Nanegal,' Sodiro s.n. [lectotype: Q!, here designated; isolectotypes: P!, GH (photo P), UC!].

Cyathea halonata R.C.Moran & B.Øllgaard, Nord. J. Bot. 18: 431–434 (1998). *Type*: Ecuador. Pichincha: Estación Biológica Río Gualajito, in Quebrada Las Palmeras, 59 km along road Chillo Gallo–Alluriquin, 00°14'S, 78°47'W, 1800–2000 m, 30.xi.1991 to 1.xii.1991, Øllgaard 99946 (holotype: QCA!; isotypes: AAU!, QCNE!).

Trunks to 4 m high, 10(–12) cm diameter, without old petiole bases or adventitious buds, appearing ruddy as a result of often long persisting spreading scales (Fig. 1A); frond scars round to weakly elliptic, crowded (Fig. 1A), weakly prominent, with an arch of vermilion pneumathodes below them; trunk apices hidden in fascicles of the youngest petioles (Fig. 1A). *Petiole* bases sometimes with 1–2 pairs of small pinnae (Fig. 1B). *Petiole scales* lanceolate, concolourous brown

PRELIMINARY KEY TO *CYATHEA* WITH BIPINNATE–PINNATIFID OR MORE COMPLEX LAMINAE FROM CONTINENTAL SOUTH AMERICA

1. Sori exindusiate.....2
- 1'. Sori indusiate.....3
2. Petioles with adventitious pinnae near the bases.....1. *C. pallescens*
- 2'. Petioles without adventitious pinnae.....(various species, see Lellinger, 1984, 1987 and references therein)
3. Indusia hemitelioid to cyatheoid.....(various species, see Tryon, 1976; Lellinger, 1984 and references therein)
- 3'. Indusia sphaeropteroid to subsphaeropteroid.....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; petioles scales almost concolourous dark brown to castaneous to strongly bicolourous with bright orange margins (in the latter case sometimes together with almost concolourous orange scales); petioles usually inermous, never with adventitious pinnae; mature spores pale brown.....*C. lechleri* group
- 4'. Petiole scurf well developed, components 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 concolourous orange–brown or with distinct white margins; petioles often strongly aculeate, sometimes with adventitious pinnae; mature spores pale to dark yellow.....5
5. Scurf a dense matted tomentum of greyish to white, branched tortuous hairs and strongly dissected squamules, only removable in clusters or larger flakes.....6
- 5'. 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.....7
6. Petioles weakly to strongly aculeate, regularly with 1–2 pairs of adventitious pinnae; petiole scales concolourous to bicolourous dark brown with paler brown narrow margins.....*C. frondosa*
- 6'. Petioles inermous, without adventitious pinnae; petiole scales bicolourous dark brown with wide greyish margins.....*C. moranii*
7. Petiole scurf brown, orange–brown, atropurpureous or castaneous, never white or bicolourous, either pulverulent or consisting of erect squamules of various sizes, never with long marginal cilia or short darkened cilia/teeth; petiole scales concolourous brown to dark brown, orange–brown or castaneous, if bicolourous then margins pale brown, orange–brown or yellowish, never purely white.....8
- 7'. Petiole scurf pale brown, tan, stramineous, cream, ivory or white, consisting of distinct erect, round to lanceolate squamules, sometimes with long marginal cilia or short darkened teeth, if squamules bicolourous then with long, often contorted, fragile whitish cilia and the pale brown (to brown) centre appressed to the petiole; petiole scales concolourous white or bicolourous with tan to white, never orange–brown margins.....9
8. Petiole scurf consisting of erect squamules of various sizes, usually cristate, brown to dark orange–brown or atropurpureous; laminae glabrous to densely hairy with pluricellular hairs to 2 mm long.....*C. fulva* group
- 8'. Petiole scurf pulverulent, consisting of fine lanceolate squamules, either dissected or with fimbriate margins, dark brown to castaneous; laminae glabrous to sparsely hairy with pluricellular hairs less than 1 mm long.*xenoxyla* group, *caracasana* group p.p.
9. Trunks to 4 cm diameter, fertile plants less than 2 m tall.....10
- 9'. Trunks 7–25 cm diameter (mostly 10–20 cm diameter), fertile plants usually 2 m or taller.....11
10. 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.....7. *C. bettinae*
- 10'. Petiole scurf well developed, long lasting in mature material; petiole scales narrowly lanceolate to ovate–lanceolate, discordantly to concordantly bicolourous brown to dark brown with tan to whitish margins, distal scales broader and lighter in colour than the basal ones; Guyana Highlands.....12. *C. simplex*
11. Petiole scales concolourous white, cream, stramineous or tan, without continuous central streak.....12
- 11'. Petioles scales at least at petiole bases bicolourous with continuous central streak, sometimes almost concolourous brown to dark brown or blackish.....13
12. Petiole scales relatively thick, firm, elastic; petiole scales and scurf squamules lacking long marginal cilia, but often with brown to dark brown marginal teeth.....13. *C. straminea*
- 12'. Petiole scales thin, papyraceous, flexuous; petiole scales and scurf squamules without brown marginal teeth but with long marginal cilia not differently coloured than the rest of the scale.....6. *C. atahuallpa*
13. Laminae indumenta with linear–lanceolate squamules and small scales, both with fimbriate to ciliate margins and often transient with branched hairs, the small scales concolourous, usually golden brown to orange–brown.....*C. caracasana* group p.p.

- 13'. Laminal indumenta without linear–lanceolate squamules that are transient with branched hairs (which may be present), usually with ovate to lanceolate squamules and small scales, white, tan or dark brown, the flat squamules often bicolourous or with dark marginal teeth, never golden brown to orange–brown. 14
14. Petiole scurf consisting of pale brown to tan, appressed to ascending small squamules with fimbriate to ciliate margins, relatively sparse, never transient with the larger petiole scales or with dark marginal teeth. 15
- 14'. Petiole scurf consisting of erect, stramineous, cream or white lanceolate squamules, often transient with the larger petiole scales and/or with dark marginal teeth. 18
15. Petiole scurf consisting of small, isodiametric squamules with spreading marginal cilia (appearing like snowflakes or cottonballs). 16
- 15'. Petiole scurf consisting of small flat, round to ovate–lanceolate squamules with paler marginal cilia, these not spreading. 17
16. Laminal indumenta 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. 5. *C. tungurahuae*
- 16'. Laminal indumenta 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. 4. *C. cystolepis*
17. Petiole scales dark brown, margins usually narrow; hairs, if present, more abundant abaxially than adaxially; laminal indumenta with bullate squamules and white tortuous hairs; petiole bases often with adventitious pinnae. 3. *C. brachypoda*
- 17'. Petioles scales brown to pale brown with wide white margins; hairs, if present, more abundant adaxially or equally frequent on both laminal surfaces; laminal indumenta without bullate squamules or white tortuous hairs; petiole bases never with adventitious pinnae. 2. *C. austropallescens* sp. nov.
18. Petiole scurf diffuse, petiolar cortex visible between petiole scales; petiole scales with relatively firm, largely persisting margins; fronds sometimes with dark fungal infection visible as black spot between veins. 19
- 18'. Petiole scurf dense, obscuring petiolar cortex between petiole scales; petiole scales with brittle, fragmenting margins; laminae without black spots between the veins. 20
19. Scurf squamules without dark marginal teeth but usually with cropped tips; petiole scales concordantly bicolourous 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. 9. *C. dintelmannii*
- 19'. Scurf squamules often with dark marginal teeth, petiole scales only pale brown to brown, discordantly bicolourous; laminae without black spots between the veins. 13. *C. straminea*
20. Largest pinnules notably stalked, stalk usually longer than width of basal segment; laminal indumenta 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. 10. *C. divergens*
- 20'. Largest pinnules sessile to subsessile, stalk length not reaching width of basal segment; laminal indumenta not appearing concolorous brown, either white or bicolourous; indusia light brown to colourless, persisting to ephemeral. 21
21. Pinnules to 9.5–12 × (0.8–)1.2–1.7(–2) cm, mostly linear with acute tips; laminal indumenta consisting of strongly bicolourous 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. 11. *C. ruiziana*
- 21'. Pinnules to 12–16 × (1.2–)2.5–4.5 cm, mostly triangular with attenuate tips; laminal indumenta fine, mainly white dissected squamules and trichomidia, sometimes 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 weakly shiny, tan to white, transparent, fragile, often ephemeral. 8. *C. corallifera*

to orange–brown or weakly bicolourous with the margins somewhat lighter. *Laminae* short–pubescent on both sides, on and between the veins. *Sori* costal, indusia absent, paraphyses shorter than sporangia.

For full description see Moran & Øllgaard (1998).

Distribution and habitat: In moist montane forests of the western Andean slope at 1550–2000 m. Most

collections were made near Mindo and in the Maquipucuna Reserve, Ecuador, Prov. Pichincha, where the species occurs in small numbers; one collection is from southern Colombia, Prov. Nariño. Thus, *C. pallescens* seems to be small ranging and genuinely rare, with less than a dozen gatherings over the last century in a relatively well-searched area.

Additional specimens examined: COLOMBIA. NARIÑO: Reserva Natural La Planada, 01°05'N, 77°25'W, 1800 m, 23.v.1994, *Bittner 2278* (MO). ECUADOR. CARCHI: Cerro Golondrinas, N-facing slope on S-side of upper Río Blanco valley, 00°52'N, 78°11'W, 1750–1800 m, 6.ii.1993, *Boyle & Boyle 1466* (MO, QCNE). PICHINCHA: Estación Biológica Gualajito, in Quebrada 'Las Palmeras,' 59 km along road Chillogallo–Alluriquin, 00°14'S, 78°49'W, 1860 m, 1.iv.1995 to 5.iv.1995, *Ankersen & Kragelund 44* (AAU, QCA); Maquipucuna, 5 km E of Nanegal, 00°07'N, 78°37'W, 1550 m, 11.ii.1991, *Gentry & Valencia 73245* (MO); Mindo Biological Station, 00°04.7'S, 78°43.9'W, 1550 m, 12.x.2002, *Lehnert 963* (GOET, QCA, UC); Santa Rosa, 18 km S of Nanegalito, 00°00'50"S, 78°29'10"W, 1900–2000 m, 1995, *Navarrete 820* (AAU, QCA); Estación Biológica Gualajito, in Quebrada 'Las Palmeras,' 59 km along road Chillogallo–Alluriquin, 00°14'S, 78°47'W, 1800–2000 m, 30.xi.1991 to 1.xii.1991, *Øllgaard 99946* (AAU, QCA); along new road Nanegal–Mindó, 1600–1800 m, 3.iii.1994, *van der Werff et al. 13400* (AAU, MO).

Notes: The misunderstanding of *C. pallescens* is based on a labelling error of a specimen at P, which Tryon (1976) mistook for the type of this species. That specimen, however, belongs to *Cyathea tungurahuae*. Its indusiate sori, firm, glabrous lamina and strongly aculeate petiole are in conflict with Sodiro's description, which explicitly states that the petioles are sparsely muricate, the laminae are membranaceous and pubescent and the sori are exindusiate. The last character must have received much attention by Sodiro because it was the distinguishing character in the contemporary generic system of the Cyatheaceae for the genus *Alsophila*, in which he placed his new species. Especially in later descriptions, Sodiro displays great scrutiny in the description of indusia, receptacles and paraphyses. However, Tryon evidently trusted more the specimen label in Sodiro's handwriting and must have believed in a misinterpretation by Sodiro.

During my stays in Quito, I took the opportunity to visit the herbaria Q and QPLS, which have been neglected by taxonomists in the past. The erratic opening hours, a low number of specimens and the bad maintenance of the collections gave the prospect of only wasting time there. With improved maintenance and easier access to the institutions, I quickly found several specimens that can be addressed as types of Sodiro's species, of which Tryon was unaware. Among them was a specimen of *C. pallescens* at Q and, although it lacked petiole material, it clearly agreed with the diagnosis of the species. Later, I found another specimen of equal quality at UC. Both

have identical labels in Sodiro's handwriting, the information on which matches the details on locality and date given in the description. When I looked for Tryon's reference specimen at P, I also found there a pinna of the real *C. pallescens*, which Tryon did not see (at least it is not annotated) and a petiole of *C. conjugata* (Hook.) Domin under the same number and with an identical label as the specimen of *C. tungurahuae*. This indicates that the specimens and labels of the Parisian Sodiro collections must have been mixed up during the transfer from Ecuador, or during the incorporation in P, and excludes the possibility of an originally mixed collection.

Cyathea pallescens sensu Sodiro (Sodiro, 1883) and *C. tungurahuae* are easily distinguished as the first species is exindusiate, has concolourous orange-brown scales, inconspicuous scurf of small brown squamules and trichomidia and a strong pubescence on both sides of the lamina and leaf axes; the latter species is indusiate, has bicolourous brown scales with white margins, conspicuous scurf of whitish, strongly dissected squamules and glabrous axes and veins, except for evanescent scurf and some scattered hairs on the veins abaxially.

Because of Tryon's misapplication of the name, the true *C. pallescens* (Sodiro) Domin was newly described as *C. halonata* R.C.Moran & B.Øllgaard (1998). The most remarkable feature of that species was the presence of small pinnae at the petiole bases that form a halo around the trunk apex. Sodiro did not mention such a structure in his description (Sodiro, 1883), but it is known from species like *Cyathea suprastrigosa* (Christ) Maxon (Tryon, 1976), *C. brachypoda* Sodiro (M. Lehnert, this publication) and *C. brevistipes* R.C.Moran (M. Lehnert, pers. observ.) that these basal pinnae are sometimes missing. Apparently Sodiro had the bad luck to find only plants without basal pinnae, if not only one: He noted that the species occurs near Nanegal, Prov. Pichincha and appears to be rare. However, I have seen about six plants of *C. pallescens* in the vicinity of the type locality and all had adventitious basal pinnae. Among the exindusiate *Cyathea* species, these aplebioid pinnae of *C. pallescens* are unique and distinguish it from species with similarly coloured petiole scales [e.g. *C. phalerata* (Mart.) Mart., *C. mucilagina* R. C. Moran].

Cyathea pallescens can be confused with species of the *C. fulva* group sensu Tryon (Tryon, 1976) because of the similar petiole scales and pubescence of the fronds; one of them, *C. suprastrigosa*, commonly has adventitious pinnae too. However, the whole group has sphaeropteroid indusia and none of the species occurs in the small range of the exindusiate *C. pallescens*. *Cyathea delgadii* Sternb., the most widely distributed species of the *C. fulva* group, can grow

from sea level to 2000 m, but has not been found above 800 m on the western Andean slope and hence is clearly separated from *C. pallescens*, which occurs here at 1550–2000 m. I cannot rule out that *C. pallescens* indeed belongs to the *C. fulva* group sensu Tryon (Tryon, 1976). Comparative field studies revealed that many *Cyathea* species are nearly identical except for the presence or absence of indusia and are undoubtedly closely related, like *C. concordia* B. León & R. C. Moran and *C. palaciosii* R. C. Moran (León & Moran, 1996) or *C. brucei* Lehnert and *C. haughtii* (Maxon) R. M. Tryon (Lehnert, 2006b).

2. *CYATHEA AUSTROPALLESSENS* LEHNERT SP. NOV.

(FIG. 2)

Type: Bolivia. La Paz: Prov. Nor Yungas, trocha al Valle de Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'N, 3250 m, 11.ix.1997, Kessler *et al.* 11832 (holotype: LPB!; isotypes: GOET!, UC!).

A *Cyathea cystolepis* Sodiro var. *cystolepis* furfure pallide brunneo (vs. albido), squamis laminarum brunneis atrobrunneisque (vs. albis usque pallide brunneis), pilis regulariter creberioribus pagina adaxiale (vs. creberioribus pagina abaxiale vel neutra), absentia squamarum bullatarum (vs. squamis bullatis frequentibus) differt.

Etymology: The name refers to the southern distribution (Latin *australis*, *austro-* = south) of this species in respect to the other species with which it had been included in *C. pallescens* (Sodiro) Domin.

Trunks to 6–(10) m high, to 15–20 cm diameter, without persistent petiole bases when old, densely covered with them when young (less than 2 m high) and then to 25 cm diameter; trunk apices hidden in fascicles of the petioles; frond scars broadly ovate, grey–brown to blackish brown like the adjacent cortex, with an arch of small round pneumathodes below them; adventitious buds usually lacking, but multiple lateral sprouting possible after injury or loss of the apex. *Fronde*s to 300 cm long, patent to slightly erect, weakly arching. *Petioles* 30–100 cm long, muricate to spiny, brown, rarely blackish basally, often stramineous distally; scurf scattered, persistent, consisting of appressed to ascending, round to ovate, pale brown squamellae with somewhat paler fringed to crested margins (Fig. 2C). *Petiole scales* (10–)21–36(–41) × (2.8–)3.5–5.5(–7.5) mm, broadly lanceolate, discordantly bicolorous, or basal scales also concordantly bicolorous, with brown to dark brown (never blackish) centres and white to yellowish margins (Fig. 2A), these sometimes with irregularly distributed brown marginal cells (Fig. 2B); margins persistent, of the same firm texture as the centres; apical scales broader and lighter in colour than the basal

ones. *Laminae* 90–200 × 50–130 cm, ovate–elliptic, bipinnate–pinnatifid to tripinnate, green to dark green, sometimes blackish when dried adaxially, pale green abaxially; apices gradually reduced. *Rhachises* inermous to muricate, stramineous to light brown or yellowish, pubescent adaxially, the hairs 1 mm long or less, white to tan, antrorsely curved; glabrous or glabrescent abaxially, with only few hairs to 1 mm long and few to many squamellae like those of the scurf; sometimes persistent scales like those on the petioles reach up to the middle of the rhachises. *Pinnae* to 70 cm long (Fig. 2D), distally not or just weakly green alate, mainly alternate, rarely subopposite. *Costae* and costules inermous, stramineous to tan, short pubescent adaxially, glabrescent abaxially, with trichomidia, thin scales to 5 mm and squamules (Fig. 2H); insertions between costae and rhachises each bearing abaxially a weakly raised elliptic aerophore, greyish to pale brown when fresh, black when dried. *Pinnules* to 5–8.2 × (0.8–)1.2–1.8(–2.5) cm, long–triangular to linear–lanceolate (Fig. 2D, E, F), the tips acute, the bases truncate to weakly rounded, basal segments may be remote from the following ones, but are connected by narrow green wings (Fig. 2E); segments with more hairs adaxially than abaxially (Fig. 2F, G) or sometimes equally hairy on both sides and then hairs sparse; hairs adaxially on and between veins, mainly close to the segment margins, abaxially evenly distributed on veins, rarely between them, here often substituted by appressed brown, unicellular trichomidia; small broadly lanceolate to ovate, brown to dark brown flattish squamules present on midveins and veins (Fig. 2H); sterile veins forked or simple, fertile veins forked (Fig. 2G). *Sori* subcostal, in forks of veins (Fig. 2G); indusia sphaeropteroid, lustrous brown, transparent, with an apical umbo (Fig. 2G), fragmenting irregularly at maturity, leaving an incomplete shallow cup or disc; paraphyses of the same length as or shorter than sporangia. *Spores* tetrahedral–globose, exospore smooth, finely porate near the laesura, perispore finely baculate.

Distribution and habitat: Grows in wet montane forests, elfin forests and *ceja de la montaña* in Bolivia and Peru at (2000–)2600–3500 m.

Additional specimens examined: PERU. CUZCO: Prov. Urubamba, Distr. Machu Picchu, Cedropata (Collpani), 13°06'S, 72°38'W, 2520 m, 7.xi.1993, Chávez Huamán 1002 (AAU); entre San Luis y Abra Málaga, 13°03'S, 72°23'W, 3050 m, 16.x.2002, Lehnert 426 (GOET, UC, USM); *ibid.*, 13°03.61'S, 72°22.89'W, 3080 m, 16.x.2002, Lehnert 431 (GOET, UC, USM). PASCO: Prov. Oxapampa, Río San Alberto valley E of Oxapampa, slopes of Cordillera Yanachaga, 10°34'S,

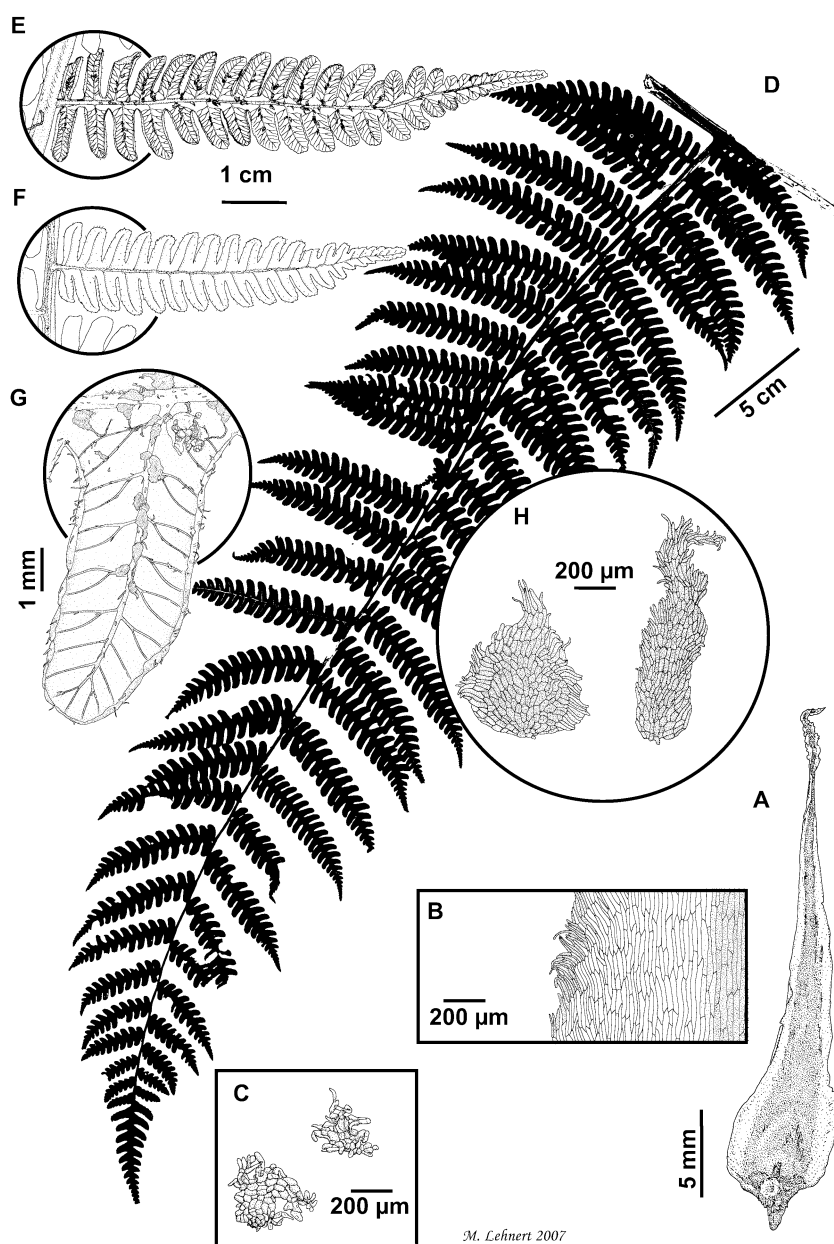


Figure 2. *Cyathea austropallescens* sp. nov. A, petiole scale. B, enlarged distal part of petiole scale from margin to darker centre, ultimate marginal cell row darker than adjacent cells. C, flat squamules with short marginal cilia from petiole scurf. D, medial pinna. E, large pinnule abaxially, showing remote basal segments and well-developed indumenta of brown squamules. F, small pinnule adaxially, showing short pubescence near segment margins. G, fertile segment abaxially, with mature sorus. H, flat squamules from laminar indument, showing variation in size and shape. All from *Lehnert 14* (GOET) with the exception of (E) (*Lehnert 15*, GOET).

75°22'W, 2400 m, 24.vii.1984, *Smith D. N. & Pretel 7972* (AAU, MO); *ibid.*, 2600 m, 25.vii.1984, *Smith D. N. & Pretel 8014* (AAU, MO).

BOLIVIA. LA PAZ. Prov. Nor Yungas, Parque Nacional Cotapata, Estación Tunquini, senda nueva del camino de la mina (curva al lado W) al pantanon, 16°11'S, 67°53'W, 2800 m, 13.ix.2000, *Bach 1003*

(GOET, LPB); *ibid.*, senda al W del pantanon, 16°11'S, 67°53'W, 3000 m, 14.vii.2002, *Bach et al. 1845* (LPB); *ibid.*, camino de la mina, 16°11'S, 67°53'W, 2700 m, 6.viii.2001, *Bach et al. 1437* (GOET, LPB); *ibid.*, camino principal a la mina, 16°12'S, 67°53'W, 2700 m, 15.viii.2002, *Bach et al. 1873* (LPB); Chuspipata, 5 km via Unduavi, 16°17'S, 67°50'W,

3150 m, 2.iv.1982, *Beck 7576* (LPB); Prov. Bautista Saavedra, Charazani, Richtung Carijna, 15°12'S, 68°52'W, 2000 m, 19.i.1994, *Herzog H500* (AAU, LPB); Charazani, östlich von Chullina, 15°09'S, 68°56'W, 3150 m, 21.i.1994, *Herzog H521* (AAU, LPB); Prov. Nor Yungas, trocha al Valle de Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3400 m, 10.ix.1997, *Kessler et al. 11765* (LPB, UC); 2 km de Chuspipata hacia Coroico, 16°22'S, 67°49'W, 2900 m, 14.ix.1997, *Kessler et al. 11904* (LPB, UC); Chuspipata, 2 km hacia Yolosa, 16°18'S, 67°48'W, 3000 m, 27.vii.2000, *Lehnert 0* (GOET, LPB, UC); Chuspipata, 16°18'S, 67°49'W, 2950 m, 3.viii.2000, *Lehnert 6* (GOET, LPB, UC); Carretera de Chuspipata a Yolosa, km 59, 16°17'S, 67°47'W, 2800 m, 3.viii.2000, *Lehnert 9* (GOET, LPB, UC); Cotapata Santa Barbara, sobre la cumbre de la montaña detras de la madona, 16°18'S, 67°52'W, 3100 m, 6.viii.2000, *Lehnert 12* (GOET, LPB, UC); entre Unduavi y Cotapata Santa Barbara, camino sobre la cumbre de la montaña antes de la bifurcation, 16°18'S, 67°53'W, 3250 m, 7.vii.2000, *Lehnert 13, 14 & 15* (GOET, LPB, UC); 500 m de Chuspipata a Yolosa, sobre loma de montaña a Coroico, 16°18'S, 67°49'W, 3000 m, 19.viii.2000, *Lehnert 31* (GOET, LPB, UC); Chuspipata–Sacramento, 16°18'S, 67°49'W, 2800 m, 10.xi.2002, *Lehnert 492* (GOET, LPB, UC); Prov. Inquisivi, Abra Sitia – climbing 1 km to the W of the road between Sita and Licoma Pampa from where it crosses Loma El Abra, 5 km NW of Inquisivi, 16°51'S, 67°10'W, 3050–3250 m, 22.xii.1989, *Lewis 36857* (MO); Prov. Inquisivi, Comunidad Choquetanga–Cuchiwasi, bajando Pabellonani, a 7 km al NE de Choquetanga, 16°48'S, 67°17'W, 3300 m, 19.i.1994, *Salinas 2137* (LPB); Prov. Inquisivi, Comunidad Choquetanga–Valle Chimu, 8–9 km de Choquetanga, 16°48'S, 67°16'W, 3200 m, 26.i.1994, *Salinas 2318* (LPB); Comunidad Choquetanga–Wichupampa, serranias de Lulini, 13.5 km al N de Choquetanga, 16°45'S, 67°20'W, 3310 m, 3.iii.1994, *Salinas 2509* (LPB); *ibid.*, 13 km al N de Choquetanga, 2–3 km al NW del Cerro Lulini, 16°45'S, 67°20'W, 3290 m, 17.iii.1994, *Salinas 2698* (LPB); Prov. Sud Yungas, Cantón Yanacachi, Mina Chojlla, camino de acceso de vehiculos a Kacapi, 15°52'S, 68°07'W, 2182 m, 5.viii.2000, *Siñani 246* (LPB); Prov. Nor Yungas, entre Cotapata y Chuspipata, 16°18'S, 67°50'W, 3100 m, 6.v.1989, *Smith D. N. & León 13134* (LPB, MO, UC); 1.2 km E of Cotapata on road between Unduavi and Chuspipata, 16°17'S, 67°50'W, 3100 m, 26.vi.1986, *Solomon 15346* (LPB, MO, UC); Prov. Murillo, Valle del Río Zongo, 24.2 km al N de la cumbre, 16°08'S, 68°07'W, 2900 m, 11.iv.1987, *Solomon & Chevalier 16550* (LPB, MO, NY, UC); Estrada de La Paz a Coroico, 72 km de La Paz, 3050 m, 28.vii.1979, *Windisch 2446* (AAU);

COCHABAMBA: Prov. Ayopaya, Sailapata, 16°51'S, 66°56'W, 3250 m, i.1935, *Cárdenas 3059* (GH, US); Sailapata, 16°51'S, 66°56'W, 3500 m, xii.1935, *Cárdenas 3150* (GH); Prov. Carrasco, 108 km antigua carretera Cochabamba–Villa Tunari, 17°09'S, 65°38'W, 2950 m, 22.vi.1996, *Kessler et al. 6548 & 6549* (LPB, UC); 116 km antigua carretera Cochabamba–Villa Tunari, 17°08'S, 65°38'W, 2400 m, 6.vii.1996, *Kessler et al. 7047* (LPB, UC, US); Puiyani, 10 km Cotapata–Cotacajes, 16°38'S, 66°41'W, 2900 m, 7.v.1997, *Kessler et al. 9329* (LPB, UC); 10 km Cocapata–Cotacajes, 16°38'S, 66°41'W, 3000 m, 9.v.1997, *Kessler et al. 9407 & 9411* (GOET, LPB, UC); Prov. Chapare, entre Villa Tunari y Cochabamba, detras Corani, arriba la montaña, 17°11'S, 65°54'W, 2800 m, 9.ix.2000, *Lehnert 61* (GOET, LPB, UC); Prov. Carrasco, Siberia, 220–222 km on the Cochabamba–Sta Cruz highway (between Pojo and Comarapa), steep pass dividing the Dept Cochabamba from that of Sta Cruz, 17°50'S, 64°40'W, 2800 m, 20.iv.1963, *Ugent & Ugent 5111* (GH, UC, US); Comarapa, aserradero Gualberto, April 1983, *Susanna 925* (LPB). SANTA CRUZ: Prov. Caballero, de Siberia 4 km al E, pequeña laguna por la cima (Laguna Tinqué?), 2600 m, 18.iii.2003, *Lehnert 720* (GOET, LPB, UC); de Siberia 5 km al E, á Torecillos, ladera fuertemente inclinada, 2650 m, 18.iii.2003, *Lehnert 721* (GOET, LPB, UC).

Notes: Identical in habit and undoubtedly closely related to *Cyathea austropallescens* are *C. cystolepis* Sodiro and *C. tungurahuae* Sodiro. The latter two species grow sympatrically in Venezuela, Colombia and Ecuador, but show no geographical overlap with *C. austropallescens*. They can be easily distinguished by the petiole scurf, which is scattered and pale brown in *C. austropallescens* and quite dense and whitish in the other two species. Structurally, the scurf consists of appressed to ascending, irregularly crested flattish squamules in *C. austropallescens* and of small erect multiciliate squamules in *C. tungurahuae* and *C. cystolepis*, in the latter species more variable in size than in the other. Usually, *C. tungurahuae* and *C. cystolepis* are less hairy adaxially than abaxially (vice versa in *C. austropallescens*); however, in northern Peru, *C. cystolepis* var. *leonis* Lehnert is abundantly hairy on both laminar surfaces as well as on all leaf axes. It can be distinguished by the presence of white to tan bullate scales on the laminae abaxially, which are common in all varieties of *C. cystolepis* but are lacking in *C. austropallescens*. In both species, the indumentum can be depauperate and virtually lacking the distinguishing lamina scales; these forms are best recognized by the petiole scurf and the geographic distribution. Glabrescent forms of *C. cystolepis* are common in the var. *boreopallescens* Lehnert from southern Ecuador, Prov.

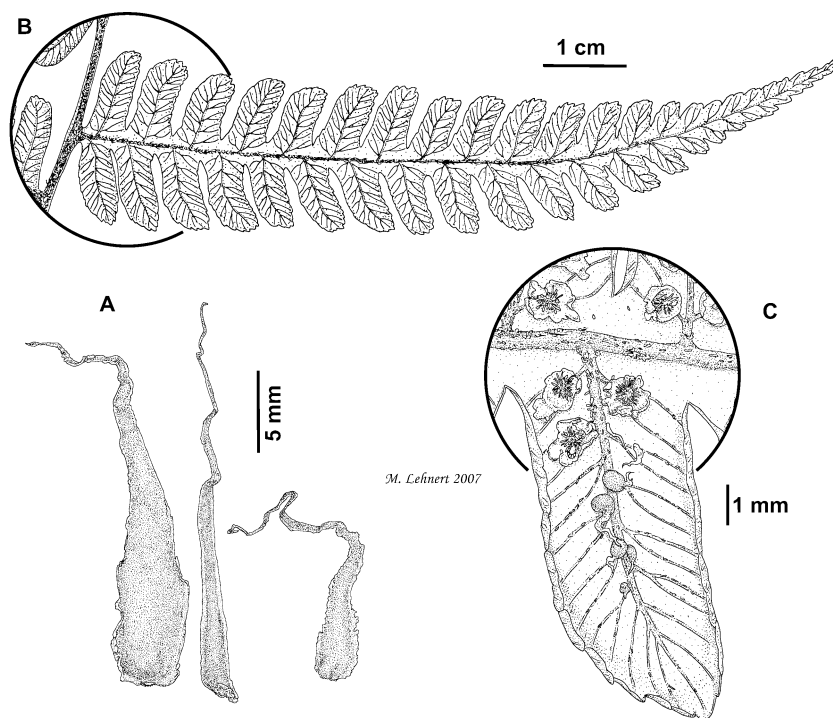


Figure 3. *Cyathea brachypoda*. A, petiole scales. B, pinnule of medial pinna adaxially. C, segment abaxially, showing fragmented indusia and weakly bullate squamules on midvein. All from *Sodi* s.n. (UC).

Zamora–Chinchi, whereas such forms of *C. austropallescens* have been often found in the Charazani region in Bolivia, Prov. La Paz. The northernmost collections of *C. austropallescens* in Peru, Prov. Pasco (Smith D. N. & Pretel 7972, 8014) do not only have almost glabrous laminae but also rather large petiole scurf squamules (to 1 mm); they may represent a local variety.

Cyathea ruiziana Klotzsch from Peru and Bolivia is distinguished from *C. austropallescens* by the fragile cretaceous petiole scale margins that are often abraded by age (vs. not fragile or abraded in *C. austropallescens*), dense white petiole scurf with the squamules intergrading to the larger scales (vs. scattered tan to pale brown scurf of only small squamules that do not intergrade to larger scales) and the presence of small white scales on the veins abaxially that always bear some distinct brown marginal teeth and often have a dark brown centre (vs. concolourous brown to tan without differently coloured marginal teeth).

Cyathea herzogii Rosenst. from Peru and Bolivia grows in the same range and habitat as *C. austropallescens* and may appear similar, but this species is much hairier, with the hairs abundant and evenly distributed on and between the veins adaxially (vs. more frequent towards the segment margins in *C. austropallescens*) and has orange–brown, deeply

bullate scales on the veins abaxially (vs. bullate scales lacking).

The species of the *Cyathea caracasana* alliance differ from *C. austropallescens* in the petiole scales which are either concolourous brown or bicolourous with brown margins (vs. white margins in *C. austropallescens*) or if the margins are whitish then the petiole scurf consists of erect, crested, dark brown squamules (vs. tan to pale brown and appressed).

3. *CYATHEA BRACHYPODA* SODIRO (FIG. 3)

Sert. Fl. Ecuad. 2: 8 (1908). *Type*: Ecuador. Pichincha: ‘Sylv. suband. vulc. Atacatzo,’ *Sodi* s.n. [lectotype: Q!, here designated; isolectotypes: SI (nos. 22795, 22707)!, US!].

Cyathea asperata Sodi, Sert. Fl. Ecuad. 2: 9 (1908). *Type*: Ecuador. Pichincha: ‘In silvis suband. m. Pichincha, iii.1903,’ *Sodi* s.n. [lectotype: SI (no. 22801)!, here designated; isolectotypes: NY!, US!].

Cyathea asperata var. *brevipes* Sodi, Sert. Fl. Ecuad. 2: 10 (1908). *Ex char.* No specimen cited.

Cyathea muricatula Sodi, Sert. Fl. Ecuad. 2: 10 (1908). *Type*: Ecuador. Pichincha: ‘In silvis suband. vulc. Corazón, xii.1907,’ *Sodi* s.n. (holotype: n.l.; isotypes: NY!, P!, US!).

Trunks to 4(–5) m tall, to 8–12 cm diameter, without old petiole bases, nevertheless appearing ruddy

because of dark brown to blackish scales; frond scars circular to weakly elliptic, inconspicuous, with small round, reddish brown pneumathodes below them; trunk apices hidden in fascicles of the youngest petioles; adventitious buds lacking. *Fronde*s to 320 cm long, patent, arching. *Petioles* 25–80 cm long, short-acute to verrucate, brown to tan, rarely stramineous with plumbeous tinge; sometimes 1–2 pairs of small adventitious (aphlebioid) pinnae at the petiole bases, to 20 cm long. *Petiole scales* narrowly lanceolate to lanceolate, 25–31 × 3–5 mm, their tips attenuate to aristate, weakly to pronouncedly helically twisted, blackish to fuscous, the narrow margins lighter coloured to whitish, not orange or rufescent (Fig. 3A); petiole scurf weakly developed, brown, consisting of small (0.2–0.3 mm) flat, round, appressed squamules with crested margins. *Laminae* to 240 × 130 cm, bipinnate–pinnatifid, firm herbaceous, gradually reduced apically, widest at or below the middle, the basal pinnae significantly reduced in fronds with short petioles; pale green abaxially, dark green abaxially, sometimes plumbeous when dried; pinnae sessile to short stalked. *Leaf axes* adaxially with hairs 0.5–1 mm long, shortly pubescent abaxially, with white scurf consisting of small, pale ciliate squamules and hairs, persisting in junctures of costae with costules and rhachises. *Pinnules* sessile to subsessile, 7.2–10.5 × 1.6–3.4 cm, bases truncate to weakly cordate, tips acute or short attenuate, the segments weakly falcate with finely serrate to crenate margins, the sinuses narrow (Fig. 3B); sterile pinnules usually broader than fertile ones. *Veins* with small flattish to weakly bullate, whitish to brown squamules abaxially (Fig. 3C); glabrous or with 1–3 hairs on midveins adaxially, shortly pubescent abaxially, with downward-curved hairs 0.2 mm long or less, sometimes substituted by appressed white trichomidia, rarely glabrous and then only partially; hairs absent between veins or only few below the sinuses abaxially. *Sori* subcostal to costal, indusia sphaeropteroid, usually with umbo, whitish–translucent, very fragile and evanescent (sometimes not detectable in mature sori); paraphyses of the same length as or shorter than sporangia. *Spores* not examined.

Distribution and habitat: Upper montane forest at 1200–2300(–2800) m, preferably along creeks in half shade. Restricted to northern Ecuador, to be expected in southern Colombia.

Additional specimens examined: ECUADOR. NAPO: Valley of Río Oyacachi, 10 km W of El Chaco, ridge SE of Río San Juan Grande, 00°17'S, 77°52'W, 1950–2020 m, 13–14.iii.1996, Øllgaard & Navarrete 1690 (AAU, QCA); Valley of Río Oyacachi, 10–15 km W of

El Chaco, trail Río San Juan Grande to Santa Maria, 00°15'S, 77°52'W, 1850–1900 m, 15.iii.1996, Øllgaard & Navarrete 1709 (AAU, QCA); Baeza, 12 ha de bosque poco disturbado y disturbado, 2 km antes de Baeza (carretera Papallacta–Baeza, parte alta de Y), 00°28'S, 77°54'W, 2000 m, 19–20.iii.1993, Valencia, Navarrete & Quintana 2896, 2897, 2911, 2914, 2917 (AAU, QCA). PICHINCHA: Lloa valley, 1-hectare plot, Hacienda Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 00°50'N, 78°38'W, 2900 m, 13–14.x.1990, Jørgensen & Yezpe 92576 (AAU, QCA); Maquipucuna Biological Field Station, c. 5 km E of Nanegalito, 34 km NW of Quito, trail Camino del Río, 00°08'N, 78°37'W, 1300 m, 4.iv.1996, Moran *et al.* 5988 (QCA); Reserva Maquipucuna, c. 5 km (airline) ESE of Nanegal, Hda. El Carmen, trail along Río Umachca, just W of research station, 00°07'N, 78°38'W, 1250–1350 m, 28.ii.1995–4.iii.1995, Øllgaard *et al.* 904 (AAU, QCA); Atacatzo, vii.1906, Sodiro *s.n.* (GH, MO) (authentic specimens of *C. brachypoda* Sodiro); Atacatzo, vii.1907, Sodiro *s.n.* (NY, US) (authentic specimens of *C. brachypoda* Sodiro); Bosque Protector Maquipucuna, crest and upper slopes of Cerro Monte Cristi, c. 9 km airline SE of Nanegalito, 00°03'N, 78°36'W, 2700 m, 08–09.ix.1993, Webster, Smith & Pastuzo 30554 (QCNE). PROV. UNKNOWN: Limones subtropico, 2300 m, 19.ix.1967, Latorre–A. 791 (Q).

Notes: The most notable feature of *C. brachypoda* is the small adventive pinnae at the petiole bases; however, these are sometimes missing. It is very similar to *C. pallescens* (Sodiro) Domin in laminar texture and pinnule shape, but differs from that species in having very fragile indusia (no indusia in *C. pallescens*), dark brown to blackish, sometimes weakly bicolourous petiole scales (vs. concolourous orange–brown) and whitish to tan squamules on the lamina abaxially (vs. orange–brown).

Judging from the descriptions, *Hemitelia subcaesia* Sodiro is the oldest name for this species. However, to date, the type could not be located. There are no good matches of the type locality description with the label information of known Sodiro specimens annotated with this name. The specimens I have seen have no petiole either; despite my confidence in the laminar indumentum as a reliable distinguishing character, I would prefer to see the petiole scurf and scales to separate this species from *Cyathea frondosa* H. Karst. with confidence (see below). Instead of selecting an ambiguous specimen as reference, I exclude *H. subcaesia* as dubious name and choose the second name in line, *C. brachypoda* Sodiro, for which complete specimens with matching references on the labels are available.

Included in *C. brachypoda* are *C. asperata* Sodiro and *C. muricatula* Sodiro, which are identical judging from Sodiro's description and the available type material. However, they have no adventive pinnae at the petiole bases; *C. muricatula* is an extreme form whose petiole scales have more pronounced whitish margins. Sodiro recognized a smaller form of his *C. asperata* as *β. brevipes* (as var. *brevipes* in Tryon, 1976). He did not cite any particular specimen but, as I understand, he refers to the species description and the cited locality of *C. asperata* in the preceding paragraphs. So I have decided to treat the *β. brevipes* among the synonyms of *C. brachypoda* and not to exclude it as illegitimate name.

Cyathea frondosa H.Karst. from Colombia and Ecuador is generally larger than *C. brachypoda*, has somewhat firmer indusia and wider pinnules. Both match in the scurf remnants on the leaf axes (white matted hairs or ciliate squamules), however, *C. frondosa* has the same type of dense scurf on the petioles whereas here *C. brachypoda* shows only scattered tan to brown squamules. The petiole scales of *C. frondosa* are only firm and bicolourous in the upper parts of the petioles and are nearly identical to those of *C. brachypoda*. Towards the petiole bases, they are concolourous or nearly so, with a softer, more papery texture than the scales of *C. brachypoda*.

Other species with basal aphlebioid pinnae are *Cyathea brevistipes* R. C. Moran and *C. suprastrigosa* (Christ) Maxon, which can be easily distinguished by their planar petiole scales that are bicolourous brown and white in the former and concolourous dull orange-brown in the latter. Their distributions do not overlap with that of *C. brachypoda* in northern Ecuador: *C. brevistipes* only occurs from southern Ecuador to Bolivia at 3000–3500 m; *C. suprastrigosa* is known only from Costa Rica and northern Colombia.

The ephemeral indusia of *Cyathea caracasana* (Klotzsch) Domin s.s. are identical to those of *C. brachypoda*. That species, however, differs from *C. brachypoda* in having wider sinuses between the segments, less hair abaxially on the lamina and in lacking white scurf on the leaf axes as well as remote basal pinnae on the petioles. The petiole scales of *C. caracasana* s.s. are broadly lanceolate with the apices not helically twisted (vs. narrowly lanceolate with apices helically twisted in *C. brachypoda*).

4. *CYATHEA CYSTOLEPIS* SODIRO. (FIGS 4, 5)

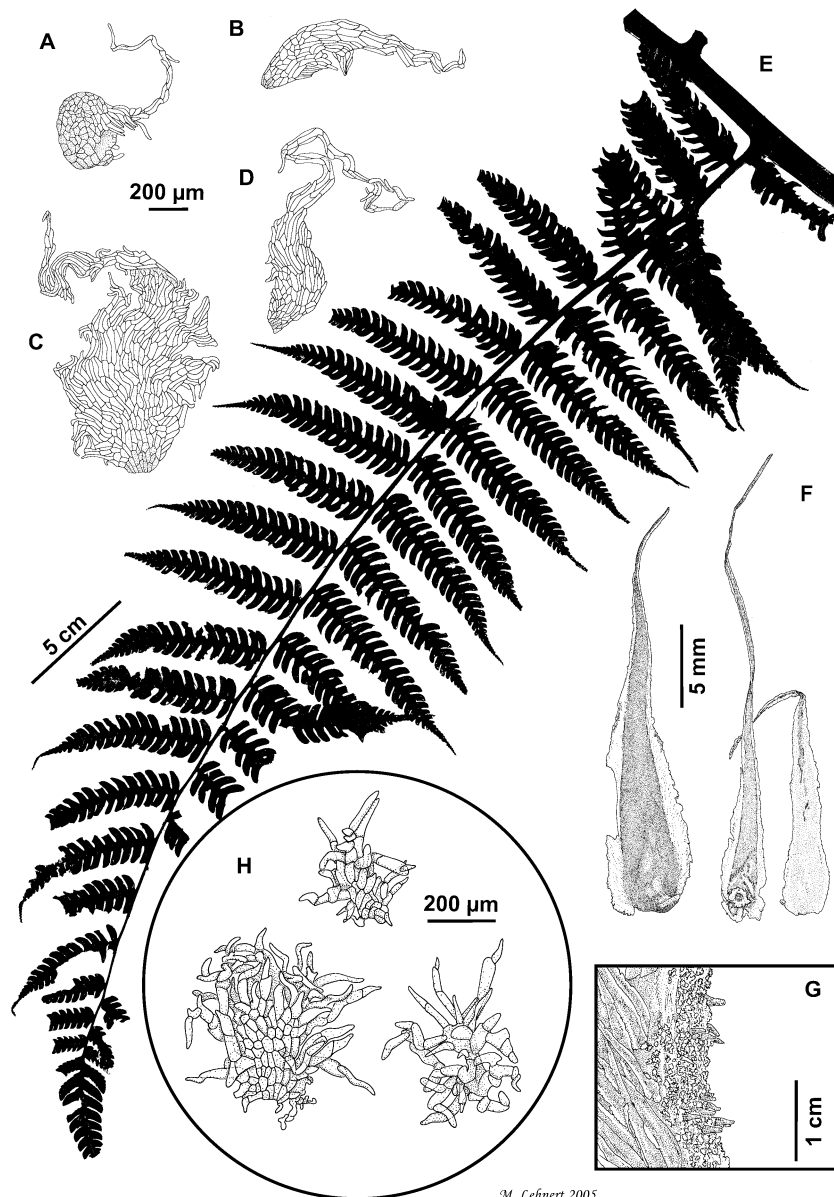
Rec. Crypt. Vasc. Quit. 15 (1883). *Type*: Ecuador. Pichincha: 'Crece en la pendiente occidental del Atacazo y del Corazón, 1600, 2000 m,' Sodiro s.n. (holotype: n.l.; isotype: NY!).

Cyathea fulva Sodiro, Rec. Crypt. Vasc. Quit. 13 (1883), not (M. Mart. & Gal.) Fée (1857). *Type*:

Ecuador. Riobamba: Tamboloma, x.1882, Sodiro s.n. [lectotype: P!, designated by Tryon (1976: 81); isolecotypes: B!, K!, NY (fragment ex K!)].

Cyathea sodiroi Christ, Ind. Fil. 195 (1905). nom. nov. for *Cyathea fulva* Sodiro.

Trunks to 8–13(–15) m high, 7–14 cm diameter, without persistent petiole bases when old, densely covered with them when young (less than 2 m high); trunk apices hidden in fascicles of the youngest petioles; frond scars broadly ovate, blackish brown like the adjacent cortex, with an arch of small round, brown to vermillion pneumathodes below them; adventitious buds lacking. *Fronds* to 300 cm long, patent to slightly erect, weakly arching. *Petioles* 30–100 cm long, muricate to spiny (Fig. 4G), stramineous to brown, rarely blackish basally; scurf dense, persistent (Fig. 4G), consisting of erect, multiciliate, whitish squamellae of different sizes (Fig. 4H). *Petiole scales* 14–30 × (1.8–)2–4 mm, narrowly lanceolate to lanceolate (Fig. 4F), discordantly bicolourous, or basal scales also concordantly bicolourous, with brown to dark brown (never blackish) centre and white or yellowish margins; margins often fragmenting, of a more brittle texture than the centres; apical scales broader and lighter in colour than the basal ones (Fig. 4F). *Laminae* 90–200 × 50–130 cm, ovate-elliptic, bipinnate-pinnatifid to tripinnate, green to dark green, when dried sometimes blackish adaxially, pale green abaxially; apices gradually reduced. *Rhachises* inermous to muricate, stramineous to light brown, rarely brown or yellowish, pubescent adaxially, with pulvicellular hairs 1 mm long or less, white to tan, antrorsely curved and somewhat appressed; glabrescent abaxially, covered with easily abraded scurf of white to greyish bullate squamellae (Fig. 4A); sometimes persistent petiole scales reach up to the middle of the rhachises. *Pinnae* to 70 cm long (Fig. 4E), distally not or just weakly green alate, alternate to subopposite. *Costae* and costules inermous, stramineous to light brown, rarely brown or yellowish, often with plumbeous tinge, shortly pubescent adaxially, densely tomentose abaxially, with small white (rarely greyish or partly brown) flat and bullate squamules, also with some small trichomidia and thin scales (to 10 mm long); the insertions bearing abaxially each a weakly raised elliptic aerophore, greyish to black already in fresh material. *Pinnules* to 5–7.8 × (0.8–)1.2–1.7(–2.5) cm, sessile to subsessile (stalked to 1 mm), long-triangular to linear, the tips acute, the bases truncate to weakly rounded (Fig. 5D–F), basal segments may be remote from the following ones, but are connected by a narrow green wing; segments oblong, weakly falcate, tips obtuse, margins crenulate (Fig. 5A–C); segments with more hairs abaxially than adaxially, or sometimes equally hairy



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Figure 4. *Cyathea cystolepis*. A–D, laminar indumenta. A, strongly bullate squamule. B, weakly bullate squamules. C, D, flat squamules. E, medial pinna. F, petiole scales, showing variation in size and colour on one petiole. G, basal part of petiole abaxially, with blunt spines and dense scurf. H, scurf squamules from one petiole; note variation in size and shape. All from *Lehnert & Kessler 1156* (GOET).

on both sides, or rarely hairs absent abaxially (Fig. 5A–C); hairs to 0.5 mm long, appressed adaxially, mainly near the segment margins on veins, erect abaxially, evenly distributed on and between veins and often substituted by appressed, tan, unicellular trichomidia; squamules on midveins and veins similar to scurf on costules, mainly bullate squamules to 1 mm long, completely white or brown with white margins, some subbullate and flattish squamules between them (Fig. 4A–D), these discordantly bicolourous tan to brown with whitish margins or completely tan to

whitish, margins often irregularly tinged brown; all squamules with one or few white apical processes; sterile veins forked or simple, fertile veins forked. *Sori* subcostal (Fig. 5A, B), in forks of veins; indusia sphaeropteroid, lustrous tan to light brown, transparent, with a weakly developed apical umbo, fragile, fragmenting irregularly at maturity, leaving a shallow cup or disc (Fig. 5A, B), sometimes completely missing; paraphyses of the same length as or shorter than sporangia. *Spores* pale yellow, tetrahedral–globose, perispore and exospore not examined.

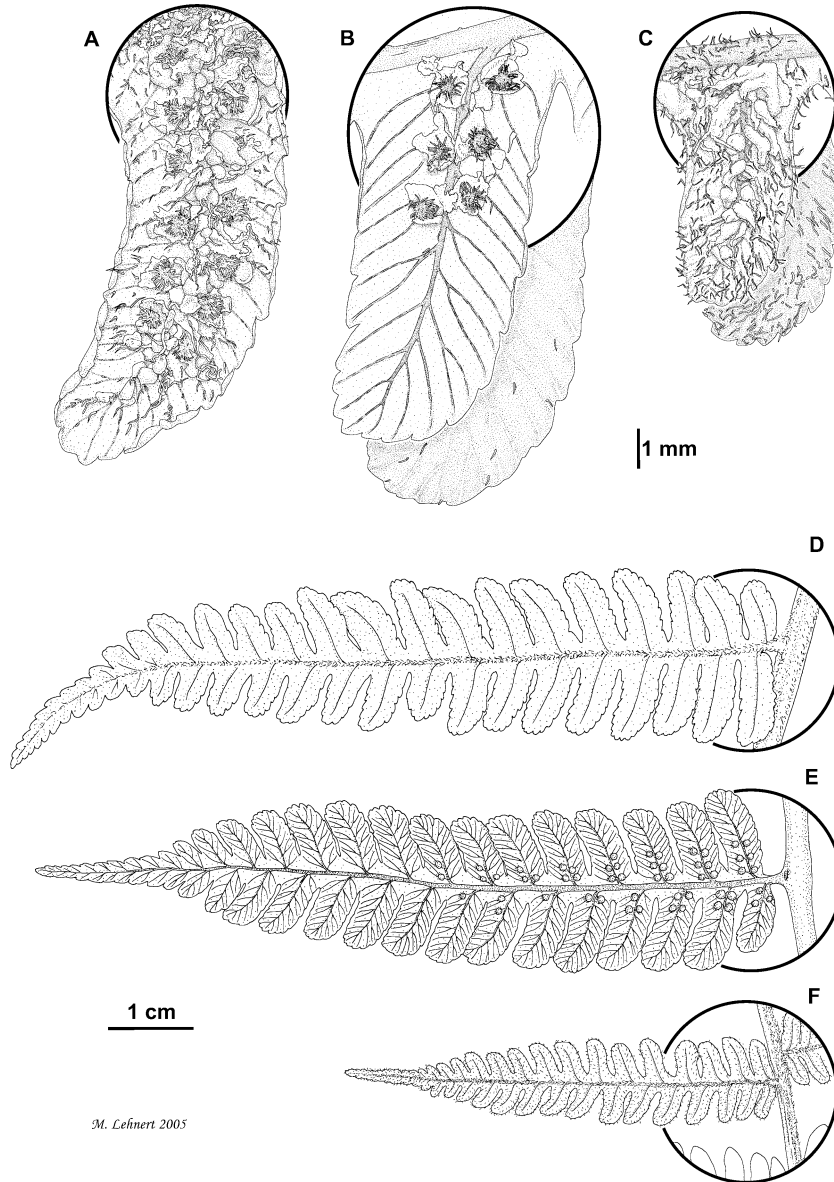


Figure 5. *Cyathea cystolepis*. A–B, variation of segments. A, var. *chimborazensis* (Lehnert & Kessler, 1156, GOET). B, var. *boreopallescens* var. nov. (Lehnert 1053, GOET). C, var. *leonis* var. nov. (Quipuscoa-S. et al. 1234, GOET). D–F, variation in pinnules. D, var. *cystolepis* (Lehnert & Kessler 1156, GOET). E, var. *boreopallescens* (Lehnert 1053, GOET). F, var. *leonis* (Quipuscoa-S. et al. 1234, GOET).

Notes: *Cyathea cystolepis* Sodiro, which was listed as a synonym under *C. pallescens* (Sodiro) Domin by Tryon (1976), was treated as a valid species by Moran & Øllgaard (1998) and listed as an endemic of the northern Cordillera Occidental in Ecuador by Valencia *et al.* (2000).

This species can be divided into three varieties, which differ considerably in the laminar characters, but are identical in the petiolar characters like scurf and petiolar scales. A similar pattern with

discrepancies in the laminar indumenta but constant petiolar characters can be found in *Cyathea delgadii* Sternb. (Lehnert, 2006a), but the amount of collections of this species is much ampler. They contain several intermediate forms between the densely hairy and sparsely hairy extremes, which reveal them as intraspecific variability connected with different growing conditions. I am convinced that future collections of *C. cystolepis* will show a similar trend in this species.

KEY TO THE VARIETIES OF *CYATHEA CHIMBORAZENSIS*

1. Hairs on the segments more abundant adaxially or equally dense on both sides, generally erect and abundant on and between the veins; bullate scales frequent abaxially, mainly pure white, rarely with brown body.....4c. var. *leonis* var. nov.
- 1'. Hairs on the segments more abundant abaxially than adaxially on and between the veins, except if hairs generally few and appressed, then sometimes few hairs adaxially and almost no hairs abaxially, hairs mainly on the veins; bullate squamules with brown body if abundant.....2
2. Hairs sparse on both laminar surfaces, often appressed, bullate squamules abaxially few, only white or lacking.....4b. var. *boreopallescens* var. nov.
- 2'. Hairs on the segments more abundant abaxially, sparse to abundant, mainly erect adaxially, appressed adaxially, bullate squamules few to many, always brown-bodied and pure white ones mixed, the brown-bodied squamules often dominating.....4a. var. *cystolepis* comb. nov.

4A. *CYATHEA CYSTOLEPIS* VAR. *CYSTOLEPIS*

(FIG. 5A, D)

Distribution and habitat: Moist montane forests in Colombia and Ecuador, south to Prov. Chimborazo, at (1500–)2000–3200 m.

Additional specimens examined: COLOMBIA. ANTIOQUIA: Prov. Jardín, Cuchilla de Ventanas, Alto de Ventanas, 2560 m, 9.vi.2000, *Giraldo & Mejía 2131* (COL). BOGOTÁ: 'Nova Grenada,' *Lindig 308* (B, COL); Fusagasugá, 2300/2600–2800 m, *Lindig 308* (B, COL). BOYACÁ: Valle del Río Cusiana, entre Sogamoso y Corinto, 2000–2200 m, 8.xii.1970, *Murillo 1378* (COL); Arcabuco, 2700–2900 m, 7.ii.1959, *Bishler 1908* (COL). CAUCA: Puracé, Parque Nacional de Puracé, 3050 m, 4.x.1984, *Lozano et al. 4490* (COL); *ibid.*, via hacia la casacada, frente a la cancha de San Nicolás, 2800–2900 m, 14.x.1992, *Orozco & Mayorga 2641* (COL). CUNDINAMARCA: Sibate, Alto de San Miguel, 31 km de la carretera a Fusagasugá, 2730 m, 2.iii.1974, *Acosta Arteaga 133* (COL); en 14.1 km de la carretera Fómeque a Chingaza, 2770 m, 27.iv.1974, *Acosta Arteaga 351* (COL); Cordillera Oriental, quebrada la Virgen, Gazaunta valley, Cordillera de Heliconia, 15 km NW of Medina, 2560 m, 2.x.1944, *Grant 10345* (COL, NY, US); San Miguel (Caserio Mun. Sibate), 2500 m, 20.x.1972, *Hagemann & Leist 1249* (COL); Sibate, below Alto de Cuchuco, 7 km SW of Sibate, 2600–2650 m, 19.x.1961, *Tryon & Tryon 6113* (COL, NY, US). HUILA: Comisaria del Caquetá, Cordillera Oriental sobre el filo divisorio, en Gabinete, 2300–2450 m, 21–22.iii.1940, *Cuatrecasas 8418* (COL); Cordillera Oriental, at Hacienda Pensilvanica, 15 km E of Baraya, 560 m, 23.vi.1944, *Little 8120* (COL). NARIÑO: Páramo El Campanero, arriba de La Botana (region Pasto), 3200 m, 31.x.1972, *Hagemann & Leist 1382* (COL). SANTANDER: Prov. Piedecuesta, Vereda Cristales, trocha que conduce al NE de la estación, 2950 m, 7.xi.1997, *Bustos et al. 178* (COL); carretera del páramo de Guantiva a Onzaga, 2970 m, 1.xii.1967, *Jaramillo Mejía 4433* (COL).

ECUADOR. BOLIVAR: 'In suband. occid. prov. Bolívar, September 1888,' *Sodirol s.n.* (SI, no. 22806) (authentic specimen of *C. fulva* Sodiro). CHIMBORAZO: 'Tamboloma, Chimborazo, x.1882,' *Sodirol s.n.* (UC) (authentic specimen of *C. fulva* Sodiro); 'in silv. suband. m. Chimborazo, ii.1905,' *Sodirol s.n.* (UC) (authentic specimen of *C. fulva* Sodiro β minor). PICHINCHA: Bellavista, entre Tandayapa y Mindo (vieja carretera Quito–Puerto Quito), 2300 m, 10.ix.2004, *Lehnert & Kessler 1156* (GOET, QCA, UC); 'In silvis subandinis prope Alaspongo, ix.1899,' *Sodirol s.n.* [SI (no. 22864)]; 'in silv. apud Niebly, i.1883,' *Sodirol s.n.* (P) (authentic specimen of *C. cystolepis* Sodiro); Quito, bei San Florencio, Exkursion nach dem Weg von Manabi, *Stuebel 806* (B); San Florencio, Camino de Manabi, 1500 m, *Stuebel 807* (B). PROV. UNKNOWN. *Sodirol s.n.* (B).

Notes: *Cyathea cystolepis* var. *cystolepis* differs from the very similar and sympatrical *C. tungurahuae* Sodiro in having a dense whitish indumentum on the axes that can be easily abraded and in having bullate scales on the laminae; *C. tungurahuae* largely lacks scurf on the axes and bullate squamules completely and also has generally wider pinnules than *C. cystolepis*. *Cyathea ruiziana* differs from *C. cystolepis* var. *cystolepis* in the larger petiolar scurf squamules and the presence of dark teeth in various types of scales and squamules (vs. always without dark marginal teeth in *C. chimborazensis*).

4B. *CYATHEA CYSTOLEPIS* VAR. *BOREOPALLESCENS*
LEHNERT VAR. NOV. (FIG. 5B, E)

Type: Ecuador. Zamora–Chinchipec: Reserva Tapichalaca, 2450–2550 m, 04°29'S, 79°07'W, 18–19.ix.2004, *Lehnert 1296* (holotype: QCA!; isotypes: AAU!, GOET!, LOJA!, UC!).

A var. *cystolepis* pilis paucioribus absentiaque squamarum bullatarum bicolorium differt.

Etymology: The name refers to the northern geographic position of this variety towards the similar

Cyathea austropallescens Lehnert (Latin *borealis*, *boreo-* = north, northern).

This variety differs from the var. *cystolepis* in having no or only very few hairs on the veins abaxially (Fig. 5B) and in lacking bicolorous bullate scales. The concolourous whitish indumentum on petiole and axes is often weakly developed (Fig. 5E).

Distribution and habitat: Moist montane forests in northern Colombia, southern Ecuador, Prov. Zamora–Chinchiipe and northern Peru, Dept. Amazonas, at 2450–2850 m.

Additional specimens examined: COLOMBIA. ANTIOQUIA: Jardín, Alto de Ventanas, 15 km SW of Jardín on road to Riosucio, 05°30'N, 75°50'W, 2400–2800 m, 6.ix.1987, *Callejas et al.* 3904 (UC, NY).

ECUADOR. ZAMORA–CHINCHIPE: Reserva Tapichalaca, trail from the station to study plots 4–7, 04°29'S, 79°07'W, 2500 m, 31.x.2003, *Lehnert 1053* (GOET, LOJA, QCA, UC); *ibid.*, study plot B1, near Sector Ventanillas, 04°29'S, 79°07'W, 2600 m, 2.xi.2003, *Lehnert 1074* (GOET, LOJA, QCA, UC); road Valladolid–Yangana, 10.4–12.3 km, 04°29'S, 79°10'W, 2450–2850 m, 18.ii.1993, *Øllgaard & León 100604* (AAU, QCA).

PERU. AMAZONAS: Prov. Bagua, Cordillera Colán SE of La Peca, 2283–2407 m, 29.ix.1978, *Barbour 3611* (AAU, MO); *ibid.*, *Barbour 3745* (US).

Notes: *Cyathea chimborazensis* var. *boreopallescens* appears to be smaller than the other two varieties. The largest plant I observed was 3.5 m high with 15 cm diameter, including the persistent petiole bases. Most plants in the Reserva Tapichalaca, Ecuador, Prov. Zamora–Chinchiipe, were fertile at just 2 m trunk height and 10 cm diameter. Plants with sparse laminar indumentum resemble *C. austropallescens* from southern Peru and Bolivia, but this species can be distinguished by the concolourous tan to pale brown petiole scurf and the flattish, concolourous brown squamellae on the veins abaxially, which do not occur in *C. cystolepis*.

4C. *CYATHEA CYSTOLEPIS* VAR. *LEONIS* LEHNERT VAR. NOV. (FIG. 5C, F)

Type: Peru. Amazonas: Prov. Leymebamba, alrededor de la Laguna de Los Condores, 06°51.201'S, 77°40.958'W, 2500–2700 m, 16.viii.1998, *Quipuscoa–S et al.* 1234 (holotype: USM!; isotypes: F!, GOET!, UC!).

A var. *cystolepe* pilis erectis in paginam superiorem crebribus absentiaque squamarum bicoloratorum in indumento laminarum differt.

Etymology: This new variety is dedicated to Dr Blanca León to reward her extensive work on pteridophytes in the Río Abiseo National Park, Peru, where the paratype was collected. The epithet is a direct translation from Spanish 'león' (= lion) to Latin *leo*, *leonis*.

This variety differs from the var. *cystolepis* in being densely hairy with erect hairs on both sides of the lamina (Fig. 5C, F) and in having only white squamellae in the laminar indumenta (Fig. 5C).

Distribution and habitat: Growing in moist montane forest at 2700 m in northern Peru, Dept. Amazonas and San Martín; to be expected farther south.

Additional specimens examined: PERU. SAN MARTÍN: Prov. Marsical Cáceres, Río Abiseo National Park, 07°S, 77°W, 2700 m, 1.ix.1985, *Young 1546* (F, USM).

Notes: *Cyathea cystolepis* var. *leonis* can be mistaken for *Cyathea straminea* H. Karst. because of the white laminar indumentum and the overall appearance. They can be distinguished by the flat, whitish lanceolate laminar scales with brown marginal teeth that are common in *C. straminea* but absent in *C. cystolepis* var. *leonis*. This variety reaches similar growth heights as var. *cystolepis* (13–15 m).

5. *CYATHEA TUNGURAHUAE* SODIRO (FIG. 6)

Sert. Fl. Ecuad. 2: 12 (1908). *Type:* Ecuador. Tungurahua: 'Sylv. suband. vulc. Tungurahuae, Ecuador,' *Sodiro s.n.* (lectotype: Q!, here designated; isolectotype: US!).

Cyathea nitens Sodiro, Sert. Fl. Ecuad. 2: 3 (1908). *Type:* Ecuador. Pichincha: 'Silvis subandin. vulc. Corazón, Ecuador, vii.1907,' *Sodiro s.n.* (lectotype: 'Corazón, viii.1907,' US!, here designated; isolectotypes: MO, P!).

Cyathea ochroleuca Sodiro, Sert. Fl. Ecuad. 2: 11 (1908). *Type:* Ecuador. Pichincha: 'Crescit in sylvis subandinis vulcani Atacazo, Ecuador, vii.1907,' *Sodiro s.n.* (lectotype: QPLS!, here designated; isolectotype: SI!).

Cyathea subinermis Sodiro, Sert. Fl. Ecuad. 2: 10 (1908). *Type:* Ecuador. Pichincha: 'Sylvis subandinis vulcani Atacazo, Ecuador, vii.1907,' *Sodiro s.n.* (lectotype: Q!, here designated).

Trunks to 10–12 m high, 12–20 cm diameter, without old petiole bases, the frond scars usually tightly packed, rhomboid, the small parts of cortex between them blackish brown, without pneumathodes or with few small ones below the scars; adventitious buds lacking. *Fronde*s to 275 cm long, patent to weakly erect, arching from the middle. *Petioles* 48–92 cm long, dark green to blackish, stramineous when dried, with strong

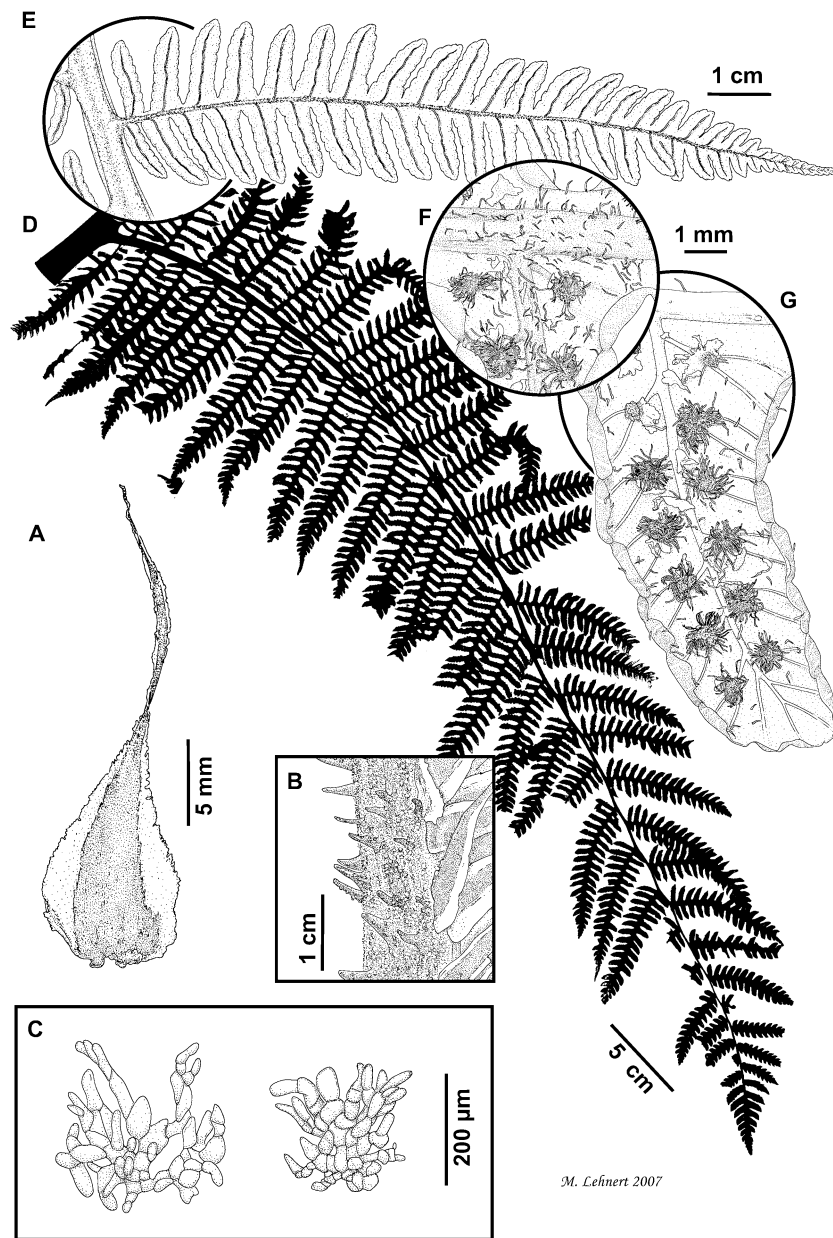


Figure 6. *Cyathea tungurahuae*. A, lower petiole scale. B, detail of basal petiole adaxially, showing fine scurf. C, squamules from petiole scurf, strongly dissected. D, medial pinna. E, basal pinnule of medial pinna, adaxially. F, detail of pinnule abaxially, with relatively dense hair on the costule. G, segment abaxially, moderately hairy. All from Lehnert 1504 (GOET) with the exception of (F) (Øllgaard & Feil 91113, AAU).

spines. *Petiole scales* large, to 30×8 mm, broadly lanceolate with long tips, discordantly bicourous, dark brown to blackish with tan to white margins abaxially (Fig. 6A), discordantly bicourous adaxially, brown, often streaked centres and yellowish to white margins; petiole scurf dense, whitish-grey to tan (Fig. 6B), consisting of clearly separated multiciliate squamellae with narrow bodies (Fig. 6C). *Rhachises* inermous or muricate in basal half, yellow to strami-

neous, glabrescent abaxially, with dense indumentum of white to tan erect squamellae to 0.4 mm long, with many long marginal processes, no larger scales similar to petiole scales present. *Laminae* to 180×90 cm, firm-chartaceous to cartilaginous, bipinnate-pinnatifid, apices gradually reduced, dull green adaxially, pale green abaxially. *Costae* yellow to stramineous, inermous or rarely some short prickles basally, weakly hairy adaxially (Fig. 6E), the hairs

white to tan, antrorsely curved, to 1 mm long; costules yellow to stramineous, inermous, moderately to densely hairy adaxially, the hairs white to tan, antrorsely curved, to 1 mm long. *Pinnules* to 12 × 2.5 cm, sessile to subsessile, linear-lanceolate, bases truncate to slightly rounded, apices long acute (Fig. 6E); segments to 3.5 mm wide, patent, straight to weakly falcate (Fig. 6F, G), the margins subentire to crenulate; sinuses narrow, acute; basal segments never remote; veins glabrous adaxially or with 1–3 white pluricellular hairs on the midveins distally, glabrous to densely hairy abaxially with white erect hairs 0.4–0.6 mm long (Fig. 6F, G), some scattered small, flat-tish, round to broadly lanceolate scales, light brown to tan with white entire margins and obtuse tips; sterile veins forked or simple, fertile veins forked. *Sori* subcostal, in fork of veins; indusia subsphaeropteroid to sphaeropteroid, colourless or tan, translucent, fragile, fragmenting to a shallow cup or disc with lacerated margins at maturity (Fig. 6F, G), hardly recognizable as indusia; sometimes indusia stop growing before sori are fully developed and may just be cyatheoid or they may fall off before the sporangia open; paraphyses of the same length as or shorter than sporangia. *Spores* pale yellow, tetrahedral-globose; exospore and perispore not examined.

Distribution and habitat: Mainly in moist montane forest and elfin forest, in open spots like clearings and road cuts. Andes of Colombia and Ecuador at 2000–3200 m, to be expected in adjacent Venezuela and Peru.

Additional specimens examined: COLOMBIA. BOYACA: Villa de Leyva, Santuario de Flora y Fauna de Iguaque, Cabaña de Carrizal, 05°44'N, 73°28'W, 2820 m, 27.iii.1993, *Betancur et al.* 4069 (COL); camino del Alto de Onzaga a Soatá, en valle lateral, 2800 m, 23.xi.1967, *Jaramillo Mejía* 4183 (COL); entre Arcabuco y Villa de Leyva, camino de Las Coloradas, 2750 m, 28.viii.1967, *Jaramillo Mejía et al.* 3001 (COL); Soatá, carretera a Onzaga, hoya de la quebrada San Antonio, 2820 m, 3.viii.1958, *Jaramillo Mejía, Hernández-Camacho & van der Hammen* 809 (COL); carretera de Chiquiquirá a Pauna, entre Los Curubitos y San Antonio, 2600 m, 2.ix.1967, *Jaramillo Mejía, Murillo M. T. & van der Hammen* 3258, 3281 (COL); Villa de Leyva, Santuario de Flora y Fauna de Iguaque, alrededores de la Cabaña Mamarros, 2750 m, 9.vi.2001, *Murillo J. et al.* 2969 (COL). CUNDINAMARCA: La Mesa, Laguna de Pedro Palo 2000 m, 14.xii.1989, *Acosta Artega et al.* 2241 (COL); road from Bogotá to Sylvania, 20 km S of Bogotá, 22.vii.1972, *Barrington* 464 (COL); Arriba de La Mesa, 2600 m, 16.xi.1964, *Jaramillo-U. s.n.* (COL); San Francisco, hacienda 'La Laja', 2880 m,

26.ix.2004, *Parra-O., Mieth & Vargas* 596 (COL). SANTANDER: Carretera del páramo de Guantiva a Onzaga, 2800 m, 1.xii.1967, *Jaramillo Mejía & van der Hammen* 4469 (COL).

ECUADOR. CAÑAR: Tipococha, 3200 m, 17.viii.1933, *Diels* 592 (QCA). IMBABURA: Cotacachi Canton, Parroquia Plaza Gutierrez, caserío Tablachupa, via a Apuela, NW de Cuicocha, 00°20'N, 78°26'W, 2800–3000 m, 13.vi.1992, *Cuamaacs, Gudiño & Tipaz* 154 (QCNE). LOJA: Between Argelia and La Palma, SW of Loja, along old road to Cata-mayo, 04°09.49'S, 79°16.86'W, 2600–2700 m, 3.xi.2004, *Lehnert* 1504 (AAU, GOET, LOJA, QCA, UC); road La Argelia (southern Loja)–La Palma, along crest of the mountain range just SW of Loja, c. 04°03'S, c. 79°14'W, 2700–2900 m, 4.iii.1989, *Øllgaard et al.* 90829 (AAU, QCA); new road Loja–Saraguro, 17 km, 03°55'S, 79°15'W, 2600–2650 m, 19.iii.1989, *Øllgaard & Feil* 91113 (AAU, MO). NAPO: Cuyuja, colecciones desde el Río Maspá siguiendo la carretera que va hacia Baeza, c. 78°00'W, 2530 m, 19.viii.1990, *Jaramillo, Grijalva & Grijalva* 11933 (AAU, QCA); Oyacachi, camino Chalpi–Baños, 00°12'S, 77°58'W, 2500–2800 m, 24.v.1996, *Navarrete* 1708 (AAU, QCA). PICHINCHA: Reserva Geobotanica Pululahua, camino a Lulumbamba, 00°05'N, 78°30'W, 2500–2610 m, 29.vi.1988, *Cerón* 4288 (QCA); one hectare plot, Lloa valley, Hda. Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 00°50'S, 78°38'W, 2900 m, 13–14.x.1990, *Jørgensen & Yepéz* 92570 (QCA, AAU); *ibid.*, 00°10'S, 78°38'W, 2900 m, 7.iv.1991, *Jørgensen et al.* 92659, 93070, 93074, 93079 & 93085 (AAU, QCA). TUNGURAHUA: 'Tungurahua, vii.1901,' *Sodiro s.n.* (P, SI) (Authentic specimens of *C. tungurahuae* Sodiro).

Notes: The specimen at P annotated as type specimen of *C. pallescens* by Tryon in 1974 belongs without any doubt to *C. tungurahuae* Sodiro. It consists of a petiole with well-developed scurf and many scales and a fertile pinna; a rare condition in so old a specimen. Lamentably, it cannot be used as a type any more because the original label belonging to that collection must have been lost and wrongly replaced, which has been the cause of Tyron's error. The typical scurf is exquisitely pictured in the revision of the genus (Tryon, 1976).

The priority of the names is not given by the publishing date as all diagnoses follow one another in the *Sertula* (Sodiro, 1908). I have chosen the name *C. tungurahuae* Sodiro because of the better condition and ampler amount of the material at Q. I have only found one authentic specimen of *C. subinermis* and two of *C. ochroleuca*, all with little scurf and scales remaining on the petioles. Furthermore, the label of *C. ochroleuca* has written on it 'sive var. *C. tun-*

gurahuae', indicating that Sodiro defined *C. tungurahuae* for himself prior to *C. ochroleuca*, although this has no value according to the Code (McNeill, 2006).

The array of synonym types cover the whole variability of the species: *C. tungurahuae* is a broad-leafed form with glabrous laminae, with well-developed spines and scurf; *C. ochroleuca* is a medium-sized form with well-developed indumentum on the lamina, strong spines and remnants of well-developed petiole scurf; the specimens at hand of *C. nitens* are identical with *C. ochroleuca*, but they lack the petiole; *C. subinermis* has a very small frond, with the short petiole only muricate (thorns are worn off and thus only verrucate now), but the petiole scurf is typical.

The type of *C. tungurahuae*, which has glabrous laminae and relatively broad segments, is distinct from the types of the other names, which generally have some hairs abaxially and narrower segments. Intermediate forms that fill this morphological gap have been found in one population in southern Ecuador (Øllgaard *et al.* 90829, Lehnert 1504). They show that, in the same plant, short hairs may occur on one lamina while they are lacking on the other.

Cyathea tungurahuae is defined by the combination of strongly ciliate, thin-bodied petiole scurf squamules, glabrescent axes, fragile indusia and the lack of bullate squamules. The pubescence may vary from having no hairs on both sides to having scattered hairs on veins adaxially and many hairs on and between veins abaxially. These hairs are always very short (to 0.6 mm) and may be replaced by evanescent appressed trichomidia. The scales on the laminae are always few, broadly lanceolate to round, light brown and have white subentire margins. The very similar *C. cystolepis* is best distinguished by the sessile bullate scales (vs. no bullate squamules in *C. tungurahuae*) which vary in colour from pure white to brown with white tips; they also form part of the easily abraded, dense scurf on rhachises, costae and costules, which also contains the same whitish squamellae that are found in *C. tungurahuae*. The petiole scales of *C. cystolepis* tend to be smaller, narrower and less contrastingly coloured than those of *C. tungurahuae* and the scurf squamellae are not so uniform in size and shape. The rhachises of *C. tungurahuae* never have been found to bear persistent scales such as is sometimes the case in *C. cystolepis*.

Other similar Andean *Cyathea* species are easily distinguished by the small stellate scurf squamules of *C. tungurahuae*: *Cyathea corallifera* Sodiro from Ecuador and *C. divergens* Kunze from the northern Andes, whose petiole scales match those of *C. tungurahuae* in size and colour, have generally larger, erect lanceolate squamules in the scurf and also

larger and broader pinnules. *Cyathea patens* H. Karst. has brown to tan scurf of round to oblong, squamellae with white fimbriate margins and smaller, less contrasted petiole scales than *C. tungurahuae*. In *C. austropallescens* Lehnert of Peru and Bolivia, the scurf consists of flat squamellae with fringed to crested margins that are generally browner than in *C. tungurahuae*; it can also be distinguished by the pubescence on the veins adaxially being denser than abaxially and the presence of small flat, brown to tan squamules on the lamina abaxially.

Without petioles at hand for identification, one can rely on the laminar scales that are usually found at the bases of pinnae and basal pinnules: *Cyathea tungurahuae* has flat, round to broadly lanceolate, tan scales with white subentire margins; other species similar in leaf cutting have brown scales with dentate–ciliate margins (*C. patens*) or white scales with dark marginal teeth and sometimes also dark central stripes (*C. straminea* H. Karst, *C. corallifera* Sodiro, *C. ruiziana* Klotzsch) or also bullate scales of white or brown colour (*C. cystolepis*).

ALLIED SPECIES

6. *CYATHEA ATAHUALLPA* (R.M. TRYON) D.B. LELLINGER (FIG. 7A–D)

Amer. Fern J. 74: 56 (1984). *Sphaeropteris atahuallpa* R. M. Tryon, Rhodora 74: 442 (1972). *Type*: Peru. Amazonas: Prov. Chachapoyas, Cerros Calla Calla, above Balsas on road to Leimebamba, 3000–3100 m, 14.x.1964, Hutchinson & Wright 6922 (holotype: GH!; isotype: UC!).

Distinguishing characters: Trunks to 13 m tall, to 12 cm diameter, without persistent petiole bases when old, densely covered with them when young; fronds to 400 cm long, patent to ascending, arching. *Petiole scales* to 45–55 × (1.8–)4–5 mm, spreading, narrowly lanceolate (Fig. 7A), concolourous, pure white to stramineous, with a tan to pale brown spot at the base, of a brittle papery texture. *Scurf* on petioles and leaf axes dense, persistent, consisting of white erect scales 1–5 mm long (Fig. 7B), with long marginal cilia; scurf scales usually conglomerated to distinct tufts. *Pinnules* to 12(–13) × 2.8(–3) cm, sessile to subsessile; squamules on veins mainly flat, white, translucent, 1–3 mm long (Fig. 7C, D), also with bullate squamules to 1 mm long distally on midveins, completely white or with brown bases; all squamules with many white marginal cilia (Fig. 7B, D). *Indusia* sphaeropteroid (Fig. 7C), firm, fragments persistent.

Distribution and habitat: In moist high montane forests in southern Ecuador and northern Peru at 2500–3200 m.

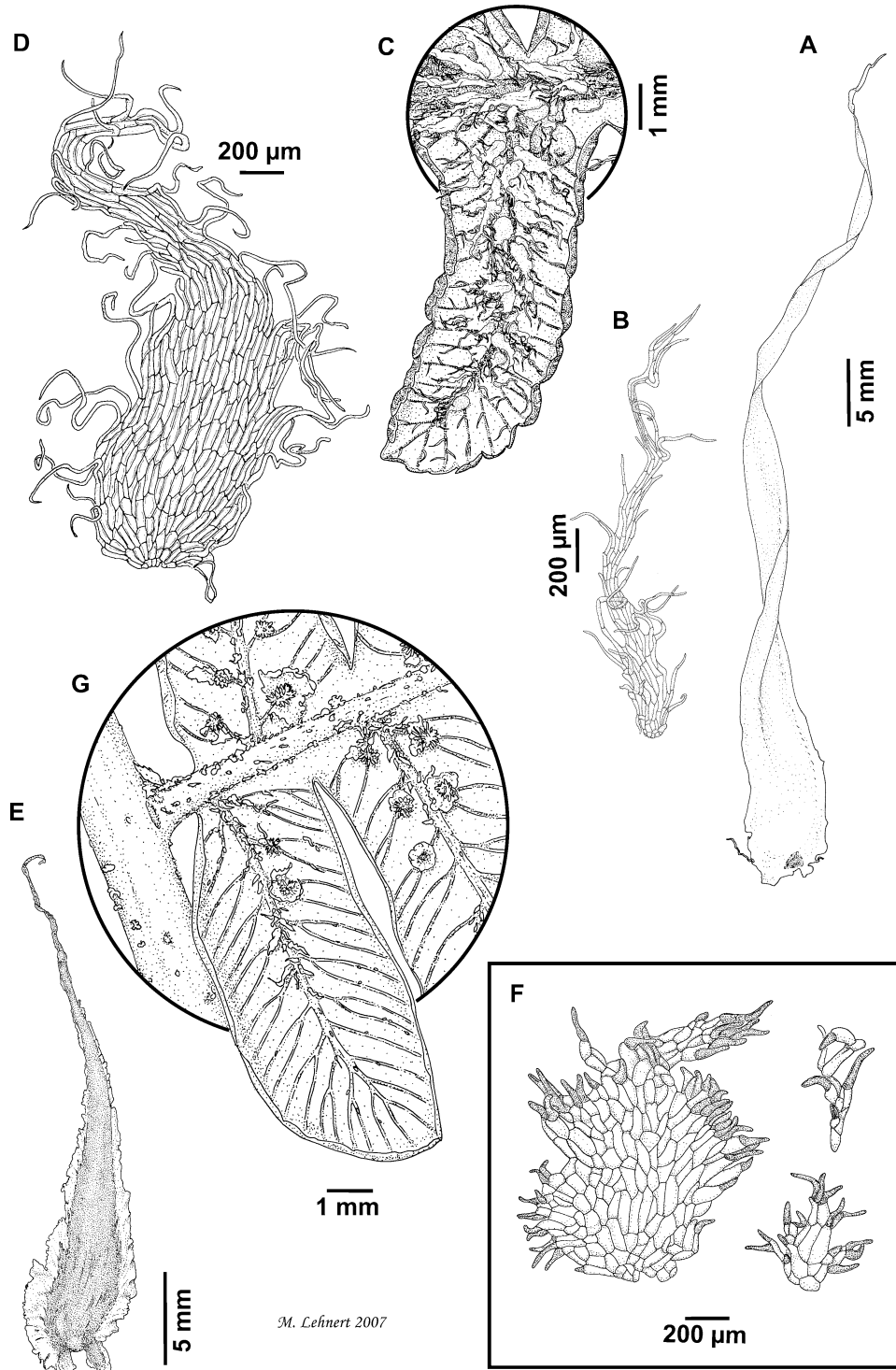


Figure 7. A–D, *Cyathea atahuallpa*. A, petiole scale. B, squamule from petiole scurf. C, fertile segment of large pinnule abaxially. D, squamule from laminar indumentum. All from *Lehnert 1563* (GOET, UC). E–G, *C. corallifera*. E, petiole scale. F, squamules from petiole scurf. G, basal segment of large fertile pinnule abaxially. All from *Lehnert 130* (UC).

Selected specimens examined: ECUADOR. AZUAY: Sevilla de Oro, old road 10–12 km N of the village, 02°46'S, 78°37'W, 2750–2850 m, 11.ix.1976, *Øllgaard & Balslev 9342* (AAU, QCNE). LOJA: Cajanuma, sendero 'Osos de Anteojos,' 2740 m, 7.viii.2003, *Lehnert 789* (GOET, LOJ, QCA, UC). MORONA-SANTIAGO: E of pass on Gualaceo–Limon road, 03°00.27'S, 78°39.10'W, 3000–3200 m, 15.xi.2004, *Lehnert 1563* (GOET, QCA, UC). ZAMORA-CHINCHIPE: New road Loja–Zamora, c. 5 km E of pass 'El Tiro,' above old landslide along road, 03°59'S, 79°08'W, 2500 m, 18.xi.2004, *Lehnert 1573* (GOET, QCA, UC). PERU. CAJAMARCA: Jaén, Sallique, localidad Quebrada Grande, 05°40'59"S, 79°55'W, 2700–2800 m, 20.vii.1998, *Campos, Dia & Guevara* (UC). LIBERTAD: Pataz, La Montañita (Dist. Buldibuyo), 08°06'S, 77°14'W, 3200 m, 15.iii.2001, *Sagástegui, Zapata & Palacios 16321* (UC).

7. *CYATHEA BETTINAE* LEHNERT

Brittonia 56: 210 (2004). *Type:* Bolivia. La Paz: Prov. Franz Tamayo, Parque Nacional Madidi, senda Keara Mojos, Chunkani, 14°38'S, 68°57'W, 2950 m, 10.xi.2001, *Jiménez & Gallegos 973* (holotype: LPB!; isotype: UC!).

Distinguishing characters: *Trunks* 0.2–0.5 m tall, c. 3 cm diameter, covered with slender lanceolate, brown to tan, lustrous scales, 16 × 4 mm, some with paler or whitish margins. *Petioles* to 40 cm long, sparsely verrucate to weakly muricate basally, smooth to tuberculate distally, dark brown to atropurpureus; scurf of minute white squamules easily abraded. *Petiole scales* broadly lanceolate to ovate, opaque white to very light brown, sometimes with a dark brown streak at tip, the margins finely serrate. *Laminae* to 40 cm long and 24 cm broad, broadly ovate to triangular, widest in the region of the second pinna pair, bipinnate–pinnatifid, the apices gradually reduced, long tapering. *Rachises*, costae and costules dull reddish brown, with many short white multicellular hairs adaxially and few white tortuous, evanescent unicellular hairs abaxially; costae base with dark prominent pneumathode. *Pinnae* to 8 cm wide, long triangular, acuminate, distally green alate. *Pinnules* to 3.5 × 0.8 cm, petiolulate (1–2 mm) to sessile, acute to short acuminate, the segments round to deltate, tips obtuse with crenulate margins, white hairs adaxially on all veins as well as between the veins along the segment margins, these visible from beneath because of revolute margins, few flattish brown scales with weakly fringed margins abaxially. *Sori* costal, situated in furcations of main and lateral veins of a segment. *Indusia* sphaeropteroid, without umbo, appearing cyatheoid or meniscoid at maturity.

Distribution and habitat: This species grew in large numbers under trees (I. Jiménez, pers. comm.) in moist forests at 2900–2950 m; apparently restricted to western Bolivia.

Additional specimen examined: BOLIVIA. LA PAZ: Prov. Franz Tamayo, trail Keara–Mojos, Chunkani (camping site), 14°38'S, 68°57'W, 2900 m, 25.vi.2005, *Jiménez et al. 2958* (LPB, UC).

Notes: *Cyathea bettinae* is distinguished from sympatric congeners by its small size combined with the bipinnate–pinnatifid laminae. This species resembles most closely *C. simplex* R. M. Tryon from the Guyana Highlands, which differs in having darker petiole scales (dark brown with paler brown margins vs. almost concolourous whitish to pale brown in *C. bettinae*) and its denser and more persistent scurf. In the 'Pteridophyta of Peru' (Tryon & Stolze, 1989), *Cyathea bettinae* will key out to *C. ruiziana* Klotzsch but that species has larger scales in the petiole scurf and spiny petioles.

Cyathea bettinae combines some characters of *C. austropallescens* Lehnert and *C. bipinnatifida* (Baker) Domin: it shares the scale colour and hair distribution on the lamina with the first species, while it has the diminutive habit of the latter. However, *C. austropallescens* has firm persisting indusia (fragile in *C. bettinae*) and is generally much larger; *C. bipinnatifida* is exindusiate and has a pinnate–pinnatifid lamina (bipinnate–pinnatifid in *C. bettinae*). As both species as well as other tree ferns did not grow nearby, a hybridogenic origin of *C. bettinae* seems unlikely.

8. *CYATHEA CORALLIFERA* SODIRO (FIG. 7E–G)

Rec. Crypt. Vasc. Prov. Quit. 11 (1883). *Type:* Ecuador. Pichincha: 'Crece en los declives del Corazon y del Atacazo (Milligallí–S. Florencio), 1500–2000 m,' *Sodiuro s.n.* [lectosyntypes: designated herewith: 'Corazón, 1882,' *Sodiuro s.n.*, P!, GH (photo P); 'Atacazo, prop. Canzacoto,' v.1882, *Sodiuro s.n.*, NY!].

Cyathea corallifera var. *alsophilacea* Sodiuro, *Rec. Crypt. Vasc. Prov. Quit.* 12 (1883). *Ex char.*, no specimen cited.

Cyathea corallifera var. *firma* Sodiuro, *Rec. Crypt. Vasc. Prov. Quit.* 12 (1883). No specimen cited. Authentic specimen: 'Ecuador,' *Sodiuro s.n.* [K, NY (fragment ex K)!].

Cyathea corallifera var. *ortholoba* Sodiuro, *Rec. Crypt. Vasc. Prov. Quit.* 12 (1883). No specimen cited. Authentic specimen: 'Corazón, 1800 m', v.1882, *Sodiuro s.n.* (NY!).

Cyathea aspidioides Sodiuro, *Rec. Crypt. Vasc. Prov. Quit.* 14 (1883), not (Blume) Moritz, *Syst. Verz. Java*

108 (1845). *Type*: 'Crece en los bosques del Corazón y del Atacazo, 1800–2000 m,' *Sodirol s.n.* (n.l.). Authentic specimens: 'Corazón, prop. Milligally,' x.1896, *Sodirol s.n.* (NY); 'Corazón,' x.1891, *Sodirol s.n.* (NY!).

Cyathea aspidiiformis Domin, Acta Bot. Bohem. 9: 94 (1930), nom. nov. for *Cyathea aspidioides* Sodirol.

Distinguishing characters: Trunks to 5 m tall, to 16 cm diameter, without persistent petiole bases when old, densely covered with them when young (less than 2 m high). Fronds to 500–570 cm long, drooping. Scurf dense, persistent on petioles, evanescent on leaf axes, consisting of erect, whitish squamellae with occasional brown marginal cells (Fig. 7F) and a basal layer of appressed, matted squamellae with long marginal cilia. Petiole scales 18–30 × 3–6 mm, narrowly lanceolate to lanceolate, discordantly bicolourous, or basal scales also concordantly bicolourous, with brown to blackish centres and white to tan margins, these often fragmenting, of a more brittle texture than the centres (Fig. 7E); apical scales broader and lighter in colour than the basal ones. Fronds to 500–570 cm long, strongly arching in the proximal half, drooping distally. Petioles to 130–170 cm long, muricate to aculeate with spines to 5 mm long, stramineous to brown, rarely blackish basally; scurf dense, persistent, consisting of erect, whitish squamellae with occasional brown marginal cells. Pinnules to 12–16 × (1.2–)2.5–4.5 cm, sessile or short-stalked to 6 mm, narrowly or broadly triangular to linear, tips long acute, bases truncate to weakly cordate, basal segments may be free but not remote from the other segments. Indusia sphaeropteroid (Fig. 7G), fragile, fragments ephemeral.

Distribution and habitat: Known only from north-western Ecuador at 1500–2300 m.

Selected specimens examined: ECUADOR. COTOPAXI: Reserva Ecológica Los Illinizas, sector II, sector Chuspitambo, W of Choasillí, Cordillera Occidental, W slope, 00°58'42'S, 79°06'22'W, 1900 m, 5.viii.2003, *Silverstone-Sopkin et al.* 9829 (CUVC, UC). IMBABURA: Catacachi, Parroquia Apuela, sector Cuellague, 00°15'N, 78°25'W, 1600 m, 10.vii.1992, *Tipaz & Aulestina 1684* (QCNE). PICHINCHA: Carretera Mindo–Nono, 00°01'N, 78°39'W, 2050 m, 2.vii.2002, *Lehnert 130* (GOET, QCA, UC).

Notes: *Cyathea corallifera* is very similar to *C. tungurahuae* and *C. cystolepis*. With *C. tungurahuae*, it shares the same indusium type, i.e. it is sphaeropteroid, very fragile and sometimes missing completely at maturity, although normally a disc with a brown ring around the receptacle remains. All three species have mainly white scurf on petioles and on

the leaf axes abaxially (in *C. tungurahuae* only on young leaves, persistent in others). *Cyathea corallifera* differs, however, in its large, broad pinnules (to 17 × 3.5 cm vs. 12.5 × 2.6 cm in *C. tungurahuae* and 7.8 × 1.7(–2.5) cm in *C. cystolepis*) and the presence of brown marginal teeth in the concolourous white squamules of the scurf and the laminar indumentum (vs. no brown marginal teeth in *C. tungurahuae* and *C. cystolepis*).

Cyathea corallifera grows in the understory of moist montane forests and in clearings. Its habit with very long fronds drooping from their bases and with large pinnules does not change with different sun exposure (M. Lehnert, pers. observ.).

9. *CYATHEA DINTELMANNII* LEHNERT

Brittonia 58: 237, figs 1–2 (2006). *Type*: Bolivia. Cochabamba: Prov. Chapare, Territorio Indígena Parque Nacional Isiboro Securé, Cordillera de Mosestenes, Laguna Carachupa, 16°14'S, 66°25'W, 1300 m, 29.viii.2003, *Kessler et al.* 13012 (holotype: LPB!; isotypes: GOET!, UC!).

Distinguishing characters: Trunks 6–12 m high, (5–)8–15 cm diameter without petiole bases, to 20 cm diameter with them; petiole bases persistent in small plants and at the base of large plants, deciduous when the trunk height surpasses the frond length; trunk apices hidden in fascicles of the youngest petioles; adventitious buds lacking. Fronds 200–330 cm long, patent to weakly ascending, weakly arching. Petioles to 90 cm long, short- to long-aculeate, dark green to blackish when fresh, stramineous to lustrous brown when dried, the bases usually dark brown; pneumathodes in one discontinuous line laterally, usually not visible. Petiole scurf white to tan, dense to scattered, easily detached and vanishing with age, consisting of fragile squamules to 0.3 mm long, with crested margins, in larger squamules the margins laterally convolute; marginal processes very fragile, with the horizontal cell walls often on one level so that the squamellae may appear trimmed when the marginal processes have fallen. Petiole scales lanceolate, their bases very narrow to broad, 17–25 × 1.8–5 mm, nearly concolourous brown to dark brown with the margins paler to white or concordantly bicolourous with dark brown to atropurpureous, often streaked centre and yellowish to white margins; scales of the adaxial petiole parts and beneath the upper scale layer on the crosiers discordantly bicolourous with most of the centre yellowish to golden like the margins; scale margins sometimes with some brown cells. Laminae ovate–elliptic, very often infected by a fungus, notable abaxially as brown to black spots restricted by the veins. Rachises muri-

cate, weakly aculeate, stramineous to pale brown, glabrous in basal parts adaxially, with some short (0.5–0.8 mm) pale brown hairs distally, glabrous abaxially except for scattered evanescent scurf similar to petiole scurf. *Pinnæ* to 45–69 cm long, distally narrowly green alate. *Pinnules* (6.1–)9.5–12.2 × (1–)1.8–2.8 cm, long linear to weakly long obovate, rarely long triangular, subsessile to short stalked to 2 mm, bases truncate to weakly cordate or rounded, apices long–acute to short attenuate; segments oblong to weakly obovate–oblong, patent to weakly ascending, with acute tips; basal segments of largest pinnules usually remote from the next segments, articulate or connected by a thin green wing to adjacent segments; glabrous adaxially or with 1–5 short (to 0.6 mm long) hairs on the midveins distally, without or with scattered white erect hairs (to 0.5 mm long) on the veins and some whitish to tan flattish to subbullate squamules abaxially, with subentire to weakly toothed margins and elongate tips. *Sterile veins* forked or simple, fertile veins forked. *Sori* costal to subcostal, in forks of veins. *Indusia* sphaeropteroid, opaque brown to tan, each with an apical umbo, remaining as shallow cups or irregularly shaped discs, sometimes appearing hemitelioid or vanishing entirely.

Distribution and habitat: *Cyathea dintelmannii* occurs in very wet montane forests at 1300–2550(–2850) m, mainly below 2000 m, in Peru and Bolivia. This is the first report of this species from Peru.

Additional specimens examined: PERU. CUZCO: La Convención, Dist. Vilcabamba, Espiritupampa, 12°54'25'S, 73°12'16'W, 1535 m, 22.vii.2004, *Calatayud et al.* 2582 (MO, UC); *ibid.*, 12°54'32'S, 73°12'43'W, 1544 m, 24.vii.2004, *Calatayud et al.* 2676 (MO, UC); *ibid.*, 12°54'31'S, 72°48'45'W, 2099 m, 19.iv.2004, *Calatayud et al.* 2714 (MO, UC); La Convención, Dist. Huayopata, Huyro, Balconpata, 12°52'01'S, 72°32'46'W, 2200 m, 20.iv.2004, *Huamantupa et al.* 4552 (MO, UC). OXAPAMPA: Dist. Oxapampa, P.N. Yanachaga–Chemillén, quebrada Yanachaga, 10°23'S, 75°28'W, 2250 m, 13.vi.2003, *Vasquez R. et al.* 28192 (MO, UC).

BOLIVIA. LA PAZ: Prov. Caranavi, Serranía Bella Vista, 44 km de Caranavi hacia Sapecho, 15°40'S, 67°29'W, 1300 m, 29.viii.1997, *Kessler et al.* 11562 (LPB, UC); PN-ANMI Madidi, sendero Keara–Mojos, desde Tokuaque antes de llegar a Chunkani, 14°38'S, 68°57'W, 2830 m, 10.xi.2001, *Jiménez & Callegos 1010* (LPB, UC); Estación Biológica de Tunquini, Hormuni Bajo, senda del campo de Dn. Pedro al pajonal atras del Río Cedrón ('senda de los monos'), 16°12'S, 67°52'W, 1850 m, 19.viii.2001, *Bach et al.* 1718 & 1720 (GOET, LPB); Serranía de Bella Vista,

15.1 km N of the bridge at Carrasco on the road to Palos Blancos (Alto Beni) 36 km N of Caranavi, 15°35'S, 67°34'W, 1500 m, 6.xii.1985, *Solomon 14845* (LPB, MO, UC). COCHABAMBA: Prov. Carrasco, 123 km antigua carretera Cochabamba–Villa Tunari, 17°08'S, 65°37'W, 2100 m, 9.vii.1996, *Kessler et al.* 7110B & 7118 (LPB, UC); Prov. Chapare, Territorio Indígena Parque Nacional Isiboro–Securú, Cordillera de Mosestenes, arriba de la Laguna Carachupa, 16°14'S, 66°25'W, 1350 m, 30.viii.2003, *Kessler et al.* 13047 (LPB, UC); entre Villa Tunari y Cochabamba, cerca del puente Río Carmen Mayu, 17°10'S, 65°44'W, 1900–1950 m, 1.iv.2000, *Lehnert 47, 48* (GOET, LPB, UC).

Notes: *Cyathea ruiziana* can be distinguished from *C. dintelmannii* by the denser and more persistent petiole scurf and by the presence of concoloured dark brown and bicoloured dark brown, white margined scales on the segments (vs. sparse petiole scurf and only concoloured whitish to tan scales on the segments of *C. dintelmannii*). Additionally, the petiole scales are generally more strongly bicoloured and often larger in *C. ruiziana* than in *C. dintelmannii*.

Cyathea straminea is easily distinguished from *C. dintelmannii* by its (almost) concoloured whitish petiole scales (vs. almost concoloured to discordantly bicoloured brown in *C. dintelmannii*). Plants of *C. straminea* with darker, discordantly bicoloured petiole scales are best distinguished from *C. dintelmannii* by the pale brown bullate squamules with whitish tips and flat whitish lanceolate squamules with dark brown marginal teeth in the laminar indumentum, which are present in all forms of *C. straminea* but absent in *C. dintelmannii*.

Another similar sympatric species is *C. austropallenscens*, which differs from *C. dintelmannii* in having tan to pale brown scurf consisting of appressed to ascending, round to lanceolate squamellae with irregularly fringed to crested margins (vs. scurf of whitish to tan squamellae with regularly crested, often abraded tips in *C. dintelmannii*), some dark brown to brown squamellae on the segments (vs. white to tan squamellae) and having few to many hairs on the veins adaxially and abaxially (vs. glabrous or nearly so abaxially).

The fungal infection in *Cyathea dintelmannii*, first visible as darker areas between the veins abaxially, eventually turning black and rising to a small cushion that stretches over the neighbouring veins, is a feature not known from any other *Cyathea* in this frequency and abundance.

10. *CYATHEA DIVERGENS* KUNZE (FIG. 8A, B)

Linnaea 9: 100 (1834). *Type:* Peru. Huánuco: Pampayaco, Jul 1829, *Poeppig s.n.* (diar. 1163) (holotype:

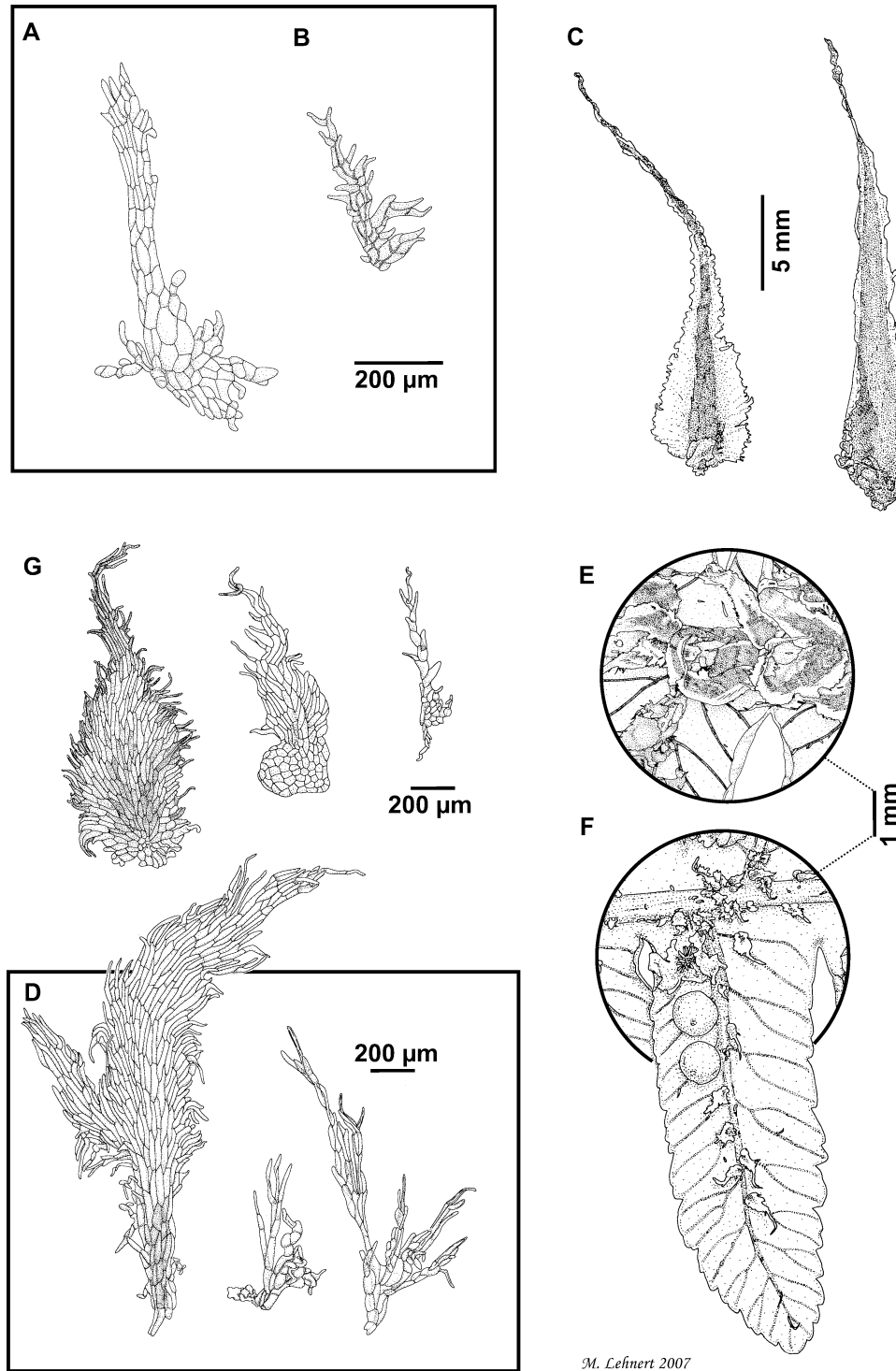


Figure 8. A, B, *Cyathea divergens*. A, white squamule from petiole scurf. B, brown squamule from laminar indumentum. All from *Cogollo et al.* 6162 (UC). C–G, *Cyathea ruiziana*. C, petiole scales, left with wide, intact margins, right with narrow, partially fragmented margins. D, squamules from petiole scurf. E, costule of sterile pinnule abaxially, with dense indumentum of larger scales. F, fertile segment abaxially, with sparse indumentum. G, variety of squamules from laminar indumentum; from left: small flat scale with dark marginal teeth, weakly bullate squamule with pale brown body and white margins, white hair-like squamule. All from *Lehnert* 69 (GOET).

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LZ, destroyed). Authentic specimens (fide Tryon, 1976): *Poeppig 219* (diar. 1152) [B!, K!, P!, GH (photo P), NY (fragments ex B, K)!].

Cyathea divergens var. *minor* Rosenst., Feddes Repert. Nov. Spec. Regni. Veg. 22: 2. 1925. *Type*: Costa Rica. La Palma, *Brade & Brade 108* (lectotype: n.l., designated by Tryon, 1976; isolectotype: NY!).

Cyathea equestris Kunze, *Linnaea*. 2: 9 (1834). *Type*: Peru. Huanuco: Pampayacu, Cerro Cristobal, July 1829, *Poeppig s.n.* [holotype: LZ, destroyed, K (fragment)!].

Cyathea globularis C.Presl, *Epim. Bot.* 30 (1849). *Ex char. Type*: 'Nova Grenada', *Linden s.n.* (holotype: n.l.).

Cyathea equestris var. *boconensis* H.Karst., *Linnaea*. 28: 456 (1856); *Fl. Columb.* 2: t.185, f.7. (1869). *Cyathea petiolulata* var. *boconensis* (H.Karst.) H. Karst., *Fl. Columb.* 2: 164. (1869). *Ex char. Type*: Venezuela. Mérida: Páramo de Bocono, Sierra de Mérida, *Karsten s.n.* (n.l.).

Alsophila petiolulata H.Karst. ex Mett., *Ann. Sci. Nat., Bot. sér.* 5, 2: 263 (nomen) (1864). *Cyathea petiolulata* H.Karst., *Fl. Columb.* 2: 163, t.185 (1869). *Type*: Venezuela. Mérida: 2000–2500 m, *Karsten 135* (holotype: B!).

Cyathea calva H.Karst., *Fl. Columb.* 2: 175, t.192 (1869). *Type*: Venezuela. Mérida: Sierra de Mérida, Escuque, 1000 m, *Karsten 127* [holotype: B!, NY (fragment B)!; isotype: K (ex. Rosenst.)!].

Cyathea firma Mett. ex Kuhn, *Linnaea* 36: 163 (1869). *Cyathea calva* var. *firma* (Kuhn) Domin, *Acta Bot. Bohem.* 9: 102 (1930). *Type*: Venezuela. Mérida: *Funck & Schlim 1228* [holotype: n.l., US (fragment)!].

Alsophila subaspera Christ in Pittier, *Prim. Fl. Costaric.* 3: 43. 190 (1901). *Cyathea subaspera* (Christ) Domin, *Pteridophyta* 263 (1929). *Syntypes*: Costa Rica. San José: Forêts du Copey, *Tonduz 11787* (A, GH!, NY!, P, US!), *11802* [B!, BR, P, NY (fragments B, BR)!], *12183* (NY!).

Tryon (1976) distinguished two varieties, var. *divergens* from Costa Rica and continental South America and var. *türckheimii* (Maxon) R. M. Tryon from Mexico to Nicaragua. Only the var. *divergens* is considered here.

Distinguishing characters: Trunks 5–8(–15) m tall, to 10–12 cm diameter, including adventitious root mantle to 25 cm, without old petiole bases, upper parts invested in pale scales. Fronds to 600 cm long, drooping. Petiole scales narrowly lanceolate to lanceolate, often falcate, 30–32 × 3 mm, their tips weakly twisted, with brown centres and white to stramineous margins, these sharply set, narrow to wide. Petiole scurf well developed, white to stramineous, mainly erect white lanceolate squamules 0.5–2 mm long (Fig. 8A), larger ones with darkened insertions, some-

times irregularly beset with dark brown to black marginal cells. Pinnules 14–17 × 3.5–5 cm, the largest ones long-stalked (14–19 mm), 1.5–4(–5) cm between the stalks, triangular, truncate at base, acute or short–attenuate at tip, the basal segments alternately placed, often remote from each other, veins glabrous abaxially except for appressed white unicellular trichomidia, few small, flattish, brown, ovate squamules with elongated tips and finely dissected dark brown squamules (Fig. 8B). *Indusia* sphaeropteroid, firm, fragments persistent.

Distribution and habitat: In moist montane forests at 1000–2500 m in Costa Rica, Panama, Colombia, Venezuela, Surinam, Ecuador and Peru.

Selected specimens examined: COSTA RICA. CARTAGO: Finca La Esperanza, c. 3 km E of Muñeco and 2 km SW of Navarro, 1200–1300 m, 13.vii.1970, *Lellinger 1120* (AAU, F).

PANAMA. Panamá: Cerro Jefe 100 m al N de la torre, 1000 m, 8.xi.1986, *Valdespino & Aranda 247* (AAU, COL).

COLOMBIA. ANTIOQUIA: Amalfi, via principal hacia Medellín, sector de la Cascada, 1650 m, 15.iv.2000, *Giraldo & Mejia 2034* (COL). CUNDINAMARCA: Pacho, bosques de Patasía, 2300 m, 27.v.1949, *Uribe Uribe 1976* (COL). CAUCA: Popayán, Río Molino & Vereda Santa Barbara, 1950 m, 14.vii.2003, *Munar & Ceballos 152* (COL). HUILA: La Argentina, Quebrada del Pueblo, 1850 m, 25.ix.1984, *Lozano et al. 3996* (COL). NARIÑO: La Unión, Cerro La Jacoba, 1990–2440 m, 31.vii.1977, *Díaz-P. et al. 872* (COL). NORTE DE SANTANDER: Loso and vicinity (N of Toledo), 2200–2400 m, 6–7.iii.1927, *Killip & Smith A. C. 20407* (COL). QUINDIO. Provincia de Mariquita, 1800 m, i.1852, *Triana 653* (COL). RISARALDA: Santuario, Vereda Las Colonias, margen derecha del Río San Rafael, 2500 m 25.ii.1983, *Torres et al. 2314* (COL). VALLE DE CAUCA: Carretera Cali–Popayán, Reserva Natural El Guayabo, 1500 m, 12.ix.1967, *Hagemann 353* (COL).

ECUADOR. NAPO: Quijos, Reserva Ecologica Antisana, Cordillera de los Guacamayos, sector oriente, cruce del oleoducto de la compañía ARCO, colección entre El Mirador y Camino de la Virgen, 00°38'S, 77°51'W, 2300 m, 12–14.i.1999, *Vargas & Navarrete 3489* (MO, QCNE).

PERU. PASCO: Oxapampa, Dist. Villa Rica, Centro Bocaz, road and trench to Purus, 10°38'S, 75°11'W, 1590 m, 19.ix.2003, *Perea et al. 376* (MO, UC); *ibid.*, centro poblado Palma (Centro Bocaz), 10°39'24'S, 75°09'42'W, 1736–1800 m, 16.i.2005, *Mellado et al. 2629* (MO).

Notes: *Cyathea divergens* is characterized by having large triangular and often long-stalked pinnules. Among the species treated here, only *C. corallifera* has similarly large pinnules, but those are usually sessile or short stalked. Both species differ in the colour and persistency of the indusia (brown and persisting in fragments in *C. divergens* vs. white to colourless and ephemeral in *C. corallifera*). The petiole scurf of both species contains white, large, long-lanceolate squamules, just as in *C. ruiziana*. These squamules have entirely white margins in the latter species, but bear dark brown marginal teeth in the other two (regularly in *C. corallifera*, irregularly in *C. divergens*). *Cyathea ruiziana* furthermore differs from *C. divergens* in sessile to subsessile pinnules and a laminar indumentum containing bicolourous scales and purely white fine scurf. The scurf on the leaf axes is mainly brown in *C. divergens* and hence similar to that of *C. carolihenrici* Lehnert (2003) and *C. meridensis* H. Karst. However, the scurf of *C. divergens* consists of small, hyaline, thin-bodied squamules whose numerous brown marginal teeth dominate the scurf colour; in *C. carolihenrici* and *C. meridensis*, these squamules are entirely dark brown to castaneous. The laminar scurf is well developed in the Peruvian collection of *C. divergens* chosen as reference material (Tryon, 1976) and in some specimens from Costa Rica and the Guyana Highlands; however, in most specimens from the northern Andes, the scurf on the leaf axes is scarce or absent. *Cyathea divergens* (as well as *C. corallifera* and *C. ruiziana*) can furthermore be distinguished from *C. carolihenrici* and *C. meridensis* by the white margined petiole scales and the white petiole scurf containing different-sized lanceolate squamules (vs. brownish to orange scale margins and dark brown, uniformly small scurf squamules in *C. carolihenrici* and *C. meridensis*).

11. *CYATHEA RUIZIANA* KLOTZSCH (FIG. 8C–G)

Linnaea 20: 439 (1847). *Type:* Peru. Huánuco (Pana-tahuas): 'In Peruviae Andium nemoribus,' Ruiz 72 (holotype: B!; isotype: US!).

Cyathea boliviana R.M.Tryon, Contr. Gray Herb. 206: 61 (1976). *Type:* Bolivia. Cochabamba: Chapare, Incachaca, Steinbach 9512 (holotype: GH; isotypes: BM!, F!, GH, GOET!, MO!, NY!, US!).

Distinguishing characters: Trunks to 15 m tall, 12–25 cm diameter, without persistent petiole bases when old, densely covered with them when young (less than 2 m high), then up to 40 cm diameter. Fronds to 250–350 cm long, patent to slightly erect, weakly arching. Petiole scurf dense, persistent, consisting of erect, whitish, multiciliate, lanceolate squamellae without marginal teeth (Fig. 8D), often

transient with larger scales. Petiole scales to 50(–70) × 6 mm, narrowly lanceolate to lanceolate with attenuate tips, discordantly bicolourous or basal scales also concordantly bicolourous, with dark brown to blackish centres and white to tan margins (Fig. 8C), margins often fragmenting, more brittle than the centres. Pinnules to 12 × 1.7(–2) cm, well spaced, sessile to subsessile (stalked to 1 mm), linear, tips long-acute to attenuate, bases truncate, basal segments never remote from the following ones; only few hairs on the midribs adaxially, few white erect hairs to 0.5 mm long scattered on and between the veins abaxially (Fig. 8F), often replaced by appressed brown unicellular trichomidia; finer squamules on midveins and veins similar to scurf on costules (Fig. 8F), larger ones completely white or brown with white margins, some small (1–2 mm long), discordantly bicolourous tan to brown scales with whitish margins and dark brown to blackish marginal teeth (Fig. 8E, G); bullate scales to 1 mm long with pale brown bodies and ciliate to fimbriate margins mainly distally on the segments (Fig. 8G). Indusia sphaeropteroid, firm, fragments persisting (Fig. 8F).

Distribution and habitat: Cool montane forests at 2000–2650 m in southern Peru and Bolivia.

Selected specimens examined: PERU. PASCO: Prov. Oxapampa, P.N. Yanachaga Chemillén, sector San Alberto, 10°32'S, 75°21'W, 2600 m, 16.iii.2003, Vasquez & Francis 28036 (UC, US). CUZCO: Prov. Paucartambo, carretera a Pilcopata, 2650 m, León 2204 (USM).

BOLIVIA. COCHABAMBA: Prov. Carrasco, 116 km antigua carretera Cochabamba–Villa Tunari, 17°08'S, 65°38'W, 2400 m, 6.vi.1996, Kessler *et al.* 7040 (GOET, LPB, UC). LA PAZ: Prov. Murillo, Valle del Río Zongo, along Río Jachcha Cruz, 32.2 km N of the pass, 16°07'S, 68°04'W, 2200–2300 m, 22.x.1987, Solomon & Moraes 17221 (LPB, MO, UC). SANTA CRUZ: Prov. Caballero, road Empalme–Karahuasi, c. 3 km down from the main road, 17°50.53'S, 64°42'6"W, 2500 m, 19.iii.2003, Lehnert 724 (GOET, LPB, UC).

Notes: *Cyathea ruiziana* was separated from *C. boliviana* by Tryon (1976) based on the following differences: occurrence of some lanceolate black scales with white fragile margins at the costa bases; white bullate scales are scarce or lacking; the squamules on laminae have less, sometimes no dark teeth in the white fragile margins. However, all these characters can be found separately or combined in *C. boliviana*. As *C. ruiziana* has priority, I include here *C. boliviana* under that name.

This species is apparently very variable in amount of laminar indument, but small white or bicolourous squamules with dark marginal cells are always present. Small plants have more of the pure white and bullate squamules. Larger plants, especially when fertile, have many bicolourous scales on the costules and concolourous dark brown, flattish squamules on the midveins. The petiole scurf of *C. ruiziana* is similar to that of *C. corallifera* and *C. divergens*, pure white, with transitions from small crested squamules to larger lanceolate scales, but petiolar squamules with dark marginal teeth, which may be present in the other two species, are absent from the scurf of *C. ruiziana*.

12. *CYATHEA SIMPLEX* R.M.TRYON (FIG. 9A–D)

Contr. Gray Herb. 206: 60 (1976). *Type*: Venezuela. Amazonas: Cerro Yutaje, Serranía Yutaje, Río Manapiare, infrequent along left fork of Caño Yutaje, 1250 m, 12.ii.1953, Maguire & Maguire 35194 (holotype: NY!; isotypes: GH, US!).

Distinguishing characters: Trunks c. 1 m tall, 3 cm diameter, without persistent petiole bases. Fronds to 150–160 cm long, patent to slightly erect, weakly arching; scurf dense, persistent, consisting of appressed, multiciliate, whitish squamellae to 0.6 mm long (Fig. 9B). Petiole scales to 25 × 3(–3.5) mm, narrowly lanceolate to ovate–lanceolate (Fig. 9A), discordantly bicolourous, or basal scales also concordantly bicolourous, with brown to dark brown (never blackish) centres and white margins with pale brown marginal cells, their apices usually concolourous brown; apical scales broader and lighter in colour than the basal ones (Fig. 9A). Pinnules to 4.7 × 1 cm, sessile to subsessile (stalked to 1 mm), linear oblong, tips acute to short–attenuate, bases truncate, basal segments never remote (Fig. 9C); segments completely glabrous on both sides or with erect white hairs 0.5 mm long along the margins (Fig. 9D), few auburn, flat, lanceolate squamules with crested margins on costules and midveins. Indusia sphaeropteroid (Fig. 9D), remaining as fragments.

Distribution and habitat: Only known from the type specimen; there is no geographical overlap with any other species treated here.

Notes: *Cyathea simplex* is similar to *C. austropallescens* regarding the petiole scurf (small pale brown squamules with short white cilia) and the hair distribution (mainly along margins of segments); both differ in the size of the fertile plants (just 1 m in *C. simplex* vs. 2–6 m in *C. austropallescens*) and in the amount and colour of laminar indumentum (very scarce, pale

brown lanceolate squamules vs. frequent, brown to dark brown, ovate to lanceolate squamules). *Cyathea bettinae* Lehnert (2004) is of similar stature as *C. simplex* but differs in having paler brown petiole scales (vs. dark brown in *C. simplex*) and less developed, often absent petiole scurf (vs. dense and mostly persistent).

13. *CYATHEA STRAMINEA* H.KARST. (FIG. 9E–G)

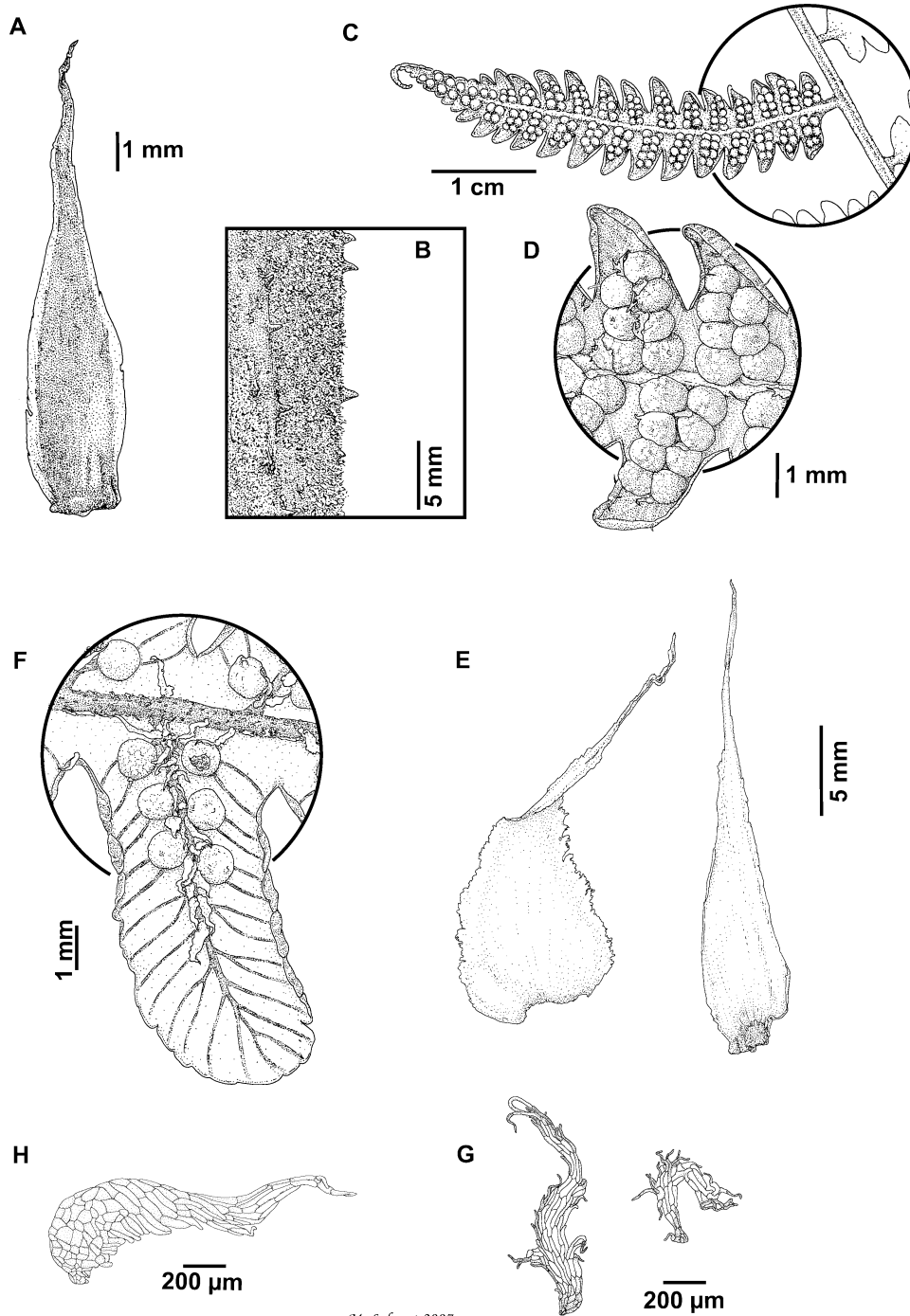
Linnaea 28: 457 (1856); Fl. Columb. II: t.182; t.183, f. III (1869). *Type*: Colombia. Quindío: ‘Crescit cum *Cyathea Quindiuensi* in declivitate montis glacialis vulcanici Tolima altitudine 2500 m,’ Karsten s.n. [holotype: n. l.; isotype: B (fragment)!].

Distinguishing characters: Trunks to 5(–8) m tall, to 11(–15) cm diameter, without persistent petiole bases when old, densely covered with them when young (less than 1.5 m high). Fronds to 210 cm long, patent, weakly to strongly arching distally, sometimes tips elongated and drooping; scurf on petioles loose, appearing flakey, not persistent, consisting of erect whitish squamellae 0.5–2 mm long with subentire margins. Petiole scales to 30 × 5 mm, lanceolate, mostly cream–white to stramineous, concolourous with only a thin brown stripe at the apex and marginal brown teeth, always darker at the pseudopeltate insertion (Fig. 9E), basal scales also irregularly striped in the centre, rarely also discordantly bicolourous, with brown to dark brown (never blackish) centres and pale brown margins; scales of a stiffly chartaceous texture, also sitting on the spines where they are long persisting. Segments without hairs on both sides or with few white hairs to 0.5 mm long on the midribs adaxially, abaxially mainly with small, white, dissected squamules on midveins and veins (Fig. 9F) and some flat (Fig. 9G) to bullate (Fig. 9H), lanceolate scales 1–4 mm long, entirely white to tan, with or without brown marginal teeth and basal brown spot (Fig. 9G), sometimes also with thin, elongate, concolourous white to brown scales. Indusia sphaeropteroid with umbo (Fig. 9F), quite fragile, fragments remaining.

Distribution and habitat: In elfin forests and open páramo scrub, rarely in forest understories at 2400–3800 m in Venezuela, Colombia, Ecuador, Peru and Bolivia.

Selected specimens examined: VENEZUELA. TRUJILLO: P.N. Guaramacal, ridge Agua Fria, 09°16.70'N, 70°08.65'W, 2700–2800 m, i–ii.1996, Stergios & Zambrano 17736 (PORT, UC).

COLOMBIA. CAUCA: 55 km on road from Totoro to Inza, (E of páramo de Guanacas), 2.viii.1972, Barrington 482 (COL). NARIÑO: Pasto, ‘Selva El Campan-



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Figure 9. A–D, *Cyathea simplex*. A, petiole scale. B, detail of petiole with scurf. C, pinnule. D, fertile segment abaxially. All from Maguire & Maguire 35194 (NY). E–H, *C. straminea*. E, petiole scales from pale variety. F, segment of pinnule abaxially. G, small lanceolate squamules with dark marginal teeth from laminar scurf. H, weakly bullate squamule from midvein. All from Jiménez 1872 (UC).

ero, 5 km SW of la Granja Botana, 8.viii.1972, Barrington 505 (COL); Pasto, Río San José, upper part of Río Bobo, 3350 m, 13.vii.1991, Ramirez-P. & Cuayal 839 (COL). PUTUMAYO: Comisariato de Putu-

mayo, S side of Laguna de la Cocha, páramo of Sta. Lucia (source of Río Alisales), 2900–3100 m, 9.i.1941, Cuatrecasas 11856 (COL). QUINDIO: 'Quindiu,' Karsten s.n. (B).

ECUADOR. CARCHI: *c.* 1/2 h E of Huaca, past Colonia Huaceña, (*c.* 00°35'S, *c.* 77°42'W), 3100–3200 m, 19.ii.1989, *van der Werff & Palacios 10605, 10611* (AAU, QCA, QCNE, UC); carretera Julio Andrade–El Carmen, 18 km, 00°38'N, 77°40'W, 3800 m, 16.v.1982, *Balslev et al. 2536* (AAU, B, QCA); road Tulcan–Maldonado, *c.* 10 km from Maldonado, 00°52'N, 78°06'W, 2550 m, 5.viii.1976, *Øllgaard & Balslev 8498* (AAU). LOJA: Parque Nacional Podocarpus, carretera Yanganá–Cerro Toledo, 04°23'S, 79°08'W, 2750 m, 1.i.1995, *Palacios & Tirado 12952* (MO, QCNE). MORONA–SANTIAGO: E of pass on Gualaceo–Limon road, 03°00.27'S, 78°39.10'W, 3000–3200 m, 15.xi.2004, *Lehnert 1565* (GOET, QCA, UC). NAPO: Oyacachi, *c.* 1.5 km SE of village, S of river, 00°13'S, 78°03'W, 3200 m, 27.x.1995, *Øllgaard & Navarrete 1244* (AAU, QCA, QCNE); Reserva Ecológica Cayambe–Coca, Cuyuja–Quito 5 km, going up the slope NE of the Hacienda 'La Flor del Bosque,' 3250 m, 23.i.1993, *Gavilanes 1085* (B, QCA, QCNE); NE side of Cerro Sumaco, 00°35'S, 77°39'W, 3100–3300 m, 27.iv.1979, *Løjtntant & Molau 12884* (AAU). PICHINCHA: Cayambe Canton, 00°07'N, 77°57'W, 3420 m, 27.xii.1999, *Cuamacas & Gudiño 456* (MO, QCNE).

PERU. AMAZONAS: Chachapoyas, carretera Leymebamba–Balsas, 16 km, 06°43.2'S, 77°50.7'W, 3300 m, 7.viii.2002, *Lehnert 252* (GOET, USM, UC). SAN MARTIN: Prov. Mariscal Caceres, P.N. Río Abiseo, en valle de Chochos, 3300 m, 28.vi.1988, *León & Young 2027* (F, USM); Prov. Mariscal Caceres, P.N. Río Abiseo, en valle de Chochos, 28.vi.1988, *León & Young 2031, 2032* (USM).

BOLIVIA. LA PAZ: Prov. Franz Tamayo, PN-AMNI Madidi, trail Pelehuco–Mojos, Tambo Quemado (camping site), going down trail to Chunkani, passing three crosses, 14°39'S, 68°57'W, 3470 m, 6.v.2003, *Jiménez 1872* (LPB, UC).

Notes: Specimens of *Cyathea straminea* from northern Peru often have bicolourous brown scales with white margins; plants with the typical concolourous whitish petiole scales are common in Ecuador and Colombia and also occur in southern Peru and Bolivia. Personal observations in southern Ecuador (Prov. Morona–Santiago) showed me that both colour forms can occur in one population under the same abiotic conditions. Despite the divergent appearance of both forms, I do not think that a distinction of varieties as in *C. cytolepis* is justified because the variability of other characters does not correlate with the change of colour (e.g. abundance of laminar indumenta, frequency of bullate squamules, pinnule size).

Specimens of *C. straminea* with bicolourous brown scales strongly resemble *C. austropallescens* and *C. cytolepis* var. *cytolepis*, but can be distinguished by the

presence of dark marginal teeth in the flat, whitish scurf squamules, which the other two species lack. Furthermore, the pale brown bullate squamules on the segments of *C. straminea* do not occur in *C. austropallescens*, which has more or less flat, predominantly dark brown squamules. The petiole scurf of *C. straminea* is rather poor; the few subentire squamules are whitish to tan and usually lack dark marginal teeth, which are typical of the larger scales on petioles and laminae. Most closely related is *C. atahuallpa*, which can be distinguished by its concolourous, paler petiole scales, denser petiole scurf and the complete lack of dark marginal teeth in scales and squamules.

DUBIOUS AND EXCLUDED NAMES

Cyathea borjae Sodiro, Crypt. Vasc. Quit. 504 (1893). Type: Ecuador. Pichincha: 'Pichincha, 900–1200 m,' Sodiro *s.n.* (holotype: n.l.) = *Alsophila cuspidata* (Kunze) D.S. Conant, J. Arnold Arbor. 64: 371 (1983). One authentic specimen seen ['Corazon, ix.1878,' Sodiro *s.n.*, SI (no. 22788)] clearly belongs to this species of *Alsophila* and fits Sodiro's description, which mentions the characteristic black spines and very narrow scales on the petiole (Sodiro, 1893).

Hemitelia subcaesia Sodiro, Crypt. Vasc. Quit. 522 (1893). Type: Ecuador. Prov. unknown: 'Bosques subandinos de la Cordillera Occidental hasta 2800 m,' Sodiro *s.n.* (holotype: n.l.). Authentic specimens determined by Sodiro apparently belong to *Cyathea brachypoda* Sodiro but lack petioles, which are crucial to determine this species confidently: 'Ecuador. Pichincha, Niebly,' Sodiro *s.n.* (NY!), 'Canzacoto, February 1882,' Sodiro *s.n.* [P!, GH (photo P)], 'Ecuador, April 1874,' Sodiro *s.n.* (US!), 'in silv. suband. m. Corazón, 2000 m,' Sodiro *s.n.* [SI (no. 22872)!].

Cyathea divergens var. *hirta* Losch, Mittl. Bot. Staatssaml. München 1: 20 (1950). Type: Costa Rica. Chirripó Grande, to 2000 m, 1.v.1932, *Kupper 1265* (holotype: M).

Listed as synonym of *Cyathea divergens* var. *divergens* by Tryon (1976). The brief description mentions a pubescence of short hairs on the pinnules abaxially, which is not characteristic of the species in general. As I have yet not been able to see the type specimen, I cannot place this name confidently under *C. divergens*.

Cyathea petiolulata var. *pastoensis* Hieron., Engl. Bot. Jahrb. 34: 437 (1904). Type: Colombia. Pasto: 'prope Altaquer et San Pablo, Cordillera de Pasto,' Lehmann 81 (holotype: n.l.). Listed as synonym of *Cyathea divergens* var. *divergens* by Tryon (1976). The description mentions a pubescence of short hairs on the pinnules abaxially, which is not characteristic of the species in general. As I have yet not been able to locate the type specimen, I cannot place this name confidently under *C. divergens*.

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NOTE ADDED IN PROOF

DUBIOUS SPECIES

Cyathea chimborazensis (Hook.) Hieron., *Hedwigia* 45: 230 (1906). *Alsophila chimborazensis* Hook., *Syn. Fil.* 37 (1866). *Cyathea caracasana* (Klotzsch) Domin var. *chimborazensis* (Hook.) R. M. Tryon, *Contr. Gray Herb.* 206: 81 (1976). *Type*: Ecuador. Chimborazo: "Chimborazo, Ecuador," 914–1219 m, *Spruce 5743* (holotype: K [2 sheets]!; isotypes: B [fragm.]!, BM!, P!, US [fragm.]!).

Early in this study, I misapplied this name to *Cyathea cystolepis* Sodiro. The laminar indumentum in the type material of *C. chimborazensis* varies in amount but generally agrees well morphologically with that of *C. cystolepis*. The pinnules, however, are much wider and more widely placed along the costae than in *C. cystolepis* and are more reminiscent of *C. corallifera* Sodiro. Furthermore, the two preserved petioles differ greatly in their type of scurf, the one at K having larger lanceolate squamules like *C. corallifera* and the one at BM having the small multiciliate squamules of *C. cystolepis*. Thus *C. chimborazensis* cannot be placed confidently in synonymy of either species. The type is either a mixed collection or a hybrid between the two species. Judging from the conflict between laminar dissection and indumentum, the latter case seems more likely.