Phytotaxa 26: 39–59 (2011)
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

Species of *Cyathea* in America related to the western Pacific species *C. decurrens*

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Abstract

The species allied to *Cyathea platylepis* are recognized as a distinct group among Neotropical *Cyathea*, and are regarded as closest relatives to the few Paleotropical members of the genus in the strict sense. All species have slender trunks that shed old petioles cleanly, inermous petioles with relatively few, ovate-lanceolate brown scales, relatively strongly dissected (to tripinnate-pinnatifid) laminae, and proximally positioned sori with hemitelioid indusia. Most of the remaining Neotropical species referred to as the *C. multiflora*-group fall into two distinct groups. The group of *Cyathea vilhelmii* differs from the *C. platylepis* group chiefly in having dense petiolar scurf, and bicolorous or concolorous white petiole scales. These species occur at high elevations in the Andes and Central America. The group of *Cyathea multiflora* is heterogeneous in habit and laminar dissection but is characterized by a medial to marginal position of the sori and a preference of lower montane and lowland forests. It includes the species allied to *C. multiflora* and *C. andina*, as well as some species formerly regarded as belonging to *Sphaeropteris*. All groups may have to include species that either have different types of indusia or lack them in order to represent natural taxa. Five names have been reinstated in the course of this study and replace commonly used names: *Cyathea austroamericana* (= *C. multiflora pro parte*), *C. boryana* (= *C. andina pro parte*), *C. leucolepismata* (= *C. amazonica*), *C. lindigii* (= *C. multiflora pro parte*), *C. traillii* (= *C. reginae*), and *C. vilhelmii* (= *C. heliophila*). *Cyathea vaupensis* is recognized at species level. A new name is chosen for *Cyathea panamensis* = *Cyathea rojasiana*. Keys to all species are included.

Key words: *Alsophila*, hemitelioid indusia, Neotropics, Paleotropics, provincialism, vegetative reproduction

Introduction

The scaly tree fern family Cyatheaceae comprises ca. 600 species distributed in the tropics and southern temperate regions (Smith *et al.* 2006). They display great ecological conservatism as most species are terrestrial plants of moist forests, and are intolerant to longer periods of drought or frost. Furthermore they show a greater provincialism and endemism than most fern groups (Tryon & Gastony 1975). Together with their good fossil record dating back to the lower Cretaceous they would be great study objects for retracing the evolution of the whole tropical rain forest biome. However, a well-resolved taxonomy, which would be the basis for such studies, is still unavailable (Holttum & Tryon 1977).

Holttum (1982) pointed out that some Cyatheaceae from the western Pacific are more closely related to South American taxa than to any other group from the Old World. He further indicated that these species, which he named the *Cyathea decurrens* (Hook.) Copeland (1929: 356)-group, have great affinity to the species of the *C. multiflora* Smith (1793: 416)-group (Tryon 1976), and among them especially to *C. platylepis* (Hook.) Domin (1929: 264). Both groups are characterized by the presence of hemitelioid indusia and fronds with bipinnate-pinnatifid or stronger dissection, but these characters alone have been proven to define only artificial groups in the family.

Recent phylogenetic studies (Conant *et al.* 1995, Korall *et al.* 2007) revealed that the *Cyathea decurrens*-group (eight species) is sister to all Neotropical *Cyathea* in the strict sense (ca. 200 species), including the

Accepted by M. Christenhusz: 30 Jun. 2011; published: 29 Jul. 2011

genera *Trichipteris*, *Cnemidaria*, *Hymenophyllopsis*, and *Sphaeropteris* subg. *Sclephropteris* (Windisch 1977, Christenhusz *et al.* 2011). While the sampling in the phylogenetic studies of Korall *et al.* (2006, 2007) was sufficient for the *C. decurrens*-group as it included a third of the species and spanned the whole morphological variability of the group (Holttum 1982), the *C. multiflora*-group *sensu* Tryon was represented by only two species (*C. multiflora*, *C. parvula* (Jenm.) Domin (1929: 264). Their distant position from each other among the Neotropical species of *Cyathea* further fomented the disutility of indusial characters for circumscribing natural groups. However, some natural groups, like the *Cnemidaria*-clade and the *C. decurrens*-group (Korall *et al.* 2007), are marked by a predominance of hemitelioid indusiate species. This could mean that more natural groups may be found in this alliance on the basis of morphology if additional characters are considered.

In this paper I present a compendium of the species with an affinity to *Cyathea decurrens sensu* Holttum and *C. multiflora sensu* Tryon, and reorganize them in an attempt to outline natural groups. These include also species without hemitelioid indusia (i.e., indusia either of different types or lacking), which are mentioned and discussed shortly under the most similar species.

Materials and methods

Material of Neotropical *Cyathea* was studied at GOET, STU, and UC, including loans made available from all herbaria mentioned in the acknowledgments but chiefly from MO, NY, and US. Material of the *C. decurrens* group including most of the types was loaned from or studied directly in B, BM, and K. Special attention was drawn to the trunk morphology. This information was obtained either personally on field trips in South America and to New Guinea, or gathered from literature and the Internet for Central American and Paleotropical species.

Terms used here largely follow Lellinger (2002). The following short glossary contains important terms that have been devised especially for the Cyatheaceae or that are equivocal because they have been used differently in previous studies.

Costa, although it translates as midrib or midvein, refers to the main axis of the pinna, and costule is the next higher order of axis that is branching from it, irreverent from the total degree of dissection of the whole lamina. Midvein refers to the main axis on the ultimate segments, and the lateral veins branching from it are just called veins.

The position of the sori between margins and midveins of the ultimate segments is traditionally defined by the terms marginal, medial, and costal. The last term is replaced here with the term proximal because of the abovementioned ambiguity of the stem word costa. The shape of the indusia is hemitelioid if they do not reach around the receptacles completely, as it is the case in all species studied here in detail. Windisch (1978) further distinguished between small, usually appressed ones (hemitelioid) and large, arching ones (flabellate), but this rarely adopted distinction is not followed here in favor of discrete measurements. All other types of indusia reach completely around the receptacles and vary in shape from disc-like (discoid) to shallow cups (meniscoid, cyatheoid) to deep urns (urceolate, subsphaeropteroid) to completely closed globes (sphaeropteroid).

Results

Four groups can be confidently defined based on morphology alone. The group of *Cyathea decurrens* contains at least eight species, which are strictly Paleotropical. The definition by Holttum (1982) is only amended here with trunk characters, which are given below. The group of *Cyathea platylepis* contains only two species from the Guayana Highlands. One of them, *C. platylepis*, is very close to *C. robertsiana* (F.v.Muell.) Domin (1929: 263) from Australia but differs in having densely scaly trunks at least at the apices; *Cyathea robertsiana* has

caduceus scales only on the petioles. As in the *C. decurrens*-group, presence of scales and hairs on the laminae are subject to strong variation between the species. The group of *Cyathea vilhelmii* Domin (1929: 264) contains five species from high elevations (2000–3200 m) in Central America and the Andes, which are characterized by having dense petiole scurf and scales that are either strongly bicolorous or almost concolorous and white.

A peculiarity of these three groups is that the petioles are inermous, are shed early and cleanly, and do not form a tight fascicle around the trunk apices (Fig. 1). Thus the crosiers of the next two or three generations of fronds are easily visible. The species further agree in having their sori proximal to subproximal to the midveins, and relatively small, mostly round frond scars that are remote from each other.

The group of *Cyathea multiflora* contains 25 species from lower elevations (0–2000 m, rarely higher) that are quite heterogenic but differ from the preceding groups in having medial to marginal sori and often aculeate petioles that are either persistent or at least not cleanly shed (Fig. 2). This group may be roughly divided between the species allied to *C. multiflora sensu stricto*, which have more or less medial sori with predominantly small indusia and mostly coarsely serrate segment margins, and to the species allied to *C. andina* (H.Karst.) Domin (1929: 263), which have supramedial to submarginal sori with mostly large indusia that split into equal halves at maturity and subentire to finely crenate or serrate margins.

Discussion

The distinction of the groups of *C. decurrens*, *C. platylepis*, *C. vilhelmii*, and *C. multiflora* based on morphology is clear and unambiguous. The split within the group of *Cyathea multiflora*, however, is not clear, as the example of *C. boryana* (Kuhn) Domin (1929: 263; subgroup of *C. andina*) and *C. leucolepismata* Alston (1958: 231; subgroup of *C. multiflora*) shows. Both show the same habit in the field, including relatively small size, erect to patent, weakly arching fronds, and pale, mostly stramineous petiole scales. While they can be easily distinguished (laminae hairy abaxially in *C. leucolepismata* vs. glabrous abaxially in *C. boryana*), the size of the indusia and the position of the sori are intermediate between the two subgroups. *Cyathea boryana* and *C. leucolepismata* are assigned to their respective subgroups based on the shape of the segment margins.

The same example nicely illustrates the affinity of the species with hemitelioid indusia to those with different indusial characters. *Cyathea leucofolis* Domin (1929: 263) from southeastern Brazil is an exindusiate species that can be easily mistaken for either *C. boryana* (Guianas) or *C. leucolepismata* (Andes). Due to its pubescence it resembles *C. leucolepismata* more than *C. boryana*, but its segment shape is divergent from both. Further examples in the group of *C. multiflora* are *C. pinnula* (Christ) Domin (1930: 148) with its reduced indusia, which resembles the exindusiate *C. pilosissima* (Baker 1874: 457) Domin (1929: 263). In the group of *C. vilhelmii*, *C. serpens* (R.M.Tryon) Lehnert (2009: 50) and trunkless plants of *C. ars* Lehnert (2009: 48) and *C. vilhelmii* may resemble the exindusiate *C. frigida* (Karsten 1859: 61) Domin (1929: 263), which is often found growing together with these species. *Cyathea holdridgeana* Nisman & L.D.Gómez (in Gómez 1971: 168), on the other side, resembles *C. moranii* Lehnert (2006: 321), which has sphaeropteroid indusia.

A noteworthy facet is the vegetative reproduction by means of lateral buds and shoots, which occurs in the groups of *Cyathea decurrens* (e.g., *C. epaleata* (Holttum) Holttum (1982: 386)*, C. stokesii* (E.Brown) Hallé & Florence (1986[1987]: 157)) and *C. multiflora* (e.g., *C. parvula, C. rufescens* (Kuhn) Domin (1929: 264)). Such asexual reproduction is widespread in the genus *Alsophila* and Paleotropical species of *Sphaeropteris*, but is rather uncommon in *Cyathea*. Species of the *Cnemidaria* clade (Korall *et al.* 2007) have prostrate rhizomes that may branch in the posterior parts with age. Similarly, *Cyathea bipinnatifida* (Baker 1874: 456) Domin (1929: 263), *C. microphylla* (Klotzsch 1844: 541) Domin (1929: 263) and their respective allies have thin erect trunks that produce buds and new erect shoots once they have inclined or fallen down. Regular formation of buds and lateral shoots is further observed in the group of *C. xenoxyla* Lehnert (2003: 175).

These species, *C. planadae* Arens & Smith (1998: 51) and *C. xenoxyla*, have aculeate petioles and sphaeropteroid indusia, but strongly resemble species of the *C. decurrens*-group in their trunk morphology. Otherwise lateral buds are formed in *Cyathea* only when the apex has been damaged or extirpated.

It can be concluded that Holttum's assumption about the relationships between the Paleotropical and Neotropical species of *Cyathea sensu stricto* is still valid and has been partially supported by recent phylogenetic studies (Korall *et al.* 2007). The age and current distribution of the genus suggest a Gondwana-centered distribution in the past or a migration of the last common ancestor between South America and Australasia across Antarctica. It is curious in this context that all Neotropical species that bear resemblance to the *C. decurrens*-group occur in the north of South America and the Andes but not in southeastern Brazil, which was evidently a stepping stone for several south-temperate and circumantarctic taxa to the Andes (Collinson 2001). Maybe species with closer affinities to the *C. decurrens*-group were once present in the Atlantic rain forests of Brazil and became extinct due to a period of unfavorable growing conditions (e.g., desiccation and lower average temperature during the glacial periods). However, this possibility seems low in the current presence of an abundant tropical fern flora in this region, which is characterized by a high percentage of endemics, including Cyatheaceae. Another possibility is that the Brazilian species close to *C. decurrens* and *C. platylepis* were outcompeted by invading species with similar ecological demands. Some species of Cyatheaceae belonging to widespread, mainly Andean-Mesoamerican species groups, are present in southeastern Brazil (e.g., *Cyathea delgadii* Sternberg (1820: 47), *C. poeppigii* (Hooker 1844: 43) Domin (1929: 263), and species allied to *C. armata* (Swartz 1788: 134) Domin (1930: 32) and *Sphaeropteris horrida* (Liebmann 1849: 279) Tryon (1970: 200)). Their absence from the Guayana Highlands indicates that they are not Gondwana relicts and probably have not originated in eastern Brazil but have colonized this area relatively recently. Because they are not directly competing, these invading species could not have led to the extinction of putative relict species belonging to the *C. decurrens* and *C. platylepis* groups in southeastern Brazil. The newcomers are mainly found in sunny, often disturbed habitats, whereas the species groups treated here prefer shady conditions.

A reconstruction of the timing of events that have led to the present pattern of diversity in Neotropical Cyatheaceae will only be possible if species of the *Cyathea platylepis*-group, which are the Neotropical group mophologically nearest to Paleotropical species of *Cyathea*, and a representative number of eastern Brazilian species are included in phylogenetic analyses.

Systematic treatment

Key to the species of the genus *Cyathea*

1 Sori strictly marginal on vein tips with bivalved indusia, fronds highly dissected, ultimate segments linear to filiform or narrowly cuneate, laminar texture thin, stomata lacking ..... ***Cyathea* subg. *Hymenophyllopsis*** (see Christenhusz 2009)

– Sori dorsal on veins, proximal to submarginal, if marginal with bivalved indusia then fronds only bipinnate and laminar texture coarse, stomata always present 2

2 Fronds pinnate to pinnate-pinnatifid, if pinnae basally pinnatisect to pinnate then free segments few and never remote ..... **Group of simply pinnate species** (Lehnert in prep.)

– Fronds bipinnate or more complex, if fronds distally only once pinnate then segments clearly remote from each other in proximal half 3

3 Fronds bipinnate, pinnules with entire to shallowly crenate margins (not incised more than 1/5 towards the costules) ..... **Group of bipinnate species** (Lehnert in prep.)

– Fronds at least bipinnate-pinnatifid 4

4 Indusia absent, but sori sometimes subtended by laminar squamules that show a cellular pattern and never reach completely around the receptacles, these scales irregularly present and ephemeral ..... **species previously treated as *Trichipteris*** (Barrington 1978) **and *Sphaeropteris* subg. *Sclephropteris*** (Windisch 1977)

– Indusia present, either scale-like (hemitelioid) but without cellular pattern or fragmented to an irregular disc reaching completely around the receptacles 5

5 Indusia cyatheoid to sphaeropteroid, sometimes fragile and evanescent but remaining as complete ring around the

receptacles ..... **Various species of *Cyathea*** (Tryon 1976, Lehnert 2008, 2009)
– Indusia hemitelioid, reaching 1/5 to ½ (rarely more) around the receptacles, larger ones often splitting into two equal halves at maturity 6
6 Sori medial to submarginal, petioles muricate to aculeate (rarely inermous), trunks usually covered in old petiole bases, petioles forming a fascicle around the apex [regular adventitious buds on trunks only in *C. parvula*, basal shoots in *C. rufescens*, Neotropics] ..... **IV. Group of *Cyathea multiflora***
– Sori proximal to subproximal, petioles inermous to weakly verrucate, trunks not covered in old petiole bases (petioles may not be shed in trunkless plants), petioles not forming fascicles around trunk apices 7
7 Petiole scales strongly bicolorous, blackish to brown with grayish to whitish margins or concolorous, stramineous to white, petiole scurf usually dense, whitish, paraphyses ± the same length of the sporangia [adventitious buds on trunks only formed after injury] ..... **III. Group of *Cyathea vilhelmii***
– Petiole scales concolorous, brown to castaneous, or weakly bicolorous with paler brown margins, petiole scurf absent or sparse, brown, paraphyses shorter to longer than the sporangia 8
8 Trunk apices with scales. Adventitious buds on trunks only formed after injury. Neotropics ..... **II. Group of *Cyathea platylepis***
– Trunk apices without scales except on crosiers. Regular adventitious buds on trunks in *C. epaleata* and *C. stokesii*. Australasia ..... **I. Group of *Cyathea decurrens***

I. Group of *Cyathea decurrens*

Trunks to 8 m tall, slender, without old petiole bases, 3–10(–15) cm in diameter, sometimes with buds below the apex that grow into lateral branches (*Cyathea epaleata*, *C. stokesii*), apices not hidden in tight fascicles of petioles, epidermis often bright green when young, darkened with age to dark brown, with relatively large pneumathodes below the frond scars, without indument except for some large caduceus scales on the apices; petioles inermous, with caduceus scales, lacking scurf, petioles soon caduceus, leaving round to elliptic, well-spaced scars, fronds bipinnate-pinnatifid to quadripinnate-pinnatifid, pinnules linear-oblong with acute to caudate tips, fine indument lacking to abundant, with flat to bullate squamules and short white hairs, sori proximal to subproximal, indusia always present, hemitelioid, either small and appressed, or large and arching, paraphyses shorter to longer than sporangia. Spore morphology variable, exospore finely pitted or with large equatorial pores, perispore lacking, echinate or baculate.

Ecology and distribution:—Species of moist montane forests and ridge top vegetation, widespread but local in the islands of the western Pacific and in northeast Australia.

Remarks:—This group may contain more, yet undiscovered or unrecognized species.

Key to the species

1 Bullate squamules abaxially on midveins and costules; fronds to quadripinnate-pinnatifid 2
– Squamules if present mostly not bullate; fronds to tripinnate-pinnatifid 5
2 Indusia distinct, not hidden by the sporangia 3
– Indusia small, hidden by the sporangia 4
3 Paraphyses thick, pale, much longer than the sporangia ..... ***Cyathea howeana***
– Paraphyses slender, shorter than the sporangia ..... ***Cyathea alata***
4 Paraphyses thick, pale, much longer than the sporangia, small appressed hairs abundant on adaxial laminar surfaces between the veins ..... ***Cyathea croftii***
– Paraphyses slender, shorter than the sporangia, small appressed hairs lacking ..... ***Cyathea decurrens***
5 Indusia distinct, not hidden by the sporangia 6
– Indusia small, hidden by the sporangia 7
6 Lamina lacking hair and scales; trunks with adventitious buds and lateral branches ..... ***Cyathea epaleata***
– Lamina abaxially with abundant scales, mostly flat, abaxially with long hairs; trunks without adventitious buds and lateral branches ..... ***Cyathea cicatricosa***
7 Paraphyses thick, pale, much longer than the sporangia, small appressed hairs abundant on adaxial laminar surfaces between the veins; trunks without adventitious buds and lateral branches ..... ***Cyathea robertsiana***
– Paraphyses slender, shorter than sporangia, small appressed hairs lacking; trunks with adventitious buds and lateral branches ..... ***Cyathea stokesii***

1. ***Cyathea alata*** (Fourn.) Copeland (1931: 377). *Alsophila alata* Fournier (1873: 349). Type:—NEW CALEDONIA. *Balansa 1589* (holotype K, isotype UC)

Distribution and habitat:—New Caledonia, widespread in humid forests at 350–1200 m.

2. ***Cyathea cicatricosa*** Holttum (1964: 274). Type:—NEW CALEDONIA. Nord: Mt Ignambi, near the summit, 1200 m, *Green 1778* (holotype K)

Distribution and habitat:—New Caledonia, endemic to Mont Ignambi, in humid montane forests on metamorphic rocks at 1200 m.

3. ***Cyathea croftii*** Holttum (1982: 387). Type:—PAPUA NEW GUINEA. Admiralty Islands: Manus Island, 500 m, *Croft 1204* (holotype K)

Distribution and habitat:—Vogelkop-Peninsular, West Papua, Indonesia, on old landslides at 1200-1600 m and Admirality Islands, Manus Island, in undergrowth of slope forests at 500 m.

Remarks:—In March 2011, I found *Cyathea croftii* (Fig. 1) on the Vogelkop Peninsular, Prov. West Papua, Indonesia, which was previously only known from Manus Island, Admirality Islands, Papua New Guinea. Its presence was anticipated because of unconfirmed reports of a scaly tree fern on the mainland of New Guinea characterized by spores with verrucate exospore (Robert Johns, David S. Conant, personal communication). Such spores are common in Neotropical *Cyathea sensu stricto*, but not known from *Alsophila* and *Sphaeropteris*, which were the only genera of Cyatheaceae hitherto known from the main island of New Guinea. A thorough comparison of both collections is still pending.

4. ***Cyathea decurrens*** (Hook.) Copeland (1929: 356). *Alsophila decurrens* Hooker (1844: 51). Type:—without locality, *Nightingale s.n.* (holotype K).

Alsophila subbullata Copeland (1939: 79). Type:—FIJI. *St. John 18304* (holotype K, isotypes MICH n.v., NSW n.v., UC).

Distribution and habitat:—New Ireland, Solomon Islands, New Hebrides, Fiji, Samoa, Cook Islands, in understory of moist montane forest at 500–1000 m.

Remarks:—Holttum (1964) recognized *Cyathea decurrens* var. *vaupelii* (Brause) Domin (1930: 110) from Samoa, which is only distinct by being larger than the average.

5. ***Cyathea epaleata*** (Holttum) Holttum (1982: 386). *Cyathea decurrens* (Hook.) Copel. subsp. *epaleata* Holttum (1964: 249). Type:—FRENCH POLYNESIA. Tahiti: Papenoo, Orofena, *Grant 4233* (holotype K).

Distribution and habitat:—Tahiti, rare in ridge top forests above 700 m.

Remarks:—This species apparently produces lateral shoots regularly (Fig. 1).

6. ***Cyathea howeana*** Domin (1929: 264), *nom. nov.* for *Hemitelia moorei* Baker (1872: 252), not *Cyathea moorei* Baker (1874: 453). Type:—AUSTRALIA. Lord Howe Island: *Moore 4, 12, 25, 68* (syntypes K)

Distribution and habitat:—Australia, Lord Howe Island.

Remarks:—The petioles are bright green and lack linear lenticels. The frond scars on the trunk are conspicuously round, like in *C. cicatricosa* (Fig. 1) and *C. stokesii*.

7. ***Cyathea robertsiana*** (F.v.Muell.) Domin (1929: 263). *Alsophila robertsiana* Müller (1865: 65). Type:—AUSTRALIA. Queensland: Rockingham Bay, *F. v. Müller s.n. [Dallachy s.n.]* (holotype MEL n.v., isotypes B, K).

Distribution and habitat:—Australia, northeast Queensland, humid tropical forests at 300–1500 m.

Remarks:—The species is usually found as a pioneer on landslides and along road cuts but it is difficult to cultivate (Large & Braggins 2004).

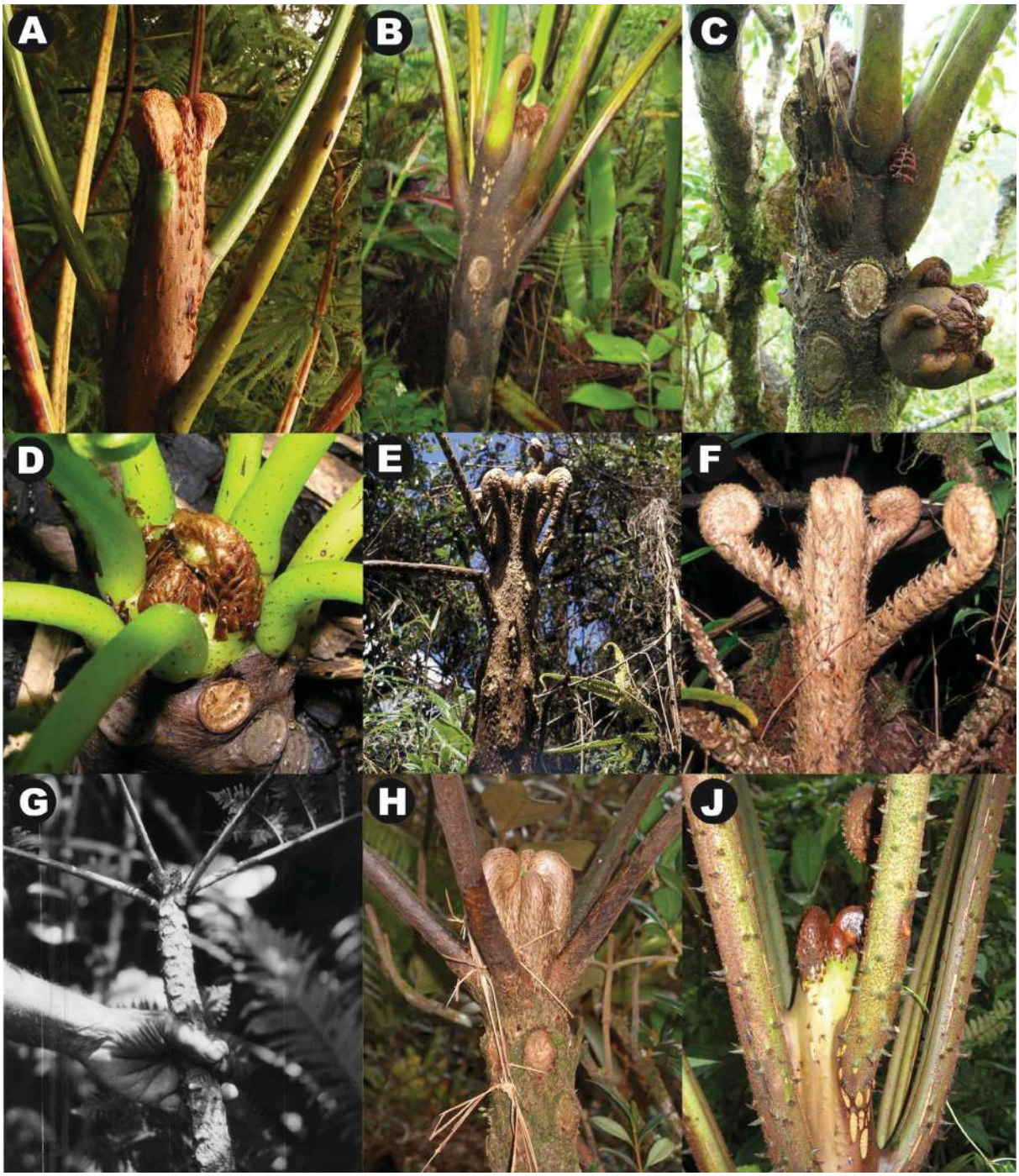

FIGURE 1. Trunk morphology. **A.** *Cyathea croftii*, Prov. West Papua, Indonesia (© Marcus Lehnert). **B–C.** *Cyathea epaleata*, Moorea, Tahiti (© Joel Nitta); **B.** Detail of trunk apex; **C.** Detail of lateral bud. **D.** *Cyathea howeana*, cultivated in Perth, Australia (© Neville Crawford). **E.** *Cyathea arnecornelii*, showing new flush of fronds, Prov. La Paz, Bolivia (© Marcus Lehnert). **F.** *Cyathea vilhelmii*, showing pale, spreading scales on trunk apex and petioles, Prov. Zamora-Chinchipe, Ecuador (© Marcus Lehnert). **G.** *Cyathea cicatricosa*, type plant, New Caledonia (reproduced from Holttum & Edwards 1982, © Kew Publishing). **H.** *Cyathea moranii,* Prov. Zamora-Chinchipe, Ecuador (© Marcus Lehnert). **J.** *Cyathea xenoxyla*, showing strong similarity with **A.** and **B.**, Prov. Zamora-Chinchipe, Ecuador (© Marcus Lehnert).

8. ***Cyathea stokesii*** (E.Brown) Hallé & Florence (1986[1987]: 157). *Hemitelia stokesii* E.Brown (in Brown & Brown 1931: 16). Type:—FRENCH POLYNESIA. Austral (Tubuai) Islands, Rapa Iti: Pariati, 850 ft, *Stokes 361* (holotype BISH n.v.).

Distribution and habitat:—Endemic to the island of Rapa between 250–350 m.

Remarks:—Holttum (1964) assumed that the species was described from "an immature plant, as it is very small." The type, however, was fertile and mature, and recent photographic evidence confirms that this

species is genuinely small. Brown & Brown (1931) report that the lateral shoots of the trunks are cooked and eaten like potatoes by the locals.

II. Group of *Cyathea platylepis*

Trunks erect, 0.5–2.0(–4.0) m tall, slender, to 5 cm in diameter, shedding old fronds cleanly, without buds, with small to large pneumathodes below the frond scars, epidermis green to brown when young, darkened with age, apices not hidden in tight fascicles of petioles, petioles inermous or weakly verrucate, petiole scales ovate-lanceolate, concolorous brown, scurf absent or very weakly developed between the petiole scales, lamina bipinnate-pinnatifid to tripinnate-pinnatifid, dimorphic or monomorphic. Sori proximal to subproximal. Indusia relatively large, paraphyses shorter to longer than sporangia, spores with verrucate exospore and no or weak perispore.

Ecology and distribution:—Species of moist lower montane forests, restricted to the Guayana Highlands, where they occur on the slopes and foothills of tepuis (table mountains).

Remarks:—The trunk morphology of this group was reconstructed from herbarium specimens only.

Key to the species

1 Fronds bipinnate-pinnatifid to tripinnate-pinnatifid, weakly dimorphic, ultimate segments with coarsely crenate margins, costae and costules with abundant white hairs to 1.5 mm abaxially ..... ***Cyathea platylepis***

– Fronds bipinnate-pinnatifid, monomorphic, ultimate segments subentire to crenulate, costae and costules without hairs abaxially ..... ***Cyathea praeceps***

9. ***Cyathea platylepis*** (Hook.) Domin (1929: 264). *Hemitelia platylepis* Hooker (1861: 100). Type:—VENEZUELA. Territorio Federal Amazonas: Dept. Río Negro, "Prope San Carlos, ad Rio Negro, Brasilia borealis," 1853–1854, *Spruce 3127* (holotype K, isotypes BM, GOET).

Hemitelia minima Morton (1951: 9). Type:—VENEZUELA. Bolivar: Ptari-tepui, on "Cave Rock" above "Cave Camp", 1810 m, 29 October 1944, *Steyermark 59481* (holotype F, isotypes MO, UC).

Distribution and habitat:—Colombia (250–900 m) and Venezuela (350–2600 m).

Remarks:—Very similar to *Cyathea robertsiana* from Australia in frond characteristics (Fig. 3), but trunks and petioles have persisting scales.

10. ***Cyathea praeceps*** Smith (1990: 253). Type:—VENEZUELA. Territorio Federal Amazonas: Dept. Río Negro, Cerro de Neblina, 6.5 km SSW of base camp, S extension of range, 00º47'N, 66º11'W, 1600 m, 18 April 1984, *Stein, Thompson, & Gentry 1655* (holotype UC, isotype MO).

Distribution and habitat:—Venezuela, 1225–1850 m.

Remarks:—Differs from *Cyathea platylepis* in being smaller, having only monomophic, bipinnate-pinnatifid fronds, and lacking hairs abaxially.

III. Group of *Cyathea vilhelmii*

Trunks 0.5–6 m tall, (3–)4–10 cm in diameter, or plants trunkless, trunks without old petiole bases, without buds, apices not hidden in tight fascicles of petioles, petioles inermous or sparsely verrucate basally, with dense grayish to white scurf consisting of matted dissected squamules and branched hairs, petiole scales blackish to brown with wide, white or grayish margins to completely white, laminae bipinnate-pinnatisect to tripinnate, pinnae subsessile to stalked, pinnules linear-lanceolate to triangular, sessile to stalked, the whole variation may occur in one plant, segment margins crenate to crenulate, sori proximal (receptacles may indeed be subproximal), indusia hemitelioid, hidden by sporangia in intact sori, paraphyses of the same length or weakly surpassing the sporangia. Spores with verrucate exospore, perispore weak or lacking.

Ecology and distribution:—Five species of moist upper montane forests, elfin forests and ridge top vegetation, above 2000 m. Patchily distributed in Central America and the Andes.

Key to the species

1 Scales on trunks and lower petioles mostly whitish to stramineous, concolorous or with brown spot near the base, few scales on upper petioles and rachises concordantly bicolorous, scales mostly spreading. (Andes) ..... ***Cyathea vilhelmii***

– Scales on trunks and lower petioles always with large darker centers and whitish to gray margins, appressed to trunks and petioles 2

2 Plants always trunkless or with short ascending rhizomes, fronds long (3–5 m), trailing over adjacent vegetation or dangling from cliffs; paraphyses longer than sporangia. (Peru) ..... ***Cyathea serpens***

– Plants with well-developed trunks, or if trunkless then fronds shorter and ± arching; paraphyses not longer than sporangia 3

3 Petiole scales reaching up to the lower rachis, larger pinnules ± linear; lanceolate, sessile to subsessile. (Ecuador) ..... ***Cyathea ars***

– Petiole scales confined to the petiole bases, larger pinnules may be triangular, partially pinnate and distinctly stalked 4

4 Sori usually covered by a weakly bullate squamule inserted at the receptacle. (Peru, Bolivia)..... ***Cyathea arnecornelii***

– Sori not covered by squamules. (Mesoamerica) ..... ***Cyathea holdridgeana***

11. ***Cyathea arnecornelii*** Lehnert (2003: 178). Type:—BOLIVIA. La Paz: Prov. Nor Yungas, Chuspipata a Yolosa, Km 7, 16°17'S, 67°48'W, 2700 m, 1 August 2000, *Lehnert 003* (holotype GOET, isotypes LPB, UC).

Distribution and habitat:—Peru, Bolivia, open ridge top vegetation, elfin forest and upper montane forests at 2580–3000 m, mostly in full sun.

Remarks:—The scales of *Cyathea arnecornelii* have grayish margins and are present only scarcely on the upper trunks and petiole bases, giving the whole plant an unkempt, worn look.

12. ***Cyathea ars*** Lehnert (2009: 48). Type:—ECUADOR. Zamora-Chinchipe: Nangaritza, Cordillera de Naguipa, Cerro Colorado, ridge 8 km SSE of Nambija, 20 km ESE of Zamora, 04°07'51"S, 78°46'36"W, 2630 m, 20 February 2002, *Cole, Delinks & Neill 258* (holotype UC, isotype MO).

Distribution and habitat:—Ecuador, open ridge top vegetation at 2575–2630 m.

Remarks:—The contrasting broad white margins of the shiny castaneous scales result in an attractive pattern on petioles and trunks.

13. ***Cyathea holdridgeana*** Nisman & L.D.Gómez (in Gómez 1971: 168). Type:—COSTA RICA. Cartago: La Chonta, at km 55 of the Interamerican Highway, 2200 m, *Nisman 104* (holotype CR n.v., isotypes F, GH).

Cyathea albomarginata Moran (1991: 88). Type:—COSTA RICA. Heredia: NW slope of Volcán Barva, between Laguna Barva and base of Cerros Las Marias, 2450–2800 m, *Grayum 7469* (holotype MO, isotypes CR, UC).

Distribution and habitat:—Costa Rica, Panama. 2200–2800 m, in wet montane forests, apparently mainly in the understory (Rojas 1999).

Remarks:—*Cyathea moranii* from southern Ecuador is almost identical but has complete sphaeropteroid indusia instead of hemitelioid ones.

14. ***Cyathea serpens*** (R.M.Tryon) Lehnert (2009: 50). *Trichipteris serpens* Tryon (1989: 126). Type:—PERU. Cuzco: Prov. La Convención, Cordillera Vilcabamba, 73º32'S, 12º37'W, 2900 m, 10 July 1968, *Dudley 10949* (holotype NA n.v., isotype GH).

Distribution and habitat:—Peru, in shrubby paramo and elfin forests at 2450–2800 m, trailing over adjacent vegetation and hanging from ledges and road cuts, in open sun.

Remarks:—*Cyathea serpens* is similar to trunkless plants of the exindusiate *C. frigida* (H.Karst.) Domin (1929: 263).

15. ***Cyathea vilhelmii*** Domin (1929: 264), *nom. nov.* for *Hemitelia lechleri* Mettenius (1859: 28). *Hemitelia lechleriana* Diels (1899: 131), *nom. superfl*. Type:—PERU. Puno: Tatanara, August 1856, *Lechler 2654* (lectotype B [Herb. Mettenius], designated by Tryon (1976: 41); isolectotype US [fragment ex Herb. Rosenst.]).

Cyathea heliophila Tryon (1986: 43). Type:—ECUADOR. Morona-Santiago: Cordillera de Cutucú, W slopes along trail from Logroño to Yaupi, 2005 m, November 1976, *Madison, Bush, & Davis 3542* (holotype GH).

Distribution and habitat:—Colombia, Ecuador, Peru, Bolivia, in montane rain forest at 2200–2900 m, most frequent in the understory along ravines (quebradas).

Remarks:—The type material of *Cyathea vilhelmii* lacks petioles and represents a very luxuriant plant with deeply tripinnate-pinnatifid fronds. Most material of *C. heliophila* has only bipinnate-pinnatisect fronds, and a considerable geographical gap was thought to exist between the documented ranges of both species. Recent findings of *C. heliophila* east and west of the type locality of *C. vilhelmii* was convincing evidence that both are best treated under one name. *Cyathea vilhelmii* has either completely white scales on trunks and petioles bases or the scales have a small brown spot near the base, which cannot be seen due to the shingle-like arrangement of the scales. Consequently, the trunks are of a striking white color. Contrary to the other species of this group, the scales are also spreading instead of being appressed, which gives the whole plant a shaggy look.

IV. Group of *Cyathea multiflora*

Trunks 0.5–10.0 m tall, 4–15 cm in diameter (reports of 25–30 cm probably included the adventitious root mantle), or sometimes trunkless, trunks densely scaly at least toward the apices, with persistent old petiole bases or these not cleanly shed, without buds (except for *C. parvula*), apices hidden in tight fascicles of petioles (Fig. 2), petioles inermous or with spines, scurf absent, or dense and consisting of matted branched hairs and dissected squamules, or sparse and consisting of distinct squamules, or sometimes replaced by spreading hairs, petiole scales blackish to brown or completely white, concolorous or with white to grayish margins, laminae bipinnate-pinnatifid to bipinnate-pinnatisect, apices gradually to abruptly reduced, pinnae subsessile to stalked, pinnules linear-lanceolate to oblanceolate, sessile to stalked, the entire variation may occur in one plant, segment margins crenate to crenulate, sori medial to submarginal, indusia hemitelioid, reaching 1/4 to 1/2 around the receptacles, small ones hidden by sporangia in intact sori, large ones often splitting into two equal lobes at maturity, paraphyses of the same length or much longer than the sporangia.

Ecology and distribution:—A group of 26 species of moist montane forests and lowland forests, mainly below 2000 m. Widely distributed in Mesoamerica and South America, with some species in the eastern Pacific (Cocos Island, Galapagos Islands) and in the Greater Antilles, with only one in eastern Brazil.

Key to the species

1 Veins anastomosing (widespread in western Amazonia)..... ***Cyathea bradei***
– Veins not anastomosing 2
2 Petiole scales persistent along the entire length of petiole and on the lower half of the rachises; plants predominantly trunkless or with trunks to 1 m tall 3
– Scales persistent only at the base of the petioles, absent from the rachises except occasionally for a few at the insertions of the costae; plants usually with trunks of 1–5 m tall 4
3 Petiole scales narrowly lanceolate to linear, with ± truncate bases, 10.0–15.0 × 0.5(–1.0) mm, dark brown to auburn with white margins, with few to many, exerted, tortuous ciliae. (Guayana Highlands, western Amazonia) ..... ***Cyathea vaupensis***
– Petiole scales lanceolate with cordate to rounded bases, to 15.0–20.0 × 4.0 mm, their apices long-attenuate; mostly concordantly bicolorous, dark brown to castaneous, the tan to white differentiated margins wide, without ciliae. (Central America) ..... ***Cyathea squarrosa***
4 Segment margins coarsely serrate to biserrate, laminar texture thin, segment tips ending in a ± triangular lobe. (IVa. Subgroup of *Cyathea multiflora*) 5

– Segment margins crenate to crenulate or subentire, rarely finely serrate, segment tips mostly ± round, if pointed then laminar texture thick and firm; indusia often large and splitting into two lobes at maturity. (IVb. Subgroup of *Cyathea andina*) 14

5 Paraphyses much enlarged and inflated, persisting. (Cocos Island) ..... ***Cyathea notabilis***

– Paraphyses not enlarged, thin, fragile if longer than the sporangia 6

6 Pinnae sessile, pinnules with obtuse to acute tips, veins of segments mostly simple (except for *C. alfonsiana*), largest pinnules 3.5–8.0 cm long 7

– Pinnae mostly short-stalked, pinnules with attenuate to caudate tips, veins of segments mostly forked, largest pinnules to 12 cm long 10

7 Fertile veins forked once to twice. (Cocos Island) ..... ***Cyathea alfonsiana***

– Fertile veins mainly simple, rarely forked once. (Mesoamerica and South American mainland) 8

8 Petiole scales dark brown to black with narrow white margins, these easily abraded, scurf if present whitish. (Guatemala to Nicaragua) ..... ***Cyathea austroamericana***

– Petiole scales orange to dark brown, concolorous or bicolorous with paler to whitish margins, rarely shiny blackish brown but then concolorous, scurf if present orange-brown 9

9 Veins adaxially glabrous except for some hairs on the midveins, abaxially glabrous to moderately hairy, hairs absent between the veins, bullate squamules scarce, pale brown, indusia small but visible. (southern Nicaragua to Panama, western slopes of the northern Andes) ..... ***Cyathea multiflora***

– Veins hairy on both sides, abaxially with hairs also present between the veins, bullate squamules frequent, orange-brown, indusia reduced to small lobes, only visible if sporangia and paraphyses are removed. (Costa Rica to Colombia) ..... ***Cyathea pinnula***

10 Petiole scales all dark brown to blackish with narrow white margins, these easily abraded, petiole bases usually with whitish scurf but lacking hairs. (Guatemala to Nicaragua) ..... ***Cyathea grayumii***

– Petiole scales rarely shiny blackish brown but if so either concolorous or quickly grading into almost white to stramineous scales more distally on the petiole, scales mostly orange to dark brown, concolorous or bicolorous with persisting broad, paler to whitish margins, scurf if present whitish to orange-brown, sometimes replaced by spreading hairs 11

11 Petioles abaxially hairy 12

– Petioles lacking hairs, at least abaxially 13

12 Veins hairy on both sides, hairs less than 1 mm long, petiole scales mostly stramineous with a pale brown central stripe, basal ones sometimes entirely brown but never blackish brown. (Mesoamerica, northern Colombia) ..... ***Cyathea acutidens***

– Veins hairy only abaxially (except for few hairs adaxially on midveins), hairs mostly 1–2 mm long, petiole scales mostly stramineous to white, basal ones sometimes strongly bicolorous blackish brown with white margins. (eastern slopes of the Andes) ..... ***Cyathea leucolepismata***

13 Petiole scales dark reddish brown to castaneous or blackish brown, concolorous to weakly bicolorous, margins never white, petiole scurf if present orange-brown. (Panama) ..... ***Cyathea rojasiana***

– Petiole scales castaneous to blackish brown with whitish margins, becoming paler in distal part of petioles, petiole scurf if present whitish. (eastern slopes of the Andes) ..... ***Cyathea lindigii***

14 Largest pinnules fully pinnate in lower half with long triangular segments with acute to attenuate tips [petiole and axes with easily abraded whitish scurf]. (northern Peru) ..... ***Cyathea rufescens***

– Largest pinnules not fully pinnate, with ± oblong segments and obtuse to round tips 15

15 Abundant dark brown bullate squamules on costae and costules. (Mesoamerica)..... ***Cyathea squamulosa***

– Bullate squamules usually lacking completely on costae, on costules rarely abundant, mostly not dark brown 16

16 Veins abaxially densely hairy with hairs to 2 mm long. (Guayana Highlands, eastern Amazonia)..... ***Cyathea surinamensis***

– Veins abaxially glabrous or with few hairs to 1 mm long 17

17 Sori submarginal, paraphyses of the same length as or shorter than the sporangia [petiole scales ovate-lanceolate to lanceolate, to 25.0 × 3.5–4.0 mm] 18

– Sori ± medial, paraphyses longer than the sporangia [petiole scales narrowly lanceolate to lanceolate, 10.0–25.0 × 1.0–3.0(–3.5) mm] 19

18 Scurf absent, petiole scales concordantly bicolorous, differentiated margins very narrow, white, fragile, usually abraded. (Greater Antilles, Andes) ..... ***Cyathea andina***

– Scurf present, dense but easily abraded, consisting of matted white tortuous hairs and dissected squamules; petiole scales discordantly bicolorous, white to pale stramineous with a continuous brown to dark brown stripe from base to tip. (Galapagos Islands) ..... ***Cyathea weatherbyana***

19 Laminae obovate, often basally tapering with basal pinnae of the same size and dissection as the pinnules of largest pinnae, petioles then virtually absent. (Guayana Highlands, eastern Amazonia) ..... ***Cyathea cyatheoides***

– Laminae ovate-elliptic, basally not gradually tapering, petioles well developed 20

20 Petiole scales stramineous, concolorous or with weak discontinuous central stripe [petiole and axes with easily abraded whitish scurf]. (periphery of Amazon basin, eastern Brazil) ..... ***Cyathea macrocarpa***
– Petiole scales discordantly to concordantly bicolorous, dark brown to auburn with white margins 21
21 Petioles aculeate, trunks with lateral buds and geotropic lateral shoots. (Greater Antilles) ..... ***Cyathea parvula***
– Petioles inermous to muricate, trunks without lateral buds or shoots 22
22 Laminar squamules ample and dark brown [petiole and axes without whitish scurf]. (Guayana Highlands) ..... ***Cyathea macrosora***
– Laminar squamules sparse and pale brown [petiole and axes with easily abraded whitish scurf]. (Mesoamerica, Amazonia) ..... ***Cyathea traillii***

IVa. Subgroup of *Cyathea multiflora*

Fronds with relatively many pinna pairs (10–15), patent to erect, planar, weakly arching, distally not drooping, laminar texture relatively soft, papyraceous, sori medial to supramedial but clearly not submarginal, indusia often small and hidden by sporangia.

16. ***Cyathea acutidens*** (Christ) Domin (1929: 264). *Alsophila acutidens* Christ (1906: 186). *Alsophila leucolepis* var. *pubescens* Christ (1901: 42). Type:—COSTA RICA. Cañas Gordas, February 1897, *Pittier 10992* (lectotype P, designated here, isolectotype US). Paratypes: Same locality, *Pittier 10981* (UC, US), *10989* (P, US)

Distribution and habitat:—Costa Rica, expected from adjacent Panama. 1100–1800 m.

Remarks:—Rojas (2001) considered *Cyathea leucolepis* (as *C. amazonica* Moran 1995: 53) to be conspecific with *C. acutidens*, which would extend the range of the species along the eastern slopes of the Andes. This view is not followed here.

17. ***Cyathea alfonsiana*** Gómez (1971: 166). Type:—COSTA RICA. Puntarenas: Cocos Island, Twin Mountains, upper Wafer valley, 400 m, *Gómez 3349* (holotype CR n.v., isotypes F, GH).

Distribution and habitat:—Cocos Island, in forest understory at 400–1000 m.

18. ***Cyathea austroamericana*** Domin (1929: 263), *nom. nov.* for *Hemitelia nigricans* Presl (1849: 31), not *Cyathea nigricans* Mettenius (1863: 56). *Amphicosmia nigricans* (C.Presl) Moore (1857: 61). Type:—NICARAGUA. "Guatemala, ad ripas fluvii S. Juan," *Friedrichsthal s.n*. (holotype W).

Distribution and habitat:—Mexico (?), Guatemala, Belize, Nicaragua, in evergreen and semi-deciduous forests between 10–700 m.

Remarks:—In laminar characters very similar to *Cyathea multiflora*, but less variable than that species. The petioles with narrowly white margined scales and whitish petiole scurf are distinct and similar to *C. grayumii*.

19. ***Cyathea grayumii*** Rojas (2001: 454). Type:—HONDURAS. Atlántida: Cordillera Nombre de Dios, Fila de La Lora, bordering Refugio de Vida Silvestre Texíguat, between Quebrada El Manchón and Quebrada San José, both flowing to the NW and their confluence with the Río Cuero, ca. 2 km N of El Manchón, 15º28´N, 87º07´30"W, 800–900 m, 10 August 1997, *Evans, Grayum & Chinchilla 2746* (holotype MO, isotype UC).

Distribution and habitat:—Honduras, Belize, in ridge-top vegetation at 350–1040 m.

Remarks:—This species looks like a larger version of the sympatric *Cyathea austroamericana* and resembles *C. rojasiana* and *C. lindigii* in the size and shape of the pinnules.

20. ***Cyathea leucolepismata*** Alston (1958: 231). Type:—COLOMBIA. Putumayo: Near San Diego de Colorado, between Umbria and Puerto Asís, 16 January 1945, *Ewan 16784* (holotype BM, isotypes S, UC, US).

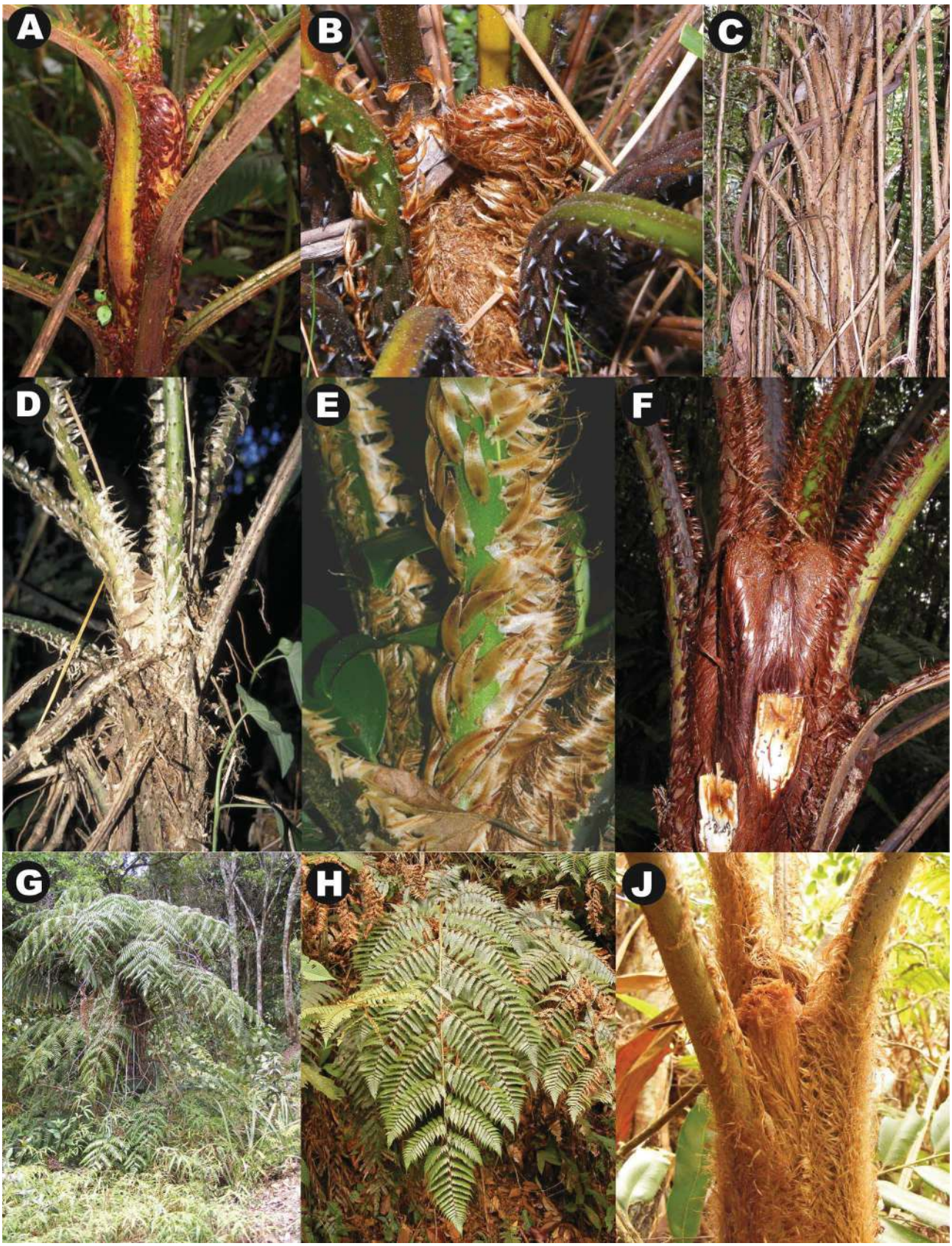

FIGURE 2. Trunk morphology. **A.** *Cyathea multiflora*, Prov. Pichincha, Ecuador. **B–C.** *Cyathea parvula*, Puerto Rico; **B.** Detail of emerging crosier; **C.** Detail of persisting spiny petioles on trunk. **D**. *Cyathea leucofolis*, Edo. Paraná, Brazil. **E.** *Cyathea boryana*, French Guiana. **F.** *Cyathea andina*, crosiers only visible after removal of two fronds, Puerto Rico. **G–J.** *Cyathea rufescens*, Dept. San Martin, Peru; **G.** Plant growing on ridge, with several small adventitious plants at the trunk base; **H.** Detail of frond; **J.** Trunk apex (**A–D, F–J.** © Marcus Lehnert, **E.** © Michel Boudrie).

Cyathea amazonica Moran (1995: 53). Type:—ECUADOR. Napo: Upper Río Tiputini, ca. 2 h from bridge on Coca-Auca oilfield road, 00º43'S 76º57'W, 300 m, 21 July 1991, *Øllgaard & Blasco 99065* (holotype AAU, isotypes K, LPB, QCA, QCNE, U, UC, US).

Distribution and habitat:—Colombia, Ecuador, Peru, Bolivia, in lower montane forests 90–1300 m.

Remarks:—This species is very similar in habit and indument to the exindusiate *Cyathea leucofolis* Domin from southeastern Brazil.

21. ***Cyathea lindigii*** (Baker) Domin (1929: 264). *Hemitelia lindigii* Baker (1874: 454). Type:—COLOMBIA. Cundinamarca: Alto del Trigo, Andes of Bogotá, *Lindig 310* (holotype K, isotypes P, GH [photo P]).

Distribution and habitat:—Colombia, Ecuador, Peru, Bolivia, in lower montane forests at 280–1250(–2000) m.

22. ***Cyathea multiflora*** Smith (1793: 416). *Hemitelia multiflora* (Sm.) Sprengel (1827: 126). *Alsophila multiflora* (Sm.) Presl (1836: 61). *Amphicosmia multiflora* (Sm.) Gardner (1842: 441). Type:—"Amer. Merid.," *Shakespeare s.n.* (holotype BM [Herb. Banks], photo GH, NY, US, fragment US).

Hemitelia denticulata Hooker (1865: 31). Type:—PITCAIRN ISLANDS. "Elizabeth Island" (= Henderson Island), *Cuming 1360* (holotype K). Holttum (1964: 274) excludes these specimens from Pacific species of *Cyathea sensu lato.* Fosberg *et al.* (1983) do not report any tree fern from Henderson Island. Most likely, a labeling error occurred. Cuming collected mainly seashells in the southeastern Pacific and ventured from Chile, via Ecuador and Panama, north to Mexico. Tryon (1976) thinks that the specimen was probably collected in Panama.

Hemitelia obscura Mettenius (1864: 264). *Cyathea columbiana* Domin (1929: 263), *nom. nov.* for *Hemitelia obscura* Mett., not *Cyathea obscura* (Mett.) Copeland (1909: 37). Type:—COLOMBIA. "Prov. de Barbacoas, via de Tuquerres," 1600 m, *Triana s.n.* (holotype not located, W?, isotypes, COL-fragment GH, K-fragment NY, P).

Distribution and habitat:—Nicaragua, Costa Rica, Panama, Colombia, Ecuador, in humid to wet forests between 400–1400 m.

Remarks:—*Cyathea multiflora* as defined here is restricted to Mesoamerica and the slopes of the western Andes. The species forms regional variations that cannot be clearly separated. Plants from the northern Andes have relatively large arching indusia and form the basis for *Hemitelia obscura* (= *C. colombiana*). Some populations in southern Ecuador produce almost black petiole scales at the petiole bases, but have the characteristic reddish brown scales in the upper parts. Plants from Costa Rica have mostly small indusia and a variable amount of hairs on the laminae abaxially.

23. ***Cyathea notabilis*** (Maxon) Domin (1930: 141). *Alsophila notabilis* Maxon (1922: 39), *nom. cons*., not *Alsophila notabilis* Saporta (1868: 329). Type:—COSTA RICA. Puntarenas: Cocos Island, Wafer Bay, *Pittier 12355* (holotype US).

Distribution and habitat:—Cocos Island, between 400–1000 m.

Remarks:—Easily recognized by the enlarged paraphyses and its restricted range.

24. ***Cyathea pinnula*** (Christ) Domin (1930: 148; Moran 1991: 90). *Alsophila pinnula* Christ (1901: 43). Type:—COSTA RICA. Limón: Río La Matina, *Pittier 10267* (holotype P n.v., fragment NY, US).

Distribution and habitat:—Costa Rica, Panama, Colombia, in wet tropical forests between 100–1500 m.

Remarks:—Moran (1991) reinstated this species unaware of the earlier combination to the genus *Cyathea* (Domin 1930: 148) and treated it as being exindusiate. Close inspection of the type material revealed that most sori have a small indusium that is hidden under the paraphyses and easily overlooked. Out of practicality, it should be treated as both indusiate and exindusiate in the keys because of the small size and irregular occurrence of the indusia.

25. ***Cyathea rojasiana*** **Lehnert, *nom.nov.*** for *Cyathea panamensis* Rojas (2001: 457), not *Cyathea panamensis* Domin (1929: 264). Type:—PANAMA. Fortuna Dam area, along quebrada Bonito to W of road, 1100 m, 8 February 1984, *Churchill et al. 4904* (holotype UC, isotype MO).

Distribution and habitat:—Panama, in moist forests at 1100 m.

Remarks:—The epithet is dedicated to Alexander Rojas who described the species. It is basically a larger form of *Cyathea multiflora* with characteristic concolorous reddish brown petiole scales, but with the habit and laminar dissection of *C. grayumii* or *C. lindigii* (i.e., pinnules with attenuate tips, most veins forked).

26. ***Cyathea squarrosa*** (Rosenst.) Domin (1929: 263). *Hemitelia squarrosa* Rosenstock (1925: 2). Type:—COSTA RICA. Limón: "Litorale atlanticum, Finca Hundriesser," August 1908, *Brade & Brade 405* (holotype S, isotypes B, NY, STU, UC, US).

Distribution and habitat:—Costa Rica, in understory of montane rainforest between 100–250 m.

Remarks:—Easily recognized by the scaly rachises and the trunkless habit of fertile plants.

IVb. Subgroup of *Cyathea andina*

Fronds with relatively few, 5–10(–12) pinna pairs, arching and distally drooping, indusia often large, arching, splitting at maturity, either sori more marginally positioned or laminar texture firmer than in the *C. multiflora*-subgroup.

27. ***Cyathea andina*** (H.Karst.) Domin (1929: 263). *Hemitelia andina* Karsten (1856: 452). Type:—COLOMBIA. Magdalena: Santa Marta, 2500 m, *Karsten s.n.* (holotype B, photo GH).

Hemitelia servitensis Karsten (1856: 451). Type:—COLOMBIA. "Crescit in silvis humidis umbrosis Novo-Granatae Provinciae Cundinamarcae altitudine 2000 metr. inter Susumuco et Servita," *Karsten s.n.* (holotype not located, W?, isotypes "Servita, Bogotá," B [Herb. Mettenius], P, photo GH).

Hemitelia escuquensis Karsten (1869: 181). *Cyathea escuquensis* (H.Karst.) Domin (1929: 263). Type:—VENEZUELA. "Sinus Maracaibensis prope Escuque, 100 m," *Karsten s.n.* (holotype not located, W?, probable isotype "Escuque, Venezuela," *Karsten 28,* B [Herb. Mettenius]).

Hemitelia joadii Baker (1891: 187). *Cyathea joadii* (Baker) Domin (1929: 263). Type:—COLOMBIA. Magdalena: Santa Marta, December 1863, *Joad s.n.* (holotype K).

Distribution and habitat:—Haiti, Puerto Rico, Colombia, Venezuela, Ecuador, Peru, Bolivia, in humid forests between 400–1900 m.

Remarks:—Plants from the Guianas treated as *Cyathea andina* belong to a separate species, *Cyathea boryana*, which is easily distinguished by its pale brown to white petiole scales (vs. dark castaneous with narrow white margins in *C. andina*, Fig. 2).

28. ***Cyathea boryana*** (Kuhn) Domin (1929: 263). *Hemitelia boryana* Mett. ex Kuhn (1869: 161). Type:—FRENCH GUIANA. *Leprieur 265a* (lectotype P, designated by Tryon (1976: 34)).

Hemitelia leprieurii Jenman (1898: 47). *Cyathea circumdentata* Kramer (1954: 491), *nom. nov.* for *Hemitelia leprieurii* Jenman (1898: 47), not Kunze (1844: 296), not *Cyathea leprieurii* (Kunze) Domin (1929: 264). Type:—FRENCH GUIANA. Cayenne, *Leprieur s.n.* (holotype NY [Herb. Jenman], photo GH).

Distribution and habitat:—Suriname, French Guiana, in understory of wet forests between 200–500 m.

Remarks:—This species is represented by material previously attributed to *Cyathea andina* in the Guianas. Both species are easily distinguished by the color of the petiole scales (dark brown in *C. andina* vs. stramineous to whitish in *C. boryana*). Probably most closely related to *C. leucolepismata*, from which it differs in the glabrosity of the petioles and abaxial laminae (vs. petioles and laminae abaxially hairy) and the slightly larger indusia.

29. ***Cyathea bradei*** (Windisch) Lellinger (1984: 166). *Sphaeropteris bradei* Windisch (1973: 372). Type:—COLOMBIA. Vaupes: Base of Cerro Mitú, *Schultes, Rauffauf, & Soejarto 24229* (holotype GH).

Distribution and habitat:—Colombia, Ecuador, Peru, on terra firme in Amazonian rain forest between 40–200 m.

Remarks:—Unique in this group because of its *Cnemidaria*-like anastomosing veins. *Cyathea bradei* is most closely related to *C. surinamensis* and *C. cyatheoides*.

30. ***Cyathea cyatheoides*** (Desv.) Kramer (1978: 39). *Hemitelia cyatheoides* Desvaux (1827: 321). Type:—FRENCH GUIANA. "Habitat in Cajenna," *anon.*, *Herb. Desvaux* (holotype P, photos GH, UC). See Windisch (1978) for synonymy.

Distribution and habitat:—Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil.

Remarks:—*Cyathea cyatheoides* is closely related to *C. surinamensis* and *C. bradei*, which share oblanceolate fronds with tapering, often strongly alternate basal pinnae.

31. ***Cyathea macrocarpa*** (C.Presl) Domin (1929: 264). *Hemitelia macrocarpa* Presl (1847: 41). *Amphicosmia macrocarpa* (C.Presl) Moore (1859: 60). Type:—BRAZIL. Bahia: *Blanchet 17* (lectotype, PRC, designated here).

Hemitelia megalosora Trevisan (1851: 164), *nom. nud.* (*Blanchet 3227* is cited, see below).

Cyathea moricandiana Moore (1861: 272), *nom. nud.* (*Blanchet 3227* is cited, below).

Hemitelia moricandiana Hooker (1865: 30). Type:—BRAZIL. Bahia: *Blanchet 3227* (lectotype PRC, designated here, fragment F, fragment HB n.v, isolectoytpe K, fragment NY, fragment RB n.v.). Paratype:—GUYANA. *Appun 193* (K, fragment NY).

Distribution and habitat:—Colombia, Venezuela, Guyana, French Guiana, Ecuador, Peru, Brazil.

Remarks:—*Cyathea macrocarpa* has an unusual distribution as it occurs sporadically in the Andean foothills, the Guayana Highlands and northeastern Brazil. Windisch (1978) doubted the correctness of its *locus classicus* in Edo. Bahia, Brazil, but the species has recently been recollected there.

32. ***Cyathea macrosora*** (Baker) Domin (1929: 263). *Alsophila macrosora* Baker in Im Thurn (1886: 211). *Hemitelia macrosora* (Baker) Jenman (1898: 45). *Sphaeropteris macrosora* (Baker) Windisch (1973: 372). Type:—GUYANA. Mount Roraima, 5750 ft, *Im Thurn 87* (holotype K, isotype US).

Distribution and habitat:—Colombia, Venezuela, Guyana, Suriname, French Guiana at 100–1700 m.

Remarks:—Windisch (1978) recognized two varieties in *Cyathea macrosora*: var. *reginae* and var. *vaupensis*, which are currently treated as separate species, *C. traillii* and *C. vaupensis*. *Cyathea macrosora* is characterized by variably bicolored scales and the general absence of scurf. The indusia of the studied material are not as variable in size as pointed out by Windisch (1978), who reports that the indusia may be almost lacking.

33. ***Cyathea parvula*** (Jenm.) Domin (1929: 264). *Alsophila parvula* Jenman (1879: 258). *Hemitelia parvula* (Jenm.) Baker (1891: 188). Type:—JAMAICA. *Jenman 97* (holotype K, fragment & photo US, photo GH, photo NY). See Tryon (1976) for synonymy.

Distribution and habitat:—Greater Antilles, in forest understory and secondary growth, on various substrates including serpentine and limestone between 500–1200 m.

Remarks:—*Cyathea parvula* is unique in the group of *C. multiflora* by having adventitious buds that grow into geotropic shoots. Jamaican plants differ by shedding their old petioles from the trunk. In phylogenetic studies, *C. parvula* clusters with the *C. armata* group (Korall *et al.* 2007), but this may be due to fragmentary sequences used in the analysis.

34. ***Cyathea rufescens*** (Mett. ex Kuhn) Domin (1929: 264). *Hemitelia rufescens* Mett. ex Kuhn (1869: 159). *Sphaeropteris rufescens* (Mett. ex Kuhn) Windisch (1973: 372). Type:—PERU. San Martin: Prov. San Martin, "in monte Guayrapurima, prope Tarapoto, Peruviae orientalis," August 1856, *Spruce 4727* (holotype BM, fragment US, isotypes K, fragment US, TCD).

Distribution and habitat:—Peru, San Martin, in mountain rainforest and ridge top vegetation between ca. 1200–1500 m.

Remarks:—*Cyathea rufescens* is easily recognized by its long triangular segments and easily detached scurf on the laminar axes. With *C. macrocarpa*, *C. macrosora*, *C. traillii*, and *C. vaupensis*, it shares a special type of narrowly triangular petiole scale, which has rectangular to hook-shaped basal lobes and narrow, fimbriate to ciliate margins.

Cyathea rufescens was long only known from the type collection in northern Peru. The type locality, Mt. Guayarapurina, is not marked on recent maps and most locals have only a faint idea where the mountain might be. In July 2002, M. Christenhusz managed to reach this *locus classicus* because Spruce's itinerary gives a fairly good description of its position, and he also collected several specimens of tree ferns there. What I first identified as *C. rufescens* among these collections, later turned out to be *C. pilosissima* (Baker) Domin (1929: 263). In November 2011, I went to Mt. Guayrapurina myself and found *Cyathea rufescens* still in fair numbers (Fig. 2). It occurs on slopes of mountains adjacent to a fertile plain, and the forest in which it grows evidently yields no valuable timber, so the species seems not directly threatened by human activity. However, the known range is very small and could be easily destroyed by one mayor fire incident. The conservation status of *C. rufescens* is therefore considered as "endangered" (EN B2a; IUCN 2001).

35. ***Cyathea squamulosa*** (I.Losch) Moran (1991: 98). *Hemitelia squamulosa* Losch (1950: 20). Type:—COSTA RICA. Cartago: Orosi, 1100 m, 14 March 1932, *Kupper 798* (holotype M, photo BM).

Distribution and habitat:—Costa Rica, Panama, in moist montane forests between 1300–2500 m.

36. ***Cyathea surinamensis*** (Miq.) Domin (1929: 264). *Hemitelia surinamensis* Miquel (1843: 191). *Alsophila surinamensis* (Miq.) Smith (1866: 244). Type:—SURINAME. Bergendaal, *Focke s.n.* (holotype U, photo GH), the fragment *ex Herb. Miquel* (K) is probably the same collection (Windisch 1978). See Windisch (1978) for synonymy.

Distribution and habitat:—Guyana, Suriname, French Guiana, Brazil, in Amazonian rainforest between 10–770 m.

Remarks:—*Cardenas 3002* (F) is a sterile juvenile plant from Prov. Pando, Bolivia, that presumably represents this species.

37. ***Cyathea traillii*** (Baker) Domin (1929: 264). *Hemitelia traillii* Baker (1891: 188). Type:—BRAZIL. Amazonas: Rio Mahues (=Maués), *Traill 1384* (holotype K, fragment US, isotypes GH, P, fragment F).

Hemitelia pumila Maxon (1949: 439). Type:—COLOMBIA. Caquetá: Cerro del Castillo, upper Apaporis basin, near confluence of the Ajuju and Macaya, *Schultes 5664* (holotype US).

Sphaeropteris macrosora (Baker) Windisch var. *reginae* Windisch (1973: 374). *Cyathea macrosora* (Baker) Domin var. *reginae* (Windisch) Smith (1990: 25). *Cyathea reginae* (Windisch) Smith (2006: 426). Type:—COLOMBIA. Vaupés: Raudal Jerijerimo, Río Apaporis, *Schultes & Cabrera 13448* (holotype GH).

Distribution and habitat:—Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, in moist lowland forest on terra firme and premontane forests between 120–1000 m.

38. ***Cyathea vaupensis*** **(Windisch) Lehnert, *comb. et stat. nov.*** Basionym: *Sphaeropteris macrosora* (Baker) Windisch var. *vaupensis* Windisch (1973: 374). Type:—COLOMBIA. Vaupés: Cerro Isibukuri, Río Kanari, Comisaria del Vaupés, *Schultes & Cabrera 13407* (holotype GH).

Distribution and habitat:—Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, in moist forests on terra firme between 75–500 m.

Remarks:—Easily recognized and distinguished from *Cyathea macrosora* by its ample cover of persistent, clearly bicolorous petiole scales, which reach along at least the lower half of the rachises. *Cyathea*

vaupensis is recognized here at the species level, because its differences with *C. macrosora* are even more evident than those of *C. macrosora* var. *reginae*, which has already been accepted at the species level as *C. traillii*.

39. ***Cyathea weatherbyana*** (C.V.Morton) Morton (1969: 65). *Hemitelia weatherbyana* Morton (1957: 188). Type:—ECUADOR. Galapagos: Indefatigable Island (= Isla Santa Cruz), *Howell 9227* (holotype US, isotype CAR n.v.).

Distribution and habitat:—Ecuador, endemic to the Galapagos Islands, mainly in the *Miconia*-zone at 550–1000 m.

40. ***Cyathea windischiana*** Smith (2006: 427). Type:—PERU. Amazonas: Bagua Distr., Cerro Tayu, ca. 1 hour from Chiriaco, 05º15'56"S, 78º22'07"W, 800 m, *van der Werff, Vasquez, & Gray 16207* (holotype MO, isotype UC).

Distribution and habitat:—Peru, in moist montane forests at 800 m.

Remarks:—*Cyathea windischiana* differs from *C. macrosora* mainly in being trunkless and having only pinnate-pinnatifid to bipinnate fronds, and may represent a precociously fertile plant of that species. Similar pedomorphic plants are common in *C. cyatheoides*, *C. surinamensis*, and *C. bradei*.

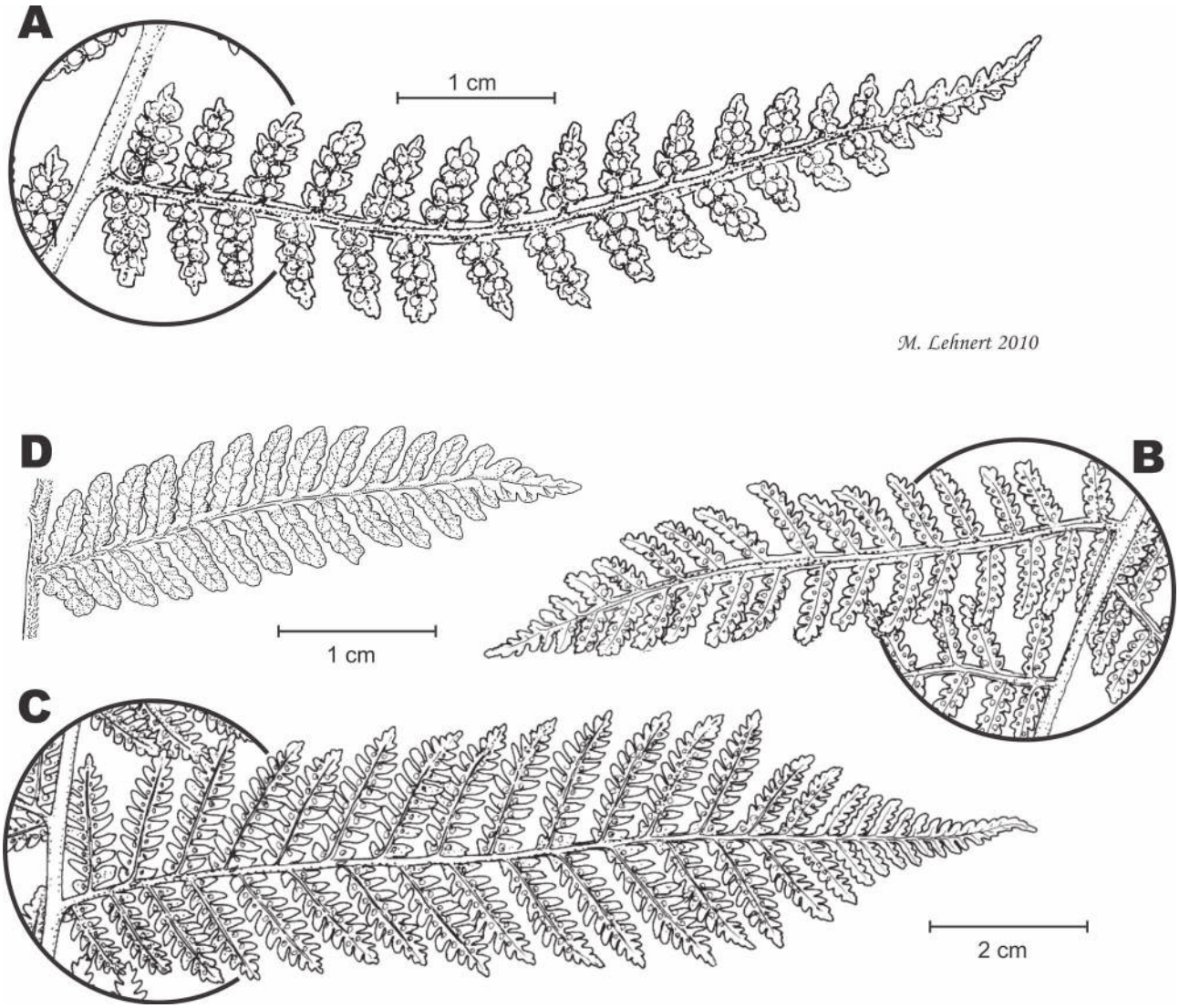

FIGURE 3. Frond morphology of the groups of *Cyathea platylepis* and *C. decurrens*. **A.** *Cyathea platylepis*, fertile pinnule abaxially, from isotype (GOET). **B.** *Cyathea robertsiana,* fertile pinnules abaxially, from isotype (B). **C.** *Cyathea croftii*, fertile pinnule abaxially, from holotype (K). **D.** *Cyathea cicatricosa*, fertile pinnule adaxially, from holotype (K).

Acknowledgments

I thank Michael Kessler (Z) and Alan R. Smith (UC) for their scientific guidance. I further thank my colleagues Dave Conant (LSC), Alexander N. Schmidt-Lebuhn (CANB), Michael Sundue (NY), Florian Werner (OLD) and Jürgen Homeier (GOET) for their company in the field. I am indebted to the curators of AAU, B, BM, CAY, COL, CUZ, F, GH, GOET, HUT, K, MBM, MO, P, Q, QCA, QCNE, QPLS, S, SCZ, SP, TUR, U, UC, USM, UPCB, UPRRP and Z for providing loans or for attending me during my visits, especially to Asunción Cano (USM), Stefan Beck (LPB) and Alison Paul (BM). Maarten Christenhusz (H) kindly provided additional specimens and helpful comments on the manuscript. Special thanks go to Joel Nitta (UC), Michel Boudrie (CAY), Neville Crawford, Perth, and the Royal Botanic Gardens, Kew, for granting permission to reproduce their excellent photographs in this treatment. Field studies that contributed to the presented results were funded by the DAAD (German Academic Exchange Service) and the DFG (German Research Foundation, grants GR 1588/7, LE 1826/3-1, LE 1826/4-1). This research received support from the SYNTHESYS Project (http://www.synthesys.info/), financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" program.

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