



The scaly tree ferns (Cyatheaceae-Polypodiopsida) of Brazil

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ABSTRACT

A synopsis of all scaly tree fern species (Cyatheaceae) occurring in Brazil is presented. We recognize 51 species in three genera [*Sphaeropteris* one species, *Alsophila* four species (one subspecies, two varieties), and *Cyathea* 45 species (one variety)] with 17 taxa being endemic to Brazil. One hybrid endemic to Brazil is recognized. Further included are five species that have not yet been recorded in Brazil, but are expected here because they are found in adjacent countries and occur literally on the border with Brazil. We present the first key covering the family for the whole territory of Brazil.

Keywords: *Alsophila*, *Cyathea*, Cyatheaceae, pteridophytes, *Sphaeropteris*, synoptical key, systematics

Introduction

Brazil covers a landmass of 8.5 million km² and encompasses several major floral regions: Amazonian lowland rainforest, Cerrado (evergreen tree savannah), Caatinga (dry scrub vegetation), Pantanal (swamp forests) and the Mata Atlântica (Atlantic rainforest) (Forzza *et al.* 2010). Its most extensive mountain range is the Planalto Central in the east but its highest peak (Pico da Neblina, 2994 m) is found at the northern border to Venezuela, which forms the southern limit of the Guayana Highlands. Because of this vast variety of habitats, the flora of Brazil is one of the most diverse on earth and contains many endemics (Forzza *et al.* 2010). Vegetation types that are almost exclusive to Brazil are the Cerrado, the Caatinga and the Mata Atlântica, which all have suffered severe degradation since colonial times (Klink & Machado 2005; Leal *et al.* 2005; Ribeiro *et al.* 2009). Of the Mata Atlântica, for example, only less than 10% of the original cover (1.29 million km²) is still present and only 1.05% lie within protected areas (Ribeiro *et al.* 2009). Although these threatened areas have been

studied almost continuously since they had been visited by the first explorers like Spix & Martius (1823–1831) and Sellow (Herter 1945), there are still new discoveries to be made in fauna (e.g. Pacheco *et al.* 1996; Simmons 1996; Rodrigues & Borges 1997; Kobayashi & Langguth 1999) and flora (e.g. Louzada & Wanderley 2011; Leme *et al.* 2012; Secco *et al.* 2012; Lima & Guilietti 2013). This includes the scaly tree ferns (Cyatheaceae), of which distinct species have long remained unnoticed (Fernandes 2000; Labiak & Matos 2009; Schwartsburd *et al.* 2015) even though they are conspicuous ferns and occur close to the densely populated areas along the coast.

The family Cyatheaceae contains ca. 600 species distributed throughout the wet tropics and the temperate southern hemisphere (Lehnert 2009). The Neotropics alone harbor ca. 210 species, with centers of endemism located in the Greater Antilles, southern Mexico plus Central America and the Andes (Tryon & Gastony 1975). Tryon and Gastony (1975) do not include Brazil as a center of endemism even though they find 37% (9 of 24) of the tree fern species to be endemic. There are conflicting accounts on the number of species in Brazil, resulting from different approaches

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and species concepts. Revisionary works on the family (Gastony 1973; Stolze 1974; Tryon 1976; Windisch 1977; 1978; Barrington 1978; Conant 1983) come up with 25 species for the whole country while local floras report even more for a single state (e.g., 29 species for Santa Catarina; Sehnem 1978). Quite recently, some new species have been described (Fernandes 2000; Labiak & Matos 2009), reinstated (Lehnert 2011b; Lehnert & Weigand 2013; Schwartsbürd *et al.* 2015) or reported from the country (Lehnert 2006; 2011b; Carvalho *et al.* 2012; Almeida & Salino 2015).

The 'Catálogo de Plantas e Fungos do Brasil' (Forzza *et al.* 2010) reports 41 species with 21 endemics for the family. However, this latest work needs to be updated regarding the generic concept (Christenhusz *et al.* 2011; Lehnert 2012) and the number of species (Carvalho *et al.* 2012; Prado *et al.* 2015; Schwartsbürd *et al.* 2015). Also, the family has never been treated systematically for the whole country. In the following, we present a revised list of the Brazilian Cyatheaceae and provide the first synoptical key for the scaly tree ferns of the country.

Materials and methods

Plant material herbaria was revised for this study: AAU, B, BM, COL, CUZ, F, FLOR, GH, GOET, HUT, JOI, K, MBM, MBML, MG, MICH, MO, NY, P, RB, S, SP, U, UC, UFP, UPCB, US, W and Z. Online resources were used for checking typifications (plants.jstor.org, apps.kew.org, science.mnhn.fr, ww2.bgbm.org) and references for the species (www.ipni.org, www.tropicos.org, see supplementary material for detailed synonymy and references).

Species of the *Gymnosphaera* Blume clade (Korall *et al.* 2007; Christenhusz *et al.* 2011) are currently treated under the genus *Alsophila* R.Br. (sensu Conant 1983), which may continue to be the nomenclaturally parsimonious solution in a phylogenetically supported classification. Previous phylogenetic studies (e.g. Korall *et al.* 2007; Janssen *et al.* 2008; Korall & Pryer 2014) have found the genus *Sphaeropteris* Bernh. (with non-marginate petiole scales) to be sister to the remainder of the Cyatheaceae, which all have marginate petiole scales. Within this clade, three monophyla are consistently retrieved, which contain the type species of the genera *Alsophila*, *Gymnosphaera* and *Cyathea* Sm., respectively, but their relationship to each other was ambiguous and weakly supported in most of the previous studies (Moran *et al.* 2008; Korall & Pryer 2014). Now with an ampler and broader sampling (M. Lehnert *et al.* unpubl. res.), the topology with the *Cyathea* clade (with non-setose petiole scales; psilate to baculate spore ornamentation if present) being sister to the *Alsophila* and *Gymnosphaera* clades (both with setate petiole scales; crested to ridged spore ornamentation) slowly emerges to most likely reflect natural relationships. Species of the *Alsophila* clade are separated morphologically only by having

16 spores per sporangia, whereas the *Gymnosphaera* clade has retained the ancestral condition with 64 spores per sporangia. Other diagnostic features are not found in all species of each clade, thus do not serve as synapomorphies. Since ranks are arbitrary (Judd *et al.* 2007) and groups not supported by synapomorphies should best be avoided in a natural classification (Christenhusz & Chase 2014), we adhere to a three genera solution for the Cyatheaceae with the genera *Sphaeropteris*, *Alsophila* and *Cyathea* for the time being. Recognizable monophyla that correspond to subgenera and sections (i.e., *Fourniera* J.Bommer ex E.Fourn., *Schizocanea* J.Sm. ex Hook., *Sarcopholis* Holttum and *Gymnosphaera* sensu Holttum 1963), we simply refer to as clades. Similarly, we here advocate the usage of the terms "*Cnemidaria* C.Presl clade" and "*Hymenophyllopsis* (K.I.Goebel) Christenh. clade" instead of referring to these distinct subunits as subgenera of *Cyathea* s.str. because the polyphyletic remainder of the genus cannot be further split up satisfactorily in morphologically defined subgenera.

Results

We report 51 species and one hybrid of scaly tree ferns for Brazil and further five species are to be expected from the country with high probability. Seventeen taxa are considered endemic for the country, all being restricted to the Atlantic rainforest.

Discussion

Even if the five non-confirmed taxa are included, Brazil has relatively few scaly tree fern species given its size (51–56 spp. on 8.5 million km²). Adjacent countries may have almost twice the diversity on a far smaller area. Peru has 83 spp. (Lehnert 2011a) on 1.28 million km², Ecuador has 86 spp. (M. Lehnert unpubl. res.) on 0.28 million km² and Colombia probably 110 spp. (M. Lehnert unpubl. res.) on 1.14 million km². With 46 spp., Bolivia has a diversity of scaly tree ferns comparable to that of Brazil (51–56 spp.) but fewer endemics (one spp. vs. 17 spp.). On 1.1 million km² of the Bolivian territory, suitable tree fern habitat is found mainly in the northern lowlands and the wet mountain forests of the so-called Yungas, both of which are contiguous with identical vegetation types in Peru. Generally, most tree ferns grow in the mountains between 1000 and 3000 m, with narrowly distributed (i.e. rare and endemic) species occurring mainly on sandstone and in the tree line ecotone. The low elevation of the mountains in the moister Atlantic coast may be seen as the main factor for the relatively low tree fern diversity in Brazil; another is the weak orographic and geologic structure of the mountain range. The result is a relatively homogenic strip of mountain forest, in which the most prominent feature that structures the habitats is the latitudinal temperature gradient.



A different picture is given by the endemism of Brazilian tree ferns. With 32–35 % (17 of 51–56 spp.), it is higher than in Colombia (ca. 10 %; ca. 11 of 110 spp.), Ecuador (14 %; 12 of 87 spp.), Peru (17%; 14 of 83 spp.) and Bolivia (0.5 %; one of 46 spp.), and only comparable to Venezuela (ca. 22 %; ca. 19 of 83 spp.).

The Brazilian species of Amazonia and the Guayana shield are all shared with the neighboring countries, and this is not surprising because these ecosystems are not delimited by national borders. On the other hand the Mata Atlantica, which harbors all Brazilian endemics, reaches only with small extensions into Paraguay, Argentina and Uruguay (Forzza *et al.* 2010). In a way, Brazilian tree fern endemics are synonymous with Mata Atlantica endemics. In total 17 species of Cyatheaceae are endemic to the Atlantic rainforest, which is 80 % of their diversity encountered here: Only *Cyathea delgadii*, *C. microdonta*, *C. poeppigii*, *C. uleana* and *C. villosa* are not restricted to this vegetation type. Given the strong fragmentation and low percentage of protected area of this vegetation type, all 17 endemic species should be categorized at least as near threatened (NT) according to the IUCN categories (IUCN 2012, 2014), with some species that are currently known from only ten or fewer localities (i.e.

Alsophila capensis, *Cyathea atrocastanea*, *C. praecincta*) also as vulnerable (VU). For the rest of the Brazilian Cyatheaceae, only least concern (LC) can be given because they are widespread and further distributed in other countries. In the case of the Guayana Highland endemics, the small ranges are in remote areas that are already classified as nature reserves and protected indigenous territories, thus they could be considered as not yet threatened (LC or NT). However, given the scarcity of collections and reported field observations from that area, a general classification as data deficient (DD) seems most adviseable.

Naturally occurring hybrids may be the reason for the observed weak morphological differences between some Brazilian taxa of scaly tree ferns. Some currently recognized species have been assumed to be hybrids or of hybridogenic origin (Conant & Cooper-Driver 1980; Lehnert & Weigand 2013). However, based on observations in the field only *Cyathea ×stella-matutina* seems to be confirmable at present to be a true hybrid (Schwartzburd *et al.* 2015). Therefore, we are not considering more hybrid taxa in the following taxonomic treatment and key. More field work and especially genetic and karyological studies are required for the solution of this topic, which will deserve a publication on its own.

Systematic Treatment

Cyatheaceae Kaulf.

Key to the genera of the Cyatheaceae

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***
- 1'. 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. Petiole scales without differentiated margins, i.e. cells of the petiole scales all of (nearly) the same size and orientation (no distinct margin of smaller cells), but dark marginal teeth, setae or pale, long cilia may be present, petiole scales basifix on ± truncate bases, never with indurated bases or with transitions to black prickles. 3
- 2'. Petiole scales with differentiated margins, i.e. cells of the petiole scale margins smaller and with different orientation than those of the scale bodies, margins may be very narrow and reduced to one row of small teeth in the distal part of the scales, but are recognizable at the bases, petiole scales pseudopeltately attached on weakly to strongly cordate bases or basally attached, in the latter case often intergrading with black prickles. 4
3. Petiole scales with small, unicellular teeth that are the end of one vertical cell row; scales of various sizes but not intergrading with branched and simple hairs; sori subcostal to costal, with deeply cyathoid to sphaeropteroid indusia; fertile plants mostly with stout, erect trunks 2–10 m tall. ***Sphaeropteris***
- 3'. Petiole scales without small black teeth but may have long, often pluricellular cilia; scales may be intergrading with branched and simple hairs; sori either exindusiate or of marginal position; fertile plants mostly without trunks, rarely with decumbent trunks to 3 m tall. ***Cyathea***
4. Scales with at least one dark apical seta protruding from the scale center (supported by more than one cell row below); stem and petioles, if prickly, with black squaminate prickles (i.e., with sharp color contrast to the cortex, breaking off cleanly at this point in dried specimens); adventitious pinnae at the petiole bases skeletonized if present. ... ***Alsophila***
- 4'. Scales without setae, although sometimes small black teeth or long cellular processes of the margin occur (supported only by one cell row or less, i.e. several marginal teeth supported by the same cell); stem and petioles only with corticinate prickles (i.e., without color contrast towards the cortex, not breaking off cleanly in dried specimens); adventitious pinnae near the petiole bases not skeletonized if present. ***Cyathea***



Sphaeropteris Bernh.

One species present (one endemic):

1. ***Sphaeropteris gardneri*** (Hook.) R.M.Tryon
Endemic; Mato Grosso, Minas Gerais, Rio de Janeiro and São Paulo at 450–600 m.

Voucher: BRAZIL. Minas Gerais: Without locality, G. Gardner 5328 (lectotype BM, designated by Tryon 1970: 17, isolectotypes F, P, US).

Reference: Tryon (1971); not considered by Windisch & Santiago (2016) due to confusion with *Cyathea mexiae* Copel. (≡*Alsophila gardneri* Hook., not *Cyathea gardneri* Hook.).

Alsophila R.Br.

Four species, three subspecies/varieties (two endemics):

Key to the Brazilian species of Alsophila

1. Adventitious pinnae absent from the base of the petioles, or if pinnae present then continuous with rest of the lamina and not differently dissected; trunks without persistent petiole bases, revealing dense cover of brown to pale scales. (*Alsophila* clade) 2
- 1'. Adventitious pinnae present at the base of the petioles, coarsely to finely dissected; trunks with persistent petiole bases, appearing dark and untidy. 3
2. Indusia dark, atropurpureous to almost black, opaque, sphaeropteroid, splitting into three ± equal parts at maturity that usually persist. (Brazil north of the Amazon; Costa Rica, northern and central Andes, Guayana Highlands) ***A. cuspidata***
- 2'. Indusia pale, whitish to medium brown, translucent, urceolate to sphaeropteroid, irregularly splitting at maturity, into two unequal parts or ephemeral fragment. (Eastern Brazil; Argentina, Paraguay) ***A. sternbergii***
3. Petioles prickly at least near base, with coarsely dissected basal pinnae; sori with wedge-shaped indusia pressed to the sporangia, reaching 1/4 to 1/3 around the receptacles, without cellular texture; plants forming colonies by stolons (sporangia with 16 spores). (*Alsophila*-clade) ***A. setosa***
- 3'. Petioles not prickly, with highly dissected basal pinnae (aphlebia); sori with spreading, scale-like, lanceolate indusia, consisting of turgid cells discernable until maturity of the sporangia or exindusiate; plants single or with small buds at the base of the trunk (sporangia with 64 spores). (*Gymnosphaera*-clade) 4
4. Fronds monomorphic; laminae bipinnate-pinnatifid to pinnatisect; segment margins serrulate; sori with spreading, scale-like, lanceolate indusia. ***A. capensis***
- 4'. Fronds dimorphic, fertile parts with less green laminar tissue than sterile ones; laminae at least partially tripinnate; segment margins crenate; sori exindusiate. ***A. salvini***

2. ***Alsophila capensis*** (L.f.) J.Sm. subsp. ***polypodioides*** (Sw.) D.S.Conant **E!**

Endemic; Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul at 120–1000 m in sheltered spots with forests, along creeks and in gorges, also directly on sandstone cliffs.

Voucher: BRAZIL. Minas Gerais: Villa Rica, G.W. Freyreis s.n. (lectotype S, inadvertently chosen by Conant 1983: 369).

Reference: Conant (1983)

Reference: Forzza et al. (2010), Prado et al. (2015)

4. ***Alsophila salvini*** Hook.

Minas Gerais at 1150–1200(–1600) m in cool humid forests; also in southern Mexico (Chiapas), Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica and Panamá with disjunct populations in northern and central Peru at 900–2600 m.

Voucher: BRAZIL. Minas Gerais: Araponga, Parque Estadual da Serra do Brigadeiro, 20°43'16"S, 42°29'00"W, 1350 m, 21.02.2014, P.B. Schwartsburd et al. 2983 (BONN, RB, VIC). *Reference:* Almeida & Salino (2015), Schwartsburd et al. (2015)

5. ***Alsophila setosa*** Kaulf.

São Paulo, Paraná, Santa Catarina, Rio Grande do Sul at 50–1000 m; reported from Bahia, Pernambuco, Espírito Santo, Minas Gerais and Rio de Janeiro by Windisch & Santiago (2016); also Paraguay and Argentina, in the understory of



Mata Atlântica, Araucaria forests and in gallery forests.
 Voucher: BRAZIL. Without locality, L.K.A. Chamisso s.n.
 (holotype LZ, destroyed, isotypes B, P).

Reference: Gastony (1973), Conant (1983), Forzza *et al.* (2010), Prado *et al.* (2015).

6. *Alsophila sternbergii* (Sternb.) D.S.Conant

Two varieties are recognized (Gastony 1973):

1. Petiole scales 'en masse' appearing pale brown to almost white, each usually with only one apical seta; petiole prickles relatively thin, to ca. 2 mm wide; indusia relatively firm, the uneven fragments usually persisting in most parts (mainly southern Brazil, reaching more inland; Argentina, Paraguay) **var. *sternbergii***
- 1'. Petiole scales 'en masse' appearing medium to dark brown, regularly with several apical and lateral setae; petiole prickles relatively thick, to ca. 4 mm wide; indusia soon caduceous, remaining as shallow cups and discs with uneven edges (mainly coastal, northeastern Brazil) **var. *acanthomelas***

6.1. *Alsophila sternbergii* var. *sternbergii*

Goiás, Minas Gerais, Rio de Janeiro, São Paulo, in the understory of Mata Atlântica and in gallery forests at 500–1300 m; also in Argentina and Paraguay.
 Voucher: BRAZIL. Minas Gerais: "Habitat in Brasiliae Capitania Goyaz ad Limoero non procul St. Izidro", J.B.E. Pohl s.n. (lectotype W, designated here, isolectotypes BM, BR, PRC).

Reference: Gastony (1973), Conant (1983)

Endemic; Pernambuco, Bahia, Rio de Janeiro, Paraná, Santa Catarina at 400–700 m in the understory of Mata Atlântica.
 Voucher: BRAZIL. Rio de Janeiro: "In Brasilia Fluminensi", Corcovado, 19.03.1865, A. Glaziou 379 (lectotype P, inadvertently designated by Gastony 1973: 135, isotypes K, P, S, US).

Reference: Gastony (1973), Conant (1983)

6.2. *Alsophila sternbergii* var. *acanthomelas* (Fée) Conant **E!**

Cyathea Sm.

Incl. *Hymenophyllopsis* K.I.Goebel. *Cyathea* subgenus *Hymenophyllopsis* (K.I.Goebel) Christenh.

Incl. *Cnemidaria* C.Presl

44 species, one variety, 14 endemics.

Key to the Brazilian 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. **Group I.**
- 1'. 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 II.**
- 2'. Fronds bipinnate or more complex, if fronds distally only pinnate then segments clearly remote from each other in proximal half. 3
3. Fronds bipinnate, pinnules with margins entire to shallowly crenate (not incised more than 1/5 towards the costules). **Group III.**
- 3'. 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. **Group IV.**
- 4'. Indusia present, sometimes scale-like (hemiteloid) but without cellular pattern, or fragmented to an irregular disc reaching completely around the receptacles. 5
5. Indusia hemiteloid, reaching 1/5 to 1/2 (rarely more) around the receptacles, larger ones often splitting into two equal halves at maturity. **Group V.**
- 5'. Indusia cyatheoid to sphaeropteroid, sometimes fragile and evanescent but remaining as complete ring around the receptacles. **Group VI.**

Group I. *Hymenophyllopsis* clade

1. Laminae 22–27 cm long; rachises villous, with shiny translucent hairs. ***C. trichomanoides***
- 1'. Laminae to 20 cm long, usually less than 15 cm; rachises glabrous, scaly or sparsely hairy. 2

2. Rhizome and petiole scales 7–10 mm long, linear, forming a tuft at the rhizome apices, lamina tripinnate; stipes and rachises with variable contorted hair-like scales. ***C. ctenitoides***
- 2'. Rhizome and petiole scales 1.5–5 cm long, lanceolate or narrowly lanceolate, not forming a conspicuous tuft at the rhizome apices 3
3. Soral valves narrowly lacerate; petioles 0.2–0.5 mm in diam.; laminae tri- to quadripinnate ***C. hymenophylloides***
- 3'. Soral valves broadly lacerate, repand, lobed or subentire; petioles (0.5–)0.7–1.0 mm in diam., laminae bipinnate to tripinnate-pinnatifid. 4
4. Laminae bipinnate to pinnate-pinnatifid; soral valves lacerate. ***C. aspleniooides***
- 4'. Laminae bi- to tripinnate-pinnatifid; soral valves shallowly and broadly lobed. ***C. dejacta***

[***Cyathea aspleniooides*** (A.C.Sm.) Christenh.]

Not native but to be expected on Mt. Roraima, where it occurs in the Venezuelan part; also on other tepuis, in Venezuela (Amazonas, Bolívar) and Guyana, in rock crevices, 1650–2450 m.

Voucher: VENEZUELA. Amazonas: Summit of Mount Duida, 5500–6000 ft, G.H.H. Tate 439 (holotype NY- fragments BM, M n.v., US).

Reference: Christenhusz (2009)

[***Cyathea ctenitoides*** (Lellinger) Christenh.]

Not native but to be expected on Mt. Roraima, where it occurs in the Venezuelan part; Venezuela (Amazonas, Bolívar), epilithic and terrestrial, in shaded crevices and

at the base of rocks often on tepui summits, 2200–2750 m.

Voucher: VENEZUELA. Bolívar: Chimantá Massif, Churi-Tepui (Muru-Tepui), lower part of lower northwest cumbres, 2100–2200 m, J.J. Wurdack 34175 (holotype US, isotypes NY, UC).

Reference: Christenhusz (2009)

7. ***Cyathea dejacta*** (Baker) Christenh.

Roraima; also Venezuela (Amazonas, Bolívar) and Guyana,

on sandstone crevices and bluffs, 2300–2800 m.

Voucher: GUYANA. Mount Roraima, E.F. Thurn 318 (lectotype K, designated by Christenhusz 2009: 39, isolectotype US).

Reference: Christenhusz (2009)

8. ***Cyathea hymenophylloides*** (L.D.Gómez) Christenh.

Amazonas, Serra do Aracá; also in Venezuela (Amazonas, Bolívar), on sandstone crevices and bluffs, 750–1850 m.

Voucher: BRAZIL. Amazonas: Barcelos, Parque Estadual da Serra do Aracá, Floresta Nebular, próxima de curso d'água, 00°55'54"N 63°21'34"W, 1400 m, 30.09.2011, R.C. Forzza et al. 6597 (SP).

Reference: Christenhusz (2009)

[***Cyathea trichomanoides*** Christenh.]

Not native but to be expected on the Serra da Neblina at the border with Venezuela (Amazonas), where it occurs in the Venezuelan part on dry rock ledges at 1400–1600 m.

Voucher: VENEZUELA. Amazonas: Cerro de la Neblina, Río Yatua, east escarpment, slopes of Caño Grande below Cumbre Camp, B. Maguire, J.J. Wurdack & C.K. Maguire 42250 (holotype US, isotype NY).

Reference: Christenhusz (2009)

Group II. Species with pinnate-pinnatifid laminae

1. Largest pinnae 2.0(–2.5) cm wide; pluricellular hairs ± 1 mm long at least present adaxially on rachises and costae, often whole plant abundantly hairy with hairs to 5 mm long, exindusiate. 2
- 1'. Largest pinnae more than 2 cm wide (mostly 3–8 cm); hairs absent or only 0.5–0.6 mm long, whole plant apparently glabrous; petiole scales white to bicolorous dark brown to blackish with white margins, indusia present (*Cnemidaria* clade) 3
2. Laminar indument consisting of short pubescence, rarely hairs longer than 1 mm; scales concolorous orange to dark brown, or strongly bicolorous with margins not white; restricted to petiole bases; petioles glabrous or glabrescent with short hairs; plants with erect trunks. ***C. bipinnatifida***
- 2'. Laminar indument with hairs 3–5 mm long, especially along rachises, scales on trunks and basal petioles narrowly triangular with long marginal cilia, intergrading with hairs in distal petiole parts, stramineous to rufescent, indusia absent, plants without trunks, rhizomes creeping to ascending. ***C. myriotricha***
3. Veins anastomosing, regularly forming areoles; lobes (=segments) acute to attenuate, sinuses acute to round; pinnae incised ± 1/2 towards the costa, pinnae ca. 20–30 pairs per frond. ***C. spectabilis***
- 3'. Veins free, only occasionally with costular areoles; lobes (=segments) obtuse to round or truncate, sinuses acute; pinnae in 10–20 pairs ***C. uleana***

9. ***Cyathea bipinnatifida*** (Baker) Domin

Amazonas; reported for Acre and Roraima by Windisch & Santiago (2016); also Colombia, Venezuela, Guyana, Ecuador, Peru and Bolivia at (430–)700–2200(–3450) m,

in lower montane rain forests at 800–1000 m.

Voucher: BRAZIL. Amazonas: Rio Negro, Rio Cauaburi, Rio Maturacá, between Missao Salesiana and Serra Pirapucú, 800–1000 m, 23.01.1966, N.T. Silva & U. Braza 60847 (NY, UC).



References: Forzza *et al.* (2010), Lehnert (2012), Prado *et al.* (2015)

10. ***Cyathea myriotricha*** (Baker) R.C.Moran & J.Prado E!

Endemic; Mato Grosso, Minas Gerais, Paraná; on wet open rocks, in crevices, or on steep rock faces at 700–1200 m.

Voucher: BRAZIL. Minas Gerais: Serra do Caraça, without date, A. Glaziou 15734 (lectotype K, inadvertently designated by Moran *et al.* 2008: 363, isolectotypes B, GH, H n.v., MICH, P).

Reference: Lehnert (2012, 2016)

11. ***Cyathea spectabilis*** (Kunze) Domin

Amazonas, Pará; also Colombia, Venezuela, Guyana, Suriname and French Guiana at (75–)130–1300(–2070) m, in forest understory, preferring slightly disturbed sites.

Voucher: BRAZIL. Amazonas: Neblina Massif, 1100 m, 24.12.2003 – 05.01.2004, F.A. Carvalho *et al.* 249 (INPA-image).

Reference: Carvalho *et al.* (2012), Prado *et al.* (2015)

12. ***Cyathea uleana*** (A.Samp.) Lehnert var. ***uleana***

Rio de Janeiro, São Paulo, Minas Gerais, Santa Catarina; reports from Amazonas dubious (Forzza *et al.* 2010); also Ecuador, Peru and Bolivia at (580–)1140–1830(–2000) m. In Mata Atlântica and wet mountain forests on the eastern Andean flanks.

Voucher: BRAZIL. Rio de Janeiro: Puerto de Nueva Friburgo, Alto da Sierra, 1898, E.H.G. Ule s.n. (holotype R n.v.-photo F, GH).

Reference: Lehnert (2012), Prado *et al.* (2015)

Group III. Species with bipinnate fronds and entire to shallowly lobed pinnules

Note:—Couplet “3” asks for the apices of the pinnae and not as commonly done for laminar apices, as in couplet “6”.

- | | |
|---|----------------------------------|
| 1. Laminae only bipinnate in lower half, distal pinnae and distal portions of proximal pinnae simply pinnatifid to entire; fertile plants often or always lacking trunks, indusia absent. (Guayana Highlands) | 2 |
| 1'. Laminae fully bipinnate except for apical sections if laminae are gradually reduced. | 3 |
| 2. Laminae herbaceous to chartaceous, margins flat. | <i>C. neblinæ</i> |
| 2'. Laminae coriaceous, margins repand. | <i>C. thysanolepis</i> |
| 3. Pinnae with abruptly reduced, pinnule-like apices. | 4 |
| 3'. Pinnae with gradually reduced, pinnatifid apices. | 5 |
| 4. Largest pinnules ca. 5 times longer than broad, more than 4.5 × 1.2 cm; sori medial to inframedial. ... | <i>C. corcovadensis</i> |
| 4'. Largest pinnules ca. 3 times longer than broad, mostly less than 4.5 × 1.2 cm (rarely to 6.4 cm long), sori subproximal to inframedial. | <i>C. feeana</i> |
| 5. Petiole scales relatively dark, shiny auburn to dark reddish brown, margins may be paler but not sharply contrasted; sori in zig-zag pattern, sometimes irregular, appearing as several discontinuous lines parallel to the costules. (Southeast Brazil). | <i>C. miersii</i> |
| 5'. Petiole scales concolorous pale, or at least with wide stramineous, sharply contrasted margins; sori in a clear line, either parallel to margins or midveins, medial to submarginal. | 6 |
| 6. Petiole scales mostly with dark brown central stripe, sometimes getting concolorous brown towards the trunk, becoming paler in upper petiole parts, never reaching lower rhachis; larger pinnules of central pinnae often pinnatifid; sori medial to supramedial, paraphyses shorter than or of the same length as the sporangia. (Southeast Brazil). | 7 |
| 6'. All petiole scales concolorous stramineous, usually reaching up to the lower rhachis; pinnules never pinnatifid; sori submarginal, paraphyses much longer than the sporangia. (Guayana Highlands). | 8 |
| 7. Sori ± medial, costae green-atale between pinnules for most of their length; whitish bullate squamules only on costules and midveins. | <i>C. dichromatolepis</i> |
| 7'. Sori supramedial, costae green-atale between pinnules in distal third, whitish bullate squamules also present on lateral veins. | <i>C. glaziovii</i> |
| 8. Laminar apices inarticulate; petiole scales often with central brown stripe. | <i>C. marginalis</i> |
| 8'. Laminar apices articulate; petiole scales concolorous. | <i>C. sipapoensis</i> |

13. ***Cyathea corcovadensis*** (Raddi) Domin E!

Endemic; Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná and Santa Catarina at 0–1000(–1300) m. Reports from the Northeast dubious (Windisch & Santiago 2016).

Voucher: BRAZIL. Rio de Janeiro: Without locality, without date, G. Raddi s.n. (lectotype FI n.v., inadvertently designated by Barrington 1978: 68, isolectotype P [“in vertiu montis Corcovado”]).

Reference: Forzza *et al.* (2010), Lehnert & Weigand (2013)

Cyathea dichromatolepis → group IV, No. 24

14. ***Cyathea feeana*** (C. Chr.) Domin E!

Endemic; Minas Gerais, São Paulo, Rio de Janeiro at 1000–1750 m, in Paraná and Santa Catarina down to 500 m.

Voucher: BRAZIL. Rio de Janeiro: “Orgaos”, A. Glaziou 3582 (lectotype K, inadvertently designated by Barrington 1978: 68, isolectotypes B, NY [fragment of K]).

Reference: Lehnert & Weigand (2013)
Cyathea glaziovii → group IV, No. 25

15. ***Cyathea marginalis*** (Klotzsch) Domin
 Amazonas, Pará; also in Guyana, Suriname and French Guiana at 600–1000(–2300) m on slopes of table mountains and hilly lowland forest on nutrient deficient soils.
 Voucher: BRAZIL. Pará: Mun. Oriximiná, Estação Ecológica Grão Pará, trilha T2, entre a parcela 03 e 05, 01°16'32.1–52.7"N, 58°41'29.2–30.7"W, 600 m, S. Maciel 789 (MG, STU).

Reference: Carvalho et al. (2012)

16. ***Cyathea miersii*** (Hook.) Domin E!
 Endemic: Minas Gerais, Rio de Janeiro and São Paulo, in Mata Atlântica at ca. 1300–2100 m.
 Voucher: BRAZIL. Rio de Janeiro: Organ Mountains, 1837, G. Gardner 117 (lectotype K, designated by Lehnert 2016: 42, isolectotype P).

Reference: Lehnert & Weigand (2013)

17. ***Cyathea neblinae*** A.R.Sm.
 Amazonas, in the Neblina range; also in Venezuela at 140–1300 m in mountain forests.
 Voucher: BRAZIL. Amazonas: Neblina Massif, 1300 m, 24.12.2003 – 05.01.2004. F.A. Carvalho et al. 308. (INPA-image).

Reference: Carvalho et al. (2012)

18. ***Cyathea sipapoensis*** (R.M.Tryon) Lellinger
 Amazonas at ca. 150–1700 m on the slopes and tops of table mountains; also in Venezuela.
 Voucher: BRAZIL. Amazonas: Neblina Massif, 1700 m, 24.12.2003 – 05.01.2004. F.A. Carvalho et al. 385. (INPA-image).

Reference: Carvalho et al. (2012)

19. ***Cyathea steyermarkii*** R.M.Tryon
 Amazonas, on the slopes of Pico da Neblina; also Venezuela at 1230–1270 m on the Cerro Autana.
 Voucher: BRAZIL. Amazonas: Neblina Massif, 1000 m, 24.12.2003 – 05.01.2004. F.A. Carvalho et al. 237 (INPA-image).

Reference: Carvalho et al. (2012)

20. ***Cyathea thysanolepis*** (Barrington) A.R.Sm.
 Amazonas, Serra da Neblina at 2115 m, and Serra do Araça at 900–1050 m; also in Venezuela at 1750 m on the Neblina massif.
 Voucher: BRAZIL. Amazonas: Barcelos Parque Estadual da Serra do Aracá. Trilha do Acampamento do Fosso para a Cachoeira do Eldorado, 20.04.2014, P.H. Labiak et al. 5646 (RB)

Reference: Lehnert & Weigand (2016)

Group IV. Species with bipinnate-pinnatifid or more complex laminae and lacking indusia

1. Petiole scales with margins reduced in distal parts to one row of cells that form short teeth to long ciliae, in basal parts with several marginal cell rows of different size and orientation, paraphyses originally longer than sporangia but fragile, or rarely just of the same length as the sporangia. 2
- 1'. Petiole scales with margins well developed, short teeth/long cilia absent or clearly the end of diverging lines of increasingly narrower cells, paraphyses shorter to longer than sporangia. 3
2. Scale margins reduced to small teeth, scales not intergrading with hairs. ***C. poeppigii***
- 2'. Scale margins with long cilia, scales intergrading with long hairs. ***C. myriotricha***
3. Largest pinnules 10 × 2 cm or larger, segments narrow, oblong to linear with double-serrate to deeply crenulate margins; pinnae predominantly to exclusively opposite, sessile or nearly so, pinnules sessile, proximal ones often reflexed and covering the rachis, firm-herbaceous petiole scales, concolorous white to bicolorous with brown to black centers, never rufous or orange-brown [laminar texture soft, usually with white spreading hairs evenly distributed]. 4
- 3'. Largest pinnules either smaller or with wider segments and/or firmer laminar texture; pinnae mostly alternate, sessile to long-stalked, pinnules never reflexed, petiole scales also concolorous brown to orange-brown to reddish [laminar texture variable, soft to often subcoraceous, hairs if present unevenly distributed]. 5
4. Petiole scales almost concolorous white to stramineous, some scales near petiole base and on trunks with pale brown center, marginal teeth not or inconsistently brown; hairs less than 2 mm long. ***C. rufa***
- 4'. Petiole scales concordantly bicolorous at least at petiole bases, with dark brown to castaneous centers and pale brown to whitish margins with a ± continuous line of dark marginal teeth, scales sometimes almost concolorous dark brown; hairs to 1.5 mm long. ***C. hirsuta***
5. Costae abaxially sparsely aculeate with thin prickles to 5 mm long. ***C. microdonta***
- 5'. Costae abaxially unarmed or scabrous with relatively thick prickles to 1 mm long. Laminae bipinnate-pinnatifid, segments fully adnate or if basal segments of largest pinnules free then with margins crenulate to entire. 6
6. Petiole abaxially with spreading multicellular hairs to 2 mm long, squamellar scurf absent or sparse, consisting of relatively large squamules; laminar squamules whitish to orange-brown, generally concolorous; leaf axes usually as hairy as petioles. 7
- 6'. Petioles without hairs, or hairs restricted to the adaxial side and the distal petiole parts, squamellar scurf absent to dense; leaf axes may be densely hairy. 9



7. Scales concolorous white to pale stramineous or with darker brown basal spot; receptacles not subtended by bullate squamules, paraphyses shorter than or of the same length as sporangia. *C. leucofolis*
- 7'. Scales bicolorous with continuous central stripe or concolorous brown, castaneous, or black; paraphyses shorter to longer than sporangia. 8
8. Midveins and veins bearing whitish bullate squamules and many hairs, hairs also frequent between veins. *C. mexiae*
8. Midveins and veins lacking whitish bullate squamules (squamules either brownish or not bullate), hairs moderately frequent on veins, scarce between veins. *C. phalerata*
9. Petiole scales concolorous white (or some scales with small brown spot near the base). *C. leucofolis*
- 9'. Petiole scales not entirely white, either concolorous pale brown to blackish, or bicolorous with continuous central portion. 10
10. Petiole scales bicolorous with broad whitish margins and predominantly dull brown centers, scurf variable, dense cover of small squamules to ephemeral pulverulent cover, but always pale, whitish, gray or very pale brown; paraphyses shorter than or of the same length as sporangia. 11
- 10'. Petiole scales concolorous black, brown, reddish, or orange-brown (the scale margins at least in the lowermost scales of the same color as the centers, in distal parts of petiole usually paler than the scale center) or bicolorous with margins not whitish; scurf always inconspicuous, often weakly developed and ephemeral, on croziers notable as tan to reddish cover; paraphyses may be much longer than sporangia. 17
11. Sori submarginal to marginal, parallel to the segment margins, laminar squamules brown [pinnules incised to 1/3 towards the costules]. *C. praecincta*
- 11'. Sori not marginal, if partially submarginal then either not parallel to segment margins but in zig-zag-pattern or laminar squamules white. 12
12. Differentiated margins on petiole scales wide (to 25% of scale width on each side), notably paler brown to pure white, most pinnules basally notably cuneate with basal segments/lobes larger than following ones. (southeastern Brazil, Mata Atlantica) 13
- 12'. Differentiated margins on petiole scales relatively narrow (central portion clearly more than 60 % of scale width), if white then inconspicuous and abraded, most pinnules basally truncate to weakly cordate, if weakly cuneate then whole pinnules oblanceolate. 14
13. Sori ± medial, costae green-alate between pinnules for most of their length. *C. dichromatolepis*
- 13'. Sori supramedial, costae green-alate between pinnules in distal third. *C. glaziovii*
14. Pinnules abaxially with brown to dark brown squamules along costules and midveins, here and on the veins abaxially with few to abundant white tortuous hairs. *C. tortuosa*
- 14'. Pinnules abaxially without dark brown squamules along costules and midveins, either absent or paler; white tortuous hairs absent. 15
15. Largest pinnules short-stalked, deeply incised, segments separated by wide sinuses, basal ones often free and remote from following segments. *C. neblinae*
- 15'. Largest pinnules sessile, incised to 1/2 towards the costae, segments separated by narrow sinuses, basal ones never free. 16
16. Petiole scales relatively wide, restricted to lower half of petioles in mature fronds. *C. pungens*
- 16'. Petiole scales relatively narrow, numerous and persistent along entire petiole and lower part of rachis. *C. oblonga*
17. Paraphyses shorter than or of the same length as sporangia. *C. iheringii*
- 17'. Paraphyses longer than sporangia. 18
18. Petiole scurf dark reddish brown, usually dense and persistent but inconspicuous because petiole epidermis ± of the same color. 19
- 18'. Petiole scurf absent or pale, usually present only in young fronds. 20
19. Laminar squamules mostly ovate-lanceolate, bullate ones lacking, segments with subentire margins and rounded apices, axes abaxially glabrous except for whitish trichomidia. *C. atrocastanea*
- 19'. Laminar squamules mostly bullate, also flat lanceolate ones, segments with finely to strongly crenulate margins and obtuse to acute apices, axes abaxially with white to reddish hairs to 1.5 mm long, sometimes abundant but glabrescent. *C. lasiosora*
20. Petiole scales castaneous, laminar squamules pale with long dark marginal teeth. *C. abbreviata*
- 20'. Petiole scales orange-brown to auburn; laminar squamules lacking long dark marginal teeth. 21
21. Lamina with tortuous hairs to 3 mm long; laminar squamules pale brown with long hair-like tips [fertile plants usually trunkless, rarely with short trunks to 2 m tall]. *C. villosa*
- 21'. Lamina without tortuous hairs but straight or curved hairs may be present; laminar squamules with acute to subulate tips [fertile plants usually with trunks]. 22

22. Veins on both sides with few to many spreading, white, uniseriate hairs to 1.5 mm long, without or with hairs between them, hairs equally abundant on both sides or more abundant abaxially, sometimes replaced by small, appressed trichomidia, especially between the veins abaxially. ***C. phalerata***
 22'. Veins glabrous on both sides except for single white, spreading uniseriate hairs to 1.0 mm long, abaxially with ephemeral tan to brown trichomidia on and between the veins, otherwise glabrous between the veins. ***C. iheringii***

21. *Cyathea abbreviata* I.Fern. E!

Endemic; Alagoas, Bahia, Ceará, Pernambuco, in closed forest remnants, usually close to water, at 480–920 m.
Voucher: BRAZIL. Pernambuco: Município de São Vicente Ferrer, 03.1999, I. Fernandes 1040 (holotype JPB n.v., isotype PARA n.v.).

Reference: Lehnert (2016)

22. *Cyathea atrocastanea* Labiak & F.B.Matos E!

Endemic; Espírito Santo, in montane forests at 600–800 m.
Voucher: BRAZIL. Espírito Santo: Santa Teresa, Estação Biológica de Santa Lúcia – Museu de Biologia Melo Leitão, 19°53'48"S, 40°36'11"W, 600 m, 11.07.2007, P.H. Labiak et al. 4008 (holotype UPCB n.v., isotypes RB, SP n.v.).

Reference: Labiak & Matos (2009), Lehnert (2016)

23. *Cyathea atrovirens* (Langsd. & Fisch.) Domin

Bahia, Goiás, Espírito Santo, São Paulo, Rio de Janeiro, Paraná, Santa Catarina, Rio Grande do Sul, reported from Minas Gerais, Mato Grosso do Sul, Pernambuco, Pará and Amazonas (Windisch & Santiago 2016); also Argentina, Paraguay and Uruguay; mainly in open swampy habitats, 10–1100 m.

Voucher: BRAZIL. Santa Catarina: Ilha Sta. Catarina, G.H. Langsdorff s.n. (lectotype LE, designated by Lehnert 2016: 32, isolectotypes BM, G n.v., LE).

Reference: Lehnert (2016), Prado et al. (2015)

24. *Cyathea dichromatolepis* (Fée) Domin E!

Endemic; Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, reported from Mato Grosso (Windisch & Santiago 2016); at 180–1000 m in Mata Atlântica.

Voucher: BRAZIL. Serra dos Órgãos, A. Glaziou 1786 (lectotype P [Herb. Cosson], inadvertently designated by Barrington 1978: 67).

Reference: Lehnert (2016), Prado et al. (2015)

25. *Cyathea glaziovii* (Fée) Domin E!

Endemic; Bahia, Pernambuco, Goiás, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, at 180–900 m in Mata Atlântica.

Voucher: BRAZIL. Rio de Janeiro: "Brasilia fluminensi", 27.12.1867, A. Glaziou 2155 (lectotype P, designated by Lehnert 2016: 37, isolectotypes B, K, P).

Reference: Lehnert (2016)

26. *Cyathea hirsuta* C.Presl E!

Endemic; Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina at 100–900 m in Mata

Atlântica.

Voucher: BRAZIL. Rio de Janeiro: Corcovado, without date, J.B.E. Pohl s.n. (lectotype PRC, designated by Lehnert 2015: 6, isolectotypes NY, W).

Reference: Lehnert (2016), Prado et al. (2015)

27. *Cyathea iheringii* (Rosenst.) Domin E!

Endemic; Bahia, Rio de Janeiro, São Paulo, Santa Catarina, at 180–1050 m in Mata Atlântica.

Voucher: BRAZIL. São Paulo: Alto da Serra, 10.1909, H. Luederwaldt 1036 (lectotype B, designated by Barrington 1976: 5, isolectotypes MICH, NY, PH, S-R, UC).

Reference: Lehnert (2016)

28. *Cyathea lasiosora* (Kuhn) Domin

Acre, Amazonas, Roraima, Pará, Amapá, reports from Bahia seem dubious (Windisch & Santiago 2016); also in Colombia, Venezuela, French Guiana, Ecuador, Peru, and Bolivia, in terra firme forest and Andean foothills at 100–1250 m, most common below 1000 m..

Voucher: Type of *Alsophila nigra* Mart.: BRAZIL. Amazonas, "Flumen Japurá in Provincia Rio Negro dicta", C.F.P. Martius s.n. (lectotype M, inadvertently designated by Barrington 1978: 47, isolectotypes B-20-0000188, NY-148719 [fragment of Herb. Martius]/-148720 [fragment of B], LE-00008117, M [3 sheets]).

Reference: Barrington (1978), Lehnert (2016), Prado et al. (2015)

29. *Cyathea leucofolis* Domin E!

Endemic; Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, at 40–1050 m in Mata Atlântica.

Voucher: BRAZIL. Minas Gerais: "Crescit in silvis umbrosis ad Mariana", [ca. 20°22"S, 43°25"W, 900 m], 1818, C.F.P. Martius s.n. (holotype M, inadvertently designated by Barrington 1978: 77).

Reference: Prado et al. (2015)

30. *Cyathea mexiae* Copel. E!

Endemic; Minas Gerais and Rio de Janeiro at 700–1400 m, gallery forests and in Mata Atlântica.

Voucher: BRAZIL. Minas Gerais: Viçosa, E of the Agricultural College, 20.07.1930, Y. Mexia 4882 (holotype UC, isotypes B, CAS, BM, E, GB, K, LA, MO, NO, P, PH, U).

Reference: Schwartzburd et al. 2015, Lehnert (2016); considered a synonym of *Cyathea phalerata* by Windisch & Santiago (2016), who erroneously treated the distinct *Cyathea mexiae* (heterotypic synonym *Alsophila gardneri* Hook. = *Trichipteris gardneri* (Hook.) R.M.Tryon) as



C. gardneri Hook., which is the basionym of the valid *Sphaeropteris gardneri* (Hook.) R.M.Tryon.

31. ***Cyathea microdonta*** (Desv.) Domin

Acre, Amazonas, Amapá, Pará, Rondônia, Roraima, Tocantins, Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Sergipe, Goiás, Mato Grosso do Sul, Mato Grosso, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo; also Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Hispaniola, Puerto Rico, Trinidad & Tobago, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil and Bolivia at 0–700 m. Typical lowland plant, found in open spots on wet to waterlogged soils, like swamps and road ditches, also in coastal forests bordering to mangroves.

Voucher: America Australi,” without date, N.A. Desvaux s.n. (lectotype P, designated by Lehnert 2016: 41, isolectotype P). *Reference:* Lehnert (2016), Prado et al. (2015)

Cyathea myriotricha → see Group II, No. 9

Cyathea neblinae → see Group II, No. 16

32. ***Cyathea oblonga*** (Klotzsch) Domin

Pará; also in Venezuela, Guyana, Suriname and French Guiana at 140–1300 m, in lowland rain forests on terra firme and in premontane forest.

Voucher: BRAZIL. Pará: Mun. Oriximiná, ESEC do Grão Pará, Serra do Acari, trilha 2 de 2.8 km, 01°16'17.4"–00.3"N, 58°41'37.6"–45.5"W, 407–600 m, 28.08.2008, M.R. Pietrobom & S. Maciel 7767 (MG, STU).

Reference: Lehnert (2016)

33. ***Cyathea phalerata*** Mart.

Mato Grosso, Minas Gerais, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, reported from Acre, Alagoas, Ceará, Pernambuco, Distrito Federal, Goiás, Rio Grande do Sul (Windisch & Santiago 2016); also eastern Bolivia at 35–1400 m in gallery forests and Mata Atlântica. *Voucher:* BRAZIL. Bahia: “Crescit in silvis montanis ad Almadam et alibi Provincia Bahiensi”, C.F.P. Martius s.n. (lectotype M, designated by Lehnert 2016: 43, isolectotypes B, BM, K, NY, US [fragment of NY]).

Reference: Forzza et al. (2010), Prado et al. (2015)

34. ***Cyathea poeppigii*** (Hook.) Domin

Goiás, Minas Gerais, Espírito Santo, Rio de Janeiro; also in Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru and Bolivia at 20–1500(–2250) m in humid to wet forests. Preferring warm climates and open sun, flourishing in disturbed habitats.

Voucher: Type of *Alsophila impressa* Féé: BRAZIL. Rio de Janeiro: “Brasilia Fluminensi”, 07.03.1867, A. Glaziou 983 (lectotype P [Herb. Féé-Cosson], inadvertently designated

by Windisch 1977: 189, isolectotype BR).

Reference: Windisch (1977), Forzza et al. (2010)

35. ***Cyathea praecincta*** (Kunze) Domin E!

Endemic; Alagoas, Bahia, Pernambuco, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, at 550–900 m in Mata Atlântica.

Voucher: BRAZIL. Bahia: Ilheos, [ca. 14°10'S, 53°05'W], 1817–1820, C.F.P. Martius 391 (lectotype B-fragment NY, chosen by Barrington 1978: 71, isolectotypes K, M, MO, NY). *Reference:* Forzza et al. (2010)

36. ***Cyathea pungens*** (Willd.) Domin

Acre, Amazonas, Pará, Rondônia, Bahia, Ceará, Paraíba, Pernambuco, Goiás, Mato Grosso do Sul, Mato Grosso, São Paulo, Paraná; also Trinidad & Tobago, Colombia, Venezuela, Ecuador, Peru, and Bolivia at 50–1250 m in lowland and premontane forests.

Voucher: BRAZIL. “Brasilia,” without date, J.C. Hoffmannsegg s.n. (holotype B [Herb. Willdenow 19716], inadvertently designated by Barrington 1978: 23, isolectotypes NY [fragment of B], US [fragment of B]).

Reference: Forzza et al. (2010)

37. ***Cyathea rufa*** (Fée) Lellinger E!

Endemic; Bahia, Espírito Santo, Minas Gerais, Espírito Santo, Rio de Janeiro; in Mata Atlântica at 100–900 m.

Voucher: BRAZIL. Rio de Janeiro: Without locality, 24.04.1868, A. Glaziou 2291 (lectotype P, designated by Riba 1969: 14; isolectotypes P, NY-[fragment of P], S).

Reference: Forzza et al. (2010), Prado et al. (2015)

38. ***Cyathea tortuosa*** R.C. Moran

Amazonas, Pará; also in Colombia, Venezuela, Ecuador, and Peru at 300–1200(–1600) m in humid lowland and premontane forests.

Voucher: BRAZIL. Amazonas, Mun. Amataura, São Domingos, 03°25'S, 68°10'W, 21.11.1986, H.C. de Lima, D.C. Daly, R.P. de Lima & W. Brazil 2764 (NY).

Reference: Lehnert (2016)

39. ***Cyathea villosa*** Willd.

Roraima, Bahia, Goiás, Distrito Federal, Minas Gerais, São Paulo, Paraná and Santa Catarina; also in Panama, Colombia, Venezuela and Bolivia at 850–1550(–1800) m in open rock outcrops, grasslands and open forests.

Voucher: Type of *Alsophila rigidula* Mart.: BRAZIL. São Paulo: “Crescit in sylvis provinciae S. Pauli”, without date, C.F.P. Martius s.n. (holotype M, inadvertently designated by Barrington 1978: 60).

Reference: Barrington (1978), Lehnert (2016)

Group V. Species with bipinnate-pinnatifid or more complex laminae and hemitelioid indusia

1. Sori proximal to subproximal, petioles inermous to weakly verrucate, petiole scales ovate with rather blunt tips,

- concolorous brown to castaneous or weakly bicolorous with paler brown margins. ***C. platylepis***
- 1'. Sori medial to submarginal, petioles muricate to aculeate (rarely inermous), petiole scales lanceolate to linear-lanceolate with acute to attenuate or filiform tips, concolorous brown to whitish or bicolorous with dark-brown center (sometimes a thin stripe) and pale margins. 2
2. Petiole scales persistent along the whole length of petiole and lower half of the rachises; plants predominantly trunkless or with trunks to 1 m. (Guayana Highlands, western Amazonia). ***C. vaupensis***
- 2'. 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 1–5 m tall. 3
3. Petioles abaxially hairy, petiole scales broadly ovate, papery, whitish to stramineous (may change quickly to strong bicolorous with blackish centers and white margins on the trunk). 4
- 3'. Petioles abaxially not hairy, petiole scales either narrowly lanceolate to hair-like, or dark brown with inconspicuous paler margins (scales on petioles and trunks ± the same in shape and color). 5
4. Lamina abaxially glabrous or with very few scattered hairs; scales on trunk of the same pale color as those on petioles. (eastern Guayana shield) ***C. boryana***
- 4'. Lamina abaxially hairy on veins; scales on trunk usually with much darker center than those on petioles. (eastern Andean foothills) ***C. leucolepismata***
5. Veins abaxially densely hairy with hairs to 2 mm long. (Guayana Highlands, eastern Amazonia) ***C. surinamensis***
- 5'. Veins abaxially glabrous or with few hairs to 1 mm long. 6
6. 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]. ***C. andina***
- 6'. Sori ± medial, paraphyses longer than the sporangia [petiole scales narrowly lanceolate to lanceolate, 10.0–25.0 × 1.0–3.0(–3.5) mm] 7
7. Laminae obovate, often basally tapering with basal pinnae of the same size and dissection as the pinnules of largest pinnae, petioles then virtually absent. (Guyana Highlands, eastern Amazonia). ***C. cyatheoides***
- 7'. Laminae ovate-elliptic, basally not gradually tapering, petioles well developed. 8
8. Petiole scales stramineous, concolorous or with weak discontinuous central stripe [petiole and axes with easily abraded whitish scurf]. (Periphery of Amazon basin, eastern Brazil). ***C. macrocarpa***
- 8'. Petiole scales discordantly to concordantly bicolorous, dark brown to auburn with white margins. 9
9. Laminar squamules ample and dark brown [petiole and axes without whitish scurf]. (Guyana Highlands). ***C. macrosora***
- 9'. Laminar squamules sparse and pale brown [petiole and axes with easily abraded whitish scurf]. (Mesoamerica, Amazonia). ***C. traillii***

[*Cyathea andina* (H.Karst.) Domin]

Haiti, Puerto Rico, Colombia, Venezuela, Ecuador, Peru, Bolivia, in humid forests at 200–1900 m.

Voucher: BOLIVIA. Cochabamba: Carrasco, 141 km antigua carretera Cochabamba - Villa Tunari, 17°07'S, 65°33' W, 1400 m, 24.08.1996, M. Kessler, T. Krömer & J. Gonzales 7709 (GOET, LPB, UC)

Reference: Lehnert (2011b), often confused with *Cyathea cyatheoides*.

[*Cyathea boryana* (Kuhn) Domin]

Suriname and French Guiana, in understory of wet forests at 200–500 m.

Voucher: FRENCH GUIANA. F.M.R. Leprieur 265a (lectotype P, designated by Tryon 1976: 34).

Reference: Lehnert (2011b)

40. *Cyathea cyatheoides* (Desv.) K.U.Kramer

Amazonas, Rondônia, Pará, Roraima and Mato Grosso at ca. 50–125 m: also Colombia, Venezuela, Guyana, Suriname and French Guiana at 40–200 m, in Amazonian lowland rainforests.

Voucher: BRAZIL. Pará: Mun. Alenquer, Floresta Estadual do Paru, trilha T2, cachoeira da Onça, 00°54'07.1"S,

53°15'56.7"W, 184 m, 07.12.2008, S. Maciel 1453 (MG).

Reference: Forzza et al. (2010), Prado et al. (2015)

41. *Cyathea leucolepismata* Alston

Amazonas; Colombia, Ecuador, Peru, Bolivia, in lower montane forests 90–1300 m.

Voucher: BRAZIL. Amazonas: Presidente Figueiredo, Reserva Biológica Uatumã, close to the easternmost point of the lake, 01°47"S, 59°17'W, 100–150 m alt., 04.02.2008, H. Tuomisto et al. 15603 (SP, TUR).

Reference: Lehnert (2011b)

42. *Cyathea macrocarpa* (C.Presl) Domin

Roraima, Bahia; also Colombia, Venezuela, Guyana, French Guiana, in the understory of humid evergreen forests; previous records from Ecuador and Peru (Lehnert 2011a, b) base on pale-scaled plants of *Cyathea traillii*.

Voucher: BRAZIL. Bahia, J.S. Blanchet 17 (lectotype PRC, designated by Lehnert 2011b: 54).

Reference: Lehnert (2011b)

43. *Cyathea macrosora* (Baker) Domin

Pará; reported from Amazonas, Rondônia and Roraima



(windisch & Santiagi 2016); also Colombia, Venezuela, Guyana, Suriname and French Guiana at 100–1700 m in Amazonian lowland forests.

Voucher: BRAZIL. Pará: Mun. Oriximiná, Estação Ecológica Grão Pará, trilha T4, gruta entre a parcela 01 e o 02, 00°54'07.1"S, 53°15'56.7"W, 450 m, 03.09.2008, S. Maciel 1071 (MG).

Reference: Lehnert (2011b), Prado *et al.* (2015)

44. ***Cyathea platylepis*** (Hook.) Domin

Amazonas; also in Colombia (250–900 m) and Venezuela (350–2600 m) in the understory of wet forests on white sands and on the slopes of sandstone mountains.

Voucher: BRAZIL. Amazonas: Rio Cuieras, 2 km from Rio Cuieras at 2 km below mouth of Rio Brancinho, 14.09.1973, G.T. Prance *et al.* 17937 (lectotype K, inadvertently designated by Tryon 1976: 38, isolectotypes BM, GOET).

Reference: Tryon (1976), Lehnert (2011b)

45. ***Cyathea surinamensis*** (Miq.) Domin

Amazonas, Amapá, Pará; also Guyana, Suriname, French Guiana, in Amazonian rainforest between 10–770 m.

Voucher: BRAZIL. Pará: Mun. Oriximiná, ESEC do Grão Pará,

Serra do Acari, trilha 2 de 2.8 km, 01°16'00.3"-17.4"N, 58°41'37.6"-45.5"W, 407–600 m, 28.08.2008, M.R. Pietrobom & S. Maciel 7772 (MG, STU).

Reference: Lehnert (2011b)

46. ***Cyathea traillii*** (Baker) Domin

Amazonas; also Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, in moist lowland forest on terra firme and premontane forests on sandstone at 120–1000 m.

Voucher: BRAZIL. Amazonas: Rio Mahues (=Maués), G.W. Traill 1384 (lectotype K, fragment US, inadvertently designated by Windisch 1978: 20, isolectotypes GH, P-fragment F).

Reference: Windisch (1978), Lehnert (2011b)

47. ***Cyathea vaupensis*** (Windisch) Lehnert

Amazonas, Roraima; also Colombia, and Peru in moist forests on terra firme at 75–500 m.

Voucher: COLOMBIA. Vaupés: Cerro Isibukuri, Río Kanari, Comisaria del Vaupés, R.E. Schultes & I. Cabrera 13407 (holotype GH).

Reference: Forzza *et al.* (2010)

Group VI. Species with bipinnate-pinnatifid or more complex laminae and indusia reaching all around the receptacles

Indusia sphaeropteroid to subsphaeropteroid, at least persisting as irregular disc around the receptacle at maturity.

1. At least petioles with scurf when young, orange-brown to brown; petiole scales orange-brown; veins abaxially with hairs. 2
- 1'. Petioles and frond axes lacking scurf although some small castaneous scales may be present on costules; petiole scales dark brown; veins abaxially without hairs. 3
2. Petiole epidermis a dull brown in dried specimens, the same color to green in fresh material; laminar hairs never between the veins, laminae usually sparsely hairy on both sides, or if pubescence evident then hairs more abundant abaxially; costules abaxially with some larger ovate scales to 5 mm long, with fimbriate margins ***C. aurea***
- 2'. Epidermis near the petiole base usually a shiny black, rarely just dark brown; laminar hairs often present between the veins abaxially but not adaxially, laminae usually evidently hairy on both sides, laminar indument with orange-brown to brown, flat ovate-lanceolate and bullate squamules 1–2 mm long with elongate tips and fimbriate to entire margins; larger scales lacking on the costules. ***C. delgadii***
3. Plants terrestrial with erect trunks several m tall, mostly in understory; petiole scale shiny castaneous; largest pinnules less than 15 mm wide, subsessile. ***C. lechleri***
- 3'. Plants epiphytic or terrestrial on ridges, with trunks to 1 m tall; petiole scales dull brown; largest pinnules to 35 mm wide, stalked. ***C. gracilis***

48. ***Cyathea aurea*** Klotzsch

Amazonas; also Venezuela, expected from adjacent Colombia, in wet mountain forests.

Voucher: BRAZIL. Amazonas: Neblina Massif, 1100 m. 24.12.2003–05.01.2004, F.A. Carvalho *et al.* 344. (INPA-image).

Reference: Carvalho *et al.* (2012)

in Mata Atlântica and gallery forests, more in the open, often surviving burnings; also on the Ilha da Trindade, where it forms dominant stands on grassy slopes. Widespread in the Neotropics from Costa Rica to Venezuela and Bolivia.

Voucher: BRAZIL. Goiás: “Gancho do Generale Delgado in via ad Caldas Novas”, without date, J.B.E. Pohl s.n. (holotype PRC-fragment GH).

Reference: Forzza *et al.* (2010)

49. ***Cyathea delgadii*** Pohl ex Sternb.

Ceará, Amazonas, Rondônia to Pernambuco, Mato Grosso to Bahia, and Espírito Santo to Rio Grande do Sul at 80–1800

Cyathea gracilis Griseb.

Amazonas, Serra da Neblina; also in Costa Rica, Panama,

Jamaica, Colombia, Ecuador and northern Peru at (770–1300–2500 m; growing as epiphyte or terrestrial in open, humid places.

Voucher: BRAZIL. Amazonas: Neblina Massif, 1100 m, 24.12.2003–05.01.2004. F.A. Carvalho et al. 347 (INPA-image).

Reference: Carvalho et al. (2012)

51. *Cyathea lechleri* Mett.

Amazonas, also in Colombia, Ecuador, Peru and Bolivia at 750–1600 m, characteristically found below ridgetops of small mountains.

Voucher: BRAZIL. Amazonas: Barcelos, Parque Estadual do Araça, 00°56'30"N, 63°24'55"W, 1412 m, 02.09.2012, R.C. Forzza et al. 6666 (RB).

Reference: Tryon (1976)

Hybrids

52. *Cyathea xstella-matutina* Schwartsb. & I. Becari-Viana

Río de Janeiro at 100–200 m in Mata Atlântica; only known from the type.

Voucher: BRAZIL. Rio de Janeiro: Cachoeiras de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03.07.2014, P.B. Schwartsbürd 3303 (holotype VIC, isotypes BONN, SP).

Reference: Schwartsbürd et al. (2015)

Dubious and excluded names

Following names may be referable to *Cyathea iheringii*, *C. mexiae* or *C. phalerata*, but an assignment to species is not possible based on the description alone:

Alsophila alutacea Kunze

Type: BRAZIL. Bahia: Ilheos, C.F.P. Martius s.n. (holotype not located). Excluded material—GUYANA. Demerara, 1830, J. Parker s.n. (K).

Alsophila pabstii Brade

Type: BRAZIL. Distrito Federal: Região da nova Capital, Brasília, 13.11.1958, C.F.J. Pabst 4935 & E. Pereira 4608 (RB [Herb. Bradeanum 7223] n.v.).

Alsophila paleolata Mart. var. *nigrescens* Hook. ex Baker

Type: BRAZIL. „Brasilia australi“, F. Sellow s.n. (syntype not located). Rio de Janeiro: Near Rio de Janeiro, A. Glaziou 2283, 2285 (syntype not located).

Alsophila paleolata Mart. var. *eriocarpa* Christ

Type: BRAZIL. Goyaz, Colombista, 04.11.1894, A. Glaziou 22628 (P); Minas Gerais: Serra do Ouro Preto, without date, C.A.W. Schwacke 11410 (holotype not located).

Alsophila phalerata var. *squamulosa* T.Moore

Voucher: BRAZIL. Bahia: Ilheos, M.E. Moricand (holotype not located).

The following names are unpublished or illegitimate:

“*Alsophila paleolata* Mart. f. *erosa* Rosenstock”, nom. ined.

The collection “BRAZIL. Paraná: Villa Nova, 1906, J. Annies s.n. [Herb. Rosenstock 246]” at (M, W) bears this name.

“*Alsophila paleolata* Sehnem” (1956: 319), hom. illeg.

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