



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

## Monograph

# A reassessment of the Neotropical *Cyathea pungens* complex (Cyatheaceae)

Marcus LEHNERT<sup>1,\*</sup>, Adrian TEJEDOR<sup>2</sup>, Michael KESSLER<sup>3</sup>,  
Wilson D. RODRÍGUEZ DUQUE<sup>4</sup> & Luis Fernando GIRALDO GALLEGOS<sup>5</sup>

<sup>1</sup>Herbarium (HAL), Martin-Luther-Universität Halle Wittenberg, Am Kirchtor 3 ,  
06108 Halle (Saale), Germany.

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,  
Leipzig 04103, Germany.

<sup>1</sup>BIOB Abt. I – Biodiversität der Pflanzen, Rheinische Friedrich-Wilhelms Universität,  
Meckenheimer Allee 170, D-53115 Bonn, Germany.

<sup>2</sup>Wildlife Conservation Society – Papua New Guinea, Rohanoka st, Goroka, Papua New Guinea.

<sup>3</sup>Institute for Systematic and Evolutionary Botany, University of Zurich, Zollikerstr. 107,  
8008 Zurich, Switzerland.

<sup>4</sup>Instituto Amazónico de Investigaciones Científicas-Sinchi, Calle 20 No. 5-44,  
Bogotá, Cundinamarca, Colombia.

<sup>5</sup>Universidad CES, Calle 10 A No. 22-04, Medellín, Antioquia, Colombia.

<sup>5</sup>Herbario Universidad de Antioquia (HUA), Calle 67 Número 53-108, Medellín,  
Antioquia, Colombia.

\*Corresponding author: [marcus.lehnert@botanik.uni-halle.de](mailto:marcus.lehnert@botanik.uni-halle.de)

<sup>2</sup>Email: [adriantejedor@gmail.com](mailto:adriantejedor@gmail.com)

<sup>3</sup>Email: [michael.kessler@systbot.uzh.ch](mailto:michael.kessler@systbot.uzh.ch)

<sup>4</sup>Email: [wrodriguez@sinchi.org.co](mailto:wrodriguez@sinchi.org.co)

<sup>5</sup>Email: [ferngiraldo@yahoo.com](mailto:ferngiraldo@yahoo.com)

**Abstract.** *Cyathea pungens*, a widespread Neotropical scaly tree fern, is reassessed taxonomically. Based on extensive field observations in South America and the Caribbean, and comparative studies of herbarium specimens and online resources, we define *C. pungens* as a mainly Amazonian species that extends into the Caribbean but neither beyond west of the Andes nor into the Brazilian Mata Atlantica. Records from west of the Colombian Cordillera Oriental belong to other species, which differ slightly but consistently in the laminar indument (i.e., abundance and color of bullate squamules, and presence of hairs variable vs constant) and prevailing pinnule shape (with only obtuse tips vs acute and obtuse tips). The weak differences in the specimens are generally corroborated by different appearances in the field (i.e., shape of the blades, and number of pinnae) and preferred elevational ranges. The distributions of *C. pungens* and *C. oblonga* overlap in the area of the Guyana shield, but *C. oblonga* is also found along the Caribbean coast and northern lowlands of Colombia and Venezuela. Both species are rarely found above 1000 m and are largely replaced in the mountains by *C. klotzschiana* (Colombian Cordillera Oriental, Sierra Nevada de Santa Marta and Venezuelan coastal ranges) and *C. pastazensis* (Colombian Cordillera Central and Occidental as well as eastern Andean slopes of Ecuador). To this group further belongs *C. dombeyi* from the Andes of Peru and Bolivia, and the reinstated *C. pycnocarpa* and *C. floribunda* from Peru and Bolivia. Several additional species are tentatively placed in this group: the northern Andean *C. squamata*, the Guayanan *C. neblinae*, Brazilian *C. praecineta* and Andean *C. werffii*.

**Keywords.** Amazonia, Andes, ecological niche, tree fern.

Lehnert M., Tejedor A., Kessler M., Rodríguez Duque W.D. & Giraldo Gallego L.F. 2025. A reassessment of the Neotropical *Cyathea pungens* complex (Cyatheaceae). *European Journal of Taxonomy* 988: 1–57. <https://doi.org/10.5852/ejt.2025.988.2883>

## Introduction

The taxonomy of tree ferns (Cyatheales; PPG 1 2016) has long lagged behind that of other fern groups because their large size involuntarily leads to fragmentary herbarium specimens, so that important characters may not be preserved for herbarium-based studies. In the last few decades, extensive field work has revolutionized our understanding of tree ferns, resulting in the discovery of many new species and taxonomic revisions (e.g., Noben & Lehnert 2013; Schwartsburd *et al.* 2015; Tejedor & Calatayud 2017; Lehnert & Coritico 2018; Lehnert & Cámara-Leret 2018, 2019). This applies particularly to the genus *Cyathea* Sm. (Cyatheaceae Kaulf.), which now is considered to include about 315 species following reassessments of many species groups (e.g., Lehnert 2008, 2009, 2011, 2014, 2016; Lehnert & Weigand 2013, 2017; Lehnert *et al.* 2021). One group that has so far not been revised in detail is the *Cyathea pungens* (Willd.) Domin group, which has a wide distribution in the Amazon basin and foothills of adjacent mountain ranges, with scattered records from the Caribbean coast of South America and some Caribbean Islands (Lehnert 2016), and which is the focus of the current study.

Lehnert (2016) united 51 species under his *Cyathea pungens* group, but this included all members of a diverse clade of exindusiate species that are phylogenetically aligned (Loiseau *et al.* 2019). Here, we define a more specific subgroup within this clade as the *Cyathea pungens* complex. This species complex is characterized by small stature, a distinct firm lamina texture and a relatively coarse bipinnate-pinnatifid blade dissection with wide and mostly rounded segments; the petiole scales are consistently bicolorous, although the extent of the white marginal color varies greatly depending on species, size and part of the plant. Morphological variation of the fine indument within the group is subtle and complex at the same time. Historically, many species had been described based on unique character combinations, while recent taxonomic treatments recognized only a few species. For instance, Barrington (1978) put only one species, *C. dombeyi* (Desv.) Lellinger, into closer relationship with *C. pungens*, each with an ample list of synonyms, and informally joined seven species with short paraphyses as a group of *Trichipteris procera* (Willd.) R.M.Tryon (= *Cyathea pungens*). This includes some taxa we later treated in different groups because of different scale color and blade dissection, i.e., with almost entire pinnules: *C. barringtonii* A.R.Sm. ex Lellinger (= *T. cordata* (Klotzsch) R.M.Tryon), *C. sagittifolia* (Hook.) Domin, *C. venezuelensis* A.R.Sm. ex Lellinger (= *T. steyermarkii* R.M.Tryon) (Lehnert & Weigand 2017); or with tripinnate blades: *Cyathea decomposita* (H.Karst.) Domin (Lehnert 2016).

Ecological observations, which in the past were only sparsely provided with the collections, may prove to be essential in separating tree fern taxa. Cremers & Boudrie (2007) were able to separate *Cyathea oblonga* (Klotzsch) Domin from *Cyathea pungens* in the Guyanas after extensive observations in the field that allowed them to correlate morphological features with environmental factors. The species, although their ranges overlap, appear to have different centers of elevational distribution and maintain their distinguishing characters where they occur together. The latest addition to this group was by Tejedor & Areces-Berazain (2018, 2021), who described *C. rutenbergiae* A.Tejedor & F.Areces from Puerto Rico.

At the start of this study, we considered the complex to include seven species (*C. pungens*, *C. dombeyi*, *C. oblonga*, *C. rutenbergiae*, *C. squamata* (Klotzsch) Domin, *C. praecincta* (Kunze) Domin and *C. werffii* R.C.Moran). Species of the *C. pungens* complex are typically found in the deep shade of the understory near water courses (Zuquim *et al.* 2008; pers. obs.) but they may also grow in more open conditions where

sufficient soil moisture is guaranteed, for example in swamps and recently logged areas. The observed morphological variation, which is reflected in the many synonyms, has generally been considered as a response to these different habitat conditions (Lehnert 2016). This variation is related mainly to the size and shape of the pinnules, which may be either blunt-tipped or conspicuously pointed (Barrington 1978). However, our observations in the central Andes (M. Lehnert and A. Tejedor, pers. obs.) have shown that large mature plants have blunt-tipped pinnules in the lower half of their leaves and pointed pinnules in the upper half, whereas smaller and immature plants tend to have only blunt pinnules.

Other characters seem to provide even less information. Petiole scurf is weakly developed and usually ephemeral. Even when it is preserved, the squamellae and branched hairs are often plastered and have not been considered reliable characters (Barrington 1978). The odd specimen with well developed scurf, which once in a while turns up, is normally filed as the exception that confirms the rule. The laminar indument of this group is also often weakly developed. Although some specimens have some whitish bullate squamules whereas others have darker brown ones, this difference has not been used for species differentiation because it appeared uncorrelated to any other character. Moreover, many samples lack bullate squamules altogether and it is not clear if they simply shed the squamules over time or were glabrous from the beginning.

The petiole scales are of an unremarkable dark brown with varying paler brown to whitish margins. Some specimens have almost concolorous scales while others have broad white-margined scales. This variation has been attributed to the age of the plants and the method of collection because in crosiers, the outer layer of scales is darker brown and the innermost layer is almost completely white, with a gradual transition of bicolorous scales in-between. Large leaves usually have more of the brown scales near the petiole bases than smaller ones, resulting from a larger outer surface of the original crosier. Depending on whether a leaf is ripped off or cut from the trunk, the appearance of the specimen may differ because the distal bicolorous scales may be shed due to handling while the basal concolorous scales are preserved, and vice versa. Therefore, an evaluation of the petiole scale morphology from herbarium specimens alone has long been considered to be of little value for recognizing more species in the complex (Barrington 1978; Lehnert 2016). However, this changes if field observations of the plant's total size, general appearance and the growing conditions are taken into account.

After extensive field observations and herbarium work in Colombia, combined with previous experiences in Ecuador, Peru, Bolivia and Puerto Rico, and aided by the increasing amount of digitized specimens available online, we are now confident in recognizing further taxa in the *Cyathea pungens* complex. In the following, we resurrect several taxa and give a brief account of the morphologically similar species.

## Material and methods

This study uses data gathered from the largest Colombian herbaria (CAUP, COAH, COL, CUCV, FMB, HUA, JAUM, MEDEL, TULV, VALLE; Thiers 2024). We further consulted collections from AAU, B, BM, BONN, F, GOET, HAL, K, L, M, MO, P, STU, UC, US, W and Z for types and comparative material. We used the websites of the pteridophyte collections consortium ([www.pteridoportal.org](http://www.pteridoportal.org)), the Universidad Nacional de Colombia ([www.biovirtual.unal.edu.co](http://www.biovirtual.unal.edu.co)) and Instituto de Pesquisas Jardim Botânico do Rio de Janeiro – REFLORA ([reflora.jbrj.gov.br/reflora/herbarioVirtual/](http://reflora.jbrj.gov.br/reflora/herbarioVirtual/)) for verifying occurrences of specimens and determinations by consulting the linked digital images. In order to properly differentiate the Caribbean specimen pool, we added all specimens identified as *Cyathea aspera* (L.) Sw. from the 'pteridoportal' database, even though this species is not considered part of the *C. pungens* complex here. A selection of specimens representing each major political subunit of the total distribution is given with each species' description; a full account of the studied material is found in the list of exsiccatae in Appendix 1.

We conducted field trips to all ecoregions of Colombia in 2015–2019; our collections are mainly stored in HUA and COAH, with duplicates deposited in BONN and Z. Further field observations were made by the authors (main initials) in Panama (AT & ML 2016), Hispaniola (ML 2014, 2024) and Jamaica (ML 2014), Puerto Rico (ML 2009; AT 2016), Ecuador (ML 2010–2015), Peru (AT 2010–2018; ML 2003, 2010) and Bolivia (ML 2002–2003). The geographic sequence of specimens follows the guidelines for Flora Neotropica ([www.nybg.org/botany/ofn/fn-gdap1.htm](http://www.nybg.org/botany/ofn/fn-gdap1.htm)), with countries listed from northwest to southeast through Mesoamerica, the Caribbean, and South America. A full list of exsiccatae can be found in the Appendix 1.

Distribution maps are based on the geographic information drawn from online resources as well as our own revisionary specimen lists (ML, WD) and were drawn using R-studio (Allaire 2012; [www.rstudio.com](http://www.rstudio.com)) with R-packages “ggplot2” and “dplyr” (<https://cran.r-project.org>).

Terminology for morphology follows Lellinger (2002) and Lehnert (2011).

Unique identifiers (barcodes, catalogue numbers) of herbarium specimens are given for type specimens like they are presented on the respective institutional home page.

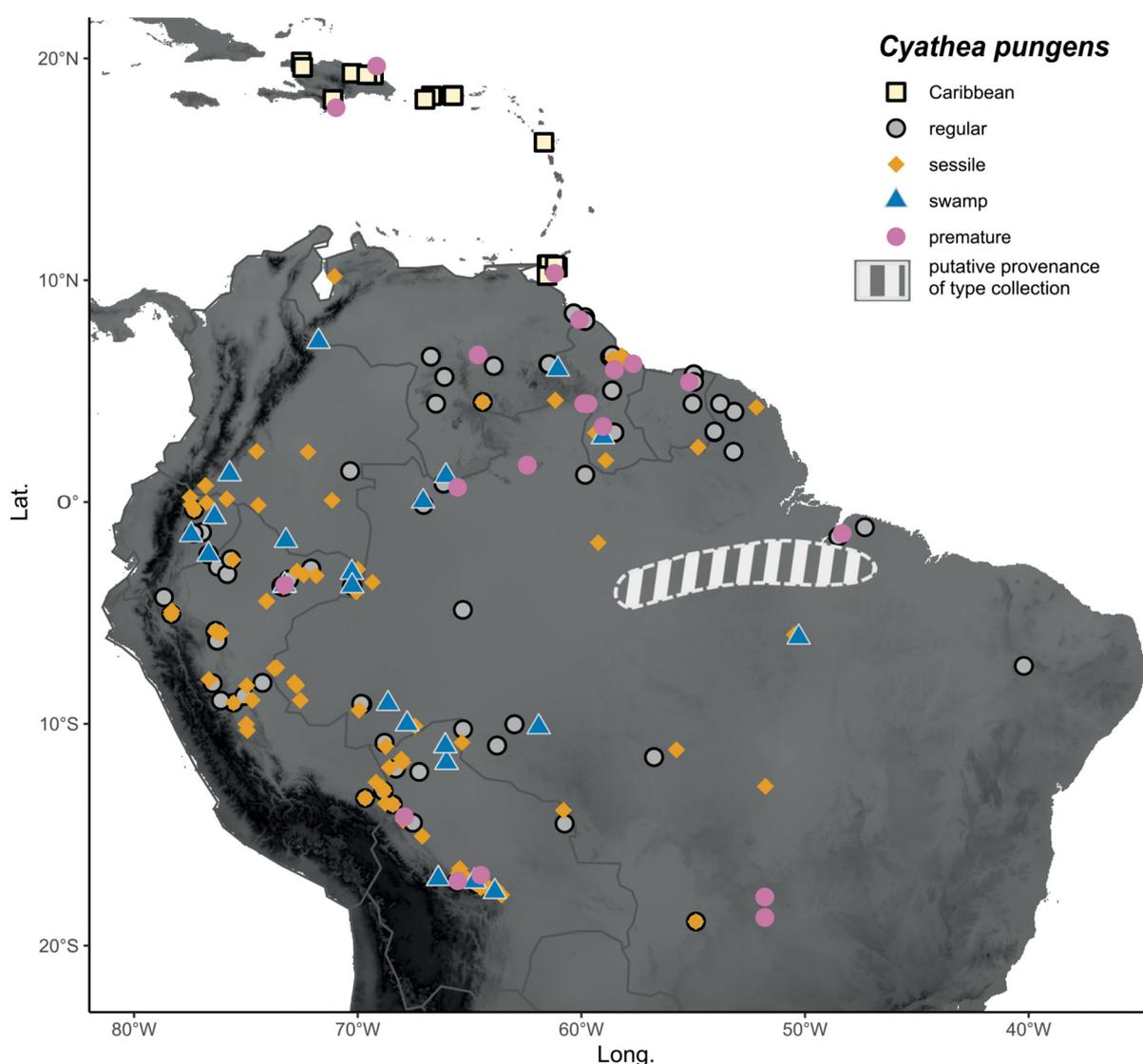
## Results

At the onset of our study, the *Cyathea pungens* complex, as defined here, had seven recognized species. For the current taxonomic reevaluation of the complex, our approach was the gradual redefinition of taxa based on field observations and study of original material, and their subsequent subtraction from the entire specimen pool. After careful evaluation of the most likely location of the locus classicus of *Alsophila pungens*, we aligned the fragmentary type material at B with recent, more complete collections from that area.

Based on this approach, we defined *Cyathea pungens* as an understory tree fern from the Amazon basin (Fig. 1) with most of the central and lower pinnae clearly stalked and being only scantily scaly on the axes and veins, differing in these aspects from most of the Andean populations, which have mostly sessile pinnae and visibly more scales on the blades. It also turns out that in *C. pungens*, as defined here, the sori strictly follow the segment margin in a submarginal line, creating an empty space of green laminar tissue on each side of the midveins and costules. Even with this narrower definition, *C. pungens* remains variable, as detailed under the discussion of that species.

As a result of our taxonomic reevaluation, we resurrect several species in the Andean region as valid. Specifically, *Cyathea klotzschiana* Domin (= *Alsophila obtusa* Klotzsch) and *C. pastazensis* (Hieron.) Domin are reinstated from synonymy with *C. pungens*, and *C. floribunda* (Hook. & Baker) Domin and *C. pycnocarpa* (Kunze) Domin are reinstated from *C. dombeyi* (Barrington 1978; Lehnert 2016). The first three (*C. klotzschiana*, *C. pastazensis*, *C. floribunda*) differ from ‘regular’ *C. pungens* (see description of morphotypes in the Taxonomic treatment below) in having sessile pinnae and pinnules, short crispate hairs on costae and costules abaxially, and few to many strongly bullate squamules on the costules, which vary between entirely dark brown (*C. pastazensis*), pale yellowish brown to whitish (*C. floribunda*) and mostly bicolorous brown with whitish tips (*C. klotzschiana*). The sori usually form a line parallel to the midvein and are more or less medially arranged; only *Cyathea klotzschiana* may have the sori in a submarginal line as in *C. pungens*, but in these cases the segments are also narrower than the average of *C. klotzschiana*. *Cyathea pycnocarpa* and *C. dombeyi* have several characters in common that distinguish them from *C. pungens*: sori arranged in a V-shape close to the midveins to almost parallel to them, bicolorous petiole scales with scattered dark teeth and often white flakey petiole scurf. Additional distinguishing characters are discussed in the taxonomic treatments.

Based on these taxonomic changes, we consider the *C. pungens* complex to include eleven species (Figs 3–13). These show clear geographic patterns with relatively little overlap (Figs 1–2): *Cyathea klotzschiana* is found in the Sierra Nevada de Santa Marta, the Colombian Cordillera Oriental and the Venezuelan Andes including the Cordillera de la Costa; *Cyathea pastazensis* is found in the Colombian Cordilleras Central and Occidental, and the eastern Andean slopes of Ecuador. Its southern distribution limit is diffuse but it seems to be replaced in Peru and Bolivia by *C. floribunda*, *C. dombeyi* and *C. pycnocarpa*. However, in the area from the Cordillera Occidental in Colombia to the coastal ranges of Venezuela several species of this complex co-occur (*C. klotzschiana*, *C. oblonga*, *C. pastazensis*). In fact, *C. klotzschiana* can be found growing together with *C. oblonga*, but there seems to be some ecological separation, with *C. klotzschiana* reaching higher up into the mountains whereas *C. oblonga* prefers the lowlands. Also occurring in this region is *Cyathea squamata*. Although it seems to be related to *C. pungens* and has a similar coloration of the scales and squamules, due to its characteristic size and proportions of scales and

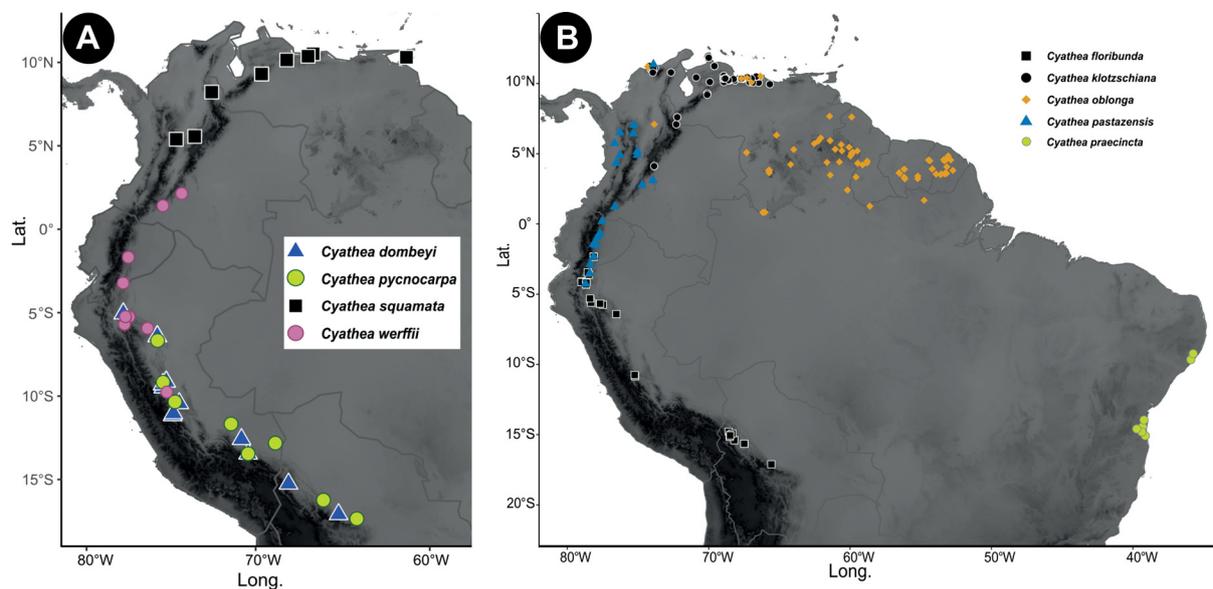


**Fig. 1.** Distribution of *Cyathea pungens* (Wild.) Domin and its different forms; most likely area of origin of the type deduced from literature research. Gaps in Peru and Brazil presumably reflect collection biases, whereas the absence in central and south Bolivia and northern parts of Colombia and Venezuela probably represent true absence.

pinnules it has rarely been confused with other species. Further fitting the diagnostic characters of this group by having bicolorous petioles scales, faint laminar indument and short paraphyses are *C. werffii*, an often trunkless species from the Andean foothills of Ecuador and Peru, *C. neblinae* A.R.Sm. from the Guayana highlands, and *C. praecincta* from eastern Brazil.

We also found that many specimens in herbaria and taxonomic treatments have been wrongly placed under the name *Cyathea pungens*. Thus, we remove the name *Alsophila eatonii* Jenman from the synonymy of *C. pungens* (Barrington 1978; Lehnert 2016) and place it in closer affinity to *C. aspera* (L.) Sw., an exclusively Caribbean taxon that itself comprises a species complex (Tejedor & Areces-Berazain 2018, 2021). Many specimens from the Brazilian Mata Atlântica had been also misidentified as *Cyathea pungens*. This was chiefly due to the specimens missing petioles with their distinctive scales, which in most exindusiate species of that area are concolorous brown to orange-brown and not white-margined as in *C. pungens*. The only two species from the area (*C. dichromatolepis* (Fée) Domin, *C. praecincta* (Kunze) Domin) that bear similarity to *C. pungens* are discussed in the taxonomic treatment under that species. Among the Neotropical exindusiate species of *Cyathea*, *C. pungens* and allies are also often confused with species of the *C. tortuosa* R.C.Moran alliance (Lehnert 2016), which are generally hairier on the axes and veins abaxially, and have concolorous dark brown scales on petioles and blades. Other taxa that we have found misidentified as *C. pungens* during our study are easily separated by either having indusia or remnants thereof, being abundantly long hairy (i.e., hairs 1 mm long or more, spreading), or having a much stronger marginal incision (e.g., *C. microdonta* (Desv.) Domin, *C. armata* (Sw.) Domin). These are not further discussed here.

Below, we provide keys and descriptions for the taxa here aligned with the *C. pungens* group. The Caribbean species assumedly allied to *C. aspera* are dealt with in more detail in a separate paper (Lehnert



**Fig. 2.** Distribution of taxa of the *Cyathea pungens* complex except *C. pungens* (Wild.) Domin s. str. **A.** *Cyathea dombeyi* (Desv.) Lellinger (blue triangles), *C. pycnocarpa* (Kunze) Domin (green dots), *C. squamata* (Klotzsch) Domin (black squares), *C. werffii* R.C.Moran (magenta dots). **B.** *Cyathea floribunda* (Hook. & Baker) Domin (black squares), *C. klotzschiana* Domin (black dots), *C. oblonga* Domin (orange diamonds), *C. pastazensis* (Hieron.) Domin (blue triangles), *C. praecincta* (Klotzsch) Domin (green dots); note that the ranges of *C. klotzschiana* in the north and *C. floribunda* in the south do not overlap but are separated by *C. pastazensis*.

*et al.* unpubl. data). All other exindusiate species of *Cyathea* should be determinable using other published treatments (Lehnert 2016; Lehnert & Tejedor 2016; Tejedor & Calatayud 2017).

**Taxonomic treatment**

Class Polypodiopsida Cronquist, Takht. & W.Zimm. (Cronquist *et al.* 1966)  
 Subclass Polypodiidae Cronquist, Takht. & W.Zimm. (Cronquist *et al.* 1966)  
 Order Cyatheales A.B.Frank in Leunis (Leunis 1877)  
 Family Cyatheaceae Kaulf. (Kaulfuss 1827)  
 Genus *Cyathea* Sm. (Smith 1793)

Group of *Cyathea pungens*

**Description**

Leaves shallowly bipinnate-pinnatifid to partially tripinnate with narrow to closed sinuses; costae adaxially ± flattened, often green alate, at least with a green edge along each side, veins excurrent into the segment margins; blades often appearing glabrous, without multicellular hairs or hairs < 1 mm long, often replaced by unicellular trichomidia, if hairs longer then tortuous and appressed, small bullate and flat squamules may occur in varying quantities and persistencies, colors ranging from whitish-gray, yellowish to dark brown, concolorous to bicolorous with white tips, never castaneous; sori exindusiate (small irregularly shaped scales subtending the receptacle may occur), paraphyses relatively short (shorter than sporangia to slightly longer than closed sporangia), their tips often hyaline, fragile and missing in mature sori, never contorted; sporangia relatively few, ca 20–30 per sorus, dark orange-brown.

**Key to the groups of *Cyathea pungens* s. str. and tree ferns most commonly mistaken for it**

1. Petiole scales bicolorous brown with white margins (sometimes grading into coconcolorous pale brown ones; mostly whitish in *C. praecincta*), scales on the trunk tend to be darker with narrower margins, sometimes appearing entirely black; petiole scurf never dark brown to castaneous, either matted grayish white, or flakey, white to medium brown; squamules on blades often pale and partially white at the tips and/or margins (except for *C. oblonga* and *C. pastazensis*) ..... ***C. pungens* complex**
- Petiole scales concolorous brown (sometimes margins slightly paler but not white), scales on the trunk of similar color, not notably darker; petiole scurf, if present, flakey, dark brown to castaneous; squamules on blades dark brown, never with white parts, but sometimes bullate squamules pale yellowish brown with darker tips ..... 2
2. Blackish spot at base of pinnules/costules present, at least in older leaves and in dried specimens, often bordering a sharp line (abscission layer); leaf axes of dried material yellowish to stramineous (= green in fresh material), rarely reddish brown, abaxially glabrous to glabrescent with hairs inconspicuous; paraphyses absent (only verrucate receptacles) to short, straight and evenly spreading, inconspicuous ..... ***C. aspera* complex** (Lehnert *et al.* unpubl. data)
- Blackish spot at base of pinnules/costules absent; leaf axes reddish brown to atropurpureous, rarely paler, abaxially often visibly hairy; paraphyses ± the same length as to longer than the sporangia, often bent near their tip and clustered at the apex of the receptacle ..... ***C. tortuosa* complex** (see Lehnert 2016)

**Key to the species of the *Cyathea pungens* complex**

1. Petiole scales reaching all along the petiole, often also on lower rachis, persistent, scales relatively narrow; all pinnules blunt-tipped (obtuse to short-acute, never attenuate) ..... 2

- Petiole scales confined to lower half of petiole, broadly lanceolate to ovate with dark center, or if reaching further up then gradually becoming paler and less sharply contrasted between the brown center and the whitish margins; larger pinnules usually with long acute to attenuate tips ..... 3
- 2. Petiole scales lanceolate, all notably bicolorous, not becoming gradually paler in distal parts; all pinnae sessile. (northern Colombia, Venezuela, Guayana, Suriname, French Guiana, northern Brazil) .....  
..... *C. oblonga* Domin
- Petiole scales broadly lanceolate, all notably bicolorous, becoming gradually paler in distal parts; lower pinnae notably stalked. (Ecuador, northern Peru) ..... *C. werffii* R.C.Moran
- 3. Petiole scales with darker brown teeth in the whitish margins; laminar indument often with larger scales persisting in the axils of leaf axes and at the base of costules; sori closer to the midveins than to the margins; sori sometimes subtended by a small scale. (Peru, Bolivia; Andean foothills) ..... 4
- Petiole scales without darker brown teeth; laminar indument without larger scales persisting in the axils of leaf axes and at the base of costules; sori closer to the margins than to the midveins; sori not subtended by a small scale ..... 5
- 4. Blades ovate-elliptic, basally cuneate; largest pinnae short stalked; largest pinnules pinnatisect almost to the costule, linear-lanceolate, tapering from beyond the middle, bases mostly cordate to truncate .....  
..... *C. dombeyi* (Desv.) Lellinger
- Blades ± triangular, basally truncate; largest pinnae ± sessile; largest pinnules subentire to pinnatifid by ½ the width, triangular-lanceolate, tapering from below the middle, bases mostly cuneate .....  
..... *C. pycnocarpa* (Kunze) Domin
- 5. Most pinnae, including medial ones, sessile, pinnules sessile; costae abaxially short villous, often also with blunt-tipped bullate squamules like found on costules and midveins; segment margins always entire ..... 6
- Most pinnae, including medial ones, notably stalked, pinnules sessile to stalked; costae abaxially glabrous, with scales and squamules if present not bullate (may be so on costules and veins); segment margins entire to dentate or serrulate at tips ..... 8
- 6. Sori in submarginal line parallel to the margins, squamules on costae and costules abaxially mostly whitish or bicolorous brown to pale brown bullate with white tips; all pinnules ± obtuse. (Colombia (Sierra Nevada de Sta Marta, Cordillera Oriental), Venezuela) ..... *C. klotzschiana* Domin
- Sori in ± medial line parallel to the midvein, small pinnules obtuse, larger ones acute to attenuate, squamules on costae and costules abaxially concolorous ..... 7
- 7. Costae and costules abaxially with yellowish white to pale brown squamules. (southern Ecuador, Peru, Bolivia) ..... *C. floribunda* (Hook. & Baker) Domin
- Costae and costules abaxially with abundant dark brown bullate squamules. (Colombia, Ecuador) .....  
..... *C. pastazensis* (Hieron.) Domin
- 8. Largest pinnules elliptic to slightly oblanceolate, with bases either truncate or inequilaterally cuneate; larger segments acute with dentate or serrulate margins; fertile veins simple (rarely some forked when pinnules more than 20 mm wide) ..... 9
- Largest pinnules linear-lanceolate, with cordate bases; larger segments rounded with (sub-)entire margins; fertile veins simple in smaller sessile pinnules, forked in larger stalked pinnules ..... 11
- 9. Sinuses between lowest segments always acute; fertile veins simple, only forked if pinnule wider than 20 mm. (Caribbean; Guayana shield, Amazonian lowland, Andean foothills) .....  
..... *C. pungens* (Willd.) Domin
- Sinuses between lowest segments blunt, widened to a trapezoid shape; fertile veins mostly forked ..... 10

10. Fertile plants trunkless or with trunks only less than 0.5 m tall; fertile leaves vary from simply pinnate-pinnatifid to bipinnate-pinnatisect with wide sinuses between sessile and adnate pinnules (or the lowest segments in fully pinnate pinnules); blade elongate-elliptic with gradually tapering apex, tips of pinnae and pinnules attenuate to caudate with coarsely serrate margins. (southern Venezuela and adjacent Brazil) ..... *C. neblinae* A.R.Sm.  
 – Fertile plants usually with trunks more than 0.5 m tall; fertile leaves mostly bipinnate-pinnatifid; blade ovate-elliptic with subconform apex, tips of pinnae and pinnules acute to attenuate with finely serrate margins. (Puerto Rico) ..... *C. ruttenbergiae* A.Tejedor & F.Areces
11. Petioles and most leaf axes dark reddish brown to atropupureous; laminar squamules scarce, all pale. (Brazil; Atlantic rainforest) ..... *C. praecincta* (Kunze) Domin  
 – Petioles and leaf axes yellowish to pale brown; laminar squamules abundant along costules, mainly whitish bullate ones, few flat ones larger, brown. (northern Andes of Colombia, Venezuela; Trinidad) ..... *C. squamata* (Klotzsch) Domin

*Cyathea dombeyi* (Desv.) Lellinger

Fig. 3

*Cyathea dombeyi* (Desv.) Lellinger (Lellinger 1987 [1988]: 94). – *Alsophila dombeyi* Desv. (Desvaux 1827: 320). – *Trichipteris dombeyi* (Desv.) Barrington (Barrington 1976: 3). – **Type:** PERU – **Huánuco** • “In Peruvia,” Cochero; 1780; *J. Dombey s.n.*; lectotype: P [P00642343]!, designated by Lehnert 2016: 36; isolectotypes: B [B 20 0000123 b]!, P [P00642344, P00642345]!

*Alsophila armigera* Kunze (Kunze 1834: 98). – **Type:** PERU – **Huánuco** • Prov. Huánuco, Ventanilla de Cassapi; Jul. 1829; *E. Poeppig s.n.*; holotype: LZ [destroyed]; lectotype: W [W0053351]!, designated by Lehnert 2016; isolectotypes: LE [LE00008089] image!, MO [MO-1858413] image!, P [P00642342]!, W [W0053352]!

*Alsophila peruviana* Klotzsch (Klotzsch 1847: 441). – **Type:** PERU • “Ad Tarma”; *Ruiz Herb.* 66; lectotype: B [B 20 0000123 a]!, designated by Lehnert 2016; isolectotypes: GH [fragment of B] n.v., NY [00148737, fragment of B]!

**Etymology**

The specific epithet honors Joseph Dombey (1742–1794), French botanist and the collector of the type specimen.

**Selected material studied**

PERU – **Amazonas, Prov. Bagua** • Distrito Imaza, Yamayakat; 5°03'20" S, 78°20'23" W; 400 m a.s.l.; 18 Nov. 1996; *R. Vasquez, P. Stern, R. Rojas & R. Aguilar 21824*; MO, UC. – **Huánuco, Prov. Leoncio Prado** • Near confluence of Río Cayumba with Huallaga; 875 m a.s.l.; 14 Oct. 1936; *Y. Mexia 8293*; UC • Tingo Maria; 700 m a.s.l.; 2 Sep. 1956; *R.M. Tryon & A.F. Tryon 5256*; BM. – **Pasco, Prov. Oxapampa** • Dist. Villa Rica, zona de amortiguamiento del Parque Nacional Yanachaga-Chemillén; 10°39'17" S, 75°10'39" W; 1290 m a.s.l.; 15 Apr. 2006; *A. Monteagudo et al. 11882*; MO. – **San Martín, Prov. San Martín** • near Tarapoto; 6°26.832' S, 76°17.741' W; 1050–1100 m a.s.l.; 3 Nov. 2010; *M. Lehnert 1998*; HAL, USM • In montibus secus flumen Mayo, prope Tarapoto; Jul.–Aug. 1856; *R. Spruce 4715* [excluded syntypes of *Alsophila floribunda*]; B [B 20 0000122], BM [BM000777032 (mix with *C. pungens*)], P [P00642346 (mix with *C. pungens*), P00642351].

BOLIVIA – **La Paz, Prov. Larecaja** • 6–10 km E of Consata along new road; 15°15' S, 68°30' W; 1350–1400 m a.s.l.; 14 Dec. 1981; *C.R. Sperling et al. 5437*; BM, GH, MO, US. – **Cochabamba, Prov. Chapare** • 159 km antigua carretera Cochabamba-Villa Tunari; 17°05' S, 65°31' W; 700 m a.s.l.; 7 Sep. 1997; *M. Kessler 8221*; GOET, UC.

## Description

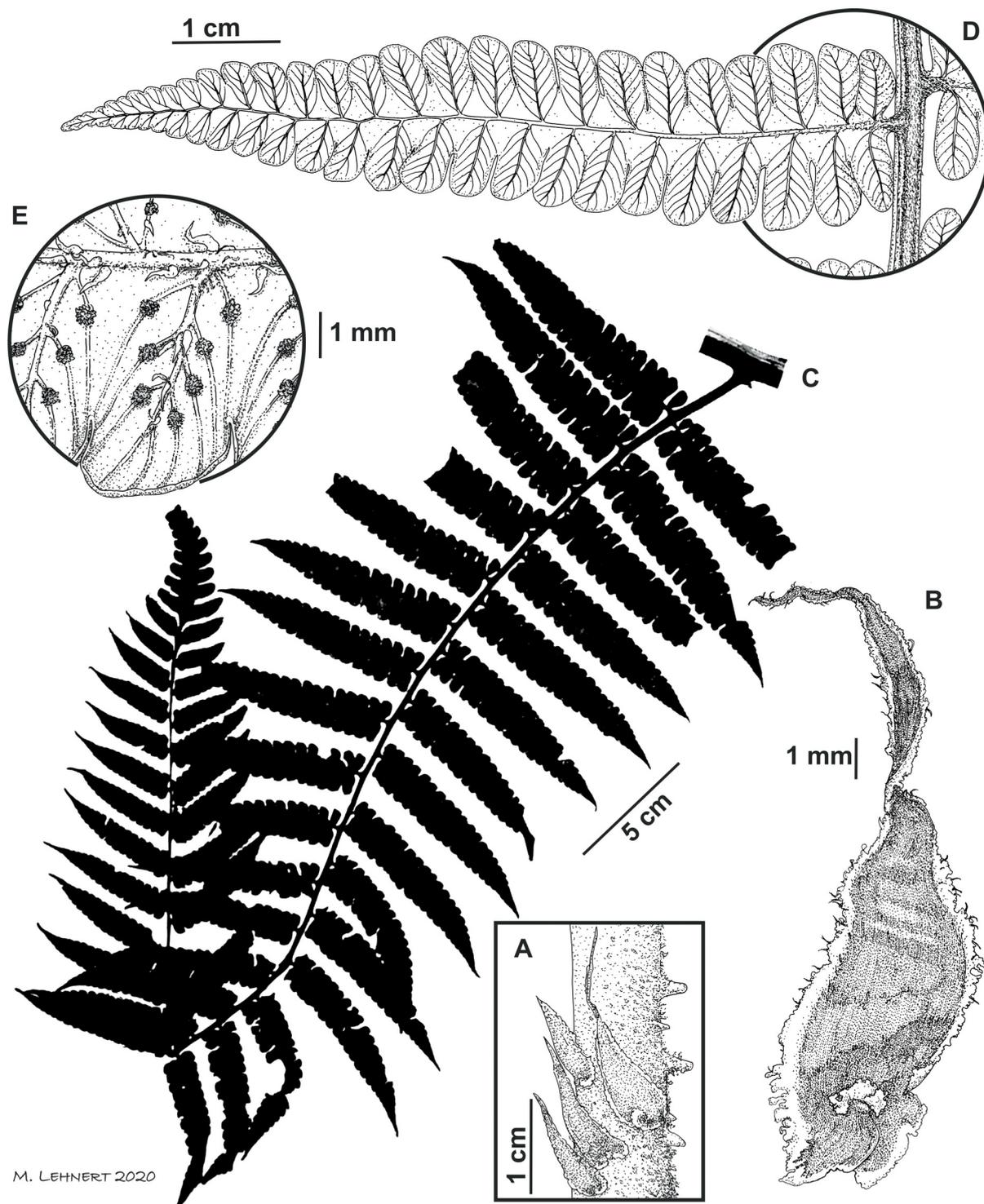
Trunks 0.5–2.4(–4.0) m tall, 5.0–12.0(–15.0) cm diam., straight, with persistent old petiole bases, spiny; apices hidden between petioles; adventitious buds absent. Leaves to 270 cm long, erect to weakly arching. Petioles 60–100 cm long, aculeate, prickles 3–5 mm long, dark brown; pneumathodes to  $10 \times 1$  mm, inconspicuously brown in dried material, whitish in fresh material; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scales lanceolate,  $25.0\text{--}32.0 \times 2.5\text{--}4.0$  mm, their tips straight to falcate, twisted, concordantly to discordantly bicolorous, shiny dark brown, with whitish margins and regular dark brown teeth; colors mostly sharply contrasted; petiole scurf a matted tomentum of small branched hairs and dissected squamules 0.2–0.4 mm long, yellowish white with brown parts, white in general aspect, soon caduceus, persistent between prickles. Blades  $100\text{--}160 \times 60\text{--}100$  cm, bipinnate-pinnatifid, elliptic to obovate, chartaceous to subcoriaceous; dark olive-green adaxially, often blackish when dried, olive-green abaxially; apices  $\pm$  gradually reduced. Rachises inermous or proximally aculeate, stramineous to yellowish brown on both sides; adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous except for scurf remnants, containing appressed, white trichomoidia and dissected squamules (0.2–0.5 mm). Largest pinnae 50–65 cm long, pinnae 10–15 pairs per leaf, sessile to stalked to 0.5 cm, alternate, ascending, distally broadly green alate, the distal segments decurrently adnate before ending in pinnatifid terminal segments; basal pinna pairs much smaller than medial pinnae, reflexed. Costae inermous, to 2.0–3.0 mm wide, adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially with scurf like on the rachises and scattered pale brown squamules, insertions into rachises abaxially weakly swollen, each with an inconspicuous planar pneumathode, dark brown, elliptic, to  $2.0 \times 1.0$  mm, area around it often black in dried specimens. Largest pinnules  $7.5\text{--}9.0(–13.5) \times (1.3\text{--})1.5\text{--}1.8(–2.0)$  cm, sessile to subsessile, articulate, alternate, 1.5–2.0 cm between the stalks, linear-oblong, incised to  $\frac{1}{2}$  or more of their width, bases truncate to weakly cordate, tapering from the middle to attenuate tips; costules with flat lanceolate bicolorous scales to  $3 \times 2$  mm and bullate squamules to 0.5–1.0 mm long with entire margins and long acute tips, varying in color from tan to deep brown, usually with white tips; costules basally with a black ring going all around their bases (abscission layer); segments oblong, to  $5.0\text{--}15.0 \times 3.0(–7.0)$  mm, patent to ascending, straight to distally weakly falcate, with entire to weakly dentate margins, tips rounded to obtuse, rarely acute and then margins weakly dentate; basal segments opposite to alternate, the lowest ones not remote from each other, sinuses triangular, acute, 1.0–2.0 mm wide, sometimes occluded; veins prominent abaxially and adaxially, midveins strongly so and adaxially ridged, lateral veins ending at segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish; glabrous adaxially except for occasional single hairs on the midveins, abaxially glabrous or with squamules and trichomoidia like on the costules (squamules on midveins darker or more strongly bicolorous than those on the costules), trichomoidia sometimes also between the veins; sterile and fertile veins mostly simple, rarely forked. Sori (0.8–)1.0–1.5 mm diam., medial and parallel to the midveins, or tapering to a subproximal position towards the segment tips (V-shape), on the back of veins, indusia absent; receptacles globose to ellipsoid, 0.3–0.4 mm diam.; paraphyses few to numerous, hyaline, tan to brown, shorter than sporangia (0.2–0.3 mm). Spores not examined.

## Distribution and ecology

Peru and Bolivia (Fig. 2A) at elevations of 700–2000 m a.s.l. in the understory of humid mountain forests.

## Remarks

*Cyathea dombeyi* and *C. pungens* differ significantly in the overall appearance of the plants and the shape of the pinnules (compare Figs 3 and 8). In fresh material with intact sori, the different position of the soral lines in these two species is even more evident, which are closer to the midveins in *C. dombeyi* and closer to the margins in *C. pungens*.



**Fig. 3.** *Cyathea dombeyi* (Desv.) Lellinger. **A.** Petiole with scurf and scales (*M. Lehnert 461*, BONN). **B.** Petiole scale, showing pseudopeltate insertion with white differentiated margin with dark marginal teeth (*M. Lehnert 461*, BONN). **C.** Pinna, silhouette (*M. Lehnert 461*, BONN). **D.** Pinnule, adaxially (*M. Lehnert 461*, BONN). **E.** Fertile segment, abaxially (*M. Lehnert 461*, BONN).

The type of *Alsophila floribunda* (Spruce 4715) was identified as a mixture of different species by Barrington (1978); the specimen P00642346 has a corresponding label, excluding the upper left pinna as belonging to *C. pungens* (as *Trichipteris procera*) and referring the rest correctly to *C. dombeyi*. However, the Kew material belongs to a third morphospecies with remotely positioned, blunt pinnules and abundant whitish bullate squamules below on veins and costules, which is clearly the condition described by Hooker & Baker (1874) for *A. floribunda*. We separate this taxon from *C. dombeyi* and transfer with it another synonym, *Alsophila bulligera* Rosenst. More material of the type collection of *A. floribunda* (Spruce 4715) can be identified as *C. pycnocarpa*, another synonym of *C. dombeyi* here reinstated. This means that the otherwise reliable Richard Spruce mixed at least four individuals, each representing a different morphotype (and likely true species), under one number.

***Cyathea floribunda* (Hook. & Baker) Domin**

Fig. 4

*Cyathea floribunda* (Hook. & Baker) Domin (Domin 1929a: 262). – *Alsophila floribunda* Hook. in Hook. & Baker (Hooker & Baker 1874: 458). – *Trichipteris floribunda* (Hook. & Baker) R.M.Tryon (Tryon 1970: 45). – **Type:** PERU • San Martín, Prov. San Martín, Mt. Campana; Aug. 1855 (isolectotypes Dec. 1855); *R. Spruce 4715*; lectotype: K [K000227562]!, designated by Lehnert 2016; isolectotypes: K [K000227563]!, W [W-Rchb. 1889-0198979]!. Excluded syntypes are discussed below.

*Alsophila bulligera* Rosenst. (Rosenstock 1928: 57). – *Cyathea bulligera* (Rosenst.) Domin (Domin 1930: 101). – *Trichipteris bulligera* (Rosenst.) R.M.Tryon (Tryon 1970: 45). – **Type:** BOLIVIA • La Paz, Prov. Larecaja, San Carlos (Mapiri Region); 850 m a.s.l.; 30 Mar. 1927; *O. Buchtien 288*; lectotype: S [S-R-199] image!, designated by Lehnert 2016; isolectotypes: GH [01100756]!, NY [00148642]!, US [01100756]!.

**Etymology**

The epithet refers to the abundant sori, which used to be likened to flowers or fruits.

**Selected material studied**

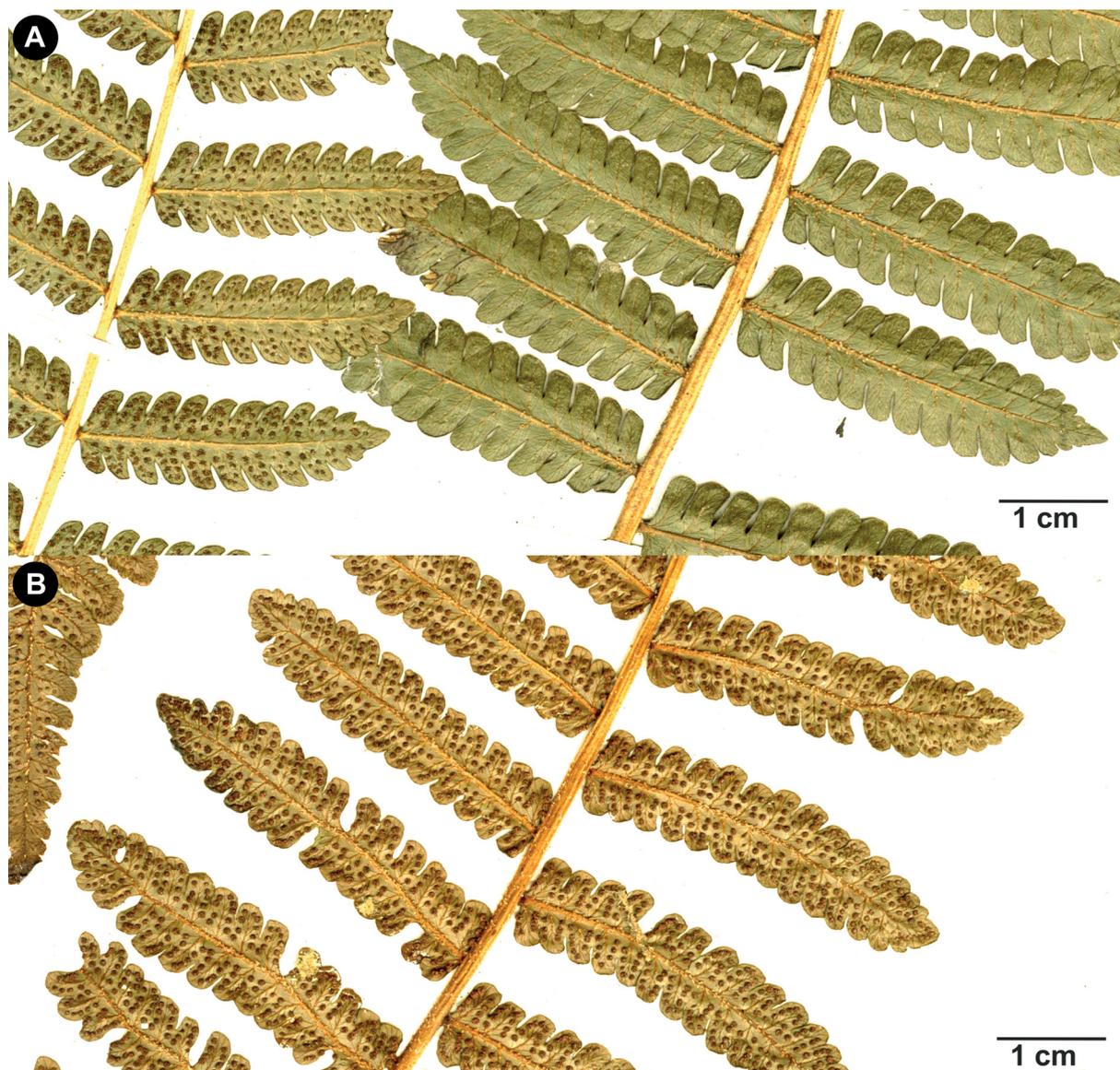
ECUADOR – **Prov. Morona-Santiago, Cantón Gualaquiza** • Off main road south of Gualaquiza, at turn-off to Bomboiza; 3.45° S, 78.55° W; 800 m a.s.l.; 8 Feb. 1993; *A. Fay & L. Fay 4219*; MO. – **Prov. Zamora-Chinchipe, Cantón El Pangui** • Campamento Shaime (Shaimi) along Río Nangaritzta, trail to the oil bird cave (“cueva de los tayos”); 4°19' S, 78°40' W; 950–1050 m a.s.l.; 6 Nov. 2004; *M. Lehnert 1524*; GOET, QCA, UC.

PERU – **Amazonas, Prov. Bagua** • Aramango, above Nueva Esperanza; 5.3558333° S, 78.3733334° W; 1271 m a.s.l.; 1 Nov. 2012; *H. van der Werff, L. Valenzuela G., G. Shareva M. & A. Reyes Barrantes 24820*; MO, UC. – **Junín, Prov. Junín** • Pichis Trail, Yapas; 10.834° S, 75.210° W; 1350–1600 m a.s.l.; 28 Jun. 1929; *E.P. Killip & A.C. Smith 25536*; NY, US. – **San Martín, Prov. Rioja** • Along road Rioja-Pedro Ruiz, in area with limestone; 5.674° S, 77.676° W; 1170 m a.s.l.; 23 Mar. 1998; *H. van der Werff, B. Gray, R. Vásquez & R. Rojas 15511*; MO, NY, UC. • Tarapoto; 1855–1856; *R. Spruce 4724*; E, K.

BOLIVIA – **Cochabamba, Prov. Carrasco** • 149 km antigua carretera Cochabamba-Villa Tunari; 17.117° S, 65.567° W; 1000 m a.s.l.; 31 Aug. 1996; *M. Kessler 7993 with J. Gonzales; T. Krömer, A. Acebey, B. Hibbits, & M. Sonnentag*; LPB, UC. – **La Paz, Prov. Franz Tamayo** • Calabatea, 44 km SW of Apolo, ca 10 km S of Correo, drainage of Río Yuyo, Transect 1; 14°55' S, 68°20' W; 1500–1550 m a.s.l.; 4 Jun. 1990; *A. Gentry & St.G. Beck 70926*; LPB, MO.

### Description

Trunks 0.5–3 m tall, 4.0–15.0 cm diam., straight to decumbent, covered with old petiole bases, due to these sparsely to strongly aculeate; apices hidden between petioles; adventitious buds absent. Leaves 125–170 cm long, held with petioles erect to ascending, blades  $\pm$  planar, weakly arching. Petioles 36–46 cm long, dark yellowish brown to stramineous, basally brown to dark brown, sparsely aculeate, prickles to 2 mm long; aerophores to  $20 \times 1$  mm, in a  $\pm$  continuous line on each side, inconspicuous in dried material, whitish in fresh material; without remote (aphlebioid) pinnae at the petiole bases; petiole scurf a tomentum



**Fig. 4.** *Cyathea floribunda* (Hook. & Baker) Domin. **A.** Type of *Alsophila bulligera* Rosenst.; showing weak dimorphism between fertile (left) and sterile (right) pinnules (*O. Buchtien* 288, lectotype S-R-199; © Swedish Museum of Natural History. CC BY-NC 4.0. <https://herbarium.nrm.se/specimens/S-R-199>). **B.** Type of *Alsophila floribunda* Hook. & Baker, representing a fully fertile leaf (*Spruce* 4715, lectotype K000227562; © The Trustees of the Royal Botanic Gardens, Kew. CC BY-NC 4.0. <https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000227562>). Note that the length of the pinnules and the distances between the costules are roughly the same in both specimens.

of small squamellae 0.2–0.4 mm long, tan with brown parts, brown in general aspect, appearing as small flakes on the epidermis, persistent but easily abraded. Petiole scales 11.0–25.0 × 2.2–3.8 mm, lanceolate to ovate-lanceolate, tapering to linear tips, straight to falcate, weakly twisted, concordantly bicolorous, shiny dark brown to castaneous, with narrow, often abraded whitish margins, scales not persistent in distal petiole parts, only scattered here and on lower rachis. Blades to 115 × 83 cm, bipinnate-pinnatifid, ovate-elliptic to obovate, chartaceous; dark olive-green adaxially, olive-green abaxially; smaller plants with long petioles and ovate-elliptic blades with 8–10 pinna pairs, basal ones ca ½ the length of longest pinnae, larger plants with short petioles and basally tapering blades with 10–16 pinna pairs, basal ones ca ½ the length of longest pinnae, patent to weakly reflexed; pinnae alternate; apices gradually reduced. Leaf axes (rachises, costae and costules) stramineous to yellowish brown on both sides, rachises sparsely aculeate in lower half, otherwise inermous; adaxially with antrorsely curved uniseriate, reddish brown hairs 0.5–1.0 mm long, abaxially with scurf remnants and small, erect curved multicellular hairs to 0.5 mm, costae and costules also with whitish to pale brown bullate squamules, 0.5–1.0 × 0.5 mm with subulate tips, larger flat squamules absent; junctions rachises/costae abaxially weakly swollen, each with an inconspicuous planar pneumathode, dark brown, elliptic, to 2.5–3.0 × 1.5 mm, area around it often black in dried specimens (foliar nectary). Largest pinnae to 41.5 cm long, sessile (appearing stalked if proximal basisopic pinnule fallen off), pinnae patent to weakly ascending, distally narrowly to broadly green alate, the pinnatifid terminal segment shortly decurrent into the costae. Largest pinnules 45–60 × 11–14 mm, linear-oblong, incised to ¾ of their width (usually 2 mm between sinuses and costules), sessile, bases truncate to weakly cuneate, tips obtuse to long acute (rarely attenuate), largest segments 9.0 × 3.0–4.0 mm, oblong, patent to ascending, distally weakly falcate, with entire to weakly dentate margins, tips rounded to obtuse; basal segments subopposite, the lowest ones not remote from each other, sinuses narrowly triangular to elliptic, acute, to 1.0 mm wide, sometimes closed; veins prominent abaxially and adaxially, midveins adaxially ridged, veins ending in cartilaginous segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish, glabrous adaxially except for occasional single hairs on the midveins, abaxially with some pale bullate squamules and short multicellular hairs on midveins, absent between the veins; sterile and fertile veins simple. Sori 0.8–1.0 mm diam., medial to supramedial (sometimes appearing submarginal when sori still complete), parallel to the midveins, indusia absent; receptacles globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few to numerous, hyaline, tan, shorter than sporangia (0.2–0.5 mm). Spores not examined.

### Distribution and ecology

Southern Ecuador, Peru and Bolivia (Fig. 2B) at elevations of ca 800–1550 m a.s.l. in the understory of humid mountain forests.

### Remarks

Excluded syntypes of *Alsophila floribunda* belong to following species:

*Cyathea dombeyi*: B [B 20 0000122]!, BM [BM000777032 p.p. (mix with *C. pungens*): “In montibus secus flumen Mayo, prope Tarapoto; Jul.–Aug. 1856”] image!, P [P00642346 p.p. (mix with *C. pungens*)!], P [P00642351]! (with scales on rachis) → rounded segments, pointed pinnules, indument flakey, flat.

*Cyathea pungens*: BM [BM000777031, BM000777032 p.p. (mix with *C. dombeyi*), BM000777346: “In montibus secus flumen Mayo, prope Tarapoto; Jul.–Aug. 1856”] image!, P [P00642346 p.p. (mix with *C. dombeyi*): “Julius 56”]!, P [P00642349: “In montibus secus flumen Mayo, prope Tarapoto; Jul.–Aug. 1856”]!, P [P00642350]!, W [W-Rchb. 0053380: “4715 var, in monte Campana pr. Tarapoto, (...) Aug. 56”]! → pointed, sessile pinnules, hardly any indument.

*Cyathea pycnocarpa*: “4715 forma pygmea, in m. Pingullu-Urku [ca 6.356° S, 76.688° W, ca 800–1500 m a.s.l.], Aug. 56”; P [P00642347, P00642348]! → with pale sub-bullate squamules in rachis axil, lower

costules with dark brown bullate and flat squamules, the larger ones with white margins; petiole scales with relatively wide white margins, dark brown teeth scattered.

The isolectotype has the original label by Spruce stating “I have not seen this growing; two imperfect fronds were brot. [sic] me - they seemed to have been about 4 feet long”. The amount and variation of the existing material suggests that Spruce has used more than these two original leaves.

Described by Hooker as having sessile blunt pinnules incised  $\frac{1}{3}$ – $\frac{1}{2}$ , medial sori and abundant minute pale scales on the veins and rachis abaxially. The excluded type material differs in one or more of these characters: *Cyathea pycnocarpa* has almost subentire pinnules; *Cyathea dombeyi* has such deeply incised pinnules but with tapering tips and the squamules below are not as notably pale as in *C. floribunda*. This mixture probably answers the question how Spruce managed to generate so many duplicates of each number. In this particular case, the different collection dates and localities are clear indicators that several individuals were combined under one catalogue number.

The type material of the synonym *Alsophila bulligera* lacks the petiole (as does that of *Alsophila floribunda*) but at least enough material is present to indicate a tapering blade base and a more or less gradually reduced blade apex. The type collections of both names appear very different at first glance, because most pinnules in *A. floribunda* are remote from each other whereas those of *A. bulligera* are close, with almost no gap between them. In pinnule length and distance as measured from costule to costule, however, both types are very similar. Fertile pinnules tend to be narrower than sterile ones in this taxon, and the different appearances stem from the fact that the material of *A. floribunda* is fully fertile, and that of *A. bulligera* predominantly sterile.

### *Cyathea klotzschiana* Domin

Figs 5–6

*Cyathea klotzschiana* Domin (Domin 1930: 128). – Replaced synonym: *Alsophila obtusa* Klotzsch (Klotzsch 1852: 41). – *Cyathea obtusata* Domin (Domin 1929a: 263), nom. illeg., not *Cyathea obtusata* Rosenst. (Rosenstock 1917: 1). – *Trichipteris obtusa* (Klotzsch) R.M. Tryon (Tryon 1970: 46). – **Type**: VENEZUELA • Without locality, cultivated by Allardt, Berlin; 1852; *H. Wagener s.n.*; holotype: B [B 20 0000322]!; putative isotype: NY [4004118, labelled “*H. Karsten*”, fragment ex B] image!.

#### Etymology

The epithet of the replacement name honors the author of the original name, Johann Friedrich Klotzsch (1805–1860), German botanist, curator and director of the Botanical Museum at Berlin Botanical Garden.

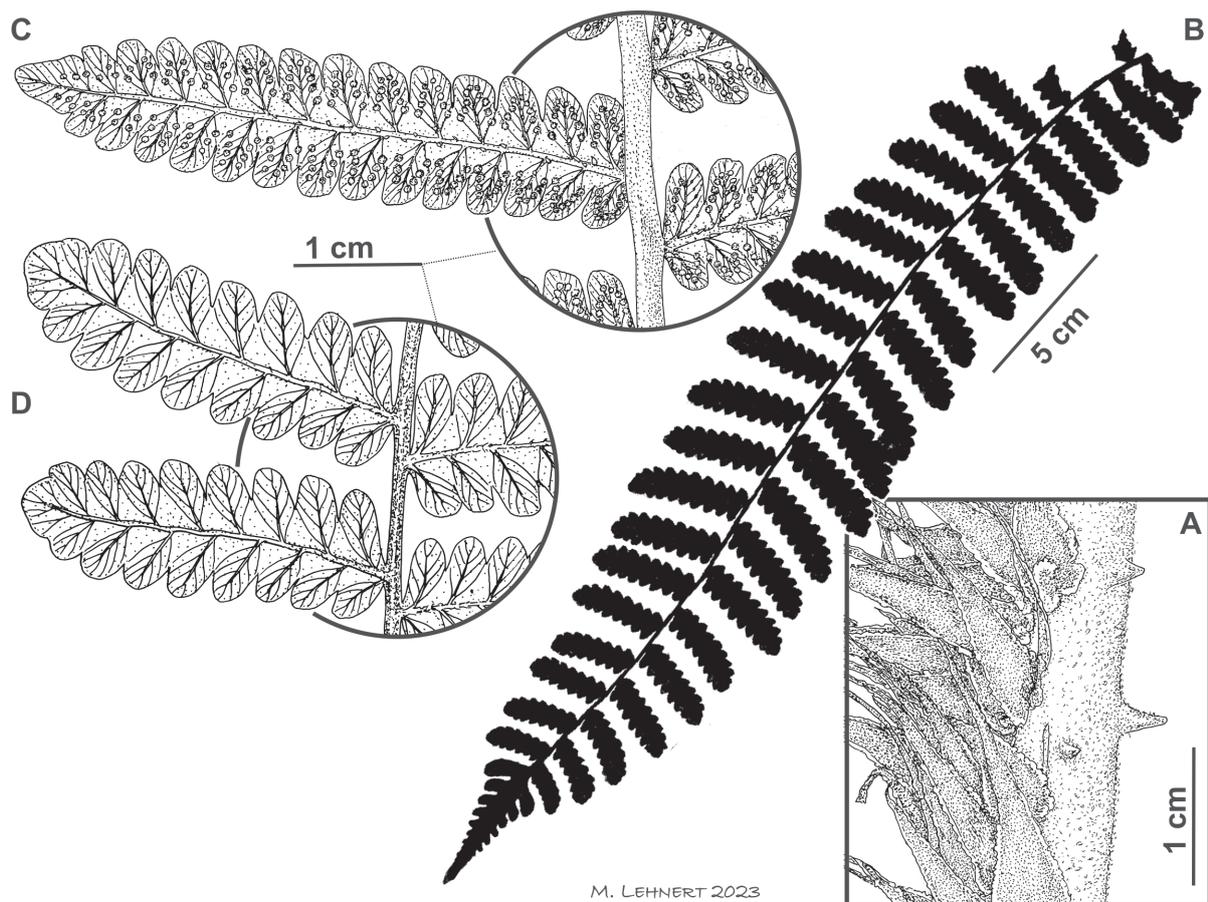
#### Selected material studied.

COLOMBIA – **Boyacá** • Puerto Boyacá, Vereda La Cunchalita, sitio El Laurel; 1200 m a.s.l.; 25 Sep. 1996; *O. Rangel 13602*; COL. – **Cundinamarca** • Medina, Vereda Periquito; ca 04°52'11" N, 74°31'28" W; 1600 m a.s.l.; 13 Jun. 2017; *A. Nassar Arboleda AN070 MEDI-070*; COAH. – **Magdalena** • Santa Marta Alto, Río Buritaca, Alto de Mira, por el camino a la Quebrada Julepia; 11.225° N, 74.136° W; 700 m a.s.l.; *S. Madriñán 185*; COL, FMB, MO. – **Meta** • Municipio de Cuabarral, sendero hacia Reserva Natural Las Palmeras; 3.832° N, 73.888° W; 1230 m a.s.l.; 21 Nov. 2021; *J.C. Castro, F. Giraldo & J. Londoño 1700*; COAH, HUA. – **Norte de Santander** • Hoya del Río Margua, quebrada del Río Negro; 11.045° N, 73.924° W; 1200–1300 m a.s.l.; *J. Cuatrecasas 12921*; COL, F, US. – **Santander** • Barrancabermeja en Valle del Magdalena, entre Sogamoso y El Río Colorado; 4.315° N, 76.363° W; *O. Haught 1422*; GH, UC, US.

VENEZUELA – **Aragua** • North slope, near La Cumbre, Parque Nacional; 900 m a.s.l.; 29 Nov. 1938; *A.H.G. Alston 5790*; MO • Rancho Grande in mountains above Maracay, trail left of road; (toward water) from research station; 10.350° N, 67.685° W; 1000 m a.s.l.; 2 Mar. 1970; *R.A. White & N.B. White 19708*; DUKE, MICH. – **Carabobo** • R. Aguada; [ca 10°10' N, 68°09' W]; 1500 m a.s.l.; 9 Jan. 1939; *A.H.G. Alston 6278*; MO • same locality as for preceding; *A.H.G. Alston 6279*; MO. – **Distrito Federal** • Along old road between 'Portachuelo' and 'Peñita' (Petaquire) and Carayaca, between Colonia Tovar-Junquito road and Hacienda El Limon, 6–8 mi. below junction of Junquito-Colonia Tovar road; 1300–1500 m a.s.l.; 12 Feb. 1966; *J.A. Steyermark & M. Rabe 94779*; US. – **Miranda** • Ocumare; ca 10°21'23" N, 67°43'10" W; 800 m a.s.l.; 2 Apr. 1937; *H.F. Pittier 13955*; F, US. – **Yaracuy** • En los canelitos cerca del caserío de San José, Aroa; [ca 10°25' N, 68°53' W]; ca 200–600 m a.s.l.; 3–4 Jul. 1953; *L. Aristeguieta & F. Pannier 1886*; US.

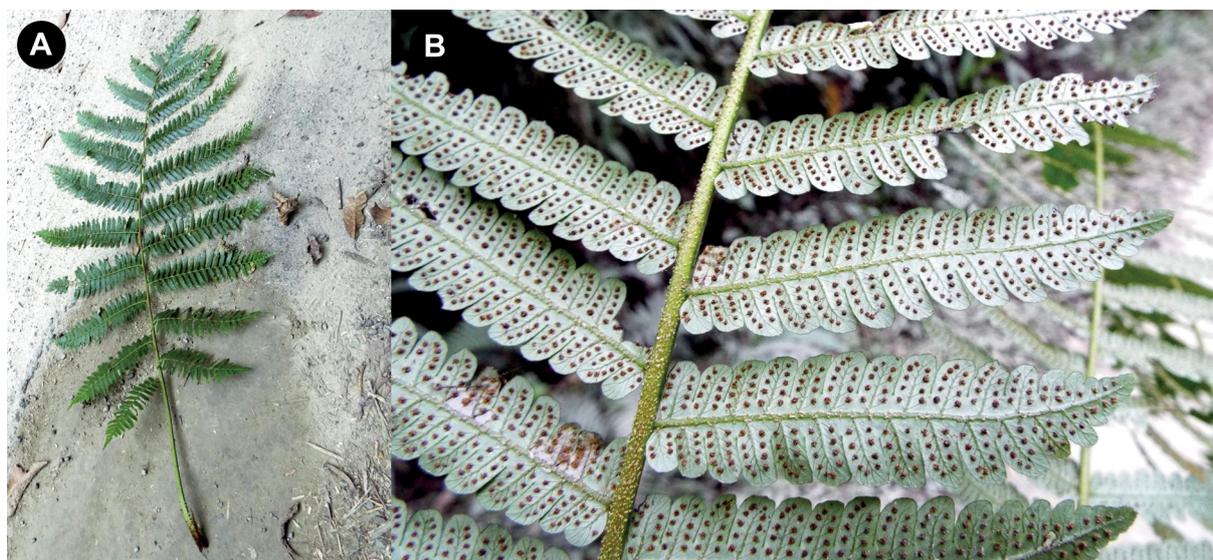
### Description

Trunks to 6 m tall, straight to decumbent, 9.0–10.0 cm diam., covered with old petiole bases, due to these sparsely to strongly aculeate; apices hidden between petioles; adventitious buds absent. Leaves 150–335 cm long, held with petioles erect to ascending, blades ± planar, weakly arching. Petioles 40–50 cm long, sparsely aculeate, prickles to 2 mm long, dark yellowish brown to stramineous, usually basally darker brown, often reddish; aerophores to 20 × 1 mm, in a ± continuous line on each side, inconspicuous



**Fig. 5.** *Cyathea klotzschiana* Domin. **A.** Petiole with scurf and scales (*F. Giraldo 2542*, BONN). **B.** Pinna, silhouette (holotype, *H. Wagener s.n.*, B 20 0000322). **C.** Pinnule, fertile, abaxially (*W. Meier; O. Escorcha & G. Forbes 11303*, UC). **D.** Small pinnules, sterile, adaxially (holotype, *H. Wagener s.n.*, B 20 0000322).

in dried material, whitish in fresh material; without remote (aphlebioid) pinnae at the petiole bases; petiole scales  $20.0\text{--}25.0 \times 2.5\text{--}5.0$  mm, lanceolate to ovate-lanceolate, tapering to linear tips, straight to falcate, weakly twisted, concordantly bicolorous, shiny dark brown to castaneous, with narrow, often abraded whitish margins, scales persistent in distal petiole parts, often reaching lower rachis, here only smaller than lower ones, remaining concordantly bicolorous (never paler or almost completely white); petiole scurf a tomentum of small branched clavate hairs  $0.2\text{--}0.4$  mm long, tan with brown parts, dark brown in general aspect, appearing as small dark dots or irregular stars on paler parts of the epidermis, persistent but easily abraded. Blades  $110\text{--}290 \times 90(\text{--}170)$  cm, bipinnate-pinnatifid, ovate-elliptic to obovate, chartaceous; dark olive-green adaxially, often blackish when dried, olive green abaxially; smaller plants with long petioles and ovate-elliptic blades with 8–10 pinna pairs, basal ones ca  $\frac{1}{2}$  the length of longest pinnae, larger plants with short petioles and basally tapering blades with 11–16(–20) pinna pairs, basal ones ca  $\frac{1}{3}$  the length of longest pinnae, patent to weakly reflexed; pinnae alternate; apices gradually reduced. Leaf axes (rachises, costae and costules) stramineous to dull orange-brown on both sides, sparsely aculate in lower half, otherwise inermous; adaxially with antrorsely curved uniseriate, reddish brown hairs  $0.5\text{--}1.0$  mm long, abaxially with scurf remnants and small, erect curved multicellular hairs to  $0.5$  mm, costae and costules also with brown to pale brown bullate squamules,  $0.5\text{--}1.0 \times 0.5$  mm, often with white flattened or elongate tips, occasionally larger flat squamules to  $2 \times 1$  mm present; junctions rachises/costae abaxially weakly swollen, each with an inconspicuous planar pneumothode, dark brown, elliptic, to  $2.5\text{--}3.0 \times 1.5$  mm, area around it often black in dried specimens (foliar nectary). Largest pinnae to  $45(\text{--}85?)$  cm long, sessile (appearing stalked if proximal basisopic pinnule has fallen off), pinnae patent to weakly ascending, distally narrowly to broadly green alate, the pinnatifid terminal segment shortly decurrent into the costae. Largest pinnules  $4.5\text{--}8.5 \times 1.1\text{--}1.7$  cm, linear-oblong, incised to  $\frac{1}{2}$  or more of their width (usually 2 mm between sinuses and costules), sessile, bases truncate to weakly cuneate, with obtuse to short acute tips; costules basally with a black spot or ring going all around their bases (abscission layer); largest segments  $8.0\text{--}9.0 \times 3.0\text{--}4.0$  mm, oblong, patent to ascending, distally weakly falcate, with entire to weakly dentate margins, tips rounded to obtuse; basal segments alternate, the lowest ones not remote from each other, sinuses narrowly triangular to elliptic, acute, to 1.0 mm wide, sometimes closed; veins



**Fig. 6.** *Cyathea klotzschiana* Domin in the field (Sierra Nevada de Santa Marta, Dept. Magdalena, Colombia); large plant. **A.** Whole leaf with ten pinna pairs and a conform apex; petiole scales restricted to the petiole base. **B.** Fertile pinnules abaxially. Note characteristic white squamules on costae and costules; the segments are more elongate than in the plants shown in Fig. 5, thus the sorol lines appear less in a zig-zag-pattern while technically still not being parallel to the midveins. (photos © M. Lehnert)

prominent abaxially and adaxially, midveins adaxially ridged, veins ending in cartilaginous segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish, glabrous adaxially except for occasional single hairs on the midveins, abaxially with some bicolorous bullate squamules and short multicellular hairs on midveins, absent between the veins; sterile and fertile veins simple. Sori 0.8–1.0 mm diam., medial to supramedial (sometimes appearing submarginal when sori still complete), parallel to the margins, on the back of veins, indusia absent; receptacles globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few to numerous, hyaline, brown to tan, of the same length as or shorter than sporangia (0.2–0.5 mm). Spores not examined.

### Distribution and ecology

Colombia (Sierra Nevada de Sta. Marta, Cordillera Oriental) and Venezuela at elevations of 600–1700 m a.s.l., predominantly in lower montane forest with Caribbean influence.

### Remarks

The type of *Alsophila obtusa* at Berlin has conflicting label information concerning the provenance (“Columbien” vs “Venezuela”) and the collection date (15 Jan. 1852 vs 23 Jul. 1855). The latter conflict may be interpreted as two separate samplings of the same cultivated plant, which were brought to Germany by H. Karsten. Other plants of this species were cultivated at Dresden Botanical Garden (1862, *Anonymous s.n.*; MO-3304121). The type consists of several pinnae, rachis parts and one petiole, but larger petiole scales or a blade apex are not preserved. The only fertile pinna is mounted face-down but the zig-zag-pattern of the sori can be recognized as impressions thorough the laminar tissue. The type is also comparatively small and pale. Some representative collections that fill the gaps are *Ortega Mendoza & Smith 2492* (NY), which matches the type in size and proportion of pinnae and pinnules, but has a darker, dull orange-brown color in petiole and rachis, and *Meier et al. 11303* (UC), which seems to represent a stouter plant with pinnule tips not rounded but tapering to a tongue-shaped lobe.

*Cyathea klotzschiana* is distinguished in the field from the similar sympatric *C. oblonga* (both have dark castaneous petiole scales with narrow white margins and blunt pinnules, similar pinnae sizes and numbers) by the different soral lines (submarginal lines, or zig-zag-pattern in *C. klotzschiana* vs parallel to midveins in *C. oblonga*) and color of the laminar indument (pale vs dark brown). *Cyathea klotzschiana* further has small erect, villose hairs on the costae and costules abaxially; *C. oblonga* has only brown appressed hairs on the veins and costules, mixed with short ribbon-like squamules.

*Cyathea klotzschiana* shows distinct variations in its key distinguishing characters related to age, environment, and region. The species’ range spans across the Cordillera de la Costa and the Andes of Venezuela to Colombian Cordillera Oriental and Sierra Nevada de Santa Marta; most of these mountain ranges, though mostly contingent, fall into several subsets of ranges that act as separate biogeographic units, which is supported by the occurrence of local endemic species (e.g., *C. barringtonii* and *C. venezuelensis*; Lehnert & Weigand 2017). This is reflected in regional morphotypes of *Cyathea klotzschiana*. For example, whereas plants from Serra do Aroa (Yaracuy state, Venezuela) have elongate blunt tipped pinnules with pale laminar squamules, which are here considered best fitting the type specimen, plants to the east in the Cordillera de la Costa have more bicolorous laminar squamules but do not differ in pinnule shape. Specimens from Santa Marta, Colombia, to the west, however, appear superficially different because of their exceptionally long pointed pinnules, but are just as pale-scaled as the plants from Serra do Aroa. Also, the short hairs abaxially on costae and costules can be lost in older leaves, which can make it hard to distinguish such plants of *C. klotzschiana* from *C. pungens* with sessile pinnules.

Among the reinstated taxa, *Cyathea klotzschiana* and *C. floribunda* are the most similar to each other regarding pinnule shape and laminar indument, with both often having a relatively dense strip of whitish bullate squamules on the costules abaxially. However, the faint leaf dimorphism of *C. floribunda* is not

observed in *C. klotzschiana*. Both taxa are geographically separated over a large part of the northern Andes by the range of *C. pastazensis*.

*Cyathea neblinae* A.R.Sm.

*Cyathea neblinae* A.R.Sm. (Smith 1990: 250). – **Type:** VENEZUELA • Prov. Amazonas, Dept. Río Negro, 0–1 km E of Cerro de la Neblina Base Camp on Río Mawarinum; 0°50' N, 66°10' W; 140 m a.s.l.; 2 Sep. 1984; *R.L. Liesner & V.A. Funk 15781*; holotype: UC [UC1506573]!; isotype: MO [MO-1873835]!

**Etymology**

The specific epithet refers to the type locality.

**Selected material studied**

VENEZUELA – **Amazonas, Dept. Río Negro** • 0 to 1 km east of Cerro de La Neblina Base Camp on Río Mawarinuma; 0°50' N, 66°10' W; 140 m a.s.l.; 9 Feb. 1984; *R.L. Liesner 15798*; MO, L, NY, UC, US. – **Bolívar, Dept. Bolívar** • Riberas del Río Canaracuni (aguas negras) y selvas adyacentes, Expedición Proyecto I.R.N.R.G. a la cuenca alta del Río Caura (Hoja NB-20-14), convenio UNELLEZ-C.V.S. (TECHIN, C.A.); 4.450° N, 64.117° W; 13 Apr. 1988; *B. Stergios 11892*; MO, UC.

BRAZIL – **Amazonas, Mun. Santa Isabel do Rio Negro** • Neblina massif; 1300 m a.s.l.; 24 Dec. 2003–5 Jan. 2004; *F.A. Carvalho et al. 308*; INPA • same locality as for preceding; *F.A. Carvalho et al. 320*; INPA.

**Description**

Trunkless or trunks 0.3 m tall, decumbent, (1.0–)2.5–4.0 cm diam., with persistent old petiole bases, spiny; apices hidden between petioles; adventitious buds absent. Leaves to 90(–100) cm long, ca 3–5 in a crown; presumably arching. Petiole to 25 cm long with prickles 2–5 mm long, dark yellowish brown to dull orange-brown, sometimes basally darker brown; aerophores to 10 × 1 mm, inconspicuously brown in dried material, without remote (aphlebioid) pinnae at the petiole bases; petiole scales lanceolate, 8.0–9.0 × 2.5 mm, their tips straight to falcate, concordantly to discordantly bicolorous, shiny dark brown with whitish margins at petiole base, scales in distal half of the petiole gradually becoming paler with wider white margins, scales only sharply contrasted in scales near petiole base and on crossiers; petiole scurf a matted tomentum of small branched hairs and dissected squamules 0.2–0.4 mm long, yellowish white with brown parts, grayish white in general aspect, soon caduceus, persistent between prickles. Blades 58 × 46–50 cm, pinnate-pinnatifid to bipinnate-pinnatifid, elliptic to ovate-lanceolate, chartaceous; blackish adaxially when dried (probably dark olive-green when fresh), olive-green abaxially; apices gradually reduced. Rachises dark stramineous to orange-brown on both sides, in basal half often with some strong prickles; adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous except for scurf remnants, containing appressed, white trichomoidia and dissected squamules (0.2–0.5 mm). Largest pinnae to 23 cm long, pinnae (6–)8–12 pairs per leaf (in fully bipinnate-pinnatifid blades, may be higher in less divided ones), subsessile to stalked to 1 cm, ascending, narrowly green alate, the distal segments adnate, decurrent into the costae, forming a pinnatisect section with long acute to attenuate tips. Costae inermous, to 1.5–2.0 mm wide, adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous or glabrescent with scurf like on the rachises, insertions into rachises abaxially weakly swollen, each with an inconspicuous planar pneumathodes, dark brown, elliptic, to 2.0 × 1.0 mm, area around it often black in dried specimens. Pinnules 1.3–6.2 × (0.4–)0.8–1.3 cm, smaller ones sessile, larger ones stalked 1.0 mm, articulate, alternate, ca 1.0–1.5 cm between costules, linear-oblong to weakly elliptic, bases notably cuneate, tapering from beyond the middle, tips blunt in entire pinnules, long actue

to attenuate to long acute to attenuate in pinnatifid pinnules, also caudate in pinnatisect pinnules; costules with ephemeral tan to brown trichomidia and whitish squamules 0.5–1.0 mm long with entire margins and acute tips; costules basally with a black ring going all around their bases (abscission layer); segments oblong, to  $7.0 \times 3.0$  mm, strongly ascending, distally weakly falcate, with entire to subentire margins, tips obtuse to acute and then margins weakly dentate; basal segments alternate, sinuses in pinnatifid pinnules triangular, acute, 1.0–2.0 mm wide, in pinnatisect to partially pinnate pinnules the lowest segments remote from each other, separated by angular sinus; veins prominent abaxially and adaxially, midveins strongly so and adaxially ridged, lateral veins ending at segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish; adaxially glabrous except for occasional single hairs on the midveins, abaxially glabrous or with squamules and trichomidia like on the costules; sterile and fertile veins mostly forked in bipinnate or less dissected blades, simple and forked in more strongly dissected blades and larger pinnules ( $> 1$  cm wide). Sori 0.6–0.8 mm diam., supramedial, parallel to the margins, on the back of veins, indusia absent; receptacles globose to ellipsoid, 0.2 mm diam.; paraphyses few hyaline, white, shorter than sporangia (0.2–0.3 mm). Spores not examined.

See Smith (1990) for an illustration.

### Distribution and ecology

Venezuela and Brazil, mainly around Cerro de la Neblina except for one outlying record from the southern base of Cerro Sarisariñama, mountain forests and scrub vegetation; at elevations of 100–1400 m a.s.l.

### Remarks

This species was described as being only pinnate-pinnatifid to partially bipinnate; later records from Brazil (F.A. Carvalho *et al.* 320, INPA) have bipinnate-pinnatifid blades with stalked pinnules (Carvalho *et al.* 2012), ultimately giving *Cyathea neblinae* the same variability in laminar dissection as *C. pungens* s. str.. Both species are also practically identical in petiole scale shape and color, laminar texture and color of the leaf axes, thus *C. neblinae* might be interpreted as a special dwarf form of *C. pungens*. However, there are some constant characters that make *C. neblinae* visibly different: the blade apex seems to be always gradually reduced (vs mostly subconform in *C. pungens*); all plants described as *C. neblinae* (Smith 1990) have pinnules with more strongly cuneate bases than *C. pungens*, irrespective of their size and degree of further dissection. In parts of the blade that mark the transition between simply pinnate and fully bipinnate, *C. neblinae* has remote adnate segments that are separated wide, asymmetric angular sinuses, formed by the decurrently alate bases at the basiscopic side of the segments. In direct comparison, such transitory sinuses are closer and more symmetric in *C. pungens*.

### *Cyathea oblonga* (Klotzsch) Domin

Figs 7–8

*Cyathea oblonga* (Klotzsch) Domin (Domin 1929a: 263). – *Alsophila oblonga* Klotzsch (Klotzsch 1844: 540). – *Trichipteris oblonga* (Klotzsch) R.M. Tryon (Tryon 1970: 46). – **Type:** GUYANA • *R. Schomburgk 1125*; lectotype: K [K000589887]!, designated by Barrington 1978; isolectotypes: B [B 20 0000323 a, B 20 0000325]!, BR [BR0000006987886] image!, LE [LE00008119] image!, NY [00148722, fragment of K] image!, P [P00631669]!, US [00066269] image!.

*Alsophila platyphylla* C. Presl (Presl 1851: 29). – **Type:** FRENCH GUIANA • “In Gujana gallica,” vicinity of Saül, ca 10 km NW from Eaux Claires; ca 03°37' N, 53°12' W; 400 m a.s.l.; *G.S. Perrottet s.n.*; lectotype: PR!, designated by Lehnert 2016; isolectotype: NY [0014874, fragment of PR] image!.

*Alosphila gleasonii* Maxon (Maxon 1925: 55). – **Type:** GUYANA [BRITISH GUIANA] • Near Rockstone, in dense up-land forest; ca 05°58'26" N, 58°31'09" W; ca 100–120 m a.s.l.; 15 Jul.–1 Aug. 1921; *H.A. Gleason 830*; holotype: US [00066252] image!; isotypes?: NY [00148678] image!, US [00715386] image!.

### Etymology

The specific epithet refers to the shape of the pinnules.

### Selected material studied

COLOMBIA – **Antioquia** • Vereda Providencia, Anorí, 500 m arriba de la carretera por el camino de la retroescabadora desde la casa de Doña María; 7.3483333° N, 75.0208333° W; 300 m a.s.l.; 15 Jun. 2011; *J. Colorado 732*; HUA.

VENEZUELA – **Amazonas, Dept. Río Negro** • Cerro de la Neblina, Río Yatua, 6–8 km S of Camp 3; 1.03° N, 65.93° W; 1200–1600 m a.s.l.; 24 Dec. 1953; *B. Maguire, J.J. Wurdack & G.S. Bunting 36870*; US. – **Bolívar, Mun. Bolivariano Angostura [= Raul Leoní]** • 50 km al SW de Guaiquinima y 72 km al W de Karún; 5°18' N; 63°59' W; 230 m a.s.l.; *A. Fernández & G. Aymard 4904*; MO, UC. – **Distrito Federal, Mun. Libertador** • Cordillera de la Costa, al noreste de Guatire, excursion Fila Juan Torres-Fila Las Perdices por el Río Guayabal hacia el pueblo Guayabal; 10.516667° N, 66.333333° W; 950–1000 m a.s.l.; 19 Feb. 1992; *W. Meier 3415*; UC.

GUYANA – **Cuyuni-Mazaruni** • Mt. Maringma, slope below sub-summit plateau; 5.20461° N, 60.5766° W; 1370 m a.s.l.; 22 Jun. 2004; *H.D. Clarke, C. Perry, E. Tripp, S.R. Stern & D. Gittens 11931*; US. – **Potaro-Siparuni** • Iwokrama Rainforest Reserve, Karupukari-Annai Road, summit of unnamed peak at end of 5 km transect; 4.471° N, 58.788° W; 700 m a.s.l.; 19 Mar. 1997; *H.D. Clarke, S.A. Mori & S. Heald 4120*; US. – **Upper Takutu-Upper Essequibo** • saddle between tops of Two-Head Mt, Kanuku Mts; 4.206° N, 59.117° W; 580 m a.s.l.; 2 Feb. 1994; *M.J. Jansen-Jacobs, B.J.H. ter Welle, A. Chanderbali, U. Raghoenandan & V. James 3535*; NY, US.

SURINAME – **Marowijne** • Marowijne [river], Nassau Mts, Plateau C; 4.83° N, 54.61° W; 500–550 m a.s.l.; 5 Feb. 2003; *M.J. Jansen-Jacobs et al. 6556*; U, UC, US. – **Sipaliwini** • Upper reaches of Grace Kreek, Tafelberg Mountain, headwaters of the Grace Kreek drainage; 3.893° N, 56.160° W; 700–790 m a.s.l.; 5 Jul. 1998; *T. Hawkins 1892*; L, MO, UC, US.

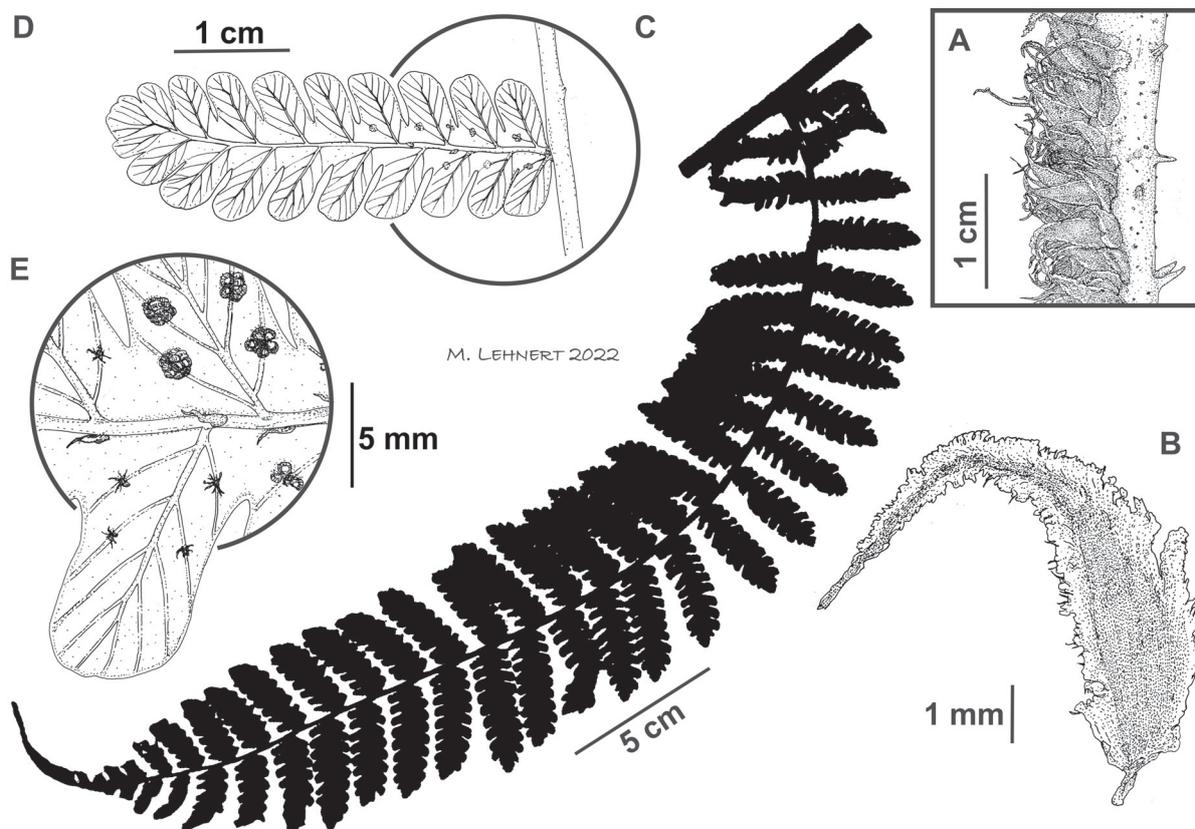
FRENCH GUIANA – **Cayenne** • D.Z. de Crique Jupiter, bassin du Sinnamary; 4.06° N, 53.16° W; 100 m a.s.l.; 25 Apr. 1991; *J.J. de Granville 11511*; CAY, L, NY, UC, US. – **Saint-Laurent-du-Maroni** • Mont Atachi Bacca, Region de l'Inini; 3.55° N, 53.91666° W; 500 m a.s.l.; 14 Jan. 1989; *G. Cremers 10227*; MO, NY.

BRAZIL – **Amapá** • Rivière Haut [= upper Río] Jari; 2.46° N, 54.76° W; 380 m a.s.l.; 19 Aug. 1993; *J.J. de Granville, P. Acevedo-Rodríguez, A. Boyer & L.A. Hollenberg 12381*; US. – **Pará** • Mun. Oriximiná Estação Ecológica Grão Pará, Córrego próximo do acampamento; 1°16'47.4" N, 58°41'28.5" W; 475 m a.s.l.; 30 Aug. 2008; *S. Maciel 983*; MCT, STU. – **Roraima** • Lower slopes of Serra da Lua, by Igarape Camarao; 2°25–29' N, 60°11–14' W; 23 Jan. 1969; *G.T. Prance, J.R. Steward, F. Ramos & L.G. Farias 9400*; F, NY.

### Description

Trunks 0.8–2.0(–8.0?) m tall, straight to decumbent, 4.0–5.0 cm diam., with persistent old petiole bases, sparsely aculeate; apices hidden between petioles; adventitious buds absent. Leaves to 165 cm long, held with petioles erect to ascending, blades ± planar, weakly arching. Petioles 27–44(–53) cm long, sparsely

to strongly aculeate, prickles 2–3 mm long, dark yellowish brown to stramineous (Andes), or dark reddish brown (Guayana shield); aerophores to  $10 \times 1$  mm, inconspicuously brown in dried material, whitish in fresh material; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scales  $15.0\text{--}20.0(-23.0) \times 2.5\text{--}4.0(-5.0)$  mm, lanceolate, tapering to linear tips, straight to falcate, weakly twisted, concordantly bicolorous, shiny dark brown to castaneous, with narrow, often abraded whitish margins, scales persistent in distal petiole parts, often reaching lower rachis, here only smaller than lower ones, remaining concordantly bicolorous (never paler or almost completely white); petiole scurf a tomentum of small branched clavate hairs  $0.2\text{--}0.4$  mm long, tan with brown parts, dark brown in general aspect, soon caduceous, persistent between spines. Blades  $80\text{--}90 \times 70\text{--}80$  cm, bipinnate-pinnatifid, elliptic to obovate, chartaceous; dark green adaxially, often blackish when dried, olive green abaxially; (8–)10–12(–24?) pinna pairs, alternate, basal ones  $\frac{1}{2}\text{--}\frac{1}{3}$  the length of longest pinnae, weakly to strongly reflexed; apices abruptly reduced to non-conform apical sections, sometimes very broad and nearly gradually reduced. Leaf axes (rachises, costae and costules) stramineous to yellowish brown on both sides, often with a reddish tinge, inermous; adaxially with antrorsely curved uniseriate hairs  $0.5\text{--}1.0$  mm long (sparse to absent on costules), abaxially glabrous except for scurf remnants, containing appressed branched brown hairs (like on petioles), dark brown bullate squamules,  $0.5\text{--}1.0 \times 0.5$  mm with subulate, rarely flattened or elongate tips (sparse to absent on rachis); junctions rachises/costae abaxially weakly swollen, each with an inconspicuous planar pneumathode, dark brown, elliptic, to  $2.0 \times 1.0$  mm, area around it often black in dried specimens. Largest pinnae 37–45 cm long, sessile or stalked to 1.5 cm (proximal basisopic pinnule reduced or fallen off), pinnae patent to weakly ascending, distally narrowly to broadly green alate, the pinnatifid terminal segment shortly decurrent into the costae. Largest pinnules  $5.0\text{--}8.0 \times 1.3\text{--}1.5$  cm,



**Fig. 7.** *Cyathea oblonga* (Klotzsch) Domin. **A.** Petiole with scurf and scales. **B.** Petiole scale, showing white differentiated margin with few dark marginal teeth. **C.** Pinna, silhouette. **D.** Pinnule, abaxially. **E.** Fertile segment, abaxially. (all from *Maciel 985*, BONN).

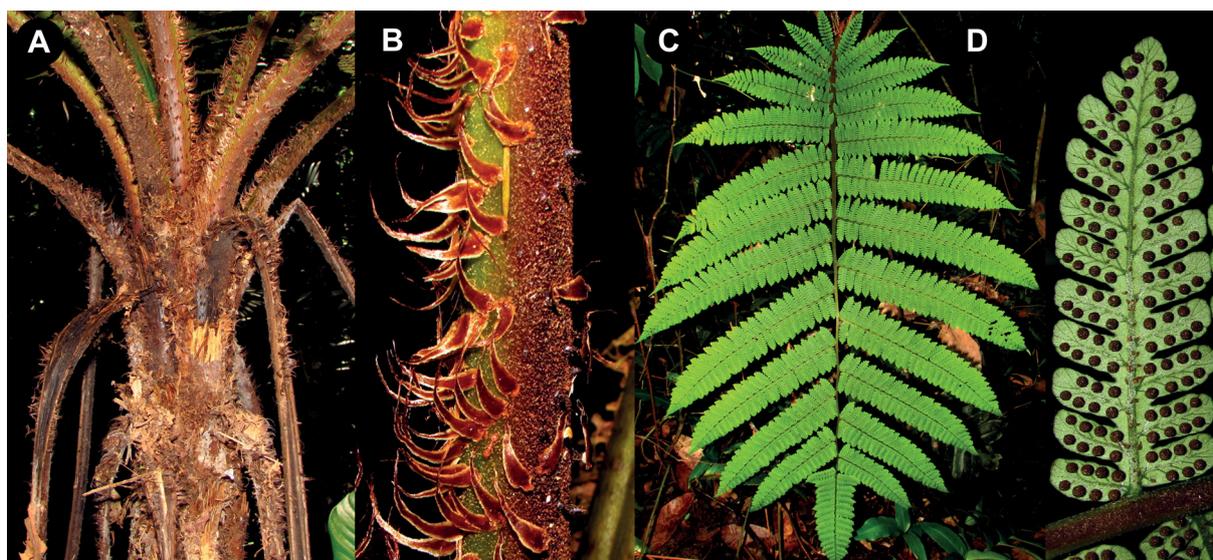
linear-oblong, incised to  $\frac{1}{2}$  or more of their width (usually 2 mm between sinuses and costules), sessile, bases truncate to weakly cuneate, tapering from beyond the middle to obtuse to acute (rarely short-attenuate) tips; costules basally with a black ring going all around their bases (abscission layer), basally without aerophore; largest segments 8.0–10.0 × 2.5–4.5 mm, oblong, patent to ascending, distally weakly falcate, with entire to weakly dentate margins, tips rounded to obtuse; basal segments alternate, the lowest ones not remote from each other, sinuses narrowly triangular, acute, to 1.0–2.0 mm wide, sometimes closed; veins prominent abaxially and adaxially, midveins adaxially ridged, veins ending in cartilaginous segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish; glabrous adaxially except for occasional single hairs on the midveins, abaxially glabrous or with squamules and trichomidia like on the costules, trichomidia sometimes also between the veins; sterile and fertile veins mostly simple, rarely forked. Sori 0.8–1.0 mm diam., appearing ± medial when intact, closer to the margins when reduced to receptacles, parallel to the margins/midveins, on the back of veins, indusia absent; receptacles globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few to numerous, hyaline, white to tan, shorter than sporangia (0.2–0.3 mm). Spores not examined.

### Distribution and ecology

Colombia, Venezuela, Guyana, Suriname, French Guiana, and northern Brazil (Fig. 2B) at elevations of (100–)140–1400(–1600) m a.s.l., in lowland rain forests on terra firme and premontane forest with Caribbean influence.

### Remarks

The maximum reported height for the plant is 8 m (*Maguire et al. 29929*), which is exceptionally high for the species and likely erroneous. The highest number of pinna pairs is twice the average for the species and might have been intended as “24 pinnae in pairs”. *Cyathea oblonga* was resurrected from the synonymy of a loosely conceived *C. pungens* by Cremers & Boudrie (2007) based on their field observations in French Guiana. Here, both species overlap in their distribution, and show consistent differences in the anatomy and distribution of the petiole scales (relatively narrow, shiny dark brown with white margins, all



**Fig. 8.** *Cyathea oblonga* (Klotzsch) Domin in the field (Kanuku Mts, Prov. Upper Takutu-Upper Essequibo, Guyana). **A.** Trunk apex. **B.** Petiole with scales, detail. **C.** Whole leaf. **D.** Fertile pinnule, abaxially. Note the small brown squamules on the costules, medial position of sori and the typical blunt segments and pinnule apex. (photos © A. Tejedor)

along the petioles without getting paler in *C. oblonga* vs petiole scales usually restricted to petiole bases or if reaching further up then becoming paler to almost white in *C. pungens*) and the laminar indument (bullate squamules and scurf remnants on costae and costules brown to dark brown, well represented vs scurf and bullate squamules pale brown to white, scant).

*Cyathea oblonga* from higher elevations at the tablemountain bases differs from those in the lowlands of eastern Guayanan in having the axes abaxially not atropurpureous but stramineous to orange brown, and being stouter plants with thicker axes and larger pinnules. Plants here reported from northern Venezuela and the Andes of Colombia look more like the stouter tablemountain variety, and although having the diagnostic characters of that species ( $\pm$  medial sori, narrow petiole scales extending to the rachis), they may turn out to be aberrations of other taxa (mostly *C. klotzschiana*, presumably) after more scrupulous investigation in the field.

Precociously fertile plants with less divided blades than regular fertile plants are the basis for the synonym *Alsophila gleasonii*. Here, also the petiole scales tend to be smaller, but full in proportion to the smaller size of the plants. These individuals look like non-sympatric dwarf species of *Cyathea*, such as *C. pseudonanna* Lellinger from Panama, which is best distinguished by the denser, stiffer hairs abaxially on the rachises and the bluish sheen of the adaxial laminar side in fresh material.

### *Cyathea pastazensis* (Hieron.) Domin

Fig. 9

*Cyathea pastazensis* (Hieron.) Domin (Domin 1929: 263). – *Alsophila pastazensis* Hieron. (Hieronymus 1906: 232). – *Trichipteris pastazensis* (Hieron.) R.M.Tryon (Tryon 1970: 46). – **Type:** ECUADOR • Prov. Tungurahua, between Baños and Jivaría de Pintuc, Río Pastaza Valley; 1870–1874; *A. Stübel 995a*; lectotype: B [B 20 0000321]!, designated by Lehnert 2016; isolectotype: NY [00148730, fragment of B]!. One excluded element (*Stübel 988*, B [B 20 0000320]!) represents *Cyathea tortuosa* R.C.Moran; other syntypes (*Stübel 975*, B [B 20 0000319 a]!; *Stübel 876a*, B [B 20 0000319 b]!) are not assignable to species.

### Etymology

The specific epithet refers to the type locality, the Río Pastaza in Ecuador; today also a province of that country.

### Selected material studied

COLOMBIA – **Antioquia** • Mun. San Carlos, between San Rafael and San Carlos; 5.1544444° N, 75.0413889° W; 1600 m a.s.l.; 21 Feb. 2015; *M. Lehnert 3162*; BONN, HUA, Z • Mun. Anori, entre Barbosa y Medellín; 7.252° N; 75.052° W; *Bro. Henri-Stanislas 1708*; MO, US. – **Caquetá** • Municipio de Belén de los Andaquíes, camino Anfaquí, reserva Andaquí, La Profunda; 1°39'39.5" N, 75°54'21.9" W; 800–1000 m a.s.l.; 13 Mar. 2016; *N. Castaño, D. Daly, E. Paki, J.A. Bustos, M. Lasso & A. Valencia 7714*; COAH. – **Cundinamarca** • Yacopí; 5.4588111° N, 74.3080083° W; 1450 m a.s.l.; *M. Morales 474*; COL, FMB. – **Meta** • Municipio de Lejanias, vereda El Triunfo, ubicado a 3 km de las escuela; 3°35'38.4" N, 74°05'52.3" W; 1295 m a.s.l.; 21 Jul. 1998; *R. López, J. Martínez, N. Cruz, M.A. Pinzón & R. Pinzón 4058*; COAH. – **Putumayo** • Trocha de el Pepino al Río Guineo, 1.084709° N, 76.707126° W; 1000 m a.s.l.; *W. Hagemann & N. Leist 2051*; COL. – **Risaralda** • Mun. Pereira, Hacienda Alejandría, Km 8 carretera Cerritos – La Virginia, extremos norte de parte ancha del valle del Río Cauca, en bosque de galería a lo largo de la quebrada; 4.850° N, 75.867° W; 960 m a.s.l.; 8 Jul. 1995; *P. Silverstone-Sopkin 7744*; CUCV. – **Tolima** • Fresno; 1.426° N, 78.384° W; 1480 m a.s.l.; *J. Cuatrecasas 9379*; COL, F, US.

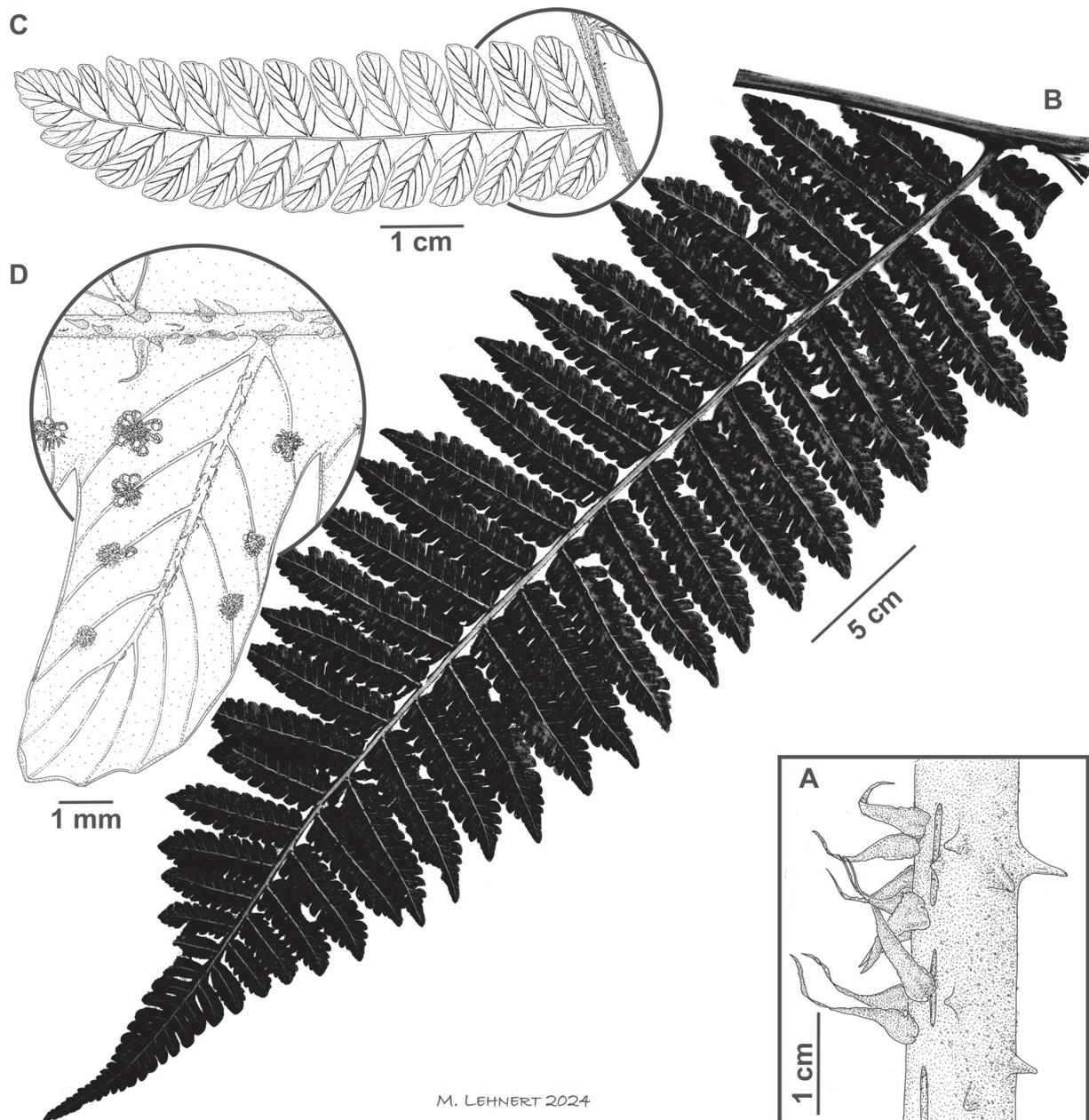
ECUADOR – **Prov. Morona-Santiago** • Macas, roadside vegetation near town of Macas; 2°19' S, 78°08' W; 1100 m a.s.l.; 3 Jul. 1993; *A. Fay & L. Fay 3957*; MO, NY, QCNE • same collection data as for preceding; *A. Fay & L. Fay 4066*; MO, UC. – **Prov. Napo** • Cantón Archidona, road Hollín-Loreto, Km 17, near Río Hollín; 0°41' S, 77°41' W; 1100 m a.s.l.; 14–22 Feb. 1989; *F. Hurtado & J. Shiguango 1624*; MO, UC. – **Prov. Pastaza** • About 0.5 km E of El Puyo; [ca 01°29'59" S, 77°58'43" W]; [ca 1000 m a.s.l.]; 5 Oct. 1974; *J. Hudson 845*; MO, UC • on E side of El Puyo; 7 Oct. 1974; *J. Hudson 896*; MO, UC. – **Prov. Sucumbios** • Shishicho ridge, Alto Aguarico drainage, above (S of) Río Cofanes, W of Puerto Libre, NW of Lumbaqui, access from Río Sieguayo, below Shishicho Camp; 0°12'01.3" N, 77°31'54.3" W; 1500–1570 m a.s.l.; 13 Aug. 2001; *R. Aguinda, N. Pitman & R.B. Foster 1302*; F, UC. – **Prov. Zamora-Chinche** • Nangaritza canton, Parroquia Guayzimi, Campamento Militar Miazi, al sur del río Nangaritza; 4.27° S, 78.70° W; 1060–1000 m a.s.l.; 21 Oct. 1991; *C.E. Cerón, M. Chango, V. Tapur & G. Aymard 16836*; MO.

PERU – **Amazonas** • Bagua, Soldado Oliva, carretera Bagua-Imaza; [ca 5.304° S, 78.388° W]; 660 m a.s.l.; 6 Feb. 1999; *C. Díaz et al. 10642*; MO.

### Description

Trunks to 3.5 m tall, straight, 5.0–8.0 cm diam. (records of 30 cm diam. likely include layer of adventitious roots), covered with old petiole bases, due to these sparsely to strongly aculeate, in lower parts petioles rotting; apices hidden between petioles; adventitious buds absent. Leaves to 275 cm long, held with petioles erect to ascending, lamina ± planar, weakly arching. Petioles 20–45(–59) cm long, sparsely aculeate, prickles to 3 mm long, dark yellowish brown to stramineous, sometimes basally darker brown; aerophores to 20 × 1 mm, in a ± continuous line on each side, inconspicuous in dried material, whitish in fresh material; without remote (aphlebioid) pinnae at the petiole bases; petiole scales 20.0–32.0 × 2.5–5.0 mm, lanceolate to ovate-lanceolate, tapering to linear tips, straight to falcate, weakly twisted, concordantly bicolorous, shiny dark brown to castaneous, with narrow, often abraded whitish margins, scales persistent in distal petiole parts, often reaching lower rachis, here only smaller than lower ones, remaining concordantly bicolorous (never paler or almost completely white); petiole scurf a tomentum of small branched clavate hairs 0.2–0.4 mm long, tan with brown parts, dark brown in general aspect, appearing as small dark dots or irregular stars on the yellowish brown epidermis, persistent but easily abraded. Blades (110–)180–255 × 90–105 cm, bipinnate-pinnatifid, ovate-elliptic to obovate, chartaceous; dark olive-green adaxially, often blackish when dried, olive green abaxially; smaller plants with long petioles and ovate-elliptic blades with 8–10 pinna pairs, basal ones ca ½ the length of longest pinnae, larger plants with short petioles and basally tapering blades with 16–18 pinna pairs, basal ones ca ⅓ the length of longest pinnae, patent to weakly reflexed; pinnae alternate; apices gradually reduced. Leaf axes (rachises, costae and costules) stramineous to yellowish brown on both sides, sparsely aculate in lower half, otherwise inermous; adaxially with antrorsely curved uniseriate, reddish brown hairs 0.5–1.0 mm long, abaxially with scurf remnants, costae and costules also with dark brown, erect shell-like to bullate squamules, 0.5–1.0 × 0.5 mm with subulate, rarely flattened or elongate tips, larger flat squamules to 2 × 1 mm rare or absent; junctions rachises/costae abaxially weakly swollen, each with an inconspicuous planar pneumathode, dark brown, elliptic, to 4.0 × 2.5 mm, area around it often black in dried specimens (foliar nectary). Largest pinnae 37–45 cm long, sessile (appearing stalked if proximal basisopic pinnule fallen off), pinnae patent to weakly ascending, distally narrowly to broadly green alate, the pinnatifid terminal segment shortly decurrent into the costae. Largest pinnules 8.0–11.5 × 2.0–2.5 cm, linear-oblong to linear-lanceolate, incised to ½ or more of their width (usually 2–3 mm between sinuses and costules), sessile, bases on smaller ones truncate to weakly cuneate, in larger ones truncate to weakly cordate, smaller pinnules (especially in lower pinna) with obtuse to rounded tip, larger pinnules tapering from beyond the middle to short-attenuate tips; costules basally with a black ring going all around their bases (abscission layer); largest segments 12.0–15.0 × 2.5–4.0 mm, oblong, patent to ascending, distally weakly falcate, with entire to weakly dentate margins, tips rounded to obtuse; basal segments alternate, the lowest ones not

remote from each other, sinuses narrowly triangular to elliptic, acute, to 1.0 mm wide, sometimes closed; veins prominent abaxially and adaxially, midveins adaxially ridged, veins ending in cartilaginous segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish, glabrous adaxially except for occasional single hairs on the midveins, abaxially glabrous except for some dark brown bullate squamules and trichomidia on midveins, absent between the veins; sterile and fertile veins mostly simple, regularly forked in the tips of larger segments. Sori 0.8–1.0 mm diam., medial to supramedial (sometimes appearing submarginal when sori still complete), parallel to the midvein or in triangular lines, on the back of veins or in fork of veins, indusia absent; receptacles



**Fig. 9.** *Cyathea pastazensis* (Hieron.) Domin. **A.** Petiole with scurf and scales, small individual (*Lehnert 3162*, BONN). **B.** Pinna, silhouette. **C.** Pinnule, adaxially (*M. Lehnert 3162*, BONN). **D.** fertile segment, abaxially (*Lehnert 3162*, BONN).

globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few to numerous, hyaline, brown to tan, shorter than sporangia (0.2–0.3 mm). Spores not examined.

### Distribution and ecology

Colombia (Cordilleras Occidental and Central), Ecuador and northern Peru (eastern Andean slopes) (Fig. 2B) at elevations of (310–)850–1600 m a.s.l., dubious records also from the western escarpment (Ecuador: El Oro; Colombia: Chocó); in the understory of lower montane forest, preferably in small valleys (quebradas) and near water courses.

### Remarks

The syntypes of *Alsophila pastazensis* have been regarded to represent one species, but we consider them to belong to at least two species, one of them *Cyathea tortuosa* R.C.Moran. This is supported by recent observations by the first author at the Jardín Botánico las Orquídeas, a private reserve near Puyo, Ecuador. Both species grew only a few meters apart in the dense forest understory, but each with a specific habit, with *C. pastazensis* having a trunk covered in old petiole bases and funnel shaped crown, and *C. tortuosa* with a clean-shed trunk and patent leaves.

*Cyathea pastazensis* is best described as a *Cyathea floribunda* with darker, concolorous squamules on the blades because both have sessile pinnae and round-tipped segments. However, *C. pastazensis* shows the typical leaf architecture of *C. pungens* with the pinnules of the lower pinnae being blunt-tipped whereas the pinnules of the distal pinnae are decidedly more acute (vs all equally blunt-tipped in *C. floribunda*, as observed so far). In the contact zone of the ranges of both species in southern Ecuador and northern Peru, it almost looks like a fluid transition between the two morphologies in a large shared range (Fig. 2B); but as we interpret it, *C. pastazensis* extends south along the lowland forests of the Amazon basin whereas *C. floribunda* reaches north along the Andean foothills.

Both *Cyathea pastazensis* and *C. floribunda* differ from *C. pungens* in soral lines that follow the midveins, thus forming parallel lines across the whole pinnule; in *C. pungens*, the soral lines are parallel to the segment margins, thus shaped in a zig-zag pattern across the whole pinnule. In *C. pastazensis* and *C. floribunda*, pinnae and pinnules are sessile whereas in *C. pungens*, at least the largest pinnae are clearly stalked, creating a visible gap between rachis and blade; pinnules tend to be remote from the costae, too, but this character is more clearly developed in eastern Amazonian population of *C. pungens*.

*Cyathea werffii* grows in the same region (e.g., Baker 5699, MO, NY), but has smaller leaves with stalked lower pinnae (vs all sessile in *C. pastazensis*), smaller pinnules with blunt, often widened tips, appearing almost rectangular; it also has scarcer scaly indument on the axes than *C. pastazensis*.

### *Cyathea praecincta* (Kunze) Domin

*Cyathea praecincta* (Kunze) Domin (Domin 1929a: 263). – *Alsophila praecincta* Kunze (Kunze 1839: 53). – *Alsophila submarginalis* Domin (Domin 1929c: 217), nom. superfl. – *Cyathea submarginalis* (Domin) Domin (Domin 1930: 163). – *Trichipteris submarginalis* (Domin) R.M.Tryon (Tryon 1970: 46). – *Trichipteris praecincta* (Kunze) R.M.Tryon (Tryon 1970: 46). – **Type:** BRAZIL • Bahia; Ilheos; ca 14°10' S, 53°05' W; 1817–1820; *C.F.P. Martius 391*; lectotype: B [B 20 0000200]!, chosen by Barrington 1978; isolectotypes: B [B 20 0000198, B 20 0000199, B 20 0000201]!, BR [BR0000006987541, labelled “Ilheos, Luschnatt”] image!, HAL [HAL-0086574]!, K [K000589886]!, L [L.1284712, L.1284714]!, LE [LE00008123] image!, M!, MO [MO-255859]!, NY [00148753, fragment of B, 00148755, 00148756] image!, P [P00631777, P00631778, P00631779]!

## Etymology

The specific epithet translates as ‘well girdled’, which may either refer to the tight, string-like arrangement of the sori or the many deep sinuses along each side of a pinnule.

## Selected material studied

BRAZIL – **Alagoas** • Poço D’Anta, ca 16–19 km NNW of Muricí by road, Mata de Muricí; 9°14’ S, 35°53’ W; 550–600 m a.s.l.; 14 May 2001; *W.W. Thomas 12419*; MO, NY. – **Bahia** • Arataca, Serra do Peito-de-Moça; 15°12’10” S, 39°24’29” W; 900 m a.s.l.; 12 Aug. 2009; *P.L.R. de Moraes, H. van der Werff, L. Daneu & R. Perdiz 2737*; HUEFS, RB • Camacã, RPPN Serra Bonita; 28 Nov. 2014; *P.L.R. de Moraes, H. van der Werff & L. Daneu 4254*; HRCB • Almadina, Serra do Corcovado; 13 Dec. 2014; *P.L.R. de Moraes, H. van der Werff & L. Daneu 4553*; HRCB • Belmonte, Fazenda Taquara; 16 Feb. 2015; *P.L.R. de Moraes, H. van der Werff & L. Daneu 4810*; HRCB • Una Reserva Biologica de Una, near Rio Maruim; 14 Nov. 2000; *I. Fernades, S.C. Sant’Ana & M. Caravallo 1498*; NY • Barro Preto, ca 13.5 km on street from Barro Preto to the access to Serra da Pedra Lascada; 14°46’22” S, 39°32’16” W; 960 m a.s.l.; 13 Aug. 2003; *P. Fiaschi, A.M. Amorim, S. C. Sant’Ana & J.L. Paixão 1574*; NY.

## Description

Trunks 0.7–1.5 m tall, ca 8–10 cm diam., with old petiole bases, straight to decumbent; without adventitious buds. Petioles ca 35–50 cm long, inermous to sparsely muricate, brown to dark purpleous, matte; scurf absent. Petiole scales lanceolate, 14.0–20.0 × 4.0–4.5 mm, their tips straight, concolorous yellowish to white, sometimes with dark central stipe, auburn to dark brown. Leaves to 230 cm long; patent and distally arching. Blades to ca 180 × 90–120 cm, bipinnate-pinnatifid, firm herbaceous to chartaceous; dark shiny green adaxially, often blackish when dried, pale olive green abaxially; apices abruptly reduced to a non-conform section. Pinnae to 35–65 cm long, number of pairs per leaf ca 8–10, stalked 1.0–2.5 cm, patent to ascending, basal pinnae ca  $\frac{2}{3}$  the length of longest pinnae, patent to weakly reflexed; pinnae distally green alate; distal pinnules free, the pinnatifid terminal segments shortly decurrent into the costae. Leaf axes brown to carnose on both sides, the costules abaxially often blackish; with whitish to brown, antrorsely curved hairs to 0.8 mm long adaxially, abaxially glabrescent with scattered, appressed, tan to brown trichomidia; abaxially with auburn to orange-brown squamules with entire margins and white tips, bullate or flat, 0.4–1.0 mm long; costae inermous, 1.5–3.0 mm wide; insertions of costae into rachises not or only abaxially weakly swollen, without clearly developed pneumathodes, usually blackened in dried specimens. Pinnules to 7.0–11.5 × 1.5–2.0 cm, short stalked to 3 mm, alternate, 1.5–3.0 cm between the stalks; linear-oblong, bases truncate to weakly cordate, long attenuate tips, and with finely serrate margins; incised to  $\frac{1}{2}$  or more of their width, with acute sinuses to 2 mm wide, weakly dimorphic, sterile part of pinnae and pinnules wider with narrower, often occluded sinuses; the carnose to brown stalks inarticulate, with a black ring at their bases (abscission layer ?), without pneumathodes; segments oblong to deltate, patent to ascending, with subentire to finely crenulate margins, in the latter case weakly revolute; tips straight to weakly falcate, rounded to obtuse; basal segments opposite to alternate, the lowest ones not remote from each other. Veins planar, carnose to dark brown abaxially and adaxially, ending shortly before the segment margins, becoming wider and reddish adaxially; glabrous adaxially, abaxially with appressed, tan trichomidia and thin, hyaline, twisted hairs to 1 mm long, with auburn to orange-brown bullate squamules with entire margins, sometimes larger, flattish squamules to 2 × 1 mm proximally on midveins and on costules; no hairs between veins; sterile simple, fertile veins forked, rarely simple. Sori 0.8(–1.0) mm diam., inframarginal to marginal, parallel to the margins, usually in the forks of veins, indusia absent; receptacles globose to ellipsoid, 0.3–0.4 mm diam., without subtending scales; paraphyses few, hyaline, tan to reddish brown, shorter than the sporangia (0.2 mm). Spores with smooth exospore, finely pitted (Gastony 1979).

### Distribution and ecology

Northeastern Brazil at elevations of 550–960 m a.s.l., in the understory of Mata Atlântica.

### Remarks

*Cyathea praecineta* has been often misidentified as *C. pungens* when petiole scales are missing (mostly concolorous white in *C. praecineta* vs strongly bicolorous with white margins in *C. pungens*), but the whole appearance and coloration of its specimens differs strongly from true *C. pungens*. Dried specimens have the blades bicolorous, with blackish adaxial side and olive to grayish green abaxial side (vs ± the same color in *C. pungens*, varying from pale green to brown depending on preservation) and the axes are a homogenous reddish brown to atropurpureus (vs yellowish to pale brown in *C. pungens*). *Cyathea praecineta* has many fertile veins forked while they are generally simple in *C. pungens*. According to our data, both species have clearly separated distributions (Figs 1–2).

From Alagoas, we have seen only images of specimens without petiole (*W.W. Thomas 12419*, MO, NY), which may be *C. macrocarpa* (C. Presl) Domin. The specimens have the lowest segments slightly smaller than the following in the pinnules, and the margins slightly dentate, which matches more *C. macrocarpa* than *C. praecineta*. *Cyathea macrocarpa* is scatteredly distributed from northeastern Brazil to the Guayana shield (Lehnert 2011). Both species occur together, have submarginal sori and very pale petiole scales, and they are often not distinguishable from photos alone (<https://www.inaturalist.org/observations/103467779>). A closer look at the sori allows a clear separation as *C. praecineta* has no indusium, which is easily discernable due to the sparse paraphyses, whereas *C. macrocarpa* has a dense mass of long persisting paraphyses that hide a well developed hemitelioid indusium.

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

Figs 10, 13B

*Cyathea pungens* (Willd.) Domin (Domin 1929a: 263). – *Polypodium pungens* Willd. (Willdenow 1810: 206). – *Alsophila pungens* (Willd.) C.Presl (Presl 1836: 61). – *Trichipteris pungens* (Willd.) R.M.Tryon (Tryon 1970: 46). – **Type:** BRAZIL • “Brasilia”; *J.C. von Hoffmannsegg s.n.*; holotype: B [B-W 19716-011, B-W 19716-012, B-W 19716-013, 3 sheets, Herb. Willdenow!]; isotypes: B [B 20 0000318, Herb. Link!], NY [00148762, fragment of B], US [00066283, fragment of B] image!.

*Polypodium procerum* Willd. (Willdenow 1810: 206). – *Alsophila procera* (Willd.) Desv. (Desvaux 1827: 319). – *Cyathea willdenowiana* Domin (Domin 1930: 171). – *Trichipteris procera* (Willd.) R.M.Tryon (Tryon 1970: 46). – **Type:** BRAZIL • “Brasilia”; *J.C. von Hoffmannsegg s.n.*; holotype: B [B-W 19717-011, B-W 19717-012, B-W 19717-013, 3 sheets, Herb. Willdenow!]; isotypes: NY [00148758, fragment of B], US [00066279, fragment of B]!.

*Alsophila infesta* Kunze (Kunze 1834: 98). – *Cyathea infesta* (Kunze) Domin (Domin 1930: 125). – *Trichipteris infesta* (Kunze) R.M.Tryon (Tryon 1970: 45). – *Alsophila phalerata* var. *infesta* (Kunze) Farw. (Farwell 1931: 250). – **Type:** PERU • Huánuco, “Peruviae ad Miss. Tocache fluv. Huallgae vicinam”; Aug. 1830; *E. Poeppig s.n.*; holotype: LZ [destroyed]; lectotype: W [W0056018, W0056019, 2 sheets]!, designated by Lehnert 2016; isoelectotypes: BM [BM000937693, fragment of W]!, MO [MO-1855206] image!.

*Alsophila subaculeata* Splitg. (Splitgerber 1840: 430). – **Type:** SURINAME • Canawappibo; Dec. 1837; *F.L. Splitgerber s.n.*; lectotype: L [L.1285146, L.1285147, 2 sheets]!, first step designated by Barrington 1978, second step **designated here**; isoelectotypes: NY [fragment of P] n.v. (fide Barrington 1978), US [00066287, fragment of P] image!.

### Etymology

The specific epithet refers to the sharp stinging prickles that are usually present on the petioles of this species.

### Selected material studied

HAITI – **Nord** • Plaisance; [ca 19.596973° N, 72.466326° W]; 609 m a.s.l.; 27 Aug. 1903; *G.V. Nash 887*; NY, US.

DOMINICAN REPUBLIC – **Barahona** • Paradis vicinity; [ca 18.149° N, 71.107° W]; 0–800 m a.s.l.; 28 Jan. 1922; *W.L. Abbott 1580*; US. – **Pacificador** • Vicinity of San Francisco de Macoris, Lo Bracito; [ca 19.326° N, 70.259° W]; 400–1000 m a.s.l.; 5 Apr. 1922; *W.L. Abbott 2030*; US. – **Samaná** • Monte Negro, about 10 miles N of Sánchez, Samaná Peninsula; ca 19.260° N, 69.591° W; 300–400 m a.s.l.; 17 Mar. 1969; *A.H. Liogier 14453*; NY.

PUERTO RICO [USA] – **Río Grande** • Luquillo Forest, Rt. 191, km 5.2; [ca 18.334° N, 65.764° W]; 286 m a.s.l.; 22 Nov. 1973; *D.S. Conant 670*; F, MO, US, VT.

GUADELOUPE – **Basse-Terre** • Marecageuse de Lamentin; [ca 16.292° N, 61.635° W]; 5–12 m a.s.l.; Jun. 1897; *A. Duss 3882*; F, NY, US.

COLOMBIA – **Amazonas** • Leticia, Quebrada Tacana, 22.5 km NNW cabecera municipal; 4.022° S, 69.999° W; 3 Aug. 2000; *J.C. Arias-G. 828*; COAH, COL, HUA. – **Caquetá** • San José del Fragua Inspección de policía de Puerto Bello, resguardo San Miguel; 1°08'67" N, 76°16'14" W; 200 m a.s.l.; 4 Oct. 2015; *L.F. Giraldo 3575*; COAH, HUA. – **Cauca** • Piamonte, aguas arriba de la desembocadura del Indayaco en el Caquetá, margen derecha; 1.02° N, 76.48° W; 400 m a.s.l.; 19 Oct. 1996; *R. Sánchez 3232*; COAH. – **Guaviare** • Municipio de San Juan del Guaviare, vereda Los Alpes, finca El Provenir, Serranía La Lindosa, 02°31'51" N, 72°48'39" W; 310 m a.s.l.; 22 Jul. 2017; *D. Cárdenas, N. Marín, M. Holguín & G. Holguín 48784*; COAH. – **Meta** • Uribe, PNN Tinigua, vereda Aires del Meta; 2.583° N, 74.333° W; 23 Apr. 2002; *M. Gaitán 7*; COAH. – **Putumayo** • Puerto Leguizamo, Río Putumayo en Puerto Ospina; 0.229° N, 75.938° W; 230 m a.s.l.; *J. Cuatrecasas 10578*; COL, F, US.

VENEZUELA – **Amazonas** • Rio Yatuá; 1.17508° N, 66.0572° W; 105 m a.s.l.; *K.M. Redden et al. 3539*; US. – **Bolívar** • Dtto. Sifontes, concesión Minera Oro Uno, 7 km al NO de la Clarita; [ca 06°13' N, 61°27' W]; 180 m a.s.l.; 3 Aug. 1985; *G. Aymard et al. 3874*; MO. – **Delta Amacuro** • Venezuela-British Guiana frontier, Sierra Imataca, upstream from San Victor, past Quebrada Piedradero and Río Matanaima; [ca 01.665° N, 62.420° W]; 65–80 m a.s.l.; 1 Nov. 1960; *J.A. Steyermark 87203*; MO, NY, US, VEN. – **Zulia** • Dtto. Bolívar, Cuenca del Embalse Burro Negro; (Pueblo Biejo), sector entre Quiros-El Pensado y el pie de Cerro Socopo, en el area aprox. 10 km en linea recta al este de Churugarita; 10.169° N, 71.0459° W; 250–300 m a.s.l.; *G.S. Bunting 9515*; UC.

TRINIDAD AND TOBAGO – **Trinidad** • Causa road, gully, near 3 mile post; 25 May 1928; *W.E. Broadway 6958*; F, MO • Without locality; 1878–1880; *A. Fendler 112*; MO, NY, US.

GUYANA – **Barima-Waini** • Barima River, Northwest District; [ca 8.33° N, 59.83° W]; [ca 110 m a.s.l.]; 19 Mar. 1923; *J.S. de la Cruz 3417*; MO, NY, US. – **Cuyuni-Mazaruni** • Arawak Matope, Cuyuni River; [ca 06.51° N, 58.91° W]; 91 m a.s.l.; 20 Jul. 1933; *T.G. Tutin 403*; US. – **Demerara-Mahaica** • Cuyuni-Mazaruni, Paruima to Conoch Tipu, S of village ± 1 km; 5.98333° N, 61.05° W; 530–610 m a.s.l.; 17 May 1990; *T. McDowell & D. Gopaul 2624 a*; US. – **Upper Takutu-Upper Essequibo** • Upper Essequibo Region, Rewa River, near Camp 2 at foot of Spider Mountains; 3°07'59" N, 58°31'59" W; 220 m a.s.l.; 13 Sep. 1999; *M.J. Jansen-Jacobs 5881*; L [formerly U], NY, UC, US.

SURINAME – **Commewijne** • Perica R., Capoerica Ridge, near km 3; ca 05.758° N, 54.973° W; 10 m a.s.l.; 27 Jan. 1954; *J.C. Lindeman 5405*; US. – **Para** • Upper Para Creek to Suriname River, ca 8 km E of Zanderij on road to Phedra; ca 5.488° N, 55.156° W; 10 m a.s.l.; 12 Feb. 1961; *R.M. Tryon Jr. & K.U. Kramer 5618*; US. – **Sipaliwini** • Inselberg Talouakem – Massif des Tumuc-Humac; 2°28'59" N, 54°45'00" W; 250 m a.s.l.; 8 Aug. 1993; *J.J. de Granville et al. 12126*; L [formerly U], US.

FRENCH GUIANA – **Cayenne** • D.Z. de Crique Jupiter, Bassin du Sinnamary; 4.0675° N, 53.1619° W; 80 m a.s.l.; 27 Apr. 1991; *J.J. de Granville, C.S. Roesel & L. Brothers 11592*; US. – **Saint-Laurent-du-Maroni** • W face of Roche Koutou 'inselberg', Upper Maroni Basin; 3.1444° N, 54.05° W; 170 m a.s.l.; 19 Aug. 1987; *J.-J. de Granville, L. Allorge, W.J. Hahn & M. Hoff 9464*; F.

ECUADOR – **Napo** • Río Lagarto Cocha, near Redondo Cocha; 0°33' S, 75°53' W; 190 m a.s.l.; 15 Jun. 1983; *J.E. Lawesson, T. Læssøe & P.M. Jørgensen 44394*; AAU, MO, QCA. – **Orellana** • Parque Nacional Yasuni, Km 92.5 rd Pompeya-Iro; 0°53.370' S, 76°13.520' W; 250–300 m a.s.l.; 12 May 1997; *M.J. Macía & A.P. Yáñez 323*; MO, QCA. – **Pastaza** • Oil exploration camp Chichirota, on the Río Bobonaza; 2°22' S, 76°40' W; 300 m a.s.l.; 26 Jul. 1980; *B. Øllgaard, E. Asanza-C., J. Brandbyge, S. Roth & C. Sperling 35264*; AAU, F, QCA, UC, US. – **Sucumbios** • Alto Río Aguarico, Río Chingual, ridge just before Ching Chingual bridge, between Rio Recodo and Río Chingual, new trail toward Bermejo, from new road to Tulcán above Puerto Libre; 0°15'22" N, 77°28'25" W; 700–800 m a.s.l.; 7 Jul. 2000; *R. Aguinda, M. Metz & T. Theim 805*; F, UC. – **Zamora-Chinchipe** • Cordillera del Condor, Miazi, flood plain forest along Río Nangaritzá. Transect #3; 4°18' S, 78°40' W; 850 m a.s.l.; 28 Jul. 1993; *A. Gentry 80578*; MO.

PERU – **Amazonas, Prov. Condorcanqui** • Dist. Imaza, Comunidad Nativa de Yamayakat; 5.057° S, 78.338° W; 350 m a.s.l.; Mar. 2002; *R. Bonino 345*; MO. – **Huanuco, Prov. Leoncio Prado** • Dtto. José Crespo y Castillo, carretera a Cotomono, cerca a Aucayacu; ca 08.950° S, 76.1176° W; 500–580 m a.s.l.; *J. Schunke V. 10507*; MO, UC. – **Loreto, Prov. Iquitos** • San Juan, río Tigre; 2°35' S, 75°40' W; 245 m a.s.l.; 17 Mar. 1987; *W.H. Lewis, M. Elvin-Lewis, D. Fast & J. Campos de la Cruz 12863*; MO. – **Madre de Dios, Prov. Tambopata** • 30 air km or 70–80 river km SSW of Puerto Maldonado at effluence to La Torre (Río D'Orbigny)/Río Tambopata (SE bank), Tambopata Nature Reserve; 12°49' S, 69°17' W; 260 m a.s.l.; 16 Apr. 1980; *P.J. Barbour 4795*; MO, UC. – **Pasco, Prov. Oxapampa** • Dist. Palcazú, San Pedro de Pichanaz-Azulis, Reserva Comunal Yanasha; 10°28'40" S, 75°06'10" W; 670 m a.s.l.; 25 Feb. 2004; *L.F. Mellado N. 0733*; MO, USM. – **Puno, Prov. Carabaya** • Río Távara base camp; 13°21' S, 69°40' W; 400 m a.s.l.; 19 May 1992; *A. Gentry, C. Reynel, R. Ortiz & P. Nuñez 76848*; MO, NY, UC. – **San Martín, Prov. Mariscal Cáceres** • Distrito Tocache Nuevo, Puerto Pizana (right margin of Río Huallaga); 350 m a.s.l.; 1 Jun. 1974; *V.J. Schunke 6866*; UC. • **Prov. San Martín** • In montibus secus flumen Mayo, prope Tarapoto; Jul.–Aug. 1856; *R. Spruce 4715* [excluded syntypes of *Alsophila floribunda*, mix with *C. dombeyi*]; BM [BM000777031, BM000777032 (mix with *C. dombeyi*), BM000777346], P [P00642346 p.p., P00642349, P00642350] • In monte Campana prope Tarapoto; Aug. 1856; *R. Spruce 4715*; W [W-Rchb. 0053380]. – **Ucayali** • Col. Prado, along new road from Parque Nacional Alexander von Humboldt to Puerto Inca, ca 5 km E of main Pucallpa-Tingo María road at Km 86; 8°17' S, 74°58' W; 500 m a.s.l.; 5 Nov. 1980; *T.B. Croat 51061*; MO, UC. • Coronel Portillo, Calleria, camino a la altura del Quebrada Mojaral, este del Río Utiquina y Quebrada Pumayacu; 8°09.13' S; 74°15.48' W; 150–175 m a.s.l.; *J. Schunke Vigo & J.G. Graham 15500*; F, UC.

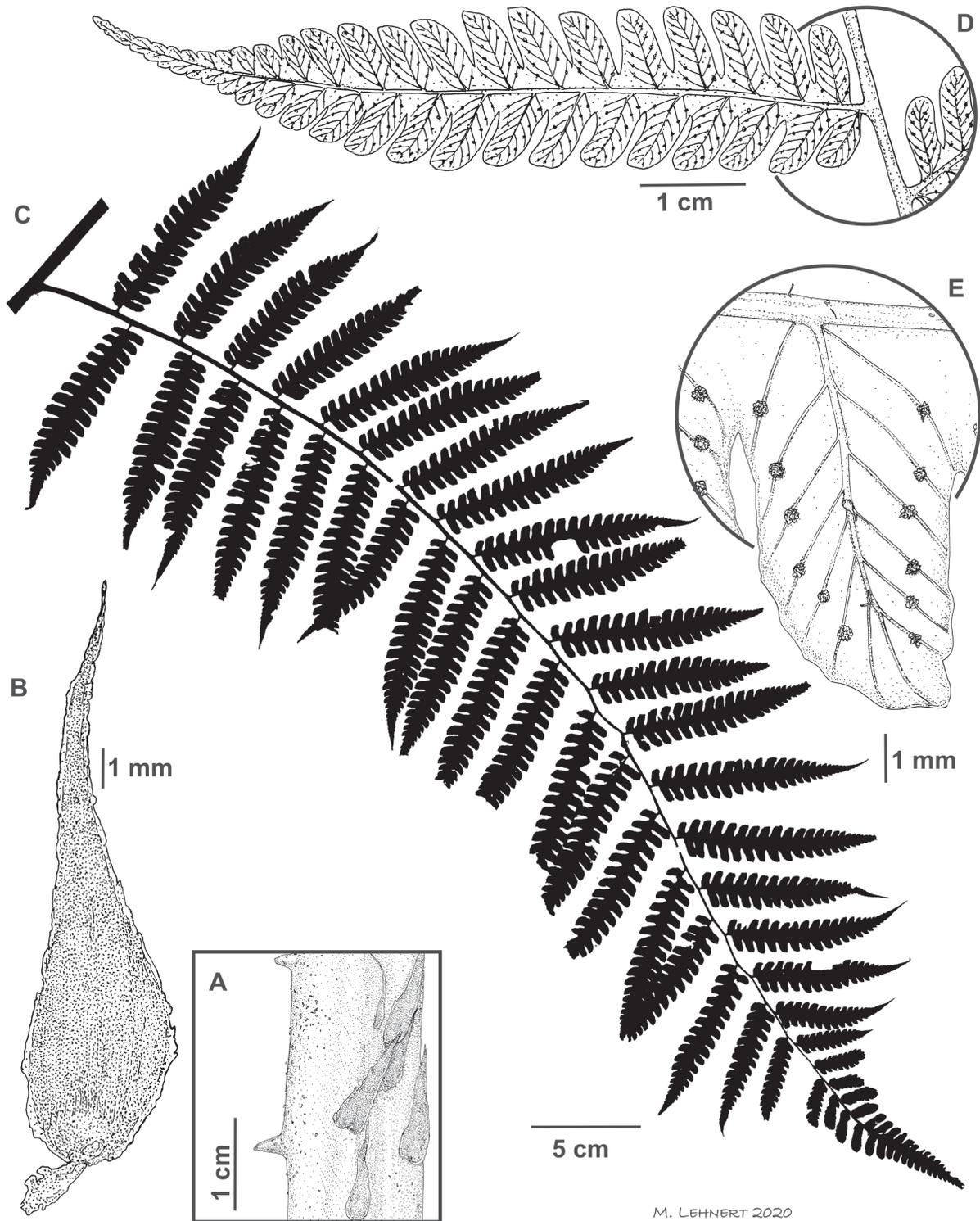
BRAZIL – **Acre** • Município de Rio Branco, BR 364, estrada Rio Branco - Porto Velho, km 11 da magem ramal que da acesso ao lugar Belo Jardim; 25 Oct. 1980; *C.A. Cid Ferreira & B.W. Nelson 3053*; NY, US. – **Amazonas** • Coari, Província Petrolífera de Urucu, arredores do pólo Arara, igarapé da Onça; 4.864454° S, 65.298671° W; 75 m a.s.l.; 2007; *M.R. Pietrobon-Silva 6928*; RB. – **Ceará** • Serra do Araripe; [ca 07.389° S, 40.216° W]; v. *Luetzelburg 25816a*; UC. – **Goias** • Jataí; [ca 17°53'26.8" S,

51°45'01.4" W]; [ca 670 m a.s.l.]; *A. Macedo 1518*; US. – **Mato Grosso** • Municipio de Porto dos Gauchos, bacia rio Patelão (afl. rio dos Peixes), ca 115 km W de Porto Atlantico (Rio Teles Pires); 11.5° S; 56.75° W; 350–400 m a.s.l.; 16 Jul. 1991; *P.G. Windisch & W. Oliveira 6493*; US. – **Mato Grosso do Sul** • Munic. Rio Verde de Mato Grosso, Serra Pimenteira, Cachoeira Anhumas, Fazenda Quartel; 18.9166667° S, 54.8833333° W; 350 m a.s.l.; 23 Feb. 1994; *M.R. Silva & C.E. Rodrigues 1298*; MO. – **Pará** • Serra dos Carajás, “Azul” near camp at Serra Norte; 5.983° S, 50.467° W; 646 m a.s.l.; 8 Dec. 1981; *D.C. Daly 1836*; MO • Alenquer, Floresta Estadual do Paru, Trilha T3; [ca 00.947° S, 53.243° W]; 53 m a.s.l.; 11 Dec. 2008; *S. Maciel 1541*; BONN, MCT • “Tanaii, ad Rio Acara, juxta Para”; [ca 01.563° S, 1.563° W]; [ca 15 m a.s.l.]; Sep. 1849; *R. Spruce 22*; K, TCD. – **Rondônia** • Rio dos Pacaás Novos, above the first cachoeira; between the river and the base of the Serra dos Pacaás Novos; 10°58'46" S, 63°46'10" W; 220 m a.s.l.; 22 Mar. 1978; *W.R. Anderson 12236*; F, NY.

BOLIVIA – **Beni, Prov. Vaca Diez** • 3 km E of Riberalta on road to Guayamerín, then 2 km SE on side road; 11°00' S, 66°05' W; 230 m a.s.l.; 19 May 1982; *J.C. Solomon 7700*; MO UC. – **Cochabamba, Prov. Carrasco** • Projecto Valle del Sacta, 241 km W of Santa Cruz, 219 km E of Cochabamba off new road between Cochabamba and Santa Cruz; 17°12' S, 64°43' W; 290 m a.s.l.; 13 Jul. 1989; *A. Fay & L. Fay 2357*; LPB, MO. – **La Paz, Prov. Abel Iturralde** • Parque Nacional Madidi, Pampas del Heath, along Río Heath, camp Maronal; 12°51' S, 68°48' W; 204 m a.s.l.; 9 Nov. 2004; *J. Gonzales, H. Nenzen, J. Choque & J.C. Cespedes 4711*; LPB, UC. – **Pando, Prov. Manuripi** • Along Rio Madre de Dios, 3 km W of Humaita; 12°01' S, 68°18' W; 150 m a.s.l.; 30 Aug. 1985; *M. Nee 31660*; LPB, NY, MO. – **Santa Cruz, Prov. Velasco** • Huanchaca I, d1, Huanchaca; 13°54' S, 60°48' W; 650 m a.s.l.; *L. Arroyo P., T.J. Killeen, J. Wellens, H. Gonzáles & P. Solíz 669*; MO, UC, UCSZ.

### Description

Trunks 0.5–4.0 m tall, 4.0–8.0(–15.0) cm diam., straight to decumbent, with persistent old petiole bases, spiny; apices hidden between petioles; adventitious buds absent. Leaves to 250(–300) cm long; smaller ones erect, in funnel-shaped crown, larger ones strongly arching. Petioles to 65 cm long, aculeate, prickles 3–5 mm long, dark yellowish brown to stramineous, sometimes basally darker brown; aerophores to 10 × 1 mm, inconspicuously brown in dried material, whitish in fresh material; without remote (aphlebioid) pinnae at the petiole bases; petiole scales lanceolate, 15.0–25.0 × 2.5–4.0(–6.0) mm, their tips straight to falcate, concordantly to discordantly bicolorous, shiny dark brown, with pale brown to whitish margins, scales in distal half of the petiole almost concolorous white except for brown spots near the base; colors only sharply contrasted in scales near petiole base and on crosiers; petiole scurf a matted tomentum of small branched hairs and dissected squamules 0.2–0.4 mm long, yellowish white with brown parts, grayish white in general aspect, soon caduceous, persistent between prickles. Blades 100–180 × 60–100 cm, bipinnate-pinnatifid, elliptic to obovate, chartaceous; dark olive-green adaxially, often blackish when dried, olive-green abaxially; apices abruptly reduced to non-conform apical sections, sometimes very broad and almost gradually reduced. Rachises stramineous to yellowish brown on both sides, in basal half often with some strong prickles; adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous except for scurf remnants, containing appressed, white trichomoidia and dissected squamules (0.2–0.5 mm). Largest pinnae 35–60 cm long, pinnae 8–12 pairs per leaf, mostly stalked to 1.5–2.5 cm, ascending, distally narrowly to broadly green alate, the distal segments free, the pinnatifid terminal segments shortly decurrent into the costae. Costae inermous, to 1.5–2.0 mm wide, adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous or glabrescent with scurf like on the rachises, insertions into rachises abaxially weakly swollen, each with an inconspicuous planar pneumathodes, dark brown, elliptic, to 2.0 × 1.0 mm, area around it often black in dried specimens. Pinnules (3.5–)5.0–8.0(–10.0) × (1.0–)1.5–1.8(–2.0) cm, smaller ones sessile, larger ones stalked 1.0–1.5(–3.0) mm, articulate, alternate, 1.5–2.0 cm between the stalks, linear-oblong, incised to ½ or more of their width, bases truncate to weakly cuneate, tapering from beyond the middle to short acute to short attenuate tips; costules with ephemeral tan to brown trichomoidia and tan to brown squamules 0.5–1.0 mm



**Fig. 10.** *Cyathea pungens* (Willd.) Domin. **A.** Petiole with scurf and scales (Tuomisto *et al.* 16679, BONN). **B.** Petiole scale from petiole base, showing only thin white differentiated margin (Tuomisto *et al.* 16679, BONN). **C.** Pinna, silhouette (S. Maciel 1541, BONN). **D.** Fertile pinnule, abaxially (E. Poeppig *s.n.*, W0056018). **E.** Fertile segment, abaxially (S. Maciel 1541, BONN).

long with entire margins and short acute tips, varying in color from white over tan, concolorous or with paler tips; costules basally with a black ring going all around their bases (abscission layer); segments oblong, to 5.0–12.0 × 3.0–5.0 mm, patent to ascending, distally weakly falcate, with entire to subentire margins, tips rounded to obtuse, rarely acute and then margins weakly dentate; basal segments opposite to alternate, the lowest ones not remote from each other, sinuses triangular, acute, 1.0–2.0 mm wide, sometimes closed; veins prominent abaxially and adaxially, midveins strongly so and adaxially ridged, lateral veins ending at segment margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish; adaxially glabrous except for occasional single hairs on the midveins, abaxially glabrous or with squamules and trichomidia like on the costules, trichomidia sometimes also between the veins; sterile and fertile veins mostly simple, rarely forked in larger pinnules (> 2 cm wide). Sori 0.6–0.8(–1.0) mm diam., supramedial to inframarginal, parallel to the margins, on the back of veins, indusia absent; receptacles globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few to numerous, hyaline, white, shorter than sporangia (0.2–0.3 mm). Spores not examined.

### Distribution and ecology

Haiti, Dominican Republic, Puerto Rico, Guadeloupe, Trinidad & Tobago, Amazonian lowland of Colombia, Venezuela, Suriname, French Guiana, Ecuador, Peru, Brazil, and Bolivia at elevations of ca 5–1100 m a.s.l., in shade along creeks or in sun on swampy soils, flourishing in tree fall gaps and small clearings; in the Caribbean mostly near mangroves and in limestone areas, often in shaded sinkholes.

### Remarks

The exact locations where the types of *Polypodium pungens* and *P. procerum*, both attributed to J.C. Hoffmannsegg, were collected are unknown. Hoffmannsegg did not travel to Brazil personally but had specimens collected and sent from there by paid collectors (Stresemann 1950). Although an accomplished botanist, Hoffmannsegg seemed to have had his main focus on animals during that time, and documentation of the Brazilian plant material in the literature is scarce. However, most of the plants seem to have been collected by Friedrich Wilhelm Sieber, who was a handyman of Hoffmannsegg, and his itinerary has been researched for the bird specimens he collected (Stresemann 1950). Sieber was almost exclusively active in today's state of Pará, along Rio Amazonas between Obidos and Gurupá, and near “Rio Preto”, which refers most likely to the town of São Benito do Rio Preto in neighboring state Maranhão. One sheet of the type of *P. pungens* bears a slip with the fragmentary information that it is “fern herb growing low, but if in dry forest at river (Sieber)”, and the type of *P. procerum* “fern herb, is a real tree, in shape of a ‘palmeiro’, in forest at river, its height was more than 6 ells (Sieber)” [personal translation from German], which are vague but still fitting descriptions of the aspect of *Cyathea pungens*. We may conclude that the types of *P. procerum* and *P. pungens* had been collected by Sieber, either in the state of Pará or Maranhão. One of the slips on the type of *P. pungens* (B 20 0000318) bears a little scribble below the location “Brazil” that may be deciphered as “Coto”; there is a location of that name in Maranhão east of São Benito do Rio Preto, which is one of the documented areas that Sieber visited. However, this particular specimen was stored in the Herbarium Link, does not bear any reference to Sieber or Hoffmannsegg, and was only aligned with the Willdenow specimen (B-W 19716) by Hieronymus. The publication of the species names in 1810 is presumably a result from Sieber's last shipment from Brazil, which arrived in 1809 (Stresemann 1950). This seems rather incredibly fast for the 19<sup>th</sup> century, but Hoffmannsegg had a network of keen and active collaborators in Europe who delivered determinations and accounts quickly after receiving specimens (Stresemann 1950). The other providers of Brazilian material sent specimens between 1801 and 1807. If the type specimen of *P. pungens* had been among them, it likely would have been published sooner. Also, these earlier shipments came from Bahia and Rio de Janeiro, from where *C. pungens* has only been erroneously reported, based on confusion with similar exindusiate species like *C. praecineta* (Kunze) Domin or *C. atrovirens* (Langsd. & Fisch.) Domin. We conclude that the location of the type of *Cyathea pungens* can be put rather confidently in the lower Amazonas region.

*Cyathea pungens* is widely distributed in the Amazonian lowland (Zuquim *et al.* 2008), and even with the narrower definition, *C. pungens* remains quite variable. Most specimens fall into a form with short stalked, asymmetrically based pinnules (including the type of the species) and a form with sessile,  $\pm$  symmetrical based pinnules (this can be tentatively aligned with the type of the synonym *Alsophila infesta*). The former seems to be more frequently encountered in eastern Amazonia-Guayana whereas the latter seems to be more dominant in western Amazonia and the Andean foothills; the map (Fig. 1), however, shows no clear regional clustering. Furthermore, small prematurely fertile plants that differ from regular mature plants in having no trunk and only pinnate-pinnatifid to partially bipinnate leaves can be found along the eastern distributional margin, where the tropical lowland rainforests border savannahs and cerrado vegetation, and in the Guayana region (Berry *et al.* 1995). A fourth morphotype seems to be restricted to open swamps; it is characterized by having small blades, short elongate pinnules with truncate bases and obtuse to short acute tips, and the scant squamules on the costules abaxially are mostly dark brown, all interpreted as adaptations to increased sun exposure; it still has stalked pinnae and often still visibly, albeit short-stalked pinnules. We dubbed these forms as “regular”, “sessile”, “precocious”, and “swamp”, respectively, but give them no taxonomic rank pending further study, preferably with molecular data included.

In the Caribbean region, including the Lesser Antilles, Trinidad & Tobago, Puerto Rico and Hispaniola, but not on Cuba or Jamaica, there is a variant of *C. pungens* with both pinnae and pinnules sessile (vs at least lower pinnae stalked in continental South America) but with the typical scant hair and pale squamules on the blades. At first glance, this form is in stark contrast with the Amazonian population and may merit formal recognition below species rank; in lack of an already published name, we refer to it simply as “Caribbean” *C. pungens* until further studies can clarify its exact status. It is not only found at lower elevations in swamps, which is a typical biotope for the species, but also in sinkholes in limestone areas.

We keep *C. rutenbergiae* from Puerto Rico (Tejedor & Areces-Berazain 2018, 2021) as separate from Caribbean *C. pungens* for now, although some of its distinguishing features (i.e., stalked pinnae and pinnules) also occur in continental *C. pungens*. Its bicolorous petiole scales and the pale laminar indument clearly align it with this species, but the branched fertile veins and the general pinnule shape (especially the truncate sinuses between the segments) of *C. rutenbergiae* are more reminiscent of *C. muricata* Willd. from the Lesser Antilles.

In the Caribbean, *Cyathea pungens* is less frequent than previous accounts suggested because of widespread confusion with *Cyathea aspera* (L.) Sw. and its segregates. The latter group is often identical in texture and dissection of the blade to the *C. pungens* group, but generally has concolorous plain brown to castaneous scales on petioles and blade (*C. pungens* has always some elements with whitish color, e.g., petiole scale margins and laminar squamules).

The central Brazilian specimen Windisch & Oliveira 6493 (US) has exceptionally wide pinnules to 25 mm across with forked fertile veins and medial sori. Regarding the indument and the stalked pinnae, it can be confidently put under *C. pungens* proper and none of the segregates here proposed, except maybe for *Cyathea rutenbergiae* (Tejedor & Areces-Berazain 2018).

Some collections from French Guiana (i.e., G. Cremers 6700, G. Cremers 7386) are plants of the regular type but have many short, stout hairs on costae and costules abaxially. Another collection from the same area (J.-J. de Granville *et al.* 9526) is slightly less hairy than these but still hairier than regular *C. pungens*, and also having dark, white tipped bullate squamules. Petiole scales are not preserved in this specimen, but the general pinnule shape strongly speaks for *C. pungens*. These aberrants may either constitute their own variant or their own unrecognized hybrid, though we do not have a suggestion for the potential other parent; an involvement of *Cyathea oblonga* would explain the squamule color but not the hairiness.

The specimen *Schunke Vigo & Graham 15500* from the Peruvian lowland is a very atypical plant of the “swamp” *Cyathea pungens*. Due to the small segments, the soral lines appear not to follow the margins in a zig-zag-pattern, as they should, but to be parallel to the midveins. Because of this, a smaller leaf at UC was determined as *C. werffii* by the first author, but the duplicate at F has a trunk and clearly surpasses the size of that species. *Cyathea werffii* from the Andean foothills of Ecuador and northern Peru is similar to precociously fertile *C. pungens*. Both species have been found growing closely together in northern Peru (Chiriaco, Dist. Baeza, Prov. Amazonas; Figs 1, 2A).

***Cyathea pycnocarpa* (Kunze) Domin**

Figs 11, 12A

*Cyathea pycnocarpa* (Kunze) Domin (Domin 1929a: 263). – *Alsophila pycnocarpa* Kunze (Kunze 1834: 97). – **Type:** PERU • Huánuco, Pampayacu; Jul. 1829; *E.F. Poeppig s.n.*; holotype: LZ [destroyed]; lectotype: B [B 20 0000124, labelled “*Poeppig 201*”]!, designated by Lehnert 2016.

*Alsophila pterorachis* Baker (Hooker & Baker 1874: 456). – *Cyathea pterorachis* (Baker) Domin (Domin 1929a: 263). – **Type:** PERU • San Martín, Tarapoto, “by rocky streams”; 1855–56; *R. Spruce 4717*; lectotype: K [K000227601]!, first step designated by Lehnert 2016, second step **designated here**; isolecotypes: B [B 20 0000362, fragment]!, NY [00148759, fragment of B] image!, US [00066280] image!.

**Etymology**

The specific epithet refers to the small size of the sori.

**Selected material studied**

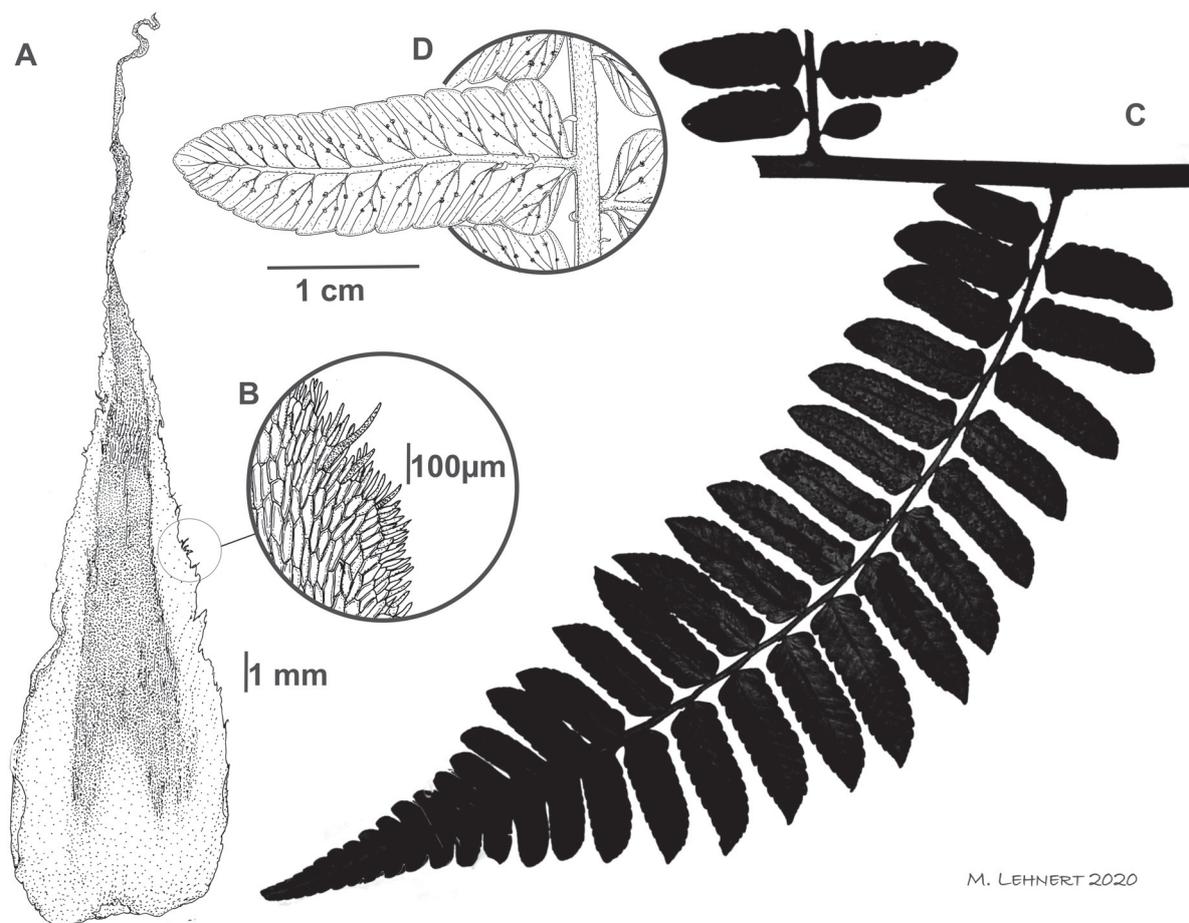
PERU – **San Martín** • San Martín, path up to the telephone antenna above Tarapoto, (Alto Ahuashiyacu), along Tarapoto; 6.45° S, 76.30° W; 1333 m a.s.l.; 10 Aug. 2002; *M.J.M. Christenhusz 2081*; GOET, TUR • “In m. Pingullu-Urku” [Cerro Pingulla?]; [ca 06.356° S, 76.689° W]; [ca 800–1500 m a.s.l.]; Aug. 1856; *R. Spruce 4715 forma pygmaea* [excluded syntypes of *Alsophila floribunda*]; P [P00642347, P00642348]. – **Cuzco** • Quispicanchi, Marcapata-Quinze Mil road, quebrada of tributary of Río Azara; 13°27.2' S, 70°54.5' W; 1570 m a.s.l.; 23 Oct. 2002; *M. Lehnert 458*; GOET, NY, UC, USM. – **Madre de Dios** • Prov. Manu, Parque Nacional Manu Rio Manu, Rio Sotileja; 11.67° S, 71.92° W; 400–500 m, 1 Oct. 1986; *R.B. Foster & B. d’Achille 11548*; US.

BOLIVIA – **La Paz** • Nor Yungas, PN Cotapata, a 600 m de la Estación Tunquini; 16.191° S, 67.869° W; 1690 m a.s.l.; 22 Aug. 1998; *A. Portugal, I. Jiménez & C. Rojas 221*; GOET, LPB, UC.

**Description**

Trunks absent or to 1.5(–3.0) m tall, slender, 6–7(–10) cm diam., straight to decumbent, with persistent old petiole bases, inermous to muricate; apices hidden between petioles; adventitious buds absent. Leaves to 150 cm long; weakly arching to strongly arching. Petioles to 55 cm long, inermous to sparsely muricate, prickles 1–2 mm long, dark yellowish brown to stramineous, sometimes basally darker brown; aerophores to 10 × 1 mm, inconspicuously brown in dried material, whitish in fresh material; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scales lanceolate, to 16 × 1.5–2.5(–3.0) mm, their tips straight, weakly twisted, concordantly to discordantly bicolorous, shiny medium to dark brown with whitish margins, scales in distal half of the petiole almost concolorous white except for brown spots near the base; colors only sharply contrasted in scales near petiole base and on crosiers; petiole scurf sparse tomentum of small branched hairs and dissected squamules 0.2–0.4 mm long, yellowish white with brown parts, grayish white in general aspect, easily abraded. Blades 80–95 × 45 cm, mostly bipinnate,

chartaceous; shiny dark green adaxially, often blackish when dried, olive-green abaxially; apices abruptly reduced to non-conform apical sections, sometimes very broad and almost gradually reduced. Rachises stramineous to yellowish brown on both sides, in basal half often with some scattered prickles less than 2 mm long; adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrous except for scurf remnants, containing a mix of appressed, white trichomoidia, dissected squamules (0.2–0.5 mm) and larger filiform scales to 20 mm long. Largest pinnae 23–39 cm long, pinnae 5–7 pairs per leaf, sessile or stalked to 1.5–2.5 cm, ascending, distally narrowly to broadly green alate, the distal segments sessile, adnate, the pinnatifid terminal section long decurrent into the costae. Costae inermous, to 1.5–2.0 mm wide, adaxially with antrorsely curved uniseriate hairs 0.5–1.0 mm long, abaxially glabrescent with scurf like on the rachises, insertions into rachises retaining larger, filiform scales from crozier, insertions abaxially weakly swollen, each with an inconspicuous planar pneumathodes, dark brown, elliptic, to  $2.0 \times 1.0$  mm, area around it often black in dried specimens. Largest pinnules (3.5–)5.2–7.8  $\times$  (1.0–)1.2 cm, sessile, articulate, alternate, 1.5 cm between the stalks, oblong-lanceolate to triangular-ovate, subentire to strongly crenate, incised to  $\frac{1}{3}$  of their width, bases truncate to weakly cuneate, tapering from beyond the middle to short acute to short attenuate tips; basal lobes pronounced to auricles; costules adaxially glabrous or with few hairs like on the costae, abaxially with ephemeral tan to light brown trichomoidia and mostly concolorous, tan to yellowish brown, flat and bullate squamules 0.5–1.0 mm long, with short subulate tips; costules basally with a black ring going all around their bases (abscission layer); segments not differentiated, outlined only by pinnate venation and short marginal lobes; veins weakly prominent



**Fig. 11.** *Cyathea pycnocarpa* (Kunze) Domin. **A.** Petiole with scurf and scales. **B.** Petiole scale from petiole base. **C.** Pinna, silhouette. **D.** Fertile pinnule, abaxially. (all from *Lehnert 458*, BONN)

abaxially and adaxially, lateral veins ending at lobe margins; midveins yellowish brown abaxially and adaxially, lateral veins yellowish to greenish brown or blackish; adaxially glabrous except for occasional single hairs on the midveins, abaxially without hairs, with squamules and trichomidia like on the costules; sterile and fertile veins simple. Sori 0.6–0.8(–1.0) mm diam., medial to subcostal, parallel to the midveins or in tight triangular lines, indusia absent; receptacles globose to ellipsoid, 0.2–0.3 mm diam.; paraphyses few, hyaline, white, shorter than sporangia (0.2–0.3 mm). Spores not examined.

### Distribution and ecology

Peru and western Bolivia at elevations of (400–)500–1690 m a.s.l., mostly in montane forests, observed along rocky creeks in shaded gullies (quebradas).

### Remarks

A relatively complete leaf of this species was included in the type material of *A. floribunda* (Spruce 4715 “forma pygmaea”; isotypes P00642347, P00642348). The type of *Alsophila pterorachis* (Spruce 4717) has serrate pinnule margins, which is atypical for *C. pycnocarpa*. It is placed here because of the matching overall appearance, pinnule shape and petiole scale morphology. Nevertheless, it may just represent a precociously fertile plant of a different, larger bipinnate-pinnatifid species.



**Fig. 12.** A. Original illustration of *Alsophila pycnocarpa* Kunze (Kunze 1846: tab. LXXXVI; CC0 1.0 Deed; <https://www.biodiversitylibrary.org/item/137895#page/429/mode/1up>), showing a whole leaf with characteristic pale indument on the leaf axes. B. Herbarium specimen of *Cyathea squamata* (Klotzsch) Domin, showing typical pinnule shape with distinct petiolule and cordate bases; whitish laminar squamules also discernable in digitized image (Cuatrecasas et al. 12585, F; © Field Museum of Natural History. CC BY-NC 4.0. <https://fm-digital-assets.fieldmuseum.org/1088/090/C0645972F.jpg> (accessed 27 Feb. 2025)).

With its overhanging leaves and subentire pinnules, *Cyathea pyncarpa* is a relatively distinct species in the Andes, but not well understood until now. It had been subsumed under either *Cyathea pungens* (because of the small sori and the general resemblance) or *C. dombeyi* (because of the presence of small brown teeth in the pale scale margins). The material was long interpreted as precociously fertile plants of *C. pungens* s. lat.

As fragmentary specimen, *Cyathea pyncarpa* bears a strong resemblance to the Brazilian *C. dichromatolepis*, where the pinnae are similarly coarsely dissected with entire pinnules and a large pinnatifid apical section. This Brazilian endemic has larger, wider petiole scales with broader white margins. It also reaches larger sizes than *C. pyncarpa*, which can already be deduced from the thickness of the petioles and leaf axes. In the field, both species are easily distinguished because *C. pyncarpa* has only 5–7 pinna pairs and blades with truncate bases whereas *C. dichromatolepis* can have twice the number of pinnae and blades with tapering bases.

*Foster & d'Achille 11548* (F, US) from Madre de Dios, Peru, is a very large specimen with most of the laminar indument relatively dark. Because of the dark squamules, it could be mistaken for *C. tortuosa*, but that species has white tortuous hairs on the blade abaxially and a dense villous hairs cover on the axes abaxially, which are both absent in this specimen.

### *Cyathea rutenbergiae* A. Tejedor & F. Areces

*Cyathea rutenbergiae* A. Tejedor & F. Areces [as *C. rutenbergii*] (Tejedor & Areces-Berazain 2018: 280).

– **Type:** PUERTO RICO • Río Grande, El Yunque National Forest, route 191, km 4.8; 18.338° N, 65.764° W; 210 m a.s.l.; 30 Jul. 2017; *F. Areces 1160*; holotype: UPRRP!, isotype: NY!.

### Etymology

The epithet honors Kathy Ruttenberg, US American artist and sculptor.

### Selected material studied

PUERTO RICO [USA] • Luquillo Mts., Rt 988 (Sabana Rd.); *D.S. Conant 4171 with J. DeCamp*; VT.

### Description (diagnostic characters)

Trunk to 2 m tall, 5–7 cm diam.; leaves to 190 cm long, ascending-arching, petioles to 60 cm long, petiole scales ovate-lanceolate, 10.0–15.0 × 4.0–5.0 mm, shiny, concordantly bicolorous brown with lighter translucent yellowish to cream margins, fragile, often abraded; blades to 90 × 70 cm; 6–7(–8) pinna pairs, basal ones strongly reflexed ca ½ the length of the longest pinnae; apices abruptly reduced. Pinnae to 45 cm long, ascending, stalked to 2.5 cm, alternate; pinnules to 12 × 2.5 cm, stalked to 4 mm, inarticulate, 2–3 cm between the stalks, elliptic-lanceolate, bases asymmetric, with a gap or missing segment on one side, tips attenuate with crenulate margins; costules green on both sides, abaxially strongly prominent, ridged, with sparse tortuous white hairs to 1 mm and flat, lanceolate whitish to beige squamules to 1.5 mm. Segments to 15 × 6 mm, basal segments strongly asymmetric, if slightly remote then connected by wide green wing; sinuses oblong to acute to 3.0 mm wide, never occluded; margins crenulate; midveins with few, tortuous, white hairs to 1 mm; veins simple or forked; sori submarginal. (Full description in Tejedor & Areces-Berazain 2018.)

### Distribution and ecology

Endemic to Puerto Rico, in the understory of perhumid rainforests.

## Remarks

Almost identical to the regular form of *Cyathea pungens* proper, but seems to have fewer pinna pairs per leaf, with basal pinnae not as much reduced as in *C. pungens* and larger pinnules (to 12 × 2.5 cm in *C. rutenbergiae* vs mostly 5–8 × 1.5–1.8 cm in *C. pungens*); due to the larger pinnules, also fertile veins are often forked (vs generally simple in *C. pungens*). Most notable are the blunt sinuses between the lowest segments of the largest pinnules; the very few samples of *C. pungens* that have pinnules wider than 2 cm still have acute sinuses between the lowest segments and not the blunt ones of *C. rutenbergiae*.

## *Cyathea squamata* (Klotzsch) Domin

Fig. 12B

*Cyathea squamata* (Klotzsch) Domin (Domin 1930: 160). – *Alsophila squamata* Klotzsch (Klotzsch 1845: 541). – **Type:** VENEZUELA • Distrito Federal, Caracas; *J. Moritz 218b*; lectotype: BR [BR0000006988319] image!, designated by Lehnert 2016; probable isoelectotypes [labelled “*J. Moritz*”]: B [B 20 000020920, B 20 0078702]!, NY [00148705] image!, P [P00642463, P00642464, P00642465, P00642466]!.

*Cyathea microphyllodes* Domin (Domin 1929a: 263), nom. nov. for *Alsophila microphylla* Klotzsch (Klotzsch 1844 [1845]: 541), not *Cyathea microphylla* Mett. (Mettenius 1856: 23, pl. 3 figs 1–6). – *Trichipteris microphylla* (Klotzsch) R.M.Tryon (Tryon 1970: 46). – **Type:** VENEZUELA • Distrito Federal; Caracas, *J. Moritz 110*; lectotype: B [B 20 0000208]!, **designated here**; isoelectotype: BR [BR0000006988319] image!.

*Alsophila caracasana* Klotzsch var. *fendleriana* Domin (Domin 1929b: 96). – **Type:** VENEZUELA • Aragua; Near Colonia Tovar, *A. Fendler 53*; lectotype: BR [BR0000006987985] image!, designated by Lehnert 2016; isoelectotypes: F [V0075843F] image!, GH [00020400, 00020401, 00020402, 00020403] image!, K? n.v., MO [MO-694350]!, NY!, US [1010709] image!, YU [YU.000669] image!.

## Etymology

The specific epithet refers to the scaly indument found on the leaves.

## Selected material studied

COLOMBIA – **Tolima** • Mariquita; 1200 m a.s.l.; Jan. 1848; *J.L. Linden 1021*; W. – **Cundinamarca** • La Palma, Murca valley, Cordillera de Helicon, 10 km SE of Gachalá; 2300 m a.s.l.; 30 Sep. 1944; *M.L. Grant 10322*; US. – **Norte de Santander** • Cordillera Oriental, region del Sarare, entre el Alto del Loro y el Alto de Santa Ines; 1800–2200 m a.s.l.; 18–21 Oct. 1941; *J. Cuatrecasas, R.E. Schultes & E. Smith 12513*; F, GH. – **Locality unknown** • *H. Karsten s.n.*; PRC.

VENEZUELA – **Aragua** • La Victoria-Colonia Tovar rd., 11.5 km N of Pie de Cerro; 10°22' N, 67°20' W; 1950 m a.s.l.; 14 Jan. 1982; *J. Luteyn, S. Mori, N. Holmgren & J.A. Steyermark 8247*; NY. – **Distrito Federal** • Cerro El Avila, S slopes; 10°32.6' N, 66°52.5' W; 2000–2050 m a.s.l.; 11 Nov. 1991; *W. Meier 902*; UC. – **Mérida** • Near summit of Cerro San Isidro, above La Carbonera; 2430–2745 m a.s.l.; 22 Apr. 1944; *J.A. Steyermark 56029*; GH, US. – **Miranda** • headwaters of the Quebrada Chacaito; 10°33' N, 66°52' W; 1990 m a.s.l.; 28 Feb. 1992; *W. Meier 1763*; UC. – **Vargas** • Monumento Natural Pico Codazzi, road Colonia Tovar-La Victoria, sector Matalpo, road Los Colonos-Pto. Cruz, 2.5 km behind Arco, SE of tourist center Villa Bahareque border with Edo. Aragua; 10°26' N, 67°13.5' W; 1850–1950 m a.s.l.; 5 Aug. 1999; *J. Mostacero & R. Castillo 261*; UC. – **Yaracuy** • Nirgua, Cerro Azul (Tucuragua), near

the limit with Edo. Cojedes, mainly of peak S of Hacienda Venezolano; 9°59' N, 68°37' W; 1400–1690 m a.s.l.; 24 Jan. 1999; *W. Meier & O. Kunert 4591*; UC.

TRINIDAD & TOBAGO – **Trinidad** • Port of Spain; [ca 10°40'32" N, 61°29'27" W]; Apr. 1874; *C.E.O. Kuntze 1684*; NY.

### Description

Trunks 0.1–3.0 m tall, 5–7 cm diam., presumably covered with old petiole bases, due to these generally spiny; apices hidden between petiole bases; without adventitious buds. Leaves 120–200 cm long. Petioles 20–40 cm long, muricate to weakly aculeate with prickles to 2 mm long, dark brown to blackish, rarely dark stramineous, opaque, basally with persistent scurf consisting of appressed reddish brown trichomidia and erect, white, lanceolate to ovate squamules to 1 mm long with subentire to erose margins; hairs absent; petioles basally with a discontinuous line of distant aerophores to  $6.0 \times 1.0$  mm on each side, gray brown and inconspicuous in dried material. Petiole scales long lanceolate, to  $15.0\text{--}25.0 \times (1.5\text{--})2.0\text{--}3.5\text{--}(4.0)$  mm, rather thin textured, bases cordate, pseudopeltately attached, apices long attenuate, straight to falcate, often strongly undulate; proximal scales concordantly to discordantly bicolorous, auburn to yellowish brown with white margins, distal ones often almost concolorous stramineous to white with a dark apical streak; differentiated margins without setae or teeth, usually persistent. Blades to  $180 \times 120\text{--}140$  cm, bipinnate-pinnatifid, firm herbaceous, matte, dark-green adaxially, dark olive green abaxially; apices gradually reduced. Rachises inermous to sparsely verrucate proximally, dark brown abaxially and adaxially; pubescent with tan to brown multicellular hairs 1.0–1.5 mm long, antrorsely curved and persistent adaxially, abaxially glabrescent with few thin hairs and appressed trichomidia, leaving the cortex smooth. Largest pinnae 24–40 cm long, pinnae sessile or stalked to 1.0(–1.7) cm, 15–20 pairs per leaf, patent to weakly ascending, alternate, inarticulate, distally narrowly green-alate, distal segments simply adnate before ending in a pinnatifid apical section; basal pairs smaller than than the medial pinnae, reflexed. Costae to 1.5–2.0 mm wide, inermous to sparsely verrucate, dark brown to grayish brown abaxially, darker adaxially; glabrous abaxially, with tan to brown, antrorsely curved multicellular hairs 0.5–1.0 mm long adaxially; junctures of costae and rachises not swollen, abaxially often black when dried, each with an inconspicuous planar, elliptic aerophore, to  $2 \times 1$  mm, dark orange-brown. Largest pinnules  $45\text{--}70 \times 11\text{--}17$  mm, short-stalked to 3 mm, inarticulate, 1.5–2.0(–2.2) cm between the stalks/costules, pinnules lanceolate, rarely linear-oblong, truncate to cordate basally, long-acute to attenuate apically with subentire to weakly crenulate margins; costules dark carnose to dark grayish brown adaxially and abaxially, proximally often darker brown; adaxially strongly prominent, ridged, and densely hairy with tan to brown, antrorsely curved multicellular hairs to 1.0 mm long, abaxially weakly prominent, glabrous or glabrescent with appressed, tan to brown unicellular trichomidia and thin tortuous hairs; also with white to brown squamules, bullate ones to 1.0 mm long, flat lanceolate ones to  $3 \times 2$  mm, with entire margins and short-attenuate tips; costules basally without pneumathodes. Segments to  $7.0\text{--}10.0 \times 3.0\text{--}4.0$  mm, rarely remote and then connected by laminar tissue, patent to strongly ascending, distally falcate, tips obtuse to rounded, proximal segments alternate to subopposite, usually a bit shorter than following segments; sinuses acute to obtuse, to 1.0(–2.0) mm wide; margins subentire to crenate; margins not differently incised in proximal segments of a pinnule; veins planar on both sides or weakly protruding adaxially, dark carnose to dark grayish brown; veins adaxially glabrous except for some multicellular hairs to 0.5 mm long on the midveins, abaxially glabrous except for some appressed trichomidia; midveins with some pure white to light brown squamules, mostly bullate ones to  $1.0 \times 0.5$  mm; sterile and fertile veins simple or forked. Sori 1.0–1.2 mm diam., medial to supramedial, indusia lacking; receptacles globose, 0.3–0.4 mm diam., paraphyses few to numerous, stiff, hyaline, tan to brown, shorter than the sporangia (0.2–0.3 mm long). Spores tetrahedral-globose, pale yellow to white, appearing hyaline.

### Distribution and ecology

Magdalena Valley and Cordillera Oriental of Colombia, Cordillera de la Costa in Venezuela at elevations of 1200–2430(–2740) m a.s.l.; one sterile specimen recorded from Trinidad (Barrington 1978).

### Remarks

*Cyathea squamata* has only rarely been confused with *C. pungens*, despite sharing the diagnostic characters of being exindusiate, having bicolorous brown petiole scales with white margins, and whitish bullate squamules on the blade. *Cyathea squamata* differs in having more pinna pairs per blade, generally smaller pinnules with notable short stalks and cordate bases, by which means the blade appears more delicate and finely dissected than in *C. pungens*. Moreover, *C. squamata* has a mixture of larger and smaller squamules on the axes and veins abaxially, giving it an untidy appearance, whereas the squamules in *C. pungens* are so small and scarce that they are hardly noticeable.

### *Cyathea werffii* R.C.Moran

Fig. 13

*Cyathea werffii* R.C.Moran (Moran 1991: 94, fig.5). – **Type:** ECUADOR • Morona-Santiago, along new road Mendez-Morona, km 55–62; 800 m a.s.l.; 23 Aug. 1989; *H. van der Werff & E. Gudiño 11386*; holotype: MO [MO-288184]!; isotypes: AAU!, QCNE [QCNE-179]!, UC [UC1564628]!.

### Etymology

The specific epithet honors Henk van der Werff, botanist at the Missouri Botanical Garden and collector of the type specimen.

### Selected material studied

COLOMBIA – **Caquetá** • Municipio de Belén de los Andaquies, Parque Natural Municipal Andaqui, cerro de Aguacata y flanco oriental hacia el sector La Mina; 1°39'17.5" N, 75°54'29.1" W; 1200–1450 m a.s.l.; *N. Castaño-A. et al. 9197*; COAH. – **Putomayo** • Municipio de Orito, Santuario de Flora de Plantas Medicinales Ingi-Andé (Nuestra Tierra); 0°41'06.2" N, 77°03'07.89" W; 944 m a.s.l.; 26 Sep. 2015; *W.D. Rodríguez, D. Cárdenas, N. Marin & J. Restrepo 9354*; COAH.

ECUADOR – **Morona-Santiago** • Along road between Santiago and Río Morona; 2°58'24" S, 77°49'36" W; 322 m a.s.l.; 10 Jul. 2004; *T.B. Croat et al. 90750*; MO • Comunidad Shuar de Mutints, faldas orientales de la Cordillera de Cutucú; 2°11' S, 77°44' W; 600 m a.s.l.; 10 Sep. 1995; *H. Navarrete 1214*; AAU, QCA • Comunidad Shuar de Mutints, faldas orientales de la Cordillera de Cutucú; 2°11' S, 77°44' W; 600 m a.s.l.; 10 Sep. 1995; *H. Navarrete 1248*; AAU, QCA • Road 3.8 km N of Santa Susana de Chiviasa (NE of Limón); 2°50' S, 78°23' W; 1380 m a.s.l.; 19 Mar. 1997; *B. Øllgaard & H. Navarrete 2506*; AAU, QCA • Road Patuca-Santiago, km 23 from Santiago; 3°01' S, 78°10' W; 830 m a.s.l.; 19 Mar. 1997; *B. Øllgaard & H. Navarrete 2492*; AAU, QCA.

PERU – **Amazonas** • Prov. Bagua, ca 40–43 km (by road) NE of Chiriaco; [1050–2400 ft a.s.l.]; 7 Nov. 1978; *P.J. Barbour 4516*; US, USM • Puerto Nazareth, 25 kms – Olmos; 540 m a.s.l.; 22 Dec. 1970; *H. Ellenberg 3489*; GOET, UC. – **Ucayali** • Prov. Coronel Portillo [Aguaytia], Rio Chino near Sinchono, between Tingo Maria and Pucallpa; [ca 9°08'30" S 75°46' W]; 1400 m a.s.l.; 2 Aug. 1948; *P. Aguilar 904*; F.

### Description

Trunkless, or trunk to 0.3 m tall, with old petiole bases, 2–4 cm diam., without adventitious shoots. Leaves erect, to 120(–140) cm long. Petioles 35–70 cm (ca 1/3–1/2 the leaf length), inermous to sparingly muricate,

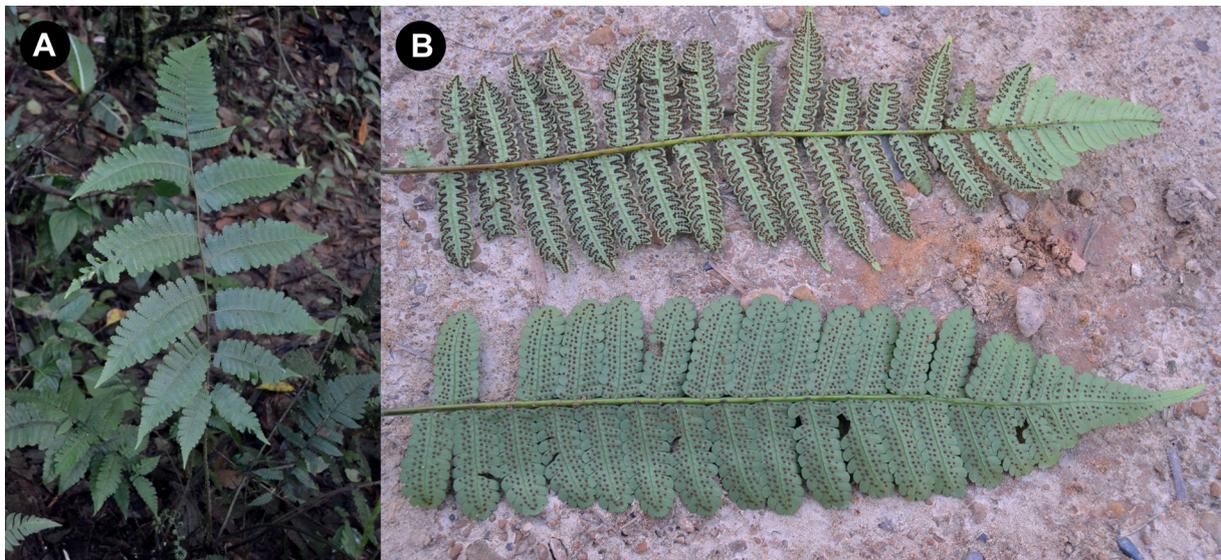
dark brown to blackish at base, green in upper parts, drying to medium brown to yellowish brown; scurf absent to scant, with ephemeral, dust-like white squamellae. Petiole scales narrowly lanceolate, 3–7 × 1–2 mm, discordantly bicolorous, castaneous to brown with whitish margins, erose with some darker cells interspersed. Blades to 50(–100) × 60(–80) cm, obovate-elliptic, with 4–7 pinna pairs (in fully bipinnate-pinnatifid leaves, 15–20 pairs in simply pinnate leaves); apex abruptly reduced. Leaf axes inermous, abaxially with short hairs 0.2–0.4 mm long, scant ephemeral squamules, and small bicolorous lanceolate scales; costae green alate throughout. Largest pinnae 31(–40) × 9(–13) cm, notably stalked by 1–2.5 cm in lower half, sessile in upper parts; basal pinnae ca ½ the length of longest pinnae, stalked by 3 cm, weakly reflexed. Pinnules to 25(–62) × 12(–17) mm, elongate to oblong, smaller ones subentire, largest ones lobed more than half way (to 4 mm) to the costa; bases truncate, tips round to truncate (rarely attenuate in largest pinnules). Costules abaxially with dark brown spot at the base, with hairs like on the costae, with few to many dark brown bullate squamules to 1.0 mm long. Segments/lobes with entire margins, rounded tips. Veins without hairs, or stronger veins adaxially with single translucent or white hairs; sterile and fertile veins simple in bipinnate parts, also forked in simply pinnate parts. Sori ca 1.2 mm diam., ± medial, forming lines across the segments parallel to costules; receptacles ca 0.2 mm diam., paraphyses few, shorter than sporangia.

### Distribution and ecology

Southern Colombia, Ecuador and northern Peru (Fig. 2A) at elevations of 150–1400 m a.s.l., in deeply shaded forest on steep rocky slopes.

### Remarks

The blades of *Cyathea werffii* vary greatly between being pinnate-pinnatifid to fully bipinnate with slightly oblanceolate, blunt-tipped pinnules with entire to coarsely lobed margins. In the general variation of plant size and blade dissection, it comes close to *C. pycnocarpa*, with which it also shares comparatively small but abundant petiole scales that may have some darker cells in the white margins. *Cyathea pycnocarpa* differs in having lanceolate to weakly hastate pinnules (i.e., widest at the base and gradually tapering to an acute tip), the blade is basally truncate with the lowest pinnae patent and barely smaller than the



**Fig. 13.** *Cyathea werffii* R.C.Moran in the field (Chiriaco, Prov. Bagua, Dept. Amazonas, Peru). **A.** Plant with upright fully bipinnate-pinnatifid leaves; note smaller and less dissected leaves left and right coming from the same rhizome. **B.** Comparison of soral lines of *C. werffii* (bottom) with “sessile” *C. pungens* (Willd.) Domin. Note the characteristic darkened spots at the base of the costules in both species. (photos © M. Lehnert)

longest pinnae (vs blades obovate-elliptic with the lowest pinnae smaller and reflexed in *C. werffii*) and the blade apex gradually reduced (vs abruptly reduced). Having seen both species in the field, we can further add that the scaly indument of the axes and veins abaxially tends to be more evident and appear more whitish in *C. pycnocarpa* than in *C. werffii*. The laminar texture is thicker and heavier in the former species than in the latter, thus the leaves are arching in *C. pycnocarpa* and held upright in *C. werffii* (Fig. 13A), presumably forming a funnel-shape in larger plants.

The occurrence in Colombia (Cárdenas *et al.* 2019) is only supported by aberrantly large specimens which look more like plants of *C. tortuosa* but with bicolorous petiole scales (vs concolorous in *C. tortuosa*) and notably stalked pinnae (vs mostly sessile or nearly so). These plants could also be a local variant of *C. pastazensis*, whose small stature with long stalked pinnae may be an adaptation to the very shady locations where they were found.

The range of *C. werffii* is sometimes reported to reach southern Peru, but as far as we can confirm, these seem to base on erroneous determinations (also by the first author) of premature plants of other species, like *C. pungens* and *C. tortuosa*. We observed *Cyathea werffii* together with both species at the paratype location in Chiriaco, Bagua, northern Peru (Ellenberg 3489), which allowed us to distinguish between them more clearly (Fig. 13).

Regarding the general size and shape of the pinnules, the soral line pattern, and composition and color combination of the fine indument, *Cyathea werffii* is practically identical to *C. oblonga* from the Guyana highlands, but that species has more numerous and persistent petiole scales that usually reach the lower half of the rachis, only sessile pinnae, and more pinna pairs per leaf (10–12 in *C. oblonga* vs 4–7 in *C. werffii*). The similarity may base merely on convergence, but a closer relationship between these two disjunct taxa is also possible, as the Amotape-Huancabamba-zone, where *C. werffii* is endemic to (Fig. 2A), has many biogeographic ties with the Guayana highlands (Lehnert & Tejedor 2016).

## Discussion

All species here newly separated should be regarded as working hypotheses to be tested further in the field and in the lab. We abstain from describing new taxa because the risk of creating redundant names is very high in the family Cyatheaceae. The geographical concentration of some variants (e.g., hairy *C. pungens* in Guyana, and the sessile pinnulate individuals in western Amazonia) may be indicative of active speciation and species introgression, and should be a valuable target for population genetic studies.

In particular, we observe a prevalence of the brown laminar squamules in the *C. pungens* complex where there is contact with superficially similar species (i.e., with exindusiate sori and not notably hairy on the blades) that generally have concolorous brown scales and laminar squamules. These species are geographically centered in Mesoamerica, i.e., *C. schiedeana* (C.Presl) Domin, *C. wendlandii* (Kuhn) Domin, and *C. darienensis* R.C.Moran (Lehnert 2016) and the Chocó-Esmeraldas region of the western Andean slopes, i.e., *C. catenata* Lehnert, F.Giraldo & W.D.Rodr., *C. kessleriana* Lehnert, F.Giraldo & A.Tejedor, *C. pholidota* Lehnert, F.Giraldo & A.Tejedor (Lehnert *et al.* 2019), and *C. brunnescens* (Barrington) R.C.Moran (Moran 1991). This geographic overlap may be indicative of some introgression or ancestral hybridization with the *C. pungens* complex leading to the morphotaxa with darker laminar squamules like *C. pastazensis*, *C. klotzschiana* or “swamp” *C. pungens*.

## Acknowledgments

We thank our colleagues Gloria Calatayud, Fabiola Areces, Ellúz Huaman, and Anna Weigand for their company and help in the field. For organisatorial assistance, we kindly thank Franklin Axelrod in Puerto Rico, Katya Romoleroux in Ecuador, Asunción Cano and Blanca León in Peru, María José Sanín and

Dairon Cárdenas in Colombia. Collection permits were kindly issued by the Ministerio del Ambiente Ecuador (N° 036-2014-FLO-DP/MAE), INRENA Peru (Resolución Directoral N° 0449-2010-DGFFS-DGEFFS) and Ministerio de Ambiente y Desarrollo Sostenible Colombia (Resolución 0790 - Permiso Marco de Recolección). Field trips that contributed to our findings were financed through the German Science Foundation (DFG; grant LE 1826/4) and the research project POPCORN (Using Population genomics, Phylogenetics, and Community Ecology for understanding Radiations in Neotropical mountains) funded by the Swiss National Fund (grant SNF-310030L\_146906 and 147630).

## References

- Allaire J.J. 2012. UseR! The R User Conference (useR! 2011) held on August 16-18 2011 at the University of Warwick in Coventry, UK. Book of contributed abstracts, compiled 28 Aug 2011. Available from <https://de.scribd.com/document/649443739/Allaire-2012> [accessed 7 Apr. 2025].
- Barrington D.S. 1976. New taxa and nomenclatural changes in the genus *Trichipteris* (Cyatheaceae). *Rhodora* 78 (813): 1–5. Available from <https://www.jstor.org/stable/23311305> [accessed 26 Feb. 2025].
- Barrington D.S. 1978. A revision of the genus *Trichipteris*. *Contributions from the Gray Herbarium of Harvard University* 208: 3–93. <https://doi.org/10.5962/p.336446>
- Berry P.E., Holst B.K. & Yatskievych K. 1995. Introduction. In: Berry P.E., Holst B.K. & Yatskievych K. (eds) *Flora of the Venezuelan Guayana, Introduction, Vol 1*: xv–xx. Missouri Botanical Garden Press, St. Louis.
- Cárdenas D., Rodríguez W.D., García N., Sua S., Lehnert M. & Giraldo F. 2019. *Libro Rojo de Plantas de Colombia Vol. 7. Helechos Arborescentes*. Instituto Amazónico de Investigaciones Científicas SINCHI, Bogotá.
- Carvalho F.A., Salino A. & Zartman C.E. 2012. New country and regional records from the Brazilian side of Neblina Massif. *American Fern Journal* 102: 228–232. <https://doi.org/10.1640/0002-8444-102.3.228>
- Cremers G. & Boudrie M. 2007. Les Ptéridophytes des Guyanes: les spécimens de référence depuis Aublet (1775) à nos jours. *Le Journal de Botanique* 40: 3–111. <https://doi.org/10.3406/jobot.2007.2039>
- Cronquist A., Takhtajan. A. & Zimmermann W. 1966. On the higher taxa of Embryobionta. *Taxon* 15: 129–134. <https://doi.org/10.2307/1217531>
- Desvaux N.A. 1827. Prodrome de la famille des fougères. *Mémoires de la Société Linnéenne de Paris* 6: 171–337.
- Domin C. 1929a. *Pteridophyta. Soustavný přehled žijících i vyhynulých kaprod'orostů*. Česká akademie věd a umění, Prague.
- Domin C. 1929b. *The Pteridophyta of the Island of Dominica, With Notes on Various Ferns from Tropical America*. Rozpravy Královské české společnosti nauk, Třída matematicko-přírodovědecká, Nová řada, číslo 2 / Memoirs of the Royal Czech Society of Sciences, Division of Natural History and Mathematics, New Series, No. 2., Dr Ed. Grégr. & Son, Prague.
- Domin C. 1929c. New ferns from Tropical America and the West Indies. *Bulletin of Miscellaneous Information (Royal Gardens, Kew)* 7: 215–222. <https://doi.org/10.2307/4113535>
- Domin C. 1930. The species of the genus *Cyathea* J.E.Sm. *Acta Botanica Bohemica* 9: 85–174.
- Farwell O.A. 1931. Fern Notes II. Ferns in the Herbarium of Parke, Davis & co. *American Midland Naturalist* 12: 231–311. <https://doi.org/10.2307/2420088>
- Hieronymus G.H.E.W. 1906. Plantae Stübelianae. Pteridophyta. *Hedwigia* 45: 215–232.

- Hooker W.J. & Baker J.G. 1874. *Synopsis Filicum*, 2<sup>nd</sup> Ed. R. Hardwicke, London. Available from <http://biodiversitylibrary.org/page/28796458> [accessed 26 Feb. 2025].
- Kaulfuss G.F. 1827. *Das Wesen der Farrenkräuter: besonders ihrer Fruchtheile zugleich mit Rücksicht auf systematische Anordnung betrachtet und mit einer Darstellung der Entwicklung der Pteris serrulata aus dem Samen begleitet. Erste Hälfte (Vol. 1)*. C. Cnobloch, Leipzig.
- Klotzsch J.F. 1844. Beiträge zu einer Flora der Aequinoctial-gegenden der neuen Welt. Filices. *Linnaea* 18: 516–556.
- Klotzsch J.F. 1847. Beiträge zu einer Flora der Aequinoctial-gegenden der neuen Welt. Filices. *Linnaea* 20: 337–445.
- Klotzsch J.F. 1852. Einige neue Baumfarn. *Allgemeine Gartenzeitung (Otto & Dietrich)* 30: 41–43.
- Kunze G. 1834. Synopsis plantarum cryptogamicarum ab Eduardo Poeppig in Cuba insaula et America meridionali collectarum. *Linnaea* 9: 1–111. <https://doi.org/10.5962/bhl.title.51054>
- Kunze G. 1839. Centuria Quarta. *Flora* 22 (1, Beibl.): 1–64.
- Kunze G. 1846. *Die Farrnkräuter in kolorirten Abbildungen naturgetreu erläutert und beschrieben, 1. Band, Taf. 81–90*. E. Fleischer, Leipzig. <https://doi.org/10.5962/bhl.title.69313>
- Lehnert M. 2008. On the identification of *Cyathea pallescens* (Sodi) Domin: typifications, reinstatements and new descriptions of Neotropical tree ferns. *Botanical Journal of the Linnean Society* 158 (4): 621–649. <https://doi.org/10.1111/j.1095-8339.2008.00887.x>
- Lehnert M. 2009. Resolving the *Cyathea caracasana* complex. *Stuttgarter Beiträge für Naturkunde A, Neue Serie* 2: 409–445. Available from [https://www.zobodat.at/pdf/Stuttgarter-Beitraege-Naturkunde\\_NS\\_2\\_A\\_0409-0445.pdf](https://www.zobodat.at/pdf/Stuttgarter-Beitraege-Naturkunde_NS_2_A_0409-0445.pdf) [accessed 26 Feb. 2025].
- Lehnert M. 2011. Species of *Cyathea* in America related to the western Pacific species *C. decurrens*. *Phytotaxa* 26: 39–59. <https://doi.org/10.11646/phytotaxa.26.1.6>
- Lehnert M. 2014. Do you know *Cyathea divergens* (Cyatheaceae-Polypodiopsida)? *Phytotaxa* 161 (1): 1–42. <https://doi.org/10.11646/phytotaxa.161.1.1>
- Lehnert M. 2016. A synopsis of the exindusiate species of *Cyathea* (Cyatheaceae-Polypodiopsida) with bipinnate-pinnatifid or more complex fronds, with a revision of the *C. lasiosora* complex. *Phytotaxa* 243 (1): 1–53. <https://doi.org/10.11646/phytotaxa.243.1.1>
- Lehnert M. & Coritico F.P. 2018. The genus *Dicksonia* (Dicksoniaceae-Cyatheaales) in western Malesia. *Blumea – Biodiversity, Evolution and Biogeography of Plants* 63 (3): 268–278. <https://doi.org/10.3767/blumea.2018.63.03.02>
- Lehnert M. & Cámara-Leret R. 2018. *Dicksonia utteridgei*, a new species of hairy tree fern (Dicksoniaceae-Cyatheaales) from New Guinea. *Blumea – Biodiversity, Evolution and Biogeography of Plants* 63 (2): 140–143. <https://doi.org/10.3767/blumea.2018.63.02.09>
- Lehnert M. & Cámara-Leret R. 2019. New species of scaly tree ferns (Cyatheaceae) from New Guinea, and new combinations for the family for Malesia. *Kew Bulletin* 74: 46. <https://doi.org/10.1007/s12225-019-9823-4>
- Lehnert M. & Tejedor A. 2016. Three new scaly tree fern species (*Cyathea*-Cyatheaceae) from the Amotape-Huancabamba Zone. *American Fern Journal* 106 (3): 175–190. <https://doi.org/10.1640/AFJ-D-16-00002.1>
- Lehnert M. & Weigand A. 2013. A proposal to distinguish several taxa in the Brazilian tree fern *Cyathea corcovadensis* (Cyatheaceae). *Phytotaxa* 155 (1): 35–49. <https://doi.org/10.11646/phytotaxa.155.1.3>

- Lehnert M. & Weigand A. 2017. A synopsis of the Neotropical species of *Cyathea* (Cyatheaceae; Polypodiopsida) with bipinnate fronds. *Brittonia* 69: 71–90. <https://doi.org/10.1007/s12228-016-9445-1>
- Lehnert M., Rodríguez Duque W.D., Giraldo Gallego L.F. & Tejedor A. 2021. The scaly tree ferns allied to *Cyathea multiflora* (Cyatheaceae) in Colombia and neighboring countries. *American Fern Journal* 111 (4): 251–307. <https://doi.org/10.1640/0002-8444-111.4.251>
- Lellinger D.B. 1987 [1988]. The disposition of *Trichopteris* (Cyatheaceae). *American Fern Journal* 77 (3): 90–94. <https://doi.org/10.2307/1547497>
- Lellinger D.B. 2002. A modern multilingual glossary for taxonomic pteridology. *Pteridologia* 3: 1–264. <https://doi.org/10.5962/bhl.title.124209>
- Leunis J. 1877. *Synopsis der Pflanzenkunde (Ed. 2) 3. Spezielle Botanik, Kryptogamen*. Hahn, Hannover.
- Loiseau O., Weigand A., Noben S., Rolland J., Silvestro D., Kessler M., Lehnert M. & Salamin N. 2019. Slowly but surely: gradual diversification and phenotypic evolution in hyper-diverse tree fern family Cyatheaceae. *Annals of Botany* 125 (1): 93–103. <https://doi.org/10.1093/aob/mcz145>
- Maxon W.R. 1925. New Tropical American ferns: II. *American Fern Journal* 15 (2): 54–57. <https://doi.org/10.2307/1544002>
- Mettenius G. 1856. In: Hohenacker R.F. (ed.) *Filices Lechlerianae, chilenses ac peruanae (Vol. 1)*. L. Voss, Leipzig.
- Moran R.C. 1991. Eight new species of tree ferns (*Cyathea*, Cyatheaceae) from the American tropics and three new combinations. *Novon* 1 (2): 88–104. <https://doi.org/10.2307/3391634>
- Noben S. & Lehnert M. 2013. The genus *Dicksonia* (Dicksoniaceae) in the western Pacific. *Phytotaxa* 155 (1): 23–34. <https://doi.org/10.11646/phytotaxa.155.1.2>
- PPG 1. 2016. Pteridophyte Phylogeny Group. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* 54 (6): 563–603. <https://doi.org/10.1111/jse.12229>
- Presl C. 1836. *Tentamen Pteridographiae*. A. Haase, Prague.
- Presl C. 1851 [1849]. *Epimeliae Botanicae*. A. Haase, Prague.
- Rosenstock E. 1917. Filices palaeotropicae novae Herbarii Lugduno-Batavi. *Mededeelingen van 's Rijks-Herbarium. Leiden* 31: 1–8. Available from <https://repository.naturalis.nl/pub/508337/MRHL1917031001001.pdf> [accessed 26 Feb. 2025].
- Rosenstock E. 1928. Filices novae a cl. Dr. O. Buchtien in Bolivia collectae. VI. *Repertorium Specierum Novarum Regni Vegetabilis* 25 (4–6): 56–64. <https://doi.org/10.1002/fedr.19280250408>
- Schwartsburd P.B., Becari-Viana I., Lopes L.R. & Lehnert M. 2015. A new hybrid and further taxonomic notes on Brazilian tree ferns (Cyatheaceae). *Phytotaxa* 231 (1): 42–52. <https://doi.org/10.11646/phytotaxa.231.1.4>
- Smith A.R. 1990. Pteridophytes of the Venezuelan Guayana: new species. *Annals of the Missouri Botanical Garden* 77 (2): 249–273. <https://doi.org/10.2307/2399539>
- Smith J.E. 1793. Tentament botanicum de filicum generibus dorsiferarum. *Mémoires de l'Academie royale des Sciences (Turin)* 5 (2): 401–422. Available from <http://onlinebooks.library.upenn.edu/webbin/gutbook/lookup?num=39534> [accessed 7 Apr. 2025].
- Splitgerber F.L. 1840. Enumeratio Filicum et Lycopodiacearum quas in Surinamo legit Splitgerber. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie* 7: 391–444.
- Stresemann E. 1950. Die brasilianischen Vogelsammlungen des Grafen von Hoffmannsegg aus den Jahren 1800–1812. *Bonner Zoologische Beiträge* 1:43–51. Available from <https://zoologicalbulletin.de/>

BzB\_Volumes/Volume\_01\_2\_3\_4/126\_143\_BZB01\_2\_3\_4\_Stresemann\_Erwin.PDF [accessed 26 Feb. 2025].

Tejedor A. & Calatayud G. 2017. Eleven new scaly tree ferns (*Cyathea*: Cyatheaceae) from Peru. *American Fern Journal* 107 (3): 156–191. <https://doi.org/10.1640/0002-8444-107.3.156>

Tejedor A. & Areces-Berazain F. 2018. *Cyathea rutenbergii*, a new tree fern (Cyatheaceae, Polypodiopsida) from Puerto Rico. *Phytotaxa* 336 (3): 279–285. <https://doi.org/10.11646/phytotaxa.336.3.6>

Tejedor A. & Areces-Berazain F. 2021. An update on the distribution and affinities of *Cyathea rutenbergii* (Cyatheaceae, Polypodiopsida). *Phytotaxa* 516 (1):108–110. <https://doi.org/10.11646/phytotaxa.516.1.9>

Thiers B. 2024 (continuously updated). *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff*. New York Botanical Garden’s Virtual Herbarium. Available from <https://sweetgum.nybg.org/science/ih/> [accessed 7 Jun. 2022].

Tryon R.M. 1970. The classification of the Cyatheaceae. *Contributions from the Gray Herbarium of Harvard University* 200: 3–53. <https://doi.org/10.5962/p.336422>

Willdenow C.L. 1810. *Species Plantarum, Ed. 4*. G.C. Nauk, Berlin.

Zuquim G., Costa F.R.C., Prado J. & Tuomisto H. 2008. *Guide to the Ferns and Lycophytes of REBIO Uatumã, Central Amazonia*. Instituto Nacional de Pesquisas da Amazonia, Manaus.

*Manuscript received: 29 February 2024*

*Manuscript accepted: 4 November 2024*

*Published on: 23 April 2025*

*Topic editor: Frederik Leliaert*

*Desk editor: Radka Rosenbaumová*

Printed versions of all papers are deposited in the libraries of four of the institutes that are members of the *EJT* consortium: Muséum national d’Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

## Appendix 1

### List of revised taxa

Group of *Cyathea pungens*:

- (1) *Cyathea dombeyi*
- (2) *Cyathea floribunda*
- (3) *Cyathea klotzschiana*
- (4) *Cyathea neblinae*
- (5) *Cyathea oblonga*
- (6) *Cyathea pastazensis*
- (7) *Cyathea praecincta*
- (8) *Cyathea pungens*
  - a. “regular”
  - b. “sessile”
  - c. “Caribbean”
  - d. “precocious”
  - e. “swamp”
  - f. “hairy/hybrid”
- (9) *Cyathea pycnocarpa*
- (10) *Cyathea rutenbergiae*
- (11) *Cyathea squamata*
- (12) *Cyathea werffii*

### List of exsiccatae

Specimens are ordered after the first collector; herbarium codes are added when collections are mixed gatherings or collection numbers are missing.

- Abbott, W.L. 347 (8c), 411 (8c), 424 (8c), 611 (8c), 1124 (8c), 1337 (8c), 1409 (8c), 1508 (8d), 1580 (8d), 2030 (8c).
- Acebey, A. 473 (8b), 518 (8b).
- Aguilar, P. 904 (12).
- Aguinda, R. 345 (8a), 1302 (6),  
[with R.B. Foster, M. Metz, T. Theim] 805 (8b).
- Aldridge, J. s.n. [NY 4004073] (8c).
- Alfonso, R. 427 (8a), 428 (8a), 498 (8a), 589 (8b).
- Alston, A.H.G. 5790 (3), 6278 (3), 6279 (3), 7554 (8d).
- Altamirano, S. [with J.P. Altamirano] 2339 (8b).
- Anderson, W.R. 12236 (8a).
- Anonymous 161 (8c), Herb. Willdenow 19717 (8a), s.n. [F C0645964F] (3), s.n. [F C0645992F] (5), s.n. [MO-3304121] (3), s.n. [NY 4004055] (8c), s.n. [NY 4004076] (8c), s.n. [NY 4004072] (8c).
- Araujo-Murakami, A. [with A.S. Poma C., A. Palabral] 883 (8a).
- Arbeláez, A. L. [with S.P. Churchill, E.L. Linares, M. Devia] 582 (3).
- Areces, F. 1160 (10).
- Arias-G., J.C. 722 (8e), 828 (8e).
- Aristeguieta, L. [with F. Pannier] 1886 (3),  
[with G. Agostini] 6360 (3).
- Arroyo P., L. [with T.J. Killeen, J. Wellens, H. Gonzáles, P. Solíz] 669 (8b).
- Ayala, F. 2484 (8b).
- Aymard, G. [with N. Cuello, G. Meza, S. Giner] 3874 (8a), 3874-B (8a),  
[with L. Delgado] 6739 (5).

- Baker, M.A. 5699 (6).  
Barbour, P.J. 2505 (2), 4440 (8d), 4445 (8d), 4516 (12), 4795 (8b).  
Barona, A., [with D. Resende, J.A. Vale, L. Lima, A. López] 3029 (8a).  
Barrington, D.S. 4337 (8c), 4338 (8c).  
Beck, S.G. 1453 (8b), 1627 (8a), 6606 (8b), 7329 (8b), 8030 (8a),  
[with R.B. Foster] 18496 (2),  
[with A. Zonta, L. Medina, G. Pardo, M. Puri] 20162 (8b).  
Beckett, J. s.n. [US 1120075] (8d).  
Beitel, J.M. 85069 (4), 85202 (8a).  
[with A. Rossman] 85252 (4).  
Bell, D. 310 (4).  
Belshaw, C.M. 3437 (2).  
Beltrán, H. [with R.B. Foster] 1241 (8a).  
Bennett, D. 14 (5).  
Betancur, J. 2126 (6), 5270 (6).  
Biganzoli, F. [with Diego Giraldo-Cañas] 415 (8a).  
Billiet, F. [with B. Jadin] 5957 (8b).  
Birschel, J.W. s.n. [YU.010024] (11).  
Bonino, R. 345 (8b).  
Boom, B.M. [with Mori S.] 1567 (5), 1576 (5),  
[with Gopaul D.] 7534 (5),  
[with G.J. Samuels] 8884 (5), 8895 (5).  
Boom, B.M. 4088 (8e).  
Botanic Gardens Herbarium 151 [US 830354] (8c), 153 [US 830355; US 830356] (8c), 159 [US  
830616; US 830615] (8c), 161 [US 830613; US 830614] (8c).  
Britton, N.L. [with T.E. Hazen] 462 (8c),  
[with T.E. Hazen, W. Mendelson] 1745 (8c),  
[with E.G. Britton, W. Freeman] 2140 (8c).  
Bro. Adolfo M. 55A (8b).  
Bro. Gines 138 (3).  
Broadway, W.E. 2407 (8d), 4222 (8c), 6958 (8c), 7080 (8c).  
Buchtien, O. 288 (2).  
Bunting, G.S. 9515 (8c), 12225 (3), 12226 (3)  
Callejas, R. 8232 (6).  
Camargo García, A. 1166 (8e).  
Cárdenas, D. [with N. Marín, M. Holguín, G. Holguín ] 48784 (8b).  
Carijano, M. 18 (8a).  
Carriker, J.W. 22 (3).  
Carvalho, F.A. [*et al.*] 308 (4), 320 (4).  
Castaño-A., N. [*et al.*] 7714 (6), 9197 (12).  
Castro, J. [with F. Giraldo, J. Londoño] 1700 (3).  
Cerón, C.E. [with M. Chango, V. Tapur, G. Aymard] 16836 (6).  
Chocce, M.A. 512 (8b).  
Christenhusz, M.J.M. 2081 (9).  
Churchill, S.P. 16892 (6).  
Cid Ferreira, C.A. [with B.W. Nelson] 3053 (8e).  
Clarke, H.D. [with S.A. Mori, S. Heald] 4120 (5), 4278 a (5),  
[with C. Perry, E. Tripp, S.R. Stern, D. Gittens] 11931 (5), 11986 (5).  
Colorado, J. 732 (5).

- Conant, D.S. 670 (8c), 4040 (8b), 4041 (8b), 4042 (8b), 4043 (8b), 4178 (8b), 4245 (10), 4246 (10), 4247 (10), 4477 (3), 4478 (3), 4486 (3),  
 [with D.S. Barrington] 4338 (8c),  
 [with J. DeCamp] 4167 (10), 4168 (10), 4169 (10), 4170 (10), 4171 (10).
- Copeland, J.J. s.n. [NY 4004229] (8c).
- Correa, M. [with F. Lara, R. Ramirez, *et al.*] 2768 (6).
- Cornejo, M. [with A.F. Fuentes, E. Ticona, S. Sompero, C. Cuqui] 128 (2).
- Cowan, R.S. [with T. R. Soderstrom] 2060 (5).
- Cremers, G. 6700 (8f), 7386 (8f) 8951 (5), 9128 (5), 9236 (5), 10270 (5), 10315 (5), 15194 (5),  
 [with J.J. de Granville, I. Hagemann, B.E. Leuenberger] 10227 (5).
- Crespi, C. s.n. [US 1879334] (6).
- Croat, T.B. 7561 (8b), 18131 (8e), 19848 (8a), 51061 (8b), 59303 (4), 59596 (12), 85359 (8b), 96937 (2), 96975 (2),  
 [with L.P. Hannon] 86940 (6),  
 [*et al.*] 90750 (12).
- Croizat, L.C.M. 757 (8a).
- Cuatrecasas, J. 9379 (6), 10578 (8b), 12921 (3), 15608 (6),  
 [with R.E. Schultes, E. Smith] 12513 (11), 12585 (11).
- Daly, D.C. 1836 (8b), 2108 (8b), 6823 (8a), 9087 (8a), 10165 (8b), 10239 (8b), 11175 (8a).
- Davis, E.W. 766 (8b).
- de Boer, M. (8e).
- DeCamp, J. [see under Conant, D.S.].
- de Granville, J.-J. 5885 (5), 12539 (8b), 13266 (5), 13350 (5), 16905 (5),  
 [with C. Feuillet, L. Hollenberg, O. Poncy, M.S. Sangrey] 8665 (5), 8690 (5), 9053 (5),  
 [with L. Allorge, W.J. Hahn, M. Hoff] 9464 (8a), 9526 (8f),  
 [with C. S. Roesel, L. Brothers] 11511 (5), 11592 (8a),  
 [with P. Acevedo-Rodriguez, A. Boyer, L. Hollenberg] 12126 (8b), 12381 (5),  
 [with F. Billiet, B. Bordenave] 12654 (5),  
 [with F. Crozier] 13655 (5).
- de la Cruz, J.A. 3417 (8a).
- de la Sota, E. 899 (8b).
- de Moraes, P.L.R. [with H. van der Werff, L. Daneu, R. Perdiz] 2737 (7),  
 [with H. van der Werff, L. Daneu] 4254 (7), 4553 (7), 4810 (7).
- Delnatte, C. 1234 (5), 1967 (5).
- Desvaux, N.A. s.n. [P01518834] (8c).
- Díaz S., C. 10642 (6).
- Díaz, W. 5421 (8a).
- Dodson, C.H. [*et al.*] 9097 (6).
- Dombey, J. s.n. [B 20 0000123-b, P00642343, P00642344, P00642345] (1).
- Dueñas, H. 245 (3).
- Duss, A. 3882 (8c), 4451 (8c).
- Eaton, D.C. 214 (3).
- Ekman, E.L. 14688 (8c), H 14688 (8b), H 14824 (8c, hybrid?), H 4751 (8c).
- Ellenberg, H. 3489 (12).
- Espina, R. [with J. Giacometto] A78 (3).
- Fay, A. [with L. Fay] 2279 (8b), 2324 (8b), 2357 (8b), 2359 (8a), 2360 (8a), 2361 (8b), 2362 (8b),  
 2675 (8e), 3644 (6), 3706 (6), 3707 (6), 3957 (6), 4048 (6), 4066 (6), 4067 (6), 4219 (2).
- Fendler, A. 55 (5), 112 (8c), 536 (11), s.n. [DUKE10156280] (3).
- Fernandes, I. [with S.C. Sant'Ana, M. Caravallo] 1498 (7).
- Fernández Casas, F.J. 7940 (8b).

- Fernández, A. 4361 (4), 4360 (4), 5388 (5), 6108 (5),  
    [with G. Aymard] 4904 (5),  
    [with E. Sanoja] 6094 (5), 6168 (5).
- Fernández-Alonso, J.L. [with A.A. Camero, Z. Marin, E. Mesa] 11006 (6).
- Ferreira, L. 117 (8b).
- Fiaschi, P. [with A.M. Amorim, S.C. Sant’Ana, J.L. Paixão] 1574 (7).
- Flora Falcón 130 (3), 135 (3), 289 (3).
- Forero, E. 6376 (8b),  
    [with R. Jaramillo, J. Espina Z., P. Palacios H.] 6438 (6), 6539 (6).
- Foster, R.B. [with B. d’Achille] 11548 (9).]
- Franco R., P. [with D. Giraldo C., L. F. Jiménez] 5457 (6).
- Freire, E. 4325 (6).
- Fuentes, A.F. [with N. Paniagua Zambrana, H. Cabrera, F. Torrico] 5350 (8b),  
    [with R. Cuevas, E. Cuevas, H. Pariamo] 7862 (2).
- Gaitán, M. [with M. Moreno, R. Valencia, A. Sanabria, E. Rojas] 7 (8b).
- García-Barriga, H. 12222 (6).
- Gentry, A.H. 80578 (8a),  
    [with B. Stein] 46550 (5), 46625 (5),  
    [with S. Estenssoro] 70307 (8b),  
    [with S.G. Beck] 70926 (2),  
    [with C. Sáenz] 76204 (3), 76211 (3), 76225 (3), 76241 (3), 76243 (3), 76252 (3), 76274 (3),  
    76306 (3),  
    [with C. Reynel Rodríguez, R. Ortiz, P. Núñez V.] 76848 (8a).
- Giraldo, L.F. 2542 (3), 3575 (8a),  
    [with S. Mejía] 2533 (5).
- Gleason, H.A. 830 (5).
- Gonzales, J. [with S. Panfil, G. Kauko] 3740 (8b),  
    [with F. Bascope, R. Justiniano] 4339 (8b),  
    [with H. Nenzen, J. Choque, J.C. Cespedes] 4711 (8b).
- Graham, J.G. [with J. Schunke V.] 15693 (8a).
- Grandez Rios, C. [with Gilmore, M.] 545 (8e).
- Grant, M.L. 10126 (3), 10322 (11).
- Hagemann, W. [with N. Leist] 2051 (6).
- Hahn, W. [with E. J. Judziewicz, S. Tiwari, D. Gopaul] 4161 (5),  
    [with E. J. Judziewicz, D. Gopaul] 4290 (5).
- Harley, R.M. [with R. Souza, R. De Castro, A. Ferreira] 10768 (8b).
- Harling, G. [with L. Andersson] 17731 (8b).
- Hart, J.H. 6353 (8d), 6920 (8c).
- Haught, O.L. 1422 (5).
- Hawkins, T. 1892 (5), 1897 (5), 2068 (5), 2213 (5).
- Henkel, T.W. 436 (8a), 928 (5), 2247 (5), 4114 (5), 4181 (5),  
    [with M. Chin, W. Ryan] 1223 (8d),  
    [with M. Chin, R. Williams, R. James] 4974 (5).
- Henri-Stanislas 1708 (6).
- Herb. G. S. Jenman s.n. [US 428914] (8c).
- Herb. of the Royal Botanic Gardens KEW 68 [YU.010055] (11).
- Hoehne, F.G. 942 (8b).
- Hoff, M. 6729 (5).
- Holm-Nielsen, L.B. [et al.] 21949 (8a).
- Homersley, A. 137 (8c).

- Huamantupa Chiquimaco, I. [et al.] 10728 (2).  
Hudson, J.E. 845 (6), 896 (6), 907 (6).  
Hurtado, F. [with J. Shiguango] 1624 (6).  
Idrobo, J.M. [with R.E. Schultes] 983 (6).  
Irwin, H.S. 55005 (5), 55075 (5).  
Jansen-Jacobs, M.J. [with C. Feuillet, P.H. Hiepko, L.E. Skog, B. Welle] 344 (8b),  
[with B.J.H. ter Welle, A. Chanderbali, U. Raghoenandan, V. James] 3535 (5), 3781 (8d),  
[with B.J.H. ter Welle, P.P. Haripersaud, O. Muller, M. van der Zee] 5881 (8a),  
[with U. Raghoenandan, A. Grant, G. Ramharrakh, H. ter Steege, O. Bánki] 6556 (5).  
Jaramillo, J. [with F. Coello, A. Freire] 31384 (8e).  
Jardim, A. 694 (8b), 2441 (8b).  
Jenman, G.S. 100 (8a), 110 ? (8a), 567 (8a), 2321 (8b).  
Jiménez, I. 1935 (8b),  
[with H. Huaylla] 2597 (8d).  
Karsten, H. s.n. [NY 4004118] (3), s.n. [PRC] (11).  
Kessler, M. 8221 (1),  
[with J. Gonzales, T. Krömer, A. Acebey, B. Hibbits, M. Sonnentag] 7993 (2), 8053 (8b), 8131  
(8d), 8302 (8), 8416 (8b), 8637 (8b) 9221 (8b),  
[with A. Acebey, J. Gonzales, M. Sonnentag] 8758 (8b), 8796 (8e), 8857 (8d),  
[with J. Gonzales, K. Bach, A. Acebey] 9776 (2), 9779 (2), 10044 (2), 10259 (2),  
[with J. Gonzales, K. Bach, I. Jiménez, A. Portugal] 10733 (8b),  
[with J. Gonzales, K. Bach, S. Theinert, E. Rapp] 11125 (8b), 11138 (8b) 11193 (8a) 11196 (8b)  
11607 (2),  
[with I. Jiménez, T. Krömer] 12935 (1).  
Killeen, T.J. 4417 (8a).  
Killip, E.P. 24579 (1), 25536 (2), 26238 (8b), 26405 (8b), 27117 (8b), 28272 (8a), 28758 (8b),  
[with A.C. Smith] 25536 (2), 25788 (2), 26238 (8b), 26405 (8b), 26746 (8b), 27117 (8b), 27120  
(8d) 27332 (8e) 28072 (8b) 28189 (8b), 28272 (8a), 28522 (8b), 28758 (8b), 29377 (8b), 29612  
(8a).  
Klug, G. 1437 (8a).  
Knapp, S.D. [with J. Mallet] 6980 (8a), 8423 (1),  
[with P.W. Alcorn] 7757 (2).  
Kral, R. 71836 (4).  
Kramer, K.U. [with W.H.A. Hekking] 2669 (8a).  
Kuntze, C.E.O. 1684 (11).  
Labiak E., P.H. 6257 (8e).  
Laegaard, S. 51972 (8b), 51981 (6), 51982 (6).  
Lawesson, J.E. [with T. Læssøe, P.M. Jørgensen] 44394 (8b).  
Lanjouw, J. [with J.C. Lindeman] 3359 (8a).  
Lehnert, M. 41 (8b), 44 (8b), 56 (8b), 202 (1), 300 (1), 305 (1), 458 (9), 461 (1), 763 (2), 795 (2), 1250  
(2), 1521 (2), 1524 (2), 1668 (8), 1998 (1), 2033 (2), 3162 (6),  
[with M. Kessler] 1255 (2).  
Leprieur s.n. [F C0645990F] (8a).  
Lewis, W.H. [with M. Elvin-Lewis, M.C. Gnerre] 10464 (8a) 10635 (8a),  
[with M. Elvin-Lewis, D. Fast, J. Campos de la Cruz] 12863 (8a), 12886 (8a).  
Liesner, R.L. 15798 (4), 17274 (4), 17419 (12), 18275 (5), 18280 (5), 23913 (5), 25603 (5),  
[with B.K. Holst] 18882 (5), 20311 (5), 21262 (8a),  
[with V. A. Funk] 15781 (4).  
Linden, J.L. 1021 (11).  
Lindeman, J.C. 5405 (8a).

- Liogier, A.H. 14453 (8c).  
Little, E.L. Jr [with R. Rice L.] 9526 (8b).  
Lleras, E. P17390 (8b).  
López M., A. 8702 (8b).  
López C., R. [with Y. Martínez, N. Cruz, M.A. Pinzón, R. Pinzón] 4058 (6).  
Lowrie, S.R. [with B. Lowy, B. Nelson, C.A. Cid Ferreira, M. Morreira] 721 (8b).  
Luteyn, J. [with S. Mori, N. Holmgren, J.A. Steyermark] 8247 (11).  
Maas, P.J.M. [with L. Westra] 3865 (5).  
Macedo, A. 1518 (8d), 2184 (8d).  
Macia, M.J. [with A.P. Yáñez] 323 (8b).  
Maciel, S. 983 (5), 985 (5), 1541 (8a).  
Madriñán, S. [with C. E. Barbosa] 162 (3), 185 (3), 492 (3).  
Maguire, B. 24543 (5), 24495a (5),  
    [with D.B. Fanshawe] 22854 (8a),  
    [with R. S. Cowan, J. J. Wurdack] 29929 (5),  
    [with J. J. Wurdack, G. S. Bunting] 36870 (5).  
Martius, C.F.P. 391 (7).  
McDaniel, S.T. [with M. Rimachi Y.] 22499 (8b), 26623 (8a), 27830 (8a), 32910 (8d),  
    [with S. Hollis, M. Rimachi Y.] 32889 (8b).  
McDowell, T. [with D. Gopaul] 2624 a (8e).  
Meier, W. 902 (11), 1515 (3), 1763 (11), 3242 (3), 3415 (5), 4449 (3),  
    [with O. Kunert] 4591 (11), 4794 (3),  
    [with M. Speckmaier] 7857 (3),  
    [with S. Nehlin] 8858 (5),  
    [with O. Escorcha] 9767 (3), 9771 (3), 9794 (3),  
    [with G. Forbes] 9919 (3), 9929 (3),  
    [with S. Nehlin, Excursionista de Caracas] 10157 (3),  
    [with Grupo Ecologico La Marroquina] 10305 (3),  
    [with N. Flauger] 10362 (3) 11025 (3),  
    [with O. Escorcha, G. Forbes] 11303 (3),  
    [with S. Jordan] 15415 (3).  
Mellado N., L.F. 0733 (8b), 1157 (1).  
Mendoza, M. [with G. Gutierrez, M. Mendizaval, F. Rojas, E. Mamani] 3169 (8b).  
Mexia, Y. 6497 (8b), 8293 (1).  
Miliken, M. 532 (8a).  
Monteagudo, A. [et al.] 11882 (1).  
Montoya Jiménez, M. [with A. Upegui, L. Monsalve, S. Ramírez, J. Muñoz] 1119 (6).  
Morales, M. 474 (6).  
Moran, R.C. 6111 (8e),  
    [with C.K. Rohrbach] 5389 (2).  
Moritz, J. 110 (11), 218b (11).  
Mostacero, J. [with R. Castillo] 261 (11).  
Nash, G.V. 887 (8c).  
Nassar Arboleda, A. AN070 MEDI-070 (3).  
Navarrete, H. 691 (8e), 708 (8e), 1214 (12), 1248 (12), 1507 (8e).  
Nee, M.H. 31660 (8a).  
Øllgaard, B. 98462 (2), 98477 (2), 99604 (6),  
    [with H. Navarrete] 2492 (12), 2506 (12), 2840 (2),  
    [with E. Asanza C., J. Brandbyge, S. Roth, C. Sperling] 35264 (8a),  
    [with J.E. Madsen, L. Ellemann, B. Eriksen] 90444 (6),

- [with B. Bergmann, M. Ruíz] 99263 (2).  
 Ortega Mendoza, F.J. [with Á.C. González] 361 (3), 383 (3),  
 [with R.F. Smith] 2388 (3), 2433 (3), 2492 (3),  
 [with R. Rivero, B. Stergios, H. van der Werff, G. Aymard] 2752 (3),  
 [with L. Marcano-Berti, L. Valverde, I. Peña S.] 3236 (8a).  
 Palacios, W.A. 5733 (8b), 6711 (2), 10303 (8e).  
 Panfil, S.N. 629 (8a).  
 Peñaranda, J.A. 383 (8b).  
 Perrottet, G.S. s.n. [PR, NY 0014874] (5), s.n. [NY 148745] (8a).  
 Phillipson, W.R. [with W.R. Philipson, J.M. Idrobo, R. Jaramillo M.] 2249 (6).  
 Pietrobom-Silva, M.R. 1298 (8a), 6928 (8a), 9128 (8a).  
 Pipoly III, J.J. 10791 (5), 15332 (8e), 15416 (8a),  
 [with H. Lall] 8124 (5),  
 [with A. Rudas, P. Palacios] 15263 (8a),  
 [with A. Cogollo P., D. Cárdenas L., M. Villa, O. Álvarez, L. Velez] 16773 (6).  
 Pittier, H.F. 5939 (3), 7090 (3), 10125 (3), 11272 (3), 12984 (3), 13837 (3), 13846 (3), 13876 (3), 13955  
 (3), 1686 (3).  
 Plowman, T.C. 5950 (8b), 3215 (8b).  
 Poeppig, E.F. s.n. [LE00008089, MO-1858413, P00642342, W0053351, W0053352] (1), s.n. [W0056018,  
 W0056019, BM (fragment of B), MO-3309247] (8b), s.n. [B 20 0000124] (9).  
 Portugal, A. [with I. Jiménez, C. Rojas] 221 (9).  
 Prance, G.T. 6644 (8a), 7573 (8b), 9400 (5), 12176 (8b),  
 [with P.J.M. Maas, K. Kubitzki, W.C. Steward, J.F. Ramos, W.S. Pinheiro, J.F. Lima] P13020 (8b).  
 Proctor, G.R. [with B. Pinto] 39970 (8c), 40706 (8c).  
 Rangel, O. 13602 (3).  
 Redden, K.M. [with R. Williams, C. Perry, C. Paul] 3539 (8e).  
 Rimachi Y., M. 6523 (8b).  
 Ríos Paredes, M.A. 739 (8b).  
 Rodríguez, L. [with O. Hokche] 1605 (5).  
 Rodríguez, W.D. 8031 (8b),  
 [with A D. Cárdenas, W. Trujillo, N. Marín, L. Maniguaaje] 6894 (8b),  
 [with A D. Cárdenas, W. Trujillo, N. Marín, E. Paqui] 6999 (8e),  
 [with A D. Cárdenas, N. Marín, J. Restrepo] 9354 (12).  
 Rudas L., A. [with P.A. Palacios, F. del Aguila Joaquin, G. Morán] 2710 (8e),  
 [with A. Prieto, C. Rodríguez] 5738 (8b).  
 Ruíz López, H. Herb. 66 (1).  
 Sagot, P.A. 726 (8a).  
 Sánchez, C. 17\_3 (8c).  
 Sánchez, R. 3232 (8b).  
 Sanoja, E. 3032 (5),  
 [with A. Fernandez] 3064 (5).  
 Sastre, C.H.L. [with C.H.L. Sastre, D.A. Bell, F. Crozier] 8076 (5).  
 Schomburgk, R. 1125 (5), s.n. [NY 148722] (5).  
 Schultes, R.E. 3835 (8e),  
 [with I. Cabrera] 12805 (8b).  
 Schunke Vigo, J.M. 269 (8b), 1900 (8b), 6866 (8b), 10507 (8a), 14031 (1), 14348 (8a), 15693 (8b),  
 [with J.G. Graham] 15340 (8a), 15430 (8a), 15500 (8c).  
 Seifríz, W. 25 (3).  
 Silva, M.R. [with C.E. Rodrigues] 1298 (8b).  
 Silveira, M. 1252 (8b).

- Silverstone-Sopkin, P. 7744 (6).  
Smith, A.C. [with B. Stergios, G. Aymard, D. Taphorn] 1544 (3).  
Smith, D.N. [et al.] 1179 (8a),  
[with J.F. Smith, G. Quintana, C. Negrete] 12962 (8b).  
Smith, H.H. 111 (8a), 1018 (3), 2224 (3), 2226 (3), 2229 (3), s.n. [NY 908505] (8a),  
Solomon, J.C. 7700 (8e).  
Souza, D.J. 14 (8b).  
Sperling, C.R. 5437 (1), 5911 (8e),  
[with S. King] 6467 (8b), 6597 (8b).  
Splitgerber, F. s.n. [L.1285146, L.1285147, US 00066287] (8a).  
Spruce, R. 22 (8a), 2115 (8e), 4323 (1), 4715 p.p. [B 20 0000122, BM000777032 (mix with 8b),  
P00642346 (mix with 8b), P00642351] (1), 4715 p.p. [K000227562, K000227563, W-Rchb.  
1889-0198979] (2), 4715 p.p. [BM000777031, BM000777032 (mix with 1), BM000777346,  
P00642346 (mix with 1), P00642349, P00642350, W-Rchb. 0053380] (8b), 4715 forma pygmea  
[P00642347, P00642348] (9), 4717 (9), 4724 (2), s.n. [US 1431488] (8a).  
Stahel, G. [with J.W. Gonggrijp] 585 (5), 638 (5).  
Stergios, B. 10588 (8a), 11892 (4),  
[with L. Delgado] 13432 (8d),  
[with J. Velazco] 14151-b (8e).  
Steyermark, J.A. 56029 (11), 58586 (5), 75598 (5), 87203 (8d), 87399 (8a), 89163 (5), 89648 (5),  
94779 (3), 100438 (3), 103595 (3), 105395 (3),  
[with S. Nilsson] 363 (5), 754 (5),  
[with G.C.K. Dunsterville, E. Dunsterville] 92753 (5),  
[with A. Braun] 94663 (3),  
[with R. Liesner, F. Delascio] 115029 (8b),  
[with J.L. Luteyn] 129763 (4),  
[with C. Sobrevila, D. Fernandez, A.B. Hernandez] 125050 (3).  
Stübel, A. 995a (6).  
Sundue, M.A. [with M. Nee, M. Soto, D. Soto] 705 (8b),  
[with M. Mendoza] 906 (8e).  
Tate, G.H.H. 140 (8a).  
Taylor, W.C. 5064 (8a).  
Thomas, W.W. [with M.R. Barbosa., A.M. Caravallo, S.C. Sant’Ana] 12419 (7).  
Tipaz, G.A. [with S. Espinoza, C. Gualinga] 580 (8a).  
Tirado, M. 1879 (8b).  
Torres J. [with G. Garces, G. Amparo, L. Urrego] 3269 (8b).  
Treacy, J. [with J. B. Alcorn] 181 (8a), 582 (8a).  
Triana, J. 653 (6).  
Trujillo, B. 16418 (3).  
Tryon, R.M. [with A.F. Tryon] 5173 (8b), 5182 (8b), 5220 (1), 5256 (1),  
[with K.U. Kramer] 5618 (8d).  
Tuomisto, H. [et al.] 3366 (8b), 8144 (8a), 16679 (8a),  
[with G. Cárdenas, M. Higgins, K. Ruokolainen] 14135 (8a),  
[with K. Ruokolainen] 11435 (8e), 11756 (8e),  
[with K. Ruokolainen, A. Duque] 12088 (8a).  
Tutin, T.G. 403 (8b).  
Tutin, T.G. 403 (8b).  
van der Werff, H. [et al.] 16780 (2),  
[with E. Gudiño] 11386 (12),  
[with R. Wingfield] 3193 (3),

- [with A.C. Gonzalez] 4797 (8e),  
[with B. Gray, R. Vásquez, R. Rojas] 15511 (2), 15555 (2),  
[with B. Gray, W. Quizhpe] 21892 (2),  
[with L. Valenzuela G., G. Shareva M., A. Reyes Barrantes] 24820 (2),  
[with R. Vásquez, B. Gray, R. Rojas, R. Ortiz, N. Davila] 18299 (12).
- Vásquez, R. [*et al.*] 21824 (1).
- Vásquez Hernández, J. s.n. [US 591371] (8d).
- Vogel, C. s.n. [F C0645983F] (3).
- von Hoffmannsegg, J.C. s.n. [B-W 19716-011, B-W 19716-012, B-W 19716-013, B 20 0000318, NY 00148762, US 00066283] (8a), s.n. [B-W 19717-011, B-W 19717-012, B-W 19717-013, NY 00148758, US 00066279] (8a).
- von Luetzelburg, P. 25816a (8a).
- von Tuerckheim, H. 2797 (8c).
- Vriesendorp, C. F. 315 (8b).
- Wagener, H. s.n. [B 20 0000322] (3).
- Wagner, W.H. s.n. [US 1833839] (8b).
- White, R.A. 197010 (3),  
[with N.B. White] 19707 (3), 19708 (3), 19710 (3), 19711 (3), 19712 (3), 19713 (3),  
[with T.W. Lucansky] 1969224 (3), 1970122 (5), 1970123 (5), 1970124 (5).
- Wilkes Explor. Exped. 24 (8a).
- Williams, L. 955 (8a), 956 (8d), 1611 (8b), 2138 (12), 4352 (8a), 4845 (8b), 8236 (8d), 10228 (3), 11380 (8b), 11388 (8a).
- Windisch, P.G. [with W. Oliveira] 6416 (8b), 6493 (8a).
- Wood, J.R.I. 12792 (8b).
- Woodbury, R.O. s.n. [MO-2385167] (8c).
- Wurdack, J.J. 1825 (8b),  
[with J.V. Monachino] 41305 (8a).