



***Danaea* (Marattiaceae) revisited: biodiversity, a new classification and ten new species of a neotropical fern genus**

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Revision of the Neotropical fern genus *Danaea* (Marattiaceae) has resulted in the recognition of ten new species, which are here for the first time presented to the scientific audience. Morphological and molecular data suggest that the genus consists of three monophyletic subgenera that are circumscribed here. A key is provided to aid species identification. The geographical ranges of the species are summarized and discussed with regard to speciation. © 2010 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2010, **163**, 360–385.

ADDITIONAL KEYWORDS: biogeography – distribution – key – marattioid ferns – speciation – subgenera.

INTRODUCTION

The fern genus *Danaea* Sm. belongs to the family Marattiaceae, one of the early diverging lineages of ferns with a long fossil history (Taylor, Taylor & Krings, 2009). *Danaea* is confined to the Neotropics and its species are readily distinguishable from other Marattiaceae by their dimorphic leaves that are usually once pinnate, but sometimes simple or partly bipinnate, and their sunken, elongated synangia that almost entirely cover the abaxial side of the fertile leaf lamina (Fig. 1; Camus, 1990; Christenhusz *et al.*, 2008). Opinions as to the degree of synonymy differ widely, and even although a much larger number of taxa have been described, the number of species in *Danaea* have traditionally been estimated to be approximately 20–25 (Tryon & Tryon, 1982; Tryon & Stolze, 1989). Recent estimates range from as few as 17 (Rolleri, 2004) to *c.* 50 species (Christenhusz *et al.*, 2008). Striking morphological variability can be found within populations, and even within individuals, often making it difficult to separate phenotypic plasticity from heritable differences. Furthermore, many

important field characters, such as habit, colour and texture, disappear when the plant is preserved as herbarium specimens and, thus, taxonomy solely based on dried material can be complicated. Also, collections of large-leaved species such as *Danaea nodosa* (L.) Sm., *Danaea cartilaginea* Christenh. & Tuomisto and *Danaea grandiflora* Underw. are often fragmentary, complicating the interpretation of type specimens and other collections (Murdock, 2008).

Since the description of the genus by Smith (1793), numerous species have been added, but many of these have later been relegated to synonymy. As a consequence, there has been considerable confusion about identity and delimitation of species within *Danaea*. Partial taxonomic revisions were prepared by Underwood (1902, 1909) and Tuomisto & Moran (2001), but these did not cover the whole geographical range of the genus. A complete monograph of all species was published by Rolleri (2004), but it was exclusively based on characters from herbarium specimens and focused on characteristics of starch granules, scales and stomata, that are not stable even in the same plant. Therefore, several species were synonymized that have similar anatomical characteristics, but differ clearly in general habit. In addition, incorrect citation of type specimens raises doubts if these were actually examined in that study. A major problem was

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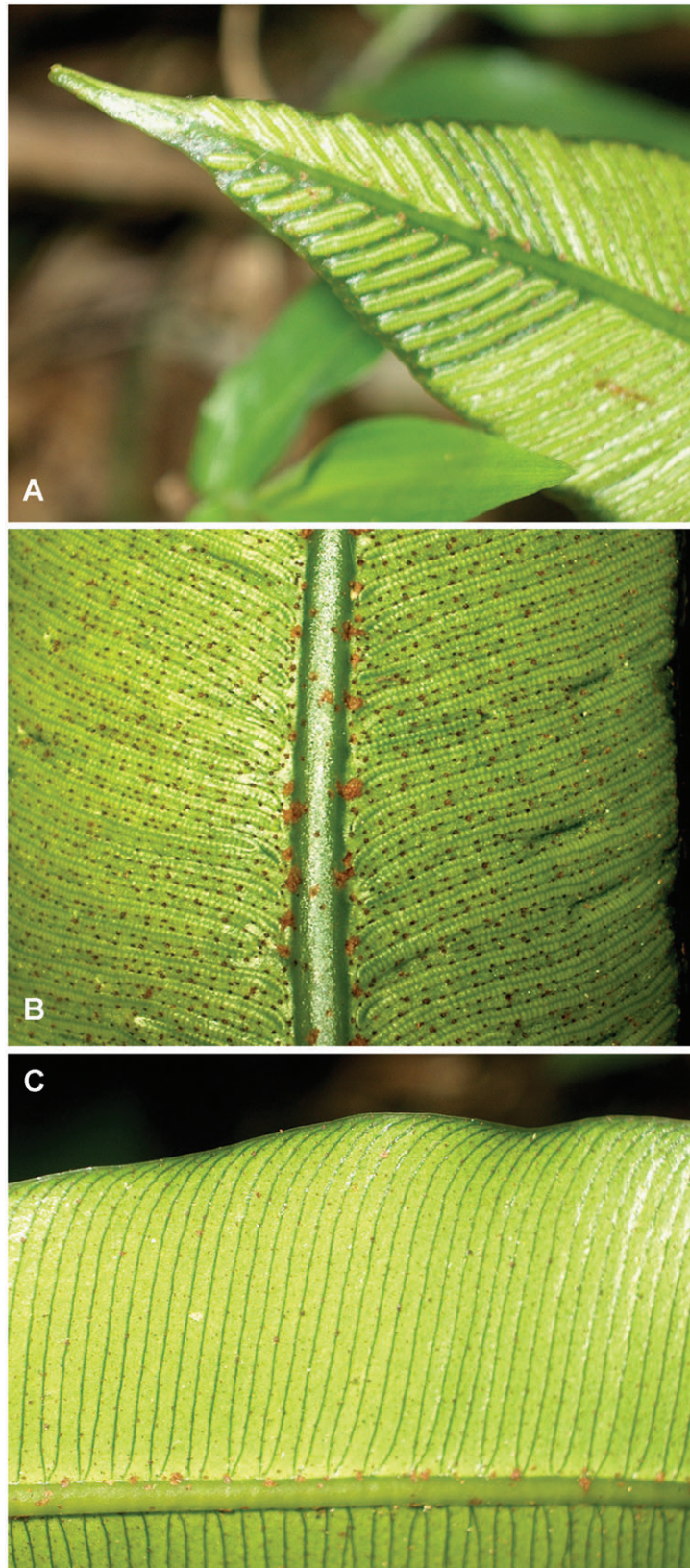


Figure 1. *Danaea arbuscula*. A, fertile pinna apex. B, detail of fertile pinna showing sori. C, detail of sterile pinna showing venation.

caused by the use of *Danaea elliptica* Sm., a name that was variously applied, but of which study of the type specimen showed this name to be referring to a juvenile *D. nodosa* (L.) Sm. Therefore *D. elliptica* was synonymized with *D. nodosa* and hence new names were provided for taxa that previously were erroneously referred to as *D. elliptica* (Christenhusz & Tuomisto, 2006). Rojas-Alvarado (2006, 2009) studied some species in the complex surrounding *D. moritziana* C.Presl, but the type of this species was not studied and no key to the complex or any genetic studies were provided. This only resulted in an increase in the synonymy of *Danaea moritziana*, a complex that needs further study at the population level to distinguish between phenotypic plasticity and heritable differences.

The present paper is based on observations made during extensive field work and consultation of specimens from 53 herbaria. Here, I present ten new species of *Danaea*, propose a subdivision of the genus into three subgenera based on my molecular studies and place all published species into these subgenera. To aid the identification to the species level, a key to all 50 currently recognized species is provided. It is based on complete specimens and field observations and may not be suitable for identifying all herbarium specimens, which are notoriously incomplete. The occurrence of species per country is presented in a table and some phytogeographical patterns are discussed.

NEW SPECIES

DANAEA CHOCOCOLA CHRISTENH., SP. NOV.

(FIG. 2A)

Type: Colombia, Chocó, Corcovada region, upper Río San Juan, ridge along Yeracúí Valley, 200–275 m, 24–25 April 1939, *E. P. Killip 35263* (holotype BM; isotype MO).

Diagnosis: Frondes steriles usque ad 48 cm longae. Stipites articulati, nodis 3–4. Pinnae laterales 19–24-jugae, maximae 3.4–5.1 × 0.7–1.2 cm, oblongae, apice acuto vel acuminato, leviter falcato, marginibus integris sed ad apicem acute serrulatis. Pinna terminalis trullati-oblonga, 3.6–5.2 × 0.7–1.2 cm. Venae plerumque simplices, rarius ad basin furcatae. Frondes fertiles et plantae juveniles non visae. Species *Danaeae humili* valde similis, a qua differt frondibus majoribus concoloribus, ad apicem acutis vel acuminatis, et venis densis plerumque simplicibus.

Description: Plant terrestrial. Rhizomes probably creeping to ascending with leaves radially arranged and roots only on the lower side (not preserved com-

pletely in the specimens observed), 1.1–1.7 cm wide at the apex; stipules 0.8 cm wide. Sterile leaves 34–48 cm long; petioles 12–17.5 cm long, with three or four nodes; rachises sparsely scaly towards the base, winged, wing 0.1–0.7 mm wide in the distal part of internodes; blades 22–32 × 6–8 cm, concolorous but a little paler below; imparipinnate with 19–24 lateral pinna pairs; largest lateral pinnae oblong, three to four times longer than wide, 3.4–5.1 × 0.7–1.2 cm, widest below the middle; pinna bases cuneate and strongly inaequilateral, apices acute to acuminate (often quite abruptly) and slightly falcate acroscopically, margins entire except sharply serrulate at apex; terminal pinnae present, trullate-oblong, 3.6–5.2 × 0.7–1.2 cm, widest below the middle, margins sharply serrulate at the gradually long-acuminate to caudate apex; veins mostly simple or paired at base, rarely forked, dense at 21–36 veins per cm. Fertile leaves and juveniles not known.

Distribution and ecology: Only known from two localities in Colombia (Chocó), in wet dense lowland rainforests, 0–300 m.

Etymology: Named for the province of Chocó from where the species is known.

Note: *Danaea chococola* was cited as *Danaea sp. F* in Christenhusz (2007). It resembles *D. humilis*, but differs in having concolorous leaves with dense and mostly simple venation.

Additional material examined (paratype): COLOMBIA: Chocó: near Quibdó, halfway to Lloró, *Mädge-frau 1474* (M).

DANAEA DANAËPINNA CHRISTENH., SP. NOV.

(FIG. 3)

Type: Suriname, Brokopondo, Brownsberg Nature Park, Koemboeval, forest on laterite near waterfall, 4°56'N, 55°11'W, 400–500 m, 8 March 2003, *M.J.M. Christenhusz & S. Bollendorff 2619* (holotype TUR; isotypes BBS, BM).

Diagnosis: Rhizomata erecta, usque ad 10 cm longa, ad apicem 1.0–2.3 cm lata. Stipites articulati, nodis 1–2 (–3). Pinnae laterales 2–5-jugae, maximae 10.4–21 × 3.2–6 cm, oblongae vel lanceolatae, apice acuto vel longe acuminato, marginibus integris. Pinna terminalis ovato-lanceolata, (10–) 13–25 × (3.3–) 3.8–6.4 cm. Frondes fertiles 2–5-jugae, stipite nodoso (0–) 1–2 nodis, pinnis lateralibus oblongo-lanceolatis.

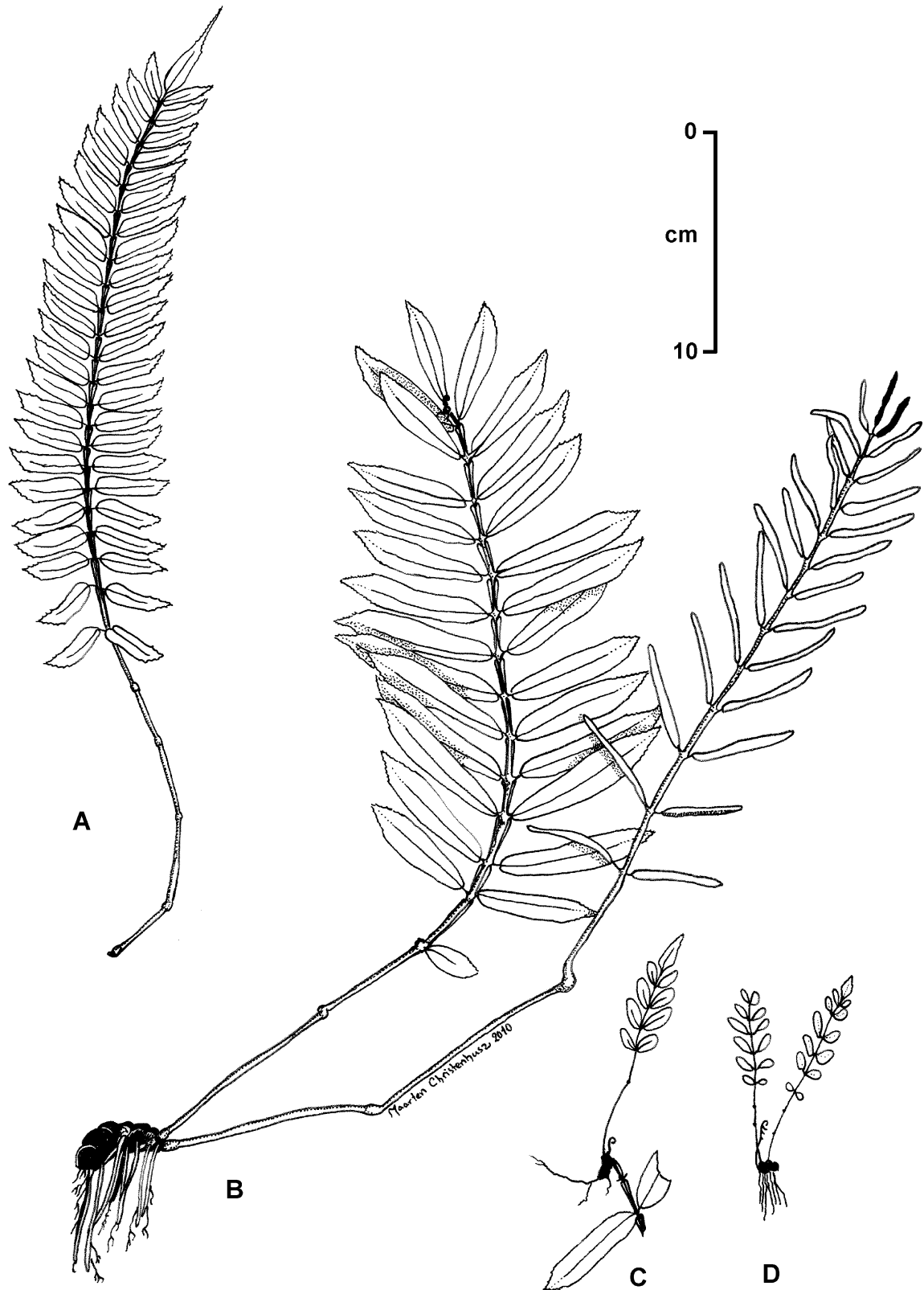


Figure 2. A, *Danaea chococola*, leaf, based on Killip 35263 (BM). B–D, *Danaea ypori*, based on Cremers *et al.* 9089 (Z). B, habit. C, plantlet from apical bulbil. D, sporeling.

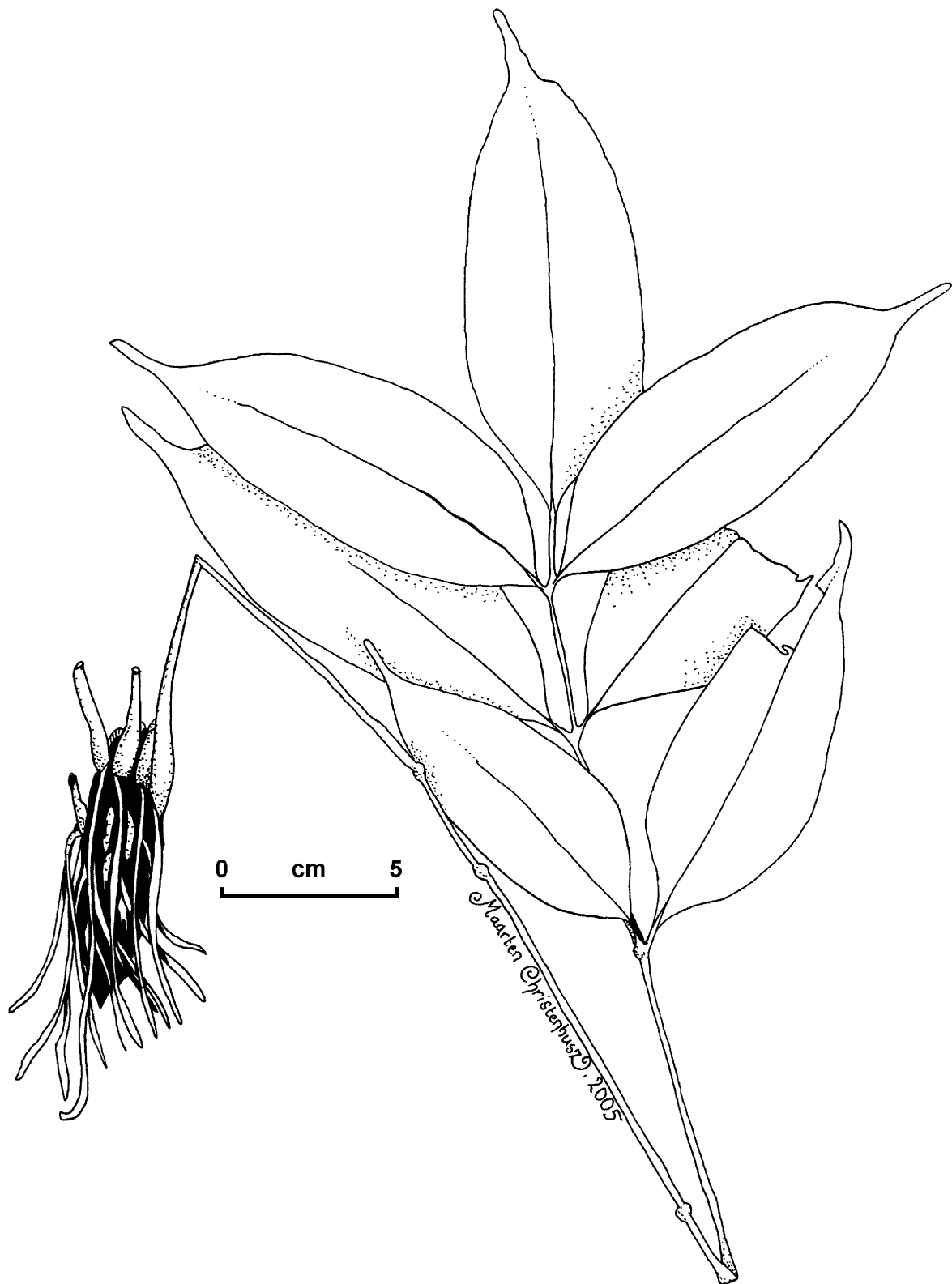


Figure 3. *Danaea danaëpinna*, based on *Christenhusz 2619* (TUR).

Description: Plant terrestrial. Rhizomes erect, 3–10 cm tall, 1–2.3 cm wide at apex, leaves and stilt roots arranged spirally; stipules 0.6–1.2 cm wide. Sterile leaves 48–68 cm long; petioles 24–44 cm long, with one or two (rarely three) nodes; rachises not scaly, not or minutely winged; blades 21–34 × 15–25 cm, concolorous, with a metallic grey sheen when dry; imparipinnate with two to five lateral pinna pairs; largest lateral pinnae oblong to lanceolate, 2.0–3.5 times longer than wide, 10.4–21.0 × 3.2–6.0 cm, widest at the middle; pinna bases acute, apices acute to (long) acuminate, margins entire throughout; terminal pinnae present, oblong–lanceolate to ovate–lanceolate, (10–) 13–25 × (3.3–) 3.8–6.4 cm, widest below the middle; veins mostly paired at base, occasionally forked, 9–13 (–14) veins per cm. Fertile leaves (33–) 57–77 cm long, petioles (22–) 33–58 cm long with (0–) 1–2 nodes, blades (11–) 15–24 × 10–20 cm with two to five pinna pairs; lateral pinnae oblong–lanceolate, largest lateral pinnae 7–10 × 1.5–2.6 cm, widest at the middle, apices acute, bases acute, margins entire; terminal pinnae present, lanceolate, 12.5–14.0 × 2.2–2.6 cm, widest below or at the middle, margins entire or minutely denticulate at apex.

Juvenile plants can produce a lateral pinna pair already when the leaf is 7 cm long, but simple leaves up to 15 cm long have been seen. The terminal pinnae are often more elongate in juveniles than adult plants. Partly fertile and partly sterile leaves seem to be common.

Distribution and ecology: Occurs throughout the eastern Guiana Shield (Guyana, Suriname, French Guiana, Amapá), in lowland and mid-elevation rainforests on laterite soils, mostly on steep slopes, c. 50–650 m elevation.

Etymology: The pinnae of this species resemble the phyllodes of *Danaë* Medik. (Asparagaceae).

Note: This species was cited as *Danaea* sp. C in Christenhusz (2007) and Christenhusz *et al.* (2008). Its leaves are crowded on a stout rhizome, which distinguish it from *D. zamiopsis*, which has slender rhizomes with spaced leaves.

Additional material examined (paratypes): SURINAME: Brokopondo: Brownsberg Nature Park, Mazaronitop, Christenhusz & Bollendorff 2633 (BBS, TUR). Brownsberg, Stahel & Grongrijp 589 (U, US). FRENCH GUIANA: Station d'écotourisme de l'Arataï, Boudrie 3762 (CAY, photocopy TUR). Réserve Volontaire Trésor, Christenhusz 2414 (CAY, TUR). Western inselberg of the Montagne de la Trinité, near creek Baboune, Cremers 7384 (CAY, U, Z). Bassin du

Maroni, 7 km east of Gobaya Soula, camp II, Cremers 10151 (B, BM, CAY, G, NY, P, U, US, Z). French Guiana, Roche Touatou, Bassin de l'Oyapock, south side of Mont Touatou, Cremers 14099 (BM, CAY, US). Maripasoula, north side of Mont Galbao, 10 km west–south-west from Saül, De Granville 1645 (CAY, Z). Eau Claire near Saül, Van der Werff 12962 (MO). BRAZIL: Amapá: Tumuc Humac, Haut Jari River, De Granville 12451 (CAY, US).

DANAEA DRACO CHRISTENH., **SP. NOV.**

(FIG. 4)

Type: Trinidad, Aripo Road, first gully on left after 2.25-mile post, 40 m in deep shade on steep loamy bank in small valley, 29 October 1974, A.C. Jermy 11025 (holotype BM).

Diagnosis: Rhizomata erecta, 7–9 cm longa, ad apicem usque ad 3 cm lata. Stipites articulati, nodis 2, rachidi alata. Pinnae laterales 2–4-jugae, maximae (11.6–) 13–21 × 3.5–5.2 cm, oblongae vel late oblanceolatae, plerumque supra medium latissimae, apice acuto vel acuminato, marginibus integris ad apicem leviter sinuatis. Pinna terminalis late ovato–lanceolata, (16–) 19.5–27.2 × 4.1–7.2 cm. Frondes fertiles 2–4-jugae, stipite nodoso 2 nodis, pinnis lateralibus satis latis lanceolatis.

Description: Plant terrestrial. Rhizomes erect, leaves and roots radially arranged, stout, 7–9 cm high, 2–3 cm wide at apex; stipules 0.8–1.1 cm wide; leaves imparipinnate; sterile leaves 41–67 cm long, petioles 17.6–33.0 cm long, with two nodes; rachises sparsely scaly below, winged, the wing up to 0.7 mm in upper part of internode; blades 22–36 × 15–36 cm, triangular, widest at the base, with 2–4 pinna pairs; largest lateral pinnae oblong to wide–oblanceolate, c. 3–4 times longer than wide, (11.6–) 13–21 × 3.5–5.2 cm, widest at or above the middle, apices acute to acuminate, bases acute, margins entire, slightly sinuate at apex; terminal pinnae much larger than the largest lateral pinna of the same leaf, widely ovate–lanceolate, (16–) 19.5–27.2 × 4.1–7.2 cm, widest below or at the middle, margins entire, slightly sinuate at apex; veins rarely simple, mostly paired at base or occasionally forked, 8–10 veins per cm; fertile leaves (42–) 67–80 cm long, petioles (24–) 42–54 cm long with two nodes, blades (19–) 23–30 × (12–) 21–24 cm with 2–4 pinna pairs; lateral pinnae rather wide, lanceolate, largest lateral pinnae 10–13.7 × 2.2–2.9 cm, widest below the middle, apices acute, bases acute, margins entire, sinuate–serrulate at apex; terminal pinnae ovate–lanceolate, 12.1–16.1 × 2.4–3.3 cm, widest below the middle, margins entire,

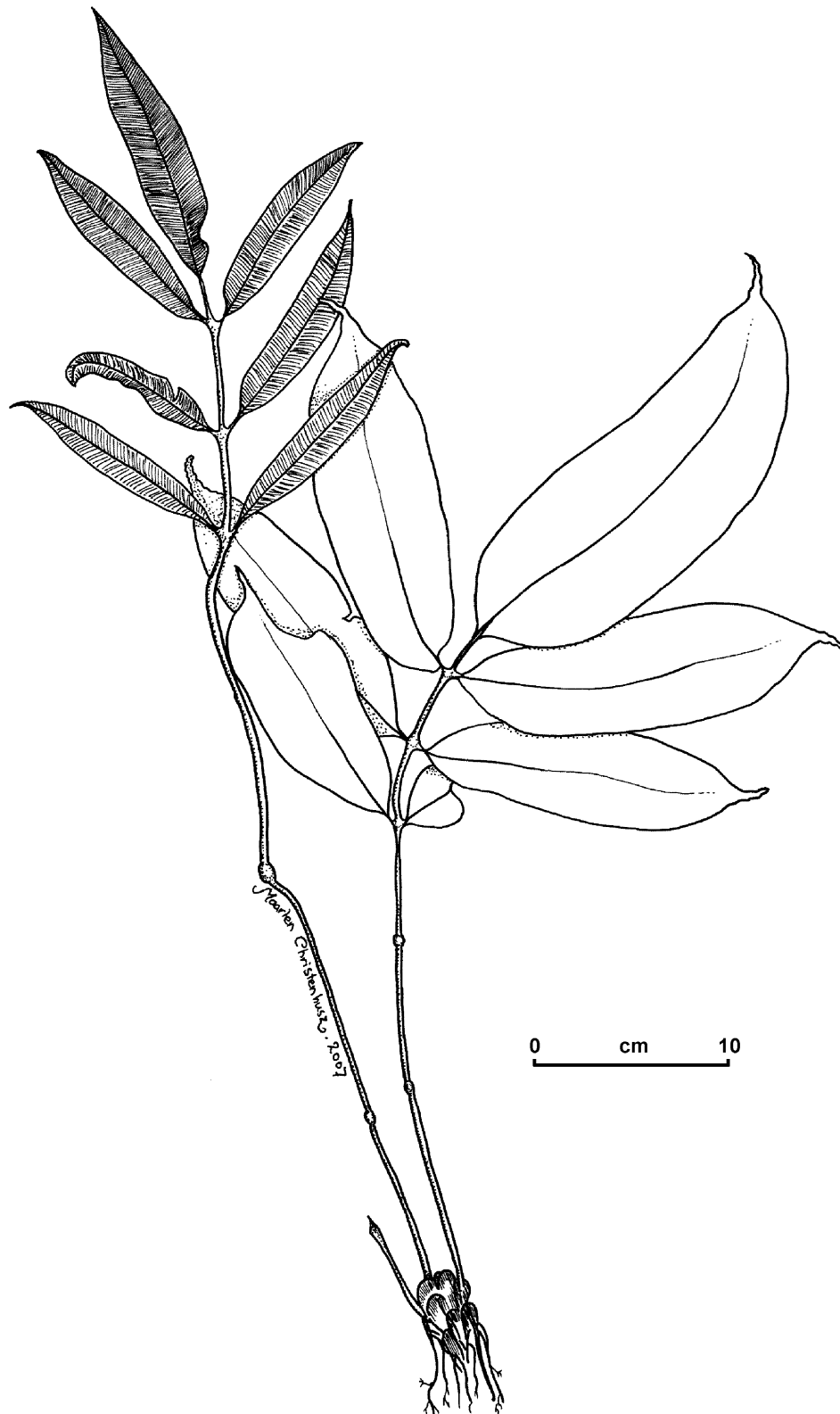


Figure 4. *Danaea draco*, based on *Jermy 11025* (BM).

sinuate at apex; juveniles with simple leaves up to 16 cm long, the first pinnae appearing at a length of 13–20 cm.

Distribution and ecology: A rare species endemic to Trinidad, found in Aripo Valley and Mount Tocuche in shady moist forests and deeply shaded gullies on steep loamy or clayey banks.

Note: *Danaea draco* was cited as *Danaea sp. D* in Christenhusz (2007). It is distinguished by its broad oblong to oblanceolate lateral pinnae that grow to 21 cm long and are usually widest above the middle.

Etymology: *Draco* meaning dragon or serpent in Latin, referring to the sinuate apices and its sticky reddish exudate, as in *Dracaena draco* (L.) L. (Asparagaceae).

Additional material examined (paratypes): TRINIDAD: Aripo Road, forest gully on densely shaded heavy clay bank, near 2.5-mile post, *Broadway 8043* (BM). Aripo Road, 13 November 1925, *Broadway s.n.* (K). Aripo Road, 3- to 4-mile posts, 15 May 1927, *Broadway s.n.* (BM). Aripo Valley, 2.5-mile gully, *Homersley 161* (BM). Aripo Valley, 2.5-mile gully, *Homersley 238* (BM). Las Cuevas Road, beyond the ridge, *Homersley 376* (BM). Tocuche, *Othmer 170* (M, P). El Tocuche, *Williams 10706* (K).

DANAEA EPIPHYTICA CHRISTENH., SP. NOV.

(FIG. 5)

Type: Ecuador, Carchi, perhumid forest on wet plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 78°17'W, 1°6'N, c. 1000 m, 7 February 1985, *B. Øllgaard et al. 57448* (holotype QCA; isotype AAU).

Diagnosis: Planta epiphytica vel terrestis. Frondes steriles usque ad 110 cm longae vel longiores. Stipites continui. Pinnae laterales (8–) 16–17-jugae, maximae 19–23 × 2.6–3.5 cm, lanceolatae vel lineari-lanceolatae, apice longe cuspidato vel caudato, marginibus integris. Pinna terminalis lanceolata, 15–20 × 2.8–3.9 cm. Venae plerumque furcatae.

Description: Epiphytic ferns, reported to grow 3 m up on tree trunks. Rhizomes probably radially arranged (not preserved completely in the specimens studied), stipules c. 0.9 cm wide; leaves imparipinnate; sterile leaves 60–110 cm long, petioles up to 41 cm long, without nodes; rachises sparsely scaly, reddish tinged, not winged; blades to 66 × 25–34 cm, concolorous, with (8–) 16–17 pinna pairs; largest lateral pinnae (linear–)lanceolate, 5.7–8.5 times longer than wide,

19–23 × 2.6–3.5 cm, parallel-sided, apices long-cuspidate to caudate, bases acute, margins entire, slightly to clearly sinuate at apex; terminal pinnae present, lanceolate, 15–20 × 2.8–3.9 cm, parallel-sided, margins entire; midveins conspicuously reddish–brown to orange, especially abaxially; veins mostly forked, with a few simple ones in between, 13–16 veins per cm. Fertile leaves and juveniles not known.

Distribution and ecology: This species occurs on the Pacific side of the Andes in Colombia and Ecuador, in extremely wet, montane rainforests, 600–1000 m. According to the collector of the type (B. Øllgaard, pers. comm.), the plants were growing fully epiphytically at a height of 1.5–3.0 m above the ground. This is the only known record of a fully epiphytic Marattiaceae.

Etymology: This is the only species in the family known to be epiphytic.

Note: *Danaea epiphytica* was cited as *Danaea sp. I* in Christenhusz (2007). This species differs from other species of section *Danaea* by its numerous parallel-sided pinnae and its epiphytic habit. More studies at the type locality should shed light on this enigmatic species.

Additional material examined (paratypes): COLOMBIA: El Valle: 'Calima' on Río Calima, Killip 11239 (NY).

DANAEA LEUSSINKIANA CHRISTENH., SP. NOV.

(FIG. 6)

Type: Costa Rica: Heredia: Sarapiquí, La Selva Biological Station, near grid post 2000:1850, 13 June 2002, *M. M. Jones 484* (holotype CR; isotype TUR).

Diagnosis: Rhizomata repentia. Frondes steriles c. 120–125 cm longae. Stipites sine nodis vel in foliis juvenilibus uninodi. Pinnae laterales 12-jugae, maximae 20–23 × 3.1–3.4 cm, lanceolatae, apice acuto, marginibus integris. Pinna terminalis lanceolata, 14.5 × 3.1 cm. Venae simplices. Species *Danaeae mediae* similis, a qua differt pinnarum apice acuto (non caudato) et frondibus maturis iridescenticaeruleis.

Description: Plant terrestrial, with creeping, dorsoventral rhizomes, but leaves arranged spirally, roots only on the lower side (M. Jones, pers. observ.); leaves imparipinnate; sterile leaves c. 120–125 cm, petioles 60–64 cm, usually without nodes in adult leaves; rachises not winged, sparsely scaly; blades c. 60 × 36–40 cm, glossy iridescent blue–green, ovate, widest at

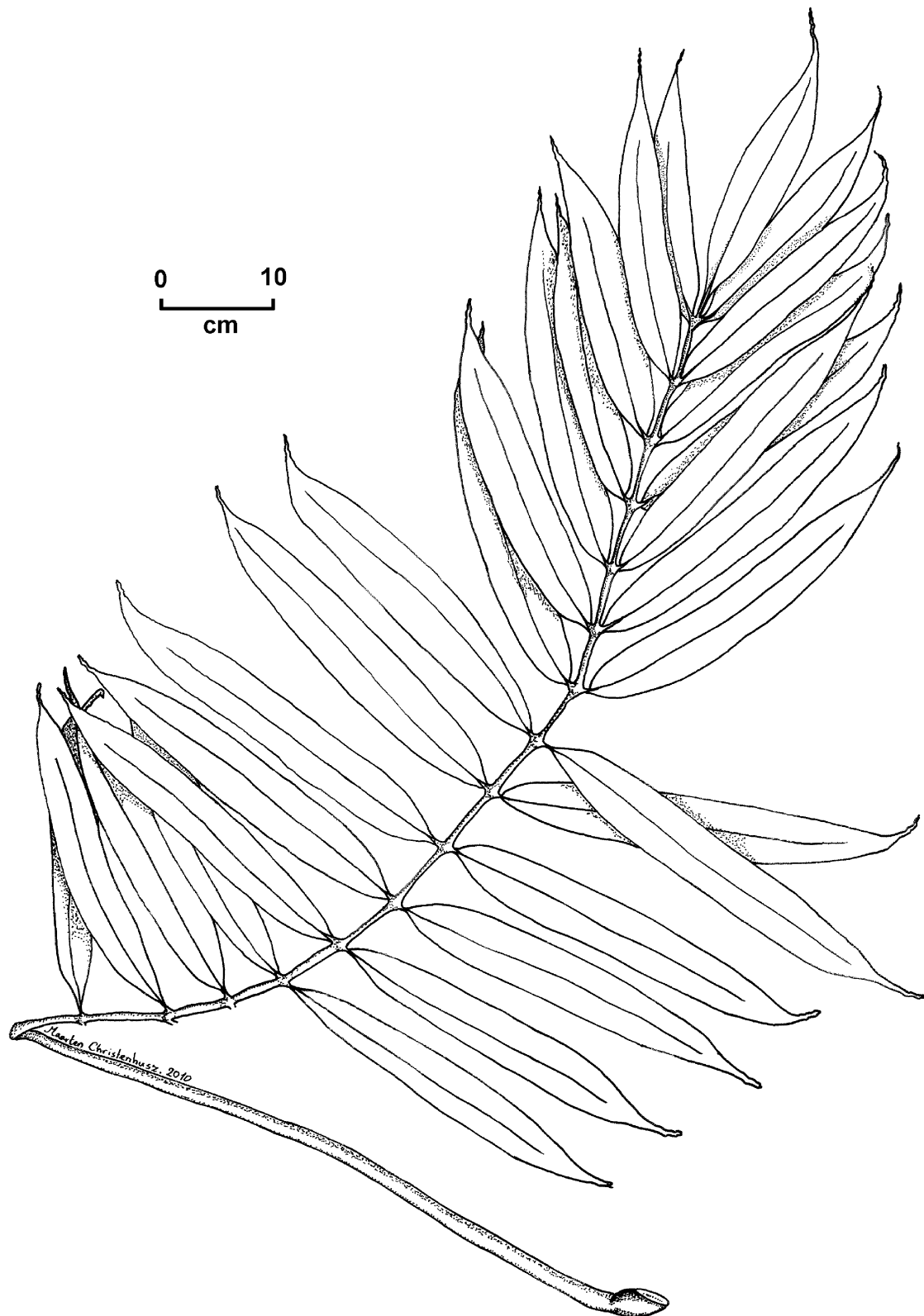


Figure 5. *Danaea epiphytica*, based on Øllgaard et al. 57448 (AAU).

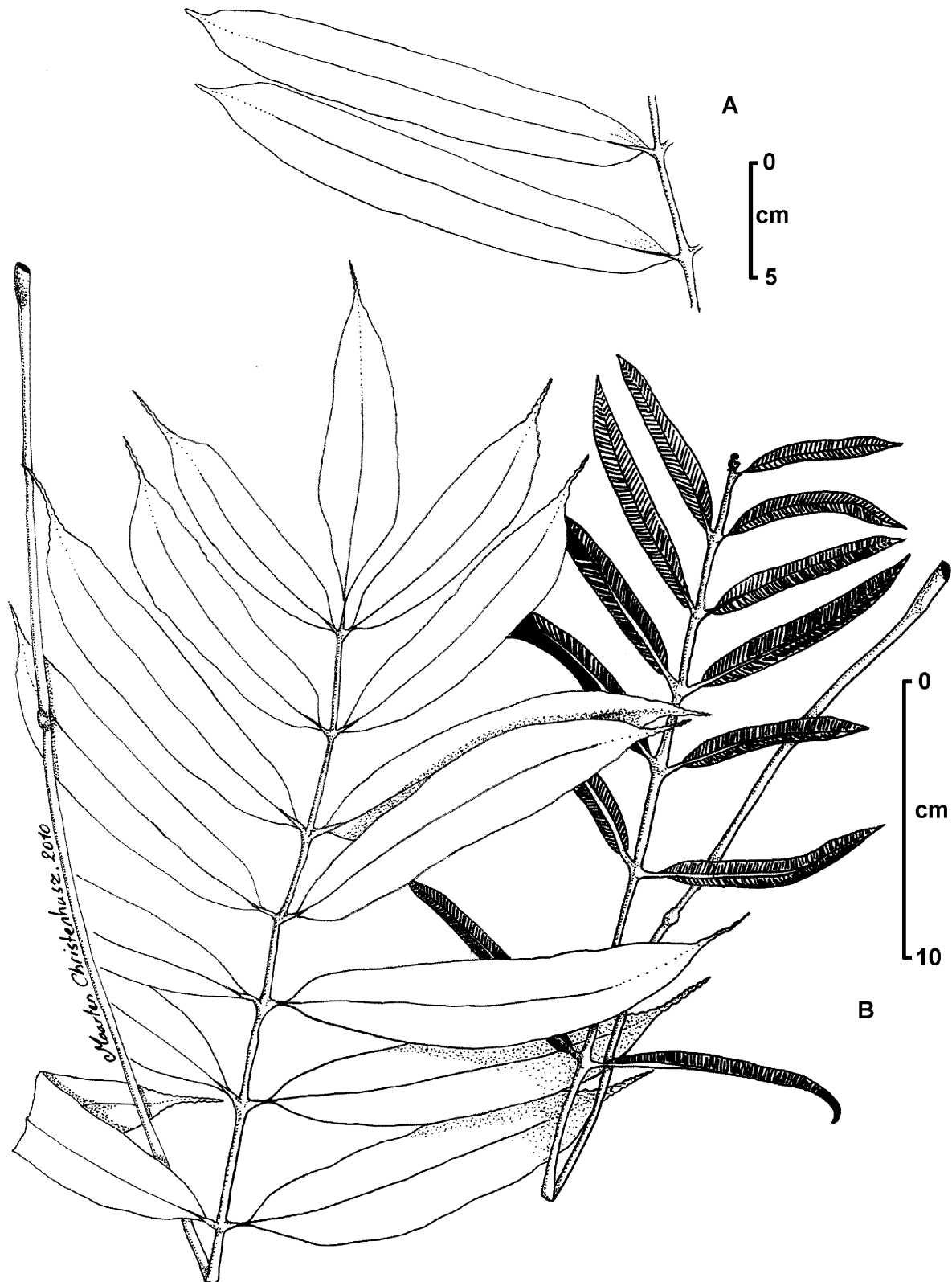


Figure 6. A, *Danaea leussinkiana*, leaf fragment, based on *Jones 484* (TUR). B, *Danaea xenium*, based on *Higgins 1266* (TUR).

base, with 12 pinna pairs; largest lateral pinnae lanceolate, *c.* 6–7 times longer than wide, 20–23 × 3.1–3.4 cm, widest at the middle or parallel sided, apices acute, bases acute, margins entire, not sinuate; terminal pinnae present, usually smaller than the lateral pinnae, lanceolate, 14.5 × 3.1 cm, parallel sided, margins entire; veins simple, 14–16 veins per cm; fertile leaves not known.

Juveniles having pinnae that are shorter, but equally wide or wider than pinnae in adult leaves. Young leaves can have nodose petioles. Young leaves soon becoming pinnate, a 12-cm long leaf already having two pairs of pinnae.

Distribution and ecology: This species is only known from Costa Rica at the La Selva Biological Station, on flat terrain and in stream valleys on residual oxisol, 50–150 m.

Etymology: Named for my mother Gerdi Leussink, who always supported me and encouraged my interest in nature.

Note: *Danaea leussinkiana* was cited as *Danaea sp.* A in Christenhusz (2007) and Christenhusz *et al.* (2008). It is remarkable in having an iridescent blue colour when adult. Several other species such as *D. nodosa* and *D. grandifolia* also have iridescent colouring but mostly when juvenile.

Additional material examined (paratypes): COSTA RICA: Heredia: Sarapiquí, La Selva Biological Station, near grid post 2200:1900, 23 July 2002, Jones 542 (TUR, CR).

DANAEA QUEBRADENSIS CHRISTENH., SP. NOV.

(FIG. 7)

Type: Colombia, Antioquia, Vic. Planta Providencia, 28 km south-west of Zaragoza, valley of Río Anorí in areas surrounding the confluence of Quebrada La Tirana and Río Anorí, *c.* 3 km upriver from Planta Providencia, 400–700 m, *c.* 75°04'W, 07°18'N, 3 April 1977, W.S. Alverson *et al.* 336 (holotype NY, 3 sheets).

Diagnosis: Rhizomata repentia vel ascendentia. Frondes steriles 57–109 cm longae. Stipites articulati, nodis (0–) 1–2. Pinnae laterales 10–13-jugae, maximae 11–20.5 × 1.8–2.9 cm, lanceolatae, apice falcati-cuspidato, marginibus integris sed ad apicem acute serrulatis. Pinna terminalis ovato-lanceolata, 7.5–10 × 1.8–2.5 cm, sed gemma saepe substituta. Venae plerumque furcatae vel geminatae. Frondes fertiles 10–13-jugae, stipite nodoso nodo unico, pinnis lateralibus lanceolatis. Species *Danaeae moritzianae*

valde similis, a qua differt venis densis, (14–) 17–21 per cm, et frondibus majoribus apice falcati-cuspidato acute serrulato.

Description: Plant terrestrial to 75 cm tall, growing in large clumps. Rhizomes creeping–ascending, sometimes almost like forming a trunk, *c.* 3 cm wide at apex, leaves spirally arranged, roots formed mostly on the ventral side; scaly throughout the rhizome, stipules, rachis and midveins below; stipules 0.9–1.2 cm wide; leaves paripinnate or imparipinnate; sterile leaves 57–109 cm long, petioles 20–51 cm long, with (0–) 1–2 nodes; rachises scaly, winged, the wing minute to 0.4 mm wide in upper part of internode, near the leaf apex; blades 34.4–58.0 × 13–23 cm, glossy green above, dull green below, with 10–13 pinna pairs; largest lateral pinnae lanceolate, 5.4–9.3 times longer than wide, 11.0–20.5 × 1.8–2.9 cm, widest below the middle, apices cuspidate, falcate, bases oblique, obtuse-cordulate, margins entire, apices sharply serrulate; terminal pinnae present or replaced by bulbils, ovate-lanceolate, 7.5–10.0 × 1.8–2.5 cm, widest below the middle, margins serrulate at apex; veins usually forked or paired at base, (14–) 17–21 veins per cm; fertile leaves 95–103 cm long, petioles 66–67 cm long with one node, blades 29.5–37.0 × 14–19 cm with 10–13 pinna pairs; lateral pinnae lanceolate, largest lateral pinnae 11–12 × 1.2–1.4 cm, widest below or at the middle, apices acute, bases cordulate, margins serrulate at apex; terminal pinnae not preserved in any of the specimens; juveniles blue iridescent, simple leaves to 4.5 cm tall, the first pinnae appear on 5-cm long leaves, then soon becoming more pinnate, 23-cm long leaves having three pairs of pinnae.

Distribution and ecology: This species is known from the departments of Antioquia, Norte de Santander and Chocó in Colombia, where it grows on hilly terrain in wet forests with *c.* 4500 mm of annual precipitation, 250–700 (–2500) m.

Etymology: After Quebrada La Tirana, one of the creeks along which it can be found.

Note: *Danaea quebradensis* was cited as *Danaea sp. K* in Christenhusz (2007). This species has sessile pinnae with sharply serrulate apices and a dense venation (17–21 per cm). The similar *D. falcata* Tuomisto & R.C.Moran has minutely stalked, coarsely denticulate apices and less crowded veins (11–16 per cm).

Additional material examined (paratypes): COLOMBIA: Antioquia: Municipio Tarazá, Corregimiento El 12, 210 km north-east of Medellín, Barro Blanco,

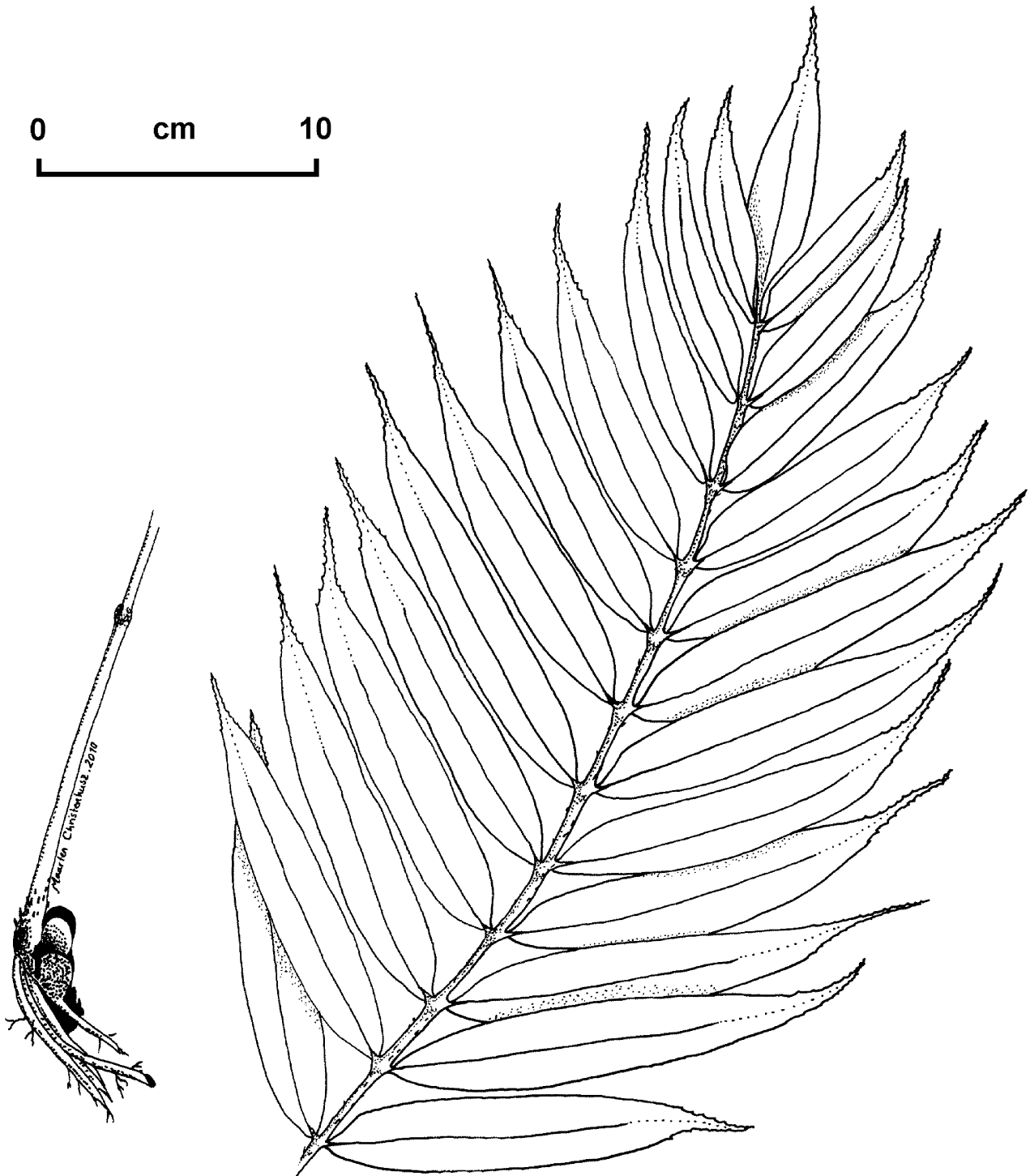


Figure 7. *Danaea quebradensis*, based on Alverson *et al.* 336 (NY).

Arbeláez 225 (NY). Peñas Blancas, *Woronow & Juzepczuk 4525* (US). Río Guapá, 6 km east of Guapá, 53 km south of Turbo, *Haught 4663* (NY). Chocó: Municipio San José del Palmar, Vereda La Holanda, *Franco 1240* (MO). Norte de Santander: Bellavista on pipeline, *Foster 1675* (A).

DANAEA TRINITATENSIS CHRISTENH. & TUOMISTO,
SP. NOV.
(FIG. 8)

Type: Trinidad, Las Lapas Road (branch of Blanchisseuse Road), on a cool shaded bank, 5 February 1926, *W.E. Broadway 5939* (holotype K; isotypes BM, Z).

Diagnosis: Rhizomata erecta, usque ad 10 cm longa et 2.5 cm lata ad apicem (in sicco). Stipites articulati, nodis (1–) 2 (–3). Pinnae laterales (1–) 3–4-jugae, maximae 6.0–16.5 × 2.0–3.9 cm, ellipticae vel lanceolatae vel oblanceolatae, apice longe acuminato vel paene cuspidato, marginibus ad apicem saepe insigniter sinuatis. Pinna terminalis oblonga vel lanceolata, (6–) 11–22 × (2.0–) 3.0–4.6 cm. Frondes fertiles (2–) 4 (–5)-jugae, stipite nodoso 1–3 nodis et pinnis lateralibus lanceolatis. Habitat in silvis umbrosis humidis in Insula Trinitatis.

Description: Plant terrestrial. Rhizomes erect, to 10 cm long and 2.5 cm wide at apex (when dried), leaves spirally arranged and stilt roots produced on all sides; stipules 0.3–0.5 cm wide. Sterile leaves 19–55 cm long; petioles (8–) 18–38 cm long, with (1–) 2 (–3) nodes; rachises sparsely scaly, not or very narrowly winged; blades (12–) 18–29 × 9–24 (–27) cm, pale and yellowish green; imparipinnate with (1–) 3–4 lateral pinna pairs, sometimes simple; largest lateral pinnae elliptic to (ob-)lanceolate, 3.0–6.5 times longer than wide, 6.0–16.5 × 2–3.9 cm, widest at (or above) the middle; pinna bases acute, apices long acuminate to almost cuspidate, margins entire but slightly irregular and often remarkably sinuate at apex; terminal pinnae present, conform but oblong to lanceolate, parallel-sided or widest at or below the middle, (6–) 11–20 cm × (2.0–) 3.0–4.6 cm; veins simple or paired at base, occasionally forked, 8–10 veins per cm. Fertile leaves 26–66 cm long, petioles 15–46 cm long with 1–3 nodes, blades 11–20 × 6–16 cm, brown, with (2–) 4 (–5) pinna pairs; lateral pinnae lanceolate, 4–8 times longer than wide; largest lateral pinnae 4–10 (–11) × 0.9–1.8 (–2.0) cm, widest below or at the middle, apices acute–acuminate, bases obtuse, margins serrulate; terminal pinnae lanceolate, (4–) 5–10 (–16) × 1–2 cm, widest below the middle, margins serrulate.

Juvenile plants may produce simple leaves up to 20 cm long and fertile leaves may already be produced at the trifoliate stage.

Distribution and ecology: Trinidad. Found in forested gullies on shaded clay and sand banks at c. 500 m elevation.

Etymology: Named after the island Trinidad, to where this species is endemic.

Note: *Danaea trinitatensis* was cited as *Danaea sp. H* in Christenhusz (2007). This species resembles *D. geniculata* but is remarkable in that the pinna apices are abruptly tapering to an elongate tip and have strongly sinuate margins (especially when juvenile). *Danaea geniculata* has more gradually tapering apices with entire or minutely sinuate margins.

Additional material examined (paratypes): TRINIDAD. Arima Ward 2.5 miles up Aripo Valley, *Walker T7066* (BM). Asa Wright Nature Centre, 7 miles north of Arima, *Mickel 9423* (NY), *Mickel 9461* (NY). Blanchisseuse Road, *Homersley 163* (BM), *Homersley 393* (BM), *Jermy 10870* (BM). 10.25-mile gully on Blanchisseuse Road, *Mickel 9599* (NY). Las Lapas Road, *Homersley 284* (BM), *Homersley 285* (BM), *Homersley 398* (BM), *Jermy 11177* (BM). Jacarigua Ward (Las Lapas Road), *Homersley 394* (BM), Maravel Valley, *Othmer 413* (M, P), *Othmer 415* (M). Without locality, *Fendler 28* (BM, BR, C, E, F, G, IJ, K, M, UC). Without locality, *Hart 6304* (K, NY, P).

DANAEA XENIUM CHRISTENH. & TUOMISTO,
SP. NOV.
(FIG. 6B)

Type: Peru, Loreto, 2 km north-east of intersection of Rio Corrientes and Lot 1AB main road, precipitously hilly, hills 30–40 m high and 150 m wide. 76.1817° W, 2.5531° S, *M. Higgins 1266* (holotype USM, isotypes BM, NY, TUR).

Diagnosis: Rhizomata repentia. Frondes steriles usque ad 118 cm longae. Stipites articulati, nodis 1–2. Pinnae laterales (4–) 6–7-jugae, maximae 15–27 × 2.7–4.8 cm, late oblanceolatae, apice cuspidato vel caudato, marginibus integris sed ad apicem serrulatis. Pinna terminalis lanceolata, 13–27 × 3.4–4.7 cm, sed gemma saepe substituta. Venae plerumque ad basin geminatae. Frondes fertiles 6–7-jugae, stipite nodoso 1–2 nodis et pinnis lateralibus oblanceolatis vel oblanceolatis. Species *Danaeae bicolori* valde similis, a qua differt laminis concoloribus ad apicem serrulatis (non crenatis).

Description: Plant terrestrial. Rhizomes creeping, 6–16 cm long, 1.6–3.0 (–4.6) cm wide at apex, dorsiventral with all roots on the ventral side and most leaves in several rows on the dorsal side; stipules

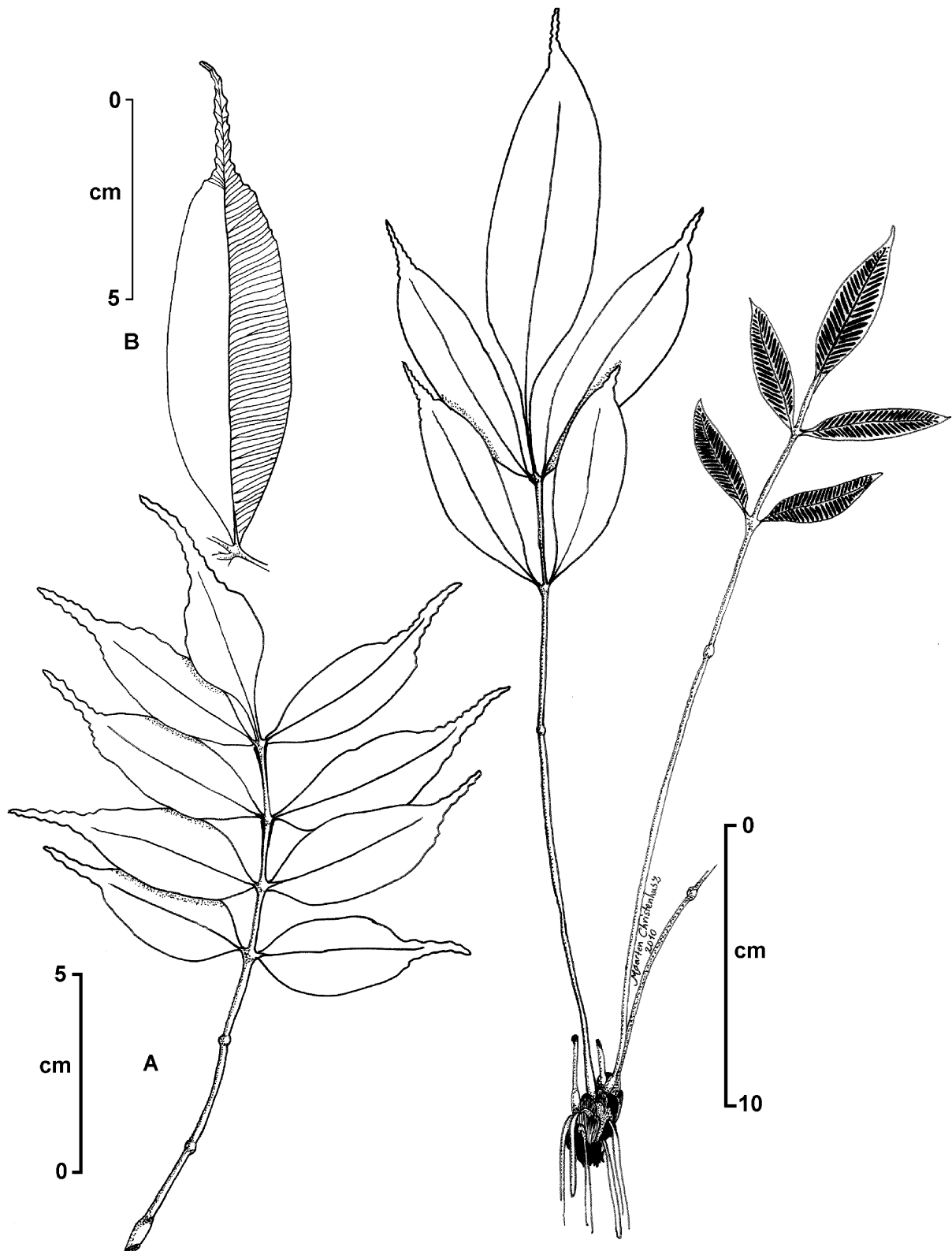


Figure 8. *Danaea trinitatensis*. A, juvenile leaf. B, pinna. C, plant. A–B, based on *Broadway 5939* (K). C, based on *Walker T7066* (BM).

0.6–1.7 cm wide. Sterile leaves (34–) 48–118 cm long; petioles 20–63 cm long, with 1–2 nodes; rachises scaly, not or minutely winged; blades (12–) 16–56 × 21–40 cm, concolorous; either paripinnate and ending in a bulbil or imparipinnate, with (4–) 6–7 lateral pinna pairs; largest lateral pinnae broadly oblanceolate, 4–7 times longer than wide, 15–27 × 2.7–4.8 cm, widest above or at the middle; pinna bases obtuse or acute, apices cuspidate to caudate, margins entire otherwise but serrulate at apex; terminal pinnae, when present, conform but lanceolate, 13–27 × 3.4–4.7 cm, widest below or at the middle; veins mostly paired at base, sometimes simple, (10–) 11–17 veins per cm. Fertile leaves 66–84 cm long, petioles 37–49 cm long with 1–2 nodes, blades 29–35 × 12–20 cm, with 6–7 lateral pinna pairs; lateral pinnae oblinear to oblanceolate, largest lateral pinnae 5–12 × 0.9–1.4 cm, widest above the middle, bases acute, apices abruptly acute-acuminate, margins denticulate at apex; terminal pinnae replaced by a bulbil or (in one of the observed specimens) linear, 8.0 × 0.9 cm, widest at the middle. Juveniles not known.

Distribution and ecology: Lowland Amazonian forests in Peru, Colombia and probably Ecuador. Closed canopy ‘tierra firme’ rainforest, usually on slopes on undulating terrain, sometimes locally dominant (M. Higgins, pers. comm.).

Etymology: From the Latin ‘*xenium*’, a present.

Note: *Danaea xenium* was cited as *Danaea sp. J* in Christenhusz (2007). This species resembles *D. nodosa* (L.) Sm., *D. nigrescens* Jenm. and *D. media* Liebm. in habit, but differs from the first two in nodose petioles and in leaves arranged in more than two rows on the rhizome, and from all three species in the terminal pinna often being replaced by a bulbil and in the pinna bases being relatively symmetrical. *Danaea xenium* resembles *D. bicolor* Tuomisto & R.C.Moran, but differs in having concolorous blades and more clearly serrulate (rather than crenate) pinna apices. *Danaea falcata* Tuomisto & R.C.Moran is a smaller plant with smaller, narrower and more falcate pinnae that are more densely arranged along the rachis.

Additional material examined (paratypes): COLOMBIA: Putumayo: Cordillera Oriental (east slope), near San Diego de Colorado, near tributary of Río Putumayo, between Umbria and Puerto Assis, *Ewan 16781* (UC). PERU: Loreto: *Cárdenas 703* (AMAZ, TUR), *Cárdenas 822* (AMAZ). Rio Pastaza, *Higgins*

410 (AMAZ, TUR), *424* (TUR), *538* (AMAZ, TUR), *714* (TUR), *901* (TUR), *1192* (TUR), *1198* (AMAZ, TUR).

***DANAEA YPORI* CHRISTENH., SP. NOV.**

(FIG. 2B–D)

Type: French Guiana, Montagne de l’Inini, zone centrale, forêt sur pente, face est, 670 m, 3°34’20”N, 53°32’30”W, 22 August 1985, *G. Cremers et al. 9089* (holotype P; isotypes B, BR, BM, CAY, MO, NY, U, UC, Z).

Diagnosis: Rhizomata repentia vel ascendentia. Frondes steriles 37–66.5 cm longae. Stipites articulati, nodis (1–) 2–3. Pinnae laterales (12–) 13–16-jugae, maximae 5.3–11.5 × 1.1–1.8 cm, oblanceolatae, apice acuto vel acuminato, marginibus acute serrulatis. Pinna terminalis trullati–lanceolata, 4.4–5.6 × 0.9–1.2 cm, sed gemma plerumque substituta. Venae densae, simplices vel raro furcatae vel geminatae. Frondes fertiles 13–15-jugae, stipite nodoso (2–) 3 (–4) nodis et pinnis lateralibus lineari–lanceolatis. Species *Danaeae moritzianae* valde similis, a qua differt venis densis plerumque simplicibus, foliis minoribus et rhizomatibus plerumque repentibus.

Description: Plant terrestrial. Rhizomes creeping–ascending, leaves and roots radially arranged, 4–6 cm long, 1.3–1.9 cm wide at apex; stipules 0.5–0.9 cm wide; leaves paripinnate or imparipinnate; sterile leaves 37.0–66.5 cm long, petioles 14–30 cm long, with (1–) 2–3 nodes; rachises slightly scaly below and along the midveins, scaly at the nodes, winged, the wing up to 0.8 mm in upper part of internode in the apical part of the leaf; blades 22–37 (–40) × 11–20 cm, dark green above, lighter green below, with (12–) 13–16 pinna pairs; largest lateral pinnae oblanceolate, 4.8–8.2 times longer than wide, 5.3–11.5 × 1.1–1.8 cm, widest above the middle, apices acute to acuminate, bases oblique truncate–obtuse, margins sharply serrulate at apex; terminal pinnae usually replaced by bulbil, rarely present, trullate–lanceolate, 4.4–5.6 × 0.9–1.2 cm, widest below the middle, apices sharply serrulate; veins dense, simple, occasionally forked or paired, 13–20 veins per cm; fertile leaves 40.0–57.5 cm long, petioles 20.0–34.5 cm long with (2–) 3 (–4) nodes, blades (16–) 23–32 × 5–9 cm with 13–15 pinna pairs; lateral pinnae linear–lanceolate, largest lateral pinnae 3.2–7.5 × 0.3–0.5 cm, widest below the middle or parallel-sided, apices obtuse to acute, bases obtuse, margins serrulate at apex; terminal pinnae usually absent and replaced by bulbil; juveniles with simple leaves up to 1.0–1.5 cm tall, soon becoming pinnate, the first pair appearing when juveniles are 4 cm tall, and 15 cm leaves already bearing seven pinna pairs.

Distribution and ecology: French Guiana, known from Inini, Sommet Tabulaire and Montagne Tortue, between rocks along creeks in primary forest, 120–670 m.

Etymology: The epithet is the Galibi (Native American Carib tribe) word for a creek, along which this species can be found.

Note: This species was cited as *Danaea sp. E* in Christenhusz (2007). This species is distinguished from other members of section *Holodanaea* by its dense simple venation and its acute to short-acuminate pinna apices.

Additional material examined (paratypes): FRENCH GUIANA: Bassin de la Comté, piste de Bélizon vers Montagne Tortue, km 31.2, *Billiet et al. 6318* (BR, BM, CAY, MO, P). Sommet Tabulaire, zone sud, crique encassé coulant entre les rochers, ± 45 km sudest de Saül, *De Granville 3602* (CAY, Z).

DANAEA ZAMIOPSIS CHRISTENH. &
TUOMISTO, **SP. NOV.**
(FIG. 9)

Type: Panama, Capira district, Cerro Campana National Park, 8°41.2'N, 79°55.3'W, 900–950 m, 25 October 2005, *H. Tuomisto & S. Aguilar 15163* (holotype PMA, isotypes AAU, BM, MO, NY, TUR, UC, Z).

Diagnosis: Rhizomata erecta, gracilia, usque ad 40 cm longa et 2 cm lata ad apicem (in sicco). Stipites articulati, nodis 2–3. Pinnae laterales (3–) 4-jugae, maximae 13.0–16.8 × 3.5–5 cm, elliptico-oblongae vel oblanceolatae, apice acuto, marginibus omnino integris. Pinna terminalis oblonga vel oblongolanceolata, 14.4–18.0 × 4.0–5.5 cm. Frondes fertiles 5-jugae, stipite nodoso 2–3 nodis et pinnis lateralibus longe petiolatis lanceolatis.

Description: Plant terrestrial. Rhizomes erect, slender, to 40 cm tall and 2 cm wide at apex (when dried), leaves and stilt roots arranged spirally; stipules 1.0–1.6 cm wide. Sterile leaves 43–67 cm long; petioles (11–) 21–35 cm long, with 2–3 nodes; rachises sparsely scaly on the abaxial side and on the midrib below, not or minutely winged in upper part of internodes; blades 24–32 × 17–25 cm, thick and coriaceous, dull green; imparipinnate with 3–4 (–5) lateral pinna pairs; largest lateral pinnae elliptic-oblong to oblanceolate, *c.* 2.5–3 times longer than wide, 13.0–16.8 × 3.5–5.0 cm, widest at or above the middle, rarely bipinnate with small extra pinnae at the terminal node; pinna bases and apices acute, margins

entire throughout; terminal pinnae present, oblong to oblong-lanceolate, 14.4–18.0 × 4.0–5.5 cm, widest below or at the middle; veins simple or paired at base, with occasionally forked ones in between, confluent with the margin, (9–) 10–11 veins per cm. Fertile leaves (52–) 61–80 cm long, petioles 29–52 cm long with 2–3 nodes, blades 23.0–30.4 × 18–22 cm with five lateral pinna pairs, the petiolules to 1 cm long; lateral pinnae lanceolate, largest 9.0–11.2 × 1.9–2.5 cm, widest below or at the middle, bases and apices acute, margins entire; terminal pinnae lanceolate, 7.4–12.0 × 1.2–2.5 cm, widest below the middle, margins entire. Juvenile plants produce the first lateral pinna pair when the leaves are *c.* 12–16 cm long.

Distribution and ecology: Montane forests in Panama at 700–1000 m elevation.

Etymology: The epithet is derived from the cycad *Zamia* L. and refers to the stiff and leathery leaves of this species.

Note: *Danaea zamiopsis* was cited as *Danaea sp. G* in Christenhusz (2007). It is most similar to *D. antillensis* Christenh., *D. arbuscula* Christenh. & Tuomisto and *D. danaëpinna* Christenh., but is distinguished by its stiff leaves and thick, leathery, elliptic-oblong pinnae with abruptly acute apices. It may form dense local populations.

Additional material examined (paratypes): PANAMA: Panamá: Distrito de Capira, Cerro Campana, trocha desde el mirador a la cima, *Galdames et al. 1819* (PMA, US). Veraguas: 5 miles west of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of Divide, *Liesner 883* (F).

SUBGENERIC CLASSIFICATION OF THE
GENUS *DANAEA*

Phylogenetic studies based on plastid DNA have demonstrated three well-supported clades within *Danaea* (Christenhusz *et al.*, 2008). All three clades have a broad distribution, spanning nearly the entire geographic range of the genus. Each clade can be relatively easily recognized on the basis of morphological characters (Christenhusz & Tuomisto, 2005). Presl (1845) described three subgeneric taxa in *Danaea*, which were initially unranked, but were later discussed by Presl as subgenera. Although Presl's circumscriptions of the subgenera do not correspond with the phylogenetic lineages (Fig. 10; Christenhusz *et al.*, 2008), the names are applicable to these.

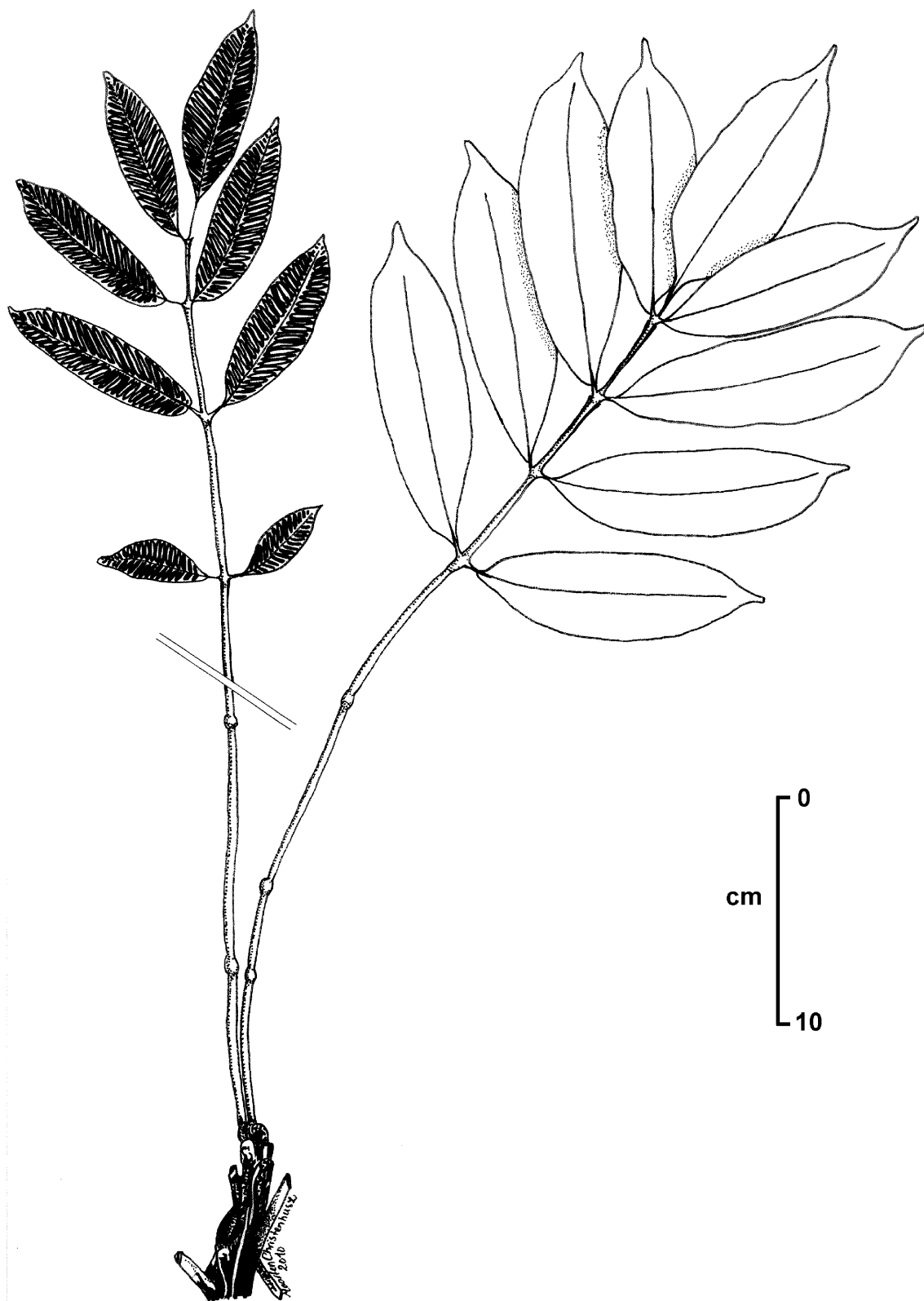


Figure 9. *Danaea zamiopsis*, based on *Tuomisto 15163* (TUR).

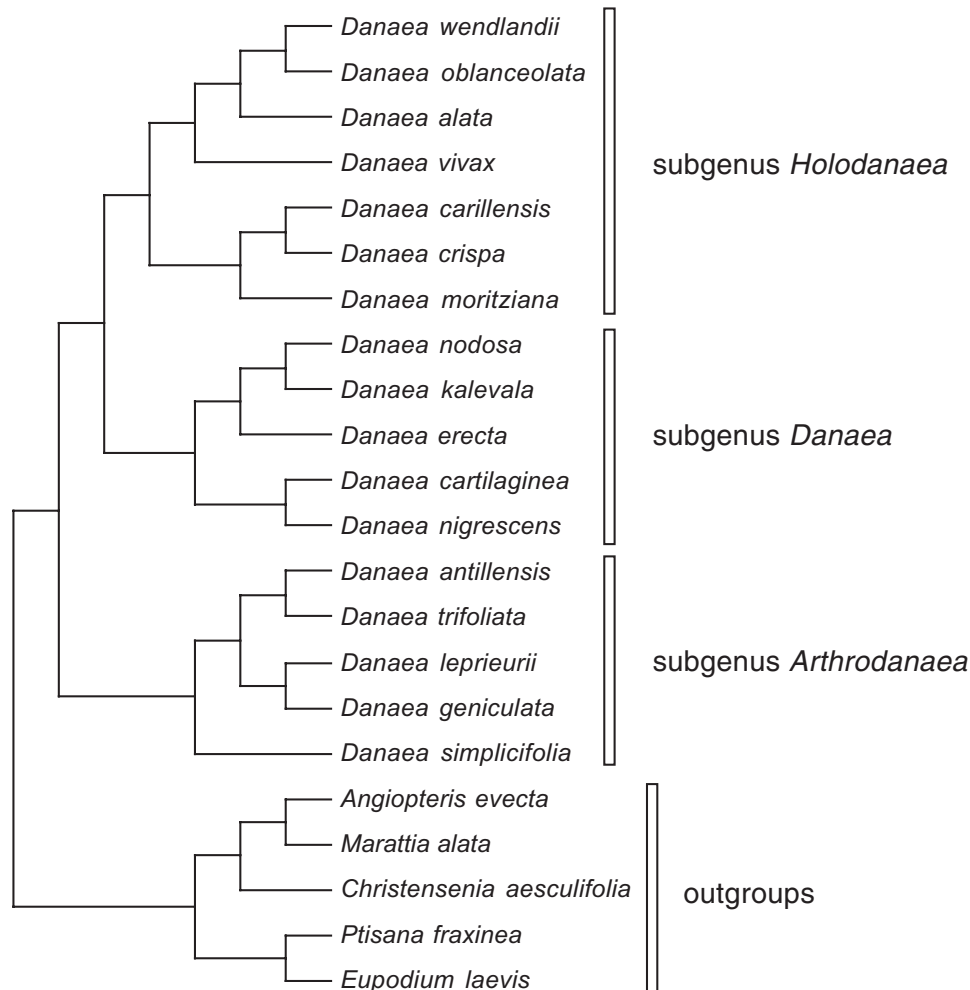


Figure 10. Simplified cladogram (‘chasogram’) of *Danaea*, based on Bayesian analysis of three plastid regions (*atpB*, *rbcL* and *trnL-trnF*), after Christenhusz *et al.* (2008). The outgroups are arranged following Murdock (2008).

I. DANAEA SM. SUBGENUS DANAEA

Synonym: *Danaea* Sm. subgenus *Eudanaea* C.Presl (1845)

Description: Generally large plants, with leaves 1–3 m long. Rhizomes either creeping and clearly dorsiventral or erect with leaves and roots arranged radially. Petiole nodes absent in most species but present in a few. Lamina green on both surfaces (never whitish underneath), with more than seven lateral pinna pairs and usually a conform terminal pinna, which may be replaced by a bulbil or plantlet in some species. Pinnae of sterile leaves generally elongate. Pinnae of fertile leaves narrowly elliptic–lanceolate. Pinna margins entire but dentate or denticulate at the apices.

Species: *Danaea nodosa* (L.) Sm., type

Synonyms: *D. angustifolia* C.Presl, *D. cordata* Fée, *D. elliptica* Sm., *D. elliptica* var. *major* Jenman, *D. elliptica* var. *repens* Jenman, *D. nodosa* var. *angustifolia* (C.Presl) T.Moore, *D. nodosa* var. *intermedia* J.Sm. ex Hassl., *D. sellowiana* C.Presl

D. cartilaginea Christenh. & Tuomisto

D. epiphytica Christenh.

D. erecta Tuomisto & R.C.Moran

D. grandifolia Underw.

D. kalevala Christenh.

D. latipinna Tuomisto & R.C.Moran

D. longicaudata Tuomisto

D. media Liebm.

Synonyms: *D. elata* Liebm., *D. pterorachis* Christ

D. nigrescens Jenm.

D. leussinkiana Christenh.

D. ushana Christenh.

II. *DANAEA* SM. SUBGENUS *ARTHRODANAEA*
C.PRESL (1845)

Description: Plants of intermediate size, with leaves 0.4–1.0 m long. Rhizomes erect, with leaves and roots arranged radially. Petioles nodose, in some species nodes are sometimes absent in some of the petioles of a plant. Lamina green on both surfaces (rarely whitish underneath) and either simple or with a few (up to eight) lateral pinna pairs and a conform terminal pinna (never replaced by a bulbil). Pinnae of sterile leaves generally (broadly) elliptic to ovate–lanceolate. Pinnae of fertile leaves narrow–elliptic. Pinna margins entire throughout (or at most sinuate at apex).

Species: Danaea leprieurii Kunze, type

D. antillensis Christenh.

D. arbuscula Christenh. & Tuomisto

D. bipinnata Tuomisto

D. danaëpinna Christenh.

D. draco Christenh.

D. geniculata Raddi

Synonym: D. elliptica Sm. var. *crispula* Rosenst.

D. lingua-cervina Christenh. & Tuomisto

D. polymorpha Lepr. ex Baker

Synonym: D. oligosora E.Fourn. ex Baker

D. simplicifolia Rudge

D. trifoliata Rchb.

D. trinitatensis Christenh. & Tuomisto

D. ulei Christ

D. zamiopsis Christenh. & Tuomisto

III. *DANAEA* SM. SUBGENUS *HOLODANAEA* C.PRESL
(1845)

Synonym: Heterodanaea Presl (1845).

Description: Small to intermediate plants with leaves 10–100 cm long. Rhizomes variable, ranging from creeping and strictly dorsiventral through intermediately decumbent or ascending to erect and radially arranged. Petioles nodose. Lamina varies from leathery to membranaceous and opaque to translucent, from strongly bicolorous with the abaxial side whitish to uniformly green in colour, simple or once pinnate with a few to many lateral pinna pairs; apical pinna in many species replaced by a bulbil. Pinnae of sterile leaves generally long and narrowly lanceolate. Pinnae of fertile leaves linear or linear–lanceolate. Pinna margins entire, undulate, crenate, (bi-)serrate or dentate, the apices denticulate to serrate.

Species: Danaea alata Sm., type

Synonyms: D. stenophylla Kunze, *D. fendleri* Underw.

D. acuminata Tuomisto & R.C.Moran

D. bicolor Tuomisto & R.C.Moran

D. carillensis Christ

D. chococola Christenh.

D. crispa Endrés

D. excurrens Rosenst.

D. falcata Tuomisto & R.C.Moran

Synonym: D. inaequilatera A.Rojas

D. humilis Spruce ex T.Moore

Synonym: D. serrulata Baker

D. imbricata Tuomisto & R.C.Moran

D. jenmanii Underw.

Synonym: D. wrightii Underw.

D. quebradensis Christenh.

D. mazeana Underw.

Synonym: D. jamaicensis Underw.

D. moritziana C.Presl (complex)

Synonyms: D. betancurii A.Rojas, *D. cuspidata*

Liebm., *D. lucens* A.Rojas, *D. moritziana* C.Presl

var. *brasiliensis* Rosenst., *D. muelleriana* Rosenst.,

D. muenchii Christ, *D. paraguariensis* Christ, *D.*

tuomistoana A.Rojas

D. oblanceolata Stolze

D. plicata Christ

D. riparia Christenh. & Tuomisto

D. tenera C.V.Morton

D. trichomanoides T.Moore

D. urbanii Maxon

D. vivax Christenh. & Tuomisto

D. wendlandii Rchb.f.

D. xenium Christenh. & Tuomisto

D. ypori Christenh.

DISTRIBUTION AND PATTERNS
OF SPECIATION

Danaea is one of the most species-rich genera of Marattiaceae, with approximately 50 species. Marattiaceae are not closely related to any other ferns and even the lineages within the family are rather isolated from each other (Pryer *et al.*, 2004). *Danaea* seems to have undergone rapid speciation in the recent past, as there are many species complexes in which species delimitation is difficult, and genetic differences among species are small (Christenhusz *et al.*, 2008). *Danaea* is obviously a genus that has not reached a static phase in its evolution, so my hypothesis of ongoing speciation processes may explain many of the problems that we experience in studies of this genus using morphological characters. This study will not be the final answer to the taxo-

onomic issues, but I hope it is a step forward in the application of the correct names in the future. Molecular studies of the genus at the population level are clearly needed to evaluate the species complexes in further detail.

Danaea is exclusive to and widely distributed in the Neotropics, occurring from Oaxaca in southern Mexico to Santa Catarina in southern Brazil. The genus is also found on all humid Caribbean Islands and on Cocos Island in the Pacific. The elevational range is from sea level to 2300 m, but the highest abundance and species diversity occurs between 100 and 1000 m elevation (Christenhusz, 2007). Most *Danaea* spp. appear to have a restricted geographical range, with only a few being widespread (Table 1). For instance, *D. carillensis*, *D. crispa* and *D. plicata* are only found in a small area of the highlands of Costa Rica and Panama, but *D. media* has a much wider range throughout Central America. The Cocos Island population morphologically matches *D. media* and must therefore be of Central American origin. This is remarkable because a majority of the fern flora of Cocos Island originated from South America (Svenson, 1938).

A different set of *Danaea* spp. is found on either side of the Andes, with very few species extending to both sides (Moran, 1995). For instance, *D. wendlandii* is found on the Pacific side of the Andes and in Central America, whereas the closely related *D. oblancoolata* is found in Amazonia (Christenhusz *et al.*, 2008). Several species with highly restricted ranges are found in the inter-Andean valleys or in the wet forests along the Pacific coast; for example, *D. chococcola*, *D. imbricata*, *D. quebradensis*, *D. tenera* and *D. trichomanoides*. This can be a result of elevational fragmentation of suitable habitats, as is the case for many pteridophytes (Moran, 1995). However, micro-environmental factors, such as physical and chemical variation of soils (Tuomisto & Poulsen, 1996), and micro-climatic conditions may also matter, because even in Amazonia, with little elevational variation, few species are widespread.

The spores of *Danaea* are relatively heavy compared with other ferns, which may influence the ability of the species to disperse to suitable habitats. In spite of this, *Danaea* has managed to reach relatively isolated islands (e.g. Cocos Island, Isla de la Juventud, Guadeloupe) and isolated patches of rainforest in otherwise inhospitable vegetation (e.g. Cerro León, Paraguay).

Phylogenetic studies based on plastid DNA have shown that *Danaea* subgenus *Danaea* is divided into two geographically separated clades (Christenhusz *et al.*, 2008). Specimens identified as *D. nodosa* were found in both clades, separated by morphologically

clearly different species, which shows that multiple species are actually involved. *Danaea nodosa* s.s. is found in the Greater Antilles and the Atlantic rainforests in Brazil. Most of the Central American specimens previously referred to *D. nodosa* belong to *D. media*. In the Lesser Antilles, *D. nodosa* is replaced by *D. kalevala* and *D. grandifolia* and, in the Andes, by *D. erecta*. *Danaea nodosa*-like specimens from Amazonia and the Guianas mostly belong to *D. nigrescens* and *D. cartilaginea*.

Danaea leprieurii has mostly been known from French Guiana, where numerous specimens have been collected. However, this species was also found to be common in western Amazonia (Colombia, Ecuador, Peru; Tuomisto & Moran, 2001) and in Central Amazonia (Amazonas state in Brazil), which makes its distribution contiguous.

After *D. arbuscula* was described from Peru (Christenhusz & Tuomisto, 2006), I decided to refer similar-looking plants from Guadeloupe to this species as well (Christenhusz, 2009). Additional specimens of *D. arbuscula* have also been found from Bolivia, Brazil (Mato Grosso), Colombia and Venezuela, which substantially expands the range of this montane forest species. *Danaea arbuscula* typically occurs at much lower elevations in the Antilles than it does in the Andes. This is a well-known pattern in many species, or closely related species (e.g. *D. alata*, *Elaphoglossum* and *Eriosorus*), shared between mountains on islands and mountains on continents (Leuschner, 1996).

Although most species of *Danaea* seem to have relatively restricted ranges, three are very widespread: *D. geniculata* of subgenus *Arthrodanaea*, *D. moritziana* of subgenus *Holodanaea* and *D. nodosa* of subgenus *Danaea*. Each of these is morphologically variable and most likely is in reality a species complex. On the basis of genetic evidence, I have already segregated the Amazonian–Guianan *D. nigrescens* from *D. nodosa* s.s., which has a disjunct distribution between the Caribbean islands and the Atlantic forests in south-eastern Brazil. Both species have considerably narrower ranges than *D. nodosa* s.l. and, if the Caribbean and south-eastern Brazilian populations prove to be different species, the geographical species ranges will be further reduced. In the case of *D. moritziana*, I have been unable to make firm conclusions about species delimitations, because the available samples are geographically too restricted. The DNA sequences (*atpB*, *rbcL*, *trnL-trnF*) used to reconstruct phylogenetic relationships were not variable enough to resolve the phylogenetic relationships of closely related *Danaea* spp. (Christenhusz *et al.*, 2008). These complexes may well be in an active state of evolution, such that they have not yet differentiated completely.

Table 1. Distribution of *Danaea* species in the neotropics

	Belize	Bolivia	Brazil (Amazonian)	Brazil (Atlantic)	Colombia	Costa Rica	Cuba	Dominica	Dominican Republic	Ecuador	French Guiana	Grenada	Guadeloupe	Guatemala	Guyana	Haiti	Honduras	Jamaica	Martinique	Mexico	Montserrat	Nicaragua	Panama	Paraguay	Peru	Puerto Rico	Saint Kitts and Nevis	Saint Lucia	Saint Vincent	Suriname	Trinidad and Tobago	Venezuela		
<i>D. acuminata</i>										X															X									
<i>D. alata</i>								X			X	X								X							X	X		X	X			
<i>D. antillensis</i>								X				X									X													
<i>D. arbuscula</i>		X	X		X					X			X												X	?		X	X			X		
<i>D. bicolor</i>										X																								
<i>D. bipinnata</i>			X							X																X								
<i>D. carillensis</i>						X																												
<i>D. cartilaginea</i>					X					X																X							X	
<i>D. chococola</i>					X																													
<i>D. crispa</i>						X																	X											
<i>D. danaëpinna</i>			X							X					X															X				
<i>D. draco</i>																														X				
<i>D. epiphytica</i>					X					X																								
<i>D. erecta</i>					X					X																								
<i>D. excurrens</i>				X																														
<i>D. falcata</i>					X					X																								
<i>D. geniculata</i>	X	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>D. grandifolia</i>					X				X								X										X						X	
<i>D. humilis</i>					X					X													X										X	
<i>D. imbricata</i>										X																								
<i>D. jenmanii</i>							X		X							X		X								X							X	
<i>D. kalevala</i>								X				X	X														X		X					
<i>D. latipinna</i>										X																								
<i>D. leprieurii</i>			X							X	X															X								
<i>D. leussinkiana</i>						X																												
<i>D. lingua-cervina</i>					X																					X								
<i>D. longicaudata</i>					X					X																								
<i>D. mazeana</i>							X		X			X				X		X								X								
<i>D. media</i>	X					X											X		X			X	X											
<i>D. moritziana</i>		X	X		X	X				X			X								X			X		X								X
<i>D. nigrescens</i>	X	X			X					X	X				X									X	X	X	X	X	X	X	X	X	X	X
<i>D. nodosa</i>			X	X			X		X							X		X						X			X							
<i>D. oblanceolata</i>					X					X																X								
<i>D. plicata</i>						X																												
<i>D. polymorpha</i>												X	X																					
<i>D. quebradensis</i>					X																													
<i>D. riparia</i>																										X								
<i>D. simplicifolia</i>			X								X				X																			X
<i>D. tenera</i>					X					X																								
<i>D. trichomanoides</i>										X																X								
<i>D. trifoliata</i>			X								X				X																		X	X
<i>D. trinitatensis</i>																																		X
<i>D. ulei</i>		X	X																							X	?							
<i>D. urbanii</i>									X							X											X							
<i>D. ushana</i>											X																							
<i>D. vivax</i>					X																				X									
<i>D. wendlandii</i>					X	X				X													X											
<i>D. xenium</i>					X																					X								
<i>D. ypori</i>											X																							
<i>D. zamiopsis</i>						X																												
Totals	2	5	12		19	9	4	3	6	20	8	3	7	3	5	6	2	4	2	3	1	2	6	3	15	6	1	2	3	5	7	9		

Total numbers of species per country are given.

Species known from a single country only are indicated with **X** in bold type.

KEY TO THE SPECIES OF *DANAEA*

1. Plants fully epiphytic, all specimens *c.* 1.5–3.0 m up in the trees, rooted on tree trunks and branches, not in the soil.....***D. epiphytica***
1. Plants terrestrial or lithophytic, when (hemi-)epiphytic, below 1 m on the tree and rooted in the soil.....2.
2. Leaves of adult plants simple or trifoliolate (juvenile plants of other species can also be simple or trifoliolate, but this key concerns only adult specimens).....3.
2. Leaves of adult plants pinnate or bipinnate, with at least two pairs of lateral pinnae.....6.
3. Pinna apices denticulate. Petioles with 2–4 nodes. Rhizomes creeping–ascending. Blades mostly simple, 2.8–4.5 cm wide. Costa Rica.....*D. carillensis*
3. Pinna apices entire. Petioles with 1–2 nodes. Rhizomes erect. Blades simple or trifoliolate, 3.8–29.0 cm wide. South America.....4.
4. Leaves bicolorous, white below, blades mostly simple and petioles with one node, if trifoliolate, then petioles without nodes.....*D. simplicifolia*
4. Leaves concolorous or sometimes paler green below, but not white, mostly trifoliolate or more divided; if blade simple, then petiole with 1–2 nodes.....5.
5. Largest lateral pinnae elliptic–oblong, two to three times longer than wide. Pinna apices acute to short–acuminate, with straight margins. Terminal pinnae 24–36 × 6.4–9.4 cm. Guianas, northern Brazil, tierra firme forests.....*D. trifoliata*
5. Largest lateral pinnae oblong–elliptic to lanceolate–elliptic, *c.* three times longer than wide. Pinna apices abruptly acuminate, with slightly sinuate margins. Terminal pinnae (12.4–) 15.5–25.0 cm × (2.8–) 4.7–6.8 cm. Western Amazonia, swamp forests.....*D. lingua-cervina*
- 6 (2). Pinna margins erose throughout, crispate–undulate, irregularly biserrate throughout. Blades transparent, always terminated by a bulbil.....*D. crispa*
6. Pinna margins entire, entire or denticulate to serrate at apices. Blades leathery or transparent, with or without terminal bulbils.....7.
7. Pinna margins dentate, denticulate, serrate, serrulate or crenulate at apices.....8.
7. Pinna margins entire, sometimes slightly sinuate at apices.....50.
8. Blades strongly bicolorous, dark green above, white below. Largest lateral pinnae 3.2–4.2 cm wide.....*D. bicolor*
8. Blades mostly concolorous, sometimes lighter green (not white) below; if (slightly) bicolorous, then the largest lateral pinnae less than 3 cm wide.....9.
9. Pinnae apices acute–acuminate with caudate–spathulate, sharply serrated tips. Pinnae linear–oblanceolate (Southern Brazil).....*D. excurrens*
9. Pinnae apices obtuse to caudate, without spathulate tips. Pinnae variously ovate to lanceolate.....10.
10. Rhizomes erect with roots on all sides. Leaves radially arranged.....11.
10. Rhizomes creeping, sometimes with the tips ascending, dorsiventrally arranged, with all roots on the lower side and leaves in two or more rows.....12.
11. Pinna apices sharply denticulate to serrulate. Petioles usually with 1–3 (–4) nodes, an occasional leaf may be without nodes.....*D. moritziana*
11. Pinna apices sinuate to crenulate. Petioles always without nodes.....*D. erecta*
12. (10). Blades thin, transparent or opaque, up to 30 cm long, usually terminated by a bulbil.....13.
12. Blades thick, leathery, longer than 30 cm, terminated by pinnae or bulbils.....18.
13. Pinnae biserrate throughout.....*D. crispa*
13. Pinnae once denticulate at apex.....14.
14. Blades with 3–6 pinna pairs. Terminal pinnae much longer than the lateral pinnae of the same leaf. Terminal pinnae usually midway aborted by bulbils.....*D. plicata*
14. Blades with 10 or more pinna pairs. Terminal pinnae, when present, as long as or shorter than the largest lateral of the same leaf. Blades with or without bulbils.....15.
15. Pinna apices acute to acuminate. Petioles 11–26 cm long with 2–4 nodes.....*D. tenera*
15. Pinna apices obtuse. Petioles to 11 cm long with 0–2 indistinct nodes.....16.
16. Pinnae crowded, often overlapping at the base. Margins coarsely serrulate to crenulate. Veins forked well above the base.....*D. imbricata*
16. Pinnae well spaced, not (or rarely) overlapping. Margins sinuate to denticulate. Veins mostly simple, but occasionally a few forked ones.....17.
17. Pinnae ovate to obovate, 1.3–3.2 × 0.6–1 (–1.3) cm. Margins sinuate to widely denticulate at pinna apices. Veins 8–11 per cm.....*D. trichomanoides*

17. Pinnae linear-oblong to lanceolate, 2–5.1 × 0.6–1.3 cm. Margins denticulate at pinna apices. Veins 11–22 per cm.....*D. wendlandii* 19.
- 18 (12). Petioles without nodes. Blades abrupt at the base, without reduced pinnae protruding from the lowest nodes. Rhizomes dorsiventral..... 19.
18. Petioles with (0–) 1–4 nodes, when nodes absent, than blades gradually tapering towards reduced, small, almost rotund pinnae at the blade bases. Rhizomes dorsiventral or radial.....23.
19. Rhizomes with two rows of leaves.....20.
19. Rhizomes with several rows of leaves.....22.
20. Pinnae elliptic-lanceolate, widest at the middle, with a darker zone around the midvein. Margins cartilaginous, apical teeth not incising the green part of the lamina.....*D. cartilaginea*
20. Pinnae oblanceolate, usually widest above the middle, concolorous. Margins usually not cartilaginous, apical teeth incising the green lamina..... 21.
21. Pinnae rounded and often cordulate to auriculate at base. Blades sometimes bipinnate. Greater Antilles and Atlantic Brazil.....*D. nodosa*
21. Pinnae acute to obtuse-truncate at base, never with extra pinnules. Continental South America.....*D. nigrescens*
- 22 (19). Pinna apices finely serrulate-sinuate to minutely serrulate-denticulate. Lesser Antilles.....*D. kalevala*
22. Pinna apices entire to sinuate(-denticulate). Central America.....*D. media*
- 23 (18). Largest lateral pinnae (2.7–) 3.0–5.0 cm wide.....24.
23. Largest lateral pinnae 0.4–2.9 cm wide.....25.
24. Pinnae strongly bicolorous, white below.....*D. bicolor*
24. Pinnae concolorous, light green below.....***D. xenium***
25. (23). Rhizomes clearly dorsiventral. Leaves up to 2 m long.....*D. media*
25. Rhizomes usually radially arranged, when dorsiventral in appearance, then leaves shorter than 1 m....26.
26. Terminal pinnae always present, more than twice the length of the largest lateral of the same leaf, usually the terminal pinna terminated by bulbil at the apex.....*D. plicata*
26. Terminal pinnae absent with the rachis terminated by bulbils or present and much shorter than the lateral pinnae of the same leaf.....27.
27. Largest lateral pinnae 2.0–5.1 cm long.....28.
27. Largest lateral pinnae 5.3–21 cm long.....34.
28. Terminal pinnae replaced (or aborted) by bulbils.....29.
28. Terminal pinnae present, never replaced or aborted by bulbils.....31.
29. Leaves with 5–11 lateral pinna pairs. Veins usually forked. Terminal pinnae aborted by or completely replaced by bulbils.....*D. jenmanii*
29. Leaves with 10–26 lateral pinna pairs. Veins simple or paired at base, when pinnae 10–12 pairs, then veins paired at the base. Terminal pinnae completely replaced, but may be present on some leaves of the plant.30.
30. Lateral pinnae acute-acuminate, somewhat falcate. Blades bicolorous, parallel sided.....*D. humilis*
30. Lateral pinnae acute, not falcate. Blades concolorous, lanceolate.....*D. wendlandii*
- 31 (28). Blades lanceolate with 8–15 pinna pairs. Veins 11–17 per cm.....32.
31. Blades parallel-sided with 12–24 pinna pairs. Veins 14–36 per cm.....33.
32. Sterile leaves all in an appressed rosette. Veins mostly paired at base. Western Amazonia....*D. acuminata*
32. Sterile leaves upright, arching. Veins mostly forked. Greater Antilles.....*D. urbanii*
- 33 (31). Blades bicolorous. Veins 14–18 per cm, mostly forked. Largest lateral pinnae 2.2–3.7 cm long....*D. humilis*
33. Blades concolorous. Veins dense, 21–36 per cm, mostly simple and paired at base. Largest lateral pinnae 3.4–5.1 cm long.....***D. chococola***
- 34 (27). Sterile leaves in a prostrate rosette or pendent, fertile leaves erect.....35.
34. Sterile leaves erect or arching, held similarly to the fertile leaves.....36.
35. Pinnae 2.3–6.2 cm long, 3–5 times longer than wide. Pinna apices abruptly acute to acuminate.....*D. acuminata*
35. Pinnae 7.5–8.5 cm long, 7–8 times longer than wide. Pinna apices gradually acute to long-acuminate.....*D. riparia*
- 36 (34). Blades (usually) terminated by bulbils, sometimes terminal pinnae present on leaves of the same plant....37.
36. Blades terminated by normal well-developed pinnae, never terminated by bulbils.....43.
37. Pinna apices abruptly acute to short acuminate.....38.
37. Pinna apices gradually (long-)acuminate to caudate.....40.
38. Veins mostly forked. Leaves with 5–11 pinna pairs. Greater Antilles.....*D. jenmanii*
38. Veins mostly simple. Leaves with 10–20 pinna pairs. South America.....39.

39. Blades weakly bicolorous, lighter below. Apices sharply serrulate. Veins dense, 13–20 per cm. French Guiana.....*D. ypori*
39. Blades concolorous. Apices denticulate. Veins 11–16 per cm. Western Amazonia.....*D. oblancoolata*
- 40 (37). Pinna apices acuminate. Veins simple.....*D. ypori*
40. Pinna apices long-acuminate to caudate, falcate. Veins usually forked or paired at base.....41.
41. Pinnae clearly stalked, longer than 1 mm. Pinna apices coarsely denticulate. Lowland.....*D. falcata*
41. Pinnae (sub-)sessile. Pinna apices sharply serrulate. Mid- to higher elevation.....42.
42. Veins *c.* 16 per cm. Fertile pinnae narrow, *c.* 0.6 cm wide.....*D. vivax*
42. Veins usually 17–21 per cm. Fertile pinnae broad, 1.2–1.4 cm wide.....*D. quebradensis*
- 43 (36). Veins mostly simple or paired at base, rarely a few forked ones.....44.
43. Veins mostly forked, sometimes paired at base or a few simple ones.....46.
44. Blades with 6–8 pinna pairs, concolorous. Lateral pinnae oblanceolate, 8 times longer than wide.....*D. excurrens*
44. Blades with 8–16 pinna pairs, lighter green below, dark glossy green above. Lateral pinnae 4–8.2 times longer than wide.....45.
45. Pinna apices sinuate to denticulate, acuminate to cuspidate. Lesser Antilles and northern Venezuela.....*D. alata*
45. Pinna apices sharply serrulate, acute to acuminate. French Guiana.....*D. ypori*
- 46 (43). Pinnae abruptly acuminate to cuspidate. Antilles.....47.
46. Pinnae gradually long-acuminate to caudate. South America.....48.
47. Pinnae rather narrow 1.0–1.5 cm wide, 5–9 cm long.....*D. urbanii*
47. Pinnae wider, 1.1–2.4 cm wide, 6.8–15.0 cm long.....*D. mazeana*
- 48 (46). Pinnae clearly stalked, longer than 1 mm. Pinna apices coarsely denticulate. Lowland.....*D. falcata*
48. Pinnae (sub-)sessile. Pinna apices sharply serrulate. Mid- to higher elevation.....49.
49. Veins *c.* 16 per cm. Fertile pinnae narrow, *c.* 0.6 cm wide.....*D. vivax*
49. Veins usually 17–21 per cm. Fertile pinnae broad, 1.2–1.4 cm wide.....*D. quebradensis*
- 50 (7). Rhizomes creeping, sometimes with the tip ascending, dorsiventrally arranged, with all roots on the lower side and leaves in two or more rows.....51.
50. Rhizomes erect, with roots and leaves radially arranged.....56.
51. Pinnae with cuspidate or abruptly caudate apices. Blades usually terminated by a bulbil, replacing the terminal pinnae.....*D. latipinna*
51. Pinnae with acute to acuminate–attenuate apices. Blades always with normally developed terminal pinnae, never replaced by bulbils.....52.
52. Rhizomes with two rows of leaves, placed alternately on the rhizomes.....53.
52. Rhizomes with several rows of leaves, these placed more or less radially but the roots all on the lower side.....54.
53. Pinna apex acuminate–attenuate. Pinnae 27–49 cm long. Leaves large, up to 3 m long.....*D. cartilaginea*
53. Pinna apex acute. Pinnae 23–28 cm long. Leaves much shorter, up to 1 m long (French Guiana).....*D. ushana*
- 54 (52). Pinna apices acute. Veins simple. Blades iridescent blue–green when plants adult.....*D. leussinkiana*
54. Pinna apices acuminate to caudate. Veins paired at base or forked. Blades only iridescent when plants juvenile.....55.
55. Pinna apices acuminate. Pinnae lanceolate, parallel-sided, widest at the middle.....*D. grandifolia*
55. Pinna apices acuminate–cuspidate to caudate. Pinnae oblanceolate, widest above the middle.....*D. media*
- 56 (50). Petioles always without nodes. Leaves mostly terminated by a bulbil.....*D. erecta*
56. Petioles usually nodose (1–4 nodes), rarely a few petioles of a plant without nodes. Leaves never terminated by bulbils.....57.
57. Leaves with more than 11 pinna pairs. Pinna apices abruptly acute–acuminate with caudate–spathulate tips.....*D. longicaudata*
57. Leaves with less than eight pinna pairs. Pinna apices not caudate–spathulate.....58.
58. Largest lateral pinnae 1–3(–4) cm wide.....59.
58. Largest lateral pinnae 3–6 cm wide.....62.
59. Pinnae abruptly tapering into an acuminate to cuspidate, somewhat falcate apex.....60.
59. Pinnae gradually tapering into an acute to acuminate apex.....61.
60. Pinna margins strongly sinuate at apex. Pinnae elliptic to (ob-)lanceolate. Trinidad.....*D. trinitatensis*
60. Pinna margins not to weakly sinuate at apex. Pinnae parallel-sided, oblong–lanceolate to oblanceolate. Continental South America.....*D. leprieurii*
- 61 (59). Pinnae ovate elliptic to oblong (rarely oblanceolate), widest at the middle.....*D. bipinnata*

61. Pinnae elliptic-oblong to oblanceolate, widest at or above the middle.....*D. geniculata*
- 62 (58). Terminal pinnae of the same size or smaller than the largest lateral pinnae of the same leaf.....63.
62. Terminal pinnae much larger than largest lateral pinnae of the same leaf.....67.
63. Rhizomes 5–8 cm thick, the leaves crowded at the tip. Pinnae 5–8 pairs per leaf, ovate–elliptic to ovate–lanceolate, gradually tapering to (long–)acuminate apices.....*D. antillensis*
63. Rhizomes 1–3 cm thick, the leaves (usually) well spaced along the rhizome. Pinnae 2–8 pairs per leaf, but when more than five pairs, the pinnae oblanceolate and/or abruptly tapering at apex.....64.
64. Lateral pinnae 4.0–6.5 times longer than wide.....65.
64. Lateral pinnae 2.0–3.5 times longer than wide.....66.
65. Rhizomes tall and slender, up to 110 cm long. Leaves well spaced. Lateral pinnae dull above, abruptly acuminate.....*D. arbuscula*
65. Rhizomes shorter and stout, up to 50 cm long. Leaves more crowded. Lateral pinnae usually glossy above, gradually acute to long–acuminate.....*D. geniculata*
- 66 (64). Leaves well spaced on slender rhizomes. Lateral pinnae elliptic-oblong to oblanceolate, lighter along the midrib above when fresh, thick and leathery. Margin cartilaginous. Pinna apices abruptly acute. 3–4 pinna pairs per leaf. Panama.....*D. zamiopsis*
66. Leaves crowded on stout rhizomes. Pinnae oblong to lanceolate, concolorous, leathery. Margin not cartilaginous. Pinna apices abruptly (long–)acuminate. 2–5 pinna pairs per leaf. Guianas.....*D. danaëpinna*
- 67 (62). Largest lateral pinnae broad–lanceolate, 5.5–7.0 cm wide.....68.
67. Largest lateral pinnae oblong to (broad–)lanceolate, 2.6–5.4 cm wide.....70.
68. Largest lateral pinnae 3–4 times longer than wide, 17–22 × 4.8–6.0 cm.....*D. ulei*
68. Largest lateral pinnae 2–3 times longer than wide, 7–18 × 2.6–7.0 cm.....69.
69. Terminal pinnae 2.0–3.4 times longer than the largest lateral of the same leaf. Lateral pinnae elliptic–oblong.....*D. trifoliata*
69. Terminal pinnae 1.5–2.0 times longer than the largest lateral of the same leaf. Lateral pinnae broad–lanceolate.....*D. ulei*
- 70 (67). Pinna apices abruptly acute to abruptly short–acuminate. Pinnae dull above. Guadeloupe, Grenada.....*D. polymorpha*
70. Pinna apices gradually acute to acuminate. Pinnae dull or glossy. South America, Trinidad.....71.
71. Pinna apices (slightly) sinuate. Terminal pinnae (12.4–) 15.5–27.2 cm long.....72.
71. Pinna apices entire, not sinuate. Terminal pinnae (19–) 24–36 cm long.....73.
72. Lateral pinnae oblong–elliptic to lanceolate–elliptic, widest at the middle, 11–15 cm long. Swamp forests of Western Amazonia.....*D. lingua-cervina*
72. Lateral pinnae oblong to broad–oblanceolate widest at or above the middle, 13–21 cm long. Mountain forests of Trinidad.....*D. draco*
- 73 (71). Lateral pinnae 7–17 cm long, elliptic–oblong. Blades 21–36 cm long.....*D. trifoliata*
73. Lateral pinnae 17–22 cm long, broadly lanceolate. Blades 30–49 cm long.....*D. ulei*

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