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Danaea (*Marattiaceae*) keeps diversifying, part 1: eighteen new species

Venni Keskiniva[1] **& Hanna Tuomisto**[1]

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Abstract: Here we describe 18 new species of the Marattialean genus *Danaea*: *D. alba*, *D. ampla*, *D. antioquiana*, *D. elongata*, *D. kessleri* and *D. panamensis* (all in *D.* subg. *Danaea*); *D. dilatata* and *D. opaca* (in *D.* subg. *Arthrodanaea*); and *D. andina*, *D. cuspidopsis*, *D. erosa*, *D. nasua*, *D. peruviana*, *D. polypinna*, *D. pumila*, *D. robbinmoranii*, *D. ubatubensis*, and *D. velona* (in *D.* subg. *Holodanaea*). We provide illustrations, maps of geographical distribution, and nomenclatural notes for the new species. We also lectotypify the name *D. media* and propose that its recent resurrection was a mistake: both *D. media* and *D. elata* are synonyms of *D. nodosa*, which is widespread in Central America and the Greater Antilles; we find that *D. pterorachis* is a valid name applicable to the Costa Rican material that has been referred to *D. media*. We consider *D. sellowiana* and *D. nigrescens* as distinct species and these names applicable to *D.* subg. *Danaea* material from the Brazilian Atlantic Forest and Amazonia, respectively, and we also lectotypify the name *D. nigrescens* here. We accept *D. cuspidata* and *D. betancurii* as species distinct from *D. moritziana*. Evolutionary relationships and an identification key for the 79 species we currently recognize in *Danaea* are published in a parallel paper (Keskiniva & al. 2024).

Keywords: *Danaea*, DNA diagnosis, ferns, *Marattiaceae*, Neotropics, new species, protologue, species descriptions, systematics, taxonomy

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Introduction

The taxonomy of the eusporangiate fern genus *Danaea* Sm. (*Marattiaceae*) has been in great flux, and opinions on the total number of species have ranged from 17 (Rolleri 2004) to 50 (Christenhusz 2010). Delimitation of species in *Danaea* is difficult: most of the morphological characteristics are quantitative rather than qualitative, they vary continuously and widely within species, there is overlap among species, and often different characteristics do not correlate very well (Keskiniva & Tuomisto 2022).

We have now revised the entire genus using an integrative approach, where morphological data from herbarium specimens and field observations were combined with phylogenetic analyses based on chloroplast DNA. In the process, we discovered that phylogenetical evidence supported a finer subdivision of the genus than has been customary, and that the obtained clades are sufficiently coherent in terms of morphology and biogeography to be recognized at the species level.

Here we describe 18 new species of *Danaea*. Most of them are supported by both morphological and genetic data, although a few lack genetic data, and for some, we have failed to find unambiguous morphological diagnostic characters. For the latter group of species, we provide diagnostic genetic differences in the protologues. Details of the phylogenetic analyses supporting these taxonomical decisions are published in a parallel paper together with an online key to all the species we currently recognize in *Danaea* (Keskiniva & al. 2024).

Material and methods

Taxonomic work

Our taxonomic work has to a large degree been based on consultation of herbarium specimens. We have visited several herbaria and had access to physical specimens in the form of loans from the following herbaria: A, AAU, BM, C, CAY, E, F, G, GH, GOET, K, L, M, MO, NY, P, S, SP, TUB, U, UC, US and Z (herbarium codes are according to Thiers 2023+). In addition, several herbaria have provided digital images of their collections upon request: B, COAH, CR, GOET, HUA, HUTI, INPA, LPB, PMA, SP, STU and UTCEC. We have also consulted the digital specimen databases of many herbaria either directly or through Pteridoportal (www.pteridoportal.org) or SpeciesLink (specieslink.net): AAU, ASU, BM, BRIT, C, CAY, CHRB, COAH, COL, F, FLAS, GOET,

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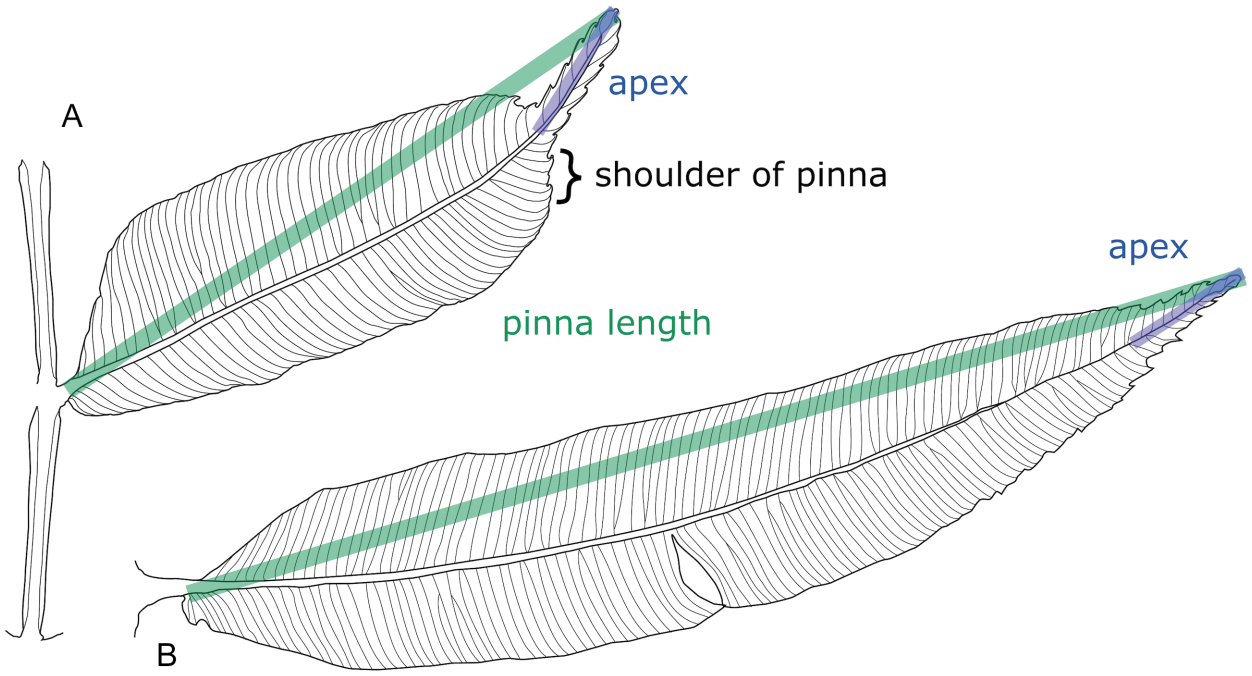

Fig. 1. Definition of pinna apex in this study; part measured for length of pinna in green, apex in blue. A: an abruptly tapering apex with shoulder of pinna serrulate and apex crenulate; B: a gradually tapering serrate apex.

H, HUA, INB, INPA, K, LPB, MICH, MO, MSC, NO, NY, P, PH, PI, PMA, PRC, SJ, SP, STU, UC, US, VT, W, WIS, WTU, WVA and YU.

Many of the new species, as well as previously described ones, have been observed and collected by us in the field, and for many others, we have obtained material from colleagues. Even so, a handful of species descriptions are based on morphological characteristics of only old herbarium material. In the specimen lists, we mention all duplicates of the cited specimens that we know of and highlight the ones we have seen and verified during this work with an exclamation mark.

All measurements mentioned in the species descriptions (including descriptions of colour) are based on herbarium specimens of adult plants except when juvenile or fresh material is mentioned explicitly. Descriptions of lamina texture are in relation to other species of *Danaea*.

Pinna size and shape, as well as detailed characteristics of the pinna apex, are often crucial in species identification, so it is important to be explicit and consistent in the use of terminology. We define pinna length as the total length of the pinna from the base of the pinna (without the petiolule) to the apex (Fig. 1). Pinna width is measured at the broadest point. In the distal part of a pinna, we differentiate between the shoulder of the pinna, which has a straight or convex outline, and the constricted apex, which starts where the pinna outline becomes concave and the pinna width is clearly constricted (Fig. 1). Serrations or other characteristics of the pinna margin are in some cases reported separately for the shoulder of the pinna and for different parts of the constricted apex. Pinna apex length is measured from the concave start of the constricted part to the very tip (Fig. 1). Since obtuse and acute pinna lack a concave constriction point, their apex length equals zero. Relative pinna shape is reported as "X times as long as wide without apex", where X = (pinna length – pinna apex length) / (pinna width). Measurements of lateral pinnae refer to the largest lateral pinna on the leaf unless explicitly stated otherwise.

The conservation status for each new species was estimated according to IUCN Red List Categories and Criteria (2012). Area of occupancy (the total area of 2 km grid cells occupied by the species) and Extent of occurrence (area of the minimum convex hull drawn around the occurrences) were calculated using the package red (Cardoso 2020) in the R environment (R Core Team 2022).

DNA diagnoses

To verify the genetic distinctness of the recognized species, we sequenced four plastid loci; the *rbcL* and *atpB* genes, and the non-coding *rpl32-trnL* (hereafter shortened as *rpl32*) and *trnL-F* regions. The details of sequencing are published in a parallel paper (Keskiniva & al. 2024). The sequences were aligned, and the same alignments were used to produce the DNA diagnoses and the phylogenetic tree shown in Keskiniva & al. (2024: fig. 2–5). Before defining diagnostic DNA-sequences, incomplete sequences and specimens that could not be identified as a named species were excluded. The exact dataset used for the DNA diagnoses is provided in the Supplemental content online. The DNA diagnoses were created with the DNAdiagnoser tool in iTaxoTools (Vences & al. 2021).

Because the reading frame of DNAdiagnoser starts from 0, the DNA diagnoses also use the number zero for the first base in the reference sequence.

Taxonomic treatment

1. *Danaea alba* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 2.
Holotype: Panama, Colón, Parque Nacional San Lorenzo. collected at PPina1, 09°08'N, 79°43'W, 181 m, 4 Sep 2008, *Jones 1212* (PMA! (72300); isotype: TUR! (mounted on 3 sheets, has separate rhizome)).

Diagnosis — Similar to *Danaea grandifolia* Underw. but differs in light yellow-green colour of laminae (vs dark blue-green); acuminate pinna apices (vs usually cuspidate); a node sometimes present on petiole (vs never); elliptic shape of juvenile pinnae (vs oblong); genetically differs in locations 562 (C vs T) of *atpB* reference sequence; 811 (C vs T) of *rbcL* reference sequence; 445 (T vs C), 912 (C vs G) of *rpl32* reference sequence.

Description — *Rhizomes* creeping, dorsiventral, 5 cm in diam., 15 cm long, leaf bases in 3–5 rows. *Sterile leaves* 160–200 cm long; *petioles* 79–90 cm long, with 0–1 node, not winged; *laminae* 75–93 × 65–90 cm, obovate, imparipinnate, terminal pinnae shorter than second distal-most pinna-pair, 8–9 pinna-pairs, pinnae equidistant and rather uniform in size, medial pinnae 5.5–6.5 cm apart, concolorous, uniformly (very) light yellowish or greyish green, texture thick and leathery to intermediately thick, pinna margins slightly cartilaginous, rachises not winged; *terminal pinnae* 12–28 × 3.7–6.2 cm, long-elliptic to oblong (to lanceolate), bases acute to cuneate; *largest lateral pinnae* 33–37 × 5.2–5.5 cm, 5.6–7.9 times as long as wide without apex, widest at middle, parallel-sided or (rarely) slightly wider above middle, bases symmetrical (acute) or asymmetrical (acute distally, obtuse proximally), apices 1.2–3 cm long, acuminate, margins of apices entire; *veins* 12–16 per cm, mostly forked at costa. *Fertile leaves* not known. *Juveniles* with creeping rhizomes with leaf bases in two rows, pinnae uniform in size, terminal pinnae lanceolate, lateral pinnae long-elliptic, margins of apices entire, smallest pinnate juvenile seen 48 cm long (already with 3 pinna-pairs).

Distribution and habitat — Known from the lowland forests of Panama (Colón, Darién, and Panamá) up to 215 m. Fig. 3.

Conservation status — We place *Danaea alba* in the Near Threatened (NT) category (IUCN 2012). It has an Area of occupancy of 16 km^2, an Extent of occurrence of 1083 km^2, and is known from only four locations, which correspond to the Endangered (EN) category. The paucity of collections, despite the large collection effort in Panama, indicates that this species is rare. However, all known collection localities are inside protected areas (Barro Colorado Island, Parque Nacional Darién, Parque Nacional San Lorenzo, and Parque Nacional Soberanía in Panama), and there appears to be no imminent threat to all subpopulations.

Etymology — Alba is Latin for white, referring to the pale colour of the dried pinnae.

Remarks — *Danaea alba* is a large species with relatively few pinna-pairs. It is similar in size and shape to *D. grandifolia*, but is distinct genetically. It can most readily be separated from *D. grandifolia* by the pale, yellow-green colour of dried samples (vs dark blue-green), the acuminate pinna apices (vs usually cuspidate), the elliptic shape of juvenile pinnae (vs oblong), and nodes sometimes present on petioles (vs never). In addition, *D. alba* has been found only in the lowlands (up to 215 m) of Panama (Fig. 3) whereas *D. grandifolia* grows at higher elevations (600–1600 m) and has a wider distribution along the Caribbean coast of Colombia and Venezuela as well as in Puerto Rico and Hispaniola.

Danaea alba belongs to the group of species that have traditionally been identified as *D. nodosa* (L.) Sm. It differs from *D. nodosa* in having rhizomes with leaf bases in 3–5 rows (vs in two rows) and generally fewer pinna-pairs (8–9 vs 8–16) that have entire apices (vs often serrate) and symmetrical bases (vs usually asymmetrical). In addition, the pinnae of *D. alba* are, on average, larger (33–37 × 5.2–5.5 cm vs 21–35 × 2.6–5.8 cm) and thicker (leathery to medium thickness vs medium thickness).

Considering other species with potentially overlapping geographical distributions, *Danaea alba* differs from *D. leussinkiana* Christenh. and *D. panamensis* in having larger pinnae (33–37 × 5.2–5.5 cm vs less than 28 × 4.9 cm) that dry yellow-green (vs blue-green). In addition, rhizomes of *D. alba* have leaf bases in 3–5 rows (vs two rows in *D. panamensis*).

Danaea megaphylla A. Rojas has a variable pinna shape, but *D. alba* differs from it by having creeping rhizomes (vs ascending to erect), fewer pinna-pairs (8–9 vs 12–18) that dry yellow-green (vs grey or brown), and by sometimes having a node on the petiole (vs never).

Danaea alba differs from *D. ampla* (described below) in having rhizomes with leaf bases in 3–5 rows (vs in two rows) and larger pinnae (33–37 × 5.2–5.5 cm vs 14–26 × 3.1–4.9 cm) that are parallel-sided (vs often oblanceolate) and thicker in texture (vs relatively thin).

Danaea alba differs from *D. erecta* Tuomisto & R. C. Moran in having creeping rhizomes (vs erect), sometimes a node on the petiole (vs never), and generally fewer pinna-pairs (8–9 vs 7–17) that dry light yellowish green (vs rather dark green or brown). *Danaea erecta* also grows at higher elevations ((300–)500–2000 m vs 50–215 m).

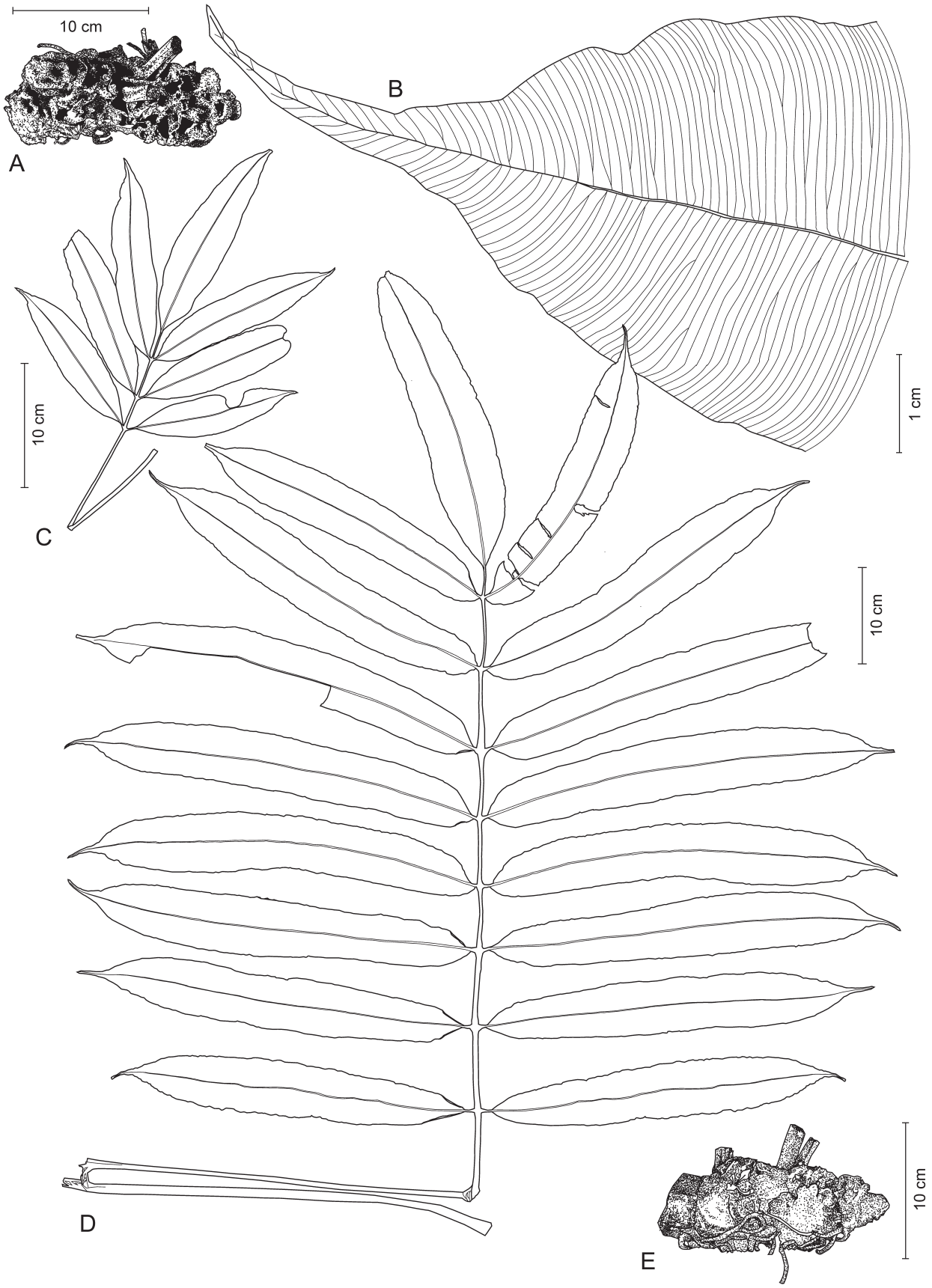

Fig. 2. *Danaea alba*: A: creeping rhizome seen from above; B: apex of sterile pinna; C: juvenile; D: sterile leaf; E: creeping rhizome seen from side. – A, B, D, E: *Jones 1212* (TUR); C: *Jones 994* (TUR). – Drawn by Venni Keskiniva.

Danaea alba differs from *D. latipinna* Tuomisto & R. C. Moran in having longer (33–37 cm vs 17–30 cm) but narrower pinnae (5.6–7.9 vs 2.4–3.4 times as long as wide without apex), terminal pinnae always present (vs often replaced by a bud), rhizomes with 3–5 rows of leaf bases (vs two rows), acuminate pinna apices (vs usually cuspidate to caudate), and a lighter lamina colour.

See *Danaea antioquiana* (described below) for comparison with that species.

Additional specimens examined — Panama: Darién: Ensenada del Guayabo, 18 km from SE Jaque, 50 m, 1983, *Garwood 163* (BM!); Panamá: Parque Nacional Soberanía, at P16, 09°08'N, 79°43'W, 182 m, 3 Apr 2008, *Jones 994* (TUR!, US!); PN Soberanía, at P8, 09°08'N, 79°45'W, 215 m, 28 Jan 2008, *Jones 686* (TUR!); Barro Colorado, 1931, *Wilson 103* (BRIT!).

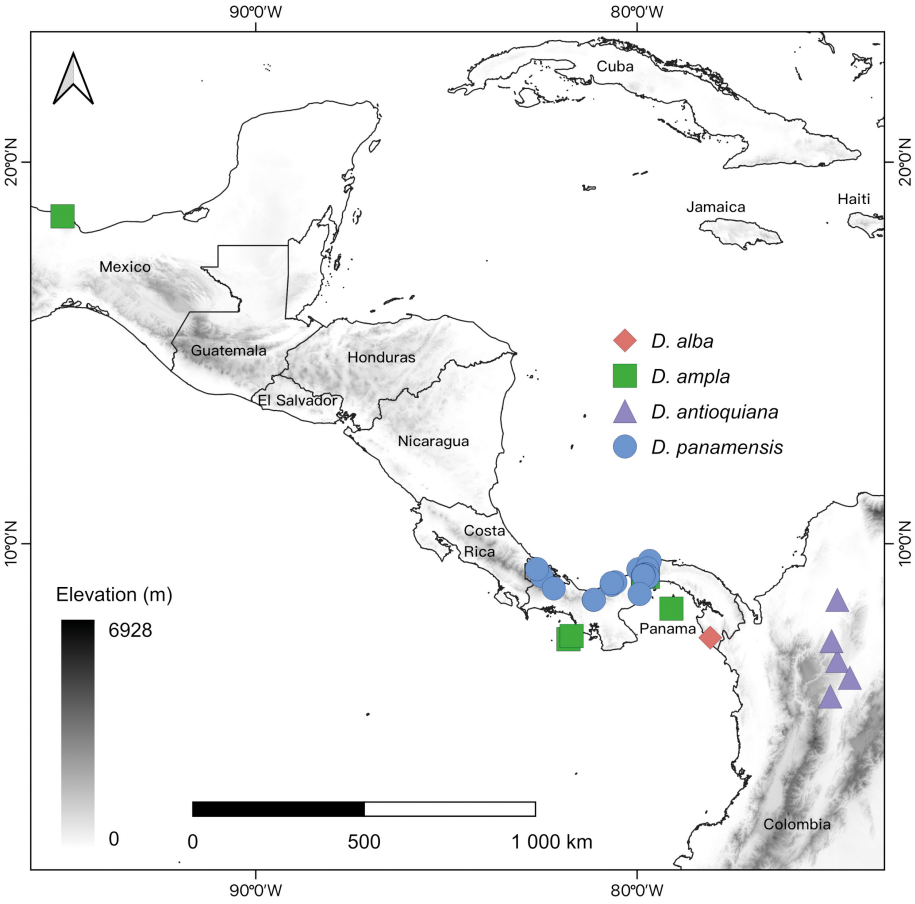

Fig. 3. Distribution of types and paratypes of *Danaea alba*, *D. ampla*, *D. antioquiana* and *D. panamensis*.

2. *Danaea ampla* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 4, 5.

Holotype: Panama, Panamá, Barro Colorado Island, close to NE corner of 50-ha plot, 09°09'N, 79°51'W, 100–150 m, 23 Oct 2005, *Tuomisto 15151* (PMA! (mounted on 2 sheets: 121546 & 121547); isotypes: TUR! (mounted on 3 sheets), UC! (mounted on 2 sheets)).

Diagnosis — Similar to *Danaea nodosa* (L.) Sm., but differs in usually fewer pairs of fertile pinnae (4–7 vs (6–)8–16); generally shorter and wider sterile pinnae (medial pinnae 2–6 vs 4–8 times as long as wide without apex); usually oblanceolate pinnae (vs usually oblong); genetically differs in locations 123 (G vs A), 282 (A vs G), 453 (G vs T) of *trnL-F* reference sequence; 621 (T vs C), 637–639 (gap vs AAA), 642 (A vs C), 673 (A vs G) of *rpl32* reference sequence.

Description — *Rhizomes* creeping, dorsiventral, 2–5 cm in diam., leaf bases in two rows, to 15 cm long. *Sterile leaves* 56–150 cm long; *petioles* 26–68 cm long, no nodes, not winged; *laminae* 29 × 73 cm, (long-)obovate, lanceolate or oblong, imparipinnate, 4–13 pinna-pairs, medial pinnae 4.0–5.0 cm apart, concolorous, light yellowish grey green to green, texture thin to intermediate (border slightly thicker), rachises usually not winged or only winged in distal part of lamina, wings to 1 mm wide; *terminal pinnae* 14–24 × 3.4–5.0 cm, oblong, elliptic or lanceolate, bases acute, apices 2–4.5 cm long, (long-)acuminate, margins of apices slightly to very sinuate; *largest lateral pinnae* 14–26 × 3.1–4.9 cm, 2.4–5.6 times as long as wide without apex, parallel-sided or widest above middle, pinna apices symmetrical (acute) or asymmetrical (obtuse proximally, acute distally), apices 1.3–4.1 cm long, (long-)acuminate (rarely cuspidate or caudate), margins of apices entire to clearly sinuate (rarely serrulate at shoulder of pinna); *veins* 10–15 per cm, mostly forked at costae, sometimes above. *Fertile leaves* 69–117 cm long; *petioles* 41–67 cm long, no nodes; *laminae* 28–50 × 17–21 cm, (long-)obovate to lanceolate, imparipinnate, 4–7 pinna-pairs; *terminal pinnae* 9–12 × 1.3–2.2 cm, lanceolate, bases acute, apices acuminate to cuneate; *largest lateral pinnae* 11–18 × 1.4–2.1 cm, long-elliptic, parallel-sided or lanceolate, bases symmetrical (acute to cuneate) or asymmetrical (obtuse proximally, acute distally), apices 1.0–2.5 cm long, acuminate to cuneate, margins of apices entire. *Juveniles* with elliptic, oblanceolate or oblong pinnae, rather wide, largest simple juvenile 7.5 cm long, smallest observed pinnate juvenile 5 cm long.

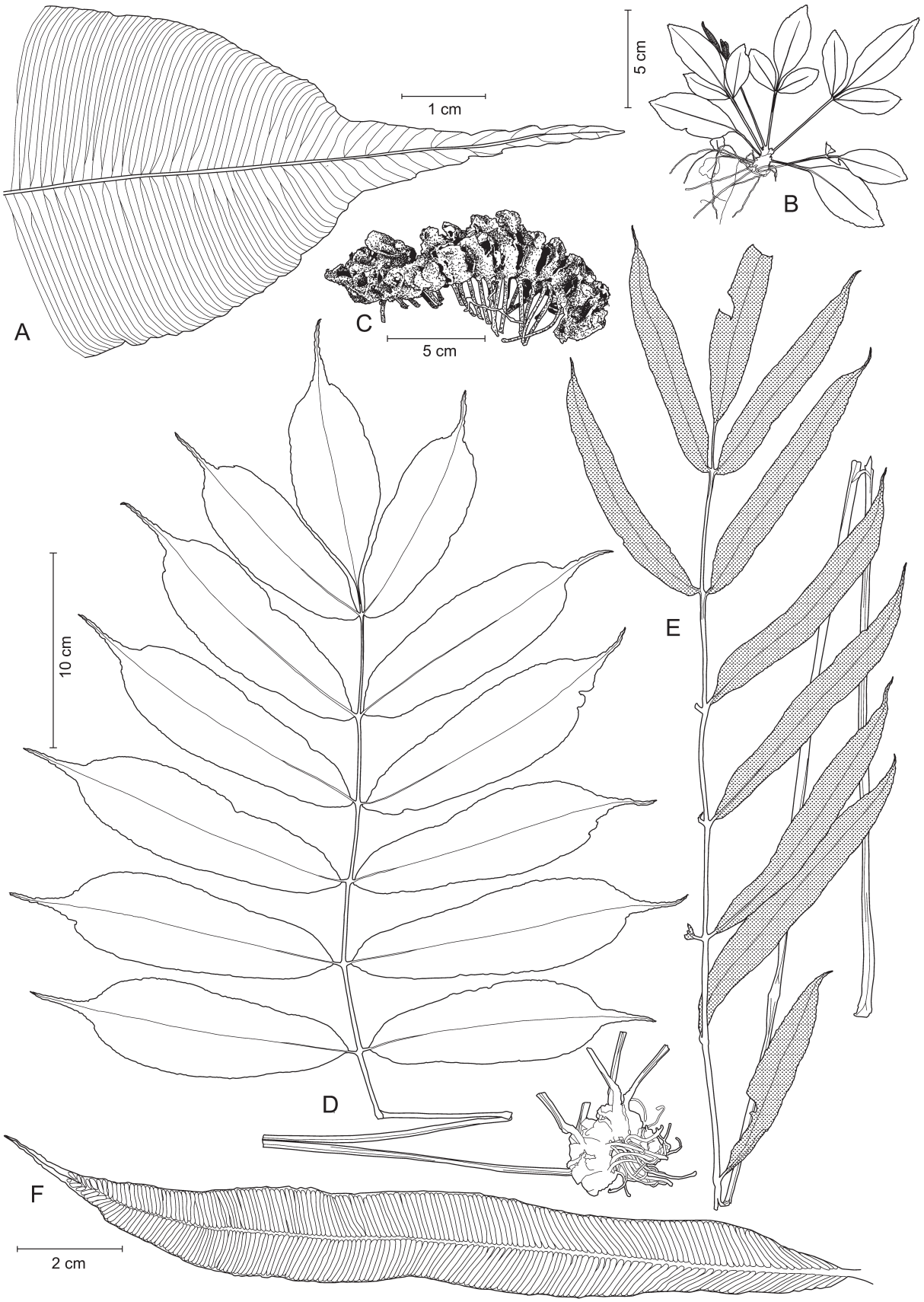

Fig. 4. *Danaea ampla*: A: medial sterile pinna apex; B: juvenile; C: creeping rhizome seen from side; D: sterile leaf and rhizome; E: fertile leaf; F: medial fertile pinna. – A, D–F: *Tuomisto 15151* (TUR); B: *Tuomisto 17494* (TUR); C: *Jones 986* (TUR). – Drawn by Venni Keskiniva.

Fig. 5. *Danaea ampla* in the field: A: entire plant with juvenile; B: entire plant; C: creeping rhizome with leaves in two rows; D: juvenile. – A–D *Tuomisto 15151*. – © Hanna Tuomisto 2005.

Distribution and habitat — *Danaea ampla* is known with certainty (based on DNA evidence) from Panama and Mexico but probably also occurs in the countries in between. It has been found in moist lowland forests up to 182 m elevation, sometimes at the edge of a creek. Fig. 3.

Conservation status — We place *Danaea ampla* in the Least Concern (LC) category (IUCN 2012). It has an Area of occupancy of 28 km^2, which corresponds to the EN category, and an Extent of occurrence of 290,615 km^2, which corresponds to the LC category. *Danaea ampla* is known from at least 10 collections, most of them from protected areas (Los Tuxtlas biological field station in Mexico, Barro Colorado Island, Parque Nacional de Isla Coiba, and Parque Nacional Soberanía in Panama) and there appears to be no imminent threat to all its subpopulations.

Etymology — Ampla is a Latin word for wide, referring to the generally wider, shorter pinnae of *Danaea ampla* in comparison to *D. nodosa*, from which it was separated.

Remarks — *Danaea ampla* is a relatively small species in *D.* subg. *Danaea*. It is similar to *D. nodosa* but has generally shorter and wider pinnae (medial pinnae 2–6 vs 4–8 times as long as wide without apex) that are usually oblanceolate (vs usually oblong). Most remarkably, fertile leaves of *D. ampla* have only 4–7 pinna-pairs (vs (6–)8–16 in *D. nodosa*), and the sterile leaves also have generally fewer pinnae (4–13 vs (6–)10–16). Unfortunately, the morphological characters overlap between *D. ampla* and *D. nodosa*, and there are cases where DNA is needed for certain identification. We have sequenced specimens of *D. ampla* from both Mexico and Panama, so it can be assumed that some of the existing specimens

from the intervening areas belong to this species, but we have not been able to identify any with confidence.

Danaea ampla co-occurs in Panama with *D. panamensis* (described below) and *D. leussinkiana*, but it has a thinner lamina texture and dries light yellow-green (vs blue-green and usually dark). In addition, *D. ampla* has generally fewer pinna-pairs than *D. panamensis* (4–13 vs 9–16) and the pinnae are broader (2–6 vs 6–12 times as long as wide without apex) and oblanceolate (vs oblong). *Danaea ampla* differs from *D. leussinkiana* in having rhizomes with leaf bases in two rows (vs 3–5 rows), generally longer pinna apices (1.3–4.1 cm vs 0.9–1.5 cm long) and broader pinnae (2–6 vs 5–7 times as long as wide without apex).

Danaea ampla differs from *D. pterorachis* Christ in having rhizomes with leaf bases in two rows (vs 3–5 rows), having no nodes on the petioles (vs petioles often with 1 or 2 nodes, especially in juveniles), and having generally broader pinnae (2–6 vs 5–8 times as long as wide without apex) that are oblanceolate (vs oblong).

See *Danaea alba* (described above) for comparison with that species.

An earlier interpretation of the types by H. Tuomisto and M. Christenhusz (cited in Mickel & Smith 2004), led to considering *D. elata* Liebm. (type from Mexico) and *D. pterorachis* Christ (type from Costa Rica) as synonyms of *D. media* Liebm. (type from Mexico) but distinct from *D. nodosa* (type from the Greater Antilles). Accordingly, Christenhusz (2010) assigned most Central American material that had previously been identified as *D. nodosa* to *D. media*. We considered these names carefully before deciding to describe *D. ampla* as a new species. We agree that the type specimens of *D. media* (*Liebmann 653*, *654*, *849* and 850 in C and P00251865 in P) are conspecific with the type of *D. elata* Liebm. (*Liebmann 848* in C): the specimens were collected in the same population (Liebmann 1849: 306), and we find it obvious that *D. media* represents the juvenile stage of *D. elata*. These specimens have a rather similar general appearance to material from La Selva Biological station in Costa Rica: the type of *D. elata* shares the narrow pinnae and some of the syntypes of *D. media* apparently have nodes on the petioles (which are common in specimens from La Selva but absent in true *D. nodosa*). However, our scrutiny of the *D. elata/media* type material suggests that they actually do not have nodes on the petiole; the naked nodes on the juvenile specimens look like they used to have pinnae that have at some stage fallen off. In addition, the *D. elata/media* material has rhizomes with leaf bases in two rows rather than in 3–5 rows as in the La Selva material. On this basis, we conclude that the La Selva material is not conspecific with *D. elata/media* but can instead be assigned to *D. pterorachis*, which we hereby lift from synonymy and consider a distinct species. The Mexican sequenced material that morphologically resembles *D. nodosa* falls into two clades, one of which also contains true *D. nodosa* from the Greater Antilles (Keskiniva & al. 2024). Although none of the Mexican sequenced material comes from the type locality of *D. elata/media*, the large number and narrow shape of pinnae in the type of *D. elata* conform with *D. nodosa* rather than with the smaller number and broader shape of pinnae of specimens in the other clade. On this basis, we consider *D. elata* and *D. media* to be synonyms of *D. nodosa* and give the material of the other clade the new name *D. ampla.* Since *D. media* has original material in two herbaria but has apparently not been lectotypified, we do so here: the lectotype is *Liebmann 653* (C) and the other specimens with the same collecting locality and date information become isolectotypes (*Liebmann 654*, *849* and *850* in C and P00251865 in P).

Additional specimens examined — Mexico: Veracruz: Los Tuxtlas biological field station, 18°35'N, 95°04'W, 100–150 m, 29 Jun 2017, *Tuomisto 17491* (TUR! (6), UC-3!, XAL-4, Z-3!); Los Tuxtlas biological field station, 18°35'N, 95°04'W, 100–150 m, 29 Jun 2017, *Tuomisto 17494* (TUR-2!, XAL-3). — Panama: Panamá: Barro Colorado, behind Casa Amarilla, 1977, *Béliz 71* (PMA!); San José Island, Perlas Archipelago, Gulf of Panama, (about 55 miles SSE of Balboa), 1944, *Johnson 263* (GH!); Parque Nacional Soberanía, at P16, 09°08'N, 79°43'W, 182 m, 2 Apr 2008, *Jones 986* (TUR!, US-2!); Canal Zone, Parque Nacional Soberania, Camino del Oleoducto, on banks of Río Limbo, 1980, *Vásquez 246* (PMA!); Veraguas: Distr. De Montijo. Isla Coiba, Río Escondido, 1995, *Araúz 287* (PMA!); Distr. De Montijo. Isla Coiba, Playa Hermosa, ascending to La Falla, 1996, *Araúz 637* (PMA!); Distr. De Montijo, Isla Coiba, N of island, Yuma trail, 07°35'N, 81°43'W, 30 m, 1995, *Galdames 2168* (PMA!).

3. *Danaea andina* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea* C. Presl) – Fig. 6, 7.

Holotype: Ecuador, Zamora-Chinchipe, Reserva Tapichalaca, sector Ventanillas, 04°29'S, 79°07'W, 2520–2600 m, 17 Sep 2004, *Lehnert 1278* (UC! (1794187); isotype: GOET! (042670)).

Diagnosis — Resembles *Danaea moritziana* C. Presl, but is usually smaller (sterile leaves to 71 cm vs to 96 cm long, sterile pinnae 4.5–13 cm vs 7.8–20 cm long, fertile pinnae to 7 cm vs to 11 cm long), has variable rhizomes (vs always erect), and its veins are mostly forked at costa (vs often forked well above costae); genetically differs in locations 985 (T vs C) of *atpB* reference sequence; 80 (C vs A), 113 (C vs A), 885 (C vs A), 886 (G vs A), 1060 (A vs T), 1136 (C vs T), 1148 (T vs G) of *rbcL* reference sequence; 233 (A vs C), 248–252 (gap vs insertion of ATTAG), 265 (G vs A), 728–731 (gap vs AATA) of *trnL-F* reference sequence; 231 (A vs G), 257 (C vs A), 396 (A vs T), 424 (C vs A), 539 (A vs C), 709–710 (TT vs gap), 713 (C vs T), 737 (A vs G), 863 (A vs G) of *rpl32* reference sequence. Similar to and co-occurs with *D. cus-*

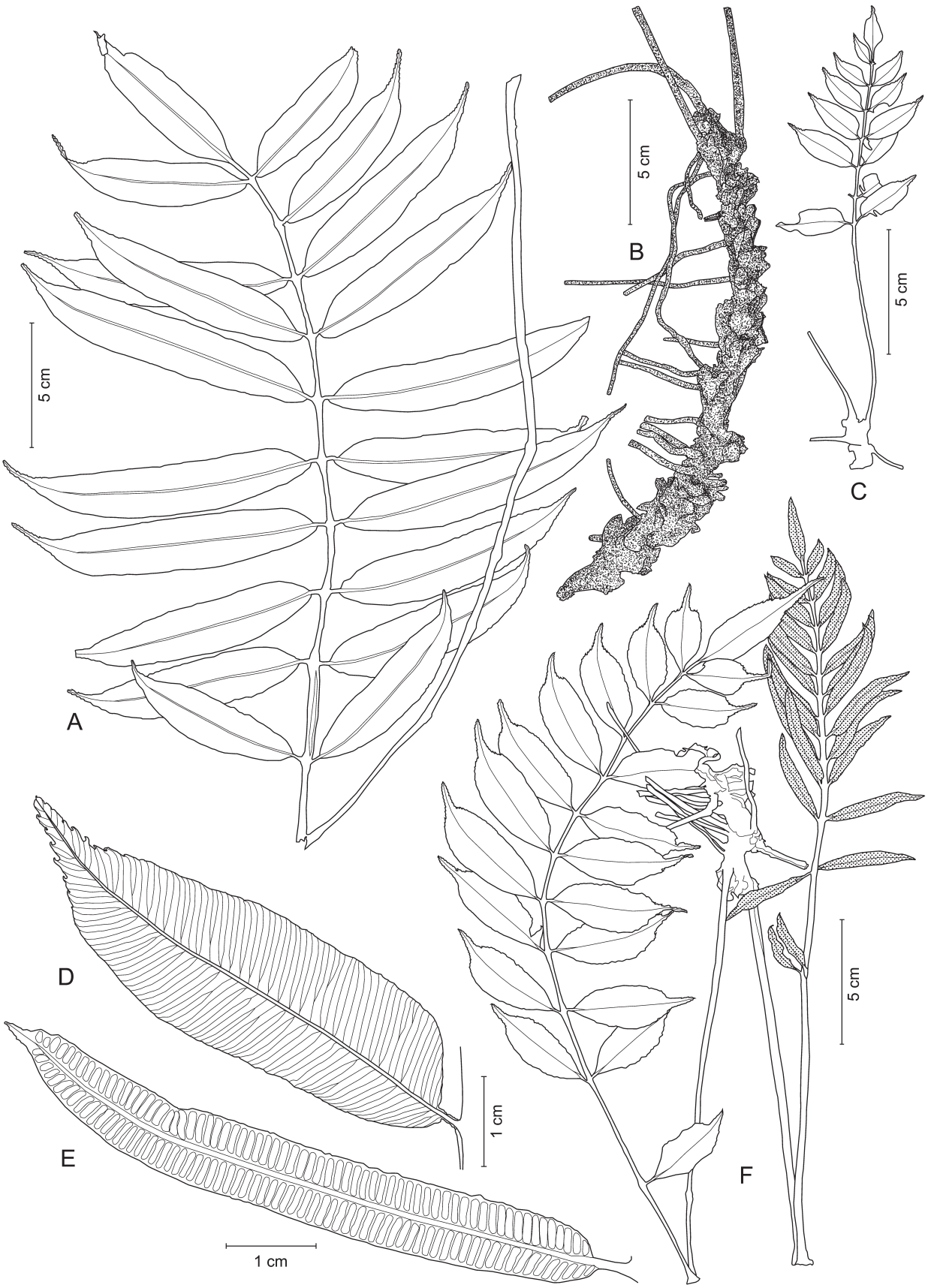

Fig. 6. *Danaea andina*: A: sterile leaf; B: rhizome; C: juvenile; D: second distal-most lateral pinna; E: medial fertile pinna; F: entire plant with fertile pinnae in grey. – A: *Lehnert 1278* (UC); B: *Lehnert 1161* (QCA); C: *Lehnert 3279* (UVMT); D: *Lehnert 1215* (QCA); E: *Øllgaard 2978* (AAU); F *Øllgaard 1664* (TUR). – Drawn by Venni Keskiniva.

Fig. 7. *Danaea andina* field habit: A: entire plant; B: sterile pinna adaxial and abaxial sides; C: sterile lamina apex. – A: Ecuador, Napo c. 5 km NW of Cosanga, Yanayacu Biological Station, 2100 m, 00°35'57"S, 77°53'26"W; B, C: Ecuador, Napo, Baeza. – © Robbin C. Moran 2005.

pidopsis Keskiniva & Tuomisto, *D. excurrens* Rosenst. and *D. betancurii* A. Rojas. Differs from *D. cuspidopsis* in generally shorter fertile pinnae (4.2–7.0 cm vs 6.5–12 cm); shorter pinna apices (0.7–1.6 cm vs 1.7–3.2 cm) that are abruptly tapering (vs usually gradually tapering); generally shorter leaves (28–)46–71 cm vs 54–120 cm); veins forked (can be simple); rhizomes creeping to erect (vs erect). Differs from *D. betancurii* in generally shorter fertile pinnae (4.2–7.0 cm vs 5.3–8.0 cm); generally wider pinnae (medial pinnae 2–6 vs 4–8 times as long as wide without apex); abruptly tapering pinna apices (vs gradually tapering); veins forked at costa (often simple or forked well above costae). Differs from *D. excurrens* in generally shorter fertile pinnae (4.2–7.0 cm vs 3.6–10.4 cm); generally longer rhizomes (to 21 cm vs to 10 cm long); acute pinna bases (vs obtuse); pinnae parallel-sided (vs often widest at base). Is unique among *Danaea* by having a deletion at positions 635–698 of *rpl32* reference sequence and at positions 382–394 of *trnL-F* reference sequence.

Description — *Rhizomes* with leaf and root bases arranged radially, variously described as creeping to erect, 0.7–2.2 cm in diam., to 21 cm long. *Sterile leaves* (28–)46–71 cm long; *petioles* 6–38 cm long, with 0–2 nodes, not winged or winged down to most distal node on petiole; *laminae* 19–43 × 7–23 cm, oblong, elliptic or (long-) lanceolate, imparipinnate (or paripinnate), 8–16 pinna-

pairs, proximal pinnae often smallest and more distant, medial pinnae 1.4–3.5 cm apart, bicolorous, dark green adaxially, light green to green abaxially, texture thin, rachises entirely or at least distally winged, wings to 0.2–0.7 mm wide; *terminal pinnae* 3.6–8.0 × 0.8–2.1 cm, lanceolate, bases acute, apices 1.1–2.8 cm long, (long-)acuminate, margins of apices crenulate to serrate; *largest lateral pinnae* 4.5–13.1 × 1.0–2.3 cm, 2.2–5.9 times as long as wide without apex, parallel-sided, slightly falcate, bases asymmetrical (acute, obtuse or slightly auriculate proximally, acute distally), apices 0.7–1.6 cm long, attenuate to acuminate, margins of apices serrate (to crenate); *veins* 12–22 per cm, mostly forked at costae (sometimes partly forked above costae or partly simple). *Fertile leaves* 45–65 cm long; *petioles* 26–37 cm long, with 1 node; *laminae* 17–28 × 5–7 cm, long-elliptic, imparipinnate (or paripinnate with a terminal bud), 13–15 pinna-pairs; *terminal pinnae* c. 2.8 × 0.5 cm, linear-lanceolate, bases acute, apices cuneate; *largest lateral pinnae* 4.2–7.0 × 0.5–0.7 cm, linear-elliptic to linear-lanceolate, slightly falcate, bases asymmetrical (obtuse or acute proximally, obtuse or acute distally), apices 0.4–0.6 cm long, cuneate to acuminate, margins of apices crenulate. *Juveniles* with parallel-sided laminae, terminal pinnae oblong to lanceolate, lateral pinnae oblong (to elliptic), apices cuspidate to acuminate.

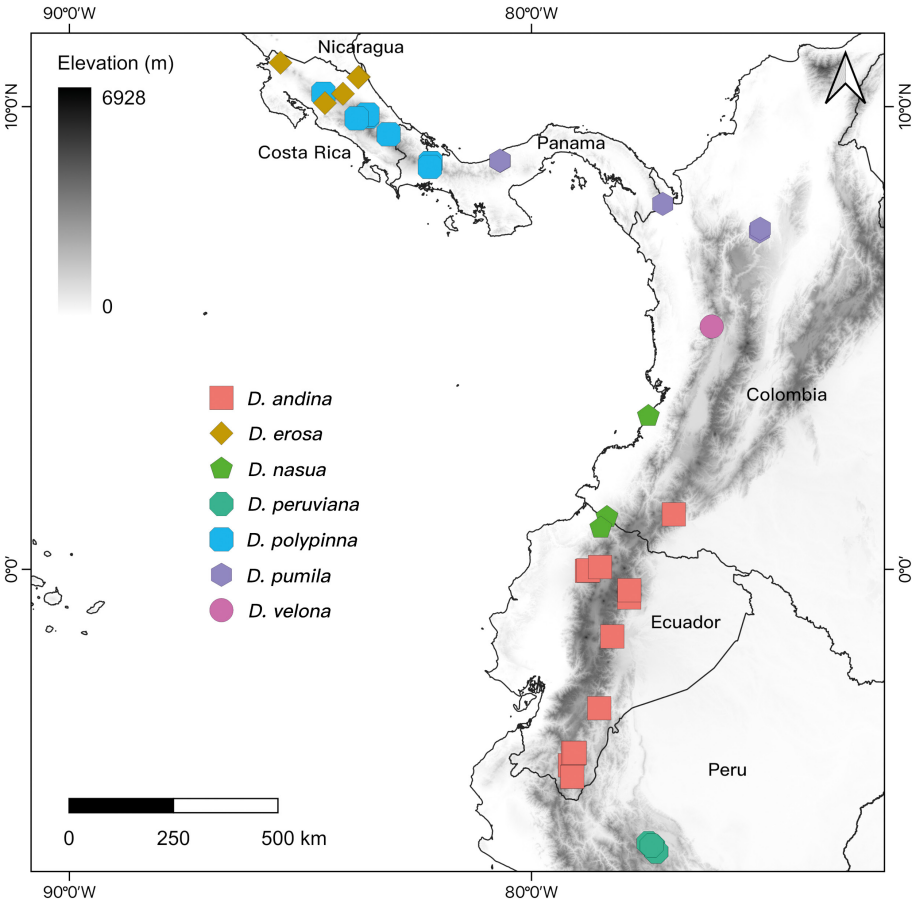

Fig. 8. Distribution of types and paratypes of *Danaea andina*, *D. erosa*, *D. nasua*, *D. peruviana*, *D. polypinna*, *D. pumila* and *D. velona*.

Distribution and habitat — *Danaea andina* is found in the tropical Andes and seems to be relatively abundant in Ecuador, where it occurs on both sides of the mountain chain at 1750–2600 m. It is also found in Colombia (Putumayo), and probably occurs in northern Peruvian Andes as well. *Danaea andina* has been found in montane rain forests, often in shady, moist and inclined spots such as stream ravines. Fig. 8.

Conservation status — We place *Danaea andina* in the Least Concern (LC) category (IUCN 2012). It has a known Area of occupancy of 56 km^2, which corresponds to the EN category, and an Extent of occurrence of at least 51,331 km^2, which corresponds to the LC category. *Danaea andina* seems to be abundant in the Ecuadorian Andes, as it is known from at least 18 collections, and some of its occurrences are inside protected areas (Tandayapa Cloud Forest Reserve, Parque National *Podocarpus*, and Reserva Tapichalaca in Ecuador). There appears to be no imminent threat to all its subpopulations.

Etymology — This species is named for its distributional area in the Andes.

Remarks — *Danaea andina* is one of the few species of *Danaea* that grow on both sides of the Andes, and it is also among the ones that reach the highest elevations. It belongs to the species complex that was previously referred to *D. moritziana*, and its distribution overlaps with several other species that have recently been segregated from that complex (*D. cuspidopsis*, *D. excurrens*, and *D. betancurii*). Although many individuals of *D. andina* are easy to identify by their characteristic appearance, within-species morphological variation and its overlap with other species is considerable. Consequently, the morphological comparisons below are rather inconclusive; *D. andina* is most reliably identified based on its unique DNA.

Danaea andina differs from *D. cuspidopsis* (and also from the Mexican *D. cuspidata*) in having generally shorter leaves (28–71 cm vs 54–120 cm long), shorter

fertile pinnae (4.2–7.0 cm vs 6.5–12 cm), and shorter pinna apices in sterile pinnae (0.7–1.6 cm vs 1.7–3.2 cm long) that are abruptly tapering (vs often gradually tapering). In addition, the rhizomes of *D. andina* can be creeping to erect (vs always erect), its veins are mostly forked at the costa (vs sometimes mostly simple), and the terminal pinna is almost always present (vs often replaced by a bud in *D. cuspidopsis*).

Danaea andina also resembles *D. moritziana* but is usually smaller (sterile leaves to 71 cm vs to 96 cm long, sterile pinnae 4.5–13 cm vs 7.8–20 cm long, fertile pinnae to 7 cm vs to 11 cm long), has more variable rhizomes (vs always erect), and its veins are mostly forked at the costa (vs often forked well above the costae). Under our current relatively narrow concept, *D. moritziana* is restricted to Venezuela and northern Colombia, and does not appear to have spread far enough south as to overlap with the distribution of *D. andina.*

Christenhusz (2010) considered *Danaea betancurii* as synonymous with *D. moritziana*, but Rojas-Alvarado (2013) argued that the two are distinct. We do not have DNA for *D. betancurii*, but the type of this species is distinctive with a simple venation and rather delicate pinnae with gradually tapering apices. We consider *D. betancurii* to be a distinct species, although it is variable in our current circumscription.

Danaea betancurii occurs on the Amazonian side of the Andes from Colombia to northern Peru and is usually found at lower elevations than *D. andina* (600–2050 m vs 1950–2600 m). The veins of *D. andina* are generally forked at the costa, unlike the simple veins in the type of *D. betancurii* (although the venation seems to be variable in *D. betancurii*). In addition, *D. andina* has generally shorter fertile pinnae (4.2–7.0 cm vs 5.3–8.0 cm) and generally wider sterile pinnae (medial pinnae 3–6 vs 4–8 times as long as wide without apex) that have abruptly tapering pinna apices (vs gradually tapering). *Danaea andina* often differs from *D. excurrens* in having shorter fertile pinnae (to 7.0 cm vs to 10 cm), longer rhizomes (to 21 cm vs to 10 cm long), and lateral pinnae that are parallel-sided (vs often widest at base) and have acute bases (vs obtuse). However, both species are variable, and we do not have reliable criteria to morphologically separate between Ecuadorian specimens of *D. andina* and Bolivian specimens of *D. excurrens.* Because we do not have genetic material of either species from Peru, we are not sure about the identity of the Peruvian specimens. This renders the distributional limits between the two species uncertain as well.

Danaea andina differs from *D. inaequilatera* A. Rojas, which occurs in the lowlands of the Pacific coast, by having clearly bicolorous pinnae that are whitish beneath (vs almost concolorous), less regularly arranged sterile pinnae of more variable shape, and narrower fertile pinnae (0.5–0.7 cm vs 0.8–1.3 cm wide).

The juveniles of *Danaea andina* have short and broad, often squarish pinnae with short, abruptly tapering apices and long, rather slender radial rhizomes that have been variously described as creeping to erect. The juveniles of *D. moritziana* have rounder and more elliptic pinnae and the juveniles of *D. excurrens* usually have narrower pinnae than those of *D. andina*.

Additional specimens examined — Colombia: Putumayo: Above Sibundoy, 2500 m, 4 May 1939, *Alston 8378* (BM!). — Ecuador: Loja: Trails to Quebrada Romerillos c. 5 km ENE of San Pedro de Vilcabamba, 04°14'S, 79°10'W, 2100–2200 m, 29 Nov 1994, *Øllgaard 105897* (AAU, NY!, QCA!, TUR-2!, UC); Trails c. 5 km ENE of San Pedro de Vilcabamba, Loma and Quebrada El Trigal, 04°14'S, 79°10'W, 2050–2250 m, 2 Dec 1994, *Øllgaard 106015* (AAU!, QCA!); Morona-Santiago: Road Plan de Milagro-Gualaceo, km 10.8, S of road, 03°00'S, 78°32'W, 2200–2250 m, 24 Nov 1997, *Øllgaard 2740* (AAU!, QCA!); Napo: Quijos Canton, Yanahyacu, 00°36'S, 77°53'W, 3 Aug 2015, *Lehnert 3279* (VT!); Baezam along road leading to radio towers behind town, 77°53'S, 00°27'W, 2080 m, 24 Feb 2005, *Moran 7540* (NY!, UC!); Pichincha: Bellavista; between Tandayapa and Mindo (old road Quito–Puerto Quito), 2300 m, 10 Sep 2004, *Lehnert 1161* (GOET, QCA!, TUR!, UC!); Tandayapa Cloud Forest Reserve, 1750–1880 m, 12 Sep 2004, *Lehnert 1214* (GOET, TUR!, QCA!); km 6 on Pela Gallo-Monte Cristi road, 00°03'N, 78°31'W, 2500 m, 26 May 1997, *Navarrete 1949* (QCA!); Tungurahua: W of Río Guambi, c. 7 km along road and trails S of Río Negro, 01°27'S, 78°15'W, 1780 m, 4 Feb 1998, *Navarrete 3053* (QCA!); Zamora-Chinchipe: Estación Cientifica San Francisco, Quebrada 2, 03°58'S, 79°04'W, 2050 m, 13 Sep 2003, *Lehnert 842* (QCA!, UC!); Reserva Tapichalaca, study plot B5, on N slope of Cerro Tapichalaca, 04°29'S, 79°07'W, 2645 m, 31 Oct 2003, *Lehnert 1044* (QCA!, UC!); Parque National *Podocarpus*, Reserva Biologica San Fransisco, Q5, MATRIX plot L6 (old label Q6), 03°58'S, 79°04'W, 1940–1960 m, 10 Sep 2010, *Lehnert 1796* (STU!); Parque Nacional *Podocarpus*, trail into Quebrada San Francisco, km 9.4 E of pass on Loja- Zamora road, 03°59'S, 79°06'W, 2000–2300 m, 25 Mar 1998, *Øllgaard 2978* (AAU-3!, QCA!); Road Loja-Zamora, 13 km E of pass, just before junction with old road, 03°58'S, 79°05'W, 2030 m, 8 Mar 1989, *Øllgaard 90898* (AAU!, QCA!); new road Loja-Zamora, km 13 E of pass, 03°58'S, 79°06'W, 2000 m, 14 Feb 1991, *Øllgaard 98814* (AAU!, QCA!); area of Estación Cientifica San Francisco, road Loja-Zamora, c. 35 km from Loja, 03°58'S, 79°04'W, 2050 m, 4 Aug 2005, *Werner 1732* (QCA!, UC!).

4. *Danaea antioquiana* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 9, 10.
Holotype: Colombia, Antioquia, San Luis, Reserva "Río Claro", 06°00'N, 74°56'W, 300 m, 1 Feb 2015, *Kessler 14754* (TUR!).

Diagnosis — Morphologically very similar to *Danaea nodosa* (L.) Sm. but genetically differs in locations 562 (T vs C) of *atpB* reference sequence; 123 (G vs A) and 282 (A vs G) of *trnL-F* reference sequence; 636–638 (gap vs AAA), 642 (A vs C) and 673 (A vs G) of *rpl32* reference sequence. Similar to *D. sellowiana* C. Presl, but generally has more parallel-sided and straight pinnae (vs narrow-elliptic and slightly curved) and dries a more yellowish colour (vs bluish to greyish green). Genetically differs from *D. sellowiana* in locations 74 (A vs G) of *trnL-F* reference sequence; 425 (T vs C) and 445 (G vs A) of *rpl32* reference sequence.

Description — *Rhizomes* creeping, dorsiventral, 4 cm in diam., leaf bases in two rows, at least to 14 cm long. *Sterile leaves* 108–217 cm long; *petioles* 55–110 cm long, no nodes, not winged; *laminae* 53–108 × 30–60 cm, long-obovate, imparipinnate, 11–19 pinna-pairs, medial pinnae 3.3–7.6 cm apart, concolorous, light brown to rather dark greenish brown, texture thin to intermediate, rachises not winged; *terminal pinnae* 8.6–16 × 1.7–4.9 cm, parallel-sided or lanceolate, bases acute, apices 1.7–3.3 cm long, acuminate, margins of apices entire, sinuate or crenulate; *largest lateral pinnae* 17–34 × 2.4–5.5 cm, 4.9–8.8 times as long as wide without apex, parallel-sided (or slightly wider at or above middle), pinna apices symmetrical (acute to obtuse) or slightly asymmetrical (obtuse proximally, acute distally), apices 1.4–3.7 cm long, (long-)acuminate, margins of apices entire, sinuate or crenulate (rarely serrulate at shoulder of pinna); *veins* 15–20 per cm, mostly forked at costa. *Largest fertile lateral pinnae* 17–19 × c. 2.3 cm, parallel-sided or long-lanceolate, bases acute, symmetrical or slightly asymmetrical, apices 1.0–1.6 cm long, acuminate to cuneate. *Juveniles* not known.

Distribution and habitat — *Danaea antioquiana* is known from the Magdalena River Valley in Colombia (Antioquia and Santander). It has been found in lowland forests at 60–820 m near ravines and rivers. Fig. 3.

Conservation status — We place *Danaea antioquiana* in the Vulnerable (VU B1ab(iii)+2ab(iii)) category (IUCN 2012). It has an Extent of occurrence of 8511 km^2 and is known from only five locations, which corresponds to the VU category. Its Area of occupancy of 20 km^2 corresponds to the EN category. *Danaea antioquiana* was said to be locally abundant in two locations and one of the collections was from inside a protected area (Reserva Río Claro in Colombia). However, the rest of the collection localities are outside protected areas, and the area, extent, and quality of suitable habitats were inferred to be suffering continuing decline from deforestation.

Etymology — The name refers to the Antioquia Department in Colombia, where the type was collected.

Remarks — *Danaea antioquiana* belongs to the clade within *D.* subg. *Danaea* that occurs outside Amazonia and includes true *D. nodosa* (which is found in Central America and the Greater Antilles) and *D. sellowiana* (which is found in the Atlantic coastal forests of Brazil and adjacent Paraguay). Although superficially similar, *D. nigrescens* Jenman (which is found in Amazonia and the Guianas) belongs to a different clade. These four species (and especially the three extra-Amazonian ones) are morphologically hard to distinguish, but genetic evidence shows that they are distinct (details are presented in Keskiniva & al. 2024).

Danaea nigrescens still remains enigmatic. It has not been lectotypified, so we do so here: the lectotype is Jenman 53, Upper Demerara River, Guyana, 1898 (US 1120090), and the other specimens with the same collecting locality and date information become isolectotypes (Jenman in E00037360 in E and 172 and 173 in NY). The type material is morphologically even more similar to *D. nodosa* than most material from the Guianas and Amazonia. Unfortunately, we do not have DNA material from the type locality, so the possibility remains that what we here call *D. nigrescens* actually consists of two species, in which case the genetic affinity of *D. nigrescens* s.s. would be unknown.

The genetic distance is especially large between *Danaea antioquiana* and *D. nodosa*, even though the morphological variation in these two overlaps almost completely. They do not seem to occur in the same geographical area, as *D. antioquiana* is (so far) known only from the Magdalena River Valley in Colombia. *Danaea antioquiana* is also morphologically similar to *D. sellowiana*, from which it differs by generally having more parallel-sided and straight pinnae (vs narrow-elliptic and slightly curved) and drying a more yellowish colour (vs bluish to greyish green). These are difficult and variable characters, however; in practice, this pair can also best be separated with genetics and biogeography.

Danaea antioquiana is also closely related to *D. alba*, *D. longicaudata* and *D. grandifolia*, but these species are relatively easy to tell apart morphologically. This is especially true for *D. longicaudata*, which is a smaller plant (leaves <1 m vs >1 m) with an erect trunk (vs creeping dorsiventral rhizome) and smaller lateral pinnae (10–16 cm vs 17–34 cm long, 1.8–2.6 cm vs 2.4–5.5 cm wide) with long-caudate (vs acuminate) apices. *Danaea antioquiana* differs from *D. alba* and *D. grandifolia* in having creeping rhizomes with leaf bases in two rows (vs 3–5 rows in the others), shorter terminal pinnae (8.6–16 cm vs 22–28 cm long in *D. alba*, 18–24 cm in *D. grandifolia*), and more pinna-pairs (11–19 vs 8–9 in *D. alba*, 8–12 in *D. grandifolia*) that are often narrower (minimum 2.4 cm wide vs 4.5 in *D. alba*, 4.2 in *D. grandifolia*), have more densely packed veins (15–20 veins per cm vs 12–13 in *D. alba*, 11–15 in *D. grandifolia*), and often have sinuate or crenulate apices (vs entire in *D. alba* and entire or slightly sinuate in *D. grandifolia*). It also differs from

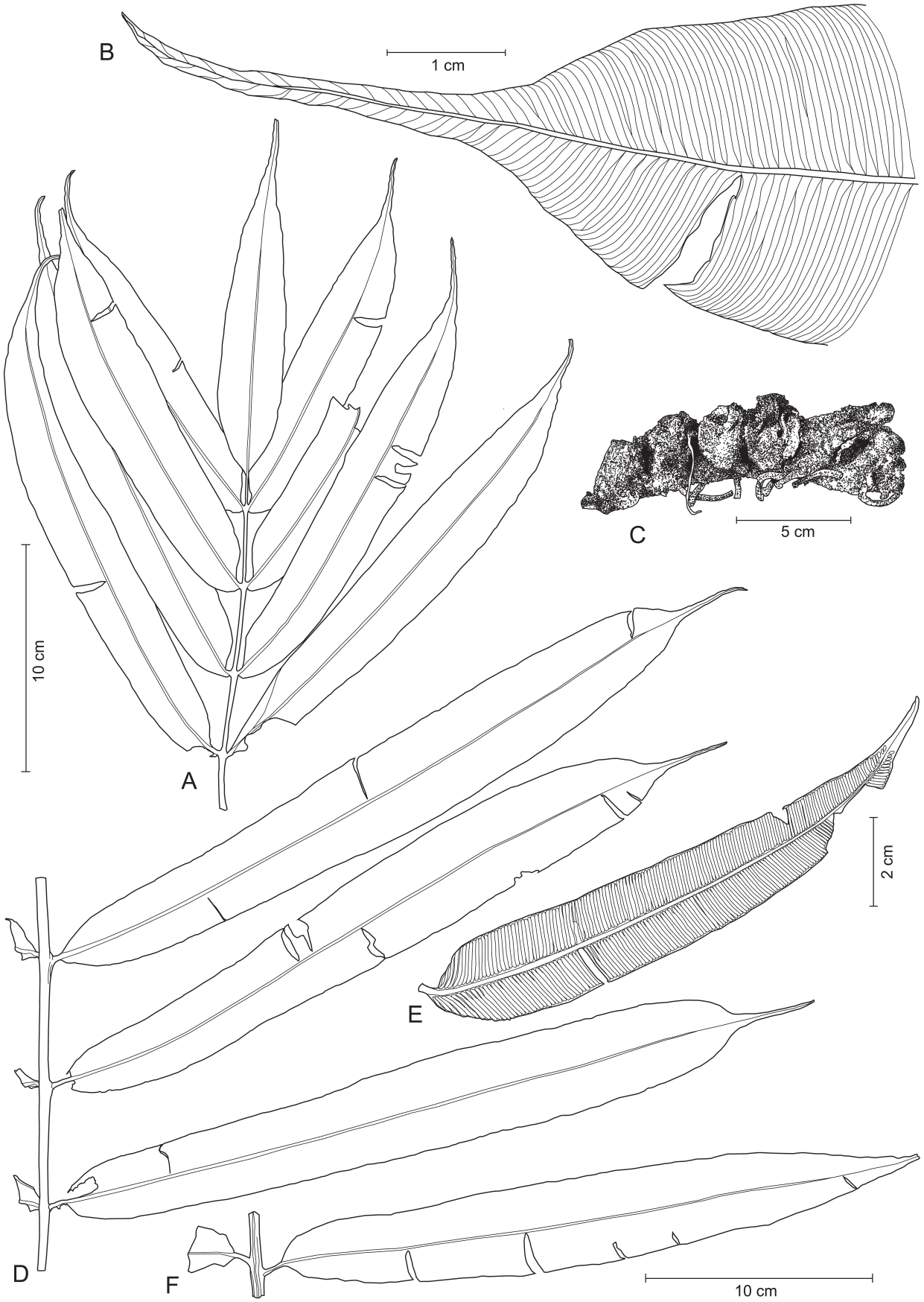

Fig. 9. *Danaea antioquiana*: A: sterile leaf apex; B: sterile medial pinna apex; C: fragment of creeping rhizome; D: sterile medial pinnae; E: fertile pinna; F: sterile proximal pinna. – A–F: *Kessler 14754* (TUR). – Drawn by Venni Keskiniva.

Fig. 10. *Danaea antioquiana* field habit: A: entire sterile leaf; B: medial sterile pinna; C: creeping dorsiventral rhizome with leaf bases in two rows. – A–C: *Kessler 14754*. – © Michael Kessler 2015.

D. grandifolia in acuminate pinna apices (vs usually cuspidate), and from *D. alba* in having petioles without nodes (vs petioles sometimes with one node), and a thinner pinnae texture and darker colour when dry. *Danaea grandifolia* is a montane species, occurring at 600–1600 m, whereas *D. antioquiana* is generally found at lower elevations (60–820 m).

Danaea antioquiana differs from the Lesser Antillean *D. kalevala* both genetically and in having rhizomes with leaf bases in two rows (vs 3–5 rows) and wider fertile pinnae (6.7–7.6 vs 8.4–9.6 times as long as wide without apex).

Additional specimens examined — Colombia: Antioquia: Remedios Municipality, Sitio Otu, 3 km from Santa Isabel, Vereda Los Lagos, 11 km S from Remedios, 06°56'N, 74°45'W, 820 m, 1987, *Callejas 4705* (NY!); Dos Bocas, on Río Nechi, near Pato, drainage of Río Nechi, 100–200 m, 23–25 Jun 1944, *Ewan 15823* (BM!, GH!, US!); Nechi Municipality, Verada Santa Maria, near chapel on edge of Santa Maria ravine, 08°82'N, 74°45'W, 60 m, 4 Mar 2010, *Rodriguez 6565* (COL-3!); Santander: Vicinity of Puerto Berio, between Carare and Magdalena Rivers, 100–700 m, 29 Jul 1935, *Haught 1841* (COL!, MICH!, S, US!).

5. *Danaea cuspidopsis* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 11, 12.
Holotype: Costa Rica, Puntarenas, Monteverde Biological Station, 10°18.2'N, 84°47.5'W, 1500 m, 16 Jul 2000, *Boyle 5971* (NY!).

Diagnosis — Morphologically very similar to but genetically distinct from *Danaea cuspidata* Liebm., differing in locations 390 (A vs G), 948 (A vs G), 1060 (T vs A) of *rbcL* reference sequence; 192 (A vs C), 233 (C vs A), 265 (A vs G), 399 (C vs T), 822 (C vs A), 249–253 (insertion of ATTAG vs gap), 729–732 (insertion of AATA vs gap) of *trnL-F* reference sequence; 170 (A vs T), 176 (A vs C), 231 (G vs A), 257 (A vs C), 396 (T vs A), 424 (A vs C), 539 (C vs A), 643 (G vs T), 678 (G vs T), 713 (T vs A), 737 (G vs A), and 867 (G vs T) of *rpl32* reference

Fig. 11. *Danaea cuspidopsis*: A: medial sterile pinna apex; B: erect rhizome; C: fertile leaf; D: sterile leaf (with incomplete pinnae filled in); E: rachis in distal part of lamina; F: fertile pinna. – A: *Maxon 5595* (NY); B: *Maxon 291* (US); C: *Standley 47774* (US); D: *Boyle 5971* (NY); E: *Kessler 14850* (TUR); F: *Burger 9780* (F). – Drawn by Venni Keskiniva.

Fig. 12. *Danaea cuspidopsis*: A: fertile (foreground) and sterile (background) laminae; B: detail of narrowly winged rachis; C: sterile leaves. – A–C *Testo 994*. – © Weston Testo 2016.

sequence. Generally differs from *D. moritziana* C. Presl in veins being simple or forked at costa (vs veins almost never simple and usually forked well above costae), veins more densely packed (17–22 vs 12–17 veins per cm), terminal pinnae often replaced by a bud (vs terminal pinnae always present), and gradually tapering pinna apices (vs abruptly tapering); genetically differs in location 192 (A vs C) of *trnL-F* reference sequence and location 678 (G vs T) of *rpl32* reference sequence. Differs from *D. andina* Keskiniva & Tuomisto in generally having longer fertile pinnae (6.5–12 cm vs 4.2–7.0 cm); longer (1.7–3.2 cm vs 0.7–1.6 cm) and gradually tapering (vs usually abruptly tapering) sterile pinna apices; generally longer sterile leaves (54–120 cm vs 28–71 cm); veins sometimes mostly simple (mostly forked); rhizomes erect (vs can be creeping to ascending). Differs from *D. robbinmoranii* Keskiniva & Tuomisto in narrower wings (to 0.1–0.7 mm vs 0.7–2 mm wide) that cover only distal part of rachises (vs usually all of rachises and sometimes part of petioles as well); generally more pinna-pairs (13–20 vs 7–16) that are usually narrower (largest lateral pinnae 5–8 vs 3–6 times as long as wide without apex), and spaced more closely together (medial pinnae 1.4–2.5 cm vs 2.9–3.5 cm apart).

Description — *Rhizomes* erect, radial, 1.5–2.5 cm in diam., to at least 25 cm long. *Sterile leaves* 54–120 cm long; *petioles* 22–57 cm long, with 1–2 nodes, not winged; *laminae* 29–65 × 12–33 cm, 13–20 pinna-pairs, oblong to lanceolate, imparipinnate or paripinnate with a terminal bud, proximal pinna-pair sometimes clearly smaller than others and more distant, medial pinnae 1.4–2.5 cm apart, bicolorous, (dark) green (to brown) adaxially, light green (to light brown) abaxially, texture thin, rachises winged

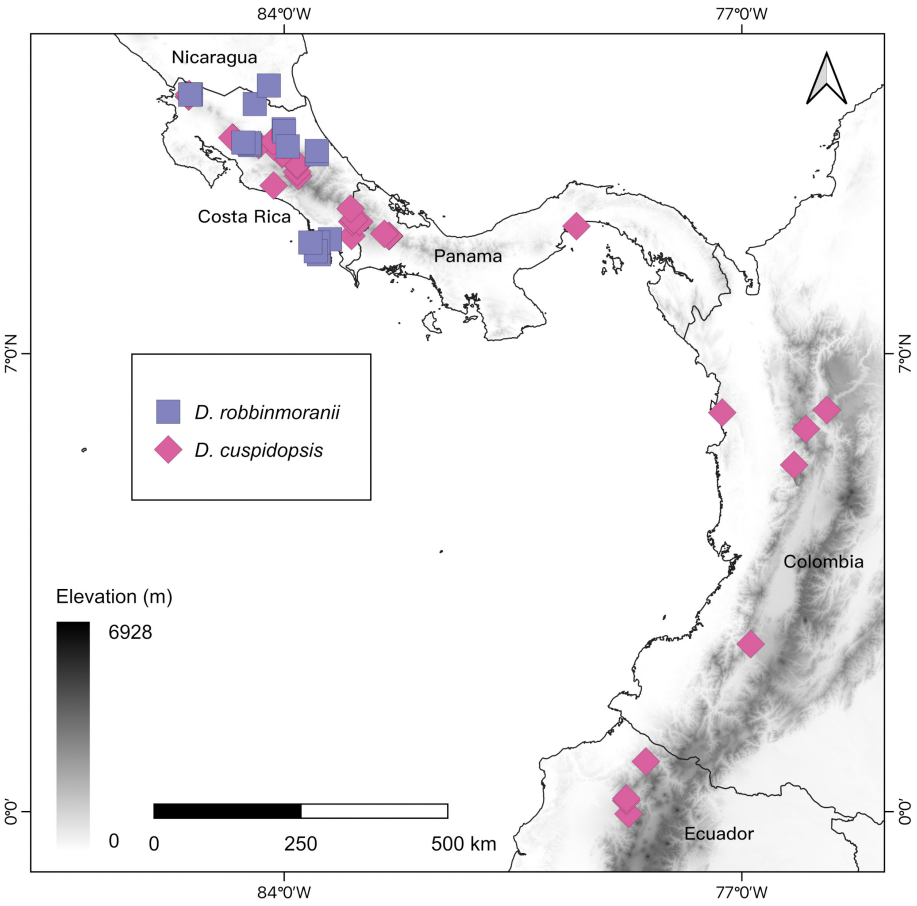

Fig. 13. Distribution of types and paratypes of *Danaea cuspidopsis* and *D. robbinmoranii*.

in distal parts of internodes in distal part of lamina, wings to 0.1–0.7 mm wide; *terminal pinnae* 5.0–15 × 1.3–3.0 cm, lanceolate, bases acute, apices 1.5–3.0 cm long, acuminate, margins of apices serrulate to serrate; *largest lateral pinnae* 8.0–16 × 1.9–2.4 cm, 5.0–7.8 times as long as wide without apex, parallel-sided, (slightly) ascending (or perpendicular to rachis), bases asymmetrical (obtuse or auriculate proximally, obtuse or acute distally), apices 1.7–3.2 cm long, (long-)acuminate, margins of apices serrulate to serrate; *veins* 17–22 per cm, usually forked at costa, only occasionally forked above costae or simple, rarely almost all simple. *Fertile leaves* 55–118 cm long; *petioles* 27–60 cm long, with 2 nodes; *laminae* 37–50 × 9–22 cm, oblong or lanceolate, imparipinnate or paripinnate with a terminal bud, 13–19 pinna-pairs; *terminal pinnae* 3.5–5.5 × 0.5–0.7 cm, linear-lanceolate, bases acute, apices acuminate to cuneate; *largest lateral pinnae* 6.5–12 × 0.5–1.0 cm, linear, slightly ascending or perpendicular to rachis, bases symmetrical (obtuse) or asymmetrical (obtuse distally, auriculate proximally), apices 0.4–1.0 cm long, acuminate to cuneate, margins of apices serrulate to serrate. *Juveniles* with lanceolate laminae, lateral pinnae oblong, rather narrow, apices acuminate.

Distribution and habitat — Abundant in Costa Rica, but also found from Panama (Chiriquí) and the Pacific side of the Andes in Colombia (Antioquia, Chocó, Risalda, Valle de Cauca) and Ecuador (Imbabura, Pichincha). Possibly extends to Nicaragua. Grows at elevations 550–2300 m, but usually found growing above 1000 m. It has been found in primary forests and disturbed secondary forests, in tall, montane forests and cloud forests, often on steep slopes and in ravines. Fig. 13.

Conservation status — We place *Danaea cuspidopsis* in the Least Concern (LC) category (IUCN 2012). It has a known Area of occupancy of at least 128 km^2, which corresponds to the EN category, and an Extent of occurrence of at least 534,564 km^2, which corresponds to the LC category. *Danaea cuspidopsis* is abundant especially in Costa Rica, and it is known from 50 collections with occurrences in several protected areas (Braulio Carillo National Park, Monteverde Nature Reserve, Tapantí Reserve, Parque Nacional La Amistad in Costa Rica, Tandayapa Cloud Forest Reserve in Ecuador). There appears to be no imminent threat to all its subpopulations.

Etymology — The name highlights the fact that *Danaea cuspidopsis* is a cryptic species morphologically very similar to but genetically clearly distinct from *D. cuspidata*.

Remarks — *Danaea cuspidopsis* is an intermediately sized *Danaea* with bicolorous leaves, pinnae with rather long acuminate apices, veins usually forked at the costa, and terminal pinnae often replaced by a bud. It is a cryptic species that we separate from *D. cuspidata* on the basis of genetic evidence: *D. cuspidopsis* is deeply embedded in a 9-species clade that does not contain *D. cuspidata*, this being resolved to another clade (Keskiniva & al. 2024). *Danaea cuspidopsis* seems to grow to a larger size than *D. cuspidata* (sterile leaves to 120 cm vs to 86 cm long), but we have been unable to find reliable morphological characters to separate the two. We have genetically verified records of *D. cuspidopsis* from Costa Rica and of *D. cuspidata* from Mexico but do not know how either species is distributed in between. *Danaea cuspidata* has

often been considered synonymous with *D. moritziana* (e.g. Christenhusz 2010; Tuomisto & al. 2018), but on the basis of both genetic and morphological evidence we are now convinced they are distinct.

Another potential name from the same geographical area is *Danaea muenchii* Christ. The protologue of *D. muenchii* written by Rosenstock (1926) cites both Costa Rican and Mexican specimens. However, the protologue also quotes a letter by Christ which says that the diagnosis of the species can be found in Christ (1905), which in turn is based on a Mexican specimen collected by Münch from San Pablo, Chiapas, Mexico in 1904. A specimen corresponding to this information, Münch 159 (P), was mentioned as a holotype in Mickel & Beitel (1988), and this can be considered a lectotypification under Art 9.23 (Turland & al. 2018). As we have identified all of the similar specimens from Mexico as *D. cuspidata*, we consider *D. muenchii* to be a synonym of that species.

Danaea cuspidopsis resembles *D. betancurii*, which is found on the Amazonian side of the Andes and between the Cordilleras in Colombia (vs *D. cuspidopsis* only on the Pacific side), but *D. cuspidopsis* is generally larger than *D. betancurii* (sterile leaves 54–120 cm vs 37–99 cm long) and almost always has wider pinnae (largest lateral pinnae 1.9–2.4 cm vs 0.9–2 cm wide, the type of *D. betancurii* having especially narrow pinnae) that are clearly bicolorous with the abaxial side whitish (vs sometimes almost concolorous). Rhizomes are always erect in *D. cuspidopsis*, whereas some specimens of *D. betancurii* seem to have a creeping to ascending rhizome.

Our current understanding is that *Danaea moritziana* has a mostly Venezuelan distribution and does not occur in the western side of the Andes, where *D. cuspidopsis* is common. *Danaea cuspidopsis* generally differs from *D. moritziana* in veins being simple or forked at the costae (vs veins almost never simple but usually forked well above the costae), a denser venation (17–22 vs 12–17 veins per cm), terminal pinnae often replaced by a bud (vs terminal pinnae always present), and gradually tapering pinna apices (vs abruptly tapering).

Danaea cuspidopsis differs from *D. stricta* Tuomisto & Keskiniva in having clearly bicolorous laminae (vs almost concolorous), narrower fertile pinnae (0.5–1.0 vs 1.0–1.5 cm wide), falcate pinnae (vs strictly linear), medial pinna apices that are asymmetrical (vs symmetrical) and obtuse or acute (vs truncate), and a thinner lamina texture. In addition, the terminal pinna is often present in *D. cuspidopsis* (vs always replaced by a bud in *D. stricta*), and the rhizome is generally shorter (up to 25 cm tall vs to 40 cm tall) and more slender (1.5–2.5 cm vs 2.2–4 cm in diam.).

Danaea cuspidopsis differs from *D. inaequilatera* in having generally narrower fertile pinnae (0.5–1.0 vs 0.8–1.3 cm wide) and sterile pinnae that are whitish abaxially (vs almost concolorous), longer (medial pinnae 5.0–7.8 vs 3.7–4.7 times as long as wide without apex), asymmetrical at bases (vs usually symmetrical), and have generally longer apices (1.7–3.2 cm vs 0.5–2.0 cm long) that are gradually tapering (vs abruptly tapering).

See *Danaea andina* (described above) and *D. robbinmoranii* (described below) for comparison with those species.

Additional specimens examined — Colombia: Antioquia: Angelópolis Municipality. Vereda Romeral, Hacienda La Argentina, Quebrada Las Animas, 06°08'N, 75°42'W, 2050–2130 m, 18 Nov 2005, *Rodriguez 5604* (NY!); Chocó: NW side of Alto del Buey, Trail along ridge from confluence of forks of Río Mutatá above Río Dos Bocas to top of Alto del Buey, 1450–1750 m, 9 Feb 1971, *Lellinger 247* (US-3!); 0.3 km E of Ciudad Bolívar-Quibdo Road across suspension bridge at c. km 141, 750 m, 3 Apr 1971, *Lellinger 881* (US-2!); Risaralda: Corregimiento de Puerto de Oro, Vereda Chirrincha, banks of Río Aguita, 800–900 m, 13 Sep 1991, *Fernández-Alonso 8993* (MO!); Valle Del Cauca: El Tambo–Munchique, between Uribe and "La 81" (La Romelia), 1800 m, 12 Feb 2015, *Kessler 14850* (HUA!, TUR!). — Costa Rica: Alajuela: Vicinity of Coliblanco, 1950 m, 30 Apr–2 May 1906, *Maxon 291* (NY!, US!); Zarcero, *Smith H261* (F!); Viento Fresco, 1600–1900 m, 13 Feb 1926, *Standley 47774* (US!); Cartago: Tapantí Reserve, 1400–1700 m, 1982, *Gómez 19287* (AAU, MO!); SE of Orosi, c. 2.2 km SSE of Purisil, above Finca La Concordia, in gorge next to house of uppermost portion of upper finca, 1800 m, 8–10 Aug 1970, *Lellinger 1481* (US!); 1923, *Maxon 8151* (US!); Turrialba, near Interamerican Institute, in Cervantes ravine, 550–650 m, 9–10 Mar 1953, *Scamman 6992* (GH!, US!); along trail leading eastward into mountains from road into Tapantí Reserve c. 1 km S of Jct. of Quebrada Salto and Río Grande de Orosi, 09°43'N, 83°47'W, 1500–1800 m, 1 Feb 1986, *Smith 2165* (CR!, NY-2!, UC!); El Munco, S of Navarro, 1400 m, 1924, *Standley 33642* (US!); Cerro de la Carpintera, *Standley 35594* (US!); Guanacaste: SW (Pacific) slope of Cerro Cacao, Cordillera de Guanacaste, 10°55'N, 85°28'W, 1300–1450 m, 10 Aug 2007, *Grayum 12581* (CR!, MO!); Liberia, Parque Nacional Guanacaste, Volcán Cacao, trail to top, 10°56'N, 85°27'W, 1450–1550 m, 8 Aug 2007, *Rojas 7709* (MO!); La Cruz, Santa Cecilia c. 5 km from Estación Pitilla, Fila Orosilito, headwaters of Río Mena (Pitilla-Volcán Cacao route), 10°58'N, 85°27'W, 1100–1200 m, 8 Apr 2008, *Rojas 8340* (MO!); Heredia: Braulio Carillo Park, Zurquí, 1700–2000 m, 1 Mar 1983, *Gómez 20219* (MO!, UC!); Braulio Carillo National Park, 10°15'N, 84°10'W, 1830 m, 8 Nov 1986, *Hennipman 6784* (AAU, BM!, CR, F!, K!, MO!, NY!, P!, U!, UC!, US!, Z!); Vara Blanca, between Poás and Barba Volcanoes, 1600–1700 m, 22 Mar 1953, *Scamman 6991* (GH!, US!); Pcia. San José, along unnamed N fork of Río Zurquí, Cordillera Central, 10°04'N, 84°01'W, 1500–1600 m, 18 Jan 1986, *Smith 1667* (AAU, CR!, MO!, NY!, UC-2!); S slopes of Cerro Zurquí, 5 km N of San Luis Norte, 10°03'N, 84°02'W, 1800 m, 20 Mar–4

Apr 1973, *Stolze 1569* (F-2!); Limón: Cordillera de Talamanca, Atlantic slope, canyon of Río Siní, 09°13'N, 82°59'W, 1800–1900 m, 15 Sep 1984, *Davidse 29113* (MO!); Puntarenas: In and around Monteverde Nature Reserve, Chomogo Trail, 10°18'N, 84°47'W, 1450–1650 m, 31 Oct–2 Nov 1975, Burger 9780 (F-2!); Coto Brus, P. I. La Amistad, Cordillera de Talamanca. Estación Pittier. Trail to Río Gemelo, 09°01'N, 82°58'W, 1650 m, 30 Jan 1995, *Fletes 26* (CR!, MO!); Upper Río Burú, 2010 m, 19 Aug 1983, *Gómez 21429* (CR!, MO!, UC!); Upper Río Burú, 2010 m, 19 Aug 1983, *Gómez 21753* (MO!, UC!); Vicinity of biological field station at Finca Wilson, 5 km S of San Vito de Java, 1200–1400 m, 4 Aug 1967, *Mickel 3114* (NY!, US!); P. N. La Amistad. Cuenca Térraba-Sierpe, Estación Pittier, Cerro Gemelo, 09°03'N, 82°56'W, 2600–2700 m, 23 May 1996, *Moraga 477* (CR!, MO!); Monteverde, Motas, 1967, *Walter 5-1968* (MO-2!); San José: San Cristobal Norte, 2000 m, 1969, *Gómez 2397* (F!); Tarrazu, San Marcos, from street crossing to San Carlos 100 m toward San Marcos, 09°34'N, 84°10'W, 1700 m, 21 Sep 2004, *Rojas 6104* (CR!, MO!); La Palma, 17 Mar 1910, *Brade 508* (NY!); La Picada de San Antonio, Cerro de la Muralla de Socorro de San Ramón, 1200–1300 m, 22 Aug 1927, *Brenes 5680* (F!); La Palma de San Ramón, 1275–1275 m, 8 Mar 1930, *Brenes 11907* (F!); 1928, *Valerjo 306* (US!); Monteverde, 28 Oct 1963, *Walter 258* (MO!). — Ecuador: Imbabura: In vicinity of Río Verde, c. 5 km SW from village of Mani, Río Cachaco, 00°46'N, 78°28'W, 1300 m, 2 Jun 1980, *Sperling 5035* (GH!, QCA!); Pichincha: Tandayapa Cloud Forest Reserve, 1750–1880 m, 2004, *Lehnert 1215* (UC-2!, QCA!); Road El Paraiso–Saguangal, 11 km from El Paraiso, 00°12'N, 78°46'W, 1250 m, 2 May 1982, *Øllgaard 37644* (AAU, QCA!); Road El Paraiso–Saguangal, 3 km from El Paraiso, 00°10'N, 78°46'W, 1500 m, 2 May 1982, *Øllgaard 37782* (AAU, QCA!, UC!); Road to Mindo, 00°02'S, 78°44'W, 1350 m, 26 May 1997, *Navarrete 1954* (AAU, QCA!). — Panama: Chiriqui: Vicinity of El Boquete, 1380 m, 1933, *Bro. Maurice 667* (US!); Vicinity of El Boquete, 1000–1500 m, 1918, *Cornman 1082* (US!); Boquete Region, Cerro Horqueta, 1900–2100 m, 30 Jul 1940, *von Hagen 2166* (NY-2!); Between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, 18 Mar 1911, *Maxon 5518* (US-2!); Upper Caldera River, above El Boquete, 1450–1650 m, 22–24 Mar 1911, *Maxon 5595* (US-2!); Along Río Caldera (Boquete region) and on slope to E, c. 3.5 km NW of Bajo Mono, 08°50'N, 82°28'W, 1600 m, 8 Feb 1986, *Smith 2506* (NY!, PMA-2!, UC-2!, US). Boquete, 08°50'12.7"N 82°27'34.3"W, 1800 m, 29 Jan 2016, *Testo 994* (NY, PMA, VT).

6. *Danaea dilatata* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Arthrodanaea* C. Presl) – Fig. 14.

Holotype: French Guiana, in sylvis montosis, comitatus de Genes, ad margines torrentium et rivulorum, 1847, *Leprieur s.n.* (GH!).

Diagnosis — Similar to *Danaea bipinnata* Tuomisto but differing in larger size (sterile leaves 60–75 cm vs 38–62 cm long); more nodes on petioles (2–4 vs 0–2); and oblanceolate fertile pinnae (vs elliptic).

Description — *Rhizomes* erect, radial, 1.5–2.5 cm in diam., to at least 7 cm long. *Sterile leaves* 60–75 cm long; *petioles* 31–43 cm long, with 2–4 nodes, not winged; *laminae* 29–32 × 21–27 cm, (long-)obovate to elliptic, imparipinnate, distal pinnae smallest, 6–7 pinna-pairs, medial pinnae 3–3.5 cm apart, almost concolorous, light to dark brown, texture thin, rachises not winged; *terminal pinnae* 12–13 × 3.0–3.9 cm, elliptic to lanceolate, bases acute to cuneate, apices 1.8–2.2 cm long, acuminate, margins of apices entire to slightly sinuate; *largest lateral pinnae* 13–17 × 3.0–3.9 cm, 4.8–5.5 times as long as wide without apex, widest at or above middle, bases symmetrical (acute) or asymmetrical (acute to obtuse proximally, acute distally), apices 2.0–3.8 cm long, (long-) acuminate, margins of apices entire to sinuate; *veins* 12–18 per cm, mostly forked at costae (sometimes mostly forked above costa or many simple). *Fertile leaves* 66–90 cm long; *petioles* 40–62 cm long, 3–4 nodes; *laminae* 26–28 × 14–18 cm, long-obovate, imparipinnate, distal pinnae smallest, 6–8 pinna-pairs; *terminal pinnae* 5.3–8.0 × 1.2–1.6 cm, lanceolate, bases acute, cuneate or acuminate, apices (long-)acuminate; *largest lateral pinnae* 7.8–11 × 1.3–1.7 cm, oblanceolate (to narrow-elliptic), bases acute, apices 1.4–2.0 cm long, (long-)acuminate, margins of apices serrulate at shoulder of pinna, sinuate at tip, synangia ascending. *Juveniles* not known.

Distribution and habitat — Known from Guyana and French Guiana. Fig. 15.

Conservation status — We place *Danaea dilatata* in the Near Threatened (NT) category (IUCN 2012). All known collections of this species are from the second half of the 19th century or the beginning of the 20th. Consequently, it is difficult to know the exact localities and their status. Based on the estimated localities, *D. dilatata* has an Extent of occurrence of 10 km^2 and it is known from only nine collections from 5 locations, which corresponds to the VU category. The locations are not inside protected areas, but there appears to be no imminent threat to all its subpopulations.

Etymology — The species epithet refers to the symmetrically outward-bending synangia that form a dilating pattern especially in the proximal part of the fertile pinnae.

Remarks — F. M. R. Leprieur was about to describe this species as *Danaea polyphylla*, which is written on several of the specimens, but we could not find a formal description of that name. We do not have genetic data for this species, but with a Guianan distribution it is geographically distant from the western Amazonian *D. bipinnata*,

Fig. 14. *Danaea dilatata*: A: medial sterile pinna apex; B: medial fertile pinna; C: fertile leaf; D: sterile lamina; E: fragment of erect rhizome. – A, B, D, E: *Leprieur s.n.* (GH); C: *Leprieur 274* (GH). – Drawn by Venni Keskiniva.

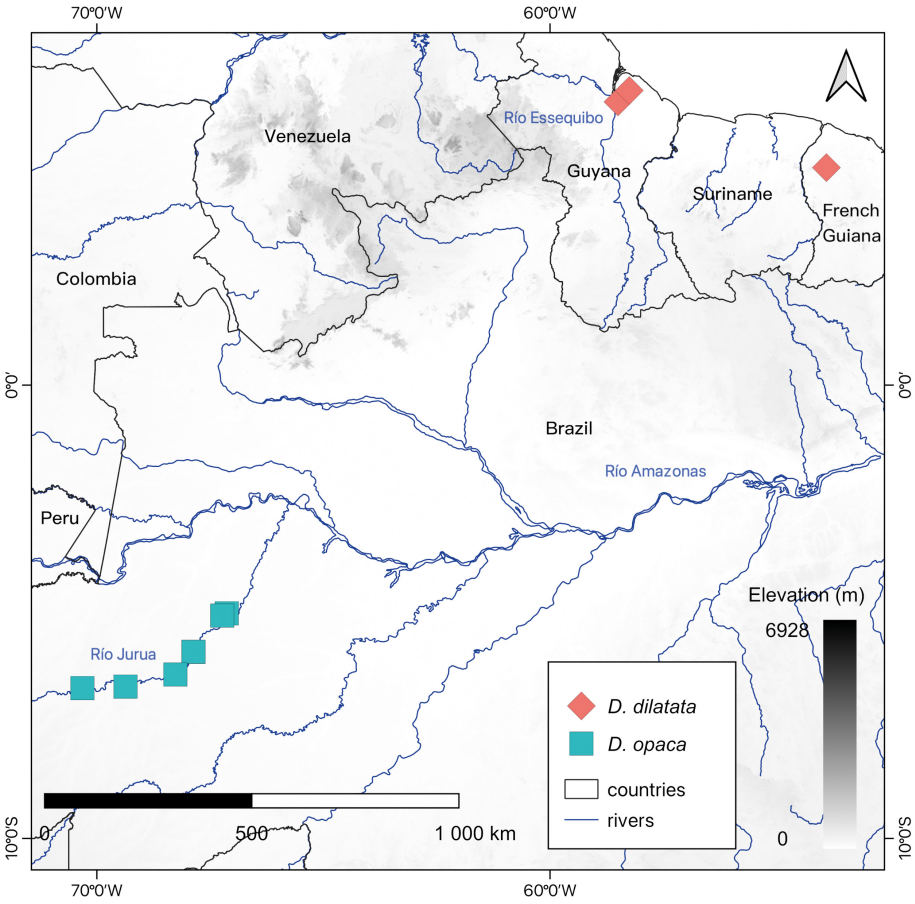

Fig. 15. Distribution of types and paratypes of *Danaea dilatata* and *D. opaca*.

which it most closely resembles. *Danaea dilatata* has generally more nodes on petioles than *D. bipinnata* (2–4 vs 0–2) and has generally larger sterile leaves (60–75 cm vs 38–62 cm long).

Danaea dilatata shares the acute to cuneate bases and (long-)acuminate apices typical of the fertile pinnae of *D. bipinnata* and *D. arbuscula* Christenh. & Tuomisto. However, the fertile pinnae of *D. dilatata* are usually oblanceolate and rather uniform in shape (vs elliptic and more variable with sometimes very long-acuminate bases and apices in *D. bipinnata* and *D. arbuscula*). Secondary veins in the fertile pinnae of *D. dilatata* resemble a fountain, curving up and then to the sides (vs usually more straight in *D. bipinnata* and especially *D. arbuscula*).

Danaea dilatata has generally more nodes per petioles than *D. arbuscula* (0–2 vs 2–4), generally more fertile pinnae (6–8 vs usually less than 6) that are generally narrower (1.3–1.7 cm vs 1.6–4.0 cm wide), and the sterile pinnae of *D. dilatata* are thinner than the often leathery, thick pinnae of *D. arbuscula*. The terminal pinna is the same size as the distal pair of lateral pinnae and smaller than other lateral pinnae (vs terminal pinnae usually as large as or larger than the largest lateral pinnae in *D. arbuscula*).

Danaea dilatata differs from *D. geniculata* Raddi, especially the northern specimens of the latter, in that its fertile pinnae are acute to cuneate (vs truncate) at bases and (long-)acuminate (vs acute to obtuse) at apices, and the sterile pinnae are usually broader (minimum 3.0 cm vs 2.1 cm wide) and have longer apices (2.0–3.8 cm vs 0.8–1.8 cm).

Danaea leprieurii Kunze is a smaller plant than *D. dilatata* (sterile leaves 15–45 cm vs 60–75 cm long) with fewer sterile pinnae (2–6 vs 6–8 pairs) that also differ in being shorter (5.2–13 vs 13–17 cm), more parallel-sided and with generally more asymmetrical bases.

Danaea trinitatensis Christenh. & Tuomisto is generally a smaller plant (23–64 cm vs 60–75 cm) with usually shorter pinnae (min. 6.2 cm vs min. 12.8 cm long), fewer pinna-pairs (1–7 vs 6–7), pinna apices that are often clearly sinuate (vs entire or only slightly sinuate), and often sterile margins on fertile pinnae (vs synangia always reaching the margins in *D. dilatata*). The leaves of *D. trinitatensis* dry to a light yellowish green colour (vs darker brown in *D. dilatata*).

The sterile leaves of *Danaea dilatata* have more pinna-pairs (6–8) than those of *D. danaëpinna* Christenh. (1–5) or *D. polymorpha* Lepr. (2–4) and they dry to a darker brown colour (vs light grey or green in *D. danaëpinna* and *D. polymorpha*).

Additional specimens examined — French Guiana: In montosis Diaboli, 1850, *Leprieur 254* (E! (E00157002), US! (US1505176)); Comitatus de Genes, ad margines torrentium et rivulorum, 1847, *Leprieur 274* (GH!, US! (00650785)); Jenman's Demerara label (with year 1897) and hand-written text: "Collected by Leprieur, French Guiana", *Leprieur s.n.* (NY!); *Leprieur s.n.* (NY 00029576!)). — Guyana: Essequibo River, Moraballi Creek, near Bartica, 1929, *Richards 751* (BM, K!); Demerara, 1897, *Jenman 55* (US! (1120091)); Jul 1847, *Leprieur s.n.* (P! (P01420459)).

7. *Danaea elongata* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 16.

Holotype: Ecuador, Zamora-Chinchipe, Bombuscaro, *Podocarpus* National Park, 950–1050 m, 16 Sep 2004, *Lehnert 1258* (QCA! (mounted on 2 sheets: 208044

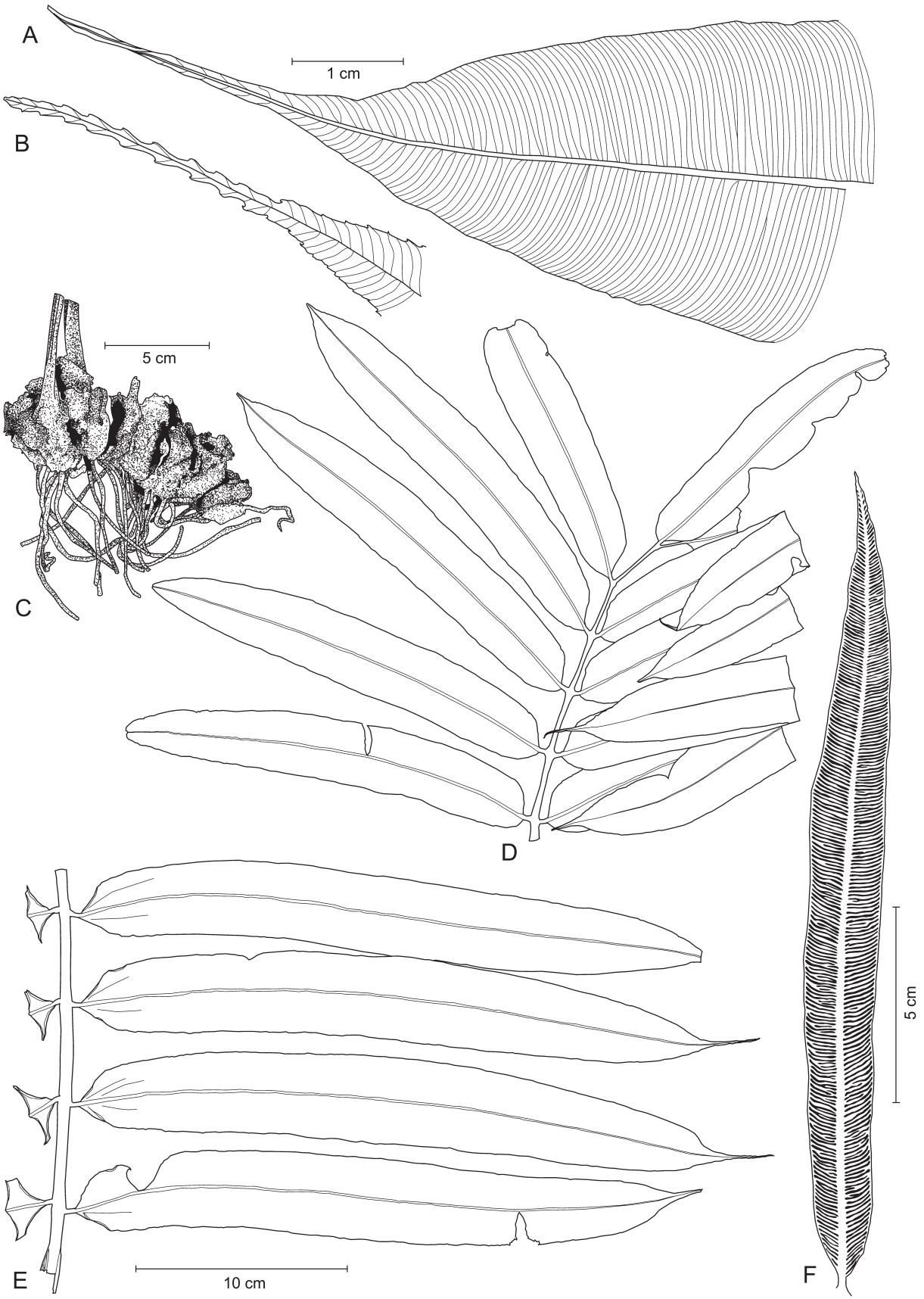

Fig. 16. *Danaea elongata*: A: medial pinna apex (typical); B: medial pinna apex (serrate form); C: fragment of creeping rhizome; D: sterile leaf apex; E: sterile leaf medial pinnae; F: fertile pinna. – A, D, E: *Lehnert 1258* (TUR); B: *Kessler 13000* (LPB); C: *Beck 7357* (F); F: *Lehnert 1523* (UC). – Drawn by Venni Keskiniva.

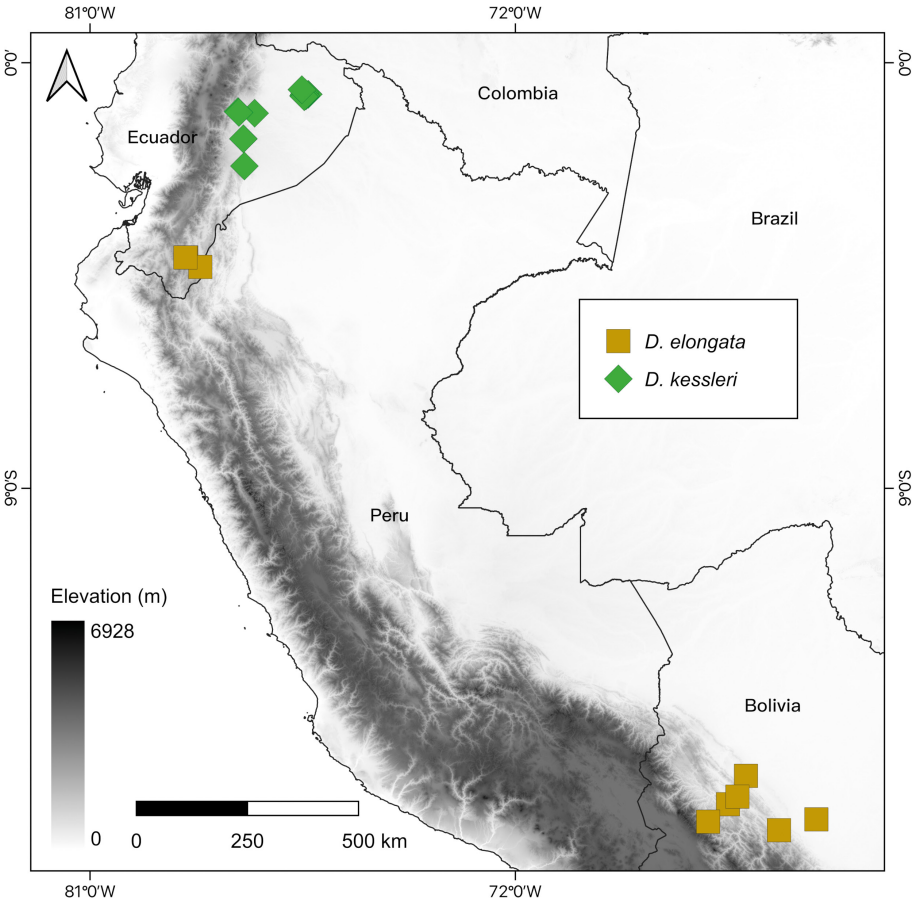

Fig. 17. Distribution of types and paratypes of *Danaea elongata* and *D. kessleri*.

& 7008041); isotypes: GOET! (042667), TUR!, UC! (mounted on 2 sheets: 1794279, 1794280)).

Diagnosis — Similar to *Danaea nigrescens* Jenman, but differing in pinna apices usually without serrations (vs almost always serrate); medial pinnae parallel-sided (vs usually oblanceolate); pinnae generally narrower (to 4.3 cm vs to 5.7 cm wide, 4.9–7.6 vs 4.1–6.7 times as long as wide without apex); genetically differs in locations 105 (G vs T), 377 (C vs T), 446 (T vs C), 480 (C vs A), 614 (G vs A), 620 (T vs C), 1004 (C vs T), 1019 (T vs A) of *atpB* reference sequence; 698 (T vs C), 752 (G vs A), 1191 (T vs C) of *rbcL* reference sequence; 48 (T vs C), 71 (T vs C), 112 (G vs T), 213 (A vs C), 293 (G vs A), 299 (G vs A), 320 (T vs G), 742–744 (TTT vs gap), 762–763 (CC vs gap), 858 (G vs A) 876 (C vs gap), 886–889 (TAAA vs gap) of *trnL-F* reference sequence; 109 (A vs G), 334 (A vs C), 424 (T vs C), 471 (C vs T), 517 (C vs T), 617 (C vs A), 630 (A vs G), 642 (G vs A), 643 (A vs G), 650 (T vs C), 670 (G vs A), 673 (A vs G), 684 (A vs C), 688 (T vs C), 690 (T vs gap), 877 (C vs T), 909 (T vs C), 958 (T vs C) of *rpl32* reference sequence. Similar to *D. erecta* Tuomisto & R. C. Moran, but differing in creeping, dorsiventral rhizomes (vs erect, radial), and sometimes having serrations in pinna apices (vs never serrate). It is unique in *D.* subg. *Danaea* by having a T (vs A or C) at position 650 of *rpl32* reference sequence and a T (vs C) at position 1191 of *rbcL* reference sequence.

Description — *Rhizomes* creeping, dorsiventral, leaf bases in two rows, 3.0–4.0 cm in diam., to at least 15 cm long. *Sterile leaves* 92–200 cm long; *petioles* 55–92 cm long, lacking nodes, not winged; *laminae* 60–69 × 45–70 cm, obovate, imparipinnate, 9–15 pinna-pairs, medial pinnae 3.5–5.0 cm apart, slightly paler abaxially than shiny green adaxial side when fresh, dries green (or brown in alcohol), texture relatively thin to intermediately thick, pinna margins sometimes slightly cartilaginous, rachises not winged; *terminal pinnae* 16–26 × 1.8–5.2 cm, oblong (to lanceolate), bases acute, apices 2.0–4.0 cm long, long-acuminate to caudate, margins of apices entire, sinuate or serrulate; *largest lateral pinnae* 22–34 × 3.9–4.3 cm, 4.9–7.6 times as long as wide without apex, parallel-sided (to slightly wider above middle), bases symmetrical, acute to obtuse, apices 2.5–3.6 cm long, acuminate to long-caudate, margins of apices entire, sinuate, serrulate or serrate; *veins* 13–19 per cm, mostly forked at costae, some simple. *Fertile pinnae* 14–22 × 1.9–2.1 cm, parallel-sided or long-elliptic, bases symmetrical, acute to obtuse, apices 0.5–2.0 cm long, acuminate to cuneate, margins of apices entire to crenulate. *Juveniles* not known.

Distribution and habitat — Grows at mid-elevations, 550–1300 m, on the Amazonian side of the Andes in Ecuador (Zamora-Chinchipe) and Bolivia (Cochabamba, El Beni, La Paz); it may occur in between as well, but we have no confirmed records from Peru. Found in (pre) humid, evergreen montane forests and lower montane forests. Individual labels mention collections made in a ravine, in disturbed vegetation, in a coffee plantation, and on sandstone. Fig. 17.

Conservation status — We place *Danaea elongata* in the Least Concern (LC) category (IUCN 2012). It has a known Area of occupancy of 36 km^2, which corresponds to the EN category, and an Extent of occurrence of 173,189 km^2, which corresponds to the LC category. Whether the lack of records from Peru indicates lack of

collecting activity or actual fragmentation of the species into two distant populations is unknown. *Danaea elongata* is known from only 10 collections, but all of these are from inside national parks (Parque Nacional Tibnis and Isiboro Sécure National Park and Indigenous Territory in Bolivia and *Podocarpus* National Park in Ecuador). There appears to be no imminent threat to all its subpopulations.

Etymology — Named for the long, narrow, parallel-sided pinnae.

Remarks — *Danaea elongata* is a rather large species with a disjunct distribution in the Ecuadorian and Bolivian Andes. It differs from the typical *D. nigrescens* in usually having entire to sinuate pinna apices (vs usually serrate) and parallel-sided medial pinnae (vs usually oblanceolate) that are generally narrower (to 4.3 cm vs to 5.7 cm wide, 5–8 vs 4–7 times as long as wide without apex). *Danaea nigrescens* usually grows at lower elevations (50–900 m vs 550–1300 m) and has a wide distribution in the Amazonian lowlands (vs found only in the foothills of the Andes). However, there is both geographical and morphological overlap, and some specimens can be reliably identified only with DNA.

The most reliable morphological difference between *Danaea elongata* and *D. erecta* is in rhizome habit (creeping and dorsiventral vs erect and radial). In addition, sometimes *D. elongata* has serrations at the pinna apices (vs margins always entire), and it usually grows at lower elevations (550–1300 m vs 500–2000 m) and only on the Amazonian side of the Andes (vs on both sides). However, reliable identification generally requires either information on rhizome habit or DNA.

Danaea elongata differs from *D. kessleri* in having generally more pinnae (9–15 vs 4–14) that are usually narrower (max. 4.3 cm vs max. 7.1 cm wide, medial pinnae 4.9–7.6 vs 3.6–7.0 times as long as wide without apex) and parallel-sided (vs often elliptic or oblanceolate), pinna apices that are usually long-acuminate (vs acute to acuminate) and can be serrate (vs always entire), and a terminal pinna that is smaller than second pinnae distally (vs usually largest or larger than second pinnae distally). In addition, *D. elongata* dries brown in alcohol (vs green), grows at higher elevations (550–1300 m vs 200–800 m), and has a more southern general distribution (Fig. 17).

Danaea elongata is a smaller plant than *D. cartilaginea* Christenh. & Tuomisto (sterile leaves to 2 m vs to 3 m long), with smaller and especially narrower pinnae (largest lateral pinnae 22–34 × 3.9–4.3 cm vs 27–49 × 4.6–10 cm). The pinnae of *D. elongata* are thinner in texture and do not have the thick cartilaginous margins usually present in *D. cartilaginea*. Both species can rarely have apices that are serrate throughout, but more typically *D. cartilaginea* has entire pinna apices with the ends of the veins protruding, whereas *D. elongata* has apices that are entire, sinuate or serrate only at the shoulder of the pinnae. In addition, *D. elongata* usually has more pinna-pairs (9–15 vs 4–10), a terminal pinna that is usually smaller than second pinnae distally (vs often larger than second pinnae distally), and lateral pinnae that are parallel-sided or seldom oblanceolate (vs seldom parallel-sided, usually elliptic or oblanceolate).

Danaea elongata is genetically clearly different from *D. nodosa*, but morphologically the two overlap almost completely and are very hard to distinguish without DNA analysis. Luckily for botanists, they do not occur in the same geographical area, as *D. elongata* is restricted to the Amazonian side of the Andes whereas *D. nodosa* is found in Central America and the Greater Antilles.

Additional specimens examined — Bolivia: Cochabamba: Prov. Chapare, Villa Tunari 34 km toward Cochabamba Trail on bank of Río Espíritu Santo, 670 m, 1905, *Beck 7357* (F!, Z!). Prov. Ayopaya, crossing Rio Ipiri in serrania de Mosetenes, 16°03'S, 66°40'W, 610 m, 27 Sep 2004, *Huaylla 1456* (GOET!, UC!); Territorio Indígena Parque Nacional Isiboro-Secure, cordillera de Mosetenez, laguna Carachupa, 16°14'S, 66°25'W, 1300 m, 2003, *Kessler 13000* (GOET!, TUR!); El Beni: Prov. Gral. Ballivian, km 16 on camino maderero to SW of km 12 Yucumo-Rurrenabaque, 15°05'S, 67°07'W, 700 m, 31 Jul 1997, *Kessler 10901* (GOET-2!, LPB, UC!); La Paz: Prov. Caranavi, serranía Bella Vista, 36 km from Caranavi toward Sapecho, 15°41'S, 67°30'W, 1300 m, 22 Aug 1997, *Kessler 11238* (GOET, UC!); Sapecho; Colonia Tupiza B, c. 3 h walk to Sapecho, 15°31'S, 67°18'W, 950 m, 14 Apr 2003, *Lehnert 769* (GOET!). — Ecuador: Zamora-Chinchipe: Lodge "Copalinga", 3 km from Bombuscaro Ranger Station of *Podocarpus* National Park, 900–1300 m, 15 Sep 2004, *Lehnert 1244* (GOET!, TUR!, QCA!, UC!); Campamento Shaime (Shaimi) along Rio Nangaritza. Trail to oil bird cave ("cueva de los tayos"), 04°19'S, 78°40'W, 950–1050 m, 6 Nov 2004, *Lehnert 1523* (GOET!, TUR!, QCA!, UC-2!); Parque National *Podocarpus*, Bombuscaro, MATRIX plot L5, along train "Higuerones", 04°07'S, 78°59'W, 1050 m, 20 Nov 2010, *Lehnert 2074* (QCA!, STU-2!), VT!).

8. *Danaea erosa* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 18 A, B, E, F.

Holotype: Costa Rica, Alajuela, about 30 km above San Ramon on road to Los Angeles Norte, 10°05'N, 84°28'W, 610 m, 10 Jul 1972, *McAlpin 1288* (US! (2682123); isotypes: DUKE, F! (C0613254F)).

Diagnosis — Similar in general appearance to *Danaea wendlandii* Rchb. f., *D. crispa* Endrés & Rchb. f. and *D. gracilis* Tuomisto & Keskiniva. Differs from *D. wendlandii* in laminae translucent (vs opaque), concolorous and dark green (vs bicolorous with abaxial side whitish); pinnae somewhat erose (vs not erose); pinna apices usually serrate (vs crenate to serrulate); larger size (sterile

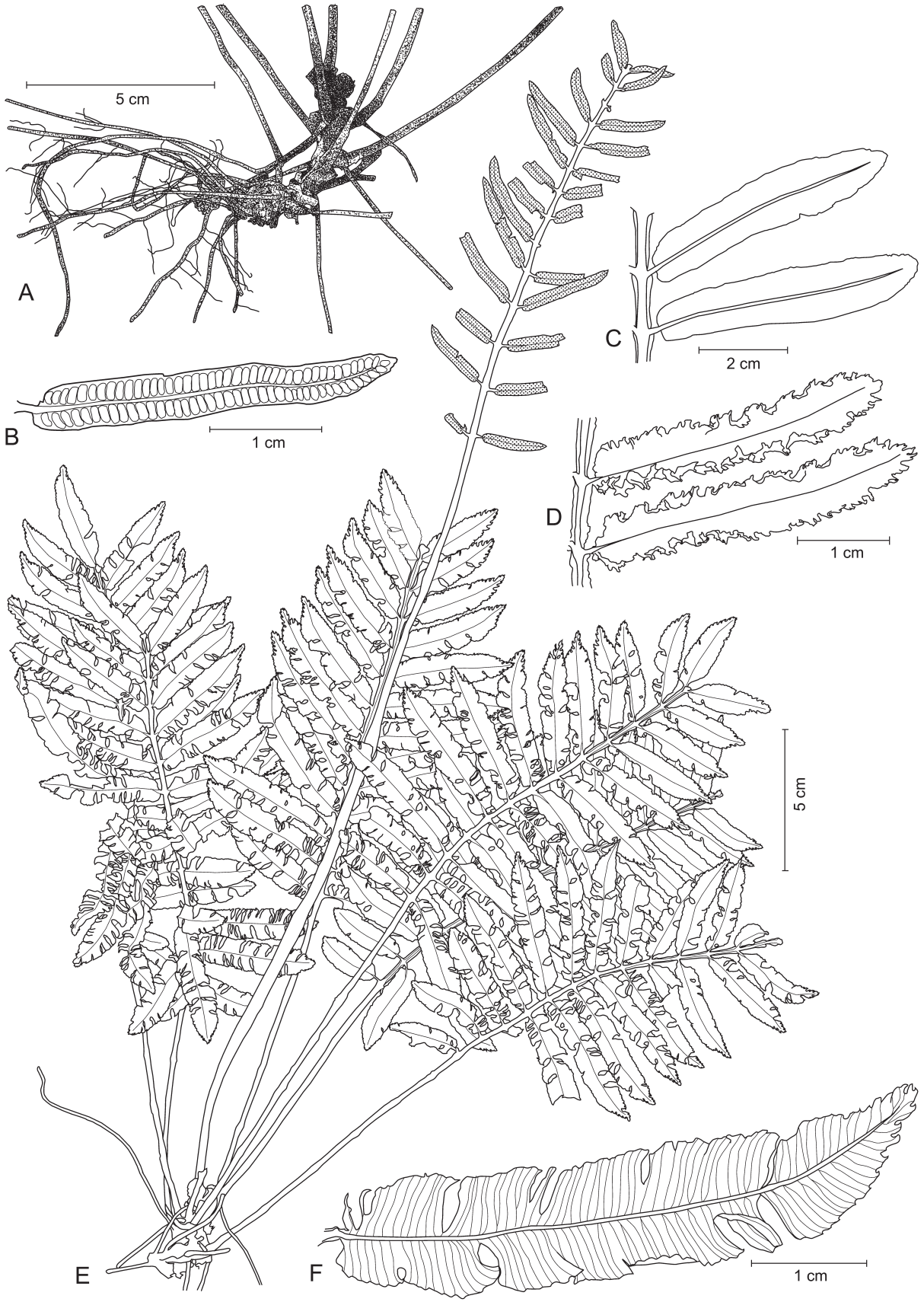

Fig. 18. A, B, E, F: *Danaea erosa*; C: *D. gracilis*; D: *D. crispa*. – A: decumbent rhizome; B: medial fertile pinna; C: sterile medial pinnae; D: sterile medial pinnae; E: plant with fertile pinnae in grey; F: sterile medial pinna. – A: *Grayum 9009* (MO); B, E, F: *Grayum 7786* (MO); C: *Gómez 23798* (BM); D: *Haught 5452* (G). – Drawn by Venni Keskiniva.

leaves 24–39 vs 13–25 cm long, 9–14 vs 4–8 cm wide); and generally more pinna-pairs (10–20 vs 10–15). Differs from *D. crispa* in pinna margins crenulate (vs crispate); generally larger size (sterile leaves 24–39 cm vs 13–26 cm long, 9–14 cm vs 6–11 cm wide); and generally fewer pinna-pairs (10–20 vs 13–25). Differs from *D. gracilis* in pinnae somewhat erose (vs not erose); pinna margins crenulate (vs entire); pinna apices usually acute-acuminate (vs obtuse to acute); margins of apices of pinnae serrate (vs crenulate to serrulate); generally larger size (sterile leaves 24–39 vs 11–32 cm long, 9–14 cm vs 5–11 cm wide); and generally fewer pinna-pairs (10–20 vs 15–25).

Description — *Rhizomes* decumbent to erect, with leaves and roots arranged radially, 1.0–1.5 cm in diam., to 9 cm long. *Sterile leaves* 24–39 cm long; *petioles* 11–14 cm long, with 0–5 nodes, not winged or winged only in distal part; *laminae* 13–23 × 9–14 cm, (long-)obovate (or lanceolate), paripinnate, 10–20 pinna-pairs, medial pinnae 1.0–1.1 cm apart, concolorous dark green, texture thin, translucent, rachises winged, wings to 1.0–1.5 mm wide; *largest lateral pinnae* 4.5–7.5 × 1.0–1.4 cm, 4.0–7.5 times as long as wide without apex, parallel-sided, perpendicular to rachises or slightly ascending, margins undulate when fresh, crenulate and partly erose when dry, bases asymmetrical (obtuse or obtuse proximally, acute distally), apices 0–0.5 cm long, acute, acuminate or cuspidate (or obtuse), margins of apices serrate (to serrulate); *veins* 11–14 per cm, variable. *Fertile leaves* 43–44 cm long; *petioles* 23–27 cm long, 0–1 nodes; *laminae* 16–21 × c. 6 cm, parallel-sided, paripinnate, 16 pinna-pairs; *largest lateral pinnae* 3.0–3.3 × 0.4–0.5 cm, linear, slightly ascending, bases symmetrical, obtuse, apices obtuse (mucronate) to acute. *Juveniles* not known.

Distribution and habitat — Known only from Costa Rica but there it has been observed from sea level to 1150 m. Locally common in primary forests and growing on the banks of small streams. One site is described as wet cloud forest. Fig. 8.

Conservation status — We place *Danaea erosa* in the Near Threatened (NT) category (IUCN 2012). It has an Area of occupancy of 20 km^2, which corresponds to the EN category, and an Extent of occurrence of 7606 km^2, which corresponds to the VU category. Despite large collection efforts in Costa Rica, *D. erosa* is known from only five collections, which indicates that it is rare. However, four of the collections are from protected areas in Costa Rica (Refugio Nacional de Vida Silvestre Barra del Colorado, Braulio Carillo National Park, Parque Nacional Guanacaste). In addition, the species was noted as locally common on the herbarium labels. There appears to be no imminent threat to all its subpopulations if conservation efforts are maintained.

Etymology — Named after the somewhat erose dried pinnae that separate this species from *Danaea wendlandii* and *D. gracilis*.

Remarks — *Danaea erosa* is a rather small, translucent species with undulate margins. In herbarium specimens, the pinnae split along the undulations, creating an incision that runs from the pinna margin toward the costa, making the pinnae appear partly erose in herbarium specimens. *Danaea erosa* is most similar to *D. crispa* but has crenulate rather than crispate pinna margins and (according to label information) less undulate margins when fresh (Fig. 18). In addition, *D. erosa* is usually larger than *D. crispa* (sterile leaves 24–34 cm vs 13–26 cm long, 9–14 cm vs 6–11 cm wide) and can have fewer pinna-pairs (10–20 vs 13–25).

In comparison to *Danaea wendlandii*, *D. erosa* has pinnae that are translucent (vs opaque), concolorous (vs bicolorous), dark green (vs lighter green), and somewhat erose when dry (vs not erose). In addition, *D. erosa* usually has sharper pinna apices (acute-acuminate vs obtuse) that are usually more sharply serrate (vs crenate or serrulate). It is also larger (sterile leaves 24–34 vs 13–25 cm long, 9–14 vs 4–8 cm wide) and can have more pinna-pairs (10–20 vs 10–15).

It is possible that *Danaea erosa* is a hybrid between *D. crispa* and *D. wendlandii*, as it has been found growing in locations with both of these present, and it is somewhat intermediate in morphology between them. However, we do not have genetic or cytological data to test this hypothesis.

Danaea gracilis is another translucent and similar looking species. It occurs in the Chocó region in Ecuador, Colombia, and southern Panama. *Danaea erosa* occurs in northern Costa Rica and differs from *D. gracilis* by having pinnae that are somewhat erose when dry (vs not erose) and have crenate margins (vs entire) and generally sharper pinna apices (acute to acuminate vs obtuse to acute) with serrate margins of apices (vs slightly crenulate or serrulate) (Fig. 18). In addition, *D. erosa* is generally larger than *D. gracilis* (sterile leaves 24–34 vs 11–32 cm long, 9–14 cm vs 5–11 cm wide), and usually has fewer pinna-pairs (10–20 vs 15–25).

Danaea tenera C. V. Morton is another translucent species from the Chocó region, from which *D. erosa* differs in being a smaller plant (sterile leaves 24–34 cm vs 35–46 cm long) with shorter pinna apices (0–0.5 vs 0.6–2.4 cm long) that are not as sharply serrate, and by having partly erose pinnae (vs rarely erose).

Additional specimens examined — Costa Rica: Alajuela: Dos Ríos, Finca Montecele, slopes of Volcán Cacao, ridge on left bank of Río Colón, 10°57'N, 85°26'W, 800 m, 15 Apr 2008, *Rojas 8446* (MO!); Heredia: between Río Peje and upper Río Guácimo, Atlantic slope of Volcán Barva, 10°17'N, 84°05'W, 950–1150 m, 11 Nov 1986, *Grayum 7797* (MO!); Limón: R. N. F. S. Barra del Colorado Llanura de Tortuguero, Sardinas, 10°39'N,

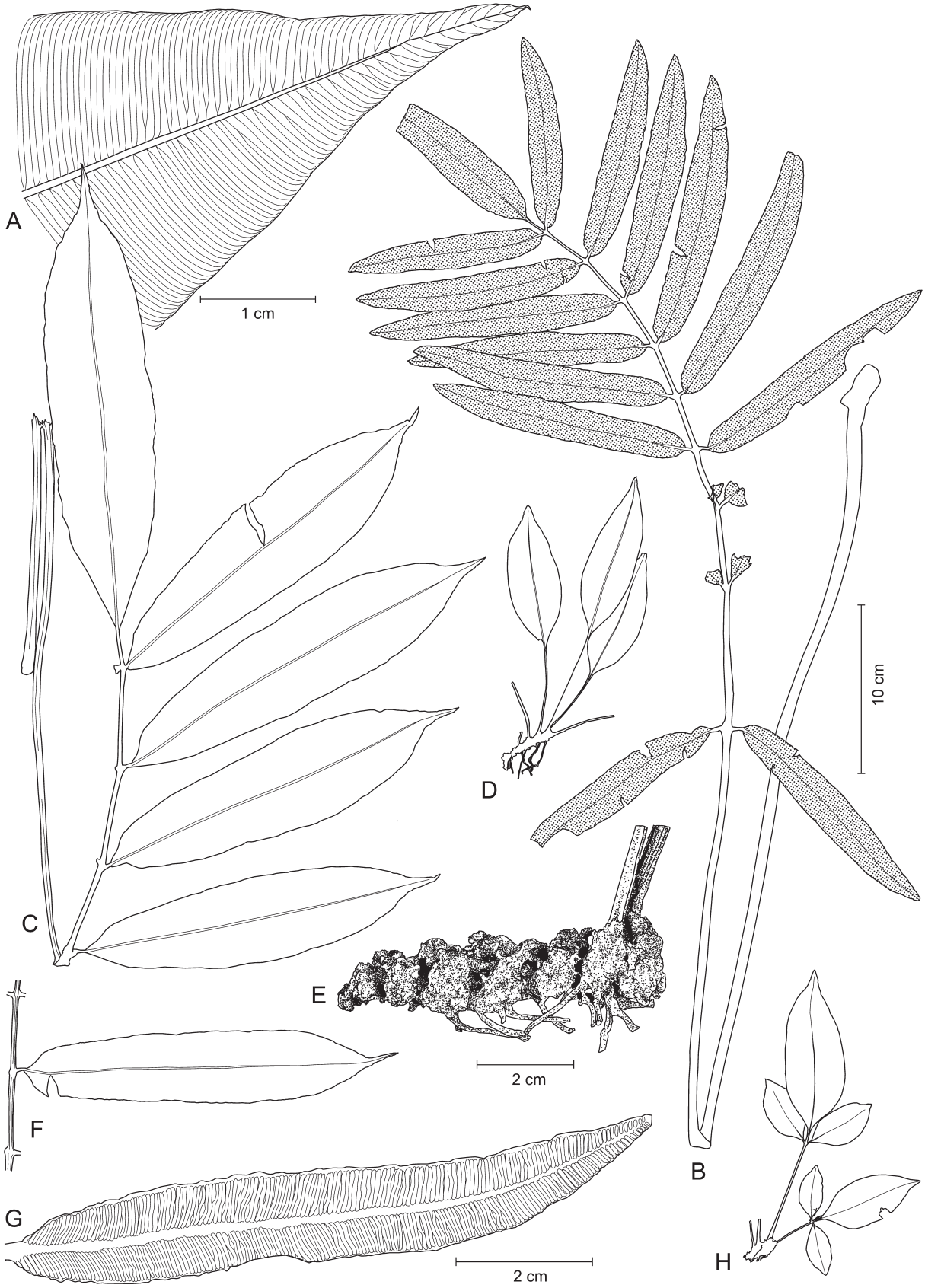

Fig. 19. *Danaea kessleri*: A: medial sterile pinna apex; B: fertile leaf; C: sterile leaf; D: simple juvenile; E: creeping rhizome of juvenile; F: medial sterile pinna; G: medial fertile pinna; H: trifoliate juvenile. C, D, F, H: same scale as B. – A: *Moran 6164* (TUR); B: *Pérez 5795* (QCA); C: *Tuomisto 10658* (TUR); D: *Moran 6217* (TUR); E, F: *Tuomisto 11934* (TUR); G: *Øllgaard 1510* (QCA); H: *Tuomisto 10658* (TUR). – Drawn by Venni Keskiniva.

Fig. 20. *Danaea kessleri* field habit. A: creeping rhizome with leaf bases in two rows; B: entire pinna apex; C: entire plant; D: lamina. – A: *Tuomisto 17897*; B–C: *Tuomisto 17962*. – A–C: © Hanna Tuomisto 2019; D: © Gabriel Massaine Moulatlet 2019.

83°44'W, 20 m, 6 Jun 1996, *Araya 879* (MO!); Refugio Barra de Colorado, between Río Chirripocito and Río Sardina, 10°38'N, 83°45'W, 10 m, 12 Nov 1988, *Grayum 9009* (MO-2!).

9. *Danaea kessleri* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 19, 20.
Holotype: Ecuador, Napo, 7 km SW of Tena, 2 km N of Río Napo, ecotourism area managed by Aventura Tours, 01°03'S, 77°51'W, 690–800 m, 30 Jul 2019, *Tuomisto 17962* (UTCEC! (00001171); isotype: TUR! (mounted on 3 sheets)).

Diagnosis — Similar to and co-occurring with *Danaea nigrescens* Jenman and *D. cartilaginea* Christenh. & Tuomisto. Differs from *D. nigrescens* in always having entire pinna margins (vs serrate to serrulate or very rarely entire); pinnae that are often wider (medial pinnae 3–5(–7) vs 4–7 times as long as wide without apex), usually parallel-sided (vs often oblanceolate); terminal pinnae often longer than second lateral pinnae distally (vs terminal pinnae usually shorter); and drying green in alcohol (vs brown). Differs from *D. cartilaginea* in having entire pinna margins or rarely with veins protruding (vs always with veins protruding or serrate); generally smaller size (sterile leaves to 2.2 m vs to 3 m long); generally smaller pinnae (17–43 × 3.6–7.1 cm vs 27–49 × 5–10 cm); margins that are not or only slightly cartilaginous (vs margins usually clearly cartilaginous); thinner texture (vs thick, leathery); genetically differs in locations 105 (T vs G), 377 (T vs C), 446 (C vs T), 480 (A vs C), 614 (A vs G), 620 (C vs T), 1004 (T vs C), 1019 (A vs T) of *atpB* reference sequence; 698 (C vs T), 752 (A vs G) of *rbcL* reference sequence; 71 (C vs T), 112 (T vs G), 213 (C vs A), 293 (A vs G), 299 (A vs G), 320 (G vs T), 741–743 (gap vs TTT), 761–762 (gap vs CC), 858 (A vs G), 864 (C vs T), 875 (gap vs C), 885–888 (gap cs TAAA) of *trnL-F* reference sequence; 109 (G vs A), 153 (A vs C), 334 (C vs A), 471 (T vs C), 517 (T vs C), 617 (A vs C), 630 (G vs A), 642 (A vs G), 643 (G vs A), 670 (A vs G), 673 (G vs A), 684 (C vs A), 688 (C vs T), 877 (T vs C), 909 (C vs T), 958 (C vs T) of *rpl32* reference sequence. *Danaea kessleri* is genetically unique among *Danaea* in having T (vs A) at position 374 of *atpB* reference sequence.

Description — *Rhizomes* creeping, dorsiventral, leaves in two rows, 1.5–5 cm in diam., to at least 20 cm long. *Sterile leaves* 85–220 cm long; *petioles* 40–130 cm long, lacking nodes, not winged; *laminae* 41 × 90 cm, lanceolate, imparipinnate, terminal pinnae shorter or longer than

second distal-most pinna-pair (or longest), 4–14 pinna-pairs, medial pinnae 3.5–6.0(–6.5) cm apart, concolorous light green to green or more bluish green adaxially and yellowish green abaxially, texture relatively thin to intermediate, margins sometimes slightly cartilaginous, rachises usually not winged (one seen with wings to 0.2 mm wide); *terminal pinnae* 18.6–27.1 × 4–6.5 cm, elliptic, lanceolate or oblong, bases acute, apices 1.6–4 cm long, acuminate to almost acute, margins of apices entire (to very slightly sinuate, crenulate or with veins protruding); *largest lateral pinnae* (17–)21–43 × (3.6–)4.1–7.1 cm, 2.6–7.0 times as long as wide without apex, widest at or slightly above middle or parallel-sided, bases symmetrical, obtuse to acute, apices 1.1–5 cm long, (long-) acuminate to attenuate, margins of apices entire (to very slightly sinuate, crenulate or with veins protruding); *veins* 12–23 per cm, mostly forked at costae. *Fertile leaves* 77 cm long; *petioles* 47 cm long, no nodes; *laminae* 30–37 × 8–28 cm, imparipinnate, obovate or parallel-sided, 6–8 pinna-pairs; *terminal pinnae* 5.5–12 × 1.2–2.2 cm, lanceolate, bases acute, apices cuneate; *largest lateral pinnae* 10–15 × 1.4–2.2 cm, parallel-sided, bases symmetrical, obtuse or acute, apices 0–0.2 cm long, acute to acuminate, margins of apices entire. *Juveniles* with terminal pinnae elliptic to lanceolate, lateral pinnae elliptic, pinna apices entire, largest simple juvenile 25 cm long, smallest pinnate juvenile 4 cm long.

Distribution and habitat — Known only from Amazonian Ecuador (Napo and Pastaza) from 100–950 m elevation. Has been found in primary lowland to montane rainforests on clayey and humus rich soils, including hilly terrain and steep slopes. Mentioned as forming dense stands. Fig. 17.

Conservation status — We place *Danaea kessleri* in the Least Concern (LC) category (IUCN 2012). It has a known Area of occupancy of 48 km^2, which corresponds to the EN category, and an Extent of occurrence of 12,073 km^2, which corresponds to the LC category. *Danaea kessleri* seems to be abundant in Amazonian Ecuador and it is known from 18 collections, many of which are inside protected areas (Reserva Forestal Putuyme, Reserva Huella Verde, and Yasuní National Park in Ecuador). There appears to be no imminent threat to all subpopulations.

Etymology — Named for Michael Kessler, who has made big contributions to fern ecology and systematics and who also collected important original material for this species.

Remarks — *Danaea kessleri* is in many ways morphologically intermediate between *D. cartilaginea* and *D. nigrescens.* Genetically it is most closely related to *D. nigrescens*, from which it differs in having entire pinna margins (vs serrate to serrulate), pinnae that are generally wider (medial pinnae minimum 2.6 vs 4.1 times as long as wide without apex) and usually parallel-sided or elliptic (vs usually oblanceolate), and the terminal pinnae usually being longer than the second lateral pinnae distally (vs terminal pinnae usually shorter). Two samples of *D. nigrescens* with entire margins are known to us, but these specimens still have narrower pinnae than *D. kessleri*. The colours of these species seem to behave differently upon drying; *D. kessleri* dries light green whereas *D. nigrescens* dries darker, such that *D. kessleri* preserved with alcohol before drying has the same colour as *D. nigrescens* that has not been in alcohol, while alcohol treatment turns *D. nigrescens* into a dark brownish green. The same difference seems to be present between *D. kessleri* and *D. elongata* as well (see *D. elongata*, described above, for further comparison).

Danaea kessleri clearly differs from *D. cartilaginea* genetically. It also differs in having entire pinna margins that are only seldom slightly cartilaginous (vs usually clearly cartilaginous) and the veins rarely protruding at the apices (vs veins protruding or sometimes apices serrate). In addition, *D. kessleri* is generally smaller than *D. cartilaginea* (sterile leaves to 2.2 m vs to 3 m long, sterile pinnae 17–43 × 3.6–7.1 cm vs 27–49 × 5–10 cm) with a thinner lamina texture (vs usually leathery and thick).

Juvenile development differs among *Danaea nigrescens*, *D. kessleri*, and *D. cartilaginea*; *D. nigrescens* becomes pinnate at the smallest size (simple juveniles to 8 cm long) and *D. cartilaginea* at the largest (simple juveniles up to 44 cm long), with *D. kessleri* being intermediate between the other two (simple juveniles to 25 cm long).

Danaea kessleri differs from the French Guianan endemic *D. ushana* Christenh. in having generally smaller terminal pinnae (19–27 × 4.0–6.5 cm vs 26–34 × 4.9–7.8 cm), more pinna-pairs (4–14 vs 3–6 in sterile leaves, 6–8 vs 3–4 in fertile leaves), and rhizomes with leaf bases in two rows (vs leaf bases in 3–5 rows).

Additional specimens examined — Ecuador: Morona-Santiago: Mutinza, foothills of Cord. Cutucú just E of village, 02°11'S, 77°44'W, 660–800 m, 19 Nov 1995, *Øllgaard 1510* (QCA!); Napo: km 50 along road traversing Yasuní National Park, 00°43'S, 76°28'W, 200–300 m, 14 Apr 1996, *Moran 6164* (AAU!, TUR!); km 21 along road traversing Yasuní National Park, 00°34'S, 76°31'W, 200–300 m, 16 Apr 1996, *Moran 6217* (AAU!, QCA!, TUR!); Yasuní National Park, permanent plot of 50 ha established for study of forest dynamics, 00°40'S, 76°23'W, 250–280 m, 30 Jan 1996, *Navarrete 1475* (AAU!, QCA!); Yasuní National Park, permanent plot of 50 ha established for study of forest dynamics, 00°40'S, 76°23'W, 250–280 m, 30 Jan 1996, *Navarrete 1486* (AAU!, QCA!); Yasuní National Park, permanent plot of 50 ha established for study of forest dynamics, 00°40'S, 76°23'W, 250 m, 30 Jan 1996, *Navarrete 1492* (AAU!, QCA!); Tena–Salcedo highway, trail to Verde Yacu, 01°02'S, 77°52'W, 620 m,

6 Aug 1993, *Navarrete 535* (AAU!, QCA!); Near Yasuní Scientific Station, 00°40'S, 76°23'W, 208–250 m, 26 Feb 1995, *Svenning 132* (AAU!); Yasuní National Park, W of oil road traversing park, 0–2.1 km from side road leading to Capirón oil well toward SW, 00°42'S, 76°29'W, 200–300 m, 18 Apr 1997, *Tuomisto 10647* (QCA!, QCNE, TUR-2!); Yasuní National Park, W of oil road traversing park, 0–2.1 km from side road leading to Capirón oil well toward SW, 00°42'S, 76°29'W, 200–300 m, 18 Apr 1997, *Tuomisto 10653* (QCA, QCNE, TUR!); Yasuní National Park, W of oil road traversing park, 0–2.1 km from side road leading to Capirón oil well toward SW, 00°42'S, 76°29'W, 200–300 m, 18 Apr 1997, *Tuomisto 10658* (QCA, QCNE, TUR-2!); Yasuní National Park, between km 38 of oil road traversing park and side road leading to Capirón oil well, 00°40'S, 76°28'W, 200–300 m, 22 Apr 1997, *Tuomisto 10821* (QCA, QCNE, TUR!); Yasuní National Park, 2–3 km toward NNE from km 38 of oil road traversing park, 00°38'S, 76°27'W, 200–300 m, 25 Mar 1998, *Tuomisto 11934* (QCA, QCNE, TUR!); Yasuní National Park, km 42+2.5 along oil road, 00°42'S, 76°26'W, 200–300 m, 27 Mar 1998, *Tuomisto 11956* (QCA, QCNE, TUR-2!); S of Río Napo, 3–4 km E from village Ahuano. Conservation area managed by Selva Viva Organization, 01°04'S, 77°31'W, 400–470 m, 23 Jul 2019, *Tuomisto 17897* (HUTI-3!, TUR-3!, UC-2!, UTCEC! (5), Z!); Pastaza: Reserva Huella Verde, 01°36'S, 77°45'W, 500 m, 31 May 2022, *Kessler 15631* (HUTI!, TUR!); Reserva Huella Verde, 01°36'S, 77°45'W, 500 m, 31 May 2022, *Kessler 15636* (HUTI!, TUR!); Arajuno Canton, Shuar Wahents Community Territory. Piedmont Evergreen Forest, 00°20' 77°40'W, 750–900 m, 3 Oct 2012, *Perez 5795* (QCA!); Reserva Forestal Putuyme, near Madre Tierra, road from Puyo to Pallora, 950 m, 26 Aug 1994, *Schneider 500* (Z-2!).

10. *Danaea nasua* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 21.
Holotype: Ecuador, Carchi, trail between Coaiquer Amerindian communities San Marcos and San Antonio before Gualpi Bajo, 01°08'N, 78°22'W, 900–1000 m, 25 Nov 1983, *Kvist 48941* (AAU!; isotype: MO).

Diagnosis — Similar to *Danaea humilis* T. Moore but differing in caudate pinna apices (vs acute); largest lateral pinnae 2.2–2.4 times as long as wide without apex (vs 2.4–3.6 times); laminae rather concolorous (vs clearly bicolorous with abaxial side whitish).

Description — *Rhizomes* erect, leaves and root bases arranged radially, 0.5–1.2 cm in diam., to at least 13 cm long. *Sterile leaves* 23–38 cm long; *petioles* 6.0–16 cm long, with 2 nodes, not winged; *laminae* 14–24 × 4.3–6.6 cm, parallel-sided, imparipinnate or possibly paripinnate, 13–20 pinna-pairs, medial pinnae 0.8–0.9 cm apart, concolorous to somewhat bicolorous, dark brownish green, texture thin, rachises winged in distal part of internodes in distal part of lamina, wings to 0.2 mm wide; *terminal pinnae* 2.2–5.8 × 0.6–0.9 cm, oblong or lanceolate, bases acute, apices 0.9–2.1 cm long, acuminate to caudate, margins of apices crenulate to serrulate; *largest lateral pinnae* 2.5–3.5 × 0.8–1.1 cm, 2.0–2.4 times as long as wide without apex, parallel-sided, perpendicular to rachises or slightly ascending, bases very asymmetrical (obtuse proximally, obtuse to acute distally), apices 0.5–0.8 cm long, short-caudate (to cuspidate), margins of apices serrulate at shoulder of pinna, crenulate at apex; *veins* 16–25 per cm, mostly simple, some forked at costa. *Fertile leaves* 38 cm long; *petioles* 24 cm long, 3 nodes; *laminae* c. 15 × 4 cm, parallel-sided, imparipinnate, 20 pinna-pairs; *terminal pinnae* c. 1.3 × 0.3 cm, lanceolate, bases acute; *largest lateral pinnae* c. 1.8 × 0.4 cm, oblong, slightly ascending, bases obtuse, apices mucronate. *Juveniles* not known.

Distribution and habitat — Known from three collections at the border of Ecuador (Carchi) and Colombia (Cauca), from 200–1000 m. Found growing in selectively logged forest and on hillsides in very wet forest. Fig. 8.

Conservation status — We place *Danaea nasua* in the Endangered (EN B1ab(iii)+2ab(iii)) category (IUCN 2012). It has an Extent of occurrence of 503 km^2, an Area of occupancy of 12 km^2, and is known from only three locations, which correspond to the EN category. None of the collection localities are inside protected areas and one of them was mentioned to be under selective logging. The area, extent, and quality of suitable habitats were inferred to be suffering continuing decline from deforestation.

Etymology — Nasua is Latin for nose, referring to the short caudate pinna apices of this species.

Remarks — *Danaea nasua* is a small species endemic to Chocó. It has conspicuous drip tips typical of many species in wet climates, and these separate it from the similar *D. chococola* Christenh., *D. humilis*, and *D. pumila* (described below), which have acute to acuminate rather than caudate (or cuspidate) apices. Like these species, *D. nasua* has parallel-sided laminae with many pairs of short, asymmetrical pinnae, but its pinnae are rounder (largest lateral pinnae 2.2–2.4 times as long as wide without apex vs 2.4–3.6 in *D. humilis* and even more in the other two relatives). In addition, *D. nasua* differs from *D. humilis* and *D. pumila* in having rather concolorous laminae (vs clearly bicolorous with abaxial side whitish) and from the concolorous *D. chococola* in that it dries to a dark, dull brownish green (vs dull green with a greyish sheen).

Danaea nasua is clearly smaller than the other species occurring in the same general area, namely *D. tenuicaulis* Tuomisto & Keskiniva, D. *velona* (described below), *D. cuspidopsis* (described above), and *D. inaequilatera* (sterile leaves < 40 cm vs > 50 cm long, largest lateral sterile pinnae < 4 cm vs > 6 cm long).

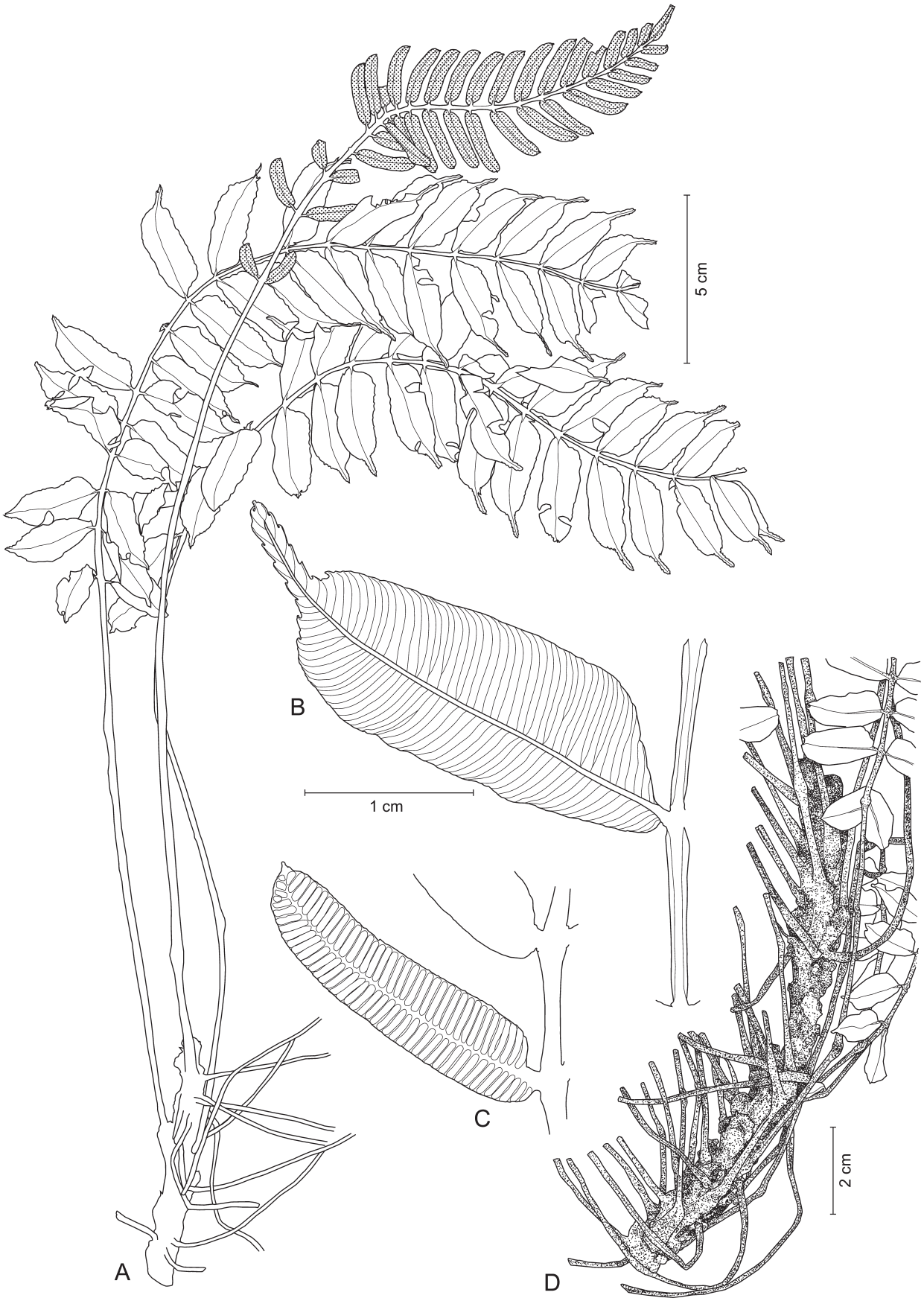

Fig. 21. *Danaea nasua*: A: plant with fertile pinnae in grey; B: medial sterile pinna; C: medial fertile pinna; D: erect rhizome. – A–C: *Kvist 48941* (AAU); D: *Haught 5391* (US). – Drawn by Venni Keskiniva.

Additional specimens examined — Colombia: Cauca: San Juan de Micay valley, 200 m, 27 Dec 1946, *Haught 5391* (US!). — Ecuador: Carchi: border area between Prov. Carchi and Esmeraldas, about 20 km past Lita on road Lita-Alto Tambo, 550 m, 24 Jun 1991, *van der Werff 11969* (MO!).

11. *Danaea opaca* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Arthrodanaea*) – Fig. 22, 23.
Holotype: Brazil, Amazonas, Río Juruá, 7 km N from town of Itamarati, 06°23'S, 68°16'W, 150 m, 10 Apr 2012, *Tuomisto 16130* (SP!; isotypes: TUR! (mounted on 2 sheets), UC!, Z!).

Diagnosis — Similar to *Danaea bipinnata* Tuomisto, but differing in fertile pinnae lanceolate (vs elliptic); sterile pinnae parallel-sided (vs elliptic); pinnae dull and pale bluish green adaxially when fresh (vs shiny and dark green); genetically differing in locations 326 (T vs C) of *rbcL* reference sequence; 32 (A vs G), 679 (C vs A) of *trnL-F* reference sequence; 413 (G vs T), 435 (G vs A), 707 (T vs G) of *rpl32* reference sequence.

Description — *Rhizomes* erect, leaves and roots radially arranged, when fresh 1.5–3.0 cm in diam., when dry 1.0–2.0 cm in diam., to 10 cm long. *Sterile leaves* 34–66 cm long; *petioles* 14–34 cm long, with 0–1(–2) nodes, not winged; *laminae* 20–32 × 16–27 cm, obovate to oblong, imparipinnate, distal pinnae usually smallest, 4–6(–7) pinna-pairs, medial pinnae 2.8–4.5 cm apart, pinnae colour dark brown when dried, often with a slightly paler zone along midvein, rather pale bluish green when fresh with a lighter yellowish zone along midvein, texture thin, rachises winged in distal part of lamina, wings to 0.2–1.0 mm wide; *terminal pinnae* 6.5–15 × 2.1–3.6 cm, lanceolate, bases acute, apices 1.0–2.1 cm long, acuminate, margins of apices entire to (slightly) sinuate; *largest lateral pinnae* 10.6–16 × 2.7–4 cm, 3.3–5.0 times as long as wide without apex, parallel-sided, bases symmetrical (obtuse to acute) or asymmetrical (obtuse proximally, acute distally), apices 1.5–2.4 cm long, acuminate to attenuate, margins of apices entire to sinuate (to crenulate at shoulder of pinna); *veins* 10–12 per cm, usually mostly paired at costa, sometimes mostly simple. *Fertile leaves* 42–67 cm long; *petioles* 28–42 cm long, not nodose (only two seen); *laminae* 15–25 × 5–12 cm, (long-)oblong or lanceolate, imparipinnate, distal pinnae smallest, 5–7 pinna-pairs; *terminal pinnae* 3.1–4.2 × 0.7–0.9 cm, lanceolate, bases acute, apices acuminate; *largest lateral pinnae* 4.2–8.5 × 0.7–1.2 cm, lanceolate, bases asymmetrical (obtuse proximally, acute distally), apices 0.3–1.0 cm long, attenuate to acuminate (or acute). *Juveniles* with terminal pinnae oblong to obovate or lanceolate, larger than lateral ones, lateral pinnae elliptic, largest simple juvenile 12 cm long, smallest pinnate juvenile 8.5 cm long.

Distribution and habitat — *Danaea opaca* has been found only in non-inundated rainforests along the Río Juruá in Amazonas, Brazil, from 90 to 550 m. Fig. 15.

Conservation status — We place *Danaea opaca* in the Least Concern (LC) category (IUCN 2012). It has an Area of occupancy of 24 km^2, which corresponds to the EN category, and an Extent of occurrence of 16,155 km^2, which corresponds to the VU category, and is known from only seven collections. However, its forest habitat is continuous over a large area, and two of the specimens were gathered in a protected area (Reserva Extrativista do Médio Juruá). There appears to be no imminent threat to all its subpopulations.

Etymology — *Danaea opaca* is named after the colour of its leaves in the field: they are dull bluish green in comparison with those of *D. bipinnata*, whose leaves are glossy dark green.

Remarks — We separate *Danaea opaca* from *D. bipinnata* based on both morphological and genetic evidence. In the field the two co-occur and can be separated by their colour, as the pinnae of *D. opaca* are dull and relatively light bluish green adaxially with the centre often yellowish and paler than the margins, whereas the pinnae of *D. bipinnata* are glossy dark green. Both species can obtain a uniformly dark brown colour when dried, but often the adaxial side of *D. opaca* retains a paler zone around the midvein, whereas *D. bipinnata* develops a darker zone around the midvein. The sterile pinnae of *D. opaca* are parallel-sided and the fertile pinnae lanceolate (vs both elliptic in *D. bipinnata*) with an abruptly tapering bases (vs gradually tapering) and short apices that can be attenuate or acute (vs usually long-acuminate).

In the field, *Danaea opaca* can easily be separated from the sympatric *D. leprieurii* by its bluish to greyish green laminar colour with a paler zone around the midvein of pinnae (vs concolorous yellowish green in *D. leprieurii*). Furthermore, *D. opaca* typically has fewer nodes on petioles (usually 0–1 vs 2–3), longer leaves (34–66 cm vs 18–38 cm long), a more elongated lamina shape (vs often almost as wide as long), and larger lateral pinnae (10.6–16 × 2.7–4 cm vs 6–10 × 1.4–2.8 cm).

Danaea opaca differs from *D. lingua-cervina* Christenh. & Tuomisto, *D. trifoliata* Rchb. ex Kunze, and *D. ulei* Christ by its shorter terminal pinnae (6.5–15 cm vs 16–26 cm in *D. lingua-cervina*, 16–33 cm in *D. trifoliata* and 18–32 cm in *D. ulei*) that are usually shorter than the second lateral pinnae distally (vs terminal pinnae usually longest), and by having generally more pinna-pairs (4–6(–7) vs 0–4 pinna-pairs in *D. lingua-cervina* and *D. trifoliata*, 2–4 in *D. ulei*). In addition, *D. opaca* differs from *D. ulei* in its generally smaller size (sterile leaves 34–66 cm vs 45–92 cm, largest lateral sterile pinnae 11–16 cm vs 16–21 cm), and usually thinner laminar texture. *Danaea opaca* develops pinnate leaves at a smaller size

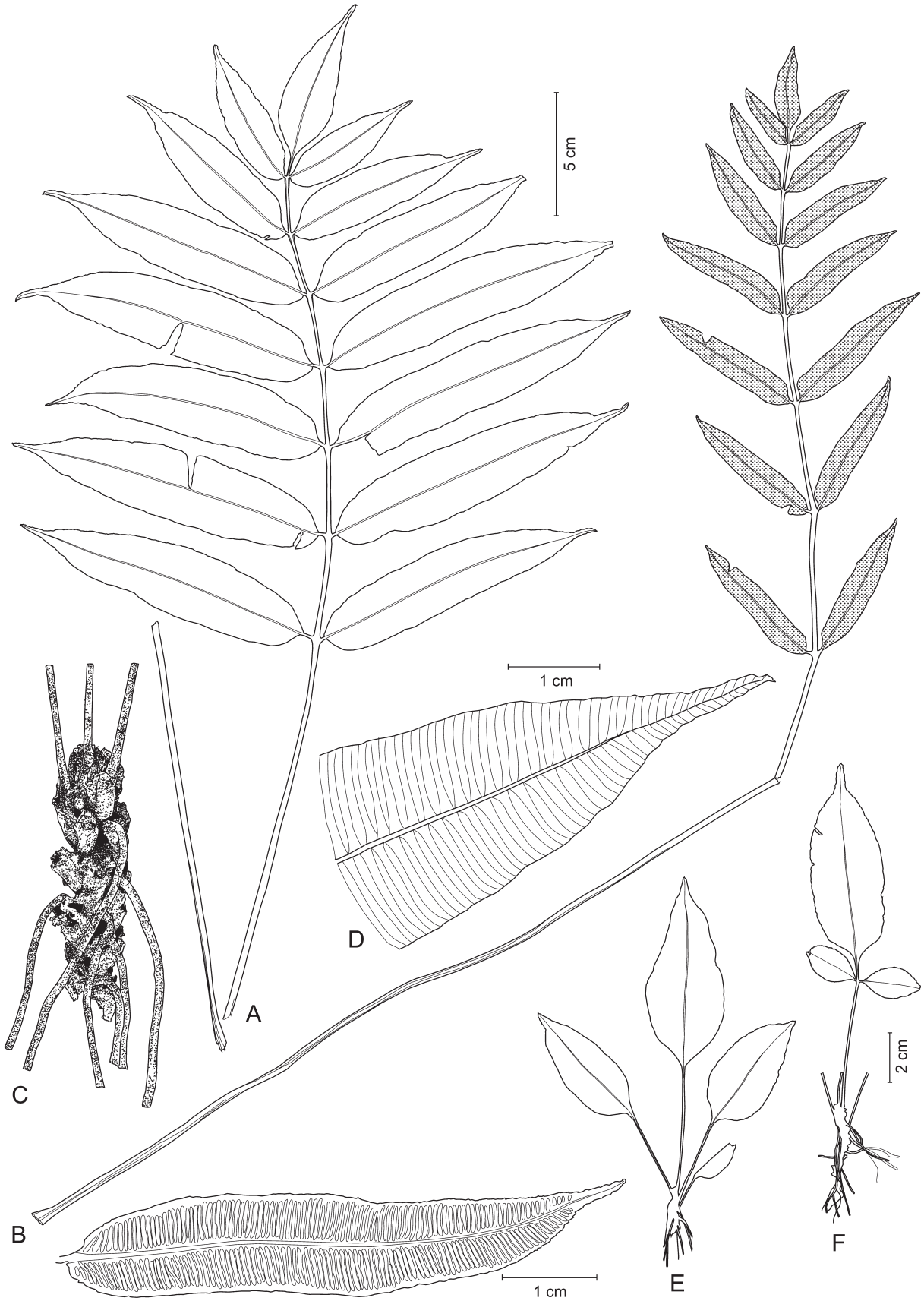

Fig. 22. *Danaea opaca*: A: sterile leaf; B: fertile leaf; C: erect rhizome; D: medial pinna apex; E: simple juvenile; F: trifoliate juvenile; G: medial fertile pinna. – A, B, D, G: *Tuomisto 16130* (TUR); C: *Tuomisto 15876* (TUR); E: *Tuomisto 15886* (TUR); F: *Tuomisto 15796* (TUR). – Drawn by Venni Keskiniva.

Fig. 23. *Danaea opaca* field habit. A: abaxial side of sterile lamina with winged rachis; B: sterile lamina; C: entire plant; D: erect rhizome. – C: *Tuomisto 16130*. – A, B, D: © Hanna Tuomisto 2012; C: © Gabriel Massaine Moulatlet 2012.

than *D. lingua-cervina* and *D. trifoliata* (simple leaves do not exceed 13 cm in length vs simple leaves may become 40 cm long in *D. lingua-cervina* and 54 cm long in *D. trifoliata*).

Fertile specimens of *Danaea alansmithii* Tuomisto & Keskiniva are readily separated from *D. opaca* by the elliptic (vs lanceolate) fertile pinnae that are larger (8.5–15 × 1.4–2.6 cm vs 4.2–8.5 × 0.7–1.2 cm), have a sterile zone of 1–4 mm on each side of the costa (vs no sterile zone), and are thinner due to slender and widely spaced synangia. *Danaea opaca* tends to have more pinnae than *D. alansmithii* (4–6(–7) vs 3–5 sterile pinna-pairs, 5–7 vs 3–4 fertile pinna-pairs). In addition, dried leaves of *D. alansmithii* have a reddish brown tint (vs greenish brown rather than reddish) and are uniform in colour (vs often lighter near the midvein).

Danaea opaca differs from *D. arbuscula* Christenh. & Tuomisto in pinna shape (sterile pinnae parallel-sided and fertile pinnae lanceolate vs both usually elliptic), generally smaller size (sterile leaves to 66 cm vs to 90

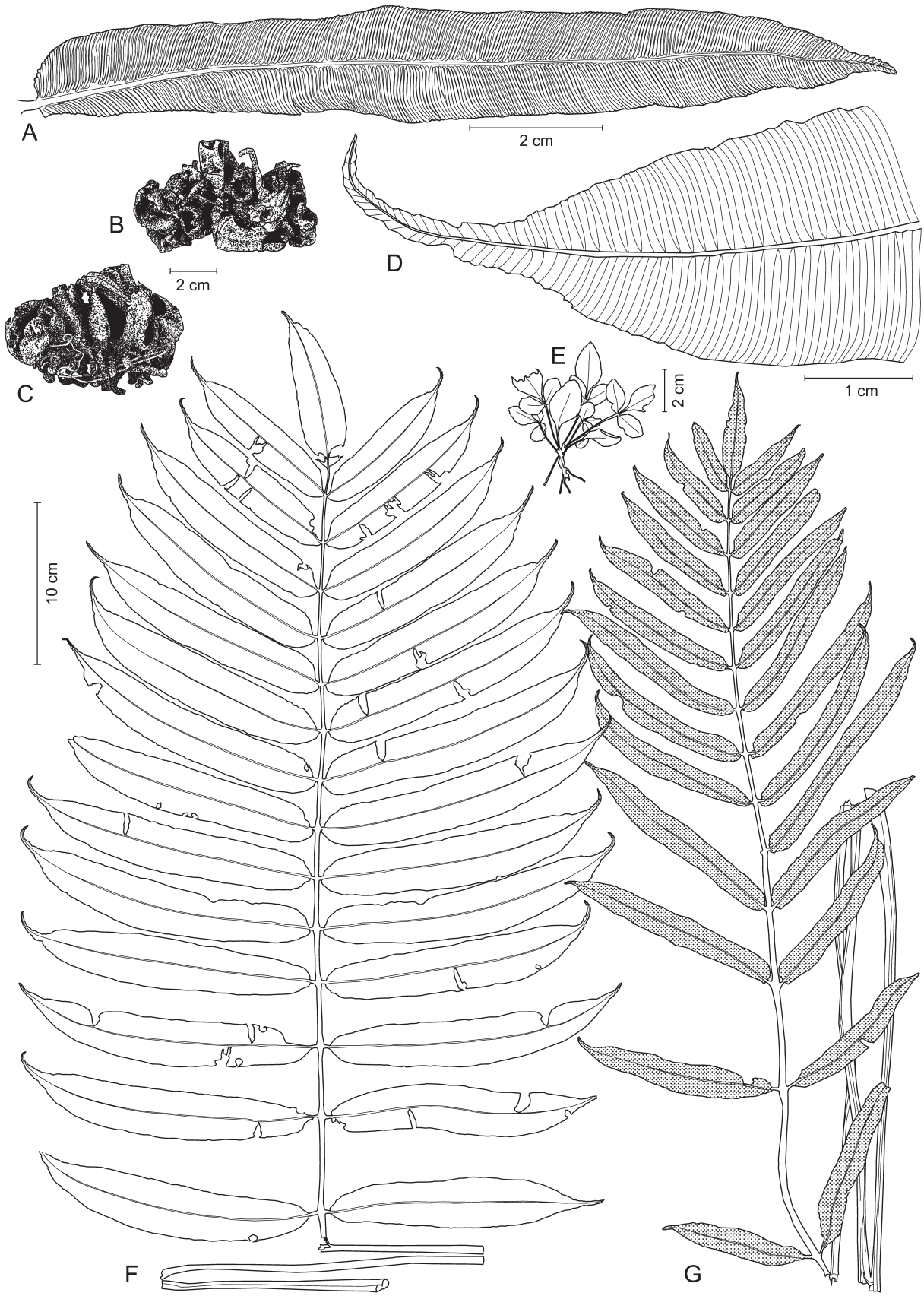

Fig. 24. *Danaea panamensis*: A: medial fertile pinna; B: creeping rhizome seen from above; C: creeping rhizome seen from side; D: medial pinna apex; E: juvenile; F: sterile leaf; G: fertile leaf. – A, D, F, G: *Tuomisto 15161* (TUR); B, C: *Jones 1051* (TUR); E: *Tuomisto 15149* (TUR). – Drawn by Venni Keskiniva.

cm long, lateral pinnae to 16 × 4 cm vs to 22 × 5 cm), and especially in smaller fertile pinnae (4.2–8.5 × 0.7–1.2 cm vs 8–18 × 1.6–4.0 cm). In addition, *D. arbuscula* often has a thicker laminar texture and its rhizomes can exceed a meter (vs to 10 cm long in *D. opaca*). *Danaea arbuscula* is a montane species mostly found in Colombia, Venezuela, Ecuador, and northern Peru above 500 m, whereas *D. opaca* has been found only in the lowlands of Brazilian Amazonia.

Danaea geniculata Raddi has a more eastern distribution than *D. opaca* in the Atlantic coast of Brazil and in French Guiana. It can have fertile pinnae with a similarly lanceolate shape as those of *D. opaca* but has elliptic sterile pinnae (vs usually parallel-sided), tends to dry dark green (vs dark brown), and often has a rachises without wings (vs rachises winged in the distal part).

Additional specimens examined — Brazil: Amazonas: Río Juruá, 1.5 km northwest from village of Xibauá, 05°53'S, 67°52'W, 110 m, 2 Apr 2012, *Tuomisto 15796* (SP!, TUR-2!); Río Juruá, 3 km northeast from village of Novo Horizonte, 05°02'S, 67°08'W, 90 m, 27 Mar 2012, *Tuomisto 15876* (SP!, TUR-4!); Río Juruá, 3 km northwest from village of Roque, 05°05'S, 67°14'W, 100 m, 28 Mar 2012, *Tuomisto 15886* (SP, AAU!, TUR!); Río Juruá, 1.5 km northwest from village of Xibauá, 05°53'S, 67°52'W, 110 m, 2 Apr 2012, *Tuomisto 16052* (SP!, MO!, TUR!); Río Juruá, 4 km northeast from village of Deixa Falar, 06°41'S, 70°19'W, 180 m, 5 May 2012, *Tuomisto 16590* (SP!, TUR-2!); Río Juruá, 4.5 km southwest from village of Monte Verde, 06°39'S, 69°22'W, 130 m, 29 May 2012, *Tuomisto 16759* (SP!, TUR!).

12. *Danaea panamensis* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Danaea*) – Fig. 24, 25.
Holotype: Panama, Panamá, Cerro Campana National Park, 08°41'N, 79°56'W, 850–900 m, 25 Oct 2005, *Tuomisto 15161* (PMA! (mounted on 2 sheets: 102072 & 102073, has separate rhizome); isotypes: AAU!, TUR! (mounted on 3 sheets), UC! (mounted on 2 sheets), Z! (mounted on 2 sheets)).

Diagnosis — Most closely related to *Danaea latipinna* Tuomisto & R. C. Moran, but differing in more pinna-pairs (12–16 vs 2–6); generally narrower pinnae (2.6–3.5 cm vs 2.8–8.7 cm). Similar to *D. nodosa* (L.) Sm., but differing in thicker laminar texture; dark blue-green colour when dry (vs light yellow green); pinnae that are generally smaller (to 27 vs to 35 cm long, to 3.5 vs 5.8 cm wide) and narrower (6–12 vs 4–8 times as long as wide without apices); pinna apices that are usually gradually tapering (vs often abruptly tapering), generally shorter (to 3.3 cm vs to 4.0 cm long), and entire, sinuate or crenulate (vs often serrulate at shoulder of pinna); can have a petiolar node (vs no nodes in petiole). Differs from *D. leussinkiana* Christenh. in rhizomes with leaf bases in two rows (vs 3–5 rows); generally narrower pinnae (2.6–3.5 cm vs 3.1–4.9 cm wide); longer pinna apices (1.3–3.3 cm vs 0.9–1.5 cm); thinner laminar texture. Differs from *D. pterorachis* Christ in rhizomes with leaf bases in two rows (vs 3–5 rows); longer pinnae (21–27 cm vs 14–21 cm long); dark blue-green colour (vs green); thicker laminar texture. Differs from *D. ampla* Keskiniva & Tuomisto in more pairs of fertile pinnae (12–14 vs 4–7); generally more pinna-pairs (12–16 vs 4–13) that are narrower (2.6–3.5 cm vs 3.1–4.9) and

Fig. 25. *Danaea panamensis*: A: field habit; B: whole plant. – A, B: *Tuomisto 15149*. – © Hanna Tuomisto.

parallel-sided (vs usually widest above middle). *Danaea panamensis* is genetically unique among *Danaea* in having a C (vs A) at position 126 of *rpl32* reference sequence and differs from all other species of *D.* subg. *Danaea* by having an A (vs G) at position 481 of *rpl32* reference sequence and a T (vs C) at position 695 of *atpB* reference sequence.

Description — *Rhizomes* creeping, dorsiventral with leaf bases in two rows, 2.5–3.5 cm in diam. when dry, 4–5 cm in diam. when fresh, to 40 cm long. *Sterile leaves* 121–157 cm long; *petioles* 66–92 cm long, with 0(–1) nodes, not winged; *laminae* 55–76 × 42–47 cm, (long-)obovate, imparipinnate, terminal pinnae shorter than second distal-most pinna-pair, 12–16 pinna-pairs, proximal pinna-pair more distant and slightly smaller, medial pinnae 2.4–4.0(–6.0) cm apart, almost concolorous, rather dark bluish green adaxially, often more yellowish toward margins, abaxial side uniformly green or brown, laminar texture relatively thick, rachises not winged or winged in distal part of lamina, wings to 0.7 mm wide; *terminal pinnae* 9.8–21 × 2.1–2.6 cm, lanceolate to oblong, bases acute, apices 1.5–3.0 cm long, (long-)acuminate, margins of apices entire, sinuate or crenulate; *largest lateral pinnae* 21–27 × 2.6–3.5 cm, 5.6–11.8 times as long as wide without apex, parallel-sided, bases symmetrical (obtuse or acute) or asymmetrical (obtuse or auriculate proximally, acute or obtuse distally), apices 1.3–3.3 cm long, acuminate (to abruptly caudate), margins of apices entire, sinuate to crenulate; *veins* 14–18 per cm, mostly forked at costae, sometimes above. *Fertile leaves* 122–145 cm long; *petioles* 72–89 cm long, lacking nodes; *laminae* 50–57 × c. 22 cm, 12–14 pinna-pairs, imparipinnate, long-elliptic to long-lanceolate, pinnae spaced proximally, crowded distally; *terminal pinnae* 6.2–9.8 × 1.3–2 cm, lanceolate, bases acute, apices acuminate; *largest lateral pinnae* 13–16 × 1.2–2.0 cm, oblong to elliptic, bases asymmetrical (obtuse or auriculate proximally, acute to obtuse distally), apices 1.3 cm long, acuminate, margins of apices entire or crenulate. *Juveniles* with terminal pinnae elliptic, oblong or lanceolate, lateral pinnae oblong when leaves are more than 10 cm long, bases asymmetrical (obtuse or auriculate proximally, acute distally), apices acuminate, smallest juveniles with elliptic pinnae, largest simple juvenile 4.4 cm long, smallest pinnate juvenile 3.9 cm long.

Distribution and habitat — Known from Panama from 70–900 m. *Danaea panamensis* has been found on steep slopes and on the banks of a ravine and a stream channel. One locality mentions clay to loam soils and hilly terrain with ravines. Fig. 3.

Conservation status — We place *Danaea panamensis* in the Least Concern (LC) category (IUCN 2012). It has an Area of occupancy of 68 km^2, which corresponds to the EN category, and an Extent of occurrence of 25,571 km^2, which corresponds to the LC category. *Danaea panamensis* seems to be rather common, and is known from 24 collections. It has been collected in several protected areas in Panama (Barro Colorado Island, Bosque Protector Palo Seco, Cerro Campana National Park, Parque Nacional Soberanía, Parque Nacional San Lorenzo, and Parque Nacional Santa Fe) and there appears to be no imminent threat to all its subpopulations.

Etymology — The species is known only from Panama.

Remarks — In the field, *Danaea panamensis* and *D. ampla* were thought to represent *D. media* and *D. nodosa*, respectively, but genetic evidence now shows that there are three distinct species involved and that *D. media* is a synonym of *D. nodosa* (see *D. ampla* for more details). *Danaea panamensis* has a thicker laminar texture than *D. nodosa* and *D. ampla* and dries a rather dark bluish green (vs often yellowish light green), with a more yellowish area around the midrib adaxially (vs concolorous); it can also have a petiolar node (vs none). It generally differs from *D. nodosa* in having smaller pinnae (to 27 cm vs to 35 cm long, to 3.5 cm vs to 5.8 cm wide) that are narrower (6–12 vs 4–8 times as long as wide without apex) and in more gradually tapering apices (vs usually rather abruptly tapering) that are shorter (to 3.3 cm vs to 4.0 cm long), almost never with serrulations (vs often serrulate at the shoulder of the pinna). *Danaea panamensis* differs from *D. ampla* in having more pairs of fertile pinnae (12–14 vs 4–7) and generally more pairs of sterile pinnae (12–16 vs 4–13) that are also narrower (2.6–3.5 cm vs 3.1–4.9 cm wide, 5.6–12 vs 2.4–5.6 times as long as wide without apex) and parallel-sided (vs usually widest above the middle).

In leaf morphology, *Danaea panamensis* is similar to the Costa Rican *D. pterorachis* but differs in having rhizomes with two rows of leaves (vs 3–5 rows) and longer pinnae (21–27 cm vs 14–21 cm long) that have a darker bluish colour (vs brighter green) and a thicker texture.

We have not seen specimens from Panama that we could confidently identify as *Danaea nodosa* or *D. pterorachis*, and it is therefore possible that these two species do not overlap in distribution with *D. panamensis*, which seems to be endemic to, and rather common in, Panama.

Genetically *Danaea panamensis* is most closely related to *D. latipinna* of coastal Ecuador but differs morphologically in having more pinnae (12–16 vs 2–6 pairs) that are narrower (2.6–3.5 cm vs 4.8–8.7 cm wide, 6–12 vs 2–3 times as long as wide without apex). *Danaea leussinkiana* co-occurs with *D. panamensis* and shares the dark blue-green colour when dry, but *D. panamensis* has rhizomes with leaf bases in two rows (vs 3–5) and narrower pinnae (2.6–3.5 cm vs 3.1–4.9 cm wide, 5–7 vs 6–12 times as long as wide without apex) with longer apices (1.3–3.3 cm vs 0.9–1.5 cm) and a thinner laminar texture.

Danaea panamensis also co-occurs with *D. alba*, but is a smaller plant (sterile leaves 121–157 cm vs 160–200 cm long) with rhizomes having pinna apices in two rows (vs 3–5) and more pinna-pairs (12–16 vs 8–9) that are smaller (21–27 × 2.6–3.5 cm vs 33–37 × 5.2–5.5 cm), and dry to a darker bluish green (vs pale yellowish or greyish green). The shape of the juveniles of these species also differs, with *D. panamensis* having oblong pinnae (vs elliptic).

Additional specimens examined — Panama: Bocas Del Toro: Bosque Protector Palo Seco, Río Changuinola, Charco La Pava. At house of Mr. Reynaldo Abrego, 09°09'N, 82°30'W, 348 m, 3 Feb 2013, *Ortiz 1204* (MO!); El Guabo District. Bosque Protector Palo Seco, Farm of Mr. Dario Araúz, 08°50'N, 82°11'W, 431 m, 6 Feb 2013, *Zapata 3148* (MO!); Bosque Protector Palo Seco, Concesión Hidro Ecológica del Teribe, near Bonyic creek, Casa máquinas, 09°20'N, 82°38'W, 355 m, 29 Sep 2013, *Zapata 3347* (MO-2!); Chiriqui: Canal Zone northwest of Gamboa along Pipeline Road, *McAlpin 1393* (D!, F!); Colón: Cocle del Norte, Escorpio 02 helipad area, taking southern route, 08°56'N, 80°40'W, 39 m, 21 Jul 2012, *Espinosa 6022* (MO-3!); Colón, Sierra Llorona, at P32, 09°21'N, 79°44'W, 285 m, 4 Mar 2008, *Jones 920* (TUR!); Colón, Parque Nacional San Lorenzo, at P2, 09°20'N, 79°58'W, 137 m, 23 Apr 2008, *Jones 1051* (PMA!, TUR!); Minera Panama, Point C24, Río San Lucas, 08°59'N, 80°34'W, 12 Mar 2010, *Martínez 531* (MO!); Minera Panama, W13 helipad area, Río Caimito area, 08°58'N, 80°40'W, 69 m, 20 Oct 2010, *Martínez 661* (MO!); Porto Bello, 5–200 m, 6–8 Apr 1911, *Maxon 5750* (US-2!); Santa Rita, STRI tree plot 32, 09°21'N, 79°44'W, 400 m, 20 Oct 2005, *Tuomisto 15142* (PMA!); Panamá: Parque Nacional Soberanía, at P8, 09°10'N, 79°45'W, 215 m, 21 Jan 2008, *Jones 635* (TUR!, US!); PN Soberanía, at P8, 09°10'N, 79°45'W, 215 m, 28 Jan 2008, *Jones 683* (TUR!); PN Soberanía, at P8, 09°10'N, 79°45'W, 215 m, Feb 2 2008, *Jones 735* (TUR!); PN Soberanía, at P20, 09°12'N, 79°46'W, 254 m, 8 Feb 2008, *Jones 753* (TUR!); PN Soberanía, at P15, 09°10'N, 79°45'W, 90 m, 15 Feb 2008, *Jones 802* (TUR!); PN Soberanía, at P19, 09°12'N, 79°46'W, 153 m, 25 Mar 2008, *Jones 957* (TUR!, US!); PN Soberanía. Collected at P16, 09°08'N, 79°43'W, 182 m, 2 Apr 2008, *Jones 982* (TUR!); Canal Zone, Pipeline Road, Agua Salud, 1 Nov 1972, *Kennedy 1889* (PMA!, US!); Barro Colorado Island, 13 Feb 1934, *Taylor 1328* (MICH-2!); Barro Colorado Island, close to beginning of Shannon Trail, 09°10'N, 79°50'W, 100–150 m, 23 Oct 2005, *Tuomisto 15149* (PMA-2!, TUR!); Veraguas: Parque Nacional Santa Fe. Alto de Piedra. First branch of Río Mulabá. Highway to Guabal, close to bridge at km 4.45, 08°32'N, 81°08'W, 663 m, 16 Nov 2012, *Ortiz 993* (MO-2!); Parque Nacional Santa Fe, Alto de Piedra, First branch of Río Mulabá, highway to Guabal, close to bridge at km 4.45, 08°32'N, 81°08'W, 676 m, 16 Nov 2012, *Ortiz 1011* (MO!, PMA!).

13. *Danaea peruviana* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 26.

Holotype: Peru, San Martín, Rioja, Alto Mayo Protected Forest (BPAM), 06°06'S, 77°18'W, 1424–1441 m, 5 Dec 2015, *Suominen 362* (TUR! (mounted on 2 sheets: 616256, 616257); isotype: USM).

Diagnosis — Morphologically most similar to *Danaea mazeana* Underw., but differs in having strictly erect rhizomes (vs creeping), generally fewer nodes on petioles (0–1(–2) vs 2–3), and straight (vs usually slightly falcate) lateral pinnae. Similar to and possibly co-occurring with *D. excurrens* Rosenst. and *D. andina* Keskiniva & Tuomisto, but differing in generally larger size (sterile leaves 64–94 cm long vs 35–62 cm in *D. excurrens* and 46–71 cm in *D. andina*); rhizomes erect (vs often creeping or ascending) and longer (to 40 cm vs to 20 cm long); pinna apices generally longer (1.5–4.0 cm vs 0.5–1.6 cm) and often rather wide (vs narrow). Also differs from *D. andina* in having longer pinnae (13–15 cm vs 4.5–13 cm). Only observed fertile leaf of *D. peruviana* is unique in *D.* subg. *Holodanaea* in having relatively long and broad fertile pinnae (c. 12 × 1.4 cm) with synangia widely spaced and sterile zones at pinna margins and around midvein.

Description — *Rhizomes* erect and radial, 1.0–2.5 cm in diam., to 40 cm long. *Sterile leaves* 64–94 cm long; *petioles* 28–43 cm long, with 0–1(–2) nodes, not winged; *laminae* 35–66 × 23–27 cm, (long-)obovate to (long-)lanceolate, imparipinnate, 11–16 pinna-pairs, if no node then proximal pinnae small, elliptic and distant, medial pinnae 1.8–2.5 cm apart, bicolorous, dark grey-brown adaxially, light grey-brown abaxially, texture thin, rachises winged in distal part of lamina, wings to 0.2–1.0 mm wide; *terminal pinnae* 9.5–13 × 1.5–2.0 cm, lanceolate to oblong, bases acute, apices 1.5–2.9 cm long, (long-)acuminate to caudate, margins of apices (deeply) serrate; *largest lateral pinnae* 13–15 × 1.4–2.2 cm, 5.0–8.6 times as long as wide without apex, usually parallel-sided, perpendicular to rachises or slightly ascending, bases asymmetrical (obtuse to auriculate proximally, acute to obtuse distally), apices 1.5–4.0 cm long, (long-)acuminate or caudate, sometimes rather wide, margins of apices (deeply) serrate; *veins* 12–14 per cm, mostly paired at costae, sometimes many simple. *Fertile leaves* 62 cm long; *petioles* 29 cm long, 1 node; *laminae* 33 × 25 cm, imparipinnate, obovate, 13 pinna-pairs; *terminal pinnae* 1.7 cm wide; *largest lateral pinnae* c. 12 × 1.4 cm, long-lanceolate, perpendicular to rachis, bases symmetrical, truncate (or asymmetrical, obtuse to auriculate proximally, acute to obtuse distally), apices 2 cm long, long-acuminate to cuneate, margins of apices serrate. *Juveniles* not known.

Distribution and habitat — Known only from a small area on the eastern slopes of the Andes in Peru (San Martín), from 1200–1500 m. Fig. 8.

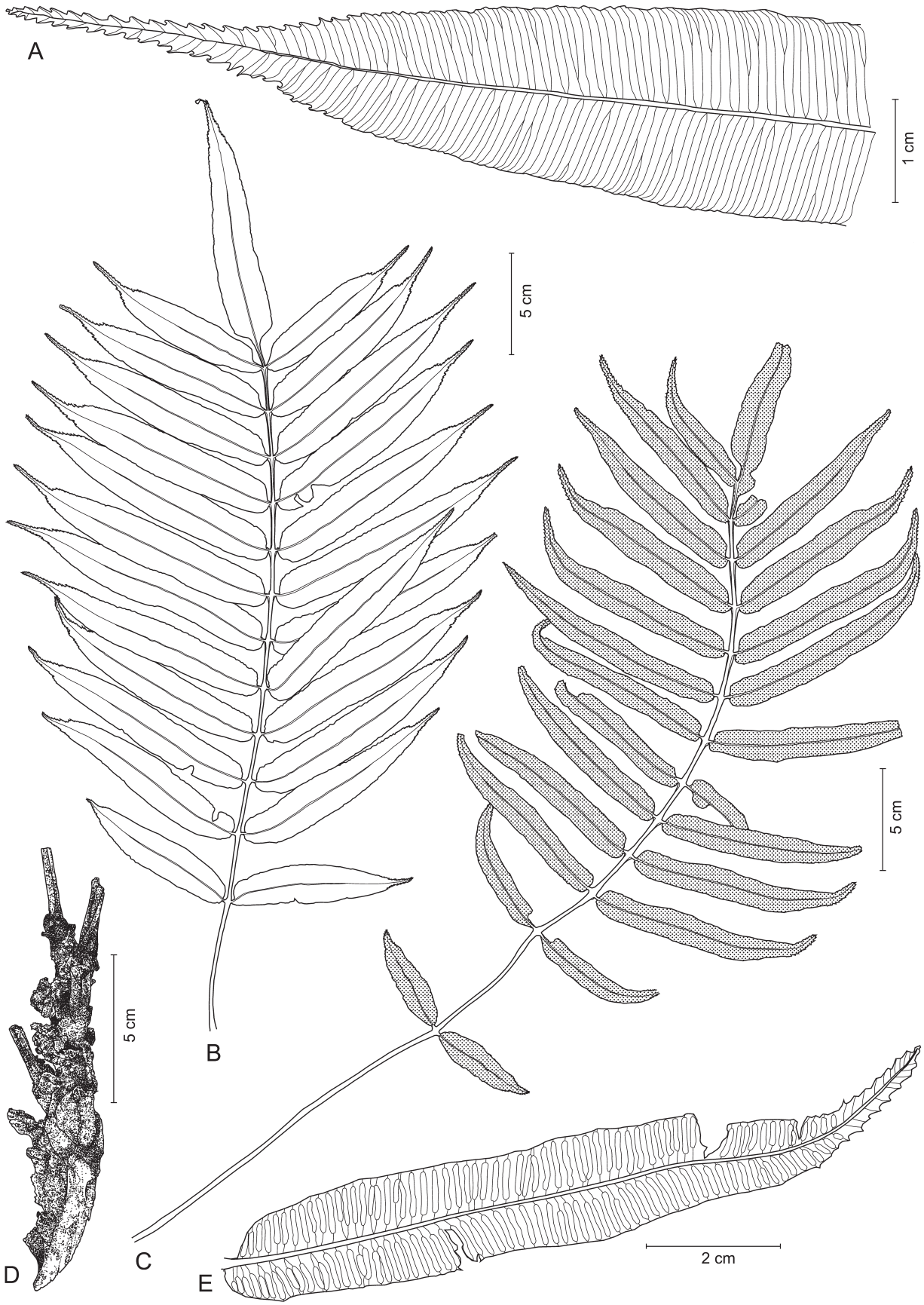

Fig. 26. *Danaea peruviana*: A: medial pinna apex; B: sterile lamina; C: fertile lamina; D: fragment of erect rhizome; E: fertile pinna. – A–C, E *Suominen 352* (TUR); D: *Suominen 242* (TUR). – Drawn by Venni Keskiniva.

Conservation status — We place *Danaea peruviana* in the Endangered (EN B1ab(iii)+2ab(iii)) category (IUCN 2012). It has an Extent of occurrence of 45 km² which corresponds to the Critically Endangered (CR) category and an Area of occupancy of 16 km² which corresponds to the Endangered (EN) category. It is known from only 9 collections, one of which was collected in a selectively logged location and the others from a single reserve (Bosque de Protección Alto Mayo in Peru). The species seems to be endemic to a small area where the extent and quality of suitable habitat is inferred to be in continuous decline from deforestation.

Etymology — This species has been found only in Peru.

Remarks — Danaea peruviana is an intermediate-sized species of the complex that was previously referred to *D. moritziana.* It has erect rhizomes and long, parallel-sided pinnae that dry to a dark greyish brown colour and have rather gradually tapering and often relatively broad apices. The fertile pinnae appear unique within *D.* subg. *Holodanaea* in that the synangia are widely spaced, and there is a sterile zone at their margins and around the midrib (vs synangia tightly packed and no sterile zones), which makes the fertile pinnae unusually long and broad. This is an excellent diagnostic character if it is consistent, but we have seen only one fertile leaf, so the possibility of aberrant growth in this individual cannot be ruled out.

In general appearance, including the relatively broad pinna apices, *Danaea peruviana* is most similar to *D. mazeana*, which is endemic to the Lesser Antilles and has creeping radial rhizomes (vs erect), more nodes on the petioles (2–3 vs 0–1(–2)), and usually slightly falcate (vs straight) lateral pinnae.

Danaea peruviana is most easily confused with *D. excurrens* and *D. andina*, which may also grow in the Peruvian Andes. *Danaea peruviana* is larger than the other two (sterile leaves 64–94 cm vs 35–62 cm long in *D. excurrens* and 46–71 cm in *D. andina*), with rhizomes that are clearly erect (vs creeping or ascending to erect) and longer (to 40 cm vs to 10–21 cm long) and pinnae that are longer than in *D. andina* (13–15 cm vs 4.5–13 cm long) and have longer but broader apices than either of the other two species (1.5–4.0 cm vs 0.5–1.6 cm long). In addition, *D. peruviana* dries to a dark greyish brown and is only slightly paler abaxially (vs green to light brown with abaxial side whitish in *D. excurrens* and *D. andina*).

Danaea betancurii also occurs in Peru, but *D. peruviana* has generally fewer pinna-pairs (11–16 vs 13–20) that can be wider (1.4–2.2 vs 0.9–2.0 cm wide), are usually longer (minimum 13.1 cm vs 7.4 cm long), and have generally longer apices (1.5–4.0 cm vs 0.9–2.0 cm long). In addition, *D. betancurii* generally has more nodes on the petioles (1–4 vs 0–1(–2)) and can also have creeping to ascending rhizomes (vs always erect) that remain shorter (to 14 vs to 40 cm long).

Additional specimens examined — Peru: San Martín: Rioja, 05°59'S 77°22'W, 1270–1295 m, 29 Jul 2014, *Suominen 148* (TUR!); Rioja, Alto Mayo Protected Forest (BPAM), 05°58'S 77°24'W, 1374–1446 m, 10 Jun 2015, *Suominen 207* (TUR!, USM); Rioja, BPAM, 05°58'S 77°24'W, 1373–1446 m, 11 Jun 2015, *Suominen 242* (TUR-2!, USM-2); Rioja, BPAM, 05°55'S 77°28'W, 1292–1358 m, 16 Jun 2015, *Suominen 260* (TUR-2!, USM-2); Rioja, BPAM, 05°55'S 77°28'W, 1292–1358 m, 16 Jun 2015, *Suominen 269* (TUR-2!, USM-2); Rioja, BPAM, 05°55'S 77°28'W, 1292–1358 m, 17 Jun 2015, *Suominen 282* (TUR!, USM); Rioja, BPAM, 06°06'S 77°18'W, 1424–1441 m, 4 Jul 2015, *Suominen 357* (TUR-3!, USM-2); Rioja, BPAM, 06°06'S 77°18'W, 1424–1441 m, 5 Jul 2015, *Suominen 373* (TUR!, USM).

14. *Danaea polypinna* Keskiniva & Tuomisto, **sp. nov.** (*D*. subg. *Holodanaea*) – Fig. 27.
Holotype: Costa Rica, Cartago, c. 22 km E of Turrialba, ridge above Platanillo, 1200–1450 m, 22 Aug 1967, *Mickel 3420* (NY!).

Diagnosis — Danaea polypinna is most closely related to *D. trichomanoides* Spruce ex T. Moore, but is a larger plant (46–72 cm vs 8–16 cm long) with much longer pinnae (6.8–11 cm vs 1.8–2.7 cm). *Danaea polypinna* co-occurs with *D. cuspidopsis* Keskiniva & Tuomisto and *D. robbinmoranii* Keskiniva & Tuomisto but differs in having almost concolorous laminae (vs bicolorous with abaxial side whitish), shorter fertile pinnae (4.8–5.1 cm vs 6.5–11.5 cm) with obtuse to acute apices (vs cuneate to (long-)acuminate), and narrower sterile pinnae (1.2–1.9 cm vs 1.9–2.4 cm). Differs from *D. humilis* T. Moore in concolorous laminae (vs bicolorous), larger size (sterile leaves 46–72 cm vs 24–42 cm long), and longer (6.8–11 cm vs 2.2–3.3 cm) and wider (1.2–1.9 cm vs 0.7–1.0 cm) pinnae. Differs from *D. chococola* Christenh. in longer (6.8–11 cm vs 3.0–4.5 cm) and wider (1.2–1.9 cm vs 0.7–1.2 cm) pinnae, thinner lamina texture, and brown colour when preserved with alcohol before drying (vs greyish). Genetically unique among *Danaea* in having a T (vs A or C) at position 529 of *rpl32* reference sequence and differing from all other species of *D.* subg. *Holodanaea* in having an A (vs C) at position 632 of *rpl32* reference sequence.

Description — Rhizomes radial, probably erect but not confirmed, 1.0–1.5 cm in diam., to 10 cm long. *Sterile leaves* 46–72 cm long; *petioles* 14–38 cm long, with 1–3 nodes, winged, winged only in distal part or not winged; *laminae* 30–40 × 12–17 cm, parallel-sided, paripinnate, 14–21 pinna-pairs, proximal pinna-pair reduced or more distant and smaller, medial pinnae 1.4–2.4 cm apart, almost concolorous, dark green or brown adaxially, laminar texture thin, rachises winged at least distally, wings to 0.3–1.5 mm wide, costae usually covered in reddish brown scales; *largest lateral pinnae* 6.8–11 × 1.2–1.9

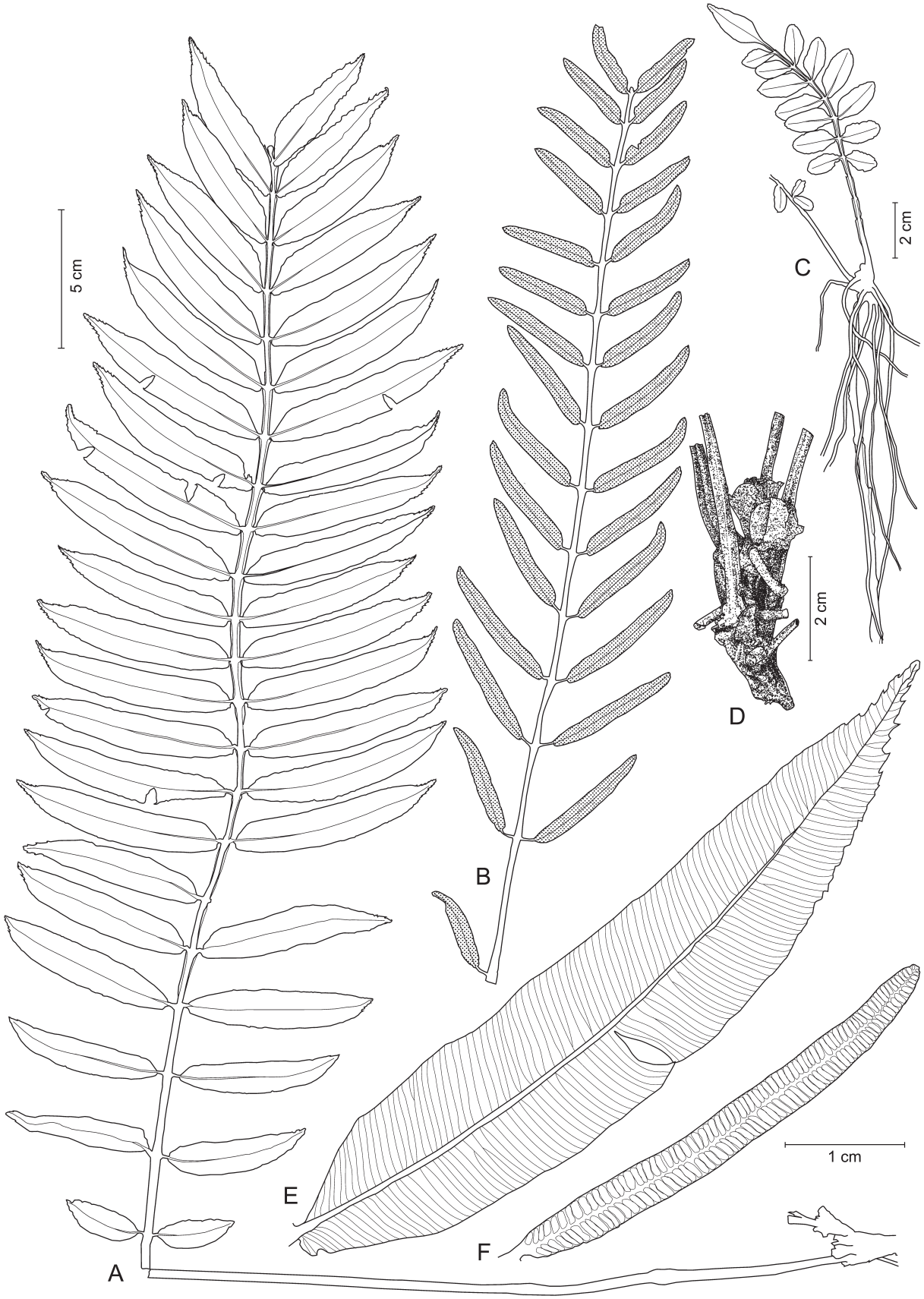

Fig. 27. *Danaea polypinna*: A: sterile leaf (with incomplete pinnae filled in); B: fertile lamina; C: juvenile leaves growing from terminal bud; D: fragment of radial rhizome; E: medial sterile pinna; F: medial fertile pinna. – A, C, E, F: *Mickel 3420* (NY); B: *van der Werff 6757* (MO); D: *Herrera 7873* (K). – Drawn by Venni Keskiniva.

cm, 5.1–6.2 times as long as wide without apex, parallel-sided, perpendicular to rachises or slightly ascending, bases asymmetrical (obtuse proximally, acute distally), apices 0.6–1.6 cm long, acuminate to attenuate, margins of apices serrate to serrulate; *veins* 17–25 per cm, mostly simple, sometimes variably simple and paired at costae. *Fertile leaves* 61 cm long; *petioles* 23 cm long, 0–1 node; *laminae* 23–38 × 7–13 cm, 15–22 pinna-pairs, paripinnate, parallel-sided; *largest lateral pinnae* 4.8–5.1 × 0.4–0.6 cm, linear-oblong, perpendicular to rachises or slightly ascending, bases obtuse, apices obtuse or acute. *Juveniles* known from one plant growing from bud of an adult specimen, this imparipinnate, 7 pinna-pairs when 8 cm long, laminae parallel-sided, terminal pinnae lanceolate, lateral pinnae parallel-sided, bases asymmetrical, apices acute.

Distribution and habitat — Known from central Panama (Chiriqui and Bocas del Toro) and Costa Rica (Limón and Cartago), from 850–1450 m. One site described as very moist upland forest. Fig. 8.

Conservation status — We place *Danaea polypinna* in the Near Threatened (NT) category (IUCN 2012). It has an Area of occupancy of 28 km^2 and an Extent of occurrence of 4184 km^2, which correspond to the EN category. It is known from only 7 collections despite considerable collection efforts in Costa Rica and Panama; this suggests that it is rare. It has been found growing in three protected areas (Reserva Forestal de Fortuna in Panama, Parque Internacional La Amistad, and Parque Nacional Tapantí in Costa Rica), and there appears to be no imminent threat to all its subpopulations.

Etymology — Named for the large number of pinna-pairs.

Remarks — *Danaea polypinna* is a rather small species with short, sausage-like fertile pinnae that are common in small species of *D.* subg. *Holodanaea*. It is characterized by many short and narrow sterile pinnae with abruptly tapering apices and rather concolorous laminae that dry to a dark brown or dark green colour, costae typically covered in reddish brown scales, and radial, probably erect rhizomes.

Danaea polypinna co-occurs with *D. cuspidopsis* and *D. robbinmoranii*, but differs in having almost concolorous laminae (vs bicolorous and clearly whitish abaxially), shorter fertile pinnae (4.8–5.1 cm vs 6.5–12 cm) with obtuse to acute apices (vs cuneate to (long-)acuminate), generally smaller size (sterile leaves 46–72 cm vs 54–120 cm long), and pinnae that are narrower (1.2–1.9 cm vs 1.9–2.4 cm) and often shorter (6.8–11 cm vs 8.0–16 cm). In addition, *D. polypinna* has generally more pinna-pairs than *D. robbinmoranii* (14–21 vs 7–16).

Out of the sequenced species, *Danaea polypinna* is most closely related to the Amazonian *D. trichomanoides*. However, *D. polypinna* is a much larger plant (46–72 cm vs 8–16 cm long) with longer pinnae (6.8–11 cm vs 1.8–2.7 cm).

Danaea polypinna is similar to *D. humilis* and *D. chococola* in having many short and narrow pinnae with short apices, but is larger (sterile leaves 46–72 cm long vs 38–48 in *D. chococola*, 27–42 cm in *D. humilis*) and its pinnae are longer (6.8–11 cm vs 3.0–4.5 cm in *D. chococola*, 2.2–3.3 cm in *D. humilis*) and wider (1.2–1.9 cm vs 0.7–1.2 cm in *D. chococola*, 0.7–1.0 in *D. humilis*). Furthermore, *D. humilis* has bicolorous laminae (vs concolorous) and *D. chococola* has a greyish sheen (vs dark brown).

Danaea wendlandii and *D. gracilis* are clearly smaller plants (sterile leaves max. 32 cm vs 46–72 cm long) with smaller pinnae (max. 5.9 cm long and 1.2 cm wide vs 6.8–11 × 1.2–1.9 cm).

Danaea polypinna is very similar in size and shape to *D. ypori* Christenh. from French Guiana but differs in having almost concolorous pinnae (vs bicolorous) that are mostly parallel-sided (vs often oblanceolate), thinner laminar texture, and by most likely having erect rhizomes (vs creeping-ascending). *Danaea polypinna* also resembles *D. inaequilatera* but differs in having narrower fertile pinnae (0.4–0.6 cm vs 0.8–1.3 cm), sterile laminae being thinner in texture and darker in colour (dark brown vs (light greyish) green), and terminal pinnae almost always being replaced by a bud (vs terminal pinnae usually present).

Additional specimens examined — Costa Rica: Limón: Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut, upper basin of Río Dapari, 09°24'N, 83°05'W, 1200 m, 9 Mar 1992, *Herrera 5250* (F!); Cartago: Turrialba, Tayutic, Jicotea, Finca La Pradera, going up Fila toward San Antonio, 09°47'N, 83°33'W, 1400 m, 14 Jun 1995, *Herrera 7873* (F!, K-2!); Orosi, P. N. Tapantí, Oropéndola trail and banks of Río Orosi, 09°45'N, 83°47'W, 1230 m, 21 Nov 2004, *Rojas 6272* (MO!); Alajuela: Along Río La Balsa about 23 km NE of San Ramón, 850 m, 29 Dec 1974, *Taylor 17805* (BRIT!). — Panama: Bocas Del Toro: Bosque Protector Palo seco, El Verrugoso trail, entering through farm of Sr. Desiderio Meneses, 08°47'N, 82°11'W, 972 m, 7 Feb 2013, *Aranda 4432* (MO!, PMA!); Chiriqui: Distrito Boquete, Fortuna Dam site, 1100 m, 8 Feb 1985, *van der Werff 6757* (GH!, MO, UC!).

15. *Danaea pumila* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 28.

Holotype: Panama, Colón, Teck Cominco Petanquilla mining concession, 08°49.7'N, 80°40.7'W, 362 m, 4 Dec 2007, *van der Werff* 22253 (PMA! (119482); isotypes: MO! (2 duplicates: 6252745, 6046894), TUR! (624450)).

Diagnosis — Similar to *Danaea humilis* T. Moore, but *D. pumila* generally has shorter sterile leaves (19–32 cm vs (27–)34–42 cm), fewer pinna-pairs (11–18 vs (16–)20–25), shorter fertile leaves (19–27 cm vs 37 cm) with

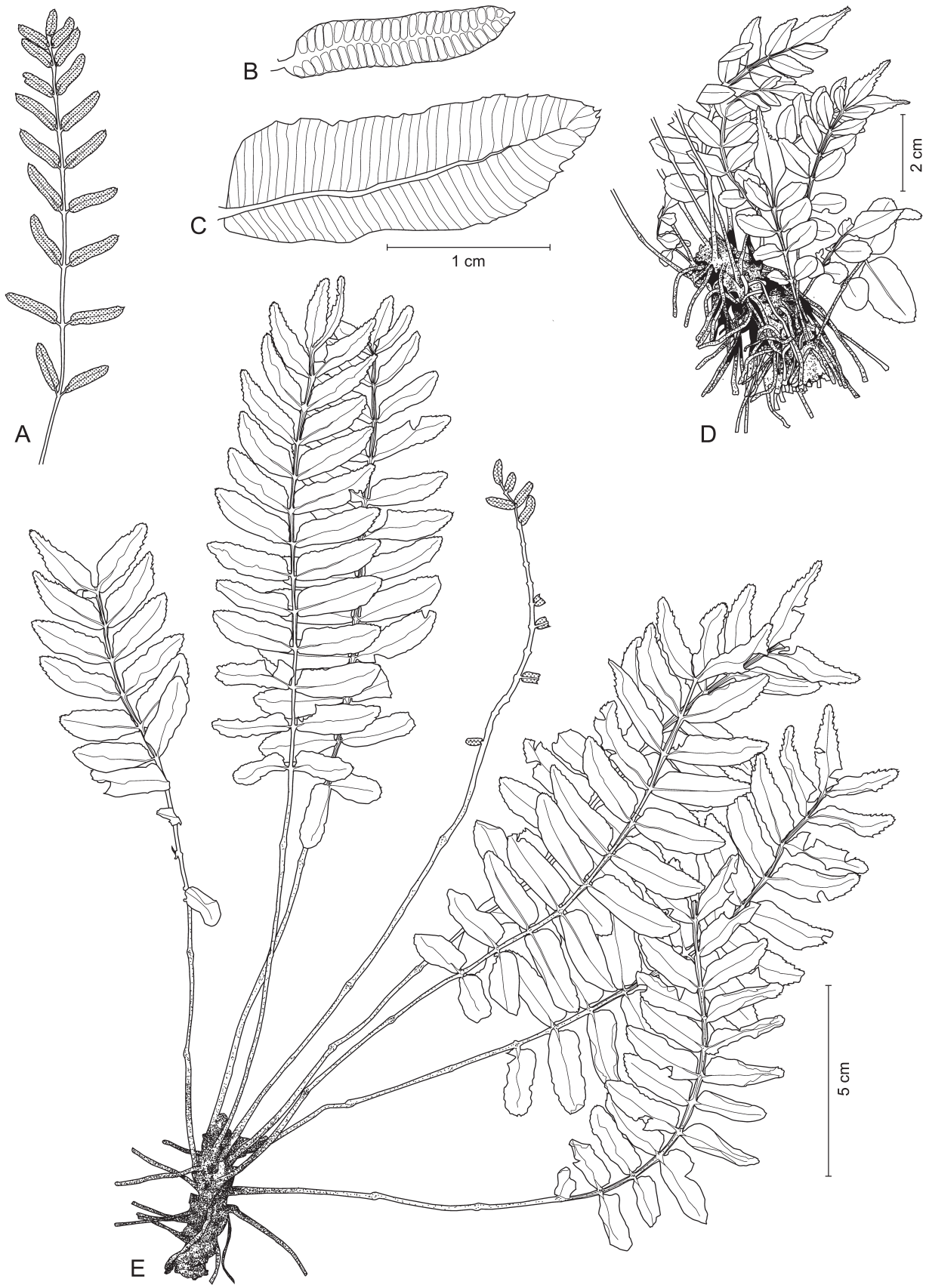

Fig. 28. *Danaea pumila*: A: fertile lamina; B: medial fertile pinna; C: medial sterile pinna; D: juvenile leaves; E: whole plant with fertile pinnae in grey. – A, B: *van der Werff 24420* (US); C, E: *van der Werff 22253* (MO); D: *van der Werff 22192* (TUR). – Drawn by Venni Keskiniva.

fewer pinna-pairs (10–17 vs 20–25), and terminal pinnae almost always replaced by a bud (vs terminal pinnae usually present). Genetically, species differs in locations 80 (C vs T), 764 (A vs G), 779 (A vs C), 1007 (T vs C), 1109 (G vs T) of *atpB* reference sequence; 80 (A vs C), 101 (A vs C), 108 (G vs C), 109 (T vs C), 158 (T vs G), 185 (G vs A), 390 (G vs A), 665 (G vs A), 758 (G vs A), 1060 (T vs A), 1148 (G vs T), 1178 (C vs T) of *rbcL* reference sequence; 218 (A vs G), 320 (G vs A), 399 (C vs T), 906 (C vs A) of *trnL-F* reference sequence; 213 (A vs T), 231 (G vs A), 257 (A vs C), 365 (G vs T), 388 (A vs G), 395 (T vs A), 396 (T vs A), 683 (C vs T), 714 (gap vs A or C), 737 (G vs A), 863 (G vs A) of *rpl32* reference sequence.

Description — *Rhizomes* radial, decumbent to erect, 0.5–1.0 cm in diam., 4–13 cm long. *Sterile leaves* 19–32 cm long; *petioles* 6.2–11 cm long, with 1–2 nodes, not winged; *laminae* 10–22 × 3.4–6.9 cm, linear to lanceolate, paripinnate (or imparipinnate), 11–18 pinna-pairs, medial pinnae 0.8–1.0 cm apart, bicolorous, dark green adaxially, light green abaxially, laminar texture thin, rachises winged (sometimes only in distal part of lamina), wings to 0.2–1 mm wide; *terminal pinnae* 2.2–3 × 0.6–1 cm, lanceolate, bases acute, apices 0.9–1.5 cm long, acuminate, margins of apices serrulate to serrate down to widest part of pinna; *largest lateral pinnae* 2.4–3.4 × 0.7–1 cm, 2.5–4.2 times as long as wide without apex, parallel-sided or widest below middle, slightly ascending, bases asymmetrical (obtuse proximally, obtuse, acute or truncate distally), apices 0–1.2 cm long, acute (to acuminate), margins of apices serrate to serrulate (serrations down to 2/3 of pinna length in distal pinnae); *veins* 13–20 per cm, variably simple or forked at costae. *Fertile leaves* 19–27 cm long; *petioles* 9.5–18 cm long, 1–2 nodes; *laminae* 7–12 × 1–4 cm, parallel-sided, paripinnate, 10–17 pinna-pairs; *largest lateral pinnae* 0.7–1.5 × 0.2–0.5 cm, linear-oblong, bases obtuse, apices obtuse to mucronate. *Juveniles* usually imparipinnate, laminae lanceolate, terminal pinnae lanceolate, lateral pinnae oblong to lanceolate, smallest pinnate juvenile leaves 2 cm long.

Distribution and habitat — Found in Colombia (Chocó, Norte de Santander, Antioquia) and Panama (Colón), in lowland wet rain forests from 250–600 m. Fig. 8.

Conservation status — We place *Danaea pumila* in the Vulnerable (VU B1ab(iii)+2ab(iii)) category (IUCN 2012). It has an Extent of occurrence of 2483 km^2 and an Area of occupancy of 20 km^2, which corresponds to the EN category, and is known from only eight locations, which corresponds to the VU category. One of the collections was from inside a protected area (Parque Nacional Natural Los Katíos in Colombia), but all other collection localities are outside protected areas (one locality was described as secondary forest), and half of the specimens were collected from inside the Minera Panama mining concession, where the area, extent and quality of suitable habitats were inferred to be suffering continuing decline from deforestation.

Etymology — The word Pumila is Latin for diminutive and refers to the small size of the plant in relation to other species of *Danaea*.

Remarks — *Danaea pumila* is a small species that morphologically most closely resembles *D. humilis*. It is smaller (sterile leaves 19–32 cm vs (27–)34–42 cm, fertile leaves 19–27 cm vs 37 cm long), has fewer pinna-pairs (11–18 vs (16–)20–25), and adult leaves mostly have terminal pinnae replaced by a bud (vs present; however, the terminal pinna is mostly present in juveniles of *D. pumila*). *Danaea pumila* grows at lower elevations than *D. humilis* (to 600 m vs 900–1600 m) and is found only west of the Andes (vs also on the Amazonian side of the Andes). Genetically the two species are clearly distinct.

Danaea pumila is smaller than *D. chococola* (sterile leaves 19–32 cm vs 38–48 cm long) and has fewer pinnae (11–18 vs (19–)23–26 pairs) that are bicolorous with abaxial side whitish (vs concolorous).

Danaea pumila differs from *D. wendlandii* in having acute to acuminate pinna apices (vs usually obtuse) that are serrulate to serrate (vs often crenulate). In addition, *D. pumila* has generally longer sterile leaves (19–32 cm vs 13–25 cm long), with generally more nodes on the petioles (1–2 vs 0–1), and its terminal pinnae, when present, are longer (2.2–3.0 cm vs 1.7–2.0 cm).

Danaea pumila differs from *D. gracilis* in having generally fewer pinna-pairs (11–18 vs 15–25) that are opaque and bicolorous (vs translucent and concolorous), wider (2.5–4.2 vs 3.0–6.2 times as long as wide without apex) and have acute apices (vs usually obtuse). If terminal pinnae are present, they are longer in *D. pumila* than in *D. gracilis* (2.2–3.0 cm vs max. 1.5 cm).

See *Danaea nasua* (described above) for comparison with that species.

Additional specimens examined — Colombia: Antioquia: Vic. Planta Providencia, 28 kms SW of Zaragoza, valley of Río Anorí, 07°18'N, 75°04'W, 400–700 m, 6 Apr 1977, *Alverson 383* (MO!, NY!, WIS!); Río Anorí valley near Planta Providencia, 360–600 m, *Shepherd s.n.* (WIS!); Chocó: Riosucio Municipality. Parque Nacional Natural Los Katíos, 250 m, 31 May 1976, *Forero 1726* (COL!, MO!); Norte De Santander: Camp 84 on pipeline, 1800 (ft), 549 m, 16 Sep 1946, *Foster 1715* (A!, COL!). — Panama: Colón: MPSA Concession, Valle Grande, Sierra 19, 08°50'N, 80°41'W, 291 m, 17 May 2012, *Hammel 26229* (MO!, PMA!, UC!); Teck Cominco Petanquilla mining concession, 08°49.9'N, 80°41.1'W, 296 m, 29 Nov 2007, *van der Werff 22192* (MO!, PMA!, TUR!); mine site of Minera Panama, Valle Grande Road, 08°50'N, 80°41'W, 250 m, 9 Sep 2012, *van der Werff 24420* (MO!, NY!, PMA!, UC!, US!).

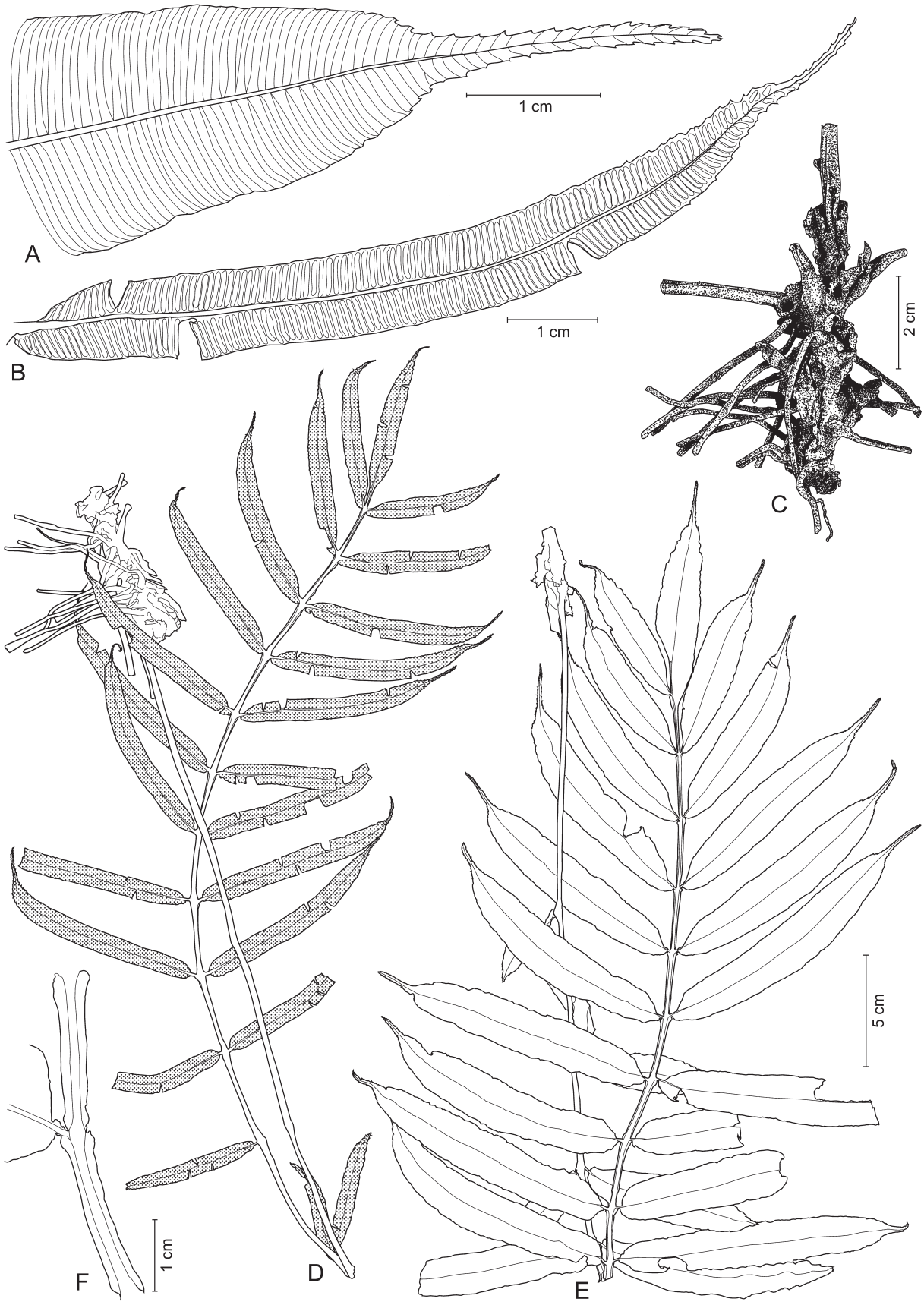

Fig. 29. *Danaea robbinmoranii*: A: medial sterile pinna apex; B: fertile pinna; C: erect rhizome; D: fertile leaf; E: sterile leaf; F: detail of winged rachis in distal part of lamina. – A, E: *Moran 6350* (NY); B, D: *Nitta 851* (UC); C: *Smith 2248* (NY); F: *Hammel 11215* (F). – Drawn by Venni Keskiniva.

Fig. 30. *Danaea robbinmoranii*: A: field habit; B: abaxial side of sterile leaf apex; C: entire plant with sterile and fertile leaf; D: detail of winged rachis and petiole; E: abaxial side of fertile leaf apex. – A–E *Nitta 851*. – © Joel Nitta 2011.

16. *Danaea robbinmoranii* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 29, 30.
Holotype: Costa Rica, San José, along entrance road to University of San Ramón's biological field station "Alberto Brenes", c. 1.5 km from main road San Ramón–La Tigra, 10°14'N, 84°38'W, 800 m, 23 Jan 2001, *Moran 6350* (CR! (INB0003704244); isotype: NY! (03881060)).

Diagnosis — Most closely related to *Danaea vanderwerffii* Tuomisto & Keskiniva but differing in proximal pinnae not as reduced (largest lateral pinnae 2–4 times as long as proximal pinnae vs over 5 times as long), generally narrower fertile pinnae (0.5–1.1 cm vs 0.8–1.6 cm wide), apices more often with serrations (vs usually crenulate), sterile pinnae generally shorter (to 16 vs to 25 cm long), generally more nodes on petioles (0–3 vs 0–1). Genetically differs in location 455 (gap vs T), 752 (T vs C) of *rpl32* reference sequence; 906 (C vs T) of *trnL-F* reference sequence. Morphologically similar to *D. cuspidopsis* Keskiniva & Tuomisto, but wings usually present along all of rachises and sometimes part of petioles (vs only in distal part of lamina) and wings wider (to 0.7–2 mm vs to 0.1–0.7 mm wide), generally fewer pinna-pairs (7–16 vs 13–20) that are stockier (largest lateral pinna length without apex 3–6 vs 5–8 times as long as wide), and spaced further apart (medial pinnae 2.9–3.5 cm vs 1.4–2.5 cm apart). Genetically differs in locations 43 (T vs A), 222 (A vs G), 231 (A vs G), 257 (C vs A), 327 (C vs T), 396 (A vs T), 424 (C vs A), 450 (T vs gap), 455 (T vs gap), 465 (T vs G), 466 (T vs A), 469 (G vs A), 587 (G vs A), 713 (C vs T), 758–762 (insertion of ATACT vs gap), 737 (A vs G), 749 (G vs T), 863 (A vs G), 865 (A vs G) of *rpl32* reference sequence; 192 (C vs A), 233 (A vs C), 248–252 (gap vs insertion of ATTAG), 265 (G vs A), 393 (G vs A), 399 (T vs C), 538 (G vs A), 665 (T vs C), 728–732 (gap vs insertion of AATA), 740 (T vs C) of *trnL-F* reference sequence. Unique among *Danaea* in location 134 (T vs C) of *rpl32* reference sequence.

Description — *Rhizomes* erect and radial, 1.0–2.5 cm in diam., short, to at least 7 cm long. *Sterile leaves* 59–94 cm long; *petioles* 19–42 cm long, with 0–3 nodes, not winged or winged only distally; *laminae* 33–63 × 10–25 cm, oblong to lanceolate or elliptic, imparipinnate or (rarely) paripinnate, 7–16 pinna-pairs, proximal pinnae smallest and more distant, medial pinnae 2.9–3.5 cm apart, bicolorous, adaxially dark green, abaxially clearly paler, whitish to light green (or dark brown adaxially, light brown abaxially when preserved in alcohol before drying), laminar texture thin, rachises winged (at least in distal part of lamina), wings to 0.7–2 mm wide; *terminal pinnae* 6.9–14.2 × 1.7–2.6 cm, lanceolate to oblong,

bases acute to obtuse, apices 1.5–2.6 cm long, acuminate, margins of apices serrate to serrulate; *largest lateral pinnae* 9.4–15.7 × 2.0–3.5 cm, 3.0–6.1 times as long as wide without apex, parallel-sided (to widest above middle), slightly ascending (or perpendicular to rachis), bases symmetrical (obtuse) to asymmetrical (auriculate proximally, obtuse (or acute) distally), apices 1.1–2.2 cm long, acuminate to caudate, margins serrate to serrulate at shoulders of pinnae, apices serrulate, serrate, crenate or crenulate; *veins* 12–17 per cm, mostly simple or mixture of simple and paired at costae. *Fertile leaves* 53–88 cm long; *petioles* 20–47 cm long, 0–3 nodes; *laminae* 27–52 × 6–17 cm, oblong or long-elliptic, imparipinnate (or possibly paripinnate), 8–15 pinna-pairs; *terminal pinnae* c. 5.2 × 0.4–0.9 cm, lanceolate, bases acute, apices acuminate; *largest lateral pinnae* 7.6–11 × 0.5–1.1 cm, linear-oblong, (slightly) ascending, bases symmetrical (obtuse) to asymmetrical (auriculate proximally, obtuse distally), apices 0.7–1.6 cm long, long-acuminate, margins of apices serrulate, crenulate or crenate. *Juveniles* not known.

Distribution and habitat — Known from Costa Rica from 50–1082 m, from primary and secondary rainforests. The species has been found growing on a steep clay creek bank and epipetric on a rock face. Fig. 13.

Conservation status — We place *Danaea robbinmoranii* in the Least Concern (LC) category (IUCN 2012). It has an Area of occupancy of 68 km^2, which corresponds to the EN category, and an Extent of occurrence of 28,079 km^2, which corresponds to the NT category. However, *D. robbinmoranii* seems to be rather abundant in the Costa Rican lowlands, is known from 17 collections, and has been collected from several protected areas (Parque Nacional Guanacaste, Nectandra Biological Preserve, Parque Nacional Braulio Carrillo, and Parque Nacional Corcovado in Costa Rica; Reserva Biológica Indio Maíz in Nicaragua). There appears to be no imminent threat to all its subpopulations.

Etymology — Named for Robbin C. Moran, who has made important contributions to fern systematics and fern-related education and who also collected the type specimen of this species.

Remarks — *Danaea robbinmoranii* is one of the species in a complex that was previously referred to *D. moritziana*. It is morphologically most similar to *D. cuspidopsis*, with which it co-occurs in Costa Rica but at lower elevations (generally below vs above 1000 m). *Danaea robbinmoranii* is perhaps best separated from *D. cuspidopsis* by the rachis wings, which are wider (to 0.7–2 mm vs to 0.1–0.7 mm wide) and usually extend along all of the rachises and sometimes part of the petioles as well (vs adult leaves only winged in the distal part of the rachis), the pinnae being further apart on the rachises (medial pinnae 3.0–3.5 cm vs 1.4–2.5 cm apart) and abaxially being even more starkly whitish. *Danaea robbinmoranii* further differs from *D. cuspidopsis* in having generally fewer pinnae (7–16 vs 13–20 pinna-pairs) that are stockier (largest lateral pinnae 3–6 vs 5–8 times as long as wide without apex), by its smaller size (sterile leaves max. 94 cm vs max. 120 cm long), and probably shorter rhizomes (to 7 cm tall vs to 25 cm tall).

Genetically, *Danaea robbinmoranii* was resolved as sister to *D. vanderwerffii* from Panama, with which it shares a starkly whitish abaxial colour but differs in the proximal pinnae being larger (vs strongly reduced; smallest pinnae ¼–½ as long as largest lateral pinnae vs at most 1/5 and usually less than 1/10). In addition, the apices of the sterile pinnae in *D. robbinmoranii* are often serrulate (vs crenate), the fertile pinnae are often narrower (0.5–1.1 cm vs 0.8–1.6 cm wide), the sterile pinnae do not grow as large (to 16 vs to 25 cm long), and there are often more petiolar nodes (0–3 vs 0–1).

Danaea robbinmoranii is similar in habit to the genetically distant *Danaea alata* Sm. that has a distribution in the Lesser Antilles and Venezuela (vs Costa Rica and Nicaragua) but differs in having erect rhizomes (vs decumbent in *D. alata*), generally stockier pinnae (largest lateral pinnae 3–6 vs 4–9 times as long as wide without apex), and often forked veins (vs always simple) that are closer (12–17 vs 7–14 veins per cm).

Additional specimens examined — Costa Rica: Alajuela: Upala, Bijagua, El Pilón, Cabaceras del Río Celeste, 10°49'N, 84°27'W, 700 m, 13 Nov 1987, *Herrera 1245* (CR!, UC!); San Ramón, Nectandra Biological Preserve, Ocotea area, 10°11'N, 84°31'W, 1082 m, 23 Jan 2011, *Nitta 851* (UC!); northern slope of ridge along quebrada draining eastward to Río Cataratitas, c. 20 km NW of San Ramón, 10°13'N, 84°32'W, 850 m, 3 Feb 1986, *Smith 2248* (MO!, NY!, UC!); Guanacaste: La Cruz, Santa Cecilia, Finca Montecele, on way to Río Colón and toward Cerro Campana, 10°58'N, 85°26'W, 650–800 m, 12 Apr 2008, *Rojas 8404* (MO!); La Cruz, Santa Cecilia, Finca Montecele, on way to Río Colón and toward Cerro Campana, 10°58'N, 85°26'W, 700–1000 m, 13 Apr 2008, *Rojas 8417* (MO-2!); Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its junction with Río Sarapiqui, 100, 22 Jun 1981, *Hammel 10905* (CR!, DUKE, F!, MO!); Along Rio Peje about 0.5 km SW of back end of Vargas property, approx. where an imaginary line between Magsasay and Puerto Viejo de Sarapiqui would cross Río Peje, 20 Feb 1982, *Hammel 11215* (DUKE, F!, MO!); Limón: Siquirres, Las Brisas de Pacuarito, 300 m, 18 Apr 1985, *Gómez 23409* (MO!); Río Danto, path to Las Brisas, Pacuarito, Siquirres, 21 May 1985, *Gómez 23622* (MO!, UC!); Puntarenas: Golfito, P. N. Corcovado, Peninsula de Osa, Cerro Rincón, 08°31'N, 83°28'W, 700–800 m, 30 Jan 1998, *Azofeifa 623* (CR!, NY!); Along road between Chacarita and Rincón de Osa, c. 6 km W of Interamerican High-

way at Chacarita, 08°45'N, 83°18'W, 160 m, 2 Mar 1985, *Croat 59710* (MO!); c. 3 miles E of Rincón de Osa, 08°42'N, 83°29'W, 250–350 m, 17 Jul 1967, *Evans 2761* (U!); Parque Nacional Corcovado, Estación Los Patos, 08°34'N, 83°31'W, 120 m, 1 Apr 1988, *Hammel 16631* (CR!, UC!); Osa Peninsula, on ridge 9.5 km W of Rincón de Osa, 600 m, 17 Jul 1967, *Mickel 2753* (NY!, U!); San José: Vazquez de Coronado, Parque Nacional Braulio Carrillo, Estación Carrillo, Quebrada Sandijuela, 500 m, 25 Jul 1984, *Gómez 22921* (UC!). — Nicaragua: Río San Juan: Reserva Indio-Maíz, Municipality of Castillo, along Caño Chontaleño, 11°06'N, 84°14'W, 150–200 m, 14 Feb 1997, *Rueda 5791* (MO!).

17. *Danaea ubatubensis* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 31, 32.
Holotype: Brazil, São Paulo, Ubatumirim, Parque Estadual da Serro do Mar, Núcleo Picinguaba, trail along Rio da Fazenda starting at Casa de Farinha, 23°20'S, 44°50'W, 125 m, 6 Mar 2008, *Christenhusz 4910* (SP! (mounted on 2 sheets: 473402); isotypes: AAU!, MO! (mounted on 2 sheets: 6303081), TUR!, UC! (1930838), Z!).

Diagnosis — Similar to and co-occurring with *Danaea excurrens* Rosenst., differing in having no serrations in pinna apices (vs pinna apices usually serrate), terminal pinnae often replaced by bud (vs always present), sometimes having more pinna-pairs (11–16 vs 5–16), generally longer pinnae (12–16 cm vs 5–15 cm) that are more elliptic (vs parallel-sided or spathulate), longer pinna apices (1.9–2.2 cm vs 0.5–1.5 cm), veins both simple and forked at costae (vs usually mostly forked either at costae or above), often symmetrical pinna bases (vs usually asymmetrical). Genetically differs from all other species of *Danaea* in locations 629 (A vs G), 857 (A vs G) of *atpB* reference sequence; 226 (G vs A or gap), 257 (T vs A or G), 685 (G vs C or T), 867 (T vs A or G) of *trnL-F* reference sequence; 417 (T vs C of *rbcL* reference sequence; 438–465 (gap vs no gap), 466 (G vs A or T), 469 (T vs A or G), 766 (T vs C) of *rpl32* reference sequence. Unique in *D.* subg. *Holodanaea* in locations 413 (G vs A or T), 435 (A vs G) of *rpl32* reference sequence; 240 (A vs C or T) of *trnL-F* reference sequence.

Description — *Rhizomes* radial, orientation not certain, 1.5–2.0 cm in diam. *Sterile leaves* 66–118 cm long; *petioles* 37–57 cm long, with 1–3 nodes, not winged; *laminae* 29–60 × 18–26 cm, lanceolate to obovate, imparipinnate or paripinnate, 11–16 pinna-pairs, medial pinnae 2.0–2.9 cm apart, bicolorous, dark green adaxially, light green abaxially (or dark brown adaxially and light brown abaxially when preserved in alcohol before drying), laminar texture rather thin, rachises not winged or very narrowly winged distally, wings to 0.1 mm wide; *terminal pinnae* 9.0–10 × 1.5–1.8 cm, oblong to lanceolate, bases acute, apices 1.4–1.6 cm long, (long-) acuminate, margins of apices sinuate at apex, serrulate at shoulder of pinna; *largest lateral pinnae* 12–16 × 1.5–2.1 cm, 5.4–7.7 times as long as wide without apex, widest at middle or parallel-sided, slightly ascending, bases asymmetrical or symmetrical, acute, apices 1.9–2.2 cm long, long-acuminate, margins of apices sinuate to crenulate at apex, crenulate to serrulate at shoulder of pinna; *veins* 10–15 per cm, simple or forked at costae or rarely above. *Fertile leaves* 100 cm long; *petioles* 57 cm long, with 1 node, not winged; *laminae* c. 43 × 14 cm, parallel-sided, paripinnate, 13 pinna-pairs, not winged; *largest lateral pinnae* c. 7.3 × 0.7–0.9 cm, parallel-sided, bases obtuse, apices mucronate to acuminate, margins of apices sinuate. *Juveniles* with elliptic, oblong or lanceolate laminae, terminal pinnae elliptic to lanceolate, lateral pinnae elliptic, apices acuminate to acute, smallest observed pinnate juvenile leaf 10 cm long with 4 pinna-pairs.

Distribution and habitat — Known only from the Brazilian Atlantic Forest in Ubatuba, São Paulo state, southern Brazil, from 125–1000 m. Fig. 33.

Conservation status — We place *Danaea ubatubensis* in the Critically Endangered (CR B1ab(iii)+2ab(iii)) category (IUCN 2012). It is known from only two specimens, which corresponds to the CR category. The collection localities were only 6 km apart, and an Area of occupancy of < 10 km^2 also corresponds to the CR category. Both collections are from Parque Estadual da Serro do Mar, Núcleo de Picinguaba, but the Atlantic forests of Brazil are only a fragment of their original size and the extent and quality of the habitats suitable for *D. ubatubensis* are continuing to decline. Given that *D. ubatubensis* is genetically distant from all the other *Holodanaea* species we have sampled, it makes an important contribution to the genetic diversity of the genus.

Etymology — Named after the municipality of Ubatuba, where both known specimens were collected.

Remarks — *Danaea ubatubensis* occurs in the same area as *D. excurrens* but is genetically clearly distinct and can most easily be identified by its larger number of pinnae (11–16 vs 5–8 pairs). However, our genetic studies suggest that *D. excurrens* is a variable species that does not always display the most striking characteristics of the type, namely the small number of pinnae that are narrow and spathulate and have sparse, simple veins. Instead, most specimens of *D. excurrens* are more similar to *D. moritziana*, although they have narrower pinnae and often creeping rhizomes (vs always erect in *D. moritziana*).

Danaea ubatubensis differs from *D. excurrens* s.l. in larger size (66–118 cm vs 35–62 cm), having entire apices (vs apices usually serrate), often with terminal pinnae replaced by a bud (vs always present but sometimes interrupted by a bud), and generally having longer pinnae (12–16 cm vs 5.3–15 cm long). The narrow-elliptic pinna shape of *D. ubatubensis* differs from both the spathulate

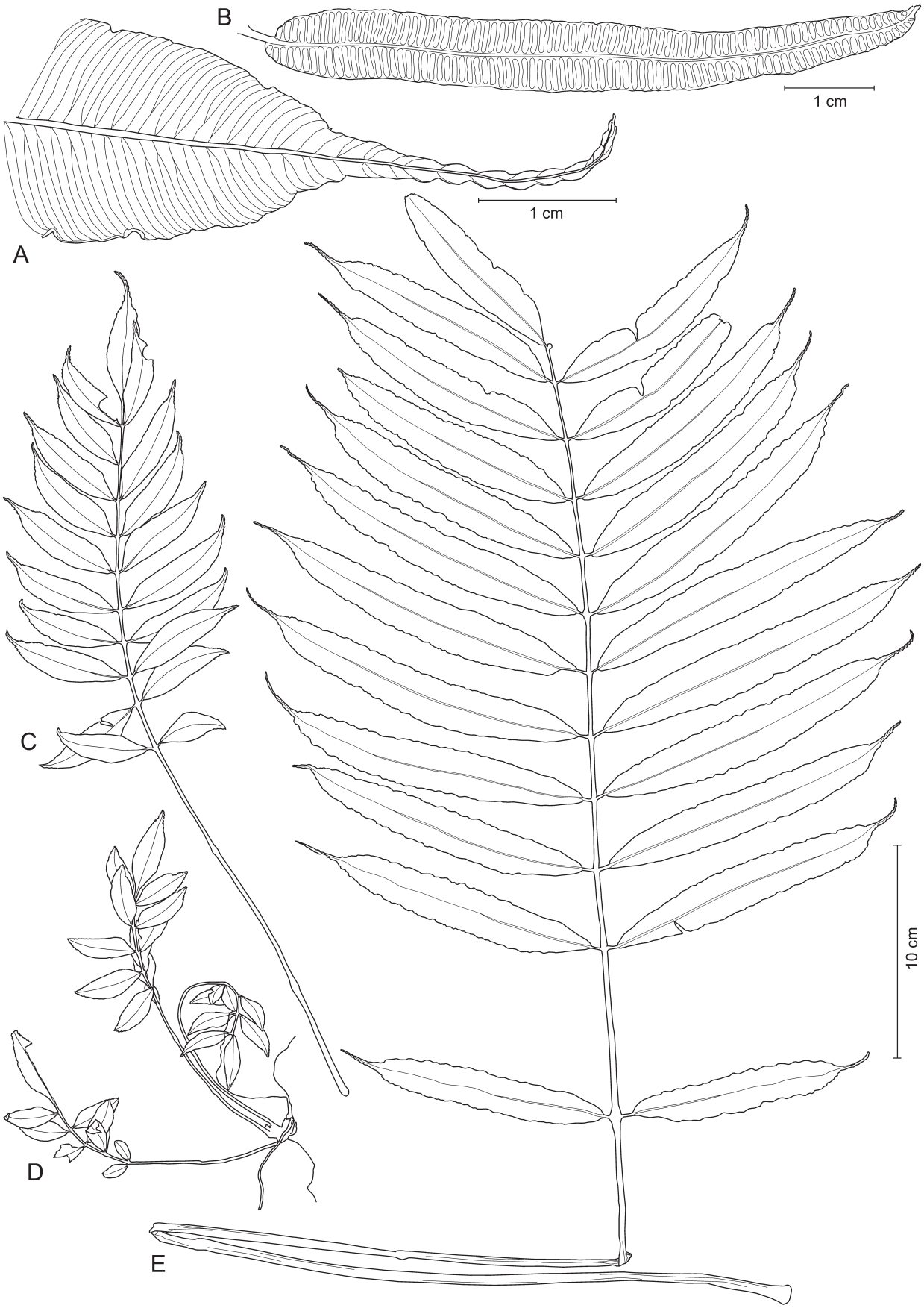

Fig. 31. *Danaea ubatubensis*: A: sterile medial pinna apex; B: fertile pinna; C: juvenile; D: juvenile; E: sterile leaf. – A–E *Christenhusz 4910* (TUR). – Drawn by Venni Keskiniva.

Fig. 32. *Danaea ubatubensis* field habit. A: juvenile; B: sterile lamina apex with a terminal bud; C: entire plant; D: fertile leaf. – A–D *Christenhusz 4910* (TUR). – © Hanna Tuomisto 2008.

shape of typical *D. excurrens* and the more parallel-sided shape of the majority of the specimens. From the latter, *D. ubatubensis* further differs in having acute pinna bases (vs obtuse) that can be symmetrical (vs always asymmetrical), longer pinna apices (1.9–2.2 cm vs 0.5–1.5 cm long), and a mixture of simple veins and veins forked at the costae (vs mostly forked at the costae or above).

Additional specimens examined — Brazil: São Paulo: Ubatuba, Parque Estadual da Serra do Mar, Núcleo de Picinguaba, Pico do Cuscuzeiro trail, close to border between Rio de Janeiro and São Paulo, 23°18'S, 44°48'W, 1000 m, 2001, *Salino 7284* (NY!)

18. *Danaea velona* Keskiniva & Tuomisto, **sp. nov.** (*D.* subg. *Holodanaea*) – Fig. 34, 35.
Holotype: Colombia, Caldas, 05°15'N 76°06'W, 1500 m, 7 Feb 2015, *Kessler 14808* (HUA! (201795); isotype: TUR!).

Diagnosis — Similar to *Danaea tenuicaulis* Tuomisto & Keskiniva, but differing in longer laminae (c. 47 cm

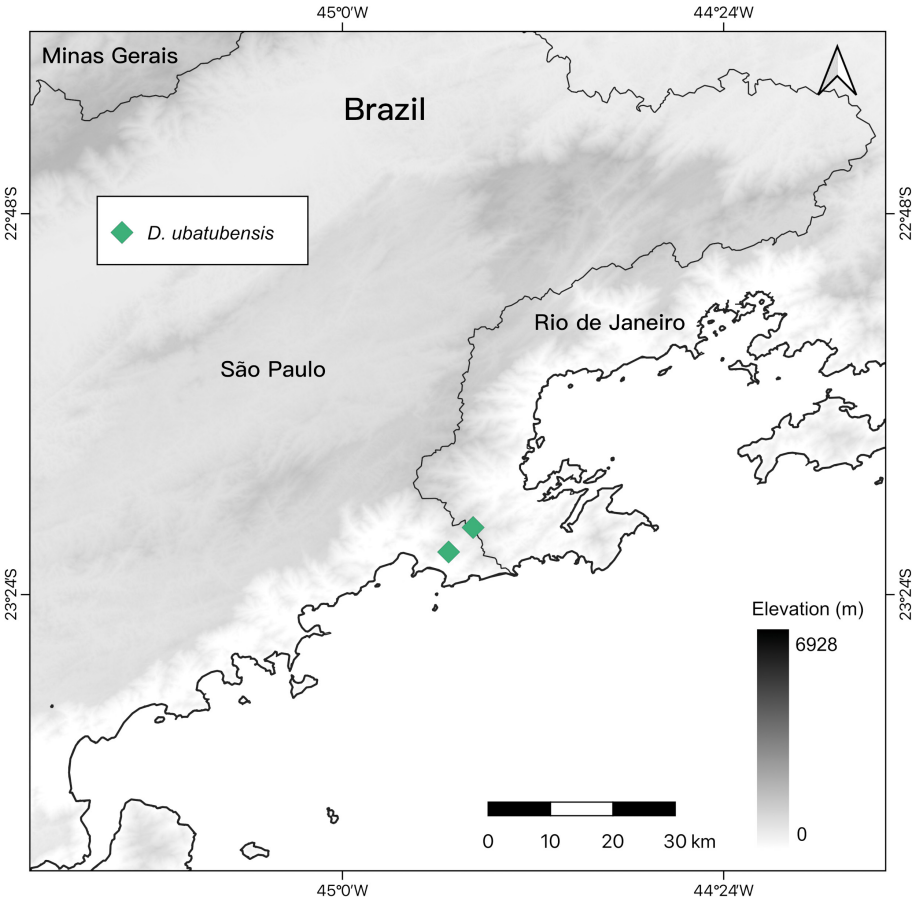

Fig. 33. Distribution of type and paratype of *Danaea ubatubensis*.

vs 23–43 cm) and more pinna-pairs (16–19 vs 9–12). *Danaea velona* has unique caudate, very long and narrow (c. 2.3 × 0.1 cm) pinna apices whose margins are mostly entire but very tip and shoulder of pinna are crenulate to serrate. Genetically unique among *Danaea* in having a T (vs A or T) at position 631 of *rpl32* reference sequence. Differs from all other species of *D.* subg. *Holodanaea* by having a T (vs C) at position 264 and an A (vs G or T) at position 867 of *rpl32* reference sequence.

Description — *Rhizomes* radial, creeping, 1 cm in diam., at least to 20 cm long, leaf and root bases 1.5–4.0 cm apart. *Sterile leaves* 77 cm long; *petioles* 31–34 cm long, with 1–2 nodes, not winged; *laminae* 47–48 × 16–20 cm, linear lanceolate, imparipinnate, 16–19 pinna-pairs, medial pinnae 1.8–2 cm apart, bicolorous, dark green adaxially, light green abaxially when fresh, dries almost concolorous green, laminar texture thin, rachises winged distally, wings to 1 mm wide; *terminal pinnae* 7.4–9.3 × 1.3–1.6 cm, oblong, bases acute, apices caudate with narrow part 2.8–5.2 cm long, margins of apices crenulate at tip, serrate at shoulder of pinna, entire in between; *largest lateral pinnae* c. 10 × 2 cm, 2.8–3.9 times as long as wide without apex, parallel-sided, slightly ascending, bases asymmetrical (obtuse proximally, concave distally), apices caudate with narrow part 2.3 cm long, spathulate, margins of apices crenulate at tip, serrate to crenulate at shoulder of pinna, entire in between; *veins* 19 per cm, mostly simple. *Fertile leaves* not known. *Juveniles* not known.

Distribution and habitat — Only one specimen is known from a montane forest in the Pacific coast of Colombia (Caldas), from 1500 m. Fig. 8.

Conservation status — We place *Danaea velona* in the Critically Endangered (CR B1ab(iii)+2ab(iii)) (IUCN 2012). It is only known from a single specimen, which suggests it is rare and endemic to a small area. The type was collected at a roadside outside of protected areas, and the area, extent and quality of the habitat were inferred to be in continuing decline from deforestation.

Etymology — Velona is a Greek word for needle, referring to the long-caudate pinna apices of this species.

Remarks — *Danaea velona* is similar in rhizome and pinna shape to *D. tenuicaulis*, having caudate pinna apices and leaf and root bases to 4 cm apart. It differs in having more pinna-pairs (16–19 vs 9–12) that are more densely packed (c. 2 cm vs 2.3–4.0 cm apart) on longer laminae (c. 47 cm vs 23–43 cm long). *Danaea velona* has unique long-caudate pinna apices that have serrations at the tip and at the shoulder of the pinnae but are entire in the middle (vs serrate to crenate all the way in *D. tenuicaulis*).

Danaea velona is genetically most closely related to *D. vanderwerffii*, *D. robbinmoranii*, *D. bicolor* Tuomisto & R. C. Moran and *D. tenera*. It differs from these species in having rhizomes with widely spaced leaf and root bases (vs more densely packed) and leaves with generally more pinna-pairs (16–19 vs 10–13 in *D. vanderwerffii*, 7–16 in *D. robbinmoranii*, 12–17 in *D. tenera*, and 3–6 in *D. bicolor*). *Danaea tenera* is a translucent species (vs opaque) that has deeply serrate pinna apices and usually has the terminal pinnae replaced by a bud (vs terminal pinnae present). *Da-*

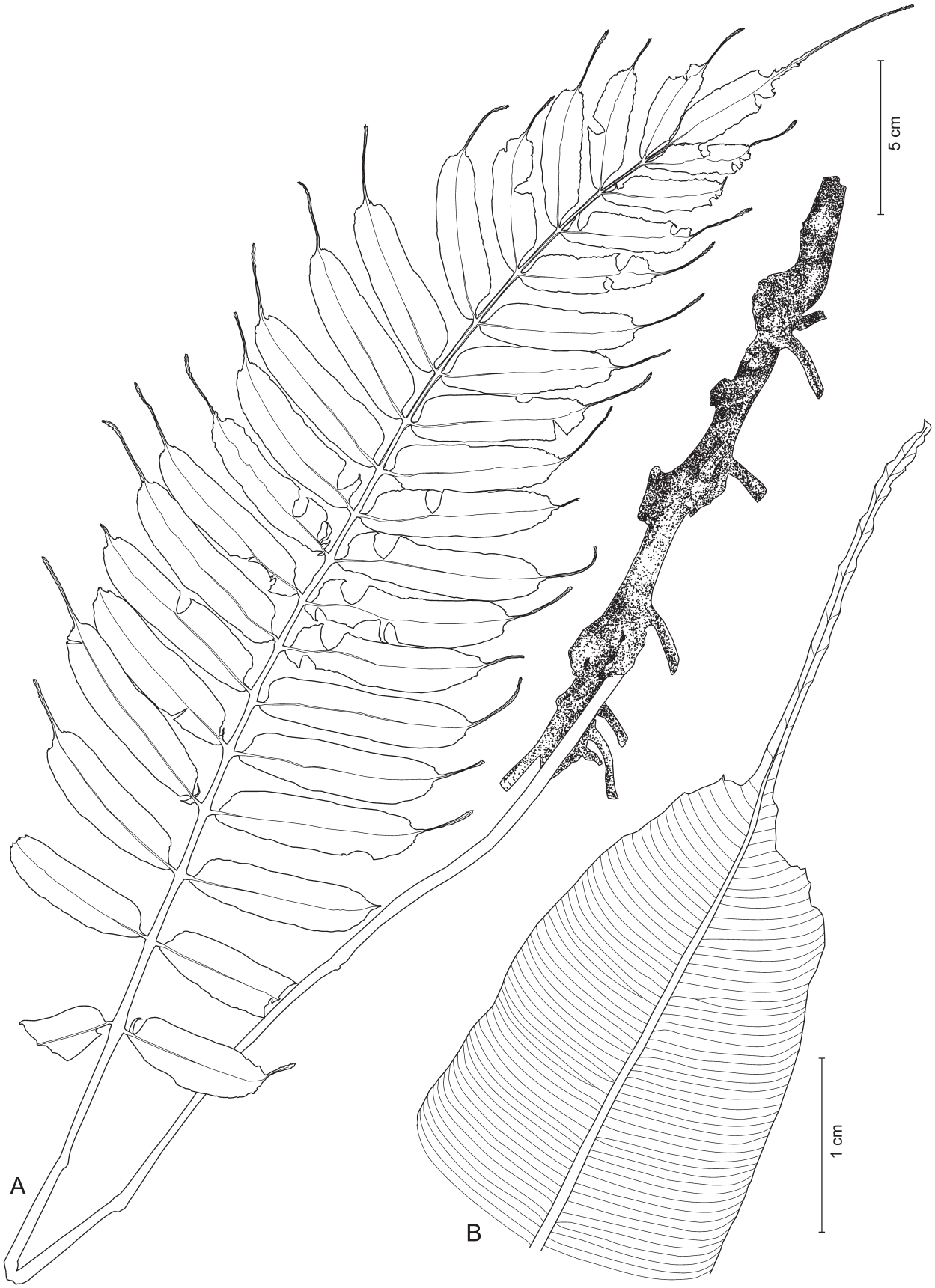

Fig. 34. *Danaea velona*: A: sterile leaf and rhizome; B: sterile medial pinna apex. – A, B: *Kessler 14808* (TUR). – Drawn by Venni Keskiniva.

Fig. 35. *Danaea velona*: A: entire plant with rhizome; B: sterile lamina abaxial (left) and adaxial (right) sides; C: medial pinna. – A–C: *Kessler 14808*. – © Michael Kessler 2015.

naea robbinmoranii has pinna apices that are serrate throughout, and its pinnae are more widely spaced (2.9–3.5 apart vs 2 cm apart). *Danaea velona* has a narrower terminal pinnae than *D. bicolor* and *D. vanderwerffii* (c. 1.3 cm wide vs 2.0–5.0 cm in *D. vanderwerffii* and 3.2–5.0 cm in *D. bicolor*). In addition, *D. vanderwerffii* has very reduced proximal pinnae (vs proximal pinnae more than half the length of largest lateral pinnae in *D. velona*).

Danaea velona differs from *D. cuspidopsis* in having abruptly caudate pinna apices (vs acuminate) that are longer and partly entire (vs serrate throughout), and creeping rhizomes (vs erect) with leaf and root bases to 4 cm apart (vs 0.5–1.5 cm apart).

Discussion

Genetic data have proved crucial in sorting out the species limits in *Danaea*. Now that we have managed to sequence specimens representing almost all known *Danaea* species, it is clear that the genus contains many species

that have not been recognized before. We have described 18 of them as new to science in the present paper, but we believe that at least as many undescribed species remain. This is because we have sequenced individual specimens that are both morphologically and genetically distinct, but we did not want to make types out of the available material. Hopefully there will be more representative specimens available in the future. The complete phylogeny is published in a companion paper together with an identification key to those 79 *Danaea* species and two hybrids that we currently recognize (Keskiniva & al. 2024).

Out of the three subgenera, *Danaea* subg. *Holodanaea* has the largest number of species, with the most morphological variation among species; some of the species have very clear diagnostic characteristics. Our work has further increased the relative diversity of *D.* subg. *Holodanaea*: here and in Keskiniva & Tuomisto (2022) we have described a total of 24 species, 16 of which are in *D.* subg. *Holodanaea*, five in *D.* subg. *Danaea* and three in *D.* subg. *Arthrodanaea*. This is consistent with the observation that *D.* subg. *Holodanaea* is also the subgenus with the highest degree of interspecific genetic variation (Keskiniva & al. 2024).

Although many of the new species were originally recognized because they were genetically distinct and formed a well-supported clade, in the vast majority of cases we were able to find diagnostic morphological characteristics for them as well. The most notable exception was the pair *Danaea cuspidata* and *D. cuspidopsis*, between which we have failed to find any morphological differences. However, we still decided to describe the latter as a new species, because both clades are well supported in the phylogeny, they are not closely related, and their distributions are allopatric.

Many of the new species were described based on existing herbarium material, which in some cases was so old that we were unable to include the species in the phylogeny (e.g. *Danaea dilatata*, *D. erosa* and *D. nasua*). In other cases, although species descriptions were based on several specimens, all of these were collected by the same person during a single ecological inventory project, and herbarium work has uncovered no additional specimens (e.g. *D. peruviana* and *D. opaca*).

Many of the new species described here are rare, geographically restricted, and under threat from deforestation. We assigned a conservation status for each new species and believe that six of the 18 new species are threatened, namely *Danaea antioquiana* (VU), *D. nasua* (EN), *D. pumila* (VU), *D. peruviana* (EN), *D. ubatubensis* (CR), and *D. velona* (CR). In addition, we placed four of the new species in the Near Threatened (NT) category (*D. alba*, *D. dilatata*, *D. erosa* and *D. polypinna*). Only eight species were sufficiently widespread and common to be placed in the Least Concern category (LC): *D. ampla*, *D. andina*, *D. cuspidopsis*, *D. elongata*, *D. kessleri*, *D. opaca*, *D. panamensis* and *D. robbinmoranii.* This highlights the importance of poorly known tropical ecosystems for maintaining global biodiversity, and the importance of taxonomic work for recognizing that biodiversity.

We feel that recognizing more *Danaea* species than before and circumscribing them more narrowly has clarified the species delimitations considerably. *Danaea* species are still not easy, but at least they make more intuitive sense than they used to, and the genus appears less messy as a result.

Author contributions

V.K. and H.T. conceptualized the study, developed the methodology, carried out the investigation, and obtained funding for the project. H.T. provided field observations and opinions, V.K. produced and analysed the data from herbarium specimens and DNA samples, drew the illustrations, and wrote the manuscript. Both authors participated in revising the manuscript and approved the final version.

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Four fasta files containing DNA aligments of the four chloroplast loci used for the DNA diagnoses.

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