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Danaea (*Marattiaceae*) keeps diversifying, part 2: phylogeny and identification key for 81 taxa

Venni Keskiniva[1], Hanna Tuomisto[1] & Samuli Lehtonen[2]

Abstract: We have produced a near-complete phylogeny for the neotropical fern genus *Danaea* (*Marattiaceae*). The phylogeny is based on four loci of the chloroplast DNA and shows reconstructions of the evolutionary relationships between 68 of the currently recognized 81 taxa of *Danaea*. A parallel paper (Keskiniva & Tuomisto 2024) draws on this phylogeny to describe 18 new species; here we discuss the phylogeny and its taxonomical implications more broadly. We propose three new synonyms: *D. atlantica* Christenh. & al. (= *D. geniculata*), *D. draco* Christenh. (= *D. polymorpha*), and *D. moralesiana* A. Rojas (= *D. erecta*). On the other hand, we consider *D. jamaicensis* Underw., which has been synonymized before, to be a distinct species. In addition, we propose that *D.* ×*ushana* is a hybrid between *D. simplicifolia* and *D. nigrescens.* We also provide an open-access online key to the 81 taxa. The key is available at https://keys.lucidcentral.org/keys/v4/neo_fern_genus_danaea/.

Keywords: *Danaea*, ferns, *Marattiaceae*, multi-entry key, Neotropics, phylogenetic analyses, species identification, systematics, taxonomic revision

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Introduction

The family *Marattiaceae* consists of often large-sized eusporangiate ferns distributed mainly in moist tropical regions around the world. It represents a very old lineage, splitting from its sister group, the leptosporangiate ferns, in the Early Carboniferous at the latest (Lehtonen & al. 2020; DiMichele & Phillips 2002). Molecular studies have clarified the previously disputed generic classification within the family; six genera are currently recognized. *Danaea* Sm. is the most species-rich of them (Murdock 2008a), and it has been resolved as the sister group to a clade containing the other five genera (Murdock 2008b; Lehtonen & al. 2020).

Danaea has diversified considerably since the year 2000 thanks to increased taxonomical interest, extensive new collections and molecular studies. The Ecuadorian species were revised by Tuomisto and Moran (2001), who recognized 18 species for the country and described 8 of them as new to science. The entire genus was soon revised by Rolleri (2004), who preferred much broader species circumscriptions and recognized only 17 species globally, synonymizing most of the new species that had been described by Tuomisto and Moran (2001). The overview provided by Christenhusz (2010) again opted for narrower species delimitation and recognized 48 species. Since then, 29 new species have been described, two species names synonymized (*D. media* Liebm. = *D. nodosa* (L.) Sm., *D. quebradensis* Christenh. = *D. lucens* A. Rojas), and eight species names raised from synonymy (*D. betancurii* A. Rojas, *D. cuspidata* Liebm., *D. inaequilatera* A. Rojas, *D. lucens* A. Rojas, *D. pterorachis* Christ, *D. sellowiana* C. Presl and *D. tuomistoana* A. Rojas) (Rojas-Alvarado 2013; Christenhusz & al. 2018; Keskiniva & Tuomisto 2022; Keskiniva & Tuomisto 2024).

Many *Danaea* species are morphologically variable, and their characteristics overlap with those of other species. Therefore, species delimitation on purely morphological grounds is difficult and strongly reliant on subjective interpretations and personal preferences. The only molecular phylogeny focusing on *Danaea* so far was published in 2008 and included 31 species (Christenhusz & al. 2008). Here we present a new phylogeny based on chloroplast DNA of 67 species. Many of the species could only be recognized as distinct thanks to the availability of this phylogeny (18 new species are described in the parallel paper Keskiniva & Tuomisto 2024).

Correct species identification is necessary both for scientific purposes, especially in ecological and evolutionary research, and for practical applications, such as con-

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servation planning. Species identification in *Danaea* has been difficult, as the most recent identification key was published over ten years ago (Christenhusz 2010), and it was not accompanied by either illustrations or detailed descriptions of the species. Since then, the taxonomy of *Danaea* has also changed a great deal (Rojas-Alvarado 2013; Christenhusz & al. 2018; Keskiniva & Tuomisto 2022). Here we provide an open-access online key for the entire genus *Danaea*. It is mainly aimed at identifying adult herbarium specimens and covers all 79 species that we currently recognize in the genus, including those described by Keskiniva & Tuomisto (2024). Two proposed hybrids, *D.* ×*plicata* Christ (Moran & Grayum 2018) and *D.* ×*ushana* Christenh. (proposed herein) are also included. The key is based on morphological features that can be seen with the naked eye, and it also includes information about geographical distribution and elevation. All species are illustrated with images of herbarium specimens, and many also with photos from the field.

Material and methods

Taxon sampling for molecular analyses

We reused the sequences from the 58 samples published in Christenhusz & al. (2008) and additionally sequenced 243 new samples specifically for this study, thereby obtaining a dataset of 301 samples of *Danaea*. To increase the resolution at the species level, we also sequenced one new locus, the highly variable *rpl32-trnL* intergenic spacer (Shaw & al. 2007), for most of the specimens. Multiple individuals across the geographical range of each species were sampled when possible (Fig. 1). We were able to obtain genetic data for 68 of the 81 taxa we recognize as well as for several specimens that we were unable to assign to any described species. Our outgroup sampling includes 13 species, with at least one representative of each of the other five genera of *Marattiaceae*. Appendix 1 lists all species with DNA material and includes voucher information and GenBank numbers for each accession.

DNA isolation

DNA was extracted from silica gel dried material with the NucleoSpin Plant II kit (Macherey-Nagel, Germany). Polymerase chain reaction (PCR) amplifications were executed using PuReTaq Ready-To-Go (PCR) Beads (GE Healthcare UK Limited). PCR was used to amplify the plastid genes *rbcL* and *atpB*, and the non-coding *rpl32-trnL* and *trnL-F* regions. The PCR reactions contained approximately 32 µl of solution composed by 25 µl of ddH_2O, 1 µl of each primer and 5 µl of the extraction template. Purification and sequencing of the PCR products was done by Macrogen Inc. (Seoul, South Korea/Amsterdam, the Netherlands). PCR and sequencing primers and protocols are detailed in Table 1.

Phylogenetic analyses

Full dataset of 301 ingroup samples representing 68 named taxa of *Danaea* and one sample for each of 13 outgroup species from the five other genera in the family *Marattiaceae* were used in the phylogenetic analyses. The four loci were aligned separately with MAFFT (Katoh & Standley 2013) on the EMBL-EBI-server (Madeira & al. 2022) with default settings. In addition, the two loci containing gaps (*rpl32-trnL* and *trnL-F*) were aligned with MUSCLE (Edgar 2004) and T-COFFEE (Notredame & al. 2000) on the EMBL-EBI-server with default settings to compare the sensitivity of the results to different alignments. All sequences are from the chloroplast genome and therefore share the same phylogenetic history, so we concatenated them into a single run with SequenceMatrix (Vaidya & al. 2011). Variation in sequence lengths appeared phylogenetically informative, so we used simple gap coding (Simmons & Ochoterena 2000) to code gaps as binary characters with the software FastGaps 1.2 (Borchsenius 2009).

The sequence data was partitioned by the 1st, 2nd, and 3rd positions of the genes and by non-coding regions, and this partition was run with the advanced greedy algorithm in ModelFinder (Kalyaanamoorthy & al. 2017) in IQ-TREE 1.6.12 (Nguyen & al. 2015). The rate of evolution at different loci was estimated with TIGER-rates (Frandsen & al. 2015), and the acquired rate file was fed into RatePartitions (Rota & al. 2018). We tested division factor values in RatePartitions ranging from 1.5 to 3.5, which resulted in differently partitioned alignments. These were fed into ModelFinder and run with the advanced greedy algorithm. The models with the best BIC values were the greedy algorithms partitioned with RatePartitions division factor 3.0. The models with the worst BIC values were the ones partitioned by genes, introns, and codon positions (Appendix 2). The gap-data for each alignment was also analysed with ModelFinder and used in subsequent analysis. The sequence and gap data were combined for the phylogenetic analysis with RAxML-NG 1.1.0 (Kozlov & al. 2019) and the models with the best BIC values were used. RAxML-NG was run with default settings, e.g. 20 maximum likelihood inferences of 10 parsimony and 10 random trees, scaled branch lengths, and the number of bootstrap replications decided by a bootstopping test (Pattengale & al. 2010). Branch supports were assessed with Felsenstein's bootstrap. Tree visualization was done using the packages ape (Paradis & Schliep 2019), ggplot2 (Wickham 2016), ggtree (Yu & al. 2017), and treeio (Wang & al. 2020) in the R environment (R Core Team 2022). The final data matrices and the resulting trees are available in TreeBASE (study number 30768). Since the trees made with the different alignments were almost identical and congruent in all well supported clades, we present and discuss here only the tree with the dataset aligned with MAFFT.

Table 1. Primers used for amplification and sequencing, PCR conditions, and appropriate references.

Primer name	**PCR conditions, primer sequence (5′ → 3′)**	**Reference**
atpB	PCR: 94° 5 min; 35 cycles of 94° 1 min, 45° 1 min, 72° 2 min; 72° 2 min	
ATPB672F	TTGATACGGGAGCYCCTCTWAGTGT	Wolf (1997)
ATPE384R	GAATTCCAAACTATTCGATTAGG	Pryer & al. (2004)
rbcL	PCR: 95° 2 min; 35 cycles of 95° 1 min, 52° 1 min, 72° 1 min; 72° 7 min	
aF	ATGTCACCACAAACAGAGACTAAAGC	Hasebe & al. (1994)
F1379R	TCACAAGCAGCAGCTAGTTCAGGACTC	Wolf & al. (1999)
rpl32-trnL	PCR: 80° 5 min; 35 cycles of 95° 1 min, 50° 1 min, 65° 4 min; 65° 5 min	
rpl32-F	CAGTTCCAAAAAAACGTACTTC	Shaw & al. (2007)
trnL	CTGCTTCCTAAGAGCAGCGT	Shaw & al. (2007)
trnL-F	PCR: 95° 2 min; 35 cycles of 95° 1 min, 52° 1 min, 72° 1 min; 72° 7 min	
c	CGAAATCGGTAGACGCTACG	Taberlet & al. (1991)
f	ATTTGAACTGGTGACACGAG	Taberlet & al. (1991)

Taxonomic work and identification key

Our species delimitation is based on morphological and genetic discontinuities between species, and the aim was to obtain biologically meaningful species that are applicable in and useful for ecological and evolutionary studies. To identify morphological groupings and discontinuities, we have extensively compared actual herbarium specimens (made possible by loans to TUR) and digital images of specimens (available online, provided by herbaria on request or photographed by us during herbarium visits). We applied species names by comparing our material with the original type specimens.

The taxonomic work was based on a total of 3362 herbarium specimens of *Danaea* collected throughout the distribution of the genus (Fig. 1). Herbarium specimens were examined from A, AAU, ASU, BM, BRIT, C, CAY, CHRB, COAH, COL, CR, E, F, FLAS, G, GOET, H, HUA, HUTI, INB, INPA, K, L, LPB, M, MICH, MO, MSC, NO, NY, P, PH, PI, PMA, PRC, QCA, S, SJ, SP, STU, TUB, TUR, U, UC, US, UTCEC, VT, W, WIS, WTU, WVA, YU, and Z. In addition, many of the species have been observed, collected and photographed by us in the field.

The identification key was built in Lucid Builder 4.0 (https://www.lucidcentral.org/, Queensland, Australia), where features are recorded on a table with a column for each taxon and a row for each feature (for quantitative traits) or state of a feature (for qualitative traits). The quantitative traits are represented by minimum and maximum values but can also have separate extreme values. We built the key using all the available material, although some specimens were considered so aberrant that they were not included in the measurements. Otherwise, the atypical specimens were labelled as extreme values in the key.

Although our species delimitations in many cases draw on field experience, we do not have characteristics of fresh material for all species, so they are not used in the key. We also chose to only use characteristics visible to the naked eye, with an emphasis on characteristics that can be seen in herbarium specimens. To keep the key manageable, we focused on the characteristics of adult plants. Juveniles would need to be treated as separate entities from the adults in the key and we do not have observations on juveniles for all species. All species are illustrated with pictures of herbarium specimens and many also with photos of live material from the field.

For species with several fertile specimens available, we used size measurements from fertile specimens only. For species with few or no fertile specimens, we used size measurements from specimens judged to be adult. Consequently, there is some uncertainty in the upper limits of the measurements, as we cannot be sure about the maximum size that the species can attain. Measurements from the earlier species descriptions were verified and supplemented with measurements of available specimens.

For the quantitative measurements, we applied a correction of measurements based on collection intensity. Measurements for species with 20 or more measured specimens were not altered, but we added and subtracted 5% of the minimum and maximum measurements for species with 10–19 measured specimens, and 10% for species with under 10 measured specimens. For elevation, we added and subtracted 100 m for species with 10–19 seen specimens, and 200 m for species with under

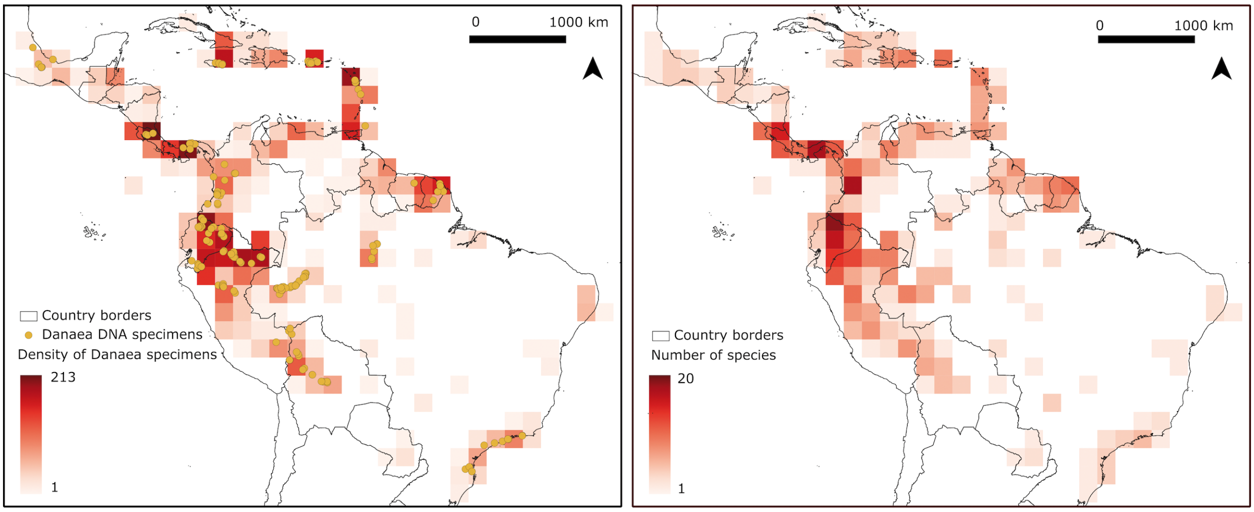

Fig. 1. Distribution in tropical America of *Danaea* specimens used in this study. – A: density of all available material is shown as a count of unique collection numbers per 2° × 2° grid cell, and DNA specimens used in phylogeny are shown as dots; B: number of recognized *Danaea* species per 2° × 2° grid cell.

10 seen specimens. These were added as extreme values.

Because any given geographical area has only a limited number of *Danaea* species, we added geographical region as a separate character in the key. One of the species, *D. excurrens*, was given two entries in the key, as it contains two forms that are morphologically too different to be keyed out together.

Results

Phylogeny and species delimitation

In our analyses, *Danaea* formed a clade consisting of three well supported subclades (Fig. 2). These correspond to the three subgenera as outlined in Christenhusz (2010): *D.* subg. *Arthrodanaea* C. Presl (Fig. 3), *D.* subg. *Danaea* (Fig. 4) and *D.* subg. *Holodanaea* C. Presl (Fig. 5). Each subgenus consisted of several well-supported subclades, many of which could be referred to a known species. However, many others could not, and those well-supported clades that had adequate material were described as new species (Keskiniva & Tuomisto 2024). In the end, we decided to assign the 301 sequenced samples to 68 recognized taxa and to leave 18 samples unidentified for the time being. The latter presumably represent several undescribed species, but we deemed the material insufficient to describe them at the present time.

The DNA sequences had 7 % missing data, with most data missing for the least informative locus (*atpB*: 12 %) and the least missing data for the two most informative loci (*rpl32-trnL*: 7 %, *trnL-F*: 1 %). Especially the newly sequenced locus *rpl32-trnL* was more variable than the other loci and helped to improve the resolution of the phylogeny, although a few problematic groups still remain.

Below we describe the phylogeny in more detail and discuss its contribution to our taxonomic decisions especially in the most difficult species complexes. We also provide a full list of accepted species and their synonyms by subgenus.

Subgeneric classification of *Danaea*

I. *Danaea* subg. *Arthrodanaea* C. Presl (Presl 1845)
Species:
Danaea leprieurii Kunze, type
D. alansmithii Tuomisto & Keskiniva
D. antillensis Christenh.
D. arbuscula Christenh. & Tuomisto (= *D. elliptica* var. *crispula* Rosenst.)
D. bipinnata Tuomisto
D. danaëpinna Christenh.
D. dilatata Keskiniva & Tuomisto
D. geniculata Raddi (= *D. atlantica* Christenh. & al.)
D. lingua-cervina Christenh. & Tuomisto
D. opaca Keskiniva & Tuomisto
D. polymorpha Lepr. ex Baker (= *D. draco* Christenh., *D. oligosora* Fourn. ex Baker)
D. simplicifolia Rudge
D. trifoliata Rchb. ex Kunze (≡ *D. simplicifolia var. trifoliata* (Rchb. ex Kunze) T. Moore)
D. trinitatensis Christenh. & Tuomisto
D. ulei Christ
D. ×ushana Christenh.
D. zamiopsis Christenh. & Tuomisto

We were able to include 15 species of *Danaea* subg. *Arthrodanaea* in the phylogeny, only lacking DNA for two species (*D. alansmithii* and *D. dilatata*). Out of the three subgenera, *Arthrodanaea* (Fig. 3) has the smallest number of species and generally also the least amount of genetic variation. There are some well supported clades, however: *D. simplicifolia* + *D. ushana* Christenh. (BP =

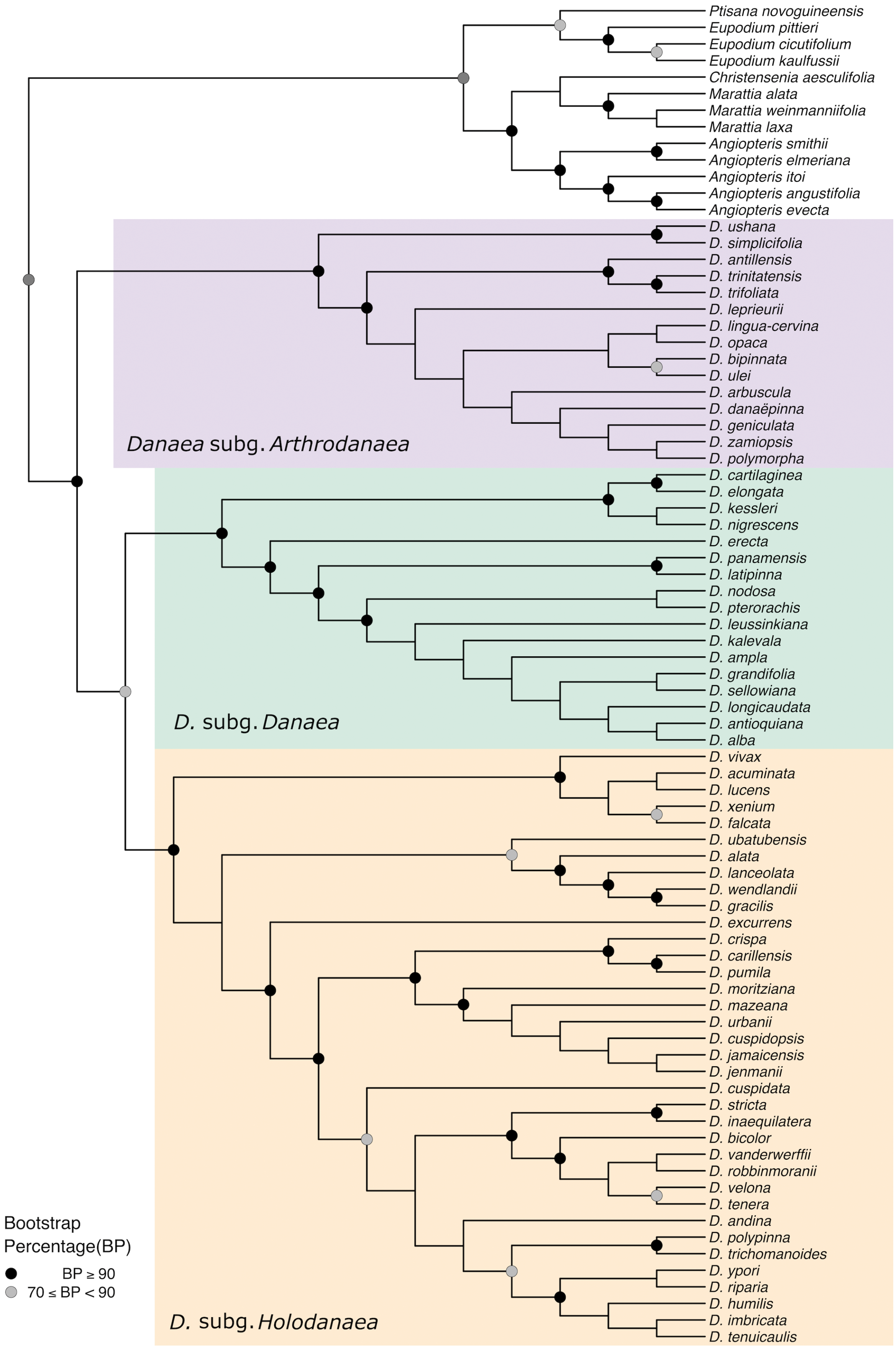

Fig. 2. Simplified cladogram of *Marattiaceae*. Taxa of uncertain identity and duplicate specimens of each species pruned using drop.tip-function in ape package (Paradis & Schliep 2019) in R environment (R Core Team 2022).

100); *D. antillensis* + *D. trinitatensis* + *D. trifoliata* (BP = 100); and *D. bipinnata* + *D. ulei* Christ (BP = 90). Six of the species in the phylogeny form clades with a bootstrap support > 80: *D. antillensis* (BP = 100), *D. danaëpinna* (BP = 82), *D. leprieurii* (BP = 86), *D. opaca* (BP = 87), *D. trifoliata* (BP = 87), and *D. trinitatensis* (BP = 84). Two species are represented by only one specimen each, so more material is needed to test their genetic coherence (*D. lingua-cervina* and *D. zamiopsis*).

The biggest problem that remains to be solved is centred around *Danaea arbuscula.* We have opted for a rather broad circumscription of this species, which has led to it becoming paraphyletic: *D. geniculata*, *D. danaëpinna*, *D. polymorpha* and *D. zamiopsis* are embedded in different parts of the same clade. In the case of *D. danaëpinna*, it is both monophyletic and morphologically distinct, while *D. polymorpha* and *D. zamiopsis* are morphologically identifiable, but the small number of DNA samples does not provide a proper test of their genetic distinctness. As to *D. geniculata*, the material from the Brazilian Atlantic coast (where the type is from) is both genetically and morphologically distinct from the type of *D. arbuscula* from northern Peru, but the relationships are complicated especially among the samples from the Amazonian side of the Andes (from Bolivia to Ecuador) and the Caribbean (including Central America). It is quite possible that both *D. arbuscula* and *D. geniculata* are species complexes, but we were unable to sort them out with the material at hand. In practice, we solved the problem by ignoring the phylogeny and assigning to *D. arbuscula* all specimens whose sterile leaves have relatively thick lamina texture and (dark) brownish colour and the fertile pinnae are elliptic with (long-)attenuate bases and apices. To *D. geniculata* we assigned those specimens whose sterile leaves have relatively thin lamina texture and greyish to bluish green colour and the fertile pinnae are lanceolate with truncate bases and acute to obtuse apices.

The placement of *Danaea ushana* in the phylogeny was a complete surprise, because until now it has been thought to belong to *D.* subg. *Danaea*: it has a creeping dorsiventral rhizome (vs erect and radially arranged in all species of *D.* subg. *Arthrodanaea*), no nodes on the petiole (vs present in almost all specimens of *D.* subg. *Arthrodanaea*) and also its pinnae look more like *D.* subg. *Danaea* than *D.* subg. *Arthrodanaea*. Nevertheless, both DNA accessions of *D. ushana* were firmly embedded within the *D. simplicifolia* clade, which suggests that they might be hybrids. The only species of *D.* subg. *Danaea* growing in French Guiana alongside *D. simplicifolia* and *D. ushana* is *D. nigrescens* Jenman. We hereby propose that *D.* ×*ushana* is a hybrid between *D. simplicifolia* and *D. nigrescens*.

Although *Danaea ulei* and *D. bipinnata* did not separate cleanly into two clades, their morphological differences are so big that we have no doubt they represent different species.

The Caribbean material that had previously been identified as *D. geniculata* formed a well-supported clade as sister to *D. trifoliata*. After comparing the voucher specimens to the material from Trinidad and Tobago, we concluded that the material from Mexico, Puerto Rico and Jamaica should be identified as *D. trinitatensis*. This resulted in a large range extension for *D. trinitatensis* from a single island (Trinidad) to much of the Caribbean, and a corresponding range contraction for *D. geniculata*.

We did not have genetic material of the type of *Danaea atlantica*, but we did have DNA of two paratypes (*M. J. M. Christenhusz 4937* and *4911*). These grouped with *D. geniculata* in the phylogeny. We were unable to find reliable morphological characteristics to separate between these two species in the herbarium and, therefore, treat *D. atlantica* as a synonym of *D. geniculata.* We also failed to find any systematic difference between *D. polymorpha* and *D. draco* Christenh. and treat *D. draco* as a synonym of *D. polymorpha*.

II. *Danaea* Sm. subg. *Danaea*
Species:
Danaea nodosa (L.) Sm., type (= *D. angustifolia* C. Presl, *D. elata* Liebm, *D. elliptica* Sm., *D. elliptica* var. *major* Jenman, *D. elliptica* var. *repens* Jenman, *D. longifolia* Desv., *D. media* Liebm., *D. nodosa* var. *angustifolia* (C. Presl) T. Moore, *D. nodosa* var. *longifolia* Hassl.)
D. alba Keskiniva & Tuomisto
D. ampla Keskiniva & Tuomisto
D. antioquiana Keskiniva & Tuomisto
D. cartilaginea Christenh. & Tuomisto
D. elongata Keskiniva & Tuomisto
D. epilithica A. Rojas
D. epiphytica Christenh.
D. erecta Tuomisto & R. C. Moran (= *D. moralesiana* A. Rojas)
D. grandifolia Underw.
D. kalevala Christenh.
D. kessleri Keskiniva & Tuomisto
D. latipinna Tuomisto & R. C. Moran
D. leussinkiana Christenh.
D. longicaudata Tuomisto
D. megaphylla A. Rojas
D. nigrescens Jenman
D. panamensis Keskiniva & Tuomisto
D. pterorachis Christ
D. sellowiana C. Presl (= *D. cordata* Fée, *D. dubia* C. Presl)

Danaea subg. *Danaea* (Fig. 4) splits into two genetically distinct clades; an Amazonian clade (BP = 99), and a clade occurring everywhere else (BP = 99). Inside the Amazonian clade, *D. elongata* + *D. cartilaginea* form a well-supported clade (BP = 100), as do *D. kessleri* + *D. nigrescens* (BP = 87). In the extra-Amazonian clade, *D. erecta* forms a sister to a well-supported clade (BP = 100)

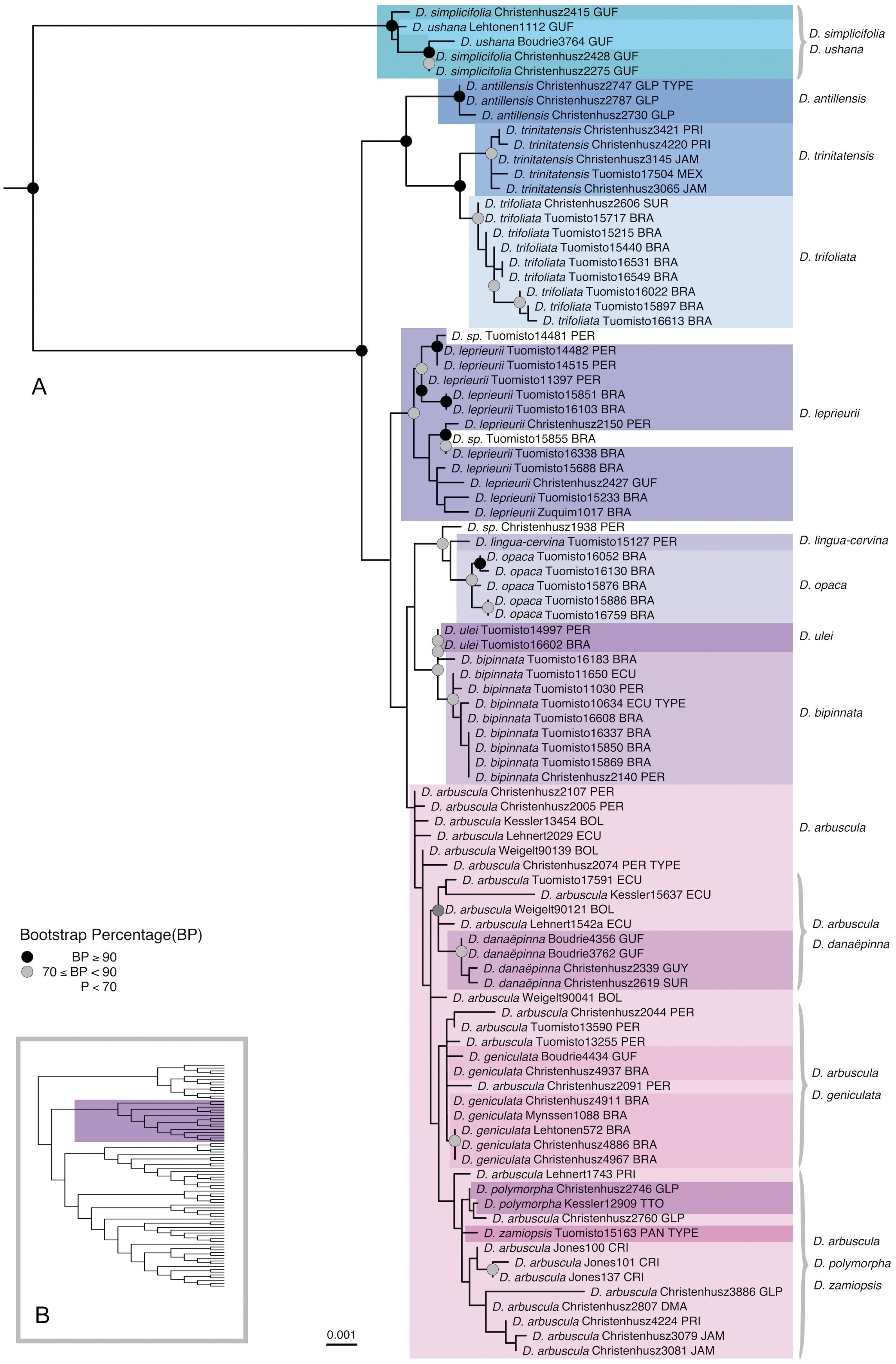

Fig. 3. A: maximum likelihood tree of *Danaea* subg. *Arthrodanaea*; B: placement of *D.* subg. *Arthrodanaea* within *Marattiaceae*.

containing the rest of the subgenus in two well supported clades, one containing *D. latipinna* + *D. panamensis* (BP = 91), another containing *D. nodosa* + the remaining nine species of *D.* subg. *Danaea* (BP = 96).

We were able to include 17 species of *Danaea* subg. *Danaea* in the phylogeny, but for three species we did not have DNA (*D. epilithica*, *D. epiphytica*, and *D. megaphylla*). Eight of the species in the phylogeny form clades with a bootstrap support > 70 (*D. alba* (BP = 89), *D. ampla* (BP = 81), *D. elongata* (BP = 78), *D. erecta* (BP = 100), *D. kalevala* (BP = 71), *D. latipinna* (BP = 82), *D. leussinkiana* (BP = 96), and *D. panamensis* (BP = 91)), two are represented by only one specimen in the phylogeny (*D. antioquiana* and *D. longicaudata*), and two form clades with a bootstrap support < 70 (*D. cartilaginea* and *D. sellowiana*). Three species pairs are somewhat ambiguous in the phylogeny, and these include the remaining five species (*D. nodosa* and *D. pterorachis*; *D. grandifolia* and *D. sellowiana*; *D. nigrescens* and *D. kessleri*).

We do not have DNA of *Danaea nodosa* from Hispaniola, from where the species was described, but the material from Jamaica and Puerto Rico is morphologically very similar, so we consider it justified to assume that they represent true *D. nodosa*. These samples form a clade with some of the Costa Rican and Mexican material that would traditionally have been identified as *D. nodosa* but has recently been assigned to *D. media*. Some of the Costa Rican specimens have nodes on the petiole and rhizomes with leaf bases in 3–5 rows, both characteristics that conflict with typical *D. nodosa* (no nodes on the petiole, rhizomes with leaf bases in exactly two rows). We assign these Costa Rican specimens to *D. pterorachis*, as scrutiny of the type material suggested that they do not conform with *D. media* and *D. elata* after all (Keskiniva & Tuomisto 2024). Unfortunately, *D. nodosa* and *D. pterorachis* do not separate to different clades, so further studies are needed to figure out their relationship.

All material of *Danaea* subg. *Danaea* from the Atlantic coastal forests of Brazil groups into one clade, which morphologically conforms with *D. sellowiana*, described from the same area. At the base of this clade is a polytomy consisting of all the specimens of *D. grandifolia*. Even though the latter does not form a clade, the two are morphologically clearly distinct (rhizome with leaf bases in two rows vs several rows, elliptic often slightly falcate pinnae vs parallel-sided straight pinnae, acuminate vs cuspidate pinna apices).

Within the Amazonian clade, the oldest available name is *Danaea nigrescens*, which we apply to the large clade containing material from the Guianas, as the species was described from that region. This species is remarkably widespread in the Amazonian lowlands and is genetically rather uniform, although three samples are separated into a polytomy with the closely related *D. kessleri*. *Danaea nigrescens* and *D. kessleri* were monophyletic with one of the alignments, albeit with poor support. Given that the two are not too difficult to tell apart based on their general appearance, we considered the evidence sufficient to recognize them as separate species.

We decided to treat *Danaea moralesiana* (from Costa Rica) as a synonym of *D. erecta* (widespread in the northern Andes) although we have no genetic material and have not seen the type of *D. moralesiana.* However, we have seen a picture of a paratype (*A. Rojas 899*, CR) and another specimen collected near the type locality (*J. T. Mickel 3049*, NY). The protologue of *D. moralesiana* provides no comparison with *D. erecta* and we were not able to find any separating morphological characters between these two.

III. *Danaea* subg. *Holodanaea* C. Presl (Presl 1845) (= *Heterodanaea* C. Presl; Presl 1845)

Species:

Danaea alata Sm., type (= *D. fendleri* Underw., *D. stenophylla* Kunze)
D. acuminata Tuomisto & R. C. Moran
D. andina Keskiniva & Tuomisto
D. betancurii A. Rojas
D. bicolor Tuomisto & R. C. Moran
D. carillensis Christ
D. chococola Christenh.
D. crispa Endrés & Rchb. f.
D. cuspidata Liebm (= *D. muenchii* Christ)
D. cuspidopsis Keskiniva & Tuomisto
D. erosa Keskiniva & Tuomisto
D. excurrens Rosenst. (= *D. moritziana* var. *brasiliensis* Rosenst., *D. muelleriana* Rosenst., *D. paraguariensis* Christ)
D. falcata Tuomisto & R. C. Moran
D. gracilis Tuomisto & Keskiniva
D. humilis Spruce ex T. Moore (= *D. serrulata* Baker)
D. imbricata Tuomisto & R. C. Moran
D. inaequilatera A. Rojas
D. jamaicensis Underw.
D. jenmanii Underw. (= *D. wrightii* Underw.)
D. lanceolata Tuomisto & Keskiniva
D. lucens A. Rojas (=*D. quebradensis* Christenh.)
D. mazeana Underw.
D. moritziana C. Presl (≡ *D. alata* var. *moritziana* (C. Presl) T. Moore)
D. nasua Keskiniva & Tuomisto
D. oblanceolata Stolze
D. peruviana Keskiniva & Tuomisto
D. ×*plicata* Christ
D. polypinna Keskiniva & Tuomisto
D. pumila Keskiniva & Tuomisto
D. riparia Christenh. & Tuomisto
D. robbinmoranii Keskiniva & Tuomisto
D. stricta Tuomisto & Keskiniva
D. tenera C. V. Morton
D. tenuicaulis Tuomisto & Keskiniva
D. trichomanoides T. Moore
D. tuomistoana A. Rojas
D. ubatubensis Keskiniva & Tuomisto

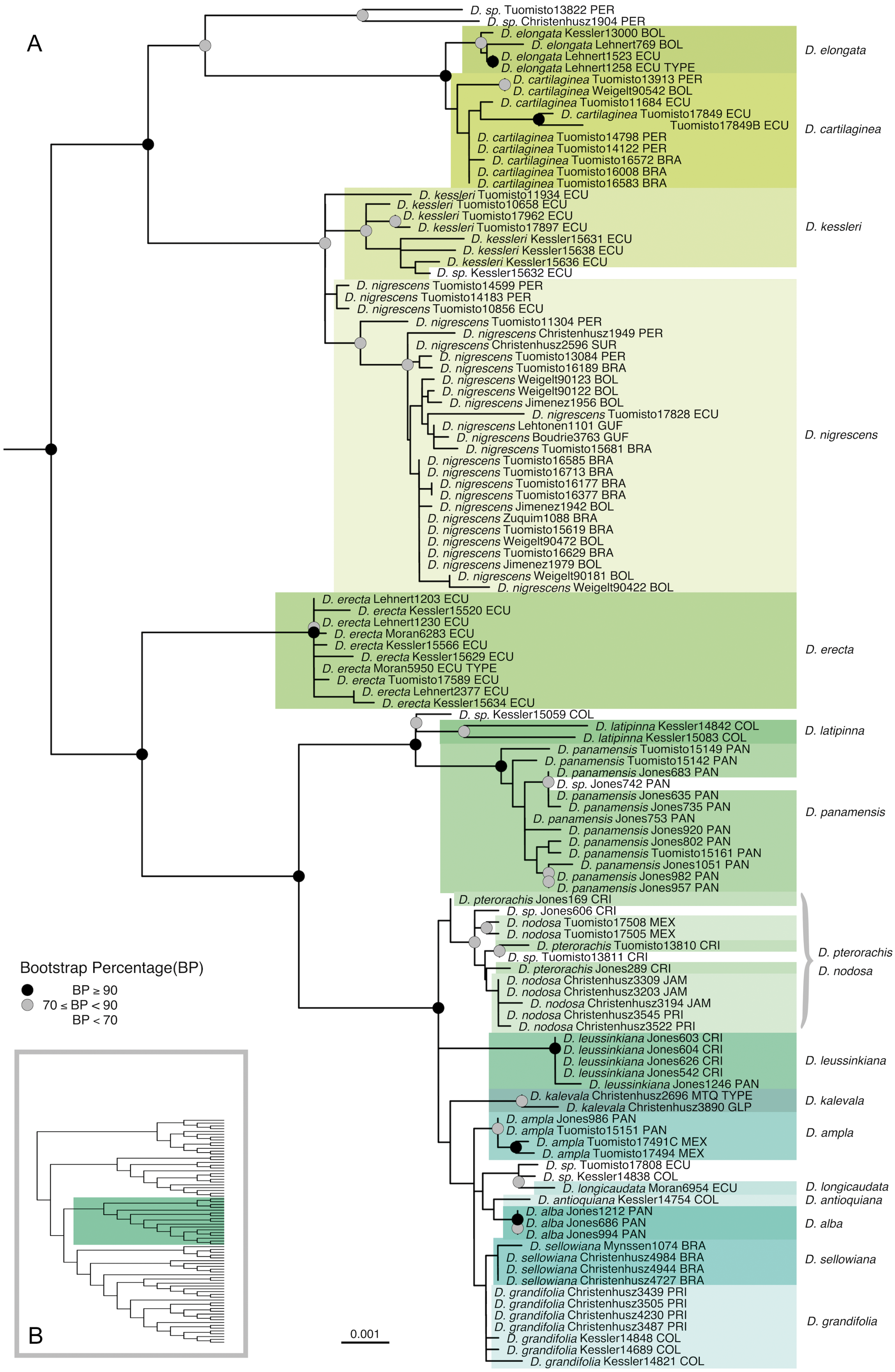

Fig. 4. A: maximum likelihood tree of *Danaea* subg. *Danaea*; B: placement of *D.* subg. *Danaea* within *Marattiaceae*.

D. urbanii Maxon
D. vanderwerffii Tuomisto & Keskiniva
D. velona Keskiniva & Tuomisto
D. vivax Christenh. & Tuomisto
D. wendlandii Rchb. f.
D. xenium Christenh. & Tuomisto
D. ypori Christenh.

Danaea subg. *Holodanaea* (Fig. 5) has the highest number of species and generally the largest genetic differences between species and clades. We were able to include 36 species of *D.* subg. *Holodanaea* in the phylogeny but did not have DNA for 7 described species and one proposed hybrid (*D. betancurii*, *D. chococola*, *D. erosa*, *D. nasua*, *D. oblanceolata*, *D. peruviana*, *D. tuomistoana*, and *D.* ×*plicata*).

Of the 36 species in the phylogeny, ten form clades with a bootstrap support > 70: *Danaea alata* (BP = 100), *D. andina* (BP = 100), *D. bicolor* (BP = 97), *D. crispa* (BP = 98), *D. cuspidata* (BP = 100), *D. excurrens* (BP = 100), *D. lanceolata* (BP = 75), *D. pumila* (BP = 79), *D. vanderwerffii* (BP = 90), and *D. wendlandii* (BP = 100). Three formed clades but with bootstrap support < 70 (*D. imbricata*, *D. mazeana*, and *D. tenuicaulis*), nine were resolved as not monophyletic, and 14 are represented by only a single specimen. The main observations for each of the six main clades of the phylogeny are described below.

Danaea acuminata clade

This is a well-supported clade (BP = 100) of five species, all of which were described in 2001–2010: *Danaea acuminata*, *D. falcata*, *D. lucens*, *D. vivax*, and *D. xenium*. The species are relatively similar in general appearance: creeping rhizomes, concolorous laminae that dry dark brown, and serrate pinna apices. The other clades in *Holodanaea* are more heterogeneous in appearance. Geographically this clade is concentrated to the Amazonian lowlands adjacent to the Andes in Peru and Ecuador, with one species (*D. lucens*) between the Cordilleras in Colombia.

Danaea alata clade

This is a moderately supported clade (BP = 72) that contains species from all corners of the wet American tropics: the Atlantic coastal forests of Brazil (*Danaea ubatubensis*), the Lesser Antilles and the Venezuelan coast (*D. alata*), Central America (*D. wendlandii*), the Pacific coast of Colombia and Ecuador (*D. gracilis*), and western Amazonia (*D. lanceolata*).

Danaea wendlandii, *D. gracilis*, and *D. lanceolata* form a well-supported clade (BP = 100) and are rather uniform in appearance, being rather small and having lanceolate laminae with narrow pinnae and terminal buds. *Danaea alata* and *D. ubatubensis* are clearly larger species, although *D. ubatubensis* shares the propensity to produce terminal buds. Three of the species were strongly supported as monophyletic, but *D. gracilis* was resolved as paraphyletic.

Danaea excurrens clade

Danaea excurrens was described from the Atlantic rainforests of Brazil, and our DNA samples from that area form a strongly supported clade (BP = 100) with similar-looking material from Bolivia. The DNA samples from Brazil represent both individuals with spathulate pinnae that conform with the type of the species and individuals that have a more classic *Holodanaea* appearance. Therefore, we have concluded that both forms belong to the same species, even though we have not discovered any obvious reason for such heterophylly.

Danaea crispa clade

This is a well-supported (BP = 100) clade containing three small-statured species from Central America that we would never have grouped together based on their morphology. One of them is unique in having simple, bicolorous laminae (*Danaea carillensis*), one resembles *D. humilis* of the *D. cuspidata* clade in having many small, bicolorous pinnae (*D. pumila*), and the third one is similar to *D. gracilis* of the *D. alata* clade in having dark green laminae that are so thin as to be translucent (*D. crispa*). The *D. crispa* clade forms a well-supported clade (BP = 93) with the *D. moritziana* clade.

Danaea moritziana clade

This clade consists of six species from the Caribbean region that are similar in having bicolorous laminae, large number of pinnae and clearly serrate pinna apices: *Danaea moritziana* (Coastal Venezuela and adjacent Colombia), *D. mazeana* (Lesser Antilles), *D. urbanii* (Greater Antilles), *D. cuspidopsis* (Costa Rica to northern Andes), *D. jamaicensis* (Greater Antilles), and *D. jenmanii* (Greater Antilles). They form a well-supported clade (BP = 98) with relatively small interspecific genetic differences.

The name *Danaea moritziana* C. Presl has traditionally been applied in a very wide sense. Our phylogenetic results suggest that the species should be circumscribed more narrowly. Our interpretation of the phylogenetic position of *D. moritziana* is based on material from the Caribbean coast of Colombia that morphologically matches the type of *D. moritziana* from Venezuela. Unfortunately, we do not have DNA from the type locality, but this interpretation leads to a morphologically coherent species whose distribution is limited to the northernmost parts of Venezuela and Colombia. Notably, none of the Mexican *Holodanaea* samples were resolved to the *D. moritziana* clade, strongly supporting the recognition of *D. cuspidata* as a distinct species. The situation was complicated by the fact that some Costa Rican and Colombian specimens were deeply embedded in the *D. moritziana* clade even though they were morphologically very similar to *D. cuspidata.* These have now been described as *D. cuspidopsis* (Keskiniva & Tuomisto 2024).

Christenhusz (2010) synonymized *Danaea jamaicensis* under *D. mazeana*, but the phylogeny shows that *D.*

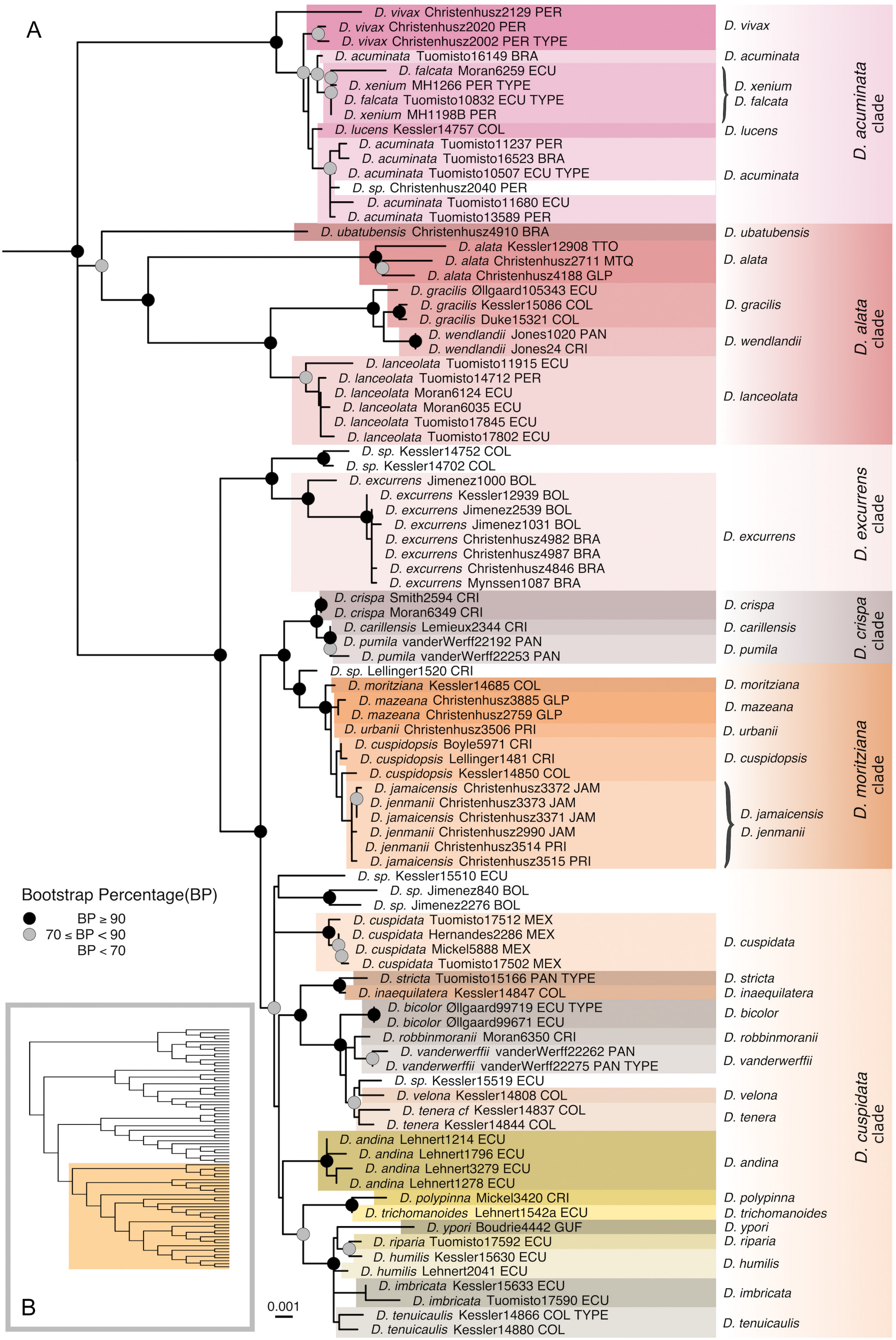

Fig. 5. A: maximum likelihood tree of *Danaea* subg. *Holodanaea* with major clades named; B: placement of *D.* subg. *Holodanaea* within *Marattiaceae*.

mazeana forms a clade of its own at the base of the *D. moritziana* clade, whereas *D. jamaicensis* groups with *D. jenmanii*. The latter two species are intermingled in the phylogeny, but we decided to keep them as separate species because of their morphological differences: *D. jenmanii* is generally smaller and has fewer pairs of shorter pinnae, shorter pinna apices, more scaly petioles and rachises, and the terminal pinna (or a part thereof) is replaced by a bud (vs terminal pinna usually present in *D. jamaicensis*). In our interpretation, *D. mazeana* is restricted to the Lesser Antilles, whereas *D. jamaicensis* and *D. jenmanii* occur in the Greater Antilles. The material from Lesser Antilles that we identified to *D. mazeana* has generally narrower pinnae and broader pinna apices, and they dry to a darker colour than *D. jamaicensis.*

Danaea cuspidata **clade**

This moderately supported (BP = 77) clade is a mixture of large and small plants, translucent and thick laminae and distributions from Mexico to Bolivia and the Guianas (including *Danaea ypori*, the only species in *D.* subg. *Holodanaea* with a Guianan distribution) but no species from the Caribbean islands.

Both *Danaea cuspidata* (from Mexico) and the newly described *D. andina* (from Ecuador) formed strongly supported clades within the *D. cuspidata* clade, confirming their distinctness from *D. moritziana*. However, their positions within the *D. cuspidata* clade varied between analyses done with different alignments and was not well resolved in any of them. In general, the species in this clade were supported by the phylogenetic results, although most of them had too few samples for their coherence to be properly tested. The morphologically relatively similar *D. imbricata* and *D. trichomanoides* were resolved to different subclades, supporting their recognition as distinct species.

Species incertae sedis

Danaea augusti H. Karst. ex Kunze
D. intermedia J. Sm.
D. nodosa var. *intermedia* J. Sm. ex Hassl.

Excluded species

Danaea evecta Spreng. = *Angiopteris evecta* (G. Forst.) Hoffm.
D. paleacea Raddi = *Bolbitis serratifolia* (Mertens) Schott

Identification key

An open-access online identification key to the 81 taxa of *Danaea* is available at https://keys.lucidcentral.org/keys/v4/neo_fern_genus_danaea/.

The list of features contains a total of 48 morphological characters. Twenty of these have negative dependencies (they disappear if an incongruent feature has been selected) and four have positive dependencies (they appear if a specific other feature has been selected). Both quantitative measurements and qualitative descriptions often overlap among species, even when they are not closely related, but a combination of traits should narrow the search down to one species when all necessary traits are present. However, often all traits are not present. For example, fertile leaves or rhizomes may be crucial to separate between two otherwise similar species, but information of them is often missing in herbarium specimens.

In general, the most useful morphological features for identifying *Danaea* species are leaf and pinna size, number of pinna pairs, number of petiole nodes, rhizome habit, fertile pinna shape, adaxial vs abaxial side colour, and the margins of the pinna apices.

Even though most species can (tentatively) be keyed out with morphological features alone, in practice the most effective way to start the identification process is to choose the geographical region where the specimen comes from. This is because the number of species that is known (or expected) to occur in any one region is almost always fewer than 20 and very often fewer than 10 (out of the total of 79 species and 2 hybrids). The main exceptions are Colombia (33 species), Ecuador (26 species), Panama (21 species), and Peru (21 species), all of which have both lowland and montane species. In the case of Colombia and Ecuador, the key also allows making a choice between the Pacific and the Amazonian side of the Andes, which reduces the number of relevant species to at most 18 per region.

Discussion

Most of the specimens in the genus *Danaea* have at some point been identified to one of three broadly distributed and variable species: *D. moritziana* in *D.* subg. *Holodanaea*, *D. nodosa* in *D.* subg. *Danaea*, and *D. elliptica* (which was synonymized and thereafter replaced by *D. geniculata*) in *D.* subg. *Arthrodanaea*. However, some species have been widely recognized due to their distinctive morphology, for example *D. simplicifolia* and *D. carillensis* (which have simple leaves), *D. alata* (which has simple veins), *D. crispa* (which has crispate pinna margins) and *D. trichomanoides* (which has very small leaves). In the phylogeny some of these do emerge as genetically distant from their nearest relatives (*D. simplicifolia*, *D. alata*) but others do not (*D. carillensis*, *D. crispa*, *D. trichomanoides*). On the other hand, some species that emerge in strongly supported clades have never been recognized as distinct before (e.g. *D. andina*, *D. elongata*, and *D. panamensis*). In addition, species that are morphologically similar can be resolved to entirely different parts of the molecular phylogeny (e.g. *D. antillensis* and *D. arbuscula* in *D.* subg. *Arthrodanaea*; *D. elongata* and *D. nodosa* in *D.* subg. *Danaea*; *D. humilis* and *D. pumila* as well as *D. cuspidata* and *D. cuspidopsis* in *D.* subg. *Holodanaea*).

The conclusion is that taxonomy based on morphology alone can be misleading in this genus. With the help of molecular data, we have now been able to divide some of the previously heterogeneous species into morphologically more coherent units that also make biogeographical sense. For example, we have split the complex formerly known as *Danaea moritziana* to about ten species. Some of these have overlapping distributions, so it is no wonder they have been identified to the same species, but genetic data now show that they are not closely related. Examples include *D. ubatubensis* and *D. excurrens* in the Atlantic coast of Brazil, *D. cuspidopsis* and *D. andina* in Ecuador, and *D. cuspidopsis*, *D. robbinmoranii*, and *D. vanderwerffii* in Costa Rica and Panama. After revisiting the samples with new information from the phylogeny, we were able to find morphological differences that allow separating between most of the genetically distinct taxa, at least the ones that are sympatric. We think that the increased morphological and genetic coherence of the recognized species gives a good foundation for future ecological and evolutionary studies, and that this by far outweighs the inconvenience of the large amount of splitting we have done.

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, V.K. and S.L. produced and analysed the data from DNA samples, and V.K. wrote the manuscript. All authors participated in revising the manuscript and have approved the final version.

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Appendix 1

Specimens included in the phylogenetic analysis in this study. Species names, voucher information, geographical origin and GenBank accession numbers are listed. Herbarium codes are according to Thiers (2023+).

Species	**Voucher information**	**Geographical origin**	**GenBank accession numbers**			
			atpB	***rbcL***	***rpl32***	***trnL-F***
Angiopteris angustifolia C. Presl	*Hortus Botanicus Leiden, acc. Nr. 8088* (TUR)	cultivated	EU221678	EU221738	–	EU221806
A. elmeriana Copel.	*Karger 210* (Z)	Philippines	OR565974	OR565975	OR565976	OR565977
A. evecta (G. Forst.) Hoffm.	*Hortus Botanicus Leiden, acc. nr. 960127* (TUR)	Malaysia	EU221679	EU221740	–	EU221808
A. itoi (Shieh) J. M. Camus	*Walker 356* (UC)	Taiwan	EU221681	EU221742	–	EU221810
A. smithii Racib.	*Whitehead 338* (UC)	Malaysia	EU221734	EU221801	–	EU221871
Christensenia aesculifolia (Blume) Maxon	*Walker 354* (UC)	Malaysia	EU221682	EU221743	–	EU221811
Danaea acuminata Tuomisto & R. C. Moran	*Tuomisto 10507* (AAU, F, K, MO, NY, QCA, QCNE, TUR, U, UC)	Ecuador	EU221683	EU221744	OR550916	EU221812
D. acuminata	*Tuomisto 11237* (AMAZ, TUR)	Peru	–	–	OR550917	OR550674
D. acuminata	*Tuomisto 11680* (QCA, QCNE, TUR)	Ecuador	–	OR541672	OR550918	OR550675
D. acuminata	*Tuomisto 13589* (CUZ, TUR, UC, USM)	Peru	OR541133	OR541673	OR550919	OR550676
D. acuminata	*Tuomisto 16149* (SP, TUR)	Brazil	OR541134	OR541674	OR550920	OR550677
D. acuminata	*Tuomisto 16523* (SP, TUR)	Brazil	OR541135	OR541675	OR550921	OR550678
D. alata Sm.	*Christenhusz 2711* (TUR)	Martinique	EU221684	EU221745	OR550922	EU221813
D. alata	*Christenhusz 4188* (TUR)	Guadeloupe	OR541136	–	OR550923	OR550679
D. alata	*Kessler 12908* (TUR)	Trinidad and Tobago	EU221685	EU221746	–	EU221814
D. alba Keskiniva & Tuomisto	*Jones 1212* (PMA, TUR)	Panama	OR541137	OR541676	OR550924	OR550680
D. alba	*Jones 686* (TUR)	Panama	OR541138	OR541677	OR550925	OR550681
D. alba	*Jones 994* (TUR, US)	Panama	OR541139	OR541678	OR550926	OR550682
D. ampla Keskiniva & Tuomisto	*Jones 986* (TUR, US)	Panama	OR541140	OR541679	OR550927	OR550683
D. ampla	*Tuomisto 15151* (PMA, TUR, UC)	Panama	OR541141	OR541680	OR550928	OR550684
D. ampla	*Tuomisto 17491* (TUR, UC, XAL, Z)	Mexico	OR541142	OR541681	OR550929	OR550685
D. ampla	*Tuomisto 17494* (TUR, XAL)	Mexico	OR541143	OR541682	OR550930	OR550686
D. andina Keskiniva & Tuomisto	*Lehnert 1214* (GOET, QCA, TUR)	Ecuador	OR541144	OR541683	OR550931	OR550687
D. andina	*Lehnert 1278* (GOET, UC)	Ecuador	OR541145	OR541684	–	OR550688
D. andina	*Lehnert 1796* (STU)	Ecuador	OR541146	OR541685	OR550932	OR550689
D. andina	*Lehnert 3279* (VT)	Ecuador	OR541147	OR541686	OR550933	OR550690

D. antillensis Christenh.	*Christenhusz 2730* (TUR)	Guadeloupe	EU221686	EU221747	–	EU221815
D. antillensis	*Christenhusz 2747* (BM, P, TUR, UC)	Guadeloupe	EU221687	EU221748	OR550934	EU221816
D. antillensis	*Christenhusz 2787* (TUR)	Guadeloupe	–	OR541687	–	OR550691
D. antioquiana Keskiniva & Tuomisto	*Kessler 14754* (TUR)	Colombia	OR541148	OR541688	OR550935	OR550692
D. arbuscula Christenh. & Tuomisto	*Christenhusz 2005* (AMAZ, TUR, USM)	Peru	OR541149	–	OR550936	OR550693
D. arbuscula	*Christenhusz 2044* (AMAZ, TUR, USM)	Peru	OR541150	–	OR550937	OR550694
D. arbuscula	*Christenhusz 2074* (AAU, AMAZ, B, BM, K, L, NY, P, TUR, UC, USM)	Peru	EU221688	EU221749	OR550938	EU221817
D. arbuscula	*Christenhusz 2091* (AMAZ, TUR, USM)	Peru	OR541151	OR541689	OR550939	OR550695
D. arbuscula	*Christenhusz 2107* (AMAZ, TUR, USM)	Peru	EU221728	EU221794	OR550940	EU221863
D. arbuscula	*Christenhusz 2760* (TUR)	Guadeloupe	–	–	OR550941	EU221818
D. arbuscula	*Christenhusz 2807* (TUR)	Dominica	OR541152	OR541690	OR550942	OR550696
D. arbuscula	*Christenhusz 3079* (IJ, TUR)	Jamaica	OR541153	OR541691	OR550943	OR550697
D. arbuscula	*Christenhusz 3081* (IJ, TUR)	Jamaica	OR541154	–	OR550944	OR550698
D. arbuscula	*Christenhusz 3886* (GUAD, TUR)	Guadeloupe	OR541155	OR541692	OR550945	OR550699
D. arbuscula	*Christenhusz 4224* (TUR, UPR)	Puerto Rico	OR541156	–	OR550946	OR550700
D. arbuscula	*Jones 100* (CR, TUR)	Costa Rica	EU221698	EU221760	OR550947	EU221829
D. arbuscula	*Jones 101* (CR, TUR)	Costa Rica	EU221699	EU221761	OR550948	OR550701
D. arbuscula	*Jones 137* (CR, TUR)	Costa Rica	EU221700	EU221762	OR550949	EU221830
D. arbuscula	*Kessler 13454* (GOET, TUR, UC)	Bolivia	OR541157	OR541693	–	OR550702
D. arbuscula	*Kessler 15637* (TUR)	Ecuador	OR541158	OR541694	OR550950	OR550703
D. arbuscula	*Lehnert 1542a* (TUR)	Ecuador	OR541159	OR541695	OR550951	OR550704
D. arbuscula	*Lehnert 1743* (STU)	Puerto Rico	OR541160	OR541696	OR550952	OR550705
D. arbuscula	*Lehnert 2029* (QCA, STU, VT)	Ecuador	OR541161	OR541697	OR550953	OR550706
D. arbuscula	*Tuomisto 13255* (CUZ, TUR, USM)	Peru	EU221701	EU221763	–	EU221831
D. arbuscula	*Tuomisto 13590* (CUZ, TUR, UC, USM)	Peru	EU221702	EU221764	OR550954	EU221832
D. arbuscula	*Tuomisto 17591* (TUR, UTCEC)	Ecuador	–	OR541698	OR550955	OR550707
D. arbuscula	*Weigelt 90041* (GOET, LPB, TUR, Z)	Bolivia	OR541162	OR541699	OR550956	OR550708
D. arbuscula	*Weigelt 90121* (GOET, LPB, TUR, Z)	Bolivia	OR541163	OR541700	–	OR550709

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D. arbuscula	*Weigelt 90139* (GOET, LPB, TUR, Z)	Bolivia	OR541164	OR541701	OR550957	OR550710
D. bicolor Tuomisto & R. C. Moran	*Øllgaard 99671* (AAU, NY, QCA, TUR, UC)	Ecuador	OR541165	OR541702	–	OR550711
D. bicolor	*Øllgaard 99719* (AAU, QCA, TUR)	Ecuador	OR541166	OR541703	OR550958	OR550712
D. bipinnata Tuomisto	*Christenhusz 2140* (AMAZ, TUR, USM)	Peru	–	–	OR550959	OR550713
D. bipinnata	*Tuomisto 10634* (AAU, NY, QCA, QCNE, TUR)	Ecuador	EU221689	EU221750	OR550960	EU221819
D. bipinnata	*Tuomisto 11030* (AMAZ, TUR, USM)	Peru	OR541167	OR541704	OR550961	OR550714
D. bipinnata	*Tuomisto 11650* (QCA, QCNE, TUR)	Ecuador	–	EU221751	OR550962	EU221820
D. bipinnata	*Tuomisto 15850* (SP, TUR)	Brazil	OR541168	OR541705	OR550963	OR550715
D. bipinnata	*Tuomisto 15869* (SP, TUR)	Brazil	OR541169	OR541706	OR550964	OR550716
D. bipinnata	*Tuomisto 16183* (SP, TUR)	Brazil	OR541170	OR541707	OR550965	OR550717
D. bipinnata	*Tuomisto 16337* (SP, TUR)	Brazil	OR541171	OR541708	OR550966	OR550718
D. bipinnata	*Tuomisto 16608* (SP, TUR)	Brazil	OR541172	OR541709	OR550967	OR550719
D. carillensis Christ	*Lemieux 2344* (CR)	Costa Rica	EU221690	EU221752	OR550968	EU221821
D. cartilaginea Christenh. & Tuomisto	*Tuomisto 11684* (QCA, QCNE, TUR)	Ecuador	EU221691	EU221753	OR550969	EU221822
D. cartilaginea	*Tuomisto 13913* (AMAZ, TUR, USM)	Peru	–	OR541710	–	OR550720
D. cartilaginea	*Tuomisto 14122* (AMAZ, TUR, UC, USM)	Peru	OR541173	OR541711	OR550970	OR550721
D. cartilaginea	*Tuomisto 14798* (AAU, AMAZ, NY, TUR, UC, USM)	Peru	OR541174	OR541712	OR550971	OR550722
D. cartilaginea	*Tuomisto 16008* (SP, TUR)	Brazil	OR541175	OR541713	OR550972	OR550723
D. cartilaginea	*Tuomisto 16572* (SP, TUR)	Brazil	OR541176	–	OR550973	OR550724
D. cartilaginea	*Tuomisto 16583* (SP, TUR)	Brazil	OR541177	OR541714	OR550974	OR550725
D. cartilaginea	*Tuomisto 17849* (HUTI, TUR, UTCEC)	Ecuador	–	OR541715	OR550975	OR550726
D. cartilaginea	*Tuomisto 17849B* (TUR)	Ecuador	–	OR541716	OR550976	OR550727
D. cartilaginea	*Weigelt 90542* (LPB, TUR)	Bolivia	OR541178	OR541717	OR550977	OR550728
D. crispa Endrés & Rchb. f.	*Moran 6349* (NY)	Costa Rica	EU221692	EU221754	OR550978	EU221823
D. crispa	*Smith 2594* (UC)	Costa Rica	EU221693	EU221755	OR550979	EU221824
D. cuspidata Liebm.	*Hernandez 2286* (Z)	Mexico	OR541179	OR541718	OR550980	OR550729
D. cuspidata	*Mickel 5888* (NY, UC)	Mexico	–	–	OR550981	OR550730
D. cuspidata	*Tuomisto 17502* (TUR XAL)	Mexico	OR541180	OR541719	OR550982	OR550731
D. cuspidata	*Tuomisto 17512* (TUR XAL)	Mexico	OR541181	OR541720	OR550983	OR550732

D. cuspidopsis Keskiniva & Tuomisto	*Boyle 5971* (CR, INB, NY, USO)	Costa Rica	EU221694	EU221756	OR550984	EU221825
D. cuspidopsis	*Kessler 14850* (HUA, TUR)	Colombia	OR541182	OR541721	OR550985	OR550733
D. cuspidopsis	*Lellinger 1481* (US)	Costa Rica	OR541183	–	OR550986	OR550734
D. danaëpinna Christenh.	*Boudrie 3762* (CAY)	French Guiana	OR541184	OR541722	OR550987	OR550735
D. danaëpinna	*Boudrie 4356* (CAY, TUR)	French Guiana	OR541185	OR541723	OR550988	OR550736
D. danaëpinna	*Christenhusz 2339* (TUR)	French Guiana	EU221729	EU221795	OR550989	EU221865
D. danaëpinna	*Christenhusz 2619* (BBS, BM, TUR)	Suriname	OR541186	OR541724	OR550990	OR550737
D. elongata Keskiniva & Tuomisto	*Kessler 13000* (GOET, TUR)	Bolivia	EU221715	EU221779	OR550991	EU221848
D. elongata	*Lehnert 1258* (GOET, QCA, TUR, UC)	Ecuador	OR541187	OR541725	OR550992	OR550738
D. elongata	*Lehnert 1523* (GOET, QCA, TUR, UC)	Ecuador	OR541188	OR541726	OR550993	OR550739
D. elongata	*Lehnert 769* (GOET)	Bolivia	–	OR541727	–	OR550740
D. erecta Tuomisto & R. C. Moran	*Kessler 15520* (TUR)	Ecuador	OR541189	OR541728	OR550994	OR550741
D. erecta	*Kessler 15566* (TUR)	Ecuador	OR541190	OR541729	OR550995	OR550742
D. erecta	*Kessler 15629* (TUR)	Ecuador	OR541191	OR541730	OR550996	OR550743
D. erecta	*Kessler 15634* (TUR)	Ecuador	OR541192	OR541731	OR550997	OR550744
D. erecta	*Lehnert 1203* (QCA, TUR)	Ecuador	EU221695	EU221757	OR550998	EU221826
D. erecta	*Lehnert 1230* (GOET, QCA)	Ecuador	OR541193	OR541732	OR550999	OR550745
D. erecta	*Lehnert 2377* (STU)	Ecuador	OR541194	OR541733	OR551000	–
D. erecta	*Moran 5950* (AAU, NY, QCA, QCNE, TUR, UC)	Ecuador	–	OR541734	OR551001	OR550746
D. erecta	*Moran 6283* (AAU, NY, QCA, QCNE, TUR)	Ecuador	OR541195	OR541735	OR551002	OR550747
D. erecta	*Tuomisto 17589* (HUTI, TUR, UTCEC)	Ecuador	–	OR541736	OR551003	OR550748
D. excurrens Rosenst.	*Christenhusz 4846* (TUR, UC)	Brazil	OR541196	OR541737	OR551004	OR550749
D. excurrens	*Christenhusz 4982* (TUR)	Brazil	OR541197	OR541738	OR551005	OR550750
D. excurrens	*Christenhusz 4987* (MO, TUR, UC)	Brazil	OR541198	OR541739	OR551006	OR550751
D. excurrens	*Jimenez 1000* (LPB, UC)	Bolivia	OR541199	OR541740	OR551007	OR550752
D. excurrens	*Jimenez 1031* (LPB)	Bolivia	OR541200	OR541741	OR551008	OR550753
D. excurrens	*Jimenez 2539* (GOET, UC)	Bolivia	–	OR541742	OR551009	OR550754
D. excurrens	*Kessler 12939* (GOET, TUR, UC)	Bolivia	–	OR541743	OR551010	OR550755
D. excurrens	*Mynssen 1087* (TUR)	Brazil	OR541201	OR541744	OR551011	OR550756
D. falcata Tuomisto & R. C. Moran	*Moran 6259* (AAU, NY, QCA, QCNE, TUR)	Ecuador	OR541202	OR541745	OR551012	OR550757
D. falcata	*Tuomisto 10832* (AAU, K, NY, QCA, QCNE, TUR, U, UC)	Ecuador	EU221696	EU221758	OR551013	EU221827
D. geniculata Raddi	*Boudrie 4434* (CAY, TUR)	French Guiana	OR541203	OR541746	OR551014	OR550758

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D. geniculata	*Christenhusz 4886* (TUR)	Brazil	OR541204	OR541747	OR551015	OR550759
D. geniculata	*Christenhusz 4911* (TUR)	Brazil	OR541205	OR541748	OR551016	OR550760
D. geniculata	*Christenhusz 4937* (MO, UC)	Brazil	OR541206	OR541749	OR551017	OR550761
D. geniculata	*Christenhusz 4967* (MO)	Brazil	OR541207	OR541750	OR551018	OR550762
D. geniculata	*Lehtonen 572* (SP, TUR)	Brazil	OR541208	OR541751	OR551019	OR550763
D. geniculata	*Mynssen 1088* (NY, SP, TUR)	Brazil	OR541209	OR541752	OR551020	OR550764
D. gracilis Tuomisto & Keskiniva	*Duke 15321* (MO, US)	Colombia	OR541210	–	OR551021	OR550765
D. gracilis	*Kessler 15086* (TUR)	Colombia	–	OR541753	OR551022	OR550766
D. gracilis	*Øllgaard 105343* (AAU, QCA, TUR)	Ecuador	OR541211	OR541754	OR551023	OR550767
D. grandifolia Underw.	*Christenhusz 3439* (MAPR, TUR, UPRRP)	Puerto Rico	EU221704	EU221766	OR551024	EU221834
D. grandifolia	*Christenhusz 3487* (MAPR, TUR)	Puerto Rico	OR541212	OR541755	OR551025	OR550768
D. grandifolia	*Christenhusz 3505* (MAPR, TUR)	Puerto Rico	EU221703	EU221765	OR551026	EU221833
D. grandifolia	*Christenhusz 4230* (TUR, UPR)	Puerto Rico	OR541213	OR541756	OR551027	OR550769
D. grandifolia	*Kessler 14689* (TUR)	Colombia	OR541214	OR541757	OR551028	OR550770
D. grandifolia	*Kessler 14821* (TUR)	Colombia	OR541215	OR541758	OR551029	OR550771
D. grandifolia	*Kessler 14848* (TUR)	Colombia	OR541216	OR541759	OR551030	OR550772
D. humilis T. Moore	*Kessler 15630* (TUR)	Ecuador	OR541217	OR541760	OR551031	OR550773
D. humilis	*Lehnert 2041* (QCA, STU)	Ecuador	OR541218	OR541761	OR551032	OR550774
D. imbricata Tuomisto & R. C. Moran	*Kessler 15633* (TUR)	Ecuador	OR541219	OR541762	OR551033	OR550775
D. imbricata	*Tuomisto 17590* (TUR, UTCEC)	Ecuador	–	OR541763	–	–
D. inaequilatera A. Rojas	*Kessler 14847* (TUR)	Colombia	OR541220	–	OR551034	OR550776
D. jamaicensis Underw.	*Christenhusz 3371* (IJ, TUR)	Jamaica	EU221712	EU221774	OR551035	EU221843
D. jamaicensis	*Christenhusz 3372* (IJ, TUR)	Jamaica	OR541221	OR541764	OR551036	OR550777
D. jamaicensis	*Christenhusz 3515* (MAPR, TUR)	Puerto Rico	OR541222	OR541765	OR551037	OR550778
D. jenmanii Underw.	*Christenhusz 2990* (IJ, TUR)	Jamaica	EU221705	EU221767	OR551038	EU221835
D. jenmanii	*Christenhusz 3373* (IJ, TUR)	Jamaica	EU221706	EU221768	OR551039	EU221836
D. jenmanii	*Christenhusz 3514* (MAPR, TUR)	Puerto Rico	EU221707	EU221769	OR551040	EU221837
D. kalevala Christenh.	*Christenhusz 2696* (NY, TUR)	Martinique	EU221708	EU221770	OR551041	EU221838
D. kalevala	*Christenhusz 3890* (GUAD, TUR)	Guadeloupe	OR541223	OR541766	–	–
D. kessleri Keskiniva & Tuomisto	*Kessler 15631* (TUR)	Ecuador	OR541224	OR541767	OR551042	OR550779

D. kessleri	*Kessler 15636* (TUR)	Ecuador	OR541225	OR541768	OR551043	OR550780
D. kessleri	*Kessler 15638* (TUR)	Ecuador	OR541226	OR541769	OR551044	OR550781
D. kessleri	*Tuomisto 10658* (QCA, QCNE, TUR)	Ecuador	OR541227	OR541770	OR551045	OR550782
D. kessleri	*Tuomisto 11934* (QCA, QCNE, TUR)	Ecuador	–	EU221787	–	EU221856
D. kessleri	*Tuomisto 17897* (HUTI, TUR, UC, UTCEC, Z)	Ecuador	–	OR541771	OR551046	OR550783
D. kessleri	*Tuomisto 17962* (TUR, UTCEC)	Ecuador	–	OR541772	OR551047	OR550784
D. lanceolata Tuomisto & Keskiniva	*Moran 6124* (AAU, QCA, TUR)	Ecuador	–	OR541773	–	OR550785
D. lanceolata	*Moran 6035* (AAU, NY, QCA, QCNE, TUR, UC)	Ecuador	–	OR541774	–	OR550786
D. lanceolata	*Tuomisto 11915* (QCA, QCNE, TUR, UC)	Ecuador	EU221723	EU221788	OR551049	EU221857
D. lanceolata	*Tuomisto 14712* (AMAZ, TUR, UC, USM)	Peru	OR541229	OR541775	OR551050	OR550787
D. lanceolata	*Tuomisto 17802* (HUTI, TUR, UTCEC)	Ecuador	OR541230	OR541776	OR551051	OR550788
D. lanceolata	*Tuomisto 17845* (HUTI, TUR, UTCEC)	Ecuador	–	–	OR551052	OR550789
D. latipinna Tuomisto & R. C. Moran	*Kessler 14842* (TUR)	Colombia	OR541231	OR541777	OR551053	OR550790
D. latipinna	*Kessler 15083* (TUR)	Colombia	OR541232	OR541778	OR551054	OR550791
D. leprieurii Kunze	*Christenhusz 2150* (AMAZ, TUR, USM)	Peru	–	–	OR551055	EU221841
D. leprieurii	*Christenhusz 2427* (CAY, TUR)	French Guiana	EU221709	EU221771	–	EU221839
D. leprieurii	*Tuomisto 11397* (AMAZ, TUR, USM)	Peru	EU221710	EU221772	OR551056	EU221840
D. leprieurii	*Tuomisto 14482* (AMAZ, TUR, USM)	Peru	OR541233	OR541779	OR551057	OR550793
D. leprieurii	*Tuomisto 14515* (AMAZ, TUR, USM)	Peru	OR541234	OR541780	OR551058	OR550794
D. leprieurii	*Tuomisto 15233* (SP, TUR)	Brazil	OR541235	OR541781	OR551059	OR550795
D. leprieurii	*Tuomisto 15688* (SP, TUR)	Brazil	OR541236	OR541782	OR551060	OR550796
D. leprieurii	*Tuomisto 15851* (INPA, SP, TUR)	Brazil	OR541237	OR541783	OR551061	OR550797
D. leprieurii	*Tuomisto 16103* (INPA, SP, TUR)	Brazil	OR541238	OR541784	OR551062	OR550798
D. leprieurii	*Tuomisto 16338* (SP, TUR)	Brazil	OR541239	OR541785	OR551063	OR550799
D. leprieurii	*Zuquim 1017* (TUR)	Brazil	OR541240	OR541786	OR551064	OR550800
D. leussinkiana Christenh.	*Jones 1246* (TUR)	Panama	OR541241	OR541787	OR551065	OR550801
D. leussinkiana	*Jones 542* (CR, TUR)	Costa Rica	–	EU221793	OR551066	EU221862
D. leussinkiana	*Jones 603* (TUR)	Costa Rica	OR541242	OR541788	OR551067	OR550802

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D. leussinkiana	*Jones 604* (TUR)	Costa Rica	OR541243	OR541789	OR551068	OR550803
D. leussinkiana	*Jones 626* (TUR)	Costa Rica	OR541244	OR541790	OR551069	OR550804
D. lingua-cervina Christenh. & Tuomisto	*Tuomisto 15127* (AMAZ, TUR, USM)	Peru	OR541245	OR541791	OR551070	OR550805
D. longicaudata Tuomisto	*Moran 6954* (NY)	Ecuador	EU221711	EU221773	OR551071	EU221842
D. lucens A. Rojas	*Kessler 14757* (HUA, TUR)	Colombia	OR541246	OR541792	OR551072	OR550806
D. mazeana Underw.	*Christenhusz 2759* (TUR)	Guadeloupe	–	–	OR551073	OR550807
D. mazeana	*Christenhusz 3885* (GUAD, TUR)	Guadeloupe	OR541247	OR541793	OR551074	OR550808
D. moritziana C. Presl	*Kessler 14685* (TUR)	Colombia	OR541248	OR541794	OR551075	OR550809
D. nigrescens Jenman	*Boudrie 3763* (CAY, TUR)	French Guiana	–	OR541795	OR551076	OR550810
D. nigrescens	*Christenhusz 1949* (TUR, USM)	Peru	EU221722	EU221786	OR551077	EU221855
D. nigrescens	*Christenhusz 2596* (BBS, TUR)	Suriname	EU221717	EU221781	OR551078	EU221850
D. nigrescens	*Jimenez 1942* (GOET, TUR)	Bolivia	OR541249	OR541796	OR551079	OR550811
D. nigrescens	*Jimenez 1956* (GOET, TUR)	Bolivia	OR541250	OR541797	OR551080	OR550812
D. nigrescens	*Jimenez 1979* (GOET, TUR, UC)	Bolivia	EU221718	EU221782	OR551081	EU221851
D. nigrescens	*Lehtonen 1101* (CAY, TUR)	French Guiana	OR541251	OR541798	OR551082	OR550813
D. nigrescens	*Tuomisto 10856* (QCA, QCNE, TUR)	Ecuador	OR541252	OR541799	OR551083	OR550814
D. nigrescens	*Tuomisto 11304* (AMAZ, TUR, USM)	Peru	EU221716	EU221780	OR551084	EU221849
D. nigrescens	*Tuomisto 13084* (CUZ, TUR, USM)	Peru	EU221720	EU221784	OR551085	EU221853
D. nigrescens	*Tuomisto 14183* (AMAZ, TUR, UC, USM)	Peru	OR541253	OR541800	OR551086	OR550815
D. nigrescens	*Tuomisto 14599* (AMAZ, TUR, USM)	Peru	OR541254	OR541801	OR551087	OR550816
D. nigrescens	*Tuomisto 15619* (SP, TUR)	Brazil	OR541255	OR541802	OR551088	OR550817
D. nigrescens	*Tuomisto 15681* (SP, TUR)	Brazil	OR541256	OR541803	OR551089	OR550818
D. nigrescens	*Tuomisto 16177* (SP, TUR)	Brazil	OR541257	OR541804	OR551090	OR550819
D. nigrescens	*Tuomisto 16189* (SP, TUR)	Brazil	OR541258	OR541805	OR551091	OR550820
D. nigrescens	*Tuomisto 16377* (SP, TUR)	Brazil	OR541259	OR541806	OR551092	OR550821
D. nigrescens	*Tuomisto 16585* (INPA, SP, TUR)	Brazil	OR541260	OR541807	OR551093	OR550822
D. nigrescens	*Tuomisto 16629* (SP, TUR)	Brazil	OR541261	OR541808	OR551094	OR550823
D. nigrescens	*Tuomisto 16713* (SP, TUR)	Brazil	OR541262	OR541809	OR551095	OR550824
D. nigrescens	*Tuomisto 17828* (HUTI, TUR, UTCEC)	Ecuador	OR541263	OR541810	OR551096	OR550825
D. nigrescens	*Weigelt 90122* (LPB, TUR)	Bolivia	OR541264	OR541811	OR551097	OR550826

D. nigrescens	*Weigelt 90123* (GOET, LPB, TUR, Z)	Bolivia	OR541265	OR541812	OR551098	OR550827
D. nigrescens	*Weigelt 90181* (LPB, TUR, Z)	Bolivia	OR541266	OR541813	OR551099	OR550828
D. nigrescens	*Weigelt 90422* (LPB, TUR)	Bolivia	OR541267	OR541814	–	OR550829
D. nigrescens	*Weigelt 90472* (LPB, TUR)	Bolivia	OR541268	OR541815	OR551100	OR550830
D. nigrescens	*Zuquim 1088* (INPA)	Brazil	OR541269	OR541816	OR551101	OR550831
D. nodosa (L.) Sm.	*Christenhusz 3194* (IJ, TUR)	Jamaica	EU221714	EU221777	OR551102	EU221846
D. nodosa	*Christenhusz 3203* (IJ, TUR)	Jamaica	OR541270	–	–	OR550832
D. nodosa	*Christenhusz 3309* (IJ, TUR)	Jamaica	–	EU221778	–	EU221847
D. nodosa	*Christenhusz 3522* (TUR, UPRRP)	Puerto Rico	OR541271	OR541817	OR551103	OR550833
D. nodosa	*Christenhusz 3545* (TUR, UPRRP)	Puerto Rico	OR541272	OR541818	OR551104	OR550834
D. nodosa	*Tuomisto 17505* (TUR, XAL)	Mexico	OR541273	OR541819	OR551105	OR550835
D. nodosa	*Tuomisto 17508* (TUR, XAL)	Mexico	OR541274	OR541820	OR551106	OR550836
D. opaca Keskiniva & Tuomisto	*Tuomisto 15876* (SP, TUR)	Brazil	OR541275	OR541821	OR551107	OR550837
D. opaca	*Tuomisto 15886* (AAU, SP, TUR)	Brazil	OR541276	OR541822	OR551108	OR550838
D. opaca	*Tuomisto 16052* (MO, SP, TUR)	Brazil	OR541277	OR541823	OR551109	OR550839
D. opaca	*Tuomisto 16130* (SP, TUR, UC, Z)	Brazil	OR541278	OR541824	OR551110	OR550840
D. opaca	*Tuomisto 16759* (SP, TUR)	Brazil	OR541279	OR541825	OR551111	OR550841
D. panamensis Keskiniva & Tuomisto	*Jones 1051* (PMA, TUR)	Panama	OR541280	OR541826	OR551112	OR550842
D. panamensis	*Jones 635* (TUR, US)	Panama	OR541281	OR541827	OR551113	OR550843
D. panamensis	*Jones 683* (TUR)	Panama	OR541282	OR541828	OR551114	OR550844
D. panamensis	*Jones 735* (TUR)	Panama	OR541283	OR541829	OR551115	OR550845
D. panamensis	*Jones 753* (TUR)	Panama	OR541284	OR541830	OR551116	OR550846
D. panamensis	*Jones 802* (TUR)	Panama	OR541285	OR541831	OR551117	OR550847
D. panamensis	*Jones 920* (TUR)	Panama	OR541286	OR541832	OR551118	OR550848
D. panamensis	*Jones 957* (TUR, US)	Panama	OR541287	OR541833	OR551119	OR550849
D. panamensis	*Jones 982* (TUR)	Panama	OR541288	OR541834	OR551120	OR550850
D. panamensis	*Tuomisto 15142* (PMA)	Panama	OR541289	OR541835	OR551121	OR550851
D. panamensis	*Tuomisto 15149* (PMA, TUR)	Panama	OR541290	OR541836	OR551122	OR550852
D. panamensis	*Tuomisto 15161* (AAU, PMA, TUR, UC, Z)	Panama	OR541291	OR541837	OR551123	OR550853
D. polymorpha Lepr. ex Baker	*Christenhusz 2746* (TUR)	Guadeloupe	EU221724	EU221789	OR551124	EU221858
D. polymorpha	*Kessler 12909* (TUR)	Trinidad and Tobago	OR541292	OR541838	OR551125	OR550854
D. polypinna Keskiniva & Tuomisto	*Mickel 3420* (NY)	Costa Rica	–	OR541839	OR551126	OR550855

Appendix 1 (continued from p. 251)

D. pterorachis Christ	*Jones 169* (CR, TUR)	Costa Rica	–	EU221776	OR551127	EU221845
D. pterorachis	*Jones 289* (CR, TUR)	Costa Rica	EU221713	EU221775	OR551128	EU221844
D. pterorachis	*Tuomisto 13810* (CUZ, TUR, USM)	Costa Rica	–	OR541840	OR551129	OR550856
D. pumila Keskiniva & Tuomisto	*Van der Werff 22192* (MO, PMA, TUR)	Panama	–	–	OR551130	OR550857
D. pumila	*Van der Werff 22253* (MO, PMA, TUR)	Panama	OR541293	OR541841	OR551131	OR550858
D. riparia Christenh. & Tuomisto	*Tuomisto 17592* (HUTI, TUR, UTCEC)	Ecuador	–	OR541842	OR551132	OR550859
D. robbinmoranii Keskiniva & Tuomisto	*Moran 6350* (CR, NY)	Costa Rica	–	–	OR551133	OR550860
D. sellowiana C. Presl	*Christenhusz 4727* (TUR)	Brazil	OR541294	OR541843	OR551134	OR550861
D. sellowiana	*Christenhusz 4944* (TUR)	Brazil	OR541295	OR541844	OR551135	OR550862
D. sellowiana	*Christenhusz 4984* (TUR)	Brazil	OR541296	OR541845	OR551136	OR550863
D. sellowiana	*Mynssen 1074* (NY, SP, TUR)	Brazil	OR541297	OR541846	OR551137	OR550864
D. simplicifolia Rudge	*Christenhusz 2275* (CAY, TUR)	French Guiana	EU221725	EU221790	OR551138	EU221859
D. simplicifolia	*Christenhusz 2415* (CAY, TUR)	French Guiana	EU221726	EU221791	OR551139	EU221860
D. simplicifolia	*Christenhusz 2428* (CAY, TUR)	French Guiana	EU221727	EU221792	OR551140	EU221861
D. sp.	*Christenhusz 1904* (TUR, USM)	Peru	EU221721	EU221785	OR551141	EU221854
D. sp.	*Christenhusz 1938* (AMAZ, TUR, USM)	Peru	EU221697	EU221759	OR551142	EU221828
D. sp.	*Christenhusz 2040* (AMAZ, TUR, USM)	Peru	OR541298	OR541847	OR551143	OR550865
D. sp.	*Jimenez 2276* (GOET)	Bolivia	OR541299	OR541848	OR551144	OR550866
D. sp.	*Jimenez 840* (LPB, MO, UC)	Bolivia	OR541300	OR541849	OR551145	OR550867
D. sp.	*Jones 606* (TUR)	Costa Rica	OR541301	OR541850	OR551146	OR550868
D. sp.	*Jones 742* (TUR)	Panama	OR541302	OR541851	OR551147	OR550869
D. sp.	*Kessler 14702* (TUR)	Colombia	OR541303	OR541852	OR551148	OR550870
D. sp.	*Kessler 14752* (HUA, TUR)	Colombia	OR541304	OR541853	OR551149	OR550871
D. sp.	*Kessler 14838* (TUR)	Colombia	OR541305	OR541854	OR551150	OR550872
D. sp.	*Kessler 15059* (TUR)	Colombia	OR541306	OR541855	OR551151	OR550873
D. sp.	*Kessler 15510* (TUR)	Ecuador	OR541307	OR541856	OR551152	OR550874
D. sp.	*Kessler 15519* (TUR)	Ecuador	OR541308	OR541857	OR551153	OR550875
D. sp.	*Kessler 15632* (TUR)	Ecuador	OR541309	OR541858	OR551154	OR550876
D. sp.	*Lellinger 1520* (US)	Costa Rica	OR541310	–	OR551155	OR550877
D. sp.	*Tuomisto 13811* (CUZ, TUR, USM)	Costa Rica	–	OR541859	OR551156	OR550878
D. sp.	*Tuomisto 13822* (AMAZ, TUR, USM)	Peru	–	–	OR551157	OR550879

D. sp.	*Tuomisto 14481* (AMAZ, TUR, USM)	Peru	OR541311	OR541860	OR551158	OR550880
D. sp.	*Tuomisto 15855* (SP, TUR)	Brazil	OR541312	OR541861	OR551159	OR550881
D. sp.	*Tuomisto 17808* (TUR, UTCEC)	Ecuador	–	–	OR551160	OR550882
D. stricta Tuomisto & Keskiniva	*Tuomisto 15166* (PMA, TUR)	Panama	OR541313	OR541862	OR551161	OR550883
D. tenera C. V. Morton	*Kessler 14837* (TUR)	Colombia	OR541314	OR541863	OR551162	OR550884
D. tenera	*Kessler 14844* (TUR)	Colombia	OR541315	OR541864	OR551163	OR550885
D. tenuicaulis Tuomisto & Keskiniva	*Kessler 14866* (HUA, TUR)	Colombia	OR541316	OR541865	OR551164	OR550886
D. tenuicaulis	*Kessler 14880* (HUA, TUR)	Colombia	OR541317	OR541866	OR551165	OR550887
D. trichomanoides Spruce ex T. Moore	*Lehnert 1542* (QCA, TUR, UC)	Ecuador	EU221730	EU221796	–	EU221866
D. trifoliata Rchb. ex Kunze	*Christenhusz 2606* (BBS, TUR)	Suriname	EU221731	EU221797	OR551166	EU221867
D. trifoliata	*Tuomisto 15215* (INPA, SP, TUR)	Brazil	OR541318	OR541867	OR551167	OR550888
D. trifoliata	*Tuomisto 15440* (SP, TUR)	Brazil	OR541319	OR541868	OR551168	OR550889
D. trifoliata	*Tuomisto 15717* (SP, TUR, Z)	Brazil	OR541320	OR541869	OR551169	OR550890
D. trifoliata	*Tuomisto 15897* (SP, TUR)	Brazil	OR541321	OR541870	OR551170	OR550891
D. trifoliata	*Tuomisto 16022* (SP, TUR)	Brazil	OR541322	OR541871	OR551171	OR550892
D. trifoliata	*Tuomisto 16531* (SP, TUR)	Brazil	OR541323	OR541872	OR551172	OR550893
D. trifoliata	*Tuomisto 16549* (SP, TUR)	Brazil	OR541324	OR541873	OR551173	OR550894
D. trifoliata	*Tuomisto 16613* (SP, TUR)	Brazil	OR541325	OR541874	OR551174	OR550895
D. trinitatensis Christenh. & Tuomisto	*Christenhusz 3065* (IJ, TUR)	Jamaica	OR541326	OR541875	OR551175	OR550896
D. trinitatensis	*Christenhusz 3145* (IJ, TUR)	Jamaica	OR541327	OR541876	OR551176	OR550897
D. trinitatensis	*Christenhusz 3421* (TUR, UPRRP)	Puerto Rico	OR541328	OR541877	OR551177	OR550898
D. trinitatensis	*Christenhusz 4220* (TUR, UPR)	Puerto Rico	OR541329	OR541878	OR551178	OR550899
D. trinitatensis	*Tuomisto 17504* (TUR, XAL)	Mexico	OR541330	OR541879	OR551179	OR550900
D. ubatubensis Keskiniva & Tuomisto	*Christenhusz 4910* (AAU, MO, TUR, UC, Z)	Brazil	OR541331	OR541880	OR551180	OR550901
D. ulei Christ	*Tuomisto 14997* (AMAZ, TUR, USM)	Peru	OR541332	OR541881	OR551181	OR550902
D. ulei	*Tuomisto 16602* (SP, TUR)	Brazil	OR541333	OR541882	OR551182	OR550903
D. urbani Maxon	*Christenhusz 3506* (TUR)	Puerto Rico	EU221732	EU221798	–	EU221868
D. ushana Christenh.	*Boudrie 3764* (CAY, TUR)	French Guiana	OR541334	OR541883	OR551183	OR550904
D. ushana	*Lehtonen 1112* (CAY, TUR)	French Guiana	OR541335	OR541884	OR551184	OR550905
D. vanderwerffii Tuomisto & Keskiniva	*Van der Werff 22262* (MO, PMA, TUR)	Panama	–	–	OR551185	OR550906

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D. vanderwerffii	*Van der Werff 22275* (MO, PMA, TUR)	Panama	OR541336	OR541885	OR551186	OR550907
D. velona Keskiniva & Tuomisto	*Kessler 14808* (HUA, TUR)	Colombia	OR541337	OR541886	OR551187	OR550908
D. vivax Christenh. & Tuomisto	*Christenhusz 2002* (AAU, AMAZ, BM, E, GOET, L, LS, NY, TUR, U, UC, US, USM, Z)	Peru	–	EU221799	–	EU221869
D. vivax	*Christenhusz 2020* (TUR, USM)	Peru	–	OR541887	OR551188	OR550909
D. vivax	*Christenhusz 2129* (AMAZ, TUR, USM)	Peru	OR541338	OR541888	OR551189	OR550910
D. wendlandii Rchb. f.	*Jones 1020* (TUR, US)	Panama	OR541339	OR541889	OR551190	OR550911
D. wendlandii	*Jones 24* (TUR)	Costa Rica	EU221733	EU221800	OR551191	EU221870
D. xenium Christenh. & Tuomisto	*Higgins 1198* (AMAZ, TUR)	Peru	OR541340	OR541890	OR551192	OR550912
D. xenium	*Higgins 1266* (AMAZ, BM, NY, TUR, USM)	Peru	OR541341	OR541891	OR551193	OR550913
D. ypori Christenh.	*Boudrie 4442* (NY, TUR)	French Guiana	OR541342	OR541892	OR551194	OR550914
D. zamiopsis Christenh. & Tuomisto	Tuomisto 15163 (AAU, BM, MO, NY, PMA, TUR, UC, Z)	Panama	OR541343	OR541893	OR551195	OR550915
Eupodium cicutifolium (Kaulf.) Lehtonen	*Christenhusz 4781* (TUR)	cultivated	MN412590	MN412590	MN412590	MN412590
E. kaulfussii (J. Sm. ex Hook.) Hook.	*Lehtonen 571* (TUR)	Brazil	MN412589	MN412589	MN412589	MN412589
E. pittieri (Maxon) Christenh.	*Christenhusz 6788* (H)	–	–	KJ716402	–	–
Marattia alata Sw.	*Christenhusz 3266* (IJ, TUR)	Jamaica	EF463486	EU221802	–	EU221872
M. laxa Kunze	*Christenhusz 1313* (TUR)	–	MN412591	MN412591	MN412591	MN412591
M. weinmanniifolia Liebm.	*Smith 2567* (UC)	Mexico	EU221737	EU221805	–	EU221875
Ptisana novoguineensis (Rosenst.) Murdock	*Karger 1721* (Z)	New Guinea	MN412592	MN412592	MN412592	MN412592

Appendix 2

The dataset in Appendix 1 was used in the phylogenetic analyses in this study. The four loci (the plastid genes *rbcL* and *atpB*, and the non-coding *rpl32-trnL* and *trnL-F* regions) were aligned separately with MAFFT (Katoh & Standley 2013) on the EMBL-EBI-server (Madeira & al. 2022) with default settings. In addition, the two loci containing gaps (*rpl32-trnL* and *trnL-F*) were aligned with MUSCLE (Edgar 2004) and T-COFFEE (Notredame & al. 2000) on the EMBL-EBI-server with default settings to compare the sensitivity of the results to different alignments. The sequence data was partitioned by the 1st, 2nd and 3rd positions of the genes and by non-coding regions, and this partition was run with the advanced greedy algorithm in ModelFinder (Kalyaanamoorthy & al. 2017) in IQ-TREE 1.6.12 (Nguyen & al. 2015). The rate of evolution at different loci was estimated with TIGER-rates (Frandsen & al. 2015), and the acquired rate file was fed into RatePartitions (Rota & al. 2018). We tested division factor values in RatePartitions ranging from 1.5 to 3.5, which resulted in differently partitioned alignments. These were fed into ModelFinder and run with the advanced greedy algorithm. The models with the best BIC values were the greedy algorithms partitioned with RatePartitions division factor 3.0 (shown in **bold**). The models with the worst BIC values were the ones partitioned by genes, introns, and codon positions. The models with the best BIC values were used for the subsequent analysis with RAxML-NG 1.1.0 (Kozlov & al. 2019). The final data matrices and the resulting trees are available in TreeBASE (study number 30768).

	MAFFT	**MUSCLE**	**T-COFFEE**
Partition by the 1st, 2nd and 3rd positions of the genes and by non-coding regions	-18794.193	-19221.385	-18823.614
Partitioned according to RatePartitions division factor 1.5	-17731.348	-18080.664	-17616.222
Partitioned according to RatePartitions division factor 2.0	-17419.613	-17781.171	-17343.308
Partitioned according to RatePartitions division factor 2.5	-17414.071	-17735.132	-17349.96
Partitioned according to RatePartitions division factor 3.0	**-17343.897**	**-17720.567**	**-17301.421**
Partitioned according to RatePartitions division factor 3.5	-18507.401	-17724.081	-17343.254