

SYSTEMATICS AND PHYLOGENY

A worldwide phylogeny of *Adiantum* (Pteridaceae) reveals remarkable convergent evolution in leaf blade architecture

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Abstract *Adiantum* is among the most distinctive and easily recognized leptosporangiate fern genera. Despite encompassing an astonishing range of leaf complexity, all species of *Adiantum* share a unique character state not observed in other ferns: sporangia borne directly on the reflexed leaf margin or “false indusium” (pseudoindusium). The over 200 species of *Adiantum* span six continents and are nearly all terrestrial. Here, we present one of the most comprehensive phylogenies for any large (200+ spp.) monophyletic, subcosmopolitan genus of ferns to date. We build upon previous datasets, providing new data from four plastid markers (*rbcL*, *atpA*, *rpoA*, *chlN*) for 146 taxa. All sampled taxa can be unequivocally assigned to one of nine robustly supported clades. Although some of these unite to form larger, well-supported lineages, the backbone of our phylogeny has several short branches and generally weak support, making it difficult to accurately assess deep relationships. Our maximum likelihood-based ancestral character state reconstructions of leaf blade architecture reveal remarkable convergent evolution across multiple clades for nearly all leaf forms. A single unique synapomorphy—leaves once-pinnate, usually with prolonged rooting tips—defines the philippense clade. Although a rare occurrence in *Adiantum*, simple leaves occur in three distinct clades (*davidii*, philippense, *peruvianum*). Most taxa have leaves that are more than once-pinnate, and only a few of these (in the *formosum* and *pedatum* clades) exhibit the distinct pseudopedate form. Distributional ranges for each of the terminal taxa show that most species (75%) are restricted to only one of six major biogeographical regions. Forty-eight of our sampled species (nearly one-third) are endemic to South America.

Keywords biogeography; leaf morphology; maidenhair ferns; Neotropics; phylogeny; vittarioids

Supplementary Material Electronic Supplement (Tables S1 & S2) and DNA sequence alignments are available from <https://doi.org/10.12705/673.3.S1> and <https://doi.org/10.12705/673.3.S2>, respectively.

■ INTRODUCTION

Molecular phylogenetic studies sometimes reveal surprisingly close relationships between extant taxa with radically different morphologies; for example, DNA data show that hippos are most closely related to whales (Gatesy & O’Leary, 2001). Among plants, one such remarkable example is the robust sister relationship between the “maidenhair” and “shoestring” ferns (Rothfels & Schuettpelz, 2014; Rothfels & al., 2015; Pryer & al., 2016). The shoestring ferns (vittarioids) are predominantly epiphytic and have highly simplified leaves (Tryon & Tryon, 1982; Schuettpelz & al., 2016), whereas the maidenhair ferns (*Adiantum* L.) are nearly all terrestrial except for a few epiphytes (*A. aneitense* Carruth., *A. christii* Rosenst.). Many species and cultivars of *Adiantum* are highly prized in horticulture because of their graceful leaves and delicate green leaf segments that contrast with their shiny, dark petioles and rachises. *Adiantum*

comprises about 220 species (Kessler & al., 2017)—the overwhelming majority of which are found in tropical and subtropical regions of the world. As Hooker & Baker (1867) aptly noted, the “headquarters” for *Adiantum* is in the Neotropics. Although some species occur in temperate regions, maidenhair ferns are not usually found in xeric or extremely cold climates. The most far-reaching species, *A. capillus-veneris* L., occurs on all continents except Antarctica.

All members of *Adiantum* share a unique and distinctive synapomorphy: their sporangia are borne on reflexed leaf margins or “false indusia” that are either continuous or interrupted (Fig. 1A, B). This single attribute has led to the long-standing acceptance of *Adiantum* as a “natural” group, despite the genus encompassing an astonishing array of leaf morphologies, from simple to many times pinnate (or even decompose), including the unique pseudopedate blade architecture (*sensu* Paris, 1991; see also Materials and Methods) as in *A. pedatum* L. and

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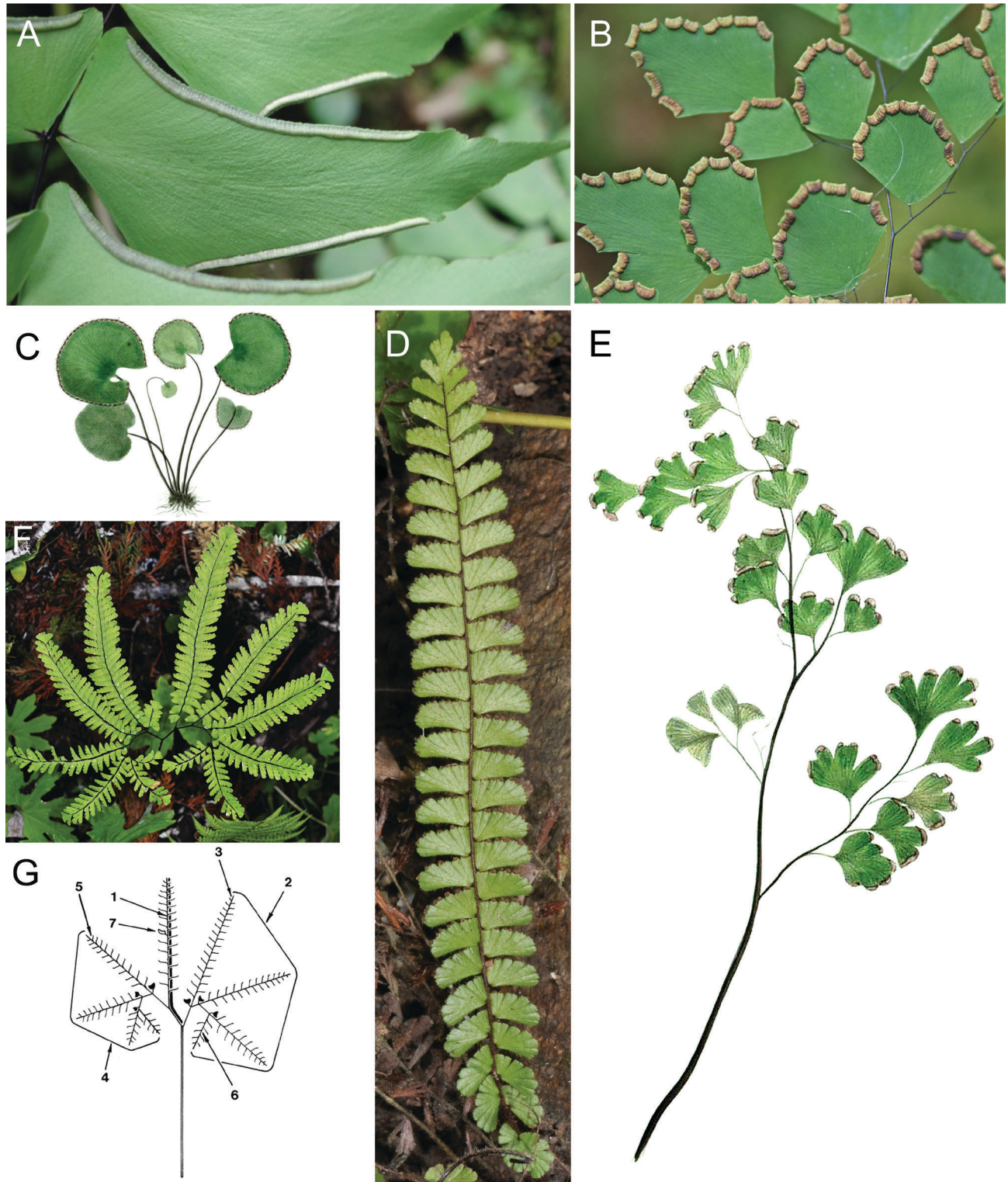


Fig. 1. Key morphological traits for *Adiantum* leaves. **A & B**, All species of *Adiantum* share a unique synapomorphy: their sporangia are borne on a reflexed leaf margin or “false indusium” that is either continuous, as in *A. macrophyllum* (**A**), or interrupted (discontinuous), as in *A. tenerum* (**B**). **C–G**, Levels of leaf architectural complexity displayed in *Adiantum*: **C**, Simple leaves of *A. reniforme*; **D**, Once-pinnate blades of *A. caudatum* L.; **E**, More than once-pinnate blades of *A. capillus-veneris*; **F**, Pseudopedate (sensu Paris, 1991) leaf architecture found in *A. pedatum*, *A. aleuticum*, and others—this is a unique type of “more than once-pinnate” dissection that is found only in *Adiantum*; **G**, Schematic explanation of the pseudopedate leaf of *A. pedatum* reproduced, with permission, from Paris (1991: fig. 1): 1 = rachis (shaded); 2 = first proximal pinna; 3 = main axis of first proximal pinna; 4 = second proximal pinna; 5 = axis of second proximal pinna; 6 = highest-order axis; 7 = medial ultimate segment. — Image credits: Robbin Moran (A); Julie Barcelona (B, D); Penfold (1845) (C, E); Robert L. Carr (F); Paris (1991: fig. 1) (G).

a few of its congeners (Fig. 1C–G). Only one segregate genus, *Hewardia* J.Sm., was ever described (Smith, 1841) to circumscribe those few species of *Adiantum* with mostly anastomosing (rather than mostly free) veins; however, it has long since been abandoned (Tryon & Tryon, 1982).

Classification schemes from the last century (e.g., Pichi Sermolli, 1977; Tryon & al., 1990) placed *Adiantum* in the Pteridaceae, but whether the pteridoid or cheilanthoid ferns were its closest relatives was disputed. More than two decades ago, the first DNA analyses of ferns revealed *Adiantum* was in fact sister to Vittariaceae (now subsumed into Pteridaceae), and both clades to be most closely related to the cheilanthoid ferns (Hasebe & al., 1994, 1995; Pryer & al., 1995). Subsequent phylogenetic analyses confirmed this relationship (Prado & al., 2007; Schuettpelz & Pryer, 2007; Schuettpelz & al., 2007; Lu & al., 2012). However, none of these studies could definitively conclude whether *Adiantum* and the vittarioids were reciprocally monophyletic; some studies suggested that a monophyletic vittarioid clade had evolved from within a paraphyletic *Adiantum* (e.g., Schuettpelz & al., 2007). Further analyses, using expanded sets of molecular markers including a mix of plastid, mitochondrial, and/or nuclear genes, have recently concluded that the two groups are indeed sister to one another (Rothfels & Schuettpelz, 2014; Rothfels & al., 2015; Pryer & al., 2016).

Hooker & Baker (1867) first classified *Adiantum* (then ca. 60 species) into eight groups based on venation, blade architecture, leaf segment and indusial morphology, and rachis indument. Kuhn (1881) proposed two sections, “*A. sect. Euadiantum*” (= *A. sect. Adiantum*) and *A. sect. Adiantellum* C.Presl, defined by whether the sporangia were confined to the veins or were also between the veins, respectively, and he assigned 113 species to these two groups. This latter classification was subsequently adopted by Diels (1902). More recently, Tryon & Tryon (1982), put forth an informal classification of *Adiantum* that circumscribed eight groups based almost exclusively on blade and pinna morphology.

Cooper-Driver & Swain (1977) made a first attempt to use molecules to resolve problems in fern taxonomy with a flavonoid study on 58 species of *Adiantum*. Since that time, and with the advent of DNA-based phylogenetics, there have been several regional studies (e.g., Brazil, New Zealand) of *Adiantum* using the plastid marker *rbcL* (Prado & al., 2007; Bouma & al., 2010) and some more targeted studies of certain species complexes, such as *A. gravesii* Hance (Wang & al., 2017), *A. philippense* L. (Kuo & al., 2016), *A. raddianum* C.Presl (Hirai & al., 2016), and *A. reniforme* L. (Wang & al., 2015). It was Lu & al. (2012), however, who undertook the first multigene phylogenetic analysis that included a broad sample of *Adiantum* species, with a focus on those found in China. Recently, Regalado & al. (2017) examined the biogeography and origins of Antillean species and assembled a comprehensive dataset of 101 species using new and previously published plastid sequences (*rbcL*, *atpA*, *atpB*, *trnL-F*).

Here, we present a worldwide 4-gene (*rbcL*, *atpA*, *rpoA*, *chlN*) plastid phylogeny of 146 taxa of *Adiantum*, exceeding the number of species previously sampled by almost 50%, to investigate relationships and underlying morphological and geographical patterns. Major goals of our study included: (1)

elucidating relationships in *Adiantum*; (2) defining any natural groups that may exist; (3) providing a framework for further morphological, molecular, and monographic studies that can focus more effectively on well-defined, monophyletic clades; (4) determining any significant distributional patterns exhibited by the various clades and subclades; and (5) shedding light on which, if any, morphological characters may be useful in defining monophyletic clades. Our results confirm previously known affinities and reveal new and remarkable relationships.

■ MATERIALS AND METHODS

Taxonomic sampling. — The eight taxonomic groups proposed by Tryon & Tryon (1982) formed the basis for our broad geographic sampling of *Adiantum*. Our ability to sample worldwide was greatly enhanced by being able to extract *Adiantum* DNA from herbarium specimens; this was supplemented by the generosity of members of the fern community who provided vouchered, silica-dried samples (see Acknowledgments). A total of 146 taxa of *Adiantum* were sampled in our study; 6 vittarioid species, representing all major lineages as identified in Schuettpelz & al. (2016), form the outgroup. Complete voucher information and GenBank accession numbers for all samples are provided in Appendix 1.

DNA isolation, amplification and sequencing. — Genomic DNA was isolated from fresh, silica-dried, or herbarium material using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.) following modifications described in Schuettpelz & Pryer (2007). Four protein-coding plastid genes were amplified and sequenced: *rbcL* and *atpA*, as described in Schuettpelz & Pryer (2007), and *rpoA* and *chlN*, as described in Schuettpelz & al. (2016). In cases where *rbcL* and/or *atpA* could not be amplified in their entirety, due to the poor quality of the DNA, sequencing primers were used to amplify smaller parts. For many species, the sequence data were confirmed from supplementary specimens of the same species; however, only a single voucher per species was included in the final analyses. A total of 453 sequences were newly published for this study, with an additional 95 from GenBank; ~6% of the targeted data are missing (Appendix 1).

Nuclear gene sequencing within ferns is especially challenging when a significant number of the DNA samples have been isolated from herbarium material (as was the case here). The quality of this DNA makes it difficult to amplify single-copy nuclear markers and so they were not utilized in this study. The application of nuclear markers in fern phylogenetics is very recent, but when used so far they have corroborated the results of plastid analyses (Rothfels & al., 2015).

Sequence alignment and datasets. — DNA sequence chromatograms were manually assembled and edited using Sequencher v.5.0.1 (Gene Codes, 2011). Sequences from each plastid region were aligned with AliView v.1.17.1 (Larsson, 2014), using MUSCLE v.3.8 (Edgar, 2004) as the default alignment program. Alignments of these protein-coding loci were straightforward to manually inspect and edit. Unsequenced portions of the plastid regions were coded as missing data. The

Table 1. Details for the DNA sequence alignments used in this study of *Adiantum* L.

Locus	Alignment length [bp]	Variable characters [bp]	Missing data (%)
<i>atpA</i>	1506	560	16.9
<i>chlN</i>	630	326	13.3
<i>rbcL</i>	1309	473	4.3
<i>rpoA</i>	616	374	6.0
Combined	4061	1733	10.6

four individual datasets, one for each plastid region (Table 1), are deposited as Supplemental Data.

Phylogenetic analyses.— For each plastid region, we first determined the best codon partitioning scheme and the associated nucleotide substitution models using PartitionFinder v.1.1.1 (Lanfear & al., 2012). Maximum likelihood (ML) analyses were then carried out in Garli v.2.0 (Zwickl, 2006) with “genthreshfortopoterm” set to 100,000 and two independent searches from random-starting trees. To infer branch support, we conducted bootstrapping (BS) in Garli with 1000 replicates. We compared the best-scoring tree from each locus and looked for topological conflicts supported by ≥ 70 bootstrap value. Because no conflicts were found, we concatenated all four loci into a single dataset.

For the combined dataset, we used PartitionFinder to determine the best data partitioning scheme (by codon position and/or by locus) and the associated substitution models (Table 2). We carried out maximum likelihood analyses, including bootstrapping, as described above using Garli. Bayesian inference was conducted using MrBayes v.3.2.4 (Ronquist & al., 2012) with two independent runs, each comprising four chains. We sampled trees every 1000 generations, and unlinked substitution parameters across each of the partitions in the optimal PartitionFinder scheme (Table 2). The rate prior was set to allow rate variation among the partitions. A total of 2.5×10^7 generations were run, and the output parameters were inspected in Tracer v.1.6 (Rambaut & al., 2014) to assess convergence; all post-burnin effective sample sizes were larger than 4000. The first 25% of the sample was discarded as burn-in and the rest was used to calculate posterior probabilities (PP).

Leaf blade architecture analysis.— *Adiantum* leaves are morphologically variable and potentially offer many valuable taxonomic characteristics. However, a fundamental misinterpretation of *Adiantum* leaf architecture persists in the literature, despite early efforts at clarification by Slosson (1906) and Wagner (1952, 1956), and a more recent and detailed explanation by Paris (1991). The confusion relates to the continued use of the term “pedate” to describe the leaf morphology that typifies *A. pedatum* (an unfortunate nomenclatural combination) and its congeners of similar form. *Adiantum pedatum* has traditionally been misinterpreted as having pedately divided leaves, with arching pinnae borne on a dichotomizing rachis. However, the primary fork in the blade axis is produced by one greatly enlarged proximal pinna laterally displacing the main rachis, and does not represent a true dichotomy (Wagner, 1952). More correctly, a modified, more than once-pinnate type of leaf architecture occurs in these species (e.g., *A. aleuticum* (Rupr.) C.A. Paris, *A. hispidulum* Sw., *A. oatesii* Baker, *A. patens* Willd., and *A. pedatum*; Fig. 1F, G; see also Paris, 1991: fig. 1). The replacement term “pseudopedate” was suggested by Paris (1991) in preference to pedate (= palmate), and we utilize that terminology here (see Fig. 1F, G).

We scored each taxon in our sample for one of five general levels of complexity commonly displayed in the laminar dissection of *Adiantum* (see Electr. Suppl.: Table S1 for scores), as determined from the literature and/or herbarium specimens: (a) simple; (b) once-pinnate, usually with prolonged, rooting tips; (c) once-pinnate, without prolonged, rooting tips; (d) more than once-pinnate (i.e., bipinnate or more divided); and (e) pseudopedate (sensu Paris, 1991).

Maximum likelihood-based ancestral state reconstructions of leaf morphology were carried out using the rerooting method (Yang & al., 1995) implemented in phytotools v.0.6.20 (Revell, 2012). Three transition models—ER (all rates equal), SYM (identical forward and reverse rates), and ARD (all rates different)—were tested based on Akaike information criterion, and the SYM model was preferred. Analyses were carried out in R v.3.3.2 (R Development Core Team, 2016).

Geography.— Each taxon sampled in this study was scored (see Electr. Suppl.: Table S2) for its distribution according to six biogeographical regions defined following Sanmartin & Ronquist (2004) and Korall & Pryer (2014), but with some

Table 2. The partition scheme and substitution models used in this study.

Subset	Models for Garli	Models for MrBayes
<i>atpA</i> 3rd codon position+ <i>rbcL</i> 3rd codon position	TVM+I+ Γ	GTR+I+ Γ
<i>atpA</i> 1st codon position+ <i>rbcL</i> 1st codon position	GTR+I+ Γ	GTR+I+ Γ
<i>rbcL</i> 2nd codon position	K81+I+ Γ	JC+I+ Γ
<i>chlN</i> 2nd codon position+ <i>rpoA</i> 2nd codon position	K81uf+I+ Γ	HKY+I+ Γ
<i>chlN</i> 3rd codon position+ <i>rpoA</i> 3rd codon position	TVM+I+ Γ	GTR+I+ Γ
<i>chlN</i> 1st codon position+ <i>rpoA</i> 1st codon position	GTR+ Γ	GTR+ Γ
<i>atpA</i> 2nd codon position	TrN+I+ Γ	HKY+I+ Γ

For Bayesian inference, different models were applied in some subsets because the optimal ones could not be implemented in MrBayes.

modification. These six regions are: (a) Eurasia (including Malaysia, Philippines, Sumatra, Borneo, and Indonesia); (b) Australasia and the Pacific (including Australia, New Zealand, and New Guinea); (c) Africa (including Madagascar); (d) South America; (e) Central America, Mexico, and the Antilles; and (f) North America. The geographical distributions for terminal taxa were gathered from herbarium collections examined and regional Floras (e.g., Moran & al., 1995; Bostock 1998; Mickel & Smith, 2004; Lin & al., 2013).

For clarity, here we note those few exceptions where we chose to more narrowly delimit a species geographical distribution: (1) Occurring as rare disjuncts in the southern U.S.A., the Antillean and/or Central/South American *A. tenerum* Sw., *A. tricholepis* Fée, and *A. melanoleucum* Willd. were not scored for having a distributional range in North America; (2) Although having escaped cultivation on a few occasions, the Old World species *A. hispidulum* was also not scored for having a distributional range in North America.

■ RESULTS

The portions of the *rbcL*, *atpA*, *rpoA*, and *chlN* genes analyzed in this study comprised 1309, 1506, 616, and 630 bp, respectively (Table 1). Maximum likelihood analyses of the four single gene datasets resulted in largely congruent topologies (trees not presented), with conflicting resolutions almost always lacking good bootstrap support (i.e., not supported by a bootstrap $\geq 70\%$; Mason-Gamer & Kellogg, 1996). Therefore, all four datasets were combined into a single dataset comprising a total of 4061 characters, of which 1733 were variable. The phylogeny resolved from the maximum likelihood analysis of the combined plastid dataset is shown in Fig. 2. Relative to the vittarioid outgroup (not shown), the monophyly of *Adiantum* is strongly supported. All *Adiantum* taxa included can be unequivocally assigned to one of nine major clades. Although the phylogenetic backbone has several very short branches (see Fig. 2A, inset) with weak support, each of the nine clades is supported with a maximum likelihood bootstrap percentage (BS) of 100 and a Bayesian posterior probability (PP) of 1.00 (*digitatum*, *formosum*, *tenerum*, *pedatum*, *capillus-veneris*, *davidii*, *philippense*, *tetraphyllum*), except for *peruvianum* (97%, 0.99, Fig. 2C). Together, the *capillus-veneris*, *davidii* and *philippense* clades form a strongly supported larger monophyletic group (Fig. 2B). The *peruvianum* and *tetraphyllum* clades are also strongly supported as sister (Fig. 2C). Sister relationships between the *tenerum* and *pedatum* clades and between the *formosum* and *digitatum* clades are weakly supported (Fig. 2A).

In Fig. 3A, we map the results of our maximum likelihood-based ancestral character state reconstructions of leaf blade architecture. Our results reveal remarkable convergent evolution, with four of the five character states scored across *Adiantum* being observed in multiple clades. An exclusive synapomorphy—leaves once-pinnate with prolonged rooting tips—mostly defines the *philippense* clade. Although a diversity of leaf forms exists throughout *Adiantum*, most taxa have leaves that are more than once-pinnate and this state is exhibited throughout eight of

the nine clades; only the *formosum* and *pedatum* clades have a few taxa that exhibit the distinct pseudopedate form (Fig. 3A). Simple leaves, although a rare occurrence in *Adiantum*, occur in three distinct clades (*davidii*, *philippense*, *peruvianum*).

Geographic distributional ranges of the terminal *Adiantum* species were usually restricted to only one of the six regions we recognized (for 109 out of 146 taxa [75%]; Figs. 3B, 4; Electr. Suppl.: Table S2). Of the remaining 37 taxa, 33 occur in only two regions, and only 4 occur in more than 2 regions (Electr. Suppl.: Table S2).

■ DISCUSSION

In recent decades, *Adiantum*, especially *A. capillus-veneris*, has occupied an increasingly prominent role as a “model plant” for the fern lineage. It was the first fern to have its chloroplast genome sequenced (Wolf & al., 2003). Kawai-Toyooka & al. (2004) developed a DNA interference (DNAi) approach for targeted gene silencing in *A. capillus-veneris*, and it has been particularly important as an experimental system in studying plant photobiology (e.g., Kawai & al., 2003; Wada, 2007). A worldwide approximation of species relationships within *Adiantum* is especially important for placing these and future experimental studies within a robust phylogenetic context.

Molecular studies of *Adiantum* to date have been mostly focused on specific geographic regions or phylogenetic groups. Prado & al. (2007) examined *Adiantum* as part of a larger study of Pteridaceae within Brazil, while Bouma & al. (2010) carried out a similar study within New Zealand. Each of these studies relied exclusively on *rbcL* to estimate species relationships. More recently, four taxon-specific, multigene studies have been carried out, but these were limited to specific monophyletic clades within *Adiantum* (McCarthy, 2012; Hirai & al., 2016; Kuo & al., 2016; Wang & al., 2017). To date, the most extensive studies of *Adiantum* focused on Chinese taxa (48 species), with limited sampling from other regions (Lu & al., 2012), and on the Antillean archipelago (Regalado & al., 2017), which had a more comprehensive sampling (101 species). Here, we sampled 146 *Adiantum* taxa, two-thirds of known species, with an aim to rigorously determine relationships that previously may have been obscured by morphological homoplasy.

***Adiantum* phylogeny, leaf morphology, and geography.**

— We recognize nine robustly supported clades in our phylogeny (Fig. 2), some of which were previously noted in Pryer & al. (2016) using representative species. Several were first resolved by Lu & al. (2012), and these were also confirmed by Regalado & al. (2017) using new and previously published plastid sequences. The backbone relationships among most of these nine clades, however, are represented by several very short branches (Fig. 2A, see inset phylogram) that are weakly supported. Nevertheless, clade membership was not ambiguous for any taxon in our large dataset; all were well resolved within one of the nine clades (Fig. 2).

The smallest recognized clade (*digitatum*) comprises just two species, *A. digitatum* C.Presl and *A. subcordatum* Sw. Both have a leaf architecture that is more than once-pinnate,

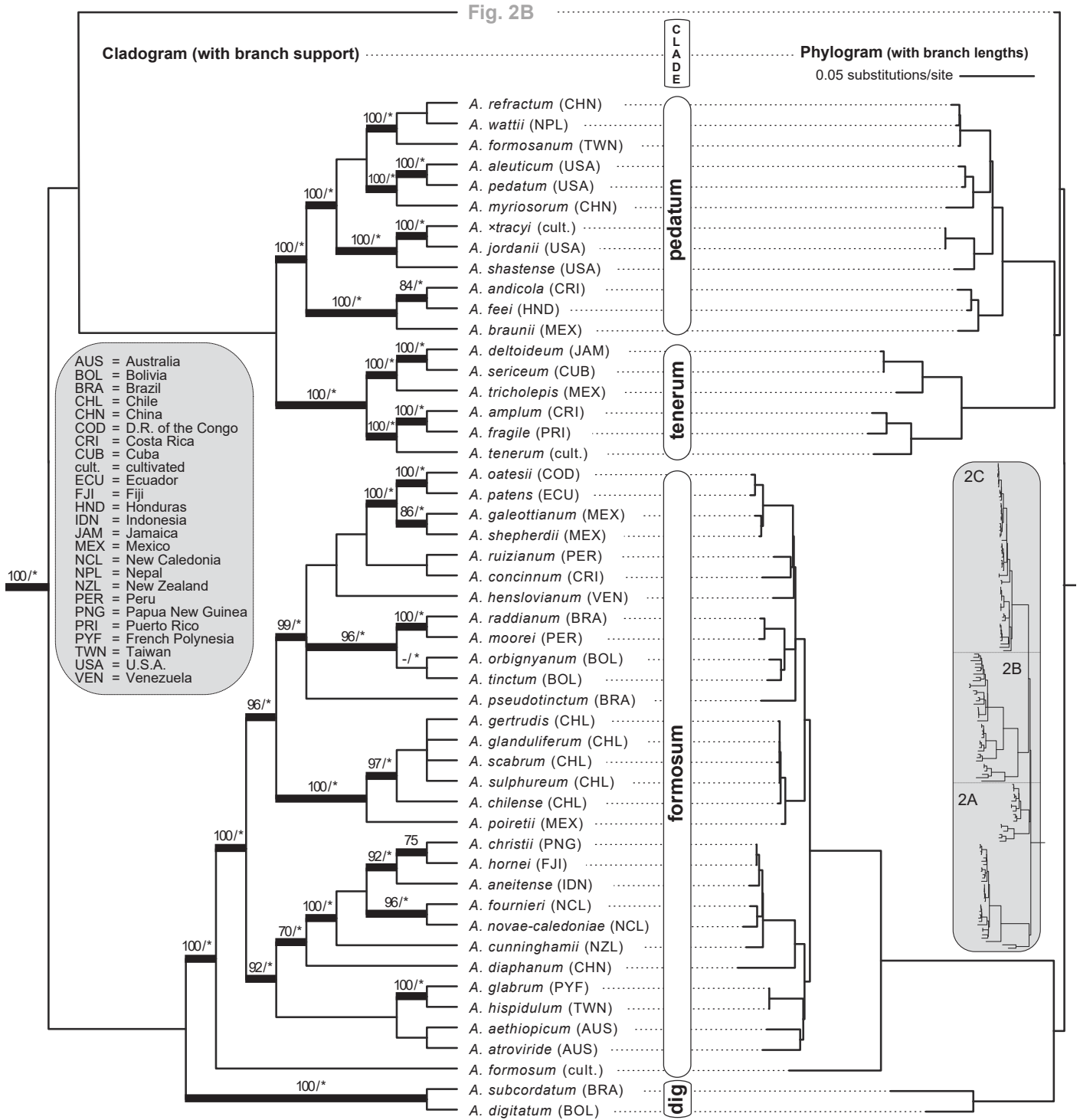


Fig. 2A. *Adiantum* phylogeny resulting from maximum likelihood analysis of plastid *rbcL*, *atpA*, *rpoA*, and *chlN* data presented both as a phylogram (right) to reveal branch lengths and a cladogram (left) to clarify relationships. On the cladogram, maximum likelihood bootstrap percentages (BS ≥ 70) and Bayesian posterior probabilities (PP ≥ 0.95; indicated with asterisks) are provided at the nodes (BS/PP); dashes indicate BS support values below 70 or PP < 0.95; thickened branches correspond to BS support ≥ 70%. Geographical provenance of each voucher used to construct the phylogeny is shown as a 3-letter country code (<https://laendercode.net/en/3-letter-list.html>) following the species name. Note that the six vittarioid fern outgroups are not shown. Major *Adiantum* clades discussed in text are indicated in vertical ellipses on tree: digitatum (dig); formosum; tenerum; pedatum. Left inset shows 3-letter country code abbreviations. Right inset depicts entire *Adiantum* phylogram (highly reduced). Phylogeny continues in Fig. 2B.

but each has a strikingly different pinnule morphology: *A. subcordatum* has large, heart-shaped ultimate segments, and *A. digitatum* has smaller, more divided segments. The two species are found in South America and are restricted geographically therein (Fig. 3B). Hooker & Baker (1867) segregated *A. digitatum* into what they called the “scandentes group” recognizing it might be unique because of its climbing habit—rare in *Adiantum*. Our phylogenetic analysis confirms its separation from essentially all other South American taxa, and from the only other species they placed in this group (*A. feii* T.Moore ex Fée) that we show here to be more distantly related (pedatum clade; see below).

The digitatum clade is weakly supported (Fig. 2A) as sister to the much larger formosum clade, where *A. formosum* (Australasia) is resolved as sister to three well-supported subclades (Figs. 2A, 3): *A. atroviride* Bostock to *A. christii* (Australasia, Africa, Eurasia), *A. poiretii* Wikstr. to *A. gertrudis* Espinosa (Eurasia, Central America, South America, Africa) and *A. pseudotinctum* Hieron. to *A. oatesii* (Central America, South America, Africa). Almost all species of the formosum clade are native to the southern hemisphere and have variations of the pinnate leaf architecture (Fig. 3A): once-pinnate (no rooting tip), more than once-pinnate, and several instances of pseudopedate (e.g., *A. hispidulum*, *A. diaphanum* Bl., *A. patens*).

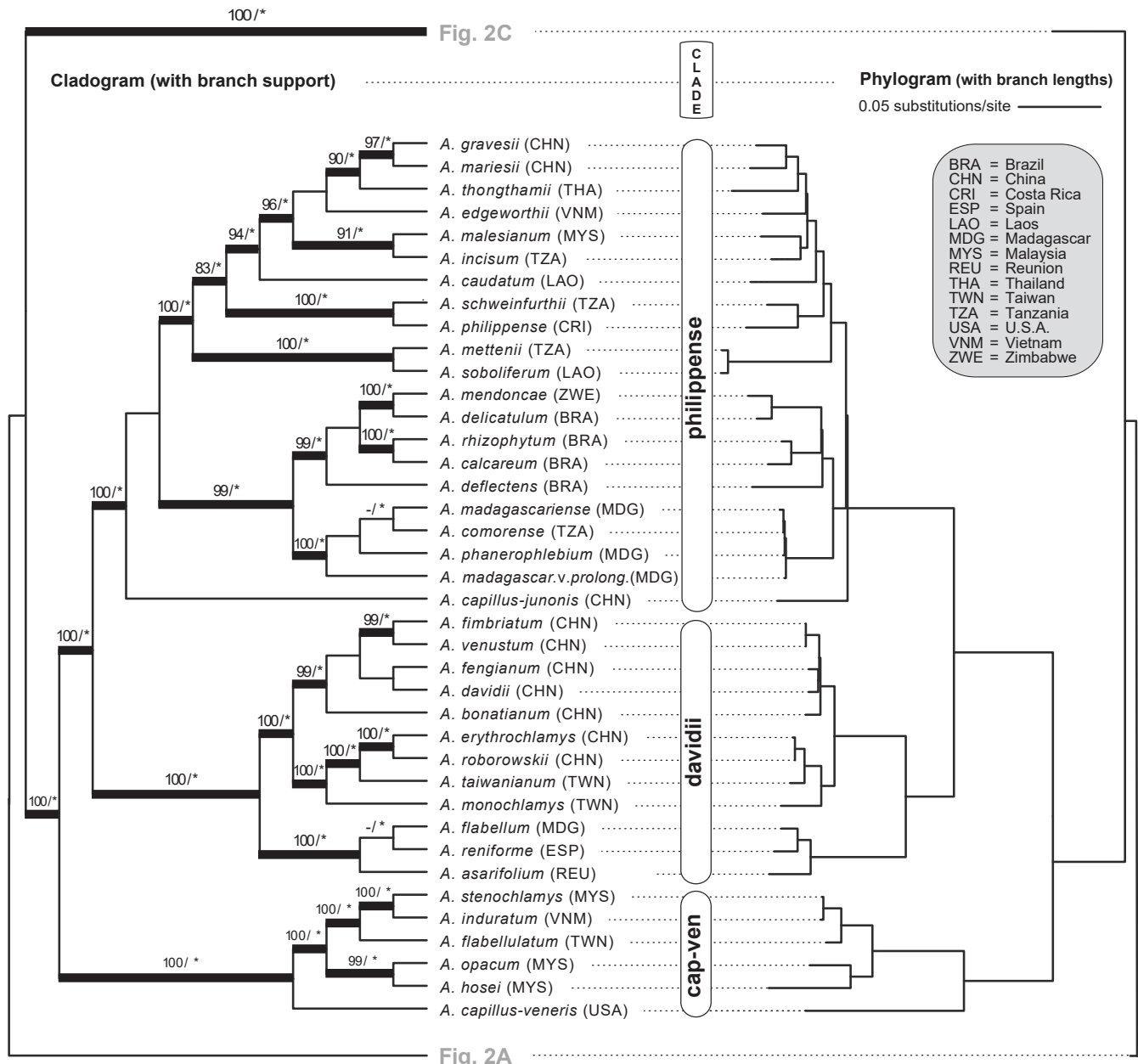


Fig. 2B. Continued from Fig. 2A. Major clades discussed in text are indicated in vertical ellipses on tree: capillus-veneris (cap-ven); davidii; philippense. Inset shows 3-letter country code abbreviations. Phylogeny continues in Fig. 2C.

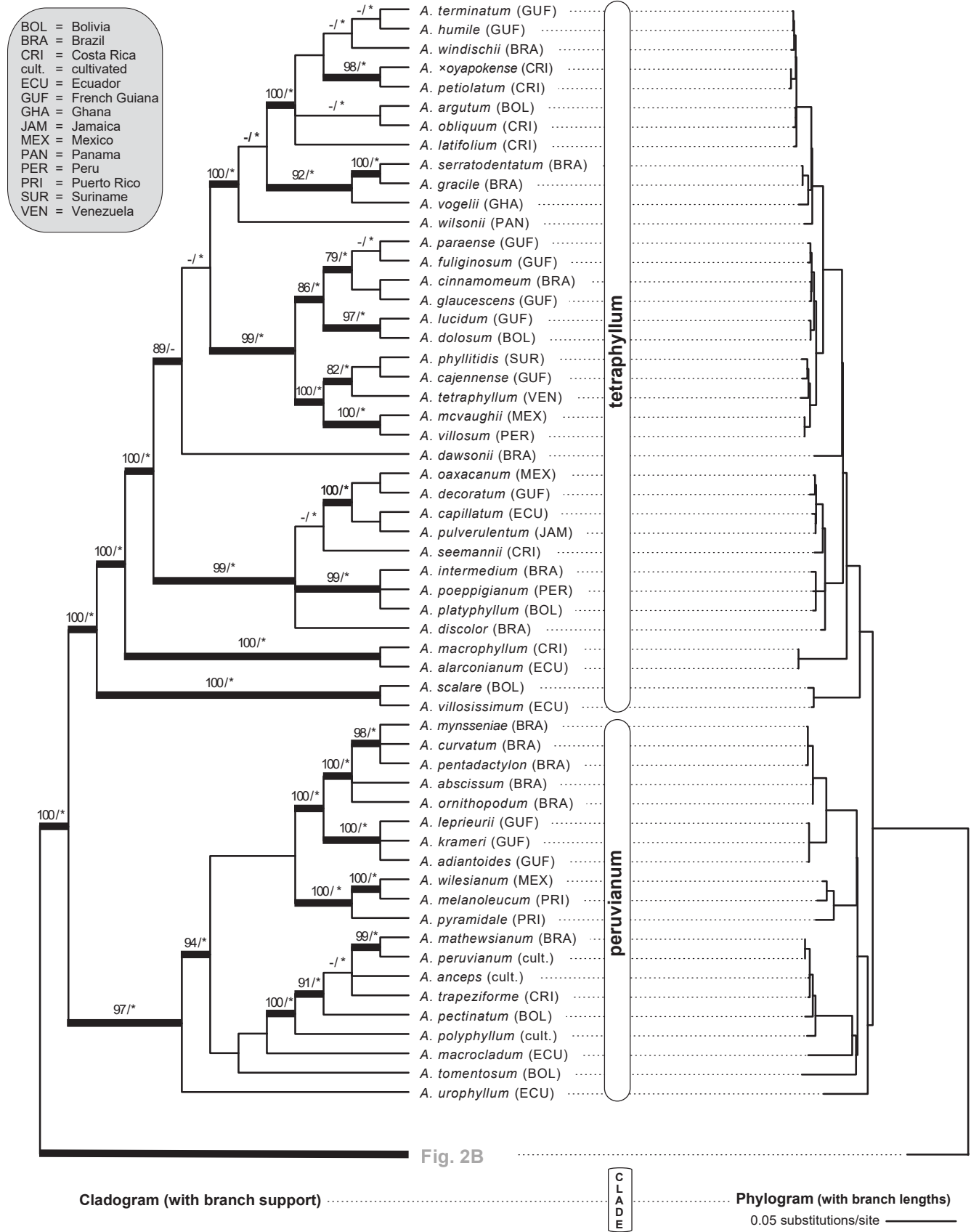


Fig. 2C. Continued from Fig. 2B. Major clades discussed in text are indicated in vertical ellipses on tree: peruvianum; tetraphyllum. Inset shows 3-letter country code abbreviations.

The pedatum and tenerum clades are resolved as sister, but again, with weak support (Fig. 2A). The tenerum clade comprises species found predominantly in Mexico, Central America and the Antilles (Fig. 3B), with a few disjunct populations in North America; the six species included in our study represent what is considered to be the entirety of the group. It is intriguing that this clade is resolved as sister to the pedatum clade, whose members are predominantly found in temperate regions of the Northern Hemisphere, except for a few species in the Neotropics (*A. andicola* Liebm., *A. feei*, *A. braunii* Mett. ex Kuhn). These neotropical species form a strongly supported (100% BS) subclade that is restricted to a subset of the same geographical range as members of the tenerum clade (Fig. 3B). Sister to this neotropical subclade within the pedatum clade are three distinct and robustly supported lineages (subclades) whose interrelationships are not well resolved (Fig. 2A). These include a subclade of Asian species (*A. refractum* Christ, *A. wattii* Baker, *A. formosanum* Tagawa), one of essentially Californian endemics (*A. jordanii* Müll.Hal., *A. shastense* Huiet & A.R.Sm., *A. ×tracyi* C.C.Hall ex W.H.Wagner), and the *A. pedatum* complex (*A. pedatum*, *A. myriosorum* Baker, *A. aleuticum*) that is found in both North America and Asia (Fig. 3B). Almost all species in the pedatum and tenerum clades have a pinnate leaf architecture (once-pinnate to mostly more than once-pinnate, including pseudopinnate; see Fig. 3A).

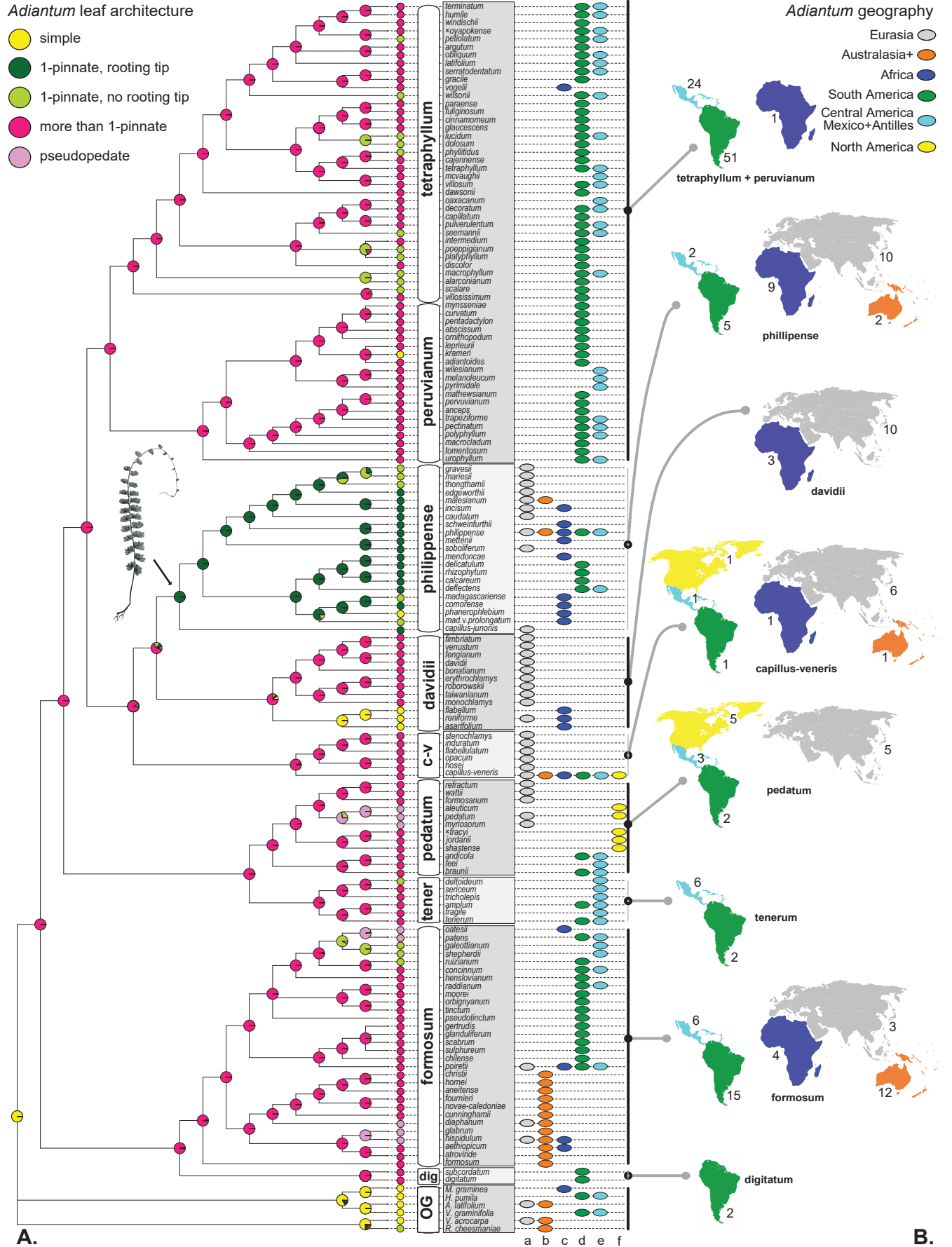
Together, three of the nine major clades (*capillus-veneris*, *davidii*, philippense) are strongly supported (100%) as a monophyletic group, as was first shown by Lu & al. (2012). Each of the three is itself strongly supported (Fig. 2B). The clade with the most wide-ranging species of *Adiantum*, *A. capillus-veneris*, is sister to a narrow-ranging group of mostly paleotropical species (Fig. 2B) within the *davidii* and philippense clades (Fig. 3B). The *davidii* clade comprises two disparate morphological lineages: one consists of simple-bladed species (*A. asarifolium* Willd., *A. reniforme*, *A. flabellum* C.Chr.) found in Eurasia and Africa, whereas the other has leaves that are more than once-pinnate and found in temperate and tropical Asia and the Himalayas (Figs. 2B, 3A, B). Species composing the philippense clade have the most constant and unique leaf morphology of any of the major clades of *Adiantum* (Fig. 3A); members are exclusively once-pinnate (except for simple-bladed *A. phanerophlebium* (Baker) C.Chr. in Madagascar). Most also have prolonged, flagelliform blade tips that are capable of rooting (hence the common name “walking ferns” that has sometimes been applied to these taxa) and the occurrence of this

character state in *Adiantum* is restricted to this clade. In previous classifications, the philippense group was frequently recognized (e.g., Hooker & Baker, 1867), and this has been confirmed here with the larger dataset. Although the philippense clade is nested well within a larger and predominantly paleotropical clade, it harbors a unique neotropical diversification comprising five species that are almost exclusively Brazilian (*A. mendoncae* Alston from Africa being the exception), and this radiation is strongly supported (99%) as sister to a small, mostly Malagasy clade (Figs. 2B, 3B).

Finally, the tetraphyllum and peruvianum clades are strongly supported as sister (100%), and together they compose the largest neotropical radiation of *Adiantum* (Figs. 2C, 3B). A single African species (*A. vogelii* Mett. ex Kuhn) is the only member of these lineages to naturally occur outside the Neotropics. Found in both clades are species that were once placed in the segregate genus *Hewardia* (Smith, 1841) characterized by the presence of anastomosing veins; *A. adiantoides* (J.Sm.) C.Chr. and *A. leprieurii* Baker are closely related in the peruvianum clade (Fig. 2C), whereas *A. dolosum* Kunze and *A. wilsonii* Hook. are members of the tetraphyllum clade and not closely related. *Hewardia* is therefore not a natural group. The peruvianum clade comprises predominantly South American species, although some have ranges extending north into Mexico, and a few are exclusive to the Antilles (Fig. 3B). With just one exception (*A. krameri* B.Zimmer), the taxa in this clade have leaves that are more than once-pinnate (Fig. 3A). Similarly, the tetraphyllum clade is also predominantly South American, but with some species additionally ranging into Mexico, Central America and the Antilles (Fig. 3B). Only a few species are limited to the northern portion of the Neotropics (e.g., *A. mcvaughii* Mickel & Beitel and *A. oaxacanum* Mickel & Beitel) and may be unique, localized hybrids (nuclear DNA data needed to confirm this hypothesis). Most species in the tetraphyllum clade are more than once-pinnate, but several are just once-pinnate (Fig. 3A). Many of the once-pinnate species have large ultimate segments (to ca. 10 cm long or more) (e.g., *A. macrophyllum* Sw., Fig. 1A).

The only previous infrageneric taxon (recognized based on a morphological character) that has molecular support in our analysis is *A. sect. Adiantellum* (Kuhn, 1881; Diels, 1902). Kuhn's (1881) two sections of *Adiantum* were characterized by whether the sporangia were borne only on the veins (“*A. sect. Euadiantum*” = *A. sect. Adiantum*) or also found between the veins (*A. sect. Adiantellum*). Of the 113 *Adiantum* species listed

Fig. 3. Visualization of *Adiantum* leaf morphology and extant geography in a phylogenetic context. **A**, Phylogeny from Fig. 2 showing the maximum likelihood-based ancestral reconstructions of five leaf architecture character state types scored for *Adiantum* (simple; once-pinnate with rooting tip; once-pinnate, no rooting tip; more than once-pinnate; pseudopinnate). Although taxon names are highly reduced (but available for online viewing), each taxon's position in the phylogeny matches exactly its position shown in Fig. 2. Pie charts at each node represent the posterior probabilities of the state of the common ancestor present at that node. Nine major *Adiantum* clades discussed in the text are indicated with vertical ellipses, as in Fig. 2. **B**, Geographic occurrence indicated for each *Adiantum* taxon sampled according to colored ovals in six columns: a, gray: Eurasia (incl. Malaysia, Philippines, Sumatra, Borneo, and Indonesia); b, orange: Australasia and the Pacific (incl. Australia, New Zealand, and New Guinea); c, dark blue: Africa (incl. Madagascar); d, green: South America; e, light blue: Mexico, Central America and the Antilles; f, yellow: North America. Geographic distributions for major clades are reflected in accompanying maps to the right. Numbers adjacent to regions on map indicate how many species in that clade occur there. Maps modified from http://commons.wikimedia.org/wiki/File:Blank_map_of_world_no_country_borders.PNG under the terms of the GNU Free Documentation License, version 1.2.



by Kuhn (1881), all 30 members of *A.* sect. *Adiantellum* are in the formosum clade, or are predicted to fall in this group (Fig. 2A).

***Adiantum* leaf architecture.** — Vast morphological diversity occurs in fern leaves (Vasco & al., 2013), and *Adiantum* is no exception. Not surprisingly, most classifications of *Adiantum* have relied predominantly on leaf dissection and to some extent on indusial morphology and venation. Our sampling attempted to include as much morphological variation within *Adiantum* leaves as possible to determine the extent of homoplasy. Homoplasy for the more than once-pinnate “capillus-veneris” leaf form and the pseudopedate form has previously been shown (Prado & al., 2007; Schuettpelz & al., 2007; Bouma & al., 2010; Lu & al., 2012). We confirm this here with a larger dataset. But, even within the formosum clade (Figs. 2A, 3A), the pseudopedate form arose at least three times independently (*A. hispidulum*/*A. glabrum* Copel.; *A. diaphanum*; *A. patens*/*A. oatesii*). This morphology also occurs as a synapomorphy for a single lineage within the pedatum clade (*A. myriosorum*, *A. pedatum*, *A. aleuticum*; Figs. 2A, 3A). In all cases, the closest relatives to these pseudopedate forms are more than once-pinnate.

Five *Adiantum* species in our phylogeny have simple blades (Fig. 3A), with three very distinct, independent origins (*A. reniforme* subgroup [davidii clade], *A. phanerophlebium* [philippense clade], and *A. krameri* [peruvianum clade]). Two additional simple-bladed taxa (*A. cordatum* Maxon and *A. parishii* Hook.) occur in *Adiantum*, but we were unable to obtain material of these for our study. Based on their morphology and geography, it is likely they are within the larger peruvianum/tetraphyllum and philippense/davidii clades, respectively, but they may have originated independently from the other simple-bladed species. The genus *Lindsaea* Dryand. ex Sm., often confused with *Adiantum* due to a morphological convergence in once-pinnate and twice-pinnate blade forms, also has several simple-bladed species. Interestingly, however, these all occur in a single clade of neotropical species (Lehtonen & al., 2010). This contrasts sharply with what is observed for simple-bladed

Adiantum species, which are found on several continents and have multiple independent origins.

In previous classification schemes (e.g., Tryon & Tryon, 1982), the once-pinnate, neotropical *Adiantum* species with large ultimate segments (mostly within the tetraphyllum clade, Fig. 3) were often segregated. However, it is clear in Fig. 3 that these species do not compose a natural monophyletic group within any neotropical lineage. Only the once-pinnate species, often with rooting tips, first recognized by Hooker & Baker (1867) and then by Lu & al. (2012), have been substantiated here as a natural group (philippense clade) with our wider sampling from multiple continents.

***Adiantum* geography.** — Of the nine clades recognized in Fig. 2, all but three have at least one species that resides an ocean away from the region where most of the species in that clade occur (e.g., digitatum, peruvianum, and tenerum clades, Fig. 3B). Also, clades dominated by strongly supported sister relationships often reflect a geographic component. For example, the capillus-veneris, davidii and philippense clades comprise species that occur predominantly in the Palearctic or in temperate Asia. On the other hand, the tetraphyllum and peruvianum clades are neotropical, with only a single unique species among them that naturally occurs outside the region (*A. vogelii* in Africa). The distributional ranges for each of the terminal *Adiantum* taxa were found to be mostly restricted to one of the six designated biogeographical regions (109 out of 146 taxa [75%]; Figs. 3B, 4; Electr. Suppl.: Table S2). Thirty-three of the remaining 37 taxa occur in only two regions (27 of the 33 taxa, 81%, are found in both South America and Mexico/Central America/Antilles), and only four taxa occur in more than two regions (Electr. Suppl.: Table S2; *A. capillus-veneris* 6 regions; *A. hispidulum* 3 regions; *A. philippense* 5 regions; *A. poiretii* 4 regions).

In 2001, Moran & Smith examined possible floristic affinities between neotropical and African-Madagascan pteridophytes. Among the 114 examples of same-species or species-pairs in their list are five for *Adiantum*, all of which were included in our study. It has already been shown within the formosum clade that *A. poiretii* from the Neotropics and Africa group together, and that neotropical *A. patens* and African *A. oatesii* are a closely related species-pair (Hirai & al., 2016). For the *A. delicatulum* Mart. (neotropical) and *A. mendoncae* (African) species-pair in the philippense clade, our molecular results support the hypothesis that these two are more closely related than either is to any other species (Figs. 2B, 3B). However, for the remaining two *Adiantum* species-pairs noted by Moran & Smith (2001), our results do not support the suggested affinities. Christensen (1932) had proposed that the simple-bladed *A. phanerophlebium* (from the philippense clade) was most likely to be closely related to a neotropical species. Our results reveal that it is part of a distinct Malagasy diversification within the philippense clade (Figs. 2B, 3B), in a subclade that is sister to the radiation that includes the *A. delicatulum* and *A. mendoncae* species-pair. Finally, Moran & Smith (2001) noted that *A. tetraphyllum* and *A. vogelii* were both bipinnate, and this shared leaf morphology does place them in the same clade; however, they are not closely related therein (Figs. 2C, 3).

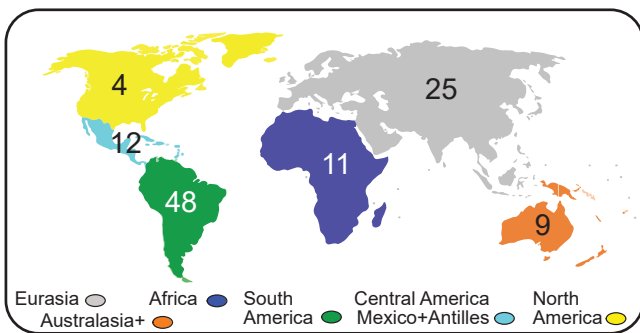


Fig. 4. Number of terminal *Adiantum* taxa sampled in this study found to be restricted to one of the six designated biogeographical regions (109 out of 146 taxa, 75%). Map legend same as for Fig. 3B. See also Electr. Suppl.: Table S2. Map modified from http://commons.wikimedia.org/wiki/File:Blank_map_of_world_no_country_borders.PNG under the terms of the GNU Free Documentation License, version 1.2.

■ CONCLUSION

We believe that our sampling includes all major lineages within *Adiantum*. Our dataset is among the most comprehensive (i.e., including sequence data for the greatest proportion of known species) for any large monophyletic, subcosmopolitan genus of ferns (see also Zhang & Zhang, 2018 [*Pteris*] and Zhang & al., 2017 [*Tectaria*]). It is remotely possible that due to the extreme homoplasy in the group there may be phylogenetically important taxa yet to be sampled. More likely, further resolution of relationships within this genus will occur only with larger datasets of either plastid and/or nuclear markers. Moving forward, this phylogenetic study on *Adiantum* and its companion study on vittarioids (using an identical set of plastid genes; Schuettpehlz & al., 2016) provide an improved framework with which to examine the evolutionary mechanisms that produced two sister lineages with radically different morphological, ecological, and genomic histories. An extreme makeover occurred during the evolutionary history of the *Adiantum*+vittarioid clade—a transformation no less spectacular than that observed between the illustrious whale and hippo sister groups. We hope that future studies will reveal the “how, when, and where” details of the evolutionary processes that led to this profound differentiation.

■ AUTHOR CONTRIBUTIONS

Conceptualization: LH, ARS, ES & KMP; *Data Curation*: LH, F-WL & T-TK; *Formal Analysis*: F-WL; *Funding Acquisition*: LH, ES & KMP; *Investigation*: LH; *Project Administration*: LH & KMP; *Resources*: LH, JP, ARS & KMP; *Supervision*: LH & KMP; *Validation*: LH, F-WL, T-TK & KMP; *Visualization*: KMP; *Writing – Original Draft Preparation*: LH & KMP; *Writing – Review & Editing*: LH, F-WL, T-TK, JP, ARS, ES & KMP — ES, <https://orcid.org/0000-0003-3891-9904>; F-WL, <https://orcid.org/0000-0002-0076-0152>; JP, <https://orcid.org/0000-0003-4783-3125>; KMP, <https://orcid.org/0000-0002-9776-6736>; LH, <https://orcid.org/0000-0001-6189-8641>; T-TK, <https://orcid.org/0000-0003-1372-7324>

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Appendix 1. Ingroup and outgroup taxa sampled in this study. For each collection, the species name, place of origin, voucher information, Fern Lab Database (<http://fernlab.biology.duke.edu>) number and GenBank accession numbers (*rbcL*, *atpA*, *rpoA*, *chlN*, in that order) are provided. Missing information is indicated with an n-dash (-); 453 newly deposited sequences are prefixed with MH.

INGROUP. *Adiantum abscissum* Schrad., Brazil, *Hirai 718* (SP), #8903, MH019532, MH019315, MH019653, MH019423; *Adiantum adiantoides* (J.Sm.) C.Chr., French Guiana, *Boudrie 3927* (UC), #2300, MH019533, MH019316, MH019654, MH019424; *Adiantum aethiopicum* L., Australia, *Nagalingum 24* (DUKE), #3895, KC984519, KC984436, MH019655, MH019425; *Adiantum alarconianum* Gaud., Ecuador, *Rubio 1819* (MO), #3721, MH019534, MH019317, MH019656, MH019426; *Adiantum aleuticum* (Rupr.) C.A.Paris, U.S.A.: Washington, *Windham 3628* (DUKE), #9505, MH019535, MH019318, MH019657, MH019427; *Adiantum amplum* C.Presl, Costa Rica, *Rothfels 08-057* (DUKE), #5177, MH019536, MH019319, MH019658, MH019428; *Adiantum anceps* Maxon & Morton, Cultivated, *Smith 2894* (UC), #2102, MH019537, MH019320, MH019659, MH019429; *Adiantum andicola* Liebm., Costa Rica, *Rothfels 2641* (DUKE), #5549, KU147272, KU147243, KU147280, KU147251; *Adiantum aneitense* Carruth., Indonesia, *Johns 10039* (K), #8964, MH019538, MH019321, MH019660, MH019430; *Adiantum argutum* Splitg., Bolivia, *Jimenez 2028* (LPB), #8970, MH019539, MH019322, MH019661, MH019431; *Adiantum asarifolium* Willd., Réunion, *Huiet 110* (UC), #4605, MH019540, MH019323, MH019662, MH019432; *Adiantum atroviride* Bostock, Australia, *Kessler 14196* (Z), #8810, MH019541, MH019324, MH019663, MH019433; *Adiantum bonatianum* Brause, China, *Kuo 1551* (TAIF), #9492, MH019542, MH019325, MH019664, MH019434; *Adiantum braunii* Mett. ex Kuhn, Mexico, *P. Rothfels 2* (UC), #6806, MH019543, MH019326, MH019665, MH019435; *Adiantum cajennense* Willd., French Guiana, *Boudrie 3931* (UC), #2296, MH019544, MH019327, MH019666, MH019436; *Adiantum calcareum* Gardner, Brazil, *Hirai 717* (SP), #8904, MH019545, MH019328, MH019667, MH019437; *Adiantum capillatum* A.R.Sm. & J.Prado, Ecuador, *Croat 95353* (MO), #8966, MH019546, -, MH019668, -; *Adiantum capillus-junonis* Rupr., China, *Sundue 988* (DUKE), #6185, MH019547, MH019329, MH019669, MH019438; *Adiantum capillus-veneris* L., U.S.A.: California, *Huiet 104* (UC), #4609, KU147273, KU147244, KU147281, KU147252; *Adiantum caudatum* L., Laos, *Sugong WS-1837* (MO), #9429, MH019548, MH019330, MH019670, MH019439; *Adiantum chilense* Kaulf., Chile, *Kelch 127* (UC), #9216, MH019549, MH019331, MH019671, MH019440; *Adiantum christii* Rosenst., Papua New Guinea, *Hoogland 6901* (UC), #9608, -, -, MH019672, -; *Adiantum cinnamomeum* Lellinger & J.Prado, Brazil, *Prado 1831* (SP), #8923, MH019550, MH019332, MH019673, MH019441; *Adiantum comorense* Fée, Tanzania, *Mwangoka 5695* (MO), #9318, MH019551, MH019334, -, MH019443; *Adiantum concinnum* Humb. & Bonpl. ex Willd., Costa Rica, *Grantham 0112-90* (UC), #2134, KX524209, KX524413, KX524360, KX524260; *Adiantum cunninghamii* Hook., New Zealand, *A.R. Smith 2914* (UC), #4727, MH019552, MH019335, MH019675, MH019444; *Adiantum curvatum* Kaulf., Brazil, *Barbosa 1227* (UC), #9409, MH019553, MH019336, MH019676, MH019445; *Adiantum davidii* Franch., China, *Kuo 1561* (TAIF), #9483, MH019554, MH019337, MH019677, MH019446; *Adiantum dawsonii* Lellinger & J.Prado, Brazil, *Prance 19082* (UC), #9147, MH019555, MH019338, MH019678, MH019447; *Adiantum decoratum* Maxon & Weath., French Guiana, *Boudrie 3760* (UC), #9410, MH019556, MH019339, MH019679, MH019448; *Adiantum deflectens* Mart., Brazil, *Schuettpelz 1390* (DUKE), #8324, MH019557, MH019340, MH019680, MH019449; *Adiantum delicatulum* Mart., Brazil, *Hirai 704* (SP), #8908, MH019558, MH019341, MH019681, MH019450; *Adiantum deltoideum* Sw., Jamaica, *Crosby 507* (UC), #9421, MH019559, MH019342, MH019682, MH019451; *Adiantum diaphanum* Bl., China, *Wuzhishan Fern Survey 67* (MO), #9322, MH019560, -, MH019683, MH019452; *Adiantum digitatum* C.Presl, Bolivia, *Wood 14432* (UC), #4673, KU147274, KU147246, KU147283, KU147254; *Adiantum discolor* J.Prado, Brazil, *Labiak 3702* (SP), #9141, MH019562, MH019344, MH019685, -; *Adiantum dolosum* Kunze, Bolivia, *Jimenez 2023* (UC), #8983, MH019563, MH019345, MH019686, MH019454; *Adiantum edgeworthii* Hook., Vietnam, *Kuo 1840* (TAIF), #9486, MH019565, MH019347, MH019688, MH019456; *Adiantum erythrochlamys* Diels, China, *Sino-Amer. Exped. 1712* (UC), #4628, MH019566, -, MH019689, -; *Adiantum feei* T.Moore ex Fée, Honduras, *Soto 95* (UC), #4680, MH019567, -, MH019690, MH019457; *Adiantum fengianum* Ching, China, *Sundue 1005* (NY), #6179, MH019568, MH019348, MH019691, MH019458; *Adiantum fimbriatum* Christ, China, *Zhang 1783* (UC), #4626, MH019569, -, MH019692, MH019459; *Adiantum flabellulatum* L., Taiwan, *Schuettpelz 1016A* (DUKE), #4759, MH019561, MH019343, MH019684, -; *Adiantum flabellum* C.Chr., Madagascar, *Rakotovoao 2310* (MO), #9325, MH019570, MH019349, MH019693, -; *Adiantum formosanum* Tagawa, Taiwan, *Li 1402* (DUKE), #8836, MH019571, MH019350, MH019694, MH019460; *Adiantum formosum* R.Br., Cultivated, *Smith s.n.* (UC), #4602, KC984520, KC984437, KU147289, KU147257; *Adiantum fournieri* Copel., New Caledonia, *Webster 14478* (DAV), #4635, MH019572, MH019351, MH019695, MH019461; *Adiantum fragile* Sw., Puerto Rico, *Axelrod 12881* (UC), #4678, MH019573, MH019352, MH019696, MH019462; *Adiantum fuliginosum* Fée, French Guiana, *Boudrie 3925* (UC), #2303, MH019574, MH019353, MH019697, MH019463; *Adiantum galeottianum* Hook., Mexico, *Mickel 7004* (UC), #4674, KX524197, KX524401, KX524348, KX524248; *Adiantum gertrudis* Espinosa, Chile, *Eyerdam 10038* (UC), #9219, MH019575, KX524422, KX524369, KX524269; *Adiantum glabrum* Copel., French Polynesia: Rapa, *St. John 15495* (UC), #9149, MH019576, -, MH019698, -; *Adiantum glanduliferum* Link, Chile, *Hartwig 54.059-S1* (UC), #9218, KX524216, KX524421, KX524368, KX524268; *Adiantum glaucescens* Kl., French Guiana, *Boudrie 3930* (UC), #2295, MH019577, MH019354, MH019699, MH019464; *Adiantum gracile* Fée, Brazil, *Prado 2242* (SP), #9137, MH019578, MH019355, MH019700, MH019465; *Adiantum gravesii* Hance, China, *Zhang 376* (MO), #6423, MH019579, MH019356, MH019701, MH019466; *Adiantum henslovianum* Hook.f., Venezuela, *Fay 1535* (UC), #9215, KX524213, KX524417, KX524364, KX524264; *Adiantum hispidulum* Sw., Taiwan, *Schuettpelz 1168A* (DUKE), #4915, MH019580, MH019357, MH019702, MH019467; *Adiantum hornei* Baker, Fiji, *Game 95/10* (UC), #4669, MH019581, -, MH019703, MH019468; *Adiantum hoseri* Baker, Malaysia, *Beaman 10302* (UC), #4666, MH019582, MH019358, MH019704, MH019469; *Adiantum humile* Kunze, French Guiana, *Boudrie 3934* (UC), #2298, MH019583, MH019359, MH019705, MH019470; *Adiantum incisum* Forssk., Tanzania, *Gereau 6840* (MO), #9203, MH019584, MH019360, MH019706, MH019471; *Adiantum induratum* H.Christ, Vietnam, *WP 963* (MO), #9323, MH019585, MH019361, MH019707, -; *Adiantum intermedium* Sw., Brazil, *Prado 1769* (SJRJ), #9134, MH019586, MH019362, MH019708, MH019472; *Adiantum jordanii* Müll.Hal., U.S.A.: California, *Li 1196* (DUKE), #9509, MH019587, MH019363, MH019709, MH019473; *Adiantum krameri* B.Zimmer, French Guiana, *van der Werff 12986* (UC), #4642, MH019588, MH019364, MH019710, -; *Adiantum latifolium* Lam., Costa Rica, *Rothfels 08-170* (DUKE), #5181, MH019589, MH019365, MH019711, MH019474; *Adiantum lepieurii* Baker, French Guiana, *Boudrie 3926* (UC), #2301, MH019590, MH019366, MH019712, -; *Adiantum lucidum* (Cav.) Sw., French Guiana, *Boudrie 3929* (UC), #2299, MH019591, MH019367, MH019713, MH019475; *Adiantum macrocladum* Kl., Ecuador, *Tuomisto 10852* (UC), #9411, MH019592, MH019368, MH019714, MH019476; *Adiantum macrophyllum* Sw., Costa Rica, *Rothfels 08-094* (DUKE), #5129, MH019593, MH019369, MH019715, MH019477; *Adiantum madagascariense* H.Rosend., Madagascar, *Trigui 531* (MO), #9319, MH019594, MH019370, -, MH019478; *Adiantum madagascariense* var. *prolongatum* (Bonap.) Tardieu, Madagascar, *Nusbaumer 2749* (MO), #9320, MH019595, MH019371, -, MH019479; *Adiantum malesianum* J.Ghatak, Malaysia, *Schuettpelz 666* (DUKE), #4079, MH019596, MH019372, MH019716, MH019480; *Adiantum mariesii* Baker, China, *Wade 2493* (TAIF), #9479, MH019597, -, MH019717, MH019481;

Appendix 1. Continued.

Adiantum mathewsianum Hook., Brazil, *Hatschbach 74482* (UC), #4631, MH019598, –, MH019718, MH019482; *Adiantum mcvaughii* Mickel & Beitel, Mexico, *Alava 1603* (UC), #9418, MH019599, –, MH019719, MH019483; *Adiantum melanoleucum* Willd., Puerto Rico, *Axelrod 12765* (UC), #4671, MH019600, MH019373, MH019720, MH019484; *Adiantum mendoncae* Alston, Zimbabwe, *Pope 266* (BM), #4692, MH019601, MH019374, MH019721, –, *Adiantum mettenii* Kuhn, Tanzania, *Massawe 364* (MO), #9208, MH019602, MH019375, MH019722, MH019485; *Adiantum monochlamys* D.C.Eaton, Taiwan, *Li 427* (TAIF), #9477, MH019603, MH019376, MH019723, MH019486; *Adiantum moorei* Baker, Peru, *Huamantupa 4525* (MO), #8968, KX524194, KX524398, KX524345, KX524245; *Adiantum mynsseniae* J.Prado, Brazil, *Mynssen 356* (UC), #4621, MH019604, MH019377, MH019724, MH019487; *Adiantum myriosorum* Baker, China, *Kuo 2128* (TAIF), #9496, MH019605, MH019378, MH019725, MH019488; *Adiantum novae-caledoniae* Keyserl., New Caledonia, *van der Werff 16105* (MO), #4633, KX524167, MH019379, KX524318, KX524220; *Adiantum oatesii* Baker, Democratic Republic of the Congo (Zaire), *Bodenghien 2029* (UC), #4689, KX524199, KX524403, KX524350, KX524250; *Adiantum oaxacanum* Mickel & Beitel, Mexico, *Mickel 5132a* (UC), #9413, MH019606, –, MH019726, MH019489; *Adiantum obliquum* Willd., Costa Rica, *Rothfels 2661* (DUKE), #5554, MH019607, MH019380, MH019727, MH019490; *Adiantum opacum* Copel., Malaysia, *Beaman 9054* (MO), #9440, MH019608, MH019381, MH019728, MH019491; *Adiantum orbignyana* Mett. ex Kuhn, Bolivia, *Kessler 9589* (UC), #9214, KX524193, KX524397, KX524344, KX524244; *Adiantum ornithopodum* C.Presl, Brazil, *Schuettpelz 1429* (DUKE), #8363, MH019609, MH019382, MH019729, MH019492; *Adiantum oyapokense* Jenman, Costa Rica, *Cruz 128* (DUKE), #5564, MH019644, MH019416, MH019763, MH019524; *Adiantum paraense* Hieron., French Guiana, *Boudrie 3932* (UC), #2302, MH019610, MH019383, MH019730, MH019493; *Adiantum patens* Willd., Ecuador, *Wilson 2612* (UC), #4617, KX524203, KX524407, KX524354, KX524254; *Adiantum pectinatum* Kunze ex Baker, Bolivia, *Seidel 8260* (UC), #4665, MH019611, MH019384, MH019731, MH019494; *Adiantum pedatum* L., U.S.A.: North Carolina, *Rothfels 3839* (DUKE), #7517, MH019612, MH019385, MH019732, MH019495; *Adiantum pentadactylon* Langsd. & Fisch., Brazil, *Prado 2003* (SP), #9138, MH019613, MH019386, MH019733, MH019496; *Adiantum peruvianum* Klotzsch, Cultivated, *Huiet 103* (UC), #2507, EF452133, EF452070, KU147292, KU147259; *Adiantum petiolatum* Desv., Costa Rica, *Rothfels 08-178* (DUKE), #5182, MH019614, MH019387, MH019734, MH019497; *Adiantum phanerophlebium* (Bak.) C.Chr., Madagascar, *J. Kluge 8039* (Z), #8814, MH019615, MH019388, –, MH019498; *Adiantum philippense* L., Costa Rica, *Rothfels 2655* (DUKE), #5552, MH019616, MH019389, MH019735, MH019499; *Adiantum phyllitidis* J.Sm., Suriname, *Bordenave 8258* (UC), #9424, MH019617, MH019390, MH019736, MH019500; *Adiantum platyphyllum* Sw., Bolivia, *Kessler 8643* (UC), #9414, MH019618, MH019391, MH019737, MH019501; *Adiantum poeppigianum* (Kuhn) Hieron., Peru, *Rojas 707* (MO), #9206, MH019619, MH019392, MH019738, MH019502; *Adiantum poiretii* Wikstr., Mexico, *Windham 513* (DUKE), #9562, MH019620, MH019393, MH019739, MH019503; *Adiantum polyphyllum* Willd., Cultivated, *Smith s.n.* (UC), #4610, MH019621, MH019394, MH019740, MH019504; *Adiantum pseudotinctum* Hieron., Brazil, *Labiak 3792* (UC), #9527, –, MH019395, MH019741, MH019505; *Adiantum pulverulentum* L., Jamaica, *Smith 2889* (UC), #2101, MH019622, MH019396, MH019742, MH019506; *Adiantum pyramidale* (L.) Willd., Puerto Rico, *Christenhusz 3524* (UC), #9437, MH019623, MH019397, MH019743, MH019507; *Adiantum raddianum* C.Presl, Brazil, *Prado 2148* (DUKE), #8429, MH019624, MH019398, MH019744, MH019508; *Adiantum refractum* Christ, China, *Sundue 980* (DUKE), #6186, MH019564, MH019346, MH019687, MH019455; *Adiantum reniforme* L., Spain: Tenerife, *Larson 61* (UPS), #9420, MH019625, MH019399, MH019745, MH019509; *Adiantum rhizophyllum* Schrad., Brazil, *Fiaschi 3568* (SPF), #8905, MH019626, MH019400, MH019746, MH019510; *Adiantum roborowskii* Maxim., China, *Kuo 2138* (TAIF), #9497, MH019627, MH019401, MH019747, MH019511; *Adiantum ruizianum* Klotzsch, Peru, *Van der Werff 16812* (UC), #4672, KX524196, KX524400, KX524347, KX524247; *Adiantum scabrum* Kaulf., Chile, *Landrum 7963* (UC), #9217, MH019628, KX524423, KX524270; *Adiantum scalare* R.M.Tryon, Bolivia, *Fuentes 4054* (MO), #8987, MH019629, MH019402, MH019748, MH019512; *Adiantum schweinfurthii* Kuhn, Tanzania, *Gereau 5966* (MO), #9317, MH019630, MH019403, MH019749, MH019513; *Adiantum seemanii* Hook., Costa Rica, *Folsom 10108A* (DUKE), #9602, MH019631, MH019404, MH019750, MH019514; *Adiantum sericeum* D.C.Eaton, Cuba, *L.B. Smith 3254* (UC), #9425, MH019632, –, MH019751, –, *Adiantum serratodentatum* Humb. & Bonpl. ex Willd., Brazil, *Prado 2222* (UC), #9426, MH019633, MH019405, MH019752, MH019515; *Adiantum shastense* Huiet & A.R.Sm., U.S.A.: California, *Alexander 994* (DUKE), #9506A, MH019634, MH019406, MH019753, MH019516; *Adiantum shepherdii* Hook., Mexico, *Matuda 31053* (UC), #4682, KX524198, KX524402, KX524349, KX524249; *Adiantum soboliferum* Wall. ex Hook., Laos, *S.K.Wu 294* (MO), #9321, MH019635, MH019407, MH019754, MH019517; *Adiantum stenochlamys* Baker, Malaysia, *Schuettpelz 900A* (DUKE), #4319, MH019636, MH019408, MH019755, –, *Adiantum subcordatum* Sw., Brazil, *Schuettpelz 1406* (DUKE), #8340, KU147277, KU147248, KU147286, –, *Adiantum sulphureum* Kaulf., Chile, *Gardner 8454* (E), #8807, KX524178, KX524383, KX524329, KX524231; *Adiantum taiwanianum* Tagawa, Taiwan, *Schuettpelz 1131A* (DUKE), #4874, MH019637, MH019409, MH019756, MH019518; *Adiantum tenerum* Sw., Cultivated, *Huiet 107* (UC), #2504, EF452134, EF452072, KU147294, KU147260; *Adiantum terminatum* Kunze, French Guiana, *Boudrie 3933* (UC), #2297, MH019638, MH019410, MH019757, MH019519; *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd., Venezuela, *Huiet 105* (UC), #2505, EF452135, EF452073, KU147295, KU147261; *Adiantum thongthamii* Suksanphan, Thailand, *Suksathan 3303* (QBG), #2076, MH019639, MH019411, MH019758, MH019520; *Adiantum tinctum* T.Moore, Bolivia, *Kessler 12373* (UC), #9213, KX524185, KX524389, KX524336, KX524237; *Adiantum tomentosum* Klotzsch, Bolivia, *Jimenez 2033* (UC), #8986, MH019640, MH019412, MH019759, MH019521; *Adiantum ×tracyi* C.C. Hall ex W.H. Wagner, Cultivated, *Smith s.n.* (UC), #9264, MH019641, MH019413, MH019760, MH019522; *Adiantum trapeziforme* L., Costa Rica, *Rothfels 2650* (DUKE), #5563, MH019642, MH019414, MH019761, MH019523; *Adiantum tricholepis* Fée, Mexico, *Rothfels 3116A* (DUKE), #6549, KU147278, KU147249, KU147287, KU147255; *Adiantum urophyllum* Hook., Ecuador, *Croat 99951* (MO), #8965, MH019643, MH019415, MH019762, –, *Adiantum venustum* D.Don, China, *Boufford 30540* (MO), #9502, MH019645, –, MH019764, –, *Adiantum villosissimum* Mett. ex Kuhn, Ecuador, *Moran 7633* (NY), #8902, MH019646, MH019417, MH019765, MH019525; *Adiantum villosum* L., Peru, *Huiet 108* (UC), #4614, MH019647, MH019418, MH019766, MH019526; *Adiantum vogelii* Mett. ex Kuhn, Ghana, *Schmidt 2216* (UC), #4690, MH019648, MH019419, MH019767, MH019527; *Adiantum wattii* Baker, Nepal, *Allard 304* (BM), #4686, MH019649, MH019420, MH019768, MH019528; *Adiantum wilesianum* Hook., Mexico, *Cowan 4691* (UC), #9132, MH019650, MH019421, MH019769, MH019529; *Adiantum wilsonii* Hook., Panama, *van der Werff 22298* (MO), #9200, MH019651, MH019422, MH019770, MH019530; *Adiantum windischii* J.Prado, Brazil, *Prance 23898* (UC), #9422, MH019652, –, MH019771, MH019531. **OUTGROUP.** *Antrophyum latifolium* Blume, Papua New Guinea, *Ranker 1774* (COLO), #3078, EF452138, EF452076, KU147297, KU147263; *Hecostopteris pumila* (Spreng.) J.Sm., Guadeloupe, *Christenhusz 3976* (TUR), #3278, KC984524, EF452097, KU147303, KU147266; *Monogramma graminea* (Poir.) Schkuhr, Réunion, *Janssen 2692* (P), #3548, EF452157, EF452102, KU147304, KU147268; *Rheopteris cheesmaniae* Alston, Papua New Guinea, *Croft 1749* (A), #3373, EF452176, EF452126, KU147301, KU147270; *Vaginularia acrocarpa* Holttum, Papua New Guinea, *Ranker 1778* (COLO), #3375, EF452156, KC984435, –, KU147267; *Vittaria graminifolia* Kaulf., Ecuador, *Schuettpelz 227* (DUKE), #2395, KU147279, EF452128, KU147302, KU147271.