SYSTEMATICS AND PHYLOGENY

Phylogeny and relationships of the neotropical *Adiantum raddianum* group (Pteridaceae)

Regina Y. Hirai,[1] Eric Schuettpelz,[2] Layne Huiet,[3] Kathleen M. Pryer,[3] Alan R. Smith[4] & Jefferson Prado[1]

1 *Instituto de Botânica, C.P. 68041, 04045-972, São Paulo, SP, Brazil*

2 *Department of Botany, Smithsonian Institution, MRC 166, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A.*

3 *Department of Biology, Duke University, Durham, North Carolina 27708, U.S.A.*

4 *University Herbarium, 1001 Valley Life Sciences Building #2465, University of California, Berkeley, California 94720-2465, U.S.A*

Author for correspondence: *Regina Y. Hirai, regina.hirai@gmail.com*

ORCID RYH, http://orcid.org/0000-0002-7570-2811; ES, http://orcid.org/0000-0003-3891-9904; JP, http://orcid.org/0000-0003-4783-3125

DOI https://doi.org/10.12705/656.1

Abstract With more than 200 species, the maidenhair fern genus *Adiantum* is among the top ten most diverse fern genera. *Adiantum* is pantropical in distribution and, due to the presence of a unique synapomorphy (sporangia borne on indusia rather than laminae), perhaps the most easily recognized fern genus. Many of its members, including numerous cultivars derived from *A. raddianum*, are grown as ornamentals. Because of its size, a comprehensive taxonomic study of *Adiantum* is difficult and the genus is perhaps better approached through a series of narrower studies. Here, we focus specifically on *A. raddianum* and putative allies. We find a newly defined *A. raddianum* group to be strongly supported as monophyletic and segregated from other maidenhair ferns on the basis of genetic as well as morphological characteristics. Bayesian inference and maximum likelihood analyses of plastid *atpA*, *chlL*, *chlN*, *rbcL*, and *rpoA* sequences support the *A. raddianum* clade as sister to *A. poiretii* and its allies. We identify round-reniform indusia to be a characteristic of the *A. raddianum* group (vs. lunate in the *A. poiretii* group). Additionally, we find species in the *A. poiretii* group to differ in having a unique 66 nucleotide deletion in our *chlN* gene alignment. The neotropical *A. raddianum* group comprises at least 17 species (14 studied here), some widely distributed; one was recently described (*A. alan-smithii*).

Keywords adiantoids; *chlN*; cpDNA; ferns; maidenhair

Supplementary Material DNA sequence alignment is available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

Adiantum L., with more than 200 species, is among the largest fern genera and accounts for approximately 20% of the diversity in the fern family Pteridaceae (Smith & al., 2006, 2008). *Adiantum* is globally distributed (most diverse in the tropics), and many species are grown as ornamentals, including many cultivars derived over the years from *A. raddianum* C.Presl and its allies (Hoshizaki, 1970; Goudey, 1985). Due to this widespread cultivation, the *A. raddianum* group has become naturalized in many countries, including Jamaica (Proctor, 1985), Hawaii (Palmer, 2003), Mexico (Mickel & Smith, 2004), and perhaps also Taiwan (Knapp, 2011). However, no one has heretofore circumscribed its constituent species, provided evidence for their interrelationships, or produced a comprehensive phylogenetic study involving the group and its relatives.

Early molecular phylogenetic studies resolved *Adiantum* as most closely related to vittarioids (e.g., Hasebe & al., 1994, 1995; Crane & al., 1995; Pryer & al., 1995; Gastony & Johnson, 2001; Schneider & al., 2004; Schuettpelz & Pryer, 2007; Bouma & al., 2010). Later, more comprehensive analyses of the Pteridaceae showed that *Adiantum* belongs to a well-supported adiantoid clade comprising *Adiantum* and the various vittarioid genera (ca. 125 spp.; Prado & al., 2007; Schuettpelz & al., 2007, 2014). Rothfels & Schuettpelz (2014), using six markers (three plastid loci: *atpA*, *atpB*, *rbcL*; one nuclear locus: *gapCp*; and two mitochondrial loci: *atp1*, *nad5*) obtained strong support for the monophyly of *Adiantum* (maximum likelihood bootstrap percentage, MLBS = 94%; Bayesian posterior probability, PP = 1.0). Results from an analysis of nuclear data by Rothfels & al. (2015) and plastid data by Pryer & al. (2016) reached this same conclusion, and it is now clear that *Adiantum* is monophyletic.

Relationships within *Adiantum* were first explicitly examined by Huiet & Smith (2004). A main objective of their study was to test the informal classification of *Adiantum* proposed by Tryon & Tryon (1982). Based on morphological characters (e.g., laminar division, ultimate segment shape, venation, and aspects of the indusia), Tryon & Tryon (1982) divided *Adiantum* into eight groups (each named after a prominent species):

Received: 7 Mar 2016 | returned for (first) revision: 25 Apr 2016 | (last) revision received: 15 Jul 2016 | accepted: 17 Jul 2016 || publication date(s): online fast track, 6 Dec 2016; in print and online issues, 22 Dec 2016 ||

A. capillus-veneris L., *A. patens* Willd., *A. pectinatum* Kunze ex Baker, *A. philippense* L., *A. phyllitidis* J.Sm., *A. platyphyllum* Sw., *A. reniforme* L., and *A. tetraphyllum* Humb. & Bonpl. ex Willd. Huiet & Smith (2004) conducted molecular analyses using 40 *Adiantum* species (widely distributed) and two plastid markers (*rps4*, *rps4-trnS*). Their analyses demonstrated that while the *A. philippense*, *A. tetraphyllum*, and *A. platyphyllum* groups were monophyletic, the *A. patens*, *A. pectinatum*, and *A. capillus-veneris* groups were not. Based on this new phylogenetic information, Huiet & Smith (2004) tentatively showed a new arrangement for *Adiantum*, with nine informal groups: *A. capillus-veneris*, *A. lunulatum* Burm.f., *A. hispidulum* Sw., *A. peruvianum* Klotzsch, *A. pedatum* L., *A. raddianum*, *A. tenerum* Sw., *A. tetraphyllum*, and *A. venustum* D.Don. Their *A. raddianum* group was strongly supported as monophyletic (MPBS = 100%), comprising species previously placed in the *A. capillus-veneris* and *A. patens* groups (sensu Tryon & Tryon, 1982), and defined by veins ending in the sinuses at the segment margins (Sundue & al., 2010).

Later, Lu & al. (2012) explored the relationships of Chinese *Adiantum* species using a dataset of 56 adiantoid taxa and five plastid markers (*atpA*, *atpB*, *rbcL*, *rps4-trnS*, *trnL-trnF*). Their results showed that temperate *Adiantum* species form a clade nested within a pantropical grade, suggesting a tropical origin for the genus. They contrasted Ching's (1957) and Lin's (1980, 1990) classifications of Chinese *Adiantum* species, based on morphological characters, where *Adiantum* was treated in six and seven series, respectively. The molecular results of Lu & al. (2012) are partially consistent with Lin's (1980, 1990) classification.

McCarthy (2012) studied the neotropical *Adiantum peruvianum* group (as defined by Huiet & Smith, 2004) to determine its constituent species. She sampled 39 taxa (using *Vittaria* as the outgroup) and two plastid markers (*atpA*, *rbcL*) and found a neotropical clade (referred to as "clade D") with two subclades (D1, D2). Subclade D1 was characterized by visible venuloid idioblasts (silica bodies resembling veins) between veins, whereas subclade D2 contained species lacking visible venuloid idioblasts between veins. The *Adiantum peruvianum* group was nested within subclade D2, as D2.III, and contained at least eight species.

Within the *Adiantum raddianum* group, the study by Huiet & Smith (2004) initially included five species: *A. raddianum*, *A. lorentzii* Hieron., *A. patens*, *A. concinnum* Humb. & Bonpl. ex Willd., and *A. poiretii* Wikstr. Later, Prado & al. (2007: fig. 8) showed that *A. raddianum* and *A. cuneatum* Langsd. & Fisch. form a strongly supported, discrete clade (PP = 100%) separate from other *Adiantum* groups. Based on these phylogenetic findings, Sundue & al. (2010), using only morphological characters, suggested the possibility of 17 species belonging to the *A. raddianum* group. According to Sundue & al. (2010), this group can be recognized by having 2–4-pinnate, decompound, non-conform laminae (lacking a terminal pinna); orbicular, obovate, rhomboid, or flabellate ultimate segments; silica bodies absent between veins; and orbicular to reniform or lunate sori.

In their study of the Chinese species of *Adiantum*, Lu & al. (2012: figs. 2 & 3) included some neotropical species (Fig. 1). Among these were several accessions of *A. raddianum* and other potentially closely related species, and their analyses supported this group as comprising a well-supported monophyletic subclade within *Adiantum* (*atpA*, *atpB*, *rbcL*, MPBS = 71%, PP = 100%; *atpA*, *atpB*, *rbcL*, *rps4-trnS*, *trnL-trnF*, MPBS = 73%, PP = 100%). Included in this subclade (their "subclade II") were *A. raddianum* (including *A. cuneatum*), *A. excisum* Kunze, and *A. chilense* Kaulf., and three unidentified individuals.

Because *Adiantum* is a large genus with a broad distribution, a comprehensive study of the group is challenging. We therefore decided to initially focus our phylogenetic studies on the group of *A. raddianum* and its close relatives. This group was selected based on three attributes: (1) the type collection of *A. raddianum* is from Brazil; (2) all of the probable closest relatives of *A. raddianum* occur in the Neotropics; and (3) we had previously studied the morphology and taxonomy of *A. raddianum* and its purported allies (Sundue & al., 2010).

Here, we aim to better define the *Adiantum raddianum* group, identify its members, and confirm its monophyly. We also look for morphological characters that support this clade. Our phylogenetic approach is a necessary first step toward the taxonomic revision of the *A. raddianum* group in the Neotropics (Hirai & Prado, in prep.).

■ MATERIALS AND METHODS

Taxonomic sampling. — Our ingroup corresponds to the clade uniting subclades I and II of Lu & al. (2012). Together, these subclades form a well-supported monophyletic group that is sister to subclade III (Fig. 1). Based on the results of Huiet & Smith (2004), Lu & al. (2012) (Fig. 1), and Pryer & al. (2016), we included the following taxa: *A. aethiopicum* L., *A. diaphanum* Blume, *A. hispidulum* (previously resolved in subclade I of Lu & al., 2012), *A. fournieri* Copel. and *A. novae-caledoniae* Keyserl. We also included *A. formosum* R.Br. as a representative of subclade III of Lu & al. (2012), to serve as our outgroup. For subclade II, we included a combination of taxa that had previously been resolved there (e.g., *A. raddianum* and *A. chilense*; Lu & al., 2012) and taxa hypothesized (based on morphological grounds) to be allied with *A. raddianum*. The first candidates for inclusion came from Tryon & Tryon (1982) and Sundue & al. (2010). From Tryon & Tryon (1982), we targeted species from their groups 1 and 2 (*Adiantum capillus-veneris* and *A. patens* groups, respectively), but not those species with veins ending in teeth (e.g., in *A. capillus-veneris*), as Huiet & Smith (2004) and Pryer & al. (2016) showed that this character was not present in the neotropical species of the *A. raddianum* group. *Adiantum sinuosum* Gardner (placed in the *A. patens* group by Tryon & Tryon, 1982) was excluded from consideration because preliminary analyses by Huiet & al. (in prep.) demonstrated that this species was resolved well outside our ingroup (in clade II of Lu & al., 2012) (Fig. 1). We also attempted to sample the 15 species (excluding *A. digitatum* Hook. and *A. sinuosum*) that were assigned to the *A. raddianum* group on morphological grounds by Sundue & al. (2010); we were able to obtain suitable material for 13 species. In all, from

Tryon & Tryon (1982) and Sundue & al. (2010), we identified 23 species as possibly belonging to the subclade II (Table 1) and were able to include 20 species in our analyses. Additionally, six specimens representing four unidentified species, but having the basic morphology of the *A. raddianum* group, were included in our sampling.

Most samples were collected from the field in Brazil and Argentina by authors of this paper. Other samples came from Australia, Bolivia, Brazil, Chile, Costa Rica, Ecuador, and Mexico, and were provided by collaborators (see Acknowledgments). The remaining samples were obtained from herbarium collections. Overall, our sampling encompassed 50 collections of *Adiantum* thought to be part of, or closely related to, the *A. raddianum* group. With 6 additional samples representing subclades I and III of Lu & al. (2012), our final five-gene dataset included 56 terminals, corresponding to 29 species. Complete voucher information and GenBank accession numbers for all samples are listed in the Appendix 1.

DNA extraction, amplification, and sequencing. — Genomic DNA was extracted using a modified CTAB protocol (Doyle & Doyle, 1987) executed in a 96-well format (Beck & al., 2011) or using the Qiagen DNeasy Plant Mini Kit. Nuclear sequencing in ferns has proven difficult, due to a lack of generalized protocols for the amplification and sequencing of the nuclear ribosomal internal transcribed spacer (ITS) region and the problematic nature of recently developed low-copy nuclear genes (Schuettpelz & al., 2008). For this reason, and also because nuclear markers (when available) have corroborated the results of plastid analyses (Rothfels & al., 2015), we exclusively targeted plastid genes in the present study. These genes (*atpA*, *chlL*, *chlN*, *rbcL*, *rpoA*), which have been previously demonstrated as sufficiently powerful to resolve relationships in *Adiantum* and across ferns (Pryer & al., 1995; Schuettpelz & Pryer, 2007; Lu & al., 2012, 2015; Pryer & al., 2016), were amplified and sequenced according to previously published protocols (Schuettpelz & al., 2006; Schuettpelz & Pryer, 2007; Cochran & al., 2014; Schuettpelz & al., 2016). Primer information is provided in Table 2. All resulting sequences were submitted to GenBank (Appendix 1).

Sequence alignment and analysis. — For each plastid gene, the corresponding sequences were assembled and manually aligned using Mesquite v.2.75 (Maddison & Maddison, 2011); one existing sequence (EF473680; Prado & al., 2007), for *Adiantum pseudotinctum* Hieron., was incorporated into the *rbcL* alignment. Regions at the ends of each alignment containing copious amounts of missing data were excluded, as were internal areas with ambiguous alignment. Statistics for each alignment are provided in Table 3.

Each of the five single-gene datasets was phylogenetically analyzed in MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001;

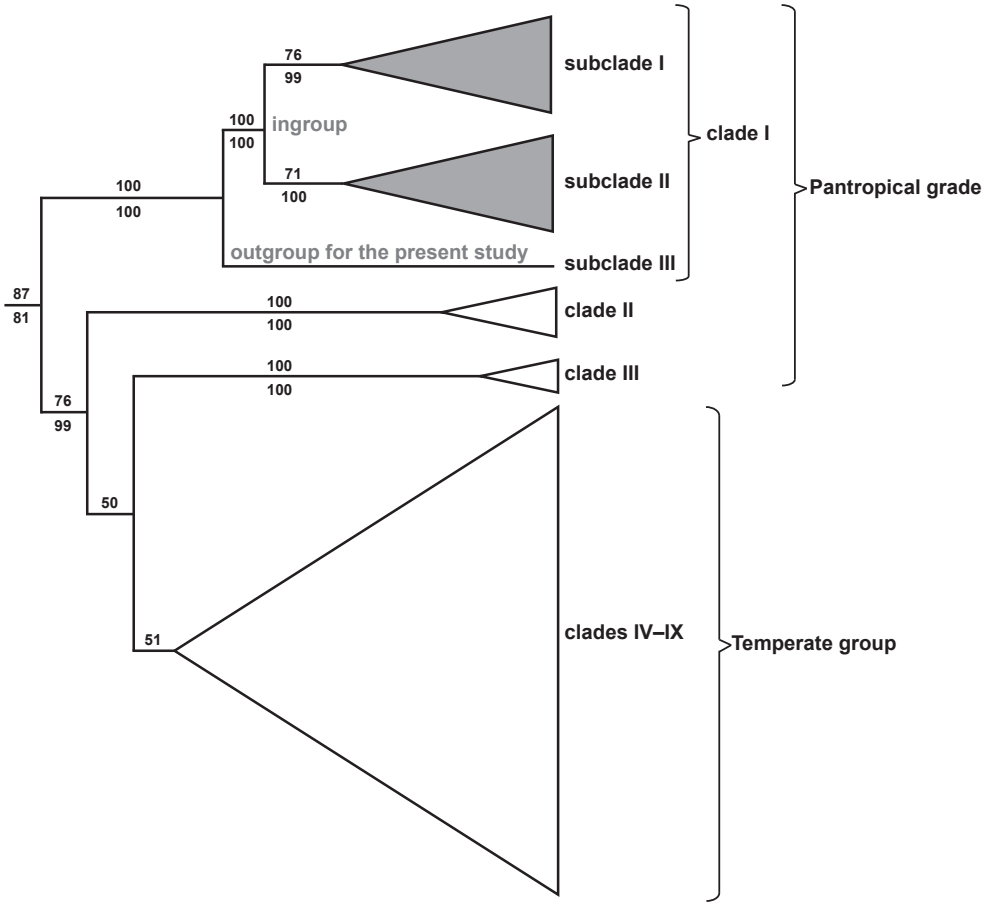

Fig. 1. Schematic phylogeny of *Adiantum* based on data presented by Lu & al. (2012: fig. 2, from analysis of plastid *atpA*, *atpB*, and *rbcL* sequences; maximum parsimony bootstrap percentages and Bayesian posterior probabilities are shown above and below the lines, respectively; outgroups not shown). *Adiantum raddianum* is resolved in subclade II. In addition to numerous species thought to be allied to *A. raddianum*, our analysis included other known members of subclades II and I (our ingroup), and *A. formosum* from subclade III (our outgroup).

Ronquist & Huelsenbeck, 2003), using the GTR+G model of sequence evolution. Each analysis incorporated four independent runs, with four chains of 10 million generations. Trees were sampled every 1000 generations. To identify when the runs had reached stationarity, the standard deviation of split frequencies between the four runs was examined, and the output parameter estimates were plotted using Tracer v.1.6 (Rambaut & al., 2014). Based on these convergence diagnostics, the first 2500 trees were (very conservatively) excluded from each analysis before obtaining a majority-rule consensus phylogeny with clade posterior probabilities.

The resulting gene trees were rooted with *Adiantum formosum*, the sister group of our ingroup as indicated by earlier studies with broader sampling of *Adiantum* (Huiet & Smith, 2004; Lu & al., 2012; Pryer & al., 2016), and then visually inspected for well-supported (PP ≥ 0.95) differences. Finding none, we concatenated the five datasets and analyzed them in unison. The combined dataset was analyzed as above, using the GTR+G model, but with parameters estimated and optimized separately for each gene. We additionally conducted a maximum likelihood analysis of the combined dataset using RAxML v.8.2.0 (Stamatakis, 2014). This analysis employed the GTRGAMMA model of sequence evolution, with parameters independently estimated for each gene, and involved 10,000 rapid bootstrap inferences followed by a thorough maximum likelihood search.

■ RESULTS

In this study, 260 new sequences were obtained and deposited in GenBank (Appendix 1). The concatenated dataset, with five plastid markers (*rbcL*, *atpA*, *chlL*, *chlN*, *rpoA*), contains 4815 characters (1309, 1764, 598, 523, and 621 characters, respectively; Table 3).

Bayesian and maximum likelihood analyses of our five-gene dataset reveal strong support for a split within our ingroup corresponding to subclades I and II of Lu & al. (2012). In our analyses, their subclade I was supported by a Bayesian posterior probability (PP) of 0.99 and a maximum likelihood bootstrap percentage (MLBS) of 80%. All species previously thought to be allied to *Adiantum raddianum* are resolved in a large well-supported (PP = 1; MLBS = 100%) clade corresponding to their subclade II (Fig. 2). Within this clade, we

Table 1. List of species previously suggested as belonging to the *Adiantum raddianum* group by Tryon & Tryon (1982; TT) or Sundue & al. (2010; S); updated affinities are also indicated, based on the results of the current study.

Species	Literature	Updated
1. *A. camptorachis* Sundue & al.	S	*A. poiretii* group
2. *A. chilense* Kaulf.	S	*A. poiretii* group
3. *A. excisum* Kunze	S	*A. poiretii* group (based on Lu & al., 2012)
4. *A. gertrudis* Espinosa	S	*A. poiretii* group
5. *A. glanduliferum* Link	S	*A. poiretii* group
6. *A. poiretii* Wikstr.	TT, S	*A. poiretii* group
7. *A. sulphureum* Kaulf.	TT, S	*A. poiretii* group
8. *A. scabrum* Kaulf.	S	*A. poiretii* group
9. *A. lorentzii* Hieron.	S	*A. raddianum* group
10. *A. concinnum* Humb. & Bonpl. ex Willd.	TT	*A. raddianum* group
11. *A. cuneatum* Langsd. & Fisch.	TT	*A. raddianum* group (= *A. raddianum*)
12. *A. galeottianum* Hook.	TT	*A. raddianum* group
13. *A. lobatum* C. Presl	TT	*A. raddianum* group (based on morphology)
14. *A. oatesii* Baker	TT	*A. raddianum* group
15. *A. orbignyanum* Mett. ex Kuhn	TT, S	*A. raddianum* group
16. *A. patens* Willd.	TT, S	*A. raddianum* group
17. *A. pseudotinctum* Hieron.	S	*A. raddianum* group
18. *A. raddianum* C. Presl	TT, S	*A. raddianum* group
19. *A. ruizianum* Klotzsch	TT	*A. raddianum* group
20. *A. rufopunctatum* Mett. ex Kuhn	S	*A. raddianum* group (= *A. moorei* Baker)*
21. *A. sessilifolium* Hook.	TT	*A. raddianum* group (= *A. henslovianum* Hook.f.)
22. *A. shepherdii* Hook.	TT	*A. raddianum* group
23. *A. subvolubile* Mett. ex Kuhn	TT, S	*A. raddianum* group (based on morphology)

* *Adiantum moorei* is the older name for *A. rufopunctatum* (Hirai & Prado, in prep.).

in turn uncover two distinct, well-supported (PP = 1; MLBS = 100%) lineages, which we refer to as the *A. poiretti* and *A. raddianum* groups (Fig. 2). The *A. poiretii* group comprises two well-supported subclades, one with *A. poiretii* and *A. camptorachis* Sundue & al. (PP = 1; MLBS = 89%) and the other consisting of *A. chilense, A. scabrum* Kaulf., and four other species (PP = 1; MLBS = 99%). The *A. poiretii* group differs from the *A. raddianum* group by a unique deletion of 66 nucleotides, at positions 288–353 in the *chlN* gene alignment (Fig. 3).

Although the *Adiantum raddianum* group is well supported (PP = 1; MLBS = 100%), internal resolution and support are poor at the deepest levels. Our Bayesian analysis reveals a trichotomy of *A. henslovianum* Hook.f. (PP = 1; MLBS = 100%), a rather poorly supported subclade including *A. pseudotinctum* and four other species (PP = 0.97; MLBS = 59%), and a very poorly supported subclade with *A. ruizianum* Klotzsch and eight other species (PP = 0.69; MLBS < 50%). Collapsing the poorly supported branches within the *A. raddianum* clade effectively results in a polytomy of six lineages. *Adiantum pseudotinctum* is isolated within the smaller subclade and *A. patens* appears to be paraphyletic relative to *A. galeottianum* Hook., *A. shepherdii* Hook., and *A. oatesii* Baker. *Adiantum ruizianum* and *A. concinnum* are, in turn, isolated within the larger subclade, although the remaining species together compose a well-supported group (PP = 1; MLBS = 99%) therein. *Adiantum lorentzii* is strongly supported (PP = 1; MLBS = 100%) as sister to a clade composed of *A. alan-smithii* R.Y.Hirai & al., *A. moorei* Baker, *A. raddianum*, and *Adiantum* sp., and these all are, together, sister to *A. orbignyanum* Mett. ex Kuhn plus *A. tinctum* T.Moore (PP = 1; MLBS = 99%).

Of the six specimens representing four unidentified species, three were found to belong to the *Adiantum raddianum* group (*A. alan-smithii*, *A. tinctum*, and *Adiantum* sp. – 2978) and one to the *A. poiretii* group (*Adiantum* sp. – 8897).

Table 2. Primers utilized in this study of the *Adiantum raddianum* group.

Region	Name	Type	Sequence	Reference
atpA	ESATPF412F	Forward	GARCARGTTCGACAGCAAGT	Schuettpelz & al., 2006
atpA	ESTRNR46F	Reverse	GTATAGGTTCRARTCCTATTGGACG	Schuettpelz & al., 2006
atpA	ESATPA856F*	Forward	CGAGAAGCATATCCGGGAGATG	Schuettpelz & al., 2006
atpA	ESATPA877R*	Reverse	CATCTCCCGGATATGCTTCTCG	Schuettpelz & al., 2006
atpA	ESATPA535F*	Forward	ACAGCAGTAGCTACAGATAC	Schuettpelz & al., 2006
atpA	ESATPA557R*	Reverse	ATTGTATCTGTAGCTACTGC	Schuettpelz & al., 2006
chlL	chlL-F1	Forward	GRATTGGMAARTCAACAACTAGCTG	Cochran & al., 2014
chlL	chlL-R1	Reverse	CBAGTACRGGCATGGGRCAAGCTTC	Cochran & al., 2014
chlN	chlN-F2	Forward	CGWTAYGCRAYGGCVGAATYGSAAG	Schuettpelz & al., 2016
chlN	chlN-R2	Reverse	CAWATTTTTTCGATCCARGCRCGTG	Schuettpelz & al., 2016
rbcL	ESRBCL1F	Forward	ATGTCACCACAAACGGAGACTAAAGC	Pryer & al., 2004
rbcL	ESRBCL1361R	Reverse	TCAGGACTCCACTTACTAGCTTCACG	Pryer & al., 2004
rbcL	ESRBCL628F*	Forward	CCATTYATGCGTTGGAGAGATCG	Pryer & al., 2004
rbcL	ESRBCL654R*	Reverse	GAARCGATCTCTCCAACGCAT	Pryer & al., 2004
rpoA	rpoA-F1	Forward	TRCAYGAGTATTCYACAATAACGGG	Schuettpelz & al., 2016
rpoA	rpoA-R1	Reverse	AATTAAARGCTCTRGCRGGTRATTC	Schuettpelz & al., 2016

*Primers used only for sequencing.

Table 3. Details for alignments analyzed in this study.

		Characters				
Dataset	Taxa	Total	Included	Variable	Parsimony-informative	Data missing*
atpA	53	1,844	1,764	217	92	6.03%
chlL	44	523	523	62	36	0.19%
chlN	54	621	621	107	58	0.03%
rbcL	54	1,309	1,309	151	79	2.06%
rpoA	56	598	598	107	52	0.59%
Combined	56	4,895	4,815	644	317	8.45%

*Calculation based on included characters

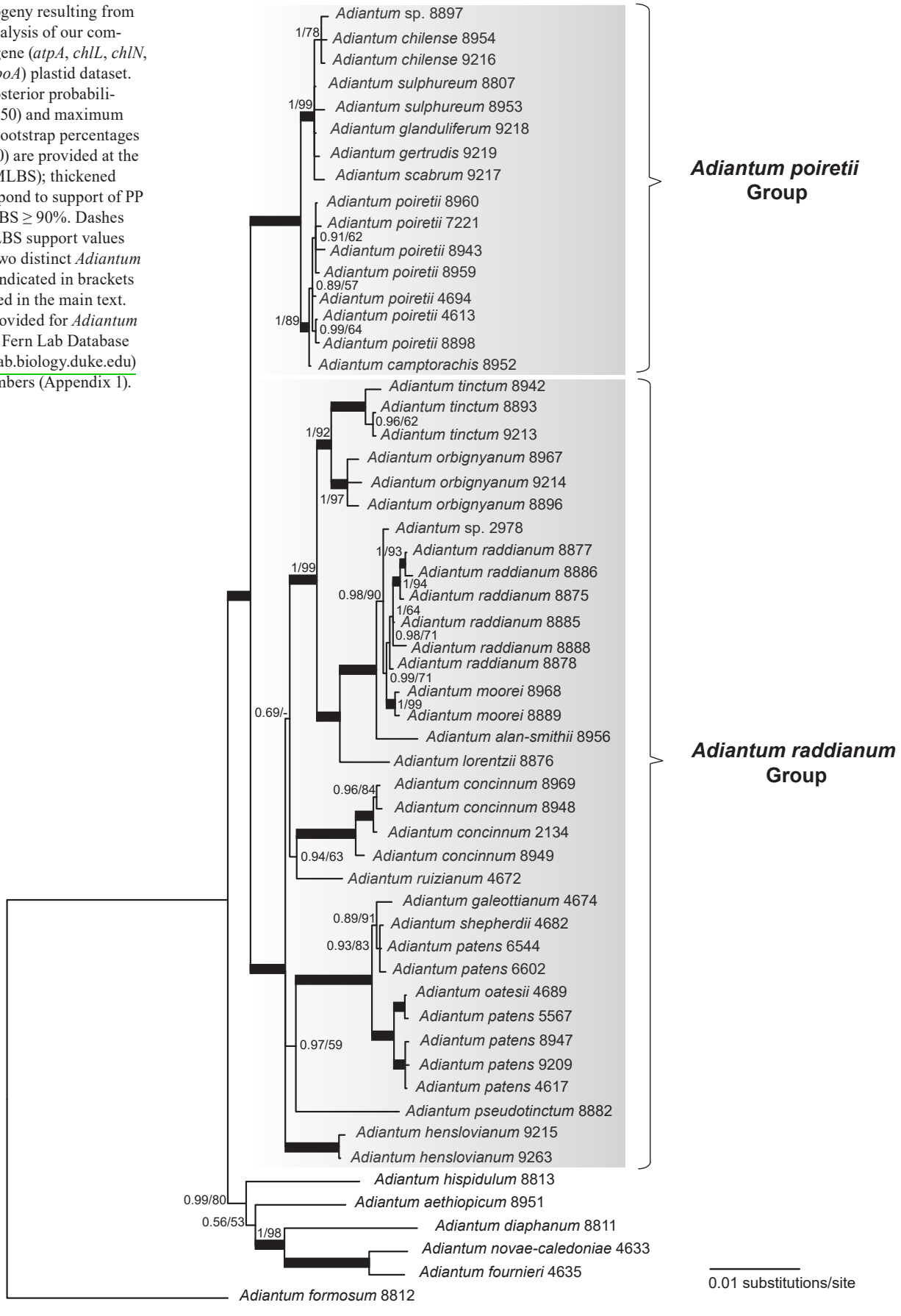

Fig. 2. Phylogeny resulting from Bayesian analysis of our combined five-gene (*atpA*, *chlL*, *chlN*, *rbcL*, and *rpoA*) plastid dataset. Bayesian posterior probabilities (PP ≥ 0.50) and maximum likelihood bootstrap percentages (MLBS ≥ 50) are provided at the nodes (PP/MLBS); thickened lines correspond to support of PP = 1 and MLBS ≥ 90%. Dashes indicate MLBS support values below 50. Two distinct *Adiantum* groups are indicated in brackets and discussed in the main text. Numbers provided for *Adiantum* samples are Fern Lab Database (http://fernlab.biology.duke.edu) voucher numbers (Appendix 1).

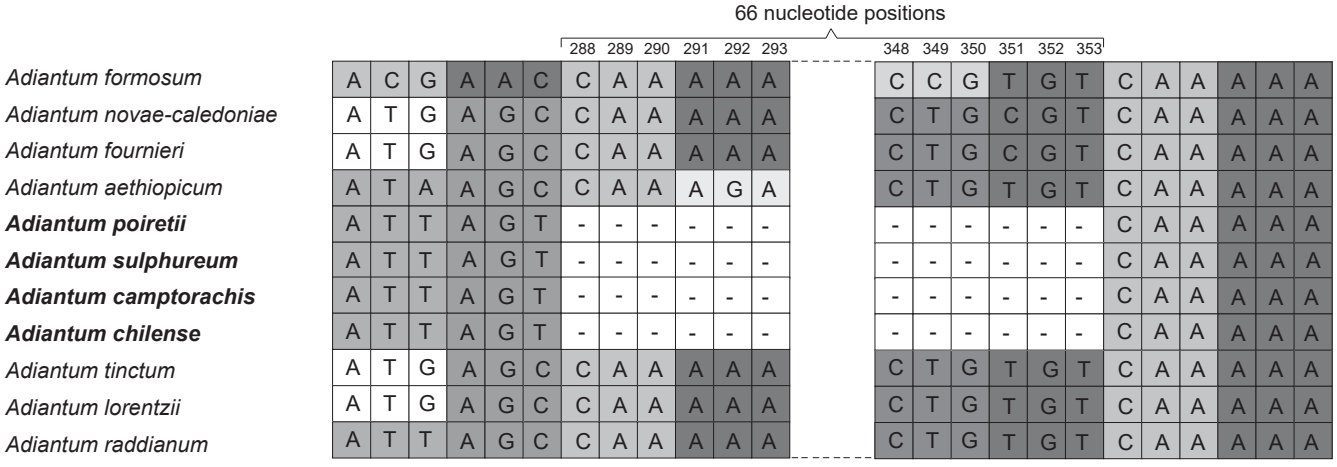

Fig. 3. Part of the *chlN* aligment showing a 66-nucleotide deletion characterizing the *Adiantum poiretii* group.

■ DISCUSSION

We resolved all our sampled species thought to be allied to *Adiantum raddianum* (Table 1) within a large clade corresponding to subclade II of Lu & al. (2012) (Fig. 1). Members of this clade can be recognized by a suite of morphological characters: pseudopedate to (1–)3–5-pinnate laminae lacking a conform terminal pinna; flabellate to flabellate-cuneate, or sometimes dimidiate to obovate, short- to long-stalked ultimate segments; laminar tissue with or without silica bodies; veins ending in sinuses at the segment margins; and orbicular, reniform, or lunate indusia. However, we also find strong support for a deep split within this larger clade and, after considering the morphology of each lineage, we favor the recognition of two informal groups: the *A. poiretii* group and the *A. raddianum* group. This choice is helpful to facilitate the taxonomic revision of each group, since both have widely distributed species.

Lu & al. (2012: figs. 2 & 3) also found this deep split within subclade II, albeit with much reduced sampling. Their sampling of the *A. poiretii* group included only three species: *A. chilense*, *A. excisum*, and *Adiantum* sp. (*Nee 53851 = A. poiretii*). Likewise, their sampling of the *A. raddianum* group comprised just three samples of *A. raddianum*, one of *A. cuneatum* (= *A. raddianum*), and two other undetermined species (*Nee 53885 = A. lorentzii*; *Wen 6893*, not seen).

In our analyses, we find *Adiantum camptorachis*, *A. chilense*, *A. gertrudis* Espinosa, *A. glanduliferum* Link, *A. poiretii*, *A. scabrum*, and *A. sulphureum* Kaulf. to compose the *A. poiretii* group (Fig. 2). Notably, all of these were previously proposed as *A. raddianum* allies (Sundue & al., 2010) (Table 1). Other species, such as *A. excisum* and *A. pearcei* Phil. (both endemic to Chile), certainly also belong to the *A. poiretii* group but were not included in our analyses. *Adiantum excisum* appears in Lu & al. (2012) in the subclade II sister to *A. chilense*. In our results, the last species is a member of the *A. poiretii* group. We find two morphological characters that support the separation of the *A. poiretii* group from the *A. raddianum* group: (1) lunate indusia (Fig. 4A, B) vs. round-reniform indusia in the *A. raddianum* group (Fig. 4C–F); and (2) a lack of 66 nucleotides at positions 288–353 in the *chlN* gene alignment (Fig. 3). The *A. raddianum* group can, in turn, be recognized morphologically by the unique combination (in *Adiantum*) of the following characters: pseudopedate to 1–5-pinnate laminae, sterile segments with veins ending in sinuses at the segment margins (vs. veins ending in teeth), and round-reniform sori (vs. oblong, lunate). Other morphological features may also distinguish these two closely related groups within *Adiantum*. Among these could be the presence/absence of silica bodies and their position in the laminar tissue (Sundue, 2009). In particular, Sundue (2009) commented that silica bodies could be a potential synapomorphy for recognizing groups within the adiantoid clade. He studied three species of the *A. raddianum* group (*A. concinnum*, *A. patens*, *A. raddianum*) and found silica bodies to be present on the veins; he also found one species of the *A. poiretii* group (*A. poiretii*) that lacked silica bodies. Before employing this character as diagnostic in *Adiantum*, additional studies are necessary, since the intra- and inter-specific variation in this character have yet to be thoroughly evaluated. Additionally, the observation of this character under the dissecting microscope is not a simple task; confirming the presence of such bodies requires wet-ashing leaf fragments.

The *Adiantum raddianum* group is well supported, but the internal polytomy that appears in our analyses still needs resolution. Studies involving nuclear or additional plastid markers might clarify these relationships. In our analyses, we sampled 14 of the 17 neotropical species that we believe belong to the *A. raddianum* group, as treated taxonomically by Hirai & Prado (in prep.). *Adiantum lobatum* C.Presl., *A. subvolubile* Mett. ex Kuhn, and *A. imbricatum* R.M.Tryon (Fig. 4F) are missing from our analyses. *Adiantum tinctum* is here found to be another member of the *A. raddianum* group, although in the past it was sometimes misidentified as *A. raddianum* (Tryon & Stolze, 1989) or *A. subvolubile* (Sundue & al., 2010). *Adiantum pseudotinctum* (Fig. 4C, D; from southern Brazil, Argentina, Paraguay, and Uruguay) is sister to a small subclade, including

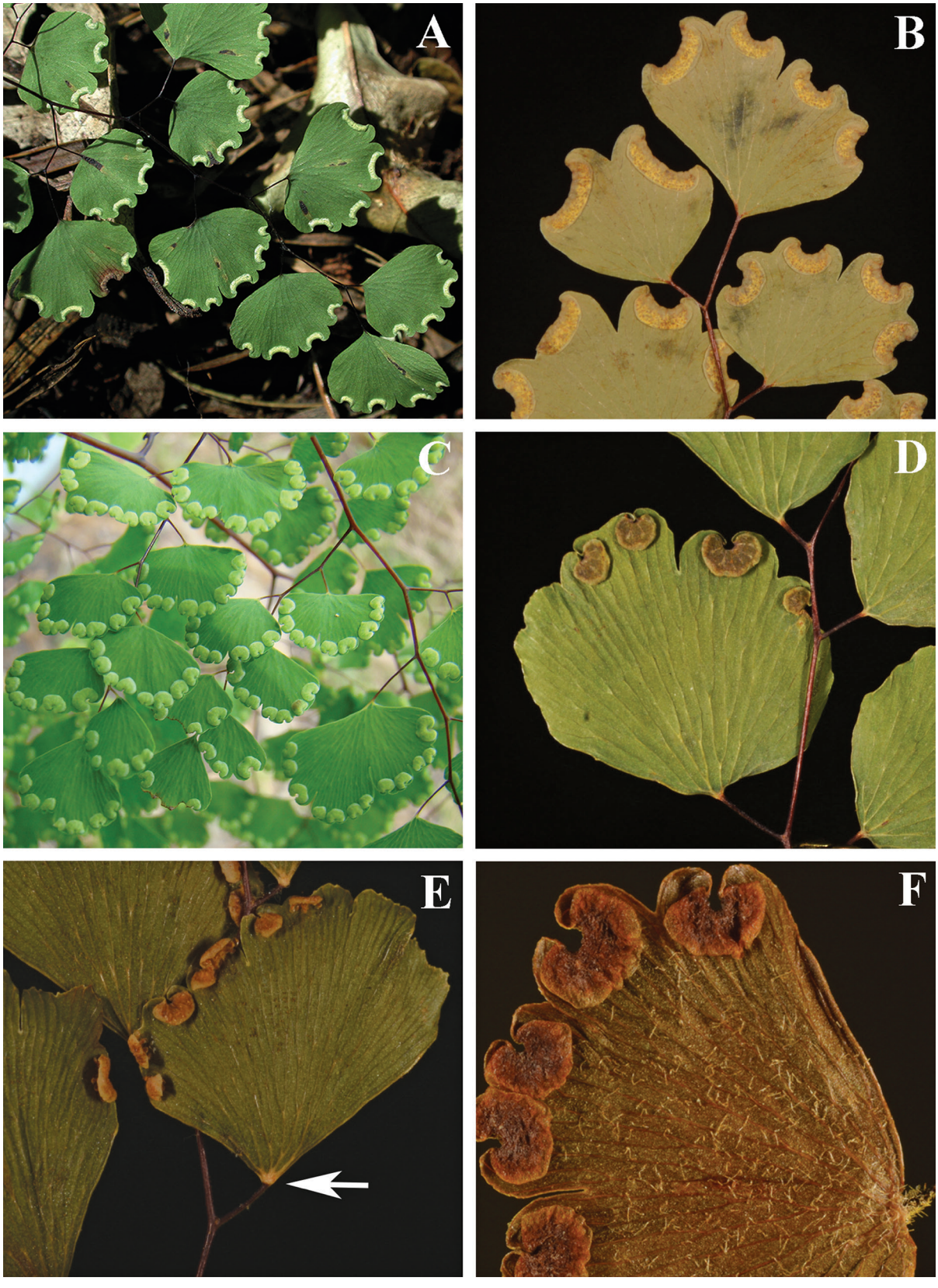

Fig. 4. A & B, *Adiantum poiretii* group. **A,** Pinnules with lunate sori (photo by M. Sundue, from *Sundue 845*, NY); **B,** Detail of pinnules showing lunate indusia with yellow farina (*Schmit & al. 324*, SP). **C–F,** *A. raddianum* group. **C,** *A. pseudotinctum* (*Hirai & Prado 691*, SP), pinnules with round-reniform sori; **D,** *A. pseudotinctum* (*Hirai & Prado 691*, SP), pinnules with detail of the sori; **E,** *A. orbignyanum*, detail of the articulate segment (arrow) (*Quirogo 1598*, MCNS); **F,** *A. imbricatum*, detail of the subarticulate segment showing sori and acicular hairs (*Bües 1305* p.p., UC).

A. galeottianum, A. patens, and *A. shepherdii*. Morphologically, these species all have similar primary laminar division (1-pinnate, pseudopedate, or subdichotomously divided; Hirai & Prado, in prep.).

Based on our analyses, *Adiantum patens* is not monophyletic, because African *A. oatesii* (sensu Burrows, 1990) and Mexican *A. shepherdii* and *A. galeottianum* nest within *A. patens* (Fig. 2). Our phylogeny suggests that two exemplars of Mexican *A. patens* (6544, 6602) could represent a different species than specimens of this species from Central America and the Andes. However, the support for this topology is not sufficiently strong (PP = 0.89; MLBS = 93%) to convincingly corroborate this hypothesis. Moran & Smith (2001) alluded to some morphological differences between specimens of *A. patens* from Central and South America. *Adiantum oatesii* has often been considered a subspecies (e.g., Schelpe, 1967; Jacobsen, 1983) or variety (e.g., Ballard, 1940) of *A. patens*, but Hyde & al. (2015) treated it as synonymous with *A. patens*. Our results suggest that *A. oatesii* may not be distinguishable, even infraspecifically, from at least some forms of *A. patens* in the Neotropics.

The sister relationship between *Adiantum lorentzii* (represented in our analyses by only one sample) and a small subclade comprising *A. raddianum*, *A. moorei*, and *A. alan-smithii* is supported morphologically only by the presence of (2)3–5-pinnate laminae. Hirai & al. (2014) recently described *A. alan-smithii*, and it was segregated from Mexican specimens previously identified as *A. raddianum* by Mickel & Smith (2004). *Adiantum moorei* is the closest relative to *A. raddianum*, differing by the presence of glandular laminar hairs (Hirai & Prado, in prep.).

Among species with veins ending in sinuses at segment margins, included by Tryon & Tryon (1982) in the *Adiantum capillus-veneris* and *A. patens* groups, 12 species were found to belong to the *A. raddianum* group and two species to the *A. poiretii* group, as circumscribed in the present study (Table 1). Of the candidates suggested as having affinities to the *Adiantum raddianum* group by Sundue & al. (2010), our results support the placement of seven in the *A. raddianum* group as defined here (Table 1). Eight others belong to the *A. poiretii* group based on our phylogenetic analyses and/or the presence of characteristic lunate sori.

■ ACKNOWLEDGMENTS

This study was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Proc. n. 2011/07164-3, to R.Y.H. and J.P.) and the National Science Foundation (NSF awards DEB-1405181 to E.S. and DEB-1145614 to K.M.P. and L.H.). We thank The New York Botanical Garden and Dr. Robbin C. Moran for providing herbarium access and facilities for the first author; curators of herbaria for loans and/or permission to examine their collections (B, DUKE, K, MCNS, MO, NY, P, S, UC, US); and Michael Kessler, Robbin C. Moran, Michael Sundue, Pedro Fiaschi, and Pedro B. Schwartsburd for providing us with silica-dried material. We also thank two anonymous referees for their comments and suggestions to improve the manuscript.

■ LITERATURE CITED

Ballard, F. 1940. Notes on ferns and fern allies: II. *Bull. Misc. Inform. Kew* 1940: 29–31. http://dx.doi.org/10.2307/4118146

Beck, J.B., Alexander, P.J., Allphin, L., Al-Shehbaz, I.A., Rushworth, C., Bailey, C.D. & Windham, M.D. 2011. Does hybridization drive the transition to asexuality in diploid *Boechera*? *Evolution* 66: 985–995. http://dx.doi.org/10.1111/j.1558-5646.2011.01507.x

Bouma, W.L.M., Ritchie, P. & Perrie, L.R. 2010. Phylogeny and generic taxonomy of the New Zealand Pteridaceae ferns from chloroplast *rbcL* DNA sequences. *Austral. Syst. Bot.* 23: 143–151. http://dx.doi.org/10.1071/SB09047

Burrows, J.E. 1990. *Southern African ferns and fern allies*. Sandton: Frandsen.

Ching, R.C. 1957. On the genus *Adiantum* L. of China with notes on some related species from neighboring regions. *Acta Phytotax. Sin.* 6: 301–354.

Cochran, A.T., Prado, J. & Schuettpelz, E. 2014. *Tryonia*, a new taenititoid fern genus segregated from *Jamesonia* and *Eriosorus* (Pteridaceae). *PhytoKeys* 35: 23–43. http://dx.doi.org/10.3897/phytokeys.35.6886

Crane, E.H., Farrar, D.R. & Wendel, J.F. 1995. Phylogeny of the Vittariaceae: Convergent simplification leads to a polyphyletic *Vittaria*. *Amer. Fern J.* 85: 283–305. http://dx.doi.org/10.2307/1547811

Doyle, J.J. & Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.

Gastony, G.J. & Johnson, W.P. 2001. Phylogenetic placements of *Loxoscaphe thecifera* (Aspleniaceae) and *Actiniopteris radiata* (Pteridaceae) based on analysis of *rbcL* nucleotide sequences. *Amer. Fern J.* 91: 197–213. http://dx.doi.org/10.1640/0002-8444(2001)091[0197:PPOLTA]2.0.CO;2

Goudey, C.J. 1985. *Maidenhair ferns in cultivation*. Lothian, Melbourne.

Hasebe, M., Omori, T., Nakazawa, M., Sano, T., Kato, M. & Iwatsuki, K. 1994. *rbcL* gene sequences provide evidence for the evolutionary lineages of leptosporangiate ferns. *Proc. Natl. Acad. Sci. U.S.A.* 91: 5730–5734. http://dx.doi.org/10.1073/pnas.91.12.5730

Hasebe, M., Wolf, P.G., Pryer, K.M., Ueda, K., Ito, M., Sano, R., Gastony, G.J., Yokoyama, J., Manhart, J.R., Murakami, N., Crane, E.H., Haufler, C.H. & Hauk, W.D. 1995. Fern phylogeny based on *rbcL* nucleotide sequences. *Amer. Fern J.* 85: 134–181. http://dx.doi.org/10.2307/1547807

Hirai, R.Y., Sundue, M.A. & Prado, J. 2014. *Adiantum alan-smithii* (Pteridaceae), a new maidenhair fern from Chiapas, Mexico. *Syst. Bot.* 39: 380–383. http://dx.doi.org/10.1600/036364414X680942

Hoshizaki, B.J. 1970. The genus *Adiantum* in cultivation (Polypodiaceae). *Baileya* 17: 97–144; 145–190.

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755. http://dx.doi.org/10.1093/bioinformatics/17.8.754

Huiet, L. & Smith, A.R. 2004. Phylogenetic relationships in *Adiantum* inferred from chloroplast coding and non-coding sequences. In: *Botany 2004*, July 31–August 5, Salt Lake City, Abstract no. 697. Botanical Society of America. http://2004.botanyconference.org/engine/search/index.php?func=detail&aid=697

Hyde, M.A., Wursten, B.T., Ballings, P. & Coates Palgrave, M. 2015. Flora of Zimbabwe: Species information: *Adiantum patens*. http://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=101030 (retrieved 22 Jul 2015).

Jacobsen, W.B.G. 1983. *The ferns and fern allies of southern Africa*. Durban, Pretoria: Butterworths.

Knapp, R. 2011. *Ferns and fern allies of Taiwan*. Taipei: KBCC Press & Yuan-Liou Publishing.

Lin, Y.X. 1980. New taxa of *Adiantum* L. in China. *Acta Phytotax. Sin.* 18: 101–105.

Lin, Y.X. 1990. Adiantaceae. Pp. 173–216 in: Ching, R.C. & Shing, K.H. (Eds.), *Flora Reipublicae Popularis Sinicae*, vol. 3. Beijing: Science Press.

Lu, J.-M., Jun, W., Lutz, S., Wang, Y.-P. & Li, D.-Z. 2012. Phylogenetic relationships of Chinese *Adiantum* based on five plastid markers. *J. Pl. Res.* 125: 237–249. http://dx.doi.org/10.1007/s10265-011-0441-y

Lu, J.-M., Zhang, N., Du, X.-Y., Wen, J. & Li, D.-Z. 2015. Chloroplast phylogenomics resolves key relationships in ferns. *J. Syst. Evol.* 53*:* 448–457*. http://dx.doi.org/10.1111/jse.12180*

Maddison, W.P. & Maddison, D.R. 2011. Mesquite: A modular system for evolutionary analysis, version 2.75. http://mesquiteproject.wikispaces.com.

McCarthy, M.R. 2012. *Molecular systematics and morphology of* Adiantum peruvianum *group (Pteridaceae).* Ph.D. thesis, Miami University, Oxford, Ohio, U.S.A.

Mickel, J.T. & Smith, A.R. 2004. The pteridophytes of Mexico. *Mem. New York Bot. Gard.* 88: 1–1054.

Moran, R.C. & Smith, A.R. 2001. Phytogeographic relationships between neotropical and African-Madagascan pteridophytes. *Brittonia* 53: 304–351. http://dx.doi.org/10.1007/BF02812704

Palmer, D.D. 2003. *Hawai'i's ferns and fern allies*. Honolulu: University of Hawai'i Press.

Prado, J., Rodrigues, C.N., Salatino, A. & Salatino, M.L. 2007. Phylogenetic relationships among Pteridaceae, including Brazilian species, inferred from *rbcL* sequences. *Taxon* 56: 355–368.

Proctor, G.R. 1985. *Ferns of Jamaica*. London: British Museum of Natural History.

Pryer, K.M., Smith, A.R. & Skog, J.E. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *Amer. Fern J.* 85: 205–282. http://dx.doi.org/10.2307/1547810

Pryer, K.M., Schuettpelz, E., Wolf, P.G., Schneider, H., Smith, A.R. & Cranfill, R. 2004. Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *Amer. J. Bot.* 91: 1582–1598. http://dx.doi.org/10.3732/ajb.91.10.1582

Pryer, K.M., Huiet, L., Li, F.-W., Rothfels, C.J. & Schuettpelz, E. 2016. Maidenhair ferns, *Adiantum*, are indeed monophyletic and sister to shoestring ferns, vittarioids (Pteridaceae). *Syst. Bot.* 41: 17–23. http://dx.doi.org/10.1600/036364416X690660

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. 2014. Tracer, version 1.6. http://beast.bio.ed.ac.uk/Tracer

Ronquist, F. & Huelsenbeck, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. http://dx.doi.org/10.1093/bioinformatics/btg180

Rothfels, C.J. & Schuettpelz, E. 2014. Accelerated rate of molecular evolution for vittarioid ferns is strong and not driven by selection. *Syst. Biol.* 63: 31–54. http://dx.doi.org/10.1093/sysbio/syt058

Rothfels, C.J., Li, F.-W., Sigel, E.M., Huiet, L., Larsson, A., Burge, D.O., Ruhsam, M., Deyholos, M., Soltis, D.E., Stewart, C.N., Jr., Shaw, S.W., Pokorny, L., Chen, T., de Pamphilis, C., De Gironimo, L., Chen, L., Wei, X., Sun, X., Korall, P., Stevenson, D.W., Graham, S.W., Wong, G.K.-S. & Pryer, K.M. 2015. The evolutionary history of ferns inferred from 25 low-copy nuclear genes. *Amer. J. Bot.* 102: 1089–1107. http://dx.doi.org/10.3732/ajb.1500089

Schelpe, E.A.C.L.E. 1967. New taxa of Pteridophyta from south east tropical Africa. *Bol. Soc. Brot., sér.* 2, 41: 203–217.

Schneider, H., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallón, S. & Lupia, R. 2004. Ferns diversified in the shadow of angiosperms. *Nature* 42: 553–557. http://dx.doi.org/10.1038/nature02361

Schuettpelz, E. & Pryer, K.M. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56: 1037–1050. http://dx.doi.org/10.2307/25065903

Schuettpelz, E., Korall, P. & Pryer, K.M. 2006. Plastid *atpA* data provide improved support for deep relationships among ferns. *Taxon* 55: 897–906. http://dx.doi.org/10.2307/25065684

Schuettpelz, E., Schneider, H., Huiet, L., Windham, M.D. & Pryer, K.M. 2007. A molecular phylogeny of the fern family Pteridaceae: Assessing overall relationships and the affinities of previously unsampled genera. *Molec. Phylogen. Evol.* 44: 1172–1185. http://dx.doi.org/10.1016/j.ympev.2007.04.011

Schuettpelz, E., Grusz, A.L., Windham, M.D. & Pryer, K.M. 2008. The utility of nuclear *gapCp* in resolving polyploid fern origins. *Syst. Bot.* 33: 621–629. http://dx.doi.org/10.1600/036364408786500127

Schuettpelz, E., Davila, A., Prado, J., Hirai, R.Y. & Yatskievych, G. 2014. Molecular phylogenetic and morphological affinities of *Adiantum senae* (Pteridaceae). *Taxon* 63: 258–264. http://dx.doi.org/10.12705/632.7

Schuettpelz, E., Chen, C.-W., Kessler, M., Pinson, J.B., Johnson, G., Davila, A., Cochran, A.T., Huiet, L. & Pryer, K.M. 2016. A revised generic classification of vittarioid ferns (Pteridaceae) based on molecular, micromorphological, and geographic data. *Taxon* 65: 708–722. http://dx.doi.org/10.12705/654.2

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H. & Wolf, P.G. 2006. A classification for extant ferns. *Taxon* 55: 705–731. http://dx.doi.org/10.2307/25065646

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H. & Wolf, P.G. 2008. Fern classification. Pp. 417–467 in: Ranker, T.A. & Haufler, C.H. (eds.), *Biology and evolution of ferns and lycophytes*. Cambridge: Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511541827.017

Stamatakis, A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. http://dx.doi.org/10.1093/bioinformatics/btu033

Sundue, M. 2009. Silica bodies and their systematic implications in Pteridaceae (Pteridophyta). *Bot. J. Linn. Soc.* 161: 422–435. http://dx.doi.org/10.1111/j.1095-8339.2009.01012.x

Sundue, M., Prado, J. & Smith, A.R. 2010. *Adiantum camptorachis* (Pteridaceae), a new species from South America with notes on the taxonomy of related species from the Southern Cone and Bolivia. *Amer. Fern J.* 100: 195–206. http://dx.doi.org/10.1640/0002-8444-100.4.195

Tryon, R.M. & Stolze, R.G. 1989. Pteridophyta of Peru. Part II. 13. Pteridaceae–15. Dennstaedtiaceae. *Fieldiana, Bot.*, n.s., 22: 1–128.

Tryon, R.M. & Tryon, A.F. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer. http://dx.doi.org/10.1007/978-1-4613-8162-4

Appendix 1. Taxonomic sampling, including voucher information and accession numbers for this study of the *Adiantum raddianum* group.

Species, collection locality, voucher information, Fern Lab Database voucher number (FLDB: http://fernlab.biology.duke.edu), GenBank accession numbers for *rbcL*, *atpA*, *rpoA*, *chlL*, and *chlN*. All but one (indicated with *) sequence newly obtained in this study. A dash (–) indicates not available.

Adiantum aethiopicum L., Australia, *Sundue s.n.* (MEL), 8951, KX524169, –, KX524320, KX524276, KX524222. ***A. alan-smithii*** R.Y.Hirai, Sundue & J.Prado, Mexico, *Lopes 941* (MO), 8956, KX524212, KX524416, KX524363, KX524313, KX524263. ***A. camptorachis*** Sundue, J.Prado & A.R.Sm., Argentina, *Morero 335* (CORD), 8952, KX524212, KX524384, KX524331, KX524287, KX524233. ***A. chilense*** Kaulf., Chile, *Lendemer 16331* (NY), 8954, KX524181, KX524385, KX524332, KX524288, –; Chile, *Kelch 127* (UC), 9216, KX524215, KX524420, KX524367, –, KX524267. ***A. concinnum*** Humb. & Bonpl. ex Willd., Costa Rica, *Grantham 0112-90* (UC), 2134, KX524209, KX524413, KX524360, KX524310, KX524260; Ecuador, *Sundue 2692* (SP, VT), 8948, KX524210, KX524414,

Appendix 1. Continued.

KX524361, KX524311, KX524261; Ecuador, *Sundue 2701* (VT), 8949, KX524211, KX524415, KX524362, KX524312, KX524262; Ecuador, *Madsen 7045* (MO), 8969, KX524183, KX524387, KX524334, KX524290, KX524235. ***A. diaphanum*** Blume, Australia, *Kessler 14206* (Z), 8811, KX524164, KX524371, KX524315, KX524271, KX524217. ***A. formosum*** R.Br., Australia, *Kessler 14218* (Z), 8812, KX524166, KX524373, KX524317, KX524273, KX524219. ***A. fournieri*** Copel., New Caledonia, *Webster 14478* (DAV), 4635, KX524168, KX524374, KX524319, KX524275, KX524221. ***A. galeottianum*** Hook., Mexico, *Mickel 7004* (NY), 4674, KX524197, KX524401, KX524348, KX524302, KX524248. ***A. gertrudis*** Espinosa, Chile, *Eyerdam 10038* (UC), 9219, –, KX524422, KX524369, –, KX524269. ***A. glanduliferum*** Link, Chile, *Hartwig 54.059-S1* (UC), 9218, KX524216, KX524421, KX524368, –, KX524268. ***A. henslovianum*** Hook.f., Venezuela, *Fay 1535* (UC), 9215, KX524213, KX524417, KX524364, –, KX524264; Ecuador, *Leveque 10+11* (K), 9263, KX524214, KX524418, KX524365, –, KX524265. ***A. hispidulum*** Sw., Australia, *Kessler 14185* (Z), 8813, KX524165, KX524372, KX524316, KX524272, KX524218. ***A. lorentzii*** Hieron., Argentina, *Prado s.n.* (SP), 8876, KX524187, KX524391, KX524338, KX524293, KX524239. ***A. moorei*** Baker, Bolivia, *Wood 13704* (LPB), 8889, KX524195, KX524399, KX524346, KX524300, KX524246; Peru, *Huamantupa 4525* (MO), 8968, KX524194, KX524398, KX524345, KX524299, KX524245. ***A. novae-caledoniae*** Keyserl., New Caledonia, *Werff 16105* (UC), 4633, KX524167, –, KX524318, KX524274, KX524220. ***A. oatesii*** Baker, Republic of the Congo, *Bodenghien 2029* (UC), 4689, KX524199, KX524403, KX524350, KX524304, KX524250. ***A. orbignyanum*** Mett. ex Kuhn, Argentina, *Hernández 1953* (SP), 8896, KX524208, KX524412, KX524359, KX524309, KX524259; Bolivia, *Vargas 312* (MO), 8967, KX524192, KX524396, KX524343, KX524298, –; Bolivia, *Kessler 9589* (UC), 9214, KX524193, KX524397, KX524344, –, KX524244. ***A. patens*** Willd., Ecuador, *Wilson 2612* (UC), 4617, KX524203, KX524407, KX524354, –, KX524254; Costa Rica, *Rothfels 2697* (DUKE), 5567, KX524200, KX524404, KX524351, KX524305, KX524251; Mexico, *Rothfels 3112* (DUKE), 6544, KX524204, KX524408, KX524355, –, KX524255; Mexico, *Rothfels 3185* (DUKE), 6602, KX524205, KX524409, KX524356, –, KX524256; Ecuador, *Sundue 2691* (VT), 8947, KX524201, KX524405, KX524352, KX524306, KX524252; Ecuador, *Sigel 201050* (DUKE), 9209, KX524202, KX524406, KX524353, –, KX524253. ***A. poiretii*** Wikstr., Argentina, *Avent AIAG-276* (UC), 4613, KX524176, KX524381, KX524327, KX524283, KX524229; Malawi, *Chapman 7365* (UC), 4694, KX524173, KX524378, KX524324, KX524280, KX524226; Mexico, *Beck 1153* (DUKE), 7221, KX524172, KX524377, KX524323, KX524279, KX524225; Argentina, *Martínez 1907* (MCNS), 8898, KX524177, KX524382, KX524328, KX524284, KX524230; Ecuador, *Sundue 2681* (VT), 8943, KX524174, KX524379, KX524325, KX524281, KX524227; Mexico, *Sundue 3026* (MEXU), 8959, KX524175, KX524380, KX524326, KX524282, KX524228; Mexico, *Sundue 3052* (MEXU), 8960, KX524171, KX524376, KX524322, KX524278, KX524224. ***A. pseudotinctum*** Hieron., Brazil, *Hirai 691* (SP), 8882, –, KX524419, KX524366, KX524314, KX524266; Brazil, *Prado 1077* (SP), EF473680*, –, –, –, –. ***A. raddianum*** C.Presl, Brazil, *Hirai 724* (SP), 8875, KX524206, KX524410, KX524357, KX524307, KX524257; Brazil, *Hirai 692* (SP), 8885, KX524190, KX524394, KX524341, KX524296, KX524242; Brazil, *Prado 2154* (SP), 8886, KX524191, KX524395, KX524342, KX524297, KX524243; Brazil, *Schwartsburd 2568* (SP), 8888, KX524207, KX524411, KX524358, KX524308, KX524258; Brazil, *Prado 2148* (SP), 8877, KX524188, KX524392, KX524339, KX524294, KX524240; Brazil, *Fiaschi 3687* (SP, SPF), 8878, KX524189, KX524393, KX524340, KX524295, KX524241. ***A. ruizianum*** Klotzsch, Peru, *Werff 16812* (UC), 4672, KX524196, KX524400, KX524347, KX524301, KX524247. ***A. scabrum*** Kaulf., Chile, *Landrum 7963* (UC), 9217, –, KX524423, KX524370, –, KX524270. ***A. shepherdii*** Hook., Mexico, *Matuda 31053* (UC), 4682, KX524198, KX524402, KX524349, KX524303, KX524249. ***A. sulphureum*** Kaulf., Chile, *Gardner 8454* (E), 8807, KX524178, KX524383, KX524329, KX524285, KX524231; Chile, *Lendemer 16155* (NY), 8953, KX524179, –, KX524330, KX524286, KX524232. ***A. tinctum*** T.Moore, Bolivia, *Tanaka ZO-017* (LPB), 8893, KX524184, KX524388, KX524335, KX524291, KX524236; Ecuador, *Sundue 2624* (SP), 8942, KX524182, KX524386, KX524333, KX524289, KX524234; Bolivia, *Kessler 12373* (UC), 9213, KX524185, KX524389, KX524336, –, KX524237. ***Adiantum* sp.,** Argentina, *Schuettpelz 333* (DUKE), 2978, KX524186, KX524390, KX524337, KX524292, KX524238. ***Adiantum* sp.,** Brazil, *Prado 2134* (SP), 8897, KX524170, KX524375, KX524321, KX524277, KX524223.