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Lectotypification of *Adiantopsis alata* (Pteridaceae) and Descriptions of New Palmate Species in the Guiana Shield

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Abstract—*Adiantopsis alata* was described by Prantl in 1883 and was distinguished from *A. radiata* based on the presence of large adaxial carinae along the stipes. Morphological and molecular analyses of specimens meeting this general description reveal four distinct species, with one endemic to eastern Brazil and three others restricted to the Guiana Shield. The syntypes for *A. alata* represent two different species, one from Brazil and the other from Guyana. Here, we designate a Brazilian syntype as the lectotype for *A. alata* and describe and illustrate three new palmate species from the Guiana Shield with adaxial carinae along their stipes: ***A. aurea***, ***A. hickeyi***, and ***A. scalariformis***. A distribution map for the new species and a key to all ten palmate members of *Adiantopsis* are provided.

Keywords—*atpA*, cheilanthoid ferns, molecular systematics, morphology, *rbcL*.

Adiantopsis radiata (L.) Fée is the most widespread member of the neotropical fern genus *Adiantopsis* Fée (Link-Pérez et al. 2011), which contains ca. 40 species with laminar architectures including pinnate, pedate, and palmate. The palmate architecture is characterized by pinnae that radiate from a central point at the stipe apex, and *A. radiata* has generally been regarded as the only species in *Adiantopsis* with palmately compound laminar morphology (Tryon and Tryon 1982), until recent work revealed several additional palmate species that were morphologically and molecularly distinct (Link-Pérez and Hickey 2011; Link-Pérez et al. 2011). A remaining question, however, concerns the application of the name *A. alata* Prantl. Prantl set this palmate species apart from *A. radiata* in 1883 based on the presence of a pair of well-developed adaxial carinae on the stipes, a feature that is typically absent on the stipes of *A. radiata* except for juvenile fronds or rarely along the extreme distal stipe.

The protologue (Prantl 1883) for *A. alata* provides a brief diagnosis and an illustration. Prantl cites two specimens, one from Brazil (*Luschnath 103*, B [scan!]) and one from British Guiana (*M.R. Schomburgk 1132*, B [scan!]). According to the *International Code of Nomenclature* (McNeill et al. 2012), the specimens Prantl cited in the protologue and their duplicates are, therefore, syntypes. Examination of these syntypes and of specimens generally matching the description of *A. alata* from the Guiana Shield and Brazil suggested that the syntypes represent two different species. Our goals were to 1) clarify the taxonomy of *A. alata* and the application of that name, and 2) resolve the remaining undescribed palmate species of *Adiantopsis*.

Materials and Methods

Morphology—We obtained morphological data from herbarium sheets using a dissecting microscope, scoring more than 70 discrete and continuous characters for each taxon and using the data to construct species descriptions. Two to six pinnules per taxon, each from different collections, were prepared as described in Link-Pérez and Hickey (2011) to observe guard cells and venation patterns. We collected spores directly from herbarium sheets using a dissecting needle (Wagner et al. 1986) and mounted them on glass slides in Hoyer's Mounting Medium (Anderson 1954; Barrington et al. 1986). After 24 hr, we measured spore diameter as described in Link-Pérez and Hickey (2011), including the perispore but not the echinae. We mounted additional spores from each taxon onto aluminum stubs using double-sided carbon adhesive tabs, sputter coated with gold, and examined with scanning electron microscopy (SEM) to observe spore ornamentation and shape. Data analyses of spore and guard cell lengths were conducted in R (R Core Team 2015) using one-way analysis of variance, with differences between means computed using Tukey's 'honest significant difference' method to identify significantly different values. We used the data from spore and guard cell lengths to generate hypotheses about ploidy level (Barrington et al. 1986). Our descriptions of planar shapes follow guidelines published by the Systematics Association Committee for Descriptive Terminology (1962); we followed Lellinger (2002) for all other morphological terminology.

DNA Extraction, Amplification, and Sequencing—Samples for DNA extraction (Appendix 1) were selected from herbarium specimens (Savolainen et al. 1995), and the tissue was disrupted with a Mini-Beadbeater (BioSpec Products, Bartlesville, Oklahoma) using zirconia/silica beads. We extracted total genomic DNA using the DNeasy Plant Mini kit (Qiagen, Valencia, California). We followed the manufacturer's protocol, including the optional five-minute centrifugation after incubating on ice during protein precipitation.

The PCR amplification of two plastid loci, *rbcL* and *atpA*, was carried out according to Link-Pérez et al. (2011). We added the trehalose-based additive TBT-PAR (Samarakoon et al. 2013) to the reaction mix at 3 μL of a 5 × concentration and adjusted the volume of water accordingly for a final reaction volume of 15 μL. TBT-PAR was added due to its ability to reduce PCR inhibition, and experiments in our lab showed it to dramatically improve our success rates in DNA amplification from herbarium specimens (data not shown). We visualized PCR products with a 1% agarose gel with SafeView Nucleic Acid Stain (Applied Biological Materials Inc., Richmond, British Columbia, Canada) in a sodium borate buffer (Brody and Kern 2004) to confirm successful amplification of DNA.

The PCR product was then purified using Exo-SAP PCR clean up (Affymetrix, Santa Clara, California) with a reaction mix of 0.5 μL of Exonuclease I (Product No. 70073Z), 0.5 μL shrimp alkaline phosphatase (SAP) (Product No. 78390) and 1 μL of 1 × SAP Buffer (Product No. 70103). We sent the purified PCR product to the DNA Analysis Facility on Science Hill at Yale University for Sanger sequencing.

Phylogenetic Analyses—We assembled newly-acquired sequences in Geneious v8.1.7 (Kearse et al. 2012) and used the MAFFT multiple alignment plugin v1.3.3 (Katoh 2013) to align sequences from all taxa, including additional sequences obtained from GenBank (Benson et al. 2013). Voucher specimen data and GenBank accession numbers are provided in Appendix 1 as well as made available from the Dryad Digital Repository: doi:10.5061/dryad.67qq8 (Link-Pérez et al. 2016). Because the chloroplast is a single, non-recombining molecule, we concatenated the amplified regions for each species. We used PartitionFinder (Lanfear et al. 2012) to identify the best model of molecular evolution for each portion of the concatenated alignment, including each codon position of *rbcL* and *atpF,* and the non-coding *atpF–A* and *atpA–trnR* spacers. Reading frames were identified by comparison to translations of previously annotated sequences downloaded from GenBank using the NCBI plugin in Geneious v8.1.7 (Kearse et al. 2012). We could not find a well-annotated sequence for the small portion of *atpA* included in the alignment, and so we did not partition it by codon. We performed maximum likelihood (ML) analyses with RAxML v8.2.3 (Stamatakis 2014), conducting a rapid bootstrap analysis

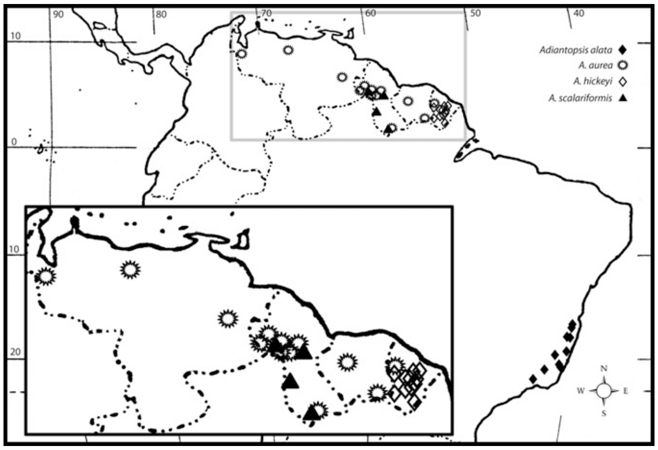

FIG. 1. Distribution of *A. alata* (black diamonds) and the three new palmate species of *Adiantopsis*. Inset shows an enlarged view of the distribution of the Guiana Shield taxa.

with 1,000 replicates and searching for the best-scoring ML tree in a single run (option "-f a"). We applied the GTR + I + Γ model using the optimal partitioning scheme identified by PartitionFinder: the first partition included only the first position of *rbcL*, and the second partition included the second positions of *atpF* and *rbcL*. The third partition included both spacers and the third positions of both genes. The final, fourth partition included *atpA* and position one of *atpF*. We used SumTrees v3.3.1 (Sukumaran and Holder 2010) to summarize support from the 1,000 bootstrap analyses on the single best-scoring ML tree.

Bayesian inference (BI) analyses were conducted using the MPI version of MrBayes v3.2.1 (Altekar et al. 2004; Ronquist et al. 2012). We used two independent runs of 20 million generations each, with four chains per run and sampling trees every 1,000 generations. Uniform priors and default chain temp of 0.2 were employed. We used the optimal partitioning scheme described above, with the optimal model identified for each partition. We assessed chain convergence, stationarity, and estimated sample size (ESS) using Tracer 1.6 (Rambaut et al. 2014), visually examining plots of parameter values and log-likelihood against number of generations. ESS values were considered satisfactory when they passed 200. We discarded the first 25% of trees from each run as burn-in, combined the remaining trees from the two runs, and produced an annotated maximum clade credibility tree using TreeAnnotator v1.8.0 (part of the BEAST package; Drummond et al. 2007, 2012). All ML and BI analyses were conducted on the HiPerGator high performance computing cluster at the University of Florida.

RESULTS

Examination of specimens revealed four distinct taxa: one restricted to eastern Brazil that matches Prantl's diagnosis for *A. alata*, and three distinct species from the Guiana Shield, described here as new: *A. aurea*, *A. hickeyi*, and *A. scalariformis*. The morphological and molecular distinctions that separate these taxa from each other and from the widespread *A. radiata* support the recognition of these taxa at the level of species. Except for *A. aurea*, which is found across the Guiana Shield, these species have narrower geographic distributions (Fig. 1). Several diagnostic characters separating these species from each other and from the widespread *A. radiata* are presented in Table 1 and described below.

Frond and Pinnae Characters—Fronds of *A. radiata*, *A. alata*, and the three new species typically bear between five and seven pinnae radiating from the stipe apex (Fig. 2C), although rarely fewer and occasionally more are observed (Table 1). *Adiantopsis aurea* is collected frequently with short pinnate fronds at the base of palmate fronds (Fig. 3A), or as young plants with only pinnate fronds present (Fig. 3F); these pinnate fronds are not found on the other nine species of palmate *Adiantopsis*, except rarely in *Adiantopsis trifurcata* (Baker) Link-Pérez & Hickey (Link-Pérez and Hickey 2011). The caudate pinna apices of *A. alata* are much longer and more narrowly tapered than all other members of the genus (Fig. 2A, B), and they are the most easily visible character separating it from the other palmate species.

Pinnule Characters—*Adiantopsis alata* and *A. scalariformis* tend to have larger pinnules than other palmate *Adiantopsis* (Table 1 and Link-Pérez and Hickey 2011), although size ranges overlap. The pinnules of *A. alata* are notable for their tapered and acute apices (Fig. 2F). Guard cell lengths of *A. alata*, *A. aurea*, *A. hickeyi*, and *A. scalariformis* are all significantly larger than those of *A. radiata* ($p < 0.001$; Table 2).

Stipe Carinae Characters—The paired carinae on the stipes *of A. alata* extend more than 1 mm in height and, in contrast to other palmate *Adiantopsis*, are obvious to the unaided eye (Fig. 2E); they are located adaxially along the distal quarter or half of the stipe. The stipe carinae of *A. aurea* are found along the distal half to 2/3 and are up to 0.64 mm tall (Fig. 3B, Table 1). *Adiantopsis hickeyi* has stipe carinae that are 0.2–0.4 mm tall with undulate margins (Fig. 4F), while *A. scalariformis* has stipe carinae that are 0.3–0.8 mm tall, often involute or revolute, with smooth margins (Fig. 5E).

Spore Characters—Spores of *A. alata* are significantly smaller than spores of the other species (Table 3); *A. hickeyi* has spores that are significantly larger than those of *A. radiata*,

TABLE 1. Characters that can be used in distinguishing the palmate members of *Adiantopsis* addressed in this study.

Taxa	Typical number of pinnae	Pinnae apices	Typical size of pinnules (excluding auricle, if present)	Pseudoindusia shape (margin)	Stipe carinae, position and height
A. alata	5–6(–9)	Basally lobate with elongate acicular apex, frequently to 1.5 cm in length	9.3–20.0 mm long; 2.4–5.2 mm wide	Lunate (entire)	Golden, distal ½ to ¼ of stipe, to 1.3 mm tall
A. aurea	(1)3–5,6(7–8 rarely)	Basally lobate with one or two lobes and acute apex, 0.5–1.0 cm in length	3.5–14.7 mm long; 1.4–4.5 mm wide	Lunate to quadrangular (entire to undulate)	Golden or reddish-gold, distal ½ to ⅔ of stipe, to 0.64 mm tall
A. hickeyi	(5)7(–9)	Basally lobate with rounded apex, 0.5–1.0 cm in length	6.8–15.8 mm long; 2.4–5.8 mm wide	Lunate to quadrangular (entire to undulate)	Golden to brown, distal ½ to ⅓ of stipe, to 0.3 (–0.4) mm tall
A. radiata	(3–)5–7(–9)	Basally pinnatifid with elongate acute apex, 0.5–1.0 cm in length	7.0–13.5 mm long; 2.0–3.5 mm wide	Lunate (entire)	Rarely present, distal end only when present, to 0.1 mm tall
A. scalariformis	5–7	Basally pinnatifid with elongate rounded apex, 0.5–1.0 cm in length	10.0–18.0 mm long; 3.0–5.0 mm wide	Lunate to quadrangular (entire to undulate)	Golden to reddish-brown, distal ¼ to ½ of stipe, 0.3–0.8 mm tall (typ. 0.6 mm)

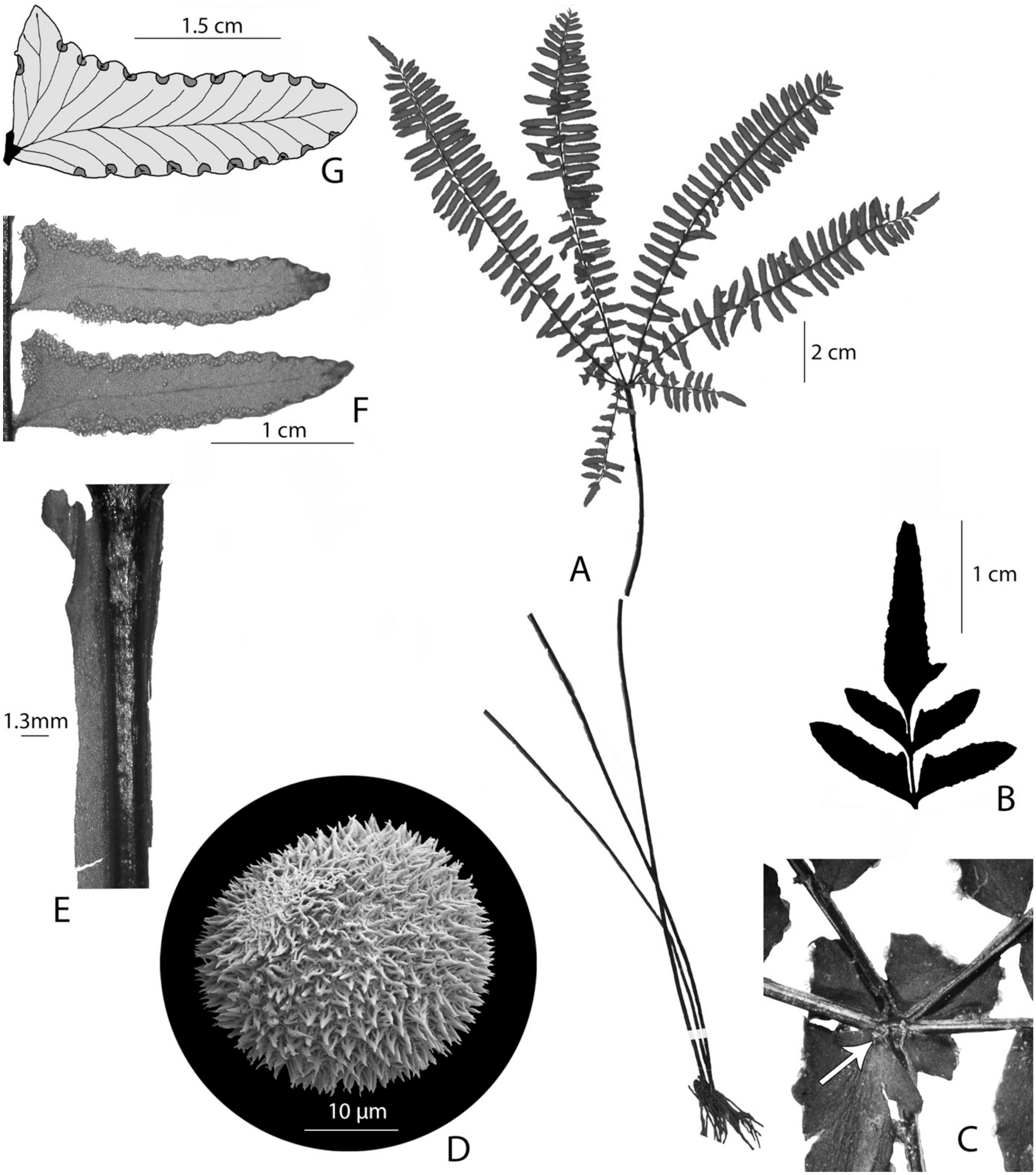

Fig. 2. *Adiantopsis alata.* A. Habit. B. Pinna apex. C. Stipe apex, indicated with white arrow. D. Spore with arachnoid-echinulate ornamentation. E. Stipe detail, showing adaxial carina to the left. F. Pinnules showing dense sporangia and lanceolate shape. G. Line drawing of a cleared pinnule showing venation and round to lunate pseudoindusia. A. *Luschnath 103* (B); B, F. *Almeida et al. 688* (BHCB); C, E. *Prantl s.n.* (US); D. *Curran 270* (US); G. *Salino et al. 10929* (BHCB).

whose spores are of similar size to *A. aurea* and *A. scalariformis*. All five species have tetrahedral-globose spores; *A. radiata* with echinate ornamentation, and the other four with arachnoid-echinulate ornamentation.

Phylogenetic Analyses—Our concatenated alignment included the genes *rbcL* and *atpF* and the non-coding *atpF–A* and *atpA–trnR* spacers, and was 3,130 base pairs in length. When all models were available to PartitionFinder, the following optimal partitioning scheme and models were selected. Partition 1 included *rbcL*, position 1, with GTR + I as the best model; Partition 2 included position 2 of *rbcL* and *atpF,* with HKY + I as the best model; Partition 3 included

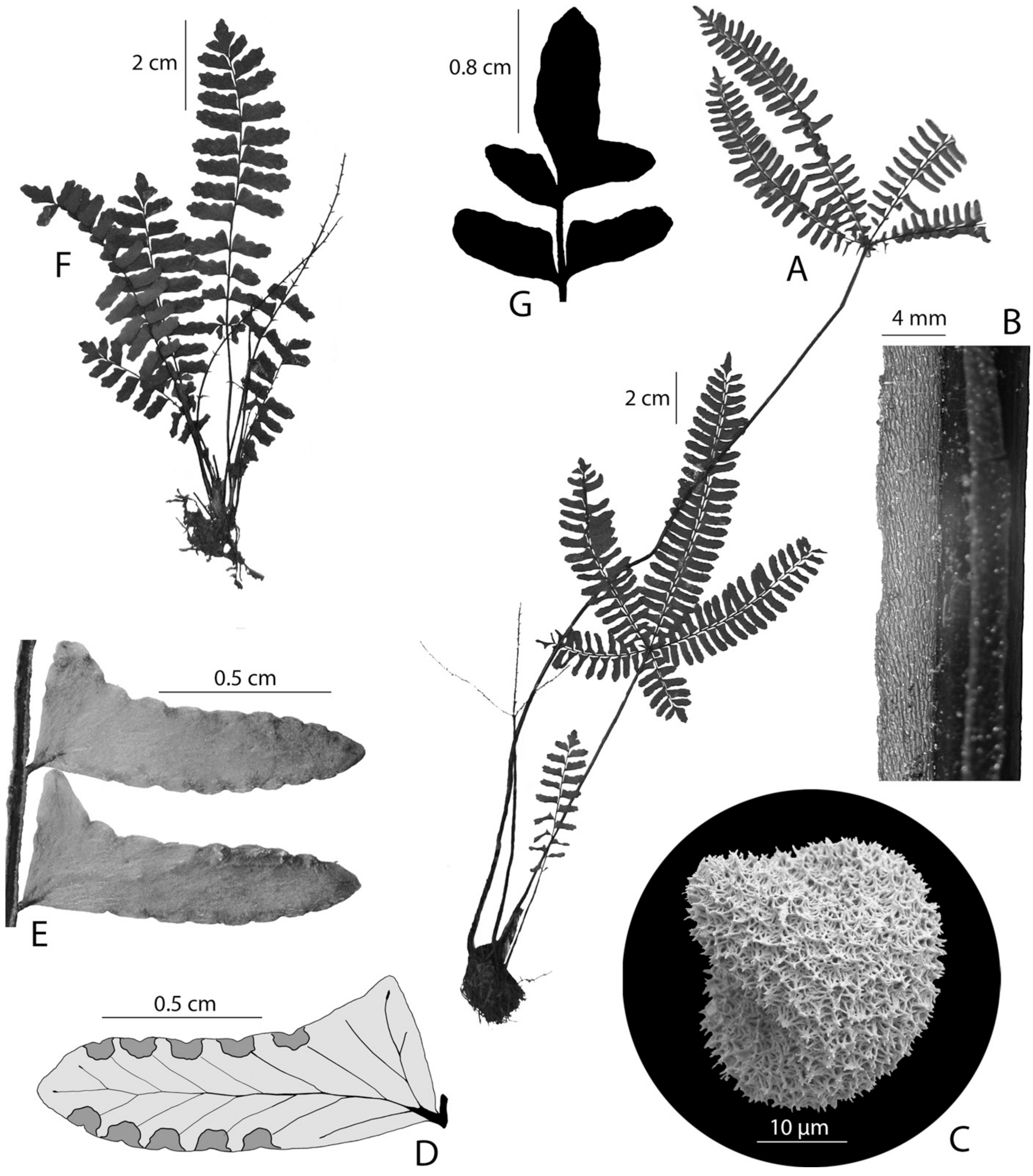

FIG. 3. *Adiantopsis aurea*. A. Habit showing pinnate, ternate (see naked axis; pinnules abscised), and palmate fronds. B. Stipe detail showing adaxial carina on the left. C. Spore showing arachnoid-echinulate ornamentation with dissected bases. D. Line drawing of a cleared pinnule showing quadrangular pseudoindusia and venation. E. Pinnules showing crenate margins and basal stalk. F. Pinnate growth habit. G. Pinna apex. A, F, G. *Henkel and Chin 5721* (NY); B. *Liesner and González 10164* (MO); C, D, E. *van der Werff and González 4944* (MO).

both spacers and the third positions of both genes, with GTR + Γ as the best model; Partition 4 included *atpA* and position one of *atpF*, with GTR + I + Γ as the best model. Maximum likelihood analysis (using only GTR + I + Γ, but partitioned as described) produced a single best tree with ln L = -8,038.76 (Fig. 6). The BI analyses produced a tree nearly identical in topology to the ML tree, with posterior probabilities (BI PP) generally similar to the ML BS values, except that the position of *Adiantopsis regularis* differed between the two. In both trees, within the ingroup *A. flexuosa* is sister to

Table 2. Guard cell lengths of palmate species of *Adiantopsis* addressed in this paper. Taxa with means that are significantly different from each other (One-way ANOVA, Tukey's HSD, $p < 0.001$) are indicated by different letters. Data for *A. radiata* from Link-Pérez and Hickey (2011).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
A. alata[a]	150	51.02	4.78	40.00	67.50
A. aurea[b,c]	125	64.40	6.56	50.0	77.50
A. hickeyi[b]	150	65.64	4.99	55.00	77.5
A. radiata[d]	75	46.44	3.29	36.45	54.00
A. scalariformis[c]	50	62.12	7.78	47.50	82.50

the remaining species of *Adiantopsis*. In the ML tree, *A. regularis* is then sister to a clade that contains the remaining species, with low support (ML BS = 53%), while in the BI tree, *A. regularis* falls in a small clade where it is sister to *A tweediana* plus *A. dichotoma*, and this clade is sister to the remaining taxa (Fig. 6).

Discussion

Our research has revealed that the syntypes for *A. alata* represent two distinct entities that we posit should be regarded as two separate species. The syntypes from Brazil, *Luschnath 103*, most closely resemble the illustration from the protologue and best demonstrate the characteristics included in Prantl's diagnosis, including the exaggerated stipe carinae and the elongated pinnules with caudate apices; for these reasons, we are selecting *Luschnath 103* (B [barcode B 20 0001553]) as the lectotype for *A. alata*. The syntype from Guyana, *Schomburgk 1132* (B), is referred to the new segregate species *A. scalariformis* (Fig. 5), which is currently known only from Guyana (Fig. 1). *Adiantopsis alata* as now circumscribed is endemic to Brazil (Fig. 1).

Palmate *Adiantopsis* from the Guiana Shield bearing adaxial carinae along their stipes, as does *A. alata*, are of three separate species and are morphologically and molecularly distinct from each other and from both *A. alata* and *A. radiata* (Fig. 6). *Adiantopsis alata* is sister to *A. scalariformis*, with which it shares the largest pinnules among the palmate members of the genus; the two species differ in the size and disposition of their paired stipe carinae, the shape of their pinna apices, and in statistically significant differences in the size of their guard cells (Table 2) and spores (Table 3).

Adiantopsis hickeyi from French Guiana is sister to the widespread *A. radiata*; these two form a clade that is sister to that containing *A. alata* and *A. scalariformis* (Fig. 6). It is important to note that the single accession of *A. radiata* used in our analyses was selected from the four accessions of *A. radiata* for which *atpA* and *rbcL* sequences were generated in Link-Pérez et al. (2011); sequences from this accession share 100% identity with two other accessions of *A. radiata* in that study and share complete consensus with a fourth accession for which there were missing data. Because the sequences for *A. radiata* generated in Link-Pérez et al. (2011) were identical throughout their alignment except for where data were missing, we opted to simplify the analyses by using just one accession (OTU1 in that study). *Adiantopsis hickeyi* is sister to *A. radiata* and not embedded within the latter, as it appears to be in the maximum clade credibility tree presented in Link-Pérez et al. (2011, Fig. 2). In that tree, two accessions of *A. hickeyi* ("Species novum 3" in that paper) form a clade sister to a clade containing the four accessions of *A. radiata* newly sequenced in that study, with two additional accessions of *A. radiata* from GenBank located just outside this clade containing *A. hickeyi* and the other four *A. radiata*. None of these relationships received support from bootstrap analyses, other than strong support for a clade containing *A. radiata* and *A. hickeyi*, and we interpret the position of the two GenBank accessions of *A. radiata* as an artifact generated by a substantial amount of missing data. In the current study, the sister relationship of *A. radiata* and *A. hickeyi* received strong support (ML BS $\geq$ 75% and BI PP $\geq$ 0.95), as did this clade's sister relationship to the clade containing *A. alata* and *A. scalariformis* (Fig. 6).

Adiantopsis aurea occupies a position sister to *A. timida*, from which it differs in pinnule size and shape, costule position in pinnule, pseudoindusia shape, and spore ornamentation (Link-Pérez and Hickey 2011). Data from spore lengths (Table 3) suggest that *A. alata*, *A. aurea*, *A. hickeyi*, and *A. scalariformis* are all diploids, based on their relation to the sizes observed in *A. radiata*, a known diploid with a base chromosome number of n = 30 (Walker 1973; see discussion about the use of spore sizes as indicators of ploidy levels in *Adiantopsis* in Link-Pérez and Hickey 2011).

Adiantopsis alata and the three new palmate taxa from the Guiana Shield are described and illustrated below, bringing the total number of palmate members of *Adiantopsis* to ten. A key to all palmate *Adiantopsis* is presented below.

Key to the Palmate Species of *Adiantopsis* (modified from Link-Pérez and Hickey 2011)

1. Lamina primarily ternate with three pinnae; pseudoindusia triangular 2
    2. Pinnae fastigiate; pseudoindusia +/− entire . . . . *A. trifurcata*
    2. Pinnae spreading; pseudoindusia laciniate . . . . *A. ternata*
1. Lamina palmate with five or more pinnae; pseudoindusia lunate to quadrangular 3
    3. Carinae with apical cells digitate, composed of separate and distinct cells oriented perpendicular to the axes . . . . *A. dactylifera*
    3. Carinae with apical cells forming a more or less entire margin, with most cells oriented parallel to the axes 4
        4. Fronds subdimorphic; pinnules generally less than 7 mm long; pinnules attached medially or sub-medially 5
            5. Pseudoindusia lunate with entire margins; carinae adaxial on stipe beginning at midpoint or proximal third . . . . *A. timida*
            5. Pseudoindusia quadrangular with erose margins; carinae absent or adaxial on extreme distal end only . . . . *A. crinoidea*
        4. Fronds monomorphic (rarely subdimorphic); pinnules generally more than 7 mm long; pinnules attached sub-basally to basally 6
            6. Stipe carinae absent or adaxial on distal 1.0 cm only, up to 0.1 mm tall . . . . *A. radiata*
            6. Stipe carinae present adaxially on distal ¼ or more, greater than 0.2 mm tall 7
                7. Stipe carinae prominent and typically 1.0 mm tall or more; pinnae apices with elongate acicular apices, these frequently to 1.5 cm in length . . . . *A. alata*
                7. Stipe carinae less than 1.0 mm tall; pinnae apices with acute or rounded apices, these typically 0.5–1.0 cm in length 8
                    8. Central pinnae 1.0–2.7 cm wide; stipe carinae present in distal half or more; frequently with additional short pinnate fronds, these fertile when rest of plant is fertile . . . . *A. aurea*

8. Central pinnae 1.9–3.4 cm wide; stipe carinae present along distal half or less; not associated with short pinnate fronds 9
   9. Fronds monomorphic; carinae 0.3–0.8 mm tall, often involute or revolute . . . . *A. scalariformis*
   9. Fronds subdimorphic; carinae 0.2–0.4 mm tall, undulate . . . . *A. hickeyi*

Taxonomic Treatment

Adiantopsis alata Prantl, Gartenfl. 32: 99. 1883.—TYPE: BRAZIL. Bahia: exact locality unknown, s.d., *Luschnath 103* (lectotype, here designated: B [barcode B 20 0001553, scan!]; isolectotypes: B [barcode B 20 0001550] B [barcode B 20 0001552]).

Rhizome erect; scales acicular, bicolorous, the central band shiny, black, occupying ½ to ⅔ of the width, the margins

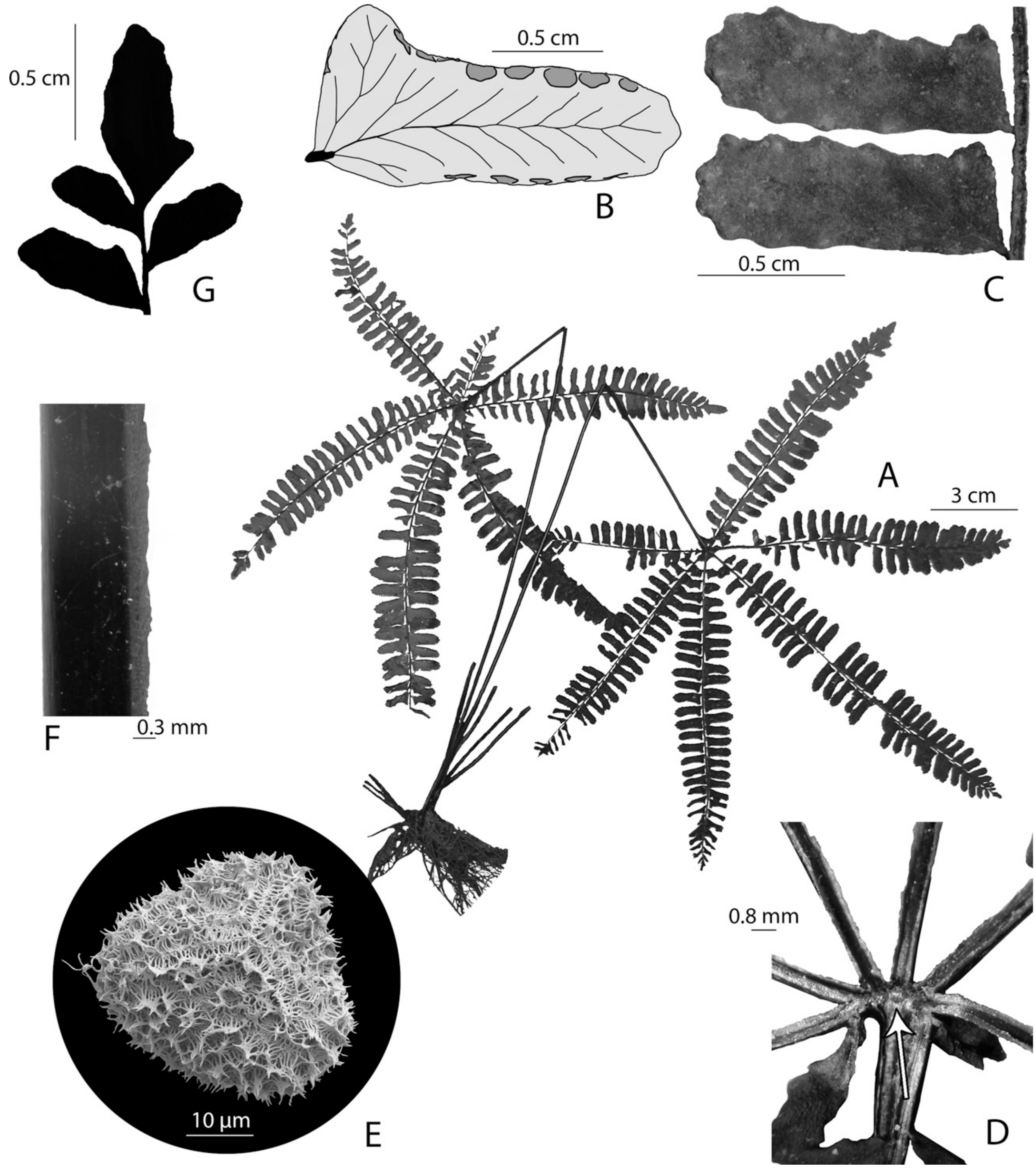

Fig. 4. *Adiantopsis hickeyi*. A. Habit. B. Line drawing of a cleared pinnule showing venation, basal stalk placement, and lunate pseudoindusia. C. Adaxial view of pinnules showing undulate margins. D. Stipe apex, indicated with white arrow. E. Spore with arachnoid-echinulate ornamentation with dissected bases. F. Detail of stipe showing adaxial carina on the right. G. Pinna apex. A. *Mori and Smith 25095* (CAY); B. *Mori and Smith 25095* (NY); C, D, F, G. *de Granville et al. 15052* (CAY); E. *Cremers and Crozier 15132* (CAY).

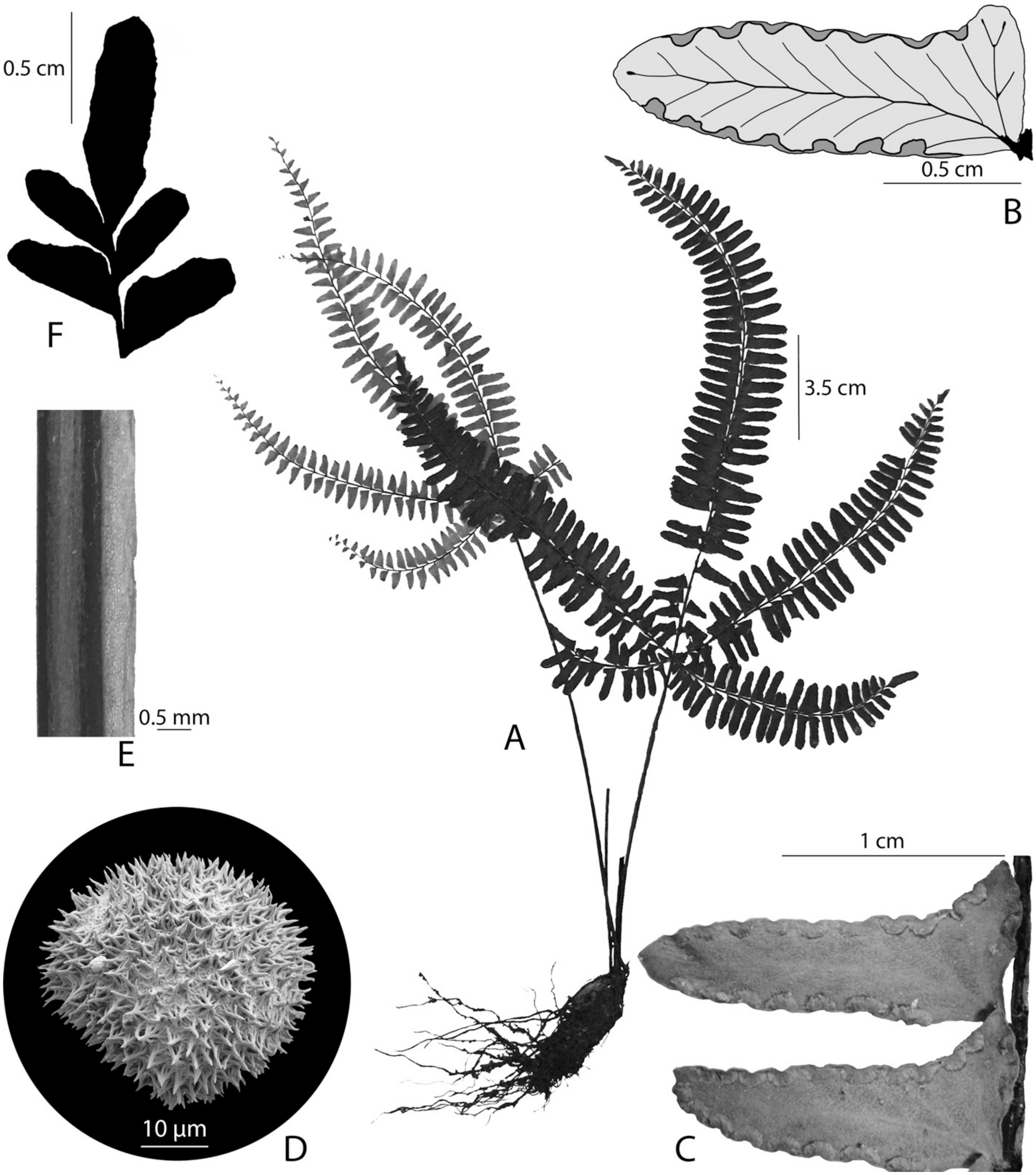

Fig. 5. *Adiantopsis scalariformis.* A. Habit B. Line drawing of a cleared pinnule showing lunate to quadrangular pseudoindusia, venation, and basal stalk placement. C. Pinnules showing lunate pseudoindusia. D. Spore with arachnoid-echinulate ornamentation with dissected bases. E. Adaxial carina on the right of the stipe. F. Pinna apex. A. *Mori et al. 24525* (NY); B, D, E. *Henkel et al. 983* (NY); C. *Clarke 2962* (CAY); F. *Jansen-Jacobs et al. 3572* (CAY).

golden, with sparse concolorous scales intermixed. Fronds erect, monomorphic, 15.0–52.8 cm long. Stipes atrocastaneous to cinnamomeous, matte to sub-lustrous, terete, about 50–80% of the frond length, 5.5–37 cm long; carinae adaxial, beginning at midpoint of stipe, occasionally in the distal ¼, golden, translucent, prominent, to 1.5 mm tall, cells large and irregular; scales brown, concolorous, rare at the stipe base, rare and biseriate at the stipe apex; catenate hairs rare. Laminae palmate, circular, geniculate, 8.0–18.0 cm long, 8.0–24.0 cm wide; spongiose to chartaceous, drying olivaceous;

Table 3. Spore lengths of palmate species of *Adiantopsis* addressed in this paper. Taxa with means that are significantly different from each other (One-way ANOVA, Tukey's HSD, $p < 0.05$) are indicated by different letters. Data for *A. radiata* from Link-Pérez and Hickey (2011).

Taxon	Sample size	Mean (μm)	Standard deviation (μm)	Min (μm)	Max (μm)
A. alata[a]	131	28.99	2.08	25.00	35.00
A. aurea[b]	144	33.49	3.14	25.00	42.50
A. hickeyi[c]	148	36.75	2.38	30.00	42.50
A. radiata[b]	75	32.91	2.39	27.00	37.80
A. scalariformis[b]	64	33.38	1.98	29.70	37.80

hydathodes marginal, green or black, occasionally dark margined; scales absent; three-celled hairs rare abaxially, absent adaxially, septate, the basal cell elongate and colorless, the middle cell short, orange to red, the apical cell white, yellow, or colorless; stomata anomocytic, the guard cells 40.0–67.5 (mean = 51.02) μm long. Costae persistent, atrocastaneous to cinnamomeous, lustrous; carinae adaxial on all costae, golden, 0.23–0.6 mm tall, the apical cells narrow, parallel to the costae and smaller than others; scales and hairs rare at abaxial costule-costa junctures. Pinnae 5–6 (–9), spreading radially from stipe apex, fusiform, ending in a generally-symmetrical ultimate segment, this basally lobate and with an elongate caudate apex to 1.5 cm long; central pinna 7.0–17.5 cm long, 1.4–3.5 cm wide, bearing 22–36 pinnule pairs; basal pinnae to 2.5–15.0 cm long, 1.0–3.2 cm wide, bearing 6–29 pinnule pairs; basal flabellate divisions attached between pinnae at stipe apex, more or less symmetrical, typically fertile when frond is fertile. Pinnules transverse (to slightly ascending), short-stalked, articulate, narrowly oblong to lanceolate, 9.3–20.0 mm long, 2.4–5.1 mm wide, length:width ratio 2.6–5.2 (mean = 3.85), the acroscopic auricles to 1.8 mm long; base excavate basiscopically, truncate (cuneate) acroscopically; margins entire, slightly crenate; apices round to acute; stalks basal, persistent, stalk apex appearing irregularly conical after pinnule abscission, to 0.65 mm long. Veins free, anadromous, obscure to occult. Sori marginal, discrete, occasionally confluent on very fertile fronds, 17–29 per pinnule. Pseudoindusia distinct, lunate, scarious to papyracious, brownish-black, often similar to lamina color or darker, usually (1.5–)2.4(–3.6) times wider than long, 0.18–0.33 mm long, 0.45–0.83 mm wide, margin entire. Sporangia subglobose, short-stalked with stalks 80–150 μm long. Spores yellow, tetrahedral-globose, 25.00–35.00 (mean = 28.99) μm long, arachnoid-echinulate, echinae dense, up to 2.5 μm long, with dissected bases, laesura visible with brightfield. Chromosome number unknown. Figure 2A–G.

Additional Specimens Examined—BRAZIL. Bahia: Mun. Arataca, Serra do Peito de Moça, Estrada Arataca-Una, com entrada no assentamento Santo Antônio, ca. 22,4 km de Arataca, RPPN Caminho das Pedras, trilha para a serra, 15°10.26′S, 39°20.31′W, 1,000 m, 21 Jul 2005, *Matos et al. 738* (UPCB); Mun. Ibirapitanga, plantação de cacau, 18 May 1966, *Belém and Pinheiro 2270* (UB); Mun. Itanhém, Estrada para o Corró, 17°7′S, 40°14′W, 451 m, 18 Aug 2004, *Stehmann et al. 3828* (BHCB); Mun. Jussari, RPPN Serra do Teimoso, floresta ombrófila densa/floresta estacional semidecidual, 15°09′S, 39°31′W, 260–400 m, 2 Nov 2002, *Salino and Jardim 8153* (BHCB); Mun. Prado, Parque Nacional do Descobrimento, floresta ombrófila densa de terras baixas, 16°59′S, 39°23′W, 50 m, 30 Oct 2002, *Salino and Jardim 8133* (BHCB); Forests of Rio Grongogy Basin, 100–500 m, Oct–Nov 1915, *Curran 270* (US). Espírito Santo: Mun. Linhares, Reserva Florestal de Linhares (CVRD), cruzamento das estradas Flamengo e Gávea, mussununga, 19°9′S, 39°56′W, 30–60 m, 9 Feb 2007, *Almeida et al. 688* (BHCB); Linhares, Reserva Natural da CVRD, Estrada: Jueirana Vermelha, Km: 1.5, 15 Oct 2002, *Folli 4382* (BHCB). Minas Gerais: Mun. Conselheiro Pena, Parque Estadual de Sete Salões, área com floresta estacional semidecidual secundária com palmeira (*Attalea* sp.) e Cactus, alem de afloramentos rochosos dentro e no entorno, 19°15′S, 41°22′W, 545 m, 7 May 2006, *Salino et al. 10929* (BHCB); Mun. Viçosa, Universidade Rural de Minas Gerais, *Kuhlmann 3924* (US). Unknown location: cultivated, Nov 1882, *K. Prantl s.n.* (HBG).

Distribution and Habitat—*Adiantopsis alata* is known only from Brazil (Bahia, Minas Gerais, and Espírito Santo), where it occurs in forests and along roadsides, from 30–1,000 m a. s. l.

Comments—The most distinguishing features of *Adiantopsis alata* are the extra long apical segment on the pinnae (frequently extending to 1.5 cm in length) and the wide carinae, often 1.0 mm wide or more and clearly visible to the unaided eye, on the stipes distally. The pinnules are narrowly oblong to lanceolate with acute apices and typically reaching 2 cm in length, larger than pinnules in most palmate members of the genus. The spores of *A. alata* are smaller than those of all the other palmate *Adiantopsis*.

Adiantopsis aurea Link-Pérez, Seabolt, and Ledford, sp. nov.—TYPE: GUYANA. Region: Potaro-Siparuni. Pakaraima Mtns., 19 July 1994, *Henkel and Chin 5721* (holotype: NY!; isotype CAY!).

Rhizome erect; scales acicular, bicolorous, the central band shiny, black or dark brown, occupying ½ to ⅔ of the width, the margins golden or reddish-gold, shiny, with conform concolorous golden scales interspersed. Fronds caespitose, monomorphic, (3.0–) 4.5–41.3 cm long. Stipes atrocastaneous, cinnamomeous, ebeneous, or atropurpureous, lustrous, typically 47–72% of the frond length, as little as 28–36% of the frond length in the young plants with pinnate fronds, 1.3–30.0 cm long; carinae adaxial, beginning at midpoint of stipe, occasionally at the proximal 1/3 on palmate fronds or at base of stipe on younger pinnate fronds, golden or reddish-gold, cells more or less with long sides parallel to stipe, to 0.64 mm tall; stipe scales tan or golden, sparse, these generally restricted to stipe base and apex; hairs sparse. Laminae palmate or ternate, circular, geniculate, 7.0–22.0 cm long, 5.0–24.0 cm wide, young fronds often once-pinnate and linear, 3.0–13.0 cm long cm and 1.0–2.3 cm wide, the smallest observed (3.0 cm long, 1.0 cm wide) was fertile; spongiose to chartaceous, drying grayish-green, olive, or brown; hydathodes marginal; scales absent; hairs rare abaxially, rare adaxially; stomata anomocytic, the guard cells 50.0–77.5 (mean = 64.4) μm long. Costae persistent, atrocastaneous, cinnamomeous, ebeneous, or atropurpureous, lustrous; carinae adaxial on all costae, golden or reddish-gold, shiny, to 0.5 mm tall, the cells more or less parallel to the costa; scales at abaxial costule-costa junctures, amber or brown, hair-like; hairs not observed. Pinnae (1)3–5(–8), spreading radially from stipe apex, fusiform, gradually diminishing in width to a small conform apex, this basally lobate with one or two lobes and with an acute apex; central pinna 5.0–18.5 cm long, 1.1–2.7 cm wide, bearing 8–33 pinnule pairs; basal pinnae no more than 20–60% of length of central pinnae, to 1.4–10.5 cm long, 0.7–2.2 cm wide, bearing 2–20 pinnule pairs; basal flabellate divisions attached between pinnae at stipe apex, more or less symmetrical, typically fertile when frond is fertile. Pinnules incurved slightly, transverse to ascending, short-stalked, articulate, narrowly oblong, 3.5–14.7 mm long, 1.4–4.5 mm wide, length:width ratio 2.8–4.2 (mean = 3.5), the acroscopic auricles to 2.2 mm long; base excavate basiscopically, truncate acroscopically; margins entire to crenate; apices round to acute; stalks basal, adaxially

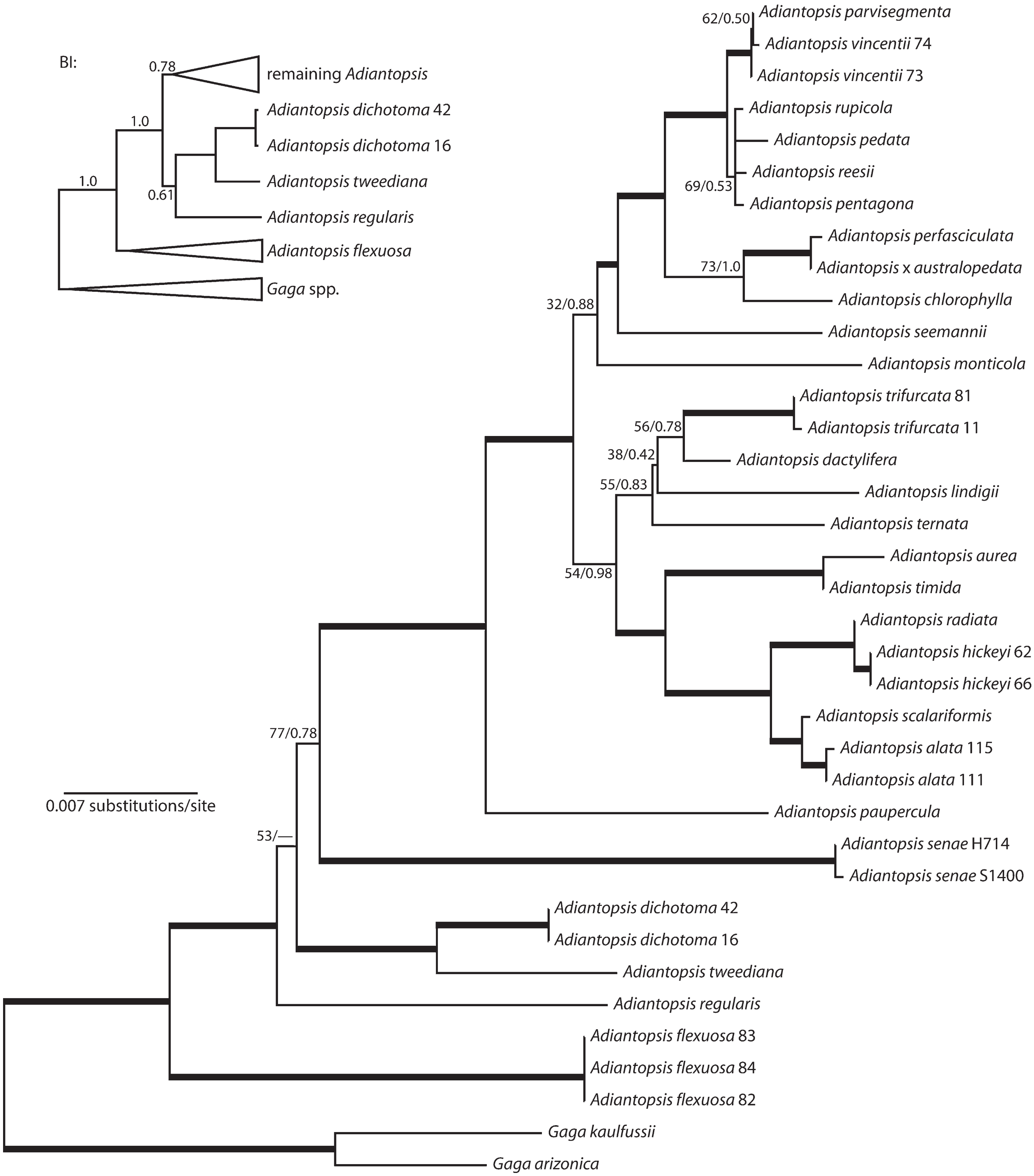

Fig. 6. ML phylogram from analysis of coding and non-coding plastid regions (ln L = -8,038.76). Thick branches received strong support (ML BS ≥ 75% and BI PP ≥ 0.95). Inset shows BI topology. Note that the position of the one taxon, *Adiantopsis regularis*, differs between the two topologies. Branch lengths are proportional to substitutions per site.

arched before entering pinnule, persistent, appearing aculeate or two-pronged after pinnule abscission, to 1.2 mm long, obvious. Veins free, anadromous, occult, ending submarginally in adaxial hydathodes. Sori marginal, discrete, 4–16 per pinnule. Pseudoindusia distinct, lunate to quadrangular, papyracious to scarious, lustrous, yellowish-tan or approaching lamina color, sometimes black maculate, usually 1.3–3 times wider than long, 0.28–0.53 mm long, 0.60–1.2 mm wide, the margin undulate to entire. Sporangia subglobose, long-stalked with stalks up to ~200 μm long. Spores yellow to dark-yellow/amber at maturity, tetrahedral-globose, 25.00–42.50 (mean = 33.49) μm long, arachnoid-echinulate, echinae to 2.5 μm long, with dissected bases, laesura visible. Chromosome number unknown. Figure 3A–G.

Additional Specimens Examined—FRENCH GUIANA. Mont Itoupé: Sommet Tabulaire - 14, versant ouest, layon A et abords, partie amont crique 1, à partir de 100 m au sud du point 600 du layon A, Station MB 973–240, 3°1′N, 53°5′W, 685 m, 24 Mar 2010, *Boudrie 4410* OSC, CAY, P); Sommet Tabulaire - 10, versant ouest, layon A, zone bota 6, layon A, de 700 à 300 m, versant ouest, Station MB 973–220, 3°01′N, 53°05′W, 710 m, 19 Mar 2010, *Boudrie et al. 4320* OSC, CAY). Mont Kotika: versant est., 3°55′N, 54°10′W, 600 m, 6 Sept 2007, *Delnatte 1381* (CAY).

GUYANA. Cuyuni-Mazaruni Region: Kamarang River-Wenamu Trail, occasional at river side by rapids, between Paruima Falls and Paruima Mission, 600 m, 8 Nov 1951, *Maguire and Fanshawe 32453* (NY); Pakaraima Mts., Mazaruni River, 0.4 miles W of Base Camp 6, 6°02′N, 60°39′W, 550 m, 13 Feb 2004, *Redden et al. 2724* (NY); Upper Mazaruni River region, Karowtipu Mountain, between camp and peak on western side of mountain, 5°45′N, 60°35′W, 920–1,080 m, 24 Apr 1987, *Boom and Gopaul 7685* (NY); At headwaters of Kangu River, W branch; +/− 4 km NW of E peak of Mt. Ayanganna, first talus slope of plateau, 5°25′N, 60°00′W, 700 m, 5 Mar 1987, *Pipoly et al. 11053* (NY); Upper Mazaruni River region, Karowtipu Mountain, slopes of eastern peak, between camp and peak, 5°45′N, 60°35′W, 920–1080 m, 19 Apr 1987, *Boom and Gopaul 7501* (NY); Pakaraima Mtns, 1–4 km NW of Mt Ayanganna on outer toe slopes of mtn., 5°25′N, 60°00′W, 800–1,100 m, 9 Nov 1992, *Hoffman and Henkel 3318* (CAY, NY). Potaro-Siparuni Region: Chenapou, Amerindian village (Patumona) 50 km upstream from Kaieteur Falls, 5°00′N, 59°34′W, 450 m, 16 Oct 1987, *Kvist et al. 348* (AAU, CAY, US); Pakaraima Mtns, upper Ireng watershed, Sukabi River, adjacent forest and base of Andu Falls, 5°06′N, 59°58′W, 625 m, 19 Oct 1994, *Mutchnick et al. 86* (CAY, NY); Pakaraima Mtns, upper Ireng River, 15–20 km upriver from Cipo settlement, Julong Falls, 5°00′N, 59°57′W, 701 m, 2 Nov 1994, *Mutchnick et al. 347* (NY); Pakaraima Mts, Mt. Wokomung, toe slope 0.5–2 km NW from northern escarpment, 5°04′N, 59°53′W, 1,300–1,400 m, 13 Nov 1993, *Henkel et al. 4348* (CAY, NY); Pakaraima Mts, Mt. Wokomung, upslope to NE 1–2 km from headwaters of Wasupubaru Creek, 5°03′N, 59°53′W, 975–1,125 m, 16 Feb 1993, *Henkel et al. 1420* (CAY); Pakaraima Mts, Mt. Wokomung ridgeline 0.5 km NE of Wokomung escarpment adjacent Ka-Mie-Wah pinnacle, 5°04′N, 59°53′W, 1,400–1,500 m, 15 Nov 1993, *Henkel et al. 4401* (CAY, NY); Potaro River, *Jenman s.n.* (NY). Upper Takutu-Upper Essequibo Region: Acarai Mts, Kashinar Mt, S slope and adjacent lowlands to the south, 1°17′N, 58°39′W, 525–750 m, 28 Feb 1994, *Henkel et al. 4862* (CAY, US).

SURINAME. Sipaliwini: Caiman Camp area (Tafelberg), trail between the Caiman Creek campsite and the East Ridge overlook of the Tafelberg, tropical forest of mixed hardwood species dominated by *Clusia* species growing on sandstone rocks or stream drainages, 3°54′N, 56°10′W, 750–900 m, 29 Jun 2001, *Hawkins 2082* (MO, NY); Talouakem - Inselberg - Monts Tumuc Humac, forêt basse sur pente d'inselberg, sommet de la face Nord, 2°29′N, 54°45′W, 600 m, 31 July 1993, *de Granville et al. 11931* (CAY; duplicates at B, BBS, U, US, Z).

VENEZUELA. Aragua: Mun. Girardot, along road between Marcay and Choroní, along S slope of northern cordillera, on steep rocky slopes near stream at km 19 from Maracay, 9°18′N, 67°′W, 1,280–1,300 m, 3 Aug 1982, *Croat 54485* (MO). Bolívar: Mun. Angostura, P.N. Canaima, O del Auyantepui, margen derecha del Río Cucurital, sector Wareipa, cuenca baja del Río Cucurital, 6°00′N, 62°47′W, 370 m, 21 Sep 2000, *García and Rodríguez 196* (GUYN); Mun. Gran Sabana, ca 10 km SW of Karaurin Tepui at junction of Rio Karaurin and Rio Asadon (Rio Sanpa), 5°19′N, 61°03′W, 900–1,000 m, 25 Apr 1988, *Liesner 23816* (MO, NY, VEN); Mun. Piar, Amaruay-tepui, slope S of SW corner of tepui, 5°54′N, 62°15′W, 470–770 m, 23 Apr 1986, *Liesner and Holst 20229* (MO, NY, VEN); Ladera sur del Amarawuay-Tepuy, 700 m, 9 May 1989, *Delascio 12689* (VEN). Federal Amazonas: Dpto. Río Negro, piedra ígnea, Cerro Aratitiyope, aprox. 70 km al SSW de Ocamo con riachuelos afluente al río Manipitare, 2°10′N, 65°34′W, 1,020 m, 24–28 Feb 1984, *Steyermark et al. 130304* (VEN). Táchira: Mun. Uribante, Empresa Las Cuevas near La Fundación, 8°50′N, 71°47′W, 900 m, 6 Jul 1983, *van der Werff and González 4944* (MO, VEN); Mun. Uribante, 10 km E of La Fundación (13–23 km by road), around Represa Dorada, 600–1,000 m, 10–13 Mar 1981, *Liesner and González 10164* (MO).

Distribution and Habitat—*Adiantopsis aurea* is a terrestrial-epipetric species that occurs in French Guiana, Guyana, Surinam, and Venezuela. It is found in forested regions near rocky areas, particularly sandstone, and around rivers and creeks, from 450–1,300 m a. s. l.

Comments—*Adiantopsis aurea* is named for the vibrant golden carinae that are found along all axes, including much of the stipe. Young plants with only once-pinnate fronds are often confused with *A. monticola* (Gardn.) T. Moore; however, the latter species is exclusively pinnate and endemic to the states of Goiás and Tocantins, Brazil. The once-pinnate fronds can be fertile and appear to begin developing into ternate fronds by the time they are eight to ten cm in height; taller fronds are always palmate with fusiform pinnae.

Adiantopsis hickeyi Link-Pérez, Seabolt, and Ledford, sp. nov.—TYPE: FRENCH GUIANA. Mont Saint-Marcel, zone du sommet central, versant sud du sommet central, rive gauche de la crique, 24 July 2002, *de Granville, Aliker, & Sarthou 15476* (holotype: NY!; isotypes B, CAY!, P, U, UC, US).

Rhizome erect to decumbent; scales acicular, bicolorous, the central band shiny, black, thickened, occupying 1/2 (to 2/3) of the width, the margins golden, with conform concolorous brown scales interspersed. Fronds erect, subdimorphic, 16.0–54.2 cm long, shorter fronds on plant often sterile. Stipes atropurpureous to atrocastaneous, lustrous, typically 50–70% of the frond length in fertile fronds, approximately 50% of the frond length in sterile fronds, 7.0–39.0 cm long; carinae adaxial, beginning at midpoint of stipe, occasionally only in the distal 1/3 of stipe, golden to brown, to 0.3(–0.4) mm tall; stipe scales golden-brown, sparse, restricted to distal and proximal stipe ends; catenate hairs absent to sparse on stipe, more numerous at apex between pinnae attachments, amber. Laminae palmate, circular, geniculate, 7.0–20.0 cm long, 9.0–27.0 cm wide; spongiose to chartaceous, drying green to greenish-black, occasionally maculate; hydathodes marginal; scales absent; hairs rare; stomata anomocytic, the guard cells 55.0–77.5 (mean = 65.64) μm long. Costae persistent, atropurpureous, lustrous to matte; carinae adaxial on all costae, golden to brown, 0.2–0.4 mm tall, the apical cells parallel to the costa axis, undulate; scales absent; catenate hairs few at abaxial costule-costa junctures, amber or brown. Pinnae (5)7(–9), spreading radially from stipe apex, fusiform to narrowly oblong, ending in a basally lobate apical segment, this with a rounded apex; central pinna to 9.0–19.6 + cm long, 1.9–3.1 cm wide, bearing 20–43 pinnule pairs; basal pinnae to 4.0–13.3 cm long, 1.5–2.8 cm wide, bearing 7–24 pinnule pairs; basal flabellate divisions attached between pinnae at stipe apex, typically fertile when frond is fertile. Pinnules transverse to slightly incurved, short-stalked, articulate, narrowly oblong, 6.8–15.8 mm long, 2.4–5.8 mm wide, length: width ratio 2.1–4.3 (mean = 3.2), the acroscopic auricles to 2.7 mm long; base excavate basiscopically, truncate to occasionally acute acroscopically; margins entire to crenate due to pseudoindusia; apices round to round-crenate; stalks basal, reflexed abaxially, persistent, appearing aculeate after pinnule abscission, to 1.0 mm long. Veins free, anadromous, prominent due to color or occult, ending submarginally in adaxial hydathodes. Sori marginal, discrete, 3–21 per pinnule. Pseudoindusia distinct, lunate to quadrangular, scarious to carnose, sometimes lustrous, yellowish to tan, often black maculate, usually 1.3–3.1 times wider than long, 0.25–0.60 mm long, 0.50–1.35 mm wide, the margin entire, undulate. Sporangia subglobose, medium-stalked with stalks to ~150 μm long. Spores yellow to amber at maturity, tetrahedral-globose, 30.00–42.50 (mean = 36.75) μm long, arachnoid-echinulate, echinae to 2.5 μm long, with dissected bases, laesurae obscured by echinae. Chromosome number unknown. Figure 4A–G.

Additional Specimens Examined—FRENCH GUIANA. Cayenne: Base camp at Pic Matécho, ca. 22.5 km NE of Les Eaux Blaires, rocky slope along stream up to low forest at top of slope, 3°45′N, 53°02′W, 500 m, 10 Sep 2000, *Mori and Smith 25095* (NY); Haute Camopi, Mont Belvédère, lisière inférieure, 200 m, 23 Nov 1984, *de Granville 6987* (CAY); Massif des Emerillons, zone sud, sommet d'une colline avec blocs et affleurement granitique, 450 m, 8 Sept 1980, *de Granville 3792* (CAY); Mont Chauve, forêt de pente sur sol bien drainé, layon partant du camp de base vers la crique, le long d'un écoulement d'eau temporaire su une dalle rocheuse en sous-bois, 3°49′N, 52°44′W, 120 m, 21 Apr 1997, *Cremers and Crozier 15132* (CAY, NY); Mont Galbao, Secteur Sud, Sommet, 3°35′N, 53°18′W, 650 m, 22 Jan 1986, *de Granville et al. 8903* (CAY, NY); Mont Itoupé, Sommet Tabulaire - 3, extrémité nord-est plateau tabulaire, fin du layon F, rebord nord-est du plateau tabulaire, Station n MB 973–251, 3°01′N, 53°04′W, 780 m, 29 Mar 2010, *Boudrie et al. 4446* (OSC, CAY, P); Montagne de l'Inini, zone est, extrèmité est, forêt sur crête, 3°34′N, 53°29′W, 650 m, 3 Sept 1985, *Cremers et al. 9280* (CAY, MO, NY); Monts Bakra, versant sud, forêt basse sur afleurements granitiques, 4 km Ouest du Pic Coudreau, 400 m, 28 Sept 1980, *de Granville 3995* (CAY); Monts d'Arawa, savane-roche centrale, pied du versant sud de la saven-roche, 2°49′N, 53°22′W, 200 m, 5 July 2002, *de Granville et al. 15052* (CAY); Pic Coudreau, Monts Bakra, Région des Emérillons, Saut de cours d'eau, 3°18′N, 52°57′W, 500 m, 16 Apr 1993, *Cremers 13133* (CAY, NY); Pic Matécho, zone sommitale 2, sommet du versant Est, sous-bois, en zone semi-éclairée, 3°45′N, 53°02′W, 420 m, 16 Sept 2000, *de Granville et al. 14166* (CAY); Station des Nouragues - Bassin de l'Arataye, forêt de basse altitude, 4°03′N, 52°42′W, 24 Aug 1987, *Feuillet 4290* (CAY). Saint-Laurent-du-Maroni: 12 km Est de Saül, Piste de Carbet Maïs, colline boisée a 1 km environ au Nord de Carbet Mitan, 500 m, 1 Jan 1980, *de Granville 3238* (CAY); Haut Tampoc, Saut Awali, récolté sur une colline de plus de 50 m au dessus du Tampoc, 220 m, 29 Mar 1977, *Cremers 4550* (CAY); Mont Atachi Bacca, Région de l'Inini, Mont Atachi Bacca, Plateau sommitale, 3°33′N, 53°55′W, 660 m, 15 Jan 1989, *Cremers et al. 10246* (CAY, NY, with duplicates at B, F, P, U, US, Z); Roche ruine Roche Koutou - Bassin du Haut-Marouini, 1 km au Nord, Eboulis d'inselberg, sous bois de bord d'Inselberg, 2°53′N, 54°03′W, 200 m, 15 Aug 1987, *de Granville et al. 9292* (CAY).

Distribution and Habitat—This terrestrial species has been collected in French Guiana. It is found among rocky areas in moist undergrowth of forests or near streams from 50–660 m a. s. l.

Comments—*Adiantopsis hickeyi* is most likely to be confused with *A. radiata*, with which it shares pinnules of similar size and shape; however, the pinnules in *A. hickeyi* are decidedly stalked, with the stalks appearing aculeate after pinnule abscission instead of peg-like as in *A. radiata*. Additionally, examination of lamina tissue of *A. radiata* reveals diffuse three-celled hairs abaxially; such hairs are almost impossible to find on *A. hickeyi*. Another useful character is the disposition of the stipe carinae: in *A. hickeyi* they are typically present in the distal half or third of the stipe, whereas they are generally absent or restricted to the upper 1/10 of the stipe in *A. radiata*, at least in mature fronds. The pinnae apices of *A. hickeyi* are generally much smaller than in *A. radiata* and have a rounded apex, rather than the distally elongate and acute apex of pinnae in *A. radiata*. The specific epithet is in honor of R. James Hickey, Professor at Miami University (Oxford, Ohio) and scholar of ferns and lycophytes. He has made a positive and powerful impact on the first author, who continues to be a fan of his two most frequently asked questions during conversations regarding science in general and research in particular: "What do you know? How do you know it?"

Adiantopsis scalariformis Link-Pérez, Seabolt, and Ledford, sp. nov.—TYPE: GUYANA. Potaro-Siparuni. Pakaraima Mts. Cipo Mtn, ca. 2 km from summit escarpment, headwaters Cipo Creek. Mixed montane forest on steep slopes, 4°54′N, 60°05′W, 1000 m, 26 Jan 1993, *Henkel, Chin & Ryan 983* (holotype: NY!; isotype CAY!).

Rhizome erect to ascending; scales acicular, bicolorous, the central band lustrous, castaneous to black, occupying 1/3 of the width, the margins golden-brown, with conform concolorous tan to brown, lanceolate scales interspersed. Fronds strict, monomorphic, 22.0–46.0 cm long. Stipes atropurpureous, castaneous, or ebeneous, lustrous, terete, typically 35–65% of the frond length, 11.0–27.0 cm long; carinae adaxial, distal ¼ to ½ of stipe, golden to reddish-brown, 0.3–0.8 mm tall (typically to 0.6 mm), frequently revolute, often forming flap-like structure at stipe apex; scales castaneous, linear triangular, sparse, these found along the proximal 1 cm of stipe; catenate hairs rare, reddish-gold. Laminae palmate, orbiculate, geniculate, 10.0–20.0 cm long, 6.0–21.0 cm wide; chartaceous to sub-spongiose, drying olive-green to dark brown; hydathodes marginal; scales absent; three-celled hairs rare abaxially, absent adaxially, septate, the basal cell elongate and colorless, the middle cell short, orange, the apical cell yellow, white, or colorless; stomata anomocytic, the guard cells 47.5–82.5 (mean = 62.12) μm long. Costae persistent, atropurpureous to ebeneous, occasionally atrocastaneous, lustrous; carinae adaxial on all costae, golden-brown to brown, 0.4–0.7 mm tall, often involute and/or revolute; scales absent; catenate hairs sparse at abaxial costule-costa junctures. Pinnae 5–7, spreading radially from stipe apex, narrowly oblong to lanceolate, distal pinnules abruptly reduced toward the pinnatifid apex, the apical segment distally elongate to 0.5 (occasionally 1.0) cm with a rounded apex; central pinna 10.0–20.2 cm long, 2.1–3.4 cm wide, bearing 35–42 + pinnule pairs; basal pinnae to 8.5–10.3 cm long, 2.1–2.8 cm wide, bearing 19–25 pinnule pairs; basal flabellate divisions attached between pinnae at stipe apex, symmetrical, typically fertile when frond is fertile. Pinnules patent to slightly ascending, short-stalked, articulate, narrowly oblong to oblong, 10.0–18.0 mm long, 3.0–5.0 mm wide (excluding auricles), length:width ratio typically 2.6–4.8, the acroscopic auricles to 4.0 mm long; base acute to excavate basiscopically, truncate (to widely acute) acroscopically; margins entire; apices round to slightly acute; stalks basal, sometimes slightly reflexed abaxially, persistent, appearing peg-like to aculeate after pinnule abscission, to 1.2 mm long. Veins free, anadromous, occult to obscure, ending submarginally in adaxial hydathodes. Sori marginal, discrete, occasionally two per pseudoindusium, (5–) 10–22 per pinnule. Pseudoindusia distinct, lunate to quadrangular, scarious to chartaceous, yellowish-brown to brown, sometimes black maculate, 1.3–2.5 times wider than long, 0.35–0.6 mm long, 0.73–1.33 mm wide, the margin entire to undulate or scalloped. Sporangia subglobose, long-stalked with stalks to ~200 μm long. Spores yellow at maturity, tetrahedral-globose, 29.70–37.80 (mean = 33.38) μm long, arachnoid-echinulate, echinae 1–2.5 μm long, with dissected bases, laesurae prominent in brightfield microscopy. Chromosome number unknown. Figure 5A–F.

Additional Specimens Examined—GUYANA. Potaro-Siparuni Region: Iwokrama Rain Forest Reserve, Karupukari, 20 mi. SW on Karupukari/Annai Road, transect to mt. peak, 4°25′N, 58°49′W, 700 m, 22 Mar 1997, *Mori et al. 24525* (NY). Upper Takutu-Upper Essequibo Region: Acari Mts., 0–1 km W of Chodikar Mountain, 1°20′N, 58°50′W, 500–600 m, 5 Nov 1996, *Clarke 2962* (CAY); Rupununi District, Kanuku Mts., Two-Head Mt., 3°09′N, 59°07′W, 730 m, 5 Feb 1994, *Jansen-Jacobs et al. 3572* (CAY). Guiana angl. s.d., *Schomburgk 1132* (B [barcode B 20 0001551, scan; this specimen was one of the original syntypes for *A. alata*]).

Distribution and Habitat—This terrestrial species is known from forested regions of mountains in Guyana. It has been collected from 500–1,000 m a. s. l.

Comments—The specific epithet for *Adiantopsis scalariformis* comes from the ladder-like appearance of the pinnules along the costa, which are almost opposite or sub-opposite and are borne horizontally like rungs. The pinnules are relatively large (in comparison to other species of *Adiantopsis* found in the Guiana Shield) and are similar in size to *A. alata*, which is endemic to several states in eastern Brazil. The pinnules frequently are closely spaced along the costae, causing their auricles to overlap adjacent pinnules. The apical segment of the pinnae has 1 or 2 lobes at the basal region, with the apical extension often 0.5 cm. The carinae are 0.3–0.8 mm tall, typically 0.5 mm, and are confined to the distal 2/3 to ½ of the stipe. The abrupt apical taper of the pinnae separates it from the other palmate taxa with which it shares its distribution.

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Literature Cited

Altekar, G., S. Dwarkadas, J. P. Huelsenbeck, and F. Ronquist. 2004. Parallel Metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* 20: 407–415.

Anderson, L. E. 1954. Hoyer's solution as a rapid permanent mounting medium for bryophytes. *The Bryologist* 57: 242–244.

Barrington, D. S., C. A. Paris, and T. A. Ranker. 1986. Systematic inferences from spore and stomate size in the ferns. *American Fern Journal* 76: 149–159.

Benson, D. A., M. Cavanaugh, K. Clark, I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and E. W. Sayers. 2013. GenBank. *Nucleic Acids Research* 41(Database issue): D36–D42.

Brody, J. R. and S. E. Kern. 2004. Sodium boric acid: A Tris-free, cooler conductive medium for DNA electrophoresis. *BioTechniques* 36: 214–216.

Drummond, A. J. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214–222.

Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.

Johnson, A. K., C. J. Rothfels, M. D. Windham, and K. M. Pryer. 2012. Unique expression of a sporophytic character on the gametophytes of notholaenid ferns (Pteridaceae). *American Journal of Botany* 99: 1118–1124.

Katoh, S. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. J. Drummond. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.

Lanfear, R., B. Calcott, S. Y. W. Ho, and S. Guindon. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701.

Lellinger, D. B. 2002. A modern multilingual glossary for taxonomic pteridology. *Pteridologia* 3: 1–263.

Li, F. W., L. Y. Kuo, C. J. Rothfels, A. Ebihara, W. L. Chiou, M. D. Windham, and K. M. Pryer. 2011. *rbcL* and *matK* earn two thumbs up as the core DNA barcode for ferns. *PLoS One* 6: E26597.

Link-Pérez, M. A. and R. J. Hickey. 2011. Revision of *Adiantopsis radiata* (Pteridaceae) with descriptions of new taxa with palmately compound laminae. *Systematic Botany* 36: 565–582.

Link-Pérez, M. A., L. E. Watson, and R. J. Hickey. 2011. Redefinition of *Adiantopsis* Fée (Pteridaceae): systematics, diversification, and biogeography. *Taxon* 60: 1255–1268.

Link-Pérez, M. A., T. G. Ludwig, C. J. Ledford, M. H. Seabolt, and E. B. Sessa. 2016. Data from: Lectotypification of *Adiantopsis alata* (Pteridaceae) and descriptions of new palmate species in the Guiana Shield. *Dryad Digital Repository.* doi:10.5061/dryad.67qq8.

McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, D. L. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, and J. Prado. W. F. Prud'Homme van Reine, G. F. Smith, and J. H. Wiersema (eds.). 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Regnum Vegetabile* 154. Königstein: Koeltz Scientific Books.

Prantl, K. 1883. *Adiantopsis alata* Prantl. *Gartenflora* 32: 99–103.

R Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

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

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Rothfels, C. J., M. D. Windham, A. L. Grusz, G. J. Gastony, and K. M. Pryer. 2008. Toward a monophyletic *Notholaena* (Pteridaceae): Resolving patterns of evolutionary convergence in xeric-adapted ferns. *Taxon* 57: 712–724.

Samarakoon, T., S. Y. Wang, and M. H. Alford. 2013. Enhancing PCR amplification of DNA from recalcitrant plant specimens using a trehalose-based additive. *Applications in Plant Sciences* 1: apps. 1200236.

Savolainen, V., P. Cuenoud, R. Spichiger, M. D. P. Martinez, M. Crevecoeur, and J.-F. Manen. 1995. The use of herbarium specimens in DNA phylogenetics: Evaluation and improvement. *Plant Systematics and Evolution* 197: 87–98.

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

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.

Sukumaran, J. and M. T. Holder. 2010. DendroPy: A Python library for phylogenetic computing. *Bioinformatics* 26: 1569–1571.

Systematics Association Committee for Descriptive Terminology. 1962. Terminology of simple symmetrical plane shapes (Chart 1). *Taxon* 11: 145–156, 245–247.

Tryon, R. M. and A. F. Tryon. 1982. *Ferns and allied plants with special reference to tropical America*. New York: Springer-Verlag.

Wagner, W. H. Jr., F. S. Wagner, and W. C. Taylor. 1986. Detecting abortive spores in herbarium specimens of sterile hybrids. *American Fern Journal* 76: 129–140.

Walker, T. G. 1973. Evidence from cytology in the classification of ferns. Pp. 91–110 in *The phylogeny and classification of ferns*, ed. A. C. Jermy. New York: Academic Press.

Appendix 1. Voucher information for sequence data generated in this study, in the following format: taxon, origin, collector name and number (herbarium), and GenBank accession numbers for *rbcL* and *atpA*, in that order. Sequences from previously published studies do not include voucher information and are designated with a superscript following the GenBank accession number as follows: [a] Link-Pérez et al. (2011), [b] Schuettpelz et al. (2014), [c] Li et al. (2011), [d] Rothfels et al. (2008), [e] Johnson et al. (2012). Numbers in brackets refer to operational taxonomic units (OTUs) for species with multiple accessions.

Adiantopsis alata Prantl. BRAZIL. Bahia. *Matos et al. 738* (UPCB). KY020078; KY020081 [OTU111]. ***Adiantopsis alata*** Prantl. BRAZIL. Bahia. *Salino and Jardim 8133* (UPCB). KY020079; KY020082 [OTU115]. ***Adiantopsis aurea*** Link-Pérez, Seabolt, and Ledford. FRENCH GUIANA. Mont Itoupé. *Boudrie et al. 4320* OSC). KY020080; KY020083. ***Adiantopsis chlorophylla*** (Sw.) Fée. JN709739[a]; JN709785[a]. ***Adiantopsis dactylifera*** Link-Pérez & Hickey. JN709759[a]; JN709805[a]. ***Adiantopsis dichotoma*** (Sw.) T. Moore. JN709728[a]; JN709774[a] [OTU16]. ***Adiantopsis dichotoma*** (Sw.) T. Moore. JN709727[a]; JN709773[a] [OTU42]. ***Adiantopsis flexuosa*** (Kunze) Link-Pérez & Hickey. JN717154[a]; JN717157[a] [OTU83]. ***Adiantopsis flexuosa*** (Kunze) Link-Pérez & Hickey. JN709722[a]; JN709769[a] [OTU84]. ***Adiantopsis flexuosa*** (Kunze) Link-Pérez & Hickey. JN709723[a]; JN709770[a] [OTU82]. ***Adiantopsis hickeyi*** Link-Pérez, Seabolt, and Ledford. JN709762[a]; JN709808[a] [OTU62/"species novum

3″ in Link-Pérez *et al*. 2011]. ***Adiantopsis hickeyi*** Link-Pérez, Seabolt, and Ledford. JN709763[a]; JN709809[a] [OTU66/“species novum 3” in Link-Pérez *et al*. 2011]. ***Adiantopsis lindigii*** (Mett.) Prantl. JN709754[a]; JN709800[a]. ***Adiantopsis monticola*** (Gardn.) T. Moore. JN709729[a]; JN709775[a]. ***Adiantopsis parvisegmenta*** M. S. Barker & Hickey. JN709750[a]; JN709796[a]. ***Adiantopsis paupercula*** (Kunze) Fée. JN709765[a]; JN709811[a]. ***Adiantopsis pedata*** (Hook.) T. Moore. JN709748[a]; JN709794[a]. ***Adiantopsis pentagona*** M.S. Barker & Hickey. JN709749[a]; JN709795[a]. ***Adiantopsis perfasciculata*** Sehnem. JN709747[a]; JN709793[a]. ***Adiantopsis radiata*** (L.) Fée. JN709760[a]; JN709806[a]. ***Adiantopsis reesii*** (Jenman) C. Chr. JN709755[a]; JN709801[a]. ***Adiantopsis regularis*** (Kunze) T. Moore. JN709726[a]; JN709772[a]. ***Adiantopsis rupicola*** Maxon. JN709753[a]; JN709799[a]. ***Adiantopsis scalariformis*** Link-Pérez, Seabolt, and Ledford. JN709766[a]; JN709812[a] [OTU67/“species novum 2” in Link-Pérez *et al*. 2011]. ***Adiantopsis seemannii*** (Hook.) Maxon. JN709731[a]; JN709777 [a]. ***Adiantopsis senae*** (Baker) Schuettp. & A. Davila. KF800703[b]; KF800705[b] [OTU-H714]. ***Adiantopsis senae*** (Baker) Schuettp. & A. Davila. KF800702[b]; KF800704[b] [OTU-S1400]. ***Adiantopsis ternata*** Prantl. JN709756[a]; JN709802[a]. ***Adiantopsis timida*** Link-Pérez & Hickey. JN709757[a]; JN709803[a]. ***Adiantopsis trifurcata*** (Baker) Link-Pérez & Hickey. JN709767[a]; JN709813[a] [OTU11]. ***Adiantopsis trifurcata*** (Baker) Link-Pérez & Hickey. JN709768[a]; JN709814[a] [OTU81]. ***Adiantopsis tweediana*** (Hook.) Link-Pérez & Hickey. JN709725[a]; JN709771[a]. ***Adiantopsis vincentii*** M. S. Barker & Hickey. JN709752[a]; JN709798[a] [OTU73]. ***Adiantopsis vincentii*** M. S. Barker & Hickey. JN709751[a]; JN709797[a] [OTU74]. ***Adiantopsis ×australopedata*** Hickey, M. S. Barker & Ponce. JN709746[a]; JN709792[a]. ***Gaga arizonica*** (Maxon) Fay W. Li & Windham. JN647784[c]; EU268727[d]. ***Gaga kaulfussii*** (Kunze) Fay W. Li & Windham. JN647807[c]; JQ855918[e].