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

Melanie A. Link-Pérez,1,4 Thomas G. Ludwig,2 Cody J. Ledford,2 Matthew H. Seabolt,2 and Emily B. Sessa3

1Department of Botany and Plant Pathology, Oregon State University, Cordley Hall 2082, Corvallis, Oregon 97331, U. S. A.
2Department of Biology, Armstrong State University, Savannah, Georgia 31419, U. S. A.
3Department of Biology, University of Florida, Gainesville, Florida 32611, U. S. A.
4Author for correspondence (melanie.link-perez@oregonstate.edu)

**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 pinnules 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 (Savoilainen 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 x 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 (Brodie 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. 700732), 0.5 μL shrimp alkaline phosphatase (SAP) (Product No. 78890) and 1 μL of 1 x 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.67q98 (Link-Pérez et al. 2016). Because the chloroplast is a single, non-recombinating 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 tool 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.
with 1,000 replicates and searching for the best-scoring ML tree in a single run (option “-a 1”). We applied the GTR + I + Γ model using the optimal partitioning scheme identified by PartitionFinder: the first partition included only the first position of rcl, and the second partition included the second positions of atpF and rcl. 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 pinnate 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.

Pinnae 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, appear to be continuous without any notches (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,
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–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...
both spacers and the third positions of both genes, with GTR + $\Gamma$ as the best model; Partition 4 included \textit{atpA} and position one of \textit{atpF}, with GTR + I + $\Gamma$ as the best model. Maximum likelihood analysis (using only GTR + I + $\Gamma$, but partitioned as described) produced a single best tree with \textit{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 \textit{Adiantopsis regularis} differed between the two. In both trees, within the ingroup \textit{A. flexuosa} is sister to

Fig. 3. \textit{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. \textit{Henkel and Chin 5721} (NY); B. \textit{Liesner and González 10164} (MO); C, D, E. \textit{van der Werff and González 4944} (MO).
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, *Lueschnath 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 *Lueschnath 103* (B [barcode B 20 0001553]) as the lectotype for *A. alata*. The syntype from Guiana, *Schomburgk 1132* (B), is referred to the new segregate species *A. scalariformis* (Fig. 5), which is currently known only from Guiana (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).

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

1. Lamina primarily ternate with three pinnae; pseudoindusia triangular ................................................................. *A. trifurcata*
2. Pinnae fastigate; pseudoindusia +/- entire .......................... 2
3. Pinnae spreading; pseudoindusia laciniate .............................. *A. ternata*
4. Carinae with apical cells digitate, composed of separate and distinct cells oriented perpendicular to the axes .......................... *A. dactylophora*
5. Carinae with apical cells forming a more or less entire margin, with most cells oriented parallel to the axes .......................... 4
6. Fronds subdimorphic; pinnules generally less than 7 mm long; pinnules attached medially or sub-medially .......................... 5
7. Pseudoindusia lunate with entire margins; carinae adaxial on stipe beginning at midpoint or proximal third .......................... *A. timida*
8. Pseudoindusia quadrangular with erose margins; carinae absent or adaxial on extreme distal end only .......................... *A. crinoidea*
9. Fronds subdimorphic; pinnules generally more than 7 mm long; pinnules attached sub-basally to basally .......................... 6
10. Stipe carinae absent or adaxial on distal 1.0 cm only, up to 0.1 mm tall .......................... *A. radiata*
11. Stipe carinae present adaxially on distal ½ or more, greater than 0.2 mm tall .......................... 7
12. Stipe carinae prominent and typically 1.0 mm tall or more; pinnule apices with elongate acicular apices, these frequently to 1.5 cm in length .......................... *A. alata*
13. Stipe carinae less than 1.0 mm tall; pinnule apices with acute or rounded apices, these typically 0.5–1.0 cm in length .......................... 8
14. 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*

**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).
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

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).
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;

**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. Henkel et al. 983 (NY); C. Clarke 2962 (CAY); F. Jansen-Jacobs et al. 3572 (CAY).
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).

<table>
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<th>Taxon</th>
<th>Sample size</th>
<th>Mean (μm)</th>
<th>Standard deviation (μm)</th>
<th>Min (μm)</th>
<th>Max (μm)</th>
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</thead>
<tbody>
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<td><em>A. alata</em></td>
<td>131</td>
<td>28.99</td>
<td>2.08</td>
<td>25.00</td>
<td>35.00</td>
</tr>
<tr>
<td><em>A. aurea</em></td>
<td>144</td>
<td>33.49</td>
<td>3.14</td>
<td>25.00</td>
<td>42.50</td>
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<tr>
<td><em>A. hickeyi</em></td>
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<td>36.75</td>
<td>2.38</td>
<td>30.00</td>
<td>42.50</td>
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<tr>
<td><em>A. radiata</em></td>
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<td>32.91</td>
<td>2.39</td>
<td>27.00</td>
<td>37.80</td>
</tr>
<tr>
<td><em>A. scalariformis</em></td>
<td>64</td>
<td>33.38</td>
<td>1.98</td>
<td>29.70</td>
<td>37.80</td>
</tr>
</tbody>
</table>

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 ⅓ of the width, the margins golden or reddish-gold, shiny, with conform concolorous golden scales interspersed. Fronds cespitose, monomorphic, (3.0–) 4.5–41.3 cm long. Stipes acroastaceous, cinnamonous, 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 and 1.0–2.3 cm wide, the smallest observed (3.0 cm long, 1.0 cm wide) was fertile; spongiophore to chartaceous, drying greyish-green, olive, or brown; hydathodes marginal; scales absent; hairs rare abaxially, rare adaxially; stomata anomocytic, the guard cells 50.0–77.5 μm long. Costae persistent, acroastaceous, cinnamonous, 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 junctions, 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 pinnule no more than 20–60% of length of central pinnule, to 1.4–10.5 cm long, 0.7–2.2 cm wide, bearing 2–20 pinnule pairs; basal flabellate divisions attached between pinnule 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 acrosopic auricles to 2.2 mm long; base excavate basiscopically, truncate acroscopically; margins entire to crenate; apices round to acute; stalks basal, adaxially

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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, acroastaceous to cinnamonous, 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 radically 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 acrosopic 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. Pseudonodium 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 sub-globose, 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.

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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, papyraceous 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

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.
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 critique 1, à partir de 100 m au sud du point 600 du layon A, Station MB 973-240, 3°11′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 Kotok: versant est., 3°55′N, 54°10′W, 600 m, 6 Sept 2007, Delnate 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 Farnhause 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, 920–1080 m, 24 Apr 1987, Boom and Gopal 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, 59°34′W, 710 m, 19 Mar 2010, Henkel et al. 1420 (NY); Pakaraima Mts, upper Ireng watershed, Sukabi River, adjacent forest and base of Andu Falls, 5°45′N, 60°00′W, 19 Oct 1987, Boudrie et al. 4320 OSC, CAY). Mont Kek: versant est., 3°55′N, 54°10′W, 600 m, 6 Sept 2007, Delnate 1381 (CAY).

Comments—Adiantopsis aurea is named for the vibrant golden carinae that are found all along 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 tertiary fronds by the time they are eight to ten cm in height; taller fronds are always palmate with fusiform pinnae.


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 atropurpureus to atroacanthous, 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 μm (mean = 65.64) μm long. Costae persistent, atropurpureus, 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-costula 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 acrosopic auricles to 2.7 mm long; base excavate basiscopically, truncate to occasionally acute acrosopically; margins entire to crenate due to pseudoindusia; apices round to rounded-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 quadranocular, scarious to carneous, sometimes lustrous, yellowish to tan, often black-maculate, usually 1.3–3.1 times wider than longer, 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 μm (mean = 36.75) μm long, arachnoideechinulate, echinate to 2.5 mm long, with dissected bases, laesura visible. Chromosome number unknown. Figure 3A–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 23905 (NY); Haute Camopi, Mont Belvédère, lisière inférieure, 200 m, 23 Nov 1984, de Granville 6597 (CAY), Massif des Emerillons, zone sud, sommet d’une colline avec blocs et affleurement granitique, 450 m, 8 Sep 1980, de Granville 3792 (CAY); Mont Chauve, forêt de pente sur sol bien drainé, layon partant du camp (CAY); Massif des Emerillons, zone sud, sommet d’une colline de plus de 50 m au dessus du Tampoc, 220 m, 29 Mar 2010, Boudrie et al. 4446 (OSC, CAY, P); Montagne de l’Inini, zone est, extrémité est, forêt sur crête, 3°34′N, 53°29′W, 650 m, 3 Sep 1985, Cremers et al. 9280 (CAY, MO, NY); Monts Bakra, versant sud, forêt basse sur affleurements granitiques, 4 km Ouest du Pic Coudreau, 400 m, 28 Sep 1990, de Granville 3995 (CAY); Monts d’Arawa, savane-roche centrale, pied du versant sud de la saven-roche, 2°49′N, 52°22′W, 210 m, 5 July 2002, de Granville et al. 15052 (CAY); Pic Coudreau, Monts Bakra, Réjion des Emerillons, Saut de cours d’eau, 3°18′N, 52°57′W, 500 m, 16 Apr 1993, Cremers 13133 (CAY, NY); Pic Matécho, sommet sismatique, 2 sommet du versant Est, sous-bois, en zone semi-éclairése, 3°45′N, 53°03′W, 420 m, 16 Sep 2000, de Granville et al. 14166 (CAY); Station des Nouragues - Bassin de l’Arayate, 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 Maït, 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, Réjion 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, US, Z); Roche ruine – versant sud de la saven-roche, 2°49′N, 52°42′W, 1 km au Nord, Eboulis d’inselberg, sous bois de bord d’inselberg, 2°33′N, 54°03′W, 200 m, 15 Aug 1987, de Granville et al. 4446 (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 50–600 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. hickeyi instead of peg-like as in A. radiata and have a rounded apex, rather than the distally elongate and acute apex of pinnule 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?”
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 pinnule has 1 or 2 lobes at the basal region, with the apical extension often 0.5 cm. The carinae are 0.3 \text{-} 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 peltate taxa with which it shares its distribution.

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Literature Cited


