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Generic Relationships and Classification of Tribe Paullinieae (Sapindaceae) with a New Concept of Supertribe Paulliniodae

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Abstract—The current study examines all genera of Sapindaceae tribe Paullinieae sensu Acevedo-Rodríguez et al. (2011). Based on molecular phylogenetic analyses of *trnL* intron and ITS sequence data along with critical evaluation of morphology, supertribe Paulliniodae is newly recognized and morphologically characterized by zygomorphic flowers, thyrses with lateral cincinni, corollas of 4 petals, and alternate leaves with a well-developed distal leaflet. Paulliniodae contains four successively nested subclades designated as tribes Athyaneae, Bridgesieae, Thouinieae, and Paullinieae. Athyaneae contains *Athyana* and *Diatenopteryx*, and is composed of trees with exstipulate pinnately compound leaves, and isopolar, spherical, colporate pollen grains. Bridgesieae contains the monospecific shrub genus *Bridgesia* with exstipulate, simple leaves, and isopolar, spherical, tricolporate pollen grains. Thouinieae is resurrected and amended to include three genera of trees or shrubs with exstipulate trifoliolate or unifoliolate leaves. Paullinieae is circumscribed to include only six genera (*Thinouia*, *Lophostigma*, *Cardiospermum*, *Paullinia*, *Serjania* and *Urvillea*) of climbers or climber-derived shrubs with stipulate leaves and a pair of inflorescence tendrils. *Guindilia*, previously considered a member of this clade, is shown to be more distantly related and not part of supertribe Paulliniodae. The following 14 new combinations are made to incorporate the results of our findings: ***Serjania biternata***, ***Serjania cristobaliae***, ***Serjania dissecta***, ***Serjania guerrerensis***, ***Serjania macrolopha***, ***Serjania serjanioides***, ***Serjania sonorensis***, ***Serjania spinosa***, ***Serjania tortuosa***, ***Thinouia trifoliata***, ***Urvillea cuchujaquense***, ***Urvillea oliveirae***, ***Urvillea procumbens***, and ***Urvillea pterocarpa***.

Keywords—Athyaneae, Bridgesieae, *Diatenopteryx*, *Guindilia*, molecular phylogenetics, Thouinieae.

Since the publication of the most recent taxonomic treatment of Sapindaceae (Acevedo-Rodríguez et al. 2011), where four subfamilies (Xanthoceroideae, Hippocastanoideae, Dodonaeoideae, and Sapindoideae) and 142 genera were recognized, four new genera (*Alatococcus* Acev.-Rodr., *Allophylastrum* Acev.-Rodr., *Balsas* J. Jiménez Ram. & K. Vega, and *Gereaua* [Capuron] Buerki & Callm.) have been described. Following the description of these new genera and the results of this analysis, we currently recognize 144 genera with ~1,900 species within the family. According to Acevedo-Rodríguez et al. (2011), the Sapindaceae in the New World contains about 925 species, of which ~475 belong to the Paullinieae (i.e. Paullinieae + Thouinieae, sensu Radlkofer 1890, 1931-1934). Paullinieae are primarily Neotropical with the exception of *Paullinia pinnata* L., *Cardiospermum corindum* L., and *C. halicacabum* L., which in addition to their Neotropical ranges, are naturally distributed in parts of the Paleotropics (Brncic et al. 2007; Gildenhuys et al. 2015). Thouinieae is by far more diverse at the generic level in the Neotropics than in the Paleotropics. However, at the species level, there are many more species (~197 species) in the Paleotropics, all of which belong to the genus *Allophylus* (Coelho 2014).

The Paullinieae was proposed by Kunth as a "section" of Sapindaceae in 1821 (Kunth 1821) to accommodate *Cardiospermum* L., *Paullinia* L., *Serjania* Mill., and *Urvillea* Kunth. This group of herbaceous or woody climbers with tendrils was characterized by the presence of well-developed petal appendages, unilateral nectaries with distinct lobes, and 3-carpellate gynoecia with uniovular locules. In 1824, de Candolle designated Kunth's Paullinieae as a tribe, which was later adopted by Radlkofer in 1890 in his tribal classification of Sapindaceae that included 14 tribes. Radlkofer further characterized Paullinieae by the presence of stipules, and compound leaves with a fully developed distal leaflet. The presence of stipules in the Paullinieae is unique within Sapindaceae, while the latter two characters are shared with members of the closely related Thouinieae. Radlkofer divided Paullinieae into the subtribes *Eupaullinieae* and *Thinouineae*. The *Eupaullinieae* was essentially the same group as the one recognized by Kunth but further characterized by the presence of zygomorphic flowers with hood-shaped petal appendages. Subtribe Thinouineae solely contained *Thinouia* Triana & Planch., described in 1862 (Triana and Planchon 1862), and was characterized by the presence of actinomorphic flowers with marginal or bifid petal appendages and an annular disc. Additional genera were later included in the *Eupaullinieae*: *Lophostigma* Radlk. was described in 1897 and is characterized by the presence of short petals and heteropolar, prolate pollen grains; *Houssayanthus* Hunz. was described in 1978 (Hunziker 1978) and is characterized by mericarps with a circumferential wing; and *Chimborazoa* H. T. Beck was described in 1992 (Beck 1992) and is characterized by wingless spherical mericarps.

Radlkofer's system of classification of 1890 placed Paullinieae in the vicinity of the Thouinieae, a tribe that included the genera *Guindilia* Gillies ex Hook. & Arn., *Bridgesia* Bertero ex Cambess., *Athyana* Radlk., *Diatenopteryx* Radlk., *Thouinia* Poit., and *Allophylus* L. The Thouinieae was characterized by an arboreal or shrubby habit and zygomorphic flowers in lateral cincinni (or a simplification of it). Radlkofer's concept of Paullinieae had survived through much of the 20th century and was only modified by Acevedo-Rodríguez (1993) who proposed placing *Thinouia* in the Cupanieae near *Allosanthus* Radlk. More recently, *Thinouia* was reinstated in the tribe Paullinieae following recent molecular phylogenetic analyses (Acevedo-Rodríguez,

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unpubl. data; Acevedo-Rodríguez et al. 2011). At the same time, *Allosanthus* was treated as congeneric with *Thinouia* as its only differentiating character, i.e. the spicate inflorescence, was not considered worthy of generic recognition (Acevedo-Rodríguez et al. 2011).

Cladistic analyses of the Paullinieae and Thouinieae, based on morphological characters, indicated a monophyletic Paullinieae nested within a paraphyletic Thouinieae (Acevedo-Rodríguez 1993). Analyses of eight DNA sequence regions from the plastid and nuclear genomes by Buerki et al. (2009, 2010, 2011) recovered a "*Paullinia group*" of genera assignable to the Paullinieae and Thouinieae. Following the conclusions suggested in Acevedo-Rodríguez (1993) and Buerki et al. (2009), Acevedo-Rodríguez et al. (2011) placed the genera of Thouinieae in a newly circumscribed Paullinieae, which encompassed 12 genera. That classification made sense in light of the then sparse molecular phylogenetic taxon-sampling, but now the results of more comprehensive analyses call for a tribal reclassification.

Our study includes genera (*Balsas* and *Allophylastrum*) assignable to the Paullinieae that were published after the treatment of Sapindaceae by Acevedo-Rodríguez et al. (2011) as well as *Sapindus oligophyllus* Merr. & Chun, proposed by Buerki et al. (2009, 2010, 2011) as a member of their *Paullinia group*. *Balsas* was described to account for a species considered closely related to *Paullinia*, but which is distinguished by its exarillate seeds and hemi-tricolporate pollen grains. *Allophylastrum*, which vegetatively closely resembles *Allophylus*, was described due to its actinomorphic, apetalous, solitary (or on short racemes) flowers, and 4–5-porate pollen grains. The position of *Sapindus oligophyllus* as sister to *Thouinia acuminata* S. Watson (Buerki et al. 2009) was clarified by analyzing sequence data from its type collection. In addition, the validity of *Chimborazoa*, already reduced to synonymy in *Serjania* (Acevedo-Rodríguez 1998), was further tested in our analyses.

The objectives of our study were to analyze molecular and morphological evidence to: 1) evaluate the current circumscription of tribe Paullinieae (sensu Acevedo-Rodríguez et al. 2011), 2) test the monophyly of the genera currently included in this tribe, and 3) elucidate the relationships among the genera once considered to belong in the Paullinieae.

Materials and Methods

Sampling—We sampled all genera of tribe Paullinieae (here recognized as supertribe Paullinioidae) sensu Acevedo-Rodríguez et al. (2011), and where possible multiple species per genus (see Appendix 1). The outgroups selected based on the family-wide phylogenies (i.e. Buerki et al. 2009, 2011), included 16 genera of subfamily Sapindoideae, which represent a successive series of nested sister clades to Paullinieae. The plastid *trnL* intron and nuclear ribosomal internal transcribed spacer, ITS, were selected as molecular phylogenetic markers because they have proven useful in Sapindaceae (e.g. Buerki et al. 2009).

Molecular Methods—DNA extractions, amplifications, and Sanger sequencing for the 184 newly generated sequences were conducted largely according to standard methods as outlined here. Silica-gel dried or herbarium leaf tissue (ca. 1.0 cm^2) was pulverized with glass and steel beads in a TissueLyser (Qiagen, Hilden, Germany). DNA extractions from the resulting tissue powder were mostly performed with the Qiagen DNeasy Plant Mini Kit according to the manufacturer's protocol. The herbarium extractions of *Allophylastrum*, *Chimborazoa*, and *Sapindus oligophyllus* included an overnight incubation with proteinase K, and each sample was not co-processed (i.e. from DNA extractions through sequencing) with any other Sapindaceae. We believe the data for each of these is authentic and not derived from contamination, based on the extra care taken during the extractions, expected correlation of DNA quality and amplification success, and the unique sequences obtained. The *trnL* intron was amplified and sequenced using primers "c" and "d" (Taberlet et al. 1991), and ITS was amplified using ITS5a (Stanford et al. 2000) and ITS4 (White et al. 1990). The amplification reactions were conducted in a final volume of 25 µl with 2.5 µl of Bioline ammonium reaction buffer (10×), 2.0 µl of dNTP mix (10 mM), 1.25 µl of magnesium chloride (50 mM), 1.0 µl of each primer (10 nM), 0.5 µl of bovine serum albumin (10 mg/ml), 14.05 µl of water, 0.2 µl of Biolase DNA polymerase (5U/µl; Bioline USA, Taunton, Massachusetts) and 2.5 µl of DNA extraction (~20 ng/µl). Amplification conditions were 95°C for 3 min, followed by 35 cycles of 94°C for 40 sec, 55°C for 40 sec and 72°C for 1 min 40 sec, with a 10 min final extension at 72°C. PCR products were treated with ExoSAP-IT (Affymetrix-USB, Santa Clara, California) prior to sequencing. Sequencing reactions were conducted using 8 µl of a cycle sequencing reaction mixture (including 0.8 µl BigDye Terminator v3.1 [Applied Biosystems, Foster City, California], 1.0 µl of 1 µM primer, 2.0 µl of 5 × buffer, 4.2 µl water) combined with 4 µl of DNA template. The cycle sequencing conditions were 30 cycles of 95°C for 30 sec, 50°C for 30 sec and 60°C for 4 min. The cycle sequencing products were purified using Sephadex G-50 (GE Healthcare Bio-Sciences, Pittsburgh, Pennsylvania) and run on an ABI 3730xl DNA Analyzer (Applied Biosystems) at the Smithsonian. The resulting reads were assembled and edited using Sequencher ver. 5.2.4 (Gene Codes, Ann Arbor, Michigan).

Phylogenetic Analyses—We assembled and did preliminary analyses on a complete data set that included our new data plus additional published *trnL* and/or ITS sequences for Paulliniodae (i.e. from Buerki et al. 2009, 2011; Urdampilleta et al. 2013; Gildenhuys et al. 2015). In our final data set we included some of this published data that complemented our taxon sampling, did not cause unnecessary taxon redundancy, and where we could confirm the identifications. The *trnL* alignment was straightforward with most indels representing tandem repeats while that of the ITS was complex with many ambiguous regions within ITS1 and ITS2. Alignments were generated using MAFFT ver.7 (Katoh and Standley 2013) under the Q-INS-i refinement method (alternative MAFFT iterative refinement methods did not greatly improve the alignment) and/or using Clustal Omega (Sievers et al. 2011). For the *trnL* alignment we first inferred the secondary structure of one outgroup with the ViennaRNA package (Lorenz et al. 2011), which was then applied as a constraint to improve the alignment using RNAsalsa (Stocsits et al. 2009). Our concatenated datasets included a 125-tip sampling with some taxa having missing data in one partition (i.e. incorporating published data such as that for *Cardiospermum*), had manual refinement of the alignment using a similarity criterion, and had a manual character deletion set made by removing matrix columns with >50% missing data. This method eliminated overlapping indels with clearly noisy characters and reduced missing data, but did not remove all ambiguously aligned regions. We also created a 99-tip sampling that minimized missing data (i.e. by removing most tips that were missing one of the partitions and which especially impacted *Cardiospermum*), was not manually refined, and used Noisy (Dress et al. 2008) as an automated approach to remove "noisy" sites.

To further assess the monophyly of Paullinieae — in particular the effect of previously unsampled *Lophostigma* and *Thinouia* on the backbone of that subclade — and to assess the suspected misidentification of *Sapindus oligophyllus* in Buerki et al. (2011), we manually added our data (*trnL* and ITS) for those taxa to their 8-marker family-wide data set archived in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S10580). Two new gaps (insertions relative to rest of the data set) were added to *trnL* and we manually refined the ITS partition to improve alignment consistency within genera of Paulliniodae and within *Harpullia* Roxb., *Lepisanthes* Blume, and *Llagunoa* Ruiz & Pav. This combined taxon sampling contained 247 tips, including five new taxa and deleting their chimeric *Haplocoelum foliosum* (Hiern.) Bullock (i.e. *trnL*, EU721250, clusters with the "Dodonaea group" and is likely mislabeled). Our concatenated matrices, along with supplemental figures are archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.p2g6p (Acevedo-Rodriguez et al. 2017)

We determined nucleotide substitution models for four data partitions (i.e. ITS1, ITS2, 5.8S, and *trnL*) in jModelTest ver. 2.1.2 (Darriba et al. 2012) using the Akaike information criterion (AIC; Akaike 1974). For both individual and concatenated matrix analyses we performed parsimony, maximum likelihood (ML), and Bayesian analyses. Parsimony analyses on the 99-tip data set were performed with TNT ver.1.5 (Goloboff et al. 2000) with a two-stage search using 100,000 replicates of TBR followed by SPR, and keeping the best 10 trees for each replicate (maximum of 100 million trees). Parsimony non-parametric bootstrap (Felsenstein 1985) analyses included 1 million replicates, using the same approach as in the tree search. ML analyses of the 99-tip data set were made with RAxML ver. 8.0.0 (Stamatakis 2014) on an unpartitioned matrix and 20 simultaneous runs, each followed by bootstrap analysis with 100,000 replicates. ML analyses

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of the 125-tip Paullinieae and 247-tip Sapindaceae data set were with GARLI ver.2.1 (Zwickl 2006) on an unpartitioned matrix; GARLI-ML bootstrap analysis included 500 replicates. Finally, Bayesian analyses under the GTR + I + Γ model were performed on the 99-tip data set using MrBayes (Ronquist and Huelsenbeck 2003) with four simultaneous runs, each with four Markov chains (three cold and one heated) for a total of 16 simultaneous chains including 1,000,000 generations. Phylogenetic trees were produced using Figtree ver. 1.4.0 (Rambaut 2015), Dendroscope ver. 3 (Huson and Scornavacca 2012), and/or Mesquite ver. 3.04 (Maddison and Maddison 2015).

Morphology—Morphological characterization of the genera is based on the treatment of the Sapindaceae by Acevedo-Rodríguez et al. (2011), Ferrucci (1991), and further study of collections at the U.S. National Herbarium (US). Pollen morphology applies Erdtman's terminology (Erdtman 1966) and the studies of van der Ham (Acevedo-Rodríguez et al. 2011), van der Ham and Tomlik (1994), and Ferrucci and Anzótegui (1993). Chromosome data come from Ferrucci (2000a), de Freitas et al. (2007), Urdampilleta et al. (2013), and the *Index to Plant Chromosome Numbers* (1979–). We have adopted the terms 'anterior' and 'posterior', as opposed to traditional terminology, to refer to specific floral parts as done by Ferrucci and Somner (2010), and Ferrucci and Urdampilleta (2011a, 2011b). Anterior is the side where the third and fifth sepals are located; and posterior is the side on which the fourth sepal is found (Fig. 1C). Other floral parts are described according to their relative position between these two points of reference.

Results

Phylogenetic Analyses—Data set statistics are summarized in Table 1 and results of our primary combined 99-tip analyses are shown in Fig. 2, with additional analyses in Suppl. Figures 1–3. Separate analyses of each locus did not reveal any strongly supported groupings that would indicate incongruence, although resolution in *trnL* was poor due to the low number of informative characters. Based on this broad congruence, we combined the loci for the total evidence approach on which we base our discussion. The 99- and 125-tip analyses had different approaches to data set polishing (automated vs. manual) and software (RAxML vs. GARLI). Both topologies are highly congruent but the 99-tip sampling is better resolved at deeper nodes and serves as the point of reference for our discussion. The long branches we observed (Suppl. Figure 2) in *Cardiospermum integerrimum* Radlk. suggest a need for caution regarding the placement of that taxon, although its inclusion or exclusion did not greatly change the topology, or bootstrap values in neighboring subclades. Inspection of the ITS matrix indicated a substitution bias that resulted in a GC content reduction to 45% in *Cardiospermum integerrimum* from an average across the rest of the data of 61% (range 58–65%). Data consistency between our sequence and that of Urdampilleta et al. (2013) contraindicates a lab-specific artifact. Our combined 99-tip DNA analyses show strong support (Bayesian posterior probability (PP) = 1; ML bootstrap percentage (MLBP) = 96) for a clade containing most taxa placed by Acevedo-Rodríguez et al. (2011) in the Paullinieae. This clade, here called supertribe Paulliniodae, contains four supported monophyletic groups, which are here classified as tribes *Athyaneae*, *Bridgesieae*, *Thouinieae* and *Paullinieae*. Tribe Athyaneae containing *Athyana and Diatenopteryx* is strongly supported (PP = 1; MLBP = 100) as basal within Paulliniodae. Tribe *Bridgesieae* with a single species (*Bridgesia incisifolia* Cambess.) is sister to the Thouinieae + Paullinieae (PP = 1; MLBP = 98). Tribe Thouinieae is strongly supported (PP = 1; MLBP = 100) as a clade including *Thouinia* as sister to *Allophylus* plus *Allophylastrum*. *Allophylastrum* is weakly embedded in a paraphyletic *Allophylus* (PP < 60; MLBP < 50) and requires additional data to be resolved. Tribe Paullinieae has strong support (PP = 1; MLBP = 94) and a basal clade formed by *Thinouia*, successively followed by *Lophostigma* and then a poorly resolved crown group of three subclades containing *Serjania*, *Paullinia*, *Urvillea*, *Cardiospermum*, *Balsas*, and *Houssayanthus*. Although *Serjania* is poorly resolved, it is clearly paraphyletic because of deeply embedded *Balsas*, *Chimborazoa* and *Houssayanthus*. *Cardiospermum* as currently

Table 1. Data set characteristics for 99 and 125-tip phylogenetic analyses.

Characteristic	ITS	*trnL*	Combined total evidence
No. terminals	122/123	101/112	99/125
Aligned length, nt	680/925	441/716	1121/1641
Characters analyzed, nt	512/636	441/507	953/1143
% missing	4.0/5.2	11.2/2.6	6.9/9.4
Constant characters, nt	300/202	329/371	513/573
Variable characters, nt	380/434	112/136	440/570
Informative characters, nt	319/383	91/82	354/465

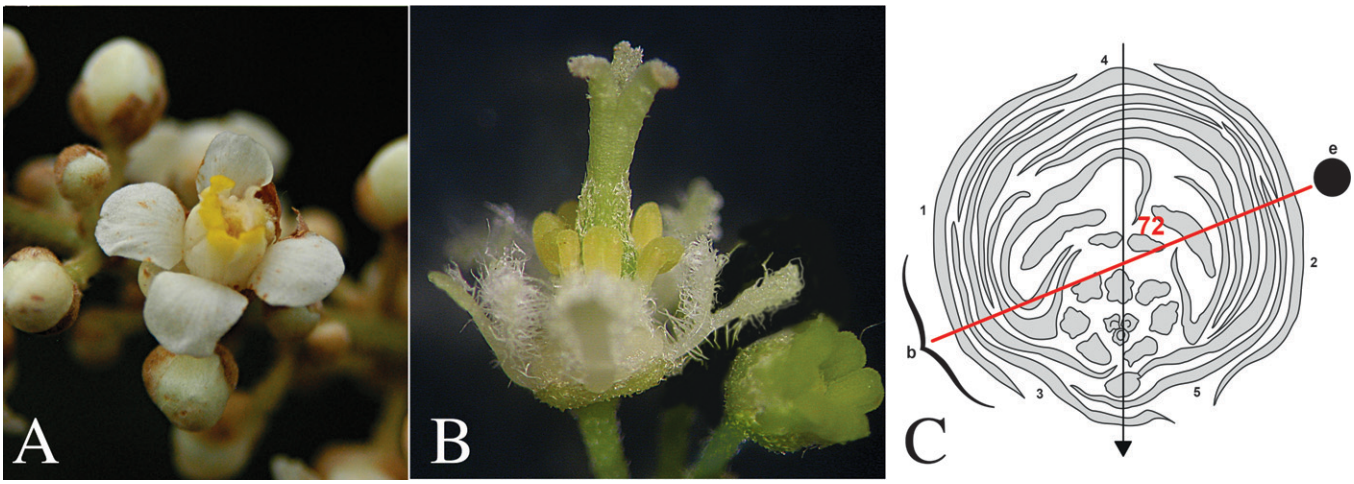

Fig. 1. Flowers in Paullinieae. A. zygomorphic flower (*Paullinia stellata* Radlk.; *Acevedo-Rodríguez 14964* (US), photo by P. Acevedo). B. actinomorphic flower (*Thinouia mucronata* Radlk.; photo by S. Maris Solís). C. Diagram of flower bud cross section of *Serjania salzmanniana* Schltdl. showing floral orientation (72°) in relation to inflorescence axis (e) and bracteole (b); numbers mark the different sepals (modified from Radlkofer 1931–1934).

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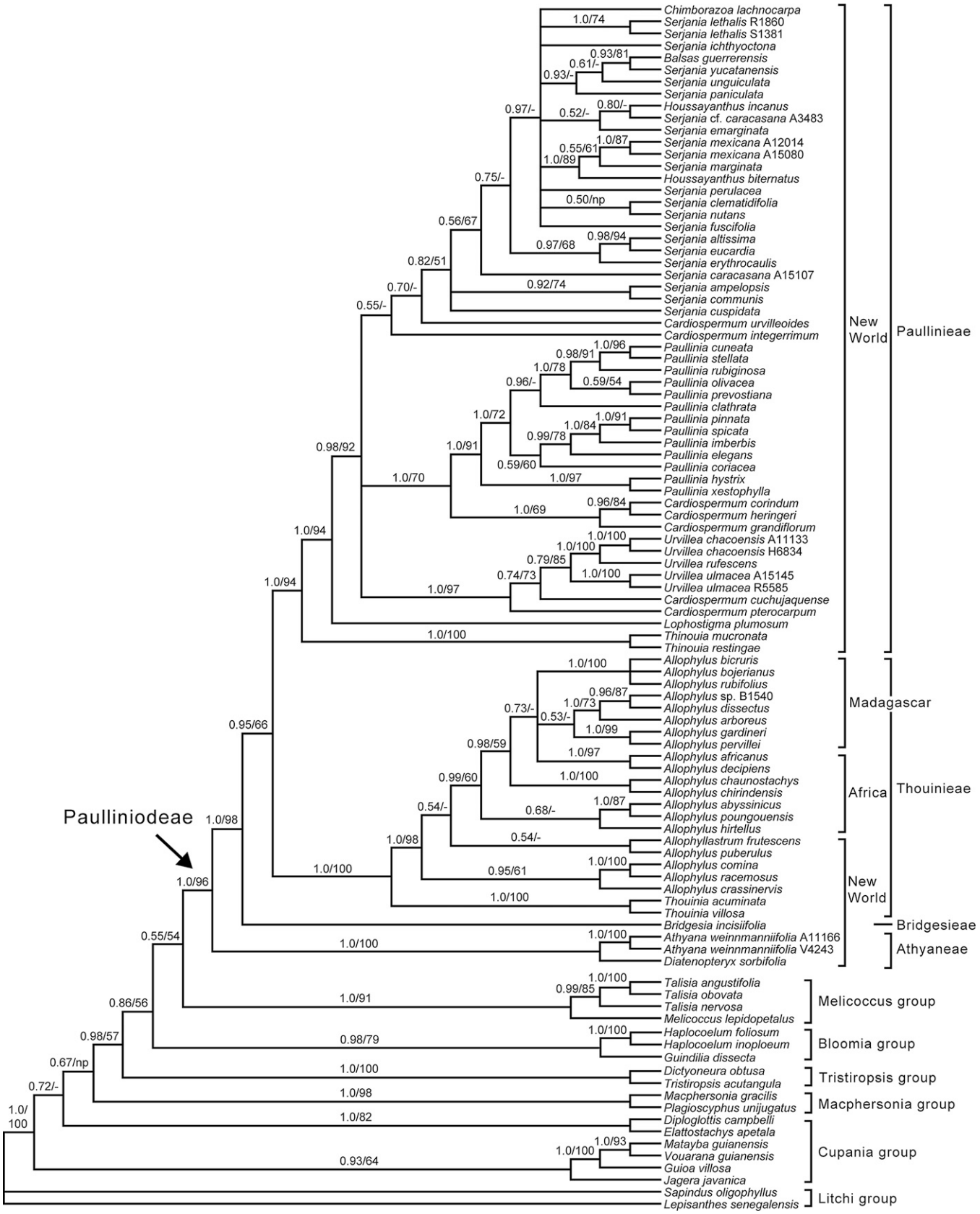

FIG. 2. Bayesian 50% majority-rule consensus tree based on the combined two marker, 99-tip data set for Paulliniodae and outgroups. Bayesian posterior probability values ≥0.50 are indicated above branches, followed by RAxML bootstrap values ≥50%. (–) = value < 0.50/50%. np = an edge recovered in the Bayesian tree but not present with ML.

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circumscribed (Ferrucci 2000b) is polyphyletic, with species grouping with *Serjania*, *Paullinia*, and *Urvillea*. The core *Cardiospermum* s. s. subclade (containing the type species *C. halicacabum*; sampled in the 125-tip analysis; Suppl. Figure 1) is sister to *Paullinia* (PP = 1; MLBP = 70). *Guindilia* is among the outgroup taxa, and although support is not strong in the 99-tip analyses as to an exact placement, it is clearly excluded from Paulliniodae.

Our analyses of the 247-tip family-wide data set show (Suppl. Figure 3) broad topological similarity among the sampled Paulliniodae to our focused 2-gene results, with two notable exceptions: (1) *Bridgesia* is sister to Thouinieae (MLBP = 93) rather than sister to Thouinieae + Paullinieae, and (2) *Guindilia* is sister to the rest of Paulliniodae (MLBP = 87) rather than farther out. *Sapindus oligophyllus* clearly groups (MLBP = 100) with *Lepisanthes*, an affiliation proposed by Xia and Gadek (2007) who transferred *S. oligophyllus* to *Lepisanthes*. Therefore, the anomalous position of this taxon within the *Paullinia* group by Buerki et al. (2009, 2010, 2013) is due to the misidentification of their sample, which is likely a species of *Allophylus*.

Discussion

Characterization of the Paulliniodae and Nested Tribes— Our best estimate (Fig. 2) of phylogenetic relationships of Paullinieae and its close relatives is incompletely resolved but makes considerable progress in a group that has been poorly sampled in prior phylogenetic studies. The examination of chromosome numbers, and important reproductive and vegetative characters (i.e. potential morphological synapomorphies) in the context of our trees reveals patterns of character state change that deserve closer examination (Fig. 3; Table 2). Supertribe Paulliniodae is characterized by the following morphological synapomorphies: leaves with a fully developed distal leaflet, thyrses with lateral cincinni, zygomorphic flowers with 4–5 sepals, 4 petals, unilateral

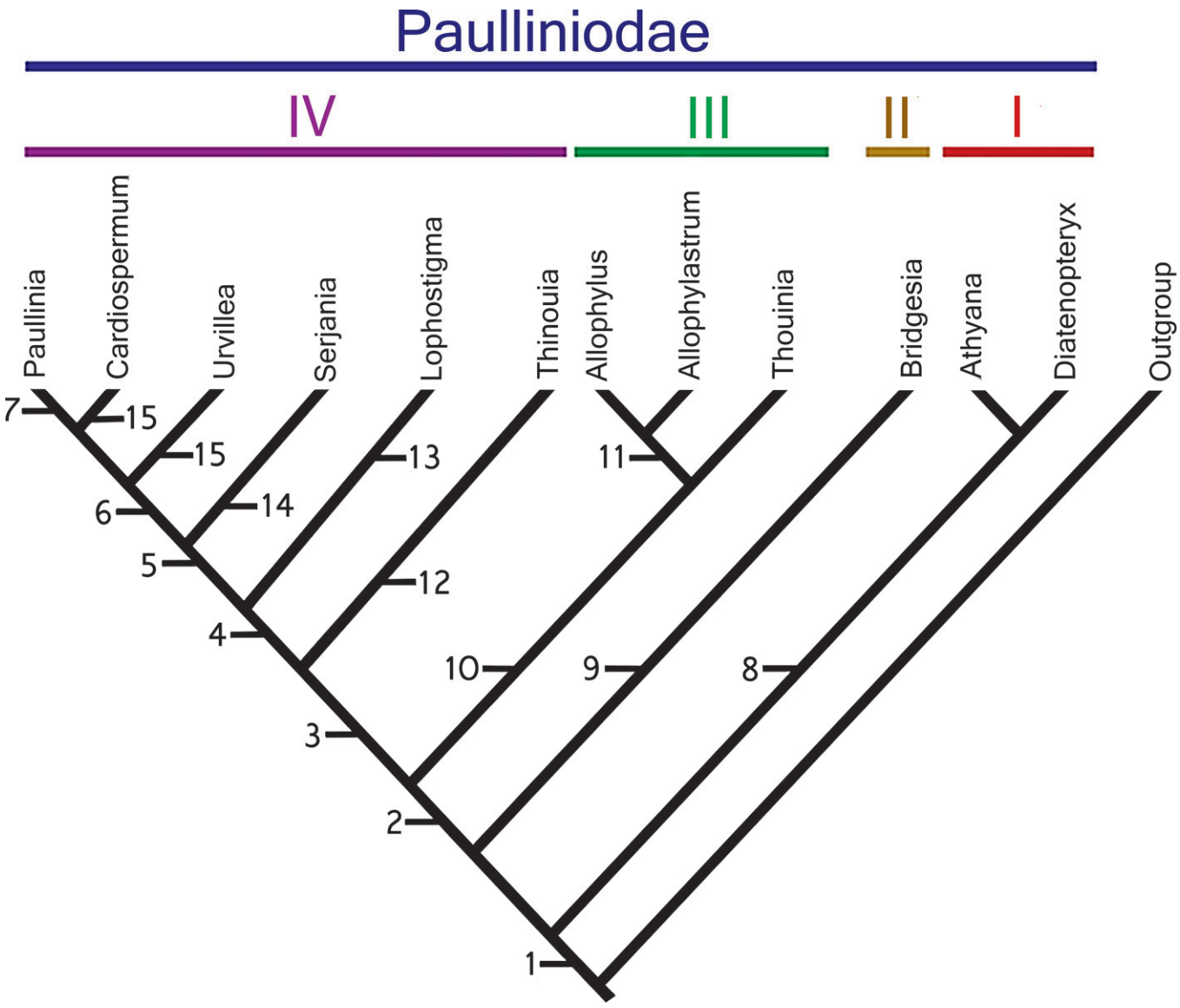

Fig. 3. Hypothetical relationships of genera in supertribe Paulliniodae, backbone based on DNA sequence and chromosome analyses; relationships within tribe Paullinieae based on morphological characters. Refer to Table 2 for synapomorphies.

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Table 2. Morphological characters (synapomorphies) for clades in supertribe Paulliniodae. Numbers correspond to synapomorphies shown in Fig. 3.

1. Leaves with a fully developed distal leaflet; thyrses with lateral cincinni; zygomorphic flowers with 4–5 sepals; 4 petals; unilateral nectary disc; schizocarpic fruits with divaricate mericarps; seeds not arillate; chromosome number $2n \leq 30$.
2. Leaves trifoliolate or trifoliolate derived; seeds basal; chromosome number $2n \leq 28$.
3. Climbers with stipules and tendrils.
4. Pollen heteropolar.
5. Pollen oblate (compressed in polar area) with triangular outline; petals as long as or longer than the sepals; chromosome number $2n \leq 24$.
6. Seeds in center of axis, with pseudo-hilum; fruit capsular.
7. Pollen hemi-isopolar, triporate; capsules coriaceous to woody; seeds arillate or sarcotestal.
8. Imparipinnate leaves.
9. Leaves simple; cincinni reduced.
10. Subglobose to oblate porate pollen grains; chromosome number $2n \leq 28$.
11. Fruits with coccate monocarps; seeds covered by fleshy endocarp.
12. Actinomorphic flowers, a reversal.
13. Pollen prolate heteropolar, 4-aperturate; petals shorter than the sepals.
14. Mericarps mostly proximally winged.
15. Capsule membranous; chromosome number mostly $2n < 24$.

nectary discs, schizocarpic fruits with divaricate mericarps, and reduced chromosome numbers ($2n \leq 30$).

Tribe Athyaneae, although distinct based on molecular data, is difficult to define with synapomorphic morphological characters. However, the tribe can be recognized by pinnately compound leaves in addition to the features that characterize the Paulliniodae. *Athyana* and *Diatenopteryx* can be distinguished by a combination of a 3-carpellate gynoecium and an indumentum lacking glandular hairs in *Athyana*, and the 2-carpellate gynoecium and indumentum with glandular hairs in *Diatenopteryx*. These two genera are currently restricted to southern South America, but according to the fossil pollen record, *Athyana* once was present in North America during the Oligocene (MacGinitie 1953).

Tribe Bridgesieae is strongly supported by molecular data and is recognized by its simple, exstipulate leaves in addition to the same floral characters as in Paulliniodae and by short, axillary cymes (a single, few-flowered cincinnus) or flowers solitary. Simple leaves and reduced cincinni are considered morphological synapomorphies for the Bridgesieae. Monospecific *Bridgesia* is currently restricted to the Andean region of Chile; however, fossil pollen records indicate its presence in North America during the Eocene (Graham 2011).

Tribe Thouinieae is characterized by trifoliolate (or trifoliolate-derived) leaves, zygomorphic flowers, thyrses with lateral cincinni and by the oblate to subglobose, porate pollen grains (Fig. 4A–B). *Thouinia*, which is sister to *Allophylus* and *Allophylastrum*, does not seem to have any morphological apomorphies, but can be differentiated from the latter two genera by its schizocarpic fruit with 3 distally winged mericarps (Fig. 5G). The subclade containing *Allophylastrum* and *Allophylus* is defined by fruits with coccate monocarps (Fig. 5H–I). Although *Allophylastrum* is easily distinguished by unique morphological features (see treatment below), its phylogenetic position is poorly resolved with respect to *Allophylus* with individual trees indicating it as either sister to, or alternatively embedded within, *Allophylus*. While our sampling of *Allophylus* is broad, sequence variation is low and additional loci are needed to resolve this point. Except for *Allophylus*, the genera of Thouinieae are restricted to the New World. *Thouinia* is currently known from the Greater Antilles (except Jamaica), Mexico and northern Central America but it has been documented in pollen samples from the Eocene to the Oligocene of North America (Muller 1981; Graham 2011). Accordingly, Thouinieae evolved in the New World, as the Neotropical genus *Thouinia* is the first diverging lineage of this clade and possibly shared a common ancestor with *Allophylus* and *Allophylastrum*. Hence, *Allophylus* evolved in the New World and later dispersed to Africa, Madagascar, and Asia. Poorly known *Allophylastrum* is restricted to northern South America, while *Allophylus* has a pantropical distribution. *Allophylus* has been documented as early as the middle Eocene from fossil pollen from the Gatuncillo Formation in Panama (Graham 1987).

Tribe Paullinieae is essentially Neotropical and the most species diverse of the four tribes. It is characterized by the presence of a climbing habit, stipules, and tendrils that seem to be homologous to the lower cincinni of the inflorescence (Darwin 1897). Floral symmetry for the most part is zygomorphic (Fig. 1A) with the exception of *Thinouia*, which has actinomorphic flowers (Fig. 1B). Actinomorphic flowers are plesiomorphic within the Paulliniodae and their occurrence in the Paullinieae can be best explained as a likely reversal. *Thinouia* is the first diverging lineage of this clade and although it does not have any morphological apomorphies, it is recognizable (in addition to the characters that define the Paulliniodae) by the presence of actinomorphic flowers, isopolar tricolporate pollen grains, and mericarps with distal wings (Figs. 1B, 5A, 6F). The next inclusive clade is formed by *Lophostigma* in a sister position to a clade containing *Serjania*, *Paullinia*, *Urvillea*, and *Cardiospermum*. The presence of heteropolar hemi-tri-syncolporate pollen grains (or its transformation) is considered synapomorphic in this clade (Fig. 6B–E). *Lophostigma* stands alone by the presence of prolate heteropolar 4-aperturate pollen grains and petals shorter than the sepals (Fig. 6E). The most inclusive clade is defined as a polytomy uniting *Serjania*, *Paullinia*, *Urvillea*, and *Cardiospermum*. This clade is characterized by the presence of petals that are as long as, or longer than, the sepals, and by oblate pollen grains (Figs. 1A, 6B–D).

The greater species richness of Paullinieae has been hypothesized to be the result of the ecological specializations in its innovative climbing habit and development of zygomorphic flowers (Buerki et al. 2013). This suggestion however, does not explain finer differences in species richness, where *Cardiospermum*, *Lophostigma*, and *Urvillea* have far fewer species than *Paullinia* and *Serjania*. Flower zygomorphism has evolved in all four subfamilies of Sapindaceae presumably from ancestors with actinomorphic flowers. Although most large genera in Sapindaceae have zygomorphic flowers, this character alone cannot explain differences in species richness. For example, *Acer* L. with about 125 species and *Dodonaea* Miller with about 68 species have actinomorphic flowers. In addition, from a total of 61 genera of Sapindaceae with zygomorphic flowers, only five have more than 30 species and 24 contain a single species. Thus, the poor correlation of habit and floral symmetry with species richness in the Sapindaceae does not seem to explain taxonomic richness in the Paullinieae.

Novel seed dispersal mechanisms in Paullinieae could have played an important role in the evolution, specialization, and diversification of *Paullinia* and also perhaps of *Serjania*. *Paullinia* is largely a forest dweller while *Serjania* favors open savannah-like formations. The presence of bird- and

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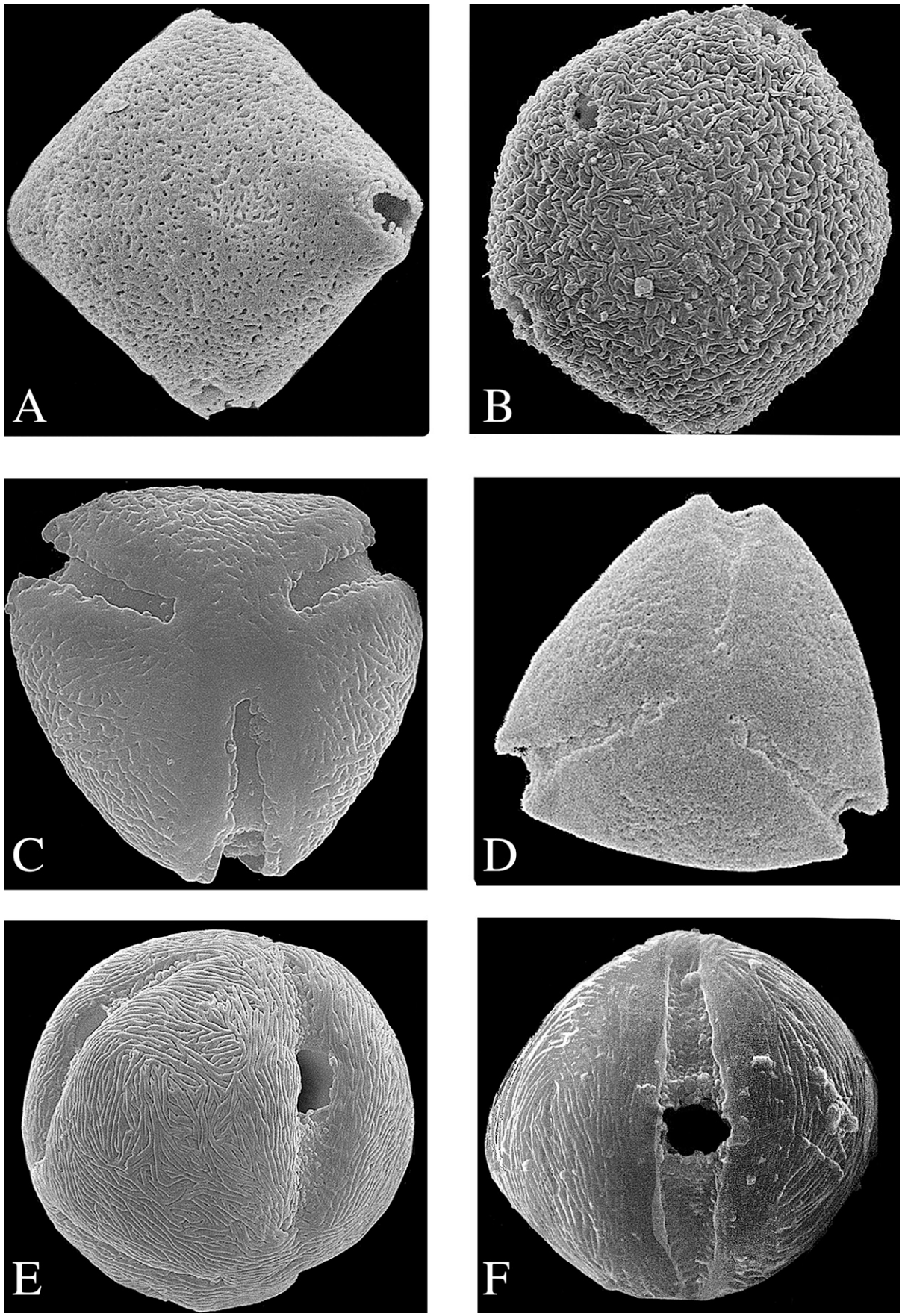

FIG. 4. Pollen grains in super-tribe Paullinoidae. A. *Thouinia striata* Radlk. (*Acevedo-Rodríguez 7869*, US). B. *Allophylastrum frutescens* Acev.-Rodr. (*Schomburgk 336*, W). C. *Diatenopteryx sorbifolia* Radlk. (*Hassler 10644*, US). D. *Athyana weinmannifolia* (Griseb.) Radlk. E. *Bridgesia incisifolia* Camb. (*Landrum 9824*, ASU). F. *Guindilia trinervis* Hook & Arn. (*Joseph 4048*, US).

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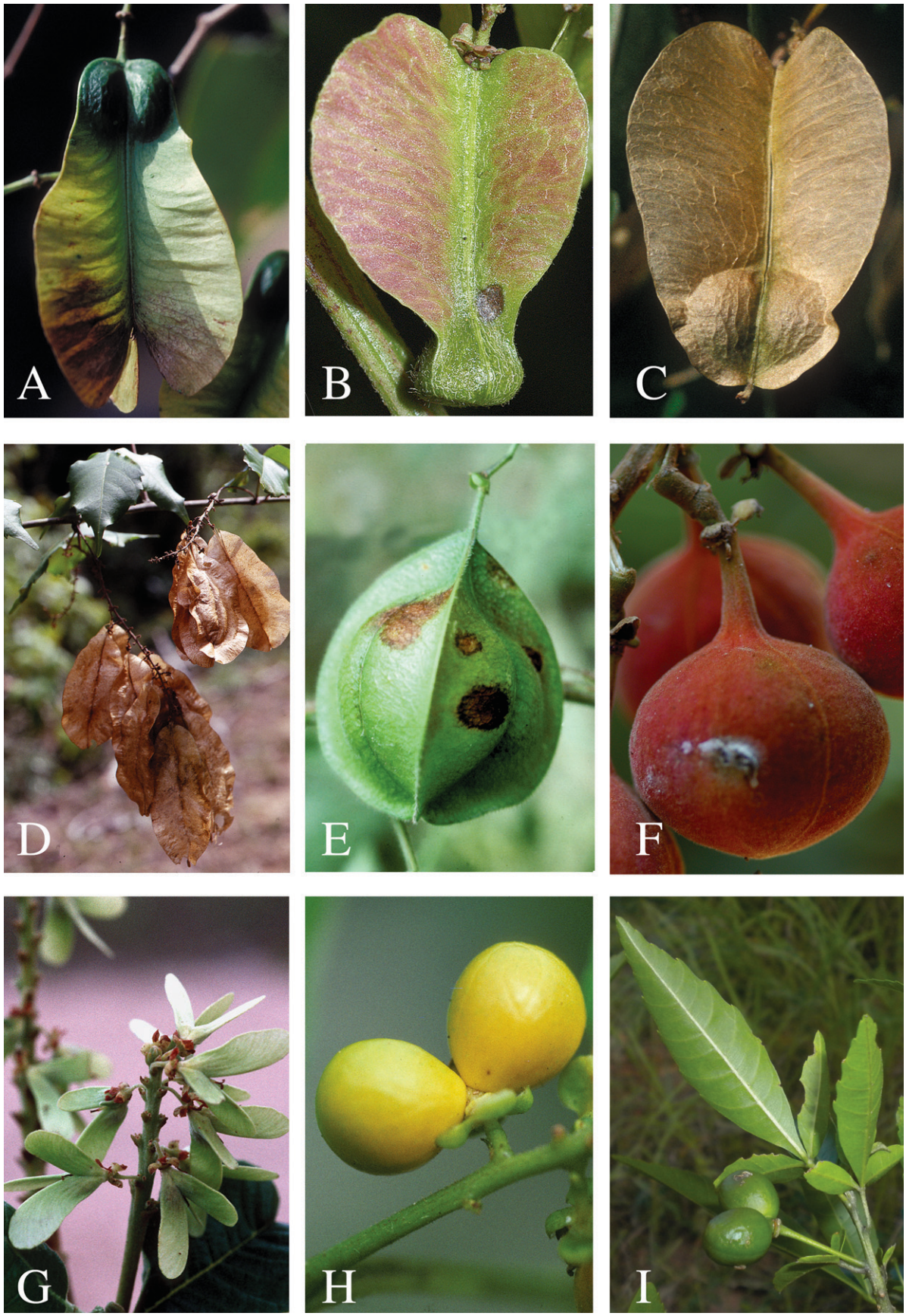

FIG. 5. Fruits in Paullinieae and Thouinieae. A. *Thinouia scandens* (*Acevedo-Rodríguez 3697*, US). B. *Serjania trachygona* Radlk. (*Acevedo-Rodríguez 15222*, US). C. *Lophostima plumosum* Radlk. (*Acevedo-Rodríguez 6568*, US). D. *Urvillea triphylla* Radlk. (*Acevedo-Rodríguez 3711*, US). E. *Cardiospermum corindum* L. (*Acevedo-Rodríguez 1349*, US). F. *Paullinia ingifolia* Juss. (*Acevedo-Rodríguez 13549*, NY). G. *Thouinia striata* Radlk.; H. *Allophylus* sp. (*Acevedo-Rodríguez 3726*, US). I. *Allophylastrum frutescens* Acev-Rodr. Photo credits: A–H, P. Acevedo; I, R. Perdiz.

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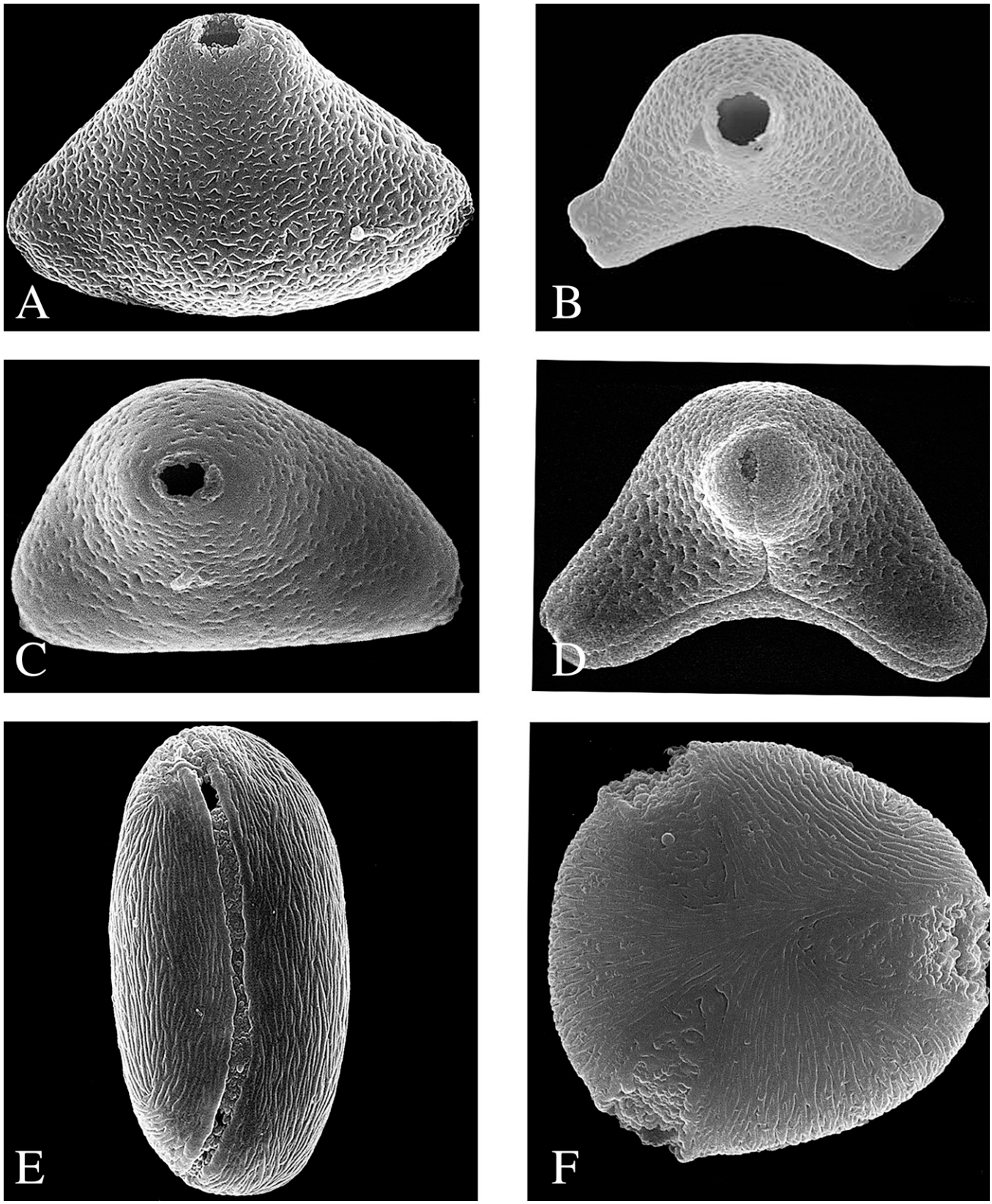

Fig. 6. Pollen grains in super-tribe Paullinoidae. A. *Allophylus sericeus* (Camb.) Radlk. (*Mexia 5202*, US). B. *Cardiospermum bahianum* Ferrucci (*Harley et al. 5266*, CTES). C. *Paullinia carpopoda* Camb. (*Irwin et al. 29394*, US). D. *Serjania squarrosa* Radlk. (*Cook & Gilbert 389*, US). E. *Lophostigma schunkei* (Acev.-Rodr.) Acev.-Rodr. (*Cerón & Cerón 4544*, US); *Thinouia myriantha* Triana & Planch. (*Tun Ortíz 2403*, US).

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water-dispersed seeds in *Paullinia* seems to be an adaptation for dispersal throughout the extensive Amazon biome, allowing *Paullinia* to reach new micro-niches and eventually to diversify into distinct species (Figs. 7A–D, 8A–B). Species richness in *Serjania*, however, cannot be explained solely by its wind-dispersed mericarps, as this feature also occurs in the much less diverse lianoid genera *Thinouia* and *Lophostigma* (Fig. 5A, C). *Serjania* may have capitalized on this dispersal mechanism by becoming a dry habitat specialist in more open environments (Acevedo-Rodríguez 1990), while *Thinouia* is mostly found in moister habitats where wind-dispersed species are less abundant (Mori and Brown 1994), and *Lophostigma* is restricted to high elevations. The poor species diversity observed in *Cardiospermum* and *Urvillea* may be due to the lack of effective dispersal mechanisms which otherwise would allow these genera to reach and radiate into novel habitats. In both genera, the seeds remain attached to the septa of the dehisced capsules and are only liberated by gravity after the decay of the septa (Fig. 8C). The suggestion that capsules of *Cardiospermum* may be water- or wind-dispersed (Harden 2002) is highly unlikely, as it has not been documented and because the capsule dehisces long before the fruit abscises from the inflorescence.

Chromosome Number—Recent studies on chromosome structure, size, and number provide additional insights into the evolution of the Paullinioidae (Ferrucci 2000a; Urdampilleta et al. 2013; *Index to Plant Chromosome Numbers* 1979–). When chromosome number is examined in the context of our trees, a pattern emerges of reduction from $2n = 32$ (*Talisia* Aubl. and *Matayba* Aubl.) to $2n \leq 30$ in Paullinioidae (Fig. 3), with occasional reports of polyploidy. This trend is evident in the Athyaneae (*Diatenopteryx*) where $2n = 30$ and in the closely related Thouinieae (*Allophylus*) and the basal taxa of Paullinieae (*Thinouia* and *Lophostigma*) where the number is further reduced to $2n = 28$. The most derived clade (*Cardiospermum*, *Paullinia*, *Serjania*, and *Urvillea*) is characterized by $2n \leq 24$, with even further reduction to $2n \leq 22$ in *Cardiospermum* and *Urvillea*.

Exclusion of Guindilia from Paullinioidae—*Guindilia*, which heretofore has been considered a member of the Paullinieae (Thouinieae sensu Radlkofer 1931-1934), is placed in our 99-tip phylogeny among the outgroup taxa, and clearly outside of the strongly supported Paullinioidae. While this suggests that it does not belong in the supertribe, its exact position within the tree may be an artifact of our limited outgroup sampling. A richer phylogenetic context still excludes *Guindilia* from Paullinioidae with placement as either sister to the supertribe (i.e. our 247-tip results in Suppl. Figure 3; also Buerki et al. 2011) or a placement further out and roughly similar to our 99-tip results (i.e. divergence dating in Buerki et al. 2013). Our data from a new accession of *Guindilia* agrees with that of Buerki et al. (2011). Morphologically, this genus differs from other Paullinioidae by the presence of opposite, simple leaves. Although the disc in *Guindilia* flowers is unilateral, it is roughly pyramidal-shaped and two-lobed, a feature that is not present in the Paullinioidae. We defer to assign *Guindilia* to any group until its phylogenetic position is better resolved.

Origin of the Paullinioidae and Nested Tribes—Our analyses do not suggest a clear affinity of the Paullinioidae with any of the outgroup taxa. However, based on pollen morphology, van der Ham and Tomlik (1994) suggested the parallel evolution of Paullinieae and Thouinieae from a *Cupania*-like ancestor. This hypothesis posits that the hemi-syncolporate pollen found in *Serjania*, *Cardiospermum*, and *Urvillea* is necessarily derived from a syncolporate or parasyncolporate pollen type that is found in the Cupanieae. Support for this claim is found in the sporadic presence of distal vestigial colpi in the pollen of these three genera, and fine traces of a parasyncolporate condition in *Athyana* (van der Ham and Tomlik 1994; Acevedo-Rodríguez 2011). From the floral morphology point of view, this hypothesis is plausible as some Cupanieae (e.g. species of *Guioa* Cav.) have zygomorphic flowers with unilateral nectary discs similar to those in the Paullinioidae. The alternative hypotheses of derivation from an ancestral group with colporate pollen such as *Sapindus* L. (Acevedo-Rodríguez 1993) or *Thinouia*-like (Ferrucci and Anzótegui 1993) would have to account for the unlikely transformation of tricolporate into the hemi-tri-syncolporate pollen present in *Serjania* and allied genera.

Buerki et al. (2013) offered a hypothesis for the origin of the Paullinioidae (their "Paullinia group") as a result of a migration event of ancestral Sapindaceae from Australia via Antarctica during the Middle Eocene. Although this hypothesis and the proposed timing of events is not supported by the available fossil record, it is possible that such a migratory route existed much earlier as suggested by the wide occurrence of *Cupaniopsis* pollen (Cupanieae) during the middle Cretaceous in Antarctica, Africa (Gabon), South America (Brazil), and North America (Coetzee and Muller 1984; Muller 1981). Although no specific ancestor is mentioned by Buerki et al. (2013), their consensus tree has *Blomia* Miranda and the Melicocceae closer to the Paullinioidae than to the Cupanieae. *Blomia* and the Melicocceae have colporate pollen grains and could share a common ancestor with the Paullinioidae.

The constraints of the van der Ham and Tomlik (1994) hypothesis do not preclude a common ancestor with isopolar colporate pollen like those of *Talisia*, and *Melicoccus* P. Browne although it would require the additional evolutionary step of becoming syncolporate. Our analyses do not provide support for either scenario but it would be an interesting hypothesis to test by expanding the molecular sampling coupled with examining the pollen of *Blomia* and the Melicocceae for vestigial Cupanieae-like pollen characters. From a palynological point of view, *Paullinia* could have been derived from a common ancestor with *Cardiospermum*, *Serjania*, and *Urvillea*. Its isopolar, triporate pollen (Fig. 5C) is seen as derived from the type found in *Serjania*. The presence of subisopolar pollen grains in a few species of *Paullinia* is seen as a vestigial character that adds weight to this argument. In addition, the presence of capsular fruits with thick walls and seeds without sarcotesta in *Balsas* (herein considered a *Serjania*) is interpreted as a step in the derivation of the capsules in *Paullinia* from an ancestor with schizocarpic, thin-walled fruits and non-sarcotestal seeds.

The persistence of plesiomorphic characters such as the trigonous-subglobose, tricolporate, striate pollen grains (Athyaneae, Bridgesieae, *Allophylus*, *Thinouia*, and *Lophostigma*) and actinomorphic flowers (*Allophylastrum* and *Thinouia*) are indicative of mosaic-like character evolution in the Paullinioidae. In addition, the occurrence of transitional plesiomorphic characters such as the sub-zygomorphic flowers in *Lophostigma* and some species of *Allophylus* provide further evidence for mosaic evolution and provide possible links between genera. For example, striate pollen and sub-zygomorphic flowers in *Lophostigma* are seen as intermediate between *Thinouia* and

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Fig. 7. Fruits in *Paullinia*. A. *P. hyxtrix* Radlk. (*Acevedo-Rodríguez et al. 14408*, US). B. *P. obovata* (Ruiz & Pav.) Pers. (*Acevedo-Rodríguez et al. 14441*, US). C. *P. verrucosa* Radlk. (*Acevedo-Rodríguez et al. 14584*, US). D. *P. caloptera* Radlk. (*Acevedo-Rodríguez et al. 14315*, US).

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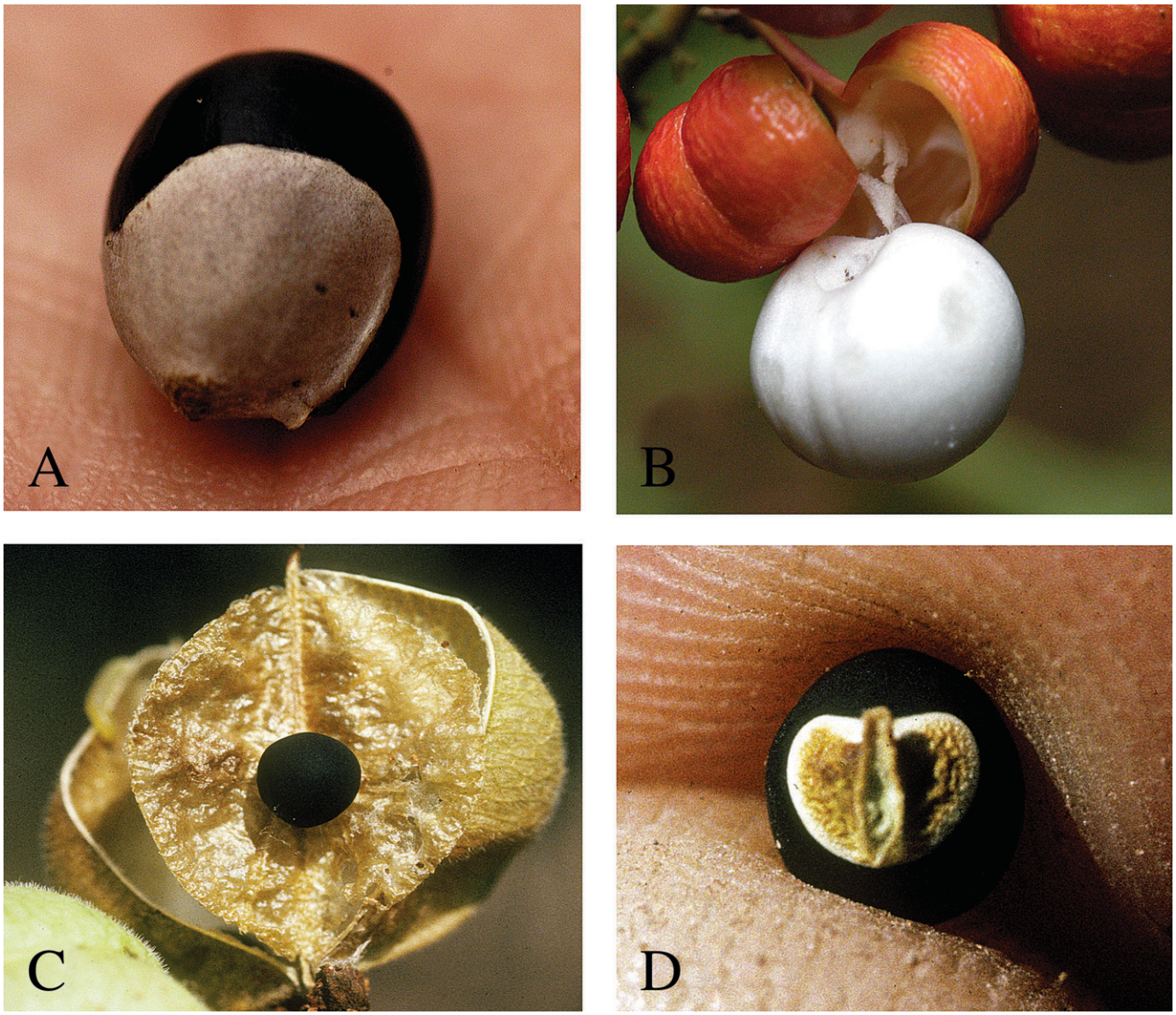

Fig. 8. Fruits and seeds in Paullinieae. A. Seed with removed arillode showing pseudo-hilum, *Paullinia verrucosa* Radlk. (*Acevedo-Rodríguez 14584*, US). B. Dehisced capsule, *Paullinia fibrigera* Radlk. (*Acevedo-Rodríguez 15233*, US). C. Dehisced capsule, *Cardiospermum corindum* L. (*Acevedo-Rodríguez 4568*, US). D. Seed with pseudo-hilum, *Cardiospermum corindum* L., (*Acevedo-Rodríguez 4568*, US).

the remaining genera (*Serjania*, *Cardiospermum*, *Urvillea*, and *Paullinia*) of Paullinieae. The presence of sub-actinomorphic flowers within *Allophylus* suggests an incipient reversal (from zygomorphic to actinomorphic flowers) and provides a connection with *Allophylastrum* where actinomorphic flowers are found. This notion also supports the interpretation of actinomorphic flowers in *Thinouia* as a reversal. Instances of intermediate or incipient characters are also found in *Serjania* where a few species show features (pseudo-hilum, and capsules) that are characteristic of *Cardiospermum*, *Urvillea*, and *Paullinia*. While our resolution of major subclades within supertribe Paulliniodae is incomplete, an examination of morphological characters with reference to the persistence of plesiomorphic and intermediate morphological characters, suggests links among genera and testable hypotheses of evolutionary trends.

Pollen fossils identified as *Allophylus*, *Bridgesia*, *Cardiospermum*, *Paullinia*, *Serjania*, and *Thouinia* indicate the wide establishment of supertribe Paulliniodae in the Americas by the late Eocene (Gray 1960; Muller 1981; Graham 1987, 2011). Moreover, the fact that *Allophylus* fossils have only been found in the Old World in recent geological times further supports the hypothesis that *Allophylus* evolved in the Americas and later dispersed to Africa and other regions of the Old World.

A New Classification—The recognition of Supertribe Paulliniodae allows for the retention of tribes that are recognizable from a suite of morphological characters. Tribe Athyaneae, although similar to the Thouinieae, contains trees with exstipulate, pinnately compound leaves with fully developed distal leaflets. Tribe Bridgesieae contains shrubs with simple, exstipulate leaves, and short, axillary cymes (a single few-flowered cincinni) or solitary flowers. Tribe Thouinieae deviates from previous classifications by excluding *Athyana*, *Bridgesia*, *Diatenopteryx*, and *Guindillia* and contains trees or shrubs with trifoliolate or unifoliolate, exstipulate leaves, and zygomorphic flowers. Finally, tribe Paullinieae agrees with previous classifications (de Candolle 1824; Radlkofer 1890), and contains climbers or climber-derived shrubs with stipulate leaves, and tendrils. We have made limited taxonomic

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changes toward the goal of recognizing only monophyletic genera, although problems still remain with regard to *Allophylastrum* and *Cardiospermum* (i.e. *Cardiospermum integerrimum*, C. *urvilleoides*). Not all of these changes are based on direct molecular phylogenetic placement, but rather some are inferred based on close morphological similarity to our sampled taxa.

Taxonomic Treatment

Supertribe Paulliniodae—Lianas, vines, trees shrubs, or hemicryptophytes. Leaves alternate, with a fully developed distal leaflet; thyrses with lateral cincinni; flowers zygomorphic, with 4–5 sepals, 4 petals, unilateral nectary disc (or exceptionally actinomorphic), and schizocarpic (or schizocarpic derived) fruits.

Key to the Tribes

1. Lianas, climbing shrubs, or less often erect or hemicryptophytic shrubs; stipules minute to foliaceous; tendrils paired at base of inflorescence rachis ..... *Paullinieae*
1. Trees or erect shrubs; stipules and tendrils wanting 2
   2. Leaves pinnately compound ..... *Athyaneae*
   2. Leaves trifoliolate, unifoliolate or simple 3
      3. Leaves trifoliolate or unifoliolate (pulvinulate at the base of blade); fruits bicoccate or schizocarpic with non-bladder-like mericarps, apically elongated into a long (distal) wing; pollen porate ..... *Thouinieae*
      3. Leaves simple; fruit schizocarpic, with bladder-like mericarps, transversely elongated into a short (dorsal) wing; pollen tricolporate ..... *Bridgesieae*

Tribe **Athyaneae** Acev.-Rodr., tribus nova—TYPE: *Athyana*

Exstipulate, small trees, leaves alternate imparipinnate with fully developed distal leaflet; flowers zygomorphic; pollen isopolar, obtusely triangular in polar view, subspherical in equatorial view, tricolporate, with colpi nearly reaching the poles.

Small trees; exstipulate. Leaves alternate, imparipinnate, distal leaflet fully developed or exceptionally rudimentary. Inflorescences of thyrses with flowers in lateral cincinni; pedicel articulate (abscission zone) below the middle. Flowers zygomorphic, structurally or functionally unisexual; calyx 4–5-merous, sepals valvate or imbricate; corolla of 4 distinct petals, each with an adaxial, basal, hood-shaped appendage; disc semiannular; stamens (6–)8, filaments usually of different lengths, anther dorsifixed; gynoecium 2- or 3-carpellate with a single ovule per carpel.

Distribution—Two genera distributed in southern South America.

Key to the Genera

1. Gynoecium 3-carpellate; leaf rachis winged ..... *Athyana*
1. Gynoecium 2-carpellate; leaf rachis unwinged ..... *Diatenopteryx*

Athyana (Griseb.) Radlk. in T. Durand, Index Gen. Phan. 73. 1887 ["1888"].—TYPE: *Athyana weinmanniifolia* (Griseb.) Radlk.

Duodichogamous trees; exstipulate. Leaves imparipinnate; leaflets (5)7–15, serrate; distal leaflet fully developed; rachis winged. Inflorescences axillary or pseudoterminal, simple or double thyrses; flowers on lateral, reduced cincinni (seemingly a depauperate dichasium); pedicels articulate. Flowers zygomorphic; calyx actinomorphic, sepals 5, valvate, of similar size, with the 2 anterior sepals connate at base; petals 4, as long as the sepals, with a single basal, hood-shaped, crested appendage; disc semiannular, lobed; stamens (7)8, filaments of unequal lengths, anthers dorsifixed; pollen isopolar, obtusely triangular in polar view, subspherical in equatorial view, tricolporate, with colpi nearly reaching the poles (Fig. 4D), finely perforate (also faintly parasyncolporate fide van der Ham and Tomlik 1994); ovary 3-carpellate; stigma capitate. Fruit schizocarpic, splitting into 3 samaroid mericarps with a dorsal-distal, ascending wing; seed exarillate. A single species found in Peru, Bolivia, Paraguay, and Argentina.

Diatenopteryx Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. Münch. 8: 284. 1878.—TYPE: *Diatenopteryx sorbifolia* Radlk.

Duodichogamous small to large trees; exstipulate. Indumentum of simple hairs. Leaves imparipinnate or paripinnate; leaflets dentate or serrate; distal leaflet fully developed; rachis unwinged. Inflorescences terminal or axillary thyrses, with flowers in lateral cincinni; pedicel articulate. Flowers zygomorphic, functionally unisexual; sepals 4, free, imbricate, the anterior sepal larger; petals 4, up to four times as long as the sepals, each with a basal hood-shaped, crested appendage; disc semiannular, crenate; stamens (6–)8, of unequal length, anthers dorsifixed; pollen isopolar, obtusely triangular in polar view, subspherical in equatorial view, tricolporate, with elongated colpi nearly reaching the poles, rugulate (Fig. 4C); ovary 2-carpellate, v-shaped; style filiform; stigma bifid. Fruits schizocarpic, splitting into 2 samaroid divaricate, mericarps with a long dorsal wing; seed exarillate. Two species from Brazil, Bolivia, Paraguay, and Argentina. $2n = 30$.

Tribe **Bridgesieae** Acev.-Rodr., tribus nova—TYPE: *Bridgesia*

Exstipulate, shrubs; leaves alternate simple; flowers zygomorphic; pollen isopolar, subspherical in polar and equatorial views, tricolporate.

Characters as in *Bridgesia*.

Distribution—A single, monospecific genus distributed in Chile, South America.

Bridgesia Bertero ex Cambess., Nouv. Ann. Mus. Hist. Nat. 3: 234. 1834, nom. cons., non Hook., 1831.—TYPE: *Bridgesia incisifolia* Cambess.

Duodichogamous shrubs; exstipulate. Leaves simple, deeply trilobed or serrate. Inflorescence a short, axillary cyme (a single few-flowered cincinni) or flowers solitary; pedicels articulate. Flowers zygomorphic; sepals 5, imbricate, lanceolate, nearly equal, the 2 anterior sepals partly connate; petals

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4, pink, with a single basal, hood-shaped crested appendage; disc semiannular, 4-lobed; gynophore with 4 tiny lobes; stamens 8, filaments of unequal lengths, anthers dorsifixed; pollen isopolar, spherical in polar and equatorial view, tricolporate, striate (Fig. 4E); ovary 3-carpellate; style filiform with 3 stigmatic branches. Fruit schizocarpic, splitting into 3 samaroid, bladder-like, papery, divaricate mericarps with a short dorsal wing; seed exarillate, black, with a large hilum. A single species from Andean Chile.

Tribe Thouinieae Blume, Rumphia 3: 186. 1847.

Small trees or shrubs; exstipulate. Leaves alternate, trifoliolate or unifoliolate. Inflorescences of thyrses with flowers in lateral cincinni, or less often solitary or in short racemes; pedicel articulate (abscission zone) below the middle or non-articulate (in *Allophylastrum)*. Flowers zygomorphic or less often actinomorphic, structurally or functionally unisexual; calyx 4(5)-merous, sepals with quincuncial imbrication; corolla of 4 distinct petals (or missing in *Allophylastrum*), usually with an adaxial or marginal petaloid appendage; disc semiannular, 2–4 lobed, or less often annular; stamens (6)8, filament usually of different lengths, anther dorsifixed; gynoecium (2)3-carpellate with a single ovule per carpel.

***Distribution*—**All genera Neotropical, except for *Allophylus* that is primarily Paleotropical.

Key to the Genera

1. Fruit schizocarpic, of 3 distally-winged mericarps ..... *Thouinia*
1. Fruits unicoccate, bicoccate or seldom tricoccate
   2. Flowers zygomorphic, petaliferous, on lateral cincinni in racemiform or paniculate thyrses; nectary disc unilateral, semiannular, 2- to 4-lobed, or rarely annular; pedicels articulate, 1–2 times as long as the calyx; pollen 3(4)-porate, triangular (seldom quadrangular) in polar view ..... *Allophylus*
   2. Flowers actinomorphic, apetalous, solitary, or in short axillary racemes; nectary disc cupular; pedicels non-articulate, >4 times as long as the calyx; pollen 4- or 5-porate, 4- or 5-angled in polar view ..... *Allophylastrum*

Thouinia Poit., Ann. Mus. Natl. Hist. Nat. 3: 70. 1804, nom. cons., non L. f., 1782.—TYPE: *Thouinia simplicifolia* Poit.

Duodichogamous shrubs or small trees; exstipulate. Leaves trifoliolate or unifoliolate. Inflorescences axillary, racemiform thyrses with flowers in reduced lateral cincinni; pedicels articulate. Flowers zygomorphic; sepals 4, imbricate, the outer two usually smaller; petals 4, with an adnate, ventral, 2-lobed appendage; disc unilateral, 4-lobed; stamens 8, filaments of equal length; pollen isopolar, obtusely triangular, quadrangular, pentagonal, or hexagonal in polar view, oblate in equatorial view, 3–6-porate, rugulate; ovary 3-carpellate, with a single ovule per carpel; style filiform, with 3 stigmatic branches. Fruit schizocarpic, splitting into 3 samaroid mericarps, each bearing a dorsal ascending wing; seeds exarillate. About 30 species from the Greater Antilles (excluding Jamaica), Bahamas, Mexico, and northern Central America.

Allophylus L., Sp. Pl. 348. 1753. —TYPE: *Allophylus zeylanicus* L. [= *Allophylus cobbe* (L.) Raeusch.]

Duodichogamous, rarely dioecious, erect shrubs, trees, or rarely scandent shrubs (in Malaysia); exstipulate. Leaves alternate, trifoliolate or less often unifoliolate or digitately 5-foliolate (few Asian species); leaflets serrate, dentate or entire; petioles elongated. Inflorescences axillary, racemiform or paniculate thyrses, flowers on lateral cincinni; pedicels articulate. Flowers zygomorphic; sepals 4(5), free, imbricate, the outer distinctly smaller than the inner ones; petals 4, with a single, adnate, 2-lobed, or a basal hood-shaped, non-crested appendage, or these represented by an elongation of petal's margins, exceptionally wanting; disc unilateral, semiannular or divided into 2 or 4 lobes, or exceptionally annular; stamens 8, filaments of unequal lengths, with posterior three shorter, anthers dorsifixed; pollen isopolar, obtusely triangular (seldom quadrangular) in polar view, oblate in equatorial view, 3(4)-porate (Fig. 6A) or less often brevicolporate, rugulate, sometimes striate, reticulate or psilate (Cruz and Melhem 1984) (pollen of *A. guaraniticus* has been shown also as quadrangular in polar view and 4-porate (da Luz and Barth 1999; in *A. edulis*, > 60% of pollen grains are reported as 4-porate by Anzótegui and Ferrucci 1998; Fig. 4A); ovary 2(3)-carpellate; style with 2–3 stigmatic branches. Fruit unicoccate (with a rudimentary coccus) or bicoccate, endocarp crustose, exocarp fleshy; seeds exarillate, with papery testa. A circumtropical genus with about 255 species (Coelho 2014). $2n = 28; 56$.

Allophylastrum Acev-Rodr., Phytokeys 5: 40. 2011.—TYPE: *Allophylastrum frutescens* Acev.-Rodr.

Dioecious (?), small trees or shrubs; exstipulate. Leaves trifoliolate; leaflets serrate. Flowers solitary, axillary or in short racemes, actinomorphic, unisexual with staminate flowers sometimes bearing a rudimentary 2-locular gynoecium; pedicels elongated, non-articulate; calyx 4-merous, sepals of similar length, in two whorls; petals wanting; disc cupular; stamens (5)6, the filaments of nearly equal length, connate at base; pollen isopolar, obtusely 4- or 5-angled in polar view, subspherical in equatorial view, 4–5-porate, with rugulate ornamentation (Fig. 4B); ovary 2-carpellate; style with 2 stigmatic branches. Fruit unicoccate (with a rudimentary coccus) or bicoccate, endocarp semi-woody, exocarp fleshy; seeds exarillate, with papery testa. A single, poorly collected species from Guyana and Brazil (Roraima).

Tribe Paullinieae (Kunth) DC., Prodr. 1: 601. 1824.—TYPE: *Paullinia*

Lianas, vines or climbing shrubs, exceptionally erect or hemicryptophytic shrubs, with a short, axillary shoot bearing a distal pair of coiled tendrils; stipules minute to foliaceous. Leaves alternate, with a well-developed distal leaflet, variously pinnate, trifoliolate, biternate, bipinnate or seldom unifoliolate. Inflorescences of thyrses with flowers in lateral cincinni; pedicel usually articulate below the middle. Flowers zygomorphic or less often actinomorphic (in *Thinouia*), structurally or functionally unisexual; calyx 4(5)-merous, sepals with quincuncial imbrication; corolla of 4(5) distinct petals, with an adaxial petaloid appendage; disc unilateral, 2- or 4-lobed, or less often annular (in *Thinouia*); stamens 8, filament

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usually of three different lengths, anther dorsifixed; gynoecium 3-carpellate with a single ovule per carpel.

***Distribution*—**Neotropical, with a couple of species naturally extending into Africa and Madagascar.

Key to the Genera*

1. Leaves trifoliolate; stipules minute; flowers actinomorphic; pollen subspherical to oblate-spherical in equatorial view ..... *Thinouia*
1. Leaves variously compound; stipules minute to foliaceous; flowers zygomorphic (sub-zygomorphic in *Lophostigma)*; pollen oblate, peroblate or prolate in equatorial view.
   2. Petals much shorter than sepals; petal appendages about ½ the length of petals, bifid; stamens of equal lengths; pollen striate, prolate or prolate-spherical in equatorial view, 4-hemicolporate, 2 colpi always diorate ..... *Lophostigma*
   2. Petals much longer than sepals; petal appendages as long or nearly as long as the petals, hood-shaped; stamens of unequal length; pollen reticulate, perforate or psilate, oblate or peroblate in equatorial view.
      3. Lianas, climbing shrubs or seldom erect shrubs; fruit always capsular, woody, coriaceous or crustaceous; seed with a partial to complete arilode (sarcotesta); pollen isopolar or subisopolar, 3-porate ..... *Paullinia*
      3. Lianas, climbing shrubs, herbaceous vines or less often erect shrubs or prostrate herbs; fruit schizocarpic or if capsular, membranaceous; seeds lacking an arillode; pollen heteropolar, hemi-syncolporate.
         4. Fruits schizocarpic with 3 winged mericarps or exceptionally capsular; seeds without a pseudo-hilum or if present then trigonous ..... *Serjania*
         4. Fruits capsular, membranaceous, with seeds persistent on septa after dehiscence; seeds with a heart-shaped, reniform, or crescent-shaped pseudo-hilum.
            5. Sepals 5; nectary disc 4-lobed; anthers usually with a more or less conspicuous apical connective expansion ..... *Urvillea*
            5. Sepals 4 or 5, when 5 nectary disc of 2 corniform lobes; anthers without an apical connective expansion ..... *Cardiospermum*

**Cardiospermum urvilloides* and *C. integerrimum* are weakly associated with *Serjania* in our analyses. However, because they are morphologically indistinguishable from *Cardiospermum* (*sensu stricto*), we defer creating new genera until additional data supporting their placement are found.

Thinouia Triana & Planchon, Ann. Sci. Nat. Bot. Ser. 4, 18: 368. 1862.—TYPE: *Thinouia myriantha* Triana & Planchon.

Allosanthus Radlkofer in A. Engler, Pflanzenr. IV. 165 (Heft 98): 1157. 1933.

Lianas. Early stems and branches with a single vascular cylinder; older stems occasionally with neoformed cortical vascular cylinders. Leaves trifoliolate; stipules minute. Inflorescences of umbelliform (racemiform in *T. trifoliata*) thyrses, seldom bearing tendrils, axillary or aggregate into terminal thyrsoid inflorescences with flowers in cincinni; pedicels articulate. Flowers actinomorphic, 5-merous; calyx cup-shaped, the sepals valvate, equal; petals 5, obovate to spatulate, with a pair of short, marginal appendages (a prolongation of petal's margins); disc annular; stamens 6–8, of unequal lengths, anthers dorsifixed; pollen isopolar, obtusely triangular in polar view, subspherical in equatorial view, tricolporate, with elongated colpi nearly reaching the poles, striate (Fig. 6F); ovary 3-carpellate; style elongated with 3 stigmatic branches. Fruit schizocarpic, splitting into 3 mericarps (Fig. 5A), each with a distal wing; seeds trigonous ellipsoid, or lenticular-ellipsoid, exarillate, with a small hilum. About 10 species from Mexico, Central America, and South America. $2n = 28$ (Urdampilleta et al. 2008a).

***New Combination*—**

Thinouia trifoliata (Radlk.) Acev.-Rodr. & Ferrucci, comb. nov.; *Allosanthus trifoliatus* Radlk. in A. Engler, Pflanzenr. [Heft 98f] 4, Fam. 165: 1157. 1933.

Lophostigma Radlk. in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1: 228. 1897.—TYPE: *Lophostigma plumosum* Radlk.

Duodichogamous woody vines. Cross section of stem with a single vascular cylinder. Leaves trifoliolate; stipules minute. Inflorescences axillary racemiform thyrses with a pair of tendrils at base of rachis and flowers in lateral cincinni. Flowers sub-zygomorphic; sepals 5, unequal, imbricate; petals 4, shorter than the sepals, with very short, bifid, basally adnate appendages; disc unilateral, 4-lobed; stamens 8, with short, equal, filaments, anthers dorsifixed (seemingly basifixed); pollen heteropolar, subspherical or subspherical-trilobed in polar view, prolate or prolate-spherical in equatorial view, 4-aperturate pollen heteropolar, subspherical or subspherical-trilobed in polar view, prolate or prolate-spherical in equatorial view, 4-aperturate (possibly an elongated variant of the hemi-tri-syncolporate pollen present in *Thinouia*), 2 colpi always diorate, striate; ovary 3-carpellate (Fig. 6E); style with 3 stigmatic branches. Fruit a schizocarp splitting into 3 mericarps with an elongated proximal wing (Fig. 5C); seeds lenticular, exarillate, with a small trigonous or ellipsoid hilum. Two species, one from Ecuador and Peru, the other from Bolivia. $2n = 28$.

Serjania Plum. ex Miller, Gard. Dic. Abrg. (ed. 4). 1754.—TYPE: *Serjania seriana* L.

Houssayanthus Hunziker, Kurtziana 11: 17. 1978.

Chimborazoa H.T. Beck, Brittonia 44: 306–311. 1994.

Balsas J. Jiménez Ramírez & K. Vega, Novon 21: 197. 2011.

Duodichogamous woody or herbaceous vines, often producing milky sap. Cross section of stem with a single or with a central vascular cylinder and (1–2)3–10 peripheral vascular cylinders. Leaves ternately compound (trifoliolate, biternate, or triternate) or 5-pinnately compound; stipules generally small, persistent, deciduous or ephemeral. Thyrse axillary and solitary with a pair of tendrils at the base of the rachis, or distal, aggregated into terminal syn-florescenses bearing no tendrils. Flowers in lateral cincinni, zygomorphic; sepals 4–5, unequal, imbricate; petals 4, with a basal, hood-shaped, crested appendage; disc unilateral, 2- or 4-lobed; stamens 8, filaments of unequal lengths, anthers dorsifixed; pollen heteropolar, obtusely triangular in polar view, oblate in equatorial view, hemi-tri-syncolporate proximally, sometimes with short distal demicolpi as well, perforate, reticulate, psilate or faintly rugulate (Fig. 6D); ovary 3-carpellate; style with 3 stigmatic branches. Fruit schizocarpic, splitting into three, winged mericarps (Fig. 5B) [wing proximal, sometimes vestigial or

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lacking (e.g. *S. lachnocarpa* (Radlk.) Acev.-Rodr., *S. cissoides* Radlk.), or less often circumferential (e.g. *S. biternata*, *S. dissecta* and *S. macrolopha*)], or fruits sometimes capsular by dissolution of septa (i.e. *S. cristobaliae*, *S. guerrerensis*, *S. tortuosa*); seeds lenticular to nearly globose, exarillate, with a small trigonous or ellipsoid hilum or sometimes with a pseudo-hilum (e.g. *S. glabrata* Kunth). About 230 species native to tropical and subtropical America. $2n = 24$.

***New Combinations*—**

Serjania biternata (Weath.) Acev.-Rodr., comb. nov.; *Urvillea biternata* Weath., Proc. Amer. Acad. Arts 45: 425. 1910.

Serjania cristobaliae (Ferrucci & Urdampilleta) Ferrucci & Steinmann, comb. nov.; *Cardiospermum cristobaliae* Ferrucci & Urdampilleta, Brittonia 63: 479. 2011.

Fruits in this species are apparently dehiscent (along the connection of the fruit wall to the partitioning wall), with flattened, circumferential winged locules; seeds lack a pseudo-hilum.

Serjania dissecta (S. Watson) Ferrucci & Steinmann, comb. nov.; *Urvillea dissecta* S. Watson, Proc. Amer. Acad. Arts 21: 447. 1886.

Serjania guerrerensis (Cruz Durán & K. Vega) Acev.-Rodr., comb. nov.; *Balsas guerrerensis* Cruz Durán & K. Vega, Novon 21: 199. 2011.

Serjania macrolopha (Radlk.) Acev.-Rodr. & Ferrucci, comb. nov.; *Cardiospermum macrolophum* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 261. 1878.

Serjania serjanioides (Rzed. & Calderón) Acev.-Rodr., comb. nov.; *Houssayanthus serjanioides* Rzed. & Calderón, Acta Bot. Mex. 76: 91. 2006.

Serjania sonorensis (S. Watson) Ferrucci & Steinmann, comb. nov.; *Paullinia sonorensis* S. Watson, Proc. Amer. Acad. Arts 24: 45. 1889.

Serjania spinosa (Radlk.) Ferrucci & Steinmann, comb. nov.; *Cardiospermum spinosum* Radlk., Contr. U. S. Natl. Herb. 1: 368. 1895.

Serjania tortuosa (Benth.) Ferrucci & Steinmann, comb. nov.; *Cardiospermum tortuosum* Benth., Bot. Voy. Sulphur 1: 9. 1844.

Urvillea Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. Pl. 5: 105. 1821.—TYPE: *Urvillea ulmacea* Kunth

Duodichogamous, herbaceous to woody vines. Stems terete and lenticellate, becoming trilobate at age, with a single vascular cylinder, producing milky or watery sap. Leaves trifoliolate; stipules minute, persistent or deciduous. Inflorescences axillary, thyrses with flowers in cincinni; pedicels articulate. Flowers zygomorphic; sepals 5, unequal, imbricate; petals 4, spatulate, with a basal hood-shaped, crested appendage on adaxial surface; disc unilateral, 4-lobed, receptacle enlarged into a short androgynophore; stamens 8; pollen heteropolar, obtusely triangular in polar view, oblate in equatorial view, hemi-tri-syncolporate proximally, sometimes with short distal demicolpi, perforate, indistinctly rugulate or reticulate; ovary 3-carpellate; style with 3 stigmatic branches. Fruit a 3-locular, thin, papery, semi-inflated capsule, mericarps flattened into a wing along dorsal margin (Fig. 5d); seeds 3 or 1, trigonous-ellipsoid, with a heart-shaped or reniform, white pseudo-hilum. About 21 species distributed in the United States (Texas), Mexico, Central America and South America. $2n = 20, 22, 24, 88$ (Urdampilleta et al. 2008b).

***New Combinations*—**

Urvillea cuchujaquensis (Ferrucci & Acev.-Rodr.) Acev.-Rodr. & Ferrucci, comb. nov.; *Cardiospermum cuchujaquense* Ferrucci & Acev.-Rodr., Novon 8: 235. 1998.

Urvillea oliveirae (Ferrucci) Acev.-Rodr. & Ferrucci, comb. nov.; *Cardiospermum oliveirae* Ferrucci, Bol. Soc. Argent. Bot. 24: 116. 1985.

Urvillea procumbens (Radlk.) Acev.-Rodr. & Ferrucci, comb. nov.; *Cardiospermum procumbens* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 262. 1878.

Urvillea pterocarpa (Radlk.) Acev.-Rodr. & Ferrucci, comb. nov.; *Cardiospermum pterocarpum* Radlk., Bull. Herb. Boissier II, 3: 806. 1903.

Cardiospermum L., Sp. Pl. 366. 1753.—TYPE: *Cardiospermum halicacabum* L.

Duodichogamous herbaceous vines. Leaves trifoliolate or biternate; stipules usually minute and persistent. Inflorescences simple, axillary, racemiform or umbelliform thyrses bearing tendrils at base of rachis, with flowers in cincinni. Flowers zygomorphic; sepals 4(5), unequal, imbricate; petals 4, with a basal, hood-shaped, crested appendage; disc unilateral, 2- or 4-lobed; stamens 8, filaments of unequal lengths, anthers dorsifixed; pollen heteropolar, obtusely triangular in polar view, oblate in equatorial view, tri-syncolporate proximally, perforate to reticulate (Fig. 6B); ovary 3-carpellate; style with 3 stigmatic branches. Fruit a 3-locular septifragal-marginicidal, inflated capsule, generally with subchartaceous walls; seeds brown or black, with a small, round to heart-shaped, light-colored area around the hilum (pseudo-hilum sensu Pijl 1957; Fig. 8D). Six or seven species native to the Neotropics, one of which is also native in Africa, and 2 that are now widely distributed throughout the tropics. $2n = 14, 18, 20, 22, 36$.

Paullinia L., Sp. Pl. 365. 1753. —TYPE: *Paullinia pinnata* L.

Duodichogamous, woody vines, usually producing milky sap. Cross section of stem with a central and 3–5 peripheral vascular cylinders, or with a single vascular cylinder. Leaves trifoliolate, 5-foliolate pinnate, partly bipinnate, bipinnate, biternate, or variously dissected; stipules minute to foliaceous. Inflorescences axillary, solitary or fascicled thyrses, with a pair of tendrils at base of rachis when solitary, sometimes cauliflorous and fascicled and bearing no tendrils. Flowers zygomorphic; sepals 4–5, unequal, imbricate; petals 4, with a basal, hood-shaped, crested appendage; disc unilateral, 2- or 4-lobed; stamens 8, filaments of unequal lengths, anthers dorsifixed; pollen isopolar or subisopolar, obtusely triangular in polar view, oblate in equatorial view, triporate, perforate (Fig. 6C); ovary 3-carpellate; style with 3 stigmatic branches. Fruit a 1–3-locular, septifragal-marginicidal capsule, locules sometimes dorsally winged or exceptionally spiny; seeds globose, oblong or ellipsoid, with a partial to nearly complete sarcotesta, leaving a scar when removed (Figs. 7C,

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8A–B). About 200 species native to the Neotropics, one species extending into Africa and Madagascar. 2*n* = 24, 210 (de Freitas et al. 2007).

Placement Pending—

Guindilia Gillies ex Hook. & Arn., Hooker's Bot. Misc. 3: 170. 1833. —TYPE: *Guindilia trinervis* Gillies ex Hook. & Arn.

Valenzuelia Bertero ex Cambessèdes, Nouv. Ann. Mus. Hist. Nat. 3: 236. 1834, non Mutis, 1810.

Duodichogamous trees. Leaves simple, opposite, entire or tridentate at apex, exstipulate. Inflorescences of axillary cymes. Flowers zygomorphic, bisexual or functionally unisexual; sepals 5, imbricate; petals 4(5), with a hood-shaped, crested, ventral appendage; disk unilateral, 2-lobed-pyramidal; stamens 8; pollen colporate, striate (Fig. 4F); ovary 3-carpellate, with a single ovule per carpel; style filiform; stigma 3-lobed. Fruit schizocarpic, splitting into (1–)3 subglobose, crustose mericarps. Seed exarillate. Three species from southern South America.

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Appendix 1. Voucher and GenBank information for taxa included in the phylogenetic analyses. Listed as: taxon, collection, herbarium, place of origin, and GenBank accession numbers (ITS, *trnL* intron). Herbarium acronyms follow Index Herbariorum (Thiers, continuously updated). Accession numbers for new data begin with KX; an en-dash (–) indicates missing data.

Allophylastrum frutescens Acev.-Rodr., *Lima 812* (K), Brazil, KX584885, KX584982. *Allophylus abyssinicus* (Hochst.) Radlk., *Desissa & Binggeli DD-318* (MO), Ethiopia, KX584886, KX584983. *Allophylus africanus* P. Beauv., *Balkwill 4206* (MO), South Africa, KX584887, KX584984. *Allophylus arboreus* Choux, *Wohlhauser & Stiefle 60072* (MO), Madagascar, KX584888, KX584985. *Allophylus bicruris* Radlk., *Barthelat 828* (MO), Mayotte, KX584889, KX584986. *Allophylus bojerianus* (Cambess.) Blume, *Ratovoson 961* (MO), Madagascar, KX584890, KX584987. *Allophylus chaunostachys* Gilg, *Mwangoko 729* (MO), Tanzania, KX584891, KX584988. *Allophylus chirindensis* Baker f., *Hizza 26* (MO), Tanzania, KX584892, KX584989. *Allophylus cominia* Sw., *Acevedo-Rodríguez 12216* (US), Mexico, KX584893, KX584990. *Allophylus crassinervis* Radlk., *Acevedo-Rodríguez s.n.* (no voucher), Puerto Rico, KX584894, KX584991. *Allophylus decipiens* (E. Mey.) Radlk., *Phillipson 4194* (MO), South Africa, KX584895, KX584992. *Allophylus dissectus* Gereau & G.E. Schatz, *Phillipson 1704* (MO), Madagascar, KX584896, KX584993. *Allophylus gardineri* Summerh., *Pignal 1834* (MO), Mayotte, KX584897, KX584994. *Allophylus hirtellus* (Hook. f.) Radlk., *Cheek 5059* (?), KX584898, KX584995. *Allophylus pervillei* Blume, *Hoffmann 399* (MO), Mayotte, KX584899, KX584996. *Allophylus poungouensis* Pellegr., *McPherson 16109* (MO), Gabon, KX584900, KX584997. *Allophylus puberulus* (Cambess.) Radlk., *Somner 1069* (US), Brazil, KX584901, KX584998. *Allophylus racemosus* Sw., *Acevedo-Rodríguez 12180* (US), Mexico, KX584902, KX584999. *Allophylus rubifolius* (A. Rich.) Engl., *Kuchar 23357* (MO), Tanzania, KX584903, KX585000. *Allophylus* sp., *Acevedo-Rodríguez 14847* (NY), Brazil, KX584904, KX585001. *Allophylus sp., Barthelat 1540* (MO), Mayotte, KX584905, KX585002. *Athyana weinmanniifolia* (Griseb.) Radlk., *Acevedo-Rodríguez 11166* (US), Bolivia, KX584906, KX585003. *Athyana weinmanniifolia* (Griseb.) Radlk., *Villalobos 4243* (MO), Bolivia, KX584907, KX585004. *Balsas guerrerensis* Cruz Durán & K. Vega, *Vega Flores 1318* (US), Mexico, KX584908, KX585005. *Blomia prisca* (Standl.) Lundell, *Acevedo-Rodríguez 12242* (US), Mexico, EU720444, EU721208. *Bridgesia incisifolia* Cambess., *Landrum 9824* (NY), Chile, KX584909, KX585006. *Cardiospermum anomalum* Cambess., *Urdampilleta 330* (UEC), Brazil, KX584910, —. *Cardiospermum bahianum* Ferrucci & Urdampilleta, *Urdampilleta 389* (UEC), Brazil, KX584911, —. *Cardiospermum corindum* L., *Harder & Bringham 3495* (MO), Zambia, KX584912, KX585007. *Cardiospermum corindum* L., *JLR291* (?), KM062239, KM062345. *Cardiospermum cristobaliae* Ferrucci & Urdampilleta, *Urdampilleta 421* (UEC), Brazil, KX584913, —. *Cardiospermum cuchujaquense* Ferrucci & Acev.-Rodr., *Van Devender 92-1012* (ARIZ), Mexico, KX584914, KX585008. *Cardiospermum grandiflorum* Sw., *ATBP 603* (MO), Uganda, KX584915, KX585009. *Cardiospermum grandiflorum* Sw., *Gildenhuys H1* (?), Hawaii, KM062277, KM062362. *Cardiospermum halicacabum* L., *Gildenhuys 280* (?), Argentina, KM062192, KM062341. *Cardiospermum halicacabum* L., *CSM 8* (?), South Africa, KM062194, KM062296. *Cardiospermum halicacabum* L., *Murata 72327* (MO), Japan, KX584916, —. *Cardiospermum heringeri* Ferrucci, *Urdampilleta 437* (US), Brazil, KX584917, KX585010. *Cardiospermum integerrimum* Radlk., *Urdampilleta 312* (UEC), Brazil, KJ845651, —. *Cardiospermum integerrimum* Radlk., *Urdampilleta 312* (US), Brazil, KX584918, KX585011. *Cardiospermum oliveirae* Ferrucci, *Urdampilleta 337* (UEC), Brazil, KX584919, — *Cardiospermum pechuelii* Kuntze, *Gildenhuys s.n.*, Namibia, KM062216, KM062299. *Cardiospermum procumbens* Radlk., *Urdampilleta 322* (UEC), Brazil, KX584920, —. *Cardiospermum pterocarpum* Radlk., *Urdampilleta 321* (US), Brazil, KX584921, KX585012. *Cardiospermum urvilleoides* (Radlk.) Ferrucci, *Urdampilleta 425* (US), Brazil, KX584922, KX585013. *Chimborazoa lachnocarpa* (Radlk.) H.T. Beck, *Wiggens 11060* (US), Ecuador, KX584923, KX585014. *Cupania dentata* DC., *Acevedo-Rodríguez 12241* (US), Mexico, KX584924, KX585015. *Cupania emarginata* Cambess., *Somner1068* (RBR),

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Brazil, KX584925, KX585016. *Diatenopteryx sorbifolia* Radlk., *Zardini 43371* (MO), Paraguay, EU720534, EU721303. *Dictyoneura obtusa* Blume, *Edwards KE142* (JCT), Australia, EU720428, EU721187. *Diploglottis campbellii* Cheel, *Chase 2048* (K), Australia, EU720457, EU721224. *Elattostachys apetala* Radlk., *Munzinger 692* (MO), New Caledonia, EU720537, EU721306. *Guindilia dissecta* (C. & Burk.) Hunz., *Ferrucci 2928* (CTES), Argentina, KX584926, KX585017. *Guioa villosa* Radlk., *McPherson 18040* (MO), New Caledonia, EU720544, EU721314. *Haplocoelum foliosum* (Hiern.) Bullock, *Edwards KE195* (JCT), Tanzania, FJ514259, FJ514265. *Haplocoelum inoploeum* Radlk., *Lap 117* (?), FJ514259, FJ514265. *Houssayanthus biternatus* (Weath) Rzed. & Calderón, *Catalán & Terán 837* (MO), Mexico, KX584927, KX585018. *Houssayanthus incanus* (Radlk.) Ferrucci, *Ferrucci 2710* (CTES), Argentina, KX584928, KX585019. *Jagera javanica* (Blume) Kalkman, *Chase 2130* (K), Bogor, EU721236, EU720468. *Lepisanthes senegalensis* (Poir.) Leenh., *Callmander 627* (MO), Madagascar, EU720492, U72126. *Lophostigma plumosum* Radlk., *Acevedo-Rodríguez 6554* (US), Bolivia, KX584929, KX585020. *Macphersonia gracilis* O. Hoffm., *Rabenantoandro 1081* (MO), Madagascar, EU720550, EU721320. *Matayba guianensis* Aubl., *Acevedo-Rodríguez 12342* (US), French Guiana, EU720527, EU721294. *Melicoccus bijugatus* Jacq., *Acevedo-Rodríguez, no voucher*, Puerto Rico, EU927391, EU721207. *Melicoccus lepidopetalus* Radlk., *Acevedo-Rodríguez 11128* (US), Bolivia, EU720443, EU721206. *Paullinia clathrata* Radlk., *Acevedo-Rodríguez 14305* (US), Peru, KX584930, KX585021. *Paullinia coriacea* Casar., *Somner 1070* (RBR), Brazil, KX584931, KX585022. *Paullinia cuneata* Radlk., *Acevedo-Rodríguez 14255* (US), Peru, KX584932, KX585023. *Paullinia elegans* Cambess., *Acevedo-Rodríguez 14976* (US), Brazil, KX584933, KX585024. *Paullinia hystrix* Radlk., *Acevedo-Rodríguez 14417* (US), Peru, KX584934, KX585025. *Paullinia imberbis* Radlk., *Schunke Vigo 14928* (US), Peru, KX584935, KX585026. *Paullinia olivacea* Radlk., *Schunke Vigo 16002* (US), Peru, KX584936, KX585027. *Paullinia pinnata* L., *Acevedo-Rodríguez 11088* (US), French Guiana, KX584937, KX585028. *Paullinia prevostiana* Acev.-Rodr., *Acevedo-Rodríguez 11113* (US), French Guiana, KX584938, KX585029. *Paullinia rubiginosa* Cambess., *Thomas 12995* (US), Brazil, KX584939, KX585030. *Paullinia rufescens* Rich., *Acevedo-Rodríguez 12350* (US), French Guiana, KX584940, KX585031. *Paullinia spicata* Benth., *Acevedo-Rodríguez 12344* (US), French Guiana, KX584941, KX585032. *Paullinia stellata* Radlk., *Acevedo-Rodríguez 14958* (US), Brazil, KX584942, KX585033. *Paullinia xestophylla* Radlk., *Hoffman 5955* (US), Suriname, KX584943, KX585034. *Plagioscyphus unijugatus* Capuron, *Buerki 145* (NEU), Madagascar, EU720475, EU721245. *Sapindus oligophyllus* Merr. & Chun, *How 70627* (US), China, KX584944, KX585035. *Serjania altissima* (Poepp.) Radlk., *Acevedo-Rodríguez 14953* (US), Brazil, KX584945, KX585036. *Serjania ampelopsis* Planch. & Lind., *Acevedo-Rodríguez 11181* (US), Bolivia, KX584946, KX585037. *Serjania caracasana* (Jacq.) Willd., *Acevedo-Rodríguez 15107* (US), Mexico, KX584947, KX585038. *Serjania* cf. *caracasana* (Jacq.) Willd., *Acevedo-Rodríguez 3483* (US), Guyana, KX584948, KX585039. *Serjania clematidifolia* Cambess., *Somner 1078* (RBR), Brazil, KX584949, KX585040. *Serjania communis* Cambess., *Somner 1334* (US), Brazil, KX584950, KX585041. *Serjania cuspidata* Cambess., *Somner 1400* (US), Brazil, KX584951, KX585042. *Serjania diversifolia* (Jacq.) Radlk., *Acevedo-Rodríguez 13462* (US), Puerto Rico, KX584952, —. *Serjania elongata* J.F. Macbr., *Acevedo-Rodríguez 13547* (US), Brazil, KX584953, —. *Serjania emarginata* Kunth, *Acevedo-Rodríguez 15135* (US), Mexico, KX584954, KX585043. *Serjania erythrocaulis* Acev.-Rodr. & Somner, *Acevedo-Rodríguez* 3729 (US), Brazil, KX584955, KX585044. *Serjania eucardia* Radlk., *Somner 1072* (RBR), Brazil, KX584956, KX585045. *Serjania fuscifolia* Radlk., *Somner 1455* (RBR), Brazil, KX584957, KX585046. *Serjania grandiceps* Radlk., *Acevedo-Rodríguez 13704* (US), Brazil, KX584958, KX585047. *Serjania grandifolia* Sagot, *Acevedo-Rodríguez 11121* (US), French Guiana, KX584959, —. *Serjania ichthyoctona* Radlk., *Somner 1081* (RBR), Brazil, KX584960, KX585048. *Serjania lethalis* St. Hil., *Roque 1860* (ALCB), Brazil, KX584961, KX585049. *Serjania lethalis* St. Hil., *Somner 1381* (RBR), Brazil, KX584962, KX585050. *Serjania marginata* Casar., *Acevedo-Rodríguez 11131* (US), Bolivia, KX584963, KX585051. *Serjania membranacea* Splitg., *Acevedo-Rodríguez 12329* (US), French Guiana, KX584964, —. *Serjania mexicana* (L.) Willd., *Acevedo-Rodríguez 12014* (US), Jamaica, KX584965, KX585052. *Serjania mexicana* (L.) Willd., *Acevedo-Rodríguez 15080* (US), Mexico, KX584966, KX585053. *Serjania paniculata* Kunth, *Acevedo-Rodríguez 15143* (US), Mexico, KX584967, KX585054. *Serjania perulacea* Radlk., *Acevedo-Rodríguez 11134* (US), Bolivia, KX584968, KX585055. *Serjania unguiculata* Radlk., *Acevedo-Rodríguez 15081* (US), Mexico, KX584969, KX585056. *Serjania yucatanensis* Standl., *Acevedo-Rodríguez 12183* (US), Mexico, KX584970, KX585057. *Talisia angustifolia* Radlk., *Zardini 43368* (MO), Paraguay, EU720558, EU721516. *Talisia nervosa* Radlk., *Pennington 628* (MO), ~, EU720474, EU721244. *Talisia obovata* A.C. Sm., *Lombello 13* (MO), Brazil, EU720485, EU721255. *Thinouia mucronata* Radlk., *Keller 6919* (US), Argentina, KX584971, KX585058. *Thinouia myriantha* Triana & Planch. *Acevedo-Rodríguez 12359* (US), French Guiana, —, KX585059. *Thinouia restingae* Ferrucci & Somner, *Somner 1074* (RBR), Brazil, KX584972, KX585060. *Thouinia acuminata* S. Watson, *Liston 633-2*, —, EU720478, EU721249. *Thouinia paucidentata* Radlk., *Acevedo-Rodríguez* 12160 (US), Mexico, KX584973, —. *Thouinia portoricensis* Radlk., *Acevedo-Rodríguez* 11435 (US), Puerto Rico, KX584974, —. *Thouinia tomentosa* DC., *Acevedo-Rodríguez* 12867 (US), Dominican Republic, —, KX585061. *Thouinia villosa* DC., *Hall 825* (US), Mexico, KX584975, KX585062. *Tristiropsis acutangula* Radlk., *Chase 1358* (K), Bogor, EU720453, EU721220. *Urvillea chacoensis* Hunz., *Acevedo-Rodríguez 11133* (US), Bolivia, KX584976, KX585063. *Urvillea chacoensis* Hunz., *Keller 6834* (US), Argentina, KX584977, KX585064. *Urvillea rufescens* Cambess., *Somner 1073* (RBR), Brazil, KX584978, KX585065. *Urvillea ulmacea* Kunth, *Acevedo-Rodríguez 15145* (US), Mexico, KX584979, KX585066. *Urvillea ulmacea* Kunth, *Reyes-García 5585* (MO), Mexico, KX584980, KX585067. *Vouarana guianensis* Aubl., *Acevedo-Rodríguez 5031* (US), French Guiana, KX584981, KX585068.

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