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RECLASSIFICATION OF THE BERTHOLLETIA CLADE OF THE BRAZIL NUT FAMILY (LECYTHIDACEAE) BASED ON A PHYLOGENETIC ANALYSIS OF PLASTOME AND TARGET SEQUENCE CAPTURE DATA

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Abstract. The Neotropical clade of Lecythidaceae—Lecythidoideae—comprises 10 genera and more than 230 woody species that are usually rainforest trees. Lecythidoideae range from Mexico to southeast Brazil but are most diverse and abundant in the central Amazon and Guiana Shield regions. Previous studies found weak support for monophyly in the two species rich Amazon-centered genera, *Eschweilera* and *Lecythis*, and ambiguous relationships within the Bertholletia clade (*Eschweilera*, *Lecythis*, *Bertholletia* and *Corythophora*). We performed a phylogenomic analysis of Lecythidoideae with focus on the Bertholletia clade, using target capture sequencing of 343 nuclear loci and 10 informative plastome regions. Our sampling included 206 individuals from 130 described Neotropical species and ca. 10 undescribed taxa. Our limited sampling outside the Bertholletia clade confirmed the monophyly of *Grias*, *Gustavia*, *Couroupita*, *Allantoma*, *Cariniana*, and *Couratari*. Within the Bertholletia clade, however, our work shows that *Lecythis* and *Eschweilera*, as currently circumscribed, are polyphyletic. To align Lecythidaceae taxonomy with phylogeny, we propose six genus name changes within the former *Lecythis* and *Eschweilera*. Our new circumscription maintains the core *Lecythis* (Ollaria clade) and *Eschweilera* (Parvifolia clade). For the clade comprising the Poiteau and Chartacea sections of *Lecythis* we reinstate *Chytroma* Miers. For the former Pisonis section of *Lecythis* we reinstate *Pachylecythis* Ledoux. For the former Tetrapetala section of *Eschweilera* we propose *Imbiriba gen. nov*. For the Corrugata clade (formerly of *Lecythis*) we propose *Guaiania gen. nov*. We propose to elevate the Integrifolia clade of *Eschweilera* as a new genus, *Scottmoria gen. nov*. We determined that the Manaus-area endemic, *Eschweilera amazoniciformis*, is an isolated sister lineage to *Corythophora* and *Imbiriba*. We recognize this species as the monotypic genus *Waimiria gen. nov*. Our proposal for taxonomic changes highlights distinct evolutionary histories and eliminates paraphyletic and polyphyletic genera, resulting in 60 name changes for species or subspecies.

Keywords: Bertholletia clade, Ericales, *Eschweilera*, phylogenomics, *Lecythis*, Neotropics, tropical rainforest

Lecythidaceae is a pantropical family of woody plants belonging to the order Ericales. It is classified into either five (APG IV, 2016) or three (Huang et al., 2015, Mori et al., 2017) subfamilies. In the latter classification, used here, Napoleonaeoideae and Scytopetaloideae are considered families, leaving Lecythidaceae with three subfamilies: Foetidioideae (predominantly in Madagascar), Barringtonioideae (synonym: Planchonioideae; Asia and Africa), and Lecythidoideae (Neotropics). Lecythidoideae is the most species-rich subfamily containing ca. 230 species (Mori et al., 2017) out of the ca. 278 known species in the family (Mori et al., 2007; Huang et al., 2015; Mori et al., 2017) with several new species described each year.

Lecythidoideae are understory, canopy, and emergent trees with distinctive woody fruits and often highly specialized zygomorphic flowers (Prance and Mori, 1979;

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Mori and Prance, 1990). Lecythidaceae are ranked as the third most abundant family of trees in Amazonian forests based on forest inventory data (ter Steege et al., 2013) with *Eschweilera* Mart. ex DC. and *Eschweilera coriacea* (DC.) S.A. Mori being the most common Amazon tree genus and species, respectively (ter Steege et al., 2013). In addition to their large role in carbon sequestration, Lecythidaceae host diverse interactions with animals: bees and bats pollinate their flowers, and the seeds are dispersed by rodents, birds, monkeys, bats, and fish (Prance and Mori, 1979; Mori and Prance, 1990). The family includes economically important timber trees (e.g., *Cariniana legalis* (Mart.) Kuntze), foods (e.g., Brazil nut, *Bertholletia excelsa* Bonpl.), ornamentals (e.g., cannonball tree, *Couroupita guianensis* Aubl.), and some of the longest-lived rain forest trees, with individual trees of *Cariniana micrantha* Ducke near Manaus, Brazil, estimated via carbon dating to be more than 1400 years old (Chambers et al., 1998). In the Amazon and Orinoco river basins, the inner bark of several species of Lecythidaceae, e.g., *Eschweilera subglandulosa* (Steud. ex O. Berg) Miers and *Lecythis alutacea* (A.C. Sm.) S.A. Mori (*J. A. Steyermark* 60767), are an ancestral source of cordage and head bands, and that of others, e.g., *Allantoma lineata* (Mart. ex O. Berg) Miers and *Couratari guianensis*, as a source of cigarette paper (Mori et al., 2010 and onwards), called *Tabarí* (Mori and Prance, 1999).

The classification of Lecythidoideae is relatively stable thanks to the comprehensive monographs published by Prance and Mori (1979) and Mori and Prance (1990). The incorporation of molecular phylogenetics using chloroplast markers and the internal transcribed spacer (ITS) confirmed Lecythidoideae as monophyletic and sister to the other two subfamilies (Mori et al., 2007). Molecular phylogenies also grouped several zygomorphic-flowered genera (*Eschweilera*, *Lecythis* Loefl., *Corythophora* R. Knuth, and *Bertholletia* Bonpl.) into the Bertholletia clade, which is nested within a grade of actinomorphic-flowered (*Grias* L., *Gustavia* L., and *Allantoma* Miers) and zygomorphic-flowered genera (*Cariniana* Casar., *Couroupita* Aubl., and *Couratari* Aubl.) (Mori et al., 2007; Huang et al. 2015; Mori et al., 2017; Vargas and Dick, 2020). All prior molecular phylogenies have inferred monophyly for *Allantoma* (8 spp.), *Cariniana* (9 spp.), *Corythophora* (4 spp.), *Couroupita* (3 spp.), *Grias* (14 spp.), and *Gustavia* (47 spp.), while the large Amazon-centered genera *Eschweilera* (ca. 97 spp.) and *Lecythis* (ca. 31 spp.) have been inferred as polyphyletic (Mori et al., 2007; Huang et al., 2015; Mori et al., 2017; Vargas and Dick, 2020). Huang et al. (2015) recognized the need for a generic circumscription within the Bertholletia clade (see Table 1 for clade names) but refrained from making nomenclatural changes because relationships among the internal clades were largely unresolved.

The goal of this study was to resolve these uncertain phylogenetic relationships within Lecythidoideae, especially within the zygomorphic-flowered and Amazon-centered Bertholletia clade. We performed phylogenomic analyses using nuclear genomic dataset based on family-specific probes developed by Vargas et al. (2019) and plastome regions shown to be informative for the subfamily (Thomson et al., 2018). Based on sampling of 130 species (~57% of Lecythidoideae), we resolved the internal clades within *Lecythis* and *Eschweilera* and propose a circumscription of genera within the Bertholletia clade that better reflects phylogenetic relationships.

MATERIALS AND METHODS

Sampling

Although we sampled broadly from the Lecythidoideae, our greatest sampling efforts were focused on the Bertholletia clade from the central Amazon and Guiana Shield regions. We sampled a total of 206 individuals comprising 130 described Neotropical species and seven outgroup species (Table S1). NYBG provided about half of our samples from their silica-dried tissue collections, whose corresponding vouchers are at NYBG. Many of the NYBG collections came from an intensively studied forest in French Guiana (Mori, 1987). About a quarter of the samples come from recent collections within a forest inventory plot of Lecythidaceae trees known as the Lecythidaceae plot (Mori and Lepsch da Cunha, 1995) within Reserve 1501 (km 41) of the Biological Dynamics of Forest Fragments Project (BDFFP) 70 km north of Manaus, Brazil. We sampled multiple individuals for some species, especially within the *Eschweilera* Parvifolia clade, because of reports of hybridization (Caron et al., 2019; Larson et al., 2021). Within the Parvifolia clade, *E. coriacea* was of special interest because of its genetic and morphological variability and taxonomic uncertainty (Heuertz et al., 2020). Voucher specimens of new collections were deposited at the BDFFP reference collection and at INPA in Manaus. While most of the species sampled are represented by Latin binomials, we included undescribed species, indicated as "sp. nov" in the cladograms, and some samples with ambiguous identities are represented only by their sample code "sp." Most of these latter samples are recent collections by coauthors and have associated herbarium vouchers (Table S1).

DNA Sequencing

To infer robust nuclear- and plastome-based phylogenies for Lecythidoideae we sequenced 344 nuclear genes previously identified as phylogenetically informative (Vargas et al., 2019) and ten informative chloroplast regions through genome skimming (Thomson et al., 2018). We performed DNA extractions using the NucleoSpin Plant Mini Kit II (Macherey-Nagel, Düren, Germany) following the manufacturer's protocol but extending the digestion step to an hour and adding 5 uL of proteinase K (20 mg/mL, Qiagen). Library preparation and HiSeq4000 (Illumina Inc.) sequencing was performed by Rapid Genomics (Gainesville, Florida) for samples with 100–1000 ng of DNA. Sequencing of bait enriched libraries (for the nuclear data) and un-enriched ones (for the plastome data) were performed independently. Our sequencing output comprised paired end reads of 150 bp that were processed with SeqyClean (Zhbannikov et al., 2017), removing low-quality reads and adaptors, and trimming read sections with a Phred score < 20 using a window of 10 bp. Sequence data are available from NCBI Bioproject PRJNA641333 in GenBank.

TABLE 1. Clades within the Bertholletia clade that we propose to recognize as distinct genera (Col. 1) are from Huang et al. (2015) with the exception of *E. amazoniciformis*. In column 3 we provide our justification for the revised classification.

GENUS AND PRIOR CLADE OR SECTION NAME	PROPOSED CHANGE	JUSTIFICATION OF NAME CHANGE
Lecythis Pisonis clade	*Pachylecythis* Ledoux	The Pisonis clade is polyphyletic in relation to core *Lecythis*.
Lecythis Poiteauii clade Chartacea clade	*Chytroma* Miers	The sister clades are polyphyletic in relation to core *Lecythis*. There is insufficient morphological variation to justify separating the clades into two genera.
Eschweilera *E. amazoniciformis* S. A. Mori	*Waimiria* C.W. Dick & O.M. Vargas *gen. nov*.	The species *E. amazoniciformis* is morphologically distinctive and polyphyletic with respect to other subclades of *Eschweilera s.l.*
Lecythis Corrugata clade	*Guaiania* O.M. Vargas & C.W. Dick *gen. nov*.	The Corrugata clade is polyphyletic in relation to core *Lecythis*.
Eschweilera Tetrapetala clade	*Imbiriba* O.M. Vargas, M. Ribeiro, & C.W. Dick *gen. nov*.	The Tetrapetala clade is polyphyletic in relation to core *Eschweilera*.
Eschweilera Integrifolia clade	*Scottmoria* Cornejo *gen. nov*.	This clade could be combined with core *Eschweilera*, but its distinctive morphology combined with the mostly Pacific pattern of distribution justify its elevation to genus.

Nuclear DNA Phylogeny

We employed HybPiper v1.3.1 (Johnson et al., 2016) to assemble the 344 target genes, of which we dropped one gene because of unsuccessful assembly. The Hybpiper pipeline uses Exonerate (Slater and Birney, 2005), BLAST+ (Camacho et al., 2009), Biopython (Cock et al., 2009), BWA (Li and Durbin, 2009), SAMtools (Li et al., 2009), GNU Parallel (Tange, 2011), and SPAdes (Bankevich et al., 2012) as dependencies. For each gene we aligned exons and introns independently and employed an exhaustive algorithm (linsi, 1k iterations) in Mafft v7.407 (Katoh and Standley, 2013). For the 39 introns for which the exhaustive alignment failed, a less exhaustive algorithm (fftnsi,1k iterations) was implemented (Table S2). Subsequently, exon and intron matrices were concatenated by gene, and these alignments were filtered with trimAl v1.4.rev22 (Capella-Gutiérrez et al., 2009) for problematic regions using the "-automated1" command, and for outlier sequences using the "-resoverlap 0.33 -seqoverlap 75" command. We employed RAxML v8.2.12 (Stamatakis, 2014) to calculate our 343 gene trees; exons and introns were treated as independent partitions. In order to identify taxa bearing extreme long branches, we employed TREESHRINK "-q 0.05" (Mai and Mirabab, 2018) for every gene tree produced by the RAxML per-gene analysis. We concatenated the 343 genes into a single matrix after removing the outlier taxa per-gene identified by THREESHRINK. We used the concatenated alignment to infer a species tree (referred from now onwards as the concatenated tree). We used ASTRAL v.5.6.3 (Zhang et al., 2018) to calculate a maximum quartet support species tree (MQSST), using trees pruned from outlier taxa identified with THREESHRINK and with nodes collapsed when bootstrap support was < 60%. We calculated the number of genes supporting every node on the RAxML concatenated tree using phyparts (Smith et al., 2015). The results were illustrated with phypartspiecharts.py (https://github.com/mossmatters/MJPythonNotebooks).

Chloroplast phylogeny

We generated a plastome phylogeny using a supermatrix consisting of 10 chloroplast regions: *ccs*A-*ndh*D, *rpl*16-*rps*3, *psb*M-*trn*D, *trn*G-*psa*B, *pet*D-*rpo*A, *psb*Z-*trnf*M, *trn*E-*trn*T, *trn*T-*psb*D and two segments of *ycf*1. These regions were identified as phylogenetically informative in a previous analysis of 24 Lecythidaceae chloroplast genomes (Thomson et al., 2018). To generate the sequences, a draft plastome was assembled for each sample using raw reads and GetOrganelle (Jin et al., 2020) with the options "-R 15 -k 21,45,65,85,105" and "-F embplant_pt" (Camacho et al., 2009; Bankevich et al., 2012; Langmead and Salzberg, 2012). In cases where multiple possible structural configurations were recovered, the first configuration was used. All contigs per assembly were merged prior to analysis. Each of the target regions were identified in one draft assembly (L289; Table S1) by using the primers reported in Thomson et al. (2018). We then identified the target regions in each of the other draft assemblies by conducting a BLAST search (Altschul et al., 1990; Camacho et al., 2009) for each region using an e-value cutoff of $1x10^{-3}$ and extracted the top hit, including bases that matched to the primers, with a custom script. We aligned sequences for each region with MAFFT v7.490 and the options "-genafpair," "-maxiterate 1000," and "-adjustdirectionaccurately." Alignments were each visually inspected for evidence of misidentified homology or other issues and primers were removed from each alignment. We also masked 10 columns of the *ccs*A-*ndh*D alignment because of suspected assembly issues and removed the last 394 columns of the *psb*Z-*trnf*M alignment because we found that it exactly matched the beginning of the *trn*G-*psa*B region. Sites with less than 50% matrix occupancy were removed with pxclsq and the 10 regions were concatenated with the program pxcat in phyx (Brown et al., 2017). An ML tree and 200 standard, non-parametric bootstraps were estimated with RAxML v8.2.11, with a single GTRCAT model partition. Conflict with the nuclear tree was assessed using the pxbp program in phyx and visualized with Figtree (http://tree.bio.ed.ac.uk/software/figtree/).

Taxonomic Circumscription

We obtained taxonomic information (e.g., accepted names, type specimen information, diagnostic characters, and specialized morphological terms) from Mori and Prance (1990) and from the Lecythidaceae Pages (Mori et al., 2010 and onward), which is an online resource maintained by the New York Botanical Garden. For nomenclatural changes at the genus level, we prioritized available names within the clade of interest, following rules of the International Code of Nomenclature (Turland et al., 2018). If there were no available generic names within a clade, we assigned a new name and provided an etymological justification. We consulted the International Plant Names Index (IPNI, 2020) for standardized taxonomic author names. We only provide synonyms if widely used; a full list of synonyms for each species is available on the Lecythidaceae Pages. We did not sample DNA from all of the new combinations. The assignment of unsampled species to a clade was based on their subgeneric classification (e.g., sections) as recognized by Mori and Prance (1990) and Mori et al. (2010 and onward). Our proposed nomenclature follows suggestions outlined by Huang et al. (2015) except in cases in which our data supported different phylogenetic relationships.

Results

Nuclear dataset

We obtained sequence data for 343 of the 344 targeted gene regions. On average, we recovered 321 regions per sample, with a maximum of 338 and minimum of 130 (Table S1). A concatenated alignment of all 343 nuclear gene regions generated 1,702,870 columns with a cell occupancy of 93.3%, with 285,682 parsimony-informative characters. We inferred a concatenated- and a coalescent-consistent topology (Fig. 1, S1); both topologies are robust with the majority of their nodes having high bootstrap support and posterior probabilities, respectively. Both trees are virtually identical regarding the relationships of genera and the major clades within Lecythidoideae. *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari* are monophyletic with full support in both phylogenies. *Eschweilera* and *Lecythis* are polyphyletic in both topologies, in agreement with previous studies (Huang et al. 2015). Both trees show the same relationships among the major clades (Pisonis, Ollaria, Poiteau, Chartacea, *Corythophora,* Tetrapetala, Corrugata, Integrifolia, Parvifolia) described by previous studies (Huang et al., 2015). We infer monophyly for the Bertholletia clade and for the first time recover high support for the polyphyly of *Eschweilera* and *Lecythis,* which confirms the results of Huang et al. (2015) and justifies recircumscribing both genera.

Corythophora's monophyly is the only exception to the congruence between the backbone topologies of the concatenated and the coalescent-consistent analyses. *Corythophora alta* R. Knuth (bearing a long branch) is sister to a clade composed of the remaining sampled *Corytophora* species and the *Eschweilera* Tetrapetala clade in the concatenated topology, rendering *Corythophora* paraphyletic; while *C. alta* is sister to the Bertholletia clade in the coalescent-consistent topology, making *Corythophora* polyphyletic.

Considering the high level of congruence between the two topologies and the finding that many gene-trees present too little phylogenetic signal to inform shallow relationships (Fig. S2), we selected the concatenated topology—with all the phylogenetic signal analyzed in a single matrix—as the best hypothesis representing the relationships among Neotropical Lecythidaceae. Therefore, from this point forward we will focus our results and discussion in the nuclear concatenated topology, which we refer to as the "nuclear tree."

Our nuclear tree suggests that *Eschweilera s.l.* contains two main clades (Tetrapetala and Integrifolia+Parvifolia), with *E. amazoniciformis* S.A. Mori outside of these two clades and sister to a clade composed of *Corythophora* and the Tetrapetala clade (Fig. 1). *Lecythis* s.l. comprises three main clades (Pisonis, Poiteaui+Chartacea, and Corrugata clades), with *L. minor* Jacq. outside of these three clades and sister to the clade composed of all members of the Bertholletia clade minus the Pisonis clade (Fig. 1).

The majority of the nuclear tree was fully supported by bootstrapping (Fig. 1). There was 100% bootstrap support along the backbone phylogeny with the exception of nodes inside the Parvifolia clade. Bootstrapping also fully supported the monophyly of the genera *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari*, and the monophyly of the clades Pisonis, Poiteaui, Chartacea, Tetrapelata, Corrugata, Integrifolia, and Parvifolia. *Corythophora* was paraphyletic, and we only sampled one species in the Ollaria clade and therefore cannot evaluate its monophyly. Support by gene was high for *Grias, Gustavia, Couroupita, Allantoma, Cariniana,* and *Couratari,* for which monophyly was supported by 322, 213, 339, 331, 124, and 308 genes, respectively, out of the 343 sequenced (Fig. S2). The clade of *Corythophora* that excludes *Corythophora alta* was supported by 184 genes. High support per gene was also found for the main *Lecythis s.l.* and *Eschweilera s.l.* clades: Pisonis, Poiteaui, Chartacea, Tetrapelata, Corrugata, Integrifolia, and Parvifolia were supported by 331, 207, 247, 286, 279, 175, and 88 genes respectively (Fig. S2).

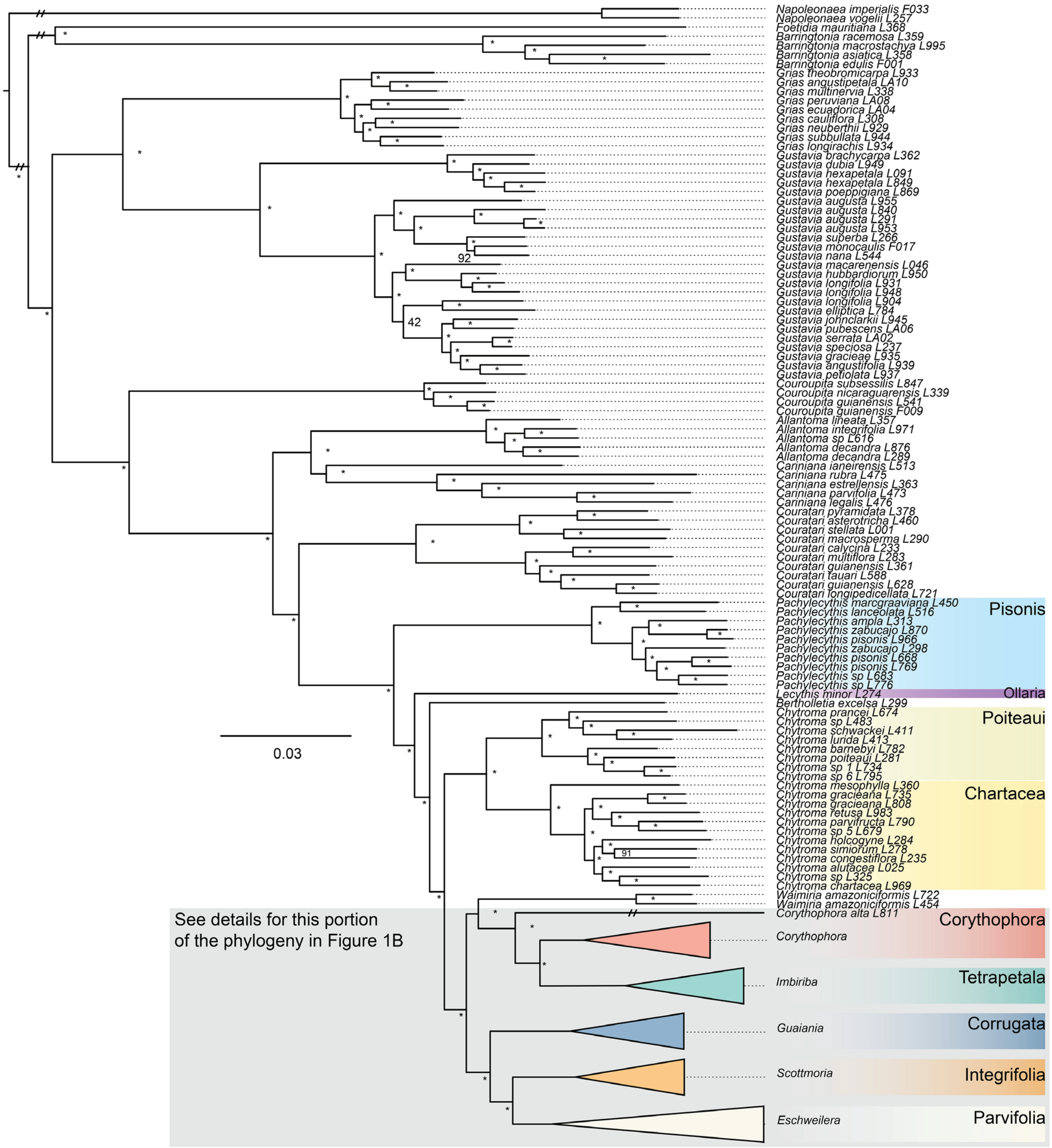

FIGURE 1A. Neotropical Lecythidaceae concatenated phylogeny of 343 nuclear genes. All shaded clades belong to the Bertholletia clade. Stars indicate full bootstrap support. Branch lengths are in units of substitutions per base pair.

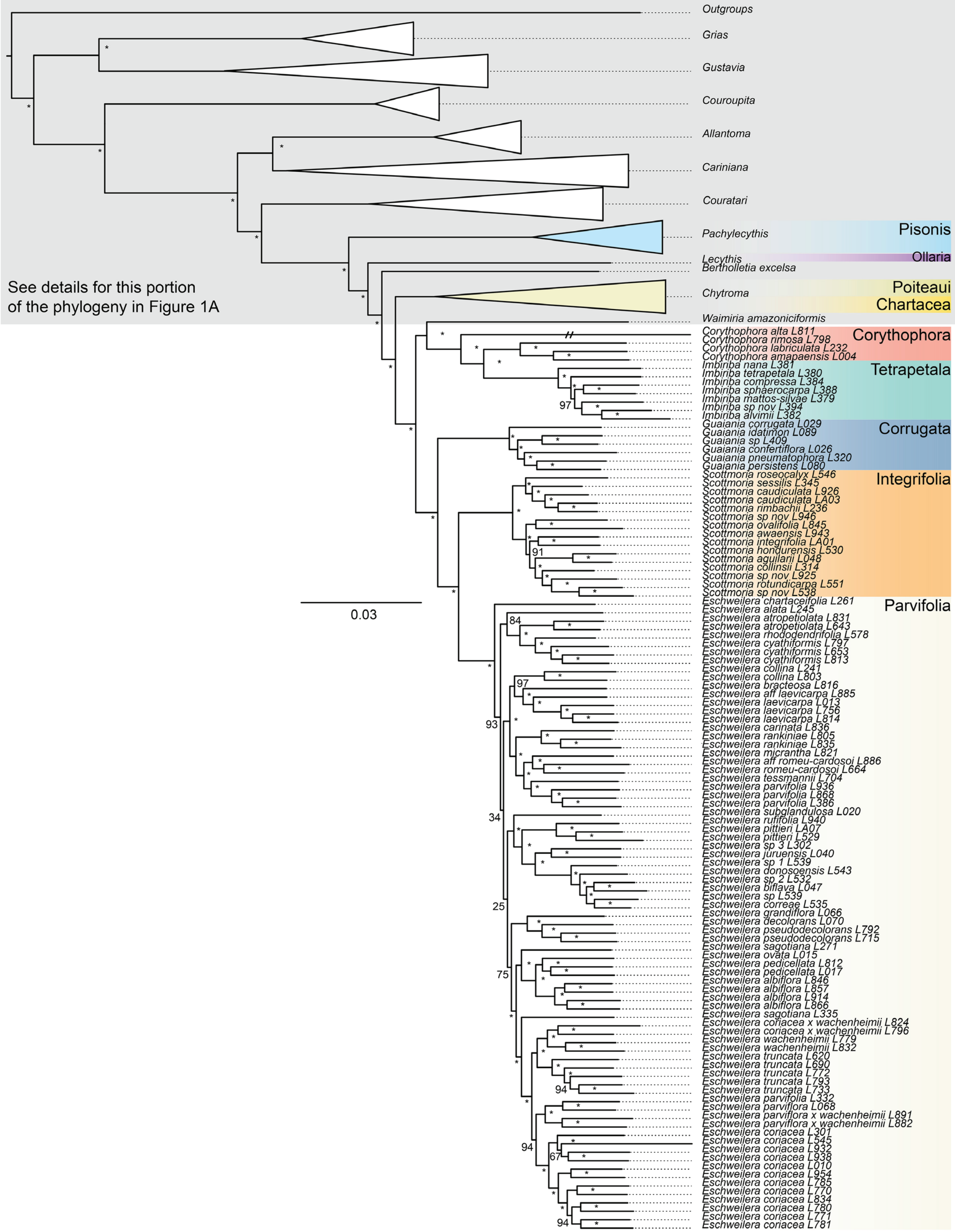
See details for this portion of the phylogeny in Figure 1A

Figure 1B. Neotropical Lecythidaceae concatenated phylogeny of 343 nuclear genes. All shaded clades belong to the Bertholletia clade. Stars indicate full bootstrap support. Branch lengths are in units of substitutions per base pair.

Plastome Dataset

The final concatenated plastome alignment contained 10,047 sites (2624 parsimony-informative) and 5.4% gaps. There was generally support for the monophyly of the major clades of Lecythidaceae in the plastome tree, though relationships among clades, in many cases, differed from those of the nuclear tree (Fig. 2). However, the Parvifolia and Integrifolia clades were not recovered as monophyletic in the plastome tree because one sample (L302, *Eschweilera* sp.) was recovered as a member of the Integrifolia clade in the plastome tree, but was placed within the Parvifolia clade in the nuclear phylogeny. With the exception of sample L302, the Parvifolia clade was monophyletic with 100% support, as was the Integrifolia clade. *Corythophora*, including *Corythophora alta*, was monophyletic in the plastome tree with 100% support. The Corrugata clade was sister to the Parvifolia clade (100% support) and *Corythophora* was sister to those (95% support). *Eschweilera amazoniciformis* was sister to the Tetrapetala clade (99% support) with those being sister to a clade consisting of the Pisonis, *Corythophora*, Corrugata, and Parvifolia clades (51% support). *Lecythis mesophylla* S.A. Mori (Chartacea clade, sample L360) was recovered as sister to a clade consisting of the Integrifolia clade and the other members of the Chartacea clade (79% support), with *Bertholletia* sister to the Chartacea + Integrifolia clades. The Guianensis and Echinata clades of *Couratari* were sister clades (100% support), with *Cariniana* sister to those (96 % support). *Couroupita* was monophyletic and *Gustavia* and *Grias* formed a clade that was sister to the rest of the Lecythidoideae. Several terminal branches in the plastome tree were inferred to have near-zero branch lengths, including individuals of different species (Figure S3).

Because plastome phylogenies are expected to be biased when hybridization is present due to the uniparental nature of it its inheritance (Rieseberg and Soltis, 1991, Vargas et al., 2017), and there is evidence of hybridization in the Bertholletia clade (Larson et al., 2021), we selected the nuclear topology as the best hypothesis to base our classification for Lecythidoideae. We provide illustrations for only one of the genera with updated names because photos and illustrations for clades are available in Huang et al. (2015).

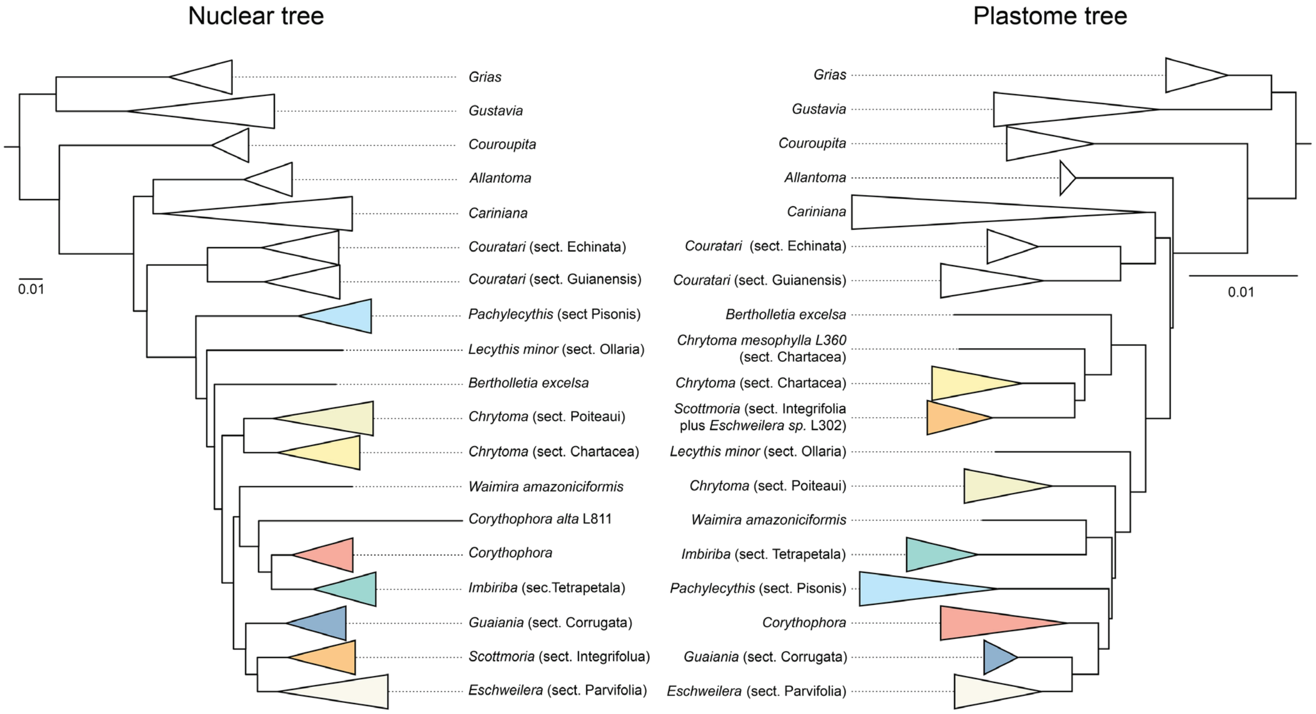

FIGURE 2. Nuclear and plastome trees with major clades collapsed. Colors correspond to those of the nuclear tree in Figure 1. Branch lengths are in units of substitutions per base pair and the scales for branch lengths differ between the two trees.

Taxonomy

Key to genera of the Bertholletia clade

See Prance and Mori (1990) and the NYBG Lecythidaceae Pages (Mori et al., 2010 and ongoing) for an explanation of the specialized fruit and floral terminology used in this key.

1a. Hypanthia and/or calyx-lobes often with mucilage ducts; petals usually pressed against the androecial hood/androecium; androecial hood often with posterior and anterior hood extensions; style linear, (2–)3–10 mm long 2

1b. Hypanthia and/or calyx-lobes without mucilage ducts; petals not pressed against the androecial hood/androecium; androecial hood without posterior and anterior hood extensions; style thickly oblongoid, up to 3 mm long 3

2a. Corolla buds enclosed by calyx; calyx with 2 lobes at anthesis; style ca. 8–10 mm long. Fruits perfectly globose, with inwardly falling operculum. Seeds with thick, bony testa, without aril, remaining inside fruit at maturity . . . . ***Bertholletia***

2b. Corolla buds not enclosed by calyx; calyx with 6 lobes at anthesis; style up to 7 mm long. Fruits usually subglobose (=depressed globose) or turbinate, and usually with freely falling operculum. Seeds without thick, bony testa, usually with an aril, usually falling out of fruit at or after maturity . . . . ***Chytroma*** (Poiteaui and Chartacea clades)

3a. Androecial hood with a single coil or no coil; ovary 2–5(–8)-locular 4

3b. Androecial hood with 2 to 4 coils; ovary 2-locular 8

4a. Pedicels and hypanthium densely rugose to muricate; androecial hood broadly open at anthesis, with a laterally expanded, concave ligule, exhibiting staminal ring. Fruits conical with horizontally oriented rugae (rugose) exterior (see exceptions for *G. corrugata*) . . . . ***Guaiania*** (sect. Corrugata)

4b. Pedicels and hypanthium smooth or nearly so; androecial hood inwardly closed or nearly closed at anthesis, usually with a narrower ligule, covering staminal ring. Fruits turbinate, globose or cupuliform (=cup-shaped), without horizontally oriented rugae/rugose exterior 5

5a. Androecial hood with a space between appendage-free ligule and coil; single coiled ligule with staminal appendages found only on the exterior part of the coil . . . . ***Lecythis*** (Ollaria clade)

5b. Androecial hood without coil, otherwise without a space between appendage-free ligule and coil 6

6a. Androecial hood with single coil, with staminal appendages arranged on both sides of coil. Seeds with basal or sub-basal aril poorly developed. Restricted to Brazilian Atlantic Forest and Cerrado . . . . ***Imbiriba*** (Tetrapetala clade)

6b. Androecial hood without coil; Seeds with long, basal aril, usually more than one-half length of seed. From Nicaragua to Ecuador, Venezuela, and throughout Guianas, Amazonia, and the Atlantic Forest 7

7a. Androecial hood ± flat, anterior staminal appendages projected forward; stylar collar present; flower tissue often oxidizing bluish-green when damaged. Fruits globose or broadly turbinate, usually ≥10–30 cm diam., with a convex operculum . . . . ***Pachylecythis*** (sect. Pisonis)

7b. Androecial hood dorsiventrally thickened and curved, anterior staminal appendages projected downwards; stylar collar absent. Fruits campanulate or cylindrical, ≤ 10 cm diam., with a flat operculum . . . . ***Corythophora***

8a. Flowers with 4 calyx lobes and 4 petals. Fruits narrowly turbinate; infracalycine zone narrow, conspicuously longer than wide. Seeds longitudinally ridged, with basal aril. Restricted to the Manaus area in Brazil . . . . ***Waimiria***

8b. Flowers with 6 calyx lobes and 6 petals. Fruits globose, globose-depressed or oblate; infracalycine zone undeveloped, otherwise broader than long. Seeds either (1) not ridged, with a lateral aril, sometimes with a soft, thin white sarcotesta, or (2) seeds surrounded by a mostly free, white rubbery coat (only in *S. awaensis*). From Mesoamerica to Amazonia 9

9a. Androecial hood with 3–4 inner coils, petals predominantly dark-purple or burgundy to rose, occasionally yellow to white. Seed covering of two types: (1) a soft, thin, white sarcotesta that is infiltrated with testa, arranged over the entire or most of the mature seed or at least present in young seeds and mostly dissolving at maturity, and with a thick, yellow to white lateral aril, often half I-beam shaped with rubber-like texture and overlapping ends on seed; or (2) seeds surrounded by a mostly free, white rubbery coat (only in *S. awaensis*). Predominantly on the Pacific side of NW South America (from Ecuador) to Mesoamerica . . . . ***Scottmoria***

9b. Androecial hood with 2 inner coils, petals usually white or yellow. Seeds with lateral, thick, white, rubbery aril with ends not overlapping; sarcotesta or rubbery coat absent. Predominantly in central and western Amazonia with a few species in Mesoamerica. . . . . . ***Eschweilera*** *s.s.*

Pachylecythis Ledoux, Lecointea 2: 2–4. 1964.
TYPE: *Pachylecythis pisonis* (Cambess.) O.M. Vargas & C.W. Dick.

Pachylecythis comprises a clade of five species informally recognized by Mori and Prance (1981) as the "sapucaia" group within *Lecythis*, and subsequently by Mori and Prance (1990) as *Lecythis* section *Pisonis*. Based on genetic and morphological evidence, Huang et al. (2015) named it the Pisonis clade (Huang et al., 2015). *Pachylecythis* species are canopy to emergent trees with deeply, vertically fissured bark and large woody fruit capsules known variously as monkey pot, *olla de mono* and *coco de mono* in Spanish (Sp.), and *sapucaia* in Portuguese (Port.). *Pachylecythis* species are found in lowland forests from Nicaragua to Brazil's Atlantic Forest. The edible seeds are consumed locally and sporadically marketed in Europe and the United States as paradise or cream nuts. The biology of the sapucaia group is discussed in Mori and Prance (1981) and Mori et al. (2017).

Diagnosis: Leaves, flowers, and fruits oxidize blue-green when bruised; flowers with short styles, flat androecium hood; fruits large and dehiscent; seeds with cord-like funicles surrounded by a large aril.

Etymology: *Pachylecythis egleri* Ledoux (1964) is the oldest Linnean synonym for *Lecythis pisonis*. *Jacapucaya brasiliensis* Marcgr. (1648) is pre-Linnaean and does not have priority following articles 32.1 and 13.1 of the International Code of Nomenclature.

Pachylecythis ampla (Miers) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis ampla* Miers, Trans. Linn Soc. London 30(2): 204–205 pl. 43, Fig. 1. 1874.

TYPE: COLOMBIA. Antioquia: without locality, no date, (fr only), *W. R. Jervis s.n.* (Lectotype: designated by Mori and Prance, 1990, K).

Habitat and distribution: Canopy to canopy-emergent trees in lowland wet or moist forest from Nicaragua and Costa Rica to the Chocó bioregion of Panama, Colombia and Ecuador; middle and lower Magdalena river valley; and Central and Western Cordilleras of Colombia (Mori and Prance, 1990).

Pachylecythis lanceolata (Poir.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis lanceolata* Poir., Encycl. Méth. 6: 27. 1804.

TYPE: MAURITIUS. Cultivated on the Île de France (=Mauritius), no date (fl), *P. Commerson 518* (Lectotype: designated by Mori and Prance, 1990, P-Juss., photograph NY; Isolectotypes: F [accession No. 537888], K, LINN [accession No. 943.3], US [accession No. 1112080]).

Habitat and distribution: Large trees (to 30 m) found in coastal moist forests of eastern Brazil from Rio de Janeiro to Pernambuco (Smith et al., 2016b). Sometimes cultivated as a street tree in Sao Paulo and Rio de Janeiro (Mori et al., 2010 and onward).

Pachylecythis marcgraaviana (Miers) O.M. Vargas & C.W. Dick. *comb. nov.*

Basionym: *Lecythis marcgraaviana* Miers (1874: 210–211, t. 48, Fig. 1).

TYPE: BRAZIL. Espirito Santo, Linhares, Reserva Natural Vale, Estrada Aceiro Marco de Ferro, 19˚9'02"S, 40˚04'13"W, 7 January 2010 (fl), *D. A. Folli 6527* (Neotype: designated by Smith et al., 2016b; CVRD; Isoneotype: NY).

Habitat and distribution: Canopy tree or shrub found in coastal Atlantic Forest between the states of Espírito Santo and Rio Grande do Norte (Smith et al., 2016a). This taxon was until recently considered part of morphologically variable species *Lecythis pisonis*.

Pachylecythis pisonis (Cambess.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis pisonis* Cambess., St. Hil., Fl. Bras. merid. 2: 377. 1829.

TYPE: BRAZIL. Espírito Santo: Without locality, 1816–1862 (fl), *A. Saint-Hilaire 365* (Lectotype: designated by Mori and Prance, 1990, P); Isolectotypes: MPU, NY [photo neg. No. 8782]).

Habitat and distribution: Canopy-emergent tree to 50 m found in lowland moist forests in the Amazon basin (especially eastern Amazonia) and in Brazil's Atlantic Forest. Common names are sapucaia (Brazil) and monkey pot (English). The species is planted along city streets in Brazil and in tropical botanical gardens around the world. The seed "castanha de sapucaia" is highly edible (Mori et al., 2010 and onward).

Pachylecythis zabucaja (Aubl.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis zabucaja* Aubl., Hist. pl. Guiane 1: 718–721. 1775, pro parte quoad fructum tantum.

TYPE: Plate 283 in Aublet (1775) (Lectotype: designated by Mori and Prance, 1990).

Habitat and distribution: Emergent trees (to 55 m) of lowland rain forest in the Guianas and eastern Venezuela and less commonly in the central and eastern Amazon.

The species epithet was originally masculine, *L. zabucajo*; however, Mori et al. (2010 and onward) changed the epithet spelling to *L. zabucaja* to agree in gender with the genus name.

Chytroma Miers, Trans. Linn. Soc. London 30: 229. 1874.

Basionym: *Lecythis schomburgkiana* O. Berg, Linnaea 27456: 230–231.1856.

TYPE: *Chytroma schomburgkiana* (O. Berg) Miers

Diagnosis: Some members of the clade have an androecial hood with appendages swept inward, mucilage ducts in the ovary and/or the calyx lobes, and a long obliquely oriented or geniculate style. No single apomorphy is yet known that unites all the species in this clade. However, Huang et al. (2015) cites the aforementioned combination of diagnostic characters.

Chytroma includes two sister clades consisting of the Lecythis section Poiteaui (Mori and Prance, 1990; Poiteaui clade of Huang et al., 2015) and the Chartacea clade described by Huang et al. (2015). The morphology of the Poiteaui clade and Chartacea clade overlaps and these groups have no uniting synapomorphies, hence we have opted to combine the two clades into the single genus *Chytroma*. The Chartacea clade and some species in the Poiteaui clade possess an androecial hood with swept-in appendages, and some species in both clades contain secondarily indehiscent fruits. Many of the same fruit and flower characters are found in *Bertholletia excelsa,* although *B. excelsa* has a dehiscent fruit with an inwardly falling operculum (Huang et al., 2015). Taxonomic treatments combined with phylogenetic studies are necessary to better delimit their morphological differences.

Etymology: *Chytroma schomburgkii* (O. Berg) Miers and *Chytroma ibiriba* Miers, both published in Miers (1874), are the earliest valid available names for species in this clade. *Cercophora* Miers is a synonym for another species in this clade and was also published in Miers (1874). However, *Cercophora* was previously published by Fuckel (1870) as a genus of fungi. The word *Chytroma* derives from the greek *chytra*, which is an earthenware cooking pot, and *oma*, meaning tumor or swollen, in likely reference to the fruits.

Chytroma alutacea (A.C. Sm.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera alutacea* A.C. Sm., American Journal of Botany 26(5): 409. 1939.

TYPE: GUYANA. Essequibo River, near the mouth of Orono Creek, ca. 1˚35'N, 17 December 1937 (fl), *A. C. Smith 2690* (Lectotype: designated by Mori and Prance, 1990, NY; Isolectotypes: F, G, K, MO, P, S, U).

Homotypic synonym: *Lecythis alutacea* (A.C. Sm.) S.A. Mori, Brittonia 33: 362. 1981.

Habitat and distribution: Canopy tree of lowland forest found primarily along rivers in eastern Venezuela, Guyana, Surinam and northern Pará state in Brazil (Mori et al., 2010 and ongoing). Chartacea clade.

Chytroma barnebyi (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis barnebyi* S.A. Mori 1981. Brittonia 33: 360.

TYPE. BRAZIL. Amazonas: Manaus-Caracarai Rd., km 130.5, 13 February 1974 (fl), *W. C. Steward et al. P.20242* (Holotype: INPA; Isotypes: COL, F, MO, NY, OXF, P, U, US, VEN).

Habitat and distribution: Understory tree restricted to *terra firme* forests in the Central Amazon region (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade (based on Mori and Prance, 1990).

Chytroma brancoensis R. Knuth (Engler) Pflanzenr. IV, fam. 291a: 84. 1939.

Homotypic synonym: *Lecythis brancoensis* (R. Knuth) S.A. Mori 1981, Brittonia 33: 359. TYPE: BRAZIL. Roraima: Rio Branco, São Marcos, 1913 (fl), *J. G. Kuhlann 913* (RB [accession No. 3517]) (Neotype: RB, designated by Mori and Prance, 1990, NY).

Habitat and distribution: Small tree (to 5 m) of savanna and forest fragments in Roraima state in northern Brazil and adjacent Guyana.

Clade: Poiteaui clade (based on Mori and Prance, 1990).

Chytroma chartacea (O. Berg) Miers Trans. Linn. Soc. London 30: 229. 1874.

Basionym: *Lecythis chartacea* Berg, Linnaea 27: 450–451. 1856. TYPE: GUYANA. Pomeroon River, Sep (fl), *R. Schomburgk 1432* (Lectotype: K).

Habitat and distribution: Medium to large tree (to 35 m) of riparian and *terra firme* forests in the Guiana Shield and Amazon basin regions.

Clade: Chartacea clade.

Chytroma congestiflora (Benoist) R. Knuth (Engler) Pflanzenr. IV, fam. 291a. 1939.

Basionym: *Lecythis congestiflora* Benoist, Notul. Syst. (Paris) 3: 177. 1915. TYPE: FRENCH GUIANA. Charvein, 11 January 1914 (fl), *R. Benoist 578* (Lectotype: designated by Mori and Prance, 1990, P).

Habitat and distribution: Canopy trees (to 25 m) known from *terra firme* forest of northern Surinam, French Guiana, and Surinam (Mori and Prance, 1990).

Clade: Chartacea clade.

Chytroma gracieana (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis gracieana* Mori, Mem. New York Bot. Gard. 75: 47–49. 1995.

TYPE: BRAZIL. Amazonas: Distrito Agropecuário, Reserve 1501 (Km 41) of the Biological Dynamics of Forest Fragments Project, 2˚24'26"–2˚25'31"S, 59˚43'40"–59˚45'50"W. ca. 50–125 m, *terra firme* forest, tree 1991, 9 January 1991 (fl), *M. A. de Freitas et al. 577* (Holotype: INPA; Isotypes: K, NY).

Habitat and distribution: Trees to 30 m in height in *terra firme* forest. Known only from the Manaus region (Mori and Lepsch da Cunha, 1995).

Clade: Chartacea clade.

Chytroma holcogyne (Sandwith) R. Knuth. (Engler) Pflanzenr. IV, fam. 291a. 1939.

Basionym: *Eschweilera holcogyne* Sandwith Kew Bulletin 1935: 126. 1935. TYPE: GUYANA. Kartabo Rd. nr. Confluence of Cuyuni and Mazaruni Rivers, 7 February 1931 (fl), *T. A. W. Davis D17* (=Forest Dept. British Guiana 1019) (Lectotype: designated by Mori and Prance, 1990, K; Isolectotypes: FDG, K).

Habitat and distribution: Canopy tree (to 35 m) found in *terra firme* forest of Guyana, French Guiana, and the northern part of Amapá state, Brazil.

Clade: Chartacea clade.

Chytroma ibiriba Miers 1874, Trans. Linn. Soc. London 30: 236–237. TYPE: BRAZIL. Alagoas, Maceió, February 1838 (imm. Fr), *G. Gardner 1312* (Lectotype: designated by Mori and Prance, 1990, K).

Homotypic synonym: *Lecythis ibiriba* (Miers) N.P. Sm., S.A. Mori, & Popovkin J. Torrey Bot. Soc. 139(4): 447. 2013.

Habitat and distribution: Small to medium trees known from the northeastern Brazilian states of Alagoas, Bahia, and Sergipe (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade (Huang et al., 2015).

Chytroma lurida (Miers) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Eschweilera lurida* Miers, Trans. Linn. Soc. London 30: 262. 1874.

TYPE: BRAZIL. Para: vicinity of Belem, 30 December 1929, *Burchell 10000* (Lectotype: designated by Mori and Prance, 1990, K; Isolectotypes: NY, OXF, P, US).

Homotypic synonym: *Lecythis lurida* (Miers) S.A. Mori, Brittonia 33: 362. 1981.

Habitat and distribution: Small to large trees of *terra firme* moist forests, secondary vegetation, and savanna, ranging from Rio de Janeiro to eastern Amazonia.

Clade: Poiteaui clade.

Chytroma mesophylla (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis mesophylla* S.A. Mori, Ann. Missouri Bot. Gard. 57: 386. 1971.

TYPE: PANAMA. Darien: N slope of Cerro Pirre, 15 November 1967 (empty fr), *S. A. Mori 364* (Holotype: WIS; Isotypes: BM, F, GH, MO, NY, UC, US).

Habitat and distribution: Large trees (to 50 m) from lowland tropical forests in lower Central America (Osa Peninsula in Costa Rica and Darien in Panama) and the Magdalena Valley in Colombia.

Clade: Chartacea clade.

Chytroma parvifructa (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis parvifructa* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 312. 1990.

TYPE: Brazil. Manaus-Itacoatiara Rd., EPLAC, km 30, 29 March 1976 (fr), *J. F. Ramos* 380 (Holotype: INPA; Isotypes: K, NY, RB).

Habitat and distribution: Trees of up to 35 m in height found in *terra firme* forest. Known only from the Central Amazon near Manaus, Brazil.

Clade: Chartacea clade.

Chytroma poiteaui (O.Berg) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis poiteaui* O. Berg Fl. Bras. (Martius) 14(1): 615. 1859.

TYPE: FRENCH GUIANA. Cayenne, no date (fl), *J. Martin s.n*. (Lectotype: designated by Mori and Prance, 1990, P, photograph NY; Isolectotypes: K, P, photograph of specimen at P, NY).

Habitat and distribution: Trees of up to 35 m in height found in *terra firme* forest in the eastern Amazon (east of Manaus), Surinam, and French Guiana (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma prancei (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov*.

Basionym: *Lecythis prancei* S.A. Mori Fl. Neotrop. Monogr. 21(2): 304. 1990.

TYPE: BRAZIL. Amazonas: Acara Trail, Reserva Ducke, km 26 Manaus-Itacoatiara Rd., 24 October 1974 (fl), *G. Prance et al. 23062* (Holotype: INPA; Isotypes: AAU, COL, FHO, K, MEXU, MO, NY, P, RB, U, US, VEN).

Habitat and distribution: Tree up to 35 m in height known only from the central Amazon region near Manaus (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma retusa (Spruce ex O. Berg) Miers, Trans. Linn. Soc. London 30(2): 243–244. 1874.

Basionym: *Lecythis retusa* Spruce ex O.Berg, Fl. Bras. (Martius) 14(1): 487. 1858. TYPE: BRAZIL. Amazonas: Vicinity of Barra (Manaus), prov. Rio Negro, flowering December–March, 1850–1851 (fl) (Lectotype: designated by Mori and Prance, 1990, *R. Spruce 1166*, BM; Isolectotypes: K, LE, M, NY).

Habitat and distribution: Canopy tree (to 30 m) of *terra firme* forest known only from the central Amazon region near Manaus, Brazil

Clade: Chartacea clade.

Chytroma schomburgkii (O. Berg) Miers, Trans. Linn. Soc. London 30(2): 230–231, t. 58. 1874.

Basionym: *Lecythis schomburgkii* O. Berg, Linnaea 27: 456. 1856.

TYPE: GUYANA. Without locality, 1868 (fl), *R. Schomburgk 792* (Lectotype, designated by Mori and Prance, 1990: BM).

Habitat and distribution: Small trees of up to 12 m in height found in the savannas of Roraima, Brazil.

The original publication names this species as *C. schomburgkiiana*; however, this termination is contrary to the standard required by the International Code of Nomenclature (art. 60.8b; the suffix "ana" applies to places not people), so we have chosen to use the corrected spelling for the epithet here, also previously corrected in Mori and Prance (1990).

Clade: Chartacea clade (Mori et al., 2017)

Chytroma schwackei (R.Knuth) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Sapucaya schwackei* R. Knuth, Repert. Spec. Nov. Regni Veg. 38: 113. 1935.

TYPE: BRAZIL. Minas Gerais: Virgem da Lapa, 9 April 1959 (fr), *M. Magalhães 15322* (Neotype: IAN, designated by Mori and Prance, 1990).

Habitat and distribution: Small trees known only from the states of Minas Gerais and Rio de Janeiro, Brazil (Mori et al., 2010 and ongoing).

Clade: Poiteaui clade.

Chytroma serrata (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis serrata* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 320. 1990.

TYPE: BRAZIL. Pará: Road to Munguba, 23 May 1969 (fl), *N. T. Silva 2035* (Holotype: IAN; Isotype: NY).

Habitat and distribution: Small to medium trees (4 to 20 m) of *terra firme* forest known from the central and eastern Amazon basin.

Clade: Likely Chartacea clade (Mori and Prance, 1990).

Chytroma simiorum (Benoist) R. Knuth, Pflanzenr. (Engler) IV, 219a: 81. 1939.

Basionym: *Lecythis simiorum* Benoist, Notul. Syst. (Paris) 3: 178. 1915.

TYPE: FRENCH GUIANA. Saint Jean du Maroni, 1 April 1914 (fr), *R. Benoist 1065* (Lectotype: designated by Mori and Prance, 1990, P; Isolectotype: K).

Habitat and distribution: Tree of up to 25 m in height found in *terra firme* forests in northern Guyana, Surinam, and French Guiana to Amapá, Brazil. Some collections from Amazonas, Brazil, suggest that the species may have a disjunct distribution.

Clade: Chartacea clade.

Waimiria C.W. Dick & O.M. Vargas, *gen. nov*.

TYPE: *Waimiria amazoniciformis* (S.A. Mori) C.W. Dick & O.M. Vargas, *comb. nov.*

Diagnosis: Flower with four petals; the androecial hood 3-coiled; fruits narrowly turbinate to turbinate; seeds with salient veins and basal aril.

Eschweilera amazoniciformis was so named because of the similarity of its fruit morphology with that of *E. amazonica* R. Knuth. *Waimiria amazoniciformis* is narrowly endemic to the vicinity of Manaus, Brazil, and is most frequently collected in the Ducke Reserve and the BDFFP reserves north of Manaus. The combination of four petals, tri-coiled hood, and narrowly turbinate fruit set this taxon apart morphologically from all other Lecythidaceae species. The narrowly endemic range and evolutionary distinctiveness of *W. amazoniciformis* should make it a conservation priority. We look forward to basic studies of its pollination, seed dispersal, and other aspects of its biology in the future.

Etymology: We name the genus for the Waimiri people whose ancestral lands overlap with the small geographic range of its eponymous genus. The Waimiri were forcibly displaced from their lands to make way for construction of the Balbina Dam (Davis, 1977). Their numbers were reduced by violence and disease, and they currently occupy a small portion of their former land.

Waimiria amazoniciformis (S.A. Mori) C.W. Dick & O.M. Vargas, *comb. nov.*

Basionym: *Eschweilera amazoniciformis* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 227. 1990.

TYPE: BRAZIL. Amazonas: Manaus-Itacoatiara Rd., km 178, May 1972 (fr), *L. Coelho 161* (Holotype: INPA; Isotype: NY).

Habitat and distribution: Canopy to emergent tree (to 40 m) of *terra firme* forest known only from the central Amazon region near Manaus, Brazil.

Imbiriba O.M. Vargas, M. Ribeiro, & C.W. Dick, *gen. nov.*
TYPE: *Imbiriba tetrapetala* (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Diagnosis: Inflorescence with horizontal scales on the rachis. Flowers with imbricated calyx lobes or fused at base and forming calycine rim; 4(–6) petals; androecium hood single coiled, with presence of staminal appendages on both sides of the single coil; ovary 2-locular, more than one row of ovules per locule. Seeds with impressed venation; basal aril poorly developed (Ribeiro et al., 2019).

Imbiriba subsumes the former *Eschweilera* sect. Tetrapetala proposed by Mori and Prance (1990) to include three species characterized by flowers with four petals and an androecium hood that does not form a complete coil. Huang et al. (2015) recognized the broader Tetrapetala clade which includes four additional species. Although the presence of four petals is unusual and one of the initial morphological characters defining section Tetrapetala (including in 3 unpublished new species, M. Ribeiro, in prep.), two species, *Imbiriba nana* and *Imbiriba mattos-silvae*, have six petals. Outside of this clade only *Waimiria amazoniciformis* and *Eschweilera perumbonata* Pittier have four petals (Mori and Prance, 1990). *Imbiriba* currently contains seven recognized taxa (three additional species are being described, M. Ribeiro, pers. comm.), all endemic to the Brazilian Atlantic Forest (Ribeiro et al., 2016a; Ribeiro et al., 2016b; Ribeiro, 2019; Smith et al., 2016b) with exception of *Imbiriba nana* which occurs in the Cerrado; six species of the genus are listed in the Brazilian endangered flora list (Lima da Venda et al., 2013; Brazil, Ministry of the Environment, 2022).

Etymology: The name *Imbiriba* is derived from the indigenous name used commonly for these species.

Although *Lecythopsis glabra* (Cambess.) O. Berg is a synonym of *Eschweilera compressa* (Vell.) Miers., *Lecythopsis* was not assigned a nomenclatural type and its description of fruit characters fit *Couratari* and do not apply to *E. compressa*. *Lecythopsis* was cited by Mori and Prance (1990) as a synonym of *Couratari*.

Imbiriba alvimii (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera alvimii* Mori, Brittonia 33: 469. 1981.

TYPE: BRAZIL. Bahia: Mun. Santa Cruz de Cabrália, vic. Pau-Brasil ecological reserve, 18 October 1978 (fl, fr), *S. A. Mori et al. 10819* (Holotype: CEPEC; Isotypes: K, RB, US).

Habitat and distribution: Small to medium trees of 4 to 30 m in height found in lowland forests in southeastern Bahia (Mori and Prance, 1990; Smith et al., 2016b).

Imbiriba complanata (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera complanata* S.A. Mori, Bol. Bot. Univ. São Paulo 14: 16. 1995.

TYPE: BRAZIL. Bahia: Mun. Porto Seguro, new road uniting BR 367 to Ajuda camp, 17 km from entrance, ca. 30 km W or Porto Seguro, 19 October 1978, *S. A. Mori et al. 10878* (Holotype: CEPEC; Isotypes: A, F, K, NY, P, RB, U, US).

Habitat and distribution: Medium sized trees (12 to 20 m) only known from the state of Bahia in Brazil's Atlantic forests (Smith et al., 2016b; Mori, 1995).

Imbiriba compressa (Vell.) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera compressa* (Vell.) Miers, Trans. Linn. Soc. London 30: 248. 1874.

TYPE: Plate 87 in Vellozo, Fl. Flum. Icon. V, t. 85. 1831 (1830) designated as Lectotype by Mori and Prance, 1990, in lieu of extant collection.

Habitat and distribution: Understory trees (3 to 10 m) of lowland moist forests endemic to Rio de Janeiro and Espírito Santo states (Mori and Prance, 1990; Ribeiro et al., 2016b).

Imbiriba mattos-silvae (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Eschweilera mattos-silvae* S.A. Mori, Bol. Bot. Univ. São Paulo 14: 22. 1995.

TYPE: BRAZIL. Bahia, Mun. Uruçuca, 7.3 km N of Serra Grande, 14°25'S, 39°03'W, 6 May 1992 (fl., immature fr), *W. W. Thomas et at. 9165* (Holotype: CEPEC; Isotypes: K, MO, NY, U, US).

Habitat and distribution: Small to medium sized tree of 10 to 25 m in height found in Brazil's Atlantic forests and endemic to southeastern Bahia.

Imbiriba nana (O. Berg) O.M. Vargas, M. Ribeiro, & C.W. Dick, *comb. nov.*

Basionym: *Lecythis nana* O. Berg, Trans. Linn. Soc. London 30: 261. 1874.

TYPE: BRAZIL. Mato Grosso: in sandy savanna near Camapuan, October (fl), *L. Riedel s.n.* (Holotype: LE fide Berg; Isotypes: P, photograph of specimen at P, NY).

Habitat and distribution: A shrub or small tree of savanna (Cerrado Biome) widely found at 400–800 m in the Planalto and northeastern Brazil (Mori and Prance, 1990; Smith et al., 2016b).

Imbiriba sphaerocarpa (M. Ribeiro & S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick. *comb. nov.*

Basionym: *Eschweilera sphaerocarpa* M. Ribeiro & S.A. Mori, Phytotaxa 255: 268. 2016.

TYPE: BRAZIL. Espírito Santo: Jaguaré, Jaguaré road toward Fátima, 18°54'50"S, 40°06'22"W, 28 December 2010, *D. A. Folli 6755* (Holotype: CVRD, Isotype: NY).

Habitat and distribution: Medium sized trees of 23 to 27 m in height, known only from one population of three trees in an Atlantic Forest fragment in the municipality of Jaguaré, Esprito Santos, Brazil and is classified as critically endangered by Ribeiro et al. (2016a).

Imbiriba tetrapetala (S.A. Mori) O.M. Vargas, M. Ribeiro, & C.W. Dick. *comb. nov.*

Basionym: *Eschweilera tetrapetala* Mori, Brittonia 33: 467. 1981.

TYPE: BRAZIL. Bahia: Mun. of Andaraí, 3 km NE of Andaraí, ca. 400 m alt., 5 March 1980 (fl), *S. A. Mori & L. S. Funch 13421* (Holotype: CEPEC; Isotypes: INPA, K, MG, MO, NY, P, RB, US).

Habitat and distribution: Medium sized tree of up to 15 m in height found in moist forest on plateaus in central Bahia, Brazil.

Guaiania O.M. Vargas & C.W. Dick, *gen. nov*.

TYPE *Lecythis idatimon* Aubl.

Diagnosis: Flowers with rugose or tuberculate pedicels and hypanthia that may persist in the fruits; androecial hood flat and thin with ligular flanges (except for *Guaiania corrugata*); seeds with basal and short aril.

Guaiania O.M. Vargas & C.W. Dick was first recognized as *Lecythis* section Corrugata by Mori and Prance (1990) and as a clade by Huang et al. (2015). All five species are located in the Guiana Shield/Central Amazon region.

Etymology: There were no published names with priority within this clade, so we propose a new name, *Guaiania*, derived from one of the Latin words for Guiana, which is the geographic center of the newly recognized genus and its ancestral area according to the biogeographic analysis of Vargas and Dick (2020). The word Guiana (Guayana, Guyana) is phonetically derived from an indigenous word meaning "land of many waters."

Guaiania confertiflora (A.C. Sm.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis confertiflora* (A.C. Sm.) Mori. Mem. New York Bot. Gard. 44: 31. 1987.

TYPE: GUYANA. Kumuparu Creek, Demerara River, 150 feet [ca. 50 m], 5 November 1937 (fl), *Forest Dept. British Guiana 2557* (Holotype: NY; Isotypes: K-2 sheets, MAD).

The aforementioned types are listed as lectotypes in Mori and Prance (2010). However, the basionym protologue indicates that the specimen *Forest Dept. British Guiana 2557* is a holotype.

Habitat and distribution: Typically canopy trees of up to 35 m in height but occasionally small trees (to 15m) found in *terra firme* forest throughout the Guianas and extending to Amapá, Brazil.

Guaiania corrugata (Poit.) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis corrugata* Poit., Mém. Mus. Hist. Nat. 13: 146. 1825.

TYPE: FRENCH GUIANA. Without locality, July 1824 (fl), *P. A. Poiteau s.n.* (Lectotype: designated by Mori and Prance, 1990, K, photo K neg. 16376 at NY)

Habitat and distribution: Large trees of up to 35 m in height found in *terra firme* forest ranging from Venezuela through the Guianas and to eastern Brazil. Two subspecies are recognized.

Guaiania corrugata *subsp.* rosea (Spruce ex O. Berg) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis rosea* Spruce *ex* Berg in Martius, Fl. bras. 14(1): 488–489. 1858. TYPE: BRAZIL. Amazonas: Rio Negro, Barcellos, November 1851 (fl), *R. Spruce 1920* (Holotype: M).

Homotypic synonym: *Lecythis corrugata* subsp. *rosea* (O.Berg) S.A. Mori, Brittonia 33: 363. 1981.

Habitat and distribution: Found in *terra firme* forest and along rivers and has been collected in Venezuela and Roraima Territory of Brazil (Mori et al., 2010 and ongoing).

Guaiania idatimon (Aubl.) O.M. Vargas & C.W. Dick. *comb. nov.*

Basionym: *Lecythis idatimon* Aubl., Hist. Pl. Guiane 2: 721. 1775.

TYPE: FRENCH GUIANA. Without locality, no date (fl), *J. B. C. F. Aublet s.n.* (Lectotype: designated by Mori and Prance, 1990, BM, photograph [F negative. 402], NY; Isolectotypes: BM-fragment, S).

Habitat and distribution: Typically an understory tree of 10 to 20 m in height and infrequently a canopy tree (to 35 m), locally common in *terra firme* forest from Suriname to Maranhão, Brazil.

Guaiania persistens (Sagot) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis persistens* Sagot, Ann. Sci. Nat., Bot. VI, 20: 201. 1885.

TYPE: FRENCH GUIANA. Without locality, 1842 (fl), [initial(s)] *E. Melinon 59* (Lectotype: Designated by Mori and Prance, 1990, P, photograph, NY).

Habitat and distribution: Understory to canopy trees of up to 35 m in height frond in *terra firme* forest in the Guiana Shield region. Known only from Guyana, French Guiana, and Amapá, Brazil. This taxon has two subspecies. In Mori et al. (2007), *Lecythis persistens* subs. *persistens* was sister to *L. persistens* subs. *aurantiaca* + L. *pneumatophora*, suggesting that the subspecies may eventually be elevated to species.

Guaiania persistens *subsp.* aurantica (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis aurantica* S.A. Mori, Memoirs of The New York Botanical Garden 44: 32. 1987.

TYPE: FRENCH GUIANA. Saul: Monts La Fume, 10 October 1982, *S. A. Mori et al 15075* (Holotype: NY; Isotypes: B, CAY, HAMAB, K, MG, MO, P, U, WIS).

Homotypic synonym: *Lecythis persistens* subsp. *aurantiaca* S.A. Mori, Mem. New York Bot. Gard. 44: 32. 1987.

Habitat and distribution: Canopy tree of unflooded forest known only from French Guiana.

Guaiania pneumatophora (S.A. Mori) O.M. Vargas & C.W. Dick, *comb. nov.*

Basionym: *Lecythis pneumatophora* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 288. 1990.

TYPE: FRENCH GUIANA. Comté River, nr. bridge of Route de l'est, 45 km S of Cayenne, 26 January 1977 (fr), *S. A. Mori & Y. Veyret 8983* (Holotype: NY; Isotype: CAY).

Habitat and distribution: Medium sized trees (to 15 m) found in dense stands along rivers in French Guiana (Oldeman, 1971).

Scottmoria Cornejo, *gen. nov.*

TYPE: *Lecythis integrifolia* Ruiz & Pav. ex Miers, Trans. Linn. Soc. London 30(2): 225. 1874, designated here.

Diagnosis: *Scottmoria* is a clade of Neotropical trees characterized by an androecial hood with three to four inner coils, as seen in medial longitudinal section, and two kinds of seed covering: (1) a thin white sarcotesta over the entire or most of the mature seed that is infiltrated with testa or a thin white sarcotesta present over the entire or most of the seed in young seeds but mostly dissolving at maturity, and with a thick, yellow to white, half I-beam shaped aril, with rubber-like texture and overlapping ends on seed; or (2) seeds with a finely tuberculate testa, surrounded by a mostly free, white rubbery coat; funicle surrounded by the aril (Fig. 3).

Etymology: The genus honors Scott Alan Mori (1941–2020), an extraordinary and prolific American botanist, who achieved the greatest discoveries on Neotropical Lecythidaceae during the past half of century (Prance et al., 2020). His profound dedication to the research and training of students throughout decades has deeply impacted our understanding of this family. The new genus is befittingly named after him.

Twenty-three new combinations are presented based on species formerly in *Eschweilera s.l.*, corresponding to the *Eschweilera integrifolia* clade (Mori et al., 2017; Vargas and Dick, 2020) to *Scottmoria*. The eight species of this clade studied in the field by Cornejo are marked with an asterisk (*).

Scottmoria aguilarii (S.A. Mori) Cornejo, *comb. nov.**

Basionym: *Eschweilera aguilarii* S.A. Mori, Monogr. Syst. Bot. Missouri Bot. Gard. 111: 903. 2007.

TYPE: COSTA RICA. Puntarenas: Cantón de Osa, Sierpe, San Juan, cuenca superior del Río San Juan, estribaciones Cerros Chocuaco, 8°43'50"N, 83°33'05"W, 580 m, 21 July 1990 (fl), *G. Herrera 3997* (Holotype: CR; Isotypes: MO, NY).

Habitat and distribution: Wet, lowland forests at less that 600 m on the Osa Peninsula, Costa Rica, and Honduras (Batista and Mori, 2017; Mori et al., 2010 and ongoing).

Scottmoria amplexifolia (S.A. Mori) Cornejo, *comb. nov.*

Basionym: *Eschweilera amplexifolia* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 210. 1990.

TYPE: PANAMA. Colón: Santa Rita Ridge Road, 26 October 1974 (fl), *S. A. Mori & J. Kallunki 2791* (Holotype: MO; Isotype: NY).

Habitat and distribution: Endemic to the wet forests from near sea level to 200 m in the Caribbean coast and lower slopes of Panama in the provinces of Colón and San Blas (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria andina (Rusby) Cornejo, *comb. nov.**

Basionym: *Lecythis andinus* Rusby, Mem. Torrey Bot. Club 6: 37. 1896.

TYPE: BOLIVIA. Mapiri: July–August 1892 (fl), *M. Bang 1522* (Lectotype: designated by Mori and Prance, 1990, NY [accession No. 1076]; Isolectotypes: K, MO, NY [accession No. 1077]).

Homotypic synonym: *Eschweilera andina* (Rusby) J.F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4): 246. 1941.

Habitat and distribution: In non-flooded Amazonian forests to ca. 800 m along the eastern slopes of the Andes from Colombia to Bolivia (Mori and Prance, 1990; Mori et al., 2010).

Scottmoria antioquensis (Dugand & Daniel) Cornejo, *comb. nov.*

Basionym: *Eschweilera antioquensis* Dugand & Daniel, Contr. Hist. Nat. Colomb. 2: 1–2. 1938.

TYPE: COLOMBIA. Antioquia: Laguna de Guarne, 2285 m, 26 June 1937 (fl), *H. Daniel 1201* (Holotype: Herbario del Colegio de San José de Medellín; Isotypes: COL, US).

Habitat and distribution: In unflooded forests, usually at elevations of 1000 m in northwestern Colombia in the departments of Antioquia, Chocó, and Cundinamarca and NW Venezuela in the state of Mérida (Mori and Prance, 1990; Mori et al., 2010 and ongoing) with a disjunct collection in Cerro Jefe region in central Panama (collection *R. Dressler 3508* at MO).

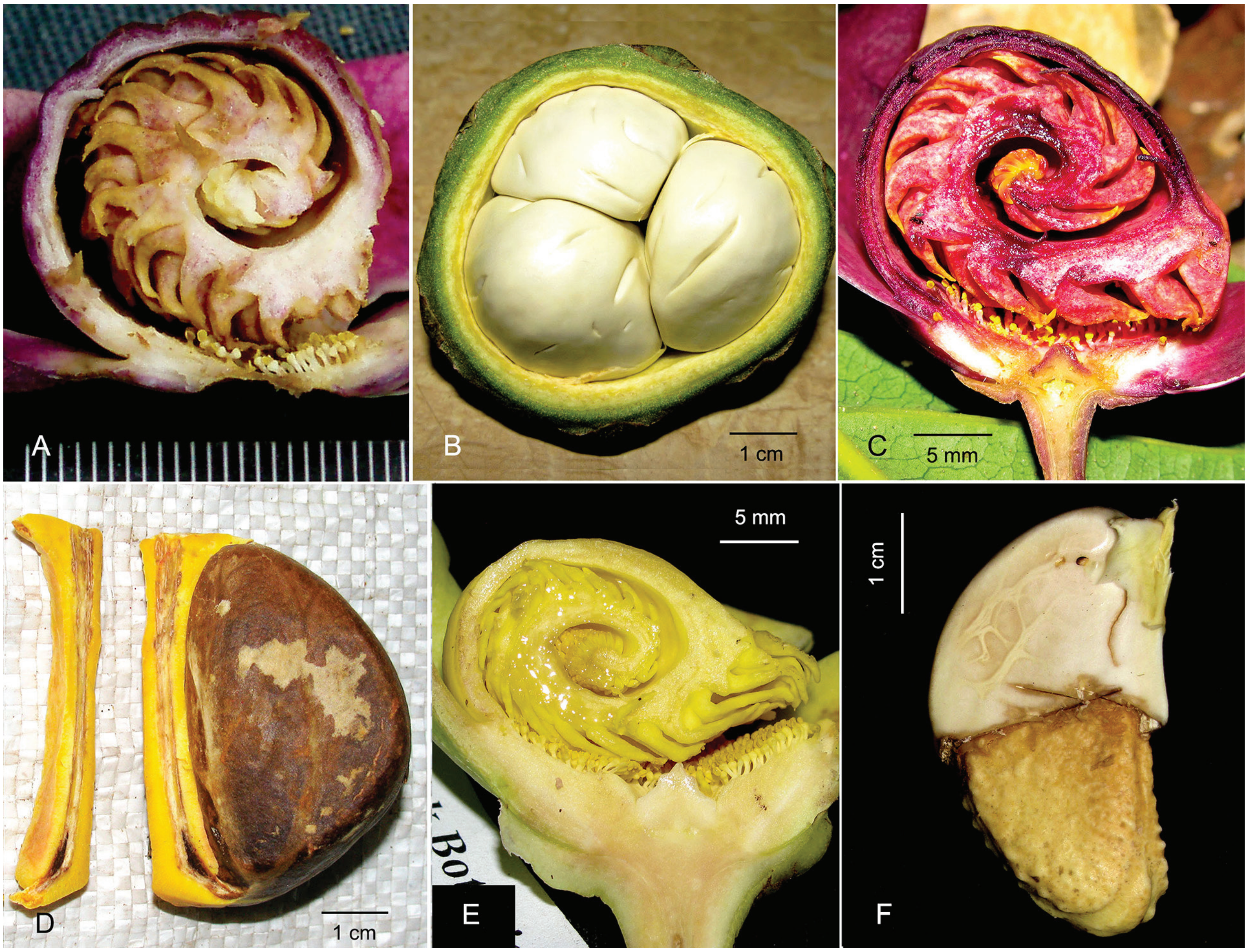

FIGURE 3. *Scotttmoria* Cornejo, morphological features. *Scottmoria integrifolia* (Ruiz & Pav. ex Miers) Cornejo: **A**, Medial section of androecial hood exhibiting a triple coil (*Cornejo & Grochowski 8057*, NY, from environs of the type area; scale in mm); **B**, Cut open fruit, the operculum removed, note three seeds fully surrounded by a fleshy white spreading aril (*Cornejo 8111*, NY). *Scottmoria rimbachii* (Standl.) Cornejo: **C**, Medial section of androecial hood exhibiting a triple coil (*Cornejo & García 8450*, NY). *Scottmoria caudiculata* (R. Knuth) Cornejo: **D**, Smooth seed with impressed nerves and a longitudinally sectioned yellow, half I-beam aril, note the funicle all the way along the interior of aril, and the irregular small relict patches of whitish thin sarcotesta (*Cornejo 8106*, NY). *Scottmoria awaensis* (S. A. Mori & Cornejo) Cornejo: **E**, Medial section of androecial hood exhibiting a triple coil; F, Seed with a white rubbery free coat, partially removed on lower half exhibiting a finely tuberculate testa (*Cornejo & Macías 8171*, NY, holotype).

Scottmoria awaensis (S.A. Mori & Cornejo) Cornejo, *comb. nov.** Fig. 3E, F.
Basionym: *Eschweilera awaensis* S.A. Mori & Cornejo, Brittonia 63: 470. 2011.
TYPE: ECUADOR. Esmeraldas: Bilsa Biological Station, Sendero Verde, 79°44'W, 0°21'N, 500 m, 16 October 2009 (fl, fr), *X. Cornejo & A. Macías 8171* (Holotype: NY; Isotypes: COL, GUAY, K, MO, QCNE, US, USM).

Habitat and distribution: Endemic to the wet forests on non-flooded soils from lowlands to 800 m in northwestern Ecuador (Cornejo and Mori, 2011).

Scottmoria brevipetiolata (S.A. Mori & Cornejo) Cornejo, *comb. nov.*
Basionym: *Eschweilera brevipetiolata* S.A. Mori & Cornejo, Phytotaxa 585: 288. 2023.
TYPE: COLOMBIA. Valle del Cauca: Bajo Calima; Concesión Pulpapel/Buenaventura, carretera al Dindo, 77°00'W, 3°55'N, ca. 100 m, 25 September 1986 (fl), *M. Monsalve 1169* (Holotype: CUVC-25917; Isotypes: MO-3701257, MO-3701347, NY-00853327).

Habitat and distribution: From 50 to 100 m elevation in wet to pluvial forests on non-flooded areas, department of Valle del Cauca, western Colombia (Cornejo, 2023b).

Scottmoria calyculata (Pittier) Cornejo, *comb. nov.*
Basionym: *Eschweilera calyculata* Pittier, Contr. U. S. Natl. Herb. 12: 97, Fig. 1, Pl. III. 1908.
TYPE: COSTA RICA. Limón: Forests between Port Limón and Moin, September 1899 (fl), *H. Pittier 16018* (Holotype: US [578009]).

Habitat and distribution: In lowland forests in *terra firme* and swamp forests at the Caribbean coast of southern Central America from a short distance N of Limón, Costa Rica to near Portobelo, Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria caudiculata (R. Knuth) Cornejo, *comb. nov.** Fig. 1D.
Basionym: *Eschweilera caudiculata* R. Knuth, Pflanzenr. (Engler) IV.219a: 95. 1939.
TYPE: COLOMBIA. Antioquia: Peñitas, 1880 (fl), *G. Kalbreyer 1860* (Holotype: B, not found or destroyed; Lectotype: designated by Mori and Prance, 1990, K, photograph NY [K neg. no. 16386]).

Eschweilera caudiculata syn. nov. was classified as a member of the Parvifolia clade in Mori and Prance (1990) but, because it has flowers with a triple coil, this species belongs in the Integrifolia clade.

Habitat and distribution: A predominantly Andean species in non-flooded forests often at 1000 to 2500 m, ranging from eastern Panama to southern Ecuador (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria collinsii (Pittier) Cornejo, *comb. nov.**
Basionym: *Eschweilera collinsii* Pittier, Contr. U. S. Natl. Herb. 12: 97, Fig. 1, Pl. III. 1908.
TYPE: COSTA RICA. Alajuela, Plains of San Carlos, 100 m, 15 April 1903 (fr), *O. F. Cook & C. B. Doyle 95* (Holotype: US [accession No. 473872]).

Habitat and distribution: In wet forests from near sea level to 1000 m elevation, Veraguas, Panama, and on the Atlantic and Pacific slopes of Costa Rica in the Provinces of Alajuela, Puntarenas, Limón, and San José (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria hondurensis (Standl.) Cornejo, *comb. nov.*
Basionym: *Eschweilera hondurensis* Standl., Field Mus. Nat. Hist., Bot. Ser. 9:318. 1940.
TYPE: HONDURAS. Atlantida: vicinity La Ceiba, lower slopes of Mt. Cangrejal, 6 August 1938 (fr), *T. G. Yuncker, J. M. Koepper & K. A. Wagner 8829* (Holotype: F; Isotypes: BM, K, MO, NY).

Habitat and distribution: In non-flooded primary forests, often collected on the lower slopes of low mountains at below 500 m elevation from Honduras to the Pacific coast of Panama (Cerro Hoya National Park and Coiba Island National Park) (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria integrifolia (Ruiz & Pav. ex Miers) Cornejo, *comb. nov.** Fig. 3A, B.
Basionym: *Lecythis integrifolia* Ruiz & Pav. ex Miers, Trans. Linn. Soc. London 30(2): 225. 1874.
TYPE: ECUADOR. Guayas: Guayaquil, no date (fl), *J. Tafalla s.n.* (Lectotype: designated by Mori & Prance, 1990, MA, photograph, GH; Isolectotype: K).
Homotypic synonym: *Eschweilera integrifolia* (Ruiz & Pavón ex Miers) R. Knuth, Pflanzenr. (Engler) IV, 219a: 97. 1939.

Habitat and distribution: Persistent in secondary moist and wet forests from sea level to ca. 800 m elevation from the Pacific coast of Colombia to western Ecuador (Mori & Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria jacquelyniae (S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera jacquelyniae* S.A. Mori, Fl. Neotrop. Monogr. 21(2): 192. 1990.
TYPE: PANAMA. Panamá. Gorgas Memorial Labs. Yellow Fever Research Camp, Campamento Cuatro, 5–10 km NE of Altos de Pacora on ridge top, 600 m, 21–24 November 1974 (fl), *S. A. Mori & J. Kallunki 3440* (Holotype: NY; Isotypes: COL, K, MO, PMA, US).

Habitat and distribution: Endemic to cloud forests 600 to 1000 m elevation in central Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria jefensis (J.E. Bat. & S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera jefensis* J.E. Bat. & S.A. Mori, Phytoneuron 62: 2. 2017.
TYPE: PANAMA. Provincia de Panamá: Parque Nacional Chagres, Alrededores de Cerro Jefe, 9°12'N, 79°22'W, 900 m, 24 January 1996 (fl), *C. Galdames et al. 2414* (Holotype: PMA; Isotypes: MO, NY, SCZ).

Habitat and distribution: Endemic to the cloud forests from 800 to 1000 m in central and eastern parts of Panama Province, Panama (Batista et al., 2017).

Scottmoria ovalifolia (DC.) Cornejo, *comb. nov.*
Basionym: *Lecythis ovalifolia* DC., Prodr. (DC.) 3: 292. 1828.
TYPE: BRAZIL. Amazonas: At mouth of Rio Negro, no date (fl), *C. Martius s.n.* (Lectotype: designated by Mori & Prance, 1990, M, photo NY; Isolectotypes: G, photographs of specimen at G at A, K, M, NY [F negative. 23206]).
Homotypic synonym: *Eschweilera ovalifolia* (DC.) Nied., Nat. Pflanzenfam. 3(7): 40. 1892.

Habitat and distribution: In periodically flooded riverine forests of Central and western Amazonia in Brazil, Bolivia, and Peru (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria pachyderma (Cuatrec.) Cornejo, *comb. nov.*
Basionym: *Eschweilera pachyderma* Cuatrec., Fieldiana, Bot. 27(2): 91. 1951.
TYPE: COLOMBIA. Valle del Cauca: Costa de Pacífico, Río Cajambre, 8 May 1944 (fl), *J. Cuatrecasas 17448* (Lectotype: designated by Mori and Prance, 1990, F [accession No.1358486]; Isolectotypes: F [accession No. 1358487], NY, U).

Habitat and distribution: Pluvial forests, Pacific coast of Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria panamensis (Pittier) Cornejo, *comb. nov.*
Basionym: *Eschweilera panamensis* Pittier, Contr. U. S. Natl. Herb. 26(1): 12. 1927.

TYPE: PANAMA. San Blas: Hills back of Puerto Obaldia, 50–200 m, August 1911(fl, fr), *H. Pittier 4338* (Holotype: US [accession No. 679481]; Isotypes: BM, F, K, NY).

Habitat and distribution: Known only from *terra firme* forests below 500 m, from Bocas del Toro to the vicinity of Puerto Obaldia, Panama (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria podoaquilae (Cornejo) Cornejo, *comb. nov.**
Basionym: *Eschweilera podoaquilae* Cornejo, Phytotaxa 579: 139. 2023.
TYPE: ECUADOR. Santo Domingo de los Tsáchilas: Centinela, área norte de las montañas de Ila, Parroquia El Esfuerzo, comuna Polanco, Cascadas Las Rocas, 79°11'W, 0°28'S, 560 m, 20 March 2022 (fl), *X. Cornejo, J. L. Clark & C. Restrepo 10032* (Holotype: GUAY; Isotype QCA).

Habitat and distribution: Endemic to the wet forests on *terra firme* areas in northwestern Ecuador (Cornejo, 2023a).

Scottmoria rimbachii (Standl.) Cornejo, *comb. nov.** Fig. 1C.
Basionym: *Eschweilera rimbachii* Standl., Trop. Woods 42: 31. 1935.
TYPE: ECUADOR. [probably Chimborazo]: Foot of Western Cordillera, 1931 (fr), *A. Rimbach 47* (Lectotype: designated by Mori and Prance, 1990, F [accession No. 677029]; Isolectotype: F [accession No. 677045]).

Habitat and distribution: Persistent after disturbance in *terra firme* secondary wet forests, southwestern Colombia, and western Ecuador (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria roseocalyx (J.E. Bat., S.A. Mori, & J.S. Harrison) Cornejo, *comb. nov.*
Basionym: *Eschweilera roseocalyx* J.E. Bat., S.A. Mori, & J.S. Harrison, Phytoneuron 62: 7. 2017.
TYPE: PANAMA. Province of Panama, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, bosque achaparrado dominado por *Colpothrinax aphanopetala* R. Evans (Arecaceae), 9°13'39"N, 79°23'20"W, 970 m, 28 May 2016 (fl), *J. Batista et al. 1680* (Holotype: PMA; Isotypes: MO, NY, SCZ, UCH, US).

Habitat and distribution: Endemic to Cerro Jefe, Chagres National Park, in central Panama, at elevations 900 to 1000 m (Batista et al., 2017).

In the protologue, *Eschweilera roseocalyx* was described and discussed as having androphores with a double coil; however, a closer examination of the illustration (Fig. 5 H in Batista et al., 2017) reveals an androphore with a triple coil. That character jointly with the spreading white aril design of seeds fully fits *Scottmoria*, as is also confirmed by the molecular results presented herein.

Scottmoria rotundicarpa (J.E. Bat. & S.A. Mori) Cornejo, *comb. nov.*
Basionym: *Eschweilera rotundicarpa* J.E. Bat. & S.A. Mori, Phytotaxa 296: 46. 2017.
TYPE: PANAMA. Provincia de Coclé, Corregimiento El Harino, Parque Nacional General de División Omar Torrijos Herrera, sendero de la Quebrada Yaya (Sendero Los Monos), 8°40'04"N, 80°35'53"W, 717 m, 22 September 2014 (fr), *J. Batista G., A. Espinosa, & J. Montenegro 1085* (Holotype: PMA; Isotypes: MO, NY, SCZ, UCH).

Habitat and distribution: Endemic to cloud forests at elevations 700 to 900 m and lowland rain forests at elevations 200 to 300 m in Panama (Batista and Mori, 2017).

The original description associated this species with the Integrifolia clade (Batista & Mori, 2017); however, its triple coil, and spreading aril in the seed, along with its phylogenetic position evidence the inclusion of this species in *Scottmoria*.

Scottmoria sclerophylla (Cuatrec.) Cornejo, *comb. nov.*
Basionym: *Eschweilera sclerophylla* Cuatrec., Fieldiana, Bot. 27(2): 92. 1951.
TYPE: COLOMBIA. Valle: Rio Calima (region del Choco), La Trojita, 5–50 m alt., 27 February 1944 (fl), *J. Cuatrecasas 16517* (Lectotype: designated by Mori & Prance, 1990, F [accession No. 1358508]; Isolectotypes: F [accession No. 1358509], NY).

Habitat and distribution: Known from pluvial forests near sea level to 100 m the departments of Valle and Chocó, Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria sessilis (A.C. Sm.) Cornejo, *comb. nov.*
Basionym: *Eschweilera sessilis* A.C. Sm., Phytologia 1: 21. 1933.
TYPE: COLOMBIA. Boyacá. In forest on Mt. Chapón, 2100 m, 17 June 1932 (fl), *A. Lawrance 239* (Holotype: NY; Isotypes: BM, K, MO).

Habitat and distribution: From 350 to 2100 m elevation in wet to pluvial forests of Colombia (Mori and Prance, 1990; Mori et al., 2010 and ongoing).

Scottmoria silverstonei (Cornejo) Cornejo, *comb. nov.*
Basionym: *Eschweilera silverstonei* Cornejo, Phytotaxa 585: 290. 2023.
TYPE: COLOMBIA. Valle del Cauca: Bajo Calima; Concesión Pulpapel/Buenaventura, 77°00'W, 3°55'N, ca. 100 m, 9 August 1984 (fl), *M. Monsalve 214* (Holotype: CUVC [accession No. 19929]; Isotype: NY [accession No. 02152729]).

Habitat and distribution: At ca. 100 m elevation in wet to pluvial forests on *terra firme* areas, department of Valle del Cauca, western Colombia (Cornejo, 2023b).

Discussion

We present a phylogeny of Neotropical Lecythidaceae based on unprecedented genomic sampling of the family, with over 300 nuclear genes and a large and variable portion of the plastome genome sampled for most of the Neotropical species. We focused our sampling on the Bertholletia clade, centered in northern South America, with the aim of obtaining a robust hypothesis for the relationships among its genera. We found strong phylogenetic support for the polyphyly of *Lecythis* and *Eschweilera*—suggested but weakly supported in previous studies (Mori et al., 2007; Huang et al., 2015)—which justifies our revised classification of these two genera. The phylogenies presented here can serve as a backbone for future taxonomic and evolutionary studies of the Lecythidaceae. We provide an updated list of all described Neotropical Lecythidaceae to date (Table S3).

Taxonomic Changes

We have divided *Lecythis* and *Eschweilera* each into four genera, with a total of six new or reinstated genera. We have reduced *Lecythis* from 26 to three species, and *Eschweilera* now circumscribes only the Amazon-centered Parvifolia clade. Mori and colleagues (Huang et al., 2015; Mori et al., 2017; Mori et al., 2010 and ongoing) anticipated these taxonomic changes. For example, "*Lecythis*, as currently circumscribed, is most likely not monophyletic; thus, generic realignments are to be expected in the future…There are 26 known species, but if the genera are circumscribed differently *Lecythis sensu stricto* will consist of only three species." (*Lecythis* description in Mori et al., 2010 and ongoing). In addition to the anticipated taxonomic changes for *Eschweilera* and *Lecythis*, we detected that *Eschweilera amazoniciformis* is sister to *Corythophora* and the Tetrapetala clade (*Imbiriba*), thus justifying its elevation to a new genus, *Waimiria*. Although it was not essential to elevate to genus the Integrifolia section of *Eschweilera s.l.*, we agreed that the morphological and geographical distinctiveness of the clade merited genus-level recognition.

The alternative to splitting *Eschweilera* and *Lecythis* was to lump the entire Bertholletia clade into *Lecythis*, thereby eliminating *Eschweilera*, *Bertholletia*, and *Corythophora*. We felt that this approach would have hidden important evolutionary and biogeographic history.

Phylogenetic conflicts

We observed phylogenetic conflict among nuclear genes, as is typical of most nuclear phylogenomic analyses. We found that the monophyly of most major clades was supported by a majority of informative gene trees, whereas there was more conflict for the relationships among recently diverged species (Fig. S2). Nearly all major clades recovered in the nuclear tree were also recovered in the plastome tree (Fig. 2). An exception was the monophyly of the Parvifolia and Integrifolia clades because one sample (i.e., L302, *Eschweilera* sp.) was recovered as sister to *Scottmoria sessilis* (Integrifolia clade) in the plastome tree but was sister to *Eschweilera juruensis* R. Knuth (Parvifolia clade) in the nuclear tree. The markedly different placements of this single sample in the two trees suggests there may have been recent introgression between the Parvifolia and Integrifolia clades, since none of the other ~90 plastomes sampled from these clades share this pattern, as might be expected if this conflict was due to incomplete lineage sorting (ILS). This sampled specimen (*S. A. Mori 25642*; collected at Los Amigos biological station, Peru) was originally determined as *Eschweilera tessmannii* R. Knuth (Parvifolia clade) by S. A. Mori in 2003, but was later re-designated as *Eschweilera* sp. by Mori in 2012. This specimen was included in the sampling of a chloroplast phylogeny of the *ndhF* and *trnL-F* genes as *Eschweilera tessmannii* by Mori et al. (2007), who also found its chloroplast genome to be closely related to the Integrifolia clade. Furthermore, the chloroplast regions from that study (GenBank accessions DQ388268 and DQ417983) matched the *de novo* chloroplast assembly produced in this study with 99.9% (a single bp mismatch across the 1992 base pairs of sequence) and 100% identity, respectively (data not shown), confirming that the placement of its plastome among the Integrifolia clade is not erroneous. Notably, *Corythophora* was recovered as monophyletic in the plastome tree (Fig. 2) but was paraphyletic in the nuclear tree. We hypothesize that the non-monophyly of *Corythophora* in the nuclear data can be explained by ILS, considering that the genus is monophyletic in the plastome tree—plastome genotypes can be fixed in a population rapidly because their effective population size is one quarter relative to that of an autosomal nuclear region (Moore, 1995), thus explaining the discordance.

Evolutionary diversity uncovered

The new taxon *Waimiria*, as a monotypic genus with distinct morphology and phylogenetic isolation, is comparable to the iconic and monotypic Brazil nut tree *Bertholletia* in its position as an evolutionary outlier within the Bertholletia clade. *Waimiria amazoniciformis* is a canopy or canopy-emergent species with a distinctive cylindrical trunk. Its flowers notably have four petals (which it shares with four of the six *Imbiriba* species), and it has a distinctive elongated fruit similar to eponymous *Eschweilera amazonica*. Despite its stature and distinctive floral and fruit morphology, and its proximity to an intensively collected forest near the city of Manaus (Nelson et al., 1990) and relatively high abundance there (147 individuals in the Lecythidaceae plot; Milton et al., 2022), it was only described as a new species in 1990. This relatively recent discovery is typical of many species in Lecythidaceae and other Amazon tree families. The small geographic ranges of narrowly endemic species make them easy to overlook, and large trees of mature Amazon Forest are difficult to collect and poorly represented in herbaria. While there are exceptions, such as hyperabundant *E. coriacea* which has been collected thousands of times, the average number of global collections per Lecythidaceae species is around 24, with 82 taxa having a single specimen collected and 137 taxa having three or less specimens collected (Medellín-Zabala, in prep.). To obtain high quality (i.e., fertile) herbarium specimens, trees in mature Amazon Forest must first be identified as being distinctive and in fertile condition, requiring some local botanical knowledge, and then they must typically be climbed, which requires expertise and is a substantial investment in labor (Mori et al., 2011). In the central Amazon, mature forest tree populations may go decades without producing perceptible quantities of flowers or fruit.

Species Boundaries and Hybridization

The "Lecythidaceae Plot" within reserve 1501 of the BDFFP is a useful case study of the diversity of Lecythidaceae in the central Amazon, and it is especially relevant for this study because we sampled all of its species. Scott Mori led the identification of Lecythidaceae (>10 cm dbh) in the 100-ha forest plot beginning in 1989. The initial census yielded 7791 trees from 39 species. *Eschweilera coriacea* was the most abundant species, with n = 1529 individuals (Milton et al., 2022). Of the 39 species in the plot, 30% (13 spp.) were described since 1978; three species (*Chytroma gracieana* [n = 40], *Eschweilera romeu-cardosoi* S.A. Mori [n = 309] and *E. rankiniae* S.A. Mori [n = 16]) were first collected in the plot. Mori recognized two additional new species ("*Lecythis* 01" [n = 8] and "*Lecythis* 05" [n = 51], both species were sampled in this study and were found to belong to *Chytroma*) on the basis of field characters but didn't formally name them for lack of flower or fruit specimens. Thirty years of monitoring have not yielded a single fruit- or flower-bearing specimen from these relatively large trees. For our team, the Lecythidaceae plot was a "living herbarium" that allowed us to sample the family level diversity and explore useful field characters including aspects of bark, stature, and tree form.

We sampled multiple individuals of hyperdominant species of *Eschweilera* s.s. (Parvifolia clade) in the Lecythidaceae plot. Hyperdominant species are members of a group of 257 tree species (out of an estimated 5000 species) that comprise >50% of stem numbers and biomass in Amazonian Forest inventories (ter Steege et al., 2013). The Parvifolia clade contains three hyperdominant *Eschweilera* species in the Lecythidaceae plot, which are also dominant at the local scale: *E. coriacea* (n = 1539), *E. truncata* (n = 1321), and *E. wachenheimii* (Benoist) Sandwith (n = 926) (Mori and da Cunha 1995). *Eschweilera coriacea* was suspected to contain cryptic diversity and/or hybridize (M. Heuertz, pers. com.), and we were interested in knowing if the taxonomic boundaries corresponded with distinctive gene pools in these and the other Lecythidaceae species. Larson et al. (2021) performed more detailed population genomic analyses which supported the hypothesis of hybridization and introgression amongst *E. coriacea, E. truncata*, and *E. wachenheimii*. Hybridization and introgression are evolutionary processes that may permit ecological generalist species like *E. coriacea* to thrive in all the major Amazon Forest types (Larson et al., 2021; Heuertz et al., 2020). Further taxonomic sampling within *E. coriacea* may reveal cryptic species diversity. It is notable that, despite evidence of hybridization in the hyperdominant *Eschweilera*, Larson et al. (2021) found that the other species exhibited distinctive gene pools that corresponded with their taxonomy, suggesting that current species circumscriptions provide a meaningful description of the diversity of Neotropical Lecythidaceae, with no evidence of widespread taxonomic "over-splitting."

Implications for Ecology and Biogeography

Lecythidaceae comprise about half of all trees in mature Amazon Forest and is an important family across networks of Amazon Forest inventory plots (e.g., ter Steege et al., 2013); and in terms of tree abundance and species richness, *Lecythis s.l.* and *Eschweilera s.l.* are its two most important genera in the basin. With the BDFFP Lecythidaceae plot as our point of reference for the central Amazon forests, our revised taxonomy will not affect most of its *Eschweilera*, as the Parvifolia clade (*Eschweilera sensu stricto*) are predominant here. In the Lecythidaceae plot, 15 of the 16 *Eschweilera* species maintain their names, with only *E. amazoniciformis* transferring to the monotypic genus *Waimiria*. In contrast, the name *Lecythis* is essentially eliminated from most Amazon forests. In the Lecythidaceae plot, eight species are transferred to *Chytroma* and the remaining two are transferred to *Pachylecythis*. *Lecythis sensu stricto*, based on our revised classification, will contain only three species that are relegated to the Guiana shield region. Our revised taxonomy corresponds geographically with the centers of origin of these taxa previously suspected to be clades (Vargas and Dick, 2020). This will increase the level of genus-level turnover (beta diversity) among regions for researchers interested in continental scale biodiversity patterns.

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Appendix

Supplementary materials can be accessed at https://dx.doi.org/10.7302/22806 (The supplementary tables are in the document titled “Supplementary information” at this website). Command and intermediate files can be found in the following repository: https://github.com/oscarvargash/lecy_taxo.

Supplementary Figure 1. The coalescent-consistent tree generated with ASTRAL. Branch-lengths are in coalescent units and node labels are ASTRAL local posterior probabilities.

Supplementary Figure 2. Phylogenetic conflict of gene trees with the nuclear tree, generated with phyparts. The proportion of gene trees that are concordant or discordant are represented in blue and red pies respectively. Uninformative gene trees, those with < 70% bootstrap support, are represented in gray. The number of gene trees that are concordant or discordant are also shown above and below individual branches, respectively.

Supplementary Figure 3. Plastome tree based on a concatenated matrix of 10 plastome regions. Node labels indicate standard, non-parametric bootstrap support. Branches that agree with the nuclear phylogeny are represented as thick black lines and conflicting branches are lighter gray.

Supplementary Table 1: Vouchers with their accession numbers and number of nuclear loci recovered.

Supplementary Table 2. Nuclear regions included in the phylogenetic analysis and their alignment method.

Supplementary Table 3. List of currently valid Neotropical Lecythidaceae names.

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