An Updated Infra-Familial Classification of Sapindaceae Based on Targeted Enrichment Data

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Publication Information

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Manuscript received 30 October 2020; revision accepted 17 March 2021.
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PREMISE: The economically important, cosmopolitan soapberry family (Sapindaceae) comprises ca. 1900 species in 144 genera. Since the seminal work of Radlkofner, several authors have attempted to overcome challenges presented by the family’s complex infra-familial classification. With the advent of molecular systematics, revisions of the various proposed groupings have provided significant momentum, but we still lack a formal classification system rooted in an evolutionary framework.

METHODS: Nuclear DNA sequence data were generated for 123 genera (86%) of Sapindaceae using target sequence capture with the Angiosperms353 universal probe set. HybPiper was used to produce aligned DNA matrices. Phylogenetic inferences were obtained using coalescence-based and concatenated methods. The clades recovered are discussed in light of both benchmark studies to identify synapomorphies and distributional evidence to underpin an updated infra-familial classification.

KEY RESULTS: Coalescence-based and concatenated phylogenetic trees had identical topologies and node support, except for the placement of Melicoccus bijugatus Jacq. Twenty-one clades were recovered, which serve as the basis for a revised infra-familial classification.

CONCLUSIONS: Twenty tribes are recognized in four subfamilies: two tribes in Hippocastanoideae, two in Dodonaeoideae, and 16 in Sapindoideae (no tribes are recognized in the monotypic subfamily Xanthoceratoideae). Within Sapindoideae, six new tribes are described: Blomieae Buerki & Callm.; Guindilieae Buerki, Callm. & Acev.-Rodr.; Haplocoeleae Buerki & Callm.; Stadmanieae Buerki & Callm.; Tristiropsideae Buerki & Callm.; and Ungnadieae Buerki & Callm. This updated classification provides a backbone for further research and conservation efforts on this family.

KEY WORDS: biogeography; infra-familial classification; new tribes; Sapindaceae; Sapindales; targeted enrichment; taxonomy.

The soapberry family (Sapindaceae, Sapindales), comprising ca. 1900 species (Acevedo-Rodriguez et al., 2011), has a predominantly pantropical distribution, although some taxa occur in temperate areas (e.g., Acer L.). Biogeographic reconstructions indicate that Sapindaceae originated in Eurasia sometime during the Late Cretaceous, with subsequent dispersals into the southern hemisphere during the Late Paleocene mediated by the Gondwanan break-up and the emergence of proto-SE Asia (Buerki et al., 2013).
Currently, >80% of the generic diversity is restricted to tropical and subtropical ecosystems of the southern hemisphere, largely resulting from three main routes of dispersal: one that connected Eurasia with Africa associated with the collision of the African and Eurasian plates; a second established between proto-SE Asia, Africa, and Madagascar, resulting from the break-up of India and Madagascar and the subsequent northern rafting of India; and a third that connected proto-SE Asia and Australia, facilitated by the existence of myriad archipelagos in the region (see Buerki et al., 2013 and references therein). Interestingly, South American lineages of Sapindaceae belonging to the Paullinia group (the only one in which llanas have evolved) were shown to have involved the third route of dispersal, via Antarctica, estimated to have occurred during the Middle Eocene (ca. 44 million years ago). The warm climate during this period (with ice probably only occurring in the Antarctic highlands and within and around the Arctic Ocean in the north) combined with the specific tectonic configuration at that time most likely mediated this type of long-distance dispersal (see Buerki et al., 2013 for more details and del la Estrella et al., 2019 for a review on the role of Antarctica in angiosperm biogeography). Sapindaceae include many economically important species used for their fruits (e.g., guara [Paullinia cupana Kunth], lychee [Litchi chinensis Sonn.], longan [Dimocarpus longan Lour.], pitho- nba [Talisia esculenta Radlk.], and rambutan [Nephelium lappa- ceum L.]), timber (e.g., buckeyes [species of Aesculus L.] and Fijian longan [Pometia pinnata J.R.Forst. & G.Forst.]), or as ornamentals (e.g., Koelreuteria paniculata Laxm. and Ungnadia speciosa Endl.).

Since the seminal work of Radlkofner (1931–1934), several authors have attempted, often with limited success, to develop an improved infra-familial classification of Sapindaceae (e.g., Klaassen, 1999; Muller and Leenhouts, 1976), which has benefited recently from molecular systematic work that has focused on the family or on particular groups. The phylogenetic study of Harrington et al. (2005), using broad sampling and two plastid markers (matK and rbcL), was the first to provide new insights into relationships within the family. This study placed the monotypic genus Xanthoceras Bunge (long included in Sapindaceae) as sister to a group comprising two clades, one comprising the historically recognized families Aceraceae and Hippocastanaceae, and another containing the remaining genera traditionally assigned to Sapindaceae. Based on these results, Harrington et al. (2005) proposed a broad definition of Sapindaceae in which four subfamilies are recognized, Dodonaeoideae, Hippocastanoidae (including taxa previously assigned to Aceraceae and Hippocastanaceae, along with the genus Handeliodendron Rehder, previously assigned to Dodonaeoideae), Sapindoideae (including the genera Koelreuteria Laxm. and Ungnadia Endl., likewise previously placed in Dodonaeoideae), and Xanthocarotidae (including just Xanthoceras). Although Harrington et al. (2005) questioned the traditional tribal delimitations proposed by Radlkofner (1931–1934), their sampling was not adequate to propose an alternative.

More recently, Buerki et al. (2009) produced a significantly expanded phylogenetic analysis of the family, increasing both the number of DNA regions used to eight (i.e., one nuclear and seven plastid regions) and the taxonomic sampling (encompassing 85 of the 141 of the genera known at the time, i.e., ca. 60%) in an attempt to test the monophyly and clarify the relationships of the 14 tribes recognized by Radlkofner (1931–1934). Their results revealed a high level of paraphyly and polyphyly at the subfamilial and tribal levels and cast serious doubt on the monophyly of several genera, including Arytera Blume, Cupaniopsis Radlk., and Haplocoelum Radlk. (see below). This prompted Buerki et al. (2009) to propose an informal tribal classification for the 14 clades they recovered in Dodonaeoideae and Sapindoideae as a basis for pursuing a more focused approach using phylogenetic and taxonomic research to identify morphological synapomorphies for each clade, thereby permitting a comprehensive re-circumscription of the tribes within the family (see also Buerki et al., 2010b, 2012).

Radlkofner (1931–1934) based his infra-familial classification mainly on the number and type of ovules per locule, fruit morphology, the presence or absence of arils or sarcotestas, leaf type, and cotyledon shape. Subsequent authors questioned the delimitation of certain tribes, although results from molecular analyses have provided support for at least some of them. For instance, in his treatment of Malagasy Sapindaceae, Capuron (1969) showed that several species of the endemic genera Tina Roem. & Schult. and Tinopsis Radlk. exhibited intermediate morphologies between tribes Cupanies and Schleichereae. Molecular analyses focusing on these and putatively related genera occurring in Madagascar confirmed Capuron’s predictions, leading to the placement of Tina in Cupanies and its re-circumscription to include Tinopsis and Neotina Capuron (previously placed in Schleichereae), both of which were nested within Tina (Buerki et al., 2011a). Muller and Leenhouts (1976) expressed doubt about Radlkofner’s use of palynological data to support his classification of the family, especially the monophyly of tribe Melicocceae and the recognition of Cupanies as distinct from Schleichereae and Nepheleeae. Acevedo-Rodriguez (2003) further challenged the monophyly of Melicocceae based on a morphological cladistic analysis, suggesting that Castanospora F.Muell., Tristira Radlk., and Tristriopsis Radlk. did not belong there. This idea was subsequently confirmed by molecular phylogenetic analyses in which Tristriopsis and Tristina formed distinct lineages from the core of Melicocceae (including Melicoccus P.Browne and Talisia Aubl.) (Harrington et al., 2005; Buerki et al., 2009). The position of Castanospora remains uncertain as it has not been included in any molecular studies to date. Finally, Acevedo-Rodriguez et al. (2017) applied a phylogenetic approach supported by morphological synapomorphies to investigate Sapindoideae supertribe Paulliniodae (corresponding to tribe Paulinieae of Acevedo-Rodriguez et al., 2011), showing that it comprises four clades, which they recognized as tribes Athyanaeae, Bridgesieae, Thouiniiaeae, and Paulinieae. Taken together, the morphological and molecular work published to date points strongly toward the need for an updated infra-familial classification of Sapindaceae and in particular a new delimitation of tribes.

A total of 141 genera were recognized in the treatment of Sapindaceae by Acevedo-Rodriguez et al. (2011), placed in four sub-families (Dodonaeoideae, Hippocastanoidae, Sapindoideae, and Xanthocarotidae). However, due to the high level of polyphyly at the infra-familial level, they only recognized six tribes that included a total of just 44 genera and refrained from placing any of the 97 remaining genera. Moreover, they cast doubt on the taxonomic status and placement of the monotypic African genus Chonopetalum Radlk., listing it as “insufficiently known.” Similarly, they questioned the placement of the monotypic genus Hirtania ’Thulin from Somalia, which Thulin (2007) had hypothesized to be closely related to the Australian genus Diploptelis Endl. (Dodonaeoideae) based on its flower morphology, but which has an intrastaminal floral disk, a character otherwise known only from the distantly related genus Acer (Hippocastanoidae). These examples further highlight the
difficulties of confidently assigning the majority of sapindaceous genera to a tribe.

The problems associated with tribal assignments of genera in Sapindaceae are compounded by uncertainties regarding the delimitation of many genera, including several shown to be polyphyletic. Since the treatment by Acevedo-Rodriguez et al. (2011), seven new genera have been described: Alatococcus Acev.-Rodr. (to accommodate a distinctive species that morphologically resembles Scyphyonychium Radlk.; Acevedo-Rodriguez, 2012), Allophyllastrum Acev.-Rodr. (for a species morphologically similar to Allophyllus; Acevedo-Rodriguez, 2011), Balsas J.Jiménez Ram. & K.Vega (now considered as a synonym of Serjania Mill.; Jiménez Ramirez et al. 2012; see Acevedo-Rodriguez et al., 2017), and Gereaua Buerki & Callm. (recognized to render Haplocoelum polyphyletic; Buerki et al., 2010a), as well as Lepidocupania Buerki et al. and Neoaorytera Callm. et al. (recognized so that the circumscriptions of Atyera and Cupaniopsis, respectively, are now monophyletic; Buerki et al., 2020; see also Buerki et al., 2012). Furthermore, over the last decade several genera have been placed in synonymy, including Neotina and Tinopsis, now included in Tina (Buerki et al., 2011a; Callmander et al., 2011). In all, 144 genera are currently recognized in Sapindaceae, assigned to four subfamilies and eight tribes (see Table 1). While molecular evidence has provided valuable information for refining our understanding of relationships within the family, 36 genera either lack molecular data or have never been assigned to a tribe or to one of the infra-familial groups defined by Buerki et al. (2009).

In this study, we present the results of a greatly expanded analysis of phylogenetic relationships within Sapindaceae using near-complete sampling at the genus level and a much larger set of nuclear markers obtained with a targeted enrichment approach. For each of the 21 clades recognized, its taxonomic composition, species richness, biogeography, and key morphological features are discussed. Based on the molecular evidence, we present an updated infra-familial classification of the family in which a total of 20 tribes are recognized (six of which are new) and their constituent genera are listed. As most genera of subfamily Sapindoideae have not previously been assigned to a tribe (Acevedo-Rodriguez et al. [2017] accepted the tribes presented by Acevedo-Rodriguez et al. [2011]), we base our decisions on the phylogenetic grouping proposed by Buerki et al. (2009, 2010a, 2010b, 2011b).

**MATERIALS AND METHODS**

**Sampling**

We aimed to sample at least one representative for all genera of Sapindaceae and sought to include collections belonging to type species, although this was not always possible, in which case, we used collections from the DNA and Tissue Collection at Royal Botanic Gardens, Kew (http://dnabank.science.kew.org/homepage.html) or from our own field-collected samples. Species representing the type genus of each tribe were also included to support the development of a tribal classification. The resulting sample set included representatives of 123 of the 144 currently recognized genera (86%), 31 of which had never been sequenced before or were not included in any previous family-wide phylogenetic analyses. All samples are vouchered by collections deposited in one or more of the following herbaria: BM (The Natural History Museum, London, UK), G (Conservatoire et Jardin botaniques de Genève, Geneva, Switzerland), K (Royal Botanic Gardens, Kew, UK), L (Naturalis, Leiden, Netherlands), MO (Missouri Botanical Garden, St, Louis, MO, USA), and P (Muséum national d'Histoire naturelle, Paris, France) (see Appendix S1 with Supplementary Data and Data Availability section for more details on data repository).

**DNA sequencing**

DNA extractions were performed with a modified CTAB method (Doyle and Doyle, 1987) using 40 mg of leaf material obtained from herbarium specimens or 20 mg of silica-gel-dried material. Extracts were subsequently cleaned using magnetic beads following the manufacturer's protocol (AMPure XP beads; Beckman Coulter, Indianapolis, IN, USA). Some DNA extracts were obtained from the Kew DNA Bank (see above). The quality and quantity of the DNA extracts were evaluated using a fluorometer (either Qubit, Thermo Fisher Scientific, Inchinnan, UK; or Quantum, Promega, Madison, WI, USA) to obtain 100–200 ng of DNA. The extracts were also run on a 1% agarose gel to determine the size of the fragments. Samples with low concentrations were further assessed using a 4200 TapeStation System with Genomic DNA ScreenTapes (Agilent Technologies, Santa Clara, CA, USA).

Before library preparation, samples with an average fragment size exceeding 350 bp were fragmented using a M220 Focus-Ultrasonicator (with microTUBES AFA Fiber Pre-Slit Snap-Cap) from Covaris (Woburn, MA, USA), with shearing times between 30 and 90 s, selected based on the estimated fragment size of a sample to obtain an average fragment size of 350 bp for each sample. Library preparation followed the standard protocol required for dual-indexed libraries of the DNA NEBNext Ultra II Library Prep Kit and the NEBNext Multiplex Oligos for Illumina from New England Biolabs (Ipswich, MA, USA). The quality of the library preparations was assessed using a 4200 TapeStation System with D1000 ScreenTapes, and subsequently quantified on a Quantus fluorometer. The resulting library preparations were pooled (8–24 samples per reaction) and enriched using the Angiosperms353 probe kit (v1; Arbor Biosciences; catalog #308196; Johnson et al., 2019), using the manufacturer's protocol and a hybridization temperature of 65°C for 24 h. The average fragment size and quality of the pooled samples were assessed again on a 4200 TapeStation System using D1000 ScreenTapes. Library pools were multiplexed for sequencing. Sequencing (2 × 150-bp paired-end reads) was either performed on an Illumina MiSeq (with v2, 300 cycles) at the Royal Botanic Gardens, Kew or on an Illumina HiSeq4000 at Genewiz (Takeley, UK).

**Gene recovery and phylogenetic tree reconstructions**

Gene-coding sequences were recovered from each specimen using HybPiper version 1.2 (Johnson et al., 2016) to find matching orthologous sequences from the Angiosperms353 target gene set (Johnson et al., 2019; https://github.com/mossmatters/Angio sperms353). First, specimen read sequences were trimmed using Trimmomatic (Bolger et al., 2019) with the following parameters: ILLUMINACLIP: <AdapterFastqFile>: 2:30:10:2:true; LEADING: 10; TRAILING: 10; SLIDINGWINDOW: 4:20; and MINLEN: 40. Successfully trimmed read pairs and singletons were then assembled in HybPiper default mode (read mapping to amino acid target...
<table>
<thead>
<tr>
<th>Clade</th>
<th>Radlkofer (1931–1934)</th>
<th>Buerki et al. (2009, 2011b)</th>
<th>Subfamily (this study)</th>
<th>Tribe (this study)</th>
<th>No. genera</th>
<th>Genera (no. of species)</th>
<th>No. species</th>
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<td>Begua (10), Camptolepis (4), Chouvia (6), Gereaua (1), Macphersonia (8), Pappea (1), Plagioscyphus (10), Pseudoperis (3), Stadmania (6), Tsingya (1)</td>
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<td>Madagascar (incl. Comoro Islands), the Mancearen, Seychelles Islands (Aldabra atoll), tropical Africa</td>
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<td></td>
<td>Schlechereae (1)</td>
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<td>21</td>
<td>Cupanieae (27),</td>
<td>Cupania (28), Not included (3), Litchi (2), Dodonaea (1)</td>
<td></td>
<td>Sapindoideae</td>
<td>34</td>
<td>Alectryon (30), Aryera (7), Castanospora (1), Cnemoscorpan (4), Cupania (45), Cupaniopsis (43), Dictyoneura (3), Diplolossus (12), Elattostachys (20), Eurycynthus (1), Gongrodiscus (8), Guioa (65), Jagera (2), Lecanodiscus (3), Lepiderama (8), Lepidocupania (21), Lepidodentalum (7), Matayba (56), Mischarytera (3), Mischocarpus (15), Molinaeae (9), Neoaryera (4), Pentagynus (1), Podonemophilum (9), Rhysophyta (14), Sarcopteryx (12), Sarcotoechia (11), Scythronychium (1), Starthocalyx (5), Symna (4), Tina (20), Toechima (7), Tragonacarya (8), Vouarana (1)</td>
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<td>Pantropical</td>
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<td>Sapindoideae</td>
<td>9</td>
<td>Bizanula (1), Chonopetalea (1), Gloeocarpus (1), Gongrospermum (1), Lychnodiscus (7), Namataea (1), Parocyritis (2), Pseudopancovia (1), Smelophyllum (1)</td>
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<td>Africa, South America, Philipines</td>
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sequences with BLASTX) except the --cov_cutoff parameter was set to 4. The same gene set was also retrieved from a transcriptome for *Aesculus pavia* L. from the One Thousand Plant (1KP) transcriptome initiative (sample HHBB; Leebens-Mack et al., 2019). Sequences for the same gene from each sample were aligned with MAFFT version 7.458 (Katoh and Standley, 2013) using the iterative refinement method (option --maxiterate 1000). Sequences with insufficient coverage (<60%) across well-occupied columns of each gene alignment were removed. Well-occupied columns were defined as those with more than 70% of positions occupied by base residues. Sequences with a total length of <85 bases were also removed. Each gene alignment were collapsed. For reconstructing the super-matrix tree, RAxML version 8.2.12 was set to perform rapid bootstrap analysis (option -f a), with the well-occupied columns in the gene trees with bootstrap support values <10% percent were collapsed. For reconstructing the super-matrix tree, RAxML version 0.9.0 was used.

**RESULTS**

**Sequence recovery and phylogenetic tree reconstructions**

For the species sequenced specifically for this study (i.e., excluding *Aesculus pavia*, which was obtained from OneKP; www.onekp.com), we recovered on average 2,634,488 reads per accession (range: 58,883–11,035,138) of which 451,877 (range: 7853–2,302,320) were on target (16.9%; range 1.14–31.95%). Of the 353 genes targeted by the Angiosperms353 probe set, we retrieved on average 335 (range: 45–349). Both ASTRAIL and concatenated analyses were performed on 343 gene alignments. All statistics concerning sequence recovery are presented in Appendix S1 (with data on vouchers and DNA accession numbers).

Angiosperms353 target gene sequences were generated for 123 genera (86%) represented by 135 samples (see Appendix S1 and Data Availability section for details on data repository). Of the 19 currently recognized genera not included in the present study, we attempted to sequence 10, but the samples failed to meet the HybPiper criteria due to the quality of the DNA and its replication (see above) and were therefore not included in further analyses. Material was unavailable for the nine other genera. Of the 19 genera not studied, only eight (viz. *Bizonula* Pellegr., *Chonopotulum* Radlk., *Gloeocarpus* Radlk., *Gongrospermum* Radlk., *Namataea* D.W. Thomas & D.J.Harris, *Pseudopancovia* Pellegr., *Scyphonychium* Cupania (Buerki et al., 2011b), and *Smelophyllum* Radlk.) were unable to include DNA sequences of these latter genera in the analyses presented here since they were represented only by plastid or nuclear ribosomal DNA sequences (rather than nuclear genes, targeted by the Angiosperms353 baiting kit; see above).

RAxML and ASTRAIL phylogenetic trees are available in Appendices S2 and S3 (newick trees are available here: https://github.com/svenbuerki/Angiosperms353_Sapindaceae/tree/master/Phylogenetic_trees). The phylogenetic trees obtained from the ASTRAIL III coalescent-based method and the RAxML concatenated maximum likelihood analysis are identical in terms of phylogenetic clustering/topologies and node support, except for the placement of *Melicoccus bijugatus* Jacq., which appears on its own in the ASTRAIL phylogenetic tree, whereas it is inferred as sister to representatives of *Talisia*, *Tripterodendron* Radlk., and *Dilodendron* Radlk. in the RAxML phylogenetic tree (see clade 20 in Appendices S2, S3). Hereafter we will only refer to the RAxML phylogenetic tree because it best supports previous phylogenetic hypotheses concerning the position of *Melicoccus* as sister to *Talisia*, *Tripterodendron*, and *Dilodendron* (e.g., Buerki et al., 2009, 2011b). A simplified, genus-level RAxML phylogenetic tree of Sapindaceae is presented in Fig. 1. Overall, 21 highly supported clades are identified, which serve as the basis for the new tribal classification presented below. Among these 21 clades, four are represented by a single genus: clades 1 (*Xanthoceras*), 11 (*Triстиrosis*), 14 (*Blomia* Miranda), and 15 (*Guindilia* Gillies ex Hook. & Arn.).

Table 1 summarizes the phylogenetic groups inferred in this study and compares them to those obtained by Buerki et al. (2009, 2011b) and to the tribes recognized by Radlkofier (1931–1934). The table also includes data on the number of genera, species richness, and overall distribution of each clade. Moreover, it lists the nine genera for which no genomic data and/or phylogenetic hypotheses are available.

**DISCUSSION**

**Overview of clades: evidence for a revised phylogenetic classification of Sapindaceae**

Although there were minor differences in the topologies of the ASTRAIL and RAxML phylogenetic trees (see Fig. 1 and Appendices S2, S3), they both overwhelmingly support the four subfamilies

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delimited by Acevedo-Rodríguez et al. (2011). Furthermore, the information provided by our analyses strongly supports the recognition of 20 tribes, each corresponding to one of the well-supported clades we have recovered within Sapindaceae (clade 1 corresponds to Xanthoceras, the only genus in subfamily Xanthoceratoideae, within which we have refrained from formally recognizing a tribe; see below and Fig. 1; Table 1). Unlike in previous molecular studies (e.g., Buerki et al., 2009; Harrington et al., 2005), the analyses presented here, which include the most complete generic coverage to date for the family (123 of 144 currently recognized genera; 86%), fully resolve the relationships between these clades (especially within the largest subfamily, Sapindoideae). Moreover, given the high level of agreement between the clades we have recovered and those reported in previous studies (e.g., Buerki et al., 2009, 2011b;
Muellner-Riehl et al., 2016), we are able to deduce the phylogenetic position of 10 genera whose placement has been particularly difficult. The placement of just nine genera, for which no sequence data are available, remains uncertain (Table 1).

Although the phylogenetic relationships among genera of Sapindaceae presented here are highly congruent with those reported in previous studies, they differ by the recovery of two groups for which limited support was previously available, i.e., the Litchi and Blomia groups (see below for more details; Fig. 1). A better understanding of the evolution and circumscription of genera within the Litchi group is especially important since it contains some of the most economically important crop species of Sapindaceae (in particular lychee, rambutan, and longan). These species are all placed in clade 9 (see below), an explicit phylogenetic hypothesis that opens up opportunities for identifying wild relatives of crops and developing long-term conservation programs that target these important taxa (see Aubriot et al., 2018 for an example regarding eggplant). Overall, the hypotheses embodied in our new infra-familial classification will not only contribute to a more robust taxonomy of Sapindaceae, but will also provide a much-improved framework for inferring the evolution and biogeography of this cosmopolitan family compared to earlier studies (e.g., Buerki et al., 2011c, Buerki et al., 2013).

The 21 clades retrieved in the present study are presented below by subfamily, following the phylogenetic sequence depicted in Fig. 1 (see Appendices S1, S2 for more details on species sampled). Morphological synapomorphies for the subfamilies follow Acevedo-Rodríguez et al. (2011). Our current understanding of each clade is reviewed, including species richness, distribution, and morphology, along with a discussion of the implications of this revised infra-familial classification (especially focusing on tribal circumscriptions). Genera not represented in our phylogenetic analyses but that were included in previous studies are also discussed.

I. Subfamily Xanthoceratoideae

Clade 1—This clade contains only the monotypic, temperate, Chinese and Korean genus Xanthoceras (Fig. 2A), the sole member of subfamily Xanthoceratoideae, which can be differentiated from taxa belonging to the other subfamilies of Sapindaceae by its large flowers (petals ca. 2 cm long) and disc with 5 horn-like appendages, the presence of 7 or 8 ovules per locule (all fertile), more than 15 seeds per fruit, and alternate, deciduous, imparipinnate leaves (Buerki et al., 2010b). Based on its phylogenetic position and unique spatiotemporal history, together with these clear morphological synapomorphies, Buerki et al. (2010b, 2011c) described the family Xanthocerataceae and recognized Aceraceae and Hippocastanaceae as distinct from a more narrowly delimited Sapindaceae nearly identical in circumscription to that used for nearly a century and a half. However, while there is strong justification for these familial delimitations (see Buerki et al., 2010b) and the decision to recognize one or four families is a matter of preference, the Angiosperm Phylogeny Group (APG IV, 2016) adopted a single, broadly defined family, and the classification presented here is aligned with their interpretation.

II. Subfamily Hippocastanoideae—This subfamily comprises five genera and ca. 130 species, primarily found in northern temperate ecosystems, with some lineages that have colonized tropical South America. Hippocastanoideae are characterized by opposite leaves and the presence of two ovules per locule (Acevedo-Rodríguez et al., 2011). Our phylogenetic analyses confirm that the subfamily comprises two clades, recognized as Aceraceae and Hippocastanaceae by Buerki et al. (2010b) but treated below as tribes within Sapindaceae.

Clade 2—This clade contains two genera, Acer L. (111 species in northern temperate and tropical Asian mountains, Fig. 2B) and Dipteronia Oliver (2 species in China), characterized by their actinomorphic flowers, petals without appendages, and an annular disk (Buerki et al., 2010b).

Clade 3—This clade includes three genera, Aesculus (13 species in Europe, North America, and Asia, Fig. 2C), Billia Peyr. (2 species from southern Mexico to tropical America), and Handeliodendron (1 species in deciduous forests of China). Its members are characterized by zygomorphic flowers, petals usually with appendages, and a unilaterally disk (Buerki et al., 2010b).

III. Subfamily Dodonaeoideae—This subfamily comprises 24 genera and ca. 140 species, characterized by alternate leaves and petals that usually lack appendages (Acevedo-Rodríguez et al., 2011). Our phylogenetic analyses placed these genera in two clades that are consistent with the corresponding tribes recognized by Acevedo-Rodríguez et al. (2011).

Clade 4—This clade contains seven genera and 18 species and is distributed across the southern United States (Florida), Central America (including the West Indies), Africa, Madagascar (including the Mascarene islands), and India, extending all the way to Australia and the Pacific Islands (Table 1). Clade 4 was previously identified by Buerki et al. (2009), who referred to it as the Doratoxylon group, to which only five genera were assigned, Doratoxylon (Fig. 2D), Filicium Thwaites ex Hook.f., Ganophyllum Blume, Hippobromus Ecklon & Zeyher, and Hypeleia P.E.Browne. In the present study, this same clade was recovered, also including Exotheca Macfad. (1 species in Florida, the West Indies, and Central America to northwestern South America) and Zanha Hiern (4 species in tropical Africa and Madagascar), for a total of seven genera, very much like Radlkofer’s tribe Doratoxyleae, with the exception that we have placed Euchorium Eckman & Radlkr. in clade 5 (see below).

Clade 5—This clade contains 16 genera with >120 species and is distributed across the Paleotropics. Eleven of these genera were previously assigned to the Dodonaeae group by Buerki et al. (2009, 2011b, 2012) and were included by Acevedo-Rodríguez et al. (2011) in Dodonaeae: viz. Arfueilea Pierre ex Radlkr. (1 species in Southeast Asia), Cosinia (4 species, disjunct between the Mascarenes islands and Australia and the Pacific islands), Diplolekeleba (2 species in South America), Diplolepsis (5 species in Australia), Dodonaea Miller (65 species distributed across the paleotropics, Fig. 2F), Euphorianthus Radlkr. (1 species in Malesia), Harpulia Roxb. (26 species in Asia, Malesia, Australia, and the Pacific islands), Lagunoa Ruiz & Pavón (3 species in tropical South America), Loxodiscus Hook.f. (1 species in New Caledonia), Magonia A.St.-Hil. (1 species in South America), and Majidea J.Kirk ex Oliv. (3 species in tropical Africa and Madagascar). Unfortunately, we were not able to include representatives of Cosinia and Diplolekeleba in our phylogenetic analyses, although they were placed in this clade by Buerki et al. (2012). In this study, we present new genomic and phylogenetic data for three additional genera that belong to clade 5: Euchorium (1 species in
FIGURE 2. (A) Xanthoceras sorbifolia, cultivated at Royal Botanic Gardens, Kew, UK. (B) Acer campbellii var. serratifolium, China (Boufford 43672). (C) Aesculus indica cultivated at Royal Botanic Gardens, Kew, UK. (D) Doratoxylon chouxii, Madagascar (Rakotovao et al. 6303). (E) Nephelium cuspidatum, Malaysia (Borneo) (Buerki et al. 359). (F) Dodonaea madagascariensis, Madagascar (Lowry 6285). (G) Paraneophelium joannis, Malaysia (Borneo) (Buerki et al. 358). (H) Erythrophysa aesculina, Madagascar (Phillipson 5704). Photo credits: © F. Forest (A, C), © C. Davidson (B, E), © C. Rakotovao (D), © P. B. Phillipson (F, H), and © M. W. Callmander (G).
Cuba), Hirania (1 species in Somalia), and Sinoradlkofera F.G.Mey. (1 species in China). Eschrium and Hirania are only known by their type specimens, which were sampled for our study. Euchrium was previously placed in Doratoxyceae by Radlkofe (1931–1934) and by Acevedo-Rodriguez et al. (2011), but its tribal placement remained uncertain due to the lack of data on fruit morphology. Our phylogenetic analyses support its placement in clade 5, close to Magonia (Fig. 1). Our results are also consistent with the morphological observations made by Thulien (2007), which prompted him to describe Hirania as a new genus and to place it in Dodonaeoideae based on its zygomorphic flowers (with five sepals with gland-tipped trichomes along margins, and four pink, subequal, clawed petals without appendages) and eight glabrous stamens. Thulien (2007) hypothesized that Hirania was closely related to Diploplexis, an interpretation that was not supported by our analyses (Fig. 1). Finally, the sole species of Sinoradlkofera was previously included in Koelreuteria (a member of Sapindoideae) by Radlkofe (1931–1934), but further morphological analyses were needed to confirm its tribal placement. Finally, genomic data presented here for the Malagasy genus Conchepetalus Radlk. strongly support its placement in Dodonaeoideae (Table 1; Fig. 1), as previously suggested by Capuron (1969) based on overall morphology, whereas the results of Buerki et al. (2009) had placed it in the Macphersonia group.

IV. Subfamily Sapindoideae—This subfamily comprises 107 genera and ca. 1400 species and is characterized by alternate leaves, petal appendages usually present, and an annular or unilateral disk (Acevedo-Rodriguez et al., 2011). Our phylogenetic analyses recovered 16 clades within Sapindoideae, which are used below to delimit the corresponding tribes in our new infra-familial classification. Because the taxa included in these clades have either one or two ovules per carpel, we consider this to represent a synapomorphy for Sapindoideae.

Clade 6—This clade exhibits a disjunct distribution between southern North America (Ungnadia, 1 species) and southwestern China and northern Vietnam (Delavaya Franch., 1 species; Fig. 3A). It is sister to the remainder of Sapindoideae, a relationship found previously by Buerki et al. (2011b). Its members are characterized by two ovules per carpel, type-A (colporate spheroidal) pollen, elongated basal petal appendages, glabrous stamens, and Cupaniana wood anatomy (Buerki et al., 2009; Klaassen, 1999).

Clade 7—This clade contains three genera and 13 species, assigned by Radlkofe to Koelreuterieae, and exhibits a disjunct distribution between Africa-Madagascar and southern China, Japan, eastern Iran, and Afghanistan (Table 1). We provide new genomic and phylogenetic data for Stocksia Benth., a monotypic genus restricted to eastern Iran and Afghanistan, which is sister to Koelreuteria (3 species) from southern China and Japan (Fig. 1). This placement is consistent with Radlkofe’s classification based on morphological similarities. The third genus in clade 7, the African-Malagasy Erythrophysa (9 species; Fig. 2H), was not included in our study, but previous phylogenetic inferences strongly support its inclusion (Buerki et al., 2011b). Buerki et al. (2011b) recovered Erythrophysa as sister to a clade comprising Koelreuteria and the South African monotypic genus Smelophyllum. We have therefore adopted their assessment, retaining these three genera in Koelreuterieae, with the caveat that additional genetic data will be necessary to confirm the placement of Smelophyllum. Members of clade 7 are characterized by zygomorphic flowers, 3-locular inflated capsules, and seeds without an aril or sarcotesta.

Clade 8—This clade contains six genera and 11 species distributed across Southeast Asia (Table 1). While we were not able to include representatives of the monotypic genus Schleichera in our study, clade 8 corresponds to the Schleicheraeae as defined by Buerki et al. (2009), with the addition of Pavieasia Pierre (3 species in southern China and northern Vietnam), Phyllotrichium Thorel ex Lecomte (1 species in Laos), and Sisyropelis Radlk. (1 species in Thailand and Cambodia), for which no genomic data were previously available (Fig. 1). These three genera were assigned to Cupanianae by Radlkofe (Table 1), a tribe that has been shown to be highly polyphyletic (e.g., Buerki et al., 2009, 2011a, b, 2012). The circumscription of Schleicheraeae, as defined by Radlkofe (1931–1934) and treated by Capuron (1969), includes 12 genera and exhibits a disjunct distribution between Africa-Madagascar and Southeast Asia (Buerki et al., 2009). The delimitation of clade 8 presented here is more biogeographically coherent than Schleicheraeae as it only contains genera occurring in Asia (Table 1). Although there is strong molecular support for this clade, further examination of morphological characters will be required to identify synapomorphies that support this circumscription. It is worth noting that the poorly known genera Phyllotrichium and Sisyropelis have zygomorphic flowers (vs. actinomorphic flowers in the other genera) and similar overall morphologies. Based on these characters, we hypothesize that they could represent a single genus, although our phylogenetic analyses do not support this and suggest instead that they belong to two distinct subclades (Fig. 1).

Clade 9—This clade includes 16 genera and 116 species, distributed across the tropics. It contains most of the economically important crop species found in Sapindaceae (belonging to Dimocarpus Lour., Litchi Sonn., and Nepheleum L.; Table 1). Clade 9 includes most of the genera of the Litchi group, as defined by Buerki et al. (2009, 2011b), along with 12 additional genera (including the type genus of Nepheleaeae): Blighia Koenig (4 species in tropical Africa), Chytranthes Hook. f. (30 species in Africa), Cabilia Blume (1 species in Malesia), Dimocarpus (4 species in Southeast Asia and Australia), Glenniea Hook. f. (8 species in tropical Africa, Madagascar, Sri Lanka, and Malesia), Haplococcolpis F.G.Davies (1 species in East Africa), Laccodiscus Radlk. (4 species in West Africa), Litchi (1 species in tropical China to West Malesia), Nepheleum (22 species in Southeast Asia and Malesia; Fig. 2E), Pancovia Willd. (13 species in tropical Africa), Pometia J.R.Forst. & G.Forst. (2 species in Malesia and the Pacific islands), and Xerospermum Blume (2 species in Indocheinese Peninsula and Malesia). These genera were previously dispersed among tribes Nepheleae, Lepisantheae, and Cupanianaee, distinguished from one another by Radlkofe (1931–1934) based on the presence of a fleshy aril in the first tribe and its absence in the second, and of a dry or fleshy aril in the third tribe. The presence of these morphological features among the members of clade 9 supports the hypothesis of convergent evolution of seed morphology, which is most likely connected to shifts in dispersal mechanisms (as discussed by Buerki et al., 2011a). In addition, four genera for which no genomic data were available before the present study belong to this clade: Aporrhiza Radlk. (6 species in tropical Africa), Otonephelium Radlk. (1 species in India), Placcodiscus Radlk. (15 species in tropical West Africa), and Radlkofera Gilg. (1 species in tropical Africa) (Fig. 1). Otonephelium was assigned to Nepheleaeae, whereas Aporrhiza was placed in Cupanianaee, and Placcodiscus and Radlkofera were included in Lepisantheae (Radlkofe, 1931–1934). We have not yet identified any morphological synapomorphies
that define this clade, but suspect that floral features may be useful for its characterization.

**Clade 10**—This clade includes 12 genera and ca. 130 species, distributed across the tropics (Table 1). Seven of these genera were placed by Buerki et al. (2009) in their Litchi group: *Atalaya* Blume (12 species in South Africa, Australia, and New Guinea), *Deinbollia* Schumach. & Thom. (40 species in tropical Africa and Madagascar), *Eriocoeleum* Hook. f. (10 species in tropical Africa), *Lepisanthes* Blume (the type genus of Lepisantheae, including 24 species in tropical Africa, Madagascar, Southeast Asia, Malesia, and Northwest Australia; Fig. 3B), *Pseudima* Radlk. (3 species in South America), *Sapindus* L. (the
type of Sapindaeae, including 13 species widely distributed across the tropics), and *Tristiropsis* (1 species in Malesia). The current study provides strong support for their inclusion in clade 10. The rest of the genera belonging to clade 10 were sequenced for the first time as part of our study: *Alatococcus* (1 species in Southeast Brazil), *Hornea* Baker (1 species in Mauritius), *Toulia* Aublet. (14 species in tropical America), *Thouinidium* Radlk. (7 species in Mexico and the West Indies), and *Zollingeria* Kurz. (3 species in Southeast Asia and Malesia) (see Table 1). Overall, six of the seven genera assigned to Sapindaeae by Radlkofe (the seventh, the tropical South American *Porocystis*, was not sampled and lacks any genomic data) were inferred to belong to clade 10. The remaining genera in this clade were previously placed in three other tribes, viz. Cupaniiaceae (*Eriocoeulum* and *Pseudima*), Lepisantheae (*Lepisanthes* and *Zollingeria*), and Melicoccaeae (*Tristiropsis*), to which the recently described Brazilian monotypic genus *Alatococcus* was subsequently added (Acevedo-Rodriguez, 2012). According to Radlkofe (1931–1934), Sapindaeae are morphologically very similar to Lepisantheae in having a single ovule per carpel and indehiscent fruits, and in lacking an aril. The placement of *Alatococcus*, *Lepisanthes*, *Tristiropsis*, and *Zollingeria* in clade 10 is supported by the presence of a single ovule per carpel and indehiscent fruits, and the absence of an arillode (Adema et al., 1994; Acevedo-Rodriguez, 2012). *Eriocoeulum* and *Pseudima* differ from the remaining genera in this clade by their dehiscent fruits and dry arils. However, despite sharing these characters, these two genera are not closely related to one another, which suggests that dehiscent fruits with dry arils may have evolved twice within the clade (Fig. 1).

**Clade 11**—This clade includes a single genus, *Tristiropsis*, with three species that occur in Malesia, Australia, and the Pacific islands (Fig. 3C, Table 1). *Tristiropsis* was assigned to Melicoccaeae by Radlkofe (1931–1934) but excluded from the tribe by Acevedo-Rodriguez (2003) due to its distinct fruit type, which is not shared with its other members. Our analyses confirm its exclusion from Melicoccaeae, and due to its distinctive fruits, which are unique within Sapindaeae (drupes with a [23]-locular stony endocarp), we have opted to place *Tristiropsis* in its own tribe (see below).

**Clade 12**—This clade includes two genera (*Haplocoeulum* and *Blighiopsis* Van der Veken) with seven species occurring in tropical Africa. Two species of *Haplocoeulum* (including the type, *H. inopaleum* Radlk.; Fig. 3D) were placed by Buerki et al. (2009, 2010a) along with *Blomia* in their Blomia group, although with poor support. The present analyses, for which *Blighiopsis* was sequenced for the first time, recover *Blomia* as a separate clade from *Haplocoeulum* and *Blighiopsis*. The latter two genera are morphologically similar, as reflected in the recent transfer of *Haplocoeulum gabonicum* Breteler to *Blighiopsis* by Hopkins (2013). They share the absence of partition walls in the fruit, resulting in a unilocular capsule (Fouilly and Hallé, 1973). In recognition of the distinctiveness of this clade, we describe a new tribe to accommodate its members (see below).

**Clade 13**—This clade includes four genera and >60 species occurring in tropical America. Three of the four genera were assigned by Buerki et al. (2009, 2011b) to their Melicoccus group: *Dilodendron* (1 species in South America), *Melicoccus* (10 species in tropical America), and *Talisia* (52 species in tropical America; Fig. 4B). We show here that the monotypic Brazilian genus *Tripterodendron* (sequenced for the first time) also belongs to this clade, within which it is sister to *Dilodendron*. Both of these genera were placed in Cupaniiaceae by Radlkofe (1931–1934), and they share similar morphologies (see Gentry and Steyermark, 1987). Acevedo-Rodriguez (2003) published a monograph of *Talisia* and *Melicoccus*, which are characterized by indehiscent fruits and sarcotestal seeds. This treatment could provide a basis for identifying morphological similarities between these genera and the species of *Dilodendron* and *Tripterodendron*, but despite the very coherent biogeography they exhibit, it remains unclear whether any morphological characters represent synapomorphies for the clade.

**Clade 14**—This clade only includes the monotypic genus *Blomia* (Fig. 3E), which occurs in Mexico, Guatemala, and Belize. As discussed above (see clade 12), this genus was previously found to be sister to the African *Haplocoeulum*, but the analyses presented here support its evolutionary distinctiveness, which has led us to describe a new tribe to accommodate it (see below).

**Clade 15**—This clade only includes the South American genus *Guindilia* (3 species; Fig. 3F), which was excluded from Paulliniaeae by Acevedo-Rodriguez et al. (2017) and inferred to be sister to supertribe Paulliniumiaeae (Appendix S3). Morphologically, *Guindilia* differs from members of Paulliniumiaeae by the presence of opposite, simple leaves (vs. alternate, compound leaves) (Acevedo-Rodriguez et al., 2017). Although the floral disc in *Guindilia* has been shown to be unilateral, it is roughly pyramidal in shape and two-lobed, a feature that is not present in Paulliniumiaeae (Acevedo-Rodriguez et al., 2017). Udampilella et al. (2016) informally recognized the *Guindilia* group based on palynological, karyological, and molecular phylogenetic data. To recognize the morphological and evolutionary distinctiveness of *Guindilia*, we have placed it in a new tribe, described below.

**Clades 16–19**—These clades correspond to supertribe Paulliniumiaeae, as defined by Acevedo-Rodriguez et al. (2017). This group is characterized morphologically by zygomorphic flowers, thyrses with lateral cincinni, corollas of four petals, and alternate leaves with a well-developed distal leaflet. Our study recovered the same phylogenetic clustering as Acevedo-Rodriguez et al. (2017), and we have therefore adopted the tribal delimitations presented in their study. Paulliniumiaeae thus contain four clades, recognized as tribes Athyaneae (clade 16), Bridgesiaeae (clade 17), Thouinieae (clade 18), and Paullineaeae (clade 19). Athyaneae comprise *Athyana* (Griseb.) Radlk. (1 species in South America; Fig. 4C) and *Diatensopteryx* Radlk. (2 species in South America), and contain trees with extipulate pinnately compound leaves and isopolar, spherical, colporate pollen grains. Bridgesiaeae contain the monotypic Chilean shrub genus *Bridgesia* Bertero ex Cambess., which has extipulate, simple leaves and isopolar, spherical, tricolporate pollen grains. Thouinieae comprise three genera of trees or shrubs with extipulate, trifoliate or unifoliolate leaves: *Allophylastrum* (1 species in Brazil and Guyana), *Allophylus* L. (250 species across the tropics), and *Thouinia* Poit. (28 species in Mexico and the West Indies; Fig. 4D). Paulliniumiaeae are circumscribed to include six genera: *Cardiospermum* (6 or 7 species in tropical America, 1 species also native to Africa; Fig. 4E), *Lophysistigma* Radlk. (2 species in South America), *Paullinia* L. (200 species in tropical America, 1 species also in Africa and Madagascar), *Serjania* (230 species in tropical America), *Thinouia* Planch. & Triana (14 species in tropical America), and *Urvillea* Kunth (21 species in tropical America). They are climbers or climber-derived shrubs with stipulate leaves and a pair of inflorescence tendrils. We were not able to include representatives of *Cardiospermum* in
our analyses, but previous studies have confirmed its placement in Paullinieae (e.g., Buerki et al., 2009; Acevedo-Rodríguez et al., 2017; Chery et al., 2019).

Clade 20—This clade comprises 10 genera and >50 species occurring in Madagascar (including the Comoro islands), the Mascarene islands, the Seychelles islands (Aldabra atoll), and tropical Africa.

It corresponds to the Macphersonia group of Buerki et al. (2009, 2010a, 2014), with the addition of the East African and Malagasy genus *Camptolepis* Radlk. (4 species) and the African-Malagasy *Stadmania* Lam. ex Poir. (6 species; Fig. 3F) (see Table 1 for a list of all genera). The first of these genera was not sequenced before the present study, although Capuron (1969) included it among Malagasy Schleichereae, along with the rest of the genera belonging...
to clade 20, based on its morphology, whereas *Stadmania* was assigned to Nepheleiae (Radlkofner, 1931–1934) and was previously recovered in the Koelreuteria group (see Buerki et al., 2011b), although its position there was not conclusive due to missing data. The placement of *Stadmania* in clade 20 is strongly supported not only by the results of our phylogenetic analyses, but also by its actinomorphic flowers (absent in *S. oppositifolia* Lam. ex Poir.), petals (when present) with basal appendage(s), a 3-carpellate ovary with a single ovule per carpel, and an indehiscent fruit with a seed covered by a fleshy, translucent aril, a suite of character shared with all the other genera in clade 20 (Capuron, 1969). In recognition of the coherence of this clade, we describe a new tribe to accommodate its members (see below).

**Clade 21**—This clade, which corresponds to the Cupania group of Buerki et al. (2009, 2012, 2013, 2020), is the most diverse lineage in Sapindaceae at the generic level, with 34 genera and >460 species occurring throughout the tropics. Buerki et al. (2013) hypothesized that the high level of species richness exhibited by this clade resulted from interactions between climate change at the Eocene-Oligocene boundary and the emergence of islands in Southeast Asia, triggering rapid biogeographic movements promoting its diversification. This interpretation was also supported by relatively short branch lengths within this clade when compared to the rest of Sapindoidea, which resulted in phylogenetic uncertainty in several lineages (for further details, see Buerki et al., 2012, 2013). Although a few nodes in clade 21 have low support in the analyses presented in this study, the information provided by the Angiosperms353 baiting kit enabled the resolution of relationships among its members, especially the early-diverging lineages (Fig. 1). Based on our results, four genera for which no genomic data were previously available have been added to the Cupania group: *Castanosperma* F.Muell. (1 species in Northeast Australia), *Cnemoscarpon* Adema (4 species in Australia and Papua New Guinea), *Pentaschys* Radlk. (1 species in Guyana), and *Trigonachras* Radlk. (8 species in Malesia). The last three of these genera were placed in Cupaneae by Radlkofner (1931–1934), and their fruit morphologies are indeed very close to *Cupania*, which would suggest that *Cupania* is not a member of Schleichereeae (sensu Radlkofner) but rather belongs to clade 20. The tropical West African *Lychnodiscus* (6 species) was also previously placed in Cupaneae by Radlkofner (1931–1934), and most of the genera he assigned to this tribe were recovered in clade 21, but apart from *Lecaniodiscus*, none occur in mainland Africa. A *matK* sequence (GenBank accession MN370324) of *L. dananensis* Aubr. & Pellegr., was produced by Janssens et al. (2020) for DNA barcoding analyses. A BLAST analysis on this sequence suggested a close relationship with species of the African genus *Chytranthus*, which would instead place *Lychnodiscus* in clade 9. *Namataea* (1 species in Cameroon) was regarded as a member of Lepisantheae by Thomas and Harris (1999) because it morphologically resembles *Chytranthus*, prompting us to hypothesize that it may also belong to clade 9. *Pseudopancovia* (1 species in tropical West Africa) was also included in Lepisantheae (Radlkofner, 1931–1934), and its flower and fruit morphologies would also suggest a close relationship with genera in clade 9. *Porocystis* (2 species), distributed in South America, was placed in Sapindeae by Radlkofner (1931–1934). A *matK* sequence of *P. toulcicoides* Radlk. was produced by Clark, Pennington and Dexter (GenBank accession MH024824) but has to be taken with caution since it is not associated with a publication or a cited voucher (at least not as of 1 June 2021). A BLAST analysis revealed that this species is genetically closely related to species of *Acteleyon* Gaertn. and *Mischarytrea* (Radlk.), H. Turner, which would suggest that *Porocystis* may belong to clade 21. Finally, we are unable to comment on the affinities of the monotypic African *Chonopetalum*, since it is only known from the type specimen and is in critical need of further study.

**TAXONOMIC TREATMENT**

The updated infra-familial classification of Sapindaceae presented below follows the sequence of the clades recovered in our phylogenetic analyses (Fig. 1; Table 1). Four subfamilies are recognized along with 20 tribes distributed as follows: two tribes in Hippocastanoideae, two in Dodonaeoideae, and 16 in Sapindoideae (no tribes are recognized in the monotypic subfamily Xanthoceroideae). Within Sapindoideae, we formally describe six new tribes, as follows: Blonieae Buerki & Callm. (tribe 13), Guindilieae Buerki, Callm. & Accv.-Rodr. (tribe 14), Haplocooeae Buerki & Callm. (tribe 11),
I. Subfamily Xanthoceroideae

Note: This taxon corresponds to clade 1 of our phylogenetic tree (Table 1; Fig. 1) and includes a single genus, *Xanthoceras* (Fig. 2A).

II. Subfamily Hippocastanoideae

1. Tribe Aceraceae (Durande) Dumort. Fl. Belg.: 113. 1827. Type: *Acer* L.

Note: This taxon corresponds to our clade 2 (Table 1; Fig. 1) and includes two genera, *Acer* (Fig. 2B) and *Dipteronia*.

2. Tribe Hipocastaneae (DC.) Dumort. Fl. Belg.: 113. 1827. Type: *Aesculus* L.

Note: This taxon corresponds to clade 3 (Table 1; Fig. 1) and includes three genera: *Aesculus* (Fig. 2C), *Billia*, and *Handeliodendron*.

III. Subfamily Dodonaeoideae


Note: This taxon corresponds to clade 4 (Table 1; Fig. 1) and includes eight genera: *Doratoxylon* (Fig. 2D), *Exothea*, *Filicium*, *Ganophyllum*, *Hipppobromus*, *Hypelate*, *Smelophyllum*, and *Zänha*.

4. Tribe Dodonaeae (Kunth) DC. Prodr. 1: 615. 1824. Type: *Dodonaea* Mill.

Note: This taxon corresponds to clade 5 (Table 1; Fig. 1) and includes 16 genera: *Arfeuillea*, *Boniodendron*, *Conchopetalum*, *Cosinia*, *Diplokeleba*, *Diplopeltis*, *Dodonaea* (Fig. 2F), *Euchorium*, *Euphorianthus*, *Harpullia*, *Hirania*, *Llagunoa*, *Locolidiscus*, *Magonia*, and *Majidea*.

IV. Subfamily Sapindoideae

5. Tribe Ungnadiae Buerki & Callm., tribus nov. Type: *Ungnadia* Endl.

Shrubs or small trees. Leaves alternate, 3-foliolate or paripinnate, stipule absent. Flowers zygomorphic, functionally unisexual. Sepals 5, imbricate. Petals 4–5, clawed, with a tuft of filiform appendages above the claw; disk wavy; stamens generally 8, glabrous; ovary stipitate, 2–3-carpellate, ovules 2 per carpel. Fruit a 2- or 3-lobed, loculicidal coriaceous capsule. Seeds without aril.

Note: This new tribe is characterized by zygomorphic flowers with clawed petals bearing a tuft of filiform appendages above the claw, glabrous stamens, and two ovules per carpel. This taxon corresponds to our clade 6 (Table 1; Fig. 1) and includes two genera, *Delavaya* (Fig. 3A) and *Ungnadia*.


Note: This taxon corresponds to clade 7 (Table 1; Fig. 1) and includes three genera: *Erythrophysa* (Fig. 2H), *Koelreuteria*, and *Stocksia*.


Note: This taxon corresponds to clade 8 (Table 1; Fig. 1) and includes six genera: *Amesiodendron*, *Paranepheleium* (Fig. 2G), *Pavieasia*, *Phyllotrichium*, *Schlecheira*, and *Sisysrolepis*.


Note: This taxon corresponds to clade 9 (Table 1; Fig. 1) and includes 16 genera: *Aporrhiza*, *Blingha*, *Chytanthus*, *Cubilia*, *Dimocarpus*, *Glenniea*, *Haplocoelopsis*, *Laccodiscus*, *Litchi*, *Nephelium* (Fig. 2E), *Ononephelium*, *Pancovia*, *Placodiscus*, *Pometia*, *Radkofera*, and *Xerospermum*.

9. Tribe Sapindeae (Kunth) DC. Prodr. 1: 607. 1824. Type: *Sapindus* L.

Note: This taxon corresponds to clade 10 (Table 1; Fig. 1) and includes 13 genera: *Alatococcus*, *Atalaya*, *Deinbollia*, *Eriocoele*, *Hornea*, *Lepisanthes* (Fig. 3B), *Porocystis*, *Pseudima*, *Sapindus*, *Thouinidium*, *Toulicia*, *Tristira*, and *Zollingeria*.


Trees. Leaves alternate, bipinnate. Inflorescences thyrses, axillary, borne towards the end of the branches. Flowers zygomorphic, bisexual or functionally unisexual; sepals 5; petals 5 or absent, clawed, with basal appendages; stamens 8(–13); disc disk annular; ovary 3(–5)-carpellate with a single ovule per carpel; style sessile, short or elongated; stigma not lobed. Fruit a (2–3)-locular; indehiscent drupe; seeds without an arilode.

Notes: This new tribe is characterized by true drupes with a (2–3)-locular stone layer, a feature that is unique among Sapindaceae. It corresponds to clade 11 (Table 1; Fig. 1) and includes a single genus, *Triptisropsis* (Fig. 3C).


Trees and shrubs. Leaves alternate, pinnate. Flowers actinomorphic, functionally unisexual; sepals 4–7; petals absent; stamens 4–7; disc hemispherical; ovary 3-carpellate with a single ovule per carpel; style short, stigma 3-lobed. Fruits a capsule, 1-locular, indehiscent to tardily dehiscent; seeds with an aril.

Note: This new tribe is characterized by alternate pinnate leaves, actinomorphic and functionally unisexual flowers, absence of petals, 3-carpellate ovary with a single ovule per carpel, and fruit that is 1-locular by abortion with an arillate seed. It corresponds to clade 12 (Table 1; Fig. 1) and includes two genera, *Blighiopsis* and *Haplocoelum* (Fig. 3D).


Note: This taxon corresponds to clade 10 (Table 1; Fig. 1) and includes four genera: *Dilodendron*, *Melicoccus*, *Tallisia* (Fig. 4B), and *Tripterodendron*.

13. Tribe Blomieae Buerki & Callm., tribus nov. Type: *Blomia* Miranda

Trees. Leaves alternate, paripinnate. Flowers actinomorphic, unisexual or bisexual; sepals 5, distinct, valvate; petals absent or...
vestigial, with a pair of minute vestigial appendages; disk annular-
lobed; stamens 5–6; ovary 1-carpellate with a single ovule per car-
pel; style short, stigma capitulate. Fruit a 1-locular, tardily loculically
dehiscent, coriaceous capsule. Seeds with a thin aril.

Note: This new tribe is characterized by paripinnate leaves, pet-
als (when present) with adaxial or marginal appendages (Acevedo-
Rodriguez, 2009), a 1-carpellate ovary, a coriaceous capsule that is
tardily loculically dehiscent, and seeds with a thin arillode. It corre-
responds to clade 14 (Table 1; Fig. 1) and includes a single genus,
Blomia (Fig. 3E).

14. Tribe Guindilieae Buerk, Calm. & Acev.-Rodr., tribus
nov. Type: Guindilia Gillies ex Hook. & Arn.

Shrubs or small trees. Leaves alternate or opposite, simple, entire
or tridentate at apex. Flowers zygomorphic, bisexual or function-
ally unisexual; sepals 5, imbricate; petals 4(–5), with a hood-shaped,
crested, ventral appendage; disk unilateral, 2-lobed-pyramidal; sta-
mens 8; pollen colporate, striate; ovary 3-carpellate with a single
ovule per carpel; style filiform, stigma 3-lobed. Fruit schizocarpic,
splitting into (1–)3 subglobose, crustose mericarps. Seed without an
aril.

Note: This new tribe is characterized by simple leaves, a uni-
ilateral 2-lobed pyramidal disc, and a schizocarpic fruit that splits
into 1–3 subglobose, crustose mericarps (Acevedo-Rodriguez et al.,
2011, 2017). It corresponds to clade 15 (Table 1; Fig. 1) and includes
a single genus, Guindilia (Fig. 3F).

Athyana (Griseb.) Radlkl.

Note: This taxon corresponds to clade 16 (Table 1; Fig. 1) and
includes two genera, Athyana (Fig. 4C) and Diatenopteryx.

Bridgessia Bertero ex Cambess.

Note: This taxon corresponds to clade 17 (Table 1; Fig. 1) and
includes a single genus, Bridgesia (Fig. 4A).

17. Tribe Thouiniaee Blume. Rumphia 3: 186. 1847. Type:
Thouinia Poit.

Note: This taxon corresponds to clade 18 (Table 1; Fig. 1) and
includes three genera: Allophylastrum, Allophylus, and Thouinia
(Fig. 4D).

18. Tribe Paulinieae (Kunth) DC. Prodr. 1: 601. 1824. Type:
Paulinia L.

Note: This taxon corresponds to clade 19 (Table 1; Fig. 1) and
includes six genera: Cardiospermum (Fig. 4E), Lophostigma, Paulinia,
Serjania, Thinouia, and Urvilea.

19. Tribe Stadmanieae Buerk & Calm., tribus nov. Type:
Stadmania Lam. ex Poir.

Trees and shrubs. Leaves simple, biparipinnate or paripinnate.
Corolla actinomorphic or absent, functionally unisexual; sepals 5 or
absent; petals 5 or absent, clawed, with basal appendages; stamens
5(6–10); disk annular to 5-lobed; ovary 3-carpellate with a single
ovule per carpel, style sessile, short or elongated, stigma 2–3-lobed
or with 2–3 stigmatic branches or lines; fruit 1–3 locular, indehis-
cent or tardily dehiscent. Seeds with an arillode.

Note: This new tribe is characterized by actinomorphic flow-
ners (perianth absent in Beguea Capuron, Tsingya Capuron, and
Stadmania oppositifolia), petals (when present) with basal appen-
dages, ovary 3-carpellate with a single ovule per carpel, and a seed
covered by an arillode. It corresponds to clade 20 (Table 1; Fig. 1)
and includes 10 genera: Beguea, Camptolepis, Chouxia, Gereaua,
Macphersonia, Pappea, Plagioscyphus, Pseudopteris, Stadmania
(Fig. 4F), and Tsingya.


Note: This taxon corresponds to clade 10 (Table 1; Fig. 1) and in-
cludes 36 genera: Alectryon, Arytera, Castanospora, Cesmocarpys,
Cupania, Cupaniopsis, Dictyoneura, Diploglottis, Elattostachys,
Euryocorymbus, Gloeocarpus, Gongrodiscus, Gongpropermum, Guioa,
Jugera, Lecaniodiscus, Lepiderema, Lepidocapnia, Lepidopetalum,
Matayba, Mischarytera, Mischocarpus, Molinaea, Nearya,terys,
Pentasychus, Podonephelium (Fig. 4G), Rhysoctoechia, Sarcopteryx,
Sarcotoechia, Scyphyochium, Storthocalyx, Synima, Tina, Toecharina,
Trigonachras, and Vouarana.

ACKNOWLEDGMENTS

This work was funded by grants from the Calleva Foundation and
the Sackler Trust to the Plant and Fungal Tree of Life Project
(PAFTOL) at the Royal Botanic Gardens, Kew. Fieldwork by S.B.,
M.W.C., J.M., and P.P.L. was supported by the Idaho Botanical
Research Foundation. We thank the curators at the following her-
baria for making their collections available for our research: BM,
BRI, CNS, G, K, KLU, L, MO, MPU, NOU, P, SAR, SAN, SUVA,
SING. We are grateful to Michail Belov (http://www.chileflora.
com), Philippe Chassot (https://philou.i234.me), Christopher
Davidson (https://floraoftheworld.org), Claire De Schrevel, G. Curt
Fieldler (http://www.umijin.com), Olga Martha Montiel, Diosdado
Nguema, Pete Phillipson, Charles Rakotovao, and Germaine
A. Parada for permission to reproduce their photos, and to Roy
Gereau for advice regarding Latin. We especially express our grati-
itude to Christopher Davidson and Sharon Christoph for their con-
tinuous support and interest in our research. Finally, we thank two
anonymous reviewers for their helpful comments on a previous
version of this paper.

AUTHOR CONTRIBUTIONS

S.B., M.W.C., and F.F. designed the study and coordinated it with
contributions from O.M. and W.J.B.; S.B., M.W.C., J.M., and
P.P.L. collected the data; G.E.B. and N.E. conducted the laboratory
work; P.B. and S.B. analyzed the data; S.B., M.W.C., P.B., P.P.L.,
and F.F. wrote the manuscript; all authors provided input on the manu-
script and gave final approval for publication. W.J.B. and F.F.
supervised the PAFTOL project at RBG Kew.

DATA AVAILABILITY

The data (a spreadsheet summarizing sampling as well as ASTRAL
and RaxML phylogenetic trees in newick format) and R code
(scripts to produce Table 1, Fig. 1, and Appendices S2 and S3) un-
derpinning this study are available on GitHub: https://github.com/
svenbuerki/Angio353_Sapindaceae

ENA (European Nucleotide Archive) accession numbers for all
samples included in this study are available in Appendix S1.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the
supporting information tab for this article.
APPENDIX S1. Statistics on gene recovery for Sapindaceae accessions included in this study and details on vouchers and ENA accession numbers.

APPENDIX S2. RAxML phylogeny of Sapindaceae based on Angiosperms353 target gene sequences. Clades (Arabic numbers correspond to tribes and Roman numbers to subfamilies) are displayed along with bootstrap support values. See Appendix S1 for more details on species sampling and node support.

APPENDIX S3. ASTRAL phylogeny of Sapindaceae based on nuclear Angiosperms353 target gene sequences. Clades (Arabic numbers correspond to tribes and Roman numbers to subfamilies) are displayed along with node support values. See Appendix S1 for more details on species sampling and node support.

LITERATURE CITED


