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Wood anatomy helps solve challenging taxonomic relationships in the tropical Sapotaceae

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Summary – The Sapotaceae (Ericales) are an average-sized pantropical family mostly known for hard and durable timber. The many impressively tall trees of this family are ecologically important in tropical forests, but ongoing (illegal) logging practices threaten many species with extinction. Conservation efforts for Sapotaceae are difficult since lineages have undergone many taxonomic changes over the past two centuries, and classifications based on morphological characters are heavily debated. Molecular phylogenies have improved our knowledge of species relationships to some extent, but a robust classification of the entire family remains lacking. Likewise, wood anatomical studies are often fragmented or unpublished, urging the need for a global study of the family. Hence, we present the first wood anatomical overview of Sapotaceae based on approx. 450 species, summarising earlier unpublished work combined with over 150 new descriptions. We found monophyletic clades can be recognised by wood anatomical traits, such as variation in mineral inclusion type (prismatic crystals, silica bodies, or crystal sand), silica body size, vessel-ray pit variation, ray width, fibre wall thickness, vessel arrangement, and axial parenchyma distribution. We used these traits to perform ancestral state reconstructions on the Chrysophylloideae and Sapotoideae, for which published molecular phylogenies are available with a limited number of chloroplast and/or nuclear markers. Likewise, we did the same on a new genus-level phylogeny made with an angiosperm target capture bait set that includes 353 low-copy nuclear markers. Several striking evolutionary patterns were revealed, such as complex evolutionary shifts in mineral inclusions and independent reversals from simple to scalariform vessel perforations. With this overview, we have summarised wood anatomical variation in the often-ignored Sapotaceae, and hope these results will aid taxonomic and evolutionary studies, as well as conservation efforts on these majestic trees.

Keywords – hardwood timber species, phylogenetic comparative methods, sapodilla, wood evolution.

Introduction

Sapotaceae are an average-sized angiosperm family of about 1300 species consisting of 74 currently accepted genera that are mostly found in the humid tropics, but a considerable number of species extend to seasonally dry or more arid regions (Govaerts *et al.* 2001). Members can be found in all regions of the world with notable biodiversity hotspots

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in Amazonian South America, Madagascar, south-east Asia, and the Pacific Islands (Govaerts *et al.* 2001; Richardson *et al.* 2014). Sapotaceae are mostly trees, varying in size from short understory trees to tall canopy trees up to 70 m (Govaerts *et al.* 2001), but plenty of species are shrubs, and there is one climber (*Donella welwitschii*). Sapotaceae species are a fundamental part of many tropical forests. In regions of tropical South America, they make up 40% of the forest's biomass (Pennington 1991), and can dominate large areas (Ter Steege *et al.* 2013). Several species provide economically important products, such as latex from the bark, cosmetic oils from seeds (e.g., shea and argan), edible fruits (e.g., sapodilla and star-apple), and high-quality and heavy hardwood timber (e.g., massaranduba and nyatoh; Pennington 1991; Charrouf & Guillaume 2008; Silva *et al.* 2008; Wilkie 2011). This hardwood is generally very dense, regularly reaching specific gravities of over 1.0 g/cm^3 (Kukachka 1978b, 1981a) that are challenging to section and require special softening methods (Kukachka 1977; MacLachlan & Gasson 2010).

Despite its ecological and economic importance, intrafamilial relationships in Sapotaceae have been contested since the introduction of the family (Jussieu 1789). Genera and clades have been frequently split and lumped based on morphological traits. Since the emergence of molecular phylogenetic methods, species relationships have been mostly investigated with a few nuclear and chloroplast markers (Anderberg & Swenson 2003; Swenson *et al.* 2023). Recently, classification efforts have been made with a more extensive angiosperm-wide bait set that includes 353 nuclear markers (Zuntini *et al.* 2024). However, a robust, family-wide phylogeny is still to be made. The taxonomic challenges notwithstanding, three subfamilies are currently recognised: Sarcospermatoideae, Sapotoideae and Chrysophylloideae (Anderberg & Swenson 2003; Swenson & Anderberg 2005). Sarcospermatoideae are the earliest diverging and consist of one Asian genus (*Sarcosperma*) with 11 species (Fig. 1). Sister to the rest of the Sapotaceae is the Asian *Eberhardtia* (three species), which has not been assigned to any of the three subfamilies, but is traditionally considered a member of the Sapotaceae. The species-rich Sapotoideae and Chrysophylloideae form sister clades. The inclusion of the pantropical *Sideroxylon* (84 species) in Sapotoideae is debated (Fig. 1), and here we treat this genus separately. The Sapotoideae (approx. 500 species) consist of two formerly recognised tribes (Isonandreae and Mimusopeae) (Pennington 1991) and a few other genera (Fig. 1). Most Mimusopeae are native to Africa, but *Manilkara* is found pantropically, while Isonandreae have an Asian distribution. Current circumscription of the Chrysophylloideae (approx. 630 species) is mostly in agreement with the Chrysophylleae as recognised by Pennington (1991; Fig. 1). It is very prominent in the Americas, includes many formerly recognised and monotypic genera (Fig. 1), and it is the first subfamily for which the evolution of morphological traits was assessed in detail (Swenson *et al.* 2023).

The wood anatomy of neotropical Sapotaceae was extensively documented by Kukachka in the 1980s. He described genera in 38 separate papers for which he sectioned and described hundreds of samples, including many type specimens (Kukachka 1978–1982). Budi described the wood anatomy of many Asian Sapotaceae (131 species) in his unpublished PhD thesis (Budi 1993). Likewise, Lens (2005) filled major gaps for African Sapotaceae (79 species) in an unpublished chapter of his dissertation on the wood anatomy of the Ericales, and this is still the most recent wood anatomical update of Sapotaceae. Other substantial wood anatomical contributions are from Detiénne & Jacquet (1983) (21 neotropical genera), and Record (1939) (17 neotropical genera); less extensive family contributions are listed in Gregory (1994). Recent studies deal with only one or two genera, often in combination with other methods to investigate Sapotaceae taxonomy or wood identification (Prasawang & Srinual 2020; Deklerck *et al.* 2021). The important works of Kukachka, Budi, Lens, and others have shown considerable variation in wood anatomy across the family. However, in the influential family treatment of Pennington (1991), Sapotaceae woods were described as anatomically uniform, which did not stimulate wood scientists to complete a wood anatomical overview of the family. Consequently, wood anatomical traits have generally not been integrated in family-wide taxonomic studies and evolutionary trends in wood anatomical traits are unknown. Our study aims to fill this knowledge gap.

Sapotaceae trees are often (illegally) logged for their valuable hardwood, which can cause serious damage to the fragile forest ecosystems they are found in (Foley *et al.* 2007). It is expected that Sapotaceae timber species will be added to the CITES Appendices (Convention on International Trade in Endangered Species of Wild Fauna and

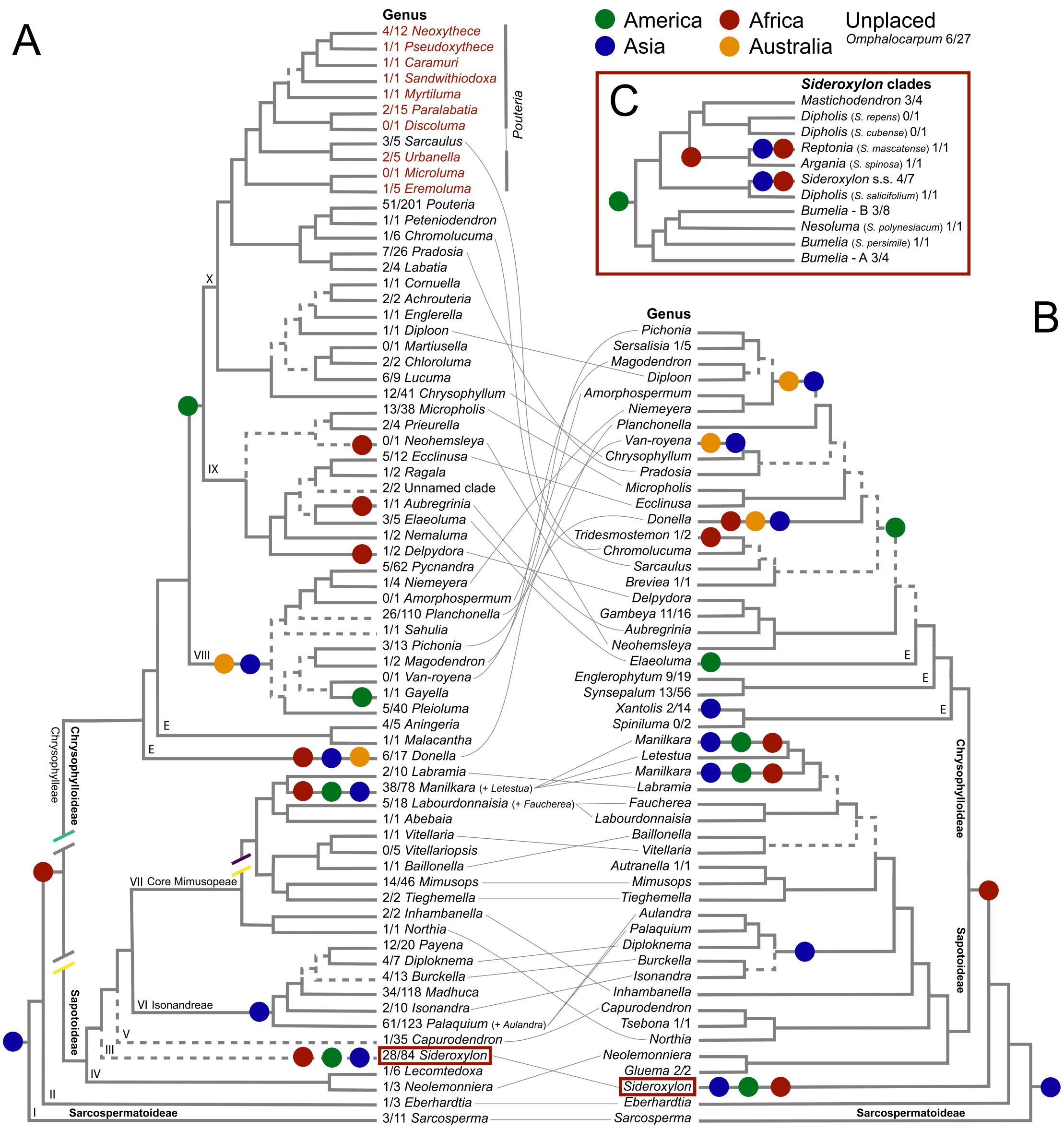


Fig. 1. Sapotaceae molecular phylogenies at the genus level. (A) Synthetic topology using several published phylogenies. The genus relationships in Sapotoideae and Chrysophylloideae are based on: the chloroplast topology of Richardson *et al.* (2014; branches between yellow dashes), nuclear phylogeny of Randriarisoa *et al.* (2023; branches following purple dash), and chloroplast + nuclear phylogeny of Swenson *et al.* (2023; branches following green dash). Genera in red are currently not accepted but suggested to be reinstated upon further sampling (Swenson *et al.* 2023). (B) Phylogenetic tree based mainly on (un)published sequence data from 353 nuclear markers (Zuntini *et al.* 2024). (C) Topology of *Sideroxylon* clades based on the chloroplast phylogeny of Richardson *et al.* (2014) with reference to the previously accepted genera. Numbers before (A) or after (B, C) genus names are the number of species investigated in proportion to the total number of species in that genus (following POWO 2024). Dashed branches represent uncertain relationships with posterior probabilities of <95%, subfamilies are indicated along the branches in bold, and several important tribes of Pennington (1991) are mentioned in regular writing. Grey lines between the topology tip labels highlight differences in taxonomic placements. Roman numbers indicate monophyletic clades, which will be referred to in the main text, while E is a paraphyletic group dealt with separately.

Flora; CITES 2023) in the near future, urging us to provide scientific tools to identify and thus protect these species. With this study, we present the first wood anatomical overview of the family, which can help in the identification of traded Sapotaceae woods. This overview includes three major objectives: 1) summarise wood anatomical variation of the entire family, 2) compare the anatomy of closely and more distantly-related clades according to molecular phylogenies and look for wood anatomical synapomorphies, and 3) investigate the evolution of several noteworthy traits within a molecular phylogenetic framework.

Materials and methods

In total 1196 slides were available for this wood anatomical overview, belonging to 68 (out of 74, see Fig. 1) currently recognised genera and 443 species. These slides were: newly made in the Naturalis laboratory (162 slides), made by Kukachka and offered as a loan by the Madison Forest Products Laboratory (630 slides), made by Budi and loaned with additional slides by the Thünen Institute (196 slides), or already available in the slide collections of Naturalis Biodiversity Center (208 slides — Lw, Uw, WAGw). See Supplementary 1 for voucher information on all slides used, including references to previous publications. Additionally, 15 descriptions from InsideWood (InsideWood 2004–onwards) were added to the dataset, as well as 2 observations from the Atlas of Chinese Woods (Luo *et al.* 2022; see Supplementary 2 for the full dataset). The new wood sections were prepared according to the protocol of Lens *et al.* (2005), with the adaptation that samples were heated in a 1:1:1 mixture of glycerol, water, and 70% ethanol at 200°C for half a day before sectioning (following an adjusted protocol used in the Thünen Institute). Particularly hard samples were treated with ethylenediamine according to the protocol of MacLachlan & Gasson (2010). Wood anatomical variation was described according to the standardised IAWA hardwood list (IAWA Committee 1989), with the following changes. Vessel grouping was classified as follows: (1) mainly solitary vessels, (2) equal presence of solitary vessels and vessels in short radial multiples of 2–5, (3) mainly short radial multiples of 2–5, (4) mainly long radial multiples of 5–15. Ray variation was described as (1) mainly uniseriate rays, (2) mainly uni- and multiseriate rays up to two cells wide, for which the multiseriate part of the ray is as wide as the uniseriate part, (3) mainly multiseriate rays of 2–4, with the multiseriate part wider than the uniseriate part. Two distinct shapes and sizes of vessel-ray pits in the same cell are typical for Sapotaceae (character 33 in IAWA hardwood list). Instead of scoring this trait as present, we scored whether this particular pitting type was present mainly in (square/upright) marginal ray cells, or also in (procumbent) body ray cells. When scoring this trait as present, we acknowledge that not all marginal or body ray cells in a single wood sample exhibit this trait, as there is quite some additional variation that can be described using other vessel-ray pitting types in the IAWA hardwood list. Quantitative trait values for vessel width, vessel density, and ray height were collected from the descriptions of Kukachka (1978–1982), Budi (1993), and Lens (2005) for the general clade descriptions, but were not included in the full dataset (Supplementary 2) due to differences in how data were presented by different authors (e.g., Kukachka mentioned averages for genera but did not provide details per sample or species). Trait values for vessel element length and fibre length are given, and the existing literature descriptions of Sapotaceae woods were supplemented with original maceration observations. We follow Sapotaceae species names as provided by Plants of the World Online (POWO 2024), which has its base in Govaerts *et al.* (2001).

Previously published Sapotaceae phylogenies were based on a small selection of markers, resulting in incongruent hypotheses on species relationships. We generated a new Sapotaceae family phylogeny for 56 representative species and one outgroup species (Fig. 1B for the genus-level topology, Supplementary 3 for sampling details, and Supplementary 4 for the phylogeny with node support values) from both published and unpublished target capture sequencing data of 353 single-copy nuclear genes (Johnson *et al.* 2019). Most sequences came from the unpublished PAFTOL project (Zuntini *et al.* 2024) and were complemented with a few sequences from the ongoing PhD project of Ryan Brewer (Naturalis Biodiversity Center). Raw data were mapped and aligned using the bioinformatic pipeline described by Hendriks *et al.* (2023), with the following improvements. HybPiper v2.1.8 (Johnson *et al.* 2016) was used to map raw sequencing data, while 'omm-macse' (Ranwez *et al.* 2011) was used instead of 'MAFFT' (Katoh & Standley 2013) to perform codon-aware alignments of each gene. We used trimAl v1.4.rev22 (Capella-Gutiérrez *et al.* 2009) with parameters resoverlap 0.75, seqoverlap 0.90, and gt 0.90 to clean gene alignments (i.e., remove short reads and poorly covered nucleotide positions). Finally, we used the 151 704 bp 'supermatrix' from the concatenation of the 283 nuclear genes that passed the pipeline in 'IQ-TREE2' (Minh *et al.* 2020) to infer the maximum likelihood species phylogeny. Ancestral state reconstructions were performed following Beckers *et al.* (2024, see Supplementary 5 for model selection).

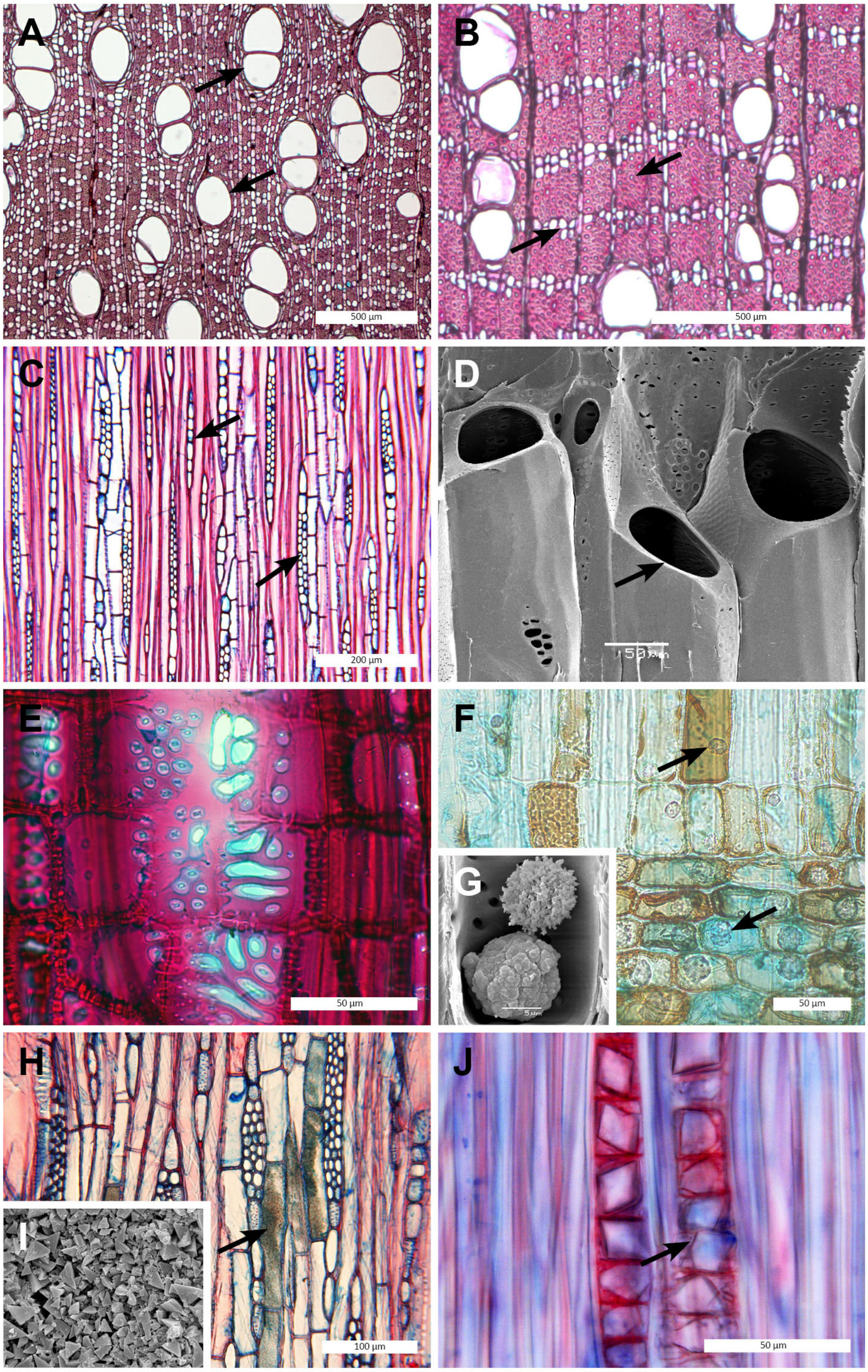
Results

General Sapotaceae descriptions

Sapotaceae woods are generally heavy and dense, coloured light to dark brown, occasionally a bit reddish. Growth rings are mostly absent, and woods are generally diffuse-porous. Vessels are mostly united in short radial multiples up to 4 cells, often in combination with solitary vessels (Fig. 2A). Average tangential vessel width ranges from 30–140 µm, vessel density varies between 2–65/mm^2, and vessel element length between 360–1050 µm. Intervessel pits are alternate, ranging in size from <4 µm up to over 10 µm. Vessel-ray pits are probably the most recognisable anatomical characteristic of Sapotaceae: all species have bordered pits similar in shape and size to intervessel pits that often co-occur with (often minutely bordered to simple) elongated or irregularly shaped pits in the same square/upright marginal ray cells and/or procumbent body ray cells (Fig. 2E). Vessel perforation plates, with a few noteworthy exceptions (e.g., scalariform with 2–10 up to 15 bars in *Palaquium*), are simple (Fig. 2D). Axial parenchyma is diffuse–in–aggregates or banded, mostly 1–2 cells wide in transverse sections (Fig. 2A–B), and varies between 4 and over 12 cells per strand. Fibres are mostly thick–walled (Fig. 2B) with simple to minutely bordered pits typically confined to the radial walls (except distinctly bordered in both walls in *Sarcosperma*), and are on average between 880–2040 µm in length. Rays are typically uni– and multiseriate (2–4 up to 5 cells wide) with the multiseriate part of the ray often as wide as the uniseriate part (Fig. 2C). The (uni- and multiseriate) rays are on average between 130–1040 µm long and consist of procumbent body ray cells with one or several rows of square and/or upright marginal ray cells (Fig. 2F). Mineral inclusions vary greatly in Sapotaceae, but generally include at least one of the following: silica bodies in ray cells (Fig. 2F–G), crystal sand in axial parenchyma (Fig. 2H–I), or prismatic crystals in axial parenchyma (Fig. 2J); occasionally both silica grains and calcium oxalate crystals are found in the same wood samples. Variable dark contents are often present in ray cells (Fig. 2F), sometimes also in axial parenchyma. A wood anatomical summary per genus can be found in Supplementary 6. The full list of wood anatomical traits for each observed species is in Supplementary 2. Below, detailed descriptions are given per subfamily. Within these subfamilies, we focused on monophyletic clades, distinct groups and occasionally non-monophyletic groups (Roman numerals in Fig. 1A).

Sarcospermatoideae

Sarcospermatoideae is the earliest-diverging Sapotaceae clade, including only *Sarcosperma* (clade I in Fig. 1A). Growth rings are absent, and the wood is diffuse-porous. Vessels in short radial multiples of 2–5, average length of vessel elements 330–950 µm. Vessel perforation plates simple, intervessel pits 6–10 µm in horizontal diameter. Vessel–ray pits similar to intervessel pitting in shape and size co-occurring with non–bordered enlarged and irregularly shaped scalariform pits in both body and marginal ray cells (Fig. 2E). Fibres thin-walled, pits distinctly bordered in tangential and radial walls (fibre-tracheids), 870–2120 µm long. Axial parenchyma diffuse-in-aggregates (Fig. 2A) and short strands (4–8 cells per strand). Uni- and multiseriate rays up to 2 cells wide, with multiseriate parts as wide as uniseriate parts (Fig. 2C); rays consisting of either exclusively upright ray cells (uniseriate) or procumbent body ray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cells with several rows of upright marginal ray cells (multiseriate). Occasionally gummy deposits in ray cells. Crystal sand present in axial parenchyma (Fig. 2H).

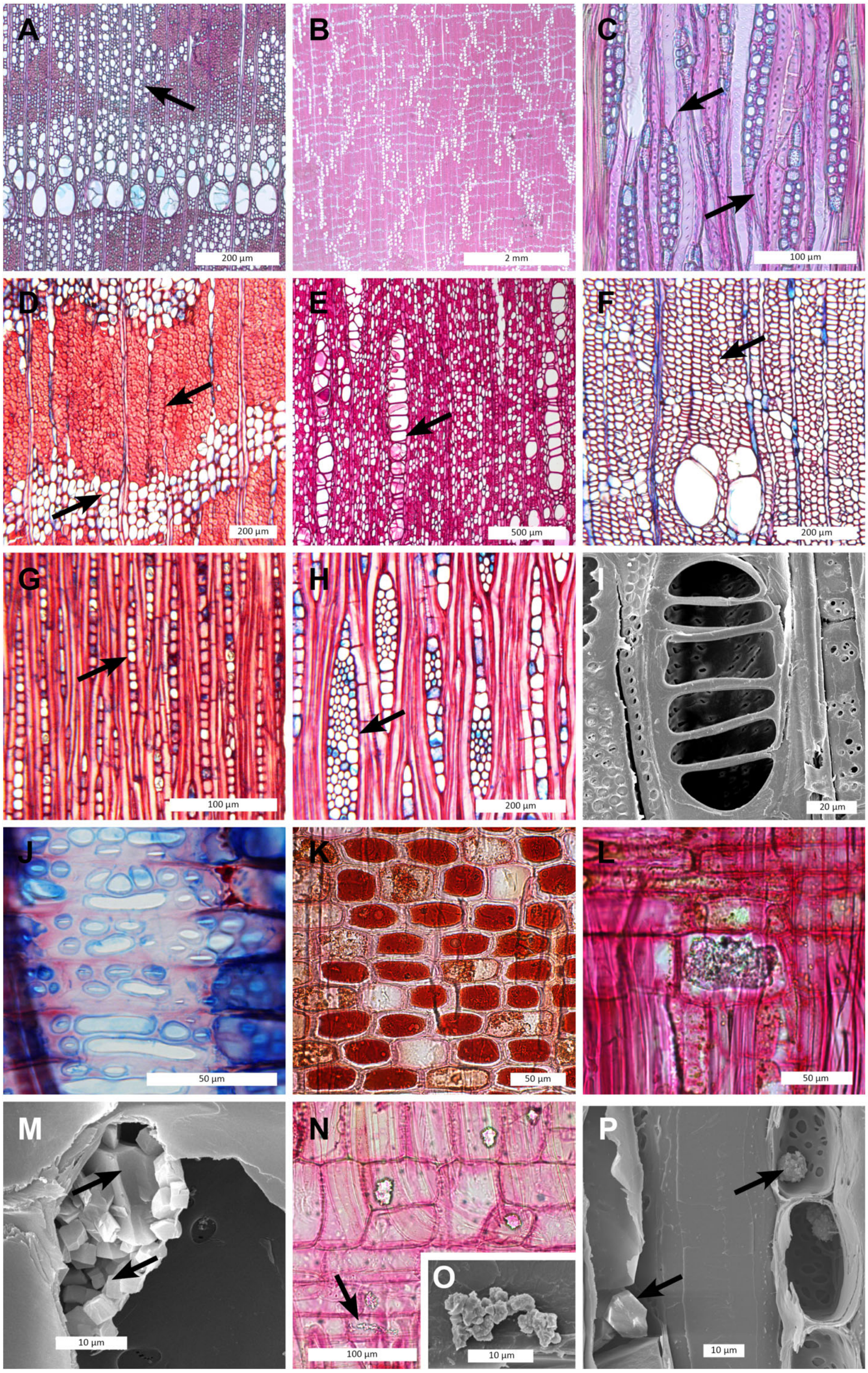
EBERHARDTIA AND *SIDEROXYLON*

Eberhardtia (clade II in Fig. 1A–B) is sister to the rest of Sapotaceae. While no slides were available for this study, one description in the Atlas of Chinese Woods (Luo *et al.* 2022) suggests a close similarity to *Sarcosperma* (Supplementary 2), except for the absence of mineral inclusions in *Eberhardtia* (fibre-tracheids presence unknown). *Sideroxylon* (clade III in Fig. 1A) is described separately from the Sapotoideae because of the unclear taxonomic position of this genus (Fig. 1A–B). This pantropical genus includes the previously accepted genera *Argania*, *Bumelia*, *Dipholis*, *Mastichodendron*, *Nesoluma*, and *Reptonia* (Fig. 1C) and is unique within Sapotaceae because it has relatively short vessel elements (average 500 µm) that are often arranged in dendritic vessel patterns (except for *Mastichodendron* and *Dipholis*) and surrounded by vasicentric tracheids (less so for *Mastichodendron* and *Dipholis*), along with very thick-walled fibres, rays of two or more cells wide, and absence (or rare occurrence) of dark content in ray cells. The position of *Sideroxylon* outside Sapotoideae is supported by a lack of silica bodies and relatively short axial parenchyma strands, two traits that are shared with early-diverging *Sarcosperma* and *Eberhardtia* (Supplementary 6).

Sideroxylon can be split into two subclades based on molecular evidence: one that includes former genera *Bumelia* and *Nesoluma*, and one that includes *Argania*, *Dipholis*, *Mastichodendron*, *Reptonia*, and *Sideroxylon* s.s. (Fig. 1C). No clear set of anatomical traits could be found to match this division, because trait variation is similar within the two groups (e.g., presence of a dendritic vessel pattern; Supplementary 6). However, at a finer taxonomic scale, wood anatomy matches, for the most part, with delimitations of the previously accepted genera according to the currently available chloroplast-based phylogeny (Fig. 1C). For instance, *Bumelia* A (*S. lycioides*, *S. lanuginosum*, *S. tenax*; Fig. 1C) has one of the most recognisable Sapotaceae woods because it is ring-porous with a dendritic vessel pattern in the latewood consisting of narrow vessels surrounded by vasicentric tracheids (Fig. 3A), and large intervessel pits of more than 6 µm in horizontal diameter (Supplementary 6). *Bumelia* B (*S. horridum*, *S. celastrinum*, *S. obtusifolium*, *S. persimile*) woods are not ring-porous, have intervessel pits smaller than 4 µm, and bear crystal sand in axial parenchyma (Supplementary 6). The inclusion of *Nesoluma* (*S. polynesiacum*) in *Bumelia* (Fig. 1C) is not supported from a wood anatomical point of view, because *Nesoluma* has prismatic crystals instead of crystal sand, narrower rays, and narrower axial parenchyma bands.

In the other major *Sideroxylon* subclade, *Sideroxylon* s.s., *Reptonia*, and *Argania* also have a dendritic vessel pattern, while the sister genera *Mastichodendron* and *Dipholis* do not (Supplementary 6, Fig. 1C). Sister group *Argania* (*S.*

Fig. 2. General wood anatomical traits across Sapotaceae. (A) *Diploknema butyracea* (Sapotoideae, clade VI): transverse section with solitary vessels (arrow pointing left) co-occurring with short radial multiples (arrow pointing right). (B) *Palaquium pseudorostratum* (Sapotoideae, clade VI): transverse section with banded axial parenchyma of 1–2 cells wide (arrow pointing right) and thick-walled fibres (arrow pointing left). (C) *Aningeria adolfi-friederici* (Chrysophylloideae, grade E): tangential section with uniseriate rays (arrow pointing left) and multiseriate rays of two cells wide with the multiseriate part as wide as the uniseriate part (arrow pointing right). (D) *Gambeya perpulchra* (Chrysophylloideae, clade IX): radial surface showing simple perforation plates (arrow). (E) *Chrysophyllum oliviforme* (Chrysophylloideae, clade X): radial section with two types of vessel-ray pits in square to upright marginal ray cells. (F) *Payena lucida* (Sapotoideae, clade VI): radial section with silica grains in procumbent/square body ray cells (arrow pointing left) and silica grains in upright marginal ray cells (arrow pointing right). (G) *Manilkara obovata* (Sapotoideae, clade VII): detail of two regularly shaped silica grains with a different surface texture in an upright marginal ray cell. (H) *Gambeya gigantea* (Chrysophylloideae, clade IX): tangential section with crystal sand in axial parenchyma cells (arrow). (I) *Sarcosperma laurinum* (Sarcospermatoideae, clade I): detail of crystal sand in an axial parenchyma cell. (J) *Gambeya albida* (Chrysophylloideae, clade IX): tangential section with prismatic crystals in chambered axial parenchyma cells (arrow). A–C, E–F, and H–I are light microscope images, and D, G, and I are scanning electron microscopic images.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spinosum) and *Reptonia* (*S. mascatense*; Fig. 1C) are indistinguishable from each other and other species from the *Sideroxylon* lineage (Supplementary 6). *Sideroxylon* s.s. is fairly similar to the genera described above, but can be split based on the mineral inclusion type: *Sideroxylon* s.s. A (*S. betsimisarakum*, *S. gerrardianum*, *S. grandiflorum*, *S. inerme*, *S. majus*, *S. saxorum*) shows prismatic crystals in axial parenchyma and rays (including irregularly shaped crystals), and *Sideroxylon* s.s. B (*S. bojeranum*, *S. puberculum*, *S. obovatum*) has crystal sand. *Sideroxylon* s.s. B is very similar to *Bumelia* B, but *Bumelia* B has slightly smaller intervessel pits (Supplementary 6).

The formerly recognised genera *Mastichodendron* and *Dipholis* form sister clades (Fig. 1C) and have a different wood anatomy from other *Sideroxylon* lineages due to a lack of a dendritic vessel pattern, diffuse-in-aggregates axial parenchyma, and longer axial parenchyma strands consisting of at least six cells per strand (Supplementary 6). *Mastichodendron* (*Sideroxylon capiri*, *S. foetidissimum*, *S. tepicense*) and *Dipholis* A (*S. portoricense*, *S. stevensonii*) have prismatic crystals in axial parenchyma and marginal ray cells in combination with crystals of other shapes and sizes (generally much smaller crystals; Fig. 3M), a trait that is only shared with *Sideroxylon* s.s. A (Supplementary 6). *Dipholis* B (*S. montanum*, *S. salicifolium*) is similar to *Mastichodendron* and *Dipholis* A, but rays are narrower and the latter two lineages have crystal sand (Supplementary 6).

Sapotoideae

There is more variation in mineral inclusions for Sapotoideae than in the equally large Chrysophylloideae. The best indicator for a sister-relationship between both subfamilies is the dominant presence of silica bodies, which probably originated in their most common recent ancestor (Fig. 4). When comparing both subfamilies, silica bodies are generally smaller, and additional prismatic crystals are more abundant in Sapotoideae compared to Chrysophylloideae (Supplementary 6). Furthermore, axial parenchyma strands are generally longer in Sapotoideae, and the variable shapes of vessel-ray pits mostly occur in marginal ray cells, as opposed to their presence in both body and marginal ray cells in the majority of Chrysophylloideae (Supplementary 6). The broad relationships within Sapotoideae are mostly congruent between nuclear and chloroplast phylogenies (Fig. 1A–B), and they also match for the most part with tribes identified by Pennington (1991). Below, short descriptions are given for well-defined Sapotoideae clades and a few lineages with unclear relationships.

Fig. 3. Diagnostic wood anatomical traits suited to identify Sapotaceae clades. (A) *Sideroxylon lycioides* (clade III): transverse section showing ring-porous wood with narrow latewood vessels surrounded by vasicentric tracheids (arrow). (B) *Syzygiopsis pachycarpa* (Chrysophylloideae, clade IX): dendritic vessel pattern of a diffuse-porous wood. (C) *Sideroxylon lycioides* (clade III): tangential section showing narrow vessels (arrow pointing left to perforation) with vasicentric tracheids (arrow pointing right). (D) *Inhambanella guereensis* (Sapotoideae, clade VII): transverse section with wide banded axial parenchyma (arrow pointing right) and very thick-walled fibres (arrow pointing left). (E) *Niemeyera prunifera* (Chrysophylloideae, clade VIII): transverse section with vessels in very long radial multiples (arrow). (F) *Aningeria superba* (Chrysophylloideae, grade E): transverse section with very thin-walled fibres (arrow). (G) *Chrysophyllum longipes* (Chrysophylloideae, clade X): tangential section with only uniseriate rays (arrow). (H) *Omphalocarpum brieyi* (Chrysophylloideae, grade E): tangential section with predominantly wide rays (arrow). (I) *Palaquium obovatum* (Sapotoideae, clade VI): detail of a scalariform vessel perforation plate. (J) *Aningeria superba* (Chrysophylloideae, grade E): radial section with two types of vessel-ray pits in procumbent body ray cells. (K) *Franchetella atabapoensis* (Chrysophylloideae, clade X): radial section showing variable dark content. (L) *Achrouteria pomifera* (Chrysophylloideae, clade X): radial surface showing one very large silica body in ray cell. (M) *Sideroxylon betsimisarakum* (clade III): a typical prismatic crystal (arrow pointing right) surrounded by prismatic crystals of variable shapes and sizes (arrow pointing left). (N) *Diploknema butyracea* (Sapotoideae, clade VI): radial section with irregularly shaped silica bodies (arrow). (O) *Isonandra lanceolata* (Sapotoideae, clade VI): detail of an irregularly shaped silica body. (P) *Palaquium dasyphyllum* (Sapotoideae, clade VI): species with small and large prismatic crystals in axial parenchyma (arrow pointing left shows prismatic crystal) and silica bodies in ray cells (arrow pointing right). A–H, J–K, and N are light microscopy images, and I, M, and O–P are scanning electron microscopic images.

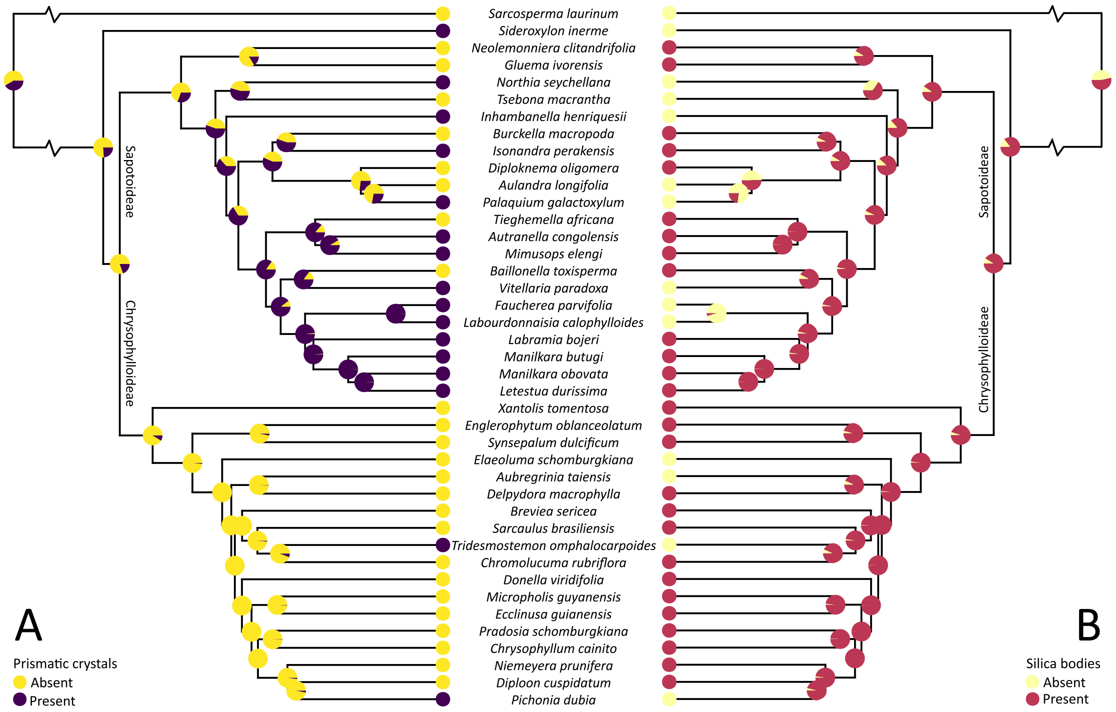

Fig. 4. Ancestral state reconstructions of mineral inclusion type based on a nuclear molecular phylogeny of the family (cf. Fig. 1B). (A) Presence or absence of prismatic crystals. (B) Presence or absence of silica bodies. Contracted lines separating *Sarcosperma* from the rest of the family are an artificial truncation of the branches for illustrative purposes.

Neolemonniera, *Lecomtedoxa*, and *Gluema* (clade IV in Fig. 1A) are supposedly the earliest-diverging clade within Sapotoideae. They are similar to each other in having rays of predominantly three or more cells wide (rather unusual in Sapotaceae), very thick-walled fibres, common presence of vasicentric tracheids, and banded axial parenchyma. *Neolemonniera* has more pronounced radial vessel multiples, and small silica bodies in body and marginal ray cells. *Lecomtedoxa* has a dendritic vessel pattern, small intervessel pits (<4 µm), two types of vessel-ray pits in both body and marginal ray cells, prismatic crystals in axial parenchyma, and occasionally also crystal sand. *Gluema* is similar to the other two genera, but has a sporadic occurrence of prismatic crystals in addition to small silica bodies. The early-diverging position of these three genera seems justified, based on a combination of distinctive wood anatomical traits shared with *Sideroxylon*, such as common vasicentric tracheid presence, wide rays, and the presence of prismatic crystals (except for *Neolemonniera*).

The early-diverging position of *Capurodendron* (clade V in Fig. 1A) within Sapotoideae can also be justified by a common presence of vasicentric tracheids, relatively wide rays, and occasional presence of crystal sand (shared with *Sideroxylon* and clade IV). Yet, the silica bodies in *Capurodendron* are much larger than almost all other Sapotoideae (>15 µm, resembling more the typical size of silica grains in Chrysophylloideae). No microscopic slides were available for *Tsebona* (Fig. 1B), but the lack of diagnostic mineral inclusions as listed in the InsideWood descriptions does not support its position as sister to *Capurodendron*, especially since several other traits are also different between the two genera, such as a difference in fibre wall thickness and vasicentric tracheid presence (Supplementary 6). The newly suggested putative relationship of *Capurodendron* and *Tsebona* with *Northia* (Fig. 1B) is also ambiguous: *Northia* shares the presence of vasicentric tracheids, but differs in mineral inclusions (only prismatic crystals in axial parenchyma) and shows exclusively uniseriate rays (Supplementary 6). We have described *Northia* within

Sapotoideae clade VII (see below), because this genus seems to be a better fit in this clade from a wood anatomical point of view (Fig. 1A).

ISONANDREAE

Isonandreae (clade VI in Fig. 1A) are a previously recognised tribe (Pennington 1991), which also group as a monophyletic clade in molecular phylogenetic studies, although the generic relationships can be different based on the markers used (Fig. 1A–B). Compared to other Sapotoideae, the wood of Isonandreae members has much thinner-walled fibres and even includes genera with very thin-walled fibres (Fig. 3F), such as in some species of *Diploknema* and *Palaquium* (Supplementary 2, 6). Additionally, *Aulandra*, *Payena*, *Diploknema*, *Burckella*, and *Madhuca* have two types of vessel-ray pits in both body and marginal ray cells (Supplementary 6; also observed in *Neolemonniera*, *Gluema* and *Capurodendron*), though less frequently than in Chrysophylloideae (see below).

Palaquium (including *Aulandra*) is an interesting genus because a significant number of its species have scalariform perforation plates (with 2–10, up to 15 bars) in addition to simple plates (Fig. 3I). Scalariform perforation plates (Supplementary 2) are also observed in *Labourdonnaisia* (also Sapotoideae), and *Donella*, *Synsepalum* and *Gambeya* (Chrysophylloideae), but *Palaquium* is the only Sapotaceae genus where scalariform perforation plates occur in low to high percentages from 5 up to 50% (Supplementary 2). *Palaquium* can be split into five groups, based on mineral inclusion types (Supplementary 6): (1) most species (41 out of 61 species studied; *Palaquium* A in Supplementary 6) have prismatic crystals, (2) some species (7 out of 61; *Palaquium* B) have prismatic crystals and silica bodies, (3) a considerable number of species (19 out of 61) only contain silica bodies, (4) two species (*Palaquium* D) have crystal sand, and (5) two species entirely lack mineral inclusions (*Palaquium* E, also true for *Aulandra* which is now considered *Palaquium*; Phang *et al.*, 2025). Misidentifications seem very probable in *Palaquium*, but most samples of the same species had similar mineral inclusions, suggesting that a division can be made within the genus based on wood anatomical traits.

Isonandra (10 species) is a relatively small genus, but unique in the family due to the presence of all mineral inclusion types in the same wood sample: prismatic crystals of several shapes mostly in axial parenchyma and sometimes also in rays, small silica bodies in body and marginal ray cells and axial parenchyma, and occasionally also crystal sand in *Isonandra lanceolata* (Supplementary 6). Moreover, it is the only genus in Isonandreae with very thick-walled fibres and predominantly simple vessel-ray pits.

Burckella, *Diploknema*, *Madhuca* and *Payena* are more similar to each other and mostly share silica bodies of variable sizes in ray cells (Supplementary 6). *Madhuca* is a large, wood-anatomically well-defined genus. However, the variation in ray width is exceptional within Sapotaceae: about one-third of the *Madhuca* species have exclusively uniseriate rays (Fig. 3G), one-third have uni-and multiseriate rays with the multiseriate part as wide as the uniseriate part, and one-third has exclusively multiseriate rays that are often more than three cells wide (Fig. 3H). *Burckella* is distinguished from other Isonandreae by the presence of large silica bodies in the marginal ray cells and smaller silica bodies in the body ray cells. About half of the *Diploknema* species (*Diploknema* B; Supplementary 6) are potentially wrongly identified or taxonomically incorrectly placed because crystal sand was observed instead of silica bodies, which is considered an important diagnostic character for taxonomic placement.

MIMUSOPEAE

Unlike its sister Isonandreae, the Mimusopeae as recognised by Pennington (1991) are a paraphyletic group. However, the 'core' Mimusopeae (clade VII in Fig. 1A) do cluster nicely in both chloroplast and nuclear molecular phylogenies, except for the exclusion of *Inhambanella* and *Northia* from this core clade in Fig. 1B. We treat these two genera as part of the core Mimusopeae based on wood anatomical similarities. The core Mimusopeae typically has more genera with prismatic crystals than Isonandreae, as well as many genera with additional silica grains, shorter vessel elements and an abundance of very thick-walled fibres (similar to *Sideroxylon*, different to many Isonandreae), and on average wider rays (often two or more cells wide; Supplementary 6). *Baillonella*, *Mimusops*, and *Tieghemella* are suggested to be closely related within Mimusopeae (Fig. 1A), which is supported by shared wood anatomical traits such as rays of three or more cells wide, large intervessel pits (>6 μm), and small silica bodies that occur only in the marginal ray cells. *Vitellaria* is hypothesised to be closely related to these three genera, but its taxonomic position is questionable based on the presence of prismatic crystals in axial parenchyma instead of silica bodies in rays (suggesting a closer relationship to *Northia* and *Inhambanella*, see further down). Additionally, *Vitellaria* is the only genus in clade VII that shows variably shaped vessel-ray pits in both body and marginal ray cells (also present in some Isonandreae, and typical of many Chrysophylloideae; Supplementary 6).

Another molecular-defined subclade with a similar wood anatomy within clade VII is formed by *Abebaia*, *Faucherea*, *Labourdonnaisia*, *Labramia*, *Letestua* and *Manilkara*. The long radial vessel multiples in this subclade are especially noteworthy compared to the vessel grouping in their sister clade (*Vitellaria*, *Baillonella*, *Mimusops*, *Tieghemella*; following Fig. 1A). Interestingly, the former clade shows much variation in mineral inclusions. Some genera have prismatic crystals in axial parenchyma (*Abebaia*, *Faucherea* B, part of *Labourdonnaisia*, and the neotropical *Manilkara* A), others show silica bodies (*Manilkara* C and *Faucherea* A), or both silica bodies and prismatic crystals (*Autranella*, *Labramia*, *Letestua*, and *Manilkara* B). This variation in mineral inclusions does not support the phylogenetic relationships as indicated by the chloroplast phylogeny of Fig. 1A (Supplementary 6). The inclusion of *Northia* and *Inhambanella* in clade VII is poorly supported (Fig. 1A–B), and the absence of silica bodies implies a closer relationship to early-diverging Sapotoideae (see above). A potential close relationship between *Northia* and *Inhambanella* is supported by wood anatomical traits, but there are also differences: *Northia* has small intervessel pits (<4 μm) and exclusively uniseriate rays with dark content, while *Inhambanella* has large intervessel pits (>6 μm) and rays of three or more cells wide without dark contents (Supplementary 6).

Chrysophylloideae

The wood anatomy of Chrysophylloideae is more homogeneous compared to Sapotoideae. The dominant mineral inclusion type is silica, especially in neotropical clades IX and X (Fig. 4B), with only a few exceptions showing additional prismatic crystals and/or crystal sand (*Aubregrinia*, *Chloroluma*, *Donella*, *Gambeya* p.p., *Magodendron*, *Malacantha*, *Omphalocarpum*, *Pichonia*, *Planchonella*, *Podoluma*, *Pouteria* s.l. p.p., *Tridesmostemon*; Supplementary 6). In addition, axial parenchyma strands are generally shorter in Chrysophylloideae compared to Sapotoideae, a trait that is shared with early-diverging Sapotaceae (*Eberhardtia*, *Sarcosperma*, *Sideroxylon*). Also, variable vessel-ray pit shapes and sizes in both body and marginal ray cells are more abundant in Chrysophylloideae, especially in clade X (Fig. 5B). Below, detailed descriptions are given for the major lineages within Chrysophylloideae as defined by current molecular phylogenetic evidence (Fig. 1A–B).

Lineages E represent a paraphyletic, poorly studied grade of early-diverging Chrysophylloideae consisting mainly of African genera *Aningeria*, *Donella* (also in Asia and Australia), *Englerophytum*, *Malacantha*, *Omphalocarpum*, *Spiniluma*, *Synsepalum*, *Tridesmostemon* and *Xantolis* (Asia; Fig. 1A–B). Vessels are solitary and in short radial multiples, fibres are very thick-walled (although thinner-walled in *Donella*, *Malacantha* and *Omphalocarpum*, and very thin-walled in *Aningeria*), axial parenchyma is arranged diffuse-in-aggregates and/or in 1–2-celled narrow bands with generally many cells per strand (often more than six, but maximum five in *Donella*), ray width is variable, and silica bodies are present (except in *Tridesmostemon*).

There are a number of peculiar wood anatomical traits in Chrysophylloideae grade E. For instance, *Aningeria*, *Donella* and *Malacantha* show irregularly shaped silica grains in their marginal ray cells (Fig. 3N–O; also present in body ray cells in *Elaeoluma* and *Ecclinusa* of clade IX). *Aningeria* can be further characterised by large intervessel pits (>6 μm) and very thin-walled fibres. Likewise, *Donella* can be easily recognised within this grade by crystal sand, short axial parenchyma strands (<5 cells per strand), and sporadic occurrences of scalariform perforation plates (also present in *Synsepalum* p.p.; Supplementary 6; Fig. 3I). It also includes one species with laticifers

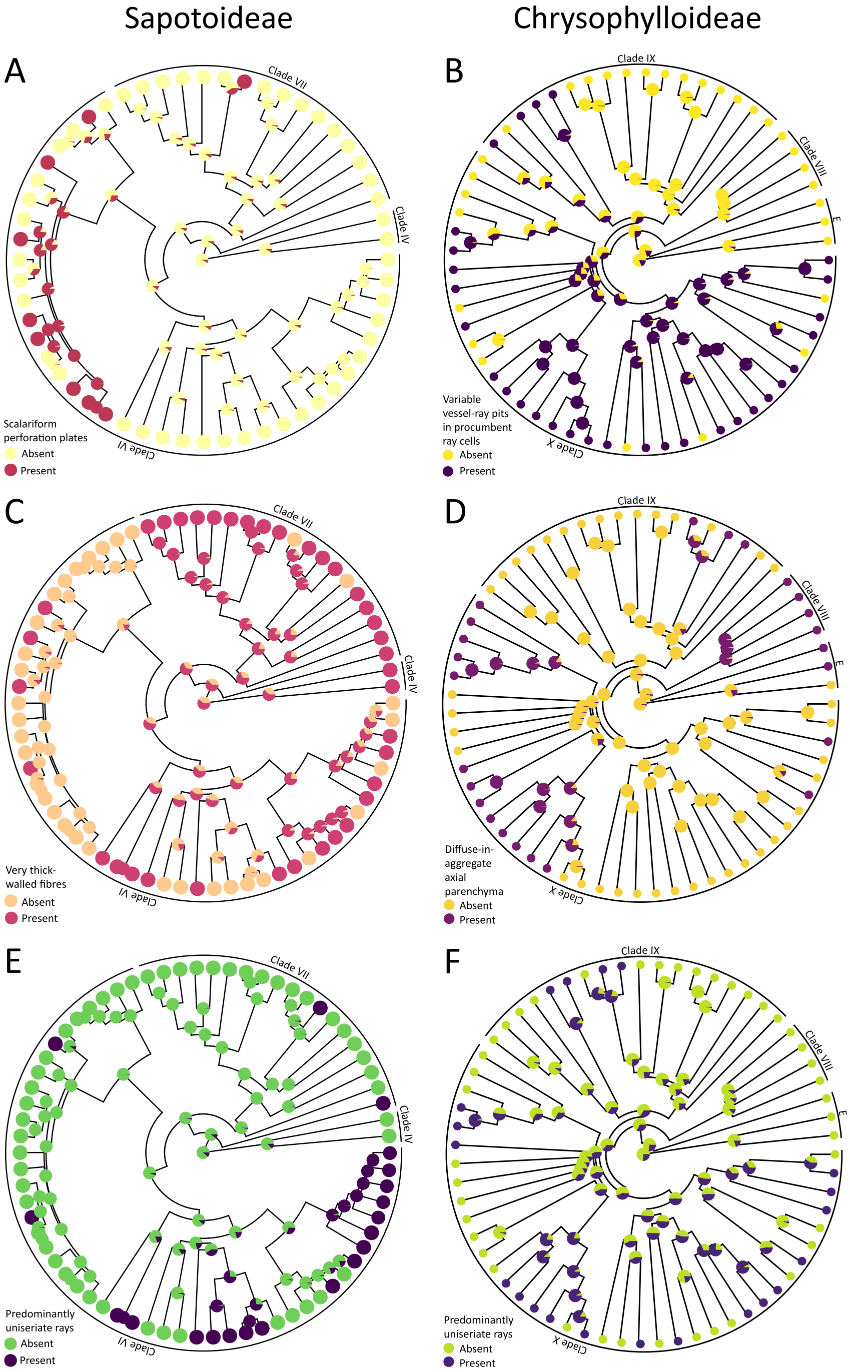

Fig. 5. Ancestral state reconstructions showing the presence/absence of a few diagnostic traits modelled for Sapotoideae (left column) and Chrysophylloideae (right column) based on chloroplast molecular phylogenies (Fig. 1A). (A) Scalariform perforation plates. (B) Two types of vessel-ray pit shapes and sizes in (procumbent) body ray cells and (square/upright) marginal ray cells (absence means that the variable vessel-ray pits are only present in the (square/upright) marginal ray cells). (C) Very thick-walled fibres. (D) Diffuse-in-aggregates axial parenchyma. (E–F) Presence of predominantly uniseriate rays in Sapotoideae and Chrysophylloideae. The Roman numbers correspond to the clades identified in Figure 1.

(*D. ubangiensis*, formerly *Chrysophyllum pruniforme*). *Malacantha* is distinguishable due to the presence of large and irregularly shaped small crystals in axial parenchyma and ray cells, in addition to the unique, irregularly shaped silica bodies in rays (Supplementary 6). Furthermore, *Tridesmostemon* is unique in grade E due to an absence of silica bodies but the presence of prismatic crystals in axial parenchyma (Supplementary 6). *Omphalocarpum* (together with *Tridesmostemon* placed in tribe Omphalocarpeae sensu Pennington 1991) is similar to *Tridesmostemon* in having prismatic crystals, but also shows additional silica bodies in ray cells. Both genera differ in their fibre wall thickness (thick-walled in *Tridesmostemon*) and intervessel pit size (at least 6 µm in *Omphalocarpum*) (Supplementary 6). The putatively close relatives *Englerophytum* and *Synsepalum* (Fig. 1B) have a similar wood anatomy: both genera have a dendritic pattern of vessels and vasicentric tracheids, very thick-walled fibres, and uniseriate rays. *Xantolis* is unique within grade E because it has only short vessel radial multiples and exclusively uniseriate rays.

Clade VIII consists of genera with a mostly Australasian distribution. *Gayella* (only in South America), *Magodendron*, *Niemeyera*, *Pichonia*, *Planchonella*, *Pleioluma*, *Pycnandra*, *Sahulia* and *Sersalisia* have silica grains as the dominant mineral inclusion type (although absent in *Planchonella*), and share mainly diffuse-in-aggregates axial parenchyma and a high abundance of long vessel multiples (solitary vessels are rare). Clade VIII can be split into genera with only silica bodies (*Pycnandra*, *Gayella*, *Pleioluma*, *Niemeyera*, *Sahulia* and *Sersalisia*), genera with silica bodies and prismatic crystals (*Magodendron*, *Pichonia*), and species with crystal sand (*Planchonella* A) and/or calcium oxalate crystals of various shapes (*Planchonella* B–C) or no mineral inclusions at all (*Planchonella* D; Supplementary 6). The genera with similar mineral inclusions are not grouped in the molecular phylogenies, but support for generic relationships in clade VII is often low (Fig. 1A–B). Interestingly, *Pycnandra* is similar to *Aningeria*, *Donella*, and *Malacantha* of grade E in having irregularly shaped silica grains. However, the silica grains in *Pycnandra* are equally present in body and marginal ray cells, while they are confined mainly to marginal ray cells in the three grade E genera, *Aningeria*, *Donella*, and *Malacantha*. The distribution of silica grains in *Gayella* is similar to *Pycnandra*, but they are not irregularly shaped in the former. The really small silica grain size in *Pleioluma* is unique within clade VIII, and only shared with *Englerella* (clade X). *Niemeyera* and *Sersalisia* are similar to the genera described above, but observations on these two genera should be interpreted with caution because few samples were available in our study (Supplementary 6). *Magodendron* and *Pichonia* are sister genera with high support (Fig. 1A) and are the only two genera in this clade with prismatic crystals in axial parenchyma in addition to silica bodies, as well as small intervessel pits (Supplementary 6). *Magodendron* is different from *Pichonia* in having a clear dendritic pattern of vessels and vasicentric tracheids, and rays of two or more cells wide. *Planchonella* is unique within the clade in having no silica grains (Supplementary 6).

Clade IX is largely neotropical and consists of *Aubregrinia*, *Breviea*, *Delpydora*, *Ecclinusa*, *Elaeoluma*, *Gambeya*, *Micropholis*, *Nemaluma*, *Prieurella*, *Ragala*, and a yet *unnamed clade* of *Pouteria cayennensis* and *P. oblanceolata* (Fig. 1A). Genera in this clade are generally characterised by thin- (to thick-)walled fibres, short axial parenchyma strands, and nearly all genera have exclusively silica bodies with exception of *Gambeya* A (only prismatic crystals in axial parenchyma), *Aubregrinia* and *Gambeya* B (only crystal sand), *Gambeya* C (occasional crystal sand with silica grains), and *Gambeya* D (no mineral inclusions observed; Supplementary 6). *Ecclinusa* is most distinct within clade IX because of its tendency to form long radial vessel multiples of more than five vessels (Fig. 3E) that occasionally form dendritic patterns with vasicentric tracheids, large (>6 µm) intervessel pits, and irregularly shaped silica grains in body and marginal ray cells. *Elaeoluma* is distinct in having very thin-walled fibres (shared with *Aubregrinia*), diffuse-in-aggregates axial parenchyma, and irregularly shaped silica grains mainly in body ray cells. The closely related *Micropholis* and *Prieurella* share narrow axial parenchyma bands, silica bodies, and irregularly shaped vessel-ray pits in both body and marginal ray cells, though this irregularity is dominant in the marginal ray cells. *Prieurella* is distinguishable from *Micropholis* in having very thick-walled fibres and tracheids, long axial parenchyma strands, and exclusively uniseriate rays. *Breviea*, *Nemaluma*, *Ragala*, and the unnamed clade are similar in wood anatomy, with relatively thin-walled fibres, banded axial parenchyma, and relatively short axial parenchyma strands.

The African genera *Aubregrinia*, *Delpydora* and *Gambeya* group with the South American *Breviea* in the nuclear molecular phylogeny (Fig. 1B), but not in the combined chloroplast-nuclear phylogeny (Fig. 1A). Like other African Sapotaceae clades, mineral inclusions vary among these genera, but results should be interpreted with caution as we only observed one specimen in both *Aubregrinia* and *Delpydora*. *Gambeya* A–D share diffuse-in-aggregates axial parenchyma with *Elaeoluma* and *Aubregrinia*, but *Gambeya* B and D occasionally have scalariform perforation plates in addition to simple ones. Furthermore, *Gambeya* is unique in clade IX in having a huge variation in mineral inclusions (prismatic crystals, crystal sand, and/or silica bodies; Supplementary 6). The absence of silica grains in most clade IX species is particularly peculiar (except for the single specimen of *Aubregrinia*).

Clade X consists of the neotropical *Achrouteria*, *Chloroluma*, *Chromolucuma*, *Chrysophyllum*, *Cornuella*, *Diploon*, *Englerella*, *Labatia*, *Lucuma*, *Peteniodendron*, *Pouteria* s.l. (including *Pouteria* s.s., and closely related genera that form *Pouteria* s.l. together with *Sarcaulus*, see Fig. 1A) and *Pradosia*. It is the only clade in the family with a dominant occurrence of variable shapes and sizes of vessel-ray pits in both body and marginal ray cells (Fig. 3J; Supplementary 6). Along with clade IX, it is also one of two clades where silica bodies outnumber the other mineral inclusions (with the notable exception of *Chloroluma* that only shows prismatic crystals and crystal sand, and *Cornuella*, that lacks mineral inclusions). Defining smaller groups within clade X is challenging, mostly because of the many monotypic genera with a few observations each, but also because relationships among the genera in this clade are not well supported and vary greatly between the nuclear and combined nuclear-chloroplast phylogenies (Fig. 1A–B). Traits that are useful in defining clades in other parts of the family are variable in clade X, such as vessel arrangement, intervessel pit size, vasicentric tracheid presence, axial parenchyma band width, axial parenchyma strand length, and ray width.

However, there are a few genera with a distinctive set of wood anatomical traits. For example, *Pradosia* and the formerly recognised *Pouteria* s.l. genera *Podoluma* and *Gomphiluma* are the only genera in clade X with silica bodies and crystal sand. Furthermore, *Achrouteria* has unique silica bodies: they are so large that they take up the entire volume of the square to upright marginal ray cells (Fig. 3L). Furthermore, *Chloroluma* is the only genus in this subgroup without silica, but with crystals of various shapes (including crystal sand), no dark content in ray cells, and irregularly shaped vessel-ray pits only in marginal ray cells, making the position of this genus within clade X questionable. Finally, *Pouteria* s.s., and the formerly recognised *Pouteria* s.l. genera *Caramuri*, *Diploon* and *Sarcaulus* are distinct from other genera in this *Pouteria* s.l. clade in having silica grains predominantly in body ray cells (Supplementary 6).

Ancestral state reconstructions

The most informative state reconstructions are shown in Figures 4 and 5, and additional state reconstructions can be found in Supplementary 7. As mentioned in the materials and methods section, we used three molecular phylogenies for Sapotaceae wood anatomical state reconstructions: (1) a Sapotoideae chloroplast phylogeny, (2) a Chrysophylloideae chloroplast-nuclear phylogeny, and (3) a family-wide nuclear phylogeny with one representative species per genus (Fig. 1, Supplementary 5). Figure 4 shows a comparison between ancestral state reconstructions of prismatic crystal and silica body presence based on the family-wide nuclear phylogeny. The common ancestor of Chrysophylloideae and Sapotoideae had silica bodies, but it is less likely that it also had prismatic crystals. However, prismatic crystals are abundant, and taxonomically clustered in Sapotoideae (Fig. 4A) and *Sideroxylon* (Supplementary 6) and are nearly absent in Chrysophylloideae. The earliest diverging Sapotaceae lineage, *Sarcosperma*, has crystal sand (Supplementary 6). However, the state reconstructions were not conclusive that crystal sand is the ancestral state of the Sapotaceae (Supplementary 7), probably due to the small sampling size of the nuclear phylogeny (Fig. 1B).

In Figure 5, ancestral state reconstructions are shown for separate analyses on Sapotoideae and Chrysophylloideae trait evolution. One of the most noteworthy evolutionary trends in Sapotaceae is the recurrent transition from species with only simple vessel perforation plates to species with both simple and scalariform perforations (see Supplementary 2 for details on the number of bars and the ratio of scalariform to simple perforations). In the Sapotoideae state reconstructions, the scalariform observations are mostly clustered within *Palaquium* (clade VI, including *Aulandra*; Fig. 5A), although not all species of *Palaquium*, and the rest of clade VI, have scalariform plates (Supplementary 2, 7). The presence of scalariform vessel perforation plates seems to coincide in Sapotoideae with an absence of very thick-walled fibres (Fig. 5C). The wood of *Palaquium* especially has thin fibre walls (Supplementary 6). Interestingly, clade VI can be split into two groups: one group has a high occurrence of simple and scalariform perforation plates (mainly *Palaquium*, Fig. 5A), and the other has many species in a range of genera with predominantly uniseriate rays (Fig. 5E). Uniseriate rays (Fig. 5F) and diffuse-in-aggregates axial parenchyma (Fig. 5D), are dominant in Chrysophylloideae clades (Fig. 5F), although the latter ancestral state is more pronounced at deeper nodes. A conspicuous observation is the dominance of two types of vessel-ray pits in both procumbent body ray cells and square/upright marginal ray cells in Chrysophylloideae clade X (Fig. 5B). This trait is only sporadically observed in other Sapotaceae lineages (Supplementary 6 and 7).

Discussion

For the first time, we present a wood anatomical overview of the entire pantropical Sapotaceae family, which is known for its many tall trees with hard, valuable timber, as well as its challenging taxonomy (Fig. 1). Altogether, we observed around 1200 slides from 450 species, including 160 original sections, comprising all major lineages and nearly all genera. In addition to the descriptive part, we analysed the evolution of a number of diagnostic wood anatomical traits with ancestral state reconstructions (Fig. 5). The remarkable variation in vessel-ray pitting (Figs 2E, 3J) and mineral inclusions (Fig. 4), together with the recurrent reversals of scalariform vessel perforations from simple ones (Fig. 5A), makes this family stand out compared to many other families of flowering plants. Furthermore, there is much variation in vessel grouping, axial parenchyma distribution, and fibre thickness. Therefore, we have to disagree with Pennington (1991), who claimed in his family treatment that the variation in Sapotaceae wood anatomy does not provide any taxonomic usefulness and that the wood anatomy is as "…equally uniform throughout the family…" as the Ebenaceae to which he compared them (Pennington 1991: p. 2). Below, more detailed information is given regarding the interpretation of the results within a taxonomic, evolutionary, and ecological framework.

PHYLOGENETIC POSITION OF SAPOTACEAE AT HIGHER TAXONOMIC LEVELS

Not only are intrafamilial relationships within Sapotaceae unclear (see introduction, Fig. 1), but the phylogenetic position of Sapotaceae to other Ericales families has also been ambiguous. In recent studies, Larson *et al.* (2020) found Sapotaceae sister to Ebenaceae, Rose *et al.* (2018) retrieved a sister relationship to Ebenaceae and Primulaceae, while Zuntini *et al.* (2024) positioned Sapotaceae as part of a paraphyletic grade that is sister to the rest of the Ericales. From a wood anatomical point of view, the Ericalean Lecythidaceae is most similar to Sapotaceae. Both families have two types of vessel-ray pitting, banded axial parenchyma, narrow multiseriate rays, crystals, and silica bodies, but Sapotaceae has vasicentric tracheids commonly present and crystal sand (unique in the order; Figs 2–3 in Lens *et al.* 2007). The presence of both crystals and silica in the same family is also shared with Ebenaceae (Jahanbanifard *et al.* 2020), Styracaceae (Dickison & Phend 1985) and Primulaceae (Lens *et al.* 2005), though silica bodies are most dominant in Sapotaceae.

Within Sapotaceae, the clades identified based on molecular (chloroplast and/or nuclear) markers (Fig. 1) show a considerable amount of incongruencies among topologies, making statements on wood anatomical synapomorphies challenging. However, there are several diagnostic wood anatomical traits at higher taxonomic levels that can be used to support molecular-based clades in the family. For instance, calcium oxalate crystals are the only mineral inclusion found in the early-diverging monotypic Sarcospermatoideae and *Sideroxylon*, while silica bodies become more dominant in Sapotoideae and, especially, in Chrysophylloideae (Supplementary 2 and 6; Fig. 4, more details on mineral inclusion evolution below). Additionally, Sapotoideae has longer axial parenchyma strands compared to Chrysophylloideae and Sarcospermatoideae, and Sarcospermatoideae show fibres with clearly bordered pits (see section on genus-level identification below).

Within these subfamilies, some of the morphologically defined tribes proposed by Pennington (1991) match well with molecular defined clades (Fig. 1A). For instance, clade VI corresponds to Isonandreae, which generally have much thinner-walled fibres compared to the rest of the family, and a noteworthy percentage of species have scalariform vessel perforation plates in addition to simple perforations (especially *Palaquium*; Fig. 5A). Sister to clade VI is clade VII, which corresponds to the majority of Mimusopeae, referred to us as the 'core' Mimusopeae (Fig. 1A). Isonandreae and core Mimusopeae share many wood anatomical traits, but the latter has more genera with prismatic crystals, shorter vessel elements, and wider rays (Supplementary 6). Noteworthy in Chrysophylloideae is clade X, which has a mix of distinctly bordered and irregularly-shaped (minutely bordered or simple) vessel-ray pits in both procumbent body and upright marginal ray cells, which occurs only sporadically in other clades (Supplementary 6; Fig. 5B).

Genus-level identification

In addition to the traits discussed above, a combination of fibre cell wall thickness, specific gravity, axial parenchyma distribution, vessel grouping pattern, presence of vasicentric tracheids, and ray width can be used to identify genera (Fig. 5; Supplementary 6) (Ter Welle 1976; Kukachka 1978–1982; Détienne & Jacquet 1983; Budi 1993; Lens 2005). For instance, *Sarcosperma* is unique within Sapotaceae by a combination of distinctly bordered fibre pits (also present in *Madhuca* section *Ganua*; Budi 1993; Lens 2005) and crystal sand (Metcalfe & Chalk 1950; Lens 2005). Sometimes only one diagnostic trait is enough to identify a genus, such as the off-white coloured wood of the neotropical *Cornuella venezuelanensis* (former *Gambeya*; Kukachka 1980d), and the very large silica grains in ray cells of the monotypic *Achrouteria* (*A. pomifera*; Fig. 3L) (Kukachka 1978d).

Wood anatomy also offers new insights into the classification of species-rich genera that have undergone many taxonomic changes. For instance, contrasting classification systems exist for the pantropical *Sideroxylon* lineage (approx. 80 species), mostly based on morphological characters (Aubréville 1964; Baehni 1965; Pennington 1991; Stride *et al.* 2014). From a wood anatomical point of view, *Sideroxylon* can be defined by a dominance of dendritic vessel patterns associated with vasicentric tracheids, multiseriate rays of two or more cells wide, and a lack of dark content in ray cells (Fig. 3A, C). Yet, there is ample evidence from molecular phylogenies and wood anatomical observations for splitting this genus and reinstating a number of former smaller genera (Richardson *et al.* 2014; Stride *et al.* 2014; Fig. 1C). For instance, *Mastichodendron* is unique in *Sideroxylon* s.l. in having no dendritic vessel pattern, small intervessel pits (<4 µm), diffuse-in-aggregates axial parenchyma, and prismatic crystals (Kukachka 1978b). Furthermore, *Bumelia* can be split into a North American clade with ring-porous wood, large intervessel pits (>6 µm) and no mineral inclusions, and a Central American clade with small intervessel pits (<4 µm), widely banded axial parenchyma bands, and crystal sand (Kukachka 1978a) (Supplementary 6). However, other relationships remain unresolved in the *Sideroxylon* lineage due to incongruence between morphological, anatomical, and molecular phylogenetic data. For instance, the former genus *Argania* is morphologically unique with fused seeds that form a woody pyrene — in contrast to the presence of free seeds in the rest of *Sideroxylon* (Pennington 1991) — but both wood anatomical characters and molecular phylogenies support the inclusion of *Argania* within *Sideroxylon* s.l. (Stride *et al.* 2014; Fig. 1C).

The most species-rich Sapotaceae genus is *Pouteria* (over 200 species, clade X). This broad circumscription based mainly on floral traits has long been controversial (Baehni 1942; Aubréville 1961, 1964). Recent molecular studies split this genus into multiple, previously accepted genera (De Faria *et al.* 2017; Swenson *et al.* 2023), a decision that also receives some wood anatomical support (Kukachka 1979b,e,f, 1980b,c,e; 1981b,d, 1982a–i) (Supplementary 6). For instance, *Pouteria* s.s. is defined by straight banded axial parenchyma, silica in procumbent and square (body) ray cells, and vasicentric tracheids common (Kukachka 1982d), while *Richardella*, a synonym of *Pouteria*, has wavy and irregular axial parenchyma bands, silica in both procumbent body and upright marginal ray cells, and rarely vasicentric tracheids (Kukachka 1982e) (Supplementary 6). The latter is currently still included in *Pouteria*, but with a note that it is likely to be resurrected to genus-level when better-sampled molecular phylogenetic studies become available (Swenson *et al.* 2023). Swenson *et al.* (2023) also introduced a new, yet, unnamed clade consisting of *Pouteria cayennensis* and *P. oblanceolata* (Fig. 1A); however, the few samples we investigated did not show any distinctive wood anatomical features compared to the rest of clade IX (Supplementary 6).

While silica bodies are dominant in *Pouteria* s.s. and s.l., there are a number of other large genera for which variation in mineral inclusions helps to support subgeneric divisions established by molecular phylogenies. *Manilkara* (approx. 80 species) is a prime example as it harbours species with only prismatic crystals, prismatic crystals and silica bodies, and only silica bodies. Interestingly, the majority of *Manilkara* species are neotropical and have prismatic crystals (Kukachka 1981a), while the African and Asian species have silica bodies occasionally with prismatic crystals (Budi 1993; Lens 2005; Supplementary 6). Whether or not this is sufficient to subdivide *Manilkara* into separate genera remains to be determined, as the wood anatomy is uniform for other traits. Other examples of large genera with a similar conspicuous variation in mineral inclusions are *Gambeya* and *Palaquium*, but for these genera, no geographical groupings could be found. Some genera are more easily defined than others, and a combination of research disciplines is needed to understand intrafamilial relationships. Morphological and anatomical traits are vulnerable to homoplasy, but also gene trees are prone to incongruences due to, for instance, hybridisation and other biological factors (Deklerck *et al.* 2021; Hendriks *et al.* 2023). Therefore, more in-depth interdisciplinary taxonomic studies of the Sapotaceae are urgently needed.

Noteworthy evolutionary trends in Sapotaceae wood anatomy

The variation in Sapotaceae mineral inclusions is remarkable (Supplementary 6). Some species have silica bodies (Fig. 2F–G), others prismatic crystals or crystal sand (Fig. 2H–J), but combinations in the same wood sample are also commonly found (Supplementary 2). Only a minority of flowering plants accumulate silica in wood, which makes it a useful diagnostic trait in plant systematics (Fig. 4B; Ter Welle 1976; Kukachka 1978–1982; Carlquist 2001). For Sapotaceae, the diversity of mineral inclusions reflects a complex evolutionary history (Fig. 4). The early-diverging Sapotaceae (*Sarcosperma*) have crystal sand, followed by clades with additional larger crystals of variable shapes and sizes (*Sideroxylon*), and the introduction of silica grains in Sapotoideae and Chrysophylloideae (Fig. 4, Supplementary 6). While prismatic crystals are still abundant in Sapotoideae (often in combination with silica), they are outnumbered by (larger) silica grains in Chrysophylloideae (Fig. 4, Supplementary 6). The dominance of silica bodies in Chrysophylloideae often co-occurs with variable vessel-ray pitting in both body and marginal ray cells that defines the majority of clade X (Fig. 5B). No family-wide state reconstructions on vessel-ray pit variation could be undertaken due to a lack of overlap between this trait and the molecular dataset, but the potential link between silica presence and vessel-ray pit variation is something that deserves further investigation.

Another intriguing evolutionary shift in the wood anatomy of Sapotaceae is the recurrent transition from simple to simple mixed with scalariform vessel perforations (5–50% scalariform per sample, generally with 2–10 bars; Supplementary 2). While simple plates are the ancestral state for Sapotaceae, there are several parallel evolutionary shifts towards species that also show scalariform plates (Fig. 5A; Supplementary 7). Vessel elements with scalariform perforations are considered a textbook example of an evolutionary intermediate cell type linking primitive water conducting tracheids with vessel elements showing simple perforations (Bailey & Tupper 1918), which were later interpreted by Carlquist (2001) in a more functional framework towards increased water transport efficiency. Hence, transitions from simple to scalariform perforation plates should be treated as evolutionary reversals, which are not so uncommon as previously thought (Oskolski & Jansen 2009; Lens *et al.* 2016; Medeiros *et al.* 2019). However, the number of parallel shifts from scalariform to simple perforations still clearly outnumber the evolutionary reversals (Baas & Wheeler 1996).

Potential functional signals in Sapotaceae wood anatomy

Building hypotheses on the functional significance of certain wood anatomical traits in Sapotaceae is challenging due to a lack of a robust time-calibrated phylogenetic backbone to reconstruct past climates and an absence of in-depth xylem functional studies. Therefore, this section uses information from other families with similar traits to speculate on the potential adaptive roles of certain wood anatomical traits. One easy-to-recognise trait with a strong ecological implication is the presence of a dendritic vessel pattern associated with vasicentric tracheids (Fig. 3A–B). Sapotaceae species with an extensive dendritic arrangement generally grow in more xeric regions and at higher latitudes than their tropical sisters, such as in northern and southern Africa (*Argania* and *Sideroxylon* s.s.) (Govaerts *et al.* 2001; Lens 2005) (Fig. 1, Supplementary 6), North America (*Bumelia*; Kukachka 1978a), and southern South America (*Gayella*; Kukachka 1981d). The role of dendritic or diagonal vessel aggregations (often mixed with vasicentric tracheids) is proposed to ensure pathways for rerouting the sap flow within the same extensive vessel cluster in case drought-induced gas bubbles obstruct one or multiple vessels (Carlquist 1984, 1987; see also review of Pratt *et al.* 2023). However, this highly connected vessel network could also facilitate embolism spread, leading to hydraulic failure via air-seeding (Loepfe *et al.* 2007; Brodersen *et al.* 2013; Choat *et al.* 2015; Bouda *et al.* 2022). To avoid potentially lethal levels of embolism inside the vessel network, the surrounding vasicentric tracheids can act as a hydraulic safety net that ensures sufficient water transport to the leaves under intense drought periods (Carlquist 2001). The Malagasy *Capurodendron* is a good example. Tracheids are common in this genus and species inhabit dry forests in the northeast, west, and south of the island (Govaerts *et al.* 2001) (Supplementary 6). Species with vasicentric tracheids are also common in many other Sapotaceae, but their environmental conditions are not always well known (Supplementary 6) (Govaerts *et al.* 2001). Often these species also have narrow vessels, which may be associated with increased embolism resistance (see the discussion of Lens *et al.* 2022, and Olson *et al.* 2023 for nuances), but also with plant height (Baas *et al.* 1983; Olson *et al.* 2014). In addition, *Bumelia lycioides*, *B. tenax*, and *B. lanuginosa* (currently *Sideroxylon*) deserve special mention because these species have the only ring-porous woods in the family (Fig. 3A), and are the only ones that thrive in seasonal temperate climates at higher latitudes (Stride *et al.* 2014).

Another functional signal in Sapotaceae wood is fibre wall thickness (Jacobsen *et al.* 2005). Fibre wall lignification is necessary for mechanical strength (Zeng *et al.* 2017), but is also associated with increased drought tolerance (Martínez-Cabrera *et al.* 2009; Greenwood *et al.* 2017; Rosner 2017; Liang *et al.* 2021; Moulin *et al.* 2022). For instance, *Sideroxylon* species typically grow in arid regions (exemplified above) and show conspicuously thick-walled fibres. Also, many other Sapotaceae species — except for members in clade VI (Isonandreae) and XI (Supplementary 6) — have thick-walled fibres and occur in seasonally dry areas. The ecological implications for a variable fibre wall thickness can be nicely summarised in *Palaquium* (clade VI, Isonandreae). This species-rich genus is widely distributed in wetter and drier habitats of Southeast Asia and is also variable in plant height (Govaerts *et al.* 2001), which has resulted in species with very thin- to very thick-walled fibres. Many *Palaquium* species also have scalariform perforation plates in addition to simple plates (Fig. 4B, Supplementary 6), indicating sufficiently wet environmental conditions that do not require a fast root-to-leaf water transport system (Christman & Sperry 2010; Lens *et al.* 2016; Medeiros *et al.* 2019). Plant height is often not recorded for wood samples in scientific collections, but *Palaquium* species with scalariform perforations are generally understory trees in wet tropical forests (van Royen 1960; Whitmore 1972; Soepadmo *et al.* 2002; Wilkie *et al.* 2008). This dark and wet understory habit is perfectly suited for species with scalariform perforations and has also been found in Lecythidaceae (Lens *et al.* 2007). Other genera with scalariform perforations (*Donella*, *Labourdonnaisia*, *Gambeya*, and *Synsepalum*) also occur in wet tropical biomes and similarly vary in size as *Palaquium* (Govaerts *et al.* 2001).

Conclusions

Sapotaceae woods generally have solitary vessels co-occurring with short radial multiples. The axial parenchyma is narrowly banded, and the fibres are often thick-walled. Dark contents are often observed in the rays and axial parenchyma, and the mineral inclusions vary. The remarkable diversity and reconstructed evolutionary history of mineral inclusions (prismatic crystals, silica grains, and/or crystal sand) is conspicuous. Two other peculiar wood anatomical traits are the recurrent reversals from simple to scalariform vessel perforation plates in a few genera, and the distribution of irregularly shaped vessel-ray pits in different ray cell types. Furthermore, genera and larger clades can be identified by a combination of wood anatomical traits, such as vessel-ray pitting, mineral inclusions, and fibre type. Specific combinations of traits may reveal functional importance, like the presence of vasicentric tracheids co-occurring with narrow vessels arranged in a dendritic pattern that suggests an adaptation to drought, or the occurrence of ring-porosity in the few Sapotaceae species occurring in temperate areas. With this wood anatomical contribution, we hope traded Sapotaceae timbers can be better recognised, resulting in increased conservation efforts of these majestic trees that are a dominant part of many tropical forests around the world.

Supplementary materials

Data is available on https://doi.org/10.1163/22941932-bja10198 under Supplementary Materials.

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References

Anderberg AA, Swenson U. 2003. Evolutionary lineages in Sapotaceae (Ericales): a cladistic analysis based on ndhF sequence. *Int. J. Plant Sci.* 164(5): 763–773. DOI: 10.1086/376818.

Aubréville A. 1961. Notes sur des Poutériées Américaines. *Adansonia* 1(2): 155–159.

Aubréville A. 1964. Les Sapotacées: taxonomie et phytogéographie. *Adansonia Mémoire* 1: 1–157.

Baas P, Wheeler EA. 1996. Parallelism and reversibility in xylem evolution: a review. *IAWA J.* 17(4): 351–364. DOI: 10.1163/22941932-90000633.

Baas P, Werker E, Fahn A. 1983. Some ecological trends in vessel characters. *IAWA J.* 4(2–3): 141–159. DOI: 10.1163/22941932-90000407.

Baehni C. 1942. Mémoires sur les Sapotacées II. Le genre *Pouteria*. *Candollea* 9: 194–475.

Baehni C. 1965. Mémoire sur les Sapotacées III. Inventaire des genres. *Boissiera* 11: 1–262.

Bailey IW, Tupper WW. 1918. Size variation in tracheary cells. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. *Proc. Am. Acad. Arts Sci.* 54: 149–204.

Beckers V, Endress M, Baas P, Smets E, Lens F. 2024. Apocynaceae wood evolution matches key morphological innovations. *Am. J. Bot.*: e16436. DOI: 10.1002/ajb2.16436111.

Borg D, Richardson JE, Harris DJ, Gautier L, Hughes M, MacKinder B. 2019. Phylogeny of two African genera of Sapotaceae — *Englerophytum* and *Synsepalum*. *Edinb. J. Bot.* 76: 231–267. DOI: 10.1017/S0960428619000040.

Bouda M, Huggett BA, Prats KA, Wason JW, Wilson JP. 2022. Hydraulic failure as a primary driver of xylem network evolution in early vascular plants. *Science* 378(6620): 642–646. DOI: 10.1126/science.add2910.

Brodersen CR, Choat B, Chatelet DS, Shackel KA, Matthews MA, McElrone AJ. 2013. Xylem vessel relays contribute to radial connectivity in grapevine stems (*Vitis vinifera* and *V. arizonica*; Vitaceae). *Am. J. Bot.* 100(2): 314–321. DOI: 10.3732/ajb.1100606.

Budi AS. 1993. Struktur des sekundären Xylems und Taxonomie der Südasiatisch-Pazifischen Sapotaceae. Thesis, University of Hamburg.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009. trimAI: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 25(15): 1972–1973. DOI: 10.1093/bioinformatics/btp348.

Carlquist S. 1984. Vessel grouping in dicotyledon woods: significance and relationship to imperforate tracheary elements. *Aliso* 10(4): 505–525. DOI: 10.5642/aliso.19841004.03.

Carlquist S. 1987. Diagonal and tangential vessel aggregations in wood: function and relationship to vasicentric tracheids. *Aliso* 11(4): 451–462. DOI: 10.5642/aliso.19871104.04.

Carlquist S. 2001. *Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood*, 2nd Edn. Springer, Berlin.

Charrouf Z, Guillaume D. 2008. Argan oil: occurrence, composition and impact on human health. *Eur. J. Lipid Sci. Technol.* 110(7): 632–636. DOI: 10.1002/ejlt.200700220.

Choat B, Brodersen CR, Mcelrone AJ. 2015. Synchrotron X-ray microtomography of xylem embolism in *Sequoia sempervirens* saplings during cycles of drought and recovery. *New Phytol.* 205(3): 1095–1105. DOI: 10.1111/nph.13110.

Christman MA, Sperry JS. 2010. Single-vessel flow measurements indicate scalariform perforation plates confer higher flow resistance than previously estimated. *Plant Cell Environ.* 33(3): 431–443. DOI: 10.1111/j.1365-3040.2009.02094.x.

CITES. 2023. Convention on international trade in endangered species of wild fauna and flora. Available online at https://cites.org/eng/app/index.php (accessed 16 April 2024).

De Faria AD, Pirani JR, Ribeiro JELDS, Nylinder S, Terra-Araujo MH, Vieira PP, Swenson U. 2017. Towards a natural classification of Sapotaceae subfamily Chrysophylloideae in the Neotropics. *Bot. J. Linn. Soc.* 185(1): 27–55. DOI: 10.1093/BOTLINNEAN/BOX042.

Deklerck V, Price E, Vanden Abeele S, Lievens K, Espinoza E, Beeckman H. 2021. Timber identification of *Autranella*, *Baillonella* and *Tieghemella* in the taxonomically challenging Sapotaceae family. *Plant Methods* 17(1): 1–11. DOI: 10.1186/s13007-021-00766-x.

Detiénne P, Jacquet P. 1983. Atlas d'identification des bois de l'Amazonie et des régions voisines. Centre Techique Forestier Tropical, Nogent-sur Marne.

Dickison WC, Phend KD. 1985. Wood anatomy of the Styracaceae: evolutionary and ecological considerations. *IAWA Bull. n.s.* 6: 3–22. DOI: 10.1163/22941932-90000903.

Foley JA, Asner GP, Costa MH, Coe MT, DeFries R, *et al.* 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Front. Ecol. Environ.* 5(1): 25–32. DOI: 10.1890/1540-9295(2007)5[25:ARFDAL]2.0.CO;2.

Govaerts R, Frodin DG, Pennington TD. 2001. *World checklist and bibliography of Sapotaceae*. The Royal Botanic Gardens, Kew.

Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, Lloret F, Kitzberger T, *et al.* 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecol. Lett.* 20(4): 539–553. DOI: 10.1111/ele.12748.

Gregory M. 1994. *Bibliography of systematic wood anatomy of dicotyledons*. Rijksherbarium/Hortus Botanicus, Leiden University, Leiden.

Hendriks KP, Kiefer C, Al-Shehbaz IA, Bailey CD, Hooft van Huysduynen A, *et al.* 2023. Global Brassicaceae phylogeny based on filtering of 1000-gene dataset. *Curr. Biol.* 33(19): 4052–4068.e6. DOI: 10.1016/j.cub.2023.08.026.

IAWA Committee. 1989. List of Microscopic Features for Hardwood Identification. *IAWA J.* 10: 219–332. DOI: 10.1002/fedr.19901011106.

InsideWood. n.d. InsideWood. Available online at http://insidewood.lib.ncsu.edu/search (accessed 28 June 2023).

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD. 2005. Do xylem fibers affect vessel cavitation resistance? *Plant Physiol.* 139(1): 546–556. DOI: 10.1104/pp.104.058404.

Jahanbanifard M, Beckers V, Koch G, Beeckman H, Gravendeel B, Verbeek F, Baas P, Priester C, Lens F. 2020. Description and evolution of wood anatomical characters in the ebony wood genus *Diospyros* and its close relatives (Ebenaceae): a first step towards combating illegal logging. *IAWA J.* 41(4): 577–619. DOI: 10.1163/22941932-bja10040.

Johnson MG, Gardner EM, Liu Y, Medina R, Goffinet B, Shaw AJ, Zerega NJC, Wickett NJ. 2016. HybPiper: extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. *Appl. Plant Sci.* 4(7): 1–7. DOI: 10.3732/apps.1600016.

Johnson MG, Pokorny L, Dodsworth S, Botigué LR, Cowan RS, *et al.* 2019. A universal probe set for targeted sequencing of 353 nuclear genes from any flowering plant designed using k-Medoids clustering. *Syst. Biol.* 68(4): 594–606. DOI: 10.1093/sysbio/syy086.

Jussieu AL. 1789. *Genera Plantarum. Vol. 151.*

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30(4): 772–780. DOI: 10.1093/molbev/mst010.

Kukachka BF. 1977. Sectioning refractory woods for anatomical studies. Research Note FPL-0236. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978–1982. Wood anatomy of the neotropical Sapotaceae. I–XXXVIII. U.S Department of Agriculture, Forestry Products Laboratory Research Papers. U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978a. Wood anatomy of the Neotropical Sapotaceae. I. *Bumelia*. Research Paper FPL 325. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978b. Wood anatomy of the Neotropical Sapotaceae. II. *Mastichodendron*. Research Paper FPL 326. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978c. Wood anatomy of the Neotropical Sapotaceae. III. *Dipholis*. Research Paper FPL 327. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978d. Wood anatomy of the Neotropical Sapotaceae. IV. *Achrouteria*. Research Paper FPL 328. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978e. Wood anatomy of the Neotropical Sapotaceae. V. *Calocarpum*. Research Paper FPL 329. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978f. Wood anatomy of the Neotropical Sapotaceae. VI. *Chloroluma*. Research Paper FPL 330. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1978g. Wood anatomy of the Neotropical Sapotaceae. VII. *Chrysophyllum*. Research Paper FPL 331. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979a. Wood anatomy of the Neotropical Sapotaceae. VIII. *Diploon*. Research Paper FPL 349. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979b. Wood anatomy of the Neotropical Sapotaceae. IX. *Pseudoxythece*. Research Paper FPL 350. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979c. Wood anatomy of the Neotropical Sapotaceae. X. *Micropholis*. Research Paper FPL 351. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979d. Wood anatomy of the Neotropical Sapotaceae. XI. *Prieurella*. Research Paper FPL 352. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979e. Wood anatomy of the Neotropical Sapotaceae. XII. *Neoxythece*. Research Paper FPL 353. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1979f. Wood anatomy of the Neotropical Sapotaceae. XIII. *Podoluma*. Research Paper FPL 354. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980a. Wood anatomy of the Neotropical Sapotaceae. XIV. *Elaeoluma*. Research Paper FPL 358. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980b. Wood anatomy of the Neotropical Sapotaceae. XV. *Sandwithiodoxa*. Research Paper FPL 359. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980c. Wood anatomy of the Neotropical Sapotaceae. XVI. *Paralabatia*. Research Paper FPL 360. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980d. Wood anatomy of the Neotropical Sapotaceae. XVII. *Gambeya*. Research Paper FPL 361. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980e. Wood anatomy of the Neotropical Sapotaceae. XVIII. *Gomphiluma*. Research Paper FPL 362. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1980f. Wood anatomy of the Neotropical Sapotaceae. XIX. *Chromolucuma*. Research Paper FPL 363. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981a. Wood anatomy of the Neotropical Sapotaceae. XX. *Manilkara*. Research Paper FPL 371. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981b. Wood anatomy of the Neotropical Sapotaceae. XXI. *Barylucuma*. Research Paper FPL 372. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981c. Wood anatomy of the Neotropical Sapotaceae. XXII. *Pradosia*. Research Paper FPL 373. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981d. Wood anatomy of the Neotropical Sapotaceae. XXIII. *Gayella*. Research Paper FPL 374. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981e. Wood anatomy of the Neotropical Sapotaceae. XXIV. *Ecclinusa*. Research Paper FPL 395. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981f. Wood anatomy of the Neotropical Sapotaceae. XXV. *Ragala*. Research Paper FPL 396. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981g. Wood anatomy of the Neotropical Sapotaceae. XXVI. *Myrtiluma*. Research Paper FPL 397. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1981h. Wood anatomy of the Neotropical Sapotaceae. XXVII. *Sarcaulus*. Research Paper FPL 398. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982a. Wood anatomy of the Neotropical Sapotaceae. XXVIII. *Labatia*. Research Paper FPL 416. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982b. Wood anatomy of the Neotropical Sapotaceae. XXIX. *Eglerodendron*. Research Paper FPL 417. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982c. Wood anatomy of the Neotropical Sapotaceae. XXX. *Pseudocladia*. Research Paper FPL 418. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982d. Wood anatomy of the Neotropical Sapotaceae. XXXI. *Pouteria*. Research Paper FPL 419. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982e. Wood anatomy of the Neotropical Sapotaceae. XXXII. *Richardella*. Research Paper FPL 420. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982f. Wood anatomy of the Neotropical Sapotaceae. XXXIII. *Englerella*. Research Paper FPL 421. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982g. Wood anatomy of the Neotropical Sapotaceae. XXXIV. *Franchetella-Eremoluma*. Research Paper FPL 422. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982h. Wood anatomy of the Neotropical Sapotaceae. XXXV. *Urbanella*. Research Paper FPL 423. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982i. Wood anatomy of the Neotropical Sapotaceae. XXXVI. *Syzygiopsis*. Research Paper FPL 423. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982j. Wood anatomy of the Neotropical Sapotaceae. XXXVII. Genus Novo? Research Paper FPL 425. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Kukachka BF. 1982k. Wood anatomy of the Neotropical Sapotaceae. XXXVIII. Miscellaneous. Research Paper FPL 426. Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, WI.

Larson DA, Walker JF, Vargas OM, Smith SA. 2020. A consensus phylogenomic approach highlights paleopolyploid and rapid radiation in the history of Ericales. *Am. J. Bot.* 107(5): 773–789. DOI: 10.1002/ajb2.1469.

Lens F. 2005. Systematic significance of wood anatomical characters in Ericales. Thesis, K.U. Leuven, Leuven.

Lens F, Jansen S, Caris P, Serlet L, Smets E. 2005. Comparative wood anatomy of the primuloid clade (Ericales s.l.). *Syst. Bot.* 30(1): 163–183. DOI: 10.1600/0363644053661922.

Lens F, Baas P, Jansen S, Smets E. 2007. A search for phylogenetically informative wood characters within Lecythidaceae S.L. *Am. J. Bot.* 94(4): 483–502. DOI: 10.3732/ajb.94.4.483.

Lens F, Vos RA, Charrier G, Van Der Niet T, Merckx V, *et al.* 2016. Scalariform-to-simple transition in vessel perforation plates triggered by differences in climate during the evolution of Adoxaceae. *Ann. Bot.* 118(5): 1043–1056. DOI: 10.1093/aob/mcw151.

Lens F, Gleason SM, Bortolami G, Brodersen C, Delzon S, Jansen S. 2022. Functional xylem characteristics associated with drought-induced embolism in angiosperms. *New Phytol.* 236: 2019–2036. DOI: 10.1111/NPH.18447.

Liang X, Ye Q, Liu H, Brodribb TJ. 2021. Wood density predicts mortality threshold for diverse trees. *New Phytol.* 229(6): 3053–3057. DOI: 10.1111/nph.17117.

Loepfe L, Martinez-Vilalta J, Piñol J, Mencuccini M. 2007. The relevance of xylem network structure for plant hydraulic efficiency and safety. *J. Theor. Biol.* 247(4): 788–803. DOI: 10.1016/j.jtbi.2007.03.036.

Luo J, Li D, Cui Y. 2022. In: Itoh T, Pan B, Sano Y, Baas P (eds.), *Anatomical database and atlas of Chinese woods*. Kaiseisha Press, Otsu.

MacLachlan IR, Gasson P. 2010. PCA of CITES listed *Pterocarpus santalinus* (Leguminosae) wood. *IAWA J.* 31(2): 121–138. DOI: 10.1163/22941932-90000010.

Martínez-Cabrera HI, Jones CS, Espino S, Jochen Schenk H. 2009. Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *Am. J. Bot.* 96(8): 1388–1398. DOI: 10.3732/ajb.0800237.

Medeiros JS, Lens F, Maherali H, Jansen S. 2019. Vestured pits and scalariform perforation plate morphology modify the relationships between angiosperm vessel diameter, climate and maximum plant height. *New Phytol.* 221(4): 1802–1813. DOI: 10.1111/nph.15536.

Metcalfe CR, Chalk L. 1950. *Anatomy of the dicotyledons*, 1st Edn. Clarendon Press, Oxford.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R, Teeling E. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* 37(5): 1530–1534. DOI: 10.1093/molbev/msaa015.

Moulin JC, De Souza Ribeiro D, Vidaurre GB, Mulin LB, Moreira SI. 2022. Effect of drought stress on the formation and lignification of eucalyptus wood cells. *IAWA J.* 55(1): 1–13. DOI: 10.1163/22941932-bja10092.

Olson ME, Anfodillo T, Rosell JA, Petit G, Crivellaro A, Isnard S, Leon-Gomez C, Alvarado-Cardenas LO, Castorena M. 2014. Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. *Ecol. Lett.* 17(8): 988–997. DOI: 10.1111/ele.12302.

Olson ME, Pace MR, Anfodillo T. 2023. The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. *IAWA J.* 1(8): 1–20. DOI: 10.1163/22941932-bja10123.

Oskolski AA, Jansen S. 2009. Distribution of scalariform and simple perforation plates within the vessel network in secondary xylem of Araliaceae and its implications for wood evolution. *Plant Syst. Evol.* 278(1–2): 43–51. DOI: 10.1007/s00606-008-0130-z.

Pennington TD. 1991. *The genera of Sapotaceae*. Royal Botanic Gardens, Kew & The New York Botanical Garden, New York, NY.

Phang A, Middleton DJ, Wilkie P. 2025. Transfer of the genus *Aulandra* into *Palaquium* (Sapotaceae) and associated nomenclatural changes. *Edinb. J. Bot.* 82: 1–10. DOI: 10.24823/ejb.2025.2063.

POWO. 2024. Plants of the World Online. Available online at http://www.plantsoftheworldonline.org (accessed 13 May 2024).

Prasawang S, Srinual A. 2020. Comparative leaf and wood anatomical characteristics of *Chrysophyllum* (Sapotaceae) relate to taxonomy of the species in Thailand. *Biodiversitas* 21(4): 1578–1587. DOI: 10.13057/biodiv/d210439.

Pratt RB, Castro V, Jacobsen AL. 2023. The functional significance of tracheids co-occurring with vessels in xylem of eudicots suggests a role in embolism tolerance. *IAWA J.* 44(3–4): 477–494. DOI: 10.1163/22941932-bja10111.

Randriarisoa A, Naciri Y, Armstrong K, Boluda CG, Dafreville S, Pouchon C, Gautier L. 2023. One in, one out: Generic circumscription within subtribe Manilkarinae (Sapotaceae). *Taxon* 72(1): 98–125. DOI: 10.1002/tax.12863.

Ranwez V, Harispe S, Delsuc F, Douzery EJP. 2011. MACSE: Multiple alignment of coding sequences accounting for frameshifts and stop codons. *PLoS ONE* 6(9). DOI: 10.1371/journal.pone.0022594.

Record SJ. 1939. American woods of the family Sapotaceae. *Trop. Woods* 59: 21–51.

Richardson JE, Bakar AM, Tosh J, Armstrong K, Smedmark J, Anderberg AA, Slik F, Wilkie P. 2014. The influence of tectonics, sea-level changes and dispersal on migration and diversification of Isonandreae (Sapotaceae). *Bot. J. Linn. Soc.* 174(1): 130–140. DOI: 10.1111/boj.12108.

Rose JP, Kleist TJ, Löfstrand SD, Drew BT, Schönenberger J, Sytsma KJ. 2018. Phylogeny, historical biogeography, and diversification of angiosperm order Ericales suggest ancient Neotropical and East Asian connections. *Mol. Phylogenet. Evol.* 122: 59–79. DOI: 10.1016/j.ympev.2018.01.014.

Rosner S. 2017. Wood density as a proxy for vulnerability to cavitation: size matters. *J. Plant Hydraul.* 4: e-001. DOI: 10.20870/jph.2017.e001.

Silva CAM, Simeoni LA, Silveira D. 2008. Genus *Pouteria*: chemistry and biological activity. *Rev. Bras. Farmacogn.* 19(2A): 501–509. DOI: 10.1590/S0102-695X2009000300025.

Soepadmo E, Saw LG, Chung RCK. 2002. *Tree Flora of Sabah and Sarawak. Vol. 4*. Forest Research Institute Malaysia.

Stride G, Nylinder S, Swenson U. 2014. Revisiting the biogeography of Sideroxylon (Sapotaceae) and an evaluation of the taxonomic status of *Argania* and *Spiniluma*. *Aust. Syst. Bot.* 27(2): 104–118. DOI: 10.1071/SB14010.

Swenson U, Anderberg AA. 2005. Phylogeny, character evolution, and classification of Sapotaceae (Ericales). *Cladistics* 21(2): 101–130. DOI: 10.1111/j.1096-0031.2005.00056.x.

Swenson U, Lepschi B, Lowry PP, Terra-Araujo MH, Santos K, Nylinder S, Alves-Araújo A. 2023. Reassessment of generic boundaries in Neotropical Chrysophylloideae (Sapotaceae): eleven reinstated genera and narrowed circumscriptions of *Chrysophyllum* and *Pouteria*. *Taxon* 72(2): 307–359. DOI: 10.1002/tax.12894.

Ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, *et al.* 2013. Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092. DOI: 10.1126/science.1243092.

Ter Welle BJH. 1976. *Silica grains in woody plants of the Neotropics, especially Surinam*. *Leiden Bot. Ser.* (*3*): 107–142.

van Royen P. 1960. Revision of the Sapotaceae of the Malaysian area in a wider sense. XXIII. *Palaquium* Blanco. *Blumea*: 432–603.

Whitmore T. 1972. *Tree flora of Malaya. Vol. I.* Forest Research Institute, Kepong.

Wilkie P, Pullan M, Richardson J, Armstrong K, Buendia J, *et al.* 2008. Sapotaceae resource centre. Available online at https://padme.rbge.org.uk/Sapotaceae/welcome (accessed 24 June 2024).

Wilkie P. 2011. Towards an account of Sapotaceae for Flora Malesiana. *Gardens' Bull. Singapore* 63(1–2): 145–153.

Zeng Y, Himmel ME, Ding SY. 2017. Visualizing chemical functionality in plant cell wall. *Biotechnol. Biofuels* 10(1): 1–16. DOI: 10.1186/s13068-017-0953-3.

Zuntini AR, Carruthers T, Maurin O, Bailey PC, Leempoel K, *et al.* 2024. Phylogenomics and the rise of the angiosperms. *Nature* 629: 843–850. DOI: 10.1038/s41586-024-07324-0.

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