



The wood anatomy of Sapindales: diversity and evolution of wood characters

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Received: 17 August 2021 / Revised: 18 October 2021 / Accepted: 20 October 2021
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Abstract

The Sapindales are a large order comprised of trees, shrubs, lianas and rarely herbs. This lineage is mostly pantropical with important temperate lineages, including some of the most diverse, highly prized woods in the world, such as mahogany (*Swietenia*). In this study, we characterized the wood anatomy across eight of the nine Sapindales families, and leverage phylogenetic comparative methods to explore the evolution of wood traits in the order. We delimited 23 characters and reconstructed them onto the most recent time-calibrated phylogeny for the group. We found that ring-porosity is derived within the order, coinciding with the occupation of more seasonal climates; marginal parenchyma is ancestrally present, but largely lost in Anacardiaceae-Burseraceae-Kirkiaceae; vessels in radial chains are ancestrally absent but gained many times; scanty paratracheal parenchyma was ancestrally present with multiple evolutions of more abundant parenchyma. Anacardiaceae-Burseraceae-Kirkiaceae share tyloses and large vessel-ray pits. Radial ducts are exclusive to Anacardiaceae-Burseraceae, while traumatic ducts are exclusive to Meliaceae-Rutaceae-Simaroubaceae. Rays are generally 2–4 cells wide, heterocellular, but with multiple lineages evolving homocellular narrow rays or more heterocellular wide rays. Prismatic crystals are commonly located in rays in Anacardiaceae-Burseraceae while in the other families they are mainly in axial parenchyma. Silica bodies are abundant in Burseraceae, but also present in Anacardiaceae and Meliaceae. Lianas are exclusively in Anacardiaceae and Sapindaceae, with Sapindaceae displaying an enormous diversity of cambial variants. Our work unravels several potential synapomorphies of Sapindales major clades, and evolutionary patterns for the enormous wood anatomical diversity of the order. In addition, our work highlights variable characters worth of more detailed studies within individual families of the Sapindales.

Keywords Cambial variants · Ducts · Gums · Silica bodies · Tyloses · Vessel-ray pits · Wood evolution

1 Introduction

The Sapindales are one of the major rosid orders, with approximately 6,500 species, distributed in 479 genera and nine families: Anacardiaceae, Biebersteiniaceae, Burseraceae, Kirkiaceae, Meliaceae, Nitrariaceae, Sapindaceae, Simaroubaceae and Rutaceae (APweb, Stevens 2001 onwards; Muellner et al. 2007; Muellner-Riehl et al. 2016; APG 2016). While Bierbersteiniaceae, Kirkiaceae and Nitrariaceae are small families with only a few species, the other six are fairly large, with a mainly pantropical distribution, albeit with important temperate lineages (e.g., *Acer* L., *Aesculus* L., *Pistacia* L. and *Rhus* L.) (Andrés-Hernández et al. 2014; Xie et al. 2014; Muellner-Riehl et al. 2016). The members of these families are typically woody, large to small trees, treelets, shrubs, lianas (in

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Sapindaceae and Anacardiaceae) and only rarely herbs (Muellner et al. 2003; Muellner-Riehl et al. 2016). Species occupy a diverse realm of habitats, from rainforests to deserts and even mangroves (Muellner et al. 2003; Groppo et al. 2008; Clayton et al. 2009; Buerki et al. 2010; Muellner-Riehl et al. 2016). One remarkable aspect of the order is the myriad of secondary compounds encountered in internal and external secretory structures such as trichomes, nectaries, cavities, resin ducts, laticifers, traumatic ducts and idioblasts (APweb, Stevens 2001 onwards; Groppo et al. 2008; Cunha Neto et al. 2017; Medina et al. 2021; Tölke et al. 2021). These secretory structures are responsible for scents that are immediately recognized when trying a citric fruit, a mango, or when lighting copal incense. The monophyly of the order and all of its nine families is well-supported (Muellner-Riehl et al. 2016), opening new avenues to explore more detailed aspects of character evolution across the lineage.

Woods from members of Sapindales are among the most prized timbers in the world, especially in the Meliaceae, such as the mahogany (*Swietenia mahogany* (L.) Jacq., *S. macrophylla* King), American/Spanish cedars (*Cedrela fissilis* Vell., *C. odorata* L.), Australian red cedar (*Toona ciliata* M.Roem), sapel trees in Africa (*Entandrophragma* C.DC. species), and andiroba/crabwood (*Carapa* Aubl. spp.), among others (Petrucci 1903; Record and Hess 1972). The intensive exploitation of aforementioned timber species has considerably impacted their natural populations, and many members of Sapindales (e.g., Mahogany species) are currently CITES protected (Miller et al. 2002; Ravindran et al. 2018; UNEP-WCMC 2021). Many wood anatomical studies have sought to help identify taxa found in the market and in criminal or legal cases in response to illegal logging (e.g., Braga et al. 2011; Pastore et al. 2011; da Silva et al. 2013; Bergo et al. 2016; Rocha et al. 2021). In several of these studies, more advanced methods have been proposed to sort look-alike species almost indistinguishable based solely on wood anatomy, such as *Cedrela odorata* and *Cedrela fissilis* or even among *Carapa*, *Cedrela* P.Browne and *Swietenia* Jacq. (Bergo et al. 2016; Ravindran et al. 2018; He et al. 2020). It is also thanks to their economic importance that we have amassed countless physical, mechanical, and wood anatomical studies to date (Kribs 1930; Record and Hess 1972; Patel 1974; Datta and Samanta 1983; Mainieri et al. 1983; Mainieri and Chimelo 1989; Nair 1991; Dong and Baas 1993; Terrazas and Wendt 1995; Tomazello et al. 2001; León 2006, 2013; Luchi 2011; Campagna et al. 2017; Amusa et al. 2020). In addition, the clear demarcation of growth rings and their annual periodicity in many taxa (e.g., *Carapa*, *Cedrela* and *Swietenia*) have rendered them invaluable models for dendrochronological research (Dünisch et al. 2002; Hietz et al. 2005; Roig et al. 2005; Marcati et al. 2006a; Espinoza et al. 2014; van der Sleen

et al. 2015; Inga and del Valle 2017; Shah and Mehrotra 2017; Lisi et al. 2020; Santos et al. 2020).

Wood anatomy in the order is extremely diverse, even when only trees are considered. For instance, their woods range from quite light such as *Bursera instabilis* McVaugh & Rzed. (Burseraceae, basic wood density = 0.24 g/cm³) to extremely heavy, such as *Schinopsis brasiliensis* Engl. (Anacardiaceae, basic wood density = 1.23 g/cm³) (Riesco-Muñoz et al. 2019). Their vessels range from very narrow (30 µm, *Helietta lucida* Brandege, Rutaceae) to quite wide (200 µm; *Tapirira guianensis* Aubl., Anacardiaceae), without any specific arrangement, to clearly in radial multiples forming chains (*Paullinia* L. species; *Thouinia paucidentata* Radlk., Sapindaceae) or even dendritic (*Orixa japonica* Thunb., Rutaceae). The fiber walls range from very thin (*Zanthoxylum kellermannii* P.Wilson, Rutaceae), to quite thick (*Trichilia japurensis* C. DC., Meliceae), to having septae (*Bursera* Jacq. ex L. species, Burseraceae) or not. The axial parenchyma can be abundant aliform confluent (*Sapindus saponaria* L., Sapindaceae), in narrow bands (*Trichilia triflora* L., Meliaceae) or rare (*Acer* spp., Sapindaceae). The rays vary from uniseriate (*Cedrelopsis grevei* Baill. & Courchet, Meliaceae) to multiseriate more than three cells wide (*Cedrela odorata*, Meliaceae). This enormous wood diversity coupled with the fact that a well-supported, fossil-calibrated phylogeny to the order is available (Muellner-Riehl et al. 2016) makes this group particularly interesting to perform detailed anatomical comparative studies to investigate the diversification of wood anatomy. Here we present the largest wood anatomy dataset of Sapindales to date, and leverage this novel dataset to explore the diversity and evolutionary history of wood features, and their possible correlates with ecological conditions and habit transitions within the order. The aims of this work are: (1) to detect the common features in the woods of the Sapindales, (2) to delimit all the variable characters in the families of the order and investigate their pattern of evolution using phylogenetic comparative methods, and (3) uncover possible wood anatomical synapomorphies to major clades of Sapindales. We also tested previous hypotheses from the systematic wood anatomy literature concerning the co-evolution of wood anatomy traits. These hypotheses are: (1) ring porosity evolve together with helical thickening, both in response to either dry regimes or freezing (Nair 1987; Carlquist 2001); (2) tyloses only evolves whenever vessel-ray pits are wide enough to allow the parenchyma cell wall intrusion (Chattaway 1949), and (3) when axial parenchyma is scanty, the fibers are septate (Carlquist 2001).

2 Material and methods

Plant material – We have investigated the wood anatomy of 257 species (166 genera), most with multiple specimens (422 specimens in total) (Appendix 1). Descriptions

followed the IAWA Committee (1989) and our own character delimitation, based on the diversity found in the order. Below we detail how we performed the character delimitation, with its strengths and limitations. While most of the species were either trees, treelets and shrubs, eight species were lianas in the genera *Cardiospermum* L., *Serjania* Vell. (Sapindaceae) and *Toxicodendron* Auct. (Anacardiaceae), and one was an herb, *Peganum mexicanum* A.Gray (Nitrariaceae). We tried to always use heartwood in our descriptions, to make sure that characters such as tyloses and gums/gum-like inclusions were scored consistently. All the studied species and specimens are listed in Appendix 1, with their respective authorships and all available details of their source, including collector, localities, and where vouchers are deposited, whenever available. Our sampling included species from eight of the nine major families of Sapindales, all but Bierbersteiniaceae, a small family of rhizomatous perennial herbs (Heywood et al. 2007) that we could not find material available in collections. Since our goal was to sample as much as possible the same species used as terminals in Muellner-Riehl et al. (2016), we leveraged the publicly available database InsideWood (InsideWood 2004–onwards; Wheeler 2011; Wheeler et al. 2020). InsideWood provides a description for each species based on the IAWA Hardwood List for Microscopic Identification (IAWA Committee 1989), almost always accompanied by high-resolution photos. We have re-analyzed each species present on InsideWood, cross-checking the available descriptions to the photos to reduce user error and guarantee we were scoring all specimens under the same criteria. We have also searched publications where the species were described to cross-check their descriptions to ours and that of InsideWood. In addition to that, we have sampled all the woods of Sapindales present in the slide collections of our Institutes (Universidad Nacional Autónoma de México—UNAM MEXU, Universidade de São Paulo—USP Angyalossy's slide collection, UNAM Terrazas' collection, and some slides available from the CTFTw collection at the Smithsonian National Museum of Natural History), which are in total 117 of the 257 species. We prioritized sampling the same exact species as represented in the Muellner-Riehl et al. (2016) phylogeny; however, in cases where this was not possible (i.e., samples not available or images not in InsideWood), we analyzed at least one other species from that given genus. These cases are noted in the phylogeny by only the genus name devoid of a species epithet. All individuals analyzed are listed in Appendix 1.

Anatomical procedures – For the MEXU xylarium species, dried woods were rehydrated by boiling in 1% v/v glycerin in water, sectioned with a steel knife with the aid of sliding microtome (15–30 µm of thickness), stained in 1% v/v safranin in 50% ethanol, dehydrated in an ethanolic series (50, 70, 80, 95, 100%), followed by a xylene series

(1:1 xylene to ethanol, then 100% xylene), then mounted in Canada balsam. Samples from the Angyalossy's or Terrazas' collections were fixated in FAA 50 (formaldehyde-acetic acid -50% ethanol), preserved in 70% ethanol, softened either with GAA (glycerin—95% alcohol—water; 1:1:1) or by boiling. The samples were sectioned with the aid of a sliding microtome in transverse and longitudinal sections (15–30 µm of thickness), and either stained exclusively with safranin or double stained with safranin-fast green or safranin-astra blue (Johansen 1940; Kraus and Arduim 1997). The sections were subsequently dehydrated in an ethanolic series, rinsed in xylene or butyl acetate, and mounted in a histological resin (Johansen 1940; Pace 2019). Newly developed slides are deposited at MEXU herbarium. All other samples used in this work were from different slide collections, to which we have no information of the anatomical procedures used.

Slides were analyzed under a Leica DM2500 and Velab prime VE-B50 compound microscope, and photographed with the software ImageView.

Phylogenetic comparative methods – Character delimitation. Considering 168 species of which we had both anatomical photos/slides and that were present in the phylogeny of Muellner et al. (2016), we delimited, described and performed ancestral character state estimations of 23 wood anatomical characters (Tables 1 and 2). Character could be divided in either neomorphic (character states absent or present) or transformational (from one state to another, e.g., from color pink to yellow), as proposed by Sereno (2007) and available in Table 1. We also provide as Supplementary Appendix 1 a complete description of all characters, following the IAWA Hardwood List (IAWA Committee 1989), for all the 257 species sampled here. In many cases, our character delimitation is independent of the features proposed by the IAWA Committee (1989); for instance: we consider that each different growth markers are independent from each other (non-homologous) (Supplementary Appendix 1), and therefore, they are delimited in separate states, e.g., radially narrow fibers, marginal parenchyma, ring porosity. Also, for some quite variable characters, as ray width and composition, and because it was common to have more than one type co-occurring, we delimited more inclusive character states to encompass this variation. One limitation we faced in the reconstruction of quantitative characters was that, because we did not have the anatomical slides for most species in the phylogeny, and scales are not available on InsideWood, we needed to discretize some of the continuous features in arbitrary ranges, a problem rightfully criticized by Olson (2005). This was done for three characters: intervessel pit size, parenchyma strand length and ray width. We decided to carry this less-optimal approach not to ignore these variable features, and their inclusion here will be explored in future

Table 1 Characters and character states included in phylogenetic reconstructions of the Sapindales using wood anatomy

Character	Character states	Character type
1	Growth ring: indistinct (0); distinct (1)	Transformational
2	Wood porosity: Diffuse (0); semi-ring to ring-porous (1)	Transformational
3	Vessel arrangement: diffuse (0); Radial and/or dendritic (1)	Transformational
4	Intervessel pits size: < 8 μm (0); > 8 μm (1)	Transformational
5	Vessel-ray pitting: equal (0); semi-bordered to simple (1);	Transformational
6	Helical thickening: absent (0); present (1)	Neomorphic
7	Tyloses: absent (0); present (1)	Neomorphic
8	Gums: absent (0); present (1)	Neomorphic
9	Septate fibers: absent (0); present (1)	Neomorphic
10	Marginal bands: absent (0); present (1)	Neomorphic
11	Axial parenchyma paratracheal: aliform (0); aliform confluent (1); vasicentric (2); vasicentric confluent (3); scanty (4)	Transformational
12	Paratracheal unilateral: absent (0); present (1)	Neomorphic
13	Apotracheal diffuse: absent (0); present (1)	Neomorphic
14	Apotracheal banded: absent (0); present (1)	Neomorphic
15	Parenchyma strand length: < 4 cells (0); > 4 cells (1)	Transformational
16	Parenchyma-like fibers: absent (0); present (1)	Neomorphic
17	Ray width > 3 cells: absent (0); present (1)	Neomorphic
18	Ray composition: exclusively homocellular (0); homo and heterocellular with one marginal row of upright/square cells (1); heterocellular with many marginal row of upright/square cells (2)	Transformational
19	Crystal location: rays (0); axial parenchyma (1); fibers (2)	Transformational
20	Storied structure: absent (0); present (1)	Neomorphic
21	Radial canals: absent (0); present (1)	Neomorphic
22	Traumatic canals: absent (0); present (1)	Neomorphic
23	Silica: absent (0); present (1)	Neomorphic

Character types as defined by Sereno (2007)

discussions in wood evolution studies and how we interpret, biologically, the diversity that occurs in wood anatomy. For the samples from our own collections (117 species), we were able to quantify exact values (Table 3), but they differ from the species in the phylogeny and these data were therefore used only to perform Principal Component Analyses, as discussed below.

Ancestral character state estimations and correlation analysis. The ancestral state estimations and tests of correlated evolution were performed using the Sapindales chronogram from Mueller-Riehl et al. (2016). This phylogeny was built with three molecular markers, plastid genes *rbcL*, *atpB* and *trnL-trnLF*, covering one-third of the species diversity for the order. For each of the analyzed characters, the phylogeny was first pruned down to those species with wood anatomy data, using the *drop.tip* function in *phytools* (Revell 2012). For each character, the best-fit model (equal rates or all rates different) was determined using a likelihood ratio test provided the log likelihood using *fitMk* for 2-state discrete traits, or *fitpolyMk* for polymorphic features (Revell 2012). Using the best-fit model, each character history was

estimated by summarizing the results of 1000 stochastic character maps obtained utilizing the *make.simmap* function (Revel 2013). A summary of character histories was visualized by jointly overlaying the 1000 character maps to display character transitions along branches and the posterior probabilities at nodes, using the *plot.simmap* function written by Dr. Michael May (UC-Berkeley). All analyses were performed in R (R Core Development Team 2021), and associated code is available at github.com/joycechery. All model statistics are reported in supplementary Appendix 2. For the correlated evolution between ring porosity and helical thickening, tyloses and vessel-ray pits and axial parenchyma type and septate fibers using a Pagel's 1994 phylogenetic test as implemented in R using the *fit.pagel* function and the ARD model of evolution in *phytools* (Supplementary Appendix 2).

Principal component analysis (PCA) – For detecting if quantitative features of the vessels, rays and axial parenchyma in woods of Sapindales had any power in sorting the families, we performed statistical analyses exclusively to the 117 specimens that were sampled from our own institutional

Table 2 Categorical matrix of anatomical characters to each species included in the phylogenetic reconstructions of the Sapindales (Number correspond to characters explained in Table 1)

Species	Growth rings			Vessel			Fiber			Axial parenchyma						Ray			Crystals				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Anacardiaceae																							
<i>Amphiterygium adstringens</i>	1	0	0	0	1	0	1	0	1	0	4	0	0	0	0	0	0	1	0	0	1	0	0
<i>Apterokarpos</i> (= <i>Loxopterygium</i>) <i>gardneri</i>	1	0	0	1	1	0	1	0	1	0	2	1	1	0	0	0	0	2	1	0	1	0	1
<i>Blepharocarya involucrigera</i>	1	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	1	0	0	0	0	0
<i>Buchanania arborescens</i>	1	0	0	1	1	0	1	0	1	1	4	1	0	0	0	0	0	1	1	0	1	0	1
<i>Choerospondias axillaris</i>	1	1	0	1	1	0	1	0	1	0	4	1	0	0	0	0	1	1	1/2	0	1	0	0
<i>Comocladia engleriana</i> (= <i>macrophylla</i>)	1	0	0	1	1	0	1	1	0	1	2	0	0	0	0	0	0	1	1	0	0	0	0
<i>Cottinus obovatus</i>	1	1	1	1	1	1	1	0	0	0	2	1	0	0	0	0	1	2	1/2	0	0	0	0
<i>Dracontomelon dao</i>	0	0	0	1	1	0	1	0	1	0	2	1	0	0	0	0	1	2	0	0	0	0	0
<i>Faguetia falcata</i>	1	0	0	0	0	0	1	0	0	1	2	0	0	0	1	0	0	1	1	0	0	0	0
<i>Fegimanra africana</i>	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	1	NA	0	0	0	NA
<i>Harpephyllum caffrum</i>	1	0	0	1	0	0	1	0	1	0	4	0	0	0	0	0	0	1	1	0	1	0	0
<i>Lannea rivae</i>	1	0	0	1	0	0	1	0	1	0	4	0	0	0	0	0	0	2	1	0	1	0	1
<i>Loxopterygium huasango</i>	1	0	0	1	0	0	1	0	1	0	2	1	1	0	0	0	0	2	1	0	1	0	1
<i>Loxostylis alata</i>	1	0	0	0	1	0	0	0	1	0	4	0	0	1	0	0	0	2	1	0	1	0	0
<i>Mangifera indica</i>	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0
<i>Metopium brownei</i>	1	0	1	1	0	0	1	1	0	1	1	1	0	0	1	0	0	2	1	0	1	0	0
<i>Micronychia macrophylla</i>	1	0	0	0	1	0	1	0	1	0	4	1	0	0	0	0	0	2	2	0	0	0	0
<i>Operculicarya decaryi</i>	0	0	0	1	0	0	0	0	1	0	4	1	0	0	0	0	0	1	0	0	1	0	0
<i>Pachycornus discolor</i>	1	0	0	1	0	0	0	0	1	0	4	0	0	0	0	0	1	2	1	0	0	0	0
<i>Pistacia chinensis</i>	1	1	1	1	0	1	0	0	1	0	4	0	0	0	0	0	0	1	2	0	1	0	0
<i>Protorhus</i> (= <i>Abrahamia</i>) <i>thouvenotii</i>	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0
<i>Rhus thourarii</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Rhus typhina</i>	1	1	1	0	1	1	0	0	0	0	4	0	0	0	0	0	0	1	1	0	0	0	0
<i>Schinus molle</i>	1	1	1	0	0	1	1	0	1	0	4	1	0	0	0	0	1	1	1/2	0	1	0	0
<i>Searsia erosa</i>	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	2	0	0	0	0	0
<i>Semecarpus forstenii</i>	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
<i>Spondias tuberosa</i>	0	0	0	1	0	0	1	0	1	0	2	1	0	0	0	0	1	2	1	0	1	0	0
<i>Tapirira bethanniana</i>	1	0	0	1	0	0	1	0	1	0	4	0	0	0	0	0	0	2	1	0	1	0	0
<i>Tapirira obtusa</i>	1	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	2	1	0	1	0	0
<i>Toxicodendron vernicifluum</i>	1	1	1	1	0	1	1	0	0	1	4	1	0	0	0	0	0	2	1	0	0	0	0
Burseraceae																							
<i>Aucoumea klaineana</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	0	0	0	0	1
<i>Beiselia mexicana</i>	0	0	0	1	1	0	0	0	1	0	4	NA	0	0	0	0	0	2	1	0	1	0	0
<i>Boswellia neglecta</i>	1	0	0	1	1	0	0	0	1	1	4	0	0	0	0	0	1	2	0	0	1	0	0

Table 2 (continued)

Species	Growth rings			Vessel			Fiber			Axial parenchyma			Ray			Crystals							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Bursera biflora</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	1	1	0	1	0	0
<i>Bursera cuneata</i>	0	0	0	1	1	0	0	0	1	0	4	0	0	0	0	0	0	2	1	0	1	0	0
<i>Bursera hindsiiana</i>	0	0	0	1	1	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	0
<i>Bursera lancifolia</i>	1	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	1	2	1	0	1	0	0
<i>Bursera microphylla</i>	0	0	0	1	1	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	0
<i>Bursera simaruba</i> (= <i>arborea</i>)	1	0	0	1	1	0	0	0	1	0	4	0	0	0	0	0	1	2	1	0	1	0	0
<i>Bursera tecomaca</i>	0	0	0	1	1	0	0	0	0	0	4	0	0	0	0	0	0	2	0	0	0	0	0
<i>Canarium decumanum</i>	0	0	0	1	1	0	0	0	1	0	4	1	0	0	0	0	0	1	1	0	0	0	0
<i>Canarium indicum</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	1/2	0	1	0	0
<i>Canarium muelleri</i>	0	0	0	1	1	0	0	0	1	0	4	1	0	0	0	0	0	2	1	0	1	0	0
<i>Canarium oleiferum</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	0	0	0	0	1
<i>Canarium ovatum</i>	0	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	1	1	0	1	0	1
<i>Canarium pilosum</i>	0	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	1	1	0	1	0	1
<i>Canarium tramdenum</i> (= <i>pimela</i>)	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	1	0	0	0	1
<i>Conniphora edulis</i>	1	0	0	1	1	0	0	0	1	0	4	1	0	0	0	0	0	2	0	0	1	0	1
<i>Conniphora falcata</i>	1	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	2	1	0	1	0	0
<i>Conniphora schimperi</i>	1	0	0	1	1	0	0	0	1	0	4	1	0	0	0	0	0	2	1	0	1	0	1
<i>Crepidospermum goudotianum</i>	1	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	1	0	0	0	1
<i>Dacryodes cuspidata</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	0	0	0	0	1
<i>Dacryodes edulis</i>	0	0	0	1	1	0	0	0	1	0	4	1	0	0	0	0	0	2	1	0	0	0	1
<i>Dacryodes rostrata</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	1	0	0	0	0	1
<i>Dacryodes rugosa</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	0	0	0	0	0
<i>Garuga floribunda</i>	1	0	0	1	0	0	0	0	1	0	4	1	0	0	0	0	1	2	1	0	1	0	0
<i>Protium copal</i>	1	0	0	1	0	0	1	0	1	0	4	1	0	1	0	0	0	1	0	0	0	0	0
<i>Protium madagascariense</i>	0	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	2	1	0	0	0	1
<i>Protium serratum</i>	1	0	0	1	1	0	1	0	1	0	4	0	0	0	0	0	0	1	1	0	1	0	0
<i>Santiria apiculata</i>	1	0	0	1	0	0	0	0	1	1	4	0	0	0	0	0	0	2	0	0	0	0	0
<i>Santiria griffithii</i>	1	0	0	1	1	0	0	0	1	1	4	0	0	0	0	0	0	2	0	0	0	0	0
<i>Santiria trimera</i>	0	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	1	0	1	0	1
<i>Tetragastris altissima</i>	1	0	0	1	0	0	1	0	1	0	4	1	0	0	0	0	0	2	1	0	1	0	0
<i>Tratinnickia demerarae</i>	1	0	0	1	1	0	1	0	1	0	4	1	0	0	0	0	0	2	0	0	0	0	1
<i>Triomma malaccensis</i>	1	0	0	1	0	0	0	0	1	1	4	1	0	0	0	0	0	2	1	0	1	0	0
Kirkiaceae																							
<i>Kirkia acuminata</i>	1	0	0	1	1	0	1	0	1	0	4	0	0	0	0	a	1	2	0	0	0	0	1

Table 2 (continued)

Species	Growth rings			Vessel			Fiber			Axial parenchyma			Ray			Crystals							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Meliaceae																							
<i>Aglaia elaeagnoides</i>	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	2	0	0	0	0
<i>Aglaia odorata</i>	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	2	0	0	0	0
<i>Azadirachta indica</i>	1	0	0	0	0	0	0	1	0	1	2	1	0	0	0	0	1	2	2	0	0	0	0
<i>Cabralea canjerana</i>	1	0	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	2	1	0	0	0	0
<i>Capuronianthus mahafalensis</i>	1	0	1	0	0	0	0	1	NA	1	4	0	0	0	0	0	0	1	2	0	0	0	0
<i>Carapa guianensis</i>	1	0	0	0	0	0	0	1	1	1	4	1	0	0	0	0	1	2	1/2	0	0	1	0
<i>Cedrela odorata (= mexicana)</i>	1	1	0	0	0	0	0	1	1	1	4	1	0	1	0	0	0	1	1/2	0	0	1	0
<i>Chukrasia tabularis</i>	1	0	0	0	0	0	0	1	0	1	4	1	0	1	0	0	1	1	1/2	0	0	1	0
<i>Dysoxylum arborescens</i>	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	2	0	0	0	0
<i>Ekebergia capensis</i>	1	0	0	0	0	0	0	1	0	1	2	1	0	0	0	0	0	1	2	1	0	0	0
<i>Guarea glabra</i>	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	2	0	0	0	1
<i>Khaya</i> sp.	1	0	0	0	0	0	0	1	1	1	4	1	0	0	0	0	1	2	1	0	0	1	0
<i>Lansium domesticum (= parasiticum)</i>	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1/2	0	0	0	0
<i>Lepidotrichilia convallariodora</i>	1	0	0	0	0	0	0	0	1	4	1	0	0	0	0	0	0	1	2/3	0	0	0	0
<i>Lovoa trichilioides</i>	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	1	2	0	0	1	0
<i>Melia azedarach</i>	1	1	1	0	1	1	0	1	0	0	2	0	0	0	0	0	1	1	2	1	0	0	0
<i>Nymphia capensis</i>	1	0	1	0	0	0	0	0	0	4	1	0	1	0	0	0	0	2	0	0	0	0	0
<i>Owenia ceptiodora</i>	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	2	1	0	0	0
<i>Reinwardtiadendron celebicum</i>	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	2	0	0	0	1
<i>Sandoricum koetjape</i>	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
<i>Swietenia macrophylla</i>	1	0	0	0	1	0	0	1	1	2	1	0	1	0	0	0	0	2	1/2	1	0	1	0
<i>Swietenia mahogany</i>	1	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	0	2	1/2	1	0	1	0
<i>Toona sinensis</i>	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	2	1	0	0	1	0
<i>Trichilia emetica</i>	1	0	0	0	1	0	0	1	0	3	1	0	0	0	0	0	0	2	2	0	0	0	1
<i>Turraea sericea</i>	1	0	0	0	0	0	0	0	1	4	1	0	0	0	0	0	0	1	1	0	0	0	0
<i>Turraeanthus africana</i>	0	0	0	0	0	0	0	1	0	4	1	0	0	0	0	0	0	1	1/2	0	0	0	0
<i>Walsura tubulata</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0
<i>Xylocarpus moluccensis</i>	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1/2	1	0	0	0
Nitriaceae																							
<i>Nitaria retusa</i>	1	0	1	0	0	1	0	1	0	1	3	0	1	0	0	0	0	2	2/3	1	0	0	0
Rutaceae																							
<i>Aegle marmelos</i>	1	0	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0
<i>Atalantia monophylla</i>	1	0	1	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Casimiroa edulis</i>	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0

Table 2 (continued)

Species	Growth rings			Vessel			Fiber			Axial parenchyma			Ray			Crystals							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Chloroxylon swietenia</i>	1	0	1	0	0	0	0	1	0	1	4	0	0	1	0	0	0	1	1/2	1	0	1	0
<i>Choisya dumosa</i> (= <i>dumosa</i> var. <i>mollis</i>)	1	1	0	0	0	1	0	0	0	1	4	0	0	0	0	0	0	2	0	0	0	0	0
<i>Citrus</i> sp.	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1/2	0	0	0	0
<i>Citrus medica</i> (= <i>limetta</i>)	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	0
<i>Clausena melioides</i>	1	0	1	0	0	0	1	0	0	1	4	0	0	1	0	0	1	1	2	0	0	0	0
<i>Cneorum tricocon</i>	1	1	1	0	0	1	0	0	0	0	4	0	0	1	0	0	0	2	1/2/3	0	0	0	0
<i>Flindersia australis</i>	1	0	0	0	0	0	0	1	0	1	4	0	0	1	0	0	0	0	2	0	0	0	0
<i>Melicope fatrainia</i>	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	2	0	0	0	1
<i>Murraya paniculata</i>	1	0	0	0	1	0	0	1	0	1	4	1	0	0	0	0	0	0	2	0	0	0	0
<i>Phellodendron amurense</i>	1	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	2	0	0	0	0
<i>Pleiospermium alatum</i>	1	0	0	0	1	0	0	1	0	NA	2	0	0	1	0	0	0	0	2	0	0	0	0
<i>Poncirus</i> (= <i>Citrus</i>) <i>trifoliata</i>	1	0	0	0	0	1	0	0	0	1	2	0	0	1	0	0	0	1	1/2	0	0	0	0
<i>Ptaeroxylon obliquum</i>	1	0	0	0	1	0	0	1	0	0	4	0	0	0	0	0	0	0	NA	1	0	0	0
<i>Ruta chapelensis</i>	1	0	1	0	1	1	0	1	0	1	4	0	0	0	0	0	0	1	0	0	0	0	0
<i>Sarcomelicope simplicifolia</i>	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	NA	0	0	0	NA
<i>Skimmia japonica</i>	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	0
<i>Spathelia sorbifolia</i>	1	0	1	0	0	0	0	0	0	1	4	0	0	0	0	0	0	1	0	0	0	0	0
<i>Tetradium daniellii</i>	1	1	1	0	1	1	0	1	0	0	2	0	0	0	0	0	1	1	2	0	0	0	0
<i>Zanthoxylum ailanthoides</i>	1	1	0	0	0	0	1	0	1	2	0	0	0	0	0	0	1	1	2	0	0	0	0
<i>Zanthoxylum nitidum</i>	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	1	2	0	0	0	0
Sapindaceae																							
<i>Acer</i> sp.	1	0	0	1	0	1	0	0	0	0	4	0	0	1	0	0	1	0	2	0	0	0	0
<i>Aesculus pavia</i>	1	0	0	0	0	1	0	1	0	1	4	0	0	0	0	0	0	0	0	1	0	0	0
<i>Alectryon connatum</i>	1	0	0	0	0	1	0	1	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0
<i>Arytera littoralis</i>	1	0	0	0	0	1	0	1	0	0	2	1	0	0	0	0	0	2	2/3	0	0	0	0
<i>Atalaya hemiglanca</i>	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	2	0	0	0	0
<i>Cardiospermum halicacabum</i>	0	0	1	0	0	0	0	1	0	2	NA	0	1	0	1	0	1	2	1/2/3	0	0	0	0
<i>Cupaniopsis anacardioides</i>	1	0	0	0	0	1	0	1	0	0	4	1	0	0	0	0	0	1	3	0	0	0	0
<i>Dilodendron bipinnatum</i>	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0
<i>Diploglottis australis</i>	1	0	0	0	0	0	1	1	0	0	4	1	0	0	0	0	0	1	2/3	0	0	0	0
<i>Diploleba floribunda</i>	?	0	NA	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	2	0	0	0	NA
<i>Dodonaea viscosa</i>	0	0	0	0	0	1	0	1	0	1	4	1	0	1	1	0	0	1	2	0	0	0	0
<i>Eurycorymbus cavaleriei</i>	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	2	0	0	0	0
<i>Filicium decipiens</i>	1	0	0	0	1	0	0	1	1	3	1	0	0	0	0	0	0	1	2	0	0	0	0
<i>Ganophyllum falcatum</i>	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	1	2	1	0	0	0

Table 2 (continued)

Species	Growth rings			Vessel			Fiber			Axial parenchyma			Ray			Crystals							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Guioa bijuga</i>	1	0	NA	0	0	0	0	1	1	0	2	1	0	1	0	0	0	1	2	0	0	0	NA
<i>Harpullia arborea</i>	1	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	2	2	0	0	0	0
<i>Hypelate trifoliata</i>	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	2	0	0	0	0
<i>Koelreuteria paniculata</i>	1	1	0	0	0	1	0	1	1	1	2	0	0	1	0	0	0	1	1/2	0	0	0	0
<i>Litchi chinensis</i>	1	0	0	0	0	1	0	1	1	0	2	1	0	0	0	0	0	1	1/2/3	0	0	0	0
<i>Nephelium lappaceum</i>	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	2	0	0	0	0
<i>Pappea capensis</i>	1	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	0	2	1/2/3	0	0	0	0
<i>Sapindus saponaria</i>	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	2	0	0	0	0
<i>Schleichera oleosa</i>	1	0	0	0	1	0	0	1	1	0	4	1	0	1	0	0	0	2	1/3	0	0	0	0
<i>Serjania</i> sp.	0	0	1	0	1	0	0	0	1	0	2	1	0	1	0	0	1	2	1/2	0	0	0	0
<i>Talisia nervosa</i>	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	2	1	0	0	0	0
<i>Thouinia portoricensis</i>	1	0	1	0	1	0	0	1	1	0	4	1	0	0	0	1	0	1	3	0	0	0	0
<i>Toechima tenax</i>	0	0	0	0	0	1	0	1	1	0	4	1	0	0	0	1	0	1	3	0	0	0	0
<i>Tristira triptera</i>	1	0	0	0	1	0	0	1	1	0	1	1	0	1	1	0	0	2	2	0	0	0	0
<i>Tristropsis acutangula</i>	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0	0	2	0	0	0	0
<i>Xanthoceras sorbifolia</i>	1	1	1	0	0	1	0	1	0	1	2	0	0	0	0	0	0	1	2/3	0	0	0	0
Simaroubaceae																							
<i>Ailanthus altissima</i>	1	1	1	0	0	1	0	1	0	1	3	1	0	0	1	0	1	1	0	1	0	0	0
<i>Ailanthus integrifolia</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0
<i>Brucea guineensis</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0
<i>Brucea javanica</i>	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0
<i>Castela coccinea</i>	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	1	0	0	0
<i>Eurycoma longifolia</i>	1	0	1	NA	NA	0	0	0	0	0	1	0	0	0	1	0	1	2	NA	0	0	0	0
<i>Holacantha emoryi</i>	0	0	1	NA	NA	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0
<i>Leitneria floridana</i>	1	1	1	1	0	1	0	0	1	4	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Nothospondias staudtii</i>	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0
<i>Odyndea (= Quassia) gabunensis</i>	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	2	1	0	0	0
<i>Perriera madagascariensis</i>	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1/2	1	0	0	0
<i>Picrasma javanica</i>	1	0	0	0	0	0	0	0	1	3	1	0	0	0	0	0	0	2	1	1	0	0	0
<i>Picrasma quassioides</i>	1	1	1	0	0	0	0	1	0	1	3	1	0	0	1	0	1	1	0	1	0	1	0
<i>Pierreodendron africanum</i>	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	0
<i>Quassia amara</i>	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0
<i>Samadera (= Quassia) indica</i>	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	0	0
<i>Simaba cedron</i>	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0
<i>Simaba orinocensis</i>	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0

Table 2 (continued)

Species	Growth rings			Vessel			Fiber			Axial parenchyma						Ray			Crystals				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Simarouba</i> sp.	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	0
<i>Soutamea</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

wood collections. The wood characters delimited were: (1) average vessel diameter (μm), (2) vessel frequency (vessels. mm^{-2}), (3) ray height (μm), (4) ray width (number of cells) and (5) the percentage of the axial parenchyma in wood (Table 3). These features were measured with ImageJ (Schneider et al. 2012) with a minimum of 25 measurements per field, with all available specimens from our own collections. We explored the variation of quantitative anatomical features applying principal component analysis (PCA) and using the two main PCA axes that explain 60% of the variation from the original data. Anatomical variables were standardized by subtracting the means and by division of the standard deviations of each variable, to give equal weight to variable in the analysis. All analytical procedures were performed using R (R Core Development Team 2021).

3 Results

General features of the Sapindales – The wood anatomy of Sapindales is very diverse, but some features may be considered general. Virtually all species have distinct growth rings varying from straight (Fig. 1a, c) to wavy (Fig. 1b), delimited by thick-walled, radially narrow fibers (Fig. 1a–c), commonly in association to other growth rings markers (Supplementary Appendix 1), which will be treated separately below. The presence of growth rings is reconstructed as ancestrally present (Supplementary Fig. 1). Having a mostly tropical distribution, diffuse-porous woods predominate (Fig. 1a–c), but ring-porous and semi-ring porous woods (e.g., tropical *Cedrela fissilis*, *C. odorata*; and temperate *Ailanthus* Desf., *Phellodendron*, *Rhus*) can be present. Typically, the vessels have simple perforation plates in slightly inclined end walls and alternate intervessel pits (Fig. 1d). However, in some isolated taxa, such as the Mexican treelet *Beiselia* Forman (the sister taxon of all other Burseraceae), although simple perforation plates predominate, scalariform perforations are also present and the vessels have scalariform intervessel pits. In general, vessels are typically solitary to multiples of 2–3 (Fig. 1a–c), however occasional cases of radial and dendritic arrangements exist. The axial parenchyma is extremely varied, but different types of paratracheal parenchyma are ubiquitous (Fig. 1a), present even when in association to other types. Parenchyma-like fibers (the alternation of thick and thin-walled bands of fibers) are fairly common in Sapindaceae [in 17% of the species according to Klaassen 1999] (Fig. 1c). The rays are usually not particularly tall (Fig. 1d–f), and heterocellular rays are the norm, composed of procumbent body cells and 1 or more rows of upright to square cells (Fig. 1g). Axial parenchyma has mostly 2–4 cells per strands (Fig. 1e), but longer strands up to 8 cells long can be found in numerous species (Fig. 1f).

Table 3 Quantitative measurements in 115 woods of Sapindales (Anacardiaceae, Burseraceae, Kirkiaceae, Meliaceae, Nitrariaceae, Rutaceae, Sapindaceae and Simaroubaceae)

Specie	Vessel diameter (μm)	Vessel frequency (vessel. mm^{-2})	Ray height (μm)	Ray width (n°cells)	Axial parenchyma (%)
Anacardiaceae					
<i>Actinocheita filicina</i>	76.74 \pm 33.19	34 \pm 7	239.82 \pm 88.67	–	–
<i>Anacardium giganteum</i>	124.23 \pm 64.26	3 \pm 1	322.36 \pm 84.05	1	5.08 \pm 0.85
<i>Astronium graveolens</i>	43.75 \pm 15.77	34 \pm 5	163.89 \pm 61.2	2 \pm 1	2.84 \pm 1.52
<i>Astronium sp.</i>	103.22 \pm 39.49	8 \pm 2	239.72 \pm 81.47	3 \pm 1	2.84 \pm 1.52
<i>Buchanania arborescens</i>	78.32 \pm 44.23	10 \pm 4	326.23 \pm 73.68	3 \pm 2	10.57
<i>Choerospondias axillaris</i>	114.3 \pm 55.28*	15 \pm 6	217.34 \pm 88.03	3 \pm 1	–
<i>Comocladia macrophylla</i> (= <i>engleriana</i>)	33.92 \pm 15.08	30 \pm 12	134.75 \pm 59.41	2 \pm 1	–
<i>Cotinus obovatus</i>	73.51 \pm 11.10*	140 \pm 97	221.8 \pm 84.16	3 \pm 1	–
<i>Cyrtocarpa procera</i>	60.25 \pm 15.53	30 \pm 4	329.6 \pm 108.53	4 \pm 1	–
<i>Dracontomelon dao</i>	135.55 \pm 37.41	4 \pm 1	372.42 \pm 106.89	–	5.65
<i>Faguetia falcata</i>	92.39 \pm 28.41	42 \pm 10	414.41 \pm 129.49	2 \pm 1	6.19
<i>Gluta tourtour</i>	151.74 \pm 56.92	30 \pm 12	280.85 \pm 91.68	2 \pm 1	8.02
<i>Harpephyllum caffrum</i>	85.84 \pm 29.64	25 \pm 5	482.03 \pm 13.81	4	0.73
<i>Loxopterygium sp.</i>	88.8 \pm 28.87	11 \pm 1	204.92 \pm 75.1	2 \pm 1	1.58 \pm 0.16
<i>Loxostylis alata</i>	39.31 \pm 15.41	45 \pm 11	215.7 \pm 69.87	2 \pm 1	2.96
<i>Mangifera altissima</i>	137.52 \pm 22.42	4 \pm 1	292.31 \pm 143.44	1	14.15
<i>Mangifera indica</i>	54.28 \pm 28.23	14 \pm 9	207.81 \pm 51.96	2 \pm 1	13.2
<i>Metopium brownei</i>	77.16 \pm 30.94	21 \pm 6	352.13 \pm 101.52	3 \pm 1	11.15 \pm 2.45
<i>Micronychia tsiramiramy</i>	60.01 \pm 13.41	22 \pm 2	319.3 \pm 129.92	2 \pm 1	4.67
<i>Mosquitoxylum jamaicense</i>	96.17 \pm 45.28	20 \pm 6	460.84 \pm 120.72	2 \pm 1	2.98 \pm 0.85
<i>Myracrodruon urundeuva</i>	47.15 \pm 18.82	27 \pm 7	141.47 \pm 42.34	3 \pm 1	4.05 \pm 0.49
<i>Pachycormus discolor</i>	71.58 \pm 17.22	36 \pm 8	343.13 \pm 198.54	3 \pm 2	–
<i>Pistacia chinensis</i>	84.6 \pm 26.36*	188 \pm 34	149.96 \pm 89.84	2 \pm 2	1.98
<i>Pistacia mexicana</i>	63.5 \pm 9.71*	118 \pm 178	267.36 \pm 91.1	3 \pm 1	6.96 \pm 2.05
<i>Poupartia chapelieri</i>	103.92 \pm 38.8	26 \pm 5	296.16 \pm 121.06	2 \pm 1	4.39
<i>Protorhus</i> (= <i>Abrahamia</i>) <i>thouvenotii</i>	69.14 \pm 26.74	32 \pm 6	298.29 \pm 99.03	2 \pm 1	10.14
<i>Rhus chondroloma</i>	55.82 \pm 24.32*	127 \pm 16	218.91 \pm 89.65	2 \pm 1	12.5 \pm 2.46
<i>Rhus</i> (= <i>Protorhus</i>) <i>perrieri</i>	106.63 \pm 36.39*	72 \pm 8	303.57 \pm 106.62	3 \pm 1	11.85
<i>Schinus molle</i>	94.7 \pm 34.95*	64 \pm 13	170.41 \pm 79.71	2 \pm 1	–
<i>Spondias mombin</i>	140.23 \pm 89.22	18 \pm 5	889.39 \pm 359.3	5 \pm 2	7.32 \pm 1.68
<i>Spondias purpurea</i>	97.71 \pm 43.8	16 \pm 5	488.15 \pm 151.31	2 \pm 1	1 \pm 0.6
<i>Tapirira guianensis</i>	131.56 \pm 38.25	10 \pm 2	356.64 \pm 128.66	3 \pm 1	1.44 \pm 0.08
<i>Tapirira mexicana</i>	88.79 \pm 33.82	16 \pm 3	224.51 \pm 70.28	3 \pm 1	5.27 \pm 1.58
<i>Toxicodendron vernix</i>	101.3 \pm 19.69*	88 \pm 21	205.7 \pm 78.55	2 \pm 1	2.2
Burseraceae					
<i>Bursera aloexylon</i> (= <i>linanoe</i>)	68.79 \pm 17.23	41 \pm 10	184.99 \pm 68.62	3 \pm 1	0.54 \pm 0.14
<i>Bursera arborea</i> (= <i>simaruba</i>)	69.96 \pm 14.28	38 \pm 8	304.57 \pm 118.61	3 \pm 2	0.43 \pm 0.07
<i>Bursera copallifera</i>	84.29 \pm 23.59	23 \pm 4	219.52 \pm 82.51	3 \pm 1	–
<i>Bursera excelsa</i>	105.62 \pm 37.09	19 \pm 3	407.38 \pm 182.4	2 \pm 1	0.45 \pm 0.16
<i>Bursera fagaroides</i>	69.56 \pm 13.66	62 \pm 1	356.86 \pm 168.97	4 \pm 2	0.55 \pm 0.27
<i>Bursera heteresthes</i>	80.66 \pm 19.28	33 \pm 2	201.04 \pm 59.83	3 \pm 1	0.47 \pm 0.05
<i>Bursera instabilis</i>	98.04 \pm 20.4	34 \pm 4	369.37 \pm 167.29	4 \pm 2	0.61 \pm 0.13
<i>Canarium madagascariense</i>	146.61 \pm 76.07	8 \pm 3	380.09 \pm 54.83	3 \pm 1	0.45
<i>Chloroxylon faho</i>	63.68 \pm 22.99	50 \pm 8	212.82 \pm 51.88	3 \pm 1	8.02
<i>Commiphora boranensis</i>	102.28 \pm 43.68	18 \pm 4	339.07 \pm 114.8	3 \pm 1	0.57
<i>Commiphora pervilleana</i>	119.41 \pm 25.26	17 \pm 2	382.01 \pm 97.1	3 \pm 1	0.79
<i>Commiphora pterocarpa</i>	93.12 \pm 32.25	16 \pm 4	397.7 \pm 139.92	4 \pm 1	0.42

Table 3 (continued)

Specie	Vessel diameter (μm)	Vessel frequency (vessel. mm^{-2})	Ray height (μm)	Ray width (n°cells)	Axial parenchyma (%)
<i>Protium copal</i>	80.59 ± 31.02	24 ± 4	303.57 ± 94.3	2 ± 1	0.51 ± 0.11
<i>Protium madagascariense</i>	88.97 ± 30.7	23 ± 6	302.78 ± 92.85	2 ± 1	0.85 ± 0
<i>Tetragastris panamensis</i>	95.13 ± 20.19	19 ± 1	252.02 ± 72.72	2 ± 1	5.17 ± 1.19
Kirkiaceae					
<i>Kirkia acuminata</i>	99.54 ± 33.20	24 ± 6	703.98 ± 284.12	2 ± 1	6.34 ± 2.13
Meliaceae					
<i>Carapa guianensis</i>	120.23 ± 30.04	8 ± 1	561.3 ± 222.04	3 ± 1	2.5 ± 1.42
<i>Cedrela fissilis</i>	143.33 ± 52.29	4 ± 2	222.51 ± 73.86	4 ± 2	25.62 ± 15.53
<i>Cedrela odorata</i> (=mexicana)	227.51 ± 60.55	4 ± 1	400.1 ± 153.97	3 ± 2	20.04 ± 7.4
<i>Cedrela salvadoriensis</i>	128.82 ± 49.82	32 ± 8	305.86 ± 98.02	3 ± 1	15.46 ± 6.31
<i>Guarea chichon</i> (=megantha)	154.83 ± 47.27	40 ± 10	393.64 ± 153.55	2 ± 1	14.51 ± 1.49
<i>Guarea glabra</i>	84.18 ± 37.12	102 ± 8	234.77 ± 102.4	2 ± 1	13.63 ± 3.64
<i>Guarea grandifolia</i> (=guidonia)	151.65 ± 38.13	9 ± 2	346.4 ± 132.16	2 ± 1	18.48 ± 6.28
<i>Khaya ivorensis</i>	131.61 ± 52.6	7 ± 1	451.16 ± 154.46	4 ± 2	1.65 ± 0.36
<i>Khaya madagascariensis</i>	104.13 ± 49.25	13 ± 6	344.06 ± 108.81	4 ± 2	3.39 ± 1.13
<i>Neobeguea leandriana</i>	118.72 ± 38.3	3 ± 1	312.78 ± 133.14	–	15.67 ± 2.91
<i>Neobeguea mahafaliensis</i>	147.63 ± 62.36	5 ± 3	273.41 ± 98.25	4 ± 2	19.84 ± 5.18
<i>Quivisianthe papinae</i>	81.72 ± 21.75	15 ± 4	241.57 ± 88.05	2 ± 1	6.03 ± 2.3
<i>Swietenia humilis</i>	105.9 ± 45.69	104 ± 16	402.12 ± 109.87	3 ± 1	10.54 ± 6.58
<i>Swietenia macrophylla</i>	137.1 ± 53.37	64 ± 22	440.44 ± 107.47	4 ± 1	9.53 ± 4.88
<i>Toona sp.</i>	154.29 ± 66.9*	8 ± 3	260.01 ± 137.7	4 ± 2	5.18 ± 3.64
<i>Trichilia glabra</i>	59.58 ± 12.04	9 ± 4	253.76 ± 71.84	1	3.78 ± 0.91
<i>Trichilia japurensis</i>	63.06 ± 15.37	15 ± 4	292.39 ± 103.3	1	3.71 ± 1.29
<i>Trichilia minutiflora</i>	27.27 ± 7.54	23 ± 2	92.25 ± 27.42	1	3.77 ± 1.7
<i>Trichilia trifolia</i>	38.97 ± 10.28	49 ± 10	258.68 ± 62.19	1	16.88 ± 2.28
Nitrariaceae					
<i>Peganum mexicanum</i>	11.24 ± 3.68*	99 ± 45	187.19 ± 67.3	5 ± 2	2.47 ± 1.28
Rutaceae					
<i>Balfourodendron riedelianum</i>	70.56 ± 11.15	55 ± 8	354.19 ± 168.34	3 ± 1	8.16 ± 5.36
<i>Casimiroa calderoniae</i>	36.9 ± 15.08	49 ± 11	145.39 ± 51.18	2 ± 1	37.78 ± 1.33
<i>Casimiroa tetrameria</i>	108.1 ± 23.48	10 ± 2	267.77 ± 100.38	3 ± 1	30.18 ± 2.06
<i>Cedrelopsis grevei</i>	30.82 ± 9.44	318 ± 40	105.72 ± 30.66	1	1.79
<i>Citrus x aurantium</i>	51.04 ± 15.43	22 ± 8	220.56 ± 94.92	5 ± 1	9.48 ± 1.56
<i>Citrus limetta</i> (=medica)	68.66 ± 18.07	38 ± 10	228 ± 75.82	4 ± 1	20.09 ± 4.88
<i>Citrus limettioides</i>	57.4 ± 12.57	41 ± 7	170.86 ± 63.49	3 ± 2	13.66 ± 5.15
<i>Citrus sinensis</i>	60.73 ± 16.63	29 ± 7	164.39 ± 65.5	3 ± 1	13.75 ± 6.36
<i>Esenbeckia berlandieri</i>	39.79 ± 10.54	141 ± 21	371.51 ± 122.47	3 ± 1	4.42 ± 0.68
<i>Esenbeckia pentaphylla</i>	52.38 ± 12.11	35 ± 6	187.59 ± 60.65	4 ± 1	–
<i>Helietta cuspidata</i> (=apiculata)	41.61 ± 11.52	128 ± 37	167.49 ± 52.89	3 ± 1	–
<i>Helietta lucida</i>	33.53 ± 13.74	211 ± 57	149.36 ± 31.14	3 ± 1	–
<i>Phellodendron amurense</i>	27.57 ± 10.34*	13 ± 5	–	–	8.47 ± 0.1
<i>Pilocarpus racemosus</i>	42.74 ± 11.76	35 ± 2	310.19 ± 130.35	3 ± 1	4.6 ± 1.65
<i>Ptelea trifoliata</i>	69.8 ± 11.4*	60 ± 24	251.32 ± 108.39	3 ± 1	12.38 ± 3.01
<i>Zanthoxylum caribaeum</i>	27.36 ± 7.87	203 ± 33	276.48 ± 93.87	3 ± 1	3.33 ± 0.45
<i>Zanthoxylum kellermanii</i>	89.75 ± 27.48	12 ± 2	286.05 ± 93.63	3 ± 1	0.64 ± 0.27
<i>Zanthoxylum madagascariense</i>	101.33 ± 23.65	9 ± 3	420.83 ± 197	3 ± 2	–
<i>Zanthoxylum tsihanimposa</i>	117.52 ± 38.62	15 ± 8	404.36 ± 335.48	3 ± 2	7.58
Sapindaceae					
<i>Acer negundo</i>	35.9 ± 10.34	50 ± 17	223.67 ± 106.26	3 ± 2	0.06 ± 0.02

Table 3 (continued)

Specie	Vessel diameter (μm)	Vessel frequency (vessel. mm^{-2})	Ray height (μm)	Ray width (n°cells)	Axial parenchyma (%)
<i>Allophylus camptostachys</i>	49.02 ± 16.72	35 ± 5	287.35 ± 77.33	3 ± 1	0.25 ± 0.11
<i>Cupania dentata</i>	88.72 ± 28.28	23 ± 6	214.1 ± 91.59	1	0.43 ± 0.18
<i>Cupania furfuracea</i>	84.93 ± 24.08	32 ± 6	110.4 ± 52.79	2 ± 1	0.84 ± 0.4
<i>Cupania glabra</i>	135.62 ± 42.78	13 ± 2	241.65 ± 113.17	2 ± 1	0.62 ± 0.29
<i>Cupania</i> (= <i>Talisia</i>) <i>macrophylla</i>	111.88 ± 39.51	11 ± 2	240.85 ± 70.14	2 ± 1	0.45 ± 0.19
<i>Filicium decipiens</i>	67.38 ± 20.1	15 ± 3	190.56 ± 72.39	2 ± 1	20.52
<i>Neotina isoneura</i>	74.21 ± 30.59	24 ± 4	175.25 ± 78.87	2 ± 1	1.81
<i>Neotina</i> (= <i>Tina</i>) <i>coursii</i>	100.33 ± 44.11	10 ± 2	183.43 ± 69.54	1	5.23
<i>Plagioscyphus louvelii</i>	63.61 ± 24.16	20 ± 4	206.16 ± 93.28	2 ± 1	24.95
<i>Sapindus saponaria</i>	81.42 ± 43.37	7 ± 3	189.6 ± 68.82	4 ± 1	40.69 ± 4.69
<i>Serjania lethalis</i>	107.22 ± 24.31**	90 ± 26	453.01 ± 376.12	3 ± 2	0.73 ± 0.3
<i>Serjania schiedeana</i>	84.9 ± 11.69**	61 ± 6	299.68 ± 163.35	2 ± 1	0.77 ± 0.37
<i>Stadmania oppositifolia</i>	62.21 ± 20.01	25 ± 5	203.89 ± 97.99	2 ± 1	12.54
<i>Thouinia paucidentata</i>	60.41 ± 27.09	61 ± 10	226.04 ± 70.41	2 ± 1	0.69 ± 0.08
<i>Thouinia serrata</i>	58.53 ± 17.51	41 ± 5	197.31 ± 40.87	2 ± 1	0.21 ± 0.06
<i>Thouinia villosa</i>	104.36 ± 32.45	20 ± 2	300.47 ± 69.29	2	0.81 ± 0.37
<i>Thouinidium decandrum</i>	81.26 ± 20.16	10 ± 1	176.93 ± 67.66	2 ± 1	24.14 ± 2.85
<i>Tinopsis</i> (= <i>Tina</i>) <i>apiculata</i>	80.9 ± 32.84	15 ± 7	186.18 ± 83.15	2 ± 1	1.6
Simaroubaceae					
<i>Ailanthus altissima</i>	180.50 ± 74.5*	35 ± 32	573.88 ± 354.51	5 ± 2	12.62
<i>Castela coccinea</i>	44.03 ± 24.59	-	159.7 ± 124.5	4 ± 1	27.64 ± 8.52
<i>Eurycoma longifolia</i>	90.49	-	1322	3 ± 2	2.95
<i>Perriera madagascariensis</i>	106.18 ± 45.48	7 ± 2	291.69 ± 126.33	4 ± 2	11.94 ± 2.45
<i>Picrasma quassioides</i>	163.15 ± 40.6*	28 ± 5	292.33 ± 184.4	4 ± 3	-
<i>Simarouba amara</i> (= <i>glauca</i>)	202.66 ± 35.3	4 ± 1	375.92 ± 132	4 ± 2	7.9
<i>Simarouba versicolor</i>	244.77 ± 49.15	2 ± 1	545.6 ± 209.9	3 ± 2	9.7

*Vessel diameter only measured in earlywood; **vessel diameter measured above 50 μm due to vessel dimorphism in lianas

Average ± Standard Deviation

Lianas are present only in two families of the order, Anacardiaceae and Sapindaceae. In Anacardiaceae, they are present in two genera, *Attilaea* E.Martínez & Ramos and *Toxicodendron* (poison-ivy). In Sapindaceae, tribe Paullinieae reunites all the lianas of the family and account for approximately 500 species (half of the Sapindaceae in the Neotropics and 25% of the family). Their anatomy reflects their habit, with very wide vessels associated with narrow vessels (vessel dimorphism) (Fig. 2a), narrow vessels typically in long radial rows in Paullinieae (Fig. 2a). Ring-porous woods are present in *Toxicodendron* (Fig. 2b). In the lianas, the rays typically have various distinct sizes (Fig. 2c), including rays above 1 mm high (Fig. 2c), typically heterocellular with square, upright and procumbent cells mixed (Fig. 2d). Variant secondary growth is absent in the Anacardiaceae lianas, but very common and of various types in Sapindaceae, tribe Paullinieae (Fig. 2f-h), which also contain many species with regular secondary growth (Fig. 2e).

Character evolution of the most variable features in Sapindales – Ring-porosity and helical thickening (Fig. 3). Diffuse-porous woods are the prevalent in Sapindales and the estimated ancestral state for the order and all of its eight family nodes (Fig. 3a, e). Almost exactly the same is true for helical thickenings (Fig. 3d), which are inferred as absent in the ancestral node of the order (Fig. 3e), except perhaps for Sapindaceae, where helical thickenings have an ambiguous ancestral reconstruction, with almost the same posterior probability for both states as ancestrally present (Fig. 3e). The Pagel 1994 test of correlated evolution showed support for the dependent model, specifically indicating the evolution of helical thickening was contingent on the evolution of ring porosity ($p = 1.13 \text{ e}^{-07}$). Both ring porosity (Fig. 3b-c) and helical thickenings have evolved multiple times in the Sapindales (Fig. 3e). Specifically, they have evolved at least three times in Anacardiaceae, once in a clade formed by *Cotinus* Mill.—*Rhus*—*Schinus* L. -*Toxicodendron*, once in

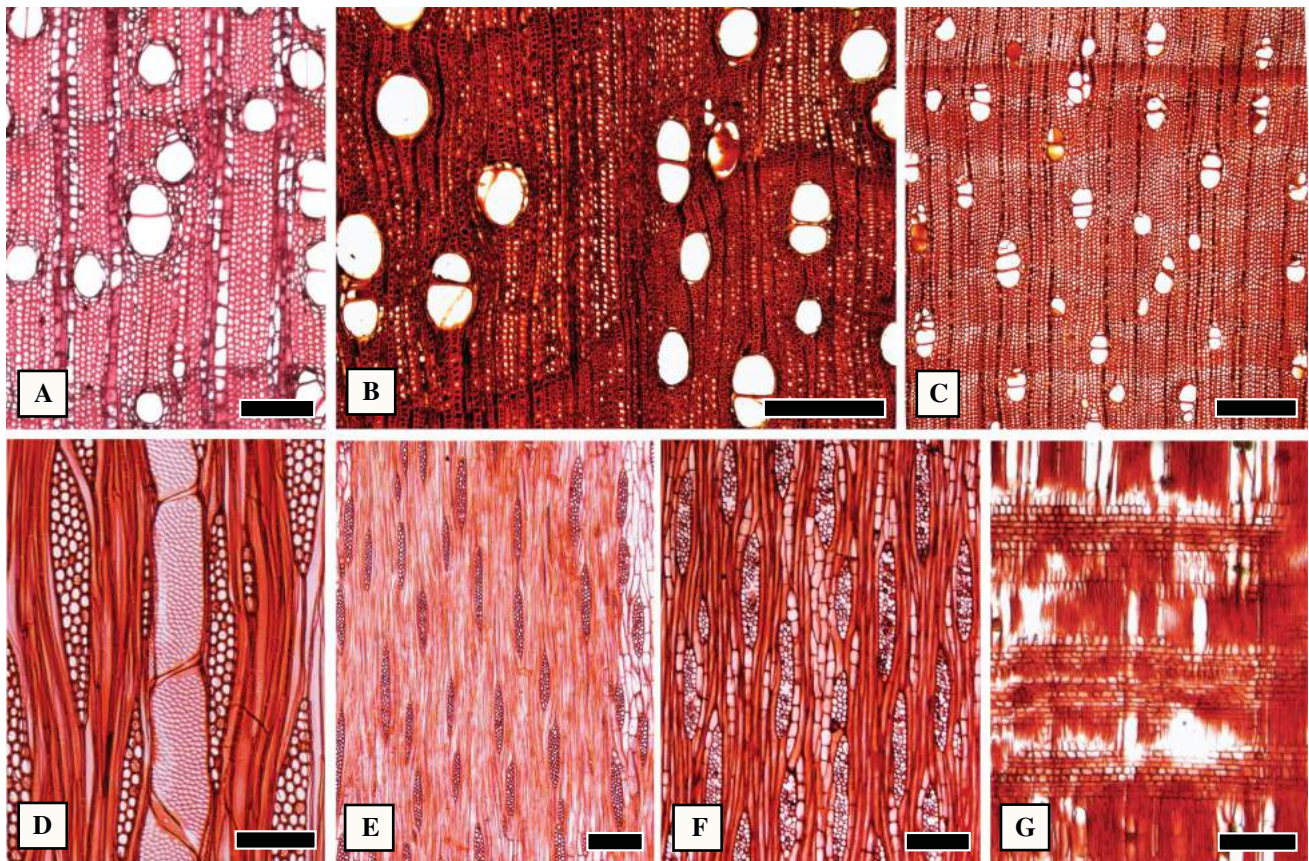


Fig. 1 General characters of the woods of Sapindales. **a** *Buchanania arborescens* F.Muell. (Anacardiaceae), growth ring marked by thick-walled, radially flattened fibers. Paratracheal vasicentric axial parenchyma. Transverse section (TS) **b** *Cupania macrophylla* Mart. (Sapindaceae), wavy growth ring delimited by thick-walled, radially narrow fibers. Axial parenchyma scanty. Fibers with dark content common in the genus (TS) **c** *Allophylus comptostachys* Radlk. (Sapindaceae), growth rings delimited by thick-walled, radially flattened fibers. Axial parenchyma scanty paratracheal. Parenchyma-like fibers forming alternating bands with thicker walled fibers (TS) **d** *Acer negundo* L. (Sapindaceae), vessels with slightly inclined perforation plates. Intervessel pits alternate. Longitudinal tangential section (LT) **e** *Sapindus saponaria* L. (Sapindaceae), rays lower than one millimeter (LT). Axial parenchyma with 2–4 cells per strand (upper right side) **f** *Cedrela odorata* L. (Meliaceae). Axial parenchyma with 5 or more cells per strand (LT) **g** *Esenbeckia berlandieri* Baill. (Rutaceae), rays heterocellular, with body procumbent and one to two rows of square to upright cells. Longitudinal radial section. Scale bars: A, C, F–G = 300 μ m; B = 400 μ m; D = 100 μ m; E = 200 μ m

Pistacia, and once in *Choerospondias* B.L.Burt & A.W.Hill, which has ring-porous wood but lacks helical thickenings. In Meliaceae ring-porosity has evolved twice, once in the clade formed by *Cedrela* and *Toona* (Endl.) M.Roem., with semi-ring porous woods, but lacking helical thickenings, and once in *Melia* L., where the woods are ring-porous and have helical thickenings (Fig. 3e). In Simaroubaceae, there were at least four independent evolutions of ring-porosity and helical thickening, once in the clade *Castela* Turpin – *Holacantha* A.Gray, once in *Ailanthus* (Fig. 3c), and once in *Leitneria* Chapm. (Fig. 3e). In *Picrasma* Blume only ring-porosity evolved, without helical thickening (Fig. 3e). In Rutaceae there were at least three independent evolutions of ring-porosity and helical thickenings, once in the clade formed by *Phellodendron* Rupr. and *Tetradium* Lour., once in *Choisya* Kunth, and once in *Cneorum* L. (Fig. 3e). *Poncirus* Raf. and *Ruta* L. have helical thickening, but no ring-porosity

(Fig. 3e). In Sapindaceae the scenario is more complex, because although the ring-porous to semi-ring porous woods of *Koelreuteria* Medik. and *Xanthoceras* Bunge do have helical thickenings (Fig. 3e), many other genera with diffuse-porous woods also exhibit helical thickenings, similarly to *Poncirus* Raf. and *Ruta* of the Rutaceae (Fig. 3e). The same case is true for *Nitraria retusa* Asch. (Nitrariaceae), where the wood is diffuse-porous, but with helical thickenings in vessel elements (Fig. 3e).

Marginal parenchyma bands (Fig. 4). Axial marginal parenchyma delimiting growth rings (Fig. 4b–c) is very common in Sapindales, and is inferred as ancestrally present in the order (Fig. 4d). It has been also lost multiple times, with the most remarkable examples in the ancestor of Anacardiaceae–Bursaceae–Kirkiaceae, and in the bulk of subfamily Sapindoideae of Sapindaceae (the entire clade, except for *Koelreuteria*; Fig. 4d). Within Simaroubaceae, it

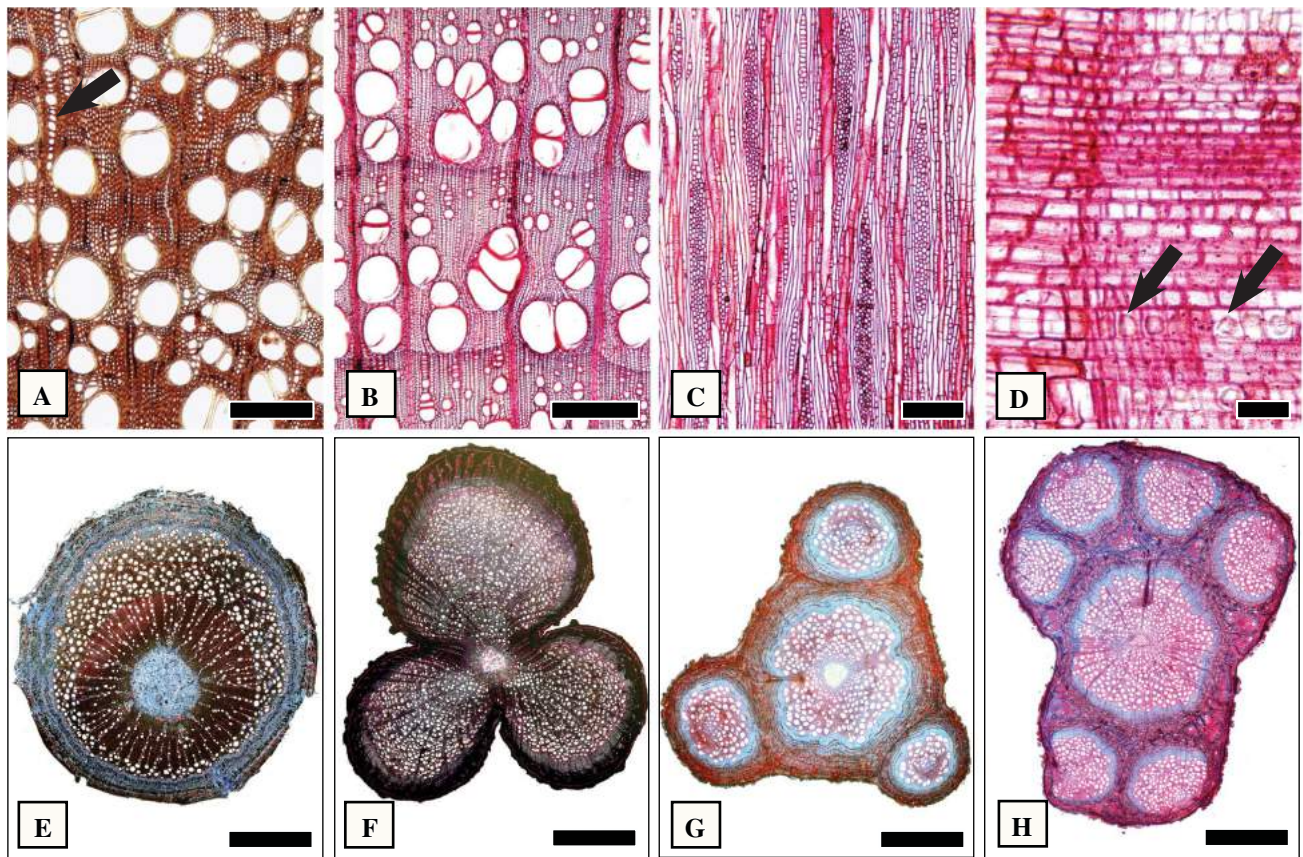


Fig. 2 General characters of lianas of Sapindales. **a** *Serjania schiedeana* Schltdl. (Sapindaceae), lianescent secondary xylem in a tropical species, with very wide vessels associated with narrow vessels. Narrow vessels commonly in radial chains (arrow). Transverse section (TS). **b-d**. *Toxicodendron radicans* (L.) Kuntze (Anacardiaceae). **b**. Lianescent secondary xylem in a temperate species. Ring-porous wood. Growth rings delimited by radially flattened fibers (TS). **c**. Most rays higher than 1 mm. Axial parenchyma with mainly 2–4 cells per strand. Longitudinal tangential section. **d**. Heterocellular mixed ray. Note prismatic crystals (arrows). Longitudinal radial section. **e**. *Cardiospermum corindum* L. (Sapindaceae), regular secondary growth. (TS). **f**. *Urvillea rufescens* Cambess. (Sapindaceae), liana with lobed stem. (TS). **g**. *Serjania lethalis* A.St.-Hil. (Sapindaceae), liana showing a central cylinder and 3 marginal cylinders. (TS). **h**. *Serjania laruoeteana* Cambess. (Sapindaceae), stem with central cylinder with 6 marginal cylinders. (TS). Scale bars: A=300 μ m; B=400 μ m; C=200 μ m; D=50 μ m; E=2 mm; F–H=4 mm; G=3 mm. Photos B–D as courtesy of Elisabeth Wheeler

was lost in the clades formed by *Castela-Holacantha* and *Brucea* J.F.Mill.- *Soulamea* Lam. (Fig. 4d). Within Meliaceae, it was lost in the clade formed by *Lansium* Rumph. – *Reinwardti dendron* Koord (Fig. 4d). All other cases represent individual losses (Fig. 4d). Marginal parenchyma was also regained within the Anacardiaceae, being present in *Faguetia* Marchand, *Gluta* L. (not in phylogeny), *Mangifera* L., *Metopium* P.Browne and some *Toxicodendron* (Fig. 4d).

Vessels in radial and dendritic arrangement (Fig. 5). A radial arrangement (Fig. 5b–c) is more common within the order than a dendritic arrangement (Fig. 5d), but are here treated together since one may grade into the other. A radial or dendritic arrangement is inferred as more likely absent in the ancestral node of Sapindales, but likely ancestrally present in the family node of Rutaceae (Fig. 5e). The radial pattern was gained multiple times in all of Sapindales major families, with exception to Burseraceae (Fig. 5e). However,

solitary to multiple of 2–3 vessels are still the most common feature in the order (Fig. 5a, e).

Tyloses and vessel-ray pit size (Fig. 6). Tyloses (Fig. 6b) are present in the heartwood (and occasionally on scattered vessels of the earlywood) of members of the clade formed by Kirkiaceae–Anacardiaceae–Burseraceae, with a few scattered losses within it (Fig. 6e). The tyloses can sometimes become sclerotic in some genera, and these tyloses may even contain large prismatic crystals within them, such as *Myracrodruon* Allemão (Anacardiaceae, Fig. 10b). Tyloses are absent in the rest of the order (Fig. 6e).

Vessel-ray pits similar to intervessel pits are the inferred ancestral states for the order (Fig. 6c, e), with one evolution of vessel-ray pits simple to semi-bordered large pits in the ancestor of Anacardiaceae–Burseraceae–Kirkiaceae (Fig. 6d, e).

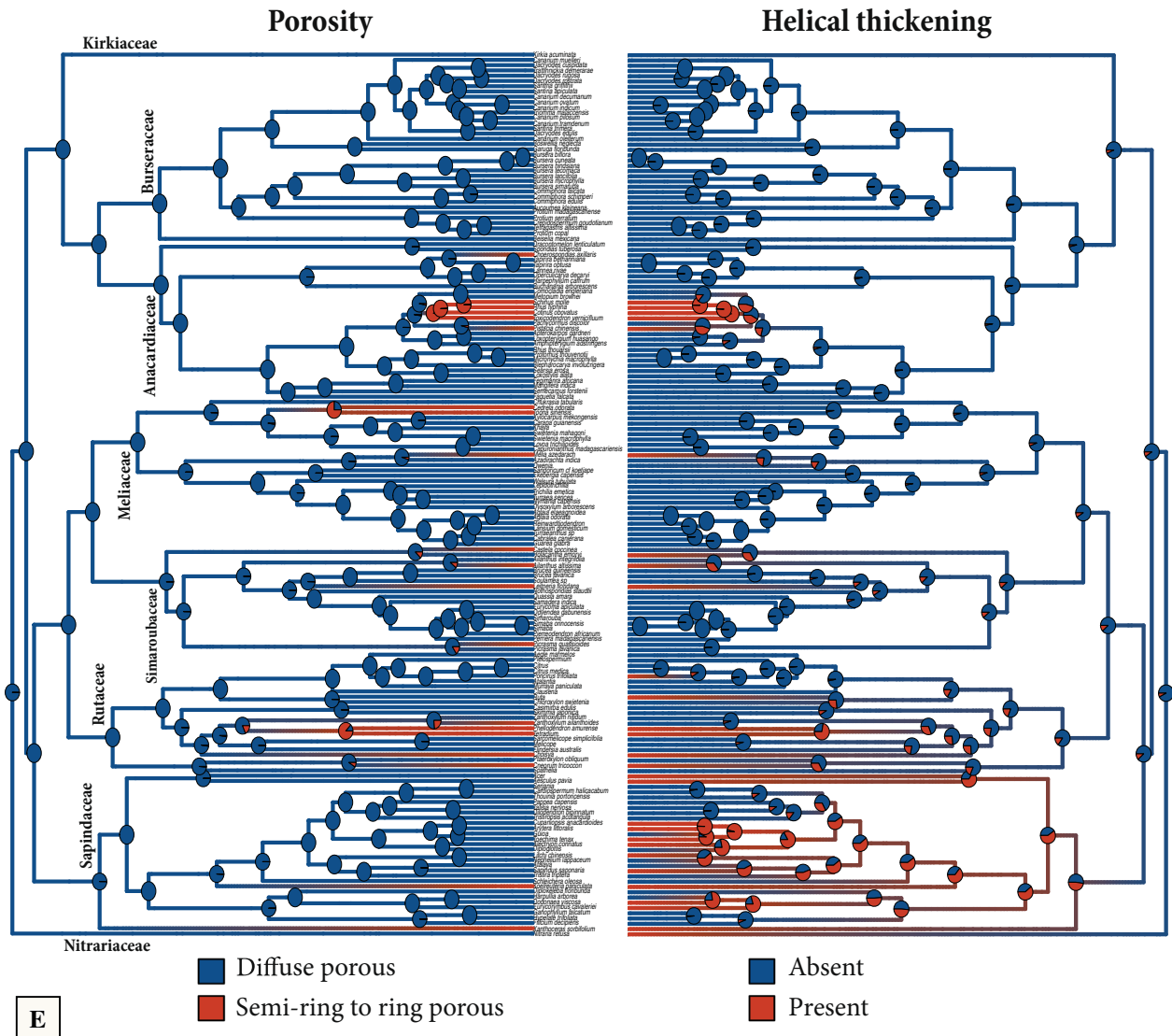
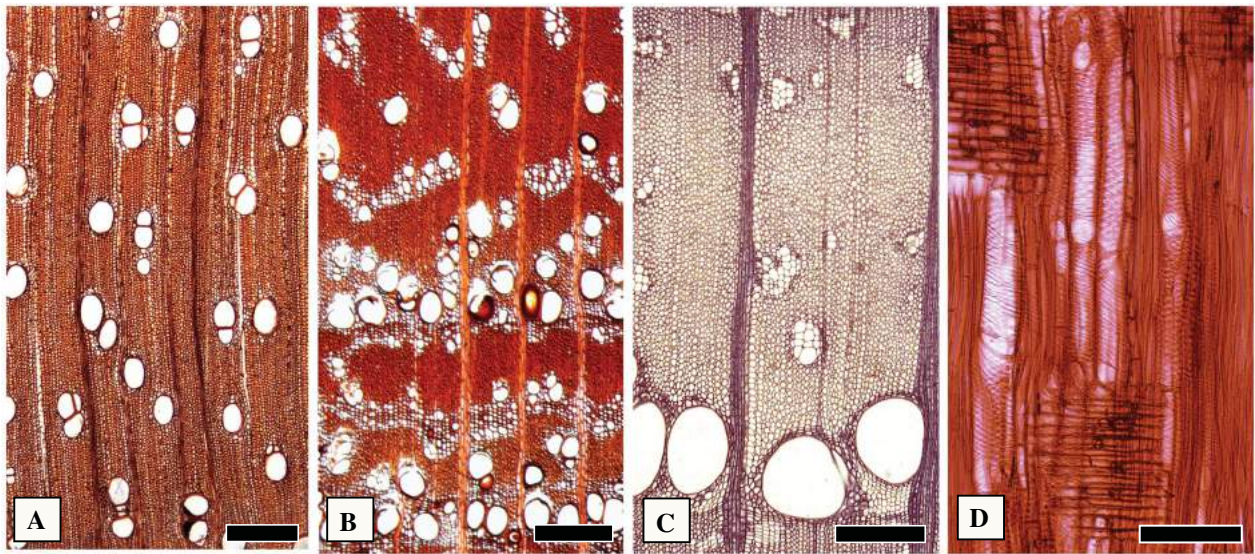


Fig. 3 Porosity and helical thickening evolution in Sapindales. **a** *Khaya ivorensis* A.Chev. (Meliaceae), diffuse-porous wood. Transverse section (TS). **b** *Ptelea trifoliata* L. (Rutaceae), ring-porous wood derived from annual dry seasons. (TS). **c** *Ailanthus latissimus* (Mill.) Swingle (Simaroubaceae), ring-porous wood derived from seasonally cold winters. (TS). **d** *Pistacia mexicana* Kunth (Anacardiaceae), helical thickening present. Longitudinal radial section. **e** Ancestral character state estimation of porosity and helical thickenings in Sapindales. Scale bars: A=250 μm ; B-C=300 μm , D=150 μm

The evolution of tyloses occurred just once, as the evolution of simple to semi-bordered large vessel-ray pits. The Pagel 94 test provides support for the dependent model of correlated evolution ($p=0.0058$) (Fig. 6d-e). We will argue how this result has to be read with caution in the discussion section.

Gums/gum-like inclusions in vessels (Fig. 7). Within Sapindales, gums or gum-like inclusions (Fig. 7b-c) are most abundant in the heartwoods of Meliaceae, Nitrariaceae, Rutaceae and Sapindaceae (Fig. 7d), and are mostly absent in Anacardiaceae, Burseraceae, Kirkiaceae and Simaroubaceae (Fig. 7d). It is inferred to be ancestrally present in the order (Fig. 7d), and ancestrally lost in Simaroubaceae, and in the clade formed by Anacardiaceae-Burseraceae-Kirkiaceae (Fig. 7d). Gums/gum-like inclusions were regained though in the clade formed by *Comocladia* P.Browne—*Metopium* within Anacardiaceae, and the distantly related genera *Simaba* Aubl. and *Ailanthus* within Simaroubaceae (Fig. 7d).

Intervessel pits (Fig. 8). The ancestral state estimation indicates that intervessel pits were likely small ($<8\ \mu\text{m}$) in the ancestral node of all Sapindales, evolving once to larger diameters in the ancestor of Anacardiaceae-Burseraceae-Kirkiaceae (Fig. 8b-c).

Septate fibers (Fig. 9). Septate fibers (Fig. 9b-c) are reconstructed as ancestrally absent in the order (Fig. 9d). They have evolved once in the ancestral node leading to the Anacardiaceae-Burseraceae-Kirkiaceae clade, two large clades of Meliaceae, and the Sapindaceae, except for the former Aceraceae (*Acer*) and Hippocastanaceae (*Aesculus*), which form a clade sister to the rest of the family (Fig. 9d). They are absent in Nitrariaceae, and Rutaceae and Simaroubaceae. Within the Anacardiaceae, two clades lack septate fibers: the clade formed by *Comocladia*-*Metopium*-*Rhus*-*Cotinus*-*Toxicodendron* (Fig. 9d), except for the genus *Schinus* and the genus *Searsia* F.A.Barkley, which do have septate fibers (Fig. 9d), and the clade formed by *Fegimanra* Pierre ex Engl. - *Mangifera* - *Semecarpus* L.f.—*Faguetia* (Fig. 9d). Within the Sapindaceae, septate fibers are absent in *Talisia* Aubl., *Hypelate* P.Browne, *Xanthoceras* and the clade formed by *Harpulia* G.Don—*Dodonaea* Mill. (Fig. 9d). In Burseraceae, they may be absent or present within different *Bursera* species (Fig. 9d).

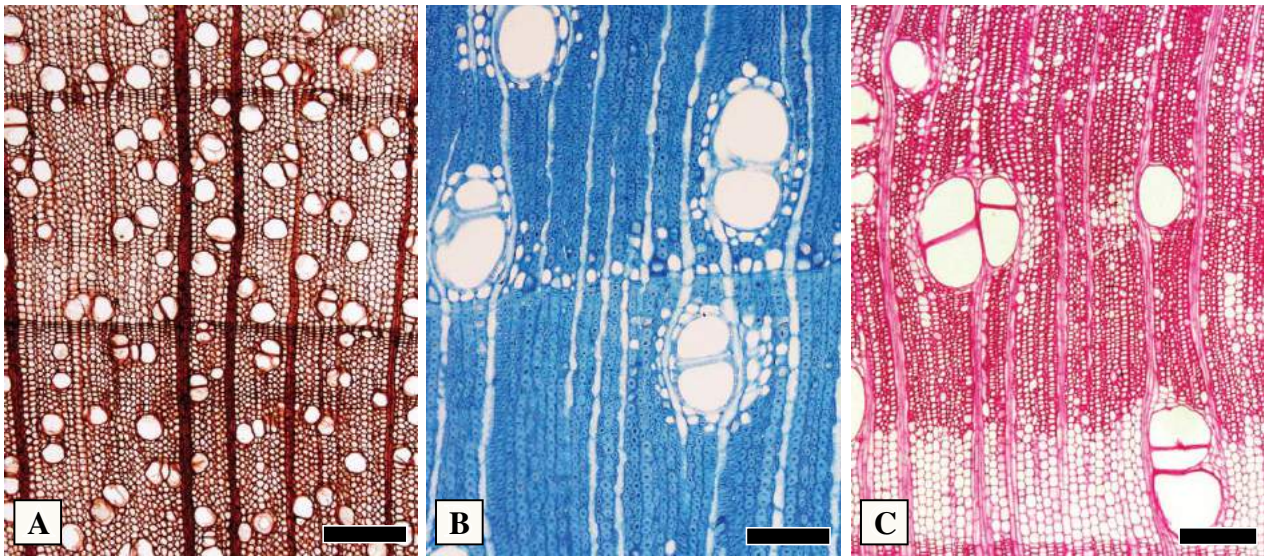
The Pagel 94 test of correlated evolution infers that septate fibers and scanty axial parenchyma are not evolving in a dependent fashion (Pagel's 94, $p=0.45$).

Axial parenchyma type (Fig. 10). Axial parenchyma is extremely varied in the order, going from absent or extremely rare (*Acer*, Sapindaceae) to paratracheal scanty (Fig. 10a), vasicentric (Fig. 10b-c), lozenge aliform, aliform winged, to confluent (Fig. 10d-f). In the order, the ancestral state is here inferred as scanty paratracheal with multiple evolutions toward aliform and vasicentric (Fig. 10g). In Burseraceae and Kirkiaceae, axial parenchyma scanty paratracheal was the only recorded state (Fig. 10g). The Anacardiaceae is more varied, with the clade formed by *Dracontomelon* Blume - *Spondias* L., which is sister to the rest of Anacardiaceae, having vasicentric axial parenchyma (Fig. 10g), a large clade formed by *Buchanania* Sm. - *Lanena* A.Rich. - *Tapirira* Aubl.—*Operculicarya* H.Perrier having scanty paratracheal axial parenchyma only (Fig. 10g), the clade formed by *Faguetia*-*Fegimanra*-*Mangifera* with more abundant, aliform or vasicentric parenchyma (Fig. 10g), while the rest of the family is quite varied (Fig. 10g). In both Nitrariaceae and Simaroubaceae, aliform winged sometimes unilateral is quite typical of most members (Fig. 10f). Both the Meliaceae and Sapindaceae are extremely varied in axial parenchyma type in all major clades (Fig. 10g).

Radial ducts/canals (Fig. 11). Radial ducts in wood (Fig. 11a-c) are exclusively found in the clade formed by Anacardiaceae-Burseraceae (Fig. 11d). The rest of the Sapindales lacks them, and the ancestral state for the order is inferred as not having radial ducts (Fig. 11d). Within both Anacardiaceae and Burseraceae, the radial ducts were lost multiple times (Fig. 11d). In Burseraceae, they were lost in the clade formed by *Dacryodes* Vahl - *Santiria* Blume - *Trattinickia* Willd., in *Aucoumea* Pierre, *Canarium* L., *Crepidospermum* Hook.f., and some species of both *Bursera* and *Protium* (Fig. 11d). In Anacardiaceae, they were lost in the clade formed by *Faguetia*-*Fegimanra*-*Mangifera*-*Semecarpus* L.f., the clade formed by *Blepharocarya* F.Muell.-*Micronychia* Oliv. - *Protorhus* Engl.- *Rhus thoursii* (Engl.) H.Perrier (Fig. 11d), the clade formed by *Cotinus*-*Pachycornus* Coville—*Rhus typhina* L. - *Toxicodendron* (Fig. 11d), and the genera *Comocladia* and *Dracontomelon* (Fig. 11d).

Axial ducts/canals of traumatic origin (Fig. 12). Traumatic ducts (Fig. 12a-b) were exclusively found in three families of the Sapindales: Meliaceae, Rutaceae and Simaroubaceae (Fig. 12c). In Meliaceae, they were especially common in clade Swietenioideae (Fig. 12c). We encountered ducts also in taxa of Rutaceae not present in our phylogeny, such as *Balfourodendron riedelianum* (Engl.) Engl., *Citrus sinensis* Pers., and *Zanthoxylum kellermanii*.

Ray composition (Fig. 13). Rays may be exclusively homocellular (Fig. 13a), heterocellular with body cells procumbent and one row of marginal upright to square cells



A Kirk *Bursera*ceae **B** *Anacardiaceae* **C** *Meliaceae* *Simaroubaceae* *Rutaceae* *Sapindaceae* *Nit*

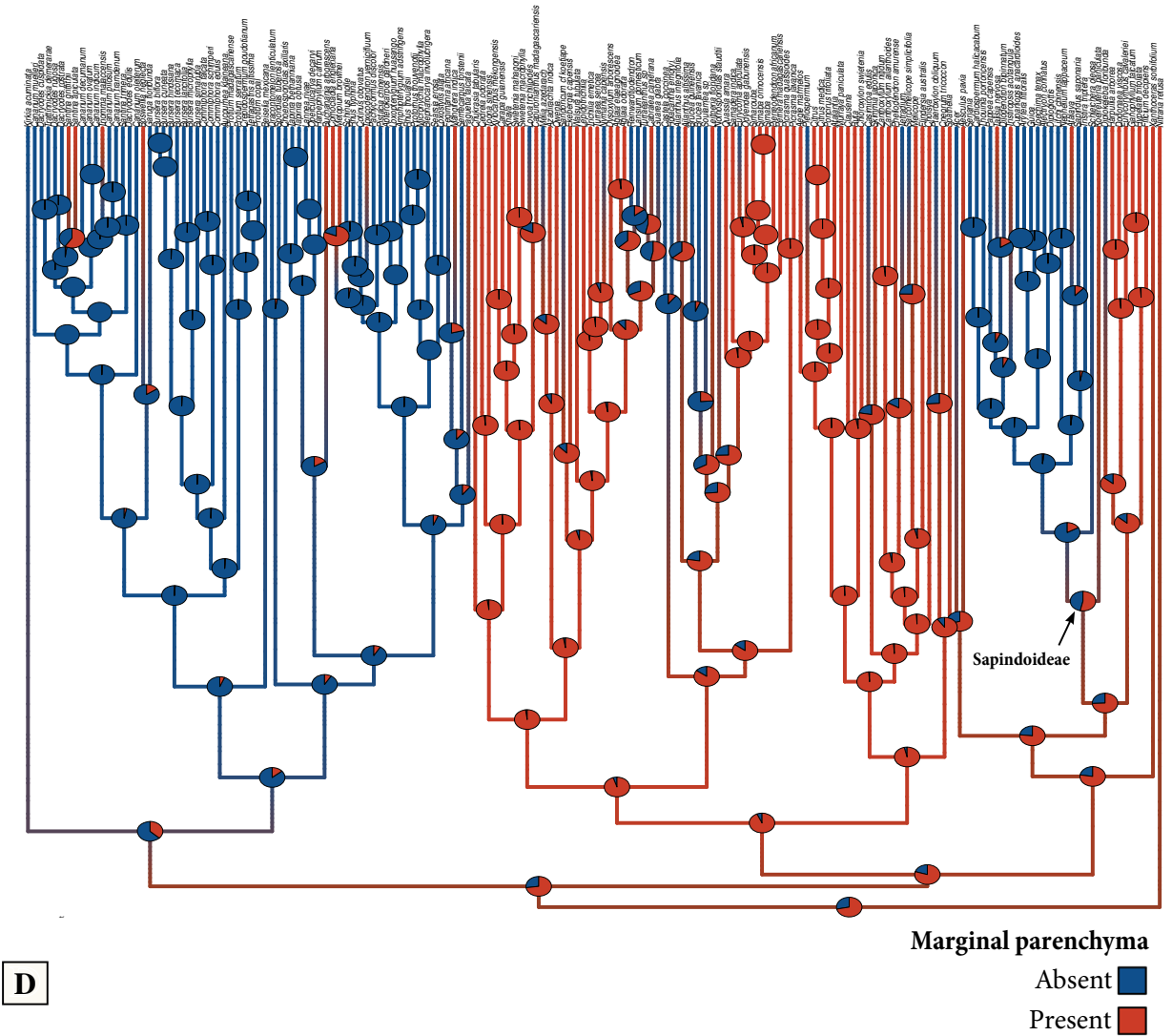


Fig. 4 Marginal parenchyma evolution in Sapindales. **a-c.** Transverse sections. **a.** *Bursera aloexylon* Engl. (Burseraceae), marginal parenchyma absent. Growth ring delimited by radially flattened fibers. Axial parenchyma scanty. **b.** *Stadmania oppositifolia* Lam. (Sapindaceae), narrow band of marginal parenchyma delimiting the growth ring. Fibers thick-walled. Axial parenchyma also vasicentric to aliform. **c.** *Cedrela fissilis* Vell. (Meliaceae), wide band of marginal parenchyma delimiting the growth ring. Axial parenchyma also vasicentric, aliform and diffuse. **D**=Ancestral character state estimation of marginal parenchyma in Sapindales. Scale bars: A-B=300 µm; C=250 µm. Kirk=Kirkiaceae, Nit=Nitrariaceae

(Fig. 13b), heterocellular with body procumbent and more than 2–3 marginal upright to square cells (Fig. 13c), or heterocellular with square, upright and procumbent cells mixed throughout the ray (Fig. 13d). In Sapindales, the predominant state is that of heterocellular rays, which is inferred as ancestral to the order (Fig. 13e). Homocellular rays are more common in Rutaceae and Sapindaceae (e.g., *Acer*, *Cupania* L.). The number of transitions to other compositions back and forth is, however, enormous and the nodes of most families have one of the two heterocellular categories of rays as more likely to have been ancestrally present (Fig. 13e).

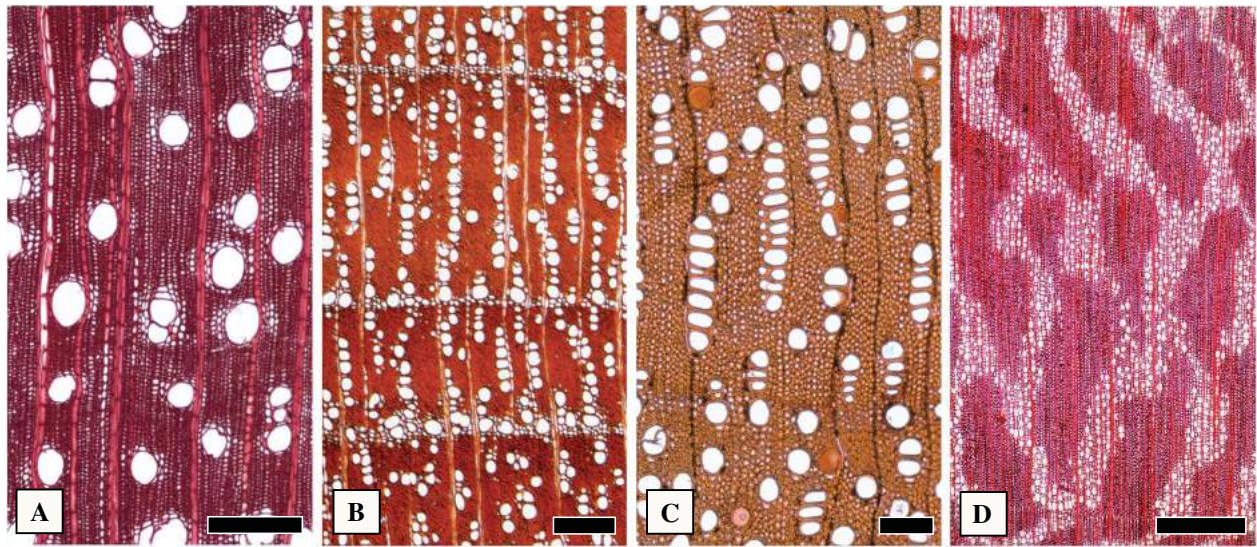
Ray width (Fig. 14). Rays are extremely diverse in Sapindales. Rays may be uniseriate (Fig. 14a), biseriate to three-seriate (14B), and wider than four cells (Fig. 14c-d). Rays uni to four-seriate (Fig. 14a-b, e) predominate in the Sapindales and are inferred as the ancestral state for the order (Fig. 14e). However, wider rays (Fig. 14c-d) are present and seem to have evolved multiple times independently (Fig. 14e). In Simaroubaceae in particular, three clades have wide rays: *Castela-Holacantha*, *Ailanthus* and the clade which contains *Simaba-Simarouba-Perriera* Courchet (Fig. 14e). The only species analyzed of Kirkiaceae (*Kirkia acuminata* Oliv.) has wide rays (Fig. 14e). In Burseraceae, they evolved in the clade formed by *Boswellia* Roxb. -*Garuga* Roxb., and in some *Bursera* (Fig. 14e). In Anacardiaceae, wider rays evolved in the clade formed by *Dracontomelon-Spondias* and appears scattered in the species of the *Cotinus-Schinus* clade, although likely ancestrally present to this clade (Fig. 14c), and in *Choerospondias*. In Rutaceae, wider rays appear in *Clausena* Burm.f., *Citrus* (Fig. 14d), *Phellodendron*, *Tetradium*, and some *Zanthoxylum* L. (Fig. 14e). In Sapindaceae, wider rays are found in some species of *Acer* (Fig. 1b) and in the Paullinieae lianas (e.g., *Cardiospermum*, *Serjania*) (Fig. 14e).

Storied structure (Fig. 15). A storied structure is inferred as absent in the ancestral node of the Sapindales (Fig. 15d). However, especially in Nitrariaceae, Meliaceae and Simaroubaceae, a storied to irregularly storied structure (Fig. 15b-c) is very common and is inferred as ancestral for Nitrariaceae and ancestrally present also for the common ancestor of Meliaceae-Simaroubaceae (Fig. 15d) and equal posterior probabilities of having been ancestrally present

also in the more inclusive clade Meliaceae-Simaroubaceae-Rutaceae (Fig. 15d), given the scattered evolutions of a storied structure in members of Rutaceae (*Chloroxylon* DC. and *Ptaeroxylon* Eckl. & Zeyh.). A few members of Sapindaceae (*Ganophyllum* Blume, *Aesculus*) can also show a storied structure (Fig. 15d).

Crystal location (Fig. 16–17). Prismatic crystals are widespread in all families of Sapindales, except for the Kirkiaceae. They may be located in axial parenchyma (Fig. 16a-b, d-e) or in rays (Fig. 16c-d); within the rays, they may be exclusively in the ray margins (Fig. 16c) or throughout the rays (Fig. 16d); they may also be present in the fibers (Fig. 16b, arrows). Our inferences indicate that crystals were ancestrally present in Sapindales, being lost multiple times, at least once in Kirkiaceae, once in Simaroubaceae, and several times in smaller clades within each family (Fig. 17a). Crystals are mostly absent in the clade formed by *Dacryodes-Santiria-Trattinickia* of Burseraceae and many other isolated cases. Crystals were regained in Simaroubaceae, in the clade formed by *Castela-Holacantha*, and in a few species of *Ailanthus*, *Picrasma*, and many other isolated cases (*Odyndea* Engl., *Simarouba*, *Pierreodendron* A.Chev. and *Perriera*) (Fig. 17a). We reconstructed each crystal occurrence location separately, since crystals may be present in more than one site simultaneously. Crystals are predominantly present in axial parenchyma in Meliaceae, Nitrariaceae, Rutaceae and Sapindaceae (Fig. 17b), and this character state is reconstructed as ancestrally present in the order (Fig. 17b). Conversely, crystals are mainly located in rays in the Anacardiaceae and Burseraceae (Fig. 17c), being reconstructed as possibly absent in the ancestral node of the order, but ancestrally present for Anacardiaceae-Burseraceae-Kirkiaceae (Fig. 17c). In Meliaceae Swietenioideae, crystals are also present in rays in addition to being present in axial parenchyma (Fig. 17b-c). Crystals in fibers are present mostly in Sapindaceae, where it has also been lost several times (Fig. 17d). Outside of Sapindaceae, it was found once in *Lepidotrichilia* (Harms) J.-F.Leroy (Meliaceae) and *Nitraria* (Nitrariaceae) (Fig. 17d). Crystals in fibers are inferred as absent in the ancestral node of the Sapindales (Fig. 17d).

Silica bodies (Fig. 18). Silica bodies in ray parenchyma (Fig. 18b-c) are reconstructed as absent in the ancestral node of Sapindales, but have evolved multiple times in Anacardiaceae, Burseraceae, Kirkiaceae, Meliaceae and Rutaceae (Fig. 18d). They are most common in Burseraceae, being inferred as most likely present in the node of the family (Fig. 18d). In Anacardiaceae, silica bodies have evolved at least three times independently, once in *Lannea*, once in *Buchanania* and once in the clade formed by *Apterokarpos* Rizzini—*Loxopterygium* Hook.f. (Fig. 18d). In Meliaceae, silica bodies are found in *Trichillia* P.Browne,



A Kirk **B** Burseraceae **C** Anacardiaceae **D** Meliaceae Simaroubaceae Rutaceae Sapindaceae Nit

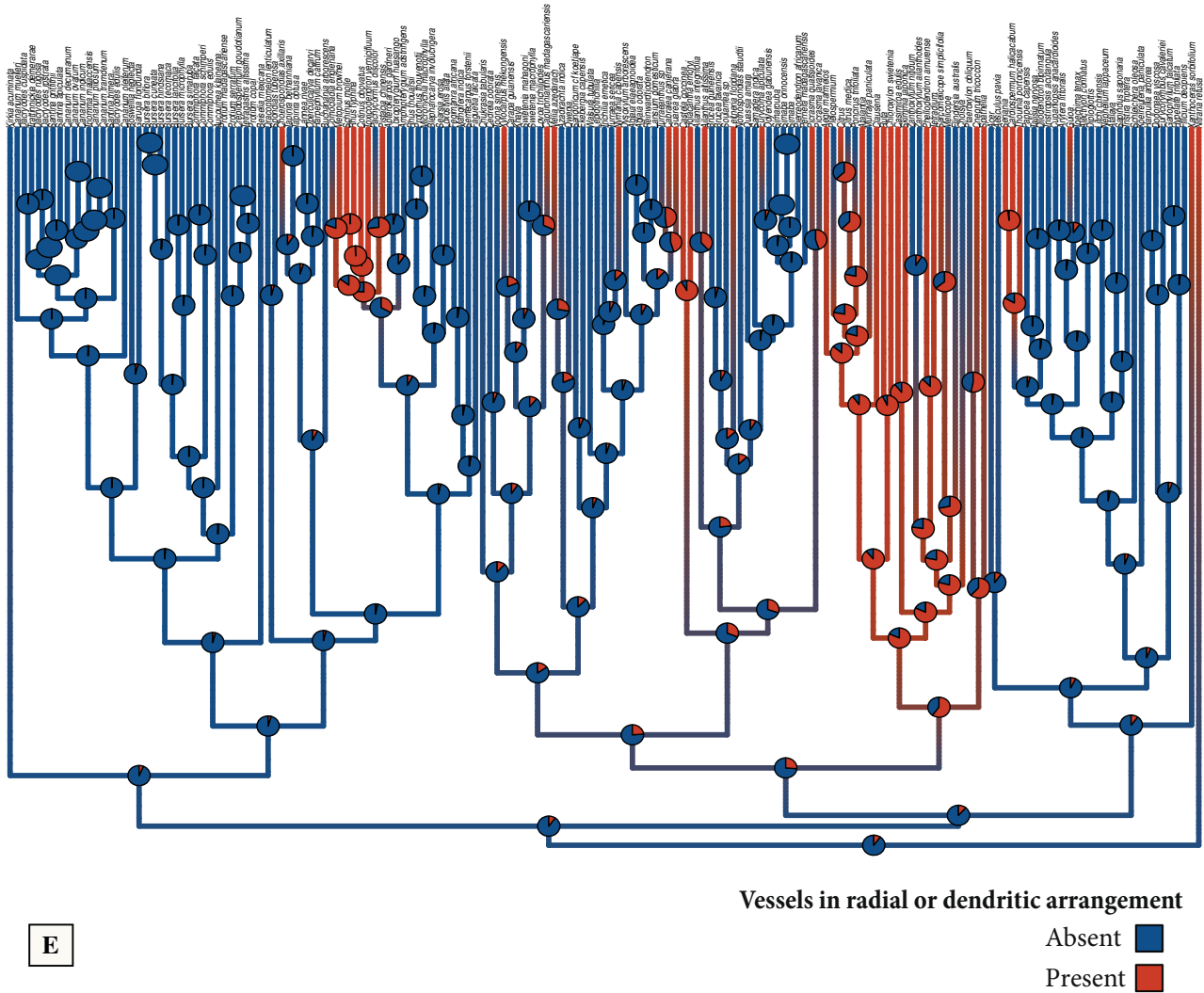


Fig. 5 Vessel arrangement diversity and evolution in Sapindales. **a–d** Transverse sections. **A.** *Protorhus thouvenotii* Lecomte (Anacardiaceae), vessels without any specific arrangement. Axial parenchyma vasicentric to aliform. **b** *Helietta lucida* Brandege (Rutaceae), vessels in a radial arrangement, growth rings marked by semi-ring porosity, thick-walled, radially narrow fibers and marginal parenchyma. **c** *Thouinia paucidentata* Radlk. (Sapindaceae), vessel in radial arrangement. Gums/gum-like deposits obstructing vessels. **d** *Orixa japonica* Thunb. (Rutaceae), vessels very narrow, in dendritic pattern. **e** Ancestral character state estimation of vessels with a radial to/or dendritic arrangement. Scale bars: A=300 μ m; B-C=200 μ m; D=500 μ m. Fig. D by courtesy of the Tsukuba Wood Collection TWTw, Japan. Kirk = Kirkiaceae, Nit = Nitrariaceae

Reinwardtiidendron and *Guarea* F.Allam. (Fig. 18d). In Rutaceae, they are present in *Melicope* J.R.Forst. & G.Forst. (Fig. 18d).

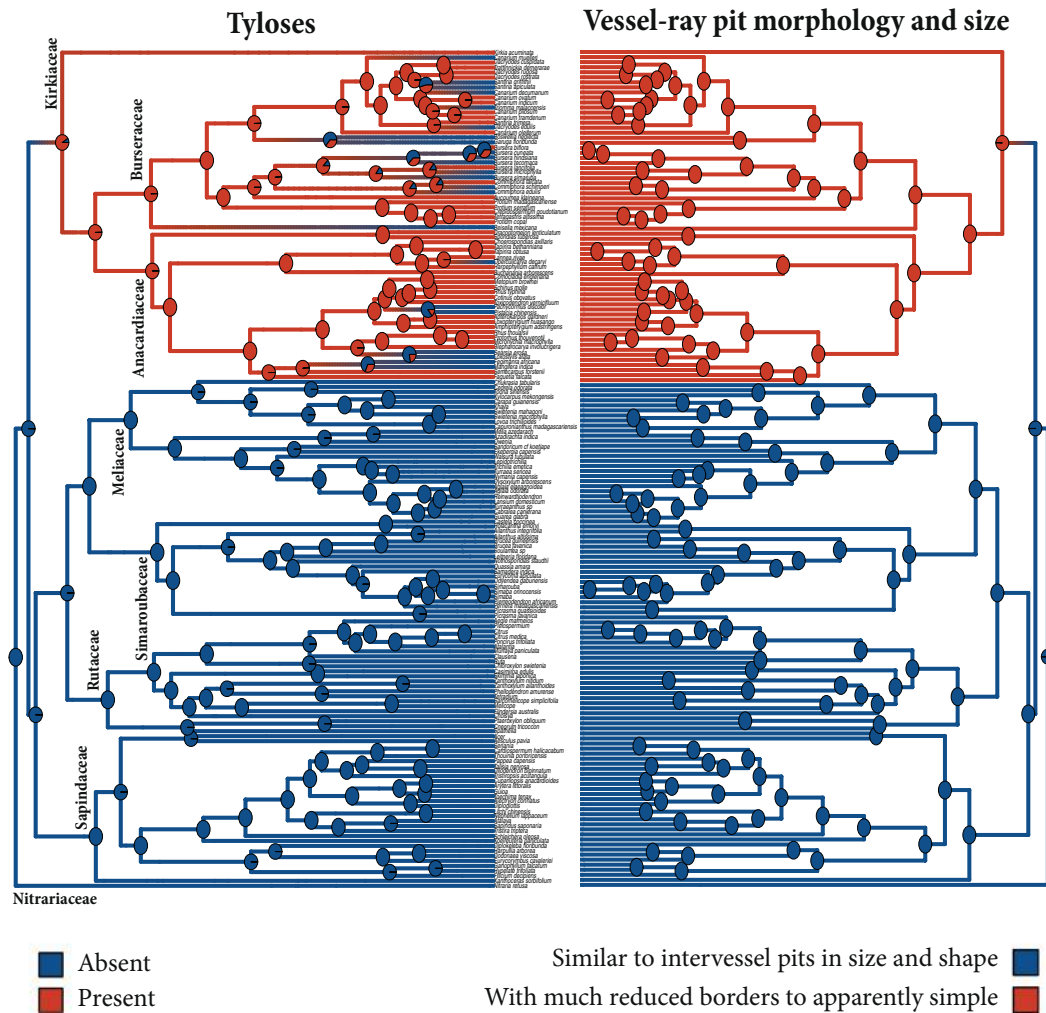
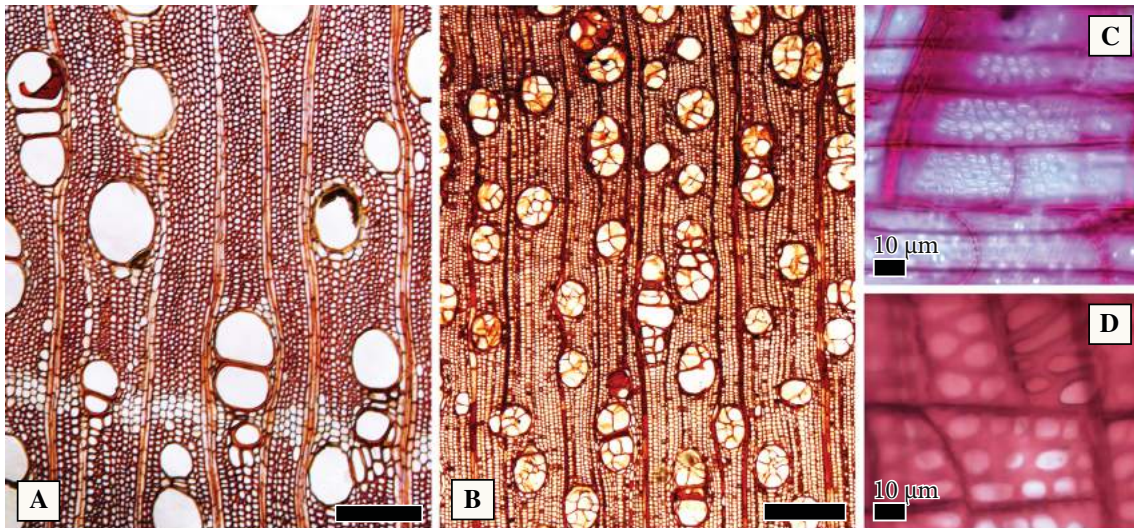
Cambial variants (Fig. 19). As mentioned in the “General Features of Sapindales,” lianas are present exclusively in two families of Sapindales: Anacardiaceae and Sapindaceae. Cambial variants are absent in lianas of the Anacardiaceae, while in Sapindaceae tribe Paullinieae, 10 different types of variant secondary growth have been described to date, although all genera have also species of regular secondary growth (Fig. 19). These different types may be extremely similar macroscopically and even microscopically when only the adult forms are considered, and it was only thanks to numerous detailed ontogenetic studies that these different forms have been established. Here we summarize and briefly explain these 10 different types of secondary growth, but specific literature on the subject will be provided in discussion for those seeking to further explore this subject. Seven of these 10 different variant types of secondary growths have in common the final aspect of a cable structure. However, their ontogenies vary. The compound stems are originated at the onset of primary growth, when independent islands of procambium generate 4 to 9 vascular cylinders in a single stem (Fig. 19). The most common compound stem has a central cylinder and three peripheral cylinders, as in *Paullinia*, or 3 to 8 peripheral cylinders, as in *Serjania* (Fig. 19). With a similar ontogeny are the divided vascular cylinders, which are by all means equal to the compound stem, except for lacking a central cylinder, and are exclusive to genus *Serjania* (Fig. 19). In some cases, a central cylinder is formed later on, derived from the formation of a cambium in the center of the stem (Fig. 19). In *Thinouia* Planch. & Triana and *Serjania meridionalis* Griseb, another type of cable structure is formed by the neof ormation of cambia derived from the pericycle forming usually 3–5 vascular cylinders around the first formed central cylinder (Fig. 19), a type named corded. Lobed stems appeared independently in *Paullinia*, *Serjania* and *Urvillea* Kunth and derive from the differential activity of certain sectors of the cambium that produce less secondary xylem than others, generating lobes (Fig. 19). In some species, one of the lobes commonly

detach in the adult, a type named fissured stem, which is exclusive of *Urvillea* (Fig. 19). Phloem wedges, which derive from portions of the cambium that produce less xylem and more phloem appeared independently in *Paullinia* and *Serjania*. Pericyclic-derived successive cambia evolved independently in both *Paullinia* section *Phygoptilium* and *Serjania pernambucensis* Radlk. (Fig. 19). Finally, again in these two genera, *Serjania* and *Paullinia*, when their stems or roots are large, one frequently encounters the formation of novel vascular strands or cylinders derived from either cortical, secondary phloem axial or ray parenchyma or even the pericycle, named neof ormations (Fig. 19).

Principal component analysis of quantitative features – The first two Principal Components, PC1 (38%) and PC2 (22%), explain 60% of the variance in the quantitative dataset. Loadings of variables related to PC1 and PC2 were used to describe the most important wood descriptors (Fig. 20; Supporting information Appendix S3). The species of Anacardiaceae and Burseraceae are most similar in terms of the variation of the quantitative characters described in Table 3. The species of these two families produce a xylem with smaller vessel diameters, less axial parenchyma and high vessel frequencies; except for *Spondias mombin* Jacq. and *Harpephyllum caffrum* Bernh. ex C.Krauss in our dataset, which have high and wide rays, respectively. Simaroubaceae and Meliaceae, on the other hand, produce a xylem with larger vessel diameter and lower vessel frequency, with the Simaroubaceae species presenting wider and taller rays while Meliaceae produces more axial parenchyma. The Rutaceae and Sapindaceae species produce a xylem with a higher vessel frequency and some species with a higher percentage of axial parenchyma, but most species in these families do not have broad and tall rays.

4 Discussion

The wood (secondary xylem) is a highly diverse and important tissue for woody plants, acting in at least four distinct roles: water conduction, mechanical support while exposing the plants to light, storage of both water and nonstructural carbohydrates, and given its role behind the longevity of trees, defense. Most of the diversity of wood will in part be related to one of these four functions, sometimes also evolving in concert with other parts of the plants such as roots and leaves (from leaf texture to leaf phenology) with different strategies to respond to their surrounding environment. Here we explore the wood diversity of over 250 species from 166 genera and patterns of evolution of 23 wood characters of the Sapindales, discussing our results considering all of these distinct roles.



E

Fig. 6 Tyloses and vessel-ray pit size diversity and evolution Sapindales. **a** *Swietenia macrophylla* King. (Meliaceae), tyloses absent, gums/gum-like deposits present. Note marginal parenchyma band and scanty paratracheal parenchyma. Transverse section (TS). **b** *Protium copal* (Schltdl. & Cham.) Engl. (Burseraceae), tyloses present. Scanty axial parenchyma. TS. **c** *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), vessel-ray pits similar to intervessel pits in size and shape. **d** *Choerospondias axillaris* (Roxb.) B.L.Burt & A.W.Hill (Anacardiaceae), vessel-ray pits with much reduced borders to apparently simple. **e** Ancestral character state estimation of tyloses and vessel-ray pit size. Scale bars: A-B = 250 μm ; C-D = 10 μm

Ancestral wood of the order – The Sapindales are estimated to have appeared in the lower Cretaceous, approximately 112 million years ago, with the diversification of all 9 families throughout the upper Cretaceous (Muellner-Riehl et al. 2016). Across this time, our work evidences that an enormous diversification of wood features have evolved within the group. According to our estimations, the wood of the ancestral Sapindales had growth rings delimited by thick-walled, radially narrow fibers (as also estimated in the broad study on seed plants of Silva et al. 2021) and a marginal parenchyma band (unlike what reconstructed by Silva et al. 2021), diffuse-porous, scanty axial parenchyma, vessels solitary to multiples of 2–3, small intervessel pits (< 8 μm), with gums/gum-like inclusions in heartwood and no tyloses, vessel-ray pits similar to intervessel pits in size and shape, non-septate fibers, no radial or traumatic axial ducts, rays 2–4 cells wide, heterocellular with body procumbent and one row of upright to square marginal cells, non-storied, with prismatic crystals and no silica bodies.

Making a search on the early to late cretaceous fossil hardwoods on the InsideWood database, using the features described above as putative ancestral to the order Sapindales, eleven potential fossil candidates come back, eight of them being Sapindalean families, strongly supporting our estimate ancestral states. Reviewing other sources of cretaceous wood fossils from different parts of the world further corroborate our reconstructions (Schönfeld 1947; Prakash 1962; Dayal 1965; Shete and Kulkarni 1982; Trivedi and Srivasta 1985, 1988; Crawley 2001; Srivastava and Guleria 2004; Huang et al. 2021).

Individual wood characters: evolution and possible relation to ecophysiological factors— Evolution of growth ring markers in Sapindales. The presence of growth rings in tropical species has been reported various times, contrary to the past belief that tropical species lacked growth rings due to the absence of severe winters (Deti  ne 1989; Worbes 1995, 1999). Today it is widely accepted that nearly half of the tropical woody species have distinctive growth rings caused by either the alternation of a favorable and unfavorable seasons or endogenous/genetic factors inherent to the studied taxa (Mainieri et al. 1983; Deti  ne 1989; Worbes 1995; Alves and Angyalossy-Alfonso 2000; Callado et al. 2001;

Marcati et al. 2006a; Wheeler et al. 2007; Lima et al. 2010; Silva et al. 2019, 2021). When caused by climate seasonality the main triggers in the tropics are either a marked dry season or periodic river floodings (Worbes 1995, 1999; Callado et al. 2001; Lima et al. 2010), and often these growth rings are annual (Marcati et al. 2006a; Brienen et al. 2016; Baker et al. 2017; Sch  ngart et al. 2017). Within this context, the Sapindalean families are no exception, and virtually all species have distinctive growth rings and this state is reconstructed as ancestrally present in the order (Supplementary Fig. 1). The most common growth ring marker are the thick-walled, radially flattened fibers, but marginal parenchyma, ring porosity or a combination of these features appear in numerous taxa. Thick-walled, radially flattened fibers are the most common growth ring markers not only in Sapindales but in woody plants as a whole, while marginal parenchyma and ring porosity have evolved many times across the diversification of woody plants (Silva et al. 2019, 2021). Physiological studies propose that the thicker, narrower fibers likely derive from a reduction in the cambial derivatives' radial expansion during maturation, due to unfavorable environmental conditions limiting water use, either cold or drought (Cuny et al. 2014; Rathgeber et al. 2016). However, other authors pose that the high frequency of this feature suggests that not only the limited expansion capacity of the cambial derivatives would likely be behind the presence of radially flattened fibers and smaller cells in general (vessels, fibers and axial parenchyma), but likely also mechanical and hydraulic selective pressures (Silva et al. 2021). More studies are needed to unravel the widespread presence of thick-walled, radially flattened fibers as wood growth ring markers.

In terms of growth rings' seasonality, detailed time series studies in members of Sapindales taxa, such as *Azadirachta indica* A. Juss., *Cedrela*, *Entandrophragma*, *Guarea*, *Toona* and *Swietenia macrophylla* (Meliaceae) showed that their growth rings are generally annual, with the cambium active during the wet season and dormant during the dry season, forming distinct growth markers in the secondary xylem (Coster 1927; Deti  ne 1989; Tomazello et al. 2001; D  nisch et al. 2002; Marcati et al. 2006b; Baker et al. 2017) and also in the secondary phloem (Angyalossy et al. 2021). However, under certain circumstances *Carapa guianensis*, *Cedrela fissilis* and *Swietenia macrophylla* (Meliaceae) formed various infra-annual growth rings (two, two and five, respectively), responding to events such as exceptional dry periods, rainfalls, and periodic flooding events across one single year (D  nisch et al. 1999, 2002; Baker et al. 2017) or even insect attack (D  nisch et al. 2002). These data evidence the high responsiveness of cambial activity to biotic and abiotic influences.

From ancestors with diffuse-porous woods and no helical thickenings, numerous lineages have evolved ring porosity

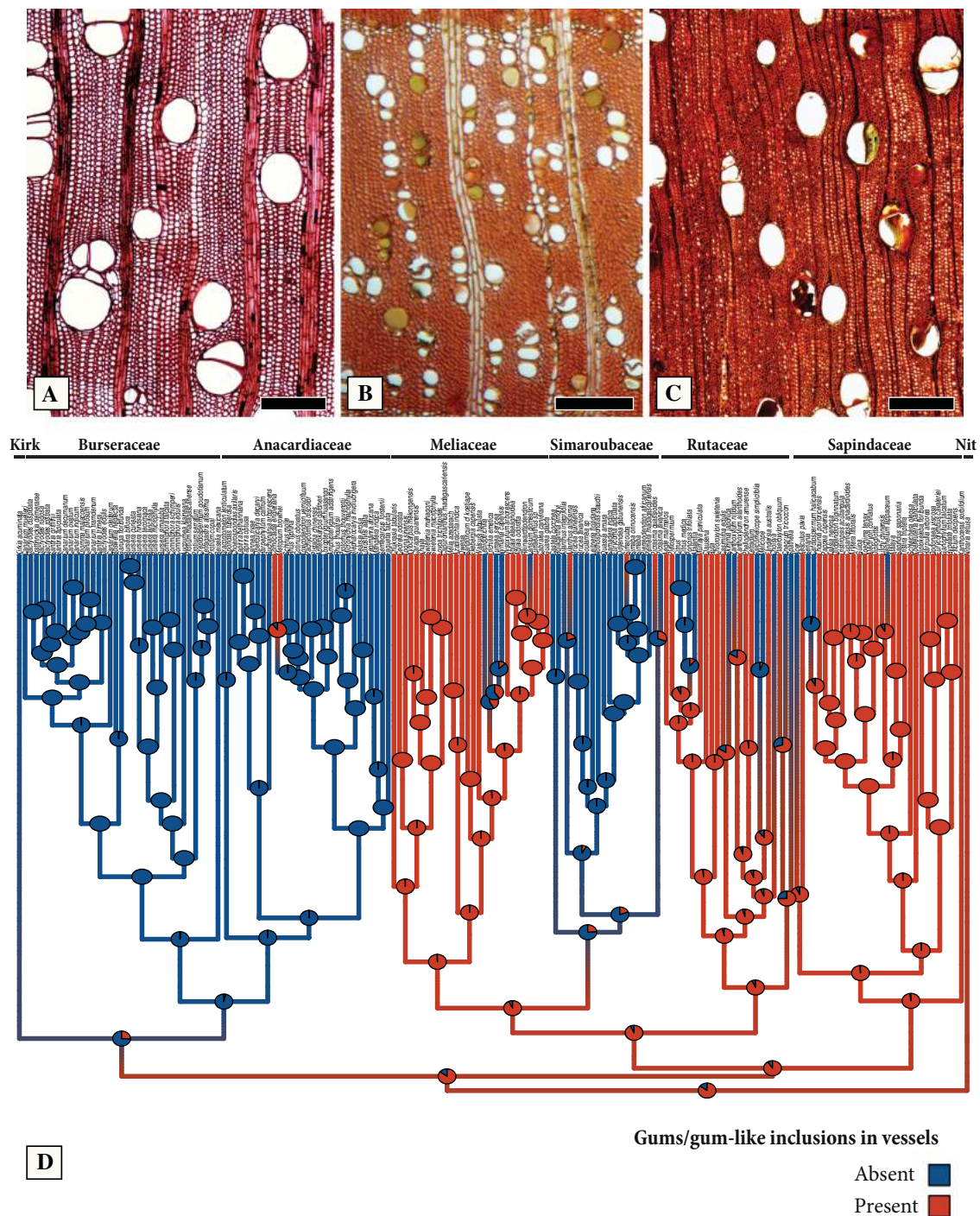


Fig. 7 Gums/gum-like deposits evolution in Sapindales. Transverse sections. **a** *Spondias mombin* L. (Anacardiaceae), gums/gum-like deposits absent. **b** *Zanthoxylum caribaеum* Lam. (Rutaceae), gums/gum-like deposits common. **c** *Cupania macrophylla* Mart. (Sapindaceae), gums/gum-like deposits common. **d** Ancestral character state estimation of gums/gum-like deposits present and their evolution in Sapindales. Scale bars: A, C = 300 μ m; B = 150 μ m. Kirk = Kirkiaceae, Nit = Nitrariaceae

and helical thickenings both in trees and lianas (i.e., *Toxicodendron*) of Sapindales. Multiple studies on the formation of ring-porous woods and helical thickenings have demonstrated they are strongly correlated to leaf deciduousness

and the occupation of seasonal environments, either with a marked cold winter in the temperate zones or a marked dry season in the tropics (Fahn 1933, 1955; Baas 1973; van den Oever et al. 1981; Baas and Vetter 1989; Wheeler

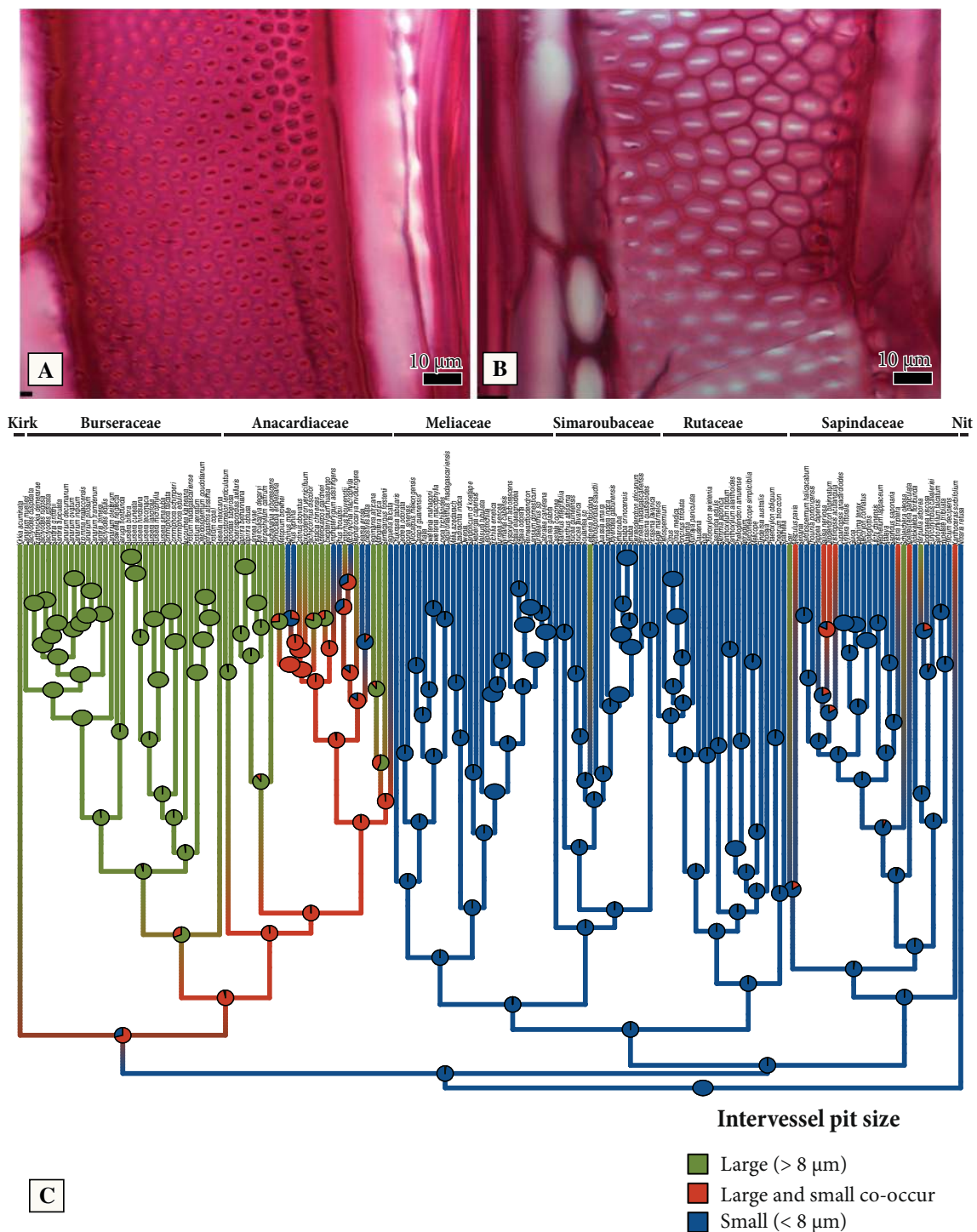


Fig. 8 Intervessel pit size diversity and evolution in Sapindales. Tangential sections. **a** *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), intervessel pits small. **b** *Loxopterygium sagotii* Hook.f. (Anacardiaceae), intervessel pits large. **c** Ancestral state reconstruction of intervesSEL pit size. Scale bars: A-B = 10 μm. Kirk = Kirkiaceae, Nit = Nitrariaceae

and Baas 1991; Schweingruber 1992, 1996; Worbes 1995, 1999; Alves and Angyalossy-Alfonso 2000; Carlquist 2001; Baas et al. 2004; Wheeler et al. 2007; Silva et al. 2021). For genera and species of wide distribution, such as *Prosopis*

L. (Leguminosae), *Buddleja* L. (Scrophulariaceae), *Dolichandra unguis-cati* (L.) L.G.Lohmann and *Catalpa* Scop. (Bignoniaceae), growth rings can vary from ring-porous all the way to diffuse-porous depending on their place of

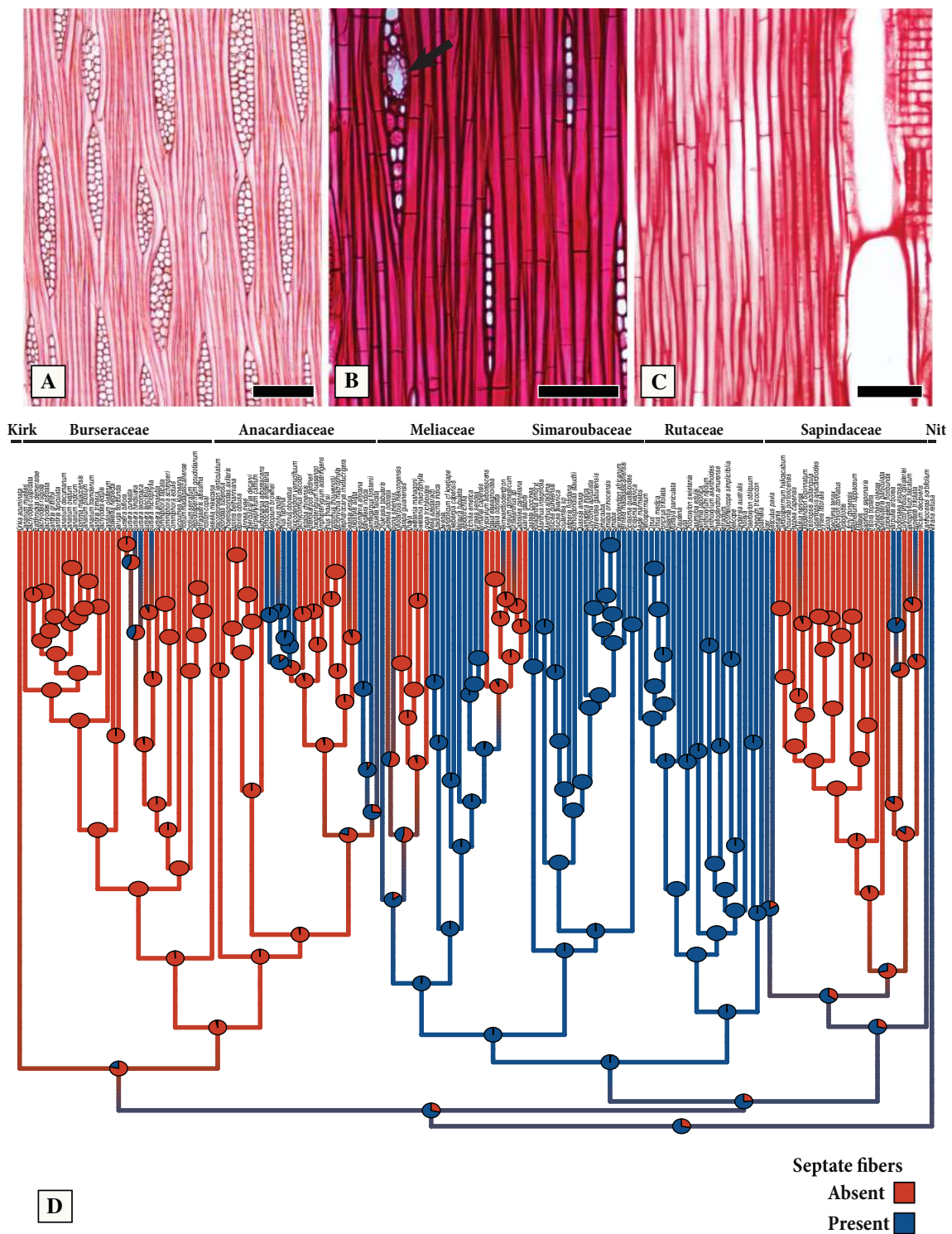


Fig. 9 Septate fiber evolution in Sapindales. **a** *Simarouba glauca* DC. (Simaroubaceae), fibers non-septate. Longitudinal tangential section (LT). **b** *Loxopterygium sagotii* Hook.f. (Anacardiaceae), septate fibers abundant. Note also radial canals (arrow). LT. **c** *Tina apiculata* Radlk. ex Choux (Sapindaceae), septate fibers abundant. Longitudinal radial section. **d** Ancestral character state estimation of septate fibers in Sapindales. Scale bars: A = 200 µm; B-C = 100 µm. Kirk = Kirkiaceae, Nit = Nitrariaceae

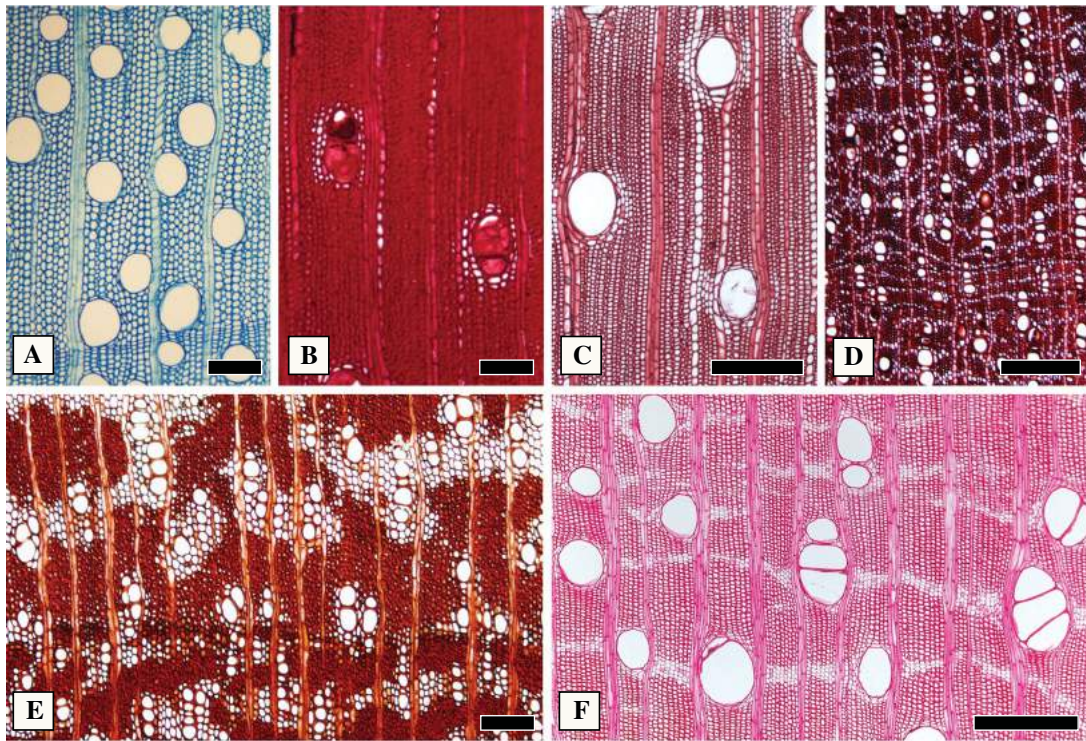
occurrence and climatic conditions, evidencing the phenotypic plasticity of this feature for some taxa (Muñiz 1986; Aguilar-Rodríguez et al. 2006; Pace and Angyalossy 2013; Pace et al. 2015). Our data support this correlation between climate and ring-porosity, with all semi-ring and ring-porous woods in Sapindales, such as *Ailanthus altissima* (Simaroubaceae) and *Phellodendron amurense* Rupr. (Rutaceae), being lineages occurring in temperate zones and being deciduous (Hu 1979; Kowarik and Sämel 2007; Wan et al. 2014). In addition, there are numerous examples of *Ailanthus* species with diffuse-porous woods when growing in non-seasonal environments of South-East Asia and being evergreen (Rajput et al. 2005; InsideWood website), therefore, supporting the suggestion of phenotypic plasticity for this genus. More studies are needed to evaluate the plasticity of these features for other genera of Sapindales. For the tropical taxa, a marked dry season was shown to be the cause of semi-ring to ring-porous woods, such as seen in *Cedrela*, *Toona* (Meliaceae; Dünisch et al. 2002), *Pistacia mexicana* Kunth (Anacardiaceae) and *Ptelea trifoliata* L. (Rutaceae). For instance, *Pistacia mexicana* and *Ptelea trifoliata* occur in the Tehuacán-Cuicatlán valley in central-south Mexico, a zone with a long, severe dry season, dominated by columnar cacti, and other xeric adapted taxa such as *Prosopis* (Leguminosae), Fouquieriaceae and Agavoideae (Dávila et al. 1995; Arias et al. 2012; Miguel-Talonia et al. 2014).

On the other hand, other studies on ring porosity indicate that in many cases a genetic control determines the presence or absence of ring porosity, independently from where the species grow (Chowdhury 1952, 1963; Brienen et al. 2016; Silva et al. 2019, 2021) and, therefore, not being phenotypically plastic. Interestingly, our data provide support also to this second hypothesis, with genera such as *Acer* (Sapindaceae), which is deciduous and of temperate distribution, or *Bursera* (Burseraceae), also deciduous and whose center of diversity is exactly the seasonally dry forests of the Tehuacán-Cuicatlán valley mentioned before (De-Nova et al. 2012), having diffuse-porous woods and no helical thickenings. Clearly, there are multiple mechanisms to cope with periodic unfavorable seasons, either dry or cold, such as early leaf shedding, photosynthetic stems, stomatal control, water storage in certain organs or deep roots which can access underground water (Méndez-Alonzo et al. 2012; Santiago et al. 2016), all of which have to be taken in account to understand the morpho-anatomy of species in relation to their environments. In particular, studies with co-occurring species in the same seasonal dry forests in the pacific coast of Mexico showed two opposed wood anatomical strategies; plants with narrower vessels, thicker fibers, denser woods were those more tolerant to drought and maintained the leaf coverage much longer through the dry season than those with wider vessels, thinner walled fibers and lighter wood, which rapidly lost their leaves (Méndez-Alonzo et al. 2012).

These results reinforce the idea that selection can shape different morpho-anatomical strategies even under similar conditions (Marks and Lechowicz 2006), the first group investing in a safer system, less efficient in water transport, with slower growth, but able to photosynthesize for longer periods, and the other more efficient in water conduction during the favorable season, but much more hydraulically vulnerable, rapidly shedding their leaves at the onset of the dry season (Méndez-Alonzo et al. 2012).

The situation of helical thickenings is even more complex. Carlquist (2001) suggested the wall ornamentation likely increased the cohesion of the water column with the vessel walls, making this feature positively selected under water stress. Here, although we did find a positive correlation between helical thickenings and ring-porousness, suggesting their relation to strongly seasonal climates (Baas 1973; Carlquist 1975; Meylan and Butterfield 1978), we have also many examples in Nitrariaceae and Sapindaceae of species with helical thickening but occurring in different habitats across the tropics (Klaassen 1999; our data). Other studies have also found conflicting results on the presence of helical thickenings and the taxa's climate of occurrence (Carlquist 1975; Schmid and Baas 1984; Nair 1987; Marcati et al. 2014; Arévalo et al. 2017), indicating that a broad study on the occurrence of helical thickenings and their possible physiological or phylogenetic correlates is needed.

The second most common growth ring marker in Sapindales is marginal parenchyma, which is inferred to be ancestral to the order, with multiple losses. Marginal parenchyma was shown to be correlated to the tropics, although not exclusively (Alves and Angyalossy-Alfonso 2000; Silva et al. 2019, 2021), being present in numerous distantly related lineages of angiosperms (Gourlay and Kanowski 1991; Klaassen 1999; Callado et al. 2001; Lima et al. 2010; Pace et al. 2015; Almeida et al. 2019). Marginal parenchyma bands may be terminal, initial or mixed, i.e., formed at the end of the growth season, at its onset, or partially in each period (Chowdhury 1934, 1936, 1947; Carlquist 1961; Marcati et al. 2014; Silva et al. 2021). Periodic cambial sampling in *Cedrela* (Meliaceae) has shown that a small part of its marginal parenchyma band is formed at the end of the growth season, while most of it is produced after the cambium resumes its activity in the next growth season, evidencing a mixed origin, and making the term marginal parenchyma preferred over terminal and initial parenchyma for this genus (Marcati et al. 2006a), as had been previously suggested (Carlquist 1975). The presence of starch and water in marginal parenchyma and their mobilization during the beginning of the growth season led authors to suggest that the marginal parenchyma bands favor rapid flushes of growth (Carlquist 1975; Gourlay and Kanowski 1991; Dünisch et al. 2002; Marcati and Angyalossy 2005). The alternative presence in several species of more abundant septate fibers in



Kirk Burseraceae Anacardiaceae Meliaceae Simaroubaceae Rutaceae Sapindaceae Nit

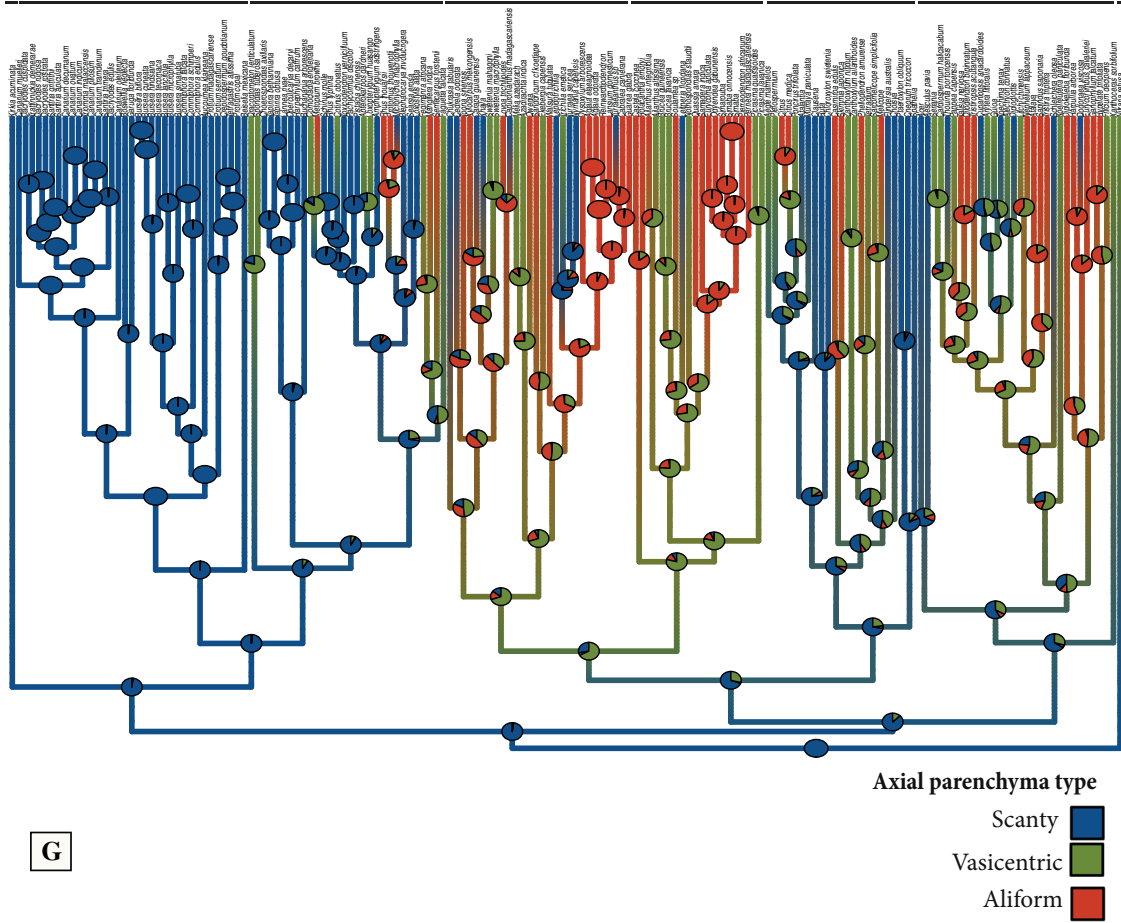


Fig. 10 Axial parenchyma diversity and evolution in Sapindales. Transverse sections. **a** *Commiphora pervilleana* Engl. (Burseraceae), axial parenchyma scanty. **b** *Myracrodruon urundeuva* Allemão, axial parenchyma vasicentric. Note also sclerotic tyloses obstructing the vessels. **c** *Dracontomelon lenticulatum* H.P.Wilk. (Anacardiaceae), axial parenchyma vasicentric to lozenge aliform. **d** *Trichilia trifolia* L. (Meliaceae), axial parenchyma winged aliform, forming confluences. **e** *Casimiroa calderoniae* F.Chiang & Medrano (Rutaceae), axial parenchyma vasicentric to aliform confluent. **f** *Simarouba amara* Aubl. (Simaroubaceae), axial parenchyma aliform winged, forming short confluences. **g** Ancestral character state estimation of axial parenchyma type in Sapindales. Scale bars: A, E=200 µm; B=100 µm; C-D=300 µm; F=500 µm. Kirk=Kirkiaceae, Nit=Nitrariaceae

the latewood and the mobilization of starch from them at the beginning of the favorable season reinforces this hypothesis of storage-related capacity created to favor flushes of growth at the onset of favorable seasons (Sauter 1973; Gregory 1978; Dünisch et al. 2002). Further observations in those Sapindales with both septate and non-septate fibers need to be done to evaluate if septate fibers are more common in latewood, as it seems from our personal observations.

Vessel arrangement, axial parenchyma, septate fibers and pit morphology—Other features found throughout the Sapindales have been traditionally attributed to wood trade-offs between safety and efficiency in hydraulic conduction. These features are: vessels in radial multiples, variation in intervessel pit size and vessel-ray pit morphology, thick-walled fibers, axial parenchyma abundance, presence of septate fibers, ray width, height and composition. Clearly, as stressed by previous authors, not necessarily all morpho-anatomical diversity need to be correlated to a function (Baas 1982), and especially in a work exploring taxa within a monophyletic group, we expect to encounter similarities also related to the phylogenetic history of these species. Therefore, we consider both scenarios here.

Within Sapindales, multiple lineages have evolved thicker walled fibers, narrower vessels in radial chains, and more abundant axial parenchyma, all features directly related to a safer hydraulic architecture in physiological studies (Hacke and Sperry 2001; Hacke et al. 2001; Jacobsen et al. 2005). Within the Rutaceae, the fibers are typically thick and vessels in radial chains were reconstructed as ancestrally present (see Fig. 5b). Vasicentric and aliform parenchyma are the most common features in Meliaceae, Sapindaceae and Simaroubaceae. In multiple studies, especially those with broad flora coverage, it has been shown that the presence of vessels in multiples, generally of lower widths, thick-walled fibers and more abundant parenchyma are correlated to more water stressful environments, and would be related to an increased hydraulic safety to the vascular system (Alves and Angyalossy-Alfonso 2000; Hacke and Sperry 2001; Appelhans et al. 2012; Fichtler and Worbes 2012), something that may be related to the multiple occupation of dry areas

by members of Sapindales. Vessels in multiples typically offer a bypass for the water column when some vessels of the group undergo cavitation, maintaining the cohesion of the water columns which is crucial to the ascent of water (Zimmermann 1982; Hacke and Sperry 2001; Wheeler and Lehman 2005; Hacke et al. 2006). A matrix of thicker wall fibers in wood is directly related to increase of wood density, consequently increasing mechanical resistance and hydraulic safety for the plant (Hacke et al. 2001; Jacobsen et al. 2005). For a long time, the axial parenchyma in contact with the vessels has been suggested to act as an accessory tissue to the vascular system (Sauter 1973; Gregory 1978; Fink 1982; Braun 1984), assisting in storage and movement of water within the secondary xylem. These cells act in a quick wound response and supporting mechanical properties. Furthermore, these cells are a potential source of surfactants, which reduce the surface tension of water altering xylem vulnerability to cavitation (Sauter 1973; Gregory 1978; Fink 1982; Braun 1984; Hacke & Sperry 2001; Dünisch and Puls 2003; Cochard et al. 2009; Brodersen et al. 2010; Fichtler and Worbes 2012; Morris et al. 2016, 2018; Słupianek et al. 2021).

The taxa in Sapindales which retained the plesiomorphic condition of scanty axial parenchyma, e.g., the clade formed by Anacardiaceae-Burseraceae-Kirkiaceae, have evolved the presence of septate fibers. Septate fibers are known to perform the roles of axial parenchyma in the storage of water and nonstructural carbohydrates, and therefore likely also have a role in embolism avoidance and repair (Carlquist 2001; Yamada et al. 2011), being sometimes even more common around vessels, such as in some species of *Anacardium* L. and *Camposperma* Thwaites (Anacardiaceae, Terrazas 1999). In numerous lineages with scanty axial parenchyma, septate fibers are also present repeatedly (Carlquist 2001; Pace and Angyalossy 2013). However, that was not the case in Sapindales. Here, although septate fibers were present in most major lineages with scanty axial parenchyma (Anacardiaceae, Burseraceae, Kirkiaceae), they are not exclusively present on these taxa. Septate fibers are present also in various Sapindaceae with aliform or vasicentric axial parenchyma. It is likely that the trade-off between septate fibers and axial parenchyma is best measured quantitatively, as it is likely the amount of septate fibers in relation to the amount of axial parenchyma, rather than the presence/absence of septate fibers in relation to the type of axial parenchyma.

One of the most important aspects in the wood hydraulic efficiency and safety are the intervessel pits. These structures are diverse in quantitatively features such as pit size, pit fraction (pit area per vessel) and ultrastructure such as thickness and porosity of the pit membrane. The relationship between these characteristics of intervessel pits and hydraulic safety seems to be quite complex (Sperry and Tyree 1988;

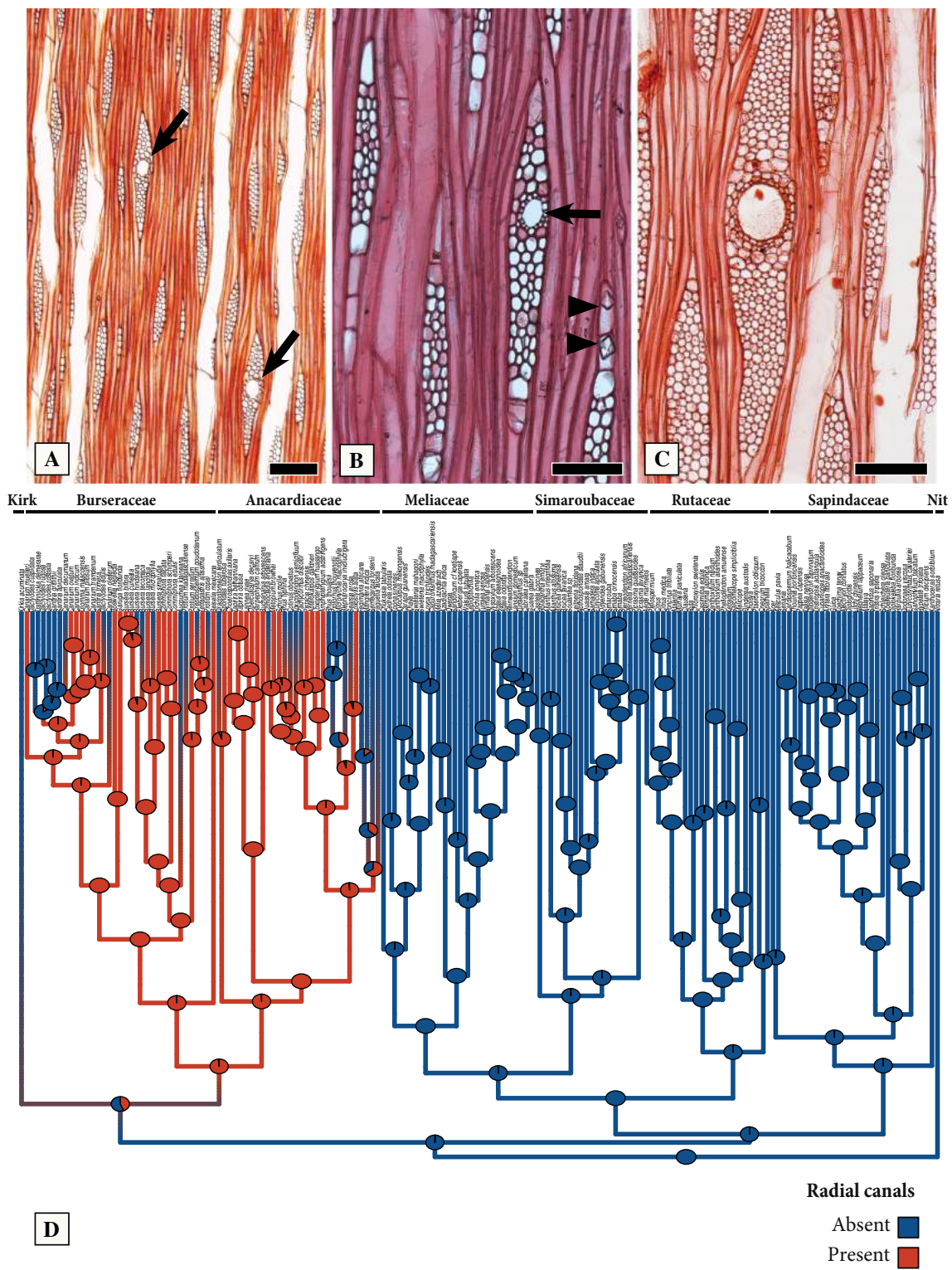


Fig. 11 Radial ducts/canals evolution Sapindales. **a-c** Tangential sections. **a** *Bursera arborea* (Rose) L.Riley (Burseraceae), radial canals present (arrows). **b** *Harpephyllum caffrum* (Anacardiaceae), radial canals. Note the epithelium lining the canal (arrow). Note also the presence of prismatic crystals on the marginal ray cells (arrowheads). **c** *Bursera instabilis* Bernh. (Burseraceae). Detail of a large radial canals, lined up by epithelial cells. **d** Ancestral state estimation of presence of radial canals in Sapindales. Scale bars: A = 200 μ m; B = 100 μ m; C = 150 μ m. Kirk = Kirkiaceae, Nit = Nitrariaceae

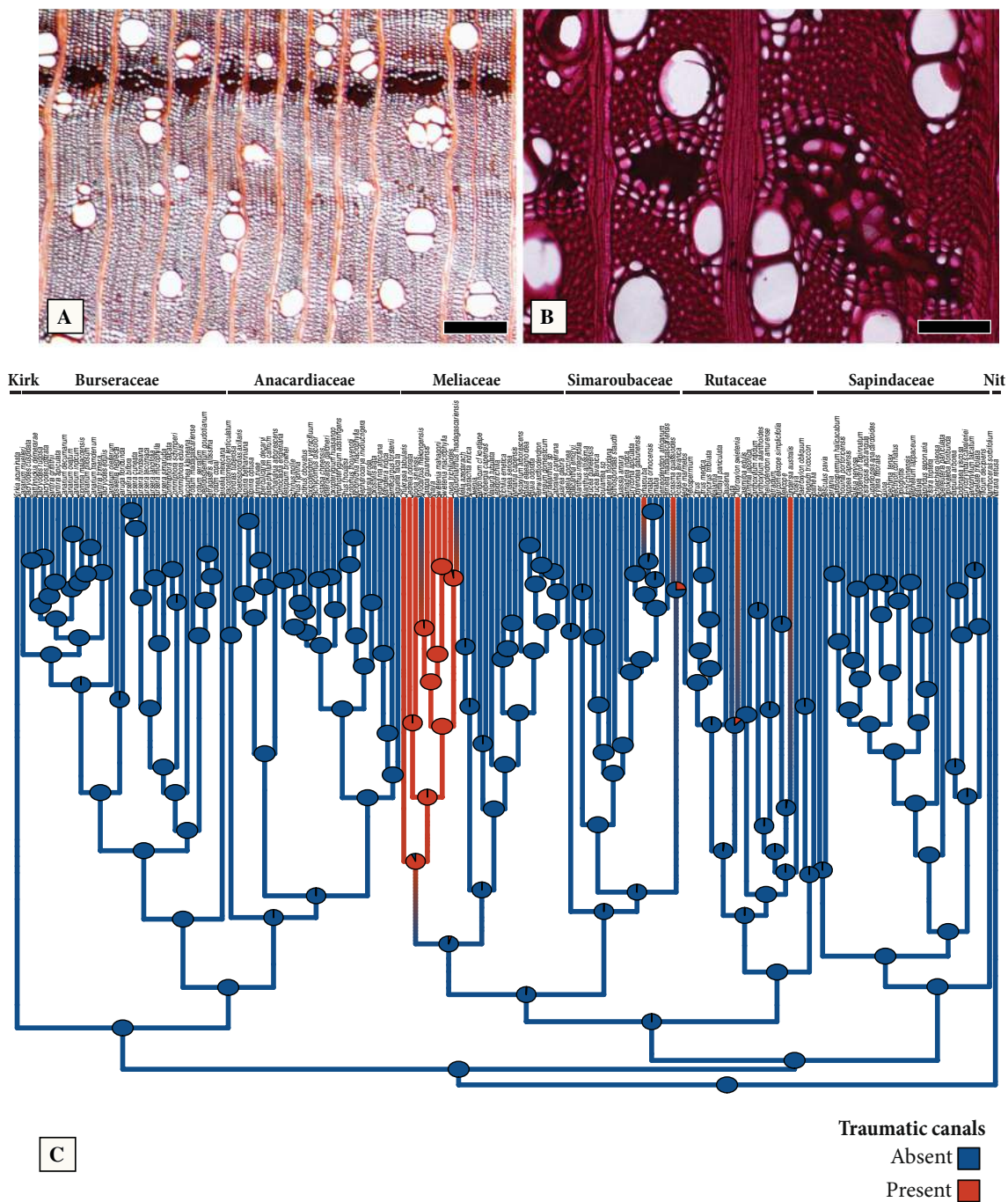
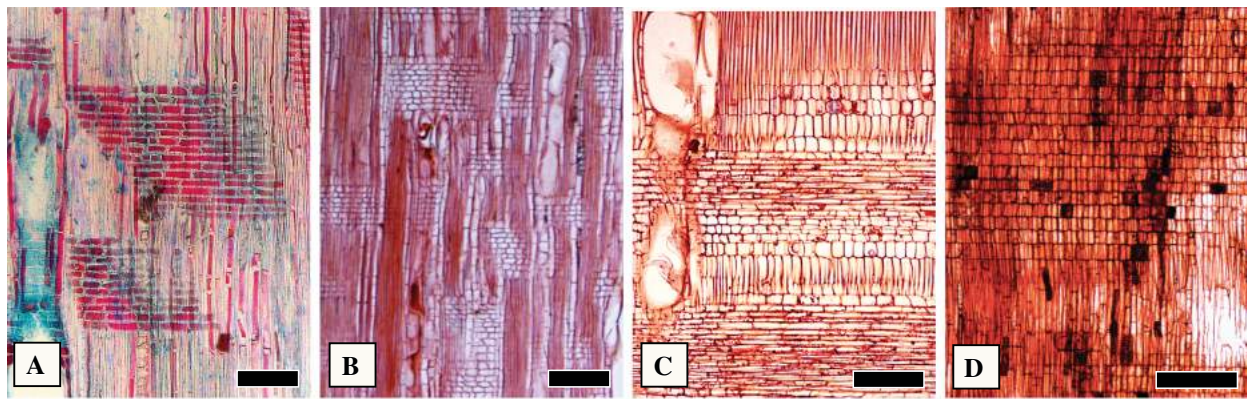


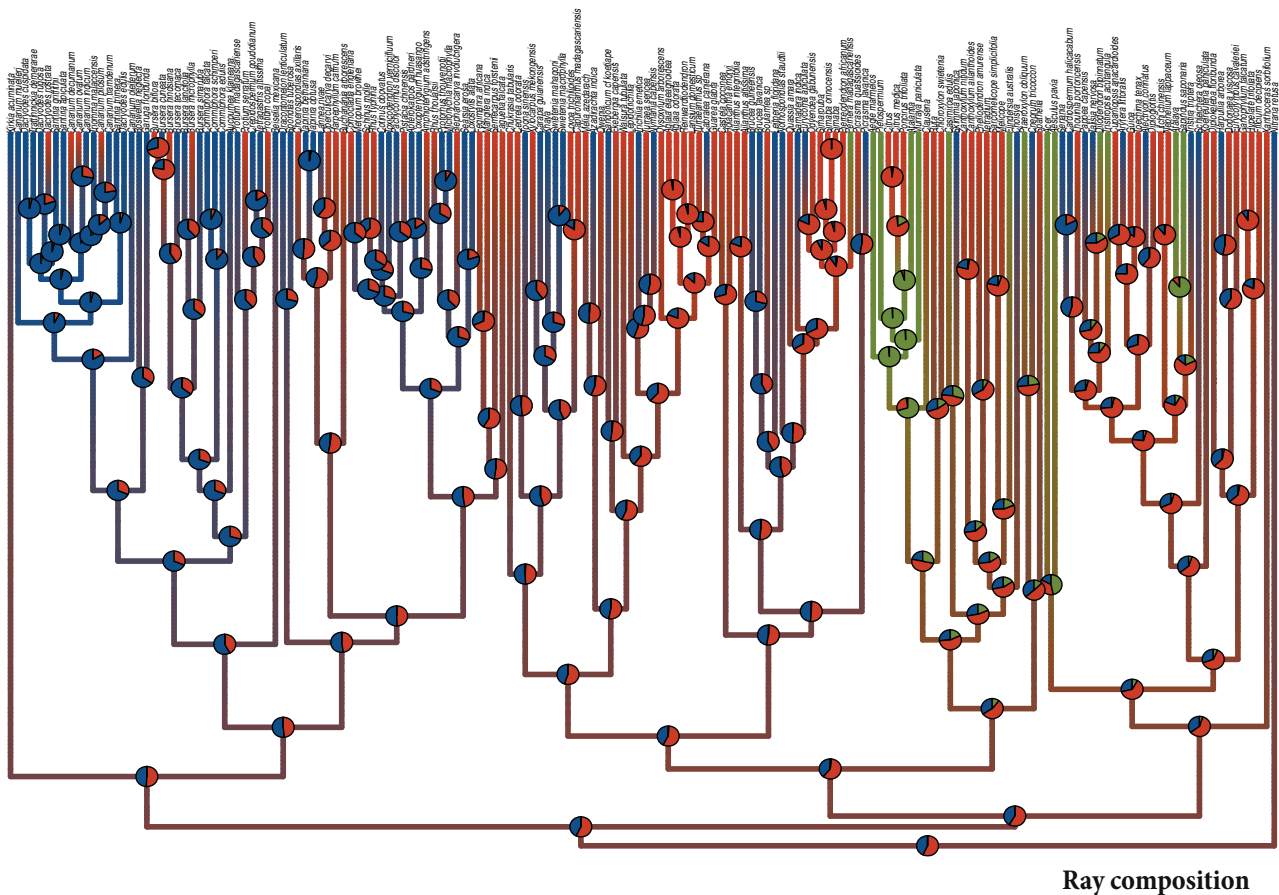
Fig. 12 Evolution of axial traumatic ducts/canals in Sapindales. **a-b.** Transverse sections. **a** *Citrus sinensis* (L.) Osbeck (Rutaceae). Note tangential row of axial canals of traumatic origin and their dark content. **b** *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae). Detail of an axial canal of traumatic origin. **c** Ancestral character state estimation of axial canals of traumatic origin in Sapindales. Scale bars: A = 200 μ m; B = 100 μ m. Kirk = Kirkiaceae, Nit = Nitrariaceae

Sperry et al. 1996; Hacke and Sperry 2001; Baas et al. 2004; Wheeler et al. 2005; Hacke et al. 2006; Jansen et al. 2009, Lens et al. 2011). Although there is no consensus, there is evidence of a reduction in hydraulic safety related to the increase in the pit membrane area for some species (Wheeler et al. 2005, Choat et al. 2005). This relationship is based on

the assumption that the large pit membrane pores responsible for air seeding are apparently rare, increases with increasing total pit membrane area per vessel (Wheeler et al., 2005). However, simply the pore width is not enough, because the pores will increase according to how much the pit membrane can deflect when pushed by an air bubble (Hacke and Sperry



Kirk Burseraceae Anacardiaceae Meliaceae Simaroubaceae Rutaceae Sapindaceae Nit



E

Ray composition

- Heterocellular with many marginal rows of upright/square cells (heterocellular mixed in lianas) ■
- Homo and heterocellular with one rows of upright/square cells ■
- Exclusively homocellular ■

Fig. 13 Ray composition diversity and evolution in Sapindales. **a-d.** Longitudinal radial sections. **a** *Cupania furfuracea* Radlk. (Sapindaceae), homocellular rays. **b** *Trichilia trifolia* L. (Meliaceae), heterocellular rays with body composed of procumbent cells and one marginal row of upright to square cells. **c** *Khaya ivorensis* A.Chev. (Meliaceae), heterocellular rays with body composed of procumbent cells and two to five rows of upright to square cells. **d** *Bursera excelsa* (Kunth) Engl. (Burseraceae), heterocellular mixed rays with procumbent, upright and square cells mixed throughout the ray. **e** Ancestral state estimation of ray composition in Sapindales. Scale bars: A-C=200 µm; D=300 µm. Kirk = Kirkiaceae, Nit=Nitrariaceae

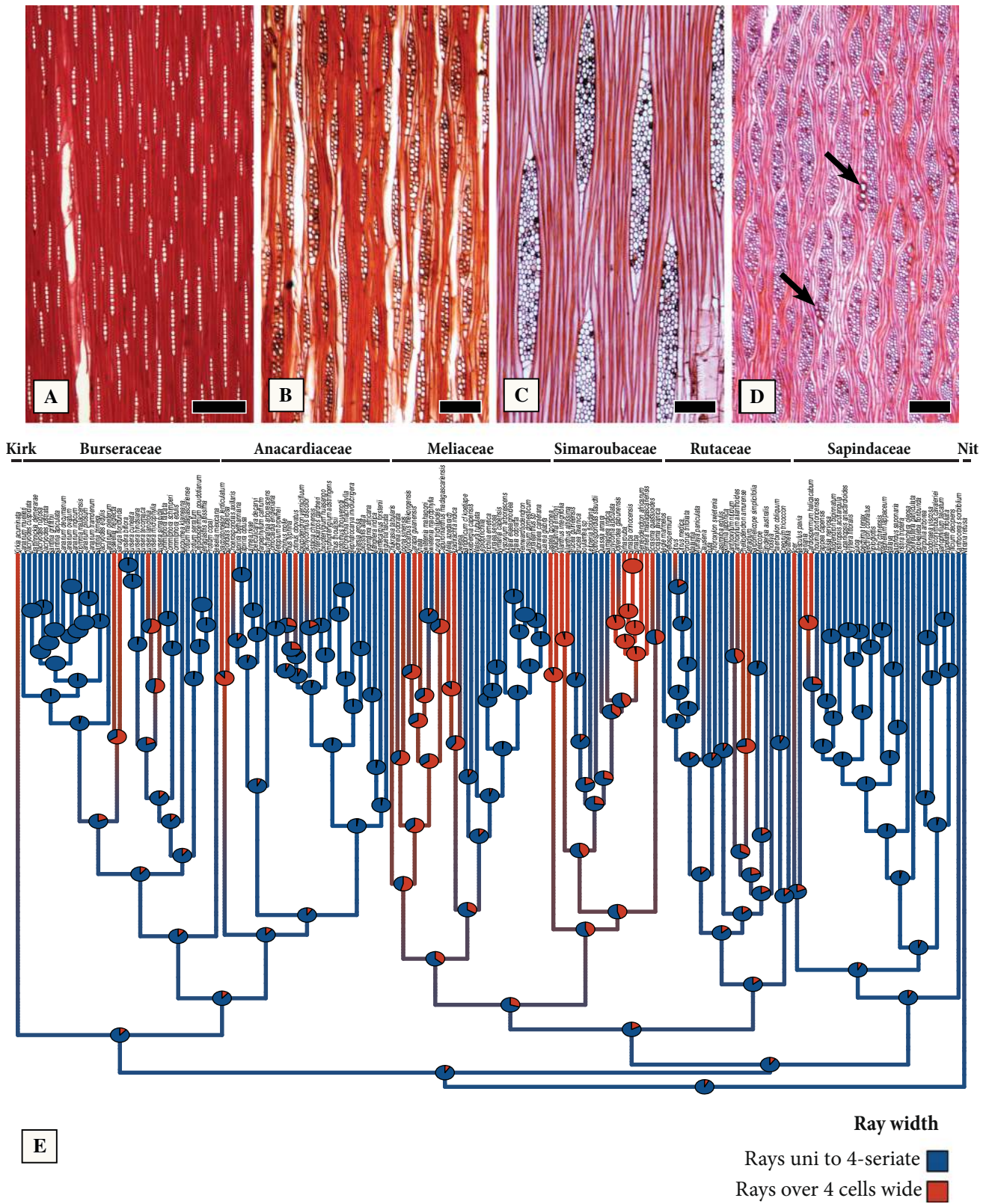


Fig. 14 Ray width diversity and evolution in Sapindales. **a-d.** Longitudinal tangential sections. **a** *Neotina coursii* Capuron (Sapindaceae), uniseriate rays. **b** *Esenbeckia berlandieri* Bail. (Rutaceae), bi-three-seriate rays. **c** *Spondias mombin* L. (Anacardiaceae), rays over 4 cells wide. **d** *Citrus x aurantium* L. (Rutaceae), rays over 4 cells wide. Note large prismatic crystals in chambered axial parenchyma cells (arrows). **e** Ancestral character state estimation of ray width in Sapindales. Scale bars: A-B, D=200 µm; C=100 µm. Kirk = Kirkiaceae, Nit = Nitrariaceae

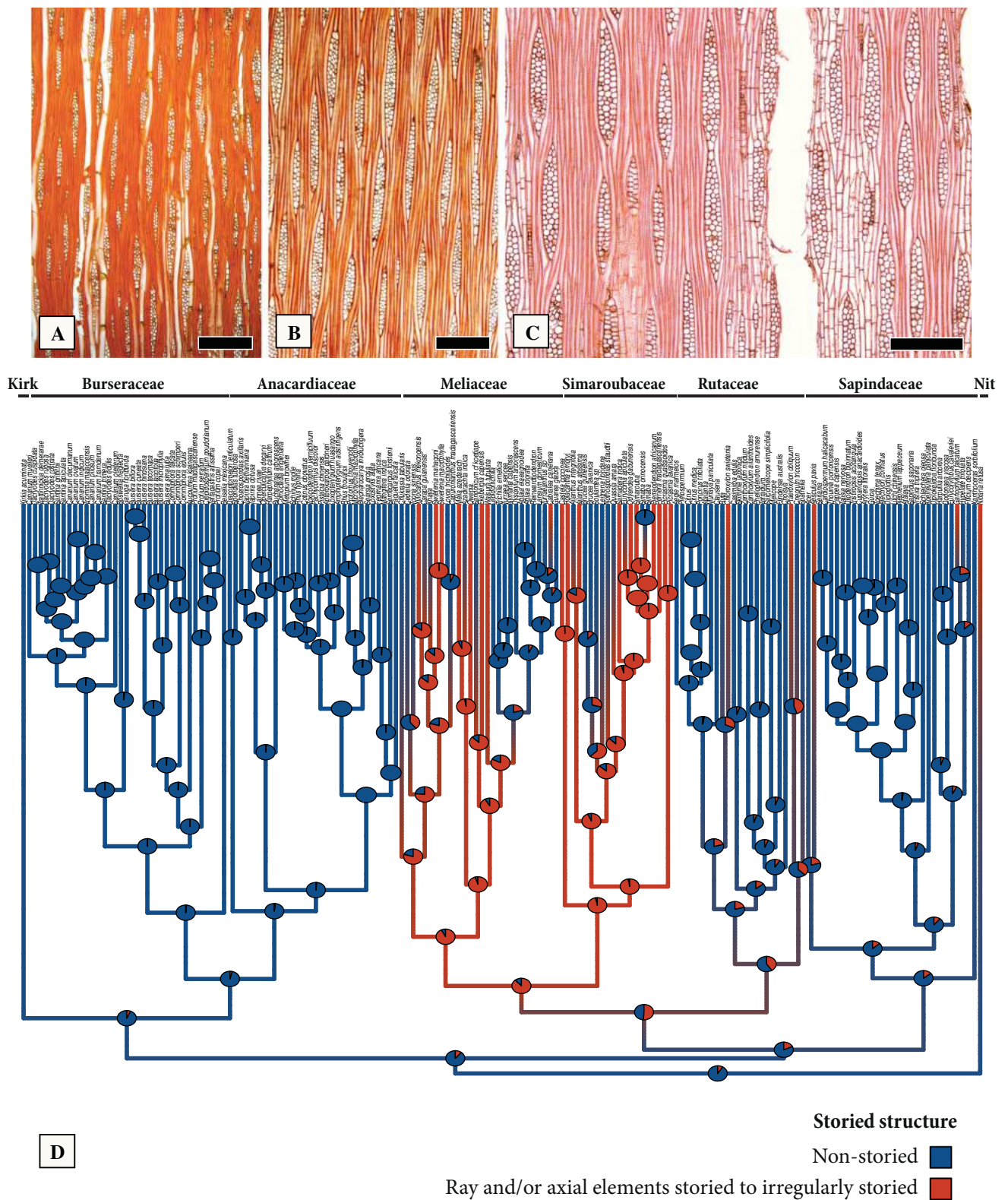


Fig. 15 Storied structure diversity and evolution in Sapindales. **a-c.** Longitudinal tangential sections. **a** *Zanthoxylum caribaeum* Lam. (Rutaceae), storied structure absent. **b** *Swietenia macrophylla* King. (Meliaceae), rays irregularly storied. **c** *Simarouba glauca* DC. (Simaroubaceae), rays and axial parenchyma storied. **d** Ancestral character state estimation of storied structure evolution. Scale bars: A-C = 300 μ m. Kirk = Kirkiaceae, Nit = Nitrariaceae

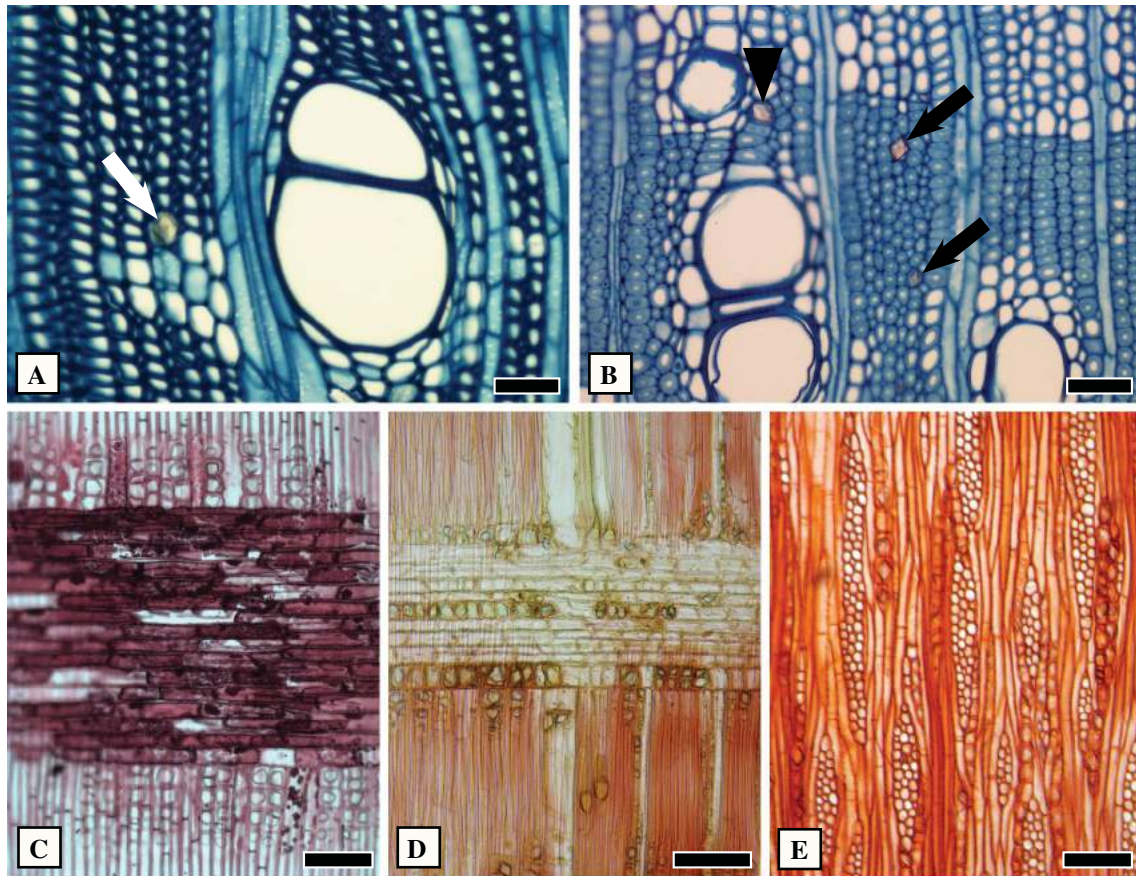


Fig. 16 Different crystal locations in the wood of Sapindales. **a** *Perriera madagascariensis* Courchet (Simaroubaceae), prismatic crystal in axial parenchyma cell (arrow). Transverse section (TS). **b** *Filicium decipiens* (Wight & Arn.) Thwaites (Sapindaceae), prismatic crystal in fibers (arrows) and in axial parenchyma (arrowhead). TS. **c** *Canarium indicum* L. (Burseraceae), prismatic crystals exclusively in chambered upright marginal ray cells, as seen in longitudinal radial section (LR). **d** *Zanthoxylum caribaeum* Lam. (Rutaceae), prismatic crystals in ray body and marginal cells and also in axial parenchyma cells. LR. **e** *Citrus medica* L. (Rutaceae), prismatic crystals in enlarged axial parenchyma cells, as seen in longitudinal tangential section. Scale bars: A–B = 50 µm; C, E = 100 µm; D = 200 µm

2001), and larger pits are expected to have larger pit chambers which allow more deflection, being therefore considered less safe than those which are small (Choat et al. 2003; Jansen et al. 2009). Most of the families in Sapindales have small intervessel pits, except for Anacardiaceae, Burseraceae and Kirkiaceae, where the pits are wide (> 10 µm). Nevertheless, these are also the only families in the order which have maintained the plesiomorphic character of large vessel-ray pits (half-bordered pits), which are known to allow more water influx through the rays and can potentially protect the vascular system by mobilizing water from other wood cell types into the vessels (Salleo et al. 2009; Nardini et al. 2011; Patrick 2013; Pfautsch et al. 2015). Therefore, we hypothesize that larger intervessel pits may indicate an advantage for water transport, but a higher risk of embolism to species of the clade Anacardiaceae–Burseraceae–Kirkiaceae, and the large vessel-ray pits of these families may counterbalance it. In fact, there is evidence of lower hydraulic safety in Anacardiaceae and Burseraceae species compared to Sapindaceae

species (Savi et al. 2018; Kiorapostolou et al. 2019; Oliveira et al. 2019). More detailed studies exploring the features of the intervessel and vessel-ray pits, including thickness and porosity of pit membrane, in these families together with physiological experiments are required to test these hypotheses. The rest of the Sapindales has evolved smaller intervessel pits and vessel-ray pits similar to intervessel pits, more axial parenchyma, evidencing a different route from the ancestral state, which again may have to do with different strategies (tissue combinations) to face similar selective pressures (Marks and Lechowicz 2006; Gerolamo et al. 2020).

Ray width, height, composition and storied structure—In Sapindales, the ray composition is predominantly heterocellular with one marginal row of upright/square cells, except in Burseraceae where rays heterocellular with multiple upright to square cells in marginal rows predominate. Similarly, Sapindaceae have half of the species sampled with heterocellular rays with many marginal rows of upright to square

Presence of crystals in the Sapindales

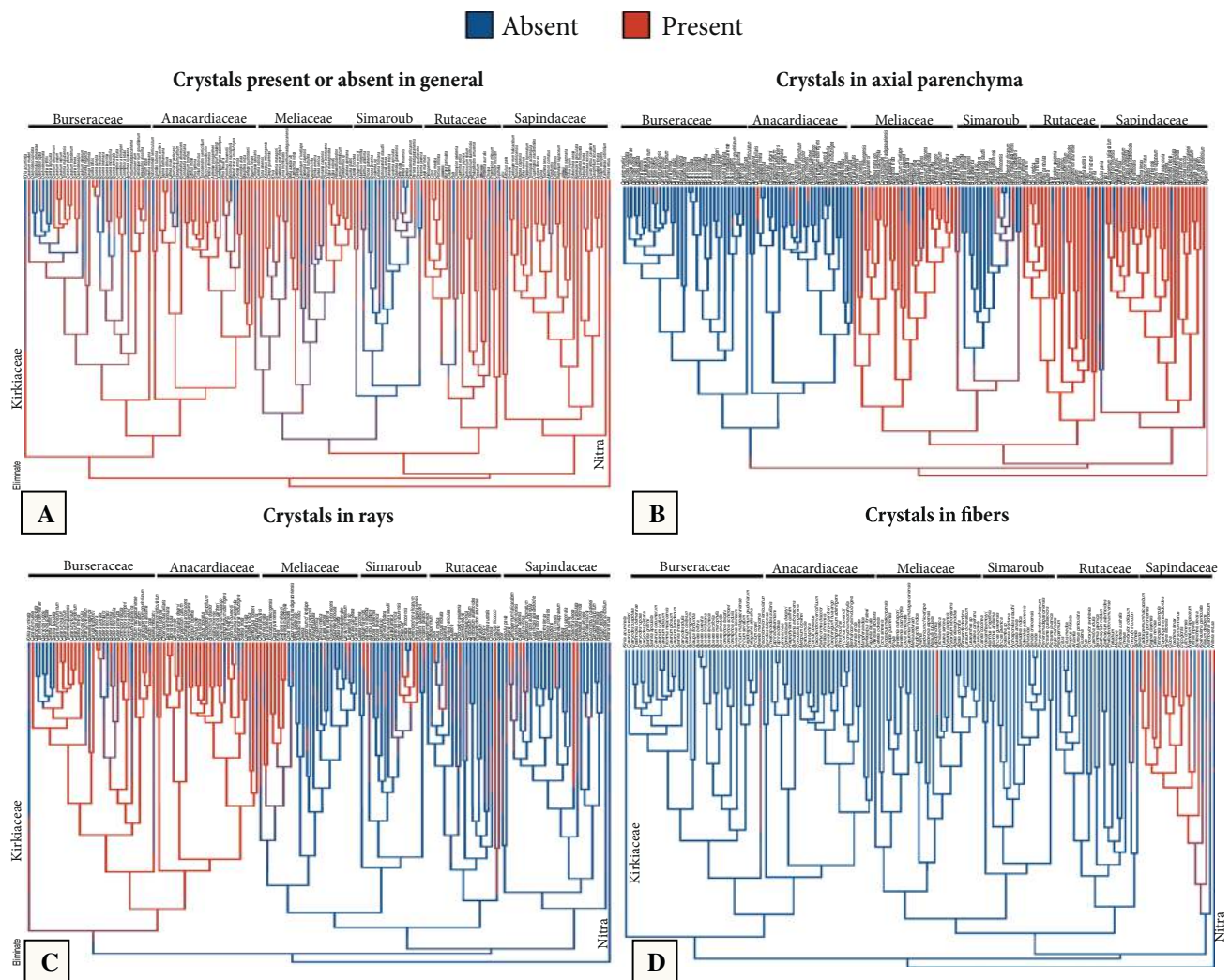


Fig. 17 Ancestral state estimation of crystals in Sapindales. **a** Crystals in general, independently on their location within the wood. **b** Crystals in axial parenchyma. **c** Crystals in rays. **d** Crystals in fibers. Simaroub = Simaroubaceae, Nitra = Nitrariaceae

cells. Homocellular rays are rare in the order, being more common in specific lineages of Rutaceae and Sapindaceae, such as *Acer*, *Cupania* (Sapindaceae), and *Casimiroa* La Llave (Rutaceae), showing an evolution from heterocellular to homocellular rays, similarly to what is seen in some distantly related lineages, such as Bignoniaceae (Pace and Angyalossy 2013; Pace et al. 2015). Studies on the origin of different cell shapes in ray composition indicate that a hormonal balance of auxin (axially transported) and ethylene (radially transported) forms a gradient responsible for the differentiation of either procumbent, square or upright cell morphologies in the ray cells (Lev-Yadun and Aloni 1991, 1995). This same balance seems to be involved in the width, height and spacing of the rays in the wood tissue (Lev-Yadun and Aloni 1991, 1995). The shapes of the cells are thought

to be related to their function, with body cells tending to be procumbent, favoring a radial distribution of sap, while the marginal cells, commonly upright or square, would promote the distribution of what is being transported by the body to their contacting cells (Lev-Yadun and Aloni 1991; Carlquist 2001). In fact, in some taxa the vessel-ray pits may even be restricted to the ray marginal rows, as in *Aesculus hippocastanum* L. (Sapindaceae), *Salix* L. and *Populus* L. (Salicaceae) (IAWA Committee, 1989). While we have this preliminary understanding on what causes different ray morphologies, there are still many questions on why such a huge diversity of ray compositions exists or has been differentially selected.

In Sapindales, the rays are predominantly uni to 4-seriate, but wider rays have evolved multiple times in the family, being especially common in the Simaroubaceae. Rays act

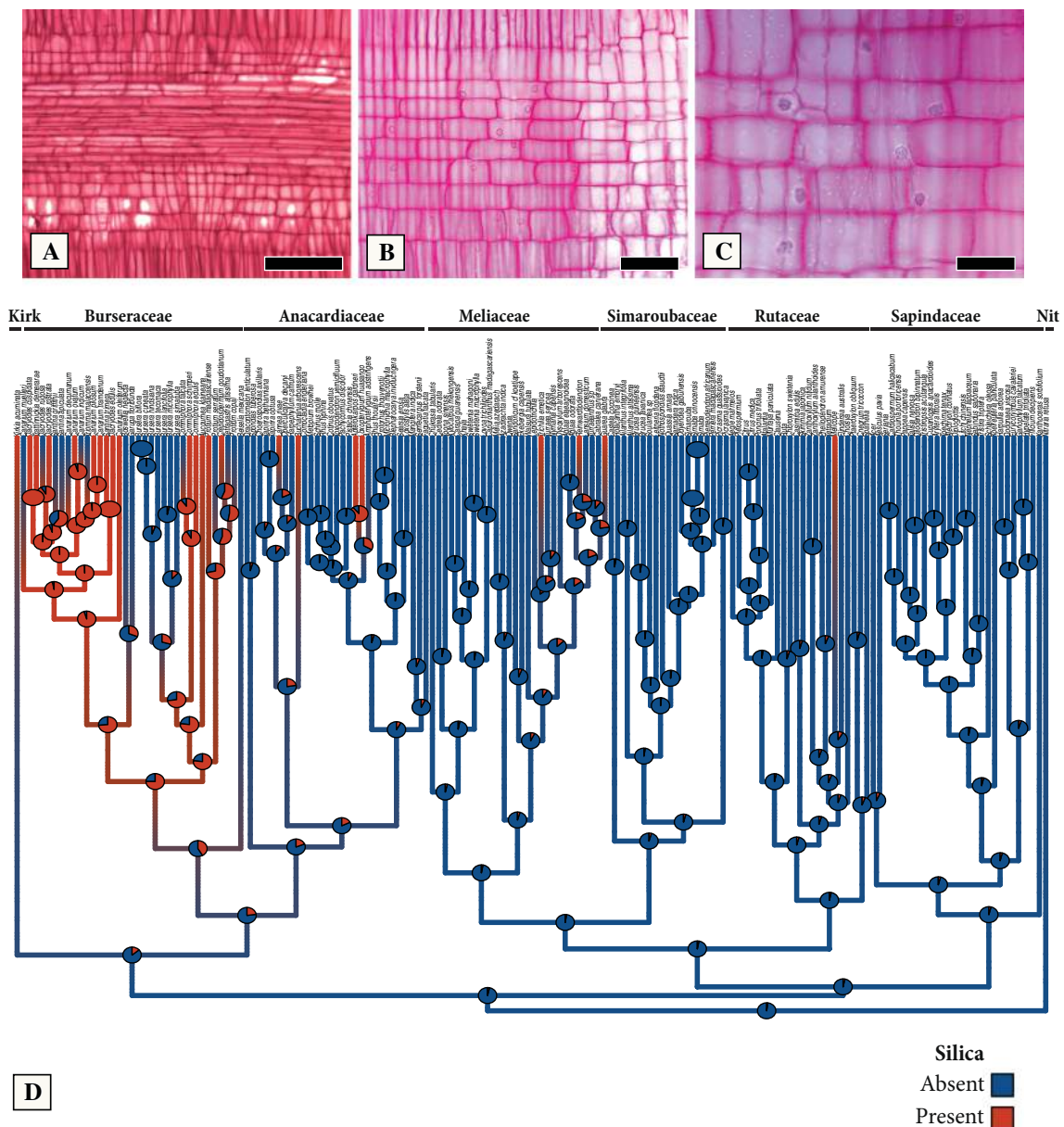


Fig. 18 Presence of silica bodies and their evolution in Sapindales. **a** *Toona* sp. (Meliaceae), rays devoid of silica bodies. **b-c** *Anacardium giganteum* Hancock ex Engl. (Anacardiaceae). **b** Silica bodies in ray cells. **c** Detail of the silica bodies in ray cells. **d** Ancestral character state estimation of silica bodies in Sapindaceae. Scale bars: A = 200 μ m; B = 100 μ m; C = 50 μ m. Kirk = Kirkiaceae, Nit = Nitrariaceae

as storage tissues for both water and nonstructural carbohydrates, and are known to be the most important cells connecting phloem and xylem, with numerous studies experimentally showing the constant exchange undergone between both tissues (Chattaway 1951; Van Bel 1990; Lev-Yadun & Aloni 1991, 1995; Pfautsch et al. 2015; Salomón et al. 2017; Stupianek et al. 2021). Surprisingly, in spite of their importance, studies investigating the connection between ray anatomical diversity and radial conductive efficiency are few (Pfautsch et al. 2015; Morris et al. 2016; Salomón et al. 2017; Pereira and Ribeiro 2018). In addition to their

role in radial conduction, it is known that ray width and height have also a role in biomechanics, with plants of wide and high rays being more flexible, and therefore explaining the more common presence of these two feature combinations in lianas (Fisher and Ewers 1989; Mattheck and Kubler 1995; Burgert and Eckstein 2001; Reiterer et al. 2002a, b; Angyalossy et al. 2012, 2015; Gerolamo and Angyalossy 2017; Gerolamo et al. 2020). In experimental studies, rays also took a pivotal role in injury repair by compartmentalization (Armstrong et al. 1981; Shigo 1984; Fisher and Ewers 1989).

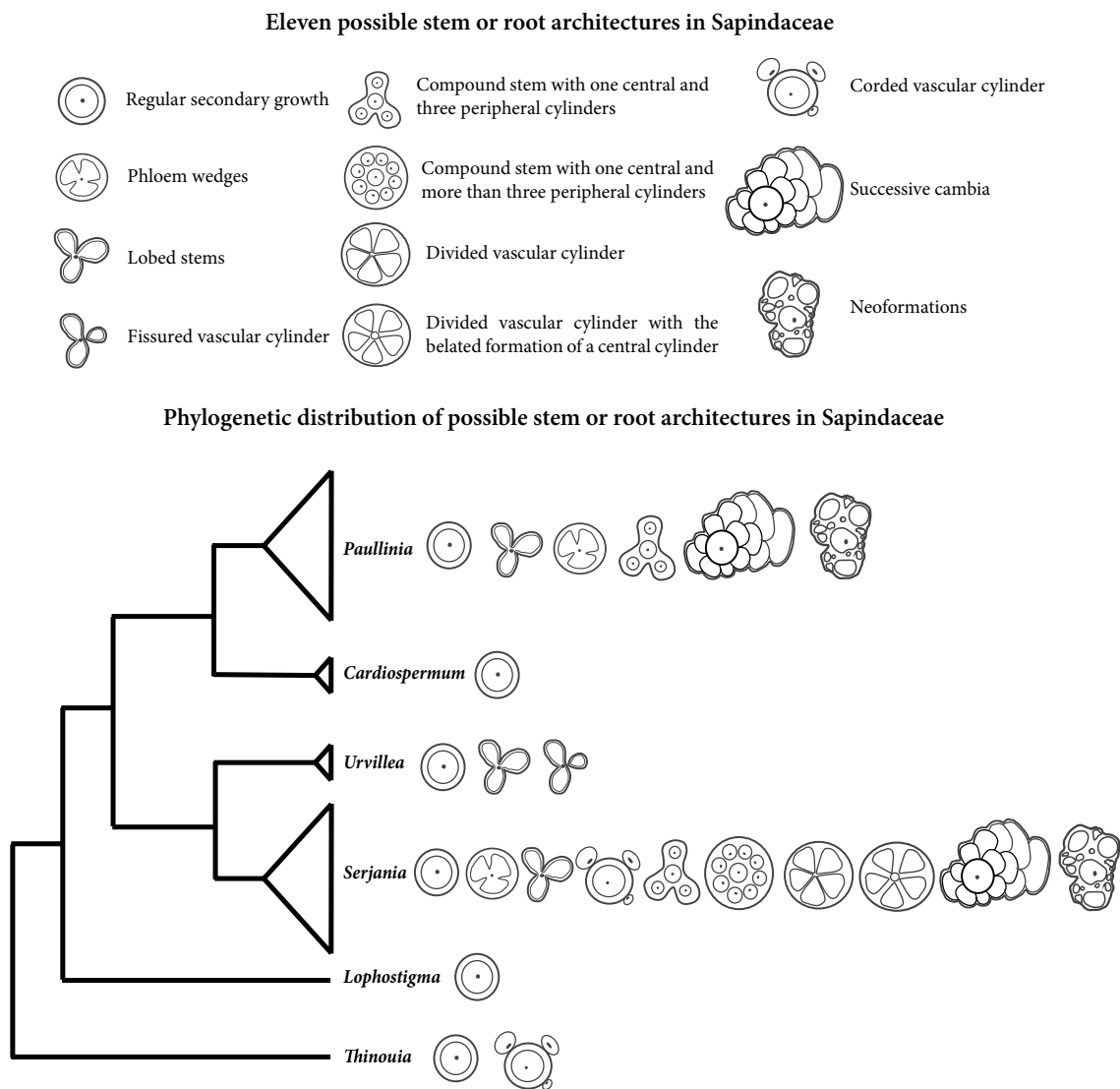


Fig. 19 Eleven different final stem or root architectures described to date in Sapindaceae, one regular and ten different types of cambial or pro-cambial variants. Inspired and updated from Bastos et al. (2016), with authorizations. Phylogeny topology based on Chery et al. (2019)

Ray width, height and composition seem to have no relation to their climatic or geographic occurrence, being more related either to phylogenetic relationships or habits. For instance, several shrubs or secondarily woody species either lack rays or have rays with mostly upright and square cells, while lianas typically have wider, higher rays, and heterocellular mixed rays (Barghoorn 1941b; Baas and Schweingruber 1987; Lev-Yadun and Aloni 1995; Angyalossy et al. 2012, 2015; Carlquist 2013; Lens et al. 2013; Morris et al. 2016, 2018). Carlquist (2001) proposed that upright cells would favor the vertical rather than the radial distribution of water in narrow stems, explaining their predominant occurrence in shrubs and lianas, and as the early stages in ray ontogeny while the stems are still narrow (Barghoorn 1940, 1941a). In fact, in our study we found the lianas to have

the heterocellular mixed ray compositions, but we found no association between different ray compositions and their provenance; therefore, this trait is likely best explained by phylogenetic relatedness and/or growth habits.

In Sapindales, when a storied structure is present, it is present in both the axial and radial elements, ranging from irregularly storied, such as in *Entandrophragma* and *Swietenia* (Meliaceae) to perfectly storied, with even the fibers storied, such as in *Quassia* L. (Simaroubaceae). Histologically, the storied structure derives from perfectly transverse divisions of the cambial initials (not pseudo-transverse or inclined), with little to no intrusive growth, and the initials are typically short and with abruptly tapering ends (Bailey 1923; Carlquist 1961; Philipson et al. 1971; Larson 1994). While it is more common that the axial elements are short

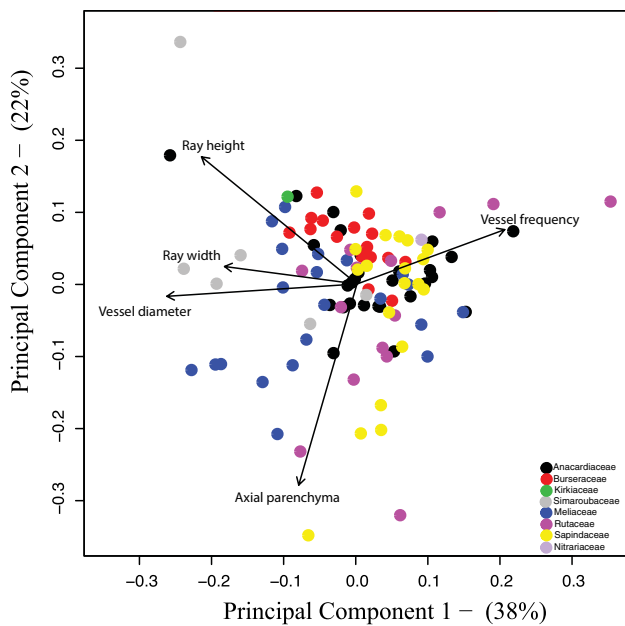


Fig. 20 Principal component analysis of anatomical features of the wood stem in 107 Sapindales species. The first two main components explain 60% of the variation in the data (in parentheses represents the proportion of variance of each principal component). Different colors represent wood stem from different Sapindales families (Anacardiaceae 37 species, Burseraceae 17 species, Kirkiaceae 1 specie, Simaroubaceae 8 species, Meliaceae 23 species, Rutaceae 20 species and Nitrariaceae 1 specie). For more details on anatomical characteristics, see Tables 2 and 3

and the rays homocellular in plants with a storied structure, that is not the case in the Sapindales, which can have a storied structure and relatively long initials (*Swietenia* has axial parenchyma cells with up to 8 cells per strand), and heterocellular rays. Storied structures are exclusive of the angiosperms, but within them they have evolved multiple times independently, in magnoliids (Aristolochiaceae and Piperaceae), rosids (Leguminosae, Malvales and Sapindales) and asterids (Asteraceae and Bignoniaceae) (Record 1919; Bailey 1923; Carlquist 1993, 2001; Pace et al. 2015; Trueba et al. 2015). Functionally it is not clear why some woods are storied, and to date there is no relation to other functional traits, geographic occupations, plant habits, plant stature or physical properties. A storied structure seems therefore to be more related to phylogeny than ecology, physiology or biomechanics. More studies exploring these relationships can help us better understand the possible causes of this pattern.

Heartwood – The presence of a distinctive heartwood versus sapwood is common in numerous Sapindales, and the different colors and durability their heartwoods can attain are the reason why many are so prized in the timber market. It is known that a myriad of secondary metabolites, also known as extractives, make the heartwood more resistant to

fungal decay, termites, and other wood-borers, and are composed of a mixture of substances such as polyphenols, resins and gums which are species-specific (Hillis 1968, 1987; Bamber 1976; Kampe and Magel 2013; Spicer 2005). The transition from sapwood to heartwood is known to be a complex process, involving the living cells of wood and sometimes even pith parenchyma cells, which completely relocate the starch and other sugars, sometimes projecting their walls to the interior of vessels forming tyloses through the half-bordered pits (vessel-parenchyma pits), and sometimes depositing substances such as resins or gums before undergoing cell death (von Alten 1909; Chattaway 1949, 1952a, b; Fahn and Arnon 1963; Hillis 1968; Nakaba et al. 2012; Spicer 2005). Tyloses are more common in heartwood, but can they can also be formed in scattered embolized vessels of the sapwood (Zimmermann 1979; De Micco et al. 2016). These different components completely block the no-longer conducting vessels before the parenchyma cells undergo cell-death, and impregnate the entire tissue (Spicer 2005).

Within the Sapindales, two opposing strategies seem to have evolved: the clade Anacardiaceae-Burseraceae-Kirkiaceae evolved tyloses (rarely co-occurring with gums, such as in *Comocladia* and *Metopium*, Anacardiaceae), while the rest of the family has maintained the plesiomorphic condition of having gums/ gum-like substances obstructing the heartwood vessels. Gums (polysaccharides) is a jargon-name in wood forestry and wood anatomy to all brown deposits that occlude the vessels and other cells (IAWA Committee 1989). However, these deposits may be either gums or resins (lipophilic substances), or even a combination of both (Hillis 1987; Spicer 2005). Specific histochemical tests or extractions are needed to unravel the nature of these deposits (Hillis 1987; Spicer 2005).

It has been suggested in the literature, with compelling evidences, that tyloses are only possible when vessel-ray pits or the pit apertures are wide (von Alten 1909; Chattaway 1949; Bonsen and Kučera 1990). While this seems to hold true for numerous taxa, there are a few exceptions, where plants with narrow vessel-ray pits form thin-walled tyloses, such as in a number of Oleaceae such as *Fraxinus* L., *Haenianthus* Griseb, *Ligustrum* L. and *Syringa* L. (Baas et al. 1988). In the Sapindales, the evolution of large vessel-ray pits and tyloses occurred once in Anacardiaceae-Burseraceae-Kirkiaceae, therefore the Pagel 94 inference that these characters evolved in a correlated fashion is to be considered with caution (Maddison and FritzJohn 2015). A broader study within the angiosperms, which accounts for multiple independent transitions of vessel-ray pitting size and the presence/absence of tyloses is necessary to test Chattaway's hypothesis correlating vessel-ray pits width with type of vessel occlusion.

The explanation to why wide enough pits would be needed stands in the fact that there would be a minimum

width necessary to allow the only nonlignified part of the wood parenchyma cells, the pit membrane, to intrude and expand within the vessels (Chattaway 1949; De Micco et al. 2016). After this expansion, the cell wall typically undergoes secondary wall deposition and lignification (Chattaway 1949; De Micco et al. 2016). This secondary wall deposition in some cases can be extreme, forming very thick, multilayered, lignified walls, also known as sclerotic tyloses, as the ones encountered in *Myracrodruon* and *Schinopsis* Engl. (Anacardiaceae), which in addition to the sclerotic tyloses had commonly also prismatic crystal within these tyloses (Terrazas 1999), making its wood extremely dense. The majority of the woods studied here were from heartwood, but for the cases where no tyloses were recorded in our sampling of Anacardiaceae-Burseraceae-Kirkiaceae, we recommend inspecting additional samples to verify the real absence of tyloses, which are known to be less-frequent, although sometimes present, in sapwood (IAWA Committee 1989; De Micco et al. 2016).

Secretory structures—Secretory structures are abundant in the order Sapindales (Solereider 1908; Melcalfe and Chalk 1950; Tölke et al. 2021) and are also present in their woods. Phenolic contents within axial parenchyma, fibers and rays are present in virtually all species (Terrazas and Wendt 1995; Tölke et al. 2021), being sometimes especially abundant in some woods such as those of *Cupania* (Sapindaceae), where all the fibers and parenchyma cells are filled with phenolic contents, even in sapwood (Fig. 1b). In addition to these cells, two specialized types of secretory structures were found in Sapindales woods: radial ducts in the clade Anacardiaceae-Burseraceae, and traumatic ducts in the clade formed by Meliaceae-Simaroubaceae-Rutaceae.

The presence of radial ducts was reconstructed as ancestrally present in Anacardiaceae-Burseraceae, but lost multiple times in different clades, corroborating previous suggestions (Terrazas 1999). The presence or absence of radial ducts is a very diagnostic character to the genus level within both Anacardiaceae and Burseraceae (Dong and Baas 1993; Terrazas 1999). Traditionally these ducts are said to produce gum (polysaccharides), but unless specific histochemical tests are performed, it is risky to make such statement. For instance, in *Tapirira* (Anacardiaceae) the ducts were shown to carry resins (lipophilic substances) (Terrazas and Wendt 1995). In addition, recent studies have shown that even in the same specimens of Sapindales, different duct systems can carry different secretions, either gums, gum-resins or resins (Tölke et al. 2021). It is well-known that the ducts are more widely distributed in the primary than in the secondary body (Solereider 1908; Weber 1936; Melcalfe and Chalk 1950; Nair et al. 1983; Babu et al. 1987; Tölke et al. 2021). For example, ducts are present in the Meliaceae and Simaroubaceae primary body (both cortex and primary phloem) (Jadin 1901; Weber 1936; Tölke et al. 2021), but

absent in their secondary body. It is also more common to have ducts in the secondary phloem than in the secondary xylem. In fact, axial and radial ducts are of common occurrence in Anacardiaceae and Burseraceae secondary phloem, while only radial ducts are present in the secondary xylem (Chattaway 1951; Fahn and Evert 1974). These radial canals are continuous between the secondary xylem and phloem, and were shown to also connect to the axial canals in the phloem (Chattaway 1951). The presence of radial ducts in the woods of Anacardiaceae and Burseraceae can be considered a synapomorphy of this clade and something that differentiates them from the Kirkiaceae, whose wood anatomy is otherwise very similar to them both.

The gum-resins produced by the cells of the ducts are believed to act as a defense mechanism, and their higher abundance in the external parts of the organs supports this scenario (Farrell et al. 1991; Pickard 2007). Ducts were also suggested as a key-innovation in vascular plants in general, with always a sensible higher number of species in the lineages with these secretory structures in comparison to their sister groups (Farrell et al. 1991). Our data support this proposal, with Anacardiaceae-Burseraceae, which have ducts, having altogether over 1600 species while their sister group Kirkiaceae, which lack them, with eight species (APweb Stevens 2001 onwards).

Traumatic axial ducts are not always present, since they are only formed when the specimens undergo an external stimulus. They were very common in the woods of the clade formed by Meliaceae-Rutaceae-Simaroubaceae. Regular ducts are present in the primary body of Meliaceae and Simaroubaceae, but absent in Rutaceae (Jadin 1901; Weber 1936; Tölke et al. 2021). However, Rutaceae have large cavities, which are similar to ducts by all means, except for the fact that ducts are more elongated than broad (Evert 2006). Here we consider that the axial traumatic structures we found are ducts in all the three families, but we are aware that the difference within the wood may be subtle and more quantitative than qualitative, and that some of these secretory spaces may resemble more a cavity than a duct in specific cases. Traumatic axial ducts are rather asymmetrical and can form either a localized or a continuous band across one entire growth ring (Babu et al. 1987; Dünisch and Baas 2006), differentiating exclusively from the fusiform initials, with the rays remaining unaltered (Weber 1936; Babu et al. 1987; Rajput et al. 2005). Ontogenetically, the wood traumatic ducts are schizolysigenous, with a constant turn-over on the epithelial cells that line them, with cells dying and being embedded within the gum/resin, consuming the tissue and making it very common that two adjacent ducts merge, something evidenced by dead cell remnants amid the gum/resin within the ducts (Nair et al. 1983; Babu et al. 1987; Larson 1994; Rajput et al. 2005; check Fig. 12b).

Many things can trigger the traumatic ducts, such as fires, fungi, insects and ever stress-induced fast growing in artificial plantations, either directly to the secondary body or to the primary body of the plants. In commercial plantations of mahogany (*Swietenia*), African mahogany (*Khaya ivorensis* A.Chev.) and Spanish cedars (*Cedrela*), attacks of *Hypsipyla* spp. larvae (Lepidoptera) to apical meristems caused long traumatic ducts to the wood (Dünisch et al. 2002; Dünisch and Baas 2006; Rinne et al. 2011). It was shown that when the injury is inflicted to the primary body, a continuous collection of concentric traumatic ducts is formed across the entire cambium cylinder, and when the damage is localized to the cambium in the secondary body, the ducts are formed only locally (Dünisch and Baas 2006). Because the ducts differentiate within parenchyma bands, infra-annual growth rings can be frequently recognized after these injuries by the formation of extra marginal parenchyma bands. More investigations are needed to unravel if clades that lost traumatic ducts are those in which axial parenchyma became scanty, since axial ducts are formed within the axial parenchyma. Because traumatic ducts are not constitutive, but dependent on an external stimulus, our reconstruction undoubtedly underestimates the occurrence of this character, with its formation after injury being likely a synapomorphy of this large clade, a statement supported by the numerous records of traumatic ducts in Meliaceae-Simaroubaceae-Rutaceae (check InsideWood; Gedalovich and Fahn 1985; Babu et al. 1987; Rajput et al. 2005).

Cell inclusions (crystals and silica bodies) – Prismatic crystals are ubiquitous in Sapindales, with the exception of Kirkiaceae and some species of the Simaroubaceae, and are estimated to be the ancestral state of the order. Other crystals shapes have not been encountered in our sampling of Sapindales, but druses have been found in enlarged axial parenchyma cells of several Chinese and Indian *Rhus* species (Anacardiaceae; Dong and Baas 1993; Agarwal and Gupta 2008) in *Castela coccinea* (Simaroubaceae; Campagna et al. 2017) and in rays and axial parenchyma of *Toona ciliata* M.Roem (Meliaceae; Negi et al. 2003). Their localization is variable, with crystals predominantly in rays in Anacardiaceae-Burseraceae and predominantly in axial parenchyma in Meliaceae, Rutaceae, Sapindaceae. The Sapindaceae and Nitrariaceae, in addition, commonly have crystals in fibers, which are sometimes also present in Meliaceae (Negi et al. 2003). In addition to crystals, we identified the presence of silica bodies predominantly in Burseraceae (except in the *Bursera* clade) and Kirkiaceae, with some species of Anacardiaceae, Meliaceae and Rutaceae also showing this character. Previous evidence for the presence of crystals and silica bodies for some of these species was found (Petrucci 1903; Chattaway 1955; Scurfield et al. 1973; Ter Welle 1976). However, individuals of the same species may or may not

have these characters in the xylem (Petrucci 1903) or they were simply not observed in the histological sections. The presence of crystals has been related to a product of plant metabolism, associated with genetic control and is widely present in flowering plants (Chattaway 1955; Prychid and Rudall 1999; Franceschi et al. 1980, 2005). Thus, depending on the species and environmental conditions, the individual may or may not produce these structures, helping to store micronutrients or defend against herbivory (Franceschi et al. 1980, 2005). Therefore, despite not having a clear taxonomic relationship or with geographical conditions, the location and presence of crystals and silica bodies in the Sapindales xylem helps taxon identification and intrafamilial groupings (Appelhans et al. 2012).

Evolution of lianas, lianescent wood anatomy and cambial variants—Lianas have evolved solely in two families of Sapindales: Anacardiaceae and Sapindaceae. Within Anacardiaceae, the lianescent habit has evolved at least twice once in the monotypic *Attilaea* and once in *Toxicodendron* (Martínez and Ramos Álvarez 2007; Acevedo-Rodríguez et al. 2015 onwards). *Toxicodendron* is a disjunct genus of root climbers or shrubs/trees with species in North America and Asia, popularly known for causing extreme allergic reactions, which has given them the name of poison-ivies (Dong and Baas 1993; Nie et al. 2009; Acevedo-Rodríguez et al. 2015 onwards). The phylogenetic position of *Attilaea* is still unknown, but morphologically it is most similar to *Spondias* (Martínez and Ramos Álvarez 2007), which is distantly related to *Toxicodendron* (Weeks et al. 2014; Muellner-Riehl et al. 2016), and likely represents an independent evolution of the scandent habit. In terms of stem macromorphologies, all the lianas of Anacardiaceae lack cambial variants.

Within Sapindaceae, the scenario is different, with tendrillate lianas having evolved just once in the branch subtending the monophyletic tribe Paullinieae, which contains over 50% of the species in the Neotropics (Buerki et al. 2010, 2011; Acevedo-Rodríguez et al. 2017; Chery et al. 2019). The evolution of lianas in Sapindaceae was accompanied by an enormous morpho-anatomical diversification, especially in leaf partition, fruit and stem anatomies with a myriad of different, and mostly unique, cambial variants (Radlkofer 1886; Schenck 1893; Pfeiffer 1926; Johnson and Truscott 1956; van der Walt et al. 1973; Acevedo-Rodríguez 1988, 1993; Klaasen 1999; Araújo and Costa 2006; Tamaio and Angyalossy 2009; Tamaio and Somner 2010; Tamaio 2011; Bastos et al. 2016; Borniego and Cabanillas 2014; Acevedo-Rodríguez et al. 2017; Cunha Neto et al. 2018; Chery et al. 2019, 2020a).

Ten different types or subtypes of cambial variants have been described to Sapindaceae and only two genera in tribe Paullinieae lack cambial variants: *Cardiospermum* and *Lophostigma* Engl. & Prantl. (Acevedo 2015 onwards; Cunha Neto et al. 2018), while all others have at least one

of the 10 types. Cambial variant type is of ultimate importance to recognize species in Sapindaceae, commonly being present in the description of new species and opening taxonomic dichotomous keys (Acevedo-Rodríguez 1988; Ferrucci and Acevedo-Rodríguez 1997, 2005; Acevedo-Rodríguez and Somner 2001). It is interesting that seven of these 10 different cambial variants converge on cable-like macromorphology: multiple vascular cylinders making a single stem (Raldkofer 1886; Schenck 1893; Carlquist 2001; Angyalossy et al. 2015). This cable-like macromorphology is observed in the corded, neoformations, successive cambia, divided (with central cylinder), and compound types.

Unlike most types of cambial variants, which have evolved multiple times across vascular plants (Angyalossy et al. 2012, 2015), the compound stems and divided vascular cylinders evolved exclusively in Sapindaceae; both originate from an unusual distribution of the procambial strands in the primary body, which result in multiple secondary vascular cylinders in the adult stem (Schenck 1893; Araújo and Costa 2006; Tamaio and Angyalossy 2009; Chery et al. 2020a). Because what causes the different stem architecture in the majority of these lianas are the different architectures of the procambial strands in the primary body, some authors name these variants as “procambial variants”, instead of the most common term cambial variants (Lopes et al. 2017). Within Sapindaceae, compound stems have evolved multiple times, being present in both *Serjania* and *Paullinia* (Schenck 1893; Carlquist 2001), the two largest genera in the Paullinieae (Acevedo-Rodríguez et al. 2017). Compound stems in *Paullinia* typically reach 3–4 peripheral cylinders maximum; however, 3–8 are frequent within *Serjania* (i.e., *S. pyramidata* Radlk.) (Tamaio and Angyalossy 2009, 2011; Tamaio 2011; Acevedo-Rodríguez et al. 2015 onwards). In *Paullinia*, compound stems have evolved at least three times independently from an ancestor with regular stems (Chery et al. 2020a), evidencing an intricate scenario in the evolution of this complex stem architecture. Divided stems—with or without the formation of a central cylinder—are also unique to *Serjania* (Acevedo-Rodríguez et al. 2015 onwards; Araújo and Costa 2006; Rizzieri et al. 2021).

In addition to the compound stems, both *Paullinia* and *Serjania* share four other cambial variants: lobed stems, phloem wedges, successive cambia and neoformations (Cunha Neto et al. 2018; Pellissari et al. 2018). Phloem wedges and neoformations can be present in both stem and roots (Bastos et al. 2016) and is a phenomenon present also in other lianescent taxa, such as Bignoniaceae (Angyalossy et al. 2015) and Rubiaceae (Leal et al. 2020), and curiously it has never been recorded in trees, unlike most cambial variants. Neoformations are round, concentric additional vascular cylinders, which differentiate from re-differentiation of parenchyma cells nonconducting phloem parenchyma, or cortex, typically appearing in older stems and roots

and without a determinate number. Successive cambia are exclusive to the stems (Bastos et al. 2016) and is present in *Serjania pernambucensis*, where the successive cambia are continuous, and species of *Paullinia* section *Phygoptilium* Radlk., where the successive cambia have a crenate pattern (Cunha Neto et al. 2018).

Lobed stems are present in *Paullinia*, *Serjania* and *Urvillea* (Bastos et al. 2016; Cunha Neto et al. 2018; Chery et al. 2020a), while in *Urvillea* one or two lobes typically break up forming a fissured stem (Cunha Neto et al. 2018). Lobed stems constitute a common type of cambial variant present in trees, lianas and shrubs, which in lianas is thought to help the stems to anchor on the surface of other plants or objects, favoring stem climbing (Cabanillas and Hurrell 2012; Sperotto et al. 2020; Luna-Márquez et al. 2021), and not uncommonly is also accompanied by the formation of adventitious roots and spiny structures in climbers (Soffiatti and Rowe 2020; Luna-Marquez et al. 2021).

Another of the Sapindaceae cambial variants that results in a cable structure is the corded stem, which is present in most of the 10 species of genus *Thinouia*, and in *Serjania meridionalis* (Tamaio and Somner 2010; Borniego and Cabanillas 2014; Cunha Neto et al. 2018). They have been considered different from neoformations because a definite number of peripheral cylinders is formed (Tamaio and Somner 2010; Borniego and Cabanillas 2014); however, their ontogenies is similar and therefore they might be considered a subtype of ‘neoformations.’

Clearly, a broad analysis of the cambial variants in Paullinieae with a well-supported and thorough phylogeny of the tribe is critical to understand the origins of some of these complex cambial variants, the diversification of these macromorphologies and how they have impacted the diversification of this neotropical species-rich liana group.

In terms of the anatomy of the secondary xylem, the lianas of Anacardiaceae from the temperate regions (*Toxicodendron*) are unique for their ring-porosity, but otherwise they share the liana features we will discuss below. As for *Attilaea*, just one specimen had its stem anatomy studied, and from a species that is described as shrubby (the species vary from scandent tree to scandent shrub; Martínez and Ramos Álvarez 2007), and its wood features are not typical of lianas (Gómez 2009). More samples of the genus when it is actively climbing are necessary, because it is known that abrupt changes in liana anatomy occur from their self-supporting to their leaning or climbing phases (Gallenmüller et al. 2001; Ménard et al. 2009; Gerolamo et al. 2020). For the other aspects, the lianas of Anacardiaceae conform to the anatomy of the family, with tyloses common, scanty axial parenchyma, heterocellular rays and septate fibers. Tyloses are not common in tropical lianas, except in injury events, and no heartwood is present in them (Lima et al. 2010; Angyalossy et al. 2015; Gerolamo and Angyalossy

2017). However, this is apparently not the case for temperate lianas, which do have heartwood. Unlike *Toxicodendron*, *Attilaea* has radial ducts (Gómez 2009), further supporting its phylogenetic distance from the former.

Numerous studies have shown that the lianas converge to a very similar wood anatomy (Schenck 1893; Carlquist 1985; Angyalossy et al. 2012, 2015), considerably reducing the phylogenetic signal of wood characters when included in phylogenetic reconstruction analyses (Lens et al. 2008). This collection of common features has been coined “the lianescent vascular syndrome” (Angyalossy et al. 2015) and represents a remarkable case of convergent evolution expressed both in qualitative and quantitative traits (Angyalossy et al. 2015; Dias-Leme et al. 2021). The lianas of Sapindaceae follow this convergent evolution in many traits, such as the presence of vessel dimorphism, with wide vessels closely associated to narrow vessels, the narrow vessels commonly in radial chains, and wide, high, and heterocellular mixed rays (Tamaio et al. 2011; Pellissari et al. 2018; Chery et al. 2020b). Contrary to what has been suggested for the lianescent vascular syndrome, though, the lianas of Sapindaceae and Anacardiaceae have scanty axial parenchyma (Tamaio et al. 2011; Pellissari et al. 2018; Chery et al. 2020b), something also recorded in lianas of Bignoniaceae (Pace et al. 2009, 2015—except for the *Fridericia* and allies clade and *Dolichandra* Cham.), some Malpighiaceae (Amorim et al. 2017) and Rubiaceae (Leal et al. 2020), evidencing that not all lianas need to have the same expression of features, despite converging to a similar anatomy. Features of Paullinieae woods that have been preserved from the other Sapindaceae are the shared presence of septate fibers, parenchyma-like fibers in alternation to thick-walled fibers, and more rarely, crystals in fibers (Pellissari et al. 2018; Chery et al. 2020b). *Paullinia* in particular differs from other members of the tribe by having crystals in axial and ray parenchyma cells (Chery et al. 2020b). This diagnostic preserved suite of features recently allowed the assignation of a fossil wood root to tribe Paullinieae (Jud et al. 2021).

Potential synapomorphies of Sapindales major clades—The combination of the ancestral character state reconstructions of 21 variable characters and the PCA analysis for quantitative features allowed us to unravel a number of features unique to certain clades within Sapindales. Given the sampling of Muellner-Riehl et al. (2016), we will limit our exploration of unique diagnostic features (potential synapomorphies) to major clades of the Sapindales and their families, while deeper wood anatomical studies are recommended within each individual family of the order to better understand character evolution at the infra-familial level. Our character delimitation and reconstructions indicate that the characters we have delimited for the order will likely be also informative to lineages under the family level. In fact, recent works with Meliaceae and Rutaceae have

independently delimited and reconstructed similar characters to ours, showing their importance to support narrower clades within these families, such as narrow rays delimiting both the crown group of subfamily Melioideae (Amusa et al. 2020) and the clade *Ptaeroxylon-Cedrelopsis* Baill.—*Bottegoa* Chiov. of Rutaceae Spathelioideae (Appelhans et al. 2012); the loss of prismatic crystals supporting both Turraeeae of the Meliaceae (Amusa et al. 2020) and the clade *Sohnreyia* K.Krause -*Dictyoloma* A.Juss.—*Spathelia* L. of Rutaceae Spathelioideae (Appelhans et al. 2012).

Our character delimitation was based on variable characters, but when the characters were very rare for the order, such as scalariform or reticulate perforation plates, parenchyma-like fibers, druses, crystals in vessels, perforated ray cells, fibers with distinct bordered pits (fiber-tracheids), coalescent pit apertures, we did not reconstruct them, but that does not mean they are not important to either understand the phylogenetic relatedness of taxa at lower levels or their ecological strategies and niche occupation (Arenas-Flores et al. 2012). For instance, multiple perforation plates, either scalariform or reticulate, have been shown in the latewood of *Ailanthus altissima* (Simaroubaceae), in the shrub *Beiselia* (Burseraeae), in *Melicope ternata* J.R.Forst. & G.Forst. (Rutaceae), in *Billia* Peyr. (Sapindaceae, former Hippocastanaceae) (Forman et al. 1989; León 2006), nine genera of Anacardiaceae (check Terrazas 1999), among others, and were already suggested as systematically important at infra-familial levels (Terrazas 1999). However, these characters are virtually absent in the bulk of Sapindales and therefore were not further investigated.

We summarized the potential synapomorphies of major Sapindales clades in Table 4. Many of the features that emerged here as diagnostic/synapomorphic of clades are intuitively known by experienced wood anatomists, especially those that are dedicated to wood identification (Record and Hess 1972; Mainieri et al. 1983; Barajas-Morales and Gómez 1989; Barajas-Morales et al. 1997; León 2006, 2013). Other synapomorphies were less expected, such as the presence of tyloses supporting the relationship of Kirkiaceae to Anacardiaceae-Burseraeae (*Kirkia* Oliv. was previously thought to be part of Simaroubaceae; Stannard 1980), crystals in fibers and helical thickenings as a synapomorphy of Sapindaceae, and traumatic ducts as a potential synapomorphy of Rutaceae-Simaroubaceae-Meliaceae. Crystals in fibers and helical thickenings were also seen in *Nitraria* (Nitrariaceae), but since we did not find them in the wood from slender samples we could gather from herbarium vouchers of *Peganum mexicanum*, we prefer to wait for additional analyses of this family.

In terms of quantitative features, we can see that more axial parenchyma distinguishes the Meliaceae, and some clades within the Rutaceae and Sapindaceae. Wider vessels are much more common in Meliaceae and Simaroubaceae.

Table 4 Potential wood anatomical synapomorphies of Sapindales major clades

Feature	Clade
Crystals in fibers	Sapindaceae
Crystals in rays	Anacardiaceae-Burseraceae
Helical thickenings	Sapindaceae
Intervessel pits small	Meliaceae-Rutaceae-Simaroubaceae; Nitrariaceae
Radial ducts/canals	Anacardiaceae-Burseraceae
Septate fibers	Anacardiaceae-Burseraceae-Kirkiaceae; core Sapindaceae
Axial parenchyma vasicentric to aliform	Meliaceae-Simaroubaceae; core Sapindaceae
Silica bodies	core Burseraceae
Storied structure	Meliaceae-Simaroubaceae; Nitrariaceae
Traumatic axial canals	possibly Meliaceae-Rutaceae-Simaroubaceae
Tyloses	Anacardiaceae-Burseraceae-Kirkiaceae
Vessels in radial rows	Rutaceae
Vessel-ray pits simple and wide	Anacardiaceae-Burseraceae-Kirkiaceae

Vessel diameter and frequency are at opposite spectra, the families with most frequent vessels being Anacardiaceae, Burseraceae, Nitrariaceae, Rutaceae and Sapindaceae, which also have the narrower vessels. Larger ray widths distinguish the Simaroubaceae and Meliaceae from Anacardiaceae, Burseraceae, Sapindaceae, Kirkiaceae and Rutaceae.

Wood is a complex tissue formed by a network of qualitative and quantitative characteristics, with many possible combinations of these characteristics. Thus, evolutionary novelties, genetic, hormonal and environmental aspects model the xylem causing some characteristics to be conserved and others altered. The result of this is the great wood diversity seen in Sapindales and woody plants in general.

In conclusion, with this broad phylogenetic study of the wood of Sapindales, we were able to unravel major transitions in the wood diversification of the order in the past 100+ million years of their history. The patterns of evolution here can largely be explained in terms of strategies to grow and survive during favorable and unfavorable conditions (amount of water available, temperature, day length) in the different environments where these taxa occur. We also raised important anatomical correlates with hydraulic efficiency versus safety in the occupation to either drier or temperate climates, protection against pathogens and injuries with secretory ducts and formation of a strong heartwoods invulnerable to most wood-borers with gums/gum-like inclusions or tyloses. Also, we were able to pinpoint major aspects of wood anatomy which still lack basic understanding of what is favoring their evolution, such as the evolution of storied structures and different ray compositions. The circumscription of the order post-APG has created a solid group in terms of wood anatomy, and with our reconstructions we were able to uncover 12 potential synapomorphies to support major clades. All information generated in this work opens avenues for future research and we believe that detailed studies within each of the nine

families of Sapindales are the next step to better understand wood diversification in the order.

Appendix 1

Studied species, authorship, family, source of wood data (book, website or wood collection). When from our own Institutions or personal slide collections includes collector, collector number, locality and place where voucher is deposited. Different specimens of the same species are separated by a semi-colon. Herbarium and wood collection acronyms follow the Index Herbariorum and Index Xylariorum, respectively (Thiers 2017). Klassen 1999 stands for his book on Anatomy of the Sapindaceae fully cited on references.

Acer amoenum Carr. (= *A. palmatum* Thunb.) (Sapindaceae), TWTw slide collection, several specimens analyzed online, Tsuba Wood Collection. *Acer negundo* subsp. *mexicanum* (DC.) Wesm. (Sapindaceae), MEXUw slide collection, FITECMA 67, Guridi Gómez, Mexico, Michoacán, Morelia, MEXU. *Actinocheita filicina* (DC.) F.A.Barkley (Anacardiaceae), MEXUw slide collection, Zendejas López 4594, Mexico, Guerrero, Eduardo Neri, Xochipala, MEXU. *Aesculus pavia* L. (Sapindaceae) InsideWood, Cerre 1367, Inst IWCS. *Aesculus hippocastanum* L. (Sapindaceae), InsideWood, FPAw 3635 J. Ilic CSIRO. *Aegle marmelos* (L.) Corrêa (Rutaceae), InsideWood, FPAw 11,332 Jugo Ilic CSIRO. *Aglaia elaeognoidea* (A.Juss.) Benth. (Meliaceae), InsideWood, AM 432 R. Aichbauer IWCS. *Aglaia odoratissima* Blume (Meliaceae), InsideWood, FPAw 28,972, Jugo Ilic. *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), Evert's slide collection; InsideWood, BWCw 8226 E. Wheeler NCSU; Uw 7286, 14,421 M. Bakker; WUE Studie 1–24 R. Aichbauer. *Ailanthus excelsa* Roxb. (Simaroubaceae), InsideWood, FPAw 3141 Jugo Ilic

- CSIRO; Uw 18,250 M. Bakker NBC; FHOw 245 E. Wheeler. *Ailanthus integrifolia* Lam. (Sapindaceae) InsideWood. Uw 18,250 M.E. Bakker NBC. *Alectryon connatum* (F.Muell.) Radlk. (Sapindaceae), Klaassen 1999. *Allophylus camptostachys* Radlk. (Sapindaceae), MEXUw slide collection, C. T. Refugio 310, Mexico, Veracruz, Reserva Biológica Los Tuxtlas, MEXU. *Amphipterygium adstrigens* (Schltdl.) Standl. (Anacardiaceae), Orduño s.n. CHAPA, Terrazas's slide collection. *Anacardium giganteum* Hancock ex Engl. (Anacardiaceae), BCTw Angyalossy's slide collection, Brazil. *Apterokarpos gardneri* (Engl.) Rizzini (= *Loxopterygium gardneri* Engl.) (Anacardiaceae), Terraza's slide collection. *Arytera divaricata* F. Muell. (Sapindaceae), Klaassen 1999; InsideWood, Agarwal and Gupta (2008). Wood anatomy of Sapindales. Bishen Singh Mahendra Pal Singh, Dehra Dun, 172 pp.; Sosef M.S.M., Hong L.T. & Prawirohatmodjo S. (eds.) 1998. Plant Resources of South-East Asia. 5(3). Timber trees: Lesser-known timbers. Backhuys Publishers, Leiden. 859 pp. *Arytera littoralis* Blume (Sapindaceae) InsideWood, FPAw ngf.3771 J. Ilıc CSIRO; Uw 33,606 M.E. Bakker NBC. *Astronium graveolens* Jacq. (Anacardiaceae), MEXUw slide collection, I. Calzada 3114, INIREB-009, Mexico, Chiapas, Nuevo Jalisco, MEXU; C. León Gómez 91, Mexico, Jalisco, La Huerta, La Salinas, MEXU. *Astronium* sp. (Anacardiaceae), BCTw Angyalossy's slide collection, Brazil. *Atalantia monophylla* DC. (Rutaceae), InsideWood. *Atalaya hemiglaucula* (F.Muell.) F.Muell. ex Benth. (Sapindaceae), Klaassen 1999; InsideWood, FHOw 12,015 R. Klaassen NBC. *Aucoumea klaineana* Pierre (Burseraceae), InsideWood, Kw 15,749 A. Campbell & P. Gasson KEW; AM379 R. Aichbauer IWCS. *Azadirachta indica* A.Juss. (Meliaceae), InsideWood, Kw MPFSL 1974 P. Gasson KEW; Kw 21,963 A. Campbell & P. Gasson KEW; FRI.s.n. Aza.ind N. Boonchai FRI; FPAw d.132 J. Ilıc CSIRO. *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), BCTw Angyalossy's slide collection, Brazil. *Beiselia mexicana* Forman (Anacardiaceae) InsideWood, Forman L.L., P. E. Brandham M. M. Harley, Lawrence T.J. 1989. *Beiselia mexicana* (Burseraceae) and its affinities. Kew Bulletin 44:1–31. *Boswellia neglecta* S.Moore. (Burseraceae), Terraza's slide collection. *Blepharocarya involucrigera* F.Muell. (Anacardiaceae), Terrazas's slide collection. *Brucea guineensis* G. Don (Simaroubaceae), Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. *Brucea javanica* (L.) Merr. (Simaroubaceae), Ogata, K. & A. Kalat. 1997. Wood anatomy of some trees, shrubs and climbers in Brunei Darussalam. After-care Programme, Brunei Forestry Research Project Special Publication No. 3. Japan International Cooperation Agency (JICA) and Forestry Department, Ministry of Industry and Primary Resources, Brunei Darussalam. *Buchanania arborescens* (Blume) Blume. (Anacardiaceae), Jacobs 4764(L), Terrazas's slide collection. *Bursera biflora* (Rose) Standl. (Burseraceae), Terraza's slide collection. *Bursera copallifera* (Sessé & Moc. ex DC.) Bullock (Burseraceae) InsideWood. Bonilla LAMA, J. Barajas-Morales & P.T. Lezama, 2004. Anatomía de Maderas de México. Árboles y Arbustos del Matorral Xerófilo de Tehuacán. Publicaciones Especiales Del Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México. *Bursera cuneata* (Schltdl.) Engl. (Burseraceae), Terraza's slide collection. *Bursera excelsa* (Kunth) Engl. (Burseraceae), MEXUw slide collection, J. Barajas Morales 39, 139, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Bursera fagaroides* (Kunth) Engl. (Burseraceae), J. Barajas Morales 224, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Bursera heteresthes* Bullock (Burseraceae), MEXUw slide collection, J. Barajas Morales 126, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Bursera hindsiana* (Benth.) Engl. (Burseraceae), Terraza's slide collection. *Bursera instabilis* McVaugh & Rzed. (Burseraceae), MEXUw slide collection, J. Barajas Morales 24, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Bursera lancifolia* (Schltdl.) Engl. (Burseraceae), Terraza's slide collection. *Bursera linanoe* (La Llave) Rzed., Calderón & Medina (= *B. aloexylon* (Schiede ex Schltdl.) Engl.) (Burseraceae), MEXUw slide collection, M. Delgado s.n. *Bursera microphylla* A. Gray. (Burseraceae), Terraza's slide collection. *Bursera morelensis* Ramírez (Burseraceae), MEXUw slide collection, Abundiz Bonilla 813, Mexico, Puebla, Tehuacán, Carretera Teotitlan-Huautla, MEXU. *Bursera simaruba* (L.) Sarg. (= *B. arborea* (Rose) L.Riley) (Burseraceae), MEXUw slide collection, C. León Gómez s.n., Mexico, Veracruz, Atoyac, MEXU; J. Barajas Morales 266, Mexico, Veracruz, San Andrés Tuxtlas, Estación Biológicas los Tuxtlas, MEXU. *Bursera tecomaca* (Sessé & Moc. ex DC.) Standl. (Burseraceae), Terraza's slide collection. *Cabralea canjerana* (Vell.) Mart. (Meliaceae), InsideWood, RBHw 5935 H. Richter BFH.UH; Tw 9900 H. Beeckman RMCA; Uw 19,213 L.Y.T. Westra NBC; Uw 6396 NBC M. Bakker NBC. *Canarium decumanum* Gaertn. (Burseraceae), Terraza's slide collection. *Canarium indicum* L. (Burseraceae), Bw19, Terrazas's slide collection. *Canarium madagascariense* Engl. (Burseraceae), Smithsonian NMNH slide collection, CTFTW 16,278. *Canarium muelleri* F.M.Bailey (Burseraceae), Terraza's slide collection. *Canarium oleiferum* Bail. (Burseraceae) InsideWood. SJRW 14,707 S. Manchester FMNH. *Canarium ovatum* Engl. (Burseraceae), Terraza's slide collection. *Canarium pilosum* A. W. Benn. (Burseraceae), Terraza's slide collection. *Canarium tramdenum* C.D.Dai & Yakovlev (= *C. pimela* K.D.Koenig) (Burseraceae). *Capuronianthus mahafalensis* J. Leroy (Meliaceae), InsideWood, CTFTW 7423 P. Detiënné CIRAD. *Carapa guianensis* Aubl. (Meliaceae), BCTw Angyalossy's slide collection, Brazil;

- InsideWood, Cerre 0015 J-C Cerre IWCS, Cerre 1199 J-C Cerre IWCS; FPAw 65 J. Ilıc CSIRO; FPRI 41,172 P. Deti enne & R. Miller Tropen; HBw 299A R.C. Rivery; Tw 23,046 H. Beeckman RMCA; Uw 10,650 L.Y.T. Westra NBC; Uw 601, 7588, 11,462 A.M.W. Mennega NBC. *Cardiospermum halicacabum* L. (Sapindaceae), InsideWood, Rock, B.N. 1972. The woods and flora of the Florida Keys: "Pinnatae". Smithsonian Contrib. Bot. 5: 1–35. *Casimiroa calderoniae* F. Chiang & Medrano (Rutaceae), MEXUw slide collection, Abundiz Bonilla 821; Mexico, Puebla, Tehuac an, al SO de Coyotepec, MEXU. *Casimiroa edulis* La Llave (Rutaceae), InsideWood, Kribs DA. 1968. Commercial foreign woods of the American market. Dover Publications, NY. *Casimiroa tetrameria* Millsp. (Rutaceae), MEXUw slide collection, Enr iquez 7488, Mexico, Chiapas, Tuxtla Guti errez, Pishtimback, MEXU. *Castela coccinea* Griseb. (Simaroubaceae), InsideWood, M.N. Campagna, M. Gattuso, M.L. Martinez, M.V.Rodr iguez & O. Di Sapio. 2016. Novel micromorphological features of wood and bark of Argentinean Simaroubaceae, New Zealand Journal of Botany, 55:134–150. *Castela galapageia* Hook.f. (Simaroubaceae), InsideWood, OUCE. LTEL 7 J. Lee OU. *Cedrela fissilis* Vell. (Meliaceae), Angyalossy's slide collection, SPFW 838–841 and BOTUw 1417–1427, BOTU. *Cedrela odorata* L. (= *C. mexicana* M.Roem.) (Meliaceae), MEXUw slide collection, Carmona 18, Mexico, Chiapas, Crucero Bonampak, INIREB 33, 58, 330; F. Miranda 5366, Mexico, Chiapas; InsideWood, CTFTWw 16,493 P. Deti enne & R. Miller Tropen; FPAw 33,724 J. Ilıc CSIRO; MADw 21,261 P. Gasson KEW. *Cedrela salvadorensis* Standl. (Meliaceae), MEXUw slide collection, Abundiz Bonilla 811, Mexico, Puebla, Tehuac an, Carretera Teotitl an-Huautla, MEXU. *Cedrelopsis grevei* Baill. & Courchet (Meliaceae), Smithsonian NMNH slide collection, CTFTw 7436. *Chloroxylon faho* Capuron (Burseraceae) InsideWood, CTFTw 11,949 P. Detienne CIRAD. *Chloroxylon swietenia* DC. (Rutaceae), InsideWood, Cerre 75, 529, J-C Cerre IWCS; FPAw 11,355 J. Ilıc CSIRO; Tw 30,364 H. Beeckman RMCA; Uw 6453 M Bakker NBC. *Choerospondias axillaris* (Roxb.) B.L.Burt & A.W.Hill (Anacardiaceae), Tw47711, Terrazas's slide collection. *Choisya dumosa* (Torr. & A.Gray) A.Gray (= *C. dumosa* var. *mollis* (Standl.) L.D.Benson) (Rutaceae), InsideWood, E. Wheeler NCSU. *Chorilaena quercifolia* Endl. (Rutaceae), Carlquist S. 1977. Ecological factors in wood evolution: a floristic approach. Am J Bot 64: 887–896. *Chukrasia tabularis* A.Juss. (Meliaceae), InsideWood, FPAw 10,235 J. Ilıc CSIRO; FPAw 9123 J. Ilıc CSIRO; Kw 22,021 A. Campbell & P. Gasson KEW. *Citrus aurantiifolia* (Christm.) Swingle (= *C. x limettioides* Yu.Tanaka) (Rutaceae), MEXUw slide collection, L. Carmona 94, Mexico, Puebla, Pahuatl an, Pahuatl an de Valle, MEXU. *Citrus x aurantium* L. (Rutaceae), MEXUw slide collection, C. Le on G omez 97, Mexico, Veracruz, San Andr es Tuxtlas, Laguna Escondida, MEXU. *Citrus medica* L. (= *C. limetta* Risso) (Rutaceae), MEXUw slide collection, L. Carmona 56, Mexico, Puebla, Pahuatl an, Pahuatl an de Valle, MEXU. *Citrus sinensis* (L.) Osbeck (Rutaceae), MEXUw slide collection, L. Carmona 16,386, Mexico, Puebla, Pahuatl an, Pahuatl an de Valle, MEXU. *Clausena melioides* Hiern (Rutaceae), InsideWood, Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. *Cneorum tricoccon* L. (Rutaceae), Appelhans et al. 2021. Phylogenetic and ecological signals in the wood of Spathelioideae (Rutaceae). IAWA J 33: 337–353; Carlquist S. 1988. Wood anatomy of Cneoraceae: Ecology, relationships and generic definition. Aliso 12:7–16. *Commiphora boranensis* Vollesen (Burseraceae), Smithsonian NMNH slide collection, CTFTW 15,458. *Commiphora edulis* (Klotzsch) Engl. (Burseraceae), Terraza's slide collection. *Commiphora falcata* Capuron (Burseraceae), Terraza's slide collection. *Commiphora pervilleana* Engl. (Burseraceae), Smithsonian NMNH slide collection, CTFTW 8827. *Commiphora pterocarpa* H.Perrier (Burseraceae), Smithsonian NMNH slide collection, CTFTW 15,457. *Commiphora schimperi* (O.Bergman) Engl. (Burseraceae), Terraza's slide collection. *Comocladia macrophylla* (Hook. & Arn.) L.Riley (= *C. engleriana* Loes.) (Anacardiaceae), J. Barajas-Morales 237, Mexico, Jalisco, La Huerta, Estaci on de Biolog a de Chamela, MEXU. *Cotinus obovatus* Raf. (Anacardiaceae), MAD2159, Terrazas's slide collection. *Crepidospermum goudotianum* (Tul.) Triana & Planch. (Burseraceae), Terraza's slide collection. *Cupania dentata* Moc. & Sess e ex DC. (Sapindaceae), Klaassen 1999; MEXUw slide collection, s.n., in Mexico, San Luis Potos . *Cupania furfuracea* Radlk. (Sapindaceae), G. Somner 1653, Brazil, Rio de Janeiro, Po o das Antas, RBR. *Cupania glabra* Sw. (Sapindaceae) MEXUw slide collection, Ibarra Manriquez G. 1304 & 1594, in Mexico, Veracruz, Reserva Biol gica Los Tuxtlas, MEXU. *Cupania macrophylla* A. Rich. (= *Talisia macrophylla* (Mart.) Radlk.) (Sapindaceae), MEXUw slide collection, J.B. Morales 198, in Mexico, Veracruz, Reserva Biol gica Los Tuxtlas, MEXU. *Cupaniopsis anacardioides* (A.Rich.) Radlk. (Sapindaceae), Klaassen 1999. *Cyrtocarpa procera* Kunth (Anacardiaceae), Abundiz Bonilla 817, Mexico, Puebla, Tehuac an, Valle de Tehuac an, MEXU. *Dacryodes cuspidata* (Cuatrec.) Daly. (Burseraceae), Terraza's slide collection. *Dacryodes edulis* (G.Don) H.J.Lam (Burseraceae), InsideWood, FPAw GAB.14 J. Ilıc CSIRO; Tw1165 H. Beeckman RMCA. *Dacryodes rostrata* (Blume) H.J.Lam. (Burseraceae) InsideWood. D tienne, P. Woods of Laos, Cambodia, Vietnam. Unpublished. *Dacryodes rugosa* (Blume) H.J.Lam. (Burseraceae), Terraza's slide collection. *Dracontomelon dao* (Blanco) Merr. & Rolfe (Anacardiaceae), PUw446, Terrazas's slide collection. *Dilodendron bipinnatum* Radlk.

- (Sapindaceae), Klaassen 1999; InsideWood DMC95 R. Klaassen NBC. *Diploglottis australis* Radlk. (= *D. cunninghamii* (Hook.) Hook.f.) (Sapindaceae), Klaassen 1999; InsideWood, E. Wheeler, North Carolina State University. *Diplokeleba floribunda* N.E.Br. (Sapindaceae), InsideWood, Tortorelli L.A. 1956. Maderas y bosques argentinos. Editorial Acme, Buenos Aires. 910 pp. *Dodonaea viscosa* (L.) Jacq. (Sapindaceae), Klaassen 1999; InsideWood, FPAw ngf.5367 J. Ilic CSIRO; Hw 8833 S. Carlquist SBBG; Uw 33,600 M.E. Bakker NBC. *Dysoxylum arborescens* (Blume) Miq. (Meliaceae), Inside Wood, FPAw ngf. 3973 Jugo Ilic. *Ekebergia capensis* Sparrm. (Meliaceae), InsideWood, Kw 22,044 A. Campbell & P. Gasson KEW; Tw 13,018 H. Beekman NBC; Tw 33,812 H. Beekman NBC; SJRW 12,441 E. Wheeler NCSU. *Esenbeckia berlandieri* Baill. (Rutaceae), MEXUw slide collection, C. León Gómez 60, Mexico, Jalisco, La Huerta, Estación de Biología de Chamela, MEXU. *Esenbeckia pentaphylla* Griseb. (Rutaceae), MEXUw slide collection, Abundiz Bonilla 3673, Turrialba. *Eurycoma longifolia* Jack (Simaroubaceae), Webber I. 1936. Systematic anatomy of the Woods of the Simaroubaceae. Am J Bot. 23: 577–587. *Eurycorymbus cavaleriei* (H.Lév.) Rehder & Hand.-Mazz. (Sapindaceae), Klaassen 1999; InsideWood, Uw 33,602 R. Klaassen NBC. *Faguetia falcata* Marchand (Anacardiaceae), Smithsonian NMNH slide collection, CTFTW 13,870; FHO11584, Terrazas's slide collection. *Fegimanra africana* (Oliv.) Pierre (Anacardiaceae) InsideWood, Détienne P. West Africa Wood Coding. CIRAD, Unpublished. *Filicium decipiens* (Wight & Arn.) Thwaites (Sapindaceae), Smithsonian NMNH slide collection, CTFTW 9003. *Flindersia australis* R.Br. (Rutaceae), InsideWood, FPAw 2735 Jugo Ilic CSIRO. *Ganophyllum falcatum* Blume (Sapindaceae), Klaassen 1999. *Garuga floribunda* Decne. (Burseraceae), InsideWood, FPAw ngf.4017 J. Ilic CSIRO. *Gluta tourtour* Marchand (Anacardiaceae), Smithsonian NMNH slide collection, CTFTW 2251. *Guarea chichon* C. DC. (= *G. megantha* A.Juss.) (Meliaceae), MEXUw slide collection, V. Carmona 43, Mexico, Chiapas, Tila, MEXU; R. Cedillo 403, Mexico, Veracruz, San Andrés Tuxtlas, Estación Biológica los Tuxtles, MEXU. *Guarea glabra* Vahl (Meliaceae), MEXUw slide collection, J. Baraja-Morales 181, Mexico, Veracruz, Catemaco, Colonia Coronel Adalberto Tejeda, MEXU. *Guarea grandifolia* DC. (= *G. guidonia* (L.) Sleumer). (Meliaceae), Angyalossy's slide collection, Brazil. *Guioa bijuga* (Hiern) Radlk. (Sapindaceae), InsideWood, Ogata K. & A. Kalat. 1997. Wood anatomy of some trees, shrubs and climbers in Brunei Darussalam. After-care Programme, Brunei Forestry Research Project Special Publication No. 3. Japan International Cooperation Agency. (JICA) and Forestry Department, Ministry of Industry and Primary Resources, Brunei Darussalam. *Harpephyllum caffrum* Bernh. (Anacardiaceae), PFP930, Terrazas's slide collection. *Harpullia arborea* (Blanco) Radlk. (Sapindaceae), Klaassen 1999; InsideWood, FPAw ngf.6210 J. Ilic CSIRO; SFEw D7948 R. Klaassen NBC. *Helietta apiculata* Benth. (= *H. cuspidata* (Engl.) Chodat & Hassl.) (Rutaceae), BCTw, Angyalossy's slide collection, Brazil. *Helietta lucida* Brandegee (Rutaceae), MEXUw slide collection, Abundiz Bonilla 827, Mexico, Puebla, Tehuacán, al SO de Coyotepec, MEXU; J. Barajas Morales 483, Cuba, Matanzas, Escaleras de Jaruco, MEXU. *Holacantha emoryi* A. Gray (Simaroubaceae), Webber I. 1936. Systematic anatomy of the Woods of the Simaroubaceae. Am J Bot. 23: 577–587. *Hypelate trifoliata* Sw. (Sapindaceae), Klaassen 1999; InsideWood, Myatt 3715G26 R. Klaassen NBC, BWCw 8749 E. Wheeler NCSU, FPAw 8942 J. Ilic CSIRO. *Khaya anthotheca* (Welw.) C. DC. (Meliaceae), InsideWood, PFAw af.8 J. Ilic CSIRO; Kw 24,705 A. Campbell & P. Gasson KEW; Tw 606, 838, 950, 26,843 H. Beekman RMCA. *Khaya ivorensis* A.Chev. (Meliaceae), Angyalossy's wood collection, Nigeria, MADw 8679. *Khaya madagascariensis* Jum. & H.Perrier (Meliaceae), Smithsonian NMNH slide collection, CTFTw 7437. *Kirkia acuminata* Oliv. (Kirkiaceae), InsideWood, FHOw 3146, 4991 E. Wheeler NCSU; Tw 28,858 J. Parrott TXSU. *Kirkia leandrii* (Capuron) Stannard (Kirkiaceae), InsideWood, CRFTw 7879 P. Detienne CIRAD. *Kirkia wilmsii* Engl. (Kirkiaceae), InsideWood, Tervuren Xylarium Wood Database, Hans Beekman. Kromhout C.P. 1977. 'N Studie van die Houtanatomie van die Vernaamste Inheemse Houtsoorte van Suid-Afrika en 'N Sleutel vir Hul Mikroskopiese Uitkennig. Unpublished PhD Thesis, Universiteit van Stellenbosch. South Africa. *Koelreuteria paniculata* Laxm. (Sapindaceae), Klaassen 1999; InsideWood, FPAw 21,706 J. Ilic CSIRO; Lw.NewGuinea 2490 W E. Wheeler NCSU; PACw 744 E. Wheeler NCSU; WLw 2490 R. Klaassen NBC, WUR Studie 2 118 R. Archbauer IWCS. *Lannea rivae* Sacleux (Anacardiaceae), Terraza's slide collection. *Lansium domesticum* Corr. (= *L. parasiticum* (Osbeck) K.C.Sahni & Bennet) (Meliaceae), InsideWood, FPAw 18,592 J. Ilic CSIRO. *Leitneria floridana* Chapm. (Simaroubaceae), InsideWood, Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. *Lepidotrichilia convallariiodora* (Baill.) J.-F. Leroy (Meliaceae), InsideWood, CTFTw 9425 P. Detienne CIRAD. *Litchi chinensis* Sonn. (Sapindaceae), Klaassen 1999; InsideWood, Uw 33,587 Klaassen NBC. *Lovoa trichilioides* (Spreng.) Harms (Meliaceae), InsideWood, AM 425 R. Aichbauer IWCS; FPAw ni.10 J. Ilic CSIRO; Kw 22,155, 31,169 A. Campbell & P. Gasson KEW; Tw 708, 1033, 7120, 7467, 13,938, 26,496 H. Beekman RMCA; Uw 20,309 M. Bakker NBC. *Loxopterygium huasango* Spruce ex Engl. (Anacardiaceae), MER3383, Terrazas's slide collection. *Loxopterygium* sp. (Anacardiaceae) BCTw, Angyalossy's slide collection, Brazil. *Loxostylis alata* A.Spreng.

- ex **Rchb.** (Anacardiaceae) InsideWood, NYBT TT1004 E. Wheeler NCSU; Terrazas's slide collection. **Mangifera indica** L. (Anacardiaceae), InsideWood, Kw 14,386 A. Campbell & P. Gasson KEW; Puw 485 P. Gasson KEW; RBHw 10,408 H.G. Richter BFH.UH. **Melia azedarach** L. (Meliaceae), InsideWood, BWCw 8315 E. Wheeler NCSU; FHOw 4291 P. Gasson KEW; FPAw a. 116 J. Ilic CSIRO; Kw 22,158 A. Campbell & P. Gasson KEW; Uw 20,735, 20,737 M. Bakker NBC. **Melicope fatraina** (H.Perrier) T.G.Hartley (Rutaceae), InsideWood, CTFTw 3024 P. Deti  ne CIRAD. **Metopium brownei** (Jacq.) Urb. (Anacardiaceae), MEXUw slide collection, E. Mart  nez 30,351, Mexico, Campeche, Calakmul, MEXU; MAD14121, Terrazas's slide collection. **Micronychia macrophylla** H. Perrier (Anacardiaceae), Terraza's slide collection. **Micronychia tsiramiramy** H.Perrier (Anacardiaceae), CFTF13437, Terrazas's slide collection. **Mosquitoxylum jamaicense** Krug & Urb. (Anacardiaceae), MEXUw slide collection, I. Calzada 2919, Mexico, Chiapas, Velasco Su  rez, INIREB-28. **Murraya paniculata** (L.) Jack (Rutaceae), InsideWood, P. Deti  ne. Woods of Laos, Cambodia, Vietnam. **Myracrodruon urundeuva** Allem  o (Anacardiaceae), Angyalossy's slide collection, identified at Wood Collection from musical instrument in Brazil. **Neobeguea leandriana** J.-F. Leroy (Meliaceae), Smithsonian NMNH slide collection, CTFTw 7980. **Neobeguea mahafaliensis** J.-F. Leroy (Meliaceae), Smithsonian NMNH slide collection, CTFTw 7981. **Neotina coursii** Capuron (= *Tina coursii* (Capuron) Callm. & Buerki) (Sapindaceae), Klaassen 1999; Smithsonian NMNH slide collection, CTFTW 8812. **Neotina isoneura** (Radlk.) Capuron (Sapindaceae), Klaassen 1999; Smithsonian NMNH slide collection, CTFTW 13,290; **Nephelium lappaceum** L. (Sapindaceae), Klaassen 1999; InsideWood, Uw 33,591 R. Klaassen NBC. **Nitraria retusa** Asch. (Nitrariaceae) InsideWood. FWB Nit.ret P. Baas. **Nothospondias staudtii** Engl. (Simaroubaceae), InsideWood, D  tienne, P. West Africa Wood Coding. CIRAD. Unpublished. **Nymanina capensis** (Thunb.) Lindb. (Meliaceae), O. Amusa et al. 2020 Wood anatomy of South African Meliaceae: evolutionary and ecological implications. Bot J Linn Soc. **Odyendea gabunensis** (Pierre) Engl. (= *Quassia gabonensis* Pierre) (Simaroubaceae), InsideWood, Uw 9524 M. Bakker NBC. **Operculicarya decaryi** H.Perrier (Anacardiaceae) InsideWood. Detienne P. Woods of Madagascar. CIRAD, Unpublished. **Owenia cepiodora** F.Muell. (Meliaceae), InsideWood, FPAw 9669 J. Ilic CSIRO. **Pachycormus discolor** (Benth.) Coville (Anacardiaceae), US30922, Terrazas's slide collection. **Pappea capensis** Eckl. & Zeyh. (Sapindaceae), Klaassen 1999; InsideWood, FPAw 5137 R. Klaassen NBC; Malaisse 8629 R. Klaassen NBC. **Peganum mexicanum** A. Gray (Nitrariaceae), Guy Nesom 6604, Mexico, San Lu  s Potos  , Guadalc  zar. MEXU; J. I. Calzada 25,452, Mexico, San Lu  s Potos  , Guadalc  zar. MEXU. **Phellodendron amurense** Rupr. (Rutaceae), InsideWood, FPAw 17,321 Jugo Ilic CSIRO; TWTw 18,444, 18,742. **Perriera madagascariensis** Courchet (Simaroubaceae), Smithsonian NMNH slide collection, CTFTw 13,398. **Picrasma javanica** Blume (Simaroubaceae), InsideWood, FPAw ngf. 4748 J. Ilic CSIRO. **Picrasma quassioides** (D.Don) Benn. (Simaroubaceae), InsideWood, TWTw 18,407, 18,468 FFPRI. **Pierreodendron africanum** (Hook.f.) Little (Simaroubaceae), InsideWood, D  tienne, P. West Africa Wood Coding. CIRAD. Unpublished. **Pilocarpus racemosus** Vahl (Rutaceae), MEXUw slide collection, E. Mart  nez 30,890, Mexico, Campeche, Calakmul, MEXU. **Pistacia chinensis** Bunge (Anacardiaceae), PUw004, Terrazas's slide collection. **Pistacia mexicana** Kunth (Anacardiaceae), MEXUw slide collection, F. Miranda 6888, Mexico, Chiapas, Tuxtla Guti  rrez, Barranca Cueva del Tigre, MEXU; J. Barajas Morales 442, Mexico, Puebla, Tehuac  n, Brecha Teontepec-Nopala, MEXU. **Plagioscyphus louvelii** Danguy & Choux (Sapindaceae), Klaassen 1999; Smithsonian NMNH slide collection, CTFTW 9088. **Pleiospermium alatum** (Wight & Arn.) Swingle (Rutaceae), InsideWood, Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. **Poupartia chapelieri** (Guillaumin) H. Perrier (Anacardiaceae), Smithsonian NMNH slide collection, CTFTW 8919. **Poncirus trifoliata** (L.) Raf. (= *Citrus trifoliata* L.) (Rutaceae), InsideWood, Eom Young Geun. 2015. Wood anatomy of Korean species. Media Wood, Ltd. Seoul, Korea. **Protium copal** (Schltdl. & Cham.) Engl. (Burseraceae), MEXUw slide collection, J. Barajas Morales 179, Mexico, Veracruz, Estaci  n Biol  gica los Tuxtlas, MEXU; E. Mart  nez 30,210, Mexico, Campeche, Calakmul, MEXU. **Protium madagascariense** Engl. (Burseraceae), Smithsonian NMNH slide collection, CTFTW 8792. **Protium serratum** (Wall. ex Colebr.) Engl. (Burseraceae), InsideWood, FPAw16522 J. Ilic CSIRO. **Protorhus thouvenotii** H.Lecomte (= *Abrahamia thouvenotii* (Lecomte) Randrian. & Lowry) (Anacardiaceae), CFTF17046, Terrazas's slide collection. **Ptaeroxylon obliquum** (Thunb.) Radlk. (Rutaceae), InsideWood, Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. **Ptelea trifoliata** L. (Rutaceae), MEXUw slide collection, J. Barajas Morales 459, Mexico, Puebla, Tehuac  n, MEXU. **Quassia amara** L. (Simaroubaceae), InsideWood, USw 16,131 E. Wheeler NCSU; Uw 2035 M. Bakker NBC. **Quassia indica** (Gaertn.) Noot. (Simaroubaceae), InsideWood, CTFTw 9842 P. Deti  ne CIRAD; FPAw 8337 J. Ilic CSIRO. **Quassia undulata** (Guill. & Perr.) D.Dietr. (Simaroubaceae), InsideWood, Tw 1412, 8029 H. Beekman RMCA. **Quivisanthe papinae** Baill. (Meliaceae), Smithsonian NMNH slide collection, CTFTw 8747. **Reinwardtiadendron celebicum** Koord. (Meliaceae), InsideWood, FPAw 13,591 J. Ilic CSIRO. **Rhus**

- chondroloma* Standl. (Anacardiaceae), MEXUw slide collection, J. Barajas-Morales 524, Mexico, Puebla, Molcaxac, SW de Izcaquixtla, MEXU. *Rhus perrieri* (Courchet) H. Perrier (= *Protorhus perrieri* Courchet) (Anacardiaceae), Smithsonian NMNH slide collection, CTFTW 13,427. *Rhus thoursii* (Engl.) H. Perrier. (Anacardiaceae) InsideWood. Detienne, P. Woods of Madagascar. CIRAD, Unpublished. *Rhus typhina* L. (Anacardiaceae), US8359, MAD18305, Terrazas's slide collection. *Ruta chalepensis* L. (Rutaceae), InsideWood, Fahn A., E. Werker, & P. Baas. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. The Israel Academy of Sciences and Humanities. *Samadera indica* Gaertn. (= *Quassia indica* (Gaertn.) Noot.) (Simaroubaceae), InsideWood, Detienne, Pierre. Woods of Madagascar. CIRAD Unpublished. *Sandoricum koetjape* (Burm. f.) Merr. (Meliaceae), InsideWood, EI 1339 R. Aichbauer IWCS; FPAw 10,345 J. Ilic; Uw 18,653 M.E. Bakker NBC. *Santiria apiculata* A.W.Benn. (Burseraceae), Insidewood, FPAw12199 J. Ilic CSIRO. *Santiria griffithii* Engl. (Burseraceae), Insidewood, R.H.M.J. Lemmens, I. Soerianegara & W.C. Wong, Plant resources of South-east Asia. No. 5(2) Timber trees. *Santiria trimera* (Oliv.) Aubrév. (Burseraceae), Insidewood Kw31165 A. Campbell & P. Gasson KEW. *Sapindus saponaria* L. (Sapindaceae), Klaassen 1999; InsideWood, BWCw 8764 E. Wheeler NCSU; MEXUw slide collection, J. Barajas-Morales & G. Ángeles 64, collected in Mexico, Veracruz, Catemaco, MEXU. *Sarcomelicope simplicifolia* (Endl.) T.G.Hartley (Rutaceae), InsideWood, FPAw 7990 J. Ilic CSIRO. *Schinus molle* L. (Anacardiaceae), U26948, Terrazas's slide collection. *Schleichera oleosa* (Lour.) Merr. (Sapindaceae), Klaassen 1999; InsideWood, FPAw 24,474 J. Ilic CSIRO. *Searsia erosa* (Thunb.) Moffett (Anacardiaceae), Terrazas's slide collection. *Semecarpus forstenii* Blume (Anacardiaceae), Terrazas's slide collection. *Serjania corrugata* Radlk. (Sapindaceae), InsideWood, Araújo G.U.C. & C.G. Costa. 2007. Anatomia do caule de *Serjania corrugata*. Acta. Bot. Bras 21(2): 489–497. *Serjania lethalis* A. St.-Hil. (Sapindaceae), Klaassen 1999; G. Somner 1628, Brazil, Rio de Janeiro, Poço das Antas, RBR. *Serjania schiedeana* Schtdl. (Sapindaceae), L. Carmona 15,630, Mexico, Morelos, Tlaquiltenango, Chimalacatlán, MEXU. *Serjania triquetra* Radlk. (Sapindaceae), MEXUw slide collection, L. Carmona 15,618, Mexico, Morelos, Tlaquiltenango, Chimalacatlán, MEXU. *Simaba cedron* Planch. (Simaroubaceae), InsideWood, Uw 215 M.E. Bakker NBC. *Simaba orinocensis* Kunth. (Simaroubaceae), InsideWood, Uw 221 M.E. Bakker NBC. *Simarouba amara* Aubl. (= *Simarouba glauca* DC.) (Simaroubaceae), BCTw Angyalossy's slide collection, Brazil; MEXUw slide collection (as *S. glauca* DC.), V. Carmona 51, Mexico, Chiapas, Macdonia, INIREB-51; R. Hernández 1246, Mexico, Campeche, Campo experimental "el tormento", MEXU. *Simarouba glauca* DC. (= *Simarouba amara* Aubl.) (Simaroubaceae), InsideWood, EI 1504 R. Aichbauer IWCS; FPAw 12,022 J. Ilic CSIRO; HBw 418 R.C. Rivery. *Simarouba versicolor* A. St.-Hil. (Simaroubaceae), BCTw Angyalossy's wood collection, Brazil. *Skimmia japonica* Thunb. (Rutaceae), InsideWood, FHOw 11,610 E. Wheeler NCSU. *Soulamea* sp. (Simaroubaceae), InsideWood, Metcalf CR. & Chalk L. 1950. Anatomy of the dicotyledons. 2 Vols. Clarendon Press, Oxford, U.K. *Spathelia sorbifolia* L. (Rutaceae), Appelhans et al. 2021. Phylogenetic and ecological signals in the wood of Spathelioideae (Rutaceae). IAWA J 33:337–353. *Spondias mombin* L. (Anacardiaceae), MEXUw slide collection, J. Barajas-Morales 254, Mexico, Veracruz, San Andrés Tuxtlas, Estación Biológica Los Tuxtlas, MEXU. *Spondias purpurea* L. (Anacardiaceae), MEXUw slide collection, O. Téllez Valdés 30,964, Mexico, Campeche, Calakmul, Al oeste de 2 lagunas, MEXU. *Spondias tuberosa* Arruda. (Anacardiaceae) InsideWood. Scheel-Ybert, R. & Gonçalves T.A.P. 2017. Primeiro Atlas Antracológico de Espécies Brasileiras. Museu Nacional—Série Livros Digital 10, Rio de Janeiro. *Stadmania oppositifolia* Lam. (Sapindaceae), Klaassen 1999; Smithsonian NMNH slide collection, CTFTW 13,279. *Swietenia humilis* Zucc. (Meliaceae), MEXUw slide collection, A. Pérez Jiménez 824, Mexico, Jalisco, La Huerta, Estación de Biología de Chamela, MEXU. *Swietenia macrophylla* King. (Meliaceae), MEXUw slide collection, I. Calzada 3107, Mexico, Chiapas, Alfredo Bonfil, MEXU; X-112, Mexico, Campeche; InsideWood, AM 308 R. Aichbauer IWCS; AO 65,120 R. Aichbauer IWCS; FPAw 24,391 J. Ilic CSIRO; Kw 4353, 24,696 P. Gasson KEW; NITw 989, 992 A.F. N. Brandes UFF; Angyalossy's slide collection, Panama, MADw 6027. *Swietenia mahogani* L. (Meliaceae), InsideWood, Cerre 3 J-C Cerre IWCS; Kw 4371 P. Gasson KEW; Uw 8358, 10,456, 11,471, 32,010 L.Y.T. Westra NBC. *Talisia nervosa* Radlk. (Sapindaceae), Klaassen 1999; InsideWood, Poveda 466 R. Klaassen NBC. *Tapirira bethanniana* J.D.Mitch. (Anacardiaceae) InsideWood. Uw 33,087 M.E. Bakker NBC. *Tapirira guianensis* Aubl. (Anacardiaceae), BCTw Angyalossy's slide collection, Brazil. *Tapirira mexicana* Marchand (Anacardiaceae), MEXUw slide collection, J. Barajas-Morales 251, Mexico, Veracruz, San Andrés Tuxtlas, Laguna Escondida, MEXU; Wendt 5321, Mexico, Chiapas, Monte Líbano, MEXU. *Tapirira obtusa* (Benth) J.D.Mitch. (Anacardiaceae), MADw26816, Terrazas's slide collection. *Tetradium daniellii* (Benn.) T.G.Hartley (Rutaceae), InsideWood, UN 441 E. Wheeler NCSU. *Tetragastris altissima* (Aubl.) Swart. (Burseraceae), Insidewood, CTFTw16667 P. Détienne & R. Miller Tropen; Tw22011 H. Beeckman RMCA; Uw658 M. E. Bakker NBC. *Tetragastris panamensis* (Engl.) Kuntze (Burseraceae), Angyalossy's slide collection, BCTw slide collection, Lâmina Permanente 37, IRENA 0254. *Thouinia paucidentata* Radlk.

(Sapindaceae), Klaassen 1999; MEXUw slide collection, C. León Gomez 64, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Thouinia portoricensis* Radlk. (Sapindaceae), Klaassen 1999. *Thouinia serrata* Radlk. (Sapindaceae), MEXUw slide collection, J. Barajas Morales 174, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Thouinia villosa* DC. (Sapindaceae), MEXUw slide collection, Guridi Gómez 4199, Mexico, Michoacán, Morelia. FITECMA 131. *Thouinidium decandrum* (Humb. & Bonpl.) Radlk. (Sapindaceae), Klaassen 1999; MEXUw slide collection, C. León Gómez 72, Mexico, Jalisco, Estación de Biología de Chamela, MEXU. *Tina apiculata* (Radlk.) Radlk. ex Choux (= *Tinopsis apiculata* Radlk.) (Sapindaceae), Smithsonian NMNH slide collection, CTFTW 16,602. *Toechima tenax* Radlk. (Sapindaceae), Klaassen 1999. *Toona sinensis* (Juss.) M. Roem. (Meliaceae), InsideWood, Cerre 1089 J-C Cerre IWCS. *Toona* sp. (Meliaceae), BCTw Angyalossy's slide collection, Brazil. *Toxicodendron vernicifluum* (Stokes) F.A. Barkley (Anacardiaceae), MADw6518, Terrazas's slide collection. *Tratinnickia demerarae* Sandwith (Burseraceae), Insidewood, FPAw17039 J. Ilic CSIRO; Tw31129 H. Beeckman RMCA; Uw2058 M. E. Bakker NBC. *Trichilia emetica* Vahl (Meliaceae), InsideWood, FPAw 4261 J. Ilic CSIRO; Kw 4430 P. Gasson KEW. *Trichilia glabra* L. (Meliaceae), Angyalossy's slide collection, M. Vales 84, HACw 84, Brazil. *Trichilia japurensis* C. DC. (Meliaceae), MEXUw slide collection, J. Barajas-Morales 56, Mexico, Veracruz, Catemaco, Colonia Coronel Adalberto Tejeda, MEXU. *Trichilia minutiflora* Standl. (Meliaceae), MEXUw slide collection, E. Martínez 30,560, Mexico, Campeche, Calakmul, MEXU. *Trichilia trifolia* L. (Meliaceae), MEXUw slide collection, C. León Gómez 27, Mexico, Jalisco, La Huerta, Estación de Biología de Chamela, MEXU. *Triomma malaccensis* Hook.f. (Burseraceae), Insidewood, FPAw12258 J. Ilic CSIRO. *Tristira triptera* Radlk. (Sapindaceae), Klaassen 1999. *Tristropsis acutangula* Radlk. (Sapindaceae), Klaassen 1999; InsideWood, FPAw ngf.4092 J. Ilic CSIRO; IFIw 11,527 R. Klaassen NBC; Waturandang 22,236 R. Klaassen NBC. *Turraea sericea* Sm. (Meliaceae), InsideWood, P. Detienne, Woods of Madagascar, CIRAD. *Turraeanthus africana* (Welw. ex C. DC.) Pellegr. (Meliaceae), InsideWood, Cerre 26 J-C Cerre IWCS; FPAw 10,304 J. Ilic CSIRO; Tw 1123, 2413 H. Beeckman RMCA; WUR 30,689 R. Aichbauer IWCS. *Walsura* (= *villosa*) *tubulata* Hiern (Meliaceae), InsideWood, FPAw 28,787, Jugo Illic. *Xanthoceras sorbifolia* Bunge (Sapindaceae), Klaassen 1999; InsideWood, UN 393 R. Klaassen NBC; Uw 33,605 M. E. Bakker NBC. *Xylocarpus moluccensis* (Lamk) M. Roem. (Meliaceae), InsideWood, FPAw 4170, 7218, 10,381 J. Ilic CSIRO; JS 1535 R. Aichbauer IWCS. *Zanthoxylum ailanthoides* Siebold & Zucc. (Rutaceae), InsideWood, Hw 9168 E. Wheeler NCSU;

TWTw 14,909 E. Wheeler NCSU. *Zanthoxylum caribaeum* Lam. (Rutaceae), MEXUw slide collection, C. León Gómez 34, Mexico, Jalisco, La Huerta, Estación de Biología de Chamela, MEXU. *Zanthoxylum kellermanii* P. Wilson (Meliaceae) InsideWood, E. Wheeler NCSU; MEXU 242, Veracruz, Catemaco, Colonia Coronel Adalberto Tejeda, Barajas-Morales & Angeles 72, MEXU. *Zanthoxylum madagascariense* Baker (Rutaceae), Smithsonian NMNH slide collection, CTFTw 13,221. *Zanthoxylum nitidum* (Roxb.) DC. (Rutaceae), MEXUw slide collection. *Zanthoxylum riedelianum* subsp. *kellermanii* (P. Wilson) Reynel ex C. Nelson (Rutaceae), MEXUw slide collection, J. Barajas Morales 68, Mexico, Veracruz, Catemaco, Colonia Coronel Adalberto Tejeda, MEXU. *Zanthoxylum tsihanimposa* H. Perrier (Rutaceae), Smithsonian NMNH slide collection, CTFTw 16,313.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40415-021-00764-2>.

Acknowledgements We are especially indebted to Elisabeth Wheeler, without whom InsideWood would not be a reality, and the present work not possible, and Alexandra Muellner-Riehl for authorizing the use of the chronogram of Sapindales. We also thank E. Wheeler for the authorization to use images of *Toxicodendron*. We thank Hisashi Abe and the staff of the TWTw wood collection for allowing the use of photos of *Orixa japonica* and Stanley Yankowski at the Smithsonian Institution for allowing the use of photos from the CTFT (Centre Technique Forestier Tropical) collection. Josefina Barajas-Morales and Calixto León Gómez for the many slides deposited in the MEXU collection that greatly contributed to this work, Carolina Lopes Bastos and André Lima, who made slides of Sapindaceae lianas for the Angyalossy's collection. We are also indebted to three anonymous reviewers and the editors for their revisions and advices. This work or the authors received funding from Programa de Apoio a Projectos de Investigación e Inovação Tecnológica (DGAPA, PAPIIT, Mexico) [Projects IA200521 to MRP, IB205419 to TT), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) [Project 2013/10679-0; 2017/17107-3; 2018/06917-7]. Joyce G. Chery was supported by Cornell University Lab Startup Funds.

Author contributions All authors contributed to the study conception and design, first conceptualized by (alphabetically): Israel L. Cunha Neto, Marcelo R. Pace and Veronica Angyalossy. Project administration and supervision was carried by Marcelo R. Pace with constant feedback from Caian Gerolamo and Joyce G. Chery. Material preparation, data collection and analyses were performed by Caian S. Gerolamo, Israel L. Cunha Neto, Joyce G. Chery, Marcelo R. Pace, Teresa Terrazas. Joyce G. Chery led the phylogenetic comparative methods. Quantitative data were acquired by Mariana Victorio and analyzed by Caian Gerolamo. The first draft of the manuscript was written by Marcelo R. Pace and all authors commented on various versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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