



Diversity and evolution of secretory structures in Sapindales

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Abstract

Sapindales comprise nine families with a mainly tropical distribution and include numerous species of high economic importance. Members of this order are known for the production of chemical constituents with medicinal properties, such as antioxidant, anti-inflammatory, and antimicrobial activity, as well as species with insecticidal properties. Such diversity of chemical compounds is attributed to a variety of secretory structures, which may occur in both vegetative and reproductive organs. During the past decades, tremendous progress has been made in anatomical and analytical chemistry studies, which has led to the next level of knowledge regarding the secretory structures of Sapindales. This comprehensive review embraces the most important data of the secretory structures of Sapindales: ducts, cavities, laticifers, floral and extrafloral nectaries, osmophores, colleters, idioblasts, and trichomes. Our review comprises structural, functional, and evolutionary aspects of these glands, which are fundamental for further studies of the diversification within Sapindales.

Keywords Cavities · Colleters · Ducts · Idioblasts · Laticifers · Nectaries · Osmophores

1 Introduction

Sapindales, with approximately 6570 spp., are a diverse order of Malvidae (Stevens 2001), currently comprising nine monophyletic families: Biebersteiniaceae, Nitrariaceae, Kirkiaceae, Burseraceae, Anacardiaceae, Sapindaceae, Simaroubaceae, Meliaceae, and Rutaceae (Muellner-Riehl et al. 2016). Species of this order vary from herbs to trees and occasionally lianas and are found in a wide range of habitats, mainly in tropical regions (Kubitzki 2011; Muellner-Riehl et al. 2016). Many species of this order are used in folk medicine and have been the subject of phytochemical

and pharmacological studies due to secretions produced by their secretory structures (Corthout et al. 1991, 1992, 1994; Farsam et al. 2000; Burris et al. 2005; Aragão et al. 2008; Muthukumran et al. 2011; Alves et al. 2014; Lv et al. 2015; Okoth et al. 2016; Zhang et al. 2017). According to these studies, antioxidant, anti-inflammatory, antimicrobial, and insecticidal properties are the pharmacological activities most commonly described for Sapindales.

Sapindales stand out as an order for which several types of secretory structures (or glands) have been reported (Kubitzki 2011 and references therein). Secretory ducts are probably the best-known secretory structure in the order, predominantly occurring in Anacardiaceae and Burseraceae (e.g., Tölke et al. 2021). They were found to be related to the protection against herbivory by producing toxic phenols and terpenes (Aguilar-Ortigoza et al. 2003; Aguilar-Ortigoza and Sosa 2004; Tölke et al. 2021). In addition, other glands have also been found in the order, such as cavities, laticifers, floral and extrafloral nectaries, osmophores, colleters, idioblasts, and trichomes, which are related to plant defense or attraction of pollinators. The occurrence, position, and type of secretory structure, as well the secretion composition, have been used to support phylogenetic relationships among different angiosperm lineages and to better understand some evolutionary patterns (Aguilar-Ortigoza and Sosa 2004;

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Marazzi et al. 2006; De-Paula OC, Sajo 2011; Weber and Keeler 2013; Vitarelli et al. 2015; Demarco 2017; Prado and Demarco 2018). Likewise, secretory structures have been also important to understand ecological interactions with pollinators and herbivores (Aguilar-Ortigoza and Sosa 2004; Kubitzki 2011; Alves et al. 2014; Lacchia et al. 2016a; Tölke et al. 2018a).

The type, distribution, and function of secretory structures might be important characters to elucidate the evolutionary history of Sapindales. The purpose of this paper is to provide a comprehensive review of the general morphological aspects of these secretory structures and the diversity of compounds that they produce, and discuss their functional and evolutionary aspects in Sapindales.

2 Secretory structures of Sapindales

Secretory ducts – Secretory ducts are observed in five out of nine families of Sapindales: Anacardiaceae, Burseraceae, Simaroubaceae, Meliaceae, and Rutaceae (Metcalf and Chalk 1950; Plowden et al. 2002; Dünisch and Bass 2006; Lacchia and Carmello-Guerreiro 2009; Kubitzki 2011; Souza et al. 2016; Palermo et al. 2018; Prado and Demarco 2018; Pace et al. 2021; Tölke et al. 2021; Fig. 1). They are ubiquitous in the clade formed by Anacardiaceae and Burseraceae, occurring in all vegetative and reproductive organs of these families (Metcalf and Chalk 1950; Lacchia and Carmello-Guerreiro 2009; Palermo et al. 2018; Pace et al. 2021; Tölke et al. 2021). In this clade, ducts occur in

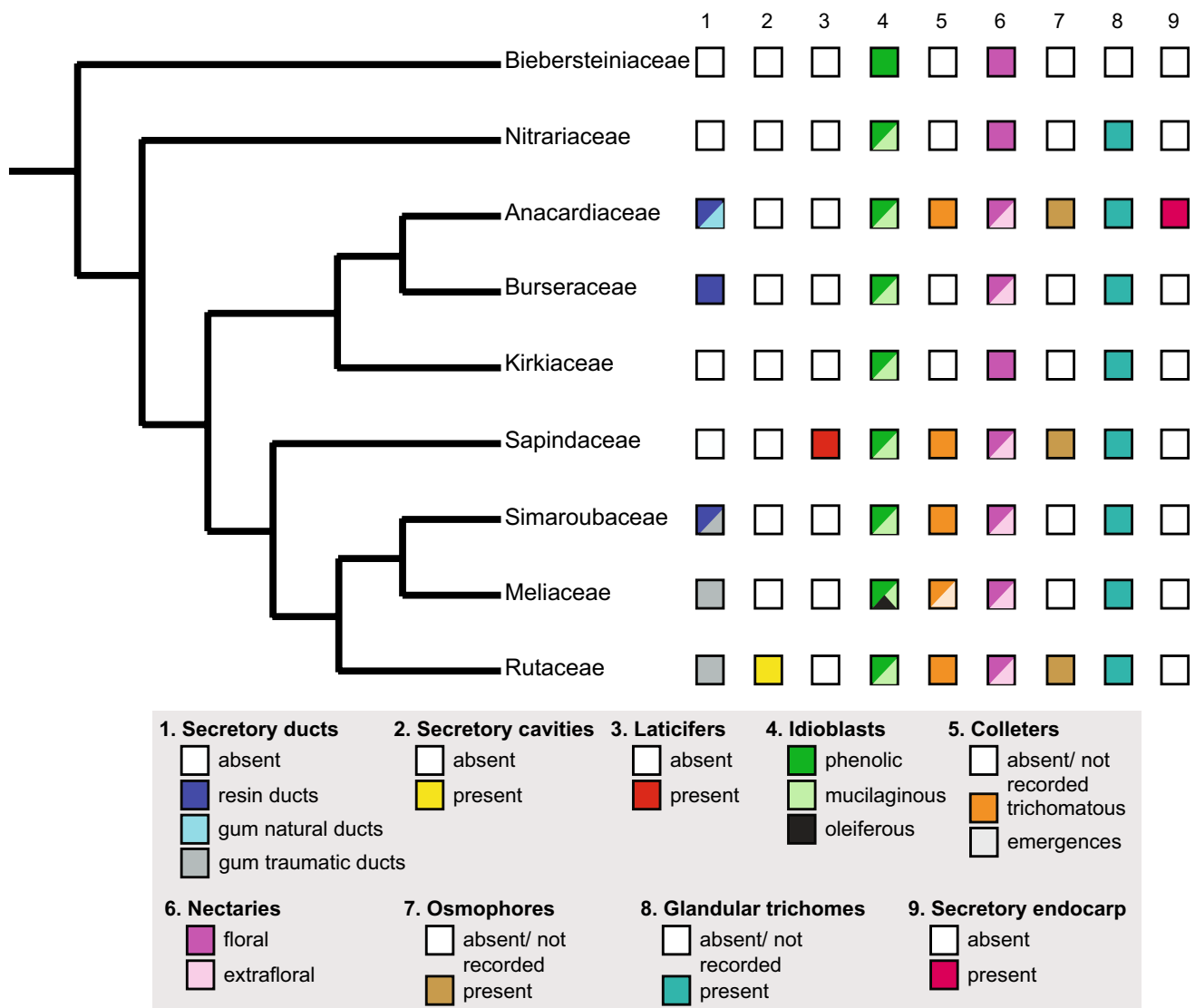


Fig. 1 Occurrence of secretory structures in families of Sapindales. Phylogenetic hypothesis based on Stevens (2011). Data obtained from cited references among the text

the phloem (primary and secondary; Fig. 2a–c), and secondary ducts are also commonly found in the wood (Heimsch 1942; Metcalfe and Chalk 1950; Pace et al. 2021; Tölke et al. 2021). In addition to the vascular ducts, some genera of Anacardiaceae stand out for having primary ducts in the pith (Metcalfe and Chalk 1950; Tölke et al. 2021). According to Solereder (1908), the ducts in the leaves of Anacardiaceae are found along the phloem either of the larger and smaller veins, and occasionally also adaxially to the vascular bundles, in which case they are connected to the pith ducts of the stem. The arrangement of the ducts may be axial, radial, tangential, or irregular, and more than one type may occur within a plant. Axial and radial ducts are the main types found in the secondary phloem of Anacardiaceae and Burseraceae, and radial ducts are also often observed in the secondary xylem of both families (Heimsch 1942; Venkaiah and Shah 1984; Agarwal and Gupta 2008; Daly et al. 2011; Pell et al. 2011; Pace et al. 2021). Remarkably, some species have an integrated ramifying duct system in the trunk, connecting the radial ducts of xylem and phloem to axial ducts of the bark (Venkaiah and Shah 1984). For instance, radial ducts are a putative synapomorphy of this clade (Pace et al. 2021; this study).

In Simaroubaceae, secretory ducts have been reported in the shoot system (Metcalfe and Chalk 1950; Babu et al. 1990; Shi et al. 2011; Alves 2015) and in the sepals and petals (Fig. 2d–e) (Alves et al. 2017) but are less frequent within each organ when compared to those of the two former families (pers. obs.). Unlike Anacardiaceae and Burseraceae, ducts of Simaroubaceae occur exclusively in the xylem (primary and secondary), besides primary ducts in the pith; only axial ducts have been reported in the family (Metcalfe and Chalk 1950; Babu et al. 1990; Shi et al. 2011; Alves 2015). Although secretory ducts naturally occur in this family, traumatic ducts have also been reported for some representatives of Simaroubaceae (e.g., *Ailanthus* Desf.) (Metcalfe and Chalk 1950; Rajput and Kothari 2005; Pace et al. 2021).

Members of Meliaceae and Rutaceae do not have constitutive ducts in their organs (e.g., Heimsch 1942); actually, the ducts observed in these families do not develop naturally and are instead formed exclusively in the secondary xylem of some genera as a result of injury (Fig. 2f–g) (Spiekerkoetter 1924; Record and Hess 1943; Metcalfe and Chalk 1950; Gedalovich and Fahn 1985; Rajput et al. 2005; Dünisch and Bass 2006; Pace et al. 2021). In this case, they are called traumatic ducts and are originated only in response to wounds, mechanical pressure, attack by microorganisms or insects, and physiological disturbances such as water stress or unfavorable environment (Fahn 1979). The injury affects cambium activity which starts to produce axial ducts into secondary xylem (Gedalovich and Fahn 1987; Rajput et al. 2005; Dünisch and Bass 2006). Traumatic ducts have also been reported in vascular bundles of leaves and fruits

infected by virus (Marques et al. 2010). Because traumatic ducts are not constitutive, their formation after injury is likely a synapomorphy of the clade Simaroubaceae–Meliaceae–Rutaceae (Pace et al. 2021).

The ducts may be single (isolated) or may fuse, that is, anastomose axially and laterally forming long, branched ducts (Fig. 2c). The ducts of Simaroubaceae and the traumatic ducts of Meliaceae and Rutaceae are single and short (Fig. 2d–g), while those of Anacardiaceae and Burseraceae anastomose profusely, originating a complex branched system of ducts, which extends throughout the plant body (Fig. 2a–c) (Lacchia and Carmello-Guerreiro 2009; Palermo et al. 2018; Tölke et al. 2021) and is responsible for the high amount of secretion that exudes when the system is ruptured.

The general structure of the ducts is very similar in all Sapindales (Fig. 2a–g). It is composed of an epithelium (usually uniseriate) lining a lumen, which stores the exudate and is surrounded by a sheath of idioblasts or parenchyma cells (Rajput et al. 2005; Lacchia and Carmello-Guerreiro 2009; Souza et al. 2016; Palermo et al. 2018; Tölke et al. 2021). However, the origin of the lumen may vary among families and within a family. One of the more complex challenges regarding ducts is understanding how their lumen is formed. There is a large number of studies on this topic and an equal amount of divergence in the literature. Most studies of ducts of Sapindales are restricted to Anacardiaceae, and there is no consensus about lumen formation in this family. Some authors have described their ducts as schizolysigenous, others as schizogenous, and according to some studies, both types may be present in the family, depending on the species (Lacchia and Carmello-Guerreiro 2009 and references therein). For the other families, the studies are much more restricted. For Burseraceae, schizolysigenous ducts have been described in *Protium* Burm. f. (Palermo et al. 2018), and for Simaroubaceae, schizogenous constitutive ducts have been reported for *Ailanthus excelsa* Roxb, while lysigenous traumatic ducts have been described for the same species (Babu et al. 1990). The traumatic ducts of *Azadirachta* A. Juss. (Meliaceae) seem to have a schizolysigenous origin (Rajput et al. 2005), while those of *Citrus* L. (Rutaceae) are schizogenous (Gedalovich and Fahn 1987).

Studies made so far indicate that the secretory apparatus is very conservative in ducts of Sapindales. Epithelial cells are rich in mitochondria with dilated cristae, rough endoplasmic reticulum, multivesicular bodies, vesicles, dictyosomes, lipid bodies, plastids, and osmiophilic droplets (Babu et al. 1990; Nair and Subrahmanyam 1998; Lacchia and Carmello-Guerreiro 2009; Palermo et al. 2018). Plasmodesmata or their rudiments are not common (Joel and Fahn 1980a; Nair et al. 1983; Nair and Subrahmanyam 1998; Lacchia and Carmello-Guerreiro 2009). The secretion mode is similar to those described for ducts of other angiosperms, including eccrine and granulocrine mechanisms (Nair and

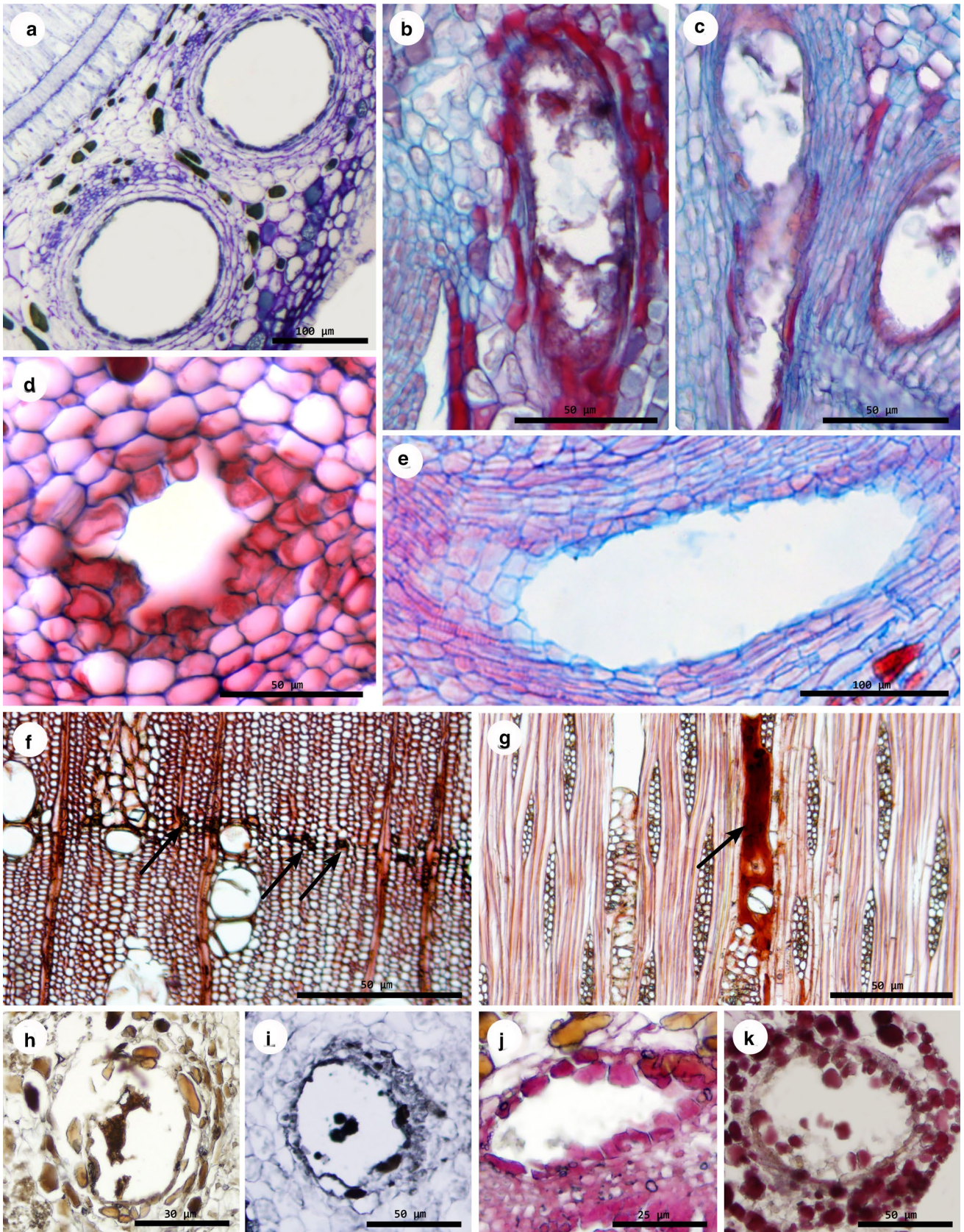


Fig. 2 Secretory ducts in Sapindales. **a, d, f, h–k** Transverse section. **b–c, e, g** Longitudinal sections. **a** Fruit of *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae). **b–c** Sepals of *Schinus molle* L. (Anacardiaceae). Note the anastomosis of ducts (**c**). **d–e** Petals of *Homalolepis cedron* (Planch.) Devecchi & Pirani (Simaroubaceae). **f–g** Traumatic ducts (arrows) in the wood of *Zanthoxylum kellermanii* P. Wilson (Rutaceae). **h–k** Histochemical tests in the ovary of *Spondias macrocarpa* Engl. (Anacardiaceae), showing positive reactions to phenolic compounds, using ferric chloride (**h**), lipids, using Sudan black (**i**), mucilage, using Ruthenium red (**j**), and polysaccharides, using Schiff reagent (**k**). Photographs **f** and **g** provided by Dr. Marcelo Pace

Subrahmanyam 1998; Lacchia and Carmello-Guerreiro 2009; Palermo et al. 2018). Sometimes, in late stages, the epithelial cells disintegrate, becoming part of the secretion, which characterizes the holocrine secretion (Joel and Fahn 1980b; Babu et al. 1990; Palermo et al. 2018).

Most secretory ducts in Sapindales are vascular (originated from procambium and/or cambium) but medullary ducts (originated from ground meristem) also occur in Anacardiaceae and Simaroubaceae (Babu et al. 1990; Tölke et al. 2021) and this distinct origin may influence the secretory activity of some ducts. Recently, it has been demonstrated in Calophyllaceae (Malpighiales) that the meristematic origin of a duct may affect some metabolic routes and change its chemical composition (Costa et al. 2021). Likewise, the type of secretion may vary depending on the duct origin in Anacardiaceae (Tölke et al. 2021). In this family, phloem ducts produce resin composed of terpenes, phenolic compounds, polysaccharides, and other non-volatile lipids (Fig. 2 h–k), while the medullary ducts of some species produce gum, with polysaccharides as the major component (Tölke et al. 2021). It is possible that this variation also occurs in species of Simaroubaceae, whose ducts produce resin, composed of terpenes, polysaccharides and other substances, with a few variations depending on the organ studied (Babu et al. 1990; Shi et al. 2011; Tölke et al. 2021), but investigations of this topic are still lacking.

For Burseraceae, only resin ducts have been reported, which produce a heterogenous secretion rich in terpenes and other metabolites, such as phenolic compounds, polysaccharides, and proteins (Setia et al. 1977; Souza et al. 2016; Palermo et al. 2018). Notably, all traumatic ducts of Sapindales produce gum instead of resin, including those of Simaroubaceae which produce constitutive resin ducts in regular conditions (Gedalovich and Fahn 1985; Rajput and Kothari 2005; Rajput et al. 2005; Dünisch and Bass 2006). Although the chemistry of the duct secretion is quite complex in Sapindales, we are able to classify them as gum or resin. Although both types of exudate may have heterogeneous composition, resin is mostly terpenic, while gum is mostly polysaccharidic (Prado and Demarco 2018; Tölke et al. 2021). In fact, Anacardiaceae and Burseraceae share the production of biflavonoids, lost in some lineages of Anacardiaceae, while in the clade formed by

Simaroubaceae, Meliaceae, and Rutaceae, flavanones, flavones, and flavonols are common (Aguilar-Otigoza et al. 2003; Aguilar-Ortigoza and Sosa 2004; Kubitzki 2011), but production of mucilaginous substances has also been reported (Marques et al. 2010).

The production of terpenoids and phenolic compounds, main constituents of resins, is almost ubiquitous in Sapindales. However, those compounds are secreted by distinct secretory structures with defensive function depending on the family. Secretion composed mostly of terpenoids is produced by ducts in Anacardiaceae, Burseraceae, and Simaroubaceae, while it is produced by oil idioblasts in Meliaceae and by cavities in Rutaceae. The probable emergence of the high molecular weight terpenoid pathway in the ancestor of Sapindales probably enabled the evolution of different types of defensive glands according to the evolutionary history of the order and diversification of families (for more information, see Sect. 3).

Oil cavities – Rutaceae is the only family of Sapindales that have secretory cavities (Fig. 1), which consist of an epithelium of secretory cells lining an isodiametric intercellular space (lumen), sometimes containing more than one epithelial layer and surrounded by a sheath (Fig. 3a) (Liu and Hu 1998; Kubitzki 2011; Turner and Lange 2015; Cruz et al. 2017; Machado et al. 2017; Franco and Albiero 2018). In contrast to secretory ducts, the cavities are rounded in shape in both cross and longitudinal planes (Fahn 1979). They are nearly universally present and correspond to the most striking feature of the family, occurring in all parts of the shoot system, and constitute the translucent dots (or pellucid glands) of leaves, a diagnostic character of Rutaceae (Liu and Hu 1998; Kubitzki 2011; Turner and Lange 2015; Oggero et al. 2016; Cruz et al. 2017; Machado et al. 2017; Franco and Albiero 2018; Andrade et al. 2020). In contrast to the core Rutaceae, in three genera of subfamily Cneoroideae, *Dictyoloma* A. Juss., *Spathelia* L. and *Sohnreyia* K. Krause, oils cavities are restricted to the margin of leaflets (Appelhans et al. 2011; Kubitzki et al. 2011).

The seven types of leaf venation defined by Dede (1962), based on observations of 80 genera of Rutaceae, are characterized by a spatial correlation between the vascular system and the secretory cavities, an association previously reported by Stern and Brizicky (1960). Dede (1962) also pointed out an allometric correlation of the number of cavities and their relative size, that is, the larger the glands the smaller their number on a leaf blade area. He considered that this ancestral condition would be found in taxa with a high number of small oil cavities in the leaves.

Regarding the reproductive organs, oil cavities may be found in sepals, petals, stamens, gynoecium (especially in the ovary) and in mesocarp of fruits (Heinrich and Schultz 1985; Liu et al. 1998; Souza et al. 2004; Caris et al. 2006;

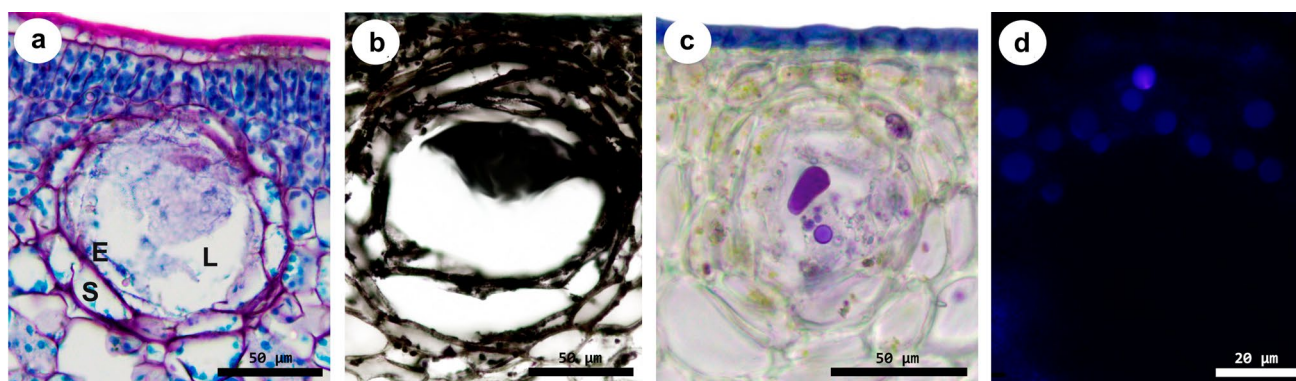


Fig. 3 Oil cavities in Rutaceae. Leaves of *Citrus sinensis* (L.) Osbeck. **a** Structure of the oil cavity. **b** Lipids stained with Sudan black B. **c** Terpenes identified by Nadi reagent. The violet staining revealed the presence of an oleoresin, i.e., a mixture of essential oils and resins. **d** Phenolic compounds (blue) detected by autofluorescence under UV. E, epithelium; L, lumen; S, sheath

Liang et al. 2006; Pirani et al. 2010; Turner and Lange 2015; El Ottra et al. 2019). In a study of flower anatomy of 29 genera of subfamily Aurantioideae, Tillson and Bamford (1938) reported a close association of these glands to the vascular tissue in several organs.

The oil cavities of Rutaceae have been reported exclusively in the parenchyma of primary organs, i.e., in the mesophyll of leaves (Fig. 3a) and cortex of stem, as well as in the corresponding portions of reproductive organs (Metcalf and Chalk 1950; Liu and Hu 1998; Muntoreanu et al. 2011; Machado et al. 2017; Franco and Albiero 2018; Andrade et al. 2020). Several reports have demonstrated the origin of the cavities from the protoderm and ground meristem (described as subprotodermal cells) or only from the ground meristem, which explains their constant position close to the epidermis (Bosabalidis and Tsekos 1982a; Bennici and Tani 2004; Rafiei and Rajaei 2007; Machado et al. 2017; Franco and Albiero 2018). There is no report of vascular cavities in the family. Despite rare reports of cavities in wood (Metcalf and Chalk 1950), only traumatic gum ducts have been confirmed for the family (see “Secretory ducts”).

Many studies about the lumen formation of cavities of Rutaceae have been performed, especially in *Citrus* L. (Thomson et al. 1976; Bosabalidis and Tsekos 1982a, b; Turner et al. 1998; Knight et al. 2001; Bennici and Tani 2004; Liang et al. 2006; Chen and Wu 2010; Liu et al. 2012; Turner and Lange 2015), but the conclusions are controversial and many conflicting reports of lysigeny and schizogeny of cavities are easily found (Turner 1999).

The cavities of the family were first described as schizogenous by Solereder (1908), then lysigenous or schizolysigenous by Engler (1931), schizogenous or lysigenous by Metcalf and Chalk (1950) and finally schizogenous by Kubitzki (2011). Turner et al. (1998) investigated the cavities of *Citrus* L. and described them as schizogenous, but a few years later Bennici and Tani (2004) clearly demonstrated

the schizolysigenous origin of cavities in *Citrus sinensis* (L.) Osbeck and *C. limon* (L.) Osbeck. Similarly, the cavities of *Pilocarpus* Vahl were considered schizogenous by Marquete (1981) but as schizolysigenous by Muntoreanu et al. (2011), as well reported by Franco and Albiero (2018) for *Esenbeckia* Kunth. In general, the disagreements are due to the fact that the studies did not use the same methodologies and only further studies using more appropriate techniques will reveal which is the main type of cavity formation in Rutaceae, or if it varies depending on the species. In a more recent work, Machado et al. (2017) concluded that the formation of cavities in *Metrodorea nigra* A. St.-Hil. occurs through a schizolysigenous process. Cavities of reproductive organs are usually larger, which may be related to the coalescence of distinct cavities. It has been observed in the ovary of some flowers that when two or more cavities are adjacent and their epithelia touch each other, they can fuse/coalesce, forming very large and often shapeless structures (El Ottra et al. 2019).

An unusual type of cavity is observed in *Dictamnus* L. (Rutaceae) and deserves special attention. This particular type of cavity is formed within a non-glandular trichome with short stalk, wide multicellular head and a beak-shaped apex, called a trichome-like cavity by Zhou et al. (2012). These authors observed this type of gland on stem, leaf blade and in all floral organs of *Dictamnus dasycarpus* Turcz. In the wide head, the cavity is originated by lysigeny, acquiring the same spheroidal shape as the other cavities of the family, composed of an oil-producing epithelium that releases the secretion into the lumen.

As observed for ducts, the oil cavities of Rutaceae usually start the production of secretion concomitantly to the formation of the lumen (Machado et al. 2017). The ultrastructure of the epithelium of these cavities is very similar to that of the resin ducts since they produce similar substances. Numerous plastids containing osmiophilic material are very

common (Heinrich and Schultze 1985; Liu et al. 1998). The cytoplasm is rich in vesicles of variable sizes, oil bodies, endoplasmic reticulum, mitochondria with unusual morphology and have a high density of ribosomes (Thomson et al. 1976; Heinrich and Schultze 1985; Liu et al. 1998, 2012; Turner and Lange 2015; Machado et al. 2017). The cavities of Rutaceae are specialized in the production and storage of terpenes (Fig. 3b–c), and it was demonstrated that plastids are the main sites of their production. These lipids are observed as plastoglobules inside the plastids, which may be transferred to the vacuoles and/or stored as lipid bodies in the cytosol (Turner and Lange 2015; Franco and Albiero 2018). After the production and transitory storage of these compounds within epithelial cells, the secretion is released into the lumen via eccrine and/or granulocrine mechanisms (Bosabadilis and Tsekos 1982b; Turner and Lange 2015; Franco and Albiero 2018), or through the collapse of the epithelial cells (holocrine mechanism) (Machado et al. 2017; Franco and Albiero 2018).

In addition to terpenoids (Fig. 3c), the secretion produced by cavities in Rutaceae may be composed of phenolic compounds (Fig. 3d) and other minority substances, such as non-volatile oils, alkaloids, proteins, and polysaccharides (Fig. 3a–d) (Castro and Demarco 2008; Machado et al. 2017; Franco and Albiero 2018; Andrade et al. 2020). Although the main composition of the oils of Rutaceae is similar to that of the resins of ducts in other Sapindales, oils are predominantly composed of volatile terpenes, such as mono- and sesquiterpenes, while resins are mostly composed of non-volatile terpenes, such as di-, tri-, and tetraterpenes (Dell and McComb 1979; Langenheim 2005). The oils of Rutaceae are attributed to the protection against herbivores and microorganisms (Champagne et al. 1992). Since among the Sapindales the cavities occur only in Rutaceae, we conclude that they evolved just once in the order, although the biosynthetic route of some classes of compounds may be shared with other secretory structures, such as ducts, laticifers, trichomes, and idioblasts. Secretory cavities are thus reported as a remarkable synapomorphy of Rutaceae, with a further lost in a clade formed by four genera within the small subfamily Cneoroideae (Stevens 2001; Appelhans et al. 2011).

Laticifers – Laticifers occur exclusively in Sapindaceae within Sapindales (Prado and Demarco 2018; Medina et al. 2021) (Fig. 1), and until recently the presence of latex is usually considered an unusual characteristic for the order (APG 2016). Taxonomic monographs refer to the presence of laticifers evidenced by milky or watery exudates in a few genera such as *Paullinia* L., *Serjania* Mill. and *Urvillea* Kunth (e.g., Radlkofer 1895; Acevedo-Rodríguez 1993; Acevedo-Rodríguez et al. 2011, 2017). Detailed descriptions of laticifers had previously been provided

for a small number of representatives of this family (Benedict 1961; Amini et al. 2008; Weckerle and Rutishauser 2005; Cunha-Neto et al. 2017), while most genera lack reports of these structures (e.g., Agarwal and Gupta 2008; Acevedo-Rodríguez et al. 2011). However, Medina et al. (2021) recently studied a large number of genera and found laticifers in 15 genera of three out of four subfamilies that constitute the family (Sapindoideae, Dodonaeoideae, and Hippocastanoideae).

Laticifers of Sapindaceae are articulated, non-anastomosing, that is, they are formed by a row of cells whose terminal walls do not dissolve. These laticifers occur in all organs of the plant, and are originated from ground meristem (primary laticifers) and/or vascular cambium (secondary laticifers) and rarely branch. The primary laticifers occur in the cortex and pith, while the secondary ones are found in the secondary phloem (Medina et al. 2021; Fig. 4a–c).

The scarcity of reports of latex in the family is due to the low frequency of laticifers in the organs and the fact that the cells constituting the laticifers do not merge (Medina et al. 2021), resulting in a small amount of latex which oozes when the tissue is ruptured (Fig. 4c). In addition, the latex of some species is colorless (Pickard 2008), making latex identification even more difficult.

Latex is the most highly complex secretion of plants and may contain all the main chemical classes of compounds, of which terpenoids predominate (Ramos et al. 2019, 2020). In Sapindaceae, the latex is usually white, composed mainly of terpenes (Fig. 4d) and as well as proteins, phenolic compounds, and carbohydrates. Alkaloids have also been detected in the latex of *Paullinia* L. (Medina et al. 2021). Phytochemical analysis of laticiferous members of the family has shown that components of latex are a toxic deterrent against insects. Flavonoids, phenols, triterpenes, and saponins detected in extracts of *Paullinia* L. and *Dodonaea* Mill. seem to be the main components responsible for the anti-insect effect, as well as for the medicinal properties of those plants (Díaz and Rossini 2012, and references therein).

To date, there have been no subcellular studies of laticifers of Sapindaceae. However, considering the fact that laticifers of the family produce lattices with similar classes of compounds to those of other families (Ramos et al. 2020), we can predict that laticifers in Sapindaceae should have a dense cytoplasm with many secretory vesicles formed by endoplasmic reticulum and plastids, numerous mitochondria, and abundant lipid bodies distributed throughout peripheral and central vacuole (Wilson and Mahlberg 1978, 1980; Inamdar et al. 1988; Roy and De 1992; Gama et al. 2017; Fang et al. 2019). The central vacuole is the most prominent organelle of laticifers in which the metabolites are stored (Medina et al. 2021). Latex remains within the cell and is only released to the outside by tissue rupture.

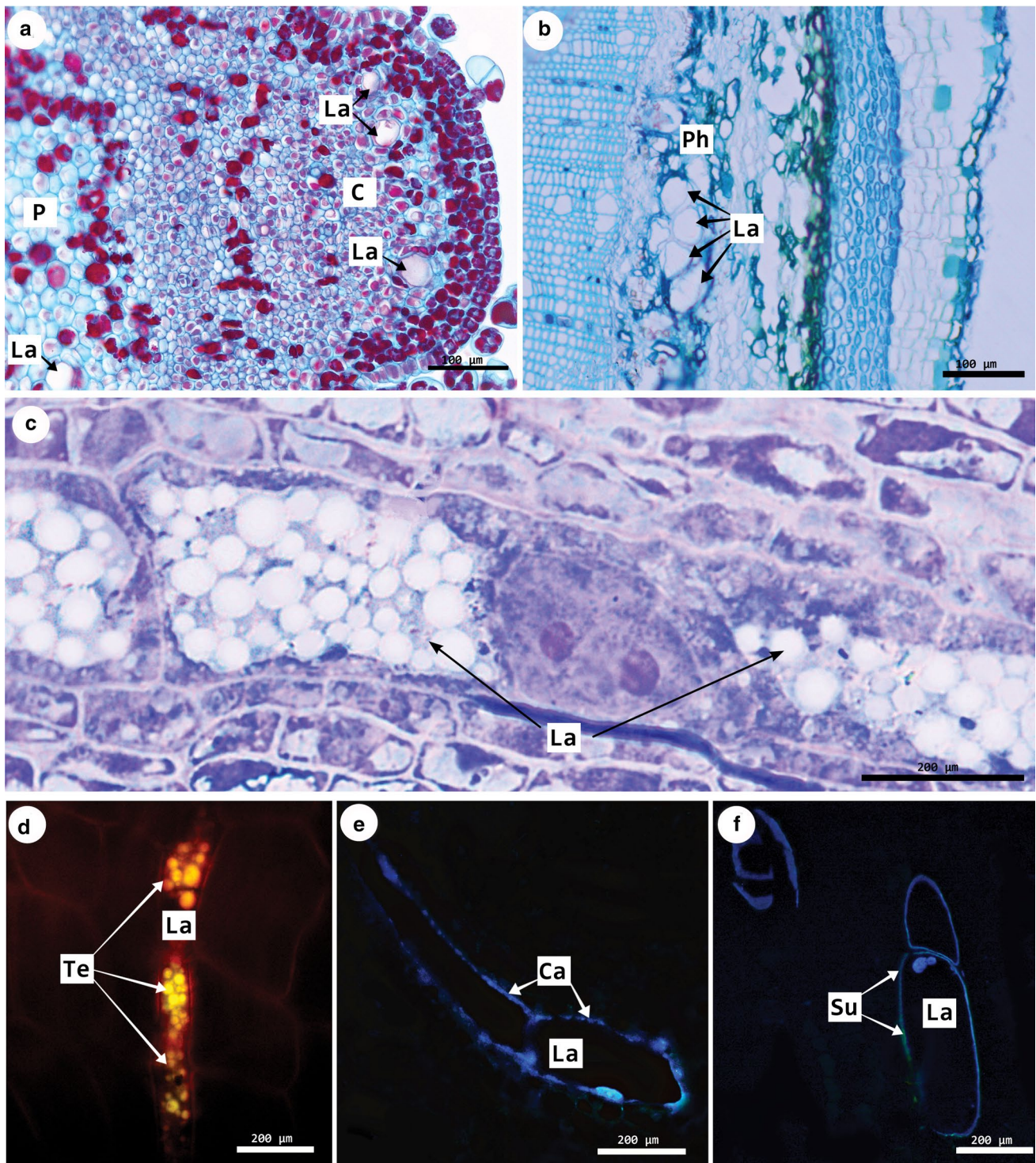


Fig. 4 Laticifers in Sapindaceae. **a–b** Transverse sections. **c–f** Longitudinal sections. **a** Primary laticifers in cortex and pith of *Serjania caracasana* (Jacq.) Willd. **b** Secondary laticifers in the phloem of *Dipteronia sinensis* Oliv. **c** *Urvillea ulmacea* Kunth. Note that the cells constituting the laticifer do not merge. **d** Terpenes detected in the latex of *Urvillea ulmacea* Kunth with neutral red observed under blue light. **e** Callose deposition in laticifer cell wall of *Paullinia seminuda* Radlk. using aniline blue test under UV light. **f** Autofluorescence of suberin in laticifer cell wall of *Thouinia tomentosa* DC. under UV light. C, cortex; Ca, callose; La, laticifers; P, pith; Ph, phloem; Su, suberin; Te, terpenes

Laticifers had at least five independent origins in Sapindaceae (Medina et al. 2021), which may be related to their different positions within the organs depending on the lineage. In Sapindoideae, the subfamily with the largest number of species, primary and secondary laticifers have been observed in the cortex and/or pith and in the secondary phloem in the subtribes Paullinieae, Thouinieae, Athyaneae, Melicoccus group, Cupania group, and Litchi group. In Dodonaeoideae, only primary laticifers are present in the cortical region, and in Hippocastanoideae only secondary laticifers have been found in the phloem (Medina et al. 2021). In addition, some distinctive features have been observed in the laticifer cell wall of some genera. In *Paullinia* L. and *Serjania* Mill., the cell walls have callose (Fig. 4e), considered an important innovation in the diversification of these genera. On the other hand, suberin is present in the laticifer walls of *Diatenopterix* Radlk., *Thouinia* Poit. and *Talisia* Aubl. (Fig. 4f) (Medina et al. 2021).

The variable features and occurrence of laticifers may have taxonomic or phylogenetic importance in some groups (Rudall 1987; Simpson 2010), as recently observed for Sapindaceae. The comprehensive study of Medina et al. (2021) indicates the secondary loss of latex in *Cardiospermum* L. within tribe Paullinieae. This unexpected result may help us to re-evaluate the circumscription of the genus since some species of *Cardiospermum* L. analyzed actually have laticifers. However, these latescent species of *Cardiospermum* L. seem to be more closely related to *Serjania* Mill. and *Urvillea* Kunth, according to the phylogenetic analysis of Acevedo-Rodríguez et al. (2017).

Secretory idioblasts – In Sapindales, idioblasts have been reported in all families of the order (Fig. 1) (Tölke et al. 2021). Like laticifers, the idioblasts keep their secretion inside the cell (Fahn 1979). They are specialized cells easily distinguished from others by their content and occur either singly or as groups of cells (Metcalfe and Chalk 1950; Fahn 1979). These structures are dispersed throughout the plant body, in all primary and secondary tissues of roots, stem, leaves, flowers, and fruits (Metcalfe and Chalk 1950; Solís and Ferrucci 2006; Bachelier and Endress 2008; Bachelier et al. 2011; Alves et al. 2017; Cunha-Neto et al. 2017; Rosalem et al. 2017; Tilney et al. 2018a, b; El Ottra et al. 2019; Medina et al. 2021). Three types of idioblasts have been recorded in the order: phenolic (Fig. 5a–c), mucilaginous, and oleiferous (Fig. 5d–e).

Phenolic (or tanniniferous) idioblasts are ubiquitous in Sapindales (Fig. 1) (Metcalfe and Chalk 1950; Bachelier et al. 2011; Kubitzki 2011; Muntoreanu et al. 2011; Alves et al. 2017; Cunha-Neto et al. 2017; Rosalem et al. 2017; Tilney et al. 2018a, b; Medina et al. 2021; Pace et al. 2021; Tölke et al. 2021; this study). They are present as the only secretory structure of the plant or as a redundant secretory

defensive system since many species have other protective glands co-occurring in their organs (this study). Phenolic idioblasts occur in all fundamental and vascular tissues of roots, stem, leaves, in all floral organs (Fig. 5a–b, f) and fruits, and have sometimes also been observed in the epidermis of leaves and floral organs (Fig. 5f). In the secondary phloem and xylem, these secretory cells are often described as phenolic-containing cells of axial and radial parenchyma (Metcalfe and Chalk 1950; Bachelier et al. 2011; Muntoreanu et al. 2011; Alves et al. 2017; Cunha-Neto et al. 2017; Rosalem et al. 2017; Tilney et al. 2018a, b; Medina et al. 2021; Pace et al. 2021; Tölke et al. 2021; this study).

Mucilage idioblasts have been reported for some species of all families, except for Biebersteiniaceae, likely due to the lack of anatomical studies (Fig. 1). These idioblasts have been found in few genera, located in the epidermis (Fig. 5c; sometimes making up the entire epidermis), hypodermis, and/or mesophyll of leaves and floral organs. Two types of mucilage idioblasts may be found in the order, with the larger ones showing an odd, restricted distribution in the organs (Metcalfe and Chalk 1950; Matthews and Endress 2006; Bachelier and Endress 2008; Bachelier et al. 2011; Kubitzki 2011; El Ottra et al. 2019). They have been called “special mucilage cells” by some authors and are located exclusively in the adaxial epidermis of leaves (Fig. 5c) and mainly in the abaxial epidermis and hypodermis of sepals, i.e., in the exposed surface of the organ, indicating a likely protective function for the leaf tissues and floral bud, respectively (Matthews and Endress 2006, and references therein). In *Citrus*, leaf mucilage idioblasts also contain crystals (Fig. 5c). The association of crystals with mucilage is rare in Sapindales and has previously been reported only in *Nitraria* (Nitrariaceae; Gregory and Baas 1989). Apparently, the water-holding capacity of mucilage is strongly influenced by calcium (Gregory and Baas 1989).

Oil idioblasts occur exclusively in Meliaceae, distributed throughout the family (Fig. 1) (Metcalfe and Chalk 1950). This third type of idioblast is a synapomorphy of the family and often stands out by its relative large size, several times larger than the phenolic idioblasts (Fig. 5d–e). Due to its usual spheroidal shape, these idioblasts have been misinterpreted as secretory cavities by some authors. Oil idioblasts occur only in the parenchyma (Fig. 5d–e), being found in the mesophyll of leaves, cortex, and pith of stem and in all floral organs (Dayanandan and Ponsamuel 2000; this study), as well as in roots, bark, and cotyledons of *Azadirachta* A. Juss. (Dayanandan and Ponsamuel 2000). Even though oil idioblasts have been described in leaves of some genera of Rutaceae (e.g., *Spathelia* L., Appelhans et al. 2011), this is a misinterpretation of smaller oil cavities.

Ultrastructural studies of idioblasts are scarce in Sapindales. However, their secretory apparatus varies according to

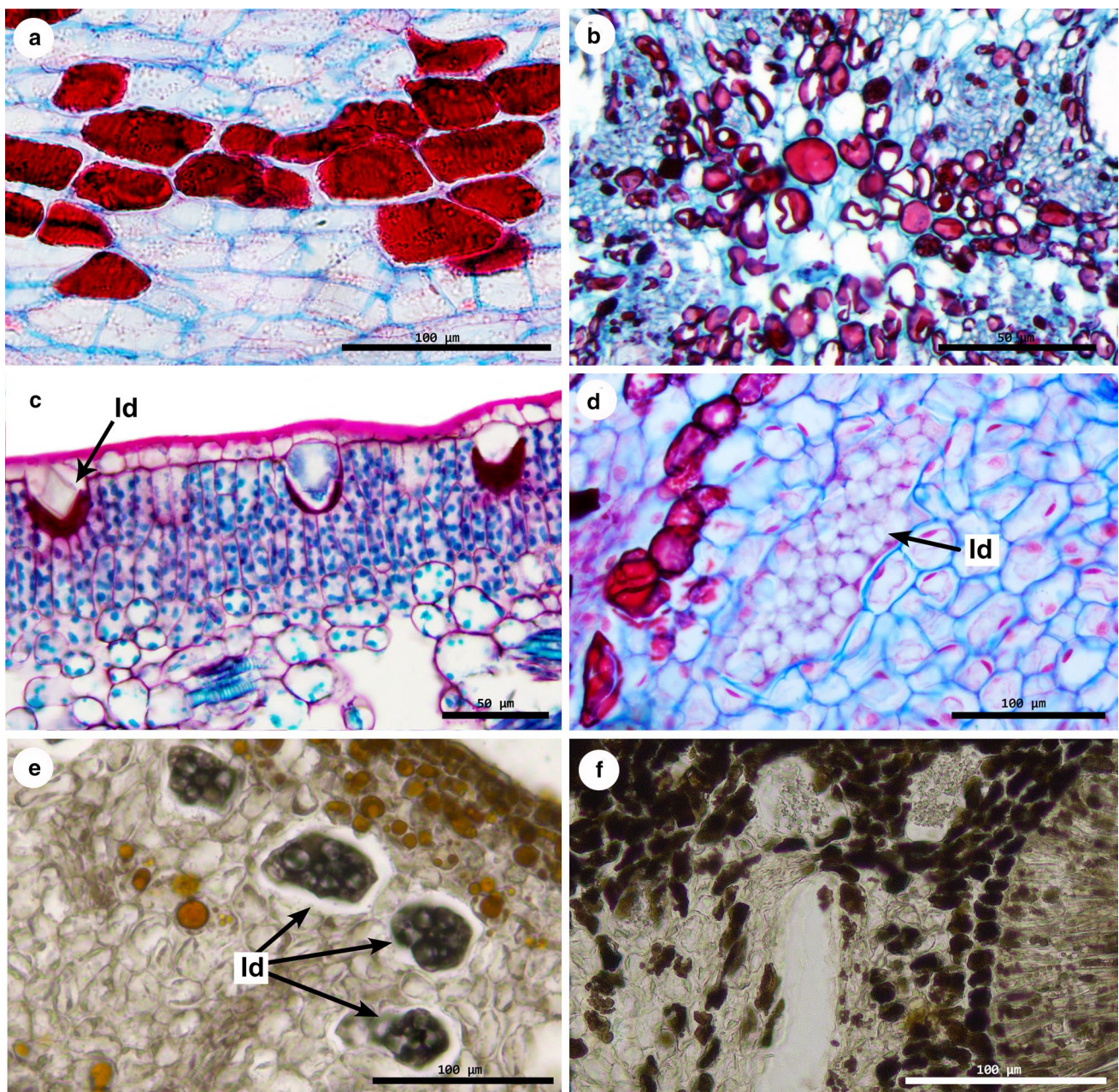


Fig. 5 Secretory idioblasts in Sapindales. **a–b, f** Phenolic idioblasts. **c** Mucilage idioblasts. **d–e** Oil idioblasts. **a** Pedicel of *Homalolepis cedron* (Planch.) Devecchi & Pirani (Simaroubaceae). **b** Pith of *Schinus molle* L. (Anacardiaceae). **c** Leaf of *Citrus sinensis* (L.) Osbeck (Rutaceae). Note the presence of a prismatic crystal within the mucilage idioblast. **d** Ovary of *Guarea macrophylla* Vahl (Meliaceae). **e–f** Histochemical tests. **e** Lipids detected with Sudan black B in *Trichilia clausenii* C. DC. (Meliaceae). **f** Phenolic compounds identified by ferric chloride in *Guarea macrophylla* Vahl (Meliaceae). Id, idioblasts

the secreted material. Phenolic idioblasts have a prominent endoplasmic reticulum and many plastids of different sizes, which are the main structures responsible for the production of secretion, which is transferred into the central vacuole, where it will be stored. Many mitochondria and ribosomes are also seen but dictyosomes are scarce. In mature idioblasts, the vacuole is filled with an electron-dense material (Lacchia and Carmello-Guerreiro 2009). Similarly, oil

idioblasts of Meliaceae have a dense cytoplasm, particularly abundant in endoplasmic reticulum and ribosomes; plastids with osmiophilic material; mitochondria; microbodies and several vesicles with terpenoid. These terpenoid vesicles appear to originate by enlargements of the endoplasmic reticulum. The small vesicles fuse and produce larger vesicles with lipid droplets, which is characteristic of the mature idioblast (Dayanandan and Ponsamuel 2000). On the other

hand, mucilage idioblasts usually do not store the secretion within the protoplast in Sapindales. In general, except when the mucilage occurs associated with crystals within the vacuole, the mucilage is stored in the periplasmic space, i.e., in the space between the cell wall and the plasma membrane (Gregory and Baas 1989; Matthews and Endress 2006). The main organelle involved in mucilage production is the dictyosome producing numerous vesicles filled with polysaccharides which are released into periplasmic space by exocytosis. Upon prolonged mucilage deposition in this space, the secretion fills almost the entire cell lumen, compressing the protoplast against the cell wall, where only thin degenerating cytoplasmic strands remain (Trachtenberg and Fahn 1981; Bakker and Gerritsen 1992; Andreeva et al. 1998; Demarco and Carmello-Guerreiro 2011).

Collecters – Collecters are secretory structures producing a sticky substance, which cover the vegetative and reproductive buds, protecting the meristems against desiccation, sometimes inhibiting microorganism proliferation and also adhering small phytophagous insects (Fahn 1979; Thomas 1991; Ribeiro et al. 2017). In Sapindales they have been reported in only a few members of Anacardiaceae, Sapindaceae, Simaroubaceae, Meliaceae, and Rutaceae (Fig. 1) (Fisher and Rutishauser 1990; Thomas 1991; Souza 2010; Lacchia et al. 2016b; Macêdo et al. 2016; Tilney et al. 2018b; Cortez et al. 2021). Two morphological types of collectors are found in Sapindales: trichomes and emergences (Fig. 6a–c).

Trichomatous collectors are the most common type in Sapindales. By the way, they are found in Anacardiaceae, Sapindaceae, Simaroubaceae, Meliaceae, and Rutaceae (Figs. 1 and 6a–c). They are observed on leaf primordia, young leaves, and prophylls, releasing a mucilaginous sticky secretion (Souza 2010; Lacchia et al. 2016b; Macêdo et al.

2016; Cortez et al. 2021). Since the trichomes are the most common type of collector in Sapindales and glandular trichomes are one of the most ordinary secretory structure in Sapindales (Kubitzki 2011; Tölke et al. 2021), it is likely that trichomatous collectors occur in many other species and families of the order.

Trichomatous collectors of Sapindales are formed by a uni- or biseriata non-glandular stalk and a multicellular secretory head (Fig. 6a–c). The secretory head is multiseriata, elongate in Anacardiaceae, Meliaceae, and Sapindaceae (Souza 2010; Lacchia et al. 2016b; Fig. 6a–c), while short, wide secretory heads are observed in collectors of Simaroubaceae and Rutaceae (Macêdo et al. 2016; Cortez et al. 2021; this study). The development of these collectors is asynchronous, originating from protoderm during the first stages of leaf development. The secretory phase occurs early, and the secretion is released to the outside from the gland, crossing the cuticle without rupturing it. After leaf expansion, collectors degenerate and fall off (Fig. 6c) (Lacchia et al. 2016b; Macêdo et al. 2016; Cortez et al. 2021; this study).

In Meliaceae emergences are also reported (Fig. 1), i.e., they originate from protoderm and subprotodermal tissues (Fahn 1990). They are conical in shape, composed of a short stalk and a head composed of a secretory epidermis surrounding a central axis of non-secretory parenchyma devoid of vascular tissues (Fig. 6d) (Tilney et al. 2018b). Morphologically, these collectors are the standard type described by Lersten (1974). In intermediate stages of leaf development, they turn brown, dry up and fall off (Tilney et al. 2018b). Although these collectors had been found in *Ekebergia* Sparrm. (Tilney et al. 2018b), they may not be the only type found in the family, since trichomes containing a wide secretory head, morphologically similar

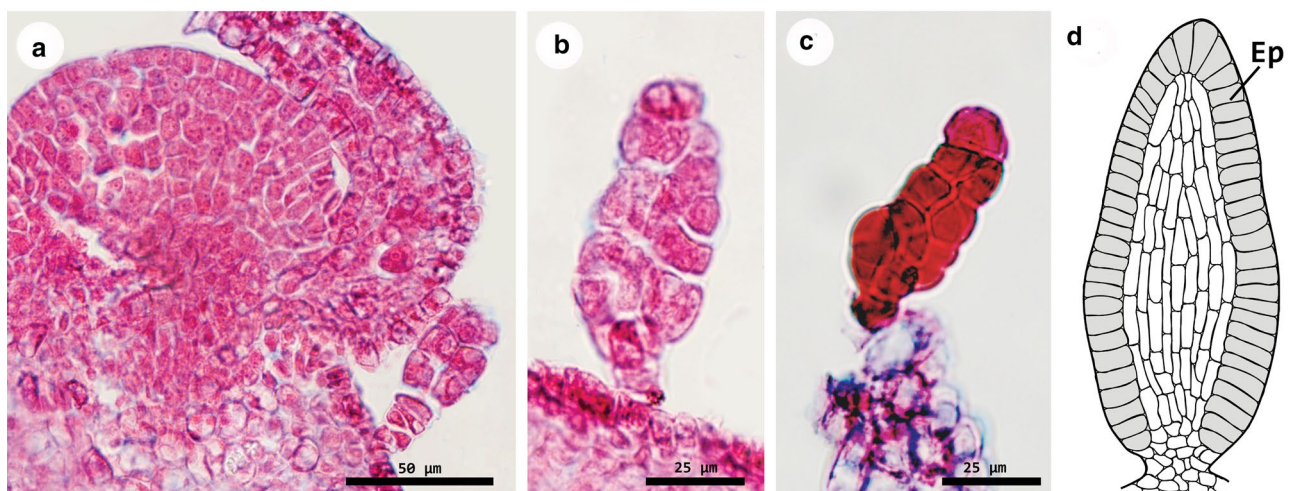


Fig. 6 Diversity of collectors in Sapindales. **a–c** Trichomatous collectors in the shoot apex of *Trichilia clausenii* C. DC. (Meliaceae). **a–b** Secretory phase. **c** Senescent phase. **d** Schematic draw of the standard collector found in Meliaceae. Ep: epidermis

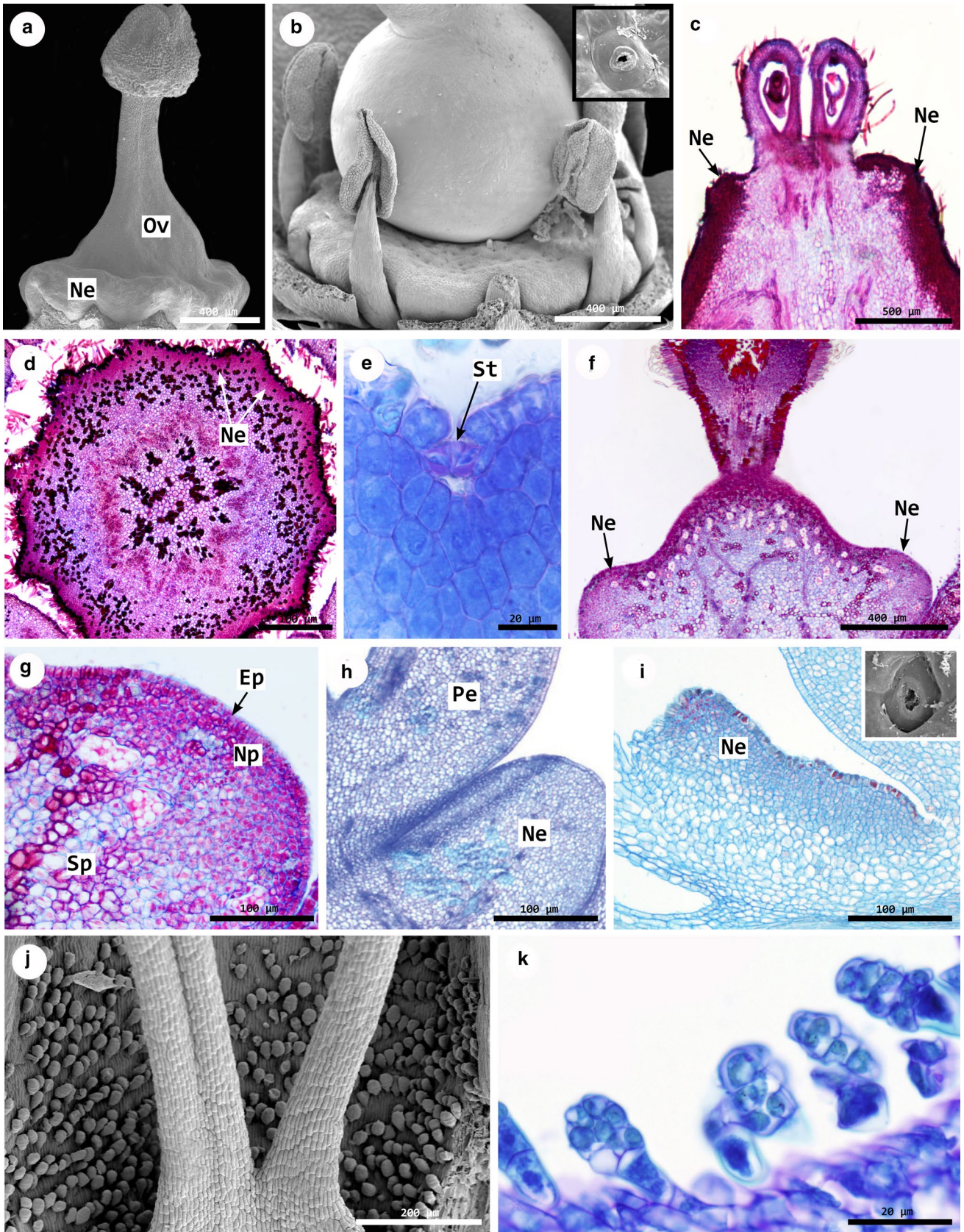


Fig. 7 Floral nectaries in Sapindales. **a** Nectary disk surrounding the ovary of *Trichilia clausenii* C. DC. (Meliaceae). **b** Nectary disk of *Schinus engleri* F.A. Barkley (Anacardiaceae). Note the stoma (inset). **c, f–i, k** Longitudinal sections. **d–e** Transverse sections. **c–e** Gynophore of *Homalolepis cedron* (Planch.) Devecchi & Pirani (Simaroubaceae), showing the peripheral nectariferous tissue (**c–d**). Note the presence of a stoma (**e**). **f–g** Nectary disk of *Trichilia clausenii* C. DC. (Meliaceae). **h** Nectary disk of *Citrus sinensis* (Rutaceae). **i** Nectary disk of *Astronium graveolens* Jacq. (Anacardiaceae), detail of a stoma in the square. **j–k** Trichomatous nectary on the petals of *Anacardium humile* A. St.-Hil. Ep, epidermis; Ne, nectary; Np, nectariferous parenchyma; Pe, petal; Sp, subnectariferous parenchyma; St, stoma; Ov, ovary

to colleters of Simaroubaceae and Rutaceae, have been observed in *Melia* L. (Tilney et al. 2018a).

The histochemical characterization of the secretions produced by colleters in Anacardiaceae, indicates the presence of a complex mixture containing mucilage, fatty acids, and phenolic compounds; however, in Rutaceae the secretion contains only mucilage and lipids, and only mucilage has been detected in colleters of Sapindaceae and Meliaceae (Souza 2010; Lacchia et al. 2016b; Macêdo et al. 2016; Tilney et al. 2018b). Mucilage is the main component responsible for avoiding desiccation due to its hygroscopic characteristic, but the presence of phenolic compounds and/or lipids in the secretion is important to prevent the proliferation of microorganisms, which can be promoted by mucilage (Ribeiro et al. 2017).

There is no ultrastructural study of the colleters of Sapindales. However, the differences in secretion composition observed so far may be related to distinct secretory apparatus and secretion release to the colleter surface, as observed in many families of angiosperms. The production of mucilage is performed in the dictyosomes and a close association between this organelle and the rough endoplasmic reticulum is commonly found in mucilaginous colleters. On the other hand, colleters which produce secretion containing lipids and phenolic compounds usually have abundant plastids containing plastoglobules. Additionally, recent studies have also reported the participation of the vacuole in the secretion mechanism of both types of colleters (Ribeiro et al. 2021 and references therein). New studies are required to ascertain whether the secretory pattern observed in colleters of other orders is also present in Sapindales.

Nectaries – Nectaries are widespread in Sapindales, occurring in all families in vegetative and reproductive organs. According to the origin/ position, three types of nectaries are recognized: floral nectaries, extrafloral nectaries (in shoots), and post-floral nectaries (in fruits).

Floral nectaries. All families of Sapindales have floral nectaries, which are morphologically diverse (Fig. 1). They

can occur, as disks, single glands (emergences) around the ovary, trichomes, and the gynophore/androgynophore surface may also be nectariferous (Fig. 7a–k). The nectariferous disk is the most common type of nectary, which is usually located surrounding the gynoecium in intrastaminal position (Fig. 7a–b) (Bachelier and Endress 2008, 2009; Kubitzki 2011; Solís et al. 2017; Tölke et al. 2018b; El Ottra et al. 2019; Alves et al. 2021; Gama et al. 2021a; Pirani et al. 2021). However, this is not the type found in the early divergent families of the order. Instead of a disk, Biebersteiniaceae have extrastaminal single glands, i.e., they are not fused to each other, and Nitrariaceae have sunken nectariferous glands in intrastaminal position, not forming a disk either (Bachelier et al. 2011; Muellner 2011). In all other families of the order, an extra- or intrastaminal disk is observed (Kubitzki 2011 and references therein). The extrastaminal nectariferous disk has been interpreted as a derived condition and a synapomorphy of Sapindaceae but also occurs in a few members of Anacardiaceae (Ronse De Craene and Haston 2006; Acevedo-Rodríguez et al. 2011; Pell et al. 2011; Muellner-Riehl et al. 2016; Solís et al. 2017; Tölke et al. 2018b). Despite the widespread occurrence of nectaries, they are completely absent in some genera of the order (e.g., *Tetradiclis* Steven ex M. Bieb. in Nitrariaceae, *Pistacia* L. in Anacardiaceae, *Dodonaea* Mill. in Sapindaceae, *Toona* (Endl.) M. Roem. in Meliaceae, *Leitneria* Chapm. in Simaroubaceae, *Lunasia* Blanco in Rutaceae) (Bachelier and Endress 2009; Bachelier et al. 2011; Kubitzki 2011; El Ottra et al. 2019).

The nectariferous disk has a diverse morphology, even within the family, ranging from inconspicuous to a large cup- and/or cushion-shaped structure, or even tubular disks longer than the ovary, sometimes united with the gynoecium, like in some species of Burseraceae, Meliaceae, Simaroubaceae, and Rutaceae (Nooteboom 1962; Bachelier and Endress 2009; Kubitzki 2011; El Ottra et al. 2019; Gama et al. 2021a, b; Lima et al. 2021; Alves et al. 2021).

Particularly in Rutaceae, structural analyses were used to support hypotheses on the origin of the disk, since the first half of the twentieth century. They may be originated from sterilized whorls, either carpels (Moore 1936; Saunders 1934) or vestigial stamens (Tillson and Bamford 1938), from both the receptacle and gynoecium base (Gut 1966) or as a proliferation from the floral axis (Tilak and Nene 1976; Ramp 1988). Additionally, the nectar-secreting floral base in *Zanthoxylum* L. has recently been described as “transitional between gynophore and disk” (Kubitzki et al. 2011, p. 281). In the subtribe Galipeinae, developmental analyses indicate that the nectary disk is not a modified floral organ, since it appears as an axillary protrusion that eventually may share a common base with inner or outer floral organs (El Ottra et al. 2019). Additional studies in Sapindales are still on demand.

Despite the variation in morphology of the disks or the occurrence of nectaries as single glands, they are all anatomically very similar, composed of an uniseriate non-secretory epidermis, a nectariferous and a subnectariferous parenchyma which may be supplied by xylem and phloem, only phloem or no own vascular tissues (Fig. 7c–i) (Ning-Xi and Wu 2005; Bachelier and Endress 2008, 2009; Solís and Ferrucci 2009; Kubitzki 2011; Tölke et al. 2015, 2018b; Avalos et al. 2017; Solís et al. 2017; El Ottra et al. 2019; Gama et al. 2021b). The surface of the nectary may be papillose, and the nectar is released through stomata, which can vary in density depending on the species (Fig. 7b, e, i) (Bachelier and Endress 2008, 2009; Tölke et al. 2015, 2018b; Avalos et al. 2017; Solís et al. 2017; El Ottra et al. 2019; this study).

In many species in which the disk and single nectaries are not observed, the function of nectar secretion is transferred to other structures, i.e., other types of nectary evolved in some lineages. In some genera of Anacardiaceae, trichomatous nectaries are found on the base of the adaxial side of petals (e.g., *Anacardium* L.) (Fig. 7j–k). These trichomes are structurally similar to the common type of glandular trichome of Anacardiaceae, composed of a non-glandular uniseriate stalk and a multicellular secretory head (Tölke et al. 2018b; see “Colleters”, “EFNs”, “Osmophores”, “Glandular trichomes” sections). The main difference in relation to the other glandular trichomes of the family is its function. The secretion of nectar characterizes this type of trichome as a nectary.

In some genera lacking nectariferous disks but containing gynophore or androgynophore, the surface of these stalk-like elongations became nectariferous (Fig. 7c–d). Gynophores and androgynophores evolved independently in Simaroubaceae, Meliaceae, and Rutaceae (Alves et al. 2021), and it is likely that nectariferous tissues occur in many of them. Nectaries have been reported at the periphery of gynophores in *Homalolepis* Turcz., *Quassia* L., *Simaba* Aubl., *Simarouba* Aubl. and likely also in *Picrolemma* Hook. f. in Simaroubaceae (Alves et al. 2017, 2021; Pirani et al. 2021), in *Adiscanthus* Ducke in Rutaceae (El Ottra et al. 2019) and *Guarea* F. Allam. ex L. in Meliaceae (ongoing study). The analysis of this nectary in *Homalolepis* Turcz. revealed that the nectary is composed of a non-secretory epidermis and many layers of nectariferous parenchyma vascularized by phloematic bundles (Fig. 7c–d). Nectar is released through stomata, as observed in the nectariferous disks and single nectaries (Fig. 7e).

The secretory apparatus of the nectariferous cells is variable in Sapindales and is linked to the substances produced, as demonstrated in Anacardiaceae (Tölke et al. 2018b). In Anacardiaceae and other Sapindales, the nectary produces not only sugars but also phenolic compounds, lipids, and polysaccharides; thus, the ultrastructure of the secretory cells is diverse among the species (Giuliani et al. 2012;

Avalos et al. 2017; Tölke et al. 2015, 2018b). In those species in which nectar contains oils, the cells have many free oil droplets in the cytosol, prominent smooth endoplasmic reticulum, and many plastids containing plastoglobules (Giuliani et al. 2012; Paiva 2012; Avalos et al. 2017; Tölke et al. 2015, 2018b). On the other hand, nectaries lacking oils have cytoplasm containing rough endoplasmic reticulum and many mitochondria, dictyosomes, and amyloplasts (Giuliani et al. 2012; Avalos et al. 2017; Tölke et al. 2015, 2018b). In both cases many secretory vesicles containing various contents are widespread in the secretory cells, indicating the granulocrine secretion from cell-to-cell, transferring the nectar across the layers of cells of the nectary until it reaches the epidermis, releasing the nectar to the outside via stomata (Giuliani et al. 2012; Paiva 2012; Avalos et al. 2017; Tölke et al. 2015, 2018b). Eccrine secretion and a combination of granulocrine and eccrine mechanisms have also been reported (Paiva 2012; Tölke et al. 2015, 2018b). In trichomes, the nectar is released through the outer periclinal cell wall and the cuticle (Tölke et al. 2018b).

Little is known about the evolution of floral nectaries in Sapindales, but their occurrence seems to be ancestral in the order, with its loss in some lineages. The nectariferous disk was indicated as a putative synapomorphy of the order (Gadek et al. 1996). The intrastaminal position of the disk is also considered ancestral, with a transition to extrastaminal position in Sapindaceae and a small clade of Anacardiaceae (Ronse De Craene and Haston 2006; Muellner-Riehl et al. 2016; Solís et al. 2017; Alves et al. 2021). Regarding the nectaries located at the surface of a gynophore, this structure was retrieved as a putative synapomorphy for the clade including *Quassia* L. and 10 other genera, a lineage which is more or less equivalent to Engler’s (1931) tribe Simaroubeae, but with further losses in some genera (Devecchi et al. 2018a; Alves et al. 2021). According to Alves et al. (2021) gynophores likely evolved independently in Simaroubaceae, Meliaceae, and Rutaceae. In a few taxa of these three families, an androgynophore evolved, such as *Cedrela* P. Browne and *Toona* (Endl.) M. Roem. (Meliaceae, Gouvêa et al. 2008; Gama et al. 2021a), *Cneorum* (Rutaceae, Caris et al. 2006), and *Ailanthus glandulosus* Desf. (Simaroubaceae, Ramp 1988). Nectar production by androgynophores remains a matter of further investigation.

Inferences about the production of diverse substances by the nectary are still hampered by the scarcity of studies. However, Tölke et al. (2018b) hypothesize that the production of lipids by the floral nectary may be widespread in Sapindales. They also demonstrated that the composition of the nectar sugars is of limited value to the systematics of Anacardiaceae, and probably to other Sapindales as well, since the composition of the nectar may largely vary among species of the same subfamily and/or genus.

Extrafloral nectaries. Extrafloral nectaries are morphologically diverse glands that vary greatly in their location, size and form (Elias 1983; Weber and Keeler 2013). Many parts of the plant may contain extrafloral nectaries, such as leaves (lamina, petiole, and stipules), stems, bracts, bracteoles, inflorescence axis, fruits, and even cotyledons (Elias 1983; Schmid 1988; Marazzi et al. 2013; Weber and Keeler 2013; Gama et al. 2019).

Extrafloral nectaries have been reported in most families of Sapindales, including Anacardiaceae, Burseraceae, Sapindaceae, Simaroubaceae, Meliaceae, and Rutaceae (Fig. 1; Table 1) (Paiva et al. 2007; Souza 2010; Devecchi and Pirani 2015; Lacchia et al. 2016a; Tilney et al. 2018a, b; Andrade et al. 2020; this study). Several studies have extensively documented EFN mainly on the leaves of species belonged to Sapindales, but they may also occur on bracts and peduncle (i.e., *Anacardium* L. in Anacardiaceae) (Wunnachit et al. 1992; Rickson and Rickson 1998; Souza 2010; Devecchi and Pirani 2015; Lacchia et al. 2016a).

The morphology of extrafloral nectaries in Sapindales is diverse, ranging from trichomatous to stalked glands, circular or slightly elliptical structures (ocelli), and sometimes the entire organ (or part of it) is modified into a nectary (Fig. 8a–g) (Bory and Clair-Maczulajtys 1990; Paiva et al. 2007; Souza 2010; Alves 2015; Devecchi and Pirani 2015; Lacchia et al. 2016a; Tilney et al. 2018a, b; Andrade et al. 2020; this study).

Nectariferous trichomes are found in Anacardiaceae (Fig. 8a–b). These nectaries are morphologically differentiated in pit-like structures on leaves and bracts, where many trichomes are observed (Rickson and Rickson 1998; Lacchia et al. 2016a). The depressions, which harbor the trichomes, are commonly misinterpreted as domatia due to their morphological appearance. However, Lacchia et al. (2016a) demonstrated the production and secretion of glucose by those trichomes in *Anacardium humile* A. St.-Hil., confirming their nectariferous nature. However, a species does not necessarily have a single type of nectary. Secretion of nectar has been detected on the inflorescence axis of the same species, *A. humile* A. St.-Hil.; and although the authors did not observe the tissue responsible for the nectar secretion (nonstructured nectary), they hypothesized that it is released through stomata (Rickson and Rickson 1998).

Extrafloral nectaries have also been reported in Burseraceae, Sapindaceae, and Simaroubaceae, but only a few studies have explored the anatomy and morphology of these glands. They generally occur on leaves (petiole, lamina, stipule) and cataphylls (Fig. 8c–g) (Bory and Clair-Maczulajtys 1990; Morellato and Oliveira 1991; Acevedo-Rodriguez 1993a, b; Fiala and Linsenmair 1995; Silva 2009; Koptur et al. 2010; Boudouris and Queenborough 2013; Devecchi and Pirani 2015). Morphologically, the foliar nectaries of Sapindaceae and Simaroubaceae are very similar. Elongate

vascularized stalked glands are found in *Paullinia* L. (Sapindaceae) (Fig. 8c–f) and *Ailanthus* Desf. (Simaroubaceae), for example. They are located on the leaf margins in *Paullinia* L. (Souza 2010) but vary in *Ailanthus* Desf. In the latter, nectaries are found at the base of petiole, abaxial side of the lamina and also on the margins of cataphylls (Bory and Clair-Maczulajtys 1990, and references therein). The diversity of nectary positions in *Ailanthus* Desf. reveals a diversity of origins of the EFNs in Simaroubaceae. The petiolar nectaries of *Ailanthus* Desf. are interpreted as modified stipules (Bory and Clair-Maczulajtys 1990), while *Homalolepis* Turcz. and *Simaba* Aubl. stands out by the presence of a nectary at the leaflet apex (Pirani et al. 2021; this study), as well as at the apex of reduced prophylls in *Homalolepis* Turcz. (Cortez et al. 2021). Despite the morphological and ontogenetic differences, all these nectaries of Sapindaceae and Simaroubaceae are composed of a nectariferous parenchyma, vascularized by xylem and phloem, and covered by a non-secretory epidermis, releasing the nectar through stomata (Bory and Clair-Maczulajtys 1990; Souza 2010; Alves 2015; Cortez et al. 2021; this study). There are also records of EFNs in *Pometia* J.R. Forst. & G. Forst., *Serjania* Mill., *Xerospermum* Blume (in Sapindaceae), *Simarouba* Aubl. and *Quassia* L. (in Simaroubaceae), and *Protium* (in Burseraceae); however, no information about their structure is provided, which hampers comparative studies in these families (Morellato and Oliveira 1991; Acevedo-Rodriguez 1993a, b; Fiala and Linsenmair 1995; Silva 2009; Koptur et al. 2010; Boudouris and Queenborough 2013; Devecchi and Pirani 2015; Pirani et al. 2021).

The EFNs in Meliaceae and Rutaceae are morphologically distinct from those described for the rest of the order. They are widespread on leaflets in Rutaceae and Meliaceae but also occur on petiole, rachis, and even on bracts in Meliaceae (Morellato and Oliveira 1994; Paiva et al. 2007; Kenfak et al. 2014; Tilney et al. 2018a, b; Andrade et al. 2020). The EFNs in both families are circular or slightly elliptical in shape, being flattened or depressed in relation to the epidermis in Rutaceae and Meliaceae or elevated in some Meliaceae (Morellato and Oliveira 1994; Paiva et al. 2007; Kenfak et al. 2014; Tilney et al. 2018a, b). All of them are similar in origin and composed of a uniseriate nectariferous epidermis and a nectariferous parenchyma (Paiva et al. 2007; Tilney et al. 2018a, b; Andrade et al. 2020). Stomata, trichomes, and vascular tissue are absent, and the nectar is released via epidermis through cuticular rupture (Morellato and Oliveira 1994; Paiva et al. 2007; Tilney et al. 2018a, b; Andrade et al. 2020). Although *Homalolepis* Turcz. and *Simaba* Aubl. (Simaroubaceae) also have ocelli scattered on the leaf blade (Fig. 8g), they are structurally similar to the apical nectaries (in the same genera) and differ from those of Rutaceae and Meliaceae by releasing the nectar through stomata (Alves 2015). In Rutaceae, in addition to the ocelli

Table 1 Extrafloral nectaries (EFNs) in genera and families of Sapindales

Genus	Distribution	Structure	Reference
Anacardiaceae			
<i>Anacardium</i> L	Leaves, inflorescence axes, bracts, fruits	Trichomatous	Wunnachit et al. (1992), Rickson and Rickson (1998), Lacchia et al. (2016a)
<i>Holigarna</i> Buch.-Ham. ex Roxb	Petiole, stipules, bracts	–	Weber et al. (2015)
Burseraceae			
<i>Protium</i> Burm. f	Leaves	–	Morellato and Oliveira (1991)
Sapindaceae			
<i>Chimborazoa</i> H.T. Beck	–	–	Weber et al. (2015)
<i>Paullinia</i> L	Leaves, stipules	Stalked glands	Souza (2010)
<i>Pometia</i> J.R. Forst. & G. Forst	Leaves, stipules	–	Fiala and Linsenmair (1995)
<i>Serjania</i> Mill	Leaves	–	Silva (2009)
<i>Xerospermum</i> Blume	Leaves	–	Fiala and Linsenmair (1995)
Simaroubaceae			
<i>Ailanthus</i> Desf	Leaves	Stalked glands	Bory and Clair-Maczulajtyś (1990)
<i>Brucea</i> J.F. Mill	–	–	Weber et al. (2015)
<i>Eurycoma</i> Jack	–	–	Weber et al. (2015)
<i>Hannoa</i> Planch	–	–	Weber et al. (2015)
<i>Homalolepis</i> Turcz	Leaflet apex, apex of reduced prophylls	Ocelli flattened or depressed	Pirani et al. (2021), Cortez et al. (2021)
<i>Mannia</i> Opiz	–	–	Weber et al. (2015)
<i>Odyndea</i> Pierre ex Engl	–	–	Weber et al. (2015)
<i>Picrasma</i> Blume	–	–	Weber et al. (2015)
<i>Pierreodendron</i> Engl	–	–	Weber et al. (2015)
<i>Quassia</i> L	Leaves	–	Weber et al. (2015)
<i>Samadera</i> Gaertn	Leaves	–	Weber et al. (2015)
<i>Simaba</i> Aubl	Leaves, bracts, fruits	Ocelli flattened or depressed	Boudouris and Queenborough (2013), Alves (2015); Devecchi and Pirani (2015); Cortez et al. (2021)
<i>Simarouba</i> Aubl	Leaves	–	Morellato and Oliveira (1991), Koptur et al. (2010), Boudouris and Queenborough (2013)
Meliaceae			
<i>Carapa</i> Aubl	Leaves, petiole, rachis, bracts	Ocelli depressed or elevated	Elias (1983), Kenfak et al. (2014)
<i>Cedrela</i> P. Browne	Leaves, petiole, rachis	Ocelli flattened or elevated	Paiva et al. (2007)
<i>Cipadessa</i> Blume	Leaves, rachis	Ocelli elevated	Lersten and Pohl (1985)
<i>Dysoxylum</i> Blume	Leaves	–	Weber et al. (2015)
<i>Ekebergia</i> Sparrm	Leaves	Ocelli flattened	Tilney et al. (2018b)
<i>Entandophragma</i> C. DC	–	–	Tilney et al. (2018a)
<i>Guarea</i> F. Allam. ex L	Leaves, petiole, fruit	Ocelli elevated	Morellato and Oliveira (1994)
<i>Heynea</i> Roxb	Leaves	–	Clark (1990)
<i>Khaya</i> A. Juss	Leaves	–	Weber et al. (2015), Tilney et al. (2018a)
<i>Melia</i> L	Petiole	Ocelli depressed or elevated	Yamawo (2015), Tilney et al. (2018a)
<i>Nymania</i> Lindb	Leaves	–	Dahlgren and van Wyk (1988)
<i>Pseudocedrela</i> Harms	Leaves	–	Weber et al. (2015)
<i>Swietenia</i> Jacq	Leaves, petiole, rachis	Ocelli flattened or elevated	Lersten and Rugenstein (1982)
<i>Trichilia</i> P. Browne	Leaves, petiole	–	Schupp and Feener (1991)
<i>Turraea</i> L	–	–	Tilney et al. (2018a)
<i>Walsura</i> Roxb	Leaves	–	Clark (1990)

Table 1 (continued)

Genus	Distribution	Structure	Reference
Rutaceae			
<i>Angostura</i> Roem. & Schult	Leaves	Trichomatous	Weber et al. (2015)
<i>Euodia</i> J.R. Forst. & G. Forst	Leaves	–	Weber et al. (2015)
<i>Harrisonia</i> R. Br. ex A. Juss	–	–	Weber et al. (2015)
<i>Melicope</i> J.R. Forst. & G. Forst	Steam	–	Weber et al. (2015)
<i>Zanthoxylum</i> L	Leaves	Ocelli flattened or depressed; trichomatous	Andrade et al. (2020)

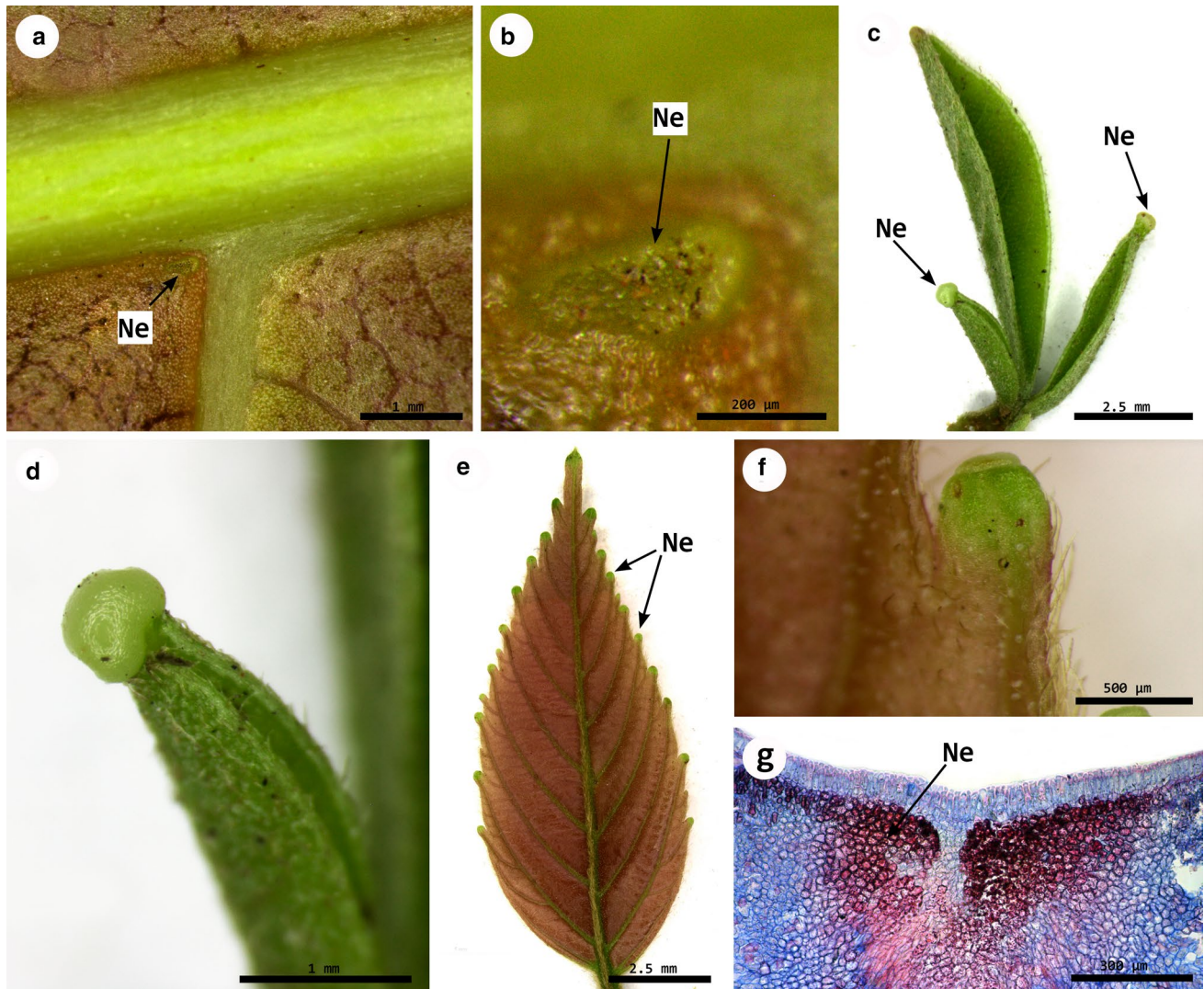


Fig. 8 Diversity of extrafloral nectaries in Sapindales. **a–b** Trichomatous nectaries. **c–f** Stalked nectaries. **g** Ocellus. **a–b** Leaf of *Anacardium occidentale* L. (Anacardiaceae). **c–d** Leaflet of *Paullinia carpopoda* Cambess. (Sapindaceae). **e–f** Leaflet of *Paullinia seminuda* Radlk. (Sapindaceae). **g** Leaflet of *Homalolepis cuneata* (A. St.-Hil. & Tul.) Devecchi & Pirani (Simaroubaceae). Ne, nectary

nectaries, trichomatous nectaries have also been found on leaves of *Zanthoxylum* (Andrade et al. 2020).

In general, the secretory activity of the EFNs begins early in leaf development and finishes before leaf maturity, reinforcing the protective function of the EFNs (Lersten and Rugenstein 1982; Lersten and Pohl 1985; Tilney et al. 2018a, b). Extrafloral nectaries of Sapindales are usually associated with the attraction of ants and other small arthropods, which protect developing leaves, shoots, and flowers from herbivores (Wunnachit et al. 1992; Rickson and Rickson 1998; Paiva et al. 2007; Marazzi et al. 2013; Alves 2015).

Studies focusing on the ultrastructure of the extrafloral nectaries in species of Sapindales are absent. The occurrence of EFNs in Sapindales as a whole appears to be underestimated, and as we have pointed out, very few studies provide information about the anatomy and substances produced by these structures. This gap of knowledge about the EFNs in the order makes it difficult to analyze the evolutionary patterns, regarding their occurrence and anatomical structure. However, there is a trend in Meliaceae and Rutaceae toward nonvascularized nectaries with rounded or elongate ocelli, while vascularized stalked glands are common in Sapindaceae and Simaroubaceae. On the other hand, EFNs seem to always be protodermal derived structures in Anacardiaceae.

Post-floral nectaries. A particular type of nectary that is not located in the flower (i.e., extrafloral) is found in Sapindales and deserves to be highlighted: post-floral nectaries. Despite the little information we have about the post-floral nectar secretion (sensu Schmid 1988) in the order, functional nectaries have been reported on fruits (pericarpial nectaries) or associated with fruits. They may be formed in the flower,

continuing the secretion of nectar during fruit development, or only after pollination, i.e., in the fruit (Schmid 1988).

Persistent floral nectaries are often observed during fruit development but they usually remain as non-functional glands, i.e., in the post-secretory phase, as observed in *Astro-nium* Jacq. (Anacardiaceae; Lima et al. 2021) and *Simaba* Aubl. (Simaroubaceae; Devecchi and Pirani 2015). However, floral nectariferous disks have been observed producing secretions in fruits of *Tapirira* Aubl. (Anacardiaceae), acting as true pericarpial glands (Tölke et al. 2015; Table 1). In other cases, nectaries are newly developed after pollination in growing fruits. In *Guarea macrophylla* Vahl (Meliaceae), numerous pericarpial nectaries are formed on fruits. Despite the distinct origin, these nectaries have the same structure of the leaf nectaries found in the family (Morellato and Oliveira 1994). These nectaries are usually associated with the promotion of seed dispersal (Faegri and van der Pijl 1979), but in *Anacardium occidentale* L. (Anacardiaceae) nectaries formed on the fruit secrete nectar only during fruit development and are associated with the attraction of ants, which protect the plant against frugivory (Wunnachit et al. 1992; Rickson and Rickson 1998).

Osmophores Osmophores are floral glands specialized in the production of volatile oils, which are mainly related to the long-distance attraction of pollinators (Vogel 1990; Tölke et al. 2019). In Sapindales, their occurrence has been documented in only a few members of Anacardiaceae, Rutaceae, and Sapindaceae (Fig. 1) (Bussel et al. 1995; Marques et al. 2015; Lima et al. 2016; Tölke et al. 2018a). In Anacardiaceae and Rutaceae (Fig. 9a–d), osmophores are located on the adaxial surface of petals and consist of a secretory epidermis (Fig. 9b).

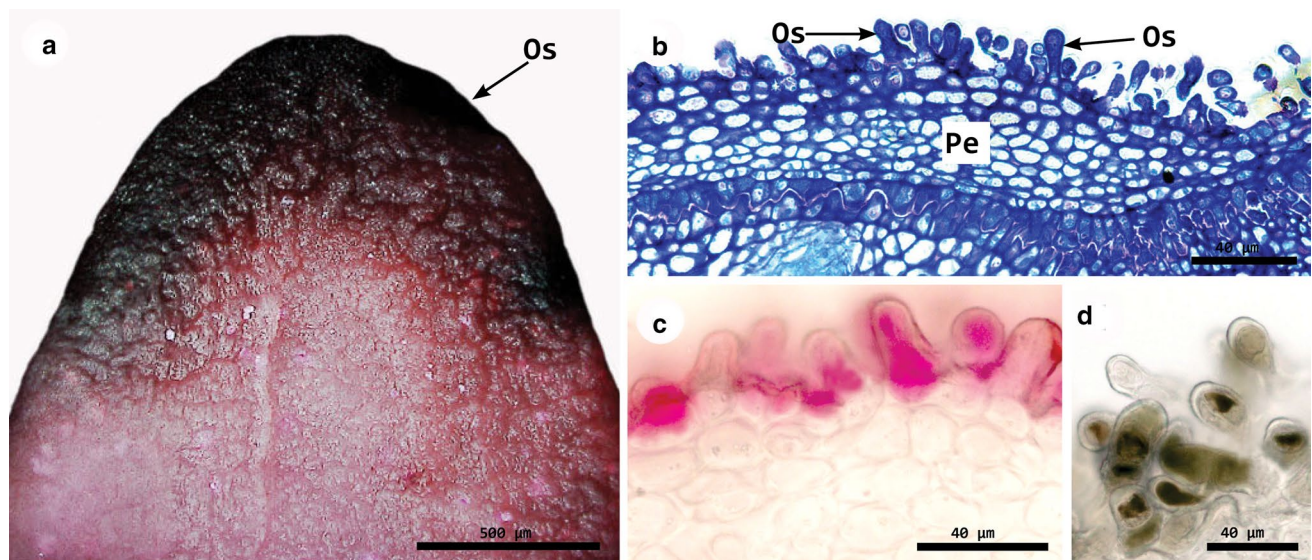


Fig. 9 Osmophores in *Citrus sinensis* (L.) Osbeck (Rutaceae). **a** Osmophore located at the tip of petal. **b** Osmophore constituted by a papillate epidermis. **c** Lipids detected using neutral red. **d** Phenolic compounds detected using ferric chloride. Os: Osmophores; Pe: petal

In *Anacardium* L. and *Mangifera* L. (Anacardiaceae), osmophores are located in the lower half of the petal, and the secretory cells are cubic to elongate (Tölke et al. 2018a). In *Citrus* L. (Rutaceae), they are located at the petal tip and are composed of papillose cells and trichomes (Fig. 9a–b) (Marques et al. 2015). No information about the structure of osmophores is available for Sapindaceae, but they have been described as being located on sepals and stamens (Lima et al. 2016).

The composition of the floral bouquet has also been analyzed. The scent consists of terpenoids, mainly sesquiterpenes and monoterpenes, in *Anacardium humile* A. St.-Hil. and *Mangifera indica* L. (Anacardiaceae; Tölke et al. 2018a) and terpenoids and phenolic compounds in *Citrus sinensis* (L.) Osbeck (Fig. 9c–d) (Rutaceae; Marques et al. 2015). These volatile oils are produced by cells, whose cytoplasm is rich in smooth and rough endoplasmic reticulum, leucoplasts, polyribosomes, and dictyosomes; the storage of starch grains is also very common. Plastids with plastoglobuli and many droplets of oil in the cytosol have been observed prior to the anthesis (Tölke et al. 2018a). In Anacardiaceae, the secretion is granulocrine, and the release of oils to the outside occurs without cuticle rupture (Tölke et al. 2018a). From an evolutionary perspective, little is known about how these secretory structures emerged and evolved in Sapindales. Since most of flowers belonging to the order are scented, osmophores might be widespread in members of Sapindales.

Glandular trichomes – The glandular trichomes are reported in all families of Sapindales, except for Biebersteiniaceae, for which detailed anatomical studies are lacking (Fig. 1) (van der Walt and van der Schijff 1969; Li et al. 1999; Caris et al. 2006; Bachelier and Endress 2008, 2009; Bachelier et al. 2011; Kubitzki 2011; Muntoreanu et al. 2011; Alves et al. 2017; Cunha-Neto et al. 2017; Tölke et al. 2017, 2021; Andrade et al. 2020; Cortez et al. 2021). The trichomes are morphologically diverse and distributed mainly on leaves, as well as on stems, inflorescences, flowers, and fruits. The most common type of trichome is the capitate, which is usually composed of a stalk and a dilated uni- or multicellular secretory head (Figs. 10a–f and 11a–d), but peltate trichomes with a large secretory head are also found in some species, as observed in *Helietta* Tul. (Rutaceae; Fig. 10f) and *Melia* L. (Meliaceae; although described as capitate by Tilney et al. 2018a). Although the capitate trichome is widespread in the order, they may vary in cell arrangement of the secretory head. Some trichomes have regular series of cell in the head as observed in Anacardiaceae and Rutaceae (Fig. 11a, b), while others have an irregular cell arrangement as found in Sapindaceae (Fig. 11c, d), Meliaceae (Fig. 6c) and Simaroubaceae (Cortez et al. 2021).

Trichomes with similar morphology may have different functions depending on their location (Bachelier and Endress

2009; Muntoreanu et al. 2011; Lacchia et al. 2016a, b; Tölke et al. 2017; Franco and Albiero 2018). The trichomes of the order may produce a variety of substances, such as phenolic compounds (including tannins), proteins, polysaccharides, and essential oils (Lacchia et al. 2016a, b; Cunha-Neto et al. 2017; Tölke et al. 2017; Andrade et al. 2020). The variation in the secretion composition may reflect distinct defensive functions in leaf trichomes (Fahn 1979; Santos-Silva et al. 2013), while inflorescence and/or flower trichomes are mainly related to pollinator attraction (Chauveau et al. 2011; Marinho et al. 2016). Therefore, some of those trichomes are classified as nectaries because they secrete nectar, others produce a mostly mucilaginous secretion next to the meristems and are identified as colleters, while other trichomes produce a scent that attract pollinators and are classified as osmophores. Remarkably, all these types of trichomes may occur in the same species (e.g., *Anacardium humile* A. St.-Hil.) (Lacchia et al. 2016a, b a, b; Tölke et al. 2018b; sections 2.5 to 2.8). Secretory trichomes could be regarded as a putative synapomorphy for Sapindales, although the evaluation of a larger number of species would be necessary to confirm this hypothesis.

Secretory endocarp – Most recently a new secretory structure has been described in Anacardiaceae, a secretory endocarp which produces mucilage and lipids in young fruits (Tölke et al. 2017). The secretory tissue is composed of the innermost cell layer of the endocarp and was detected only in drupes of *Tapirira guianensis* Aubl. (Fig. 12a–e). This secretion covers the seed and may facilitate seed imbibition, mediate germination, avoid the proliferation of microorganisms, and promote seed dispersal by attachment to animals (Tölke et al. 2017, and references therein). This is the only report of secretory endocarp for Sapindales (Fig. 1).

3 Diversity of substances produced by the secretory structures in Sapindales

Among the chemicals produced by the secretory structures of Sapindales, phenolics and terpenoids are the predominant compounds. However, other components such as alkaloids, saponins, and organic acids may occur (Fig. 13). Terpenoids, steroids, and saponins share the mevalonate pathway, whereas alkaloids belong to the shikimic acid pathway (Fig. 14). On the other hand, phenolics, known as aromatic polyhydroxylated compounds, are bioproducts from both pathways (e.g., tannins and flavonoids), and lignoids and coumarins are exclusively produced by the shikimic acid pathway (Fig. 14). In addition, the polyketide pathway produces mostly organic acids (Fig. 14) (Damasceno et al. 2018, and references therein). Therefore, all families of Sapindales

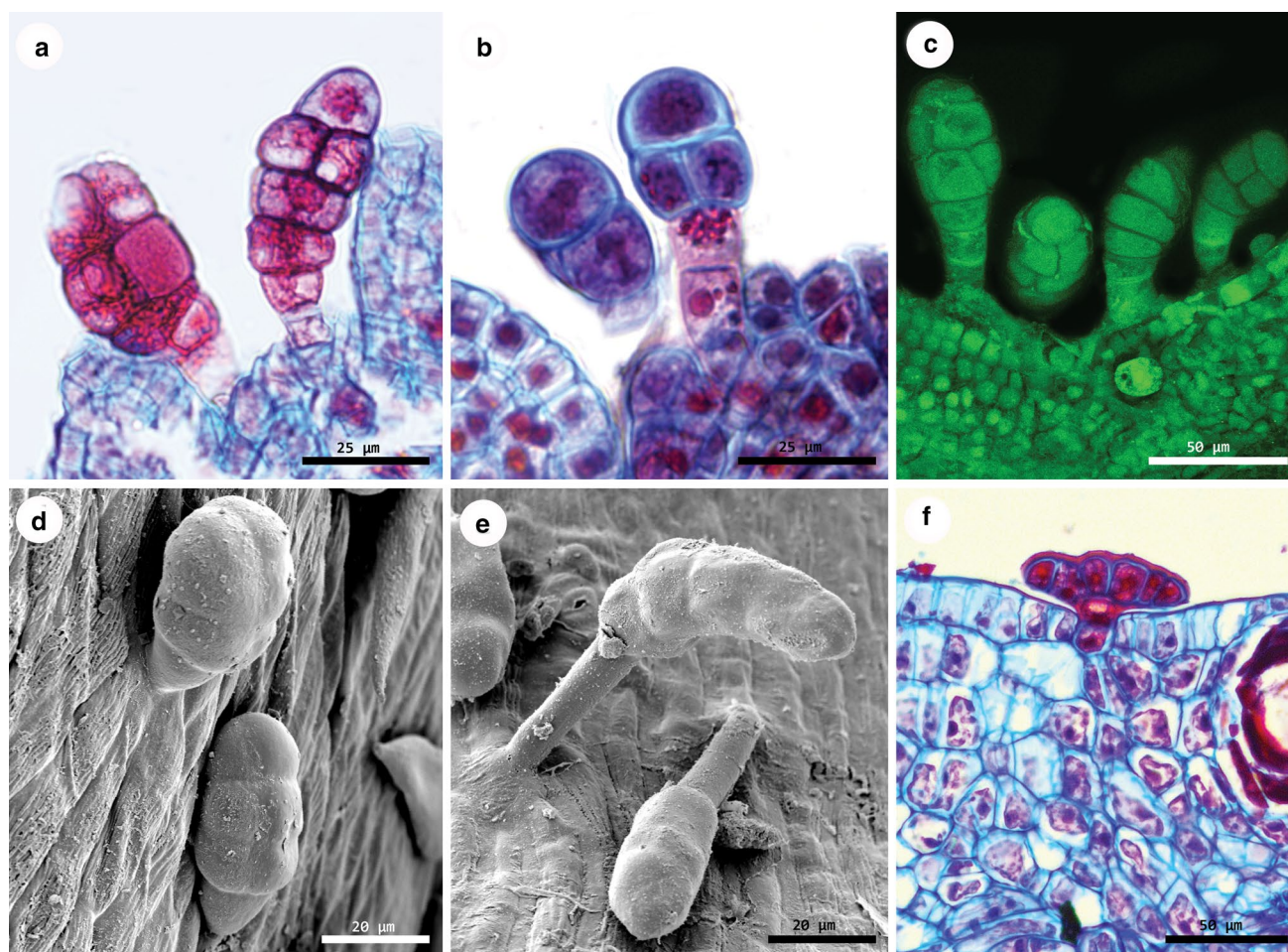


Fig. 10 Diversity of glandular trichomes in Sapindales. **a–c** Shoot apex. **d–e** Flower pedicel. **f** Fruit. **a–b, f** Bright-field microscopy. **c** Confocal microscopy. **d–e** SEM. **a–e** Capitate trichomes. **f** peltate trichome. **a** Pedunculate trichomes with secretory head organized in a variable number of series. *Serjania caracasana* (Jacq.) Willd. (Sapindaceae). **b–c** Shorter trichomes with an irregular pattern of distribution of cells in the secretory head. *Urvillea ulmacea* Kunth (Sapindaceae). **d** Trichome with a secretory head formed by two series of cells. *Anacardium occidentale* L. (Anacardiaceae). **e** Long-pedunculate trichome in *Schinus terebinthifolius* Raddi (Anacardiaceae). **f** Peltate trichomes in *Helietta glaziovii* (Engl.) Pirani (Rutaceae)

share the mevalonate and shikimate pathways, likely evolving from a common ancestor of the order (Fig. 13).

Regarding the mevalonate pathway, its metabolites are initiated by the condensation of isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAP), clearly recognizable as isoprene units, which may be polymerized by further addition of IPP units (Fig. 14). Monoterpenoids, for instance, are formed by the condensation of two isoprene units, whereas sesquiterpenoids are formed by three isoprene units, also known as farnesyl pyrophosphate. Regarding triterpenoids and steroids, they are formed by two farnesyl pyrophosphate units, which are linked together in a head-to-head mode of condensation in a two-step reaction, catalyzed by squalene synthase. These isoprene units, after the corresponding condensation, cyclization, and isomerization reactions, produce several types of steroids, as well as mono-,

sesqui-, and triterpenoid skeletons. As for the biosynthesis of saponins, they may occur after glycosylation reactions forming triterpenoids or steroids, leading to triterpenoid and steroidal saponins, respectively. The mono- and bidesmosidic saponins with triterpene sapogenins are characteristic of Sapindaceae, mostly known for its ichtiotoxic and detergent properties (Hegnauer 1990).

More complex chemical structures, such as protolimonoids, limonoids, and quassinoids, have appeared only in the most recent families of the order (Simaroubaceae, Meliaceae, and Rutaceae; Fig. 13). Thus, limonoids are an important chemotaxonomic marker correlated with these three families (Clayton 2011). Limonoids are classified as tetranortriterpenes, originated through structural modification of tetracyclic triterpene skeletons, such as tirucallane and euphane. The structural modification is initiated

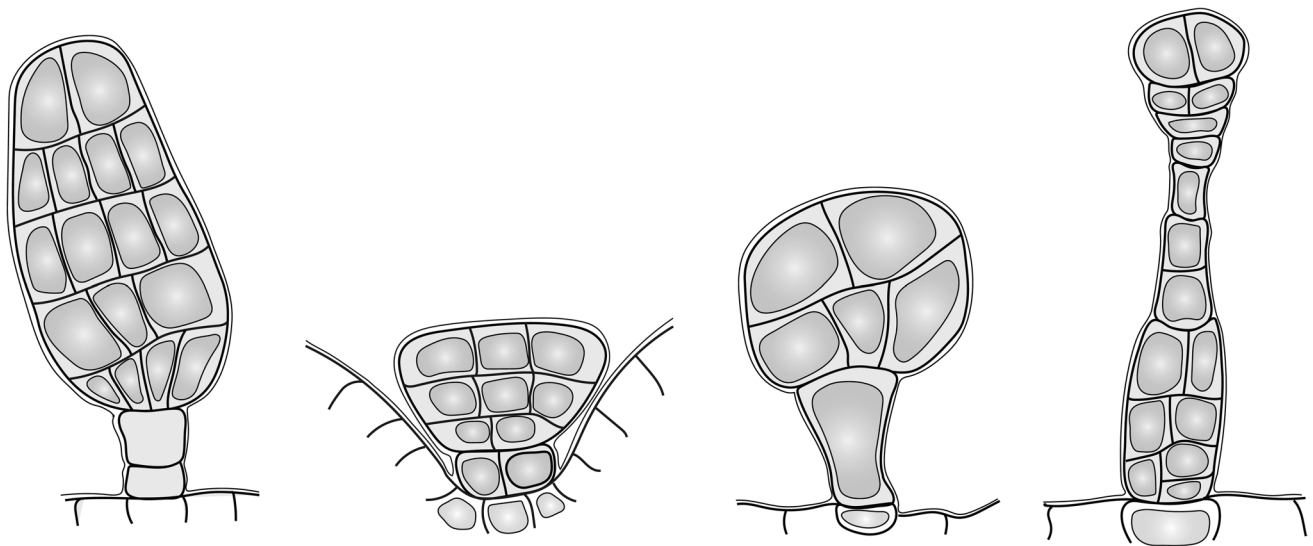


Fig. 11 Morphological diversity of glandular trichomes in Sapindales. **a** Anacardiaceae. **b** Rutaceae, **c–d** Sapindaceae. Note that the secretory head is composed of regular series of cells in Anacardiaceae (**a**) and Rutaceae (**b**) but has an irregular cell arrangement in Sapindaceae (**c–d**)

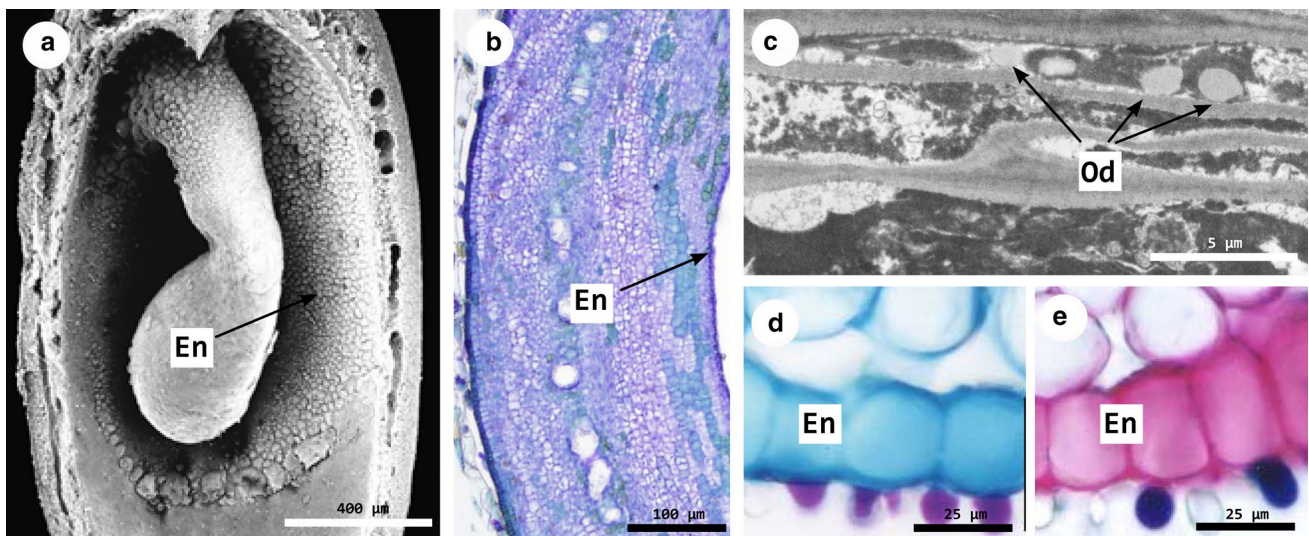


Fig. 12 Secretory endocarp in *Tapirira guianensis* Aubl. (Anacardiaceae). **a** SEM. **b, d–e** Bright-field microscopy. **c** TEM. **a** Endocarp with small droplets of secretion. **b** Endocarp with a parenchymatous aspect in young fruit. **c** Oil droplets produced by endocarp cells. **d–e** Histochemical tests showing a positive reaction for lipids using Nile Blue (**d**) and polysaccharides using PAS reaction (**e**). En: endocarp; Od: oil droplets. Photographs **a, d** and **e** provided by Dr. Ana Paula S. Lacchia

by oxidation and cyclisation reactions toward the C-17 side chain, leading to protolimonoids, which are subjected to ring fission and recyclization of the ring-A and ring-D, resulting in a limonoid structure. In relation to quassinoids, they are produced after further steps down the oxidative pathway of limonoids (Dreyer 1983). Besides their chemotaxonomic importance, limonoids may be considered an important natural source of pesticides. For instance, azadirachtin, a limonoid found in *Azadirachta indica* A. Juss. (Meliaceae),

commonly known as neem tree, is one of the most efficient plant-based pesticides, due to its broad spectrum and low mammalian toxicity (Rattan 2010). It is important to note that limonoids in Rutaceae are produced by oil cavities, but in Meliaceae, they are produced by oil idioblasts, which reinforces the fact that different secretory structures may produce similar chemical components.

In Burseraceae, the most characteristic trait is the strong diversification of its terpenoid chemistry, mostly

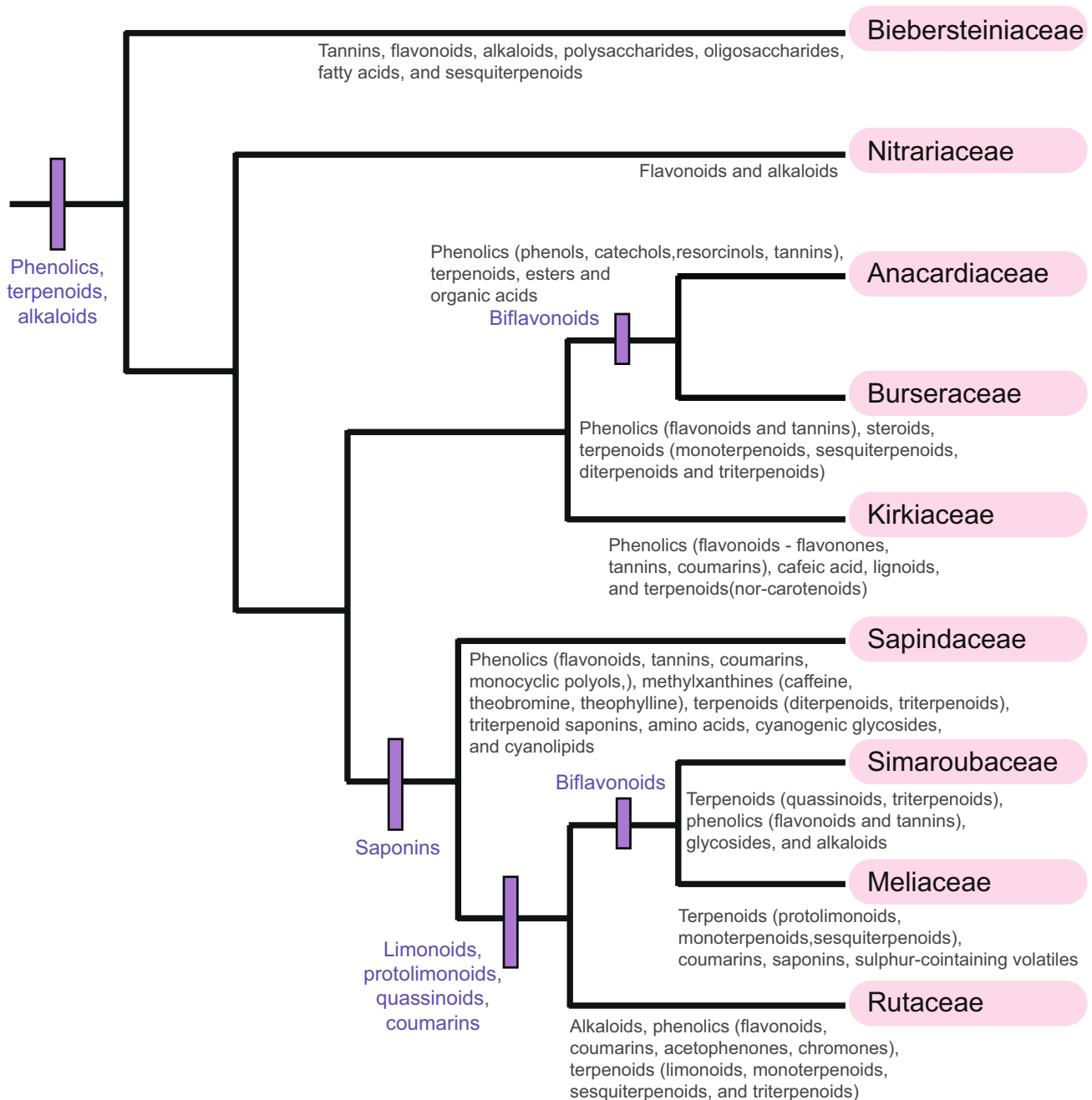


Fig. 13 Evolutionary hypothesis of the main compounds produced by the secretory structures in Sapindales. Phylogenetic hypothesis based on Stevens (2011). Data obtained from cited references among the text

accumulated as a resin, consisting of volatile and non-volatile components (Boer and Ella 2000). However, terpenoids are also components of the resin of their sister family Anacardiaceae (Aguilar-Ortigosa and Sosa 2004; Tölke et al. 2021, and references therein). The volatile part, composed mostly of mono- and sesquiterpenes, plays an important ecological function, serving as communication mechanism to attract pollinators and as a defense mechanism to deter herbivores. Moreover, it may function as an

antibiotic, competitive phytotoxin, herbivore repellent, and toxin (Becerra 2003; Aguilar-Ortigosa and Sosa 2004; Fine et al. 2005; Langenheim 2005; Marques et al. 2015). The non-volatile part is represented by di- and triterpenes, and macrocyclic cembranoid diterpenes (Waterman and Grunton 1983), whereas the most commonly reported triterpenes are related to the ursane and oleanane series (Lima et al. 2004).

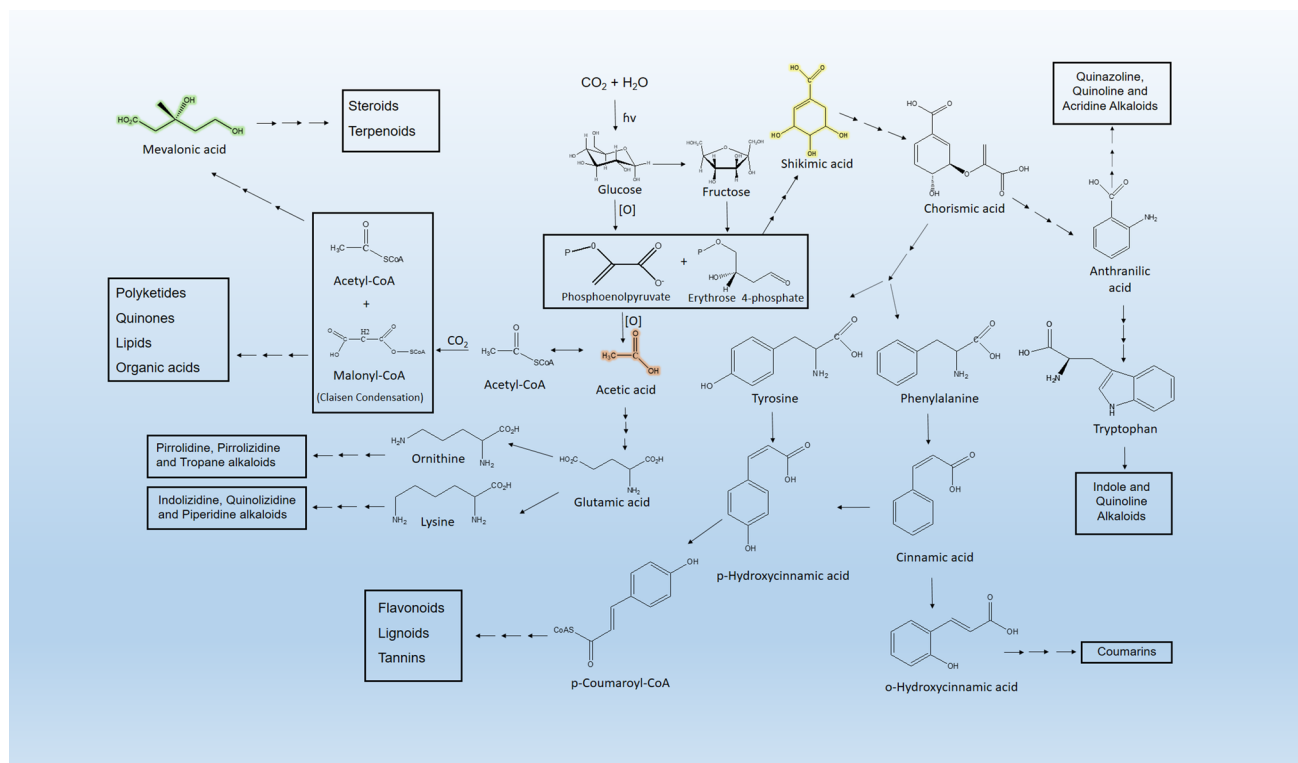


Fig. 14 General overview of the major metabolic pathways in plants

Phenolic compounds are the second most important chemicals in Sapindales, occurring in all families of the order (Mitchell 1990; Becerra 2003; Mulholland et al. 2003; Chen et al. 2005; Aguilar-Ortigoza and Sosa 2004; Fine et al. 2005; Langenheim 2005; Prado and Demarco 2018; Kubitzki 2011; Tölke et al. 2021). Most of the toxic components investigated within members of Anacardiaceae are phenolic compounds, known especially for their defensive functions, including antimicrobials, antifungal, and insect/herbivore repelling compounds (Cojocaru et al. 1986; Saxena et al. 1994; Chen et al. 2005). The toxic components are distributed in approximately 32 genera of Anacardiaceae (Mitchell 1990; Aguilar-Ortigoza et al. 2003; Aguilar-Ortigoza and Sosa 2004). They are stored mainly in the resin ducts and are represented by phenols, primarily catechols and resorcinols, including anacardic acid (*Anacardium occidentale* L.), moreakol (*Gluta usinata*), iacol, and urushiol (*Toxicodendron* Mill.), among others (Behl and Captain 1979). The main mode of action concerning these toxic compounds is through the generation of an immune system reaction upon binding with skin proteins (Drewes et al. 1998; Mitchell 1990). Among the flavonoids, biflavonoids may be considered as biomarker of Anacardiaceae and Burseraceae, since they share the production of these compounds. However, the biflavonoids evolved at least one more time in the order, in the ancestor of Simaroubaceae and Meliaceae (Mulholland

et al. 2003; Aguilar-Ortigoza and Sosa 2004; Clayton 2011; Tölke et al. 2021 and references therein; Fig. 13). The phenolic compounds (usually described as tannins) are mainly produced by idioblasts, a ubiquitous secretory structure of the order. However, as discussed in the previous sections, secretory ducts, trichomes, and even nectaries may contribute to the phenolic production in the families of Sapindales.

Alkaloids have a more restricted pattern of distribution in the order, occurring only in five out of nine families: Biebersteiniaceae, Nitrariaceae, Sapindaceae, Simaroubaceae, and Rutaceae (Fig. 13). However, Rutaceae is noteworthy when it comes to biosynthesis of alkaloids as a great variety of subclasses derived from tryptamine, tyrosine, and phenylalanine have been reported. Moreover, quinolones and acridones derived from anthranilic acid stand out for being highly diversified and extremely restricted to Rutaceae (Waterman 1993).

4 Final remarks

Sapindales are an order extremely rich in types of glands that occur in vegetative and reproductive organs, such as ducts, cavities, laticifers, secretory idioblasts, colleters, nectaries, osmophores, secretory trichomes, and even secretory endocarp. These secretory structures have a great diversity of

forms and produce a wide variety of compounds that play a protective role against pathogens, herbivory or frugivory, or an attractive role for pollinators and seed dispersers. The occurrence of the same compounds in different lineages (e.g., terpenoids), sharing the same metabolic pathways, may have allowed the diversification of glands in Sapindales and represent synapomorphies of some clades, such as resin ducts in Anacardiaceae, Burseraceae, and Simaroubaceae; laticifers in Sapindaceae; oil cavities in Rutaceae; and oil idioblasts in Meliaceae. Further studies combining morphological, phylogenetic, and phytochemical studies are needed for more thorough analysis of Sapindales evolution.

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Declarations

Conflict of interest Diego Demarco is the Editor-in-chief and Elisabeth D. Tölke is an Associate Editor of the Brazilian Journal of Botany, and we assure this article was entirely handled by an Associate Editor.

References

- Acevedo-Rodríguez P (1993a) A revision of *Lophostigma* (Sapindaceae). *Syst Bot* 18:379–388
- Acevedo-Rodríguez P (1993b) Systematics of *Serjania* (Sapindaceae). Part I: a revision of *Serjania* sect. *Platycoccus*. *Mem N Y Bot Gard* 67:1–93
- Acevedo-Rodríguez P, van Welzen PC, Adema F, van der Ham RWJM (2011) Sapindaceae. In: Kubitzki K (ed) The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin, pp 357–407
- Acevedo-Rodríguez P, Wurdack KJ, Ferrucci MS et al (2017) Generic relationships and classification of Tribe Paullinieae (Sapindaceae) with a new concept of Supertribe Paullinioidae. *Syst Bot* 42:96–114
- Agarwal M, Gupta S (2008) Wood anatomy of Sapindales. Bishen Singh Mahendra Pal Singh, Dehra Dun
- Aguilar-Ortigoza CS, Sosa V (2004) The evolution of toxic phenolic compounds in a group of Anacardiaceae genera. *Taxon* 53:357–364
- Aguilar-Ortigoza CS, Sosa V, Aguilar-Ortigoza M (2003) Toxic phenols in various Anacardiaceae species. *Econ Bot* 57:354–364
- Alves GGN (2015) Estudos estruturais como subsídio à taxonomia de *Simaba* Aubl. (Simaroubaceae). Master Thesis, Universidade de São Paulo, São Paulo
- Alves IABS, Miranda HM, Soares LAL, Randau KP (2014) Simaroubaceae family: botany, chemical composition and biological activities. *Rev Bras Farmacogn* 24:481–501
- Alves GGN, El Ottra JHL, Devecchi MF, Demarco D, Pirani JR (2017) Structure of the flower of *Simaba* (Simaroubaceae) and its anatomical novelties. *Bot J Linn Soc* 183:162–176
- Alves GGN, Fonseca LHM, Devecchi MF, El Ottra JHL, Demarco D, Pirani JR (2021) What reproductive traits tell us about the evolution and diversification of the Tree-of-Heaven family, Simaroubaceae. *Braz J Bot* 6:66
- Amini T, Zare H, Assadi M (2008) *Acer mazandaranicum* (Aceraceae), a new species from Northern Iran. *Iran J Bot* 14:81–86
- Andrade CRB, Martins FM, Brandão HN, Alves CK, Freitas-Silva L (2020) Leaf anatomy and histochemistry of secretory structures of *Zanthoxylum caribaeum* Lam. (Rutaceae). *Braz J Bot* 43:961–968
- Andreeva AV, Kutuzov MA, Evans DE, Hawes CR (1998) The structure and function of Golgi apparatus: a hundred years of questions. *J Exp Bot* 49:1281–1291
- APG (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot J Linn Soc* 181:1–20
- Appelhans MS, Smets E, Razafimandimbison SG, Haevermans T, van Marle EJ, Couloux A, Rabarison H, Randrianarivelosia M, Keßler PJA (2011) Phylogeny, evolutionary trends and classification of the *Spathelia-Ptaeroxylon* clade: morphological and molecular insights. *Ann Bot* 107:1259–1277
- Aragão GF, Cunha MC, Nogueira P, Gomes TL, Barros V (2008) Analgesic and anti-inflammatory activities of the isomeric mixture of alpha- and beta-amyrin from *Protium heptaphyllum* (Aubl.) March. *J Herbal Pharmacother* 7:31–47
- Avalos AA, Lattar EC, Galati BG, Ferrucci MS (2017) Nectary structure and ultrastructure in two floral morphs of *Koelreuteria elegans* subsp. *formosana* (Sapindaceae). *Flora* 226:29–37
- Babu AM, John P, Nair GM (1990) Ultrastructure of gum-resin secreting cells in the pith of *Ailanthus excelsa* Roxb. *Acta Bot Neerl* 38:389–398
- Bachelier JB, Endress PK (2008) Floral structure of *Kirkia* (Kirkiaceae) and its position in Sapindales. *Ann Bot* 102:539–550
- Bachelier JB, Endress PK (2009) Comparative floral morphology and anatomy of Anacardiaceae and Burseraceae (Sapindales), with a special focus on gynoecium structure and evolution. *Bot J Linn Soc* 159:499–571
- Bachelier JB, Endress PK, Ronse De Craene LP (2011) Comparative floral structure and development of Nitrariaceae (Sapindales) and systematic implications. In: Wanntorp L, Ronse De Craene LP (eds) *Flowers on the tree of life*. Cambridge University Press, New York, pp 181–217
- Bakker ME, Gerritsen AF (1992) The development of mucilage cells in *Hibiscus schizopetalus*. *Acta Bot Neerl* 41:31–42
- Becerra JX (2003) Evolution of Mexican *Bursera* (Burseraceae) inferred from ITS, ETS, and 5S nuclear ribosomal DNA sequences. *Mol Phylogenet Evol* 26:300–309
- Behl P, Captain RM (1979) Skin-irritant and sensitizing plants found in India. S. Chand & Co, New Delhi
- Benedict AH (1961) The floral anatomy of *Dipteronia*. *Am J Bot* 48:918–924
- Bennici A, Tani C (2004) Anatomical and ultrastructural study of the secretory cavity development of *Citrus sinensis* and *Citrus limon*: evaluation of schizolysigenous ontogeny. *Flora* 199:464–475

- Boer E, Ella AB (2000) Plant resources of South-East Asia. No. 18. Plants producing exudates. Backhuys Publishers, Leiden
- Bory G, Clair-Maczulajty D (1990) Importance of foliar nectaries in the physiology of tree of heaven (*Ailanthus glandulosa* Desf., Simaroubaceae). *Bull Soc Bot Fr Lett Bot* 137:139–155
- Bosabalidis A, Tsekos I (1982a) Ultrastructural studies on the secretory cavities of *Citrus deliciosa* Ten. I Early stages of the gland cells differentiation. *Protoplasma* 112:55–62
- Bosabalidis A, Tsekos I (1982b) Ultrastructural studies on the secretory cavities of *Citrus deliciosa* Ten. II Development of the essential oil-accumulating central space of the gland and process of active secretion. *Protoplasma* 112:63–70
- Boudouris J, Queenborough SA (2013) Diversity and distribution of extra-floral nectaries in the Cerrado savanna vegetation of Brazil. *PeerJ* 1:e219
- Burris TP, Montrose C, Houck KA, Osborne HE, Bocchinfuso WP, Yaden BC, Cheng CC, Zink RW, Barr RJ, Hepler CD, Krishnan V, Bullock HA, Burris LL, Galvin RJ, Bramlett K, Stayrook KR (2005) The hypolipidemic natural product guggulsterone is a promiscuous steroid receptor ligand. *Mol Pharmacol* 67:948–954
- Bussel BM, Considine JA, Spadek ZE (1995) Flower and volatile oil ontogeny in *Boronia megastigma*. *Ann Bot* 76:457–463
- Caris P, Smets E, De Coster K, Ronse De Craene LP (2006) Floral ontogeny of *Cneorum tricoccon* L. (Rutaceae). *Plant Syst Evol* 257:223–232
- Champagne DE, Koul O, Isman MB, Scudder GGE, Towers GHN (1992) Biological activity of limonoids from the Rutales. *Phytochemistry* 31:377–394
- Chauveau O, Eggers L, Raquin C, Silvério A, Brown S, Couloux A, Cruaud C, Kaltchuk-Santos E, Yockteng R, Souza-Chies TT, Nadot S (2011) Evolution of oil-producing trichomes in *Sisyrinchium* (Iridaceae): insights from the first comprehensive phylogenetic analysis of the genus. *Ann Bot* 107:1287–1312
- Chen Y, Wu H (2010) Programmed cell death involved in the schizogen formation of the secretory cavity in *Citrus sinensis* L. (Osbeck). *Chin Sci Bull* 55:2160–2168
- Chen T, Wiemer D, Howard JJ (2005) A volatile leafcutter ant repellent from *Astronium graveolens*. *Naturwissenschaften* 71:97–98
- Clark TP (1990) Studies in *Trichilia*—*Walsura* complex (Meliaceae). PhD Dissertation, Oxford University, Oxford
- Clayton JW (2011) Simaroubaceae. In: Kubitzki K (ed) The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin, pp 408–423
- Cojocar M, Droby S, Glotter E, Goldman A, Gottlieb HE, Jacoby B, Prusky D (1986) 5-(12-heptadecenyl)-resorcinol, the major component of the antifungal activity in the peel of mango fruit. *Phytochemistry* 25:1093–1095
- Cortez PA, Ferreira CL, Santos GNH, Pirani JR, Urbano KD, Devecchi MF, Cruz R, Gabia VS, Melo-de-Pinna GFA (2021) Strategies for the protection of shoot buds in phanerophyte and geophyte species of *Homalolepis Turcz.* (Simaroubaceae, Sapindales). *Braz J Bot*. <https://doi.org/10.1007/s40415-021-00757-1>
- Corthout J, Pieters LA, Claeys M, Vanden Berghe DA, Vlietinck AJ (1991) Antiviral ellagitannins from *Spondias mombin*. *Phytochemistry* 30:1129–1130
- Corthout J, Pieters LA, Claeys M, Vanden Berghe DA, Vlietinck AJ (1992) Antiviral caffeoyl esters from *Spondias mombin*. *Phytochemistry* 31:1979–1981
- Corthout J, Pieters LA, Claeys M, Geerts S, Vanden Berghe D, Vlietinck AJ (1994) Antibacterial and molluscicidal phenolic acids from *Spondias mombin*. *Planta Med* 60:460–463
- Costa ER, Tangerina MMP, Ferreira MJP, Demarco D (2021) Two origins, two functions: the discovery of distinct secretory ducts formed during the primary and secondary growth in *Kielmeyera*. *Plants* 10:877
- Cruz R, Duarte M, Pirani JR, Melo-de-Pina GFA (2017) Phylogenetic analysis and evolution of morphological characters in *Metrodorea* and related species in Rutoideae (Rutaceae). *Plant Syst Evol* 303:927–943
- Cunha-Neto IL, Martins FM, Sommer GV, Tamaio N (2017) Secretory structures in stems of five lianas of Paullinieae (Sapindaceae): morphology and histochemistry. *Flora* 235:29–40
- Dahlgren R, Van Wyk AE (1988) Structures and relationships of families endemic to or centered in southern Africa. *Monogr Syst Bot Mo Bot Gard* 25:1–94
- Daly DC, Harley MM, Martínez-Habibe MC, Weeks A (2011) Burseraceae. In: Kubitzki K (ed) The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin, pp 76–104
- Damasceno GAB, Souto AL, da Silva IB, Roque A, Ferrari M, Giordani RB (2018) *Prosopis juliflora*: phytochemical, toxicological, and allelochemicals. In Merillon JM, Ramawat K (eds) Co-evolution of secondary metabolites. Reference series in phytochemistry. Springer, Cham, pp 1–21
- Dayanandan P, Ponsamuel J (2000) Ultrastructure of terpenoid secretory cells of neem (*Azadirachta indica* A. Juss.). In: Gupta PD, Yamamoto H (eds) Electron Microscopy in medicine and biology. Science Pub Inc, Oxford, pp 179–195
- De-Paula OC, Sajo MG (2011) Morphology and development of anthers and ovules in *Croton* and *Astraea* (Euphorbiaceae). *Nord J Bot* 29:505–511
- Dede RA (1962) Foliar venation patterns in the Rutaceae. *Am J Bot* 49:490–497
- Dell B, McComb AJ (1979) Plant resins—their formation, secretion and possible functions. *Adv Bot Res* 6:277–316
- Demarco D (2017) Floral glands in asclepiads: structure, diversity and evolution. *Acta Bot Bras* 31:477–502
- Demarco D, Carmello-Guerreiro SM (2011) Pericarp ontogeny and histochemistry of the exotesta and pseudocaruncle of *Euphorbia milii* (Euphorbiaceae). *Rodriguésia* 62:477–489
- Devecchi MF, Pirani JR (2015) A new species of *Simaba* sect. *Grandiflorae* (Simaroubaceae) from Jalapão region, Tocantins. *Brazil Phytotaxa* 227:167–174
- Díaz M, Rossini C (2012) Bioactive natural products from Sapindaceae deterrent and toxic metabolites against insects. In: Perveen F (ed) Insecticides—pest engineering. IntechOpen, London, pp 287–308
- Drewes SE, Horn MM, Mabaso NJ (1998) *Loxostylis alata* and *Smodingium argutum*—a case of phytochemical bedfellows? *S Afr J Bot* 64:128–129
- Dreyer DI (1983) Limonoids of the Rutaceae. In: Waterman PG, Grundon MF (eds) Chemistry and chemical taxonomy of the Rutales. Academic Press, London, pp 215–245
- Dünisch O, Bass P (2006) On the origin of intercellular canals in the secondary xylem of selected Meliaceae species. *IAWA J* 27:281–297
- El Ottra JHL, Demarco D, Pirani JR (2019) Comparative floral structure and evolution in Galipeinae (Galipeae: Rutaceae) and its implications at different systematic levels. *Bot J Linn Soc* 191:30–101
- Elias TS (1983) Extrafloral nectaries: their structure and distribution. In: Bentley B, Elias TS (eds) The biology of nectaries. Columbia University Press, New York, pp 174–203
- Engler A (1931) Rutaceae. In: Engler A, Prantl K (eds) Die Natürlichen Pflanzenfamilien, 2nd edn. Engelmann, Leipzig, pp 187–359
- Faegri K, van der Pijl L (1979) The principles of pollination ecology, 3rd edn. Pergamon Press, Oxford
- Fahn A (1979) Secretory tissue in plants. Academic Press, London

- Fahn A (1990) Plant anatomy. Pergamon Press, Oxford
- Fang X, Zhang Y, Wang M, Li P, Zhang Q, Si J, Wei B, Miao Y, Tian L, Cai X (2019) Lysosome and proteasome pathways are distributed in laticifers of *Euphorbia helioscopia* L. *Physiol Plant* 166:1026–1038
- Farsam H, Amanlou M, Reza Dehpour A, Jahani F (2000) Anti-inflammatory and analgesic activity of *Biebersteinia multifida* DC. root extract. *J Ethnopharmacol* 71:443–447
- Fiala B, Linsenmair E (1995) Distribution and abundance of plants with extrafloral nectaries in the woody flora of a lowland primary forest in Malaysia. *Biodivers Conserv* 4:165–182
- Fine PVA, Daly DC, Muñoz GV, Mesones I, Cameron KM (2005) The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. *Evolution* 59:1464–1478
- Fisher JB, Rutishauser R (1990) Leaves and epiphyllous shoots in *Chisocheton* (Meliaceae): a continuum of woody leaf and stem axes. *Can J Bot* 68:2316–2328
- Franco MJCS, Albiero ALM (2018) Estruturas secretoras em folha e caule de *Esenbeckia febrifuga* (A.St.-Hil.) A. Juss. ex Mart. e *Esenbeckia grandiflora* Mart. (Rutaceae). *Hoehnea* 45:468–483
- Gadek PA, Fernando ES, Quinn CJ, Hoot SB, Terrazas T, Sheahan MC, Chase MW (1996) Sapindales: Molecular delimitation and infraordinal groups. *Am J Bot* 83:802–811
- Gama TSS, Rubiano VS, Demarco D (2017) Laticifer development and its growth mode in *Allamanda blanchetii* A. DC. (Apocynaceae). *J Torrey Bot Soc* 144:303–312
- Gama TSS, Cordeiro I, Demarco D (2019) Floral structure and development in *Alchornea sidifolia* (Acalyphoideae) and the evolution of wind pollination in Euphorbiaceae. *Braz J Bot* 42:307–317
- Gama RL, Muellner-Riehl AN, Demarco D, Pirani JR (2021a) Evolution of reproductive traits in the mahogany family (Meliaceae). *J Syst Evol* 59:21–43
- Gama RL, El Ottra JHL, Pirani JR, Demarco D (2021b) Gynodioecy in *Trichilia* (Meliaceae) and a peculiar case of male sterility due to tapetal necrotic cell death. *Braz J Bot*. <https://doi.org/10.1007/s40415-021-00746-4>
- Gedalovich E, Fahn A (1985) The development and ultrastructure of gum ducts in *Citrus* plants formed as a result of brown-rot gummosis. *Protoplasma* 127:73–81
- Giuliani C, Bini LM, Lippi MM (2012) Two structures and functions in the nectary of frankincense tree (*Boswellia sacra* Flueck.). *Flora* 207:74–79
- Gouvêa CF, Dornelas MC, Rodriguez APM (2008) Floral development in the tribe Cedreleae (Meliaceae sub-family Swietenioideae): *Cedrela* and *Toona*. *Ann Bot* 101:39–48
- Gregory M, Baas P (1989) A survey of mucilage cells in vegetative organs of the dicotyledons. *Isr J Bot* 38:125–174
- Gut BJ (1966) Beiträge zur Morphologie des Gynoeciums und der Blütenachse einiger Rutaceen. *Bot Jahrb Syst* 85:151–247
- Hegnauer R (1990) Chemotaxonomie der Pflanzen, Bd. 9. Birkhäuser, Basel
- Heimsch C Jr (1942) Comparative anatomy of the secondary xylem in the “Gruinales” and “Terebinthales”, of Wettstein with reference to taxonomic grouping. *Lilloa* 8:83–198
- Heinrich G, Schultze W (1985) Composition and site of biosynthesis of the essential oil in fruits of *Phellodendron amurense* Rupr. (Rutaceae). *Isr J Bot* 34:205–217
- Inamdar JA, Murugan V, Subramanian RB (1988) Ultrastructure of non-articulated laticifers in *Allamanda violacea*. *Ann Bot* 62:583–588
- Joel DM, Fahn A (1980a) Ultrastructure of the resin ducts of *Mangifera indica* L. (Anacardiaceae). 3. Secretion of the protein-polysaccharide mucilage in the fruit. *Ann Bot* 46:785–790
- Joel DM, Fahn A (1980b) Ultrastructure of the resin ducts of *Mangifera indica* L. (Anacardiaceae). 1. Differentiation and senescence of the shoot ducts. *Ann Bot* 46:225–233
- Kenfak D, Tindo M, Gueye M (2014) Extranuptial nectaries in *Carapa* Aubl. (Meliaceae-Cedreloideae). *Adansonia* 36:335–349
- Koptur S, William P, Olive Z (2010) Ants and plants with extrafloral nectaries in fire successional habitats on Andros (Bahamas). *Fla Entomol* 93:89–99
- Knight TG, Klieber A, Sedgley M (2001) The relationship between oil gland and fruit development in Washington navel orange (*Citrus sinensis* L. Osbeck). *Ann Bot* 88:1039–1047
- Kubitzki K (2011) The families and genera of vascular plants. Vol. X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin
- Lacchia APS, Carmello-Guerreiro SM (2009) Aspectos ultra-estruturais dos canais secretores em órgãos vegetativos e reprodutivos de Anacardiaceae. *Acta Bot Bras* 23:376–388
- Lacchia APS, Tölke ED, Demarco D, Carmello-Guerreiro SM (2016a) Presumed domatia are actually extrafloral nectaries on leaves of *Anacardium humile* (Anacardiaceae). *Rodriguésia* 67:19–28
- Lacchia APS, Tölke ED, Carmello-Guerreiro SM, Ascensão L, Demarco D (2016b) Foliar colleters in Anacardiaceae: first report for the family. *Botany* 94:337–346
- Langenheim JH (2005) Higher plant terpenoids: a phyto-centric overview of their ecological roles. *J Chem Ecol* 20:1223–1280
- Lersten NR (1974) Morphology and distribution of colleters and crystals in relation to the taxonomy and bacterial leaf nodule symbiosis of *Psychotria* (Rubiaceae). *Am J Bot* 61:973–981
- Lersten NR, Pohl RW (1985) Extrafloral nectaries in *Cipadessa* (Meliaceae). *Ann Bot* 56:363–366
- Lersten NR, Rugenstein SR (1982) Foliar nectaries in Mahogany (Swietenia Jacq.). *Ann Bot* 49:397–401
- Li JX, Baskin JM, Baskin CC (1999) Pericarp ontogeny and anatomy in *Rhus aromatica* Ait. and *R. glabra* L. (Anacardiaceae). *J Torrey Bot Soc* 126:279–288
- Liang S, Wu H, Lun X, Lu D (2006) Secretory cavity development and its relationship with the accumulation of essential oil in fruits of *Citrus medica* L. var. *sarcodactylis* (Noot.) Swingle. *Acta Bot Sin* 48:573–583
- Lima MP, Braga PAC, Macedo ML, Silva MFGF, Ferreira AG, Fernandes JB, Vieira PC (2004) Phytochemistry of *Trattinnickia burserifolia*, *T. rhoifolia*, and *Dacryodes hopkinsii*: chemosystematic implications. *J Braz Chem Soc* 15:385–394
- Lima HA, Somner GV, Giulietti AM (2016) Duodichogamy and sex lability in Sapindaceae: the case of *Paullinia weinmannifolia*. *Plant Syst Evol* 302:109–120
- Lima EA, Tölke ED, Silva-Luz CL, Demarco D, Carmello-Guerreiro SM (2021) Fruit morphoanatomy of *Astronium* Jacq. and *Myracrodruon Allemão* (Anacardiaceae): taxonomic implications and development of the calycinal wings. *Braz J Bot*. <https://doi.org/10.1007/s40415-021-00732-w>
- Liu WZ, Hu ZH (1998) Comparative anatomy of secretory cavities in leaves of the Rutaceae in China. *Acta Phytotax Sin* 36:119–127
- Liu WZ, Zhang H, Hu ZH (1998) Ultrastructural studies on the secretory cavity development and essential oil accumulation in the fruits of *Evodia rutaecarpa*. *J Acta Bot Sin* 40:401–404
- Liu P, Liang S, Yao N, Wu H (2012) Programmed cell death of secretory cavity cells in fruits of *Citrus grandis* cv. Tomentosa is associated with activation of caspase 3-like protease. *Trees Struct Funct* 26:1821–1835
- Lv M, Xu P, Tian Y, Liang J, Gao Y, Xu F, Zhang Z, Sun J (2015) Medicinal uses, phytochemistry and pharmacology of the genus *Dictamnus* (Rutaceae). *J Ethnopharmacol* 171:247–263
- Macêdo TP, Cortez PA, Costa LCB (2016) First record of colleters in *Zanthoxylum* Linn. species (Rutaceae Juss., Sapindales): structural, functional and taxonomic considerations. *Flora* 224:66–74

- Machado SR, Canaveze Y, Rodrigues TM (2017) Structure and functioning of oil cavities in the shoot apex of *Metrodorea nigra* A. St.-Hil. (Rutaceae). *Protoplasma* 254:1661–1674
- Marazzi B, Endress PK, Paganucci de Queiroz L, Conti E (2006) Phylogenetic relationships within *Senna* (Leguminosae, Cassiinae) based on three chloroplast DNA regions: patterns in the evolution of floral symmetry and extrafloral nectaries. *Am J Bot* 93:288–303
- Marazzi B, Bronstein JL, Koptur S (2013) The diversity, ecology and evolution of extrafloral nectaries: current perspectives and future challenges. *Ann Bot* 111:1243–1250
- Marinho CR, Oliveira RB, Teixeira SP (2016) The uncommon cavitated secretory trichomes in *Bauhinia* s.s. (Fabaceae): the same roles in different organs. *Bot J Linn Soc* 180:104–122
- Marques JP, Kitajima E, Freitas-Astúa J, Apezato-da-Glória B (2010) Comparative morpho-anatomical studies of the lesions caused by *Citrus leprosis* virus on sweet orange. *Ann Braz Acad Sci* 82:501–511
- Marques JPR, Amorim L, Silva-Júnior GJ, Spósito MB, Apezato-da-Glória B (2015) Structural and biochemical characteristics of citrus flowers associated with defense against a fungal pathogen. *AoB Plants* 7:plu090
- Marquete O (1981) Anatomia e vascularização foliar e floral de *Pilocarpus organensis* Oechioni & Rizzini (Rutaceae). *Arq Jard Bot RJ* 25:117–159
- Matthews ML, Endress PK (2006) Floral structure and systematics in four orders of rosids, including a broad survey of floral mucilage cells. *Pl Syst Evol* 260:199–221
- Medina MC, Sousa-Baena MS, Prado E, Acevedo-Rodríguez P, Dias P, Demarco D (2021) Laticifers in Sapindaceae: structure, evolution and phylogenetic importance. *Front Plant Sci* 11:612985
- Metcalf CR, Chalk L (1950) Anatomy of the dicotyledons: leaves, stem, and wood in relation to taxonomy with notes on economic uses. Clarendon Press, Oxford
- Mitchell JD (1990) The poisonous Anacardiaceae genera of the world. *Adv Econ Bot* 8:103–129
- Moore JA (1936) Floral anatomy and phylogeny in the Rutaceae. *New Phytol* 35:318–322
- Morellato LPC, Oliveira PS (1991) Distribution of extrafloral nectaries in different vegetation types of Amazonian Brazil. *Flora* 185:33–38
- Morellato LPC, Oliveira OS (1994) Extrafloral nectaries in the tropical tree *Guarea macrophylla* (Meliaceae). *Can J Bot* 72:157–160
- Muellner AN (2011) Biebersteiniaceae. In: Kubitzki K (ed) The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin, pp 72–75
- Muellner-Riehl AN, Weeks A, Clayton JW, Buerki S, Nauheimer L, Chiang YC, Cody S, Pell SK (2016) Molecular phylogenetics and molecular clock dating of Sapindales based on plastid *rbcL*, *atpB* and *trnL-trnF* DNA sequences. *Taxon* 65:1019–1036
- Mulholland D, Cheplogoi P, Crouch N (2003) Secondary metabolites from *Kirkia acuminata* and *Kirkia wilmsii* (Kirkiaceae). *Biochem Syst Ecol* 31:793–797
- Muntoreanu TG, Cruz RS, Melo-de-Pinna GF (2011) Comparative leaf anatomy and morphology of some neotropical Rutaceae: *Pilocarpus* Vahl and related genera. *Plant Syst Evol* 296:87–99
- Muthukumran P, Begumand VH, Kalaiarasan P (2011) Antidiabetic activity of *Dodonaea viscosa* (L) leaf extracts. *Int J Pharm Tech Res* 3:136–139
- Nair MNB, Subrahmanyam SV (1998) Ultrastructure of the epithelial cells and oleogumresin secretion in *Boswellia serrata* (Burseraceae). *IAWA J* 19:415–427
- Nair GM, Venkaiah K, Shah JJ (1983) Ultrastructure of gum-resin ducts in cashew (*Anacardium occidentale*). *Ann Bot* 51:297–305
- Ning-Xi HN, Wu P (2005) The structural and developmental characteristics of floral nectaries of *Litchi chinensis* and their biological significance. *Acta Phytotaxon Sin* 44:523–537
- Nooteboom HP (1962) Generic delimitation in Simaroubaceae tribus Simaroubeae and a conspectus of the genus *Quassia* L. *Blumea* 11:509–528
- Oggero A, Arana MD, Reinoso HE (2016) Comparative morphology and anatomy of the leaf and stem of species of *Zanthoxylum* (Rutaceae) from Central Argentina. *Polibotánica* 42:121–136
- Okoth DA, Akala HM, Johnson JD, Koorbanally NA (2016) Alkyl phenols, alkenyl cyclohexenones and other phytochemical constituents from *Lannea rivae* (chiov) Sacleux (Anacardiaceae) and their bioactivity. *Med Chem Res* 25:690–703
- Pace MR, Gerolamo CS, Chery JG, Terrazas T, Victorio MP, Cunha-Neto IL, Angyalossy V (2021) The wood anatomy of Sapindales: diversity and evolution of wood characters. *Braz J Bot* 6:66
- Paiva EAS (2012) Anatomy, ultrastructure, and secretory activity of the floral nectaries in *Swietenia macrophylla* (Meliaceae). *Am J Bot* 99:1910–1917
- Paiva EAS, Buono RA, Delgado MN (2007) Distribution and structural aspects of extrafloral nectaries in *Cedrela fissilis* (Meliaceae). *Flora* 202:455–461
- Palermo FH, Rodrigues MIA, Nicolai J, Machado SR, Rodrigues TM (2018) Resin secretory canals in *Protium heptaphyllum* (Aubl.) Marchand. (Burseraceae): a tridimensional branched and anastomosed system. *Protoplasma* 255:899–910
- Pell SK, Mitchell JD, Miller AJ, Lobova TA (2011) Anacardiaceae. In: Kubitzki K (ed) The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales. Springer, Berlin, pp 7–50
- Pickard WF (2008) Laticifers and secretory ducts: two other tube systems in plants. *New Phytol* 177:877–888
- Pirani JR, El Ottra JHL, Menezes NL (2010) Morfoanatomia de flores de cinco espécies de *Galipea* Aubl. e seu significado na evolução de flores tubulosas entre as Rutaceae neotropicais. *Rev Bras Bot* 33:301–318
- Pirani JR, Majure LC, Devecchi MF (2021) An updated account of Simaroubaceae with emphasis on American taxa. *Braz J Bot*. <https://doi.org/10.1007/s40415-021-00731-x>
- Plowden C, Uhl C, Oliveira FA (2002) Breu resin harvest by Tembé Indians and its dependence on a bark-boring beetle. In: Stepp JR, Wyndham FS, Zarger RK (eds) Ethnobiology and biocultural diversity. University of Georgia Press, Athens, pp 365–380
- Prado E, Demarco D (2018) Laticifers and secretory ducts: similarities and differences. In: Hufnagel L (ed) Ecosystem services and global ecology. IntechOpen, London, pp 103–123
- Radlkofer L (1895) Monographie der Sapindaceen – Gattung *Paullinia*. Verlag der K.B. Akademie, München
- Rafiei M, Rajaei H (2007) Structural and developmental studies on oil producing reproductive organs in Lime (*Citrus aurantifolia* Swingle). *J Biol Sci* 7:848–853
- Rajput KS, Kothari RK (2005) Formation of gum ducts in *Ailanthus excelsa* in response to fungal infection. *Phyton* 45:33–43
- Rajput KS, Rao KS, Vyas H (2005) Formation of gum ducts in *Azadirachta indica* A. Juss J Sustain For 20:1–13
- Ramos MV, Demarco D, Souza ICC, Freitas CDT (2019) Laticifers, latex, and their role in plant defense. *Trends Plant Sci* 24:553–567
- Ramos MV, Freitas CDT, Morais FS, Prado E, Medina MC, Demarco D (2020) Plant latex and latex-borne defense. In: Nawrot R (ed) Latex, laticifers and their molecular components: from functions to possible applications. Advances in Botanical Research, Vol 93. Academic Press, Cambridge, pp 1–25
- Ramp E (1988) Struktur, Funktion und Systematische Bedeutung des Gynociums bei dem Rutaceae und Simaroubaceae. Dissertation

- zur Erlangung der philosophischen Doktorwürde. Universität Zürich, Zürich
- Rattan RS (2010) Mechanism of action of insecticidal secondary metabolites of plant origin. *Crop Prot* 29:913–920
- Record SJ, Hess RW (1943) *Timbers of the New World*. Yale University Press, New Haven
- Ribeiro JC, Ferreira MJP, Demarco D (2017) Colleters in Asclepiadoideae (Apocynaceae): protection of meristems against desiccation and new functions assigned. *Int J Plant Sci* 178:465–477
- Ribeiro JC, Tölke ED, Demarco D (2021) Secretory patterns in colleters of Apocynaceae. *Plants* 6:66
- Rickson FR, Rickson MM (1998) The cashew nut, *Anacardium occidentale* (Anacardiaceae), and its perennial association with ants: extrafloral nectary location and the potential for ant defense. *Am J Bot* 85:835–849
- Ronse De Craene LP, Haston E (2006) The systematic relationships of glucosinolate-producing plants and related families: a cladistic investigation based on morphological and molecular characters. *Bot J Linn Soc* 151:453–494
- Rosalem PF, Picão TB, Rodrigues-Lisoni FC, Martins AR (2017) Leaf anatomy of *Protium ovatum* and its antiproliferative potential in cervical cells. *Rev Bras Farmacog* 27:673–678
- Roy AT, De DN (1992) Studies on differentiation of laticifers through light and electron microscopy in *Calotropis gigantea* (Linn.) R.Br. *Ann Bot* 70:443–449
- Rudall PJ (1987) Laticifers in Euphorbiaceae—a conspectus. *Bot J Linn Soc* 94:143–163
- Santos-Silva J, Tozzi AMGA, Simon MF, Urquiza NG, Morales M (2013) Evolution of trichome morphology in *Mimosa* (Leguminosae—Mimosoideae). *Phytotaxa* 119:1–20
- Saunders ER (1934) On carpel polymorphism. VI. *Ann Bot* 48:643–692
- Saxena G, McCutcheon AR, Farmer S, Towers GHN, Hancock REW (1994) Antimicrobial constituents of *Rhus glabra*. *J Ethnopharmacol* 42:95–99
- Schmid R (1988) Reproductive versus extra-reproductive nectaries—Historical perspective and terminological recommendations. *Bot Rev* 54:179–232
- Schupp EW, Feener DH (1991) Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In: Huxley CR, Cutler DF (eds) *Ant-plant interactions*. Oxford University Press, Oxford, pp 175–197
- Setia RC, Parthasarathy MV, Shah JJ (1977) Development, histochemistry and ultrastructure of gum-resin ducts in *Commiphora mukul* Engl. *Ann Bot* 41:999–1004
- Shi HY, Zhou YF, Guo JS, Liu WZ (2011) Development and cytochemistry of secretory ducts in *Ailanthus altissima*. *Acta Bot Boreal-Occid Sin* 31:1291–1296
- Silva TFP (2009) *Biologia floral e aspectos botânicos de Serjania pernambucensis* Radlk (Sapindaceae). Master Thesis. Universidade Federal do Recôncavo da Bahia, Cruz das Almas
- Simpson MG (2010) *Plant systematics*, 2nd edn. Elsevier, San Diego
- Solereder H (1908) *Systematic anatomy of the dicotyledons*, vol 1. Clarendon Press, Oxford
- Solís SM, Ferrucci MS (2006) Comparative leaf morpho-anatomical studies of two South American species of *Cardiospermum* (Sapindaceae) with special reference to adaxial domatia. *Blumea* 51:153–164
- Solís SM, Ferrucci MS (2009) The floral nectary of *Cardiospermum grandiflorum* and *Urvillea chacoënsis* (Sapindaceae): morpho-anatomy and ontogeny. *Ann Bot Fenn* 46:485–495
- Solís SM, Zini LM, González VV, Ferrucci MS (2017) Floral nectaries in Sapindaceae s.s.: morphological and structural diversity, and their systematic implications. *Protoplasma* 254:2169–2188
- Souza LA (2010) *Estruturas secretoras nos órgãos vegetativos aéreos de Paullinia rubiginosa* Cambess. (Sapindaceae). Master Thesis. Universidade Federal de Viçosa, Viçosa
- Souza LA, Moscheta IS, Mourão KSM, Rosa SM (2004) Morphology and anatomy of the flower and anthesis of *Metrodorea nigra* St. Hill. (Rutaceae). *Braz Arch Biol Technol* 47:107–112
- Souza LR, Trindade FG, Oliveira RA, Costa LCB, Gomes VM, Da Cunha M (2016) Histochemical characterization of secretory ducts and essential oil analysis of *Protium* species (Burseraceae). *J Essent Oil Res* 28:166–171
- Spiekerkoetter H (1924) Untersuchungen zur Anatomie und Systematik ostafrikanischer Meliaceen, Burseraceen und Simarubaceen. *Bot Arch* 7:274–320
- Stern WL, Brizicky GK (1960) The morphology and relationships of *Diomma*, gen. inc. sed. *Mem NY Bot Gard* 10:38–57
- Stevens PF (2001 onwards) *Angiosperm Phylogeny Website*. Version 14, July 2017 [and more or less continuously updated since]. <http://www.mobot.org/MOBOT/research/APweb/>
- Thomas V (1991) Structural, functional and phylogenetic aspects of the colleter. *Ann Bot* 68:287–305
- Thomson WW, Platt-Aloia K, Endress AG (1976) Ultrastructure of oil gland development in the leaf of *Citrus sinensis* L. *Bot Gaz* 137:330–340
- Tilak VD, Nene PM (1976) The disc in the Rutaceae. *J Univ Bombay* 45:49–53
- Tillson AH, Bamford R (1938) The floral anatomy of the Aurantioideae. *Am J Bot* 25:780–793
- Tilney PM, Nel M, van Wyk AE (2018a) Foliar secretory structures in *Melia azedarach* (Meliaceae), a widely cultivated and often invasive tree. *N Z J Bot* 56:198–215
- Tilney PM, Nel M, van Wyk AE (2018b) Foliar secretory structures in *Ekebergia capensis* (Meliaceae). *Heliyon* 4:e00541
- Tölke EEAD, Galetto L, Machado SR, Lacchia APS, Carmello-Guerreiro SM (2015) Stages of development of the floral secretory disk in *Tapirira guianensis* Aubl. (Anacardiaceae), a dioecious species. *Bot J Linn Soc* 179:533–544
- Tölke ED, Lacchia APS, Demarco D, Carmello-Guerreiro SM (2017) Pericarp ontogeny of *Tapirira guianensis* Aubl. (Anacardiaceae) reveals a secretory endocarp in young stage. *Acta Bot Bras* 31:319–329
- Tölke ED, Bachelier JB, Lima EA, Ferreira MJP, Demarco D, Carmello-Guerreiro SM (2018a) Osmophores and floral fragrance in *Anacardium humile* and *Mangifera indica* (Anacardiaceae): an overlooked secretory structure in Sapindales. *AoB Plants* 10:ply062
- Tölke ED, Bachelier JB, Lima EA, Galetto L, Demarco D, Carmello-Guerreiro SM (2018b) Diversity of floral nectary secretions and structure, and implications for their evolution in Anacardiaceae. *Bot J Linn Soc* 187:209–231
- Tölke ED, Capelli NV, Pastori T, Alencar AC, Cole TCH, Demarco D (2019) Diversity of floral glands and their secretions in pollinator attraction. In: Mérillon JM, Ramawat KG (eds) *Coevolution of secondary metabolites*. Reference Series in Phytochemistry. Springer, Cham, pp 1–46
- Tölke ED, Lacchia APS, Lima EA, Ascensão L, Demarco D, Carmello-Guerreiro SM (2021) Secretory ducts in Anacardiaceae revisited: updated concepts and new findings based on histochemical evidence. *S Afr J Bot* 138:394–405
- Trachtenberg S, Fahn A (1981) The mucilage cells of *Opuntia ficus-indica* (L.) Mill.—development, ultrastructure, and mucilage secretion. *Bot Gaz* 142:206–213
- Turner GW (1999) A brief history of the lysigenous gland hypothesis. *Bot Rev* 65:76–88
- Turner GW, Berry AM, Gifford EM (1998) Schizogenous secretory cavities of *Citrus limon* (L.) Burm. f. and a re-evaluation of the lysigenous gland concept. *Int J Plant Sci* 159:75–88

- Turner GW, Lange BM (2015) Ultrastructure of grapefruit secretory cavities and immunocytochemical localization of (1)-limonene synthase. *Int J Plant Sci* 176:643–661
- van der Walt JJA, van der Schijff HP (1969) The anatomy of the petiole as an aid to the identification of South African *Commiphora* species. *Kirkia* 9:95–107
- Venkaiah K, Shah JJ (1984) Distribution, development and structure of gum ducts in *Lannea coromandelica* (Houtt.) Merrill. *Ann Bot* 54:175–186
- Vitarelli NC, Riina R, Caruzo MBR, Cordeiro I, Fuertes-Aguilar J, Meira RMSA (2015) Foliar secretory structures in Crotonaceae (Euphorbiaceae): diversity, anatomy, and evolutionary significance. *Am J Bot* 102:833–847
- Vogel S (1990) The role of scent glands in pollination: on the structure and function of osmophores. Amerind, New Delhi
- Waterman PG (1993) Phytochemical diversity in the order Rutales. In: Downum KR, Romeo JT, Stafford HA (eds) *Phytochemical potential of tropical plants*. Plenum Press, New York, pp 203–233
- Waterman PG, Grundon MF (1983) *Chemistry and chemical taxonomy of the Rutales*. Academic Press, New York
- Weber MG, Keeler KH (2013) The phylogenetic distribution of extrafloral nectaries in plants. *Ann Bot* 111:1251–1261
- Weber MG, Porturas LD, Keeler KH (2015) World list of plants with extrafloral nectaries. <http://www.extrafloralnectaries.org>, Accessed 3 May 2020
- Weckerle CS, Rutishauser R (2005) Gynoecium, fruit and seed structure of Paullinieae (Sapindaceae). *Bot J Linn Soc* 147:159–189
- Wilson KJ, Mahlberg PG (1978) Ultrastructure of non-articulated laticifers in mature embryos and seedlings of *Asclepias syriaca* L. (Asclepiadaceae). *Am J Bot* 65:98–109
- Wilson KJ, Mahlberg PG (1980) Ultrastructure of developing and mature nonarticulated laticifers in the milkweed *Asclepias syriaca* L. (Asclepiadaceae). *Am J Bot* 67:1160
- Wunnachit W, Jenner CF, Sedgley M (1992) Floral and extrafloral nectar production in *Anacardium occidentale* (Anacardiaceae): an andromonoecious species. *Int J Plant Sci* 153:413–420
- Yamawo A (2015) Extrafloral nectaries of *Melia azedarach* (Meliaceae): the first record for genus *Melia*. *J Jap Bot* 90:404–406
- Zhang M, Wang J, Zhu L, Li T, Jiang W, Zhou J, Peng W, Wu C (2017) *Zanthoxylum bungeanum* Maxim. (Rutaceae): a systematic review of its traditional uses, botany, phytochemistry, pharmacology, pharmacokinetics, and toxicology. *Int J Mol Sci* 18:2172
- Zhou Y, Shi H, Liu W (2012) Ontogenesis of trichome-like cavities in *Dictamnus dasycarpus*. *Flora* 207:63–73