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SYSTEMATICS, PHYLOGENY & FLORISTICS - REVIEW

An updated account of Simaroubaceae with emphasis on American taxa

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Abstract
Simaroubaceae are among the families whose circumscription radically changed over time, because phylogenetic analyses undertaken since 1995 demonstrated it was a polyphyletic group in its traditional delimitation. Currently, Simaroubaceae sensu stricto are a mostly pantropical, highly supported monophyletic group composed of 22 genera and approximately 120 species. Growing knowledge about members of the family has allowed several advances over the last couple of decades. The primary center of diversity for Simaroubaceae is in tropical America, and new contributions have been recently made regarding members of the family in the region, including descriptions of several new taxa. Hence, we undertook an updated overview of general information available for the group, with focus on American taxa of Simaroubaceae, and highlighting numerous data published after the 2011 monograph. Besides aiming to contribute to a better knowledge of a family with past controversial limits, we emphasize research topics in which the current scarcity of data demands further investigation.

Keywords Eudicots · Morphology · Rutales · Sapindales · Taxonomy

1 Introduction

Several traditional families of plants have a history going back to the XVIIIth century, when they were first described by botanists such as Antoine-Laurent de Jussieu (1748–1836), Michel Adanson (1727–1806), and Augustin-Pyramus de Candolle (1778–1841). Along the following centuries, great progress was gradually achieved toward a better knowledge of the general diversity and morphology of the components of each family. With a continuous increase in new evidence from other sources, such as anatomy, palynology, chemistry, cytology and genetics, a great improvement of the circumscription of the plant families was achieved. Integration of data from some or all of these sources characterizes most systems of classification produced in the nineteenth and twentieth centuries. Among the remarkable ones are those elaborated by H. G. Adolf von Engler (1844–1930), John Hutchinson (1884–1972), Armen Takhtajan (1910–2009), Arthur Cronquist (1919–1992), Robert F. Thorne (1920–2015) and Rolf M. T. Dahlgren (1932–1987). The advent and flourishment of the *Phylogenetic Systematics* approach after ideas of Emil Hans Willi Hennig (1913–1976) opened a new era when the use of explicit principles to define taxa was required, especially the search for synapomorphies to diagnose monophyletic groups, as did Dahlgren et al. (1985) for families and other taxa of the monocotyledons. The full access to DNA sequencing from the early 1990 years on allowed a rapid construction of phylogenies, and this brought a new age of tests of monophyly of the traditional groups.

Simaroubaceae are among the families whose circumscription radically changed over time, because its traditional delimitation (Engler 1931) was showed to be an "artificial construct" (Fernando et al. 1995). Five of the six subfamilies recognized by Engler (1931) were excluded from the family, while a few genera were included in it. Growing knowledge about members of Simaroubaceae allowed several advances, such as phylogenies based on larger sampling and number of gene regions (Clayton et al. 2007; Devecchi et al. 2018a), biogeographical analysis (Clayton et al. 2009), and a worldwide taxonomic monograph (Clayton 2011).

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The primary center of diversity for Simaroubaceae is in tropical America (e.g., Thomas 1990), and new contributions have been recently made regarding members of the family in the region, mainly as descriptions of several new taxa (e.g., Schrader & Davis 2011; Devecchi & Pirani 2015; Palacios 2015; Devecchi et al. 2016, 2018b, c; Noa-Monzón and González-Gutiérrez 2019; Majure et al. 2021a), a genus synonymization (*Euleria* Urb. in *Picrasma* Blume, Thomas et al. 2011), and a genus revision (*Homalolepis* Turcz., Devecchi et al. 2018b), as well as regional floras (e.g., Hahn and Thomas 2001; Thomas and Franceschinelli 2005; Devecchi and Pirani 2016, 2020; Devecchi et al. 2021) and broad floristic projects, such as a checklist of the vascular plants of the Americas (Ulloa Ulloa et al. 2017), a catalogue and an illustrated guide to the trees of Peru (Brako and Zarucchi 1993; Pennington et al. 2004), catalogues of Southern Cone (Zuloaga et al. 2008), Bolivia (Pirani and Thomas 2014) and Colombia (Bernal et al. 2016) and Flora do Brasil (2020), the latter with a monographic treatment for the family (Devecchi et al. 2020). Taxonomy at the species level has been improved also by detailed studies on two complex species (*Simaba guianensis* Aubl., Thomas 1985; *Homalolepis ferruginea* (A.St.-Hil.) Devecchi & Pirani, Devecchi et al. 2018d), and phenetic analyses quantifying the variation of diagnostic features in related species of *Simarouba* (Franceschinelli and Yamamoto 1993; Franceschinelli et al. 1999). A general treatment in a book on the Neotropical families of flowering plants was presented by Thomas (2004).

On the other hand, most floras and other works on Neotropical Simaroubaceae published earlier that 2000 include surpassed descriptions and taxa that do not belong in the group ever since (e.g., Small 1911; Fawcett and Rendle 1920; Macbride 1949; Brizicky 1962; Porter 1975; Jansen-Jacobs 1979; Pirani 1987a, b; Thomas 1990; Killeen et al. 1993; Pirani 1997). A couple of floras published after 2000 still included genera, such as *Picramnia* Sw (currently in Picramniaceae, Picramniales), as authors had to follow the general rules of each floristic plan (Pirani 2002; Pennington et al. 2004).

Thus, this is a conducive time for undertaking an update of general information on the group, with a focus on American taxa of Simaroubaceae. Our aim is to contribute to a better knowledge of a family with past controversial limits, and about which still there is a scarcity of data from some fields of research, while the other needs complimentary investigation and prospects.

2 A brief historical overview, with emphasis in taxonomy and phylogeny

Simaroubaceae was first published by De Candolle (1811) "as Simarubeae", including *Ailanthus* Desf., *Brucea* J.F. Mill., *Castela* Turpin, *Quassia* L., *Samadera* Gaertn., *Soulamea* Lam., *Simaba* Aubl., and *Simarouba* Aubl. These genera were previously described from 1762 to 1806, classified first within the classes Decandria and Polygamia of Linnaeus' classification, and were later transferred to the "ordo" Terebinthacearum by Jussieu (1789). Circumscription of this latter taxon remained somewhat controversial for some decades, but subsequently the concept of Terebinthaceae became limited to genera currently included in Anacardiaceae and Burseraceae (e.g., Marchand 1869), and the definition of the family Simaroubaceae by De Candolle (1811) prevailed.

A revisional account on the family was elaborated by Planchon (1846), who proposed the first attempt to an infrafamilial classification, placing 17 genera into four tribes: Simaroubeae, Harrisonieae, Ailantheae, Spathelieae, based mainly on carpel union (free or connate), number of ovules per carpel, type of embryo and number of stamens and petals. Later on, Bentham and Hooker (1862) proposed a classification recognizing only two tribes, Simaroubeae with free carpels, and Picramnieae with a syncarpous gynoecium.

Engler (1874) in his treatment for Martius' *Flora brasiliensis* recognized three tribes in Simaroubaceae (spelled Simarubaceae at that time): Surianeae, Eusimarubeae and Picramnieae, based on the structure of ovaries and styles, and the number of ovules. In the worldwide monograph of the family, Engler (1897, 1931) excluded the subtribe Dictyolomeae (formerly in tribe Eusimarubeae, then transferred to Rutaceae), but largely expanded the circumscription of Simaroubaceae, recognizing eight subtribes and nine tribes in six subfamilies: Alvaradoideae, Irvingioideae, Kirkioideae, Picraminoideae, Simarouboideae (the largest one) and Surianoideae. Besides the gynoecium features previously used, he also took into account characters of the androecium, such as the presence or lack of scale-like appendages at the filaments base, and leaf traits, such as the division of the lamina. Simaroubaceae sensu Engler (1931) became a large family comprising about 30 genera and 200 species of tropical and subtropical trees and shrubs. This classification persisted in subsequent editions of Engler's Syllabus der Pfanzenfamilien (Melchior 1964, ed. 12).

Growing evidence from several sources gradually revealed the heterogeneous nature of Simaroubaceae as defined by Engler (1931), such as through the analysis of wood anatomy (e.g., Webber 1936; Heimsch 1942), general anatomy (Metcalfe and Chalk 1950), pollen morphology (Erdtman 1952, 1986; Basak 1963, 1967; Moncada and Machado 1987) and phytochemistry (e.g., Hilditch and Williams 1964; Gibbs 1974; Waterman 1983; Simão et al. 1991). Webber (1936) and Heimsch (1942) suggested the exclusion of some of the subfamilies, based on anatomic evidences, as did Gibbs (1974) on chemical grounds. Even though one or more of the subfamilies were excluded in systems of classification proposed during the second half of the twentieth century, such as the ones proposed by Takhtajan (1980), Dahlgren et al. (1985), Cronquist (1981, 1988) and Thorne (1992), the Simaroubaceae continued to encompass considerable diversity in secondary chemistry, macro- and micromorphology.

However, based on structural studies of the gynoecium structure of ten genera by Ramp (1988) suggested that Simaroubaceae sensu lato represented a polyphyletic group. This suggestion was later corroborated by a study of fruit anatomy by Fernando and Quinn (1992), and eventually by the first molecular phylogenetic analysis focusing on Simaroubaceae (Fernando et al. 1995). Although limited to sequences of a single gene (*rbcL*) of seven genera, the latter study recovered Simaroubaceae s.l. as not monophyletic, with at least five separate lineages. Only members of Kirkioideae and Simarouboideae (except *Harrisonia*) clustered within the Sapindales clade, while those of Irvingioideae, Surianoideae, Alvaradoideae and Picramnioideae emerged well outside the order. The two latter currently constitute Picramniaceae, Picramniales (see Stevens et al. 2002); Irvingioideae and Surianoideae had been long before removed as Irvingiaceae (currently in Malpighiales), and Surianaceae are embedded in Fabales (see Stevens et al. 2002 onwards). Thus, Simaroubaceae sensu stricto was recircumscribed as a well-supported monophyletic group, composed only by the genera of Simarouboideae, with the inclusion of *Leitneria* (formerly Leitneriaceae), and the exclusion of *Harrisonia*, which is nested within Rutaceae (Fernando et al. 1995). Leitneriaceae were formerly included in Leitneriales in Engler's *Syllabus* (Melchior 1964) and also by authors, such as Takhtajan (1980) and Cronquist (1988), within subclass Hamamelidae on account of its reduced, naked, wind-pollinated flowers. However, this family was treated as a member of Rutales (= Sapindales) by Thorne (1992) and later also by Takhtajan (1997). *Kirkia* as the only genus of Kirkiaceae was already proposed by authors as Takhtajan (1980) and remains within Sapindales (Gadek et al. 1996; Stevens et al. 2002).

Further evidences based on morphological and molecular grounds help support Simaroubaceae s.s. as a monophyletic group (Gadek et al. 1996; Clayton et al. 2007, 2009; Muellner et al. 2007, 2016). The latest comprehensive phylogenetic studies of the family were conducted by Clayton et al. (2007, 2009), based on four molecular regions and a broad taxon sampling. A recent phylogeny based on six gene regions from a richer sampling of neotropical taxa (Devecchi et al. 2018a) improved the knowledge about the neotropical lineages, and most clades from Clayton's study (2009) were also corroborated.

Putative synapomorphies of Simaroubaceae are the exclusive triterpenoid compounds of the quassinoid type (Fernando et al. 1995), five carpels united only by their styles and separating in fruit and one ovule per locule (e.g., Stevenson et al. 2002; Alves et al. 2021—this issue).

Regarding the suprafamilial relationships, Simaroubaceae form a well-supported clade with Rutaceae and Meliaceae in Sapindales (Gadek et al. 1996; Källersjö et al. 1998; Savolainen et al. 2000; Soltis et al. 2000; Muellner-Riehl et al. 2016), but the sister relationship between the families is still uncertain, with possible topologies—Rutaceae sister to Simaroubaceae (Gadek et al. 1996), or Meliaceae sister to Simaroubaceae (Chase et al. 1999, Muellner et al. 2007, Muellner-Riehl et al. 2016), or Rutaceae sister to Meliaceae (Fernando et al. 1995). Majure et al. (2021b—this issue) resolved Simaroubaceae strongly supported as sister to Rutaceae using plastome data. These three families share the presence of unusual triterpenoids, bitter substances, which are based on degraded forms of triterpenes and uncommon in other Angiosperms: the limonoids in Meliaceae and Rutaceae, and the quassinoids in Simaroubaceae (Kubitzki and Gottlieb 1984; Gadek et al. 1996; Kubitzki et al. 2011). The Simaroubaceae are related to the Rutaceae in terms of chemical composition, wood anatomy, and in the free stamens (which are mostly united in Meliaceae), but it is remarkably distinct from Rutaceae in its absence of secretory cavities containing aromatic oils in leaves and floral parts, and by its uniovulate carpels, as well as by the absence of quassinoids in Rutaceae (Fernando and Quinn 1992). The alternative sister group relationship of Simaroubaceae and Meliaceae is supported also by some morphological features shared by both families, as discussed by Gama et al. (2021) and Alves et al. (2021—this issue).

A general treatment of the family since its new circumscription made by Fernando and Quinn (1995) was provided by Clayton (2011), including a complete synopsis with identification keys and descriptions of all genera. Several decades before, important contributions to the knowledge of neotropical genera were provided by Arthur Cronquist, who produced synopses of *Castela* (Cronquist 1944a, 1945), *Simarouba* (1944b) and *Simaba* (1944c), and eventually a resume of the remaining American genera (1944d). Later, the largest genus *Simaba* was reviewed by Cavalcante (1983), mostly following species circumscriptions presented in Cronquist (1944c). Even though there were proposals to reduce *Simaba* to a section of *Quassia*, along with other extra-neotropical genera of subfamily Simarouboideae, by Pierre (1896) and Nooteboom (1962), in the Americas *Simaba*, *Quassia,* and *Simarouba* were maintained as distinct genera in regional floras and monographs (e.g., Cronquist 1944c; Porter 1973; Arrázola 1993; Cavalcante 1983; Feuillet 1983; Thomas 1985, 1990; Pirani 1987a, b, 2015; Hahn and Thomas 2001; Thomas and Franceschinelli 2005; Devecchi and Pirani 2015, 2016; Devecchi et al. 2021). Molecular phylogenies by Clayton et al. (2007, 2009) also refuted the broad circumscription of *Simaba* as proposed by Nooteboom (1962), until eventually a phylogenetic study (Devecchi et al. 2018a) based on data of five molecular regions, including two nuclear (ETS, ITS) and three plastidial ones (psbA-trnH, rps16 and trnL-trnF) provided strong evidence that *Simaba* was not monophyletic. The genus was there reduced to include only the species of *S.* sect *Tenuiflorae* Engl., while the species belonging to the two mostly extra-Amazonian sections (*S.* sect. *Floribundae* Engl., and *S.* sect. *Grandiflorae* Engl.) were transferred to the reinstated *Homalolepis* Turcz., which emerged closely related to *Simarouba* (Devecchi et al. 2018a). *Homalolepis* is currently the largest genus of the family and was subject of a detailed taxonomic revision (Devecchi et al. 2018b).

Except for *Castela*, *Simaba* and *Picrasma*, the remaining American genera have been maintained under the circumscription, such as presented in Engler's monograph (1931) and Cronquist's synopses (1944a; 1944b, 1944d). Neotropical species of *Picrasma* were treated by Engler (1931) in a distinct genus, *Aeschrion* Vell., but were synonymized under the former by Cronquist (1944d). *Holacantha* A. Gray, a genus maintained separately from *Castela* by Engler (1931) and Cronquist (1944a), was synonymized with *Castela* by Moran and Felger (1968) based on a putatively morphologically intermediate species between the two genera. This broader circumscription of *Castela* was maintained by Thomas (1990) and Majure et al. (2021b), although Clayton (2011) considered two distinct genera. Also, it is important to highlight the inclusion of *Leitneria,* formely in Leitneriaceae, endemic of the southeastern USA.

Thus, the circumscription of Simaroubaceae changed drastically over the last few decades, but currently, they are a highly supported monophyletic group composed of 22 genera and approximately 120 species (Devecchi et al. 2021).

3 General morphology, with accounts on special anatomic traits

All Simaroubaceae species are woody, ranging from large trees, up to 60 m as in *Ailanthus*, to treelets, shrubs and subshrubs, these occasionally suffrutescent with the leaves clustered at ground level, as seen in some dwarf species of *Homalolepis* from Central Brazil. The latter are geophytes, with apparently protective structures of cauline buds, as prophylls and cataphylls, recently investigated through morphoanatomical and histochemical techniques (Cortez et al. 2021—this issue). A detailed structural analysis of the underground system of these geophytic species is presented by Melo-de-Pinna et al. (2021—this issue).

Thorns at the branch tips or axillary are present only in the genus *Castela.* This taxon also demonstrates reduced, simple leaves and generally green, photosynthetic stems, which are often devoid of leaves, a feature likely related to their occurrence in deserts, southern South American Chaco vegetation and seasonally dry tropical forests, where they are especially diverse in the Greater Antilles (Majure et al. 2021b—see this issue).

Detailed wood anatomy is described by Webber (1936), Record and Hess (1943) and Metcalfe and Chalk (1950, 1972). All these authors refer that the only common characters to all species studied were vessels in a diagonal and/or radial pattern; vessel outline circular to oval; simple perforation plates; and alternate intervessel pits. Webber (1936) and O'Donnell (1937) also observed ring porous wood in *Picrasma* and *Ailanthus*, and semi-ring-porous in *Castela*. Vessel size or diameter is among the quantitative characters useful to help distinguish wood of these latter three genera (O'Donell 1937). Some genera may have rays exclusively uniseriate (*Picrasma, Quassia),* while others are mostly 2–4 cells wide, but up to 7 cells wide rays are found in *Castela* and *Simarouba,* or sometimes even more than 10 cells wide in *Ailanthus* (Metcalfe and Chalk 1950). Besides the thorny habit, *Castela* also diverges from all other genera of the family studied so far mainly because the greatest part of their wood consists of libriform fibers, rather than fibers with distinctly bordered pits (Webber 1936). Additionally, the spiral thickenings observed in vessels of *Castela* and *Leitneria* are rare or absent in the remaining taxa.

Solitary or clustered crystals are widespread in the family, especially the latter type, and their size and distribution seem to bear taxonomic relevance at the generic level; clustered crystals are particularly large in *Castela* (Boas 1913; Metcalfe and Chalk 1950).

Secretory canals are often present along vascular bundles, and secretory cells occur in the cortex and pith. Either cells and canals contains volatile oils and resins, but in smaller amounts compared to the related families Rutaceae and Meliaceae (Hegnauer 1983). The presence or absence of medullary secretory canals seems to be a feature of generic diagnostic value (Boas 1913; Heimsch 1942; Metcalfe and Chalk 1950).

Hairs are mostly simple, unicellular or multicellular, sometimes glandular-capitate (Boas 1913; Metcalfe and Chalk 1950, 1972; Macedo et al. 2005); trichomes with secretory basal cells were found in leaves of *Quassia amara* L. (Macedo et al. 2005). Taxonomic relevance of the indumentum is mostly related to variations in density and size of trichomes at the species level (e.g., Engler 1874; Cronquist 1944b, c; Devecchi et al. 2018b). Glandular trichomes on leaves of *Ailanthus* release a secretion with an unpleasant smell that is repulsive to insects (Bory and Clair-Maczulajtys 1980). Trichomes are especially common in inflorescence axes, bracts and floral organs (e.g., Nair and Joshi 1958; Clayton 2011).

Leaves are alternate, spirally arranged, generally crowded at apex of branches, mostly pinnately compound, seldom simple (*Castela, Leitneria*) or unifoliolate (two species of *Simaba,* with petiole pulvinate at apex). Leaflets are alternate, opposite or subopposite, and the petiole and rachis are distinctively winged in *Quassia amara* and slightly so in *Picrolemma* Hook. f.

Stipules are mostly lacking, though stalked extrafloral nectaries located at the base of the petiole of young leaves of *Ailanthus* are interpreted as reduced stipules by Clair-Maczulajtys and Bory (2011). Early caducous pseudostipules are reported in some *Picrasma* (Weberling and Leenhouts 1966).

The margin of the leaf or leaflet lamina usually is entire, while serrate to crenate leaflets are conspicuous in *Picrasma*, toothed in *Ailanthus*, and sometimes with pitted, concave, or flattish glands (*Ailanthus, Homalolepis, Picrolemma, Quassia, Simaba, Simarouba*). The marginal glands are mainly located at the basal tooth in *Ailanthus* and were anatomically studied by Bory and Clair-Maczulajtys (1990), who considered them as foliar nectaries acting as systems allowing for the elimination of excess sugars, probably playing an important role in the regulation of photosynthetic activity. The tissue structure of these marginal nectaries is similar to that of the stalked nectaries of the petiole (Clair-Maczulajtys and Bory 2011). In the closely related *Homalolepis, Simaba* and *Simarouba,* there are glandular structures on the leaf blade; these may be located at the leaflet apex (either at the very tip of the midvein or flanking it) or elsewhere; they are usually immersed in the mesophyll and may be found in both surfaces or only in the adaxial one (Metcalfe and Chalk 1950; Devecchi et al. 2018a); these variable patterns seem to bear taxonomic significance (Devecchi et al. in prep.; Devecchi et al. 2018a). Particularly, the apical gland located at the tip of the midvein is very conspicuous in leaflets of almost all species of *Homalolepis* and *Simaba,* while in *Simarouba* there are small glands flanking both sides of the midvein distal portion (Devecchi et al. in prep.). Such a remarkable feature is often mentioned in descriptions of these plants in botany manuals and floras (e.g., Engler 1874, 1931; Franceschinelli and Thomas 2000; Thomas and Franceschinelli 2005; Clayton 2011; Devecchi and Pirani 2016). Like *Simarouba*, species of *Quassia* bear laminar glands only toward the apex, and some extra-American taxa also have leaf glands. Apical and laminar glands seem to function as extrafloral nectaries in young leaflets, when ants are often seen foraging on them (Devecchi et al. 2018a).

Very peculiar sclereids, generally crossing the mesophyll, are found in several genera of Simaroubaceae (Boas 1913; Engler 1931). The sclereids exhibit a wide range of form and variations in thickness of the cell wall (Metcalfe and Chalk 1950; Saraiva et al. 2002; Macedo et al. 2005). Franceschinelli and Yamamoto (1993) described variation in form and size of the sclereids among three continental species of *Simarouba* and their usefulness in distinguishing them from each other. Although quite conspicuous, they seem to lack enough variation among species to subsidize taxonomy in genera, such as *Simaba* and *Homalolepis* (e.g., Alves 2015).

Flowers are arranged in inflorescences that can be axillary or terminal, bracteate. The most common types found in the family are the thyrse and the thyrsoid, which is a determinate thyrse and is much more widespread in the family. Most other inflorescence types found in a few genera can be interpreted as modifications from the basic thyrsoid. In *Picrasma,* there are cymoids, which are more or less rounded, modified thyrsoids; these are sometimes greatly reduced to 1–4-flowered inflorescences (Noa-Monzón 2020, Majure et al. 2021a), which may be treated as botryoids or depauperate thyrsoids. These latter pauciflorous inflorescence types also characterize *Simaba*, while *Quassia amara* has botryoids usually referred to as racemes in the literature. Inflorescences in *Castela* are often very reduced, pauciflorous fascicles, solitary or clustered in leaf axils. The peculiar catkin-like male inflorescences of *Leitneria* are pendulous or erect (Schrader & Graves 2011) and have been interpreted as reduced thyrses by anatomical studies (Abbe and Earle 1940; Tobe 2013). Evolution of inflorescence types within the family is discussed in Devecchi et al. (2018a) and especially in Alves et al. (2021—this issue).

The flowers are generally small, pedicellate (sessile in *Leitneria*), actinomorphic and mostly pentamerous. Even though the majority of core eudicots families present a stable merism with a predominance of pentamerous flowers, taxa from many families are more prone to meristic variations (Ronse De Craene and Smets 2016), as is the case of Simaroubaceae. The presence of flowers either tetramerous or pentamerous or occasionally hexamerous in a same species is found in some genera (e.g., *Ailanthus* and *Homalolepis*), and a hexamerous to octomerous perianth became fixed in the *Holacantha* clade of *Castela* (sensu Majure et al. 2021b—this issue). There is anatomical evidence that flowers of occasional tetramerous flowers of species of *Homalolepis* maintain traces concordant with pentamery, since one of the four petals has two vascular traces, indicating it originated by the fusion of two petals (Alves et al. 2017). The perianth underwent an extreme reduction in *Leitneria* female flowers, which lack petals and have vestigial sepals, while male flowers are naked.

The calyx is gamosepalous at the base. Petals are free, mostly imbricate, with cases of induplicate-valvate or valvate corolla, commonly pale green or white and less frequent red, pink, orange and yellow, and usually haired. *Quassia amara* has distinctive reddish flowers with an elongate, tubular corolla formed by coherent petals (e.g., Clayton 2011); flowers in *Homalolepis* sect. *Grandiflorae* may be large, with petals surpassing 3.5 cm long, and stamens coherent by the basal appendages of the filaments (Alves et al. 2017; Devecchi et al. 2018a, b).

The androecium is usually described as obdiplostemonous in most simaroubaceous genera. In the Americas, only *Picrasma* is haplostemonous (antesepalous stamens) and *Picrolemma* is obhaplostemonous (antepetalous stamens, a rare feature in angiosperms according to Ronse De Craene and Smets 1995). Phylogenetic analysis and ancestral character state reconstruction reveal lability in the stamen number within the family, with pleiostemonous and haplostemonous flowers having evolved a couple of times, independently, from the typically diplostemonous pattern (Clayton et al. 2007; Alves et al. 2021—this issue). The obdiplostemony of *Ailanthus* was considered to have resulted from the adnation of the traces to petals and antipetalous stamens by Nair and Joshi (1958). The current controversy on the nature of the (ob)diplostemonous androecium in most rosids shows the need for more developmental studies (e.g., Ronse De Craene and Bull-Hereñu 2016; Alves et al. 2021—this issue).

Anthers are bithecal, dorsifixed or basifixed, often versatile, usually introrse, dehiscing by longitudinal slits. In *Homalolepis*, the anther wall has a uniseriate epidermis and a conspicuous endothecial layer of columnar cells with lignified secondary wall thickening forming trabeculae (Alves et al. 2017).

Twelve out of the 22 genera of the family present a laminar, adaxial appendage on the base of the filaments, a remarkable feature. The staminal appendages vary in length, pubescence and form of the apex, may be erect or curved, and are taxonomic valuable. Engler (1931) defined tribe Simaroubeae essentially on the basis of the presence of appendaged stamens, and the phylogeny indicates that this is a remarkable trait of a highly supported lineage containing 11 genera, four of which occur in the Neotropics: *Quassia, Simaba, Simarouba*, and *Homalolepis.* This lineage holds the highest number of species in Simaroubaceae, and only two extra-American genera probably lost these appendages (Alves et al. 2021—this issue). The appendages may be slightly post-genitally coherent to each other by intertwining trichomes, in *Simaba* and especially in species of *Homalolepis* sect. *Grandiflorae,* forming a "pseudotube" (Alves et al. 2017; Devecchi et al. 2018a, b).

Staminodes are present in female flowers of several Simaroubaceae genera, but only three genera have staminodes in male flowers, two of them American: *Picrolemma* and *Simaba.* In the former genus, staminodes alternate with petals and stamens are opposite the petals. In *Simaba,* rudimental staminodes were recently detected forming a partial whorl between the base of the petals and the stamens (Devecchi et al. 2018a).

An intrastaminal disk is found in most genera, usually nectariferous, as seen in most representatives of Sapindales (the disk is extrastaminal only in Sapindaceae). In some simaroubaceous genera, a disk is inconspicuous, and in most of them, the nectariferous tissue is placed on the entire surface of a small to conspicuously elongated and stout gynophore (Alves et al. 2017), as in *Quassia, Simarouba, Simaba, Homalolepis,* and likely also *Picrolemma*. The nectary tissue at the periphery of the gynophore is vascularized only by small phloematic bundles, and the nectar is released through stomata found in depressions or at the same level as the epidermis (Alves et al. 2017).

The gynoecium is formed predominantly by five carpels, sometimes less or more. *Amaroria* and *Leitneria* are the only two genera in the family with a single carpel, and six to eight carpels occur in the *Holacantha* clade of *Castela* (sensu Majure et al. 2021b—this issue). Carpels are generally antepetalous and dorsally bulged above the level of the style base (hence anacrostylous) (Alves et al. 2017). Carpels are completely free from each other (*Picrolemma),* or they may be connate for a short extent at the base of the ovaries (e.g., *Homalolepis, Simaba*), but most genera have carpels partially and weakly united only by the styles (Nair and Joshi 1958; post-genital union, Alves et al. 2017). It is important to highlight that the vascularization of each carpel remains independent throughout the entire gynoecium; for example, the style is vascularized by five bundles, each corresponding to the dorsal bundle of the carpel with vascular bundles splitting into smaller bundles in the stigmatic region (Alves et al. 2017). Along the free (unfused) region of the ovary, carpels remain tightly coherent, often by means of dense intertwining trichomes. After fertilization, styles and stigmas fall down and carpels separate from each other forming fruitlets. Similar gynoecia with partially, postgenitally connate carpels are common in other families of Sapindales (e.g., Endress et al. 1983; Ramp 1988). The post-genital fusion of carpels in the apices of ovaries, as observed in most genera of Simaroubaceae, is considered as evidence of a probable derivation from a syncarpic ancestor (Endress et al. 1983; Alves et al. 2021—this issue).

The stigma shape varies from punctiform to lobate or with elongate stylar lobes, which are separate and divergent in several genera. Some studied stigmas have a papillose secretory epidermis (e.g., Alves et al. 2017).

There is a single ovule per locule, and the placentation is marginal. The ovule is anatropous or syntropous, suspended, or sometimes amphitropous and suberect (*Picrasma*), bitegmic and crassinucellate (Corner 1976; Alves et al. 2017). In *Homalolepis,* the inner integument of the ovule overgrows the outer and forms the micropyle (Alves et al. 2017). Pistillodes are found in male flowers of most genera that are not hermaphroditic.

Regarding the sexual systems, Simaroubaceae are hermaphroditic, monoecious, (sub)dioecious, or polygamous, this latter condition being the most common, with the presence of dimorphic flowers where each morphotype has rudimentary organs of the opposite sex, such as staminodes or pistillodes. Among the American genera, *Castela, Leitneria,* *Picrolemma* and *Simarouba* have distinctive unisexual flowers in dioecious plants, a feature traditionally used in floristic and taxonomic works to distinguish them from related genera (e.g., Engler 1931; Cronquist 1944a, b, d; Pirani 1987b; Thomas 1990; Clayton 2011). Male flowers in these five genera present a very reduced to vestigial pistillode, and small, sterile staminodes are found in female flowers. *Quassia* is hermaphroditic, with bisexual flowers known to be self-compatible (Roubki et al. 1985).

Among the remaining genera represented in the Americas, there are controversial references and more field and laboratory investigations are needed. *Ailanthus* and *Picrasma* are usually referred to either as monoecious and dioecious (Nooteboom 1962; Clayton 2011), or polygamous (e.g., Engler 1931). However, detailed studies revealed that flowers of *Ailanthus* fomerly described as bisexual are in fact female flowers whose staminodes are similar to fertile stamens but smaller and not releasing pollen (e.g., Nair & Joshi 1958; Alves et al. 2021—this issue). Thus, it is probable that only unisexual flowers, in monoecious or dioecious species, occur in this genus, as described by Clayton (2011). Conversely, *Picrasma* is traditionally referred to as an androdioecious genus with hermaphroditic and staminate flowers on separate plants (Thomas et al. 2011, Noa-Monzón et al. 2019, Majure et al. 2021a). In *Homalolepis* and *Simaba,* the flowers are morphologically bisexual, and the genera were described by some authors as hermaphroditic (e.g., Cavalcante 1983). Nevertheless, their flowers may be functionally bisexual or unisexual, either in polygamous plants (according to Engler 1931; Clayton 2011), or incompletely dioecious (according to Cronquist 1944b). This is supported by recent findings of scattered flowers bearing abortive ovules in some species of these two genera (Franceschinelli and Thomas 2000; Alves et al. 2017; Devecchi et al. 2018a, b). Flowers that are morphologically perfect but functionally unisexual are reported also to some extra-American simaroubaceous genera, as well as in many other groups of Sapindales [e.g., Meliaceae (Styles 1972; Franceschinelli et al. 2015), Anacardiaceae and Burseraceae (Bachelier and Endress 2009), Sapindaceae (Avalos et al. 2019) and Rutaceae (Kubitzki et al. 2011)]. Evolutionary paths of sexual structures and systems in Simaroubaceae and related families are discussed in Alves et al. (2021—this issue) and in Gama et al. (2021).

The fruit in Simaroubaceae is formed by one to five drupaceous fruitlets, each one derived from a single carpel, one-seeded, usually with a fleshy mesocarp, and less frequently woody and fibrous or dry (*Leitneria*). Drupaceous fruits are likely synapomorphic for the family (Stevenson et al. 2002; Alves et al. 2021—this issue). When mature, the fruits are cream to red or purple-blackish, with a bitter taste. Sclereids are found in the epicarp, mesocarp and endocarp (Fernando and Quinn 1992). As is common in drupelike fruits, the endocarp constitutes the hard portion of the pericarp, and it is described as a broad homogeneous layer with irregularly arranged isodiametric sclereids (Hartl 1958; Fernando and Quinn 1992). Nevertheless, the endocarp is thin in *Homalolepis,* while the mesocarp has a thick, fibrous and hard layer (Devecchi et al. 2018a, b). Globose fruitlets seem to be conservative in the family, but more specialized types are also found. In some *Simaba,* drupelets may be strongly laterally flattened (*S. obovata* Spruce ex Engl. and *S. orinocensis* Kunth), or they are lenticular (*Simaba guianensis, Castela*) or lenticular and flattened (*Castela* sp. nov.; Majure et al. accepted). Samaroid fruitlets as those of *Ailanthus* are rare in the family.

The seed has a thin, membranaceous but hard coat, scanty endosperm, and a straight or curved embryo with two large plane-convex cotyledons (Corner 1976; Stevens 2001). Detailed embryological data on some of the genera represented in the Neotropics are provided by Wiger (1935), Mauritzon (1935) and Narayana (1957).

4 Floral biology and dispersal

Entomophily prevails in most simaroubaceous genera, whose flowers are often reported to be fragrant and attract a wide range of generalist insects, including bees and moths (e.g., Hardesty et al. 2005; Clayton 2011; Devecchi et al. 2018a). However, floral diversity ranges from wind-pollinated catkin-like inflorescences in *Leitneria* (Cronquist 1981) to hummingbird-pollinated tubular red flowers in *Quassia amara* (Roubik et al. 1985). In the several genera with larger appendaged stamens, the nectar is concealed beneath those structures, which in some species of *Homalolepis* may even form a long staminal pseudotube. This is probably related to restrictions of animal visitors, but pollination system remains to be investigated.

Numerous species of bees and wasps were observed at populations of *Castela emoryi* (A. Gray) Moran & Felger, a desert species from Northern Mexico to Arizona and California; as blooming occurs during hot mid-summer time, when few other plants produce flowers, *C. emoryi* is believed to be locally essential for those foraging insects (Bell and Herskovits 2013).

The samaroid mericarps of *Ailanthus* disperse over small distances by wind. *Leitneria* grows in freshwater and brackish swamps, and as its fruits have an air chamber between the seed and the endocarp, they fluctuate and are water dispersed (Clayton 2011).

As drupaceous fruits prevail in the family, with a more or less fleshy pericarp, animal dispersion is common. Ichtyochory is reported to some species of *Simaba,* as *S. obovata* and *S. orinocensis,* inhabiting Amazonian seasonally flooded forests ("mata de várzea") or permanently flooded ("mata de igapó"). The drupelets of these two species are laterally flattened and float on water; they have a fleshy and edible mesocarp and are dispersed by fishes (Gottsberger 1978; Honda 1974).

Drupelets of *Homalolepis* are subglobose and can be very large, the largest ones in *H. cedron* (Planch.) Devecchi & Pirani (up to 10 cm long) and *H. trichilioides* (A.St.-Hil.) Devecchi & Pirani (around 4 cm long); their fruit wall is very hard, with a thick, fibrous mesocarp, and only a few animals can crack them, so it is likely that some rodents such as agoutis are dispersers (Devecchi et al. (2018a, b).

As the fruits of *Castela, Picrasma* and *Simarouba* are small, bird-dispersed drupelets, Clayton et al. (2009) suggested that north–south dispersal may be facilitated by the migratory patterns of fruit-eating birds. Majure et al. (2021b—this issue) likewise provided support for this hypothesis, showing that the modern distribution of *Castela* likely is the result of multiple long-distance dispersal events.

Drupaceous fruitlets of the widespread *Simarouba amara* Aubl. are known to be vertebrate-dispersed, mainly by large birds and mammals, including chachalacas, flycatchers, motmots, thrushes, howlermonkeys and tamarins (Hardesty et al. 2006), and also by fruit-eating phyllostomid bats (Kelm et al. 2008). Leaf-cutter ants have been observed to disperse the seeds of *S. amara* in Panama forests (Hardesty et al. 2005), and also of *S. versicolor* A.St.-Hil. in the Brazilian cerrado (Lopes et al. 2018). Seeds of *S. amara* that are eaten by monkeys are more likely to germinate than seeds that have not (Stevenson et al. 2002), as well as seeds of *S. versicolor* cleaned by ants germinate faster than seeds with tegument and seeds with tegument removed manually (Lopes et al. 2018). However, investigation of *S. amara* populations in Panama revealed that the seed dispersal effectiveness by leaf-cutter ants "appears to be ephemeral and likely contributes inconsequentially to the long-term recruitment and distribution patterns of the species" (Hardesty 2011).

5 Palynology

Studies on pollen morphology of Simaroubaceae are relatively scarce. The available palynological data are mostly based only on light microscopy, and pollen grains are considered relatively homogeneous, mostly isopolar, tricolporate, small or medium in sized, with lalongate endoapertures. The pollen shape varies among the genera and also between species of a genus, from oblate, oblate-spheroidal, prolate, prolate-spheroidal to subprolate, and the surface pattern is mostly finely to coarsely reticulate or sometimes verrucate (Erdtman 1952; Basak 1963, 1967; Caccavari De Filice and Villar 1980; Zavada and Dilcher 1986; Moncada and Machado 1987; Moura et al. 2004; Clayton 2011; Cartaxo-Pinto et al. in prep.). Cartaxo-Pinto et al. (in prep.) present also SEM pollen analyses and describe five distinct pollen types based mainly on sexine sculpture.

A survey on pollen morphology of the Sapindales elaborated by Gonçalves-Esteves et al. (2021—this issue) presents data from 15 genera of Simaroubaceae, including the 10 genera represented in the Americas.

It is noteworthy to highlight that pollen morphology provides important characters for the taxonomy of the family. For instance, pollen data supported the exclusion of *Kirkia* from Simaroubaceae, erected as Kirkiaceae (Erdtman 1952, 1986), as well as they helped to refute Nooteboom's proposal (1962) to merge some genera in *Quassia* sl. (Basak 1967).

6 Chromosome numbers

A survey of chromosome numbers and their evolutionary significance in Sapindales includes published and original data on Simarubaceae taxa (Guimarães and Forni-Martins 2021—this issue). Although basic chromosome numbers of 8–13 were reported by Stevens (2001 onwards), there is a probable range of chromosome number in Simaroubaceae of 7–16.

Karyotypes are known only for a few genera. In *Leitneria,* the basic number is $X=16$ (Raven 1975), and in *Castela coccinea* $2n=26$ (Bernardello et al. 1990). For *Simarouba,* the basic number reports are variable: *S. amara* has $X=16$ (Guimarães 2017), while in *S. glauca* there are two distinct reports: $X=16$ (Bawa 1973), and $X=15$ (Baratakke and Patil 2010). Polyploid numbers are reported in *Ailanthus altissimus* with $2n=80$ (Desai 1960), and to *Ailanthus integrifolia* with $2n=64$, which is probably an octoploid (Bennett and Leitch 2005a, b). In *Homalolepis arenaria* (Devecchi & Pirani) Devecchi & Pirani*, H. bahiensis* (Moric.) Devecchi & Pirani*, H. floribunda* (A.St.-Hil.) Devecchi & Pirani and *H. warmingina* (Engl.) Devecchi & Pirani, chromosome numbers $2n=32$ were found by Romero-da-Cruz et al. (2021—this issue), who also present additional cytogenetic data for this genus, which allowed the inference of a caryotypical history for Simaroubaceae.

7 Chemistry

Plants of Simaroubaceae have long been characterized in the literature by their bark with bitter taste, with several medicinal uses. Such bitter principles are quassinoids, which are triterpenoid derivatives, biosynthetically related to the limonoids of Rutaceae and Meliaceae (Dreyer 1983; Waterman 1983; Silva and Gottlieb 1987). Quassinoids are present throughout vegetative tissues and are also present in the fleshy fruits of most genera. Furthermore, the exclusive presence of the quassinoids is a putative chemical synapomorphy of the family (Fernando et al. 1995; Stevens 2001).

Bitter principles widely known in Simaroubaceae are quassin isolated from *Quassia amara* and *Picrasma excelsa* (Sw.) Planch., glaucarubin isolated from seeds of *Simarouba glauca* DC., cedrin from seeds of *Homalolepis cedron* (Planch.) Devecchi & Pirani (as *Simaba cedron*) (Gibbs 1974). However, a single genus, such as *Picrasma,* may produce 35 different structural types (Silva and Gottlieb 1987). The common structure to these substances is the lactone function and the isoprenoid structure (sesquiterpens or diterpens), and so they are related to the limonoids typical of Rutaceae, whose carbonskeleton is based on triterpenes however (Gibbs 1974).

Those authors reviewed the information regarding the chemistry of the main genera of the family. Besides the quassinoids, secondary metabolites reported for several genera in the family include alkaloids, mostly tryptophan-derived, coumarins, flavonols, flavones, flavonol glycosides and glycoflavons, and small amounts of volatile oils (e.g., Hegnauer 1983), and also canthinones and β-carbolines (Simão et al. 1991). Proportions of secondary metabolites isolated from species of *Simaba* and *Homalolepis* by Barbosa et al. (2011) were identified as quassinoids (34.5%), triterpenes (17.7%), alkaloids (16.8%) and others (31%: coumarins, steroids, phenolic compounds, anthraquinones, organic acid, flavonoid, essential oil and lignans).

Simão et al. (1991) suggested that a "specialization of quassinoid skeletons is accompanied by a West to East spatial radiation of the simaroubaceous lineage." According to them, a diversification of oxygenation and unsaturation patterns, and an increase in oxidation level of the quassinoids, are observed as one compares taxa from the Americas and West Africa to the East African and Asian genera.

8 Biogeography and ecology

Simaroubaceae are a mostly pantropical family, but include some subtropical and temperate elements. Among the American genera, *Castela* and *Picrasma* include one or more subtropical species, while only *Leitneria* is warm temperate and *Ailanthus altissimus* temperate.

The primary center of diversity of Simaroubaceae (in number of species) is found in the Neotropical region, with over half (65) species grouped in ten genera. Other species-rich areas are West Africa, Asia and Australasia (Clayton 2011). Brazil is home to a great diversity of Simaroubaceae, consisting of 36 species in seven genera of which 21 are endemic (Devecchi et al. 2020). Although forming a very minor part of the distribution of the family, the Greater Antilles also are a hotspot for the family, with at least 16 species occurring there, 13 of those endemics (Majure et al. 2021b—this issue). Distribution maps of the American genera are depicted in Figures 1, 2, 3, 4, 5, 6, 7, 8, 9.

Nine genera are monospecific or with only two species, with restricted distribution. Among these, only *Leitneria* and *Quassia* occur in the Americas. The largest genus is *Homalolepis*, with 28 species, exclusively neotropical. *Quassia* and *Picrasma* are the only American genera that also occur disjunctly in other continents. Some remarkable disjunct patterns are also present within the Americas, the most expressive shown by species of *Castela* and *Picrasma,* found in Central America and the West Indies (and occasionally in northernmost South America), as well as in southern South America (Figs. 1g and 4f) (Thomas 1990); *Castela* also is found in western North American deserts, where it likely originated (see Majure et al. 2021b—this issue).

A few species are widespread throughout tropical America, as *Homalolepis cedron* and *Simarouba amara*, the latter also with dense populations, but the former is more rare. Most species show a more restricted distribution, and there are some microendemics (e.g., *Castela macrophylla* Urb., *Picrasma longistaminea* W. Palacios, *Homalolepis pumila* Devecchi and Pirani, and at least seven other species of the later genus).

Simaroubaceae as a lineage probably diverged from the larger families of Sapindales during the Late Cretaceous (Clayton et al. 2009; Muellner-Riehl et al. 2016), and the crown-group Simaroubaceae are dated to approximately 65 Ma, in the Cretaceous-Maastrichian (Clayton et al. 2009). Although the remarkable disjunct pantropical distribution of the family could suggest vicariance events related to continental split, the dates of divergence of several clades revealed that multiple recent range shifts through long-distance dispersal might have also occurred. Simaroubaceae is likely to have a North American origin with an early history of range expansion between major continental areas in the Northern Hemisphere, including migration via Beringia by ancestral taxa. Long-distance dispersal events probably took place particularly in the Late Oligocene and later, including dispersals across the Atlantic Ocean in both directions, as well as between Africa and Asia, and around the Indian Ocean basin and Pacific islands (Clayton et al. 2009).

The family is a geographically widespread and ecologically diverse, but mainly found in moist lowland tropical forests, including Amazonian seasonally flooded forests (some *Simaba*). They also inhabit seasonally dry (semi)deciduous forests, subandean montane forests, highland vegetation at the Guyana Shield, open savannas, sandy habitats as coastal *restingas* in Eastern Brazil, swamp forests (only *Leitneria*), and deserts and dry scrubs in northwestern Mexico and southwestern USA (*Castela*). The latter genus consists of thorny plants, and leaves are generally rudimentary in several species. *Homalolepis* is remarkable for its broad habit span, from tall, sometimes palmlike forest trees, to shrubs

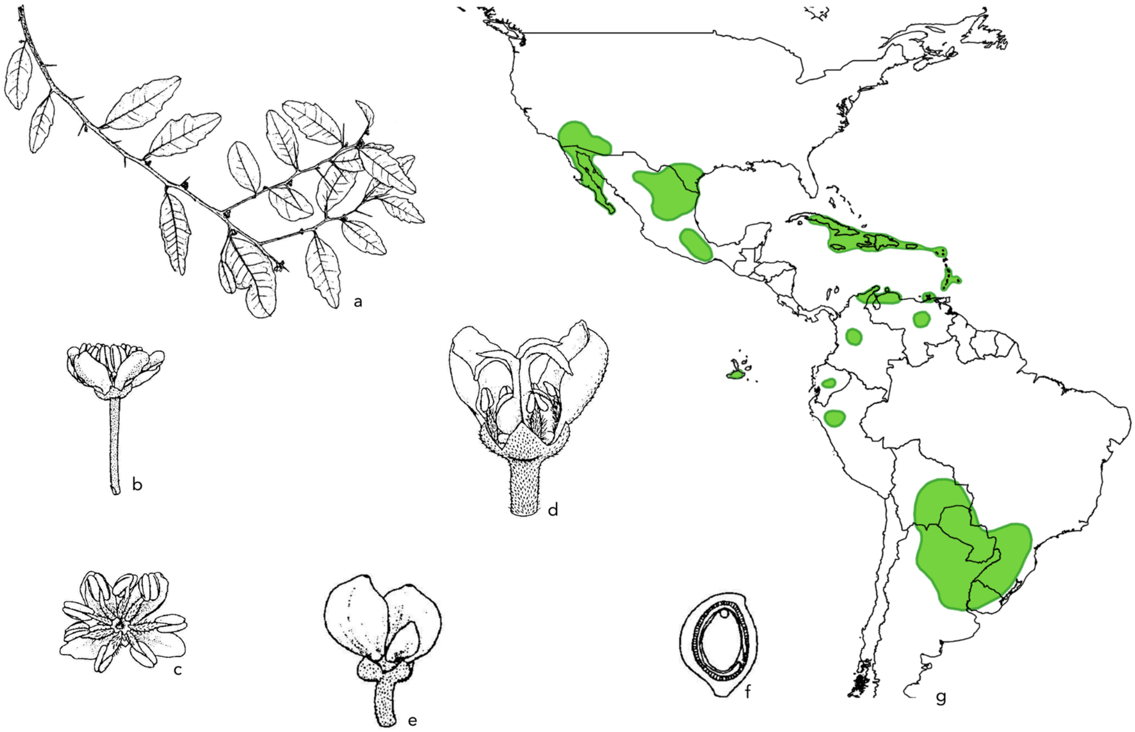


Fig. 1 *Castela*—**a**–**f** *C. tweediei* Planch. **a** Flowering twig, **b** male flower in lateral view, **c** male flower in front view, **d** female flower, **e** a fruit with two fruitlets and a small one aborted, **f** longitudinal section of a fruitlet, **g** distribution map of the genus (**a**–**f** modified from Pirani 1997)

and small subshrubs inhabiting South American savannas, including eight geophytic species, which are dwarf plants provided with a woody underground perennial axis, with a less persistent aerial system that can be deciduous and resprout, the leaves usually clustered at the soil surface. This geophytic life-form seems to have evolved at least three times independently among the members of *Homalolepis* (Devecchi et al. 2018a), including distinct structural variations of the underground system as shown by Melo-de-Pinna et al. (2021—this issue).

9 Ethnobotany/economic uses

Wood and bark of several species of Simaroubaceae yield bitter principles—the quassinoids—traditionally employed as therapeutic agents and thus, are used locally as medicinal plants. According to Alves et al. (2014), the quassinoids are "secondary metabolites responsible for a wide spectrum of biological activities such as antitumor, antimalarial, antiviral, insecticide, feeding deterrent, amebicide, antiparasitic and herbicidal." Other properties include antidysenterics and antihelmintics. The main study about antimalarial properties of the quassinoids of *Homalolepis cedron* (as *Simaba cedron)* was elaborated by O'Neill et al. (1986). Almeida et al. (2007) add to these the antineoplastic property. In vitro anthelmintic activity of *Picrolemma sprucei* Hook.f. was demonstrated (Nunomura et al. 2006), and the antiplasmodial activity of the same species was due presumably to quassinoid and non-quassinoid active components (Amorim et al. 2013). Members of the family are included in official compendia, as Brazilian, British, French and German pharmacopoeias, and some patent registrations have been made (Alves et al. 2014). However, only a few species have been studied in detail and more phytochemical and pharmacological investigations are needed.

Several species produce timber of local importance for various purposes (Record & Hess 1943), and some of them are exported. A few species are cultivated and planted as ornamentals, as the "Tree of Heaven" (*Ailanthus altissimus* (Mill.) Swingle), the "Surinam Quassia" (*Quassia amara* L.) and the "Paradise Tree" (*Simarouba glauca* DC.) (Brizicky 1962; Clayton 2011).

Bark extracts from species, such as *Quassia amara* and *Picrasma excelsa* (Sw.) Planch., are traditionally used as flavoring in drinks.

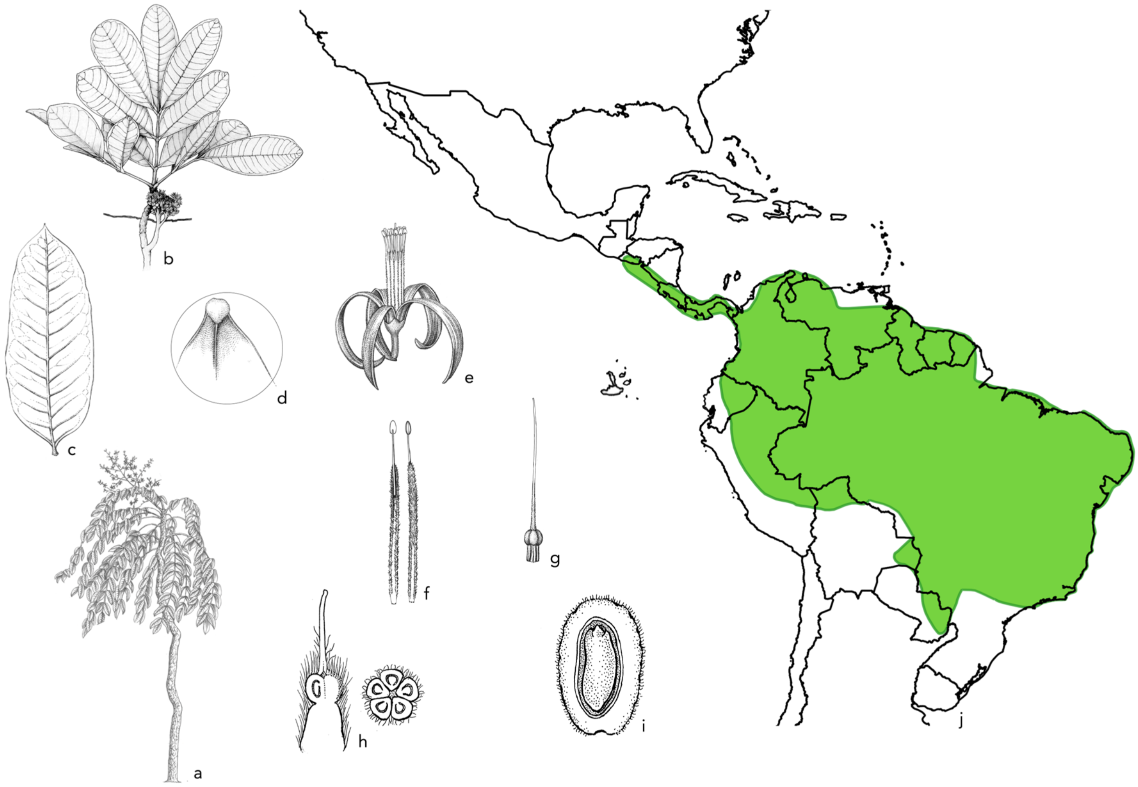


Fig. 2 *Homalolepis*—**a** Habit of *H. arenaria*, **b** Habit of *H. pumila* Devecchi & Pirani, **c** Leaflet of *H. arenaria*, **d** Leaflet apical gland of *H. arenaria*, **e** Flower at anthesis of *H. cedron*, **f** Stamen in ventral and dorsal views of *H. cedron*, **g** Gynoecium on top of a long gynophore of *H. cedron*, **h** Longitudinal and transverse section of the gynoecium of *H. guajirensis* Devecchi, Thomas & Pirani, i. Longitudinal section of a fruitlet of *H. guajirensis*, **j** Distribution map of the genus (**a**, **c**, **d** modified from Devecchi et al. (2016), **b** from Devecchi et al. (2018c), **e**–**g** from Devecchi et al. (2018b), **h**, **i** from Devecchi et al. (2018d)

Fig. 3 *Leitneria floridana*—**a** elongate male catkins, **b** male flower, **c** stamen, **d** female flower, **e** fruits, **f** longitudinal section of a fruitlet, **g** distribution map of the genus (**a**–**f** modified from Hooker 1867)

Fig. 4 *Picrasma*—**a**–**e**—*P. excelsa:* **a** flowering twig, **b** male flower, **c** male flower in longitudinal section, **d** female flower, **e** fruit, **f** distribution map of the genus (**a**–**c** modified from Engler 1897; **d**, **e** from Fawcett and Rendle 1920)

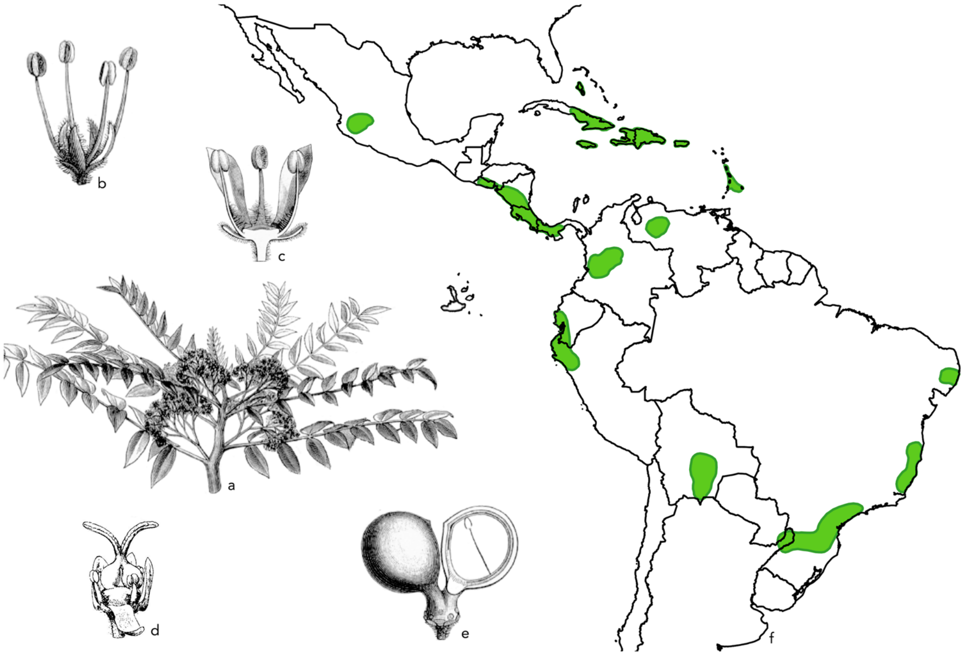
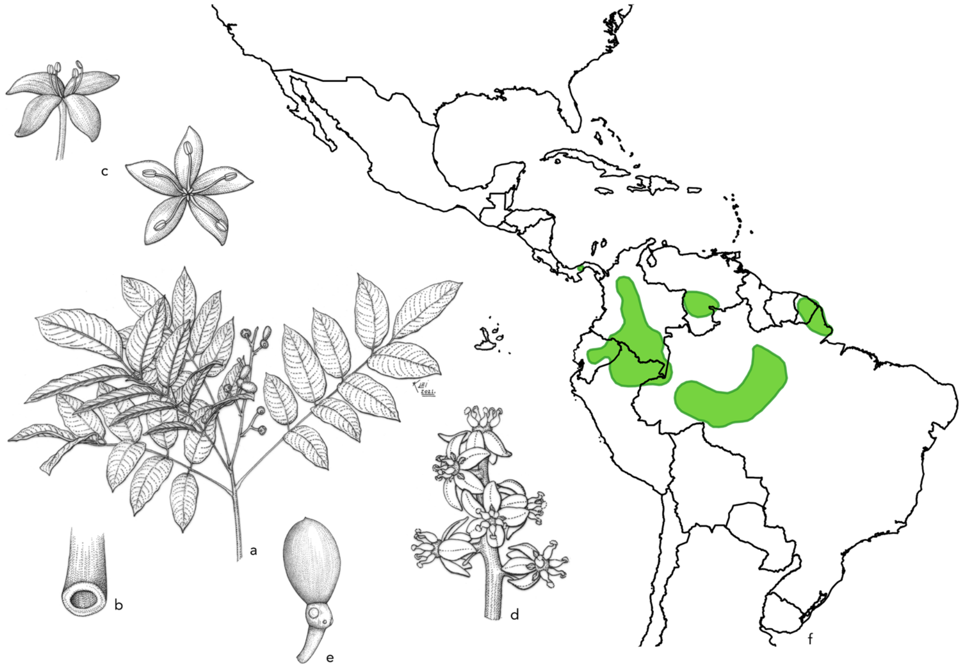


Fig. 5 *Picrolemma sprucei*—**a** fruiting twig, **b** detail of the hollow stem, **c** male flower in lateral and front view, **d** female thyrsoid, **e** fruit, **f** distribution map of the genus (Artwork: Klei Souza)



10 Brief taxonomic account of American taxa (native and naturalized)

Simaroubaceae DC., nom. cons., Nouv. Bull. Sci. Soc. Philom. Paris sér.2: 209. 1811, as Simarubae. Type: *Simarouba* Aubl., *nom. cons.*

Key to the native and naturalized genera occurring in the Americas

1. Fruit with samarids (winged fruitlets); leaves pinnately compound with a conspicuous gland at the basal lobes of proximal leaflets ……….….. 9-*Ailanthus* (naturalized)

1′. Fruit with drupaceous fruitlets; leaves absent, or simple, or reduced to scales, or seldom unifoliolate, when pinnately compound with leaflets without glandular basal lobes … 2

2. Flowers lacking a perianth or this vestigial, surrounded by large bracts … 3-*Leitneria*

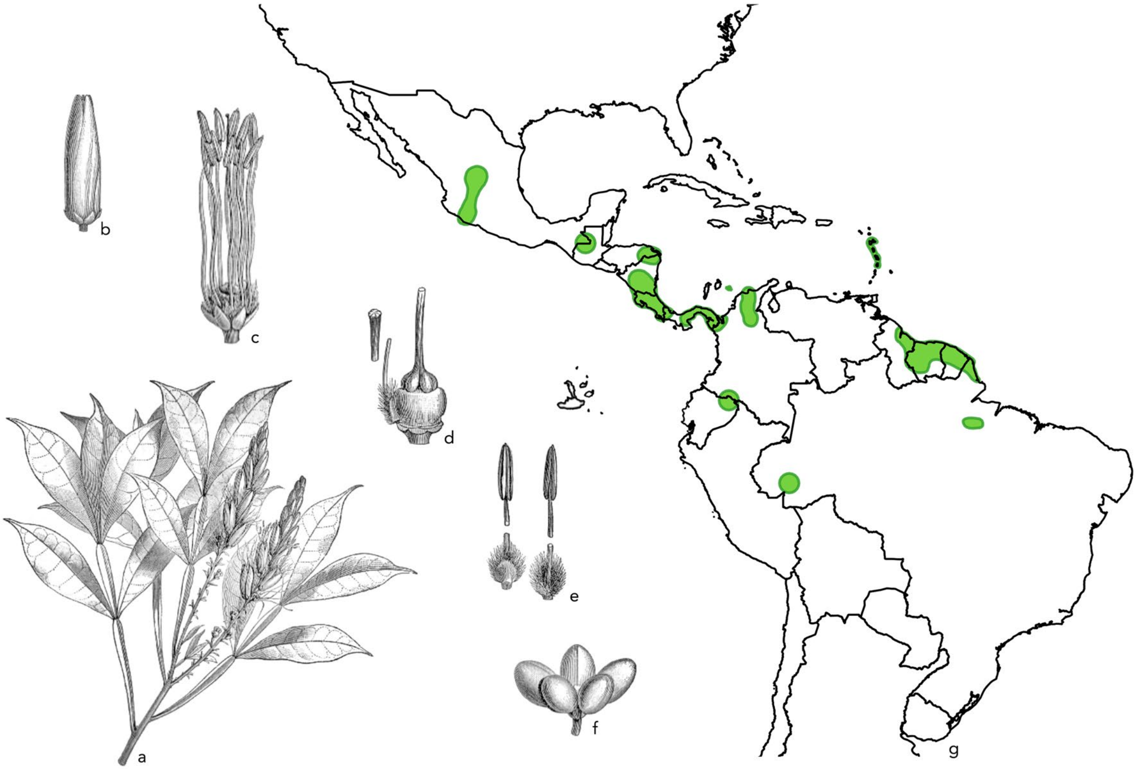


Fig. 6 *Quassia amara*—**a** flowering twig, **b** floral bud, **c** flower with the petals omitted, **d** Gynoecium, **e** Stamen in dorsal and ventral view, **f** Fruit, **g** Distribution map (**a**–**f** modified from Engler 1897)

2. Flowers with conspicuous calyx and corolla; bracts small, not surrounding the flowers 3

3. Leaf pinnately compound, rachis winged and articulate .... 6-*Quassia.*

3′. Leaf pinnately compound but the rachis nor winged nor articulate, or leaves simple, or reduced to scales, or seldom unifoliolate, or absent .... 4.

4. Flowers isostemonous .... 5.

4′. Flowers diplostemonous .... 6.

5′. Twigs hollow, inhabited by ants; stamens opposite to the petals; inflorescence elongate, pyramidal in shape; styles distinct at anthesis; fruitlets ellipsoid .... 5-*Picrolemma.*

5. Twigs solid, not hollow, not inhabited by ants; stamens alternate with the petals; inflorescence broad and rounded, often (sub)corymbiform; styles united at anthesis; fruitlets globose .... 4-*Picrasma.*

6. Plants unarmed; leaves pinnately compound, seldom scattered unifoliolate leaves present; stamens with appendage fillaments .... 7.

6′. Plants commonly armed with conspicuous thorns; leaves simple or reduced to scales or absent; stamens with unappendaged filaments .... 1-*Castela.*

7. Leaflets alternate or occasionally subopposite with laminar glands immerse at the blade adaxial surface; flowers unisexual, style shorter than the elongate, linear, divergent stigmas .... 8-*Simarouba.*

7′. Leaflets (sub)opposite or sometimes unifoliolate with an apical gland at the end of the midvein and laminar glands immerse in the mesophyll; flowers bissexual (though some may bear sterile stamens or sterile ovary in some species); style longer than the small stigmas 8

8. Leaflet laminar glands only on adaxial surface; vegetative and reproductive organs bearing only tector trichomes; anthers with connective smooth; stigmas short-divergent .... 7-*Simaba.*

8′. Leaflet laminar glands often on both surfaces; vegetative and reproductive organs bearing tector and often also glandular trichomes; anthers with connective papillate; stigma punctiform to slightly lobed 2-*Homalolepis*

1. ***Castela*** Turpin, Ann. Mus. Natl. Hist. Nat. 7: 78. 1806. Figure 1

Holacantha A Gray, Pl. Nov. Thurb. 310. 1854.

Small trees or shrubs, armed with axillary thorns or branches terminating in multibranched thorns, leaves simple (although sometimes lobed or toothed), these sometimes reduced to scales or lacking, lacking apical and laminar glands. Dioecious. Flowers in small axillary fascicles to larger, dense axillary thrysoids. Petals 4(5–8); stamens

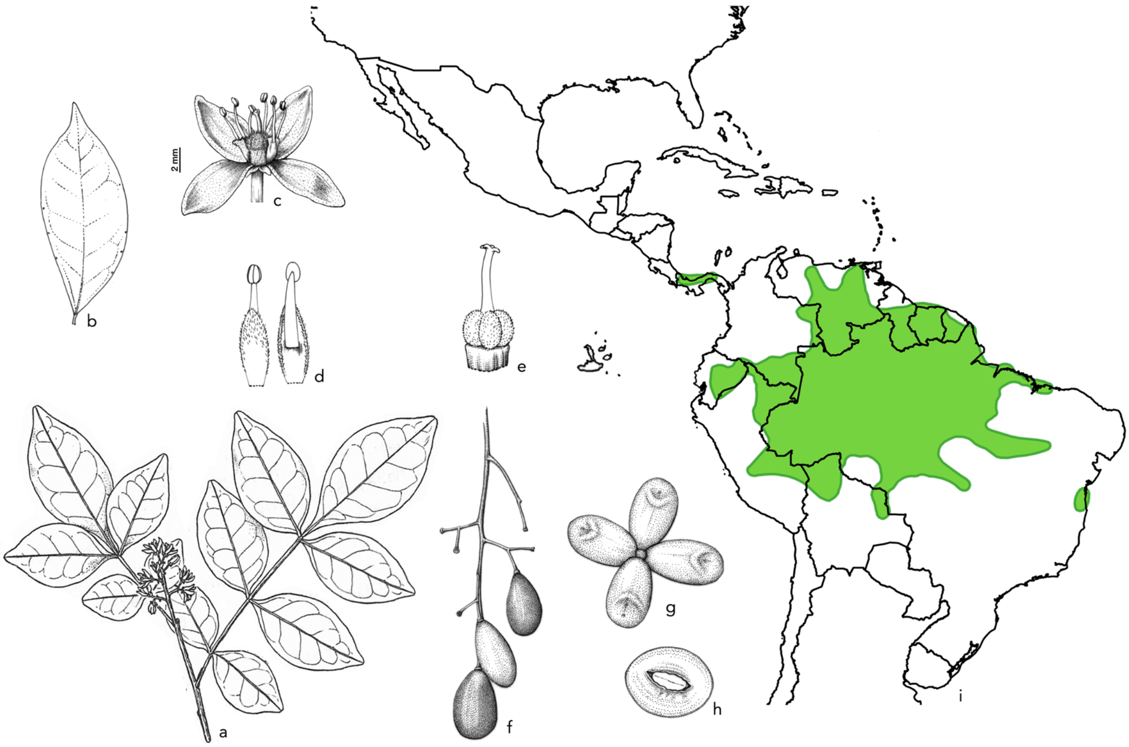


Fig. 7 *Simaba*—**a** Flowering twig of *S. guianensis*, **b** Leaflet with marginal laminar glands of *S. guianensis*, **c** Flower with a petal and four stamens removed showing the gynoecium of *S. pubicarpa* Devecchi, Franceschinelli & Thomas, **d** Stamen in dorsal and ventral view of *S. guianensis*, **e** Gynoecium of *S. guianensis*, **f** Fruiting branch of *S. orinocensis*, **g** Fruit of *S. orinocensis*, **h** Transversal section of a fruitlet of *S. orinocensis*, **i** Distribution map of the genus (**a** modified from Thomas (1985), **b** from Devecchi 2017, **c**–**e** from Devecchi et al. 2021, **f**–**h** by Klei Souza)

8(10–16), filaments unappendaged; carpels 4(5–8) weakly united only at the styles, on a short gynophore, stigma branches linear, divergent. Fruit with free, lenticular, lenticular-flattened or subovoid drupelets.

Sixteen species, in disjunct edaphically dry areas: in southwestern USA and northern Mexico (including Baja California), West Indies, northern South America including Ecuador and Peru, the Galapagos Islands and southern South America (Bolivia, Paraguay, Uruguay, Argentina and southwestern Brazil). There are endemic species in most of these areas; only one species, *C. erecta*, is widespread.

Revision: Cronquist (1944a, d, 1945).

Phylogenetic relationships (Clayton et al. 2007): *Castela* emerged as sister to *Holacantha,* in a clade which also included *Picrasma*. Majure et al. (2021a) and Majure et al. (2021b—this issue) recovered *Castela* s.s. as sister to the *Holacantha* clade, all of which were sister to the rest of Simaroubaceae.

2. ***Homalolepis*** Turcz., Bull. Soc. Imp. Naturalistes Moscou 21(1): 575. 1848.

Figure 2; see also the illustrated Field Guide by Devecchi et al. (2018e)

Trees, shrubs or dwarf geophytes. Leaves pari- or imparipinnate, leaflets mostly opposite, occasionally with a conspicuous apical nectariferous gland, laminar glands scattered usually on both surfaces. Hermaphroditic or polygamous. Flowers in (sub)terminal many-flowered thyrsoids or thyrses. Petals (4)5(6). Stamens (8)10(12), filaments appendaged at base; carpels (4)5 weakly united, on a conspicuous gynophore, stigma punctiform or slightly lobed. Fruit with 1(5) free, (sub)globose to obovoid or ellipsoid drupelets.

Species of this genus were traditionally treated as *Simaba* (e.g., Engler, 1874; Cronquist 1944c; Clayton 2011). A phylogenetic analysis showed that *Simaba* s.l. is not monophyletic and hence, *Homalolepis* was reinstated (Devecchi et al. 2018a, b). As currently circumscribed, *Homalolepis* comprises 28 species mainly distributed throughout tropical South America, except for Chile and Uruguay, with most species in open formations of Central Brazil (cerrados). Eight species are geophytes. The widespread species *H. cedron* ranges from southeastern Brazil to northern South America and Costa Rica and El Salvador in Central America. Moist forests to seasonally dry forests, cerrado (savanna) and restinga (coastal sandy formation).

Revision: Devecchi et al. (2018b).

Phylogenetic relationships: In Clayton et al. (2007, updated by Alves et al. 2021—this issue)) the sister group relationships are: ((*Simaba, Homalolepis*) (*Simarouba,*

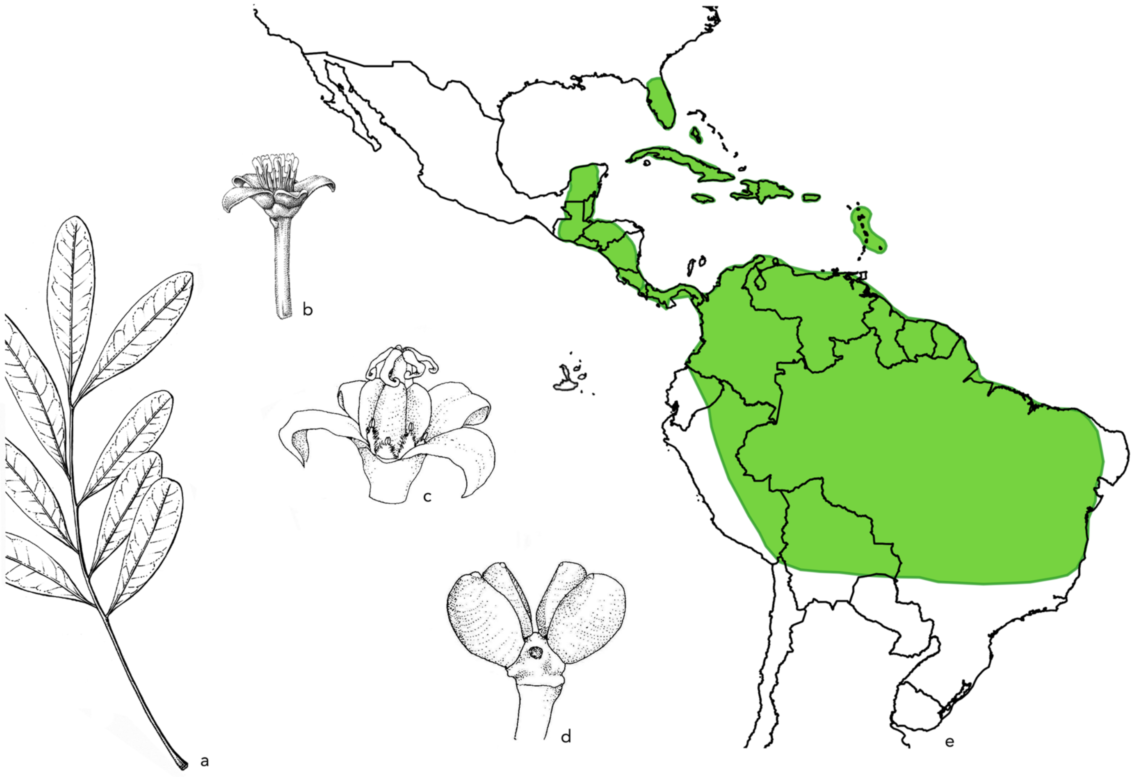


Fig. 8 *Simarouba amara*—**a** imparipinnate leaf, **b** male flower, **c** female flower, **d** fruit with four fruitlets, **e** distribution map of the genus (**a**, **b** modified from Devecchi & Pirani 2016, **c**, **d** from Pirani 1987b)

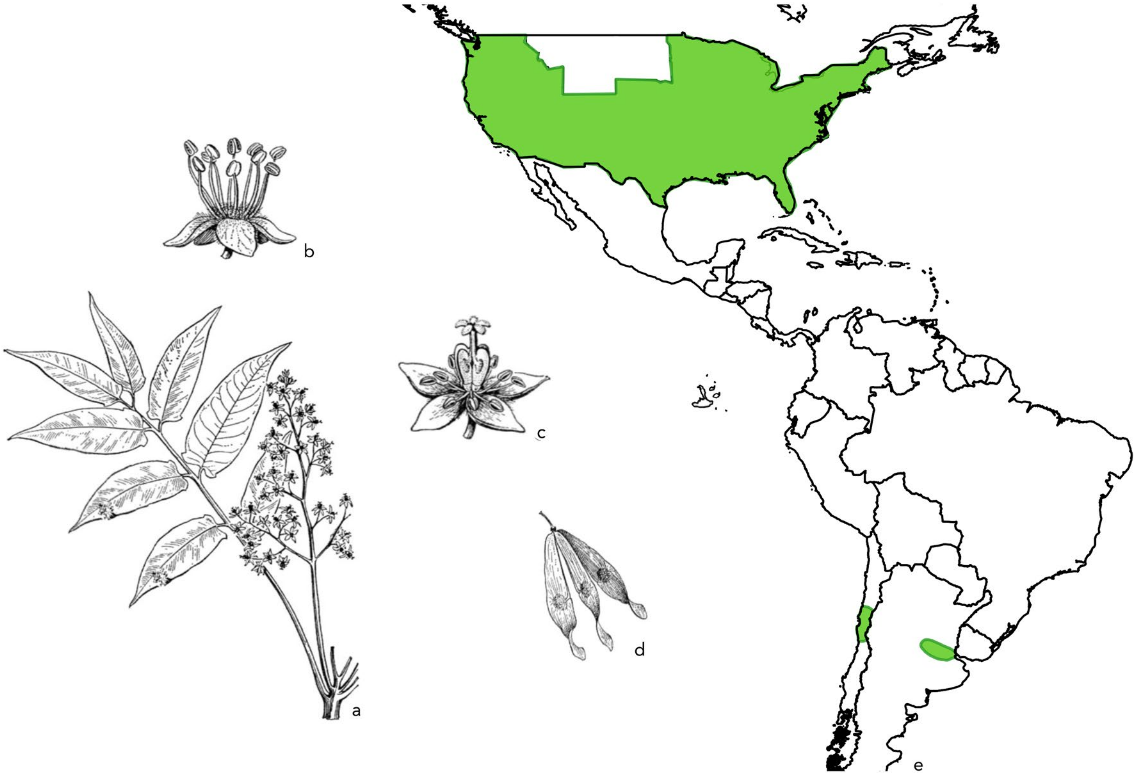


Fig. 9 *Ailanthus altissimus*—**a** flowering twig, **b** male flower, **c** female flower, **d** fruit, **e** distribution map (**a**–**d** modified from Takhtajan 1981)

Pierreodendron)). According to Devecchi et al. (2018a, b), *Homalolepis* emerges as sister to *Simarouba,* in a clade which includes also *Simaba* s.s.

3. ***Leitneria*** Chapm., Fl. South. U.S. 427. 1860.

Figure 3

Treelets with simple leaves, lacking apical and laminar glands. Dioecious. Flowers solitary (female) or in catkin-like thyrsoids (male). Hermaphroditic or polygamous. Perianth lacking (male flowers) or vestigial (female flowers), surrounded by large bracts. Stamens (1)4, filaments unappendaged; carpel 1, stigma elongate; disk and gynophore lacking. Fruit a narrowly ellipsoid drupe.

A genus endemic to southeastern USA, traditionally recognized as monospecific (*Leitneria floridana* Chapm.) until a second species, *L. pilosa* Shrader & Graves was described in 2011. Both inhabit swamp forests.

Phylogenetic relationships (Clayton et al. 2007): *Leitneria* emerges as sister to a clade formed by three extra-American genera (*Brucea, Soulamea* and *Amaroria).*

4. ***Picrasma*** Blume, Bijdr. Fl. Ned. Ind.: 247. 1825.

Figure 4

Aeschrion Vell., Fl. Flum. 58. 1825.

Trees or treelets. Leaves imparipinnate, leaflets (sub) opposite, lacking apical and laminar glands. Monoecious, dioecious or polygamous (androdioecious). Flowers in broad, rounded cymoids (modified thyrsoids) or reduced cymes with 1–4 flowers. Petals (4)5. Stamens (4)5, alternate with the petals, filaments unappendaged; carpels (2)4–5 distinct but united by the styles, on a conspicuous gynophore or surrounded by an intrastaminal disk, stigma branches linear, divergent. Fruit with 1–3(5) free, globose drupelets.

Eleven species, two of which occur in Asia; one species found in southern and eastern South America, and the remaining distributed from northern South America to Mexico and the West Indies. There are species endemic to Ecuador, Cuba, Dominican Republic and Mexico. Moist to semideciduous, lowland or submontane forests, although two species occur in seasonally dry tropical forest (Noa-Monzón et al. 2020; Majure et al. 2021a).

Revision: Cronquist (1944d); three species described later: *P. longistaminea* W. Palacios, from Ecuador, *P. pauciflora* A.Noa & P.A.González, from Cuba, and *P. nanophylla* Majure & Clase, from Dominican Republic.

Phylogenetic relationships (Clayton et al. 2007): *Picrasma* emerges as sister to a clade formed by *Castela* + *Holacantha* (*Castela* s.l.) or as sister to the rest of Simaroubaceae after *Castela* s.l. (Majure et al. 2021a, 2021b—this issue).

5. ***Picrolemma*** Hook.f., Gen. Pl. 1: 312. 1862.

Figure 5

Slender shrubs with hollow stems (myrmecophytes) and imparipinnate leaves, leaflets mostly opposite without a gland at the leaflet apex, laminar glands present only on abaxial surface. Dioecious. Flowers in elongate, narrow or broad pyramidal thyrsoids. Petals (4)5; stamens (4)5, opposite to the petals and alternate with small staminodia, filaments unappendaged; carpels (4)5, distinct, each with a terminal style, on a conspicuous gynophore, stigma capitate. Fruit with 1–2 free, ellipsoid drupelets.

This genus comprises two Amazonian rainforest species, *P. huberi* Ducke found in Colombia, Ecuador and Peru, and *P. sprucei* Hook.f. widespread throughout lowland Amazonia, from Brazil, Ecuador, French Guiana, Guyana and Peru to Venezuela.

Revision: Cronquist (1944d).

Phylogenetic relationships: According to Clayton et al. (2007), *Picrolemma* emerges as sister to the large clade formed by 11 genera, most with staminal appendages (only two extra-American genera have unappendaged stamens). According to Devecchi et al. (2018a), it is sister to *Quassia,* with strong support.

6. ***Quassia*** L., Sp. Pl. (ed. 2) 1: 553. 1762.

Figure 6

Shrubs or treelets with imparipinnate leaves, the petiole and rachis winged; leaflets opposite, without a gland at the leaflet apex, laminar glands present only on adaxial surface, toward the apex. Hermaphroditic. Flowers in narrow thyrsoids or botryoids. Petals 5; stamens 10, filaments appendaged at base; carpels 5, weakly united by the styles, on a short gynophore, stigma capitate or slightly lobed. Fruit with 1–2 drupelets.

Two species, one in tropical West Africa, other neotropical (*Q. amara* L.) from northern South America north to Nicaragua and the West Indies. As the latter species has been widely used as a medicinal plant, and cultivated and naturalized, its natural distribution is difficult to determine with confidence. It is found mainly in lowland rainforests.

Revision: Cronquist (1944d).

Phylogenetic relationships (Clayton et al. 2007, updated by Alves et al. 2021—this issue): *Quassia* emerges as the early diverging member of a clade of 11 genera mostly provided with staminal appendages (only two extra-American genera have unappendaged stamens). According to Devecchi et al. (2018a), it is sister to *Picrolemma,* with strong support.

7. ***Simaba*** Aubl., Hist. Pl. Guiane 1: 400. 1775.

Figure 7

Trees or shrubs with imparipinnate or seldom unifoliolate leaves (petiole pulvinate at apex); leaflets (sub)opposite, usually with an inconspicuous nectariferous gland present at the apex and laminar glands scattered only on adaxial surface. Hermaphroditic or polygamous. Flowers in depauperate thyrsoids to botryoids. Petals (4)5(6); stamens (8–)10(–12), filaments appendaged, vestigial staminodes; carpels (4)5, weakly united by the styles up to the slighlty lobed stigma. Fruit with 1–5 free, lenticular to obovoid drupelets.

In its current circumscription, *Simaba* s.s. comprises about ten mostly Amazonian species (Devecchi et al. 2018a, b). They are concentrated at northern South America, with only two disjunct occurrences, one in the Atlantic forest in northeast of Brazil, and the other in the Caribbean coast of Panama (Devecchi and Pirani, subm.). They inhabit mainly lowland flooded and non-flooded forests, and also highland Amazonian savanas and the Guiana Shield.

Revision: Cronquist (1944c); Cavalcante (1983).

Phylogenetic relationships: According to Devecchi et al. (2018a, b), *Simaba s.s.* emerges as sister to a clade formed by *Homalolepis* + *Simarouba.* In Clayton et al. (2007, updated by Alves et al. 2021—this issue)) the sister group relationships are: ((*Simaba, Homalolepis*)(*Simarouba, Pierreodendron*)).

8. ***Simarouba*** Aubl., Hist. Pl. Guiane 2: 859. 1775.

Figure 8

Trees or shrubs with leaves pari- or imparipinnate, persistent; leaflets alternate or occasionally subopposite, with laminar glands scattered on adaxial surface Dioecious. Flowers in many-flowered thyrsoids. Petals (4)5; stamens (8)10, filaments appendaged at base; carpels (4)5, weakly united only by the short styles, on a short gynophore, stigmas long and divergent. Fruit with 1–3 free, ovoid or ellipsoid drupelets.

A genus of six species, found from Florida (United States), Mexico and the Greater Antilles to Bolivia and southeastern Brazil. Three clearly distinct species are each endemic to one of the Greater Antilles: Cuba, Hispaniola and Puerto Rico; one species is found primarily in Mexico and Central America (*S. glauca*); one is restricted to South America (*S. versicolor*), and one is broadly distributed from tropical South America to Guatemala and Belize (*S. amara*).

Revision: Cronquist (1944b).

Phylogenetic relationships: According to Clayton et al. (2007, updated by Alves et al. 2021—this issue), the relationships are: ((*Simaba, Homalolepis*) (*Simarouba, Pierreodendron*)). In Devecchi et al. (2018a, b), *Pierreodendron* was not sampled and the hypothesis is (*Simaba* (*Homalolepis, Simarouba*)).

9. ***Ailanthus altissimus*** (Miller) Swingle - a nonative, naturalized and invasive species.

Figure 9.

Trees with leaves pari- or imparipinnate, deciduous; leaflets usually (sub)opposite, with conspicuous glands at the tip of the basal lobes of proximal leaflets. Polygamous-dioecious. Flowers in many-flowered thyrses. Petals 5(6); stamens (5)10(12), filaments unappendaged; carpels 5(6) weakly united only by the styles, stigma branches peltate and divergent. Fruit with 1–5 free, oblong samarids, each with a flattened seed at the middle of the membranaceous wing.

Commonly known as the "Tree of Heaven",— this species was introduced from China in North America in 1784, where it is cultivated but escaped and became naturalized throughout most of the USA (from northern Florida and northward) (Hu, 1979). It is occasionally cultivated in Southern South America (Argentina, Bolivia, Chile and south Brazil), and it has become naturalized in some parts of Argentina and Chile. Plants of *A. altissimus* are polyploid (2n = 80, Desai, 1960) and, once established, they become very difficult to eradicate, for they can sprout from the stumps and on any portion of a root, and also because a female tree is a prolific seed producer; its winged fruits spread and germinate nearby and far away from the mother plant (e.g., Hu 1979). For these reasons, the species is considered as a weedy tree, an aggressive colonizer of disturbed habitats such as old fields, forest edges, and roadsides and also invades undisturbed habitats, suppressing growth of surrounding plants through release of allelopathic compounds (e.g., Brizicky 1962).

Five species are currently accepted in *Ailanthus,* a genus originally distributed in northeastern to southern Asia to northern Australia (Clayton 2011).

Phylogenetic relationships: According to Clayton et al. (2017), Devecchi et al. (2018a, b) and Majure et al. (2021b) the genus *Ailanthus* emerges as sister to a clade formed by all genera of the family except for *Castela* and *Picrasma*.

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Declarations

Conflict of interest No potential conflict of interest was reported by the authors.

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