



A review of systematics studies in the *Citrus* family (Rutaceae, Sapindales), with emphasis on American groups

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Abstract

The Rutaceae are the largest family in number of species in the order Sapindales, with 162 genera and ca. 2085 species, mainly in (sub)tropical regions. The family is well distributed in the Americas, with 51 genera and 412–415 species, most of them in the tropical America, with 48 genera (46 endemic to this region), and 350–400 species. Forty-nine genera are restricted to America, only *Thamnosma* (also present in African) and (sub)tropical worldwide *Zanthoxylum* also occurring in other continents. Growing knowledge about the group, especially along the last 25 years, has led to a great internal rearrangement in the family systematics, mainly due to phylogenetic studies based on molecular data. In addition, studies of group reviews, descriptions of new species, and anatomical, cytogenetic, phytochemical, biogeographic and other studies have greatly expanded the knowledge about the evolution of the group. The present work provides a comprehensive overview of these studies in the Rutaceae, with an emphasis on taxa that occur in the American continent, notably in the Neotropical Region, and indicates groups that still need more in-depth studies, specially in a systematic point of view.

Keywords Biogeography · Central America · Cytogenetics · Neotropics · Phytochemistry · Plant anatomy · South America

1 Introduction

Rutaceae is a large, predominantly tropical, and subtropical family, consisting of c. 162 genera and c. 2085 species, being the largest family in number of species in the order Sapindales. Species are found mainly in (sub)tropical regions worldwide, with three main centers of diversity: Tropical America, southern Africa (especially in the Cape Province, with the tribe Diosmeae), and Australasia (Kubitzki et al. 2011; Groppo et al. 2012; Appelhans et al. 2021). The family is best known due to *Citrus* L., a speciose genus of Asian

origin, broadly cultivated worldwide on account of its edible fruits (oranges, lemons, tangerines, and grapefruits). Apart *Citrus*, other groups in Rutaceae are important as sources of aromatic oils (as *Boronia* Sm., *Ruta* L., and even *Citrus*), drugs (as *Pilocarpus* Vahl, source of pilocarpine, used against glaucoma), and bitter beverages used to treat fevers (as *Angostura* Roem. & Schult. and *Galipea* Aubl.). Species of some genera are commercially used as timbers (e.g., *Flindersia* R.Br., *Balfourodendron* Corr.Mello ex Oliv., *Euxylophora* Huber, and *Zanthoxylum* Lam.), and many more are used locally as log or in small works of carpentry. Antimicrobial and antifungal properties of rutaceous compounds are being exploited as natural pesticides (e.g., Oliva et al. 2000), herbicides (e.g., Aliotta et al. 1996), and antimicrobials (e.g., Mandalari et al. 2007), while others are reputed as medically useful (e.g., Holmstedt et al. 1979; Moraes et al. 2003).

Rutaceae are variable in their habit, being trees or shrubs, less often subshrubs or herbs (*Apocaulon* R.S.Cowan, *Ertela* Adans.), seldom lianas (as in *Luvunga* Buch.-Ham., some *Paramignya* Wight and *Zanthoxylum*); the leaves are compound, impari or paripinnate (bipinnate in *Bottegoa* Chiov. and *Dictyoloma* DC.), 1-3-(5-7)-foliolate, or simple, alternate or opposite; most species are unarmed, but there

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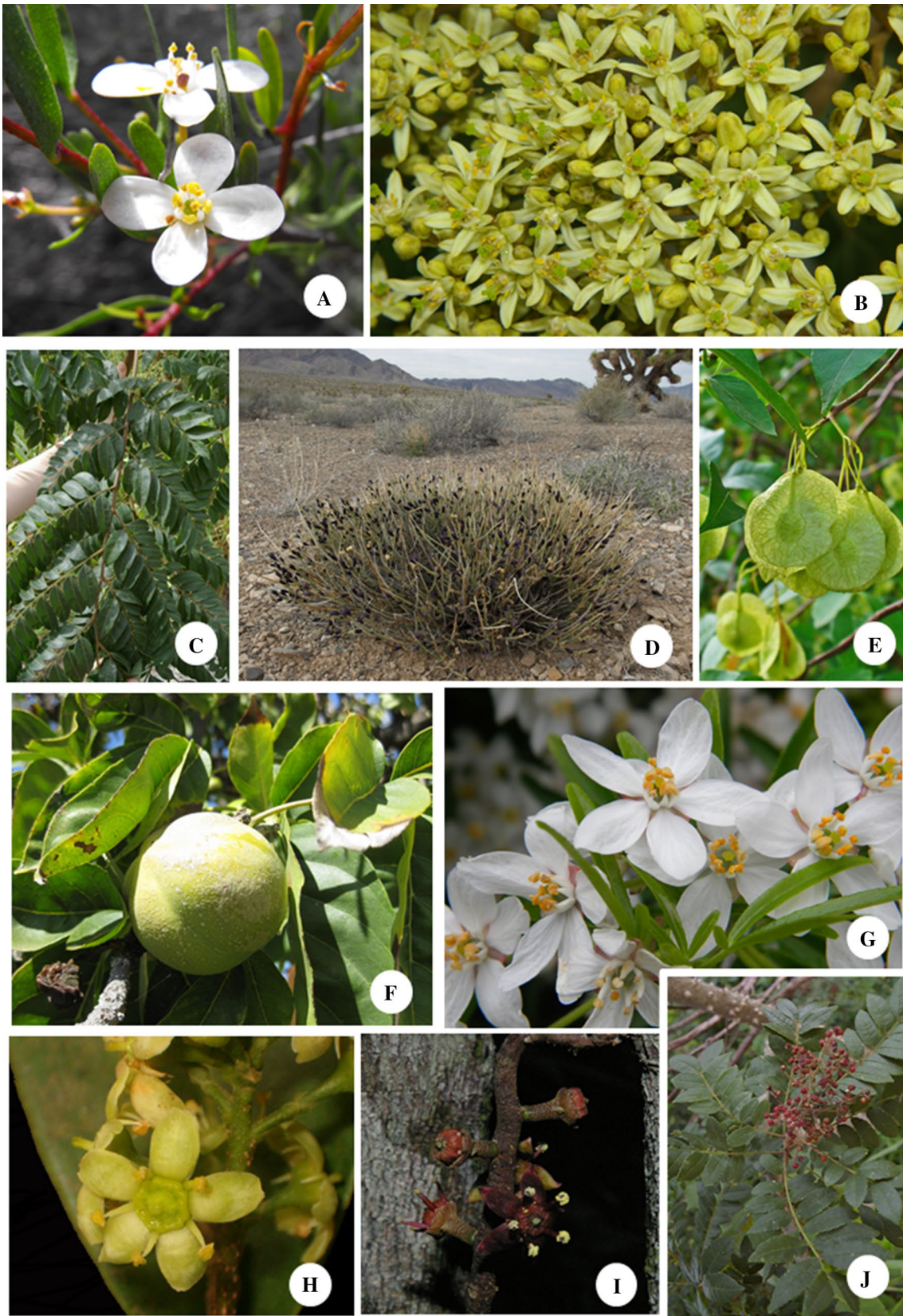


Fig. 1 Some representatives of American Rutaceae. Subfamily Amyridoideae: **A** *Cneoridium dumosum*, flowers. Subfamily Cneoroideae: *Dictyoloma vandellianum*, **B** flowers. **C** Branch showing bipinnate leaf. Subfamily Rutoideae: **D** *Thamnosma texana*, habit. Subfamily Zanthoxyloideae: **E** *Ptelea trifoliata*, fruits (samaras). **F** *Casimiroa edulis*, fruit (baccate). **G** *Choisya ternata*, flowers. **H** *Esenbeckia grandiflora*, flower. **I** *Pilocarpus grandiflorus*, cauliflorous, pendulous inflorescence. **J** *Zanthoxylum rhoifolium*, branch with fruits, note pinnate leaves **B**, **C**, **H**, **I**, **J** by Milton Groppo, **C** by Stickpen (public domain), Torrey Pines State Reserve, San Diego, California, USA, **D** by Jim Morefield, Nevada, USA (License: <https://creativecommons.org/licenses/by-sa/2.0/deed.en>, **E** by H. Zell, license Creative Commons Attribution-Share Alike 3.0 Unported license, **F** by Raffi Kojian, Gardenology.org, <http://www.gardenology.org>, **G** by Bildoj—Propra verko, wikicommons (https://commons.wikimedia.org/wiki/File:Choisya_ternata_%27Aztec_Pearl%27.JPG#/media/Dosiero:Choisya_ternata_'Aztec_Pearl'.JPG)

are thorns in most *Zanthoxylum* (trunks, branches and/or leaves), and in many representatives of subfamily Aurantioideae, in this case persistent, solitary or paired thorns in on one or both sides of an axillary bud, also present in *Raulinoa* R.S.Cowan (*Zanthoxyloideae* sensu Appelhans et al. 2021). Flowers are usually actinomorphic and small, usually white or cream, except for the Neotropical subtribe Galipeinae (*Zanthoxyloideae*) in which most members have zygomorphic and showy flowers (Groppo et al. 2021); the fertile stamens and carpels range from many to two, and the carpels are united or free with two to several ovules, and the ovary, with very few exceptions, is superior, surrounded by an intrastaminal nectariferous disc. Fruits in the family are quite variable, being dry or fleshy, dehiscent or indehiscent, but many genera present species with capsules or fruits with 1–5 dehiscent fruitlets, often with a detaching elastic endocarp that ejects the seeds when mature, as observed in most Euphorbiaceae. Baccate (e.g., the hesperidia in the *Citrus* subfamily, Aurantioideae), as well samaras, samaroids and drupes are also found (Groppo et al. 2008; Kubitzki et al. 2011; Appelhans et al. 2021). See Figs. 1 and 2, which some American representatives of Rutaceae.

Rutaceae are distinguished from all other families of the order Sapindales by the possession of secretory cavities containing aromatic ethereal oils scattered throughout almost all organs, a synapomorphy to the family (Groppo et al. 2008). The oil cavities are found only on the parenchyma of primary organs (e.g., Metcalfe and Chalk 1950), and they are easily observed in the field as pellucid dots, mainly in the leaves (similar to those encountered in the Myrtaceae), but also in other parts of the plants, such as in the fruits, flowers, and sometimes in young axes (Turner et al. 1998; Kubitzki et al. 2011; Groppo et al. 2012). This character is present in almost all Rutaceae except for some genera of the subfamily Cneoroideae Webb (Appelhans et al. 2012); these cavities may be also inconspicuous in some groups or species, as in *Phellodendron amurense* Rupr. (Kubitzki et al. 2011), and *Esenbeckia leiocarpa* Engl. (Kaastra 1982).

In the last 25 years, phylogenetic studies conducted with molecular data have changed our view of the internal relationships in Rutaceae, leading to rearrangements in the classification of its infrafamilial groups. As a consequence, the understanding of the evolution of the group, its morphological characters, biogeography and ecology has been significantly advanced. At the same time, alpha-taxonomy studies, such as floristic surveys focused on Rutaceae, descriptions of new species and other anatomical, palynological, cytogenetic, phytochemical and reproductive biology studies have been carried out. Many of these studies have been focused in groups of Rutaceae from the Neotropical Region, one of the centers of diversity of the family.

The objectives of this work are to present a comprehensive review of the phylogenetic, taxonomic, and floristic studies on Rutaceae, with emphasis on works undertaken in the Neotropical Region, but expanding this scope to the taxa that occur in the Americas as a whole; additionally, anatomic, palynological, cytological, phytochemical, and reproductive biology studies are also addressed. Finally, a discussion on the current state of floristics and taxonomic/systematics of the American groups of Rutaceae are presented, highlighting gaps in the knowledge of studies of Rutaceae in this continent, notably from the Tropical groups, which shall be addressed in forthcoming studies.

Portions of the text from some topics below have been moved to the “Supplementary Material” due to limited space for references. The entire bibliography used for the preparation of this text can also be consulted in that section.

A brief systematic background of Rutaceae – New data on phylogeny and current infrafamilial classification of Rutaceae are presented in the next topic. As a brief systematic background of the family, it can be said that the circumscription of Rutaceae presented by Bentham and Hooker (1862) is similar to the current concept of the family. These authors recognized seven tribes and other infrafamilial groups, quite similar to those presented later by Engler (1874) in his treatment of Rutaceae on Martius *Flora brasiliensis*, and in his monographs for *Die natürlichen Pflanzenfamilien* (Engler 1896, 1931). Engler (1931) presented keys to the internal groups and genera, with detailed descriptions on morphology, anatomy and geographic distribution, as well as a subfamilial division that has been influential for many decades and only started to be revisited recently. This author divided the Rutaceae in seven subfamilies—Aurantioideae (not Citroideae, see Mabberley 1998, p. 333), Dictyolomatoideae, Flindersioideae, Rhabdodendroideae, Rutoideae, Spathelioideae, and Toddaloideae, those further divided in tribes and subtribes, based in morphological traits as the degree of connation and number of carpels, fruit characters (e.g., dehiscent vs. indehiscent, fleshy vs. dry, winged or not), the histology of the glands (schizogenous, lysigenous

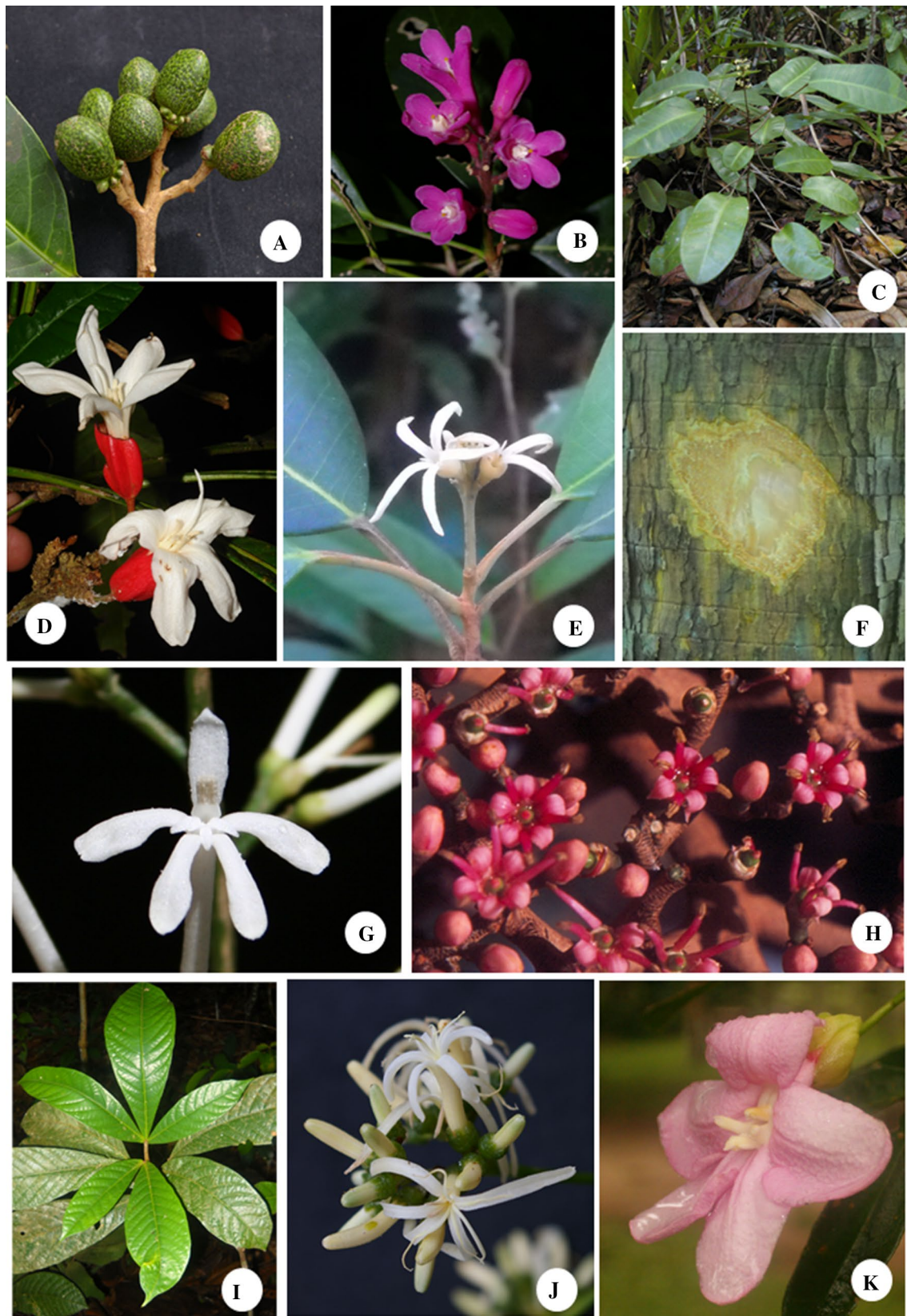


Fig. 2 Some representatives of American Rutaceae, all from Subfamily Zanthoxyloideae, Tribe Galipeae, subtribe Galipeinae. **A** *Andreadoxa flava*, immature fruits. **B** *Conchocarpus ruber*, flowers. **C** *Dryades concinna*, habit. **D** *Erythrochiton brasiliensis*, flowers. *Euxylophora paraensis*. **E** Flower. **F** Wood. **G** *Galipea jasminiflora*, flower. **H** *Hortia arborea*, flowers. **I** *Raputia praetermissa*, 3-foliolate, opposite leaves. **J** *Rauia* sp., flowers. **K** *Ravenia spectabilis*, flower. All photographs by Milton Groppo except D. by Cláudio Nicoletti Fraga

or schizo-lyigenous), the habit of the plants, and their geographic distribution. Englerian view of Rutaceae was maintained with minor changes by Scholz (1964) in the latest revision of the *Syllabus der Pflanzenfamilien*. Of the seven subfamilies only Rhabdodendroideae was later excluded from Rutaceae constituting the Rhabdodendraceae (Caryophyllales, cf. APG 2016). A detailed discussion of the characteristics of the Englerian subfamilies can be found in Chase et al. (1999) and in Groppo et al. (2008).

Works prior to Bentham and Hooker (1862) for Rutaceae can be consulted in the “Supplementary Material”.

New data on phylogeny and current infrafamilial classification – Englerian infrafamilial classification of Rutaceae began to be criticized in the 70’s to 2000’s due to the accumulation of evidences from morphological (e.g., Hartley 1974, 1981, 1982), phytochemical (Fernandes da Silva et al. 1988), and chromosomal (Stace et al. 1993; Guerra et al. 2000) studies. Molecular phylogenetic studies also demonstrated a need of revisions in the englerian infragroups in Rutaceae (see Chase et al. 1999; Scott et al. 2000; Samuel et al. 2001; Poon et al. 2007; Groppo et al. 2008), specially in Rutoideae and Toddalioidae that not appear as monophyletic in the molecular studies. On the other hand, englerian Aurantioideae (*Citrus* and allies) appeared as monophyletic in all those studies, being also the subject of internal phylogenetic scrutinization (Samuel et al. 2001; Morton et al. 2003; Bayer et al. 2009).

A phylogenetic molecular analysis by Groppo et al. (2008), based on samples from all Rutaceae tribes, demonstrated that geographic distribution of the genera could be more relevant than traditionally used characters of the fruit to an understanding of diversification within the family. Additionally, these authors showed that *Ptaeroxylon* Eckl. & Zeyh. (Ptaeroxylaceae) and *Cneorum* L. (Cneoraceae) were closely related to *Dictyoloma* (englerian subfamily Dictyolomatoideae) and *Spathelia* L. (subfamily Spathelioideae), and those two families should be merged in Rutaceae. Later Groppo et al. (2012) expanded their analysis, proposing only two subfamilies in Rutaceae: the Rutoideae (encompassing englerian Rutoideae, Toddalioidae, Flindersioideae, and Aurantioideae) and Cneoroideae (composed by the genera of Cneoraceae and Ptaeroxylaceae plus englerian Dictyolomatoideae and Spathelioideae). Other rearrangements were proposed by other authors, as Kubitzki et al. (2011), with three subfamilies—Aurantioideae, Cneoroideae and a non-monophyletic Rutoideae, and Morton and Telmer (2014), with three subfamilies (Amyrioidae, Aurantioideae and Rutoideae).

Appelhans et al. (2021) presented the most recent phylogeny for Rutaceae, using six molecular markers and the largest sampling so far for the family, with 135 genera representing 87.7% of the recognized genera for Rutaceae.

These authors proposed the division of the family into six subfamilies—Amyridoideae, Aurantioideae, Cneoroideae, Haplophylloideae, Rutoideae, and Zanthoxyloideae. Subfamilies Aurantioideae (*Citrus* and its relatives) and Haplophylloideae (constituted only by *Haplophyllum* Rchb.) do not have native representatives in the Americas. Appelhans et al (2021) subfamilial division to Rutaceae is used in all following topics below.

Studies like Chase et al. (1999), Groppo et al. (2008), Morton and Telmer (2014) and Appelhans et al. (2021) reinforced that the characters used by Engler (1874, 1896, 1931) and Scholz (1964) to delimit the internal groups of Rutaceae (subfamilies or equivalent), such as dehiscence/indehiscence of the fruit and its type, degree of conation of carpels and ontogeny of the oil glands, did not held strong phylogenetic signal, as previous molecular studies had indicated. Rather, biogeography seems to better explain the evolutionary history of the internal groups of Rutaceae, as pointed out by Groppo et al. (2008) and Bayly et al. (2013). Further discussions on this topic can be found in these works and in Groppo et al. (2012) and Appelhans et al. (2021).

Phylogenetic position of Rutaceae within the angiosperms

– The positioning of Rutaceae among angiosperms has been relatively stable in most modern classification systems. The family has been associated with other close families such as Meliaceae and Simaroubaceae, and to a slightly more distant degree with Anacardiaceae, Burseraceae, and Sapindaceae. All these families (and some smaller ones) have been grouped in the classification systems of Cronquist (1981, 1988) in the order Sapindales, or Rurales (as in Thorne 2007). Dahlgren (1989) prefers to treat all these families as Superorder Rutanae, separating Rutaceae, Meliaceae, and Simaroubaceae in the order Rurales and Sapindaceae, Burseraceae, and Anacardiaceae as Sapindales. This is the same treatment given by Takhtajan (1997), who considers the Rurales and Sapindales as separate orders within the Superorder Rutanae.

Gadek et al. (1996) in the first major molecular analysis of the Sapindales (or Rurales) group showed Rutaceae nested within this order with strong support, forming a clade with the major families Simaroubaceae, Sapindaceae, and Meliaceae. These authors preferred to use the Sapindales sensu Cronquist (1981, 1988), which encompassed all these families, even though the internal relationships obtained showed two strongly sustained clades formed by Rutaceae, Meliaceae, and Simaroubaceae and the other by Anacardiaceae, Burseraceae, and Sapindaceae. The close phylogenetic relationship among these major families was also obtained in subsequent phylogenetic studies (e.g., Soltis et al. 2011); APG (1998) accepted the delimitation of Sapindales by Gadek et al. (1996), maintaining this order named as Sapindales in all subsequent editions, within the Malvids

group (APG 2016). Morphological synapomorphies of the Sapindales include extipulate, compound leaves, and a well-developed nectary disk. On the other hand, Rutaceae share with Meliaceae and Simaroubaceae bitter, triterpenoid compounds (Waterman 1983), but are distinguished from them by glandular-punctate leaves and secretory cavities containing aromatic ethereal oils scattered in almost all organs, a synapomorphy of the family as stated above.

Fossil record and age of Rutaceae – Fossil records in Rutaceae are better represented in the Northern Hemisphere (see Xie et al. 2013), with relatively poor samples in the Southern Hemisphere. The oldest certain Rutaceae fossil are seeds from *Rutaspermum biornatum* Knobloch & Mai, (Knobloch and Mai 1986), around 65 My, from the Maastrichtian (Late Cretaceous) of Walbeck, Germany, followed by seed fossils belonging to the extant genera *Acronychia* J.R.Forst. & G.Forst., *Euodia* Gaertn., *Fagaropsis* Mildbr., *Toddalia* Juss. (today = *Zanthoxylum*), and *Zanthoxylum* (Tiffney 1980; Gregor 1989), from the Paleocene to the Holocene. Rutaceous fossil seeds and fruits from the Eocene to Miocene (55–5 My) of Europe (as in Tiffney 1981; Collinson et al. 2012), North America (Tiffney 1980), and Asia (as in Li et al. 2013) were reported. Leaves (Pan 2010; Guo 2011) and woods are reported from the Cenozoic in Africa, Asia, and Europe (Gregory et al. 2009); fossil fruits (samaras) from North American belonging to *Ptelea* from the Miocene and Eocene (55–5 My) were revised by Call and Dilcher (1995), and Manchester and O’Leary (2010). Fischer and Butzmann (1998), and Xie et al. (2013) presented data on fossil leaf of *Citrus*—*C. meletensis* T.C.Fisch. & Butzmann from the Pliocene (5–2 My) of Italy, and *C. linczangensis* Xie, Manchester, Liu, Wang & Sun from the late Miocene (c. 5 My) of Yunnan, China, respectively. A Cenozoic (c. 65.5 My to the present) fossil history for extant and endemic Rutaceae from East Asian was provided by Manchester et al. (2009).

Given the fossil record, Raven and Axelrod (1974) stated that Rutaceae was already widely dispersed across the two hemispheres in the lower Tertiary (equivalent to the Paleocene, 66–56 My). Appelhans et al. (2018) suggest that the family may be Eurasian in origin, while Schwartz et al. (2015) suggested that *Citrus* may have moved from west to east Malesia and Australia some time in the Miocene/Pliocene.

Rutaceae diversification dates based on molecular data show wide variation, with studies showing the age of the most recent crown groups from c. 40–39 My (Wikström et al. 2001; Bell et al. 2010) to 82–72.9 My (Muellner et al. 2006, 2007; Pfeil and Crisp 2008) or even as ancient as 93.3–84.6 My (Muellner-Riehl et al. 2016). For dates of some internal groups in Rutaceae, see Pfeil and Crisp (2008, for Aurantioideae), and Appelhans et al. (2012, Cneoroideae).

Cytology – Cytological data in Rutaceae began with Engler (1931), who records the number of chromosomes for some genera, having already found haploid numbers of 9, 18, and 45 (South American *Erythrochiton* Nees & Mart.). Desai (1960) presented chromosomal counts for 10 species belonging to eight genera, including the Americans *Ptelea* L. and *Zanthoxylum*. Forni-Martins and Martins (2000) found $x = 12$ as basic chromosome number in *Hortia oreadica* Groppo, Kallunki & Pirani, this number contrasting with the $x = 18$ or 9, commonly found in Rutaceae (Stace et al. 1993, see also discussion below).

Guerra and collaborators presented a series of works on Rutaceae cytogenetics, as Guerra (1984a, b, 1985, 1987). In Guerra (1984a), there are chromosome counts to 61 species of Rutaceae, belonging to 33 genera. In subsequent articles, this author focused on different cytogenetic aspects in several species of Rutaceae, these works as recent as 2020 (Guerra et al. 2020) and 2021 (Santos et al. 2021).

Stace et al. (1993) made an important synthesis of the known data on 73 genera of 9 (englerian) tribes of Rutaceae, proposing cytoevolutionary patterns for the family. Their findings included an abundance dysploidy and infragenic polyploidy in the large Rutoideae/Toddalioideae complex (Zanthoxyloideae sensu Appelhans et al. 2021); the diploid number $x = 18$, typical of the Zanthoxyloideae and Toddalieae tribes (both included in Zanthoxyloideae sensu Appelhans et al. 2021), and probably ancestral in other tribes of Rutoideae, would be ancestral in the family; Citroideae (Aurantioideae) presented invariably $x = 9$, which can represent the displacement reduction product. Santos et al. (2021), studying the chromosome number and genome size in *Dictyoloma vandellianum* A.Juss. (subfamily Cneoroideae) found $x = 9$ was the most probably basic chromosome number to the family and that the CMA/DAPI banding pattern and the relatively high genome size ($2C = 2.6$ pg) of *D. vandellianum* suggest that its chromosomal organization is highly divergent from Aurantioideae, where $x = 9$ is dominant.

Phytochemistry – According to Price (1963), Rutaceae have one of the most diverse array of secondary metabolites in flowering plants. Secondary compounds include quinolones and acridones (both derived from anthranilic acid), a class of compounds quite diversified in the family, with many restricted to this family (Price 1963).

Hegnauer (1973, 1990) and Waterman and Grundon (1983) surveyed the phytochemistry of the family, discussing the distribution of the secondary metabolites in terms of evolution and systematics. Waterman (1983) presented data of classes of metabolites in Rutaceae, postulating four genera—*Fagaropsis*, *Phellodendron* Rupr., *Toddalia* Juss. (= *Zanthoxylum*), and *Zanthoxylum* as old representatives of the family on basis of these metabolites, calling this group the “proto-Rutaceae,” with the other genera of the family

originating from these ancestral (a gradist view not followed today given the modern phylogenetic paradigm). Although these groups indeed constitute a well-supported group within the Rutaceae (together with other genera, see Appelhans et al. 2018), nowadays they are not reputed as “ancestors” of the remaining Rutaceae. Quader et al. (1991) pointed out that this group, called for him the “*Euodia* Alliance” (*Acradenia* Kippist, *Euodia* Gaertn., *Geijera* Schott, *Melicope* J.R.Forst. & G.Forst, and *Zanthoxylum*), presents acetophenones, restricted to this group within Rutaceae. On the other hand, chromones have a more restricted distribution, occurring in genera as *Angostura*, *Flindersia*, *Maclurodendron* T.G.Hartley, *Skimmia* Thunb., while *Ptaeroxylon*-type chromones have been found in *Cedrelopsis* Baill., *Cneorum*, *Dictyoloma*, *Harrisonia* R.Br. ex A.Juss., *Ptaeroxylon*, and *Spathelia* (Gray 1983). These last six genera belong nowadays to the subfamily Cneoroideae, and the presence of chromones of this type is reputed as a synapomorphy of the group (see Groppo et al. 2012; Appelhans et al. 2021; Fernandes da Silva et al. 2021). Monoterpenes, sesquiterpenes, and phenylpropanes as volatile oils are universally present in the family according Kubitzki et al. (2011).

Fernandes da Silva et al. (1988) proposed a series of suggestions for an evolutionary interpretation of Rutaceae, based on the survey of various secondary metabolites (fundamentally alkaloids, coumarins, and limonoids) and their biosynthetic derivation, rearranging the internal groups of Rutaceae in provisional informal tribes. However, Waterman (1990) argued that such an approach, based on a single group of characters, many of which are not yet available for several genera or entire subtribes that time, would be useless in the search for a new classification for Rutaceae. In fact, phylogenies produced later using molecular data proved to be more effective in recovering the evolutionary history of the Rutaceae internal groups, as seen above.

Works dealing with phytochemical data on American species of Rutaceae are extensive and cited in the “Supplementary Material” section, together with the respective references. An extensive review of nortriterpenes, chromones, anthraquinones and their chemosystematics significance in Meliaceae, Rutaceae, and Simaroubaceae (Sapindales) are presented by Fernandes da Silva et al. (2021).

Reproductive biology and dispersion – Engler (1931) stated that the vast majority of Rutaceae are entomophilous; Brizicky (1962) reinforced this view, emphasizing that insects would be attracted by the intense odor of flowers and/or by abundant nectar, and often by showy corollas; however he recalls that cases of ornithophily have also been presumed for family members (e.g., in Australian *Correa* Andrews). Also according to this author, cross-fertilization would be the rule in Rutaceae, in some genera through dicliny or protandry (e.g., *Barosma* Willd., *Ravenia* Vell., *Ruta*), or

through the relative position of stigma and anthers (*Dictamnus* L., *Triphasia* Lour.). In other genera, however, both autogamy and xenogamy seem equally possible and effective (e.g., *Choisya* Kunth, *Citrus*, *Murraya* J.Koenig, *Skimmia*). Cleistogamy has also been reported in a New Zealand species of *Melicope* (Brizicky 1962). Pirani (1987) observed in a Brazilian population of monoecious *Dictyoloma vandellianum* that all male flowers of one individual releases their pollen either before or after the period of receptivity of the female flowers, with unsynchronized flowering pattern in the population, thus increasing the chances of cross-pollination.

According to Kuhlmann and Kühn (1947), most Brazilian species in the family have entomophilous flowers, which are pollinated by flies and wasps. Piedade and Ranga (1993) studied the pollination biology of *Galipea jasminiflora* (A. St.-Hil.) Engl., while the pollination of *Metrodorea nigra* A. St.-Hil. and *M. stipularis* Mart. were studied by Pombal (1994). In these two genera, the flowers were protandrous, with intrafloral, complete and asynchronous dichogamy; in *Galipea* nocturnal anthesis and phalaenophily were observed, while *Metrodorea* A-St-Hil. have diurnal myophilic flowers. The fetid and red/purple flowers of some *Pilocarpus* species appear to be sapromyophilous, according to Skorupa (1996). Barbosa (1999) noticed insects, more precisely bees, visiting *Hortia oreadica*; however, this author stated that passeriform birds are the effective pollinators, when they alight on the inflorescences and collect nectar. El Ottra et al. (2016a) studied the floral biology and pollination of *Angostura bracteata* (Engl.) Kallunki and *Conchocarpus macrophyllus* J.C.Mikan (Galipeinae), and found pollination by butterflies and less frequently pollination by medium-sized bees in *C. macrophyllus*, and butterflies, settling moths or by hummingbirds in *A. bracteata*. These same authors studied *Conchocarpus ruber* (A.St.-Hil.) Bruniera & Groppo, whose pinky flowers are pollinated by a single species of hermit hummingbird (*Phaethornis idaliae* Bourcier and Mulsant) and by butterflies (Pyrginae and Pierinae) (El Ottra et al. 2016b).

The dispersion of fruits and seeds in the family takes place in several ways, as a consequence of the diversity of types of fruits found there. Thus, there are autochorous, mechanical dispersion processes, as occurs with the elastic endocarp, detached from the rest of the pericarp, from the capsules and fruitlets of Galipeinae and Pilocarpinae (both Zanthoxyloideae sensu Appelhans et al. 2021), an efficient seed disperser device (e.g., Kuhlmann and Kühn 1947; Kaastra 1982; Skorupa 1996); dispersion by animals, as is the case of the edible fruits of *Citrus* and related genera (Citraceae), or also of the seeds covered with the luminous testa of *Zanthoxylum* (Rutoideae), which attract numerous types of granivorous birds (Kuhlmann and Kühn 1947); many fruits are adapted to dispersal at short distance by the wind, such as the samaras of *Spathelia* (Cneoroideae) and certain

genera of the subfamily Zanthoxyloideae, as *Balfourodendron*, *Helietta*, and *Ptelea*, or even the seeds themselves are winged, which is observed in *Dictyoloma*. The baccate fruits in *Hortia* Vand. are dispersed by mammals, as observed in *H. brasiliensis* Vand. ex DC., with common agoutis [(*Cuniculus paca* L., 1766, Groppo et al. 2012)], and black-rumped agoutis [(*Dasyprocta prymnolopha* Wagler) (Melo and Tabarelli 2003)] being the most observed dispersers.

Apomixis resulting from nuclear embryogenesis has already been demonstrated in several genera, such as *Aegle Dulac*, *Citrus*, *Esenbeckia* Kunth, *Murraya*, *Ptelea*, *Triphasia*, and *Zanthoxylum*, with numerous cases of polyembryony, particularly in *Citrus*. On the other hand, zygotic (or gametic) polyembryony seems much rarer in the group (Brizicky 1962).

Palynology – Pollen morphology of several species of the family, as seen under optical microscopy, is described in Erdtmann (1952). Ortrud M. Barth studied the pollen of some genera of Rutaceae native to Brazil, under optical and scanning microscope, including *Zanthoxylum* (Barth 1980), *Hortia* and *Dictyoloma* (Barth 1983), *Pilocarpus* (Barth 1985), and a general summary of pollen variations in several genera in the family (Barth 1982). The main conclusion of her works is that most genera are well characterized by a particular pollen type. Noteworthy is the palynotaxonomic analysis of Galipeinae carried out by Morton and Kallunki (1993), where the support of several genera is well demonstrated, and their interrelations suggested. This study also demonstrated that Zanthoxyloideae (Rutoideae in that work) exhibits the largest spectrum of variation, as the pollen variability described for the family is entirely reflected in this subfamily, except for the 2-colporate state. In the review of *Pilocarpus* made by Skorupa (1996), the pollen of all species of the genus was worked, confirming the previous general characterization by Barth (1985) but expanding and detailing the variations in each type and species. Groppo et al. (2010) studied the palynology of all species of *Hortia*. Dutra and Gasparino (2018) surveyed the pollen morphology of Rutaceae from Brazilian forest fragments in the São Paulo state.

Pollen has provided useful in the definition of some groups in phylogenetic analysis of in the descriptions of new species in the “*Almeidea* A.St.-Hil.-*Conchocarpus* J.C.Mikan complex,” as in the descriptions of *Conchocarpus albiflorus* (Bruniera & Groppo) Bruniera & Groppo (Bruniera et al. 2011), *C. hendrixii* Groppo, IG Costa & Bruniera (Groppo et al. 2019), and in the phylogenetic analysis focused in Galipeinae (Zanthoxyloideae) by Bruniera et al. (2015), and Groppo et al. (2021).

Anatomy – In addition to the external morphological characterization (studied in several floristic works, descriptions

of new taxa and revisions) and palynology, there are several works dealing with the anatomy (internal morphology) of the Rutaceae. Anatomical data are present in Engler’s monographs (1896, 1931), including anatomical and developmental characteristics of the ethereal oil cavities are used as subsidies for the recognition of some infrafamilial groups. Other earlier studies are those by Urban (1883) and Schulze (1902) that carried out studies on various aspects of the anatomy (only leaf in the second case) of family members. Record and Hess (1940) presented an anatomical description of wood from several American Rutaceae, still very useful today. Heimsch (1942) studied the secondary xylem anatomy of all (englerian) subfamilies of Rutaceae, with the exception of Spathelioideae (Cneoroideae *pro parte*, cf Appelhans et al. 2021).

Metcalf and Chalk (1950) provided a description of the general anatomy of Rutaceae. These last authors mention that, in addition to oil cells and glands, there are also resin cells in the pith, primary cortex and rays of young stems; the trichomes in the family are generally unicellular, sometimes uniseriate, and peltate, stellate trichomes and glandular multicellular trichomes may appear. Based on the detailed anatomical studies of Heimsch (1942), these authors claim that the xylem structure is uniform across the Rutaceae as a whole and exhibits a relatively high level of specialization. A comprehensive review of studies on the anatomy, histology and chemical products of the oil cavities of the Rutaceae, as well other secretory structures, under evolutionary approach, is presented by Tölke et al. (2021).

Dede (1962) studied species from 80 genera of Rutaceae, distinguishing seven types of leaf venation in the family, each venation type based on the spatial relationship of the vascular system with that of the glandular cavities, and also on the pattern of vascularization, finding a definite correlation between the vascular system and the secretory cavities. According to this author, there also seems to be a correlation between the number of cavities and their relative size; that is, the larger the size of the glands, the smaller their number in the leaf blade. The close association of the glandular cavities with the vascular system, observed in the leaves in the aforementioned articles and by Stern and Brizicky (1960), was also found in the floral parts by Tillson and Bamford (1938). Other works include a detailed description of the leaf venation of Amazonian *Zanthoxylum* species presented by Albuquerque (1969). Solis (1997) carried out an anatomical study of the foliar domatia of *Balfourodendron riedelianum* (Engl.) Engl. and in two species of *Zanthoxylum*. Hermoso and Escala (2002) studied the leaf anatomy of *Pilocarpus goudotianus* Tul., and Muntoreanu et al. (2014) studied leaf anatomy in *Pilocarpus* and related genera, while Ferreira (2017) conducted an extensive study of leaf anatomy among the Galipeinae (subfamily Zanthoxyloideae), providing subsidies for the recognition of the genus *Dryades*

Groppo, Kallunki & Pirani (Groppo et al. 2021). Margalho et al. (2014) and Costa et al. (2014) presented data on morphology and wood anatomy of *Euxylophora paraensis* Huber and *Zanthoxylum rhoifolium* Lam., respectively. Cruz et al. (2017) performed a phylogenetic analysis of *Metrodorea* and related species, studying the evolution of morphological characters, many of them from anatomy.

Floral morphology and anatomy works have been carried out by several authors. Earlier studies include some focused in the morphology and origin of the nectariferous disc in Rutaceae, as Saunders (1934), Moore (1936), Tillson and Bamford (1938), Gut (1966), and Tilak and Nene (1978), who worked also on morphology gynoecium in Rutaceae. Gut (1966) also showed that the various members of Rutaceae studied are similar not only in the possession of oil glands and in the structure of the endocarp, as previously shown by Hartl (1957, 1958), but also in the general construction of the carpel, position of the ovules and role that the floral axis plays within the flower. Other studies dealing with gynoecium and/or carpel morphology were carried out by Guédes (1973); Ramp (1988), on the floral structure in an ontogenetic context based on 32 genera, compared to other genera of Simaroubaceae; and Beurton (1994), who analyzed the gynoecium of *Zanthoxylum* as a subspecies to keep or not *Fagara* (= *Zanthoxylum*) as a distinct genus.

Pirani et al. (2010) performed a morphoanatomical study of the flower in five species of *Galipea* concluding that there is the formation of a true floral tube through the connation of filaments and the adnation of this staminal tube to the petals in this genus, in a group—the subtribe Galipeinae—that presents different degrees of connation of petals. Floral morphoanatomical studies in Galipeinae were deepened by El Ottra et al. (2013, 2019), who carried out extensive anatomical studies in the subtribe, relating the characteristics raised to evolutionary patterns among the Neotropical Rutaceae and comparing them to other Sapindales. Floral anatomical data were also used in studies to distinguish *Dryades* from *Conchocarpus* (Groppo et al. 2021), and in the characterization of new species, such as *Conchocarpus hendrixii* (Groppo et al. 2019).

Regarding fruit anatomy, Hartl (1957, 1958) published two studies on endocarp structure in Rutaceae. More recently, Brückner (1991) presented an anatomical study of the fruit of four species in the genera *Dictamnus*, *Ptelea*, *Ruta*, and *Zanthoxylum*. The fruits of Rutaceae are also one of the highlights in the extensive work by Barroso et al. (1999) who mentions the carpel of the family flowers as poorly adherent, becoming multiple with the development of the fruit. According to Barroso et al. (1999), many species of Rutaceae with autochoric fruits have the participation of the endocarp in the ejection of seeds in mature fruits. Afonso (2018) studied the development of different fruits in the tribe Galipeae (subfamily Zanthoxyloideae), comparing

the formation of the different tissues that make up the fruit in species with fruits dispersed by the wind (such as *Balfourodendron* and *Helietta* Tul.), animals (*Hortia*), and those autochoric (*Conchocarpus*, *Ertela*).

Data on the internal structure of the seed are represented by Martin (1946) and Corner (1976). According to Corner (1976), the ovules in Rutaceae are anatropous, bitegumented, and crassinucellate; and the fundamental characteristics of the seeds are the predominance of the testa as a mechanical layer (both exotesta and mesotesta), the absence of differentiation in the endotesta, and, especially, the tracheoidal construction of the tegmen. Souza et al (2005) studied the morphology and developing anatomy of *Pilocarpus pennatifolius* Lem.

Ovule and testa development are detailed in *Ruta*, *Zanthoxylum*, *Skimmia*, *Poncirus* Raf. (= *Citrus*), *Citrus* L., *Fortunella* Swingle, *Citropsis* Swingle & Kellerman, *Murraya* (Boesewinkel 1977, 1978), and *Glycosmis arborea* (Roxb.) DC (Boesewinkel and Bouman 1978). The most thorough study of Rutaceae embryology, however, was done by Mauritson (1935), who analyzed species from all (Englerian) subfamilies. Johri and Ahuja (1957) carried out a study of the embryology associated with anther, ovule and seed development and aspects of the floral morphology in *Aegle marmelos* (L.) Corrêa.

Taxonomic and floristic treatments in the American Continent – In addition to the more comprehensive works on Rutaceae mentioned above carried out in the nineteenth century (see “Historical Background”), as those by Engler (1874) in Martius *Flora brasiliensis*, and Saint-Hilaire (1825), many works focused on descriptions of new species, floristic studies and later revisions of genus have been published, mainly in richer species regions in Americas, as in the Neotropics, as a consequence of the continued exploration of new South and Central American regions. Earlier works in American Rutaceae in the twentieth century (largely before the 60’s of the twentieth century) are referred in the “Supplementary Material.”

Beginning in the 60’s (twentieth century), several contributions for the American Rutaceae, notably from Brazil, were made by Albuquerque, including studies of *Fagara* L. (= *Zanthoxylum*) from the Amazonas state, Brazil (Albuquerque 1968a), and a complete study of the family for that state (Albuquerque 1976). Albuquerque and Honda (1971) also described a new Brazilian species of that genus. Albuquerque also published treatments for the Rutaceae of the Guanabara (today included in the Rio de Janeiro state, Brazil), and Goiás state (Albuquerque 1968b, 1985, respectively). Albuquerque (1981) also published many new combinations in *Angostura*, transferring to this genus the taxa previously recognized in *Cusparia* Humb., an invalid name (see Elias 1970).

Rodrigues and Silva (1971) published a new species of *Rauia* Nees & Mart. from the Brazilian Amazonia. Another species of the same genus from Venezuela was described by Steyermark (1988). Steyermark (1980, 1988) and Kallunki and Steyermark (1987) described a new species of *Raveniopsis* Gleason from the Venezuelan Guayana Shield, the later authors reporting the first occurrence of this genus in northern Brazil.

Waterman (1975) proposed several new combinations from *Fagara* to *Zanthoxylum*, proposing that the former should be synonymized with the latter. Emmerich (1978) redefined the generic circumscription in the *Raputia* Aubl. Group, describing *Neoraputia* Emmerich ex Kallunki, *Raputiarana* Ennerich, and *Sigmatanthus* Huber ex Emmerich. *Neoraputia* would be later revised by Kallunki (2009), who validated this generic name and all other combinations (invalidly) made by Emmerich. Kaastra (1977) described new taxa in the subtribe Pilocarpiinae (tribe Galipeeae, Zanthoxyloideae). Later, this author published a complete monograph on Pilocarpiinae (Kaastra 1982), recognizing four genera: *Esenbeckia*, *Metrodorea*, *Pilocarpus*, and *Raulinoa*. *Pilocarpus* was the object of a new review by Skorupa (1996), who brought new data and new taxa to this genus, with new Brazilian species formally described later (Skorupa 1998; Pirani and Skorupa 2004).

Treatments focused in American Rutaceae from 1970 to 1980 decades include Fournet (1978), who published the treatment of Rutaceae to Guadalupe and Martinique; Croat (1978) to Barro Colorado Island (Panama); Porter and Elias (1979) carried out the study of Rutaceae for the Flora of Panama; Spichiger and Stutz-de-Ortega (1987) published the Rutaceae treatment for the Flora of Paraguay. A taxonomic treatment to *Angostura* was presented by Rizzini (1990), including five new species. Chiang (1984) presented a synopsis of the North American *Helietta*, including a new Mexican species for that genus. Correll and Correll (1982) presented a detailed treatment of the family for the Flora of the Bahamas. Two new species of *Zanthoxylum* from Peru were described by Simpson (1982), while Gereau (1990) worked with the Cuspariinae (= Galipeinae) from that country. In this work, he proposed the new genus *Achuaria* Gereau, later synonymized under *Raputia* by Kallunki (1994). Gereau also published a treatment of the genus *Amyris* P.Browne to the South America, including two new species from eastern Amazonia (Gereau 1991). Brako and Zaruchi (1993) cataloged 25 genera with 67 species of Rutaceae for Peru. Maguire and Boom (1989) published a treatment of the Rutaceae of the Guayana Highland.

A series of publications on Rutaceae from the Neotropical Region, notably from Brazil, were published by Pirani, including family treatments for regional floras, such as for the Parque das Fontes do Ipiranga, in São Paulo state (Pirani 1984), Serra do Cipó, Minas Gerais state (Pirani 1987), Pico

das Almas (Pirani 1995), and Mucugê (Pirani 1986), both in Bahia (Brazil), Flora of Parati in state of Rio de Janeiro (Pirani 1997), for the Mato Grosso state (Pirani 1998a), and for the Flora of São Paulo (Pirani 2002), to Ducke Reserve in Manaus, state of Amazonas (Pirani 2005), and Grão-Mogol (Minas Gerais, Pirani 2006). Other contributions include descriptions of new taxa in *Zanthoxylum* (Pirani 1993), *Esenbeckia* (Pirani 1999), *Spiranthera* A.St.-Hil. (Pirani 2010), *Galipea* (Pirani 2004; Pirani and Kallunki 2007), and a review of *Helietta* and *Balfourodendron* (Pirani 1998b).

Together with his former students and collaborators, Pirani also presented decisive contributions in the Rutaceae from Brazil, as the treatment of Rutaceae to the Flora of Brazil project (Pirani and Groppo 2010, 2020), descriptions of new species, as in *Pilocarpus* (Pirani and Skorupa 2004), *Conchocarpus*, and *Zanthoxylum* (Groppo and Pirani 2017), and other local floras, as the Flora of Distrito Federal, Brazil (Groppo and Pirani 2007), Flora of Paraná, Brazil (Pirani and Groppo 2014), Pirani and Devecchi (2018) on the Rutaceae from the “Flora das Cangas,” Carajás Mountain chain, Pará (Brazil), and also in accounts of Rutaceae from other countries, as in the Flora of Bolivia project (Pirani et al. 2014).

Dias et al. (2013a) described *Metrodorea conccina* Pirani & P.Dias from the state of Bahia and epitypified *Esenbeckia cowanii* Kaastra in the same year (Dias et al. 2013b); two years later Dias et al. (2015) study the phylogeny and biogeography of *Metrodorea*. Brito et al. (2019) synonymized the monotypic *Nycticalanthus* Ducke into *Spiranthera*, and Colli-Silva and Pirani (2019) published a study on phylogeographic patterns of Galipeinae (Galipeeae) in Brazil.

Other studies in the period 2000–2020 in Rutaceae from the Americas, notably from the Neotropical Region, were carried out by Groppo in collaboration with his students, his previous advisor Pirani, and also involving Dr. Jacquelyn Ann Kallunki. These studies were focused on groups such as *Hortia*, with the description of new species (Groppo et al. 2005; Groppo and Pirani 2005), works focused on typing and synonymization (Groppo and Pirani 2008; Groppo 2010a); and a revision of the genus (Groppo and Pirani 2012). Other works include regional floras focused on Rutaceae, as the Flora of Sergipe, Brazil (Groppo and Erbert 2015), descriptions of new species in *Almeidea* (= *Conchocarpus*) (Bruniera et al. 2011), taxonomic notes in the same genus (Groppo and Bruniera 2010), and an account of the Neotropical Rutaceae (Groppo 2010b). Other contributions included a broad phylogenetic analysis of Rutaceae (Groppo et al. 2008), and later the proposition of an infrafamilial classification of the family (as pointed out above) and an investigation of the phylogenetic position of Chilean *Pitavia* Molina (Groppo et al. 2012), a first analysis of the Galipeinae (tribe Galipeeae), with the synonymization of *Almeidea* under *Conchocarpus* (Bruniera et al. 2015), and description of new

species in this genus (Groppo et al. 2019); a revision of the former *Almeidea* (= *Conchocarpus*, see Bruniera et al. 2021) and the recognition of the genus *Dryades*, with five species from the Brazilian Atlantic Rainforest, segregated from *Conchocarpus* (Groppo et al. 2021). Other studies from the same period involved descriptions of new species, such as *Conchocarpus kalunkiae* Londoño-E., Ana Trujillo, Pérez Zab. & Groppo (Londoño-Echeverri et al. 2021a), and *Lubaria heterophylla* Londoño-Ech., Trujillo-López & Pérez-Zab. (Londoño-Echeverri et al. 2021b), both from Colombia, the latter being the first record of this genus for that country. Londoño-Echeverri et al. (2021c) also published on floral morphology, geographical distribution and sexual dimorphism in *Zanthoxylum magnifrutum* Reynel (Rutaceae), a recently described species from tropical dry forest in Colombia. Wurdack (2017) described a new species of *Raveniopsis* from the Pakaraima Mountains in Guyana.

Reynel (1995) described three new Andean species of *Zanthoxylum*. The same author concluded an extensive work on this genus, published in *Flora Neotropica* series (Reynel 2017), recognizing 77 species. The phylogeny and biogeography of the same genus was studied world-wide by Appelhans et al. (2018), who also proposed the synonymization of the monotypic *Toddalia* under *Zanthoxylum*.

Jacquelyn A. Kallunki presented a series of works in the subtribe Galipeinae, including descriptions of new species of *Raveniopsis* (Kallunki and Steyermark 1987), *Galipea* from Nicaragua and Costa Rica (Kallunki 1988), a revision of *Erythrochiton* and related genera (Kallunki 1992), a revision and emended description and new combinations in *Raputia* (Kallunki 1990, 1994), a revision of *Ticorea* Aubl. (Kallunki 1998a), and the validation and revision of *Neoraputia* (Kallunki 2009). Kallunki also described the monotypic *Andreodoxa* Kallunki, endemic to southern Bahia, Brazil (Kallunki 1998b). The treatment of the Rutaceae to the central French Guiana was published by Kallunki (2002).

Kallunki and Pirani (1998) published a synopsis of *Angostura* and *Conchocarpus* (both from subtribe Galipeinae) resurrecting the later from illegitimate *Cusparia* and defining the circumscription of these taxonomically complex genera. This publication brought also three new species of *Angostura* and 21 new species of *Conchocarpus*, mostly from coastal forests within the Atlantic Forest Domain, from Rio de Janeiro to south Bahia, eastern Brazil. Many of the new species were collected by the authors for the first time, highlighting the need of botanical explorations in areas such as the Brazilian Atlantic Forest. This study was also the base to other studies that were carried out later, as Bruniera et al. (2015, 2021), and Groppo et al. (2021), whose main objective was the understanding of the Galipeinae as a whole.

Rutaceae in the Americas – A survey in the available treatments published in Rutaceae for the America (most cited

above) reveals that this family is represented in this continent by 51 genera and 412–415 species. Most of its representatives are found in the tropical America, with 48 genera (46 restricted to this region), and c. 350 species (Kallunki 2004) to 400 species. Species of *Cneoridium* Hook.f. (one *Thamnosma* Torr. & Frém., some *Zanthoxylum*, *Ptelea* and *Choisya* occur in desertic or temperate areas in North America. Monospecific *Pitavia*, represented only by *Pitavia punctata* Molina occurs in temperate areas from Chile (Groppo et al. 2012). Data on genera and species of the different subfamilies of Rutaceae presented in America are summarized in Table 1.

Native genera of Rutaceae in America are restricted to this continent with just two exceptions: the pantropical *Zanthoxylum*, with c. 225 species occurring in tropical and subtropical areas of America, Africa, Asia, and Oceania (Appelhans et al. 2018), 78 of them in the Americas (Reynel 2017; Groppo and Pirani 2017) and *Thamnosma*, with eight species (Thulin 1999; Kubitzki et al. 2011), 3–4 of them in North America (Texas, USA, Kubitzki et al. 2011), and the remaining in Africa. Another genus that was reported having species in America and elsewhere is *Cneorum*, with one species—*Cneorum trimerum* (Urban) Chodat, known only by its type collection (from 1861), from Cuba, and two other species from the Mediterranean vegetation in continental Spain and Canary Islands. However, the specimen from Cuba was analyzed by Appelhans et al. (2010) and reduced to the synonymy of *C. tricoccon* L. (from Mediterranean region), these authors stating that the transatlantic distribution of *C. tricoccon* is probably the result of an introduction in Cuba by humans.

Some genera of Rutaceae are cultivated in the Americas, but not native to this continent. These genera include some of the subfamily Aurantioideae, as *Citrus*, cultivated worldwide because its edible fruits, and species of *Clausena* Burm.f., *Murraya*, *Swinglea* Merr., and *Triphasia*, cultivated as ornamentals, all of them (including *Citrus*) of Asian origin (cf. Swingle and Reece 1967). Other species cultivated as ornamentals include *Phellodendron amurense* Rupr., and *Dictamnus albus* L., both from Asia. Two species of rue, *Ruta* (from Mediterranean region, Macaronesia and southwest Asia), *R. chalepensis* L., and *R. graveolens* L., are cultivated as ornamental, as sources of aromatic oil and essences or to “avoid envy” in some countries, as in Brazil, where they are widely known as “arruda.” Other native species of Rutaceae from America are cultivated out of their place of origin, both in America or in other continents, as *Casimiroa edulis* La Llave & Lex. (“zapote blanco”), native from Mexico to Nicaragua, but cultivated as an ornamental and edible fruits; *Choisya ternata* Kunth (Mexican Orange), from Mexico and cultivated as ornamental and *Ravenia spectabilis* (Lindl.) Planch. Ex Griseb., from Cuba, also cultivated as ornamental because its showy, pink flowers.

Table 1 Summary of genera and number of species of Rutaceae in the Americas. Genera arranged under subfamilies, these according to Appelhans et al. (2021); only tribe Galipeae (and its subtribes Galipeinae and Pilocarpinae) and Polyaster Alliance (both under subfamily Zanthoxyloideae) are discriminated. Delimitation of Galipeae and its subtribes (Galipeinae and Pilocarpinae) follows Groppo et al. (2017). *Polyaster* Alliance according to Kubitzki et al. (2011). *Rutaneblina* tentatively positioned in Galipeinae (see Kubitzki et al. 2011). Number of genera and species between brackets—genera/species (total world and for America)

Subfamily/tribe, subtribe or alliance/genera	Number of species	Habit	Geographic range
Subfamily Amyridoideae (3/42, all in America)			
<i>Amyris</i> P.Browne	c. 40	Shrubs or trees	USA (Texas, Florida), Mexico, Central America (including West Indies) to Peru and Brazil
<i>Cneoridium</i> Hook.f.	1	Shrubs	Southern North America (California and Baja California, Mexico)
<i>Stauranthus</i> Liebm.	1	Shrubs or small trees	Mexico (southeastern) to Panama
Subfamily Aurantioideae (27–28/206, no native species in America)			
Subfamily Cneroideae (8/35 total, 3/14 in America)			
<i>Dictyoloma</i> DC.	1	Small trees	Bolivia, Peru, Brazil (Acre, Rondônia, with a disjunction to Eastern Brazil)
<i>Sohnreyia</i> K.Krause	4	Unbranched trees	Northern South America (Guayana, Venezuela, Brazil, Peru, Colombia)
<i>Spathelia</i> L.	9	Unbranched trees	Bahamas, Cuba, Jamaica
Subfamily Haplophyloideae (1/66, no native species in America)			
Subfamily Rutoideae (5/20 total, 1/3–4 in America)			
<i>Thamnosma</i> Torr. & Frém.	8 (3–4 in America)	(Sub)shrubs	Southern USA and southern Mexico (also in Africa)
Subfamily Zanthoxyloideae (109/ca. 1700 total, 44/371–373 in America)			
Zanthoxyloideae, Tribe Galipeae (33/246, all in America)			
Zanthoxyloideae Galipeae, Subtribe Galipeinae (27/183)			
<i>Adiscanthus</i> Ducke	1	Shrubs	Brazil, Venezuela, Peru, lowland forests
<i>Andreadoxa</i> Kallunki	1	Trees	Brazil, state of Bahia, Atlantic Forest
<i>Angostura</i> Nees & Mart.	8	Trees or shrubs	Cuba, Nicaragua to Venezuela; south to northern Bolivia and southern Brazil
<i>Apocaulon</i> R.S.Cowan	1	Decumbent herbs	Venezuela, (Guayana Shield), montane forests
<i>Conchocarpus</i> J.C.Mikan	50	Shrubs or small trees, often unbranched	Nicaragua to southern Bolivia and southern-eastern Brazil
<i>Decagonocarpus</i> Engl.	2	Shrubs or small trees	Venezuela (Guayana Shield), northern Brazil, and eastern Colombia
<i>Desmotes</i> Kallunki	1	Shrubs	Panama, Coiba Island
<i>Dryades</i> Groppo, Kallunki & Pirani	5	Shrubs or small trees, often unbranched	Brazil, Atlantic Forest
<i>Ertela</i> Adans	2	Erect herbs to subshrubs	Mexico through South America to Peru, Bolivia, and Brazil (Rio de Janeiro as southern limit)
<i>Erythrochiton</i> Nees & Mart	7	Shrubs or small trees, often unbranched	Costa Rica to northern South America; south to Bolivia and Brazil
<i>Euxylophora</i> Huber	1	Tall trees	Brazil (eastern Amazonia) and Peru
<i>Galipea</i> Aubl.	15	Trees or shrubs	Costa Rica to Brazil and Bolivia
<i>Hortia</i> Vand.	10	Trees or Shrubs	Panama and tropical South America to São Paulo state (Brazil)
<i>Leptothyrsa</i> Hook.f.	1	Shrubs or small trees, not ramified	Brazil, Colombia, Peru, Amazonian lowland forests
<i>Lubaria</i> Pittier	2	Trees	Costa Rica, Venezuela, and Colombia
<i>Naudinia</i> Decne. ex Triana	1	Shrubs	Colombia
<i>Neoraputia</i> Emmerich ex Kallunki	6	Trees	Venezuela, French Guiana, Peru and Brazil
<i>Raputia</i> Aubl.	11	Shrubs or trees	Northern South America, lowland forests
<i>Raputiarana</i> Emmerich	1	Shrubs	Brazil, Colombia, Peru, Amazonian lowland forests
<i>Rauia</i> Nees & Mart.	c. 10	Shrubs of small trees	Northern South America to Rio de Janeiro (Brazil)
<i>Ravenia</i> Vell.	11	Shrubs or small trees	Greater Antilles and Trinidad & Tobago, and Honduras to Brazil and Peru

Table 1 (continued)

Subfamily/tribe, subtribe or alliance/genera	Number of species	Habit	Geographic range
<i>Raveniopsis</i> Gleason	19	Shrubs or small trees	Guayana Shield, southern Venezuela to northern Brazil
<i>Rutaneblina</i> Steyerm. & Luteyn	1	Shrubs	Venezuela (Guayana Shield)
<i>Sigmatanthus</i> Huber ex Emmerich	1	Small trees or shrubs	Northeast Brazil
<i>Spiranthera</i> A.-St.-Hil.	6	Shrubs or trees	Peru, Brazil, Bolivia, Amazonian and Atlantic Forests
<i>Ticorea</i> Aubl.	5	Trees or shrubs	Ecuador, Peru, Bolivia, Brazil (Amazonian) and the Guianas
<i>Toxosiphon</i> Baill.	4	Shrubs or small trees, often unbranched	Southern Mexico to Panama, and from Ecuador to northern Bolivia and Brazil
Zanthoxyloideae, Galipeeae, Subtribe Pilocarpinae (6/63)			
<i>Balfourodendron</i> Corr.Mello ex Oliv.	2	Trees or treelets	Northeastern to southern Brazil, Paraguay and Argentina
<i>Esenbeckia</i> Kunth	30	(Sub)shrubs or small trees	USA (Texas) and Mexico to north Argentina
<i>Helietta</i> Tul.	8	Shrubs or trees	Mexico and USA (Texas), Cuba, northern South America (Peru) and south-eastern Brazil, Paraguay and Argentina
<i>Metrodorea</i> A.St.-Hil.	6	Shrubs or trees	Surinam through Brazil and Bolivia
<i>Pilocarpus</i> Vahl	16	Shrubs or trees	Mexico, Central America (including Antilles) to Argentina
<i>Raulinoa</i> R.S.Cowan	1	Shrubs	Brazil, Santa Catarina
Zanthoxyloideae, Polyaster Alliance (5/9)			
<i>Decatropis</i> Hook f.	2	Small trees or shrubs	Southern Mexico, Guatemala, Honduras
<i>Decazyx</i> Pittier & S.F.Blake	2	Trees	Mexico, Guatemala, Honduras, Costa Rica
<i>Plethadenia</i> Urb.	2	Small shrubs	Central America (Cuba and Hispaniola)
<i>Polyaster</i> Hook.f.	1	Shrubs	Mexico
<i>Peltostigma</i> Walp.	2	Small trees or shrubs	Central America (Jamaica and continental part), Ecuador, Peru
Other American Zanthoxyloideae (6/244–247)			
<i>Casimiroa</i> La Llave	c. 10	Shrubs or trees	Mexico (highlands) and USA (Texas) to Costa Rica
<i>Choisya</i> Kunth	6	Shrubs	Mexico and south-western USA (Arizona)
<i>Megastigma</i> Hook.f.	2	Shrubs or small trees	Southern Mexico, Guatemala, Honduras, Nicaragua
<i>Ptelea</i> L.	1–3	Shrubs or small trees	North America (Mexico and USA)
<i>Pitavia</i> Molina	1	Small trees or shrubs	Chile (costal cordillera)
<i>Zanthoxylum</i> Lam.	225 (78 in America)	Trees, shrubs, lianas	Pan(sub)tropical, in America from USA to north Argentina and Chile
Total: (162/ca. 2085 total worldwide, 51/412–415 in America)—49 genera endemic to this continent, except <i>Thamosma</i> (also in Africa) and (sub)tropical worldwide <i>Zanthoxylum</i>			

Pilocarpus microphyllus Stapf ex Holm (“jaborandi”) is cultivated in Northeastern Brazil as source of pilocarpine, used in the treatment of glaucoma.

From the six subfamilies of Rutaceae sensu Appelhans et al. (2021), four are natively presented in the Americas, being the Aurantioideae (with some species cultivated in this continent, as seen above) and the Haplophyllioideae both absence in this continent. Most of the genera and species belong to Zanthoxyloideae, with 44 genera, and 371–373 species. This subfamily is better represented in the Americas by the “American Clade” sensu Groppo et al. (2012),

or “Clade C” in Appelhans et al. (2021), which includes the Neotropical Galipeinae and Pilocarpinae (both from tribe Galipeeae), plus species of Rutaceae from Central and North America (Mexico and Southern USA), such as *Choisya*, *Plethadenia*, *Peltostigma*, and *Ptelea*, all sampled by Appelhans et al. (2021) and positioned in other groups than Galipeeae. It is reasonable to assume that other genera of Central American Rutaceae such as *Decatropis* Hook. f., *Decazyx*, *Megastigma* Hook.f., *Peltostigma* Walp., and *Polyaster* Hook.f., all not yet sampled in phylogenetic studies and treated as *Polyaster* Alliance by Kubitzki et al. (2011)

are also part of the American Clade. Tribe Galipeeae is the most speciose group in the American Clade, with 33 genera and 246 species, being the subtribe Galipeinae the most diverse, with 27 genera and 183 species, 50 of these species belonging to *Conchocarpus*. These numbers include *Hortia* (10 species), after preliminary results of Groppo et al. (2017). The other subtribe of Galipeeae is Pilocarpinae, with six genera (including *Balfourodendron* and *Helietta*, see Groppo et al. 2017) and 63 species.

In addition to the groups of the “American Clade” mentioned above, the Rutaceae of the subfamily Zanthoxyloideae are represented in the Americas by *Zanthoxylum*, with 78 species (in a total of 225 species worldwide), present in (sub)tropical areas; *Casimiroa* La Llave, with about 10 species distributed throughout Central and North America (northern limit in Texas, USA); and *Pitavia punctata*, a species of small trees or shrubs restricted to areas of the Chilean costal cordillera. These three genera are phylogenetically closer to non-American groups: *Zanthoxylum* to *Fagaropsis*, *Phellodendron* Rupr. and *Tetradium* Lour., all from East Asia and Oceania (Appelhans et al. 2018); *Casimiroa* to *Orixa* Thunb., *Skimmia* (East Asia) and *Dictamnus* (Europe and West Asia), see Appelhans et al. (2021); and finally *Pitavia* to Australasian and Pacific groups (Groppo et al. 2012; Appelhans et al. 2021).

The other subfamilies with representatives in the Americas are much smaller when compared with the Zanthoxyloideae. Subfamily Amyrioidae are exclusively American, formed by three genera and 42 species, almost all of them belonging to *Amyris*, with 40 species ranging from Texas and Florida (USA) throughout America to Peru and West Brazil. The other two genera are from North America, both monotypic, *Cneoridium*, with *C. dumosum* Hook.f., that are shrubs from sub-desert areas of California (USA) and Mexico (Baja California) and *Stauranthus perforatus* Liebm., shrubs or small trees from the south. Mexico to Panama. Subfamily Rutoideae, with five genera and 20 species distributed in the Old World (Europe, Asia and Africa), are represented in America only by *Thamnosma*, with 3–4 (sub) shrubs from the southern USA and Mexico (plus about four species in Africa). Finally, the subfamily Cneoroideae (8 genera/35 species) presents three genera in the neotropics, the monotypic *Dictyoloma*, represented only by *D. vandellianum* A.Juss., from Bolivia, Peru and Brazil (absent in the Amazon), and other two genera represented by unbranched trees with leaves concentrated at the apex of the trunk: *Sohnreya* K.Krause, with four species from the north of South America and *Spathelia*, with four species from the insular part of Central America (Bahamas, Cuba and Jamaica).

The occurrence of Rutaceae groups from different clades in America suggests that the occupation of the family on the continent occurred at different times in the past. Vicariance events of Gondwanic origin can be hypothesized to explain

the split between the American Clade and the Diosmeae tribe (subfamily Zanthoxyloideae), given that these two groups are sisters according to Groppo et al. (2008) and Appelhans et al. (2021). Likewise, the current distribution of Cneoroideae (present in Tropical America and Africa-Europe) suggests a Gondwanic origin. On the other hand, long-distance dispersion hypotheses are more adequate to explain the pantropical distribution of *Zanthoxylum* (Appelhans et al. 2018) and *Pitavia*, closer to Australasian and Pacific Island groups (Groppo et al. 2012; Appelhans et al. 2021). The distribution of *Thamnosma*, with species in dry areas in North America and Africa, would need to be better investigated. More biogeographical studies focused in American Rutaceae are necessary to access the history of the geographic occupation of its representatives in the continent.

Future perspectives – Floristic and taxonomic studies in Rutaceae have been carried out preferable in the Neotropical region, given the greater diversity of the group in this region. Cariological, palynological, and phytochemistry studies also have been focused in Neotropical species, notably in Brazil, where there is a great biological diversity and research groups working in Rutaceae in different fields.

Despite the largest volume of work focused in the Neotropical groups of Rutaceae in the Americas, there are still gaps in the knowledge of the family that can be addressed in future studies. These gaps, from the point of view of basic knowledge of the species, are noted in regions that still lack sufficient botanical collections such as the Amazonia (spread across several countries) and other regions that are densely forested and/or such as those at high altitudes, as the Atlantic Forest in eastern Brazil, and the northern regions of South America such as the Guyana Shield (including the Tepuis). Other areas where there is a need for more extensive botanical collections include the mainland of Central America, where there are still unexplored forested areas.

The number of new species found in Rutaceae in recent years, even in more densely populated areas such as the Brazilian Atlantic Forest, shows that there is still work to be done in terms of botanical collections. Many of these new species were previously detected on visits to botanical collections (herbaria), but in several cases exploratory expeditions reported new species in the field, as reported by Kallunki and Pirani (1998), and Groppo et al. (2019) to *Conchocarpus*. These new findings reinforces the need for more intensive fieldwork in tropical areas of the Americas.

The knowledge of the phylogeny of Rutaceae groups around the world has increased fast in recent years, with new, more comprehensive studies, such as those involving the whole family (as Appelhans et al. 2021), but also those focused on more specific groups (e.g., Bruniera et al. 2015). The taxon that has been most studied in America is the tribe Galipeeae with its tribes Galipeinae and Pilocarpinae. Step

by step, the phylogenetic relationships in Galipeeae are being studied, with the construction of evolutionary hypotheses that may better reflect what happened in the past in this group. However, some genera from the Galipeeae are still to be better understood and sampled, as Amazonian *Lep-tothyrsa*, and *Rutaneblina* (from the Venezuelan Guayana Shield). Other groups that can be accessed for phylogenetic and biogeographic studies are those from the *Polyaster* Alliance (sensu Kubitzki et al. 2011), an informal group concentrated in Central and North America (Mexico) and still poorly understood in its delimitation and internal relationships. More accurate phylogenetic hypotheses are essential for understanding the evolution of morphological, anatomical and palynological traits, as well as the biogeography story of any biological group. The use of new techniques for obtaining phylogenies with molecular data, such as those of next-generation sequencing (NGS) can be useful in the production of more robust phylogenies, especially in groups with shorter branches of divergence, such as those found in tropical American groups of Rutaceae (see Groppo et al. 2008; Appelhans et al. 2021).

Particularly to the Rutaceae, these phylogenetic hypotheses can be useful also to optimize the search for new drugs, since the family is extremely diverse in secondary metabolites as seen above. Works dealing with the use of NGS to infer phylogenies in American groups of Rutaceae are still in the beginning (cf Allevato et al. 2019). Population genetic studies in species of American Rutaceae are also scarce, e.g., Guidugli et al (2012) who accessed the genetic diversity from small populations of *Metrodorea nigra* A.St.-Hil. in a southeastern Brazil forest remnant. This type of study is important to assess the genetic viability of wild populations, with effects on conservation and recovery programs for degraded areas.

The advancement of research on Rutaceae in the Americas will depend on collaborative work between researchers from different areas, which include systematists, specialists in floral and reproductive biology, anatomists, palynologists, biogeographers and other professionals who work with diversity. Besides this collaborative work, the activity of training of young botanists is essential not only in Rutaceae, but also to the knowledge of the flora. There is a global lack of academic education in taxonomy and of properly trained taxonomists (see Engel et al. 2021), a problem that becomes more serious in areas of high biological diversity, as in the Tropical America, which may have extinct species even before they are known to science.

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Declarations

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

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