LEAF VENATION OF BRAZILIAN SPECIES OF *CRYPTOCARYA* R. BR. (LAURACEAE)

Pedro Luís Rodrigues de Moraes[1] and Carlos Alberto Moysés Neto[2]

Abstract. With the aim of recognizing and identifying both fertile and sterile specimens of *Cryptocarya* from Brazil, we analyzed the leaf venation pattern of 14 taxa, 6 of them being described and illustrated for the first time. A dichotomous identification key was built from a matrix of 12 leaf venation characters and 30 character states, which distinguishes among taxa.

Keywords: Laurales, leaf venation, morphology, Neotropics, taxonomy

The genus *Cryptocarya* (Lauraceae) was described by Robert Brown (1810: 402), with three species from Australia: *C. glaucescens* R. Br., *C. obovata* R. Br., and *C. triplinervis* R. Br., of which Kostermans (1939: 112) designated *C. glaucescens* as lectotype. It is a pantropical genus of monoecious trees, present in Central and South America, East Africa (Tanzania, Zimbabwe, Malawi, Mozambique), South Africa, Madagascar, Asia, Australia, and Oceania (van der Werff, 1992; Rohwer, 1993; Diniz, 1996; Moraes, 2007; Moraes and van der Werff, 2010). The number of known species is uncertain, since the genus has never been revised in full (de Kok, 2015, 2016). Regardless, some estimates have been proposed, but they are inconsistent among authors: a more conservative one ranges from 200 to 250 species, which is the one most usually cited (e.g., Kostermans, 1957b, 1995; Vattimo-Gil, 1966, 1979; Klucking, 1987; Mabberley, 1987; Rohwer and Richter, 1987; Hyland, 1989; Tressens, 1997; Le Cussan et al., 2007; Li Xiwen et al., 2008; Cooper, 2013; de Kok, 2015, 2016), whereas more liberal ones assume ca. 300 (e.g., Mabberley, 2017; Fasila et al., 2020), more than 300 (e.g., van der Werff, 2001; Gangopadhyay and Chakrabarty, 2005; Nishida et al., 2016), 300–350 (Moraes, 2007), 250–350 (Carter, 2017), or ca. 350 species (Kostermans, 1974; Rohwer, 1993; Moraes et al., 2007; van der Werff, 2008; Moraes and van der Werff, 2010; Morden et al., 2015; Munzinger and McPherson, 2016; Moraes and Vergne, 2018), the latter considered to be too high (Rohwer et al., 2014; Morden et al., 2015; van der Merwe et al., 2016). Several of the previous estimates did not consider another 30 Malagasy species originally named under *Ravensara* Sonnerat (1782), the latter being sunk in synonymy of *Cryptocarya* (see Kostermans, 1958; van der Werff, 1992, 2008, 2013, 2017; Rohwer et al., 2014; Kottaimuthu and Rajendran, 2018). This difference in estimates of about 100 species may reflect different opinions on the more than 500 specific binomials of *Cryptocarya* enumerated in Index Kewensis (e.g., Kostermans, 1937, 1964, 1968, 1990; Vattimo-Gil, 1966; Frodin, 1976; Kochummen, 1989; Ng, 2005; Moraes, 2007; de Kok, 2016), since there is no list of currently accepted names encompassing the homotypic and heterotypic synonyms. Therefore, *Cryptocarya* is in need of a comprehensive taxonomic revision (Rohwer, 1993; van der Werff, 2017). However, its large size and widespread distribution make revision of the genus difficult to accomplish, being beyond the scope of most botanists.

The increase in knowledge of *Cryptocarya* diversity over the last 210 years can be summarized as follows: in *Systema laurinarum*, the first general monograph of all known Lauraceae, Nees von Esenbeck (1836) recognized 13 species, of which 7 are currently accepted, 4 are heterotypic synonyms, and 2 belong to other genera. In Meissner's treatment (1864), the second complete monograph of the family, 37 species were recognized, of which currently 25 are accepted, 7 are heterotypic synonyms, and 5 belong to other genera; in addition, 3 species listed in *species exclusæ* are also currently accepted, thus totalling 28 species. Gamble (1912) reported ca. 40 species, Lecomte (1914) ca. 55 species, and Liou (1932) ca. 173 species. Kostermans (1957b) noted the existence of 303 (318) binomials, whereas in 1964 he listed 327 binomials (with several homonyms), from the literature through 1962. At present, the Tropicos database lists 519 taxa, whereas 544 are listed in the International Plant Name Index (IPNI) database.

There are several modern regional treatments (or accounts) of the genus, which help in understanding its variability and distribution and also provide evidence of a relatively high level of endemism for most of the analyzed regions and territories: 48 Australian species are accepted (Hyland, 1989; Le Cussan et al., 2007; Cooper, 2013), of which 39–40 (81–83%) are considered to be endemic; 21 species are recognized from the Indian subcontinent (Gangopadhyay and Chakrabarty, 2005; Gangopadhyay, 2006, 2008; Bachan et al., 2018; Fasila et al., 2020), of

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[1] Universidade Estadual Paulista "Júlio de Mesquita Filho," Instituto de Biociências, Departamento de Biodiversidade, Av. 24 A 1515, Bela Vista, Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil; pedro.r.moraes@unesp.br

[2] Alumnus of Undergraduate Biological Sciences Program, Universidade Estadual Paulista "Júlio de Mesquita Filho," Instituto de Biociências, Rio Claro, SP, Brazil.

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which 16 (76%) are considered to be endemic; 21 Chinese taxa have been revised by Li Xiwen et al. (2008), of which 15 (71%) are considered to be endemic; 22 endemic species (100%) are recognized from New Caledonia (Morat et al., 2012; Munzinger and McPherson, 2016); 17 species have been recognized from Thailand and Indochina (Laos, Cambodia, and Vietnam), with 14 recorded (3 endemic) from Thailand, 10 (1 endemic) from Vietnam, 8 from Laos, and 5 from Cambodia, of which 7 species (41%) are endemic for the region as a whole (de Kok, 2015; Zhang et al., 2020); among the 17 taxa currently recognized from Peninsular Malaysia, only three (18%) are endemic (de Kok, 2016); about 40 Malagasy species are recognized, of which 39 (97%) are endemic (van der Werff, 2017); and 31 species are recognized from the Philippines, of which 16 (52%) are endemic (Collantes and Pelser, 2020).

In his monograph on the American Lauraceae, Mez (1889) recognized 9 species of *Cryptocarya*. He accepted all species treated by Meissner except *C. dubia* Kunth [= *Aiouea dubia* (Kunth) Mez] and *C. emarginata* [= *Beilschmiedia emarginata* (Meisn.) Mez]. He also described *C. aschersoniana* Mez and *C. saligna* Mez, and reduced *Aydendron floribundum* Meisn. to the synonymy of *C. minima* Mez. Later, Mez (1892, 1893, 1902, 1907) and described another five Brazilian taxa as new: *Cryptocarya hypoleuca* Mez, *C. longistyla* Mez, *C. minutiflora* Mez, *C. schwackeana* Mez, and *C. subcorymbosa* Mez. Kostermans (1937) revised the American species and recognized 7 of them, including the Chilean *C. alba* (Molina) Looser [= *C. rubra* (Molina) Skeels]. More recently, Moraes (2005b) lectotypified the names of Brazilian *Cryptocarya*, accepting 8 species, which were further revised by Moraes (2007), then recognizing 13 species, 5 of them being newly described and 11 being endemic (85%). Another 2 species were described by Moraes and van der Werff (2010), increasing to 16 the number of currently accepted species to the Americas. Furthermore, extra Brazilian specimens collected in Costa Rica, Ecuador, Peru, Venezuela, and Bolivia likely represent undescribed species, but they still lack flowering herbarium material for a proper description (Moraes, 2007; Moraes and van der Werff, 2010).

Cryptocarya can be easily distinguished from other laurel genera by its bisexual and invariably trimerous flowers, which are very typical in shape, with six equal to subequal tepals, nine fertile stamens with disporangiate anthers, staminal glands only in the third androecial whorl, three relatively big cordate to sagittate staminodes, a usually slender, deeply urceolate, apically narrowed receptacular tube and immersed ovary. Its characteristic fruit is completely enclosed in the receptacular tissue and appears to be inferior, hence its etymology: from Greek κρυπτός, "kruptós," hidden, and κάρυον, "káruon," nut, that is, the fruit is covered by the accrescent flower tube (Kostermans, 1957b; Ng, 2005; Moraes, 2007; Nishida et al., 2016). Its leaves generally do not bear domatia, which are only found in a few Australian and Papuasian species (e.g., *C. alleniana* C.T. White, *C. erythroxylon* Maiden & Betche ex Maiden, *C. foveolata* C.T. White & Francis, *C. rigida* Meisn., and *C. triplinervis*; Brouwer and Clifford, 1990). It is placed in tribe Cryptocaryeae Nees sensu van der Werff and Richter (1996), as bearing "paniculate-± cymose inflorescences," or as "paniculate" in van der Werff (2001); however, according to Endress and Lorence (2020), botryoids, thyrsoids, and compound botryoids and thyrsoids are the most common forms. This tribe is also known as the *Cryptocarya* group (Rohwer, 1993), which was first recognized by Richter (1981) on the basis of wood and bark anatomy and which currently encompasses the genera *Aspidostemon* Rohwer & H.G. Richt., *Beilschmiedia* Nees, *Endiandra* R.Br., *Eusideroxylon* Teijsm. & Binn., *Dahlgrenodendron* J.J.M. van der Merwe & A.E. van Wyk, *Potameia* Thouars, *Potoxylon* Kosterm., *Sinopora* J. Li, N.H. Xia & H.W. Li, *Triadodaphne* Kosterm., and *Yasunia* van der Werff (Chanderbali et al., 2001; Rohwer et al., 2014; Rohwer, 2017).

A molecular phylogenetic study by Rohwer et al. (2014) supported the monophyly of *Cryptocarya*, although based on only 20 species sampled from the genus. Within *Cryptocarya*, their results showed a split between a group comprising *C. alba*, *C. oubatchensis* Schltr. (see below), and *C. pluricostata* Kosterm. (the latter two from New Caledonia) and all the remaining species. Among the latter, three major well-supported clades were retrieved: the Asian-Australian clade, the southeastern Brazilian (including all Brazilian *Cryptocarya* species investigated, *C.* aff. *aschersoniana* Mez, *C. botelhensis* P.L.R. Moraes, *C. citriformis* [Vell.] P.L.R. Moraes, *C. mandioccana* Meisn., *C. moschata* Nees & Mart., *C. saligna* Mez, and *C. wiedensis* P.L.R. Moraes), and the two Malagasy species, *C. subtriplinervia* (Kosterm.) van der Werff and *Ravensara elliptica* Kosterm. (≡ *Cryptocarya rigidifolia* van der Werff). Therefore, the origin of *C. alba* has been shown to be different from that of the other South American species, indicating two independent colonization events. In the phylogenetic study by van der Merwe et al. (2016), which was focused on Australian species, *C. alba* was found as sister to five Australian species not included in Rohwer's study (*C. erythroxylon*, *C. oblata* F.M. Bailey, *C. onoprienkoana* B. Hyland, *C. rhodosperma* B. Hyland, and *C. rigida*), thus indicating that this lineage is present also in Australia. Moreover, the phylogenetic study by Carter (2017), focused on New Caledonian species, indicated that at least another New Caledonian species, *C. aristata* Kosterm., would belong to that lineage. However, Carter's work also suggests the possibility that the sample of *C. oubatchensis* used by Rohwer et al. (2014; and later by Morden et al., 2015), *McPherson 19131* (MO-398160; as determined by the collector in 2004), actually belongs to *C. aristata*, or is closely related to it, as determined by J. Munzinger & G. McPherson in March 2018 on a duplicate at the Paris Herbarium (P02033187). Another sample of *C. oubatchensis* used by Carter (2017), *Munzinger 7078* (MPU026704, NOU082910, P00806970), formed a strongly supported clade with *C. phyllostemon* Kosterm., which in turn was sister to a clade formed by *C. chinensis* (Hance) Hemsl. and *C. densiflora* Blume., which all together were sister to a clade formed by *C. subtriplinervia* and *Ravensara elliptica*.

As pointed out by van der Merwe et al. (2016), although molecular phylogenies have supported the monophyly of the Cryptocaryeae and the genus *Cryptocarya*, there has been little success in finding morphological characters that can elucidate subgeneric or species-level relationships (Chanderbali et al., 2001; Rohwer et al., 2014). With regard to the Australian *Cryptocarya*, two attempts to arrange species into morphologically distinguishable groups have been made by Hyland (1989) and by Christophel and Rowett (1996), who evaluated relationships among species on the basis of morphological similarity. However, the molecular phylogenetic study by van der Merwe et al. (2016) has shown that just a few of Hyland's (1989) morphology-based groups reflected the phylogenetic relationships, whereas none of the groups proposed by Christophel and Rowett (1996), based on leaf and epidermal characters, has been congruent with the evolutionary relationships assessed by molecular data. For instance, *Cryptocarya* species with triplinerved leaves, which is a much smaller group than the one having pinnately veined leaves (the great majority), have a convergent origin as evidenced for *C. densiflora*, *C. subtriplinervia*, and *C. triplinervis* (Rohwer et al., 2014; Carter, 2017) and reinforced by van der Merwe et al. (2016), as exemplified by the placement of *C. grandis* B. Hyland, *C. pleurosperma* C.T. White & Francis, and *C. triplinervis*, which did not form a clade. Nevertheless, de Kok (2016) assembled the *Cryptocarya* species of Peninsular Malaysia in three groups on the basis of a single morphological character (i.e., leaf venation: pinnate vs. acrodromous) and their geographical distribution. The first two groupings comprise (i) a bigger group of species with pinnately veined leaves and (ii) a smaller group of species with triplinerved leaves (i.e., *C. densiflora*, *C. laevigata* Blume, and *C. wrayi* Gamble).

As for the Brazilian *Cryptocarya*, Moraes (2007) was unable to arrange species into morphologically clearly distinguishable groups (de Kok, 2016; Nishida et al., 2016), because of their morphological homogeneity. Regardless, Moraes (2005a) evaluated isozymic data in combination with morphological criteria for classifying Brazilian species of *Cryptocarya*. Through the analysis of 19 enzyme systems, 41 putative isozyme loci (polymorphic in at least one population), 124 alleles were recorded from 739 adult trees of 35 natural populations of 10 species of *Cryptocarya* native to the southeastern Atlantic rain forest. Results demonstrated that discriminant analysis of isozymic data can be used for efficient marker-based allocation of individual trees into predefined groups of populations and species of *Cryptocarya*, complementing and/or confirming information obtained from traditional taxonomic studies; as pointed out by Moraes (2007), unsupervised classification through cluster analysis revealed that *C. mandioccana* and *C. moschata*, as well as *C. citriformis* and *C. saligna*, are closely related species, corroborating morphological evidence and a former indication by Moraes et al. (2002).

Despite the apparent morphological uniformity of Brazilian *Cryptocarya*, which makes their circumscription a difficult task, particularly because of the lack of exclusive diagnostic characters, several studies have demonstrated their diversity and variability through characters other than those traditionally used. For instance, Flörsheim and Barbosa (1983–1985) studied the wood anatomy of samples of *Cryptocarya aschersoniana*, *C. mandioccana*, *C. moschata*, and *C. saligna* collected at Serra da Cantareira, São Paulo. Whether or not the variability they found, among the three different taxa considered (*C. aschersoniana*, *C. mandioccana*, and *C. moschata*, which may actually represent just *C. mandioccana*), was caused by adaptive responses to different environment conditions and/or by different cambial age is a matter awaiting further evaluation. Moraes and Alves (2002) studied the biometry of mature fruits of *C. mandioccana* ($N = 1892$, from 27 trees of 1 population) and *C. moschata* ($N = 1487$, from 37 trees of 11 populations). Despite their differences in shapes and sizes, fruits of *C. moschata* showed a tendency to positive allometry, that is, greater increase of the equatorial radius than of the polar radius when increasing in size, whereas fruits of *C. mandioccana* from all trees investigated have shown a tendency to isometry, that is, a constancy of shape for both small and large fruits. For 12 natural populations (267 individuals) of *C. moschata*, genetic structure, differentiation, and diversity were determined by Moraes and Derbyshire (2002, 2003) by analyzing 39 polymorphic isozyme loci. Those results indicated that individuals within populations might be panmitic and that the diversity among populations was fairly high, being superior to what would be expected for groups of plants having a full-sib family structure, suggesting the existence of significant genetic drift and/or natural selection effects between populations. The within-sample gene diversity accounted for 66.12% of overall gene diversity, indicating a greater variability occurring within populations than among them. Similarly, Moraes and Derbyshire (2004) published results of the genetic structure of 11 natural populations (335 individuals) of *C. mandioccana* from southeastern Brazilian Atlantic rain forest. Results indicated that individuals within populations must be panmitic and that the diversity among populations is fairly high, being superior to what would be expected for groups of plants having a full-sib family structure in a single generation. In addition, the pronounced populational differentiation might be more related to drift and founder effects than to selection.

Phytochemical studies are another important source of information for around 40 *Cryptocarya* species, which have isolated and provided structural identification of more than 140 secondary metabolites. With regard to the Brazilian species, studies were conducted on *C. botelhensis*, *C. mandioccana*, *C. moschata*, and *C. saligna* and included intraspecific variability of secondary metabolites from *C. mandioccana* and *C. moschata*. In earlier phytochemical investigations of the essential oils of these species, the presence of linalool was reported in leaf oil of *C. moschata* and *C. aschersoniana* (current status: *C. mandioccana* and *C. moschata*, respectively; Moraes, 2005b), although the latter also contained β-myrcene, 1,8-cineol, and stereo-isomeric linalool oxides (Naves et al., 1963). Detailed

composition of essential oil from leaves of *C. mandioccana* has been determined by Telascrea et al. (2007), yielding the identification of 64 compounds with a predominance of isomeric sesquiterpenes with molecular weight of 204. The intraspecific chemical variability of essential oil obtained by steam distillation was evaluated within populations of trees growing at three separate locations in the state of São Paulo, Brazil. Three distinct chemical groups could be characterized on the basis of differences in the relative percentages of the three main sesquiterpenes from essential oil: CGB, BCG, and GCB (i.e., with a predominance of β-caryophyllene [C], germacrene-D [G], and bicyclogermacrene [B], respectively). Individuals from groups CGB and BCG were found more frequently in southern locations, while group GCB, with a predominance of germacrene, occurred more frequently in the northern region of the Atlantic rain forest. A comparison of essential oils from leaves of four species of *Cryptocarya* was reported by Telascrea et al. (2008). Monoterpenes were found to be the main constituents of essential oils from *C. moschata* and *C. botelhensis,* with a predominance of acyclic and menthane monoterpene skeletons in the former and pinane monoterpene skeletons in the latter. However, the major sesquiterpenes identified in essential oil from leaves of *C. mandioccana* belong to two main classes, from distinct sesquiterpene synthases, each associated with a different mode of cyclization of the C15-precursor, while the main constituents of essential oil from *C. saligna* were formed by C1-C11 cyclization, which is indicative of a preferential cyclization way of farnesyl diphosphate precursor in this species.

Phytochemical studies of the bark of *Cryptocarya mandioccana* have shown that styrylpyrones are the typical secondary metabolites present in this species (Cavalheiro and Yoshida, 2000), whereas flavonoid glycosides, as well as styrylpyrones, have been detected in leaves and fruits. The qualitative and quantitative intraspecific variability of these secondary metabolites has been determined by Nehme at al. (2002). A more detailed study on the polar chemical variability of flavonoids and styrylpyrones was undertaken by Nehme et al. (2008), who analyzed leaves of 57 trees of *C. mandioccana* from three sites of Atlantic rain forest in São Paulo state. The flavonoid glycosides profiles were very conservative in all individuals, with a predominance of quercetin. In addition, four chemotypes were recognized by qualitative and quantitative differences in the styrylpyrone composition. Chemotype F could be characterized by a predominance of flavonoid glycosides (F1–F6) and low content of styrylpyrones. Chemotypes FS1, FS2, and FS3 each presented at least one intense peak attributed to styrylpyrones, while differing from each other in the number of acetate units in their polyketides: in chemotype FS1, the most intense peak was attributed to deacetylcryptocaryalactone (S5); in chemotype FS2 there were three intense styrylpyrone peaks, which were attributed to cryptomoschatone E3 (S1), cryptomoschatone F1 (S4), and cryptomoschatone E1 (S6); and in chemotype FS3, the most intense peak was attributed to cryptomoschatone D1 (S2). The distribution of these chemotypes revealed inter- and intrapopulational chemical variability, with a predominance of trees with higher levels of styrylpyrones in southern regions with soils of higher K^+, Ca^{2+}, and Mg^{2+} content. The northern population of Ubatuba showed trees with a clear predominance of flavonoids (chemotype F) and a good correlation with lower levels of Mg^{2+}, K^+ and Ca^{2+}, suggesting some possible influence of soil nutrients on styrylpyrone profiles of *C. mandioccana*. However, evidence that chemical variability would also be under genetic control has been provided by some pairs of trees that presented different chemical profiles, in spite of being located just a few meters apart from each other. Moreover, the genetic studies by Moraes and Derbyshire (2004) and Moraes et al. (2007) have demonstrated that individuals of *C. madioccana* from different populations formed distinct genetic groups (among them the north and south groups) closely related to geographical origin. Furthermore, locus Skdh-2 was significantly related to production of quercetin-3-*O*-β-D-glucopyranoside (F2) and the diastereoisomers cryptofolione and cryptomoschatone E2 (S6/S7), indicating that shikimate dehydrogenase could affect differential regulation on these chemotypes of *C. mandioccana*. Moraes and Derbyshire (2004) have shown relatively weak genetic differentiation among large areas of sampled populations, which indicated no significant differences in genetic structure among different regions. Since the greatest environmental differences are related to the different regions, it is probable that selective differences were of little or no importance and that the fixation indexes were essentially measures of random drift due to endogamous mating in populations, and probably accidental differences in the founding individuals among the populations (Wahlund effect), which are largely smoothed out in the regions.

According to Wilf et al. (2016), understanding the extremely variable and complex angiosperm leaf architecture (shape and venation characters) is one of the most challenging problems in botany. Nevertheless, leaf features of the Lauraceae have long been reported and demonstrated to be helpful for identification of taxa, being used as taxonomic descriptors (Christophel and Rowett, 1996). This type of information is relatively scarce for the Brazilian species of the family, however, and therefore for the species of *Cryptocarya*.

Data on leaf venation of *Cryptocarya* species can be found in treatments of local floras or florulas, being usually restricted to information on the venation pattern of secondary veins and the "number of pairs of secondaries." Concerning the species treated here, such information has been recorded by Vattimo-Gil (1957) for collections from Monte Sinai and by Quinet and Andreata (2002) for collections from Nova Friburgo, Rio de Janeiro state; Pedralli (1987) for collections from Rio Grande do Sul state; Brotto et al. (2009) for collections from Paraná state; Gomes-Bezerra et al. (2011), for collections of the Federal District (Brasília); Barbosa et al. (2012), for collections from Santa Teresa, Espírito Santo state; and Poszkus Borrero et al. (2016), for collections from Misiones, Argentina. From these reports, it is possible to verify how constant these features are across a wider geographical range for each species and in different populations and/or environments.

Material and Methods

This study is based on the Brazilian species of *Cryptocarya* recognized in Moraes (2007), where a more detailed account on the species and specimens analyzed can be consulted. In that publication, narrow species concepts were used in order to maintain the boundaries among species. Nevertheless, in the particular case of *C. aschersoniana*, Moraes's concept has been more inclusive, since he had not evaluated in the field all the variability detected in herbarium collections, especially from the south of Brazil. Here, we kept discriminating specimens of the "true" *C. aschersoniana* from southern Brazil, Uruguay, and Argentina, from those determined by Moraes (2007) as *C.* aff. *aschersoniana* from some populations of São Paulo state (e.g., Base Ecológica da Serra do Japi [*Moraes 2243*] and Parque Estadual de Campos do Jordão [*Moraes 2403*, *Robim 588*]) and from Espírito Santo state (e.g., Linhares [*Moraes 2543*] and Santa Teresa [*Moraes 3242*]). Whenever available, herbarium leaf samples of at least four specimens of each species were used for this study, which are listed in Table 1. Most specimens are deposited in herbarium HRCB, and just a few are from samples taken from ALCB, CEPEC, HUEFS, MG, MO, NY, and RB (acronyms according to Thiers, 2020 [continuously updated]).

For description of basic venation patterns—that is, the major secondary vein framework—samples of entire leaves of all *Cryptocarya* species from Brazil were digitally X-rayed in a Faxitron® LX-60 cabinet X-ray system coupled to a computer with the software Faxitron DX version 1.0, where the images were captured using an X-ray exposure time of 19 seconds at a voltage of 30 kV. For illustration and description of the reticulation, closed-up images of the former leaves were captured with a magnification of about 10x by placing the leaves very close to the X-ray source.

For description of minor venation patterns—that is, the patterns of higher-order veins, areolations, and veinlets—we employed the following clearing technique. Leaf samples of 1 cm^2 were taken from the middle part of the lamina of mature leaves. To rehydrate the herbarized, dry leaf, the samples were boiled in water for about 10 min. Afterward, samples were soaked in a 20% solution of NaOH at room

Table 1. *Cryptocarya* species and voucher specimens analyzed in this study.

Species[a]	Voucher[b]
C. aff. *aschersoniana* Mez	*Moraes 2243, 2403* (HRCB)/SP, *Moraes 2543, 2544, 3242, 3696, 3735* (HRCB)/ES, *Robim 588* (HRCB)/SP
C. aschersoniana Mez	*Brotto 2547, 2550* (HRCB)/PR, *Klein 3187* (HRCB)/SC, *Moraes 2295, 2297* (HRCB)/SP, *Moraes 5362* (HRCB)/RS, *Moraes 5402* (HRCB)/PR
C. botelhensis P.L.R. Moraes	*Moraes 1252, 1254, 1264, 3349* (HRCB)/SP
C. citriformis (Vell.) P.L.R. Moraes	*Barreto 1784* (HRCB)/MG, *Folli 320, 6123* (HRCB)/ES, *Moraes 2154, 2456* (HRCB)/RJ, *Moraes 3199, 3712, 3746* (HRCB)/ES, *Paixão 17* (CEPEC)/BA
C. guianensis Meisn.	*Bondar 65* (RB)/BA, *Goulding 1117 (MG)/RO, Jardim 1263* (MO)/BA, *Pires s.n.* (NY 51511)/AP, *Prance 25443* (MG)/PA, *Thomas 4752* (MG)/MT
C. mandioccana Meisn.	*Moraes 2505, 4099* (HRCB)/SP, *Moraes 3509* (HRCB)/MG, *Santos 2811* (CEPEC)/BA
C. micrantha Meisn.	*Moraes 2155, 2458, 2468, 2469* (HRCB)/RJ, *Moraes 2449* (HRCB)/SP
C. moschata Nees & Mart.	*Bertoni 425* (HRCB)/SP, *Hoehne s.n.* (MO 3600631)/SP, *Moraes 2237, 2257, 2259, 2264, 3491* (HRCB)/SP, *Moraes 2277* (HRCB)/MG, *Pereira PCD 1753* (CEPEC)/BA
C. riedeliana P.L.R. Moraes	*Braga s.n.* (RB 358589)/RJ, *Farias 80* (RB)/RJ, *Jardim 2104* (ALCB)/BA, *Kollmann 4413* (HRCB)/ES, *Moraes 3126* (HRCB)/BA, *Moraes 4716* (HRCB)/ES
C. saligna Mez	*Folli 88* (ESA)/ES, *Magnago 1471* (HRCB)/ES, *Moraes 3182, 3226, 3682* (HRCB)/ES
C. sellowiana P.L.R. Moraes	*Luz 196* (HRCB)/MG
C. subcorymbosa Mez	*Moraes 5161* (HRCB)/SP
C. velloziana P.L.R. Moraes	*Braga s.n.* (RB 358585)/RJ, *Lombardi 7150* (HRCB)/BA, *Lombardi 8950* (HRCB)/MG, *Moraes 2621* (HUEFS)/ES, *Moraes 3227* (HRCB)/ES
C. wiedensis P.L.R. Moraes	*Kollmann 2464* (HRCB)/ES

a) Species determination by the first author, according to Moraes (2007).

b) Samples from vouchers deposited in several herbaria, acronyms indicated in parentheses, followed by abbreviations of Brazilian states: AP, Amapá; BA, Bahia; ES, Espírito Santo; MG, Minas Gerais; MT, Mato Grosso; PA, Pará; PR, Paraná; RJ, Rio de Janeiro; RO, Rondônia; RS, Rio Grande do Sul; SC, Santa Catarina; SP, São Paulo.

temperature for 12–24 hours, then rinsed three times with tap water. The samples were decolorized with household bleach (50%) for 12 hours, then thoroughly washed (3 times) with distilled water. Dehydration of the cleared samples was done in alcohol series before staining them in 1% safranin in 50% ethanol for 1 min. They were mounted on microscope slides in Entellan.® Photomicrographs were obtained with a photomicroscope (Leica DM500) coupled with a camera (Leica ICC50), using the software LAS (Leica Application Suite) EZ v.3.0.0.

An interactive multiple-entry key was created using the program *Lucid* 3 v3.5 (https://www.lucidcentral.org/), based on a matrix of 12 leaf venation characters, with a total of 30 states and 14 taxa (Table 2). A dichotomous key was built from this matrix.

Terminology

Two basic venation patterns occur within the Lauraceae (Christophel and Rowett, 1996): (1) pinnate (Hickey, 1973, 1979; Dilcher, 1974) or penninerved (Hyland, 1989), in which there is a central midvein (primary vein) from which arise lateral veins; and (2) acrodromous (Hickey, 1973, 1979; Dilcher, 1974) or triplinerved (Hyland, 1989), in which a basal pair of veins is strengthened to the point of being similar in size to the midvein. For convenience of comparison with other works on the Lauraceae, we have used Hyland's terminology. The nature of the midvein course can be monopodial, where its trunk is not deflected by lateral veins, or sympodial, where the midvein axis is deflected at each branch point (Ellis et al., 2009).

For the pattern of secondary veins, Hickey's classification (1973, 1979) is adopted here. For Lauraceae leaves, the relevant categories include (1) brochidodromous, in which the secondaries join together in a series of prominent arches; and (2) eucamptodromous, in which the secondaries are upturned, gradually diminish apically inside the margin, and are connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops. Cases in which proximal secondaries are eucamptodromous but distal secondaries form loops of secondary gauge (subcategory "Eucamptodromous becoming brochidodromous distally"; Ellis et al., 2009) are termed here eucamptodromous-brochidodromous. An additional category was described by Pole (1991) and labelled by Christophel and Rowett (1996) as pseudobrochidodromous, in which the leaf appears brochidodromous but the loops are formed by strengthened tertiary veins and not by the secondary veins themselves.

The number of secondary veins per side of the midvein is recorded for each species, rather than the "number of pairs of secondary veins," as some species have different numbers of veins on either side of the midvein; moreover, when counting secondary veins, the apical 10% of the lamina is excluded, since veins there are generally so much smaller as to make determining relative orders difficult (Christophel and Rowett, 1996). The major features of secondary venation proposed by Klucking (1987) are adopted here; we list only the subcategories observed from the analyzed material: (1) the nature of the course of the secondary vein: (a) straight—the secondary vein extends laterally in an essentially straight line; or (b) curved—the secondary vein curves gently apically as it extends laterally from the midvein; (2) the spacing of the secondary veins along the midvein: (a) broad—secondary veins are noticeably spaced more than 1/10 the length of the leaf apart; (b) medium—secondary veins are spaced about 1/10th the length of the leaf apart; or (c) narrow—secondary veins are noticeably less than 1/10th the length of the leaf apart; and (3) the angle between the secondary course and the midvein: (a) high—most of the lateral course of the secondary veins is oriented at 55 degrees or more to the midvein; (b) moderate—most of the lateral course of the secondary veins is oriented at about 45 degrees to the midvein; or (c) low—most of the lateral course of the secondary veins is oriented at 40 degrees or less to the midvein. The angle of secondary courses usually varies from the apex to the base of the leaf, but it is more or less constant in the middle region of the leaf, for each species (Coe-Teixeira, 1980). For this reason, in the present study the angles of secondary courses are recorded from the middle part of the lamina.

Regarding tertiary-order veins, Christophel and Rowett (1996) recognized two major types for the Lauraceae: (1) percurrent, in which the tertiary veins directly connect two adjacent secondary veins; this category can be divided into two further categories: (a) strongly percurrent, having a ladder-like appearance; and (b) weakly percurrent, appearing to meander or arch in their course; and (2) reticulate, in which a pattern of tertiary veins anastomoses with other tertiary or secondary veins and does not directly connect two secondary veins; reticulate tertiary veins can be (a) orthogonal, forming mainly right-angled anastomoses; or (b) random, in which they are either curved or form a variety of anastomoses.

As for higher-order venation patterns, the discriminating character is the number and relative size of vein orders in the reticulum, and the veinlet pattern (Nishida and Christophel, 1999). According to Christophel and Rowett (1996), "veins of leaves keep dividing into smaller, higher orders, until ultimately they form small enclosed areas called areoles which fairly uniformly cover the lamina surface in a pattern often referred to as the reticulum." The areoles themselves are described in terms of (1) development: (a) well developed, forming meshes of relatively consistent size and shape; (b) imperfect, with meshes of irregular shape, more or less variable in size; or (c) incompletely closed meshes, in which one or more sides of the mesh is not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape; (2) arrangement: (a) random, areoles showing no preferred orientation; or (b) oriented, areoles having a similar alignment or pattern of arrangement within blocks or domains; (3) shape: (a) quadrangular, or (b) polygonal, here defined as having more than 4 sides; (4) size: (a) very large, > 2 mm; (b) large, 1–2 mm; (c) medium, 0.3–1.0 mm; or (d) small, < 0.3 mm (Hickey, 1973, 1979; Dilcher, 1974). With regard to the development and size of the areoles, the appearance of the minor venation pattern can be divided into two categories: (1) fine—the highest vein order is sixth or more, and areoles are usually less than 0.5–0.7 mm diam.; and (2) coarse—the highest vein order is less than fifth, with larger areoles over 1.0 mm diam. In Hickey's terminology (1973, 1979), the veinlets

TABLE 2. Leaf venation features of Brazilian *Cryptocarya*.

SPECIES	NUMBER 2RY VEINS	VENATION PATTERN[a]	MIDVEIN[b]	NATURE 2RY COURSE[c]	SPACING 2RY VEINS[d]	ANGLE 2RY COURSE[e]	3RY VEINS[f]	RETICULUM[g]	DEVELOPMENT[h]	AREOLE SHAPE[i]	SIZE[j]	VEINLET[k]	FIGURE
C. aff. *aschersoniana*	5–12	BRO/PB	MON	STR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	4A–H
C. aschersoniana	5–12	EU-BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG/MOD	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	1A, 2A, 4I–N
C. botelhensis	4–8	EU-BRO/BRO	MON/SYM	STR/CUR	BRO/MED	HIG/MOD	RET, RAN	FIN	IMP/INC	POL	MED/LAR	BON/BTW/DEN	1B, 2B, 4O–P
C. citriformis	6–9	EU-BRO/PB	MON/SYM	CUR/STR	BRO	HIG/MOD	RET, RAN/ PER, weakly	FIN	WDE	POL/QUA	SMA	ABS/[LIN]	1C, 2C, 4Q–T
C. guianensis	6–12	EU-BRO/ BRO/PB	MON	CUR/STR	BRO	HIG/MOD	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	1D, 2D, 4U–X
C. mandioccana	5–9	EU-BRO	MON/SYM	CUR/STR	BRO/MED	HIG-[LOW]	RET, RAN/ PER, weakly	FIN	WDE/IMP	POL/QUA	SMA	LIN/BON/BTW/DEN	1E, 2E, 4Y–B’
C. micrantha	7–12	EU-BRO/PB	MON/SYM	STR/CUR	BRO-NAR	HIG/MOD	RET, RAN	FIN	IMP/WDE	POL/QUA	MED/SMA	ABS/LIN/BON/BTW/DEN	1F, 2F, 5A–H
C. moschata	5–12	EU-BRO/ BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/CUR/BON/BTW	1G, 2G, 5I–L
C. riedeliana	5–11	EU-BRO/PB	MON/SYM	CUR/STR	BRO-NAR	MOD/LOW	RET, RAN	FIN	WDE/IMP	POL/QUA	SMA/MED	LIN/BON/DEN	1H, 2H, 5M–P
C. saligna	4–14	EU-BRO/PB/ BRO	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	MED/SMA	ABS/LIN/BTW/DEN	1I, 2I, 5Q–T
C. sellowiana	6–10	EU-BRO	MON/SYM	CUR	BRO	HIG/MOD	RET, RAN	FIN	WDE/IMP	POL	SMA/MED	DEN	1J, 2J, 5U–V
C. subcorymbosa	4–10	BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	QUA/POL	SMA	ABS/LIN	1K, 2K, 5W–X
C. velloziana	6–11	EU-BRO/PB/ BRO	MON/SYM	CUR/STR	BRO	HIG/MOD	RET, RAN	FIN	WDE	POL	SMA	ABS/LIN/BON/DEN	1L, 2L, 5Y–B’
C. wiedensis	4–7	BRO	MON/SYM	STR/CUR	BRO	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN	1M, 3A–C

a) Venation pattern (major secondary vein framework): EU-BRO, mixed eucamptodromous-brochidodromous; BRO, brochidodromous; PB, pseudobrochidodromous.

b) Nature of the midvein course: MON, monopodial; SYM, sympodial.

c) Nature of the secondary course: STR, straight; CUR, curved.

d) Spacing of secondary veins along the midrib: BRO, broad (> 1/10th the length); MED, medium (≈ 1/10th the length); NAR, narrow (< 1/10th the length).

e) Angle secondary course makes with the midrib: HIG, high (≥ 55°); MOD, moderate (≈ 45°); LOW, low (≤ 40°).

f) Tertiary veins: RET, RAN, random reticulate; PER, percurrent reticulate.

g) Reticulum (minor venation pattern—pattern of higher-order veins): FIN, fine (the highest vein order is sixth or more, and areoles are usually less than 0.5–0.7 mm diam.); COA, coarse (the highest vein order is less than fifth with larger areoles over 1.0 mm diam.).

h) Areole development: WDE, well developed; IMP, imperfect; INC, incomplete.

i) Areole shape: QUA, quadrangular; POL, polygonal.

j) Areole size: LAR, large (1–2 mm); MED, medium (0.3–1.0 mm); SMA, small (< 0.3 mm).

k) Veinlet: ABS, absent; LIN, linear; CUR, curved; BON, branched once; BTW, branched twice; DEN, dendritic.

are freely ending ultimate veins (FEV; i.e., the veins of the finest gauge) of the leaf and veins of the same order, which occasionally cross areoles to become connected distally. They can be classed as (1) veinlets none; (2) simple, without branches, either (a) linear or (b) curved; or (3) branched, giving rise to ramifications by dichotomizing (a) once, (b) twice, (c) thrice, etc. (= dendritic, i.e., branching unequally) (Hickey, 1973, 1979; LAWG, 1999; Ellis et al., 2009).

Results

All leaf venation characters and states are summarized in Table 2, with respective figures for each taxon indicated. Fig. 1 shows X-ray images of an entire leaf of each species, and Fig. 2–3 show closed up images of the intercostal region from the middle part of the leaf. Fig. 3–5 show photomicrographs of the reticulum and areoles from cleared leaves of each taxon.

All species show leaves with the secondary veins forming marginal loops variously prominent, which fall into the various categories of brochidodromous venation. Most species present leaves predominantly with proximal secondaries eucamptodromous becoming brochidodromous distally. Only *Cryptocarya wiedensis* (Fig. 1M) presents leaves strictly brochidodromous; they

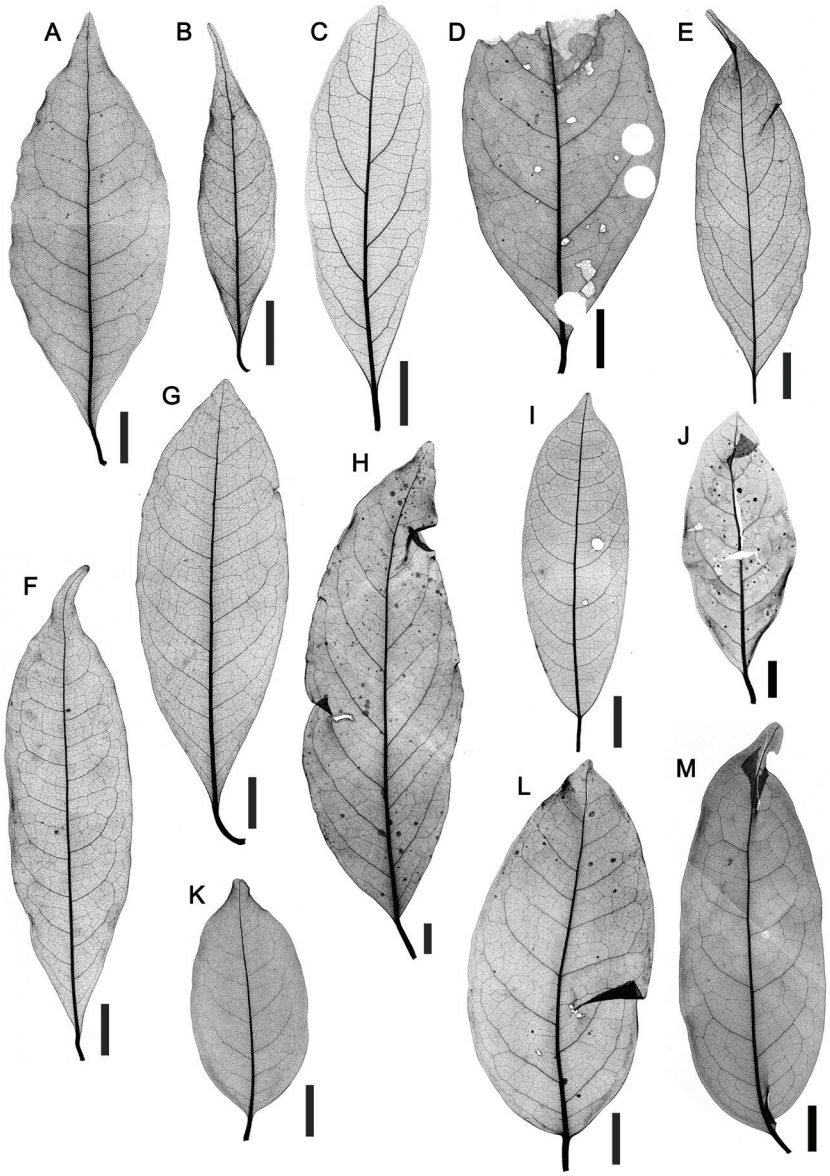

Figure 1. X-ray images of *Cryptocarya* leaves. **A,** *C. aschersoniana* Mez (*Moraes 5362*); **B,** *C. botelhensis* P.L.R. Moraes (*Moraes 1254*); **C,** *C. citriformis* (Vell.) P.L.R. Moraes (*Moraes 2456*); **D,** *C. guianensis* Meisn. (*Prance 25443*); **E,** *C. mandioccana* Meisn. (*Moraes 4099*); **F,** *C. micrantha* Meisn. (*Moraes 2155*); **G,** *C. moschata* Nees & Mart. (*Moraes 2259*); **H,** *C. riedeliana* P.L.R. Moraes (*Kollmann 4413*); **I,** *C. saligna* Mez (*Magnago 1471*); **J,** *C. sellowiana* P.L.R. Moraes (*Luz 196*); **K,** *C. subcorymbosa* Mez (*Moraes 5161*); **L,** *C. velloziana* P.L.R. Moraes (*Lombardi 8950*); **M,** *C. wiedensis* P.L.R. Moraes (*Kollmann 2464*). Bars = 1 cm.

are mixed brochidodromous and pseudobrochidodromous in *C*. aff. *aschersoniana* and *C*. *subcorymbosa* (Fig. 1K). Monopodial midveins are constant only in *Cryptocarya* aff. *aschersoniana* and *C*. *guianensis* (Fig. 1D), while in the remaining species the midveins are slightly sympodial mainly from the middle part of the leaf toward the apex, at least in some leaves (e.g. Fig. 1A,B,J,M).

The number of secondary veins per side of the midvein varies between species with a relatively small number (up to 7 [*Cryptocarya wiedensis*] or 8 [*C*. *botelhensis*]), and those with 9 to as many as 14 secondaries, as in *C*. *saligna*. Only *C*. *sellowiana* (Fig. 1J) has leaves with secondary veins strictly curved, whereas they are strictly straight in *C*. aff. *aschersoniana*. Another five species have leaves with mainly curved secondaries mixed with straight ones (Fig. 1C,D,E,H,L), while in another seven species they are mainly straight mixed with curved ones (Fig. 1A,B,F,G,I,K,M).

Five species (*Cryptocarya citriformis*, *C*. *guianensis*, *C*. *sellowiana*, *C*. *velloziana*, and *C*. *wiedensis*) have leaves with the secondary veins broadly spaced, whereas they are mixed broadly and medium-spaced in another seven species, or mixed broadly, medium-, and narrowly spaced in *C*. *micrantha* and *C*. *riedeliana*. Five species (*Cryptocarya* aff. *aschersoniana*, *C*. *moschata*, *C*. *saligna*, *C*. *subcorymbosa*, and *C*. *wiedensis*) have leaves with secondary veins diverging at strictly high angles to the midvein, whereas in *C*. *riedeliana* (Fig. 1H) their courses run at moderate and low angles, and in the remaining species the courses are mainly highly to moderately angled.

The tertiary veins are randomly reticulate in all species (e.g., Fig. 2A,B,D,F–L; 3A), except for *Cryptocarya citriformis* (Fig. 2C) and *C*. *mandioccana* (Fig. 2E), whose tertiary veins vary from randomly reticulate to weakly percurrent. All species have a fine reticulum. Areoles vary

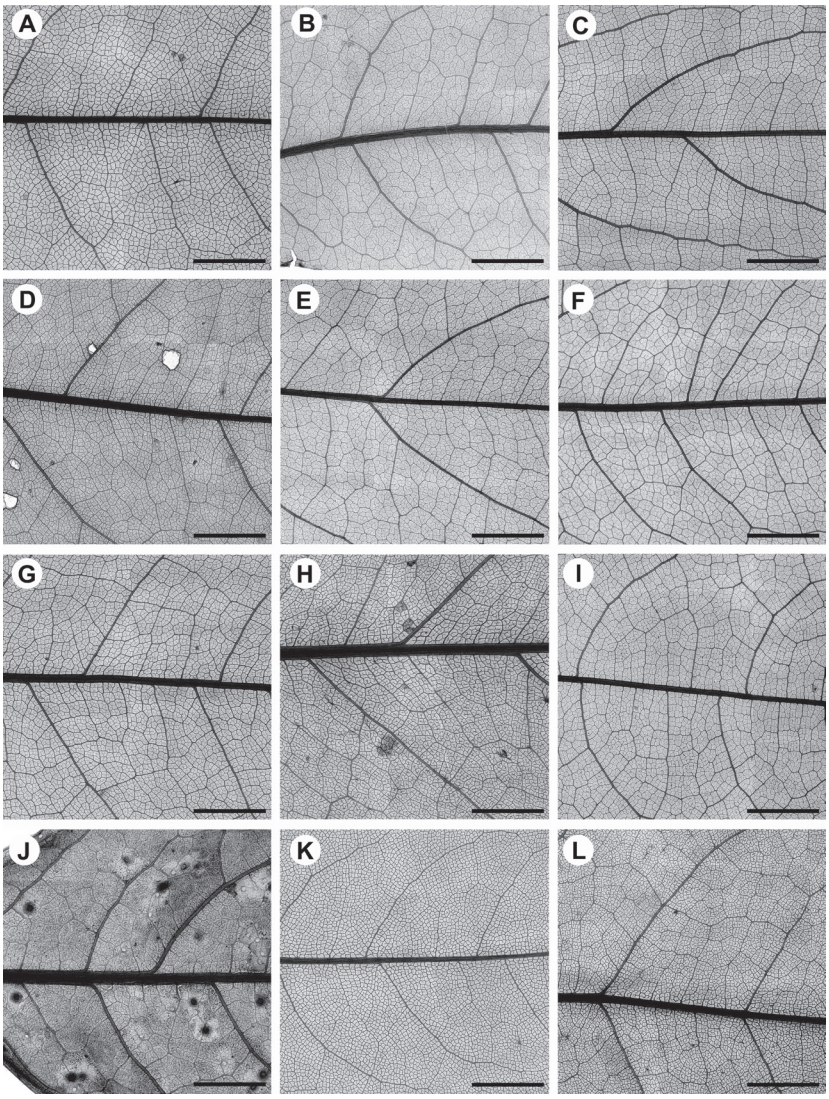

FIGURE 2. X-ray images (closed up) of the leaf venation of *Cryptocarya*. **A,** *C*. *aschersoniana* Mez (*Moraes 5362*); **B,** *C*. *botelhensis* P.L.R. Moraes (*Moraes 3349*); **C,** *C*. *citriformis* (Vell.) P.L.R. Moraes (*Moraes 2456*); **D,** *C*. *guianensis* Meisn. (*Prance 25443*); **E,** *C*. *mandioccana* Meisn. (*Moraes 4099*); **F,** *C*. *micrantha* Meisn. (*Moraes 2458*); **G,** *C*. *moschata* Nees & Mart. (*Moraes 2259*); **H,** *C*. *riedeliana* P.L.R. Moraes (*Kollmann 4413*); **I,** *C*. *saligna* Mez (*Magnago 1471*); **J,** *C*. *sellowiana* P.L.R. Moraes (*Luz 196*); **K,** *C*. *subcorymbosa* Mez (*Moraes 5161*); **L,** *C*. *velloziana* P.L.R. Moraes (*Lombardi 8950*). Bars = 5 mm.

among and within taxa in terms of development and size. Nine species have areoles strictly well developed (Fig. 2A,C,D,G,I,K,L; 3A–C; 4A–N,Q–X; 5I–L,Q–T,W–B'), whereas the other species present areoles with two types of development, with the one indicated first in Table 2 being predominant (Fig. 2B,E,F,H,J; 4O,P,Y–B'; 5A–H,M–P,U,V). Areoles strictly small are present in nine species, whereas they are mixed medium and small in *Cryptocarya micrantha* (Fig. 2F; 5A–H), *C. riedeliana* (Fig. 2H; 5M–P), *C. saligna* (Fig. 2I; 5Q–T), and *C. sellowiana* (Fig. 2J; 5U,V), or mixed medium and large in *C. botelhensis* (Fig. 2B; 4O,P). Areoles strictly or predominantly polygonal are found in all species, except for *C. subcorymbosa* (Fig. 2K; 5W–X), whose areoles are predominantly quadrangular.

With regard to veinlets, *Cryptocarya citriformis* (Fig. 2C; 4Q–T), *C. subcorymbosa* (Fig. 2K; 5W–X) and *C. wiedensis* (Fig. 3A–C) present areoles with mixed absent and simple linear veinlets, while only *C. sellowiana* (Fig. 2J; 5U,V) presents veinlets strictly dendritic. In the remaining species, areoles have mixed veinlets of several sorts, involving absent, linear, curved, branched once and/or twice, and/or dendritic ones (Fig. 4A–P,U–B'; 5A–T,Y–B').

Altogether, these characters and states allow recognition of the studied taxa, which can be determined through the following dichotomous identification key.

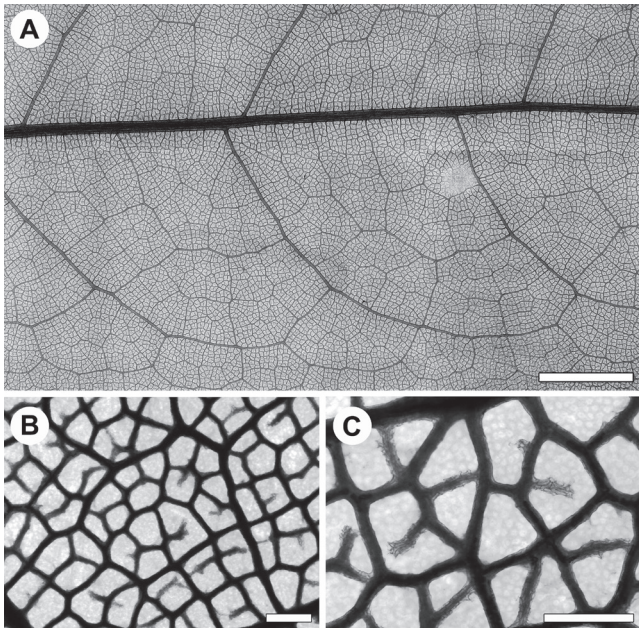

FIGURE 3. X-ray image (close up) and photomicrographs of *Cryptocarya wiedensis* P.L.R. Moraes (*Kollmann 2464*). Bars = 5 mm (A), 250 μm (B–C).

KEY TO THE BRAZILIAN SPECIES OF *CRYPTOCARYA*, BASED ON LEAF VENATION CHARACTERS

1a. Veinlets strictly dendritic . . . . . *C. sellowiana*
1b. Veinlets other 2
2a. Veinlets mixed absent and linear 3
2b. Veinlets other 5
3a. Venation eucamptodromous-brochidodromous to pseudobrochidodromous, 6–9 secondary veins per side of the midvein, course of secondary veins predominantly curved, spacing of secondary veins broad, angle of secondary courses mixed high and moderate, tertiary veins mixed randomly reticulate and weakly percurrent . . . . . *C. citriformis*
3b. Venation strictly brochidodromous to mixed brochidodromous and pseudobrochidodromous 4
4a. 4–10 secondary veins per side of the midvein, spacing of secondary veins mixed broad and medium, shape of areoles predominantly quadrangular . . . . . *C. subcorymbosa*
4b. 4–7 secondary veins per side of the midvein, spacing of secondary veins broad, shape of areoles predominantly polygonal . . . . *C. wiedensis*
5a. Areoles strictly small (< 0.3 mm) 6
5b. Areoles other 11
6a. Areoles strictly well developed 7
6b. Areoles mixed well developed and imperfect . . . . . *C. mandioccana*
7a. Midvein strictly monopodial 8
7b. Midvein sympodial toward the apex, at least in some leaves 9
8a. Venation brochidodromous to pseudobrochidodromous, course of secondary veins strictly straight, spacing of secondary veins mixed broad and medium, angle of secondary veins strictly high . . . . . *C.* aff. *aschersoniana*
8b. Venation eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous, course of secondary veins predominantly curved, spacing of secondary veins broad, angle of secondary veins mixed high and moderate . . . . . *C. guianensis*
9a. Course of secondary veins predominantly curved, spacing of secondary veins broad, areoles polygonal . . . . . *C. velloziana*
9b. Course of secondary veins predominantly straight, spacing of secondary veins mixed broad and medium, areoles mixed polygonal and quadrangular 10
10a. Venation eucamptodromous-brochidodromous to pseudobrochidodromous, angle of secondary veins mixed high and moderate, veinlets mixed absent and linear and branched once . . . . . *C. aschersoniana*
10b. Venation eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous, angle of secondary veins strictly high, veinlets mixed absent and linear and curved and branched once and twice . . . . . *C. moschata*
11a. Areoles mixed medium (0.3–1.0 mm) and large (1–2 mm) . . . . . *C. botelhensis*
11b. Areoles mixed medium (0.3–1.0 mm) and small (< 0.3 mm) 12
12a. Areoles strictly well developed . . . . . *C. saligna*
12b. Areoles mixed well developed and imperfect 13
13a. 7–12 secondary veins per side of the midvein, course of secondary veins predominantly straight, angle of secondary veins mixed high and moderate . . . . . *C. micrantha*
13b. 5–8(–11) secondary veins per side of the midvein, course of secondary veins predominantly curved, angle of secondary veins mixed moderate and low . . . . . *C. riedeliana*

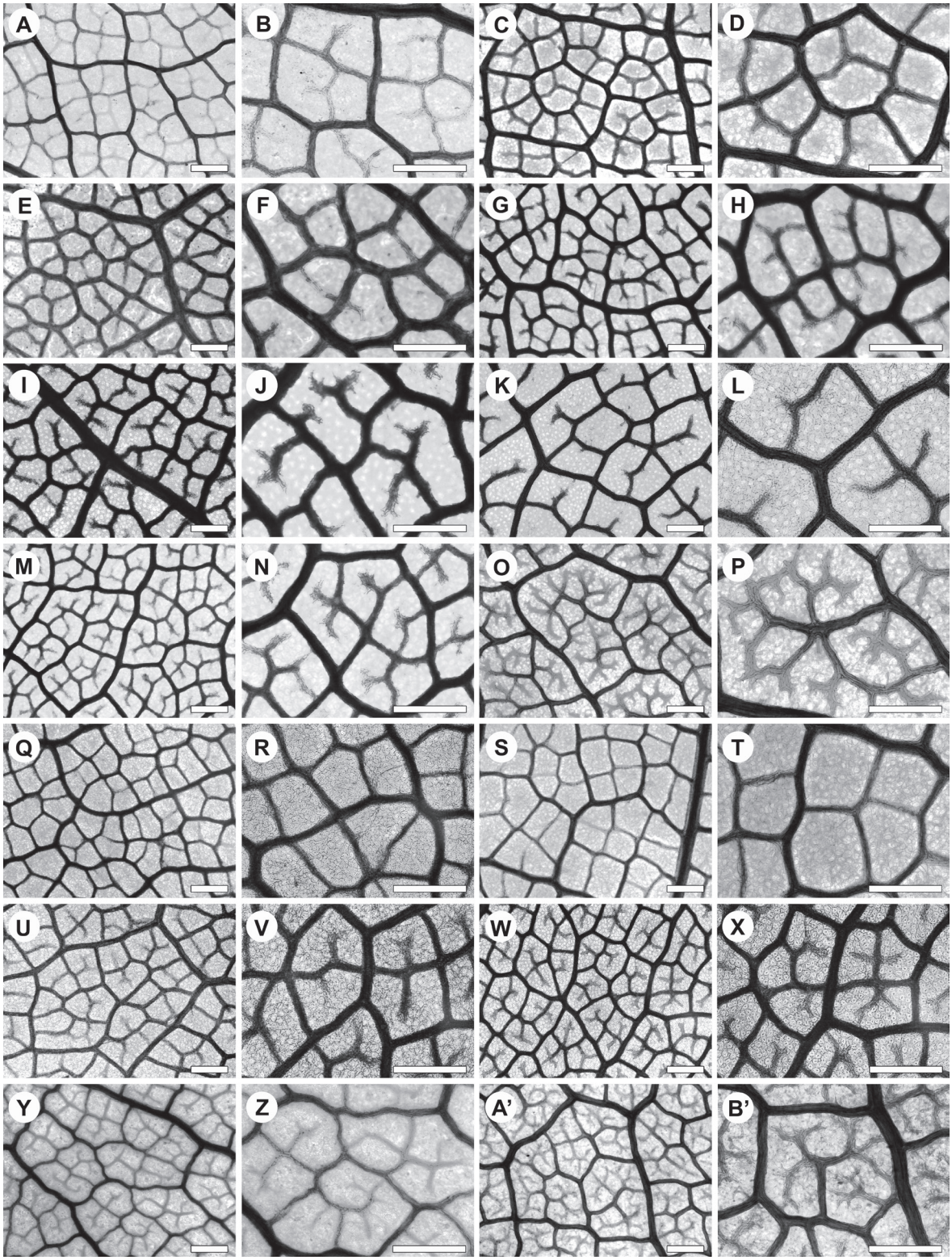

FIGURE 4. Photomicrographs of *Cryptocarya* leaves. **A–B,** *C*. aff. *aschersoniana* Mez (*Moraes 2243*); **C–D,** *C*. aff. *aschersoniana* Mez (*Moraes 2543*); **E–F,** *C*. aff. *aschersoniana* Mez (*Moraes 3242*); **G–H,** *C*. aff. *aschersoniana* Mez (*Robim 588*); **I–J,** *C*. *aschersoniana* Mez (*Moraes 2295*); **K–L,** *C*. *aschersoniana* Mez (*Moraes 5362*); **M–N,** *C*. *aschersoniana* Mez (*Moraes 5402*); **O–P,** *C*. *botelhensis* P.L.R. Moraes (*Moraes 3349*); **Q–R,** *C*. *citriformis* (Vell.) P.L.R. Moraes (*Moraes 2154*); **S–T,** *C*. *citriformis* (Vell.) P.L.R. Moraes (*Moraes 3199*); **U–V,** *C*. *guianensis* Meisn. (*Prance 25443*); **W–X,** *C*. *guianensis* Meisn. (*Thomas 4752*); **Y–Z,** *C*. *mandioccana* Meisn. (*Moraes 3509*). **A'–B',** *C*. *mandioccana* Meisn. (*Moraes 4099*). Bars = 250 μm.

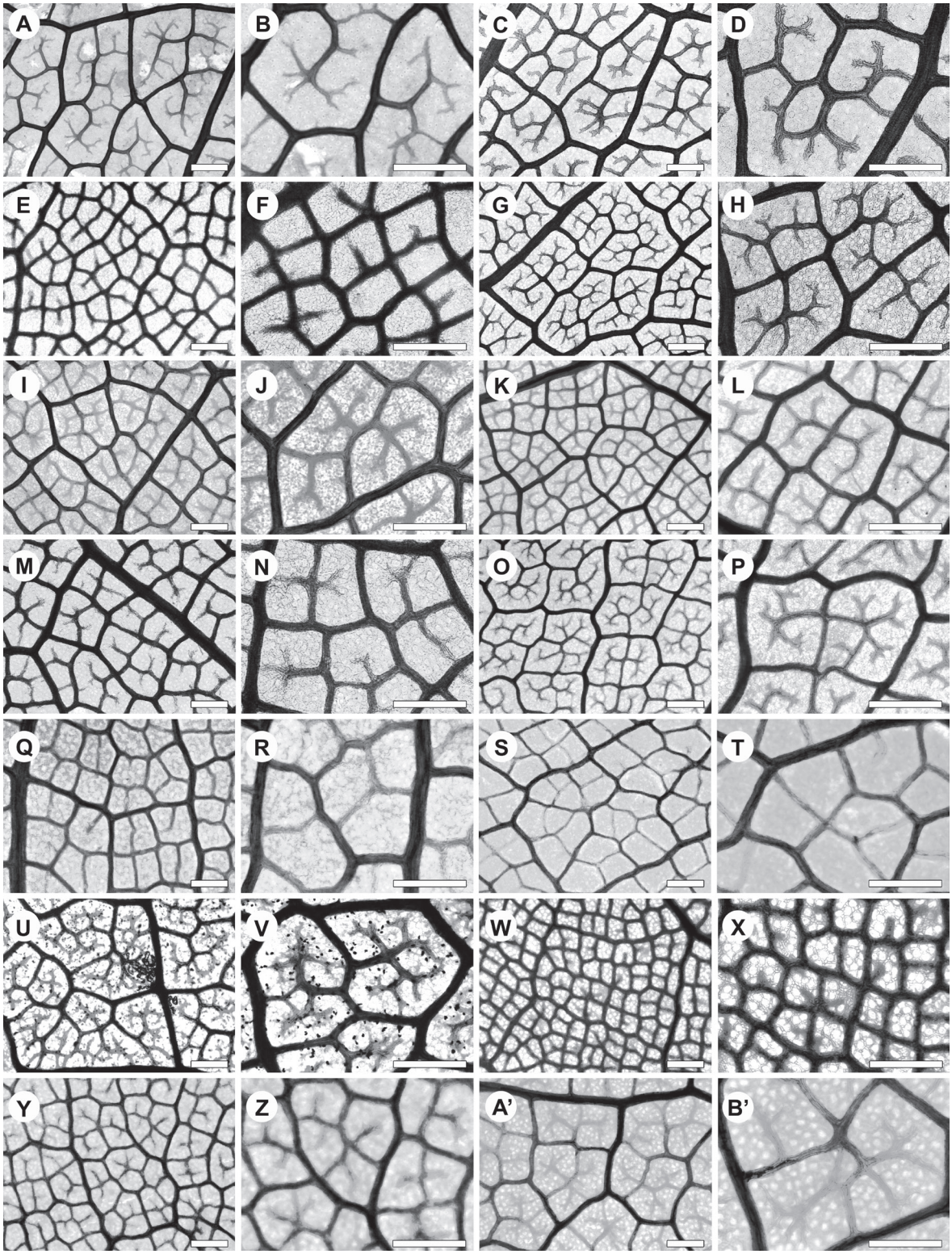

FIGURE 5. Photomicrographs of *Cryptocarya* leaves. **A–B,** *C. micrantha* Meisn. (*Moraes 2155*); **C–D,** *C. micrantha* Meisn. (*Moraes 2449*); **E–F,** *C. micrantha* Meisn. (*Moraes 2458*); **G–H,** *C. micrantha* Meisn. (*Moraes 2468*); **I–J,** *C. moschata* Nees & Mart. (*Moraes 2259*); **K–L,** *C. moschata* Nees & Mart. (*Moraes 2264*); **M–N,** *C. riedeliana* P.L.R. Moraes (*Kollmann 4413*); **O–P,** *C. riedeliana* P.L.R. Moraes (*Moraes 4716*); **Q–R,** *C. saligna* Mez (*Magnago 1471*); **S–T,** *C. saligna* Mez (*Moraes 3226*); **U–V,** *C. sellowiana* P.L.R. Moraes (*Luz 196*); **W–X,** *C. subcorymbosa* Mez (*Moraes 5161*); **Y–Z,** *C. velloziana* P.L.R. Moraes (*Lombardi 8950*). **A'–B',** *C. velloziana* P.L.R. Moraes (*Moraes 3227*). Bars = 250 μm.

Discussion

The most comprehensive study on leaf venation of Lauraceae has been undertaken by Klucking (1987), in the second volume of his series of leaf architectural atlases. According to Klucking, since many individual leaves may have one kind of venation in the basal part of the leaf, another kind in the middle part of the leaf, and a third kind in the upper part, each of these types of venation—the basal, middle, and apical—have different characteristics and are distinct. These kinds of venation are distinguished by the nature of the secondary venation and the type of intercostal venation, as the secondary venation of a leaf begins to form in the basal part of the leaf and develops progressively apically or acropetally. Consequently, each of these types of venation is formed during a different phase of development, with the venation in the basal part of the leaf formed first (Early Phase Venation), that in the middle part of the leaf next (Middle Phase Venation), and that in the apical part last (Late Phase Venation). Since the three types of venation are usually not present on a leaf in equal amounts, the venation pattern for the leaf has been named by Klucking after the dominant type of venation (i.e., presence on half the leaf or more).

For species of *Cryptocarya*, Klucking (1987) examined leaves of 245 species, from which specimens of 49 species were cleared for description. Leaves of another 13 species of *Ravensara* were also examined, from which specimens of 6 species were cleared for description. From Brazil, only *C. aschersoniana* was cleared from the collection of "*L. B. Smith and R. Klein 7528*, Santa Catarina, Brazil, UC M080142; plate 44, fig. 1" (also B 10 0002525, F, R, RB00128594, US01350763), being classified as having the "Predominant Venation Pattern," that is, "Early Phase Pinnate Venation dominant with small amounts of Middle Phase and Late Phase Venation present in the apical part of the leaf... most leaves with 8 to 10 pairs of secondary veins, courses curved or geniculate, curving sharply distally at closure and merging into a marginal looping; secondary courses running at low or moderate angles, spacing broad, narrow or a mixture of broad and narrow." Pedralli (1987) reported the leaves as brochidodromous, with secondary veins oriented at 45–60 degrees to the midvein (from specimens treated by him as *C. aschersoniana*) or with secondary veins oriented at 30–60 degrees to the midvein (from specimens treated by him as *C. moschata*). In Moraes (2007, thus including specimens of *C.* aff. *aschersoniana*), leaves were described as having camptodromous-brochidodromous venation, 5–12 secondary veins per side of the midvein, but in Brotto et al. (2009) as having 6–10 pairs of secondaries. Poszkus Borrero et al. (2016) recorded the leaves as brochidodromous, 7–11 pairs of secondary veins (vs. 6–12 pairs in Tressens, 1997), areoles quadrangular to polygonal, and veinlets linear to branched once. Here, our results corroborate the findings of Moraes et al. (2021), which showed that specimens from Linhares (*C.* aff. *aschersoniana*), despite their morphological similarity with those from southern Brazil (*C. aschersoniana*), partially match these former descriptions of the latter taxon, mainly disagreeing with the nature of the secondary veins (courses, angles, and spacing) as indicated by Klucking (1987). Evidence provided by DNA sequences prepared by Suganuma (2012), Rohwer et al. (2014), and Bolson et al. (2015) further indicates that at least the specimens from Espírito Santo, which have been formerly treated by Moraes (2007) as *C.* aff. *aschersoniana*, actually belong to *C. wiedensis*, according to the phylogenies inferred by Rohwer et al. (2014) and Carter (2017). Moreover, evidence provided by discriminant and cluster analyses based on isozymic data (Moraes, 2005a; P. L. R. Moraes, unpubl.) have shown that the populations of Serra do Japi and Campos do Jordão had genetic support to be treated as *C.* aff. *aschersoniana* (by Moraes, 2007), since they were clearly different from those belonging to *C. botelhensis*, *C. mandioccana*, and *C. moschata* (later also corroborated by the DNA sequences prepared by Suganuma, 2012).

With regard to *Cryptocarya botelhensis*, leaves were originally described by Moraes (2007) as having a brochidodromous venation pattern. However, they are better classified here as having mixed eucamptodromous-brochidodromous and brochidodromous venation.

Leaves of *Cryptocarya citriformis* were described by Kostermans (1937) (as *C. minima* Mez) and by Moraes (2007) as having camptodromous-brochidodromous venation, with 6–9 secondary veins per side of the midvein. Leaves of Bahian specimens are slightly different from those studied by Moraes et al. (2021) from specimens of Linhares. The leaves in the former have secondary veins broadly to narrowly spaced (vs. broadly), and courses highly to moderately angled (vs. highly) to the midvein. Nevertheless, the species remains poorly collected, which undermines the evaluation of its real variability. Regardless, it is the only American species of *Cryptocarya*, along with *C. mandioccana*, that shows some leaves with tertiary venation with a weakly defined percurrency. However, it is quite different from the degree of percurrency presented by many species of the genus, which often exhibit clearly scalariform tertiary venation. This organization of the tertiary venation has been used in *Cryptocarya* species identification (de Kok, 2016) in a number of studies: Christophel and Rowett (1996) described the leaf venation of 48 species of *Cryptocarya* from Australia (46 or 47 species respectively treatened by Hyland [1989] and Le Cussan et al. [2007], and 1 undescribed species), from which 32 species presented tertiary veins percurrent; and 14 out of 22 New Caledonian species of *Cryptocarya* have leaves with tertiary veins percurrent (Kostermans, 1974; Munzinger and McPherson, 2016). Leaves with tertiary veins percurrent to scalariform were found in 21 species from the Indian subcontinent (Gangopadhyay and Chakrabarty, 2005; Gangopadhyay, 2006, 2008; Bachan et al., 2018; Fasila et al., 2020); 14 out of 17 species from Thailand and Indochina (de Kok, 2015; Zhang et al., 2020); 16 out of 17 species from Peninsular Malaysia, where only 2 species feature a tertiary venation that could be classified as reticulate (i.e., *C. enervis* Hook.f. and *C. malayana* de Kok; Kostermans, 1975; de Kok, 2016); 12 out of 40 species from Madagascar (Kostermans, 1939, 1950, 1957a, 1958; van der Werff, 2008, 2013, 2017); 2 out

of 7 species from South Africa and the Flora Zambesiaca area (Kostermans, 1938; Diniz, 1996); and most of the species from Papua New Guinea (e.g., Teschner, 1923; Allen, 1942; Kostermans, 1988, 1990).

With regard to leaves of *Cryptocarya guianensis*, Kostermans (1937) described them as having 6–10 secondary veins per side, whereas Moraes (2007) reported them as brochidodromous, with 6–12 secondary veins per side. Here, after a more thorough investigation on the leaf venation, the classification of leaves as varying from eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous is seen to be more accurate.

Leaves of *Cryptocarya mandioccana* were studied by Moraes and Paoli (1999) (as *C. moschata* Nees & Mart.; see Moraes, 2005b, 2007) and reported as camptodromous-brochidodromous, with (4–)5–8(–9) pairs of secondary veins (7–9 in Coe-Teixeira, 1965), courses curved to geniculate, running at moderate to high angles to the midvein, spacing broad to narrow, areoles mostly imperfect to well developed, small, with random arrangement, shape irregular, and intrusive veinlets mostly multibranched or multiforked (dendritic). The minor venation of *C. mandioccana* varied among different individuals of the population analyzed from Carlos Botelho State Park. Both perfect and imperfect reticulation were found, composed of subrotund or polygonal areoles, with low to highly ramified veinlet terminations. Genetical, environmental, and/or ontogenetical variation would explain the variability at this level, which has been shown to be present in different collections from different populations. It is worth noting that the cleared leaf of an unnamed species of *Cryptocarya* from tropical America, presented by Ettingshausen (1861: 45–46, fig. 14), mainly resembles the major venation pattern of eophylls of *C. mandioccana* but also of some of its nomophylls.

Quinet and Andreata (2002) reported the leaves of *Cryptocarya micrantha* as brochidodromous, with 7–12 pairs of almost-straight secondary veins, diverging at 30–35 degrees from the midvein. In Moraes (2007), leaves were described as camptodromous-brochidodromous, with 7–12 secondary veins per side of the midvein, rather patent, arcuate toward margin, whereas Barbosa et al. (2012) reported 10–12 pairs of secondaries. Here, leaves are better classified as eucamptodromous-brochidodromous to pseudobrochidodromous, differing from the former description by Quinet and Andreata (2002) in the angle mixed high and moderate to the midvein, and course of secondary veins predominantly straight to curved.

Cryptocarya moschata was reported by Moraes (2007) as bearing leaves camptodromous-brochidodromous, with 5–11 secondary veins per side. In Gomes-Bezerra et al. (2011), from specimen *Ratter 3887* (UB) (as *C. aschersoniana* Mez), leaves were given as brochidodromous, with 8–11 pairs of secondary veins, areoles quadrangular to polygonal, and veinlets linear to branched. Specimens from Bahia differ from the former descriptions and other collections in the venation pseudobrochidodromous, up to 12 secondary veins per side, and veinlets mixed curved and branched once and twice.

Leaves of *Cryptocarya riedeliana* were described by Moraes (2007) as camptodromous-brochidodromous, with 5–8 secondary veins per side, whereas Barbosa et al. (2012) reported 8–10 pairs of secondary veins. The Bahian specimens slightly surpass the number of secondary veins (up to 11) and their leaves are pseudobrochidodromous.

As for *Cryptocarya saligna*, Kostermans (1937) and Vattimo-Gil (1957) reported leaves with 8–14 secondary veins per side of the midvein. Coe-Teixeira (1965) described the course of secondary veins as oriented at 50–85 degrees to the midvein. Moraes (2007) reported leaves with camptodromous-brochidodromous venation, 4–14 secondary veins per side, whereas Barbosa et al. (2012) with 8–11 pairs of secondaries. The venation pattern described by Moraes et al. (2021), from specimens of Linhares, is virtually the same as that found in other populations from different regions. In Bahia, the collection by *Monteiro 23556* (ESA, HST, HUEFS—2 sheets, PEUFR) is the only one known so far, differing in the course of secondary veins curved (vs. predominantly straight), and broadly spaced (vs. broadly to medium-spaced).

Since its description by Moraes (2007), *Cryptocarya sellowiana* remains known only from the type and two other collections from the region of Rio Piracicaba, Minas Gerais state. Its leaf venation pattern has been shown to fall within the variability found in leaves of *C. mandioccana*, corroborating the assertion by Moraes (2007) that it could be a local variation of the latter species. However, the species was evaluated here from only one collection, and further collections and study are needed to clarify the relationships between these taxa (including in terms of their leaf venation).

Leaves of *Cryptocarya subcorymbosa* were described by Moraes (2007) as brochidodromous, with 4–10 secondary veins per side of the midvein. The species remains poorly collected and is known only from a few collections from Rio de Janeiro, São Paulo, and Paraná states. Regardless, the species presents leaves usually small, being the smallest among the Brazilian species, and also with the smallest areoles, thus giving the tightest mesh.

Cryptocarya velloziana was described by Moraes (2007), on the basis of a few collections from Estação Biológica de Santa Lúcia, in Santa Teresa, Espírito Santo. Its leaves were described as having camptodromous-brochidodromous venation, with 6–10 secondary veins per side of the leaf. Some Bahian specimens show leaves better classified here as having pseudobrochidodromous to brochidodromous venation, and they can present up to 11 secondaries per side of the leaf.

Cryptocarya wiedensis was described by Moraes (2007), on the basis of four collections from the region of Santa Maria de Jetibá and Santa Teresa, Espírito Santo. Here, although only a sample of the type collection was analyzed, its leaf venation pattern is shown to be quite similar to that presented by other espírito-santense samples previously determined as *C.* aff. *aschersoniana*.

The leaf venation patterns of species, much less genera, cannot be accurately described because they must be generalized from the patterns of a large number of

individuals (Klucking, 1987). Variation in venation patterns can be seen in individual leaves from the base of the leaf to the apex, as well as among individual leaves from different specimens of a species and among the different species of a genus. Another source of variability in observed patterns arises when leaves from the same collection are formed during different periods of secondary venation development, which is seen in several taxa of the present study. Although this variability adds additional difficulty to the intrinsic complexity of the venation patterns, it is not an impediment for describing and using them in a taxonomic sense, as an additional tool for discriminating taxa. Here, the major venation pattern has been demonstrated to be more conservative and, along with minor leaf venation, has proved to be useful for detecting possible misidentifications between taxa that are alike in their leaf venation characters.

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