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Taxonomy of *Cryptocarya* species of Brazil

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Taxonomy of *Cryptocarya* species of Brazil

by

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Cover illustration: *Cryptocarya moschata* Nees & Martius: ripe fruit, still coloured green at São Pedro, SP, January 2006 (Picture by author).

"What the Gods give they sell", the Greeks rightly said.
Fernando Pessoa

"Concedo nulli"
(Device of Erasmus)

Preface

This revision of the genus *Cryptocarya* was carried out at the Herbarium Rioclarense of the Universidade Estadual Paulista (HRCB), the Herbarium of the Escola Superior de Agricultura Luiz de Queiroz (ESA), and the Herbarium of the Universidade Estadual de Campinas (UEC).

As André Joseph Guillaume Henri Kostermans, to whom I here pay homage for his achievements on Lauraceae, I have done my best to make the enumeration of the specimens of *Cryptocarya* collected in Brazil as complete and as reliable as possible. For this purpose I have verified 2079 specimens, representing 1146 different collections deposited in 106 different herbaria. This embodies nearly all known herbarium collections of Brazilian species of *Cryptocarya*.

Loans of Brazilian specimens were obtained from nearly all Brazilian and several non-Brazilian herbaria (abbreviations follow Holmgren *et al.*, 1990). In addition various herbaria (ALCB, B, BHCB, BR, CEN, CEPEC, CVRD, ESA, F, HB, HBG, HBR, HPNI, HRCB, HXBH, IAC, IAN, INPA, KIEL, M, MBM, MBML, MG, NY, OUPR, R, RB, SP, SPF, SPFR, SPSF, UEC, UPCB and VIC) were visited in order to find additional specimens belonging to *Cryptocarya*. This was done by examining the entire Lauraceae collections, the specimens identified in genera related to *Cryptocarya* and the unidentified material of the above herbaria. Information and/or images from type and non-type material were kindly provided by various other institutions (A, AAU, B, BC, BHUPM, BM, BO, BR, C, CGE, CTES, FI-W, FR, G, G-DC, GB, GH, GOET, GZU, H, HAL, HBG, K, KIEL, L, LE, LINN, LISU, LZ, M, MA, MO, NY, OXF, P, PI, PR, QCNE, S, SGO, SI, STR, U, UPS, US, VT, and WRSL). Collections of Lauraceae from some other herbaria (BOTU, COR, HTO, PMSP, and UFMT) were also analysed, but no specimens of *Cryptocarya* were retrieved in these collections. The herbaria BA, BHU, BHUPM, BREM, FCAB, GLAM, HEID, HUEM, JE, LD, LIV, MAF, MANCH, NHV, NMW, PAD, PAMG, PORT, RO, ROST, SBT, STU, TUB, TUR, and VAL informed me that they do not house neotropical species of *Cryptocarya*.

Photographs from the *Type Photograph Collection of the Field Museum of Natural History*, Chicago, U.S.A, photographed by J. Francis Macbride (Grimé & Plowman, 1986) are mentioned here as *Photo F Neg. No._*. I have decided to cite these photographs mainly because all *Cryptocarya* type specimens deposited in the Herbarium Berolinense were destroyed during World War II.

In complement to the examination of the collections, an extensive revision of the literature was also done as to contextualise and update available taxon information.

Authors of plant names are based on Brummitt & Powell (1992), and book abbreviations are as proposed by Stafleu & Cowan (1976-1988).

Distribution maps of species were built from the digitised georeferenced 'map 14' of the *World Geographical Scheme for Recording Plant Distributions* (http://www.rbgkew.org.uk/gis/tdwg; with the permission of the Trustees of the Royal Botanic Gardens, Kew) (Brummitt, 2001) and the Americas Base Map (Bletter *et al*., 2004), using the program DIVA-GIS (version 5.2.0.2). When the coordinates of localities were not available from the labels, they were taken from the Instituto Brasileiro de Geografia e Estatística's Catalog of Cities and Villages.

The official classification system of Brazilian vegetation (Veloso & Góes-Filho, 1982; Veloso *et al.*, 1991) was adopted for indicating the phytoecological regions.

For the descriptions of the venation pattern, the general terminology of Hickey (1973, 1979) was employed. All other morphological terms were used as defined by Stearn (1992). Measurements of flower parts were taken from rehydrated herbarium material as well as from ca 1200 SEM micrographs from floral pieces of types, historical voucher specimens and 53 different recent collections (Moraes *et al.*, 2001).

I take the opportunity to thank the Belgian National Focal Point to the Global Taxonomy Initiative (GTI) for sponsoring a research visit to the National Botanic Garden of Belgium (BR) that houses the important private Herbarium Martii and for inviting me to write this volume for the *Abc Taxa series*. This was a unique opportunity for me to liberate my knowledge on the *Cryptocarya* species of Brazil into the lingua franca of English.

Campinas, 7 September 2006.

Abstract

The Brazilian species of *Cryptocarya* are revised. The systematic treatment of its species is provided, and its typification, synonym, general descriptions for morphology, distribution, and ecological features are discussed. As a result, 13 species were recognised with five newly described: *Cryptocarya botelhensis* P.L.R. de Moraes, *C. riedeliana* P.L.R. de Moraes, *C. sellowiana* P.L.R. de Moraes, *C. velloziana* P.L.R. de Moraes, and *C. wiedensis* P.L.R. de Moraes. Illustrations and a key to the species are presented.

Keywords – *Cryptocarya*; Lauraceae; *C. aschersoniana*; *C. botelhensis*; *C. citriformis*; *C. guianensis*; *C. mandioccana*; *C. micrantha*; *C. moschata*; *C. riedeliana*; *C. saligna*; *C. sellowiana*; *C. subcorymbosa*; *C. velloziana*; *C. wiedensis*; new taxon; key; descriptions; plant taxonomy; Brazilian flora.

Resumo

Revisaram-se as espécies brasileiras de *Cryptocarya*. O tratamento sistemático das espécies é apresentado e sua tipificação, sinonímia, descrições gerais morfológicas, de distribuição e ecológicas são discutidas. Como resultado, 13 espécies foram reconhecidas, cinco das quais descritas como novas: *Cryptocarya botelhensis* P.L.R. de Moraes, *C. riedeliana* P.L.R. de Moraes, *C. sellowiana* P.L.R. de Moraes, *C. velloziana* P.L.R. de Moraes, e *C. wiedensis* P.L.R. de Moraes. Ilustrações e uma chave para as espécies são apresentadas.

Palavras-chave – *Cryptocarya*; Lauraceae; *C. aschersoniana*; *C. botelhensis*; *C. citriformis*; *C. guianensis*; *C. mandioccana*; *C. micrantha*; *C. moschata*; *C. riedeliana*; *C. saligna*; *C. sellowiana*; *C. subcorymbosa*; *C. velloziana*; *C. wiedensis*; táxon novo; chave; descrições; taxonomia de plantas; flora brasileira.

Taxonomic novelties

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1. Introduction

When Kostermans (1952) published 'A Historical survey of Lauraceae' he pointed out that the family contains more than 190 generic names holding some 5200 binomials. Of these 190 generic names only about 50 are currently accepted, the exact number depending on generic concepts, which are still a matter of discussion (Rohwer, 1993a, 1993b; van der Werff & Richter, 1996). More recently, two new genera were described for the Neotropics, viz. *Mocinnodaphne* Lorea-Hernández (1995) and *Sextonia* van der Werff (1997). According to van der Werff (2003) the family encompasses 55 genera that are recognised on the basis of combinations of characters that intergrade among taxa. To circumscribe genera, floral and fruiting characters are mostly used; for instance: number and kind of fertile androecial whorls, number of sporangia in the anthers, extent of development of staminodia in the fourth androecial whorl, and the extent of hypanthium development in the fruit (Lorea-Hernández, 1996).

The family Lauraceae belongs to the Order Laurales that is classified in the Subclass Magnoliidae (*sensu* Cronquist, 1981, 1988). Currently, it has been inserted in the Superorder Magnoliidae, in association with Magnoliales, Piperales and Canellales (APG II, 2003). The family is pantropical, including about 50 genera with a probable number of 2500 to 3500 species (Rohwer, 1993a, 1993b). The estimated number of extant Neotropical species is around 700 to 800, belonging to 30 genera (van der Werff, 1988, 1991). Brazil has the majority of the species diversity for this family in the Neotropics (c. 360 known, most probably an underestimation) distributed in 21 genera, and its species are important components of the functional and structural composition in the Atlantic rain forest, Cerrado (Brazilian savanna) and Amazonian forests. *Cryptocarya* R. Brown is one of the largest pantropical genera in the Lauraceae, comprising some 300 to 350 species. *Cryptocarya* can be distinguished from other laurel genera by its bisexual and trimerous flowers, which are very typical in shape (usually slender, urceolate, apically narrowed tube and immersed ovary, six equal to subequal tepals, nine fertile stamens with disporangiate anthers, staminal glands only in the third androecial whorl), and by the characteristic fruit that is enclosed by the accrescent flower tube.

The present taxonomic revision of the *Cryptocarya* species of Brazil is based on intensive fieldwork, mainly in the southeast of the country, but also on more than 2000 specimens that are deposited in 1146 collections (Herbarium abbreviations follow Holmgren *et al.*, 1990).

2. Historical survey

Kostermans (1952) and Bernardi (1962) provided a historical overview of the taxonomy of the Lauraceae. A chronological overview of the names attributed to *Cryptocarya,* mainly based on Kostermans (1952), is provided hereunder.

Feuillée (1725) was the first to describe the Chilean plant called "Boldo" ("*Boldu arbor olivifera*"). Adanson (1763) redescribed *Boldu* Feuillée, and validated the name by diagnosing it properly. However he did not add a specific epithet. Looser

(1935) objected to these descriptions that he found rather confusing. He argumented that Feuillée, in his diagnosis, had mixed the leaves and other vegetative parts of what is called “Boldo” in Chile (Monimiaceae) with the fruit of another Lauraceae species, maybe the Chilean “Peumo”. The latter species currently is referred to either *Cryptocarya alba* (Molina) Looser or to *Bellota miersii* Gay (current status: *Beilschmiedia miersii* (Gay) Kosterm.) (Mez, 1889; Kuntze, 1891). The complete history of the nomenclatural intricacies of *Cryptocarya alba* are covered by Looser (1935, 1950, 1963), and Kostermans (1939a, 1952). According to Kostermans (1952), if one cites *Boldu* (Feuillée) Adanson it should only be *pro parte*, *i.e.* without the description of the fruit.

Kostermans (1939b, 1958) treated the Madagascan genus *Ravensara* monographically and recognised 27 species. Recently, van der Werff (1992) successfully (cf. Brummitt, 1994) put forward a proposal to conserve *Cryptocarya* R. Brown 1810 against *Ravensara* Sonnerat 1782. The main argumentation given was that the two genera were separated solely on one fruit character, *i.e.* presence of ruminate cotyledons in *Ravensara* versus non-ruminate cotyledons in *Cryptocarya* (or endocarpic versus nucellar ruminations *sensu* Corner, 1976). More recently, Hyland (1989) corroborated this by documenting ruminate cotyledons for 11 Australian *Cryptocarya* species. He showed that these species did not differ in other characters from the *Cryptocarya* species with non-ruminate cotyledons. Still, Mez (1889) described a fruit of *C. minima* Mez [= *C. citriformis* (Vellozo) de Moraes], collected by *T. Peckolt* in Brazil, as having an imperfectly bicarpellate ovary (*i.e.* with septa intruding into the cotyledons).

The genus *Cryptocarya* was first described by Robert Brown (1810) as a new genus for Australia, with three species, *C. glaucescens*, *C. obovata* and *C. triplinervis*, of which Kostermans (1939b) designated *C. glaucescens* R. Brown as type species. Nees von Esenbeck (1833a) described the first Brazilian species for the genus, *Cryptocarya moschata* Nees & Martius, based on two specimens: the fruiting one of *von Martius*, and the flowering one of *Sellow*. The species was also cited in the same year by Nees (1833b). In 1836, Nees published the first general treatise (*Systema laurinarum*) of all known Lauraceae at his time, describing 13 species under *Cryptocarya*. *Cryptocarya moschata* Nees & Martius was the only species described from tropical America. In the same work, Nees also published the genus *Caryodaphne* with Blume as authority. The latter is comprehensible as it was Blume who suggested the genus, albeit as subgenus, to Nees. Blume’s subgenus comprised two species of *Cryptocarya*: *C. laevigata* Blume and *C. densiflora* Blume (1826), to which Nees added a third species, *C. triplinervis* R. Brown. The species were cited as *Caryodaphne laevigata* (Blume) Nees, *C. densiflora* (Blume) Nees, and *C. browniana* Nees. Bentham (1870; 1880) reduced *Caryodaphne* to the synonymy of *Cryptocarya* R. Brown, a decision that is now generally accepted.

The second volume of *Nova genera et species plantarum* (Humboldt, Bonplandt & Kunth, 1817/1818) is of importance to the present work as one of the genera recognised by Kunth (who was the author of the descriptions, see Stafleu & Cowan, 1979) was *Cryptocarya*. One species, *C. canelilla* Kunth, was introduced. Mez (1889) however transferred it to *Aniba*, a decision that still holds.

In 1845, Blanco described *Salgada lauriflora* Blanco (misprinted as *Salgada laurifolia*). Vidal y Soler (1886) later referred the species to *Cryptocarya luzoniensis* Vidal. Merrill (1909, 1918) likewise relegated Blanco's species to *Cryptocarya*, making the combination: *C. lauriflora* (Blanco) Merrill.

Gay (1851/1852), described *Cryptocarya berteroana* Gay, from specimens collected by *Bertero*. In 1857, Philippi described *Icosandra* Phil. with one species: *I. rufescens* Phil. [current status: *C. alba*]. Mez (1889), however reduced *Icosandra* to the synonymy of *Cryptocarya*, a decision that still holds today.

Meissner (1864) elaborated a complete monograph of Lauraceae, accepting 37 species in *Cryptocarya*, from which four were new descriptions for Brazil: *Cryptocarya emarginata* Meissn., *C. mandioccana* Meissn., *C. micrantha* Meissn., and *C. riedelii* Meissn.. The same American species of *Cryptocarya* were also described in the *Flora Brasiliensis* (Meissner, 1866). They were complemented with two additional species: *C. guianensis* Meissn. and *C. moschata* Nees & Martius.

Beccari (1880) coined the generic name *Massoia*, with one species *M. aromatica* Becc.. Kostermans (1949: 169) relegated the genus to *Cryptocarya* R. Brown, giving the name *Cryptocarya aromatica* (Becc.) Kosterm. [current status: *Cryptocarya massoy* (Oken) Kosterm.].

Mez (1889) published a classical monograph on American Lauraceae, adopting chiefly Bentham's (1880) classification of genera (Kostermans, 1952). In his specific circumscription, Mez recognised nine species of *Cryptocarya*: he accepted all species treated by Meissner, except *C. dubia* Kunth [= *Aiouea dubia* (Kunth) Mez; Andean species] and *C. emarginata* [= *Beilschmiedia emarginata* (Meissn.) Mez]. He described *C. aschersoniana* Mez and *C. saligna* Mez, and put *Aydendron floribundum* Meissn. in synonymy with *C. minima* Mez, which has been generally accepted. *Cryptocarya moschata* Nees & Martius was described in a broader sense, including the proposal of *C. moschata* forma *angustifolia* Mez. Mez later (1892, 1893, 1902, 1907) described five new Brazilian species: *Cryptocarya hypoleuca* Mez, *C. longistyla* Mez, *C. minutiflora* Mez, *C. schwackeana* Mez, and *C. subcorymbosa* Mez.

In 1923, Teschner erected the genus *Pseudocryptocarya* Teschner, to accomodate *P. pauciflora* (Lauterbach & K. Schumann) Teschner, a species originally classified in *Cryptocarya*. Kostermans (1937) reduced *Pseudocryptocarya* to the synonymy of *Cryptocarya* R. Brown. Later, Kostermans (1950) synonymised *P. pauciflora* with *Cryptocarya laevigata* Blume.

The last revision of the American species of *Cryptocarya* was done by Kostermans (1937), who studied the historical collections deposited in European and US herbaria. He accepted the following species for Brazil: *Cryptocarya guianensis*, *C. mandioccana*, *C. micrantha*, *C. minima*, *C. moschata* and *C. saligna*. In 1938, after examining the syntype specimen of *Cryptocarya moschata* collected by *von Martius s.n.*, Kostermans (1938a) accepted *C. aschersoniana* and reduced *C. mandioccana* to the synonymy of *C. moschata*. Since Kostermans' monographic revision, voucher material of Brazilian *Cryptocarya* has dramatically increased.

In 1957 (a, b), Kostermans gave a classification of Lauraceae; and proposed three subgenera for *Cryptocarya*: (i) *Cryptocarya* = *Enneanthera* Kosterm., with 9 fertile anthers; (ii) *Hexanthera* Kosterm., with 6 fertile anthers; (iii) *Triandra* Kosterm., with 3 fertile anthers. More recently, Rohwer & Richter (1987) described the genus *Aspidostemon* for a group of eleven closed related lauraceous species from Madagascar, which were previously included in the genus *Cryptocarya*, including those that were assigned under subgeneric rank *Hexanthera* and *Triandra* by Kostermans.

In Brazil, Ida de Vattimo-Gil was the first to systematically study the taxonomy of Lauraceae. In 1956, she published "Lauraceae do Itatiaia", based on the specimens collected by *W.D. de Barros* in the Parque Nacional de Itatiaia, RJ. She described *Cryptocarya saligna* and one unidentified *Cryptocarya* sp. [current status: *C. riedeliana* P.L.R. de Moraes]. In a following work (Vattimo-Gil, 1957), she treated the species from "Monte Sinai, Governador Portela", RJ, and recognized *C. micrantha*, *C. moschata*, and *C. saligna*. In 1959, the "Flora da cidade do Rio de Janeiro-Lauraceae" was published with the citation of *C. moschata* and *C. saligna*. In all of three of her works, *Cryptocarya* species circumscriptions were based on Kostermans (1937, 1938a).

In 1965, Beulah Coe-Teixeira studied the *Cryptocarya* species of the state of São Paulo from specimens kept in herbaria NY, RB and SP. She adopted Kostermans' treatment and presented a key to the species, describing *C. aschersoniana*, *C. moschata* and *C. saligna*.

In 1966, Vattimo-Gil (1966a) published "Lauraceae do Estado da Guanabara", citing *Cryptocarya moschata* and *C. saligna*. In the same year, Vattimo-Gil (1966b) also published a preliminary study of the Brazilian species of *Cryptocarya*, based mainly on Kostermans' criteria, but with several different interpretations of synonyms and specific status. She also provided drawings for all species and described three new ones: *C. granulata* Vattimo-Gil, *C. jacarepaguensis* Vattimo-Gil and *C. nigropunctata* Vattimo-Gil.

In 1978, Vattimo-Gil started a series of publications on the geographic distributions of Lauraceae species. In the first one (Vattimo-Gil, 1978), she incorporated specimens of *C. aschersoniana* from Paraná and Rio Grande do Sul, *C. moschata* [current status: *C. mandioccana*] from Paraná, and *C. saligna* from São Paulo. Vattimo-Gil (1979a) treated the genus *Cryptocarya* for the "Flora Ilustrada Catarinense", describing *C. aschersoniana* and *C. moschata* [current status: *C. mandioccana*], basically from the collections made by *Reitz & Klein* housed in HBR. In the same year, she gave the localities of occurrence for *C. guianensis*, *C. micrantha*, *C. moschata*, and *C. saligna* (Vattimo-Gil, 1979b), and new localities of occurrence for *Cryptocarya aschersoniana* from Paraná and Rio Grande do Sul, and for *C. moschata* [current status: *C. mandioccana*] from Paraná (Vattimo-Gil, 1979c).

In the taxonomic treatment of the Lauraceae for the "Flora Fanerogâmica do Parque Estadual das Fontes do Ipiranga", SP, Baitello & Coe-Teixeira (1987) described *C. moschata* Nees [current status: *C. mandioccana*]. In this same

year, Pedralli (1987) published part of his dissertation on Lauraceae from Rio Grande do Sul (Pedralli, 1983), with recognition of *C. aschersoniana* and *C. moschata*.

In 1997, Sara Tressens was the first to report *Cryptocarya aschersoniana* for Argentina, providing it with a detailed and illustrated description. Nicolau (1999) presented her study on the Lauraceae species of Serra da Juréia, SP. In the taxonomic treatment, she recognised *C. aschersoniana*, *C. moschata* [current status: *C. mandioccana*] and *C. saligna*.

Quinet & Andreata (2002), after the study of Quinet (2001), published the taxonomic treatment of Lauraceae for the Reserva Ecológica de Macaé de Cima, Nova Friburgo, RJ, citing the occurrence of *C. moschata* sensu Kostermans and *C. micrantha*.

In the "Flora Fanerogâmica do Estado de São Paulo", Moraes (2003) presented the taxonomic study of *Cryptocarya* species from collections of São Paulo herbaria and HB, R and RB. Based on Kostermans' revision (1937; 1938a), *C. aschersoniana*, *C. moschata*, and *C. saligna* were recorded for the state.

Moraes (2005a) published the lectotypification of names of Brazilian species of *Cryptocarya*, accepting eight species: *Cryptocarya aschersoniana*, *C. citriformis* (Vellozo) P.L.R. de Moraes (comb. nov., = *C. minima*), *C. guianensis*, *C. mandioccana*, *C. micrantha*, *C. moschata*, *C. saligna*, and *C. subcorymbosa*. In the same year, the synopsis of Lauraceae from the states of Goiás and Tocantins was published (Moraes, 2005b; see also Moraes & Oliveira, 2007), with *C. moschata* Nees & Martius as a new record for Goiás. In the same year, Baitello & Moraes (2005) presented a taxonomic treatment of Lauraceae for the "Flora Fanerogâmica da Ilha do Cardoso", SP, describing *Cryptocarya* aff. a*schersoniana* and *C. mandioccana*.

In his taxonomic synopsis of Lauraceae for the state of Rio de Janeiro, Quinet (2005) recognised eight species, viz. *Cryptocarya aschersoniana*, *C. granulata*, *C. jacarepaguensis*, *C. micrantha*, *C. minima*, *C. moschata*, *C. nigropunctata* and *C. saligna*, accepting Kostermans' treatment (1937, 1938a) and the species described by Vattimo-Gil (1966b). Both *C. granulata* and *C. nigropunctata* are species only known from their type locality, the former from Minas Gerais, the latter from Amazonas. *C. jacarepaguensis* is only known by the type collection from Rio de Janeiro, which is so far missing. Assis *et al*. (2005) treated *C. micrantha* from the Reserva Biológica da Represa do Grama, Descoberto, MG.

3. Morphology and anatomy

3.1. Leaf[1]

The leaves of Brazilian *Cryptocarya* are evergreen, simple, entire, petiolate, without stipules, alternate in arrangement, mostly coriaceous or leathery in nature,

[1] Section authored by Pedro Luís Rodrigues de Moraes & Marília de Moraes Castro.

with a pinnate secondary venation pattern. Venation is always pinnate with secondary veins alternately arranged and evenly spaced along the midrib. Secondary veins range in number from 4 to over 14 per side, but usually number 6 to 8 pairs. Even if rarely found in Australia and Papua New Guinea (Brouwer & Clifford, 1990), *Cryptocarya* species generally do not bear domatia. The presence of pellucid dots is a distinct macromorphological character of the leaf laminae.

3.1.1. Epidermis

According to Faggetter (1987), the micromorphology of the outer leaf surface provides few characters of diagnostic value within the Lauraceae. The trichomes are always simple and unicellular, they can vary in respect to presence/absence, distribution, and size. The outer periclinal walls of the epidermal cells may be flat (and the cells are consequently tabular), more or less convex, or domed, while those of the abaxial epidermis may be papillate. The occurrence of cells with the pattern of straight walls is the preponderant epidermal character of the family (Petzold, 1907). Another important diagnostic trait that occurs in a small number of species is the presence of cell wall undulation in the adaxial epidermis. Petzold (1907), who dealt with the American members of the genus, reported that *Cryptocarya aschersoniana*, *C. mandioccana*, *C. moschata*, and *C. schwackeana* present such cell wall undulation, with the degree of undulation being constant, in the abaxial epidermis. *Cryptocarya minutiflora*, by exception, shows cell wall undulation in the adaxial epidermis, and straight cell walls in the abaxial one. The lateral walls of the epidermal cells of both *C*. *minutiflora* and *C. subcorymbosa* were described as bending in a zig-zag manner with ridge-like projections, which protrude in the apices of the angles.

Moraes (1993), summarised in Moraes & Paoli (1999), found that the adaxial epidermis of eophylls (first pair of leaves) of seedlings of *Cryptocarya mandioccana* is similar to that of nomophylls (mature leaves) of adult trees, composed of cells with strongly undulate and thick walls; in costal regions, cells are more longitudinally elongated, with almost straight walls (Fig. 1 A-B, D-E). The abaxial epidermis is composed of cells that are similar to those of the adaxial epidermis. They are nevertheless smaller, with slightly undulate and less thick walls, in the possession of more trichomes, and with paracytic stomata, two subsidiary cells completely enclosing the guard cells and with parallel long axes (Fig. 1 C, F-H). However, the observation that the leaves of the studied species show a pronounced variation in the epidermal cell wall outlines, makes that this is not the best taxonomic character.

Petzold (1907) reported that, in Brazilian species of *Cryptocarya*, the stomata seen from surface view (paradermal section) show only a narrow aperture of subsidiary cells, strongly thickened, over the guard cells. In mid position, he reported two apertures, one from the subsidiary cells and one from the guard cells, giving a cruciform appearance. In an inner position, the proper stomatal pore can be observed. Apart from three species (*C. guianensis*, *C. micrantha*, and *C. minima*), which Petzold did not have at his disposal, and from *C. saligna*, all other Brazilian species of *Cryptocarya* were described as possessing depressed stomata, viz. *Cryptocarya aschersoniana*, *C. longistyla*, *C. mandioccana*, *C. moschata* Martius (= *C. moschata* Nees & Martius), *C. schwackeana*, and *C. subcorymbosa*.

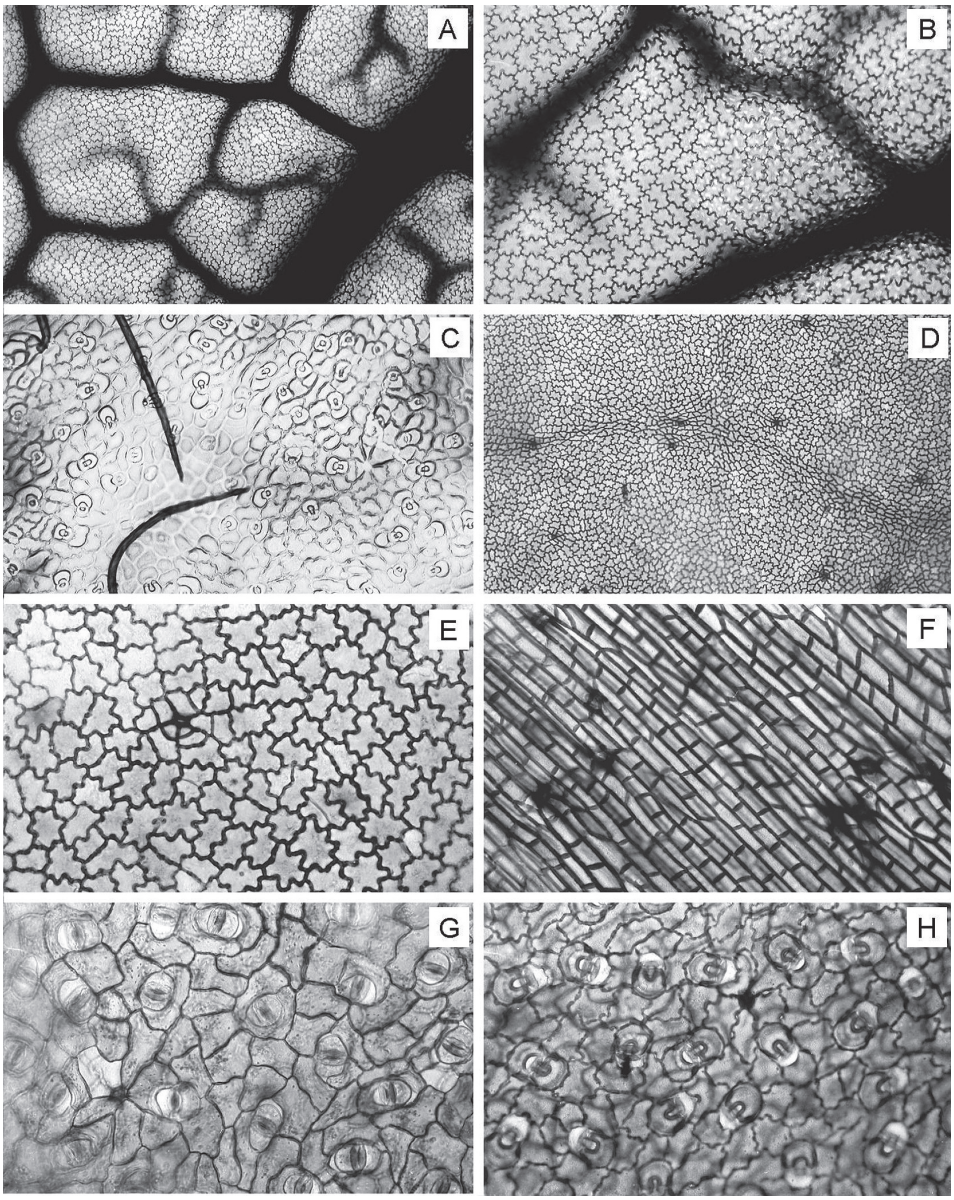

Fig. 1. Leaf surface view of *Cryptocarya mandioccana* Meissner. A-B. Eophylls: adaxial epidermis over intercostal region (A ×30; B ×100); C. Eophylls: abaxial epidermis, paracytic stomata and trichomes (×100). D-E. Nomophylls: adaxial epidermis over intercostal region (D ×30; E ×300); F. Nomophylls: abaxial epidermis over midrib (×300); G-H. Nomophylls: abaxial epidermis, paracytic stomata (×300). (Photomicrographs by author).

Van der Merwe & van Wyk (1994) studied leaf epidermal, particularly stomatal, characters in all southern African species of Lauraceae (five *Cryptocarya* spp.). Anatomically, infrageneric groups were discernible in *Cryptocarya*, but individual species could not always be distinguished. They found that all taxa have paracytic stomata, with small sunken guard cells, abaxially overarched by the subsidiary cells.

According to Christophel *et al*. (1996), "the paracytic arrangement is uniform across the family, and all species are hypostomatic", that means stomata are only found on the abaxial surface of the leaves. However, they also reported that the exclusive use of cuticular features within Australian species of *Cryptocarya* proved to be challenging, since they found no good generic delimiting characters, even with the examination of approximately 20 additional species from this genus occurring outside of Australia.

Christophel & Rowett (1996) described the leaf architecture and cuticular features of all leafy Australian species of Lauraceae (including 50 *Cryptocarya* species) from a taxonomic perspective, based on the treatment made by Hyland (1989). Within *Cryptocarya*, Christophel & Rowett (1996) recognised five groups on the basis of the degree of undulation of the anticlinal wall of the epidermal cells of both surfaces. This is in contrast to Hyland (1989) who recognised nine groups with a tenth group consisting of five species which he considered not fitting elsewhere. Christophel & Rowett (1996) concluded that the genus *Cryptocarya* is either: (i) a non-natural taxon, (ii) a taxon with a lot of parallel evolution – perhaps reflecting its relative antiquity, or (iii) a taxon wherein foliar features are inappropriate for consideration at generic level, at least for Australian species.

3.1.2. Mesophyll

Petzold (1907) showed that in *Cryptocarya* leaves are dorsiventral, hypostomatic, and have two to three layers of palisade parenchyma (Brazilian species with two layers). In some cases the spongy parenchyma contains large lacunae, which are filled with stellate tissue. The latter is however not the case with *Cryptocarya aschersoniana*, *C. minutiflora*, and *C. subcorymbosa*. Hypodermis, in the form of a single cell layer, was recorded on the adaxial side of the leaf in all *Cryptocarya* species examined. According to Kostermans (1957a), *Cryptocarya* and *Endiandra* however tend to form a hypodermis with two layers. Sclerenchymatic cells are often seen in the leaf margins.

3.1.3. Secretory idioblasts and crystals

According to Solereder (1908), Lauraceae are characterised by the constant presence of oil cells, and occurrence of mucilage cells in many genera. These secretory cells frequently give rise to transparent dots in the leaf laminae; they are found both in the palisade and spongy parenchyma. They are generally spherical in shape; those situated in the palisade appear as enlarged sac-like cells. The walls of the secretory cells are suberised, and their contents are homogeneous and in most cases yellowish. In the survey of Baas & Gregory (1985) concerning oil and mucilage cells and Gregory & Baas (1989) reviewing mucilage cells, the occurrence of these secretory idioblasts is mentioned to a few Lauraceae genera such as *Cinnamomum*, *Laurus*, *Persea*, *Sassafras,* and

Umbellularia. Bakker *et al*. (1992), in their comprehensive study of leaf anatomy of *Cinnamomum*, described the morphology and distribution of oil and mucilage cells in the leaf of 150 species, ascertaining that these idioblasts were always present in the palisade and the spongy parenchyma.

Petzold (1907) stated that mucilage cells are present only in the palisade parenchyma of *Cryptocarya* species. However, he also noted that such cells are absent in *C. aschersoniana*, *C. mandioccana*, *C. minutiflora*, *C. moschata*, and *C. subcorymbosa*. Oil cells occurring only in the palisade parenchyma were found in *Cryptocarya moschata* Martius and *C. saligna*, while in *C. schwackeana* they are present only in the spongy parenchym.

Crystals occur mostly in the form of small needles or spindles, not only in the mesophyll, but, although rarely, also in the epidermis of the leaves in Lauraceae. In a recent anatomical study of leaves of *Cryptocarya* aff. *aschersoniana* Mez, Castro & Watanabe (ined.) found that leaves are structurally dorsiventral (Fig. 2). The adaxial and abaxial epidermises are both uniseriate. Stomata are restricted to the abaxial side. Secretory hypodermis with lipophilic substances (revealed by buffered neutral formalin fixative; FNT) are also uniseriate and occur in both sides of the laminae; in the abaxial surface, hypodermis is interrupted by substomatal chambers. The chlorenchyma presents one layer of palisade parenchyma, and five to nine layers of spongy parenchyma. Secretory idioblasts with lipophilic content (revealed by FNT) are observed in the palisade and spongy parenchyma. Single raphides and prismatic crystals are found in parenchyma cells. Vascular bundles are collateral and surrounded by a lignified bundle-sheath. The bundle-sheath and bundle-sheath extensions of the vascular bundles are composed of thick-walled parenchyma cells, which walls become impregnated with lignin.

Sclerified cells are also observed as supporting tissues in the midrib and at the leaf margins.

3.1.4. Venation pattern

Similarly to what has been described by Nishida & Christophel (1999) for the Neotropical species of *Beilschmiedia*, all the Brazilian species of *Cryptocarya* have penninerved leaves (pinnately nerved). Klucking (1987) gave a comprehensive account on this topic; it is here succinctly repeated.

Many leaves have one kind of venation in their basal part, another kind in the middle part and a third kind in the upper part of the leaf. The secondary venation of a leaf begins to form in the basal part of the leaf and develops progressively apically or acropetally. Since the secondary venation develops acropetally, the venation in the basal part of the leaf is formed first, that in the middle part of the leaf next, and that in the apical part last. Each of these venation types – the basal, middle, and apical – has different characteristics and is distinct. As each of these venation types are formed during a different phase of development, they are commonly termed *early phase venation*, *middle phase venation*, and *late phase venation*. These three types of venation usually are not present in equal amounts on the leaf. One or another type commonly makes up half or more of

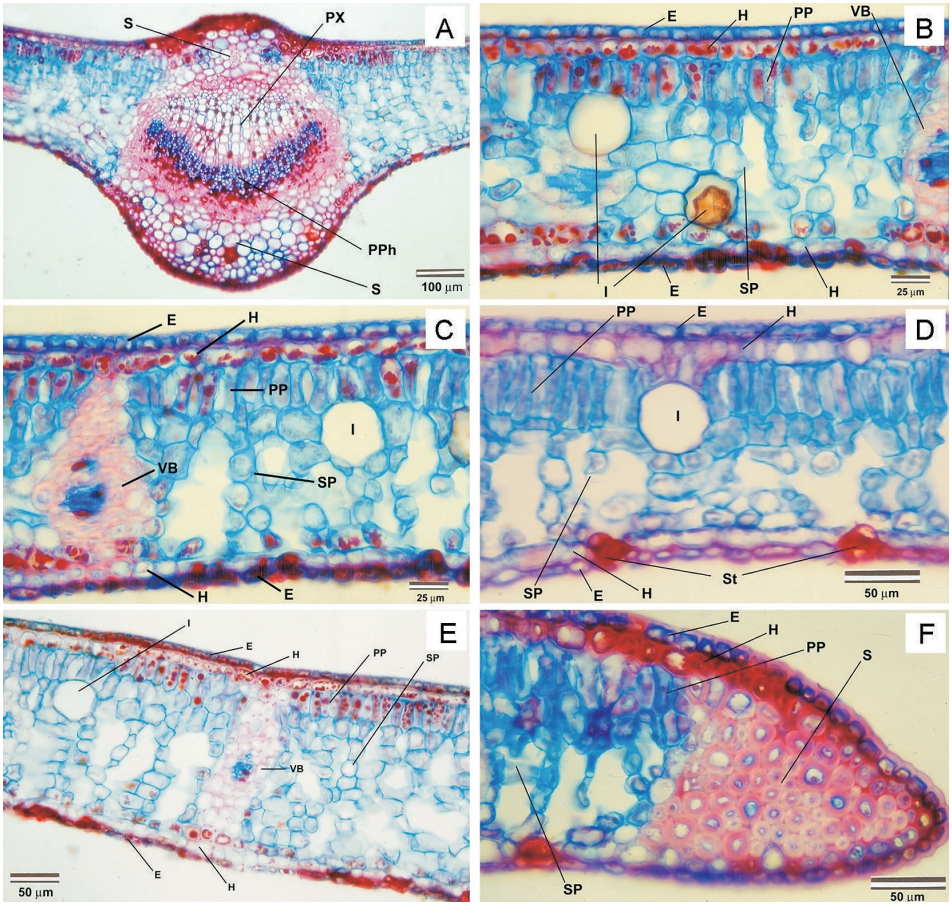

Fig. 2. Transections of leaves of *Cryptocarya* aff. *aschersoniana* Mez (from *Moraes 2389*). A. Midrib; B-D. Intermediary region; E-F. Marginal region. (A-C, E fixed in FNT; D, F fixed in FAA). (E = epidermis, H = secretory hypodermis, I = secretory idioblast, PP = palisade parenchyma, PPh = primary phloem, PX = primary xylem, S = sclerified cells, SP = spongy parenchyma, St = stomata, VB = vascular bundle). (Photomicrographs by M. de M. Castro & T.M. Watanabe).

the total pattern and so the leaf venation pattern is named after that dominant type of venation, (e.g. if early phase venation is present on half or more of the leaf, one terms the venation pattern for that leaf '*early phase venation*').

"Secondary veins are veins that depart from the midvein or primary vein. They are termed *pinnate* if they are directed more laterally; they're called *acrodromal* if they are directed more apically than laterally.The area between the secondary veins is termed the *intercosta* or *intercostal area*. The inner boundary of the intercosta is the midvein. Its outer or marginal boundary is formed when the secondary vein branches and the distal branch continues the secondary course apically terminating by connecting with the basally directed branch from the secondary vein above. This boundary that boxes in the intercostal area is called

closure. Secondary veins are termed *brochidodromous* when the closure connection is arched and definite (adapted from Hickey, 1973).

Klucking (1987) examined the leaf structure of 245 species of *Cryptocarya*. Of 49 species he gave a description. From Brazil, only *C. aschersoniana* was cleared, and described. This species had the predominant venation pattern of the genus, *i.e.* "Early Phase Pinnate Venation dominant with small amounts of Middle Phase and Late Phase Venation present in the apical part of the leaf".

Moraes (1993; see also Moraes & Paoli, 1999), studied the leaf venation pattern of *C. mandioccana*, for eophylls and nomophylls (Fig. 3 A-B), the latter also showed the predominant venation pattern as described by Klucking (1987).

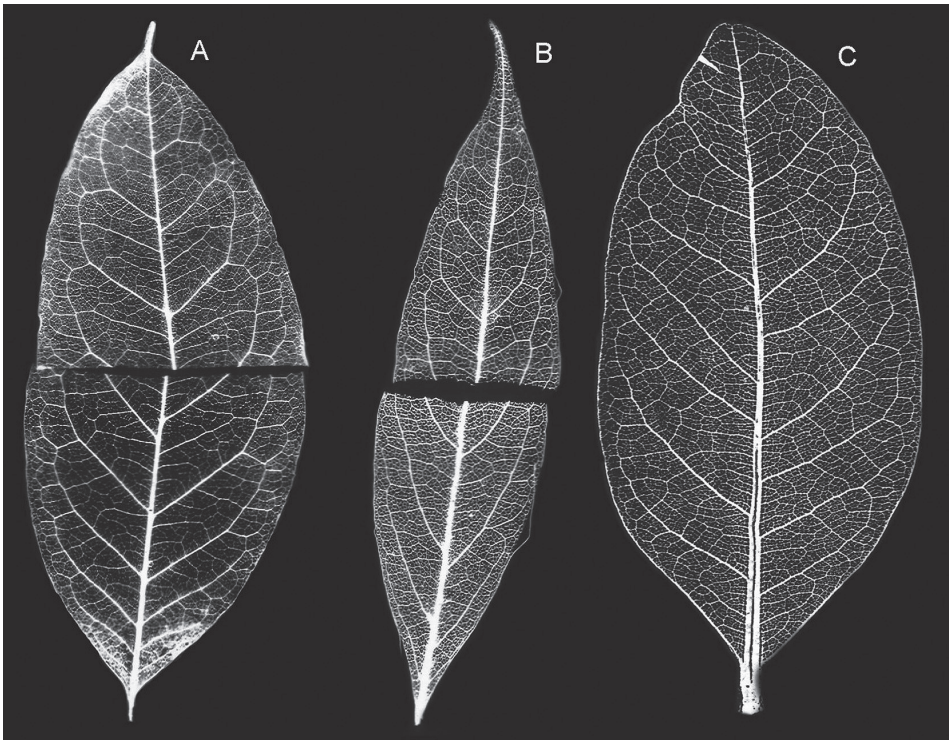

Fig. 3. Cleared leaves of *Cryptocarya*. A-B. Eophyll and nomophyll of *C. mandioccana* Meissner, respectively, from Parque Estadual Carlos Botelho (Photographs by author). C. "*Cryptocarya* sp. nov.", from tropical America (ex von Ettingshausen, 1861; fig. 14, p. 45).

They found eophylls and nomophylls presenting pinnate, camptodromous-brochidodromous venation pattern (secondary veins not terminating at the margin or secondary veins joined together in a series of prominent arches). However, eophylls differed from nomophylls in arrangement, number and course of secondary veins, as well as in reticulation, size and type of areoles and veinlets. Most eophylls with 5 to 8 pairs of secondary veins, mainly 6 pairs and a few with 4 pairs, courses curved, curving gently apically as it extends laterally from the midrib, merging into the marginal looping; secondary courses running at high