

angles (most of the lateral course of the secondary veins is oriented at 55 degrees or more to the midrib), spacing broad, narrow, or a mixture of broad and narrow; marginal vein and/or marginal thickening present; intercostal venation scalariform or random reticulate; areoles are incomplete, larger than those of nomophylls, with random arrangement, shape irregular, intrusive veinlets multi-branched or multi-forked (pattern dendroid), sometimes with more than one veinlets per areole, with less freely ending veinlets than those of nomophylls (Fig. 4 A-B). Nomophylls with laminae narrow-elliptical to elliptical, apices acute to acuminate, base cuneate; most of nomophylls with 5 to 8 pairs of secondary veins, some with 4 pairs and a few with 9 or more pairs, courses curved or geniculate (the secondary vein departs at a high angle to the midrib and after a short distance it has an abrupt apical change in its course direction), curving sharply distally at closure and merging into the marginal looping; secondary courses running at moderate or high angles, spacing broad and/or narrow; marginal vein and intersecondary veins present; intercostal venation scalariform or random reticulate; areoles are imperfect, small or large, with random arrangement, shape irregular, intrusive veinlets mostly multi-branched or multi-forked (pattern dendroid), sometimes with more than one veinlets per areole; some with perfect reticulation; in young leaves, open reticulation, without branched endings (Fig. 4 C-J).

The minor venation of *Cryptocarya mandioccana* is variable between different individuals of a population (Moraes, 1993). Both perfect and imperfect reticulation was 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. However, major venation of *C. mandioccana* is much more conservative and thus useful for identifying the species.

3.2. Wood and bark

Richter (1987) gave a summary of the structural features of the secondary phloem, based on barks from about 400 specimens representing 310 species and 35 genera of Lauraceae. I have here retaken the information relevant to *Cryptocarya* species.

Sclerenchymatous tissue (mechanical tissue) is always present in lauraceous bark. "True" or normal phloem fibres are lacking entirely in *Cryptocarya*. Sclereids are present in nearly all lauraceous barks and show great variability in type, form and distribution. The morphology of these sclereids permits them to be classified in two categories, viz: columnar sclereids longitudinally elongated, usually with blunt but rarely with pointed ends, typically hexagonal in transverse section; or, polygonal, isodiametric sclereids clustered into small or large nests or tangential groups.

A combination of both columnar and isodiametric sclereids occurs in individual species of *Beilschmiedia* and *Cryptocarya*. Lignified parenchyma (of sclerotic cells with extremely thick, polylamellate walls) is developed exclusively in the non-functional phloem and often very clearly demarcates the functional part, being typical of *Cryptocarya*. Some species of *Cryptocarya* present dilated rays expanding into wedge-shaped ends in the outer phloem. Most of such dilated tissue is sclerotic.

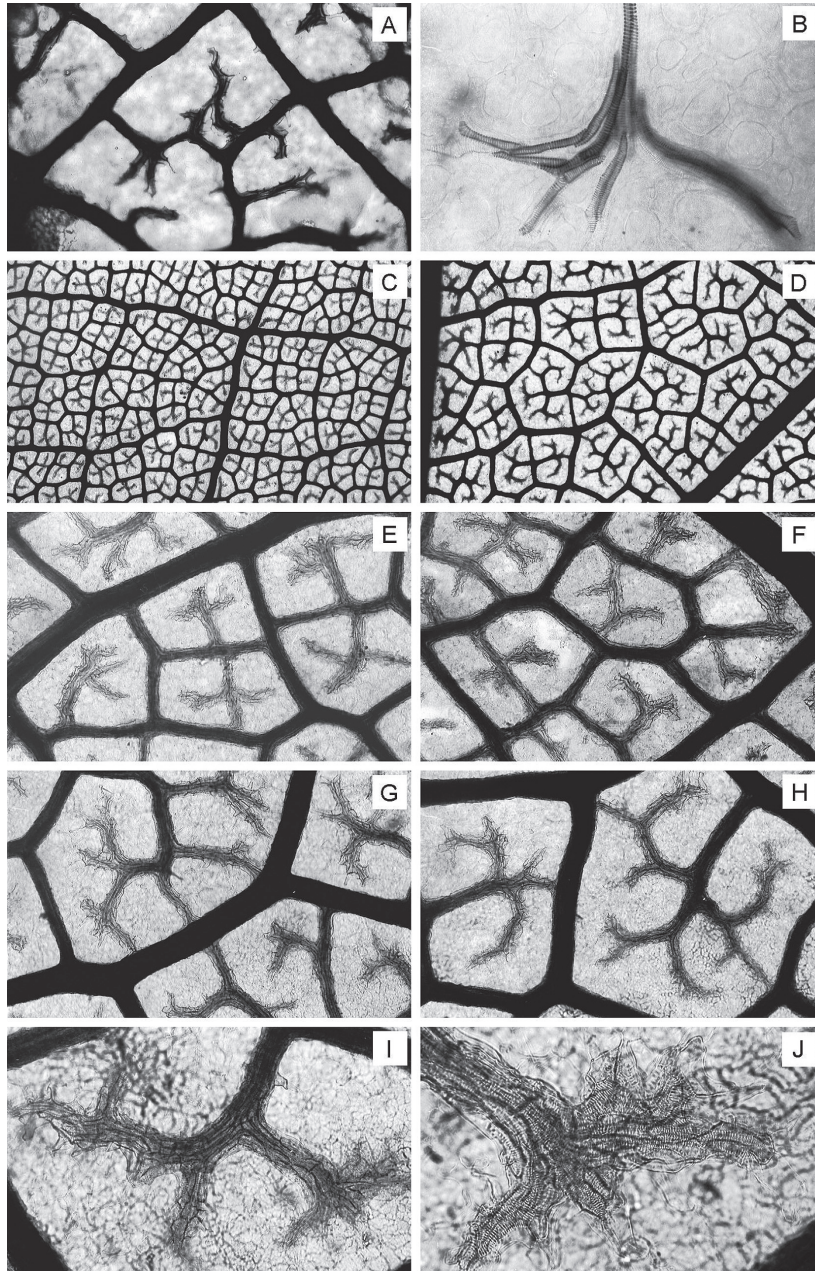


Fig. 4. Minor venation in leaves of *Cryptocarya mandioccana* Meissner. A. Eophylls: incomplete reticulation, detail of anastomosis ($\times 30$); B. Eophylls: detail of veinlet ($\times 300$). C. Nomophylls: perfect reticulation, veinlet termination few-branched, intercostal region ($\times 18.75$); D. Nomophylls: imperfect reticulation, dendroid veins, intercostal region with secondary vein ($\times 18.75$); E-H. Nomophylls: detail of areoles and veinlet termination ($\times 30$); I-J. Nomophylls: detail of veinlet termination (I $\times 100$; J $\times 300$). (Photomicrographs by author).

Lauraceae commonly have inorganic inclusions such as large rhomboid crystals. These are diagnostically valuable. They are associated with all types of sclereids in *Cryptocarya* (the Brazilian *C. aschersoniana* and *C. moschata*, current status *C. mandioccana*, being the exception). Compact blocks or plugs of “vitreous” or “dense” silica in fibre and/or sclereid lamina are characteristic of the barks of *C. aschersoniana* and *C. moschata*. Oil and mucilage cells are common throughout the entire secondary phloem, being particularly numerous in some species of *Cryptocarya*.

In mature secondary xylem, vessels are never exclusively solitary; rather they mostly appear as mixed solitary and in short (2-4) radial multiples in varying proportions. In species of *Cryptocarya* they are typically arranged in a radial pattern (multiple of up to 10 vessels). Perforations are typically simple in *Cryptocarya* although scalariform perforations are found to a very limited degree in species of the “Longotra” group of Madagascar (*Cryptocarya humbertiana* Kosterm., *C. lacrimans* Kosterm., *C. louvellii* Danguy, *C. percoriacea* Kosterm., *C. perrieri* Danguy, *C. scintillans* Kosterm. and *C. trianthera* Kosterm.). All species except *C. louvellii* are now classified under *Aspidostemon* (Rohwer & Richter, 1987).

Fibres are predominantly libriform and arranged in radial rows, being horizontally stratified in *Cryptocarya*; with numerous pits restricted almost exclusively to radial walls, small (2-4 µm) and slightly conspicuous. Fibres are for the most part non-septate in *Cryptocarya* (except in “Longotra” group). Solid organic contents (“gums”) are extremely rare and were reported to “Longotra” group.

In *Cryptocarya* (except the “Longotra” group) and *Ravensara*, the parenchyma (axial) is basically paratracheal, with distribution sparse to weakly vasicentric, in combination with multiseriate (2-4 up to 8) marginal bands. Rays are predominantly 2-3 cells wide and less than 1 mm high. Uniseriates and multiseriates up to four cells wide are characteristic for *Cryptocarya*. Rays are conspicuously heterogeneous, *i.e.* uniseriates are composed of mostly upright cells, whereas multiseriates have one to several marginal rows of upright cells. The occurrence of aggregate rays within the family is restricted to a few species of *Cryptocarya* from the South East Asian and Australo-Pacific regions [*C. australis* (Cunn. ex Hook.) Benth. (current status: *C. laevigata*), *C. chinensis* (Hance) Hemsl., *C. corrugata* C.T. White & Francis, *C. densiflora*, *C. glaucescens*, *C. mannii* Hillebr., *C. meissneri* F. Muell. (current status: *C. glaucescens*), and *C. nitens* Kood. & Valet.]. Sheath cells are developed sporadically in several species of *Cryptocarya*. Rays are typically storeyed in the “Longotra” group of Madagascar.

Inorganic deposits are quite frequent in lauraceous wood. However, simultaneous occurrence of both calcium-oxalate (CaC_2O_4) crystals and silicon dioxide (SiO_2) is extremely rare and restricted to a few species of *Cryptocarya* and *Beilschmiedia*. In the “Longotra” group, no crystals have been observed in the secondary xylem, and the presence of silica is restricted to some species of *Cryptocarya*.

The work of Richter (1981), based on the anatomy of 41 Lauraceae genera (830 species, represented by more than 1600 specimens), has shown that

certain groups of genera show a high degree of anatomical uniformity. This, in turn, makes that wood and/or bark structure cannot be used to corroborate the generally accepted generic distinctions. This applies particularly to the large *Beilschmiedia* complex (comprising *Beilschmiedia*, *Endiandra*, *Potameia*, *Triadodaphne*), and the *Cryptocarya* complex consisting of *Cryptocarya* and *Ravensara*. Richter (1987) further proposed that wood and bark anatomy suggest a bipartite subdivision of the family. One subdivision holds the *Beilschmiedia* and *Cryptocarya* complexes, while the other houses the remaining taxa except for the parasitic climber *Cassytha* (Richter, 1987).

3.3. Inflorescence

Inflorescences of Lauraceae are rarely terminal, sometimes pseudoterminal, usually axillary. Inflorescences originate from the axils of frondose or bracteose leaves of a proliferating main axis and, as a rule, have a determinate growth. In the tribe Cryptocaryeae Nees (*sensu* van der Werff & Richter, 1996), inflorescences are paniculate to \pm cymose (basically of thyrsoïd or thyrso-paniculate type in the sense of Weberling, 1989) (Fig. 5), *i.e.* they start with a racemose branching pattern, but are cymose (usually dichasial) in their distal parts (Rohwer, 1993a). The lateral flowers of a “cyme” are not quite opposite, and flowers can appear individually placed along an inflorescence axis (van der Werff & Richter, 1996).

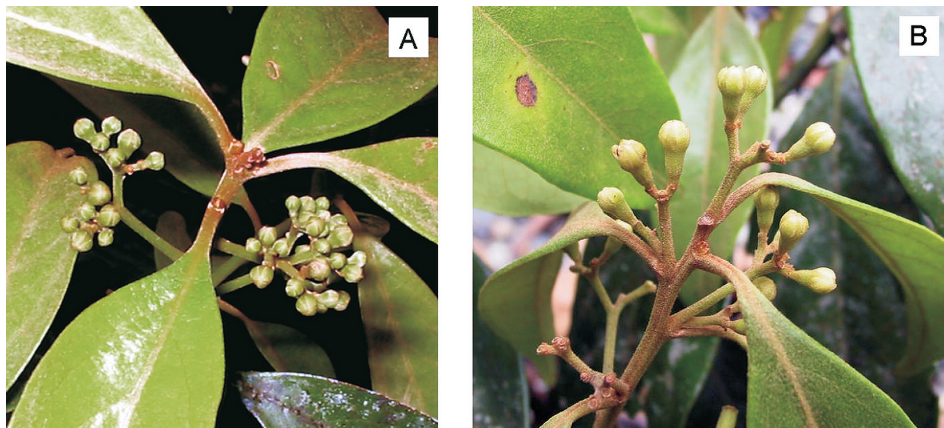


Fig. 5. Inflorescences of *Cryptocarya mandioccana* Meissner. A. Axillary, with flower buds; B. Axillary and pseudoterminal, with flowers almost at anthesis and scars of fallen flowers. (Photographs by author and A.J. Cavalheiro, respectively).

3.4. Flower

Species of Brazilian *Cryptocarya* have a typical lauracean flower structure, as described by van der Werff (1991, 2001) and Rohwer (1993a, 1994). Flowers are actinomorphic, perigynous, pedicellate, bracteate, hermaphroditic (bisexual), trimerous, with “complete” floral diagram (Fig. 6), *i.e.*, there are two perianth whorls of three sepaloïd tepals each, which are usually equal in size and shape; the androecium is arranged in three whorls of three fertile stamens each, and

one whorl of well-developed staminodes (Fig. 7 F), while the gynoecium is the central pistil. Whorls are counted from the outside to the centre of the flower. Whorl I is positioned opposite the outer tepals, whorl II is facing the inner tepals, whorl III is opposite whorl I, and whorl IV (staminodes) opposite whorl II. The stamens of whorls I and II are nearly identical and seemingly form one whorl of six stamens, with introrse anthers. The stamens of whorl III have a pair of basal-lateral appendages (glands; Fig. 7 F), and the anthers are lateral or lateral-extrorse (Fig. 7 F). Anthers are disporangiate, with one functional, valvately dehiscent pollen sac per theca (*i.e.*, one sporangium per theca, which opens by a valve) (Fig. 7, 8). The receptacle is enlarged, urceolate, and completely enclosing the gynoecium, which invariably consists of a single carpel with superior ovary containing a single ovule.

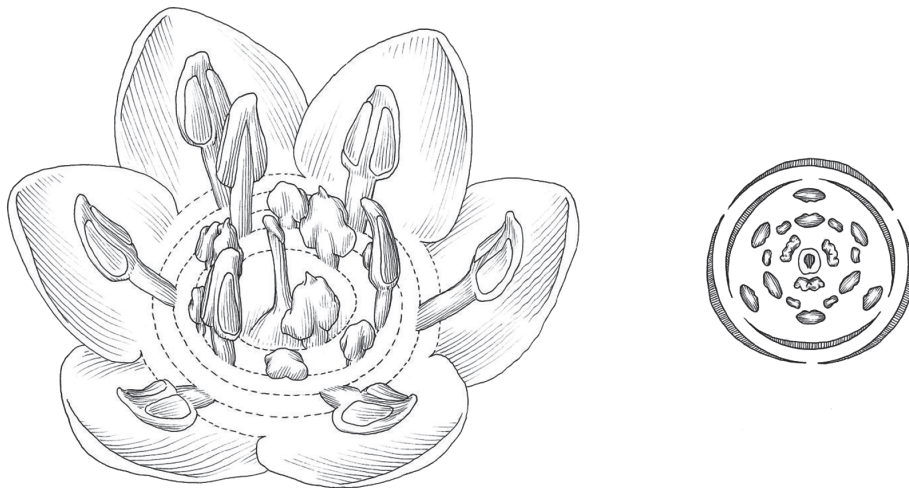


Fig. 6. Schematic flower and floral diagram of *Cryptocarya*.
Floral formula: \ominus P: 3 + 3; A: 3 + 3 + 3 + (3); G: 1.

Within the limits of this basic organization, Brazilian *Cryptocarya* species do not show pronounced floral variation. Flower shape is rather infundibular (funnel-shaped) with erect or erect-patent tepals. The androecium is also little variable. Stamens of the outer androecial whorls are (sub-)equal and in all species the filaments are as long as or (slightly) shorter than anthers (rarely stamens are stipitate). Two different anther types occur in whorl I and II stamens. In species of the *Cryptocarya moschata* group (*C. aschersoniana*, *C. botelhensis*, *C. guianensis*, *C. micrantha*, *C. moschata*, *C. riedeliana*, *C. subcorymbosa*), and *Cryptocarya mandioccana* group (*C. mandioccana*, *C. sellowiana*, *C. wiedensis*), anthers are (nearly) ovate with protruding connectives that emerge between and beyond locelli. Locelli are elliptical, occupying almost all the available space and sterile tissue is located mostly above locelli. In the *Cryptocarya citriformis* group (*C. citriformis* and *C. saligna*), anthers are depressed-oblong to broad-ovate in shape, and connective tissue is either reduced between or level with the two locelli, the latter being suborbicular. Glands of whorl III stamens are either sessile or raised on short to long stalks.

After the anthesis the tepals usually fall off as a continuous ring, together with all stamens, and staminodes (Fig. 7 A; also illustrated in Meissner, 1866). As a rule, remnants of flower parts on the apex of the accrescent tube are only found in some immature fruiting material (except for *C. sellowiana* and *C. subcorymbosa*). According to Endress & Hufford (1989), in the Lauraceae, each pollen sac opens independently via an uplifting flap, which is hinged at its apex (Fig. 7 A). Mez (1888) pointed out that the anther does not deform at dehiscence, except for the valves that may shrink to one-third of the original size, remarkably in *Ayden-dron* and *Acrodiclidium*. In *Cryptocarya*, shrunken flaps of valves are found in all Brazilian species, but most visible in *C. aschersoniana*, *C. citriformis*, *C. mandioccana*, *C. micrantha*, and *C. saligna* (cf. Fig. 7 B, D; 8 A-B). Another noteworthy feature in the Lauraceae is the stickiness of the pollen grains (see Kubitzki & Kurz, 1984). This stickiness holds pollen together, whereby they adhere to the surface of the pollinator's body or to the flaps. This seems to be a mechanism of exhibition and release of pollen (also reported for *Endlicheria* by Chanderbali, 2004) (Fig. 7 C-E).

As discussed by Rohwer (1994), the number of pollen sacs per anther and their position are traditionally regarded as very important systematic characters in the Lauraceae, although with diverging opinions about the evolutionary direction in these characters. According to Drinnan (cited by Rohwer, 1994), disporangiate anthers represent the plesiomorphic condition in the family, since all close outgroups (Monimiaceae-Atherospermatoidae, Gomortegaceae, Hernandiaceae), and the earliest known fossil lauraceous flowers (Drinnan *et al.*, 1990) have disporangiate anthers.

Like indicated by Rohwer (1994) for *Brassiodendron fragrans* C.K. Allen (Rohwer, 1994 – Fig. 4; current status: *Endiandra montana* C.T. White) and several species of *Endiandra* (Hyland, 1989 – Fig. 76F, 78B, 79B; Rohwer, 1994 – Fig. 5), Brazilian *Cryptocarya* spp. have four pollen sacs, but the two pollen sacs of each theca open by means of a common, sometimes slightly two-lobed, flap (Fig. 7 B, E; 8 A-D; 30 C; 36 D). This represents one of the three transitional (intermediate) forms between disporangiate and tetrasporangiate anthers. As these intermediate forms are distributed over several genera, the transition must have occurred several times within the family, weakening the argument that disporangiate anthers represent the primitive state. Rohwer (1994) also pointed out that a reduction from four pollen sacs to two appears much more likely and can be interpreted as both more economical and allowing a better pollen presentation. Even if disporangiate anthers were plesiomorphic within the Lauraceae, one would have to allow for independent reversals from the tetrasporangiate to the disporangiate condition.

3.5. Fruit and seed

The mature fruit of *Cryptocarya* is completely covered by the accrescent hypanthium (receptacular tube or receptacle). According to Rohwer (1993a), “the fruit of the Lauraceae can be described as a one-seeded berry or as drupe with a weakly developed endocarp”. Under the systematic treatment of fruit types proposed by Spjut (1994), the fruits of *Cryptocarya* are classified in Eucarpia (one or more closed carpels), Category I – Simple Fruits, Series A – Angiocarpi,

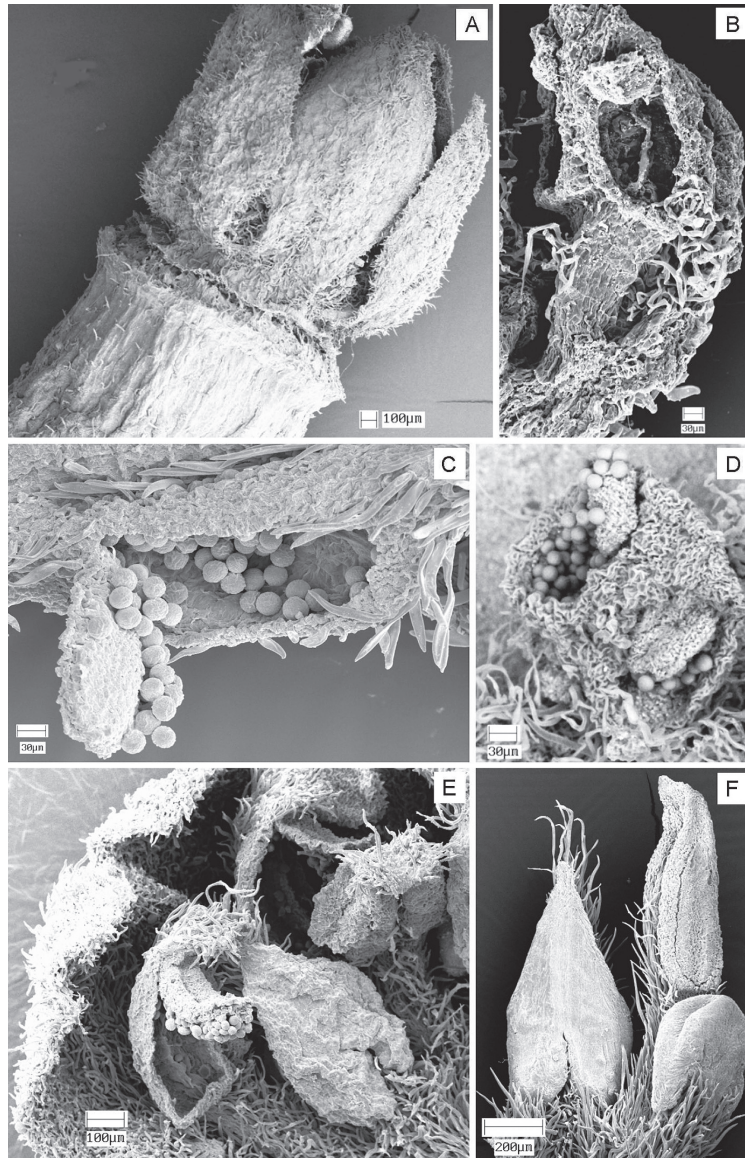


Fig. 7. SEM micrographs. A. *Cryptocarya moschata* Nees & Martius, detachment of tepals and androecial parts from the flower tube after fertilization; B. *Cryptocarya citriformis* (Vellozo) P.L.R. de Moraes, stamen of androecial whorl I showing shrunken flaps (from Peckolt 166); C. *Cryptocarya botelhensis* P.L.R. de Moraes, stamen of androecial whorl III, detail of valvate dehiscence via an uplifting flap, hinged at its apex (from Moraes 2329); D. *Cryptocarya saligna* Mez, stamen of androecial whorl II (from Moraes 2305); E. *Cryptocarya moschata* Nees & Martius, stamens and staminode (from Moraes 2241); F. *Cryptocarya mandioccana* Meissner, staminode (left), gland (right), and stamen of androecial whorl III with anther lateral (from Santos 2811). (Photomicrographs by author).

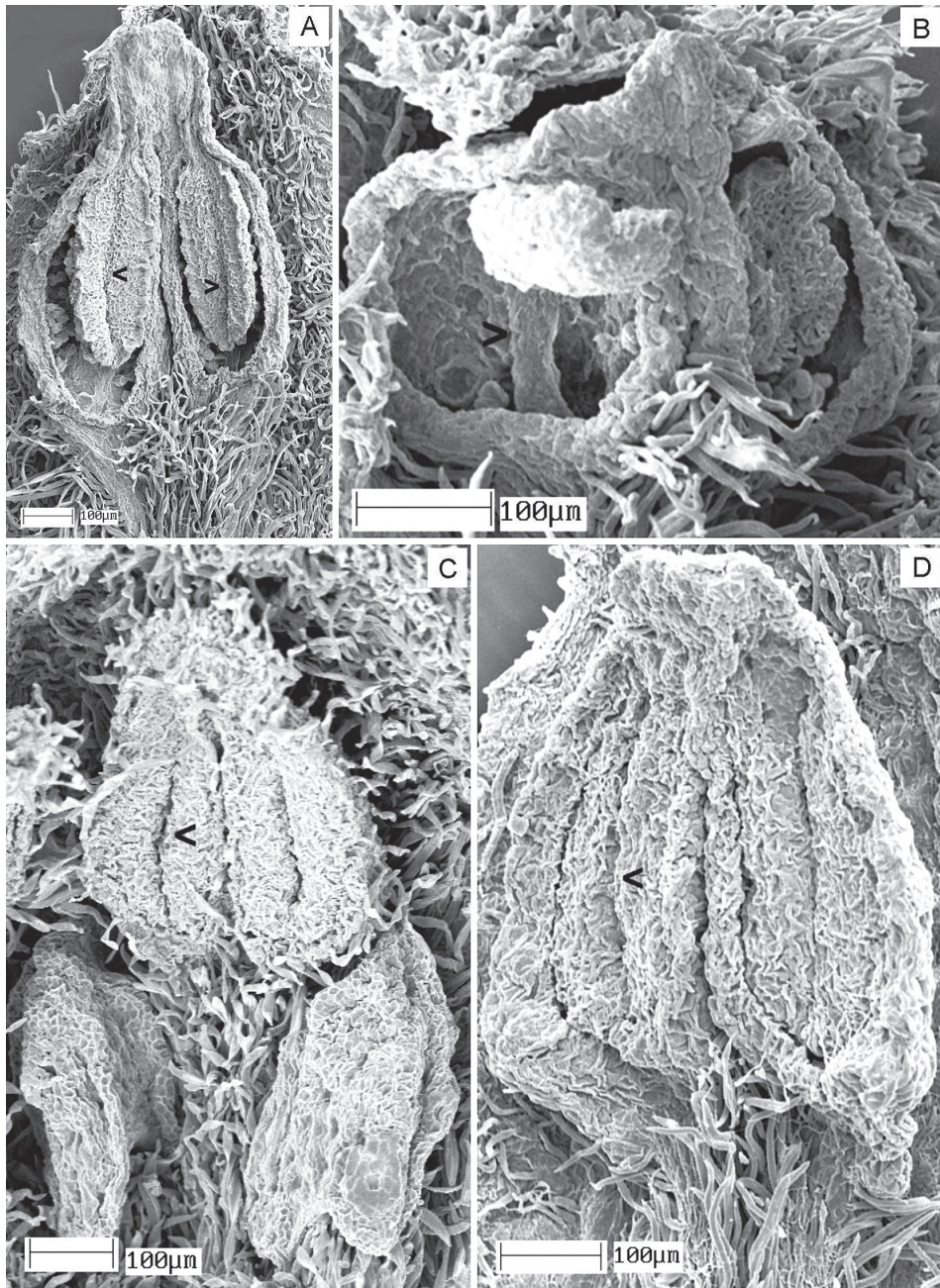


Fig. 8. SEM micrographs of adaxial side of stamens of androecial whorls II and II, introrse. A. *Cryptocarya mandioccana* Meissner (from Esteves 16, SPSF); B. *Cryptocarya micrantha* Meissner (from Heringer 913, VIC); C. *Cryptocarya riedeliana* P.L.R. de Moraes (from Duarte 7991, RB); D. *Cryptocarya subcorymbosa* Mez (from Glaziou 18436, OUPR).

Note furrow in the middle of the flaps (A, C, D) and longitudinal septum in the middle of the anther locule in B (<). (Photomicrographs by author).

Acrosarcum (simple indehiscent fruit with an undifferentiated pericarp lacking a stony endocarp and surrounded by an accrescent fleshy exocarp derived from perianth or receptacle) or Pseudodrupe (anthocarpous fruit with an undifferentiated indurate pericarp surrounded by a fleshy or coriaceous exocarp). Under the classification of fruits proposed by Barroso *et al.* (1999) for Brazilian Dicotyledons, the fruit of *Cryptocarya* is classified as Nucoid (Hertel, 1959), Nucula type.

When the fruit is completely enclosed in the accrescent receptacular tube the latter assumes the function of the exocarp and mesocarp (Kostermans, 1957a), and usually takes over the attractive colouring (Rohwer, 1993a). In *Cryptocarya* the pericarp of the fruit becomes woody and is often ribbed. The accrescent flower tube becomes entirely adnate to the fruit, although the ovary in the flower is still free from the tube.

In Lauraceae, as a rule, mature fruits are black in colour, sometimes red, rarely yellow (Kostermans, 1957a). For instance, in 43 of the 46 species of Australian *Cryptocarya* described by Hyland (1989), the fruits were indicated as black, blue-black, purple or black, bluish black, or purplish black when perfectly ripe; the three remaining species had more vivid colours (*i.e.* yellow, orange or red in *C. laevigata*; red, orange-red, pinkish orange or orange in *C. oblata* Bailey and pink or red in *C. pleurosperma* C. White & Francis). From the 20 species of *Cryptocarya* occurring in China, 13 are described with black fruits when ripe, and only *C. chingii* Cheng with red fruits (Li Xi-wen *et al.*, *ined.*; but black in Allen, 1942). According to van der Merwe *et al.* (1988), the prevailing colour in all African species of *Cryptocarya* is black or red. Brazilian species of *Cryptocarya* have their ripe fruits coloured yellow (or at least yellowish, in *Cryptocarya aschersoniana*, *C. botelhensis*, *C. guianensis*, *C. mandioccana*, *C. micrantha*, *C. moschata*, *C. riedeliana*, *C. subcorymbosa*), yellow, orange or red (*C. saligna*), brown (*C. citriformis*), and black (*C. sellowiana*). Finally, it can be noted that, Kostermans (1937) reported that the fruits of *C. alba* are red or pink. Looser (1963) on the other hand states that they can sometimes be white or whitish, at least partially.

The shape of the fruits of Brazilian *Cryptocarya* is usually globose, sometimes ellipsoid (*C. citriformis*, *C. saligna*), and often provided with a neck at the base, presenting considerable variation (Fig. 9). To highlight the variation in the shape of fruits Moraes (1993) collected 1892 fruits of *C. mandioccana* from 27 trees of the population at Parque Estadual Carlos Botelho. Most trees (16) presented fruits that are strictly prolate (polar radius > equatorial radius), whereas 11 trees presented fruits prolate, spherical and oblate (equatorial radius > polar radius), from which only one tree bore fruits strictly oblate (Fig. 10).

The size of mature fruits is to be measured with the accrescent receptacular tube, also called anthocarp (see Spjut, 1994). More details on the biometry of mature fruits of *C. mandioccana* and *C. moschata* can be found in Moraes & Alves (2002).

According to Endress (1972, 1990), Corner (1976), Heel (1981), Rohwer (1986), and Endress & Igersheim (1997) the ovary of the Lauraceae is unicarpellate,

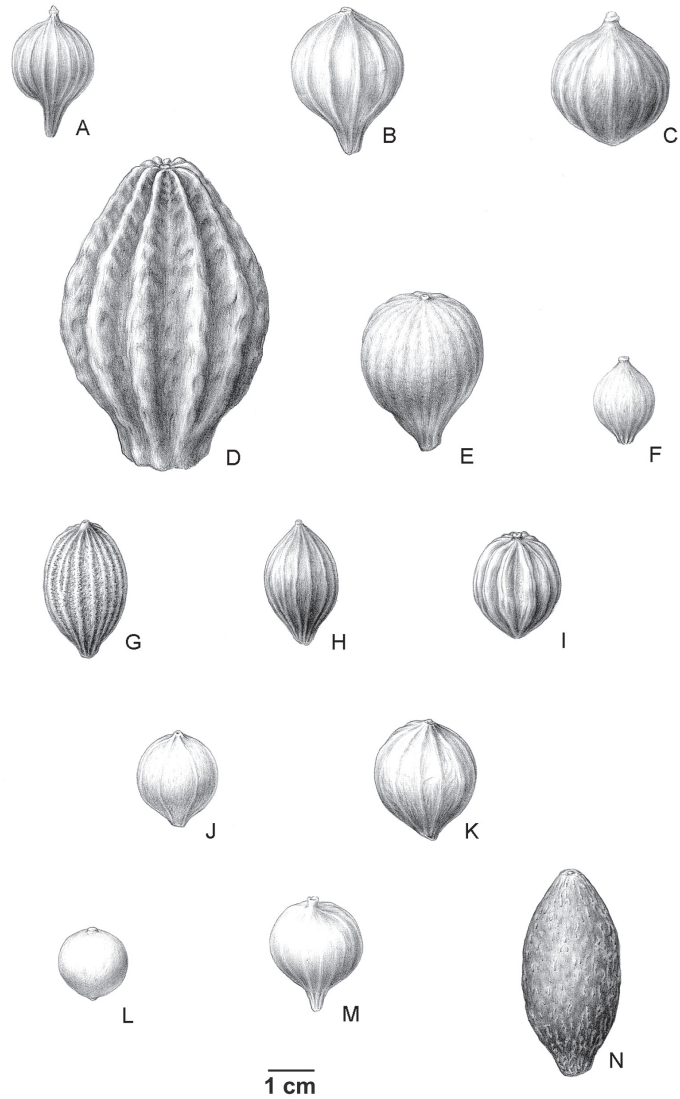


Fig. 9. Diaspores of Neotropical *Cryptocarya*. A-C. *Cryptocarya guianensis* Meissner (from Lescure 356, Prévost & Grenand 2016, and Oldeman 1816, respectively); D. *Cryptocarya citriformis* (Vellozo) P.L.R. de Moraes (from Moraes 2154); E & G. *Cryptocarya micrantha* Meissner (from Moraes 2156 and Moraes 2449, respectively); F. *Cryptocarya aschersoniana* Mez (from Moraes & Oliveira 2504); H. *Cryptocarya mandioccana* Meissner (from Moraes 2452); I. *Cryptocarya botelhensis* P.L.R. de Moraes (from Moraes 1243); J-K. *Cryptocarya moschata* Nees & Martius (from Moraes 2101 and Moraes 2115, respectively); L-M. *Cryptocarya aschersoniana* Mez (from Reitz & Klein 2633 and Moraes 2424, respectively); N. *Cryptocarya saligna* Mez, without remotion of the accrescent receptacular tube (from Kuhlmann s.n. – RB, fruit collection 1576).

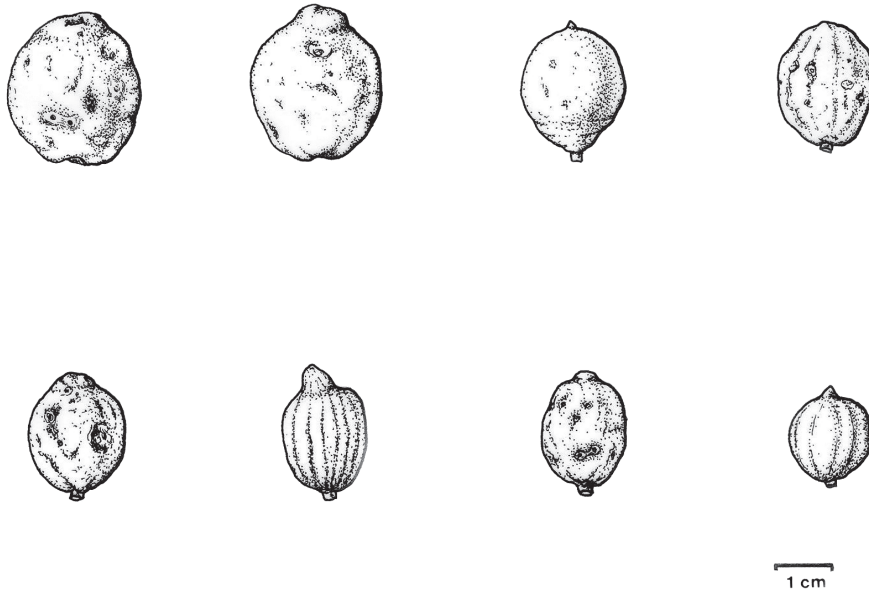


Fig. 10. Variation in shape and size of mature fruits (without remotion of the accrescent receptacular tube) of *Cryptocarya mandioccana* Meissner from the population of Parque Estadual Carlos Botelho, São Miguel Arcanjo, SP (from Moraes, 1993).

small to medium, ascidiate (pitcher-shaped), with the ovarial cavity being almost completely filled by the solitary ovule in central median placentation. The carpel is closed at anthesis and its mode of angiospermy is represented by postgenital fusion of the stylar (and ovarial) slit. The ovule is anatropous, pendent, with dorsal raphe and the micropyle on the placental side with overarching funicle, bitegmic, pachychalazal (or perichalazal), crassinucellate; ovule size at maturity varies between 750-1400 μm ; *o.i.* (outer integument) 3-5 cells thick, semiannular; *i.i.* (inner integument) 2-4 cells thick (integument thickness is quite uniform in Lauraceae); micropyle closed by the endostome or by the nucellus; chalaza massive, unspecialised; embryo-sac often large and elongate.

The reduction to a single carpel makes that the single ovule can develop into a large and exalbuminous seed. According to Corner (1976), this structure secures rapid establishment of the seedling in the forest.

The structure of the seed in Lauraceae has been described by Corner (1976). The seed is massive, with thin testa, 4-20 cells thick, more or less multiplicative, most layers persistent or the inner crushed (crushed entirely in *Cryptocarya* except for the inner epidermis), without stomata, outer epidermis as a layer of cuboid cells with tannin, or unspecialised; mesophyll unspecialised, without oil cells; inner epidermis typically composed of longitudinally and tangentially elongate, narrow tracheids with spiral or annular thickening, slightly lignified or not, 2-3 layers of tracheids at the micropyle; tegumen not or scarcely thickening, soon crushed; nucellus soon absorbed or persistent as ruminations (*Cryptocarya*, *Ravensara*); endosperm nucellar, absorbed by the embryo.

For *Cryptocarya wightiana* Thwaites, Corner (1976) described the ovule with the “o.i. 3 cells thick, i.i. 2-3 cells thick; testa 4-5 cells thick, thin-walled, unspecialised (except inner epidermis) and becoming crushed; i.e. composed of longitudinal tracheids with annular or closely spiral, lignified thickening, differentiating soon after fertilization, forming a pellicle over the embryo; tegumen not multiplicative, soon crushed; vascular bundle of the raphe not branching, becoming a flattened band in the perichalaza, with a thin brownish hypostase; chalaza extending into a perichalaza in the lower part of the seed; nucellus well-developed, forming a crescentic ingrowth from the perichalaza between the cotyledons, appearing as a rumination, eventually drying up”. Still, “the persistent perianth-tube, surrounding the immersed pericarp, gives to the fruit in section the appearance of a large seed in which the perianth-tube would represent the testa, the pericarp the tegmen, the testa the nucellus, and the nucellus the endosperm”.

Moraes (1993), summarised in Moraes & Paoli (1996), studied the morphology of fruits and seeds of *Cryptocarya mandioccana* from material collected at Parque Estadual Carlos Botelho. Fruits were classified as nucoids (*sensu* Hertel, 1959), one-seeded, surrounded by the fleshy accrescent hypanthium. The pericarp is thick and lignified, forming indentations in the fleshy portion (Fig. 11). The diaspores are constituted by pericarp plus seed, presenting pronounced variation in shape, within and among individual trees (Fig. 12). The pericarp is externally whitish, with the inner epidermis brown; apex mucronate, with a small pore, which internally (in the seed) corresponds to the site of micropyle (Fig. 11). Seeds are anatropous, endotestal, exalbuminous, with crushed tegumen, not adhered to pericarp, ellipsoid. External colour of integument is dark brown, glossy. Seed cavity entirely filled by the embryo (Fig. 11). Embryo is constituted by fleshy cotyledons, massive, whitish, asymmetric, plane-convex, and mucronate at apex, completely covering the radicle-hypocotyl axis, which is minute, flattened, and rhombic; axis is ascendant and the plumule is turned towards the centre of cotyledons; below the plumule, in the centre of radicle-hypocotyl axis there are two minute lateral appendices that articulate with the cotyledons.

4. Karyology

Up till now relatively few studies have been performed on the cytogenetics of South American Lauraceae. Okada & Tanaka (1975) provided a summary. The base number is $x = 12$ ($2n = 24$), with very little variation in the karyotype throughout the family. Polyploidy has however been observed in *Cassytha*, *Laurus*, *Litsea* and *Sassafras* ($2n = 48$), and in species of *Laurus* and *Neolitsea aciculata* ($2n = 72$). Metaphase chromosomes are 1-3 μm long (5-7 μm in *Cassytha*); position of centromere varies from median to subterminal; heterochromatin is found only in the proximal regions of both arms (more evenly distributed in *Cassytha*). Fig. 13 (from Moraes & Gardingo, 1996) shows a typical *Cryptocarya* karyotype

More recent information on the karyology of the Lauraceae can be found in Contim *et al.* (2005) and Oginuma & Tobe (2006). It can be concluded that more studies are needed to clarify chromosome evolution in the Lauraceae.

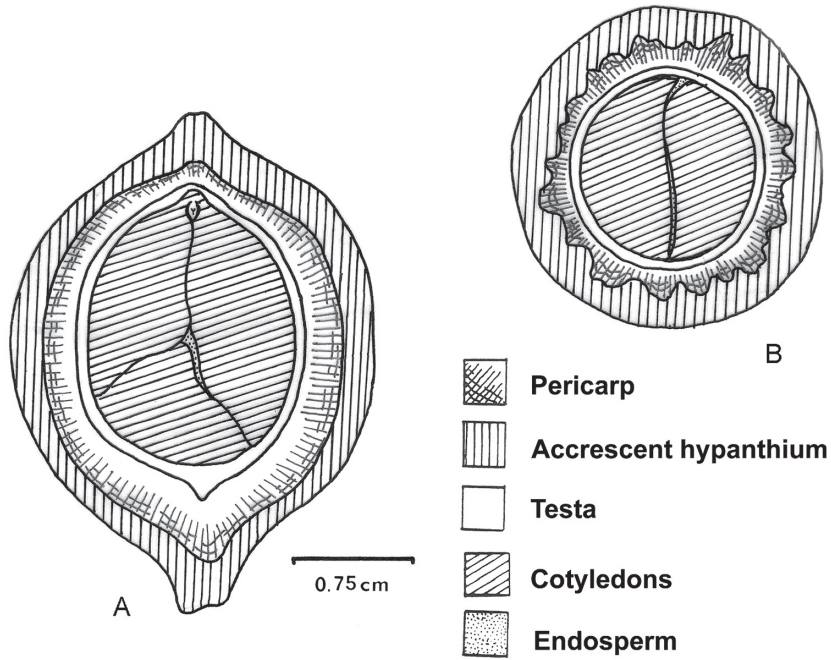


Fig. 11. Fruit diagrams of *Cryptocarya mandioccana* Meissner. A. Longitudinal section; B. Transversal section (adapted from Moraes, 1993, and Moraes & Paoli, 1996).

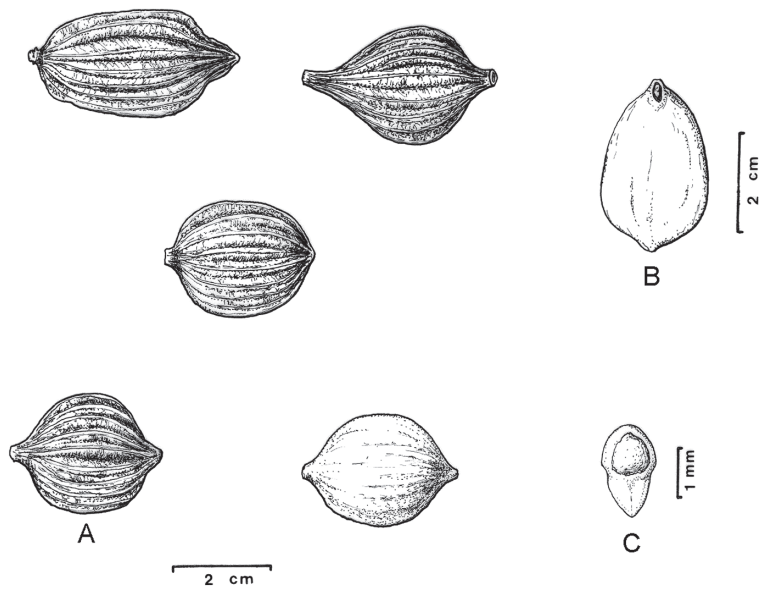


Fig. 12. *Cryptocarya mandioccana* Meissner. A. Morphological variation of diaspores (pericarp and seed); B. Embryo with one of the cotyledons detached; C. Radicle-hypocotyl axis (from Moraes, 1993, and Moraes & Paoli, 1996).

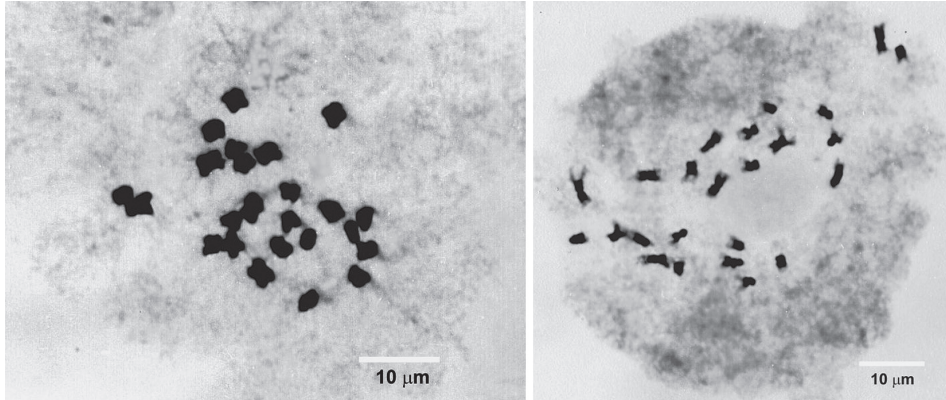


Fig. 13. Photomicrographs of somatic chromosomes of *Cryptocarya mandioccana* Meissner ($2n = 24$). (Photomicrographs by J.R. Gardingo & author).

5. Palynology

The pollen grains of species of *Cryptocarya* have been described as inaperturate, spheroidal, with a characteristic pollen wall, that has an “extreme thinness of exine and a massive nature of the intine” (Veloso & Barth, 1962; Raj & van der Werff, 1988). However, in southern African *Cryptocarya* species, the pollen grains are strongly flattened, peroblate/oblate (van der Merwe *et al.*, 1988, 1990). The exine surface of a pollen grain can be either more or less smooth or variously verrucate (wrinkled).

Examples of descriptions of pollen grains can be found in Veloso & Barth (1962), Raj & van der Werff (1988) or (Rohwer, 1993a).

It is interesting to note that palynological studies can provide important windows for understanding the evolutionary history of the taxon. For instance, Raj & van der Werff (1988) put forward the hypothesis that, *Cryptocarya* is isolated from other neotropical genera, because its pollen grains are quite different, as they seem to be devoid of spinules and spinuloid excrescences in the exine surface. However, Rohwer (1993a) reported that the exine sculpture in some species of *Cryptocarya* presents a pattern densely covered with minute spinules. This variability registered from the palynological record made Rohwer (1993a) suspect that the genus may not be a natural group.

Figure 14 shows some SEM micrographs of flower pieces of herbarium specimens. Pollen grains of some of the species are shown.

However, it must be noted that, according to Drinnan *et al.* (1990) and Herendeen *et al.* (1994), the palynological record of the Lauraceae is very poorly documented because their pollen grains have thin exine with little sporopollenin in the mature pollen wall and consequently are seldom preserved (see also Kubitzki, 1981; Hesse & Kubitzki, 1983). For Eklund & Kvaček (1998), this might explain why the family is completely absent in Early Cretaceous palynofloras.

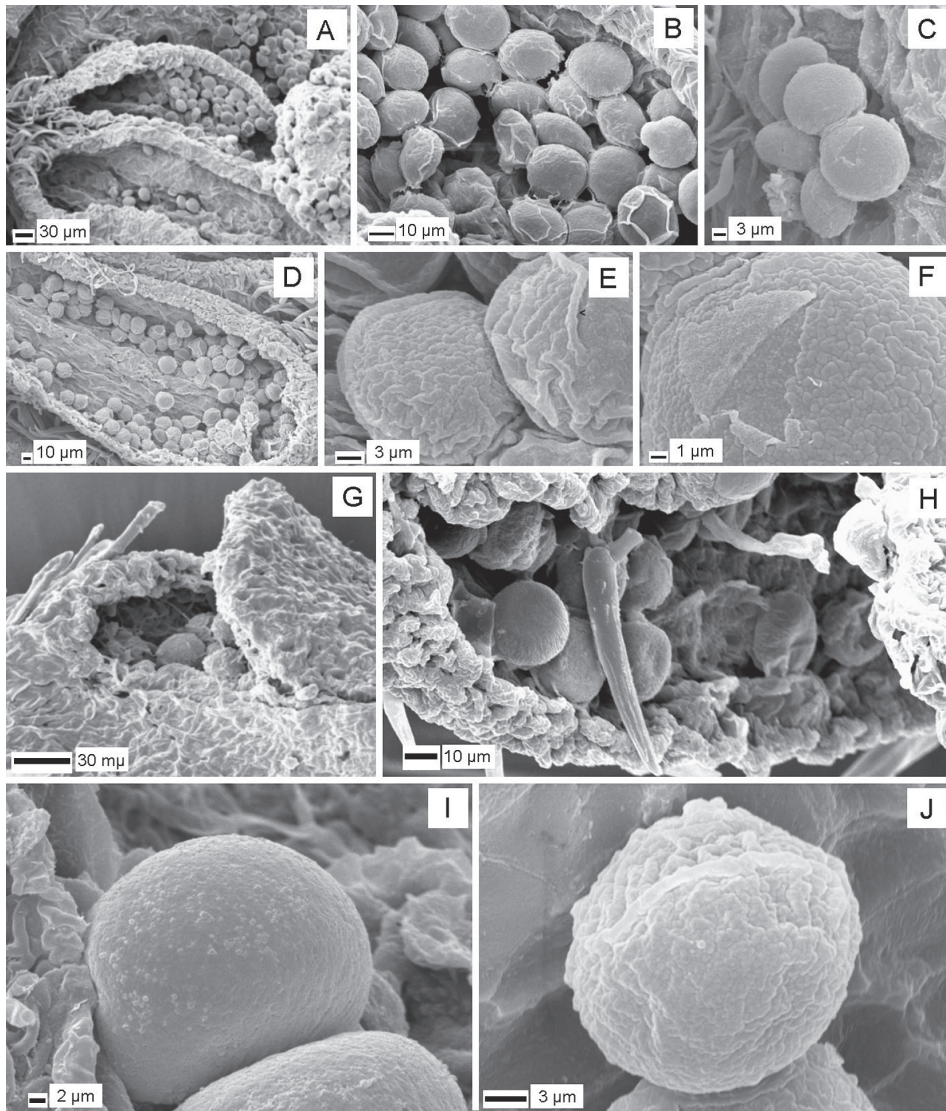


Fig. 14 SEM micrographs of pollen grains. *Cryptocarya aschersoniana* Mez: A-B. Klein 3960 (HBR); C, F. Smith & Reitz 13266 (HBR); D-E. Barbosa & Abe 397 (MBM). *Cryptocarya guianensis* Meissner: G. Pires & Silva 1388 (Herbário Jari). *Cryptocarya mandioccana* Meissner: H. Santos 2811 (CEPEC); I. Hatschbach 5175 (MBM).

Cryptocarya moschata Nees & Martius: J. Hoehne s.n. (HB-53855).

(Ridges – < – are due to shrivelled exine surface when dry).

(Photomicrographs by author).

6. Distribution

According to Chanderbali *et al.* (2001), species of Cryptocaryeae are predominantly southern hemispheric, with a distribution that indicates a Gondwanan history. *Beilschmiedia* and *Cryptocarya* are the most widespread genera of Lauraceae. From molecular data, the genetic distance-based age estimations have shown that these genera diverged from their most recent common ancestor about 90 ± 20 million years ago, indicating also a direct migration throughout Gondwana, and a widespread pre-drift distribution for both genera. *Cryptocarya* is present in South America, South Africa, Madagascar, Asia, Australia and Oceania (van der Werff, 1992). Although species relationships have not been investigated yet, Kostermans (1938b) indicated a possible connection between the African species *C. angustifolia* E. Meyer and the Chilean *C. alba*, since their fruits are strongly alike.

In the Neotropics, *Cryptocarya* ranges from Costa Rica to south Brazil, northeast Argentina, Uruguay and central Chile, with species registered for Andean Venezuela, Guyana, Surinam, French Guiana, Brazilian Amazon, Bolivia, Peru, and Ecuador (Fig. 15). Southeastern Brazil is the main centre of diversity of Neotropical *Cryptocarya*, with 12 species, nine of them endemic to this region. Except for the Chilean endemic, *Cryptocarya alba*, which occurs in semiarid vegetation (Mediterranean-type vegetation-sclerophyllous shrublands and woodlands), the other species occur in moist forest habitats from elevations of around sea level to 2000 m at Andean Upper Montane Forest in Cajamarca, Jaén, Peru. However, according to Armesto & Martinez (1978) and Celis-Diez & Bustamante (2005), *C. alba* inhabits south-facing slopes and humid ravines supporting the inference of a topographic moisture gradient, with the south-facing slope representing the mesic end and the north-facing slope the xeric end.

Cryptocarya is present in three out of the four biomes of the Brazilian flora. It is present in the Amazon Forest, the Atlantic Forest (“Mata Atlântica” *sensu lato*), and the Savanna (which comprises the “Cerrado” *sensu lato* and also the Brazilian swampland – the “Pantanal”), and absent from the Steppe (which comprises both the Semiarid northeast – “Caatinga” and the southern grasslands – “Campos Sulinos” or “Pampas”). The absence of *Cryptocarya* species from the Caatinga indicates that low water availability restricts their spreading (*C. alba* being an exception).

The sparse and scattered distribution of *C. guianensis* in the Amazon Basin and the relatively low distribution of species from West-central states can be explained as a collecting artefact. The presence of *C. guianensis* in the south of Bahia is an example of an Amazonian species that has invaded the Atlantic forest. According to Joly *et al.* (1991), the occurrence of some typical Amazonian species in the Atlantic forest in the south of the state of Bahia and north of Espírito Santo, on one hand, and the presence of species typical to the Paraná and Uruguay river basins in the Atlantic forest of Santa Catarina, Paraná and the south of São Paulo state, on the other hand, suggests that the Atlantic rain forest has gone through a process of expansion and retraction mainly as a consequence of climatic variations (see also Joly *et al.*, 1999). The deposition of the Formação



Fig. 15. Distribution of Neotropical *Cryptocarya*, excepting for *C. alba* from Chile.

Barreiras (Berier Formation), during the Tertiary Period, allowed the expansion of the Amazonic formations into the Atlantic forest. The existence of Hiléia Bahiana as far south as the region of Colatina, Espírito Santo, shows that the periods of high humidity that occurred at the end of the Tertiary or beginning of the Quaternary Period had a strong influence on the floristic composition of the coastal formations. According to Behling *et al.* (2000), only the cold and very wet climatic conditions with short annual dry seasons characteristic of the late glacial period allowed an expansion of mountain forests, floodplain forest and gallery forests along NE Brazilian rivers. Floristic exchanges between the Atlantic and Amazon rain forest were possible during the Late glacial period. De Oliveira (2005) reported that from the transition Pleistocene/Holocene up to c. 10540 years B.P. the climate of the Caatinga region in northeastern Brazil was humid and relatively colder than is currently the case. This favoured the establishment of an exuberant tropical forest that has a large floristic affinity with Amazonian and Atlantic coast rain forests.

Pollen spectra of this period represent the first botanical evidence of the forest corridor between the Amazon and the Atlantic rain forest, which could explain the great floristic similarity between both biomes. A gradual drying of landscape eliminated such vegetation up to c. 6790 years B.P. The establishment of the modern Caatinga vegetation has been dated at 4535 years B.P. from the fossil sand dunefields of Bahia (De Oliveira *et al.*, 1999). The register from the marine core GeoB 3104-1 (Behling *et al.*, 2000) also indicated that between 15500 and 11800 year B.P. there was an impressive increase in rainfall, making it the wettest recorded period for NE Brazil. The palaeoenvironmental observations made by Behling *et al.* (2000) support the biogeographical hypothesis of a connection between the Amazonian and Atlantic rainforests, by migration routes in Late Pleistocene when wetter and colder climate conditions persisted. This is also supported by botanical data (Ducke & Black, 1954; De Andrade-Lima, 1966), the palynological record and paleontological data (Cartelle & Hartwig, 1996; Hartwig & Cartelle, 1996; De Oliveira *et al.*, 1999).

For the southern and south-eastern states which have been relatively well-sampled, some species have a narrow or scattered distribution and/or may be rare. The latter is the case for *C. citrifomis*, *C. micrantha*, *C. riedeliana*, *C. sellowiana*, *C. velloziana*, and *C. wiedensis* for which the known populations are composed of only few individuals. On the other hand, *C. botelhensis* is known from only a few localities, but its populations have relatively many individuals in protected areas. The presence of *Cryptocarya moschata* in the Savanna domain is due to a contact with the riparian forests or due to contact with semi-deciduous forests, the latter representing its predominant habitat.

In the vegetation of southern Brazil, *Cryptocarya aschersoniana* is a preferential species of the Ombrophilous Mixed Forest ("Araucária Pine Forest", "Mata-de-araucária", "Pinhal", or "Pinheiral"; Klein, 1975), *i.e.* it is more or less abundant in various forest formations, but it predominates or reaches better vitality in *Araucaria* forests. According to Reitz *et al.* (1983, 1988), in Rio Grande do Sul, the distribution of *C. aschersoniana* is almost restricted to areas of the East plateau and North of the state, where the "araucária" is present. The species has

not been found in forests of the Upper Uruguay River and from the Central Depression region, where it is very rare or completely absent. In “Pinhais” of Santa Catarina, it behaves as a hygrophytic selective species, preferring foothills, river banks, as well as the well-drained soils, where it can become one of the most frequent species of the forest’s upper layer. It has a wide geographic distribution in the plateau of Santa Catarina, occurring under high abundance, always in moist or slightly undulated soils of the Araucária Formation region. It is also fairly frequent in the Atlantic pluvial forest, especially in deep valleys, lower slopes, and in floodplains along rivers (Klein, 1974, 1975; Reitz *et al.*, 1978).

7. Intergeneric relationships

Intergeneric relationships within Lauraceae remain poorly understood, despite the recognised economical and ecological importance of many of its species (van der Werff, 1991).

Poor generic concepts are a central problem, allied to the variability of species that are difficult to recognise and that are usually poorly represented in herbaria (Hammel, 1986; Burger, 1988; Burger & van der Werff, 1990). Confusion at generic level is partially due to conflicting evidence from characters of fruits, flowers and wood anatomy (van der Werff & Richter, 1985).

Neotropical species of *Cryptocarya* and *Beilschmiedia* share morphological similarities except for the length of the pistils (long or short), depth of the receptacles (deep or shallow), and enclosure of the fruits (enclosed by floral tube or without cupules) (Nishida, 1999).

According to Rohwer (2000), essentially the same limited set of characters (listed by Kostermans, 1957a) has been used in nearly all classification systems proposed (Nees von Esenbeck, 1836; Meissner, 1864; Bentham, 1880; Mez, 1889; Pax, 1889; Kostermans, 1957a; Hutchinson, 1964; Rohwer, 1993a), but the resulting classification has depended on the author’s opinion on the reliability and inferred taxonomic importance of these characters. Bentham (1880), Mez (1889) and Hutchinson (1964) considered the presence vs. absence of an involucre around several flowers as an important phylogenetic character (Rohwer, 1993b). Rohwer (1993a) followed the latter line of reasoning and recognised only two tribes, Laureae with an involucre, and Perseeae (including *Cryptocarya*) without an involucre. On the other hand, Kostermans (1957a) placed more emphasis on the development of the flower tube in fruit, *i.e.* whether the fruit is (nearly) free on the pedicel at the base surrounded by a cupule, or completely enclosed in receptacular tissue. According to Rohwer (1993b), who does not deny the importance of development of the flower tube in fruit, it often conflicts with flower structure and/or wood anatomy (Richter, 1981). Van der Werff & Richter (1996) reviewed the classifications proposed for the Lauraceae and concluded that androecial characters such as the number of sporangia were not useful in a generic classification of the family. They proposed a classification based on inflorescence structure as well as on wood and bark anatomy.

From the most recent phylogenetic investigation of the Lauraceae (Rohwer & Rudolph, 2005), the tribe Cryptocaryeae showed to be clearly monophyletic. The authors also pointed out that “the genus *Beilschmiedia* is clearly paraphyletic in its current circumscription, with respect to *Endiandra* and *Potameia*”. Still, “the genera *Brassiodendron* and *Triadodaphne*, which both were included in *Endiandra* (the former by Kostermans, 1957a, and Hyland, 1989, the latter by Rohwer, 1993a) can safely be placed in *Beilschmiedia* s.l., although they have not been studied with molecular markers yet”. Last but not least, “the rare South African *Dahlgrenodendron* and the possibly extinct Malaysian *Hexapora* most likely also belong to the *Cryptocarya* group”.

8. Infrageneric relationships

The tentative grouping of the Brazilian species of *Cryptocarya* as proposed here is based on overall gross morphological similarity. The groups are heterogeneous and have not been defined by single characters. Thus, they neither necessarily represent monophyletic groups, nor intend to reconstruct phylogeny. The reason for this approach is due to the fact that Brazilian *Cryptocarya* species usually share quite similar flowers and fruits and thus make it difficult to discuss their relationships based solely on reproductive characters. Additionally, there is no single character that shows a clear-cut discrimination of possible groups.

Similarly to what has been stated by Rohwer (1993b) in his treatment of *Nectandra*, the circumscription of *Cryptocarya* species faces a considerable morphological variability, with the occurrence of intermediate forms between some species, which makes the identification of taxa to species level a difficult task, especially from herbarium specimens. This scenario of overlapping ranges of morphological variation can be notably apprehended from the circumscriptions proposed by Nees von Esenbeck (1833a, 1836), Meissner (1864, 1866), Mez (1889), Kostermans (1937, 1938a), and Vattimo-Gil (1966b), which denote many incongruities and disagreements.

In the present revision of *Cryptocarya*, minor leaf venation pattern, presence of papillae and pubescence type on lower leaf surface, pubescence of floral parts, and morphology of elements of androecial whorls as well as persistence of tepals in fruit, are some of the characters used for taxonomic segregation of taxa. Regardless of the fact that floral characters have been inadequately used for diagnostic (identification) or discriminatory (classification) purposes, within the specific context of Lauraceae (as discussed by van der Werff & Richter, 1996), Moraes *et al.* (2001) accepted the proposed synonyms of *Cryptocarya schwackeana*, *C. hypoleuca*, and *C. longistyla* under *C. micrantha*, *C. minima*, and *C. saligna*, respectively, after studying in detail their flowers through SEM micrographs. Flower characters used here for characterization of species showed to be a helpful tool for their discrimination as well. Similar to the systematic revision of Neotropical species of *Cinnamomum* (Lorea-Hernández, 1996, 1997), here the assumption of independent genetic control for these characters was made, expecting that morphological entities corresponded to biological species. Likewise, all the specimens coming from different populations, but with similar set of characters, were linked to the same species.