

THREE NEW SPECIES OF *Ocotea* (LAURACEAE) FROM THE BRAZILIAN ATLANTIC FOREST¹

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ABSTRACT

(Three new species of *Ocotea* (Lauraceae) from Brazilian Atlantic forest) Three new species of *Ocotea* – *O. calliscypha* L. C. S. Assis & Mello-Silva, from the state of Minas Gerais, *O. ciliata* L. C. S. Assis & Mello-Silva, from the state of Espírito Santo, and *O. marcescens* L. C. S. Assis & Mello-Silva, from the states of Bahia, Espírito Santo and Rio de Janeiro – are described. The species are illustrated, and comments on their relationships to other species of *Ocotea*, distribution, habitat, and phenology are provided.

Key words: Brazilian Atlantic Forest, Lauraceae, *Ocotea*, taxonomy.

RESUMO

(Três espécies novas de *Ocotea* (Lauraceae) da floresta atlântica brasileira) Três novas espécies de *Ocotea* – *O. calliscypha* L. C. S. Assis & Mello-Silva, do estado de Minas Gerais, *O. ciliata* L. C. S. Assis & Mello-Silva, do estado do Espírito Santo e *O. marcescens* L. C. S. Assis & Mello-Silva dos estados da Bahia, Espírito Santo e Rio de Janeiro – são descritas. As espécies são ilustradas e comentários, distribuição, habitat, fenologia e relações com outras espécies de *Ocotea* são fornecidos.

Palavras-chave: floresta atlântica brasileira, Lauraceae, *Ocotea*, taxonomia.

INTRODUCTION

Ocotea Aubl. is the largest Neotropical genus of Lauraceae, comprising ca. 300-350 species in the Neotropics plus ca. 50-60 species in Africa and Madagascar (Rohwer 1993, Madriñán 2004). It is not taxonomically well defined, but their species can be distinguished by stamens with four pollen sacs arranged in two pairs above each other, together with additional features such as flowers that generally lack papillae, have free tepals, and either are unisexual or bisexual (van der Werff 1991, 2002). The genus is very diverse in Neotropical rain forests (Rohwer 1986, van der Werff 2002, Madriñán 2004), and it is highly rich in the Atlantic forest of Brazil, where 20-30% of the species of *Ocotea* occur (cf. Rohwer 1986, Baitello & Marcovino 2003, Assis *et al.* 2005, Quinet 2005). It is a quite threatened biome in need of conservation (Myers *et al.* 2000), a task that the three new endemic species described here reinforces.

MATERIALS AND METHODS

This work is based on the analysis of collections housed at B, BHCB, CEPEC, CVRD, K, MO, NY, RB, SPF, SPSF, and UEC herbaria (Thiers, continuously updated). Measures of flowers include the pedicel. The taxonomic species concept is followed, by which a species (as a natural kind; Assis & Brigandt 2009) is defined by an exclusive feature or a combination of them (Stuessy, 1990). Geographic distribution and habitat complement species circumscription. The classification of vegetation is based on Oliveira-Filho & Fontes (2000).

RESULTS AND DISCUSSION

Ocotea calliscypha L. C. S. Assis & Mello-Silva, *sp. nov.* **Type:** BRAZIL. MINAS GERAIS: Itambé do Mato Dentro, Distrito de Sant'Ana do Rio Preto, Cabeça de Boi, APA do Parque Nacional da Serra do Cipó, terras de José Agostinho, alto do morro, vegetação

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aberta, perturbada, 19°23'46.9"S, 43°24'07.4"W, 23.X.2008, fr., M. F. Santos & J. B. C. Marques 380 (Holotype, SPF; Isotypes, K, MO, RB).

Fig. 1

Species nova O. indecorae accedit sed nervis secundariis plus numerosis, areolis minoribus receptaculo intus glabro, apice antherarum breviore, cupula margine duplique differt. Proxime est etiam affinis O. odoriferae a qua cataphyllis inferne pubescentibus vel sericeis, receptaculo extus pubescenti apiceque antherarum breviore differt.

Trees 8–12 m tall. Branchlets with rhythmic growth, young branchlets gray to black, glabrous, glabrescent to sparsely pubescent, rhytidome absent, old branchlets gray, glabrous. Leaves generally clustered on the tips of the branchlets; petiole (5–)11–18(–22) × 1.5–2.5 mm; lamina (3.1–)10–16.3 × (1.3–)3–4.3(–5.1) cm, plane, narrowly elliptic to oboval, base acute to obtuse, rarely rounded, apex caudate to slightly caudate, rarely rounded or emarginate, adaxial surface glabrous, venation raised, flat or sunken, abaxial surface glabrous, venation raised, secondary veins 10–16 pairs, angles with primary vein 35–75°, areoles 0.2–0.5 mm diam., domatia absent. Cataphylls ca. 5 × 1.5 mm, abaxial surface sparse to densely pubescent to sericeous. Inflorescences 2.7–8.5 cm long, botryoid to thyrsoid, in the axils of cataphylls or the leaves to extra-axillary, axes sparsely pubescent. Flowers 3.8–9 mm long; pedicel, 1–6 mm long; receptacle 1–2 × 1–2.5 mm, outside sparsely pubescent, inside glabrous; tepals 1.5–2 × 0.5–1.5 mm, elliptic, oval to oblong, adaxial surface sparse to densely papilose, abaxial surface glabrous, glabrescent to sparsely pubescent; stamens 9, whorls I and II 0.9–1.5 mm long, filaments 0.4–0.6 mm long, sparse to densely pubescent, anthers 0.5–0.7 × 0.5–0.6 mm, elliptic, oval to oblong, sparsely papilose, apex 0.05–0.1 mm long, rounded, obtuse, acute, emarginate to truncate, upper and lower pollen sacs introrse to latero-introrse, whorl III 1–1.5 mm long, filaments 0.4–0.7 mm long, densely pubescent, anthers 0.5–0.7 × ca. 0.5 mm, elliptic, oblong to trapeziform, sparsely

pubescent-papilose, apex rounded, truncate to emarginate, upper pollen sacs latrorse, lower pollen sacs latero-extrorse, pair of glands at the base of the whorl III stamens present, staminodia 3 (whorl IV), 0.5–0.7 mm long, clavate to sagittate, sparse to densely pubescent; ovary 1–1.2 mm long, ellipsoid, style 0.5–0.8 mm long. Cupules 0.9–1.6 × 1.5–2.1 cm, obconic, margin double and thick, entire to slightly undulate after development of fruits, lenticels densely present, tepals deciduous. Immature fruits 0.8–1 × 0.8–1 cm, ellipsoid to ovoid.

Ocotea calliscypha are trees endemic to lower montane semi-deciduous forest from Minas Gerais state. It flowers from January to October and fruits from March to October.

Ocotea calliscypha is included in the *O. indecora* group (Rohwer 1986; Assis *et al.* 2005), which has 20 species and is defined by a unique morphological synapomorphy, the rhythmic growth of the branchlets (Assis 2009). Within the group, the new species can be distinguished by the leaves with 10–16 pairs of secondary veins and areoles 0.2–0.5 mm diam., by the cataphylls with pubescent to sericeous abaxial surface, the receptacle pubescent outside and glabrous inside, the apex of the anthers ca. 0.1 mm long, and cupules with double and thick margin. *Ocotea calliscypha* is quite similar to *O. indecora* (Schott) Mez and *O. odorifera* (Vell.) Rohwer, and one of the paratypes has been misidentified as *O. odorifera* (e.g., Chanderbali *et al.* 2001, p. 110). However, *O. indecora*, a widespread and morphologically variable species, has leaves with 7–12(–14) secondary veins per side and areoles 0.5–1.5 mm diam., the receptacle inside pubescent and outside glabrous to pubescent, and the apex of the anthers 0.1–0.5 mm long, and cupules with a single margin. Nevertheless, *Ocotea odorifera* is widespread and has the abaxial surface of the cataphylls and the outer surface of the receptacle glabrous, the apex of the anthers 0.1–0.4 mm long, and cupules with inconspicuous double margin.

Paratypes: Belo Horizonte, Parque Ecológico da CEMIG, approx. 3 km ao SE de Belo Horizonte, mata, 20.I.1995, fl., F.G. Lorea 5578 (MO not seen, SPSF);

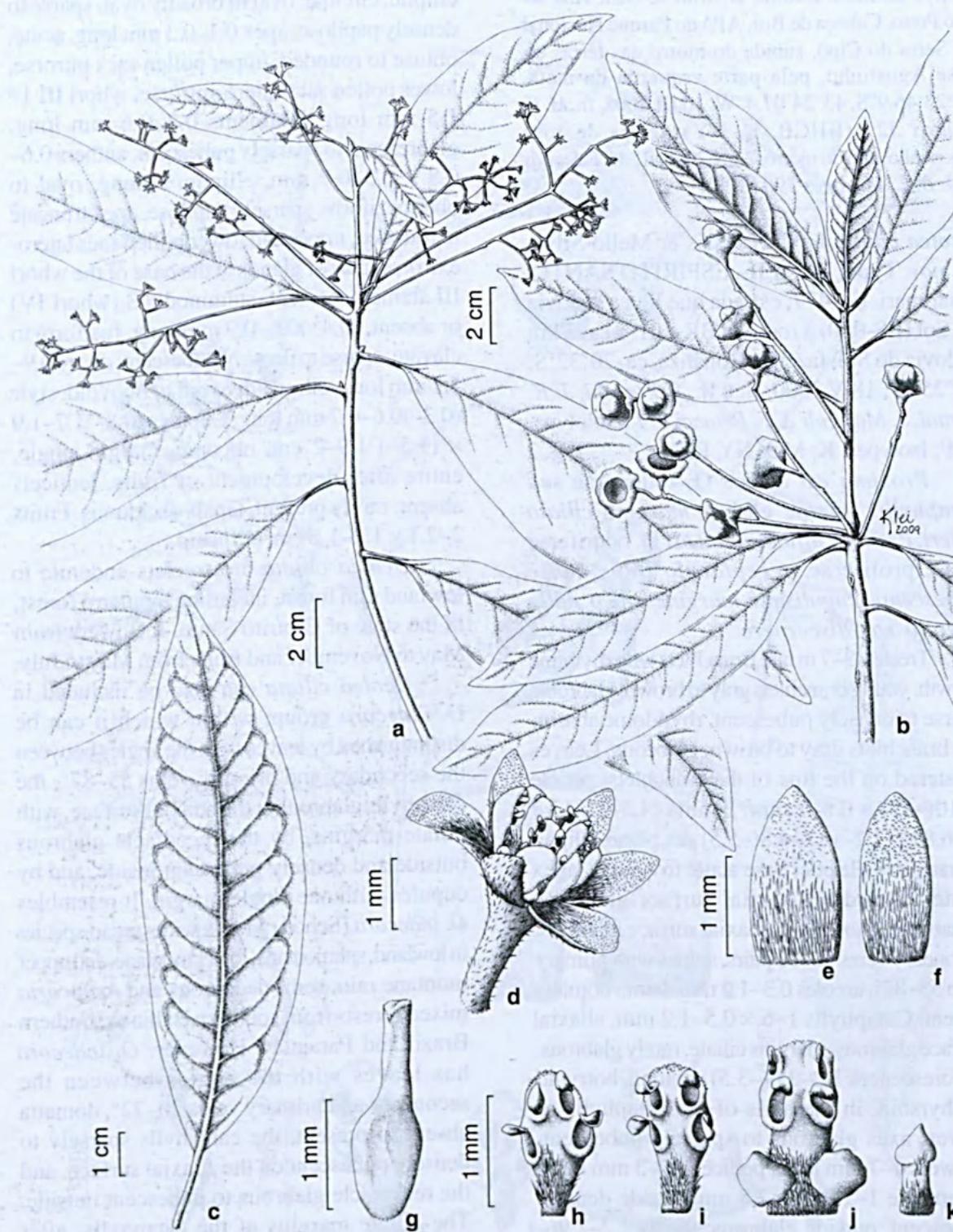


Figure 1 – *Ocotea calliscypha* L. C. S. Assis & Mello-Silva – a. flowering branchlet; b. fruiting branchlet; c. detail of abaxial surface of leaf; d. detail of flower; e. adaxial side of petal of the outer whorl; f. adaxial side of petal of the inner whorl; g. gynoecium; h. abaxial side of stamen of the whorl I; i. abaxial side of stamen of the whorl II; j. adaxial side of stamen of the whorl III; k. adaxial side of staminodium of the whorl IV. (a, c-k F. G. Lorea 5578, SPSF; b M. S. Santos & J. B. C. Marques 380, SPF).

Itambé do Mato Dentro, Distrito de Sant'Ana do Rio Preto, Cabeça de Boi, APAdo Parque Nacional da Serra do Cipó, subida do morro das terras de José Agostinho, pela parte esquerda da mata, 19°23'46.9"S, 43°24'07.4"W, 16.III.2008, fr., M. F. Santos 322 (BHCB, K, NY); terras de José Agostinho, alto do morro, 23.X.2008, fl., M. F. Santos & J. B. C. Marques 390 (SPF).

Ocotea ciliata L. C. S. Assis & Mello-Silva, sp. nov. Type: BRAZIL. ESPÍRITO SANTO: Guarapari, ES-477, estrada que liga a rodovia do Sol (ES-060) à rodovia BR-101, a ca. 3 km rodovia do Sol, fazenda Bonanza, ca. 20°32'S, 40°25'W, 18.V.2000, fl. e fr., P. Fiaschi, J. R. Pirani, J. Mafezoli & F. Petacci 271 (Holotype, SPF; Isotypes, K, MO, NY, RB). Fig. 2

Proxima est affinis O. indecorae sed cataphyllis inferne glabris margine ciliato differt. Proxime affinis etiam est O. odoriferae et O. proliferae, receptaculo intus dense pubescenti, cupulisque margine unico nullo negotio eas discernere.

Treelets 3–7 m tall. Branchlets with rhythmic growth, young branchlets gray to brown, glabrous, sparse to densely pubescent, rhytidome absent, old branchlets gray to brown, glabrous. Leaves clustered on the tips of the branchlets; petiole 4–10(–13) × 0.8–1 mm; lamina (4.5–)7–13.7 (–16.8) × (1.2–)1.8–4.8(–5.5) cm, plane, elliptic to narrowly elliptic, base acute to obtuse, apex acute to caudate, adaxial surface glabrous, venation flat to raised, abaxial surface glabrous, secondary veins 10–13 pairs, angles with primary vein 55–87°, areoles 0.3–1.2 mm diam., domatia absent. Cataphylls 1–6 × 0.5–1.2 mm, abaxial surface glabrous, margins ciliate, rarely glabrous. Inflorescences 1.2–2.6(–3.5) cm long, botryoid to thyrsoid, in the axils of the cataphylls or leaves, axes glabrous to sparsely pubescent. Flowers 4–7 mm long; pedicel 0.5–3 mm long; receptacle 1–1.8 × 2–2.8 mm, inside densely pubescent, outside glabrous; tepals 2.2–2.9(–3.3) × 1.2–1.7 mm, oval, narrowly oval, oblong to oboval, adaxial surface sparse to densely papilose, abaxial surface glabrous; stamens 9, whorls I and II 1.2–1.6 mm long, filaments (0.2–)0.4–0.7 mm long, sparse to densely pubescent, anthers 0.7–1.2 × (0.4–)0.7–1.1 mm,

elliptic, circular, oval to broadly oval, sparse to densely papilose, apex 0.1–0.3 mm long, acute, obtuse to rounded, upper pollen sacs introrse, lower pollen sacs latero-introrse, whorl III 1–1.5 mm long, filaments 0.3–0.6 mm long, glabrescent to sparsely pubescent, anthers 0.6–0.8 × 0.3–0.7 mm, elliptic, oblong, oval to obtrapeziform, sparsely papilose, apex truncate to rounded, upper and lower pollen sacs latero-extrorse, pair of glands at the base of the whorl III stamens present, staminodia 3 (whorl IV) or absent, (0.4–)0.6–0.9 mm long, fusiform to clavate, sparse to densely pubescent; ovary 0.9–1.1 mm long, ellipsoid, ovoid to obovoid, style (0.3–)0.6–0.7 mm long. Cupules (0.8–)1.7–1.9 × (1.5–) 1.9–2 cm, obconic, margin single, entire after development of fruits, lenticels absent, rarely present, tepals deciduous. Fruits 2–2.1 × 1.2–1.8 cm, ellipsoid.

Ocotea ciliata are treelets endemic to lowland rain forest, including tabuleiro forest, in the state of Espírito Santo. It flowers from May to November and fruits from May to July.

Ocotea ciliata can also be included in *O. indecora* group, within which it can be distinguished by leaves with the angles between the secondary and primary veins 55–87°, the cataphylls glabrous at the adaxial surface, with ciliate margins, by the receptacle glabrous outside and densely pubescent inside, and by cupules with one single margin. It resembles *O. indecora* (Schott) Mez, a widespread species in lowland, submontane, lower montane, and upper montane rain, semi-deciduous and *Araucaria* mixed forests from southern Bahia to southern Brazil and Paraguay. However, *O. indecora* has leaves with the angles between the secondary and primary veins 20–72°, domatia absent to present, the cataphylls sparsely to densely pubescent on the adaxial surface, and the receptacle glabrous to pubescent outside. The ciliate margins of the cataphylls, after which the species is named, also occur in other species of *O. indecora* group, namely *O. fasciculata* (Nees) Mez, *O. odorifera* (Vell.) Rohwer, and *O. prolifera* (Nees & Mart.) Mez. Nevertheless, *O. fasciculata* has arcuate leaves and anthers of the whorls I, II, and III

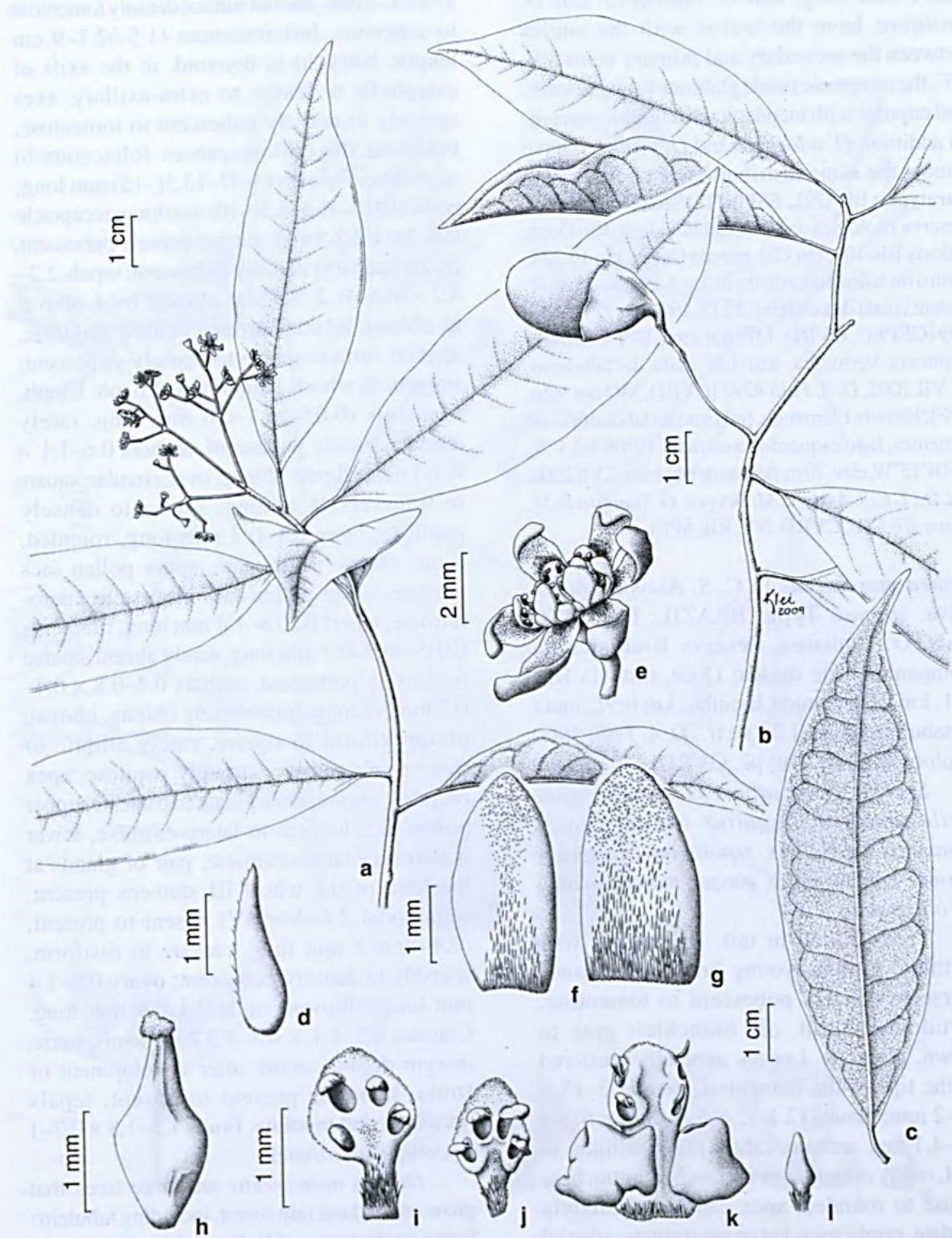


Figure 2 – *Ocotea ciliata* L. C. S. Assis & Mello-Silva – a. flowering branchlet; b. fruiting branchlet; c. detail of abaxial surface of leaf; d. detail of abaxial side of cataphyll; e. detail of flower; f. adaxial side of tepal of the outer whorl; g. adaxial side of tepal of the inner whorl; h. gynoecium; i. abaxial side of stamen of the whorl I; j. abaxial side of stamen of the whorl II; k. adaxial side of stamen of the whorl III; l. adaxial side of staminodium of the whorl IV. (a-l P. Fiaschi et al. 271, SPF).

0.3–1 mm long; and *O. odorifera* and *O. prolifera* have the leaves with the angles between the secondary and primary veins 30–75°, the receptacle inside glabrous to glabrescent, and cupules with inconspicuous double margin. In addition, *O. odorifera* and *O. prolifera* have almost the same distribution as *O. indecora*. **Paratypes:** BRAZIL. ESPÍRITO SANTO: Linhares, Reserva Biológica da Companhia Vale do Rio Doce, rodovia BR-101, km 120, estrada Gávea, km 16.324, centro ou lado esquerdo do bloco 4, ensaio de prod. sustent., mata de tabuleiro, 22.IX.1982, fl., D.A. Folli 399 (CEPEC, CVRD, MO not seen, SPF); Estrada Sapucaia Vermelha, km 1.8, mata de tabuleiro, 17.VII.2002, D.A. Folli 4292 (CVRD, MO not seen, SPF); Estrada Flamengo, próximo ao laboratório de sementes, lado esquerdo da estrada, 19°09'02.1"S, 40°04'15"W, elev. 70m, floresta de tabuleiro, 7.VII.2006, fl. e fr., L.C.S. Assis, L.M. Borges, G. Siqueira & M. Trovo II63 (B, CVRD, NY, RB, SPF).

Ocotea marcescens L. C. S. Assis & Mello-Silva, sp. nov. **Type:** BRAZIL: ESPÍRITO SANTO: Linhares, Reserva Biológica da Companhia Vale do Rio Doce, rodovia BR-101, km 120, estrada Bicuiba, km 0.91, mata de tabuleiro, 4.VIII.2004, fr., D.A. Folli 5090 (Holotype, SPF; Isotype, CVRD). Fig. 3

Species quam affinis O. mosenii quae facile tamen distinguitur coflorescentiis squamatis vel foliatis, tepalis inferne sparce dense pubescens quoque marcescentibus revolutisque.

Trees 20–30 m tall. Branchlets with rhythmic growth, young branchlets brown, sparse to densely pubescent to tomentose, rhytidome absent, old branchlets gray to brown, glabrous. Leaves generally clustered on the tips of the branchlets; petiole 3–15 × 1.5–2 mm; lamina (2.1–)2.6–7.8(–8.5) × (0.8–)1.4–4.1 cm, arcuate, rarely plane, elliptic to oval, rarely orbicular or narrowly elliptic, base obtuse to rounded, apex caudate to slightly caudate, rarely rounded or emarginate, adaxial surface glabrous, venation raised, flat or sunken, abaxial surface glabrous to glabrescent, venation raised, secondary veins 7–11 pairs, angles with primary vein 45–60(–80°), areoles 0.5–1.7 mm diam., domatia absent. Cataphylls

1–5 × 1–2 mm, abaxial surface densely tomentose to sericeous. Inflorescences (1.5–)2.1–9 cm length, botryoid to thyrsoid, in the axils of cataphylls or leaves to extra-axillary, axes sparsely to densely pubescent to tomentose, bracts of the coflorescences foliaceous to scale-like. Flowers (4–)7–13.5(–15) mm long; pedicel (0.5–)1.5–8.5(–10) mm long; receptacle 0.8–2 × 1.2–2.5 mm, outside densely pubescent, inside sparse to densely pubescent; tepals 2.2–4.2 × (0.8–)1.2–2.5 mm, elliptic, oval, oboval to oblong, adaxial surface densely papilose, abaxial surface sparse to densely pubescent; stamens 9, whorls I and II 0.9–1.6 mm length, filaments (0.05–)0.1–0.6 mm long, rarely absent, densely pubescent, anthers 0.6–1.1 × 0.5–1 mm, elliptic, oblong, oval, circular, square to transversely oblong, sparse to densely papilose, apex 0.1–0.3 mm long, rounded, acute, obtuse to truncate, upper pollen sacs introrse, lower pollen sacs introrse to latero-introrse, whorl III 0.8–1.4 mm long, filaments (0.05–)0.3–0.7 mm long, rarely absent, sparse to densely pubescent, anthers 0.4–0.8 × 0.4–0.7 mm, oblong, transversely oblong, oboval, obtrapeziform to square, rarely elliptic or transversely elliptic, sparsely papilose, apex rounded, obtuse, emarginate to truncate, upper pollen sacs latrorse to latero-extrorse, lower pollen sacs latero-extrorse, pair of glands at the base of the whorl III stamens present, staminodia 3 (whorl IV) absent to present, (0.4–)0.6–1 mm long, clavate to fusiform, sparsely to densely pubescent; ovary 0.8–1.4 mm long, ellipsoid, style 0.4–0.9 mm long. Cupules 0.7–1.1 × 0.8–1.3 cm, hemispheric, margin double, entire after development of fruits, lenticels present to absent, tepals persistent and revolute. Fruits 1.5–1.8 × 0.7–1 cm, ellipsoid to ovoid.

Ocotea marcescens are large trees that grow on lowland rain forest, including tabuleiro forest, in the states of Bahia and Espírito Santo, and lowland and submontane rain forests in the state of Rio de Janeiro. It flowers from June to September and fruits from May to July.

Ocotea marcescens can also be included in the *O. indecora* group. Within the group,

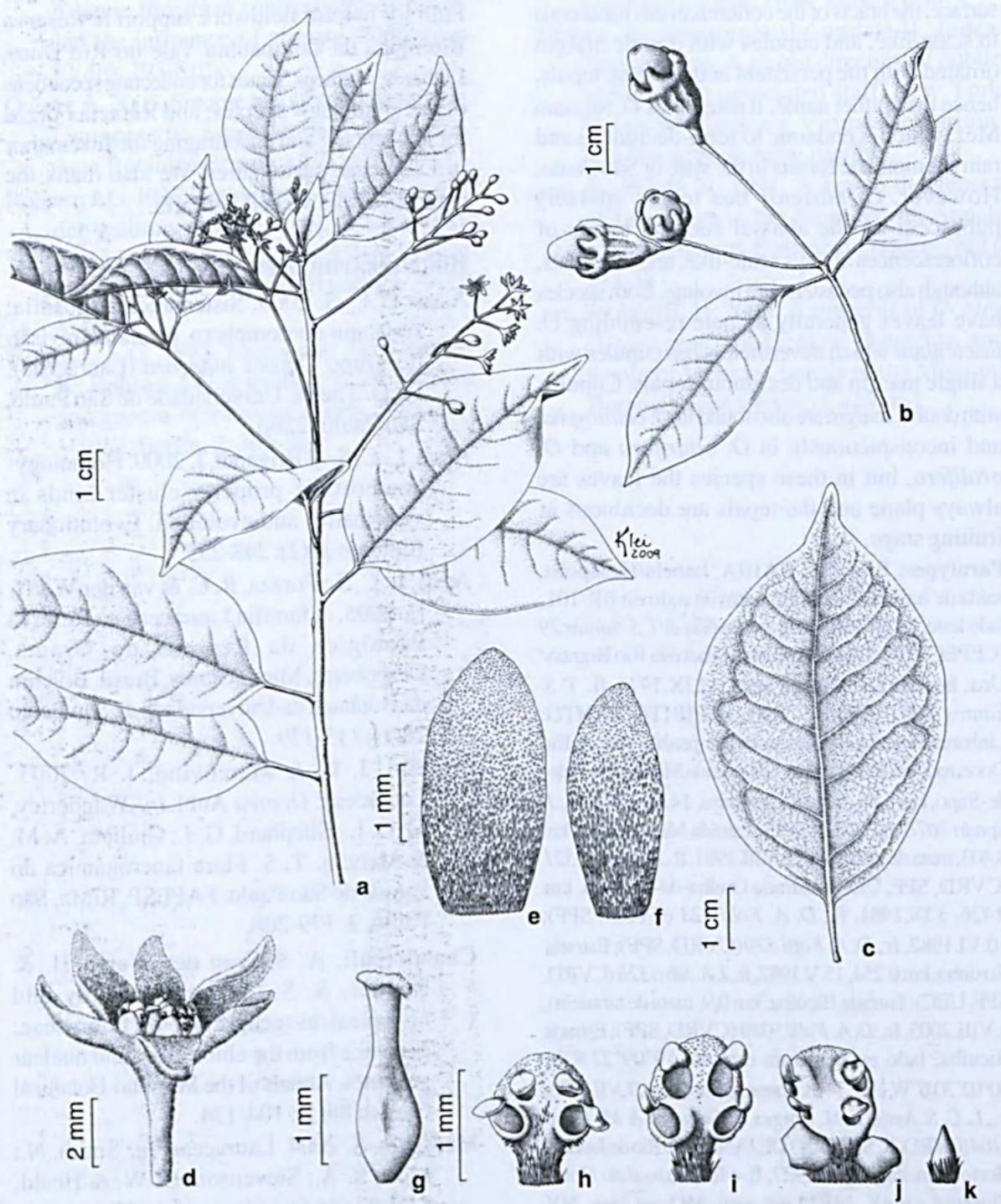


Figure 3 – *Ocotea marcescens* L. C. S. Assis & Mello-Silva – a. flowering branchlet; b. fruiting branchlet; c. detail of abaxial surface of leaf; d. detail of flower; e. adaxial side of petal of the outer whorl; f. adaxial side of petal of the inner whorl; g. gynoecium; h. abaxial side of stamen of the whorl I; i. abaxial side of stamen of the whorl II; j. adaxial side of stamen of the whorl III; k. adaxial side of staminodium of the whorl IV. (a, c-k D. A. Folli 321, SPF; b D. A. Folli 5090, SPF).

the new species can be distinguished by the tepals sparse to densely pubescent on the abaxial surface, the bracts of the coflorescences foliaceous to scale-like, and cupules with double margin ornated with the persistent and revolute tepals, hence the epithet name. It resembles *O. mosenii* Mez, which is endemic to semi-deciduous and rain submontane forests in the state of São Paulo. However, *O. mosenii* has tepals sparsely pubescent on the abaxial surface, bracts of coflorescences always scale-like, and the tepals, although also persistent, are involute. Both species have leaves generally arcuate resembling *O. fasciculata* which nevertheless has cupules with a single margin and deciduous tepals. Cupules with double margin are also found in *O. calliscypha*, and inconspicuously in *O. odorifera* and *O. prolifera*, but in these species the leaves are always plane and the tepals are deciduous at fruiting stage.

Paratypes: BRAZIL. BAHIA: Itabela/Eunápolis, saída de Itabela/Eunápolis, 1 km da rodovia BR-101, lado leste, 13.IX.1968 (fl.), J. Almeida & T.S. Santos 29 (CEPEC, RB); Una, km 40 of the rodovia Rio Branco/Una, fazenda Dendhevea, mata, 11.IX.1974, fl., T. S. Santos 2801 (CEPEC, RB). ESPÍRITO SANTO: Linhares, Reserva Biológica da Companhia Vale do Rio Doce, rodovia BR-101, km 120, estrada Macanaíba-Pelede-Sapo, km 3.45, mata de tabuleiro, 14.IX.1973, fl., J. Spada 307/73 (CVRD, SPF); Estrada Mantegueira, km 0.403, mata de tabuleiro, 25.VIII.1981, fl., D.A. Folli 321 (CVRD, SPF, UEC); Estrada Orelha-de-Macaco, km 0.426, 3.IX.1981, fl., D. A. Folli 323 (CVRD, SPF); 10.VI.1982, fr., D. A. Folli 379 (CVRD, SPF); Estrada Roxinho, km 0.254, 15.V.1982, fr., J.A. Silva 328 (CVRD, SPF, UEC); Estrada Bicuiba, km 0.9. mata de tabuleiro, 4.VIII.2005, fr., D.A. Folli 5089 (CVRD, SPF); Estrada Bicuiba, lado esquerdo da estrada, 19°09'27.8"S, 40°02'20.6"W, elev. 74m, floresta de tabuleiro, 7.VII.2006, fr., L.C.S. Assis, L.M. Borges, G. Siqueira & M. Trovó 1164 (CVRD, K, SPF). RIO DE JANEIRO: Rio de Janeiro, Horto Florestal, 27.VI.1927, fl. e fr., Pessoal do Horto Florestal s.n. (K, MBM not seen, MO not seen, NY not seen, RB 139859, SI not seen, SPF).

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Polydactyl stem (from Greek *poulos*, many, and *daktylos*, finger).

Author's name

Osvaldo Vassalini (Argentina) - Sennarossa's approach on the terminology adopted for the distinct features of a stem is sustained as follows: "a compound vascular cylinder" and "typical of the family" from the Lauraceae family. In the present the *Sennarossa* approach is accepted, so a central vascular cylinder is assumed to be a more simpler as well as the term "typical of the family". In this study, the use of the univascular and one, it was preferred than eight polydactyl vascular, called the new nomenclature of a *multidactyl vascular cylinder*, with the former referring to the central axis. With the beginning of the new glaciogenesis cycle the latter axis is called "trigona cylinder". The term adopted here "multidactyl vascular cylinder" is proper, because it reflects the relationship between the vascular cylinders and comes along through the presented origin. This approach is a simplification that enables the concept under discussion, also keeps the linguistic agreement with the original term — *varius lignotriches et ramea*. We repeat the term "multidactyl stem" and "polydactyl stem" because the terms "whetted herbaceous" to the presence of a single pade at the start.

Key words: *ocotea*, *lauraceae*, *new nomenclature*.

Introduction

The genus *Ocotea* (Lauraceae) describes a morpho-anatomical complexly scandent and arborescent, evergreen coniferous tree up to 100m x 100cm DBH with different types of trunks (Schubert 1993). Different parts of the trunk are variously called (e.g. Schubert 1993; Pfeiffer 1962; Chacon Henriquez 1982; Philipson et al. 1973). Denyer (1974) described "a large, cylindrical stem consisting of a single, continuous, longitudinal axis" (Philipson 1973).

Angulo (1970, 1973, 1976) and Pfeiffer (1962)

described the stem as "a single, longitudinal axis" (Angulo 1970, 1973, 1976; Pfeiffer 1962).

Barbosa (1970) described the stem as "a single, longitudinal axis" (Barbosa 1970).

Philipson (1973) described the stem as "a single, longitudinal axis" (Philipson 1973).

Chacon Henriquez (1982) described the stem as "a single, longitudinal axis" (Chacon Henriquez 1982).

Denyer (1974) described the stem as "a single, longitudinal axis" (Denyer 1974).

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