TWO NEW SPECIES OF LAURACEAE FROM ESPÍRITO SANTO, BRAZIL

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Abstract. Two new species from the Brazilian Atlantic rainforest of Espírito Santo State, *Licaria spiritusanctensis* and *Ocotea teresae*, are described and illustrated. Their putative relationships within the respective genera are discussed. We also provide illustrations and comments on micromorphological and anatomical features of leaves of these new species, comparing them to those of congenerics and showing that they can be useful for recognition of different taxa.

Keywords: leaf cuticle, leaf vascular bundle, *Licaria*, *Ocotea*, taxonomy

In this study, two new species are described respectively for *Licaria* Aubl. and *Ocotea* Aubl. The work is a by-product of the treatment of the Lauraceae for the Flora of Espírito Santo, Brazil. The descriptions and illustrations of the new species are presented below, as well as a discussion on their possible relationships with congenerics.

Licaria is a Neotropical genus of about 65 species (Trofimov and Rohwer, 2018 [although 77 names are currently in use by different authors]), distributed from southern Florida and Mexico to southern Brazil and Bolivia (Kurz, 2000; Moraes, 2018; Moraes and Vergne, 2018; Trofimov and Rohwer, 2018; van der Werff, 2009b). The latest revision of *Licaria* was carried out by Kurz (1983), in his Ph.D. dissertation, which was only published years later (Kurz, 2000), at which time the author updated it with the addition to some taxa of some new synonyms and a few newly examined specimens. Kurz (2000) also described three subgenera of *Licaria* on the basis of stamen characters, particularly on the manner of opening of the locelli: subgen. *Licaria*, subgen. *Canella* H.W. Kurz, and subgen. *Armeniaca* H.W. Kurz. A detailed account of those three subgenera can be found in van der Werff (2009b). The genus is characterized by the combination of flowers with two-celled anthers, a well-developed cupule, often double-rimmed, and alternate or opposite leaves (Moraes, 2018; Moraes and Vergne, 2018; Rohwer, 1993; van der Werff, 2009b).

Ocotea is the largest genus among the Neotropical Lauraceae, estimated to have ca. 400 recognized species in the Americas (Trofimov et al., 2019; van der Werff, 2011). However, since 2011, another 74 species have been published and one transferred to the genus (see Moraes, 2018; Moraes and Vergne, 2019; van der Werff, 2018a,b), which make such estimates somewhat obsolete. As pointed out by Moraes and Vergne (2019), the last revision of *Ocotea* sensu Kostermans (1957), including *Nectandra* Rol. ex Rottb. and *Pleurothyrium* Nees, dates back to the *Lauraceae americanae* of Mez (1889). Rohwer (1986) published a synopsis of the genus, proposing its subdivision into smaller informal entities, which encompassed 29 groups of species sharing morphological affinities, and 54 species treated singly. No subsequent monographic treatments of these groups have been published, except for the study of the *Ocotea indecora* (Schott) Mez group (Assis and Mello-Silva, 2010). A synopsis of the Central American species was published by van der Werff (2002), but the South American species are still less well known (Moraes and van der Werff, 2011; van der Werff, 2011). Several studies have shown that *Ocotea* is polyphyletic, or paraphyletic with respect to other Neotropical genera of Lauraceae (Chanderbali, 2004; Chanderbali et al., 2001; Rohde et al., 2017; Trofimov et al., 2016, 2019) and in need of a revision. Its large size, however, makes the revision of the genus difficult to accomplish (Rohwer, 1993), being beyond the scope of most botanists (van der Werff, 2014). Recently, Trofimov et al. (2019) have reinstated the genus *Mespilodaphne* Nees & Mart. as a first step toward a phylogenetic classification, therefore transferring to *Mespilodaphne* eight species that had been positioned in *Ocotea*.

Ocotea is characterized by having paniculate-cymose inflorescences with the lateral flowers of the terminal cymes strictly opposite, flowers with six equal tepals, nine four-celled stamens with the locelli arranged in two superposed pairs, staminodes of fourth whorl, when present, stipitiform, and the fruits seated in a more or less well-developed cupule (van der Werff, 2009a, 2011, 2013). As currently circumscribed, both species with unisexual and bisexual flowers have been placed in *Ocotea* (van der Werff, 2011, 2013). Although the combination of characters listed above is unique to *Ocotea*, each is individually present in other genera of Lauraceae and there are no features known to be exclusive for *Ocotea* (van der Werff, 2013). For these reasons, the genus is regarded as a "dustbin" for species that do not fit into better-defined genera of the tribe Perseeae Nees (Rohwer, 1993).

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Material and Methods

This study was based on literature review and morphological analysis of specimens deposited in the following herbaria: BHCB, BR, CEPEC, COL, CVRD, ESAL, F, G, G-DC, GZU, HBG, HBR, HRCB, HUEFS, IAN, INPA, K, KIEL, L, LE, M, MBM, MBML, MG, MO, NY, OXF, P, R, RB, RFA, SPSF, U, UEC, UPCB, US, VEN, and VIES (acronyms according to Thiers, continuously updated).

Photographs of floral structures of the new species of *Licaria* were obtained with a stereomicroscope (Leica MZ125) equipped with a camera (Leica DFC290). Photographs of other morphological characters, particularly the indument, and of floral structures of the new species of *Ocotea* were acquired by a stereomicroscope (Leica M80) equipped with a camera (Leica IC80 HD), using the software LAS (Leica Application Suite) version 4.3.0. Photographs of specimens analyzed at the Kew Gardens were obtained with a stereomicroscope (Leica MZ12) equipped with a camera (ToupCam XCam Full HD). Electron micrographs of floral parts and leaf cuticles were acquired using a Hitachi (TM3000) scanning electron microscope. Prior to observation in the SEM, the specimens were coated with gold in a BAL-TEC SCD 050 sputter coater for 180 s at 50 mA, depositing 10 nm of gold on the material surface.

In order to compare the new species of *Licaria* with congenerics from the Amazon region and the Atlantic rainforest, the following species have also been analyzed in more detail: *L. armeniaca* (Nees) Kosterm. (Kostermans, 1936: 732, 1937: 584), *L. bahiana* H.W. Kurz (Kurz, 2000: 146), *L. debilis* (Mez) Kosterm. (Kostermans, 1936: 737, 1937: 596), and *L. subbullata* Kosterm. (Kostermans, 1962: 286). The specimens examined and used in the micromorphological and anatomical analyses are listed after the paratypes of the new species.

For the study of leaf cuticles, leaf samples of 1 cm^2, taken from the median region of mature leaves of herbarium specimens of each species, were boiled in a water bath until the material felt pliable (usually for 5–10 min). After that, the samples were macerated in Jeffrey's solution (Jeffrey, 1917; we slightly modified it to be equal parts 20% chromic and bench concentrated nitric acids; Johansen, 1940; Stace, 1965), for about 16 hr, in order to isolate the cuticular membrane. After maceration, cuticles were thoroughly (three times) rinsed with distilled water, then dehydrated in alcohol series before staining them in 1% safranin in 50% ethanol for 5–10 min. For the anatomical analysis of cross sections of blade midribs and petioles, leaf samples of herbarium specimens were boiled in a water bath for about 10 min. Freehand transverse sections were made at the median region of the blade and of the petiole, and the sections were partially decolorized with household bleach (20%), then thoroughly (three times) washed with distilled water. Dehydration of the cleared samples was done in alcohol series before staining them with safranin and Astra Blue (Safrablau) (Bukatsch, 1972, modified by Kraus and Arduin, 1997). All preparations were mounted on microscope slides in Entellan.® Photomicrographs were obtained with a photomicroscope (Leica DM500) coupled with a camera (Leica ICC50) and the software LAS EZ v.3.0.0.

Descriptive terminology of leaf cuticles follows Barthlott and Ehler (1977), Wilkinson (1979), Faggetter (1985, 1987), and Trofimov and Rohwer (2018). Terminology of leaf venation follows Hickey (1973, 1979), Coe-Teixeira (1980), Christophel and Rowett (1996), and Ellis et al. (2009). Terminology of the vascular bundle arrangement in midribs and petioles follows Howard (1979), Santos and Oliveira (1988, 1995), Nishida and Christophel (1999), and Vaz et al. (2019). Abbreviations used in the text are as follows: fl. = flower; fr. = fruit; immat. fr. = immature fruit; l. = left; r. = right.

Taxonomy

Licaria spiritusanctensis P.L.R. Moraes & T.D.M. Barbosa, *sp. nov*.

TYPE: BRAZIL. Espírito Santo: Santa Teresa, terreno do Boza, 26 October 1999, bud, fl., *V. Demuner, E. Bausen & W. Pizziolo 173* (Holotype: MBML [11290]; Isotypes: HRCB, RB, UEC). Fig. 1.

Licaria spiritusanctensis can be recognized by the combination of leaves glabrous above, glabrous to glabrescent below, trichomes short, straight, appressed, sparse trichomes mainly on midrib, often somewhat bullate above, inflorescences pubescent to dense pubescent, flowers glabrescent to sparse pubescent, floral tube glabrous to sparse pubescent inside, tepals subequal, stamens free, elongate, apical-extrorse, staminal valves large, locelli opening away from the center of the flower, the flaps laterally swinging toward the center of anthers, filaments as wide as or narrower than the anthers, with two large basal glands, elongate, almost as long as the filament, appressed, sagittate, sessile, staminodes of fourth whorl in irregular numbers, 1 to 3 or wanting, pistils glabrous, and fruits seated on a distinctly swollen and turbinate pedicel that gradually merges into a shallow cupule, conspicuously double-rimmed.

Small *trees* up to 10 m tall. Cortex slightly aromatic. *Terminal buds* ovoid to elongate, densely covered with short, straight, appressed-to-ascending trichomes. Young *branchlets* angular, glabrous or with short, straight, appressed, whitish trichomes, moderately sparse to dense immediately below terminal bud, and slowly glabrescent on older parts of the twig; twigs in living material glossy, gray-bluish. *Petioles* 1.0–1.8 cm long, glabrous to glabrescent, densely pubescent in young leaves, indument ± as on twigs, (±) roundish below, canaliculate above, flat, or irregularly ridged. *Leaves* alternate, evenly distributed along branchlets, mostly elliptic to lanceolate, varying toward (sub)oblong or obovate, 5.4–27.0 × 1.7–8.5 cm, subcoriaceous to chartaceous, glabrous above, glabrous to glabrescent below, with short, straight, appressed, sparse trichomes mainly on midrib, papillate (but the papillae are not well developed; outer periclinal walls

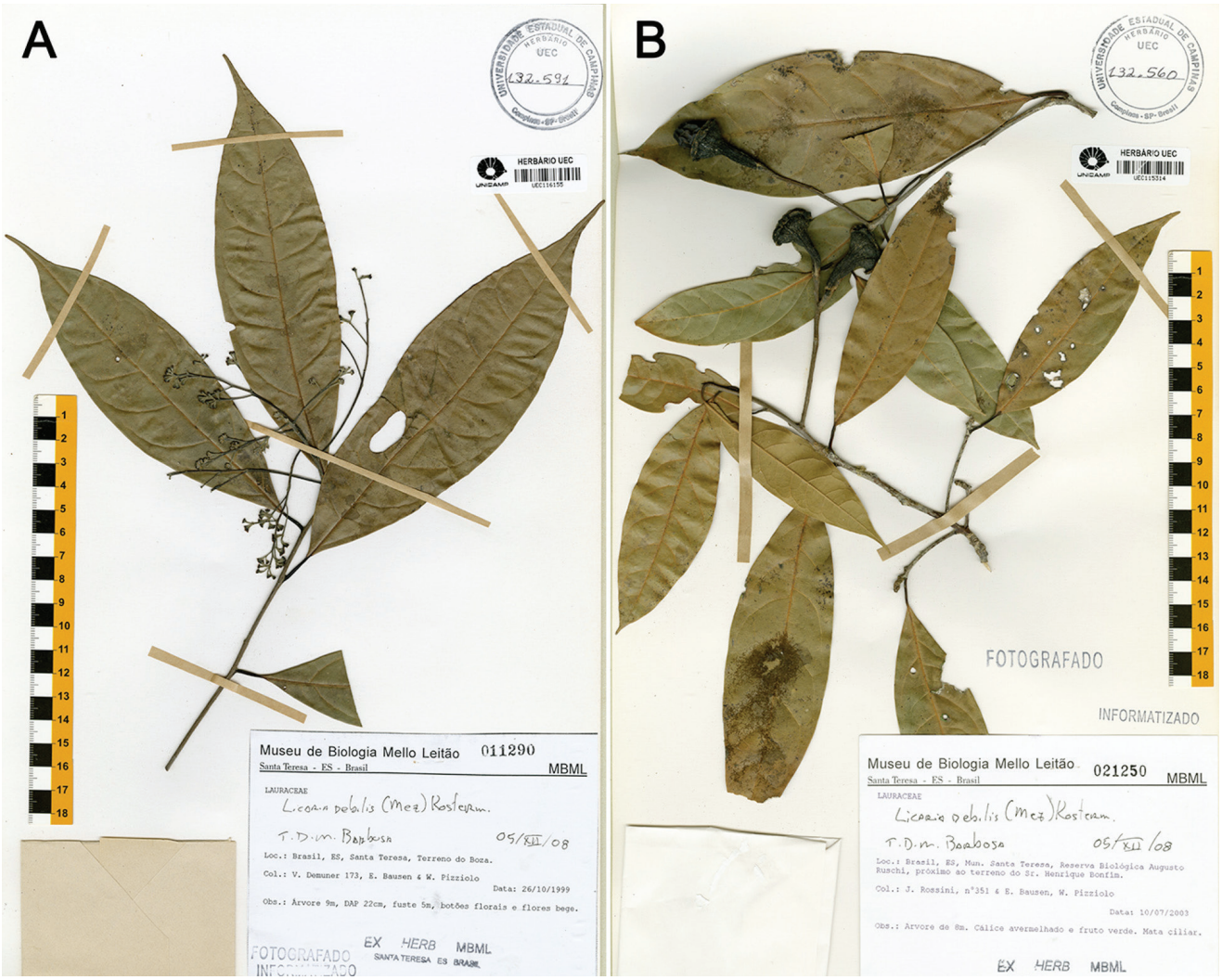


FIGURE 1. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, isotype (*Demuner 173*, UEC); **B**, paratype (*Rossini 351*, UEC).

variously convex, low domed), glossy above, paler below, tip often long acuminate to cuspidate, base attenuate, cuneate or subrounded (mostly obtuse), mostly symetrical, margin sclerified, flat to minutely revolute; upper surface somewhat bullate in several specimens; venation pinnate, eucamptodromous to brochidodromous, reticulation imperfect, areoles randomly arranged (not oriented), irregular, veinlets linear to branched once, or absent; midrib above usually prominulous to slightly prominent in a distinct impression, sometimes flat to level toward the base, (very) prominent below, secondary veins above usually convex in an often slight impression to flat to level, prominulous to prominent below, 6–11 on each side of the midrib, reticulation flat to level to immersed above, prominulous below. *Inflorescences* paniculate, 1.25–9.70 cm long, in the axils of foliage leaves as well as in the axils of cataphylls at the base of the new growth, below the terminal bud, or on axillary brachyblasts, few-flowered to (sub)many-flowered, much shorter than leaves, pubescent to densely pubescent, trichomes grayish to whitish, short, appressed to ascending. *Pedicels* 2.7–3.2 mm long, 0.29–1.10 mm thick, indument denser than peduncles. *Flowers* yellow in living material (but also recorded as white, beige, orange, green, green-yellowish, or yellow-greenish), blackish in dried material, 2.3–2.8 × 1.9–2.7 mm, glabrescent to sparse pubescent, trichomes short, appressed, floral tube relatively shallow, ca. 0.6–0.9 mm deep, infundibuliform, glabrous to sparse pubescent inside, trichomes whitish, short, appressed; tepals 6, subequal, inner ones slightly longer than outer ones, erect to spreading at anthesis, 0.80–1.96 × 0.9–1.7 mm, ovate to depressed ovate, mainly glabrous to sparsely pubescent, trichomes short, appressed; staminodes of first and second whorl foliaceous, almost panduriform to rectangular, narrowed toward the base, apex obtuse to truncate, glabrous at the base, first whorl 0.8–1.1 × 0.5–0.6 mm, second whorl 0.8–1.2 × 0.5 mm; stamens of third whorl free, elongate, 0.79–1.40 × 0.39–0.70 mm, apical-(sub)extrorse, staminal valves relatively large (in proportion to stamen size), the locelli opening away from the center of the flower, with the flaps laterally swinging toward the center of anthers, from

the borders of the septum separating the locelli, filaments as wide as or narrower than the anthers, pilose, with two basal glands, large, 0.44–1.00 mm long, elongate, almost as long as the filament, appressed, sagittate, (sub)sessile; staminodes of fourth whorl 1 to 3 when present, 0.54–0.88 mm long, liguliform to conic, pilose; pistil glabrous, 1.5–1.9 mm long, ovary ellipsoid, 0.64–0.80 mm long, style relatively stout, 0.7–1.1 mm long, stigma minute, ovule ellipsoid, 0.48–0.64 mm long. *Fruits* 1.9–2.8 × 1.1–1.9 cm, ellipsoid, smooth, seated on a distinctly swollen and turbinate pedicel that gradually merges into a shallow cupule; cupules red in living material, 0.4–1.6 × 1.48–2.30 cm, hemispheric to infundibuliform, verrucose, double-rimmed, margin 4.0–8.0 mm thick, pedicels 1.3–1.9 cm long. Fig. 2–4, 5A–D.

Phenology: flowers collected from June to January. Immature fruits collected from September to July.

Etymology: the species name refers to the Brazilian state of Espírito Santo, where the species has been collected so far.

Distribution and habitat: *Licaria spiritusanctensis* is known only from two municipalities of the state of Espírito Santo, Águia Branca and Santa Teresa, in the Atlantic rainforest domain. However, in the region of Santa Teresa, which has been thoroughly surveyed for many years, the species seems to be relatively frequent in the understory of the Montane Atlantic rainforest. Evidence of that are the 43 specimens collected in that region, a number that is notably higher than the average of collections of the other Lauraceae recorded there (see Barbosa et al., 2012). (Fig. 4).

Additional specimens examined [*Licaria spiritusanctensis*]: BRAZIL. Espírito Santo: Águia Branca, Córrego Jabuticaba, propr. Rosangela Fausti, 19°01'22"S, 40°38'52"W, 190–550 m, 30 November 2006, immat. fr., *L. F. S. Magnago et al. 1659* (MBML); Santa Teresa, Alto São Lourenço, sítio da Cachoeira (Lídio), 25 October 2000, fl., *V. Demuner et al. 1489* (HRCB, MBML, RB, UEC); idem, Sítio L. Bringhenti, 19°58'22"S, 40°35'36.1"W, 819 m, 10 September 2011, immat. fr., *P. L. R. de Moraes et al. 3228* (HBG, HRCB); idem, Estação Biológica de Santa Lúcia, divisa à direita depois da trilha Bonita, 750 m, 25 November 1998, fl., *L. Kollmann et al. 1109* (HRCB, MBML, RB, UEC); idem, Estação Biológica de Santa Lúcia, trilha do Tapinoã, 30 December 1999, fl., *V. Demuner et al. 434* (HRCB, MBML, RB, UEC); idem, Estação Biológica de Santa Lúcia, 1 October 2004, *F. A. G. Guilherme 373* (ESAL, MBML, RFA); idem, Estação Biológica de Santa Lúcia, 11 October 2004, bud, *F.A.G.Guilherme 388* (MBML, RFA); idem, Estação Biológica de Santa Lúcia, 19°58'05.4"S, 40°31'57.4"W, 623 m, 20 December 2012, fl., *P. L. R. de Moraes 3555* (HBG, HRCB); idem, Mata da Prefeitura, 8 December 1999, fl., *V.Demuner & E.Bausen 284* (MBML, RB, SPSF); idem, São Lourenço, terreno de Clério Loss, 750 m, 28 October 1998, fl., *L. Kollmann et al. 830* (MBML, RB, SPSF); idem, Mata Fria, terreno de Clério Loss, lado direito do asfalto, 9 December 1999, fl., *V. Demuner & E. Bausen 316* (HRCB, MBML, RB, UEC); idem, Nova Lombardia, Reserva Biológica Augusto Ruschi, 800 m, 16 October 2001, fl., *L. Kollmann & E. Bausen 4835* (HRCB, MBML, RB, UEC); idem, beira da estrada, 800 m, 6 November 2001, fl., *L. Kollmann & E. Bausen 4946* (HRCB, MBM, MBML, RB, UEC); idem, estrada para Goiapaba-Açu, 850 m, 11 December 2001, fl., *L. Kollmann et al. 5177* (ESAL, MBML, RB, UEC); idem, 11 December 2001, fl., *L. Kollmann et al. 5181* (MBM, MBML, RB, UEC); idem, estrada de Nova Lombardia, 850 m, 9 January 2002, fl., *L. Kollmann et al. 5229* (MBML, RB, UEC); idem, estrada para João Neiva, 24 September 2002, fl., *R. R. Vervloet et al. 1060* (BHCB, MBM, MBML, RB, UEC); idem, estrada para Goiapaba-Açu, parte final, 800 m, 24 October 2002, fl., *R. R. Vervloet et al. 1265* (MBML, RB, UEC); idem, Goiapaba-Açu (marcos 78, 77, 76), 850 m, 29 October 2002, fl., *R. R. Vervloet et al. 1317* (BHCB, MBML, RB, UEC); idem, Nova Lombardia, Reserva Biológica Augusto Ruschi, trilha da Tronqueira, 800 m, 30 October 2001, fl., *L. Kollmann et al. 4939* (MBML, RB, UEC); idem, valão à direita da sede velha, 800 m, 29 November 2001, fl., *L. Kollmann et al. 5102* (BHCB, MBML, RB, UEC); idem, 775 m, 5 November 2002, fl., *R.R.Vervloet et al. 1341* (MBML, RB, UEC); idem, trilha da Preguiça, 810 m, 3 December 2002, fl., *R. R. Vervloet & E. Bausen 1396* (MBML, RB, UEC); idem, trilha da Cachoeira, partindo da sede, 790 m, 4 December 2002, fl., *R. R. Vervloet & E. Bausen 1430* (ESAL, MBML, RB, UEC); idem, linha de divisa, marco 108, 825 m, 10 December 2002, fl., *R. R. Vervloet et al. 1451* (BHCB, MBML, RB, UEC); idem, trilha da Cachoeira, partindo da nova sede, 11 March 2003, immat. fr., *R. R. Vervloet & E. Bausen 1967* (MBML, RB, UEC); idem, próximo ao terreno do Sr. Henrique Bonfim, 10 July 2003, immat. fr., *J. Rossini et al. 351* (HRCB, MBML, RB, UEC); idem, trilha da Roda d'Água até área aberta, 19°54'39"S, 40°33'15.3"W, 787 m, 10 December 2012, fl., *J. A. Lombardi et al. 9822* (HRCB, UPCB); idem, São Lourenço, estrada do Caravage, Reserva da Prefeitura (Estação Biológica da Caixa D'Água), 750 m, 27 October 1998, fl., *L. Kollmann et al. 809* (MBML, UEC); idem, estrada do Caravagem (Caravaggio), 850 m, 18 November 1998, fl., *L. Kollmann et al. 1045* (MBML, RB, SPSF); idem, Mata da Prefeitura, estrada do Caravaggio, 19°55'05"S, 40°36'50.1"W, 780 m, 11 September 2011, immat. fr., *P. L. R.de Moraes et al. 3238* (HBG, HRCB); idem, Rio Saltinho, 13 May 2005, immat. fr., *L. Kollmann & A. P. Fontana 7787* (MBML); idem, Santo Antônio, terreno do Boza, 750 m, 7 October 1998, bud, *L. Kollmann et al. 734* (MBML, RB, SPSF, UEC); idem, 7 October 1998, fl., *L. Kollmann et al. 739* (MBML, RB, UEC); idem, 750 m, 29 October 1998, fl., *L. Kollmann et al. 854* (MBML, RB, SPSF); idem, 29 October 1998, fl., *L. Kollmann et al. 855* (MBML, RB, SPSF); idem, 850 m, 17 November 1998, fl., *L. Kollmann et al. 1034* (MBML, RB, SPSF, UEC); idem, 29 October 1999, fl., *V. Demuner et al. 154* (MBML, RB, SPSF); idem, 24 October 2000, fl., *V. Demuner et al. 1454* (MBML, RB, UEC); idem, 19°54'37"S, 40°35'41"W, 800 m, 8 June 2012, immat. fr., *F. Z. Saiter et al. 472* (MBML); idem, São Lourenço, Caixa d'Água, 30 November 1999, fl., *V. Demuner & W. Pizziolo 276* (MBML, RB, SPSF); idem, Vale do Canaã, 18 June 1985, fl., *J. M. Vimercat 283* (MBML, MO, SPSF); idem, estrada para Santa Maria de Jetibá, 19°56'12"S, 40°41'17.7"W, 828 m, 11 September 2011, bud, immat. fr., *P. L. R. de Moraes et al. 3245* (HBG, HRCB).

FIGURE 2. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A–B**, **D–J**, **O**. Flowers from *Kollmann 5181* (UEC). **C**, **K–N**, **P–Q**. Flowers from *Vervloet 1396* (UEC). **R**. Flower from *Vervloet 1060* (UEC). **A**, flower with erect tepals; **B**, flower with two tepals and two staminodes removed; **C**, anomalous flower, tetramerous, with spreading tepals; **D**, outer tepal and staminode of first whorl, adaxial surface; **E**, inner tepal and staminode of second whorl, adaxial surface; **F**, outer tepals, adaxial (l.) and abaxial (r.) surfaces; **G**, inner tepals, adaxial (l.) and abaxial (r.) surfaces; **H**, staminodes of first whorl, abaxial (l.) and adaxial (r.) surfaces; **I**, staminodes of second whorl, abaxial (l.) and adaxial (r.) surfaces; **J–L**, stamens of third whorl with glands, abaxial (l.) and adaxial (r.) surfaces; **M–N**, staminodes of fourth whorl; **O–P**, pistils; **Q–R**, pistils showing the ovule. Bars = 2 mm (A, B, C); 1 mm (D, E, F, G); 0.5 mm (H, I, J, K, L, M, N, O, P, Q, R).

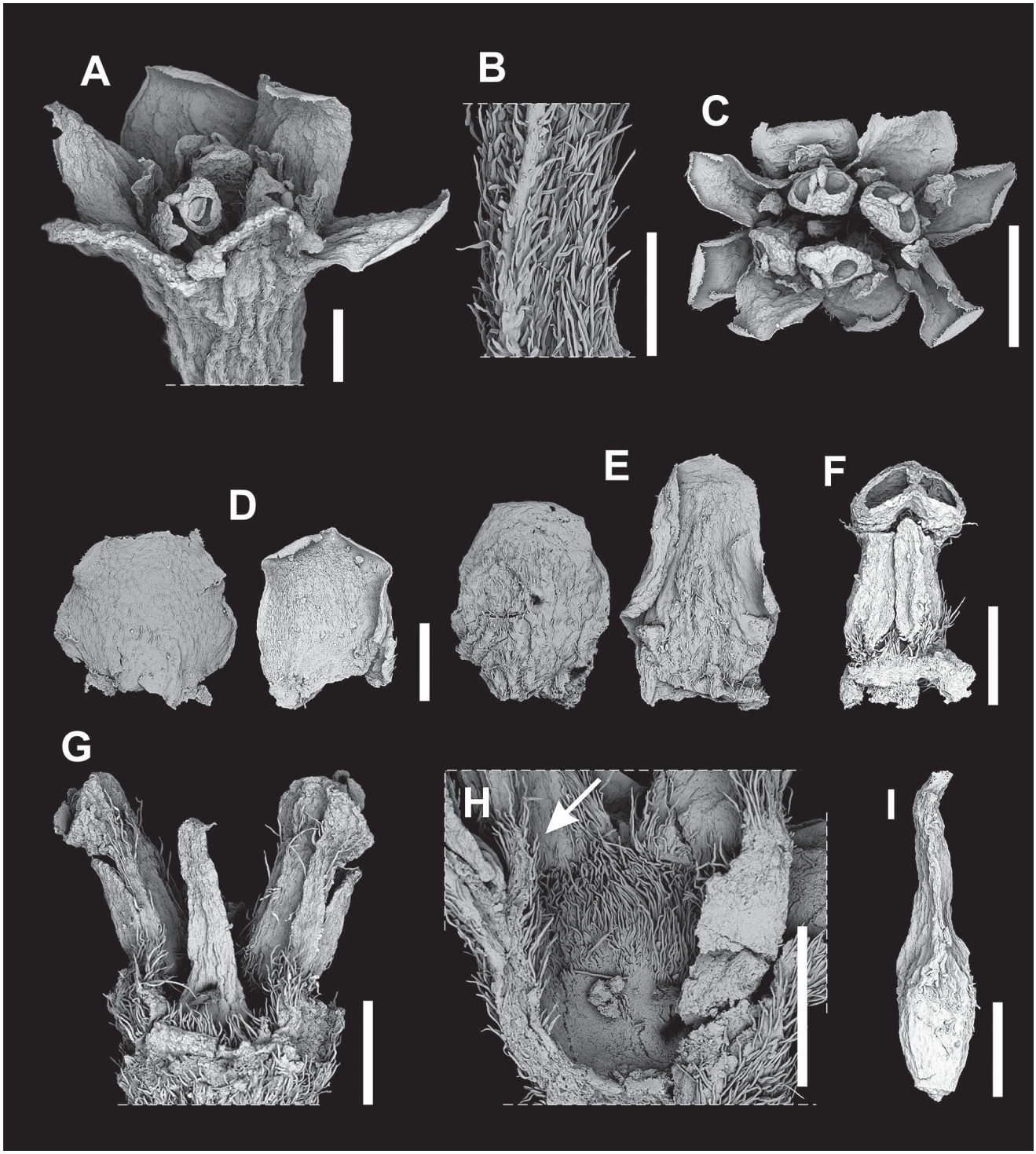


FIGURE 3. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, **E**. Flowers from *Kollmann 5229* (UEC). **B**. Flower from *Demuner 173* (UEC). **C**, **F–I**. Flowers from *Vervloet 1396* (UEC). **D**. Flower from *Lombardi 9822* (HRCB). **A**, flower with patent tepals; **B**, detail of pedicel; **C**, anomalous tetramerous flower, top view; **D**, outer tepals, abaxial (l.) and adaxial (r.) surfaces; **E**, inner tepals, abaxial (l.) and adaxial (r.) surfaces; **F**, stamen of third whorl with glands; **G**, side view of stamens of third whorl and pistil; **H**, view of floral tube inside and staminode of fourth whorl (arrow); **I**, pistil. Bars = 1 mm (B); 0.5 mm (A, D, E, F, G, H, I); 0.3 mm (C).

FIGURE 4. Geographic distribution of *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, South America; **B**, Brazil; **C**, State of Espírito Santo.

Additional specimens examined [*Licaria armeniaca* (Nees) Kosterm.]: BRAZIL. Amazonas. Borba, BR 230, estrada Transamazônica, 1–5 km upstream from Sucunduri, along margin of river, 06°50'S, 59°00'W, 9 May 1985, *A. Henderson et al. 407* (HRCB, INPA, MO), *A. Henderson et al. 429* (F, HRCB, INPA, MBM, MO); near mouth of Rio Embira, 7°30'S, 70°15'W, 5 July 1933, *B. A. Krukoff 5185* (LE, MO, NY, US); Humaitá, near Três Casas, 14 September–11 October 1934, *B. A. Krukoff 6155* (LE, MO, NY). Paraná. Adrianópolis, Tatupeba, estrada para João Surrá, 24°42'01"S, 48°45'26"W, 130 m, 30 November 2016, *J. M. Silva et al. 9661* (HRCB, HUEFS, MBM). Rio Grande do Sul. Morrinhos do Sul, Perdida, 6 October 2016, *P. L. R. de Moraes et al. 5385* (HRCB). Rio de Janeiro. "in umbr. sylvaticis R. Jan.," June–July 1832, *L. Riedel 478* (LE, Lectotype of *Mespilodaphne parviflora* Meisn.; Isolectotypes: G, K—3 sheets, NY, US); idem, Serra dos Órgãos, April 1833, *B. Luschnath s.n.* (BR, KIEL, LE; syntype of *M. parviflora* Meisn.). Santa Catarina. Sombrio, Garapuvu, Vista Alegre, 19 March 1960, *R. Reitz & R. M. Klein 9593* (RB, holotype of *Licaria reitzkleiniana* Vattimo-Gil; isotype: HBR). São Paulo. Sete Barras, Parque Estadual Intervales, Saibadela, May 2002, *F. A. G. Guilherme 341* (HRCB). COLOMBIA. Amazonas-Vaupés. Río Apaporis, Soratama, entre el Río Pacoa y el Río Kananari, 1 August 1951, *R. E. Schultes & I. Cabrera 13237* (P). PERU. "Maynas circa oppidum Tocache ad fl. Huallagan," June 1831, *E. F. Poeppig 1787* (W [not seen], lectotype of *Evonymodaphne armeniaca* Nees; isolectotypes: B†, F, G, GZU, L, LE—2 sheets, M, NY, OXF, P—2 sheets); "Tocache," 1830/1831, *E. F. Poeppig 1861 ex parte* (B, F, GZU—2 sheets, NY, P, US; syntype of *E. armeniaca* Nees).

Additional specimens examined [*Licaria bahiana* H.W. Kurz]: BRAZIL. Bahia. km 25 da rod. Guaratinga/São Paulinho, 2 April 1973, *R. S. Pinheiro 2085* (HBG-509810, Holotype; CEPEC [9182], RB00133993, Isotype). Pedras Pretas, 29 May 1918, *H. M. Curran 364* (NY; paratype). Porto Seguro, Reserva Biológica do Pau-Brasil, 11 December 1971, *A. Eupunino 83* (CEPEC, HBG, RB; paratype); idem, RPPN Estação Veracel, 30 November 2014, *P. L. R. de Moraes et al. 4267* (HRCB). Prado, Rod. BA 284, trecho Prado/Itamaraju, ca. 65 km a NW de Prado, 18 September 1978, *S. A. Mori et al. 10638* (CEPEC, HBG, NY, RB; paratype), *S. A. Mori et al. 10671* (CEPEC, HBG, K, NY, RB; paratype); idem, km 31 da Rod. Prado/Itamaraju, (Rod. BA 284), 17°12'S, 39°24'W, 31 October 1979, *L. A. Mattos Silva & H. S. Brito 699* (CEPEC, HBG; paratype). Santa Cruz de Cabrália, arredores da Est. Ecológica do Pau-Brasil, 18 October 1978, *S. A. Mori et al. 10783* (HBG, NY, RB; paratype); idem, antiga rodovia que liga a Estação Ecológica Pau-Brasil à Sta. Cruz de Cabrália, 28 November 1979, *S. A. Mori et al. 13041* (CEPEC, HBG; paratype). Una, ca. 35 km S of Itabuna, 27 September 1979, *K. Kubitzki & H.-H. Poppendieck 79-259* (HBG, NY; paratype). Uruçuca, Lagoa Encantada, 4 June 1971, *R. S. Pinheiro 1286* (BHCB, CEPEC, HBG; paratype). Espírito Santo. Linhares, Reserva Natural Vale, 6 September 2011, *P. L.R. de Moraes et al. 3166* (CVRD, HRCB, MBM).

Additional specimens examined [*Licaria debilis* (Mez) Kosterm.]: BRAZIL. Pará. Bragança, 24 October 1926, *A.Ducke s.n.* (HBG, RB00128046, U [1359273]); Breves, Rio Tajapuru in aestuario amazonico loco Antonio Lemos, 8 July 1923, *A. Ducke s.n.* (RB00129178, U [1359288]); plantation de Paricatuba, route de Belém-Mosqueiro, 13 March 1968, *C. Sastre & F. Sastre 157* (P); Capitão Poço, Colônia S. José, 12 August 1966, *J.E.dePaula 289* (MG). FRENCH GUIANA. Cayenne, *J. B. Patris 53* (G00368864, holotype of *Acrodiclidium debile* Mez; isotype: F [1023382]); Fleuve Kourou, sur la crique Couy, 19 September 1967, *R. A. A. Oldeman B-1326* (P, U); idem, 21 September 1967, *R. A. A. Oldeman B-1354* (K). GUYANA. Kangaruma-Potaro landing, 25–27 June, 1921, *H. A. Gleason 230* (K, NY, US); Kanaku Mountains, near Nappi Creek, Pirara River, ca. 200 m, 8 October 1931, *Davis in Forest Department 2218*

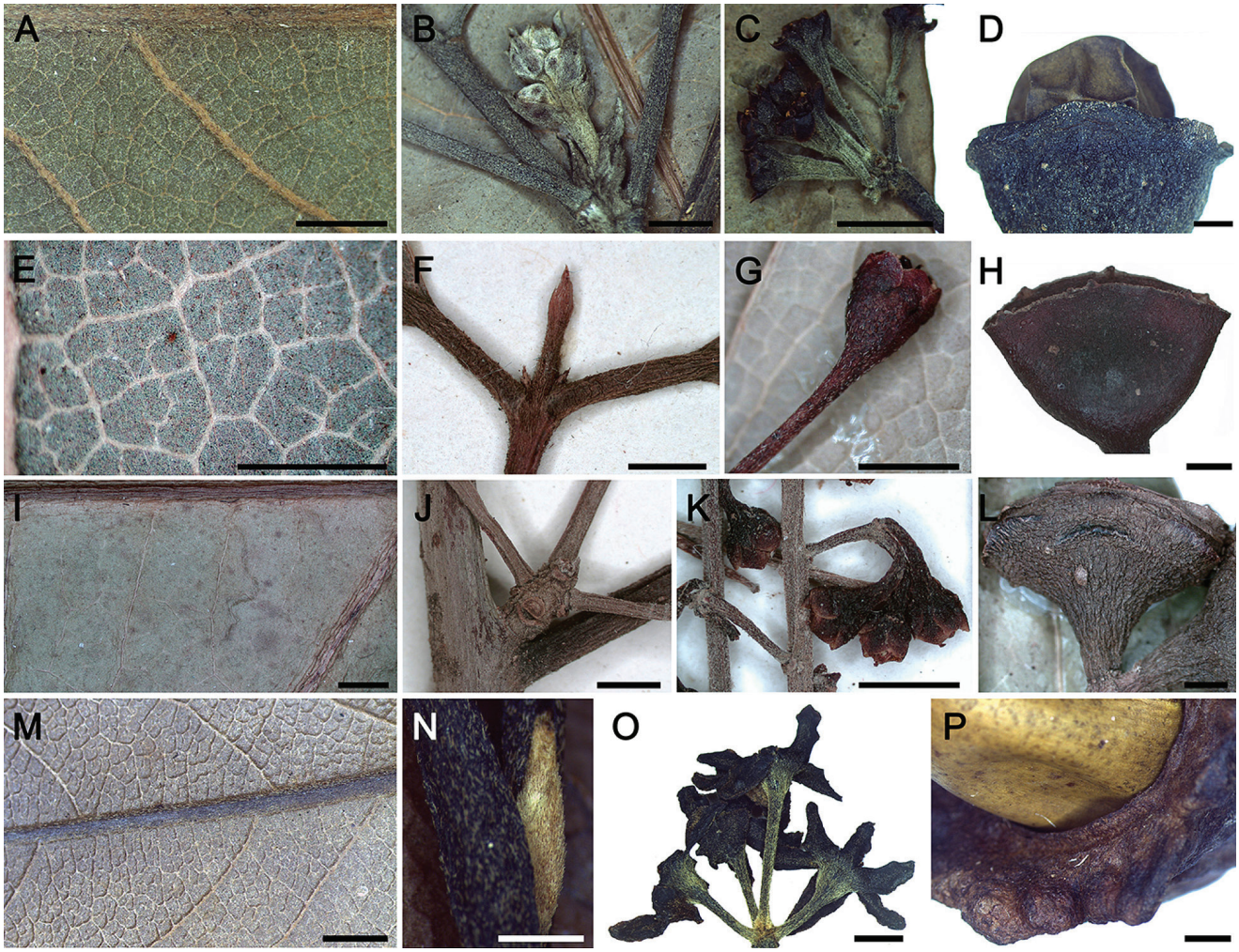


FIGURE 5. **A–D**. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **E–H**. *L. debilis* (Mez) Kosterm. **I–L**. *L. subbullata* Kosterm. **M–P**. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A**, leaf abaxial surface (*Demuner 316*, UEC); **B**, detail of peduncles and buds (*Kollmann 739*, UEC); **C**, detail of flowers (*Demuner 173*, UEC); **D**, detail of cupule and young fruit (*Vervloet 1967*, UEC); **E**, leaf abaxial surface (*Gleason 230*, K); **F**, petioles and bud (*Gleason 230*, K); **G**, flower (*Lindeman 285*, K); **H**, detail of cupule (*Gleason 230*, K); **I**, leaf abaxial surface (*Forest Department 5595*, K); **J**, detail of peduncles and petiole (*Forest Department 5595*, K); **K**, detail of peduncle and flowers (*Forest Department 5595*, K); **L**, detail of cupule (*Mori 8454*, K); **M**, leaf abaxial surface (*Kollmann 1171*, UEC); **N**, detail of petioles and bud (*Kollmann 2557*, UEC); **O**, flowers (*Demuner 334*, UEC); **P**, detail of margin of cupule (*Kollmann 2557*). Bars = 2.5 mm (A, B, C, D, E, F, G, H, I, J, K, L, M, O, P); 1.25 mm (N).

(K); Puruhi River, 1 April 1953, *Forest Department 7748* (K, NY); Kanaku Mountains, slope of Nappi Mountains, Camp 2, 03°20'N, 59°34'W, 450 m, 12 November 1987, *M. J. Jansen-Jacobs et al. 902* (K, U); Barima-Waini Region, Barima River Head, 7°38'N, 60°07'W, 1 m, 2 August 1986, *J. J. Pipoly III & H. Lall 8187* (F, MO); Kamoa River, Toucan Mountain, 01°33'N, 58°50'W, 260–360 m, 22 September 1989, *M. J. Jansen-Jacobs et al. 1741* (K, MO, U); Cuyuni-Mazaruni region, Aurora, 06°47'30"N, 59°44'30"W, 4 October 1989, *L. J. Gillespie & S. Tiwari 2090* (MO, U, US); U. Takutu-U. Essequibo region, Maparri River, 03°20'N, 59°15'W, 8 June 1996, *D. Clarke & T. McPherson 2062* (MO, U, US); idem, Sipu River, 01°24'N, 58°57'W, 245 m, 23 August 1998, *D. Clarke et al. 7087* (MO, U, US); idem, Acarai Mountains, 8 km S of Sipu River, 01°21'N, 58°57'W, 610 m, 3 September 1998, *D. Clarke et al. 7406* (MO, U, US). SURINAME. Brownsberg, 12 September 1924, *B.W. 6653* (U—2 sheets); Lely Mountains, 24 September 1975, *J. C. Lindeman et al. 285* (F, K, P, U); Jodensavanne-Mapane kreek area (Suriname River), 13 June 1953, *J. C. Lindeman 4054* (F, K, NY, U), 15 June 1953, *J. C. Lindeman 4086* (INPA, NY, U). VENEZUELA. Territorio Delta Amacuro, Rio Amacuro, Venezuela-Guyana frontier, Sierra Imataca, 65–80 m, 1 November 1960, *J. A. Steyermark 87206* (F, NY, U, US, VEN). Fig. 5E–H.

Additional specimens examined [*Licaria subbullata* Kosterm.]: BRAZIL. Amazonas. Manaus, Distrito Agropecuário, Reserva 1501 (km 41) da WWF/INPA Projeto da Dinâmica Biológica dos Fragmentos Florestais, 2°24'26"S–2°25'31"S, 59°43'50"W, 50–150 m, 28 September 1989, *N. M. Lepschda Cunha & E. C. Pereira 400* (INPA, MO, NY, U); idem, Reserva Florestal Ducke, 02°53'S, 59°58'W, 12 July 1994, *A. Vicentini & P. A .C. L. Assunção 595* (INPA, K, MG, MO, NY, RB, U); idem, 17 January 1995, *P. A. C. L.*

Assunção 150 (INPA, K, MG, MO, NY, RB, U, UEC); Maués, Rio Parauari, entre os lugares Laranjal e Vila Darcy ao longo do rio, 17 July 1983, *C. A. Cid Ferreira 4199* (INPA, K, MO, NY, RB, US). Pará. Peixe Boi, 30 August 1949, *N.T.Silva 334* (IAN, U); BR 163, km 1305, vicinity of Igarapé José Preto, 23 November 1977, *G. T. Prance et al. 25679* (F, HBG, MG, U); Parauapebas [Marabá], Serra Norte, clareira à direita da estrada para o acampamento Azul, N1, 29 May 1982, *R. S. Secco et al. 381* (F, K, MG, MO, NY, RB, US); Serra Norte, 3 km southeast of AMZA mining camp 3-Alfa and west along secondary logging road, 5°49'S, 50°32'W, 225–250 m, 15 June 1982, *C. R. Sperling et al. 6190* (MG, MO, NY, US). FRENCH GUIANA. Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 8 September 1982, *S. A. Mori et al. 14887* (NY, P); idem, La Fumée Mountain Trail, vicinity of Antenne Nord, 28 July 1987, *S. A. Mori 18593* (K, MG, MO, NY, P). GUYANA. 75 miles Bootica-Potaro Road, Wallaba forest on white sand, 21 November 1947, *Forest Department 5595* (K000602008, holotype); Rupununi District, between Kuyuwini Landing and Kassikaityu River, 21 October 1992, *M. J. Jansen-Jacobs et al. 3032* (F, K, P); slopes of Mountain Makarapan, along Makarapan Creek, 3°59'N, 58°57'W, 250 m, *P. J. M. Maas et al. 7523* (K). SURINAME. Wilhelmina Gebergte, lower slopes of Frederik Top, 2 km southeast of Juliana Top, 325 m, 7 August 1963, *H. S. Irwin et al. 54585* (K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, ca. 3 km S of Juliana top, 12 km N of Lucie River, 3°39'N, 56°32'W, 500 m, 24 August 1963, *H. S. Irwin et al. 55018* (COL, F, K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, 325 m, 23 August 1963, *H.S. Irwin et al. 55028* (NY, holotype of *L. wilhelminensis* C.K. Allen; isotypes: F, K, U, US, VEN); idem, 3.5 km SSE of Juliana Top, 11.5 km north of Lucie River, 450 m, 8 August 1963, *H. S. Irwin et al. 54590* (COL, F, K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, West Rivier, 4 km south of Juliana Top, 450–700 m, 1 September 1963, *H. S. Irwin et al. 55307* (K, NY; paratype of *L. wilhelminensis* C.K. Allen); Lely Mountains, SW plateaus covered by ferrobauxite, 550–710 m, 20 September 1975, *J. C. Lindeman et al. 99* (F, K, U); idem, 175 km SSE of Paramaribo, 500–700 m, 12 October 1976, *S. A. Mori & A. Bolten 8454* (K, HBG). Fig. 5I–L.

In the revision of *Licaria* by Kurz (2000), a collection of 1985 from Santa Teresa, ES, *J. M. Vimercat 283* (MBML, MO, SPSF), was listed under *L. debilis*, therefore representing a disjunct distribution between the Amazon and the Atlantic rainforest domains. The known distribution of *L. debilis* is concentrated in the Guiana Highlands (in the three Guianas) and also recorded in Venezuela and the Brazilian state of Pará, being found in the understory of the Terra Firme forest, preferably on the border with flood forest, but also on white sand and in high savannah vegetation. Particularly related to Vimercat's collection, Kurz pointed out that it "has some characteristics that are related to *L. bahiana*" (but he did not specify them). In Barbosa et al. (2012), the authors have accepted Kurz's circumscription of *L. debilis*, thus including the specimens from Santa Teresa as belonging to that species. Nevertheless, after the analyses of specimens of *L. debilis* from the Guiana Highlands and the Brazilian Amazon, it has become clear to us that the specimens from Espírito Santo belong to a different taxon that had not been described so far.

Based on Kurz's (2000) key to subgenera, *Licaria spiritusanctensis* will key to subgen. *Armeniaca*, since it has stamens with anthers with valvate dehiscence, ovary glabrous, twigs glabrous or pubescent, apical-extrorse anther cells with flaps opening away from the stigma (i.e., the center of the flower), tepals often spreading, and staminodes 6 or 9. Nevertheless, in his key to the species of subgen. *Armeniaca*, the characters of *L. spiritusanctensis* fit up to the couplet 4, "stamens free. Staminodes of fourth whorl lacking or present," which then leads to couplet 5 and forward, where the characters of the former species do not fit at all. The couplet 5a leads to couplets 6, which encompass *L. macrophylla* (A.C. Sm.) Kosterm. and *L. subbullata*, whereas couplet 5b leads to couplets 7, encompassing *L. bahiana* and *L. debilis*. Taking the former four species for comparison with *L. spiritusanctensis*, *L. macrophylla* has stamens clearly forming a shield around the stigma, with very small valves (whereas *L. spiritusanctensis* does not have such stamens and the valves are relatively large), stalked glands (vs. sessile glands), floral tube inside with silky, rusty-brown trichomes (vs. glabrous to sparse pubescent, trichomes whitish), leaves 15–40 cm long (vs. 5.4–27.0 cm long), shortly narrowed at the base (vs. base attenuate, cuneate, or subrounded), clustered at the end of branchlets (vs. evenly distributed), and petioles 2–5 cm long (vs. 1.0–1.8 cm).

In terms of general morphological appearance of dried specimens and some flower features, *Licaria subbullata* has a combination of morphological characters that best resemble those found in *L. spiritusanctensis*: both species are small trees (up to 15 m height vs. 10 m height), with leaves alternate, evenly distributed, glabrous, with almost similar shapes and sizes (13.0–21.0 × 5.0–10.0 cm vs. 5.4–27.0 × 1.7–8.5 cm), tip cuspidate to acuminate, upper surface somewhat bullate, similar number of secondary veins on each side of the midrib (7–11 vs. 6–11), petioles of similar size (1.0–2.0 cm long vs. 1.0–1.8 cm), floral tube glabrous inside (vs. glabrous to sparse pubescent), stamens of third whorl free, elongate, with extrorse anthers, two large basal glands, elongate, almost as long as the filament, staminodes of fourth whorl present, and pistil glabrous. However, in spite of these similarities, *L. subbullata* differs from *L. spiritusanctensis* by leaves often asymmetrical at the base (vs. mostly symmetrical), with secondary veins strongly sunken on the upper surface, reticulation incomplete (vs. imperfect), coarse (vs. relatively fine), veinlets multibranched (vs. linear to branched once), flowers smaller (ca. 2.0 mm long vs. 2.3–2.8 mm long), glabrous (vs. glabrescent to sparse pubescent), staminal valves medium (vs. relatively large in proportion to stamen size), fruits smaller, 1.2–1.8 × 0.8 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules 1.0 × 0.8–1.5 cm (vs. 0.4–1.6 × 1.48–2.30 cm), and pedicels short, slightly obscure (vs. 1.3–1.9 cm long). It is worth mentioning that Richter (1985) says that *L. subbullata* is "the literally most 'outstanding' species of the entire genus." According to him, its wood and bark features are incongruous with all other species of *Licaria*, which puts in doubt its position in the genus, or raises doubts regarding the present circumscription of the genus based on floral and vegetative morphology.

As for *Licaria bahiana*, whose distribution is also in the Atlantic rainforest domain and is sympatric in the region of Santa Teresa with *L. spiritusanctensis*, this species has been recently illustrated by Moraes and Vergne (2018). Both species can be easily distinguished, since *L. bahiana* is usually taller, reaching up to 22 m height, with flowers glabrous, pedicels relatively long, 3.6–4.0 mm long (vs. 2.7–3.2 mm long), stamens without basal glands, staminodes of fourth whorl wanting, pistil 2.2–2.4 mm long (vs. 1.5–1.9 mm long), fruits larger, 2.5–4.0 × 1.5–3.0 cm (vs. 1.9–2.8 × 1.1–1.9 cm), and cupules larger, 2.0–4.0 × 2.0–4.0 cm (vs. 0.4–1.6 × 1.48–2.30 cm).

Licaria debilis appears similar to *L. spiritusanctensis* at first glance because of the general morphological appearance of dried specimens of both species, which resemble each other. However, in *L. debilis*, the indument of buds, branchlets, petioles, and inflorescences consist of rusty trichomes of different sizes (vs. only short, grayish-to-whitish trichomes), the leaves on average are smaller, 6.0–16.0 × 2.0–5.5 cm (vs. 5.4–27.0 × 1.7–8.5 cm), often opposite to subopposite (vs. alternate), glabrescent on both sides, with long-persistent trichomes (longer than 0.5 mm) on midrib (vs. glabrous to glabrescent below, short trichomes), petioles slender, 0.3–1.0 cm long (vs. 1.0–1.8 cm long), inflorescences reddish in dried material (vs. blackish), flowers glabrous or nearly so (vs. glabrescent to sparsely pubescent), 1.0–2.0 mm long (vs. 2.3–2.8 mm long), pedicels thin, 2.0–5.0 mm long (vs. 2.7–3.2 mm long), stamens rather thick, ca. 1.0 mm long (vs. 0.79–1.40 mm long), filaments not distinct (vs. filaments as wide as or narrower than the anthers, therefore distinct), staminal valves medium (vs. staminal valves relatively large), basal glands in irregular numbers, 2–6 (vs. always 6), minute (vs. large, elongate), pin-shaped (vs. sagittate), located far to the side of the filaments (vs. along the abaxial surface of filaments), staminodes of fourth whorl wanting (vs. present), floral tube densely sericeous inside, with brown-yellowish trichomes (vs. glabrous to sparsely pubescent, trichomes whitish), fruits smaller, 2.0 × 1.0 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules in average smaller, 0.8–1.2 × 0.8–1.5 cm (vs. 0.4–1.6 × 1.48–2.3 cm), scarcely recognizable with double margins (margin 1.0–2.0 mm thick; vs. conspicuously double-rimmed, margin 4.0–8.0 mm thick), reddish in dried material (vs. blackish), pedicels ca. 1.0 cm long (vs. 0.4–1.6 cm long).

In addition to the species compared above with *Licaria spiritusanctensis*, *L. armeniaca* is another species with distribution in the Atlantic rainforest domain that could be confused with the former by the seeming vegetative resemblance. However, *L. armeniaca* can be distinguished by the leaves on average usually smaller and narrower, 8.0–18.0 × 2.5–6.0 cm (vs. 5.4–27.0 × 1.7–8.5 cm), lower number of secondary veins on each side of the midrib, 5–9 (vs. 6–11), petioles slender, smaller, 0.3–1.5 cm long (vs. 1.0–1.8 cm long), inflorescences larger, 2.0–13.0 cm long (vs. 1.25–9.70 cm long), glabrous to sparsely pubescent (vs. pubescent to densely pubescent), flowers smaller, 1.0–2.0 mm long (vs. 2.3–2.8 mm long), glabrous (vs. glabrescent to sparsely pubescent), pedicels thin, long, (3.0–)8.0–15.0 mm long (vs. 2.7–3.2 mm long), floral tube sericeous inside (vs. glabrous to sparsely pubescent), tepals unequal, inner ones conspicuously larger than outer ones (vs. subequal, inner ones slightly longer than outer ones), stamens with apical-introrse valves, the locelli always opening outward from the center of the flower, and the flaps swinging toward the tip of the anthers (vs. apical-(sub)extrorse, the locelli opening away from the center of the flower, and the flaps laterally swinging toward the center of anthers), staminodes of fourth whorl wanting (vs. wanting to present, then 1 to 3), fruits relatively smaller, 1.5–2.5 × 0.8–1.5 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules smaller, 0.4–1.5 × 0.6–1.5 cm (vs. 0.4–1.6 × 1.48–2.3 cm), pedicels up to 2.5 cm long (vs. 1.3–1.9 cm long).

Ocotea teresae P.L.R. Moraes & T.D.M. Barbosa, *sp. nov.* TYPE: BRAZIL. Espírito Santo: Santa Teresa, São Lourenço, Country Club, 16 December 1999, fl., *V. Demuner, E. Bausen & W. Pizziolo 334* (Holotype: MBML [11393]; Isotypes: HRCB, RB, UEC). Fig. 6.

Ocotea teresae can be recognized by the combination of leaves alternate to subopposite, evenly distributed along branchlets, without domatia, flowers large, densely pubescent, floral tube pubescent inside, tepals patent, spreading at anthesis, subequal, sparsely papillate outside, moderately papillate inside, stamens papillate, with short, pilose filaments, pistil glabrous, and relatively large fruits seated on large, hemispheric, hexalobed, double-rimmed cupules.

Small *trees* up to 12 m tall. *Terminal buds* elongate, densely covered with short, straight, appressed to ascending, yellow trichomes. *Branchlets* subangular, pubescent, trichomes short, straight, mostly appressed, yellowish, dense immediately below terminal bud, and slowly glabrescent on older parts of the twig. *Petioles* 0.5–1.1 cm long, blackish, glabrous to sparsely pubescent, densely pubescent in young leaves, indument ± as on twigs, (±) roundish below, canaliculate above. *Leaves* alternate to subopposite, evenly distributed along branchlets, elliptic, varying towards suboblong or obovate, 6.4–13.0 × 2.5–4.1 cm, subcoriaceous to coriaceous, glabrous above, sparsely pubescent below, with short, straight, mostly appressed trichomes mainly on midrib, glossy on both surfaces, paler below, tip obtuse, long acuminate to acuminate, base acute to cuneate, margin sclerified, flat; venation pinnate, eucamptodromous to brochidodromous, reticulation perfect to imperfect, areoles randomly arranged (not oriented), irregular, veinlets branched once, or absent; midrib prominent on both surfaces, secondary veins prominulous on both surfaces, 7–10 on each side of the midrib, without domatia, reticulation subdense, prominulous on both surfaces, conspicuous. *Inflorescences* racemose to paniculate, in the axils of foliage leaves and subterminal apical buds, or lateral, few-flowered, shorter than leaves, pubescent, trichomes yellowish, short, mostly appressed, peduncles angular, 1.8–4.5 cm long. *Flowers* bisexual, white in living material, blackish in dried material, large,

FIGURE 6. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A**, isotype (*Demuner 334*, UEC); **B**, paratype (*Kollmann 2557*, UEC).

ca. 6.0–8.0 × 5.0–6.0 mm at anthesis, densely pubescent, trichomes short, straight, mostly appressed, floral tube suburceolate, relatively shallow, ca. 1.0 mm deep, pubescent inside, trichomes grayish, relatively long (ca. 0.4 mm long), mostly appressed; tepals patent at pre-anthesis, spreading at anthesis, subequal, outer ones slightly larger than inner ones, ca. 2.2–4.1 × 1.1–2.0 mm, narrow ovate to suboblong, sparse pubescent to glabrescent, trichomes short, straight, appressed, sparse papillate outside, moderately papillate inside; stamens of first and second whorl almost of same size and shape, 0.7–1.0 mm long, upper pair of locelli introrse, lower pair lateral-introrse, anthers almost orbicular to roundish-trapeziform to trapeziform, glabrous, connective papillate, mainly on apex, the latter obtuse to truncate, filaments very short, ca. 0.15–0.3 mm long, shorter than anthers, pilose; stamens of third whorl 0.7–1.0 mm long, anthers subrectangular, glabrous, papillate, apex truncate, upper locelli lateral-extrorse, lower ones extrorse, filaments slightly shorter than anthers, pilose, with two basal glands, large, 0.48–0.70 × 0.57–0.67 mm, globose, short stalked; staminodes of fourth whorl stipitiform to subsagittate, pilose; pistil glabrous, 1.6–2.4 mm long, ovary ovoid, 0.9–1.4 mm long, style stout, 0.7–0.9 mm long, stigma robust, discoid, trilobed. *Fruits* 2.0–5.0 × 1.0–3.0 cm, ellipsoid, smooth, cupules 1.5–4.0 × 1.5–5.0 cm, hemispheric, hexalobed, double-rimmed, margin 4.0–8.0 mm thick, pedicels short. Fig. 5M–P, 7–8.

Phenology: flowers collected in November and December. Unripe fruits collected in January and June.

Etymology: the species name refers to the municipality of Santa Teresa, where the species has been collected so far.

Distribution and habitat: *Ocotea teresae* is known only from five specimens collected in the municipality of Santa Teresa, Espírito Santo, in the Atlantic rainforest domain; the localities are virtually the same as those shown in Fig. 4 for *Licaria spiritusanctensis*.

Additional specimens examined: BRAZIL. Espírito Santo: Santa Teresa, Reserva Biológica da Caixa D'água, alt. 700 m, 24 November 1998, bud, fl., *L. Kollmann et al. 1070* (HRCB, MBML, RB, SPSF, UEC); Santa Teresa, São

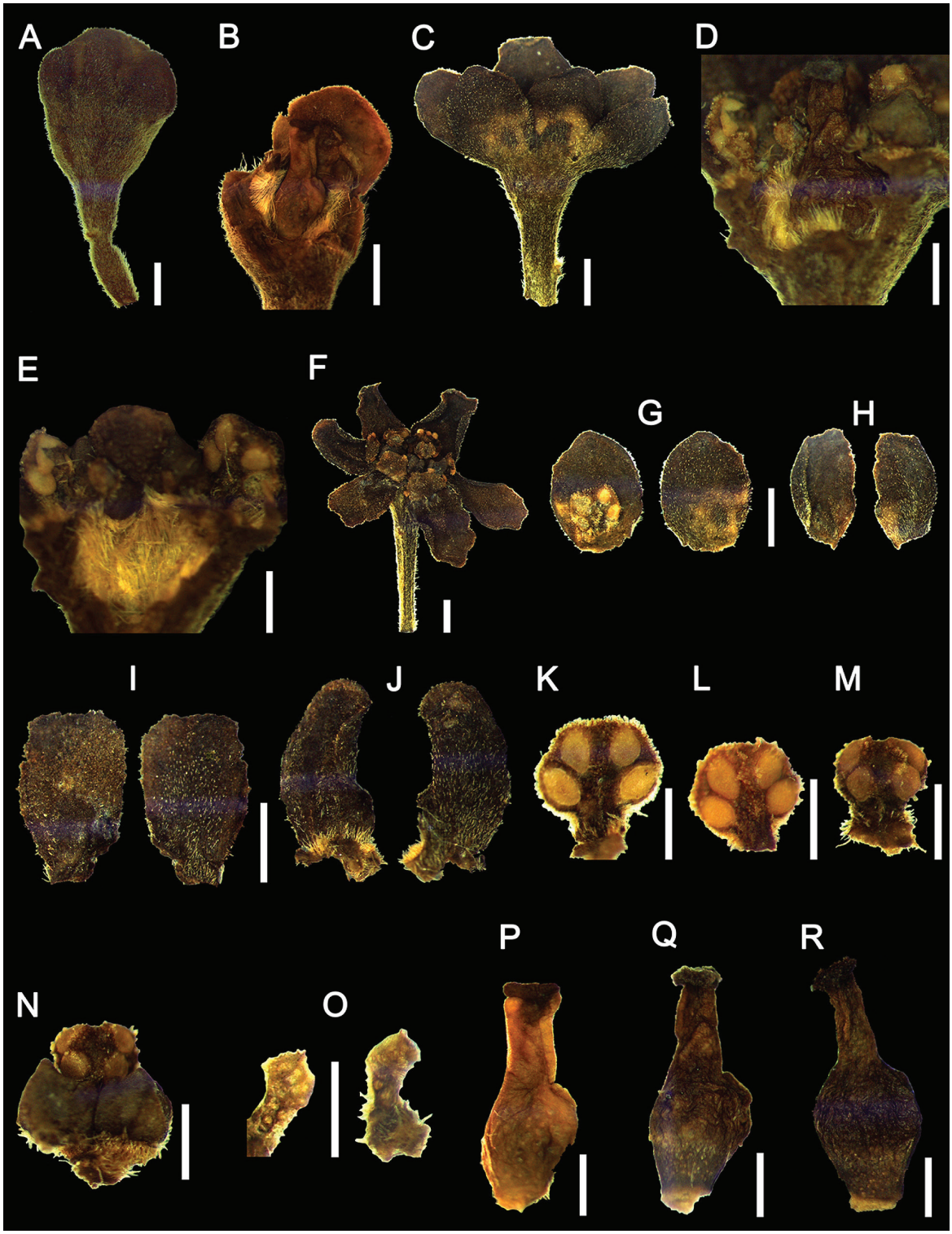


FIGURE 7. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A–B**, **P**. Flower buds from *Kollmann 1070* (UEC). **C–O**, **Q–R**. Flowers at pre-anthesis and post-anthesis from *Kollmann 1171* (UEC). **A**, bud; **B**, detail of pistil insertion in the floral tube from the previous bud; **C**, flower at pre-anthesis with patent tepals; **D**, detail of pistil insertion in the floral tube from the previous flower; **E**, detail of floral tube inside; **F**, flower at post-anthesis with spreading tepals; **G**, outer tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in C; **H**, inner tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in C; **I**, outer tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in F; **J**, inner tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in F; **K**, stamen of first whorl from flower at pre-anthesis; **L**, stamen of second whorl from flower at pre-anthesis; **M**, stamen of third whorl from flower at pre-anthesis; **N**, stamen of third whorl with basal glands from flower at pre-anthesis; **O**, staminodes of fourth whorl from flower at pre-anthesis; **P**, pistil from flower bud; **Q**, pistil from flower at pre-anthesis; **R**, pistil from flower at post-anthesis. Bars = 1 mm (A, B, C, F, G, H, I, J); 0.5 mm (D, E, K, L, M, N, O, P, Q, R).

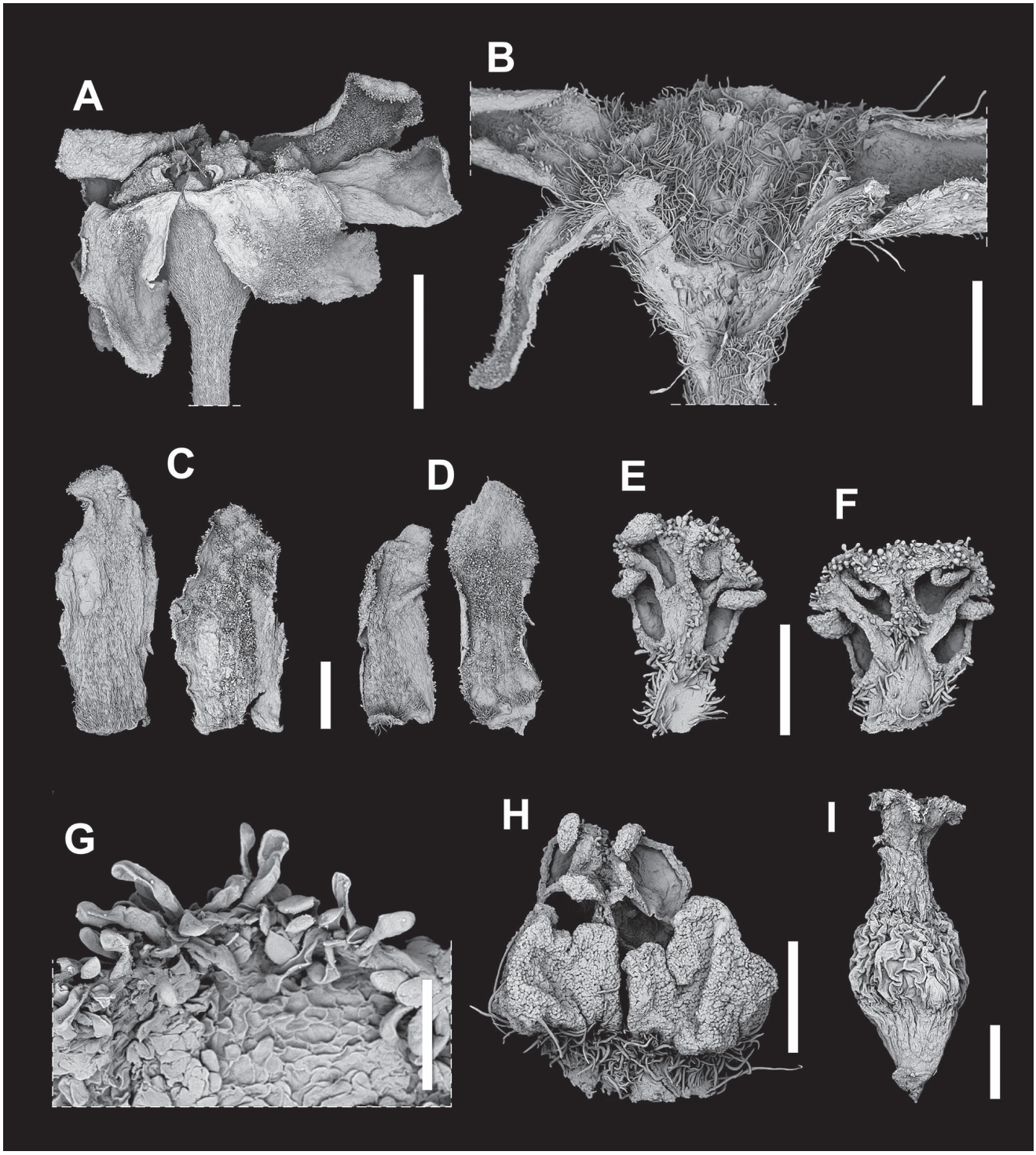


FIGURE 8. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. Flowers at post-anthesis from *Demuner 334* (UEC). **A**, sideview; **B**, sideview showing floral tube inside; **C**, outer tepals, abaxial (l.) and adaxial (r.) surfaces; **D**, inner tepals, abaxial (l.) and adaxial (r.) surfaces; **E**, stamen of second whorl; **F**, stamen of first whorl; **G**, detail of papillae on surface of anther apex; **H**, stamen of third whorl with basal glands; **I**, pistil. Bars = 2 mm (A); 1 mm (B, C, D); 0.5 mm (E, F, H, I); 0.1 mm (G).

Lourenço, Mata Fria, terreno de Clério Loss, valão à direita do asfalto, alt. 750 m, 2 December 1998, fl., *L. Kollmann et al. 1171* (HRCB, MBML, RB, UEC); Santa Teresa, Santo Antônio, terreno do Boza, alt. 750 m, 14 January 1999, immat. fr., *L. Kollmann & E. Bausen 1557* (ESAL, MBML, UEC); idem, alt. 850 m, 15 June 1999, immat. fr., *L. Kollmann et al. 2557* (MBML, RB, UEC).

From the combination of morphological characters found in *Ocotea teresae*, its placement in the informal groups of species proposed by Rohwer (1986) must be among those with bisexual flowers. It seems to fit best in the *O. indecora* group, which encompasses species with stamens with distinct, pubescent filaments, anthers usually somewhat papillate, staminodes present, floral tube usually deeply tubular; cupule in most species for most of its development hemispherical to almost spherical, sometimes double-rimmed. Nevertheless, it does not appear to present rhythmic growth of the branchlets, showing growth units starting with a long internode, and leaves and branches often more or less crowded, which are characteristic of this group.

In the general morphological aspect, *O. teresae* resembles *O. complicata* (Meisn.) Mez and *O. elegans* Mez, but differs from them by the flowers larger, ca. 8.0 × 6.0 mm (vs. 4.0–6.0 × 3.0–6.0 mm and 2.3–5.0 × 1.3–5.0 mm, respectively) and cupules double-rimmed. Several species of the *O. indecora* group develop double-rimmed cupules, like *O. calliscypha* L.C.S. Assis & Mello-Silva, *O. marcescens* L.C.S. Assis & Mello-Silva, *O. mosenii* Mez, *O. oppositifolia* S. Yasuda, *O. pumila* L.C.S. Assis & Mello-Silva, and *O. virgultosa* (Nees) Mez (= *O. lobbii* (Meisn.) Rohwer). However, none of them has cupules similar to those of *O. teresae*, which are different in shape, larger, thicker, with margins fairly conspicuous, resembling those of *Licaria bahiana*. *Ocotea teresae* is also vegetatively similar to *O. catharinensis* Mez and *O. oppositifolia* S. Yasuda, but both species have domatia in the leaves, which are not found in the former. The large flowers of *O. teresae*, with papillate tepals, are also found in species of *Nectandra*. However, both tepals and stamens of the former are less papillate than those usually found in *Nectandra*, besides other differences.

Micromorphological and Anatomical Notes

Further characters for the description of *Licaria spiritusanctensis* are provided here on the basis of investigation of its leaf cuticle and vascular bundles of midrib and petioles as compared with those of selected congenerics. Similarly, these characters are presented for *Ocotea teresae*, for both flowering and fruiting specimens, in order to verify their matching. No effort has been made here for a complete and detailed description of all epidermal features that could be analyzed in a more comprehensive study.

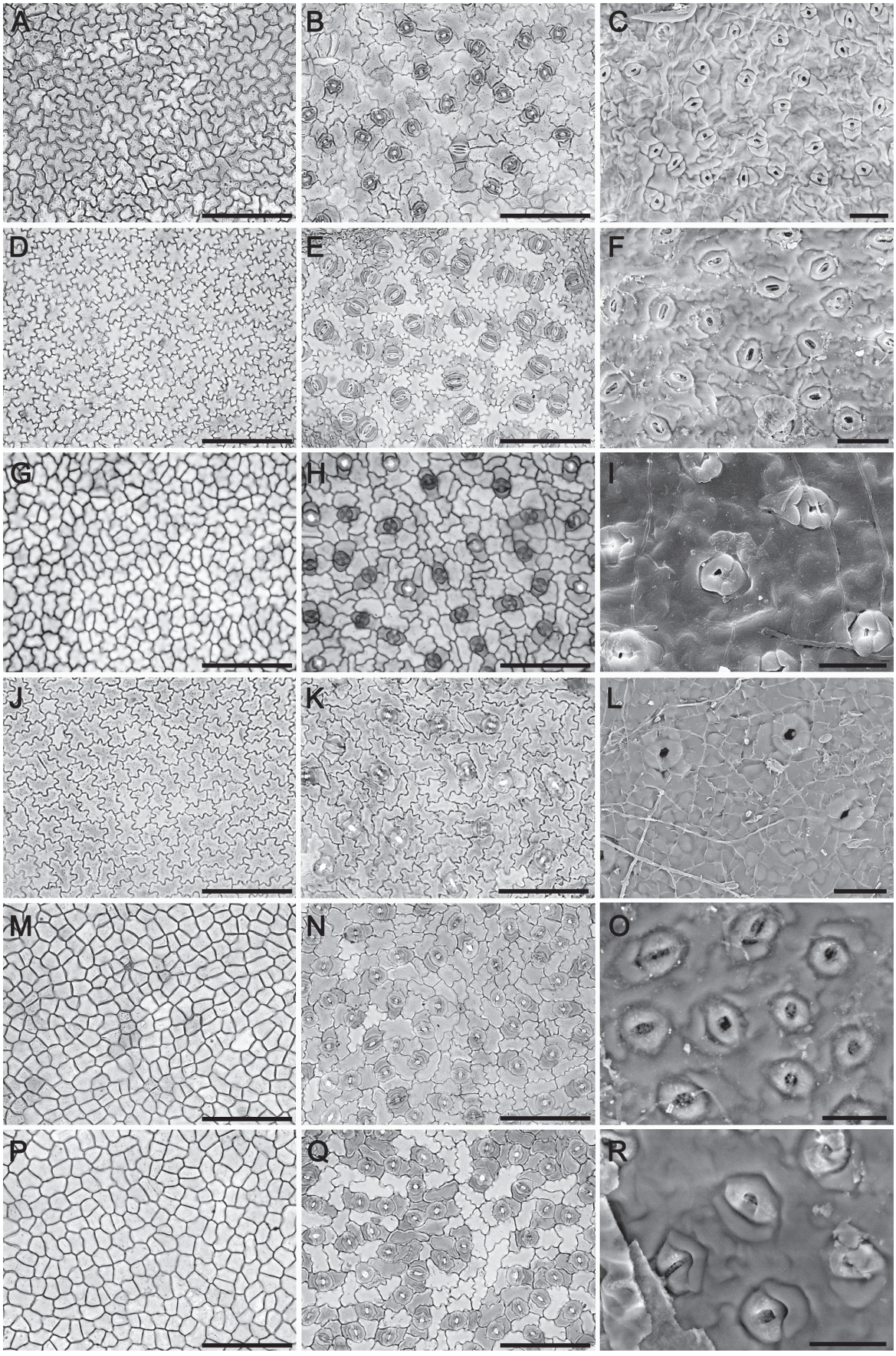
Leaf cuticles: Figure 9 shows the straightness of the epidermal anticlinal walls, in frontal view, for both adaxial and abaxial sides, as well as the overall shape of the stomatal complex. For the adaxial side of the epidermis, the epidermal anticlinal walls of *Licaria spiritusanctensis* are sinuate (Fig. 9A), whereas they are Ω-shaped in *L. armeniaca* and *L. subbullata* (Fig. 9D and J, respectively), and undulate to sinuate in *L. bahiana* (Fig. 9G). For *Ocotea teresae*, the anticlinal walls are curved and the cells are of the same size in both the flowering and fruiting specimens examined (Fig. 9M and P, respectively). On the abaxial side, *L. spiritusanctensis* shows cells slightly larger than those of the adaxial side, with sinuate to almost Ω-shaped walls (Fig. 9B), whereas in the other species the cells are of the same size and the anticlinal walls are as straight as on the adaxial side, that is, Ω-shaped in *L. armeniaca* and *L. subbullata* (Fig. 9E and K, respectively), and undulate to sinuate in *L. bahiana* (Fig. 9H). In *O. teresae*, the cells of both specimens examined are slightly larger than those on the adaxial side, and the anticlinal walls are sinuate to almost Ω-shaped (Fig. 9N and Q, respectively).

The overall shape of the stomatal complex is elliptic in *Licaria spiritusanctensis* and *L. bahiana* (Fig. 9C and I, respectively), and elliptic to broadly circular in *L. armeniaca* and *L. subbullata* (Fig. 9F and L, respectively). In *Ocotea teresae*, both specimens show the overall shape mostly elliptic to almost broadly circular (Fig. 9O and R, respectively).

According to Nishida and van der Werff (2011), an increasing number of studies on cuticular characters of extant Lauraceae have been conducted after the report of their usefulness for the family by Christophel et al. (1996). Nevertheless, there are few studies on these characters involving species of *Licaria* (e.g., Faggetter, 1985; Kostermans and Baas, 1976; Nishida and van der Werff, 2011; Petzold, 1907; Trofimov and Rohwer, 2018).

Petzold (1907) was the first to report general information on the anatomy of leaves of the American Lauraceae, on the basis of collections housed at the Berlin-Dahlem herbarium (B), following the taxonomic treatment undertaken by Mez (1889). Petzold presented anatomical descriptions for 15 species of *Licaria*, which were classified by Mez under *Acrodiclidium* Nees or *Misanteca* Cham. & Schltdl. Particularly referring to the straightness of the epidermal anticlinal walls, for both adaxial and abaxial sides, he discriminated only between straight and undulate walls, remarking when the undulation was more pronounced on one of the sides but not providing any illustration. Following this criterion, Petzold reported that *Acrodiclidium brasiliense* Nees (≡ *Licaria brasiliensis* (Nees) Kosterm.) shows anticlinal walls undulate on the adaxial side and straight on the abaxial, an exception to his observations that

Figure 9. (Shown on next page.) Leaf cuticles and stomata complex of *Licaria* species and *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A–C**. *L. spiritusanctensis* (*Kollmann 4946*, UEC). **D–F**. *L. armeniaca* (*Henderson 407*, HRCB). **G–I**. *L. bahiana* (*Moraes 4267*, HRCB). **J–L**. *L. subbullata* (*Secco 381*, MG). **M–O**. *O. teresae* (*Demuner 334*, UEC). **P–R**. *O. teresae* (*Kollmann 2557*, UEC). **A–B**, **D–E**, **G–H**, **J–K**, **M–N**, **P–Q**, adaxial and abaxial surfaces, respectively, by optical microscopy; **C**, **F**, **I**, **L**, **O**, **R**, stomatal complex by SEM. Bars = 100 μm (A–B, D–E, G–H, J–K, M–N, P–Q); 25 μm (C, F, I, L, O, R).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the species usually have cells with anticlinal walls more undulate on the abaxial side, as he has pointed out for *A. guianense* Nees (= *Licaria polyphylla* (Nees) Kosterm.) and *A. parviflorum* (Meisn.) Mez (= *Licaria armeniaca*). Under *Misanteca*, *M. capitata* Cham. & Schltdl. (≡ *Licaria capitata* (Cham. & Schltdl.) Kosterm.) and *M. pittieri* Mez (= *Licaria triandra* (Sw.) Kosterm.) were indicated with anticlinal walls undulate only on the abaxial side, whereas in *M. jurgensenii* Mez (= *L. triandra*) and *M. triandra* (Sw.) Mez (≡ *L. triandra*) the anticlinal walls were undulate on both sides. As for *L. armeniaca*, our results partially agree with Petzold, from the specimens examined for leaf cuticles (*Guilherme 341*, *Henderson 407*, *Moraes 5385*, and *Silva 9661*), since their epidermal anticlinal walls were shown to be Ω-shaped on both sides, without any pronounced difference between them. A similar result has been found by Trofimov and Rohwer (2018). Regarding *L. capitata*, photographs of epidermal anticlinal walls of both sides are available at the Cuticle Database Project (http://cuticledb.eesi.psu.edu/; former Leaf Cuticle Database Project; Barclay et al., 2007), from a sample of *E. Keber 410* (F), Mexico, prepared by David Dilcher (Contributor specimen no. 00169). The images show anticlinal walls curved adaxially, and curved to undulate to sinuate abaxially, therefore agreeing with Petzold. For *L. triandra*, Nishida and van der Werff (2011) examined a sample from *Vasquez 25139* (MO), Peru, which shows anticlinal walls "with tight U-shaped curves" (equivalent to sinuate and/or Ω-shaped walls, as used by Trofimov and Rohwer, 2018, and here) on both surfaces, agreeing with Petzold's findings for *M. jurgensenii* and *M. triandra*, but not for *M. pittieri*. In Vaz et al. (2019), *L. triandra* is said to have anticlinal walls straight adaxially and curved abaxially (but no voucher is reported for the sample used). In the protologue of *M. pittieri*, Mez (1903) cited only the fruiting specimen of "*Tonduz in herb. inst. phys.-geogr. Costar. 11612*," in "Herb. Berol., Mez," (duplicates in BM, BR, G, GH, K, NY, P, US), which most likely was the specimen analyzed by Petzold. This species was placed in the synonymy of *Licaria limbosa* (Ruiz & Pav.) Kosterm. by Kostermans (1937), which was not accepted by Allen (1945), who positioned it in *Licaria*, combining it as *L. pittieri* (Mez) C.K. Allen. Nevertheless, Kurz (1983, 2000) synonymized both *L. limbosa* and *L. pittieri* under *L. triandra*, thus widening the circumscription of the latter. Burger and van der Werff (1990) accepted the synonymy of *L. pittieri* in *L. triandra* but commented that the Costa Rican larger-leaved highland collections, which are well matched by the description and type of *L. pittieri*, contrasting with smaller-leaved lowland collections, would be worthy of subspecific rank. Despite the different opinions of taxonomists about the delimitation of *L. triandra*, it is worth mentioning that "the anticlinal walls of epidermal cells vary so much in the extent to which they are straight, curved, or undulating that the use of the surface view appearance of cells in taxonomic studies is severely limited" (Metcalfe, 1979) and should be used with caution (see Moraes and Paoli, 1999; Vaz et al., 2019).

Kostermans and Baas (1976) described the leaf anatomy of the type of *Licaria guianensis* Aubl. (*J. B. C. F. Aublet s.n.*, French Guiana; P00128471, P00128472). According to them, the unspecialized epidermal cells show strongly undulating (anticlinal) walls of about equal size adaxially and abaxially, but those on the abaxial side with very lowly dome-shaped, lignified, outer periclinal walls (in transverse section). In Nishida and van der Werff (2011), photographs of the epidermal anticlinal walls of both surfaces and the overall shape of the stomatal complex are presented from the collection of *Sabatier 3645* (MO), French Guiana.

The Ph.D. dissertation of Faggetter (1985) was a detailed study of the leaf cuticle in selected Laurales. She included two species of *Licaria* sampled from specimens deposited at Kew. The first was *A. J. G. H. Kostermans 15018*, from Trinidad (duplicates also in B, BO, L, NY, P, RB, U, and others), which was identified by Kostermans as *L. guianensis*, the name used by Faggetter. Later, in 1992, it was identified as *L. subbullata* by Henk van der Werff and confirmed by Holger Kurz in 2000 in the specimen housed at Utrecht. The second specimen was *J. de J.Jiménez 1395*, from the Dominican Republic (duplicate in US), correctly identified as *L. triandra*. From Kostermans's specimen, she described epidermal anticlinal walls as straight, which does not agree with our results from the specimens *Secco 381* and *Sperling 6190,* which showed anticlinal walls Ω-shaped on both sides. As for *Jiménez 1395*, Faggetter reported curved anticlinal walls.

In the study by Nishida and van der Werff (2011), four species of *Licaria* were included: *L. cannella* (Meisn.) Kosterm. (correct name: *L. crassifolia* (Poir.) P.L.R. Moraes), *L. guianensis*, *L. martiniana* (Mez) Kosterm., and *L. triandra*. According to the authors, all of them presented epidermal anticlinal walls "with tight U-shaped curves" (ca. sinuate and/or Ω-shaped walls) on both surfaces. These species appear to form a clade in the phylogeny inferred by Chanderbali et al. (2001), which was supported by the cuticular characters analyzed by Nishida and van der Werff (2011), since they did not vary within the group. However, those cuticular characters were be incongruent with the subgenera proposed by Kurz on the basis of stamen characters, since *L. cannella* belongs to subgen. *Canella* and the other three species belong to subgen. *Licaria*.

Trofimov and Rohwer (2018) have examined and illustrated the leaf cuticle and stomatal complex in 85 species of the *Ocotea* complex by optical and scanning electron microscopy. They included samples of four species of *Licaria* subgen. *Armeniaca*: *L. armeniaca* (*Kvist & Ruiz 1052* (AAU), from Loreto, Peru), *L. bahiana* (*Moraes 3166* (HRCB), from Linhares, Espírito Santo, Brazil), *L. pachycarpa* (Meisn.) Kosterm. (*Henkel 3021* (HBG), from U. Takutu-U. Essequibo, Guyana), and *L. rodriguesii* H.W. Kurz (*Silva 1960* (HBG), from Pará, Brazil). Results from these samples showed epidermal anticlinal walls Ω-shaped on both sides for *L. armeniaca*, whereas they were sinuate on both sides for *L. bahiana* and *L. rodriguesii*, and undulate adaxially and sinuate abaxially for *L. pachycarpa*. For the overall shape of the stomatal complex and the surface appearance of epidermal periclinal walls, *L. armeniaca* showed stomata circular with a circular and protruding surface appearance of periclinal walls forming a symmetric

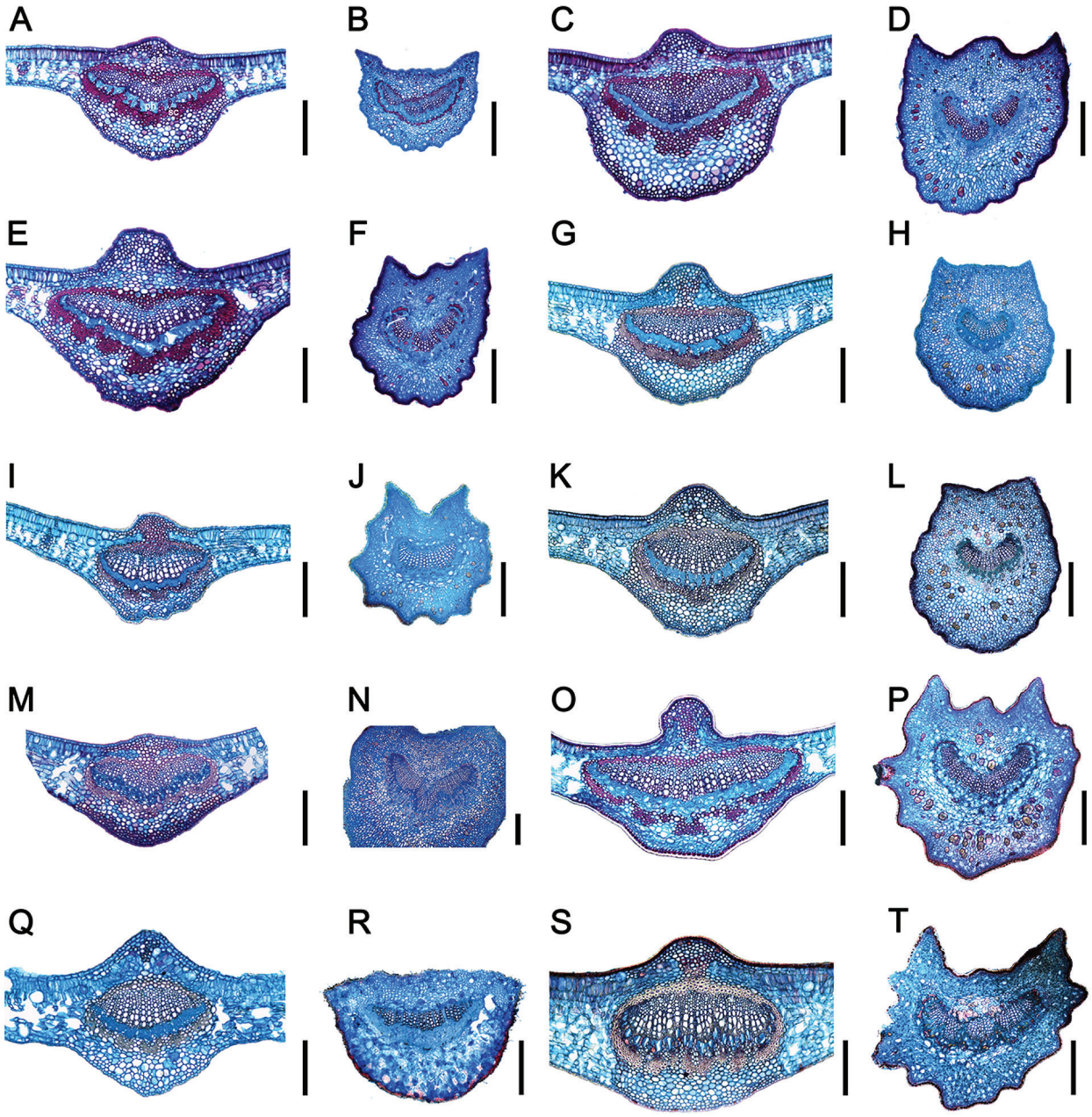

FIGURE 10. Leaf cross sections of *Licaria* species and *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa through blade midribs and petioles. **A–B**. *L. spiritusanctensis* (*Kollmann 4946*, UEC). **C–D**. *L. spiritusanctensis* (*Moraes 3238*, HRCB). **E–F**. *L. spiritusanctensis* (*Moraes 3245*, HRCB). **G–H**. *L. armeniaca* (*Guilherme 341*, HRCB). **I–J**. *L. armeniaca* (*Henderson 407*, HRCB). **K–L**. *L. armeniaca* (*Moraes 5385*, HRCB). **M–N**. *L. bahiana* (*Moraes 3166*, HRCB). **O–P**. *L. subbullata* (*Secco 381*, MG). **Q–R**. *O. teresae* (*Demuner 334*, UEC). **S–T**. *O. teresae* (*Kollmann 2557*, UEC). **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**, **S**, blade midrib; **B**, **D**, **F**, **H**, **J**, **L**, **N**, **P**, **R**, **T**, petiole. Abbreviations: ph, phloem; sc, sclerenchyma; se, sheath extension; xy, xylem. Bars = 250 μm (A, C, E, G, I, K, M, O, Q, S); 500 μm (B, D, F, H, J, L, N, P, R, T).

circle, whereas in the other species they were elliptic with a surface appearance narrowly circular, protruding, with evenly wide margin. Our results from samples of *L. armeniaca* showed that stomata can vary between elliptic to circular in almost equal proportions, making it difficult to select the most frequent type as typical for the specimen or species.

Regarding *Licaria debilis*, Kurz (2000) has pointed out that it is one of the few species in the genus that could be safely recognized vegetatively. Under a reflected light microscope, or even under a magnifying glass with a 50-fold magnification, it is possible to see that the epidermal anticlinal walls are strongly wavy (ca. sinuate to Ω-shaped) and shine more brightly than their surroundings. Although

we had no sample at hand to illustrate this feature, we have observed it in specimens at Kew, through a stereomicroscope. Unfortunately, we did not succeed in obtaining pictures of high enough quality to include here.

As pointed out by van der Werff (2009b), fruiting specimens of *Licaria* can often be identified only by matching them with flowering ones from the same area. This is also often true in *Ocotea*, and the leaf epidermal features have been useful for confirming the identity of our samples of *O. teresae*.

Leaf vascular bundles: Figure 10 shows leaf cross sections through blade midribs and petioles. All *Licaria* species presented midribs and petioles supplied with single collateral vascular bundles, with xylem adaxially and phloem abaxially. Midrib bundles are arranged in flattened arches and are sheathed by a continuous sclerenchyma (somewhat discontinuous close to phloem in *L. subbullata*); bundle sheath extensions touch only the adaxial surface (Fig. 10A, C, E, G, I, K, M, O). The various specimens of *L. spiritusanctensis* (Fig. 10A, C, E) and *L. armeniaca* (Fig. 10G,I,K) show a closer anatomical similarity within each species, as would be expected, despite the overall similarity among them and in comparison with the specimens of *L. bahiana* (Fig. 10M) and *L. subbullata* (Fig. 10O). However, among their differences, *L. armeniaca* and *L. bahiana* have the presence of two palisade layers, whereas *L. spiritusanctensis* and *L. subbbullata* have an uniseriate palisade layer; and *L. armeniaca* shows a relatively narrower midrib bundle, whereas *L. subbullata* presents the widest one in comparison to the others. As for the petioles, the vascular bundles are crescent-shaped or in arch (ca. U- or V-shaped) in all species of *Licaria* (Fig. 10B, D, F, H, J, L, N, P). The presence of a sclerenchymatic sheath surrounding the bundle varied among the specimens of *L. spiritusanctensis* and *L. armeniaca*, and was clearly perivascular only in the sample of *Kollmann 4946* (Fig. 10B), whereas it was adaxially absent or discontinuous in the other specimens. All species presented large sclereids isolated and dispersed in the cortex.

In the specimens of *Ocotea teresae*, midribs (Fig. 10Q, S) and petioles (Fig. 10R, T) have a single collateral vascular bundle, with xylem adaxially and phloem abaxially. Midrib bundles are semicircular to arch with a perivascular sclerenchymatic sheath that can be discontinuous close to the phloem. The petioles also varied between the samples, with the bundle arranged in a flattened arch in *Demuner 334*, and crescentic in *Kollmann 2557*.

The anatomy of the leaf midrib and the petiole in Lauraceae has been studied in only a few genera and species, for example: several Philippine species of *Cinnamomum* Schaeff. by Santos (1930); *Umbellularia californica* (Hook. & Arn.) Nutt. and *Laurus nobilis* L. by Kasapligil (1951); several species of *Aniba* Aubl. by Vattimo (1968a,b,c,d, 1969a,b,c); three species of *Nectandra* Rol. ex Rottb. by Gonzalez et al. (1997); *Beilschmiedia* Nees by Nishida and Christophel (1999); several species of *Ocotea* by Santos and Oliveira (1988, 1995), Farago et al. (2005), and Coutinho et al. (2006a,b); one species of *Cryptocarya* R. Br. by Moraes and Castro (2007); and species of the *Mezilaurus* Kuntze ex Taub. clade by Vaz et al. (2019). Vaz et al. (2019) pointed out that *Licaria triandra* shows a midrib bundle arranged in arch, similar to what we have shown for the examined species.

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