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Original article

Revised delimitation of *Croton campestris* (Euphorbiaceae), including description of two new species, molecular phylogenetic, anatomical and micromorphological data

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ABSTRACT

Croton section *Adenophylli* is the largest section in the genus, with around 223 species distributed in the neotropical region. One of the main diagnostic characteristics of this section is the fruit columella, which has three prominent ascending terminal appendages. During a taxonomic review of this section in Brazil, we observed that *C. campestris* has a problematic taxonomic circumscription, thereby being confused with some other congeners. We investigate the circumscription of *C. campestris* through the examination of several herbarium specimens across its entire geographic range, and in its different habitats. We conducted macro- and micro-morphological studies as well as molecular analyses based on DNA sequences. Our results allow us to propose two new species (*C. hatschbachii* and *C. stellatorotatus*), update the nomenclature of *C. campestris* and *C. subvillosus*, and define the systematic positions, phylogenetic relationships, morphology and leaf anatomy of the above-mentioned taxa. The species are described, and their geographic distributions, morphological relationships, flowering and fruiting times, and conservation statuses are commented on. The two new species are also illustrated. Seventeen new synonyms, thirteen lectotypes and two neotypes are proposed. We also provide a key for the identification of 11 taxa belonging to the section *Adenophylli*, previously confused with *C. campestris*.

Keywords: Brazilian flora, Cerrado, Crotoneae, *Croton* sect. *Velamea*, phylogeny, taxonomy

Introduction

Croton is the second largest genus of Euphorbiaceae, with from 1200 to 1300 species widely distributed in the tropics and subtropics (Govaerts *et al.* 2000; Berry *et al.* 2005). These species inhabit dry or moist vegetation regions and exhibit habits ranging from small herbs, shrubs, and lianas to large trees, and display a wide diversity of trichomes, floral and extrafloral nectary glands, and interesting floral patterns (van Ee *et al.* 2011; Thaowetsuwan *et al.* 2020). *Croton* is represented by approximately 700 species in the

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Americas (van Ee *et al.* 2011), of which 300 are cited for Brazil and 230 considered endemic (Caruzo *et al.* 2021). A phylogenetic study of *Croton* has identified four major clades, three of them American, and one restricted to the Old World (van Ee *et al.* 2011). Among the American clades, *Croton* subg. *Adenophylli* comprises 270 species distributed in two sections: *Croton* sect. *Cyclostigma* (47 spp. according to Farias *et al.* (2019)) and *C.* sect. *Adenophylli* (223 spp.) (van Ee *et al.* 2011).

Croton sect. *Adenophylli* is the largest section of the genus, with species distributed from southern United States to Argentina (van Ee *et al.* 2011), and *C. bonplandianus*, native to the Southern Cone, has become naturalized in the Old World (Berry *et al.* 2017). In Brazil, we estimate that the section *Adenophylli* is represented by about 45 species. The monophyletic nature of this section has been supported by studies by Berry *et al.* (2005), Riina *et al.* (2009), and van Ee *et al.* (2011), including the former *C.* sect. *Velamea*, *C.* sect. *Cyclostigma* subsect. *Xalapensis*, and *C.* sect. *Cascarilla* sensu Webster (1993), even though based on low sampling (only 28 % of the species). The section includes species that are subshrubs, shrubs or, less commonly, trees, usually with stellate trichomes, leaves with or without acropetiolar/basilaminar nectary glands, leaf margins often entire, bisexual thyrses with cymules usually unisexual, pistillate flowers sessile or subsessile, with valvate sepals of equal lengths and often without glands, and capsule columella with three prominent, smooth, ascending terminal appendages (van Ee *et al.* 2011).

According to van Ee *et al.* (2011), *Croton* sect. *Adenophylli* needs to be taxonomically revised using tools that can help resolve the delimitations of its species in light of the existence of many synonyms among published names, and likely other undescribed species. Among those species, *Croton campestris* is prominent, since it has been reported from Argentina, Bolivia, and all regions of Brazil (Lima & Pirani 2003; Carneiro-Torres 2009; Silva *et al.* 2010; Jørgensen *et al.* 2014; Sodré *et al.* 2017), and it appears to encompass wide morphological variation. Analyzing herbarium collections and the available literature, we found that the name *Croton campestris* has been applied to very distinct species from distant locations by several authors (*e.g.*, Lima & Pirani 2003). On the other hand, several species and varieties related to *C. campestris* with type collections from the same geographical area were described by Baillon (1864) and Müller Argoviensis (1866; 1873) but differentiated only by superfluous characteristics. The resulting confused taxonomy is evidenced by the difficulty that many researchers have encountered in identifying the morphological limits of *C. campestris,* and differentiating it from related species.

During the revisional study of *C.* sect. *Adenophylli*, it was observed that the collections of *C. campestris* as well as the literature reflected errors of identification for including the concept of other species such as *C. intercedens*, *C. heliotropiifolius*, *C. lanatus*, *C. subacutus*, *C. subvillosus* and two undescribed species (see Tab. 1). Detailed examinations of all of these species led us to: a) update the circumscriptions of *C. campestris* as well as *C. subvillosus* - a species that is often confused with the former in taxonomic and floristic studies of the genus in the midwestern region of Brazil (Sodré *et al.* 2014; 2017; Secco *et al.* 2018); b) describe and illustrate *C. hatschbachii* and *C. stellatorotatus* as new species; c) propose 17 new synonyms and 14 lectotypes for names related to *C. campestris*; and d) update the geographic distributions, conservation statuses, and phenologies of all recognized species, with illustrations, photographs and maps. We also compared *C. campestris*, *C. hatschbachii*, *C. stellatorotatus* and *C. subvillosus* in terms of the anatomies of their leaves and the micromorphologies of their foliar trichomes, as studies of that nature have frequently been found to be valuable for separating taxa in the genus (*e.g.*, Caruzo *et al.* 2016; Sodré *et al.* 2019; Sodré & Silva 2020). We positioned the new species, as well as *C. campestris* and *C. subvillosus,* in a molecular phylogeny derived from *trnL-F* (cpDNA) and ITS (nrDNA) markers to confirm their phylogenetic positions and better understand the relationships between them. We also present a key to differentiate *C. campestris* from the other 11 species of *Croton* sect. *Adenophylli* with which it has previously been confused.

Materials and Methods

Phylogenetic Studies

Our sampling included accessions of 69 species of all four subgenera of *Croton* L., among them 34 species of the section *Adenophylli* Griseb., ten species of section *Cyclostigma* Griseb., *C. chimboracensis* P.E. Berry & Riina (species sister to *C.* sect. *Adenophylli* according to Riina & Berry 2010) and one species of genus *Brasiliocroton* P.E. Berry & Cordeiro as an outgroup. Two datasets were built: one with 70 samples for the nuclear ribosomal ITS region and another with 65 samples for the plastid spacer *trnL-trnF* region. Sequences were retrieved from GenBank depending on DNA availability, except for five of them (*C. campestris* A.St.-Hil., *C. echioides* Baill., *C. hatschbachii* Sodré & M.J. Silva sp.nov., *C. stellatorotatus* Sodré & M.J. Silva sp.nov. and *C. subvillosus* Müll. Arg.), which were generated in this study. Information about all sequences used in this study with their vouchers and GenBank accession numbers are presented in Tab. S1.

DNA was extracted from silica-dried specimens following the cetyltrimethyl ammonium bromide (CTAB) protocol of Doyle & Doyle (1987) with modifications. ITS and trnL-F regions of DNA were amplified with PCR and sequenced with primers from White *et al.* (1990), Taberlet *et al.* (1991) and Urbatsch *et al.* (2000) followed the same laboratory procedures as in previous phylogenetic studies in the genus (van Ee *et al.*

Table 1. Authors who misinterpreted different materials such as *C. campestris*, with their respective vouchers, locations and valid species to which they correspond.

Author(s)	Voucher(s)	Country/State or Province	Correct species
Croizat (1941)	*E.L. Ekman 444* (US); *J.E. Montes 450* (LIL)	Argentina; Paraguay	*Croton lanatus* Lam.
Lima & Pirani (2003)	*F. Barros 2649* (SP)	Brazil, São Paulo	*Croton fulvus* Mart.
	L.B. Smith et al. *14862* (R, US)	Brazil, Paraná	*Croton fulvus* Mart.
	M.P.M. Lima et al. *119* (RB)	Brazil, Pará	*Croton hadrianii* Baill.
	F.C.F. Silva 183 (RB)	Brazil, Ceará	*Croton heliotropiifolius* Kunth
	S. Ginzbarg et al. *724* (UB)	Brazil, Distrito Federal	*Croton intercedens* Müll. Arg.
	J. Semir 20513 (UEC)	Brazil, Goiás	*Croton intercedens* Müll. Arg.
Cordeiro (2004)	*R.M. Harley 25091* (SPF)	Brazil, Minas Gerais	*Croton hatschbachii* Sodré & M.J. Silva sp. nov.
Sátiro and Roque (2008)	*L.P. de Queiroz 4765* (HUEFS, SP)	Brazil, Bahia	*Croton heliotropiifolius* Kunth
Carneiro-Torres (2009)	*R.P. Belém* and *J.M. Mendes 128* (RB)	Brazil, Goiás	*Croton fulvus* Baill.
	A.S.F. Castro s.n. (EAC31168)	Brazil, Piauí	*Croton echioides* Baill.
	G. Hatschbach et al. *36262* (MBM)	Brazil, Goiás	*Croton subacutus* (Baill.) Müll. Arg.
	G. Hatschbach et al. *72220* (MBM)	Brazil, Minas Gerais	*Croton subferrugineus* Müll. Arg.
	D.S. Carneiro-Torres et al. *612* (HUEFS)	Brazil, Bahia	*Croton stellatorotatus* Sodré & M.J. Silva sp. nov.
Silva *et al.* (2010)	*G. Fotius 3761* (IPA, HUEFS)	Brazil, Pernambuco	*Croton echioides* Baill.
Jørgensen *et al.* (2014)	*T. Killeen 1332* (F)	Bolivia, Santa Cruz	*Croton fulvus* Mart.
Sodré *et al.* (2014)	*M.J. Silva* et al. *3104* (UFG)	Brazil, Goiás	*Croton subvillosus* Müll. Arg.
Sousa *et al.* (2014)	without voucher	Brazil, Paraíba	*Croton heliotropiifolius* Kunth
Sodré *et al.* (2017)	*E.P. Heringer et al. 4054* (UFG)	Brazil, Distrito Federal	*Croton subvillosus* Müll. Arg.
Secco *et al.* (2018)	*W.G. Garcia 14026* (UEC)	Brazil, Mato Grosso do Sul	*Croton subvillosus* Müll. Arg.
Caruzo *et al.* (2021)	*Markgraf 3438* (R)	Brazil, Minas Gerais	*Croton glandulosobracteatus* Carn.-Torres & Cordeiro

2011; Riina *et al.* 2009). The sequences were aligned using the CLUSTALW in MEGA version 6 (Tamura *et al.* 2013). The data matrix obtained was analyzed by Bayesian Inference, using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003). The evolutionary model was previously selected by JModelTest 2.1.5 (Darriba *et al.* 2012) based on Akaike Information Criterion (AIC) (Akaike 1973). The model used to analyze the ITS datasets was SYM + G and to analyze the *trn*L-*trn*F was TVM + G). The analysis consisted of two independent runs of four Markov chain Monte Carlo, each run with 10,000,000 generations, with trees sampled every 1,000 generations. After 25 % of the initial samples collected (burn in) being discarded, the remainder were used to determine the values of posterior probability (PP). The statistical support of each node of the cladograms obtained was estimated through the bootstrap statistics (Felsenstein 1985) from 10,000 heuristic pseudo-replicates using a random addition of taxa and TBR branch swapping performed in PAUP* version 4.0b10. Well-supported clades are defined as those with Bayesian posterior probabilities (PPs) and bootstrap support (BS) greater than or equal to 0.95 and 85 %, respectively.

Scanning Electron Microscopy

For the scanning electron microscopy (SEM) analyses, the leaves of the two new species, *C. subvillosus* and *C. campestris* were removed from field and herbarium specimens, fixed on stubs, and coated with gold using a spray applicator (Leica EM SCD050, Heidelberg, Germany). The samples were examined using a scanning electron microscope (Zeiss EVOMA100, Jena, Germany) at the High-Resolution Microscopy Multiuser Laboratory (LabMic), at the Institute of Physics, Federal University of Goiás (UFG). The trichomes were classified according to the terminology of Webster *et al.* (1996).

Anatomical studies

Adult leaves from four fresh specimens of *C. campestris* (*R.C. Sodré 3437-3440*) and *C. subvillosus* (*R.C. Sodré 1054*, *1199*, *1561*, *3464*), two specimens of *C. hatschbachii* (*R.C. Sodré et al. 3464, 3465*) and one of *C. stellatorotatus* (*R.C. Sodré 3309*) were fixed in the field with FAA (formaldehyde, acetic acid, and 50 % ethanol; 1:1:18, v:v:v) for 48 hours, and preserved in 70 % ethanol (Johansen 1940); vouchers were deposited in the BOTU and UFG herbaria (acronyms according to Thiers 2021, continuously updated). Cross sections were made from those samples using a razor blade, cleared with sodium hypochlorite (10-20 %), stained in 1 % astra blue aqueous solution and 1 % safranin (9:1, v:v) (Bukatsch 1972), and mounted on slides with coverslips in an aqueous glycerin solution (1:1, v:v). Imaging was performed using a light microscope (Leica DM 500®) equipped with a digital camera (Leica ICC 50®). Cross sections and SEM photographs were viewed, edited, and merged with Adobe Photoshop CS vers. 8.0.1. Anatomical analyses of the leaves were conducted at the Plant Anatomy Laboratory, at the Botany Department, Institute of Biological Sciences, Federal University of Goiás (UFG).

Taxonomic Studies

Fieldwork was carried out between December 2017 and January 2019 in the states of Goiás, Minas Gerais, and Bahia, Brazil. We analyzed approximately 400 specimens identified as *Croton campestris* in 39 Brazilian and foreign herbaria during personal visits or through loans (A, ALCB, BHCB, BM, BOTU, C, CEN, CEPEC, EAC, ESA, F, G, G-DC, GH, HRCB, HUEFS, IAN, IBGE, INPA, IPA, K, LD, LIL, M, MBM, MPU, NY, P, PAMG, R, RB, SPF, U, UB, UEC, UFG, UFMT, US, W; acronyms according to Thiers 2021, continuously updated). The flowers were dissected after rehydration in hot water and their components measured. Information concerning latex colors, indument types, and flowers and fruits was primarily based on field observations. Species identifications and the confirmation of new species were based on the specialized literature (*e.g.*, Müller Argoviensis 1866; 1873; Smith *et al.* 1988; Webster 1993; Lima & Pirani 2003; Caruzo & Cordeiro 2007; Secco 2008; Carneiro-Torres 2009; Silva *et al.* 2010; van Ee *et al.* 2011; Sodré *et al.* 2014; 2017), analyses of types and original descriptions, and comparisons with collections from the aforementioned herbaria.

Type collections were consulted using the online image banks of the B, BR, F, G, K, NY, P and W herbaria, as well as websites such as Jstor Global Plants (https://plants.jstor.org/), GBIF - Global Biodiversity Information Facility (https://www.gbif.org/), Specieslink (http://www.splink.org.br/index?lang=pt), Herbário Virtual Reflora (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/) and Jabot (http://jabot.jbrj.gov.br/v2/consulta.php).

The conservation statuses of the species were assessed according to IUCN (2017) criteria, with the Extent of Occurrence (EOO) calculated using the Geospatial Conservation Assessment Tool GeoCAT (Bachman *et al.* 2011). Our descriptions follow the terminology of the specialized literature on *Croton*. Geographic distributions were based on georeferenced data from the herbarium specimens analyzed, and were plotted using QGIS v. 2.14 (QGIS 2020 development team).

The typifications of the species were based on literature review and consultations of high-resolution photographs of type collections available on the aforementioned websites. The lectotype proposals follow article 9.3 of the Shenzhen Code (Turland *et al.* 2018). When the protologue of a specific taxon indicated an herbarium with only a single exsiccatae type collection, it was considered the holotype, while any other exsiccatae in other herbaria were considered isotypes. However, when the taxon was described without any mention of a host herbarium, and if only a single exsiccatae was found, we chose to treat it as a syntype (considering that other exsiccatum from that same collection might be found in other herbaria during further studies).

The synonymizations proposed here are based on analyses of protologue descriptions, type collections, and variations found in populations in their respective areas of occurrence. None of the varieties or forms previously described for the species are recognized here, as we consider the characteristics that differentiate them as being continuous between populations of their respective species.

Results and Discussion

Molecular phylogeny

Bayesian reconstruction based on individual ITS and *trn*L-*trn*F datasets resulted in different topologies, mainly in the relationships between the sections *Adenophylli* and *Cyclostigma*, as already noted in phylogenies with the genus *Croton* (Riina *et al.* 2009; van Ee *et al.* 2011). The trees with Bayesian posterior probabilities (PP) and bootstrap percentages (BS) based on ITS dataset are shown in Fig. 1 and on *trn*L-*trn*F dataset in Fig. 2. The tree resulting from the ITS analysis supports the section *Cyclostigma* as sister to the clade containing *C. chimboransensis* + section *Adenophylli* with 100 % BS and 1.00 PP. In the *trn*L-F tree *C. chimboracensis* emerged as sister to the members of the three largest subgenera of *Croton* (C. subg. *Adenophylli*, *C.* subg. *Croton* and *C.* subg. Geiseleria) while *C.* sect. *Adenophylli* was a sister of the clade containing *C.* sect. *Cyclostigma* + subgenera *Croton* + subgenera *Geiseleria*. *Croton* sect. *Adenophylli* emerged as monophyletic in both datasets, if *C. chimborancensis* is considered separate, with results from ITS analyses given better support for this clade (PP 1.00; BS 99 %), and moderate bootstrap support by trnL-F data (PP 1.00; BS 78 %). Our results are in agreement with the topology found by Riina *et al.* (2009) and van Ee *et al.* (2011), in which *Croton* sect. *Adenophylli* was represented by only 7 % and 6 % of its species respectively. Additionally, we made the first sampling of *C. campestris*, the type species of *Croton* sect. *Velamea*, which is currently synonymous with the *C.* sect. *Adenophylli*.

The members of the *C. campestris* group sampled here (*C. campestris*, *C. hatschbachii*, *C. heliotropiifolius*, *C. stellatorotatus* and *C. subvillosus*) form a clade well supported in the analysis of ITS (PP 1.00; BS 100 %) and *trn*L-F data (PP 1.00; BS 99 %). This subclade is mainly characterized by leaves without nectary glands covered by dense indument of stipitate stellate or multiradiate trichomes with pinnate venation, thyrses always with unisexual cymules, stamens usually around 15 or 16, sessile or subsessile pistillate flowers with eglandular sepals, and always 2-fid styles, characters similar to those indicated by Webster (1993) to define *C.* sect. *Velamea*. *Croton campestris* group must include approximately 10 species distributed mainly in South America in semiarid vegetation in Caribbean Islands, Venezuela, Colombia, Peru, and northeastern Brazil, or in areas of Chaco and Cerrado (neotropical savanna) in Argentina, Brazil, Paraguay, and Bolivia.

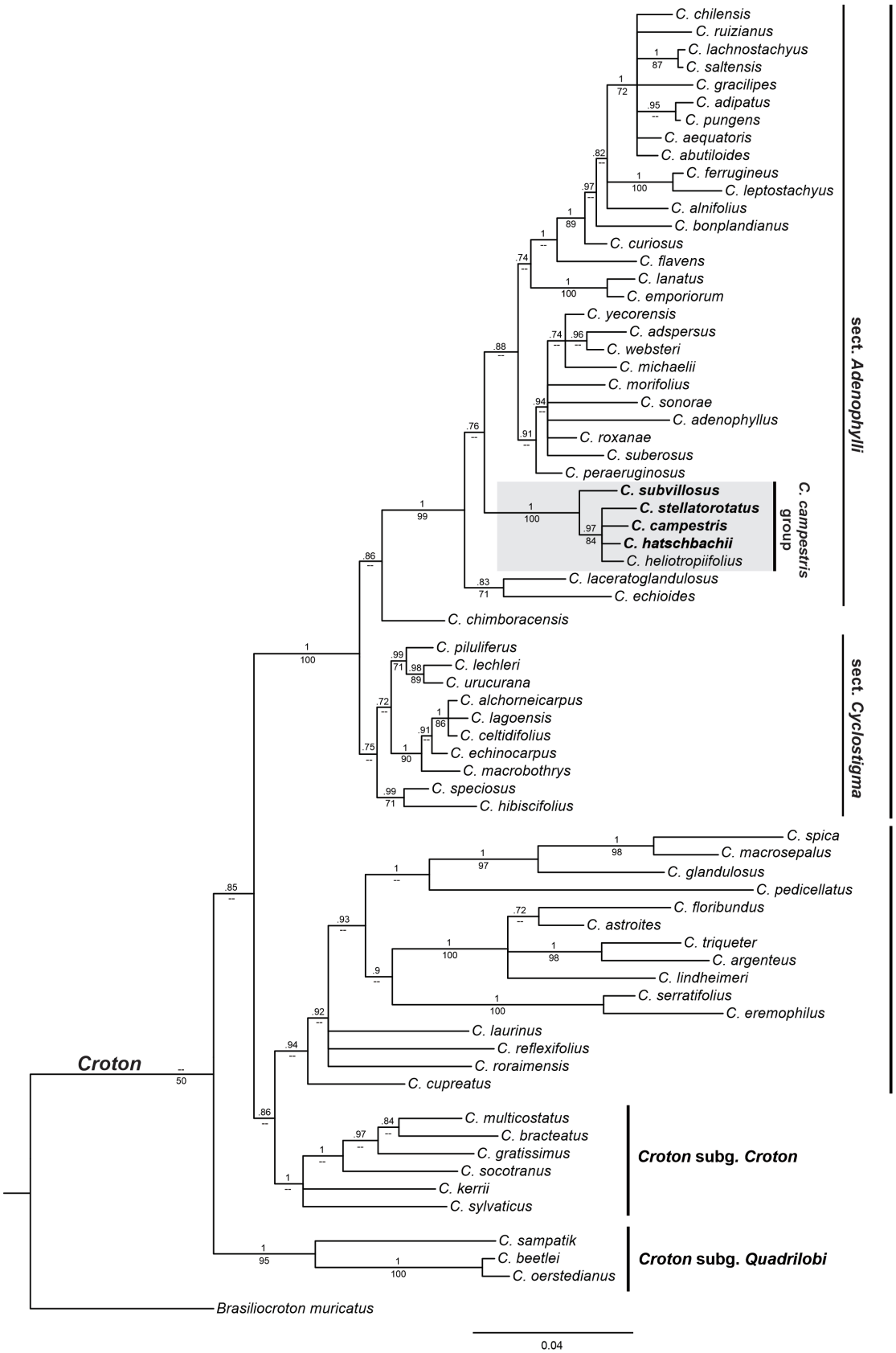

Figure 1. Tree obtained from the Bayesian analysis of ITS sequences. Values above and below the branches are Bayesian posterior probabilities and bootstrap percentages respectively. The scale bar indicates the mean number of nucleotide substitutions per site. In bold the species treated in this study. Asterisk indicates that the sample identification has been updated.

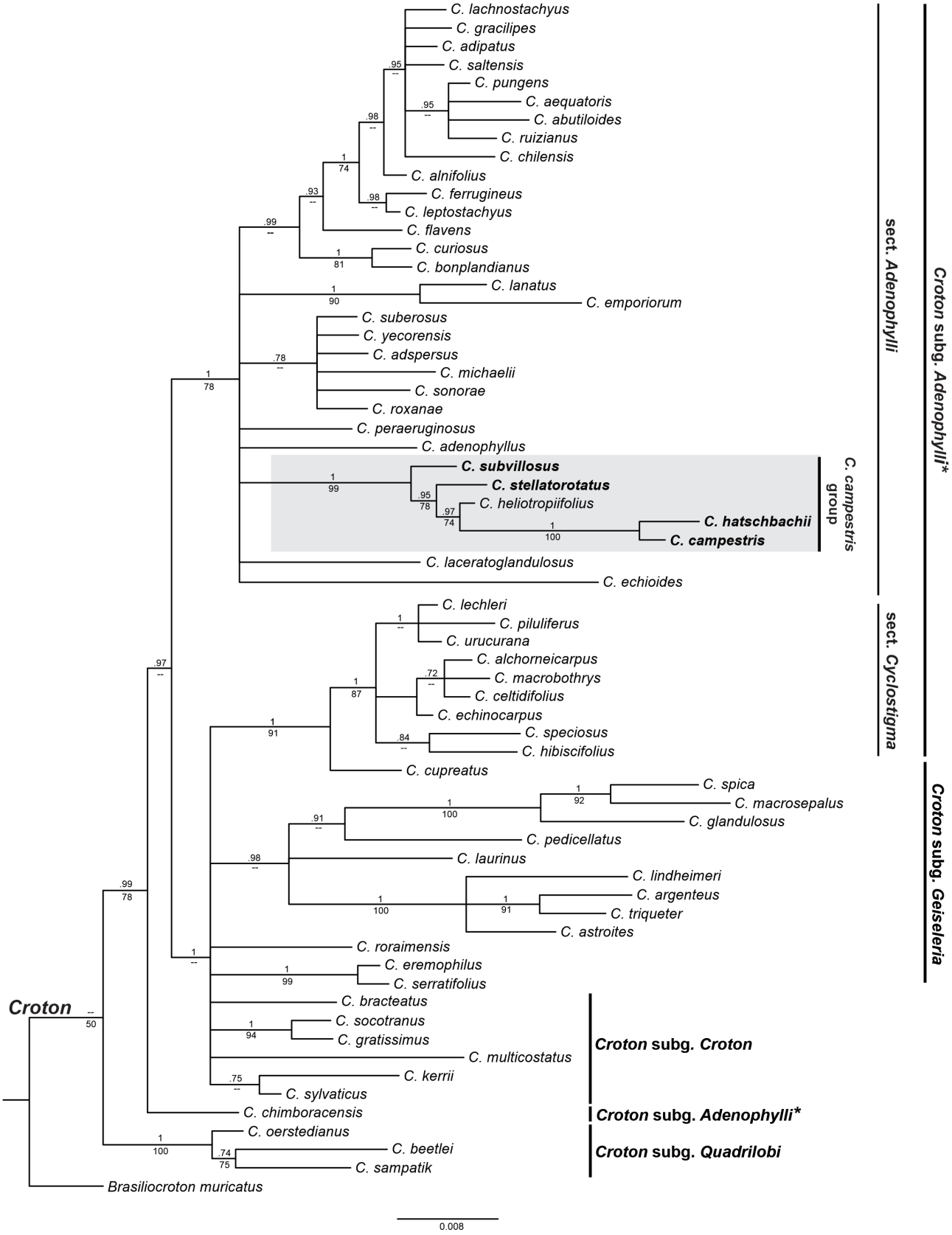

Figure 2. Tree obtained from the Bayesian analysis of *trn*L-*trn*F sequences. Values above and below the branches are Bayesian posterior probabilities and bootstrap percentages respectively. The scale bar indicates the mean number of nucleotide substitutions per site. In bold the species treated in this study. Asterisk indicates that the sample identification has been updated.

Croton subvillosus appeared as sister to the other sampled species of the *C. campestris* group in the analysis of the ITS and *trn*L-F data. Morphologically, *C. subvillosus* differs from the others mainly by its subshrub habit up to 50 cm in height (vs. shrubs 1-4 m tall in *C. campestris*, *C. heliotropiifolius*, *C. hatschbachii* and *C. stellatorotatus*) leaf trichomes with long lateral rays 1-2 mm long (vs. 0.3-0.7 mm long), and petiole 0.5-5 mm long (vs. 2.5-40 mm). With sequence data of ITS, *C. campestris*, *C. heliotropiifolius*, *C. hatschbachii,* and *C. stellatorotatus* appear in a polytomy. Although in results from *trn*L-F analyses *Croton stellatorotaus* was positioned as sister to the rest of the taxa, which formed a clade (PP 0.97; BS 74%), in which *C. heliotropiifolius* was sister to *C. campestris* + *C. hatschbachii*, which together also formed a well-supported clade (PP 1.00; BS 100%).

Future molecular and morphological studies will need to increase the sampling of the section *Adenophylli*, including species previously admitted in the section *Velamea* and species related to *C. chimboracensis*. Although we don't admit *C. chimboracensis* as a member of section *Adenophylli*, due to low or absent support in the ITS and *trn*L-F analysis, it will have fundamental importance in future studies with the section. This species appears as a sister to the *C.* sect. *Adenophylli* in ITS analysis, and still presents differentiated columella with an entire apex, rare in species of the section, which can help in the investigation of how this unique pattern of fruit columella emerged in the genus. Regarding the sampling of the *C.* sect. *Velamea*, it may come to confirm whether the group could emerge as a subsection within the section *Adenophylli*.

Leaf anatomy

Leaf blade - glabrous on the adaxial surface in some individuals of *Croton subvillosus,* and indumented on both surfaces of *C. campestris*, *C. hatschbachii,* and *C. stellatorotatus*. The indumentum is composed of multicellular, sessile, or stipitate trichomes of three types: 1) stellate-porrect (*C. campestris* Figs. 3 A-C, 4A, B; and *C. subvillosus* Figs. 3J, K, 4 N, O) or 2) multiradiate (*C. hatschbachii* Figs. 3D-F, 4E, F, and abaxial surface of *C. campestris*), or 3) stellate-rotate (*C. stellatorotatus*, Figs. 3G-I, 4J, K) varying in length, number, size, and arrangement of their rays. The trichomes have slightly thickened cell walls, and some of them show hexagonal cell structures with transverse openings externally - interpreted here as secretory structures of epidermal origin (Fig. 4P). Regarding their density, the trichomes are slightly dense in *C. campestris* (Fig. 3A), sparsely distributed in *C. hatschbachii* (Fig. 3D) and *C. subvillosus* (Fig. 3J), and strongly dense in *C. stellatorotatus* (Fig. 3G). The stellate-porrect trichome type is characterized by having lateral rays (7-13) arising in a single plane (Fig. 3B, C, J, K) (with a more developed central ray (0.2-1 mm), called the porrect ray (Fig. 3B, C, J, K)) on both leaf surfaces of *C. campestris* (Fig. 4A) and *C. subvillosus* (Fig. 4N, O). The multiradiate trichomes of *C. hatschbachii* show 16 to 30 lateral rays arising in 2 or 3 whorls (Fig. 3E, F). The stellate-rotate trichomes show 13-20 lateral rays joined along $^{1}/_{10}$ of their lengths, and (usually) a vestigial central ray (20-50 μm long); they are exclusive to *C. stellatorotatus* among the species studied here (Fig. 3H, I). The species also differ in terms of the lengths of the lateral rays of the trichomes, being (usually) short in *C. hatschbachii* (250-350 μm), of medium length in *C. stellatorotatus* (300-600 μm) and *C. campestris* (350-1000 μm), and long in *C. subvillosus* (500-2000 μm).

The leaves of *C. campestris* are hypostomatic, but amphistomatic in *C. hatschbachii*, *C. stellatorotatus* and *C. subvillosus*, with stomata distributed at the same level as the common epidermal cells, with discrete substomatal chambers (Fig. 4C, G, L, Q). The epidermis in all species is unistratified, has rectangular and quadrangular cells with straight internal periclinal and anticlinal walls, and slightly sinuous external periclinal walls covered by a thin cuticle (*e.g.*, Fig. 4I, L). *Croton hatschbachii* also shows a discontinuous hypodermis composed of longitudinally rectangular cells with thin walls on the adaxial surface (Fig. 4S). All of the species also show sessile or shortly stipitate ovoid, ellipsoidal, or subglobose colleters along the leaf margins, or on the base of the leaf blade, as seen in *C. campestris* (Fig. 4T).

The mesophyll is dorsiventral, with a palisade parenchyma composed of a layer of juxtaposed cells in *C. campestris, C. hatschbachii,* and *C. stellatorotatus* (Fig. 4C, G, L), and one or two layers in *C. subvillosus* (Fig. 4Q), as well as spongy parenchyma composed of cells of different sizes and shapes, with conspicuous intercellular spaces (Fig. 4C, G, L, Q). Druses occur in the palisade and spongy parenchyma of all species (*e.g.*, *C. hatschbachii* (Fig. 4H), and *C. subvillosus*, (Fig. 4Q)), as well as laticifers, as seen in *C. hatschbachii* (Fig. 4S). The leaf margins of all species have obtuse outlines, with parenchymatous cells in subepidermal positions (Fig. 4D, I, M, R).

The vascular bundles are collateral and of large calibers, with annular collenchyma cells adjacent to the phloem on the abaxial surface (Fig. 4U); the smaller caliber vascular bundles are surrounded by a conspicuous parenchymatous sheath (Fig. 4V). Figure 4u shows cells of the epidermis with external periclinal walls with conspicuous pectocellulosic thickenings.

Midrib - the indument in that region is composed of the same types of trichomes as the leaf blade itself. The epidermis is unistratified, and composed of rectangular, rounded, or quadrangular cells with thin walls, covered by a thin cuticle, and without stomata (Fig. 5A-H).

The cortex consists predominantly of annular and angular collenchyma, and the ground parenchyma has rounded cells of different sizes (Fig. 5 A-H). A palisade parenchyma continuity is also noted between the two faces of the leaf blade (Fig. 5A, C, E, G). Druses were observed throughout the cortex tissues on both surfaces (*e.g.*, *C. campestris* (Figs. 5B, I) and *C. hatschbachii* (Fig. 5D)), and laticifers

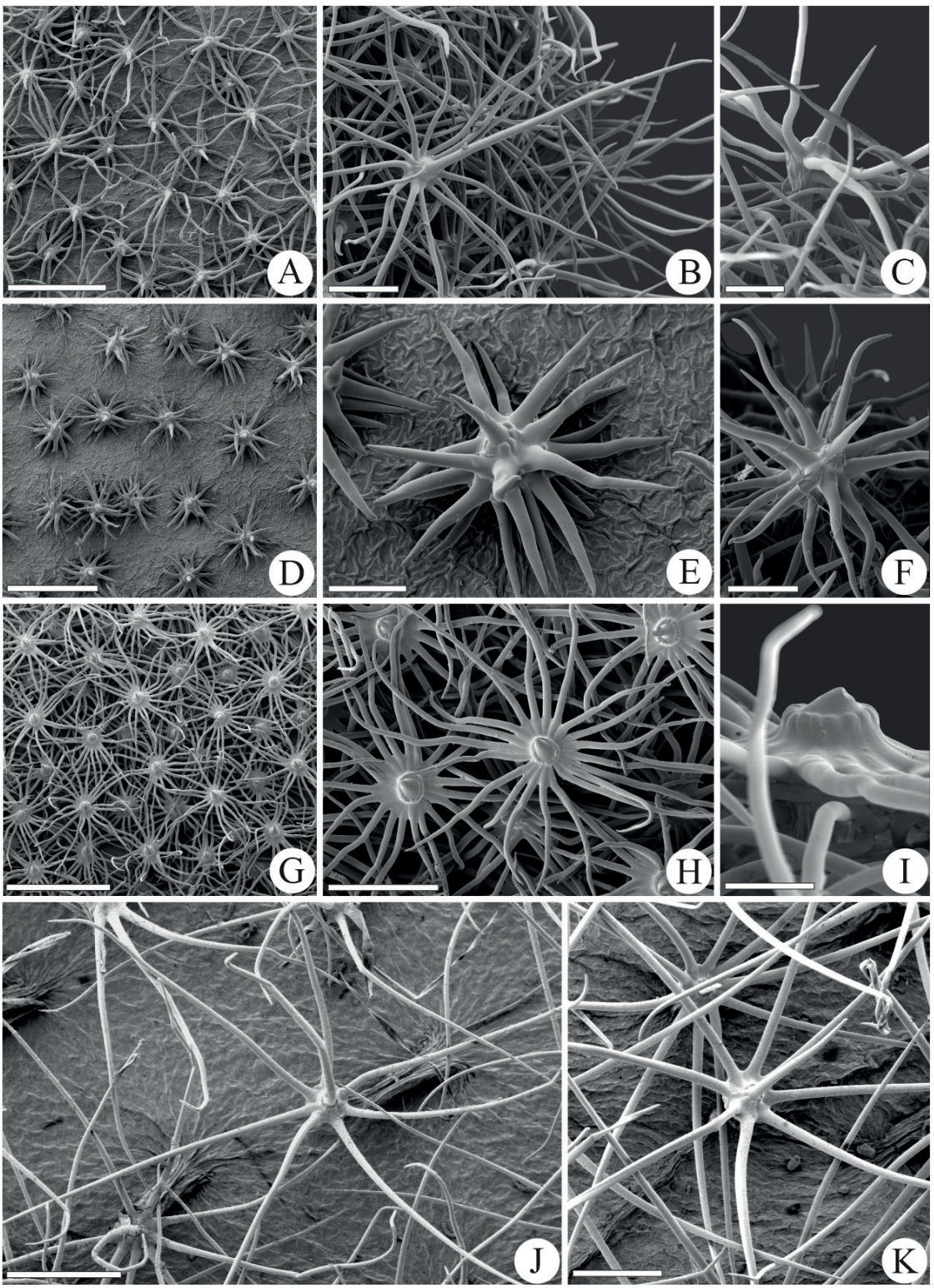

Figure 3. Scanning electron microscope (SEM) images of the foliar trichomes of *Croton campestris* (**A-C**), *C. hatschbachii* (**D-F**), *C. stellatorotatus* (**G-I**), and *C. subvillosus* (**J-K**). **A.** Indument on the adaxial surface of *C. campestris*. **B.** Stellate-porrect trichomes of *C. campestris* in frontal view. **C.** Stellate-porrect trichomes of *C. campestris* in lateral view. **D.** Indument of the adaxial surface of *C. hatschbachii*. **E.** Multiradiate trichomes of *C. hatschbachii* in frontal view. **F.** Multiradiate trichomes of *C. hatschbachii* in lateral view. **G.** Indument of the adaxial surface of *C. stellatorotatus*. **H.** Stellate-rotate trichomes of *C. stellatorotatus* in frontal view. **I.** Stellate-rotate trichomes of *C. stellatorotatus* in lateral view. **J-K.** Stellate-porrect trichomes on the adaxial surface of *C. subvillosus*. Scale bars: **A**, **D**, **G**, **J**, **K** = 500 µm; **B**, **H** = 200 µm; **C**, **E**, **F** = 100 µm; **I** = 50 µm. (**A-C:** *R.C. Sodré et al. 3439*, BOTU; **D-F:** *R.C. Sodré et al. 3464*, BOTU; **G-I:** *R.C. Sodré et al. 3309*, BOTU; **J-K:** *R.C. Sodré 3495*, BOTU).

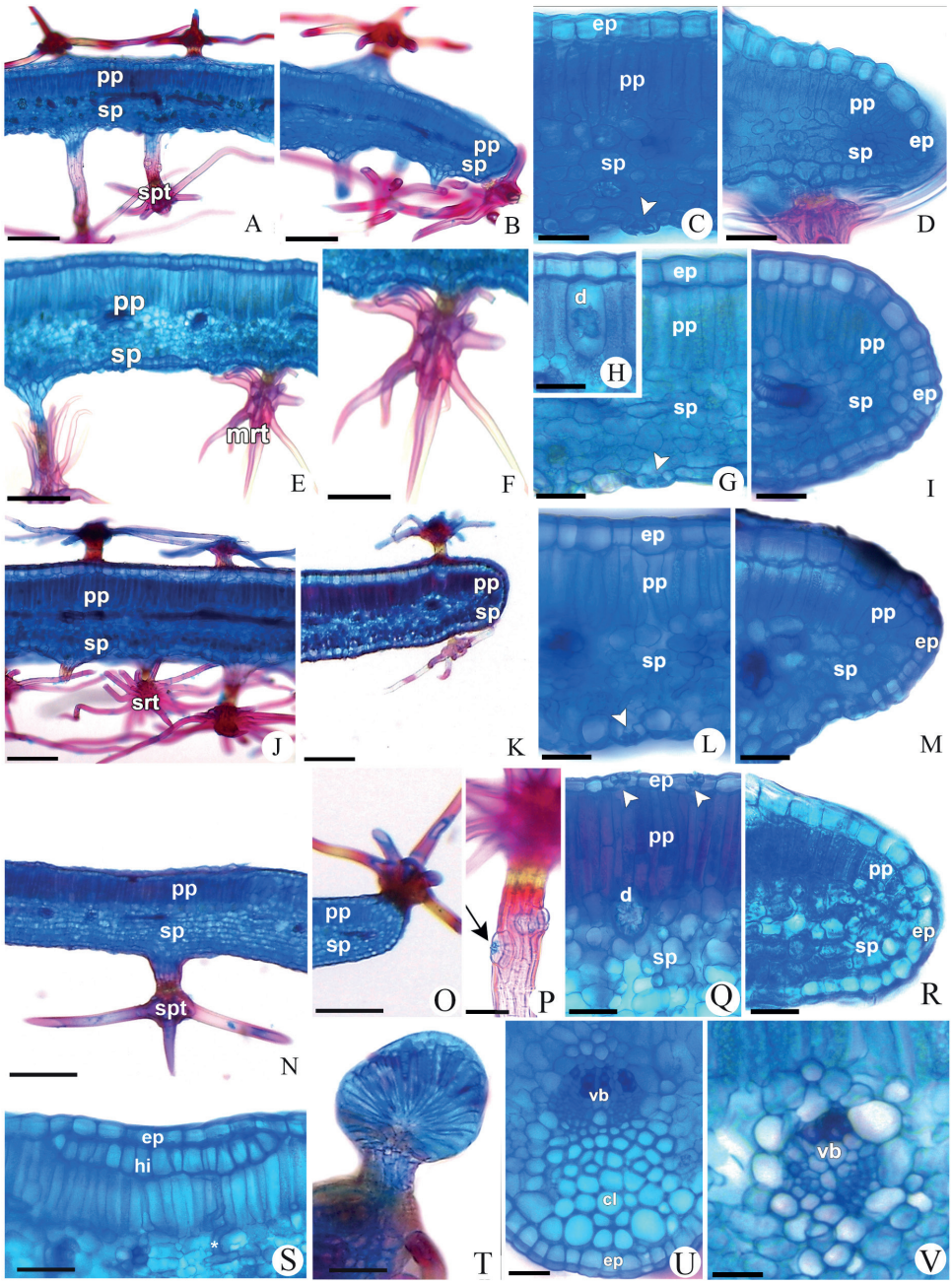

Figure 4. Cross section of the median portions and leaf blade margins of *C. campestris* (**A-D**, **P**, **T**), C. *hatschbachii* (**E-I**, **S**, **U**, **V**), *C. stellatorotatus* (**J-M**) and *C. subvillosus* (**N**, **O**, **Q**, **R**). **A.** Median portion of the leaf blade of *C. campestris*, note the stellate-porrect trichomes in lateral view. **B.** Leaf margin of *C. campestris*. **C.** Median portion of the leaf blade of *C. campestris*. **D.** Leaf margin of *C. campestris*. **E.** Median portion of the leaf blade of *C. hatschbachii*, note the subsessile or stipitate multiradiate trichomes on the abaxial surface. **F.** Detail of a subsessile multiradiate trichome in lateral view of *C. hatschbachii*, observe the ascending and descending rays. **G-H.** Median portion of the leaf blade of *C. hatschabachii*. **I.** Leaf margin of *C. hatschbachii*. **J.** Median portion of the leaf blade of *C. stellatorotatus*, note the stipitate stellate-rotate trichomes in lateral view. **K.** Leaf margin of *C. stellatorotatus*. **L.** Median portion of the leaf blade of *C. stellatorotatus*. **M.** Leaf margin of *C. stellatorotatus*. **N.** Median portion of the leaf blade of *C. subvillosus*, observe the stipitate stellate-porrect trichome on the abaxial surface, in lateral view. **O.** Leaf margin of *C. subvillosus*. **P.** Epidermal secretory structure indicated by an arrow on the stipe of a multiradiate trichome on the adaxial surface of *C. campestris*. **Q.** Median portion of the leaf blade of *C. subvillosus*. **R.** Leaf margin of *C. subvillosus*. **S.** Hypodermis and laticifers of *C. hatschbachii*. **T.** Colleter on the leaf margin of *C. campestris*. **U-V.** Vascular bundle of *C. hatschabachii*. Scale bars: **A**, **J** = 130 μm; **B** = 100 μm; **C, G**, **H**, **I** = 30 μm; **D**, **L**, **M**, **Q**, **R**, **T** = 50 μm; **E** = 150 μm; **F** = 70 μm; **K** = 170 μm; **N**, **O** = 230 μm; **P** = 60 μm; **S** = 60 μm; **U** = 40 μm; **V** = 20 μm. Abbreviations: cl = collenchyma, d = druses, ep = epidermis, hi = hypodermis, pp = palisade parenchyma, sp = spongy parenchyma, spt = stellate-porrect trichome, srt = stellate-rotate trichome, mrt = multiradiate trichome, vb = vascular bundle, arrowheads indicate stomata. (**A-D**, **P**, **T** *R.C. Sodré et al. 3439*, BOTU; **E-I, S**, **U**, **V** *R.C. Sodré et al. 3464*, BOTU; **J-M** *R.C. Sodré et al. 3309*, BOTU; **N**, **O**, **Q**, **R** *R.C. Sodré 3495*, BOTU).

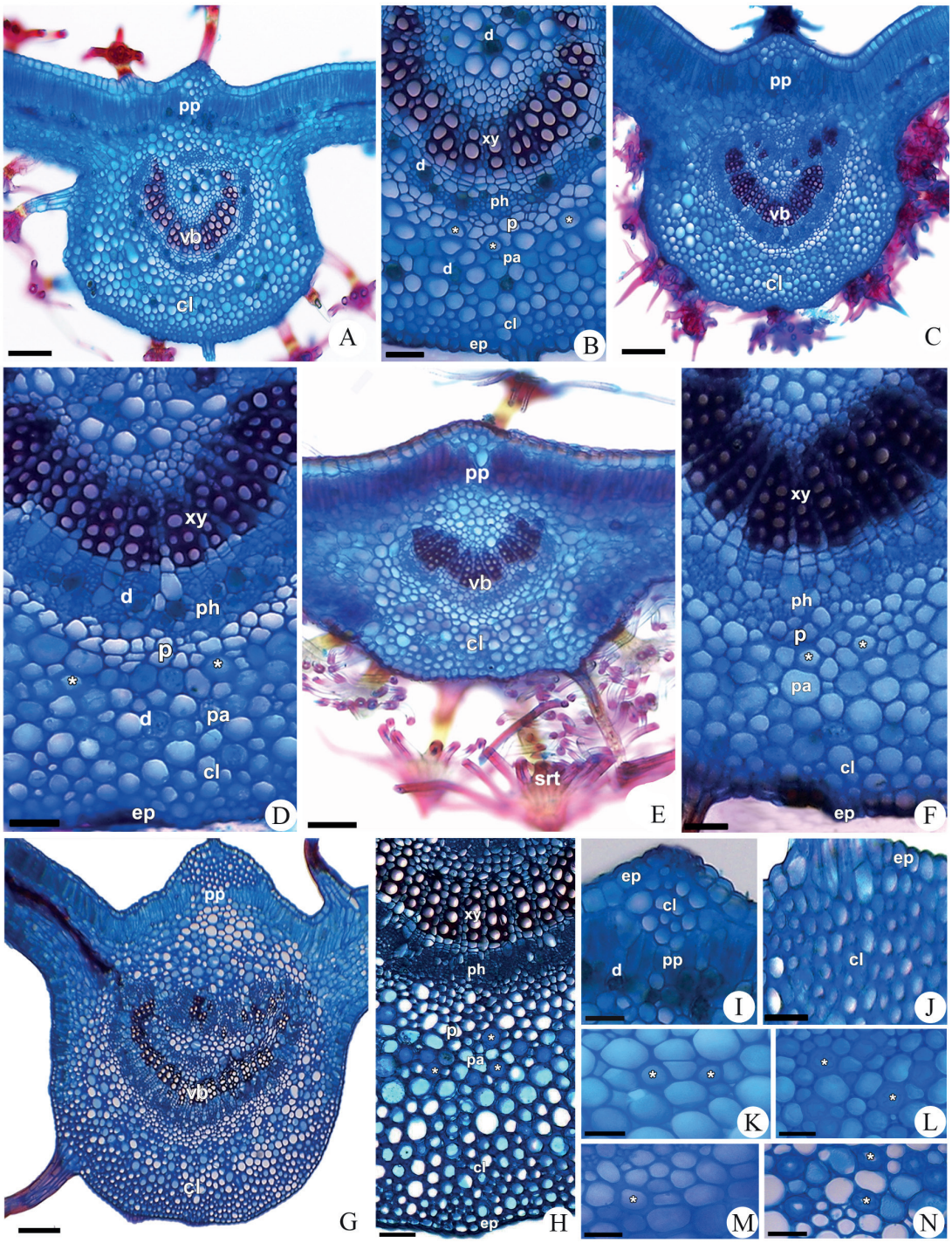

Figure 5. Cross sections of the midribs of *C. campestris* (**A**, **B**, **I**, **K**), *C. hatschbachii* (**C**, **D**, **L**), *C. stellatorotatus* (**E**, **F**, **M**), *C. subvillosus* (**G**, **H**, **J**, **N**): **A.** Midrib of *C. campestris*, note the distributions of the trichomes on both surfaces of the midrib and the continuous palisade parenchyma. **B.** Details of the cortex and vascular cylinder of *C. campestris*. **C.** Midrib of *C. hatschbachii*. **D.** Details of the cortex and vascular cylinder of *C. hatschbachii*. **E.** Midrib of *C. stellatorotatus*, note the distributions of the trichomes on both surfaces of the midrib and the continuous palisade parenchyma. **F.** Details of the cortex and vascular cylinder of *C. stellatorotatus*. **G.** Midrib of *C. subvillosus*. **H.** Details of the cortex and vascular cylinder of *C. subvillosus* and distribution of the vascular system and cortex. **I.** Collenchyma at the adaxial surface of *C. campestris*. **J.** Collenchyma at the adaxial surface of *C. subvillosus*. **K.** Laticifers in the cortex of *C. campestris*. **L.** Laticifers in the cortex of *C. hatschbachii*. **M.** Laticifers in the cortex of *C. stellatorotatus*. **N.** Laticifers in the cortex of *C. subvillosus*. Scale bars: **A** = 110 µm; **B** = 50 µm; **C** = 130 µm; **D**, **I**, **N** = 40 µm; **E** = 100 µm; **F** = 35 µm; **G** = 190 µm; **H** = 65 µm; **J** = 60 µm; **K**, **L**, **M** = 25 µm. Abbreviations: cl = collenchyma, d = druses, ep = epidermis, pa = ground parenchyma, p = pericycle, ph = phloem, pp = palisade parenchyma, str = stellate-rotate trichome, vb = vascular bundle, xy = xylem, asterisks indicate laticiferous. (**A**, **B**, **I**, **K** *R.C. Sodré et al. 3439*, BOTU; **C**, **D**, **L** *R.C. Sodré et al. 3464*, BOTU; **E**, **F**, **M** *R.C. Sodré et al. 3309*, BOTU; **G**, **H**, **J**, **N** *R.C. Sodré 3495*, BOTU).

(showing different thicknesses of their primary walls) are dispersed among the tissues adjacent to the vascular bundle (Fig. 5B, D, F, H), and the walls of the species studied here show distinct outlines (Fig. 5K-N).

The vascular bundles are collateral and U-shaped, with phloem surrounded by a pericycle of parenchyma cells (Fig. 5A-H). Druses were observed only in the phloematic parenchyma of *C. campestris* and *C. hatschbachii* (Fig. 5B, D).

Petiole - The petiolar indumenta are similar to those described for the leaf blades and midribs, with stellate-porrect trichomes having secretory structures of epidermal origins (Fig. 6H, L). The petiolar outline in the cross section is planar-convex (Fig. 6A, C, E, G), with the epidermis composed of common round cells with a thin cuticle, but without stomata.

The cortex is composed of annular collenchyma and ground parenchyma, both with cells of varying sizes (*e.g.*, *C. campestris* (Fig. 6B) and *C. stellatorotatus* (Fig. 6F)). Druses were found in the petioles of all species, as exemplified by *C. hatschbachii* (Fig. 6D).

The vascular bundles are collateral in *C. campestris*, *C. hatschbachii,* and *C. stellatorotatus* (Fig. 6B, D, F), with parenchymatous pericycles, but bicollateral in *C. subvillosus* with the pericycle showing libriform fibers and parenchyma cells (Fig. 6I, J). The vascular bundles are isolated, being nine in *C. campestris* (Fig. 6A), seven in *C. hatschbachii* (Fig. 6C) and *C. stellatorotatus* (Fig. 6E), and six in *C. subvillosus* (Fig. 6G). Accessory vascular bundles in the cortex on the adaxial surface of the petioles were found in *C. hatschbachii* (Fig. 6C) and *C. subvillosus* (Fig. 6G). Druses occur in the cortical parenchyma (*e.g.*, *C. stellatorotatus* (Fig. 6D)) and phloematic parenchyma (*e.g.*, *C. campestris* (Fig. 6K)), while laticifers are found in the cortical parenchyma adjacent to the phloem.

Additional notes - The anatomical characteristics observed in the studied species, their trichome types, the presence of a discontinuous hypoderm, the distribution patterns of the stomata, the presence of accessory vascular bundles in the petiole, the presence libriform fibers in the pericycle, and the numbers of vascular bundles in the petiole all proved useful in species differentiation (Tab. 2), as was reported by Barros & Soares (2013) and Vitarelli *et al.* (2015) for other *Croton* species. Among these features, the types of trichomes can be highlighted, as they have been used to differentiate species in the genus even since Müller Argoviensis (1873), and were emphasized by Webster *et al.* (1996) and other authors such as Inamdar & Gangadhara (1977), Nepumoceno & Oliveira (1979) and Lucena & Sales (2006). Despite the taxonomic value of the trichomes in some cases at both sectional and species levels, we emphasize that different type of trichomes appear to have evolved independently within the genus, as they occur in taxa from distinct sections. The stellate-rotate trichomes reported here for *C. stellatorotatus*, for example, were cited by Webster *et al.* (1996), Gordillo & Matías (2005) and Gomes *et al.* (2018), for members of the sections *Lasiogyne*, *Barhamia*, and *Astraeopsis*. respectively; the multiradiate trichomes of *C. hatschbachii* were likewise observed in taxa belonging to the sections *Barhamia*, *Cyclostigma,* and *Geiseleria* by Gordillo & Matías (2005), Feio *et al.* (2018), and Sodré *et al.* (2019) respectively. Similarly, the stellate-porrect trichomes observed here in *C. campestris* and *C. subvillosus*, seem to be the most frequent in the genus (*e.g.*, Lucena & Sales 2006; Carneiro-Torres *et al.* 2011; Feio *et al.* 2018). We also highlight the structures interpreted here as trichomes truly represent those structures - unlike structures with similar appearances reported for other species of the genus by Vitarelli *et al.* (2016) and Sodré *et al.* (2019), which are simply trichome-like emergences, not found in the species here studied. Those observations evidence the micromorphological richness found in *Croton,* and likewise point to the need to determine the correct type of indument in the genus.

Table 2. Comparison of *C. campestris*, *C. hatschbachii*, *C. stellatorotatus* and *C. subvillosus* based on SEM analyses of the foliar trichomes and leaf anatomy.

Characters/Species	*C. campestris*	*C. hatschbachii*	*C. stellatorotatus*	*C. subvillosus*
Type of foliar trichomes	stellate-porrect (ad. surf.) or multiradiate (ab. surf.)	multiradiate	stellate-rotate	stellate-porrect
Number of lateral rays of the trichomes	7-13 (ad. surf.) or 14-18 (ab. surf.)	16 to 30	13-20	7-11
Length of the lateral rays (μm)	350-1000	250-350	300-600	500-2000
Degree of union of the lateral rays	free	free	10 %	free
Length of the central rays (μm)	250-1000	100-250	20-50	400-1000
Stomata position on leaf	hypostomatic	amphistomatic	amphistomatic	amphistomatic
Discontinuous hypodermis on leaf blade	absent	present	absent	absent
Number of layers of the palisade parenchyma of dorsiventral mesophyll	one	one	one	two
Type of the vascular bundle in the petioles	collateral	collateral	collateral	bicollateral
Numbers of vascular bundle in the petioles	nine	seven	seven	six
Accessory vascular bundles in the petioles	absent	present	absent	present
Libriform fibers in the petiole pericycle	absent	absent	absent	present

Abbreviation = ad. surf. - adaxial surface; ab. surf. - abaxial surface

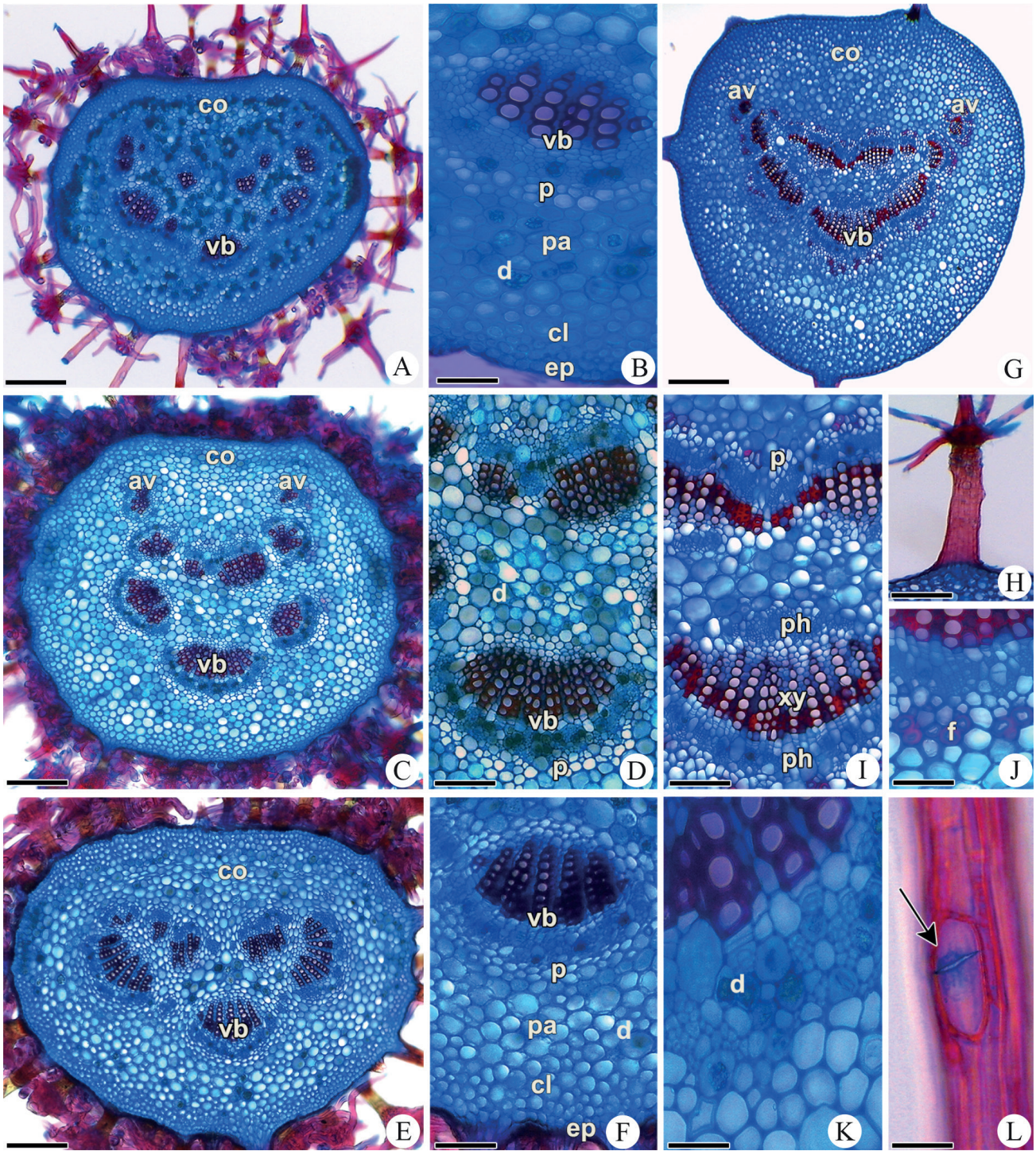

Figure 6. Cross sections of the petioles of *C. campestris* (**A**, **B**, **L**), *C. hatschbachii* (**C**, **D**, **K**), *C. stellatorotatus* (**E**, **F**), *C. subvillosus* (**G**-**J**): **A.** Median portion of the petiole of *C. campestris*. **B.** Detail of the epidermis, cortex and vascular bundle of *C. campestris*. **C.** Median portion of the petiole of *C. hatschbachii*. **D.** Detail of the vascular bundles and medulla of *C. hatschbachii*. **E.** Median portion of the petiole of *C. stellatorotatus*. **F.** Detail of the epidermis, cortex, and vascular bundle of *C. stellatorotatus*. **G.** Median portion of the petiole of *C. subvillosus*. **H.** Stipe of the trichome of *C. subvillosus*. **I.** Detail of the vascular bundles and medulla of *C. subvillosus*. **J.** Libriform fibers in *C. subvillosus*. **K.** Druses in *C. hatschbachii*. **L.** Secretory structure (indicated by arrow) in the stipe of a stellate trichome of *C. campestris*. Scale bars: **A**, **H** = 250 µm; **B** = 60 µm; **C**, **E** = 170 µm; **D**, **F** = 80 µm; **G** = 450 µm; **I** = 125 µm; **J** = 70 µm; **K** = 30 µm; **L** = 20 µm. Abbreviations: co = cortex, cl = collenchyma, d = druses, ep = epidermis, f = libriform fibers, pa = ground parenchyma, p = pericycle, ph = phloem, vb = vascular bundle, xy = xylem. (**A**, **B**, **L** *R.C. Sodré et al. 3439*, BOTU; **C**, **D**, **K** *R.C. Sodré et al. 3464*, BOTU; **E**, **F** *R.C. Sodré et al. 3309*, BOTU; **G**-**J** *R.C. Sodré 3495*, BOTU).

Leaf anatomical characters such as a unistratified epidermis, the presence of druse crystals, laticifers, angular collenchyma, and parenchyma cells in the primary veins, as well as collateral vascular bundles are common in *Croton* species as well as in Euphorbiaceae in general (*e.g.*, Metcalfe & Chalk 1950; Mendonça *et al.* 2008; Barros & Soares 2013; Vitarelli *et al.* 2016). Although the species studied here preferentially occupy environments with certain water restrictions (such as Cerrado, and the Caatinga domain), they show an epidermis covered by only a thin cuticle, with the pericycle usually composed of parenchymal cells - different from reports by Morretes & Ferri (1959), Morretes (1969), and Bieras & Sajo (2009), who described a thickened cuticle on the epidermis and sclerified cells surrounding vascular tissues, for example, in Cerrado species from different plant families. The lack of a thickened cuticle on the leaf epidermis of the studied *Croton* species is possibly compensated with the presence of trichomes which sometimes form a dense indument, as already observed in other species of *Croton* by Sodré *et al.* (2019). Our observations show that living in the aforementioned dry environments does not necessarily lead to the development of obvious xeromorphic anatomical adaptations.

Taxonomic treatment

Croton campestris A. St.-Hil., Pl. Usuel. Bras. [12]: t. 60. 1827. *Oxydectes campestris* (A. St.-Hil.) Kuntze, Revis. Gen. Pl. 2: 611. 1891. *Croton campestris* var. *genuinus* Müll. Arg., Prodr. 15(2): 633. 1866. nom. inval. Type: BRAZIL. Minas Gerais: Congonhas, XI/1816-1821, *A.F.C.P. Saint-Hilaire 2155bis* (lectotype: P 00623075!, designated by Sodré *et al.* (2017); isolectotypes: P 00623073!, P 00623074!, MPU 015220!) (Fig. 7)

Croton campestris var. *dupraei* Baill., Adansonia 4: 317. 1864. Type: BRAZIL. "Brésil Meridional", 1842, *Dupré s.n.* (holotype: P 00623076!).

Croton campestris var. *nigricans* Baill., Adansonia 4: 317. 1864. Type: BRAZIL. Minas Gerais: 1816-1821, *A.F.C.P. Saint-Hilaire B1 1131* (holotype: P 00623078!; isotype: A 00257894!).

Croton campestris var. *atratus* Baill., Adansonia 4: 321. 1864. *Croton versicolor* Müll. Arg. Prodr. 15(2): 630. 1866. *Oxydectes atrata* Kuntze, Revis. Gen. Pl. 2: 610. 1891. Type: BRAZIL. Minas Gerais: 1816-1821, *A.F.C.P. Saint-Hilaire cat. B*[1] *1114* (holotype: P 00623077!; isotype: A 00257895!), syn. nov.

Croton agrarius var. *augustinianus* Baill., Adansonia 4: 320. 1864. *Croton grandivelus* var. *augustinianus* (Baill.) Müll. Arg., Prodr. 15(2): 631. 1866. Type: BRAZIL. *S.loc.*, 1816-1821, *A.F.C.P. Saint-Hilaire s.n.* (holotype: P 00623595!), syn. nov.

Croton agrarius var. *cremostachyus* Baill., Adansonia 4: 321. 1864. *Croton grandivelus* var. *cremostachyus* (Baill.) Müll. Arg., Prodr. 15(2): 631. 1866. Type: BRAZIL. *S.loc.*, 1816-1821, *A.F.C.P. Saint-Hilaire s.n.* (holotype: P 00623587!), syn. nov.

Croton agrarius var. *laetifolius* Baill., Adansonia 4: 321. 1864. *Croton campestris* var. *laetifolius* (Baill.) Müll. Arg., Prodr. 15(2): 632. 1866. Type: BRAZIL. Minas Gerais, 1816-1821, *A.F.C.P. Saint-Hilaire cat. B*[2] *2387* (lectotype designated here: P 00623079!, isolectotypes: A 00257879!, F V0093330F!, P 00623080!, P 00623081!). Syntype: BRAZIL. Minas Gerais: 1816-1821, *A.F.C.P. Saint-Hilaire cat. B1 210* (P, not found), syn. nov.

Croton sellowianus var. *tomentosus* f. *brevifolius* Müll. Arg., Linnaea 34: 121. 1865. *Croton campestris* var. *tomentosus* Müll. Arg. nom. nud. Type: BRAZIL. Minas Gerais: Serra da Moeda, *s.d.*, *Sellow s.n.* (holotype: B†, photo in F 249181); without further locality, *s.d.*, *P. Claussen s.n.* (neotype designated here: G 00312253!).

Croton sellowianus var. *tomentosus* f. *angustifolius* Müll. Arg., Linnaea 34: 121. 1865. *Croton campestris* var. *angustifolius* (Müll. Arg.) Müll. Arg., Prodr. 15(2): 633. 1866. Type: BRAZIL. Minas Gerais: Serra do Ouro Branco, *s.d.*, *Sellow s.n.* (holotype: B†); *ca.* 13 km E of Diamantina, 14/III/1970, *H.S. Irwin, S.F. da Fonsêca, R. Souza, R. Reis dos Santos* & *J. Ramos 27502* (neotype designated here: UB 150550; isoneotypes: K 1184405!, MG 56280!, MO 2934616!, NY 870844!, RB 19988!).

Croton vauthierianus Baill., Adansonia 4: 317. 1864. *Oxydectes vauthieriana* (Baill.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. *Croton campestris* var. *vauthieriana* nom. nud. Type: BRAZIL, Minas Gerais: Serra do Frio, 1833, *A.C. Vauthier 91* (lectotype designated here: P 00634760!; isolectotypes: G 00312240!, G 00434723!, P 00634761!).

Croton agrophilus Müll. Arg., Fl. Bras. 11(2): 175. 1873. *Oxydectes agrophila* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Minas Gerais: "in campis siccis in Serra da Piedade et prope Caëté", IX/1824, *L. Riedel 559* (lectotype designated here: LE [the sheet annotated with Müller's handwriting]; isolectotypes: LE! [2 more sheets, none with annotations by Müller], P 00623659!, G 00434408!, GH 00047219!, K 000186130!). Syntypes: BRAZIL. Minas Gerais: "ad Lagoa Santa", 11/XI/1863, *J.E.B. Warming 1645/3* (C 10011155!); BRAZIL, Minas Gerais: "prope Lagoa Santa", XI/1863, *J.E.B. Warming 1645/2* (A 00257880!, C 10011154!, G 00434409!, P 00623657!, P 00623658!, US 00109493!), syn. nov.

Croton albellus Müll. Arg., Fl. Bras. 11(2): 180. 1873. *Oxydectes albella* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Minas Gerais: "prope Lagoa Santa", *s.d.*, *J.E.B. Warming 1645/4* (lectotype designated here: C 10011156!; isolectotypes: A 00404022!, G 00434405!), syn. nov.

Croton ferruginellus Müll. Arg., Fl. Bras. 11(2): 175. 1873. *Oxydectes ferruginella* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. "in campis glareosis Brasiliae", *s.d.*, *L. Riedel s.n.* (lectotype designated here: LE!; isolectotype: G 00434475!, photo in F 24479!), syn. nov.

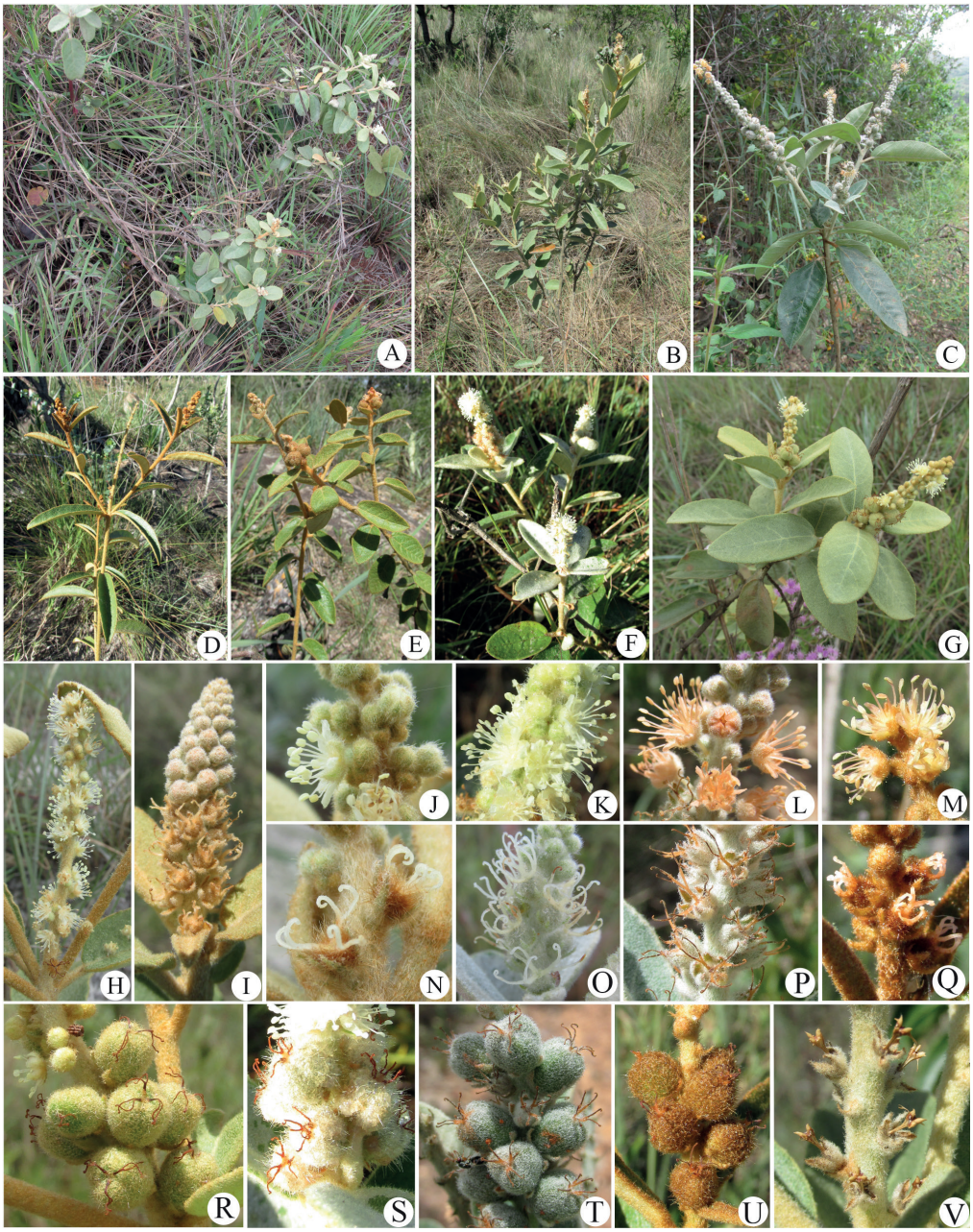

Figure 7. *Croton campestris* A. St.-Hil.: **A.** Subshrub with pendent branches in *campo sujo* vegetation in the municipality of Belo Horizonte, MG, Brazil, *R.C. Sodré 3439*. **B.** Subshrub with erect branches in *campo sujo* vegetation in the municipality of Santana do Riacho, MG, *R.C. Sodré 3443*. **C.** Flowering branch showing whitish indument, large and elliptic leaf blades, and elongate inflorescences in *cerrado denso* vegetation in the municipality of Diamantina, MG, *R.C. Sodré et al. 3456*. **D.** Flowering branch showing ferruginous indument and narrowly elliptic leaf blades in *cerrado rupestre* vegetation in the municipality of Datas, MG, *R.C. Sodré 3449*. **E.** Flowering branch showing ferruginous indument, short leaves, and inflorescences in *cerrado rupestre* vegetation in the municipality of Diamantina, MG, *R.C. Sodré et al. 3454*. **F.** Flowering branch showing whitish dense indument of the leaves and inflorescences in *campo limpo* vegetation in the municipality of Gouveia, MG, *R.C. Sodré 3450*. **G.** Flowering branch showing the yellowish indument in *campo limpo* vegetation in the municipality of Belo Horizonte, MG, *R.C. Sodré 3438*. **H.** Inflorescences with one pistillate flower near the base, and numerous staminate flowers along the axes, *R.C. Sodré 3437*. **I.** Young inflorescences with *ca.* 15 pistillate flowers towards the base, and staminate buds towards the distal end, *R.C. Sodré 3437*. **J**-**K.** Staminate flowers with greenish-yellow calyxes and whitish petals. **L.** Salmon-colored staminate flowers, note whitish indument on the calyx. **M.** Staminate flowers with ferruginous calyxes. **N.** Inflorescence base with only two sparsely distributed pistillate flowers, note brownish and hirsute indument of the ovary. **O.** Inflorescence base with *ca.* 10 whitish and densely distributed pistillate flowers. **P.** Fecundated pistillate flowers, note dark styles and whitish indument on the sepals and ovary. **Q.** Young pistillate flowers with brownish indument. **R.** Greenish-yellow capsules. **S.** Whitish capsules. **T.** Clear green capsules. **U.** Brownish capsules. **V.** Dehisced capsule, showing the columella with three apical lobes (**J, N, R** *R.C. Sodré 3438*; **K**, **O**, **S** *R.C. Sodré 3450*; **L**, **P**, **T** *R.C. Sodré 3456*; **M**, **Q**, **U** *R.C. Sodré 3449*) Photographs by R.C. Sodré.

Croton incertus Müll. Arg., Fl. Bras. 11(2): 177. 1873. *Oxydectes incerta* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. São Paulo: s.d., *C.F.P. Martius 579* (lectotype designated here: M 0089089!; isolectotype: G 00434521!), syn. nov.

Croton lapanus Müll. Arg., Fl. Bras. 11(2): 258. 1873. *Oxydectes lapanus* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Minas Gerais: Serra da Lappa, *s.d.*, *L. Riedel s.n.* (lectotype designated here: G 00434567!; isolectotype: P 00623507!) syn. nov.

Croton petraeus Müll. Arg. Fl. Bras. 11(2): 172. 1873. *Oxydectes petraea* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. *Croton petraeus* var. *ovatus* Müll. Arg., Fl. Bras. 11(2): 172. 1873. nom. inval. Type: BRAZIL. Minas Gerais: "in petrosis Serra da Lapa", *s.d.*, *L. Riedel 1001* (lectotype designated here: LE! [the sheet with four fragments of branches mounted upside down and one branch normally mounted]; isolectotype: LE! [the sheet with all its five fragments of branches mounted upside down], [P 00634592!), syn. nov.

Croton petraeus var. *oblongifolius* Müll. Arg., Fl. Bras. 11(2): 172. 1873. Type: BRAZIL. Minas Gerais: "in petrosis Serra da Lapa", *s.d.*, *L. Riedel 1001 pr. p.* (lectotype designated here: LE!; isolectotype: G 00434649!), syn. nov.

Croton semivestitus Müll. Arg., Prodr. 15(2): 628. 1866. *Oxydectes semivestita* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Without further locality, *s.d.*, *s.col.* (holotype: MEL n.v.; isotype: G-DC 00312257!, photo in F 34026), syn. nov.

Croton velame Müll. Arg., Fl. Bras. 11(2): 181. 1873. *Oxydectes velame* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Minas Gerais: "ad Lagoa Santa", 2/XI/1863, *J.E.B. Warming 1645/1* (lectotype designated here: C 10011199!; isolectotypes: A 00404023!, C 10011200!, G 00434722!, P 00634762!), syn. nov.

Croton tejucensis Müll. Arg., Fl. Bras. 11(2): 181. 1873. *Oxydectes tejucensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. *S.loc*, *s.d.*, *L. Riedel s.n.* (lectotype designated here: P 00634738!; isolectotype: G 00434668!). Syntypes: BRAZIL. Minas Gerais: "ad Tejuco", 1833, *A.C. Vauthier 90* (G 00434667!, F V0056205F!), syn. nov.

Subshrub, 0.5-2 m tall, xylopodium not seen, erect or with pendent branches, latex hyaline to whitish, branches cylindrical, not striated, indument tomentose, yellowish, ferruginous or grayish, trichomes stellate-porrect with 11-16 lateral rays 0.4-2 mm long, in a single whorl, central ray 0.1-1 mm long, stipe 0.4-0.7(-1.0) mm long. Leaves alternate, or subopposite or subwhorled below the stem bifurcations and/or inflorescences, leaf blades 4-8(-10) times longer than petioles, nectary glands absent; stipules reduced to 2-4 glands 0.3 × 0.2 mm, ovoid, greenish, reddish or orange, covered by the indument; petiole 0.25-1.7 cm long; leaf blades 2.6-8.9 × 0.9-4.2 cm, commonly elliptic, sometimes narrowly elliptic, lanceolate, ovate, oboval-elliptic, oboval-oblanceolate, oblong, widely ovate or obovate, membranaceous, base obtuse or slightly cordate, sometimes acute, with 1 or 2 sessile globose glands (colleters), apex obtuse, acute or rounded, margins usually entire, sometimes serrulate, rarely serrate, with sessile, globose or ellipsoidal glands (colleters), venation brochidodromous with 5-10 pairs of secondary veins impressed on both surfaces or slightly prominent on abaxial surface, bifacial, whitish, yellowish or ferruginous, adaxial surface with tomentose indument of stellate-porrect trichomes with 7-13 lateral rays in a single whorl, each ray 0.35-1 mm long, central ray 0.2-0.8 mm long, stipe 0.1-0.3 mm long, abaxial surface whitish or clear yellow with tomentose indument of multiradiate trichomes with 10-25 lateral rays in 1 or 2 whorls, each ray 0.5-1 mm long, central ray 0.15-0.5 mm long, stipe 0.4-0.7 mm long. Thyrses 2.3-25 cm long, terminal or in the bifurcations of the branches, bisexual, (2-)5-15 solitary pistillate flowers, densely arranged on basal $^{2}/_{5}$-$^{1}/_{2}$ of the inflorescence axis, staminate cymules with (1-)3-5 flowers; bracts of both flowers 1.2-2.3 × 0.2-0.4 mm, linear or lanceolate, with 2 globose glands (colleters) at base, external surface with stellate-porrect trichomes, shortly stipitate, internally glabrous. Staminate flowers 4.3-7 mm long, pedicel 0.8-2 mm long, glabrous, glabrescent or tomentose, stellate-porrect trichomes shortly stipitate, 7-8 lateral rays in a single whorl, each ray 0.4-0.7 mm long, calyx 5-partite, valvar or slightly imbricate prefloration, lobes 2-2.3 × 1.2-2 mm, ovate or largely ovate, apex acute, minutely tomentose, sometimes pubescent or hirsute externally, trichomes stellate-porrect, rarely multiradiate trichomes, shortly stipitate, lateral rays 7-10, porrect ray 0.8-1 mm long, glabrous internally, petals 2.5-3 × 0.9-1.5 mm, obovate, sometimes oboval-oblanceolate or oblong-oblanceolate, glabrous externally, villous basally or $^{2}/_{5}$-$^{2}/_{3}$ of their length, mainly along the margins, stamens (14-)16, 3.5-5 mm long, filaments 2.8-4 mm long, villous basally, anthers 0.7-1 × 0.4-0.5 mm, oblongoid, ellipsoidal or ovoid, disk 5-segmented, segments transversely oblong, yellowish. Pistillate flowers 3.5-5.5 mm long, pedicel 0.2-0.5 mm long, sepals 5, equal or slightly unequal, (1.3-)1.8-2.5(-3.7) × (0.35-)0.6-1(-1.5) mm, lanceolate, narrowly-lanceolate, ovate or triangular, glabrescent or glabrous internally, indument minutely tomentose externally, whitish or ferruginous, trichomes stellate-porrect, shortly stipitate, petals 0.1-0.7 × 0.1-0.3 mm, glanduliform or plane, ovoid, lanceolate or linear, glabrous or glabrescent; ovary 1.3-1.5 × 1.6-2.2 mm, subglobose, indument hirsute with stellate-porrect trichomes, styles 2-fid, 3.5-5 mm long, united for lower $^{1}/_{8}$-$^{1}/_{4}$ of their length, with stellate porrect trichomes externally up to $^{5}/_{6}$ of the length, disk 5-segmented or, less commonly, 5-lobed, with segments/lobes transversely oblong, or sometimes entire and ring-shaped. Capsules 4.5-6 × 5-5.5 mm, subglobose, with carpels visually delimited, indument tomentose or hirsute, yellowish or ferruginous, trichomes stellate-porrect, shortly stipitate, pedicel 1-2.5 mm long; seeds 3.5-4.8 × 2.1-3 mm long, oblongoid to ellipsoidal, rarely ovoid, dark-brown or grayish, smooth and

minutely foveolate surfaces, caruncle 1.5-2.1 mm width, hat-shaped, sessile.

Distribution and habitat - Although *Croton campestris* has been cited for Bolivia (Jørgensen *et al.* 2014), Paraguay, Argentina, and other Brazilian states (Lima & Pirani 2003; Carneiro-Torres 2009; Silva *et al.* 2010; Sodré *et al.* 2014, 2017; Caruzo *et al.* 2021), we found that the specimens cited in those works represent different species of *Croton* sect. *Adenophylli*, or other sections of the genus, as summarized in Tab. 1. Therefore, according to the circumscription proposed here, *Croton campestris* is endemic to Brazil (the states of Bahia, Goiás e Minas Gerais) (Fig. 8), and cited with some uncertainty for the state of São Paulo, based on the type collection of *C. incertus*, *Martius 579*. It grows in *campos limpos*, *campos sujos*, *cerrado rupestre*, *cerrado típico*, and *cerrado ralo* vegetation, on sandy or rocky soil, between 680 and 1515 m a.s.l.

Phenology - Collected with flowers and fruits throughout the year, but flowering mainly between October and April, and fruiting from November to May.

Remarks - *Croton campestris* was described and illustrated by Saint-Hilaire (1827) based on his own collection (A.F.C.P. Saint-Hilaire 2155bis) from the Congonhas da Serra region, in rocky fields of the south-central portion of Minas Gerais State. Baillon (1864) described the *Croton* sect. *Velamea* and allocated ten species to it, including *C. campestris*. That author complemented its description and recognized four varieties for the species: vars. *subacutum*, *nigricans*, *atratum*, and *dupraei*, differentiated, mainly by the type and color of the branches, leaves and capsules, the size and shape of the leaves, and length of the racemes. Müller Argoviensis (1866) recognized two other new varieties for *C. campestris*: *C. campestris* var. *angustifolius* and *C. campestris* var. *laetifolius,* and elevated *Croton campestris* var. *atratum* to the level of species, naming it *Croton versicolor*, which stresses its variable colors and long inflorescences with congested flowers. In the *Flora Brasiliensis*, Müller Argoviensis (1873) maintained the varieties of *Croton campestris* recognized until then, except for *C. campestris* var. *subacutus,* which he treated as a distinct species, *Croton subacutus*, by having branches with smooth and yellow-whitish trichomes, stamens with glabrous filaments, and small fruits. However, while analyzing the type collections of *Croton campestris*, its varieties, *C. versicolor*, and several specimens from the same geographic area, we observed great variations and overlaps in the characters identified as important for differentiating them, even in the same

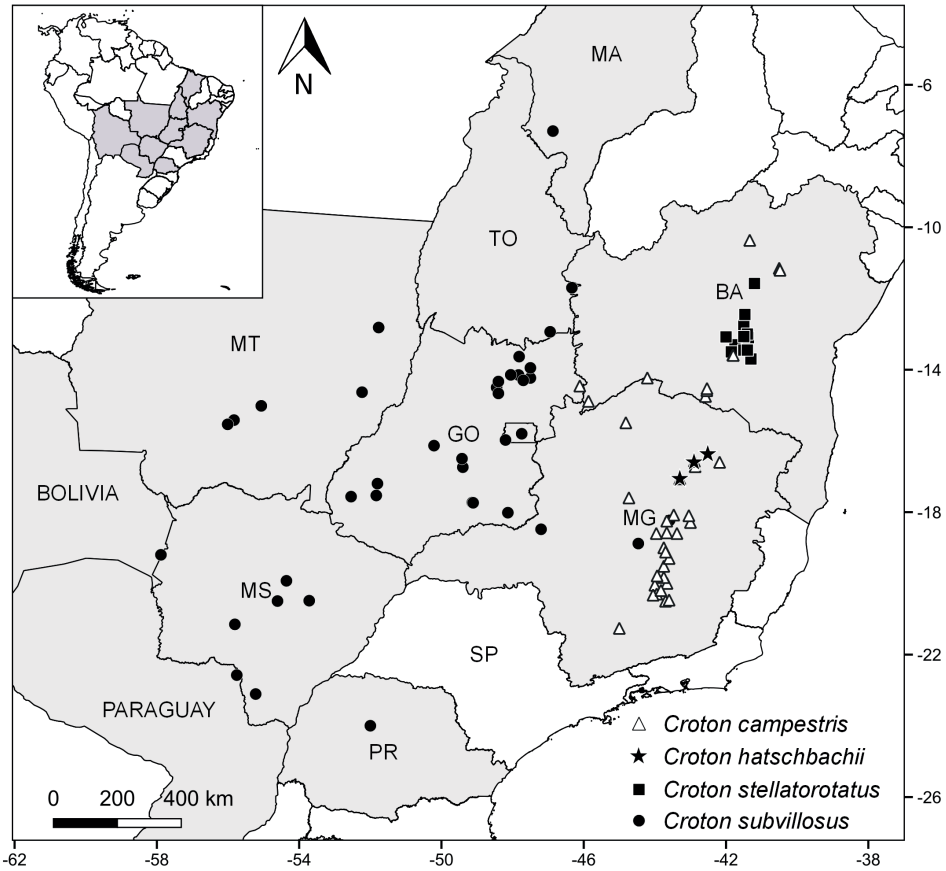

Figure 8. Geographic distributions of *Croton campestris*, *C. hatschbachii*, *C. stellatorotatus* and *C. subvillosus*. *BA* Bahia State, *GO* Goiás State, *MA* Maranhão State, *MG* Minas Gerais State, *MS* Mato Grosso do Sul State, *MT* Mato Grosso State, PR Paraná State, *TO* Tocantins State.

population, or being continuous between populations, and we therefore treat them as synonyms.

In contrast, *Croton subacutus* proved to be different from *Croton campestris* in terms of characters other than those already mentioned by Müller Argoviensis (1873), such as discrete bracts 0.5-1.1 mm (vs. 1.2-2.3 mm long), stamens 1.8-2.3 mm long (vs. 3.5-5 mm), staminate calyx lobes, 1.4-1.9 × 0.7-1.2 mm (vs. 2-2.3 × 1.2 -2 mm), staminate petals 1.4-2 × 0.4-0.8 mm (vs. 2.5-3 × 0.9-1.5 mm), and oblong capsules (vs. subglobose).

Müller Argoviensis (1873) described approximately 20 new *Croton* species morphologically related to *Croton campestris* in the Flora Brasiliensis, based on material collected mainly in the states of Goiás and Minas Gerais. Nine of those species (*Croton agrophilus*, *C. albellus*, *C. ferruginellus*, *C. incertus*, *C. petraeus*, *C. semivestitus*, *C. tejucensis*, *C. vauthierianus*, and *C. velame*) caught our attention as sharing with *C. campestris* several characteristics, such as subshrub or shrub habits, branches with stellate trichomes tomentose to the touch, leaves conspicuously petiolate and without nectary glands, and racemes usually with congested flowers. Those species were differentiated in the key by Müller Argoviensis (1873) by few and overlapping characteristics related to the dimension of the petiole, indument density on the adaxial surfaces of the leaf blades, presence of trichomes on the petals and stamens, and capsule shape. With the exception of *C. incertus* and *C. ferruginellus*, the former described based on a collection from São Paulo State, and the latter from an unknown location in Brazil, all of the other species were described based on collections from the grasslands and rocky fields of Minas Gerais, as well as *C. campestris* and its varieties. Additionally, while analyzing the populations of *Croton campestris* in the field, as well as approximately 100 other exsiccatum (collected in rocky fields in the municipality of Ouro Preto to the municipality of Diamantina in Minas Gerais), we were able to observe wide variation, sometimes within the same population, in the characters used until then to differentiate them. The indumentum can be whitish, yellowish, or ferruginous, usually dense, tomentose or hirsute to the touch, but sometimes sparse, especially on the adaxial surface of the leaf blade; the leaves are usually elliptic, from wide to narrow, sometimes oblong, lanceolate, oval or oboval, and the thyrsus can be short to elongated (2.3-25 cm long) with varying numbers and densities of pistillate flowers/capsules (2-)5-15 per inflorescence. Additionally, we collected most of the representative morphotypes of those species, and found no reproductive or vegetative characteristics that could actually differentiate them from *C. campestris*, and therefore consider them all as conspecific.

Still considering the works of Baillon (1864) and Müller Argoviensis (1866, 1873), two varieties of *Croton agrarius* described by the first author (*C. agrarius* var. *cremostachyus* and *C. agrarius* var. *augustinianus)* and later circumscribed in the concept of *Croton grandivelus* by Müller Argoviensis (1866), demonstrated morphologies most similar to *C. campestris* by the smooth or slightly striate branches and axes of the inflorescences, stipules reduced to 2-4 glands, leaf blades only 4-8(-10) times longer than the petioles, and tiny bracts (1.2-2.3 mm long). In contrast, *C. grandivelus,* the stipules are narrowly lanceolate and 2-8 mm long with numerous glands at the base, leaf blades 15-25 times larger than the petioles, and bracts 3.4-6.3 mm long; in *C. fulvus* (species that currently includes *C. agrarius* in its concept) the branches and axes of the inflorescences are strongly striate, the leaf blades are usually 10-12 times longer than petioles, and the bracts 3.5-5 mm long.

Historically, *C. campestris* has been confused by different authors with several other species (see Tab. 1): *C. echioides*, *C. fulvus*, *C. glandulosobracteatus*, *C. hadrianii*, *C. heliotropiifolius*, *C. grandivelus*, *C. intercedens*, *C. lanatus*, *C. subacutus*, *C. subferrugineus*, *C. subvillosus* and two species here described, *C. hatschbachii* and *C. stellatorotatus*. In order to more easily recognize those species, we provide here a key to their identification, and photographs (Fig. 14), but did not include *C. hadrianii* (C. sect. *Geiseleria*) and *C. glandulosobracteatus* (*C.* sect. *Barhamia*), the only taxa that does not belong to the sect. *Adenophylli* and are therefore easily differentiated by the absence of three prominent and ascending appendices at the apex of the columella.

In the circumscription proposed here for *Croton campestris*, it can be recognized by its shrubby habit up to 2 m tall, cylindrical, and smooth (non-striate) branches, generally densely branched, petioles 0.25 to 1.7 cm long, without nectary glands, a maximum of 10 times shorter than the leaf blades, brochidodromous leaf venation with 5-10 pairs of secondary veins not prominent on either surface, or slightly prominent on the abaxial surface, short pedicellate staminate flowers (0.8-2 mm long), and subglobose capsules 4.5-6 × 5-5.5 mm, with well-defined mericarps.

Proposed conservation status - *Croton campestris* is evaluated here as of Least Concern, as the species is known from many locations along the Espinhaço Chain (EOO 265,546 km^2), and many sites are located in protected areas (*e.g.*, the Serra do Cipó National Park, Rola Moça State Park, Biribiri State Park). Additionally, the species is relatively common where it occurs.

Additional specimens examined - BRAZIL. Bahia: Abaíra, Campo da Pedra Grande, 13°14'S, 41°54'W, 1400 m a. s. l., 19/II/1992, fl., *B. Stannard & R.F. Queiroz 52118* (NY, SPF); Barreiras, rodovia BR-020, 30 km O de Barreiras, 11/III/1979, fl., fr., *G. Hatschbach 42079* (MBM); upper slopes of Espigão Mestre, *ca.* 32 km W of Barreiras, *ca.* 600 m elev., 5/III/1971, fl., fr., *H.S. Irwin et al. 31540* (NY). Cocos, Fazenda Trijunção, próximo à sede da Fazenda Santa Luzia, 14°54'14"S, 45°56'25"W, 845 m a. s. l., 12/XII/2001, fl., *M.L. Fonseca et al. 3096* (IBGE); *ibid.*, estrada que dá acesso à Fazenda Olhos d'Água, 14°53'12"S, 45°51'59"W, 860 m a. s. l., 11/XII/2001, fl., *M.L. Fonseca et al. 3068* (IBGE). Feira da Mata, Médio São Francisco, próximo ao

rio Carinhanha, 14°13'54"S, 44°12'45"W, 454 m a. s. l., 7/V/2007, fl., fr., *M.L. Guedes et al. 13343* (ALCB, HUEFS). Iraquara, Serra da Água de Rega, *ca.* 22 km N of Seabra, road to Água de Rega, 1000 m a. s. l., 26/II/1971, fl., fr., *H.S. Irwin et al. 31104* (LD, NY). Jacobina, Serra da Jacobina, Toca da Areia, 11°9'9"S, 40°30'16"W, 932 m a. s. l., 5/VII/1996, fl., fr., *H.P. Bautista PCD 3412* (ALCB, HUEFS); Serra do Cruzeiro, 11°12'24"S, 40°28'55"W, 1040 m a. s. l., 7/IV/2001, fl., fr., *N.G. Jesus et al.1301* (ALCB, HUEFS). Licínio de Almeida, estrada para Urandi, 14°44'58"S, 42°34'35"W, 930 m elev., 3/XI/2006, fl., fr., *A. Rapini & R. Souza-Silva 1330* (HUEFS); Serra Geral, Riacho Fundo, 14°35'11"S, 42°32'25"W, 849 m elev., 10/V/2012, fl., fr., *F. Hurbath et al. 269* (ALCB); Garimpo das ametistas, 14°31'48"S, 42°32'6"W, 815 m a. s. l., 22/I/2013, fl., *F. Hurbath et al. 444* (ALCB). Minas do Mimoso, 16 km north west of Lagoinha (which is 5,5 km SW of Delfino) on side road to Minas do Mimoso, 41°20'S, 10°22'W, 950-1000 m a. s. l., 8/III/1974, fl., fr., *R.M. Harley 16957* (P). Rio de Contas, estrada para Mato Grosso, 20/I/1984, fl., fr., *G. Hatschbach 47386* (BHCB); arredores, 13°35'50"S, 41°47'44"W, 1090 m a. s. l., 8/XI/2018, fl., *J. Cordeiro & M.L. Brotto 5642* (MBM). **Goiás**: Mambaí, *ca.* 500 m da Vila Baru, 14°27'28.5"S, 46°6'40.7"W, 19/II/2003, fl., *M.L. Fonseca et al. 4163* (IBGE). **Minas Gerais**: Belo Horizonte, Jardim Botânico, 28/I/1933, fl., fr., *M. Barreto 2705* (BHCB); Barreiro, 31/I/1933, fl., fr., *M. Barreto 2704* (BHCB); Serra do Mutuca, 1000 m a. s. l., 16/XI/1938, fl., fr., *F. Markgraf & A.C. Brade 3609* (BHCB); Serra do Curral, 18/XII/1941, fl., *G. Black & J. E. Oliveira 1023* (BHCB); *ib*., 18/XII/1941, fl., fr., *J.E. Oliveira s.n.* (IAN 015047); Lagoa Secca, 22/II/1942, fl., fr., *M. Magalhães 1488* (BHCB, MBM);/VIII/1953, fl., fr., *L. Krieger 16734* (MBM, ESA); Serra do Curral, 11/XI/1975, fl., *M.B. Ferreira 5309* (PAMG); Morro do Chapéu, 20/III/1996, fl., fr., *M. Brandão 25437* (PAMG); Parque Estadual do Rola Moça, à esquerda da estrada para Casa Branca, *ca.* 100 m após o portal do Parque, 20°3'7"S, 44°0'10"W, 1340 m a. s. l., 08/I/2019, fl., fr., *R.C. Sodré et al. 3437* (BOTU), *3438* (BOTU), *3439* (BOTU); à esquerda da estrada para Casa Branca, campo oposto ao Mirante dos Planetas, 20°3'18"S, 44°1'11"W, 1440 m a. s. l., 08/I/2019, fl., fr., *R.C. Sodré et al. 3440* (BOTU). Brumadinho, Serra do Rola-Moça, 20°3'S, 44°1'W, 1350 m a. s. l., 13/X/2000, fl., *R.C. Vicent 230* (BHCB); Retiro das Pedras, 20°5'35"S, 43°59'1"W, 1400 m a. s. l., 11/X/2001, fl., *P.L. Viana 271* (BHCB). Caeté, Serra Gandarela, Caeté-Rio Acima, 04/XI/1992, fl., fr., *M. Brandão 19835* (PAMG); *ib*., Projeto Mina Apolo, 20°00'52"S, 49°40'31"W, 1515 m a. s. l., 21/I/2011, fl., fr., *T. Mansur & C.V. Vidal 170* (BHCB). Coronel Murta, UHE Murta, Serra da Lagoa Nova, III/1997, fl., fr., *E. Tameirão Neto 2485* (BHCB). Couto de Magalhães de Minas, 50 km após Couto Magalhães - Acauã, 10/XII/1983, fl., *M. Brandão 10507* (PAMG). Cristália, Bem Querer, 10/II/1991, fl., fr., *G. Hatschbach*, *M. Hatschbach & D.D. Guimarães 55001* (MBM). Cunha Magalhães, rio Jequitinhonha, 16/XI/1971, fl., *G. Hatschbach 28072* (MBM). Datas, estrada para Congonhas do Norte, *ca.* 500 m após a entrada, acesso pela rodovia Datas-Serro, 27/I/2004, fl., fr., *F.N. Costa & P.N. Costa 730* (ESA); *ca.* 10 km S de Datas pela MG-259, *ca.* 5 km a direita da rodovia por uma estrada vicinal, 18°34'53"S, 43°40'22"W, 1120 m a. s. l., 09/I/2019, fl., fr., *R.C. Sodré et al. 3448* (BOTU). Diamantina, Boa Vista, 09/XI/1937, fl., *M. Barreto 9691* (BHCB); *ca.* 12 km NE of Diamantina, road to Mendanha, 1300 m a. s. l., 28/I/1969, fl., fr., *H.S. Irwin et al. 22742* (LD), *22795* (MBM); *ca.* 13 km E of Diamantina, 1000 m a. s. l., 14/III/1970, fl., fr., *H.S. Irwin et al. 27505* (INPA); *ca.* 3 km N of São João da Chapada, 1200 m a. s. l., 24/III/1970, fl., fr., *H.S. Irwin et al. 28202* (MBM); 20 km S de Diamantina, serra na estrada para Conselheiro da Mata, 17/V/1977, fl., fr., *P.E. Gibbs*, *R. Abbott & J.B. Andrade 5207* (MBM, UEC); Biri-Biri, 23/I/1978, fl., fr., *G. Hatschbach 40856* (MBM); estrada entre Diamantina e Conselheiro Mata, 06/VIII/1990, fl., fr., *C.M. Sakuragui* & *V.C. Souza 227* (ESA); 02/XII/1991, fl., *M.M.N. Braga et al. 407* (BHCB, ESA), *s.n.* (BHCB 011485); 03/XII/1991, fl., fr., *M.M.N. Braga & A.L.F. Chaves 455* (BHCB), *471* (BHCB); 04/XII/1991, fl., fr., *M.M.N. Braga & A.L.F. Chaves 504* (BHCB); 2 km de Diamantina, em direção a Mendanha, 06.VII.1996, fl., *V.C. Souza et al. 11858* (ESA); Área de Proteção Ambiental Pau-de-fruta, COPASA, 18°15'1"S, 43°39'8"W, 13/II/2001, fl., fr., *J.R. Stehmann et al. 2763* (BHCB), *2891* (BHCB); 11 km de Diamantina em direção a Milho Verde, 18°18'36.9"S, 43°33'24.6"W, 993 m a. s. l., 08/I/2003, fl., *A.O. Araujo*, *G.O. Romão & S. Vieira 220* (ESA); Parque Estadual do Biribiri, *ca.* 1.2 km na estrada à esquerda antes da UFVJM, sentido Diamantina-Mendanha, 18°12'20.7"S, 43°35'28.9"W, 1427 m a. s. l., 02/II/2015, fl., fr., *T.A. Pontes & H. van der Werff 361* (HRCB); estrada Diamantina, próximo a São João da Chapada, 03/II/2015, fl., fr., *T.A. Pontes & H. van der Werff 375* (HRCB); *ca.* 24 km de Diamantina em direção a Conselheiro Mata (MG-220), 18°17'33"S, 43°47'42"W, 1300 m a. s. l., 17/VII/2017, fr., *V.C. Souza 40813* (ESA). Felício dos Santos, APA Felício, 18°10'S, 43°17'W, 1000-1400 m a. s. l., 08/X/2004, fl., fr., *P.L. Viana et al. 2243* (BHCB); *ca.* 23 km S de Diamantina, 10/I/2019, fl., fr., *R.C. Sodré 3453* (BOTU); *ca.* 20 km S de Diamantina, 18°20'38"S, 43°40'52"W, 1390 m a. s. l., 10/I/2019, fl., fr., *R.C. Sodré et al. 3454* (BOTU); BR-367, imediações do Parque Estadual do Biribiri, *ca.* 2 km a sudeste do povoado de Mendanha, 18°9'5"S, 43°30'10"W, 780 m a. s. l., fl., fr., *R.C. Sodré et al. 3456* (BOTU). Gouveia, Serra do Espinhaço, 13/XI/1971, fl., fr., *G. Hatschbach & P. Pelanda 27881* (MBM); rodovia BR-259, subida Serra do Espinhaço, 12/III/1982, fl., fr., *G. Hatschbach 44649* (MBM); rodovia Curvelo-Diamantina, *ca.* 37 km de Gouveia em direção a Curvelo, 18°35'39.6"S, 43°57'50.4"W, 05/IV/1998, fl., fr., *V.C. Souza et al. 20882* (ESA); about 8 km N of Gouveia on road to Diamantina, 1220 m a. s. l., 3/II/1972, fl., fr., *W.R. Anderson*, *M. Stieber & J.H. Kirkbride Jr. 35308* (MBM); proximidades do trevo Diamantina/Gouveia/Datas, 7 km

N de Gouveia, 18°25'5"S, 43°41'32"W, 1320 m a. s. l., 10/I/2019, fl., fr., *R.C. Sodré et al. 3450* (BOTU), *3451* (BOTU), *3452* (BOTU). Grão Mogol, rodovia para Cristália, 22/IV/1978, fl., *G. Hatschbach 41406* (MBM); arredores, 23/IV/1978, fl., *G. Hatschbach 41417* (MBM); vale do Córrego Alegre, 24/X/1991, fl., fr., *M.G. Carvalho & S.T. Silva 695* (BHCB), *696* (BHCB). Ibirité, *ca.* 10 km da cidade em direção a Belo Horizonte, 14/X/1995, fl., *J.P. Souza*, *D.G. Souza & L.M.P.P. Souza 212* (ESA); Serra do Rola Moça, 05/XII/1996, fl., fr., *M. Brandão 275416* (PAMG). Itabirito, Pico do Itabirito, 12/III/1994, fl., fr., *W.A. Teixeira s.n.* (BHCB 011516); *ca.* 10 km da cidade em direção a Belo Horizonte, 14/X/1995, fl., *J.P. Souza*, *D.G. Souza & L.M.P.P. Souza 212* (BHCB); região da Gerdal, próximo à BR-040, Mina Várzea do Lopes, 20°18'6.5"S, 43°55'57.3"W, 1260 m a. s. l., 25/I/2007, fl., fr., *S.G. Rezende et al. 1919* (BHCB). Itacambira, Serra de Itacambira, 2/III/1993, fl., fr., *M. Brandão 18583* (PAMG). Jaboticatubas, Lagoa de D. Ignacia, 20/XII/1939, fl., fr., *M. Barreto 10443* (BHCB). Lavras, 6/XII/1982, fl., *L.H.S. Cunha 1383* (PAMG). Moeda, Serra da Moeda, 04/X/1989, fl., fr., *P.H.A. Pequeno et al. 143* (BHCB). Nova Lima, Morro do Chapéu, 1250 m a. s. l., 31/III/1982, fl., fr., *T.S.M. Grandi & P.M. Andrade 923* (BHCB); 22/VIII/1982, fl., fr., *T.M.S. Grandi & P.M. Andrade 1143* (BHCB); Serra do Cachimbo, 14/III/1999, fl., fr., *M. Pompeu 388* (BHCB); Serra do Rola-Moça, 20°3'S, 44°1'W, 1350 m a. s. l., 28/VI/2000, fr., *R.C. Vicent 167* (ESA); *ib.*, 22/V/2001, fl., fr., *R.C. Vicent 443* (ESA). Mina de Capão Xavier, 20°2'59.93"S, 43°59'13.24"W, XI/2008, fl., fr., *F.S.R. Pena & L. Maielo-Silva 24* (BHCB). Ouro Branco, Serra de Ouro Branco, em direção à antena, 20°29'30.2"S, 43°42'6,7"W, 1401 m a. s. l., 12/I/2003, fl., fr., *A.O. Araújo*, *G.O. Romão & S. Vieira 335* (ESA). Ouro Preto, Serra do Itatiaia, 28/I/1942, fl. e fr., *M. Magalhães 1234* (BHCB); estrada velha Ouro Branco - Ouro Preto, *ca.* 15 km de Ouro Branco, 20°28'39.4"S, 43°35'32"W, 1000 m a. s. l., 09/III/1995, fl., fr., *V.C. Souza, P.H. Miyagi & J.P. Souza 8043* (ESA, BHCB); Serra Itatiaia, 28/I/1942, fl., fr., *M. Magalhães 1234* (IAN). Rio Acima, rodovia de Ouro Preto para Belo Horizonte, próximo ao Pico do Itabirito, 20°12'8"S, 43°50'33"W, 1230 m a. s. l., 12/VII/2001, fl., *P. Fiaschi*, *A.Q. Lobão & F.N. Costa 910* (MBM); 20°2'37"S, 43°45'00"W, 1229 m a. s. l., 07/V/2010, fl., fr., *E. Tameirão Neto & T. Mansur 4854* (BHCB). Rio Vermelho, Pedra Menina, Fazenda Vargem do Anjo - Morro Espigão do Meio, 13/X/1984, fl., *R. Mello-Silva et al. CFCR5418* (SPF, MBM); Serra do Ambrósio, 18°6'28"S, 43°2'20"W, 1450 m alt., 10.I.2006, fl., fr., *P.L. Viana et al. 2416* (BHCB), *ib.*, 18°7'29"S, 43°2'24"W, 1260 m a. s. l., 28/IV/2013, fl., fr., *M.L. Brotto et al. 1271* (MBM). Sabará, Mina do Segredão, 19°50'S, 43°46'W, 1200 m a. s. l., 21/XII/2007, fl., *R.C. Mota*, *L.M. dos Santos & S.A.T. dos Santos 3424* (BHCB). Santa Luzia, Lagoa Santa, 11/IX/1932, fl., *M. Barreto 2707* (BHCB); *ib.*, 26/II/1933, fl., fr., *M. Barreto 2708* (BHCB); *ib.*, 25/III/1933, fl., *M. Barreto 2709* (BHCB); Serra do Cipó, 12/I/1934, fl., fr., *M. Barreto 2706* (BHCB). Santana do Pirapama, Serra do Cipó (Serra da Lapa), distrito de São José da Cachoeira, trilha da captação da Fazenda Toucan Cipó, 19°00'20"S, 43°45'25"W, 680 m a. s. l., 17/II/2007, fl., *V.C. Souza et al. 32515* (ESA, BHCB). Santana do Riacho, Serra do Cipó, Vale da Mãe D'Água, 01/V/1993, fl., fr., *V.C. Souza & C.M. Sakuragui 3388* (ESA); estrada para Lapinha, *ca.* 8 km após Santana do Riacho, 19°07'4.5"S, 43°41'56.2"W, 1100 m a. s. l., 01/III/2002, fl., fr., *V.C. Souza*, *G.O. Romão & D. Sampaio 28736-A* (ESA); Serra do Cipó, MG-010, margem da estrada para a fazenda Mãe D'água, 19°18'9"S, 43°36'5"W, 1030 m a. s. l., 09/I/2019, fl., fr., *R.C. Sodré et al. 3443* (BOTU). Serro, rodovia MG-2, entre Serro e Datas, 19/I/1972, fl., fr., *G. Hatschbach*, *L.B. Smith & E. Ayensu 238954* (MBM); estrada para Gouveia, 11/X/1996, fl., fr., *W. Marcondes-Ferreira*, *A.O. Simões & R. Belinello 1365* (UEC). Várzea da Palma, fazenda Serra do Cabral Agro-Industrial, 9/XI/1997, fl., *G. Hatschbach*, *M. Hatschbach & E. Barbosa 67270* (MBM). Without municipality, Serra do Cipó, 28/X/1989, fl., *A.M. Monteiro s.n.* (BHCB 011448).

Croton hatschbachii Sodré & M.J. Silva, sp. nov. Type: BRAZIL. Minas Gerais: Mun. Grão Mogol: Parque Estadual de Grão Mogol, cerca de 1 km ao norte da cidade pela trilha do Barão, 16°33'17.9"S, 42°53'27.1"W, 890 m a. s. l.., 11/I/2019, fl., fr., *R.C. Sodré, I.S. Santos* & *T.P. Mendes 3465* (holotype BOTU!; isotypes: UFG!, RB!, NY!, K!) (Figs. 9, 10)

Croton hatschbachii differs from related species by having branches and leaves with a floccose indumentum of multiradiate trichomes, rough to the touch, petioles 0.5-3 cm long, adaxial surface of leaf blades lime-green with usually sparse trichomes, thyrses 1.5-6.5 cm long with sparse flowers; staminate flowers with long pedicels (2-3.2 mm) and small stamens (2.5-3.2 mm), petals (1.8-2.2 × 0.8-0.9 mm) and calyx lobes (1.5-2 × 0.8-1 mm), and oblong capsules with carpels not visually delimited.

Subshrub or shrub, 0.5-1.5 m tall, xylopodium not seen, erect, ramifying in 2 or 3-furcations, old branches cylindrical and not striated, young branches flattened and slightly striate, latex clear or orange, indument floccose, rough to the touch, yellowish, with multiradiate trichomes with 20-25 lateral rays in 2 or 3 whorls, each ray 0.15-0.4 mm long, central ray 0.2-0.5 mm long, stipitate (stipe 0.2-0.4 mm long), or less commonly sessile. Leaves spiral, alternate or subopposite, or subwhorled below the stem bifurcations and/or inflorescences, leaf blades 2-5 times longer than the petioles, nectary glands absent; stipules lanceolate, 0.3-0.4 mm long, with 1-3 ovoid or globose glands (colleters) laterally, covered by indument; petiole 0.5-3 cm long; leaf blade 2.1-5.9 × 0.9-4.9 cm, membranaceous, ovate, largely ovate, oblong, suborbicular, elliptic, or less commonly oval-lanceolate, base rounded, retuse or slightly cordate, apex obtuse, slightly truncate, mucronate, retuse or acute, margins entire or sometimes serrulate, with globose glands (colleters), venation brochidodromous with 5-9 pairs of secondary veins impressed on both surfaces, bifacial,

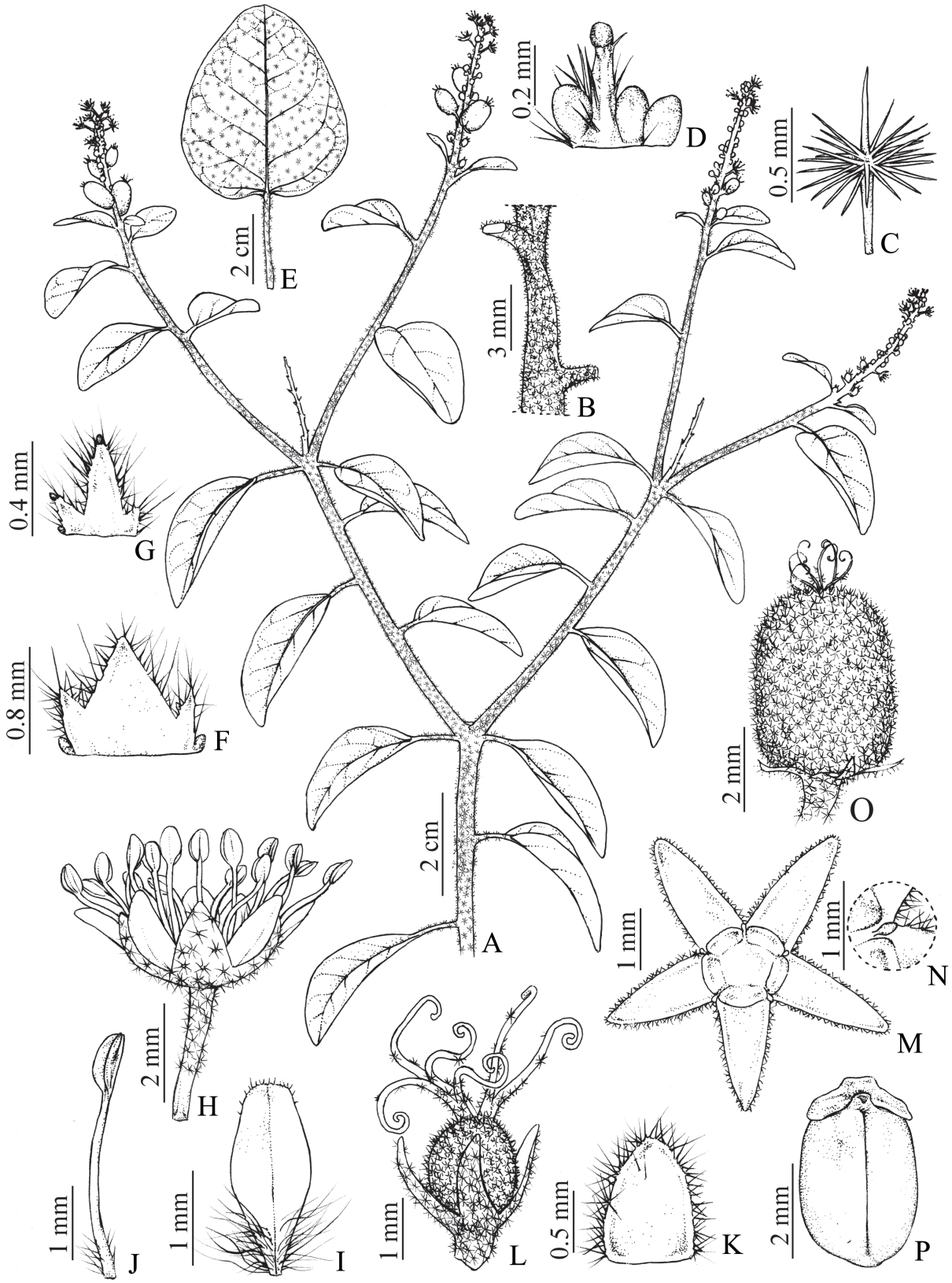

Figure 9. *Croton hatschbachii* Sodré & M.J. Silva, sp. nov.: **A.** Fertile branch. **B.** Detail of young branch. **C.** Multiradiate trichome on a branch. **D.** Stipule. **E.** Leaf blade. **F.** Staminate bract. **G.** Staminate bracteole. **H.** Staminate flower. **I.** Ventral surface of a staminate petal. **J.** Stamen. **K.** Pistillate bract. **L.** Pistillate flower. **M.** Top view of a pistillate flower with the ovary removed to show the 5-segmented nectary disk and calyx spread open. **N.** Detail of pistillate petals reduced to inconspicuous glands. **O.** Capsule. **P.** Ventral side of seed. Drawn by R. Galhardo Neto from the holotype.

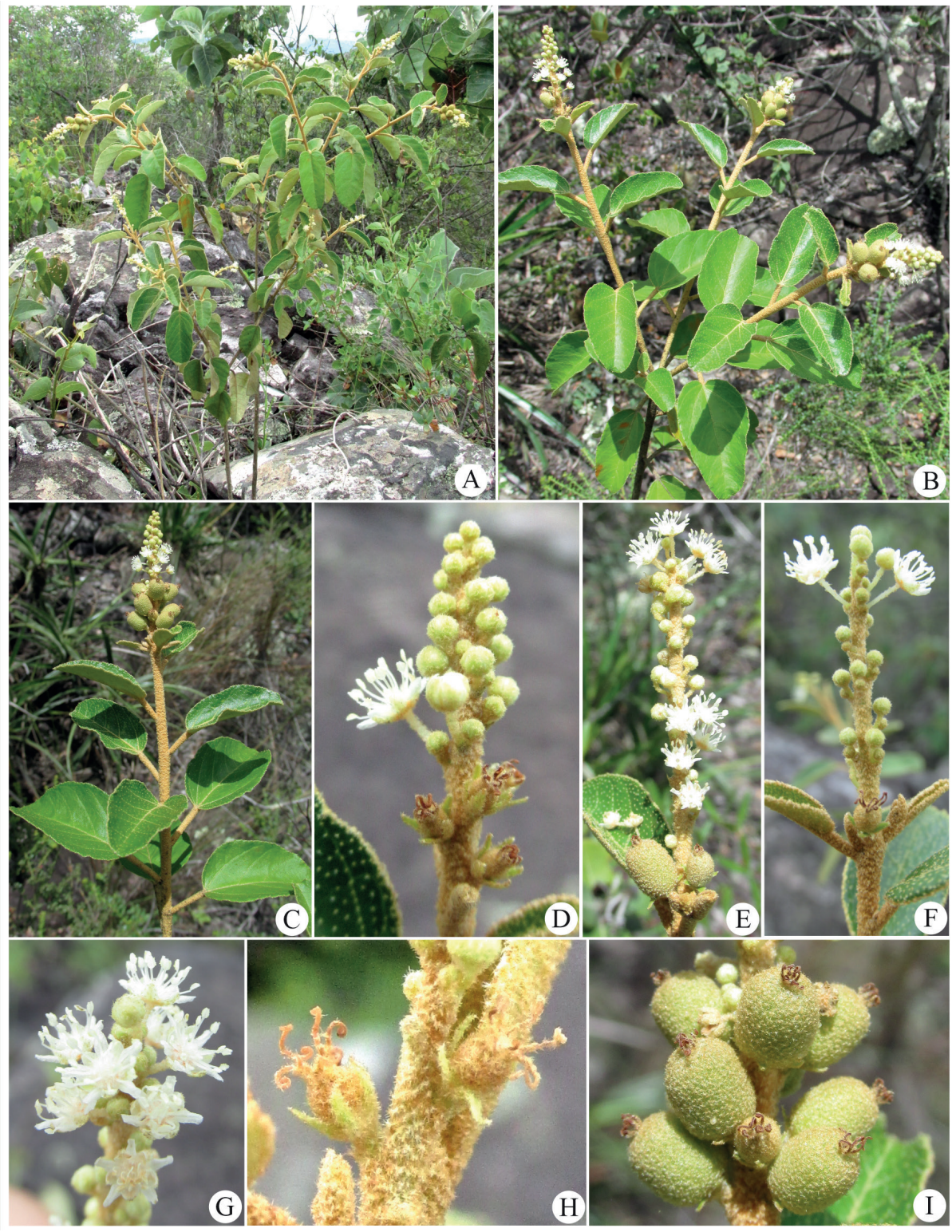

Figure 10. *Croton hatschbachii* Sodré & M.J. Silva, sp. nov.: **A.** Subshrub habit in "cerrado rupestre" vegetation. **B.** Fertile branch ramifying in trifurcations. **C.** Fertile branch showing spiral alternate leaves, with lime-green adaxial surfaces. **D.** Short inflorescence showing sparse pistillate flowers, whitish and long-pedicellate staminate flower, and greenish-yellow buds, note the inconspicuous bracts. **E.** Inflorescence showing two capsules at base, one of them still young, and staminate flowers and buds along the axes. **F.** Inflorescence showing one developing fruit at base, and sparse staminate cymules along the axes, note the long pedicels of the staminate flowers. **G.** Staminate cymules, with flowers and buds, note whitish petals and stamens, and greenish calyx. **H.** Inflorescence base with two pistillate flowers, note floccose indument of the axes, greenish sepals, and brownish ovary and styles. **I.** Oblong clear-green capsules. Photographs by R.C. Sodré from *R.C. Sodré et al. 3464* and *3465*.

adaxial surface light green with sparse or rarely overlapping multiradiate sessile trichomes, (10-)16-26 lateral rays, usually in 2 whorls, each ray 0.25-0.35 mm long, central ray *ca.* 0.25 mm long, abaxial surface clear yellow or whitish with dense indument of multiradiate stipitate trichomes, 16-30 lateral rays in 2 or 3 whorls, each ray *ca.* 0.3 mm long, central ray 0.2 mm long, stipe 0.25 mm long. Thyrses 1.5-6.5 cm long, terminal, or in branch bifurcations, bisexual, with (1-)2-10 solitary pistillate flowers sparsely arranged on $^1/_8$-$^1/_4$ of the inflorescence axis, staminate cymules with 2 or 3 flowers; bracts of both flowers 0.9-1.2 × 0.2-0.3 mm, triangular or lanceolate, internally glabrous or glabrescent, externally with dense indument of stellate trichomes, subglobose glands (colleters) at the base. Staminate flowers 4.5-5.5 mm long, pedicel 2-3.2 mm long, pubescent, trichomes multiradiate, calyx 5-partite, valvar prefloration, lobes 1.5-2 × 0.8-1 mm, ovate or oblong, apex acute, indument pubescent externally with multiradiate trichomes, petals 1.8-2.2 × 0.8-0.9 mm, elliptic or oblong, villous basally for up to $^1/_3$ of their length, stamens 16, 2.5-3.2 mm long, filaments 2-2.7 mm long, villous basally, anthers 0.35-0.6 mm long, ellipsoidal, disk 5-segmented, segments transversely oblong, whitish, receptacle pubescent. Pistillate flowers 3.5-5 mm long, pedicel 0.2-0.7 mm long, sepals 5, 1.2-2 × 0.5-0.8 mm, equal, triangular, narrowly triangular or lanceolate, apex acute, externally with pubescent indument of multiradiate trichomes, internally glabrous, petals 5, 0.2-0.7 × 0.1 mm, globose or linear with a subglobose gland at the apex, ovary 1.1-1.3 × 1.3-1.5 mm, widely oblongoid, yellowish, indument pubescent with multiradiate trichomes shortly stipitate, styles 2-fid, 2-4 mm long, united for $^1/_8$-$^1/_6$ of their length, with stellate-porrect trichomes externally up to $^5/_6$ of their length, disk 5-segmented or 5-lobed, lobes or segments transversally oblong, or less commonly entire and ring-shaped, orange. Capsules 5-5.5 × 4.5-4.8 mm, oblong, greenish; pedicel 1.6-2.5 mm long; seeds 3.9-4.1 × 1.9-2.1 mm, oblongoid, with carpels not visually delimited, grayish, smooth with slightly foveolate surfaces, caruncle 1.5-1.8 mm width, hat-shaped, slightly truncate at apex, sessile.

Distribution and habitat - *Croton hatschbachii* is endemic to Minas Gerais State, with known distributions in the municipalities of Grão Mogol, Padre Carvalho, and Itacambira (Fig. 8). It grows in *cerrado rupestre* vegetation on sandy-stony soils, between 600 and 890 m a.s.l.

Phenology - Flowering and fruiting from September to June.

Remarks - *Croton hatschbachii* is closely related to *C. campestris* by sharing a subshrub or shrub habit, 0.5-1.5 m tall, branches with usually yellowish and dense indument, stipules with 1-3 glands (colleters), covered by indument, leaves conspicuously petiolate and without nectary glands. *Croton hatschbachii*, however, has branches and leaves with multiradiate trichomes with 16-30 lateral rays in 2 or 3 whorls, each ray 0.15-0.4 mm long (vs. stellate-porrect with 11-16 lateral rays in a single whorl, and each ray 0.4-2 mm long in *C. campestris*), adaxial surfaces of the leaf blades lime-green, with usually sparse trichomes rarely overlapping even on young leaves (vs. whitish, yellowish, ferruginous or dark green, usually with dense indument, especially on young leaves), thyrses 1.5-6.5 cm long with sparse flowers (vs. 2.3-25 cm long with usually dense flowers), pedicels of staminate flowers 2-3.2 mm long (vs. 0.8-2 mm), lobes of the staminate calyx 1.5-2 × 0.8-1 mm (vs. 2-2.3 × 1.2-2 mm), staminate petals 1.8-2.2 × 0.8-0.9 mm, elliptic or oblong (vs. 2.5-3 × 0.9-1.5 mm, obovate, sometimes oboval-oblanceolate or oblong-oblanceolate), staminal filaments 2-2.7 mm long (vs. 2.8-4 mm long), anthers 0.35-0.6 mm long (vs. 0.7-1 mm long), and oblong capsules with inconspicuous locule delimitations (vs. subglobose with conspicuous locule delimitations). Additionally, the branches of *C. hatschbachii* have a floccose indumentum that is rough to the touch, leaf blades only 2-5 times longer than the petioles (petioles 0.5-3 cm long), small bracts 0.9-1.2 mm long; *C. campestris*, on the other hand, has branches tomentose and not rough to the touch, blades 4-10 (-13) times longer than the petioles (petioles 0.25-1.7 mm long), and bracts 1.2-2.3 mm long.

The new species also resembles *Croton heliotropiifolius* by petioles up to 3 cm long, branches and abaxial surface of the leaf blades with multiradiate trichomes, pedicel of staminate flowers with 2-4 mm long and oblong capsules. However, *C. hatschbachii* has branches with floccose indument (vs. hirsute, hirtellous or tomentose in *C. heliotropiifolius*); adaxial surface of leaf blades covered with multiradiate trichomes (vs. stellate-porrect or fasciculate); thyrses 1.5-6.5 cm long (vs. 1.7-15 cm long), with (1-)2-10 solitary pistillate flowers sparsely arranged thyrses (vs. 12-20 pistillate flowers densely arranged). In addition, *C. hatschbachii* is endemic to *cerrado rupestre* in northern Minas Gerais, Brazil; while *C. heliotropiifolius* is widely distributed in the Caatinga, in eastern Brazil, and in dry forests of Peru, Venezuela and Colombia.

The name *Croton heliotropiifolius* has been accepted by several authors to designate the most widely distributed species of section *Adenophylli* in the east and northeast of Brazil (*e.g.*, Govaerts *et al.* 2000, Carneiro-Torres 2009, Caruzo *et al.* 2021). We analyzed specimens of *C. heliotropiifolius* from the type locality in the Andes and an extensive list of Brazilian materials, especially from the northeast region, and we agree that the specimens are very similar. Therefore, until population level phylogenetic studies are conducted on this species covering its entire range, it will not be possible to know whether they are cryptic species.

Proposed conservation status - *Croton hatschbachii* has an Extent of Occurrence (EOO) of 526.4 km^2, is known from approximately ten localities in three municipalities in Minas Gerais (EOO) and only one known population occurs in a protected area (the Grão Mogol State Park). Although the species inhabit rocky areas at high altitude and of difficult access that are not always suitable for agriculture,

we consider it Endangered (EN B1ab (i, ii)), due to limited EOO (< 5,000 km^2) and strongly recommend increased efforts to map new populations.

Etymology - The epithet honors Gert Günter Hatschbach, one of the most prolific collectors of plants of the Brazilian flora, and who collected the paratypes selected for the new species.

Additional specimens analyzed (paratypes) - BRAZIL. Minas Gerais: Grão Mogol, Serra do Pipiri, 22/III/1980, fl., *G. Hatschbach 42875* (MBM); campos rupestres atrás da cidade, 13/IV/1981, fl., *I. Cordeiro et al. CFCR 778* (SPF); vale do Rio Itacambiruçu, 04/IX/1985, fl., fr., *J.R. Pirani et al. CFCR 8384* (SPF); próximo da saída na estrada para Francisco Sá, 900 m elev., 07/I/1986, fl., *I. Cordeiro et al. CFCR 9052*-A (SPF); *ib.*, *J.R. Pirani et al. CFCR 9046* (SPF); Ribeirão do Bois, 02/IX/1986, fl., fr., *I. Cordeiro & R. Mello-Silva CFCR 9996* (SPF); *ib.*, 16°33'S, 42°52'W, 22/III/2000, fl., fr., *L.R. Lima et al. 97* (SPF); Rio das Mortes, 17/V/1988, fl., *G. Hatschbach & M. Hatschbach 52108* (MBM, SPF); *ca.* 5-15 km ao norte da cidade, 16°32'S, 42°47'W, 900 m elev., 16/X/1988, fl., fr., *R.M. Harley et al. 25091* (SPF); Francisco Sá-Salinas, km 87, 21/X/1990, fl., fr., *M. Brandão 17849* (PAMG); estrada da Serra do Barão, 16°32'S, 42°55'W, 22/III/2000, fl., *L.R. lima et al. 95* (SPF); Parque Estadual de Grão Mogol, 13/VI/2006, fl., fr., *C.V. Vidal 109* (BHCB); *ib.*, 11/I/2019, fl., fr., *R.C. Sodré*, *I.S. Santos & T.P. Mendes 3464* (BOTU); cerca de 1 km após a ponte para Cristália, 16°35'41,9"S, 42°53'55.4"W, 682 m, 08/II/2015, fl., *T.A. Pontes & H. van der Werff 431* (HRCB). Itacambira, 5 km de Itacambira, a leste da cidade, na estrada para Montes Claros, 29/XI/1984, fl., fr., *M.L. Kawasaki et al. CFCR 6616* (SPF); Serra de Itacambira, 05/X/1990, fl., *M. Brandão 18971* (PAMG); *ib.*, 2/III/1993, fl., fr., *M. Brandão 21721* (PAMG); 16°59.616'S, 43°20.42'W, 1250 m, 13/XI/2001, fl., *A.M.G.A. Tozzi & D.A.A. Vilhalva 2001-453* (UEC). Padre Carvalho, BR 251, km 400, 13/XII/2010, fl., *J. Cordeiro*, *E. Barbosa & E.F. Costa 3905* (MBM).

Croton stellatorotatus Sodré & M.J. Silva, sp. nov. Type: BRAZIL. Bahia: Abaíra, estrada Abaíra-Catolés, *ca.* 300 metros a leste do Riacho Machado, 13°17'22.5"S, 41°44'42.7"W, 878 m a. s. l., 17/XII/2017, fl., fr., *R.C. Sodré*, *A.O. Souza* & *U.S. Amaral 3309* (holotype BOTU!; isotypes NY!, UFG!) (Figs. 11, 12)

Croton stellatorotatus is similar to *C. campestris* Baill. by having dense indument on the branches and leaves, foliar nectary glands absent, and petioles up to 1.7 cm long, but differs in having stellate-rotate trichomes (vs. stellate-porrect or multiradiate in *C. campestris*), leaf blades orbicular, ovate or largely elliptic (vs. usually elliptic, oboval-oblanceolate or narrowly elliptic), thyrses up to 6 cm long (vs. 2.3-25 cm long), and flowers with small stamens and styles, both up to 2.8 mm long (vs. 3.5-5 mm long).

Subshrub, 0.4-1.7 m tall, xylopodium not seen, erect, latex clear, branches cylindrical, smooth (not striate), indument tomentose, whitish or yellowish, trichomes stellate-rotate with 14-19 lateral rays in a single whorl, each ray 0.5-1 mm long, united up to $^1/_{10}$ of their length, stipe 0.2-1 mm long, central ray vestigial, up to 0.05 mm long, or sometimes developed, 0.1-0.6(-1.3) mm long. Leaves alternate, subopposite or subwhorled below the stem bifurcations and/or inflorescences, leaf blades 5-11 times longer than the petioles, nectary glands absent; stipules 0.2-0.5 × 0.1-0.15 mm, lanceolate or linear, with two globose or oblongoid glands on the base and with, or without, a gland at the apex, with stellate-porrect trichomes externally, stipules sometimes reduced to glands; petiole 0.3-0.8 cm long, with two or three subglobose glands (colleters) at the apex; leaf blades 1.7-4.5 × 1.4-3.0 cm, orbicular, ovate or widely elliptic, or less commonly elliptic, oval-lanceolate or oblong, apex rounded, obtuse, emarginate, retuse or acuminate, base obtuse or slightly cordate, margins entire, sometimes with globose glands (colleters) similar to those at the apex of the petiole, venation brochidodromous, with 4-7 pairs of secondary veins impressed on both surfaces or prominent on the abaxial surface, bifacial, adaxial surface with stellate-rotate trichomes with 13-17 lateral rays, 0.3-0.6 mm long, central ray vestigial, *ca.* 15 µm long, or sometimes developed and 26 mm long, stipe 0.1-0.3 mm long., abaxial surface whitish with a tomentose indument of stellate-rotate trichomes with 14-20 lateral rays in a single whorl, each ray 0.35-0.6 mm long, united for $^1/_{10}$ of their length, central ray vestigial and *ca.* 15 µm long, or sometimes developed and 0.2-1(-1.3) mm long, stipe 0.2-0.5 mm long, grayish or green-yellowish. Thyrses 1-6 cm long, terminal or in branch bifurcations, bisexual, 3-7 solitary pistillate flowers basally, staminate cymules with (1-)2-3 flowers; staminate bracts 1-1.3 × 0.2-0.3 mm, triangular, oval-lanceolate, with two small globose or ovoid glands (colleters), shortly stipitate at the base, externally with stellate-porrect trichomes with 10-14 lateral rays 0.3-0.5 mm long, central ray 0.5 mm long, shortly stipitate (stipe *ca.* 0.1 mm long); pistillate bracts 0.7-1.5 × 0.3-0.8 mm, lanceolate, triangular or ovate, with two pairs of ovoid or ellipsoidal glands, shortly stipitate at the base, internally glabrous, externally with dense indument of stellate-porrect trichomes shortly stipitate, with 12-14 lateral rays, central ray vestigial. Staminate flowers 3.7-5 mm long, pedicel 1.1-2.2 mm long with stellate-porrect trichomes, calyx 5-partite, united for $^1/_6$-$^1/_{10}$ of their length, lobes 1.4-2.2 × 0.7-1.4 mm, ovate or largely ovate or less commonly elliptic, apex acute or obtuse, internally glabrous, externally with stellate-porrect trichomes, with 12-17 lateral rays *ca.* 0.4 mm long, central ray vestigial or less commonly developed, stipe 0.1-0.3 mm long; petals 1.6-2.2 × 0.6-1.1 mm, obovate, oboval-lanceolate or sometimes oboval-elliptic, apex obtuse or rounded, villous basally, stamens (15-)16(-18), 2.1-2.8 mm long, filaments 1.7-2.2 mm long, glabrous, or sometimes villous basally, anthers 0.4-0.65 × 0.4-0.5 mm, orbicular, oblongoid or largely ellipsoid, disk 5-segmented, segments transversely oblong, orange. Pistillate flowers 3.5-4.2 mm

Figure 11. *Croton stellatorotatus* Sodré & M.J. Silva, sp. nov.: **A.** Fertile branch. **B.** Stellate-rotate trichome on a branch. **C.** Stipule. **D.** Leaf blade. **E.** Staminate bract. **F.** Staminate flower. **G.** Ventral surfaces of staminate petals. **H.** Stamen. **I.** Pistillate bract. **J.** Pistillate flower. **K.** Top view of pistillate flower, with ovary removed to show the 5-segmented nectary disk, and calyx spread open. **L.** Detail of pistillate petals reduced to inconspicuous glands. **M.** Capsule. **N.** Ventral side of seed. Drawn by R. Galhardo Neto from the holotype.

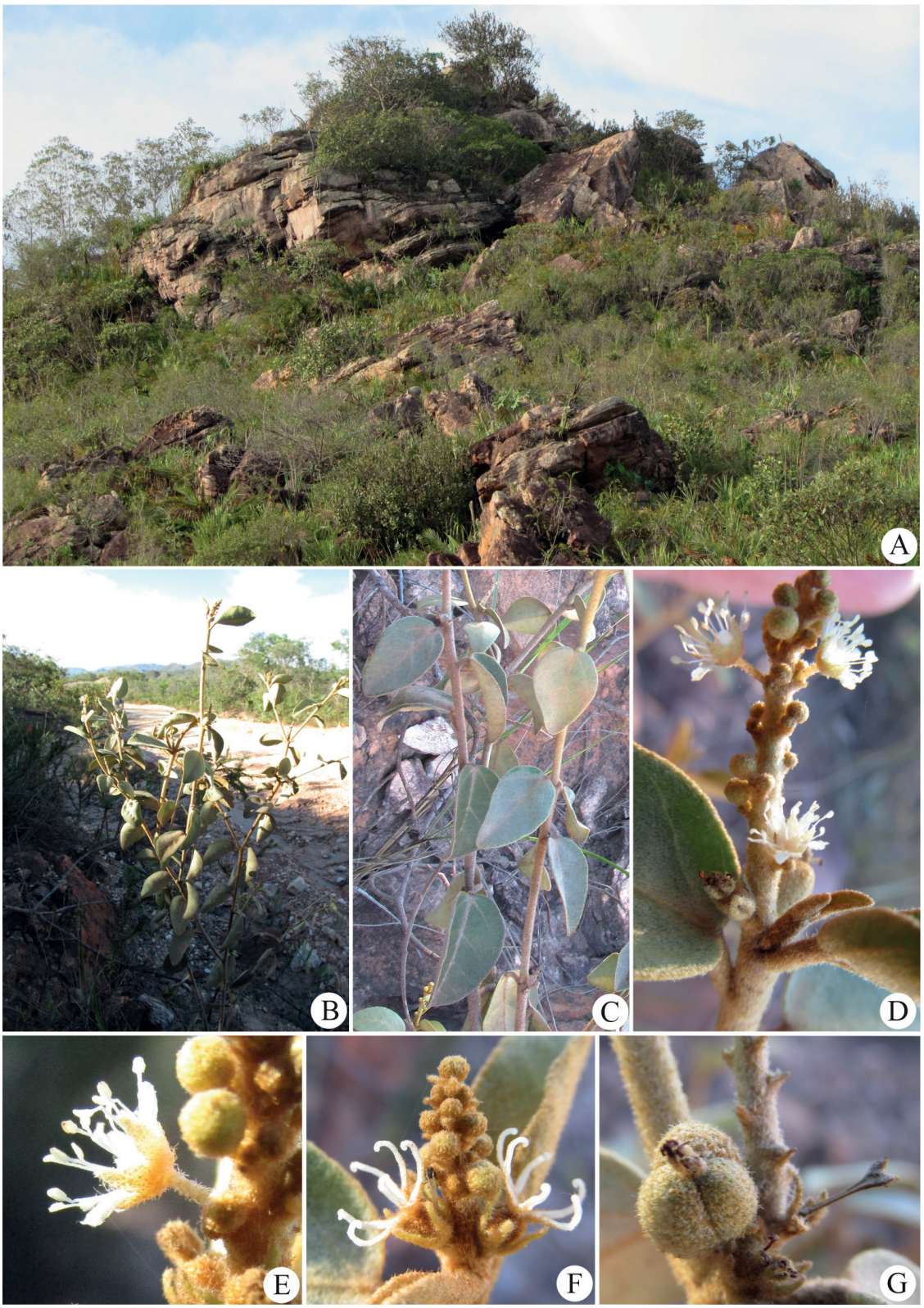

Figure 12. *Croton stellatorotatus* Sodré & M.J. Silva, sp. nov.: **A.** Habitat in "campo rupestre" vegetation in the municipality of Abaíra, Bahia State. **B.** Habit. **C.** Detail of branch, showing spiral alternate leaves with short petioles and cinereous indumentum. **D.** Inflorescence showing one developing fruit at base and sparse staminate cymules along the axes. **E.** Staminate flower. **F.** Young inflorescences, with two pistillate flowers towards the base and staminate buds towards the distal end. **G.** Inflorescence base, with a globose capsule with conspicuous locule delimitations, and a dehisced capsule showing the columella with three apical lobes. Photographs by R.C. Sodré from *R.C. Sodré et al. 3309*.

long, pedicel 0.2-0.5 mm long, sepals 5, slightly unequal, 1.6-2.2 × 0.6-1 mm, triangular, lanceolate or oblong, apex acute, internally glabrous or glabrescent, externally with stellate-rotate trichomes shortly stipitate with *ca.* 13 lateral rays united for $^1/_{10}$ of their length, central ray vestigial, petals 0.15-0.2 mm diam., subglobose, sessile, or shortly stipitate, disk 5-segmented, segments transversely oblong, ovary 1.4-1.6 × 1.8-2 mm, subglobose, with stellate-rotate trichomes with 15-17 lateral rays in a single whorl, each ray 0.4-0.8 mm long, central ray 0.2-0.5(-1.3) mm long, styles 2-partite, 2.2-2.8 mm long, united for $^1/_3$ of their length, externally with stellate-porrect trichomes for up to $^1/_2$ of their length. Capsules 5.5-6.5 × 5.5-6 mm, globose, with carpels visually delimited, yellowish-green; seeds 4.8-5 × 2.7-2.9 mm, ellipsoidal, brownish, with smooth and minutely foveolate surfaces, caruncle 1.3-2.2 mm, large, reniform or hat-shaped, slightly bilobed at apex, orange or yellowish, sessile.

Distribution and habitat - *Croton stellatorotatus* is found only in the Bahia State, in the Chapada Diamantina region, in *campo rupestre*, in gravelly or lateritic sandy soils, between 878 and 1823 m a.s.l. (Fig. 8).

Phenology - Found flowering and fruiting throughout the year.

Remarks - *Croton stellatorotatus* has usually been identified in herbaria as *C. campestris,* and it was described and illustrated under that name by Carneiro-Torres (2009), as it is a non-viscous subshrub or shrub with branches and leaves with dense yellowish or whitish indument of stellate trichomes, leaves without nectary glands, petioles up to 1.7 cm long, shortly pedicellate pistillate flowers (pedicels up to 0.5 mm long), with 2-partite styles. *Croton stellatorotatus* differs, however, by having stellate-rotate trichomes with 13-20 lateral rays united for $^1/_{10}$ of their length, and the central ray usually vestigial (*ca.* 15 µm long) on its branches, leaves, axes of the thyrses, sepals of the pistillate flowers and ovary; leaf blades usually orbicular, ovate or largely elliptic, thyrses up to 6 cm long with 3-7 pistillate flowers, staminate flowers with small petals (1.6-2.2 mm long) and stamens (2.1-2.8 mm long), and styles 2.2-2.8 mm long. In *C. campestris,* the trichomes are stellate-porrect with 7-16 free lateral rays and a developed central ray (0.1-1 mm long), or multiradiate on the abaxial surfaces of the leaves; leaf blades elliptic, oblong, narrowly elliptic, lanceolate, ovate, oboval-elliptic, oboval-oblanceolate, widely ovate, or obovate, thyrses are usually long, 2.3-25 cm, with (1-)5-15 pistillate flowers, staminate flowers have long petals (2.5-3 mm long) and stamens (3.5-5 mm long), and styles 3.5-5 mm long.

Proposed conservation status - Although populations of *Croton stellatorotatus* occur in protected areas in Bahia State (*e.g.*, the Chapada Diamantina National Park), its limited Extent of Occurrence (9,730.7 km^2) leads us to recognize it as Vulnerable (VU B1ab(i, ii, iii)).

Etymology - The epithet "stellatorotatus" refers to the stellate-rotate trichomes that cover the vegetative and reproductive organs of the species.

Additional specimens analyzed (paratypes) - BRAZIL. Bahia: Abaíra, Catolés, 13°17'S, 41°51'W, 1000-1100 m a. s. l., 20/XII/1991, fl., *R.M. Harley et al. 50160* (MBM); cachoeira das Anáguas, 13°16'S, 41°53'W, 1400 m a. s. l., 26/I/1992, fl., fr., *J.R. Pirani*, *B. Stannard & A. McRobb 51309* (ESA, SP); base da encosta da Serra da Tromba, 13°17'S, 41°48'W, 1150 m a. s. l., 22/II/1992, fl., *J.R. Pirani et al. 51486* (SP, SPF); distrito Catolés, encosta da serra do Atalho em frente ao Mendonça, 13°16'S, 41°49'W, 1100 m a. s. l., 03/IV/1992, fl., fr., *W. Ganev 16* (HUEFS, NY); caminho Samambaia-Serrinha, *ca.* 4 km de Catolés, 13°19'S, 41°51'W, 1300 m a. s. l., 22/V/1992, fl., fr., *W. Ganev 343* (HUEFS, NY); campo das Anáguas, acima da cachoeira, à beira do córrego, 13°17'S, 41°53'W, 1340 m a. s. l., 10/X/1992, fl., fr., *W. Ganev 1217* (HUEFS, NY); Água Limpa, Morro do Cuscuzeiro, 13°18'S, 41°53'W, 1400 m a. s. l., 29/IV/1994, fl., *W. Ganev 3174* (HUEFS, NY); caminho Boa Vista-Bicota, 13°19'S, 41°51'W, 1200-1400 m a. s. l., 23/VII/1994, fl., fr., *W. Ganev 3432* (HUEFS, NY); encosta da Serra do Tromba, 13°17'S, 41°46'W, 1823 m a. s. l., 7/IX/1996, fl., fr., *R.M. Harley et al. 28359* (ESA); *ib*., 24/X/1999, fl., fr., *D.S. Carneiro-Torres et al. 169* (HUEFS); Catolés, subida para a Serra do Barbado, 13°17'19"S, 41°57'27"W, 1663 m a. s. l., 17/XI/2015, fl., *D.S. Carneiro-Torres et al. 1358* (HUEFS). Barra da Estiva, *ca.* 6 km N of Barra da Estiva on Ibicoara road, 13°35'S, 41°18'W, 1100 m alt., 28/I/1974, fl., *R.M. Harley et al. 15522* (NY, US); estrada Barra da Estiva-Mucugê, km 31, 13°23'S, 41°26'W, 1280 m a. s. l., 04/VII/1983, fl., *L. Coradin et al. 6430* (CEN, P); Morro do ouro, 9 km ao S da cidade na estrada para Ituaçú, 13°42'S, 41°18'W, 1100 m a. s. l., 19/XI/1998, fl., fr., *R.M. Harley*, *D.J.N. Hind & T.B. Cavalcanti 26926* (CEPEC, NY); saída de Barra da Estiva, em direção a Brumado, *ca.* 7 km de Barra da Estiva, 13°41'27"S, 41°19'0"W, 9/I/2006, fl., *T.S. Nunes et al. 1527* (HUEFS); BA-sentindo Itauçu, 13°41'20"S, 41°17'55"W, 1147 m a. s. l., 18/XI/2015, fl., *D.S. Carneiro-Torres et al. 1458* (HUEFS). Ibicoara, Cascavel, 28/I/2011, fl., fr., *H.A. Ogasawara & Equipe Labea 61* (ALCB, MBM); proximidades do Capão da Volta, estrada pra Jussiape, 13°27'23"S, 41°29'46"W, 1300 m a. s. l., 10/VIII/2013, fl., fr., *E. Melo 12134* (HUEFS). Ituaçú, Morro do Ouro, 28/VIII/1988, fl., *E.P. Gouveia s.n.* (ALCB 20671). Morro do Chapéu, Morrão, 11°35'12"S, 41°12'32"W, 1213 m a. s. l., 5/V/2007, fl., *D.S. Carneiro-Torres et al. 905* (HUEFS). Mucugê, Estrada Mucugê-Guiné, a 28 km de Mucugê, 07/IX/1981, fl., *A. Furlan et al. CFCR 2043* (SPF); estrada Mucugê-Capão da Volta-Jussiape, próximo ao entroncamento da estrada, 13°26'34"S, 41°24'12,5"W, 30/V/2002, fl., fr, *L.R. Lima & A. Conceição 175* (BHCB); Serra do Gobira, 13°5'16"S, 41°22'40"W, 1206-1250 m a. s. l., 20/II/2005, fl., fr., *P.L. Ribeiro*, *A.C.S. Pereira & E.C. Oliveira 117* (HUEFS, BHCB); Morro do Beco, Serra do Esbarrancado, PARNA Chapada Diamantina, 12°45'S, 41°30'W, 1250 m

a. s. l., 20/VI/2005, fl., fr., *A.A. Conceição & D. Cardoso 1431* (HUEFS, RB); estrada para Guiné, 12°53'6"S, 41°31'43"W, 1071 m a. s. l., 29.X.2005, fl., *J.G. Carvalho-Sobrinho & A.J. Neto 603* (HUEFS); trilha do Guiné para a Serra Esbarrancado, 12°46'20"S, 41°32'0"W, 13/III/2007, fl., fr., *A.K.A. Santos et al. 1086* (HUEFS); 13°0'S, 41°22'W, 18/VII/2007, fl., fr., *M.L. Guedes et al. 16229* (ALCB); 25/VIII/2009, fl., fr., *P.L.R. Moraes & H.V. der Werff 2908* (HUEFS); Chapada Diamantina, trilha para o Rio Paraguaçu, início na estação de tratamento de água, 13°0'1"S, 41°23'29"W, 941 m a. s. l., 22/V/2010, fl., fr., *N. Roque & Alunos de Botânica III 2819* (ALCB, MBM); caminho para Abaíra, 13°4'20"S, 41°29'54"W, 1021 m a. s. l., 14/VI/2010, fl., fr., *M.L. Gomes et al. 17182* (ALCB, MBM). Palmeiras, Serras dos Lençóis, lower slopes of Morro do Pai Inácio, *ca.* 14.5 km N.W. of Lençóis just N. of the main Seabra-Itaberaba road, 12°27'S, 41°28'W, 700-1000 m a. s. l., 21/V/1980, fl., *R.M. Harley 22253* (SPF, U, US); Morro do Pai Inácio, 12°27'S, 41°28'W, 1100-1200 m a. s. l., 13/II/1994, fl., fr., *V.C. Souza et al. 5219* (ESA); *ib.*, 12°27'20"S, 41°28'15"W, 1110 m a. s. l., 29/VIII/1994, fl., *M.L. Guedes et al. PCD 400* (CEPEC); Morro da Mãe Inácia, próximo ao Morro Pai Inácio, 27/V/2002, fl., fr., *L.R. Lima & A. Conceição 163* (SPF). Piatã, *ca.* 9 km de Piatã, 1250 m a. s. l., 5/II/1987, fl., fr., *R.M. Harley et al. 24238* (SPF, K); estrada Piatã-Inúbia a *ca.* 25 km NW de Piatã, Serra do Atalho, 13°4'48"S, 41°55'59"W, 1450 m a. s. l., 23/II/1994, fl., fr., *P.T. Sano et al. CFCR 14478* (ESA); 13°3'39"S, 41°53'11"W, 1300 m a. s. l., 05/XI/1996, fl., fr., *D.J.N. Hind et al. 4051* (ALCB, SPF). Rio de Contas, near Junco, *ca.* 15 km W.N.W. of the town of Rio de Contas, 13°32'S, 41°55'W, 1200 m, 22/I/1974, fl., fr., *R.M. Harley et al. 15592* (NY, US); arredores, 15/V/1983, fl., *G. Hatschbach 46430* (MBM); *ib.*, 16/V/1983, fl., fr., *G. Hatschbach 46460* (ALCB, MBM); campo da aviação, 1200 m a. s. l., 6/IV/1992, fl., fr., *G. Hatschbach*, *M. Hatschbach & E. Barbosa 56727* (MBM); *ca.* 7 km da cidade, em direção ao vilarejo de Bananal, 13°31'38"S, 41°51'13"W, 1200-1250 m a. s. l., 05/III/1994, fl., fr., *N. Roque et al. CFCR 14926* (ESA, SPF), Pico das Almas, *ca.* 500 m após o riacho, 13°31'7"S, 41°57'27"W, 1500 m a. s. l., 2/V/2003, fl., *L.R. Lima et al. 269* (SPF).

Croton subvillosus Müll. Arg., Fl. Bras. 11(2): 168. 1873. *Oxydectes subvillosa* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. Goiás: prope Gamelleira, *s.d.*, *J.B.E. Pohl 1617*, catalogue number 2164 (lectotype: W 0051217!, designated by Sodré *et al.* (2017); isolectotypes: G 00434673!, M 0089120!, K 000186135!, K 000186136!) (Fig. 13).

Croton occidentalis Müll. Arg., Fl. Bras. 11(2): 159. 1873. *Oxydectes occidentalis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. Type: BRAZIL. "Brasilia occidentali", *s.d.*, *Tamberlik s.n.* (lectotype designated here: W 0051235!, photo in F 32534!; isolectotypes: G, photo in F 24509!, F V0056171F!, W 0051234!). Syntype: BRAZIL. Mato Grosso do Sul: "in campis siccis secus Pardo", *s.d.*, *L. Riedel 510* (P 00634532!), syn. nov.

Croton agrarius var. *neuwiedii* Baill., Adansonia 4: 320. 1864. *Croton grandivelus* var. *neuwiedii* (Baill.) Müll. Arg., Prodr. 15(2): 631. 1866. Type: BRAZIL. "Province de Mato Grosso", 1833, *C. Gaudichaud-Beaupré 252* (lectotype designated here: P 00623588). Syntype: BRAZIL. *S.loc. s.d.*, *s.col.* (Wied-Neuwied?) (P?, not located), syn. nov.

Croton pedersenii Ahumada, Candollea 53: 120. 1998. Type: PARAGUAY. Caaguazú: "In campo pr. flumen Capibary", IX/1898-1899, *E. Hassler 4470a* (holotype: G 00392398; isotypes: BM 000504251!, G 00392394!, G00392399!, P 00634599!), syn. nov.

Subshrub, 0.1-0.35 m tall, arising from a xylopodium, few-branched, erect or sometimes with pendent branches, latex whitish or orange, branches cylindrical, usually smooth (not striate), indument hirsute, ferruginous, yellowish or whitish, trichomes stellate-porrect with 7-13 lateral free rays in a single whorl, each ray 0.7-2 mm long, porrect ray 0.2-3 mm long, erect or slightly inclined, stipe 0.1-0.9 mm long. Leaves spiral, alternate, or subopposite below stem bifurcations and/or inflorescences, leaf blades (6-)15-90(-180) times larger than petioles, nectary glands absent; stipules reduced to 2-6 globose or ovoid sessile glands (colleters), ferruginous or yellowish, glabrous; petiole 0.5-5(-15) mm long, without glands; leaf blades 3.6-18 × 1.4-5.4 cm, narrowly elliptic, narrowly oblong, elliptic, oblanceolate, or oboval-oblanceolate, sometimes obovate or oblong, rarely lanceolate, apex acute, obtuse, shortly acuminate or less commonly rounded, base acute or sometimes obtuse, margins entire, usually with subulate, subglobose, or ovoid glands (colleters), venation brochidodromous with (7-)9-24 pairs of secondary veins prominent, or rarely impressed, on the abaxial surface, impressed on the adaxial surface, membranaceous or chartaceous, bifacial, whitish, clear-green or slightly ferruginous, abaxial surface with tomentose, hirsute, or pubescent indument of stipitate stellate-porrect trichomes with 7-11 lateral rays in a single whorl, each ray (0.6-)1-2 mm long, free, porrect ray 0.1-1.5 mm long, stipe 0.1-1.2 mm long, adaxial surface yellow-ferruginous, clear-green or dark-green, glabrous, glabrescent, pubescent or sometimes with tomentose indument of sessile or stipitate stellate-porrect trichomes with 7-12 lateral rays in a single whorl, each ray 0.5-1.8 mm long, free, porrect ray 0.3-1.5 mm long, stipe 0.5-1 mm long. Thyrses 1-19.5 cm long, terminal, or less commonly in branch bifurcations, bisexual or unisexual, pistillate thyrses glomeruliform, sessile, or sometimes stipitate, with 10-14 flowers, bisexual thyrses with 4-24 pistillate flowers densely or sparsely arranged along lower $^{1}/_{4}$-$^{1}/_{2}$ of the inflorescence axis, staminate cymules with (1-)2-3 flowers; staminate bracts 1.2-2.8 × 0.3-0.9 mm, ovate, oval-lanceolate, lanceolate, or oblong, apex acute, with 2-4 ovoid or subglobose glands (colleters) at base, external surface with sessile or shortly stipitate stellate-porrect trichomes, internally glabrous; bracteoles 0.6 × 0.2 mm, linear-lanceolate; pistillate bracts 1-2.2(-3.7) × 0.3-1.2 mm, ovate, triangular, lanceolate or narrowly

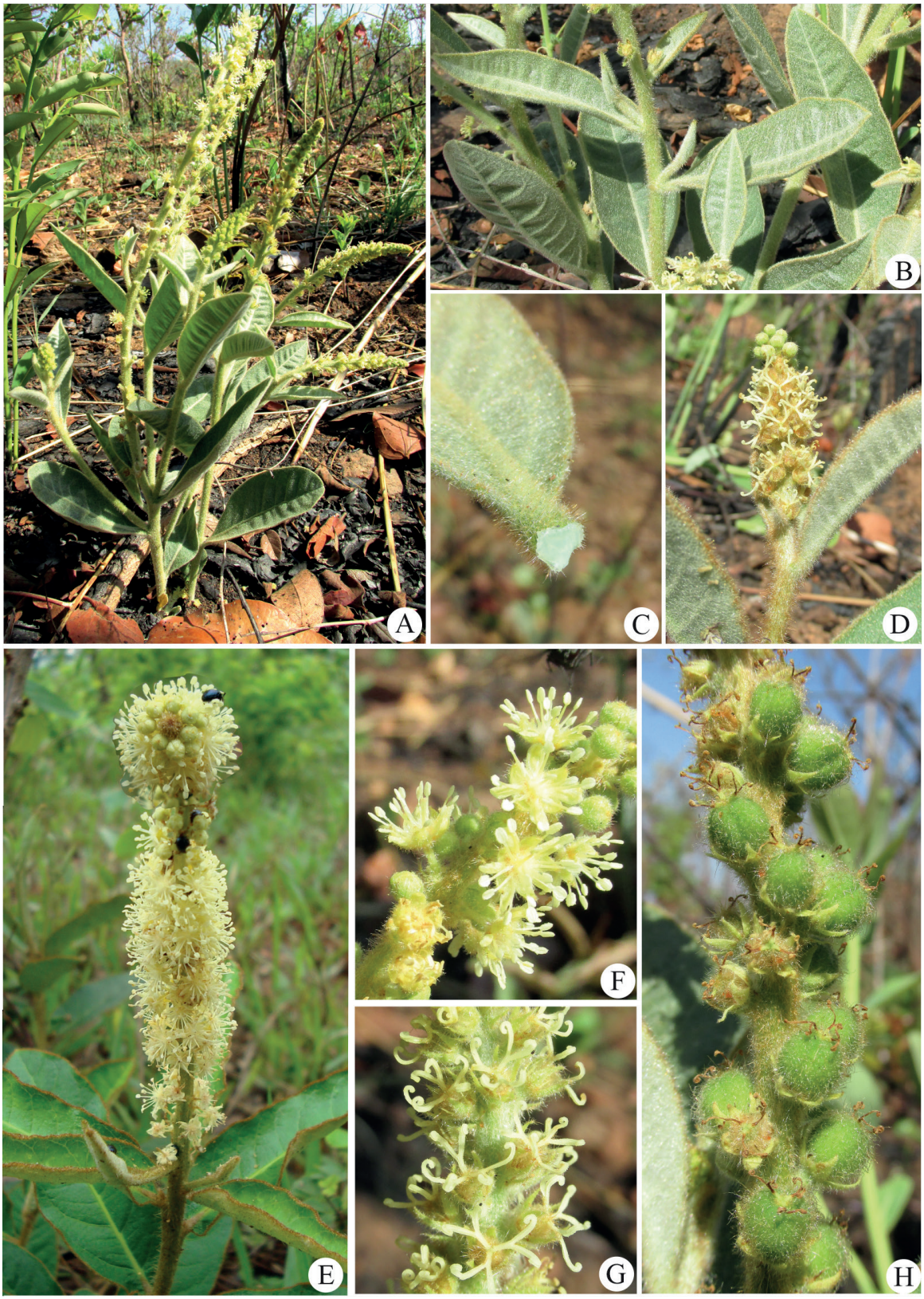

Figure 13. *Croton subvillosus* Müll. Arg.: **A.** Subshrub in "campo ralo" vegetation in the municipality of Mossâmedes, GO, *R.C. Sodré 3495*. **B.** Detail of a branch, showing spiral alternate leaves with inconspicuous petioles, whitish indument, and secondary veins prominent on the abaxial surface. **C.** Whitish latex. **D.** Young inflorescences with *ca.* 15 pistillate flowers towards base, and some staminate buds towards the distal end. **E.** Staminate unisexual inflorescence. **F.** Staminate flowers. **G.** Pistillate flowers. **H.** Pistillate flowers and capsules. Photographs by R.C. Sodré from *R.C. Sodré* et al. *3495*.

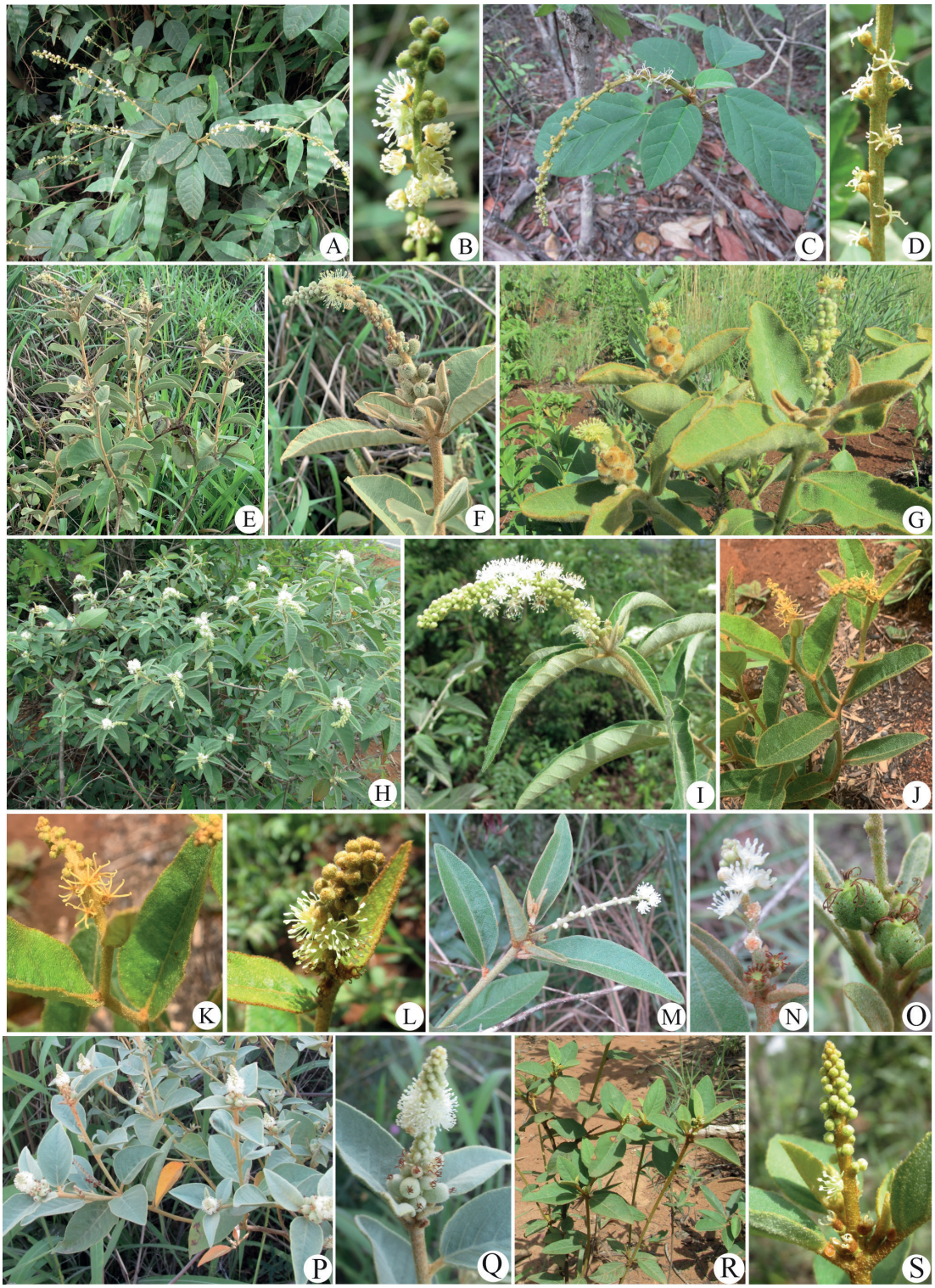

Figure 14. Species of *Croton* section *Adenophylli* that have been confused with *Croton campestris*. **A-D.** *C. echioides*. **A.** Habit. **B.** Detail of inflorescence, showing staminate flowers and buds. **C.** Branchlet with inflorescence, showing pistillate flowers and staminate buds. **D.** Detail of the inflorescence, showing pistillate flowers. **E-F.** *C. fulvus*. **E.** Fertile branchlet. **F.** Branchlet with inflorescence showing capsules and staminate flowers. **G.** Fertile branches of *C. grandivelus*. **H-I.** *C. heliotropiifolius*. **H.** Habit. **I.** Branchlet with inflorescence, showing staminate flowers. **J-L.** *C. intercedens*. **J.** Fertile branch. **K.** Branchlet with inflorescence, showing pistillate flowers and staminate buds. **L.** Branchlet, showing staminate flowers and buds. **M-O.** *C. lanatus*. **M.** Branchlet with inflorescence. **N.** Inflorescence showing pistillate and staminate flowers. **O.** Fruits. **P-Q.** *C. subacutus*. **P.** Fertile branches. **Q.** Branchlet with inflorescence, showing young fruits and staminate flowers. **R-S.** *C. subferrugineus*. **R.** Fertile branches. **S.** Inflorescence showing pistillate flowers, staminate flowers, and buds. Photographs by R.C. Sodré.

triangular, apex acute, globose glands at the base, sometimes with two short lobes, externally with hirsute indument of stellate-porrect trichomes with 6-7 lateral rays 0.7-1.5 mm long, porrect ray 1.2-1.5 mm long, sessile or subsessile, stipe up to 0.1 mm long, or covered by simple trichomes the same length as the rays, internally glabrous. Staminate flowers 5.5-8.5 mm long, pedicel 2.3-4.7 mm long with sessile stellate-porrect trichomes with 6-7 lateral rays, sparse or slightly dense, sometimes glabrous, calyx 5-partite, united along lower $^1/_8$-$^1/_{12}$ of their length, prefloration slightly imbricate, lobes 1.2-2.9 × 0.7-1.7 mm, ovate, sometimes largely ovate, oval-lanceolate or elliptic, apex obtuse, rarely acute, slightly unequal, internally glabrous, externally with stellate-porrect trichomes with (6)7-9(-13) lateral rays in a single whorl, each ray 0.4-0.9 mm long, porrect ray 0.7-1.1 mm long, stipe 0.05 mm long; petals 2.8-4 × 0.8-1.5 mm, oblanceolate or oboval-oblanceolate, apex acute or obtuse, suprabasal reticulate perfect actinodromous venation, villous basally along $^1/_5$-$^2/_5$ of its length; stamens 15-16(-20), (2.8-)4-5 mm long, filaments (2-)3.2-4 mm long, villous or glabrescent basally, anthers 0.7-1 × 0.6-0.8 mm, oblongoid, largely ellipsoidal, orbicular or ellipsoidal, disk 5-segmented, segments transversally oblong, yellowish. Pistillate flowers 4-7 mm long, pedicel 0.6-1.7 mm long, glabrous or densely indumented; sepals 5, 1.3-4.3 × 0.3-1.5 mm, triangular, narrowly triangular or ovate, sometimes lanceolate, equal or slightly unequal, apex acute, yellowish or whitish, venation hyphodromous, internally glabrous or villous basally, externally hirsute, sparse or slightly dense, hyaline or ferruginous, stellate-porrect trichomes, sessile or subsessile (stipe up to 0.05 mm long), 7-9 lateral rays 0.4-0.8 mm long, porrect ray 0.7-1.4 mm long, or with simple or 2-4-radiate trichomes mainly along the margin; petals absent, or when present, 0.6-3.3 × 0.2-0.6 mm, linear, lanceolate or narrowly triangular, sometimes ovate or triangular, apex acute or acuminate, whitish, villous basally along the margins, rarely with stellate-porrect trichomes externally; ovary 1.2-2.2 × 1.3-1.8 mm, subglobose, indument hirsute or ferruginous with stellate-porrect trichomes with 6-12 lateral rays, each ray 0.8-2(-2.5) mm long, porrect ray 1-3 mm long, stipe 0.2-0.25 mm long, styles 2-partite, united along lower $^1/_7$-$^1/_6$ of their length, 5.5-7 mm long, with stellate-porrect trichomes along up to $^1/_3$-$^1/_2$ of their length, involute at the apex, disk 5-segmented, subentire, ring-shaped or sometimes 5-lobed, segments or lobes transversally oblong, yellowish or orange. Capsules 7-8 mm long, subglobose, with carpels visually delimited, greenish, pedicel 1.5-3 mm long; seeds 5-6 × 2.8-3.5 mm, oblongoid or ellipsoidal, grayish, smooth and with minutely foveolate surfaces, caruncle 2-2.5 mm width, hat-shaped, sessile, whitish or yellowish.

Distribution and habitat - *Croton subvillosus* was cited as endemic to Brazil (Goiás and Tocantins) by Sodré *et al.* (2017), however, its distribution is expanded here to Paraguay, Bolivia, and also to other Brazilian states (Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, and the Federal District) (Fig. 8). It grows in *campos limpos*, *campos sujos*, *cerrados ralos*, *cerrados típicos,* or *cerrados densos* vegetation on sandy, gravelly, or hydromorphic soils, between 353 and 1447 meters a.s.l.

Phenology - Flowering from August to December, and fruiting from September to February.

Remarks - Sodré *et al.* (2017), when considering the species of the Crotoneae tribe for the Chapada dos Veadeiros region, Goiás State, separately described and illustrated *C. subvillosus* and *C. campestris*, and differentiated them by trichome densities on the adaxial surfaces of their leaf blades, the presence of trichomes on the pedicels of the flowers, and style orientation. After studying larger numbers of collections of those two putative species, as well as field observations, we found that the differences pointed out by Sodré *et al.* (2017) were not consistent in terms of their differentiation, as they show variability among individuals in the same population.

As such, the specimens identified as *C. campestris* by those authors, by Sodré *et al.* (2014), and by Secco *et al.* (2018), are *C. subvillosus*, which is different from *C. campestris* in terms of its herbaceous or subshrub habit up to 50 cm in height, with little branching, with leaf trichomes with lateral rays 1-2 mm long, short petiolate leaves ((petioles (6-) 12-50 times smaller than the leaf blades)), leaf blades with an acute or short attenuate base, 7-15 pairs of secondary veins, axes of the thyrses and external surfaces of the floral calyxes of both sexes with a hirsute indument, as well as the pedicels of staminate flowers 2.3-4.7 mm long. *Croton campestris*, however, is characterized by a subshrub or shrub habit up to 2 meters tall, densely branched, lateral rays of leaf trichomes 0.35-1 mm long, petiole only 3.8-10 (-13) times smaller than the leaf blade, the leaf blades with obtuse bases, slightly cordate, or less commonly acute, 5-10 pairs of secondary veins, the axes of the thyrsus and external surfaces of the calyxes of the flowers of both sexes tomentose, and pedicels of the staminate flower up to 2 mm long.

Croton occidentalis was synonymized under *C. grandivelus* by Caruzo & Cordeiro (2007), although the latter differs by having stipules 2-8 mm long, narrowly lanceolate with numerous glands, petioles 2-15 mm long, leaf blades 5.2-9.0 cm wide, with cordate, slightly cordate, or rarely obtuse base, with 6-10 pairs of secondary veins, staminate bracts 3.4-6.3 × 0.4-0.8 mm, and pistillate floral sepals 3-3.7 × 1.2-1.4 mm, oval-lanceolate. In *C. occidentalis*, synonymized here under *C. subvillosus*, the stipules are only glanduliform (with 5 glands) and are *ca.* 0.5 mm long, the petioles are 0.5-2 mm long, the leaf blades 1.4-5.4 cm wide, with acute, obtuse, or sometimes attenuated base, and 9-24 pairs of secondary veins, staminate bracts 1.3-1.8 × 0.3-0.7 mm, and pistillate sepals 1.3-2.7 × 0.3-0.9 mm, narrow-triangular, triangular or oval. *Croton occidentalis* and *C. subvillosus* were described in the same publication, so either one could be used as the valid species name. We chose *C. subvillosus*

because it is the most frequent name on the labels of the herborized collections of the species.

Chodat & Hassler (1905) described six taxa of *Croton occidentalis* for the flora of Paraguay: *C. occidentalis* var. *intermedius*, *C. occidentalis* var. *oblongifolius*, *C. occidentalis* var. *ovalifolius*, C. *occidentalis* var. *parvifolius*, *C. occidentalis* var. *parvifolius* f. *rupestris,* and *C. occidentalis* var. *setosus*. After analyzing the type collections of those taxa, and other specimens from the same location, we conclude that they are morphologically closest to *C. curuguatyensis* Ahumada (recently described for the Paraguayan province of Canindeyú (Ahumada 1998)) than to any specimen of *C. subvillosus;* thus we do not accept these varieties in the concept of *C. subvillosus*.

Proposed conservation status - *Croton subvillosus* has an Extent of Occurrence of 1,553,821 km^2, and so its conservation status is classified here as Least Concern.

Additional specimens examined - BOLIVIA. **Santa Cruz**: Chiquitos, Cerro Mutún, 7 km al NE de la pista de aterrizaje del campamento minero (25 km al S de Puerto Suárez), 19°11.4'S, 57°52.7'W, 730 m, 17-20/X/1994, fl., fr., *I.G. Vargas*, *R. Foster & M. Peña 3257* (F). **BRAZIL. Distrito Federal**: Brasília, Bacia do rio São Bartolomeu, quadrícula n° 141, 17/III/1980, *E.P. Heringer et al. 4054* (UFG). Gama, a esquerda do km 19 da BR-060, sentido Brasília, 15°58'28.7"S, 48°11'27.1"W, 1023 m, 28/I/2014, *R.C. Sodré et al. 1157* (UFG). **Goiás**: Alto Paraíso de Goiás, without locality, 18/IX/1977, *A. Allem & G. Vieira 1062* (UFG); Parque Nacional da Chapada dos Veadeiros, descida para as cachoeiras de 80 e 120 metros no rio Preto, 14°9'47"S, 47°50'2"W, 10/IX/1996, *R.C. Mendonça et al. 2693* (IBGE); PNCV, campo limpo, 1.8 km a partir do rio Preto em direção ao Morro Peito de Moça, 03/VIII/2013, fl., *M.J. Silva et al. 5230* (UFG); cerca de 5 km do morro da Baleia, na estrada que leva ao rio Preto, 13/VII/2013, fl., *M.J. Silva, A.O. Souza & P.H.B. Santos 5122* (UFG), *5124* (UFG), *5128* (UFG), *5129* (UFG); estrada que leva ao Vale da Lua, 14°10'17.9"S, 47°46'48.2"W, 1020 m a. s. l., 15/X/2010, *M.J. Silva et al. 3053* (UFG); GO-118, km 153, entre São João d'Aliança e Alto Paraíso de Goiás, 14°14'3.8"S, 47°29'12.2"W, 10/X/2013, fl., *R.C. Sodré et al. 872* (UFG), *874* (UFG), *875* (UFG), *876* (UFG); GO 118, km 155, São João d'Aliança/ Alto Paraíso de Goiás, 14°12'49.4"S, 47°29'15.9"W, 1122 m a. s. l., 10/X/2013, *M.J. Silva et al. 5425* (UFG), *5437* (UFG); GO 239, entre o povoado de São Jorge e Colinas do Sul, 13/XII/2013, fr., *R.C. Sodré et al. 1062* (UFG), *1063* (UFG), *1064* (UFG); a 1.2 km da entrada para o Vale da Lua, 12/X/2013, fl., *R.C. Sodré et al. 908* (UFG), *911* (UFG); cerca de 30 km a esquerda da GO 118 (sentido São João d'Aliança a Alto Paraíso de Goiás), na estrada que leva a catarata do rio dos Couros, 14°17'23.6"S, 47°42'33.2"W, 1049 m a. s. l., 31/X/2014, *R.C. Sodré et al. 1492* (UFG); *ib*., 14°17'35"S, 47°42'32"W, 1028 m a. s. l., 31/X/2014, *R.C. Sodré et al. 1502* (UFG); *ib*., 02/I/2015, *R.C. Sodré, M.J. Silva & C.H.G. Machado-Filho 1580* (UFG); imediações da fazenda Campo Seco, cerca de 15 km após a vila São Jorge, em direção a Colinas do Sul, 14°13'39.9"S, 47°53'41.2"W, 700 m a. s. l., 22/II/2014, *R.C. Sodré*, *T.M.S. Melo & M.J. Silva 1247* (UFG); *ib*., 14°13'37.5"S, 47°53'39.3"W, 705 m a. s. l., 14/XII/2014, *R.C. Sodré et al. 1561* (UFG), *1562* (UFG); a esquerda do km 131 da GO-118, sentido São João d'Aliança a Alto Paraíso de Goiás, próximo à divisa dos municípios, 14°25'20,7"S, 47°30'35"W, 1000 m, 20.II.2014, *R.C. Sodré*, *T.M.S. Melo & M.J. Silva 1215* (UFG); Parque Nacional da Chapada dos Veadeiros, trilha para os Saltos, a 300 metros da bifurcação para as corredeiras do rio Preto, 14°9'42.3"S, 47°50'12.6"W, 863 m a. s. l., 31/X/2014, *R.C. Sodré et al. 1474* (UFG); *ca.* 1 km após a casa dos pesquisadores, 14°8'27.4"S, 47°46'2.8"W, 1115 m a. s. l., 04/I/2015, *R.C. Sodré*, *M.J. Silva & C.H.G. Machado-Filho 1631* (UFG); estrada Alto Paraíso-Teresina, 11/X/1979, *E.P. Heringer et al. 2490* (IBGE). Caiapônia, Serra do Caiapó, *ca.* 33 km S of Caiapônia on road to Jataí, 17°12'S, 51°47'W, 800-1000 m a. s. l., 20/X/1964, fl., *H.S. Irwin & T.R. Soderstrom 7097* (NY, K); *ca.* 45 km S of Caiapônia on road to Jataí, 17°12'S, 51°47'W, 800-1000 m alt., 22/X/1964, fl., *H.S. Irwin & T.R. Soderstrom 7205* (NY). Caldas Novas, Parque Estadual da Serra de Caldas Novas, 17°43'41"S, 49°7'54"W, 766 m a. s. l., *T.M. Moura et al. 494* (CEN). Cavalcante, PNCV, *ca.* 23 km a norte de Alto Paraíso de Goiás, cruzeiro, 13°56'39"S, 47°29'38"W, 1410 m a. s. l., 12/XI/1996, *M.L. Fonseca*, *A.J. Santos & F.C.A. Oliveira 1315* (IBGE); *ib.*, *M. Aparecida da Silva & A.J.V. dos Santos 3234* (IBGE); RPPN Serra do Tombador, 13°38'4"S, 47°49'6"W, 857 m a. s. l., 29/X/2011, *A.R.O. Ribeiro et al. 283* (UB); reserva da fazenda Gavião, 14°8'37"S, 47°52'45.5"W, 01/XI/2013, fl., *R.C. Sodré*, *M.J. Silva & P.H.B. Santos 947* (UFG), *948* (UFG), *949* (UFG), *958* (UFG), *960* (UFG); final do Parque, sentido Teresina de Goiás, *ca.* 150 m a partir da estrada, 13°54'54.4"S, 47°25'40.4"W, 1447 m a. s. l., 20/XI/2015, fl., *D.O. Diniz-Neres et al. 674* (UFG). Colinas do Sul, estrada de acesso a fazenda Gavião, cerca de 3 km a direita da GO 239, sentido Alto Paraíso de Goiás a Colinas do Sul, 01/XI/2013, fl., fr., *R.C. Sodré*, *M.J. Silva & P.H.B. Santos 925* (UFG), *930* (UFG), *934* (UFG); *ibd.*, 13/ XII/2013, fr., *R.C. Sodré et al. 1054* (UFG); estrada para a fazenda Gavião, cerca de 4 km da GO 239, 14°10'1"S, 47°58'8.5"W, 650 m, 29/I/2014, *R.C. Sodré et al. 1199* (UFG). Goiânia, a esquerda da estrada de Goiânia para Guapó, 10 km de Goiânia, 07/VIII/1968, fl., *J.A. Rizzo & A. Barbosa 1945* (UFG); a esquerda da rodovia Goiânia para Trindade no Km 12, 06/IX/1968, fl., fr., *J.A. Rizzo & A. Barbosa 2221* (UFG). Goiandira, Fazenda do Chapéu, 18°0'43-54"S, 48°8'3-15"W, 19/XI/2004, fl., *J.A. Rizzo et al. 12512* (UFG). Goianira, a 2 km da margem esquerda do Rio Meia Ponte, na fazenda Louzandira, 17/X/1970, fl., *J.A. Rizzo & A. Barbosa 4839* (UFG). Jataí, estrada de Jataí para Serranópolis, a 20 km do Ribeirão Ariranha, 18/X/1972, fl., *J.A. Rizzo 8459* (UFG); fazenda em direção a Caiapônia, 17°32'S, 51°50'W, 789 m a. s. l., 3/XI/2012, fl., fr., *J.P. Santos 801* (UFG). Mineiros, Parque Nacional das Emas, Jacuba, 17/X/1990, fl., *H.D.*

Ferreira et al. 2271 (UFG). Morrinhos, rodovia BR-153, km 146, 30/IX/1975, fl., *G. Hatschbach & R. Kummrow 37286*. Mossâmedes, Serra Dourada, 1º transecto, na cabeceira do rio Índio Grande, 17/VI/1994, fr., *J.A. Rizzo et al. 11495* (UFG); 2º transecto, da Reserva Biológica até os córregos Cafundó e Piçarrão, 18/X/1994, fl., *J.A. Rizzo et al. 11899* (UFG); *ib*., fl., fr., *J.A. Rizzo et al. 11939* (UFG); área próximo ao alojamento, 26/X/1997, fl., *V.L. Gomes-Klein et al. 3295* (UFG); Parque Estadual da Serra Dourada - Reserva Biológica Prof. José Ângelo Rizzo, proximidades do alojamento, 30/X/2010, fl., *A.M. Teles et al. 949* (UFG); *ib*., encosta de morro, na margem direita da estrada que leva à Reserva Biológica Prof. José Ângelo Rizzo, 16°5'30"S, 50°11'8"W, 800 m a. s. l., 19/X/2019, fl, *R.C. Sodré 3495* (BOTU). Niquelândia, estrada para o DNPM, Placa do IBAMA, 14°29'46"S, 48°27'0"W, 830 m a. s. l., 19/X/1996, *R. Marquete et al. 2679* (IBGE); *ib*., *A.F. Vaz et al. 1109* (IBGE), *1112* (IBGE); estrada de chão em direção a reserva do IBAMA, *ca*. 5 km de Niquelândia, 14°29'46"S, 48°27'0"W, 635 m a. s. l., 19/X/1996, *M.L. Fonseca et al. 1236* (IBGE); fazenda Engenho, *ca*. 11 km de Niquelândia/Dois Irmãos, cabeceira do rio Traíras, 14°40'28"S, 48°25'25"W, 680 m a. s. l., 14/VIII/1997, *M.L. Fonseca et al. 1549* (IBGE); Companhia de Níquel Tocantins-CNT, estrada à esquerda da mina de níquel, *ca*. 2 km da entrada, 14°20'37"S, 48°23'57"W, 1040 m a. s. l., 01/X/1997, *R.C. Mendonça et al. 3099* (IBGE), *ibd.*, *M.L. Fonseca et al. 1578* (IBGE); próximo ao povoado de Macedo, 14°23'48"S, 48°25'59"W, 17/IX/1996, *M. Aparecida da Silva & C.C.S. Ferreira 3091* (IBGE); morro do Cristo, 14°27'8"S, 48°27'26"W, 19/IX/1996, *M.L. Fonseca et al. 1195* (IBGE). Sem município, Parque Nacional das Emas - Área 1A6, 20/X/1989, fl., *H.D. Ferreira 2272* (UFG). **Maranhão**: Parque Nacional Chapada das Mesas, Morro do Arcançu, Gleba II, 7°18'41"S, 46°52'41"W, 353 m a. s. l., 22/X/2015, fl., *A.C. Sevilha et al. 5552* (CEN). **Mato Grosso**: Chapada dos Guimarães, Sta. Anna da Chapada, 20/VII/1902, fl., *A. Robert 398b* (K); *ib*., 1/VIII/1902, fl., *A. Robert 436b* (K); behind Colegio de Buriti, 720 m a. s. l., 12/X/1973, fl., fr., *G.T. Prance*, *E. Lleras & D.F. Coelho 18862* (NY, UFMT); 15°25'S, 55°50'W, 650 m a. s. l., 15/IX/1991, fl., *M. Schessi 5283* (UFMT); arredores, 20/X/1995, fl., *G. Hatschbach et al. 63613* (MBM); estrada Nova Brasilândia-Campo Verde, *ca*. 20 km de Nova Brasilândia, 15°1'S, 55°14'W, 08/X/1997, fl., *V.C. Souza et al. 20359* (ESA, UFMT); Véu de Noiva, 04/X/2005, fl., *O.S. Nasser 499* (UFMT). Cuiabá, Burity N.E. of Cuyabá, 685 m a. s. l., IX/1927, fl., *C.L. Collenette 180* (K). Nova Xavantina, *ca*. 6 km S. of Xavantina (R & A transect), 14°38'S, 52°14'W, fl., 11/X/1967, *G. Argent et al. 6697* (K, NY). Ribeirão Cascalheira, by roadside just S. of base camp, 12°49'S, 51°46'W, 22/IX/1968, fl., *R.M. Harley 10184* (K); *ca*. 12 km south south west of base camp., 12°49'S, 51°46'W, 5/X/1968, fl., *R.M. Harley 10483* (K, NY, P). **Mato Grosso do Sul**: Amambai, Lagoa Bonita, 11/XII/1982, fl., *G. Hatschbach 45893* (MBM); rodovia para Coronel Sapucaia, 14/X/1984, fl., *G. Hatschbach & R. Kummrow 48403* (MBM), *48407* (MBM); Reserva indígena, 21/X/1987, fl., fr., *G. Hatschbach & J.M. Silva 51525* (MBM). Bandeirantes, rodovia BR-163, 11/XI/1973, fl., fr., *G. Hatschbach & C. Koczicki 33042* (MBM). Campo Grande, Fazenda das Moças, 09/IX/1936, fl., *W. Archer & A. Gehrt 145 (*US). Nioaque, Rod. BR-060, 10-15 km S de Nioaque, 15/X/1995, fl., fr., *G. Hatschbach, M. Hatschbach & E. Barbosa 63386* (MBM). Rio Pardo, 1824-1829, fl., *L. Riedel s.n.* (NY 02431398). **Minas Gerais**: Coromandel, km 6,6 após córrego bonito de baixo-Bocaina 988, 04/XI/1988, fl., *M. Brandão 15688* (PAMG). Diamantina, entre Diamantina et A. Dattas, 18/IV/1892, fl., *A. Glaziou 19828* (P). Sem localidade, IX/1892, fl., *A. Glaziou 19828* (K); Curvelo, 15 km ao sul da cidade na estrada BR-135 para Paraopeba, 18°53'S, 44°28'W, 11/X/1998, fl., *R.M. Harley et al. 24827* (MBM). **Paraná**: Campo Mourão, 11/XII/1960, fl., *G. Hatschbach 7642* (MBM); Aeroporto, 20/X/1973, fl., *G. Hatschbach 32920* (MBM); 17/X/1966, fl., *J. Lindeman & H. Haas 2743* (MBM) 23/VIII/1998, fl., *Rosana s.n.* (UFG 29369); 11/XI/2003, fl., fr., *A.E. Bianek 114* (MBM). **Tocantins**: Arraias, 5-10 km a oeste na rodovia para Paranã, 10/XI/1991, fl., fr., *G. Hatschbach & M. Hatschbach 56009* (MBM). Dianópolis, 11°42'32"S, 46°20'10"W, 603 m a. s. l., 30/IX/2003, fl., *T.B. Cavalcanti et al. 3430* (CEN, UFG). **PARAGUAY. Amambay**: Pedro Juan Caballero, arredores, 11/XI/2006, fr., *J.M. Silva & E. Barbosa 5211* (MBM).

Identification key to ***Croton campestris*** *and species with which it has previously been confused*

1. Leaves with nectary glands at the apex of the petioles, or at the base of the blades.
   2. Nectary glands stipitate; petiole 1-4 cm long; thyrses lax, 5-15 cm long; staminate cymules with 3-5 flowers ..... *C. echioides*
   2'. Nectary glands sessile; petiole 0.1-0.8 cm long; thyrses congested, 1.5-4 cm long; staminate cymules with 1-3 flowers.
      3. Nectary glands basilaminar; leaf margin entire; stamens 15-20; styles 2-4-fid ..... *C. lanatus*
      3'. Nectary glands acropetiolar; leaf margin subentire or serrulate; stamens 10 or 11; styles 2-fid ..... *C. subferrugineus*
1'. Leaves without nectary glands.
   4. Subshrub, 0.2-0.6 m tall, or sometimes up to 1 m tall, little branched; leaves subsessile, with blades 15-90 times longer than petioles.

5. Stipules 2-8 mm long, with 20 or more colleters at their base; staminate bracts 3.5-6.3 mm long, narrowly lanceolate; capsule 7-9 mm long, with long stipitate trichomes ..... *C. grandivelus*

5'. Stipules up to 1 mm long, with 2-6 colleters at their base; staminate bracts 0.7-2.7 × 0.35-0.8 mm, ovate or lanceolate; capsules 5.5-6.5 × 6-6.5 mm, with sessile or shortly stipitate trichomes.

6. Foliar trichomes with short lateral rays *ca.* 0.3-0.7 mm long; thyrses with sparse flowers; staminate flowers 4-5.5 mm long, subsessile, pedicel 0.6-1.6 mm long ..... *C. intercedens*

6'. Foliar trichomes with long lateral rays (0.5-)1-2 mm long; thyrses usually with dense flowers; staminate flowers 5.5-8.5 mm long, with pedicel 2.3-4.7 mm long ..... *C. subvillosus*

4'. Subshrub or shrub, 1-2.5 m tall, densely branched; leaves with conspicuous petioles, blades 4-12 times longer than petioles.

7. Branches and abaxial surface of leaves with multiradiate trichomes.

8. Branches with floccose indument; adaxial surface of leaf blades covered with multiradiate trichomes, thyrses with (1-)2-10 solitary pistillate flowers sparsely arranged; endemic to *cerrado rupestre* in northern Minas Gerais, Brazil ..... *C. hatschbachii*

8'. Branches usually with hirsute, hirtellous or tomentose indument, rarely floccose; adaxial surface of leaf blades covered with stellate-porrect or fasciculate trichomes, thyrses with 12-20 pistillate flowers densely arranged; widely distributed in the Caatinga, in northeastern Brazil, and in dry forests of Peru, Venezuela and Colombia ..... *C. heliotropiifolius*

7'. Branches and abaxial surface of leaves with stellate-porrect or stellate-rotate trichomes.

9. Branches, leaves, axes of the thyrses, sepals of the pistillate flowers and ovary with stellate rotate trichomes with 13-20 lateral rays united for $^1/_{10}$ of their length, and the central ray usually vestigial; leaf blades usually orbicular, ovate or largely elliptic; endemic to rocky field in Bahia state, Caatinga Domain ..... *C. stellatorotatus*

9'. Branches, leaves, axes of the thyrses, sepals of the pistillate flowers and ovary with stellate-porrect trichomes with 6-10 free lateral rays; leaf blades usually elliptic; species distributed mainly in Brazil (except *Croton fulvus*, which also occurs in Bolivia, Paraguay and Argentina), growing in several vegetations of the Cerrado Domain.

10. Staminate bracts 0.5-1 mm long; staminate flowers 2.5-4 mm long, stamens 1.8-2.5 mm long, styles 1.5-2 mm long, capsules oblong with inconspicuous locule delimitations and shortly tomentose indument ..... *C. subacutus*

10'. Staminate bracts 1.2-5 mm long; staminate flowers 4.2-7 mm long; stamens 2.5-5 mm long; styles 2.5-5 mm long, capsules oblong or globose, with conspicuous locule delimitations and dense tomentose or hirsute indument.

11. Branches and axes of the thyrses striate; leaf blades 10-12 times longer than petioles, with obtuse and mucronate apex; staminate bracts 3-5 mm long ..... *C. fulvus*

11'. Branches and axes of the thyrses smooth; leaf blades 4-8(-10) times longer than petioles, with acute or obtuse apex, not mucronate; staminate bracts 1.2-2.3 mm long ..... *C. campestris*

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