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Research article

Croton restingae sp. nov. (Euphorbiaceae), a new species of section *Adenophylli* from the state of Rio de Janeiro, Brazil, and its phylogenetic relationships

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Abstract. We describe and illustrate *Croton restingae* Sodré & Riina sp. nov., a new species endemic to a restricted area in the state of Rio de Janeiro, Brazil, characterized by a particular type of vegetation of the Atlantic Forest known as restinga. The new species belongs to *Croton* sect. *Adenophylli* subsect. *Laceratoglandulosus*, which is supported by morphology and a phylogenetic analysis based on nrDNA ITS sequence data. *Croton restingae* is most closely related to *C. echioides* and *C. laceratoglandulosus*, also in subsect. *Laceratoglandulosus*, with which it shares the fruit columella with three non-inflated, flat or slightly ascending apical appendages. *Croton restingae* differs from them by its sessile or shortly stipitate leaf nectaries, revolute pistillate sepals, styles distally 2-fid and basally united forming a column, and larger capsules (7.5–8 × 8.5–9.3 mm). *Croton restingae*'s habitat, conservation status, phenology, morphology and phylogenetic relationships are discussed, and a map with its geographic distribution is also included.

Keywords. Atlantic Forest, Crotoneae, Neotropics, restinga, taxonomy.

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Introduction

Croton section *Adenophylli* Griseb. (~200 spp.) is the most species-rich lineage within the giant genus *Croton* L. (~1200 spp.). Species of this section are predominantly distributed in semiarid environments

and secondary vegetation of the Americas (van Ee *et al.* 2011; Sodré & Silva 2020). The section includes subshrubs, shrubs, and less commonly small trees, usually with leaf nectaries at the apex of the petiole or base of the blade, sessile or shortly pedicellate pistillate flowers, and fruit columella usually with three inflated and ascending apical appendages. The latter is the main character used to distinguish members of this section from the rest of the species in the genus (Riina *et al.* 2009; Sodré & Silva 2020; van Ee & Berry 2021). Section *Adenophylli* is also recognized as one of the most taxonomically complex groups of *Croton* given its high number of species and low morphological differentiation. Recently, van Ee & Berry (2021) proposed a preliminary classification based on molecular data for this section, recognizing six subsections (*C.* subsections *Adenophylli* (Griseb.) B.W.van Ee & P.E.Berry, *Caribaeus* B.W.van Ee & P.E.Berry, *Laceratoglandulosus* B.W.van Ee & P.E.Berry, *Meridionalis* B.W.van Ee & P.E.Berry, *Pungentes* Croizat and *Velamea* (Baill.) B.W.van Ee & P.E.Berry). In addition, the taxonomic knowledge of section *Adenophylli* has been improved with studies that focused on species with poorly resolved taxonomy and/or species that are difficult to identify, including *C. grandivelus* Baill. (Sodré & Silva 2020), *C. flavens* L. (van Ee & Berry 2021) and *C. campestris* A.St.-Hil. (Sodré *et al.* 2022). These studies resulted in many synonymizations, lectotypifications and descriptions of new species.

Ongoing taxonomic and phylogenetic studies on *Croton* sect. *Adenophylli* (Sodré 2022) have so far recorded 23 species in Brazil, distributed in almost all phytogeographical domains of the country. Due to its preferentially shrubby or subshrubby habit, little diversity of *C.* sect. *Adenophylli* would be expected for the Amazon and the Atlantic Forest Domains, where the arborescent growth form predominates (Santos *et al.* 2017). However, a particular type of vegetation of the Atlantic Forest Domain known as 'restinga', which occurs in sandy soils of the Brazilian coastal plain zone (Araújo 1992), has been recognized as a favorable habitat for many shrub and herbaceous lineages of *Croton* (Sodré *et al.* 2019). We came across collections from the restinga of the state of Rio de Janeiro that could not be attributed to any of the known species of *Croton*. *Croton restingae* Sodré & Riina sp. nov. is here described and illustrated, and included in a molecular phylogenetic analysis based on nrDNA ITS sequences to determine its phylogenetic position within the genus.

Material and methods

Croton restingae Sodré & Riina sp. nov. was established and described based mainly on morphological evidence obtained from eleven specimens from the herbaria ASE, BHCB, R, RB, SLUI and SP, abbreviations following Thiers (2022, continuously updated), but also integrating geographic, ecological and molecular data. Terminology about secretory structures follow recent anatomical works on *Croton* lineages by Vitarelli *et al.* (2015) and Feio *et al.* (2016, 2018). The species distribution map was made using the QGIS Geographic Information System software (ver. 3.12 – QGIS.org) with geographic coordinates contained in the labels of the specimens listed below. For those without georeferencing data, we used the coordinates (centroids) of the municipality where the specimens were collected. This same dataset of geographic coordinates was used to estimate the species' Extent of Occurrence (EOO) through GeoCAT (Bachman *et al.* 2011) and determine its preliminary conservation status according to IUCN (2012).

We included a newly generated ITS sequence of the new species in a molecular dataset with 38 species of *Croton*: 27 in section *Adenophylli*, five in section *Cyclostigma* Griseb., and three (*C. tetradenius* Baill., *C. pulegiodorus* Baill. and *C. chimboracensis* P.E.Berry & Riina) with uncertain sectional placement, but frequently allied to section *Adenophylli* in previous studies (Riina *et al.* 2021; van Ee & Berry 2021). As outgroups within *Croton*, we included *C. cupreatus* Croizat, *C. argenteus* L. and *C. sampatik* Müll.Arg. The sample of *Croton restingae* Sodré & Riina sp. nov. used for DNA was taken from an herbarium collection (Table 1). All other sequences were obtained from previous studies through GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Voucher information and GenBank accession numbers are listed in Table 1. For the newly generated sequence, DNA extraction, PCR amplification, sequencing and chromatogram editing followed the procedures in Masa-Iranzo *et al.* (2021). Sequence alignment was performed using the software MAFFT available online (Katoh *et. al.* 2017) with subsequent minor manual adjustments.

Table 1. List of species of *Croton* L. used in the phylogenetic analysis with their respective voucher information, locality, and Genbank accessions.

Taxon	Locality	Voucher	Genbank accession
C. abutiloides Kunth	Tunguragua, Ecuador	*Riina 1391* (WIS)	EU586903
C. adenophyllus Spreng.	St. Andrew, Jamaica	*van Ee 770* (A)	EU497728
C. adipatus Kunth	Bagua Grande, Ecuador	*Riina 1468* (QCNE)	KP764612
C. adspersus Benth.	Michoacán, Mexico	*Steinmann 1680* (WIS)	EF421767
C. alchorneicarpus Croizat	São Paulo, Brazil	*Caruzo 71* (SP)	HM044788
C. alnifolius Lam.	Trujillo, Peru	*Mostacero 1459* (MO)	KP764608
C. argenteus L.	Guanacaste, Costa Rica	*van Ee 297* (WIS)	EU478094
C. bonplandianus Baill.	Santa Cruz, Bolivia	*Killeen 4272* (MO)	AY971185
C. caboensis Croizat	Baja California Sur, Mexico	*Carter 4849* (WIS)	EU477897
C. campestris A.St.-Hil.	Minas Gerais, Brazil	*Sodré 3438* (BOTU)	OQ756123
C. celtidifolius Baill.	São Paulo, Brazil	*Caruzo 32* (SP)	EU586920
C. chilensis Müll.Arg.	Chile	*Quezada 313* (M)	EU586905
C. chimboracensis P.E.Berry & Riina	Chimborazo, Ecuador	*Berry 7618* (WIS)	AY971204
C. cupreatus Croizat	Pichincha, Ecuador	*Riina 1408* (WIS)	EU586919
C. curiosus Croizat	Argentina	*Zuloaga 8438* (SI)	EU586906
C. discolor Willd.	Puerto Rico	*van Ee 547* (WIS)	EF421774
C. disjunctus V.W.Steinm.	Chihuahua, Mexico	*Wilson 96213* (WIS)	EU477903
C. echioides Baill.	Bahia, Brazil	*Sodré 3314* (UFG)	OQ756122
C. flavens L.	Puerto Rico	*van Ee 540* (WIS)	EU477905
C. fragilis Kunth	Sucre, Venezuela	*Riina 1295* (VEN)	MW263128
C. francoanus Müll.Arg.	Oaxaca, Mexico	*Torres 10048* (DAV)	EU477914
C. fruticulosus Torr.	Texas, USA	*van Ee 338* (WIS)	EU477916
C. gracilipes Baill.	Bolivia	*Nee 47412* (NY)	EU586909
C. heliotropiifolius Kunth	Bolívar, Venezuela	*Berry 5542* (MO)	AY971195
C. hibiscifolius Kunth ex Spreng.	Ecuador	*Riina 1413* (WIS)	EU586925
C. laceratoglandulosus Caruzo & Cordeiro	Santa Cruz, Bolivia	*Wood & Mamani 14095* (USZ)	DQ836744
C. lachnostachyus Baill.	Argentina	*Zuloaga 8600* (SI)	EU586912
C. magdalenae Millsp.	Baja California Sur, Mexico	*Carter 3886* (WIS)	EU477936
C. menthodorus Benth.	Imbabura, Ecuador	*Riina 1412* (WIS)	KP764621
C. piluliferus Rusby	Bolivia	*Riina 1500* (WIS)	EU586932
C. pulegiodorus Baill.		*Carneiro-Torres 726* (HUEFS)	MW678656
C. pungens Jacq.	Aragua, Venezuela	*Riina 1272* (WIS)	AY971241
C. restingae Sodré &Riina sp. nov.	Arraial do Cabo, Rio de Janeiro, Brazil	*Vasconcelos s.n.* (BHCB)	OQ756127
C. ruizianus Müll.Arg.	Peru	*Riina 1487* (WIS)	EU586910
C. sampatik Müll.Arg.	Pasco, Peru	*Riina 1447* (WIS)	EF421792
C. subvillosus Müll.Arg.	Goiás, Brazil	*Sodré 3422* (BOTU)	OQ756125
C. tetradenius Baill.	Bahia, Brazil	*Carneiro-Torres 381* (HUEFS)	MW678657
C. urucurana Baill.	Minas Gerais, Brazil	*Riina 1317* (WIS)	EU586937

The data matrix was analyzed using Bayesian inference (BI) under an evolutionary model (SYM+G), which was selected in JModelTest ver. 2.1.5 (Darriba *et al.* 2012) based on the Akaike information criterion (Akaike 1973). The phylogenetic analysis was conducted in MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003) and consisted of two independent runs of four Markov Monte Carlo Chains, each for 10 million generations, with one tree sampled every 1000 generations. 25% of the sampled trees (burn-in) were discarded; the remaining were used to calculate the tree of maximum clade credibility (MCC) using TreeAnnotator in the BEAST package ver. 1.7 (Drummond *et al.* 2012), with clade support indicated as posterior probabilities (PP). Tracer ver. 1.6 (Rambaut *et al.* 2013) was used to confirm the quality of the parameters of the Bayesian inference. The MCC tree was visualized and edited using FigTree ver. 1.4.0 (Rambaut 2014).

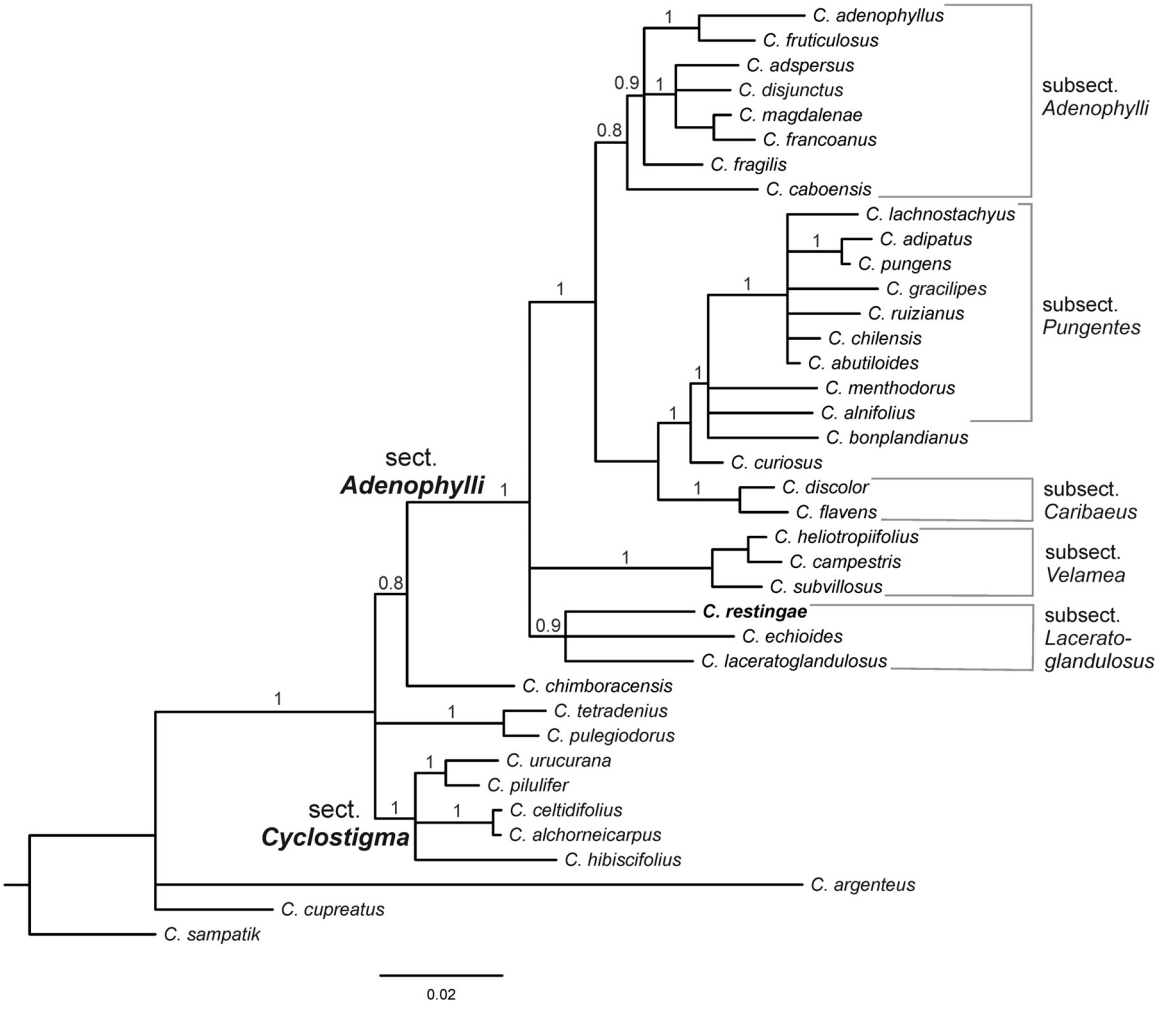

Fig. 1. Bayesian majority consensus phylogram of ITS nuclear data from a selection of taxa of *Croton* L. including an accession of *Croton restingae* Sodré & Riina sp. nov. The relevant clades are named. Values above the branches are Bayesian posterior probabilities. The scale bar indicates the average number of nucleotide substitutions per site.

Results

Phylogenetic analysis

The proposed new species, *Croton restingae* Sodré & Riina sp. nov., was recovered within the *C.* sect. *Adenophylli* clade (1 PP) as part of a well supported subclade (0.9 PP) along with *C. echioides* Baill. (*C.* subsect. *Pungentes*) and *C. laceratoglandulosus* Caruzo & Cordeiro (*C*. subsect. *Laceratoglandulosus*) (Fig. 1). This clade was in turn nested in a large polytomy with the other two main clades of *C.* sect. *Adenophylli* recovered, one formed by *C.* subsect. *Velamea* and the other including species of subsections *Adenophylli*, *Caribaeus* and *Pungentes* as well as species not yet assign to a subsection (*C. bonplandianus* Baill. and *C. curiosus* Croizat) (Fig. 1). *Croton chimboracensis* emerged as sister to the *Croton* sect. *Adenophylli* clade with relative high support (0.8 PP) and *C.* sect. *Adenophylli* + *C. chimboracensis* emerged in a polytomy with *C.* sect. *Cyclostigma* and *C. tetradenius* + *C. pulegiodorus* (Fig. 1).

Taxonomy

Class Magnoliopsida Brongn.
Order Malpighiales Juss. ex Bercht. & J.Presl
Family Euphorbiaceae Juss.
Genus *Croton* L.

Croton restingae Sodré & Riina sp. nov.
urn:lsid:ipni.org:names:77315910-1
Figs 2, 4P–T

Diagnosis

Croton restingae Sodré & Riina sp. nov. shares with *C. echioides* and *C. laceratoglandulosus* a fruit columella with three non-inflated, flat or slightly ascending apical appendages; however, it differs by having entire stipules with 2 sessile glands at the base, 2(–6) sessile or shortly stipitate acropetiolar / basilaminar leaf nectaries, entire bracts, 2–2.3 × 1.5–1.6 mm, staminate flowers with 15–18 stamens, revolute and eglandular pistillate sepals, 4.2–5 × 2.6–3 mm, styles 2-fid with 6 apical terminal arms, basally united forming a column ca 0.8 mm long, and larger capsules, 7.5–8 × 8.5–9.3 mm, vide Table 2.

Etymology

The specific epithet refers to the restinga vegetation where the species occurs.

Material examined

Type

BRAZIL – **Rio de Janeiro** • Saquarema, Reserva Ecológica Estadual de Jacarepiá; 18 Nov. 1992; fl.; *C. Farney et al. 3290*; holotype: RB[299275]; isotypes: ASE[17676], SLUI[5310].

Paratypes

BRAZIL – **Rio de Janeiro** • Arraial do Cabo, Pontal do Atalaia; 2 Jan. 2000; *M.F. Vasconcelos s.n.*; BHCB[035062] • Saquarema, Reserva Ecológica Estadual de Jacarepiá; 22 Jan. 1993; *J. Fontella, R. Paixão, C. Farney & D. Garcia 2899*; SP • ibid.; *J. Fontella, R. Paixão, C. Farney & D. Garcia 2900*; RB • ibid.; Sep.–Dec. 1992; *C. Farney et al. 3663*; RB • ibid.; 20–21 Aug. 1990; *A. Souza et al. 3163*; R • ibid.; 20–21 Aug. 1990; *A. Souza s.n.*; R[174495] • ibid.; 21 Aug. 1990; fl.; A. *Souza et al. 3161*; R • ibid.; restinga de Ipitanga, 2º cordão; s.d.; *s.col.*, *s.n.*; R[203793] • Reserva Ecológica de Massambaba, estrada do Joazeiro, trilha dos Micos Leões; 8 Apr. 1995; *M.G. Bovini, V.S. Fonseca & L.C. Giordano 757*; RB, SP • without locality [probably Rio de Janeiro State]; s.d.; *s.col.*, *s.n.*; R[99957].

Table 2. Morphological comparison between *C. restingae* Sodré & Riina sp. nov., *C. echioides* Baill. and *C. laceratoglandulosus* Caruzo & Cordeiro.

Character		***C. echioides***	***C. laceratoglandulosus***	***C. restingae* sp. nov.**
Stipule	length	1–3.5 mm	3.5–20 mm	4–10 mm
	shape	entire	entire or 2–7-palmatisect	entire
	glands	with or without 2 sessile glands	5–30 stipitate glands on the margin	2 sessile glands on the base
Basilaminar nectaries	number per leaf	2	absent	2(–6)
	stipe	0.5–1.4 mm long	–	sessile or stipe 0.1–0.4 mm
	position	abaxial surface	–	both surfaces
Staminate bracts	dimension	0.7–1.2 × 0.4–0.7 mm,	2.3–6.5 × 1.2–4 mm	2–2.3 × 1.5–1.6 mm
	margin	entire	laciniate, sometimes dentate or entire	entire
Pistillate sepals	dimension	1.3–3 × 0.6–1.3 mm	2.4–4.2 × 0.8–3.5 mm	4.2–5 × 2.6–3 mm
	aspect	plane	plane	revolute
	glands	absent	5–numerous, rarely absent	absent
Number of stamens		16–19	(32–)39–55(–74)	15–18
Styles	basal column	absent	0.3–1.1 mm long	ca 0.8 mm long
	ramification	2-fid with 6 terminal arms	(6–)8-fid with (18–)24 terminal arms	2-fid with 6 terminal arms
Capsule size		4.8–5.5 × 5.5–6 mm	4.9–5 × 5–5.3 mm	7.5–8 × 8.5–9.3 mm

Description

Shrub 1.7–3.5 m tall, latex yellowish, orange or reddish; stems erect, dichotomous or trichotomous, cylindrical, slightly striate, puberulent, sometimes hirsute, hirtellous or glabrescent, yellow-ferrugineous, trichomes stellate-porrect, 6–11 lateral rays 0.3–0.6(–0.9) mm long, one or two whorls, central ray (0.2–)0.4–2.1 mm long, with stipe 0.05–0.25 mm long, or with simple trichomes 1–2 mm long. Leaves alternate; stipules 4–10 × 0.5–0.8 mm, linear or narrowly lanceolate, dorsal surface pubescent or puberulent with trichomes multiradiate, stellate-porrect or simple, sessile, ventral surface puberulent or glabrescent with the same trichomes, with 2 ovoid, sessile colleters at the base, and an ovoid or subglobose colleter at the apex; petioles 1.5–6 cm long; 2(–6) acropetiolar / basilaminar nectary glands, two of them facing the abaxial surface, 0.8–1.3 mm diam., sometimes another two or four facing the adaxial surface, 0.35–0.6 mm diam., both patelliform, sessile or with stipe 0.1–0.4 mm long; leaf blade 6.7–9.5 × 3.2–6.3 cm, 1.7–4 times as long as petioles, ovate or ovate-lanceolate, membranaceous, base truncate, rounded, obtuse or cordate, apex acute or acuminate, margin serrulate, sometimes entire, with subglobose colleters usually at the apex of teeth, subsessile, venation brochidodromous with 4–6 pairs of secondary veins impressed on the adaxial surface and prominent on the abaxial surface, leaf blade discolorous, dark-green adaxial surface, pubescent, with simple trichomes, 0.1–0.3 mm long, with 4–12 quadrangular glands (idioblasts) at the base, stellate or multiradiate trichomes, in both rays 0.2–0.6 mm long, sessile or with stipe 0.05 mm long, abaxial surface clear green, tomentose or pubescent, with multiradiate trichomes, stipe 0.2–0.7 mm long, or subsessile stellate-porrect trichomes. Thyrses 9.5–21 cm long, bisexual, terminal or in the dichotomies or trichotomies of branches, sessile or with peduncle up to 1.5 cm long, sparse flowers, bisexual cymules in the basal portion with 1 pistillate flower and 6–8 staminate flowers, followed by staminate cymules with (4–)6–8 flowers; bracts of both flowers 2–2.3 × 1.5–1.6 mm, elliptic or oblong, entire, with globose glands at the base, tomentose on ventral surface and pubescent on dorsal surface, both with stellate or multiradiate trichomes; bracteoles 0.7–1.1 × 0.2–0.5 mm, triangular, linear or lanceolate, with globose

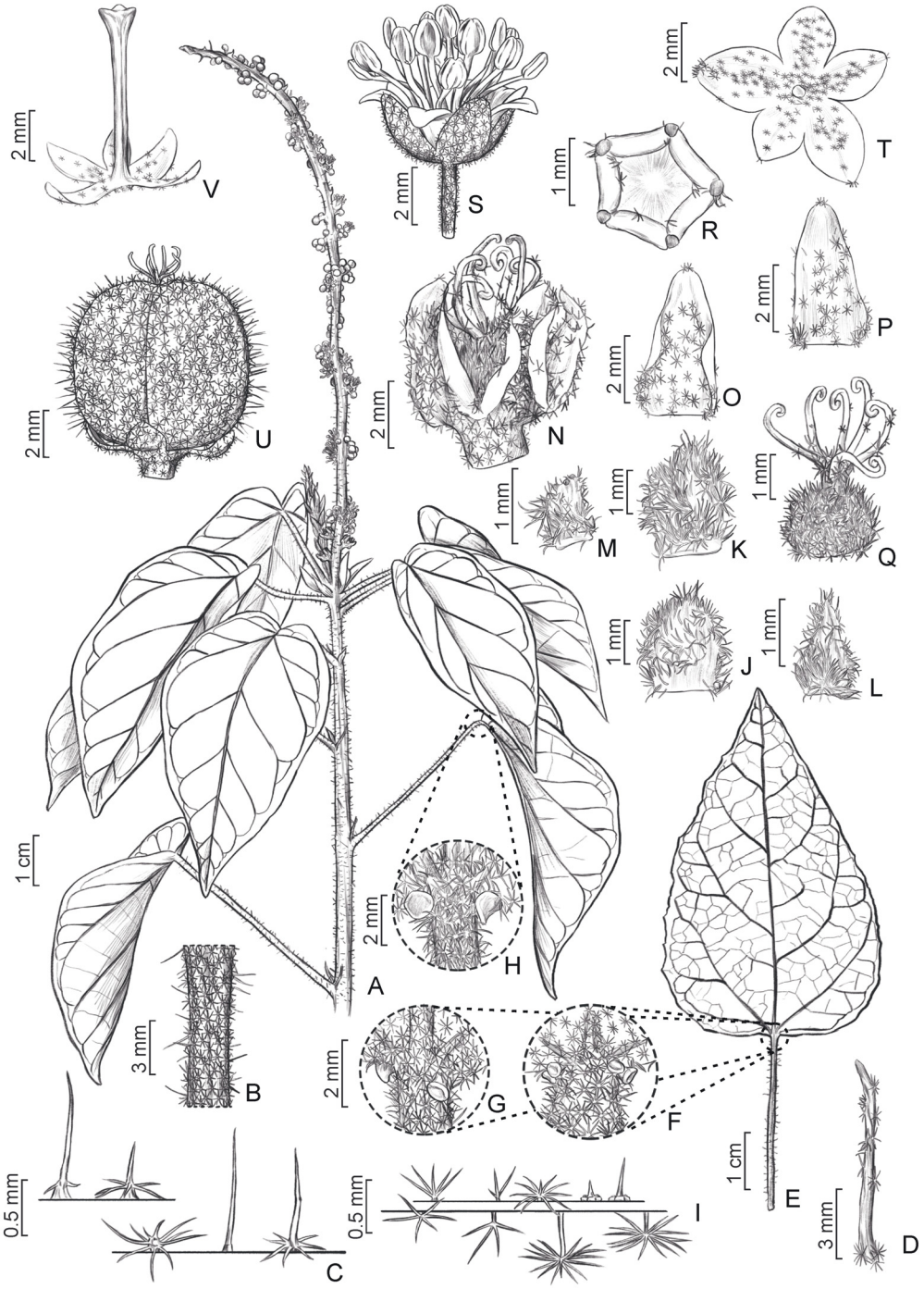

Fig. 2. *Croton restingae* Sodré & Riina sp. nov. **A**. Flowering branch. **B**. Indument of branch. **C**. Trichomes of branches. **D**. Stipule. **E**. Leaf. **F–G**. Foliar base (adaxial surface) showing the nectaries. **H**. Foliar base (abaxial surface) showing the nectaries. **I**. Trichomes of adaxial and adaxial surfaces of the leaf blade. **J**. Pistillate bract, dorsal surface. **K**. Pistillate bract, ventral surface. **L–M**. Pistillate bracteoles, dorsal surface. **N**. Pistillate flower. **O**. Pistillate sepal, dorsal surface. **P**. Pistillate sepal, ventral surface. **Q**. Gynoecium. **R**. Nectary disk of pistillate flower and glandular petals. **S**. Staminate flower. **T**. Calyx of staminate flower, dorsal view. **U**. Capsule. **V**. Carpophore showing the columella with discrete appendages at the apex. Drawn by Renato Galhardo Neto. A–R, T from *M.F. Vasconcelos s.n.*; S from *J. Fontella 2899*; U from *s.col. s.n.* R[99957]; V from *A. Souza et al. 3163*.

glands at the apex, indument similar to those of bracts. Staminate flowers 3.5–4.2 mm long; pedicel 1–2 mm long; receptacle villous; sepals 5, 2.7–3.4 × 2.1–2.8 mm, slightly unequal, shortly united at the base, ovate or largely elliptic, apex acute, obtuse or rounded, dorsal surface pubescent with stellate-porrect trichomes, shortly villous at the apex, ventral surface glabrous; petals 2–2.5 × ca 1 mm, oblong, apex rounded, glabrous on both surfaces, villous apex; stamens 15–18, ca 2 mm long, anthers elliptic or largely elliptic; nectary disk with 5 segments. Pistillate flowers 5–6.7 mm long; pedicel ca 1.2 mm long; sepals 5, 4.2–5 × 2.6–3 mm, slightly unequal, free, ovate or oblong, acute apex, margin entire, eglandular and revolute, dorsal surface shortly tomentose with trichomes stellate-porrect or multiradiate, ventral surface pubescent with trichomes fasciculate, stellate-porrect or simple; petals 5, ca 0.15 mm diam., reduced to ovoid glands, glabrous, whitish; ovary ca 1.6 × 2.2 mm, globose, hirsute-tomentose, trichomes stellate-porrect or multiradiate, shortly stipitate; styles 3, ca 3 mm long, united basally in a column ca 0.8 mm long, 2-fid, with 6 terminal arms; nectary disk with 5 segments oblong. Capsules 7.5–8 × 8.5–9.3 mm, globose, hirsute-tomentose, ferrugineous, pedicel 1–1.5 mm long, apex of columella with three discrete, flat or slightly ascending appendages, seeds not seen.

Distribution, habitat and phenology

Croton restingae Sodré & Riina sp. nov. is endemic to the coast of Rio de Janeiro (Fig. 3), in the municipalities of Saquarema and Arraial do Cabo, where it grows in restinga vegetation, on sandy soil, between 5–50 m of elevation. This vegetation is included in the Brazilian Atlantic Forest Domain and is floristically highly diverse and includes different phytophysiognomies such as forest, dense shrubland, open shrubland, savanna and pasture (Eiten 1983; Araújo 1992). The new species was collected with flowers in January, April, August and November.

Preliminary conservation status

Croton restingae Sodré & Riina sp. nov. has a limited Extent of Occurrence (45.7 km^2) and is tentatively categorized as Critically Endangered (CR; B1ab[iii]). Although the new species occurs in the Massambaba Environmental Protection Area (EPA), a special Conservation Unit called 'sustainable use' that covers 9000 hectares of the coastal strip between the municipalities of Saquarema and Arraial do Cabo, in general EPAs are very poorly preserved and urbanization is allowed without major restrictions (Macedo *et al.* 2019). Sá (2002) in a series of studies on the regeneration of restinga in the municipality of Saquarema reported significant disturbance in the area of occurrence of *C. restingae*, even within the limits of an Ecological Reserve (former Jacarepiá Ecological Reserve). Such disturbance was caused by deforestation to plant pineapple, opening of roads, logging, extractivism of ornamental plants, in addition to the use of plants for various purposes by the local community. Additionally, the only record of *C. restingae* for the municipality of Arraial do Cabo, comes from a region with intense tourism, representing a potential risk to its natural populations.

Discussion

Our phylogenetic analysis based on the ITS region (Fig. 1) supports *C. restingae* Sodré & Riina sp. nov. as a member of *C*. sect *Adenophylli*, which is also supported by several morphological characteristics, such as its shrub habit, indument of stellate trichomes, pistillate flowers shortly pedicellate with styles 2-fid and staminate flowers with 15–18 stamens. Despite this, the apex of the fruit columella, a feature that has been treated as a potential synapomorphy of *Croton* sect. *Adenophylli* (van Ee *et al.* 2011; van Ee & Berry 2021), is somewhat different in *C. restingae*, having three discrete, flat and non-inflated appendages. The new species emerges in a well-supported clade (0.9 PP) along with *C. laceratoglandulosus* and *C. echioides*, which shares the same columella features. Recently, van Ee & Berry (2021) proposed a new subsection *Laceratoglandulosus* B.W.van Ee & P.E.Berry with *C. laceratoglandulosus* Caruzo & Cordeiro as its only species. Although *C. echioides* had previously been found to be related to *C. laceratoglandulosus* (Riina *et al.* 2009; van Ee *et al.* 2011), these authors did so based on a sequence obtained from a wrongly

identified sample, as explained in van Ee & Berry (2021). Thus, here we confirmed the phylogenetic position of *C. echioides* based on a correctly identified material (*Sodré 3314*, UFG), and expand the circumscription of subsection *Laceratoglandulosus* to include *C. echioides* and *C. restingae*. The three species in the subsection share conspicuous stipules (usually more than 2 mm long), long petioles (1.5–8(–12) cm long), leaf blades often ovate and lax thyrses often reaching 20–30 cm in length. In addition, these are the only species of the *Adenophylli* section lacking the typical *Adenophylli* columella, having instead the apex of the columella with three non-inflated, flat or slightly ascending apical appendages (Fig. 4E, O, T). Furthermore, *C. laceratoglandulosus* and *C. restingae* have styles basally united into a column, an unusual feature in the section *Adenophylli*. The three species are distributed mainly in the eastern portion of Brazil, except for *C. laceratoglandulosus*, which also occurs in dry forests of eastern Bolivia. *Croton echioides* and *C. laceratoglandulosus* occur, often in sympatry, in an extensive area of caatinga, whereas *C. restingae* has a restricted distribution in the restinga area which show some floristic similarities with the caatinga (Ab'Saber 2003). The main characteristics that differentiate *C. restingae* from *C. laceratoglandulosus* and *C. echioides* are detailed in Table 2, some of which are shown in Fig. 4.

Among the other species of *Croton* sect. *Adenophylli*, *C. restingae* Sodré & Riina sp. nov. could also be confused with *C. gracilipes* Baill. because of its ovate or oval-lanceolate leaf blades, usually with

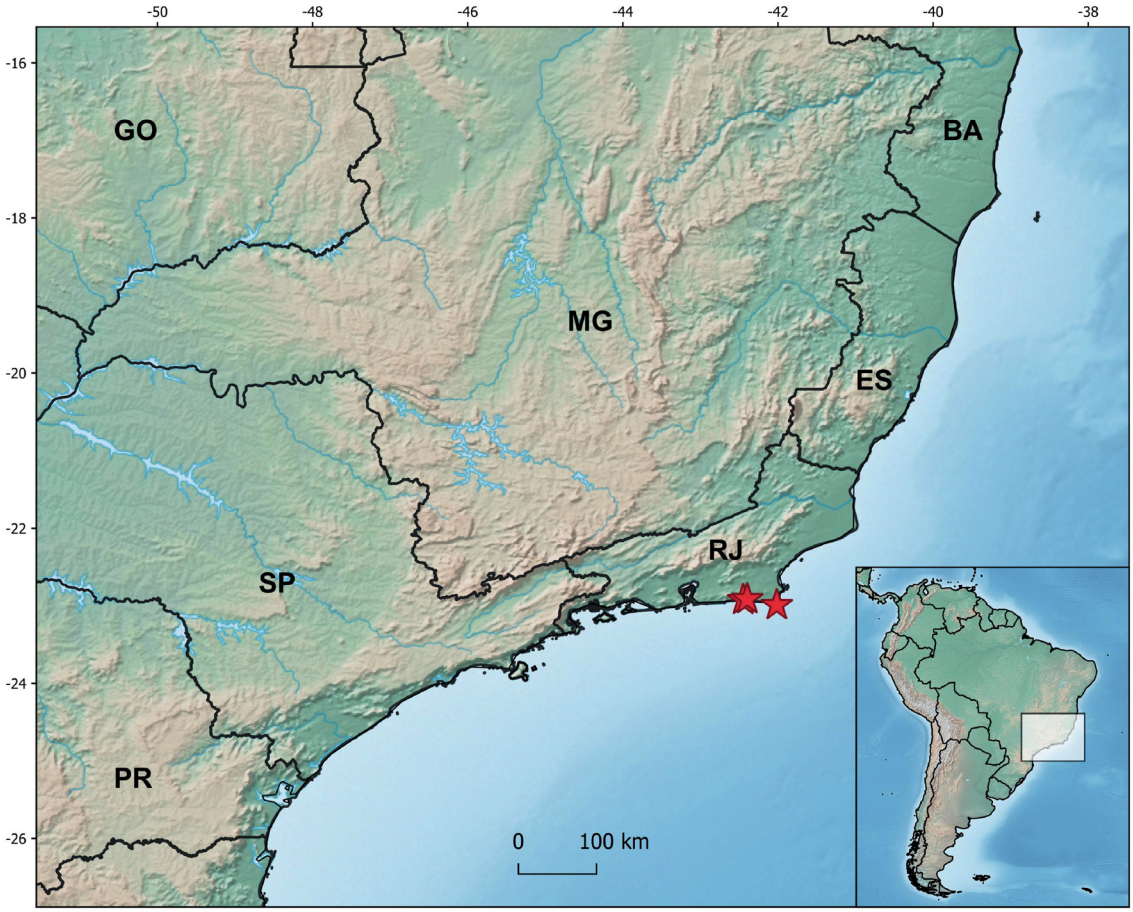

Fig. 3. Distribution map of *C. restingae* Sodré & Riina sp. nov. State abbreviations: BA = Bahia; ES = Espírito Santo; GO = Goiás; MG = Minas Gerais; PR = Paraná; RJ = Rio de Janeiro; SP = São Paulo.

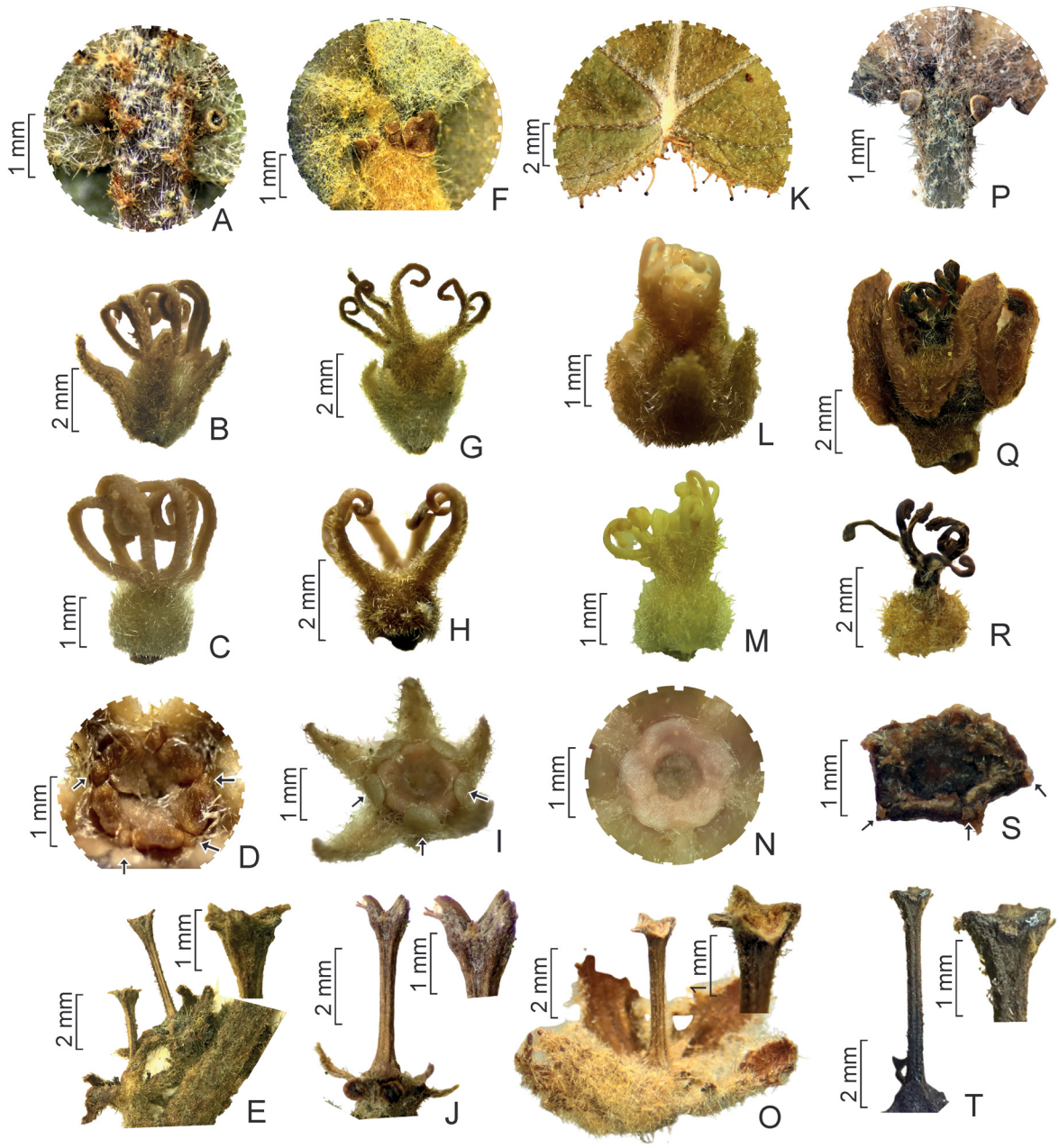

Fig. 4. Morphological comparison of *C. restingae* Sodré & Riina sp. nov. and related species. **A–E**. *Croton echioides* Baill. **A**. Basilaminar nectaries. **B**. Pistillate flower. **C**. Gynoecium. **D**. Nectary disk and glandular petals (arrows) of pistillate flower. **E**. Carpophore showing the columella, detail of the apical appendages. – **F–J**. *C. gracilipes* Baill. **F**. Basilaminar nectaries. **G**. Pistillate flower. **H**. Gynoecium. **I**. Nectary disk and glandular petals (arrows) of pistillate flower. **J**. Carpophore showing the columella, detail of the apical appendages. – **K–O**. *C. laceratoglandulosus* Caruzo & Cordeiro. **K**. Basilaminar colleters. **L**. Pistillate flower. **M**. Gynoecium. **N**. Nectary disk of pistillate flower. **O**. Carpophore showing the columella, detail of the apical appendages. – **P–T**. *C. restingae* sp. nov. **P**. Basilaminar nectaries. **Q**. Pistillate flower. **R**. Gynoecium. **S**. Nectary disk and glandular petals (arrows) of pistillate flower. **T**. Carpophore showing the columella, detail of the apical appendages. Photos: A–E from *R.C. Sodré 3314*; F–J from *R.C. Sodré 3413*; K–O from *R.C. Sodré 3461*; P–S from *M.F. Vasconcelos s.n.*; T from *A. Souza et al. 3163*.

two sessile or short stipitate patelliform nectaries, inflorescences with basal, bisexual cymules, pistillate flowers and capsules shortly pedicellate (ca 0.5–1.2 mm long), 15–18 stamens, and 2-fid styles. However, *C. restingae* can be differentiated from the latter by the size of the bracts (2–2.3 × 1.5–1.6 mm), the size of the pistillate sepals (4.2–5 × 2.6–3 mm) and their revolute margin (Fig. 4Q), petals ca 0.15 mm wide (Fig. 4S), styles united into a column (Fig. 4R), and fruit columella with three discrete, flat or slightly ascending apical appendages (Fig. 4T). *Croton gracilipes* has bracts 0.6–1.2 × 0.2–1 mm, sepals of pistillate flowers 1–2.2 × 0.4–1 mm with flat margin (Fig. 4G) and petals 0.3–1 mm wide (Fig. 4I), free styles (Fig. 4H), and fruit columella with three prominent and ascending apical appendages (Fig. 4J). Additionally, *C. restingae* has stipules 4–10 mm long (vs 0.7–3.4 mm long in *C. gracilipes*), petioles 1.5–6 cm long (vs up to 19.8 cm), leaf blades with 4–6 pairs of secondary veins (vs 8–20), pedicel of staminate flowers 1–2 mm long (vs 2.2–9 mm), and capsules with 7.5–8 × 9–9.3 mm (vs 5.5–6.5 × 6–6.8 mm).

Some specimens of *Croton restingae* Sodré & Riina sp. nov. were identified in scientific articles (e.g., Sá 1996) and in herbarium collections as *C. hemiargyreus* Müll.Arg. (*C. Farney et al. 3290*, RB; *Souza et al. 3163*, R), and *C.* cf. *pseudopopulus* Baill. (*C. Farney et al. 3663*, RB; *s.col., s.n.*, R[203793]). *Croton hemiargyreus* is a tree in *C.* sect. *Cleodora* (Klotzsch) Baill. (Caruzo *et al.* 2011), easily distinguished from *C. restingae* by its height of up to 10 m, lepidote trichomes throughout the plant, pistillate calyx with lobes united at the base and accrescent, and 4-fid styles. *Croton pseudopopulus* (Caruzo *et al.* 2022) appears to belong to *C.* sect. *Cyclostigma*, sister of *C.* sect. *Adenophylli*, but it has not yet been included in a molecular phylogenetic study (the species is only known from the type). It can be distinguished from *C. restingae* by its arborescent habit up to 10 m tall, dendritic trichomes on branches, leaf nectaries with a long stipe (1–2 mm long) and pistillate flowers with pedicel 2–5 mm long.

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