









Research article

Croton maranonensis: a new species of Euphorbiaceae from the tropical inter-Andean dry valleys

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Abstract. We describe *Croton maranonensis* Riina & Martín-Muñoz sp. nov., a species in *Croton* section *Julocroton* (Mart.) G.L.Webster from the seasonally dry tropical forests and shrublands of the inter-Andean valleys. This species is a small shrub occurring along the Marañón river valley in Peru and similar dry areas in southern Ecuador. We surveyed morpho-anatomical characters of the new species and closely related taxa. To confirm the placement of the new species in *C.* section *Julocroton*, we conducted a molecular phylogenetic analysis including three accessions of the new species and selected representatives of section *Julocroton* and related groups within *Croton* L. Micro- and macro-morphological evidence, and molecular data support *C. maranonensis* sp. nov. as an independent lineage within the *C.* section *Julocroton* clade. We compared the new species with morphologically similar species in the same section that also occur in the Andean region, including *C. flavispicatus* Rusby, *C. triqueter* Lam., and *C. hondensis* (H.Karst.) G.L.Webster.

Keywords. Anatomy, *Croton* section *Julocroton*, dry vegetation, morphology, Neotropics, taxonomy.

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Introduction

Croton section *Julocroton* (Mart.) G.L.Webster is a monophyletic group (Van Ee *et al.* 2011) that consists of 42 species including the new species here described. Species in this section are monoecious herbs or shrubs with usually dense stellate indumentum, leaves without basilaminar/petiolar nectary glands, highly congested bisexual inflorescences composed of staminate flowers with 10–12 stamens and pistillate flowers with lacinate and unequal sepals (Van Ee *et al.* 2011). The section is mainly distributed in tropical areas of South America, with southern Brazil and Paraguay as the main centers of diversity (Cordeiro 1990; Van Ee *et al.* 2011; Caruzo *et al.* 2022). Only one species, *C. argenteus* L., has expanded its range outside South America, occurring also in Central America, Mexico, southern United States and the Caribbean (Van Ee *et al.* 2011).

Croton maranonensis sp. nov. occurs in the seasonally dry forests of the tropical Andes biodiversity hotspot, the most species-rich among the world's hotspots (Myers *et al.* 2000). The new species has been extensively collected along the Marañón Valley and in a few localities in southern Ecuador. The Marañón Valley is part of the Central inter-Andean valleys floristic group identified by DRYFLOR (2016), along with 11 other floristic nuclei of dry forest vegetation in the Neotropics. The levels of plant endemism in the Marañón Valley is extremely high (Marcelo-Peña *et al.* 2016), with many new endemic species being described from this area in the last decade (Moura *et al.* 2013; Michelangeli & Ulloa Ulloa 2016; Esquerre-Ibañez 2017; Jara *et al.* 2020; Montesinos-Tubée *et al.* 2020; Wood & Uría 2021). This suggests that the diversity of Marañón's flora has been underestimated and that there are probably more new plant species waiting to be described (Särkinen *et al.* 2011).

In the last floristic survey of the Marañón Valley flora, Euphorbiaceae was recorded as the second family in number of species, after Leguminosae, and *Croton* and *Senna* Mill. were the most species-rich genera with 12 and 11 species, respectively (Marcelo-Peña *et al.* 2016). When considering the entire area covered by the Central inter-Andean valleys floristic group (northern Peru and Ecuador; DRYFLOR 2016), *Croton* also stands out as the genus with the highest number of species and high levels of abundance in many of the forest plots measured so far (DRYFLOR 2016; Quintana *et al.* 2017). In some of these areas, *Croton* plants are the dominant woody elements of the landscape, acting as ecosystem engineers (Espinosa *et al.* 2019).

In this paper we add to the floristic knowledge of the Central inter-Andean valleys and the Neotropical dry forest by describing *Croton maranonensis* sp. nov., a taxon in the understudied *C.* section *Julocroton*. We used both morphological and anatomical data to characterize the species and to compare it to its closest relatives in the section. We also performed a molecular phylogenetic analysis based on the ITS region to test the placement of the new species in *C.* section *Julocroton*, as initially suggested by morphology. Finally, we propose a preliminary assessment of the conservation status of the new species.

Material and methods

We examined collections of *Croton maranonensis* sp. nov. and related taxa in *C.* sect. *Julocroton* deposited in herbaria A, BKL, BM, BR, COL, E, ESA, F, GH, HUTPL, IAC, ICN, K, MA, MICH, MO, MOL, NY, P, RFA, SP, SPF, UB, US, USM, and WIS. The type material and additional specimens available from morphologically similar species in *C.* sect. *Julocroton* were also examined (see Appendix 1). Acronyms of herbaria follow Index Herbariorum (<https://sweetgum.nybg.org/science/ih/>). For

morphological descriptions we used a stereomicroscope with 10–60× magnification. The morphological and anatomical descriptions follow recent taxonomic and anatomical studies about *Croton* (Van Ee *et al.* 2011; Vitarelli *et al.* 2015, 2021; Riina *et al.* 2021). For trichome terminology, we follow the classification proposed by Pinto-Silva *et al.* (2023).

For the anatomical study, we sampled leaves, young leaves, shoots and stipules of six specimens of *Croton maranonensis* sp. nov.: Van der Weff 14623, 14806 (MICH); Cumbicus & Camacho 1924 (MA); Riina 1469 (MA); Campos 2139 (MICH); Vásquez 27094 (WIS), three specimens of *C. flavispicatus* Rusby: Sacha 14613 (MO); Souza 6401 (MO); Riina 1450 (MICH) and three specimens of *C. triqueter* Lam.: E. Valduga 749, 815 (ICN); L.C. Bernacci *et al.* 997 (IAC). These materials were prepared for light and scanning electron microscopy following the methods described in similar anatomical studies (Johansen 1940; Bozzola & Russel 1992; Meira & Martins 2003; Vitarelli *et al.* 2015, 2021; Feio *et al.* 2018).

For the phylogenetic analysis we used sequences from the ITS (Nuclear ribosomal internal transcribed spacers) region using a selection of species of *C.* subgenus *Geiseleria* A.Gray (Van Ee *et al.* 2011) obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) along with newly generated sequences of *C. maranonensis* sp. nov., *C. hondensis* (H.Karst.) G.L. Webster, and several specimens of *C.* sect. *Julocroton*, including the widespread *C. triqueter* (see Appendix 2).

DNA extraction, amplification, sequencing, and alignment followed the same procedures as in Masa-Iranzo *et al.* (2021). The aligned ITS matrix was trimmed on both ends to minimize missing data (the alignments, in fasta format, are provided as [Supp. file 1](#)). Phylogenetic analysis was performed in MrBayes ver. 3.2.7 (Ronquist *et al.* 2012) applying the GTR+I+G model (Masa-Iranzo *et al.* (2021)). We did 2 runs for 10 million generations sampling every 1000th generation, monitoring the standard deviation of split frequencies (< 0.01) for assuring convergence. Tracer ver. 1.7.2 (Rambaut *et al.* 2014) was used to evaluate the Markov chains. As burn-in, the first 25% of MCMC samples were discarded. Using the *sumt* command we obtained a Bayesian tree with posterior probability (PP) values by computing a majority rule consensus of the post-burn-in trees. We used FigTree ver. 1.4.4 (Rambaut 2006) to edit the consensus tree.

A preliminary assessment of the conservation status, including estimation of the area of occupancy (AOO) and extent of occurrence (EOO) were conducted using the GeoCat software (Bachman *et al.* 2011) and the coordinates available from the examined herbarium collections of the new species. For those without coordinates, we estimated them with Google Earth using locality and habitat information provided in the collection labels.

Results

Class Magnoliopsida Brongn.
Order Malpighiales Mart.
Family Euphorbiaceae Juss.
Genus *Croton* L.

Croton maranonensis Riina & Martín-Muñoz sp. nov.

[urn:lsid:ipni.org:names:77347325-1](https://nomenclature.ipni.org/names/77347325-1)

Figs 1–2

Diagnosis

Croton maranonensis sp. nov. is morphologically most similar to *C. hondensis* and can be distinguished from the latter mainly by its bifid styles (4-fid in *C. hondensis*), shorter petioles (0.2–1 cm vs 1.8–5.3 (–7.8) cm in *C. hondensis*), leaf blades that are 2–6(–8) cm long (5.5–6.6(–10.2) cm long in *C. hondensis*), bracts 1–1.2 mm long (3.2–5 mm in *C. hondensis*) and the presence of a conspicuous, usually persistent, colleter at the leaf apex (vs an inconspicuous caducous colleter in *C. hondensis*) (Table 1).

Etymology

The specific epithet of the new species refers to Marañón river valley, the location where the majority of specimens of *C. maranonensis* sp. nov. have been collected.

Type material

PERU • Amazonas, Utcubamba, Dtto. Bagua Grande, carretera Corral Quemado a Lonya Grande, bordeando el valle del alto Río Marañón; 06°04'20" S, 78°32'24" W; elev. 600 m; 20 May 2004; R. Riina & J. Campos 1469; holotype: MA [MA 874921], isotypes: E, MICH, MO, USM.

Other material examined

ECUADOR • Loja, Cantón Catamayo, Parroquia el Tambo, sector San Bernabé, 500 m de la entrada del desvío desde San Bernabé a Malacatos; 04°05'32.2" S, 79°20'11.8" W; elev. 1950 m; 23 Nov. 2013; N. Cumbicus, F. Tinitana & O. Cabrera 1890; HUTPL • Loja, Cantón Catamayo, Parroquia el Tambo, sector San Bernabé, 500 m de la entrada del desvío desde San Bernabé a Malacatos; 04°05'32.2" S, 79°20'11.8" W; 1950 m; 20 May 2008; N. Cumbicus & V. Camacho 1924; HUTPL, MA.

PERU • Amazonas, Bagua Grande, El Parco, bosque seco espinoso; 05°40'00" S, 78°25'00" W; elev. 700 m; 5 Dec. 2001; R. Vásquez, R. Rojas & L. Campos 27094; MO, USM [198077], WIS • Amazonas, along road Bagua Grande and Pedro Ruiz in dry and semideciduous scrub; 05°54'48" S, 78°07'38" W; elev. 500–1000 m; 10 Mar. 1998; H. van der Werff, B. Gray, R. Vásquez & R. Rojas 14623; MICH, MO, WIS • Amazonas, Bongorá, Pedro Ruiz-Chachapoyas, km 35; 06°12'53" S, 77°54'21" W; Oct. 1990; F. Kahn & F. Moussa 2854; USM [115945] • Amazonas, Along road Tingo-Kuelap, Choctamal, moderately wet scrub, originally forest; 06°23'43" S, 77°57'53" W; elev. 2400 m; 12 Mar. 1998; H. van der Werff, B. Gray, R. Vásquez & R. Rojas 14806; USM [201908] • Cajamarca, Jaén; 9 Jun. 1877; E.D. Andre 4713; K • Amazonas, Valley of the Marañón river, past Tingo on road to Lambeyque, property of Lola and Perico Heredia, on eastern bank of Río Utcubamba; -6.432583333, -77.873305556; elev. 1820 m; 8 Mar. 2012; K.G. Dexter, J.L. Marcelo Peña, A. Daza Yomona & R.T. Pennington 5935; E • Cajamarca, Jaén, 29 km E of Pucara on road to Bagua, very dry tropical forest along Río Huancabamba; elev. 710 m; 10 Jun. 1978; A. Gentry, M. Dillon, J. Aronson & C. Diaz 22750; F [2100677], MICH • Cajamarca, Jaén, Dtto. Jaén, Sector El Huito, bosque seco; 05°40'47" S, 78°47'55" W; elev. 890 m; 18

Table 1. Main differences between *Croton maranonensis* sp. nov. and its most morphologically similar species *C. flavispicatus* Rusby, *C. hondensis* (H.Karst.) G.L. Webster and *C. triquetus* Lam. in section *Julocroton* (Mart.) G.L. Webster.

	<i>C. maranonensis</i> sp. nov.	<i>C. flavispicatus</i>	<i>C. hondensis</i>	<i>C. triquetus</i>
Leaf blade (cm)	2-6(-8) × 1-2(-4)	4.2-11 × 1.2-7	5.5-6.6(-10.2) × 2.9-3.8(-4.2)	7.4-14 × 3-5.6
Colleter at leaf apex	Conspicuous, usually persistent (Figs 1D, 2C)	Inconspicuous, caducous	Inconspicuous, caducous	Inconspicuous, caducous
Petiole anatomy	Absence of accessory bundles	Presence of 2 accessory bundles	Unknown	Presence of 2 accessory bundles
Petiole length (cm)	0.2-1	0.7-3.3(-5)	1.8-5.3(-7.8)	1-4.5
Stipules length (mm)	0.5-3	4.1-9	4.8-7β	5-9
Inflorescences (cm)	1-3(-3.5) × 0.5-1	2-4 × 1	2-3 × 1-1.2	1.5-2.5(-3) × 1-1.5
Bracts length (mm)	1-1.2	2.5-4	3.2-5	3-4
Styles	Bifid (6 tips)	4-fid (12 tips)	4-fid (12 tips)	4-fid (12 tips)
Longest sepals in fruit	< 1/2 the length of capsule	≥ length of capsule	≥ length of capsule	≥ length of capsule
Fruit size (mm)	4.0-5.0 × 3.0-3.5	2.5-3.5 × 3-4.5	4.5-4.9 × 4.2-4.5	4-5 × 4-5
Habitat	Dry forests, dry shrublands	Moist forest and along rivers	Dry forests	Moist to mesic habitats
Elevation (m)	600-2400	200-1100	340-600	800-1600

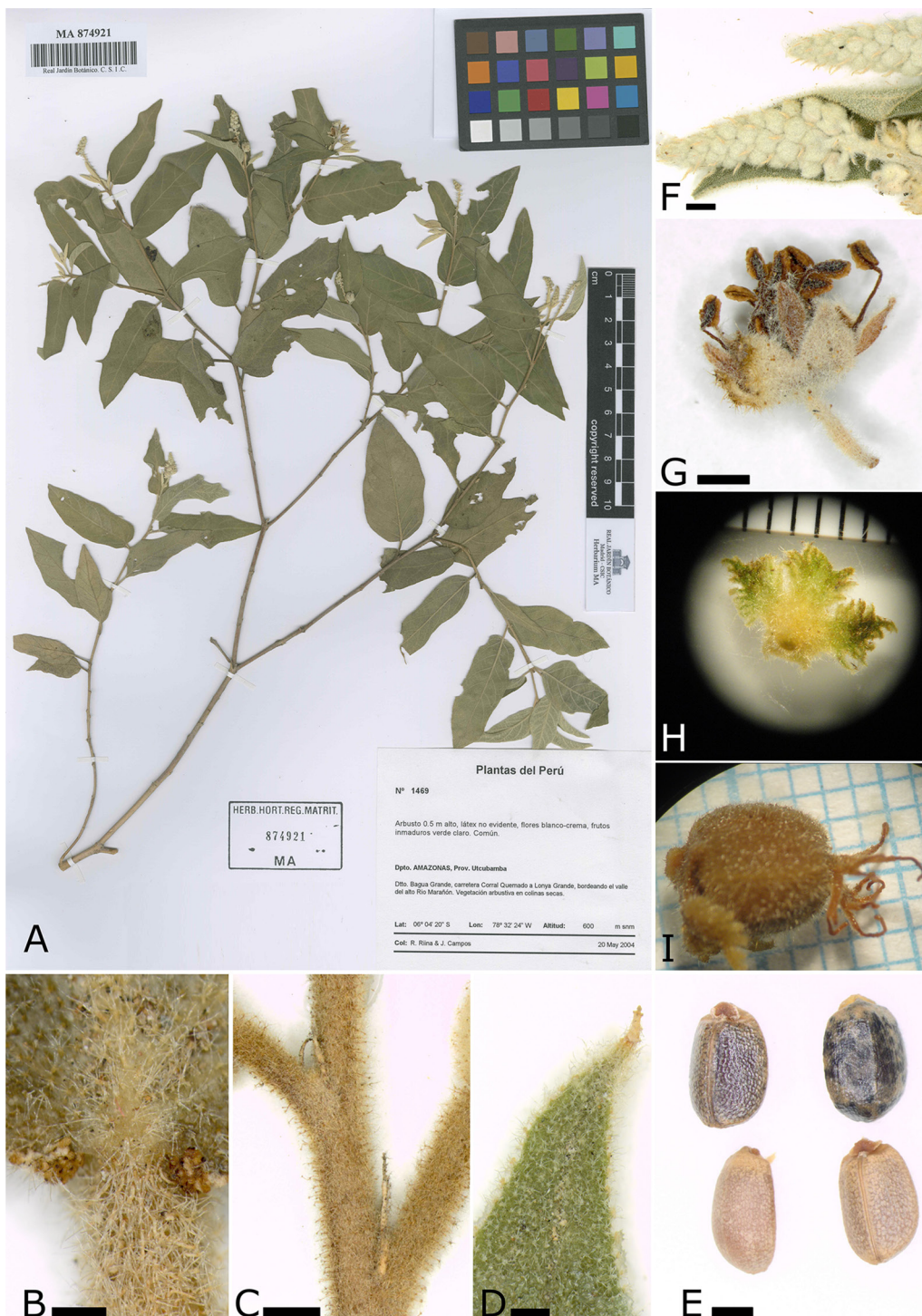


Fig. 1. *Croton maranonensis* sp. nov. **A.** Image of the holotype: MA[874921]. **B.** Clusters of no longer active colleters at the base of the lamina. **C.** Detail of the stipules. **D.** Leaf apex bearing a colletel (no longer active) at the tip. **E.** Seeds in different views. **F.** Inflorescences showing mainly the staminate portion (distal) with flowers in bud. **G.** Individual staminate flower. **H.** Detail of the calyx showing the three conspicuous and dissected lobes and the two highly reduced ones. **I.** Detail of the fruit showing the bifid styles. A from *R. Riina & J. Campos* 1469 (MA); B, E from *van der Werff* 14623 (MICH); C from *Rojas* 0863 (WIS); D, F. from *van der Werff* 16399 (WIS); G from *Campos* 2139 (MICH, MO); H–I from *Cumbicus & Camacho* 1924. Scale bars: B, D = 500 μ m; C, F = 2 mm; E, G–I = 1 mm.

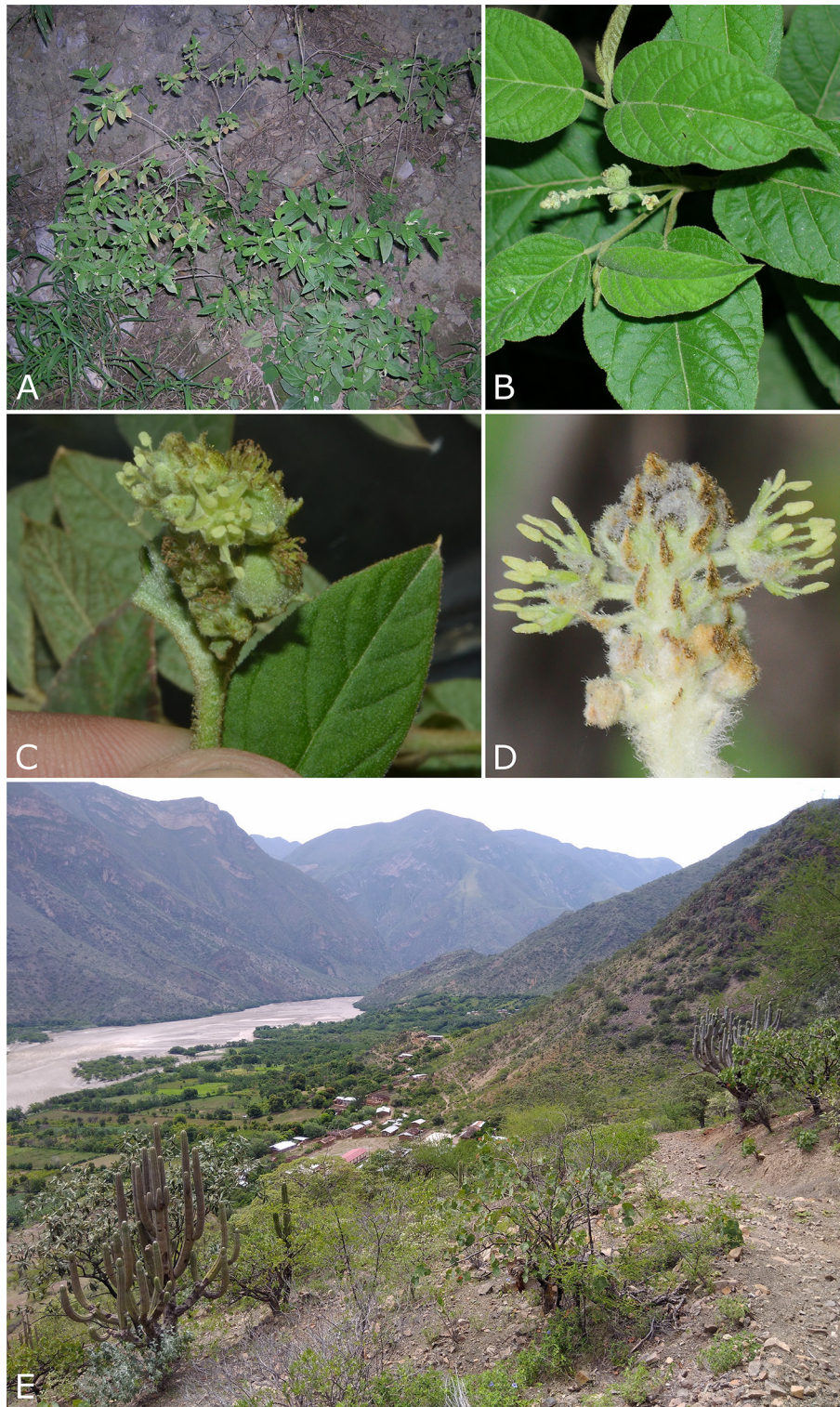


Fig. 2. *Croton maranonensis* sp. nov. **A.** Small individual growing in dry forest understory. **B.** Fertile branch. **C.** Inflorescence showing both pistillate and staminate flowers; note the conspicuous colletar at the apex of the leaf on the right. **D.** Detail of inflorescence with two staminate flowers in anthesis. **E.** A view of the open dry vegetation associated with the seasonally dry tropical forest in the Marañón Valley where the new species occur. A–B from R. Riina 1478; C from Cumbicus 1924; D from González 6491. Photographs by R. Riina (A–B), N. Cumbicus (C), and P. González (D–E).

Jul. 2005; *J.L. Marcelo-Peña, A. Tapia N. & J. Dilas J. 1761*; MICH, MOL • Cajamarca, Jaén, Yanayacu, bosque seco; 05°40'47.8" S, 78°46'12.3" W; elev. 623 m; *J.L. Marcelo Peña 2057*; MOL • Cajamarca, Jaén, El Huito, bosque seco; 05°41'17" S, 78°48'60" W; elev. 780 m; 14 Dec. 2006; *J.L. Marcelo Peña & U. Hipler 2235*; MOL • Cajamarca, Jaén, Dtto. Jaén, Sector San Isidro, bosque estacionalmente seco; 05°42'30" S, 78°46'54.4" W; elev. 734 m; 18 Apr. 2007; *J.L. Marcelo-Peña & V. Marcelo-Peña 2601*; MICH • Cajamarca, Dtto. Jaén, Sector El Huito, bosque excepcionalmente seco; 05°41'17" S, 78°48'59" W; elev. 780 m; 24 Mar. 2008; *J.L. Marcelo-Peña, C. Carrasco & R. Carhuatocto 3107*; E [E00664543] • Cajamarca, Jaén, Pucará (On the Río Huancabamba), km 127 east of Olmos, north of town up creek in Quebrada de las Breas in vicinity of waterfall, ca 20 minutes by foot; 05°58'17.6" S, 79°11'59.5" W; 11 Jan. 1964; *P.C. Hutchison & J.K. Wright 3520*; F, K [000111643], USM • Cajamarca, Jaén, at Gota de Agua, privately owned conservation área 15 minute drive away from central Jaén. Collected as part of plot work, plot located close to a path leaving from the main gate of the estate; 05°41'33" S, 78°46'04" W; elev. 800 m; 9 Apr. 2008; *T.E. Sarkinen, A. Daza, H. Vandrot & S. D'ugard 3026*; E [E01007877], FHO, MOL, USM • Cajamarca, Jaén, Dtto. Morro Solar, camino de Jaén a Chililique. Ladera con vegetación seca, suelo arenoso y pedregoso; 05°43'02" S, 78°48'56" W; elev. 700 m; 22 May 2004; *R. Riina & J. Campos 1478*; MA • Cajamarca, Jaén, Pucará, bosque secundario, 06°03'00" S, 79°10'00" W; elev. 1000 m; 28 Dec. 1999; *R. Rojas, J. Campos & S. Flores 863*; WIS • Cajamarca, Jaén, Colasay, bosque seco; 05°55'00" S, 79°10'00" W; elev. 1600 m; 8 Dec. 2001; *R. Vásquez, R. Rojas & L. Campos 27200*; USM [196679], WIS • Cajamarca, Jaén, dry scrub along Marañón, between Chamayo and Corral Quemado; 05°42' S, 78°48' W; elev. 700 m; 25 Mar. 2001; *H. van der Werff, R. Vásquez & B. Gray 16399*; USM [178708] • Cajamarca, San Ignacio, Distrito de Chirinos, Patociego; 05°19' S, 78°44' W; elev. 500–800 m; 27 Jan. 1996; *J. Campos & O. Díaz 2210*; MO, MOL • Cajamarca, San Ignacio, Dtto. Chirinos, La Catahua, 05°24' S, 78°47' W; elev. 500–800 m; 24 Jan. 1996; *J. Campos 2139*; MA, MICH, MO, USM • Dtto. La Libertad, Sánchez Carrión, Chugay, 4 km abajo El Convento en la ruta Huamachuco - Calemar; 07°36'21" S, 77°51'45" W; elev. 1695 m; 16 Feb. 2020; *P. Gonzáles, Z.A. Goodwing, J.L. Marcelo-Peña, W. Aparco & R. Balvin 6491*; E [E01059878], USM • Dtto. La Libertad, Sánchez Carrión, Chugay, 4 km abajo El Convento (margen derecho del Río Chusgón); 07°36'21" S, 77°51'45" W; elev. 1695 m; 13 Feb. 2020; *J.L. Marcelo-Peña, P. Gonzáles, Z.A. Goodwin, W. Aparco & R. Balvin 11142*; E, USM • Dtto. La Libertad, Sánchez Carrión, Chugay, 4 km abajo El Convento (margen derecho del Río Chusgón); 07°36'21" S, 77°51'45" W; elev. 1695 m; 13 Feb. 2020; *J.L. Marcelo-Peña, P. Gonzáles, Z.A. Goodwin, W. Aparco & R. Balvin 11146*; E, USM.

Description

Monoecious shrub, up to 2 m high; young branches with dense indumentum of stellate trichomes, often stipitate; without evident latex. *Stipules* 0.5–3 mm long, linear to narrowly subulate, with colleters (ovoid glands) at the base, margin, and apex. *Petiole* 0.2–1 cm long, with dense indumentum of stellate trichomes and stipitate stellate trichomes; petiolar nectary glands absent; colleters present at the apex of petioles, sometimes arranged into two clusters at both sides of the petiole. *Leaf blade* ovate-lanceolate 2–6(–8) × 1–2(–4) cm; indumentum on the adaxial side more or less dense with stipitate porrect stellate trichomes, simple trichomes also present; indumentum on the abaxial side very dense with long-stipitate porrect stellate trichomes; base cordate or rounded, sometimes asymmetrical; apex acute, usually mucronate with a single conspicuous colleter (no longer active); margin entire; colleters (no longer active) along the margin; venation palmate-pinnate, 3–5 veined at base, brochidodromous; primary and secondary veins raised only on the abaxial side. *Inflorescences* terminal, 2–4.5 cm long, axis slightly costate, with a dense indumentum of mostly stipitate porrect stellate trichomes, bracts linear and curved, ca 1–1.2 mm long; basal cymules pistillate; upper cymules with staminate flowers, all flowers regularly spaced or sometimes with a gap in the middle, between the pistillate and staminate portions, with persistent bracts and rounded scars of the fallen flowers. *Staminate flowers* pedicellate; pedicel 0.5–2.0 mm; sepals valvate, triangular-ovate, 1.3–2.0 × 1.0–1.2 mm, adaxial side glabrous with simple

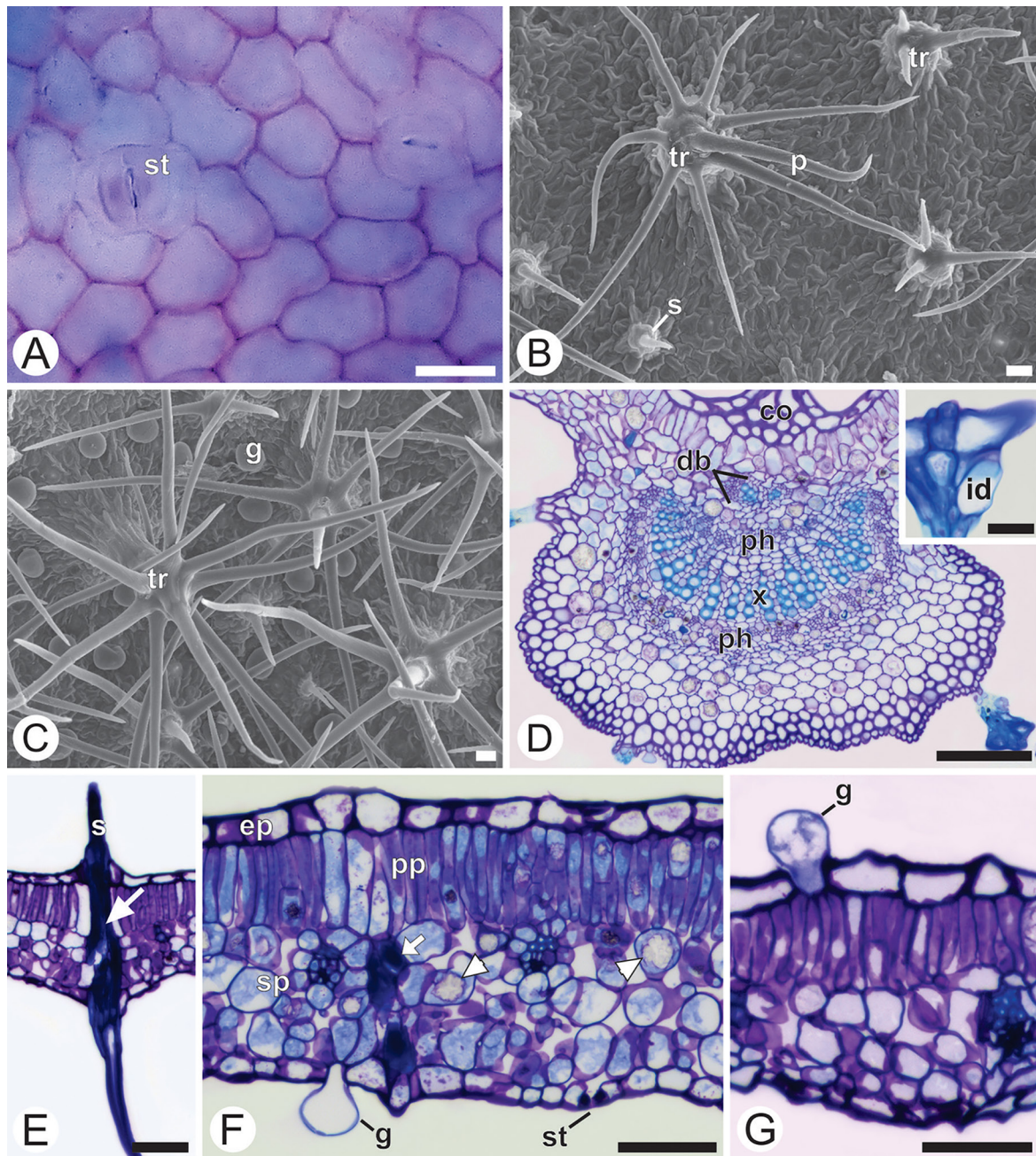


Fig. 3. Leaf anatomy features of *Croton maranonensis* sp. nov., based on diaphanization of leaf blade (A); scanning electron microscopy from the adaxial (B) and abaxial (C) surface; and transverse sections (D–G). **A.** Cells with straight contour and paracytic stomata (st) on the adaxial surface. **B.** Epidermal appendages of simple (s) and porrect (p) stellate trichomes (tr) with a variable number of radial cells. **C.** Porrect stellate trichomes and knob-like glandular trichomes (g). **D.** Biconvex midrib and secretory idioblast (id) at the base of the stellate trichome in detail. **E.** Simple trichomes connected to sclereids crossing the mesophyll (arrow). **F.** Middle region of the blade with dorsiventral mesophyll and knob-like glandular trichome (g) on the abaxial side; note druses (arrow head only) dispersed on the mesophyll and sclereid (arrow). **G.** Knob-like glandular trichome on the adaxial side. Abbreviations: co: collenchyma; db: dorsal bundles; ep: epidermal cells; g: glandular trichome; id: idioblast; p: porrect ray; ph: phloem; pp: palisade parenchyma; s: simple trichome; sp: spongy parenchyma; st: stoma; tr: trichome; x: xylem. Scale bars: A–C = 20 μ m; D = 100 μ m (detail = 20 μ m); E–G = 50 μ m.

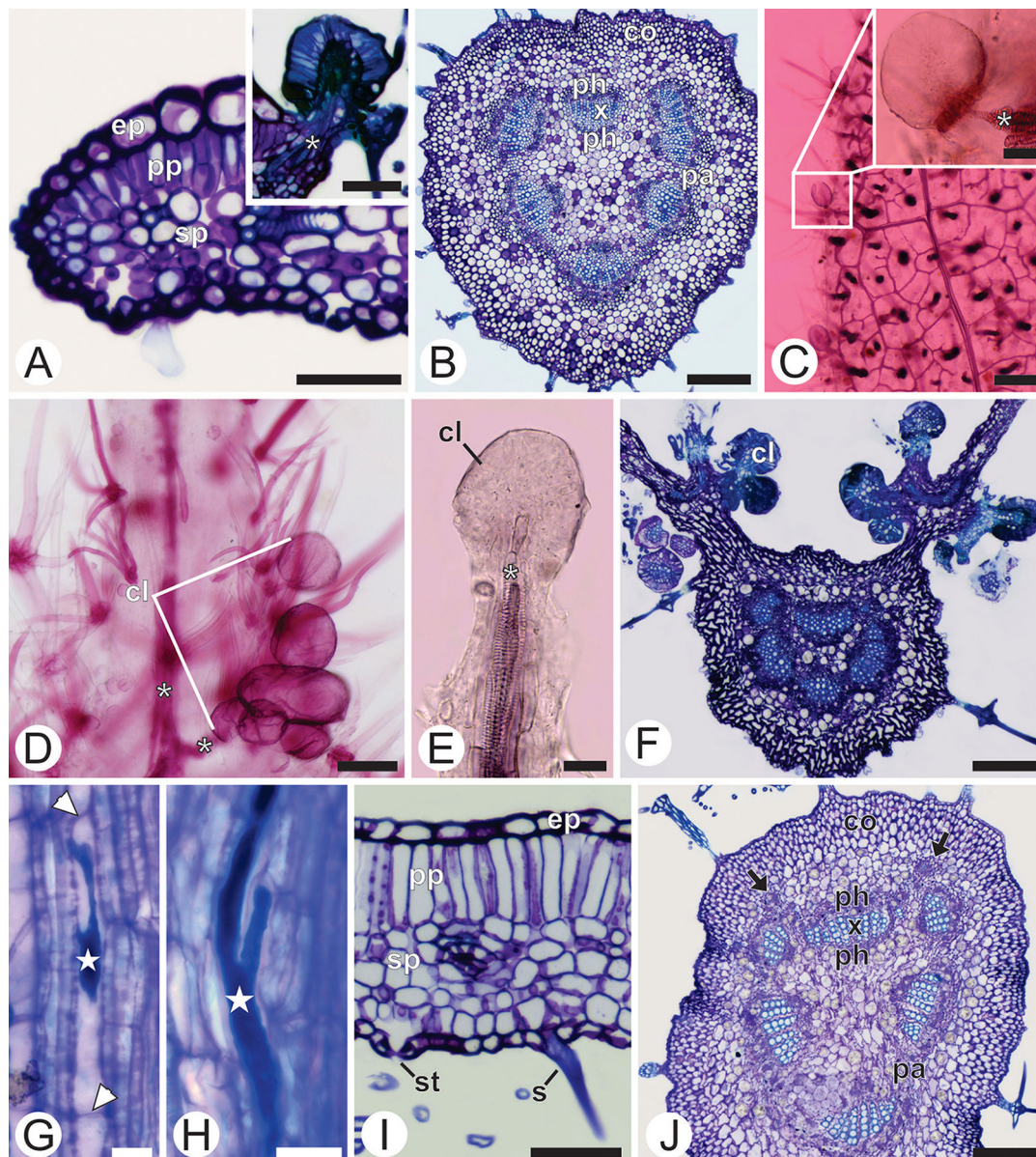


Fig. 4. Leaf anatomy features of *Croton maranonensis* sp. nov. (A–H), *C. triqueter* Lam. (I) and *C. flavispicatus* Rusby (J), based on transverse (A, B, F–J) and longitudinal (G–H) sections; diaphanization of leaf blade (C) and stipules (D–E). **A.** Blade margin with non-continuous palisade parenchyma; note standard vascularized coléter in detail (asterisk). **B.** Petiole with bicollateral vascular system organized in a closed arch with the bundles separated by parenchyma and without accessory bundles. **C.** Standard colleters along the margin, note vascularization at the base (asterisk). **D.** Clusters of vascularized (asterisks) colleters (cl) at the base of the stipule. **E.** A single colleter at the apex of the stipule, note the vascularization at the base (asterisk). **F.** Cluster of basilar/acropetiolar colleters at both sides of the petiole. **G.** Non-anastomosed articulated laticifers; note the transverse walls (arrow head) and the latex content (star). **H.** Y-shaped laticifers (star). **I.** Dorsiventral mesophyll and simple trichome (s) on abaxial surface. **J.** Petiole with bicollateral vascular system organized in a closed arch with the bundles separated by parenchyma and one pair of accessory bundles (arrow). Abbreviations: cl: colleter; co: collenchyma; ep: epidermal cells; pa: parenchyma; ph: phloem; pp: palisade parenchyma; s: simple trichome; sp: spongy parenchyma; st: stoma; x: xylem. Scale bars: A, D = 100 µm; B–C, F, J = 200 µm (detail of C = 20 µm); E, I = 50 µm; G–H = 10 µm.

trichomes at the apex, abaxial surface with a dense indumentum of stellate trichomes; petals narrow-elliptic $1.2\text{--}2.0 \times 0.5\text{--}0.7$ mm, simple trichomes scattered on adaxial side and toward the apex, abaxial side glabrous; receptacle densely pilose; stamens 11–12, filaments 2.5–3.0 mm long, with trichomes toward the base, anthers $0.6\text{--}0.8 \times 0.3\text{--}0.5$ mm. *Pistillate flowers* pedicellate, pedicel 0.5–1 mm long; sepals triangular-ovate, valvate, unequal, the 3 large sepals $1.8\text{--}2.0 \times 0.8\text{--}1.2$ mm, often with a dissected margin, sometimes with a long acuminate apex, the 2 small sepals $1.0\text{--}1.2 \times 0.3\text{--}0.5$ mm, with margin entire, adaxial and abaxial sides with stellate trichomes; petals absent; nectary disc entire; ovary densely covered with stellate trichomes; styles bifid, covered in part with stellate trichomes. *Fruits* subglobose, $4.0\text{--}5.0 \times 3.0\text{--}3.5$ mm, columella 2.5–3.0 mm long; seeds elliptical, $2.7\text{--}3.0 \times 1.3\text{--}1.5$ mm, usually mottled (brownish with black spots), surface slightly foveolate, shiny; caruncle $0.2\text{--}0.3 \times 0.2\text{--}0.3$ mm. (Figs 1–2).

Main micromorphological features of *Croton maranonensis* sp. nov.

Leaves are amphi-hypoestomatic, with paracytic stomata and epidermal cells exhibiting straight contour (Fig. 3A) on both faces. Simple trichomes and stipitate stellate porrect trichomes were present (Figs 3B–C); trichome stipes were shorter on the adaxial sides than on the abaxial side. Sometimes idioblasts were observed at the base of the radial cells of stellate trichomes (Fig. 3D, in detailed image). Sclereids, connecting both leaf sides across the mesophyll, were present at the base of stellate trichomes (Fig. 3E). Unicellular, glandular trichomes were relatively abundant on the abaxial side (Fig. 3C) and rare on the adaxial side (Fig. 3B). Glandular trichome had a knob-like appearance with a narrow base and a dilated distal portion (Figs 3F–G). Epidermal cells were tabular with mucilage content (Fig. 3F); the mesophyll is dorsiventral (Fig. 3F). The contour of the midrib is biconvex, with 2–3 layers of annular subepidermal collenchyma (Fig. 3D).

The bicollateral vascular system is organized in an open arch with a dorsal bundle (Fig. 3D). The blade margin is straight with non-continuous palisade parenchyma (Fig. 4A). The petiole has a flat-convex shape (Fig. 4B) and is covered by a uniseriate epidermis. Three to five subepidermal layers of annular collenchyma surround the entire petiole (Fig. 4B). The bicollateral vascular system is organized in a closed arch with the bundles separated by parenchyma (Fig. 4B). Both young and fully expanded leaves present standard colleters scattered along the blade margin (Figs 4A, C). Clusters of colleters were observed at the base of stipules (Fig. 4D) and on the basilaminar/acropetiolar region of the leaf (Fig. 4F), while only a single colleter was present at the stipule apex (Fig. 4E). Standard colleters consist of one-layer secretory palisade epidermis, and parenchyma, which are vascularized by xylem and phloem (Fig. 4A, E). Idioblasts with druse occur in the mesophyll (Fig. 3F), midrib, and petiole. Non-anastomosed articulated laticifers (Fig. 4G) were observed in shoots and fully expanded leaves, always associated with phloem, often exhibiting a Y-shaped form (Fig. 4H). Specimens of *C. flavispicatus* and *C. triqueter* had similar anatomical features (Fig. 4I), with the exception of the presence of a pair of accessory bundles in the petiole (Fig. 4J, Table 1), which was absent in *C. maranonensis* sp. nov. (Fig. 4B), and the absence of simple trichomes on the blade abaxial side. The presence of simple trichomes on the abaxial side of the blade (Fig. 4I) and the occurrence of idioblasts at the base of the radial cells of stellate trichomes of *C. triqueter* were the only anatomical differences observed between *C. triqueter* and *C. flavispicatus*.

Phylogenetic placement and relationships

The ITS matrix, with 63 aligned positions, consisted of 32 sequences representing 24 species of *Croton*, including 9 from the focal group (*C. sect. Julocroton*). Overall the topology of the represented *Croton* clades or sections (Fig. 5) was congruent with previous *Croton* phylogenetic analyses (Berry *et al.* 2005; Van Ee *et al.* 2011). *Croton* sect. *Julocroton*, *C. sect. Lasiogyne* (Klotzsch) Baill. and *C. sect. Heptallon* (Raf.) Müll. Arg. were recovered as highly supported monophyletic groups (Posterior Probability, PP = 1). The three specimens of *C. maranonensis* sp. nov. were clustered together in a highly supported clade (PP = 1) within the *C. sect. Julocroton* clade. The new species was recovered sister to a clade including

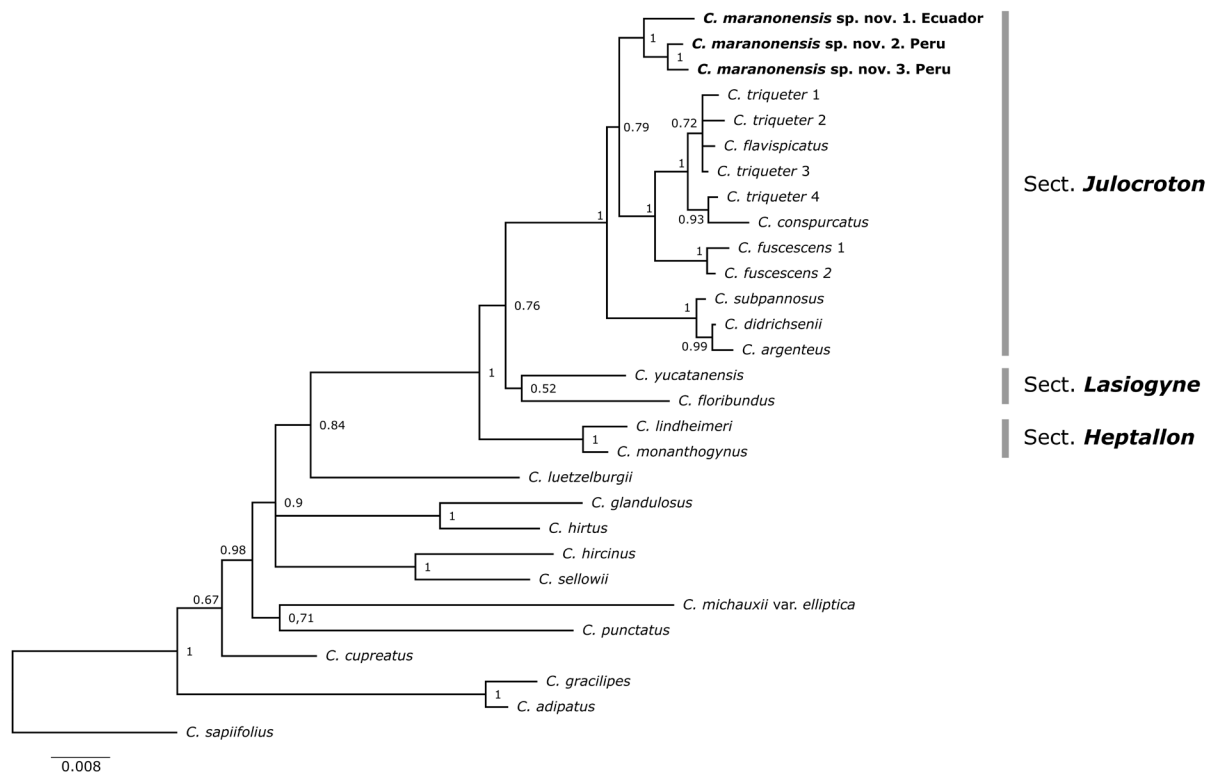


Fig. 5. Bayesian phylogram based on ITS sequences of the selected *Croton* species including *C. maranonensis* sp. nov. and representatives of sections *Julocroton*, *Lasiogyne*, *Heptallon*, and other sections of *Croton*. Numbers at nodes indicate Bayesian posterior probability values (PP). Numbers distinguishing accessions of the same species are also indicated in Appendix 2. The country of origin of the sample is indicated only for the samples of the new species..

C. triqueter, *C. flavispicatus*, *C. hondensis*, *C. conspurcatus* Schldl. and *C. fuscescens* Spreng., albeit with relatively low support (PP = 0.79). The three accessions of *C. hondensis* and the two specimens of *C. fuscescens* were recovered as monophyletic groups, while the four representatives of *C. triqueter* emerged as unresolved within the largest clade including *C. flavispicatus*, *C. hondensis*, *C. triqueter*, and *C. conspurcatus*. The clade including *C. argenteus* was recovered sister to the rest of the *C. sect. Julocroton*.

Distribution, ecology, and phenology

Croton maranonensis sp. nov. is distributed in the Marañón Valley in northern Peru and in the Province of Loja, southern Ecuador. According to information from specimens labels, the species grows in seasonally dry tropical forest and dry shrublands, along semideciduous shrubs from different plant families, giant columnar cacti, ferns, and epiphytic bromeliads (Fig. 6). Examined specimens were in flower and fruit throughout the year.

Preliminary conservation status assessment

The extent of occurrence (EOO) and area of occupancy (AOO) resulted in 26,335.574 km² for EOO and 72,000 km² for AOO. Following the IUCN criteria (IUCN 2012), *Croton maranonensis* sp. nov. cannot be classified as vulnerable (VU) using the B1 criterion due to its disjunct distribution with relatively isolated populations in southern Ecuador and a few records (*González 6491* and *Marcelo-Peña 11142*,

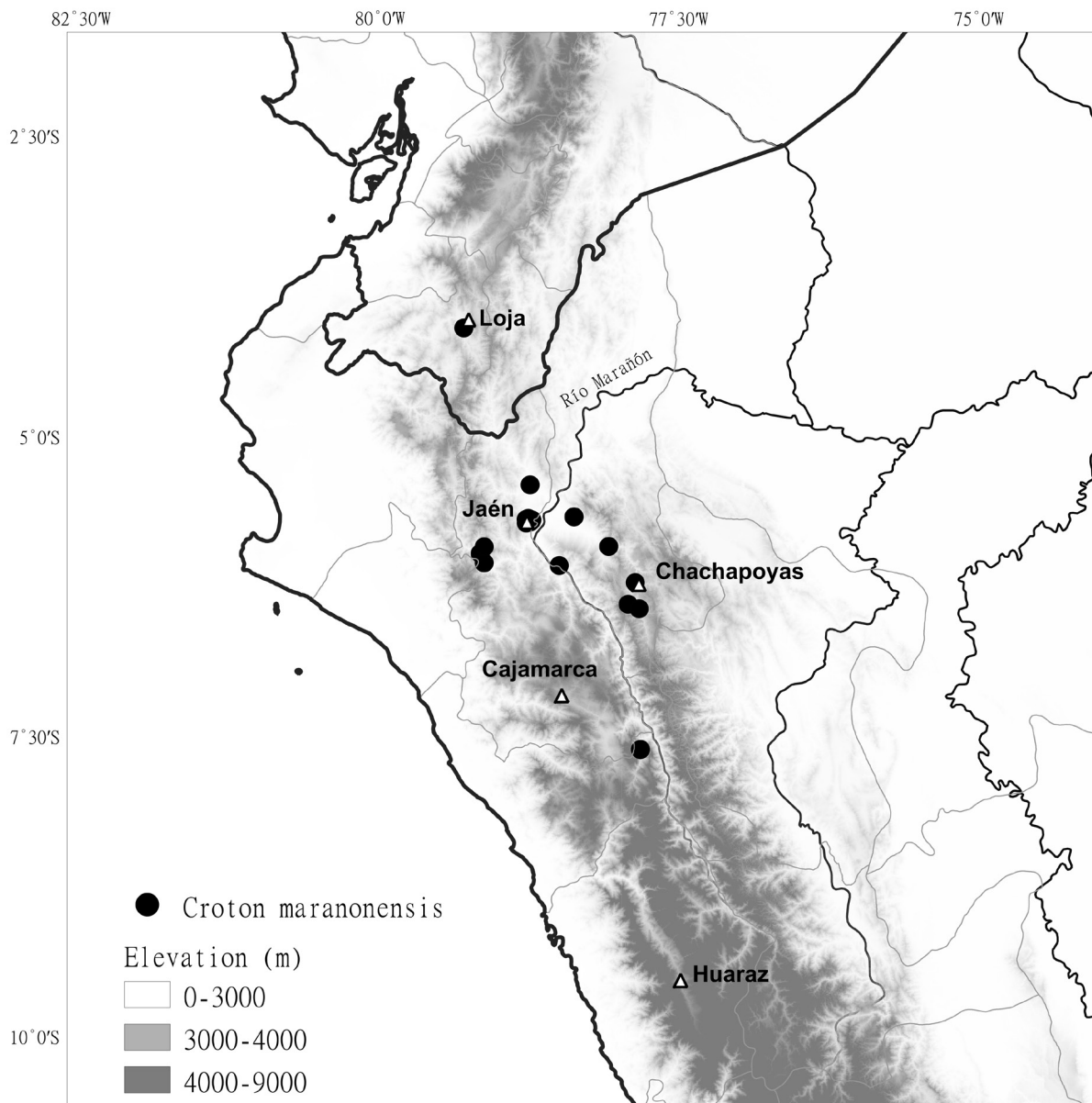


Fig. 6. Map showing the location of the known herbarium collections of *Croton maranonensis* sp. nov. (solid circles). Main cities in the area are indicated by white triangles.

11146) collected upstream (south) in the Marañón Valley (Fig. 5). For this reason we classify the species tentatively as nearly threatened (NT).

Discussion

New species discovery, elaboration of morphological description, and the final publication of a new taxon is often a long process which could extend for decades (Bebber *et al.* 2010; Riina *et al.* 2015; Goodwin *et al.* 2020). This is the case of *Croton maranonensis* sp. nov., whose first specimen was collected in 1877, about 145 years ago, by the famous french botanist and explorer Édouard François André (Smith 1965; Padilla 1984). We provide strong evidence from multiple sources that support the recognition of this species as an independent *Croton* lineage within *C.* section *Julocroton*. Both morphological (including anatomy) and molecular data provide strong support for establishing *C. maranonensis*

sp. nov. Although our phylogenetic analysis is limited in genome representation (only ITS) and in taxon sampling (21% of the *C. sect. Julocroton* diversity), the molecular evidence is relatively strong in support of *C. maranonensis* sp. nov. because its clade, including accessions from Peru and Ecuador, is both strongly supported and highly divergent from all the other central-northern Andean species known in the section. Key morphological characters separating the new species from its most closely similar Andean species (*C. hondensis* and *C. flavispicatus*) include cylindrical and smooth stems opposed to costate stems in *C. flavispicatus* and *C. triqueter*, shorter petioles without a pair of accessory bundles and smaller leaves, stipules and bracts. *Croton maranonensis* sp. nov. also occupies different habitats (dry forests and shrublands) than *C. flavispicatus*, and it can be found at higher elevations, up to 2400 m (Table 1). Finally, *C. maranonensis* occurs in northern Peru and southern Ecuador while *C. hondensis* is known only from Colombia, where it also grows in dry forests.

We observed slight morphological differences between the Peruvian and Ecuadorian populations of *C. maranonensis* sp. nov., such as the presence of sparse, dark ferruginous, stellate trichomes (interspersed with whitish trichomes) on the apical parts of branches and inflorescences and the more costate stems in the Ecuadorian specimens. However, scattered ferruginous stellate trichomes were also observed in some specimens from Peru, especially on young leaves and young inflorescences.

Croton maranonensis sp. nov. might be the undetermined *Croton* species (as ‘*Croton* sp.’) reported by Marcelo-Peña *et al.* (2016) in their study of the Marañón flora. However, the authors did not include voucher information that could allow us to verify the species identity. Similarly, researchers conducting ecological studies in the southern Ecuadorian dry shrublands, where *C. maranonensis* sp. nov. could occur, were unable to identify the focal *Croton* taxa under study because of incomplete taxonomic knowledge of the species dominating those dry habitats and the possibility of hybridization involving populations of closely related species (Vélez-Mora *et al.* 2022). Additional systematics studies, including a phylogeographic approach, are needed to understand species boundaries among these abundant *Croton* shrubs from arid Andean ecosystems (e.g., Luján *et al.* 2015).

In our dissections of specimens of *C. flavispicatus* and *C. maranonensis* sp. nov. flowers, we found that style branches are very fragile and they are often broken in herbarium specimens. This may lead to confusion when this character is used to separate these species. Morphological differences between *C. triqueter*, *C. hondensis*, and *C. flavispicatus* are very subtle, which is also reflected in the results of the phylogenetic analysis, where specimens from the three species are embedded in a polytomy. A specimen of *C. conspurcatus* is also part of this polytomy but is well resolved in a clade with one of the accessions of *C. triqueter* (accession 4). These preliminary phylogenetic results indicate that further phylogenetic studies using a wider taxon sampling of section *Julocroton* and related clades will be needed to better establish species limits within this understudied section of Neotropical *Croton*.

The presence of the acropetiolar/basilaminar clusters of colleters (Figs 1B, 3I) is a novel finding for the genus *Croton* as a whole. So far, this feature is only known for *C. maranonensis* sp. nov., but it is possible that it could be present in other *Julocroton* species. Interestingly, these raceme of petiolar colleters are situated in the usual position of nectary glands in other *Croton* sections. However, it is unlikely that these colleters have the same function (ant attraction) of extrafloral nectaries in *Croton* (Aguirre *et al.* 2013; Leal *et al.* 2015) since colleters are only active in their early stage of leaf development (Vitarelli *et al.* 2015; Meira *et al.* 2020).

Similar to other *Croton* species that occur in dry environments (Vitarelli *et al.* 2015, 2021; Sodr e *et al.* 2019), *C. maranonensis* sp. nov. bears sclereids associated with epidermal trichomes in leaves. Therefore, our results reinforce previous findings about the functional role of these structures as capable of atmospheric water absorption, which has been suggested as a survival strategy for *Croton*

species that live in environments with strong soil water restrictions (Vitarelli *et al.* 2016, 2021). In fact, *C. maranonensis* sp. nov. occurs in extreme dry habitats, subject to a severe dry season (8–9 months) with an average annual rainfall of ca 550 mm in the Marañón Valley (Marcelo-Peña *et al.* 2016) and 317 mm in the southern Ecuadorian inter-Andean valleys (Vélez-Mora *et al.* 2022).

Regarding the suggested conservation status for the new species, it will be important to explore possible under-collected areas within the two gaps, in Peru and Ecuador, shown in the distribution map (Fig. 6), since there are areas of dry forest in those areas (DRYFLOR 2016; Quintana *et al.* 2017) where *C. maranonensis* sp. nov. populations could be present.

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Supplementary files

Supp. file 1. ITS alignments.

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Appendix 1. Specimens of *Croton flavispicatus* Rusby, *C. hondensis* (H.Karst.) G.L.Webster, and *C. triqueter* Lam. examined for morphological and anatomical analysis.

Croton flavispicatus Rusby

BOLIVIA • 20 Dec. 1921; 800 ft.; *M. Cárdenas 2026*; A [A00003150], BKL [BKL00000631], GH [GH00047295], NY [NY 00246540], US [US00109559].

PERU • Dpto. San Martín, Tarapoto; 6 Jan. 1855; *R. Spruce 4290*; BM [BM000777935], BR [BR000006999223], K [K000601111], P [P00623189] • Dpto. San Martín, Juanjul, Tarapoto; 07°05' S, 76°55' W; elev. 400 m; 5 Feb. 1984; *A. Gentry & D.N. Smith 44940*; COL [COL000390386], MO • Dpto. San Martín, Prov. Lamas, Caserío Lamas, en chacra cerca de nacimiento de quebrada; 06°25'13" S, 76°30'51" W; elev. 800 m; 18 May 2004; *R. Riina & J. Campos 1450*; MA, USM.

Croton hondensis (H.Karst.) G.L.Webster

COLOMBIA • Dpto. Antioquia, Olaya, Carretera que conduce al corregimiento de Llanadas; 06°40'59" N, 75°49'0" W; elev. 800–1000 m; 1 Mar. 2003; *J.C. Marrugo G. 875*; COL [COL000220351] • Dpto. Antioquia, Santa Fe de Antioquia, Finca Cotove, margen derecha del Río Tonusco, 1 km antes de la desembocadura; 06°33'35" N, 75°49'41" W; elev. 700–750 m; 20 Feb. 1981; *G. Galeano 383*; COL [COL000390653] • Dpto. Antioquia, Santa Fe de Antioquia, vega del río Tonuzco; elev. 600 m; Aug. 1962; *J. Murillo 567*; COL [COL000390662] • Dpto. Cudinarca, Girardot; elev. 326 m; 19 Mar. 1962; *I. Baptiste 16*; COL [COL000396921] • Dpto. Tolima, Armero, I.F.A., Campo Exp. de Bledonia; 15 Jun. 1960; *J.A. Barreneche 27*; COL [COL000390659] • Dpto. Cudinarca, Municipio de Nariño, Quebradas de Apauta, Pitalito, Juanchiquito y Los Mangos; elev. 350–600 m; 13–15 Sep. 1989; *J.L. Fernández Alonso & R. Jaramillo Mejía 8093*; MA [MA-491555] • Dpto. Cudinarca, Poblado de Nariño, Carretera de Los Mangos; elev. 340 m; 15 Feb. 1986; *Fernández Alonso & R. Jaramillo Mejía 5256*; MA [MA-517068] • Dpto. Cudinarca, Nariño; elev. 340 m; 15 Feb. 1986; *Fernández Alonso & R. Jaramillo 5257*; MA [MA-851531] • Dpto. Cudinarca, Tocaima, Prov. Bogota; elev. 450 m; Jan. 1853; *Triana 5827-1*; A [A00003143] • Dpto. Tolima, Armero, I.F.A.- Campo Exp. de Bledonia; 15 Jun. 1960; *J.A. Barreneche E. 27*; COL [COL000390659] • Dpto. Tolima, Honda; *Karsten s.n.*; F [F871326] • Without locality; 1783–1808; *J.C. Mutis 1473*; MA [MA-663646], [MA-663647], [MA-663648], [MA-663649]; Without locality; *J.C. Mutis 1479*; MA [MA-663650], [MA-663651].

Croton triqueter Lam.

BRAZIL • Rio de Janeiro, des environs Rio de Janeiro; Jun. 1767; *Commerson s.n.*; P (P00634801) • Minas Gerais, Santana do Riacho, Morro da Pedreira; 19°18'27" S, 43°36'50" W; 900 m; 5 Mar. 2002; *L.R. Lima 134*; SPF [SPF00150863] • Minas Gerais, Diamantina, Turmalina; 16°59'51" S, 42°47'51" W; 445 m; 24 Jan. 2004; *Riina 1356*; SPF [SPF00164171] • São Paulo, Eldorado, Estrada para o Mirante do Cruzeiro; 10 Apr. 2004; *S.E. Martins 834*; SP [SP0369873] • São Paulo, Itararé; 13 Mar. 2004; *M.B.R. Caruzo et al. 27*; ESA [ESA052603], F [2260700], RFA [RFA39534], SP [SP0367404], UB [UB150891].

Appendix 2. Taxa, localities, vouchers, and GenBank accession numbers for all sequences of the nuclear ITS region analyzed in this study. Newly generated sequences are marked with an asterisk (*).

Croton adipatus Kunth; Ecuador, Bagua Grande; *Riina 1468* (QCNE); KP764612. *C. argenteus* L.; Costa Rica, Guanacaste; *Van Ee 297* (WIS); EU478094. *C. conspurcatus* Schltld.; Mexico, Jalisco; *Santana 5921* (WIS); EU478095. *C. cupreatus* Croizat; Ecuador, Pichincha; *Smith 473* (WIS); HM564077. *C. didrichsenii* G.L.Webster; Brazil, Tocantins, Natividade; *Mello-Silva 2361* (SPF); OR622585*. *C. flavispicatus* Rusby; Perú, San Martín, Tarapoto; *Riina 1450* (MA, MICH, USM); OR622586*. *C. floribundus* Spreng.; Brazil, São Paulo, Jundiaí; *Santos 3* (SP); OR622587*. *C. fuscescens* Spreng. [1]; Brazil, Ceará, Meruoca; *Sousa 4* (HUEFS); OR622588*. *C. fuscescens* Spreng. [2]; Brazil, São Paulo; *Van Ee 502* (WIS); HM564081. *C. glandulosus* L.; U.S.A., Wisconsin; *Van Ee et al. 512* (WIS); EU478066. *C. gracilipes* Baill.; Bolivia, Santa Cruz; *Nee 47412* (NY); EU586909. *C. hircinus* Vent.; Venezuela, Distrito Federal; *Riina 1291* (VEN); EU477889. *C. hirtus* L'Hér.; Brazil, Pernambuco; *Van Ee 481* (WIS); EU478071. *C. hondensis* (H.Karst.) G.L.Webster [1]; Colombia, Cudinamarca; *Fernández Alonso & Jaramillo 5256* (MA); OR622589*. *C. hondensis* (H.Karst.) G.L.Webster [2]; Colombia, Cudinamarca; *Fernández Alonso & Jaramillo 5257* (MA); OR622591*. *C. hondensis* (H.Karst.) G.L.Webster [3]; Colombia, Cudinamarca; *Fernández Alonso & Jaramillo 8093* (MA); OR622590*. *C. lindheimeri* (Englem. & A.Gray) Alph.Wood; U.S.A., Louisiana; *Van Ee et al. 517* (WIS); EU478106. *C. luetzelburgii* Pax & K.Hoffm.; Brazil, Bahia; *Conceição 1457* (HUEFS); HM564087. *C. maranonensis* sp. nov. [1]; Ecuador, Loja; *Cumbicus & Camacho 1924* (MA); OR622592*. *C. maranonensis* sp. nov. [2]; Peru, Amazonas, Bagua Grande; *Vásquez 27094* (MO); OR622593*. *C. maranonensis* sp. nov. [3]; Peru, Amazonas; *Dexter 5935* (E); OR622594*. *C. michauxii* G.L.Webster var. *elliptica* (Willd.) B.W.van Ee & P.E.Berry; U.S.A., Missouri; *Archer 40* (MO); EU478004. *C. monoanthogynus* Michx.; U.S.A., Illinois; *Van Ee et al. 515* (WIS); EU478113. *C. punctatus* Jacq.; Mexico, Veracruz; *Van Ee et al. 528* (WIS); EU478022. *C. sapiifolius* Müll.Arg; Brazil, Bahia; *Lima 677* (CEPEC); EF421754. *C. sellowii* Baill.; Brazil, Bahia; *Van Ee 498* (WIS); HM564095. *C. subpannosus* Griseb.; Brazil, Matto Grosso do Sul; *Webster 25374* (MO), AY971253. *C. triqueter* Lam. [1]; Brazil, Minas Gerais, Santana do Riacho; *L.R. Lima 134* (SPF); OR622595*. *C. triqueter* [2]; Bolivia, Santa Cruz; *Nee 40034* (NY); AY971256. *C. triqueter* [3]; Brazil, Minas Gerais; *Riina 1356* (SPF); OR622596*. *C. triqueter* [4]; Brazil, São Paulo, Eldorado; *S.E. Martins 834* (SP); OR622597*. *C. yucatanensis* Lundell; Mexico, Yucatán; *Van Ee & May-Pat 121* (WIS); DQ227537.
