Research manuscript

Untangling taxonomic knots: the intricate case of *Croton anomalus* (Euphorbiaceae), a seasonally dry tropical forest specialist

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Abstract

Croton anomalus was described by Henri Pittier in 1930 from a collection made in Estado Lara, Venezuela, and its use has so far been restricted to several states in Venezuela. A reevaluation of the species here has led here to its recircumscription and recognition in several other countries, including Suriname, Brazil, Bolivia, and Mexico. Previously, it was confused with several species referred to here as the "*Croton anomalus* group", namely *C. acapulcensis*, *C. blanchetianus*, *C. chiapensis*, *C. jacobinensis* (=*C. sonderianus*), and *C. stahelianus*. We integrated morphological, phylogenetic, and ecological evidence to understand species limits and relationships within the *Croton anomalus* group. We first studied ca. 650 herbarium specimens covering the geographic range of the group, and we inferred species phylogenetic relationships using DNA sequences from the nuclear and plastid regions (ITS and *trnL-F*). We also used ecological niche modeling to infer potential suitable areas for the occurrence of the studied species and to determine the variables that most contribute to their distribution model. Both morphological and phylogenetic data provide evidence for the synonymization of *C. acapulcensis*, *C. chiapensis*, and *C. stahelianus* under *C. anomalus*. On the other hand, our results support the recognition of *C. blanchetianus* and *C.*

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jacobinensis are two independent lineages, both distinct from *C. anomalus*. An amended description of *C. anomalus* is provided, as well as the designation of a lectotype, illustrations, updates of distribution data, and morphological comparisons with closely related species. Regarding niche modeling, annual precipitation was the most important variable explaining species distributions. *Croton anomalus* showed suitable areas in most Seasonally Dry Tropical Forests in the Neotropics, while *C. blanchetianus* and *C. jacobinensis* had their suitable areas restricted to the Caatinga Dry Forest (Brazil), and Caatinga + northern South America, respectively. Our study shows the importance of taxonomic revisions using integrative approaches to disentangling species boundaries and to elucidate their biogeography and conservation.

Keywords - *Croton blanchetianus*; *Croton sonderianus*; marmeleiros; Neotropics, integrative taxonomy.

Introduction

The delimitation of cryptic or morphologically very similar species is a long-standing challenge in taxonomy, and it is a common problem in megadiverse lineages. Properly recognizing such cryptic species is crucial for understanding species distributions, assessing biological conservation, and more accurately estimating biodiversity (Bickford et al., 2007; Padial et al., 2010). Since occurrence data are one of the most important pieces of evidence when designating new species, delimitation is more difficult when the putative taxa present disjunct distributions (Padial et al., 2010; Medina et al. 2012; Salvador-Montoya et al., 2015; Guimarães et al., 2021; Sassone et al., 2021), which in some cases may be artifactual due to poorly explored areas or collection gaps (Feeley, 2015; Riina et al., 2018; Ondo et al., 2024). Thus, the use of integrative approaches becomes an efficient alternative to achieve more assertive taxonomic decisions (Padial et al., 2010; Frajman et al., 2019).

Croton L. is the most species-rich genus occurring in the Caatinga Dry Forest (Fernandes et al., 2020) with ca. 70 species (Carneiro-Torres, 2009; Caruzo et al., 2020). It is also an important genus in many of the Seasonally Dry Tropical Forests (SDTF) areas of the Americas (DRYFLOR, 2016; Quintana et al. 2017). The SDTF biome has long been under-appreciated by the scientific community when compared to other biomes such as Savannas and Tropical Rainforests (Moonlight et al., 2020). Although recent studies have increased our understanding of SDTFs (DRYFLOR, 2016; Escribano-Avila et al. 2017; Quintana et al. 2017; BFG, 2021; Carrión et al., 2022; Wurdack, 2023), the diversity of the Caatinga, the largest and the most species-rich area of SDTF, is still understudied (Queiroz et al., 2017; Fernandes et al., 2020).

The taxonomic knowledge of *Croton*, a genus with over 1,200 species (Moonlight et al., 2024), is still incomplete and problematic for many species groups within it (Berry et al., 2005; van Ee et al., 2011). For example, *C. sonderianus* Müll.Arg. is a frequent name in studies spanning taxonomy, phytochemistry, pharmacology, and ecology (*e.g.* Craveiro et al., 1981; Craveiro & Silveira, 1982; Lucena & Sales, 2006; Lôbo et al., 2011; Souza et al., 2017). However, the

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application of this name in northeastern Brazil to various *Croton* species, particularly those locally known as *'marmeleiros'* (Carneiro-Torres, 2009), poses a taxonomic challenge. Despite the proposal of Gomes et al. (2010) that *C. sonderianus* should be synonymized under *C. jacobinensis* Baill., the use of the former persists in the scientific literature, including Flora & Funga do Brasil (2020). In addition, in numerous cases the name *C. sonderianus* has also been misapplied to specimens of *C. blanchetianus* Baill. ~~as if they were synonyms~~.

After an extensive revision of specimens identified as *C. sonderianus*, we realized that a third species (*C. anomalus* Pittier) was involved, which had never been cited for Brazil. *Croton anomalus* was published nearly a century ago (Pittier, 1930) and it was known only from Venezuela (Hockche et al. 2008). Additionally, three other species, very similar to *C. anomalus*, were noted during our ongoing revision of *C.* sect. *Lasiogyne* (Klotzsch) Baill. and were also considered for this study. These species are *C. acapulcensis* Mart.Gord. & J.Jiménez Ram. and *C. chiapensis* Lundell, both from Mexico, and *C. stahelianus* Lanj., known from Suriname (Lanjouw, 1931; Lundell, 1942; Gordillo & Ramírez, 1990). Based on these morphological observations, we proposed the following hypotheses: i) *Croton blanchetianus* and *C. jacobinensis* are separate lineages independent of *C. anomalus*; and ii) *C. anomalus* includes *C. acapulcensis*, *C. chiapensis*, and *C. stahelianus* as synonyms, and has a broad geographic range.

The taxonomic riddle concerning *C. anomalus* and other names/species in the *Croton anomalus* group is discussed and disentangled here. We use morphological, ecological, geographic, and phylogenetic data to elucidate the taxonomy of this group. We also employ ecological niche modeling to uncover potential suitable areas for the occurrence of the studied species. An amended description and designation of a lectotype for *C. anomalus*, distribution maps, illustrations, preliminary conservation assessments, and a historical discussion about this taxonomic complex are provided.

Material and Methods

Sampling

We analyzed ca. 650 herbarium specimens identified as *Croton anomalus*, *C. acapulcensis*, *C. chiapensis*, *C. blanchetianus* (see Appendix 1 in Rossine et al., 2023), *C. jacobinensis* (see Appendix 1 in Rossine et al., 2023), *C. sonderianus*, and *C. stahelianus.* The specimens deposited in A, CA, CEPEC, EAC, HESBRA (not indexed), HUEFS, HUESB, HST, K, MA, MICH, MO, MOSS, NY, PEUFR, UFP, US, VEN, W (acronyms follow Thiers, continuously updated) were analyzed, and complemented by virtual specimens from other herbaria available at SpeciesLink (https://specieslink.net/search/), Southeast Regional Network of Expertise and Collections - SERNEC (https://sernecportal.org/portal/) or directly from herbarium online data portals.

For the phylogenetic analyses, we included a total 37 specimens, representing 29 putative species (28 of *Croton*, and *Brasiliocroton muricatus* Riina & Cordeiro as the outgroup), of which 16 samples were part of the *Croton anomalus* group (Table 1). Unfortunately, we were not able to sample *C. chiapensis* for phylogenetic analyses due to the lack of material (the species is only known from the type).

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DNA extraction, amplification, sequencing, and alignment

Total genomic DNA was extracted according to the CTAB protocol (Doyle, 1991). The nuclear ribosomal internal transcribed spacer (ITS) region, and the plastid intergenic spacer *trnL-trnF* (hereafter called *trnL-F*) were amplified using the PCR settings of Masa-Iranzo et al. (2021) and sent to Macrogen (Macrogen, Madrid) for sequencing. Primers and references are given in Table 2. The aforementioned regions have been widely used and proven to be informative in previous studies of *Croton* (*e.g.* van Ee et al., 2011; Masa-Iranzo et al., 2021; Riina et al., 2021). Sequences were assembled and aligned with MAFFT (default parameters), followed by a manual edition in Unipro UGENE (Okonechnikov et al., 2012). Summary statistics of each data matrix were estimated in PAUP v.4.0a169 (Swofford, 2002).

Phylogenetic analyses

Bayesian Inference (BI) was used to reconstruct phylogenetic relationships of the nuclear and plastid regions individually. Since no incongruences were found after visual examination of the two topologies, a concatenated dataset was generated using SequenceMatrix (Vaidya et al., 2011). Incongruences between topologies were considered as such if the clades in question were supported with > 0.95 posterior probability (PP), following Alfaro et al. (2003). The BI was performed in MrBayes v.3.2.7a (Ronquist et al., 2012). The best substitution models were determined in JModelTest2 v.2.1.10 using the Akaike Information Criterion (AIC) and were SYM+I+G for ITS, TIM1+G for *trnL-F*. These were substituted for the most similar and compatible models implemented in MrBayes: GRT+I+G for ITS and GTR+G for *trnL-F*. The aforementioned analyses were all run on the XSEDE-CIPRES platform (Miller et al., 2010). Bayesian PP were generated from two runs each of four chains. The parameters set were the following: 30 million generations with sampling in every 1,000th generation; default priors, and discarding the first 25% sampled trees and parameters for burn-in. Estimated sample size (ESS) values (> 200) were checked in Tracer v.1.6 (Rambaut & Drummond, 2007).

The phylogenetic trees were visualized and edited in FigTree (Rambaut, 2010) followed by a vector edition for publishing. The support values for Bayesian Posterior Probability (PP) were considered moderate when ≥ 0.75 to < 0.95 PP and strong when ≥ 0.95 PP.

Taxonomic treatment

Protologues, type specimens, historical and general collections were examined and compared for all names/species treated here. The nomenclatural decisions were made under the recommendations of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018). The general terminology used in the taxon descriptions follows Simpson (2006). Specific terminology for section *Lasiogyne* follows previous works on the group (Rossine et al., 2023) with additions from Pinto-Silva et al. (2023) for trichomes.

Distribution maps, conservation status, and ecological niche modeling

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Geographic coordinates were obtained from the labels of herbarium specimens. When only locality was available, without coordinates, the approximate coordinates were estimated using Google Earth (https://earth.google.com/web/). Distribution maps were produced in the Quantum Geographic Information System (QGIS) version 3.4.13 (QGIS Development Team, 2020), using cartographic data from OpenDataSoft (https://public.opendatasoft.com) for World administrative boundaries, and the DryFlor network (http://www.dryflor.info/) for SDTFs areas. The preliminary assessments of the species conservation status were based on the guidelines from the IUCN Red List Categories and Criteria v.15.1 (IUCN, 2022) under B criteria, applying the estimated values of Extent of Occurrence (EOO) and Area of Occupancy (AOO), obtained from GeoCAT (http://geocat.kew.org/), following Bachman *et al*. (2011).

Using the same set of georeferenced records cited above, we modeled the ecological niche of each putative species using MaxEnt v.3.4.3 (Phillips et al., 2017). Default parameters were used with 10,000 background points (pseudoabsence). Replicates were performed 3 times. The variables used (Table 3) had 30 arc-sec resolution and were: bioclimatic from WorldClim (Fick & Hijmans 2017), elevation from the Shuttle Radar Topographic Mission (NASA – SRTM), and soil quality (Fischer et al., 2008). The area under the curve (AUC) was used to evaluate the projections.

RESULTS

Phylogenetic relationships within the Croton anomalus *group*

The data matrix included 74 sequences, of which 30 were newly generated in this study (15 of ITS and 15 of *trnL-F*). Voucher information and GenBank numbers for all the sequences used in the analyses are included in Table 1. The data alignment needed few manual adjustments after the automatic alignment. The aligned matrices of ITS and *trnL-F* are provided in Supplementary File 1 and Supplementary File 2. The ITS region had more variable characters and parsimony informative sites than *trnL-F* (Table 4). Summary statistics for each data matrix are shown in Table 4. Both nuclear ITS and plastid *trnL-F* analyses recovered similar topologies on the resulting trees, and no incongruences were found between the two datasets regarding the lineages formed by *C. anomalus*, *C. blanchetianus*, and *C. jacobinensis* (phylogenetic trees not shown, see Supplementary material, Figs. S1, S2).

~~We conducted the most representative phylogenetic analysis of *C.* sect. *Lasiogyne* to date, even if it only includes 10 of the more than 40 species currently assigned to the section (Fig. 1).~~ The phylogenetic reconstruction of the concatenated dataset recovers section *Lasiogyne* as a monophyletic lineage, with strong support (PP = 1; Fig. 1). Similarly, the topology of the backbone of the genus, including 10 other sections (Fig. 1), is in agreement with previous phylogenetic analysis at the genus level (Berry et al., 2005; van Ee et al., 2011). Section *Julocroton* was recovered as the sister clade of section *Lasiogyne*, and section *Heptallon* as sister of the former two with high support (PP = 1; Fig. 1).

~~The phylogenetic position of *C. anomalus* and *C. blanchetianus* as members of section *Lasiogyne* was demonstrated here for the first time (Fig. 1).~~ The concatenated (ITS + *trnLF*)

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phylogenetic analysis recovered the specimens of *C. blanchetianus* and *C. jacobinensis* as separate monophyletic lineages with high support (PP = 1), both independent of *C. anomalus* (Fig. 1). *Croton acapulcensis* and *C. stahelianus* were recovered in a highly supported clade along with all the *C. anomalus* specimens (1 PP; Fig. 1).

Taxonomic treatment

Croton anomalus Pittier, J. Wash. Acad. Sci. 20: 4. 1930. – TYPE: VENEZUELA. Lara: Los Rastrojos, between Sarare and Barquisimeto, in bushes, 10°04'29'' N, 69°15'31''W, Apr. 9, 1925, *H. Pittier 11757* (**lectotype, designated here**: A barcode A00047223!; isolectotypes: US barcode US00109497!, VEN barcode VEN6465!). Figures 2-3.

=*Croton acapulcensis* Mart. Gord. & J. Jiménez Ram., Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 60: 40. 1990. – TYPE: MEXICO. Guerrero: Acapulco, Parque Nacional "El Veladero", El Mirador, 16º45'00'' N, 99º43'55'' W, alt. 350 m, Jul. 6, 1985, *N. Noriega Acosta 599* (holotype: FCME [not seen]; isotype: MEXU barcode MEXU00511553!), ***syn. nov.***

=*Croton chiapensis* Lundell, Contr. Univ. Michigan Herb. 7: 18. 1942. TYPE: MEXICO. Chiapas: Escuintla, 160 m, Jul. 1938, *E. Matuda 2614* (holotype: MICH barcode MICH1191498!; isotypes: LL barcodes LL00371633! and LL00208230!, F barcode F0056020F!, A barcode A00047090!, MEXU barcode MEXU00078286!, EAP barcode EAP112178!), ***syn nov.***

=*Croton stahelianus* Lanj., Euphorb. Surinam, 17. 1931. –Type: SURINAME. Upper Koetarie R., 16 Oct. 1926, *B.W. n. 7002 = Stahel n. 611* (lectotype: U [not seen]; isolectotypes: IAN barcode IAN049296!, K barcodes K000254419! And K000254420!, RB barcode RB00538444!, US barcode US00109761!), ***syn nov.***

Monoecious shrubs, 0.7–2 m, latex not reported, monopodial ramification, branches brown, glabrescent, young ones greenish to yellowish with stellate trichomes. Leaves alternate; stipules linear to narrowly lanceolate, 5–8.8 × 1–1.4 mm, persistent, trichomes stellate; petiole 0.5–2 cm, trichomes stellate to multiradiate; leaf blade oval to elliptic, membranous, 2.5–9.5 × 1–4 cm, base rounded to cordate, margins entire, irregularly sinuate to slightly serrate, apex acuminate, discolorous, adaxial surface dark green with stellate-porrect trichomes, abaxial surface light green to yellowish with stellate trichomes, venation eucamptodromous to brochidodromous, 4–7 secondary veins, curved, ascendant. Inflorescences terminal or axillary, unisexual staminate or bisexual, 1–5 cm long, trichomes stellate to multiradiate, peduncle 3–5 mm, congested, 3–7 pistillate flowers per inflorescence; bracts linear or 3-lobed, 5–6 mm long, margins entire, apex acuminate, trichomes stellate-porrect, 1 bract per cymule, persistent. Staminate flowers with pedicels 3-4 mm, sepals yellowish, oval, 2 × 1 mm, margins entire, apex acute, united only near the base, trichomes stellate, indument dense externally and absent to sparse internally; petals white to yellowish, oblong, 3 × 1 mm, margins entire, apex rounded, trichomes simple; stamens (11-)14–17(-18), filaments ca. 2 mm, anthers elliptic, 1 × 0.5 mm; nectary disk rounded, unlobed, trichomes simple. Pistillate flowers with pedicels 2–5 mm (up to 10 mm in fruit), sepals 5–6 (7), equal to slightly unequal in size (when having 7 sepals), light green to whitish externally, dark green internally, oval to widely oval, 2.5–5 × 1.5–2.9, margins entire, apex acute, reduplicate lateral and vertically, ⅕ united at the base, trichomes stellate and stellate-porrect, indument dense externally

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and sparse internally; petals absent or rarely with vestigial petals, yellowish, linear to narrowly lanceolate, ca. 2–2.3 × 0.2–0.4 mm, margins entire, apex acuminate, trichomes simple; ovary globose, 2.1–2.8 mm diam., trichomes stellate-porrect; styles 3, ascendant, ~~4-fid to~~ multifid, free, with a total of 12–32(–48) stigmatic tips, trichomes stellate-porrect; nectary disk 5-lobed, lobes rounded, glabrescent. Capsules light green to yellowish, yellow when dry, globose, 3.5–8 mm diam., unlobed, surface hispid, with stellate-porrect trichomes, slightly 3-lobed to unlobed; columella ca. 4 mm, flattened, without prominent lobes; seeds brown to blackish, widely ovoid to slightly globoid, 3.6–4 × 3.2–3.6 mm, smooth to slightly papillate, with cream to greyish blotches, caruncle reniform.

Additional Specimens Examined

BOLIVIA. Santa Cruz: Cordillera, al sur de Bañados del Izozog, Estancia Toborochi y Cerro Toborochi, 18º49’52”S, 62º00’55”W, 520 m, 09.I.1993, fr., *G. Navarro 1728* (USZ); reas, Cerro Toborochi, 10–12 km por brecha abandonada al SE de Estancia Toborochi, fr., 5–15.I.1993, *I.C. Vargas et al. 1915* (WIS, USZ). **BRAZIL. Bahia:** Côcos, estrada Côcos – Feira da Mata, 14º15’12”S, 44º22’14”W, 484 m, fl., 09.I.2008, *R.F. Souza-Silva et al. 283* (HUEFS). Feira de Santana, Distrito de Ipuaçu, 12º13’58”S, 39º04’35”W, 230 m, 05.V.2005, fr., *A.P.L. Couto et al. 58* (HUEFS, HUESB). Morpará, estrada para Morpará, Beira do Rio Paramirim., 11º43’50”S, 43º13’39”W, 396 m, fl., 15.XII.2007, *A.A. Conceição 2642* (HUEFS). **Ceará:** Apuiarés, Triângulo marmelheiro rasteiro, 03º94’88.89”S, 39º43’17.01”W, 09.III.2008, fr., *Otilio & Chaguinha s.n.* (EAC42392, HUEFS138379). Paramoti, Fazenda São João, fl., fr., 17.X.1986, *E. Nunes s.n.* (EAC0014856, HUEFS111097). Pentecoste, Fazenda Experimental Vale do Curu, fl., 29.I.2015, *J.C. Alves s.n.* (EAC57488). **Espírito Santo:** Santa Teresa, São João de Petrópolis, Escola Agrotécnica Federal, 19º43’20”S, 40º38’48”W, 180 m, 11.XII.1985, fr., *H.Q. Boudete Fernandes 1720* (SP). Colatina, Rio Doce, 19º31’48”S, 40º42’02”W, 40 m, 13.II.2019, fr., *F. Marinero* (MBM). **Minas Gerais:** Jaíba, 47 km da cidade, estrada de chão sentido cidade, 15º14’13”S, 43º20’10”W, 577 m, 22.IV.2006, *D.S. Carneiro-Torres 731* (HUEFS, HUESB, SP). Mato Verde, margens da rodovia Mato Verde – Monte Azul (BR 122), 8 km ao norte da cidade, 15º20’07”S, 42º53’25”W, 520 m, 31.III.2004, fr., *J.R. Pirani et al. 5372* (HUEFS, SP, SPF). **Piauí:** Caracol, área de entorno de lagoa, 09º12’48”S, 43º29’50”W, 533 m, 22.XI.2010, fl., *E. Melo et al. 8775* (HUEFS). Castelo do Piauí, cerrado entre Castelo do Piauí e São João da Serra, 05º38’29”S, 41º72’09”W, 414 m, 26.XI.1980, fr., *A. Fernandes et al. S.n.* (EAC9077). São Jõao do Piauí, descida da Serra da Capivara, próximo a São Raimundo Nonato (10-11 km de Várzea Grande), 08º47’26”S, 42º28’41”W, 562 m, 05.XII.1971, fl., *D. Andrade-Lima et al. 1187* (HUEFS, IPA, MAC). **MEXICO. Jalisco:** La Huerta, Rancho Cuixmala and environs. Teopa, a ranch along the Arroyo Cajones near the Puerto Vallarta – Barra de Navida Hwy, 19º25’45”N, 104º59’30”W, 30 m, 11.IX.1991, fl., *E.J. Lott et al. 3726* (WIS); reas, Chamela, Dry deciduous forest, 17.VIII.1991, fr., *A. Gentry & L. Woodruff 74399* (DAV); reas, Estación de Investigación, Expirmentación y Difusión Chamela, 02.IX.1981, *J.A.S. Magallanes 3098* (DAV, MEXU). **Chiapas:** Cintalapa, thorn forest near and northwest of Cintalapa along road to colonia Francisco I. Madero, 29.III.1981, *D.E. Breedlove 50502* (CAS). **VENEZUELA. Carabobo:** Road from San Diego to Valencia,

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XIII.1941, *J. Saer 816* (US). **Guárico:** El Valle and Laguna de Espino, 18.VI.1891, *Eggers 13143* (US). ~~**Maracay:** Aragua~~, Puerto Escondido, on dry slopes, ~~10º21'48"N, 67º34'25"W, 1505 m~~, 18.IV.1930, *H.F. Pittier 13421* (F). **Mérida:** Entre Estanques y Puente de la Victoria, 700 m, 7.V.1953, *Bernardi 498* (P). **Miranda:** Caracas, reforested hills of the Caracas Botanical Gardens, 980 m, 10.XI.1974, *P.E. Berry 99* (VEN); reas, bosque decidio secundario y perturbado entre las quebradas afluentes al Río Guarita, al sur del Cementerio Monumental del Este Miranda, 1000 m, 17.VIII.1975, fr., *J.A. Steyermark & P.E. Berry 112078* (F, NY, VEN); reas, *J.A. Steyermark & P.E. Berry 112082* (NY); Guaicaipuro, Sector Begonia-Caobal, Parcela Loma Brisa. Bosque seco en laderas que dan al NE, 10º16'36.57" N, 66º56'30.27" W, 785 m, 23.VII.2009, *R. Riina & C. Reyes 1843* (MA). **Monagas:** Roadside between Caicara and San Felix, 7.VI.1967, fl., *R.A. Purcell 9220* (NY). **SURINAME. Sipaliwini:** lower slopes of Voltzberg, 04º58'19.64"N, 56º16'54.8"W, 150–175 m, 02.VIII.1979, fl., fr., *G.L. Webster 24136* (DAV, TEX, WIS); ibid, Central Suriname Nature Reserve, Voltzberg top I, 13.IV.2002, fr., *A. Gröger et al. 1300* (U); ibid, op helling van Voltzberg, op humus re op rease rots, Boven-Coppename, 22.IX.1954, fl., *A.M.W. Mennega 62* (U).

DISCUSSION

Distribution, phenology, conservation status, and ecological niche modeling

Croton anomalus was found here to be a widely distributed species in the Neotropics, occurring in Brazil, Bolivia, Mexico, Venezuela, and Suriname (Fig. 4, Table 6). This broader geographic range is the result of the synonymization of *C. acapulcensis*, *C. chiapensis* and *C. stahelianus*, as well as by the numerous new records recently discovered in Bolivia and throughout Brazil. Records of *C. anomalus* were found primarily in SDTFs, and secondarily in transition areas of STDF with Savanna (Cerrado phytogeographic domain) or Tropical Rainforest (Fig. 4). The species altitudinal range varied from 30 to 1100 m. Herbarium labels reported the species growing in sandy and clayey soils, and rocky outcrops. *Croton anomalus* was most frequently found inside forest vegetation, growing in shadow and glade zones. Although largely restricted to the Caatinga, *C. blanchetianus* and *C. jacobinensis* were widely distributed, occurring in open areas (*C. blanchetianus*) or transition zones to montane and Atlantic forests (*C. jacobinensis*) (Fig. 5, Table 6). *Croton anomalus* has been recorded flowering and fruiting in January (Bolivia), April (Venezuela), June to August (Mexico, Venezuela, Suriname), and from October to May (Brazil).

Based on its EOO of 13,865,766.407 km^2 and AOO of 124,000 km^2, we tentatively classify *C. anomalus* as Least Concern (LC). The species is found in protected areas, including national parks, in Venezuela, Bolivia, and Brazil.

The distribution modeling for all species demonstrated good performance in our analysis (Table 5). Annual precipitation (bio12) was an important bioclimatic variable for the distribution of the three species (Table 5). The suitability of areas of occurrence (Fig. 6) followed the distribution pattern of the SDTFs for *C. anomalus* and overlapped with the majority of the areas where the three species have been recorded (only Caatinga Dry Forest for *C. blanchetianus* and *C. jacobinensis*). Nonetheless, the Caribbean region and the coastal region of Ecuador and Peru were indicated as

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moderately suitable areas for *C. anomalus* (Fig. 6), as was northern South America for *C. jacobinensis*, even if there are no records of these species in those areas, respectively (Figs. 4, 5).

Discussion

Typification and new synonyms

Croton anomalus was described based on a collection of Henri Pittier, from Venezuela, with *Pittier 11757* indicated as the type material. The author (Pittier, 1930) did not mention where the type material was deposited nor if there was only one specimen (automatically to be considered the holotype [Art. 9.1 of the ICN, Turland et al., 2018]). Three specimens of *Pittier 11757* are found in A, US, and VEN, containing matching information with the protologue (locality and date), and are considered syntypes (Art. 9.6 of the ICN, Turland et al., 2018). Since the name *C. anomalus* was published based on syntypes, one of them must be designated as lectotype (Art. 9.11 and 9.12 of the ICN, Turland et al., 2018). The specimen in best conditions is A00047223 and it is designated here as the lectotype of *C. anomalus*.

Croton stahelianus was described by Lanjouw (1931) based on specimens from Suriname collected by Gerold Stahel *n. 611*. According to the Euphorbiaceae of Suriname index (Lanjouw, 1931), when 'B.W.' is indicated in the protologue it means that the material was collected by the '*Boschwesen'* (Forestry Department), with which Stahel was involved at the time (Stafleu & Cowan, 1985). So, *B.W. n. 7002* represents the collection *Stahel n. 611*, as indicated in the labels of the type material. Lanjouw (1931) did not assign *C. stahelianus* to any infrageneric group, but described the species as related to *C. doctoris* S.Moore and *C. flavens* var. *flavens* Müll.Arg., both representatives of *C.* section *Adenophylli* Griseb. (van Ee et al., 2011). Both aforementioned species can be distinguished from *C. stahelianus* for their acropetiolar glands, bifid styles and columella with prominent apex (all absent in *C. stahelianus*). The morphological characteristics included in the protologue of *C. stahelianus* that are discordant with those of *C. anomalus* are: axillary or terminal inflorescences (*vs*. only terminal on *C. anomalus*), 11 stamens (vs. 16 on *C. anomalus*), pistillate flowers with 5 sepals of glabrous inner surface (*vs*. 6–7 sepals of villous inner surface on *C. anomalus*).

The original description of *Croton chiapensis* is somewhat controversial because some character states described by Lundell (1942) are not seen in the type collection, namely staminate flower of 6 sepals and 6 petals, and pistillate flowers with bifid styles. The staminate flowers are pentamerous and the styles are 4-fid in the few open pistillate flowers (the inflorescences mostly have pistillate flower buds). Also, other authors have indicated 5 sepals and petals for the staminate flowers (Pittier, 1930; Gordillo & Ramírez, 1990). Based on this, we believe that Lundell (1942) confused the number of sepals in staminate flowers with those in the pistillate ones (5–6) when describing *C. chiapensis*. The only character in *C. chiapensis* differing from *C. anomalus,* based on the protologue, is the presence of 18 stamens (*vs.* 14–17 in *C. anomalus*).

Gordillo & Ramírez (1990), in their description of *C. acapulcensis*, mentioned only *C. alamosanus* Rose as its closest relative. These authors used traits of leaves, stipules, and flowers to

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differentiate the two species. However, our revision of the protologues and type specimens of species in *Croton* sect. *Lasiogyne* shows a strong morphological resemblance between *C. acapulcensis* and *C. anomalus* from Venezuela, prompting us to further study and compare these two taxa. According to the protologues, *C. anomalus* differs from *C. acapulcensis* by the ovate to ovate-lanceolate leaf blades (*vs.* oblong-lanceolate in *C. acapulcensis*), irregularly sinuate or dentate to serrate leaf margins (*vs.* entire), linear to lanceolate stipules (*vs.* subulate), inflorescences of 5–7 cm long (*vs.* 2.5–5 cm long), 16 stamens (*vs.* 14–15), and the pistillate flowers with 6 to sometimes 7 sepals (*vs*. 5 or sometimes 6 in *C. acapulcensis*) (Table 6).

After examining numerous specimens from Brazil, Bolivia, Mexico, Suriname and Venezuela (including the type collections), we determine that the characteristics listed above overlap within and among populations. Character states such as entire or serrate leaf blade margins are found on the same individual (even on the same branch). The presence of pistillate flowers with 7 sepals (probably responsible for the epithet "anomalus") is a rare state for this species, although not so abnormal in the genus, where even 10 sepals have been observed in *C. sincorensis* Mart. ex Müll. Arg. (Sodré et al., 2019). Thus, we find weak morphological evidence to sustain *C. acapulcensis*, *C. anomalus*, *C. chiapensis* and *C. stahelianus* as four distinct taxonomic entities. As shown by the morphological data, *C. acapulcensis* and *C. stahelianus* are better positioned as synonyms of *C. anomalus*. Additionally, the phylogenetic reconstruction also agrees with the morphological evidence where the two specimens of *C. acapulcensis* and *C. stahelianus* are intermingled in a highly supported clade along with *C. anomalus* specimens representing most of the geographic range of the species (Fig. 1).

Systematics of the Croton anomalus group

The phylogenetic position of all the sampled species is congruent with previous phylogenetic analyses of *Croton* (Berry et al., 2005; van Ee et al., 2011; Arevalo et al., 2017). In contrast with van Ee et al. (2011), section *Lasiogyne* is strongly supported as monophyletic (PP = 0.95; Fig. 1), being more closely related to section *Julocroton* rather than to section *Heptallon* as in van Ee et al. (2011). The latter section is in turn sister to the clade formed by sections *Lasiogyne* and *Julocroton* (Fig. 1). However, the monophyletic status of section *Lasiogyne* remains to be confirmed by the inclusion of a more comprehensive taxon sampling in future phylogenetic analyses (Y. Rossine et al., unpublished results). Our results are in accordance with previous taxonomic classifications based on morphology, which placed *C. anomalus* and *C. blanchetianu* as members of *C.* sect. *Lasiogyne* (*e.g.* van Ee et al., 2011; Rossine et al., 2023).

Based on our taxon sampling and emended morphological description (capsules and seeds were not described in the protologues of *C. anomalus* and *C. acapulcensis* [Pittier, 1930; Gordillo & Ramírez, 1990]), *C. anomalus* is definitely a member of section *Lasiogyne*, as indicated by van Ee et al. (2011) based on morphology alone. This species is characterized by a stellate indumentum, lack of nectaries in leaves, bracts and sepals, reduplicate-valvate pistillate sepals, and multifid styles, all character states that are widely present in section *Lasiogyne* (van Ee et al. 2011; Rossine et al., 2023).

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Morphologically, *C. anomalus* is most similar to *C. blanchetianus* (Fig. 6; Table 6). The two species share the monopodial branching, lanceolate stipules, general aspects of the leaves, such as the stellate indumentum (making the leaf blade light green on the abaxial surface), ovate leaf blades, entire leaf margins, eucamptodromous venation, multifid styles, and smooth seeds. Both species are morphologically variable and plastic, showing some overlap in character states among species. For example, the shared lanceolate stipules can also be reniform or auriculate and the ovate leaf blade can also be cordiform in *C. blanchetianus* (Rossine et al., 2023). On the other hand, the entire leaf margin can be irregularly sinuate to slightly serrate, and the venation can be brochidodromous instead of eucamptodromous (the most frequent state) in *C. anomalus*.

The comparison between *C. anomalus* and *C. jacobinensis* (Fig. 6, Table 6) shows that they share the lanceolate stipules, coloration of leaf blades, eucamptodromous venation, linear to 3-lobate bracts, 14–17 stamens, and free styles (Rossine et al., 2023). Again, some character states can be polymorphic in *C. anomalus* (brochidodromous venation). The main differences between *C. anomalus*, *C. blanchetianus*, and *C. jacobinensis* are indicated in Table 6.

Species distributions and ecological niche modeling

Croton anomalus is rediscovered here after more than 90 years of its publication. Conversely, *C. blanchetianus* and *C. jacobinensis* are well-documented species, particularly in terms of their geographic distribution, as described in studies dealing with *Croton* of the Brazilian Caatinga dry forest region (*e.g.* Silva et al., 2010; Oliveira et al., 2023; Rossine et al., 2023).

Our results show that *C. anomalus* represents a new species record for the Brazilian Caatinga dry forest and other dry areas of Brazil in the transition zones with the Tropical Rainforest biome (state of Espírito Santo), or with the Savanna biome (state of Piauí). We also report the first records of *C. anomalus* for Bolivia, where it occurs in the Gran Chaco region, in fragments of the Chiquitano dry forest. Populations of *C. anomalus* from Mexico, Suriname, and Venezuela, are also found in SDTFs. According to DRYFLOR (2016), the Caatinga shares less than a hundred species with Mexico's SDTFs, and about 241–409 species with northern South American nuclei of SDTFs. *Croton anomalus* can now be added to that group of species shared between distant dry forest areas across the Neotropics. Recent biogeographic studies feature dry forest plant groups, but with species restricted to one or two dry forest areas across the Neotropics (e.g., Lavor et al., 2019; Silva et al., 2020; Hurbath et al., 2021; Pezzini et al., 2021). When including species present in more than two distinct fragments, they often present corridors connecting those regions (Colli-Silva et al., 2021). Conducting studies including taxa that are widespread across most or all the Neotropical dry forests would be interesting to complete our knowledge regarding the floristic assembly and configuration of the SDTF biome in evolutionary time. However, as our study shows, insufficient taxonomic knowledge is probably hiding widely distributed dry forest species, such as *C. anomalus*.

The only dry forest nuclei where *C. anomalus* has not yet been found is the coastal regions of Ecuador and Peru, which are indicated as potential areas of occurrence in our analyses (Fig. 7-A). The Andean Mountains can act as a geographic barrier for the dispersal of species from the surrounding areas (Hazzi et al., 2018). However, given the presence of *C. anomalus* in Bolivia and

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Brazil, it is possible that its absence in Ecuador and Peru is just a matter of lack of botanical information, once both areas are both plant biodiversity hotspots and darkspots (places predicted to contain undescribed and not yet recorded species) (Ondo et al., 2024). There could also be specimens of *C. anomalus* from Ecuador and Peru waiting in herbaria backlogs to be processed and identified. Interestingly, the Caribbean region also shows favorable climatic conditions for the occurrence of *C. anomalus* but so far collections records are absent from all Caribbean islands (Fig. 7-A). One possible explanation for this pattern is that *C. anomalus* has not yet been able to disperse overseas.

As in the *C. anomalus* case, the niche analysis of *C. jacobinensis* shows suitable areas in northern South America (coastal areas of Venezuela and Ecuador) where that species is not present (Fig. 7-C). The Amazon rainforest could represent a strong geographic and climatic barrier for the south-to-north direction of dispersal of *C. jacobinensis*, since populations of this species are found in all other suitable areas south of the Amazon region.

Niche modeling of past periods, biogeographic and phylogeographic studies are necessary to understand the age of colonization events and dispersal trajectories, as well as ecological and climatic processes leading to the nowadays distribution of *C. anomalus* and other plant lineages occurring in fragments of SDTFs across the Americas.

Impacts of misidentification in herbaria

The case of *Croton anomalus* highlights the importance of updating taxonomic revisions in the Neotropics, especially in plant groups specialized in fragmented biomes as the SDTF. It also highlights the effect of specimen misidentifications on biogeographic knowledge and consequently on species conservation assessments. Many specimens of *Croton anomalus* were found in Brazil misidentified as *C. sonderianus* (a synonym of *C. jacobinensis*) or as *C. blanchetianus*. In fact, these species are very similar morphologically, but we have demonstrated that there are morphological characters distinguishing them. These can be used to correctly identify species, even those with populations overlapping in the same biogeographic region such as the Brazilian Caatinga. *Croton anomalus* was also found in Bolivia and Suriname identified only at the genus level (as *Croton* sp.), whereas in Mexico it has been identified as *C. acapulcensis* and *C. chiapensis* (proposed here as new synonyms) and as *C. stahelianus* in Suriname (also a new synonym proposed here).

Brazil is the country where most of the taxonomic problems related to *C. anomalus* have arisen. The use of the name *C. sonderianus* to treat specimens of *C. anomalus*, *C. blanchetianus* and *C. jacobinensis* seems to have been popularized since the 1980s due to misidentifications by Euphorbiaceae experts, which were followed subsequently by local taxonomists. Also, it seemed that the specimens were not identified by comparing them with the protologue and type collection of *C. sonderianus*. Specimens of either *C. blanchetianus* or *C. jacobinensis* have been routinely identified as *C. sonderianus* in herbaria over the decades. The lack of knowledge of the presence of *Croton anomalus* in Brazil has caused divergence even among *Croton* experts due to the close morphological affinities among these species in question. The synonymization of *C. sonderianus* under *C. jacobinensis* (Gomes *et al.* (2010) is reinforced here, and we recommend avoiding the use

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of *C. sonderianus* other than as a synonym of *C. jacobinensis*. The various sources of evidence shown here support the recognition of three species in the *Croton anomalus* group: *C. anomalus*, *C. blanchetianus*, and *C. jacobinensis*.

Acknowledgements

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Figure Legends

Figure 1 Phylogenetic reconstruction of the *Croton anomalus* group illustrated by a majority consensus tree obtained from the Bayesian analysis of combined ITS and *trnL-F* datasets. Names in bold are those newly generated in this study.

Figure 2 Main morphological features of *Croton anomalus*. (A) flowering branch, showing the monopodial branching, disposition of stipules and leaves, and terminal inflorescences. (B-E) leaf blades, (B) leaf blade with entire margins; (C) stellate-porrect trichomes found on petioles; (D) leaf blade with slightly serrate margins, showing the detail of a section of the margin; (E) leaf blade with irregularly erose margins; (F) narrowly lanceolate stipule; (G) linear (right) and 3-lobed (left)

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bracts; (H) staminate flower; (I-J) pistillate flower, (I) pistillate flower with 6 sepals; (J) pistillate flower with 5 sepals, showing a detail of the trichomes on the stigmatic tips; (K) capsule, showing a detail of the inner surface of the sepals with stellate and stellate-porrect trichomes; (L) ventral (left) and dorsal (right) view of a seed.

Figure 3 *Croton anomalus* general aspects. (A) shrubby habit; (B) general aspect of leaves and inflorescences, (C) stipules, (D) adaxial and (E) abaxial view of the leaf blade; (F) early anthesis of the inflorescences with only pistillate flowers open; (G) branches with unisexual staminate inflorescences; (H) bisexual inflorescence; (I) infructescence and (J) capsule showing the stellate porrect trichomes, and (K) ventral and dorsal views of a seed. Photographs: A, B, F, G (C. Domínguez-Rodríguez); C, D (J. Mota); H (E. S. Velásquez Arellanes), reproduced with permission.

Figure 4 Distribution map of *Croton anomalus*. Red star: previously known record (type locality); blue circles: new records. New records from Mexico and Suriname are based on the synonymizations proposed here. Shapefiles were downloaded from http://www.efrainmaps.es. (Americas) and http://www.dryflor.info/data/datasets (Dry Forests).

Figure 5 Distribution maps of *C. blanchetianus* and *C. jacobinensis* in the Caatinga phytogeographic domain. Records outside the Caatinga are in transition zones with Atlantic Forest.

Figure 6 Point-wise mean of the modeled distribution for species recognized in the *Croton anomalus* group. (A) *Croton anomalus*, (B) *C. blanchetianus*, and (C) *C. jacobinensis*.

Figure 7 Morphological comparison of species in the *Croton anomalus* group. (A-C) *Croton anomalus*, (D-F) *C. blanchetianus*, and (G-I) *C. jacobinensis*. (A, D, G) General aspects of leaves and inflorescences, (B, E, H) pistillate flowers of five and (B) six sepals, and (C, F, I) capsular fruit. Photographs: A–B (A. S. Farias-Castro), reproduced with permission.

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TABLE 6. Morphological comparison between the species included in the Croton anomalus group.

Character	*Croton anomalus*	*Croton blanchetianus*	*Croton jacobinensis* (=*C. sonderianus*)
Indumentum	Stellate to multiradiate, porrect	Stellate, sublepidote to lepidote	Stellate to multiradiate
Leaf blade	Ovate to elliptic, margins entire, irregularly sinuate or slightly serrate	Ovate to ovate-lanceolate, elliptic, margins entire	Cordiform, margins entire
Venation	Eucamptodromous to brochidodromous	Eucamptodromous	Actinodromous
Inflorescences	Unissexual staminate or bisexual (1–5 cm long)	Bisexual (3–12 cm long)	Bisexual (5–18 cm long)
Number of pistillate sepals	5-6 (7)	5	5
Inner surface of pistillate sepals	Sparsely hirsute, trichomes stellate, porrect	Glabrous	Densely velutine, trichomes stellate to multiradiate
Styles	Ascending, free	Ascending, united forming a small column	Patent or ascending, free (rare slightly united at the base)
Capsule trichomes	Stellate to multiradiate, porrect	Lepidote, rarely sublepidote	Stellate to multiradiate
Seed surface	Smooth, slightly papillose	Smooth	Rugose
Geographic distribution	SDTFs of Bolivia, Brazil, Mexico, Suriname and Venezuela	Caatinga SDTF (Brazil)	Caatinga SDTF (Brazil)

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