



Research article

Croton calcareus: a new species of dragon's blood (Euphorbiaceae) from dry forest in the state of Chiapas, Mexico

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Abstract. We describe *Croton calcareus* Riina & Mateo-Ram. sp. nov., a new species in *Croton* section *Cyclostigma* (dragon's blood trees) from the state of Chiapas (Mexico). This species is a small tree growing in dry forest on calcareous substrates. Both morphological and molecular data support *C. calcareus* sp. nov. as a new species closely related to *C. redolens*, another dry forest taxon from northern Venezuela. We provide illustrations, a distribution map and suggestions for species conservation status. The new species along with *Croton draco* are the only known representatives of *C.* section *Cyclostigma* occurring in Mexico.

Keywords. *Croton* section *Cyclostigma*, dry forest, Euphorbiaceae, Neotropics, phylogeny.

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Introduction

Croton L. species popularly known as dragon's blood ('sangre de drago' or 'sangre de grado' in Spanish) belong to *C.* sect. *Cyclostigma* Griseb. This section is an arborescent clade of 48 species occurring mainly in lowland and montane forests along the Andes (Riina *et al.* 2009; van Ee *et al.* 2011) and the Atlantic Rain Forest region in south-eastern Brazil (Santos *et al.* 2017; Farias *et al.* 2019). In the northern Neotropics, only one species in the section, *Croton draco* Schltdl., was previously known to reach Mexico.

As part of a revision of the common and widespread *Croton draco*, which occurs from Mexico to Panama, we noticed several specimens from Mexico that had obvious morphological differences with *C. draco* as well as differences in habitat. Further examination of these specimens revealed an undescribed taxon, which we assign here to *C.* sect. *Cyclostigma* based on its morphological affinities with species in this section and support from molecular phylogenetic evidence.

Members of sect. *Cyclostigma* have laticifers that produce conspicuous reddish latex (Wiedenhoeft *et al.* 2009; Feio *et al.* 2018a) that is widely used for its medicinal properties in several Latin American

countries (Jones 2003; Salatino *et al.* 2007). Species from sect. *Cyclostigma* occur predominantly in mesic forests (Riina *et al.* 2009; Arévalo *et al.* 2017); however, a small number of species are restricted to seasonally dry forest vegetation in different areas of the Neotropics, such as *C. churutensis* Riina & Cornejo (Riina *et al.* 2007) in Ecuador, *C. tumbesinus* Riina (Feio *et al.* 2018b) in Peru, *C. redolens* Pittier in northern Venezuela and *C. charaguensis* Standl. in Bolivia. In this paper, we describe and illustrate a new species from the state of Chiapas (Mexico), which adds to the list of dry forest specialists of this diverse and medicinally important Neotropical *Croton* clade.

Material and methods

We examined collections of the new taxon and *C. draco* deposited in BM, DAV, MA, MEXU, MICH and MO. Acronyms of herbaria follow *Index Herbariorum* (Thiers, continuously updated). For morphological descriptions we used a 10–60 × magnification stereo microscope. Morphological terminology follows recent taxonomic papers on *Croton* (e.g., Santos *et al.* 2017; Feio *et al.* 2018b; Riina *et al.* 2018), and anatomical studies on trichomes and secretory structures (Webster *et al.* 1996; Vitarelli *et al.* 2015; Feio *et al.* 2016; Feio *et al.* 2018a).

For the phylogenetic analysis, we used a subset of the nuclear rDNA internal transcribed spacers (ITS) dataset from Riina *et al.* (2009), including species of sect. *Cyclostigma* sampled there, a selection of other *Croton* sections and one outgroup (*Brasiliocroton mamoninha* P.E.Berry & Cordeiro). To this dataset, we added two newly generated sequences of the new species, *C. calcareus* Riina & Mateo-Ram. sp. nov., and two sequences of *C. draco* from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). GenBank accession numbers of all the sequences used in the analysis are shown in Table 1. DNA extraction, amplification and sequencing of ITS followed the same laboratory procedures as in previous *Croton* phylogenetic studies (Riina *et al.* 2009; van Ee *et al.* 2011). Sequences were aligned manually using Mesquite ver. 3.2 (Maddison & Maddison 2017). The aligned matrix, in fasta format, is provided as [Supplementary file 1](#).

The phylogenetic analysis was performed in MrBayes 3.2.6 (Ronquist *et al.* 2012) using the GTR+I+G substitution model as estimated with jModelTest 2.1.6 (Darriba *et al.* 2012) using the Akaike Information Criterion (AIC). The analysis included two runs of 10 million generations in MrBayes, sampling trees every 1000 generations. One-fourth (25%) of the MCMC samples from each run was discarded as ‘burn-in’. Tracer ver. 1.7.1 (Rambaut *et al.* 2014) was used to determine run convergence and stationarity as indicated by the effective sample size (ESS) values, which should be higher than 200. Node posterior probability (PP) values were obtained by computing a 50% majority rule consensus of the post-burn-in trees from both MCMC chains using the sumt command. We used FigTree ver. 1.3.1 (Rambaut 2006) to visualize and edit the consensus tree.

We ran a preliminary analysis with all the *Cyclostigma* accessions from Riina *et al.* (2009) to assess the phylogenetic position of *C. calcareus* sp. nov. within the section (data not shown). Based on this preliminary phylogeny, we reduced the sampling within the *Cyclostigma* clade to exclude taxa distantly related from *C. calcareus* sp. nov. (i.e., all the Brazilian species from the Atlantic Rain forest and most species from the south-central Andes). We ran the final Bayesian analysis on the reduced dataset (Table 1) following the steps indicated above.

The species distribution map was produced using R software (<https://www.r-project.org>) and the *dismo* package (Hijmans *et al.* 2010). Only two of the seven available collections had geographic coordinates on their labels, so we estimated coordinates for the remainder with the locality information using Google Earth. The proposed conservation status was based on the criteria of the *International Union for the Conservation of Nature Guidelines* (IUCN 2012). Extent of occurrence (EOO) was assessed using GeoCat (Bachman *et al.* 2011).

Table 1. List of GenBank accession numbers of the ITS sequences used to provide a phylogenetic context to the new species (shown in Fig. 1).

<i>Brasiliocroton mamoninha</i> P.E.Berry & Cordeiro	EU586944
<i>Croton arboreus</i> Millsp.	EU478029
<i>C. beetlei</i> Croizat	EU586916
<i>C. calcareus</i> Riina & Mateo-Ram. sp. nov.; <i>Hampshire et al. 1161</i> ; Mexico: Chiapas	MT106663
<i>C. calcareus</i> Riina & Mateo-Ram. sp. nov.; <i>Webster et al. 12966</i> ; Mexico: Chiapas	MT106664
<i>C. caracasanus</i> Pittier	DQ227525
<i>C. chilensis</i> Müll.Arg.	EU586905
<i>C. conduplicatus</i> Kunth	EU477957
<i>C. coriaceus</i> Kunth	EU586921
<i>C. cuneatus</i> Klotzsch	EU497735
<i>C. cupreatus</i> Croizat	EU586919
<i>C. curiosus</i> Croizat	EU586906
<i>C. discolor</i> Willd.	EU497736
<i>C. draco</i> Schltdl. & Cham. 1	EU478006
<i>C. draco</i> 2	EF421776
<i>C. echioides</i> Baill.	EU586907
<i>C. eichleri</i> Müll.Arg.	EU586949
<i>C. emporiorum</i> Croizat	EU586908
<i>C. gossypifolius</i> Vahl	EU586924
<i>C. goudotii</i> Baill.	EU586946
<i>C. gratissimus</i> Burch. (as <i>C. zambesicus</i> in GenBank)	AY971260
<i>C. hibiscifolius</i> Kunth ex Spreng.	EU586925
<i>C. lundellii</i> Standl.	EF421735
<i>C. niveus</i> Jacq.	EU478046
<i>C. pachypodus</i> G.L.Webster (as <i>C. megistocarpus</i> in GenBank)	EU586953
<i>C. priscus</i> Croizat	EU586950
<i>C. pungens</i> Jacq.	AY971241
<i>C. redolens</i> Pittier	EU586935
<i>C. rimbachii</i> Croizat	EU586936
<i>C. saltensis</i> Griseb.	EU586911
<i>C. sampatik</i> Müll.Arg.	EF421792
<i>C. sapiifolius</i> Müll.Arg.	EF421754
<i>C. schiedeianus</i> Schltdl.	AY971246
<i>C. speciosus</i> Müll.Arg.	AY971251
<i>C. suberosus</i> Kunth	EU477979
<i>C. verapazensis</i> Donn.Sm.	EF421750
<i>C. xalapensis</i> Kunth	EU477987
<i>C. yavitensis</i> Croizat	EU586918

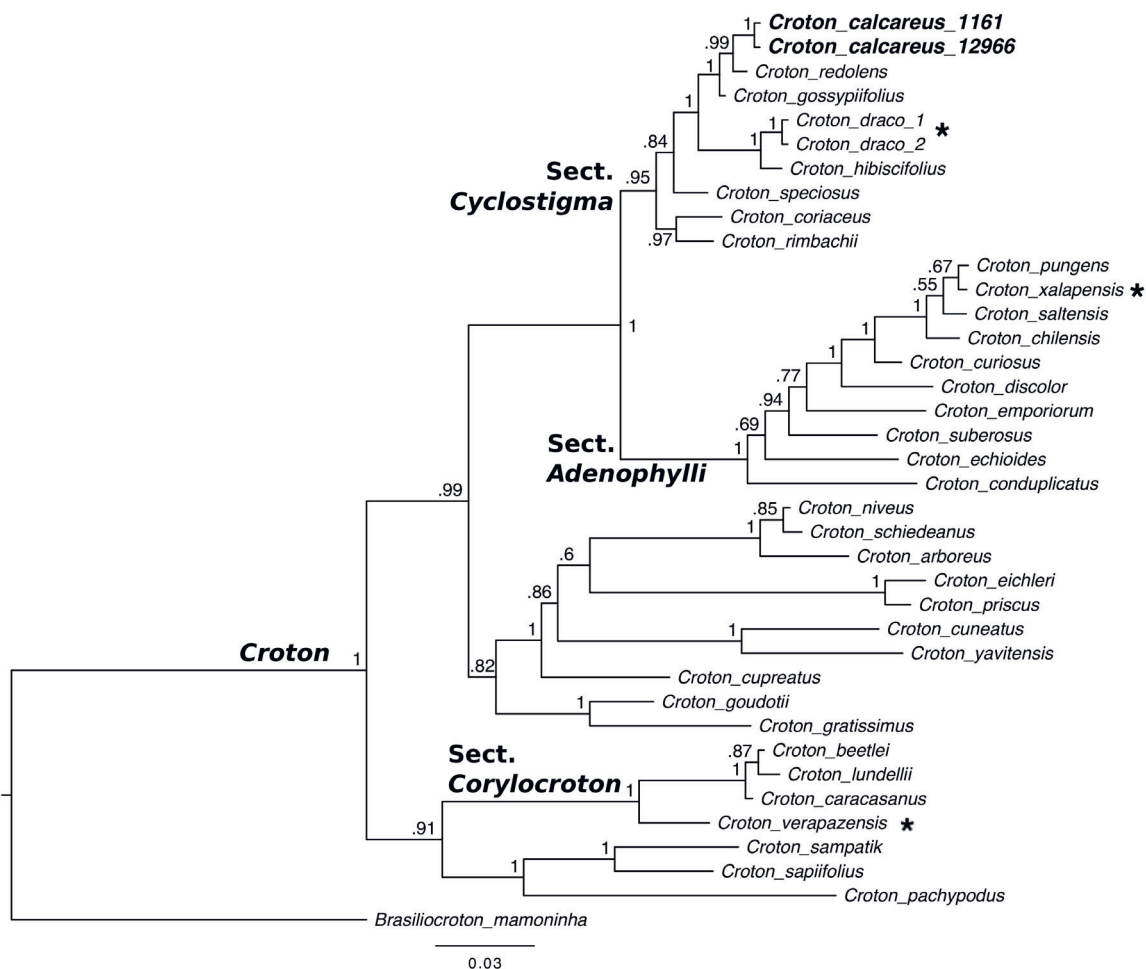


Fig. 1. Bayesian majority rule consensus phylogram of nuclear ITS data from a selection of *Croton* L. taxa including two accessions of *Croton calcareus* Riina & Mateo-Ram. sp. nov. Species marked with an asterisk correspond to those with which *C. calcareus* sp. nov. has been previously confused. The relevant clades are labelled on the left side. Numbers next to nodes indicate clade support (Bayesian posterior probabilities).

Results

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

***Croton calcareus* Riina & Mateo-Ram. sp. nov.**

[urn:lsid:ipni.org:names:77209678-1](https://nomenclature.ipni.org/names/77209678-1)

Figs 2–4

Diagnosis

Croton calcareus Riina & Mateo-Ram. sp. nov. is most closely related to *C. redolens* Pittier and can be distinguished from the latter mainly by its larger fruits (12–13 × 12–15 mm in *C. calcareus* sp. nov. vs 5–6 × 7–8 mm in *C. redolens*) and an indumentum of sessile, stellate, multiradiate, porrect trichomes on the adaxial side of leaves (vs stipitate, stellate, porrect trichomes in *C. redolens*). The new species

has been confused with *C. draco* Schltdl., another dragon's blood from Mexico, but it differs from this species in having shorter inflorescences (8–10 cm vs 15–43 cm in *C. draco*) and larger fruits (only 4–7 × 4–7 mm in *C. draco*).

Etymology

The specific epithet refers to the calcareous substrates where the species occurs.

Type material

MEXICO • Chiapas, Mpio, La Trinitaria, 4 km E of La Trinitaria along Mex 190; 16°8' N, 92°2' W; alt. 1480 m; 8 Jul. 1990; *R.J. Hampshire, A. Reyes García and L. Hernández 1161*; holotype: MEXU[858873]; isotypes: BM, MA[540108], MO[4323513].

Paratypes

MEXICO – **Chiapas** • Mpio, Ocozocoautla, steep-walled canyon at the head of the Río de la Venta at the Chorreadero near Derna; 16 Dec. 1972; *D.E. Breedlove, R.F. Thorne 30301*; MEXU • El Aguacero, 13 km al NO de Ocozocoautla; 29 Mar. 1985; *E. Cabrera and H. de Cabrera 7870*; MEXU • El Aguacero, canyon of the Río La Venta; alt. 540–660 m; 19 Nov. 1984; *G. Davidse, M. Sousa, O. Tellez, E. Martinez and J. Davidse 30083*; MA, MO • 13 km E of Ocozocoautla on Rte 190, then N on road to Aguacero; alt. 630–700 m; 2 Oct. 1984; *M.J. Huft, E. Cabrera and R. Torres 2253*; MEXU, MO • “Cascada El Aguacero en el Río La Venta” [El Aguacero waterfall on the river La Venta]; 16°45'17" N, 93°31'20" W; alt. 600 m; 12 Dec. 1987; *E. Martinez and A. Reyes 22018*; MEXU, MICH • El Aguacero, “a 33 km al E de Cintalapa” [33 km E of Cintalapa]; alt. 540–660 m; 19 Nov. 1984; *O. Tellez, M. Sousa, E. Martinez, G. Davidse and J. Davidse 8120*; MO, MEXU • 7 mi SW of Tuxtla Gutierrez; alt. 3000 ft.; 11 Aug. 1962; *G.L. Webster, K. Miller and L. Miller 12966*; DAV, MO.

Description

Small monoecious trees, up to 6 m high; young branches with a dense indumentum of rosulate (sometimes also stipitate) trichomes; latex from the main trunk and branches reddish to dark red (observation from herbarium specimens). Stipules short-triangular when young (ca 1.5 mm) to filiform 8–13.5 mm long, covered with a dense indumentum of rosulate and multiradiate trichomes, colleters (ovoid glands) at base, margin and apex. Leaf blade ovate to broadly ovate, 5–13 × 3.5–11 cm; base rounded to cordate; apex acute to obtuse; margin entire or slightly dentate; colleters (ovoid glands) along the margin; venation 3–5-plinerved, brochidodromous; primary and secondary veins raised on both surfaces; petiolar nectary glands 2–6, patelliform, sessile, subsessile or stipitate, attached to the petiole on the adaxial side, but also sometimes visible from the abaxial side; petiole 1.5–8 cm long, with a more or less dense indumentum of stellate adpressed trichomes; adaxial leaf indumentum very dense on young leaves to nearly glabrous on old leaves, sessile, stellate-porrect and stellate-multiradiate trichomes; abaxial leaf surface very densely pubescent on young leaves to sparser with age, with sessile or stipitate stellate or multiradiate trichomes. Inflorescences terminal, erect thyrses 8–10 cm long, axis costate, with a dense indumentum of stellate-multiradiate trichomes; bracts triangular, ca 1 × 1 mm; cymules usually bisexual, regularly spaced at the base and more congested toward the apex. Staminate flowers shortly pedicellate, pedicels 1–2 mm long; sepals valvate, triangular-ovate, 2–2.8 × 1.1–2 mm, adaxial surface with scattered simple trichomes, abaxial surface with a dense indumentum of stellate-multiradiate trichomes; petals narrow-elliptical, 1.7–1.8 × 0.7–0.8 mm, with scattered simple or stellate hairs on both surfaces, margin lanate; receptacle densely pilose; stamens 16; filaments glabrous, 2–3 mm long, anthers 0.6–0.9 × 0.4–0.5 mm. Pistillate flowers with pedicels 1.5–2 mm long, with stellate-multiradiate trichomes; sepals valvate, triangular-ovate, 2–2.2 × 1.2–1.3 mm, adaxial and abaxial surfaces with dense covering of stellate-multiradiate trichomes; petals absent or reduced to a filament with a colleter at the tip; ovary subglobose, densely covered with stellate-multiradiate trichomes; styles bifid, with six terminal tips, the lower half of the

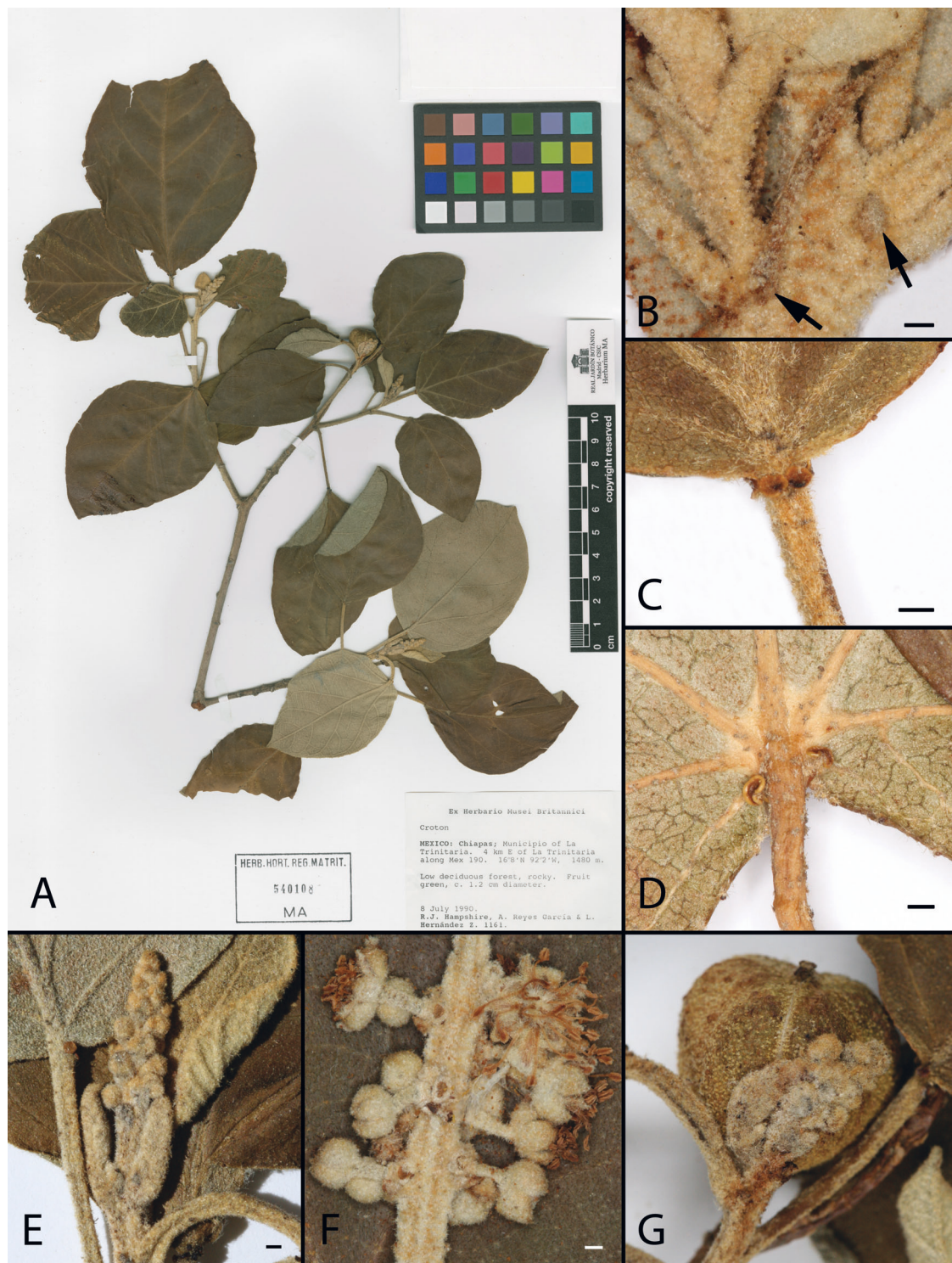


Fig. 2. *Croton calcareus* Riina & Mateo-Ram. sp. nov. **A.** Image of an isotype (MA). **B.** Apical portion of a young branch showing the short young stipule (right arrow) and fully developed stipule (left arrow); the arrows point to the base of each stipule. **C.** Petiolar nectary glands visible from the adaxial side on a leaf with a rounded base. **D.** Petiolar nectary glands visible from the abaxial side on a leaf with a cordate base. **E.** Branch showing a young inflorescence. **F.** Section of inflorescence with detail of male flowers. **G.** Mature fruit. Scale bars = 1 mm. Vouchers: A, C, E, G: *Hampshire et al.* 1161 (MA); B, D, F: *Davidse et al.* 30083 (MA).



Fig. 3. Image of one of the paratypes of *Croton calcareus* Riina & Mateo-Ram. sp. nov. (Cabrera and Cabrera 7870, MEXU), previously identified as *C. xalapensis* Kunth, to show the variation in leaf shape and indumentum density. It also shows immature fruits (younger than those in the type specimens).

styles with stellate-multiradiate trichomes. Capsules depressed-subglobose, slightly trilobate, 12–13 × 12–15 mm; columella 9–10 mm long; seeds ovoid, 7–8 × 5.5–6 mm, brown, surface smooth, shiny, caruncle trapezoid, 0.6 × 1.2 mm.

Phylogenetic placement and relationships

The ITS alignment consisted of 686 aligned positions. The resulting tree topology (Fig. 1) was congruent with previous analyses of *Croton* using the ITS region for the clades involved (Riina *et al.* 2009; van Ee *et al.* 2011). This phylogeny indicates that *Croton calcareus* sp. nov. is indeed a member of *Croton* sect. *Cyclostigma* and that it is most closely related to *C. redolens* and *C. gossypifolius* Vahl (Fig. 1). The two sequences of *C. calcareus* sp. nov. are identical and share two unique positions with respect to the rest of sequences in the matrix. The accessions of Mexican species with which *C. calcareus* sp. nov. has been confused in the past (i.e., *C. draco*, *C. xalapensis* Kunth and *C. verapazensis* Donn.Sm.) are indicated with an asterisk in the phylogeny (Fig. 1). Of these, *C. draco* is the most closely related to the new species, coming out in the same clade (sect. *Cyclostigma*), the other two species belong to two different sections/clades of *Croton* (Fig. 1).

Distribution, ecology and phenology

Croton calcareus sp. nov. appears to be restricted to the state of Chiapas (Mexico) where it grows on limestone outcrops, in low deciduous forests on rocky slopes, steep river canyons and river floodplains,

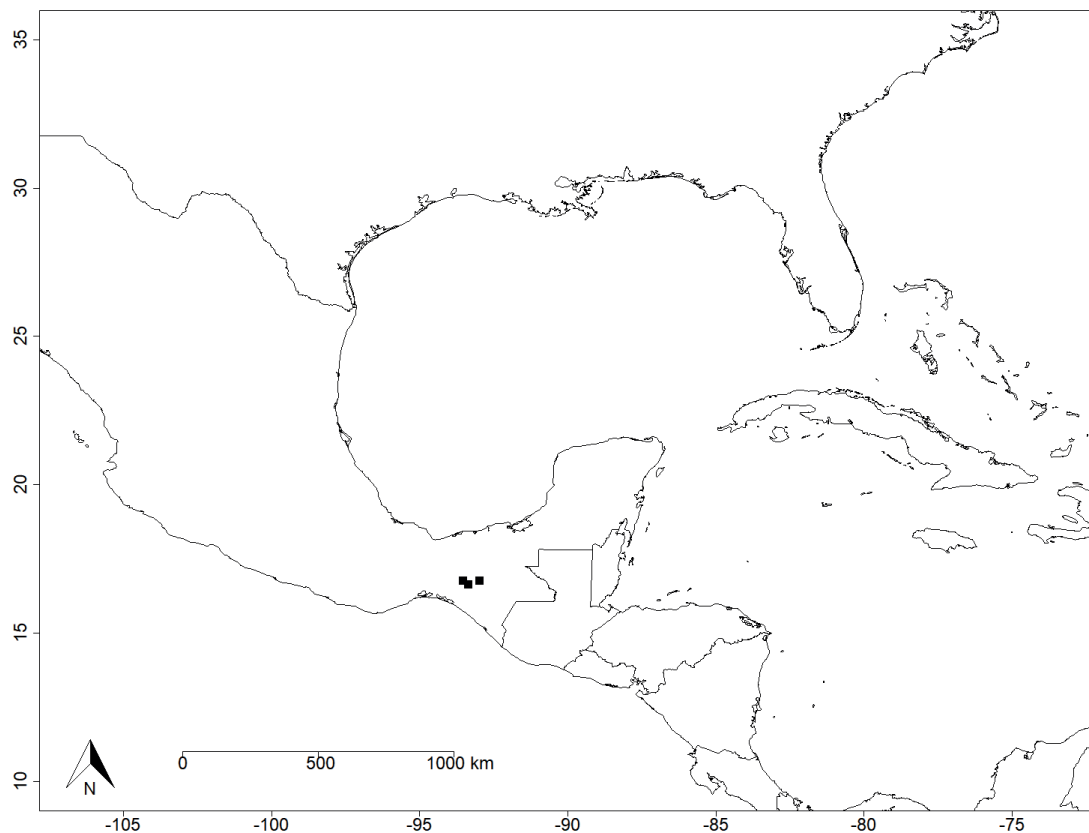


Fig. 4. Distribution map showing the localities (black squares) of *Croton calcareus* Riina & Mateo-Ram. sp. nov., all known from southern Mexico.

between 550–1500 m elevation (Fig. 4). Flowering between August and February and probably fruiting between March and July.

Conservation status

The species could be categorized as Vulnerable (VU D2; IUCN 2012). The extent of occurrence of *Croton calcareus* sp. nov. is only 2718 km² and it is only known from four different localities in two not-adjacent municipalities. The species appears to be under low human pressure since three of the known localities (Municipality of Ocozocoautla) are within the buffer zone of the Selva el Ocote Biosphere Reserve (Ochoa-Gaona 1996; UNESCO 2012). Most of the known localities are of limited access due to their vicinity to limestone rocky formations along rivers.

Discussion

Our phylogenetic analysis supports *Croton calcareus* sp. nov. as a distinct lineage in *C.* sect. *Cyclostigma* sensu van Ee *et al.* (2011), which, combined with the observed distinct morphological features, warrants recognition at the species level. Based on the ITS phylogeny and morphology, the new species is most closely related to *C. redolens*, a dendroid shrub (up to 3 m tall) occurring in dry forest vegetation associated with rocky outcrops in northern Venezuela. *Croton calcareus* sp. nov. also belongs to the same clade that includes *C. draco*, the only other species in sect. *Cyclostigma* known to occur in Mexico. Characters shared among *C. calcareus* sp. nov., *C. draco*, *C. redolens* and other members of sect. *Cyclostigma* include, but are not limited to, arborescent habit, indumentum of stellate trichomes, red latex, conspicuous stipules, petiolar nectary glands, bisexual cymules at the lower portion of the inflorescence axis, bifid styles and more than 15 stamens. For this reason, it is not surprising that specimens of *C. calcareus* sp. nov. have been confused with *C. draco* in the past.

Among the many morphological differences between *C. calcareus* sp. nov. and both *C. redolens* and *C. draco* (Table 2), the most obvious ones are fruit size and inflorescence length; although the latter is only relevant in the case of *C. draco*. Inflorescences are much longer in *C. draco* and fruits are much larger in *C. calcareus* sp. nov. (Table 2). Unfortunately, only one of the examined collections (*Hampshire et al.* 1161, the type) had fully mature fruits and seeds. Plant stature and habitat preference are also important features setting the two Mexican species (*C. draco* and *C. calcareus* sp. nov.) apart (Table 2).

There are also differences, although with some overlap, in the leaves among the three species in question. In *Croton calcareus* sp. nov. leaves can have a rounded or cordate base (Fig. 1C–D) and acute to obtuse apex, whereas in *C. redolens* the base is mostly rounded and rarely cordate and the apex is acute, and in *C. draco* the base of the leaves is usually cordate and the apex acuminate (Table 2). In addition, the texture of the adaxial leaf surface is soft to touch in *C. draco* and *C. redolens*, while in *C. calcareus* sp. nov. it has a rough texture. Stipules are usually informative distinguishing species within sect. *Cyclostigma* (Riina *et al.* 2009; Farias *et al.* 2019). In *Croton calcareus* sp. nov., there is variation in the shape of stipules depending on their state of development. When young, stipules in *C. calcareus* sp. nov. are triangular in shape and they become more linear and much longer as they grow (Fig. 1B), whereas in *C. redolens* and *C. draco* young and old stipules have more or less the same shape (Table 2).

Croton calcareus sp. nov. occurs in a diverse and relatively poorly explored area of Mexico in which species from different plant groups continue to be described (e.g., Martínez-Meléndez *et al.* 2014; Hirai *et al.* 2014; Ruiz-Sánchez 2015; Ortiz-Díaz *et al.* 2016; Steinmann & Carrillo-Reyes 2018; Areces-Berazain & Vega-Lopez 2019). Several specimens of *C. calcareus* sp. nov. have previously been misidentified in herbaria as *C. draco*, *C. xalapensis* or *C. verapazensis*. Besides *C. draco*, which belongs to the same section as the new species, the other two species belong to different sections or clades (Fig. 1). *Croton xalapensis* is a shrub in *C.* sect. *Adenophylli* Griseb., the largest section of

Table 2. Main differences between *Croton calcareus* Riina & Mateo-Ram. sp. nov., *C. redolens* Pittier and *C. draco* L. (the only other species in *C.* sect. *Cyclostigma* Griseb. occurring in Mexico).

Feature	<i>Croton calcareus</i> sp. nov.	<i>Croton draco</i>	<i>Croton redolens</i>
Stipules	Short triangular to long filiform	Subulate to broadly subulate	Short filiform
Leaf size (max. cm)	5–13 × 3.5–11	9.9–22.9 × 6.6–17.7	7.8–8.3 × 4.8–6.3
Leaf base	Rounded or cordate	Cordate, rarely rounded	Rounded, rarely cordate
Leaf apex	Acute to obtuse	Acuminate	Acute
Adaxial leaf texture	Rough	Soft	Soft
Adaxial leaf trichomes	Sessile, stellate porrect and stellate multiradiate	Stipitate, stellate multiradiate	Stipitate, stellate porrect
Adaxial leaf indument	Sparse to glabrescent	Dense to very dense	Dense
Inflorescence length (cm)	8–10	14.6–42.5	5.7–15.6
Fruit size (mm)	12–13 × 2–15	4–7 × 4–7	5–6 × 7–8
Seed surface	Smooth	Rugose	Slightly rugose
Plant stature (max. height, m)	6	25	3
Habitat	Dry forest	Moist forest	Dry forest
Distribution	Restricted to Chiapas	Widespread (Mexico to Panama)	Northern Venezuela

Croton and the sister clade of sect. *Cyclostigma* (van Ee *et al.* 2011). It is also one of the few sections of *Croton* with a distinct synapomorphy, i.e., the presence of three inflated lobes at the apex of the fruit columella (Riina *et al.* 2009; van Ee *et al.* 2011). So, *C. xalapensis* can be easily distinguished from *C. calcareus* sp. nov. by its shrubby habit and its trilobed columella apex. *Croton verapazensis*, from Central America, is superficially similar to *C. calcareus* sp. nov. and it also grows in dry forest. However, it is member of a different clade of Neotropical *Croton*, namely *C.* sect. *Corylocroton* G.L.Webster, and can be distinguished from any member of sect. *Cyclostigma*, including *C. calcareus* sp. nov., mainly by its unique petiolar nectary gland morphology (apical part with almost the same diameter as the stipe; in sect. *Cyclostigma* it is much wider than the stipe), presence of stellate-lepidote trichomes, leaf margins serrate to coarsely dentate and presence of unisexual cymules at the base of the inflorescence axis. Finally, as in *C. draco*, both *C. xalapensis* and *C. verapazensis* also have much longer mature inflorescences and smaller capsules and seeds than *C. calcareus* sp. nov.

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Supplementary material

[Supplementary file 1](#)

ITS alignment (fasta file) used in phylogenetic analysis including the newly generated sequences of *Croton calcareus* Riina & Mateo-Ram. sp. nov.

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