

## Sectional rearrangement of arborescent clades of *Croton* (Euphorbiaceae) in South America: Evolution of arillate seeds and a new species, *Croton domatifer*

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**Abstract** Most of the arborescent *Croton* species in the New World were treated by Webster as belonging either to *C. sect. Cyclostigma* Griseb. or *C. sect. Luntia* (Neck. ex Raf.) G.L. Webster. The circumscription of *C. sect. Cyclostigma* has been treated recently. In this paper we focus on *C. sect. Luntia*, which was subdivided by Webster into two subsections, *C. subsect. Matourenses* and subsect. *Cuneati*. Using chloroplast *trnL-F* and nuclear ITS DNA sequence data, morphology and a broader sampling of additional *Croton* lineages, we found that the two subsections are not closely related and form distinct monophyletic groups. Substantial morphological differences support the molecular data. A taxonomic recircumscription of the two subsections, elevated to sectional level, is proposed. A key and taxonomic revision, with new synonyms, is provided for *C. sect. Cuneati*; together with the description of a new species from the coastal mountains of Venezuela, *Croton domatifer*. The new species is the only one in the genus known to possess leaf domatia. We infer that species in the *Cuneati* clade have lost the typical *Croton* caruncle, and some of them have evolved a different, specialized type of aril. We hypothesize that the arillate seeds are an adaptation to dispersal by fish in the Orinoco and Amazon river basins.

**Keywords** arillate seeds; *Croton domatifer*; *Croton* section *Cuneati*; *Croton* section *Luntia*; Euphorbiaceae; leaf domatia; molecular phylogeny; wood anatomy

### ■ INTRODUCTION

*Croton* L. is the second largest genus in Euphorbiaceae, with an estimated 1250 species worldwide (Govaerts & al., 2000; Frodin, 2004; Berry & al., 2005). The majority of the species are shrubs adapted to seasonally dry areas of the tropics and subtropics, but there are a substantial number of tree species on different continents that occur in generally moister habitats in both lowland and montane regions. One of the main reasons why *Croton* trees are ecologically important is because of their role as pioneer species in disturbed forest vegetation in the tropics. For example, on Barro Colorado Island (Panama), *Croton* is among the most common pioneers, with 367 reproductive-sized individuals recorded in a census of a 50-ha plot (Dalling & Brown, 2009). This ecological characteristic makes *Croton* trees ideal candidates for restoration of degraded forests, such as the use of *C. urucurana* Baill. in Brazil (Lorenzi, 1992; Carrenho & al., 1997). Most of the arborescent *Croton* species from the New World were treated by Webster (1993) as belonging to one of two sections, either *C. sect. Cyclostigma* Griseb. or *C. sect. Luntia* (Neck. ex Raf.) G.L. Webster. Webster (1993, 2001) also recognized two subsections within *C. sect. Luntia* and four within *C. sect. Cyclostigma*. Riina & al. (2009) used nuclear ITS and chloroplast *trnL-F* DNA sequence data,

as well as morphology, to determine that Webster's circumscription of *C. sect. Cyclostigma* was widely polyphyletic, with species treated in that section emerging in at least nine separate clades in a broader sampling of *Croton* species. Two of these nine clades represented the two subsections of *Croton* sect. *Luntia* sensu Webster (1993), namely *C. subsect. Matourenses* G.L. Webster and subsect. *Cuneati* G.L. Webster. Both Berry & al. (2005) and Riina & al. (2009) showed that these two subsections or clades are not part of *C. sect. Cyclostigma* s.str., and that they are not sister to each other, but rather represent two morphologically distinct and not closely related lineages within a larger clade of New World species.

Webster (1993) defined *C. sect. Luntia* based on a set of morphological characters (e.g., lepidote indumentum, leaves biglandular, stipules entire, inflorescences terminal and often clustered, sepals valvate, stamens 10–15, styles multifid, etc.), however he did not indicate any single synapomorphy to support the section. The two subsections of *C. sect. Luntia*, *C. subsects. Cuneati* and *Matourenses*, were separated by Webster (1993) based on four morphological differences: presence or absence of bisexual cymules, pistillate flowers sessile or long-pedicellate, chorisepalous or gamopetalous pistillate calyx, and capsules oblong or obovate, respectively. Although Webster indicated that *C. sect. Luntia* was entirely

Neotropical, he mentioned that some African species, such as *C. mubango* Müll. Arg. from western central Africa, could be closely related.

*Croton* sect. *Luntia* subsect. *Matourenses* was originally circumscribed to include only two species, the type, *C. matourensis* Aubl., and *C. lanjouwensis* Jabl. (Webster, 1993). The latter name, however, has since been treated as a synonym of the variable *C. matourensis* (Webster & al., 1999). Berry & al. (2005) then showed that the previously unplaced *C. megalodendron* Müll. Arg. is sister to *C. matourensis* in their analysis, and Riina & al. (2009) showed that three species formerly treated by Webster as members of *C. sect. Cyclostigma* subsect. *Palanostigma* Mart. ex Baill. (*C. chocoanus* Croizat, *C. palanostigma* Klotzsch, *C. smithianus* Croizat) are sister to *C. megalodendron* (*C. matourensis* was not included in this analysis).

*Croton* sect. *Luntia* subsect. *Cuneati* was originally circumscribed by Webster (1993) to include about ten Neotropical species, the type being *C. cuneatus* Klotzsch, a name applied to a widespread Amazonian riparian tree. Other lowland Amazonian or Orinocoan species in the subsection included *C. tessmannii* Mansf., *C. monachinoensis* Jabl., and *C. subcoriaceus* Jabl. Webster also included some montane species in the subsection, such as *C. kaieteuri* Jabl. and *C. neblinae* Jabl., both from the Guayana Shield, *C. pachypodus* G.L. Webster (a mainly Andean species from Costa Rica to Bolivia), and *C. poecilanthus* Urb. (endemic to the Luquillo mountains of Puerto Rico). Van Ee & al. (2008), however, showed that *C. poecilanthus* belongs to an early diverging clade of *Croton* that is not at all closely related to *C. cuneatus*. Riina & al. (2009) similarly showed that *C. pachypodus* belongs to another early diverging branch within *Croton*, and hence is not a member of the same clade as *C. cuneatus* either. Berry & al. (2005) were the first to suggest a close relationship between *C. cuneatus* and *C. malambo* Karst., which was previously placed by Webster (1993) in the mainly Old World section, *C. sect. Tiglium* (Klotzsch) Baill., due to its nearly glabrous foliage. Most recently, Riina & al. (2009) placed *C. yavitensis* Croizat in the same clade with *C. cuneatus* based on molecular phylogenetic analyses. Finally, we are now treating *C. kaieteuri*, *C. monachinoensis*, and *C. subcoriaceus* as synonyms of *C. cuneatus* as a result of our taxonomic revision of the pertinent type specimens.

This study focuses on the phylogeny and taxonomy of *Croton* subsect. *Matourenses* and subsect. *Cuneati*. These groups are important because they include tree species that are prominent in primary and secondary forests of the Neotropics, and they may provide insights into the evolution of reproductive and vegetative characters within *Croton*, such as the loss or modifications of the seed caruncle, reduplication of the pistillate calyx, and the types of leaf glands and trichomes. *Croton cuneatus* and *C. malambo* are also important as medicinal plants in South America (Webster & al., 1999; Salatino & al., 2007; Suárez & al., 2003, 2004, 2005, 2006, 2008). A taxonomic recircumscription of both subsections is proposed, with emphasis on *C. subsect. (now sect.) Cuneati*, for which we include an identification key and a taxonomic synopsis. Finally, we describe and illustrate a new species of *C. sect. Cuneati*,

*Croton domatifer*, the only one in the genus known to possess well-developed leaf domatia.

## ■ MATERIALS AND METHODS

**Molecular sampling.** — Species with characters consistent with *Croton* sect. *Luntia* subsections *Matourenses* and *Cuneati* sensu Webster (1993) were targeted for molecular sampling. These were combined with a selection of taxa representing nine of the eleven clades identified by Berry & al. (2005). The nuclear ribosomal ITS (ITS1, 5.8s, ITS2) and plastid *trnL-F* (*trnL* exon, intron, and 3' intergenic spacer) loci were sequenced employing the same methods as described in Berry & al. (2005). These two loci have been used in all species-level phylogenies of *Croton* to date (Berry & al., 2005; Van Ee & al., 2008; Cordeiro & al., 2008; Riina & al., 2009; Van Ee & Berry, 2009). Two outgroup taxa, *Astraea lobata* (L.) Klotzsch and *Brasiliocroton mamoninha* P.E. Berry & Cordeiro, were included following the results of Berry & al. (2005). Our finalized taxon sampling contains 41 taxa for which ITS and *trnL-F* sequence data are available for all accessions except *C. smithianus*, for which only ITS is available. Indels were noted but not scored for inclusion in the phylogenetic analyses. The data matrix is archived in TreeBASE (Study accession number = S2577; Matrix accession number = M4924), and sequences are deposited in GenBank (Appendix). Two sequences were newly generated for this study, ITS and *trnL-F* sequences of the new species *C. domatifer*.

**Phylogenetic analyses.** — DNA sequences were edited and assembled using the Staden Package v.2003.0b1 (Staden, 1996), and then aligned manually using MacClade v.4.08 (Maddison & Maddison, 2001). Incongruence between the nuclear and chloroplast loci was evaluated with the incongruence length difference (ILD) test (Farris & al., 1994) as implemented in PAUP\* v.4.0b10 (Swofford, 2002). The ILD test was conducted using 1000 partition homogeneity replicates of 10 random addition sequence replicates (RASR) each, tree bisection and reconnection (TBR), holding one tree at each step, nchuck = 100, and excluding uninformative and gapped characters. *Croton smithianus*, for which only ITS sequence data is available, was excluded from the ILD test.

Maximum parsimony (MP) analyses were conducted in PAUP\*. We performed MP heuristic searches with 100 random taxon addition replicates using TBR branch swapping, multrees in effect, and not limiting the number of trees saved. All characters were equally weighted, and gaps were treated as missing data.

The *gI* statistic (Hillis & Huelsenbeck, 1992) and the parsimony permutation tail probability test (PTP) (Faith & Cranston, 1991) were conducted on the combined ITS and *trnL-F* dataset for assessing the phylogenetic signal of the combined data. The Templeton test (Templeton, 1983), as implemented in PAUP\* under a maximum parsimony framework and with same settings as in the MP analyses above, was used to evaluate Webster's suggestion that *Croton* sect. *Cuneati* and sect. *Luntia* form a clade.

The best fitting likelihood models for each of the loci, as well as for the combined data, were selected with Modeltest

v.3.07 (Posada & Crandall, 1998) using the Akaike Information Criterion (AIC). Ten independent likelihood analyses of the loci in combination and separately were conducted in GARLI v.0.96b8 (Zwickl, 2006). Each likelihood analysis used the program's default settings, the substitution model selected by Modeltest, and allowing GARLI to estimate the model parameters. In the combined likelihood analyses, the data were treated as a single partition. Maximum likelihood (ML) bootstrap (BS) values were calculated from the combined and separate loci from 100 likelihood replicates run in GARLI, also using the default stop criterion settings. Each BS replicate consisted of four search replicates. Maximum parsimony BS values of the combined and separate loci were calculated in PAUP\* from 1000 replicates of 100 RASR each, TBR, and nchuck = 100. Bayesian posterior probabilities (PP) of the combined loci were calculated in MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) from two Markov chain Monte Carlo (MCMC) analyses, each consisting of four linked chains (heat = 0.2), 1,000,000 generations, and sampling every 50 generations. The burn-in period was estimated by visual examination of the likelihood-by-generation plot. After removing the trees from the burn-in period PP values were obtained by computing a majority rule consensus of the trees from both MCMC chains.

**Wood anatomy.** — Wood samples from *Croton domatifer* and other species in *C. sect. Cuneati* were prepared for microscopic observation and measured following standard microtechnique protocols as in Berry & Wiedenhoft (2004).

## ■ RESULTS

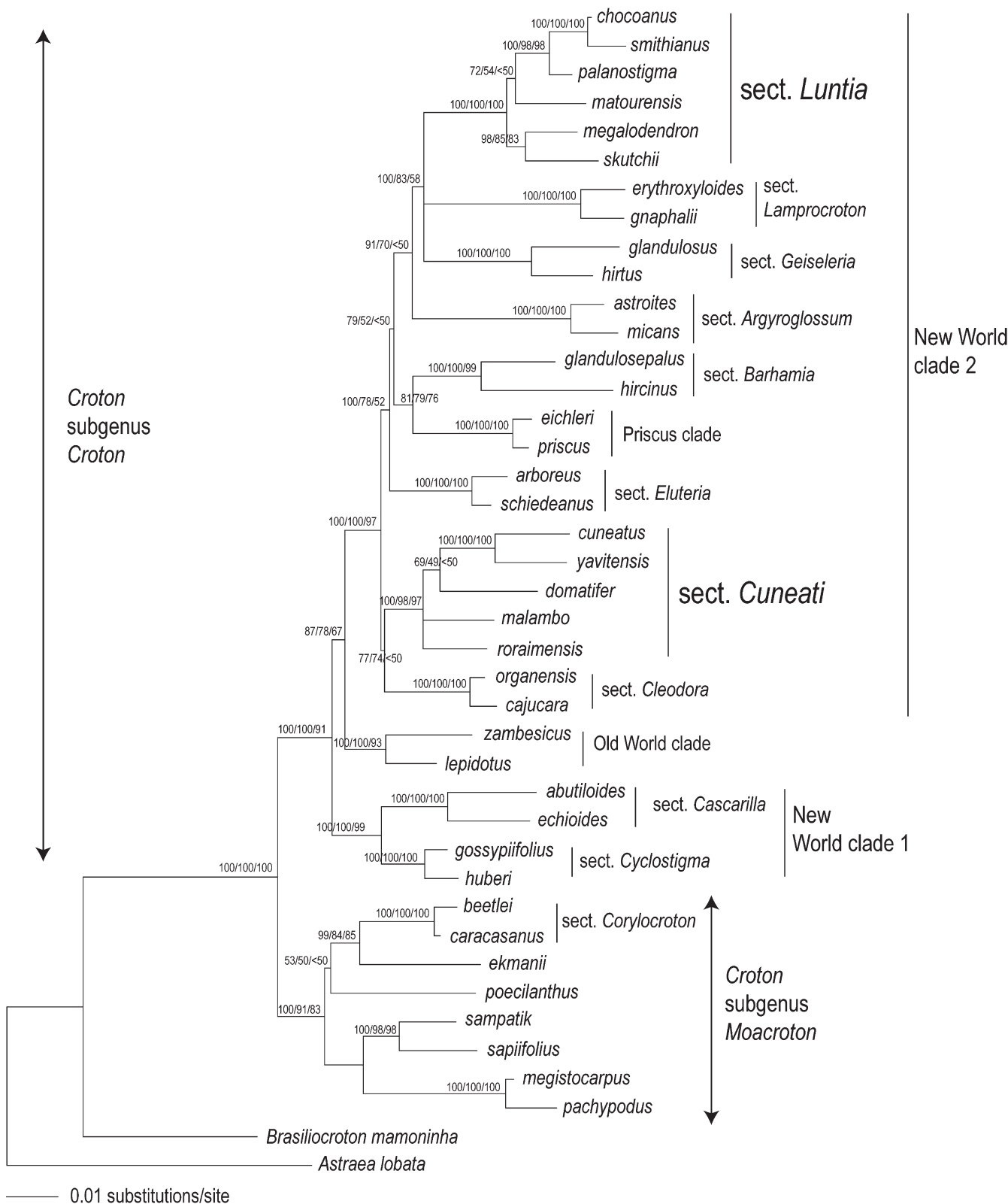
**Datasets.** — The aligned length of the ITS dataset is 704 positions, of which 326 (46.3%) are variable and 237 (33.7%) are parsimony-informative. The aligned *trnL-F* dataset is 1251 positions long, of which 279 (22.3%) are variable and 131 (10.5%) are parsimony-informative. A visual inspection of the data matrices did not reveal any obviously ambiguously aligned regions, therefore no portions were excluded. The ILD test failed to reject ( $P = 0.314$ ) the hypothesis of no meaningful conflict between the two loci given this sampling. The phylogenetic signal in the combined data matrix was significant ( $gI = -0.73$ ,  $P < 0.01$ , and  $P = 0.01$  in the PTP test). In contrast, the Templeton test was not significant ( $P = 0.1537-0.2350$ ), and the hypothesis that *Croton sect. Luntia* and *sect. Cuneati* form a clade, given these data, cannot be rejected.

The MP search of the combined ITS and *trnL-F* dataset resulted in a single most parsimonious tree (not shown,  $L = 1388$ , consistency index = 0.595 and retention index = 0.654), with both indices calculated including parsimony uninformative characters. Modeltest, using AIC, selected SYM+I+G for the ITS data, TIM+I+G for the *trnL-F* data, and GTR+I+G for the combined data. The ML model selected for the ITS data (SYM+I+G) specifies equal codon frequencies (statefrequencies = equal), which is suggested to be a poor option (Zwickl, 2006). Therefore, the ITS ML search was also conducted allowing GARLI to estimate the codon frequencies (statefrequencies = estimate), and the results were compared.

Although the ITS and *trnL-F* loci were analyzed separately as well as together using parsimony, likelihood, and Bayesian methods, only the result of the Bayesian analysis of the combined data is presented here (Fig. 1), and where relevant the results of the separate analyses are discussed. All ten independent likelihood analyses of the combined loci recovered the same topology (not shown), suggesting that the program has converged on the best, or nearly best, topology. There were no differences in the topology of the Bayesian analysis and the likelihood analyses, and no strongly supported differences between these and the results of the parsimony analysis. Likewise, the separate ITS and *trnL-F* analyses do not differ from each other or the combined analysis in any strongly-supported way, with the exception that the *trnL-F* analysis recovered *Croton sect. Cyclostigma* apart from *C. sect. Cascarilla* Griseb., a result discussed in greater detail in Riina & al. (2009).

**Phylogenetic patterns.** — *Croton cuneatus* and four other species, *C. yavitensis*, *C. domatifer*, *C. roraimensis* Croizat, and *C. malambo*, form a strongly supported monophyletic group (100% PP/98% ML/97% MP BS; from here on the Bayesian PP, ML bootstrap, and the MP bootstrap values are given in that order), now labeled *sect. Cuneati* in Fig. 1 (previously *subsect. Cuneati*). *Croton sect. Cuneati* is separate and not sister to the well-supported (100%/100%/100%) *C. sect. Luntia* clade (previously *C. subsect. Matourenses*), which contains *C. skutchii* Standl., *C. megalodendron*, *C. matourensis*, *C. palanostigma*, *C. smithianus*, and *C. chocoanus* (Fig. 1). Although the overall *Croton* sampling in this work is reduced and skewed compared to previous publications, the Bayesian consensus tree (Fig. 1) shows the same overall topology as in previous *Croton* phylogenies in which two reciprocally monophyletic subgenera are recovered. Also, New World clade 2 goes sister to the Old World clade, and together these go sister to New World clade 1 (*sensu* Berry & al., 2005). Both *C. sects. Cuneati* and *Luntia* belong to New World clade 2, equivalent to clades C-4 through C-11 of Berry & al. (2005).

*Croton sect. Cuneati* is recovered as sister to *C. sect. Cleodora* (Klotzsch) Baill. with weak support (77%/74%/<50%), and *C. sect. Luntia* is recovered with moderate support (100%/85%/58%) sister to a clade including *C. sect. Lamprocroton* (Müll. Arg.) Pax and *sect. Geiseleria* (Klotzsch) Baill. (Fig. 1). The *C. sect. Luntia* clade is formed by two sister subclades, the first (top) with the entire and penninerved-leaved *C. matourensis* sister to the lobed and palminerved-leaved group of *C. palanostigma*, *C. smithianus*, and *C. chocoanus*. The second, (bottom) subclade consists of *C. megalodendron* and *C. skutchii*, both of which are entire and penninerved-leaved species and are morphologically more similar to *C. matourensis* (Fig. 1). The species relationships within *C. sect. Cuneati* are not as well resolved as in *C. sect. Luntia*, and only *C. cuneatus* and *C. yavitensis* together form a highly supported clade (100%/100%/100%). Within *C. sect. Cuneati*, the lone dry forest species, *C. malambo*, and the montane forest species, *C. roraimensis*, form a polytomy with a clade containing the other three species sampled, namely *C. domatifer*, *C. yavitensis*, and *C. cuneatus* (Fig. 1).



**Fig. 1.** Bayesian consensus tree of combined *trnL-F* and ITS data. The numbers represent support values in the following order: Bayesian posterior probability/Maximum likelihood bootstrap support/Maximum parsimony bootstrap support. Names on the right of vertical bars represent the sectional or informal clade assignment of the species.



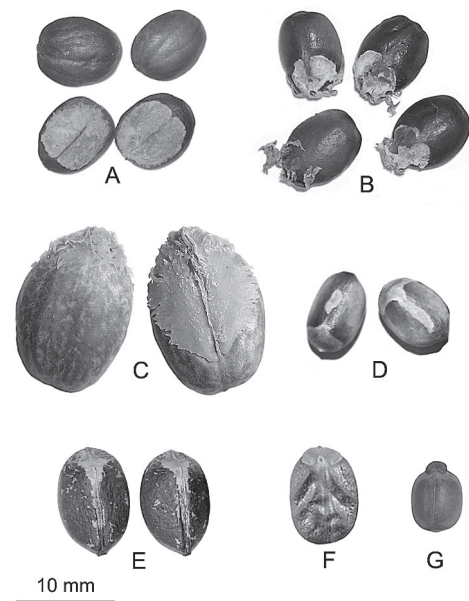
## DISCUSSION

Two distinct and separate clades represent the two subsections of *Croton* sect. *Luntia* sensu Webster (1993), and given their disparate positions in the phylogram (Fig. 1) and their morphological differences, we recognize them as distinct sections, *C. sect. Cuneati* (G.L. Webster) Riina & P.E. Berry and *C. sect. Luntia* (Neck. ex Raf.) G.L. Webster (see Taxonomic Treatment below). The results presented in Fig. 1 give strong Bayesian PP support, but not strong ML or MP bootstrap support, for *C. sects. Cuneati* and *Luntia* not being sister to each other. However, the results of Berry & al. (2005) do provide that support, further indicating that these clades are not closely related to each other, unlike Webster's (1993) hypothesis that they were part of the same section. This pattern is also supported by clear morphological differences between the two sections, which we describe in more detail below.

*Croton* sect. *Cuneati* is supported by two morphological synapomorphies, namely loosely crenate to dentate leaf margins with sessile to shortly stipitate discoid glands in the sinuses, and the loss of the typical *Croton* caruncle (Fig. 2A–E). All of these species effectively lack a caruncle on their seeds, which otherwise is characteristic of almost all *Croton* species, including all members of *C. sect. Luntia*. *Croton roraimensis* and *C. yavitensis* both have unusually large seeds for the genus (1.5–2.5 cm diam.), and *C. domatifer* has stellate-fasciculate trichomes with unusually long radii and is the only species known in the genus that has evident domatia-like structures on the undersides of the leaves. Lastly, *C. cuneatus* and *C. yavitensis* are strongly supported (100%/100%/100%) as sister species, as previously reported by Riina & al. (2009). These are both lowland riparian species, with seeds that have an arillate structure that may be adapted to attract fish (Murillo, 1999) (Fig. 2A–C). If this observation is confirmed by future studies, it will indicate an interesting evolutionary shift of secondary seed dispersal in *Croton* from ant to fish dispersal (nearly all species of *Croton* have explosively dehiscent capsules that initially scatter the seeds close to the mother plant). Additional taxon sampling and a better resolved phylogeny is still needed to identify the evolutionary trends in seed morphology in this group and the evolution of an elaborate aril that could be an adaptation to riparian habitats and seasonally inundated lowland forests (Fig. 2A–C). Other genera of Euphorbiaceae, such as *Hevea* and *Mabea*, have been documented to have seeds that are eaten by fish in the same habitats, although these generally lack an arillate structure (Kubitzki & Ziburski, 1994).

Based on its similar habitat and morphology to *C. cuneatus*, we hypothesize that *C. tessmannii* also belongs in *C. sect. Cuneati*. Moreover, we predict that it will cluster with *C. cuneatus* and *C. yavitensis* once molecular data is obtained given that it is very similar morphologically to *C. cuneatus*, the main difference being the seed size and the aril size and shape of specimens of *C. tessmannii*. Two species placed by Webster (1993) in his *C. sect. Luntia* subsect. *Cuneati* (here re-ranked as *C. sect. Cuneati*), namely *C. pachypodus* and *C. poecilanthus*, are confirmed here as belonging to *C. subg. Moacroton*, a finding that is consistent with the results of Van

Ee & al. (2008) and Riina & al. (2009). *Croton* sect. *Cuneati* shares several morphological features with *C. sections Geiseleria* and *Corylocroton* G.L. Webster. Although not closely related (Fig. 1), these three sections share bifid styles, stellate to lepidote trichomes, a pair of glands at the base of the leaf blade, and the presence of glands in the sinuses of the leaf margins. All these shared character states are symplesiomorphic, therefore they do not indicate close phylogenetic relationship. Many species of *C. sect. Geiseleria* are annual herbs, but the shrubby species can be distinguished from the other two sections by having unequal sepals in the pistillate flowers. Only two species of *C. sect. Corylocroton*, *C. caracasanus* Pittier and *C. beetlei* Croizat, occur in South America, and these can be distinguished from those of *C. sect. Cuneati* by their carunculate seeds, very reduced pistillate sepals that are never reflexed in fruit, and epipetiolar glands at the base of the lamina in the adaxial position. Our phylogenetic results indicate that the presence of glands in the sinuses of the leaf margins is a character that arose independently at least four times in *Croton*, three times in the Neotropical sections, *C. sects. Cuneati*, *Corylocroton* (see Van Ee & al., 2008), and *Geiseleria*, and one or more times on Madagascar. All Old World species of *Croton* sampled to date form a monophyletic clade (Berry & al., 2005; Van Ee & al., 2008; Riina & al., 2009), and within



**Fig. 2.** Seeds and aril morphology of several members of *Croton* sect. *Cuneati* and other *Croton* species. **A**, *C. cuneatus*, Vasquez 7472 (AMAZ), showing ventral (bottom two) and dorsal (upper two) sides; **B**, *C. tessmannii*, Rimachi 11575 (AMAZ), showing dorsal (lower left) and ventral (other three) sides; **C**, *C. yavitensis*, Beck 10126 (LPB), showing ventral and dorsal sides; **D**, ecarunculate seeds of *C. malambo*, Karsten s.n. (W), showing ventral sides; **E**, vestigial caruncle of *C. domatifer*, Morillo 2601 (VEN), showing ventral sides; **F–G**, ventral side of seeds of *C. ruizianus* Mull.Arg., Ruiz & Pavón s.n. (G-DC), and *C. serratifolius* Baill., Nee 4439 (USZ), showing more typical *Croton* caruncles.

those all the Malagasy species form a monophyletic group of their own (Berry & al., 2009). This finding contradicts Webster’s hypothesis that *C. sect. Luntia* may have some Old World members, such as the African *C. mubango*.

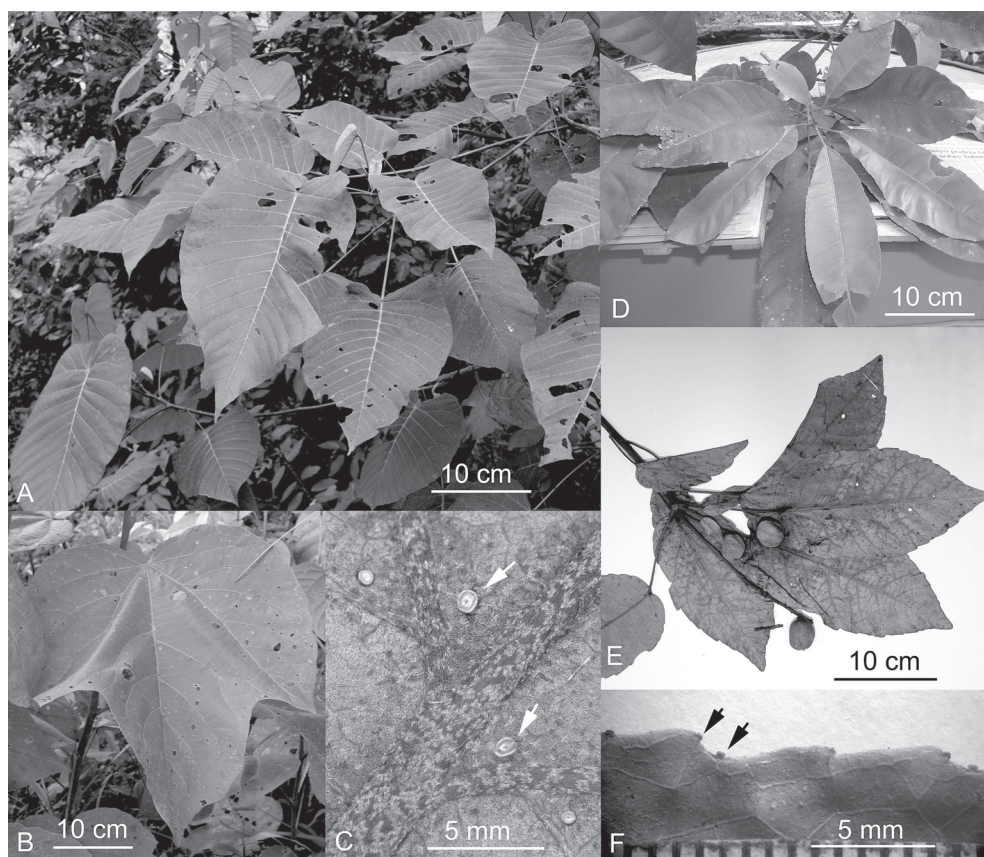
The placement of *C. megalodendron* and *C. skutchii* in *C. sect. Luntia* (Fig. 1) confirms their close relationship to *C. matourensis*, which was first discovered by Riina & al. (2009). Based on morphological similarities, described in detail in the following paragraph, we hypothesize that *C. costatus* Kunth from Colombia and Andean Venezuela will be placed with *C. megalodendron* and *C. skutchii* once it is sampled molecularly. The additional three species recovered in *C. sect. Luntia*, namely *C. chocoanus*, *C. palanostigma*, and *C. smithianus*, belong to what Webster treated as *C. sect. Cyclostigma* subsect. *Palanostigma* Mart. ex Baill., and because *C. palanostigma* is the type of *C. subsect. Palanostigma*, we synonymize it with *C. sect. Luntia*. We predict that several more species previously placed in *C. subsect. Palanostigma*, but not all, are actually members of *C. sect. Luntia* rather than of *C. sect. Cyclostigma* (see Taxonomic Treatment below).

In addition to the molecular characters, *C. sect. Luntia* is defined by several floral characters, including a robust and strongly reduplicate calyx in the pistillate flowers, highly divided styles, a low number of stamens (usually 10), and conspicuous linear-lanceolate bracts (3–4) subtending each cymule (the bracts are deciduous as the inflorescence matures).

Unlike floral characters, foliar characters are not as uniform across *C. sect. Luntia*, and there are two different types of leaf morphology within the clade. There are species with pinnate venation and unlobed leaves, such as *C. matourensis*, *C. megalodendron*, *C. skutchii*, and *C. costatus*, which also lack laminar glands, and species with lobed and palmatinerved leaves, which bear cup-shaped or patelliform glands on the lamina (Fig. 3A–C). Within *C. sect. Luntia*, our molecular phylogeny (Fig. 1) supports an evolutionary trend from unlobed, penninerved, eglandular leaves to deeply lobed, palmatinerved leaves with numerous patelliform glands on both surfaces of the lamina.

Although the Templeton test failed to reject the hypothesis that *C. sections Cuneati* and *Luntia* are not sister clades, the consistency of our phylogenetic pattern (Fig. 1) with previous phylogenetic work on *Croton* (Berry & al., 2005; Van Ee & al., 2008; Riina & al., 2009; Van Ee & Berry, 2009), and the morphological differences between the two sections suggest that they are not sister to each other. These two clades are in a region of the *Croton* phylogeny (New World clade 2, Fig. 1) with low resolution and support, which could explain the results of the Templeton test. Additional taxon and molecular marker sampling are needed to improve resolution and support along the backbone of New World clade 2, which should support or reject our hypothesis that *C. sections Cuneati* and *Luntia* do not form a clade.

**Fig. 3.** Diagnostic leaf characters of *Croton* sect. *Luntia* (A–C) and sect. *Cuneati* (D–F): **A**, entire and penninerved leaves of *C. costatus*, Riina 1829 (VEN); **B**, lobed and palmately veined leaves of *C. palanostigma*, Riina 1492 (MICH); **C**, cup-shaped or patelliform laminar glands (arrows) of *C. palanostigma*, Morillo 9555 (VEN); **D**, leaves of *C. cuneatus* with subentire or loosely dentate margins, Riina 1493 (MICH); **E**, leaves of *C. yavitenensis* with conspicuously dentate margins; **F**, glandular leaf margin of *C. tessmannii*; the arrows indicate two types of marginal glands, ovoid glands on the teeth and discoid glands in the sinuses, Vásquez 11509 (USM).





■ TAXONOMIC TREATMENT

*Croton* sect. *Luntia* (Neck. ex Raf.) G.L. Webster in Taxon 42: 804. 1993 – *Luntia* Neck. ex Raf. – Type: *Luntia sericea* Raf., nom. illeg. (*C. sericeus* Lam., nom. illeg. ≡ *C. matourensis* Aubl.).

= *Croton* (sect. *Cyclostigma* Griseb.) subsect. *Palanostigma* Mart. ex Baill. in Étude Euphorb.: 358. 1858 – Type: *Croton palanostigma* Klotzsch.

Monoecious trees; indumentum lepidote or stellate-lepidote; leaves alternate, pinnately or palmately veined, entire or tri-lobed (Fig. 3A–B), usually with sessile cup-shaped or patelliform glands on one or both sides of the lamina (Fig. 3C) and a pair of acropetiole glands at the base of the lamina in an abaxial position, stipules entire, deciduous; inflorescences terminal, often clustered, unisexual or bisexual, bisexual cymules sometimes present, conspicuous bracts (3–4) subtending each cymule (more noticeable in very young inflorescences), stamens 10–15; pistillate flowers with sepals entire, partially united at the base, eglandular, reduplicate-valvate, styles repetitively divided, with 6–12 or more branches each; capsules obovate, trilobular, seeds carunculate.

Included species: *C. caryophyllus* Benth., *C. cearensis* Baill., *C. costatus* Kunth, *C. chocoanus* Croizat, *C. grazielae* Secco, *C. huitotorum* Croizat, *C. javarisensis* Secco, *C. kilipianus* Croizat, *C. matourensis* Aubl., *C. megalodendron* Müll. Arg., *C. nuntians* Croizat, *C. palanostigma* Klotzsch, *C. perimetralensis* Secco, *C. pullei* Lanj., *C. skutchii* Standl., *C. smithianus* Croizat, *C. tonantinensis* Jabl., *C. uribei* Croizat.

Necker (1790) first described *Luntia* as a genus. However, generic names published in his work are not accepted as validly published (McNeill & al., 2006: Article 32.9). The validly published *Luntia* Neck. ex Raf. therefore had to wait until Rafinesque’s (1838) validation of the name. In this publication, Rafinesque made the new name *Luntia sericea* Raf. for Lamarck’s (1786) *C. sericeus* Lam., which is illegitimate and superfluous given that in the protologue, Aublet’s (1775) earlier name *C. matourensis* Aubl. is cited.

There are still a number of taxonomic and nomenclatural issues that need to be clarified for several species in *Croton* sect. *Luntia*, and this will be done at a later date. However, a report of a new synonym for *C. skutchii* follows. With further study, *C. skutchii* may also prove to be conspecific with *C. costatus* Kunth, which is the earliest name available.

*Croton skutchii* Standl. in Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 86. 1940 – Type: Costa Rica. San José: vicinity of El General, 670 m, A.F. Skutch 4377 (holotype, F!; isotypes, K!, MO!, US!).

= *Croton stipuliformis* J. Murillo in Caldasia 21: 159, fig. 6. 1999 – Type: Colombia. Boyacá: Pauna, vereda Manote Alto, 1250 m, 3 Nov 1975, H. Rueda s.n. (holotype, COL!).

*Croton* sect. *Cuneati* (G.L. Webster) Riina & P.E. Berry, **stat. nov.** ≡ *Croton* subsect. *Cuneati* G.L. Webster in Taxon 42: 804. 1993 – Type: *C. cuneatus* Klotzsch.

Monoecious trees; indumentum lepidote, stellate-lepidote,

and stellate; leaves alternate, pinnately or palmately veined, margin loosely crenate or sinuous, crenate or dentate, usually with sessile or shortly stipitate discoid glands in the sinuses, and sometimes less obvious ovoid glands on the teeth (Fig. 3D–F), and a pair of acropetiole glands at the base of the lamina in an abaxial position, stipules entire, deciduous; inflorescences terminal, often clustered, unisexual or bisexual, bisexual cymules sometimes present, styles 2-fid to 4-fid; stamens 10–20; pistillate flowers with sepals entire and eglandular, free, valvate; capsules oblong, trilobular, rarely bilobular, seeds ecarunculate (Fig. 2D) or with a vestigial caruncle (Fig. 2E), sometimes with a distinctive aril (Fig. 2A–C).

Key to the species of *Croton* sect. *Cuneati*

1. Leaf blades broadly ovate, palmately 3–5-veined at the base, less than twice as long as broad, indumentum of dense ferruginous appressed-stellate to rosulate trichomes, with tufts of longer trichomes present in the axils of abaxial leaf veins and forming domatia; in cloud forests of the Venezuelan Coastal Cordilleras . . . . . *C. domatifer*
1. Leaf blades elliptic or ovate, penninerved or sometimes 3-veined at the base, more than twice as long as broad, indumentum dense to very sparse (subglabrous), of lepidote or stellate (but not ferruginous) trichomes, domatia absent; in lowland Amazonian forests, dry coastal forests, or montane forest of the Guayana Shield . . . . . 2
2. Leaf blades nearly glabrous, if trichomes present, then very sparse . . . . . 3
2. Leaf blades sparsely to densely pubescent, at least on the lower surface. . . . . 4
3. Leaf blades narrowly elliptic to lanceolate, apex acuminate, base cuneate, petioles less than 1/5 the length of the blade; pistillate flowers subsessile, ovary stellate tomentose, fruits and seeds unknown; upland forests of the Guayana Shield in SE Venezuela and SE Colombia . . . . . *C. icabarui*
3. Leaf blades ovate, apex acute, base rounded to subcordate, petioles 1/4–1/3 the length of the blade; pistillate flowers with pedicels 5–10 mm long, sepals of pistillate flowers reflexed in fruit, capsules glabrous, seeds without aril or caruncle; dry Caribbean coastal forests of NE Colombia and NW Venezuela. . . . . *C. malambo*
4. Young growth and undersides of leaves with stellate to stellate-lepidote trichomes (becoming somewhat glabrescent); seeds 13–15 × 9–10 mm, aril with dissected margin covering half or most of the ventral side of the seed, and the upper part of the dorsal side (Fig. 2C); seasonally flooded lowland vegetation (forests and savannas) in the Amazon and Orinoco basins. . . . . *C. yavitensis*
4. Young growth and undersides of leaves with lepidote trichomes; seeds 6–9 × 4–6 mm or, if larger (15–25 × 10–15 mm), then lacking an aril; montane forests of the Guayana Shield as well as seasonally flooded riverine forests of the Amazon and Orinoco basins. . . . . 5
5. Lowland tress (<500 m elevation) in seasonally flooded riverine forests of the Amazon and Orinoco basins; leaf

- blades 3–5 times as long as wide; seeds ecarunculate but with a ventral aril . . . . . 6
5. Trees of moist montane forests of the Guayana Shield (>1000 m elevation); leaf blades 2–3 times as long as wide; mature seeds (not known in *C. neblinae*) 15–25 mm long × 10–15 mm thick, seeds ecarunculate but with a broad ventral scar lighter than the brown seed coat. . . . . 7
6. Leaf margin serrulate to subentire; aril with an entire margin covering most of the ventral side of the seed (Fig. 2A); widespread in the Amazon and Orinoco basins (incl. Guyana, French Guiana, and Suriname) . . . *C. cuneatus*
6. Leaf margin serrate; aril with an irregularly dissected margin covering the upper part of the ventral side of the seed (Fig. 2B); restricted to the Colombian and Peruvian Amazon. . . . . *C. tessmannii*
7. Leaf margins serrulate, petioles 2–4 cm long; slopes of tepuis of eastern Venezuela and western Guyana . . . . . *C. roraimensis*
7. Leaf margins entire, petioles 6–10 cm long; only known from the Sierra de la Neblina along the Venezuelan-Brazilian border . . . . . *C. neblinae*

**Synopsis of the species of *Croton* sect. *Cuneati***

1. *Croton cuneatus* Klotzsch in London J. Bot. 2: 49. 1843 – Type: Guyana. Roraima expedition, 1839, *Richard Schomburgk s.n.* (lectotype, designated here, K!; isolectotypes, B destroyed, F-neg. 5079!, G!); Brazil. On the Amazon river, 1836, *E.F. Poeppig 2593* (syntype, G!); Brazil. Rio Negro: in sylvis Japurensibus, *C.F.P. Martius s.n.* (syntype, M 0089073!).
- = *Croton surinamensis* Müll. Arg. in Linnaea 34: 82. 1865 ≡ *Croton cuneatus* Miq. in Linnaea 21: 477. 1848, non *C. cuneatus* Klotzsch (1843) – Type: Suriname. *Fr. W.R. Hostmann 1094* (lectotype, designated here, G!; isolectotypes, B destroyed, F-neg. 5184!, K!, G-DC!); Suriname. *A. Kappler 1505* (syntype, G!); Suriname. *H.C. Hocke s.n.* (syntype, U?).
- = *Croton martii* Müll. Arg. in Martius, Fl. Bras. 11(2): 88. 1873 ≡ *C. martii* var. *latifolius* Müll. Arg. in Martius, Fl. Bras. 11(2): 88. 1873 – Type: Brazil. Pará: in silvis prope Pará, *C.F.P. Martius s.n.* (lectotype, designated here, M 0089098!).
- = *Croton martii* Müll. Arg. var. *longifolius* Müll. Arg. in Martius, Fl. Bras. 11(2): 88. 1873 – Type: Brazil. Pará: prope Pará, *C.F.P. Martius s.n.*, (lectotype, designated here, M 0089099!).
- = *Croton mimeticus* S. Moore in Trans. Linn. Soc. London 4: 453. 1895 – Type: Brazil. Matto Grosso: Villa Maria, Dec 1891, *S. Moore 843* (lectotype, designated here, BM; isotype, B destroyed, F-neg. 5134!).
- = *Croton kaieteuri* Jabl. in Mem. New York Bot. Gard. 12(3): 155. 1965 – Type: Guyana. Kaieteur Plateau, along Potaro River above Kaiatuk, 10 May 1944, *B. Maguire & D.B. Fanshawe 23352* (holotype, NY!; isotypes, GH!, S!, US!, VEN!).
- = *Croton monachinoensis* Jabl. in Mem. New York Bot.

- Gard. 12: 157. 1965 – Type: Venezuela. Bolívar: Río Suapure, 17 Jan 1956, *J.J. Wurdack & J. Monachino 41251* (holotype, NY!; isotypes, GH!, US!, VEN!).
- = *Croton subcoriaceus* Jabl. in Mem. New York Bot. Gard. 12(3): 156. 1965 – Type: Venezuela. Amazonas: Río Orinoco, just below the mouth of Caño Yapacana, 125 m, 17 Mar 1953, *J.J. Wurdack & L.S. Adderley 43028* (holotype, NY!; isotypes, NY!, S!).
- = *Croton bilocularis* J. Murillo in Caldasia 21: 156. 1999 – Type: Colombia. Amazonas: Quebrada el Achote, afluente del río Caquetá, frente a Peña Roja, Feb 1992, *J. Murillo & A. Matapí 85* (holotype, COL!; isotype, COAH!).
- After examining the types of *C. martii* var. *latifolius* and var. *longifolius*, and designating that of the former as lectotype of the species name, we concluded that *C. martii* and both its varieties should be synonymized with *C. cuneatus*. *Croton bilocularis* was described as differing from *C. cuneatus* in having bilocular capsules (Murillo, 1999). However, we found that bilocular capsules are also present in some specimens of typical *C. cuneatus*, and sometimes there are individuals with both bilocular and trilocular capsules on the same inflorescences. Murillo (1999) also indicated that *C. bilocularis* differed from *C. cuneatus* in having the abaxial surface of the lamina covered by a dense lepidote indumentum without spaces between the scales. A dense lepidote indumentum is well within the range of variation of this character in *C. cuneatus*, however, and we could not find other significant differences between them.
- Croton cuneatus* is widespread in seasonally flooded riparian forests of the Amazon and Guayana regions, including Venezuela, Guyana, Suriname, French Guiana, Brazil, Colombia, Ecuador, Peru, and Bolivia.
2. *Croton icabarui* Jabl. in Mem. New York Bot. Gard. 12(3): 158. 1965 – Type: Venezuela. Bolívar: región de los ríos Icabaru, Hacha, y cordillera sin nombre a 280° de las cabeceras del río Hacha, 450–850 m, 9 Jan 1956, *A.L. Bernardi 2853* (holotype, NY!; isotype, VEN!).
- This species is known from the type locality in southeastern Venezuela and from one other locality in southeastern Colombia (*Schultes & Cabrera 19469*, COL, U, from the Vaupés/Caquetá border).
3. *Croton malambo* H. Karst. in Linnaea 28: 418. 1856 – Type: Colombia. Bolívar: Cartagena, *H. Karsten s.n.* (lectotype, designated here, LE!; isolectotype, W!).
- This species is distributed in the Guajira region of northwestern Venezuela (Estado Zulia) and the northeastern coastal region of Colombia (Departamentos Bolívar, Atlántico, Magdalena, and La Guajira).
4. *Croton neblinae* Jabl. in Mem. New York Bot. Gard. 12(3): 155. 1965 – Type: Venezuela. Amazonas: Cerro de la Neblina, Río Tatua: Cano Grande, SSE of Cumbre Camp, 26 Dec 1957, *B. Maguire 42529* (holotype, NY!; isotype, MO!).
- This species is only known from the type locality in southernmost Venezuela along the border with Brazil.



5. *Croton roraimensis* Croizat in Bull. Torrey Bot. Club 67: 290. 1940 – Type: Venezuela. Bolívar: Mount Roraima, southwestern slopes, about 7400 feet, 6 Jan 1939, *A. Pinkus 122* (holotype, A!; isotypes, F!, NY!, US!).
- = *Croton roraimensis* var. *subinteger* Steyerf. in Fieldiana, Bot. 28: 315. 1952 – Type: Venezuela. Bolívar: Ptari-tepui, along base of east-facing high sandstone bluff, 2410–2450 m, 7 Nov 1944, *J.A. Steyermark 59925* (holotype, F!).
- This species is an occasional tree of wet montane forests of the Guayana region (Venezuela and Guyana).

6. *Croton tessmannii* Mansf. in Notizbl. Bot. Gart. Berlin-Dahlem 9: 264. 1925 – Type: Peru. Loreto: Ucayali River, flooded areas, Yarina Cocha, 150 m, 20 Nov 1923, *G. Tessmann 3438* (holotype, B, destroyed; lectotype, designated here, G!; isolectotypes, NY!, S!). Peru. Loreto: upper Ucayali, Cumaria, s.d., *G. Tessmann 3434* (paratypes: B destroyed, F-neg. 5186!, F!, NY!).

In several major herbaria, the name *Croton tessmannii* has mistakenly been applied to many specimens of *C. pachypodus*, which is a medium-elevation montane forest species that is widespread along the foothills of the Andes and also occurring in Panama and Costa Rica. *Croton pachypodus* can be distinguished from *C. tessmannii* by its large fruits (the largest fruit of all Neotropical *Croton* species, 3–5 cm diam.), petiolar glands acropetiolar and in adaxial position (vs. glands on the abaxial side in *C. tessmannii*), 2-fid styles (vs. 4-fid in *C. tessmannii*), and axillary inflorescences (vs. a terminal cluster of inflorescences in *C. tessmannii*). *Croton pachypodus* was erroneously described as having 4-fid styles (Webster & Huft, 1988), but, like its close relatives *C. megistocarpus* J.A. González & Poveda and *C. jorgei* J. Murillo, it has bifid styles.

*Croton tessmannii* is known quite locally from riparian lowland forests in Loreto, Peru.

7. *Croton yavitensis* Croizat in J. Arnold Arbor. 26: 189. 1945 – Type: Venezuela. Amazonas: Yavita, *L.W. Williams 14029* (holotype, A!; isotypes, G!, US!, VEN!).

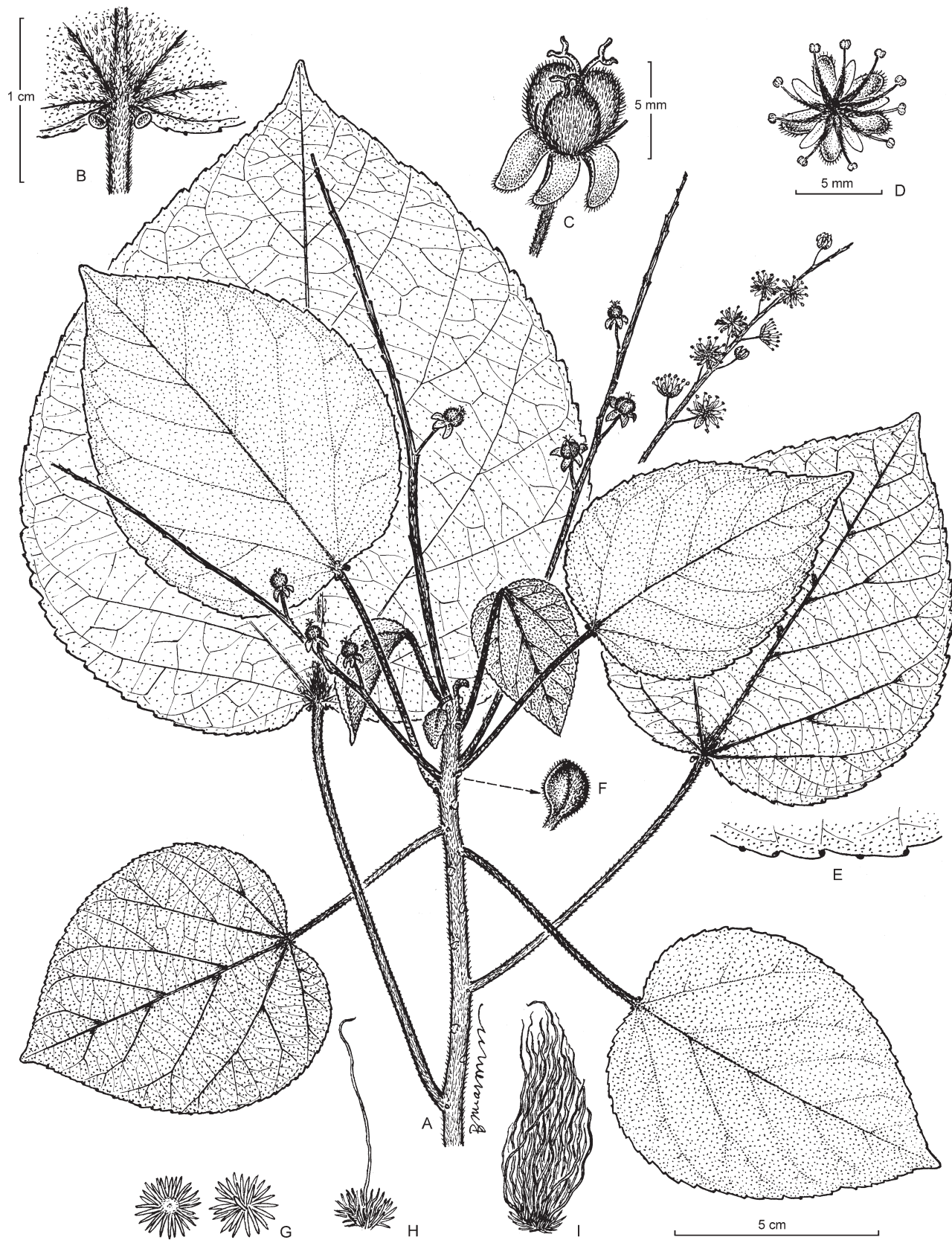
This species occurs in seasonally flooded riparian forests of the Amazon and Orinoco basins in Venezuela (Amazonas), Colombia (Guainía), Brazil (Rondônia, Goiás, Tocantins, Mato Grosso), and northern Bolivia (Beni, La Paz, Pando, Santa Cruz). Individuals from the southernmost part of the species distribution exhibit more stellate-lepidote trichomes (50% webbing of the trichome radii), whereas individuals around the type locality (Amazonas, Venezuela) show more stellate trichomes (<5% of webbing of the trichome radii).

8. *Croton domatifer* Riina & P.E. Berry, **sp. nov.** – Type: Venezuela. Aragua: Parque Nacional Henri Pittier, 1700 m, selva nublada superior, 1 Jul 1992, *A. Cardozo, D. Hidalgo & R. Hidalgo 1992* (holotype, MY!; isotypes, MICH!, MY!, VEN!). Figures 2E and 4.

Arbor 5–25-metralis *Crotoni roraimensis* affinis, sed differt: foliis cordato-ovatis margine haud crenato-dentatis, trichomatibus porrectis 0.7–1.0 mm longis, domatiis abaxillaribus praesentibus.

Monoecious tree 5–25 m high, indumentum of stellate, rosulate, to stellate-lepidote trichomes; latex from the trunk and young branches dark orange to reddish. Stipules cupulate to cucullate, 1.8–2.5 × 1.8–2.5 mm, persistent on young branches. Leaves alternate, petioles 6–13 cm long, lamina broadly ovate to cordate, 9–19 × 5–16 cm, apex acute, base usually cordate or less commonly rounded; margin irregularly crenate-dentate, minute patelliform glands usually present in the sinuses, venation palmate with 3–5 veins from the base and 4–7 lateral veins per side of the midrib further up the lamina, the primary and secondary veins raised on the abaxial surface; indumentum on both sides of the lamina of mature leaves sparse to dense, denser along the veins, trichomes appressed-stellate, stellate-lepidote to rosulate, sometimes with a longer porrect central ray; vein axils on the abaxial surface of the lamina and both sides of the leaf base covered with dense clusters of rosulate, ferruginous trichomes with long rays 0.7–1.0 mm long, forming domatia; petiolar glands 2, acropetiolar, patelliform, 0.6–0.8 mm diam., sessile to shortly stipitate. Inflorescences terminal, 1–5 inflorescences per apical branch, erect, 10–20 cm long; young inflorescences with basal bisexual cymules, mature inflorescences bearing either pistillate or staminate flowers, rachis densely covered by appressed-stellate trichomes. Staminate flowers 2–3 mm long, 3–5 mm wide; pedicels 3–11 mm long; sepals 5, ovate, 2.7–3.0 × 1.8–2.0 mm, slightly imbricate at the base, abaxial surface glabrous and papillose, adaxial surface sparsely villous, apex acute and densely villous at the tip, base truncate; petals 5, oval-oblong, 2.0–2.8 × 1.0–1.6 mm, apex acute to rounded, villous at the tip, glabrous and papillate on both sides, margins sparsely villous; receptacle densely villous; stamens 10–11; filaments 0.5–0.6 mm long, densely villous; anthers 0.8–1.0 mm long. Pistillate flowers with pedicels 5–13 mm long; sepals 5, valvate, broadly obovate, slightly imbricate in young flowers, reflexed in fruit, 3.5–4.0 × 3.0–3.2 mm, apex acute, adaxial surface pilose, abaxial surface covered with sparse stellate trichomes; ovary globose, ± trilobed, 3.0–4.5 × 2.5–5.0 mm, covered with a dense indumentum of light golden stellate and stellate-lepidote trichomes; petals absent or reduced to narrow glandular filaments; styles bifid. Fruits globose, 1.0–1.2 cm diam.; columella 6–7 mm long; seeds ovoid, 6.0–7.0 × 4.0–5.0 mm, dorsally compressed, base ending in a pointed tip, apex obtuse, aril reduced to a small, irregular appressed structure above the hilum.

**Wood anatomical description.** — *Macroscopic features:* Growth rings not distinct with a hand lens. Wood white to light brown, heartwood absent or not distinct. Basic specific gravity: 0.38. *Microscopic features:* Growth increments indistinct or absent. Wood diffuse-porous; vessels solitary and in radial multiples of 2–4; 6 vessels/mm<sup>2</sup> (Fig. 5A); helical thickenings occasionally present in tails of vessel elements. Vessel outline rounded; average tangential diameter 99 μm. Vessel elements 737 μm long. Perforation plates exclusively simple. Intervessel pits non-vestured, alternate; 11 μm diameter (Fig. 5F); with rounded outline. Vessel-ray pits similar to intervessel pits in size and shape, and vessel-ray pits larger than intervessel pits and simple (Fig. 5E). Fibers non-septate; thin- to thick-walled; without helical thickenings; angular outline; 1226 μm long.



**Fig. 4.** *Croton domatifer*. **A**, flowering branch; **B**, petiolar glands; **C**, pistillate flower; **D**, staminate flower; **E**, marginal leaf glands; **F**, stipule; **G**, stellate-lepidote and rosulate trichomes; **H**, rosulate trichome with a single, long porrect central ray; **I**, rosulate trichome with numerous long rays, forming domatia on the abaxial surface of leaves in vein axils and at the base. Note: items E–I are not to scale.



Fiber pits distinctly bordered (Fig. 5E). Fiber length to vessel element length ratio 1.66. Paratracheal parenchyma scanty and sparsely aliform. Apotracheal parenchyma diffuse to diffuse-in-aggregate, with the diffuse-in-aggregate parenchyma in confluent-like arrangement (Fig. 5B). Parenchyma strands 4-celled. Rays 1–2-seriate; 11 per linear mm; 228  $\mu\text{m}$  in average height; tallest ten rays average 340  $\mu\text{m}$  (Fig. 5D). Rays composed of square, upright, and procumbent cells, upright cells in marginal rows of more than four common (Fig. 5C). Disjunctive ray cell end walls common, especially in upright cells. Crystals rare to absent in both axial and ray parenchyma. Wood never storied.

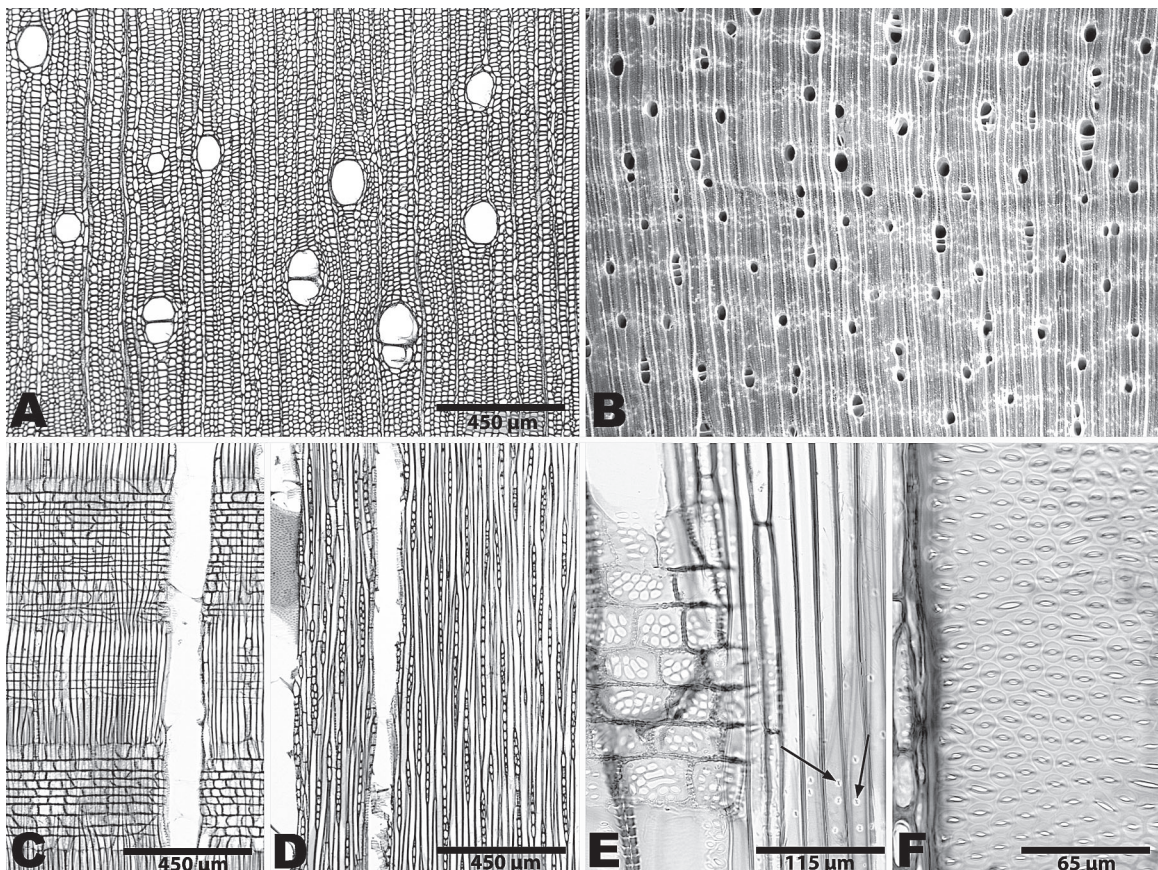
**Distribution and habitat.** — Known from Aragua, Sucre, and Yaracuy states in northern Venezuela (Fig. 6). *Croton domatifer* occurs in montane cloud forests of the Coastal Cordillera, between 760 and 1850 m elevation.

**Etymology.** — The specific epithet refers to the presence of leaf domatia.

**Additional specimens examined.** — VENEZUELA. Aragua: Parque Nacional Henri Pittier, Pico Guacamaya 1850 m, 14 Apr 1990, A. Cardozo & E. Garcia 1372 (MY); 1



**Fig. 6.** Collection localities of *Croton domatifer* in northern Venezuela indicated by dots.



**Fig. 5.** Light micrographs of the wood of *Croton domatifer*, Riina 1537 (VEN). **A, C–F**, transmitted light micrographs; **B**, stereomicrograph. **A**, transverse section showing relatively large vessels and thin walled fibers; **B**, transverse surface showing the diffuse-in-aggregate parenchyma in confluent-like arrangement; **C**, radial section showing heterocellular rays; **D**, tangential section showing uniseriate rays; **E**, transverse section showing ray-vessel pits ranging from the same as intervessel pits to larger and simple (unbordered), and distinctly bordered fiber pits indicated by arrows; **F**, tangential section showing intervessel pits.



Jul 1990, *A. Cardozo & al. 1490* (MY); Parque Nacional Henri Pittier, 1700 m, 23 Jun 1991, *A. Cardozo & D. Hidalgo 1795* (MY); 1450–1500 m, 21 May 1992, *A. Cardozo & al. 1983* (MICH, MY); Rancho Grande camino hacia Pico Guacamayo, 1400 m, 4 Jan 1976, *O. Huber 360* (DAV, VEN); entre Cumbre de Rancho Grande y Pico Guacamayo, 1430 m, 28 Jan 1976, *O. Huber 378* (VEN); 1570 m, *G. Markina 5* (MER); camino hasta la Cumbre de Rancho Grande, 1340–1450 m, 23 Apr 2006, *R. Riina & al. 1537* (VEN). Sucre: Península de Paria, Cerro Humo, 62°36'W, 10°41'N, 12 Jul 1972, *K. Dumont & al. VE-7578* (NY), *G. Morillo 2601* (MY, VEN); entre Roma y Santa Isabel, 1273 m, 2 Mar 1966, *J.A. Steyermark 94900*

(NY, VEN); 10°41'–42'N, 62°36'–37'W, 760–1000 m, 24 Feb 1980, *J.A. Steyermark & al. 121742* (F, DAV, MO, VEN). Yaracuy: Sierra de Aroa, Cerro Negro, 1200–1800 m, 10°17'N, 69°01'W, 1–2 April 1980, *R. Liesner & A. González 9905* (VEN); Río Cocorotico, arriba de San Felipe, 1150–1350 m, 14 Nov 1967, *J.A. Steyermark & G. Wessels-Boer 100463* (DAV, NY, VEN).

Specimens from Sucre state in northeastern Venezuela have smaller, ovate-lanceolate leaves with a rounded base in comparison with the larger, broadly and deeply cordate leaves of specimens from Aragua and Yaracuy states. The description of fruits and seeds is based on *Morillo 2601* (VEN, MY),

**Table 1.** Morphological and wood anatomical differences between *Croton domatifer* and several representatives of *Croton* sect. *Cuneati*.

	<i>C. cuneatus</i>	<i>C. domatifer</i>	<i>C. malambo</i>	<i>C. roraimensis</i>	<i>C. yavitensis</i>
Stipules	Linear-narrowly triangular	Cupulate-cucullate	Linear-lanceolate	Linear-subulate (asymmetric)	Linear-narrowly triangular
Leaf base	Cuneate	Deeply cordate to rounded	Slightly cordate to rounded	Cuneate to rounded	Cordate to rounded
Leaf margin	Entire to crenate-dentate	Crenate-dentate	Loosely crenate	Dentate	Crenate to dentate
Leaf domatia	Absent	Present	Absent	Absent	Absent
Stamens	16	10–11	18–20	12–15	10
Pedicel of pistillate flowers	1–2 mm	10–13 mm	17–20 mm	4–6 mm	1–2 mm
Ovary indument; trichomes	Dense; lepidote	Very dense; stellate to stellate-lepidote	Glabrous (caducous)	Dense; lepidote	Very dense; stellate-lepidote
Style	4-fid	2-fid	2-fid	2-fid	4-fid
Fruit length	13–16 mm	10–12 mm	10–11 mm	25–30 mm	20–25 mm
Caruncle	Absent	Absent	Absent	Absent	Absent
Aril	Present, conspicuous	Present, inconspicuous	Absent	Absent	Present, conspicuous
Habitat	Riparian lowland forests	Montane forests	Dry lowland forests	Montane forests	Riparian lowland forests
Distribution	Amazon and Orinoco basins	Northern Venezuela, Coastal Cordillera	Guajira region (Venezuela and Colombia)	Guayana Highlands	Amazon basin
Vessels per square mm	7–13	6	21–43	9	9
Tangential vessel diameter	70–123 µm	99 µm	79–83 µm	114 µm	77 µm
Ray-vessel pit type	Same as intervessel pits	Same to smaller and simple	Same as intervessel pits	Same to unilaterally coarse and compound	Smaller than intervessel pits
Intervessel pit diameter	10–11 µm	11 µm	6 µm	12 µm	12 µm
Fiber pitting	Distinctly bordered	Distinctly bordered	Indistinctly bordered	Indistinctly bordered	Indistinctly bordered
Helical thickenings in vessel elements	In tails	In tails	Absent	Absent	In tails

the only collection with mature fruits. *Croton domatifer* is remarkably distinctive from other species of *Croton* because of the leaf domatia which consist of dense clumps of large stellate-rosulate trichomes. Apparently, this is the first report of leaf domatia in the genus.

*Croton domatifer* shows morphological affinities to the species in *Croton* sect. *Cuneati*, and DNA sequence data (*trnL-F*, ITS) support its position in this clade (Fig. 1). Table 1 shows the main morphological and wood anatomical differences and similarities between the new species and several representatives of the *Cuneati* clade (*C. cuneatus*, *C. yaviten-sis*, *C. malambo*, *C. roraimensis*). Species in *C. sect. Cuneati* and *C. domatifer* share characters such as dentate to loosely crenate leaf margins (sometimes subentire in *C. cuneatus*), discoid or patelliform glands along the leaf margin, indumentum of lepidote or stellate-lepidote trichomes, patelliform petiolar glands, a very reduced caruncle or ecarunculate seeds, some species have a non-carunculate aril covering a large area of the ventral surface of the seed (Fig. 2A–D), and preferences for mesic habitats such as riversides, seasonally flooded evergreen forests, and montane cloud forests. The only apparent exception to this syndrome is *C. malambo*, which occurs in dry forests. *Croton domatifer* displays a wood anatomical pattern typical of mesic, arborescent *Croton*, consistent with other members of the *Cuneati* clade (Wiedenhoeft, 2008). An intriguing feature of the wood of *C. domatifer* is the presence of diffuse-in-aggregate parenchyma in confluent-like bands, which cannot be seen clearly with transmitted light microscopy, but is easily observed with a stereomicroscope or a hand lens (Fig. 5B). Parenchyma of this type is not common, and the IAWA list does not recognize it as a separate character (IAWA Committee, 1989). The presence of distinctly bordered fiber pits (Fig. 5E) in this new species is an important character linking it to *C. sect. Cuneati*, these distinctive pits have been found in most species of *C. sect. Cuneati* examined to date (*C. cuneatus*, *C. domatifer*, *C. neblinae*, *C. roraimensis*), although they are not found in *C. malambo* and *C. yaviten-sis* (Wiedenhoeft, 2008). These distinct pits are also found in *C. sampatik* and *C. poecilanthus* (Wiedenhoeft, 2008), a species once thought to be in *C. sect. Cuneati* (as subsect. *Cuneati*) by Webster (1993).

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**Appendix.** Taxa, vouchers, localities, and GenBank accession numbers for all sequences analyzed.

Taxon, origin, voucher, GenBank accession numbers: (*trnL-F*; ITS). Missing data: –.

*Astraea lobata* (L.) Klotzsch, BRAZIL, Bahia, Van Ee 486 (WIS), (EU586999; EU586945); *Brasiliocroton mamoninha* P.E. Berry & I. Cordeiro, BRAZIL, Espírito Santo, Pirani 4947 (SPF), (EU586998; EU586944); *Croton abutiloides* Kunth, ECUADOR, Tunguragua, Riina 1391 (WIS), (EU586957; EU586903); *C. arboreus* Millsp., MEXICO, Quintana Roo, Van Ee 472 (WIS), (EU497701; EU478029); *C. astroites* Dryand., PUERTO RICO, Van Ee 537 (WIS), (EU586955; EU586902); *C. beetlei* Croizat, BOLIVIA, Santa Cruz, Riina 1512 (WIS), (EF408090; EU586916); *C. cajucara* Benth., BRAZIL, Caruzo 95 (SP), (EU586968; EU586913); *C. caracasanus* Pittier, VENEZUELA, Riina 1288 (VEN), (DQ227557; DQ227525); *C. chocoanus* Croizat, ECUADOR, Esmeraldas, Riina 1415 (WIS), (EU586995; EU586941); *C. cuneatus* Klotzsch, VENEZUELA, Berry 7589 (WIS), Riina 1491 (WIS), (AY794698; EU497735); *C. domatifera* Riina & P.E. Berry, VENEZUELA, Aragua, Riina 1537 (VEN), (GU296103; GU296102); *C. echioides* Baill., BRAZIL, Santos 795 (HUEFS), (EU586967; EU586907); *C. eichleri* Müll. Arg., BRAZIL, Rio de Janeiro, Riina 1525 (WIS), (EU587001; EU586949); *C. ekmanii* Urb., CUBA, Holguín, HAJB 81845 (WIS, HAJB), (EF408137; EF421760); *C. erythroxyloides* Baill., BRAZIL, Caruzo 74 (SP), (EU586992; EU586938); *C. glandulosepalus* Millsp., BELIZE, Vincent 6058 (MU), (EU478126; EU477888); *C. glandulosus* L., USA, Wisconsin, Van Ee 512 (WIS), (EU497713; EU478066); *C. gossypifolius* Vahl., VENEZUELA, Riina 1261 (WIS), (AY971301; AY971212); *C. helicoideus* Müll. Arg. (= *C. micans* Sw.), BOLIVIA, Wood 14086 (LPB), (EU586956; EU586902); *C. hircinus* Vent., VENEZUELA, Caracas, Riina 1291 (WIS), (EU478127; EU477889); *C. hirtus* L'Her., BRAZIL, Lima 345 (SPF), (EU478160; EU478070); *C. huberi* Steyerem., VENEZUELA, Miranda, Berry 7590 (WIS), (AY971305; AY971217); *C. lepidotus* A.DC., MADAGASCAR, Schatz 3845 (MO), (EU497719; EU497740); *C. malambo* Karst., COLOMBIA, Zarucchi 3856 (MO), (AY971315; AY971228); *C. megalodendron* Müll. Arg., VENEZUELA, Miranda, Riina 1290 (WIS), (EU586996; EU586942); *C. megistocarpus* J.A. González & Poveda, COSTA RICA, Jimenez 1527 (MO), (EF408130; EF421787); *C. organensis* Baill., BRAZIL, Rio de Janeiro, Caruzo 90 (WIS), (EU586969; EU586914); *C. pachypodus* G.L. Webster, COSTA RICA, San José, Valverde 1043 (MO), (EU587004; EU586953); *C. palanostigma* Klotzsch; PERU, Loreto, Riina 1492 (WIS), (EU586997; EU586943); *C. poecilanthus* Urb., PUERTO RICO, Van Ee 551 (WIS), (EF408122; EF421782); *C. priscus* Croizat, BRAZIL, Sao Paulo, Riina 1535 (WIS), (EU587002; EU586950); *C. sampatik* Müll. Arg., PERU, Pasco, Riina 1447 (WIS), (EF408133; EF421792); *C. sapiifolius* Müll. Arg., BRAZIL, Bahia, Lima 667 (CEPEC), (EF408150; EF421754); *C. schiedeana* Schldtl., COSTA RICA, Aguilar 886 (MO), (AY971331; AY971246); *C. skutchii* Standl., COSTA RICA, Cartago, Van Ee 597 (WIS), (EU478166; EU478100); *C. smithianus* Croizat, COSTA RICA, Aguilar 2263 (MO), (–; EU478101); *C. gnaphalii* Baill., ARGENTINA, Belgrano 423 (SI), (EU586994; EU586940); *C. yavitensis* Croizat, BOLIVIA, Beck 5710 (LPB), (EU586973; EU586918); *C. gratissimus* Burch., ZAMBIA, Songwe Gorge, Zimba 901 (MO), (AY971341; AY971260).