

A revised infrageneric classification and molecular phylogeny of New World *Croton* (Euphorbiaceae)

Benjamin W. van Ee,¹ Ricarda Riina^{2,3} & Paul E. Berry²

¹ Black Hills State University Herbarium, 1200 University Street, Spearfish, South Dakota 57799, U.S.A.

² University of Michigan Herbarium, Department of Ecology and Evolutionary Biology, 3600 Varsity Drive, Ann Arbor, Michigan 48108, U.S.A.

³ Real Jardín Botánico, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain

Author for correspondence: Benjamin van Ee, bvanee@uwalumni.com

Abstract *Croton* (Euphorbiaceae) is a large and diverse group of plants that is most species-rich in the tropics. We update the infrageneric classification of the New World species of *Croton* with new evidence from phylogenetic analyses of DNA sequence data from all three genomes. The relationships of species that were previously placed in conflicting positions by nuclear and chloroplast data, such as *C. cupreatus*, *C. poecilanthus*, and *C. setiger*, are further resolved by adding the nuclear *EMB2765* and mitochondrial *rps3* genes to the molecular sampling. Analyses of *rps3* reveal an accelerated rate of evolution within *Croton* subg. *Geiseleria*, the only one of the four subgenera that contains numerous herbaceous, annual species. We provide morphological descriptions, species lists, and a key to the 31 sections and 10 subsections recognized in the New World. New taxa that we describe include *C.* sects. *Alabamenses*, *Argyranthemii*, *Cordiifolii*, *Corinthii*, *Cupreati*, *Luetzelburgiorum*, *Nubigeni*, *Olivacei*, *Pachypodi*, *Prisci*, and *C.* subsections. *Cubenses*, *Jamaicensis*, and *Sellowiorum*. Additional transfers are made to the ranks of subgenus, section, and subsection. A total of 712 species of *Croton* are currently recognized for the New World, with 702 of them assigned here to section.

Keywords *Croton*; *EMB2765* exon 9; Euphorbiaceae; infrageneric classification; molecular phylogenetics; New World; *rps3*; taxonomy

■ INTRODUCTION

Croton L. (Euphorbiaceae) is a characteristic genus of dry to moist vegetation in the tropics and subtropics worldwide, and its species can usually be recognized in the field by their pungent odor, stellate or lepidote pubescence, clear to colored latex, and leaves that turn orange before dehiscing. It has long been considered one of the “giant genera” of the angiosperms (Brown, 1883; Frodin, 2004) and was last tabulated by Govaerts & al. (2000) to consist of over 1200 species. Its large size, great morphological diversity, and broad distribution have made it challenging to study, even with molecular data.

Webster (1993) reviewed earlier work on the infrageneric relationships of *Croton* worldwide and proposed a system in which he recognized 40 sections. Although he provided a concise description for each section as well as a key to the sections, he only listed representative species for most groups, with the result that a majority of *Croton* species remained unplaced to section. Unlike Müller (1865, 1866, 1873), Pax (1890), and Pax & Hoffmann (1931), Webster (1993) did not attempt to organize these sections hierarchically. The first molecular phylogeny of *Croton* and tribe Crotoneae by Berry & al. (2005) helped define the limits of the genus and made an initial evaluation of the monophyly and relationships of the sections recognized by Webster (1993). The only change in the circumscription of the genus that emerged was the removal of *Croton* sect. *Astraea* (Klotzsch) Baill. and its return to generic status. The recircumscribed tribe Crotoneae resulted in seven genera: the large

Croton sister to the monotypic *Brasiliocroton* P.E. Berry & Cordeiro, these sister to a clade comprised of *Astraea* Klotzsch and the sister genera *Acidocroton* Griseb. and *Ophellantha* Standl., and all of these sister to a clade composed of *Sagotia* Baill. and *Sandwithia* Lanj. (Berry & al., 2005; Wurdack & al., 2005). Together, the other six genera of Crotoneae comprise fewer than 30 species, compared to over 1200 in *Croton*.

Subsequent molecular phylogenetic work on *Croton* has focused on specific groups within the genus, such as *C.* subg. *Moacroton* (Croizat) B.W. van Ee & P.E. Berry (= *C.* subg. *Quadrilobi* (Müll. Arg.) Pax in Engl. & Prantl; Van Ee & al., 2008), the Jamaican species of *Croton* (Van Ee & Berry, 2009a), *C.* sects. *Cyclostigma* Griseb. (Riina & al., 2009), *Cuneati* (G.L. Webster) Riina & P.E. Berry (Riina & al., 2010b), *Luntia* (Neck. ex Raf.) G.L. Webster (Riina & al., 2010b), *Heptallon* (Raf.) Müll. Arg. (Van Ee & Berry, 2010a), *Pedicellati* B.W. van Ee & P.E. Berry (Van Ee & Berry, 2011), and *Cleodora* (Klotzsch) Baill. (Caruzo, 2010). There has also been recent monographic work on *C.* sects. *Argyroglossum* Baill. (= *C.* sect. *Lasiogyne* (Klotzsch) Baill.; Gomes, 2006), *Cleodora* (Caruzo, 2010), *Crotonopsis* (Michx.) G.L. Webster (Van Ee & Berry, 2009b), *Cyclostigma* (Smith, 2002; Riina, 2006), *Eluteria* Griseb. (León Enríquez, 2007), *Heptallon* (Van Ee & Berry, 2010a), and *Lamprocroton* (Müll. Arg.) Pax in Engl. & Prantl (Lima, 2006; Lima & Pirani, 2008).

We estimate that approximately two-thirds of the species of *Croton* occur in the New World, with the other third scattered across the Old World. Webster (1993) admitted to providing a

more cursory treatment of the Old World groups and species of *Croton* compared to those in the New World. We have the same bias, although we are making major strides in understanding the phylogenetic relationships of the nearly 150 species of *Croton* from Madagascar and neighboring islands in the Indian Ocean (Berry & al., 2009; Haber & al., 2010). Consequently, we focus this study on the New World species of *Croton*. Our goals are to expand the molecular and taxonomic sampling of Berry & al. (2005), recognize and name new infrageneric taxa, recircumscribe others, provide an update to Webster's (1993) sectional key (excluding the Old World sections), and place to section as many of the New World species as possible.

■ MATERIALS AND METHODS

Taxonomic and molecular sampling. — Berry & al. (2005) were unable to sample 11 of the 40 sections of *Croton* recognized by Webster (1993), and these were specifically targeted for the molecular analyses presented here. We also targeted New World species potentially representing a distinct section, whether suggested by morphology or by prior molecular evidence (i.e., Van Ee, 2006; Riina, 2006). Nine Old World samples were included as placeholders for the estimated 400 Old World *Croton* species, which form a monophyletic clade in the molecular analyses completed to date (Berry & al., 2005, 2009; Van Ee & al., 2008; Riina & al., 2009; Haber & al., 2010). Each molecular sample is represented by an herbarium voucher specimen (Appendix). Overall, we analyze 112 accessions representing 108 ingroup *Croton* species, of which 99 are New World species. This represents 100% of the New World sections that we recognize, and 14% of the 712 New World species of *Croton* that we currently recognize. It is important to note, however, that molecular sequence data are available for many more species of *Croton* than are presented in this paper, both published and unpublished. These are being used to develop species-level phylogenies of the larger clades or sections, and to verify the sectional delimitations proposed here. To date, we have completed studies on *Croton* sect. *Cleodora* (Caruzo, 2010, 15 of 18 species sampled); *C.* sect. *Cyclostigma* (Riina & al., 2009, 23 of 41 species sampled); *C.* sect. *Cuneati* (Riina & al., 2010b, 5 of 11 species sampled); *C.* sect. *Heptallon* (Van Ee & Berry, 2010a, 9 of 9 species sampled); *C.* sect. *Luntia* (Riina & al., 2010b, 6 of 19 species sampled); *C.* sect. *Moacroton* (Van Ee & al., 2008, 7 of 8 species sampled); and *C.* sect. *Pedicellati* (Van Ee & Berry, 2011, 8 of 20 species sampled). The molecular phylogeny of *Croton* by Berry & al. (2005) includes 26 species beyond those used in the analyses in this paper, and Van Ee (2006) provides 63 additional species, which add substantially to groups such as *C.* sects. *Adenophylli* Griseb., *Corylocroton* G.L. Webster, and others. Regional-based studies with molecular data such as Van Ee & Berry (2009a), or ones focusing on new taxa and their phylogenetic placement (Cordeiro & al., 2008; Riina & Berry, 2010; Riina & al., 2010b) further increase our sampling across the New World species.

The nuclear ribosomal internal transcribed spacer (ITS: ITS1, 5.8S, and ITS2) and the plastid *trnL-F* (*trnL* exon, intron,

and 3' intergenic spacer) markers employed by Berry & al. (2005) were supplemented by sequences of exon 9 of the coding low-copy nuclear gene *EMB2765* (*EMBRYO DEFECTIVE 2765*, At2g38770), and by the mitochondrial protein-coding *rps3* gene, thereby providing evidence from all three genomes. Samples for which one of the four markers is lacking were included in the combined analysis with the missing sequences coded as missing. The phylogenetic signal within *Croton* found in other chloroplast markers, such as *ndhF*, *rbcL* (Van Ee & al., 2008), *matK* (Riina, 2006), and *trnH-psbA* (Berry & al., 2009; Haber & al., 2010; Caruzo, 2010), has been shown to be highly congruent with that of *trnL-F*.

DNA extraction, amplification, and sequencing. — Total genomic DNA from silica-dried samples, or from leaf fragments picked from herbarium specimens, was extracted and purified using the Qiagen DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.). ITS was amplified with PCR and sequenced using the primers ITS-I and ITS4 (White & al., 1990; Urbatsch & al., 2000), following the methods described in Berry & al. (2005), with the exception that the PCR reactions were scaled down from 50 μ L to 25 μ L. For material obtained from herbarium collections, and for silica-dried collections that failed to amplify in one piece, the region was amplified with two primer pairs: ITS-I with ITS2 and ITS3 with ITS4 (White & al., 1990). The *trnL-F* region was similarly amplified and sequenced as one fragment with primers "C" and "F," or in two pieces, with "C" paired with "D" and "E" paired with "F" (Taberlet & al., 1991). Exon 9 of *EMB2765* was amplified and sequenced using primers "9F" and "9R" following the methods described in Wurdack & Davis (2009). Similar to the results of Wurdack & Davis (2009), *EMB2765* exon 9 usually amplified well, and when successful it always yielded single bands. Upon sequencing, some accessions had multiple peaks, which were coded as ambiguities. The mitochondrial *rps3* gene was amplified and sequenced in two fragments, using the same PCR conditions as for *EMB2765* exon 9, and the primer combinations "F1" with "R1.5," and "F2" with "R1" (Wurdack & Davis, 2009). Primer sequences and their respective references are given in Table 1.

DNA sequence alignment and phylogenetic analyses. — Forward and reverse chromatograms were edited and assembled into DNA fragments using Sequencher v.3.1.1 (Gene Codes Corp., Ann Arbor, Michigan). Aligned datasets were generated manually in MacClade v.4.08 (Maddison & Maddison, 2005). All sequences are deposited in GenBank, and species names, vouchers, and GenBank accession numbers are given in the Appendix.

The data were concatenated and arranged into four partitions corresponding to the four loci: nuclear ITS, nuclear *EMB2765* exon 9, chloroplast *trnL-F*, and mitochondrial *rps3*. The best-fitting maximum likelihood model for each of the four partitions, as well as for all the data combined, were selected using Modeltest v.3.07 (Posada & Crandall, 1998) using the results obtained from the Akaike information criterion (AIC). Maximum likelihood bootstrap support values were obtained from one hundred pseudoreplicates run in GARLI v.1.0 (Zwickl, 2006). Two independent search replicates were executed for each bootstrap replicate. The substitution models

Table 1. Amplification and sequencing primers used.

Primer name	Primer sequence	Reference
ITS-I	5' GTCCACTGAACCTTATCATTAG 3'	Urbatsch & al., 2000
ITS2	5' GCTGCGTTCTTCATCGATGC 3'	White & al., 1990
ITS3	5' GCATCGATGAAGAACGCAGC 3'	White & al., 1990
ITS4	5' TCCTCCGCTTATTGATATGC 3'	White & al., 1990
trnL-F "C"	5' CGAAATCGGTAGACGCTACG 3'	Taberlet & al., 1991
trnL-F "D"	5' GGGGATAGAGGGACTTGAAC 3'	Taberlet & al., 1991
trnL-F "E"	5' GGTTC AAGTCCCTCTATCCC 3'	Taberlet & al., 1991
trnL-F "F"	5' ATTTGAACTGGTGACACGAG 3'	Taberlet & al., 1991
EMB2765 exon 9 "9F"	5' TGATACCTGAGATTCCGTAACGAG 3'	Wurdack & Davis, 2009
EMB2765 exon 9 "9R"	5' TTGGTCCAYTGTGCWGCAGAAGGRT 3'	Wurdack & Davis, 2009
rps3 "F1"	5' GTTCGATACGTCCACCTAC 3'	Wurdack & Davis, 2009
rps3 "F2"	5' CCCGTCGTAGTTCTCAATCATTTYG 3'	Wurdack & Davis, 2009
rps3 "R1"	5' GTACGTTTCGGATATRGAC 3'	Wurdack & Davis, 2009
rps3 "R1.5"	5' CTATTCCTTTATCAATTCTCCTAT 3'	Wurdack & Davis, 2009

selected in Modeltest, and the default automated stop criterion settings were used. Bootstrap analyses were performed on each of the four partitions separately and in combination. In the combined likelihood bootstrap analyses, the data were treated as a single partition.

Bayesian posterior probabilities (PP) were calculated for each of the four partitions and for the combined data using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Posterior probabilities were obtained from two Markov chain Monte Carlo (MCMC) analyses, each consisting of four linked chains (heat = 0.02), 10,000,000 generations, starting from random trees, default priors, and sampling every 10,000 generations. In the combined analysis, the data were divided into four partitions, allowing the program to estimate the model parameters separately for each of the four loci (Brown & Lemmon, 2007). The best-fitting models for each of the data partitions, and the combined data, were the same as those used in the ML analyses. The burn-in period was estimated by viewing the parameter distributions in Tracer v.1.5 (Rambaut & Drummond, 2007). After removing the trees from the burn-in period, PP values were obtained by computing a majority rule consensus of the post-burn-in trees from both MCMC chains using the sumt command.

Evaluation of accepted New World species of *Croton* and their sectional affiliation. — In order to evaluate the number of species of *Croton* occurring in the New World and to assign them to section, we examined a large body of literature and type specimens. We used the list of more than 800 New World *Croton* species accepted in the World Checklist of Selected Plant Families (2010) as a starting point in developing a checklist of New World species that we accept, and their subsequent sectional placement. Protologues and type specimens on loan, photographed at major herbaria that we visited, and scanned types on the JSTOR Plant Science website (www.plants.jstor.org) were consulted. In some cases,

names that were treated as synonyms in the World Checklist are treated here as accepted species when examination of their types and other specimens showed them to be distinct taxa. We also determined that numerous names accepted in the World Checklist are either synonyms, erroneous citations, or are not possible to verify. For the species that have not been sampled molecularly, we focused on the combinations of morphological characters that distinguish the different sections, and in most cases we were able to assign them to section. Based on this, we developed an avowedly artificial but practical key to the sections.

■ RESULTS

Summary statistics for the data matrices and information about the analyses, such as the substitution models, are presented in Table 2. To assess the relative utility of each marker in addition to the number of variable and informative sites, the well- and weakly supported internal branches recovered in the consensus Bayesian trees from each analysis were counted. These are also expressed as a percentage of the total number of internal branches possible (number of terminals minus 3), and the well- and weakly supported branches as a percentage of the total internal branches recovered (Table 2). Well-supported branches are defined as those with $\geq 90\%$ Bayesian PP and $\geq 75\%$ ML BS. Seventy-five percent ML bootstrap support was chosen as the cut-off after reviewing the results of the ML BS analyses in which most clades have either 75% or greater support, or less than 60% support. In all analyses there are several clades recovered with $\geq 90\%$ Bayesian PP but low (<60%) ML BS support. Given the potential for having selected the incorrect model, which could create overly high Bayesian PP values, these are treated as weakly supported, although individual clades are discussed (Ronquist, 2004).

Table 2. Summary statistics for the aligned molecular data matrices and analyses. The number of internal branches recovered is also expressed as a percentage of the total number of branches possible (number of terminals minus 3), and the well- and weakly supported branches as a percentage of the total branches recovered.

	<i>rps3</i>	<i>EMB2765</i> exon 9	ITS	<i>trnL-F</i>	Combined
Number of accessions	107	103	112	108	112
Aligned length	1861	819	708	1371	4759
Variable characters	361 (19%)	278 (34%)	408 (58%)	474 (35%)	1519 (32%)
Informative characters	206 (11%)	175 (21%)	330 (47%)	235 (17%)	945 (20%)
Number of internal branches recovered	58 (53%)	67 (67%)	94 (86%)	60 (57%)	102 (94%)
Number of well-supported internal branches	23 (40%)	27 (40%)	56 (60%)	23 (38%)	66 (65%)
Number of weakly supported internal branches	35 (60%)	40 (60%)	38 (40%)	37 (62%)	36 (35%)
Model of nucleotide substitution	K81uf+I+G	TIM+I+G	SYM+I+G (hLRT: GTR+I+G)	TIM+I+G	GTR+I+G
Number of missing accessions	5	9	0	4	N/A (~4.5% of total data missing)

Phylogenetic analyses. — Analysis of the four regions in combination produced the most resolved and strongly supported phylogeny (Fig. 1). Of the 31 New World sections of *Croton* recognized here, 14 are recovered as strongly supported clades in the combined analysis (Fig. 1). *Croton* sect. *Cleodora* is also resolved as monophyletic in the combined analysis, but with less statistical support (100% Bayesian PP and 73% ML BS). Of the remaining 16 sections, 12 are represented by a single accession and therefore their monophyly is not being tested. *Croton* sect. *Eluteria*, as it is more broadly circumscribed here, is not recovered as a clade, but our results do not reject the hypothesis that it is a monophyletic group. The three remaining sections, *C.* sects. *Geiseleria*, *Lasiogyne*, and *Moacroton*, have one or more members that fall outside of a core clade, and these sections are each discussed individually.

Phylogenetic informativeness among the four sequenced loci. — The two nuclear markers, ITS (Fig. 2) and *EMB2765* exon 9 (Fig. 3), contain the highest proportion of informative characters. They provide resolution in roughly the same portions of the phylogeny, and both leave the backbone of *C.* subg. *Geiseleria* relatively unresolved. The chloroplast *trnL-F* (Fig. 4) and the mitochondrial *rps3* (Fig. 5) markers contain proportionally fewer informative characters and provide roughly equal resolution. However, they differ markedly in where they provide resolution. The *trnL-F* region provides resolution in approximately the same portions of the phylogeny as ITS and *EMB2765* exon 9, whereas *rps3* provides resolution within *C.* subg. *Geiseleria* and little elsewhere.

Number of New World *Croton* species and their distribution by sections. — Of more than 800 New World *Croton* species treated as accepted by the World Checklist, we now recognize 712 species, some of which had been treated there as synonyms. Of these, we assign 702 to sections, albeit with doubts in a few cases. Ten species defy placement to section by reference to their morphological features. Most of these are known from only one or a few collections, and some of them

may be resolved to section if further material is obtained. A selection of characters used in the key, such as glands, styles, and sepals, are illustrated in Figures 6 and 7.

DISCUSSION

Although there is widespread agreement between the four markers in the overall topology and in the support values for most clades, there are a few topological conflicts between the gene trees, mostly between *rps3* and the others. Heterogeneity among datasets can yield misleading results (De Queiroz & al., 1995), but it has also been argued that simultaneous analyses provide the best explanatory power in phylogenetic inference (Nixon & Carpenter, 1996). Our combined analysis (Fig. 1) provides the most resolution and support, and our separate analyses (Figs. 2–5) allow for comparison among the different datasets. Our phylogenetic hypotheses, as illustrated by the subgenera and sections labeled on the phylogenetic figures, are informed by all of these, even though none of the phylogenetic trees (Figs. 1–5) perfectly reflect our hypotheses.

An updated classification of *Croton* based on molecular data. — The classification system presented here attempts to establish monophyletic sections to account for all New World species of *Croton*. We divide the genus into four subgenera. We describe ten new sections, bringing the number of New World sections to 31, 11 of which are monotypic. We also recognize ten subsections, three of which are newly described. This is in addition to two sections and two subsections that were described or recognized recently (Riina & al., 2010b; Van Ee & Berry, 2011). The circumscriptions of *C.* sects. *Geiseleria* and *Lasiogyne* presented here are broad, and monographic and molecular phylogenetic work is currently underway that may allow them to be further subdivided. Likewise, *C.* sects. *Adenophylli*, *Cyclostigma*, and *Julocroton* are large and diverse groups within which subsections may be recognized in the future.

Fig. 1. Bayesian phylogram of combined ITS, *EMB2765* exon 9, *trnL-F*, and *rps3* data of *Croton* species and four outgroups. Strongly supported clades ($\geq 90\%$ Bayesian PP and $\geq 90\%$ ML BS) are indicated with thick branches, moderately supported clades ($\geq 90\%$ Bayesian PP and $\geq 75\%$ ML BS) with thick dashed branches, and thin branches represent clades with less support. The number of strong, moderate, and less supported branches is given. Labeled groups represent *Croton* and the subgenera and sections recognized in this work. Names on the right are sections. Labeled sections that are not recovered as monophyletic groups in this analysis are indicated with an asterisk.

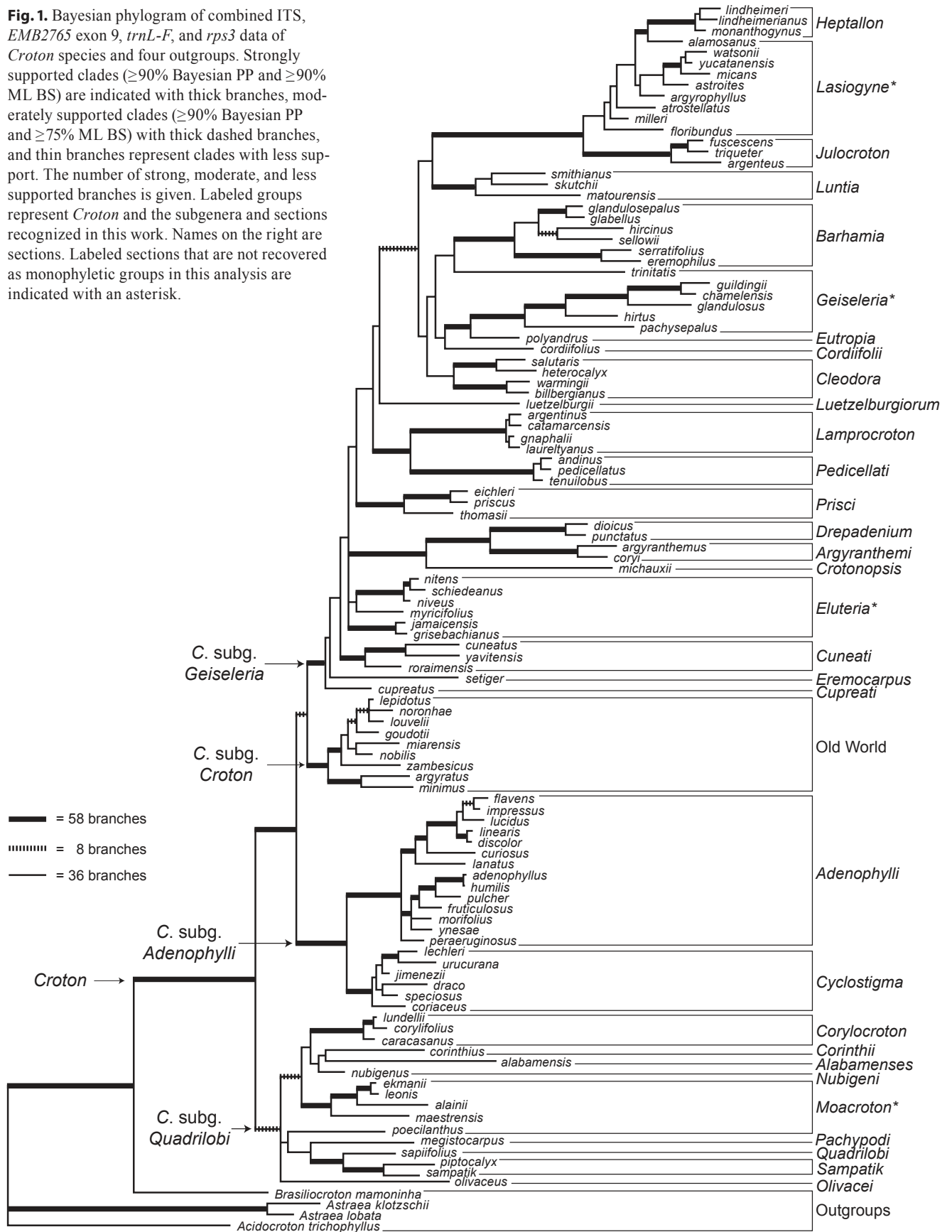


Fig. 2. Bayesian phylogram of nuclear ITS data of *Croton* species and four outgroups. For explanation see Fig. 1.

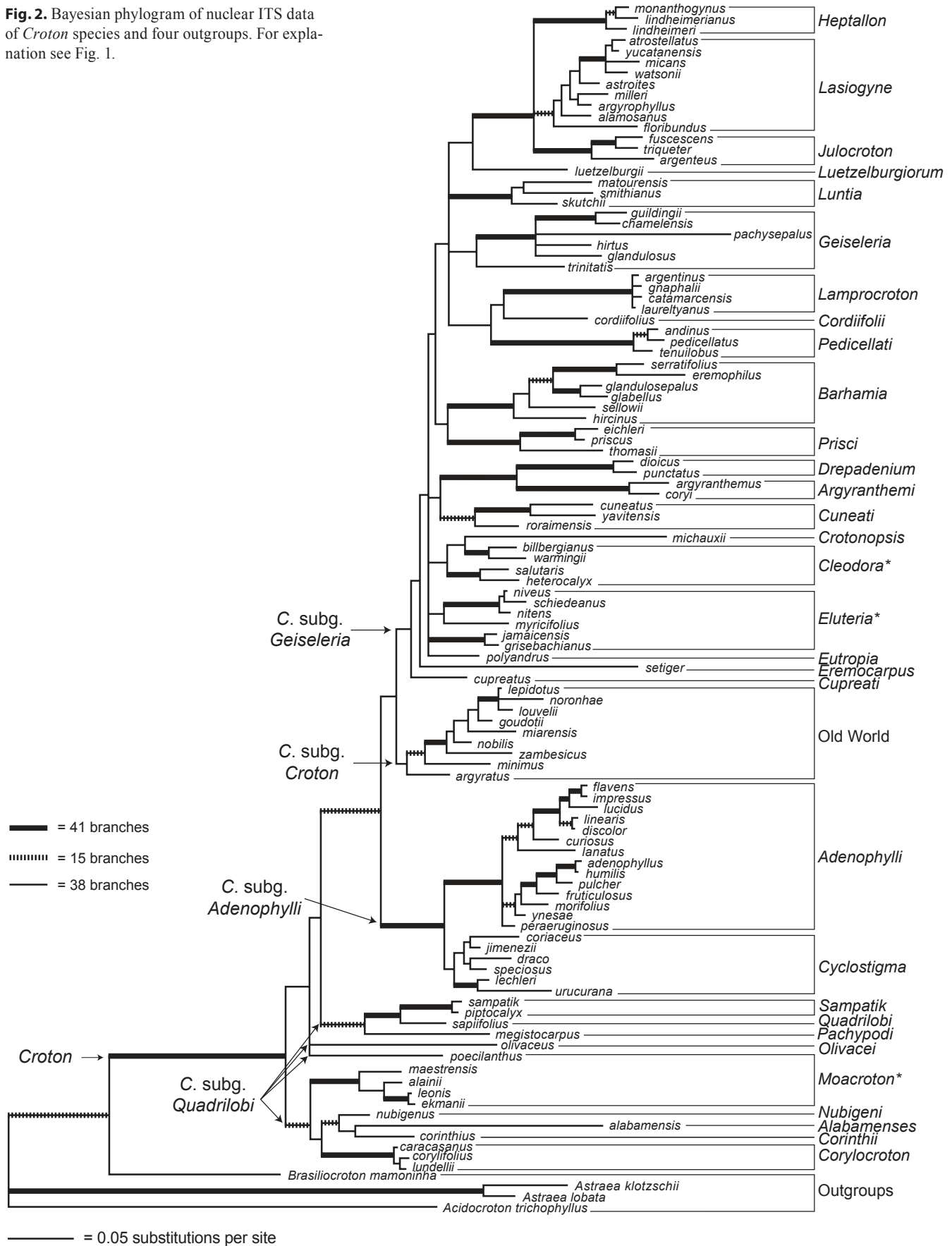


Fig. 3. Bayesian phylogram of nuclear *EMB2765* exon 9 data of *Croton* species and four out-groups. For explanation see Fig. 1.

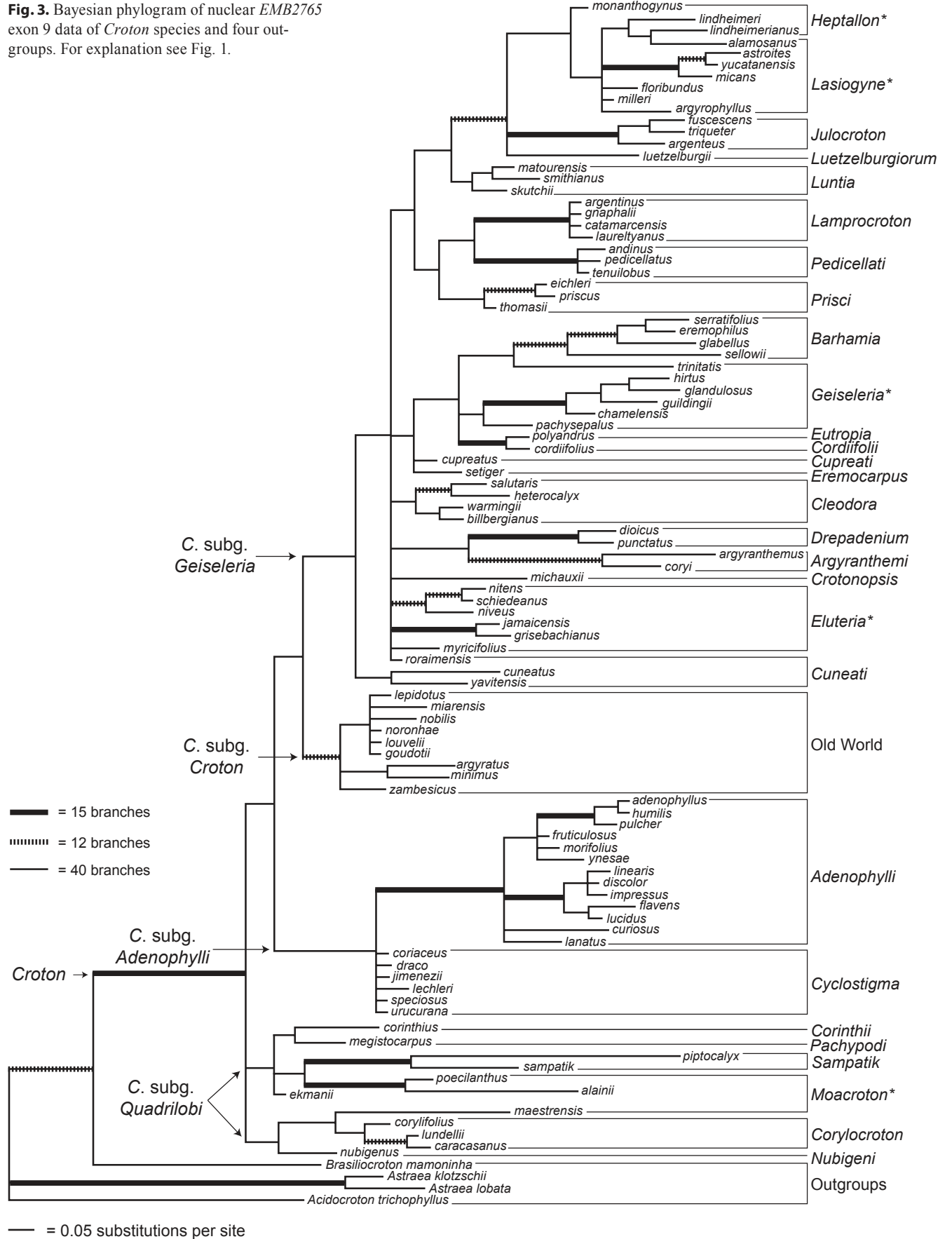


Fig. 4. Bayesian phylogram of chloroplast *trnL-F* data of *Croton* species and four out-groups. For explanation see Fig. 1.

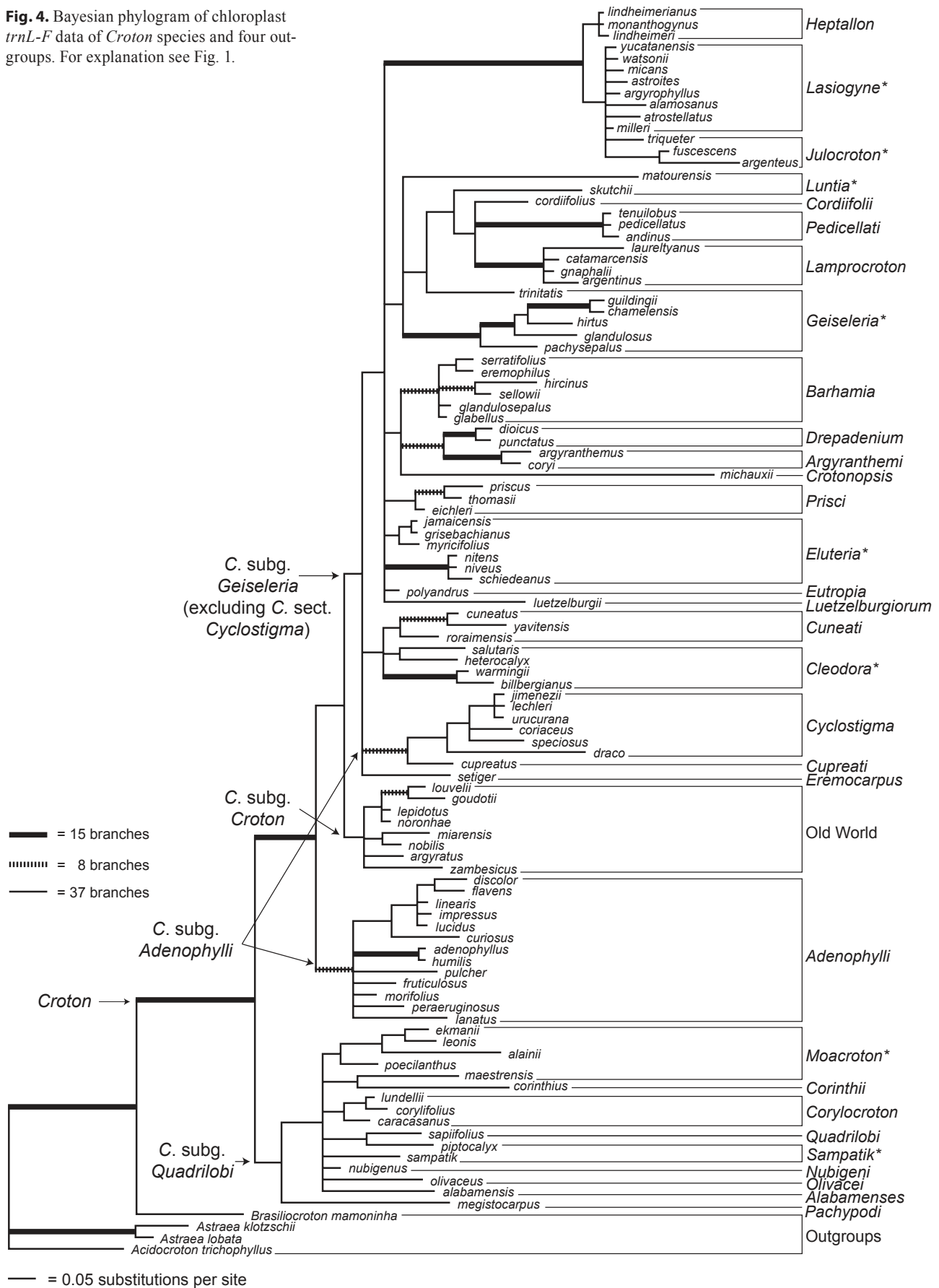
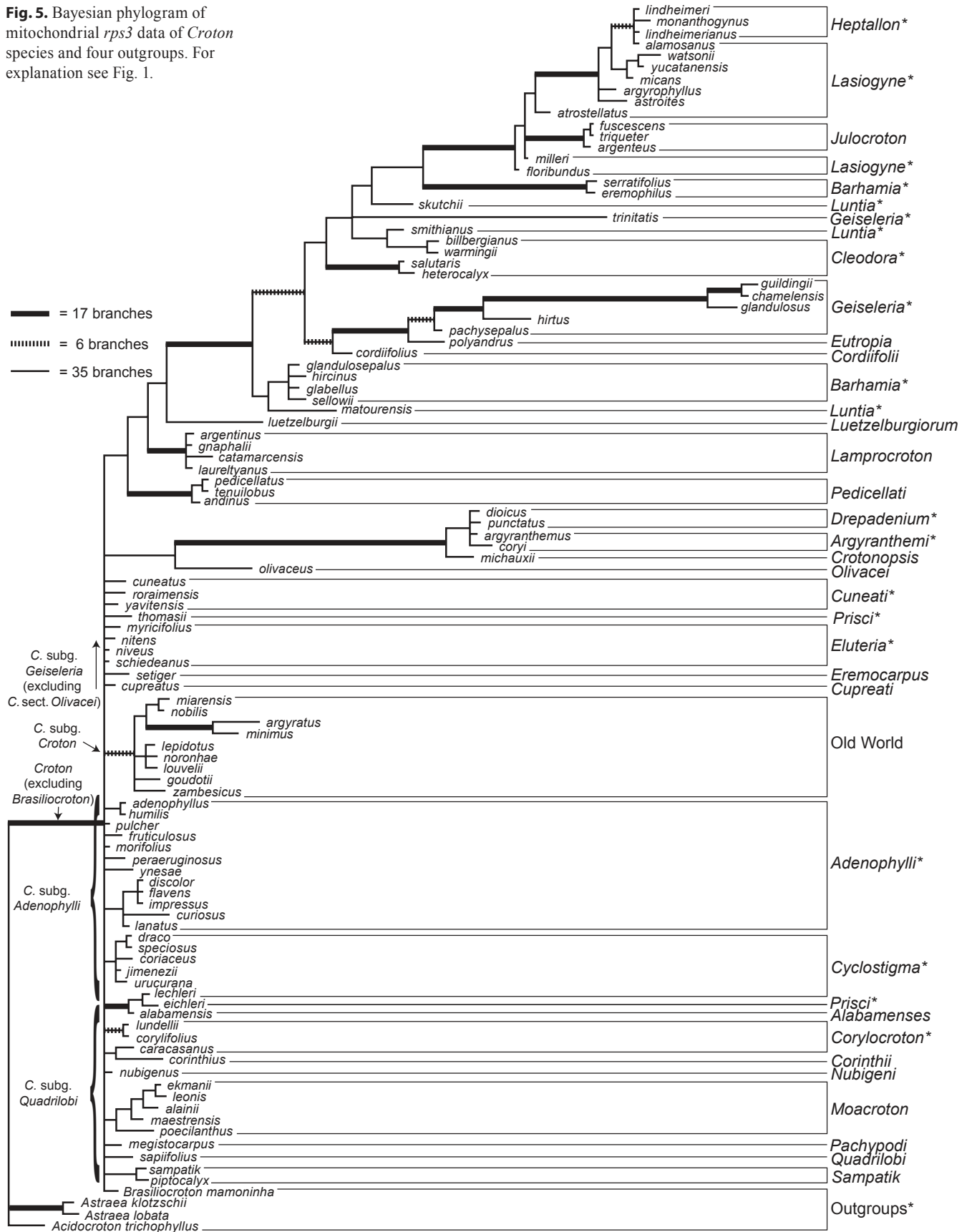


Fig. 5. Bayesian phylogram of mitochondrial *rps3* data of *Croton* species and four outgroups. For explanation see Fig. 1.



— = 0.05 substitutions per site

Geographical and morphological patterns within New World *Croton*.

— Although *Croton* is most species-rich in South America, all three of its New World subgenera are widely distributed in the Americas. Narrowly endemic species are found in all groups, but nearly all species of *C. subg. Quadrilobi* are rare and restricted, whereas many species of *C. subgenera Adenophylli* and *Geiseleria* are common and widespread. *Croton subg. Adenophylli* consists of two of the largest sections, one of which, *C. sect. Cyclostigma*, consists primarily of trees, and the other, *C. sect. Adenophylli*, of shrubs. The inflated columella tip unique to *C. sect. Adenophylli* (Riina & al., 2009) allows for easy identification of this section, which accounts for over a fifth of the species in the genus. Shrubs and trees characterize most sections and subgenera of *Croton*, but annual herbs are found only in *Croton subg. Geiseleria*.

Nearly all of the morphological characters that have been used to infer relationships within *Croton*, such as those used in the key, are homoplasious across the genus. Most of the larger sections are characterized by a suite of characters, which often overlap with other sections. Geography is often a good indicator of phylogenetic relatedness within the genus, with several morphologically convergent sections found in distinct areas, such as *C. sect. Heptallon* which is entirely North American, and the superficially similar *C. sect. Pedicellati*, which is mainly South American. *Croton sect. Pedicellati* is recovered sister to the sympatric *C. sect. Lamprocroton* (Fig. 1), and although there are morphological similarities between the two, it was not until molecular evidence was obtained that their close relationship was revealed.

Monophyletic formal groups. — Our hypotheses are that each of the formally named taxa that we recognize is monophyletic. However, due to a lack of resolution, or to “wild card” species such as *C. trinitatis* Millsp., or to species potentially of hybrid origin such as *C. poecilanthus* Urb., four of the sections that we recognize are recovered as non-monophyletic groups in the combined analysis (Fig. 1, indicated there with an asterisk).

Additional work is underway to address the relationships within *Croton sect. Lasiogyne* and its relationship to *C. sects. Heptallon* and *Julocroton*, and preliminary results (not shown) support the topology recovered in the ITS analysis (Fig. 2), which is the same as that found by Berry & al. (2005) and Van Ee & Berry (2010a), in which the three sections are each monophyletic groups within an unresolved trichotomy.

Croton sect. Geiseleria is rendered paraphyletic by *C. trinitatis*, which is recovered without support sister to *C. sect. Bahamia* in the combined analysis (Fig. 1). All of the remaining accessions of *C. sect. Geiseleria* otherwise make a highly supported clade. In the ITS phylogeny (Fig. 2) *C. trinitatis* is recovered within a monophyletic *C. sect. Geiseleria*, while in the *EMB2765* exon 9 phylogeny (Fig. 3), it is sister to *C. sect. Bahamia*. Berry & al. (2005) also recovered *C. trinitatis* within a well-supported *C. sect. Geiseleria*. Given that *C. sect. Geiseleria* is a morphologically cohesive group, and *C. trinitatis* is a very characteristic species within it, this may be a problem caused by an elevated rate of molecular substitution within *C. trinitatis*, and further investigation of its genome is warranted. *Croton sect. Geiseleria* is an otherwise well-supported natural group.

Croton sect. Eluteria, as circumscribed here in a broad sense, is not recovered as a monophyletic group; the combined (Fig. 1) and ITS (Fig. 2) analyses place *C. myricifolius* Griseb. (*C. subsect. Cubenses*) sister to *C. subsect. Eluteria*, while the *trnL-F* analysis (Fig. 4) places it sister to *C. subsect. Jamaicensis*. The *EMB2765* exon 9 and *rps3* analyses (Figs. 3 and 5) recover the three subsections of *C. sect. Eluteria* unresolved with respect to each other. There is no support for *C. sect. Eluteria* not being monophyletic, and given the morphological and geographic evidence (Van Ee & Berry, 2009a), we group these three groups as subsections of *C. sect. Eluteria*.

Croton sect. Moacroton is rendered paraphyletic by *C. poecilanthus* in the combined (Fig. 1) and ITS (Fig. 2) analyses. In the *EMB2765* exon 9 (Fig. 3), *trnL-F* (Fig. 4), and *rps3* (Fig. 5) phylogenies, *C. poecilanthus* is recovered in *C. sect. Moacroton* rather than with species of the “South American Grade” (sensu Van Ee & al., 2008). The striking morphological resemblance between *C. poecilanthus* and species of *C. sect. Moacroton*, and the close relationship recovered in their *rbcl*, *ndhF*, and *trnL-F* analyses, led Van Ee & al. (2008) to place it there, and to hypothesize that it may be of hybrid origin. The additional nuclear and mitochondrial gene trees presented here corroborate the placement of *C. poecilanthus* within *C. sect. Moacroton*.

Evolution of life history. — The mitochondrial *rps3* phylogeny (Fig. 5) shows a remarkable increase in the substitution rate in the branch leading to *C. sects. Argyranthemis, Crotonopsis, and Drepadanium*, and in the branches leading to *C. sect. Pedicellati* and others in the upper part of the figure. In contrast, the branch lengths in the analyses of the other loci are more even. A similar pattern of variable and elevated substitution rates in the mitochondrial genome has been reported for *Silene* L. (Caryophyllaceae; Städler & Delph, 2002) and *Plantago* L. (Plantaginaceae; Cho & al., 2004). Given their reputation for overall slower rates of evolution, mitochondrial genes have been identified as being suitable for resolving deep phylogenetic relationships (Knoop, 2004; Qiu & al., 2006). In our analyses, the mitochondrial *rps3* gene provides resolution between *Croton* and two of the three outgroup genera, namely *Astraea* and *Acidocroton*, whereas the third outgroup, *Brasiliocroton*, is recovered within *Croton* (Fig. 5). It also provides supported resolution at higher levels within *Croton*, such as recovering *C. sects. Argyranthemis, Crotonopsis, and Drepadanium* as a highly supported clade, and *C. sects. Heptallon, Julocroton, and Lasiogyne* as another highly supported clade (Fig. 5). The sections with longer branches leading to them in the *rps3* phylogeny have in common that many of their members are annual herbs, compared to the tree and shrub habits of the sections with short branch lengths distributed along the polytomy towards the bottom of the phylogram (Fig. 5). Smith & Donoghue (2008) evaluated rates of molecular evolution in angiosperms and demonstrated that a shift from the tree/shrub habit to an herbaceous habit correlated with an increased rate of evolution. One possibility is that the groups in *Croton* that display elevated rates of *rps3* evolution represent a shift from the perennial tree and shrub habit to an herbaceous habit, along with several reversals to the perennial habit. Such a reversal was demonstrated by Van Ee & Berry (2010a) in *C. sect.*

Heptallon, in which the perennial *C. pottsii* (Klotzsch) Müll. Arg. is embedded within a group of annual species.

Conclusions. — The work presented here, and the earlier papers that it builds on, bring us closer to a global understanding of the phylogenetic relationships and a comprehensive taxonomic classification of the complex and megadiverse genus *Croton*. Besides the need to assess the Old World species and their sectional delimitations, more phylogenetic and species-level taxonomic work needs to be done in the New World, such as the circumscription of *C. sect. Lasiogyne* and relationships and species circumscriptions within the large *C. sects. Adenophylli* and *Geiseleria*. Molecular data have been invaluable for resolving phylogenetic relationships within *Croton* and as an aid in identifying and circumscribing taxa. The insights they have provided and the careful examination of hundreds of type specimens and species protologues, together with the sectional key we developed, have enabled us to confidently assign to section 702 of the 712 species we recognize in the New World. In the Taxonomic Treatment below, we group the sections into four named subgenera, which facilitates discussion of larger assemblages of sections and avoids awkward references to informal clade names, such as “New World clade I”, “New World clade II”, and “Old World clade” that have been used in previous works. Although the subgenera are difficult to distinguish morphologically because they are each so diverse, and thus no key to them is provided, this is similar to the difficulties in trying to use nonmolecular characters to characterize many of the orders recognized by the Angiosperm Phylogeny Group (2009). We use the taxonomic categories of subgenus, section, and subsection to provide properly named and ranked groups, but we do not consider that all taxa of the same rank are necessarily equivalent.

■ TAXONOMIC TREATMENT

Croton subg. *Croton*, which is restricted to the Old World, is listed here to complete the four subgenera that we recognize within the genus. The number of species belonging to each section or subsection is given below and in parentheses at the start of the lists of included species. Species for which molecular sequence data are available in GenBank, published here or previously, appear in bold face in the individual section lists.

Synopsis of the subgenera and the New World sections and subsections of *Croton*

- I. *Croton* subg. *Croton* (exclusively Old World)
- II. *Croton* subg. *Quadrilobi* (Müll. Arg.) Pax in Engl. & Prantl
 1. *C. sect. Olivacei* Berry — 1 sp.
 2. *C. sect. Sampatik* (G.L. Webster) Riina — 4 spp.
 3. *C. sect. Quadrilobi* Müll. Arg. — 1 sp.
 4. *C. sect. Pachypodi* B.W. van Ee — 5 spp.
 5. *C. sect. Moacroton* (Croizat) B.W. van Ee & P.E. Berry — 8 spp.
 6. *C. sect. Nubigeni* B.W. van Ee — 1 sp.
 7. *C. sect. Alabamenses* B.W. van Ee — 1 sp.

8. *C. sect. Corinthii* B.W. van Ee — 1 sp.
9. *C. sect. Corylocroton* G.L. Webster — 11 spp.
- III. *Croton* subg. *Adenophylli* (Griseb.) Riina, B.W. van Ee & P.E. Berry
 10. *C. sect. Cyclostigma* Griseb. — 41 spp.
 11. *C. sect. Adenophylli* Griseb. — 223 spp.
- IV. *Croton* subg. *Geiseleria* A. Gray
 12. *C. sect. Cupreati* Riina — 1 sp.
 13. *C. sect. Eremocarpus* (Benth.) G.L. Webster — 1 sp.
 14. *C. sect. Cuneati* (G.L. Webster) Riina & P.E. Berry — 11 spp.
 15. *C. sect. Eluteria* Griseb. — 22 spp.
 - 15a. *C. subsect. Eluteria* (Griseb.) B.W. van Ee & P.E. Berry — [15 spp.]
 - 15b. *C. subsect. Cubenses* B.W. van Ee & P.E. Berry — [4 spp.]
 - 15c. *C. subsect. Jamaicensis* B.W. van Ee & P.E. Berry — [3 spp.]
 16. *C. sect. Crotonopsis* (Michx.) G.L. Webster — 1 sp.
 17. *C. sect. Argyranthemii* B.W. van Ee — 2 spp.
 18. *C. sect. Drepadenium* (Raf.) Müll. Arg. — 6 spp.
 19. *C. sect. Prisci* Riina — 3 spp.
 20. *C. sect. Pedicellati* B.W. van Ee & P.E. Berry — 20 spp.
 21. *C. sect. Lamprocroton* (Müll. Arg.) Pax in Engl. & Prantl — 37 spp.
 - 21a. *C. subsect. Lamprocroton* (Müll. Arg.) B.W. van Ee & P.E. Berry — [17 spp.]
 - 21b. *C. subsect. Argentinii* B.W. van Ee & P.E. Berry — [20 spp.]
 22. *C. sect. Luetzelburgiorum* Riina — 1 sp.
 23. *C. sect. Cleodora* (Klotzsch) Baill. — 18 spp.
 24. *C. sect. Cordiifolii* Riina — 1 sp.
 25. *C. sect. Eutropia* (Klotzsch) Baill. — 1 sp.
 26. *C. sect. Geiseleria* (A. Gray) Baill. — 82 spp.
 27. *C. sect. Barhamia* (Klotzsch) Baill. — 84 spp.
 - 27a. *C. subsect. Barhamia* (Klotzsch) B.W. van Ee — [19 spp.]
 - 27b. *C. subsect. Astraeopsis* (Baill.) B.W. van Ee — [4 spp.]
 - 27c. *C. subsect. Medea* (Klotzsch) Pax in Engl. & Prantl — [45 spp.]
 - 27d. *C. subsect. Micranthi* (Baill.) B.W. van Ee — [13 spp.]
 - 27e. *C. subsect. Sellowiorum* B.W. van Ee — [3 spp.]
 28. *C. sect. Luntia* (Neck. ex Raf.) G.L. Webster — 19 spp.
 29. *C. sect. Julocroton* (Mart.) G.L. Webster — 41 spp.
 30. *C. sect. Lasiogyne* (Klotzsch) Baill. — 45 spp.
 31. *C. sect. Heptallon* (Raf.) Müll. Arg. — 9 spp.

Artificial key to the New World sections of *Croton*

1. Herbs, subshrubs, or shrubs 2
1. Small to large trees (rarely lianas) 27
2. Leaves without glands at the base of the leaf blade or apex of the petiole 3

- 2. Leaves with glands at the base of the leaf blade or apex of the petiole **19**
- 3. Annual herbs; ovary 1-locular **4**
- 3. Annual to perennial herbs, subshrubs, or shrubs; ovary (2-) 3-locular **5**
- 4. Low, mat-forming plants; leaves bristly stellate; inflorescences congested, hidden in the leaf axils or in dichotomies of stems; style 1, simple; fruit dehiscent; staminate flowers apetalous; western U.S.A. **13. C. sect. *Eremocarpus***
- 4. Erect, loosely branching plants; leaves stellate-lepidote; inflorescences racemose; styles 3, simple to twice bifid; fruit indehiscent; staminate flowers with petals; eastern and central U.S.A. **16. C. sect. *Crotonopsis***
- 5. Sepals of pistillate flowers serrate, deeply divided, lacinate, or glandular-toothed. **6**
- 5. Sepals of pistillate flowers entire and eglandular **9**
- 6. Sepals of pistillate flowers deeply divided (lacinate), eglandular, strongly unequal in size **29. C. sect. *Julocroton***
- 6. Sepals of pistillate flowers divided < 1/2 their length, usually glandular-toothed, and nearly equal in size **7**
- 7. Stamens 10–45; columella persistent, with three prominent, smooth lobes angling outwards **11. C. sect. *Adenophylli***
- 7. Stamens 3–20; columella lacking prominent, smooth lobes. **8**
- 8. Stamens (3–)8–15(–20); numerous species, herbs to shrubs, widespread **27. C. sect. *Barhamia***
- 8. Stamens 15; single low shrubby species from campos rupestres of Bahia, Brazil **22. C. sect. *Luetzelburgiorum***
- 9. Sepals of pistillate flowers reduplicate-valvate (the sepals are creased in the middle and flare outwards where they adjoin) **30. C. sect. *Lasiogyne***
- 9. Sepals of pistillate flowers valvate (rarely imbricate), but not reduplicate **10**
- 10. Shrubs, usually > 1 m tall **11**
- 10. Annual to perennial herbs or subshrubs, mostly < 1 m tall but occasionally robust individuals larger **15**
- 11. Pistillate flowers sessile or subsessile, without petals; the columella persistent, with three prominent, smooth lobes angling outwards **11. C. sect. *Adenophylli***
- 11. Pistillate flowers pedicellate, with or without petals; the columella lacking prominent, smooth lobes **12**
- 12. Inflorescences terminal and/or axillary. **13**
- 12. Inflorescences terminal **14**
- 13. Indumentum stellate to stellate-lepidote **30. C. sect. *Lasiogyne***
- 13. Indumentum lepidote, or stellate on species only from Cuba and Jamaica **15. C. sect. *Eluteria***
- 14. Styles multifid (≥ 12 terminal tips). **30. C. sect. *Lasiogyne***
- 14. Styles simple (3 terminal tips), or slightly flabellate at the tips. **7. C. sect. *Alabamenses***
- 15. Dioecious or occasionally monoecious; staminate flowers without petals. **18. C. sect. *Drepadenium***
- 15. Monoecious; staminate flowers with petals **16**
- 16. Staminate flowers with lepidote petals **17. C. sect. *Argyranthemis***
- 16. Staminate flowers with glabrous or villous petals **17**
- 17. Sepals of staminate and pistillate flowers with open aestivation; pistillate flowers pedicellate, pedicels often recurved **20. C. sect. *Pedicellati***
- 17. Sepals of staminate and pistillate flowers valvate; pistillate flowers subsessile to pedicellate, pedicels straight to recurved **18**
- 18. Annual herbs or perennial subshrubs from a ligneous base, indumentum stellate; pistillate flowers pedicellate; North America **31. C. sect. *Heptallon***
- 18. Perennial shrubs, indumentum lepidote or stellate; pistillate flowers sessile to shortly pedicellate; South America **21. C. sect. *Lamprocroton***
- 19. Stamens (2–)4–6, anthers subsessile, anthers not inflexed in bud (or else filamentous anthers 2 or 3 and inflexed in bud); Cuba. **5. C. sect. *Moacroton***
- 19. Stamens 5 to many, anthers filamentous, inflexed in bud; widespread **20**
- 20. Sepals of pistillate flowers markedly connate at base and then free, lobes imbricate or quincuncial; styles multifid and forming one or more fused styler columns. **23. C. sect. *Cleodora***
- 20. Sepals of pistillate flowers free or slightly connate at base, lobes valvate, reduplicate, open, or imbricate; styles bifid to multifid but not united into styler columns. **21**
- 21. Dioecious shrubs; stigmas bifid with 6 stigmatic tips; eastern Brazil (Bahia). **22**
- 21. Monoecious or occasionally dioecious herbs or shrubs; stigmas bifid to multifid; widespread **23**
- 22. Flowers 5-merous; capsules muricate, 3-locular **24. C. sect. *Cordiifolii***
- 22. Flowers 4-merous; capsules smooth, mostly 2-locular **3. C. sect. *Quadrilobi***
- 23. Basalmost cymules of the inflorescence with both staminate and pistillate flowers. **24**
- 23. Basalmost cymules of the inflorescence unisexual **25**
- 24. Indumentum stellate; sepals valvate or reduplicate-valvate; widespread in the Neotropics. **10. C. sect. *Cyclostigma***
- 24. Indumentum lepidote to stellate-lepidote; sepals of pistillate flowers small and imbricate; a single species endemic to coastal restinga vegetation in Brazil (Bahia). **25. C. sect. *Eutropia***
- 25. Leaves usually dentate, generally with a pair of stipitate glands at the base and sometimes with glands in the leaf sinuses; sepals of pistillate flowers often free and unequal **26. C. sect. *Geiseleria***
- 25. Leaves usually entire or serrulate, with sessile or sometimes stipitate glands at the base, lacking glands in the leaf sinuses; sepals of pistillate flowers valvate and equal in size **26**
- 26. Pistillate flowers sessile to subsessile, stigmas bifid to multifid, with 6 to numerous terminal tips; staminate flowers with short pedicels of similar length; widespread, with numerous species **11. C. sect. *Adenophylli***
- 26. Pistillate flowers subsessile to shortly pedicellate, stigmas bifid, with 6 terminal tips; staminate flowers with pedicels of varying lengths; single species from montane Ecuador and Peru **1. C. sect. *Olivacei***

27. Leaves without glands at the base of the blade or apex of the petiole **28**
27. Leaves with glands at the base of the blade or apex of the petiole. **30**
28. Inflorescences terminal and axillary; pistillate flowers usually with well-developed petals . . . **15. C. sect. *Eluteria***
28. Inflorescences terminal; pistillate flowers without petals **29**
29. Pistillate flowers sessile or subsessile, the sepals valvate but not reduplicate, the columella with three prominent, smooth lobes angling outwards. **11. C. sect. *Adenophylli***
29. Pistillate flowers subsessile or pedicellate, the sepals reduplicate-valvate (the sepals are creased in the middle and flare outwards where they adjoin), the columella lacking prominent, smooth lobes **30. C. sect. *Lasiogyne***
30. Stamens (2–)4–6 (if >3, then lacking filaments); styles simple or bifid, with 3 or 6 stigmatic tips; Cuba **5. C. sect. *Moacroton***
30. Stamens > 5, filaments always present; styles bifid or multifid; widespread. **31**
31. Sepals of pistillate flowers noticeably reduplicate-valvate; styles multifid **32**
31. Sepals of pistillate flowers valvate, imbricate, or basally connate, but not reduplicate; styles bifid or multifid . . . **34**
32. Styles divided into 18–36 stigmatic tips; stamens 10–15; fruits smooth **28. C. sect. *Luntia***
32. Styles divided into 12–24 stigmatic tips; stamens 15–100 (–350); fruits smooth or muricate **33**
33. Leaves palmately veined (or lobed), the margins entire to dentate, eglandular; stamens 16–100 (–350) **10. C. sect. *Cyclostigma***
33. Leaves pinnately veined, the margins crenate-dentate with sessile glands at the apices of the teeth; stamens 15–18 **19. C. sect. *Prisci***
34. Sepals of pistillate flowers distinctly imbricate. **35**
34. Sepals of pistillate flowers valvate **37**
35. Inflorescences axillary and terminal; pistillate flowers subsessile, small, <5 mm diam., sepals inconspicuous, stigmas bifid with 6 stigmatic tips; stamens 10–15; a single species endemic to coastal restinga vegetation in Brazil (Bahia) **25. C. sect. *Eutropia***
35. Inflorescences terminal (rarely axillary); pistillate flowers subsessile to clearly pedicellate, >5 mm diam., sepals generally persistent and conspicuous, stigmas multifid, with 12–30 stigmatic tips; stamens 15–25; multiple species from Mexico to South America **36**
36. Adult leaves stellate or lepidote; leaf margins entire or dentate, without glands in the sinuses; sepals of pistillate flowers noticeably connate at the base, styles multifid with 12–30 terminal tips and basally connate, usually forming 1 or 3 styler columns; stamens 15–25 . . . **23. C. sect. *Cleodora***
36. Adult leaves nearly glabrous; leaf margins crenate-dentate, with glands in the sinuses; sepals of pistillate flowers barely connate at the base, styles quadrifid, with 12 terminal tips, not forming a styler column; stamens 15–16 **19. C. sect. *Prisci* (*C. thomasi*)**
37. Pistillate flowers sessile or subsessile, the columella with three prominent, smooth lobes angling outwards; small trees (mostly shrubs) **11. C. sect. *Adenophylli***
37. Pistillate flowers sessile to pedicellate, the columella lacking prominent smooth lobes; small to large trees. **38**
38. Leaf blades pinnately veined, margins dentate with stipitate glands along the margins, or on the lamina near the margins; styles distinct, bifid; capsules 3-lobed; seeds laterally compressed **2. C. sect. *Sampatik***
38. Leaf blades pinnately or palmately veined or lobed, margins entire or dentate, but usually without marginal stipitate glands; styles distinct to partly connate, bifid or multifid; capsules terete to slightly lobed, seeds not laterally compressed **39**
39. Indumentum on leaves lepidote or lepidote-stellate . . . **40**
39. Indumentum on leaves stellate or subglabrous **44**
40. Leaf venation palmate-pinnate (3- or 5-nerved at base and pinnate above) **41**
40. Leaf venation pinnate **42**
41. Indumentum lepidote-stellate, never densely coppery-lepidote; stipules narrow and entire; various species, widespread. **9. C. sect. *Corylocroton***
41. Indumentum densely coppery-lepidote; stipules foliose and dentate; one species, *C. cupreatus*, from montane Ecuador and Colombia. **12. C. sect. *Cupreati***
42. Leaf margins dentate, crenate, or loosely crenate to sinuous, usually with sessile or shortly stipitate discoid glands in the sinuses; seeds with the caruncle reduced, absent, or modified into an arillate structure **14. C. sect. *Cuneati***
42. Leaf margins entire, without glands; seeds carunculate **43**
43. Inflorescences axillary and terminal, sometimes branched, terete; styles bifid, with 6 terminal tips; seeds large, 1–3 cm long; Costa Rica, Panama, and South America **4. C. sect. *Pachypodi***
43. Inflorescences terminal, unbranched, and angular in cross-section; styles simple or flabellate, with 3 terminal tips; seeds <1 cm long; cloud forests of Puerto Rico. **5. C. sect. *Moacroton* (*C. poecilanthus*)**
44. Leaf venation palmate or triplinerved, leaves sometimes 3-lobed; styles bifid to multifid, with 6–30 terminal tips **45**
44. Leaf venation pinnate or palmate-pinnate (3-nerved at base and parallel above); styles bifid, with 6 terminal tips (except *C. sect. *Corinthii**, which is twice bifid with 12+ terminal tips) **46**
45. Leaf blades entire to variously toothed or lobed, but without glands in the sinuses, also lacking domatia in the vein axils; stamens 16–100 (–350); seeds carunculate; numerous species, widespread. **10. C. sect. *Cyclostigma***
45. Leaf blades crenate-dentate, with small glands in the sinuses, with dense, long tufts of trichomes (forming domatia) in the major leaf axils on the lower leaf surface and on both sides of the base; stamens 10–12; seeds without a caruncle; two species (*C. aripoensis* and *C. domatifer*) from cloud forests of Trinidad and northern Venezuela **14. C. sect. *Cuneati***
46. Leaf margins serrate to coarsely dentate, sometimes with glands in the sinuses; various species, widespread **9. C. sect. *Corylocroton***

46. Leaf margins entire or subentire, if sinuous with glandular teeth and glands in the sinuses (*C. sect. Quadrilobi*) then the flowers 4-merous; all monotypic sections of narrow distributions. 47
47. Dioecious; leaf margin sinuous with glands in the sinuses; stipules gland-tipped; flowers 4-merous; staminate inflorescences axillary, pistillate inflorescences terminal; one species in eastern Bahia, Brazil. 3. *C. sect. Quadrilobi*
47. Monoecious; leaf margins entire or subentire, without glands; stipules eglandular; flowers 5-merous; inflorescences terminal 48
48. Mature leaves sparsely to densely pubescent, lower surface with scattered glands in the axils of the secondary veins; styles twice bifid, with 12 or more terminal tips; one species in Atlantic coastal Costa Rica 8. *C. sect. Corinthii*
48. Mature leaves sparsely pubescent to nearly glabrous, without glands on the lower surface; styles bifid, with 6 terminal tips; one species in Nicaragua and Honduras, another in South America 49
49. Petioles with pulvini at both ends (difficult to see when dried); stamens 13–15; one species in montane Nicaragua and Honduras. 6. *C. sect. Nubigeni*
49. Petioles without evident pulvini; stamens 30–40; one species in montane Ecuador and Peru 1. *C. sect. Olivacei*

Croton L., Sp. Pl.: 1004. 1753 ≡ *Oxydectes* L. ex Kuntze, Revis. Gen. Pl. 2: 609. 1891, nom. illeg. & superfl. – Type: *C. tiglium* L., lectotype designated by Britton (1918: 207).

Although Webster (1993) superseded Small's (1913) choice of *C. tiglium* L. as the lectotype of *Croton* and designated *C. aromaticus* L., the valid lectotype of the genus is *C. tiglium* (Britton, 1918; Van Ee & Berry, 2010b).

Trees, shrubs, or herbs, annual or perennial, monoecious or rarely dioecious; indumentum stellate to lepidote; latex usually present, clear to reddish. Leaves alternate or sometimes clustered or whorled below the inflorescences, simple, often with a lemony, pungent, or acrid odor when crushed, older leaves often turning orange before dehiscing; stipules present or absent; petiole present or absent; blade margins entire to toothed or lobed, glands present or absent at the base or along the margins and occasionally on the lamina; venation pinnate, or palmate at base and pinnate above. Inflorescences unisexual or bisexual with proximal pistillate flowers and distal staminate ones, terminal or axillary, spikes, heads, racemes, or thyrses. Staminate flowers: sepals (3–)5(–6), distinct or connate basally, valvate to imbricate; petals (3–)5(–6) or 0, distinct, imbricate; disc extrastaminal, usually of 5 glands opposite the sepals; stamens (2–)4–100(–350), filaments inflexed in bud (nearly obsolete in *C. sect. Moacroton*), distinct, anthers basifixed, dehiscent longitudinally; pistillode absent. Pistillate flowers: sepals (3–)5(–10), distinct, imbricate, valvate, or reduplicate-valvate, distinct or connate basally; petals 5 or 0 (rudimentary), imbricate; disc annular or of 5 lobes opposite the sepals, or absent; pistils (1-, 2-) 3-carpellate, styles 1–3, simple, bifid, or multifid. Fruits capsules, rarely indehiscent. Seeds 1 per locule, seed coat dry, caruncle present, rarely absent or arillate.

I. *Croton* subg. *Croton* – Type: *C. tiglium* L.

Croton sect. *Croton* ≡ *Tiglium* Klotzsch in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 418. 1843 ≡ *Croton* sect. *Tiglium* (Klotzsch) Baill., Étude Euphorb.: 361. 1858 ≡ *Croton* sect. *Eucroton* Baill., Étude Euphorb.: 354. 1858, nom. inval. – Type: *C. tiglium* L.

II. *Croton* subg. *Quadrilobi* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 ≡ *Croton* sect. *Quadrilobi* Müll. Arg. in Linnaea 34: 78. 1865 – Type: *C. sapiifolius* Müll. Arg.

Croton subg. *Moacroton* was circumscribed by Van Ee & al. (2008) to include species of *C. sects. Alabamenses, Corinthii, Corylocroton, Moacroton, and Nubigeni*, and they recovered species of *C. sects. Olivacei, Pachypodi, and Sampatik* as a grade at the base of this clade. The subgeneric classification of *Croton* adopted here places all of these into a single subgenus. However, the inclusion of *C. sapiifolius*, the type of the earlier name *C. subg. Quadrilobi*, which was not sampled by Van Ee & al. (2008), requires that this clade now be called *C. subg. Quadrilobi* instead of *C. subg. Moacroton*. This is somewhat of a misnomer for the group, since the only 4-merous species in the entire group is the type species, *C. sapiifolius*. This subgenus is characterized by its tree or large shrubby habit, and with the exception of *C. corinthius*, all species have simple or bifid styles with three or six stigmatic tips.

1. *Croton* sect. *Olivacei* P.E. Berry, **sect. nov.** – Arbores frutescens parce stellata, foliis basi biglandulosis, stipulis integris; racemis terminalibus, pedicellis staminatis disparibus, staminibus 30 ad 40; sepalis pistillatis integris, valvatis; stylis bifidis. – Type: *C. olivaceus* Müll. Arg.

Description. – Monoecious shrubs or trees 2–7 m tall; indumentum sparsely stellate; latex present; leaves with 2 glands at the base; margins subentire; venation pinnate; stipules entire; inflorescences terminal, bisexual, lower cymules unisexual; stamens 30–40; sepals of pistillate flowers with open aestivation; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips.

Distribution and habitat. – This monotypic section is known from tropical premontane forests in Ecuador and Peru from 900 to 1600 m.

Included species (1). – *C. olivaceus* Müll. Arg.

2. *Croton* sect. *Sampatik* (G.L. Webster) Riina, **stat. nov.** ≡ *Croton* (sect. *Cyclostigma* Griseb.) subsect. *Sampatik* G.L. Webster in Taxon 42: 802. 1993 – Type: *C. sampatik* Müll. Arg.

Description. – Monoecious trees to 25 m tall; indumentum stellate or stellate-lepidote; leaves with 2 glands at base, glands sessile, on adaxial side of petiole; margins slightly sinuous to dentate, with an ovoid gland on each tooth and stipitate patelliform glands positioned at each sinus or near the margin on the abaxial side of the lamina; venation pinnate or palmate; stipules entire, linear; inflorescences terminal, bisexual, lower cymules unisexual; stamens 15–20; sepals of pistillate flowers

with open to valvate aestivation; petals of pistillate flowers reduced; styles bifid for a total of 6 stigmatic tips; capsules 3-lobed; seeds compressed laterally.

Distribution and habitat. – Widespread in South America in the Amazon-Orinoco basins to the foothills of the Andes and in the Mata Atlántica forests of southeastern Brazil, from 100 to 900 m.

Notes. – *Croton sampatik*, *C. piptocalyx*, and *C. trombetensis* were previously placed in *C. sect. Cyclostigma* (Webster, 1993; Secco & al., 2001). An examination of their morphology and the molecular data supports this group as a separate lineage well removed from *C. sect. Cyclostigma* (Riina & al., 2009). Webster (1993) listed six species in the description of *C. subsect. Sampatik*, and these have been shown to belong to five different sections, none of which are closely related.

Included species (4). – *C. ater* Croizat, *C. piptocalyx* Müll. Arg., *C. sampatik* Müll. Arg., *C. trombetensis* Secco, P.E. Berry & N.A. Rosa.

3. *Croton* sect. *Quadrilobi* Müll. Arg. in *Linnaea* 34: 78. 1865 – Type: *C. sapiifolius* Müll. Arg.

Description. – Dioecious shrubs or trees 2–14 m tall; indumentum stellate to stellate-lepidote; leaves with 2 (4) glands at base, glands sessile, on adaxial side of petiole; margins entire to sinuous or dentate with glands in the sinuses and glandular-tipped teeth; venation pinnate; stipules glandular-tipped; staminate inflorescences axillary; pistillate inflorescences terminal; flowers 4-merous; stamens 10–15; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips; capsules obovate, 2-(3)-locular.

Distribution and habitat. – Endemic to low-elevation moist forests in southern Bahia, Brazil.

Notes. – At the time of the description of *C. sect. Quadrilobi* (Müller, 1865), *C. sapiifolius* was known only from the type collection. It was recently recollected, and Riina & al. (2010a) published additional details about the species' morphology, including evidence that it is probably dioecious, and that despite having three styles, nearly all the capsules are 2-locular. This section is unique in *Croton* in being 4-merous.

Included species (1). – *C. sapiifolius* Müll. Arg.

4. *Croton* sect. *Pachypodi* B.W. van Ee, **sect. nov.** – Arborea lepidota foliis basi inaequaliter biglandulosis, stipulis integris; racemis terminalibus axillaribusve; staminibus 14 ad 16; sepalis pistillatis integris, valvatis; stylis bifidis; capsulis 2–5 cm longis. – Type: *C. pachypodus* G.L. Webster.

Description. – Monoecious trees to 30 m tall; indumentum lepidote; leaves with 2 glands at the base, the glands generally facing towards the abaxial side of the leaf; margins entire; venation pinnate; stipules entire; inflorescences terminal or terminal and axillary, bisexual or staminate, lower cymules unisexual, some cymules bisexual; stamens 14–16; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips; mature capsules and seeds generally large, up to 5 × 4 cm and 3 × 2 cm respectively.

Distribution and habitat. – *Croton* sect. *Pachypodi* is a mainly South American group that reaches its northern limit

in Costa Rica. It is found in humid montane and lower montane forests in Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia, from 50 to 1200 m.

Notes. – This small section of at least five species possesses some of the largest fruits and seeds of all New World groups. Webster & Huft (1988) incorrectly described *C. pachypodus* as having multifid styles; in this group, all species have bifid styles.

Included species (5). – *C. diasii* Pires ex Secco & P.E. Berry, *C. jorgei* J. Murillo, *C. maasii* Riina & P.E. Berry, *C. megistocarpus* J.A. González & Poveda, *C. pachypodus* G.L. Webster.

5. *Croton* sect. *Moacroton* (Croizat) B.W. van Ee & P.E. Berry in *Bot. Rev. (Lancaster)* 74: 158. 2008 ≡ *Moacroton* Croizat in *J. Arnold Arbor.* 26: 189. 1945 ≡ *Croton* subg. *Moacroton* (Croizat) B.W. van Ee & P.E. Berry in *Bot. Rev. (Lancaster)* 74: 158. 2008 – Type: *Moacroton leonis* Croizat ≡ *C. leonis* (Croizat) B.W. van Ee & P.E. Berry.

= *Cubacroton* Alain in *Candollea* 17: 116. 1960 – Type: *Cubacroton maestrensis* Alain ≡ *Moacroton maestrensis* (Alain) Radcl.-Sm. ≡ *Croton maestrensis* (Alain) B.W. van Ee & P.E. Berry.

= *Moacroton* sect. *Glaucifoliae* Borhidi in *Acta Bot. Acad. Sci. Hung.* 36: 8. 1990 [1991] – Type: *Moacroton trigonocarpus* (Wright ex. Griseb.) Croizat ≡ *Croton trigonocarpus* Wright ex. Griseb.

Description. – Monoecious shrubs or trees to 15 m tall; indumentum lepidote; leaves with 2 glands at base; margins entire or toothed; venation pinnate; coriaceous; stipules entire; inflorescences terminal, bisexual, lower cymules unisexual or bisexual; stamens (2–)4–6(–30); sepals of pistillate flowers with open aestivation; petals of pistillate flowers absent; styles simple, bifid, or flabellate for a total of 3 or 6 stigmatic tips.

Distribution and habitat. – Serpentine barrens in Cuba, and cloud forests in Cuba and Puerto Rico, from sea level to 1500 m.

Notes. – Six species in this section are restricted to serpentine outcrops in Cuba, and sister to this serpentine radiation is *C. maestrensis* (Fig. 1), which is found in cloud forests on igneous substrates in the Sierra Maestra mountains of southeastern Cuba (Van Ee & al., 2008). *Croton maestrensis* has staminate flowers with only two or three stamens and pistillate flowers with simple styles. *Croton poecilanthus*, endemic to the rainforests of the Luquillo mountains of eastern Puerto Rico, is placed in this section given its remarkable morphological similarity to the Cuban species, with the exception of it having up to 30 stamens compared to a maximum of six in any of the other members. This relationship is supported by the phylogenetic signal of the chloroplast genome (Fig. 4; Van Ee & al., 2008), and at least in part by the nuclear *EMB2765* exon 9 and the mitochondrial *rps3* gene trees (Figs. 3 and 5).

Included species (8). – *C. alainii* B.W. van Ee & P.E. Berry, *C. cristalensis* Urb., *C. ekmanii* Urb., *C. leonis* (Croizat) B.W. van Ee & P.E. Berry, *C. maestrensis* (Alain) B.W. van Ee & P.E. Berry, *C. poecilanthus* Urb., *C. revolutus* (Alain) B.W. van Ee & P.E. Berry, *C. trigonocarpus* Wright ex. Griseb.

6. *Croton* sect. *Nubigeni* B.W. van Ee, **sect. nov.** – Arbores parce stellata foliis basi biglandulosis, stipulis integris; pulvinibus ad basin et apicem petiolo; racemis terminalibus; staminibus 13 ad 15; sepalis pistillatis integris; stylis bifidis. – Type: *C. nubigenus* G.L. Webster.

Description. – Monoecious trees to 7 m tall; indumentum stellate but mostly nearly glabrous; leaves with 2 glands at the base; margins subentire; venation pinnate; petioles with pulvini at both ends; stipules entire; inflorescences terminal, bisexual or unisexual, lower cymules unisexual; stamens 13–15; sepals of pistillate flowers with open aestivation; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips.

Distribution and habitat. – This monotypic section is endemic to humid forests from 200 to 1200 m in Honduras and Nicaragua.

Notes. – Webster (1988) suggested that *Croton nubigenus* was closely related to the Jamaican *C. lucidus* L. (as *C. wilsonii* Griseb.) and the Mexican *C. ynesae* Croizat, and ultimately referred them to the mainly Old World *C. sect. Croton* (as *C. sect. Tigium* (Klotzsch) Baill.). *Croton lucidus* and *C. ynesae* are members of *C. sect. Adenophylli* (Fig. 1), and their main similarity with *C. nubigenus* is that they are nearly totally glabrous. Webster (1988) also suggested that *C. nubigenus* might be closely related to the Brazilian *C. sapiifolius* (*C. sect. Quadri-lobi*) or the Old World *C. verreauxii* Baill., but ultimately its relationship lies with geographically closer species, rather than with those that appear similar morphologically. Webster (1988) described *C. nubigenus* as dioecious, but additional field work has revealed that it is monoecious, although most inflorescences and collections are unisexual.

Included species (1). – *C. nubigenus* G.L. Webster.

7. *Croton* sect. *Alabamenses* B.W. van Ee, **sect. nov.** – Frutices lepidoti foliis eglandulosis, estipulatis; racemis terminalibus; staminibus 10 ad 15; sepalis pistillatis integris, valvatis, petalis viridis evolutis; stylis simplicibus. – Type: *C. alabamensis* E.A. Sm. ex Chapm.

Description. – Monoecious shrubs to 3 m tall; indumentum lepidote; leaves without visible glands when fully developed, but vestigial glands distinguishable at the base of developing leaf blades on the adaxial side; stipules absent; inflorescences terminal, bisexual or staminate, lower cymules unisexual; stamens 10–15; sepals of pistillate flowers valvate; petals of pistillate flowers well developed; styles simple to flabellate at the tips for a total of 3 stigmatic tips, although these may sometimes appear slightly divided at the tips.

Distribution and habitat. – This monotypic section is endemic to the southern United States, with *C. alabamensis* var. *alabamensis* found in Bibb and Tuscaloosa counties in Alabama, and *C. alabamensis* var. *texensis* Ginzburg in Coryell, Bell, and Travis counties in Texas (Ginzburg, 1992; Van Ee & al., 2006; Wurdack, 2006). It occurs above the coastal plain on limestone, dolomite, and shale outcroppings and adjacent outwashes, from 50 to 300 m.

Notes. – This is one of the few groups that have simple styles (Fig. 6B).

Included species (1). – *C. alabamensis* E.A. Sm. ex Chapm., with two varieties: *C. alabamensis* var. *alabamensis* and *C. alabamensis* var. *texensis* Ginzburg.

8. *Croton* sect. *Corinthii* B.W. van Ee, **sect. nov.** – Arbores stellata foliis basi biglandulosis, glandulis in axillis venarum secundariis abaxialis; stipulis integris; pulvinibus ad basin et apicem petioloracemis terminalibus; racemis terminalibus; staminibus 15 ad 17; sepalis pistillatis integris, valvatis; stylis bisbifidis vel plus. – Type: *C. corinthius* Poveda & J.A. González.

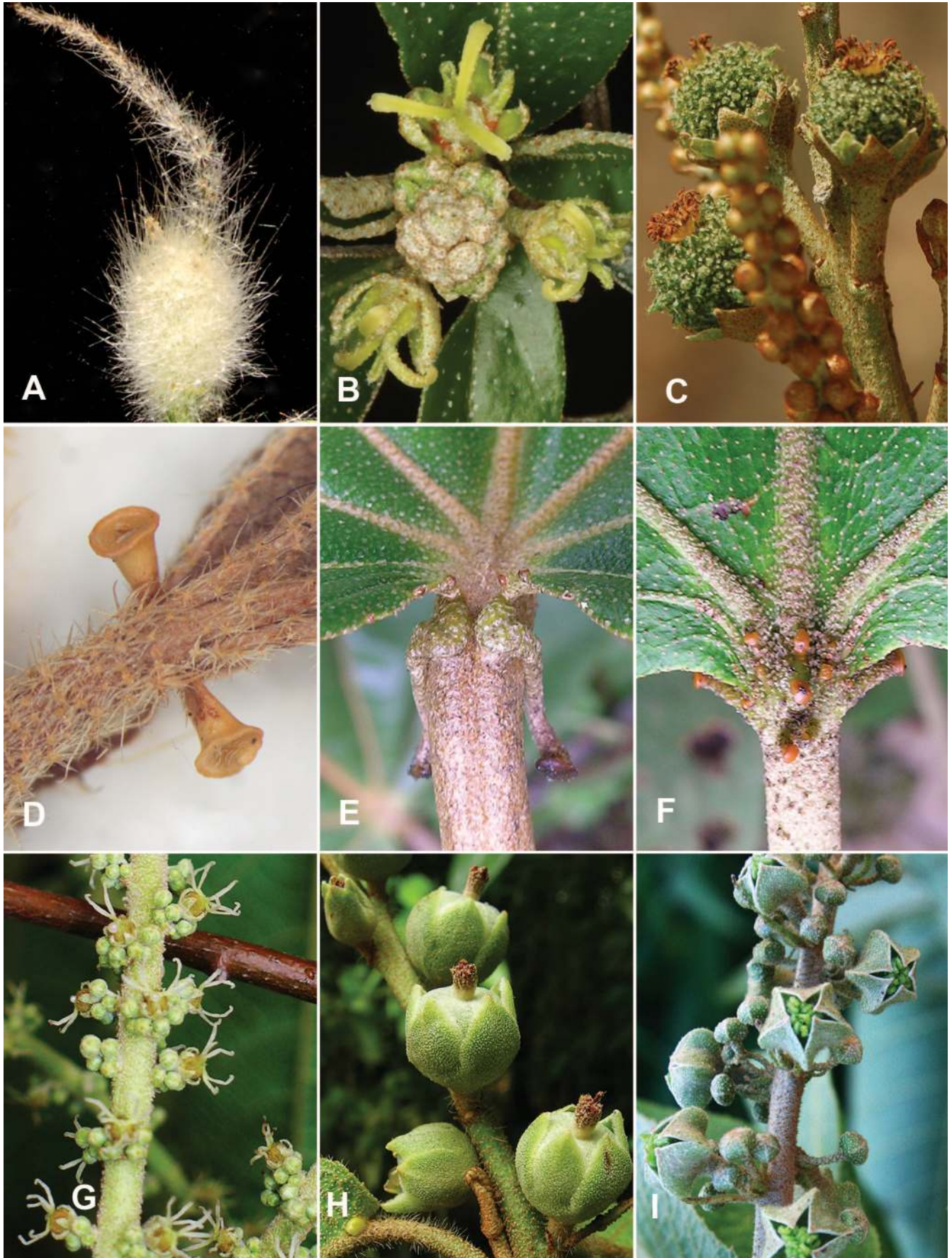
Description. – Monoecious trees to 10 m tall; indumentum stellate; leaves with 2 glands at the base and scattered glands in the axils of the secondary veins on the abaxial side; margins subentire; venation pinnate; petioles with pulvini at both ends; stipules entire; inflorescences terminal, bisexual, lower cymules unisexual; stamens 15–17; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles twice bifid or more for a total of 12 or more stigmatic tips per flower.

Distribution and habitat. – This monotypic section is endemic to humid forests between 50 and 250 m of Limón, Costa Rica, near the Atlantic coast. It has been located at one more locality in addition to the two published in González Ramírez & Poveda Álvarez (2003; J. González Ramírez, pers. comm.).

Notes. – The scattered glands in the axils of the secondary veins on the abaxial leaf surface of *C. corinthius* is a distinctive characteristic that also appears in Leandri’s “*Groupe Adenophorum*” (Leandri, 1939) from Madagascar, and similar glands are found in *C. sect. Luntia* (Riina & al., 2010b). The presence of pulvini at both ends of the petioles appears to be a synapomorphy shared with the closely related *C. sect. Nubigeni*. These pulvini shrink when dry and are not readily visible on herbarium specimens.

Included species (1). – *C. corinthius* Poveda & J.A. González.

Fig. 6. Diagnostic floral and vegetative features of *Croton* used in the sectional key. **A**, Unilocular ovary and simple style of *Croton setiger* (*C. sect. Eremocarpus*). Trichomes are stellate with a long, porrect central ray (ex cult., MICH). **B**, Pistillate flowers of *Croton alabamensis* (*C. sect. Alabamenses*), showing simple styles from a trilocular ovary, petals, and discrete disk glands (ex cult., MICH). **C**, Pistillate flowers of *Croton arboreus* (*C. sect. Eluteria* subsect. *Eluteria*), showing multifid styles, petals, and muricate ovaries (Van Ee 472, WIS). **D**, stalked acropetiolar glands of *Croton sipaliwinensis* (*C. sect. Geiseleria*) (Prance 4293, NY). **E**, recurved, stipitate petiolar glands of *Croton cupreatus* (*C. sect. Cupreati*) (Riina 1408, WIS). **F**, multiple acropetiolar and epipetiolar sessile to stipitate glands of *Croton lechleri* (*C. sect. Cyclostigma*) from central Ecuador (Riina & López 1393, WIS). **G**, bisexual cymules along the inflorescence axis of *Croton lechleri* (*C. sect. Cyclostigma*) from eastern Peru, showing open pistillate flowers with bifid styles and no petals, and staminate flowers still in bud (Riina & Ruiz 1490, WIS). **H**, pistillate flowers of *Croton sphaerogynus* (*C. sect. Cleodora*), showing quincuncial sepal aestivation and basal styler column (Sant’Ana & al. 1122, CEPEC). **I**, bisexual inflorescence cymules of *Croton eichleri* (*C. sect. Prisci*), showing smaller staminate flowers in bud and larger pistillate flowers opening, with reduplicate-valvate sepals (Riina & Caruzo 1525, SP). All photos by the authors.



9. *Croton* sect. *Corylocroton* G.L. Webster in Taxon 42: 806. 1993 – Type: *C. corylifolius* Lam.

Description. – Monoecious shrubs or trees to 15 m tall; indumentum stellate to stellate-lepidote; leaves with 2 glands at base, glands usually stipitate, on adaxial side of petiole; margins serrate to coarsely dentate, with or without glands in the sinuses; venation pinnate, 3-veined at the base; stipules entire; inflorescences terminal; bisexual or staminate, lower cymules bisexual or pistillate; stamens 10–18; sepals of pistillate flowers valvate; petals of pistillate flowers reduced or absent; styles bifid for a total of 6 stigmatic tips.

Distribution and habitat. – Deciduous forests of the Antilles, southern Mexico, and South America, and evergreen cloud forests of Central America, from sea level to 1600 m.

Notes. – In the description of this section Webster (1993) included only four species. Several members were previously placed in *C.* sects. *Adenophylli* and *Cyclostigma* (Webster, 1993; Martínez Gordillo, 1996), but the phylogenetic results of Van Ee & al. (2008) and Riina & al. (2009) confirm their placement here. Webster (2001) assigned the closely related *C. mcvaughii* G.L. Webster and *C. repens* Schldl. to *C.* sect. *Corylocroton*, based in part on their coarsely dentate leaves, but they have since been shown to belong in *C.* sect. *Geiseleria* (Van Ee, 2006). The species of this section require a taxonomic revision, given that some names, such as *C. lundellii* Standl. and *C. beetlei* Croizat, may represent more than one taxon.

Included species (11). – *C. beetlei* Croizat, *C. caracasana* Pittier, *C. corylifolius* Lam., *C. grewiaefolius* Müll. Arg., *C. lundellii* Standl., *C. mexicanus* Müll. Arg., *C. oerstedianus* Müll. Arg., *C. pagiveteris* Croizat, *C. quercetorum* Croizat, *C. tonduzii* Pax, *C. verapazensis* Donn. Sm.

III. *Croton* subg. *Adenophylli* (Griseb.) Riina, B.W. van Ee & P.E. Berry, *stat. nov.* ≡ *Croton* sect. *Adenophylli* Griseb., Fl. Brit. W.I.: 40. 1859 (*Adenophyllus*) – Type: *C. adenophyllus* Bertero ex Spreng.

This subgenus contains two of the largest sections of the genus. *Croton* sect. *Cyclostigma* consists of large shrubs to large trees, nearly all of which have copious latex. Species of *C.* sect. *Adenophylli* rarely get larger than shrub-size. Both of these sections are otherwise very diverse, and numerous species belonging to them have been erroneously placed elsewhere, and vice versa. We rely here on the more extensive molecular sampling in the revisions of Van Ee (2006) and Riina & al. (2009) to help place species in these two sections.

10. *Croton* sect. *Cyclostigma* Griseb., Fl. Brit. W.I.: 42. 1859 ≡ *Croton* subsect. *Cyclostigma* (Griseb.) Müll. Arg. in Linnaea 34: 81. 1865 ≡ *Croton* ser. *Cyclostigma* (Griseb.) Müll. Arg. in Martius, Fl. Bras. 11(2): 91. 1873 – Type: *C. gossypifolius* Vahl.

= *Cyclostigma* Klotzsch in Seemann, Bot. Voy. Herald: 104. 1853, nom. illeg. non *Cyclostigma* Hochst. ex Endl. (1842) – Type: *Cyclostigma panamense* Klotzsch, lectotype designated by Wheeler in Taxon 24: 535. 1975 ≡ *Croton panamensis* (Klotzsch) Müll. Arg. = *C. draco* Schldl. & Cham.

Description. – Monoecious trees or large shrubs; indumentum stellate; yellow, orange, or more usually red latex present; leaves with 2 or more glands at base, glands sessile or stipitate, on abaxial or adaxial side of petiole; lamina entire or lobed, margins entire, serrate, or dentate; venation palmate or triplicated; stipules conspicuous, entire or dissected, filiform, foliose, auriculate, or subulate; inflorescences terminal, bisexual, lower cymules bisexual or rarely just staminate; stamens 16–100(–350); sepals of pistillate flowers valvate, reduplicate-valvate, rarely imbricate; petals of pistillate flowers reduced to a glandular filament or absent; styles bifid to multifid for a total of 6–24+ stigmatic tips per flower.

Distribution and habitat. – Secondary vegetation, roadsides, river banks, and landslide areas of dry to wet forests from central Mexico and Central America to tropical and subtropical South America, from sea level to 3000 m.

Notes. – We concur with Webster (1993) that Griseb's (1859: 37–42) *C.* sect. *Cyclostigma* is not based on Klotzsch's (1853) illegitimate genus *Cyclostigma*, and therefore is not typified by it. Therefore, *C. gossypifolius* Vahl, which was the only species mentioned by Griseb (1859: 37–42), is the obligate type of the section. There is great morphological diversity within *C.* sect. *Cyclostigma* in the stipules, petiolar glands (Fig. 6F), stamen number, and style branching (Figs. 6G and 7A–B). In a recent survey of the wood anatomy of *C.* sect. *Cyclostigma* and other sections, Wiedenhoft & al. (2009) found secondary xylem rays containing laticifers only in species of *C.* sect. *Cyclostigma*. These laticifer-containing rays can be regarded as the only known morphological synapomorphy for the section. Laticifers in the pith and bark are common in several sections of *Croton*.

Riina & al. (2009) identified *C.* sect. *Cyclostigma* as a source of incongruence, with ITS placing it sister to *C.* sect. *Adenophylli*, and *trnL-F* placing it embedded within *C.* subg. *Geiseleria* sister to *C. cupreatus* Croizat (*C.* sect. *Cupreati*), which is also where our analysis of *trnL-F* places it (Fig. 4). The analysis of *EMB2765* exon 9 recovers *C.* sects. *Adenophylli* and *Cyclostigma* as a strongly supported clade (Fig. 3), while the analysis of *rps3* does not resolve the position of *C.* sect. *Cyclostigma*, but neither does it place it with *C. cupreatus* (Fig. 5). It is not surprising to find cases of incongruence between gene trees such as this in a large group such as *Croton*, in which there have probably been multiple events of reticulation and incomplete lineage sorting. Possible cases of hybridization events deep in the phylogeny have been identified and discussed in previous studies (Van Ee & al., 2008; Riina & al., 2009).

Included species (41). – *C. alchorneicarpus* Croizat, *C. anisodontus* Müll. Arg., *C. aristophlebius* Croizat, *C. boavitanus* Croizat, *C. caldensis* Müll. Arg., *C. celtidifolius* Baill., *C. charaguensis* Standl., *C. churutensis* Riina & X. Cornejo, *C. coriaceus* Kunth, *C. draco* Schldl. & Cham., *C. echinocarpus* Baill., *C. erythrochilus* Müll. Arg., *C. erythrochloides* Croizat, *C. fastuosus* Müll. Arg., *C. floccosus* B.A. Sm., *C. gossypifolius* Vahl, *C. hibiscifolius* Kunth ex Spreng., *C. huberi* Steyerem., *C. jimenezii* Standl. & Valerio, *C. lagoensis* Müll. Arg., *C. lechleri* Müll. Arg., *C. macrobothrys* Baill.,

C. medusae Müll. Arg., *C. mutisianus* Kunth, *C. perspeciosus* Croizat, *C. pilulifer* Rusby, *C. plagiograptus* Müll. Arg., *C. pseudopopulus* Baill., *C. purdiei* Müll. Arg., *C. quadrisetosus* Lam., *C. redolens* Pittier, *C. rimbachii* Croizat, *C. rusbyi* Britton ex Rusby, *C. sibundoyensis* Croizat, *C. speciosus* Müll. Arg., *C. turumiquirensis* Steyererm., *C. tyndaridum* Croizat, *C. urucurana* Baill., *C. vulnerarius* Baill. Placed here with some uncertainty: *C. buchii* Urb., *C. lindmanii* Urb.

11. *Croton* sect. *Adenophylli* Griseb., Fl. Brit. W.I.: 40. 1859 ('*Adenophyllus*') – Type: *C. adenophyllus* Bertero ex Spreng.

= *Semilta* Raf., Sylva Tellur.: 63. 1838 – Type: *S. althaeifolia* (Mill.) Raf. = *C. flavens* L.

= *Croton* sect. *Velamea* Baill. in *Adansonia* 4: 316. 1864 – Type: *C. campestris* A. St.-Hil., lectotype designated by Webster in *Taxon* 42: 808. 1993.

= *Croton* subsect. *Xalapenses* G.L. Webster in *Contr. Univ. Michigan Herb.* 23: 356. 2001 – Type: *C. xalapensis* Kunth.

Description. – Monoecious (rarely dioecious) shrubs or subshrubs, rarely small trees; indumentum stellate, rarely lepidote; leaves with or without glands at the base; margins entire, serrate, or dentate, occasionally glandular; venation palmate, triplinerved, or pinnate; stipules lobed, dissected, glandular, or entire; inflorescences terminal, bisexual, lower cymules unisexual; stamens 10–45; sepals of pistillate flowers valvate, sometimes glandular; petals of pistillate flowers reduced or absent; columella tipped with three smooth, ascending, inflated apical lobes; styles bifid or twice bifid for a total of 6 or 12 stigmatic tips.

Distribution and habitat. – In a wide variety of habitats, many of them semiarid and often in secondary vegetation, in the southern United States, Mexico, Central America, the West Indies, and all countries of South America, from sea level to 3000 m.

Notes. – As defined here, *Croton* sect. *Adenophylli* is the largest and most ubiquitous New World section of *Croton*. It includes *C.* sect. *Velamea* Baill., *C.* (sect. *Cyclostigma*) subsect. *Xalapenses* G.L. Webster, and Webster's (1993) concept of *C.* sect. *Cascarilla* Griseb. The recognition of *Croton cascarilla* (L.) L. as a synonym of *C. eluteria* (L.) W. Wright (Van Ee & Berry, 2010b), requires a change of name relative to that used by Webster (1993). The species of *C.* sect. *Adenophylli*, as circumscribed more narrowly by Webster (1993), have twice bifid styles and glandular leaves, stipules, and sepals, and are embedded as a monophyletic subclade of *C.* sect. *Adenophylli*. The inflated distal columella lobes identified as a synapomorphy for the section by Riina & al. (2009), combined with their typically sessile to subsessile pistillate flowers and unisexual cymules, serve to identify members of this section.

Croton sect. *Adenophylli* is by far the largest of the New World sections and will require considerable work to resolve synonymies among the many published names. The list below is our current best estimate of accepted species, although we expect to find some of them to be conspecific, and also some additional new species to be found and described.

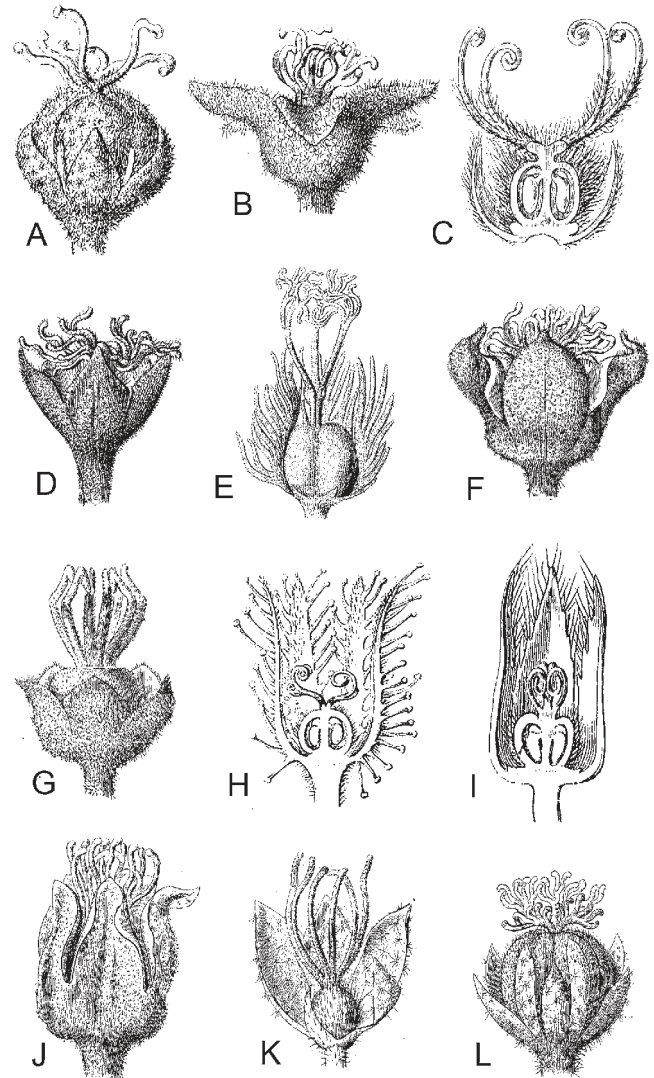


Fig. 7. Pistillate flower diversity of *Croton* in the New World. **A**, *Croton urucurana* (*C.* sect. *Cyclostigma*) with valvate sepals, reduced filamentous petals, bifid styles, and stellate trichomes; **B**, *Croton caldensis* (*C.* sect. *Cyclostigma*) with valvate sepals that are joined at the base, multifid styles, and stellate trichomes; **C**, *Croton grandivelus* (treated as *C. pohlianus* Müll. Arg. in Müller, 1873) (*C.* sect. *Adenophylli*) with valvate sepals and bifid styles; **D**, *Croton palanostigma* (*C.* sect. *Luntia*) with valvate sepals, multifid styles, and lepidote trichomes; **E**, *Croton stipularis* (*C.* sect. *Julocroton*) with lacinate and unequal sepals, the two inner sepals (facing towards the axis of the inflorescence) are much reduced compared to the three outer sepals, and multifid styles; **F**, *Croton floribundus* (*C.* sect. *Lasiogyne*) with reduplicate-valvate sepals, multifid styles, and lepidote trichomes; **G**, *Croton sphaerogynus* (*C.* sect. *Cleodora*) with quincuncial sepals that are joined less than half their length; **H**, *Croton chaetocalyx* (*C.* sect. *Barhamia* subsect. *Barhamia*) with valvate, glandular sepals; **I**, *Croton timandroides* (*C.* sect. *Barhamia* subsect. *Medea*) with lacinate sepals and multifid styles; **J**, *Croton sellowii* (*C.* sect. *Barhamia* subsect. *Sellowiorum*) with reduplicate-valvate sepals and multifid styles; **K**, *Croton bidentatus* (*C.* sect. *Geiseleria*) with unequal sepals, bifid styles, and stellate trichomes; **L**, *Croton sincorensis* (*C.* sect. *Geiseleria*) with unequal sepals, multifid styles, and stellate trichomes. Illustrations reproduced from *Flora Brasiliensis* (Müller, 1873), not to scale.

Included species (223). – *C. abeggii* Urb. & Ekman, *C. abutilifolius* Croizat, ***C. abutiloides*** Kunth, *C. acunae* Borhidi, ***C. adenophyllus*** Bertero ex Spreng., *C. adipatus* Kunth, ***C. adpersus*** Benth., ***C. aequatoris*** Croizat, *C. agrarius* Baill., *C. agrophilus* Müll. Arg., *C. albellus* Müll. Arg., *C. alloephyllus* Urb., *C. alnifolius* Lam., *C. alnoideus* Baill., *C. amphileucus* Briq., *C. angustifolius* Ham., *C. apicifolius* Croizat, *C. araripensis* Croizat, *C. artibonitensis* Urb., *C. azuensis* Urb., *C. balsameus* Müll. Arg., ***C. balsensis*** V.W. Steinmann & M.J. Martínez Gordillo, *C. bangii* Rusby, *C. barahonensis* Urb., *C. barbatus* Kunth, *C. betaceus* Baill., *C. boliviensis* Müll. Arg., ***C. bonplandianus*** Baill., *C. borhidii* O. Muñiz, *C. brachytrichus* Urb., *C. bryophorus* Croizat, ***C. caboensis*** Croizat, *C. campestris* A. St.-Hil., *C. cardenasii* Standl., *C. catharinensis* L.B. Sm. & Downs, *C. chamanus* Steyererm., ***C. chilensis*** Müll. Arg., ***C. chimboracensis*** P.E. Berry & Riina, *C. chrysocladus* Müll. Arg., *C. churumayensis* Croizat, ***C. ciliatoglandulifer*** Ortega, *C. cinerascens* Radcl.-Sm. & Govaerts, *C. clavuliger* Müll. Arg., *C. comayaguanus* Standl. & L.O. Williams, ***C. conduplicatus*** Kunth, *C. corallicola* Borhidi, *C. cordobensis* Ahumada, ***C. cortesianus*** Kunth, *C. corumbensis* S. Moore, ***C. craspedotrichus*** Griseb., ***C. curiosus*** Croizat, *C. curuguatyensis* Ahumada, *C. curvipes* Urb., *C. cycloideus* Borhidi & O. Muñiz, ***C. discolor*** Willd., ***C. disjunctus*** V.W. Steinmann, *C. doctoris* S. Moore, ***C. echioideus*** Baill., *C. eggersii* Pax, ***C. ehrenbergii*** Schldtl., ***C. empriorum*** Croizat, *C. excisus* Urb., *C. ferruginellus* Müll. Arg., *C. ferrugineus* Kunth, ***C. flavens*** L., *C. flavescens* Greenm., *C. flaviglandulosus* Lundell, *C. fragilis* Kunth, ***C. francoanus*** Müll. Arg., *C. fraseri* Müll. Arg., *C. frieseanus* Müll. Arg., ***C. fruticulosus*** Torr., *C. fulvus* Mart., *C. glyptospermus* Müll. Arg., ***C. gracilipes*** Baill., *C. grandivelum* Baill., *C. guillemianum* Baill., *C. heliotropifolius* Kunth, ***C. heterochrous*** Müll. Arg., *C. heteroneurus* Müll. Arg., *C. hieronymi* Griseb., *C. hilarii* Baill., *C. holguinensis* Borhidi, *C. holtonii* Müll. Arg., *C. horridulus* (Baill.) Müll. Arg., *C. huajuapansensis* M.J. Martínez Gordillo & Cruz Durán, ***C. humilis*** L., ***C. hypoleucus*** Schldtl., ***C. impressus*** Urb., *C. incanus* Kunth, *C. incertus* Müll. Arg., *C. intercedens* Müll. Arg., *C. jacmelianus* Urb., *C. jamesonii* Müll. Arg., *C. japiensis* Müll. Arg., *C. jucundus* Brandegees, *C. kalkmannii* Müll. Arg., *C. kleinii* L.B. Sm. & Downs, ***C. laceratoglandulosus*** Caruzo & Cordeiro, *C. lachnocladus* Mart. ex Müll. Arg., *C. lachnostachyus* Baill., *C. laeticapsulus* Croizat, ***C. lanatus*** Lam., *C. lapanus* Müll. Arg., ***C. lasiopetaloides*** Croizat, *C. lehmannii* Pax, ***C. leptostachyus*** Kunth, *C. leucophlebius* C. Wright ex Griseb., ***C. limnocharis*** Croizat, ***C. linearis*** Jacq., *C. longifolius* Müll. Arg., ***C. lucidus*** L., ***C. magdalenae*** Millsp., ***C. mazapensis*** Lundell, *C. medians* Müll. Arg., *C. megaladenus* Urb., ***C. menthodorus*** Benth., *C. meridenensis* Croizat, ***C. michaelii*** V.W. Steinmann, *C. micradenus* Urb., *C. miradorensis* Müll. Arg., *C. miraflorensis* Borhidi, *C. missionum* Croizat, *C. mollis* Benth., *C. monogynus* Urb., ***C. morifolius*** Willd., *C. munizii* Borhidi, ***C. nephrophyllus*** Urb. & Ekman, *C. nitidulifolius* Croizat, *C. nudulus* Croizat, *C. olanchanus* Standl. & L.O. Williams, *C. ophiticola* Borhidi, *C. orbignyanus* Müll. Arg., *C. orientesensis* Borhidi,

C. organifolius Lam., *C. pachyrachis* Alain, *C. pallidus* Müll. Arg., *C. panduriformis* Müll. Arg., *C. paraensis* Müll. Arg., *C. patrum* L.B. Sm. & Downs, *C. pavonis* Müll. Arg., ***C. payaquensis*** Standl., *C. pedersenii* Ahumada, *C. pellitus* Kunth, *C. peltophorus* Müll. Arg., ***C. peraeruginosus*** Croizat, *C. peraffinis* Müll. Arg., *C. perlongiflorus* Croizat, *C. persicaria* Baill., *C. peruvianus* Briq., *C. pervestitus* C. Wright ex Griseb., *C. petraeus* Müll. Arg., *C. piauihensis* Müll. Arg., *C. poitaei* Urb., *C. polygonoides* L.B. Sm. & Downs, *C. polytomus* Urb., *C. priorianus* Urb., *C. prostratus* Urb., ***C. pulcher*** Müll. Arg., ***C. pungens*** Jacq., *C. pycnanthus* Benth., *C. rehderianus* Croizat, *C. reitzii* L.B. Sm. & Downs, *C. rhamnifolioides* Pax & K. Hoffm., *C. rivinifolius* Kunth, *C. rosarianus* M.J. Martínez Gordillo & Cruz Durán, ***C. roxanae*** Croizat, ***C. ruizianus*** Müll. Arg., *C. sagraeanus* Müll. Arg., ***C. saltensis*** Griseb., *C. sanctae-crucis* S. Moore, ***C. sancti-lazari*** Croizat, *C. sapiiflorus* Croizat, *C. scouleri* Hook.f., *C. seminudus* Müll. Arg., *C. semivestitus* Müll. Arg., *C. shreveanus* Croizat, ***C. soliman*** Cham. & Schldtl., ***C. sonorae*** Torr., ***C. soratensis*** Müll. Arg., ***C. sphaerocarpus*** Kunth, *C. spurcus* Croizat, *C. stenopetalus* G.L. Webster, *C. stenophyllus* Griseb., *C. stenosepalus* Müll. Arg., *C. stenotrichus* Müll. Arg., ***C. stipulaceus*** Kunth, ***C. suaveolens*** Torr., *C. suavis* Kunth, *C. subacutus* (Baill.) Müll. Arg., *C. subcomosus* Müll. Arg., *C. subdecumbens* Borhidi & O. Muñiz, ***C. suberosus*** Kunth, *C. subferrugineus* Müll. Arg., *C. subfragilis* Müll. Arg., *C. subjucundus* Croizat, *C. subsuavis* Croizat, *C. subvillosus* Müll. Arg., ***C. suyapensis*** Ant. Molina, *C. tarapotensis* Müll. Arg., *C. tejucensis* Müll. Arg., *C. tenuifolius* Pax & K. Hoffm., *C. thurifer* Kunth, *C. timotensis* Pittier, *C. tremulifolius* Croizat, *C. turnerifolius* S. Moore, *C. vacinioides* A. Rich., *C. vaillantii* Geiseler, *C. vauthierianus* Baill., *C. velame* Müll. Arg., *C. vepretorum* Müll. Arg., *C. versicolor* Müll. Arg., *C. viminalis* Griseb., ***C. virletianus*** Müll. Arg., ***C. vitifolius*** Lundell, *C. wagneri* Müll. Arg., ***C. websteri*** M.J. Martínez Gordillo & J. Jiménez Ram., ***C. xalapensis*** Kunth, *C. xanthochylus* Croizat, ***C. yecorensis*** V.W. Steinmann & Felger, ***C. ynesae*** Croizat, *C. ypanemensis* Müll. Arg., *C. yungensis* Croizat.

IV. *Croton* subg. ***Geiseleria*** A. Gray, Manual, ed. 2: 391. 1856 – Type: *C. glandulosus* L.

Croton subg. *Geiseleria* is the only subgenus in which annual species are found. Although the annual habit is clearly derived within *Croton*, Van Ee & Berry (2010a) documented a reversal from annual to perennial in *C. sect. Heptallon*.

12. *Croton* sect. ***Cupreati*** Riina, **sect. nov.** – Arbores lepidota foliis basi biglandulosis, glandulis stipitatis, recurvatis; stipulis foliaceis dentatis; racemis terminalibus; staminibus 10 ad 12; sepalis pistillatis integris, valvatis; stylis bifidis. – Type: *C. cupreatus* Croizat.

Description. – Monoecious trees to 20 m tall; indumentum minutely lepidote; leaves with 2 elongate, recurved glands at the base; margins entire to serrate, sometimes with sessile ovoid glands in the sinuses towards the base of the leaf; venation palmate or pinnate; stipules foliaceous, dentate; inflorescences

terminal, bisexual; lower cymules bisexual; stamens 10–12; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips.

Distribution and habitat. – Andean cloud forests of northern Ecuador and southeastern Colombia, from 1800 to 2200 m.

Notes. – This monotypic section has unusual stipitate petiolar glands that arise from an expanded rounded base on the adaxial side of the petiole, and then curve down towards the abaxial side ending in a clavate head (Fig. 6E).

Included species (1). – *C. cupreatus* Croizat.

13. *Croton* sect. *Eremocarpus* (Benth.) G.L. Webster in Novon 2: 270. 1992 ≡ *Eremocarpus* Benth., Bot. Voy. Sulphur: 53. 1844 ≡ *Piscaria* Piper in Contr. U.S. Natl. Herb. 11: 382. 1906, nom. illeg. & superfl. ≡ *Croton* subg. *Eremocarpus* (Benth.) Radcl.-Sm. & Govaerts in Kew Bull. 52: 184. 1997 – Type: *Eremocarpus setigerus* (Hook.) Benth. ≡ *C. setiger* Hook.

Description. – Monoecious annual prostrate herbs; indumentum bristly-stellate; leaves without glands at the base; margins entire; venation palmate; stipules absent; inflorescences pseudoterminal at dichotomies of the stems, bisexual, lower cymules unisexual (but inflorescences very congested); staminate flowers apetalous, stamens 5–10; sepals of pistillate flowers absent; petals of pistillate flowers absent; ovary 1-locular, style simple with 1 stigmatic tip.

Distribution and habitat. – Roadsides, fencerows, vineyards, and disturbed areas in western Mexico and U.S.A., naturalized elsewhere, as in Chile, South Africa, and Australia, from 50 to 1800 m.

Notes. – This monotypic section stands apart both morphologically and molecularly, with no close relatives identified by either method. The reduction of the pistillate flower to a single carpel (Fig. 6A) has occurred independently in *C. sect. Crotonopsis* and in at least one Old World species (*C. miarensis* Leandri). Berry & al. (2005) identified *Croton setiger* and *C. insularis* Baill., an Old World species, as sources of incongruence between ITS and *trnL-F*, although this was primarily restricted to their maximum parsimony analyses. In the combined analyses (Fig. 1), we recover *C. setiger* in the same position as Berry & al. (2005) did in their combined Bayesian analysis, and none of the separate analyses place it anywhere else with any support.

Included species (1). – *C. setiger* Hook.

14. *Croton* sect. *Cuneati* (G.L. Webster) Riina & P.E. Berry in Taxon 59: 1153. 2010 ≡ *Croton* (sect. *Luntia* (Neck. ex Raf.) G.L. Webster) subsect. *Cuneati* G.L. Webster in Taxon 42: 804. 1993 – Type: *C. cuneatus* Klotzsch.

Description. – Monoecious trees to 20 m tall; indumentum lepidote, stellate-lepidote, and stellate; leaves with 2 glands at the base; margins 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; venation pinnate; stipules entire; inflorescences terminal, often clustered, unisexual or bisexual; lower cymules unisexual or bisexual; stamens 10–20; sepals of pistillate flowers valvate;

petals of pistillate flowers absent; styles bifid or twice bifid for a total of 6–12 stigmatic tips; seeds with a reduced or absent caruncle, or with the caruncle modified into an arillate structure.

Distribution and habitat. – This entirely South American section, including the adjacent Caribbean island of Trinidad, consists of rainforest trees found from seasonally flooded riparian Amazonian lowland forests on the slopes of tepuis in the Guayana Shield and the Venezuelan Coastal Range, from 100 to 2500 m.

Notes. – *Croton* sect. *Cuneati* is most diverse in northern South America, with one species, *C. cuneatus*, being widespread throughout the Amazon and Orinoco river basins of South America. The section includes *C. ariposensis* Philcox and *C. domatifer* Riina & P.E. Berry, the only known species of *Croton* with domatia on the leaves. *Croton* sect. *Cuneati* is distinctive in having some lowland riverine species that have seeds with caruncles modified into arils, which was hypothesized by Riina & al. (2010b) as an adaptation for dispersal by fish. Riina & al. (2010b) provide a phylogeny and detailed synonymy for the section.

Included species (11). – *C. ariposensis* Philcox, *C. cuneatus* Klotzsch, *C. domatifer* Riina & P.E. Berry, *C. icabarui* Jabl., *C. malambo* H. Karst., *C. neblinae* Jabl., *C. roraimensis* Croizat, *C. tessmannii* Mansf., *C. yavitensis* Croizat. Placed here with some uncertainty: *C. polypleurus* Croizat, *C. subasperrimus* Secco, P.E. Berry & Rosário.

15. *Croton* sect. *Eluteria* Griseb., Fl. Brit. W.I.: 39. 1859 ≡ *Croton* subg. *Eluteria* (Griseb.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 38. 1890 – Type: *Croton eluteria* (L.) W. Wright ≡ *Chutia eluteria* L.

= *Cascarilla* Adans., Fam. Pl. 2: 355. 1763 ≡ *Croton* sect. *Cascarilla* (Adans.) Griseb., Fl. Brit. W.I.: 38: 1859 – Type: *Croton cascarilla* (L.) L. ≡ *Chutia cascarilla* L. = *Croton eluteria* (L.) W. Wright.

Description. – Monoecious trees and shrubs; indumentum lepidote to stellate; leaves without glands at the base; margins entire to serrate; venation pinnate or palmate; stipules rudimentary or absent; inflorescences axillary and terminal, bisexual, lower cymules unisexual; stamens 10–16; sepals of pistillate flowers valvate; petals of pistillate flowers well-developed to reduced; styles multifid for a total of more than 12 stigmatic tips.

Notes. – Several species of *Croton* sect. *Eluteria* have been described recently (Martínez Gordillo & Cruz Durán, 2002; Webster, 2005; León Enríquez & Vester, 2006; León Enríquez & Martínez Gordillo, 2008; Van Ee & Berry, 2009a), but the biggest change since Webster (1993) is the return to Grisebach's (1859: 37–42) concept of the group suggested by the molecular results of Van Ee & Berry (2009a). Here we describe the three clades of *C. sect. Eluteria* as subsections, and although they appear superficially to be quite distinct, they share axillary inflorescences, lepidote trichomes, a lack of glands on the leaves, and multifid styles (Fig. 6C). All species of *C. subsect. Eluteria* are lepidote, and one of the three species in each of the other two subsections is lepidote while the others are stellate. Both *C. subsects. Cubenses* and *Jamaicenses* have members that are multiple-stemmed shrubs.

Key to the subsections of *Croton* sect. *Eluteria*

1. Petals of pistillate flowers well developed; stipular spines absent; indumentum lepidote; widespread **15a. *C.* subsect. *Eluteria***
1. Petals of pistillate flowers reduced or absent; stipular spines present or absent; indumentum lepidote or stellate; Cuba and Jamaica **2**
2. Spines present or absent, if spines absent then leaves <1 cm long; Cuba **15b. *C.* subsect. *Cubenses***
2. Spines absent, leaves >5 cm long; Jamaica **15c. *C.* subsect. *Jamaicenses***

15a. *Croton* subsect. *Eluteria* (Griseb.) B.W. van Ee & P.E. Berry, **stat. nov.** ≡ *Croton* sect. *Eluteria* Griseb., Fl. Brit. W.I.: 39. 1859 – Type: *C. eluteria* (L.) W. Wright.

Description. – Single-stemmed trees and shrubs; petals of pistillate flowers present, well developed; spines absent; leaf margins entire; indumentum lepidote. (Fig. 6C).

Distribution and habitat. – Widely distributed in the West Indies, and from Mexico to tropical South America. Dry, open vegetation to rainforests, from sea level to 1700 m.

Included species (15). – *C. arboreus* Millsp., *C. carpostellatus* B.L. León & M.J. Martínez Gordillo, *C. eluteria* (L.) W. Wright, *C. fantzianus* F. Seym., *C. gomezii* G.L. Webster, *C. guatemalensis* Lott, *C. icche* Lundell, *C. mayanus* B.L. León & H.F.M. Vester, *C. nitens* Sw., *C. niveus* Jacq., *C. pseudoniveus* Lundell, *C. reflexifolius* Kunth, *C. schiedeanus* Schldl., *C. sousae* M.J. Martínez Gordillo & Cruz Durán, *C. tenuicaudatus* Lundell.

15b. *Croton* subsect. *Cubenses* B.W. van Ee & P.E. Berry, **subsect. nov.** – Frutices spinosi vel non spinosi, lepidoti vel stellati, foliis marginibus integris vel serratis; petalis pistillatis nullis vel deminutis. – Type: *C. bispinosus* C. Wright.

Description. – Single or multiple-stemmed shrubs; petals of pistillate flowers reduced or absent; spines present or absent; leaf margins entire or serrate; indumentum lepidote to stellate.

Distribution and habitat. – Endemic to Cuba. Dry, scrubby vegetation from sea level to 500 m.

Notes. – Given its small, lepidote leaves, *C. myricifolius* was placed by Webster (1993) in *C.* sect. *Lamprocroton*, but using molecular data Van Ee & Berry (2009a) placed it in a highly supported clade with two spinose Cuban species with which it shares axillary inflorescences.

Included species (4). – *C. bispinosus* C. Wright, *C. brittonianus* Carabia, *C. jaucoensis* Borhidi, *C. myricifolius* Griseb.

15c. *Croton* subsect. *Jamaicenses* B.W. van Ee & P.E. Berry, **subsect. nov.** – Frutices lepidoti vel stellatis, non spinosi, foliis marginibus integris vel serratis; petalis pistillatis nullis vel deminutis. – Type: *C. jamaicensis* B.W. van Ee & P.E. Berry.

Description. – Multiple-stemmed shrubs and small single-stemmed trees; petals of pistillate flowers reduced or absent; spines absent; leaf margins entire or serrate; indumentum lepidote to stellate.

Distribution and habitat. – Endemic to Jamaica. Dry, scrubby vegetation on limestone and moister upland areas, from sea level to 700 m.

Notes. – *Croton laurinus* is a small tree, while *C. grisebachianus* and *C. jamaicensis* are multiple-stemmed shrubs from drier and lower elevations of the southern part of Jamaica. *Croton laurinus* was placed by Grisebach (1859: 37–42) in *C.* sect. *Eluteria*, and its exclusion from the section by Müller (1865) had been followed until molecular data confirmed its relationship with the more traditional, lepidote-leaved species of *C.* subsect. *Eluteria* (Van Ee & Berry, 2009a).

Included species (3). – *C. grisebachianus* Müll. Arg., *C. jamaicensis* B.W. van Ee & P.E. Berry, *C. laurinus* Sw.

16. *Croton* sect. *Crotonopsis* (Michx.) G.L. Webster in Novon 2: 270. 1992 ≡ *Crotonopsis* Michx., Fl. Bor.-Amer. 2: 185. 1803 ≡ *Leptemon* Raf. in Med. Repos. 5: 353. 1808, nom. superfl. & illeg. ≡ *Friesia* Spreng., Anleit. Kenntn. Gew. 2(2): 885. 1818, nom. superfl. & illeg. ≡ *Croton* subg. *Crotonopsis* (Michx.) Radcl.-Sm. & Govaerts in Kew Bull. 52: 183. 1997 – Type: *Crotonopsis linearis* Michx. ≡ *Croton michauxii* G.L. Webster.

Description. – Monoecious annual erect herbs; indumentum appressed-stellate to stellate-lepidote; leaves without glands at the base; margins entire; venation pinnate; stipules lacking; inflorescences terminal and axillary, bisexual, lower cymules unisexual; stamens 5–6; sepals of pistillate flowers with open aestivation; petals of pistillate flowers reduced; ovary 1-locular; styles 3; styles simple to twice bifid for a total of 3–12 stigmatic tips; fruit indehiscent.

Distribution and habitat. – Endemic to the United States along the east and Gulf coasts, and inland along the Mississippi River. Sandy soils, forest openings, and rocky outcrops, from sea level to 300 m.

Notes. – Many workers have recognized two species in *Croton* sect. *Crotonopsis*, but Pursh (1814) and Van Ee & Berry (2009b) joined them as varieties of a single species. The unilocular ovaries of *Croton* sect. *Crotonopsis* have what appear to be three multifid styles, and its fruits are indehiscent.

Included species (1). – *C. michauxii* G.L. Webster, with two varieties: *C. michauxii* var. *michauxii* and *C. michauxii* var. *elliptica* (Willd.) B.W. van Ee & P.E. Berry.

17. *Croton* sect. *Argyranthemis* B.W. van Ee, **sect. nov.** – Herbae annuae vel perennes interdum robusta, stellata vel lepidota, foliis eglandulosis, integris; racemis terminalibus; staminibus 10 ad 16, petalis staminatis valde lepidotis; stylis bis- vel terbifidis. – Type: *C. argyranthemus* Michx.

Description. – Monoecious erect herbs or subshrubs, annual or perennial; indumentum lepidote or stellate and lepidote; leaves without glands at the base; margins entire; stipules entire or lacking; inflorescences terminal, bisexual, lower cymules unisexual; stamens 10–16; petals of staminate flowers densely covered with lepidote scales on the abaxial side; sepals of pistillate flowers equal or unequal, valvate; petals of pistillate flowers absent; styles twice or three times bifid for a total of 12–24 stigmatic tips.

Distribution and habitat. – Sandy soils of the coastal plains of the southern United States and northeastern Mexico, from sea level to 100 m.

Notes. – This section of two known species is endemic to North America. *Croton argyranthemus* was previously placed in the Old World *C. sect. Argyrocroton* (Müll. Arg.) G.L. Webster by Webster (1967, 1993), and Croizat (1942) hypothesized that *C. coryi* was related to members of *C. sect. Heptallon*. These two species, although appearing overall very different (*C. argyranthemus* has lepidote foliage, and *C. coryi* has stellate foliage), share the synapomorphy of having a dense covering of lepidote scales on the abaxial side of the petals of their staminate flowers.

Included species (2). – *C. argyranthemus* Michx., *C. coryi* Croizat.

18. *Croton* sect. ***Drepadenium*** (Raf.) Müll. Arg. in *Linnaea* 34: 79. 1865 ≡ *Drepadenium* Raf., *Neogenyton*: 2. 1825 ≡ *Croton* subg. *Drepadenium* (Raf.) Pax in Engler & Prantl, *Nat. Pflanzenfam.* 3(5): 40. 1890 – Type: *Drepadenium maritimum* (Walter) Raf. ≡ *C. maritimus* Walter = *C. punctatus* Jacq.

= *Hendecandra* Eschsch. in *Mém. Acad. Imp. Sci. St. Pétersbourg, Hist. Acad.* 10: 287. 1826 – Type: *Hendecandra procumbens* Eschsch. ≡ *C. californicus* Müll. Arg.

= *Penteca* Raf., *Sylva Tellur.*: 62. 1838 – Type: *Penteca tomentosa* Raf. = *C. dioicus* Cav.

= *Astrogyne* Benth., *Pl. Hartw.*: 14. 1839 – Type: *Astrogyne crotonoides* Benth. = *C. dioicus* Cav.

= *Banalia* Raf., *Autik. Bot.*: 50. 1840 – Type: *B. muricata* Raf. = *C. texensis* (Klotzsch) Müll. Arg.

Description. – Monoecious or dioecious shrubs, subshrubs, and herbs; indumentum appressed-stellate to stellate-lepidote; leaves without glands at the base; margins entire; venation pinnate to slightly 3-veined at the base; stipules reduced or lacking; inflorescences terminal, unisexual or rarely bisexual, lower cymules unisexual; stamens 8–12; petals of staminate flowers absent; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles multifid for a total of 24 or more stigmatic tips; columella stout, winged, readily breaking off from the receptacle.

Distribution and habitat. – *Croton* sect. *Drepadenium* is a primarily North American group which would be endemic to Mexico and the United States except for the widespread, sand dune species *C. punctatus*, which extends along the Atlantic coast to northern South America. Deserts, prairies, sand dunes, limestone and igneous mountains, open, disturbed vegetation, from sea level to 2000 m.

Notes. – The lack of petals in the staminate flowers is a synapomorphy for *C. sect. Drepadenium*. Species of *C. sect. Drepadenium* are dioecious, with the exception of *C. punctatus*, although most collections of this species are unisexual.

Included species (6). – *C. californicus* Müll. Arg., *C. dioicus* Cav., *C. parksii* Croizat, *C. punctatus* Jacq., *C. texensis* (Klotzsch) Müll. Arg., *C. wigginsii* L.C. Wheeler.

19. *Croton* sect. ***Prisci*** Riina, **sect. nov.** – Arbores fruticesve stellati, foliis basi biglandulosis, marginibus glanduloso-dentatis; racemis terminalibus, cymulis inferioribus bisexualibus; staminibus 15 ad 18; sepalis pistillatis reduplicatis vel imbricatis; stylis bisbifidis. – Type: *C. priscus* Croizat.

Description. – Monoecious trees 2–7 m tall; indumentum stellate-appressed or stellate-rosulate; leaves with 2–4 glands at the base; margins crenate-dentate, with sessile glands at the apex of the teeth; venation pinnate; stipules linear, entire or divided; inflorescences terminal, bisexual, lower cymules bisexual; stamens 15–18; sepals of pistillate flowers reduplicate, reduplicate-valvate, or slightly imbricate; petals of pistillate flowers absent; styles quadrifid for a total of 12 stigmatic tips.

Distribution and habitat. – Occurring in moist forests of the Brazilian states of São Paulo, Rio de Janeiro, and Bahia, from 100 to 800 m.

Notes. – *Croton priscus* was placed by Webster (1993) in *C. sect. Cyclostigma*, however molecular and morphological evidence indicate that this species forms a separate monophyletic group with *C. eichleri* and *C. thomasi* (Riina & al., 2009; 2010a).

Included species (3). – *C. eichleri* Müll. Arg., *C. priscus* Croizat, *C. thomasi* Riina & P.E. Berry.

20. *Croton* sect. ***Pedicellati*** B.W. van Ee & P.E. Berry in *Syst. Bot.* 36: 93. 2011 – Type: *C. pedicellatus* Kunth.

Description. – Monoecious subshrubs 0.5–1.0 m tall; indumentum stellate to stellate-lepidote; leaves without glands at the base; margins entire; venation pinnate to slightly 3-veined at the base; stipules entire, inconspicuous; inflorescences terminal, bisexual or staminate, lower cymules unisexual; stamens 6–12; pedicels of pistillate flowers often recurved; sepals of pistillate flowers with open aestivation; petals of pistillate flowers absent; styles bifid for a total of 6 stigmatic tips, columella with a prominent tip.

Distribution and habitat. – *Croton* sect. *Pedicellati* is distributed disjunctly between Mexico and South America, with its greatest diversity in eastern Brazil. It is found in scrubby tropical deciduous forests in Mexico and Brazil, as well as in dry inter-Andean valleys in Colombia, Peru, and Bolivia, from 200 to 2500 m.

Notes. – A preliminary list of species included in *C. sect. Pedicellati* was prepared by Van Ee & Berry (2011), although many of these are very similar and several may prove to be synonymous. The molecular phylogeny of Van Ee & Berry (2011) indicates that molecular data may be able to resolve species boundaries.

Included species (20). – *C. acradenius* Pax & K. Hoffm., *C. andinus* Müll. Arg., *C. angustifrons* Müll. Arg., *C. breedlovei* B.W. van Ee & P.E. Berry, *C. burchellii* Müll. Arg., *C. catinganus* Müll. Arg., *C. cerinodentatus* Müll. Arg., *C. corchoropsis* Baill., *C. cuyabensis* Pilg., *C. dracunculoides* Baill., *C. eriocladoides* Müll. Arg., *C. eriocladus* Müll. Arg., *C. horminum* Baill., *C. linearifolius* Müll. Arg., *C. longicolumellus* B.W. van Ee & P.E. Berry, *C. pachecensis* S. Moore, *C. pedicellatus* Kunth, *C. tenuicaulis* B.W. van Ee & P.E. Berry, *C. tenuilobus* S. Watson, *C. tridentatus* Mart. ex Müll. Arg.

21. *Croton* sect. **Lamprocroton** (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 ≡ *Croton* ser. *Lamprocroton* Müll. Arg. in Martius, Fl. Bras. 11(2): 244. 1873 – Type: *C. ceanothifolius* Baill., lectotype designated by Webster in Taxon 42: 815. 1993.

Description. – Monoecious or dioecious shrubs or subshrubs 0.2–3.0 m tall; indumentum stellate, stellate-lepidote, or lepidote; leaves without glands at the base; margins entire; venation pinnate; stipules entire, inconspicuous or absent; inflorescences terminal, bisexual or unisexual, lower cymules unisexual; stamens 9–16; sepals of pistillate flowers equal or unequal, imbricate, valvate, or reduplicate-valvate; petals of pistillate flowers reduced or absent; styles bifid or twice bifid for a total of 6–12 stigmatic tips.

Notes. – Müller (1873) included species with both bifid and twice bifid styles in this group, while Webster (1993) recircumscribed the section to include only those with bifid styles. Lima & Pirani (2008) returned to Müller's (1873) circumscription of the group by including species with both bifid and multifid styles. This broader concept of the section was supported by the molecular phylogenetic analysis of Van Ee & Berry (2011), in which the bifid-styled species were recovered as a clade sister to the multifid-styled species. This led them to recognize each clade as a subsection of *C.* sect. *Lamprocroton*.

Key to the subsections of *Croton* sect. *Lamprocroton*

1. Styles bifid, stigmatic tips 6 21a. *C.* **subsect. Lamprocroton**
 1. Styles twice or more bifid, stigmatic tips 12 or more 21b. *C.* **subsect. Argentini**

- 21a. *Croton* subsect. **Lamprocroton** (Müll. Arg.) B.W. van Ee & P.E. Berry in Syst. Bot. 36: 93. 2011 ≡ *Croton* ser. *Lamprocroton* Müll. Arg. in Martius, Fl. Bras. 11(2): 244. 1873 – Type: *C. ceanothifolius* Baill.

Description. – Indumentum primarily lepidote; styles bifid, stigmatic tips 6.

Distribution and habitat. – This South American group is most diverse in Brazil, but extends into adjacent Paraguay, Argentina, Uruguay, and Bolivia. It is found most commonly in open vegetation on sandy or rocky ground, including rock outcrops, from 100 to 2800 m, but some members are also known from riparian and swampy habitats (Lima & Pirani, 2008).

Included species (17). – *C. ceanothifolius* Baill., *C. chloroleucus* Müll. Arg., *C. dichrous* Müll. Arg., *C. dusenii* Croizat, *C. ericoides* Baill., *C. erythroxyloides* Baill., *C. imbricatus* L.R. Lima & Pirani, *C. muellerianus* L.R. Lima, *C. myrianthus* Müll. Arg., *C. pallidulus* Baill., *C. perintricatus* Croizat, *C. pseudoadipatus* Croizat, *C. pygmaeus* L.R. Lima, *C. splendidus* Mart. ex Colla, *C. subcinerellus* Croizat, *C. tenellus* Müll. Arg., *C. uruguayensis* Baill.

- 21b. *Croton* subsect. **Argentini** B.W. van Ee & P.E. Berry in Syst. Bot. 36: 93. 2011 – Type: *C. argentinus* Müll. Arg.

Description. – Indumentum primarily stellate; styles twice or more bifid, stigmatic tips 12 or more.

Distribution and habitat. – *Croton* subsect. *Argentini* is also entirely South American, but its center of diversity appears to be south of Brazil in Uruguay and Argentina.

Included species (20). – *C. argentinus* Müll. Arg., *C. bresolinii* L.B. Sm. & Downs, *C. catamarcensis* Ahumada, *C. chamaepitys* Baill., *C. cinerellus* Müll. Arg., *C. echinulatus* (Griseb.) Croizat, *C. eskucheii* Ahumada, *C. gnaphalii* Baill., *C. isabellei* Baill., *C. julopsidium* Baill., *C. lachnostephanus* Baill., *C. laurelyanus* Ahumada, *C. leptophyllus* Müll. Arg., *C. paraguayensis* Chodat, *C. pycnocephalus* Baill., *C. ramellae* Ahumada, *C. serpyllifolius* Baill., *C. tartonraira* Müll. Arg. Placed here with some uncertainty: *C. santolinus* Baill., *C. tartonrairoides* Pax & K. Hoffm.

22. *Croton* sect. **Luetzelburgiorum** Riina, **sect. nov.** – Frutices stellati foliis marginibus glanduloso-dentatis, racemis terminalibus; staminibus 15; sepalis pistillatis valvatis, glandulosis; stylis multifidis. – Type: *C. luetzelburgii* Pax & K. Hoffm.

Description. – Monoecious shrubs 0.5–2.5 m tall; indumentum stellate; leaves without glands at the base; margins entire to slightly dentate, with shortly stipitate glands on the apex of the teeth; venation pinnate; stipules fimbriate, glandular; inflorescences terminal, bisexual, lower cymules unisexual; stamens 15; sepals of pistillate flowers valvate, glandular; petals of pistillate flowers absent; styles multifid for a total of 12–15 stigmatic tips.

Distribution and habitat. – This monotypic section is restricted to the Chapada Diamantina of Bahia, Brazil, occurring in “campos rupestres” and high-elevation “cerrado”, from 800 to 1800 m.

Included species (1). – *C. luetzelburgii* Pax & K. Hoffm.

23. *Croton* sect. **Cleodora** (Klotzsch) Baill., Étude Euphorb.: 369. 1858 ≡ *Cleodora* Klotzsch in Arch. Naturgesch. 7: 196. 1841 – Type: *Cleodora sellowiana* Klotzsch ≡ *Croton pachycalyx* Müll. Arg. = *C. sphaerogynus* Baill.

= *Croton* sect. *Stolidanthi* Baill. in Adansonia 4: 323. 1864 – Type: *C. heterocalyx* Baill., lectotype designated by Webster in Taxon 42: 800. 1993.

Description. – Monoecious trees and shrubs; indumentum stellate to stellate-lepidote; leaves with 2 glands at the base; margins entire; venation pinnate or palmate; stipules entire; inflorescences terminal, rarely axillary, bisexual; lower cymules bisexual, rarely unisexual, sometimes falsely unisexual; stamens 15–25; sepals of pistillate flowers partly to mostly connate at the base, aestivation imbricate or quincuncial; petals of pistillate flowers absent, rarely reduced; styles twice bifid or multifid for a total of 12 or more stigmatic tips; styles with varying degrees of connation, usually forming 1 or 3 columns at the top of the ovary.

Distribution and habitat. – Species of *Croton* sect. *Cleodora* inhabit moist or seasonally dry forests in tropical South America, Central America, and into central Mexico.

Notes. – Members of *Croton* sect. *Cleodora* share the synapomorphy of having styles that are fused into a column extending beyond the top of the ovary (Figs. 6H and 7G). The section may be able to be divided into two equally sized

groups by distinguishing those whose pistillate flowers have sepals that are mostly free, usually fleshy at the base, and with quincuncial aestivation, from those whose sepals of the pistillate flowers are not fleshy, usually united at least half of their length, and have imbricate aestivation (Caruzo, 2010; Caruzo & al., 2010). *Croton cajucara* is a widespread species in the Amazon basin that has an extensive history of ethnobotanical uses to treat diarrhea and other ailments (Le Cointe, 1934; Salatino & al., 2007).

Included species (18). – *C. billbergianus* Müll. Arg., *C. cajucara* Benth., *C. campanulatus* Caruzo & Cordeiro, *C. fragrans* Kunth, *C. fragrantulus* Croizat, *C. hemiargyreus* Müll. Arg., *C. heterocalyx* Baill., *C. hoffmannii* Müll. Arg., *C. organensis* Baill., *C. orinocensis* Müll. Arg., *C. pseudo-fragrans* Croizat, *C. rottlerifolius* Baill., *C. rufolepidotus* Caruzo & Riina, *C. salutaris* Casar., *C. sexmetralis* Croizat, *C. sphaerogynus* Baill., *C. spruceanus* Benth., *C. stellatoferugineus* Caruzo & Cordeiro.

24. *Croton* sect. *Cordiifolii* Riina, **sect. nov.** – Frutices dioici stellati, foliis basi biglandulosis, stipulis linearibus; racemis axillaribus; staminibus 10 ad 12; sepalis pistillatis valvatis; stylis bifidis; fructibus muricatis. – Type: *C. cordiifolius* Baill.

Description. – Dioecious shrubs 0.5–2.0 m tall; indumentum stellate; leaves with 2 glands at the base; margins entire to serrulate; venation pinnate; stipules entire, linear; inflorescences axillary, unisexual; stamens 10–12; sepals of pistillate flowers valvate; petals of pistillate flowers absent; styles bifid, for a total of 6 stigmatic tips; fruits muricate.

Distribution and habitat. – This monotypic section is restricted to semiarid caatinga vegetation of Bahia, Brazil; it occurs in seasonally semideciduous forests from 300 to 1000 m.

Included species (1). – *C. cordiifolius* Baill.

25. *Croton* sect. *Eutropia* (Klotzsch) Baill., Étude Euphorb.: 357. 1858 ≡ *Eutropia* Klotzsch in Arch. Naturgesch. 7: 196. 1841 ≡ *Croton* subsect. *Eutropia* (Klotzsch) Müll. Arg. in Linnaea 34: 101. 1865 ≡ *Croton* ser. *Eutropia* (Klotzsch) Müll. Arg. in Martius, Fl. Bras. 11(2): 87. 1873 – Type: *C. polyandrus* Spreng. ≡ *Eutropia brasiliensis* Klotzsch, nom. illeg. & superfl.

Description. – Monoecious shrubs or trees; indumentum lepidote to stellate-lepidote, plants nearly glabrous; leaves with 2 glands at the base; margins crenate, revolute; venation pinnate; stipules entire; inflorescences terminal and axillary, bisexual, lower cymules bisexual; stamens 10–15; sepals of pistillate flowers imbricate; petals of pistillate flowers absent or reduced; styles bifid for a total of 6 stigmatic tips.

Distribution and habitat. – Endemic to scrubby vegetation on sandy ‘restinga’ soils of eastern Brazil from sea level to 150 m.

Notes. – The terminal and axillary inflorescences of *C. polyandrus* differ from other species of *Croton* with axillary inflorescences by being elongated, rather than contracted and congested as in *C.* sect. *Eluteria* and *C.* sect. *Lasiogyne* (*C. alamosanus* N.E. Rose and *C. axillaris* Müll. Arg.).

Included species (1). – *C. polyandrus* Spreng.

26. *Croton* sect. *Geiseleria* (A. Gray) Baill., Étude Euphorb.: 359. 1858 ≡ *Croton* subg. *Geiseleria* A. Gray, Manual, ed. 2: 391. 1856 ≡ *Geiseleria* Klotzsch in Arch. Naturgesch. 7: 254. 1841, nom. illeg. – Type: *Geiseleria glandulosa* (L.) Klotzsch ≡ *C. glandulosus* L.

= *Decarinium* Raf., Neogenyton: 1. 1825 ≡ *Croton* sect. *Decarinium* (Raf.) Müll. Arg. in Linnaea 34: 78. 1865 ≡ *Croton* subg. *Decarinium* (Raf.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 – Type: *Decarinium glandulosum* (L.) Raf. ≡ *C. glandulosus* L.

= *Aldinia* Raf., Autik. Bot.: 50. 1840 – Type: *A. glechomoides* Raf. = *C. betulinus* Vahl

= *Pleopadium* Raf., Autik. Bot.: 50. 1840 – Type: *P. ciliatum* Raf.

= *Ocalia* Klotzsch in Arch. Naturgesch. 7: 195. 1841 ≡ *Croton* sect. *Ocalia* (Klotzsch) Baill., Étude Euphorb.: 366. 1858 – Type: *C. perdicipes* A. St.-Hil., lectotype designated by Baillon in Étude Euphorb.: 366. 1858 = *C. antisiphiliticus* Mart.

= *Podostachys* Klotzsch in Arch. Naturgesch. 7: 193. 1841 ≡ *Croton* sect. *Podostachys* (Klotzsch) Baill., Étude Euphorb.: 365. 1858 ≡ *Croton* subsect. *Podostachys* (Klotzsch) Müll. Arg. in Linnaea 34: 134. 1865 – Type: *Podostachys subfloccosa* Didr., lectotype designated by Wheeler in Taxon 24: 537. 1975 = *C. lundianus* (Didr.) Müll. Arg.

= *Brachystachys* Klotzsch in London J. Bot. 2: 47. 1843 – Type: *Brachystachys hirta* (L’Hér.) Klotzsch ≡ *C. hirtus* L’Hér.

= *Heterocroton* S. Moore in Trans. Linn. Soc. London, Bot., ser. 2, 4: 461. 1895 ≡ *Croton* subg. *Heterocroton* (S. Moore) Pax in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1: 211. 1897 – Type: *Heterocroton mentiens* S. Moore ≡ *C. mentiens* (S. Moore) Pax.

= *Croton* sect. *Octolobium* Chodat & Hassl. in Bull. Herb. Boissier ser. 2, 5: 496. 1905 – Type: *C. guaraniticus* Chodat & Hassl. = *C. aberrans* Müll. Arg.

Description. – Monoecious or dioecious herbs and shrubs, annual or perennial; indumentum stellate; leaves with 2 stalked (occasionally sessile or subsessile) glands at the base, alternate or opposite; margins dentate to serrate, often with stipitate glands in the sinuses; venation palmate to pinnate; stipules entire; inflorescences terminal, lower cymules unisexual; stamens 5–15; sepals of pistillate flowers usually unequal, aestivation open, valvate, or rarely reduplicate-valvate, sepals 5, 6 (–10); petals of pistillate flowers absent (occasionally present); styles bifid or multifid for a total of 6, 12, or more stigmatic tips.

Distribution and habitat. – Fields, roadsides, waste places, open and mostly dry vegetation, deciduous to occasionally moist forests, widespread in the New World from the United States to Argentina, from sea level to 1800 m. *Croton glandulosus* and *C. hirtus* have been introduced as weeds in Africa and Australia.

Notes. – *Croton* sect. *Geiseleria* has a high proportion of annual or short-lived species. With the additional groups included in synonymy here, it contains species with both bifid and multifid styles, although nearly all of them have pistillate flowers with unequal sepals (Fig. 7K–L), as well as a pair of stalked glands at the base of the leaves (Fig. 7D).

Included species (82). – *C. abaitensis* Baill., *C. aberrans* Muell. Arg., *C. adamantinus* Müll. Arg., *C. adenodontus* (Müll. Arg.) Müll. Arg., *C. agoensis* Baill., *C. antisiphiliticus* Mart., *C. araracuarae* J. Murillo, P.E. Berry & M.V. Arbeláez, *C. arenosus* Carn.-Torres & Cordeiro, *C. asperrimus* Benth., *C. betulinus* Vahl, *C. bidentatus* Müll. Arg., *C. brevipes* Pax, *C. carandaitensis* Croizat, *C. chamelensis* E.J. Lott, *C. chiribiquetensis* Cardiel, *C. comes* Standl. & L.O. Williams, *C. crustulifer* Croizat, *C. cupulifer* McVaugh, *C. desertorum* Müll. Arg., *C. fluminensis* (Kuntze) K. Schum., *C. galeopsifolius* Lanj., *C. gardnerianus* Baill., *C. glandulosus* L., *C. glechomifolius* Müll. Arg., *C. goyazensis* Müll. Arg., *C. gracilescens* Müll. Arg., *C. grewioides* Baill., *C. grosse-dentatus* Pittier, *C. guildingii* Griseb., *C. gynopetalus* Croizat, *C. hadriani* Baill., *C. harleyi* Carn.-Torres & Cordeiro, *C. hirtus* L'Hér., *C. hostmannii* Miq. ex Schldl., *C. inaequilobus* Steyerl., *C. itzaeus* Lundell, *C. junceus* Baill., *C. jutiapensis* Croizat, *C. krukoffianus* Croizat, *C. leptobotrys* Müll. Arg., *C. liebmannii* Müll. Arg., *C. longinervius* Müll. Arg., *C. lotorius* Croizat, *C. lundianus* (Didr.) Müll. Arg., *C. macradenis* Görts & Punt, *C. macrodontus* Müll. Arg., *C. malvaviscifolius* Millsp., *C. martinianus* V.W. Steinmann, *C. mcvaughii* G.L. Webster, *C. megaponticus* Müll. Arg., *C. mentiens* (S. Moore) Pax, *C. mucronifolius* Müll. Arg., *C. nepetifolius* Baill., *C. odontadenius* Müll. Arg., *C. ortegae* Standl., *C. ortholobus* Müll. Arg., *C. pachysepalus* Griseb., *C. pardinus* Müll. Arg., *C. parodianus* Croizat, *C. pulegioidorus* Baill., *C. pycnadenius* Müll. Arg., *C. ramillatus* Croizat, *C. repens* Schldl., *C. sclerocalyx* (Didr.) Müll. Arg., *C. sincorensis* Mart. ex Müll. Arg., *C. sipaliwinensis* Lanj., *C. spiraeifolius* Jabl., *C. strobiliformis* Secco, *C. subincanus* Müll. Arg., *C. sublepidotus* Müll. Arg., *C. subserratus* Jabl., *C. tamberlikii* Müll. Arg., *C. tetradenius* Baill., *C. teucridium* Baill., *C. triangularis* Müll. Arg., *C. trinitatis* Millsp., *C. varelae* V.W. Steinmann, *C. virgulatus* Müll. Arg., *C. waltherioides* Urb., *C. wittianus* Ule, *C. yacaensis* Croizat. Placed here with some uncertainty: *C. santaritensis* Huft.

27. *Croton* sect. *Barhamia* (Klotzsch) Baill., Étude Euphorb.: 367. 1858 ≡ *Barhamia* Klotzsch in Seemann, Bot. Voy. Herald 3: 104. 1853 – Type: *Barhamia panamensis* Klotzsch, lectotype designated by Wheeler in Taxon 24: 534. 1975 = *C. hircinus* Vent.

Description. – Monoecious or dioecious perennial herbs, subshrubs, or shrubs; indumentum stellate to lepidote; leaves without glands at the base; margins entire, crenulate, serrate, or dentate; venation pinnate or palmate; some species with viscid foliage; stipules glandular, glandular-lobed, dissected, or obsolete; inflorescences terminal, bisexual, lower cymules unisexual; inflorescence bracts glandular; stamens (3–)8–15(–20); sepals of pistillate flowers reduplicate-valvate or lacinate, glandular or eglandular; petals of pistillate flowers reduced or absent; styles multifid for a total of 12 or more stigmatic tips.

Notes. – Glandular inflorescence bracts are shared by all species of this otherwise diverse and variable section, in which pistillate flowers with glandular or dissected sepals are found in all of the subsections (Fig. 7H–I).

Key to the subsections of *Croton* sect. *Barhamia*

1. Dwarf subshrubs or perennial herbs; leaves <1 cm long **27d. *C.* subsect. *Micranthi***
1. Shrubs; leaves ≥1 cm long **2**
2. Leaf margins dentate or serrate **3**
2. Leaf margins entire **4**
3. Leaf venation palmate, evident or less commonly obscured; foliage of some species viscid; indumentum densely stellate to nearly glabrous; stipules glandular-lobed or dissected **27a. *C.* subsect. *Barhamia***
3. Leaf venation pinnate, evident or obscured; foliage not viscid; indumentum densely stellate, stellate-lepidote, or sparse but not subglabrous; stipules glandular-lobed, dissected, or obsolete **27c. *C.* subsect. *Medea***
4. Leaves lepidote (rarely stellate); sepals of pistillate flowers eglandular; eastern Brazil **27e. *C.* subsect. *Sellowiorum***
4. Leaves stellate or stellate-lepidote; sepals of pistillate flowers glandular or dissected (rarely eglandular); more widely distributed **5**
5. Leaf venation palmate or pinnate, indumentum sparse to appressed-stellate, but not woolly; Central America, Mexico, and the West Indies **27b. *C.* subsect. *Astraeopsis***
5. Leaf venation pinnate, indumentum often woolly; Brazil, Paraguay, Uruguay, and Argentina **27c. *C.* subsect. *Medea***

27a. *Croton* subsect. *Barhamia* (Klotzsch) B.W. van Ee, **stat. nov.** ≡ *Barhamia* Klotzsch in Seemann, Bot. Voy. Herald 3: 104. 1853 – Type: *Barhamia panamensis* Klotzsch, lectotype designated by Wheeler in Taxon 24: 534. 1975 = *C. hircinus* Vent.

= *Calypteriopetalon* Hassk. in Flora 40: 531. 1857 – Type: *Calypteriopetalon brasiliense* Hassk. = *Croton urticifolius* Lam.

Description. – Indumentum stellate, loosely or appressed-stellate, not woolly, to nearly glabrous; some species with viscid foliage; leaf margins serrate to dentate; venation palmate; stipules glandular-lobed or dissected; sepals of pistillate flowers valvate to reduplicate-valvate, glandular.

Distribution and habitat. – *Croton* subsect. *Barhamia* is widespread in the West Indies and Central and South America, with its greatest diversity in Brazil. It is found in mostly open, dry vegetation from 100 to 1200 m.

Notes. – Although Martínez Gordillo & Espinosa Matías (2005) included *Croton agoensis* Baill. in *C.* sect. *Barhamia*, which corresponds to our concept of *C.* subsect. *Barhamia*, the presence of stipitate glands at the base of the leaves and the lack of glands on the inflorescence bracts exclude it from the section, and its overall morphology is instead consistent with *C.* sect. *Geiseleria*.

Included species (19). – *C. adenocalyx* Baill., *C. betulaster* Müll. Arg., *C. catariae* Baill., *C. chaetocalyx* Müll. Arg., *C. essequiboensis* Klotzsch, *C. glandulosodontatus* Pax & K. Hoffm., *C. glutinosus* Müll. Arg., *C. guianensis* Aubl., *C. hircinus* Vent., *C. klaenzei* Müll. Arg., *C. longibracteatus* M.J. Martínez Gordillo & de Luna, *C. muscicapa* Müll.

Arg., *C. paucistamineus* Müll. Arg., *C. perviscosus* Croizat, *C. rhexiifolius* Baill., *C. rudolphianus* Müll. Arg., *C. senescens* Croizat, *C. urticifolius* Lam., *C. yerbalium* Chodat & Hassl.

27b. *Croton* subsect. *Astraeopsis* (Baill.) B.W. van Ee, **stat. nov.** ≡ *Croton* sect. *Astraeopsis* Baill., Étude Euphorb.: 362. 1858.

Description. – Indumentum appressed-stellate, dense to sparse; foliage not viscid; leaf margins entire; venation palmate or pinnate; stipules glandular-lobed or linear; sepals of pistillate flowers reduplicate-valvate, entire or glandular.

Distribution and habitat. – West Indies and the Yucatan peninsula of Mexico and adjacent parts of Belize. Open, scrubby vegetation, usually on limestone, from sea level to 300 m.

Included species (4). – *C. ameliae* Lundell, *C. glabellus* L., *C. glandulosepalus* Millsp., *C. sutup* Lundell.

27c. *Croton* subsect. *Medea* (Klotzsch) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890 ≡ *Medea* Klotzsch in Arch. Naturgesch. 7: 193. 1841 ≡ *Croton* sect. *Medea* (Klotzsch) Baill., Étude Euphorb.: 368. 1858 ≡ *Croton* ser. *Medea* (Klotzsch) Müll. Arg. in Martius, Fl. Bras. 11(2): 144. 1873 – Type: *Medea hirta* Klotzsch = *C. timandroides* (Didr.) Müll. Arg.

= *Timandra* Klotzsch in Arch. Naturgesch. 7: 197. 1841 – Type: *Croton serratus* Müll. Arg., lectotype designated by Wheeler in Taxon 24: 538. 1975.

= *Myriogomphos* Didr. in Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1857: 142. 1857 – Type: *Myriogomphos fuscus* Didr. ≡ *C. fuscus* (Didr.) Müll. Arg.

= *Croton* sect. *Codonocalyx* Klotzsch ex Baill., Étude Euphorb.: 369. 1858 – Type: *C. montevidensis* Spreng., lectotype designated by Webster in Taxon 42: 820. 1993.

= *Croton* sect. *Hesperidium* Baill. in Adansonia 4: 306. 1864 – Type: *C. matronalis* Baill., lectotype designated by Webster in Taxon 42: 818. 1993 = *C. vestitus* Spreng.

= *Croton* sect. *Calycireduplicati* Allem in Bol. Soc. Argent. Bot. 18: 76. 1979 – Type: *Croton calycireduplicatus* Allem.

Description. – Indumentum stellate to stellate-lepidote, often woolly; foliage not viscid; leaf margins entire to serrate; venation pinnate, often obscure; stipules glandular, glandular-lobed, dissected, or obsolete; sepals of pistillate flowers lacinate, or reduplicate-valvate and glandular, entire, or dentate.

Distribution and habitat. – Brazil, Paraguay, Uruguay, and Argentina; temperate and subtropical, generally open vegetation, from sea level to 1000 m.

Notes. – In the classification adopted here, species with pistillate flowers with both reduplicate-valvate and lacinate calyces are included in *C.* subsect. *Medea*.

Included species (45). – *C. arlineae* D. Medeiros, L. Senna & R.J.V. Alves, *C. atrorufus* Müll. Arg., *C. avulsus* Croizat, *C. berberifolius* Croizat, *C. borbensis* Secco & P.E. Berry, *C. calyciglandulosus* Allem, *C. calycireduplicatus* Allem, *C. chaetophorus* Müll. Arg., *C. cuchillae-nigrae* Croizat, *C. decipiens* Baill., *C. dissectistipulatus* Secco, *C. eremophilus* Müll. Arg., *C. faroensis* Secco, *C. fuscus* (Didr.)

Müll. Arg., *C. garckeanus* Baill., *C. glandulosobracteatus* Carn.-Torres & Cordeiro, *C. gnidiaceus* Baill., *C. helichrysum* Baill., *C. heterodoxus* Baill., *C. integrilobus* Croizat, *C. josephinus* Müll. Arg., *C. landoltii* Ahumada, *C. langsdorffii* Müll. Arg., *C. lenheirensis* D. Medeiros, L. Senna & R.J.V. Alves, *C. luzianus* Müll. Arg., *C. megalocalyx* Müll. Arg., *C. melanoleucus* Müll. Arg., *C. montevidensis* Spreng., *C. parvifolius* Müll. Arg., *C. pradensis* D. Medeiros, L. Senna & R.J.V. Alves, *C. quintasii* Allem, *C. ramboi* Allem, *C. rubiginosus* Croizat, *C. serratifolius* Baill., *C. serratoideus* Radcl.-Sm. & Govaerts, *C. serratus* (Klotzsch) Müll. Arg., *C. siderophyllus* Baill., *C. spica* Baill., *C. staechadis* Baill., *C. subdioecus* (Kuntze) K. Schum., *C. subglaber* (Kuntze) K. Schum., *C. timandroides* (Didr.) Müll. Arg., *C. vestitus* Spreng. Placed here with some uncertainty: *C. ariramba* Huber, *C. thymelinus* Baill.

27d. *Croton* subsect. *Micranthi* (Baill.) B.W. van Ee, **stat. nov.** ≡ *Croton* sect. *Micranthi* Baill., Étude Euphorb.: 355. 1858 – Type: *C. galeottianus* Baill. = *C. nummulariifolius* A. Rich.

= *Merleta* Raf., Autik. Bot.: 49. 1840 – Type: *Merleta microphylla* Raf. = *C. nummulariifolius* A. Rich.

= *Comatocroton* H. Karst. in Wochenschr. Gärtnerei Pflanzenz. 2: 6. 1859 – Type: *Comatocroton ovalifolia* (Vahl in H. West) H. Karst. ≡ *Croton ovalifolius* Vahl in H. West.

= *Croton* sect. *Microcroton* Griseb. in Mem. Amer. Acad. Arts ser. 2, 8: 159. 1860 – Type: *C. serpylloides* Griseb. = *C. nummulariifolius* A. Rich.

Description. – Indumentum appressed-stellate; foliage not viscid; leaf margins entire; venation palmate or pinnate; stipules glandular-lobed; sepals of pistillate flowers reduplicate-valvate, glandular, or valvate and entire.

Distribution and habitat. – Mexico, West Indies, and Central and South America; sand barrens, coastal regions, waste places, and other open vegetation, from sea level to 1500 m.

Notes. – Webster (1993) suggested that what he recognized as *Croton* sect. *Micranthi* could perhaps be treated as a subsection of *C.* sect. *Barhamia*, and the molecular data support this.

Included species (13). – *C. cerinus* Müll. Arg., *C. gonaivensis* Urb. & Ekman, *C. haitiensis* P.T. Li, *C. lombardianus* Croizat, *C. microcarpus* Ham., *C. microphyllinus* Radcl.-Sm. & Govaerts, *C. nummulariifolius* A. Rich., *C. nummularius* Baill., *C. ovalifolius* Vahl, *C. paludosus* Müll. Arg., *C. radlkoferi* Pax & K. Hoffm., *C. refractus* Müll. Arg., *C. velutinus* Baill.

27e. *Croton* subsect. *Sellowiorum* B.W. van Ee, **subject. nov.** – Frutices lepidotis vel stellatis, foliis integris; stipulis bracteisque glanduloso-lobatis; sepals pistillatis reduplicate-valvatis, integris, eglandulosis. – Type: *C. sellowii* Baill.

Description. – Indumentum lepidote or stellate; foliage not viscid; leaf margins entire; venation pinnate, obscure; stipules glandular-lobed; sepals of pistillate flowers reduplicate-valvate, entire, eglandular.

Distribution and habitat. – Sandy soils in open vegetation in eastern Brazil. *Croton sellowii* Baill. occurs at lower elevations in “restinga” vegetation from sea level to 100 m. *Croton myrsinites* Baill. and *C. schultesii* Müll. Arg. occupy “campo rupestre” habitats from 800 to 1500 m.

Notes. – Müller (1873) placed *Croton sellowii* in *C. ser. ArgyroGLOSSUM*, with which it shares pistillate flowers with reduplicate-valvate sepals (Fig. 7J), but it keyed out by itself given its glandular stipules. Although these species are unusual in *C. sect. Barhamia* for being at least partly lepidote amid otherwise stellate species, the glandular inflorescence bracts and stipules of these three species are shared with the rest.

Included species (3). – *C. myrsinites* Baill., *C. schultesii* Müll. Arg., *C. sellowii* Baill.

28. *Croton* sect. *Luntia* (Neck. ex Raf.) G.L. Webster in *Taxon* 42: 804. 1993 ≡ *Luntia* Neck. ex Raf., *Sylva Tellur.*: 62. 1838 ≡ *Croton* subsect. *Matourenses* G.L. Webster in *Taxon* 42: 804. 1993 – Type: *C. matourensis* Aubl. ≡ *C. sericeus* Lam., nom. illeg. ≡ *Luntia sericea* Raf., nom. illeg.

= *Croton* subsect. *Palanostigma* Mart. ex Baill., *Étude Euphorb.*: 358. 1858 – Type: *C. palanostigma* Klotzsch.

Description. – Monoecious shrubs, trees, or lianas, 3–25 m tall; indumentum lepidote or stellate; leaves with 2 glands at the base, lamina entire or lobed, sometimes with cup-shaped glands; margins entire; venation palmate or pinnate; stipules entire; inflorescences terminal, bisexual or unisexual, lower cymules bisexual or unisexual; stamens 10–15; sepals of pistillate flowers valvate to reduplicate; petals of pistillate flowers reduced or absent; styles multifid for a total of 18–36 stigmatic tips.

Distribution and habitat. – *Croton* sect. *Luntia* is widespread across tropical South America and extends into Central America in Panama, Costa Rica, and Nicaragua. Its members are found in primary to secondary moist forests and disturbed sites, often near streams, from sea level to 3000 m.

Notes. – *Croton ascendens* Secco & N.A. Rosa, *C. grazieleae* Secco, *C. javarisensis* Secco, *C. pullei* Lanj. and *C. nuntians* Croizat represent a shift from the typical free-standing habit found in nearly all species of *Croton* to a semi-self-supporting liana growth form (Medeiros Carreira & al., 1996; Gallenmüller & al., 2001, 2005). Although none of these have been sampled molecularly, the lobed leaves and cup-shaped laminar glands of *C. ascendens* and *C. nuntians* are very similar to those of *C. palanostigma*, and we expect that they are closely related. The other lianas have unlobed leaves and lack the cup-shaped glands, suggesting that there may have been more than one shift to the liana habit within *C. sect. Luntia*.

Included species (19). – *C. ascendens* Secco & N.A. Rosa, *C. caryophyllus* Benth., *C. cearensis* Baill., *C. chocoanus* Croizat, *C. costatus* Kunth, *C. grazieleae* Secco, *C. huitotorum* Croizat, *C. javarisensis* Secco, *C. killipianus* 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.

29. *Croton* sect. *Julocroton* (Mart.) G.L. Webster in *J. Arnold Arbor.* 48: 354. 1967 ≡ *Julocroton* Mart. in *Flora* 20 (2, Beibl.): 119. 1837 ≡ *Croton* subg. *Julocroton* (Mart.) Radcl.-Sm. & Govaerts in *Kew Bull.* 52: 184. 1997 – Type: *Julocroton phagedaenicus* Mart. = *C. triqueter* Lam.

= *Cieca* Adans., *Fam. Pl.* 2: 355. 1763, nom. rej.

= *Heterochlamys* Turcz. in *Bull. Soc. Imp. Naturalistes Moscou* 16: 61. 1843 – Type: *Heterochlamys quinquinervia* Turcz. = *C. argenteus* L.

= *Julocroton* subg. *Eremadenia* Didr. in *Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn* 1857: 134. 1857 – Type: *J. triqueter* (Lam.) Didr. ≡ *C. triqueter* Lam.

= *Julocroton* subg. *Oligonychia* Didr. in *Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn* 132. 1857 – Type: *J. argenteus* (L.) Didr. ≡ *C. argenteus* L., lectotype designated by Webster in *Novon* 2: 270. 1992.

= *Centrandra* Karst. in *Linnaea* 28: 440. 1857 – Type: *Centrandra hondensis* Karst. ≡ *C. hondensis* (Karst.) G.L. Webster.

Description. – Monoecious herbs or shrubs; indumentum stellate; leaves without glands at the base; margins entire or dentate; venation palmate or pinnate; stipules entire to lacinate; inflorescences terminal, bisexual, congested, lower cymules unisexual; stamens 10–12; sepals of pistillate flowers lacinate and unequal, valvate to reduplicate-valvate; petals of pistillate flowers reduced or absent; styles multifid, occasionally bifid, for a total of 12, or occasionally 6, stigmatic tips.

Distribution and habitat. – This is a primarily South American group with its greatest diversity in Brazil, but a few species extend into the rest of tropical South America, and one species, *C. argenteus*, extends throughout Central America, the Caribbean, and up to the southern United States. It has a somewhat disjunct distribution between eastern and western South America (Cordeiro, 1990). Species of the section are found in open, generally dry vegetation from sea level to 2000 m.

Notes. – The congested inflorescences and pistillate flowers with highly dissected and unequal sepals make this one of the easier sections to recognize (Fig. 7E).

Included species (41). – *C. abutilopsis* G.L. Webster, *C. ackermannianus* (Müll. Arg.) G.L. Webster, *C. acuminatissimus* (Pittier) G.L. Webster, *C. agrestis* (Pax & K. Hoffm.) Radcl.-Sm. & Govaerts, *C. allemii* G.L. Webster, *C. apostolon* Radcl.-Sm. & Govaerts, *C. argentealbidus* Radcl.-Sm. & Govaerts, *C. argenteus* L., *C. calonervosus* G.L. Webster, *C. chodatii* (Croizat) P.E. Berry, *C. conspurcatus* Schltldl., *C. cooperianus* (Croizat) Radcl.-Sm. & Govaerts, *C. doratophylloides* (Croizat) G.L. Webster, *C. doratophyllus* Baill., *C. flavispicatus* Rusby, *C. fuscescens* Spreng., *C. geraesensis* (Baill.) G.L. Webster, *C. herzogianus* (Pax & K. Hoffm.) Radcl.-Sm. & Govaerts, *C. hondensis* (G. Karst.) G.L. Webster, *C. lepidus* (S. Moore) Radcl.-Sm. & Govaerts, *C. malvoides* (Croizat) Radcl.-Sm. & Govaerts, *C. nigricans* (Mart. ex Schltldl.) Radcl.-Sm. & Govaerts, *C. phyllanthus* (Chodat & Hassl.) G.L. Webster, *C. pyrosoma* (Croizat) Radcl.-Sm. & Govaerts, *C. robustior* (L.B. Sm. & Downs) Radcl.-Sm. & Govaerts, *C. rupestris* (Chodat & Hassl.) G.L. Webster, *C. rutilus* (Chodat & Hassl.) G.L. Webster, *C. salzmännii*

(Baill.) G.L. Webster, *C. solanaceus* (Müll. Arg.) G.L. Webster, *C. spissirameus* Radcl.-Sm. & Govaerts, *C. stipularis* (Müll. Arg.) G.L. Webster, *C. subpannosus* Müll. Arg. ex Griseb., *C. thellungianus* (Herter ex Arechav.) Radcl.-Sm. & Govaerts, *C. tocaninsensis* Radcl.-Sm. & Govaerts, *C. trichophilus* (Pax & K.Hoffm.) Radcl.-Sm. & Govaerts, *C. triqueter* Lam., *C. verbascooides* G.L. Webster, *C. vergarenae* (Jabl.) Gillespie, *C. villosissimus* (Chodat & Hassl.) Radcl.-Sm. & Govaerts, *C. viridulus* (Croizat) Radcl.-Sm. & Govaerts. Placed here with some uncertainty: *C. calocephalus* Müll. Arg.

30. *Croton* sect. *Lasiogyne* (Klotzsch) Baill., Étude Euphorb.: 370. 1858 ≡ *Lasiogyne* Klotzsch in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 418. 1843 ≡ *Croton* subsect. *Lasiogyne* (Klotzsch) Müll. Arg. in Linnaea 34: 81 (95). 1865 – Type: *Lasiogyne brasiliensis* Klotzsch = *C. compressus* Lam.
- = *Croton* sect. *Gonocladium* Baill. in Adansonia 4: 299. 1864 ≡ *Croton* ser. *Gonocladium* (Baill.) Müll. Arg. in Martius, Fl. Bras. 11(2): 126. 1873 ≡ *Croton* subsect. *Gonocladium* (Baill.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890 – Type: *C. compressus* Lam.
- = *Croton* sect. *Argyroglossum* Baill. in Adansonia 4: 289. 1864 ≡ *Croton* ser. *Argyroglossum* (Baill.) Müll. Arg. in Martius, Fl. Bras. 11(2): 118. 1873 ≡ *Croton* subsect. *Argyroglossum* (Baill.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890 – Type: *C. argyroglossum* Baill. = *C. argyrophyllus* Kunth.
- = *Croton* sect. *Decalobium* Müll. Arg. in Linnaea 34: 78. 1865 ≡ *Croton* subg. *Decalobium* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 – Type: *C. decalobus* Müll. Arg.
- = *Croton* sect. *Anadenocroton* G.L. Webster in Taxon 42: 806. 1993 – Type: *C. axillaris* Müll. Arg.

Description. – Monoecious shrubs and trees; indumentum stellate to lepidote; leaves without glands at the base; margins entire although frequently with crenations at the base on either side of the petiole; venation palmate or pinnate; stipules entire; inflorescences terminal or axillary, bisexual or unisexual, lower cymules unisexual; stamens 10–20; sepals of pistillate flowers reduplicate-valvate, occasionally just valvate; petals of pistillate flowers reduced or absent; styles multifid, free or sometimes basally connate, for a total of approximately 24 stigmatic tips.

Distribution and habitat. – *Croton* sect. *Lasiogyne* is widespread in the New World tropics and subtropics, occurring mostly in dry forest and scrub vegetation, from sea level to 1000 m.

Notes. – *Croton* sect. *Lasiogyne* is circumscribed here more inclusively than how Baillon (1858, 1864), Müller (1865, 1873), and Webster (1993) treated it. Webster (1993) recognized *C. sect. Argyroglossum* as distinct from *C. sect. Lasiogyne* based on lepidote pubescence in the former and stellate pubescence in the latter, but this distinction is not supported by the molecular data. The reduplicate-valvate sepals of the pistillate flowers of most species (Fig. 7F) are the most readily recognized characteristic of this section, although these are

shared homoplasiously with some species of *C. sects. Barhamia* (Fig. 7J), *Cleodora*, *Cyclostigma*, *Luntia* (Fig. 7D), and *Prisci* (Fig. 6I). Webster (1993) indicated that *C. sect. Decalobium* was highly suggestive of *C. sect. Barhamia*, and Martínez Gordillo & Espinosa Matías (2005) effectively synonymized the two by including *C. decalobus*, the type of *C. sect. Decalobium*, in *C. sect. Barhamia*. However, DNA sequence data (Van Ee, 2006) place *C. decalobus* and *C. pendens* within a more broadly circumscribed *C. sect. Lasiogyne*. Whether this broader sectional concept can be maintained as a monophyletic group, and what subsections can be recognized within it, will require additional phylogenetic and taxonomic work.

Included species (45). – *C. acapulcensis* M.J. Martínez Gordillo & J. Jiménez Ram., *C. alamosanus* Rose, *C. anomalus* Pittier, *C. argyrophyllus* Kunth, *C. astroites* Dryand., *C. atrostellatus* V.W. Steinmann, *C. axillaris* Müll. Arg., *C. blanchetianus* Baill., *C. bolivarensis* Croizat, *C. chiapensis* Lundell, *C. compressus* Lam., *C. cucutensis* Croizat, *C. culiacanensis* Croizat, *C. curranii* S.F. Blake, *C. decalobus* Müll. Arg., *C. deserticola* Steyererm., *C. floribundus* Spreng., *C. heliaster* S.F. Blake, *C. jacobinensis* Baill., *C. janeirensis* Radcl.-Sm. & Govaerts, *C. katoae* Croizat, *C. limae* A.P.S. Gomes, P.E. Berry & M.F. Sales, *C. mansfeldii* Urb., *C. masonii* I.M. Johnston., *C. micans* Sw., *C. moustiquensis* Urb., *C. pendens* Lundell, *C. potaroensis* Lanj., *C. rosmarinoides* Millsp., *C. sacaquinha* Croizat, *C. scaber* Willd., *C. schomburgkianus* A.P.S. Gomes & M.F. Sales, *C. sidifolius* Lam., *C. spiralis* Müll. Arg., *C. subcompressus* Müll. Arg., *C. sucrensis* Steyererm., *C. tabascensis* Lundell, *C. tricolor* Klotzsch ex Baill., *C. umbratilis* Kunth, *C. watsonii* Standl., *C. yucatanensis* Lundell. Placed here with some uncertainty: *C. astrophorus* Urb., *C. clausenianus* Baill., *C. coronatus* Urb., *C. stahelianus* Lanj.

31. *Croton* sect. *Heptallon* (Raf.) Müll. Arg. in Linnaea 34: 78. 1865 ≡ *Anisepta* Raf., First Cat. Gard. Transylv. Univ.: 13. 1824, nom. inval. ≡ *Heptallon* Raf., Neogenyton: 1. 1825 ≡ *Heptanis* Raf., Neogenyton: 1. 1825, nom. superfl. ≡ *Croton* subg. *Heptallon* (Raf.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 – Type: *Heptallon graveolens* Raf. ≡ *C. capitatus* Michx.
- = *Pilinophytum* Klotzsch in Arch. Naturgesch. 7: 255. 1841 ≡ *Croton* subg. *Pilinophytum* (Klotzsch) A. Gray, Manual, ed. 2: 391. 1856 – Type: *Pilinophytum capitatum* (Michx.) Klotzsch ≡ *C. capitatus* Michx.
- = *Engelmannia* Klotzsch in Arch. Naturgesch. 7: 253. 1841, nom. illeg. non *Engelmannia* A. Gray ex Nutt., 1840 (Asteraceae) ≡ *Angelandra* Endl., Gen. Pl. Suppl. 5: 91. 1850, nom. illeg. non *Angelandra* Endl., 1843 (Asteraceae) ≡ *Croton* sect. *Angelandra* Müll. Arg. in Linnaea 34: 79. 1865 ≡ *Croton* subg. *Angelandra* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 ≡ *Gynamblosis* Torr. in Marcy, Explor. Red River Louisiana 295. 1853 ≡ *Croton* subg. *Gynamblosis* (Torr.) A. Gray, Manual, ed. 2: 392. 1856 – Type: *Engelmannia nuttaliana* Klotzsch, nom. illeg. = *C. monanthogynus* Michx.

Description. – Monoecious herbs or subshrubs, annual or perennial; indumentum stellate to stellate-lepidote; leaves

without glands at the base; margins entire; venation pinnate; stipules entire, sometimes absent; inflorescences terminal or terminal and axillary, bisexual or unisexual, lower cymules unisexual; stamens 4–15; sepals of pistillate flowers valvate, occasionally unequal, aestivation occasionally open; petals of pistillate flowers absent; styles bifid or twice bifid for a total of (4) 6–12 stigmatic tips; columella usually tipped with 3 recurved appendages; ovary 2-carpellate in one species.

Distribution and habitat. – Eastern, central, and southern United States to central Mexico. Pastures, roadsides, sand dunes, deserts, and disturbed areas, from sea level to 1800 m.

Notes. – This section of eight annual species and a single perennial species, *C. pottsii*, is endemic to North America. Like some other sections, it includes closely related species with bifid and twice bifid styles, indicating the ease with which these characters can change within *Croton*. Van Ee & Berry (2010a) provide a more detailed phylogeny of this section, a list of the extensive synonymy, and an explanation for why its correct name is sect. *Heptallon*, as it was called by Webster (1967), rather than “section *Pilinophytum*”, as it was treated by Webster (1993).

Included species (9). – *C. capitatus* Michx., *C. elliotii* Chapm., *C. heptalon* (Kuntze) B.W. van Ee & P.E. Berry, *C. leucophyllus* Müll. Arg., *C. lindheimeri* (Engelm. & A. Gray) Alph. Wood., *C. lindheimerianus* Scheele, *C. monanthogynus* Michx., *C. palmeri* S. Watson, *C. pottsii* (Klotzsch) Müll. Arg.

Accepted species of unknown affinity

Croton abonari Riina & P.E. Berry, *C. amazonicus* Müll. Arg., *C. astianus* Croizat, *C. boissieri* Müll. Arg., *C. carinatus* Müll. Arg., *C. confinis* L.B. Sm. & Downs, *C. guaiquinimae* Steyerf., *C. ichthygaster* L.B. Sm. & Downs, *C. microgyne* Croizat, *C. scutatus* P.E. Berry (10 in total).

These are all distinctive species, with either anomalous characters that require further evaluation, or in need of more material that might provide additional characters to help place them.

Total number of New World species recognized: 712.

ACKNOWLEDGEMENTS

We are grateful to the numerous colleagues who have provided samples and facilitated field work, as well as to the curators of the herbaria cited in the Appendix who allowed us to sample specimens. This work was supported by NSF grants DEB-0212481 to P.E. Berry and DEB-0508725 to P.E. Berry & B. van Ee, grants from the Latin American Caribbean & Iberian studies (LACIS) program of the University of Wisconsin-Madison to R. Riina & B. van Ee, an award from the International Association of Plant Taxonomy (IAPT), the American Society of Plant Taxonomists (ASPT), and the Lawrence Memorial Award of the Hunt Institute to R. Riina, and by support from the University of Michigan Department of Ecology and Evolutionary Biology. We thank the three anonymous reviewers for their extensive and useful comments.

LITERATURE CITED

- Angiosperm Phylogeny Group.** 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–121.
- Baillon, H.** 1858. *Étude générale du groupe des Euphorbiacées*. Paris: Masson.
- Baillon, H.** 1864. Species Euphorbiacearum. Euphorbiacées Américaines. Première partie: Amérique austro-orientale. *Adansonia* 4: 257–377.
- Berry, P.E., Hipp, A.L., Wurdack, K.J., Van Ee, B. & Riina, R.** 2005. Molecular phylogenetics of the giant genus *Croton* and tribe Crotonae (Euphorbiaceae sensu stricto) using ITS and *trnL-trnF* DNA sequence data. *Amer. J. Bot.* 92: 1520–1534.
- Berry, P.E., Riina, R., Van Ee, B. & Haber, E.** 2009. The radiation of *Croton* (Euphorbiaceae) on Madagascar—how did this group become so speciose and diversified there compared to other Old World areas? Botany & Mycology 2009, Snowbird, Utah, July 25–29, Abstract. <http://2009.botanyconference.org/engine/search/index.php?func=detail&aid=816>.
- Britton, N.L.** 1918. *Flora of Bermuda*. New York: Charles Scribner's Sons.
- Brown, J.M. & Lemmon, A.R.** 2007. The importance of data partitioning and the utility of Bayes Factors in Bayesian phylogenetics. *Syst. Biol.* 56: 643–655.
- Brown, N.E.** 1883. The “*Genera Plantarum*.” *Gard. Chron.*, II, 19: 733–734.
- Caruzo, M.B.R.** 2010. *Sistemática de Croton sect. Cleodora (Euphorbiaceae s.s.)*. Dissertation, Universidade de São Paulo, Brasil.
- Caruzo, M.B.R., Cordeiro, I., Berry, P.E. & Riina, R.** 2010. A new species of *Croton* section *Cleodora* (Euphorbiaceae s.s.) from Minas Gerais, Brazil. *Phytotaxa* 3: 27–33.
- Cho, Y., Mower, J.P., Qiu, Y.-L. & Palmer, J.D.** 2004. Mitochondrial substitution rates are elevated and variable in a genus of flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* 101: 17741–17746.
- Cordeiro, I.** 1990. Aspectos taxonômicos e distribuição geográfica de *Julocroton* Mart. (Euphorbiaceae). *Acta Bot. Brasil.* 4: 83–90.
- Cordeiro, I., Berry, P.E., Caruzo, M.B.R. & Van Ee, B.** 2008. *Croton laceratoglandulosus* (Euphorbiaceae s.s.), a new glandular-stipulate species from Brazil and Bolivia, and its systematic position based on molecular analysis. *Bot. J. Linn. Soc.* 158: 493–498.
- Croizat, L.** 1942. New and critical Euphorbiaceae chiefly from the southeastern United States. *Bull. Torrey Bot. Club* 69: 445–460.
- De Queiroz, A., Donoghue, M.J. & Kim, J.** 1995. Separate versus combined analysis of phylogenetic evidence. *Annual Rev. Ecol. Syst.* 26: 657–681.
- Frodin, D.G.** 2004. History and concepts of big plant genera. *Taxon* 53: 753–776.
- Gallenmüller, F., Müller, U., Rowe, N. & Speck, T.** 2001. The growth form of *Croton pullei* (Euphorbiaceae)—functional morphology and biomechanics of a neotropical liana. *Pl. Biol. (Stuttgart)* 3: 50–61.
- Gallenmüller, F., Rowe, N. & Speck, T.** 2005. Development and growth form of the neotropical liana *Croton nuntians*: The effect of light and mode of attachment on the biomechanics of the stem. *J. Pl. Growth Regulat.* 23: 83–97.
- Ginzburg, S.** 1992. A new disjunct variety of *Croton alabamensis* (Euphorbiaceae) from Texas. *Sida* 15: 41–52.
- Gomes, A.P.S.** 2006. *Revisão das espécies sul-americanas de Croton sect. Argyroglossum Baill. (Crotonoideae—Euphorbiaceae)*. Dissertation, Universidade Federal Rural de Pernambuco, Brasil.
- González Ramírez, J. & Poveda Álvarez, L.** 2003. Dos nuevas especies de *Croton* (Euphorbiaceae) en el neotrópico. *Lankesteriana* 8: 7–12.
- Govaerts, R., Frodin, D.G. & Radcliffe-Smith, A.** 2000. *World checklist and bibliography of Euphorbiaceae (and Pandaceae)*, 4 vols. Kew: Royal Botanic Gardens.

- Grisebach, A.H.R.** 1859. *Flora of the British West Indian Islands*. London: Reeve.
- Haber, E., Van Ee, B., Oyserman, B. & Berry, P.E.** 2010. Origin and diversification of *Croton* (Euphorbiaceae) in Madagascar, and the Mascarene and Comoros islands. *Botany* 2010, Providence, Rhode Island, July 31–August 4. Abstract. <http://2010.botanyconference.org/engine/search/index.php?func=detail&aid=535>.
- Huelsenbeck, J.P. & Ronquist, F.** 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- Klotzsch, J.F.** 1853. Euphorbiaceae. Pp. 99–106 in: Seemann, B.C. (ed.), *Botany of the voyage of H.M.S. Herald ... during the years 1845–1851*. London: Reeve.
- Knoop, V.** 2004. The mitochondrial DNA of land plants: Peculiarities in phylogenetic perspective. *Curr. Genet.* 46: 123–139.
- Le Coite, P.** 1934. *Arvores e plantas úteis (indígenas e aclimatadas)*. Belém: Livraria Clássica.
- Leandri, J.** 1939. Les *Croton* de Madagascar et des îles voisines. *Ann. Inst. Bot.-Géol. Colon. Marseille* 7: 1–100.
- León Enriquez, B.L.** 2007. *Caracterización arquitectónica, molecular y cromosómica del género Croton sección Eluteria (Euphorbiaceae)*. Dissertation, Colegio de la Frontera Sur, Chetumal, Mexico.
- León Enriquez, B.L. & Martínez Gordillo, M.** 2008. Especie nueva de *Croton* sección *Eluteria* (Euphorbiaceae) de Chiapas, México. *Novon* 18: 189–191.
- León Enriquez, B.L. & Vester, H.F.M.** 2006. *Croton mayanus* (section *Eluteria*: Euphorbiaceae), a new species, endemic to the Yucatán Peninsula, México. *Novon* 16: 505–507.
- Lima, L.R.** 2006. *Estudos taxonômicos em Croton seção Lamprocroton (Müll. Arg.) Pax (Euphorbiaceae)*. Dissertation, Universidade de São Paulo, Brasil.
- Lima, L.R. & Pirani, J.R.** 2008. Revisão taxonômica de *Croton* sect. *Lamprocroton* (Müll. Arg.) Pax (Euphorbiaceae s.s.). *Biota Neotrop.* (Sao Paulo) 8: 203–257.
- Maddison, D.R. & Maddison, W.P.** 2005. *MacClade: Analysis of Phylogeny and Character Evolution*. Version 4.08. Sunderland, Massachusetts: Sinauer.
- Martínez Gordillo, M.** 1996. *El género Croton (Euphorbiaceae) en Mesoamerica*. Thesis, Universidad Nacional Autónoma de México, Mexico City.
- Martínez Gordillo, M. & Cruz Durán, R.** 2002. Especie nueva de la sección *Eluteria* Griseb. del género *Croton* (Euphorbiaceae) de Veracruz, México. *Anal. Inst. Biol. Univ. Nac. Autón. México, Bot.* 73: 141–145.
- Martínez Gordillo, M. & Espinosa Matías, S.** 2005. Tricomas foliares de *Croton* sección *Barhamia* (Euphorbiaceae). *Acta Bot. Mex.* 72: 39–51.
- Medeiros Carreira, L.M., de Souza Secco, R. & Barth, O.M.** 1996. Pollen morphology of the lianescent species of the genus *Croton* (Euphorbiaceae). *Grana* 35: 74–78.
- Müller, J.** 1865. Euphorbiaceae. Vorläufige Mittheilungen aus dem für De Candolle's Prodrromus bestimmten Manuscript über diese Familie [conclusion]. *Linnaea* 34: 1–224.
- Müller, J.** 1866. Euphorbiaceae. Pp. 189–1261 in: Candolle, A.P. de (ed.), *Prodromus systematis naturalis regni vegetabilis*, vol. 15(2). Paris, Strasbourg, & London: Treuttel & Würtz.
- Müller, J.** 1873. *Croton*. Pp. 81–274 in: Martius, C.F.P. von, *Flora Brasiliensis*, vol. 11(2). Munich, Vienna & Leipzig.
- Nixon, K.C. & Carpenter, J.M.** 1996. On simultaneous analysis. *Cladistics* 12: 221–241.
- Pax, F.** 1890. Crotonaeae. Pp. 36–41 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, vol. 3(5). Leipzig: Engelmann.
- Pax, F. & Hoffmann, K.** 1931. Crotonaeae. Pp. 83–88 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, ed. 2, vol. 19c. Leipzig: Engelmann.
- Posada, D. & Crandall, K.A.** 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Pursh, F.T.** 1814. *Flora Americae septentrionalis*. London: printed for White, Cochran, and Co.
- Qiu, Y.-L., Li, L., Hendry, T.A., Li, R., Taylor, D.W., Issa, M.J., Ronen, A.J., Vekaria, M.L. & White, A.M.** 2006. Reconstructing the basal angiosperm phylogeny: Evaluating information content of the mitochondrial genes. *Taxon* 55: 837–856.
- Rambaut, A. & Drummond, A.J.** 2007. Tracer. Version 1.5. <http://tree.bio.ed.ac.uk/software/tracer/>.
- Riina, R.** 2006. *Molecular systematics of the Neotropical Dragon's Blood trees Croton sect. Cyclostigma (Euphorbiaceae)*. Dissertation, University of Wisconsin, Madison, U.S.A.
- Riina, R. & Berry, P.E.** 2010. Two new South American species of *Croton* (Euphorbiaceae) and their phylogenetic affinities. *Anales Jard. Bot. Madrid* 67: 23–27.
- Riina, R., Berry, P.E. & Van Ee, B.W.** 2009. Molecular phylogenetics of the dragon's blood *Croton* section *Cyclostigma* (Euphorbiaceae): A polyphyletic assemblage unraveled. *Syst. Bot.* 34: 360–374.
- Riina, R., Cordeiro, I., Amorim, A. & Berry, P.E.** 2010a. *Croton thomasi* Riina & P.E. Berry (Euphorbiaceae), a new species from the Atlantic Forest in the State of Bahia (Brazil) and typification of *Croton sapiifolius* Müll. Arg. *Candollea* 65: 101–107.
- Riina, R., Van Ee, B., Wiedenhoef, A.C., Cardozo, A. & Berry, P.E.** 2010b. Sectional rearrangement of arboresecent clades of *Croton* (Euphorbiaceae) in South America: Evolution of arillate seeds and a new species, *Croton domatifer*. *Taxon* 59: 1147–1160.
- Ronquist, F.** 2004. Bayesian inference of character evolution. *Trends Ecol. Evol.* 19: 475–481.
- Ronquist, F. & Huelsenbeck, J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Salatino, A., Salatino, M.L.F. & Negri, G.** 2007. Traditional uses, chemistry and pharmacology of *Croton* species (Euphorbiaceae). *J. Brazil. Chem. Soc.* 18: 11–33.
- Secco, R.S., Berry, P.E. & Rosa, N.A.** 2001. *Croton diasii* and *Croton trombetensis*, two new Euphorbiaceae from Amazonian Brazil. *Novon* 11: 119–123.
- Small, J.K.** 1913. *Croton*. Pp. 454–455 in: Britton, N.L. & Brown, A. (eds.), *An illustrated flora of the Northern United States*, ed. 2, vol. 2. New York: Charles Scribner's Sons.
- Smith, B.A.** 2002. *A systematic revision of Croton section Cyclostigma (Euphorbiaceae) in Ecuador*. Dissertation, University of California, Davis, U.S.A.
- Smith, S.A. & Donoghue, M.J.** 2008. Rates of molecular evolution are linked to life history in flowering plants. *Science* 322: 86–89.
- Städler, T. & Delph, L.F.** 2002. Ancient mitochondrial haplotypes and evidence for intragenic recombination in a gynodioecious plant. *Proc. Natl. Acad. Sci. U.S.A.* 99: 11730–11735.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J.** 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1109.
- Urbatsch, L.E., Baldwin, B.G. & Donoghue, M.J.** 2000. Phylogeny of the cone-flowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast DNA restriction site data. *Syst. Bot.* 25: 539–565.
- Van Ee, B.W.** 2006. *Molecular phylogenetics within Croton (Euphorbiaceae s.s.)*. Dissertation, University of Wisconsin, Madison, U.S.A.
- Van Ee, B.W. & Berry, P.E.** 2009a. A phylogenetic and taxonomic review of *Croton* (Euphorbiaceae s.s.) on Jamaica including the description of *Croton jamaicensis*, a new species of section *Eluteria*. *Syst. Bot.* 34: 129–140.
- Van Ee, B.W. & Berry, P.E.** 2009b. The circumscription of *Croton* section *Crotonopsis* (Euphorbiaceae), a North American endemic. *Harvard Pap. Bot.* 14: 61–70.
- Van Ee, B.W. & Berry, P.E.** 2010a. Taxonomy and phylogeny of *Croton* section *Heptallon* (Euphorbiaceae). *Syst. Bot.* 35: 151–167.
- Van Ee, B.W. & Berry, P.E.** 2010b. Typification notes for *Croton* (Euphorbiaceae). *Harvard Pap. Bot.* 15: 73–84.
- Van Ee, B.W. & Berry, P.E.** 2011. *Croton* section *Pedicellati*

- (Euphorbiaceae), a novel New World group, and a new subsectional classification of *Croton* section *Lamprocroton*. *Syst. Bot.* 36: 88–98.
- Van Ee, B.W., Berry, P.E., Riina, R. & Gutiérrez Amaro, J.E. 2008. Molecular phylogenetics and biogeography of the Caribbean-centered *Croton* subgenus *Moacroton* (Euphorbiaceae s.s.). *Bot. Rev. (Lancaster)* 74: 132–165.
- Van Ee, B., Jelinski, N., Berry, P.E. & Hipp, A.L. 2006. Phylogeny and biogeography of *Croton alabamensis* (Euphorbiaceae), a rare shrub from Texas and Alabama, using DNA sequence and AFLP data. *Molec. Ecol.* 15: 2735–2751.
- Webster, G.L. 1967. The genera of Euphorbiaceae in the southeastern United States. *J. Arnold Arbor.* 48: 303–430.
- Webster, G.L. 1988. A new species of *Croton* (Euphorbiaceae) from Nicaragua. *Madroño* 35: 117–120.
- Webster, G.L. 1993. A provisional synopsis of the sections of the genus *Croton* L. (Euphorbiaceae). *Taxon* 42: 793–823.
- Webster, G.L. 2001. Synopsis of *Croton* and *Phyllanthus* (Euphorbiaceae) in western tropical Mexico. *Contr. Univ. Michigan Herb.* 23: 353–388.
- Webster, G.L. 2005. A new Mexican species of *Croton* section *Eluteria* (Euphorbiaceae). *Lundellia* 8: 12–16.
- Webster, G.L. & Huft, M. 1988. Revised synopsis of Panamanian Euphorbiaceae. *Ann. Missouri Bot. Gard.* 75: 1087–1144.
- White, T.J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis M.A., Gelfand D.H., Sninsky J.J. & White T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press.
- Wiedenhoft, A.C., Riina, R. & Berry, P.E. 2009. “Ray-intrusive” laticifers in species of *Croton* section *Cyclostigma* (Euphorbiaceae). *I.A.W.A. J.* 30: 135–148.
- World Checklist of Selected Plant Families. 2010– (continuously updated). The Board of Trustees of the Royal Botanic Gardens, Kew. Published on the Internet at <http://www.kew.org/wcsp/> (accessed 28 September 2010).
- Wurdack, K.J. 2006. The lectotypification and 19th century history of *Croton alabamensis* (Euphorbiaceae s.s.). *Sida* 22: 469–484.
- Wurdack, K.J. & Davis, C.C. 2009. Malpighiales phylogenetics: Gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. *Amer. J. Bot.* 96: 1551–1570.
- Wurdack, K.J., Hoffmann, P. & Chase, M. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcL* and *trnL-F* DNA sequences. *Amer. J. Bot.* 92: 1397–1420.
- Zwickl, D.J. 2006. *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Dissertation, University of Texas at Austin, U.S.A.

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

Taxon; locality; voucher; *rps3*; *EMB2765* exon 9; ITS; *trnL-F*. Missing data: –.

Outgroup: *Acidocroton trichophyllus* Urb.; Cuba, Holguín; *HABJ 81844* (MICH); HM564101; HM564234; EF421766; EF408087. *Astraea klotzschii* Didr.; Brazil, Bahia; *Van Ee 484* (WIS); HM564102; HM564235; HM564073; HM564209. *A. lobata* (L.) Klotzsch; Cuba, Havana; *HABJ 81999* (MICH); HM564103; HM564236; –; –. Costa Rica, Guanacaste; *Van Ee 296* (WIS); –; –; EF421720; EF408089. *Brasilicroton mamoninha* P.E. Berry & Cordeiro; Brazil, Espírito Santo; *Pirani 3411* (NY); HM564104; HM564237; AY971175; AY971267.

Ingroup: *Croton adenophyllus* Bertero ex Spreng.; Jamaica, St. Andrews; *Van Ee & al. 770* (A); HM564105; HM564238; EU497728; EU497700. *C. alabamensis* E.A. Sm. ex Chapm.; U.S.A., Alabama; *Van Ee & al. 369* (WIS); HM564106; –; DQ227513; DQ227545. *C. alainii* B.W. van Ee & P.E. Berry; Cuba, Holguín; *HABJ 81770* (MICH); HM564107; HM564239; EF421756; EF408138. *C. alamosanus* Rose; Mexico, Sonora, *Van Devender 2006-1284* (MICH); HM564108; HM564240; –; –. Mexico, Michoacán; *Steinmann 1659* (WIS); –; –; EU477863; EU478123. *C. andinus* Müll. Arg.; Argentina, Catamarca; *Van Ee & al. 657* (US); HM564109; HM564241; FJ614761; FJ614801. *C. argenteus* L.; Costa Rica, Guanacaste; *Van Ee 297* (WIS); HM564110; HM564242; EU478094; EU497702. *C. argentinus* Müll. Arg.; Argentina, Córdoba; *Van Ee & al. 638* (US); HM564111; HM564243; –; HM564210. Argentina, Córdoba; *Van Ee & al. 644* (US); –; –; EU497729; –. *C. argyranthemus* Michx.; U.S.A., Texas; *Jones 8262* (MICH); HM564112; HM564244; HM564074; –. U.S.A., Texas; *Fryxell 4967* (MO); –; –; HM564211. *C. argyratus* Blume; Malaysia, Selangor; *Van Ee & Sugumarani 790* (A); HM564113; HM564245; HM564075; HM564212. *C. argyrophyllus* Kunth; Brazil, Pernambuco; *Carneiro-Torres 881* (SP); HM564114; HM564246; –; –. Brazil, Pernambuco; *Van Ee 476* (WIS); –; –; HM564076; HM564213. *C. astroites* Dryand.; Puerto Rico; *Van Ee 537* (WIS); HQ654591; HQ654592; EU586901; EU586955. *C. atrostellatus* V.W. Steinmann; Mexico, Michoacán; *Steinmann 1681* (WIS); HM564115; –; EU477875; EU478124. *C. billbergianus* Müll. Arg.; Costa Rica, Alajuela; *Van Ee & Redden 342* (WIS); HM564116; HM564247; EU477998; EU478148. *C. caracasanus* Pittier; Venezuela, Distrito Federal; *Riina 1288* (WIS); HM564117; HM564248; DQ227525; DQ227557. *C. catamarcensis* Ahumada; Argentina, Córdoba; *Van Ee & al. 653* (US); HM564118; HM564249; HM071949; HM071969. *C. chamelensis* E.J. Lott; Mexico, Guerrero; *Moore & Wood 4739* (A); HM564119; HM564250; FJ614707; FJ614775. *C. cordifolius* Baill.; Brazil, Bahia; *Queiroz 12041* (HUEFS); HM564120; HM564251; –; –. Brazil, Bahia; *Thomas 13601* (CEPEC); –; –; EU586917; EU586971. *C. coriaceus* Kunth; Ecuador; *Riina & López 1403* (WIS); HM564121; HM564252; EU586921; EU586976. *C. corinthius* Poveda & J.A. González; Costa Rica, Limón; *Van Ee & Van Ee 600* (WIS); HM564133; HM564264; HM564079; HM564253; EF421751; EF408110. *C. coryi* Croizat; U.S.A., Texas; *Van Ee & al. 520* (WIS); HM564123; HM564254; EU478012; EU478152. *C. corylifolius* Lam.; Jamaica, Manchester; *Van Ee & al. 775* (A); HM564124; HM564255; EU497734; EU497709. *C. cuneatus* Klotzsch; Peru; *Riina 1491* (MICH); HM564125; HM564256; EU478005; EU497710. *C. cupreatus* Croizat; Ecuador, Pichincha; *Smith 473* (WIS); HM564126; HM564257; HM564077; HM564214. *C. curiosus* Croizat; Argentina, Tucumán; *Zuloaga 8438* (SI); HM564127; HM564258; EU586906; EU586960. *C. dioicus* Cav.; U.S.A., Texas; *Yang 5* (MICH); HM564128; HM564259; HM564078; HM564215. *C. discolor* Willd.; Puerto Rico; *Van Ee 547* (WIS); HM564129; HM564260; EU497736; EU497711. *C. draco* Schltdl. & Cham.; Costa Rica; *Van Ee & Redden 347* (WIS); HM564130; HM564261; EU478006; EU497712. *C. ekmanii* Urb.; Cuba, Holguín; *Van Ee 393* (WIS); –; –; HM564262; –; –. Cuba, Holguín; *HABJ 81888* (MICH); HM564131; –; EF421763; EF408147. *C. eichleri* Müll. Arg.; Brazil, Rio de Janeiro; *Riina & Caruzo 1525* (SP); HM564132; HM564263; EU586949; EU587001. *C. eremophilus* Müll. Arg.; Brazil, Minas Gerais; *Carneiro-Torres 707* (SP); HM564133; HM564264; HM564079; HM564216. *C. flavens* L.; Puerto Rico; *Van Ee 540* (WIS); HM564134; HM564265; EU477905; EU478134. *C. floribundus* Spreng.; Brazil, São Paulo; *Berry 7686* (MICH); HM564135; HM564266; HM564080; –. *C. fruticosus* Torr.; U.S.A., Texas; *Van Ee & al. 338* (WIS); HM564136; HM564267; EU477916; EU478136. *C. fuscescens* Spreng.; Brazil, São Paulo; *Van Ee 502* (WIS); HM564137; HM564268; HM564081; HM564217. *C. glabellus* L.; Jamaica, St. Thomas; *Van Ee & al. 771* (A); HM564138; HM564269; EU477892; EU497719. *C. glandulosepalus* Millsp.; Belize, Cayo District; *Vincent 6058* (MU); HM564139; –; EU477888; EU478126. *C. glandulosus* L.; U.S.A., Wisconsin; *Van Ee & al. 512* (WIS); HM564140; HM564270; EU478066; EU497713. *C. gnaphalii* Baill.; Argentina, Entre Rios; *Belgrano & al. 423* (SI); HM564141; HM564271; EU586940; EU586994. *C. goudotii* Baill.; Madagascar, Fianarantsoa; *Hoffmann 248* (K); HM564142; HM564272; EU586946; EU587000. *C. grisebachianus* Müll. Arg.; Jamaica, St. Andrew; *Van Ee & al. 767* (A); –; HM564273; EU497737; EU497714. *C. guildingii* Griseb. subsp. *tiarensis* P.E. Berry & Riina; Venezuela, Aragua; *Riina 1274* (WIS); HM564143; HM564274; AY971254; AY971336. *C. heterocalyx* Baill.; Brazil, Bahia; *Caruzo 108* (SP); HM564144; HM564275; HM044794; HM044775. *C. hircinus* Vent.; Venezuela, Distrito Federal; *Riina 1291* (VEN); HM564145; –; EU477889; EU478127. *C. hirtus* L’Her.; Brazil, Pernambuco; *Van Ee 481* (WIS); HM564146; HM564276; EU478071; EU497715. *C. humilis* L.; Jamaica, St. Andrews; *Van Ee & al. 769* (A); HM564147; HM564277; HM564083; HM564218. *C. impressus* Urb.; Puerto Rico; *Van Ee 543* (WIS); HM564148; HM564278; EF421775; EF408113. *C. jamaicensis* B.W. van Ee & P.E. Berry; Jamaica, St. Catherine; *Van Ee & al. 772* (A); –; HM564279; EU497733; EU497708.

Appendix. Continued.

C. jimenezii Standl. & Valerio; Costa Rica, San José; *Van Ee 326* (WIS); HM564149; HM564280; EF421777; EF408115. *C. lanatus* Lam. var. *tatacuensis* (Ahumada) P.E. Berry; Argentina, Corrientes; *Belgrano & al. 256* (SI); HM564150; HM564281; HM564084; HM564219. *C. laureltyanus* Ahumada; Argentina, Corrientes; *Belgrano & al. 281* (SI); HM564151; HM564282; HM071953; HM071970. *C. lechleri* Müll. Arg.; Peru, San Martín; *Riina & Campos 1449* (WIS); HM564152; –; EU586927; EU586983. *C. lechleri* Müll. Arg.; Peru, San Martín; *Riina 1497* (WIS); –; HQ654593; –; –. *C. leonis* (Croizat) Van Ee & P.E. Berry; Cuba, Holguín; *HABJ 81773* (MICH); HM564153; –; EF421758; EF408140. *C. lepidotus* Aug. DC.; Madagascar, Toamasina; *Van Ee & al. 998* (MICH); HM564154; HM564283; HM564085; HM564220. *C. lindheimerianus* Scheele; Mexico, Tamaulipas; *Van Ee & al. 521* (WIS); HM564155; HM564284; EU478111; EU478168. *C. lindheimeri* (Engelm. & A.Gray) Alph.Wood; U.S.A., Louisiana; *Van Ee & al. 517* (WIS); HM564156; HM564285; EU478106; FJ614778. *C. linearis* Jacq.; Jamaica, St. James; *Van Ee & al. 745* (A); –; HM564286; –; –. Bahamas, Cat Island; *Richey 99387* (MU); –; –; EU477933; EU478138. *C. louvelii* Leandri; Madagascar; *Hoffmann 194* (K); HM564157; HM564287; HM564086; HM564221. *C. lucidus* L.; Jamaica; Manchester; *Van Ee & al. 776* (A); –; HM564288; EU497743; EU497726. *C. luettelburgii* Pax & K.Hoffm.; Brazil, Bahia; *Conceição 1457* (HUEFS); HM564158; HM564289; HM564087; HM564222. *C. lundellii* Standl.; Mexico, Yucatán; *Van Ee & May-Pat 123* (WIS); HM564159; HM564290; EF421733; EF408099. *C. maestrensis* (Alain) B.W. van Ee & P.E. Berry; Cuba, Granma; *HABJ 81958* (MICH); HM564160; HM564291; EF421753; EF408127. *C. matourensis* Aubl.; Brazil, Amazonas; *Van Ee 492* (WIS); HM564161; HM564292; EU478096; EU497720. *C. megistocarpus* J.A.González & Poveda; Costa Rica, Puntarenas; *Gardner s.n.* (WIS); *Van Ee & al. 998* (MICH); EF421779; EF408118. *C. miarensis* Leandri; Madagascar, Toliar; *Van Ee & al. 903* (MICH); HM564163; HM564294; HM564088; HM564223. *C. micans* Sw.; Dominica; *Whitefoord 4449* (BM); HM564164; HM564295; –; –. Dominica; *Hill 24051* (MO); –; –; EU497731; EU497705. *C. michauxii* G.L. Webster var. *elliptica* (Willd.) B.W. van Ee & P.E. Berry; U.S.A., Missouri; *Archer 40* (MO); HM564165; HM564296; EU478004; HM564224. U.S.A., Missouri; *Cusick 33275* (MICH); HM564166; HM564297; HM564089; HM564225. *C. milleri* J.R. Johnst.; Venezuela, Nueva Esparta; *Riina 1269* (WIS); HM564167; HM564298; AY971232; AY971319. *C. minimus* P.I. Forst.; Australia, Queensland; *Forster 28146* (WIS); HM564168; HM564299; HM564090; –. *C. monanthogynus* Michx.; U.S.A., Illinois; *Van Ee & al. 515* (WIS); HM564169; HM564300; EU478113; EU478169. *C. morifolius* Willd.; Costa Rica, Guanacaste; *Van Ee 295* (WIS); HM564170; HM564301; EU477943; –. Costa Rica, Guanacaste; *Van Ee 286* (WIS); –; –; EU478140. *C. myricifolius* Griseb.; Cuba, Havana; *Van Ee 379* (WIS); HM564171; HM564302; HM564091; HM564226. *C. nitiens* Sw.; Jamaica, St. James; *Van Ee & al. 744* (A); HM564172; HM564303; EU478042; EU497724. *C. niveus* Jacq.; Costa Rica, Heredia; *Van Ee & Van Ee 593* (WIS); HM564173; HM564304; EF421780; EF408119. *C. nobilis* Baill.; Madagascar, Toliar; *Van Ee & al. 938* (MICH); HM564174; HM564305; HM044797; HM044778. *C. noronhae* Baill.; Madagascar, Toamasina; *Van Ee & al. 1001* (MICH); HM564175; HM564306; HM564092; HM564227. *C. nubigenus* G.L. Webster; Nicaragua, Región Autónoma del Atlántico Norte; *Van Ee & Coronado 587* (HULE) [= *Coronado & al. 3404* (HULE, MO)]; HM564176; HM564307; EU478103; –. Nicaragua, Región Autónoma del Atlántico Norte; *Van Ee & Coronado 589* (HULE); –; –; EF408121. *C. olivaceus* Müll. Arg.; Ecuador, Napo; *Neill 11163* (MO); HM564177; –; AY971237; AY794694. *C. pachysepalus* Griseb.; Cuba, Guantánamo; *HABJ 81930* (MICH); HM564178; HM564308; HM071957; HM071974. *C. pedicellatus* Kunth; Colombia, Cundinamarca; *Plowman 3766* (GH); HM564179; HM564309; FJ614766; FJ614804. *C. peraeuginosus* Croizat; Mexico, Yucatán; *Van Ee 128* (WIS); HM564180; –; EU477953; EU478141. *C. piptocalyx* Müll. Arg.; Brazil, São Paulo; *Caruzo 54* (SP); HM564186; HM564310; EF421791; EF408132. *C. poecilanthus* Urb.; Puerto Rico; *Van Ee 551* (WIS); HM564181; HM564311; EF421782; EF408122. *C. polyandrus* Spreng; Brazil, Bahia; *Nunes 1376* (HUEFS); HM564182; HM564312; –; HM564228. Brazil; Bahia; *Cordeiro 3017* (SP); –; –; HM564093; –. *C. priscus* Croizat; Brazil, São Paulo; *Riina 1535* (WIS); –; HQ654594; EU586950; EU587002. *C. pulcher* Müll. Arg.; Mexico, Oaxaca; *Walker 3005* (WIS); HM564184; HM564314; EU477994; EU478147. *C. punctatus* Jacq.; Mexico, Veracruz; *Van Ee & al. 528* (WIS); HM564185; HM564315; EU478022; EU478153. *C. roraimensis* Croizat; Venezuela, Bolívar; *Riina 1539* (VEN); HM564187; HM564316; HM564094; EF408149. *C. salutaris* Casar.; Brazil, Rio de Janeiro; *Caruzo 89* (SP); HM564188; HM564317; HM044804; HM044783. *C. sampatik* Müll. Arg.; Perú, Pasco; *Riina 1447* (WIS); HM564189; HM585372; EF421792; EF408133. *C. sapiifolius* Müll. Arg.; Brazil, Bahia; *Lima 677* (CEPEC); HM564190; –; EF421754; EF408150. *C. schiedeanus* Schldt.; Mexico, Yucatán; *Van Ee 458* (WIS); HM564191; HM564318; EU478051; EU478156. *C. sellowii* Baill.; Brazil, Bahia; *Van Ee 498* (WIS); HM564192; HM564319; HM564095; HM564230. *C. serratifolius* Baill.; Argentina, Córdoba; *Van Ee & al. 639* (US); HM564193; HM564320; HM564096; HM564231. *C. setiger* Hook.; U.S.A., California; *Berry 7688* (WIS); HM564194; HM564321; HM564097; –. California; *Hughey s.n.* (US); –; –; AY794697. *C. skutchii* Standl.; Costa Rica, Cartago; *Van Ee & Van Ee 597* (WIS); HM564195; HM564322; EU478100; EU478166. *C. smithianus* Croizat; Costa Rica, Heredia; *Van Ee s.n.* (A); HM564196; HM564323; HM564098; –. *C. speciosus* Müll. Arg.; Venezuela, Distrito Federal; *Berry 7590* (WIS); HM564197; HM564324; AY971251; AY794699. *C. tenuilobus* S. Watson; Mexico, Sonora; *Van Devender & al. 2006-993* (MICH); HM564198; –; –; Mexico, Jalisco; *Webster & Lynch 17169* (GH); –; HM564325; FJ614764; FJ614803. *C. thomasii* Riina & P. E. Berry; Brazil, Bahia; *Lima 654* (CEPEC); HM564201; HM564327; EU586951; EU587003. *C. trinitatis* Millsp.; Brazil, Amazonas; *Van Ee 507* (WIS); HM564199; –; EU478092; HM564232. *C. triqueter* Lam.; Brazil, São Paulo; *Caruzo 27* (SP); HM564200; HM564326; –; –. Bolivia, Santa Cruz; *Nee 40034* (NY); –; –; AY971256; AY794700. *C. urucurana* Baill.; Brazil, São Paulo; *Amaral 2002-09* (UEC); HM564202; –; –; –. Brazil, Minas Gerais; *Riina & al. 1317* (MICH); –; HQ654595; EU586937; EU586991. *C. warmingii* Müll. Arg.; Brazil, São Paulo; *Caruzo 56* (SP); HM564203; –; EU586915; EU586970. *C. watsonii* Standl.; Mexico, Tamaulipas; *Dwyer & al. 90* (GH); HM564204; –; HM564099; HM564233. *C. yavitensis* Croizat; Bolivia, Beni; *Beck 5710* (LPB); HM564205; HM564328; EU586918; EU586918. *C. ynesae* Croizat; Mexico, Nayarit; *Webster & Breckon 15774* (GH); HM564206; HM564329; HM564100; –. *C. yucatanensis* Lundell; Mexico, Yucatán; *Van Ee & May-Pat 121* (WIS); HM564207; HM564330; DQ227537; DQ227569. *C. zambeus* Müll. Arg.; Zambia, Songwe Gorge; *Zimba & al. 901* (MO); HM564208; HM564331; AY971260; AY971341.