

Realignments in American *Croton* (Euphorbiaceae)

Grady L. Webster

Department of Botany, University of California, Davis, California 95616, U.S.A.

ABSTRACT. Revisional studies in *Croton* to achieve a more nearly phylogenetic classification necessitate a number of nomenclatural changes. The genera *Crotonopsis* and *Eremocarpus* are reduced to sections of *Croton*, and the new names *Croton michauxii* and *C. willdenowii* are proposed for the two species of *Croton* sect. *Crotonopsis*. For *Croton* sect. *Julocroton*, the 25 species accepted are enumerated, including 19 new names or new combinations.

In the course of an unpublished review of the sections of *Croton* L., I have found it necessary to make a number of changes in classification. Consequently, in order to be able to cite representative species for the 38 sections of *Croton*, a number of nomenclatural changes must be validated.

The generic circumscription of *Croton* that has been almost universally accepted by systematists for more than a century is that proposed by Jean Mueller (1865, 1866, 1873). In contrast to the earlier classification of Baillon (1858), Mueller recognized only four genera in the *Croton* alliance (subtribe *Crotoneae* Muell. Arg.): *Croton* L., *Julocroton* Mart., *Crotonopsis* Michaux, and *Eremocarpus* Benth. These four taxa have in common (with rare exceptions in individual species) the diagnostic characters of stellate or lepidote indumentum, thyrsoïd inflorescence with pistillate flowers at base, stamens inflexed in the bud, and carunculate seeds.

Although Benth (1880) noted that *Julocroton* was excessively close to *Croton*, he accepted it hesitatingly. A more definite rejection of the Muellierian circumscription was made by Macbride (1951), who refused to recognize *Julocroton* as a distinct genus and incorporated the Peruvian species into *Croton*. Mueller (1866) had distinguished *Julocroton* from *Croton* by a supposed difference in the relative position of the sepals to the subtending bract, although in subsequent taxonomic treatments (as by Macbride), the highly asymmetrical and lacinate pistillate calyx of *Julocroton* was used as the distinguishing character. In agreement with Benth (1880), who was one of the first to question the generic distinctness of *Julocroton*, I find the topology of sepal position versus bract an unusable character; and I concur with Macbride that the irregular la-

ciate calyx does not adequately distinguish *Julocroton* from various South American species of *Croton*.

In a review of the Euphorbiaceae in the southeastern United States (Webster, 1967), I reduced *Julocroton* to a section of *Croton*, but rather diffidently accepted *Crotonopsis* as a distinct genus. However, in reviewing all of the sections of *Croton*, it has become apparent to me that *Crotonopsis* is excessively close to *Croton* sect. *Gynamblosis* (Torrey) A. Gray. In particular, the main generic character of *Crotonopsis*—unicarpellate gynoecium and indehiscent fruit—represents merely the end-point in a reduction series from the 3-carpellate gynoecium of most *Croton* species through the 2-carpellate gynoecium of *Croton monanthogynus* Michaux to the 1-carpellate gynoecium of *Crotonopsis*. Consequently, there appears to be a much stronger case for treating *Crotonopsis* as a section of *Croton* than as an independent genus.

Although I did not consider the problem of *Eremocarpus* earlier, its situation is comparable to that of *Crotonopsis*. When Hooker (1838) described *Croton setigerus* Hook., he expressed doubt as to its position in his citation of the name as *Croton* ? *setigerus*. Following the creation of the monotypic genus *Eremocarpus* to accommodate this species (Benth, 1844), it has been almost universally accepted (except by Greene (1891), who is hardly renowned as a "lumper"). However, *Eremocarpus setigerus* (Hook.) Benth. has a habit reminiscent of various herbaceous species of North American *Croton*, such as *C. capitatus* Michaux of section *Pilinophyton* (Klotzsch) A. Gray and *C. lindheimerianus* Scheele of section *Gynamblosis* (Torrey) A. Gray. The obsolete pistillate perianth was used by Mueller (1866) as the main generic character for *Eremocarpus*, but the staminate flowers are typical for *Croton*; and the 1-carpellate gynoecium apparently represents a reduction parallel to that discussed above for *Crotonopsis*. Thus, although I earlier accepted both *Crotonopsis* and *Eremocarpus* as distinct from *Croton* (Webster, 1975), their claim to generic separation now appears no better founded than that for *Julocroton*.

For all three of these satellite genera of *Croton*, a serious argument against their acceptance at the

generic rank is that it would lead to a blatantly nonphylogenetic classification; or, to use cladistic parlance, it would make *Croton* a thrice-paraphyletic genus. The only way to salvage such genera as *Julocroton* would be to split *Croton* into a large number of segregate genera, as Klotzsch (1841) attempted. Such an alternative, I believe, would be highly unacceptable because of problems in defining and recognizing the segregates, and because it would obscure the phyletic coherence of this great genus of nearly 1,000 species. Consequently, the three segregates are here treated as sections of *Croton*, and the necessary nomenclatural adjustments are proposed.

Croton L., Sp. Pl. 1004. 1753. Lectotype: *Croton aromaticus* L. (designated by Webster, 1967).

SECTION *CROTONOPSIS*

Croton sect. **Crotonopsis** (Michaux) Webster, stat. nov. Basionym: *Crotonopsis* Michaux, Fl. Bor.-Amer. 2: 185. 1803. *Leptemon* Rafinesque, Med. Repos. II. 5: 353. 1808, nom. superfl. TYPE: *Crotonopsis linearis* Michaux.

Friesia Sprengel, Anleit. Halle Gewächs. 2(2): 885. 1818. TYPE: *Friesia argentea* Sprengel [= *Crotonopsis linearis* Michaux].

This section contains two species, sometimes combined but well discriminated by Pennell (1918), followed by Correll & Johnston (1970). Unfortunately, both species have to be renamed because all available epithets are preoccupied in *Croton*.

1. **Croton michauxii** Webster, nom. nov. Replaced name: *Crotonopsis linearis* Michaux, Fl. Bor.-Amer. 2: 185. 1803, non *Croton linearis* Jacq., 1760. *Crotonopsis argentea* Pursh, Fl. Amer. Sept. 1: 206. 1814, nom. superfl.; non *Croton argenteus* L., 1753. TYPE: U.S.A. South Carolina: Long Bay, Michaux s.n. (lectotype, selected here, Michaux Herbarium, P; microfiche seen). The only specific location given by Michaux was Long Bay, which is in South Carolina according to Ewan (1974); it seems appropriate to select it as the lectotype.

Crotonopsis spinosa Nash, Bull. Torrey Bot. Club 22: 157. 1895, non *Croton spinosus* Forsk., 1775. TYPE: U.S.A. Florida: Marion Co., Dunnellon, Swingle 1397a (holotype, NY).

2. **Croton willdenowii** Webster, nom. nov. Replaced name: *Crotonopsis elliptica* Willd., Sp. Pl. 4: 380. 1805, non *Croton ellipticus* Gei-

seler, 1807. TYPE: U.S.A. South Carolina: Muehlenberg s.n. (lectotype, selected here, Willdenow Herbarium 17490, B).

Crotonopsis abnormis Baillon, Etude Euphorb. 381. 1858 non *Croton abnormis* Baillon, 1864. TYPE: without locality, *Leconte* s.n. (P not seen).

Although Merrill (1949) listed three species of Rafinesque as synonymous with *Crotonopsis elliptica* Willd., Rafinesque did not cite Willdenow, and all three Rafinesque species—in the absence of clear typification—could possibly be synonyms of *Crotonopsis linearis* Michaux. It seems preferable, therefore, to apply a new name to the species that can be securely based on a type specimen.

SECTION *EREMOCARPUS*

Croton sect. **Eremocarpus** (Benth) Webster, stat. nov. *Eremocarpus* Benth, Bot. Voy. Sulphur 53. 1844. *Piscaria* Piper, Contr. U.S. Natl. Herb. 11: 382. 1906, nom. superfl. TYPE: *Croton setigerus* Hooker.

1. **Croton setigerus** Hooker, Fl. Bor.-Amer. 2: 141. 1838. TYPE: U.S.A. Oregon: Menzies' Island, and banks of Columbia River, *Douglas* s.n. (not seen; presumably at K).

SECTION *JULOCROTON*

Croton sect. **Julocroton** (Mart.) Webster, J. Arnold Arbor. 48: 354. 1967. *Julocroton* Mart., Flora Beibl. 1837(2): 119. 1837, nom. cons. TYPE: *Julocroton phagedaenicus* Mart. [= *Croton triquetus* Lam.].

Cieca Adanson, Fam. Pl. 2: 355. 1763, nom. rej. TYPE: *Croton argenteus* L.

Heterochlamys Turcz., Bull. Soc. Imp. Naturalistes Moscou 16: 61. 1843. TYPE: *Heterochlamys quinqueria* Turcz. [= *Croton argenteus* L.].

Centrandra Karsten, Linnaea 28: 440. 1857. TYPE: *Centrandra hondensis* Karsten [= *Croton hondensis* (Karsten) Webster].

Julocroton subg. *Eremadenia* Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 134. 1857. TYPE: *Julocroton triquetus* Didr.

Julocroton subg. *Oligonychia* Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 132. 1857. TYPE: *Croton argenteus* L. (lectotype, selected here).

In the only general revision of *Julocroton* so far, Croizat (1943, 1944) recognized about 25 species. Species discrimination in the genus is difficult, and much work remains to be done in order to evaluate Croizat's proposals and determine how many valid binomials there are. Here I am making new combinations only for those species being cited as rep-

representatives of section *Julocroton* in an unpublished survey of the sections of *Croton*. This includes most of the species cited by Mueller (1873), as well as those names of Croizat that I have been able to evaluate. Pending a critical revision of section *Julocroton*, it is not possible to evaluate all of the binomials that have been proposed, but possible synonyms have been indicated where appropriate. In the following enumeration the correct names under *Croton* are given for those species of *Julocroton* that could be verified and judged distinct. Unless otherwise noted, microfiches and photographs cited are at DAV.

1. ***Croton abutilopsis*** Webster, nom. nov. Replaced name: *Julocroton abutiloides* Spencer Moore, Trans. Linn. Soc. Bot. II. 4: 465. 1895, non *Croton abutiloides* HBK, 1817. TYPE: Brazil. Matto Grosso do Sul: Corumbá, Moore 968 (holotype, BM not seen; photograph, B).
2. ***Croton ackermannianus*** (Muell. Arg.) Webster, comb. nov. Basionym: *Julocroton ackermannianus* Muell. Arg., Fl. Bras. 11(2): 283. 1873. TYPE: Brazil. Minas Gerais: *Ackermann s.n.* [var. β *ovatus*] (holotype, G not seen).
3. ***Croton acuminatissimus*** (Pittier) Webster, comb. nov. Basionym: *Julocroton acuminatissimus* Pittier, J. Wash. Acad. Sci. 20: 11. 1930. TYPE: Venezuela. Yaracuy: between La Piedra and Yaritagua, Pittier 11175 (holotype, US).
4. ***Croton allemii*** Webster, nom. nov. Replaced name: *Julocroton ramboi* Smith & Downs, Sellowia 11: 153. 1959, non *Croton ramboi* Allem, 1979. TYPE: Brazil. Santa Catarina: Itapiranga, 1951, *Rambo s.n.* (PACA 49824) (holotype, US).

It is appropriate to rename this species for my colleague Antonio Allem, who has contributed important publications on the systematics of *Croton* in southern Brazil.
5. ***Croton argenteus*** L., Sp. Pl. 1004. 1753. TYPE: America (probably in Hortus Cliffortianus Herbarium, BM not seen; possible isotype, 1140.8 in LINN, microfiche).

Probable synonyms, mostly indicated by Croizat (1943), include: *Julocroton camporum* Chodat & Hassler, *J. elaeagnoides* Spencer Moore, and *J. integer* Chodat & Hassler. Although accepted by Croizat as a distinct species, *J. montevidensis* Klotzsch ex Muell. Arg. may prove to be synony-

mous with *C. argenteus*; hence no new name is provided for it here.

6. ***Croton calonervosus*** Webster, nom. nov. Replaced name: *Julocroton nervosus* Baillon, Adansonia I. 4: 369. 1864, non *Croton nervosus* Klotzsch, 1843. TYPE: Brazil. Minas Gerais: St. Hilaire B² 2369 (lectotype, selected here, P not seen; photograph, DAV).
 7. ***Croton conspurcatus*** Schldl., Linnaea 7: 380. 1832. *Julocroton conspurcatus* (Schldl.) Klotzsch, Arch. Naturgesch. 7: 193. 1841. *Julocroton triquetus* var. *conspurcatus* (Schldl.) Muell. Arg., DC. Prodr. 15(2): 705. 1866. TYPE: Mexico. Veracruz (?): "in dumetis prope Tioselo," Schiede 39 (holotype, HAL not seen).
 8. ***Croton cordeiroae*** Webster, nom. nov. Replaced name: *Julocroton riedelianus* Muell. Arg., Fl. Bras. 11(2): 278. 1873, non *Croton riedelianus* Muell. Arg., Linnaea 34: 104. 1865. TYPE: Brazil. São Paulo: São Carlos, Riedel s.n. (holotype, G not seen; photograph, DAV).
- The specific epithet acknowledges the contributions of my colleague, Iris Cordeiro, to the systematics of Euphorbiaceae (including sect. *Julocroton*) in São Paulo and adjacent areas of Brazil.
9. ***Croton didrichsenii*** Webster, nom. nov. Replaced name: *Julocroton humilis* Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 132. 1857, non *Croton humilis* L., 1753. TYPE: Brazil. São Paulo: Mugi, Lund s.n. (holotype, C not seen; microfiche of isotype at G).
 10. ***Croton doratophylloides*** (Croizat) Webster, comb. nov. Basionym: *Julocroton doratophylloides* Croizat, Revista Argent. Agron. 10: 139. 1943. TYPE: Argentina. Misiones: Salto Iguazú, Rodriguez 438 (holotype, A).
 11. ***Croton flavispicatus*** Rusby, Mem. New York Bot. Gard. 7: 283. 1927. *Julocroton peruvianus* Muell. Arg. var. *flavispicatus* (Rusby) Croizat, Revista Argent. Agron. 10: 136. 1943. TYPE: Bolivia. La Paz: Ixiamas, Cardenas 2026 (holotype, NY not seen; photograph, DAV).

Julocroton peruvianus Muell. Arg., DC. Prodr. 15(2): 704. 1866, non *Croton peruvianus* Briq., 1900. TYPE: Peru. Loreto: Tarapoto, Spruce 4290 (holotype, G, microfiche seen).

Julocroton paniculatus Pax & Hoffm., Meded. Rijks-Herb. Leiden 40: 22. 1921, non *Croton paniculatus* Lam., 1786. TYPE: Bolivia. Santa Cruz: Río Pirai, Herzog 1486 (holotype, B, photograph).

- 12. *Croton fuscescens*** Sprengel, Syst. Veg. 2: 874. 1826. *Julocroton fuscescens* (Sprengel) Baillon, Adansonia I. 4: 367. 1864. TYPE: Brazil. Possibly from Rio de Janeiro, *Sellow s.n.* (not seen; microfiche of possible isotype at G).
- Probable synonym: *Julocroton paulensis* Usteri, as pointed out by Croizat (1943).
- 13. *Croton geraesensis*** (Baillon) Webster, comb. nov. *Julocroton geraesensis* Baillon, Adansonia I. 4: 370. 1864. TYPE: Brazil. Minas Gerais: St. Hilaire B¹ 1295 (holotype, P not seen; photograph, DAV).
- Possible synonym: *Julocroton valenzuella* (Chodat & Hassler) Croizat.
- 14. *Croton hondensis*** (Karsten) Webster, comb. nov. Basionym: *Centrandra hondensis* Karsten, Linnaea 28: 440. 1857. *Julocroton hondensis* (Karsten) Muell. Arg., DC. Prodr. 15(2): 704. 1866. TYPE: Colombia. Tolima: Honda, *Karsten s.n.* (not seen).
- 15. *Croton lanceolaris*** Webster, nom. nov. Replaced name: *Julocroton lanceolatus* Klotzsch ex Muell. Arg., DC. Prodr. 15(2): 702. 1866, non *Croton lanceolatus* Cav., 1800. TYPE: Brazil. São Paulo: Alegres, *Riedel 2806* (holotype, B presumed destroyed; photograph, DAV).
- 16. *Croton microcalyx*** (Muell. Arg.) Webster, comb. nov. Basionym: *Julocroton microcalyx* Muell. Arg., Linnaea 34: 142. 1865. TYPE: Brazil. São Paulo: Salto Ytú, *Riedel 2180* (holotype, G not seen; photograph of isotype, DAV).
- 17. *Croton phyllanthus*** (Chodat & Hassler) Webster, comb. nov. Basionym: *Julocroton phyllanthus* Chodat & Hassler, Bull. Herb. Boiss. II. 5: 501. 1905. TYPE: Paraguay. La Cordillera (?): Río Carimbatay, *Hassler 4576* (photograph of holotype, G).
- 18. *Croton rupestris*** (Chodat & Hassler) Webster, comb. nov. Basionym: *Julocroton rupestris* Chodat & Hassler, Bull. Herb. Boissier II. 5: 498. 1905. TYPE: Paraguay. Paraguari: Cordillera de Altos, *Hassler 3090, 3554* (syn-types, both at G; not seen).
- Julocroton velutinus* (Chodat & Hassler) Croizat, based on a variety of *J. rupestris*, is doubtfully distinct.
- 19. *Croton rutilus*** (Chodat & Hassler) Webster, comb. nov. Basionym: *Julocroton rutilus* Chodat & Hassler, Bull. Herb. Boissier II. 5: 501. 1905. TYPE: Paraguay. Canindeyu: Sierra de Maracayu [Mbaracayú], Ipe hu [Ype Jhu], *Hassler 5226* (holotype, G not seen; isotype, UC). Possible synonym: *J. pulcher* Croizat.
- 20. *Croton salzmännii*** (Baillon) Webster, comb. nov. Basionym: *Julocroton salzmännii* Baillon, Adansonia I. 4: 369. 1864. *Julocroton pycnophyllus* Schldl. ex Muell. Arg., DC. Prodr. 15(2): 705. 1866. TYPE: Brazil. Bahia: *Salzmänn s.n.* (holotype, P not seen; microfiche of possible isotype at B).
- Julocroton pycnophyllus*, as originally proposed by Schlechtendal (Linnaea 19: 245. 1847), was not validly published. Although Mueller validated it in the *Prodromus*, Baillon had already provided a description under the name *Julocroton salzmännii*.
- 21. *Croton solanaceus*** (Muell. Arg.) Webster, comb. nov. Replaced name: *Julocroton humilis* var. *solanaceus* Muell. Arg., DC. Prodr. 15(2): 701. 1866. *Julocroton solanaceus* (Muell. Arg.) Muell. Arg., Fl. Bras. 11(2): 279. 1873. TYPE: Brazil. São Paulo: Rio Verde, *Riedel 261* (holotype, B destroyed; isotype, G not seen).
- The original type collection of Sellow at B cited by Mueller (1866) having been destroyed, the Riedel specimen cited by Mueller (1873) can be chosen as neotype because it has a specific locality. There is a photograph of the Sellow specimen at B.
- Probable synonym: *Julocroton typhaecephalus* Croizat.
- 22. *Croton subpannosus*** Muell. Arg. ex Griseb., Pl. Lorentz. 48. Dec. 1874. TYPE: Argentina. Córdoba: Aschochinga, *Lorentz 291* (holotype, GOET not seen; isotype, G not seen; photograph of presumed isotype at B, DAV). *Julocroton subpannosus* Muell. Arg., J. Bot. 12: 203. July 1874. TYPE: Argentina. Córdoba: Aschochinga, *Lorentz 291* (lectotype, selected here, G not seen).
- Owing to the curious history of publication of this species, the holotype of *Julocroton subpannosus* Muell. Arg. is the same specimen as the isotype of *Croton subpannosus* Muell. Arg. ex Griseb. Croizat (1941) discussed the priority of the names of Mueller over those of Grisebach.
- Croton dentosus* Griseb., Pl. Lorentz. 49. 1874. TYPE: Argentina. Córdoba: Córdoba, *Lorentz 292* (holotype, GOET not seen; photograph of isotype at B). *Julocroton serratus* Muell. Arg., J. Bot. 12: 227. Aug.

1874. TYPE: Argentina. Córdoba: Córdoba, *Lorentz* 292 (lectotype, selected here, G).

There is the same relation between the two names and their types as in the preceding paragraphs. Croizat (1943) appears to be correct in combining *C. dentosus* with *C. subpannosus*.

Julocroton brittonianum Morong, Ann. New York Acad. Sci. 7: 222. 1893. TYPE: Paraguay. Río Pilcomayo, *Morong* 864 (holotype, NY not seen).

Croizat (1943) reduced Morong's species to the synonymy of *C. subpannosus*.

23. *Croton stipularis* (Muell. Arg.) Webster, comb. nov. *Julocroton montevidensis* α [var.] *stipularis* Muell. Arg., DC. Prodr. 15(2): 703. 1866. *Julocroton stipularis* (Muell. Arg.) Muell. Arg., Fl. Bras. 11(2): 277. 1873. TYPE: Brazil. Goyaz: *Pohl* 1647 (holotype, B destroyed).

24. *Croton triqueter* Lam., Encycl. 2: 214. 1786. *Julocroton triqueter* (Lam.) Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 134. 1857. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Commerson s.n.* (holotype, Herb. Jussieu 16339, P).

Julocroton phagedaenicus Mart., Flora 20, Beibl. 2: 119. 1837. TYPE: Brazil. *Martius* 164 (holotype, M not seen; microfiche of isotype at G).

25. *Croton verbascoides* Webster, nom. nov. Replaced name: *Julocroton verbascoifolius* Muell. Arg., DC. Prodr. 15(2): 701. 1866, non *Croton verbascoifolius* Willd., 1803. TYPE: Brasilia meridionalis, *Sellow s.n.* (lectotype, selected here, G not seen; microfiche, DAV). Typification was effected by the Royal Air Force in destroying the other syntype at B.

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