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A provisional synopsis of the sections of the genus *Croton (Euphorbiaceae)*

Grady L. Webster[1]

Summary

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The 19th century classification of *Croton* by Müller Argoviensis is highly artificial. A revised system that incorporates the sections proposed by Baillon and Grisebach is presented, with a key to the 40 sections recognized. For each section, types and synonymy are indicated, along with a description and list of representative species. Described as new are 2 sections *(C.* sect. *Anadenocroton,* sect. *Corylocroton)* and 3 subsections *(C.* subsect. *Cuneati,* subsect. *Matourenses,* subsect. *Sampatik);* 2 new sectional names *(C.* sect. *Argyrocroton,* sect. *Luntia)* represent changes in rank.

Croton is a large and diverse genus of *Euphorbiaceae* comprising at least 800 species of the tropics and subtropics. In the most recent general synopsis of the family (Webster, 1994), it is associated in the tribe *Crotoneae* with the Old World genera *Mildbraedia* and *Fahrenheitia. Croton* differs from those genera in having staminate flowers with filaments inflexed in the bud, and pistillate flowers with the petals usually reduced. Furthermore, most species of *Croton* have a characteristic habit, with terminal thyrses of flowers that have mostly solitary pistillate flowers below and cymules of staminate flowers distally.

The present article is a contribution towards a better understanding of phyletic relationships within the genus *Croton.* In contrast to the other large genera of *Euphorbiaceae* (e.g., *Acalypha, Euphorbia, Phyllanthus*), no coherent system of sections has heretofore been available in *Croton.* The classification of Müller (1866, 1873) was patently artificial (as Müller himself implied in various comments on individual species), and was criticized as such by Bentham (1880). Unfortunately, Pax (1890) accepted Müeller's system, and in the latest general treatment by Pax & Hoffmann (1931) Müller's taxa were retained but inflated in rank (by raising sections to subgenera, etc.). In contrast, Baillon (1858, 1861, 1864) and Grisebach (1859) recognized a considerable number of sections that by and large represent natural groups. These were cited in synonymy by Müller and Bentham, but have never been generally adopted because of the prevailing authority of the Müllerian system. In the 20th century, there have been a number of critical regional studies of *Croton*: in the United States (Ferguson, 1901); Texas (Johnston, 1959; Johnston & Warnock, 1962); Panama (Webster, 1968, 1988); Cuba (Carabia, 1942; Borhidi & Muñiz, 1977); Hispaniola (Liogier, 1986); Santa Catarina, Brazil (Smith & al., 1988); Rio Grande do Sul, Brazil (Allem, 1978, 1979); Argentina (Croizat, 1941), Congo (Léonard, 1962); tropical east Africa (Radcliffe-Smith, 1987); Madagascar (Leandri, 1939); Borneo (Airy Shaw, 1975); New Guinea (Airy Shaw, 1980a); Australia (Airy Shaw, 1980b). Airy Shaw and Croizat, in a considerable number of publications, have

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described many species and provided valuable discussions of interspecific relationships, but have not revised particular taxa except for the study of Croizat (1943) on *Croton* sect. *Julocroton*. Some workers, such as Leandri (1939) and Johnston (1959), abandoned Müller's formal classification in the *Prodromus* and used informal groups, apparently because of the perceived irrelevancy of the Müllerian sectional classification.

The lack of an intelligible arrangement of taxa within *Croton* has, in my opinion, greatly impeded progress in understanding relationships between species and species groups. Since species of *Croton* are prominent in subtropical and tropical vegetational communities (especially secondary ones), and have potential utility as sources of medicinal compounds, the lack of a meaningful classification is particularly deplorable. Biochemically, *Croton* is very diverse in alkaloids, terpenoids, and other compounds (Farnsworth & al., 1969), and it appears that biochemical data could provide important systematic characters, but this potential has gone unrealized at least partly because of the unintelligibility of the Müllerian classification.

Croizat (1940, 1941, 1944) rejected the classification of Müller but declined to provide a new one utilizing the sections of Baillon and Grisebach, partly because he lacked material of critical Madagascar species but also because he felt that it was premature to offer a revision. I sympathize with his point of view, but after several decades have passed feel that it is now timely to provide at least the scaffolding of a classification that can serve as a precursor to a truly phylogenetic system.

In the present synopsis of *Croton*, 40 sections are recognized, and a key is provided. For the first time, the various sections proposed by Baillon are integrated into an overall classification. In some respects, the writing of this paper has taken on the character of an archeological dig, as a considerable number of taxa have been rescued from oblivion. Clearly, some of the sections provisionally accepted in this synopsis (e.g. *Croton* sect. *Quadrilobus*, sect. *Decalobium*, and sect. *Decapetalon*) are of dubious standing. However, this synopsis does have the merit of accounting for all of the proposed sectional (and generic) names that have been applied to *Croton*. Perhaps more importantly, it exposes problems that will need to be addressed by future workers on the genus.

Although I earlier (Webster, 1975) followed previous workers in accepting the genera *Crotonopsis* and *Eremocarpus* as distinct from *Croton*, reconsideration during this study has led me to question that judgement. As earlier writers have noted, *Crotonopsis* is morphologically similar to *Croton* sect. *Gynamblosis* except for its indehiscent fruit. *Eremocarpus*, although distinctive in having highly reduced pistillate flowers (apparently correlated with a shift to wind pollination), is quite similar in vegetative characters to North American species of *Croton* sect. *Pilinophyton* and sect. *Velamea*. Continued recognition of *Crotonopsis* and *Eremocarpus* as distinct genera would clearly involve a starkly paraphyletic concept of *Croton*. Consequently, I see no reasonable alternative to treating these two small "satellite" genera as sections of *Croton* (Webster, 1992). This still leaves two West Indian genera, *Cubacroton* Alain and *Moacroton* Croizat as apparent satellites of *Croton*; but those taxa are much more distinctive and their status remains to be critically evaluated.

In this synopsis, in addition to the synonymy and description for each section, the constituent species, or a representative selection of them, are enumerated by geographical areas. For the first time, patterns of geographical distribution that have been obscured by the Müllerian classification now begin to emerge. Croizat, in

various publications on individual species, has made some perceptive comments about distributional relationships, but these have been largely ignored by the botanical community.

A significant fact that may not be immediately apparent is that a considerable number of species are not listed under any section. In a few instances, especially in *Croton* sect. *Cascarilla* and sect. *Velamea*, this is done for expediency because of the large number of species involved. In many instances, however, omissions of species are due to uncertainty about their position. I have deliberately tried to avoid describing new taxa to accommodate these doubtful species, but have sometimes listed them parenthetically within the section to which they show the greatest resemblance.

This is not the place for an extended discussion of the morphological characters important in the sectional classification of *Croton*. The key and descriptions in fact mostly use the classical characters of Müller (1866, 1873), with the important difference that vegetative characters are given much greater weight. Because of his uncompromising Linnean principles of classification, Müller used only reproductive characters for his major divisions, and these were applied in a rigidly hierarchical fashion (Webster, 1987). However, one of the most fertile sources of characters in *Croton* is the indumentum, which shows great diversity (Froembling, 1896). Unfortunately, due to the incompleteness of available data, it has seemed necessary in this study to mainly utilize the rather crude distinction between stellate and lepidote trichomes; by further studies one should be able to achieve considerable refinement, especially in elucidating the transitional stellate-lepidote types. The presence of glands on leaves and stipules (as well as perianths) is another important character that was justifiably used by Baillon and Müller. In a large number of species, there is a pair of glands (sometimes accompanied by additional ones) at the junction between the lamina and petiole; these paired glands are referred to in this work as the leaf base glands. In addition, there are in some species glands on the margin and/or midrib of the leaf; these are morphologically different (smaller, globose rather than flattened, often stalked), and generally species with conspicuous marginal foliar glands do not have well-differentiated basal ones.

With regard to reproductive characters, Müller (1866, 1873) placed excessive weight on the number and degree of symmetry of perianth parts. A particularly problematical character, upon which Müller heavily relied, is that of the degree of development of petals in the pistillate flower. Müller (1866) brought together in *Croton* sect. *Eluteria* all the species in which the pistillate flowers have well-developed petals. However, as Radcliffe-Smith (1987) and other workers have indicated, there are all degrees of reduction of these petals, even within individual species. It is quite clear that *Croton* sect. *Eluteria* in the sense of Müller is unnatural. Another character used by Müller that is similarly problematic because of transitional states is that of the presence of bisexual cymules in the inflorescence (i.e., staminate flowers associated with the pistillate ones at the lower nodes). This feature, as with well-developed petals in pistillate flowers, appears to be primitive (plesiomorphic) within *Croton*, and thus cannot be used as a diagnostic criterion except when it is correlated with other features. Furthermore, there is widespread variability in inflorescence expression in *Croton*; a common and misleading situation in some groups (e.g. *C.* sect. *Cleodora* and sect. *Cyclostigma*) is the production of purely staminate inflorescences; individual specimens may appear entirely staminate, and this has led to some species being incorrectly described as dioecious.

More justifiable is Müller's use of the term "reduplicate" to refer to calyces of the pistillate flowers in which adjacent pairs of valvate sepals form a projection at the base; reduplicate calyces are usually distinctly angular and recognizable even in the bud stage. A character that has been treated rather arbitrarily is the degree of stylar division, a feature greatly favored by Müller. In the present treatment, the term "multifid" has been used to apply to styles in which the branches are divided, whether once (quadrifid) or many times. Fruit and seed characters have scarcely been used at all at the sectional level, even though they often supply distinctions between species; they need to be looked at attentively in the future.

It is only fair to point out here a major bias in this study: my personal lack of familiarity with the living plants in Africa, Madagascar, and Asia; as a result, the treatment of Old World taxa is much more cursory than that of New World taxa. The Madagascar species have been particularly exasperating to deal with, despite the review by Leandri (1939) and his later publications. Baillon (1858, 1861) based several of his sections on Madagascar plants, and I am far from confident that I have correctly assigned African or Asian plants to these sections. It is striking that the majority of Madagascar species, whether with stellate or lepidote indumentum, have opposite or subopposite leaves – a feature rare in other parts of the world. Baillon (1861) suggested that this opposite phyllotaxy is correlated with sympodial branching; and Leandri (1971) has provided a plausible scenario, that the many shrubby sympodial species in Madagascar may have evolved from ancestors such as *Croton goudotii* with arboreal habit and alternate leaves. This suggests that in a future revision of *Croton* these Madagascar taxa may need to be brought together into a single group. However, it should be noted that sympodial branching with opposite or subopposite leaves does occur in a number of extra-Madagascar species, especially in herbs. The character therefore may show a high degree of homoplasy.

One of the reasons why the systematic arrangement of *Croton* is difficult at the supraspecific level is the pervasiveness of parallelism and convergence (homoplasy) in many of the classical characters. There may have been several instances of independent transitions between multifid and bifid styles, stellate and lepidote indumentum, and leaves with and without basal glands. On the other hand, a few of the characters used by Müller may represent truly shared derived characters (synapomorphies); examples include the presence of glandular stipules and calyces, reduplicate-valvate calyces, and possibly the opposite phyllotaxy in Malagasian species. More critical studies of morphological features such as trichomes and foliar glands may provide additional synapomorphies that may greatly facilitate construction of a truly phyletic classification of *Croton*.

In the following synopsis, 40 sections are enumerated, with. types generally cited in accordance with Farr & al. (1979); they, however, overlooked the article by Wheeler (1975), in which a significant number of generic typifications were proposed. A number of new lectotypifications, made in this text, are indicated as such. A reviewer has pointed out that this proposed classification is retrogressive inasmuch as it relies almost exclusively on the single rank of section, in contrast to Müller's complex hierarchical system. My plea to this is "guilty", and it must be kept in mind that the present system is provisional and intended as only the starting point for critical investigations. Very likely, subgenera, subsections, and series will creep back into use as our knowledge of the evolutionary patterns in *Croton* becomes more refined.

Conspectus of the sections and subsections of Croton

1. sect. *Cleodora* (Klotzsch) Baill.
2. sect. *Cyclostigma* Griseb.
   2a. subsect. *Cyclostigma* (Griseb.) Müll. Arg.
   2b. subsect. *Sampatik* G. L. Webster
   2c. subsect. *Palanostigma* Mart. ex Baill.
3. sect. *Klotzschiphytum* (Baill.) Baill.
4. sect. *Eutropia* (Klotzsch) Baill.
5. sect. *Luntia* (Raf.) G. L. Webster
   5a. subsect. *Cuneati* G. L. Webster
   5b. subsect. *Matourenses* G. L. Webster
6. sect. *Eluteria* Griseb.
7. sect. *Croton*
8. sect. *Ocalia* (Klotzsch) Baill.
9. sect. *Corylocroton* G. L. Webster
10. sect. *Anadenocroton* G. L. Webster
11. sect. *Tiglium* (Klotzsch) Baill.
12. sect. *Quadrilobus* Müll. Arg.
13. sect. *Cascarilla* Griseb.
14. sect. *Velamea* Baill.
15. sect. *Andrichnia* Baill.
16. sect. *Anisophyllum* Baill.
17. sect. *Furcaria* Boivin ex Baill.
18. sect. *Monguia* Baill.
19. sect. *Decapetalon* Müll. Arg.
20. sect. *Podostachys* (Klotzsch) Baill.
21. sect. *Octolobium* Chodat & Hassl.
22. sect. *Geiseleria* (Klotzsch) Baill.
23. sect. *Pilinophyton* (Klotzsch) A. Gray
24. sect. *Eremocarpus* (Benth.) G. L. Webster
25. sect. *Gynamblosis* (Torr.) A. Gray
26. sect. *Crotonopsis* (Michx.) G. L. Webster
27. sect. *Argyrocroton* (Müll. Arg.) G. L. Webster
28. sect. *Lamprocroton* (Müll. Arg.) Pax
29. sect. *Julocroton* (Mart.) G. L. Webster
30. sect. *Adenophyllum* Griseb.
31. sect. *Barhamia* (Klotzsch) Baill.
32. sect. *Decalobium* Müll. Arg.
33. sect. *Micranthis* Baill.
34. sect. *Medea* (Klotzsch) Baill.
35. sect. *Lasiogyne* (Klotzsch) Baill.
36. sect. *Argyroglossum* Baill.
37. sect. *Astraeopsis* Baill.
38. sect. *Codonocalyx* Klotzsch ex Baill.
39. sect. *Astraea* (Klotzsch) Baill.
40. sect. *Drepadenium* (Raf.) Müll. Arg.

Key to the sections of Croton

1. Lower nodes of inflorescence with bisexual cymules; leaves usually biglandular at base 2
1. Lower nodes of inflorescence with only pistillate flowers; leaves with or without glands at base 6
2. Sepals of pistillate flower distinctly imbricate 3
2. Sepals of pistillate flower valvate 4
3. Styles multifid; sepals of pistillate flower ± connate; indumentum stellate . . . . . 1. sect. *Cleodora*
3. Styles bifid (tips at most emarginate); sepals of pistillate flower distinct; indumentum stellate-lepidote . . . . . 4. sect. *Eutropia*
4. Indumentum stellate . . . . . 2. sect. *Cyclostigma*
4. Indumentum lepidote 5
5. Styles multifid . . . . . 5. sect. *Luntia*
5. Styles bifid . . . . . 27. sect. *Argyrocroton*
6. Sepals of pistillate flowers well developed 7
6. Sepals of pistillate flowers obsolete; ovary 1-locular, styles unbranched . . . . . 24. sect. *Eremocarpus*
7. Petals ± equalling sepals in both staminate and pistillate flowers 8
7. Petals reduced or absent in pistillate flowers 11
8. Indumentum stellate; leaves glandular at base 9
8. Indumentum lepidote 10
9. Stamens over 20; leaves alternate, palmately veined . 3. sect. *Klotzschiphytum*
9. Stamens under 20; leaves opposite or subopposite, pinnately veined . . . . . 15. sect. *Andrichnia*
10. Leaves glandular at base; inflorescences terminal . . . . . 18. sect. *Monguia*
10. Leaves eglandular at base; inflorescences axillary . . . . . 6. sect. *Eluteria*
11. Petals present in staminate flowers 12
11. Petals absent in staminate flowers . . . . . 40. sect. *Drepadenium*
12. Staminate receptacle usually copiously villose (or else leaves copiously pubescent); seeds ellipsoidal to globose 13
12. Staminate receptacle glabrate to sparsely villose; indumentum stellate; seeds more or less tetragonal . . . . . 39. sect. *Astraea*
13. Sepals of pistillate flower valvate but not reduplicate 14
13. Sepals of pistillate flower reduplicate-valvate (or with epicalyx); styles multifid 43
14. Stipules and/or sepals not laciniate or glandular-toothed 15
14. Stipules and/or sepals laciniate or glandular-toothed 39
15. Indumentum stellate or dendritic 16
15. Indumentum lepidote, at least in part 32
16. Inflorescence without a distinct gap between pistillate and staminate flowers 17
16. Inflorescence with a distinct gap between pistillate and staminate flowers; sepals of pistillate flower more or less unequal 31
17. Leaves opposite or subopposite (at least in part); species mainly of Madagascar 18
17. Leaves alternate (rarely opposite, in extra-Madagascar species 19

18. Styles multifid; leaves often with laminar glands . . . 16. sect. *Anisophyllum*
18. Styles bifid; leaves eglandular beneath on lamina . . . . . 17. sect. *Furcaria*
19. Sepals of pistillate flower not markedly unequal; mainly shrubs or trees; bracts not glandular (or bracteal glands similar to laminar ones) 20
19. Sepals of pistillate flower distinctly unequal; herbs or subshrubs, leaves with paired basal glands; bracts with clusters of small glands . 22. sect. *Geiseleria*
20. Styles multifid 21
20. Styles bifid 26
21. Leaves glandular at base 22
21. Leaves eglandular at base (or glands rudimentary) 24
22. Stamens 15 or more; leaves not duplicidentate 23
22. Stamens 7-12; leaves coarsely duplicidentate . . . . . 8. sect. *Ocalia*
23. Sepals of pistillate flower distinctly imbricate . . . . . 1. sect. *Cleodora*
23. Pistillate sepals not distinctly imbricate . . . . . 7. sect. *Croton*
24. Sepals of pistillate flower (4) 5 25
24. Sepals of pistillate flower 7-10 . . . . . 23. sect. *Pilinophyton*
25. Leaves distinctly pinnately veined or triplinerved; shrubs or trees . . . . . 10. sect. *Anadenocroton*
25. Leaves obscurely veined, indumentum appressed; herbs or subshrubs . . . . . 34. sect. *Medea*
26. Indumentum depressed-stellate, extremely scanty; leaves glandular at base 27
26. Indumentum not strongly appressed, ± copious; leaves entire or denticulate 29
27. Trichomes stellate; leaves entire or denticulate 28
27. Trichomes appressed-stellate to stellate-lepidote; leaves coarsely dentate . . . . . 9. sect. *Corylocroton*
28. Calyx 5-merous . . . . . 11. sect. *Tiglium*
28. Calyx 4-merous . . . . . 12. sect. *Quadrilobus*
29. Leaves glandular at base . . . . . 13. sect. *Cascarilla*
29. Leaves eglandular at base; stipules often reduced 30
30. Trees or shrubs, stems not dichotomously branching; pistillate flowers sessile or subsessile . . . . . 14. sect. *Velamea*
30. Subshrubs or herbs, stems more or less dichotomously branching; pistillate flowers distinctly pedicellate, often reflexed . . . . . 25. sect. *Gynamblosis*
31. Sepals of pistillate flower 5 . . . . . 20. sect. *Podostachys*
31. Sepals of pistillate flower 6-8 . . . . . 21. sect. *Octolobium*
32. Leaves mainly alternate 33
32. Leaves opposite or subopposite (at least distally) 38
33. Leaves glandular at base 34
33. Leaves eglandular at base 36
34. Styles multifid . . . . . 5. sect. *Luntia*
34. Styles bifid 35
35. Leaves ± entire . . . . . 27. sect. *Arygyrocroton*
35. Leaves coarsely dentate, stellate-lepidote . . . . . 9. sect. *Corylocroton*
36. Fruit dehiscent, ovary trilocular; shrubs, perennial or annual herbs 37
36. Fruit indehiscent, ovary unilocular; annual herbs . . . . 26. sect. *Crotonopsis*

37. Shrubs; indumentum definitely lepidote, at least on twigs and underside of leaves; pistillate flowers sessile or subsessile, never recurved . . . . . 28. sect. *Lamprocroton*
37. Subshrubs or herbs; indumentum stellate-lepidote or appressed-stellate; pistillate flowers long-pedicellate, often recurved . . . . . 25. sect. *Gynamblosis*
38. Leaves glandular at base . . . . . 18. sect. *Monguia*
38. Leaves eglandular at base . . . . . 19. sect. *Decapetalon*
39. Stamens 20-40 . . . . . 30. sect. *Adenophyllum*
39. Stamens 6-15 40
40. Sepals of pistillate flowers not deeply laciniate nor strongly unequal . . . 41
40. Sepals of pistillate flowers deeply laciniate and strongly unequal . . . . . 29. sect. *Julocroton*
41. Racemes elongated; leaves large (over 1 cm long), palmately veined . . . . . 31. sect. *Barhamia*
41. Racemes abbreviated, or leaves less than 1 cm long 42
42. Leaves rounded, less than 1 cm long; hairs appressed; stems erect to procumbent . . . . . 33. sect. *Micranthis*
42. Leaves elongated, pointed, mostly more than 1 cm long; pubescence loose, often tomentose; stems erect . . . . . 34. sect. *Medea*
43. Stipules and sepals of pistillate flower not laciniate or glandular-lobed . . 44
43. Stipules and sepals of pistillate flower laciniate or glandular-toothed . . . 45
44. Indumentum stellate . . . . . 35. sect. *Lasiogyne*
44. Indumentum lepidote . . . . . 36. sect. *Argyroglossum*
45. Epicalyx absent in pistillate flower 46
45. Epicalyx of 5 small segments present in pistillate flower 32. sect. *Decalobium*
46. Monoecious; indumentum appressed . . . . . 37. sect. *Astraeopsis*
46. Dioecious; indumentum loose . . . . . 38. sect. *Codonocalyx*

Croton L., Sp. Pl.: 1004. 1753 ≡ *Oxydectes* Kuntze, Revis. Gen. Pl.: 609. 1891 (nom. superfl.). – LT. (Webster, 1967): *C. aromaticus* L. (supersedes the earlier designation, accepted by Farr & al., 1979, of *C. tiglium* L. by Small (1913).

A pantropical genus of c. 800 described species; detailed generic descriptions are provided by Webster (1967, 1988).

1. ***Croton*** sect. ***Cleodora*** (Klotzsch) Baill., Etude Euphorb.: 369. 1858 ≡ *Cleodora* Klotzsch in Arch. Naturgesch. 7: 196. 1841 ≡ *Croton* subsect. *Cleodora* (Klotzsch) Müell. Arg. in Martius, Fl. Bras. 11(2): 133. 1873. – T.: *Cleodora sellowiana* Klotzsch [= *Croton sphaerogynus* Baill.]. (Some uncertainty remains as to the application of this name because no type material of *Cleodora sellowiana* has been seen; the disposition of Müller (1866: 591) is being followed in the lack of contrary evidence.)

= *Croton* sect. *Stolidanthus* Baill. in Adansonia 4: 323. 1864 – LT. (designated here): *C. heterocalyx* Baill. The lectotype species is chosen because it fits Baillon's sectional description in having both distinctly unequal and broadly imbricate pistillate sepals.

Monoecious trees or shrubs; indumentum appressed-stellate; leaves alternate, pinnately or palmately veined, glandular at base; inflorescences terminal, lower cymules

bisexual or sometimes unisexual; petals present in staminate, reduced or absent in pistillate flowers; sepals of staminate flowers imbricate; stamens 15-20; pistillate flowers distinctly pedicellate, sepals 5, basally connate and/or distinctly imbricate, entire; styles multifid.

This neotropical section of about 10 species (or less) has a curious disjunct distribution in Costa Rica, Amazonia, and eastern Brazil. The synonymy of *Croton* sect. *Stolidanthus* with *C.* sect. *Cleodora* seems secure, since these plants of eastern Brazil are closely related. The character of lower bisexual cymules appears to be inconsistent within the section. Müller (1866) at first listed *C. sphaerogynus* among species with unisexual lower cymules but subsequently (Müller, 1873) among those with bisexual lower cymules. In fact, most specimens of *C. sphaerogynus* have strictly unisexual cymules; in any event, it is clear that this character is not diagnostic for the section. Two additional species recorded by Müller (1873) as having slightly imbricate calyces, *C. organensis* Baill. and *C. piptocalyx* Müll. Arg., are of dubious affinity but perhaps are better placed in *C.* sect. *Cyclostigma*. The Central American species *C. billbergianus* Müll. Arg. strongly resembles *C. hoffmannii* Müll. Arg. in habit, but has distinctly nonimbricate pistillate sepals.

Representative species. – [Costa Rica:] *Croton hoffmannii* Müll. Arg.; [Brazil:] *C. cajucara* Benth., *C. calycularis* Huber, *C. hemiargyreus* Müll. Arg., *C. heterocalyx* Baill., *C. maracayuensis* Chodat & Hassl., *C. sepotubensis* Hoehne, *C. sphaerogynus* Baill.

2. ***Croton*** sect. ***Cyclostigma*** Griseb., Fl. Brit. W. I.: 42. 1859 ≡ *Cyclostigma* Klotzsch in Seemann, Bot. Voy. Herald: 104. 1853 (non *Cyclostigma* Hochst. ex Endl., 1842) ≡ *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. – T.: *Croton gossypiifolius* Vahl. (Grisebach cited only one species and did not indicate the illegitimate basionym of Klotzsch; however, his intent seems clear; and *C. gossypiifolius* as treated by Müller (1866) includes *C. hibiscifolius*, which was enumerated by Klotzsch. There seems to be no reason to adopt the designation by Wheeler (1975) of *Cyclostigma panamense* Klotzsch as lectotype.)

Monoecious trees or shrubs; indumentum stellate; stems often exuding reddish sap; leaves alternate, mostly palmately veined or lobed, biglandular at base; inflorescences terminal, basal cymules bisexual; petals present in staminate flowers, usually reduced in pistillate flowers; stamens 11-100 or more; pistillate flowers distinctly pedicellate, sepals entire, eglandular, valvate or reduplicate-valvate; styles bifid to multifid.

As delimited here, sect. *Cyclostigma* includes 40-50 mainly neotropical species. The section is quite diverse, and tentatively may be divided into 3 subsections:

2a. ***Croton*** subsect. ***Cyclostigma*** (Griseb.) Müll. Arg. in Linnaea 34: 81. 1865. – T.: *C. gossypiifolius* Vahl.

Leaves palmately or pinnately veined, subentire or denticulate, copiously stellate beneath; stamens 15-65; calyx of pistillate flower not reduplicate-valvate; styles bifid. Mainly New World. Some species included by Müller (1866) probably do not belong here, including e.g. *Croton suberosus* Kunth with eglandular leaves.

Representative species. – [North America:] *Croton draco* Cham. & Schltdl., *C. verapazensis* Donn. Sm., *C. xalapensis* Kunth; [South America:] *C. anisodontus* Müll. Arg., *C. chilensis* Müll. Arg., *C. densiflorus* Pax & K. Hoffm., *C. echinocarpus* Müll. Arg., *C. funckianus* Müll. Arg., *C. gracilipes* Baill., *C. huberi* Steyerm., *C. lechleri* Müll. Arg., *C. macrobothrys* Baill., *C. magdalenensis* Müll. Arg., *C. mutisianus* Kunth, *C. pungens* Jacq., *C. purdaei* Müll. Arg., *C. redolens* Pittier, *C. ruizianus* Müll. Arg., *C. sarcopetalus* Müll. Arg., *C. sarcopetaloides* S. Moore, *C. urucurana* Baill.; [Africa:] *C. draconopsis* Müll. Arg.; [Madagascar:] *C. mongue* Baill., *C. oreades* Leandri. (Several other African species, including *C. congensis* De Wild., *C. pynaertii* De Wild., and *C. wellensii* De Wild., have inflorescences of *C.* sect. *Cyclostigma* but indumentum more similar to *C.* sect. *Andrichnia*; their status requires further study.)

2b. ***Croton*** subsect. ***Sampatik*** G. L. Webster, **subsect. nov.** – Folia penninervia, crenata, pilis stellatis; stamina 15-20; sepalis floris femeneus non reduplicativis; styli bifidi. – T.: *C. sampatik* Müll. Arg.

Leaves pinnately veined, crenate, sparsely appressed-stellate; stamens 10-20; pistillate flowers long-pedicellate; sepals of pistillate flower not reduplicate-valvate; styles bifid.

This new subsection is proposed to accommodate some South American species that differ from most other species of *Croton* sect. *Cyclostigma* in their elongated, nearly glabrous leaves and long inflorescence with unusually long-pedicellate pistillate flowers. The habit is reminiscent of some species in *C.* sect. *Tiglium*.

Representative species. – [Amazonian South America:] *Croton sampatik* Müll. Arg.; [Brazil:] *C. cordiifolius* Baill., *C. organensis* Baill., *C. piptocalyx* Müll. Arg., *C. priscus* Croizat. (*C. echioides* Baill., from Bahia, appears similar in habit but has subsessile pistillate flowers.)

2c. ***Croton*** subsect. ***Palanostigma*** Mart. ex Baill., Etude Euphorb.: 358. 1858. – T.: *C. palanostigma* Klotzsch (Klotzsch, 1843, cited "*Palanostigma* Mart." in synonymy, but the name does not appear to have been validly published at the generic level.)

Leaves mostly palmately veined and copiously stellate beneath; stamens 10-100+; pistillate flowers distinctly pedicellate, sepals ± reduplicate-valvate; styles multifid.

There are no typical species of *Croton* subsect. *Palanostigma* confined to North America, although species such as *C. smithianus* Croizat extend north to Costa Rica and Nicaragua. *C. grewiifolius* Müll. Arg., although technically fitting into this subsection because of the quadrifid styles, differs in its nearly pinnately veined leaves. *C. goudotii* Baill. is exceptional in having both bisexual cymules and well-developed pistillate petals, as well as in its striking geographical disjunction from its American relatives.

The only neotropical species of *Croton* known to be lianas, *C. adscendens* Secco & N. Rosa and *C. pullei* Lanj., are close relatives in the Amazon forest (Secco & Rosa, 1992). They appear to belong to *C.* subsect. *Palanostigma* because of their reproductive characters, although they differ in the climbing habit and short-pedicellate flowers. Possibly further study will show that these climbing species should be referred to a separate subsection.

Representative species. – [South America:] *Croton abutiloides* Kunth, *C. benthamianus* Müll. Arg., *C. caldensis* Müll. Arg., *C. callicarpifolius* Vahl, *C. celtidifolius* Baill., *C. coriaceus* Kunth, *C. fastuosus* Baill., *C. killipianus* Croizat, *C. lagoensis* Müll. Arg., *C. medusae* Müll. Arg., *C. polycarpus* Benth., *C. pycnanthus* Benth., *C. quadrisetosus* Lam., *C. rimbachii* Croizat, *C. smithianus* Croizat, *C. sordidus* Benth., *C. speciosus* Müll. Arg., *C. warmingii* Müll. Arg.; [Madagascar:] *C. chypreae* Leandri, *C. goudotii* Baill.

3. ***Croton*** sect. ***Klotzschiphytum*** Baill. in Adansonia 1: 169. 1861 ≡ *Halecus* Raf., Sylva Tellur.: 62. 1838 ≡ *Klotzschiphytum* Baill., Etude Euphorb.: 382. 1858, nom. illeg. – T.: *H. mauritianus* (Lam.) Raf. (*K. mauritianum* (Lam.) Baill., *C. mauritianum* Lam.)

Monoecious trees or shrubs; indumentum of leaves depressed-stellate; leaves alternate, palmately veined, glandular at base; inflorescences terminal, not bisexual below; petals present in staminate and pistillate flowers; stamens 20-60; pistillate flowers pedicellate, sepals entire, valvate; styles bifid to multifid.

This section in the strict sense would include only *Croton mauritianus* Lam. and *C. boutonianus* Müll. Arg. of Mauritius and Reunion. Its status must be regarded as dubious, since it differs from *C.* sect. *Andrichnia* only in the alternate leaves and larger stamen number.

Species included. – [Madagascar:] *Croton chypreae* Leandri; [Mauritius & Reunion:] *C. boutonianus* Müll. Arg., *C. mauritianus* Lam.

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

Monoecious trees or shrubs; indumentum lepidote or stellate-lepidote; leaves alternate or opposite, palmately or pinnately veined, biglandular at base; stipules entire; inflorescences terminal, with bisexual cymules at base, bracts persistent; petals present in staminate flowers, reduced in pistillate flowers; sepals of staminate flower imbricate; stamens 10-15; pistillate flowers subsessile, sepals entire, imbricate; styles bifid (style-branches at most emarginate).

As circumscribed here (as monotypic), *Croton* sect. *Eutropia* is much smaller than in the treatments of Müller (1873, as subsection) and Pax & Hoffmann (1931), who included all of the species with bisexual lower cymules in the inflorescences. Even *C.* ser. *Eutropia* of Müller (*C.* subsect. *Eutropia* of Pax) is more inclusive, with all of the lepidote species of *C.* sect. *Eutropia*. However, the type species of *C.* sect. *Eutropia*, *C. polyandrus*, from coastal Brazil, differs from all the associated species in its pistillate flowers with discrete, distinctly imbricate sepals. The species assigned to *C.* ser. *Eutropia* by Müller (1873) seem better placed in either *C.* sect. *Cleodora* or sect. *Luntia*. There are a number of paleotropical species, such as *C. argyratus* Blume, *C. insularis* Baill., and *C. macrostachys* Del., that share characters with *C.* sect. *Eutropia*; however, until further studies can be made, it would be premature to include any of them in this section.

The relationships of *Croton* sect. *Eutropia* may be closest with *C.* sect. *Cleodora*, in which the sepals of the pistillate flowers are also (usually) distinctly imbricate. At

present, it appears reasonable to maintain *C.* sect. *Eutropia* as distinct because its type, *C. polyandrus*, differs from the species of *C.* sect. *Cleodora* in having dentate leaves, persistent bracts, chorisepalous calyces, and bifid styles.

5. ***Croton*** sect. ***Luntia*** (Raf.) G. L. Webster, **stat. nov.** ≡ *Luntia* Necker ex Raf., Sylva Tellur.: 62. 1838. – T.: *L. sericea* Raf., nom. illeg. (*C. sericeus* Lam., nom. illeg.; *C. matourensis* Aubl.).

Monoecious trees or shrubs; indumentum lepidote; leaves alternate, pinnately veined, entire, biglandular at base, stipules entire, deciduous; inflorescences terminal, often clustered, unisexual or bisexual, the latter with or without bisexual cymules at base; stamens 10-15; pistillate flowers subsessile or pedicellate, sepals entire and eglandular, valvate (or somewhat reduplicate); styles multifid.

This well-characterized section appears to be entirely neotropical, although there are some African species (e.g. *Croton mubango* Müll. Arg.) that might prove to be related. Jablonski (1965) treated the South American taxa under an informal designation ("*C. matourensis*" group). Species of *C.* sect. *Luntia* are easily distinguished from *C.* sect. *Eutropia* by their entire leaves and valvate sepals. Species of *C.* sect. *Argyrocroton* that have bisexual cymules are distinguishable from *C.* sect. *Luntia* by their bifid styles.

The species of *Croton* sect. *Luntia* fall into two distinctive groups that merit recognition as subsections.

5a. ***Croton*** subsect. ***Cuneati*** G. L. Webster, **subsect. nov.** – Inflorescentia glomerulis infimis bisexualibus ferentibus; floribus foemineorum subsessilibus, ca-lycibus chorisepalis. – T.: *C. cuneatus* Klotzsch.

Leaves scattered-lepidote beneath; inflorescences staminate or bisexual, the latter (at least in part) usually with bisexual cymules at base; pistillate flowers subsessile (pedicels in flower shorter than calyx); sepals more or less free; capsules oblong (1 cm high or more).

Croton subsect. *Cuneati* includes about 10 species mainly of South America. Most of these were reviewed by Jablonski (1965), who proposed a number of very similar species that need to be critically evaluated.

Representative species. – [West Indies:] *Croton poecilanthus* Urb.; [Panama & Colombia:] *C. pachypodus* G. L. Webster; [Amazonia:] *C. cuneatus* Klotzsch, *C. tessmannii* Mansf.; [Guyana Highlands:] *C. kaieteuri* Jabl., *C. monachinoensis* Jabl., *C. neblinae* Jabl., *C. subcoriaceus* Jabl. From Jablonski's descriptions, it seems doubtful that *C. pakaraimae* Jabl. belongs here because of the eglandular leaves, and *C. icaburui* Jabl. is even more doubtful because of the imbricate sepals in the pistillate flower.

5b. ***Croton*** subsect. ***Matourenses*** G. L. Webster, **subsect. nov.** – T.: *C. matourensis* Aubl.

Inflorescentia infimis glomerulis bisexualibus destitutis; floribus foemineorum longe pedicellatis, ± gamosepalis.

Leaves usually metallic-lepidote beneath; inflorescences staminate or bisexual, without bisexual cymules at base; pistillate flowers long-pedicellate, calyx ± gamophyllous; fruit oblate (less than 1 cm high).

This primarily South American subsection includes only 2 closely related species that were first clearly descriminated by Lanjouw (1931). None of the other species enumerated by Jablonski (1965) appear to be closely related; these are mostly referable to *Croton* subsect. *Cuneati*.

Species included. – [Panama & South America:] *Croton lanjouwensis* Jabl.; [Venezuela to Brazil:] *C. matourensis* Aubl.

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

Monoecious trees or shrubs; indumentum of foliage lepidote; leaves alternate, entire and unlobed, pinnately or palmately veined, without petiolar glands; stipules rudimentary or absent; inflorescences mostly axillary, without bisexual cymules; petals present in both staminate and pistillate flowers; stamens mostly 10-16; pistillate flowers pedicellate, sepals entire, valvate, eglandular; ovary with stellate or lepidote trichomes; styles multifid.

As defined here, *Croton* sect. *Eluteria* is an entirely American group of about a dozen species. Old World species that were included in the section by Müller (1866) and by Pax & Hoffmann (1931), which differ in having leaves with laminar glands, are referable to *C.* sect. *Andrichnia*, sect. *Klotzschiphytum*, and sect. *Monguia*.

Representative species. – [Caribbean America:] *Croton niveus* Jacq.; [North America:] *C. arboreus* Millsp., *C. fantzii* Seym., *C. guatemalensis* Lotsy, *C. pseudoniveus* Lundell, *C. pyriticus* Croizat, *C. reflexifolius* Kunth, *C. schiedeanus* Schltdl.; [West Indies:] *C. eluteria* (L.) Sw., *C. nitens* Sw.

7. ***Croton*** sect. ***Croton*** [*C.* sect. *Eucroton* Baill., Etude Euphorb.: 354. 1858, nom. inval.] – LT.: *C. aromaticus* L. (see above).

Monoecious trees or shrubs; indumentum of foliage stellate; leaves alternate, unlobed, ± palmately veined, glandular at base; stipules entire; inflorescences terminal, without bisexual cymules; petals absent in pistillate flowers; stamens 15-35; pistillate flowers pedicellate, sepals entire, eglandular, valvate; ovary with stellate trichomes; styles multifid.

As here interpreted, *Croton* sect. *Croton* includes about 10 Old World species of the Mascarene islands, tropical Asia, and northern Australia. A few American species such as *C. astrogynus* Baill. and *C. billbergianus* Müll. Arg. would be referable here on the basis of their characters but are probably not closely related.

Representative species. – [Africa:] *Croton megalobotrys* Müll. Arg.; [Mascarene Islands:] *C. tiliifolius* Lam.; [India & Sri Lanka:] *C. aromaticus* L., *C. lacciferus* L., *C. zeylanicus* Müll. Arg.; [Southeast Asia:] *C. crassifolius* Geiseler; [Australia:] *C. phebalioides* Müll. Arg., *C. tomentellus* Müll. Arg.

8. ***Croton*** sect. ***Ocalia*** (Klotzsch) Baill., Etude Euphorb.: 366. 1858 ≡ *Ocalia* Klotzsch in Arch. Naturgesch. 7: 195. 1841. – LT. (Baillon, 1858): *C. perdicipes* A. St.-Hil. [= *C. antisiphiliticus* Mart.]

Monoecious or dioecious shrubs; indumentum stellate; leaves alternate (sometimes opposite), unlobed, pinnately or palmately veined, ± coarsely serrate, glandular at base; stipules entire; inflorescences terminal, without bisexual cymules; petals

absent in pistillate flowers; stamens 7-12(15); sepals of pistillate flower entire, eglandular, valvate; ovary with stellate trichomes; styles multifid.

This section includes about 10 species with a disjunct distribution between North America, the West Indies, and extra-Amazonian Brazil. Judging from the description (Léonard, 1962), *Croton laciniatistylus* Léon., an African species from Katanga, may be related to the Brazilian species.

Representative species. – [North America:] *Croton brevipes* Pax, *C. macrodontus* Müll. Arg.; [West Indies:] *C. betulinus* Vahl; [Brazil:] *C. antisiphiliticus* Mart., *C. caperoniifolius* Müll. Arg., *C. crustulifer* Croizat, *C. glechomifolius* Müll. Arg., *C. inaequilobus* Steyerm., *C. junceus* Baill., *C. tetradenius* Baill.

Another group of Brazilian species shows vegetative similarities to species of *Croton* sect. *Ocalia* but differs in having bifid styles: *C. goyazensis* Müll. Arg., *C. gracilescens* Müll. Arg., *C. mucronifolius* Müll. Arg., *C. nepetifolius* Baill.

9. ***Croton*** sect. ***Corylocroton*** G. L. Webster, **sect. nov.** – Arbores fruticesve foliis alternis dentatis, glandulosis, stipulis integris; pilis stellatis; racemis termina-libus; sepalis florum foemineorum integris; stylis bifidis. – T.: *C. corylifolius* Lam.

Monoecious trees or shrubs; indumentum stellate-lepidote; leaves alternate, pinnately veined, coarsely dentate, glandular at base; stipules entire, reduced; inflorescences terminal, with or without bisexual cymules; petals reduced in pistillate flowers; stamens 10-18; pistillate flowers subsessile or pedicellate, sepals entire, not glandular, valvate; styles bifid.

This small American section has a basically Caribbean distribution.

Species included. – [Mexico & Central America:] *Croton mexicanus* Müll. Arg., *C. oerstedianus* Müll. Arg.; [West Indies:] *C. corylifolius* Lam.; [Venezuela:] *C. caracasanus* Pittier.

10. ***Croton*** sect. ***Anadenocroton*** G. L. Webster, **sect. nov.** Frutices foliis alternis, eglandulosis, stipulis integris; pilis stellatis, racemis terminalibus axillaribusve; sepalis florum foemineorum integris; stylis bifidis. – T.: *C. axillaris* Müll. Arg.

Monoecious or dioecious shrubs; indumentum stellate; leaves alternate, pinnately veined, entire, without basal glands; stipules entire; inflorescences unisexual or bisexual, without basal bisexual cymules; stamens 10-15; pistillate flowers sessile or pedicellate, sepals entire, eglandular, valvate; petals absent; styles multifid.

The species of this section in some respects resemble *Croton* sect. *Velamea*, but differ in their multifid styles. *C. axillaris* diverges from the other species in its dioecious, axillary inflorescence production, but is similar in other characters.

Species included. – [Mexico & Central America:] *Croton alamosanus* Rose, *C. axillaris* Müll. Arg., *C. sutup* Lundell; [West Indies:] *C. astroites* Aiton, *C. laurinus* Sw.; [South America:] *C. sucrensis* Steyerm., *C. umbratilis* Kunth.

11. ***Croton*** sect. ***Tiglium*** (Klotzsch) Baill., Etude Euphorb.: 361. 1858 ≡ *Tiglium* Klotzsch in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1: 418. 1843. – T.: *T. officinale* Klotzsch (*C. tiglium* L.).

= *Croton* sect. *Gymnocroton* Baill., Etude Euphorb.: 356. 1858. – T.: *C. verreauxii* Baill.

Monoecious or dioecious shrubs or trees; indumentum sparse, appressed-stellate; leaves alternate, pinnately or palmately veined, glandular at base; stipules entire; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-20; pistillate sepals distinctly pedicellate, entire, eglandular, valvate, sometimes accrescent; styles bifid.

This section, as here defined, includes about 20 species of America and the Old World. In the strict sense, as treated by Müller (1866), *Tiglium* is a group of species with triplinerved leaves and inflated capsules. If the species with strictly pinnate venation were separated, they would fall into Baillon's *Croton* sect. *Gymnocroton*; however, it seems preferable to adopt a broader definition to emphasize the overall similarities.

Representative species. – [Nicaragua:] *Croton nubigenus* G. L. Webster; [Jamaica:] *C. wilsonii* Griseb.; [Colombia:] *C. malambo* Karst.; [Ecuador:] *C. fraseri* Müll. Arg.; [Brazil:] *C. microgyne* Croizat; [Kenya:] *C. alienus* Pax, *C. talaeporos* Radcl.-Sm.; [Sri Lanka:] *C. nigro-viridis* Thwaites; [Southeast Asia:] *C. griffithii* Hook. f., *C. hookeri* Croizat, *C. nanus* Gagnep.; [Indonesia:] *C. jatrophifolius* Müll. Arg., *C. oblongus* Burm. f.; [Philippines:] *C. colubrinoides* Merr., *C. palawanensis* Croizat; [New Guinea:] *C. antae* Airy Shaw, *C. choristadenius* K. Schum., *C. muriculatus* Airy Shaw, *C. prunifolius* Airy Shaw, *C. semunculus* Croizat; [Australia:] *C. verreauxii* Baill.; [Fiji:] *C. leptopus* Müll. Arg., *C. microtiglium* Burkill.

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

Monoecious shrubs; indumentum sparse, appressed-stellate; leaves alternate, pinnately veined, glandular at base; stipules rudimentary; inflorescences apparently terminal, without bisexual cymules; petals absent in pistillate flowers; stamens c. 11; pistillate flowers short-pedicellate, sepals entire, eglandular, valvate; styles bifid.

This monotypic section of Brazil scarcely differs from sect. *Tiglium* except in the tetramerous perianth. The single species, *Croton sapiifolius*, is still imperfectly known; when better studied, the section can perhaps be amalgamated with sect. *Tiglium*.

13. ***Croton*** sect. ***Cascarilla*** Griseb., Fl. Brit. W. I.: 38. 1859. ≡ *Cascarilla* Adans., Fam. Pl. 2: 355. 1763. – T.: *Croton cascarilla* (L.) L. According to Farr & al. (1979) *Clutia cascarilla* L. is the type of *Cascarilla* Adans. Even though Grisebach did not explicitly base his section on Adanson's genus, *Croton cascarilla*, the name of the species listed first in his treatment, provides the obligate type for the sectional name.

Monoecious (or sometimes dioecious) shrubs or trees; indumentum stellate, often dense; leaves alternate, pinnately veined, glandular at base; stipules entire; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-30; pistillate flowers mostly sessile or subsessile, sepals entire, eglandular, valvate; styles bifid (sometimes emarginate or lobed at tip).

As presently defined, this is the largest section of *Croton*, with over 100 species. In terms of the diagnostic characters used here, *C.* sect. *Cascarilla* only differs from *C.* sect. *Velamea* in having paired glands at the leaf base. The boundary between the two sections may be an artificial one, and both sections are probably unnatural.

However, there is a striking difference in geographic distribution, since *C.* sect. *Cascarilla* is present in the Old World as well as the New World. In contrast to *C.* sect. *Velamea*, the species in *C.* sect. *Cascarilla* are concentrated in the West Indies and South America, and are somewhat less well represented in mainland North America.

There are problems with discriminating *Croton* sect. *Cascarilla* from other sections. *C. xalapensis* Kunth resembles species of *C.* sect. *Cyclostigma* in leaf shape and stamen number. A number of neotropical species, such as *C. jutiapensis* Croizat and *C. repens* Schltdl., resemble *C.* sect. *Ocalia* in leaf morphology but have bifid styles. The evident diversity among species of *C.* sect. *Cascarilla* suggests that subdivisions into subsections would be desirable, but that will require much more study.

Representative species. – [Mexico & Central America:] *Croton adspersus* Benth., *C. itzaeus* Lundell, *C. jimenezii* Standl. & Valerio, *C. jutiapensis* Croizat, *C. lasiopetaloides* Croizat, *C. malvaviscifolius* Millsp., *C. mexicanus* Müll. Arg., *C. ortholobus* Müll. Arg., *C. ramillatus* Croizat, *C. repens* Schltdl.; [West Indies:] *C. abeggii* Urb. & Ekman, *C. alloeophyllus* Urb., *C. azuensis* Urb., *C. barahonensis* Urb., *C. cascarilla* (L.) L., *C. discolor* Willd., *C. flavens* L., *C. impressus* Urb., *C. linearis* Jacq., *C. origanifolius* Lam., *C. pallidus* Müll. Arg., *C. panduriformis* Müll. Arg., *C. plumieri* Urb., *C. poiteai* Urb., *C. priorianus* Urb., *C. sagraeanus* Müll. Arg., *C. vaillantii* Geiseler, *C. yunquensis* Griseb.; [South America:] *C. abaitensis* Baill., *C. abutilifolius* Croizat, *C. betaceus* Baill., *C. bonplandianus* Baill., *C. collinus* Kunth, *C. ferrugineus* Kunth, *C. guaiquinimae* Steyerm., *C. hasslerianus* Chodat, *C. hieronymii* Griseb., *C. hilarii* Baill., *C. kleinii* L. B. Sm. & Downs, *C. lachnostachyus* Baill., *C. leptostachyus* Kunth, *C. lorentzii* Müll. Arg., *C. macrostigma* Chodat & Hassl., *C. mollis* Benth., *C. pellitus* Kunth, *C. pavonis* Müll. Arg., *C. reitzii* L. B. Sm. & Downs, *C. subincanus* Müll. Arg., *C. tarapotensis* Müll. Arg., *C. zehntneri* Pax & K. Hoffm.; [Africa:] *C. polytrichus* Pax, *C. scheffleri* Pax, *C. sylvaticus* Hochst.; [Asia:] *C. caudatus* Geiseler, *C. columnaris* Airy Shaw, *C. kongensis* Gagnep., *C. krabas* Gagnep., *C. lachnocarpus* Benth., *C. laoticus* Gagnep., *C. luzoniensis* Müll. Arg., *C. murex* Croizat, *C. wallichii* Müll. Arg.; [Australia:] *C. arnhemicus* Müll. Arg.

14. ***Croton*** sect. ***Velamea*** Baill. in Adansonia 4: 316. 1864. – LT. (designated here): *C. campestris* A. St.-Hil.

Monoecious or dioecious shrubs, subshrubs, or herbs; indumentum stellate, often dense and trichomes pedicellate; leaves alternate, pinnately veined, eglandular at base; stipules entire; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-20; pistillate flowers sessile or short-pedicellate, sepals entire, eglandular, valvate; styles bifid.

This section includes a considerable number of widespread neotropical species. It appears that *Croton* sect. *Velamea*, with over 50 American species, may be confined to the New World, although it cannot be excluded that some Old World species may prove to belong here. For example, *C. rivularis* E. Mey. ex Müll. Arg., from South Africa, possibly may belong to *C.* sect. *Velamea* on the basis of diagnostic characters. The section as here defined may prove to be unnatural, but it seems premature to attempt to discriminate the different species complexes.

Representative species. – [Texas:] *Croton fruticulosus* Torr., *C. lindheimerianus* Scheele, *C. pottsii* (Klotzsch) Müll. Arg.; [Mexico:] *C. cortesianus* Kunth, *C. fran-*

coanus Müll. Arg., *C. heterochrous* Müll. Arg., *C. sancti-lazari* Croizat, *C. sphaerocarpus* Kunth, *C. suaveolens* Torr., *C. torreyanus* Müll. Arg.; [Central America:] *C. payaquensis* Standl.; [Cuba:] *C. acunae* Borhidi, *C. pervestitus* Wright, *C. viminalis* Griseb.; [Hispaniola:] *C. poitaei* Urb.; [South America:] *C. acradenius* Pax & K. Hoffm., *C. alnifolius* Lam., *C. andinus* Müll. Arg., *C. campestris* A. St.-Hil., *C. conduplicatus* Kunth, *C. fragilis* Kunth, *C. grandivelum* Baill., *C. horridulus* (Baill.) Müll. Arg., *C. lapanus* Müll. Arg., *C. missionum* Croizat, *C. morifolius* Willd., *C. moritibensis* Baill., *C. occidentalis* Müll. Arg., *C. orbignyanus* Müll. Arg., *C. piauhiensis* Müll. Arg., *C. regnellianus* Müll. Arg., *C. rhamnifolius* Kunth, *C. rivinifolius* Kunth, *C. seminudus* Müll. Arg., *C. stahelianus* Lanj., *C. subacutus* Müll. Arg., *C. wagneri* Müll. Arg.

15. ***Croton*** sect. ***Andrichnia*** Baill., Etude Euphorb.: 362. 1858. – T.: *C. bracteatus* Lam.

Monoecious trees or shrubs; indumentum appressed-stellate; leaves opposite or subopposite (at least above), pinnately veined, glandular at base but without laminar glands; inflorescences pseudo-terminal, not bisexual below; petals present in staminate, present or reduced in pistillate flowers; stamens 10-20; pistillate flowers pedicellate, sepals entire, valvate; styles bifid to multifid.

This Old World section remains ill-defined. The type species, *Croton bracteatus* Lam., is unusual in its accrescent bracts, but *C. nudatus* Baill., associated with it by Müller (1866), appears not to have such striking bracts. These two species have multifid styles, and it is not clear whether they belong in the same section with such species as *C. mongue* Baill., with much denser and looser stellate pubescence and bifid styles. The common Madagascar species *C. cassinoides* Lam., although having eglandular leaves, may belong in this section.

Representative species. – [Madagascar:] *Croton ankarensis* Leandri, *C. appertii* Leandri, *C. bracteatus* Lam., *C. danguyanus* Leandri, *C. heteranthus* A. DC., *C. leandrii* Croizat, *C. nitidulus* Baker, *C. nudatus* Baill.

16. ***Croton*** sect. ***Anisophyllum*** Baill. in Adansonia 1: 154, 170. 1861. – LT. (designated here): *C. payerianus* Baill.

Monoecious trees or shrubs; indumentum appressed-stellate, often dense and pale; leaves mostly opposite, subopposite, or subverticellate, pinnately veined, usually glandular at base and often on lamina beneath; inflorescences pseudoterminal, not bisexual below; petals reduced in pistillate flowers; stamens 15-20; pistillate flowers pedicellate, sepals entire, valvate; styles multifid.

Croton sect. *Anisophyllum* includes about 10-15 species of Madagascar. The section as defined by Baillon included *C. muricatus* Vahl, but that species was referred to *C.* sect. *Eluteria* by Müller (1866). Leandri (1939) included most of the species in his "groupe *Adenophorum*", and also treated *C. payerianus* as a synonym of *C. adenophorus* Baill. It is not clear whether a number of Asiatic species such as *C. cascarilloides*, that have pseudo-verticillate leaves, should be referred to this section.

Representative species. – [Madagascar:] *C. adenophorus* Baill., *C. bathianus* Leandri, *C. crocodilorum* Leandri, *C. decaryi* Leandri, *C. farinosus* Lam., *C. ihosianus* Leandri, *C. muricatus* Vahl, *C. scottii* Baill., *C. tulasnei* Baill.

17. ***Croton*** sect. ***Furcaria*** Boivin ex Baill., Etude Euphorb.: 356. 1858. – T.: *C. bovinianus* Baill.
= *Triplandra* Raf., Sylva Tellur.: 62. 1838. – T.: *T. lanata* (Lam.) Raf. (*Croton lanatus* Lam.) [= *C. lasianthus* Pers.].

Monoecious shrubs; indumentum of foliage sparse, appressed-stellate; leaves opposite or verticillate (at least distally), glandular or eglandular at base; stipules entire or reduced; inflorescences pseudoterminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 6-12; pistillate flowers ± pedicellate, sepals entire, eglandular, valvate; styles bifid.

The type species of this section, *Croton boivinianus*, is aberrant in its nearly eglandular leaves and reduced stamen number. However, a number of other Old World species with appressed-stellate indumentum can tentatively be associated with it.

Representative species. – [Malagasia:] *Croton boivinianus* Baill.; [Sri Lanka:] *C. thwaitesianus* Müll. Arg.; [Southeast Asia:] *C. dodecamerus* Gagnep., *C. dongnaiensis* Pierre ex Gagnep., *C. lasianthus* Pers.; [Indonesia:] *C. glabrescens* Miq., *C. heterocarpus* Müll. Arg., *C. morotaeus* Airy Shaw.; [Fiji:] *C. heterotrichus* Müll. Arg.

18. ***Croton*** sect. ***Monguia*** Baill. in Adansonia 1: 146. 1861. – LT. (designated here): *C. chrysodaphne* Baill.

Monoecious trees or shrubs; indumentum lepidote; leaves opposite or subopposite (at least in part), pinnately veined, glandular at base; inflorescences pseudoterminal, not bisexual below; petals equalling sepals or reduced to obsolete pistillate flowers; stamens 10-35; pistillate flowers pedicellate, sepals entire, valvate; styles multifid or greatly dilated.

In the circumscription of Baillon, *Croton* sect. *Monguia* included 2 species, the lectotype plus *C. argyrodaphne* Baill. However, Müller (1866) reported the pistillate petals of the latter species as reduced ("subulata, exigua") and Leandri (1939) described them as absent. It is clear that only *C. chrysodaphne* corresponds to the sectional diagnosis, and it is therefore chosen as lectotype. However, Leandri (1939) regarded the specimens of *C. chrysodaphne* as representing a possibly "abnormal" form of *C. argyrodaphne*. Judging from other instances reported in the literature, it seems likely that development of pistillate petals is variable within *C. argyrodaphne*.

As defined here, *Croton* sect. *Monguia* includes the Madagascar species with opposite, glandular, lepidote leaves and multifid styles. It is not clear whether there are any extra-Malagasian species, although *C. cascarilloides* Raeusch. of southeast Asia is suggestively similar.

Representative species. – [Comoro Islands:] *C. humblotii* Baill.; [Madagascar:] *C. antanosiensis* Leandri, *C. argyrodaphne* Baill., *C. bernieri* Baill., *C. boinensis* Leandri, *C. bojerianus* Baill., *C. noronhae* Baill. Some Madagascar species, such as *C. nobilis* Baill., are similar but have alternate leaves.

19. ***Croton*** sect. ***Decapetalon*** Müll. Arg. in Linnaea 34: 78. 1865. ≡ *C.* subg. *Decapetalon* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – LT. (designated here): *C. squamigerus* Baill. [= *C. jennyanus* Gris ex Baill., fide Leandri, 1939].

Monoecious shrubs; indumentum of foliage lepidote; leaves opposite or subopposite, entire, pinnately veined, eglandular at base; stipules entire or obsolete; inflorescences pseudoterminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-15; pistillate sepals equal, entire, valvate; styles bifid.

When it was first defined by Müller (1865), no species were enumerated in *Croton* sect. *Decapetalon*, but in Candolle's *Prodromus* (Müller, 1866) he listed two: *C. squamigerus* and *C. laevigatus* Vahl. These are surely not related to one another and have in common only the unusual character of petaloid staminate glands. Leandri (1939) noted that the petaloid glands in *C. squamigerus* appear to be an abnormality and reduced the species to a synonym of *C. jennyanus*. However, Leandri (1939) also recognized *C. lepidotus* A. DC. as having petaloid glands, and used that feature as a key character for the species. It seems expedient to try to salvage Müller's name by typifying the section with *C. squamigerus* so that it can accommodate those Madagascar species with lepidote indumentum, eglandular leaves, and bifid styles.

Representative species. – [Madagascar:] *Croton brevispicatus* Baill., *C. jennyanus* Baill., *C. lepidotus* A. DC., *C. trichotomus* Geiseler.

20. ***Croton*** sect. ***Podostachys*** (Klotzsch) Baill., Etude Euphorb.: 365. 1858 ≡ *Podostachys* Klotzsch in Arch. Naturgesch. 7: 193. 1841 ≡ *C.* subsect. *Podostachys* Müll. Arg. in Linnaea 34: 134. 1865. – LT. (Wheeler, 1975): *P. subfloccosa* Didr. [= *C. lundianus* (Didr.) Müll. Arg.].

Monoecious shrubs; indumentum stellate; leaves alternate, ± palmately veined, dentate, glandular at base; stipules entire; inflorescences terminal, with a distinct gap between staminate and pistillate flowers, without bisexual cymules; petals reduced in pistillate flowers; stamens 5-12; pistillate sessile or pedicellate, sepals entire to laciniate, valvate; styles usually multifid.

This section of c. 10 American species appears to be unnatural as defined by Müller (1873); the species with bifid styles are here assigned to *Croton* sect. *Octolobium*. The section is close to *C.* sect. *Geiseleria*, and could perhaps be combined with it. In fact, Smith & al. (1988) have proposed treating *C. lundianus* as a variety of *C. glandulosus*, in *C.* sect. *Geiseleria*!

Representative species. – [North America:] *Croton liebmannii* Müll. Arg., *C. meissneri* Müll. Arg.; [South America:] *C. carandaitensis* Croizat, *C. lundianus* (Didr.) Müll. Arg., *C. macradenius* Görts & Punt, *C. odontadenius* Müll. Arg., *C. sclerocalyx* (Didr.) Müll. Arg., *C. sipaliwinensis* Lanj., *C. spiraeifolius* Jabl., *C. subserratus* Jabl., *C. teucridium* Baill., *C. yacaensis* Croizat.

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

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

Monoecious shrubs or subshrubs; indumentum stellate; leaves alternate, palmately veined, glandular at base; stipules entire or nearly so; inflorescences terminal, with a distinct gap between staminate and pistillate flowers, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-15; pistillate flowers sessile or subsessile, sepals 6-8, dentate, valvate; styles bifid to multifid.

It is rather doubtful that this section of 2 or 3 South American species can be maintained as distinct from *Croton* sect. *Podostachys*. It is possible that *C. mentiens* is conspecific with *C. aberrans*, although from descriptions they differ in stamen number and stylar configurations. Müller (1873) also included 2 other species, *C. teucridium* Baill. and *C. subferrugineus* Müll. Arg., in this affinity, but their relationships are doubtful.

Species included. – [South America:] *Croton aberrans* Müll. Arg., *C. guaraniticus* Chodat & Hassl., *C. krukoffianus* Croizat, *C. mentiens* (S. Moore) Pax.

22. ***Croton*** sect. ***Geiseleria*** (Klotzsch) Baill., Etude Euphorb.: 359. 1858 ≡ *Geiseleria* Klotzsch in Arch. Naturgesch. 7: 254. 1841. – T.: *G. chamaedryfolia* Klotzsch [= *C. trinitatis* Millsp.].

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

= *Brachystachys* (L'Hér.) Klotzsch in London J. Bot. 2: 47. 1843. – T.: *B. hirta* Klotzsch [= *C. hirtus* L'Hér.].

Monoecious herbs or small shrubs; indumentum stellate; leaves alternate, ± palmately veined, dentate, glandular at base; stipules entire; inflorescences terminal, without bisexual cymules, bracts ± glandular; petals reduced in pistillate flowers; stamens 8-11; pistillate flowers sessile or pedicellate, sepals distinctly unequal, entire, not glandular; styles bifid.

As delimited here, *Croton* sect. *Geiseleria* includes c. 10 species of the New World, with most of the diversity in Brazil. Species with multifid styles, larger stamen number, or eglandular leaves are excluded, in contrast to the treatment of Müller (1873). The species show strong resemblances to those in *C.* sect. *Podostachys*.

Representative species. – [America (widespread):] *Croton glandulosus* L., *C. hirtus* L'Hér., *C. trinitatis* Millsp.; [North America:] *C. comes* Standl. & L. Williams; [South America:] *C. adenodontus* (Müll. Arg.) Müll. Arg., *C. bidentatus* Müll. Arg., *C. larensis* Steyerm., *C. tamberlikii* Müll. Arg., *C. verbenifolius* Müll. Arg.

23. ***Croton*** sect. ***Pilinophytum*** (Klotzsch) A. Gray, Manual, ed. 2: 391. 1856 ≡ *Pilinophytum* Klotzsch in Arch. Naturgesch. 7: 255. 1841. – T.: *C. capitatus* Michx.

= *Heptallon* Raf., Neogenyton: 1. 1825 ≡ *Croton* sect. *Heptallon* (Raf.) Müll. Arg. in Linnaea 34: 78. 1865 ≡ *C.* subg. *Heptallon* (Raf.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – T.: *H. graveolens* Raf. [= *C. capitatus* Michx.].

Monoecious annual herbs; indumentum of foliage stellate; leaves alternate, ± palmately veined, entire, eglandular at base; stipules entire; inflorescences terminal, contracted, without bisexual cymules; petals reduced in pistillate flowers; stamens 8-15; pistillate flowers subsessile, sepals mostly 7 or 8 (6-10), entire, not glandular; styles multifid.

This is one of the few sections of *Croton* that is mainly confined to the United States. The 3 species resemble North American species of *C.* sect. *Gynamblosis* and

sect. *Velamea*, such as *C. leucophyllus* and *C. lindheimerianus*, but differ in having quadrifid rather than bifid styles. *C. coryi* is very unusual in having stellate foliar indument but lepidote scales on the staminate petals. Although differing in its distinctive stellate-lepidote pedicellate trichomes, the South American species *C. pycnocephalus* Baill. may belong to this section.

Species included. – [North America:] *Croton capitatus* Michx., *C. coryi* Croizat, *C. elliottii* Chapm.

24. ***Croton*** sect. ***Eremocarpus*** (Benth.) G. L. Webster in Novon 2: 270. 1992 ≡ *Eremocarpus* Benth., Bot. Voy. Sulphur: 53. 1844. – T.: *E. setigerus* (Hook.) Benth. [= *C. setigerus* Hook.).

Monoecious annual herbs; indumentum bristly-stellate; leaves mostly clustered at forks of dichotomizing stems, entire, palmately veined, eglandular; stipules obsolete; inflorescences pseudoterminal at dichotomies of stems, bisexual; pistillate perianth obsolete, staminate flowers apetalous; stamens 6-10; ovary 1-locular, style unlobed.

This monotypic section, confined to western North America, has been regarded as a distinct genus since soon after Hooker described it (with doubt) as a *Croton*. The flowers, which are possibly wind-pollinated, are more highly reduced than in any other group of *Croton*. However, the habit, including pubescence and leaf shape, is highly suggestive of species of *C.* sect. *Pilinophytum* and related species of *C.* sect. *Velamea*. From an evolutionary point of view, it seems clear to me that *Eremocarpus* must be regarded as a highly specialized and florally reduced species of *Croton*.

25. ***Croton*** sect. ***Gynamblosis*** (Torr.) A. Gray, Manual, ed. 2: 392. 1856 ≡ *Gynamblosis* Torr. in Marcy, Explor. Red River Louisiana: 282. 1854. – T.: *G. monanthogyna* (Michx.) Torr. (*C. monanthogynus* Michx.).

= *Engelmannia* Klotzsch in Arch. Naturgesch. 7: 253. 1841 (non *Engelmannia* A. Gray ex Nutt., 1840) ≡ *Angelandra* Endl., Gen. Pl. Suppl. 5: 91. 1850 ≡ *Croton* sect. *Angelandra* (Endl.) Müll. Arg. in Linnaea 34: 79. 1865 ≡ *C.* subg. *Angelandra* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – T.: *E. nuttalliana* Klotzsch, nom. illeg. (*C. lindheimerianus* Scheele).

Monoecious annual or perennial herbs or subshrubs, ± dichotomously branching; indumentum of foliage appressed-stellate or stellate-lepidote; leaves alternate, entire, eglandular; stipules suppressed; inflorescences abbreviated, without bisexual cymules; petals rudimentary or absent in pistillate flowers; stamens 4-11; pistillate flowers distinctly pedicellate, ± reflexed in fruit; sepals narrow, entire, not glandular, valvate; styles bifid.

This American section of 5 species was recognized by Müller on the basis of the asymmetrical staminate flowers. The South American species have not previously been associated with the North American ones, but their resemblance is so close that there can be little doubt they belong here. The plants appear to be reduced forms perhaps derived from within *Croton* sct. *Velamea*, and could be accommodated as a subsection within that group.

Species included. – [North America:] *Croton lindheimerianus* Scheele, *C. monanthogynus* Michx.; [South America:] *C. corchoropsis* Baill., *C. cuyabensis* Pilg., *C. pedicellatus* Kunth.

26. ***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., ser. 2, 5: 353. 1808, nom. illeg. – T.: *Crotonopsis linearis* Michx. (*Croton michauxii* G. L. Webster). Renaming of the type species is necessitated by the fact that Michaux's epithet, in *Croton*, is preoccupied by *Croton linearis* Jacq.

Monoecious annual herbs; indumentum appressed-stellate and stellate-lepidote; leaves mostly alternate, entire, pinnately veined, eglandular; stipules obsolete; inflorescences pseudoterminal, reduced, usually with a single pistillate flower below the staminate; petals reduced in pistillate flowers; stamens 5 or 6; pistillate flowers sessile, sepals sometimes unequal, entire, not glandular; ovary 1-locular, style multifid; fruit indehiscent, achene-like.

Although I earlier (Webster, 1967) followed tradition in recognizing *Crotonopsis* as a genus distinct from *Croton*, its close relationship has always been apparent; and it is significant that authors such as Correll & Johnston (1970) have suggested that it could easily be combined. The relationship to such groups as *C.* sect. *Gynamblosis* is unmistakable, and it seems significant that there is a reduction series from 3 to 2 carpels within *C.* sect. *Gynamblosis*. On the other hand, the indumentum is quite different in the two groups, since the trichomes are distinctly lepidote in *Crotonopsis*; furthermore, the style in *Crotonopsis* is multifid, not bifid. The indehiscent fruit in *Crotonopsis* is rather similar in size and shape to the 2-locular capsule of *Croton monanthogynus*, and there does not appear to be a great morphological difference. Clearly, *Crotonopsis* is a highly specialized group derived from taxa within *Croton*, and it seems quite appropriate to treat it as a section of the latter rather than an independent genus.

Species included. – [North America:] *Croton michauxii* G. L. Webster, *C. willdenowii* G. L. Webster.

27. ***Croton*** sect. ***Argyrocroton*** (Müll. Arg.) G. L. Webster, stat. nov. ≡ *Argyrodendron* Klotzsch in Peters, Naturw. Reise Mossambique 6: 100. 1861 (non *Argyrodendron* F. Müller, 1858) ≡ *C.* ser. *Argyrocroton* Müll. Arg. in Martius, Fl. Bras. 11(2): 133. 1873 ≡ *C.* subsect. *Argyrocroton* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890. – LT. (designated here): *A. bicolor* Klotzsch [= *C. menyharthii* Pax].

Monoecious or dioecious trees or shrubs; indumentum lepidote; leaves alternate, pinnately veined, glandular (rarely eglandular) at base; stipules entire; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-20; pistillate flowers ± pedicellate, sepals entire, eglandular, valvate; styles bifid.

Croton sect. *Argyrocroton* is poorly represented in the New World, and the bulk of the species appear to be African and Madagascan.

Representative species. – [North America:] *Croton argyranthemus* Michx.; [South America:] *C. hilarii* Baill., *C. stenotrichus* Müll. Arg.; [Africa:] *C. dichogamus* Pax, *C. longipedicellatus* Léonard, *C. megalocarpus* Hutch., *C. menyharthii* Pax, *C. somalensis* Vatke & Pax, *C. zambesicus* Müll. Arg.; [Madagascar:] *C. brevispicatus* Baill., *C. elliottianus* Baill., *C. geayi* Baill., *C. pulchellus* Baill., *C. trichotomus* Geiseler; [India:] *C. joufra* Roxb., *C. roxburghii* N. P. Balakr.; [Southeast Asia:] *C. delpyi* Gagnep., *C. kongensis* Gagnep.; [New Guinea:] *C. hentyi* Airy Shaw; [New

Caledonia:] *C. cordatulus* Airy Shaw; [Fiji:] *C. metallicus* Seem. ex Müll. Arg. Despite its bisexual cymules, *C. insularis* Baill. may belong in this section.

28. ***Croton*** sect. ***Lamprocroton*** (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890 ≡ *C.* ser. *Lamprocroton* Müll. Arg. in Martius, Fl. Bras. 11(2): 244. 1873. – LT.: *C. ceanothifolius* Baill.

Monoecious or dioecious shrubs; indumentum of foliage lepidote at least in part, scales shallowly toothed; leaves alternate, entire, pinnately veined, eglandular; stipules reduced or absent; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-15; pistillate flowers mostly sessile or subsessile, sepals equal to distinctly unequal, entire, eglandular, valvate; styles bifid.

As defined here, *Croton* sect. *Lamprocroton* is a South American group of c. 20-30 species (boundaries between species are controversial). The redefined section includes not only the species with bifid styles placed in *C.* ser. *Lamprocroton* by Müller (1873), but also the species with bifid styles, eglandular leaves, and shallowly lobed scales in Müller's *C.* ser. *Argyrocroton*.

Representative species. – [North America:] *Croton alabamensis* E. A. Sm., *C. ehrenbergii* Schltdl., *C. hypoleucus* Schltdl.; [West Indies:] *C. myricifolius* Griseb., *C. rosmarinoides* Millsp.; [South America:] *C. burchellii* Müll. Arg., *C. ceanothifolius* Baill., *C. cinerellus* Müll. Arg., *C. dichrous* Müll. Arg., *C. ericoides* Baill., *C. fallax* Müll. Arg., *C. gaudichaudii* Baill., *C. migrans* Casar., *C. oleoides* Müll. Arg., *C. puncticulatus* Müll. Arg., *C. riedelianus* Müll. Arg., *C. russulus* Croizat, *C. tenuissimus* Baill.

29. ***Croton*** sect. ***Julocroton*** (Mart.) G. L. Webster in J. Arnold Arbor. 48: 354. 1967 ≡ *Julocroton* Mart. in Flora 20, Beibl. 2: 119. 1837.– T.: *J. phagedaenicus* Mart. [= *C. triqueter* Lam.].

= *Heterochlamys* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 16: 61. 1843. – T.: *H. quinquinervia* Turcz. [= *Croton argenteus* L.].

= *Julocroton* subg. *Eremadenia* Didr. in Vidensk. Meddel. Dansk Naturhist. Foren. Kjbenhavn 1857: 134. 1857. – T: not designated.

= *Julocroton* subg. *Oligonychia* Didr. in Vidensk. Meddel. Dansk Naturhist. Foren. Kjbenhavn 1857: 132. 1857. – LT. (designated here): *J. argenteus* (L.) Didr. (*Croton argenteus* L.).

= *Centrandra* G. Karst. in Linnaea 28: 440. 1857. – T.: *Centrandra hondensis* G. Karst. (*Croton hondensis* (Karst.) G. L. Webster).

Monoecious shrubs or herbs; indumentum stellate; leaves alternate, pinnately or palmately veined, entire or dentate, eglandular; stipules entire to laciniate; inflorescences terminal, ± congested, without bisexual cymules; petals reduced in pistillate flowers; stamens mostly 11; pistillate flowers sessile or subsessile, sepals strongly unequal and ± deeply laciniate; styles bifid or more often multifid.

Although generally treated as a distinct genus, *Julocroton* does not appear to merit separation unless *Croton* is divided up into a large number of segregate genera, as Klotzsch attempted to do in the 19th century. Over 50 species of *Julocroton* have been described, the vast majority from South America, but despite the partial revision of Croizat (1943) the group remains very poorly understood. A general review of geographic distribution patterns in the group is given by Cordeiro (1990), and a provisional enumeration of species accepted by Webster (1992).

Representative species. – [America (widespread):] *Croton argenteus* L.; [North America:] *C. conspurcatus* Schltdl.; [South America:] *C. abutilopsis* G. L. Webster, *C. ackermannianus* (Müll. Arg.) G. L. Webster, *C. allemii* G. L. Webster, *C. calonervosus* G. L. Webster, *C. cordeiroae* G. L. Webster, *C. didrichsenii* G. L. Webster, *C. doratophylloides* (Croizat) G. L. Webster, *C. flavispicatus* Rusby, *C. fuscescens* Spreng., *C. hondensis* (G. Karst.) G. L. Webster, *C. lanceolaris* G. L. Webster, *C. microcalyx* (Müll. Arg.) G. L. Webster, *C. phyllanthus* (Chodat & Hassl.) G. L. Webster, *C. rupestris* (Chodat & Hassl.) G. L. Webster, *C. rutilus* (Chodat & Hassl.) G. L. Webster, *C. salzmannii* (Baill.) G. L. Webster, *C. solanaceus* (Müll. Arg.) G. L. Webster, *C. subpannosus* Müll. Arg. ex Griseb., *C. stipularis* (Müll. Arg.) G. L. Webster, *C. triqueter* Lam., *C. verbascoides* G. L. Webster.

30. ***Croton*** sect. ***Adenophyllum*** Griseb., Fl. Brit. W. I.: 40. 1859. – T.: *C. adenophyllus* Spreng.
= *Pleopadium* Raf., Autik. Bot.: 50. 1840. – T.: *P. ciliatum* Raf. [? = *C. ciliatoglandulifer* Ortega].

Monoecious shrubs; indumentum stellate; leaves alternate, palmately veined or triplinerved, with stalked glands on margins; stipules lobed or dissected, ± glandular; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 20-40; pistillate sepals valvate, mostly glandular on margins; styles multifid.

This is an entirely American section of c. 10 closely related species; it is very similar to *Croton* sect. *Barhamia* except for the larger stamen number.

Representative species. – [Mexico:] *Croton ciliatoglandulifer* Ortega, *C. gaumeri* Millsp., *C. humilis* L., *C. jucundus* Brandegee, *C. subjucundus* Croizat; [Cuba:] *C. clavuliger* Müll. Arg.; [Hispaniola:] *C. chaetodus* Urb., *C. fuertesii* Urb.

31. ***Croton*** sect. ***Barhamia*** (Klotzsch) Baill., Etude Euphorb.: 367. 1858 ≡ *Barhamia* Klotzsch in Seemann, Bot. Voy. Herald: 104. 1853. – LT. (designated by Wheeler, 1975): *B. panamensis* Klotzsch [= *C. hircinus* Vent.].
= *Calypteriopetalon* Hassk. in Flora 40: 531. 1857. – T.: *Calypteriopetalon brasiliense* Hassk. [= *Croton urticifolius* Lam.].

Monoecious shrubs, stems sometimes viscid; indumentum loosely or appressed-stellate, not woolly; leaves alternate, pinnately or palmately veined, usually dentate, without basal glands; stipules ± glandular-lobed or -dissected; inflorescences terminal, elongated, without bisexual cymules; petals reduced in pistillate flowers; stamens (5-)8-12; sepals of pistillate flowers often glandular on back or margins; styles multifid.

Croton sect. *Barhamia* is entirely American, but unlike *C.* sect. *Adenophyllum* it is well represented in South America. The section shows considerable variability: South American species such as *C. betulaster* Müll. Arg. and *C. glutinosus* Müll. Arg. are very distinctive in their nearly glabrous, extremely viscid foliage and probably should be segregated in a separate subsection or section. Two other Mesoamerican species, *C. brevipes* Pax and *C. macrodontus* Müll. Arg., resemble species of *C.* sect. *Barhamia* in habit, but lack clearly glandular-lobed stipules and pistillate calyces; their affinity remains uncertain, but in this synopsis they are tentatively referred to *C.* sect. *Ocalia.*

Representative species. – [Mexico & Central America:] *Croton ameliae* Lundell, *C. decalobus* Müll. Arg., *C. glandulosepalus* Millsp., *C. escathos* Croizat; [Caribbean:] *C. hircinus* Vent., *C. ovalifolius* Vahl; [South America:] *C. adenocalyx* Baill., *C. agoensis* Baill., *C. betulaster* Müll. Arg., *C. essequiboensis* Klotzsch, *C. glandulosodentatus* Pax & K. Hoffm., *C. glutinosus* Müll. Arg., *C. muscicapa* Müll. Arg., *C. paucistamineus* Müll. Arg., *C. perviscosus* Croizat, *C. rhexiifolius* Baill., *C. rudolphianus* Müll. Arg., *C. urticifolius* Lam.

32. ***Croton*** sect. ***Decalobium*** Müll. Arg. in Linnaea 34: 78. 1865 ≡ *C.* subg. *Decalobium* (Müll. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – T.: *C. decalobus* Müll. Arg.

Monoecious shrubs; indumentum stellate; leaves alternate, pinnately veined, eglandular at base; stipules glandular-lobed or sometimes nearly entire; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-18; pistillate sepals with stipitate-glandular margins, subtended by an epicalyx of 5 smaller segments; styles multifid.

This small section of 2 species is confined to southern Mexico and Central America. Although the stipules in some specimens of *Croton decalobus* have the glands highly reduced, the pistillate calyx with copious stalked glands is highly suggestive of that in *C.* sect. *Barhamia*. It is possible that a more accurate match of phylogeny to classification would result in demoting *C.* sect. *Decalobium* to a subsection of *C.* sect. *Barhamia*.

Species included. – [Mesoamerica:] *Croton decalobus* Müll. Arg., *C. pendens* Lundell.

33. ***Croton*** sect. ***Micranthis*** Baill., Etude Euphorb.: 355. 1858. – T.: *C. galeottianus* Baill. [= *C. nummulariifolius* A. Rich.].

= *Merleta* Raf., Autik. Bot.: 49. 1840. – T.: *M. microphylla* Raf. [? = *C. nummulariifolius* A. Rich.]. (That *Merleta* is synonymous with sect. *Micranthis* seems probable, although not certain.)

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

Monoecious dwarf subshrubs or perennial herbs; indumentum appressed-stellate; leaves alternate, small (less than 1 cm long), pinnately veined, crenulate, blunt, eglandular at base; stipules glandular-lobed; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 5-10; pistillate sepals valvate, ± entire or glandular; styles multifid.

The species of this small American section have a very characteristic habit, but species such as *Croton escathos* Croizat and *C. ovalfolius* Vahl represent forms transitional between *C.* sect. *Barhamia* and *C.* sect. *Micranthis*. It is possible that further study will show that *C.* sect. *Micranthis* should be treated as a subsection of *C.* sect. *Barhamia*. The distribution of *C.* sect. *Micranthis* is curious, with a disjunction between the Greater Antilles and Brazil. The position of *C. nanus* Urb. & Ekman from Hispaniola remains unsettled; it has the small leaves of *C.* sect. *Micranthis* but the woolly indumentum of *C.* sect. *Medea*.

Species included. – [Cuba & Hispaniola:] *Croton nummulariifolius* A. Rich., *C. prostratus* Urb. (*C. gonaivensis* Urb. & Ekman may also belong here); [Brazil:] *C. nummularius* Baill., *C. radlkoferi* Pax & K. Hoffm., *C. refractus* Müll. Arg.

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

= *Timandra* Klotzsch in Arch. Naturgesch. 7: 193. 1841. – LT. (Wheeler, 1975): *T. serrata* Klotzsch (*Croton serratus* (Klotzsch) Müll. Arg.).

= *Myriogomphos* Didr. in Vidensk. Meddel. Dansk Naturhist. Foren. Køjbenhavn 1857: 142. 1857. – T.: *M. fuscus* Didr. (*Croton fuscus* (Didr.) Müll. Arg.).

= *Croton* sect. *Hesperidium* Baill. in Adansonia 4: 306. 1864. – LT. (designated here): *C. matronalis* Baill. [= *C. vestitus* Spreng.]. (Since Baillon took the sectional name from the resemblance of the lectotype species to *Hesperis matronalis*, this seems a logical choice.)

Monoecious subshrubs or herbs, stems not viscid; indumentum stellate, often woolly; leaves alternate, pinnately or palmately veined, entire or dentate, without basal glands; stipules ± glandular or dissected; inflorescences terminal, contracted, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-12; pistillate flowers sessile or subsessile, sepals laciniate or glandular; styles multifid.

Müller (1873) applied the name *Croton* ser. *Medea* to such a large diverse residue of Brazilian species with stellate indumentum that his concept is essentially meaningless. However, in the concept of Baillon that is accepted here, *C.* sect. *Medea* is a reasonably well characterized temperate and subtropical South American group of c. 30 named species. The diversity among the species is suggested by the generic synonymy, and further study may result in a rational subdivision of *C.* sect. *Medea* into subsections. Some Brazilian species such as *C. parvifolius* Müll. Arg. and *C. santolinus* Baill. have the habit of *C.* sect. *Medea* but lack glandular stipules; they may nevertheless be related.

Representative species. – [South America:] *Croton cerinodentatus* Müll. Arg., *C. chaetophorus* Müll. Arg., *C. fuscus* (Didr.) Müll. Arg., *C. garckeanus* Baill., *C. heterodoxus* Baill., *C. langsdorfii* Müll. Arg., *C. luetzelburgii* Pax & K. Hoffm., *C. melanoleucus* Müll. Arg., *C. myriodontus* Müll. Arg., *C. senescens* Croizat, *C. serratifolius* Baill., *C. timandroides* (Didr.) Müll. Arg., *C. venturii* Croizat, *C. vestitus* Spreng.

C. schultesii Müll. Arg. is aberrant in its shrubbier habit, suborbicular leaves, and entire pistillate sepals; but it has the glandular stipules and bracts of *C.* sect. *Medea.*

35. ***Croton*** sect. ***Lasiogyne*** (Klotzsch) Baill., Etude Euphorb.: 370. 1858 ≡ *Lasiogyne* Klotzsch in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1: 418. 1843 ≡ *C.* sect. *Gonocladium* Baill. in Adansonia 4: 299. 1864 ≡ *C.* subsect. *Lasiogyne* (Klotzsch) Müll. Arg. in Linnaea 34: 81, 95. 1865 ≡ *C.* ser. *Gonocladium* Müll. Arg. in Martius, Fl. Bras. 11(2): 126. 1873 ≡ *C.* subsect. *Gonocladium* (Baill.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890.– T.: *L. brasiliensis* Klotzsch [= *C. compressus* Lam.].

Monoecious trees or shrubs; indumentum stellate (or partly stellate-lepidote); leaves alternate, pinnately or palmately veined, minutely denticulate, glandular or eglandular at base; stipules usually entire, sometimes foliaceous; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 15-20;

pistillate flowers pedicellate, sepals reduplicate-valvate, entire, not glandular; styles multifid.

In the sense of Müller (1866, 1873), *Croton* subsect. *Lasiogyne* included all species of *Croton* with reduplicate-valvate calyces in the pistillate flowers. Here *C.* sect. *Lasiogyne* is construed more narrowly in the sense of Klotzsch and of Baillon, to include c. 25 species widely dispersed in the New World. Despite its lower stamen number and entire stipules, *C. santaritensis* appears to belong here because of its resemblance to *C. fragrans*.

Representative species. – [Mexico:] *Croton tabascensis* Lundell; [Panama:] *C. santaritensis* Huft; [West Indies:] *C. astroites* Aiton, *C. sidifolius* Lam.; [South America:] *C. bredermeyeri* Müll. Arg., *C. compressus* Lam., *C. fragrans* Kunth, *C. jacobinensis* Baill., *C. katoae* Croizat, *C. scaber* Lam., *C.sonderianus* Müll. Arg.

36. ***Croton*** sect. ***Argyroglossum*** Baill. in Adansonia 4: 289. 1864 ≡ *C.* ser. *Argyroglossum* (Baill.) Müll. Arg. in Martius, Fl. Bras. 11(2): 118. 1873 ≡ *C.* subsect. *Argyroglossum* (Baill.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 39. 1890. – T.: *C. argyroglossum* Baill.

Monoecious trees or shrubs; indumentum lepidote; leaves alternate, pinnately or palmately veined, ± entire, not glandular at base; stipules not glandular; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-15; pistillate flowers pedicellate, sepals reduplicate-valvate, entire, not glandular; styles multifid.

As defined here, *Croton* sect. *Argyroglossum* has a narrower circumscription than that of *C.* ser. *Argyroglossum* of Müller (1873), as it excludes species with glandular stipules or calyces. The section appears to be entirely American, with a total of c. 15 species. *C. sellowii* Baill. is anomalous in having lepidote indumentum and reduplicate-valvate pistillate sepals as in *C.* sect. *Argyroglossum* but glandular-dissected stipules as in *C.* sect. *Codonocalyx*; its position must be regarded as uncertain.

Representative species. – [Mexico:] *Croton culiacanensis* Croizat, *C. masonii* I. M. Johnst., *C. watsonii* Standl., *C. yucatanensis* Lundell; [West Indies:] *C. bixoides* Vahl, *C. cascarilloides* Geiseler; [South America:] *C. adipatus* Kunth, *C. alagoensis* Müll. Arg., *C. argyroglossum* Baill., *C. argyrophylloides* Müll. Arg., *C. blanchetianus* Baill., *C. cucutensis* Croizat, *C. floribundus* Spreng., *C. nervosus* Klotzsch, *C. tricolor* Müll. Arg.

37. ***Croton*** sect. ***Astraeopsis*** Baill., Etude Euphorb.: 362. 1858. – T.: *C. hookeri-anus* Baill. [= *C. lucidus* L.].

Monoecious shrubs; indumentum appressed-stellate, sparse; leaves alternate, pinnately veined, entire, eglandular at base; stipules glandular-lobed; inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-12; pistillate sepals reduplicate-valvate, ± glandular-dentate; styles multifid.

Croton sect. *Astraeopsis* is confined to North America and is largely a Caribbean group, with less than 5 species. *C. guyanensis* Aubl., which was cited under *C.* sect. *Astraeopsis* by Müller (1866), differs in its glandular quintuplinerved leaves and does not appear to be closely related to *C. lucidus*. Despite its non-reduplicate sepals, it is possible that *C. soliman* Schltdl. & Cham. may be related to species in this section.

Representative species. – [Yucatan & West Indies:] *Croton hjalmarsonii* Griseb., *C. lucidus* L.

38. ***Croton*** sect. ***Codonocalyx*** Klotzsch ex Baill., Etude Euphorb.: 369. 1858. – LT. (designated here): *C. montevidensis* Spreng. (Baillon cited a number of manuscript names of Klotzsch in protologue, but *C. montevidensis* is the earliest species name available for typification purposes, and the species seems morphologically typical for the section.)
= *Croton* sect. *Calycireduplicati* Allem in Bol. Soc. Argent. Bot. 18: 76. 1979. – T.: *C. calycireduplicatus* Allem.

Monoecious or dioecious subshrubs or perennial herbs; indumentum stellate or stellate-lepidote, densely tomentose or loosely stellate-lepidote; leaves alternate, pinnately veined, entire, eglandular at base; stipules ± glandular-lobed (sometimes ± obsolete); inflorescences terminal, without bisexual cymules; petals reduced in pistillate flowers; stamens 10-15; pistillate flowers pedicellate, sepals reduplicate-valvate, entire or dentate; styles multifid.

Croton sect. *Codonocalyx*, which is confined to temperate and subtropical South America, includes about 10-12 species. The section is variable, and the type of *C.* sect. *Calycireduplicati* differs from the type of *C.* sect. *Codonocalyx* in being dioecious rather than monoecious and in having dentate rather than entire pistillate sepals. However, there are transitional species such as *C. helichrysum* that are monoecious but have dentate pistillate sepals. Perhaps *C.* sect. *Calycireduplicatae* can be retained at subsectional rank. Allem (1978) has reduced many of the proposed names to *C. montevidensis*. A species from Bolivia, *C. avulsus* Croizat, although lacking glandular stipules and reduplicate-valvate pistillate calyx, may represent a specialized member of this section.

Representative species. – [South America:] *Croton calyciglandulosus* Allem, *C. calycireduplicatus* Allem, *C. cuchillae-nigrae* Croizat, *C. gnaphalii* Baill., *C. helichrysum* Baill., *C. lanuginosus* Baill., *C. lombardianus* Croizat, *C. montevidensis* Spreng., *C. nitrariifolius* Baill., *C. quintasii* Allem, *C. ramboi* Allem, *C. tartonraira* Müll. Arg.

39. ***Croton*** sect. ***Astraea*** (Klotzsch) Baill., Etude Euphorb.: 363. 1858 ≡ *Astraea* Klotzsch in Arch. Naturgesch. 7: 194. 1841 ≡ *C.* subg. *Astraea* (Klotzsch) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – LT.: *A. lobata* (L.) Klotzsch (*C. lobatus* L.).

Monoecious shrubs or herbs; indumentum stellate, often sparse; leaves alternate, mostly palmately veined or lobed, glandular at base; stipules mostly entire, sometimes glandular or reduced; inflorescences terminal, with or without bisexual cymules; floral receptacle nearly or quite glabrous; petals reduced in pistillate flowers; stamens 12-15; pistillate flowers pedicellate, sepals entire or denticulate; styles mostly multifid; seeds cylindric-tetragonous.

This American section of c. 10 species is one of the more sharply defined within the genus. However, the status of the common weedy species *Croton bonplandianus* Baill. (treated as *C. pauperulus* by Müller) is doubtful. It differs in its prominent basal foliar glands, bifid styles, and smooth seeds; possibly it has independently lost the receptacular indumentum characteristic of *C.* sect. *Astraea*.

Representative species. – [America (widespread):] *Croton lobatus* L.; [South America:] *C. aureo-marginatus* Chodat & Hassl., *C. cinctus* Müll. Arg., *C. comosus* Müll. Arg., *C. douradensis* Steyerm., *C. gardneri* Müll. Arg., *C. klotzschii* (Didr.) Müll. Arg., *C. paulinus* (Didr.) Müll. Arg., *C. praetervisus* Müll. Arg., *C. subcomosus* Müll. Arg.

40. ***Croton*** sect. ***Drepadenium*** (Raf.) Müll. Arg. in Linnaea 34: 79. 1865 ≡ *Drepadenium* Raf., Neogenyton: 2. 1825 ≡ *C.* subg. *Drepadenium* (Raf.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 40. 1890. – T.: *D. maritimum* (Walter) Raf. [= *C. punctatus* Jacq.].
= *Hendecandra* Eschsch. in Mém. Acad. Imp. Sci. St. Pétérsbourg, Hist. Acad. 10: 287. 1826. – T.: *H. procumbens* Eschsch. [= *Croton californicus* Müll. Arg.].
= *Penteca* Raf., Sylva Tellur.: 62. 1838. – T.: *P. tomentosa* Raf. [= *Croton dioicus* Cav.].
= *Astrogyne* Benth., Pl. Hartw.: 14. 1839. – T.: *A. crotonoides* Benth. [= *Croton dioicus* Cav.].

Monoecious or dioecious subshrubs or herbs; indumentum appressed-stellate or stellate-lepidote; leaves alternate, entire, pinnately veined, eglandular at base; stipules rudimentary or absent; inflorescences terminal, mostly unisexual; petals absent in both staminate and pistillate flowers; stamens 8-12; pistillate flowers ± pedicellate, sepals entire, eglandular, valvate; styles multifid.

All students of *Croton* have recognized this well-defined section that includes 5 or 6 species of North America and the Caribbean. The species recognized by Müller (1866) have not all been accepted by later workers.

Representative species. – [North America & Caribbean:] *Croton punctatus* Jacq.; [United States & Mexico:] *C. californicus* Müll. Arg., *C. dioicus* Cav., *C. parksii* Croizat, *C. texensis* (Klotzsch) Müll. Arg., *C. wigginsii* L. C. Wheeler.

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