**Brasiliocroton**, a New Crotonoid Genus of Euphorbiaceae s.s. from Eastern Brazil

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Communicating Editor: Paul S. Manos

**ABSTRACT.** A new genus and species of Euphorbiaceae s.s., Brasiliocroton mamoninha, is described from two disjunct areas of lowland forest remnants in eastern and northeastern Brazil. It is a member of tribe Crotonae and was previously confused with *Croton* and *Micrandra*. The resemblance to *Micrandra* is based on the branched inflorescences and terminal position of the pistillate flowers, trigonous capsules, and ovate leaves with basal glands, but the stamens are more numerous and the pollen is inaperturate (like *Croton*). *Brasiliocroton* has a stellate-rosulate indumentum like some *Croton* species, but its anthers are erect in bud, and the position of the pistillate flowers is anomalous in *Croton*. Molecular data place *Brasiliocroton* as the closest sister group to *Croton", once *Astraea* has been removed from *Croton* and placed sister to Acidocroton and *Ophellantha*. Wood anatomical features support the generic status of *Brasiliocroton*.

*Croton* is one of the ten largest genera of flowering plants, with 1,223 species recognized in the recent World Checklist and Bibliography of Euphorbiaceae (Govaerts et al. 2000). Webster (1993) proposed a revised sectional classification of the genus in which he recognized 40 sections. However, many of the currently recognized species of *Croton* were not identified to section by Webster, and others simply defy placement to section using his key and descriptions of sections. To better understand the circumscription of the genus and the delimitation of sections within *Croton*, a molecular sampling of representatives of many *Croton* sections and potential outgroups was carried out by Berry et al. (in press). Based on molecular and morphological data, we discovered a new crotonoid taxon from Brazil that is distinct from *Croton* but is closely related to it. This paper describes the new genus and its placement in tribe Crotonae.

After extensive herbarium searches, we located 39 separate collections of the new taxon. Some of these specimens were previously identified as *Micrandra* (tribe Micrandreae) because of the general similarity of the leaves, the inflorescence, and the position of the pistillate flowers. Many of the characters of the new genus are crotonoid, however, including the numerous stamens, stellate pubescence, and inaperturate pollen with a croton exine pattern. The erect anthers in bud, however, exclude it from *Croton* as currently defined. To determine the position of the new taxon in relation to *Croton* and members of the Crotonae [as defined by Webster (1994) and modified by Wurdack and Chase (2002)], two accessions of the new taxon were included in a molecular survey of the Crotonae (Berry et al. 2002, in press). The results, summarized in Fig. 1 and supported by a more extensive analysis by Wurdack et al. (in press), strongly support the new genus as the sister group to all but two species of *Croton* sampled. Those two species belong to section *Astraea*, which should be excluded from *Croton* and placed sister to the Caribbean and Central American genera *Acidocroton* and *Ophellantha* [following the generic circumscription of Radcliffe-Smith (2001)]. Based on these molecular results, we feel justified in designating the new taxon as a new genus and recognizing it as the closest living sister group to the core *Croton* clade.

In accordance with Article 42 of the International Code of Botanical Nomenclature (Greuter et al. 2000), a single Latin diagnosis is provided below for the new genus and its single species.

**Brasiliocroton mamoninha** P.E. Berry & I. Cordeiro, gen. et sp. nov.—TYPE. BRAZIL. Espirito Santo: Município de Marilândia, rodovia Marilândia–Rio Bananal ca. 1 km N de Marilândia, remanescente de floresta tropical pluvial junto a “Cerâmica Floresta,” 6 Dec 1994 [1], J.R. Pirani, M.A.G. Magenta & A.A. Conceição 3411 (holotype: SPF; isotypes: NY!, SP!, WIS!). Figs. 2-5.

Arbor usque 15 m alta, ramulis inflorescentiisque trichomatibus densis dendritico-rosulatis in centro fuscis obtectis; foliis plerumque ovatis, apice acuminatis, basi rotundata vel truncata, penninerviis praeter basin

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Habitat and Distribution. The species grows as a \( \text{terminal bisexual panicle, with a main terminal } \) habit.

**Etymology and Common Names.** The generic name derives from the species' restricted distribution in Brazil and its close affinity to *Croton*. The specific epithet refers to the common name ("mamoninha") recorded from several specimens collected in Espírito Santo. This literally means "little castor bean," since "mamona" is the Brazilian name for *Ricinus communis*. One collection from Maranhão lists "murucutuzinho" as the common name, while others include "velame buriti" and "velame branco." These latter names are all variants of ones applied to different species of *Croton*.

**Habitat and Distribution.** The species grows as a...
small to medium-sized tree in non-flooded, primary or secondary (sometimes liana) forests and in low, coastal plateau forests (‘matas de tabuleiro’) at elevations of 50–300 m. There are two disjunct areas where the new genus has been collected, one in remnants of the Mata Atlântica in southern Bahia, Espírito Santo, and eastern Minas Gerais states, and the other in northern Maranhão state (Fig. 3).


Pollen Description. Pollen from Fiaschi et al. 951 (SP, SPF) was used for both optical and scanning electron microscopy (SEM). For both optical and SEM images, pollen was acetylated as outlined by Erdtman (1966). The pollen grains of Brasiliocroton are spheroidal, inaperturate, and possess the characteristic croton exine pattern, which consists of triangular supratectal elements (subunits) attached to a network of muri with short columellae (Erdtman 1952, 1966; Punt 1962; Nowicke 1994; Fig. 4). The mean diameter of acetylated grains is 48.6 μm, with the subunits of the muri arranged in rings of 5–8. The rings of subunits have a mean diameter of 3.5 μm. The individual subunits have a striate surface and sometimes attenuate tips (Fig. 4G) that resemble those of Sagotia racemosa Baill. (Nowicke 1994), a genus close to the Crotoneae. In the optical microscope view (Fig. 4 B–D), the subunits of
Fig. 2. *Brasiliocroton mamoninsha*. A. Flowering branch with a detail (circled) of the distal position of a pistillate flower (Fiaschi et al. 951). B. Recently germinated seedling (Pirani et al. 4947). C. Leaf with details of the basal glands and trichomes (Fiaschi et al. 951). D. Nearly mature capsule and dorsal and ventral views of a seed (Muniz B656). E. Young pistillate flower (left), with a detail of the ovary and the bifurcate, patent stigmas (right), and the calyx cut and spread open (lower right). F. Enlargement
Brasiliocroton pollen are circular to triangular and are in turn arranged in circular groups. These characters are all consistent with Brasiliocroton belonging in tribe Crotoneae, but it is clearly distinct from Micrandra, which has tricolpate pollen.

**Wood Anatomy.** Two stem wood specimens [Rosa & Vilar 3026 (MG), Vilhena et al. 979 (MADw)] and two twigs from herbarium specimens [Belem 3869 (WIS), Hatschbach et al. 58035 (DAV)] were sectioned using standard microtechnique protocols for light microscopy. Sections and macerations were observed by light microscopy, and anatomical measurements were taken in part by a computer-assisted digitizing tablet and in part by a calibrated ocular micrometer. Fifty fibers were measured for fiber data, 25 vessel elements for vessel data, and 50 rays for ray data. Quantitative data are expressed as the range of averages from the two stem wood samples. Most frequent ranges were reported for intervessel pit sizes and ray widths. The IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989) was used as a guideline for description. Characters not mentioned are absent or not applicable. SEM-coupled energy dispersive X-ray analysis was used to confirm the presence of silica bodies.

The mature wood specimens were taken from trees in the northern part of the species’ range, whereas the herbarium twig specimens came from the southern disjunct section of the range. Because the twig specimens represent immature wood, a comparison of quantitative features was not made. It would still be desirable to examine additional mature wood specimens from the southern part of the range to confirm generic features, particularly the quantitative features regarding element lengths and widths, and thus know if any geographically related differences exist within the species.

**Macroscopic Features.** Wood (Rosa & Vilar 3026) has a density of 0.65 g/cm³ at 0% moisture content, basic specific gravity approximately 0.56. Growth rings not distinct with a lens. Wood light brown, heartwood absent or not distinct.

**Microscopic Features.** Growth increments distinct due to thickening of fiber walls. Diffuse-porous, vessels solitary and occurring in radial multiples of 2–6 (12+), sometimes tangentially paired or in small clusters; 20–40/mm² (ave. 31–36/mm²). Vessel outline rounded; tangential diameter 75–85 µm (Fig. 5A). Vessel element length 641–710 µm. Perforation plates exclusively simple. Intervessel pits non-vestured, alternate; 10–12 µm with rounded to angular outline. Vessel-ray pits with reduced borders; 6–8 µm. Fibers non-septate; thick-walled, without helical thickenings, distinctly angular outline; 1158–1308 µm long. Fiber pits apparently bordered, common in radial walls, occasionally present in tangential walls; pits small, 2–3 µm diam. Fiber length to vessel element length ratio 1.81–1.84. Paratracheal parenchyma scanty. Apotracheal parenchyma diffuse in aggregate to banded, wavy, 1–2 cells wide, often touching vessels (Fig. 5A). Parenchyma strands typically 2- to 8-celled, sometimes with prismatic crystals in chambered or unchambered cells. Rays 1–3-seriate; mostly 13 per linear mm. Tall rays with 1–3(10+) rows of square marginal cells (Fig. 5B, D); rays 361–602 µm high, highest 10 rays average 697–1272 µm, procumbent cells in the body of the multiserate rays several times longer than tall. Uniserate rays composed solely of square cells or upright cells. Weakly disjunctive ray cell end walls sometimes present, typically more pronounced in the uniserate
Fig. 4. Pollen of Brasiliocroton mamoninha. A–D. Optical microscope images. A. Single grain showing the Croton exine pattern and lack of apertures. B–D. Different focal planes of the sexine showing triangular supratectal elements arranged in rings of 5–8 subunits and striate surface in C. E–H. Scanning electron micrographs. E. Whole grain. F–H. Surface of pollen grain. Rosettes of subunits are recognizable in G and H, and striate surface of subunits is visible in G. All images from Fiaschi et al. 951.
Fig. 5. Light micrographs of wood anatomical features of Brasiliocroton and related taxa. A–E. Brasiliocroton mamoninha. A. Transverse section showing vessel and parenchyma patterns. Note the apparent growth increment boundary (arrow). B. Radial section showing a heterocellular ray (upper arrow), the body of which is composed of many rows of distinctly elongated procumbent cells. Note also the axial file of crystalliferous cells (lower arrows); this region corresponds to the end of a growth increment. C. Tangential section showing the width and height of the rays. D. Crystals in chambered (arrowheads) and unchambered (arrows) upright cells in a ray. E. A rough silica body (arrow) occupying the majority of the lumen of an upright cell. F. Croton lobatus. Radial section showing ray tissue composed entirely of upright cells. G. Croton rusbyi. Radial section showing an intrusively growing non-articulated laticifer displacing and deforming the upright cells of a ray.

Common to the rays or the marginal cells of the multiseriate rays. Wood not storied. Prismatic crystals common in chambered or unchambered upright or square cells (Fig. 5D), particularly in areas that appear to correspond with growth increment boundaries (Fig. 5B). Prismatic crystals occasionally present in procumbent cells. Large, rough silica bodies sometimes present in upright and procumbent cells, generally occupying the majority of the cell lumen (Fig. 5E).

Comparative Wood Anatomy. Wood anatomical
features of Brasiliocroton mamoninha were compared to those of Micrandra elata Muell. Arg. (MADw 22383), M. simpsonoides Benth. (MADw 48731), Acidocroton cf. lobatus Urb. (SJ Ru 16163), A. trichophyllus Urb. (HAJB 81844), Croton alabamensis E. A. Smith ex Chapman var. alabamensis (Van Ey et al. 365, WIS), Croton alabamensis var. texensis Ginzburg (Van Ey et al. 349, WIS), Croton rusbyi Britton (Riina 1481, WIS), Croton klotschii (Didr.) Baill. (Van Ey 485, WIS), Croton lobatus L. (MADw 46559), Croton praetervisus Muell. Arg. (Sant'Ana et al. 1123, CEPEC) Macroton ekmannii (Urb.) Croizat (HAJB 81786), Macroton lanceolatus Alain (HAJB 81772), and Macroton revolutus Alain (HAJB 82006).

The presence of distinctly elongated procumbent cells in the body of the multiseriate rays is a distinct character that sets Brasiliocroton apart from the Astrarea, Acidocroton, Macroton, and Croton alabamensis clades. In these taxa, the rays are uniseriate, and ray composition is either entirely of upright cells (Astrarea clade, Fig. 5F) or of upright cells and square cells in the body of the ray (Acidocroton and Macroton clades). However, Micrandra, Croton rusbyi, and some other species of Croton also have elongated procumbent cells in the ray cells. In Micrandra and C. rusbyi, each of which has some floral or vegetative similarities to Brasiliocroton, there are additional anatomical differences. Both Micrandra (Berry and Wiedenhoeft 2004) and C. rusbyi have laticifers in the rays; in Micrandra they are the typical articulated laticifers common to some Euphorbiaceae and Apocynaceae woods. In C. rusbyi, however, the laticifers are non-articulated and have clearly penetrated the ray intrusively (Fig. 5G), as is common in Croton macrobothrys Baill. and other species in the ‘sangre de drago’ group, Croton sect. Cyclostigma (Rudall 1989; Wiedenhoeft, pers. observ.). The wood of Brasiliocroton lacks laticifers of any kind, and it also differs from the Micrandra species investigated and from Croton rusbyi in intervessel pit diameter and ray-vessel pitting characteristics. In Brasiliocroton the ray-vessel pits are smaller than the intervessel pits, whereas in Micrandra the apparently simple intervessel pits are larger than the ray-vessel pits.

Carquist (2001) cautioned that it can be misleading to compare the ray structure of taxa when wood samples come from different diameters or developmental stages in the life of the plant. In the case of the taxa in the Astrarea group (Croton lobatus and C. praetervisus), they are shaggy or barely woody species that never form larger diameter stems as Brasiliocroton does. For this reason, small diameter stems of Brasiliocroton were also observed to determine if Brasiliocroton could be displaying paedomorphic ray ontogeny. The small diameter twig specimens showed ray structure similar to the adult material; heterocellular rays with distinctly elongated procumbent cells were present even in samples of less than 1 cm in diameter, although the rays were conspicuously shorter than those of the mature wood. Because the twig samples were roughly the same diameter as the Astrarea stem specimens, we assume they are in a developmentally similar condition. Since both the twigs and the mature wood samples of Brasiliocroton were qualitatively similar, we suggest that this wood anatomical feature is a characteristic of the taxon, making Brasiliocroton distinct from the other taxa considered above.

Although the wood anatomy of Brasiliocroton appears amply distinct from its closest relatives, Croton is a very large and diverse genus with hundreds of species for which wood anatomy has not yet been studied, so there could yet be other Croton species with wood more similar to Brasiliocroton. Wiedenhoeft et al. (2003) found a wide range of wood anatomical characters within a small number of Old World Croton species, implicating a high degree of variability across the genus. To date, however, no species of Croton examined has shown the presence of silica bodies in the ray cells that characterize the wood of Brasiliocroton (Welle 1976; Wiedenhoeft, pers. observ.).

**DISCUSSION**

Some of the collections cited above were found filed under Micrandra, which is most likely due to similarities in the inflorescence structure and the distal position of the female flowers and fruits on the side shoots of the panicle. The leaf shape and glands are reminiscent of some Micrandra species, but when leaf glands are present in Micrandra they are usually embedded in the tissue of the blade near the base, whereas the glands of Brasiliocroton are located at the apex of the petiole and are sometimes stipitate, a feature more consistent with Croton. A number of characters exclude the new genus from Micrandra, including the inaperturate pollen, the lack of laticifers in the wood, more numerous stomates (only 5–10 in Micrandra), the patent, bifurcate stigmas, the lack of a pistillode in staminate flowers, and the dense, dendritic or stellate-rosulate pubescence. Many of these characters are found in Croton, however. The main morphological character that excludes Brasiliocroton from Croton is the erect stamens in bud—the main synapomorphy of Croton is the anthers inflexed in bud. The complex, branched inflorescence and the distal position of the pistillate flowers are also out of place in Croton, although C. rusbyi from Bolivia and Peru has short side branches and distal pistillate flowers as well. The long, dark, and horizontally bifurcating stigmas of Brasiliocroton are very distinctive, although they would probably fit within the broad diversity of stigma types found among the 1,223 recognized species of Croton (Govaerts et al. 2000). Also, the stem and rachis pubescence of Brasiliocroton is unusual—composed of tiny, densely and dendritically branched or rosulate trichomes [following the ter-
minology of Webster et al. (1996) with a dark base that gives a characteristic rusty appearance to the stems and fruits, but that character alone is not distinctive enough to exclude it from Croton.

The molecular data that are being reported in a separate paper (Berry et al., in press) includes two accessions of Brasiliocroton along with 60 taxa of Croton and additional outgroups. This study used nuclear ribosomal ITS and chloroplast trnL–F sequences, which were analyzed using parsimony and Bayesian analyses. The simplified tree shown in Fig. 1 shows the position of Brasiliocroton as sister (with a Bayesian posterior probability support value of 1.00 and a bootstrap value of 91%) to all of the Croton taxa examined plus the Cuban endemic Moacroton, with one exception. Croton sect. Astraeae (sampled by Croton lobatus and C. pratersissus) falls outside the Brasiliocroton–Croton clade and is strongly supported as the sister group of the Antillean and Central American clade of Acidocroton + Ophellantha. In the molecular paper, section Astraeae will be restored to its former generic status. Moacroton differs from Croton in lacking inflexed stamens in bud, but the filaments in that group are so short that inflexing of the stamens is not possible. Ongoing molecular studies by P. Berry and B. Van Ee at UW-Madison will determine if Moacroton should eventually be sunk into Croton.

In light of these molecular results, it is now clear that Croton, and probably the entire tribe Crotoneae, is Neotropical in origin. Webster (1994) placed Croton in tribe Crotoneae together with the Old World genera Mildbraedia and Paracroton (=Fahneleitonia), but rbcL and trnL–F analyses by Wurdack and Chase (2002) and Wurdack et al. (in press) place these instead in the mainly Old World tribe Riciocarpae. A realigned tribe Crotoneae should now include Acidocroton, Ophellantha, Astraeae (formerly Croton sect. Astraeae), Sagotia, and Sandwithia, in addition to Croton and Brasiliocroton (with Moacroton and Cubacroton possibly included within, or immediately sister to Croton). Of these genera, Sagotia and Sandwithia both inhabit lowland rainforests in the Amazon basin, Astraeae and Brasiliocroton are centered in eastern Brazil, and Acidocroton, Ophellantha, and at least some of the basal members of the core Croton clade are centered in the Antilles or pan-Caribbean region. Continuing molecular work will examine more closely the biogeographic relationships among these genera.

Acknowledgments. This paper was supported by National Science Foundation grant DEB-0212481 to the senior author. We thank Emiko Naruto for the fine line illustration and Kandis Elliot for preparing the map and figures for publication. Bruno Manara kindly revised the Latin description. Kenneth Wurdack, Paul Manos, and another reviewer made very helpful comments to an earlier draft of the paper. We especially thank Dr. Jacqueline Kallunki of the New York Botanical Garden for first bringing specimens of this taxon to our attention and for her keen sense in recognizing botanical novelties.

Literature Cited


