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

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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 Crotoneae 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 Crotoneae.

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 Crotoneae [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 Crotoneae (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 ''Cerámica Floresta,'' 6 Dec 1994 [fl], *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 acuminato, basi rotundata vel truncata, penninerviis praeter basin

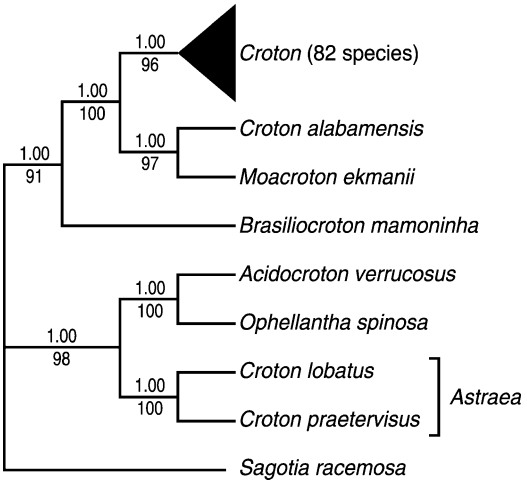

FIG. 1. Cladogram of the relationships of *Brasiliocroton* with *Croton* and other members of the Crotoneae based on combined nuclear ITS and chloroplast *trnL–F* sequences. This is extracted from a larger analysis of separate and combined data sets (Berry et al., in press). The topology shown is identical in both maximum parsimony and Bayesian analyses. Posterior probabilities from the Bayesian analysis are given above the branches, and percentage bootstrap values from the maximum parsimony analysis are given below the branches.

triplinerviis, glandulis binis saepe stipitatis ad apicem petiolis adaxialiter, petiolis plerumque laminis dimidio brevioribus; inflorescentiis terminalibus, paniculatis, bisexualibus, rhachidibus primariis 9–20 cm longis, ramulis secundariis 2–7 cm longis, ramulis tertiariis 1–3 cm longis, floribus confertis et pistillatis ad apicem ramulorum; staminibus 20–30 (plerumque 25), in alabastro erectis, pollinis granulo inaperturato; ovario loculis 3(4), 1-ovulatis, stylis bifurcatis, stigmatibus cilindricis verrucosis atropurpureis; seminibus oblongoideis, castaneis, 6–10 × 4–7 mm, caruncula parva munitis.

Monoecious tree 3–15 m tall, diameter of main trunk to 30 cm; trunk sulcate with smooth bark. Young stems covered by a whitish-ferrugineous indument of small dendritic-rosulate trichomes with a dark brown center, the young leaf buds ± congested at the tips. Leaves alternate, discolorous (lighter and more venose on the abaxial side), ovate or occasionally obovate, (4–)8–12(–15) × (2.5–)4–6(–8) cm, base rounded to truncate, apex acuminate, pinnately veined except for the tripliveined base, secondary veins 7 or 8 (rarely 9) per side, abaxial surface with scattered stellate trichomes, adaxial surface with more scattered trichomes, sometimes remaining only along the veins and then those dendritic, or glabresent; stipules filiform, 2–6 mm long or sometimes inconspicuous, deciduous; petioles 1.5–6(–8) cm long, with two sessile to shortly stipitate glands 0.5–1.0 mm diam on the adaxial side of the petiole at its junction with the leaf blade. Inflorescence a terminal bisexual panicle, with a main terminal rachis and several subterminal axillary branches; the main central rachis 9–20 cm long, the subterminal rachi 4–12 cm long, both in turn can have with widely spaced, alternate side branchlets 2–7 cm long and angled upwards at a ca. 45° angle, with flowers clustered on short, single or branched side branchlets 1–2(–3 cm in fruit) long, all covered by trichomes similar to those on the young stems. Flowers cream to white, greenish in bud, mostly staminate, these with pedicels 1–2.5 (–3) mm long, subtended by linear-lanceolate bracteoles 0.5–1.5 mm long, the distal ones opening earliest. Pistillate flowers, when present, single and at the distalmost position of the flower clusters, the pedicels 2–5 mm long and noticeably thicker than the staminate ones. Staminate flowers with 5(6) valvate calyx lobes, these thick, densely covered by stellate-dendritic trichomes ca. 0.3 mm diam on the outer surface, glabrous within, broadly triangular-oblong, 2 × 1.5 mm, slightly connate at the base, spreading at anthesis, a nectary gland ca. 1 mm wide opposite the base of each sepal; petals 5(6), membranaceous, ca. 2 × 1.2 mm, densely short-villous on the outside, sparsely villous on the inside, the tips recurved at anthesis; stamens (20–)25 (–30), receptacle with long-villous trichomes; filaments erect in bud, 2–3 mm long at anthesis, villous in basal portion; anthers broadly elliptic, bilobed, 1 × 1 mm. Pistillate flowers with 5 valvate sepals 2.5–3.5 mm long, basally connate for 1/2 to 2/3 their length, the triangular apices slightly recurved at anthesis, densely stellate-rosulate outside, short-villous inside; ovary ca. 2.5 mm diam, densely covered by dendritic trichomes; a nectary gland ca. 1 mm wide opposite the base of each sepal; ovary 3(4)-locular, locules 1-ovulate; stigmas 3, apically bifid, 4–5 mm long and disposed in a horizontal plane at anthesis, the branches cylindrical, ca. 1 mm diam, dark purplish and conspicuously verrucose on the adaxial (receptive) surface, pale tan-pubescent on the abaxial side, basally connate into a short column. Schizocarps spherical-trigonous (rarely tetragonous), 15–20 × 10–15 mm, indumentum ochraceous to brown, with stipitate trichomes, each coccus 8–13 mm tall; columella 8–12 mm long, the exocarp separating from the woody cocci. Seeds oblongoid, dorsally angled, brown, 6–10 × 4–7 mm, with a small caruncle.

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 ''murucututuzinho'' 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 nonflooded, 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).

Additional Specimens Examined. BRAZIL. Bahia: Município de Mucuri, vale do rio Mucurí, ao lado da Rodovia BR 101, mata de terra firme, 16 Jul 1968 [fr], *R.P. Belem 3869* (CEPEC, NY, WIS), 2 Abr 1971 [fl], *T. S. dos Santos 1543* (CEPEC); Município de Teixeira de Freitas, vale do rio Alcobaça, 13 Oct 1971 [fl], *T. S. dos Santos 2114* (CEPEC, R). Espírito Santo: Município de Colatina, estrada velha de Pancas, Rio Doce, Floresta Atlântica, 26 Mar 1934 [fl, fr], *J.G. Kuhlmann 62* (RB); Rodovia ES-080, trevo donde nace el camino a Governador Lindemberg y Bananal, aprox. 19°13′S, 40°38′W, 200–300 m, 29 Jan 1997 [fr], *M.M. Arbo, A.M. de Carvalho, M.S. Ferrucci, J.G. Jardim, & S.C. de Sant'Ana 7819* (CEPEC, CTES, DAV, NY, SP); Município de Conceição da Barra, 9 Oct 1998 [fl], *G. Hatschbach, M. Hatschbach & J.M. Silva 68380* (MBM, SP); Município de Linhares, Reserva Florestal da Companhia do Vale do Rio Doce—CVRD, estrada Cinco Folhas, km 0.027, lado direito, 23 Oct 1984 [fl], *G.L. Farias 20* (DAV); estrada Cinco Folhas, lado esquerdo, 7 Mar 1972 [fr], *A.M. Lino 13* (K, RB); estrada Mantegueira, ant. 154, km 1.030, lado esquerdo, 24 Oct 1978, *D.A. Folli 46* (HRB, SPF, CVRD); próximo estrada 161, Talhão 604, 8 Oct 1973 [fl], *A.M. Lino 130* (RB); MME, floresta de tabuleiro secundária, área experimental RFL 89, 19°07′57″S, 40°04′58″W, ca. 80 m, 1 Feb 2002, *J.R. Pirani, A.C. Marcato, M. Groppo, P. Fiaschi, & D. Folli 4947* (SP, SPF, WIS, CVRD); Córrego Santa Rita de Cássia, Pinheiros, 23 Nov 1991 [fl], *V. C. de Souza 266* (DAV, K); Docemade, 30 Jan 1972 [fr], *D. Sucre 8285* (RB), 4 Feb 1972 [fl, fr], *D. Sucre 8470* (RB); Reserva Ecológica de Sooretama, 14 Oct 1992 [fr], *G. Hatschbach, A.C. Cervi & J.M. Silva 58035* (MBM, DAV); Reserva Biológica de Sooretama, floresta de tabuleiro, matas de Quirino, 50–100 m, 5 Dec 1985 [fr], *G. Martinelli, F. Zuloaga, M. Varquez, I. Caruso 10971* (RB); Município de Montanha, Distrito de Vinhático, Fazenda Boa Vista, de propriedade do Sr. Alicio Britti, 9 Nov 1990 [fl], *E.N. Moraes 59* (DAV, PEUFR); Município de Pancas, Chapadão, Rio Doce, 2 Dec 1943 [fl], *J.G. Kuhlmann 6594* (DAV, RB, SPF); Município de Pinheiros, Reserva Biológica do Córrego do Veado, 62 m.s.m., 17 jun 2004 [fr], *L.S.Leoni 5803* (GFJP, SP); Município de Santa Teresa, São Sebastião, Várzea Alegre, Propriedade de Djalma Novelli, 19°50′48″S 40°43′10″, 180 m, 30 Jan 2002 [fl, fr], *P. Fiaschi, J.R. Pirani, M. Groppo, A.C. Marcato, & V. Demuneri 951* (SP, SPF); Reserva Biológica de Nova Lombardia, 700 m, 5 Feb 1985 [fr], *A. Peixoto, A. Gentry, E. Zardini, C. Proença & O. Peixoto 3489* (MO, RB); Município de São Mateus, Reserva Biológica de Sooretama, Lagoa do Macaco, 30 m, 15 May 1977 [fr], *G. Martinelli et al. 2179* (RB); entre São Mateus e Nova Venécia, 14 Nov 1953 [fl], *A.P. Duarte 3874* (RB); Córrego da Preguiça, 26 Feb 1965 [fl], *A.P. Duarte 8985* (RB). Maranhão: Município de Açailândia, Parque Florestal Rio Doce, 20–6–1991 [fl], *L.R. Marinho 1410* (IAN), *1410-A* (IAN); Município de Buriticupu, Reserva Florestal da Companhia Vale do Rio Doce—CVRD, área de experimento, 29 Aug 1991 [fr], *M.R. Cordeiro 2131* (IAN); estrada para a Reserva Florestal da CVRD, 31 Aug 1991 [fr], *M.R. Cordeiro 2140* (IAN); estrada do Arame km 20, floresta de cipó, 14 Jul 1987 [fl, fr], *M.S. Menandro 102* (CVRD, K, PEUFR); Reserva Florestal da CVRD, 8 Nov 1995, *F.H. Muniz B656* (HRCB, SP), 8 Dec 1995, *F.H. Muniz B2056* (ESA, SPF); Município de Santa Luzia, Fazenda Agripec da VARIG, margem esquerda do Rio Pindaré, mata de terra firme, solo arenoso, relevo ondulado, 2 Apr 1983 [fr], *M.G. Lobo, E.L. Taylor, N.A. Rosa, M.R. Santos, J.B. Silva & T. Rebbeck 340* (NY, MG); Municipio de Tuntum, Fazenda Violão, 9 Abr 1974, [fl], *F. Paiva 58* (PEUFR); Fazenda Santa Maria, margem esquerda da Rodovia BR-222, km 45 de Açailândia, floresta de terra firme, relevo plano, 17 Dec 1978, *N.A. Rosa & H. Vilar 3026* (F, MG, MO); Reserva Florestal da CVRD, margem da Rodovia Buriticupu-Arame, mata de terra firme com muitos cipós, 9 Sep 1985 [fr], *N.A. Rosa, R.P. Salomão & R.P. Bahia 4898* (MG); Reserva Florestal da CVRD Buriticupu, mata de terra firme, muito seca e bastante cipó, relevo ondulado, 5–30 [month not given] 1975 [fr], *N.A. Rosa, R.P. Salomão & R.P. Bahia 5178* (MG); estrada a direita entre Grajaú e Arame, km 52, 3 Oct 1983 [fl, fr], *R. Vilhena, E. Taylor, G.C. Schatz, T. Richard, C. Rosário & M.R. dos Santos 979* (NY− 2 sheets, WIS, MG). Minas Gerais. Figueira, Estrada de Ferro Vitória-Minas, 25 Sep 1929 [fl], *J.G. Kuhlmann 260* (DAV, RB).

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 acetolyzed 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 acetolyzed 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

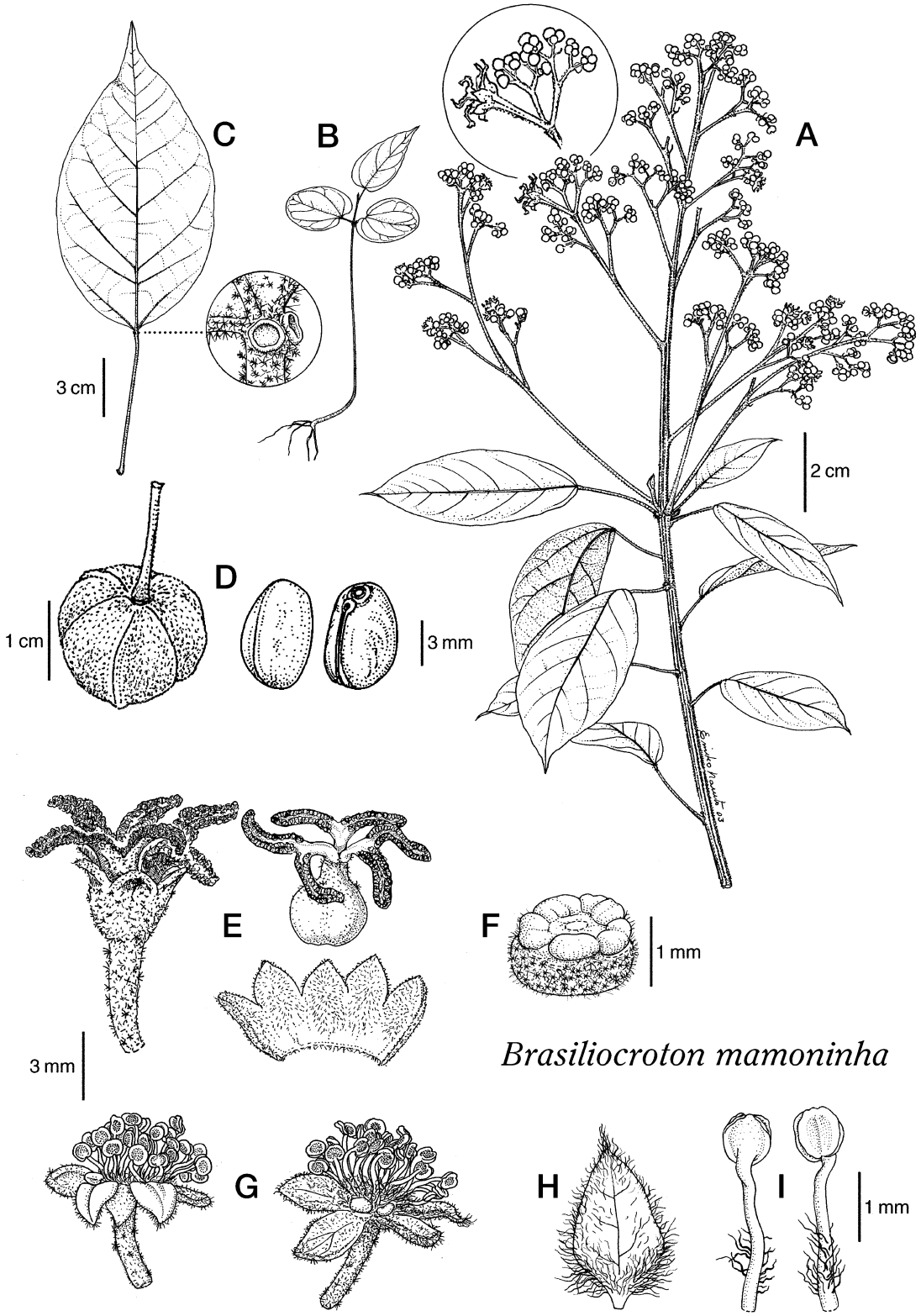

FIG. 2. *Brasiliocroton mamoninha*. A. Flowering branch with a detail (circled) of the distal position of a pistillate flower (*Fiaschi et al. 951*). B. Recently germinated seedling (*Pirani et al. 4947*). C. Leaf with details of the basal glands and trichomes (*Fiaschi et al. 951*). D. Nearly mature 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

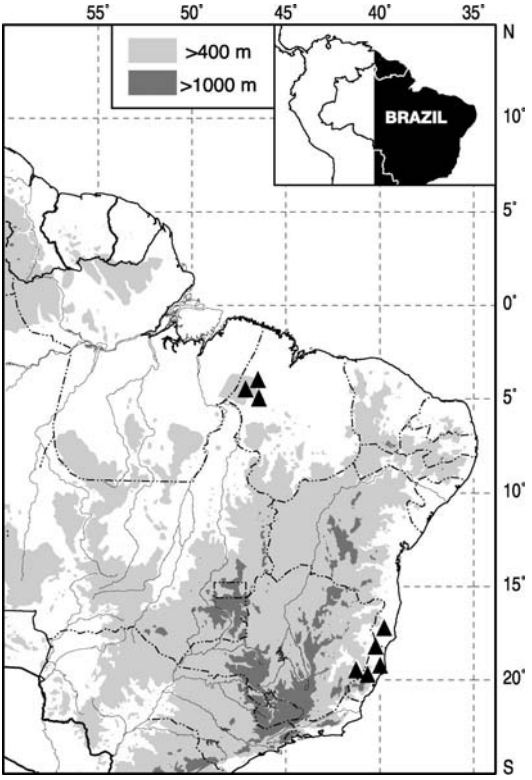

FIG. 3. Map of known localities of *Brasiliocroton mamoninha*. Note the very large disjunction between the Maranhão populations and those from Espirito Santo and southern Bahia.

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/cm^3 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/mm^2 (ave. 31–36/mm^2). 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 nonseptate; 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 multiseriate rays several times longer than tall. Uniseriate rays composed solely of square cells or upright cells. Weakly disjunctive ray cell end walls sometimes present, typically more pronounced in the uniseriate

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FIG. 2. of the pistillate receptacle showing the nectary glands. G. Staminate flowers at anthesis showing the recurving petals (left) and a flower with the petals removed (right) to show the antesepalous nectaries. H. Adaxial view of a petal. I. Dorsal and ventral views of a stamen. All floral details from *Muniz B2065.*

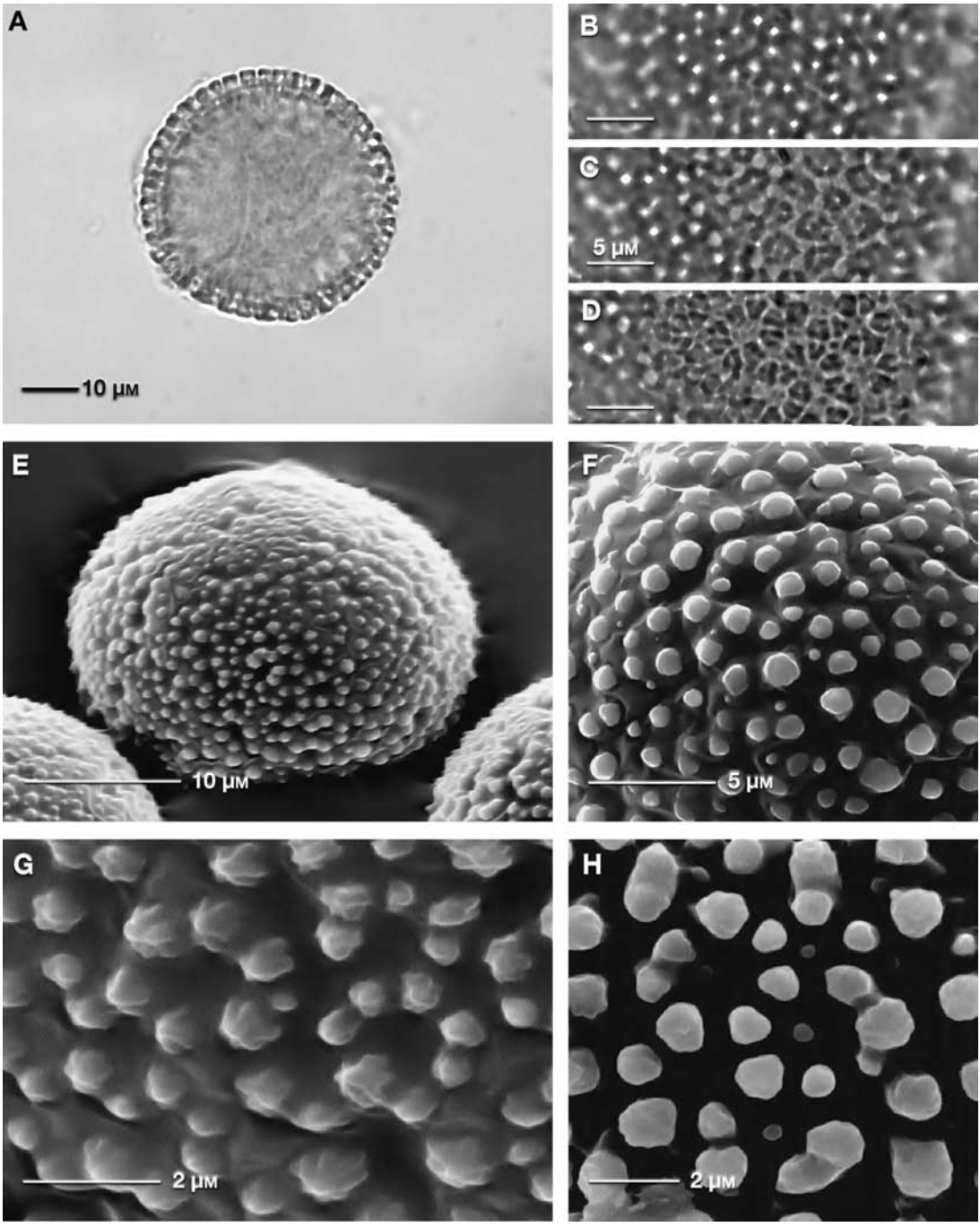

FIG. 4. Pollen of *Brasiliocroton mamoninha*. A–D. Optical microscope images. A. Single grain showing the *Croton* exine pattern and lack of apertures. B–D. Different focal planes of the sexine showing triangular supratectal elements arranged in rings of 5–8 subunits and striate surface in C. E–H. Scanning electron micrographs. E. Whole grain. F–H. Surface of pollen grain. Rosettes of subunits are recognizeable in G and H, and striate surface of subunits is visible in G. All images from *Fiaschi et al. 951*.

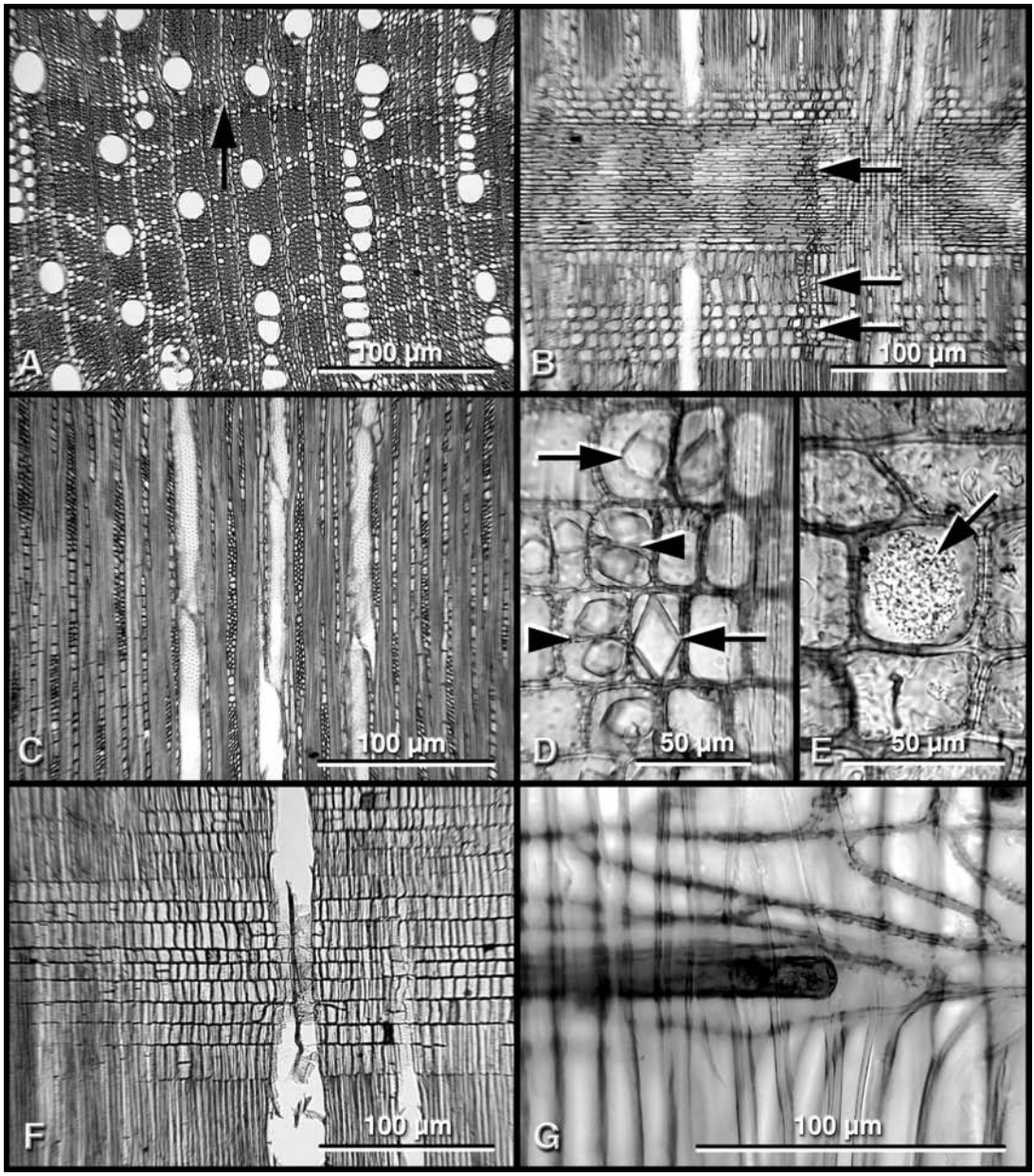

FIG. 5. Light micrographs of wood anatomical features of *Brasiliocroton* and related taxa. A–E. *Brasiliocroton mamoninha*. A. Transverse section showing vessel and parenchyma patterns. Note the apparent growth increment boundary (arrow). B. Radial section showing a heterocellular ray (upper arrow), 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.

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. siphonioides* Benth. (*MADw 48731*), *Acidocroton* cf. *lobulatus* Urb. (*SJRw 16163*), *A. trichophyllus* Urb. (*HAJB 81844*), *Croton alabamensis* E. A. Smith ex Chapman var. *alabamensis* (*Van Ee et al. 365,* WIS), *Croton alabamensis var. texensis* Ginzbarg (*Van Ee et al. 349,* WIS), *Croton rusbyi* Britton (*Riina 1481,* WIS), *Croton klotzschii* (Didr.) Baill. (*Van Ee 485,* WIS), *Croton lobatus* L. (*MADw 46550*), *Croton praetervisus* Muell. Arg. (*Sant'Ana et al. 1123,* CEPEC) *Moacroton ekmannii*(Urb.) Croizat (*HAJB 81786*), *Moacroton lanceolatus* Alain (*HAJB 81772*), and *Moacroton 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 *Astraea*, *Acidocroton*, *Moacroton*, and *Croton alabamensis* clades. In these taxa, the rays are uniseriate, and ray composition is either entirely of upright cells (*Astraea* clade, Fig. 5F) or of upright cells and square cells in the body of the ray (*Acidocroton* and *Moacroton* 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.

Carlquist (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 *Astraea* group (*Croton lobatus* and *C. praetervisus*), they are shrubby 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 *Astraea* 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 stamens (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. *Astraea* (sampled by *Croton lobatus* and *C. praetervisus*) 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 *Astraea* 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* (=*Fahrenheitia*), 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 Ricinocarpeae. A realigned tribe Crotoneae should now include *Acidocroton*, *Ophellantha*, *Astraea* (formerly *Croton* sect. *Astraea*), *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, *Astraea* 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.

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