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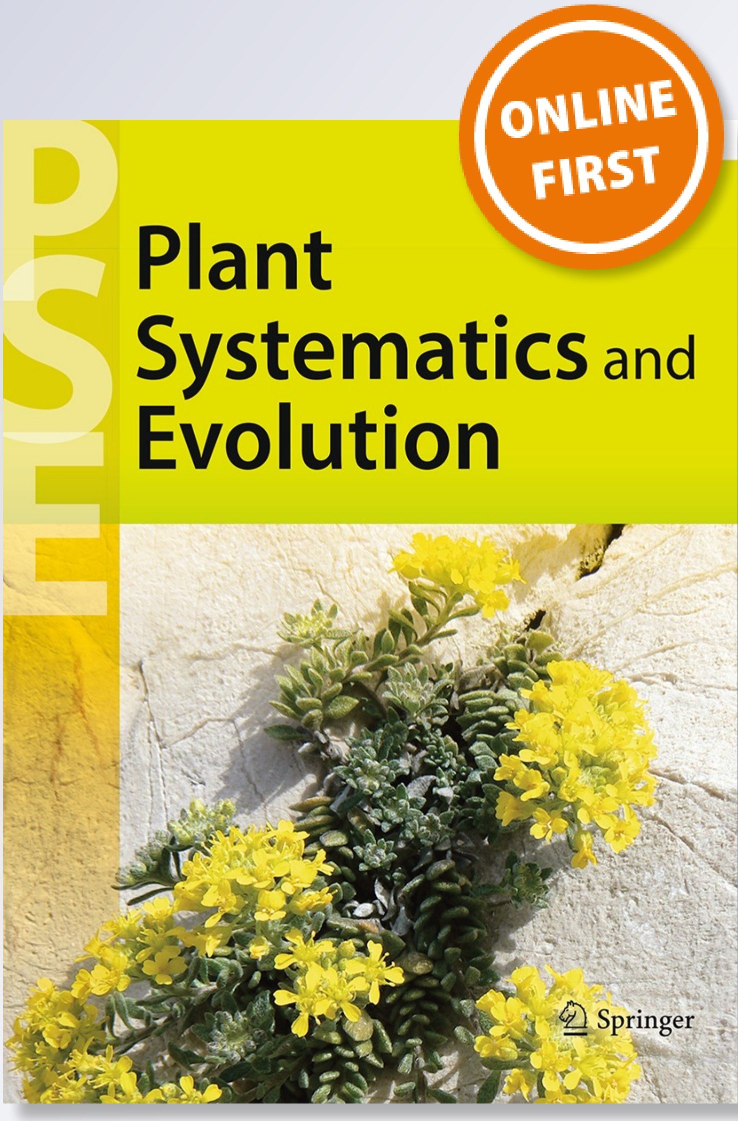

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ORIGINAL ARTICLE

Pollen morphology of Crotonoideae (Euphorbiaceae) from Seasonally Dry Tropical Forests, Northeastern Brazil

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Abstract Crotonoideae is a subfamily of Euphorbiaceae, a plant family that is characterized by the presence of laticifers and pollen grains with *Croton* pattern exine. We analysed 48 species of Crotonoideae from Seasonally Dry Tropical Forests within Caatinga vegetation aiming to contribute to the pollen morphology of this subfamily, focusing on endemics to these forests. Pollen samples were obtained from specimens of the herbarium. Pollen grains were acetolyzed, measured, photographed and described using light and scanning electron microscopy methods. Three pollen types and seven subtypes were recognized based on aperture type, polarity, shape, size and details of the exine sculpture. The exine ornamentation and the type and number of apertures are the most important characteristics for recognizing genera in Crotonoideae. Inaperturate pollen grains with surface pila plicate were observed in representatives of *Croton* and *Jatropha*; 4–8 pantoporate pollen grains and a 3-colpate one with psilate pila were observed in *Cnidoscolus,* and 10–22 pantoporate pollen grains with rugulate pila were observed in *Manihot*. Due to the high diversity of Crotonoideae pollen morphology, we highlighted its eurypalynous properties, in addition to its taxonomic relevance, for the identification of groups.

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Keywords Caatinga · Crotonoideae · Euphorbiaceae · Pollen grains

Introduction

Seasonally Dry Tropical Forests (SDTFs) are disjointed areas of xeric vegetation in the Neotropics (Pennington et al. 2006). SDTFs are included in a biome with a peculiar phytophysiognomy—a morphological characteristic of vegetation that is primarily determined by the growth form and life form of the dominant or codominant plant taxonomy and morphological adaptations to a deciduous dry season (Felfili et al. 2007). These forests have a high rate of animal and plant endemics (Mooney et al. 1995), being one of the most threatened in the world due to logging activities (Janzen 1988) yet one of the least studied (Werneck 2011).

Most Seasonally Dry Tropical Forests are scattered throughout South America, with the Caatinga biome (Fig. 1) being the largest (Santos et al. 2011). This biome is entirely located in Brazil in an area of 734,000 km^2, comprising almost all of the northeastern states, including northern Minas Gerais. This biome corresponds to 70 % of northeastern Brazil and 9.92 % of the Brazilian territory (Bucher 1982; Silva et al. 2004). Different phytophysiognomies can be found within Caatinga SDTFs, from tall dry forests to open grasslands, rocky fields, evergreen forests, Caatingas and savannas (Giulietti et al. 2006). The diversity of phytophysiognomies can be explained by the interaction of current and historic factors (Queiroz 2008). The floristic diversity of the Caatinga is extremely high, and there is a significant number of endemic and rare taxa (Giulietti et al. 2002), with 4320 species of flowering plants, of which 744 are endemic (Forzza et al. 2010). One of the most diverse families of flowering plants within Caatinga vegetation is the Euphorbiaceae. This family

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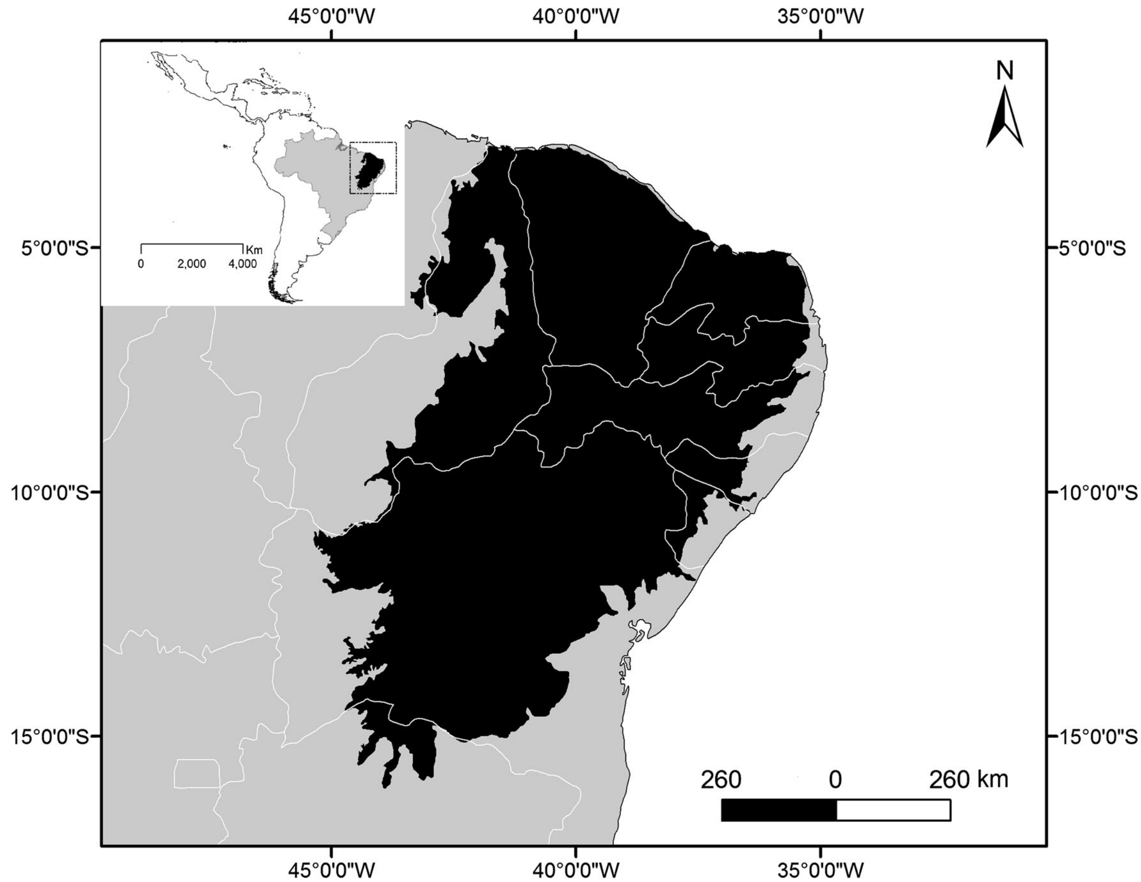

Fig. 1 Area covered by Caatinga Biome (sense Velloso et al. 2002), in *black*

figures is the fourth most diverse family of flowering plants in this biome (Forzza et al. 2010). Crotonoideae is one of the uniovulate subfamilies belonging to Euphorbiaceae that have been rearranged by Chase et al. (2002). This subfamily comprises 12 tribes and approximately 73 genera that are characterized by the presence of latex and pollen grains with *Croton*-type exine (Webster 1975, 1994; Wurdack et al. 2005). This subfamily is palynologically characterized by tricolporate pollen grains, or rarely porate to inaperturate pollen grains, with a *Croton* pattern of exine ornamentation (Webster 1994).

Palynological studies of this subfamily are rare, with a few studies restricted to a single genus (Ybert 1975; Thanikaimoni et al. 1984; Allem 1993; Carreira et al. 1996; Lima et al. 2007; Vieira et al. 2012) or to floristic inventories and general pollen catalogues (Erdtman 1952; Punt 1962; Salgado-Laboriau 1967; Zavaleta and Palacios-Chávez 1980; Palacios-Chávez et al. 1991; Roubik and Moreno 1991; Cruz-Barros et al. 2006; Corrêa et al. 2010). The main studies on Crotonoideae pollen were conducted by Nowicke (1994) and Lobreau-Callen and Cervera (1997). Recently, Matamoro-Vidal et al. (2012) conducted an important study of the pollen evolution of Euphorbiaceae in a phylogenetic context, including Crotonoideae species.

We present a palynological study of Crotonoideae species occurring in Seasonally Dry Tropical Forests of the Caatinga biome, focusing on its endemic species. A morphological characterization of pollen grains is presented for each analysed species, along with a taxonomic discussion aiming to contribute to the taxonomy of the group, as well as to applied palynology.

Materials and methods

A total of 123 specimens distributed in 48 species and four genera of Crotonoideae from Caatinga vegetation (Fig. 1) were analysed. We collected flowers and/or flower buds from all of the analysed specimens, which were deposited at the CEPEC, HUEFS, HUNEB and SP herbaria. All of the examined specimens are listed in the "Appendix".

Pollen grains were acetolyzed following Erdtman (1960) and mounted on slides immediately after using glycerin jelly sealed with paraffin.

Measurements of pollen grains were made following the most important morphometric parameters. In apolar pollen grains, a single diameter was measured. For isopolar pollen grains, the diameters were measured to the equatorial, polar and equatorial diameters in polar view. Measurements were taken whenever possible in 25 pollen grains that were randomly chosen from three slides to make uniform the sampling. Apertural and exine parameters apocolpium side, aperture dimensions, sexine and nexine thickness (Fig. 2), rosette diameter (Fig. 2), pilum diameter (Fig. 2), and diameter of rosette central spaces (Fig. 2) were measured in ten pollen grains. The mean (x), standard deviation (SX), standard error (s), 95 % confidence interval (CI) and coefficient of variation (CV) were calculated for all of the diameters of the pollen grains with a sample size of 25. For samples with 10 data points, we calculated the average and standard deviation. The results are shown in Tables 3, 4. The data were analysed visually using box plot graphs produced by Minitab 17.

For Scanning Electron Microscope (SEM) analysis, all of the acetolyzed pollen grains were washed and dehydrated in an ascending hydroacetonic series (50, 70, 90 and 100 %), remaining for 10 min in each series. Absolute acetone with pollen grains was directly dropped over the SEM stubs, which were metalized by high-vacuum gold evaporation. Pollen grains were analysed and photographed using LEO 1430 VP JSM and JEOL 6390LV microscopes.

Pollen characteristics, such as size, shape, polarity, aperture, ornamentation and exine sculpture, were illustrated using optical and SEM photographs. Pollen descriptions followed Punt et al. (2007) and Erdtman (1952) for pollen size: medium, 25–50 µm; large, 50–100 µm; and very large, 100–200 µm.

Results

Pollen grains from the Crotonoideae subfamily are characterized by monads, varying from medium to very large in size, with a predominance of large sizes, followed by very large and medium sizes. Apolar and spheroid pollen grains were found in almost all of the analysed species (Figs. 3, 4, 5 6a–i), with the exception of *Cnidoscolus quercifolius* Pohl ex Baill., in which pollen grains are isopolar, suboblate to oblate spheroidal (Fig. 6j–l).

Inaperturate pollen types were predominant (Figs. 3, 4a–i), occurring in all species of *Croton* L. and *Jatropha* L. Colpate pollen types were recorded only for *Cnidoscolus quercifolius,* whereas porate types were found only in *Cnidoscolus* Pohl. and *Manihot* Mill.

Croton pattern exine ornamentation was recorded for all of the analysed species, but with peculiarities regarding ornamentation units and subunits. A variation in size, shape, number, arrangement and ornamentation of subunits (pila) was observed. We also recorded a pattern of the absence or presence of sexine elements (clavae, bacula, and pila) in the lumen of ornamentation units (rosettes). All of the species of *Croton* and *Jatropha* showed those elements (Fig. 7), whereas in the species of *Cnidoscolus* and *Manihot*, these elements were absent from the rosette lumen (Fig. 8).

Based on aperture, size, and pila surface, we could recognize three main pollen types in Crotonoideae, divided into seven subtypes (Table 1). Pollen grains from the studied species were described and illustrated according to their main palynological characteristics (Figs. 3, 4, 5, 6, 7, 8, 9, 10; Tables 2, 3, 4).

Type 1: inaperturate pollen grains with plicate pila

Represented by species with pollen grains that were apolar and spheroidal, with a rosette disposed in a wall, a lumen greater than 1 µm in diameter, pila with plicate surfaces, the presence of sexine elements inside the rosette lumen and the sexine thicker than the nexine.

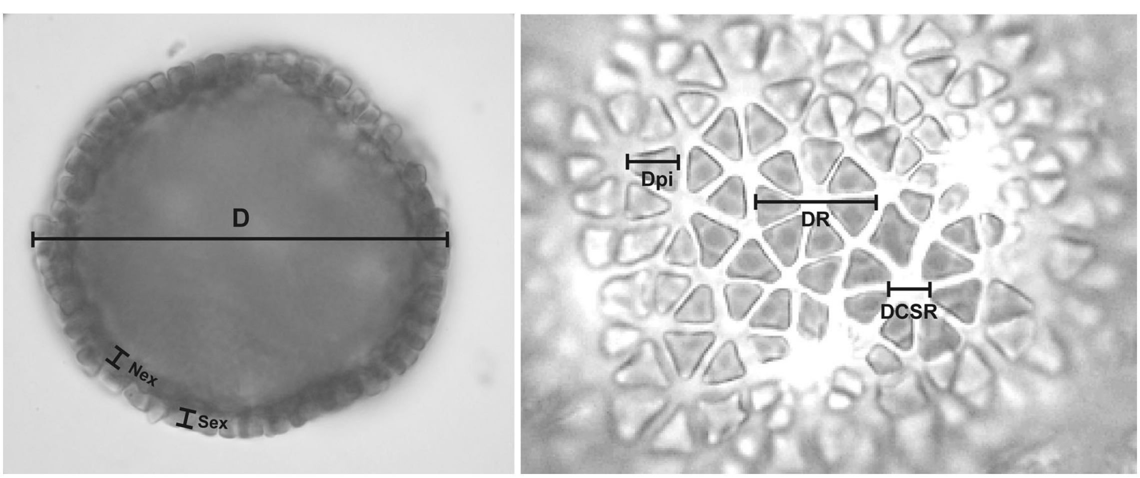

Fig. 2 Schematic representation of the morphometric characters of the grains pollen (*D* pollen grains diameter, *Sex* Sexine, *Nex* Nexine) and of exine ornamentation in the *Croton*-pattern (*DR* diameter of rosettes, *DPi* diameter of pila, *DCSR* diameter of central space of to rosettes)

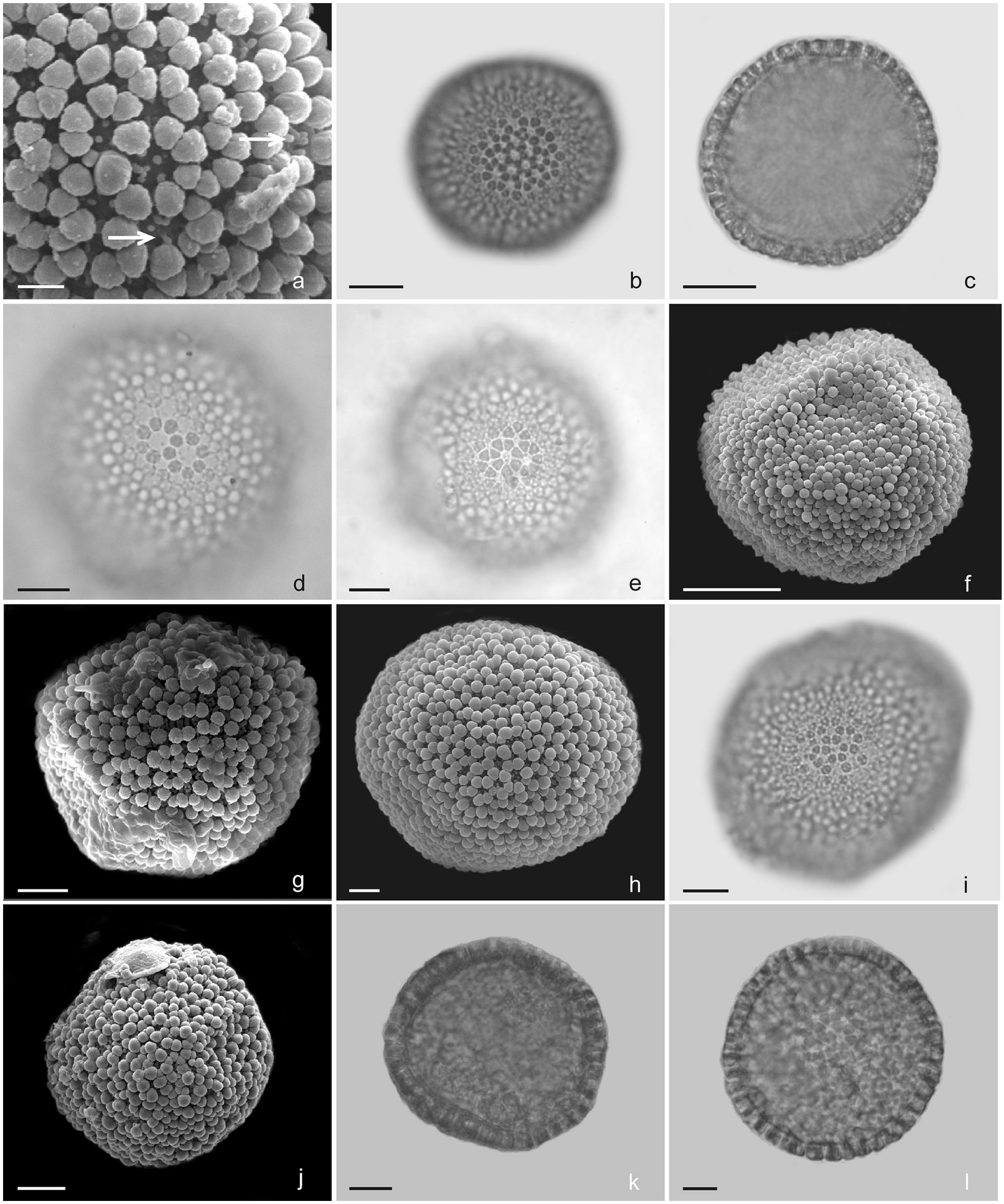

Fig. 3 Light micrographs (LM) and scanning electron micrographs (SEM) of the pollen grains of species of Crotonoideae, Types 1.1–1.3. Type 1.1- *Croton arenosus*: **a** detail of the surface (SEM), showing the clavae (*arrow*); *C. echioides*: **b** surface (LM); *C. grewioides*: **c** optical section (LM). Type 1.2- *C. adamantinus*: **d** surface (LM); *C. anisodontus*: **e** surface (LM); *C. imbricatus*: **f** surface (SEM); *C. laceratoglandulosus*: **g** surface (SEM). Type 1.3- *C. blanchetianus*: **h** surface (SEM); *C. glandulosudentatus*: **i** surface (LM); *C. luetzelburgii*: **j** surface (SEM); *C. nepetifolius*: **k** optical section (LM); *C. sonderianus*: **l** optical section (LM). *Scale bars* 10 μm

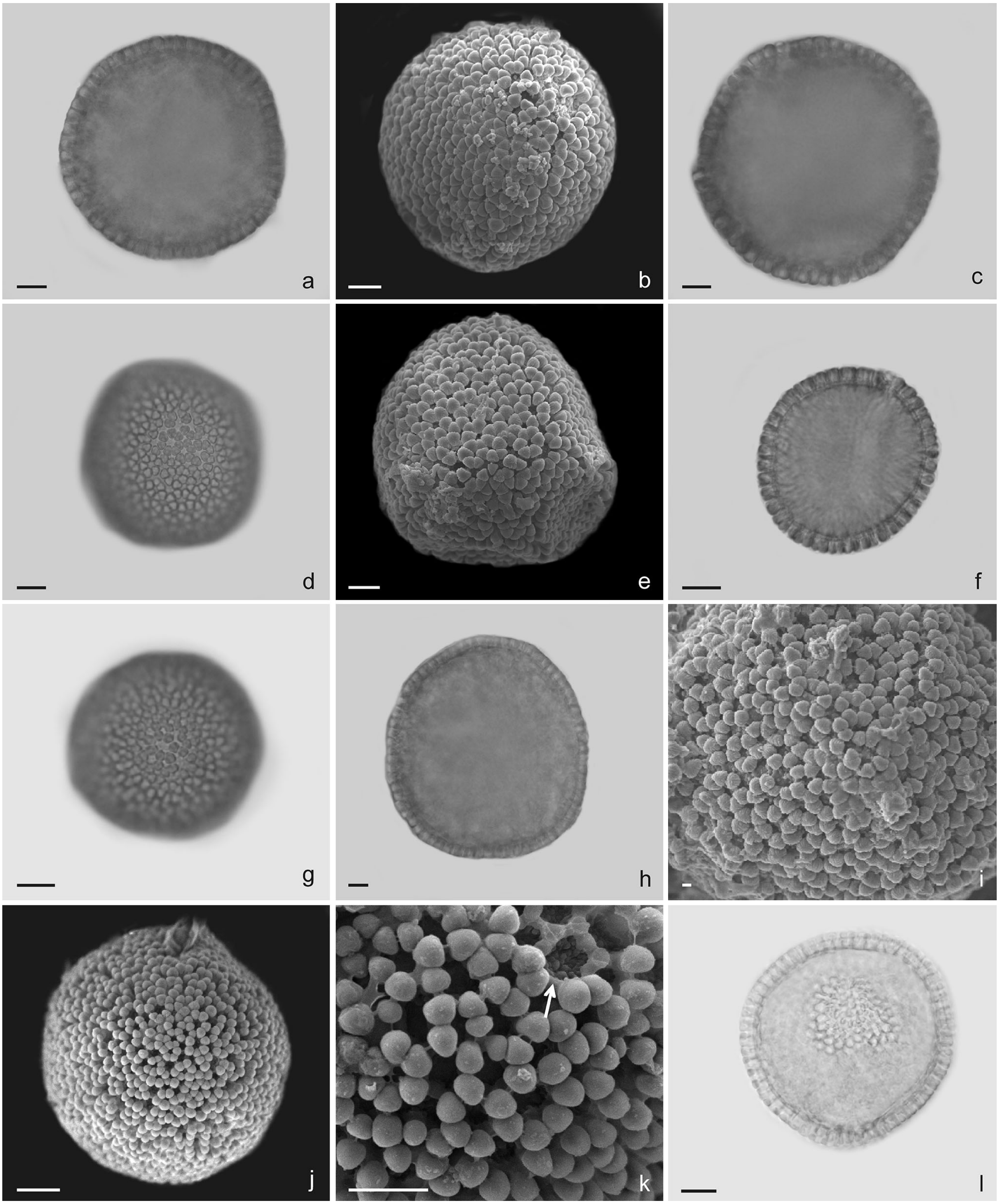

Fig. 4 Light micrographs (LM) and scanning electron micrographs (SEM) of the pollen grains of species of Crotonoideae, Types 1.3–2.1. Type 1.3- *Jatropha hastifolia*: **a** optical section (LM); **b** surface (SEM); *J. mutabilis*: **c** optical section (LM); **d** surface (LM); **e** surface (SEM); *J. ribifolia*: **f** optical section (LM); **g** surface (LM). Type 1.4- *J. catingae*: **h** optical section (LM); **i** detail of the surface (SEM). Type 2.1- *Cnidoscolus hamosus*: **j** overview (SEM); **k** detail of the surface (SEM), showing the pore (*arrow*); *C. infestus*: **l** optical section (LM). *Scale bars* **a**–**j**, **l** 10 µm; **k** 5 µm

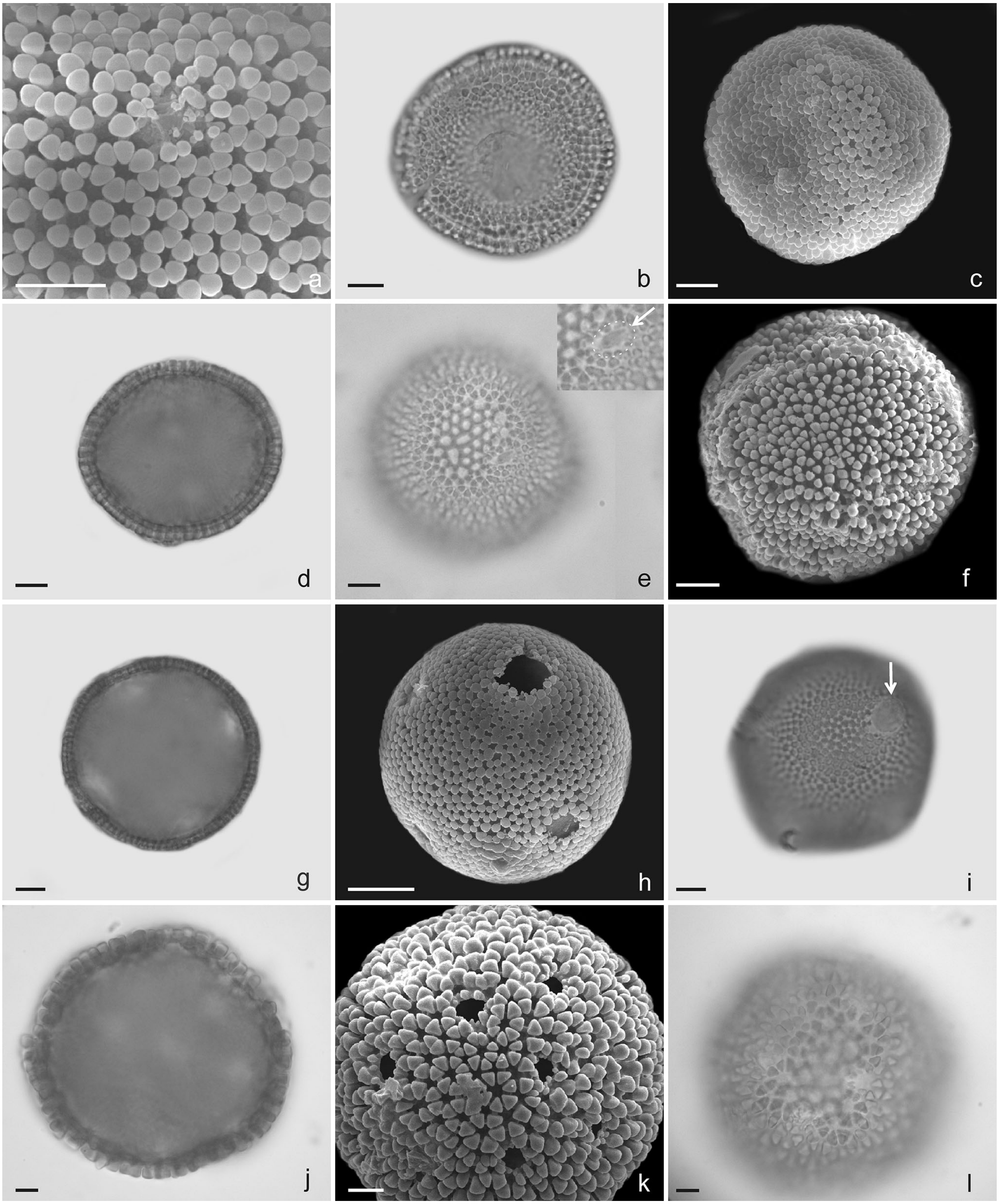

Fig. 5 Light micrographs (LM) and scanning electron micrographs (SEM) of the pollen grains of species of Crotonoideae, Types 2.1–2.2. Type 2.1- *Cnidoscolus infestus*: **a** detail of the surface (SEM) showing the pore (*arrow*); *C. pubescens*: **b** surface (LM); **c** surface (SEM); *C. ulei*: **d** optical section (LM); **e** detail of the surface (LM), detail on the *top right* of the operculum; **f** surface (SEM); *C. urnigerus*: **g** optical section; **h** surface (SEM); **i** surface (LM), detail of the pori with operculum (*arrow*). Type 2.2- *Manihot brachyandra*: **j** optical section (LM); **k** surface (SEM); *M. caerulescens*: **l** surface (LM). *Scale bars* 10 μm

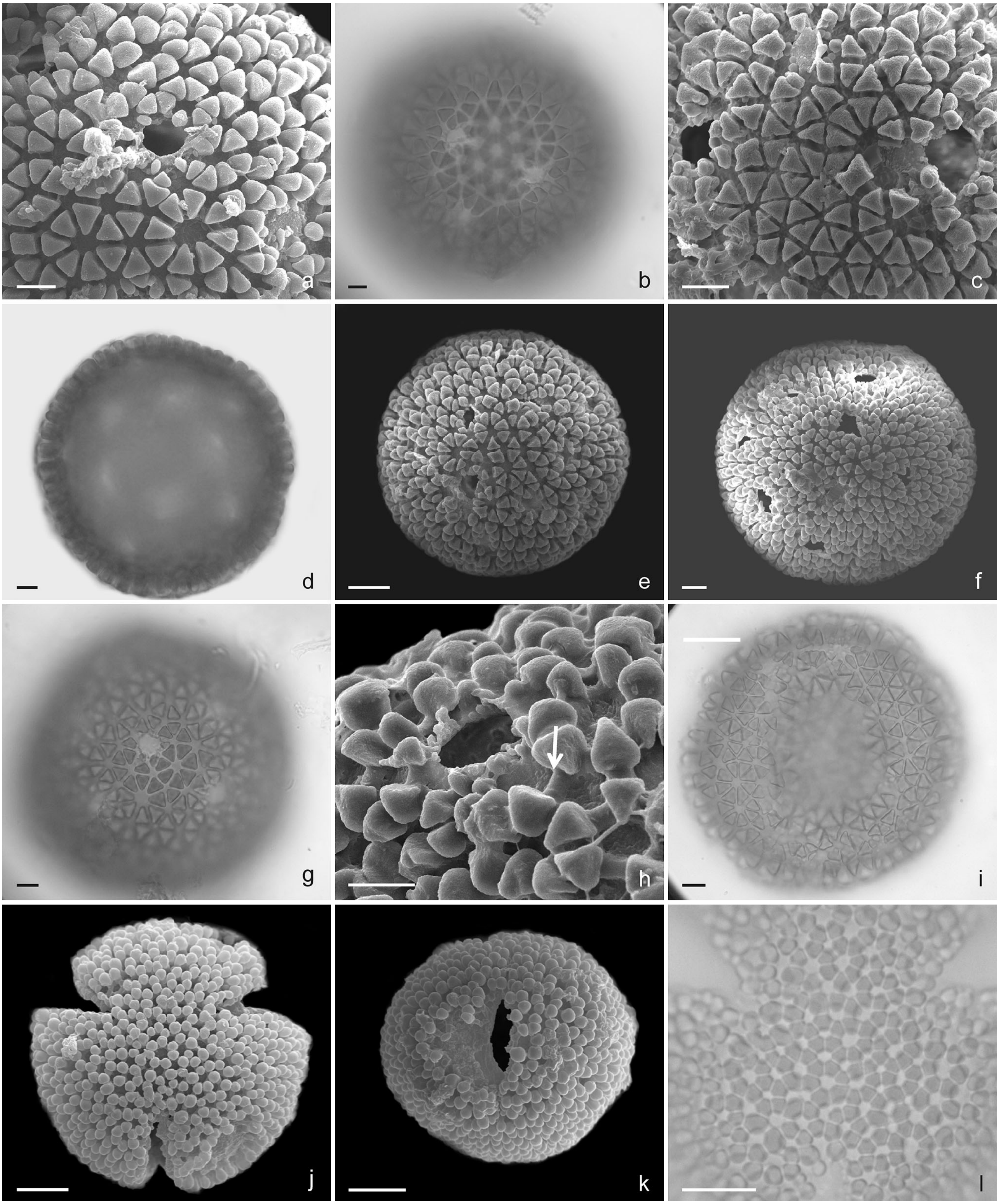

Fig. 6 Light micrographs (LM) and scanning electron micrographs (SEM) of the pollen grains of species of Crotonoideae, Types 2.2. and Type 3. Type 2.2- *Manihot catingae*: **a** detail of the surface, showing the pori (SEM); *M. dichotoma*: **b** surface, showing the pori (LM); **c** detail of the surface, showing the pori (SEM); *M. epruinosa*: **d** optical section (LM); **e** surface (SEM); *M. heptaphylla*: **f** surface (SEM); *M. maracasensis*: **g** surface (LM); **h** detail of the pori (SEM), showing murus (*arrow*) supporting pila; *M. pseudoglaziovii*: **i** surface (LM). Type 3- *Cnidoscolus quercifolius*: **j** surface, *polar view* (SEM); **k** surface, *equatorial view*, showing the aperture (SEM); **l** apocolpium (LM). *Scale bars* 10 μm

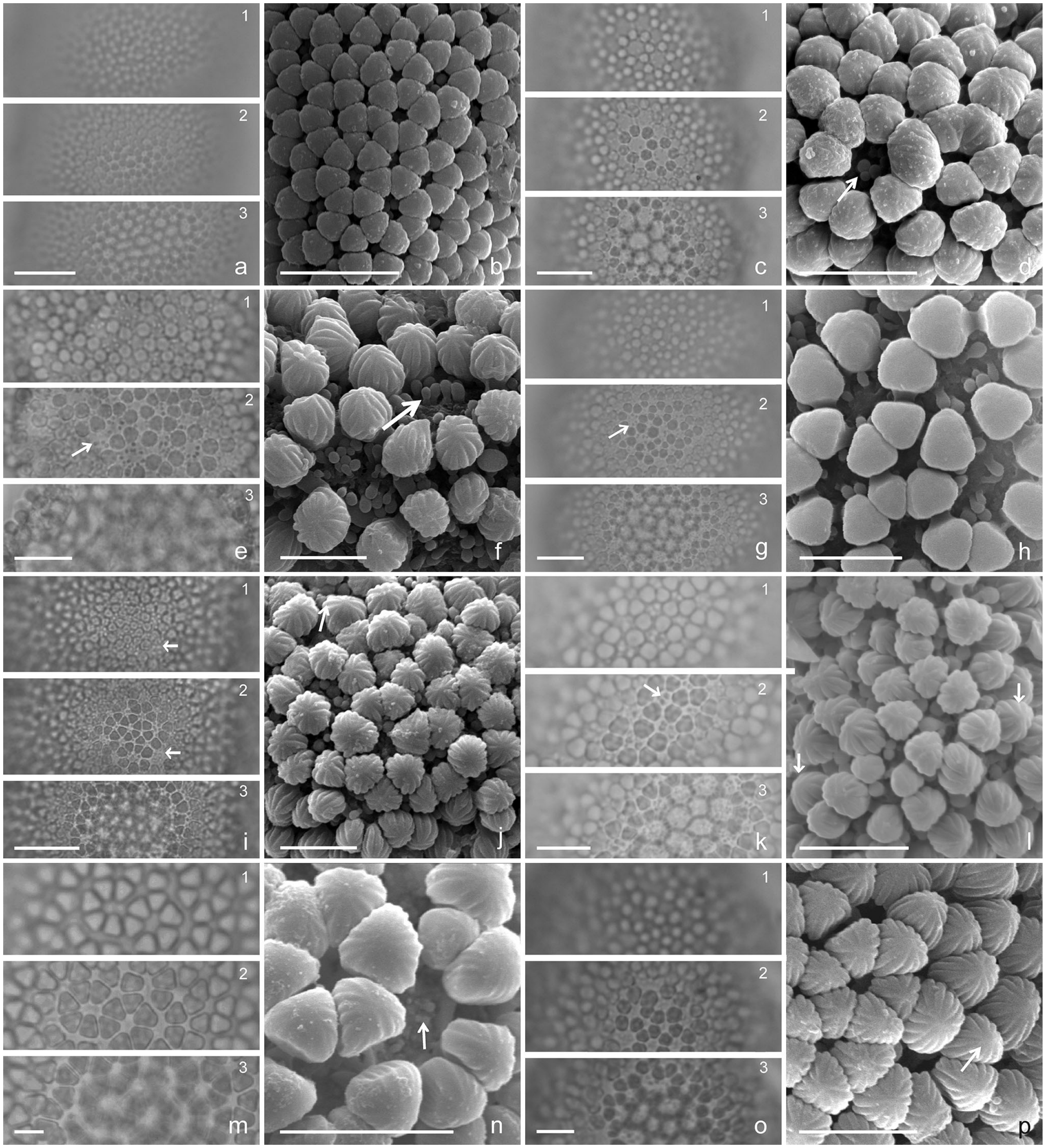

Fig. 7 Pollen surface analyses under light microscope (LM), LO analysis, and under scanning electron microscope (SEM) of species of Crotonoideae (Type 1). Type 1.1- *Croton pulegioides*: **a** L.O.; **b** detail of the surface (SEM), showing the lightly plicate pilum surface. Type 1.2- *C. adamantinus*: **c** L.O.; **d** detail of the surface (SEM), showing the free sexine elements in the lumen of the rosettes (*arrow*), notice plicate pilum surface. Type 1.3- *C. adenocalyx*: **e** L.O., showing the free sexine elements inside the lumen of the rosettes (*arrow*); **f** detail of the surface (SEM), showing the smaller pila and clavae in the lumen of the rosettes (*arrow*), notice plicate pilum surface; *C. blanchetianus*: **g** L.O., showing the free sexine elements in the lumen of the rosettes (*arrow*); **h** detail of the surface (SEM), showing the pila and clavae in the lumen of the rosettes; *C. luetzelburgii*: **i** L.O., highlighting the sexine elements in the lumen of the rosettes (*arrow*); **j** detail of the surface (SEM), notice plicate pilum surface; *C. rudolphianus*: **k** L.O., showing the sexine elements in the lumen of the rosettes (*arrow*); **l** detail of the surface (SEM), notice plicate pilum surface; *Jatropha mutabilis*: **m** L.O.; **n** detail of the surface (SEM), showing the clavae (*arrows*) inside rosette; *J. ribifolia*: **o** L.O.; **p** detail of the surface (SEM), notice plicate pilum surface. *Scale bars* **a**, **c**, **e**, **g**, **n** 10 μm; **b**, **d**, **f**, **h**, **i–l**, **m**, **o–p** 5 μm

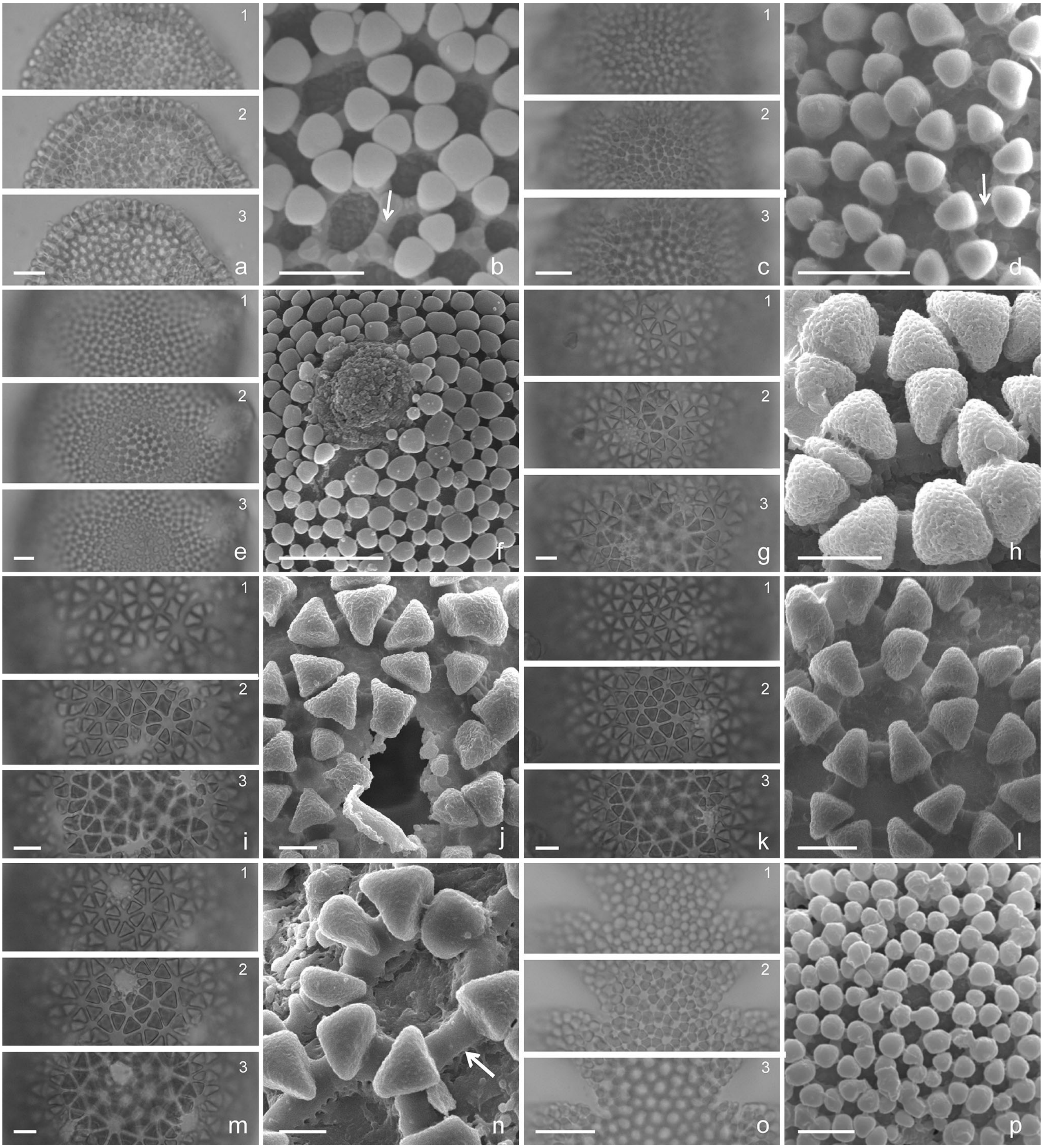

Fig. 8 Pollen surface analyses under light microscope (LM), LO analysis, and under scanning electron microscope (SEM) of species of Crotonoideae (Types 2 and 3). Type 2.1- *Cnidoscolus hamosus*: **a** L.O.; **b** detail of the surface (SEM), showing the murus (*arrow*); *C. infestus*: **c** L.O.; **d** detail of the surface (SEM), showing the murus (*arrow*); *C. urnigerus*: **e** L.O.; **f** detail of the surface (SEM), showing the pori. Type 2.2- *Manihot caerulescens*: **g** L.O.; **h** detail of the surface (SEM), notice rugulate pilum surface; *M. epruinosa*: **i** L.O.; **j** detail of the surface (SEM); *M. heptaphylla*: **k** L.O.; **l** detail of the surface (SEM); *M. maracasensis*: **m** L.O.; **n** detail of the surface (SEM), notice murus (*arrow*). Type 3- *Cnidoscolus quercifolius*: **o** L.O.; **p** detail of the surface (SEM). *Scale bars* **a**, **c**, **e**, **g**, **i**, **k**, **m**, **o** 10 µm; **b**, **d**, **f**, **h**, **j**, **l**, **n**, **p** 5 µm

Table 1 Summary of pollen characteristics of Crotonoideae (Euphorbiaceae) of dry vegetation in Northeastern Brazil

Pollen types		Genera	Species	Size	Apertural type	Apertural number	Pilum surface
Types	Subtypes						
1	1.1	*Croton*	*C. arenosus* Carn.-Torres & Cordeiro, *C. echioides* Baill., *C. grewioides*- Baill., *C. jaripensis* Müll.Arg., *C. piauhiensis* Müll.Arg., *C. pulegiodorus* Baill. and *C. pulegioides* Müll.Arg	Medium	Inaperturate	0	Plicate
	1.2	*Croton*	*C. adamantinus* Müll.Arg., *C. anisodontus* Müll.Arg, *C. cordiifolius* Baill., *C. harleyi* Carn.-Torres & Cordeiro, *C. imbricatus* L.R.Lima & Pirani, *C. laceratoglandulosus* Caruzo & Cordeiro, *C. paludosus* Müll.Arg. and *C. tridentatus* Mart. ex Müll.Arg.	Medium-large			
	1.3	*Croton* and *Jatropha*	*Croton adenocalyx* Baill., *C. argyrophylloides* Müll.Arg., *C. betulaster* Müll.Arg., *C. blanchetianus* Baill., *C. catinganus* Müll.Arg., *C. glandulosodentatus* Pax & K.Hoffm., *C. jacobinensis* Baill., *C. limae* A.P.S.Gomes, M.F.Sales & P.E.Berry, *C. luetzelburgii* Pax & K.Hoffm., *C. muscicapa* Müll.Arg., *C. nepetifolius* Baill., *C. rhexiifolius* Baill., *C. rudolphianus* Müll.Arg., *C. schultessi* Müll.Arg., *C. sonderianus* Müll.Arg., *Jatropha hastifolia* Fern.Casas, *J. mutabilis* Baill.and *J. ribifolia* Baill.	Large			
	1.4	*Jatropha*	*Jatropha catingae* Ule.	Very large			
2	2.1	*Cnidoscolus*	*C. hamosus* Pohl, *C. infestus* Pax & K.Hoffm., *C. pubescens* Pohl, *C. ulei* (Pax) Pax and *C. urnigerus* Pax.	Large	Porate (pantoporate)	4–8 pori	Psilate
	2.2	*Manihot*	*M. brachyandra* Pax & K.Hoffm., *M. caerulescens* Pohl., *M. catingae* Ule, *M. dichotoma* Ule, *M. epruinosa* Pax & K.Hoffm., *M. heptaphylla* Ule, *M. maracasensis* Ule and *M. pseudoglaziovii* Pax & K.Hoffm.	Very large		10–22 pori	Rugulate
3	3	*Cnidoscolus*	*Cnidoscolus quercifolius* Pohl ex Baill.	Large	Colpate	3 colpi	Psilate

Type 1.1: inaperturate and medium-sized pollen grains (Figs. 3a–c, 7a–b)

Pollen grains with a rosette formed by 5-(7)-8 pila, subcircular to subtriangular, less frequent, spheroidal or triangular, pila slightly to densely plicate, rosette central space well delimited (mostly) to reduced, and the presence of clavae inside the rosette lumen.

Type 1.2: inaperturate and medium-large sized pollen grains (Figs. 3d–g, 7c–d)

Pollen grains with rosettes that were formed by (4)-5-7-(-8) pila, subcircular to subtriangular or subcircular, less frequent, spheroidal, pila slightly plicate to plicate, rosette central space well delimited (mostly) to reduced, and the presence of clavae and bacula inside the rosette lumen (Fig. 7d).

Type 1.3: inaperturate and large-sized pollen grains (Figs. 3h–l, 4a–g, 7e–p)

Pollen grains with rosettes that were formed by (4)-5-(7)-8-(9) pila, subcircular to triangular, less frequent, spheroidal to triangular, pila slightly plicate to densely plicate, rosette central space well delimited (mostly) to reduced, and the presence of clavae, bacula, and granula inside the rosette lumen.

In *Jatropha* species, we observed free sexine elements inside the rosette lumen as clavae (Fig. 7n), while in representatives of *Croton*, these elements are variable, as clavae, bacula and granula (Fig. 7f, h, l).

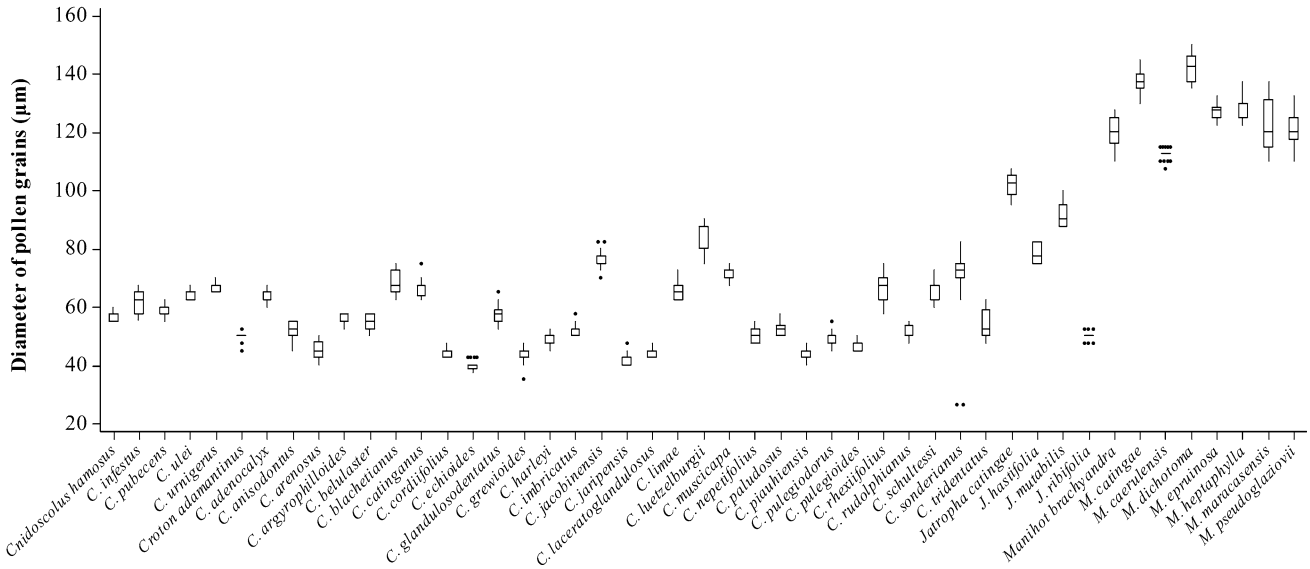

Fig. 9 Boxplot graph of the distribution of variable diameter pollen grain. The *horizontal bar* inside the *rectangle* is the median, the *rectangle* shows 50 % of interquartile, ends show the amplitude variation and the *asterisks* correspond to the outlier

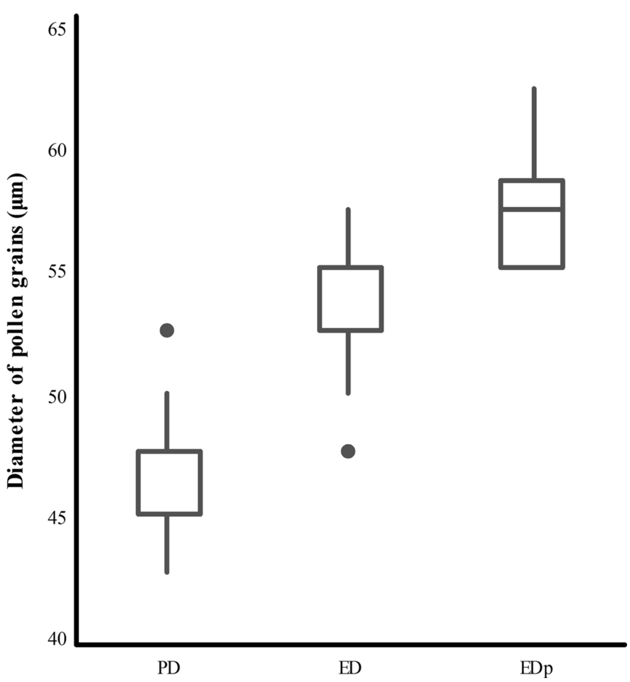

Fig. 10 Boxplot graph of the distribution of variable diameter pollen grain of the *Cnidoscolus quercifolius* Pohl ex Baill. The *horizontal bar* inside the *rectangle* is the median, the *rectangle* shows 50 % of interquartile, ends show the amplitude variation and the *asterisks* correspond to the outlier. *PD* polar diameter, *ED* equatorial diameter, *EDp* equatorial diameter in polar view

Type 1.4: inaperturate and very large sized pollen grains (Fig. 4h–i)

Pollen grains with rosettes that were formed by 4–7 pila, triangular, pila densely plicate, rosettes centrally spaced and well delimited, and the presence of clavae inside the rosette lumen.

Type 2: pantoporate pollen grains

These grains are composed of species with pollen grains that were apolar and spheroidal, with rosettes disposed on a wall, a lumen greater than 1 µm in diameter, the absence of sexine elements inside rosettes lumen, and the sexine thicker than the nexine.

Type 2.1: 4-8-pantoporate and medium sized pollen grains with psilate pila (Figs. 4j–l, 5a–i, 8a–f)

Pollen grains (4)-5-6-(7)-(8) pantoporate, pores with an oval outline, spheroidal, irregular and inconspicuous, rosettes formed by (4)-5-7-(8) pila, subcircular to subtriangular, less frequent, spheroidal or triangular, and rosette central space well delimited to reduced (mostly).

In *Cnidoscolus urnigerus* Pax., we observed that the pila from rosettes are more closely united than in the other studied species, setting a reduced central space in rosettes that is transfigured in irregularities in rosette formation (Figs. 5i, 8f). This species is the only one in which the *Croton* pattern is not evident by LM analysis. However, these characters could only be verified by scanning analysis. Moreover, muri-supporting rosettes are not visible as they are in the pollen of other taxa (Figs. 5i, 8e–f). We also observed the presence of an operculum in *Cnidoscolus ulei* (Pax) Pax. (Fig. 5e) and in *C. urnigerus* Pax (Fig. 5i).

Table 2 Morphological characters of pollen grains of Crotonoideae occurring in dry vegetation in Northeastern Brazil

Specie	Size	Apertural type	Composition *Croton* pattern rosettes	SEIR	SIR	Figures
Cnidoscolus Pohl.						
Cnidoscolus hamosus	L	6-porate	5–7 subtriangular pila	–	Well delimited to reduced	Figs. 4j–k; 8a–b
Cnidoscolus infestus	L	(6)-8-porate	5–7 subcircular pila	–	Well delimited	Figs. 4l; 5a; 8c–d
Cnidoscolus pubescens	L	4-(5)-porate	5–7 subcircular to subtriangular pila	–	Well delimited to reduced	Fig. 5b–c
Cnidoscolus quercifolius	L	3-colpate	5–7 subcircular to subtriangular pila	–	Well delimited to reduced	Figs. 6j–l; 8o–p
Cnidoscolus ulei	L	4-porate	4–8 circular to triangular pila	–	Well delimited to reduced	Fig. 5d–f
Cnidoscolus urnigerus	L	5-(6)-7-porate	4–6 subcircular pila	–	Well delimited to reduced	Figs. 5g–i; 8e–f
Croton L						
Croton adamantinus	M-L	Inaperturate	4–8 triangular to subcircular pila	+	Well delimited	Figs. 3d; 7c–d
Croton adenocalyx	L	Inaperturate	5–8 subcircular to circular pila	+	Well delimited	Fig. 7e–f
Croton anisodontus	M-L	Inaperturate	5–7 subcircular to triangular pila	+	Well delimited	Fig. 3e
Croton arenosus	M	Inaperturate	5–8 subcircular pila	+	Well delimited	Fig. 3a
Croton argyrophylloides	L	Inaperturate	5–8 subtriangular pila	+	Well delimited	–
Croton betulaster	L	Inaperturate	5–7 subcircular to circular pila	+	Well delimited to reduced	–
Croton blanchetianus	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited	Figs. 3h; 7g–h
Croton catinganus	L	Inaperturate	5–7 subtriangular pila	+	Well delimited	–
Croton cordiifolius		Inaperturate	5–7 subcircular pila	+	Well delimited	–
Croton echioides	M	Inaperturate	5–7 subcircular to triangular pila	+	Well delimited	Fig. 3b
Croton glandulosodentatus	L	Inaperturate	5–7 subcircular to subtriangular pila	+	Well delimited	Fig. 3i
Croton grewioides	M	Inaperturate	5–8 subcircular to subtriangular pila	+	Well-delimited to reduced	Fig. 3c
Croton harleyi	M-L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited	–
Croton imbricatus	M-L	Inaperturate	5–7 subcircular pila	+	Well delimited	Fig. 3f
Croton jacobinensis	L	Inaperturate	4–8 subcircular to triangular pila	+	Well delimited to reduced	–
Croton jaripensis	M	Inaperturate	5-8 subcircular to subtriangular pila	+	Well delimited to reduced	–
Croton laceratoglandulosus	M-L	Inaperturate	5–8 subcircular pila	+	Well delimited	Fig. 3g
Croton limae	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited to reduced	–
Croton luetzelburgii	L	Inaperturate	5–8 subcircular to triangular pila	+	Well-delimited to reduced	Figs. 3j; 7i–j
Croton muscicapa	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well-delimited	–
Croton nepetifolius		Inaperturate	5–7 subcircular to subtriangular pila	+	Well-delimited	Fig. 3k
Croton paludosus	M-L	Inaperturate	5–7 subcircular to subtriangular pila	+	Well delimited to reduced	–
Croton piauhiensis	M	Inaperturate	5–8 subtriangular to triangular pila	+	Well delimited	–
Croton pulegiodorus	M	Inaperturate	5–7 circular pila	+	Well delimited	–
Croton pulegioides	M	Inaperturate	5–8 subcircular pila	+	Well delimited	Fig. 7a–b
Croton rhexiifolius	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited	–
Croton rudolphianus	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited to reduced	Fig. 7k–l
Croton schultessi	L	Inaperturate	5–7 subcircular pila	+	Well delimited	–
Croton sonderianus	L	Inaperturate	5–8 subtriangular pila	+	Well delimited to reduced	Fig. 3l
Croton tridentatus	M-L	Inaperturate	5–7 subtriangular to triangular pila	+	Well delimited to reduced	–
Jatropha L.						

Table 2 continued

Specie	Size	Apertural type	Composition *Croton* pattern rosettes	SEIR	SIR	Figures
Jatropha catingae	VL	Inaperturate	4–7 triangular pila	+	Well delimited	Fig. 4h–i
Jatropha hastifolia	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited to reduced	Fig. 4a–b
Jatropha mutabilis	L	Inaperturate	4–9 subtriangular to triangular pila	+	Well delimited	Figs. 4c–e; 7m–n
Jatropha ribifolia	L	Inaperturate	5–8 subcircular to subtriangular pila	+	Well delimited	Figs. 4f–g; 7o–p
Manihot Mill.						
Manihot brachyandra	VL	(16)-18-porate	5–8 triangular pila	–	Well delimited to reduced	Fig. 5j–k
Manihot caerulescens	VL	10-(12)-14-porate	5–7 triangular (rare quadrangular) pila	–	Well delimited	Figs. 5l; 8g–h
Manihot catingae	VL	(12)-14-porate	5–8 triangular pila	–	Well delimited	Fig. 6a
Manihot dichotoma	VL	12-14-(16)-18-porate	4–8 triangular pila	–	Well delimited	Fig. 6b–c
Manihot epruinosa	VL	14-16-(18)-20-22-porate	4–8 triangular pila	–	Well delimited	Figs. 6d–e; 8i–j
Manihot heptaphylla	VL	14-(16)-22-porate	4–9 triangular pila	–	Well delimited	Figs. 6f; 8k–l
Manihot maracasensis	VL	(14)-16-18-20-22-porate	5–8 triangular pila	–	Well delimited to reduced	Figs. 6g–h; 8m–n
Manihot pseudoglaziovii	VL	14-(16)-18-20-porate	5–8 triangular pila	–	Well delimited to reduced	Fig. 6i

SEIR free sexine elements inside to pilum rosettes, *SIR* space inside to pilum rosettes; size: *M* medium, *L* large, *VL* very large; [−] absent, [+] present

Type 2.2: 10-22-pantoporate, very large sized pollen grains, with rugulate pila (Figs. 5j–l, 6a–i, 8g–n)

Pollen grains (10)-(12)-14-(16)-18-(20)-(22)-pantoporate, pores with a circular outline, undefined to irregular (*Manihot caerulescens* Pohl.), rosettes formed by (4)-5-(7)-8-(9) pila, triangular, presence of a few quadrangular shaped, and rosette central space well-delimited (mostly) to reduced.

We realized that among the studied species, in the region next to apertures, the pila might be irregularly shaped and smaller.

Type 3: colpate pollen grains (Figs. 6j–l, 8o–p)

Represented by large, isopolar, suboblate to oblate spheroidal pollen grains, with rosettes disposed on a wall with lumen greater than 1 µm in diameter, psilate pila, the absence of sexine elements inside the rosette lumen, and the sexine thicker than the nexine.

Pollen grains are spheroidal, with a small polar region, colpi with extremities slightly acute, rosettes formed by 5–7 pila, and subcircular to subtriangular. Pila form a well-delimited to reduced central space in rosettes.

Discussion

Crotonoideae species showed marked pollen diversity, mainly regarding the size, polarity, aperture type, apertural number, and exine ornamentation and sculpture. However, these species showed a pollen characteristic that unites them all, consisting of a single pattern of exine ornamentation: the *Croton* pattern.

Spheroidal shapes and polarity types are already well documented in the literature, being associated with its inaperturate and pantoaperturate characteristics (Erdtman 1952; Punt 1962; Salgado-Laboriau 1967; Roubik and Moreno 1991; Allem 1993; Nowicke 1994; Carreira et al. 1996; Lobreau-Callen and Cervera 1997; Cruz-Barros et al. 2006; Lima et al. 2007; Corrêa et al. 2010; Vieira et al. 2012). Consequently, we highlight *Cnidoscolus quercifolius* to show pollen grains that are suboblate to oblate spheroidal, isopolar, and 3-aperturate (colpate).

Large-sized pollen grains have been observed in most of the studied species, except for *Manihot*, in which pollen grains are magnified and regarded as giant, >200 µm (Roubik and Moreno 1991; Allem 1993).

The largest pollen grains were observed in pollen grains of *Manihot maracasensis*, ranging from 137.5 to 172.5 µm. However, specimens of some species presented a pollen diameter (confidence interval) varying from medium to large, highlighting the plasticity of pollen size, which may

Table 3 Morphometric characters of the pollen grains of species studied of Crotonoideae occurring in dry vegetation in Northeastern Brazil

Genera/species	*D*		DR	DPi	DCSR	Sex	Nex	Exine
	$\bar{x} \pm S\bar{x}$	*R*						
***Cnidoscolus* Pohl**								
Cnidoscolus hamosus								
Irecê, 20 Jan 1984, *G. Fotius 3705* (HUEFS)	57.1 ± 0.14	55.0–60.0	5.7	1.4	1.5	3.0	2.0	5.0
Cnidoscolus infestus								
Conceição de Feira, Jun 1980, *Grupo Pedra do Cavalo* (HUEFS)	62.2 ± 0.24	57.2–67.5	6.6	1.5	2.0	3.4	1.0	4.4
Cnidoscolus pubescens								
Paulo Afonso, 29 Nov 2005, *R.M. Castro 1277* et al. (HUEFS)	58.3 ± 0.18	55.0–62.5	5.2	1.4	1.0	3.0	1.6	4.6
Itaberaba, 23 Oct 2005, *E. Mello 4144* et al. (HUEFS)	60.0*	55.0–67.5	7.0	1.6	2.1	3.4	1.8	5.2
Bendengó, 23 Feb 2000, *A.M. Giulietti 1775* and *R.M. Harley* (HUEFS)	51.2 ± 0.18	49.0–52.5	3.8	0.6	1.3	2.4	1.5	3.9
Cnidoscolus quercifolius								
Rodelas, 30 Oct 2009, *E. Melo 6971* et al. (HUEFS).	–	–	6.0	2.0	1.3	3.9	1.0	4.9
Rodelas, 30 Oct 2009, *E. Melo 7006* (HUEFS)	–	–	5.0	1.9	1.4	3.9	1.8	5.7
Rodelas, 13 Nov 2011, *E. Melo 10684* et al. (HUEFS)	–	–	5.4	1.4	1.3	2.9	1.0	3.9
Cnidoscolus ulei								
Caetité, 18 Dec 2009, *L.T. Alves 122* et al. (HUEFS)	60.6 ± 0.11	57.5–62.5	6.7	1.7	3.1	3.6	1.3	4.9
Mucugê, 14 Feb 1992, *L.P. Queiroz 2629* (HUEFS)	66.4 ± 0.20	62.5–70.0	6.7	1.8	3.1	3.1	2.0	5.1
Caetité, 8 Feb 1997, *M.L. Guedes 5212* et al. (HUEFS)	64.2 ± 0.11	62.5–67.5	6.4	1.5	2.6	2.6	1.9	4.5
Cnidoscolus urnigerus								
Maracás, 22 Jan 2004, *D.S. Carneiro-Torres 302* et al. (HUEFS)	71.5 ± 0.19	67.5–75.0	–	–	–	2.0	1.1	3.1
Livramento do Brumado, 15 Jun 2002, *L.P. Queiroz 7069* et al. (HUEFS)	69.7 ± 0.21	67.5–75.0	–	–	–	1.5	1.0	2.5
Casa Nova, 9 Feb 2004, *L.P. Queiroz 9153* et al. (HUEFS)	66.4 ± 0.14	65.0–70.0	4.4	1.2	1.7	2.2	1.4	3.6
***Croton* L.**								
Croton adamantinus								
Pindobaçú, 16 Dec 2008, *L.A Sousa 210* (HUNEB)	47.3 ± 0.34	40.0–55.0	5.8	2.0	2.8	3.6	1.0	4.6
Rio de Contas, 6 Sep 2003, *R.M. Harley 54674* and *A.M. Giulietti* (HUEFS)	56.0 ± 0.25	50.0–60.0	7.9	2.0	3.1	3.1	1.0	4.1
Campo Formoso, 13 Apr 2006, *R.D. Souza 17* et al. (HUEFS)	47.8 ± 0.18	42.5–50.0	7.4	2.0	2.4	2.9	1.0	3.9
Mucugê, 20 Dec 2007, *M. Ibrahim 55* and *S.F. Conceição* (HUEFS)	49.8 ± 0.09	45.0–52.5	6.1	1.4	3.2	2.5	1.0	3.5
Croton adenocalyx								
Aiubá, 21 Mar 1980, *A. Gomes s.n.* (HUEFS 106414)	63.4 ± 0.16	60.0–67.5	10.0	3.2	4.1	4.2	1.1	5.3
Aiubá, 21 Mar 1980, *A. Gomes s.n.* (HUEFS 106387)	69.5 ± 0.21	67.5–75.0	9.7	2.6	4.2	4.1	0.9	5.0
Cratéus, 27 Feb 2002, *F.S. Araujo 1346* (HUEFS)	66.5 ± 0.30	60.0–75.0	9.6	5.0	4.5	3.5	1.0	4.5
Croton anisodontus								
Capistrano, 27 Apr 1994, *J.B.L.P Medeiros 51* and *M.A. Figueiredo* (HUEFS)	52.2 ± 0.19	47.5–55.0	6.3	1.8	1.8	2.8	0.9	3.7
Guaraciaba do Norte, 6 May 1984, *Fernandes s.n.* and *Matos* (HUEFS)	48.8 ± 0.17	40.3–57.2	5.7	1.5	2.6	2.5	1.0	3.5
Guaraciaba do Norte, 6 May 1984, *A. Fernandes s.n.* and *Matos* (HUEFS)	52.0 ± 0.23	47.5–55.0	5.7	1.5	1.7	2.6	0.8	3.5
Croton arenosus								
Canudos, 18 Feb 2004, *E.B. Miranda 613* et al. (HUEFS)	45.1*	40.0–50.0	5.3	1.4	2.7	2.6	1.0	3.6
Croton argyrophylloides								
Itaberaba, 15 Feb 1984, *G.C. Pereira-Pinto 544184* (HUEFS)	63.8 ± 0.27	60.0–67.5	8.7	2.1	3.0	2.5	1.0	3.5
Tucano, 19 Jan 1964, *A.L. Costa s.n.* (HUEFS)	56.4 ± 0.21	52.5–60.0	6.1	1.6	1.8	3.3	0.8	4.1
Itambé, 9 Jan 1986, *A.M. Carvalho 2118 A. Chautems* (HUEFS)	55.7 ± 0.25	50.0–60.0	6.4	1.9	2.4	3.6	1.0	4.6

Table 3 continued

Genera/species	*D*		DR	DPi	DCSR	Sex	Nex	Exine
	$\bar{x} \pm S\bar{x}$	*R*						
Croton betulaster								
Rio de Contas, 16 Aug 2006, *A.K.A Santos 846* et al. (HUEFS)	54.4 ± 0.21	50.0–57.5	6.5	1.8	1.3	3.9	1.0	4.9
Érico Cardoso, 4 Jul 2001, *M.P Bautista 3286* et al. (HUEFS)	61.4 ± 0.19	57.5–65.0	6.9	1.9	2.0	3.6	1.0	4.6
Rio de Contas, 18 Jan 2003, *A.M. Miranda 4054* et al. (HUEFS)	54.9 ± 0.27	50.0–62.5	5.5	1.4	1.9	3.6	1.1	4.7
Croton blachetianus								
Aiuaba, 9 Jan 1997, *L.V. Lima-Verde 368* et al. (HUEFS)	68.7 ± 0.30	62.5–75.0	7.4	1.9	3.0	3.4	0.7	4.1
Croton catinganus								
Amarante, 24 Jan 1970, *L.J. Goorje 10369* et al. (SP)	66.3 ± 0.23	62.5–75.0	5.6	1.3	2.1	2.3	0.8	3.1
Croton cordiifolius								
Rio de Contas, 24 Jan1994, *Ganev 2873* (HUEFS)	44.8 ± 0.14	42.5–47.5	4.9	1.1	1.3	2.5	1.0	3.5
Rui Barbosa, 17 Jan 2006, *L.P. Queiroz 12041* and *D. Cardoso* (HUEFS)	51.2 ± 0.18	47.5–55.0	5.9	1.3	2.6	2.0	1.0	3.0
Abaíra, 27 Dec 1992, *D.J.N. Hind 50467* et al. (HUEFS)	44.3 ± 0.23	40.0–50.0	5.0	1.2	2.0	2.1	1.0	3.1
Croton echioides								
Cafarnaum, 14 Jan 2012, *J.G Carvalho-Sobrinho 3227* et al. (HUEFS)	36.6 ± 0.16	32.5–37.5	5.4	1.1	1.2	2.3	0.9	3.2
Moreilândia, 4 Mar 1995, *E. Silveira s.n.* (HUEFS)	39.8 ± 0.12	37.5–42.5	5.1	1.2	1.9	2.3	1.0	3.3
Croton glandulosodentatus								
Canudos, 18 Feb 2004, *E.B. Miranda 622* et al. (HUEFS)	57.2 ± 0.24	52.5–65.0	6.3	1.7	2.0	2.9	0.9	3.8
São Raimundo Nonato, 19 Dec 1978, *A. Fundes s.n.* (HUEFS)	50.0 ± 0.31	40.0–55.0	6.9	1.9	1.3	3.7	0.8	4.5
Croton grewioides								
Pindobaçú, 16 Nov 2008, *L.A. Sousa 213* (HUNEB)	34.6 ± 0.23	32.5–37.5	4.0	1.3	1.7	2.8	1.0	3.8
Jequié, 5 Nov 2009, *J.C Nascimento 21* and R.M. Aguiar (HUEFS)	45.9 ± 0.17	42.5–50.0	6.2	1.7	2.5	2.4	0.7	3.1
Jequié, 5 Nov 2009, *J.C. Nascimento 20* and *R.M. Aguiar* (HUEFS)	43.6 ± 0.20	35.0–47.5	6.1	1.4	2.6	2.1	1.0	3.1
Jaguarari, 10 Nov 2005, *A.A. Conceição 1608* et al. (HUEFS)	36.1 ± 0.13	32.5–37.5	5.3	1.0	1.9	2.0	1.0	3.0
Croton harleyi								
Morro do Chapéu, 1 Feb 2008, *F.B.L. Silva 79* and *F. França* (HUEFS)	48.7 ± 0.22	45.0–52.5	5.9	1.5	2.2	2.8	1.0	3.8
Casa Nova, 29 Feb 2008, *A.C. Correia 412* et al. (HUEFS)	51.3*	47.5–57.5	7.3	1.8	2.5	3.4	1.0	4.4
Sertão de Dentro, 1 Mar 1980, *M. Del Arco s.n.* (HUEFS)	52.7*	47.5–55.0	7.2	2.0	3.6	3.2	0.9	4.1
Croton imbricatus								
Rio de Contas, 20 Apr 2003, *A.C. Serrão-Neto 16* et al. (HUEFS)	45.3 ± 0.18	42.5–50.0	5.0	1.0	2.0	2.7	1.0	3.7
Caetité, 20 Nov 2006, *M.M. Silva-Castro 1052* (HUEFS)	50.2 ± 0.24	42.3–55.0	5.3	2.0	2.5	2.1	1.1	3.2
Rio de Contas, 12 Jun 2003, *M.M. Silva-Castro 681* et al. (HUEFS)	52.0 ± 0.17	50.0–57.5	5.6	1.2	2.7	2.5	1.0	3.5
Croton jacobinensis								
Campo Formoso, 5 Dec 2003, *E.B. Miranda 601* et al. (HUEFS)	76.9 ± 0.24	70.0–80.0	8.4	2.3	2.7	3.2	1.0	4.2
Pindobaçú, 24 May 2008, *L.A. Sousa 85* (HUNEB)	78.3 ± 0.40	70.0–87.5	6.2	2.4	3.4	–	–	3.7
Crato, 13 Feb 2007, *D.S. Carneiro-Torres 873* et al. (HUEFS)	73.4 ± 0.25	67.5–80.0	8.7	2.7	3.7	3.7	1.0	4.7
Croton japirensis								
Macaúbas, 12 Jan 2008, *A. Rapini 1500* et al. (HUEFS)	41.7 ± 0.16	40.0–47.5	4.4	1.1	1.8	2.7	1.1	3.8
Petrolina, 21 Mar 1984, *G. Fotius 3804* (HUEFS)	41.0 ± 0.21	37.5–45.0	5.9	1.3	1.9	2.6	0.8	3.5
Casa Nova, 8 Feb 2004, *L.P. Queiroz 9109* (HUEFS)	43.1 ± 0.18	40.0–45.0	5.8	1.4	2.2	2.1	1.0	3.1
Croton laceratoglandulosus								
São Félix do Coribe, 11 Apr 2007, *L.P. Queiroz 12818* (HUEFS)	51.2 ± 0.11	52.5–55.0	5.0	1.2	2.4	2.1	1.0	3.1
São Félix do Coribe, 9 Jan 2008, *A. Rapini 1432* et al. (HUEFS)	44.8 ± 0.18	42.5–50.0	5.0	1.1	2.8	2.0	1.0	3.0
São Félix do Coribe, 11 Jan 2008, *R.F. Souza-Silva 300* et al. (HUEFS)	42.1 ± 0.12	40.0–45.0	4.9	1.0	2.8	2.8	0.9	3.8

Table 3 continued

Genera/species	D		DR	DPi	DCSR	Sex	Nex	Exine
	$\bar{x} \pm S\bar{x}$	R						
Croton limae								
Abaíra, 28 Dec 1992, *R.M. Harley 50514* et al. (HUEFS)	65.1 ± 0.38	60.0–75.0	7.8	2.5	1.7	3.6	1.7	5.2
Abaíra, 20 Dec 1991, *R.M. Harley 50157* et al. (HUEFS)	65.6 ± 0.27	62.5–72.5	9.3	2.4	2.8	3.0	1.1	4.1
Rio de Contas, 23 Jan 2008, *R.M. Harley 55788* et al. (HUEFS)	71.3*	67.5–75.0	9.2	2.8	2.5	3.3	1.0	4.3
Croton luetzelburgii								
Lençóis, 3 Oct 2007, *A.A. Conceição 2614* (HUEFS)	82.5 ± 0.36	75.0–90.0	7.1	1.8	3.0	3.9	1.0	4.9
Palmeiras, 8 Aug 2007, *T.F.B. Pastore 2162* et al. (HUEFS)	71.0 ± 0.27	65.0–77.5	5.4	1.1	1.0	2.8	1.0	3.8
Abaíra, 26 Oct 1992, *W. Ganev 1377* (HUEFS)	87.4 ± 0.17	82.5–90.0	8.9	3.2	3.1	3.7	1.0	4.7
Croton muscicapa								
Pindobaçú, 24 May 2008, *L.A. Sousa 78* and *R. B. Carvalho* (HUNEB)	72.6 ± 0.44	67.5–87.5	7.5	2.2	3.0	3.7	1.2	4.9
Pindobaçu, 26 Oct 2008, *L.A. Sousa 155* (HUNEB)	71.6 ± 0.15	67.5–75.0	9.3	2.7	3.5	3.5	1.0	4.5
Jacobina, 02 Apr 1999, *R.M. Harley 53690 A.M. Giulietti* (HUEFS)	63.8*	62.5–70.0	7.4	2.7	2.5	4.2	1.0	5.2
Croton nepetifolius								
Itaueira, 11 Nov 1979, *A. Fernandes s.n.* and *Matos* (HUEFS)	57.4 ± 0.21	52.5–62.5	5.8	1.6	1.8	3.0	1.0	4.0
Pedra Branca, 11 Feb 2007, *Carneiro-Torres 849* (HUEFS)	50.2 ± 0.19	47.5–55.0	5.9	1.8	2.0	2.7	1.0	3.7
Croton paludosus								
Pilão Arcado, 18 Mar 2006, *D.S. Carneiro-Torres 620* (HUEFS)	53.3 ± 0.25	50.0–60.0	6.7	2.0	2.0	3.7	0.7	4.4
Pilão Arcado, 19 Mar 2006, *D.S. Carneiro-Torres 624* (HUEFS)	52.2 ± 0.19	50.0–58.0	4.6	1.2	1.5	3.1	0.6	3.7
Casa Branca, 8 Feb 2004, *L.P. Queiroz 9100* et al. (HUEFS)	47.0 ± 0.19	40.0–50.0	7.4	2.0	2.3	3.1	1.0	4.1
Croton piauhiensis								
Crato, 12 Feb 2007, *D.S. Carneiro-Torres 869* (HUEFS)	47.0 ± 0.17	45.0–50.0	4.7	1.0	1.5	2.3	0.9	3.2
Exu, 13 Feb 2007, *D.S. Carneiro-Torres 876*	41.2 ± 0.29	37.5–50.0	7.4	2.1	2.1	2.8	0.8	3.6
Brejo da Madre de Deus, 29 Feb 2000, *L.M. Nascimento 327* and *A.G. Silva* (HUEFS)	43.7 ± 0.13	40.0–45.0	6.0	1.5	2.3	2.1	1.1	3.2
Croton pulegiodorus								
Bom Jesus da Lapa, 9 Feb 2000, *L.P. Queiroz 5776* et al. (HUEFS)	46.6 ± 0.19	42.5–50.0	2.2	0.6	1.2	1.8	1.0	2.8
Morada Nova, 11 Mar 1983, *E. Nunes s.n.* et al. (HUEFS)	48.9 ± 0.18	45.0–52.5	2.2	0.5	1.3	1.8	1.0	2.8
Croton pulegioides								
Ipuaçu, Sep 1980, *Grupo Pedra do Cavalo 749* (HUEFS)	47.4 ± 0.24	42.5–52.5	3.6	1.0	1.4	2.0	1.0	3.0
Feira de Santana, 13 Nov 1986, *L.P. Queiroz 1022 J.M. Lemes* (HUEFS)	46.9 ± 0.14	45.0–50.0	4.4	1.1	2.2	1.7	1.0	2.7
Croton rhexiifolius								
Almadina, 12 Aug 2007, *D. Cardoso 2128* et al. (HUEFS)	57.3 ± 0.35	52.5–65.0	4.9	1.3	1.6	3.0	0.8	3.8
Almadina, 12 Aug 2007, *R. Funch 603* (HUEFS)	67.5*	62.5–75.0	6.5	1.9	2.0	2.6	0.6	3.2
Caetité, 28 Aug 1999, *E. Melo 2863* et al. (HUEFS)	66.4 ± 0.32	60.0–75.0	7.3	1.9	3.1	2.8	1.0	3.8
Croton rudolphianus								
Itatim, 28 Jan 1996, *F. França 1543* et al. (HUEFS)	54.5 ± 0.36	50.0–60.0	6.7	1.8	2.1	3.0	1.0	4.0
Tucano, 4 Jan 2006, *D. Cardoso 902 A. Amado* (HUEFS)	51.0 ± 0.21	47.5–55.0	5.5	1.6	1.5	3.1	0.8	3.9
Itatim, 15 Dec 1996, *E. Melo 1914* et al. (HUEFS)	50.0 ± 0.19	45.0–52.5	5.3	2.0	2.3	3.4	1.0	4.4
Croton schultessi								
Rio de Contas, 18 Aug 2006, *A.K.A Santos 865* et al. (HUEFS)	65.1*	60.0–72.5	4.7	1.3	2.1	3.1	1.0	4.1
Croton sonderianus								
s.loc., s.d., M.L.Guedes 15997 et al. (HUEFS)	59.1 ± 0.35	50.0–67.5	7.8	2.3	3.8	3.6	1.0	4.6
Aiuaba, 4 Feb1997, *M.A. Figueiredo 690* and *L.W. Lima-Verde* (HUEFS)	72.5 ± 0.42	62.5–82.5	8.1	2.3	4.1	3.5	0.9	4.5

Table 3 continued

Genera/species	D		DR	DPi	DCSR	Sex	Nex	Exine
	$\bar{x} \pm S\bar{x}$	R						
Croton tridentatus								
Pilão Arcado, 10 Nov 2005, *A.A Conceição 1582* et al. (HUEFS)	60.6 ± 0.41	55.0–75.0	3.1	1.0	1.0	2.2	0.7	2.9
Petrolina, 11 Aug 1983, *G. Fotius 3544* (HUEFS)	44.8 ± 0.21	34.4–55.1	3.2	1.0	1.2	2.0	0.7	2.7
Sobradinho, 5 Aug 1985, *G. Fotius 4096* (HUEFS)	54.4 ± 0.38	47.5–62.5	3.5	1.0	1.4	1.4	1.0	2.4
***Jatropha* L.**								
Jatropha catingae								
Manoel Vitorino, *s.d.*, *Mori 11244* et al. (CEPEC)	101.1 ± 0.31	95.0–107.5	11.8	3.7	4.6	3.8	1.0	4.8
Jatropha hastifolia								
Paulo Afonso, 6 Jun 2006, *M. Calaço 141* (HUEFS)	78.7 ± 0.22	75.0–82.5	10.0	3.7	2.8	4.1	1.5	5.6
Carinhanha, 24 Nov 2007, *L.M. Guedes 13957* et al. (HUEFS)	76.1 ± 0.27	67.5–80.0	8.4	2.0	2.1	2.9	0.9	3.8
Jatropha mutabilis								
Glória, 10 Aug 2004, *S. Leal 109* and *L. Barreto* (HUEFS)	86.9 ± 0.13	85.0–90.0	11.8	3.6	4.2	5.0	1.0	6.0
Barra, 19 May 2010, *L.P. Queiroz 14658* et al. (HUEFS)	91.8 ± 0.35	87.5–100.0	11.6	3.4	8.2	4.6	1.0	5.6
Jaguarari, 26 Nov 2010, *E. Melo 8909* et al. (HUEFS)	92.3 ± 0.36	87.5–100.0	12.0	4.1	4.4	4.7	1.9	6.6
Jatropha ribifolia								
São Gabriel, 5 Apr 2009, *R.F. Machado 203* et al. (HUEFS)	53.6 ± 0.28	50.0–60.0	6.0	1.7	3.3	3.8	1.0	4.8
Morro do Chápeu, 14 Apr 2007, *E. Melo 4702* et al. (HUEFS)	50.0 ± 0.15	45.0–52.6	6.7	2.1	3.0	3.4	1.0	4.4
Glória, 5 Jun 2004, *M.V.M. Oliveira 681* (HUEFS)	50.0 ± 0.11	47.5–52.5	6.8	1.9	2.8	2.8	1.1	3.9
***Manihot* Mill.**								
Manihot brachyandra								
Piatã, 19 Oct 1992, *W. Ganev 1276* (HUEFS)	120.0 ± 0.39	110.0–127.0	16.7	5.4	5.0	5.5	4.2	9.7
Manihot caerulescens								
Correntina, 28 Apr 1995, *R.C. Mendonça 2304* et al. (HUEFS)	112.2 ± 0.14	107.5–115.0	15.9	5.9	4.4	5.7	4.7	10.4
Wanderley, 1 Dec 2011, *A.M. Miranda 6478* and *J. Ferraz* (HUEFS)	119.3 ± 0.38	115.0–125.0	15.9	5.5	5.5	6.2	4.5	10.7
Manihot catingae								
Queimadas, 16 Nov 1986, *L.P. Queiroz 1146* et al. (HUEFS)	137.8 ± 0.31	130.0–145.0	20.5	6.7	6.7	7.5	5.2	12.7
Manihot dichotoma								
Caldeirão Grande, 8 Dec 1987, *A.C. Allem 3726* and *W.L. Werneck* (HUEFS)	128.0 ± 0.42	120.0–145.0	19.9	6.7	5.2	5.8	4.7	10.6
Espinosa, 4 Dec 1987, *A.C. Allem 3707* and *W.L. Werneck* (HUEFS)	141.9 ± 0.34	135.0–150.0	22.6	7.0	5.4	7.0	5.4	12.4
Brumado, 16 Dec 1987, *A.C. Allem 3720* and *W.L. Werneck* (HUEFS)	152.7 ± 0.42	145.0–160.0	20.2	7.6	6.5	6.4	5.3	11.9
Manihot epruinosa								
Itaberaba, 7 Feb 1995, *A.C. Allem 4518* and *V.S. Silva* (HUEFS)	119.1*	115.0–125.0	16.2	6.0	4.1	6.0	4.5	10.4
Itacarambi, 3 Dec 1987, *A.C. Allem 3595* and *W.L. Werneek* (HUEFS)	131.9 ± 0.27	127.5–140.0	19.5	7.0	5.5	6.9	4.5	11.4
Itacarambi, 3 Dec 1987, *A.C. Allem 3697* and *W.L. Werneek* (HUEFS)	126.9 ± 0.19	122.5–132.5	17.7	5.2	7.8	5.0	3.7	8.7
Manihot heptaphylla								
Barra, 26 Oct 2000, *A.T.A. Rodarte 128* (HUEFS)	119.6 ± 0.20	115.0–125.0	16.1	5.6	4.2	5.2	4.5	9.7
Lençóis, 7 Sep 1999, *F.F. Focha 42* and *L.S. Funch* (HUEFS)	140.7 ± 0.34	135.0–150.0	16.8	5.4	5.8	5.4	4.1	9.5
Palmeiras, 20 Nov 2003, *A.A. Conceição 1149* (HUEFS)	129.3 ± 0.35	122.5–137.5	17.4	6.2	6.8	5.7	4.2	9.9

Table 3 continued

Genera/species	*D*		DR	DPi	DCSR	Sex	Nex	Exine
	$\bar{x} \pm S\bar{x}$	*R*						
Manihot maracasensis								
Tocantinópolis, 19 Feb 2005, *G. Pereira-Silva 9368* et al. (HUEFS)	122.3 ± 0.69	112.5–137.5	15.5	6.4	3.9	6.8	5.2	12.0
Rui Barbosa, 18 Dec 2004, *L.P. Queiroz 9904* et al. (HUEFS)	119.5 ± 0.52	107.5–130.0	18.6	6.6	5.9	6.0	4.6	10.6
Itamaraju, 6 Dec 1981, *A.M. Carvalho 915 G.P. Lewis* (HUEFS)	148.8 ± 0.67	137.5–172.5	20.7	6.4	7.8	6.0	4.9	10.9
Manihot pseudoglaziovii								
Salgueiro, 19 Jan 2010, *D. Araújo 1122* et al. (HUEFS)	120.6 ± 0.37	112.5–130.0	17.3	5.7	5.6	6.7	4.9	11.6
s.loc., s.d., V.D. Silva 26 et al. (HUEFS)	121.8 ± 0.56	110.0–135.2	16.3	5.9	4.5	6.3	5.2	11.5
Petrolina, 22 Jan 2009, *J. Antunes 95* et al. (HUEFS)	123.9 ± 0.32	120.0–132.5	17.8	6.7	5.8	6.6	4.4	11.0

D pollen grains diameter, *R* range, *DR* diameter of rosettes, *DPi* diameter of pila, *DCSR* diameter of to central space of to rosettes, *Sex* Sexine, *Nex* Nexine

* $n < 25$ measures for pollen grain diameter; measurements in µm and indices in absolute numbers

Table 4 Morphometric characters of the pollen grains of *Cnidoscolus quercifolius* Pohl ex Baill. occurring in dry vegetation in Northeastern Brazil

Specimen	PD		ED		EDp		*P/E*	Aperture	PAI
	$\bar{x} \pm S\bar{x}$	Fv	$\bar{x} \pm S\bar{x}$	Fv	$\bar{x} \pm S\bar{x}$	Fv			
Rodelas, 30 Oct 2009, *E. Melo 6971* et al. (HUEFS)	48.1 ± 0.17	45.0–55.0	55.6 ± 0.21	52.5–57.5	61.5 ± 0.34	55.0–70.0	0.90	22.0 × 2.0	0.39
Rodelas, 30 Oct 2009, *E. Melo 7006* (HUEFS)	46.5 ± 0.21	42.5–52.5	53.7 ± 0.22	47.5–57.5	57.3 ± 0.19	55.0–60.0	0.86	–	0.38
Rodelas, 13 Nov 2011, *E. Melo 10684* et al. (HUEFS)	45.8*	42.5–47.5	54.5*	52.5–57.5	62.0 ± 0.27	57.5–67.5	0.84	23.0 × 4.0	0.40

PD polar diameter, *ED* equatorial diameter, *EDp* equatorial diameter in polar view, *P/E* polar diameter/equatorial diameter, *PAI* polar area index

* $n < 25$; measurements in µm and indices in absolute numbers

be modified, e.g., due to the methodology that was used for the analysis. Therefore, this pollen characteristic is not informative for taxonomy (Melhem 1978).

Aperture

There are three apertural types in Crotonoideae: pollen grains without apertures (inaperturate) and pollen grains with pores and colpi. Inaperturate pollen grains are not unusual for Crotonoideae species (Webster 1987; Nowicke 1994), and colpi are less frequent in this group (Erdtman 1952).

Inaperturate pollen grains displaying a *Croton* pattern ornamentation of the exine are diagnostic characteristics for the studied species of *Croton* and *Jatropha*. This result corroborates phylogenetic studies that indicate *Jatropha* as a sister group of the Crotoneae tribe, in which Croton is placed (Berry et al. 2005). Porate pollen grains have been recorded in all *Manihot* and *Cnidoscolus* species, except for *Cnidoscolus quercifolius*, which showed 3-colpate pollen grains. According to Allem (1993), large-sized and pantoporate pollen grains are diagnostic of *Manihot*. For Nowicke (1994), the tribe Manihoteae (including *Manihot* and *Cnidoscolus*) is palynologically characterized by pantoporate pollen grains.

In this study, the 3-colpate pollen type that was observed in *Cnidoscolus quercifolius* diverged from the pattern that was recorded in the literature for other species from this genus (pantoporate). Palacios-Chávez et al. (1991) observed the same pollen type for *C. souzae* Mc Vaugh and *C. aconitifolius* (Mill.) I.M. Johnston, the latter of which was described by Zavaleta and Palacios-Chávez (1980) as inaperturate. Nowicke (1994) reported *Cnidoscolus* species as pantoporate, as also indicated by Lobreau-Callen and Cervera (1997).

The apertural pollen type is one of the most important phylogenetic characters in flowering plant pollen grains (Walker and Doyle 1975). The aperture pattern is relatively conserved in the Euphorbiaceae as most species in this group (for which palynological data are available) produce pollen grains with (generally three) equatorial apertures, a condition that is specified in the work Matamoro-Vidal et al. (2012) as plesiomorphic. The equatorial aperture pattern is plesiomorphic and underwent two or three independent transitions across the phylogenetic tree that was presented by the authors. In this paper, the authors present a clade that is formed by inaperturate crotonoids + articulated crotonoids + Gelonieae, indicating that the equatorial aperture pattern changed to a global pattern (pantoaperturate) and subsequently to an inaperturate in the inaperturate crotonoids, where *Croton* and *Jatropha* are positioned. In this sense, the apertural type found in *Cnidoscolus quercifolius* is a precursor in other species of the genus and in *Manihot*.

Exine ornamentation

Erdtman (1952) described the *Croton* pattern as triangular or sexine elements or somewhat spheroidal in transversal section, over a baculate or spongy wall. This ornamentation type occurs in other families besides Euphorbiaceae, such as in Buxaceae (Erdtman 1952), Thymelaeaceae (Rosello and Melhem 1998), Icacinaceae (Lobreau-Callen 1972), Callitrichaceae (Martinsson 1993) and in some Orobanchaceae genera studied by Santos and Melhem (2000), such as Scrophulariaceae.

The arrangement of pila is defined as forming a central space at the rosettes, which has a lumen with a diameter greater than 1 µm. This space is well delimited or reduced in studied species. This characteristic was also observed by Lima et al. (2007) in using the terms spaced or aggregate for this disposition. Inside rosette lumens there may or may not be sexine elements. In *Croton,* we observed elements varying from clavae, to bacula and granula, whereas the *Jatropha* species had only clavae. In pollen grains of *Cnidoscolus* and *Manihot,* any free sexine elements inside the rosette lumen were recorded. Pila are variable in transversal sections, from subcircular, spheroidal, subtriangular, triangular to quadrangulate. However, in *Manihot* species, triangular shapes were more frequent than were angulate shapes. Similar results were found by Salgado-Laboriau (1967), Allem (1993) and Nowicke (1994). The pila surface was also an important diagnostic characteristic for separating genera, as *Croton*, *Jatropha* and *Manihot* show an ornamented surface, whereas in *Cnidoscolus,* the pila are notably psilate.

We observed basic patterns in pila ornamentation: plicate and rugulate. The first occurs in *Croton* and *Jatropha* species. It is possible to establish three categories in this pattern: slightly plicate, plicate and densely plicate. These patterns are corroborated by Lima et al. (2007), although the second type occurred in *Manihot* (Figs. 6c, e; 8 h, j, l, n) and is described for the first time in this study. According to Ybert (1975), Allem (1993), Lobreau-Callen and Cervera (1997), and Vieira et al. (2012), the surface of pila is described as thinly foveolate, granulose and psilate.

The ornamentation of the sculptural elements that compose the *Croton* pattern is diversified in this pattern, which might be related to pollination mechanisms (Thanikaimoni et al. 1984). According to Muller (1979), some of these structures are probably the result of adding sporopollenin in an irregular shape angulated by exine.

Taxonomic implications of pollen morphology

Exine ornamentation has a characteristically *Croton* pattern, making this pattern a synapomorphy of this subfamily (Webster 1994; Wurdack et al. 2005).

Webster (1994) used macromorphological characteristics to segregate *Manihot* and *Cnidoscolus*, but pollen characteristics, such as the presence or absence of ornamentation in pila, pore number, and size, might also be used for this purpose.

Pollen characteristics are of great use for separating genera within Crotonoideae. Webster (1994) used macromorphological and pollen characteristics to propose a generic revision and a rearrangement of suprageneric taxa. This author separated tribes within Crotonoideae based on aperture type, in which species showing colporate or porate pollen grains were readily assigned to the tribes Micrandreae, Manihoteae, Adenoclineae and Gelonieae, whereas inaperturate pollen grains were readily assigned to the tribes Elateriospermeae, Jatropheae, Codiaeae, Trigonostemoneae, Rinicocarpeae, Crotoneae, Ricinodendreae and Aleuritideae.

Wurdack et al. (2005); Tokuoka (2007) and, recently, Matamoro-Vidal et al. (2012) reconstructed a molecular phylogeny for Euphorbiaceae in which Crotonoideae is not monophyletic. This subfamily is readily divided into four lineages: Adenoclineae s.l., Gelonieae, articulate Crotonoids and inapertured Crotonoids, the latter two with representatives in this study.

Pollen grain apertures may corroborate this topology as Adenoclineae s.l., Gelonieae and articulate Crotonoids have pollen grains varying from porate and colpate to, less frequently, colporate. In inapertured Crotonoids, all species show pollen grains without pores, corroborating in part what Webster (1994) cited using morphological data.

Based on literature for the apertural type found on articulate Crotonoid lineages, *senso* Wurdack et al. (2005), *Hevea*, *Micrandra* (Nowicke 1994) and *Glycydendron* (Lobreau-Callen and Cervera 1997) have colpate pollen grains, whereas *Cnidoscolus*, *Manihot* (Nowicke 1994) and *Elateriospermum* (Lobreau-Callen and Cervera 1997), have porate pollen grains. However, Nowicke (1994) reported the latter as having inapertured pollen grains.

Thus, we can note that the apertural types that were found in this study for species of *Cnidoscolus* showed porate pollen grains, whereas those in *C. quercifolius* pollen grains are colpate, which is one plesiomorphic condition for that genus, for *Manihot*, and for the Crotonoideae subfamily.

Conclusions

The results presented here corroborate the eurypalynous origin of the Crotonoideae subfamily as the morphological variation in pollen grains of the studied genera is taxonomically and phylogenetically significant. The size, shape, type and number of apertures, in addition to details of exine sculpture, constitute characteristics of great importance in the segregation of tribes and genera from Crotonoideae.

The apertural type and number of apertures were important characters for species grouping, being well conserved within the studied genera. There is only one exception: *Cnidoscolus*, which showed two apertural types: colpate and porate. The pollen size was also useful for setting the pollen types, consisting of a well-marked characteristic in *Manihot*. A single pollen character, the *Croton* pattern exine, might unite all of the studied species, being a synapomorphy for Crotonoideae. Although having a conserved exine type, we recorded some taxonomically significant variation in the disposition of ornament shape, size, number, disposition and surface ornamentation of pila, in addition to the presence of sexine elements inside the rosette lumen.

The morphology of pollen grains in the studied species will contribute to taxonomic and phylogenetic studies to clarify phylogenetic relationships in Crotonoideae as new descriptions and illustrations are presented for this group. Some morphological characters are recorded for the first time in this study and will contribute to the pollen flora of widely distributed, rare and endemic species of the Caatinga biome, an important unit of Seasonally Dry Tropical Forests.

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Compliance with ethical standards

This study was conducted following the accepted principles of ethics and professional conduct.

Conflict of interest Author Lidian Ribeiro de Souza has received research grant from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (BR). Author Francisco de Assis Ribeiro dos Santos has received research grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (BR) (#303862/2013-0).

Appendix: specimens investigated

Cnidoscolus hamosus Pohl. Brazil: Bahia, Irecê, 20 Jan 1984, *G. Fotius 3705* (HUEFS). *Cnidoscolus infestus* Pax & K.Hoffm. Brazil: Bahia, Conceição de Feira, Jun 1980, *Grupo Pedra do Cavalo 225* (HUEFS).

Cnidoscolus pubescens Pohl. Brazil: Bahia, Bendengó, 23 Feb 2000, *A.M. Giulietti 1775* and *R.M. Harley* (HUEFS); Bahia, Itaberaba, 23 Oct 2005, *E. Mello 4144* et al. (HUEFS); Bahia, Paulo Afonso, 29 Nov 2005, *R.M. Castro 1277* et al. (HUEFS). *Cnidoscolus quercifolius* Pohl ex Baill. Brazil: Bahia, Rodelas, 30 Oct 2009, *E. Melo 6971* et al. (HUEFS); Bahia, Rodelas, 30 Oct 2009, *E. Melo 7006* (HUEFS); Bahia, Rodelas, 13 Nov 2011, *E. Melo 10684* et al. (HUEFS).

Cnidoscolus ulei (Pax) Pax. Brazil: Bahia, Caetité, 8 Feb 1997, *M.L. Guedes 5212* et al. (HUEFS); Bahia, Caetité, 18 Dec 2009, *L.J. Alves 122* et al. (HUEFS); Bahia, Mucugê, 14 Feb 1992, *L.P. Queiroz 2629* (HUEFS).

Cnidoscolus urnigerus Pax. Brazil: Bahia, Casa Nova, 9 Feb 2004, *L.P. Queiroz 9153* et al. (HUEFS); Bahia, Livramento do Brumado, 15 Jun 2002, *L.P. Queiroz 7069* et al. (HUEFS); Bahia, Maracás, 22 Jan 2004, *D.S. Carneiro-Torres 302* et al. (HUEFS). *Croton adamantinus* Müll.Arg. Brazil: Bahia, Campo Formoso, 13 Apr 2006, *R.D. Souza 17* et al. (HUEFS); Bahia, Mucugê, 20 Dec 2007, *M. Ibrahim 55* and *S.F. Conceição* (HUEFS); Bahia, Pindobaçú, 16 Dec 2008, *L.A. Sousa 210* (HUNEB); Bahia, Rio de Contas, 6 Sep 2003, R.M. Harley 54674 and *A.M. Giulietti* (HUEFS). *Croton adenocalyx* Baill. Brazil: Ceará, Aiubá, 21 Mar 1980, *Gomes s.n.* (HUEFS); Bahia, Aiuaba, 21 Mar 1980, *A. Gomes s.n.* (HUEFS); Bahia, Cratéus, 27 Feb 2002, *F.S. Araujo 1346* (HUEFS).

Croton anisodontus Müll.Arg. Brazil: Ceará, Capistrano, 27 Apr 1994, *J.B.L.P. Medeiros 51* and *M.A. Figueiredo* (HUEFS); Ceará, Guaraciaba do Norte, 6 May 1984, *A. Fernandes s.n.* and *Matos* (HUEFS); Ceará, Guaraciaba do Norte, 6 May1984, *A. Fernandes s.n.* and *Matos* (HUEFS).

Croton arenosus Carn.-Torres & Cordeiro. Brazil: Bahia, Canudos, 18 Feb 2004, *E.B. Miranda 613* et al. (HUEFS).

Croton argyrophylloides Müll.Arg. Brazil: Bahia, Itaberaba, 15 Feb 1984, *G.C. Pereira-Pinto 544184* (HUEFS); Bahia, Itambé, 9 Jan 1986, *A.M. Carvalho 2118 A. Chautems* (HUEFS); Bahia, Tucano, 19 Jan 1964, *A.L. Costa 2050* (HUEFS).

Croton betulaster Müll.Arg. Brazil: Bahia, Érico Cardoso, 4 Jul 2001, *M.P. Bautista 3286* et al. (HUEFS);

Bahia, Rio de Contas, 18 Jan 2003, *A.M. Miranda 4054* et al. (HUEFS); Bahia, Rio de Contas, 16 Aug 2006, *A.K.A. Santos 846* et al. (HUEFS). *Croton blanchetianus* Baill. Brazil: Ceará, Aiuaba, 9 Jan 1997, *L.V. Lima-Verde 368* et al. (HUEFS).

Croton catinganus Müll.Arg. Brazil: Piauí, Amarante, 24 Jan 1970, *L.T. Eiten 1036 G. Eiten* (SP).

Croton cordiifolius Baill. Brazil: Bahia, Abaíra, 27 Dec 1992, *D.J.N. Hind 50467* et al. (HUEFS); Bahia, Rio de Contas, 24 Jan1994, *W. Ganev 2873* (HUEFS); Bahia, Rui Barbosa, 17 Jan 2006, *L.P. Queiroz 12041* and *D. Cardoso* (HUEFS).

Croton echioides Baill. Brazil: Pernambuco, Moreilândia, 4 Mar 1995, *E. Silveira s.n.* (HUEFS); Bahia, Cafarnaum, 14 Jan 2012, *J.G. Carvalho-Sobrinho 3227* et al. (HUEFS).

Croton glandulosodentatus Pax & K.Hoffm. Brazil: Bahia, Canudos, 18 Feb 2004, *E.B. Miranda 622* et al. (HUEFS); Piauí, São Raimundo Nonato, 19 Dec 1978, *A. Fundes s.n.* (HUEFS).

Croton grewioides Baill. Brazil: Bahia, Jaguarari, 10 Nov 2005, *A.A. Conceição 1608* et al. (HUEFS); Bahia, Jequié, 5 Nov 2009, *J.C Nascimento 21* and *R.M. Aguiar* (HUEFS); Bahia, Jequié, 5 Nov 2009, *J.C. Nascimento 20* and *R.M. Aguiar* (HUEFS); Bahia, Pindobaçú, 16 Nov 2008, *L.A. Sousa* 213 (HUNEB).

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