

## Croton aleuritoides P.E. Berry (Euphorbiaceae), a Distinctive New Tree Species from Montagne des Français in Northern Madagascar

Authors: Berry, Paul E., Ee, Benjamin van, Kainulainen, Kent, and

Razafindraibe, Hanta

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# Croton aleuritoides P.E. Berry (Euphorbiaceae), a distinctive new tree species from Montagne des Français in northern Madagascar

Paul E. Berry, Benjamin van Ee, Kent Kainulainen & Hanta Razafindraibe

### **Abstract**

BERRY, P.E., B. VAN EE, K. KAINULAINEN & H. RAZAFINDRAIBE (2016). Croton aleuritoides P.E. Berry (Euphorbiaceae), a distinctive new tree species from Montagne des Français in northern Madagascar. *Candollea* 71: 181-188. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2016v712a3

Croton aleuritoides P.E. Berry (Euphorbiaceae) is described from deciduous forests on tsingy limestone in the Antso River basin of Montagne des Français in northern Madagascar. This remarkable new species is distinguished by its arborescent habit; large, broadly ovate-cordate, deciduous leaves; adaxial epipetiolar glands; sparsely lepidote pubescence; elongate stipules; large seeds with a whitish fleshy covering when fresh; and cinerescent fruits that are indehiscent when dispersing from the tree and only dehiscing much later on the ground. It is remarkable that such a large tree from a relatively small massif close to the regional capital has gone undetected for so long. With its very limited area of occupancy and small population size, it should be considered an endangered species.

### Résumé

BERRY, P.E., B. VAN EE, K. KAINULAINEN & H. RAZAFINDRAIBE (2016). Croton aleuritoides P.E. Berry (Euphorbiaceae), un nouvel arbre caractéristique de la Montagne des Français au nord de Madagascar. *Candollea* 71: 181-188. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2016v712a3

Croton aleuritoides P.E. Berry (Euphorbiaceae) est décrit comme une espèce nouvelle des forêts décidues sur tsingy calcaires du bassin de la rivière Antso à la Montagne des Français, dans le nord de Madagascar. Cette remarquable espèce nouvelle se distingue par son port arborescent; ses grandes feuilles largement ovées-cordées et caduques; ses glandes adaxiales épi-pétiolaires; sa pubescence lépidote clairsemée; ses stipules allongées; ses grosses graines avec un revêtement charnu blanchâtre à l'état frais et ses fruits cendrés qui sont indéhiscents lors de la dispersion de l'arbre et ne sont déhiscents que beaucoup plus tard sur le sol. Il est étonnant que ce grand arbre d'un relativement petit massif près de la capitale régionale soit resté inaperçu pendant si longtemps. Avec sa zone d'occupation très réduite et la petite taille de sa population, il doit être considéré comme une espèce en danger d'extinction.

### **Keywords**

EUPHORBIACEAE - Croton - Madagascar - Montagne des Français

Addresses of the authors:

PEB, KK: Herbarium, Department of Ecology and Evolutionary Biology, 3600 Varsity Drive, Ann Arbor, Michigan 48108, U.S.A. Email: peberry@umich.edu BE: Department of Biology, Universidad de Puerto Rico, Recinto Universitario de Mayagüez, PR 00680, Puerto Rico, U.S.A.

HR: Parc Botanique et Zoologique de Tsimbazaza, rue Kasanga Fernand, Antananarivo 101, Madagascar.

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### Introduction

Croton L. (Euphorbiaceae) is one of the ten largest genera of flowering plants, with an estimated 1,200 species worldwide (Govaerts et al., 2000). Although roughly two-thirds of that diversity is found in the New World (VAN EE et al., 2011), Madagascar represents the major hotspot of diversity of *Croton* in the Old World, with an estimated 150 species (SCHATZ, 2001). That makes it the second or third most speciose genus of plants on the island, after Dombeya Cav. (Malvaceae) and possibly Diospyros L. (Ebenaceae), according to the MADAGAS-CAR CATALOGUE (2016) (see also Buerki et al., 2013). The last botanist to systematically review Croton in the Western Indian Ocean region was Leandri (1939), who recognized 94 species. By the time Leandri published the last of multiple updates on Croton in the region (Leandri, 1976), he had increased that number to 132 species. Since that time, numerous additional collections have been made in Madagascar, particularly by botanists associated with the Missouri Botanical Garden, and a number of them correspond to as yet undescribed species.

While examining undetermined specimens of Croton at P in 2006, the senior author came across an unusual specimen collected by René Capuron in northern Madagascar in the late 1950s. The label described it as a tree 15 m tall and 40 cm in diam., which is unusual for the genus, particularly coming from a seasonally dry limestone area of northernmost Madagascar. The specimen also had some characteristics that made us doubt initially if it was even a Croton - the leaves are large and ovate, with petioles nearly as long as the blade, and they have scattered, almost imperceptible appressed scales on the leaf surfaces. It also has long, linear stipules nearly 1.5 cm long and a pair of petiolar glands positioned well below the apex of the petiole, where they normally would be found in Croton. In the pistillate flowers, the ovaries and fruits are covered by an ashy, finely farinose indument that is quite uncharacteristic for Croton. Finally, the mature fruits have no signs of dehiscence, whereas all other species of the genus in Madagascar, with the exception of some populations of C. mongue Baill., have dehiscent capsules. In November 2009, we attempted to relocate the species on a trip to northern Madagascar. Since we had no idea where on the Montagne des Français Capuron had collected his specimen, we hiked to the base of the westernmost escarpments where some forest remnants remained. The closest we came to a tree matching the description of Capuron's collection were some individuals of Thespesia gummiflua Capuron (Malvaceae), which has very similar looking leaves, but the fruits of that species are clearly dehiscent on the tree and they have a cupular calyx remnant not found in any species of Croton.

After returning to the capital Antananarivo from our visit to the Diego Suarez area, we visited the TAN herbarium at the Parc Botanique et Zoologique de Tsimbazaza. Among the undetermined specimens of *Croton* there, we found a collection

from 2005 (Randrianarivelo et al. 199) that agreed with the earlier Capuron collection at P. It too came from the Montagne des Français massif, but had a more precise location with GPS coordinates that placed it on the eastern side of the mountain range. We were able to return to Diego Suarez in early 2016, whereupon we set out to search for this new location. With the help of a local guide who was present on the trip in 2005 and along with the GPS coordinates of the collection, we successfully found several individuals of the tree in question. We apparently arrived shortly after the fruiting season had ended, because even though there were no fruits visible on the tree branches, we were able to collect fruits off the ground and find recently germinated seedlings, and we made specimens of leafy branches and leaf tissue samples dried in silica gel for DNA extraction. Here we present the results of our herbarium and field work, describing this unusual new species of Croton and discussing its likely relationships among the Malagasy species.

## **Systematics**

Croton aleuritoides P.E. Berry, spec. nova (Fig. 1-3).

Typus: MADAGASCAR. Prov. Antsiranana: DIANA, Montagne des Français, à l'E de Diégo-Suarez, 26.XI.1958, fl. & fr., Service Forestier 20088 (holo-: P [P00312410]!; iso-: B, G [G00341674] image seen, K, MO!, P [P00206489]!, S!, TEF!, WAG).

In its large, ovate-cordate, nearly glabrous, long-petiolate leaves, Croton aleuritoides P.E. Berry is closest to C. bemaranus Leandri but differs in being a much larger tree (to 25 m vs. 2-4 m tall) with larger fruits (2.5-3 cm vs. less than 1 cm in diam.) that are ashy-farinose and indehiscent until after they have fallen to the ground (vs. glabrous and dehiscent).

Trees to 25 m tall and 50 cm dbh, bark tan and slightly flaky, trunk with reddish resin when cut. Young twigs green when fresh, lenticellate, with prominent leaf scars lower down where leaves have dehisced. Leaves alternate, deciduous; stipules linear, 7-14 mm long, caducous; petioles 4-8(-11) cm long, finely lepidote, pulvinate at base for c. 1 cm (noticeable only when fresh), with a pair of glands on the adaxial surface of the petiole near the junction with the leaf blade or up to 1 cm below it, glands crateriform, c. 1 mm in diam., sessile or stalked to c. 1 mm long, sometimes obliquely aligned. Leaf blades firmly membranaceous, broadly ovate-cordate,  $6-9(-12.5) \times 6-8$ (-11) cm, apex acuminate, base shallowly and broadly cordate, palmately 5-veined from the base, sometimes with a rounded, reddish or orange-tinged patch where these veins join at the petiole, 3 or 4 secondary veins above that on either side of the midvein, margins subentire to shallowly crenate, green and sparsely lepidote adaxially, paler and densely lepidote with very



Fig. 1. – Holotype of Croton aleuritoides P.E. Berry. [Service Forestier 20088, P] [@ Muséum national d'Histoire naturelle, Paris. Reproduced with permission]

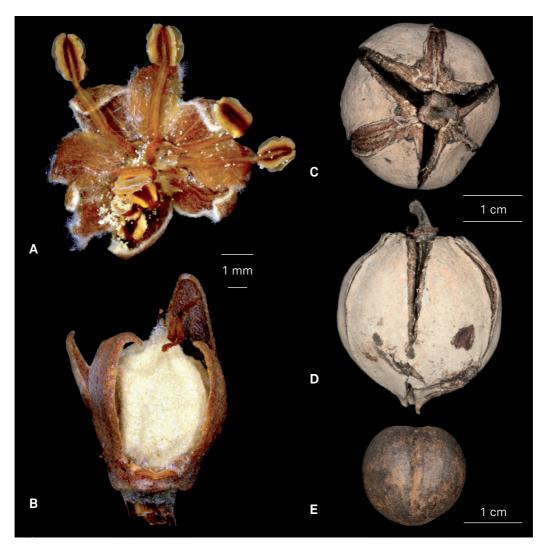


Fig. 2. – Croton aleuritoides P.E. Berry. A. Staminate flower (three stamens broken off); B. Pistillate flower, with one sepal removed and two of the three styles broken off. Note the minute petals; C-D. Capsule dehiscing both septicidally (exo- and endocarp) and loculicidally (exocarp only); E. Seed (partially dried). [Service Forestier 20088, P]

fine appressed scales abaxially. *Inflorescence* terminal, 8-15 cm long at anthesis, mostly staminate, with 1-4 pistillate flowers at the base, leaflike bracts to 2 cm long subtending the pistillate flowers and small linear bracts 1-1.5 mm long subtending the staminate flowers. *Staminate flowers* subsessile or with short pedicels to 1 mm long, buds spherical, 1-1.5 mm in diam., ashy-pubescent; sepals 5, connate at base, lobes broadly triangular-ovate, c. 2.5 × 2 mm, inflexed at anthesis, apex acute, abaxially lepidote, adaxially pilose; petals 5, obovate, c. 2.5 × 1.6 mm, abaxially lepidote, adaxially pilose; stamens c. 11, filaments c. 3 mm long, glabrous, anthers elliptic, c. 1.5 mm long; receptacle pilose. *Pistillate flowers* with pedicels 3-6 mm long and 2-3 mm thick, sepals 5, elliptic-ligulate, 8-11 × 3-5 mm, scattered lepidote abaxially, more sparsely lepidote adaxially, petals 5, spatulate-lanceolate,

minuscule, c.  $1.2 \times 0.5$  mm, abaxially lepidote, adaxially sparsely pilose; ovary spherical, beaked, finely ashy-lepidote, stigmas 3, 5-10 mm long, bifurcate (a total of 6 terminal tips), abaxially lepidote, adaxially glabrous, persistent. *Fruit* subspherical, 2.5-3 cm in diam., farinose, slightly beaked at the apex or at times broadly depressed, ridged along the septal sutures and slightly impressed in the middle of the locules, indehiscent when falling from the tree but eventually dehiscing on the ground, with an ashy external exocarp c. 2 mm thick splitting both septicidally and loculicidally and an inner woody endocarp 2-4(-5) mm thick splitting only septicidally, both opening acropetally, the endocarp persistent but the exocarp evanescent; columella stout, 3-angled, 15-17 mm long, fimbriate at apex. *Seeds* orbicular, 15-17 mm wide, 16-18 mm long, 10-12 mm thick (when partially dried, probably

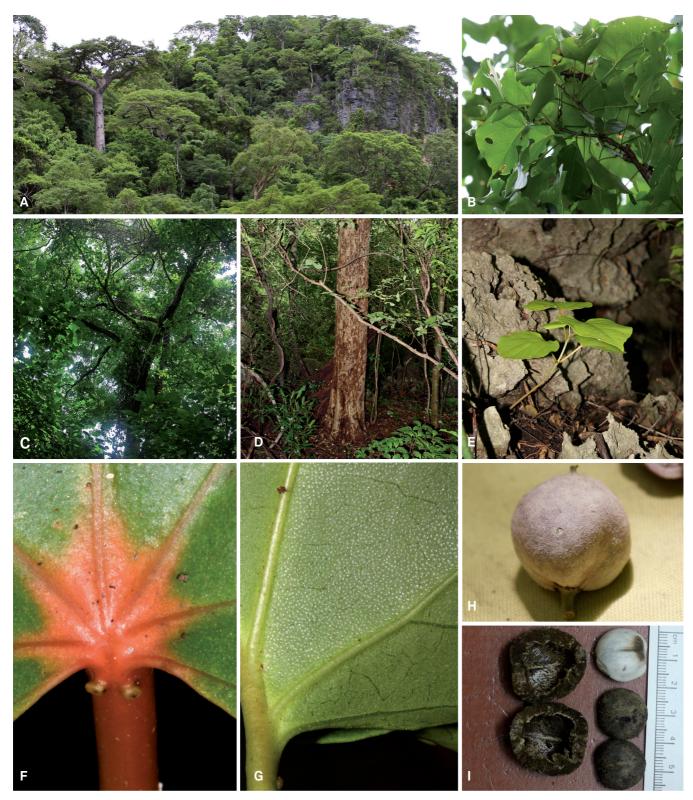


Fig. 3. – Croton aleuritoides P.E. Berry. A. Typical habitat in Montagne des Français, deciduous forest on limestone "tsingy"; B. Canopy leaves; C. Canopy from below; D. Trunk (c. 40 cm in diam.); E. Seedling growing in a crack of a block of limestone tsingy; F. Close-up of the adaxial side of a leaf base showing the epipetiolar glands and the distinct reddish coloration at the junction of the secondary veins; G. Close-up of the abaxial leaf surface showing the minute lepidote pubescence; H. Fruit, already fallen to the ground and still indehiscent; I. Endocarps and seeds; note the white fleshy cover of the fresh seed on the upper right.

[Photos: A, C, D, F, G, I: P. Berry; B, E, H: K. Kainulainen]

larger when fresh), dorsally grooved (where the endocarp is impressed), covered with a thin, fleshy, whitish arillate layer when freshly removed from the locule (this layer quickly drying and later disappearing when exposed to the air), caruncle minute or absent.

Etymology. – The specific epithet alludes to the similar arborescent habit and the typically large, cordate, acuminate leaf blades of *Aleurites* J.R. Forst. & G. Forst. (candlenut tree, *Euphorbiaceae*). It is even closer in appearance to *Vernicia fordii* (Hemsl.) Airy Shaw, the tung oil tree, which was originally described as *Aleurites fordii* Hemsl.

Distribution, habitat, and ecology. – Croton aleuritoides is known from the Montagne des Français massif, east of the city of Diego Suarez in northern Antsiranana Prov., Madagascar. The only known populations occur in the Antso River basin south of the Andavakoera River, on the eastern side of the range, in mixed deciduous forests on or alongside outcrops of jagged limestone (tsingy formations), at elevations of 90-200 m (Fig. 4).

Phenology. – From the few specimens available, *C. aleuritoides* flowers in November and fruits from November to February. Based on the strongly deciduous nature of the Montagne des Français forests and the way the leaves are produced in flushes at the branch tips, *C. aleuritoides* is likely strongly deciduous, probably losing most of its leaves from June to October.

Conservation Status. – Croton aleuritoides is so far known only from two populations in a single valley on the eastern side of the Montagne des Français massif. Those two populations are a few kilometres apart and can be considered as two locations. The massif is now part of the newly designated protected area called "Ambohitr'Antsingy – Montagne des Français". Despite its protection, the dry forests of the massif are threatened by human activities such as charcoal production and cattle grazing. The known populations of C. aleuritoides are therefore under continuing decline in the extent and quality of its habitat. Its extent of occurrence is restricted (< 1 km²) and the new species should be assign a preliminary conservation status of "Endangered" [EN B1ab(i,ii, iii, iv, v)+ B2ab(i,ii, iii, iv, v)] following IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – This is one of the most distinctive species of C. on Madagascar, which harbors over 150 species in the genus (Schatz, 2001). It is first of all a large tree, part of a minority of the Croton species on the island (Fig. 3C, D). Its pubescence is atypical for Croton, with tiny lepidote trichomes on the leaves that are not immediately evident (Fig. 3F, G). The fruits have a much denser pubescence and appear farinose

with a dense tan or ashy, mealy covering of minute trichomes (Fig. 2C, D). Its long, linear stipules are unusual for Croton from Madagascar, as are the epipetiolar glands that are often found well below the junction with the leaf blade. Certainly the most distinctive character of C. aleuritoides are the fruits, which are among the largest in the genus on Madagascar (only C. nobilis Baill. and C. mongue Baill. rival them in size), and more significantly, they are indehiscent until well after they fall to the ground (Fig. 2H). They also have an exocarp that separates from the woody endocarp when the fruit finally dehisces (Fig. 3C, D), and the seeds are very large for Croton; they lack a caruncle but instead have a thin membranous aril-like structure surrounding the entire seed when fresh (Fig. 2I). When we collected *C. aleuritoides* in March of 2016, we observed several crowned lemurs (Eulemur coronatus) browsing amid the branches of one of the trees, and it is possible that they have a role in the dispersal of the fruits, perhaps gnawing them open to access the seeds or else foraging on the ground after the fruits have fallen.

The only other species to which Croton aleuritoides bears some resemblance is C. bemaranus, which also occurs in northern Madagascar in the same limestone tsingy deciduous forest habitat. Its leaves are very similar to C. aleuritoides both in shape and texture, and they also often have a brightly colored reddish spot where the petiole connects to the leaf blade, but they are smaller, even more glabrous, and have stipules that are usually more divided or glandular. The glands on the leaves are more clearly basilaminar rather than epipetiolar, and the pistillate sepals are wider, more imbricate, and persistent in fruit, with evident vertical striations on the adaxial surface. The fruits of C. bemaranus share the unusual character of having a thin exocarp that splits both septicidally as well as loculicidally, but the fruits are clearly dehiscent while still on the plant. Finally, both the sepals and ovary of C. bemaranus are ± glabrous, and the species grows as a shrub no more than 2 or 3 m high.

The isotype specimen at TEF was annotated in 2001 by Alan Radcliffe-Smith as *C. bemarana* var. *pseudolepidotus* [ined.] and was included as such in his unpublished manuscript on *Croton* in Madagascar and the Comoro Islands. We believe this was an insightful placement of the new taxon, but clearly it is specifically distinct from *C. bemaranus*, and Radcliffe-Smith failed to remark on the significant differences in fruit size and dehiscence between the two.

We found populations of *C. aleuritoides* by returning to the site where it was collected in 2005 by Clairemont Randrianarivelo and collaborators (*Randrianarivelo et al. 199*), using the GPS coordinates provided on the label and in the Tropicos database [www.tropicos.org]. This is on the eastern side of Montagne des Français, fairly easily accessible from the village of Andavakoera, close to where the east-flowing Andavakoera creek flows into the larger Antso River coming from the south



**Fig. 4.** – Distribution of known collections of *Croton aleuritoides* P.E. Berry from northern Madagascar, in the Montagne des Français massif (stars). [Google earth Image. © 2016 DigitalGlobe. Reproduced per attribution guidelines]

(names from Service Géographique de Madagascar, 1969). Along the Antso River in the flatter and less rocky part of the valley, there are many signs of cultivation or cutting of the forest, with remains of plantations or extensive spiny Lantana L. thickets. As one approaches the steeper sides of the valley below the cliffs that delimit it, there are remains of intact forest interspersed with areas that were clearly cut for some kind of plantation. Our local guide, who was part of the 2005 collecting trip, indicated that the area close to the spot where they collected C. aleuritoides had been recently cut at that time to grow Cannabis L. By the time we returned in 2016, there was no evidence of this cultivation, although the area that had been deforested was clearly discernable by its coverage with a single leguminous tree that had successfully colonized it within the last decade.

The first individual of *Croton aleuritoides* we found in 2016 was a large tree around 25 m tall and 40 cm dbh (Fig. 3D). It was growing adjacent to a small, jagged

block of limestone that had likely eroded off the western wall of the valley which was about 200 m farther upslope (Fig. 3A). What led us to this tree, besides the GPS coordinates, were the remnants of fruits we found on the ground and a number of seedlings that were growing in the shade in cracks of the limestone block below the canopy. We subsequently found additional mature trees and some younger, smaller trees that were growing along the edge of another former clearing. Under most of the large individuals, we could find seedlings probably a month or so old on the soil or rocks underneath (Fig. 3E). On our return walk from the Randrianarivelo et al. 199 site back to the village of Andavakoera, we crossed another small tsingy area just west of the crossing of the Antso River, and there we found some additional individuals of C. aleuritoides in a small forest remnant. Now that we have confirmed the presence of this species in the area, we think that a more detailed survey should be carried out to determine if there are more sites in the same valley, or in adjacent valleys of the Montagne des Français massif, where *C. aleuritoides* also occurs.

We are delighted that we were able to relocate this species and are now able to properly describe it and confirm that it is indeed a novel species of Croton, as well as to find that there are still breeding populations in at least one part of the Montagne des Français system. However, the natural vegetation of much of Montagne des Français has been severely impacted by farmers and charcoal producers over the past decades, making tree species like this extremely vulnerable to extinction. During our visit to the lower Antso River valley of Montagne des Français in 2016, there was little evidence of active deforestation occurring in the vicinity of the main population we found in the middle section of the valley, but the second population we found in the lower part of the valley alongside the river was in a small forest patch surrounded by deforested pasturelands. We are hopeful that the recently designated protected zone of Montagne des Français overseen by the NGO SAGE (Service d'Appui à la Gestion de l'Environnement) and the nearby Protected Zone of Orangea co-administered by the Missouri Botanical Garden will contribute to the preservation of remaining natural forest habitats in this area, and that increased knowledge of unusual endemic species like C. aleuritoides will assist them with these efforts. With the information provided here about the new species of Croton, we strongly encourage local botanists, such as those working in the Missouri Botanical Garden office in Ramena, to better survey some of the remaining forests of the Montagne des Français massif to determine if there are any additional populations of *C. aleuritoides* that can be located.

Paratypi. – MADAGASCAR. Prov. Antsiranana: DIANA, Montagne des Français, 21.V.1951, ster., *R-I50-44* (TEF); Comm. Mahavanona, Fkt. Andranomanitra, Campement Antafiankovoka, Montagne des Français, 3.II.2005, 12°21'15"S 49°21'40"E, 166 m, fr., *Randrianarivelo et al. 199* (MICH, MO, P, TAN); Montagne des Français, E side of massif, E side of Antso River (S of Andavakoera stream), c. 150 m from the steep cliff walls, 12°21'16"S 49°21'41"E, 168 m, 1.III.2016, *van Ee et al. 2305* (MICH, MO, P, TAN); *ibid. loc.*, 12°21'14"S 49°21'43"E, 176 m, *van Ee et al. 2306* (MICH, TAN); *ibid. loc.*, small tsingy outcrop on W side of river, c. 20 min walk from village of Andavakoera, 12°20'26"S 49°21'39"E, 90 m, 1.III.2016, *van Ee et al. 2311* (MICH, MO, P, TAN).

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### References

- BUERKI, S., D.S. DEVEY, M.W. CALLMANDER, P.B. PHILLIPSON & F. FOREST (2013). Spatio-temporal history of the endemic genera of Madagascar. *Bot. J. Linn. Soc.* 171: 304-329.
- Govaerts, R., D.G. Frodin & A. Radcliffe-Smith (2000). *World checklist and bibliography of Euphorbiaceae*. 4 vol. Royal Botanic Gardens, Kew.
- IUCN (2012). IUCN Red List Categories and Criteria Version 3.1.
  2nd ed. IUCN Species Survival Commission, IUCN, Gland & Cambridge.
- Leandri, J.D. (1939). Les Croton de Madagascar et des Iles Voisines. *Ann. Mus. Colon. Marseille* 7: 5-100.
- Leandri, J.D. (1976). Croton appertii, Euphorbiacée nouvelle du sud-ouest de Madagascar. *Adansonia* ser 2, 15: 331-332.
- MADAGASCAR CATALOGUE (2016). Catalogue of the Vascular Plants of Madagascar. Missouri Botanical Garden, St. Louis & Antananarivo [http://www.efloras.org/madagascar].
- Schatz, G.E. (2001). *Generic tree flora of Madagascar*. Royal Botanic Gardens, Kew & Missouri Botanical Garden, St. Louis.
- Service Géographique de Madagascar (1969). Feuille U.V.-30, Diégo Suarez. Carte de Madagascar au 1/100.000. 3° ed. Antananarivo
- VAN EE, B., R. RIINA & P.E. BERRY (2011). A revised infrageneric classification and molecular phylogeny of New World *Croton* (Euphorbiaceae). *Taxon* 60: 791-823.