New species and species reports of Croton L. (Euphorbiaceae) from the eastern forest corridor of Madagascar

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

Abstract


Six species of Croton from the Moramanga District of the Alaotra-Mangoro Region of eastern Madagascar (Toamasina Prov.) are newly described here, five of which occur in the Ambatovy mining concession. A seventh new species is described from the Ankerana Forest in the Atsinanana Region, some 80 km to the northeast of the town of Moramanga, which is one of the offset areas intended to mitigate the deforestation incurred by the Ambatovy mining project. Of the new species, Croton ferricretus Kainul., B.W. van Ee & P.E. Berry is the one mostly closely associated with the ultramafic soils where nickel and cobalt is being extracted. Although it is locally common, it is only known from the mine concession. Croton enigmaticus P.E. Berry & B.W. van Ee is considerably less common on the mine concession but is also known from two other sites. Croton droguetioides Kainul. & Radcl.-Sm. is known from Ambatovy and three other areas in the Alaotra-Mangoro Region, and Croton radiatus P.E. Berry & Kainul. is known only from forests in the Ambatovy mining concession and from the area of Zahamena National Park. Croton indrisilvae Kainul., B.W. van Ee & P.E. Berry is a small-leaved species known only from Analamazaotra National Park, and Croton ankeranae Kainul. is another small-leaved species known so far only from Ankerana. Croton plurispicatus P.E. Berry, Kainul. & B.W. van Ee is a distinctive small tree known mainly from the Lakato and Vohibe forests in the southern part of the Ankeniheny-Zahamena Corridor and one other location east of Analamazaotra. Croton hypochalibaeus Baill. is reinstated from synonymy and is now known from the Ambatovy area as well as in several forest remnants within the “tampoketsa” vegetation on the high central plateau of Madagascar, and in canyons of Isalo National Park. An additional species (Croton lasiopyrus Baill.) is identified from the Moramanga area for the first time, but is not currently known from Ambatovy. Amended descriptions are provided for both Croton hypochalibaeus and Croton lasiopyrus, and lectotypes are designated.

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Résumé

Six espèces de Croton L. (Euphorbiaceae) du district de Moramanga de la région Alaotra-Mangoro à Madagascar (Prov. de Toamasina) sont nouvellement décrites ici, dont cinq se trouvent dans la concession minière d’Ambatovy. Une septième nouvelle espèce est décrite de la forêt d’Ankerana dans la région Atsinanana à quelque 80 km au nord-est de la ville de Moramanga. Cette forêt est l’une des zones de compensation visant à atténuer la déforestation subie par le projet minier Ambatovy. Croton ferricretus Kainul., B.W. van Ee & P.E. Berry est parmi les nouvelles espèces celle qui est la plus étroitement associée aux sols ultramafiques d’où le nickel et le cobalt sont extraits. Bien que localement commune, elle n’est connue que de cette zone minière. Croton enigmaticus P.E. Berry & B.W. van Ee est moins commune sur cette zone, mais elle est également connue de deux autres sites. Croton drogoetioides Kainul. & Radcl.-Sm. est connu d’Ambatovy et de trois autres zones de la région Alaotra-Mangoro, alors que l’espèce Croton radiatus P.E. Berry & Kainul. est connue des forêts de la concession minière d’Ambatovy et de la région du parc national de Zahamena. Croton indrisilvae Kainul., B.W. van Ee & P.E. Berry est une espèce à petites feuilles connue seulement du parc national d’Analamazaotra, tandis que Croton ankeranae Kainul., autre espèce à petites feuilles n’est connue à ce jour que de l’Ankerana. Croton plurispicatus P.E. Berry, Kainul. & B.W. van Ee est un petit arbre distinctif connu principalement des forêts Lakato et Vohibe dans la partie sud du corridor Ankeniheny-Zahamena et dans une autre localité à l’est d’Analamazaotra. Croton hypochalibaeus Baill. est rétabli comme nom accepté et est maintenant connu de la zone d’Ambatovy, ainsi que dans plusieurs vestiges de forêts des « tampo ketsa », la végétation du haut plateau central de Madagascar. Il est répertorié aussi dans les canyons du parc national de l’Isalo. Une autre espèce (Croton lasiopyrus Baill.) est identifiée dans la zone de Moramanga pour la première fois, mais n’est pas connue d’Ambatovy. Des descriptions amendées sont fournies pour Croton hypochalibaeus et Croton lasiopyrus et des lectotypes sont désignés.

Keywords
EUPHORBIACEAE – Croton – Madagascar – Ambatovy – Ankeniheny – Zahamena Corridor – Toamasina – Ultramafic soil
Introduction

The Ambatovy mining project is the largest-ever foreign investment in Madagascar, with a total project cost of US $8 billion (Ambatovy, 2016). It is an open-pit operation on ultramafic, lateritic crust deposits in a relatively pristine forested area at around 1000 m elevation, located in the eastern moist forests north of the town of Moramanga in the Alaotra-Mangoro Region, Toamasina Prov. The southern portion of the concession is known as Ambatovy, while the northern part is known as Analamay. The main products of the venture are nickel, cobalt, and ammonium sulphate, and these are transported to the processing site on the coast near Tamatave in a slurry pipeline about 220 km long. Construction on the project began in 2007, and full production was attained in 2014, with an estimated life span extending for 29 years. From the beginning of the project, there has been a concerted effort to study the biotic life span extending for 29 years. From the beginning of the project, there has been a concerted effort to study the biotic features of the area, with the aim of mitigating or offsetting the effects of deforestation of the mining sites. The Missouri Botanical Garden has been the main partner in efforts to collect and document the local flora, and by 2009 their collectors had amassed over 7,700 new herbarium specimens from the Ambatovy-Analamay area (Phillipson et al., 2010). They also tabulated that there are 1,580 higher plant species known from the 7,026 ha area leased by the mining company (2,126 ha in the mine footprint itself plus 4,900 ha of surrounding areas destined for conservation management). This number of species is a remarkable 14% of the total described native vascular plant flora of Madagascar, which was tabulated at around 11,200 species (Callmander et al., 2011). Besides this high species richness in a small area, Phillipson et al. (2010) estimated that 196 of the plant species were “Species of Concern”, meaning that they were known only from the mine concession and no more than three other locations. In a subsequent internal report to the Ambatovy mining company after further inventory effort, the number of Species of Concern was reduced down to 109 (P. Phillipson, pers. comm).

Croton L. (Euphorbiaceae) is one of the three largest woody plant genera in Madagascar, with an estimated 150 species there (Schatz, 2001). In their botanical inventory of the Ambatovy-Analamay mine site, Phillipson et al. (2010) listed 15 species and two additional varieties of Croton (see Table 1). Quite notably, out of these 17 taxa, at the time seven had not been formally described, of which five were technically nomina nuda, based on an unpublished manuscript by the late Alan Radcliffe-Smith.

As part of an ongoing revision of the genus Croton in Madagascar, we have examined closely the available herbarium specimens (primarily at MO, P, and TAN) from Ambatovy-Analamay and surrounding areas such as the Analamazaotra-Mantadia national park complex (which includes the area known as the Perinet or Andasibe forest) to the east, and the southern part of the Ankeniheny-Zahamena forest corridor to the southeast. After making preliminary determinations of the herbarium specimens, we made a site visit to the Ambatovy-Analamay mining concession in March of 2016, aiming to confirm the presence and extent of both the previously described and the new species of Croton in the area. We also visited both Analamazaotra and Mantadia National Parks, and we collected along the road from Andasibe to Lakato. This paper presents the results of our work on Croton from the Ambatovy-Analamay mine and nearby areas, further confirming that the area harbours a diverse array of species and a number of local endemics.

Compared to Phillipson et al. (2010), we now recognize 13 (vs. 15) species from the mining area itself, with four species newly described here (Table 1). We also provide amended descriptions and designate lectotypes for the poorly known Croton hypochalibaeus Baill. and C. lasiopyrus Baill., which were previously not recognized from this area. Lastly, we add five more species from the adjacent areas of Andasibe, Lakato, and the offset area of Ankerana, with three of these also newly described in this article. Throughout the following descriptions we refer to the elements of the indumentum as trichomes, following Webster et al. (1966), although technically they may actually represent subepidermal emergences (see Vitarelli et al., 2016).

Since the Missouri Botanical Garden staff in Madagascar is currently engaged in making Red List assessments of the Species of Concern present in the Ambatovy mining concession area, we will refrain from making our own conservation assessments in this paper.

Systematics

New species

Croton ankeranae Kainul., spec. nova (Fig. 1C, 2).


Croton ankeranae Kainul. can be distinguished from the similar small-leaved shrub Croton indrisilvae Kainul., B.W. van Ee & P.E. Berry by its taller habit (to 12 m vs. <1 m) and smaller leaves (4.5–10.5 × 3.9–6.3 mm vs. 9–28 × 5–12 mm) that are entire (vs. crenate) with the apex acute to obtuse (vs. obtuse to rounded).
Table 1. – Comparison of Croton L. taxa from the Ambatovy mining area between the PHILLIPSON et al. (2010) floristic survey of the Ambatovy-Analamay mine site and the present study.

<table>
<thead>
<tr>
<th>PHILLIPSON et al. (2010) report</th>
<th>This study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Croton alceicornu Radcl.-Sm. [ined.]</td>
<td>Included under Croton hypochalibaeus Baill.</td>
</tr>
<tr>
<td>Croton droguedioides Radcl.-Sm. [ined.]</td>
<td>Croton droguedioides Kainul. &amp; Radcl.-Sm.</td>
</tr>
<tr>
<td>Croton hovarum Leandri</td>
<td>Incorrect determinations, one is C. macrobuxus Baill., another is C. hypochalibaeus Baill.</td>
</tr>
<tr>
<td>Croton humbertii Leandri</td>
<td>Croton humbertii Leandri</td>
</tr>
<tr>
<td>Croton jennyanus Gris. ex Baill.</td>
<td>Incorrect determinations, now Croton hypochalibaeus Baill.</td>
</tr>
<tr>
<td>Croton lepidotoides Radcl.-Sm. [ined.]</td>
<td>Croton ferricretus Kainul., B.W. van Ee &amp; P.E. Berry</td>
</tr>
<tr>
<td>Croton lichenisilvae Leandri</td>
<td>Croton lichenisilvae Leandri</td>
</tr>
<tr>
<td>Croton macrobuxus Baill. (var. uncertain)</td>
<td>Croton macrobuxus Baill.</td>
</tr>
<tr>
<td>Croton macrobuxus var. glandulifer Radcl.-Sm. [ined.]</td>
<td>Not recognized here; it is insufficiently distinct from other populations of Croton macrobuxus Baill.</td>
</tr>
<tr>
<td>Croton nitidulus Baker</td>
<td>Croton nitidulus Baker</td>
</tr>
<tr>
<td>Croton nitidulus var. cinereum Radcl.-Sm. [ined.]</td>
<td>Not recognized here; the specimen cited as the type (in sched.) is Croton submetallicus Baill.</td>
</tr>
<tr>
<td>Croton noronhae Baill.</td>
<td>Incorrect determination, now Croton hypochalibaeus Baill.</td>
</tr>
<tr>
<td>Croton sp. nov. A aff. C. nitidulus Baker</td>
<td>We are not sure what this refers to</td>
</tr>
<tr>
<td>Croton submetallicus Baill.</td>
<td>Croton submetallicus Baill.</td>
</tr>
<tr>
<td>Croton thouarsianus Baill.</td>
<td>Incorrect determination, this may correspond to Croton lasiopyrus Baill.</td>
</tr>
<tr>
<td>Croton trichotomus Geisel.</td>
<td>Incorrect determination, now Croton macrobuxus Baill. or C. nitidulus Baker</td>
</tr>
<tr>
<td>[not previously recognized in the mine area]</td>
<td>Croton catatii Baill.</td>
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<tr>
<td>[not previously recognized in the mine area]</td>
<td>Croton enigmaticus P.E. Berry &amp; B.W. van Ee</td>
</tr>
<tr>
<td>[not previously recognized in the mine area]</td>
<td>Croton lasiopyrus Baill.</td>
</tr>
<tr>
<td>[not previously recognized in the mine area]</td>
<td>Croton radiatus P.E. Berry &amp; Kainul.</td>
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<tr>
<td>[near mine along pipeline, possibly planted]</td>
<td>Croton mongue Baill.</td>
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<tr>
<td>[outside the mining footprint in offset area]</td>
<td>Croton ankeranae Kainul.</td>
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<tr>
<td>[outside the mining footprint, in Analamazaotra National Park]</td>
<td>Croton indrisilvae Kainul., B.W. van Ee &amp; P.E. Berry</td>
</tr>
<tr>
<td>[outside the mining footprint, near Andasibe and on Andasibe-Lakato road]</td>
<td>Croton plurispicatus P.E. Berry, Kainul. &amp; B.W. van Ee</td>
</tr>
<tr>
<td>[outside the mining footprint, in Mandraka area and along road to Lakato]</td>
<td>Croton goudoti Baill.</td>
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<tr>
<td>[outside the mining footprint, in Mandraka area and Mantadia National Park]</td>
<td>Croton myraster Baker</td>
</tr>
<tr>
<td>15 species and 2 varieties in mine area</td>
<td>13 species in mine area, 18 overall</td>
</tr>
</tbody>
</table>
Shrubs to small trees 0.8-12 m tall, dichotomously branching, internodes sometimes contracted giving the appearance of whorled branches. Branches ± flattened on new growth and densely covered by dark gray-brown fasciculate trichomes with rays c. 0.2 mm long, pale gray to whitish, becoming terete and glabrous with age. Stipules absent or vestigial. Leaves sub-opposite, ± congested at nodes. Petioles 0.7-1.8 mm, adaxially canaliculate, sometimes with a pair of acropetolar, stipitate (0.2-0.4 mm long), discoid (c. 1.5 mm diam.) glands. Leaf blades thinly coriaceous, entire, (broadly) elliptic to obovate, 4.5-10.5 × 3.9-6.3 mm, apex acute-obtuse, base cuneate; adaxial surface glabrous, glossy, dark green when fresh and drying dark green; secondary venation indistinct; abaxial surface sparsely fasciculate, pale green when fresh and drying pale brown; secondary venation indistinct, midrib prominent. Inflorescences comprising 1-2 staminate flowers or a solitary pistillate flower, axillary or terminal; bracts triangular, c. 3.0 × 0.2 mm. Staminate flowers with fasciculate, subglobose buds c. 0.9 mm diam., pedicels to 1.5 mm long; sepals 5, shortly connate at base, lobes triangular to ovate, c. 0.7 × 0.3 mm, apex acute, inflexed at anthesis, abaxially fasciculate, adaxially glabrous, margins densely ciliate, pale green; petals 5, white, narrowly obovate to spatulate, c. 1.0 × 0.2 mm, recurved at anthesis, abaxially sparsely papillate, adaxially glabrous, margins densely ciliate; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoid, c. 0.1 × 0.05 mm; stamens 3-5, white, filaments c. 1.5 mm long, ciliate, anthers broadly ellip-tic, c. 0.2 mm long; receptacle pilose. Pistillate flowers with fasciculate-pubescent buds c. 0.9 mm diam., pedicels 0.5-0.9 mm long; sepals 5, elliptic, spreading at anthesis, 1.2 × 0.6 mm, apex rounded, abaxially stellate-pubescent, abaxially sparsely fasciculate, pale green; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoid, c. 0.3 × 0.2 mm; glandular filaments (in petal position alternating with the nectary lobes) 5, linear, c. 0.5 × 0.07 mm, erect; ovary globose, c. 0.8 mm diam., densely stellate, styles 3, c. 2.5 mm long, bifurcate, spreading, recurved at the apices, with some fasciculate trichomes and a few pilose trichomes at the base, white, turning brown, persistent. Capsules 3-4 × 6.7 mm, smooth, with fasciculate trichomes; columella 2.8-3.5 mm long, cornute, capitulate. Seeds not seen.

Etymology. – The specific epithet refers to the Ankerana forest where this species is found.

Distribution, Habitat and Ecology. – Croton ankeranae is to date only known from the Ankerana-Vohimanana montane forest in the Antsiranana Region of Toamasina Prov., at 400-1050 m elevation (Fig. 1C).

Notes. – This species is probably most closely related to C. indrisivae Kainul., B.W. van Ee & P.E. Berry described below, which has similar whitish stems with brown-fasciculate pubescence, small leaves with indistinct venation, and reduced inflorescences. However, both the leaves and flowers of C. ankeranae are smaller and among the smallest of any Malagasy Croton, and the staminate flowers have only 3 to 5 stamens.


Croton droguetioides Kainul. & Radcl.-Sm., spec. nova (Fig. 1B, 3-4).

Typus: MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Disttr., Andasibe, Berano, Ambatovy mine concession, 18°47’59”S 48°20’31”E, 1009 m, 22.III.2016, van Ee, Antilahimena, Kainulainen & Berry 2447 (holo: MICH [MICH1513195]!, iso: MO!, P!, TAN!).

Croton droguetioides Kainul. & Radcl.-Sm. is similar to C. incisus Baill, but differs in its smaller leaves with serrate (vs. incised to lobed) leaf margin; distinct abaxial venation; apiculate (vs. acute) apex; and rounded to cordate (vs. cuneate) leaf base.

Shrubs or small trees, 0.8-7.0 m tall, to 6 cm diam., dichotomously branching, internodes sometimes contracted giving the appearance of whorled branches. Branches ± flattened on young growth and densely covered by villous white-gray stellate trichomes, gray, becoming terete and glabrous with age. Stipules linear, 1.1-1.6 mm. Leaves alternate, ± congested and whorled towards the branch tips and nodes. Petioles 3-15 mm, with a pair of stipitate glands at the junction of the blade and the petiole, usually on the abaxial side, the stipe 0.4-1.9 mm long, the glandular portion cupular. Leaf blades papyraceous, serrate, ovate to elliptic, 10-28 × 7-16 mm, apex apiculate, base rounded-cordate; adaxial surface sparsely stellate-pubescent or glabrescent, glossy, dark green when fresh and drying matte (brownish) green; with 3-6 pairs of brochidodromus, ± penninerved secondary veins; abaxial surface sparsely stellate-pubescent, mostly on the midrib; pale green, venation distinct and midrib prominent. Inflorescences racemose (often apically congested and umbel-like), to 20 mm long, axillary or terminal, with mostly staminate flowers, sometimes with a pistillate flower at the base; axes densely stellate-pubescent, flattened; bracts linear to lanceolate, 1.7-2.2 mm.
Fig. 1. – Distribution maps. The grey squares or white arrow on the inset maps of Madagascar show the location of the area depicted. **A.** Croton ferricretus Kainul., B.W. van Ee & P.E. Berry (red); **B.** Distribution of Croton droguetioides Kainul. & Radcl.-Sm. (turquoise) (Cours 4111 not shown), C. enigmaticus P.E. Berry & B.W. van Ee (light green) (Ratimanana et al. 1402 not shown), C. indrisilvae Kainul., B.W. van Ee & P.E. Berry (yellow), and C. plurispicatus P.E. Berry, Kainul. & B.W. van Ee (light purple); **C.** Croton ankeranae Kainul. (yellow), C. radiatus P.E. Berry & Kainul. (red), and Croton lasiopyrus Baill. (white). The collection in grey represents presumed hybrids between C. lasiopyrus and C. enigmaticus (van Ee et al. 2215 and 2216); **D.** Croton hypochalibaeus Baill. in Madagascar. [Google Earth Image © 2016 DigitalGlobe. Reproduced per attribution guidelines]
Staminate flowers with stellate-pubescent, subglobose buds 1.0-1.2 mm diam., pedicels elongating from bud to anthesis, 2.0-4.2 mm long; sepals 5, shortly connate at base, lobes broadly triangular-ovate, 0.9-1.2 × 0.8-1.0 mm, apex acute, abaxially stellate-pubescent, adaxially sparsely ciliate, margins densely ciliate, pale green; petals 5, white, narrowly obovate; stipules, 1.4-1.7 × 0.5-0.6 mm, recurved at anthesis, abaxially papillate, adaxially ciliate, margins densely ciliate; disc glands 5, opposite the sepals, sessile, ellipsoid with an apical depression, c. 0.4 × 0.3 mm, yellow; staminodes 13-16, white to pale yellow, filaments 1.3-1.8 mm long, ciliate, anthers elliptic, 0.3-0.5 mm long; receptacle pilose. Pistillate flowers with stellate-pubescent, subglobose buds c. 1.3 mm diam., pedicels 2.6-3.5 mm long; sepals 5, elliptic, spreading at anthesis, 2.0-3.8 × 0.7-1.5 mm, adaxially ciliate, margins densely ciliate, petals 5, white, narrowly obovate-spatulate, 4.2 mm long.

Leaves with a rounded to cordate base and distinct abaxial venation. In his unpublished manuscript on Malagasy Croton, Alan Radcliffe-Smith had selected *Cours 4111* as the type collection for another proposed species (“C. parietarioides”), but we see no significant differences in it from the other specimens of *C. droguedioides* listed here.

Paratypes. – MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Dist., Ambatovy-Analamay forest, 18°48’55”S 48°18’21”E, 1086 m, 18.V.2011, Andriamarinaivo 211 (MO, P, TAN); ibid. loc., 18°47’51”S 48°20’33”E, 1036 m, 11.X.2005, Antilahimena et al. 3953 (MO, P, TAN); ibid. loc., 18°49’56”S 48°18’47”E, 1200 m, 12.X.2005, Antilahimena & Edmond 4017 (G, MO, P, TAN); ibid. loc., 18°51’36”S 48°17’29”E, 1059 m, 21.X.2005, Antilahimena & Edmond 4006 (MO, P, TAN); ibid. loc., 18°50’22”S 48°18’47”E, 1142 m, 24.I.2007, Antilahimena 5206 (G, MO, P, TAN); ibid. loc., 18°51’04”S 48°17’23”E, 1059 m, 9.II.2007, Antilahimena 5253 (MO, P, TAN); ibid. loc., 18°48’49”S 48°18’32”E, 1074 m, 5.III.2009, Antilahimena et al. 6998 (MO, P, TAN); Andasibe, Ampangalatsara, Ambimbodimiky forest, 18°59’07”S 48°25’53”E, 966 m, 17.III.2012, Antilahimena 8228 (MICH, MO, P, TAN).}

Etymology. – The specific epithet refers to the similarity of the leaves of this species to those of species of *Droguetia* Gaudich. (Urticaceae).

Vernacular name. – “Hazomby”.

Phenology. – We have seen flowering and fruiting specimens from January to May and from October. It is likely this species flowers more or less continuously throughout the year, although possibly less so in the drier months of the year.

Distribution, habitat and ecology. – Besides the Ambatovy-Analamay forests, *C. droguedioides* is also found in the Mantadia forests, in the Ambimbodimiky forest (S of Route Nationale 2 near the Hotel Edrophiella); and at a more distant site north of Didy at Ambatoharanana (near Antsabe); all are in the Alaotra-Mangoro Region of Toamasina Prov., at elevations of 975-1200 m (Fig. 1B). The species occurs in the understory of evergreen montane forests.

Notes. – *Croton droguedioides* can be readily distinguished from other small-leaved species of Malagasy *Croton* by its stems with pale, woolly and stellate trichomes, and its serrate leaves with a rounded to cordate base and distinct abaxial venation. In his unpublished manuscript on Malagasy Croton, Alan Radcliffe-Smith had selected *Cours 4111* as the type collection for another proposed species (“C. parietarioides”), but we see no significant differences in it from the other specimens of *C. droguedioides* listed here.
Fig. 2. – Croton ankeranze Kainul. A. Flowering branch with two staminate flowers; B. Staminate flower; C. Pistillate flower. Note bifurcate stigmas and greenish sepals; D. Branch with nearly mature capsule; E. Staminate flower; F. Staminate flower with stamens removed to show the five nectaries; G. Pistillate flower, showing bifurcate stigmas and filamentous structure in the position of petals; H. Pistillate flower with ovary and two sepals removed to show the five nectaries. Note the glandular filament in the petal position.

[A-C-H: Antilahimena 7554; B: Ravelonarivo & Edmond 4082] [Photos: A, C-D: P. Antilahimena; B: D. Ravelonarivo]
Subshrubs to shrubs 0.3–2 m tall or occasionally lianescents 3–4 m tall, often with a profusion of adventitious roots in the leaf litter layer (Fig. 6B). Stems, leaves, and inflorescence rachis densely pubescent, with stellate-lipidiate trichomes having a stiff, porrect, whitish central ray 2–3 mm long, the basal portion of the trichomes brown to coppery. Stipules lanceolate to falcate, often somewhat recurved, 5–10 mm × 2–4 mm, light green, foliaceous, caducous, or sometimes seemingly absent. Leaves alternate at the base of stems, but becoming more congested near the tips and then becoming opposite or whorled, persistent, varying from patent to often ± drooping from the stems; petioles 6–15(-20) mm long, hispid, with a pair of laterally divergent, stipitate glands at the apex, each 2–3.5 mm long, with a glandular, knobby tip. Leaf blades papyraceous-membranous, (broadly) ovate to elliptic, 5–9(-12) × 2.5–6 cm, apex acuminate, base rounded, venation brochidodromous with 6–7 pairs of secondary veins, these ± impressed on upper surface, margins dentate-serrate, both surfaces and margins densely hispid. Inflorescences terminal, erect to drooping when elongate, 1-8(-14) cm long (very variable from plant to plant), unisexual or bisexual, with or without conspicuous light green to brown bracts resembling the stipules; pistillate flowers from 1–10 numerous in proximal portion, stationed flowers distal and in single or in few-flowered cymes of varying pedicel lengths, the pedicels of both sexes usually ± divergent (perpendicular) from the rachis. Staminate flowers with hispid, globose buds 2–3 mm in diam., pedicels usually variable in length on same inflorescence, 1–5(-8) mm long; sepals 5, valvate, c. 3 × 1.5 mm, triangular, inflexed at anthesis; petals 5, ligulate, white, pubescent, c. 2 × 1 mm, slightly recurved at anthesis; stamens 15–20, white to pale yellow, filaments 2.5–3.5 mm long, ciliate, anthers elliptic, c. 0.8 mm long. Pistillate flowers with hispid pedicels 3–8(-15) mm long; sepals usually 5 but up to 7–9 on some flowers, imbricate, somewhat unequal in size, 8–10(-15) × 3–5 mm, narrowly triangular to elliptic-lanceolate, acuminate, foliaceous and green on both sides, the midvein and two additional lateral veins visible, hispid on both sides and along margins, persistent in fruit; glandular filaments (in petal position alternating with the sepals) 5, c. 1 mm long (Fig. 5G); ovary hispid, green, with scattered coppery-based scales, globose-ellipsoid, c. 3 mm diam., styles 3, each bifurcating 2–3 times near the base with a total of c. 24 stigmatic tips, curved when young, creamy-white, turning coppery-brown, patent. Capsules ellipsoid to subglobose, greenish, densely hispid, c. 10 mm diam.; columella c. 7 mm long, with a fimbriate tip. Seeds ± compressed-ellipsoid (Fig. 7J), c. 5.5 × 4.0 × 2.5 mm, covered by a thin, translucent-white, fleshy coating when fresh; testa glossy, rugulose, dark brown; caruncle reniform, white when fresh, c. 1.0 mm wide, 0.7 mm long.

Etymology. – The specific epithet refers to the enigmatic nature of the species, showing at times unusual characters such as foliaceous, curved stipules, prominent bract-like pistillate calyces, elongate inflorescences, markedly serrate leaves, and mats of adventitious rootlets in the leaf litter, but other times the inflorescences are short, the stipules absent, and the leaf margins are subentire. Individuals of this species can either appear to be nearly herbaceous, scraggily shrubs, or even lianas.

Phenology. – From the four sets of specimens available, C. enigmaticus is known to flower and fruit in January, June, August, and October, so it appears to be quite aseasonal in its phenology.

Distribution, habitat and ecology. – Croton enigmaticus is known from just two sites in the mountains of Moramanga Distri. in the Alaotra-Mangoro Region of Toamasina Prov. (Fig. 1B) and from the Tsarahanonena forest near Didy, at elevations of 950–1075 m. One of these sites is in the Ambatovy mine area, the second is about 15 km due south in a similarly forested region, and the Didy collection is considerably farther north. In the two Moramanga Distri. sites, C. enigmaticus grows in the understory or along road cuts of dense, montane evergreen forest, often together with lianescent bamboos prevalent in the understory.

Notes. – This species is remarkable for its densely hispid pubescence and variable-sized inflorescences, which can be very congested or quite elongate. It also has unusual foliaceous stipules and bracts, however, these may be lacking (or early caducous?) on some plants. Finally, it shows extensive local vegetative reproduction by proliferous production of adventitious roots in the litter layer. It co-occurs with plants that are included here under C. lasiopyrus Baill., but they have intermediate traits that indicate they may be hybrids between these two species.

Paratypes. – MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Distri., Andasibe, Ambatovy, Analantrongy, 18°55′13″S 48°20′26″E, 997 m, 9.VI.2009, Antahibjena et al. 7106 (MICH, MO, P, TAN); ibid. loc., Antahibjena et al. 7107 (MICH, MO, P, TAN); Ambatovy, 18°55′13″S 48°20′49″E, 1075 m, 9.X.2007, Bernard & Phillips 605 (MICH, MO, P, TAN); Ambatondrazaka Distri., Didy, Tsarahanonena forest, 4.3 km NE from Didy, 18°05′05″S 48°34′17″E, 15.I.2010, Ralimananana et al. 1402 (BR, G, K, MO, TAN); Moramanga Distri., dirt road N of Route Nationale 2 past village of Savahoana, 18°55′28″S 48°20′57″E, 972-989 m, 14.VIII.2015, van Es et al. 2209 (MICH, MO, P, TAN); ibid. loc., van Es et al. 2210 (MICH, MO, P, TAN); ibid. loc., van Es et al. 2211 (MICH, MO, P, TAN); ibid. loc., van Es et al. 2212 (MICH, MO, P, TAN); ibid. loc., van Es et al. 2213 (MICH, MO, P, TAN).
Fig. 3. – Croton droguetioides Kainul. & Radcl.-Sm. A. Habit and habitat in rainforest; B. Flowering branch with staminate flowers; C. Underside of branch showing the stipitate glands, the sparsely stellate-pubescent leaves and the villous petioles and stem; D. Inflorescence with staminate flowers and buds; E. Inflorescence with pistillate flower; F. Immature fruit.

[Photos: A: K. Kainulainen; B-F: P. Berry]
**Croton ferricretus** Kainul., B.W. van Ee & P.E. Berry, spec. nova (Fig. 1A, 5H-M, 7A-B, 8).

**Typus**: MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Distr., Andasibe, Berano, Ambatovy mine concession, on “cuirasse” between the workers houses and the Ambatovy supply road, within sight of the Ambatovy office building, 18°51’02"S 48°18’29"E, 1142 m, 21.III.2016, van Ee, Antlibinena, Kainulainen & Berry 2436 (holo- MICH [MICH1513194]); iso- : Gl, K!, MAPR!, MO!, P!, TAN!).

**Croton ferricretus** Kainul., B.W. van Ee & P.E. Berry is similar to *C. antanosiensis* Leandri in its medium-sized, lepidote leaves and elongate inflorescences, but differs from it in the more ferrugineous indumentum (vs. silvery), shorter petioles, and obloid (vs. globose) capsules.

**Shrubs** 0.4–4 m tall, dichotomously branching, internodes sometimes contracted giving the appearance of whorled branches. **Branches** ± flattened on new growth and densely ferrugineous-lepidote, brown or gray, becoming terete and glabrous with age. **Stipules** linear-triangular, 0.5–1 mm. **Leaves** alternate along stem, subopposite or whorled at apex. Petioles 3–17(-28) mm, adaxially canalicular, without any apparent glands. Leaf blades subcoriaceous, entire, elliptic, 18–85 × 9–28 mm, apex acute to shortly acuminate (rarely obtuse), base cuneate; adaxial surface glabrous, glossy, dark green when fresh (turning orange in old leaves) and drying gray-green; venation impressed, obscure, with 10–20 pairs of brochidodromus, × penninerved secondary veins; abaxial surface densely silvery-lepidote and ferrugineous-punctate, the ferrugineous scales scattered among silvery ones, but more prevalent on the leaf veins; midrib prominent, ferrugineous-lepidote. **Inflorescences** racemose, 20–85 mm long, axillary or terminal, with mostly stamine flowers, usually with 1–2(5) pistillate flowers at the base; axes densely ferrugineous-lepidote, flattened; bracts linear-lanceolate, 1–3 mm long. **Staminate flowers** with ferrugineous-lepidote, subglobose buds 1.5–2.5 mm in diam., pedicels elongating from bud to anthesis, 2–5 mm long; sepals 5, firm, connate about halfway from the base, becoming broadly triangular to ovate, 1.0–1.4 × 0.8–1.7 mm, apex acute, inflexed at anthesis, abaxially ferrugineous-lepidote, adaxially glabrous, pale green; petals 5, white, narrowly obovate-spatalate, 1.8–2.5 × 0.5–1.1 mm, recurved at anthesis, abaxially lepidote, adaxially ciliate, margins densely ciliate; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoid with an apical depression, 0.6–0.8 × 0.5–0.7 mm, yellow; stamens 14–19, white to pale yellow, filaments 1–2 mm long, ciliate, anthers elliptic, 0.5–0.7 mm long; receptacle pilose. **Pistillate flowers** with ferrugineous-lepidote, elliptic buds 2.8–3.0 × 1.7–2.5 mm, pedicels 1–8 mm long; sepals 5, firm, narrowly triangular, ascending at anthesis, 1.8–5.3 × 0.5–1.3 mm, apex acute, shortly connate at base, abaxially ferrugineous-lepidote, adaxially glabrous, pale green, persistent in fruit; petals absent/reduced; disc glands/nectaries 5, opposite the sepals, sessile, pentagonal, 0.8–1.0 × 0.6–0.8 mm, yellow; ovary obloid, 2.0–2.5 mm diam., lepidote, styles 3, c. 3 mm long, each bifurcating twice (or ultimately thrice), spreading, recurved at the apices, abaxially ferrugineous-lepidote, adaxially glabrous but with yellowish pilose trichomes at the base, white, turning brown, persistent. **Capsules** 4.5–9.0 × 3.5–6.0 mm, smooth, gray-green, lepidote, exocarp not separating, endocarp woody, c. 0.2 mm thick; columella 4–6 mm long, corunate, capitate. **Seeds** ± compressed-ellipsoid, c. 5 × 3 × 2 mm; testa glossy, rugulose, punctate, dark brown; caruncle reniform c. 1.3 × 0.5 mm.

**Etymology.** – The specific epithet refers to the ultramafic ferricrete soils to which this species is restricted.

**Vernacular names.** – “Fotsiavadika”, “Lazalaaza”.

**Phenology.** – Flowering and fruiting specimens have been collected from May through March, indicating that *Croton ferricretus* is quite aseasonal in its phenology.

**Distribution, habitat and ecology.** – *Croton ferricretus* is so far only known from the Ambatovy-Analamay forest in Madagascar’s Moramanga Distr., occurring at 1000–1150 m altitude on ultramafic ferricrete soils (Fig. 1A, 8A). It is a common and sometimes dominant component of the scrublands found on the most extreme rock-like crusts, and it also occurs in adjacent evergreen forests with better-developed soils. When growing on bare ferricrete (“cuirasse”), *C. ferricretus* does not occur with other species of *Croton*, but in forested areas it can be found growing alongside *C. lepidotoides* (Fig. 2B-C). Other species that have these characteristics tend to have glomerulate inflorescences in the leaf axils, such as *C. jennyanus* Gris ex Baill. and *C. hypochalibaeus* Baill., rather than racemose inflorescences (Fig. 8D-F). It resembles *C. antanosiensis* Leandri from southeastern Madagascar, but differs in its much more coppery-lepidote indumentum, shorter petioles, and more obloid capsules (Fig. 7A).

**Notes.** – *Croton ferricretus* was recognized in the inventory of the Ambatovy-Analamay forest by PHILLIPSON et al. (2010) under the working name “Croton lepidotoides” (ined. by the late Radcliffe-Smith), and considered a species of concern (SOC2, i.e., found only in the area of the mining footprint and the surrounding conservation zone). This is a very distinctive species among Malagasy *Crotons* that have small– medium-small leaves with coppery-lepidote indumentum (Fig. 8B-C). Other species that have these characteristics tend to have glomerulate inflorescences in the leaf axils, such as *C. jennyanus* Gris ex Baill. and *C. hypochalibaeus* Baill., rather than racemose inflorescences (Fig. 8D-F). It resembles *C. antanosiensis* Leandri from southeastern Madagascar, but differs in its much more coppery-lepidote indumentum, shorter petioles, and more obloid capsules (Fig. 7A).
Since this is a locally common species that is capable of growing on bare, ferricrete substrates, we believe that it may be an excellent candidate for revegetation efforts once the mining operations at Ambatovy-Analamay have ceased. Its shrubby habit would enable it to reproduce more quickly than tree species, and it could help stabilize slopes in previously mined areas.


**Croton indrisilvae** Kainul., B.W. van Ee & P.E. Berry, spec. nova (Fig. 1B, 7G–H, 9).

**Typus**: MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Distr., Analamazaotra National Park, on trail to the east of the visitor center, 18°56′45″S 48°25′33″E, 975 m, 11.VIII.2015, *van Es, Berry & Razafindraive 2175 (holo.– MICH [MICH1513201]); iso.– G, MO, TAN).

Croton indrisilvae Kainul., B.W. van Ee & P.E. Berry is distinguished from *C. droguetioides* Kainul. & Radl. – 5m by its whiteish branches with brown, fasciculate trichomes (vs. gray branches with villous, whitish trichomes); obovate crenate leaves with obtuse to rounded apex and cuneate base (vs. ovate dentate leaves with apiculate apex and rounded to cordate base); the absence of stipitate petiolar glands; and the lower number of stigma lobes (6 vs. >30). It is sometimes confused with *Croton incisus* Baill. but is differentiated by its crenate leaves (vs. incised to lobed) with obtuse to rounded (vs. acute) apex and the absence of stipitate petiolar glands.

**Shrubs**: 0.3–0.8 m tall, dichotomously branching, internodes sometimes contracted giving the appearance of whorled branches. Branches ± flattened on new growth and densely covered by dark reddish-brown, fasciculate trichomes with rays c. 0.5 mm long, pale gray-whitish, becoming terete and glabrous with age. Stipules absent or vestigial. Leaves whorled at apex and nodes. Petioles 1–3 mm long, adaxially canaliculate, without any apparent glands. Leaf blades thinly coriaceous, slightly revolute, crenate towards apex, obovate, 9.8–× 5.12 mm, apex obtuse to rounded or emarginate, base cuneate; adaxial surface glabrous, glossy, dark green; secondarily venation indistinct, with 2–5 pairs of brochidodromus, ± penninerved secondary veins, midrib prominent except near apex; abaxial surface sparsely covered with a mixture of white and brown fasciculate trichomes, glossy, pale green when fresh and drying gray-green; venation ± indistinct except for the midrib. *Inflorescences* racemose, reduced, to 3 mm long, terminal or axillary, bracts linear to lanceolate, 0.5–1.0 mm. *Staminate flowers* with stellate-pubescent, subglobose buds c. 1.1 mm diam., pedicels c. 1.0 mm long; sepals 5, shortly connate at base, lobes triangular to ovate, c. 0.9 × 0.7 mm, apex acute, inflexed at anthesis, abaxially stellate-pubescent, adaxially glabrous, margins ciliate; petals 5, narrowly obovate to spatulate, c. 1.2 × 0.4 mm, revurred at anthesis, abaxially sparsely papillate, adaxially glabrous, margins ciliate; disc glands/nectaries 5, opposite the sepals, sessile, triangular, c. 0.2 × 0.1 mm; stamens c. 5, filaments c. 1.3 mm long, ciliate, anthers broadly elliptic, c. 0.4 mm long; receptacle pilose. *Pistillate flowers* with pedicels 1.5–7.0 mm long; sepals 5, oblong-spatulate, 2.3–3.3 × 0.7–1.5 mm, apex rounded, abaxially stellate, adaxially glabrous, pale green, persistent in fruit; disc glands/nectaries 5, opposite the sepals, sessile, triangular, c. 0.2 × 0.1 mm; testa glossy, rugulose, pale brown; caruncle elliptic, c. 0.6 × 0.2 mm.
Etymology. – The specific epithet refers to the forests where this species grows, which are inhabited by the large, tail-less lemur species, Indri indri Gmelin, 1788.

Distribution, habitat and ecology. – Croton indrisilvae is only known from Analamazaotra in the Alaotra-Mangoro Region at 900-1000 m elevation, where it forms part of the primary montane forest understory (Fig 1B).

Notes. – This is one of several Malagasy Croton shrubs with small leaves (< 30 mm long) from moist montane forests in eastern Madagascar, including C. ambanivoulensis Baill., C. ankeranae, C. inciscus Baill. These species all have pale stems with contrasting dark fasciculate trichomes and leaves with cuneate bases and ± indistinct venation. They are mainly distinguished on the basis of the shape and size of the leaves. Both C. ankeranae and C. indrisilvae have obovate leaves, but the leaves of C. indrisilvae are larger (< 28 × 12 mm vs. < 10.5 × 6.3 mm), somewhat revolute, and crenate (vs. entire). The poorly known (and possibly conspecific) C. indrisilvae and C. inciscus have rhombic leaves that are serrate in the former and incised in the latter. Unlike C. indrisilvae they also have stipitate petiolar glands.

Paratypes. – MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga Dist., Station forestière d’Andasibe (Perinet), 900 m, 8.XII.1989, Evrard 11244 (P, TAN); Analamazaotra, 18°56’14”S 48°25’62”E, 910 m, 20.IV.2010, Rajaomarina 258 (K, P, TAN); Perinet, Rauh 477 (TAN); Analamazaotra, 8.III.1950, Service Forester 715 (K, P); ibid loc., 8.IV.1961, Service Forester 2037 (F); Analamazaotra NP, 18°56’42”S 48°25’28”E, 929 m, 11.VIII.2015, van Ex et al. 2176 (MICH, MO, P, TAN).

**Croton radiatus** P.E. Berry & Kainul., spec. nova (Fig. 1C, 11).


Croton radiatus P.E. Berry & Kainul. is similar to Croton incissus Baill., but differs in its leaves that are entire to shallowly serrulate or undulate (vs incised), and in the foliaceous, glabrous sepals (vs. densely stellate-pubescent). In its tightly clustered, medium-sized leaves that are separated by long internodes it resembles Croton hypochalibaeus Baill., but differs in its sparser pubescence with scattered stellate trichomes on the leaves (vs. densely silvery white-lepidote and brown punctulate leaves).

Shrubs to 0.8-2 m tall, dichotomously or trichotomously branching, with elongate internodes 2-7 cm long separating clusters of opposite or ternate leaves (vs. sessile), which are much denser along the young shoots.

Etymology. – The specific epithet refers to the radiate nature of the prominent trichomes, which are rather sparsely scattered on the abaxial leaf surface but much denser along the young shoots.
The genus Croton (Euphorbiaceae) in the eastern forest corridor of Madagascar

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Phenology. – Of the four known specimens, one was collected in flower in December and the others in April and late July, which indicates the species is probably aseasonal in its flowering.

Distribution, habitat and ecology. – Croton radiatus is known so far from four collections, in dense, humid, montane forests along the eastern escarpment of Madagascar in the Ankeniheny-Zahamena forest corridor in the Alaotra-Mangoro and Analanjirofo Regions of Toamasina Prov., at elevations of 900-1120 m (Fig. 1C).

Notes. – Croton radiatus shows a similar sylleptic growth pattern to other species like C. hypochalibaeus, in which long internodes separate nodes where the leaves are clustered (Fig. 11A, 13A). This may just represent growth spurts stimulated by periodic periods of rains following warmer, dry periods. The new species is distinctive in the ± foliaceous sepals of the pistillate flowers along with the stiffly hirsute ovary.

According to the classification of foliar trichomes in Webster et al. (1996), the larger brownish trichomes of C. radiatus are fasciculate or multiradiate, with the radii ascending rather than in one plane, and they vary from up to 8 radii per trichome (fasciculate) to more than 8 per trichome (radiate). The smaller, interspersed, whitish trichomes are stellate-lepidote with a larger, porrect, and brown central radius (see Fig. 11C-D). Similar, but much shorter trichomes are also characteristic of C. ankeranae and C. indrisilvae.

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**Fig. 5.** – *Croton enigmaticus* P.E. Berry & B.W. van Ee (**A-G**) and *C. ferricretus* Kainul., B.W. van Ee & P.E. Berry (**H-M**). **A.** Side view of staminate flower; **B.** Top view of staminate flower; **C.** Top view of staminate flower with the stamens removed to show the nectaries; **D.** Side view of pistillate flower with one of the sepals removed; **E.** Top view of pistillate flower with one of the sepals removed; **F.** Top view of pistillate with the ovary removed to show the five nectaries; **G.** Close-up of the base of a pistillate flower with the ovary and sepals removed, showing the five glandular filaments in the position of the petals (alternating with the sepals); **H.** Side view of staminate flower; **I.** Top view of staminate flower; **J.** Top view of staminate flower with stamens removed to show the five nectaries; **K.** Side view of pistillate flower. Note basally connate sepals and parallel sides; **L.** Top view of pistillate flower, showing the patent, bifurcating stigmas; **M.** Top view of pistillate flower with ovary removed to show the five nectaries.

[A-G: van Ee et al. 2214; H-M: van Ee et al. 2436]
Croton plurispicatus P.E. Berry, Kainul. & B.W. van Ee, spec. nova (Fig. 1B, 7C-D, 10, 12A-F).

**Typus**: MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region. Moramanga Distr., along road heading S from RN 2 towards Lakato, c. 9.8 km S by line-of-sight from RN 2, 19°03’05”S 48°21’32”E, 1030-1060 m, 13.VIII.2015, van Ee, Berry & Razafindraibe 2198 (holo: MICH [MICH1513198]); isotype: G!, MAPR!, MO!, MICH [MICH1513199], P!, TAN!.

**Description**

**Croton plurispicatus P.E. Berry, Kainul. & B.W. van Ee is similar in pubescence and habit to Croton chrysodaphne Baill. and C. submetallicus Baill., but differs in its smaller flowers grouped in multiple, axillary, spicate thyrses along the distal nodes of the fertile stems.**

**Shrubs** or small **trees** to 8 m tall, to 7 cm diam. at base, densely branched with sharply ascending branches producing copious red sap when cut. **Branches** ± flattened on new growth, ridged and furrowed, densely covered by overlapping, coppery-ferrugineous lepidote trichomes. **Stipules** absent or vestigial. **Leaves** alternate, ± congested towards the branch tips. **Petioles** 1.0–2.5(–4.0) cm long, adaxially canaliculate. Leaf **blades** subcoriaceous, elliptic to narrowly elliptic-ob lanceolate, 3–5 × 5–15 cm (to 6 × 20 cm on vigorous basal branches), apex obtuse to broadly acute or rounded, base acute to cuneate, margin entire, with a pair of prominent globose glands 0.6–1 mm diam. at the junction of the blade and petiole, usually on the abaxial side, the top of the gland generally with a narrow hollowed opening, sometimes with a second or a third pair of similar but smaller glands on the edge of the blade shortly above the base; venation brochidodromous, with 9–11 pairs of secondary veins, barely noticeable on adaxial side but more visible and subprominent on abaxial side, adaxially coppery-lepidote (young leaves densely coppery-lepidote, but as the leaf expands the scales become more sparse and the underlying green cuticle becomes visible), abaxially silvery-white-lepidote with ± evenly dispersed brown lepidote trichomes, the midvein raised and prominent on abaxial side, with more coppery-lepidote trichomes than rest of blade. **Inflorescences** spicate–thyrsoid, ascending, 3–8(–9) cm long, axillary with up to 12 in successive leaf axils on a single branch, the rachis slightly flattened or ridged, sometimes entirely stamine or else with 1–3 basal pistillate flowers followed by many cymes of staminate flowers in the distal portion. **Staminate flowers** with densely coppery-lepidote, orbicular buds c. 2 mm diam., pedicels 1–3(–4) mm long at anthesis; sepals 5, valvate, deltate, c. 1.5 × 1.5 mm, inflexed at anthesis, abaxially coppery-lepidote; petals 5, ligulate, c. 1.2 × 1.5 mm, recurved at anthesis, abaxially coppery-lepidote, adaxially glabrous, margins densely crispate-villous; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoid, c. 0.8 × 0.4 mm, yellow; stamens 15–25, white to pale yellow, filaments 1.5–2 mm long, densely villous towards the base and on the receptacle, anthers oblong, c. 0.5 mm long. **Pistillate flowers** with short pedicels 0.5–1.5 mm long, with a narrowly lanceolate bracteole c. 0.2 × 1.0 mm at base, sepals 5, valvate, narrowly triangular, patent at anthesis, abaxially coppery-lepidote, adaxially pale-greenish lepidote with coppery dots, dorsally ridged, 1.5–2.0 × 3.0–4.0 mm; petals absent; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoid, c. 0.6 × 0.4 mm, yellow; ovary densely coppery-lepidote, globose, 2.5 mm diam.; styles 3, to 3 mm long, up to five times bifurcate with numerous stigmatic tips, pale greenish–cream on upper surface, patent at anthesis. **Capsules** (Fig. 7C) densely coppery-lepidote, globose, 7–8 mm diam.; columella 5–6 mm long, cornute, fimbriate. **Seeds** (Fig. 7D) dark grey or brown, lenticular, 4–6 × 3–4 mm, caruncle c. 0.5 × 1.0 mm, with a conspicuous raphe on ventral side below the caruncle.

**Etymology.** – The specific epithet refers to the multiple, spike-like inflorescences that are clustered along the flowering branches of this species.

**Phenology.** – So far, this species has been found in flower and fruit in February, March, May, June, and August, so it is likely that it flowers fairly continuously throughout the year.

**Distribution, habitat and ecology.** – Croton plurispicatus is known from a relatively restricted area of primary montane moist forest from adjoining areas of the Alaotra-Mangoro and Atsinanana regions of Toamasina Prov., at elevations of 600–1100 m (Fig. 1B). So far it has mainly been found south of Andasibe (principally along the road to Lakato), but it has also been collected in a locality north of Route Nationale 2 near the southeastern corner of Mantadia National Park. Along the Lakato road, it grows in association with the more common and widespread C. submetallicus.

**Notes.** – Within Malagasy Croton, C. plurispicatus belongs to a diverse group of species that have in common large penninerved leaves with a dense covering of coppery- or silvery-lepidote trichomes on the underside. Leandrī (1972) published a note about this group in which he recognized seven species from Madagascar and one from the Comoro Islands. Berry et al. (2011) clarified the tangled history of one of these, C. chrysodaphne Baill., and Berry & van Ee (2011) established C. multicostatus Müll. Arg. as the correct name for another member of this group. Nonetheless, there are quite a few other specimens from various parts of the island that fall into this morphological group that still remain unidentified, often because they lack sufficient flowering or fruiting material.
Fig. 6. – Croton enigmaticus P.E. Berry & B.W. van Ee. A. Climbing habit, here together with a climbing bamboo; B. Adventitious roots emerging from the stems; C. Typical trichotomous branching; D. Leaves; E. Close-up of the densely hirsute newly emergent leaves. Note the falcate stipules and stipitate acropetiolar glands; F. Inflorescence with the pedicels of the staminate flowers perpendicular to the axis of the rachis; G. Pistillate flower. Note the somewhat unequal, foliaceous sepals and thrice bifurcating stigmas; H. Inflorescence showing an immature fruit, foliaceous bracts along the rachis, and staminate pedicels of varying lengths.

[Photos: P. Berry]
We believe that the most distinctive character of this new taxon are the multiple narrow thyrses that appear individually in the axis of successive leaves on young branches, whereas most *Croton* species have a single axillary or terminal inflorescence (Fig. 10E–F). The young stems and leaves are characterized by a very dense, coppery-lepidote indumentum that changes as the leaves expand and develop (Fig. 10E, I). On the leaf undersurface, the trichomes completely cover the blade at maturity, but the outer fringes of the scales then become visible and are lighter in color than the coppery center of the scales. On the upper surface, the scales are less dense and they degenerate more, leaving some of the underlying green cuticle exposed and visible when fully expanded. The basal leaf glands are narrow having a narrow hollow opening on top (Fig. 10F). The stems and inflorescences are noticeably ridged and partially flattened (Fig. 10D). The paucity of pistillate flowers in this species is noteworthy (only 1–3 per inflorescence when present, with some inflorescences being entirely staminate); the pistillate flowers also have very short, stout pedicels, small calyces, a lepidote inner surface, and intricate, highly divided styles. In contrast, the staminate flowers are far more numerous and longer-pedicellate, with numerous (15–25) stamens.

Where we collected *C. plurispicatus* along the road from Andasibe to La Piste, it was most often growing in association with the more abundant and widespread *C. submetallicus*. That species is generally a lower-growing and more spreading shrub or tree, with the pistillate flowers having much larger sepals and much more elongate pedicels, as well as leaves with much sparser indumentum on the underside, but the two do seem to intergrade and possibly hybridize in this area. In particular, van Et al. 2203 (MAPR, MICH, MO, P, TAN) was a plant that had many intermediate characters between the two species.

**Paratypes.** Madagascar, Provincia Tsasmania: Alao-a-Mangoro Region, Moramanga Dist., Ambatovola, Fianarano, forêt de Vohima, 18°55′13″S 48°30′49″E, Andriatsifara et al. 2559 (MO, P, TAN); La Foa, VII.1973, Guillaumet 4227 (P); village d’Ambodigavo, forêt d’Analanjaka à 1W d’Ambodigavo, 19°07′39″S 48°23′51″E, 900 m, 31.V.2007, Razanatsimina et al. 290 (MO); Lafo, village Manasamena, forêt corridor Andikinkina, 19°04′02″S 48°22′02″E, 1041 m, 19.IX.2007, van Et al. 984 (MO); Atsinanana Region, Vatomandry Dist., Ambalabe, Ambinanindroso II, le long de la piste vers SW du Tobin’I Foara, 19°10′11″S 48°34′40″E, 610 m, 12.III.2005, Ranarivoana & Razanatsimina 1173 (K, MICH, MO); ibid. loc., 19°09′08″S 48°34′47″E, 610 m, 14.III.2005, Randrianaolo & al. 1028 (K, MICH, MO); Sahaniakoa, forêt de Vohibe, chute Tsimonekina, 19°10′49″S 48°32′27″E, 763 m, 2.VI.2010, Razanatsimina 858 (MO); Alao-a-Mangoro Region, Moramanga Dist., along unpaved road from RN 2 to La Piste, 19°03′35″S 48°21′49″E, 1015 m, 27.II.2009, van Et al. 981 (MAPR, MICH, MO, P, TAN); ibid. loc., van Et al. 982 (MAPR, MICH, MO, P, TAN); ibid. loc., 19°04′25″S 48°22′04″E, 906 m, 27.II.2009, van Et al. 984 (MICH, TAN); ibid. loc., 19°03′08″S 48°21′32″E, 1030–1060 m, 13.VIII.2015, van Et al. 2199 (MAPR, MICH, MO, P, TAN); ibid. loc., van Et al. 2200 (MAPR, MICH, MO, P, TAN); ibid. loc., van Et al. 2202 (MAPR, MICH, MO, P, TAN).

**Reinstated species**

*Croton hypochalibaeus* Baill. in Bull. Mens. Soc. Linn. Paris 2: 262. 1890 (Fig. 1D, 12G–L, 13).

**Lectotypus** (designated here): Madagascar: sine loc. (K [K001040371]); isolecto: P (P00133213, P00133661)).

**Shrubs or trees** to 5 m tall, dichotomously branching, with internodes 2-14 cm long separating tight clusters of leaves at the nodes, giving the appearance of whorled branches. Branches ± flattened on new growth and densely brown-lepidote, brown or gray, becoming terete and glabrous with age. Stipules awn-shaped, 0.9-1.5 mm. Leaves congested and ± whorled at apex and nodes. Petioles 1-15 mm, adaxially canaliculate, without any apparent glands. Leaf blades papyraceous, entire or with shallow irregular undulations, narrowly elliptic to obovate, (7)-21-77(-145) × (5)-9-31(-45) mm, apex acute to long acuminate (rarely obtuse), base attenuate to cuneate; adaxial surface silvery-lepidote (young leaves appear silvery), glossy, (dark) green when fresh (turning orange in old leaves) and drying matte gray-green; venation impressed, not prominent, with 4-11 pairs of brochidodromous, ± penninerved secondary veins; abaxial surface densely silvery-lepidote and brown punctulate, the brown scales ± evenly scattered among silvery white scales; venation indistinct except for the brown-lepidote midrib. Inflorescences shortly racemose to fasciculate, 2-8(-10) mm long, axillary or terminal, with mostly staminate flowers, sometimes with 1-2 pistillate flowers at the base; axes densely brown-lepidote, flattened; bracts linear to spatulate, to 6.5 × 1.2 mm. Stamine flowers with brown-lepidote, subglobose buds 1.0-1.4 mm diam., pedicels elongating from bud to anthesis, 1-4 mm long; sepals 5, firm, shortly connate at base, lobes broadly triangular to ovate, 1.0-1.6 × 0.9-1.5 mm, apex acute to rounded, inflexed at anthesis, abaxially brown-lepidote, adaxially glabrous, white; petals 5, white, elliptic to spatulate, 2.0-2.9 × 0.7-1.1 mm, recurved at anthesis, abaxially papillate, adaxially glabrous, margins densely ciliate; disc glands/nectaries 5, opposite the sepals, sessile, triangular with an apical depression, 0.4-0.5 × 0.3-0.5 mm, yellow; stamina 10-18, white to pale yellow, filaments 1.1-3.2 mm long, ciliate, anthers elliptic, 0.5-0.9 mm long; receptacle pilose. Pistillate flowers with brown-lepidote buds 1.5-1.8 mm diam., pedicels 1-3(-5) mm long; sepals 5, firm, broadly elliptic, spreading at anthesis, 1.6-2.4(-5.5) × 0.9-2.2(-2.7) mm, apex acute and inflexed, shortly connate at base, abaxially lepidote, adaxially ± lepidote and ciliate towards apex, greenish white-green, persistent in fruit; petals usually absent/reduced; disc glands/nectaries 5, opposite the sepals, sessile, elliptoidal with a short apex, 0.2-0.6 × 0.6-1.0 mm, pale yellow; glandular filaments (in petal alternating with the nectary lobes) 5, 0.3-
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Fig. 7. – Croton ferricretus Kainul., B.W. van Ee & P.E. Berry (A–B), C. plurispicatus P.E. Berry, Kainul. & B.W. van Ee (C–D), C. hypochalibaeus Baill. (E–F), C. indrisivae Kainul., B.W. van Ee & P.E. Berry (G–H), and C. enigmaticus P.E. Berry & B.W. van Ee (I–J). A, C, E, G, I. Capsule; B, D, F, H, J. Seed. [A–B: van Ee et al. 2436; C: van Ee et al. 2198; D: Ranaivojoana & Razanatsima 1173; E–F: van Ee et al. 2472; G–H: van Ee et al. 2176; I–J: van Ee et al. 2214]
Fig. 8. – Croton ferricretus Kainul., B.W. van Ee & P.E. Berry. **A.** Typical habitat on ultramafic crust, with *C. ferricretus* dominating the understory; **B.** Habit; **C.** Underside of branch showing the silvery-lepidote and ferrugineous-punctate leaves; **D.** Inflorescence with staminate flowers and buds; **E.** Inflorescence with pistillate flower and bud; **F.** Inflorescence with immature fruits; **G.** Mature capsule.

[Photos: C-D, F: P. Berry; A-B, E, G: K. Kainulainen]
0.8 mm long; ovary subglobose, c. 2.0 mm diam., lepidote, styles 3, 2.3-5.0 mm long, flattened, each bifurcating 3-4 times, often with the first bifurcation congested and fused to appear 4-furcate, spreading, recurved at the apices, abaxially lepidote, adaxially glabrous (but appearing lepidote in some specimens where the edges of the style branches are rolled up), white, turning brown, persistent. Capsules 4.6-6.7 × c. 4.3 mm (Fig. 7E), smooth, (pale) brown, lepidote, exocarp not separating, endocarp woody, c. 0.2 mm thick; columnella 3.8-5.2 mm long, cornute, capitate. Seeds ± compressed-ellipsoid (Fig. 7F), c. 4.0 × 3.0 × 2.5 mm; testa glossy, punctate, brown; caruncle reniform c. 0.7 × 0.5 mm.

Etymology. – The epithet refers to the steel-colored lepidote indumentum on the underside of the leaves.

Phenology. – Both flowering and fruiting specimens have been collected from October to April (we have not seen any specimens collected between May and September), indicating that *C. hypochalibaeus* is aseasonal in its phenology.

Distribution, habitat and ecology. – *Croton hypochalibaeus* is mostly restricted to the eastern montane forests and the central highland plateau of Madagascar (“tampoketsa”) at elevations of 800-1600 m, but also occurs as low as 675 m at Ankenra. Most collections are from Toamasina Prov. (Ambatovy, Andasibe, Ankenra, and Zahamena), but it has also been collected in Ambositrandehy and Sohissika (Antananarivo Prov.) and as far south as Ivohibe in Fianarantsoa Prov. and Isalo National Park in Toliara Prov. Some doubtful specimens from Antsirananana Prov. are also mapped (see Fig. 1D). It typically grows in primary forest understory but it also occurs along the edges of forests or in secondary woody vegetation.

Vernacular names. – “Lazalaza madinidravina,” “Lazalaza madinika,” “Tsiavalika.”

Notes. – The two specimens of *Baron* 5635 at P are sparser fragments of the more complete specimen at K. Since Leandri (1939) treated *C. hypochalibaeus* as a synonym of *C. noronhae*, the name has not been applied to contemporary Malagasy Crotons, but the two species differ both morphologically and ecologically. *Croton noronhae* is restricted to littoral, sandy-soil forests along the eastern coast of Madagascar and has dark reddish velvety shoots compared to smooth, brown-lepidote shoots in *C. hypochalibaeus*; it also has evident acropetal glands, which are lacking in *C. hypochalibaeus*. In the Ambatovy checklist of Phillipson et al. (2010, Table 1), some of the specimens of *C. hypochalibaeus* listed below were determined either as *C. jennyanus*, *C. noronhae*, *C. sp.* nov. B aff. *jennyanus*, or the nom. nud. “Croton alceicornu Radcl.-Sm.” These all form part of a complex of small-leaved Crotons in Madagascar that have silvery- or coppery-lepidote leaf undersides and very condensed inflorescences. Just as with the group of large-leaved silvery *Croton* species that were first highlighted by Leandri (1972), it takes detailed field experience and careful examination of flowering and fruiting material to be able to successfully distinguish among the component species. The true *C. jennyanus* is restricted to northern Antsiranana Prov. at low altitudes and shows less evidence of sylleptic branching than *C. hypochalibaeus*. Also, its leaves have an acute to mucronate apex and a cuneate to rounded base (vs. an acute to long-acuminate apex and attenuate to cuneate base in *C. hypochalibaeus*), and the leaves usually dries a nitid green above (vs. a matte grey-green in *C. hypochalibaeus*), and are ferrugineous-punctate and (silvery) glossy below (vs. brown-punctulate and matte [greenish- or grayish-] white in *C. hypochalibaeus*). Specimens that were previously identified as “Croton alceicornu Radcl.-Sm., ined.” have smaller, rounder leaves than typical *C. hypochalibaeus* specimens, but we could find no consistent differences in floral characters between them. Still, closer study in the field and examination of better reproductive material may in the future justify recognition of a separate taxon for this entity.

There are some geographically outlying specimens that are referred here with some reservation; they are represented on the distribution map (Fig. 1D) by the four dots at the northern tip of the island. Ramirison 631 from the Ampondraboka forest in Daraina (12°57’29”S 49°41’50”E, 580 m, 11.IV.2004, G, P) seems to be a more reduced version of this species in terms of leaf size and compact growth. However, the label alludes to the sympatric *C. hypochalibaeus* and is ferrugineous-punctate and (silvery) glossy below (vs. brown-punctulate and matte [greenish- or grayish-] white in *C. hypochalibaeus*). Specimens that were previously identified from the Ampondrabe forest in Daraina, *Nusbaum* 986 (13°13’02”S 49°33’11”E, 950 m, 15.I.2004, G, P) and *Rakotondrafararana et al.* 358 (13°13’06”S 49°33’02”E, 790 m, 1.XI.2005, MO, P). On the northeastern side of the island, Harder et al. 1590, from Montagne d’Ambre (12°30’48”S 49°10’59”E, 990 m, 15.IV.1993, MO, P), is also a close match to this species, but since it is the only collection we have seen from this isolated massif, we would like to see further material to confirm its presence there. Finally, *Barivavao* 186, from Andrafiama, Manjato forest, 18°06’19”S 47°14’49”E (MO, P), is also represented on the distribution map (Fig. 1D) by the four dots at the northern tip of the island. Ramirison 631 from the Ampondraboka forest in Daraina (12°57’29”S 49°41’50”E, 580 m, 11.IV.2004, G, P) seems to be a more reduced version of this species in terms of leaf size and compact growth. However, the label alludes to the sympatric *C. hypochalibaeus* and is ferrugineous-punctate and (silvery) glossy below (vs. brown-punctulate and matte [greenish- or grayish-] white in *C. hypochalibaeus*). Specimens that were previously identified as “Croton alceicornu Radcl.-Sm., ined.” have smaller, rounder leaves than typical *C. hypochalibaeus* specimens, but we could find no consistent differences in floral characters between them. Still, closer study in the field and examination of better reproductive material may in the future justify recognition of a separate taxon for this entity.

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**Additional specimens examined.** — **MADAGASCAR. Prov. Antananarivo:** Analamanga Region, Ankazobe Dist., Ankazobe, Firaraza, Ankafobe forest, 18°06’30”S 47°11’12”E, 1492 m, *Ambanjafy* 1910 (MIC, MO, P, TAN). *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN); *ibid.* loc., *Ambanjafy* 1914 (MO, P, TAN).
Fig. 9. – Croton indrisilvae Kainul., B.W. van Ee & P.E. Berry. A. Habit; B. Stem showing smooth, tan bark; C. Branch with nearly mature capsule; note the rounded sepal that are green and subglabrous adaxially; D. Underside of branch showing whorled leaves; E. Detail of nearly mature capsule; note stiff, brown-stellate trichomes and triangular outline; F. Staminate flower, rehydrated; G. Pistillate flower, rehydrated.

[F: van Ee et al. 2176; G: Service Forestier 715] [Photos: A-E: P. Berry]
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Fig. 10. – Croton plurispicatus P.E. Berry, Kainul. & B.W. van Ee. A. Top of felled tree with dense ascending branches; B. Cross-section of woody stem, showing reddish sap at cambial layer; C. Young twig cut to show reddish latex that is exuded; D. Twig with flattened and angled shoots; E. Flowering branch showing the multiple thyrses along a single stem, some of them entirely staminate; F. Inflorescence with staminate flowers and buds. Note also the basilaminar glands (lower right); G. Pistillate flower at anthesis showing the lepidote inner surface of the sepals and the intricately divided, patent styles; H. Inflorescence with three basal pistillate flowers at varying stages of fruit development; I. Inflorescence with a basal fruit and a staminate flower above it.

[Photos: P. Berry].
Croton lasiopyrus Baill. in Bull. Mens. Soc. Linn. Paris 2: 926. 1890 (Fig. 1C, 14).

**Lectotypy** (designated here): **MADAGASCAR**: “Central Madagascar”, X.1882, Baron 1951 (P [P00133406]); isotype: K [K001040378?], P [P00133407]).

**Syntypy**: **MADAGASCAR**: “Central Madagascar”, X.1882, Baron 2114 (K [K001040377?], P [P00133408]); “Central Madagascar”, s.d., Baron 4078 (K [K001040376?]); Fort Dauphin, s.d., Scott-Elliot 1557 (P P00133052 packet in upper right)).

**Shrubs 1-4 m tall. Branches with fuzzy reddish-brown indument. Young shoots, petioles, and inflorescence axes hirsute, with densely ferrugineous-fasciculate trichomes, with copious red sap emerging when young stems are cut. Bark on older stems conspicuously longitudinally striate with whitish fissures on smooth grayish brown background, branching di- or trichotomous. Stipules minute, often hidden by pubescence. Leaves alternate to mostly opposite or ternate, the emerging ones usually whitish from the dense indument and anisophyllous (one of the pair or trio much smaller than the others). Petioles 0.8-2.0 cm long, with two subsessile to shortly stipitate discoid glands c. 1 mm diam. at the apex or just beneath the leaf blade. Leaf blades (broadly) elliptic to ovate, 4-5 × 2.5-8 cm, apex rounded to acutely acuminate, rounded to truncate at base, margin entire or somewhat serrate in distal half, firmly chartaceous, upper surface stellate-pubescent (densely so when young but becoming glabrescent with age except for pubescent midvein), softly and densely pubescent on lower surface, dark green above, only slightly paler on lower surface, brochiodyrominous, with 5-7 pairs of secondary veins. Inflorescences shortly racemose, terminal or axillary, epedunculate, 1.0-3.5 cm long, few-flowered, bisexual or all stamine, when bisexual with somewhat-pedicellate pistillate flowers close to the node, the pedicel 2-3 mm long, the staminate flowers with divergent pedicels 2-6 mm long. *Stamine flowers with densely stellate-hirsute, globose buds; sepals 5, lanceolate, 3.0 × 1.5 mm, abaxially stellate-pubescent; petals 5, oblong, obtuse, 2 × 1 mm, sericeous on both surfaces and margins, white; glands 5, discoid, c. 0.5 mm diam.; stamens 15, filaments 1-2 mm long, basally pilose, anthers 0.6-0.8 mm long; receptacle villous. *Pistillate flowers: sepals 5, lanceolate, 6.0-7.0 × 1.5-2 mm, abaxially densely stellate; petals lacking or subulate and c. 1 mm long; ovary globose, c. 5 mm diam., densely stellate-hirsute; styles short, stellate-lepidoite (branching pattern not discernible with available material). *Capsules depressed globose, densely ferrugineous-hirsute, c. 10 × 8 mm; columnella 7-8 mm long, coriaceous and fimbriate at apex. Seed oblong-ellipsoid, c. 6.5 × 3.5 mm, smooth, dark brown; caruncle c. 0.5 × 0.5 mm.

**Etymology.** – The specific epithet alludes to the woolly fruit of this species.
Fig. 11. – Croton radiatus P.E. Berry & Kainul. A. Holotype specimen of Croton radiatus at MICH; B. Inflorescence with a pair of basal pistillate flowers and five distal staminate flower buds; C. Underside of a leaf showing both whitish stellate-lepidote trichomes and brown fasciculate to multiradiate trichomes; D. Leaf base with a pair of stipitate, discoid glands emerging from the lamina; E. Stamine flower (7 anthers missing); F. Stamine flower with stamens removed to show the nectaries; G. Pistillate flower; H. Top view with the ovary removed to show the five nectaries and glandular filaments.

[E-F: Cours 1257; G-H: Razanatsoa & Marcellin 279]
Fig. 12. – **Croton plurispicatus** P.E. Berry, Kainul. & B.W. van Ee (A-F) and **C. hypochalibaeus** Baill. (G-L). **A.** Side view of staminate flower; **B.** Top view of staminate flower; **C.** Top view of staminate flower with stamens removed to show the five nectaries; **D.** Side view of pistillate flower; **E.** Top view of pistillate flower; **F.** Top view of pistillate flower with ovary removed to show the five nectaries; **G.** Side view of staminate flower; **H.** Top view of staminate flower; **I.** Top view of staminate flower with stamens removed to show the five nectaries; **J.** Side view of pistillate flower; **K.** Top view of pistillate flower; **L.** Top view of pistillate flower with ovary removed to show the five nectaries.

[A-F: van Ee et al. 2198; G-I: van Ee et al. 2465; J-L: van Ee et al. 2464]
Fig. 13. – *Croton hypochalibaeus* Baill. **A.** Habit; **B.** Stem (diam. c. 2.5 cm) with cauliflorous flowers; **C.** Close-up of the underside of a leaf; **D.** Staminate flower; **E-F.** Pistillate flowers; **G-H.** Fruits. 
[Photos: P. Berry]
Phenology. – Based on the few known collections, Croton lasiopyrus does not appear to be a prolific flowerer. There are remains of staminate flowers, as well as a fruit and a dehisced capsule, from August, with additional flowering collections in April, August, November, and December.

Distribution, habitat and ecology. – Croton lasiopyrus grows in ravines and the understory of montane moist forests on the eastern side of Madagascar, in Antananarivo and Toamasina Prov., at altitudes of 900-1200 m. (Fig. 1C).

Notes. – Key distinguishing characters of C. lasiopyrus include the rusty, woolly pubescence on the stems and leaves, the short-petiolate, elliptic to ovate, acuminate-tipped leaves, the new leaves tightly clustered at a node and often anisophyllous (of different sizes in the same pair or cluster), and the short inflorescences that appear axillary in the leaf clusters (Fig. 14). The syntype Scott-Elliot 1557 is not this species at all, but rather C. cassinoides Lam., from the Fort Dauphin area of Toliara Prov. There is another Scott-Elliot specimen from Fort Dauphin that is close to, but probably not conspecific with, C. lasiopyrus, namely Scott-Elliot 2699 (K, P), so there may have been a mix-up in the numbers cited by Bailon (1890).

Two collections (van Ee et al. 2215 and 2216) from the forest north of Route Nationale 2 between Andasibe and Ambatovy share many characters with C. lasiopyrus (18°54′57″S 48°20′43″E, 978 m, 14.VIII.2015, MICH, MO, P, TAN), but they were growing in close proximity to denser populations of C. enigmaticus, and we suspect they may be the result of introgression with that species. This is evidenced by noticeably serrate and acuminate-tipped leaves, more stipitate petiolar glands, and somewhat larger inflorescences and longer pistillate pedicels. Additional specimens examined. – MADAGASCAR. Prov. Antananarivo: Analamanga Region. La Man德拉, 7.II.1937, Herb. Jard. Bot. Tan. 2380 (P); ibid. loc., 7.XII.1959, Schlözen 8140 (G, K); ibid. loc., 8.X.1961, Service Forêtier 20332 (G, K, MO, P). Prov. Toamasina: Alaotra-Mangoro Region, [Ambatondrazaka Dist.], forêt d’Ambodiapiso, près d’Antsobe, 1200 m, 12.I.1945, Courrè 2293 (K, MO, P); Anony, forêt du N aux confins du pays Sihanaka, [17°13′S 48°32′E], 3.IX.1937, Herb. Jard. Bot. Tan. 2957 (P); Moramanga Distr., Ambihibolakey, Corridor Forêtier Analamay Manantadi, forêt d’Ambosary, 1019 m, 25.IV.2012, 18°47′11″S 48°23′00″E, Rakotovao 5812 (MO, P, TAN). Lacoto, forêt E de Manasamena village, along the Ankarandrabe trail, 1062-1100 m, 27.II.2007, Randrianasolo et al. 1148 (MO, P, TAN); along road to Lakato, 1080 m, 19°03′10″S 48°22′20″E, 11.XI.2003, Schatz et al. 4186 (MO, P); ibid. loc., 1022 m, 19°02′47″S 48°21′25″E, 27.II.2009, van Ee et al. 978 (MICH, MO, P, TAN); ibid. loc., 1022-1038 m, 19°02′52″S 48°21′24″E, 13.VIII.2015, van Ee et al. 2197 (MICH, MO, P, TAN); ibid. loc., van Ee et al. 2204 (MICH, MO, P, TAN).

Other species records from nearby areas

In Table 1 we list four tree species of Croton that have been collected in the Ambatovy region or in similar montane forest habitats between Moramanga and Antananarivo. Croton catatii Baill. (van Ee et al. 971, 2223, and 2431, MICH, MO, P, TAN) and C. goudotii Baill. (van Ee et al. 970 and 2225, MICH, MO, P, TAN) are both found near Mandraka in Antananarivo Prov., but C. goudotii has also been found along the road from Andasibe to Lakato near the village of Ambodiriana (van Ee et al. 972 and 973, MICH, MO, P, TAN). Croton lasiopyrus is now known from Ambatovy as well (Antilahinema et al. 7116, MO, P, TAN). Croton mongue Baill. is also found above Ambodiriana (van Ee et al. 974, 975 and 2205, MICH, MO, P, TAN) and appears to hybridize in that area with C. goudotii. It also occurs in the Ambodimandresy forest near the Hotel Euolphiiela (van Ee et al. 2221, MICH, MO, P, TAN). In 2016 we collected C. mongue along the pipeline and road descending from Ambatovy towards the coast just east of the mine (van Ee et al. 2468, MICH, MO, P, TAN), but it may actually have been planted there some years ago as part of reforestation efforts (Antilahinema, pers. obs.). Croton myriaster Baker was also found in the Mandraka area along the railroad tracks at PK 68 (van Ee et al. 2432, MICH, MO, P, TAN), as well as in Mantadia National Park along the road from Andasibe (van Ee et al. 2187, MICH, MO, P, TAN).

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Fig. 14. – Croton lasiopyrus Baill. A. Habit, with patent leaves; B. Cross-section of woody stem (diam. c. 4 cm), showing reddish sap at cambial layer; C. Young twig cut to show the reddish sap that is exuded; D. Leaves. Note the atypical serrate leaf margin of this specimen (van Ee et al. 2215), which may be introgressed with C. erigmaticus; E. Shoot apex with anisophyllous leaves; F. Close up of shoot showing the reddish, wooly pubescence. Note the acropetilolar gland at the lower side of the blade; G. Inflorescence with old staminate flowers and bud. Note the divergent pedicels; H. Pistillate flower; I. A nearly mature capsule and the remaining calyx and columella of an already dehisced capsule.

[A, C-E, G, I: van Ee et al. 2197; B, F: van Ee et al. 978; H: van Ee et al. 2215] [Photos: A, C-E, G-I: P. Berry; B, F: B. van Ee]
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