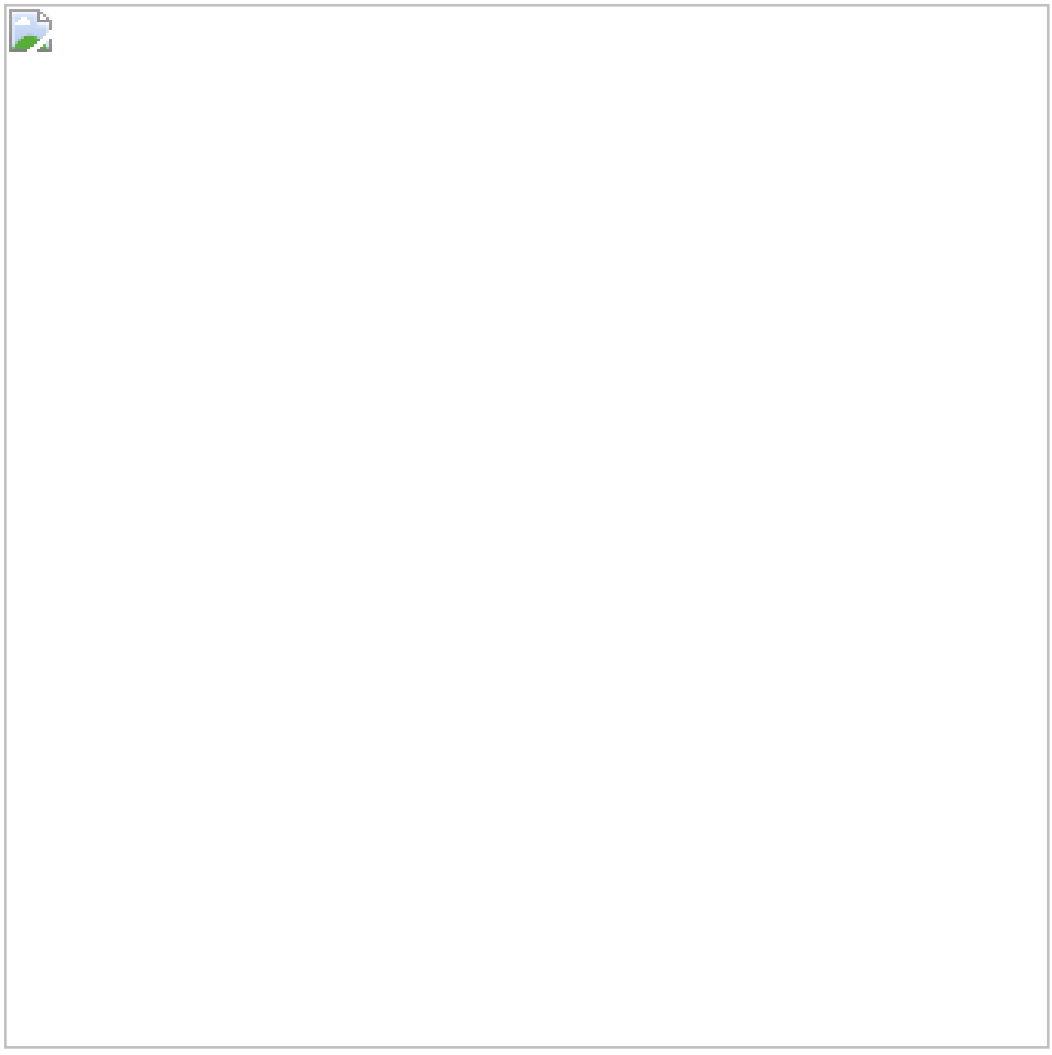

A revision of the Adenophorus Group and other glandular-leaved species of Croton (Euphorbiaceae) from northern Madagascar and Mayotte, including three new species

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A revision of the Adenophorus Group and other glandular-leaved species of Croton (Euphorbiaceae) from northern Madagascar and Mayotte, including three new species

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Abstract

KAINULAINEN, K., B. VAN EE, H. RAZAFINDRAIBE & P.E. BERRY (2017). A revision of the Adenophorus Group and other glandular-leaved species of Croton (Euphorbiaceae) from northern Madagascar and Mayotte, including three new species. *Candollea* 72 : 371-402. In English, English abstract. DOI: http://dx.doi.org/10.15553/c2017v722a15

This paper provides a revision of the species of *Croton* L. *(Euphorbiaceae)* from northern Madagascar (mainly Antsiranana and northern Mahajanga Provinces) and Mayotte in the Comoros Archipelago that bear glands on the undersides of the leaves. This includes members of the Adenophorus Group as well as two species that do not belong to that group, namely *Croton nudatus* Baill. and *Croton stanneus* Baill. *Croton nudatus* has been a problematic name since its publication due to the leafless state of its type. We were able to match the type with material recently collected near the type locality, and we provide an amended description for this species. *Croton stanneus* is another previously poorly understood species, which is actually one of the most widespread species of *Croton* in Madagascar. We also re-evaluate species delimitations in members of the Adenophorus Group from northern Madagascar and Mayotte, and we describe three new species, *Croton mayottae* P.E. Berry & Kainul., *Croton orangeae* Kainul. & P.E. Berry, and *Croton sahafariensis* Kainul. & P.E. Berry. *Croton loucoubensis* Baill. is resurrected from synonymy, and nine other species names and eight varieties are reduced to synonymy under *Croton adenophorus* Baill., *Croton loucoubensis*, *Croton nudatus*, *Croton scoriarum* Leandri, *Croton stanneus*, or *Croton tsiampiensis* Leandri. Full descriptions are provided for these species as well as for *Croton bathianus* Leandri, another misunderstood species in the group. A key to the seven species of the Adenophorus Group and the two look-alikes from northern Madagascar and Mayotte is provided. An epitype is designated for *Croton nudatus*, and lectotypes are designated for *Croton adenophorus*, *Croton bathianus*, *Croton loucoubensis*, *Croton scoriarum*, *Croton stanneus*, and *Croton tsiampiensis*.

Keywords

EUPHORBIACEAE – *Croton* – Taxonomy – Mayotte – Madagascar

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Introduction

Several species names of *Croton* L. *(Euphorbiaceae)* from Madagascar have been misapplied or overlooked since they were published by Baillon (1861). In his treatise of Malagasy *Croton*, Baillon (1861) described the closely related *Croton adenophorus* Baill., *C. loucoubensis* Baill., and *C. payerianus* Baill., all from the island of Nosy Be off the northwestern coast of Madagascar, and he included them in *C.* sect. *Anisophyllum* Baill. Two additional names, *Croton subaemulans* Baill. and *C. tenuicuspis* Baill., were later described by Baillon (1890, 1891) based on Malagasy specimens collected by Richard Baron, but which lacked further locality information. In his conspectus of the Malagasy species of *Croton*, Leandri (1939) revised these species and placed them in his "Groupe Adenophorum" [referred to as the Adenophorus Group from here on], whose species were categorized as having glands on the lower surface of the leaf blades (not just at the base of the blade or apex of the petioles), mainly stellate trichomes (no lepidote ones), and more than 12 stamens in the staminate flowers. He recognized both *C. adenophorus* and *C. subaemulans* as distinct species, but treated *C. payerianus* and *C. loucoubensis* as synonyms of *C. adenophorus* and then *C. tenuicuspis* as a synonym of *C. subaemulans*. After careful examination of the type material and detailed studies of populations in the wild, we now have a revised concept of these species and conclude that both *C. subaemulans* and *C. tenuicuspis* should be synonymized with *C. adenophorus*, but that *C. loucoubensis* represents a distinct species that should be resurrected.

Since *Croton* is a mega-genus with around 1,200 species worldwide, the rank of section has been used since Baillon (1861) to recognize more cohesive smaller groups within the genus. Webster (1993) made a comprehensive re-evaluation of the genus, in which he recognized 40 sections worldwide. An update of his system was made for the New World by van Ee et al. (2011), which showed that all of Webster's sections containing both New World and Old World species are polyphyletic. An initial refinement of some sections from the Old World was attempted by van Ee et al. (2015), but this work focused mainly on the Australian species. Overall, the sectional delimitations of Webster (1993) for the Old World have proven quite unsatisfactory, and Madagascar has been particularly problematic in that sense. One exception to this is *Croton* sect. *Anisophyllum*, for which Webster (1993) designated *C. payerianus* (considered here a synonym of *C. adenophorus*) as the lectotype, and which appears to be both molecularly and morphologically well circumscribed (see Haber et al., 2017). This section is equivalent to the Adenophorus Group of Leandri (1939), and it includes 14 described species (including three that are described in this paper), as well as another two species from Mahajanga and Toliara Provinces that we are in the process of describing as new in a forthcoming paper. The species of the Adenophorus Group are distributed in dry regions of Madagascar from the far north to the far south, but the group is not known from the humid eastern parts of the island. However, several species occur in subhumid northwestern Madagascar, such as in the Ampasindava Peninsula and along the Sambirano River. At least one species of this group also occurs on the island of Mayotte, about 350 km west of the closest populations of related species from Madagascar.

Currently, the species of the Adenophorus Group can be most readily recognized by the following suite of characters: opposite leaves with a rounded or cordate base; the proximal pairs of the secondary leaf veins palmately arranged; glands present on the abaxial side of the leaf; and terminal spike- or raceme-like thyrses in which the flowers mature from the base upwards. There is considerable variation in pubescence within the group (Fig. 1), comprising a diversity of stellate trichomes, but completely lacking lepidote scales. A number of species in the group have conspicuous petals in the pistillate flowers, while others usually have apetalous pistillate flowers.

One of Baillon (1861)'s least understood species is *C. nudatus* Baill. His description was based on a leafless specimen from the bay of Diego Suarez (Antsiranana Province), and because its leaves were unknown and the specimen was mainly in fruit, the name has not been subsequently applied beyond the type specimen. In this study we have been able to match the type to recently collected material from the same area as well as other areas in northern Madagascar, and are now able to provide an expanded description of this species, as well as designating an epitype with leaves and flowers. Since the leaves of *C. nudatus* are opposite and usually have some glands on the abaxial surface of the blade, and there are petals in the pistillate flowers, it would seem to fit into the Adenophorus Group, but other features of the inflorescence and flowers, as well as molecular data, rule that out (see discussion after the description of *C. nudatus*).

Another species described by Baillon (1890) that has been generally overlooked is *C. stanneus* Baill. The type is a Baron collection that lacks locality information (other than central Madagascar), but we have now found that *C. stanneus* is one of the most widely distributed species of *Croton* in Madagascar, ranging from Montagne d'Ambre in the north (Antsiranana Province) to southeastern Toliara Province in the south. Like *C. nudatus, C. stanneus* would appear to belong to the Adenophorus Group due to its opposite leaves with glands on the abaxial surface, but it has much laxer inflorescences than members of the group, and unlike all other members of the Adenophorus Group, it has lepidote trichomes on the leaves, stems, and flower buds.

The specific aim of this paper is to resolve the identity of *C. adenophorus* and related species from northern Madagascar and Mayotte in the nearby Comoros Archipelago, as well as some other species that have been confused with the Adenophorus Group because they also have glands on the lower surface of the leaf blades, namely *C. nudatus* and

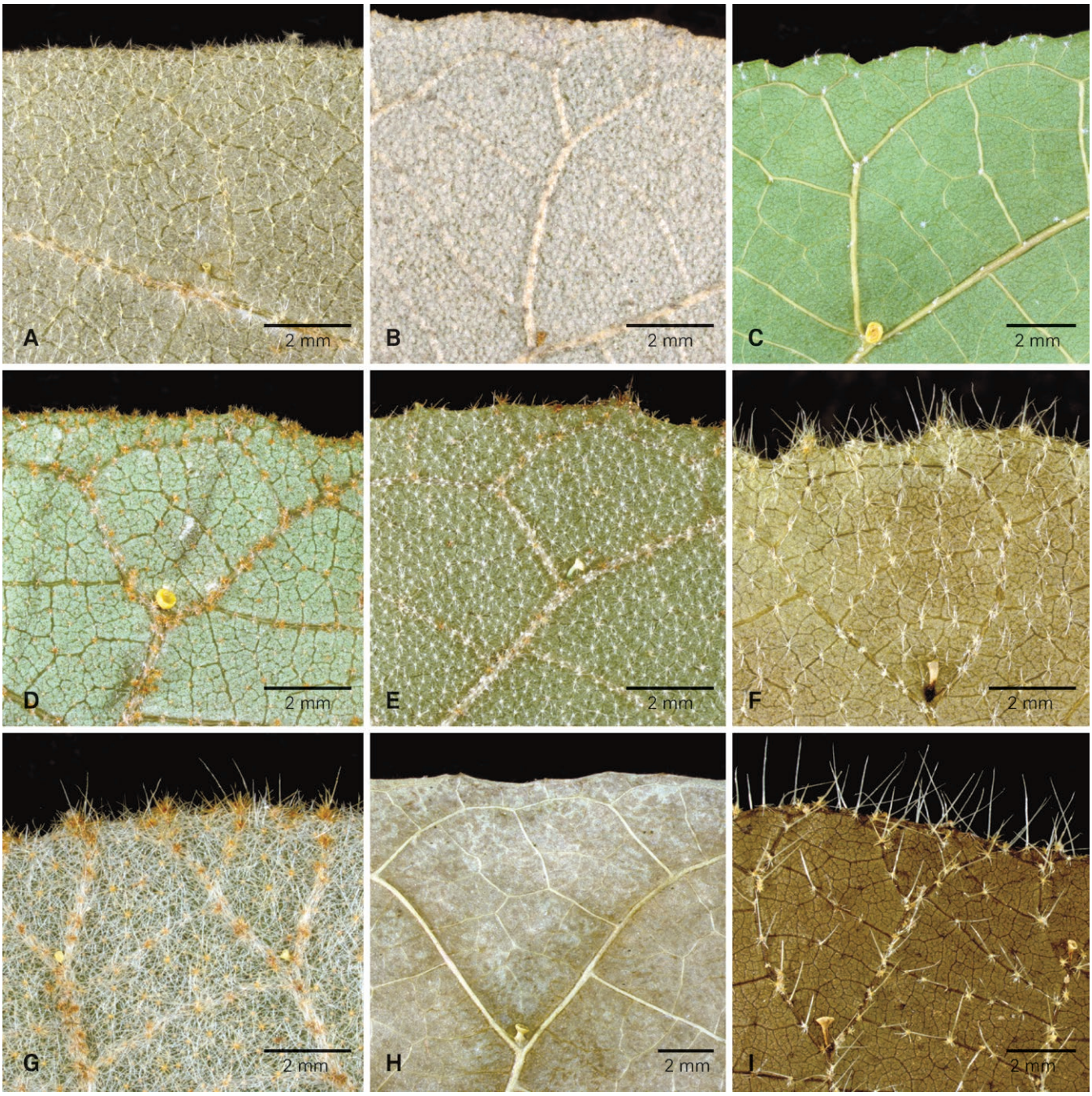

Fig. 1. Abaxial side of leaves showing laminar glands and pubescence **A.** *Croton nudatus* Baill.; **B.** *Croton stanneus* Baill.; **C.** *Croton adenophorus* Baill.; **D.** *Croton bathianus* Leandri; **E.** *Croton loucoubensis* Baill.; **F.** *Croton orangeae* Kainul. & Berry; **G.** *Croton sahafariensis* Kainul. & Berry; **H.** *Croton scoriarum* Leandri; **I.** *Croton tsiampiensis* Leandri.
[**A:** *van Ee et al. 2340*; **B:** *van Ee et al. 2160*; **C:** *van Ee et al. 1135*; **D:** *van Ee et al. 1138*; **E:** *Ammann et al. 378*; **F:** *van Ee et al. 2353*; **G:** *van Ee et al. 1089*; **H:** *van Ee et al. 2329*; **I:** *Nusbaumer LN 902*]

C. stanneus. A key for distinguishing the species from northern Madagascar and Mayotte that may have laminar glands on the lower leaf surface is provided below. A list of additional examined specimens is cited for each treated species, and we have made an effort to enter all of these in Tropicos (2017), where detailed distribution maps and photographs, when available, can be obtained.

Key to the species of Croton from northern Madagascar and Mayotte with glands on the underside of the leaf blades

1. Flower buds maturing evenly along the inflorescence, not tightly packed into a catkin-like structure, with anthesis occurring either ± simultaneously or sporadically along the length of the inflorescence **2**
1a. Flower buds maturing acropetally, with anthesis occurring sequentially from the base of the inflorescence, the distal end very compact and catkin-like **3**

2. Floral buds evenly distributed along the inflorescence axis, inflorescence 0.2-1(-2) cm long; staminate and pistillate pedicels 2-5 mm long in bud; plants with stellate trichomes only..... ***C. nudatus***
2a. Floral buds clustered in interspersed cymules along the inflorescence axis, inflorescence 3-10(-18) cm long; staminate pedicels 0.5-1 mm long in bud, pistillate pedicels 1-3.5 mm long in bud; plants with lepidote trichomes or a mixture of stellate and lepidote ones ..... ***C. stanneus***

3. Ovaries and capsules hirsute or bristly (trichomes with long-protruding porrect rays)..... **4**
3a. Ovaries and capsules with stellate trichomes (rays of the trichomes not porrect or long-protruding)..... **6**

4. Stipules fimbriate; mature capsules ≥ 10 mm diam., the endocarp c. 2 mm thick..... ***C. loucoubensis***
4a. Stipules entire or shallowly incised; mature capsules < 7.5 mm diam., the endocarp < 1 mm thick **5**

5. Leaves markedly shaggy-hirsute with long-porrect trichomes; bracts not extending beyond the buds..... ..... ***C. tsiampiensis***
5a. Leaves with woolly pubescence trichomes on the abaxial side; bracts extending well beyond the buds .... ***C. sahafariensis***

6. Sepals of pistillate flowers usually green-foliaceous, unequal in size; stipules usually foliaceous, narrowly ovate, often with an auriculate base..... ***C. adenophorus***
6a. Sepals of pistillate flowers not green or foliaceous, all of equal size; stipules narrowly lanceolate to acicular, the base not auriculate **7**

7. Young branches glossy dark reddish-brown; mature leaves ± entire, glabrous (softly pubescent when young), the base rounded to truncate or shallowly cordate..... ***C. scoriarum***
7a. Young branches dull pale gray or tan; mature leaves denticulate to dentate, with stellate trichomes, scabrous to scurfy on young leaves, the base cordate..... **8**

8. Petioles, inflorescences, and young shoots densely covered by reddish, granulate trichomes; pistillate flowers with well-developed petals ..... ***C. bathianus***
8a. Petioles, inflorescences, and young shoots covered by whitish stellate trichomes, or tan scurfy ones; pistillate flowers lacking petals or with reduced, filamentous petals **9**

9. Stipules lanceolate, serrate-margined, aristate, 10-20 mm long; inflorescences 6-10 cm long..... ***C. mayottae***
9a. Stipules awn-shaped, entire-margined, 5-10 mm long; inflorescences 1-6.5 cm long..... ***C. orangeae***

Systematics

Glandular-leaved species outside of the Adenophorus Group

Croton nudatus Baill. in Adansonia 1: 168. 1861 [as *nudatum*] (Fig. 1A, 2A, 3, 4A-B).

≡ *Oxydectes nudata* (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Typus: Madagascar. Prov. Antsiranana: «Baie de Diego-Suarès», XII.1848, *Boivin 2659* (holo-: P [P00389498]!). **Epitypus** (designated here): **Madagascar. Prov. Antsiranana:** Diana Reg., Antsiranana II, Orangea, road going uphill from military checkpoint at entrance to Orangea, 12°14'08"S 49°21'40"E, 50 m, 25.X.2009, *van Ee et al. 1081* (epi-: MICH [MICH1517189]!; isoepi-: P, TAN).

= *Croton boivinianus* var. *brevifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 12. 2016. **Typus: Madagascar. Prov. Antsiranana:** à 79 km au S d'Antsiranana par route RN6, et 15 km à l'E de l'ancien chantier du Colas à Marotaolana, Campement à l'E du village d'Ampantsona, 12°51'20"S 49°18'10"E, 394-551 m, 3-6.VI.1997, *Andrianantoanina & Bezara 1068* (holo-: K; iso-: MO, P [P00433267]!), **syn. nov.**

= *Croton hirsutissimus* Radcl.-Sm., Gen. Croton Madag. Comoro 99. 2016. **Typus: Madagascar. Prov. Antsiranana:** versant E du massif de l'Ankarana (partie S du massif de Mafokovo), au N de Vohémar, 50-450 m, 17.XII.1966, *Service Forestier 27363* (holo-: P [P00154439]!), **syn. nov.**

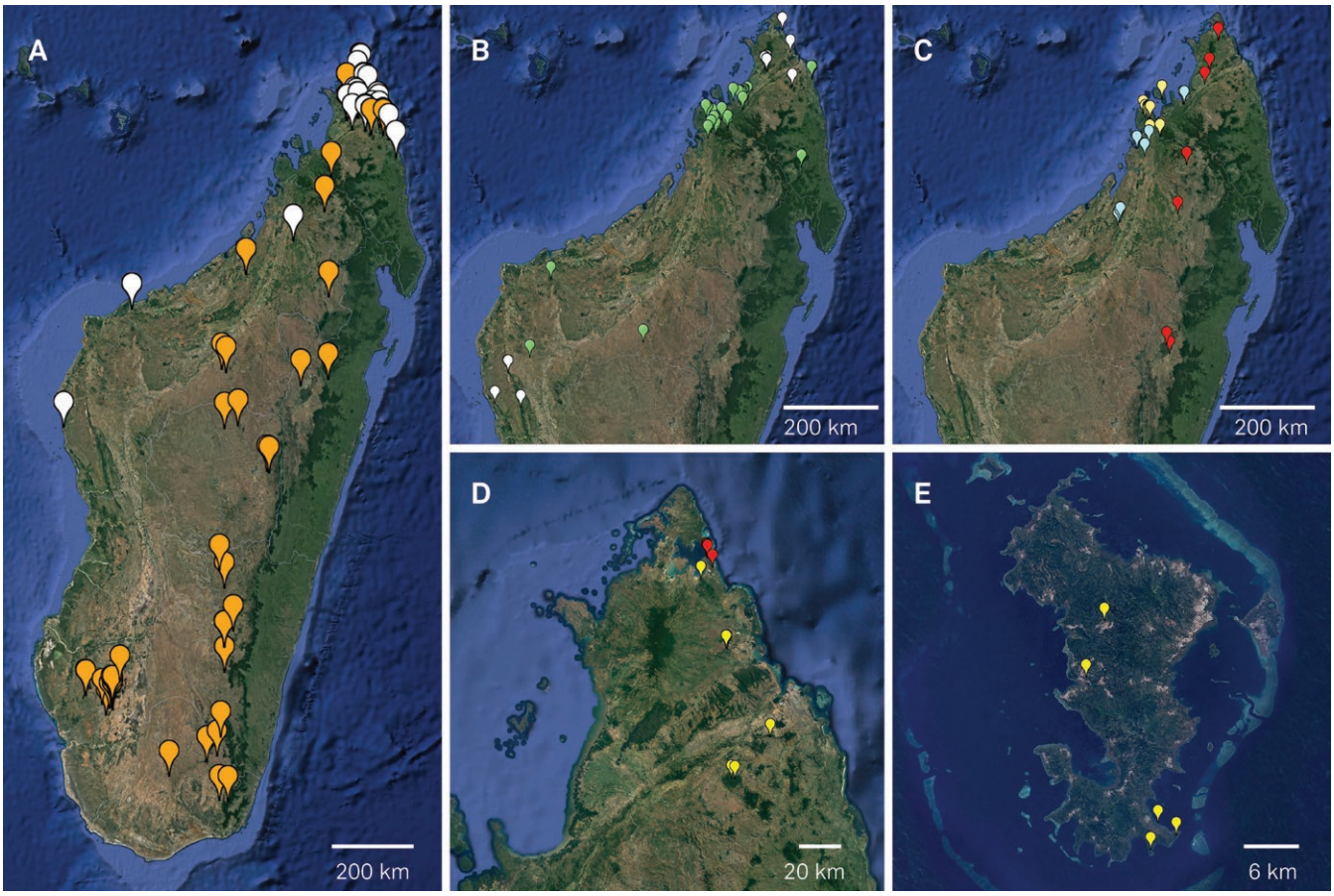

Fig. 2. Distribution maps. **A.** *Croton nudatus* Baill. (white), *C. stanneus* Baill. (yellow); **B.** *Croton adenophorus* Baill. (green) and *C. tsiampiensis* Leandri (white); **C.** *Croton bathianus* Leandri (light blue), *C. loucoubensis* Baill. (yellow), and *Croton scoriarum* Leandri (red); **D.** *Croton orangeae* Kainul. & Berry (red) and *C. sahafariensis* Kainul. & Berry (yellow); **E.** *Croton mayottae* P.E. Berry & Kainul.

= *Croton menabeensis* var. *furfuraceus* Radcl.-Sm., Gen. Croton Madag. Comoro 101. 2016. **Typus: Madagascar. Prov. Mahajanga:** Sofia Reg., Antsohihy Distr., Antsatrana, Bora, 17.VII.1970, *Service Forestier 30011* (holo-: P [P00154438]!), **syn. nov.**

Shrubs 0.5-4(5) m tall, dichotomously branched, internodes sometimes so short as to appear whorled, twigs terete, from green when newly emergent to dark gray or almost black, becoming noticeably lenticellate. Young shoots and inflorescence axes with a whitish to ferrugineous indument of stellate trichomes (rarely nearly glabrous). Stipules minute, inconspicuous. *Leaves* opposite, deciduous. Petioles 0.5-10 (-30) mm long, adaxially canaliculate, stellate, with 2 minute, shortly stipitate, discoid acropetiolar glands c. 0.1-0.3 mm diam., usually obscured by the surrounding trichomes. Leaf blades softly membranaceous, entire, narrowly to broadly ovate, 1.5-4(-7.7) × 0.5-2(-4) cm, apex shortly acuminate, base rounded to shallowly cordate, young leaves usually densely white-woolly, becoming more discolorous as they expand, the adaxial surface with stellate trichomes with a long porrect central ray, abaxial surface with a denser stellate indument; venation 3-palminerved at the base, remaining secondaries in 3-4 pairs and widely spaced, veins somewhat prominent below and sometimes with scurfy ferrugineous-stellate indument along the midrib and secondaries, sometimes with a few sparse, yellowish globular glands between the midvein and the margin, these sometimes associated with the vein junctions (Fig. 1A). *Inflorescences* terminal, racemose, 2-10(-20) mm long, few-flowered (2-10 buds), bracts inconspicuous, c. 1 mm long, buds globose, 1.5-2.5 mm diam., densely yellowish-stellate, the trichomes with an elongate porrect central ray (Fig. 3D, F, H), pedicels 2-5 mm long and divergent from the axis. *Staminate flowers* with 5 broadly triangular sepals, 5 oblong-spathulate petals, and 8-10 stamens, anthers oblong, c. 0.6 mm long, basifixed, filaments 1.5-2.5 mm long,

Fig. 3. *Croton nudatus* Baill. **A.** Leafless branch with young inflorescences.; **B.** Understory dwarf shrub; **C.** Leaves; **D.** Young inflorescence. Note the white woolly pubescence on the young leaves and shoots of this specimen; **E.** Leaves of a more hirsute specimen; **F.** Pistillate flower; **G.** Inflorescences with predominantly staminate flower; **H.** Close up of staminate and pistillate flowers; **I.** Immature capsules on a specimen with subglabrous leaves.
[**A:** *van Ee et al. 1064*; **B:** *van Ee et al. 2302*; **C:** *van Ee et al. 2321*; **D:** *van Ee et al. 2341*; **E-F:** *Callmander et al. 253*; **G-H:** *Burivalova 34*; **I:** *Randrianaivo et al. 1424*] [Photos: **A:** B. van Ee; **B:** K. Kainulainen; **C-D:** P. Berry; **E-F:** M. Callmander; **G-H:** Z. Burivalova; **I:** R. Randrianaivo]

curving inwards; receptacle villous. *Pistillate flowers* with 5 bluntly triangular sepals 1.5-2.5 mm long, basally connate, densely stellate-rosulate; petals 5, oblong-subspatulate, ciliate, 2-2.5 × 0.6-1.4 mm, ovary trilobate-subglobose, c. 2 mm diam., fulvous-hirsute, the trichomes with elongate porrect central rays; styles 3, 1-1.5 mm long, 4-fid (with 12 terminal tips), reddish-brown, basally stellate. *Bisexual flowers* occasionally present, with 5 stamens opposing the petals, filaments 1.5-2 mm long, anthers broadly elliptic-ovate, c. 0.5 × 0.5 mm. *Capsules* globose, c. 5 × 5 mm, lightly to densely hirsute, the exocarp separating, endocarp thinly woody, c. 0.3 mm thick; columella 3.5-5 mm long, triquetrous, tricornute, erect and persistent (Fig. 4A). *Seeds* ovoid, 3.5-4 × 2.5-3 × 1.5-2 mm, rounded-apiculate, biconvex in cross-section, smooth, shiny, yellowish-brown to brown (Fig. 4B); caruncle transversely oblong, slightly curved, 0.7-0.9 × 0.5 mm, whitish to golden.

Phenology. – *Croton nudatus* drops its leaves towards the end of the dry season, which typically runs from April to November in northern Madagascar. It can retain floral buds for much of the year and presumably flowers with the first heavy rains, usually in November-December, followed by leaf flush and fruiting, but there appears to be much variability in rainfall regimes across its distribution and from year to year.

Distribution, habitat and ecology. – *Croton nudatus* occurs in deciduous forests and secondary scrub vegetation in northern Antsiranana and in Mahajanga Province, from sea level to about 500 m elevation, growing mainly on sandy or rocky soils (Fig. 2A).

Conservation assessment. – *Croton nudatus* occurs in Antsiranana Prov., in northern Madagascar, where it is known from 17 locations, including the protected areas of Andrafiamena, Ankarana, and Orangea (Oronjia). Three localities are also known from Mahajanga (Bora, Maintirano, Soalala), although these collections are more than 40 years old. We recommend that *C. nudatus* should be assigned as "Least Concern" [LC] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Lazalaza" *(Be et al. 11),* "Mamalifolay" *(Service Forestier 16390).*

Notes. –The species epithet *nudatus* refers to the "naked" (leafless) branches of the type.

The holotype of *C. nudatus* is leafless, and no botanist since Baillon (1861) had successfully matched it to any other collection. However, the stems have opposite leaf scars, and the locality is clearly given as coming from the area of the bay of Diego Suarez in Antsiranana Province. The protologue also mentions the presence of petals in the pistillate flowers as well as some hermaphroditic flowers, which is very rare in Malagasy *Croton*. We have observed that several recent collections from northern Antsiranana Province, namely *Be et al. 11*, *van Ee et al. 1079*, and *van Ee et al. 1081*, all have some hermaphroditic flowers as well as opposite leaves and petals in the pistillate flowers, and consequently we are quite confident that these specimens represent the same species as the type. To better document the leaves and fruits of the species, we designate an epitype *(van Ee 1081)* that comes from the type locality area and has leaves and fruits, with photographs available in Tropicos (2017).

Croton nudatus is usually a spindly understory shrub, with thin dark gray to blackish branches. It may also form a compact dwarf shrub that is no more than 0.5 m tall, with all leaves level in a single plane (Fig 3B). The leaves are opposite and entire, but quite variable in shape and degree of pubescence. The short, raceme-like inflorescences with pedicellate, buff-colored buds are characteristic, as are the well-developed petals of the pistillate flowers (Fig 3C-E), and the smooth glossy seeds (Fig 4B). Despite having opposite leaves and sometimes a few laminar glands, it does not belong to the Adenophorus Group. In the molecular phylogenetic study by Haber et al. (2017), *C. nudatus* did not form part of the highly supported Adenophorus-Mongue clade.

Two of Radcliffe-Smith (2016)'s names, *Croton hirsutissimus* and *C. boivinianus* var. *brevifolius*, are synonymized here. They were both described from single specimens, one from Ankarana the other from nearby Ampantsona. They differ markedly in the degree of pubescence, and they could be considered as representing the extremes in a gradient within *C. nudatus*. *Service Forestier 27363*, for instance, is hirsute, whereas *Andrianantoanina & Bezara 1068* is nearly glabrous. Both have laminar glands, although there are very few in the latter specimen. Preliminary phylogenetic analyses of nrDNA strongly support the inclusion of *Andrianantoanina & Bezara 1068* in *C. nudatus*. The type of *C. menabeensis* var. *furfuraceus* Radcl.-Sm., from northern Mahajanga (see Fig. 2A), also shows the characteristic raceme-like inflorescences with buff-colored buds, and we therefore consider it to be another synonym of *C. nudatus*. The young leaves of this specimen are stellate on both sides, whereas the older leaves are nearly glabrous. Two specimens from western Mahajanga are included here, namely *Morat 997* (Soalala) and *Service Forestier 16390* (Beleza). The former is nearly leafless, but both specimens conform to *C. nudatus* in their opposite leaves and the buff-colored buds.

Additional specimens examined. – **Madagascar. Prov. Antsiranana:** Diana Reg., Mahamasina Massif de l'Ankarana, Betsimipohaka, 12°57'23"S 49°08'52"E, 13.V.2007, *Bardot-Vaucoulon 1788* (MO, P); Analabolona, 3 km à l'W d'Irodo, 12°37'21"S 49°30'01"E, 102 m, 20.VII.2004, *Be et al. 11* (CNARP, MO, P, TAN); Andrafiamena, forêts aux alentours d'Anjahankely, 12°54'50"S 49°19'13"E, 361 m, 23.XI.2010, *Burivalova et al. 34* (G, MICH);

ibid loc., 12°54'58"S 49°20'01"E, 512 m, 27.XII.2010, *Burivalova et al. 137* (G, MICH); massif de l'Ankerana, S du massif de Mafokovo, 13°18'S 49°52'E, 206 m, 22.X.2004, *Callmander et al. 253* (G, MO, P); Daraina, forêt de Bekaraoka, partie N, 13°04'58"S 49°42'04"E, 140 m, 22.XI.2006, *Gautier & Chatelain 4898* (G, MICH); Forêt d'Analamaitso entre Anivorano Nord et les falaises de l'Ankarana, III.1962, *Keraudren 1708* (K, P); SE of Ambilobe, near Daraina on road to Vohemar (Iharana), 13°12'S 49°46'E, 200 m, 20.XII.1989, *McPherson 14737* (MO, P); Daraina, Ambohitsitondroina forest, 13°07'48"S 49°27'55"E, 248 m, 5.I.2006, *Nusbaumer & Ranirison 1842* (G, MICH, MO); Daraina, Antsahraingy forest, 12°55'08"S 49°40'31"E, 95 m, 28.II.2005, *Nusbaumer & Ranirison 2301* (G); Ampisikina, Tsaratanana, Antsiraka forest, 12°57'50"S 49°41'38"E, 500 m, 8.XI.2005, *Rakotonandrasana et al. 977* (CNARP, G, MO, P, TAN); Daraina, Befarafara, 13°04'33"S 49°34'45"E, 260 m, 7.XII.2006, *Randrianaivo et al. 1424* (CNARP, MICH, MO, P, TAN); Daraina, Ambohitsitondroina forest, 13°08'55"S 49°27'36" E, 200 m, 9.I.2006, *Ranirison & Nusbaumer 1068* (G, MICH, MO); Vohimarina, Fanambana, Antsatoby, 13°35'52"S 49°59'33"E, 171 m, 3.VII.2007, *Rasoafaranaivo 204* (MO, P); W slope of Montagne des Français, 12°22'02"S 49°19'10"E, 300 m, 23.X.2009, *van Ee et al. 1064* (MICH, P); Orangea, 12°14'08"S 49°21'40"E, 50 m, 25.X.2009, *van Ee et al. 1079* (MICH, MO, P); Sahafary forest in the Saharaina River basin, 12°34'51"S 49°27'02"E, 270 m, 26.X.2009, *van Ee et al. 1104* (MICH, MO, P); *ibid loc.*, 12°35'38"S 49°26'04"E, 280 m, 26.X.2009, *van Ee et al. 1107* (MICH); Betsiaka, Andavakoera forest, 13°07'26"S 49°13'52"E, 500 m, 27.X.2009, *van Ee et al. 1127* (MICH, P); Ambatomikiny forest, 12°49'53"S 49°16'15"E, 311 m, 28.II.2016, *van Ee et al. 2302* (MICH, TAN); Sahafary forest, 12°35'03"S 49°26'59"E, 231 m, 2.III.2016, *van Ee et al. 2321* (MICH, TAN); *ibid loc.*, 12°34'54"S 49°26'25"E, 191 m, 4.III.2016, *van Ee et al. 2333* (MICH, TAN); *ibid loc.*, 12°34'53"S 49°26'24"E, 192 m, 4.III.2016, *van Ee et al. 2336* (MICH, TAN); *ibid loc.*, 12°34'57"S 49°26'07"E, 182 m, 4.III.2016, *van Ee et al. 2339* (MICH, TAN); *ibid loc.*, 12°34'56"S 49°26'06"E, 180 m, 4.III.2016, *van Ee et al. 2340* (MICH, TAN); *ibid loc.*, *van Ee et al. 2341* (MICH, TAN); Orangéa peninsula, 12°13'59"S 49°21'33"E, 24 m, 5.III.2016, *van Ee et al. 2344* (MICH, TAN); *ibid loc.*, 12°14'47"S 49°22'46"E, 30 m, 5.III.2016, *van Ee et al. 2360* (MICH, TAN); Ankarana National Park, 12°57'11"S 49°07'45"E, 101 m, 7.III.2016, *van Ee et al. 2374* (MICH, TAN). **Prov. Mahajanga:** Boeny Reg., X.1964, route de Soalala, *Morat 997* (P); Melaky Reg., Forêt de Beleza, Campement de Beleza, Maintirano, 30.V.1956, *Service Forestier 16390* (P).

Croton stanneus Baill. in Bull. Mens. Soc. Linn. Paris 2: 850. 1890 [as *stanneum*] (Fig. 1B, 2A, 4C-D, 5).

Typus: MADAGASCAR: "Central Madagascar", rec'd. XI.1885, *Baron 3382* (holo-: K [K001040368]!, iso-: P [P00133580]!).

= *Croton perrieri* Leandri in Bull. Mus. Natl. Hist. Nat., sér. 2, 3: 369. 1931. **Lectotypus** (designated here): **MADAGASCAR. Prov. Mahajanga:** Le Berizoka [Le Beritsoka], X.1897, *Perrier de la Bâthie 353* (P [P00404485]!; isolecto-: K [K001040360]!, P [P00404484, P00404486, P00404487]!), **syn. nov.**

= *Croton baldauffii* Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7: 55. 1939 [as *baldauffi*]. **Lectotypus** (designated here): **MADAGASCAR. Prov. Toliara:** Forêt de Besomaty, entre le Fiherenana et l'Isahena (Mangoky), 750-800 m, X.1933, *Humbert 11249* (P [P00301487]!; isolecto-: P [P00127468]!), **syn. nov.**

= *Croton ikopae* Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7: 83. 1939. **Lectotypus** (designated here): **MADAGASCAR. Prov. Antananarivo:** Analamanga Reg., vallée de l'Ikopa, au NW d'Ankazobe, 15.III.1930, *Decary 7554* (P [P00154394]!; isolecto-: K [K001040362]!, P [P00154395, P00154396, P00154397]!), **syn. nov.**

= *Croton crocodilorum* var. *platyaster* Radcl.-Sm., Gen. Croton Madag. Comoro 113. 2016. **Typus: MADAGASCAR. Prov. Toliara:** Forêt du Zombitsy, près de Sakaraha, III.1960, *Keraudren 510* (holo-: P [P00154485]!), **syn. nov.**

= *Croton parvifructus* Radcl.-Sm., Gen. Croton Madag. Comoro 122. 2016. **Typus: MADAGASCAR. Prov. Toliara:** Forêt de Zombitsy, au NE de Sakaraha (150 km NE Tuléar), 600-800 m, 2.XI.1960, *Leandri & Ratoto 3605* (holo-: P [P00132992]!), **syn. nov.**

= *Croton stanneus* var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro 64. 2016. **Typus: MADAGASCAR. Prov. Fianarantsoa:** Ivohibe Distr., Antambohobe, Lomanosiny, Andranovola, 13.VIII.1967, *Service Forestier 26381* (holo:- P [P00133592]!), **syn. nov.**

Shrubs or small *trees* 3-7(-10) m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches. Young stems yellowish-gray or occasionally rusty-brown, flattened and ridged, later becoming terete, somewhat broadened below the nodes. Stems, petioles, rachis, and flower buds yellowish to rusty-colored, with lepidote to stellate trichomes. Stipules 4-15 × 2-5 mm, lanceolate to narrowly falcate, caducous or semipersistent. *Leaves* opposite or ternate, sometimes subopposite, semideciduous. Petioles 2-5 cm long, adaxially canaliculate, stellate, with 2 shortly stipitate to subsessile discoid, concave, acropetiolar glands (c. 0.5 mm diam). Leaf blades firmly membranaceous, entire to minutely crenate, broadly ovate, 4-8(-14) × (2-)3-5(-9) cm, apex acuminate, base rounded to truncate or shallowly cordate, adaxial surface green and minutely stellate with impressed veins, abaxial surface gray to silvery or yellow-green, with a dense indument (sometimes hirsute) of lepidote to stellate-lepidote trichomes and an underlaying of stellate to stellate-lepidote trichomes each with a porrect central radius; venation 3-5 palminerved at the base then penninerved with the more distal lateral nerves in 4-7 pairs, veins prominent below, usually with stipitate cylindrical glands with a discoid head at the junction of the secondary veins with the midvein (Fig. 1B), rarely also at the junction of secondary and tertiary veins. *Inflorescences* terminal thyrses 3-10(-18) cm long, the flowers densely grouped in cymules that are irregularly packed along the rachis, sometimes with bare sections of the rachis in between (Fig. 5A, B), most cymules staminate,

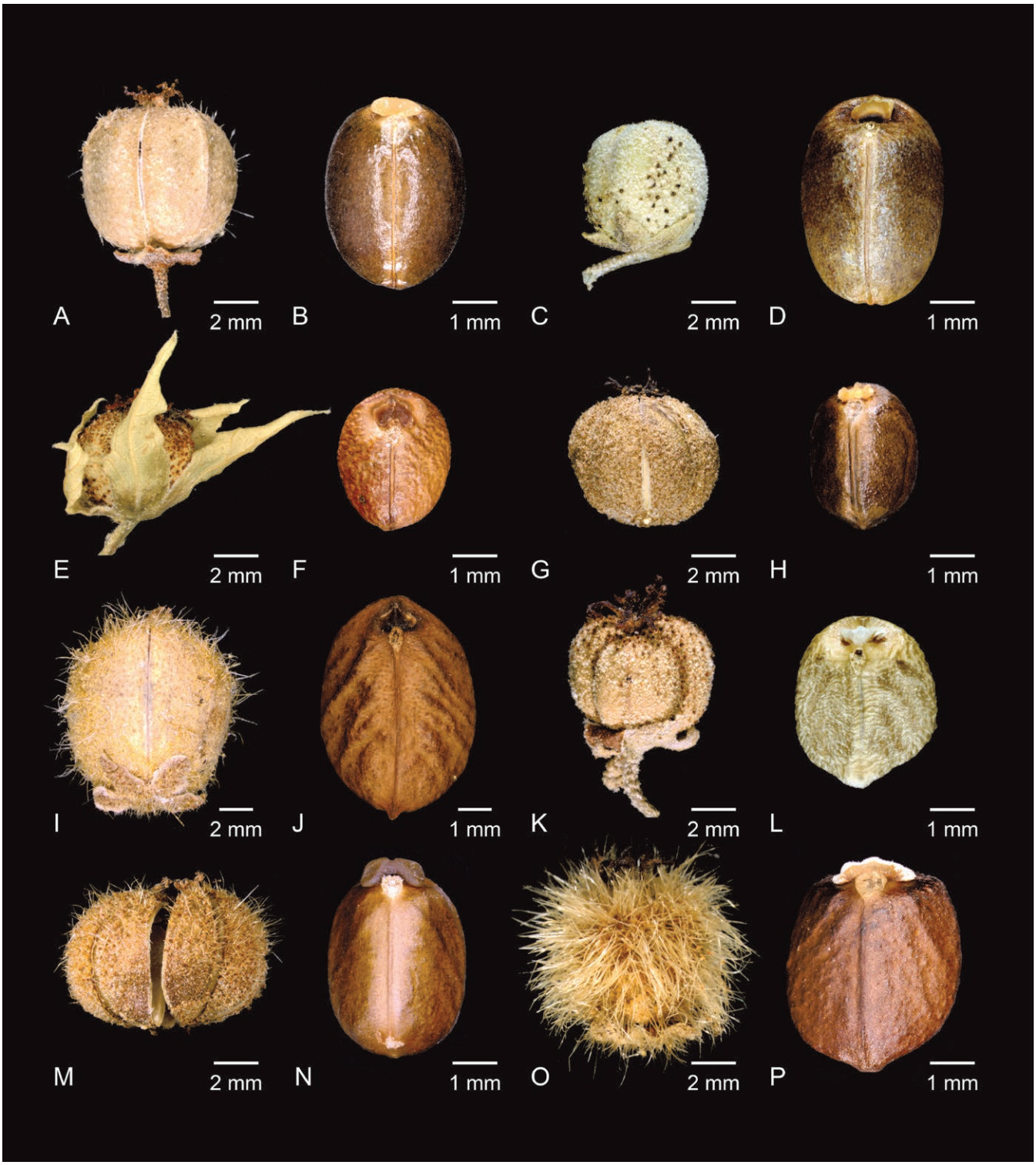

Fig. 4. Capsules (**A, C, E, G, I, K, M, O**); Seeds (**B, D, F, H, J, L, N, P**). **A-B.** *Croton nudatus* Baill.; **C-D.** *Croton stanneus* Baill.; **E-F.** *Croton adenophorus* Baill.; **G-H.** *Croton bathianus* Baill.; **I-J.** *Croton loucoubensis* Baill.; **K-L.** *Croton orangeae* Kainul. & P.E. Berry; **M-N.** *Croton sahafariensis* Kainul. & P.E. Berry; **O-P.** *Croton tsiampiensis* Leandri.
[**A:** *Randrianaivo et al. 1424*; **B:** *Gautier & Chatelain 4898*; **C:** *Gillespie 10802*; **D:** *Nusbaumer LN 906*; **E:** *van Ee et al. 1165*; **F:** *van Ee et al. 2294*; **G:** *van Ee et al. 2406*; **H:** *van Ee et al.1138*; **I:** *Nusbaumer 2536*; **J:** *Bernard et al. 1192*; **K-L :** *Razafitsalama et al. 692*; **M-N:** *van Ee et al. 2314*; **O-P:** *Nusbaumer 902*]

but bisexual cymules often present at the base (Fig. 5H, I), bracts inconspicuous, 1-2 mm long. *Staminate flowers* in dense cymules with densely lepidote, depressed-globose, pale yellow-brown buds 2-3 mm diam., pedicels 0.5-1 mm long in bud, to 1.5 mm at anthesis; sepals 5, broadly triangular-ovate, c. 2 × 1.5 mm, lepidote to stellate-lepidote abaxially; petals 5, spathulate, c. 2 × 1 mm, ciliate, yellowish-white; disc-glands 5, minute, triangular; stamens 15-20, filaments 2-2.5 mm long, distally glabrous, pubescent in lower half, anthers broadly ovate, c. 0.7 × 0.5 mm; receptacle densely pubescent. *Pistillate flowers* few to many in basal portion of rachis, either solitary or in mixed cymules with staminate flowers, pedicels 1-3.5 mm long, stouter than in the staminate flowers; sepals 5, firm, triangular, sulcate, c. 2 × 1 mm, lepidote to stellate-lepidote abaxially, adaxially glabrous and yellow to green when fresh, persistent, not accrescent; petals 0; ovary depressed-globose, c. 2 mm diam., densely lepidote to stellate-lepidote, light golden and often specked with darker or rusty trichomes (Fig. 5G, I); styles 3, 1-2 mm long, suberect, bifid, the 6 arms abaxially stellate-lepidote, adaxially glabrous, semi-persistent in fruit. *Capsules*, depressed-globose, 4.5-6.5 × 5-7(-8) mm, lepidote to stellate-lepidote (Fig. 4C); columella 3.5-4 mm long, capitate. *Seeds* broadly ovoid, 4-4.5 × 3-3.6 × 2.4-2.5 mm (Fig. 4D), finely pitted or sometimes ventrally obliquely 2-3-grooved on each facet, dorsally with 2-3 somewhat irregular oblique ribs per facet, slightly shiny, dark brown to blackish on the ridges, paler brown in the grooves; caruncle obcordate, bilobate, c. 0.5 × 1 mm, whitish.

Phenology. – This is a species that usually loses most of its leaves towards the end of the dry season (generally September to November). Plants often retain inflorescences with floral buds throughout the year, but flowering occurs during rainy periods, which varies across the wide range of the species.

Distribution, habitat and ecology. – This is a widespread species and one of just six species of *Croton* that have been found in all six provinces of Madagascar (Fig. 2A). It occurs in dry to moist forests on sandy, lateritic- or volcanic soils, as well as on inselbergs, at c. 300-1500 m elevation. *Croton stanneus* is found from Montagne d'Ambre in the north to Andohahela in the southeast, with its range centered in the phytogeographical Central Domain of Humbert (1955). It may be locally common and sometimes grows in hedgerows, and it is reported to have a spicy odor when crushed or boiled.

Conservation assessment. – Given the very widespread distribution of this species in all provinces of Madagascar, it should be assigned as "Least Concern" [LC] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Andriambolafotsy" *(Cours 5215),* "Karimbola" *(Andriamihajarivo et al. 879),* "Molanga" *(Lehavana & Rasolofonirina 391),* "Mongy" *(Service Forestier 26381).*

Notes. – The species epithet *stanneus* refers the tin-colored undersides of the leaves.

Croton stanneus has been confused with members of the Adenophorus Group due to its opposite leaves with stipitate glands on the lower surface. However, analyses of nrDNA data indicate that it is not closely related to this group, but rather is part of a clade with *C. trichotomus* Geisel. and *C. salviformis* Baill. *Croton stanneus* can best be distinguished by its long-petiolate, ovate-cordate, bicolored leaves often with large, falcate stipules and terminal, dense, spike-like inflorescences with depressed-globose buds in irregularly spaced clusters. Unlike most members of the Adenophorus Group, which have laminar glands in the axis of both secondary and tertiary veins, those of *C. stanneus* are usually limited to the junctions of the secondary veins with the midvein, and only rarely at the junctions of the secondaries and tertiaries (see Fig. 1B). Although the stems, buds, and emerging leaves are generally covered in lepidote scales, the fully expanded leaves may have stellate-lepidote or stellate trichomes (in both cases often with an ± elongated, porrect, central radius) that are initially covered by the lepidote scales. The extent to which the central radius protrudes varies (even in the Anja population), with the more hirsute type represented by *Decary 7554* (type of *C. ikopae*), *van Ee et al. 804* and *2038* (see Fig. 5H and I). In these specimens a long protruding central radius is present in most trichomes, even in the lepidote trichomes on the shoots and buds. In comparison, the type of *C. stanneus* var. *hirsutus* is not particularly hirsute. Besides *C. stanneus* var. *hirsutus*, Radcliffe-Smith (2016) also described *C. crocodilorum* var. *platyaster* and *C. parvifructus*, both typified by specimens from Zombitsy, in Toliara Province, and he furthermore considered them part of the Adenophorus Group (as opposed to *C. stanneus* and *C. ikopae*, which he placed in his Stanneus and Tiliifolius Groups, respectively). The type of *C. baldauffii* approaches the type of *C. ikopae* in its dense, stiff indument, and has relatively small leaves and short inflorescences, but it conforms well to the characterization of *C. stanneus* given above, including the presence of laminar glands along the midrib. The type of *C. perrieri* has only young leaves (with laminar glands), but these, and the inflorescences, match well those of the type of *C. stanneus*.

Leandri (1939) placed *Croton stanneus* in his Stanneus Group, which was characterized by the silvery lepidote undersides of the leaf blades (which separated it from the Adenophorus Group), staminate flowers with more than 12 stamens, no petals in the pistillate flowers, and the leaf blades at least half as wide as long. It was distinguished from the other three species recognized in the group by having glands at the insertion of the secondary veins on the leaf undersides, whereas the others lack them.

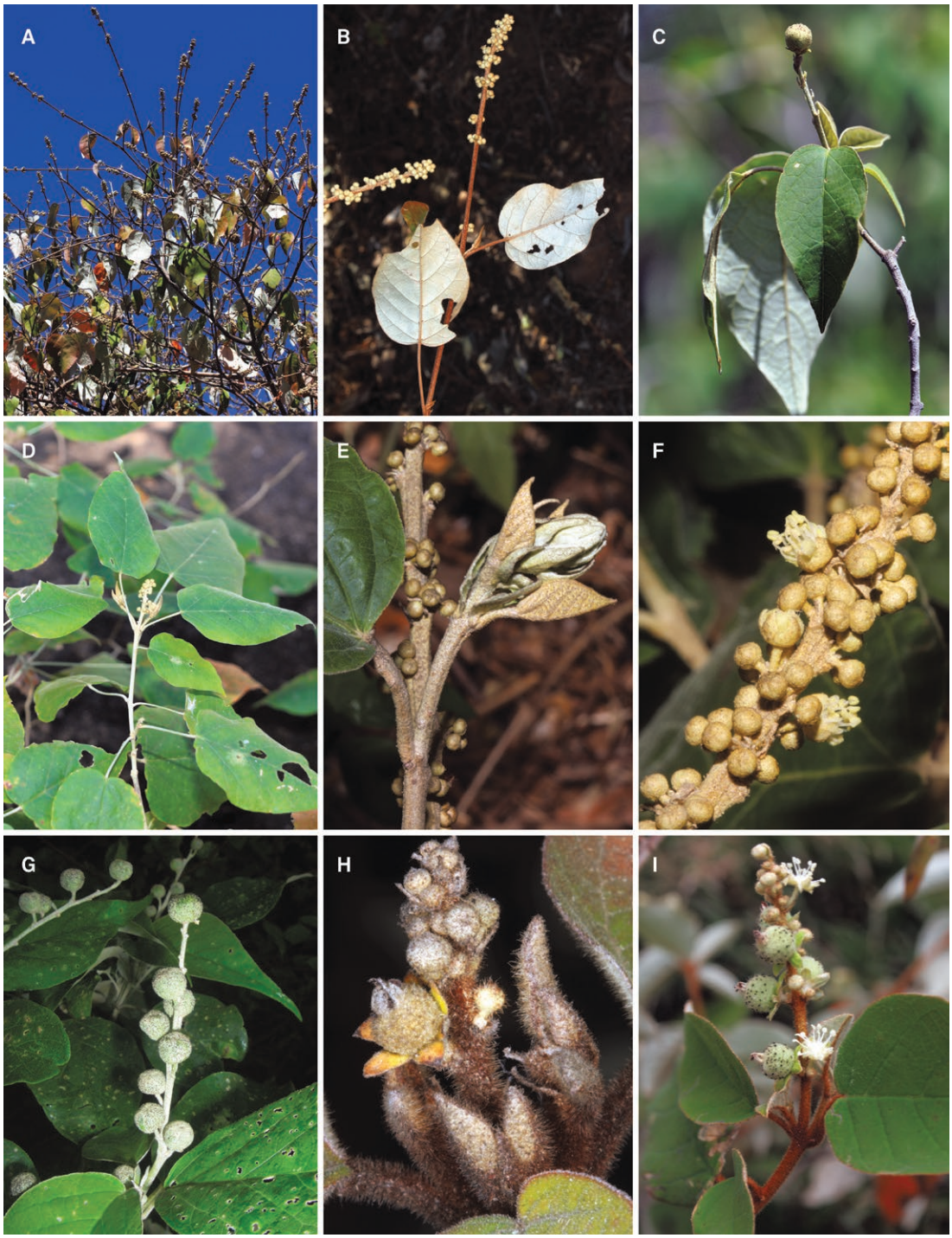

Fig. 5. *Croton stanneus* Baill. **A.** Fertile branches of a small tree in the middle of the dry season, showing senescent leaves and partially deciduous habit, and unusually elongate inflorescences with irregular spacing of the cymules; **B.** Underside of leaves, showing the typical silvery ("stanneus") color and conspicuous divergent glands at the junctions of the secondary veins with the midvein; **C.** Branch showing contrasting leaf surfaces and single fruit and short persistent sepals; **D.** Branch showing the terminal position of the inflorescence; **E.** Base of an inflorescence and an axillary shoot showing young leaves and the conspicuous falcate stipules; **F.** Inflorescence showing unevenly spaced cymules of staminate flowers and depressed globose buds; **G.** Infructescence with immature capsules showing scattered darker trichomes; **H-I.** Inflorescences and young capsules in more hirsute, ferrugineous forms. Note the mixed cymules and young fruits with erect styles and speckled surface in I.
[**A-B:** *van Ee et al. 2039*; **C:** *Gillespie 10802*; **D:** *van Ee et al. 2158*; **E-F:** *van Ee et al. 2160*; **G:** *Nusbaumer 3379*; **H:** *van Ee et al. 2038*; **I:** *van Ee et al. 804*] [Photos: **A-B, D-F, I:** P. Berry; **C:** L. Gillespie; **G:** L. Nusbaumer]

Additional specimens examined. – **Madagascar. Prov. Antananarivo:** Analamanga Reg., Ankazobe Distr., Talata-Angavo, Manontanitsiloza, Ankafobe forest, 18°07'09"S 47°11'36"E, 1455 m, 31.VII.2005, *Lehavana & Rasolofonirina 391* (MO, P, TAN); Sur le Manambolo, affluent de la Betsiboka, 900 m, XI.1925, *Perrier de la Bâthie 17401* (P); Angavokely, 8.VI.1971, *Schmitt 374* (P); Carion [Nandihizana], 28.VI.1971, *Schmitt 487* (P). **Prov. Antsiranana:** Diana Reg., Ambanja Distr., Tsaratanana, Camp III (piste vers Camp II), 16.II.1966, *Debray H362D* (P); SAVA Reg., Vohemar Distr., Daraina, Bobanora forest, 13°13'13"S 49°46'19"E, 410 m, 3.III.2003, *Gautier 4204* (G); *ibid. loc.,* Antsahabe forest, 13°12'36"S 49°33'25"E, 550 m, 11.I.2004, *Nusbaumer 906* (G, MICH, MO); Montagne d'Ambre, 12°34'56"S 49°07'44"E, 1106 m, 4.I.2002, *Nusbaumer 3379* (G); Antsahabe forest, 13°12'36"S 49°33'41"E, 420 m, 6.XI.2005, *Razafitsalama et al. 786* (CNARP, G, MO, P, TAN); Montagne d'Ambre, 12°34'56"S 49°07'45"E, 1020 m, 7.I.2008, *Razanajatovo et al. 26* (G). **Prov. Fianarantsoa:** Amoron'i Mania Reg., Ambatofinandrahana, P.K. 2 route de Fenoarivo, Centre Ouest, IX.1956, *Bosser 9862* (MO, P); Ihorombe Reg., Ambia, c^{ton} et poste Iakora, bord de l'Ianaivo, 570 m, 16.V.1957, *Cours 5200* (P); Anketsihetsy, c^{ton} Begogo, poste Iakora, 600 m, 18.VII.1957, *Cours 5202* (P); Atsimo-Atsinanana Reg., Antamboara, c^{ton} de Ranotsara Sud, distr. Midongy du Sud, massif de l'Ivakoany, montagne Analanavelo, s.d., *Cours 5215* (P); Haute Matsiatra Reg., Anja Community Reserve, E of RN 7, c. 9.5 km W of Ambalavao, 21°51'04"S 46°50'37"E, 970 m, 29.XI.2012, *Gillespie 10802* (CAN, MICH, MO, TAN); Ambatofinandrahana, X.1963, *Morat 122* (P); Haie autour d'un village près du Mt Ambohimalaza (Bassin du Mahatriaka), 1500 m, VI.1912, *Perrier de la Bâthie 9661* (P); Route Nationale 7, c. 15 km S of Fianarantsoa, c. 30 km N of Ambalavao [village of Anjamana], 21°34'51"S 47°01'12"E, 1170 m, 7.II.2009, *van Ee et al. 804* (MICH); *ibid. loc.*, 1148 m, 23.VII.2015, *van Ee et al. 2038* (MICH, TAN); Anja Park, 21°51'09"S 46°50'44"E, 940-971 m, 6.VIII.2015, *van Ee et al. 2157* (MICH, TAN); *ibid. loc.*, *van Ee et al. 2158* (MICH, TAN); *ibid. loc.*, 21°51'09"S 46°50'46"E, 941-970 m, 6.VIII.2015, *van Ee et al. 2159* (MICH, TAN); *ibid. loc.*, 21°51'07"S 46°50'43"E, 941-970 m, 6.VIII.2015, *van Ee et al. 2160* (MICH, TAN). **Prov. Mahajanga:** Betsiboka Reg., Maevatanana Distr., Antsiafabositra, Bemanevika, 17°13'28"S 46°59'37"E, 350 m, 7.V.2005, *Andrianjafy et al. 1000* (MO; P, TAN); Sofia Reg., env. de Mandritsara, IV.1974, *Morat 4467* (MO, P); Soalala, 12.VII.1977, *Rakotozafy 1920C* (MO, TAN); Borziny Distr., Tsiningia, Amberoverobe, 15°34'13"S 47°21'55"E, 60 m, 23.XI.2004, *Razakamalala et al. 1877* (MO, P, TEF); au lieu dit Analankeboka, à l'W de Bealanana, 20.XI.1966, *Service Forestier 27103* (G, K, MO, P). **Prov. Toamasina:** Alaotra-Mangoro Reg., Amparafaravola Distr., Petites forêts à l'W d'Analamanatrika, c^{ton} d'Ambohijanahary, 1200 m, 5.I.1945, *Cours 2167* (MO, P); avant la chute de Maningory, 850 m, 15.XII.1944, *Homolle 1966* (P). **Prov. Toliara:** Atsimo-Andrefana Reg., Sakaraha Distr., Zombitsy National Park, 22°53'06"S 44°41'47"E, 800 m, 16.I.2006, *Anderberg et al. 120* (MO, S); *ibid. loc.*, 22°46'21"S 44°40'25"E, 540 m, 8.IV.2006, *Andriamihajarivo et al. 879* (MO, P); Sakaraha Distr., Mahaboboka, Marotsiraka, Analavelona forest, 22°39'08"S 44°11'19"E, 1055 m, 21.II.2009, *Andriamihajarivo et al. 1670* (MO; P, TAN); Zombitsy, XII.1959, *Bosser 13873* (P); *ibid. loc.*, XII.1960, *Bosser 13995* (P); 20 km de Sakaraha, route d'Ankazoabo, 21.II.1970, *Bosser 19969* (P); Vallée du Fiherenana, 300-500 m, 1-2.VIII.1928, *Humbert & Swingle 5067* (P); Anosy Reg., Bassin supérieur du Mandrare (SE): col et sommet de Marosoui, 1000-1400 m, 14-15.XI.1928, *Humbert 6592* (MO, P); Ivakoany Massif de l'Ivakoany (centre S), pentes occidentales, 1000-1200 m, 17.XII.1928, *Humbert 7029* (P); Haute vallée de la Manambolo, affluent de l'Ionaivo, 900-1100 m, XI.1933, *Humbert 12144* (P); forêt d'Analamarina, vallée de l'Hazoroa (affluent de la Taheza, bassin de l'Onilahy) au Sud de Sakaraha, c. 300 m, 6-9.XII.1946, *Humbert 19647* (MO); Zombitsy, III.1960, *Keraudren 482* (P); *ibid. loc.*, 600-800 m, 1.XI.1960, *Leandri 3544* (P); *ibid. loc.*, 600-800 m, 1.XI.1960, *Leandri 3570* (P); *ibid. loc.*, 600-800 m, 2.XI.1960, *Leandri 3611* (P); forêt d'Analavolona, entre le Fiherenana et la Manombo, 1000 m, V.1933, *Perrier de la Bâthie 19190* (P); Sakaraha, Mahaboboka, Marotsiraka Betsileo, Analavelona forest, 22°39'36"S 44°11'51"E, 923 m, 13.XI.2010, *Rakotoarivelo et al. 407* (MO, P, TAN); Andohahela, 24°31'S 46°38'E, 600-1700 m, 5-22.VII.1993, *Randriamampionona 522* (K, MICH, MO); Zombitsy, 22°53'S 44°38'E, 700-800 m, 23.IV.1998, *Randrianaivo et al. 192* (MO, P); *ibid. loc.*, 22°49'14"S 44°42'26"E, 817 m, 22.V.2004, *Rogers 599* (MO); Androy Reg., Ampandrandava, 1000 m, 1943, *Seyrig 53* [= *Herb. Jard. Bot. Tana 5733*] (P); Zombitsy, 22°53'09"S 44°41'32"E, 810 m, 24.VII.2015, *van Ee et al. 2039* (MICH, TAN). **Sine loc.:** 1952-1963, *Dequaire E39* (P).

Species of the Adenophorus Group from northern Madagascar and Mayotte

Croton adenophorus Baill. in Adansonia 1: 153. 1861 [as *adenophorum*] (Fig. 1C, 2B, 4E-F, 6).

– *Croton adenophorus* var. *genuinus* Müll. Arg. in A. DC., Prodr. 15(2): 589. 1866 [nom. inval.].

≡ *Oxydectes adenophora* (Baill.) Kuntze, Revis. Gen. Pl. 2: 610. 1891.

Lectotypus (designated here): **Madagascar. Prov. Antsiranana:** Diana Reg.: Nossi-bé, 1837, *Richard 214* (P [P00123689]!; isolecto-: P [P00123690]!). **Syntypi: Madagascar. Prov. Antsiranana:** Nossi-bé, s.d., *Richard 574* (P [P00123691]!); *ibid. loc.*, 1849, *Boivin 2187* (G [G00446358, G00446359]!, P [P00301515]!).

= *Croton payerianus* Baill. in Adansonia 1: 154. 1861 [as *payerianum*]. ≡ *Oxydectes payeriana* (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891. **Lectotypus** (designated here): **Madagascar. Prov. Antsiranana:** " Nossibé", 1849, *Boivin 2187* (P [P00389508]!; isolecto-: G-DC [G00311984]!, G [G00446358, G00446359]!, P [P00389509, P00404480, P00404481, P00123684]!).

= *Croton subaemulans* Baill. in Bull. Mens. Soc. Linn. Paris 2: 850. 1890. **Typus: Madagascar:** "Central Madagascar", *Baron 5795* (holo-: K [K000422590]!; iso-: P [P00133593]!), **syn. nov.**

= *Croton tenuicuspis* Baill. in Bull. Mens. Soc. Linn. Paris 2: 927. 1891. **Typus: Madagascar:** "Madag. centr.", *Baron 5846* (holo-: P [P00133364]!, iso-: K [K000422590]!), **syn. nov.**

= *Croton tulasnei* Baill. in Adansonia 1: 156. 1861. ≡ *Oxydectes tulasnei* (Baill.) Kuntze, Revis. Gen. Pl. 2: 613. 1891. **Lectotypus** (designated here): **France. Dept. Mayotte:** Bouzi, 1850, *Boivin s.n.* (P [P00133305]!; isolecto-: P [P00133306, P00466148]), **syn. nov.**

Shrubs or *trees*, 1-9 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches. Branches flattened on new growth but becoming terete with age, bright green and sparsely covered with whitish stellate indument, soon turning reddish brown, glabrous, ± glossy. Bark smooth and conspicuously lenticellate. Stipules 6-17 × 2-4 mm, lanceolate or auriculate, tapering to a

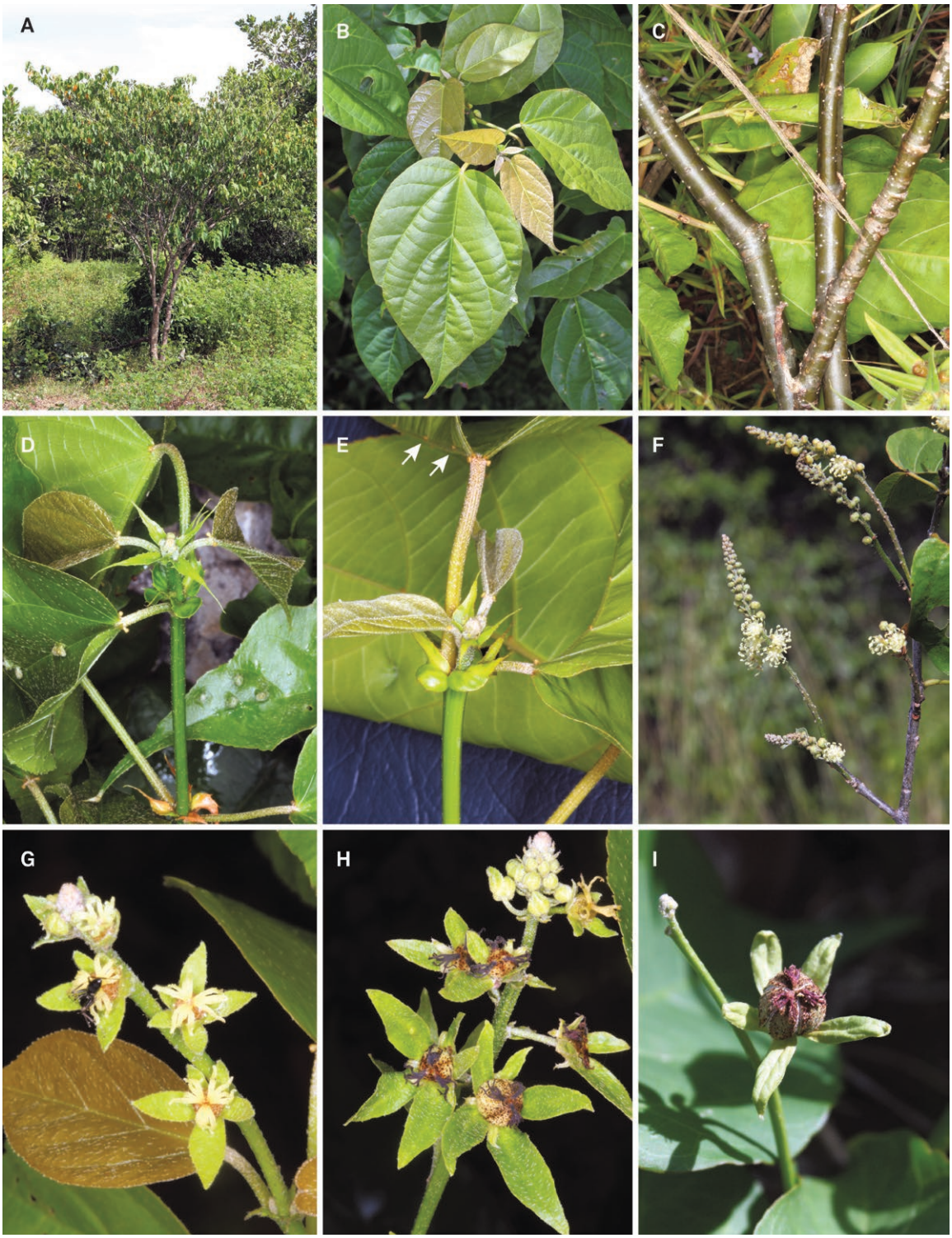

Fig. 6. *Croton adenophorus* Baill. **A.** Habit, in a heavily disturbed and cultivated area along RN 6, near turnoff for Ampampamena airstrip; **B.** Leaves; **C.** Smooth bark on young twigs; **D-E.** Close-ups of stipules and leaf bases; note the auriculate, elongate stipules, the acropetiolar glands, and the laminar glands on the adaxial side of the lamina (arrows); **F.** Inflorescence with staminate flowers and buds; **G-H.** Inflorescences with pistillate flowers; note the green, unequal sepals, the patent stigmas, and the variable occurrence of petals; **I.** Capsule.
[**A, F:** *van Ee et al. 2288*; **B, G:** *van Ee et al. 2382*; **C:** *van Ee et al. 2287*; **D, H:** *van Ee et al. 2384*; **E:** *van Ee et al. 2295*; **I:** *van Ee et al. 1165*]
[Photos: **A, F:** K. Kainulainen; **B-E, G-I:** P. Berry]

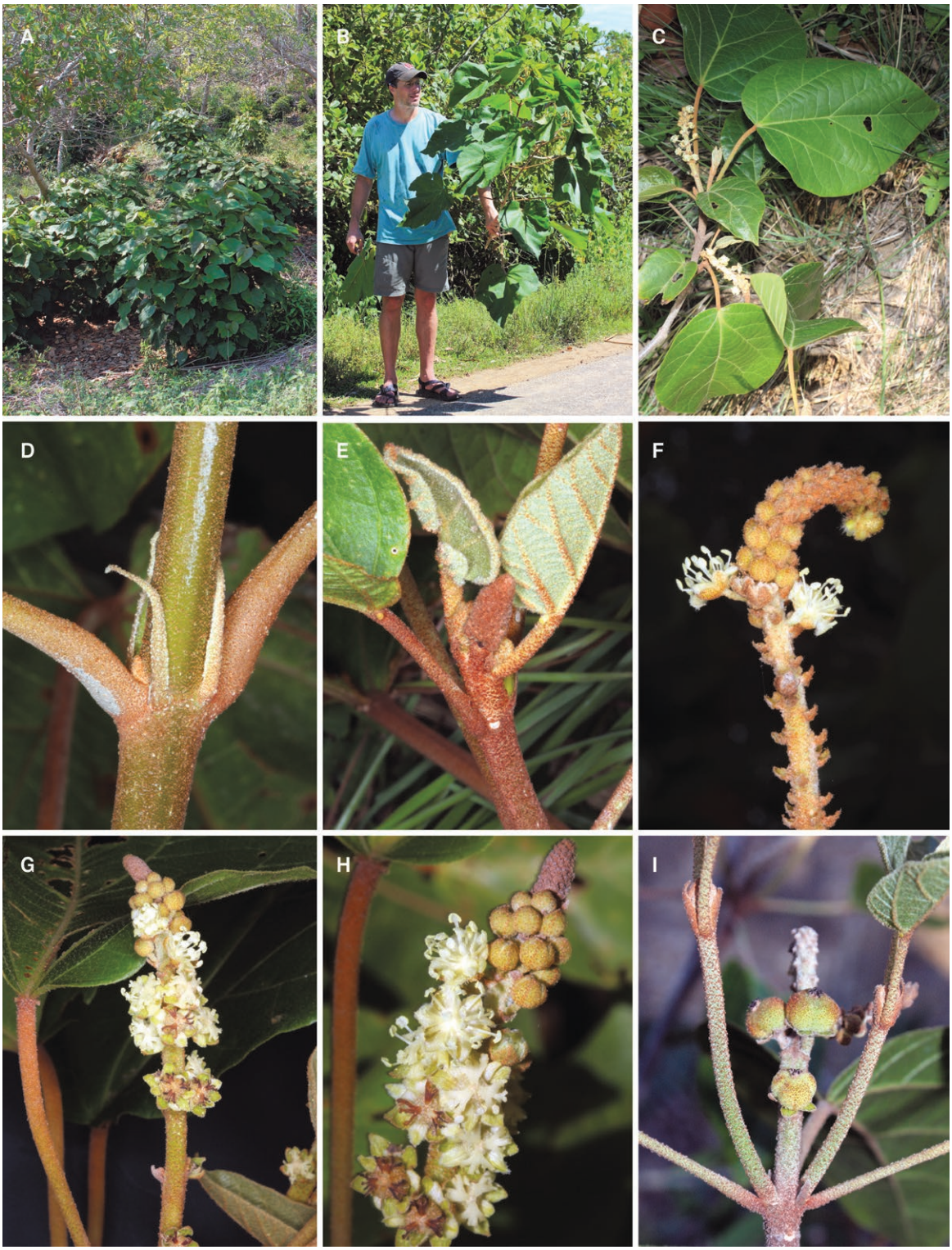

Fig. 7. *Croton bathianus* Leandri **A.** Coppiced individuals; **B.** BVE with a sucker shoot; **C.** Leaves; **D.** Stipules; **E.** Young leaves and inflorescence; note the dense covering of ferrugineous, granulate trichomes; **F.** Staminate flowers; **G-H.** Inflorescence with staminate and pistillate flowers; note the presence of petals in the pistillate flowers; **I.** Young fruits.
[**A:** *van Ee et al. 1139*; **B:** *van Ee et al. 2290*; **C, I:** *van Ee et al. 1140*; **E:** *van Ee et al. 2296*; **D, F:** *van Ee et al. 2383*; **G-H:** *van Ee et al. 2289*]
[Photos: **A:** B. van Ee; **B-I:** P. Berry]

thin apex, sometimes with marginal glands (and glandular filaments), caducous. *Leaves* opposite. Petioles 0.6-8.5 cm, adaxially canaliculate, stellate-pubescent, usually with a pair of subsessile, concave, discoid, yellow, glabrous glands (0.3-0.8 mm in diam.) by the base of the lamina. Leaf blades membranaceaous to chartaceous, glandular crenulate, denticulate, or serrate, ovate, 4.2-17.0 × 2.3-11.5 cm, apex acute to acuminate, base rounded to cordate; abaxial and adaxial surfaces sparsely stellate-pubescent on young leaves, ± glabrous on older leaves, pale green when fresh (turning orange in old leaves) and drying matte pale green to brown; venation evident on the adaxial side, prominent below, with 5-10 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation; glands are usually present in some of the axils of the secondary veins on the abaxial side (Fig 1C). *Inflorescences* terminal, raceme-like thyrses, 1.5-22 cm long, terminal, often appearing unisexual, or bisexual with pistillate flowers at the base and staminate flowers at the distal end, axes stellate-pubescent, flattened; bracts narrowly triangular, 1.0-3.5 mm long. *Staminate flowers* with stellate-pubescent, subglobose buds 1.8-2.3 mm diam., pedicels elongating from bud to anthesis, 1.0-3.5 mm long; sepals 5, pale green, shortly connate at base, lobes broadly triangular to ovate, often unequal in size, 1.5-3.5 × 1.3-2.0 mm, apex acute, inflexed at anthesis, abaxially stellate-pubescent, adaxially sparsely ciliate, margins densely ciliate; petals 5, yellowish, elliptic-spatulate, 1.9-2.4 × 0.7-1.0 mm, recurved at anthesis, abaxially stellate-pubescent and papillose, adaxially ciliate towards apex, margins densely ciliate; disc glands 5, opposite the sepals, sessile, deltoid, truncate or with an apical depression, c. 0.3 × 0.5 mm, yellow; stamens 10-16, white, filaments 1.6-3.1 mm long, ciliate, anthers broadly elliptic, c. 0.7 × 0.6 mm; receptacle pilose. *Pistillate flowers* with stellate-pubescent buds, 2-3 mm diam., pedicels 2-4(-9) mm long; sepals 5, elliptic, spreading at anthesis, often unequal in size, 2.5-11.5 × 1.1-2.5 mm, apex acute, shortly connate at base, glandular margin, abaxially and adaxially subglabrous, sometimes bearing glands similar to those on the leaves, bright green, persistent in fruit; petals usually absent/reduced, but when present, c. 1.5 × 0.3 mm, abaxially stellate-pubescent, adaxially glabrous, margin ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.3 × 0.6 mm, pale yellow; ovary densely covered by ferruginous to dark brown, stellate trichomes, pale green, globoid-ellipsoid, 2-3 mm in diameter, styles 3, 2-3 mm long, each branch flattened and 1-3 times bifurcate, the first bifurcation often congested and fused, spreading, recurved at the apices, abaxially stellate-pubescent, adaxially glabrous, (pale) yellow, turning brown, persistent. *Capsules*, 5.0-6.0 × 5.5-8.0 mm, smooth, pale brown, covered with contrasting dark brown stellate trichomes, exocarp not separating, endocarp woody, 0.3-0.4 mm thick (Fig. 4E); columella 3-4 mm long, cornute, capitate. *Seeds* ± compressed-ellipsoid, 3.1-4.1 × 2.3-3.1 × 1.8-2.5 mm (Fig. 4F); testa glossy, verrucose, brown; caruncle reniform, c. 0.5 × 1 mm.

Phenology. – We have seen flowering specimens from August to April, and in bud in May (we have not seen any specimens from June or July), so it is likely that this species flowers more or less continuously throughout the year.

Distribution, habitat and ecology. – *Croton adenophorus* occurs both in evergreen forest and in secondary or degraded vegetation, and it is often collected in riparian or moist habitats. It occurs from sea level to c. 450 m elevation. It is locally frequent in the Sambirano Domain (Humbert, 1955), and there is also a population from the littoral forest of Analabe in northernmost Vohémar, Antsiranana Province on the north-east coast (Fig. 2B). *Cours 3207*, collected in the Mainampango forest (Andapa, SAVA Reg.), was indicated as a shade plant in a vanilla plantation. It is possible that the disjunct outliers from southern Mahajanga, i.e., *Decary 2359* from Morafenobe, *Service Forestier 16* from Tsingy de Namoroka, and *van Ee et al. 1165* from Ambodiriana, were also escaped from cultivation, since this species is not only used as a shade plant but also in hedgerows (see *Randrianarivelo et al. 145*). The only known specimen from Mayotte is *Boivin s.n.* (the type of *C. tulasnei*), collected in 1850, and it is therefore uncertain whether *C. adenophorus* still occurs there, and if the gathering was made from a native or introduced plant.

Conservation assessment. – Since *C. adenophorus* is widespread and known from numerous localities, including the protected areas of Ampasindava, Galoko, and Manongarivo, we assign the species as "Least Concern" [LC] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Bemasaho" *(Rabenantoandro et al. 1070),* "Hazomafaiky" *(Madiomanana & Ammann 181),* "Hazomafaitra" *(Nusbaumer & Tahinarivony 2977),* "Matifioditra" *(Cours 3207),* "Mavokely" *(Decary 999),* "Sakaiala" *(Randrianarivelo 145),* "Sakaitomendry" *(Randrianarivelo 145).*

Notes. – The species epithet *adenophorus* means "bearer of glands."

This species is distinct in the glabrous and glossy reddish-brown bark; acuminate leaves that usually dry matte green; contrasting white stellate hairs on the young leaves (and shoots), whereas the mature leaves are ± glabrous (Fig. 1C); the usually large, foliaceous stipules that may be auriculate at the base and then taper to a fine point (Fig. 6D-E); the flattened, patent stigmas; and the often unequal and foliaceous, bright green sepals that sometimes have glands similar to those

on the leaves. The lectotype of *C. adenophorus* (P [P00123689]), which was collected by Achille Richard, bears a label with the name "Croton acuminatum" in Richard's hand, which Baillon (1861) cited in his protologue. Baillon (1861) also cited *Boivin 2187* at P [P00301515] as a syntype of *C. adenophorus*, which he annotated as such, despite citing and annotating other sheets of the same collection number as syntypes of *C. payerianus* on the next page. Since *C. adenophorus* and *C. payerianus* were published in the same article, either one could be the accepted name, but we follow the precedent of Leandri (1939), who synonymized *C. payerianus*.

It is important to note that our concept of *C. adenophorus* differs from that of Leandri (1939). By including *C. loucoubensis* as a synonym of *C. adenophorus*, Leandri confounded this group, and his description of *C. adenophorus* corresponds to what we recognize here as *C. loucoubensis*. He then went on to recognize *C. subaemulans*, which is really the same as the true *C. adenophorus*. Baillon (1861) separated *C. tulasnei* from his *C. payerianus* (to us, a synonym of *C. adenophorus*) by its poorly developed or absent laminar glands, somewhat different leaf shape (oval-ovate and acute vs cordate and acuminate), linear stipules, and different branching pattern of the stigma. However, similar variation in the shape of the leaves and stipules, and in the number of laminar glands, is also seen within populations of *C. adenophorus* in Madagascar, and the stigma branches may vary from 1-3 times bifurcate (Fig. 6G-H). We therefore do not consider *C. tulasnei* as a distinct species from *C. adenophorus*.

Additional specimens examined. – **Madagascar. Prov. Antsiranana :** Diana Reg., Nosy Be, env. d'Ambatozavany, 50-250 m, 14.XII.1967, *Bernardi 11863* (G, K, P); Nosy Be, 1847-1852, *Boivin s.n.* (G, P); SAVA Reg., forêt de la montagne de Mainampango Est, village Ambalavoanio, c. 450 m, 1.III.1949, *Cours 3207* (P); Ampasindava, 10 m, 14.VIII.1957, *Cours 5232* (P); Analanantsoa, Ambodisakoana, 14°04'S 48°15'E, 40 m, 1.XI.1994, *Derleth 145* (G, K, MO, P, TAN); *ibid. loc.*, 14°04'S 48°15'E, 50 m, 3.IV.1996, *Gautier 2966* (G, K, MO, P); Manongarivo RS, Beraty, 14°01'51"S 48°14'53"E, 65 m, 22.X.2012, *Gillespie et al. 10651* (CAN, MICH, MO, TAN); Ambanja, Antsatsaka-Ambato, 13°27'23"S 48°32'39"E, 26 m, 30.VIII.2002, *Hong-Wa 71* (MO, P, TAN, TEF); Vallée de la Lokoho (NE), près d'Ambalavohino, 75-300 m, 9-10.I.1949, *Humbert & Cours 22834* (K, P); Ampasindava, 7.IX.1967, *Jacquemin H501J* (P); Ampasindava, 13°45'39"S 48°06'38"E, 370 m, 29.XI.2008, *Madiomanana & Ammann 181* (G, K, MO, P, TEF, WAG); Vohemar Distr., Nosibe, Anjiabe, Anaborano, Analabe forest, 13°04'08"S 49°54'20"E, 5 m, 9.XII.2004, *Manjakahery & Sola 80* (MO); Ampasindava, 13°48'17"S 48°10'48"E, 218 m, 29.XI.2007, *Nusbaumer 2615* (G, K, MO, P, TEF); *ibid. loc.*, 13°43'59"S 48°04'15"E, 141 m, 23.XI. 2008, *Nusbaumer & Tahinarivony LN 2966* (G, MO, P, TEF); *ibid. loc.*, 13°46'09"S 48°06'12"E, 312 m, 24.XI.2008, *Nusbaumer & Tahinarivony LN 2977* (G, K, MO, P, TEF); Anaborano, 13°04'42"S 49°54'13"E, 25 m, 2.XI.2002, *Rabenantoandro et al. 1070* (MICH, MO, P); Analabe forest, 13°04'14"S 49°53'40"E, 22.II.2003, *Rabevohitra et al. 4481* (MO, P, TEF); *ibid loc.*, 13°04'09"S 49°54'08"E, 18 m, 11.X.2004, *Randrianarivelo et al. 145* (MICH, MO); Ambilobe Distr., Beramanja, Anketrabe Bilinta, Ambahatra, Galoko forest, 13°36'11"S 48°42'37"E, 430 m, 7.X.2013, *Randriatsivery et al. 479* (G, MO, P, TAN); Analabe forest, 13°04'43"S 49°54'04"E, 13.V.2004, *Razakamalala et al. 1270* (MO, P, TEF); Nosy Be, 25.IX.1951. *Reserves Naturelles 2992* (P); *ibid loc.*, s.d., *Richard 180* (P); *ibid loc.*, 12.III.1971, *Schmitt 252* (P); RN [Route Nationale] 6, 41 km N of Ambanja, 13°28'41"S 48°44'03"E, 25 m, 2.XI.2009, *van Ee et al. 1133* (MICH); *ibid loc.*, *van Ee et al. 1134* (MICH); *ibid loc.*, *van Ee et al. 1135* (MICH); RN 6, 41 km N of Ambanja, 13°31'23"S 48°41'28"E, 20 m, 2.XI.2009, *van Ee et al. 1141* (MICH); RN 6, close to turn off for Ampampamena airstrip, 13°29'33"S 48°38'12"E, 8 m, 27.II.2016, *Van Ee et al. 2287* (MICH, TAN); *ibid loc.*, *van Ee et al. 2288* (MICH, TAN); RN 6, N of the turnoff to Belinta, 13°30'22"S 48°42'05"E, 17 m, 27.II.2016, *van Ee et al. 2291* (MICH, TAN); *ibid loc.*, 13°30'09"S 48°42'20"E, 22 m, 27.II.2016, *van Ee et al. 2292* (MICH, TAN); *ibid loc.*, *van Ee et al. 2293* (MICH, TAN); *ibid loc.*, 13°28'56"S 48°43'36"E, 17 m, 27.II.2016, *van Ee et al. 2294* (MICH, TAN); RN 6 E of Ampampamena, 13°30'46"S 48°40'30"E, 34 m, 27.II.2016, *Van Ee et al. 2295* (MICH, TAN); RN 6 E of Ampampamena and south of Ambatomainty, 13°28'26"S 48°44'20"E, 21 m, 27.II.2016, *van Ee et al. 2299* (MICH, TAN); RN 6, PK [Pointe Kilometrique roadmarker] 525, 57 km N of Ambanja, 13°26'12"S 48°47'34"E, 17 m, 8.III.2016, *van Ee et al. 2382* (MICH, TAN); Ambanja, Nosy Be, 16.XII.1921, *Waterlot 289* (P); *ibid loc.*, *Waterlot 291* (P); Manongarivo, Ambahatra, 13°58'S 48°27'E, 400 m, 15.III.1999, *Wohlhauser 60050* (G, K, MO, P); Manongarivo, Antafia Be, Amatolary, Moyen Ambahatra, 13°55'S 48°27'E, 230 m, 7.V.1999, *Wohlhauser SW60113* (G, K, MO, P). **Prov. Mahajanga :** Sofia Reg., Analalava Distr., Maromandia (Befotaka), 16.IX.1922, *Decary 999* (P); Haut Bemarivo, VIII.1907, *Perrier de la Bâthie 9556* (P); Melaky Reg., env. de Morafenobe, 3.X.1923, *Decary 2359* (P); Boeny Reg., Tsingy de Namoroka, 4.IV.1933, *Service Forestier 16* (P); RN 6, PK 449, 19 km S of Ambanja, 13°46'56"S 48°20'59"E, 25 m, 3.XI.2009, *van Ee et al. 1142* (MICH); RN 6, PK 413, 55 km S of Ambanja, 14°00'04"S 48°10'06"E, 100-140 m, 3.XI.2009, *van Ee et al. 1147* (MICH); Betsiboka Reg., RN 4, PK 227, 88 km S of Moevaharana, 17°31'03"S 46°58'41"E, 200 m, 6.XI.2009, *van Ee et al. 1165* (MICH); RN 6 south of Ambanja, 13°55'44"S 48°12'58"E, 201 m, 8.III.2016, *van Ee et al. 2384* (MICH, TAN); Along Route Nationale 6, at PK 399, 14°05'22"S 48°06'42"E, 214 m, 8.III.2016, *van Ee et al. 2386* (MICH, TAN); *ibid loc.*, *van Ee et al. 2388* (MICH, TAN).

Croton bathianus Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7 : 80. 1939 [as *bathiana*] (Fig. 1D, 2C, 4G-H, 7).

Lectotypus (designated here) : **Madagascar. Prov. Mahajanga :** Haut Bemarivo, X.1907, *Perrier de la Bâthie 9545* (P [P00301483]! ; isolecto- : P [P00127503]!). **Syntypi : Madagascar. Prov. Mahajanga :** Maromandia, presqu'île Radama, 13.X.1922, *Decary 1133* (P [P00389631]!), *ibid. loc.,* 11.X.1922, *Decary 1174* (P [P00301482]!); collines sèches du Haut Bemarivo, X.1906, *Perrier de la Bâthie 9633* (P [P00389630]!).

Shrubs or small *trees* 2-4 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches. Branches flattened on new growth but becoming terete with age, young shoots pale green and densely covered with a reddish, granulate, stellate indument, soon turning glabrous and matte pale gray. Stipules 4-20 × 1.2-2 mm, lanceolate, early caducous. *Leaves* opposite. Petioles 2-9(-43) cm, adaxially canaliculate, stellate, usually with a pair of subsessile, concave, discoid acropetiolar glands (0.5-1 mm diam.). Leaf blades chartaceous, subentire to shallowly undulate or denticulate, ovate, 5-16(-38) × 4-12(-30) cm, apex acuminate, base rounded to cordate ; both sides with

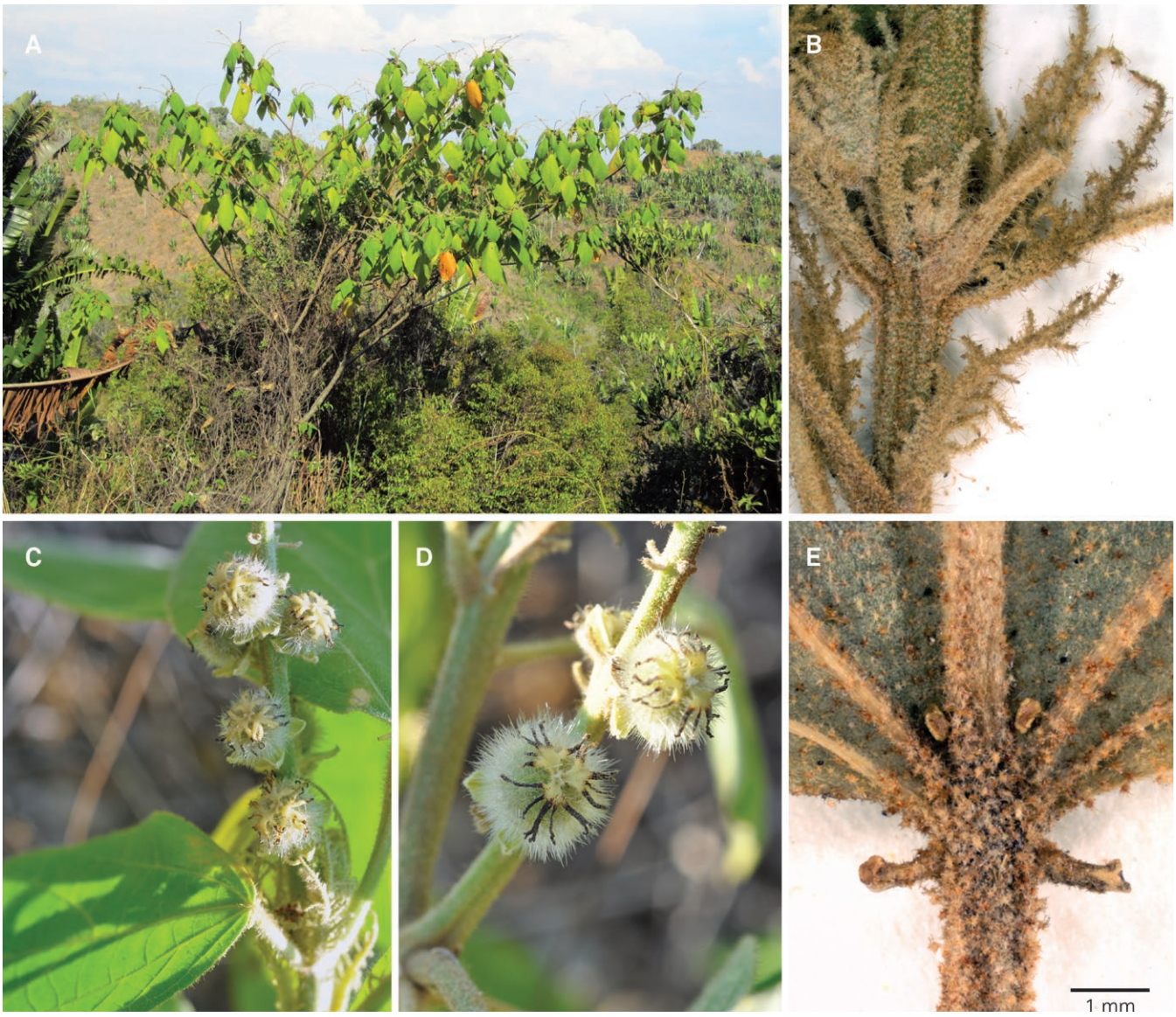

Fig. 8. *Croton loucoubensis* Baill. **A.** Habit, growing in secondary vegetation in Mahajanga Province, S of Ankaromyhely, 111 km N of Antsohihy along RN 6; **B.** Fimbriate stipules; **C.** Inflorescence with pistillate flowers; note the persistent bracts; **D.** Pistillate flowers, with patent, multiply bifurcating stigmas; **E.** Underside of a leaf showing the pubescent, stipitate acropetiolar glands, the palmate venation of the first pairs of secondary veins, and a pair of laminar glands.
[**A-D:** *Gillespie et al. 10646*; **E:** *Antilahimena 154*] [Photos: **A, C-D:** G. Levin; **E:** P. Antilahimena]

a persistent, scabrous stellate indument, green when fresh, drying matte brownish green; venation evident, with 6-11 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation; venation prominent abaxially, with conspicuous, stipitate, compressed-discoid glands in the axils of some of the secondary veins (Fig. 1F), rarely absent. *Inflorescences* terminal, raceme-like thryses 3-15 cm long, with 1-3(-4) pistillate flowers near the base and numerous staminate flowers in the upper ½ to 2/3, axes stellate, flattened; bracts ovate to triangular, c. 0.7-2.3 mm long, caducous. *Staminate flowers* with stellate, subglobose buds 2-2.6 mm diam., pedicels elongating from bud to anthesis, 1-5 mm long; sepals 5, pale green, shortly connate at base, lobes broadly triangular-ovate, 2-2.6 × 1.3-3 mm, apex acute, inflexed at anthesis, abaxially stellate-pubescent, adaxially sparsely pubescent, margins ciliate; petals 5, greenish white, elliptic to spatulate, 2-3 × 0.8-1.3 mm, recurved at anthesis, abaxially stellate and papillose, adaxially glabrous, margins densely ciliate; disc glands 5, opposite the sepals, sessile, triangular, truncate, c. 0.6 × 0.6 mm; stamens 12-17, white, filaments 1.5-2.7 mm long, glabrous, anthers broadly elliptic, 0.7-1 × 0.6-0.9 mm; receptacle pilose. *Pistillate flowers* with stellate-pubescent ellipsoid buds c. 2 mm diam., pedicels 1-5 mm long; sepals 5, elliptic-ovate, spreading at anthesis, 3-4.5 × 1.7-2 mm, apex acute, shortly connate at base, abaxially and adaxially stellate-pubescent, persistent in fruit; petals, 3-3.5 × 1 mm, spatulate, abaxially stellate-pubescent and papillose, adaxially glabrous, margin ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal, 0.5 × 0.7 mm, yellow; ovary densely covered by ferrugineous to dark brown, stellate trichomes, globoid-ellipsoid, 2-3 mm diam., styles 3, 2-2.5 mm long, each branch flattened and 3-4 times bifurcate, often with the first bifurcation congested and fused to appear 4 furcate, spreading, recurved at the apices, abaxially stellate-pubescent, adaxially glabrous, persistent. *Capsules* broadly globoid, 4.5-5.6 × 6.5-7.5 mm, smooth, pale brown, covered with dark brown stellate trichomes (Fig. 4G), exocarp not separating, endocarp woody, 0.5-0.7 mm thick; columella 3.0-4.5 mm long, cornute, capitate, the angles fimbriate. *Seeds* ± compressed-ellipsoid, 3.3-4 × 2.5-3 × 2-2.5 mm (Fig. 4H); testa glossy, verrucose, brown; caruncle reniform, 0.4-0.7 × 0.7-1.3 mm.

Phenology. – Specimens in flower have been collected in August, October, November, February and March and in fruit in March and November.

Distribution, habitat and ecology. – *Croton bathianus* inhabits remnants of semi-deciduous and semi-evergreen forests in Antsiranana and Mahajanga Provinces, from near sea level to roughly 400 m elevation (Fig. 2C). It is sometimes cultivated in hedgerows, either to delimit parcels of land or as a shade plant, and it is sometimes coppiced and then produces gigantic leaves (see the upper extremes of leaf dimensions above).

Conservation assessment. – *Croton bathianus* was first described from three collections from the hills in the "haute Bemarivo" of Mahajanga Province in the XXth century that probably represent three different locations. We found at least six more locations of this species in semi-deciduous to semi-evergreen forests in Antsiranana and Mahajanga Provinces in the last two decades. Even if this species has a substantial geographical range, the populations are severly fragmented. We therefore consider this species as "Near Threathened" [NT] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Hazomafaitra" *(van Ee et al. 2290).*

Notes. – *Croton bathianus* was named in honor of J.M.H.A. Perrier de la Bâthie (1873-1958), who collected the type and collected extensively throughout Madagascar.

This species can be distinguished by the rusty-reddish, granulate pubescence on young shoots (Fig. 7E), with the stems soon turning glabrous, dull gray, and striate. The glands in the vein junctions on the lower side of the leaves can be among the largest and most conspicuous found on any *Croton* species. Compared to the other species of the Adenophorus Group from northern Madagascar, *C. bathianus* has more compact inflorescences, with the pistillate flowers in particular often being nearly sessile, as well as having well-developed petals (Fig. 7G-H). Like *C. adenophorus,* this species is sometimes cultivated, and it is used for hedgerows (e.g., *van Ee et al. 2406*). Coppiced plants have been observed to grow enormous leaves, to c. 38 × 30 cm (Fig. 7A-B). Leandri (1939) indicates in his protologue that the diagnosis of the species was done based on characters noted by Perrier de la Bâthie in living specimens. The lectotype selected above includes a lengthy description in the hand of Perrier de la Bâthie, with a note on the top saying "sur le frais" (from fresh material).

Radcliffe-Smith (2016) recognized three additional varieties under *Croton bathianus*. We consider *C. bathianus* var. *ihosianus* Radcl.-Sm. to be a synonym of *C. ihosianus* Leandri, *C. bathianus* var. *toliarae* Radcl.-Sm. to be a synonym of *C. crocodilorum* Leandri, and *C. bathianus* var. *ambatondrazakae* Radcl.-Sm. to be a synonym of *C. scoriarum* Leandri.

Additional specimens examined. – **Madagascar. Prov. Antsiranana:** Diana Reg., RN 6, 43 km N of Ambanja, 13°30'33"S 48°41'51"E, 20 m, 2.XI.2009, *van Ee et al. 1138* (MICH); *ibid loc.*, *van Ee et al. 1139* (MICH); *ibid loc.*, *van Ee et al. 1140* (MICH); RN 6, just north of the turnoff to Belinta, 13°30'47"S 48°41'44"E, 24 m, 27.II.2016, *van Ee et al. 2289* (MICH, TAN); *ibid loc.*, *van Ee et al. 2290* (MICH, TAN); RN 6 E of Ampampamena, 13°30'46"S 48°40'30"E, 34 m, 27.II.2016, *van Ee et al. 2296* (MICH, TAN);

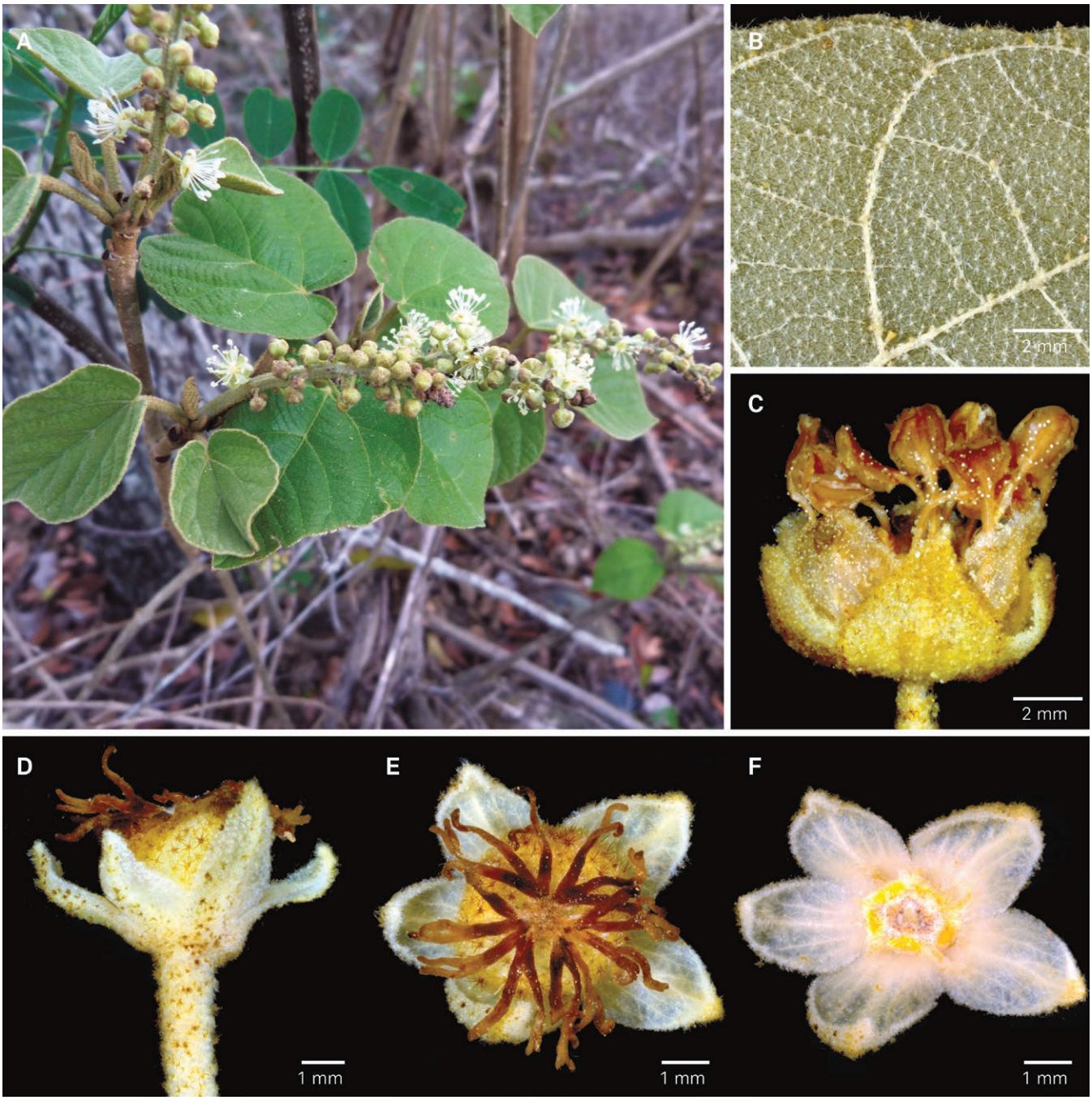

Fig. 9. *Croton mayottae* Berry & Kainul. **A.** Flowering branch with staminate flowers; **B.** Abaxial side of leaves showing laminar glands and pubescence; **C.** Staminate flower; **D-F.** Pistillate flower; **F.** Top-view with the ovary removed to show the five nectaries.
[Photo: **A:** Sébastien Traclet; **B-F:** *Barthelat et al. 225*]

along RN 6, at village of Ambatoharanana, 13°30'46"S 48°41'44"E, 33 m, 8.III.2016, *van Ee et al. 2383* (MICH, TAN). **Prov. Mahajanga:** Sofia Reg., Analalava Distr., Route Nationale 6, gorge off to the E of highway between PK 359 and 360, 14°23'26"S 48°01'14"E, 30 m, 22.X.2009, *Van Ee et al. 1043* (MICH, TAN); RN 6, between PK 388 and 389, 14°10'20"S 48°05'32"E, 20 m, 22.X.2009, *Van Ee et al. 1048* (MICH, TAN); RN 6 approximately 18 km N of Port Berge (Boriziny), 15°27'47"S, 47°35'57"E, 97 m, 26.II.2016, *Van Ee et al. 2282* (MICH, TAN); RN 6, between PK 170 and 171, north of Port Berger, 15°30'07"S 47°34'58"E, 115 m, 9.III.2016, *van Ee et al. 2406* (MICH, TAN); track heading into Bongolava Hills to west of RN6, 15°33'10"S 47°33'31"E, 79 m, 10.III.2016, *van Ee et al. 2408* (MICH, TAN); *ibid loc.*, *van Ee et al. 2409* (MICH, TAN).

Croton loucoubensis Baill. in Adansonia 1: 155. 1861 [as *loucoubense*] (Fig. 1E, 2C, 4I-J, 8).

≡ *Croton adenophorus* var. *loucoubensis* (Baill.) Müll. Arg. in A. DC., Prodr. 15(2): 589. 1866.

Lectotypus (designated here): **Madagascar. Prov. Antsiranana:** Diana Reg., Nossibé, forêt de Loucoubé, III.1851, *Boivin s.n.* (P [P00133453]!). **Syntypus: France. Dept. Mayotte:** *sine loc.,* VI.1848, *Boivin 3382* (P [P00133452]!).

= *Croton adenophoroides* Radcl.-Sm., Gen. Croton Madag. Comoro 117. 2016. **Typus: Madagascar. Prov. Antsiranana:** Besinkara, Ambalafary, Andvakena: premier cours d'eau sur le chemin de Bekolosy, 14°04'S 48°17'E, 500 m, 12.XI.1994, *Gautier & Derleth 2529* (holo-: K!; iso- G [G00341696]!, MO!, P [P00433174]!), **syn. nov.**

Shrubs or *trees* 1.5-10 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches; in all parts covered in whitish to ferrugineous, stellate trichomes many of which have a bristly, porrect (to c. 3 mm) central radius. Branches ± flattened and striate on new growth but becoming terete with age, reddish-brown to gray, with stellate trichomes, with orange latex. Stipules 0.8-2.0 cm long, lanceolate, fimbriate, glandular, caducous. *Leaves* alternate to ± opposite along stem, opposite at the apex. Petioles 3-15(-20) cm, adaxially canaliculate, densely stellate, usually with a pair of acropetiolar, ± reclined, stipitate (to 2.5 mm long), stellate-pubescent glands with a concave discoid apex (0.3-0.5 mm diam.). Leaf blades chartaceous, glandular-denticulate or undulate, ovate, 5-20 × 3-13.5 cm, apex acute to acuminate, base rounded to truncate or rarely cordate; adaxial surface velvety to bristly stellate-pubescent, pale green when fresh (turning orange in old leaves) and drying matte pale green to brown; venation with 4-9 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation; abaxial surface velvety stellate-pubescent, matte, paler than the adaxial side when dry; venation prominent and very distinct, with stipitate glands in some of the axils of the secondary veins (Fig 1E). *Inflorescences* terminal, raceme-like thryses 3.5-22.5 cm long, with numerous staminate flowers towards the distal end and 0-6 pistillate flowers towards the base; axes densely stellate-pubescent, flattened and striate; bracts awn-shaped, 1-5 mm long, usually persistent. *Staminate flowers* with brown, hirsute-stellate, subglobose buds 2.0-3.5 mm diam., pedicels elongating from bud to anthesis, 1-8 mm long; sepals 5, yellowish pale green, shortly connate at base, lobes broadly triangular-ovate, 2.2-2.8 × 1.3-2.0 mm, apex acute to rounded, abaxially stellate-pubescent, adaxially cilate towards apex, margins densely ciliate; petals 5, white, elliptic to spatulate, 2.4-3.5 × 1.2-2.2 mm, recurved at anthesis, abaxially and adaxially ciliate, margins densely ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.4 × 0.4 mm, pale yellow; stamens 16-18, white, filaments c. 2.5 mm long, ciliate, anthers broadly elliptic, c. 1.0 × 0.8-1.0 mm; receptacle pilose. *Pistillate flowers* with stellate-pubescent buds c. 2.5 mm diam., pedicels 1-6 mm long; sepals 5, triangular to ovate, spreading at anthesis, 2.5-5.0 × 1.8-3.0 mm, apex acute to rounded, somewhat inflexed, shortly connate at base, abaxially and adaxially stellate, pale green, persistent in fruit; petals absent or reduced to short filaments c. 1 mm long; disc glands 5, opposite the sepals, sessile, ellipsoidal, 0.4-0.6 × 0.8-1.2 mm, pale yellow; ovary densely covered in bristly, stellate trichomes, green, globoid, 2-6.5 mm in diameter, styles 3, 4-5.5 mm long, each branch flattened and 3-4 times bifurcate, with the first bifurcation congested and fused, spreading, recurved at the apices, abaxially stellate-pubescent, adaxially glabrous, yellowish, turning brown, persistent. *Capsules* 1-1.5 × 1-1.5 cm, smooth, pale greenish-brown, hirsute, exocarp separating, endocarp woody, c. 2 mm thick (Fig. 4I); columella 7-10 mm long, cornute. *Seeds* ± compressed-ellipsoid, apiculate, 6.3-6.9 × 4.4-4.8 × 2.5-3.4 mm (Fig. 4J); testa matte brown, diagonally ridged, verrucose; caruncle reniform, 0.5-0.8 × 1.1-1.7 mm.

Phenology. –There are specimens in flower collected in September to December and in March, which suggests either a bimodal flowering season, or else just a lack of collections from the generally rainy months of January and February.

Distribution, habitat and ecology. – *Croton loucoubensis* is known from northwestern Madagascar, from sea level to about 900 m elevation, where it is found in moist evergreen forests as well as secondary vegetation. It appears to be restricted to the subhumid Sambirano Domain, following the phytogeographical domains described by Humbert (1955), and has mainly been collected in Ampasindava Peninsula, the Manongarivo RS, and on the islands of Nosy Be and Nosy Komba (Fig. 2C). The syntype from Mayotte *(Boivin 3382)* is unfortunately sterile, and, in this condition, it is not clear if it represents this species or *C. mayottae*.

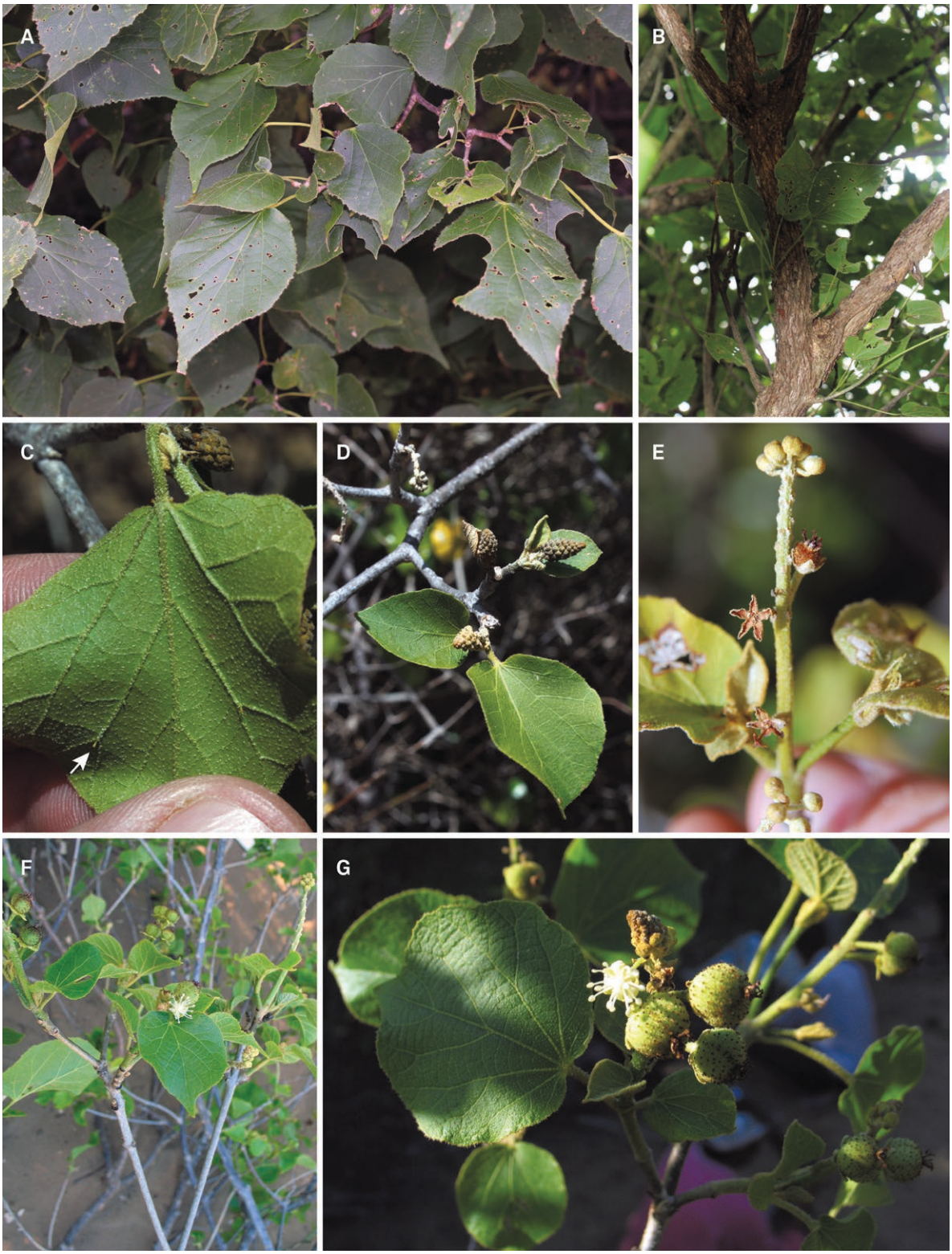

Fig. 10. *Croton orangeae* Kainul. & Berry **A.** Leaves; **B.** Bark; **C.** Underside of leaves; note the scabrous, stellate, indument and the laminar glands (arrow); **D.** Young inflorescences; **E.** Flowering branch with staminate flower and young fruits; **F.** Staminate flower and young fruits; **G.** Staminate flower in anthesis and mature fruits below.
[**A-B:** *van Ee et al. 2351*; **C-E:** *van Ee et al. 1080*; **F-G:** *Razafitsalama et al. 692*] [Photos: **A-D:** P. Berry; **E:** B. van Ee; **F-G:** R. Randrianaivo]

Conservation assessment. – *Croton loucoubensis* occurs in the protected areas of Ampasindava, Lokobe, and Manongarivo. Only one recent collection has been made outside these areas *(Gillespie et al. 10646)*. We estimate that the extent of occurrence is no more than 3000 km², and we therefore consider this species as "Near Threatened" (NT), according to IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Hazomafaika" *(Reserves Naturelles 9215),* "Kimiramira" *(Gautier et al. 3078),* "Lazakatalaotra" *(Reserves Naturelles 4896),* "Tsimiramira" *(Ammann et al. 91a).*

Notes. – The species epithet *loucoubensis* refers to the type locality in the Lokobe forest on the island of Nosy Be in Antsiranana Province.

Baillon (1861), followed by Leandri (1939), included a specimen of *Croton loucoubensis (Boivin 2185)* in *C. muricatus* Vahl, a species from southeastern Madagascar, a factor that has contributed to the confusion surrounding these species and the taxonomy of the Adenophorus Group as a whole. Leandri (1939) treated *C. loucoubensis* as a synonym of *C. adenophorus*, but his concept of *C. adenophorus*, as shown in his key and description, conforms here to the type of *C. loucoubensis*. Radcliffe-Smith (2016) also failed to recognize the type of *C. loucoubensis* as distinct from *C. adenophorus*; instead he described *C. adenophoroides* based on newer material. *Croton loucoubensis* is readily distinguished from *C. adenophorus* by its fimbriate stipules, velvety leaves, stipitate and pubescent petiolar glands, and larger woody capsules (10-15 × 10-15 mm vs 5-6 × 5.5-8 mm) with bristly pubescence (Fig. 4I).

Additional specimens examined. – **Madagascar. Prov. Antsiranana:** Diana Reg., Ambanja Distr., Ampasindava, Bongomihiravavy forest, 13°46'07"S 48°05'52"E, 323 m, 27.XI.2008, *Ammann et al. 91a* (G, MO, TEF); Ampasindava, Betsitsika forest, 13°46'09"S 48°04'06"E, 317 m, 7.XII.2008, *Ammann et al. 159* (G, MICH, MO, TEF); Ampasindava, Andranomatavy forest, 13°40'02"S 47°59'13"E, 205 m, 24.XI.2009, *Ammann et al. MYA 378* (G, K, MICH, MO, P, TEF); Nosy Be, Lokobe Reserve, 13°24'46"S 48°18'45"E, 0-100 m, 5.IX.1994, *Antilahimena 154* (MO, P); Ampasindava, Ambohimirahavavy forest, 13°45'43"S 48°05'40"E, 410 m, 13.XI.2008, *Bernard et al. 1192* (G, MICH, MO, P, TAN); Nosy Be, n.d., *Boivin 56* (P); Nosy Komba, VII.1850, *Boivin 2185* (P); Nosy Be, Lokobe forest, X.1960, *Bosser 14738* (MO, P, TAN); Manongarivo Reserve, 14°02'S 48°18'E, 880 m, 20.IX.1996, *Gautier et al. 3078* (G, MO, P); Nosy Be, Lokobe forest, 1.IX.1967, *Jacquemin H457J* (K, P); Ampasindava, Bongomihiravavy forest, 13°45'43"S 48°05'25"E, 435 m, 11.XI.2008, *Madiomanana et al. MAD 110* (G, MO, P, TEF); *ibid. loc.*, 13°45'28"S 48°04'10"E, 270 m, 26.XI.2007, *Nusbaumer 2536* (G, MO, TEF); *ibid. loc.*, 13°45'36"S 48°06'36"E, 505 m, 28.XI.2007, *Nusbaumer 2600* (G, MICH, TEF); Ampasindava, Betsitsika forest, 13°44'37"S 48°01'18"E, 333 m, 22.XI.2008, *Nusbaumer & Tahinarivony 2955* (G, K, MO, P, TEF, WAG); Manongarivo Reserve, 14°03'09"S 48°17'03"E, 240 m, XII.1993, *Rakotomalala et al. 16* (G, MO, P); [Ampasindava], 13°46'59.5"S 48°04'33.0"E, 317 m, 2.V.2012, *Rasoanaivo et al. 50* (G, MO); Lokobe Reserve, 28.IX.1952, *Réserves Naturelles 4360* (K, P); Nosy Be, 17.XI.1952, *Réserves Naturelles 4896* (P); Lokobe Reserve, 5.XII.1953, *Réserves Naturelles 5936* (K, P, TAN); Nosy Be, Andranokomba, 30.X.1956, *Réserves Naturelles 9215* (G, K, MO, P, WAG); Nosy Be, Hellville, 30.X.1956, *Réserves Naturelles 9441* (G, K, MO, P); Nosy Be, 12.III.1971, *Schmitt 255* (P); *ibid. loc.*, 13.III.1971, *Schmitt 272* (P). **Prov. Mahajanga:** Sofia Reg., Analalava Distr., 111 km N of Antsohihy along RN 6, S of Ankaromyhely, 14°04'31"S 48°06'25"E, 245 m, 21.X.2012, *Gillespie et al. 10646* (CAN, MICH, MO, TAN); Andranomohavelona, Ambaliha, Ambanja, 18.X.1953, *Service Forestier 7702* (P).

Croton mayottae P.E. Berry & Kainul., **spec. nova** (Fig. 2E, 9).

Typus: France. Dept. Mayotte: Grande-Terre, Chiconi, village, 16.I.2001, *Barthelat, M'Changama & Sifary 225* (holo-: P [P00229211]!; iso-: G [G00341697]!, K!, MAO, MO!).

= *Croton regeneratrix* var. *mayottensis* Radcl.-Sm., Gen. Croton Madag. Comoro 202. 2016. **Typus: France. Dept. Mayotte:** Rassi Maoussi, 30 m, 24.IV.1997, *Pascal 915* (holo-: K!; iso-: BR, G [G00341698]!, MO!, P [P00144592]!, WAG), **syn. nov.**

Croton mayottae P.E. Berry & Kainul. is similar to C. loucoubensis Baill. but differs in its cordate (vs rounded) leaf bases, serrulate stipules (vs fimbriate), stellate-pubescent (vs bristly hirsute) ovary, and smaller and thinner-walled capsules (c. 7 mm diam. with endocarp c. 0.4 mm thick vs ≥ 10 mm diam. with endocarp c. 2 mm thick).

Shrubs 2-3 m tall, dichotomously branching. Branches terete, with a scurfy indument of short, tan-colored, fasciculate-stellate trichomes. Older stems smooth, matte tan to pale gray, glabrescent, with lighter-colored oval lenticels, with reddish latex. Stipules 10-20 mm long, narrowly lanceolate, finely serrate along the margins, with an aristate tip, caducous. *Leaves* opposite, apparently deciduous; leaf scars conspicuous and drying much darker than the adjacent stem tissue. Petioles 1.5-6 cm long, densely scurfy-pubescent like the young stems, with a pair of subsessile, concave, discoid glands (0.4-0.6 mm diam.) on the lower side of the base of the lamina. Leaf blades firmly papyraceous, finely denticulate, ovate, 5-10 × 3-6 cm, apex acuminate, base cordate; both sides covered with a moderately dense cover of stellate trichomes (these not overlapping, so leaf surface can be seen underneath), green when fresh and drying matte pale green; venation 5- or 7-palmate at the base, with 2-6 pairs of penninerved secondary veins from around the middle of the blade, veins prominent and lighter-colored on abaxial side, usually with some acetabuliform glands in the axils of some of the secondary and tertiary veins (Fig. 9B). *Inflorescences* terminal, raceme-like thyrses, 6-10 cm long, with c. 4-12 pistillate flowers in the basal part and numerous staminate flowers distally, axes densely tan-scurfy with tightly fasciculate trichomes; bracts triangular, 2-4 × 1-2 mm, semipersistent. *Staminate flowers* with densely scurfy, subglobose buds 1.5-2.5 mm diam., pedicels 2-7 mm long; sepals 5, shortly connate at base, lobes broadly triangular-ovate, 2-2.5 × 2.2-3 mm, apex

Fig. 11. *Croton sahafariensis* Kainul. & Berry **A.** Branch with young inflorescences. Note the awn-like bracts; **B.** Underside of the leaves showing whitish woolly pubescence with contrasting ferrugineous hairs along the veins. Note laminar glands (arrow); **C-D.** Inflorescences with staminate and pistillate flowers; **E.** Young fruit.
[**A, D-E:** *van Ee et al. 2313*; **B-C:** *van Ee et al. 1089*] [Photos: **A-B, D-E:** P. Berry; **C:** B. van Ee]

acute, inflexed at anthesis, abaxially stellate-pubescent, adaxially stellate towards apex, margins ciliate; petals 5, elliptic to spatulate, 2-2.8 × 1-1.7 mm, recurved at anthesis, abaxially stellate and papillose, adaxially glabrous, margins densely ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal with an apical depression, c. 0.5 × 0.5 mm, yellow; stamens c. 14, white, filaments 2-3 mm long, glabrous, anthers broadly elliptic, c. 1 × 0.9 mm; receptacle pilose. *Pistillate flowers* with densely scurfy-stellate buds 2-2.5 mm diam., pedicels 3-6 mm long; sepals 5, triangular, 2-3.5 × 1.5-2.5 mm, apex acute, densely tan-scurfy abaxially and adaxially stellate, petals absent or reduced to short filaments ca 1.5 mm long; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.4 × 0.8 mm, yellow; ovary globoid, 2.7-4 mm diam., densely covered by compact, golden-stellate trichomes; styles 3, 1.5-3.3 mm long, each branch flattened and twice bifurcate, spreading, abaxially stellate-pubescent, adaxially glabrous, persistent. *Capsules* c. 6 mm long, light brown, puberulent, the endocarp woody, c. 0.4 mm thick; columella 4.5-5 mm long, the apex cornute with partially recurved fibers. *Seeds* broadly compressed-ellipsoid, c. 4.7 × 3.8 × 2.7 mm; testa matte, light brown, slightly rugulose; caruncle shield-shaped, c. 1 × 1.5 mm.

Etymology. – Named after the island of Mayotte, in the Comoros Archipelago, where this species is endemic.

Phenology. – Specimens in bud have been collected in March and April, flowering specimens in October–November and in January, and a specimen in fruit in November.

Distribution, habitat and ecology. – *Croton mayottae* occurs in seasonally dry forest, mainly near the coastline, on the Grande-Terre island of Mayotte at elevations from sea level to 170 m (Fig. 2E).

Conservation assessment. – Since the species in endemic to the island of Mayotte and restricted there to coastal forest remnants in only four localities, we consider it to be "Endangered" [EN B1ab(iii)] according to IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "M'Houvé" *(Soumille 992),* "Mouhouve" *(Hoffman & Ranmanana 363),* "Muhuve [in Shibushi, Shimahorais]" *(Barthelat & Rolland 1324),* "Sary lazalaza" *(Barthelat & Rolland 1324).*

Notes. – Radcliffe-Smith (2016) based his description of *C. regeneratrix* var. *mayottensis* on a single collection in early bud, and he failed to note that it had opposite leaves and glands on the undersides of the leaves, whereas *C. regeneratrix* has alternate leaves that lack laminar glands. He treated another specimen of *C. mayottae (Pascal 724)* as *C. adenophorus*. Rather than making a combination based on the type of Radcliffe-Smith's variety, we prefer our choice of type for *C. mayottae,* which has open pistillate and staminate flowers and is much more diagnostic for the species. The other native *Croton* species on Mayotte include *C. humblotii* Baill., which also occurs on the three islands of the Union of the Comoros; *C. bifurcatus* Baill., and *C. emeliae* Baill., which like *C. mayottae* are found only on Mayotte; and finally *C. adenophorus*, which occurs mainly on mainland Madagascar in Antsiranana Province.

Additional specimens examined. – **France. Dept. Mayotte:** Saziley, 21.III.2004, *Barthelat & Rolland 1324* (G, K, MAO, MO, P); Combani, Parcelle de Bakar, 11.IV.2001, *Hladik 6534* (P); Saziley, 12.IV.2001, *Hladik 6558* (P); *ibid loc.*, 12°58'S 45°11'E, 170 m, 11.XI.2002, *Hoffman & Ralimanana 363* (G, K, MAO, MO, P, TAN); *ibid loc.*, 80 m, 17.X.1996, *Pascal 724* (MO, P); Sazilé Bé, 12°58'39"S 45°12'01"E, 100-150 m, 11.IV.1999, *Pignal 1111* (G, K, P); Saziley, 0 m, 14.XI.1997, *Soumille 992* (G, K, MO, P, WAG).

Croton orangeae Kainul. & P.E. Berry, **spec. nova** (Fig. 1F, 2D, 4K-L, 10).

Typus: Madagascar. Prov. Antsiranana: Diana Reg., Ramena, Ankorikakely, Baie des Sakalava, 12°16'40"S 49°23'01"E, 25 m, 9.XII.2004, *Razafitsalama et al. 692* (holo-: MICH [MICH1517188]!; iso-: CNARP, MO!, P [P05484901]!, TAN).

Croton orangeae Kainul. & P.E. Berry is similar to C. adenophorus Baill. in its denticulate, cordate leaves and glabrous stems, but differs in its stipules that are awn-shaped (vs foliaceous), its mature leaves that are scabrously stellate-pubescent (vs subglabrous), and the bark of the branches matte and tan to gray (vs ± glossy and reddish brown) and soon turning flaky (vs smooth).

Shrubs 1-4 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches. Branches flattened on new growth but becoming terete with age, pale green and sparsely covered with whitish stellate indument, soon turning tan to gray, glabrous, matte. Bark flaky, gray to brown (Fig. 10B). Stipules 5-10 mm long, awn-shaped, early caducous. *Leaves* opposite, deciduous. Petioles 0.5-10 cm long, adaxially canaliculate, stellate-pubescent, usually with a pair of subsessile, concave, discoid glands 0.4-0.6 mm diam. at the junction with the lamina. Leaf blades chartaceous, (subentire) dentate to denticulate, ovate, 2.2-14.0 × 2.5-14 cm, apex (acute) acuminate, base (truncate) cordate; both sides with a persistent, scabrous stellate indument, green when fresh, drying matte pale green to brown; venation evident, with 6-10 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation; venation prominent, sometimes with glands in some

of the axils of the secondary veins on the lower surface (Fig. 1F), but absent in most leaves. *Inflorescences* terminal, raceme-like thryses 1-6.5 cm long, bisexual with pistillate flowers towards the base and staminate flowers towards the distal end, axes stellate-pubescent, flattened; bracts narrowly triangular, c. 2.5 mm long, caducous. *Staminate flowers* with stellate-pubescent, subglobose buds, c. 1.8 mm diam., pedicels elongating from bud to anthesis, 1-5 mm long; sepals 5, pale green, shortly connate at base, lobes broadly triangular-ovate, 2-2.5 × 1.5-1.8 mm, apex acute, inflexed at anthesis, abaxially stellate-pubescent, adaxially glabrous, margins ciliate; petals 5, elliptic to spatulate, 1.5-2.5 × 0.7-0.9 mm, recurved at anthesis, abaxially glabrous and papillose, adaxially ciliate towards apex, margins densely ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.4 × 0.6 mm, yellow; stamens 13-21, white, filaments 1.5-2.5 mm long, ciliate, anthers broadly elliptic, c. 0.8 × 0.7 mm; receptacle pilose. *Pistillate flowers* with stellate-pubescent buds 2-2.5 mm diam., pedicels 1.5-5.5 mm long; sepals 5, elliptic, not spreading at anthesis, 1.8-2.8 × 1-1.7 mm, apex acute, shortly connate at base, abaxially and adaxially stellate-pubescent, persistent in fruit; petals sometimes absent or reduced, when present 1.4-1.8 × 0.7-0.9 mm, spatulate, glabrous except for the ciliate margin, abaxially papillose; disc glands 5, opposite the sepals, sessile, ellipsoidal, 0.3 × 0.7 mm, yellow; ovary densely covered by ferrugineous to dark brown, stellate trichomes, globoid-ellipsoid, 2-3 mm diam., styles 3, c. 2 mm long, each branch flattened and twice bifurcate, spreading, recurved at the apices, abaxially stellate-pubescent, adaxially glabrous, persistent. *Capsules* broadly globoid, 5 × 6.5 mm, smooth, pale brown, covered with contrasting dark brown stellate trichomes (Fig. 4K), exocarp not separating, endocarp woody, c. 0.5 mm thick; columella 4-5 mm long, cornute, capitate. *Seeds* ± compressed-ellipsoid, c. 3.5 × 3 × 2 mm; testa matte, verrucose, pale brown; caruncle narrowly reniform c. 0.4 × 1 mm (Fig. 4L).

Etymology. – The epithet refers to the Orangea (Oronjia) Peninsula in Antsiranana Province, where the type was collected and the species is apparently restricted.

Phenology. – Only a few specimens are known, collected in bud in March, in flower in August-December, and in fruit in December.

Distribution, habitat and ecology. – This species is so far only known from the Orangea (Oronjia) Peninsula in northern Antsiranana Province where it grows in dry scrub vegetation and littoral forest on limestone and sand, from sea level to c. 50 m in elevation (Fig. 2D).

Conservation assessment. – *Croton orangeae* is known only from the Orangea Peninsula. The deciduous forests of Orangea are currently threatened by deforestation despite their recent additon to Madagascar's protected area network. Deforestation is mostly related to agricultural practices. Given this and the extent of occurrence is < 5000 km^2, the new species is assigned as "Endangered" [EN B1 ab(iii)], according the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – *Croton orangeae* is distinct for its glabrous, grayish branches with flaky bark, and dentate to denticulate leaves with a persistent, scabrous indument on both sides. In the shape of the leaves and in the pale brown capsules with white and contrasting brown stellate trichomes, it may appear similar to *C. adenophorus*, but that species has a glossy reddish bark and subglabrous leaves, and also differ in its usually longer inflorescences (1.5-22 cm vs 1-6.5 cm in *C. orangeae*), and distinctly foliaceous stipules and calyces. No vernacular names have been noted for this species.

Additional specimens examined. – **Madagascar. Prov. Antsiranana:** Diana Reg., Antsiranana Distr., Orangea, 25.XI.1970, *Debray 1525-D* (K, P); *ibid. loc.*, 12°14'20"S 49°21'49"E, 13 m, 29.VIII.2001, *Rabenantoandro & Razanatsoa 579* (MO, P); *ibid. loc.*, 12°14'08.2"S 49°21'40.3"E, 50 m, 25.X.2009, *van Ee et al. 1080* (MICH); *ibid. loc.*, 12°13'54"S 49°21'28"E, 19 m, 5.III.2016, *van Ee et al. 2343* (MICH, TAN); *ibid. loc.*, 12°14'08"S 49°21'41"E, 30 m, 5.III.2016, *van Ee et al. 2351* (MICH, TAN); *ibid. loc.*, 5.III.2016, *van Ee et al. 2352* (MICH, TAN); *ibid. loc.*, 5.III.2016, *van Ee et al. 2353* (MICH, TAN).

Croton sahafariensis Kainul. & P.E. Berry, **spec. nova** (Fig. 1G, 2D, 4M-N, 11).

Typus: Madagascar. Prov. Antsiranana: Diana Reg., Sahafary forest in the Saharaina river basin, road off of RN 6 to the E towards the "red tsingy", 12°36'19"S 49°26'23"E, 250 m, 26.X.2009, *van Ee et al. 1089* (holo-: MICH [MICH1517187]!; iso-: P!, TAN).

Croton sahafariensis Kainul. & P.E. Berry is similar to C. tsiampiensis Leandri, from which it differs in that the leaves are not markedly hirsute but instead have a whitish woolly pubescence on the abaxial side, and in having bracts which are usually extended well beyond the buds. In its opposite, woolly leaves and awn-like bracts C. sahafariensis may also be superficially similar to C. danguyanus Leandri, but that species lacks laminar glands and its pistillate flowers have an inflated, conduplicate calyx.

Shrubs 1.5-5 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches; in all parts covered in whitish or ferrugineous, stellate trichomes many of which have a bristly, porrect (to c. 2 mm) central radius. Branches flattened on new growth but becoming terete with age, pale grayish-green and hirsute with ferrugineous, stellate indument, soon turning a glabrous, matte gray to brown bark. Stipules 10-15 mm, lanceolate, entire,

with marginal glands, caducous. *Leaves* deciduous, opposite. Petioles 1-10 cm, adaxially canaliculate, stellate-pubescent to markedly hirsute, usually with a pair of subsessile (stipe <1 mm), concave, discoid, yellow, glands (c. 0.5 in diam) by the base of the lamina. Leaf blades chartaceous, glandular denticulate, broadly ovate to subreniform, 2.4-15 × 2.3-11.5 cm, apex rounded, acute or shortly acuminate, base cordate; adaxial surface stellate-pubescent, pale green when fresh (turning orange in old leaves) and drying matte greenish-brown; venation evident, with 5-8 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation; abaxial surface light green, densely covered by ± woolly, whitish stellate-pubescent hairs with contrasting ferrugineous hairs scattered along the veins; venation prominent, with glands in some of the axils of the secondary veins (Fig. 1G). *Inflorescences* terminal, spike-like thryses to 8 cm long, with pistillate flowers more prevalent toward the base and staminate flowers towards the distal end, axes densely ferrugineous stellate-pubescent, flattened; bracts narrowly triangular to lanceolate, ± inflected, 3-7 mm long. *Staminate flowers* with stellate-pubescent, subglobose buds 1.6-2.5 mm in diam., pedicels elongating from bud to anthesis, 1.5-2 mm long; sepals 5, whitish, shortly connate at base, lobes broadly triangular-ovate, 1.5-2 × 1-1.3 mm, apex acute, inflexed at anthesis, abaxially ferrugineous stellate-pubescent, adaxially glabrous, margins ciliate; petals 5, white, elliptic-spatulate, c. 2.6 × 1.4 mm, recurved at anthesis, abaxially papillose and densely stellate-pubescent, adaxially glabrous, margins densely ciliate; disc glands 5, opposite the sepals, sessile, ellipsoidal with an apical depression, c. 0.4 × 0.5 mm, yellow; stamens 14-15, white, filaments 2-3.7 mm long, glabrous, anthers broadly elliptic, c. 0.6 × 0.5 mm; receptacle pilose. *Pistillate flowers* with stellate-pubescent buds, c. 1.5 mm in diam., subsessile; sepals 5, triangular-ovate, spreading at anthesis, c. 2.5 × 1.2 mm, apex acute, shortly connate at base, abaxially and adaxially stellate-pubescent, greenish yellow, persistent in fruit; petals absent or vestigial; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.3 × 0.6 mm, pale yellow; glandular filaments sometimes alternating with the disc glands, 0.2-0.4 mm long; ovary globose, 2-2.5 mm in diameter, densely hirsute by whitish to pale brown, long-rayed stellate trichomes, styles 3, 1.5-2.0 mm long, each branch flattened and 2-3(-4) times bifurcate, spreading, recurved at the apices, abaxially stellate-pubescent, adaxially glabrous, greenish white, turning brown, persistent. *Capsules* globoid, c. 6.5 mm in diam., smooth, brown, covered with brown stellate trichomes (Fig. 4M), exocarp not separating, endocarp woody, c. 0.4 mm thick; columella 4.5-7 mm long, cornute, capitate. *Seeds* ± compressed-ellipsoid, 4-5.8 × 3-4.1 × 2.5 mm (Fig. 4N); testa glossy, verrucose, brown; caruncle narrowly reniform c. 0.6 × 1.4 mm.

Etymology. – The epithet refers to the Sahafary forest in Antsiranana Province, where the type was collected.

Phenology. – Only a few specimens are known, collected in flower in October-November and January-March, and in fruit in October, January, and March.

Distribution, habitat and ecology. – *Croton sahafariensis* occurs in deciduous forests in northern Antsiranana Province, on sandy or lateritic soils, at 150-300 m elevation (Fig. 2D).

Conservation assessment. – *Croton sahafariensis* is known only from small and fragmented populations at just four localities of threatened deciduous forests in Antsiranana Province (Ambohitsitondroina, Montagne des Français, Sahafary, and Tsaramborona). With an extent of occurrence < 5,000 km^2 and an area of occupancy of < 500 km^2 and with each of the four known localities representing separate threat locations, we assign this species as "Endangered" [EN B1ab(iii)+B2ab(iii)] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – This species can be recognized by its whitish, ± woolly pubescence on the abaxial side of the leaves with contrasting ferrugineous trichomes prevalent along the veins, and in its awn-like bracts that usually extend well beyond the buds (Fig. 1G, 11). In these characteristics it may be superficially similar to *C. danguyanus* Leandri, however, that species has pistillate flowers with large, inflated, and conduplicate sepals, and the leaves lacks laminar glands; also, *C. danguyanus* is not part of the Adenophorus Group. *Gautier & Chatelain 4876* is tentatively included here, but the leaves of this specimen are very young and small. The sterile specimen *van Ee et al. 2363* from Montagne des Français probably also belong here. The leaves of this specimen are not woolly, but since it grew in the understory it is possible this represents phenotypical variation. There are currently no vernacular names recorded for this species.

Additional specimens examined. – **Madagascar. Prov. Antsiranana:** SAVA Reg., Vohemar Distr., Daraina, Tsaramborona forest, 12°57'47"S 49°37'12"E, 150 m, 20.XI.2006, *Gautier & Chatelain 4876* (G, MICH, P); Daraina, Ambohitsitondroina forest, 13°07'44"S 49°27'29"E, 286 m, 6.I.2006, *Nusbaumer & Ranirison 1862* (G, MO); *ibid loc.*, 13°07'56"S 49°28'21"E, 210 m, 12.I.2006, *Ranirison & Nusbaumer 1077* (G, K, P); Diana Reg., Antsiranana II Distr., Sadjoavato, Saharenana, Andranomadiro forest SW of Sahafary, 12°36'18"S 49°26'35"E, 300 m, 14.II.2005, *Schatz et al. 4269* (CNARP, G, MO, P, TAN); *ibid loc.*, 12°36'20"S 49°26'22"E, 258 m, 2.III.2016, *van Ee et al. 2312* (MICH, TAN); *ibid loc.*, *van Ee et al. 2313* (MICH, TAN); *ibid loc.*, *van Ee et al. 2314* (MICH, TAN); Montagne des Français, 12°19'25"S 49°20'10"E, 235 m, 5.III.2016, *van Ee et al. 2363* (MICH, TAN).

Fig. 12. *Croton scoriarum* Leandri **A.** Habit; **B.** Bark; **C.** Mature leaves; **D.** Underside of young leaf; **E.** Inflorescence with staminate flowers and buds; **F-G.** Inflorescences with pistillate flowers; **H.** Young fruits.
[A, C, D: *van Ee et al. 2329*; **B, E-F:** *van Ee et al. 1118*; **G-H:** *van Ee et al. 1129*] [Photos: **A, C:** K. Kainulainen; **B, D-H:** P. Berry]

Croton scoriarum Leandri in Adansonia, sér. 2, 12 : 68. 1972. (Fig. 1H, 2C, 12).

Lectotypus (designated here) : **Madagascar. Prov. Mahajanga :** Centre, au lieu dit Analankeboka, à l'W de Bealanana, 20.XI.1966, *Service Forestier 27107* (P [P00706283]! ; isolecto- : K [K000895678]!, P [P00706284]!, TEF [TEF000183]!).

= *Croton bathianus* var. *ambatondrazakae* Radcl.-Sm., Gen. Croton Madag. Comoro 114. 2016. **Typus : Madagascar. Prov. Toamasina :** Alaotra-Mangoro Reg., Ambatondrazaka Distr., Menaloha, 900 m, XI.1937, *Cours 587* (holo- : P [P00127483]!), **syn. nov.**

Shrubs or *trees* 1.5-8 m tall, dichotomously branching. Branches flattened on new growth but becoming terete with age, initially green with a farinose cover of whitish, stellate trichomes, but soon turning reddish-brown and glabrous. Mature bark papery and flaky. Stipules 2-7 × 1-1.5 mm, lanceolate, with marginal glands, early caducous. *Leaves* opposite, deciduous. Petioles 1-10 cm long, adaxially canaliculate, stellate-pubescent at first, soon glabrous, usually with a pair of acropetiolar, ± stipitate glands with a concave, discoid, yellow apex (0.5-1 mm diam.). Leaf blades chartaceous, ± entire, ovate, 4.5-22 × 3-15.5 cm, apex acuminate, base rounded to cordate ; young leaves with a dense, farinose cover of whitish, stellate trichomes with brownish trichomes also present along the abaxial veins, both sides soon becoming glabrous, pale green when fresh and drying matte yellowish green to dark green-brown ; venation prominent, with 6-9 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation ; with ± stipitate glands in some of the axils of the secondary veins (Fig. 1H). *Inflorescences* terminal, raceme-like thyrses 2-11 cm long, with pistillate flowers on the lower and middle part of the axis and staminate flowers towards the distal end, axes stellate-pubescent, flattened ; bracts triangular, c. 2.5 mm long, caducous. *Staminate flowers* with stellate, subglobose buds 1.8-2 mm in diam., pedicels 1-4 mm long ; sepals 5, shortly connate at base, lobes ovate, c. 2 × 1.8 mm, apex acute, inflexed at anthesis, abaxially stellate, adaxially sparsely ciliate, margins ciliate ; petals 5, white, elliptic-obovate, 2.5-3 × 1-1.3 mm, recurved at anthesis, abaxially stellate and papillose, adaxially glabrous, margins ciliate ; disc glands 5, opposite the sepals, sessile, ellipsoidal with an apical depression, c. 0.5 × 0.8 mm, yellowish ; stamens 15-20, white, filaments 2-3 mm long, pilose at base, anthers broadly elliptic, c. 0.8-1 × 0.7-0.9 mm ; receptacle pilose. *Pistillate flowers* with stellate ellipsoid buds, c. 1.8 mm diam., pedicels 1-3 mm long ; sepals 5, ovate, spreading at anthesis, c. 2.5 × 1.3-2.0 mm, pale green, apex acute, shortly connate at base, abaxially stellate, adaxially sparsely pubescent, petals often reduced, if present similar to the petals of the staminate flower ; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.5 × 0.3-1.3 mm ; ovary stellate, globoid, c. 2.5 mm diam ; styles 3, 2-3 mm long, each branch flattened and twice bifurcate, spreading, abaxially stellate, adaxially glabrous, yellow, turning brown, persistent. *Capsules* and seeds not seen.

Phenology. – This species has only been collected from September to March, presumably because it is deciduous during the dry season. Specimens in flower have been collected from September to December, with immature fruits in October.

Distribution, habitat and ecology. – This species has a disjunct distribution and has been collected in deciduous forests in western Antsiranana Province (Ambilobe, Ankarana National Park, and Sakaramy), northern Mahajanga (Ambodimotso and Bealanana), and in the Lac Alaotra area in Toamasina Province, growing on basalt, lateritic and sandy soils at 100-900 m in elevation (Fig. 2C).

Conservation assessment. – *Croton scoriarum* has been collected only rarely from rather scattered localities, but may be extant in a wide area in central to northern Madagascar. With probably more than ten locations in three Provinces, we assigned this species as "Least Concern" [LC] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Vernacular names. – "Hazompondra" *(Herb. Jard. Bot. Tana 5252)*.

Notes. –The species epithet *scoriarum* refers to the volcanic substrate on which the type was collected.

The species can be distinguished from its congeners by its large mature leaves that are ovate with a rounded-truncate base and entire to shallowly undulate or denticulate margins. The leaves are densely whitish stellate-pubescent on both sides when young but then become almost completely glabrous with age (Fig. 1H, 12C-D). The shoots likewise become smooth, and usually dry a glossy dark reddish-brown. The mature bark is papery and thinly flaky. In the molecular phylogenetic study of Malagasy *Croton* by Haber et al. (2017), *C. scoriarum* was called "*Croton* sp. nov. K", and it formed a clade with *C. adenophorus* and *C. bathianus* (therein called "*C.* cf. *loucoubensis*") ; all three accessions share an asparagine-arginine insert in maturase K. In his protologue, Leandri (1972), mentioned the specimen *Service Forestier 26207* (P) from the Antsalova District of Mahajanga Province as possibly belonging to *C. scoriarum*. We think that this specimen may be better included in *C. crocodilorum* Leandri, or else treated as a separate species. *Croton crocodilorum* is similar to *C. scoriarum* but has smaller leaves with a cordate base and denticulate margin, and it appears to retain a dense stellate indument, at least on

the abaxial side of the leaves. The specimens from the Lac Alaotra surroundings, some of which have been recognized as *C. bathianus* var. *ambatondrazakae* Radcl.-Sm., all appear to have been collected at the onset of the rainy season (November) and have no leaves, or else very small leaves. This makes it difficult to confidently determine them to species, but the thinly flaky, glossy, and dark brown bark is consistent with their placement in *C. scoriarum*, although further collections may prove them to be a distinct species.

Additional specimens examined. – **Madagascar. Prov. Antsiranana :** Diana Reg., Ambilobe, 26.VII.1939, *Decary 14584* (P); Two-track road from Sakaramy towards Mahatsinja, west of road from RN 6 to Joffreville, 12°25'59"S 49°16'19"E, 340 m, 27.X.2009, *van Ee et al. 1118* (MICH); *ibid loc.*, *van Ee et al. 1120* (MICH); *ibid loc.*, *van Ee et al. 1129* (MICH); *ibid loc.*, 12°24'33"S 49°17'05"E, 321 m, 3.III.2016, *van Ee et al. 2329* (MICH, TAN); Ankarana National Park, 12°56'52"S 49°07'33"E, 118 m, 7.III.2016, *van Ee et al. 2379* (MICH, TAN). **Prov. Mahajanga :** Sofia Reg., Ambodimotso, bas-Befandriana Nord, 14.IX.1942, *Herb. Jard. Bot. Tana 5252* (P). **Prov. Toamasina :** Alaotra-Mangoro Reg., Antsihanaka, XI.1936, *Herb. Jard. Bot. 2202* (P); *ibid loc.*, XI.1936, *Herb. Jard. Bot. 2287* (P); Lac Alaotra (G), s.d., *Herb. Jard. Bot. 3959* (P).

Croton tsiampiensis Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7 : 79. 1939. (Fig. 1I, 2B, 4O-P, 13).

Lectotypus (designated here) : **Madagascar. Prov. Mahajanga :** Tsiampihy, près de l'embouchure de la Soahanina, 15.X.1932, *Leandri 311* (P [P00389521]!; isolecto- : P [P00133302]!).

= *Croton tsiampiensis* var. *ankaranensis* Radcl.-Sm., Gen. Croton Madag. Comoro 110. 2016. **Typus : Madagascar. Prov. Antsiranana :** Diana Reg., Massif de l'Ankarana, 4.XI.1990, *Bardot-Vaucoulon 224* (holo- : P [P00123706]!), **syn. nov.**

= *Croton tsiampiensis* var. *macrophyllus* Radcl.-Sm., Gen. Croton Madag. Comoro 110. 2016. **Typus : Madagascar. Prov. Mahajanga :** Reserve Naturelle Bemaraha, Ambodiriana, c. 9 km E of Antsalova, 18°39'S 44°43'E, 100-125 m, 13-15.XII.1990, *Gillespie 4139* (holo- : K!; iso- : MICH!, MO), **syn. nov.**

= *Croton tsiampiensis* var. *microphyllus* Radcl.-Sm., Gen. Croton Madag. Comoro 111. 2016. **Typus : Madagascar. Prov. Antsiranana :** Diana Reg., P.K. 10 de la route Diego Suarez-Orangea, 13.XII.1963, *Service Forestier 22956* (holo- : P [P00123706]!), **syn. nov.**

Shrubs or *trees* 2-6 m tall, dichotomously branching, internodes sometimes so short as to give the appearance of whorled branches ; in all parts covered in whitish to ferrugineous, stellate trichomes many of which have a bristly, porrect (to c. 4 mm) central radius. Branches flattened on new growth but becoming terete with age, green at first, soon turning a matte pale gray (to reddish brown) ; red latex present in freshly cut stems. Stipules 8-30 × 1-5 mm, lanceolate, entire or incised, with marginal glands, caducous. *Leaves* deciduous, opposite. Petioles 1.2-12 cm long, adaxially canaliculate, stellate-pubescent, usually with a pair of acropetiolar, ± stipitate glands with a concave, discoid, yellow apex (0.5-1 mm diam.). Leaf blades membranaceous to papyraceous, glandular-denticulate, broadly ovate to suborbicular, 3-18 × 3-15 cm, apex acuminate, base rounded to cordate ; abaxially and adaxially conspicuously hirsute, pale green when fresh and drying matte pale green to brown ; venation evident on both sides, prominent below, with 5-9 pairs of brochidodromus, ± penninerved secondary veins (the lowermost pairs congested and appearing palmate), and cross-venulate tertiary venation ; with ± stipitate glands in some of the axils of the secondary veins (Fig. 1I). *Inflorescences* terminal, raceme-like thryses 5-20 cm long, with pistillate flowers toward the base and staminate flowers towards the distal end, axes stellate, flattened ; bracts triangular, 1.0-2.5 mm long, caducous. *Staminate flowers* with stellate, subglobose buds 1.5-2.9 mm diam., pedicels 1-3 mm long ; sepals 5, shortly connate at base, lobes ovate, c. 2 × 1.2 mm, apex acute, inflexed at anthesis, abaxially stellate, adaxially glabrous, margins ciliate ; petals 5, white, elliptic-spatulate, 2.5-2.7 × 1-1.5 mm, recurved at anthesis, abaxially subglabrous and papillose, adaxially glabrous, margins ciliate ; disc glands 5, opposite the sepals, sessile, ellipsoidal with an apical depression, c. 0.4 × 0.3-0.6 mm, yellowish ; stamens 12-15, white, filaments 1.5-3.3 mm long, glabrous or pilose at base, anthers broadly elliptic, c. 0.5-1 × 0.5-0.8 mm ; receptacle pilose. *Pistillate flowers* with stellate, ellipsoid buds c. 2.2 mm diam., pedicels 1-4 mm long ; sepals 5, ovate, spreading at anthesis, 2.5-3 × 1.3-2.3 mm, apex acute, shortly connate at base, abaxially stellate, adaxially glabrous except towards the apex, persistent in fruit ; petals often reduced, 0.8-2.5 2.5 × 0.2-1 mm, linear to spathulate, recurved, glabrous but with a ciliate margin ; disc glands 5, opposite the sepals, sessile, ellipsoidal, c. 0.4 × 0.8 mm ; ovary densely hirsute, globoid, 1.5-3.7 mm diam ; styles 3, 3-4.2 mm long, each branch flattened and 2-3 times bifurcate, spreading, abaxially stellate, adaxially glabrous, persistent. *Capsules* 4-8 × 5-8 mm, densely hirsute, exocarp not separating (Fig. 4O), endocarp woody, 0.4-0.6 mm thick ; columella 3.5-5.5 mm long, cornute, capitate. *Seeds* ±compressed-ellipsoid, 3.5-5.6 × 3-4.3 × 2-2.9 mm (Fig. 4P) ; testa glossy, verrucose, brown ; caruncle narrowly reniform c. 0.7 × 2 mm.

Phenology. – This species has been collected only from October to March, presumably because it is deciduous during the remaining drier months of the year. Specimens in flower have been collected from October to February, and in fruit from October to January.

Distribution, habitat and ecology. – *Croton tsiampiensis* has a disjunct distribution in northern Antsiranana and southern

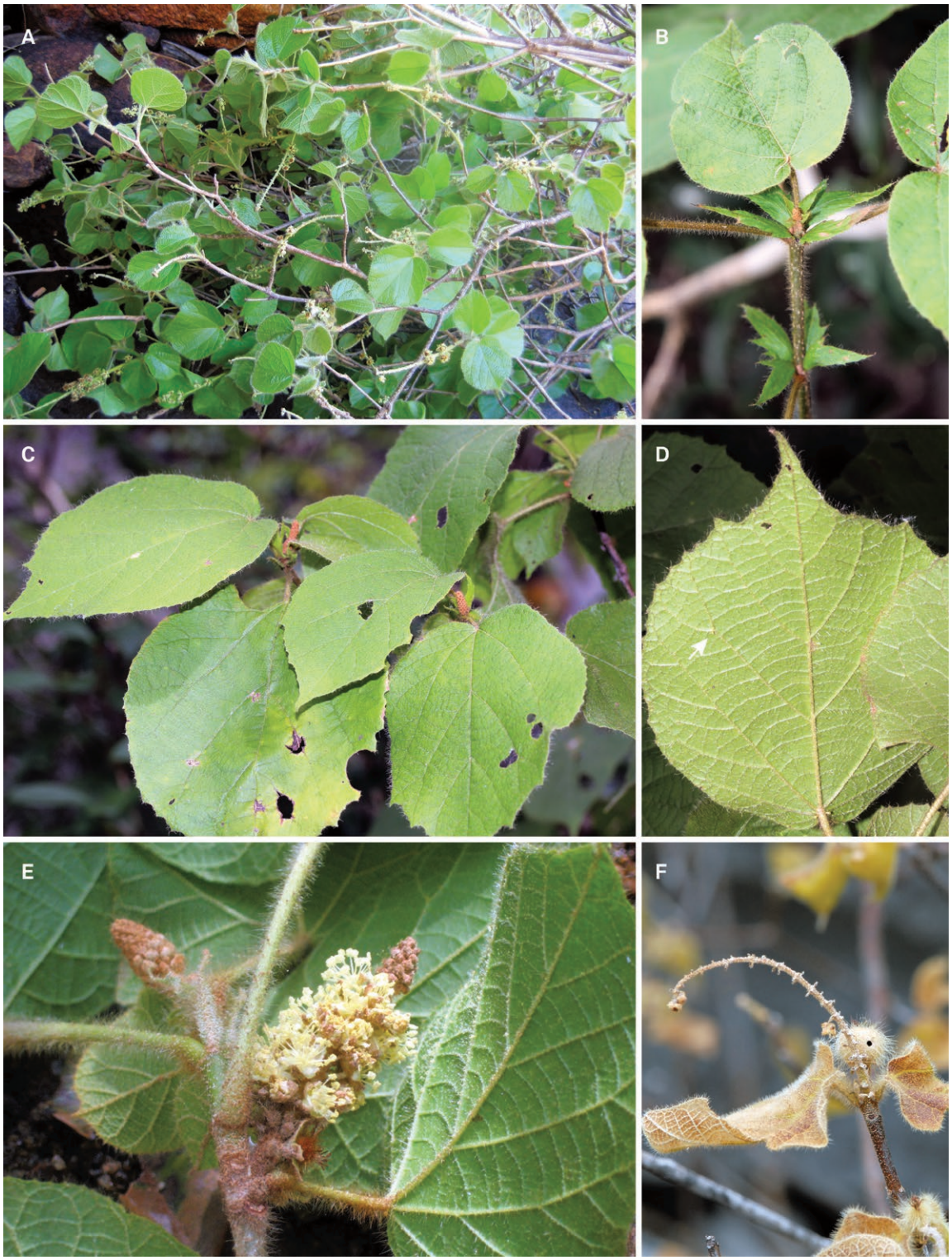

Fig. 13. *Croton tsiampiensis* Leandri **A.** Habit of a felled shrub; **B.** Laciniate stipules; **C.** Leaves; note the compact young inflorescences; **D.** Underside of leaf showing the prominent (palmate) secondary venation and the transvenulose tertiary venation; note the petiolar and laminar glands (arrow); **E.** Inflorescence with pistillate and staminate flowers; **F.** Brach with senescent leaves and infructescence with a mature capsule. [**A, E:** *Randrianaivo et al. 1400*; **B-D:** *van Ee et al. 2370*; **F:** *Gillespie et al. 10696*] [Photos: **A, E:** R. Randrianaivo; **B:** K. Kainulainen; **C-D:** P. Berry; **F:** L. Gillespie]

Mahajanga Provinces, respectively (Fig. 2B). It has been collected in deciduous, semideciduous, and evergreen forests, as well as in anthropogenic savannas, at 45-500 m in elevation, on sandy substrates and on tsingy limestone.

Conservation assessment. – This species appears to be widespread with fragmented populations in deciduous forests of northern and western Madagascar, including the the protected areas Ankarana, Beanka, Bemaraha, and Daraina. We therefore treat this species as "Near Threatened" [NT] according the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – The species epithet *tsiampiensis* refers to the type locality, the Tsiampihy forest in Mahajanga Province.

Croton tsiampiensis is distinct for its broadly cordate leaves, large incised stipules, and very hirsute pubescence. It is superficially similar to *C. ankarensis* Leandri, and Leandri's description of that species was likely based on specimens representing different taxa, one of which is likely *C. tsiampiensis*. The type of *C. ankarensis*, *Perrier de la Bâthie 9830* from Ankara (Betsiboka Reg.), lacks laminar glands and has alternate leaves, as well as sparsely stellate-pubescent capsules. It is clearly different from *C. tsiampiensis* and does not belong in the Adenophorus Group (it was placed in the Ankarensis Group by Leandri, 1939). The *Leandri 103bis* syntype from Bemaraha is nearly leafless, but the leaf scars are opposite. The pistillate flowers are much larger than in *Perrier de la Bâthie 9830*, but they conform to *C. tsiampiensis*, as does the markedly hirsute and pale gray bark of the young branches. We therefore tentatively include *Leandri 103bis* in *C. tsiampiensis*.

The varieties *C. tsiampiensis* var. *macrophyllus* and var. *microphyllus* that Radcliffe-Smith (2016) described based on differences in leaf size are synonymized here. As with many of the new names in his manuscript, only single specimens are cited, and from our studies of a broader sample of specimens that are now available, it is evident that more variation in leaf size is found within, rather than between, populations. Nor is it meaningful to recognize *C. tsiampiensis* var. *ankarensis*, which Radcliffe-Smith (2016) distinguished from the type variety by its shorter petioles (< 1 cm vs > 1.5 cm) and inflorescences, as well as slightly larger fruits. We have collected large-leaved specimens *(van Ee et al. 2371)* from the Ankarana population with leaves up to 16 × 11 cm and petioles up to 11 cm long, and *Gillespie et al. 10696*, also from Ankarana, is closer in inflorescence length and fruit size to the type of *C. tsiampiensis* than to *C.* var. *ankarensis*. There are currently no vernacular names recorded for *Croton tsiampiensis*.

Additional specimens examined. – **Madagascar. Prov. Antsiranana :** Diana Reg., Ankarongana, Analafandro, 12°37'50"S 49°31'28"E, 46 m, 23.II.2006, *Andrianjafy et al. 1619* (CNARP, MICH, MO, P, TAN) ; Ankarana, 13.X.1990, *Bardot-Vaucoulon 131* (P) ; *ibid. loc.*, 4.XI.1990, *Bardot-Vaucoulon 224* (P) ; *ibid. loc.*, 12°55'S 49°05'E, 150 m, 5.XI.1990, *Bardot-Vaucoulon 252* (P, TAN) ; *ibid. loc.*, 19.I.1991, *Bardot-Vaucoulon 392* (P) ; *ibid. loc.*, 200 m, 3.II.1960, *Cours & Humbert 5614* (P) ; *ibid. loc.*, 12°54'S 49°07'E, 150 m, 29.XI.1990, *Gillespie 4085* (MICH, MO) ; *ibid. loc.*, 12°55'23"S 49°05'09"E, 110 m, 2.XI.2012, *Gillespie et al. 10696* (CAN, MICH, MO, TAN) ; *ibid. loc.*, 30-350 m, 24.I-29.II.1960, *Humbert 32654* (P) ; SAVA Reg., Vohemar Distr., Daraina, Antsahabe forest, 13°12'37"S 49°33'27"E, 520 m, 11.I.2004, *Nusbaumer 902* (G, MICH, MO, P) ; *ibid. loc.*, 13°12'36"S 49°33'43"E, 500 m, 21.I.2004, *Nusbaumer 1076* (G, MICH, MO) ; *ibid. loc.*, 13°12'35"S 49°33'38"E, 500 m, 5.XI.2006, *Randrianaivo et al. 1400* (CNARP, MICH, MO, P, TAN) ; Ankarana National Park, Maeva trail, 12°57'23 "S 49°07'04"E, 128 m, 6.III.2016, *van Ee et al. 2370* (MICH, TAN) ; *ibid. loc.*, 12°57'23 "S 49°07'00"E, 153 m, 6.III.2016, *van Ee et al. 2371* (MICH, TAN) ; *ibid. loc.*, Benavony trail, 12°56'55 "S 49°07'39"E, 124 m, 7.III.2016, *van Ee et al. 2378* (MICH, TAN). **Prov. Mahajanga :** Melaky Reg., collines au N d'Antsalova, bord de la Soahanina, 18.X.1932, *Leandri 281* (K, P, TAN) ; *ibid loc.*, *Leandri 283* (P) ; Beanka, partie S, Ambinda-Est, 18°02'41 "S 44°30'08"E, 261 m, 24.XI.2011, *Gautier & Tahinarivony 5718* (G, MO) ; Tsingy du Bemaraha, 4.X.1932, *Leandri 103bis* (K, P) ; Beanka, partie S ; Ambinda-Est, 18°02'59"S 44°30'17"E, 260 m, 11.XII.2011, *Nusbaumer et al. 3051* (G, MICH).

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