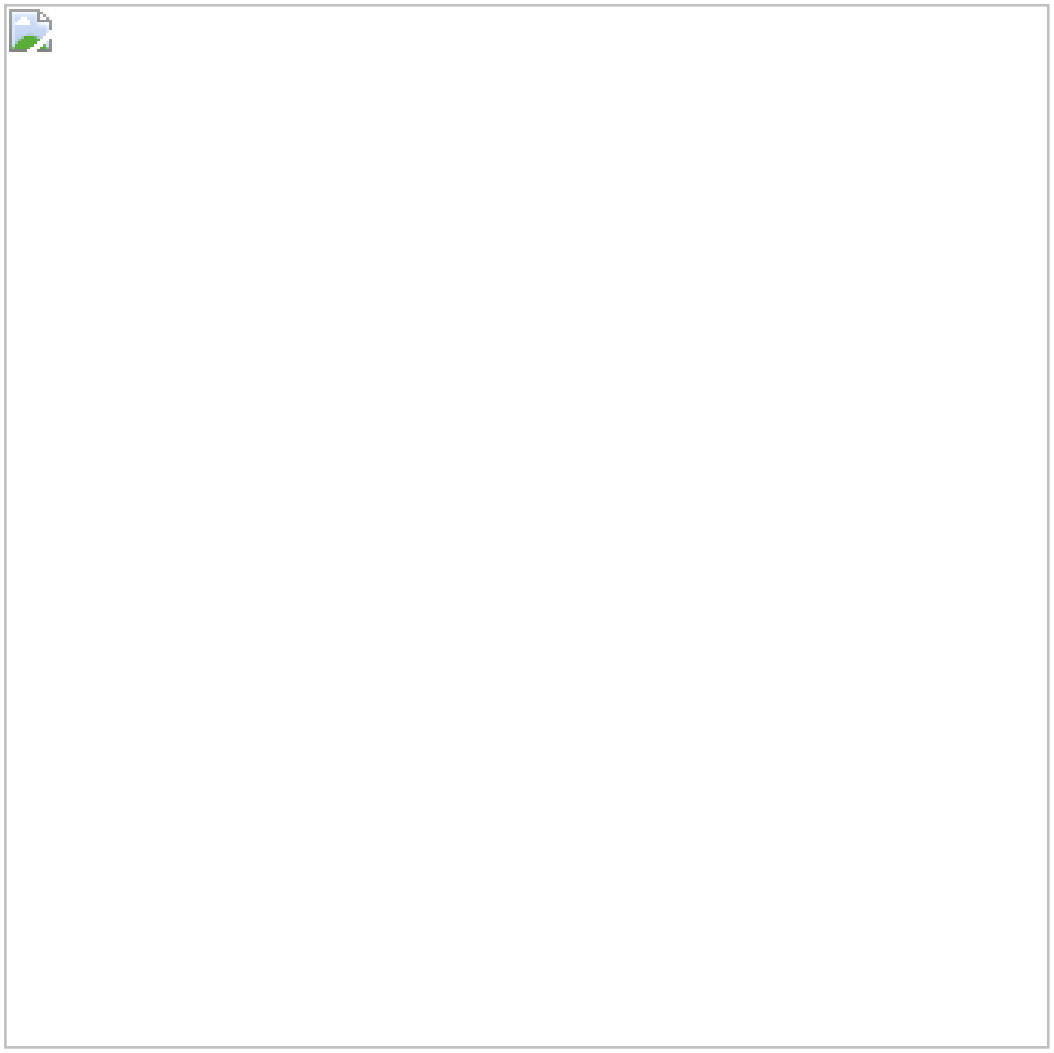

Rediscovery of two species of Croton (Euphorbiaceae) from littoral habitats of eastern Madagascar

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Rediscovery of two species of Croton (Euphorbiaceae) from littoral habitats of eastern Madagascar

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Abstract

KAINULAINEN, K., P.E. BERRY & B. VAN EE (2017). Rediscovery of two species of Croton (Euphorbiaceae) from littoral habitats of eastern Madagascar. *Candollea* 72: 35-44. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2017v721a5

Two species of *Croton* L. *(Euphorbiaceae)* previously reported only from their type specimens, *Croton chapelieri* Baill. and *Croton vatomandrensis* Leandri, are reevaluated here and found to be geographically widespread along the eastern coastline of Madagascar. We provide updated descriptions, lists of selected additional specimens, distribution maps, and photographs of both species. We also designate an epitype for *Croton chapelieri* and a lectotype for *Croton vatomandrensis*. *Croton chapelieri* was the source of considerable taxonomic confusion, and we treat as synonyms here for the first time *Croton aymoninorum* Leandri, *Croton louvelii* Leandri, *Croton daphniphylloides* Radcl.-Sm., *Croton daphniphyllum* Radcl.-Sm., *Croton daphniphyllum* var. *hirsutus* Radcl.-Sm., and *Croton rhododendroides* Radcl.-Sm. *Croton chapelieri* var. *longepetiolata* Radcl.-Sm. is considered to be a synonym of *Croton submetallicus* Baill. With our improved understanding of the geographical ranges of *Croton chapelieri* and *Croton vatomandrensis*, we provide IUCN Red List conservation assessments for both species.

Résumé

KAINULAINEN, K., P.E. BERRY & B. VAN EE (2017). Redécouverte de deux espèces de Croton (Euphorbiaceae) des habitats littoraux de l'est de Madagascar. *Candollea* 72: 35-44. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2017v721a5

Deux espèces de *Croton* L. *(Euphorbiaceae), Croton chapelieri* Baill. et *Croton vatomandrensis* Leandri, sont étudiées dans ce travail. Connues jusqu'alors uniquement par leur type, elles s'avèrent en fait distribuées tout au long de la côte orientale de Madagascar. Nous fournissons des descriptions mises à jour, un choix de spécimens supplémentaires, des cartes de distribution et des photographies des deux espèces. Nous désignons également un épitype pour *Croton chapelieri* et un lectotype pour *Croton vatomandrensis*. Un chaos taxonomique planait autour de *Croton chapelieri.* Nous considérons ici comme synonymes: *Croton aymoninorum* Leandri, *Croton louvelii* Leandri, *Croton daphniphylloides* Radcl.-Sm., *Croton daphniphyllum* Radcl.-Sm., *Croton daphniphyllum* var. *hirsutus* Radcl.-Sm., et *Croton rhododendroides* Radcl.-Sm. *Croton chapelieri* var. *longepetiolata* Radcl.-Sm. est considéré comme un synonyme de *Croton submetallicus* Baill. Grâce à une meilleure compréhension de la distribution géographique de *Croton chapelieri* et de *Croton vatomandrensis*, nous pouvons proposer une évaluation du degré de menace selon la Liste Rouge de l'UICN pour les deux espèces.

Keywords

EUPHORBIACEAE – *Croton* – Madagascar – Taxonomy – Littoral forests

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Introduction

Among the numerous species of *Croton* L. *(Euphorbiaceae)* described from Madagascar, there are many that are still known only from their type collections, which implies that they are either extremely rare, their area of occurrence is very under-collected, or that their circumscription has been misunderstood. Two such names, *C. chapelieri* Baill. (Baillon, 1861) and *C. vatomandrensis* Leandri (Leandri, 1939), are associated here with more recent collections and determined to be geographically widespread but ecologically specialized and confined to sandy, littoral forests on the moister, eastern side of the island.

The type of *C. vatomandrensis*, *Perrier de la Bâthie 14084* (P), comes from southeasternmost Toamasina Province, whereas the origin of the type of *C. chapelieri*, *Chapelier s.n.* (P), was not specified, although it is known that Louis Armand Chapelier (1779-1806) collected mainly along the eastern coast of Madagascar, where he lived for years in the Foulpointe area north of the city of Toamasina (Tamatave), in Toamasina Province (Dorr, 1997). Two additional species were described from the eastern coast by Leandri (1939, 1973), namely *C. aymoninorum* Leandri and *C. louvelii* Leandri. The former name is based on material from the Fort Dauphin area of southeastern Toliara Province, and the latter from the coastal forest of Tampina in Toamasina Province. Both are recognized here as synonyms of *C. chapelieri* for the first time. Further obfuscation was provided by the recent, posthumous publication of a manuscript left by Alan Radcliffe-Smith (1938-2007) in 2002 (Radcliffe-Smith, 2016), in which four more taxa were published from the Fort Dauphin area in southeastern Madagascar, namely *C. daphniphylloides* Radcl.-Sm., *C. daphniphyllum* Radcl.-Sm., *C. daphniphyllum* var. *hirsutus* Radcl.-Sm., and *C. rhododendroides* Radcl.-Sm. (Radcliffe-Smith, 2016). All are determined here to be mere variants of *C. chapelieri* (see Notes section of that species). A new variety of *C. chapelieri* proposed by Radcliffe-Smith (2016), namely *C. chapelieri* var. *longepetiolata* Radcl.-Sm., is based on a single specimen from Zahamena National Park in Toamasina Province, and we consider it to be a synonym of *C. submetallicus* Baill.

Although much of Madagascar's littoral forests have been destroyed, a substantial area of littoral forest is protected at Mahabo in Fianarantsoa Province as part of a project overseen by the Missouri Botanical Garden (MBG, 2016). At this site, we have located additional populations of *Croton* that include both *C. chapelieri* and *C. vatomandrensis*. In the case of the latter, this is the second site where the species has been found so far. The concept of *Croton chapelieri* recognized here is that of a species distributed very sporadically at low elevations from the Antsiranana Province (on the Masoala Peninsula) south to southeasternmost Toliara Province, where it is the most common species of *Croton* in the remaining littoral forests of Sainte Luce, Mandena, and Petriky. As a result of these discoveries, we provide expanded and updated descriptions, distribution maps, lists of specimens examined, and photographs of both *Croton chapelieri* and *C. vatomandrensis*. Since the type specimen of *C. chapelieri* is very depauperate, an epitype is also designated.

Given the apparent disjunction between Mahabo and the other populations of the two species, we speculate that there are other intervening coastal populations of these species yet to be found. We encourage botanists collecting in coastal areas of eastern Madagascar to collect these and any other *Croton* species they may find, as this will undoubtedly help fill important gaps in their known distributions.

Besides these two species of *Croton*, other species in the genus that are known from littoral forests on sandy substrates in eastern and southeastern Madagascar include *C. anisatus* Baill., *C. cassinoides* Lam., *C. noronhae* Baill., and C. *trichotomus* Lam. All are shrubs, but they are readily distinguishable from *C. chapelieri* and *C. vatomandrensis* as follows:

- *Croton anisatus* has ± whorled, anisophyllous, and sparsely lepidote leaves, as well as congested inflorescences.
- *Croton cassinoides* has crenate to serrate and sparsely stellate-pubescent leaves.
- *Croton noronhae* has dark-reddish velvety (young) stems, densely whitish-lepidote and brown-punctulate (abaxial) leaves, and congested inflorescences.
- *Croton trichotomus* has densely silvery-lepidote and ferruginous-punctate (abaxial) leaves and elongate inflorescences.

The key provided below will help in the determination of *Croton* specimens collected from littoral forests on sandy substrates near sea level along the eastern and southeastern coast of Madagascar. To the best of our knowledge this includes all of the *Croton* species found in such forests from Masoala southwards.

Key to the species of Croton found in littoral forests on sandy substrates in eastern and southeastern Madagascar

1. Abaxial surface of leaves densely covered with lepidote trichomes 2
1a. Abaxial surface of leaves glabrous or sparsely covered with stellate, lepidote, or stellate-lepidote trichomes..... 3
2. Young stems lepidote; petiolar glands sessile; inflorescences elongate..... ***C. trichotomus***
2a. Young stems velvety; petiolar glands stipitate; inflorescences congested ..... ***C. noronhae***
3. Inflorescences elongate, spike- or raceme-like; largest leaf blades 5-16 cm long..... 4
3a. Inflorescences glomerate; largest leaf blades less than 5 cm long..... 5

4. Inflorescences 1-4(-7.5) cm long, divergent; petioles 4-40(-60) mm long; leaves drying ± glossy; ovary and fruit stellate-pubescent..... ***C. chapelieri***

4a. Inflorescences 5-15 cm long, erect; petioles 2-15 mm long; leaves drying matte; ovary and fruit glabrous ..... ***C. vatomandrensis***

5. Leaf blades sparsely lepidote, margins entire; petioles less than 5 mm long..... ***C. anisatus***

5a. Leaf blades sparsely stellate, margins toothed; petioles 5-10 mm long ..... ***C. cassinoides***

Systematics

Croton chapelieri Baill. in Adansonia 1: 166. 1861 (Fig. 1, 2, 4A-F, 5A-B).

≡ *Oxydectes chapelieri* (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

– *Aubertia glandulosa* Chapel. ex Baill. in Adansonia 1: 166. 1861 [nom. nud.].

Typus: Madagascar: Prov. Toamasina: *sine loc., Chapelier s.n.* (holo-: P [P00389523]!).

Epitypus (designated here): **Madagascar. Prov. Toliara:** Sainte Luce, at entrance to reserve just past thatched huts, 24°46'46"S 47°10'17"E, 10 m, 17.II.2009, *van Ee, Berry, Dorsey & Razanatsoa 925* (MICH [MICH1514617]!; isoepi-: G!, K!, MAPR!, MO!, NY!, P!, TAN!).

= *Croton louvelii* Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7: 40. 1939. **Typus: Madagascar. Prov. Toamasina:** forêt côtière, Tampina, I.1924, *Louvel 217* (holo-: P [P00312340]!) [as *louveli*], **syn. nov.**

= *Croton aymoninorum* Leandri in Adansonia ser. 2, 13: 175. 1973. **Typus: Madagascar. Prov. Toliara:** Fort Dauphin, forêt de Mandena, 19.X.1970, *Keraudren-Aymonin & Aymonin 24940* (holo-: P [P00312374]!), **syn. nov.**

= *Croton daphniphylloides* Radcl.-Sm., Gen. Croton Madag. Comoro: 164. 2016. **Typus: Madagascar. Prov. Toamasina:** Ambila-Lemaitso, 7.XI.1951, *Service Forestier 4228* (holo-: P [P00133469]!), **syn. nov.**

= *Croton daphniphyllum* Radcl.-Sm., Gen. Croton Madag. Comoro: 161. 2016. **Typus: Madagascar. Prov. Toliara:** Fort Dauphin in Mandena, 2 km E of Botanic Garden, 24°58'S 47°00'E, 9.X.1990, *Faber-Langendoen, Dumetz & Randrianasolo 2226* (holo-: P [P00133462]!; iso-: MO!), **syn. nov.**

= *Croton daphniphyllum* var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro: 163. 2016. **Typus: Madagascar. Prov. Toliara:** Petriky Forest, c. 1.5 km W of large dune near N shore of Lake Andranany, c. 12 km WSW of Tôlañaro [Fort Dauphin], 25°03'S 46°53'E, 14.IV.1989, *Gereau, Rabevohitra & Dumetz 3374* (holo-: K!; iso-: MO!, P [P00133120]!), **syn. nov.**

= *Croton rhododendroides* Radcl.-Sm., Gen. Croton Madag. Comoro: 163. 2016. **Typus: Madagascar. Prov. Toliara:** Préfecture Tôlañaro (Fort Dauphin), forêt à 5 km de Ste. Luce, au N de Maliafolaky, 24°47'S 47°10'E, 21.X.1989, *Dumetz, McPherson & Rabevohitra 775* (holo-: P [P00133460]!; iso-: MO!), **syn. nov.**

Shrubs or *trees* to 10 m tall, with bifurcating branching. Branches ± flattened on new growth but becoming terete with age, gray, usually sparsely covered with brown stellate-lepidote indumentum (hairs sometimes with a porrect central radius, resulting in the young shoot being villous). Stipules absent or vestigial. *Leaves* alternate along stem, but (sub)opposite and ± whorled towards the apex. Petioles 4-40(60) mm long, adaxially canaliculate, sparsely brown stellate-lepidote (sometimes villous), usually with a pair of ± stipitate (0.1-1 mm) concave discoid glands 0.5-1.0 mm in diam. at the base of the blade. Leaf blades coriaceous, slightly revolute, entire or serrate towards the apex, elliptic to obovate or occasionally lance-obovate, 2.8-15.5 × 1.5-6.5 cm, apex (acuminate) apiculate or acute to rounded, base cuneate or rounded; adaxial surface glabrous, glossy, bright green with a pale green or reddish midrib when fresh, turning orange in old leaves, drying ± glossy, brown or olive green; venation usually readily seen, with 3-11 pairs of brochidodromous, ± penninerved secondary veins; abaxial surface glabrous or sparsely brown stellate-lepidote (in particular along the midrib), pale green; venation and midrib ± prominent. *Inflorescences* short racemes 1.0-4.0(-7.5) cm long, terminal, bisexual, the staminate flowers towards the distal end and more numerous than the 1-6(8) pistillate flowers at the base, generally divergent; axes stellate-lepidote (sometimes villous), flattened; bracts narrowly triangular, 1-5 mm long. *Staminate flowers* with brown stellate-lepidote (sometimes villous), subglobose buds 1-2 mm diam., pedicels elongating from bud to anthesis, 1-6 mm long; sepals 5, pale green, shortly connate at base, lobes broadly triangular-ovate, 2.0-2.5 × 1.0-1.5 mm, apex acute, inflexed at anthesis, abaxially stellate-lepidote, adaxially pilose, margins densely ciliate; petals 5, white, elliptic-spatulate, c. 2.5 × 0.8 mm, recurved at anthesis, abaxially stellate-lepidote and papillate, adaxially pilose, margins densely ciliate; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoidal with an apical depression, 0.3-0.5 × 0.3-0.4 mm, pale yellow; stamens 10-17, white, filaments 1.5-2.6 mm long, ciliate, anthers elliptic, 0.5-0.9 × 0.4-0.7 mm; receptacle pilose. *Pistillate flowers* with stellate-lepidote (sometimes villous) buds 1-2 mm diam., pedicels 1-4 mm long; sepals 5, elliptic, spreading at anthesis, 2-9.5 × 0.5-2.5 mm, apex acute, abaxially and adaxially sparsely

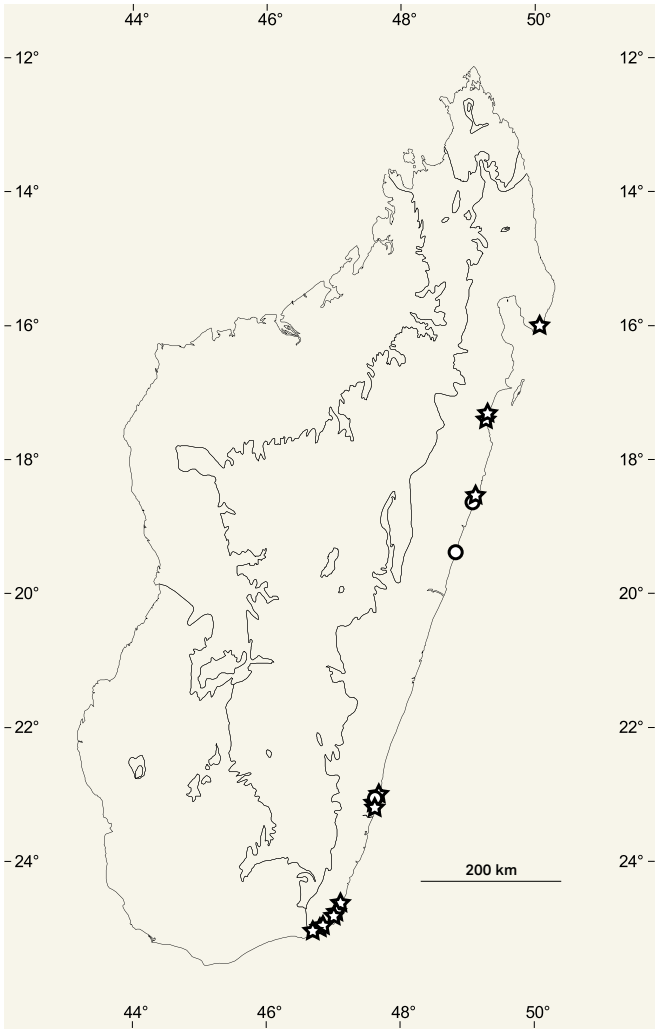

Fig. 1. – Geographic distribution of *Croton chapelieri* Baill. (stars) and *C. vatomandrensis* Leandri (circles), mapped on the bioclimatic zones of Madagascar (after Cornet, 1974; see Schatz, 2000).

stellate-lepidote, pale green, persistent in fruit; petals absent/reduced; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoidal, 0.4-0.7 × 0.3-0.5 mm, pale yellow; glandular filaments (petals?) alternating with the sepals, 0.7-2.0 mm long, ciliate; ovary densely stellate-pubescent (sometimes villous), subglobose, 1-2 mm diam., styles 3, 2.0- 3.5 mm long, each branch flattened and twice (rarely thrice) bifurcate for a total of 12 stigmatic tips, spreading, recurved at the apices, adaxially glabrous, abaxially sparsely stellate-pubescent, white, turning brown, persistent. *Capsules* c. 6-8 × 6-8 mm, smooth, brown, stellate-pubescent, exocarp not separating, endocarp woody, 0.2-0.4 mm thick; columella 4-5 mm long, cornute, capitate. *Seeds* ± compressed-ellipsoid, 3.5-4.3 × 2.7-3.1 mm; testa glossy, granulate, brown; caruncle narrowly reniform, c. 0.6 × 0.5 mm.

Distribution, habitat, and ecology. – *Croton chapelieri* is known from coastal Antsiranana, Fianarantsoa, Toamasina, and Toliara Provinces. It is sometimes locally frequent in littoral forest and scrub, mostly on white sands, from sea level to 40 m elevation (Fig. 1, 2A-B).

Phenology. – *Croton chapelieri* appears to be aseasonal and flowers throughout the year.

Vernacular names. – *Croton chapelieri* has numerous recorded common names, which include: Fotsiavadika" *(Jacquemin 1267),* "Hazomanitra" *(Louvel 217),* "Sagnira" *(Ludovic 1660),* "Sarihafotra vavy" *(Randrianaivo et al. 1976),* "Sily" *(Service Forestier 7289),* "Tsinjeny" *(Rabevohitra 2024)* and "Tsivoanjo" *(Hoffmann 194).* They probably reflect both the morphological variation of the species and its widespread distribution that spans numerous different dialects of the Malagasy language.

Conservation status. – *Croton chapelieri* can be locally abundant, but its sandy littoral habitat is very restricted, and it is known so far from seven sites, three in Toliara, one in Antsiranana, one in Fianarantsoa and two in Toamasina provinces. We therefore recommend that it be assessed as "Near Threatened" [NT] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Although Leandri (1939) recognized *C. chapelieri* and even named his "Groupe Chapelieri" after it, he characterized the species as being "incomplètement connue." This was presumably due to the poor condition of the type, which consists of a leafy branch with only the naked axis of one inflorescence [no flowers remain, although Baillon (1861) did describe them]. Also, there was no collecting location given. However, we know from Dorr (1997) that Chapelier (1779-1806) spent most of his time in Madagascar living near Foulpointe north of Tamatave, and it is quite likely that this is the area where the type of *C. chapelieri* came from. In the same treatise by Leandri (1939), he described *C. louvelii* as part of Groupe Chapelieri and recognized that both it and *C. chapelieri* have the same distinctive foliaceous pistillate calyces. His key simply separated *C. louvelii* from *C. chapelieri* as having "parties jeunes non hirsutes" vs. "parties jeunes un peu hirsutes." The type locality of *C. louvelii* is the littoral forest of Tampina, which is farther south of Foulpointe in Toamasina Province. Comparing the two types, they are a very good match, and there are some trichomes on the young growth of *C. louvelii* that are similar to those on the type of *C. chapelieri*. These similarities are the justification for our decision to synonymize *C. louvelii*. Also, because of the lack of flowers on the single type specimen of *C. chapelieri*, we designate here an epitype from a recent collection (*van Ee et al. 925*) for which multiple duplicates, photos of live material, and DNA sequence data are available.

Leandri (1973) described the first of a series of taxa from the southeastern coast of Madagascar that are also treated here as synonyms of *C. chapelieri*. His *C. aymoninorum* Leandri came from the littoral forest of Mandena, along the coast north of Fort Dauphin. Instead of assigning it to one of the groups that he recognized in his earlier treatise (Leandri, 1939), he instead treated *C. aymoninorum* as part of a bewilderingly diverse array of species whose only character in common was that of their contracted inflorescences. Largely for that reason, we believe, its affinities to *C. chapelieri* went unnoticed, and later Radcliffe-Smith (2016) described *C. daphniphyllum* from the same forest that *C. aymoninorum* came from. Mandena is a relatively small area of sandy littoral forest that has been extensively collected by botanists over many decades, including ourselves, and we are quite confident that only three species of *Croton* occur there – *C. chapelieri*, *C. cassinoides*, and *C. trichotomus*.

Croton chapelieri is morphologically quite variable, particularly in leaf shape and pubescence. The leaves are typically elliptic but vary from lanceolate to obovate. Similarly, the apex can vary from acuminate to rounded, the base can be cuneate or rounded, and the margin can be entire or serrate towards the apex. Extensive collections and our own field studies from coastal areas of southeastern Toliara Province (Mandena, Petriky, and Sainte Luce) show that the types of both *C. aymoninorum* and *C. daphniphyllum* correspond to a locally common species found in sandy, littoral forests to the west and north of Fort Dauphin, in the Mahabo area of Fianarantsoa Province, and then in Toamasina Province farther north. In the Sainte Luce and Petriky areas of southeastern Toliara Province, besides the more typical stellate-lepidote form, there are populations in which the shoots, leaves, and inflorescences are villous due to the presence of a porrect central radius to the stellate-lepidote trichomes (Fig. 2C). These forms correspond to what Radcliffe-Smith (2016) described as *C. chapelieri* var. *hirsutus* Radcl.-Sm. (from the Petriky forest) and *C. rhododendroides* Radcl.-Sm. (from the Sainte Luce forests), both of which are included here in synonymy as well. Finally, Radcliffe-Smith (2016) described *C. daphniphylloides* Radcl.-Sm., differing only slightly from his *C. daphniphyllum* and whose type comes from Ambila-Lemaitso, which is very close to the Tampina, the type locality of *C. louvelii*. The other paratype of *C. daphniphylloides* is from Tampolo, farther north in Toamasina Province and presumably close to the type locality of *C. chapelieri* itself.

The name *C. chapelieri* var. *longepetiolata* Radcl.-Sm. is based on a single specimen *(Malcomber et al. 2511)* from 500-750 m elevation in Zahamena National Park in Toamasina Province. It appears to be a fairly typical specimen of *C. submetallicus* Baill.

Beyond the specimens cited below, there are many more specimens of *C. chapelieri* that we have identified, particularly from the well-collected forests of Petriky, Mandena and Sainte Luce in Toliara Province and in the Mahabo Reserve of Fianarantsoa Province. These have all been entered into the Madagascar Catalogue (2016) with our determination and can be found in the specimen list under *Croton chapelieri*.

Selected additional specimens examined. – **Madagascar. Prov. Antsiranana**: Antalaha-CR Vinanivao, Cap Masoala, PD3 Beankora, 15°57'S 50°13'E, 10 m, 23.IX.2003, *Callmander & Bohnenstegel SW 685* (G). **Prov. Fianarantsoa**: Atsimo-Atsinanana Region, Farafangana District, Réserve Spéciale de Manombo, Agnalazaha Forest, 23°04'53"S 47°45'25"E, 25.X.2000, *Hoffmann 295* (K, MO, P, TAN); Mahabo-Mananivo, Mahabo, 23°10'36"S 47°42'01"E, 3.XI.2001, *McPherson & Rabenantoandro 18310* (K, MO, P, TEF); Farafangana, 27.VII.1955, *Service des Eaux et Forêts 13969* (K, P); Mitsevo-Farafangana, [23°00'S 47°45'E], 23.VI.1952, *Service des Eaux et Forêts 7289* (P, TEF); Mahabo Reserve, 23°10'41"S 47°42'07"E, 0-50 m, 11.XI.2009, *van Ee et al. 1181* (MICH, MO, TAN). **Prov. Toamasina**: Analanjirofo Region, Fenerive Est District, Ampasina, Tanambao-Tampolo, Station forestière de Tampolo, 17°16'S 49°25'E, 0-10 m, 5-7.IV.1997, *Birkinshaw et al. 381* (MO); Atsinanana Region, Brickaville District, Ambinaninony, Andranokoditra, Vohibola forest, 18°33'34"S 49°15'01"E, 5 m, 12.II.2003, *Lowry 6081* (MO). **Prov. Toliara**: Anosy Region, Toalanaro District, Mandena forest, 20.II.1972, *Debray 1759* (P); Nord Fort-Dauphin, Sud Massif Tsingafiafy, 2.III.1973, *Debray 1997* (K, P); Mandena, 0-10 m, 17.IV.1989, *Dumetz et al. 654* (MO, P, TAN, TEF); [Mahatalaky], Sainte Luce forest, 24°47'S 47°10'E, 0-10 m, 21.X.1989, *Dumetz et al. 774* (MO, P, TAN, TEF); Sainte Luce, 24°46'42"S 47°10'15"E, 0 m, 13.X.2000, *Hoffmann et al. 194* (K, P); Forêt IIe d'Esetra entre la scierie et la R.N.12 a S/P Fort-Dauphin, 11.XII.1972, *Jacquemin 1185* (K, P); Ambandrika, Etazo forest, 24°49'00"S 47°07'43"E, 16 m, 9.IX.2012, *Ludovic 1660* (MO, TAN); Mahatatalaky, Ebakika, Magnindriavia forest, 24°45'50"S 47°08'35"E, 22 m, 10.IX.2012, *Ludovic 1710* (MO, P, TAN); Mandena, 24°57'S 47°02'E, 10 m, 17.X.1989, *Rabevohitra 2024* (MO, P, TAN, TEF); *ibid. loc.*, *Rabevohitra 2028* (MO, TEF); Ampasy Nahampoa, Ambavarano forest, 24°57'28"S 47°03'16"E, 6 m, 8.XII.2006, *Ramison 123* (MICH, MO, P, TAN); Belavenoko forest, 24°49'07"S 47°07'52"E, 17 m, 25.XI.2011, *Ratovoson 1781* (MICH, MO, P, TAN); Tsiaronampasy, Antongoranambo, 24°48'54"S 47°08'32"E, 30 m, 22.X.2012, *Ratovoson 1998* (MICH, MO, P, TAN); Mandena, 24°57'10"S 47°00'10"E, 12-25 m, 31.VII.2015, *van Ee et al. 2135* (MICH, MO, TAN).

Croton vatomandrensis Leandri in Ann. Mus. Colon. Marseille, sér. 5, 7: 71. 1939 (Fig. 1, 3, 4G-L, 5C-D).

Lectotypus (designated here): **Madagascar. Prov. Toamasina:** env. de Vatomandry, près des lagunes, XI.1921, *Perrier de la Bâthie 14084* (P [P00248926]!; isolecto-: P [P00154409, P00154410]!).

Shrubs or *small trees* 1-3(-7) m tall, sparsely branched with dichotomous branching, stems ascending and semi-succulent, often with distinct horizontal or reticulate furrows in the bark, internodes sometimes contracted, giving the appearance of whorled branches. Branches ± flattened on new growth but becoming terete with age, gray, densely covered with red-brown stellate-lepidote indumentum that soon turns pale gray. Stipules absent or vestigial. *Leaves* alternate along stem, but (sub)opposite towards the apex. Petioles 2-15 mm long, adaxially canaliculate, densely red-brown stellate-lepidote, usually with a pair of concave discoid glands c. 1 mm in diam. near the base of the blade. Leaf blades coriaceous, entire or

Fig. 2. – *Croton chapelieri* Baill. **A.** Typical littoral habit at Mahabo, Atsimo-Atsinanana Region, Fianarantsoa Province; **B.** Shrubs growing on sand at Sainte Luce, Anosy Region, Toliara Province; **C.** Branch with leaves; note the villous pubescence on this specimen from Sainte Luce; **D.** Branch with staminate flowers and immature fruits; **E.** Staminate flowers; **F-G.** Pistillate flowers; **H.** Mature fruit. [**C:** *van Ee et al. 2148;* **D:** *van Ee et al. 927;* **E-G:** *van Ee et al. 2138;* **H:** *van Ee et al. 926*] [Photos: P. Berry]

very shallowly serrulate towards the apex, elliptic to obovate, 3-16 × 1.8-3 cm, apex acute, obtuse, or rounded, base cuneate; adaxial surface ± glabrous, glossy, bright green when fresh, turning orange in old leaves, drying matte pale green; venation not prominent, with 5-10(-16) pairs of brochidodromus, ± penninerved secondary veins; abaxial surface sparsely brown stellate-lepidote, pale green and glossy; venation not prominent except for the midrib. *Inflorescences* spike-like or pseudoracemose cymes, 5-15 cm long, terminal, erect, bisexual, the staminate flowers towards the distal end and more numerous than the pistillate flowers at the base; axes densely stellate-lepidote, flattened; bracts narrowly triangular, 0.9-1.6 mm long. *Staminate flowers* with brown stellate-lepidote, subglobose buds 1.6-2.6 mm diam., pedicels elongating from bud to anthesis, to 4 mm long; sepals 5, pale green, shortly connate at base, lobes broadly triangular-ovate, 1.2-1.8 × 1.0-1.6 mm, apex acute, inflexed at anthesis, abaxially sparsely stellate-lepidote and papillose, adaxially glabrous, margins ciliate; petals 5, white, elliptic-spatulate, c. 2 × 1 mm, recurved at anthesis, abaxially papillate and pilose towards base, adaxially glabrous, margins densely ciliate; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoidal with an apical depression, c. 0.6 × 0.3 mm, yellow; stamens 13-16, white, filaments 1.3-2.5 mm long, ciliate, anthers elliptic, c. 0.6 × 0.5 mm; receptacle pilose. *Pistillate flowers* with stellate-lepidote buds 1.8-2.8 mm diam., pedicels to 4 mm long; sepals 5, firm, elliptic, not spreading at anthesis, 2.2-3.5 × 1.1-1.6 mm, apex acute, shortly connate at base, abaxially brown stellate-lepidote, adaxially glabrous, pale green, persistent in fruit; petals absent/reduced; disc glands/nectaries 5, opposite the sepals, sessile, ellipsoidal, c. 0.6 × 0.3 mm, pale yellow; glandular filaments alternating with the sepals, 0.8-1.5 mm long; ovary glabrous, green, globoid-ellipsoid, c. 2.5 mm diam., styles 3, 3.0–3.5 mm long, each branch flattened and twice (or thrice) bifurcate for a total of 12 stigmatic tips, spreading, recurved at the apices, abaxially and adaxially glabrous, white, turning brown, persistent. *Capsules* 4.5-5.0 × 4.5-6.8 mm, smooth, green to brown, glabrous, exocarp not separating, endocarp woody, c. 0.2 mm thick; columella c. 4.5 mm long, cornute, capitate. *Seeds* ± compressed-ellipsoid, c. 4.6 × 3.3 mm; testa glossy, granulate, dark brown; caruncle narrowly reniform, c. 0.6 × 0.2 mm.

Distribution, habitat, and ecology. – *Croton vatomandrensis* is known from three sites so far, two in Toamasina Province and one in Fianarantsoa Province, all in sandy, swampy, littoral habitats, from sea level to around 30 m elevation. The type collection from Vatomandry was collected at the edge of a lagoon, and the specimens from Mahabo are from moist, somewhat boggy areas within the littoral forest and grassland zone, where they were growing mostly at the edge of patches of shrubs or *Ravenala* in areas with standing water, *Sphagnum*, ferns, grasses, and sedges (Fig. 1, 3A-B).

Phenology. – Based on the few known collections, *Croton vatomandrensis* appears to flower and fruit most heavily towards the end of the calendar year (November). In July at Mahabo we found plants mostly in the young bud stage, and the collection from Vohibola in Toamasina Province was fruiting in August.

Conservation status. – Besides the type locality near Vatomandry in southeastern Toamasina Province, *Croton vatomandrensis* is presently known from the forest of Vohibola farther north in Toamasina, and a small area near Mahabo, in Fianarantsoa Province. No collections have been made of it from the type locality near Vatomandry since the type was collected in 1921. Whereas *C. chapelieri* was locally common in the sandy forests at Mahabo, we saw very few individuals of *C. vatomandrensis* there. Given the restricted occurrences in just three known localities and the threat of habitat destruction in those sites, we recommend that this species be assessed as "Endangered" [EN B2ab(ii, iii, iv)], following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – *Croton vatomandrensis* is distinct with its sparsely branched habit and slightly succulent stems, the glabrous leaves and fruits, and the stellate-lepidote indumentum on young shoots that is reddish brown when young but turns pale gray with age (Fig. 3D). The erect spike-like inflorescences are also characteristic (Fig. 3G). It is notable that they appear to be dormant for extended periods of time before the onset of flowering. When Leandri (1939) described this species, he placed it in the informal "Groupe Fothergillifolium" together with *C. fothergillifolius* from Mauritius and *C. furcellatus* Baill. from Madagascar. Although he included all three species in his key to the group, there was no corresponding species entry for *C. furcellatus*. Instead, he included that species at the end of the article in his list of insufficiently known or doubtful species, mentioning that it might represent an introduction or a mislabeling. Although the type label of *C. furcellatus* indicates it is a Scott-Elliot collection from Fort Dauphin in southeastern Madagascar, it was actually mislabeled at Paris in a shipment that had been received from Kew (an error documented by Humbert, 1948). The type specimen of *C. furcellatus* is in reality a New World *Croton, C. sonorae* Torr., most likely an Edward Palmer collection *(Palmer 180)* from northern Mexico.

Both Leandri's "Groupe Fothergillifolium" and "Groupe Chapelieri" were characterized as having staminate flowers with more than 12 stamens, a lack of lepidote scales, two acropetiolar glands (with no other glands on the leaf surface), leaves glabrescent on the abaxial surface, and petals of the pistillate flowers rudimentary or lacking (Leandri, 1939). The only difference in Leandri's key between the groups was one of leaf blade proportions (blade at least twice as long as

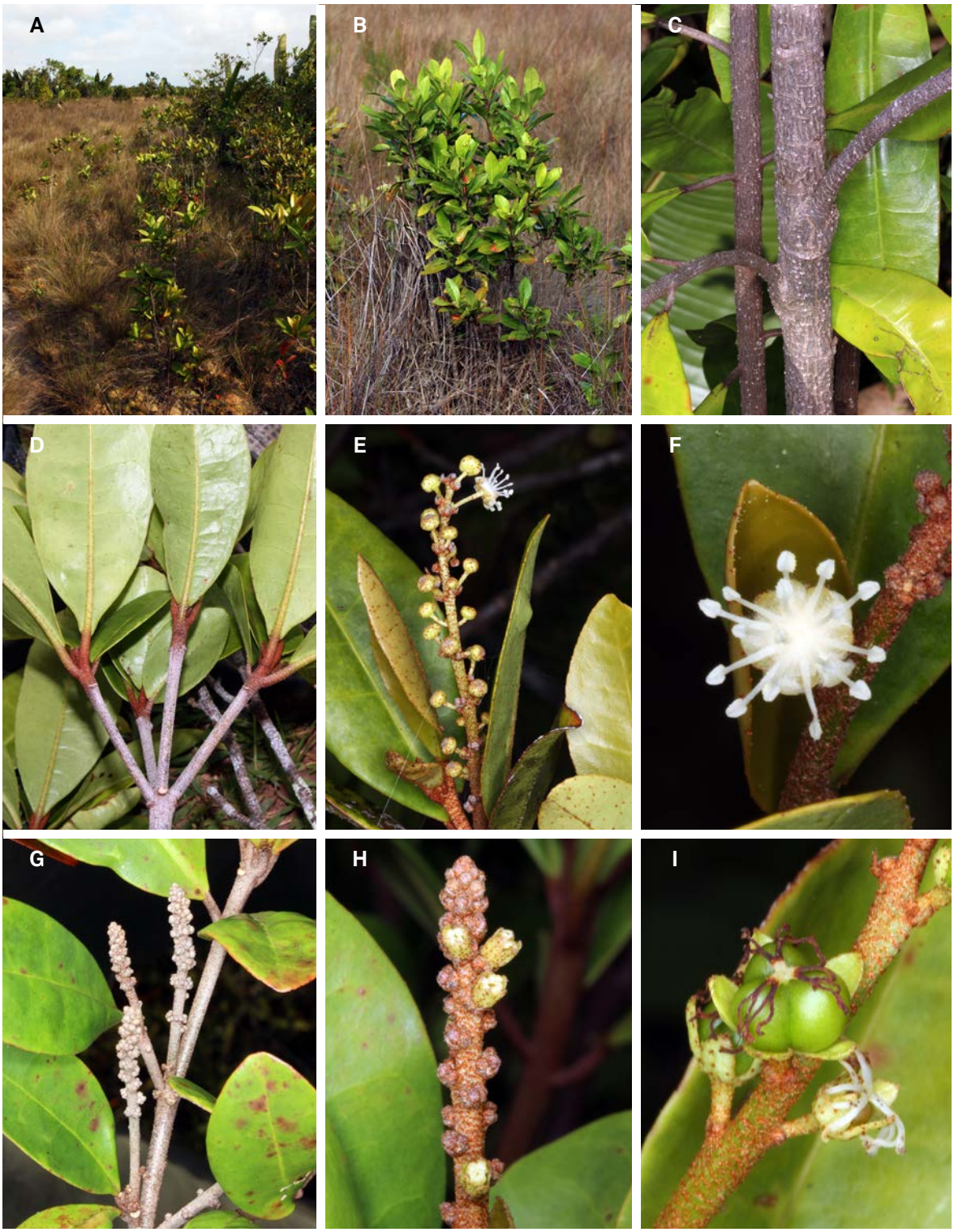

Fig. 3. – *Croton vatomandrensis* Leandri. **A.** Typical littoral habitat at Mahabo, Atsimo-Atsinanana Region, Fianarantsoa Province; **B.** Habit; **C.** Bark; note the characteristic horizontal furrows; **D.** Branch; note the subverticillate branching and how the young shoots soon turn from reddish brown to pale gray; **E.** Inflorescence with staminate flower and buds; **F.** Staminate flower; **G.** Immature inflorescences; **H.** Inflorescence with pistillate flowers; note the erect sepals; **I.** Pistillate flower and immature fruit; note the glabrous ovary. [**A-C, G-H:** *van Ee et al. 2028*; **D-F, I:** *van Ee et al. 1194*] [Photos: P. Berry]

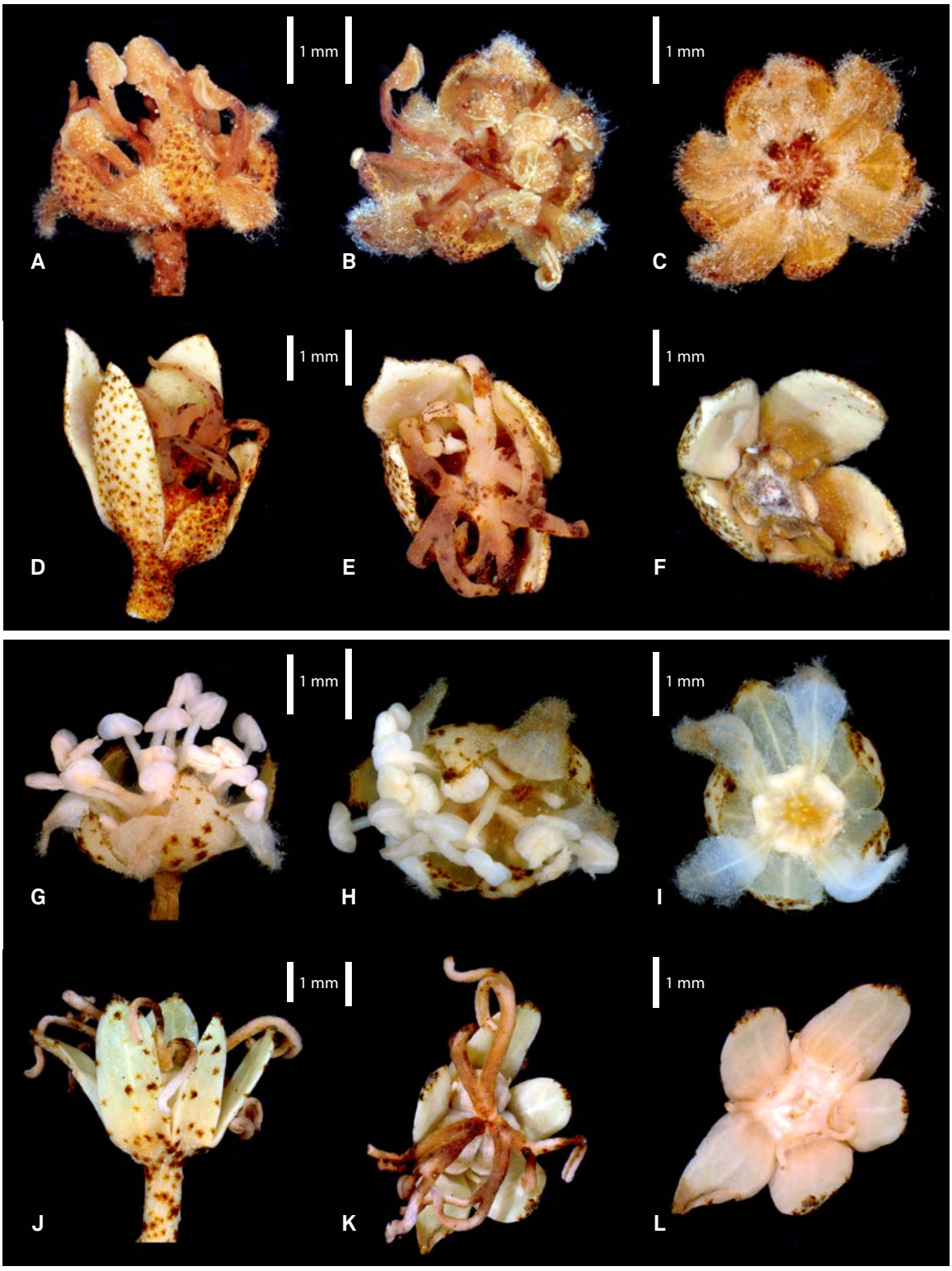

Fig. 4. – *Croton chapelieri* Baill. (**A-F**) and *C. vatomandrensis* Leandri (**G-L**). **A-C.** Staminate flower: side view (**A**), top view (**B**) and top view with stamens removed to show the five nectaries (**C**). **D-F.** Pistillate flower: side view (**D**), top view (**E**), and top view with ovary removed to show the five nectaries (**F**). **G-I.** Staminate flower: side view (**G**), top view (**H**), and top view with stamens removed to show the five nectaries (**I**). **J-L.** Pistillate flower: side view (**J**), top view (**K**), and top view with ovary removed to show the five nectaries (**L**). [**A-F:** *van Ee et al. 1181;* **G-L:** *van Ee et al. 1194*]

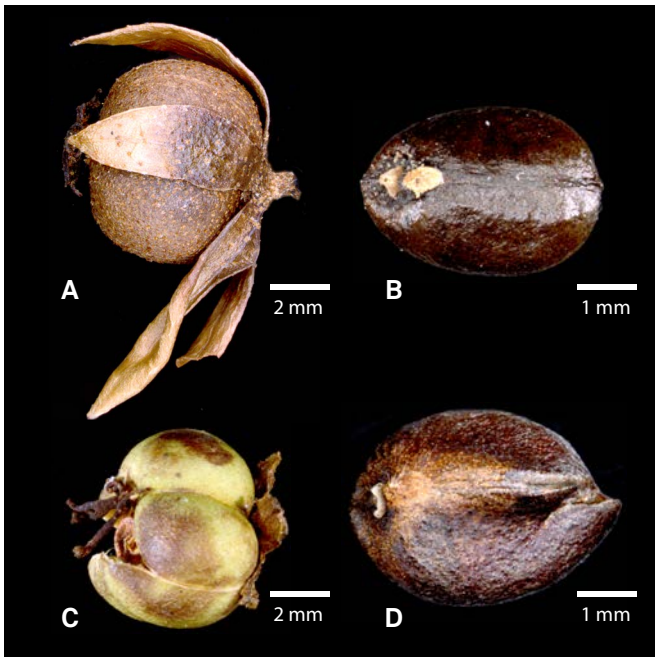

Fig. 5. – Capsules and seeds of *Croton chapelieri* Baill. (**A-B**) and *C. vatomandrensis* Leandri (**C-D**). **A.** Capsule; **B.** Seed; **C.** Capsule; **D.** Seed. [**A:** *Rabevohitra 2028*; **B:** *van Ee et al. 925*; **C-D:** *van Ee et al. 1194*].

wide in Groupe Chapelieri and blade at least half as wide as long in Groupe Fothergillifolium). In a recent molecular study of Western Indian Ocean species of *Croton* (Haber et al., in press), *C. fothergillifolius* is part of a highly supported clade of four species confined to the Mascarene island of Mauritius, whereas *C. chapelieri* and *C. vatomandrensis* are both embedded within a broader group of Malagasy, African, and Comoro Islands species, and they furthermore form part of the same, albeit poorly supported clade together with *C. bracteatus* and another undescribed species. This shows at least that *C. vatomandrensis* does not belong in the same group as C. *fothergillifolius*, and that the circumscription of Groupe Chapelieri needs to be examined in greater detail to determine whether *C. vatomandrensis* is actually closely allied to *C. chapelieri* or not.

Additional specimens examined. – **Madagascar. Prov. Fianarantsoa**: Atsimo-Atsinanana Region, Farafangana District, Mahabo-Mananivo, Baboaka, forêt Marovahatry, au bord du marécage Andranokena, 23°10'41"S 47°43'49"E, 23 m, 21.IV.2004, *Ludovic 737* (MO); Mahabo, 23°11'09"S 47°42'22"E, 15 m, 9.XI.2001, *McPherson & Rabenantoandro 18384* (K, MO, P); *ibid. loc.*, 23°10'13"S 47°43'27"E, 22 m, 26.VII.2003, *Rabehevitra et al. 550* (K, MO, P, TEF); *ibid. loc.*, 23°10'20"S 47°42'23"E, 29 m, 23.IX.2002, *Rabenantoandro et al. 957* (K, MICH, MO); *ibid. loc.*, 11.XI.2002, *Razakamalala & Ludovic 329* (K, MICH, MO); *ibid. loc.*, 23°10'21"S 47°43'11"E, 0-50 m, 11.IX.2009, *van Ee et al. 1194* (MICH, TAN); *ibid. loc.*, 23°10'16"S 47°41'58"E, c. 15 m, 19.VII.2015, *van Ee et al. 2028* (MICH, MO, P, TAN); *ibid. loc.*, 23°10'19"S 47°41'48"E, 15 m, 19.VII.2015, *van Ee et al. 2029* (MICH, MO, P, TAN). **Prov. Toamasina**: Atsinanana Region, Brickaville Distr., Andrananonkoditra, Ankanin'ny nofy, Vohibola forest, 18°33'56"S 49°15'24"E, 8 m, 4.VIII.2003, *Rabehevitra et al. 405* (K, MICH, MO).

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References

Baillon, M.H. (1861). Species Euphorbiaceorum. Euphorbiacées Africaines. 2e partie. *Adansonia* 1 : 139-173.

Cornet, A. (1974). *Essai de cartographie bioclimatique à Madagascar.* Notice Explicative No. 55. ORSTOM.

Dorr, L.J. (1997). *Plant collectors in Madagascar and the Comoro Islands*. Royal Botanic Gardens, Kew.

Haber, E.A., K. Kainulainen, B.W. van Ee, B.O. Oyserman & P.E. Berry (2017). Phylogenetic relationships of a major diversification of Croton (Euphorbiaceae) in the Western Indian Ocean region. *Bot. J. Linn. Soc.* 183 : 532-544.

Humbert, H. (1948). Au sujet des récoltes de Scott Elliot à Madagascar. *Not. Syst.* 13 : 163.

IUCN (2012). *IUCN Red List Categories and Criteria, Version 3.1.* 2nd ed. IUCN Species Survival Commission, IUCN, Gland & Cambridge.

Leandri, J. (1939). Les Croton de Madagascar et des îles voisines. *Ann. Mus. Colon. Marseille, sér. 5*, 7 : 1-100.

Leandri, J. (1973). Quelques Croton malgaches nouveaux. *Adansonia* ser. 2, 13 : 173-176.

Madagascar Catalogue (2016). *Catalogue of the Vascular Plants of Madagascar.* Missouri Botanical Garden, Saint-Louis & Antananarivo [http ://www.efloras.org/madagascar].

MBG [Missouri Botanical Garden] (2016). Botanical inventories at Mahabo Forest. [http ://www.mobot.org/MOBOT/research/littoral/mahabo_forest.shtml]

Radcliffe-Smith, A. (2016). *The genus Croton in Madagascar and the Comoro Is.* Preprint deposited in the libraries of K, BM and WSY on 23.XII.2016 by Martin Cheek.

Schatz, G.E. (2000). Endemism in the Malagasy tree flora. *In:* Lourenço, W.R. & S.M. Goodman (ed.), *Diversity and endemism in Madagascar:* 1-9. Mémoires de la Société de Biogéographie, Paris.