

A Nomenclator of *Croton* (Euphorbiaceae) in Madagascar, the Comoros Archipelago, and the Mascarene Islands

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Abstract

All published names of *Croton* from Madagascar, the Comoros, and the Mascarenes are treated here. We indicate which names are currently accepted (123 native species and 1 introduced), which ones we consider to be heterotypic synonyms (188), which ones are doubtful (25), and which ones should be excluded (5). We newly designate lectotypes for 108 names, and epitypes for *C. anisatus* Baill., *C. nobilis* Baill., and *C. submetallicus* Baill. A total of 133 names are newly treated as synonyms. One new combination is made, *Croton basaltorum* (Leandri) P.E.Berry for *C. antanosiensis* var. *basaltorum* Leandri, and one new name is proposed, *Croton toliarensis* B.W.vanEe & Kainul. for *C. tranomarensis* var. *rosmarinifolius* Radcl.-Sm.

Keywords

Euphorbiaceae, *Croton*, Madagascar, Comoros, Mascarenes, nomenclator, synonymy

Introduction

This work is part of an effort to lay the taxonomic foundation for a thorough phylogenetic-based revision of *Croton* (Euphorbiaceae) in the Western Indian Ocean Region (WIOR). Madagascar alone harbors around one third of the roughly 450 species recognized to occur in the Old World (Van Ee et al. 2011). There are also several species

known to occur on the Mascarene Islands (Mauritius and the French Department of Réunion), as well as on the Comoros Islands (Union of the Comoros and the French Department of Mayotte). There are no known species of *Croton* in the Seychelles or in any of the smaller, “Scattered Islands” of the WIOR. Because of the relative proximity of these islands to Madagascar, and the phylogenetic findings of Haber et al. (2017) that recovered all sampled *Croton* species from the Comoros and Mascarenes within a Malagasy clade, all described *Croton* taxa from this region are treated together here. The main purpose of this paper is to provide a comprehensive nomenclatural index of the published names of *Croton* from the Western Indian Ocean Region and to indicate their current taxonomic and nomenclatural status, based on our ongoing taxonomic and phylogenetic work on the genus.

Until 2016, taxa of *Croton* native to the Comoros, Madagascar, and the Mascarenes were published by just eight botanists in the following 27 books or journal articles: Lamarck (1786); Geiseler (1807); Baillon (1861, 1890, 1891a); Müller (1864, 1865, 1866); Baker (1882, 1883, 1887); De Candolle (1901); Leandri (1931, 1935, 1939, 1948, 1957, 1970a, 1970b, 1970c, 1972a, 1972b, 1973a, 1973b, 1974, 1976); and Croizat (1944). In 2016, a large number of new *Croton* taxa from the WIOR were described. Ten new species of *Croton* from Madagascar were published by Kainulainen et al. (2016) and Berry et al. (2016a, 2016b). Then, taking advantage of an overly literal interpretation of Article 29.1 of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012), Martin Cheek of the Royal Botanic Gardens, Kew, submitted three “preprint” copies of a long-dormant manuscript on Malagasy *Croton* by the late botanist Alan Radcliffe-Smith to the libraries of Kew, Wisley, and the Natural History Museum in London toward the end of December 2016. By early January 2017, most of the names from that manuscript had been posted on the International Plant Names Index website (www.ipni.org), with an effective publication date of 23 December 2016 (Radcliffe-Smith 2016). This manuscript added 150 newly described names of *Croton* from Madagascar and the Comoros Archipelago, consisting of 26 new species, three new subspecies, and 121 new varieties. All of these recent names have been evaluated here, and our assessment of their current taxonomic status is presented in Tables 1 and 2 and in the “Incertae Sedis” section at the end of the nomenclator.

Materials and methods

The main herbaria consulted for the WIOR *Croton* types were G, K, MICH, MAO, MO, P, TAN, and TEF. Scanned images of types from these and other herbaria available on JSTOR Global Plants (<http://plants.jstor.org/>) were also consulted. All original literature sources were also reviewed.

Specimens are considered holotypes when a single gathering in a particular herbarium is cited in the protologue, and there is only one specimen of that gathering housed there, or if there was a single gathering with no herbarium mentioned in the

protologue, or else a single specimen exists in the herbarium where the author was based (ICN Art. 9.1, McNeill et al. 2012; McNeill 2014). In some publications, such as Leandri (1970b, 1973a, 1974) and Radcliffe-Smith (2016), the protologue indicates a holotype, but there is more than one sheet of that collection at the herbarium cited. In such cases, we rely on the notations on the sheets to determine whether a holotype can be identified; if not, a lectotype is designated. When two or more syntypes were cited in the protologue, a lectotype is designated, using our informed assessment of the most appropriate specimen. In a few cases, an epitype is also newly designated, when the condition of the holotype or lectotype is so poor as to make the identity of the species unclear.

Since the name *Croton* is derived from the Greek κροτών (tick), which is masculine, this is the proper gender for *Croton*. However, it was sometimes treated as neuter or as feminine by Baillon and Leandri, and this now requires that the epithets with those endings be orthographically corrected to the masculine ending. In such cases, the original spelling of an epithet is given, and users should be aware of the need to search databases using both the original spelling and subsequent, corrected spellings.

Within the taxon citations, if a lectotype is designated among the extant syntypes, the remaining syntypes are also cited. Type locality information is taken directly from the type specimen labels, even if it does not entirely agree with the location given in the protologue. If we add information not present on the specimen labels, such as the province name, or a more modern or accepted spelling of a place name, that information is placed within brackets. Barcode numbers of type specimens are cited when available, but as of late October 2017, the type specimens cited by Radcliffe-Smith (2016) have not yet been assigned barcodes and do not yet appear on the JSTOR Global Plants website. Whenever we newly treat a taxon as a synonym, we include the annotation “**syn. nov.**” at the end of the entry. Lastly, under the “Habit and Distribution” section of each entry from Madagascar, we list the general distribution of the species on the island and include the former province names where they occur in parentheses.

Results and discussion

In the present treatment we recognize 114 accepted species native to Madagascar. All of these species are endemic to the island, with the exception of *C. adenophorus* Baill., which also occurs on Mayotte in the Comoros. Besides this species, there are four species endemic to the Comoros (*C. bifurcatus* Baill., *C. emeliae* Baill., *C. humblotii* Baill., and *C. mayottae* P.E.Berry & Kainul.). Another four species are endemic to Mauritius (*C. fothergillifolius* Baill., *C. grangerioides* Bojer ex Baill., *C. tiliifolius* Lam., and *C. vaughanii* Croizat), and a fifth (*C. mauritanus* Lam.) is endemic to Réunion. *Croton bonplandianus* Baill., a native of South America, is the only documented non-native, naturalized species of *Croton* in the WIOR, having previously been reported from the Mascarenes (Mauritius, Réunion, and Rodrigues; Croizat 1944, Coode 1982). We also report here the occurrence of *C. bonplandianus* from Mayotte. Other species that

are likely to become naturalized weeds, but have not been reported from the region, include *Astraea lobata* L. (formerly *Croton lobatus* (L.) Klotzsch), *C. hirtus* L'Hét., and *C. glandulosus* L. Several non-native species have been cultivated on the islands in the past, presumably for their medicinal or shade properties, such as *C. aromaticus* L., *C. haumanianus* J.Léonard, *C. laccifer* L., and *C. tigilium* L., but there is no evidence that they have persisted.

For the 114 species that are native to Madagascar, only six are truly widespread throughout the island, occurring in all six former provinces, namely *C. catatii* Baill., *C. goudotii* Baill., *C. macrobuxus* Baill., *C. mongue* Baill., *C. myriaster* Baker, and *C. stanneus* Baill. Three others occur in five provinces (*C. chrysodaphne* Baill., *C. hypochalibaes* Baill., and *C. nitidulus* Baker), five in four provinces, six in three provinces, and 29 in two provinces. Sixty-five species are known from just a single province. Of the six provinces, Toliara is the richest in *Croton* species with 53, followed by Antsiranana with 43, Toamasina with 39, Mahajanga with 35, Fianarantsoa with 27, and Antananarivo with 15. While we realize that these six administrative provinces of Madagascar have been superseded by a system of 22 administrative regions that represent subdivisions of the provinces, we did not attempt to further refine the distribution of species, although this will be a promising avenue to pursue in the future for conservation planning efforts. See Fig. 2 for a summary of these figures.

Given the small size of the islands in the Mascarenes and the Comoros Archipelago, and the small area of existing natural habitats, we believe that it is fairly unlikely that any additional *Croton* taxa will be discovered there. On the other hand, Madagascar harbors a large number of undescribed species, which are currently under study by the authors and awaiting formal description. We anticipate the description of at least 20 more new species from Madagascar based on the material we now have on hand. Many of these come from recently explored areas in the eastern part of the island, but also from relatively well-explored areas in the north and south but belonging to difficult species complexes, such as the coppery, lepidote-leaved species.

The sometimes extensive synonymy presented in this nomenclator (viz., *C. adenophorus*, *C. catatii*, *C. chapelieri*, or *C. stanneus*) suggests that many species have been poorly understood in the past, sometimes known only from sparse descriptions or poor type material, and numerous taxa are based on a single or just a few specimens. For instance, from Baillon (1861) to Leandri (1939) to Radcliffe-Smith (2016), all three authors recognized *Croton chapelieri* as an accepted species, but known only from the type, which was of unspecified provenance. The re-evaluation of this species by Kainulainen et al. (2017a), and again in this paper, reveals that *C. chapelieri* is in fact a widespread species along the eastern littoral zone, and we now consider that it has eight heterotypic synonyms. We should point out that without first-hand knowledge of the species in the field, it may have been impossible to sort out the variability of this species and recognize its restriction to a fairly narrow ecological and elevational zone in sandy coastal habitats. Among earlier workers on the genus in the region, the only one who had any first-hand knowledge of Madagascar was Jacques Leandri. In contrast, we

have made four collecting trips to Madagascar dedicated to studying *Croton*, covering much of the geography of the island, although there are still numerous areas we have not been able to visit. Especially for deciduous species, it is important to collect specimens at different times of the year, since some species flower when leafless and produce their leaves during the rainy season. Ultimately, the greatest progress in understanding the diversity of a large, complex genus like *Croton* on Madagascar will be achieved by local botanists who are able to study populations in the field, revisit sites at different phenological stages, and assess their local and regional variability.

Another instructive example of a previously misunderstood species is *Croton chrysodaphne* Baill., a tree species that Baillon (1861) described based on three syntypes from Madagascar. Baillon's concept of this species was followed by both Leandri (1939) and Radcliffe-Smith (2016), but Berry et al. (2011) determined that the three syntypes in the protologue actually represent three different species, and while one of the others had a valid name (*C. argyrodaphne*), it took several more years to determine with certainty that the third one was a new species, *C. cupreolepis* P.E.Berry, B.W.van Ee, & Kainul. (Berry et al. 2016b). As a further example, Berry and Van Ee (2011) also deciphered the history of *C. multicostatus* Müll.Arg., a Malagasy species which had erroneously been attributed to Hispaniola in the Caribbean, and included as synonyms two species names from Madagascar, *C. vernicosus* Baker and *C. sclerodorus* Baill. Figure 1A shows an example of foliage that is similar in all these coppery-lepidote tree species, while Fig. 1B–G show major differences in flowers of four species in this assemblage in terms of sepal shape, stigma morphology, and presence or absence of petals in the pistillate flowers, as well as differences in the number of stamens in the staminate flowers.

The recent, hastily published work of Radcliffe-Smith (2016) appears to us to illustrate the problem of a lack of field knowledge in the region and the consequent lack of understanding of the variability in many *Croton* species. In some cases, Radcliffe-Smith picked up on important differences in specimens, but he was very inconsistent in how he treated them. Out of the 150 new taxa that he described, 89 were known only from the type collection, and another 29 were known from just two collections. Such a narrow circumscription tends to recognize every minor variation as a separate taxon. On the other hand, in some cases very distinctive new species were treated as varieties of previously known species. For example, *Croton bemarkanus* Leandri is a small shrub, and what Radcliffe-Smith (2016) described as *C. bemarkanus* var. *pseudolepidotus* Radcl.-Sm. is a very distinctive large tree that was rediscovered in the field and described by Berry et al. (2016a) a few months earlier as *C. aleuritoides* P.E.Berry. Our general stance for recognizing varieties for Malagasy crotons is that we do not yet have a sufficient level of understanding of the majority of the species to make meaningful subspecific designations. This may come in time, but the fact that more of Radcliffe-Smith's (2016) published varieties fell into synonymy under different species than the ones to which they were assigned (see below) is an indication that we are not yet at the stage where widespread designations of infraspecific taxa are advisable.

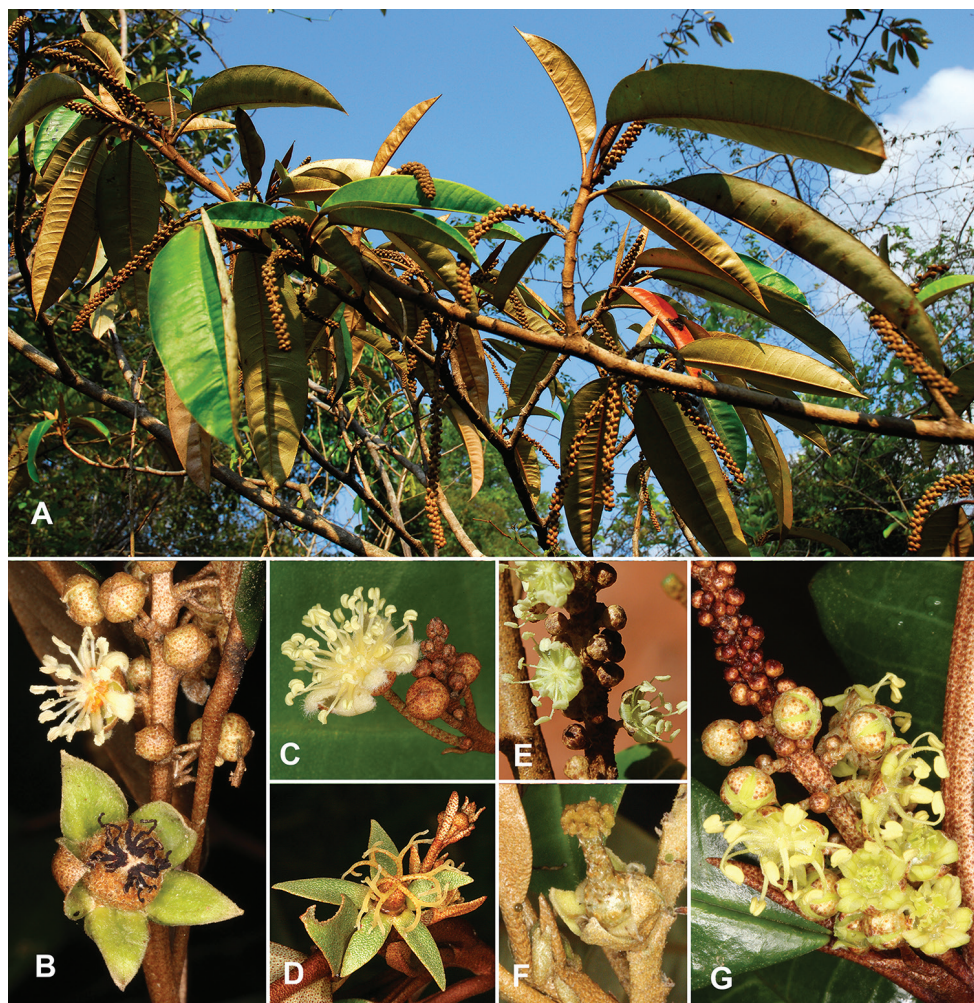


Figure 1. Diversity of flowers in coppery-lepidote tree species of *Croton* from Madagascar that are vegetatively very similar. **A** *Croton argyrodaphne*, with leaves that are similar to those of several other species **B** Part of an inflorescence of *Croton nobilis* showing pistillate flower (below) with thick, reduplicate sepals and no petals, and staminate flower (above) with an intermediate number of stamens (ca. 18) **C** Staminate flower of *C. chrysodaphne*, with numerous (ca. 40) stamens and the unusual feature of ten (vs. normally five) petals **D** Pistillate flower of *C. chrysodaphne*, with patent, slender bifurcating styles and no petals **E** Staminate flowers of *C. argyrodaphne*, with only 11 stamens **F** Pistillate flower of *C. argyrodaphne*, with a stylar column topped by tightly bunched, short stigmas and also with recurved petals between the sepals (typically the pistillate flowers of this species are apetalous) **G** Base of an inflorescence of *C. multcostatus* showing three open pistillate flowers at the base (with well-developed, ligulate petals) and several open staminate flowers showing a low stamen number of 10 or 11. Photos by P. Berry.

The overall disposition of the taxa described by Radcliffe-Smith (2016) is given in Tables 1 and 2. Of the 26 species and three subspecies that he described, only four are maintained here as accepted taxa (Table 1), and all others are considered to be

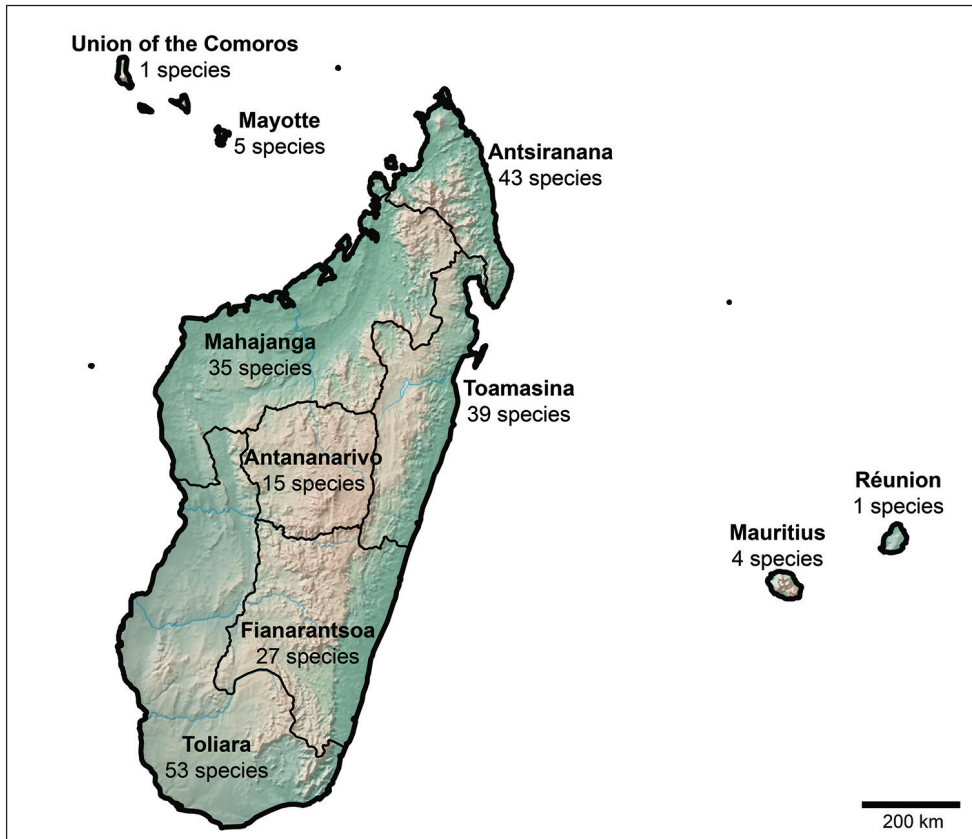


Figure 2. Distribution of the number of native species of *Croton* in the Western Indian Ocean Region. There are 123 native species overall in the region, with 114 native to Madagascar; one of them (*C. adenophorus*) is shared with Mayotte, and the single species in the Union of the Comoros (*C. humblotii*) also occurs on Mayotte. The species on Mauritius and Réunion only occur there. The map of Madagascar shows how many species occur in each of the six former provinces (there are varying levels of overlap between provinces; see text for details).

synonyms of previously described species. Of the 121 new varieties described, we synonymize 97, more often than not under different species than the ones to which they were assigned (Table 2). Of the remaining 24 varieties described, 22 are included in the ‘Incertae Sedis’ section and two are not validly published (see Names Not Validly Published). Based on this outcome, we contend that the manner in which the new taxa in Radcliffe-Smith (2016) were brought to effective and valid publication, namely by the hand-delivering of three copies of a minimally reviewed and edited manuscript to several London libraries while simultaneously having the taxa entered into IPNI at Kew, avoided a badly needed, more rigorous review of the manuscript and led to the useless creation of a great many names, in contravention of Preamble paragraph 1 of the ICN (McNeill et al. 2012). In our view, the Radcliffe-Smith (2016) publication

Table 1. New species and subspecies of Malagasy *Croton* described by Radcliffe-Smith (2016) and their treatment in this paper. Radcliffe-Smith described 26 new species and 3 new subspecies, besides the 121 varieties treated in Table 2. The four Radcliffe-Smith names in bold below are the only ones maintained here as accepted taxa.

Radcliffe-Smith (2016) name	As treated in this paper
<i>C. adenophoroides</i> Radcl.-Sm.	<i>C. loucoubensis</i> Baill.
<i>C. alaotrensis</i> Radcl.-Sm.	<i>C. droguetioides</i> Kainul. & Radcl.-Sm.
<i>C. alceicornu</i> Radcl.-Sm.	<i>C. hypochalibaeus</i> Baill.
<i>C. alchorneifolius</i> Radcl.-Sm.	<i>C. alchorneifolius</i> Radcl.-Sm.
<i>C. bracteatus</i> subsp. <i>manongarivensis</i> Radcl.-Sm.	<i>C. nitidulus</i> Baill.
<i>C. bracteatus</i> subsp. <i>populifolius</i> Radcl.-Sm.	<i>C. danguyanus</i> Leandri
<i>C. commiphoroides</i> Radcl.-Sm.	<i>C. indrisilvae</i> Kainul., B.W.vanEe & P.E.Berry
<i>C. daphniphylloides</i> Radcl.-Sm.	<i>C. chapelieri</i> Baill.
<i>C. daphniphyllus</i> Radcl.-Sm.	<i>C. chapelieri</i> Baill.
<i>C. dasygyne</i> Radcl.-Sm.	<i>C. radiatus</i> P.E.Berry & Kainul.
<i>C. delicatulus</i> Radcl.-Sm.	<i>C. menabeensis</i> Leandri
<i>C. domohineifolius</i> Radcl.-Sm.	<i>C. chapelieri</i> Baill.
<i>C. droguetioides</i> Radcl.-Sm.	<i>C. droguetioides</i> Kainul. & Radcl.-Sm.
<i>C. echinatus</i> Radcl.-Sm.	<i>C. dissimilis</i> Baill.
<i>C. gracilior</i> Radcl.-Sm.	<i>C. gracilior</i> Radcl.-Sm.
<i>C. hirsutissimus</i> Radcl.-Sm.	<i>C. nudatus</i> Baill.
<i>C. lepidotoides</i> Radcl.-Sm.	<i>C. ferricretus</i> Kainul., B.W.vanEe & P.E.Berry
<i>C. minimimarginiglandulosus</i> Radcl.-Sm.	<i>C. minimimarginiglandulosus</i> Radcl.-Sm.
<i>C. mocquerysii</i> subsp. <i>meridionalis</i> Radcl.-Sm.	<i>C. thoursianus</i> Baill.
<i>C. neoholstiifolius</i> Radcl.-Sm.	<i>C. menabeensis</i> Leandri
<i>C. oligostemon</i> Radcl.-Sm.	<i>C. hypochalibaeus</i> Baill.
<i>C. parietarioides</i> Radcl.-Sm.	<i>C. droguetioides</i> Kainul. & Radcl.-Sm.
<i>C. parvifructus</i> Radcl.-Sm.	<i>C. stanneus</i> Baill.
<i>C. remotiflorus</i> Radcl.-Sm.	<i>C. trichotomus</i> Geisel.
<i>C. rhododendroides</i> Radcl.-Sm.	<i>C. chapelieri</i> Baill.
<i>C. scorpistogyne</i> Radcl.-Sm.	<i>C. heteranthus</i> Aug.DC.
<i>C. submetallicoides</i> Radcl.-Sm.	<i>C. chrysodaphne</i> Baill.
<i>C. ustulatus</i> Radcl.-Sm.	<i>C. ustulatus</i> Radcl.-Sm.
<i>C. vohemarensis</i> Radcl.-Sm.	<i>C. argyrodaphne</i> Baill.

is not at all an accurate reflection of our current knowledge of Malagasy *Croton* taxonomy, and it should not be consulted as such. Rather, with this paper, previous ones we have published (Berry and Van Ee 2011; Berry and Kainulainen, 2017; Berry et al. 2011, 2016a, 2016b; Kainulainen et al. 2016, 2017a, 2017b), our initial molecular results (Van Ee et al. 2011, 2015; Haber et al. 2017) and with more complete molecular studies forthcoming shortly, as well as additional taxonomic novelties and revisions in preparation, we are generating a significantly different and better substantiated vision of the rich diversity of *Croton* in the Western Indian Ocean Region.

Table 2. New varieties of Malagasy *Croton* described by Radcliffe-Smith (2016) and their treatment in this paper. Radcliffe-Smith described 121 new varieties besides the 26 new species and 3 new subspecies listed in Table 1. Of the 121 new varietal names, 97 are reduced to synonymy (45 under the nominal species name and 52 under a different species), 22 are considered as Incertae Sedis, and two are invalid.

Radcliffe-Smith (2016) name	As treated in this paper
<i>C. adabolavensis</i> var. <i>hippophaëoides</i>	<i>C. adabolavensis</i> Leandri
<i>C. adabolavensis</i> var. <i>microlepidotus</i>	<i>C. adabolavensis</i> Leandri
<i>C. adabolavensis</i> var. <i>ovalifolius</i>	<i>C. adabolavensis</i> Leandri
<i>C. adabolavensis</i> var. <i>stellatipilus</i>	<i>C. adabolavensis</i> Leandri
<i>C. alaotrensis</i> var. <i>integrifolius</i>	<i>C. dissimilis</i> Baill.
<i>C. ambovombensis</i> var. <i>lepidotus</i>	nom. inval. (Excluded Taxa)
<i>C. anisatus</i> var. <i>hirsutus</i>	<i>C. hovarum</i> Leandri
<i>C. ankarensis</i> var. <i>ankarafantsikae</i>	Incertae Sedis
<i>C. anosiravensis</i> var. <i>pilosus</i>	<i>C. anosiravensis</i> Leandri
<i>C. antanosiensis</i> var. <i>ambohibyi</i>	<i>C. trichotomus</i> Geisel.
<i>C. antanosiensis</i> var. <i>fianarantsoae</i>	<i>C. hypochalibaeus</i> Baill.
<i>C. antanosiensis</i> var. <i>pubescens</i>	<i>C. greveanus</i> Baill.
<i>C. bastardii</i> var. <i>bongolavae</i>	Incertae Sedis
<i>C. bastardii</i> var. <i>meridionalis</i>	<i>C. muricatus</i> Vahl
<i>C. bathianus</i> var. <i>ambatondrazakae</i>	<i>C. scoriarum</i> Leandri
<i>C. bathianus</i> var. <i>ihosianus</i>	<i>C. ihosianus</i> Leandri
<i>C. bathianus</i> var. <i>toliarae</i>	<i>C. crocodilorum</i> Baill.
<i>C. bemarkanus</i> var. <i>parvistipulatus</i>	Incertae Sedis
<i>C. bemarkanus</i> var. <i>pseudolepidotus</i>	<i>C. aleuritoides</i> P.E.Berry
<i>C. betiokensis</i> var. <i>haplostylis</i>	Incertae Sedis
<i>C. bifurcatus</i> var. <i>humblotii</i>	<i>C. bifurcatus</i> Baill.
<i>C. boinensis</i> var. <i>parcelepidotus</i>	<i>C. greveanus</i> Baill.
<i>C. boinensis</i> var. <i>tomentosus</i>	<i>C. catatii</i> Baill.
<i>C. boivinianus</i> var. <i>brevifolius</i>	<i>C. nudatus</i> Baill.
<i>C. cassinoides</i> var. <i>alaotrensis</i>	<i>C. hovarum</i> Leandri
<i>C. catatii</i> var. <i>schizoplepis</i>	Incertae Sedis
<i>C. catatii</i> var. <i>setosus</i>	<i>C. catatii</i> Baill.
<i>C. catatii</i> var. <i>tricholepis</i>	<i>C. catatii</i> Baill.
<i>C. chapelieri</i> var. <i>longepetiolata</i>	<i>C. submetallicus</i> Baill.
<i>C. chrysodaphne</i> var. <i>meridionalis</i>	<i>C. cupreolepis</i> P.E.Berry, B.W.vanEe, & Kainul.
<i>C. crocodilorum</i> var. <i>meridionalis</i>	<i>C. crocodilorum</i> Leandri
<i>C. crocodilorum</i> var. <i>platyaster</i>	<i>C. stanneus</i> Baill.
<i>C. daphniphyllodes</i> var. <i>hirsutus</i>	<i>C. nitidulus</i> Baker
<i>C. daphniphyllodes</i> var. <i>stellatipilus</i>	Incertae Sedis
<i>C. daphniphyllodes</i> var. <i>triplinervius</i>	Incertae Sedis
<i>C. daphniphyllum</i> var. <i>hirsutus</i>	<i>C. fianarantsoae</i> Leandri
<i>C. decaryi</i> var. <i>subglaber</i>	<i>C. muricatus</i> Vahl

<i>C. elaeagni</i> var. <i>antsirananae</i>	<i>C. elaeagni</i> Baill.
<i>C. elaeagni</i> var. <i>argyrocarpos</i>	Incertae Sedis
<i>C. elaeagni</i> var. <i>brevipedicellatus</i>	Incertae Sedis
<i>C. elaeagni</i> var. <i>chrysocarpos</i>	<i>C. catatii</i> Baill.
<i>C. fianarantsoae</i> var. <i>ambremontanus</i>	<i>C. minimimarginiglandulosus</i> Radcl.-Sm.
<i>C. fianarantsoae</i> var. <i>coursii</i>	<i>C. fianarantsoae</i> Leandri
<i>C. fianarantsoae</i> var. <i>masoalae</i>	<i>C. glomeratus</i> Aug.DC.
<i>C. fianarantsoae</i> var. <i>microphyllus</i>	<i>C. fianarantsoae</i> Leandri
<i>C. fianarantsoae</i> var. <i>obovalifolius</i>	<i>C. submetallicus</i> Baill.
<i>C. fianarantsoae</i> var. <i>petiolaris</i>	Incertae Sedis
<i>C. fianarantsoae</i> var. <i>ranomafanae</i>	<i>C. fianarantsoae</i> Leandri
<i>C. fianarantsoae</i> var. <i>tandrokensis</i>	<i>C. fianarantsoae</i> Leandri
<i>C. geayi</i> var. <i>paucisquamatus</i>	<i>C. geayi</i> Leandri
<i>C. geayi</i> var. <i>pubescens</i>	<i>C. geayi</i> Leandri
<i>C. goudotii</i> var. <i>tsaratananae</i>	<i>C. goudotii</i> Baill.
<i>C. greveanus</i> var. <i>ambositrensis</i>	<i>C. hovarum</i> Leandri
<i>C. greveanus</i> var. <i>micraster</i>	<i>C. catatii</i> Baill.
<i>C. hovarum</i> var. <i>hirsutifructus</i>	Incertae Sedis
<i>C. hovarum</i> var. <i>lepidotus</i>	<i>C. hovarum</i> Leandri
<i>C. hovarum</i> var. <i>subglaber</i>	<i>C. hovarum</i> Leandri
<i>C. incisus</i> var. <i>minor</i>	<i>C. incisus</i> Baill.
<i>C. isomonensis</i> var. <i>microcarpus</i>	<i>C. trichotomus</i> Geisel.
<i>C. ivohibensis</i> var. <i>aesculops</i>	<i>C. minimimarginiglandulosus</i> Radcl.-Sm.
<i>C. ivohibensis</i> var. <i>alaotrensis</i>	<i>C. humbertii</i> Leandri
<i>C. ivohibensis</i> var. <i>ankaranaënsis</i>	<i>C. minimimarginiglandulosus</i> Radcl.-Sm.
<i>C. ivohibensis</i> var. <i>furfuraceus</i>	<i>C. heteranthus</i> Aug.DC
<i>C. ivohibensis</i> var. <i>integrifolius</i>	Incertae Sedis
<i>C. ivohibensis</i> var. <i>lepidotus</i>	<i>C. hovarum</i> Leandri
<i>C. ivohibensis</i> var. <i>macrocalyx</i>	Incertae Sedis
<i>C. ivohibensis</i> var. <i>polygynus</i>	Incertae Sedis
<i>C. ivohibensis</i> var. <i>puncticulatus</i>	<i>C. bracteatus</i> Lam.
<i>C. ivohibensis</i> var. <i>verticillatus</i>	Incertae Sedis
<i>C. kimosorum</i> var. <i>pubescens</i>	<i>C. kimosorum</i> Leandri
<i>C. leandri</i> var. <i>pubescens</i>	<i>C. toliarensis</i> B.W.vanEe & Kainul.
<i>C. lichenisilvae</i> var. <i>oligostemon</i>	<i>C. lichenisilvae</i> Leandri
<i>C. macrobuxus</i> var. <i>dolichobotrys</i>	<i>C. macrobuxus</i> Baill.
<i>C. macrobuxus</i> var. <i>glandulifer</i>	<i>C. macrobuxus</i> Baill.
<i>C. macrobuxus</i> var. <i>polygynus</i>	<i>C. chapelieri</i> Baill.
<i>C. macrobuxus</i> var. <i>subfoliaceus</i>	<i>C. macrobuxus</i> Baill.
<i>C. macrobuxus</i> var. <i>substrigosus</i>	<i>C. macrobuxus</i> Baill.
<i>C. manampetsae</i> var. <i>angustifolius</i>	<i>C. manampetsae</i> Leandri
<i>C. manampetsae</i> var. <i>chaetogyne</i>	<i>C. manampetsae</i> Leandri

<i>C. manampetsae</i> var. <i>lepidotus</i>	Incertae Sedis
<i>C. mavoravina</i> var. <i>concinus</i>	<i>C. boiteaui</i> Leandri
<i>C. mavoravina</i> var. <i>gracilis</i>	<i>C. mavoravina</i> Leandri
<i>C. mavoravina</i> var. <i>gymnolepis</i>	<i>C. mavoravina</i> Leandri
<i>C. mavoravina</i> var. <i>imanombensis</i>	<i>C. mavoravina</i> Leandri
<i>C. mavoravina</i> var. <i>rotundifolius</i>	<i>C. mavoravina</i> Leandri
<i>C. mavoravina</i> var. <i>thysanolepis</i>	<i>C. crossolepis</i> P.E.Berry & Kainul.
<i>C. menabeensis</i> var. <i>furfuraceus</i>	<i>C. nudatus</i> Baill.
<i>C. menarandrae</i> var. <i>pubescens</i>	<i>C. menarandrae</i> Leandri
<i>C. meridionalis</i> var. <i>latifolius</i>	Incertae Sedis
<i>C. meridionalis</i> var. <i>pseudolepidotus</i>	<i>C. meridionalis</i> Leandri
<i>C. meridionalis</i> var. <i>stipularis</i>	Incertae Sedis
<i>C. miarensis</i> var. <i>monadenius</i>	<i>C. miarensis</i> Leandri
<i>C. mongue</i> var. <i>borealis</i>	<i>C. mongue</i> Baill.
<i>C. nitidulus</i> var. <i>acuminatus</i>	<i>C. submetallicus</i> Baill.
<i>C. nitidulus</i> var. <i>angustiglandis</i>	<i>C. nitidulus</i> Baker
<i>C. nitidulus</i> var. <i>bekolosiensis</i>	<i>C. nitidulus</i> Baker
<i>C. nitidulus</i> var. <i>cinereus</i>	<i>C. submetallicus</i> Baill.
<i>C. nitidulus</i> var. <i>eglandulosus</i>	Incertae Sedis
<i>C. nitidulus</i> var. <i>fuscicrampus</i>	<i>C. nitidulus</i> Baker
<i>C. nitidulus</i> var. <i>hypopoliotes</i>	<i>C. submetallicus</i> Baill.
<i>C. nitidulus</i> var. <i>macrophyllus</i>	<i>C. submetallicus</i> Baill.
<i>C. nitidulus</i> var. <i>microphyllus</i>	<i>C. macrobuxus</i> Baill.
<i>C. nitidulus</i> var. <i>pubescens</i>	<i>C. macrobuxus</i> Baill.
<i>C. oreades</i> var. <i>borealis</i>	<i>C. mongue</i> Baill.
<i>C. oreades</i> var. <i>craspedadenius</i>	<i>C. mongue</i> Baill.
<i>C. oreades</i> var. <i>periphoradenius</i>	<i>C. mongue</i> Baill.
<i>C. peltieri</i> var. <i>hazofotsiensis</i>	<i>C. miarensis</i> Leandri
<i>C. regeneratrix</i> var. <i>mayottensis</i>	<i>C. mayottae</i> P.E.Berry & Kainul.
<i>C. regeneratrix</i> var. <i>ranomafanae</i>	<i>C. myriaster</i> Baker
<i>C. rubricapitirupis</i> var. <i>macrophyllus</i>	Incertae Sedis
<i>C. stanneus</i> var. <i>hirsutus</i>	<i>C. stanneus</i> Baill.
<i>C. subaemulans</i> var. <i>tsingyensis</i>	<i>C. bemarkanus</i> Leandri
<i>C. submetallicus</i> var. <i>tomentosus</i>	<i>C. submetallicus</i> Baill.
<i>C. thuarsianus</i> var. <i>angustifolius</i>	Incertae Sedis
<i>C. thuarsianus</i> var. <i>longifolius</i>	Incertae Sedis
<i>C. thuarsianus</i> var. <i>macrocalyx</i>	<i>C. minimimarginiglandulosus</i> Radcl.-Sm.
<i>C. thuarsianus</i> var. <i>robustior</i>	<i>C. thuarsianus</i> Baill.
<i>C. tranomarensis</i> var. <i>rosmarinifolius</i>	<i>C. toliarensis</i> B.W.vanEe & Kainul.
<i>C. tsiampiensis</i> var. <i>ankaranensis</i>	<i>C. tsiampiensis</i> Leandri
<i>C. tsiampiensis</i> var. <i>macrophyllus</i>	<i>C. tsiampiensis</i> Leandri
<i>C. tsiampiensis</i> var. <i>microphyllus</i>	<i>C. tsiampiensis</i> Leandri

Nomenclator of Malagasy, Comoros, and Mascarene *Croton*

1. *Croton adabolavensis* Leandri, *Ann. Mus. Colon. Marseille, sér. 5*, 7(1): 34. 1939

Croton adabolavensis var. *hippophaeoides* Radcl.-Sm., Gen. *Croton* Madag. Comoro 92. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Cap Ste. Marie Reserve, SW of Tsiombe, 25°35'S, 45°09'E, 27 Dec 1988, *P.B. Phillipson* 3008 (holotype: K!; isotypes: MO!, P [P00433074]!).

Croton adabolavensis var. *microlepidotus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 92. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Réserve Naturelle Intégrale d'Andohahela, along border road, 25°00'S, 46°40'E, 19 Oct 1990, *A. Randrianasolo, D. Faber-Langendoen, N. Dumetz & R. Rabevohitra* 174 (holotype: K!; isotypes: MO!, P [P00433039]!).

Croton adabolavensis var. *ovalifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 92. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beza Mahafaly Reserve, near Betioky, ridge E of Sakamena River, valley of Analafahy River, 23°58'S, 44°39'E, 28 Nov 1987, *P.B. Phillipson* 2621 (holotype: K!; isotype: MO!, P [P00133395]!).

Croton adabolavensis var. *stellatipilus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 93. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: 27 km from Tulear (Toliara), 23°21'S, 43°51'E, 30 Dec 1987, *P.B. Phillipson* 2759 (holotype: K!; isotype: MO!, P [P00133397]!).

Type. MADAGASCAR. Prov. Toliara: Anosy Region, vallée moyenne du Mandrare, près d'Anadabolava, forêt sèche, 200–250 m, Dec 1933, *H. Humbert* 12498 (lectotype, designated here: P [P00248927]!; isolectotype: P [P00312384]!).

Habit and distribution. Shrubs; southeastern Madagascar (Toliara).

Notes. Leandri (1939) named the species after the type locality, Anadabolava, but he may have inadvertently or even purposely omitted the first two letters of the name. The different varieties described by Radcliffe-Smith (2016) all appear to be just minor variants within the normal variability of this species that do not merit taxonomic status, but more intensive work is needed on this and the other small-leaved species from Toliara Province.

2. *Croton adenophorus* Baill., *Adansonia* 1: 153. 1861, as '*adenophorum*'

Croton payerianus Baill., *Adansonia* 1: 154. 1861, as '*payerianum*'.

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Nossibé, 1849, *L.H. Boivin* 2187 (lectotype, designated here: P [P00389508]!; isolectotypes: G-DC [G00311984]!, G [G00446358]!, G [G00446359]!, P [P00389509]!, P [P00404480]!, P [P00404481]!, P [P00123684]!).

Croton tulasnei Baill., *Adansonia* 1: 156. 1861.

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Bouzi [Ilot M'Bouzi], 1850, *L.H. Boivin s.n.* (lectotype, designated by Kainulainen et al. 2017b, pg. 382: P [P00133305]!; isolectotypes: P [P00133306]!, [P00466148]).

Croton subaemulans Baill., *Bull. Mens. Soc. Linn. Paris* 2: 850. 1890.

Type. MADAGASCAR. sin. loc., *R. Baron* 5795 (holotype: K [K000422590]!; isotype: P [P00133593]!).

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

Type. Based on *Croton adenophorus* Baill.

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

Type. Based on *Croton payerianus* Baill.

Oxydectes tulasnei (Baill.) Kuntze, *Revis. Gen. Pl.* 2: 613. 1891.

Type. Based on *Croton tulasnei* Baill.

Croton tenuicuspis Baill., *Bull. Mens. Soc. Linn. Paris* 2: 927. 1891.

Type. MADAGASCAR. sin. loc., *R. Baron* 5846 (holotype: P [P00133364]!; isotype: K [K000422590]!).

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Nossi-bé [Nosy Be], 1837, *J.M.C. Richard* 214 (lectotype, designated by Kainulainen et al. 2017b, pg. 382: P [P00123689]!; isolectotype: P [P00123690]!). MADAGASCAR. Prov. Antsiranana: Diana Region, Nossi-bé [Nosy Be], *J.M.C. Richard* 574 (syntype: P [P00123691]!); *ibid.* loc., 1849, *L.H. Boivin* 2187 (syntype: P [P00301515]!).

Habit and distribution. Shrubs or small trees; northern and northwestern Madagascar (Antsiranana, Mahajanga) and Mayotte in the Comoros Archipelago.

Notes. *Croton adenophorus* was substantially recircumscribed from the concept of Leandri (1939) and Radcliffe-Smith (2016) by Kainulainen et al. (2017b). In both earlier publications, *C. loucoubensis* was treated as a synonym of *C. adenophorus*, and *C. subaemulans* was recognized as a distinct species. This earlier synonymy was due to a fundamental misunderstanding of *C. adenophorus*. See Kainulainen et al. (2017b) for further details and the distinguishing features of *C. adenophorus* and *C. loucoubensis*.

The sheet P00466148 is listed in Sonnerat under *Croton tulasnei*, but without an image. We never saw this specimen at P either before or after the herbarium renovation in 2015, and the whole folder of *C. tulasnei* was missing during visits to P in 2016 and 2017.

Radcliffe-Smith (2016) mentioned *Boivin* 2187 at P as the lectotype for *Croton adenophorus* but failed to state “designated here” or an equivalent statement, so his designation was not validly published.

3. *Croton alchorneifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 135. 2016

Type. MADAGASCAR. Prov. Antsiranana: SAVA Region, summit of Marojejy on path from Mandena, 14°26'56"S, 49°43'58"E, 30 Sep 1994, *B. Lewis, F. Rasoavimbahoaka & J. Rastefanonirina* 1206 (holotype: K!; isotypes: MO!, P [P00131484]!).

Habit and distribution. Small trees; restricted to the Marojejy Massif in northern Madagascar (Antsiranana).

Notes. This is a distinctive high-elevation species with well-developed petals in the pistillate flowers and large capsules, belonging to the Mongue Group of Leandri (1939).

4. *Croton aleuritoides* P.E.Berry, *Candollea* 71: 182. 2016 [17 Jun 2016]

Croton bemarkanus var. *pseudolepidotus* Radcl.-Sm., Gen. Croton Madag. Comoro 209. 2016 [23 Dec 2016], as '*bemarkana*', **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Montagne des Français, à l'Est de Diego Suarez, 26 Nov 1958, *Service Forestier 20088* (lectotype, designated here: P [P00312410]!; isolectotypes: B, G [G00341674]!, K [K001040349]!, MO!, P [P00206489]!, S!, TEF!, WAG).

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Montagne des Français, à l'Est de Diégo-Suarez, 26 Nov 1958, *Service Forestier 20088* (holotype: P [P00312410]!; isotypes: B, G [G00341674]!, K [K001040349]!, MO!, P [P00206489]!, S!, TEF!, WAG).

Habit and distribution. Trees; known only from Montagne des Français in northernmost Madagascar (Antsiranana).

5. *Croton ambanivoulensis* Baill., *Adansonia* 1: 165. 1861, as '*ambanivoulense*'

Oxydectes ambanivoulensis (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton ambanivoulensis* Baill.

Type. MADAGASCAR. Prov. Toamasina: [region of the] Ambanivoules, [west of] Tamatave, dans les forêts, Dec. 1836, *J.P. Goudot s.n.* (lectotype, designated here: G [G00446336]!; isolectotype: P [P00301514]!).

Habit and distribution. Shrubs; eastern lowland Madagascar (Toamasina).

Notes. There are two sheets of *Goudot s.n.* at G within the same jacket, meaning they are considered as being part of the same collection (see Gautier et al. 2016). However, they do not fit the criterion of bearing a single label in common. Each sheet has its own label, and they are not identical. One, the lectotype, has a precise collecting date and the locality name of Ambanivoules, whereas the other sheet (G00446337) does not, and the written field description of the plants differs between the two. Also, the lectotype has mainly pistillate flowers open whereas the other syntype has only staminate flowers open. This leads us to conclude that the two sheets are actually different gatherings, even though both were annotated in Baillon's hand as "*Croton ambanivoulense*." We have designated the sheet that is most consistent with the protologue (G00446336) as the lectotype.

Ambanivoules were an ethnic group of eastern Madagascar located approximately 80–100 km west of Tamatave, their name derived from the Malagasy "Antanbanivolo," or "people living at the base of the mountains covered with bamboos" (Schatz 2013).

6. *Croton ambovombensis* Radcl.-Sm. & Govaerts, Kew Bull. 52: 186. 1997

Croton divaricatus Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 59. 1939, as '*divaricata*', nom. illeg. non *Croton divaricatus* Sw., 1788.

Type. MADAGASCAR. Prov. Toliara: Androy Region, Ambovombe, 19 Dec 1924, *R. Decary 3174* (lectotype, designated by Radcliffe-Smith 2016, pg. 191: P [P00133060]!; isoelectotype: TAN [TAN000529]!). MADAGASCAR. Prov. Toliara: Androy Region, environs d'Ambovombe (extrême sud), 9 Sep 1928, *H. Humbert & C.F. Swingle 5631* (syntypes: G [G00446382]!, P [P00133062]!; MADAGASCAR. Prov. Toliara: Andrahomana, 21 Jun 1926, *R. Decary 4017* (syntype: P [P00133061]!).

Habit and distribution. Shrubs; southern lowland Madagascar (Toliara).

7. *Croton androiensis* (Leandri) Leandri, Adansonia, n.s., 9: 507. 1970

Croton geayi var. *androiensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 35. 1939.

Type. MADAGASCAR. Prov. Toliara: Androy/Anosy Regions, Bevilany, limite entre l'Anosy et l'Androy, 14 Nov 1932, *R. Decary 10940* (lectotype, designated here): P [P00123697]!; isoelectotypes: G, K [K001044841]!, TAN [TAN000533]!. MADAGASCAR. Prov. Toliara: Androy Region, Ambovombe, 6 Jan 1931, *R. Decary 8361* (syntypes: P [P00123696]!), TAN [TAN000532]!). MADAGASCAR. Prov. Toliara: Kotoala, sables et dunes littorales, 21 Jan 1931, *R. Decary 8408* (syntypes: K [K001040395]!, MO [sheet #04861163]!, P [P00404477]!, P [P00123698]!).

Type. Based on *Croton geayi* var. *androiensis* Leandri

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. Radcliffe-Smith (2016) mentioned *Decary 10940* as the lectotype for *Croton geayi* var. *androiensis*, but this is not validly published as he failed to state "designated here" or an equivalent phrase.

8. *Croton anisatus* Baill., Adansonia 1: 159. 1861, as '*anisatum*'

Oxydectes anisata (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton anisatus* Baill.

Type. [Cult. ex Madagascar]: Cultivated in the garden of M. Hubert, Saint Benoît, Réunion, s.d., *M. Lepervanche s.n.* (holotype: P [P00301513]!). MADAGASCAR. Prov. Toamasina: Atsinanana Region, Vohibola, N to NNW of village of Andranokoditra, N of Lac Ampitabe, 18°33'34"S, 49°15'01"E, 5 m, 12 Feb 2003, *P. Lowry, R. Rabevohitra, J. Rabenantoandro, R. Razakamalala & S.W.J. Lowry 6072* (epitype, designated here): P [P00548219]!; additional duplicates: DAV!, K!, MICH [MICH1210799]!, MO [sheet # 5902002]!).

Habit and distribution. Shrubs; eastern coast of Madagascar (Toamasina).

Notes. Since the holotype of *Croton anisatus* has only young inflorescences in bud and is known only from cultivation on a quite different island, we designate an epitype with open flowers. This littoral species can be characterized by its very congested inflorescences and the pseudoverticillate, anisophyllous, and sparsely lepidote-pubescent leaves with an entire margin. The plant is apparently quite aromatic as indicated by the descriptions of both the holotype and epitype, as well as by its specific epithet.

9. *Croton ankarensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 75. 1939

Type. MADAGASCAR. Prov. Mahajanga: Causse d'Ankara, bois rocailleux et secs sur calcaire jurassique, Dec 1900, *H. Perrier de la Bâthie* 9830 (lectotype, designated here: P [P00123702]!; isoelectotype: P [P00123703]!). MADAGASCAR. Prov. Mahajanga: Tsingy du Bemaraha (9° Réserve), 4 Oct 1932, *J. Leandri* 103bis (syntypes: K [K001040394]!, P [P00123700]!, P [P00123701]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

Notes. The *Leandri* 103bis syntype corresponds to *Croton tsiampiensis*.

10. *Croton ankeranae* Kainul., Candollea 71: 329. 2016

Type. MADAGASCAR. Prov. Toamasina: Atsinanana Region, District Brickaville, Commune Maroseranana, Fokontany Ambodilendemy, Andrangato River, 18°26'37"S, 48°46'31"E, 446 m, 13 Mar 2011, *P. Antilahimena* 7554 (holotype: MICH [MICH1513200]!; isotypes: MO!, P!, TAN!).

Habit and distribution. Shrubs to small trees; eastern Madagascar (Toamasina).

11. *Croton anosiravensis* Leandri, Adansonia, n.s., 12: 69. 1972

Croton anosiravensis var. *pilosus* Radcl.-Sm., Gen. Croton Madag. Comoro 207. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Analamera, 50–400 m, Jan 1938, *H. Humbert* 19141 (lectotype, designated here: P [P00133307]!; isoelectotype: P [P00133308]!).

Type. MADAGASCAR. Prov. Antsiranana: Base des escarpements de l'Anosiravo, poteau kilométrique 6 de la route de Diego Suarez à Orangéa, 12 Dec 1963, *Service Forestier* 22930-SF (holotype: P [P00404432]!; isotypes: K [K001040369]!, TEF [TEF000193]!).

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

Notes. In its stellate-pubescent and cordate leaves, *Croton anosiravensis* is superficially similar to some of the species in the Adenophorus Group. However, it does not have opposite leaves or laminar glands, and is probably not closely related. It appears to be a rare species, because besides the type from the northern slopes of Montagne des Français, it is otherwise only known from Analamera (*Humbert 19141* [P]) and Befarafara in Daraina (*Rakotonandrasana et al. 1048* [CNAR, MICH, MO, P, TAN]). Radcliffe-Smith (2016) stated “holo: P” for var. *pilosus*, but there are two sheets of the type collection there, so we have selected the more complete of the sheets at P as the lectotype.

12. *Croton antanosiensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 45. 1939

Type. MADAGASCAR. Prov. Toliara: environs de Fort-Dauphin, près de Bévilany, 200–300 m, 14 Sep 1928, *H. Humbert & C.F. Swingle 5695* (lectotype, designated here: P [P00123716]!; isoelectotype: P [P00123717]!). MADAGASCAR. Prov. Toliara: Massif de Beampingaratra (Sud-Est), du col de Bevava au sommet de Bekoho, forêt sur latérite de gneiss, 1100–1500 m, 6–7 Nov 1928, *H. Humbert 6416* (syntypes: P [P00123718]!, P [P00154301]!, TAN [TAN000521]!). MADAGASCAR. Prov. Toliara: Fort Dauphin, *J. Cloisel 60* (syntype: P [P00123710]!). MADAGASCAR. Prov. Toliara: Behara, 9 Jul 1926, *R. Decary 4321* (syntypes: P [P00123711]!, S [S07-14102]). MADAGASCAR. Prov. Toliara: Ranofotsy, 29 Jul 1932, *R. Decary 10175* (syntypes: G [G00446368]!, P [P00123712]!).

Habit and distribution. Shrubs to small trees; southern Madagascar (Toliara).

Notes. We believe that the lectotype chosen here best conforms to the protologue among the syntypes cited by Leandri (1939). Although most of the other syntypes correspond to the same species, one of them, *Humbert 6416*, appears to belong instead to *C. trichotomus*.

13. *Croton argyrodaphne* Baill., Adansonia 1: 146. 1861

Oxydectes argyrodaphne (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton argyrodaphne* Baill.

Croton argyrodaphne var. *occidentalis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 44. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: région du Cap Saint-André, dunes, 8 Jun 1930, *R. Decary 7893* (lectotype, designated here: P [P00127457]!). MADAGASCAR. Prov. Toliara: bassin de la Tsiribihina, Jul 1911, *H. Perrier de la Bâthie 9656* (syntypes: P [P00127460]!, P [P00127461]!, P [P00127462]!). MADAGASCAR. Prov. Toliara: Morondava, received 26 Dec 1878, *H. Grévé 11* (syntype: P [P00127459]!).

Croton argyrodaphne var. *boinensis* Leandri, *Adansonia*, sér. 2, 12: 404. 1972, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Ampalony, 9 Aug 1971, *L.P. Schmitt* 515 (holotype: P [P00389629]!).

Croton argyrodaphne var. *orientalis* Leandri, *Adansonia*, sér. 2, 12: 404. 1972, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Intendro, près de Fénérive, 9 Jul 1958, *Serville Forestier* 19160-SF (holotype: P [P00418607]!).

Croton vohemarensis Radcl.-Sm., *Gen. Croton Madag.* Comoro 78. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Mantamena, Bekaroaka Range, 7 km N of Daraina (Vohemar), 13°08'S, 49°42'E, 112–330 m, 26 Nov 1990, *D. Meyers* 206 (holotype: MO!).

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Nossibé, 1837, *J.M.C. Richard* 218 (lectotype, first step designated by Leandri 1972b, pg. 404, second step designated here): P [P00127450]!; isolectotype: K [K001040357]!. MADAGASCAR. Prov. Antsiranana: Diana Region, Nossibé, *L.M.A. Du Petit-Thouars* s.n. (syntype: P [P00123733]!), *ibid.* loc., 1837, *J.M.C. Richard* 571 (syntypes: P [P00127451]!, K [K000347495]!), *ibid.* loc., 15 Nov 1840, *A. Pervillé* 236 (syntypes: K [K000347493]!, P [P00127436]!, P [P00127437]!). MADAGASCAR. Prov. Antsiranana: Loucoubé, 1848, *L.H. Boivin* 2182 (syntypes: G-DC [G00311741]!, G [G00311741]!, K [K000347494]!, P [P00123729]!, P [P00123730]!, P [P00835716]!).

Habit and distribution. Trees to large shrubs; mainly in northern Madagascar, but extending as far south as northern Toliara Province on the west coast and northern Toamasina on the east coast (Antsiranana, Mahajanga, Toamasina, Toliara).

Notes. Leandri (1972b) designated *Richard* 218 as the type of *Croton argyrodaphne*. Given that he did not specify an herbarium in his selection of this collection, we complete the lectotypification here by designating P00127450 as a second-step lectotype. The type of *C. argyrodaphne* var. *orientalis* comes from an area in northern Toamasina that is well south of the range of most other *C. argyrodaphne* specimens. However, there is a second collection of the species from the same area, *SF-10816* (TEF), which confirms its occurrence near Fénérive.

The type of *Croton vohemarensis* consists of two small twigs with leaves that are unusually small and wide for *C. argyrodaphne*. However, the low stamen number (11) and the characteristic stylar column are very typical of *C. argyrodaphne* (see Fig. 1E–F), and it falls within the geographic and altitudinal range for the species. An additional paratype cited by Radcliffe-Smith (2016), *Meyers & Bolz* 170 (G, MO), comes from the type locality and is a tree 7 m tall, again with unusually wide and long-petiolate leaves for *C. argyrodaphne*, but it only has young floral buds.

What Leandri recognized as *Croton argyrodaphne* var. *occidentalis* is a rather distinctive element of this species, with a western, subcoastal distribution. The plants are small trees, and the leaves have yellowish pigmentation along the midvein on the adaxial leaf surfaces, but other than that they conform well to the general aspect of *C. argyrodaphne*.

14. *Croton aubrevilecta* Leandri, *Adansonia*, sér. 2, 10: 309. 1970

Type. MADAGASCAR. Prov. Toliara: Sud-Ouest, s.d., *M.G. Cours 4641* (holotype: P [P00312369]!; isotypes: K [K001044848], MO [sheet # 5737746]!), P [P00380443]!, P [P00380444]!).

Habit and distribution. Shrubs; southwestern Madagascar (Toliara).

Notes. Leandri (1970b) designated *Cours 4641* as the holotype of *C. aubrevilecta* but there are three sheets of this collection at P. One of them, P00312369, has a label in Leandri's handwriting saying "type," and the other two duplicates at P have labels stating "isotype." The isotypes at P have preprinted labels stating "Itinéraire de Didy à Brickaville (forêt orientale)," but P00380444 has a note added later stating "Localité très douteuse, voir récolte *Homolle 1944* (avec *M.G. Cours*)." The holotype has a penciled note stating "Probablement région de Tranoroa." In the protologue, Leandri (1970b) also alluded to the erroneous labels from Didy and states that the collection likely came from far southern Madagascar close to Lake Tsimanampetsotsa.

15. *Croton barorum* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 66. 1939

Type. MADAGASCAR. Prov. Toliara: Antanimora, 16 Jun 1926, *R. Decary 4346* (holotype: P [P00301486]!; isotype: K [K001044842]!).

Habit and distribution. Shrubs; southwestern Madagascar (Toliara).

16. *Croton basaltorum* (Leandri) P.E.Berry, *comb. et stat. nov.*

urn:lsid:ipni.org:names:77167302-1

Croton antanosiensis var. *basaltorum* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 46. 1939.

Type. MADAGASCAR. Prov. Mahajanga: Pl. [Plateau] d'Antanimena, entre la Mahavavy et le Betsiboka, Jun 1906, *H. Perrier de la Bâthie 9593* (lectotype, designated here: P [P00123726]!; isolectotype: P [P00123725]!).

Type. Based on *Croton antanosiensis* var. *basaltorum* Leandri

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

Notes. Geographically and morphologically, this species is sufficiently distinct from *C. antanosiensis* to merit recognition at the species level. Morphologically, it appears more similar to *C. cupreolepis*.

17. *Croton bastardii* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 64. 1939, as ‘*bastardi*’

Croton appertii Leandri, Adansonia, sér. 2, 15: 331. 1976, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beharana, près de Manja, 300 m, 17 Nov 1961, O. Appert 37 (holotype: P [P00312368]!; isotypes: K [K001044847]!, MO [sheet # 2287361]!, Z [Z-000015970]!, Z [Z-000015971]!).

Type. MADAGASCAR. Prov. Toliara: forêt de Besomaty, entre le Fiherena et l’Isahaina (Mangoky), 750–800 m, Dec 1933, H. Humbert 11236 (lectotype, designated here: P [P00404492]!; isolectotypes: K [K001044843]!, P [P00127500]!).

Habit and distribution. Shrubs; southwestern Madagascar (Mahajanga, Toliara).

18. *Croton bathianus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 80. 1939, as ‘*bathiana*’

Type. MADAGASCAR. Prov. Mahajanga: Haut Bemarivo, Oct 1907, H. Perrier de la Bâthie 9545 (lectotype, designated by Kainulainen et al. 2017b, p. 386: P [P00301483]!; isolectotype: P [P00127503]!). MADAGASCAR. Prov. Mahajanga: collines sèches de haut Bemarivo, Dec 1906, H. Perrier de la Bâthie 9633 (syntype: P [P00389630]!). MADAGASCAR. Prov. Mahajanga: Maromandia, presqu’île Radama, 13 Oct 1922, R. Decary 1133 (syntype: P [P00389631]!), ibid. loc., 11 Oct 1922, R. Decary 1174 (syntype: P [P00301482]!).

Habit and distribution. Shrubs; northwestern Madagascar (Antsiranana, Mahajanga).

19. *Croton bemarkanus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 69. 1939, as ‘*bemarkana*’

Croton subaemulans var. *tsingyensis* Radcl.-Sm., Gen. Croton Madag. Comoro 120. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Tsingy du Bemaraha (9e Réserve), reçu Feb–Apr 1933, J. Leandri 116 (holotype: K!; isotypes: P [P00133368]!, P00133369!)).

Type. MADAGASCAR. Prov. Mahajanga: cause d’Ankara, Oct 1900, H. Perrier de la Bâthie 1153 (lectotype, designated here: P [P00206491]!; isolectotypes: K [K001040396]!, P [P00389502]!). MADAGASCAR. Prov. Mahajanga: Bemara, partie Nord de l’Antsingy, entre Ambatomiloloha et Anjohinomby, 29 Nov 1932, J. Leandri 656 (syntypes: P [P00127512]!, P [P00389503]!).

Habit and distribution. Shrubs; western and northern Madagascar (Antsiranana, Mahajanga).

20. *Croton bemarivensis* Leandri, *Adansonia*, sér. 2, 13: 423. 1974

Type. MADAGASCAR. Prov. Antsiranana: entre Andrangana et la rivière Anjambazamba, route de Sambava à Antsirabe-Nord, 2-7 Oct 1966, *Service Forestier* 27197-SF (holotype: P [P00312371]!; isotypes: K [K001044846]!, MO [sheet #04861161]!, P [P00404483]!, TEF [TEF000192]!).

Habit and distribution. Shrubs; northeastern Madagascar (Antsiranana, Toamasina).

21. *Croton bergassae* Leandri, *Adansonia*, sér. 2, 13: 176. 1973

Type. MADAGASCAR. Prov. Toamasina: Menagisy, Brickaville, 11 Oct 1956, *Service de Eaux et Forêts de Madagascar* 12358-SF (lectotype, designated here: P [P00312375]!; isolectotypes: P [P00127519]!, TEF!).

Habit and distribution. Shrubs or small trees; eastern lowland Madagascar (Antsiranana, Toamasina).

Notes. Although the sheet designated here as lectotype has a sticker stating "TYPE" and the other sheet at P has one stating "ISOTYPE," it is not clear who applied those labels and if it was done after Leandri's publication. In any case, there is no annotation in Leandri's hand on either sheet to indicate which of the two he intended to be the holotype.

22. *Croton bernieri* Baill., *Adansonia* 1: 152. 1861

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

Type. Based on *Croton bernieri* Baill.

Croton bernieri var. *namorokensis* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 54. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Tsingy de Namoroka (8^e Réserve), 1933, *Service Forestier* 11 (holotype: P [P00127543]!).

Type. MADAGASCAR. Prov. Antsiranana: Diégo-Suarez, 1835, *A.C.J. Bernier* 306 (lectotype, designated here: P [P00127520]!; isolectotypes: G [G00434420]!, P [P00127521]!, P [P00301481]!). MADAGASCAR. Prov. Antsiranana: Baie de Diégo-Suarez, Dec 1848, *L.H. Boivin* 2657 (syntypes: G [G00311744]!, G-DC [G00311744]!, P [P00127522]!, P [P00127523]!, P [P00127524]!, P [P00301480]!).

Habit and distribution. Shrubs to small trees; northern and northwestern Madagascar (Antsiranana, Mahajanga).

23. *Croton betiokensis* Leandri, *Adansonia*, sér. 2, 10: 183. 1970

Type. MADAGASCAR. Prov. Toliara: Plateau Mahafaly à l'ouest de Betioky, 100–300 m, 17–20 Mar 1955, *H. Humbert & R. Capuron* 29489 (holotype: P [P00312386]!; isotypes: P [P00127545], P [P00127546]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

24. *Croton bifurcatus* Baill., *Adansonia* 1: 164. 1861, as '*bifurcatum*'

Croton bifurcatus var. *genuinus* Müll.Arg. in A.P.de Candolle, Prodr. 16(2): 584. 1866, nom. inval.

Oxydectes bifurcata (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton bifurcatus* Baill.

Croton bifurcatus var. *humblotii* Leandri ex Radcl.-Sm., Gen. Croton Madag. Comoro 25. 2016, **syn. nov.**

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: forêt de Mazé, M. Bini [Majimbini], 24 May 1884, *L. Humblot* 1162 (holotype: K; isotype: P [P00196067]!).

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Cascade du Msapéré, 1849, *L.H. Boivin* 3380 (holotype: P [P00196066]!; isotypes: G-DC [G00311982]!, G [G00446373]!, P [P00196065]!, P [P00466147]!).

Habit and distribution. Shrubs; known only from the French island of Mayotte in the Comoro Islands.

Notes. The type of *C. bifurcatus* var. *humblotii* differs in only minor ways from typical *C. bifurcatus*.

25. *Croton bocquillonii* Baill., *Adansonia* 1: 161. 1861, as '*bocquillonii*'

Oxydectes bocquillonii (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton bocquillonii* Baill.

Croton brevispicatus var. *bocquillonii* (Baill.) Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 27. 1939.

Type. Based on *Croton bocquillonii* Baill.

Type. MADAGASCAR. Prov. Mahajanga: Ambongo, 16 Feb 1841, *A. Pervillé* 648 (lectotype, designated here: P [P00127552]!; isolectotypes: P [P00127553]!, P [P00127554]!, P [P00131420]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

Notes. The sheet chosen here as lectotype bears two labels, one on the left that lists *Pervillé* 648 as the collector, and one on the right in Baillon's hand that seemingly attributes the collection to Boivin, stating "ex Ambongo, cum cl. Pervillé et Bernier

comm. (1846).” Baillon lists this in his protologue as a separate collection, but it looks identical to the other syntypes, so we believe it is actually part of the same collection by Pervillé.

The types lack pistillate flowers, but they are distinctive from *C. brevispicatus* in bearing a pair of sessile acropetiolar glands and in having relatively long petioles for the size of the leaf, and blades with a rounded-cuneate base and an acuminate apex.

26. *Croton boinensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 29. 1939

Type. MADAGASCAR. Prov. Mahajanga: Bongolava, Boïna, Nov 1906, *H. Perrier de la Bâthie* 9567 (lectotype, designated here: P [P00127563]!). MADAGASCAR. Prov. Mahajanga: Ankarafantsika, 7^e reserve, chemin de Ste. Marie, Ankorika, 150-200 m, *Service Forestier Madagascar* 154 (syntypes: K [K001040380]!, P [P00127566]!). MADAGASCAR. Prov. Mahajanga: environs de Madirovalo, Boïny, Nov 1902, *H. Perrier de la Bâthie* 9803 (syntypes: P [P00127564]!, P [P00127565]!). MADAGASCAR. sin. loc., *Service Forestier Madagascar* 64 (syntype: P [P00127567]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

27. *Croton boiteau* Leandri, Adansonia, sér. 2, 10: 313. 1970

Croton mavoravina var. *concinus* Radcl.-Sm., Gen. Croton Madag. Comoro 31. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: environs d’Ampanrandava, entre Bekily et Tsivory, 1000 m, Nov 1942, *Herbier du Jardin Botanique de Tananarive* 5730 (holotype: P [P00154405]!).

Type. MADAGASCAR. Prov. Toliara: environs de Bekily, 12 Oct 1966, *P. Boiteau* 384 (lectotype, designated here: P [P00312385]!; isolectotypes: P [P00131001]!, P [P00131002]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

28. *Croton boivinianus* (Baill.) Baill., Adansonia 1: 163. 1861, as ‘*boivinanum*’

Furcaria boiviniana Baill., Étude Euphorb.: 356. 1858.

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Ile Nossibé, 1841, *A. Pervillé* 267 (lectotype, designated here: P [P00312458]!; isolectotypes: G [G00446376]!, P [P00131010]!). MADAGASCAR. Prov. Antsiranana: Diana Region, Nossibé, 1847-1852, *L.H. Boivin* 2183 (syntype: P [P00312459]!).

Oxydectes boiviniana (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Furcaria boiviniana* Baill.

Type. Based on *Furcaria boiviniana* Baill.

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

Notes. Baillon (1858) did not cite any specific specimens in the description of *Furcaria boiviniana*, just “*F. boiviniana* (herb. Mus.)” Baillon (1861) cited *Boivin* 2183 and *Pervillé* 267 when he transferred the taxon to *Croton*. Both specimens are annotated in Baillon's hand as “*Croton (Furcaria) boivinianum* H. Bn., Et. Gen. Euph., 356,” so we therefore consider them to be original material for the taxon.

29. *Croton bojerianus* Baill., *Adansonia* 1: 151. 1861, as ‘*bojerianum*’

Croton bakerianus Baill., Bull. Mens. Soc. Linn. Paris 2: 849. 1890, as ‘*bakeriana*’.

Type. MADAGASCAR. sin. loc., s.d., *R. Baron* 2091 (holotype: K [K001040351]!; isotype: P [P0013152]!).

Oxydectes bojeriana (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton bojerianus* Baill.

Type. MADAGASCAR. sin. loc., s.d., *W. Bojer s.n.* (holotype: P [P00131353]!; isotypes: K [K000347489]!, M [M0110365]!).

Habit and distribution. Shrubs; central highland Madagascar (Antananarivo, Fianarantsoa, possibly Mahajanga).

30. *Croton bonplandianus* Baill., *Adansonia* 4: 339. 1864, as ‘*bonplandianum*’

Type. ARGENTINA. Prov. Corrientes: 1833, *A. Bonpland s.n.* (lectotype, designated here: P [P00623061]!; isolectotype: P [P00623060]!). PARAGUAY: Apr–May 1845, *H.A. Weddell* 3207 (syntypes: P [P00623063]!, P [P00623062]!).

Habit and distribution. Herbs to subshrubs; native to southern South America, but naturalized in the Mascarene islands of Mauritius, Réunion, and Rodrigues (Croizat 1944, Coode 1982), as well as on Mayotte (Grande Terre – Mamoudzou, Kawéni, 9 Sep 2005, *Barthelat & Changama* 1504, K).

Notes. *Croton bonplandianus* is currently the only non-native, naturalized species of *Croton* in the Western Indian Ocean Region. Oddly, it is known from Mayotte and the Mascarenes, but it has not yet been observed or collected in Madagascar.

31. *Croton bracteatus* Lam., *Encycl.* 2: 208. 1786, as ‘*bracteatum*’

Andrichnia bracteata (Lam.) Baill., Étude. Euphorb. 362. 1858.

Type. Based on *Croton bracteatus* Lam.

Oxydectes bracteata (Lam.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton bracteatus* Lam.

Croton ivohibensis var. *puncticulatus* Radcl.-Sm., Gen. Croton Madag. Comoro 150. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Farafangana, Réserve spéciale de Manombo, 23°03'42"S, 47°44'26"E, 30 m, 25 Aug 1995, *P. Rakotomalaza et al.* 452 (holotype: K!; isotype: MO!).

Type. MADAGASCAR. sin. loc., s.d., *P. Commerson s.n.* (holotype: P-LA [P00382050]!; isotypes: G-DC [G00311196]!, G [G00446380]!, MPU [MPU014765]!, MPU [MPU014766]!, P [P00312457]!; probable isotype: P-JU (P00131377)!).

Habit and distribution. Shrubs or small trees; eastern coastal Madagascar (southern Fianarantsoa).

Notes. The collection locality of the type of *Croton bracteatus* is uncertain. Although most of Commerson's collections from Madagascar came from the Fort Dauphin area in Toliara Province, the type of *C. bracteatus* matches well specimens from the Manombo Reserve south of Farafangana in Fianarantsoa Province.

32. *Croton brevispicatus* Baill., *Adansonia* 1: 152. 1861, as '*brevispicatum*'

Croton brachybotryus Müll.Arg., Prodr. 15(2): 571. 1866, nom. superfl.

Type. Based on *Croton brevispicatus* Baill.

Oxydectes brevispicata (Baill.) Kuntze, Revis. Gen. Pl. 2: 609. 1891.

Type. Based on *Croton brevispicatus* Baill.

Type. MADAGASCAR. Prov. Antsiranana: [Diana Region] côte orientale, Baie de Rigny, Dec 1848, *L.H. Boivin* 2658 (holotype: P [P00131378]!; isotypes: G [G00018191]!, G-DC [G00311751]!), P [P00131406]!).

Habit and distribution. Shrubs; northern and western Madagascar (Antsiranana, Mahajanga).

Notes. Boivin's collection number 2658 was applied to several different collection events. Baillon (1861) was apparently aware of this given the greater detail in which he cited Boivin's specimens, such as "Boivin (1848), n. 2658, Madag., baie de Rigny (h. Mus.)" under *Croton brevispicatus* and "Boivin, n. 2658, cap d'Ambre" under *C. squamiger* Baill. Müller (1866) cited *C. brevispicatus* Baill., as well as the type of that species ("Boivin n. 2658! in hb. Mus. Paris"), in his treatment of *C. brachybotryus*, which we interpret as an illegitimate name for *C. brevispicatus*. The isotype at P was a gift from the Caen herbarium received by the Paris herbarium in 1974, and it was never annotated by Baillon, although it had been annotated by Müller.

33. *Croton campenonii* Baill., Bull. Mens. Soc. Linn. Paris 2: 847. 1890, as ‘*campenoni*’

Type. MADAGASCAR. “Madagascar central,” *P. Campenon s.n.* (lectotype, designated here: P [P00389501]!; islectotype: P [P00131482]!).

Habit and distribution. Trees; central and northern upland Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga).

34. *Croton cassinoides* Lam., Encycl. 2: 211. 1786

Oxydectes cassinoides (Lam.) Kuntze, Revis. Gen. Pl. 2: 610. 1891.

Type. Based on *Croton cassinoides* Lam.

Croton delphinianus Baill., Bull. Mens. Soc. Linn. Paris 2: 928. 1891.

Type. MADAGASCAR. Prov. Toliara: Fort Dauphin, s.d., *G.F. Scott-Elliot 1557* (lectotype, designated here: P [P00133052]!). MADAGASCAR. Prov. Toliara: Fort Dauphin, s.d., *G.F. Scott-Elliot s.n.* (possible original material: P [P00131487]!).

Type. MADAGASCAR. sin. loc., s.d., *P. Commerson s.n.* (lectotype, designated here: P [P00131494]!; islectotypes: G-DC [G00311976]!, MPU [MPU014767]!), P-JU [Catal. 16372]!).

Habit and distribution. Shrubs; southeastern coastal Madagascar (Toliara).

Notes. Unlike most other Malagasy *Croton* species described by Lamarck from Commerson specimens, there is no specimen of *C. cassinoides* found in the Lamarck Herbarium at P, so we designate the sheet in the general herbarium at P as lectotype. Most of Commerson's collections from Madagascar came from the Fort Dauphin area in Toliara Province, and all other specimens of *C. cassinoides* that we have determined are from near Fort Dauphin, so this is likely where the type came from. In the description of *C. delphinianus* (Baillon 1891a), there was no collection or locality cited (it was the last in the section of Baillon's text and appeared to be cut off). In the descriptions of other new species in the same publication, the Latin description was always followed by a paragraph containing specimen information. At P there is a sheet [P00133052] that has a label with a note in ink stating “*Croton cassinoides* Lamk. et type du *C. Delphinianus* H. Bn.” It also has a small envelope that reads “*Croton Delphinianus* Scott-Elliot. n. 1557 Fort-Dauphin.” Based on that information, we designate it as lectotype for *C. delphinianus*.

35. *Croton catatii* Baill., Bull. Mens. Soc. Linn. Paris 2: 851. 1890, as ‘*catati*’

Croton hilaris Baill., Bull. Mens. Soc. Linn. Paris 2: 927. 1891.

Type. MADAGASCAR. Prov. Toliara: Fort-Dauphin, *G.F. Scott-Elliot 2650* (holotype: P [P00131522]!; isotype: K [K001040342]!).

Croton ranohirae Leandri, *Adansonia*, sér. 2, 9: 502. 1970, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Plateaux et vallées de l'Isalo à l'Ouest de Ranohira, 900 m, 2 Nov-4 Dec 1946, *H. Humbert 19591* (lectotype, designated here: P [P00312378]!; isolectotypes: K [K000422598]!, K [K000422599]!, P [P00389515]!, P [P00389516]!).

Croton boinensis var. *tomentosus* Radcl.-Sm., *Gen. Croton Madag. Comoro* 78. 2016, **syn. nov.**

Type. MADAGASCAR. "NW Madagascar", sin. loc. cert., recd. Sep 1887, *R. Baron 5477* (holotype: K!).

Croton catatii var. *setosus* Radcl.-Sm., *Gen. Croton Madag. Comoro* 45. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Forêt de Sahafary, S/P de Diego Suarez, 2 Dec 1970, *M. Debray 1554* (holotype: P [P00154364]!).

Croton catatii var. *tricholepis* Radcl.-Sm., *Gen. Croton Madag. Comoro* 45. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: bassin de réception de la Mananara, affluent du Mandrare, entre l'Andohahela et l'Elakelaka, près de Mahamavo, Jan-Feb 1934, *H. Humbert 13876* (holotype: K!; isotypes: P [P00127556]!, P00127557!, P00127558]!).

Croton elaeagni var. *chrysocarpos* Radcl.-Sm., *Gen. Croton Madag. Comoro* 91. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Monte Isalo, in nemore Zombitsy, 800 m, 7 Nov 1967, *L. Bernardi 11281* (holotype: K!; isotypes: G!, P [P00154383]!).

Croton greveanus var. *micraster* Radcl.-Sm., *Gen. Croton Madag. Comoro* 41. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antananarivo: Ambatotsipihina, Tsinjoarivo, 21 Nov 1949, *Service Forestier 1041-SF* (holotype: P [P00133806]!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Didy, 14 Aug 1889, *L.D.M. Catat 1819* (holotype: P [P00131523]!).

Habit and distribution. Shrubs to normally trees; widespread in forested areas of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

Notes. In this circumscription, *Croton catatii* is a variable but distinctive species. It is usually a tree and typically occurs in montane habitats, but in the drier areas of Isalo and Zombitse area in Fianarantsoa and Toliara Provinces, it can be shrubby, and plants there have more verrucose fruits than elsewhere. Although plants of *C. catatii* are typically finely lepidote, plants such as what was described as *C. catatii* var. *setosus* from Sahafary in Antsiranana Province can be softly pubescent, with trichomes having long-protruding central rays.

36. *Croton chapelieri* Baill., *Adansonia* 1: 166. 1861

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

Type. Based on *Croton chapelieri* Baill.

Croton louvelii Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 40. 1939, as ‘*louveli*’.
Type. MADAGASCAR. Prov. Toamasina: forêt côtière, Tampina, Jan. 1924, *M. Louvel* 217 (holotype: P [P00312340]!).

Croton aymoniniorum Leandri, Adansonia, sér. 2, 13: 175. 1973, as ‘*aymoninorum*’.
Type. MADAGASCAR. Prov. Toliara: Forêt de Mandena, Fort Dauphin, 19 Oct 1970, *M. Keraudren-Aymonin & G. Aymonin* 24940 (holotype: P [P00312374]!).

Croton daphniphylloides Radcl.-Sm., Gen. Croton Madag. Comoro 164. 2016.
Type. MADAGASCAR. Prov. Toamasina: Ambila-Lemaitso, 7 Nov 1951, *Service Forestier* 4228 (holotype: P [P00133469]!).

Croton daphniphyllus Radcl.-Sm., Gen. Croton Madag. Comoro 161. 2016, as ‘*daphniphyllum*’.

Type. MADAGASCAR. Prov. Toliara: Fort Dauphin in Mandena, 2 km E of Botanic Garden, 24°58'S, 47°00'E, 9 Oct 1990, *D. Faber-Langendoen, N. Dumetz & A. Randrianasolo* 2226 (holotype: P [P00133462]!; isotype: MO).

Croton daphniphyllus var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro 163. 2016.
Type. MADAGASCAR. Prov. Toliara: Préfecture de Tôlañaro (Fort Dauphin), Canton de Mananbaro, 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 Apr 1989, *R. Gereau, R. Rabevohitra & N. Dumetz* 3374 (holotype: K!; isotypes: MO [sheet # 3683138], P [P00133120]!).

Croton domohineifolius Radcl.-Sm., Gen. Croton Madag. Comoro 157. 2016, **syn. nov.**
Type. MADAGASCAR. Prov. Fianarantsoa: Fanajazana-Mananjary, Jan 1955, *Service Forestier* 15451-SF (holotype: P [P00133471]!).

Croton macrobuxus var. *polygynus* Radcl.-Sm., Gen. Croton Madag. Comoro 177. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: near Fort Dauphin, s.d., *J. Cloisel* 178 (holotype: P [P00133612]!).

Croton rhododendroides Radcl.-Sm., Gen. Croton Madag. Comoro 163. 2016.
Type. MADAGASCAR. Prov. Toliara: Préfecture Tôlañaro (Fort Dauphin), forêt à 5 km de Ste. Luce, au nord de Maliafolaky, 24°47'S, 47°10'E, 21 Oct 1989, *N. Dumetz, G. McPherson & R. Rabevohitra* 775 (holotype: P [P00133460]!; isotype: MO!).

Type. MADAGASCAR. sin. loc., s.d., *L.A. Chapeliers* s.n. (holotype: P [P00389523]!). MADAGASCAR. Prov. Toliara: Sainte Luce, at entrance to preserve, 24°46'46"S, 47°10'17"E, 10 m, 17 Feb 2009, *B. van Ee, P.E. Berry, B.L. Dorsey & H. Razanatsoa* 925 (epitype, designated by Kainulainen et al. 2017a, pg. 37: MICH [MICH1514617]!; additional duplicates: G, K, MAPR, MO, NY, P, TAN).

Habit and distribution. Shrubs; southeastern and eastern coastal Madagascar (Antsiranana, Fianarantsoa, Toamasina, Toliara).

Notes. *Croton chapelieri* was accepted by Leandri (1939) but was restricted to the type specimen, due at least in part to the meager type specimen and the lack of any reported collection locality. Similarly, *C. aymoniniorum* has been recognized only from

the type collection. Extensive collections and our own field studies from coastal areas of southeastern Toliara Province (Mandena, Petriky, and Sainte Luce) show that both of these type specimens correspond to a locally common species found in sandy, littoral forests to the west and north of Fort Dauphin, in the Mahabo area of Fianarantosa Province, and then in Toamasina Province much farther north. Chapelier collected mainly in the Foulpointe and Tamatave area (Dorr 1997), and his specimen is similar to the type of *C. louvelii*, from a nearby area. Many herbarium specimens of this species were identified by the late Alan Radcliffe-Smith and subsequent botanists as *Croton daphniphyllus* Radcl.-Sm., or sometimes as *Croton rhododendroides* Radcl.-Sm. for a more pubescent form. See Kainulainen et al. (2017a) for more details about the circumscription of *C. chapelieri*. Newly added to the synonymy here are *C. domohineifolius* Radcl.-Sm. and *C. macrobuxus* var. *polygynus* Radcl.-Sm., both from littoral sites on the east coast where *C. chapelieri* is one of the few species to occur.

37. *Croton chauvetiae* Leandri, *Adansonia*, sér. 2, 10: 310. 1970

Type. MADAGASCAR. Prov. Toliara: P.K. 30, route de Tulear à Tana, 16 Feb 1962, *F. Chauvet* 273 (lectotype, designated here: P [P00312370]!; isolectotypes: G [G00074264]!, K [K001044839]!, MO [sheet #04861159]!, P [P00380439]!, P [P00380440]!, P [P00380441]!, TEF [TEF000188]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

38. *Croton chlaenacomes* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 50. 1939

Croton arenicola Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 57. 1939, nom. illeg. non *Croton arenicola* Small 1905, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Ambovombe, 10 Aug 1924, *R. Decary* 2949 (lectotype, designated by Radcliffe-Smith 2016, pg. 187: K [K001040383]!; isolectotypes: BR [BR0000009424357]!, GB [GB-0047690], G [G00446374]!, P [P00131546]!, P [P04787784]!, S [S07-14591]!, TAN [TAN000523]!). MADAGASCAR. Prov. Toliara: Ambovombe, 1-50 m, 9 Sep 1928, *R. Decary* 9182 (syntypes: MO [5598316]!), P [P00131547]!, *ibid.* loc., 9 Sep 1928, *H. Humbert & C.F. Swingle* 5624 (syntype: P [P00418490]!). MADAGASCAR. Prov. Toliara: Ampasimpolaka, 13 Jun 1924, *R. Decary* 2872 (syntypes: P [P00133410], MO [1604979]!). MADAGASCAR. Prov. Toliara: environs de Fort-Dauphin, près de Bevilany, 200-300 m, 14 Sep 1928, *H. Humbert & C.F. Swingle* 5679 (syntypes: K [K001040350]!, MO [1709286]!, MO [1842163]!, P [P00422331]!, P [P00422332], TAN [TAN000522]); Bevilany, District de Fort-Dauphin, 8 Aug 1932, *R. Decary* 10254 (syntypes: MO [1592371]!, P [P00133412]). MADAGASCAR. Prov. Toliara: Manampany, s.d., *M.F. Geay* 6385 (syntype: P [P00131548]). MADAGASCAR. Prov. Toliara: moyenne Mananara, à la limite orientale de l'Androy,

27 Nov 1931, *R. Decary* 9443 (syntypes: G [G00446375], MO [5598315]!, MO [5608957]!, P [P00133411]! = *Croton toliarensis*).

Croton leandrii Croizat, *Trop. Woods* 77: 15. 1944, as '*leandri*', **syn. nov.**

Type. Based on (replacement name for) *Croton arenicola* Leandri

Type. MADAGASCAR. Prov. Toliara: vallée moyenne du Mandrare, près d'Anadabolava, mont Vohitrotsy, 850 m, Dec 1933, *H. Humbert* 12659 (lectotype, designated here: P [P00131549]!; isolectotypes: G [G00018190]!, K [K001040365]!, P [P00131550]!, TAN [TAN000527]!).

Habit and distribution. Shrubs or small trees; southern Madagascar (Toliara).

Notes. Radcliffe-Smith (2016) noted that *Croton leandrii* and *C. chlaenacomes* are very similar, and in fact there is no reason to keep them separate. Some specimens that were identified under these names in the past, but with pubescence on the upper surface of the leaves as well as below, are now treated under *C. toliarensis* B.W. vanEe & Kainul.

39. *Croton chrysodaphne* Baill., *Adansonia* 1: 147. 1861

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

Type. Based on *Croton chrysodaphne* Baill.

Croton lepidotus Aug.DC., *Bull. Herb. Boissier*, sér. 2, 1: 565. 1901.

Type. MADAGASCAR. Prov. Toamasina: Maroantsetra, forêts à l'intérieur de la baie d'Antongil, 1897, *A. Mocquerys* 274 (holotype: G-DC [G00018155]!; isotypes: Z [Z-000015984], Z [Z-000015985]).

Croton meeusei Leandri, *Notul. Syst. (Paris)* 13: 184. 1948, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Soanierana-Antasibe, 350 m, 13 Oct 1938, *H.J. Lam* & *B. Meeuse* 5957 (holotype: P [P00312381]!; isotypes: L [L0234889]!, WAG!).

Croton submetallicoides Radcl.-Sm., *Gen. Croton Madag. Comoro* 58. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Betampona Réserve Naturelle Intégrale, 40 km NW of Toamasina, 275–650 m, 17°31'S, 49°07'E, 28 Sep 1993, *B. Lewis* & *S. Razafimandimbison* 656 (holotype: K!; isotypes: MO!, P [P00433129]!).

Type. MADAGASCAR. Prov. Toamasina: Foulpointe or near Tamatave, 21 Jul 1794 [date on attached letter], *L.A. Chapelier s.n.* (lectotype, designated by Leandri 1972b: P [P00389522]!; isolectotype: P [P00133024]!). MADAGASCAR. sin. loc., s.d., *L.M.A. Dupetit-Thouars s.n.* (syntype: P [P00133022]! = *C. cupreolepis*). MADAGASCAR. Prov. Mahajanga: in montosis in Mazangay, s.d., *W. Bojer s.n.* (syntype: P [P00133021]! = *C. argyrodaphne*); MADAGASCAR. Prov. Toamasina: Analalava Forest Reserve, 7 km W of Foulpointe, 17°42.586'S, 49°27.175'E, 22 m, 2 Mar 2009, *B. van Ee*, *P.E. Berry* & *H. Razanatsoa* 998 (epitype, designated by Berry et al. 2011, pg. 113: MICH [MICH1514785]!; additional duplicates: G!, MO!, P!, TAN).

Habit and distribution. Large shrubs or trees; eastern lowland Madagascar (Antsiranana, Fianarantsoa, Mahajanga, Toamasina, eastern Toliara).

Notes. Baillon (1861) included material of *Croton argyrodaphne* (Bojer s.n.) and *C. cupreolepis* (Dupetit-Thouars s.n.), among the syntypes of *C. chrysodaphne*, which was lectotypified on a Chapelier specimen by Leandri (1972b). See Berry et al. (2011) and Berry et al. (2016b) for further discussions.

Both *Croton meeusei* and *C. submetallicoides* fit well within the variation of leaf size and shape of *C. chrysodaphne*, but they are reported to have the normal five petals in staminate flowers, whereas specimens from the Foulpointe area (the presumed lectotype locality as well as the epitype locality) have the unusual number of ten petals. We judge this to be somewhat of an anomaly and not a feature that has been fixed in the species overall. The type of *C. meeusei* lacks pistillate flowers altogether, whereas the type of *C. submetallicoides* has the short, curved inflorescence and pistillate flowers that are typical of *C. chrysodaphne*.

40. *Croton chypreae* Leandri, *Adansonia*, sér. 2, 9: 498. 1970

Type. MADAGASCAR. Prov. Antsiranana/Mahajanga border: Massif du Tsaratanana, crête séparant les bassins du Sambirano et de la Mahavavy, entre la cote 2362 et la base du piton coté 2831 m, 11-13 Nov 1966, *Service Forestier 27057-SF* (holotype: P [P00312380]!; isotype: TEF [TEF000189]!).

Habit and distribution. Shrubs or small trees; high elevations of north-central Madagascar (border area of Antsiranana and Mahajanga).

41. *Croton cotoneaster* Müll.Arg., *Flora* 47: 484. 1864

Oxydectes cotoneaster (Müll.Arg.) Kuntze, *Revis. Gen. Pl.* 2: 611. 1891.

Type. Based on *Croton cotoneaster* Müll.Arg.

Croton mahafaliensis Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 75. 1939.

Type. MADAGASCAR. Prov. Toliara: plateau Mahafaly, Menarandra, Feb 1910, *H. Perrier de la Bâthie 9776* (lectotype, designated here: P [P00312455]!; isolectotype: P [P00133488]!) MADAGASCAR. Prov. Toliara: Beheloka, 80 m, Jun 1910, *H. Perrier de la Bâthie 9767* (syntypes: P [P00312456], P [P00133487]). MADAGASCAR. Prov. Toliara: environs de Tuléar, Aug 1919, *H. Perrier de la Bâthie 12804* (syntype: P [P00312454]). MADAGASCAR. Prov. Toliara: Lac Manampetsa [Tsimanampetsotsa], Apr 1933, *H. Perrier de la Bâthie 19047* (syntype: P [P00312453]).

Type. MADAGASCAR. Prov. Toliara: St. Augustin, 1837, *L. Bouton s.n.* (holotype: K [K001040358]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

42. *Croton crocodilorum* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 80. 1939

Croton bathianus var. *toliaerae* Radcl.-Sm., Gen. Croton Madag. Comoro 115. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beza Mahafaly Reserve near Betioky, E of Sakamena River, near Ambinda, 23°40'S, 44°38'E, 3 Nov 1987, *P.B. Phillipson* 2511 (holotype: K!; isotypes: MO, P [P00127504]!).

Croton crocodilorum var. *meridionalis* Radcl.-Sm., Gen. Croton Madag. Comoro 112. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Ihosy, in monte Lalanandro, 6 Nov 1967, *L. Bernardi* 11259bis (holotype: K!; isotypes: G!, P [P00154382]!).

Type. MADAGASCAR. Prov. Mahajanga: vallée de la Betsiboka à Marovoay, colline de Marovoay, 50 m, 4–5 Sep 1924, *H. Humbert & H. Perrier de la Bâthie* 2347 (lectotype, designated here: G [G00018189]!; isolectotypes: P [P00133026]!, P [P00312451]!, TAN [TAN000528]!). MADAGASCAR. Prov. Mahajanga: Boiny, Nov., *H. Perrier de la Bâthie* 9831 (syntypes: P [P00133027]!, P [P00312452]!).

Habit and distribution. Shrubs; mainly southern and western Madagascar (Mahajanga, Toliara), but also in Fianarantsoa Province.

Notes. The Geneva sheet was chosen as the lectotype of *Croton crocodilorum*, since it is the most complete sheet among the syntypes and contains many seeds in the packet. It was annotated by Leandri as '*Croton crocodilorum* Leandri n. sp.' before it was acquired by Geneva as part of the Herbarium Delessert in 1949.

The type of *Croton bathianus* var. *toliaerae* supposedly differs from the type of *C. crocodilorum* in its rugulose (vs. smooth) seeds (Radcliffe-Smith 2016). However, wrinkled seeds were also seen in the type of *C. crocodilorum*, whereas the type of *C. bathianus* has no fruits. The type of *C. crocodilorum* var. *meridionalis* supposedly differs from the type of *C. crocodilorum* by its denser cinereous indumentum on the lower side of the leaves and larger capsules and seeds (Radcliffe-Smith 2016), but we consider this merely an extreme pubescence outlier in the morphological variation of the species.

43. *Croton crossolepis* P.E.Berry & Kainul., Phytotaxa 307(1): 95. 2017

Croton mavoravina var. *thysanolepis* Radcl.-Sm., Gen. Croton Madag. Comoro 32. 2016.

Type. MADAGASCAR. Prov. Toliara: environs de Tuléar, 10–12 Jan 1947, *H. Humbert* 19816 (holotype: K!; isotype: P [P00433491]!).

Type. MADAGASCAR. Prov. Toliara: Atsimo-Andrefana Region, along Route Nationale 7 on S side of road, ca. 30 km as the bird flies E of Toliara, 23°19'54"S, 43°55'15"E, 190 m, 8 Feb 2009, *B. van Ee, P.E. Berry, B.L. Dorsey & H. Razanatsoa* 823 (holotype: MICH [MICH1210791]!; isotypes: G!, MO!, P!, TAN!).

Habit and distribution. Shrubs; dry forest and scrub in southwestern Madagascar (Toliara).

44. *Croton cupreolepis* P.E.Berry, B.W.van Ee & Kainul., Syst. Bot. 41: 977. 2016

Croton nobilis var. *delphinensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 48. 1939.

Type. MADAGASCAR. Prov. Toliara: Anosy Region, environs de Fort-Dauphin, forêt de Manantantely, 60–300 m, 15 Sep 1928, *H. Humbert & C.F. Swingle* 5742 (lectotype, designated by Berry et al. 2016b, pg. 977: P [P00133655]!; isolectotypes: G, [00446398]!, P [P00133656]!).

Croton chrysodaphne var. *meridionalis* Radcl.-Sm., Gen. Croton Madag. Comoro 62. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Préfecture de Fort-Dauphin, Forêt de Manantantely, 50–200 m, 9 Nov 1990, *R. Rabevohitra* 2428 (holotype: K!; isotypes: MO!, P [P00133653]!).

Type. MADAGASCAR. Prov. Toliara: Anosy Region, Domaine de la Cascade private preserve (Manantantely-Soanerana), several km north of Route Nationale 13 at Point Kilométrique 9 west of Fort Dauphin, 24°59'05"S, 46°55'39"E, 168–283 m, 2 Aug 2015, *B. van Ee & P.E. Berry* 2153 (holotype: MICH!; isotypes: MO, P, TAN!).

Habit and distribution. Trees, eastern montane forests of Madagascar (Antsirana, Fianarantsoa, Toamasina, Toliara).

45. *Croton danguyanus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 66. 1939, as ‘danguyana’

Croton bracteatus subsp. *populifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 138. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Route Tananarive-Majunga, environs de la Betsiboka, Jan 1949, *Service des Eaux et Forêts* 148SF (holotype: P [P00154434]!).

Type. MADAGASCAR. Prov. Mahajanga: environs de Madirovalo (Boïny), Nov 1907, *H. Perrier de la Bâthie* 9832 (lectotype, designated here: P [P00389520]!; isolectotype: P [P00327989]!). MADAGASCAR. Prov. Mahajanga: Bongolava, Boïny, Nov 1906, *H. Perrier de la Bâthie* 9565 (syntypes: P [P00389519]!, P [P00133040]!). MADAGASCAR [probably Prov. Mahajanga, Réserve de Namoroka], *Service Forestier* 76 (syntype: P [P00389517]!). MADAGASCAR. sin. loc., received 4 Apr 1933, *Service Forestier* 104 (syntype: P [P00389518]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

46. *Croton decaryi* Leandri, Bull. Mus. Natl. Hist. Nat., sér. 2, 3: 370. 1931

Croton bevilaniensis Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 79. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: confins de l’Anosy et de l’Androy, Bevilany, 8 Aug 1932, *R. Decary* 10258 (lectotype, designated here: P [P00127548]!; isolectotypes: K [K000253646]!, TAN [TAN000525]!).

Type. MADAGASCAR. Prov. Toliara: Massif de l'Angavo, à l'Est d'Antanimora, 19 Jul 1926, *R. Decary* 4446 (lectotype, designated here: P [P00133044]!; isoelectotypes: K [K000253647]!, P [P00133043]!, TAN [TAN000531]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

47. *Croton dissimilis* Baill., Bull. Mens. Soc. Linn. Paris 2: 861. 1890

Croton echinatus Radcl.-Sm., Gen. Croton Madag. Comoro 13. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: environs d'Antalaha, 23 Nov. 1948, *H. Humbert & R. Capuron* 21918 (holotype: P [P00131511]!).

Croton alaotrensis var. *integrifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 11. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Mananara Avaratra, Antanambe, above Mahavohobe River, 16°27'S, 49°47'E, 26 Oct 1994, *G. Prance & J. Andriantiana* 30783 (holotype: K!).

Type. MADAGASCAR. Prov. Toamasina: Fito (Ambanivoules), 1833, *J.P. Goudot* 7 (holotype: P [P00154404]!).

Habit and distribution. Shrubs; eastern lowland Madagascar (Antsiranana, Toamasina).

Notes. Leandri (1939) considered *Croton dissimilis* to be a synonym of *C. ambanivoulensis*, but *C. dissimilis* differs in its larger, usually crenate leaves and echinate ovary with trichomes with a long, porrect central ray. Although the type of *C. echinatus* has entire leaves (the type of *C. dissimilis* has crenate leaves), it has similar whitish bark with contrasting tufts of brown trichomes, acropetiole glands that are cylindrical and shortly stipitate, and the ovary shares the distinctive feature of being covered by long porrect trichomes that give it the appearance of being “echinate.” Similarly, the type of *C. alaotrensis* var. *integrifolius* has entire to slightly crenate leaves, and it comes from eastern lowland Toamasina Province, near the presumed type locality of *C. dissimilis*.

48. *Croton droguetioides* Kainul. & Radcl.-Sm., Candollea 71: 331. 2016 [23 Nov 2016]

Croton droguetioides Radcl.-Sm., Gen. Croton Madag. Comoro 16. 2016 [23 Dec 2016].

Type. MADAGASCAR. Prov. Toamasina: marais et bordures de Torotorofotsy, 18°52'S, 48°20'E, 24 Feb 1997, *P. Rakotomalaza et al.* 1170 (holotype: K!; isotype: MO!), nom. illeg.

Croton alaotrensis Radcl.-Sm., Gen. Croton Madag. Comoro 10. 2016, **syn. nov.**

Type. MADAGASCAR. “Central Madagascar”, received Dec 1883, *R. Baron* 3006 (holotype: K!, isotype: P [P00131488]!).

Croton parietarioides Radcl.-Sm., Gen. Croton Madag. Comoro 16. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatoharanana, près Antsevabe, 1000 m, 6 Mar 1951, *G. Cours 4111* (holotype: K!; isotype: P [P00418635]!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga District, Andasibe, Berano, Ambatovy mine concession, 18°47'59"S, 48°20'31"E, 1009 m, 22 Mar 2016, *B. van Ee, P. Antilahimena, K. Kainulainen & P.E. Berry 2447* (holotype: MICH [MICH1513195]!, isotypes: MO!, P!, TAN!).

Habit and distribution. Shrubs; eastern montane Madagascar (Toamasina).

Notes. Radcliffe-Smith (2016) erroneously placed the type of *Croton parietarioides* in Antananarivo Province, mistaking Antsevabe for Antsirabe. Antsevabe is close to the Ankeniheny-Zahamena eastern montane forest corridor and lies ca. 25 km southeast of Ambatondrazaka.

49. *Croton elaeagni* Baill., Bull. Mens. Soc. Linn. Paris 2: 848. 1890

Croton elaeagni var. *antsingyensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 34. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Andranoboka, 21 Nov 1932, *J. Leandri 551* (lectotype, designated here: P [P00133092]!; isolectotypes: P [P00133093]!, S [S07-14588]!). MADAGASCAR. Prov. Mahajanga: Amborokontsy, 6 Oct 1932, *J. Leandri 124* (syntypes: P [P00133090]!, P [P00133091]!).

Croton elaeagni var. *antsirananae* Radcl.-Sm., Gen. Croton Madag. Comoro 90. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Réserve Spéciale d'Ankarana, à environ 106 km au Sud d'Antsiranana par route, et 12 km à l'Ouest de Mahamasina au Lac Vert, 12°55'13"S, 49°05'10"E, 12 Dec 1995, *O. Andrianantoanina & R. Bezara 908* (holotype: K!, isotypes: MO, P [P00433269]!).

Type. MADAGASCAR. Prov. Toliara: Andakabé, près Morondava, s.d., *H. Grevé 82* (lectotype, designated here: P [P00133081]!; isolectotypes: G [G00018188]!, K [K001040385]!, P [P00133082]!, P [P00133083]!, P [P00133084]!, P [P00133085]!, P [P05481486]!).

Habit and distribution. Shrubs; northern, western and southern Madagascar (Antsiranana, Mahajanga, Toliara).

50. *Croton elliotianus* Baill., Bull. Mens. Soc. Linn. Paris 2: 863. 1890

Type. MADAGASCAR. Prov. Toliara: Fort-Dauphin, s.d., *G.F. Scott-Elliot 2970* (lectotype, designated here: P [P00133118]!, isolectotype: K [K000347488]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

51. *Croton emeliae* Baill., *Adansonia* 1: 166. 1861

Croton bifurcatus var. *emeliae* (Baill.) Müll.Arg. in A.P.de Candolle, Prodr. 15(2): 584. 1866.

Type. Based on *Croton emeliae* Baill.

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Jul 1849, *H. Boivin* 3381 (lectotype, designated here: P [P00404495]!; isolectotypes: G-DC [G00311983]!, P [P00133119]!, P [P00213565]!).

Habit and distribution. Shrubs; known only from the French island of Mayotte in the Comoro Islands.

52. *Croton enigmaticus* P.E.Berry & B.W.van Ee, *Candollea* 71: 333. 2016

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, along dirt road north of Route Nationale 2, past village of Savahoana, 981 m, 18°55'06"S, 48°20'38"E, 14 Aug 2015, *B. van Ee*, *P.E. Berry* & *H. Razafindraibe* 2212 (holotype: MICH [MICH1513196]!; isotypes: MICH [MICH1513197]!, MO, P, TAN).

Habit and distribution. Shrubs; montane forests of eastern Madagascar (Toamasina).

53. *Croton ericius* Leandri, *Cat. Pl. Madag., Euphorb.*: 32. 1935

Croton horridulus Baill., Bull. Mens. Soc. Linn. Paris 2: 977. 1891, nom. illeg. non *Croton horridulus* (Baill.) Müll.Arg., 1866.

Croton lapiazicola Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 42. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Tsingy du Bemaraha (9° Réserve), Feb. 1933, *J. Leandri* 945 (lectotype, designated here: P [P00312338]!; isolectotype: P [P00133400]!). MADAGASCAR. Prov. Mahajanga: Tsingy du Bemaraha (9° Réserve), 5 Oct 1932, *J. Leandri* 139 (syntype: P [P00312339]!), *ibid.* loc., Oct 1932, *J. Leandri* 162 (syntype: P [P00389500]!).

Type. MADAGASCAR. *R. Baron* 5579 (holotype: P [P00133163]!); isotype: K [K000422591]!

Habit and distribution. Shrubs; northern and western Madagascar (Antsiranana, Mahajanga).

54. *Croton farinosus* Lam., *Encycl.* 2: 211. 1786

Oxydectes farinosa (Lam.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton farinosus* Lam.

Croton scottii Baill., Bull. Mens. Soc. Linn. Paris 2: 967. 1891, as '*scotti*', **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Fort-Dauphin, s.d., *G.F. Scott-Elliot* 2987 (holotype: P [P00154436]!; isotype: K [K000253644]!).

Croton moraharivensis Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 68. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: vallée de la Manambolo, rive droite (bassin du Mandrare) aux environs d'Isomono (confluent de la Sakamalio), Mont Morahariva, 1000-1400 m, Dec 1933, *H. Humbert* 13176 (lectotype, designated here: P [P00132989]!; isolectotypes: G [G00018151]!, P [P00132990]!). MADAGASCAR. Prov. Toliara: bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, 600-800m, Feb 1934, *H. Humbert* 14041 (syntypes: K [K000815882]!, P [P00132991]!).

Croton vohibariensis Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 78. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: vallée moyenne du Mandrare, près d'Anadabolava, Mont Vohibaria (sommets), 800-810 m, Dec 1933, *H. Humbert* 12627 (lectotype, designated here: P [P00133322]!; isolectotypes: G [G00446404]!, K [K000253645]!, P [P00133323]!, P [P00133324]!). MADAGASCAR. Prov. Toliara: vallée moyenne du Mandrare, près d'Anadabolava, Mont Vohitrotsy, sommets, vers 850 m, Dec 1933, *H. Humbert* 12673 (syntype: P [P00133325]!).

Type. MADAGASCAR: sin. loc., s.d., *P. Commerson s.n.* (holotype: P-LA [P00382067]!; isotypes: G [G00446383]!, G [G00446384]!, LINN [LINN-HS1492-5], P [P00404490]!).

Habit and distribution. Shrubs; southeastern Madagascar (Toliara).

Notes. Although there is a wide elevational variation in this species as here circumscribed, the three names listed in synonymy share the characteristic glaucous-farinosous lower leaf surface, and all appear to have an affinity for igneous outcroppings.

55. *Croton ferricretus* Kainul., B.W.van Ee & P.E.Berry, *Candollea* 71: 337. 2016 [23 Nov 2016]

Croton lepidotoides Radcl.-Sm., Gen. Croton Madag. Comoro 71. 2016 [23 Dec 2016],

syn. nov.

Type. MADAGASCAR. Prov. Toamasina: ca. 15 air-km NE of Moramanga, ca. 11 km E of Antanambao, Ambatovy, 18°51'08"S, 48°18'40"E, 30 Jan 1997, *P. Rakotomalaza et al.* 1024 (holotype: K!; isotype: MO!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga district, Andasibe, Berano, Ambatovy mine concession, on "cuiresse" between the workers houses and the Ambatovy supply road, 18°51'02"S, 48°18'29"E, 1142 m, 21 Mar 2016, *B. van Ee, P. Antilahimena, K. Kainulainen & P.E. Berry* 2436 (holotype MICH [MICH1513194]!; isotypes: G!, K!, MAPR!, MO!, P!, TAN!).

Habit and distribution. Shrubs; eastern Madagascar (Moramanga District of Toamasina Province).

56. *Croton fianarantsoae* Leandri, *Adansonia*, sér. 2, 13: 295. 1973

Croton nitidulus var. *grandifolius* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 39. 1939, as '*grandifolia*'.

Type. MADAGASCAR. Prov. Fianarantsoa: Vondrozo, 17 Sep 1926, *R. Decary* 5333 (holotype: P [P00133643]!; isotypes: K [K001040382]!, P [P00425637 - wood], S [S07-17118]!, TAN [TAN000539]!).

Croton nitidulus var. *tandrokensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 39. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Massif d'Andringitra, col du Tandroka, versant Est, 1200 m, Sep 1910, *H. Perrier de la Bâthie* 9749 (holotype: P [P00133638]!).

Croton fianarantsoae var. *grandifolius* Leandri, *Adansonia*, sér. 2, 13: 297. 1973, as '*grandifolia*', **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Sahasanato, Antajonombay, Canton Befody, Distr. Nosy-Varika [N de Manajary], 21 May 1955, *Service Forestier* 14556 (lectotype, designated here: P [P00154399]!; isolectotypes: P [P00154400]!, P [P00154401]!, TEF [TEF000191]!).

Croton daphniphylloides var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro 165. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Parc National de Ranomafana, Talakately, 21°15'S, 47°27'E, 27 Jul–6 Aug 1993, *A. Kotozafy* 131 (holotype: K!; isotypes: MO, P [P00433137]!).

Croton fianarantsoae var. *coursii* Radcl.-Sm., Gen. Croton Madag. Comoro 154. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Rahobevava, 1300 m, 14 Mar 1951, *G. Cours* 4370 (holotype: P [P00133614]!).

Croton fianarantsoae var. *microphyllus* Radcl.-Sm., Gen. Croton Madag. Comoro 155. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Parc National de Ranomafana, SE of Savondronona, Maharira, 21°18'S, 47°23'E, 1200–1400 m, 21–23 Apr 1993, *S. Malcomber*, *C. Hemingway* & *A. Randriamanantena* 2441 (holotype: K!; isotypes: MO, P [P00422457]!).

Croton fianarantsoae var. *ranomafanae* Radcl.-Sm., Gen. Croton Madag. Comoro 156. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Parc National de Ranomafana, trail S from Cabine de Recherche to Vato camp, 21°15'S, 47°27'E, 1060 m, 11–15 Nov 1991, *S. Malcomber*, *A. Leeuwenberg*, *C. Rakotomazana*, *H. Ranarljadna* & *G. Rahajasoa* 1042 (holotype: K; isotypes: MO, P [P00422461]!).

Croton fianarantsoae var. *tandrokensis* (Leandri) Radcl.-Sm., Gen. Croton Madag. Comoro 156. 2016, **syn. nov.**

Type. Based on *Croton nitidulus* var. *tandrokensis* Leandri

Type. MADAGASCAR. Prov. Fianarantsoa: Andrambovato, Parcelle B5 [Fort Carnot], 23 Mar 1954, *Service Forestier 10169-SF* (holotype: P [P00338570]!; isotype: P [P00154402]!, TEF [TEF000190]!).

Habit and distribution. Shrubs to small trees; eastern Madagascar (Antsiranana, Fianarantsoa, Toamasina).

Notes. *Croton fianarantsoae* is part of a difficult species complex, and further work is needed to differentiate it from similar species such as *C. nitidulus*.

57. *Croton fothergillifolius* Baill., *Adansonia* 1: 150. 1861, as '*fothergillifolium*'

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

Type. Based on *Croton fothergillifolius* Baill.

Type. MAURITIUS. sin. loc., *L.M.A. Du Petit-Thouars s.n.* (lectotype, designated here: P [P00404184]!; isolectotype: P [P00404183]!).

Habit and distribution. Shrubs; Mauritius.

Notes. Bojer (1837) listed a plant from the Grand Bassin of Mauritius as *Croton muricatus* Vahl, a native Malagasy species. Based on this, the name "*C. muricatus* Bojer, nom. nud." has been included in several indices, including IPNI, Tropicos, and Govaerts et al. (2000). In the same manner as Leandri (1939), we interpret Bojer (1837) as a misidentification of what Baillon (1861) later described as *C. fothergillifolius*, rather than the publication of a nomen nudum.

58. *Croton geayi* Leandri, *Bull. Mus. Natl. Hist. Nat., sér. 2, 3*: 368. 1931

Croton geayi var. *paucisquamatus* Radcl.-Sm., *Gen. Croton Madag. Comoro* 94. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Plateau Mahafaly à l'Ouest de Betioky, 17-20 Mar 1955, *H. Humbert & R. Capuron 29490* (holotype: P [P00123679]!).

Croton geayi var. *pubescens* Radcl.-Sm., *Gen. Croton Madag. Comoro* 95. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: vallée inférieure de l'Onilahy, 12 Aug 1928, *H. Humbert & C.F. Swingle 5235* (holotype: P [P00133137]!; isotype: G!).

Type. MADAGASCAR. Prov. Toliara: sin. loc., 1906, *M.F. Geay 28* (holotype: P [P00133132]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. The two varieties of *Croton geayi* described by Radcliffe-Smith (2016) only differ from the nominal species in degree and type of pubescence, and this does not seem to justify their recognition as distinct taxonomic entities.

59. *Croton glomeratus* Aug.DC., Bull. Herb. Boissier, sér. 2, 1: 566. 1901

Croton lamianus Leandri, Notul. Syst. (Paris) 13: 184. 1948, as '*Lamiana*', **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Soanierana-Ambahoabe, 50 m, 5 Dec 1938, *H.J. Lam & B. Meeuse* 5756 (lectotype, designated here: P [P00312383]!; isolecotypes: K [K001040375]!, L [93970419], P [P00312382]!). MADAGASCAR. Prov. Toamasina: Soanierana-Ambahoabe, 100 m, 3 Dec 1938, *H.J. Lam & B. Meeuse* 5604 (syntypes: P [P00133398]!, L [939171491]).

Croton fianarantsoae var. *masoalae* Radcl.-Sm., Gen. Croton Madag. Comoro 154. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Manarivola, Sahamalaza, Vinanivao, Antalaha, Parc Masoala, 15°48'25"S, 50°17'15"E, 12–22 Feb 1996, *R. Bernard et al.* 213 (holotype: K!; isotypes: MO, P [P00433259]!).

Type. MADAGASCAR. Prov. Toamasina: Maroa [Maroantsetra], 1898, *A. Mocquerys* 298 (lectotype, designated here: G [G00446385]!). MADAGASCAR. Prov. Toamasina: Maroa [Maroantsetra], s.d., *A. Mocquerys* 317 (syntype: G [G00446386]!).

Habit and distribution. Shrubs; northeastern Madagascar (Antsiranana, Toamasina).

60. *Croton goudotii* Baill., Adansonia 1: 157. 1861

Croton platanifolius Bojer ex Baker, J. Bot. 20: 268. 1882.

Type. MADAGASCAR. edges of woods in East Betsileo, received Jul 1880, *R. Baron* 262 (holotype: K [K000422589]!; isotype(fragment): P [P00133700, upper packet]!).

Croton emirnensis Baker, J. Linn. Soc., Bot. 20: 252. 1883.

Type. MADAGASCAR. sin. loc. s.d., *R. Baron* 1854 (lectotype, designated here: K [K000422588]!). MADAGASCAR. sin. loc., s.d., *R. Baron* 1841 (syntypes: K [K001040356]!, P [P00133701]!).

Oxydectes goudotii (Baill.) Kuntze, Revis. Gen. Pl. 2: 611. 1891.

Type. Based on *Croton goudotii* Baill.

Croton mollivelus Baill. Bull. Mens. Soc. Linn. Paris 2: 926. 1891, as '*mollivelum*'.

Type. MADAGASCAR. sin. loc., s.d., *C.M. Le Myre de Vilers s.n.* (holotype: P [P00310180]!).

Croton tsaratananae Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 74. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana/Mahajanga border: Mont Tsaratanana, 2000 m, Dec 1912, *H. Perrier de la Bâthie* 9720 (lectotype, designated here: P [P00389496]!; isolecotypes: P [P00154411]!, P [P00154412]!).

Croton goudotii var. *tsaratananae* (Leandri) Radcl.-Sm., Gen. Croton Madag. Comoro 128. 2016, **syn. nov.**

Type. Based on *Croton tsaratananae* Leandri

Type. MADAGASCAR. Prov. Antananarivo: environs de Tananarivo, rec'd. 1840, *J.P. Goudot s.n.* (holotype: G [G00018187]!; isotype (fragment from G): P [P00133700, lower packet]!

Habit and distribution. Trees; upland forests across Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

61. *Croton gracilior* Radcl.-Sm., *Gen. Croton Madag. Comoro* 108. 2016

Type. MADAGASCAR. Prov. Mahajanga: Tsingy de Bemaraha, N of the Malambo River, 19°09'S, 44°49'E, 27 Nov 1996, *C.C.H. Jongkind, J. Andriantiana & H. Razanatsoa* 3235 (holotype: K!; isotypes: MO!, WAG).

Habit and distribution. Shrubs; western Madagascar (Mahajanga – Melaky Region).

62. *Croton grangerioides* Bojer ex Baill., *Adansonia* 1: 149. 1861

Croton boutonianus Müll.Arg., *Linnaea* 34: 80. 1865.

Type. MAURITIUS. in sylvis montosis, 1833, *W. Bojer s.n.* (lectotype, designated here: G-DC [G00311198]!; isolectotypes: G [G00446409]!, M [M0110371]!).

MAURITIUS. 1857, *L. Bouton s.n.* (syntype: G-DC [G00311197]!).

Oxydectes boutoniana (Müll.Arg.) Kuntze, *Revis. Gen. Pl.* 2: 611. 1891.

Type. Based on *Croton boutonianus* Müll.Arg.

Oxydectes grangerioides (Bojer ex Baill.) Kuntze, *Revis. Gen. Pl.* 2: 610. 1891.

Type. Based on *Croton grangerioides* Bojer ex Baill.

Type. MAURITIUS. s.d., *J. Néraud s.n.* (lectotype, designated here: G [G00446387]!; possible isolectotype: P [P00404205]!). MAURITIUS. à l'embrasure, au-dessous du Pouce, s.d., *L.M.A. Du Petit-Thouars s.n.* (syntypes: P [P00404204]!, P [P0040179]!). MAURITIUS. crêtes de la montagne de Port-Louis, vers l'extrémité au-dessus de l'anse Courtois, Oct 1849, *L.H. Boivin s.n.* (syntype: P [P00404203]!). MAURITIUS. 1850, *J.N.E. Vesco s.n.* (syntype: P [P00404180]!). MAURITIUS. *W. Bojer s.n.* (original material: MAU [1402; specimen not seen], possible type: G [G00446413]!, M [M0110457]!).

Habit and distribution. Shrubs; Mauritius.

Notes. Baker (1877) distinguished *Croton boutonianus* from *C. grangerioides* in his key by the former having entire leaves and pistillate flowers with petals and the latter obscurely crenulate leaves and pistillate flowers that lack petals. Leandri (1939) accepted *C. grangerioides*, but appears to have overlooked mentioning *C. boutonianus*, even as a synonym. Coode (1982) treated *C. boutonianus* as a synonym of *C. grangerioides*, describing the petals of the staminate flowers as small and delicate, and the crenulation of the leaf margins as variable. We follow here the taxonomy of Coode (1982) in treating *C. boutonianus* as a synonym of *C. grangerioides*.

63. *Croton greveanus* Baill., Bull. Mens. Soc. Linn. Paris 2: 849. 1890

Croton greveanus var. *borealis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 45. 1939.

Type. MADAGASCAR. Prov. Mahajanga: région littorale, entre Masoarivo et Ambato, Nov 1932, *J. Leandri* 536 (lectotype, designated here: P [P00133803]!; isolectotypes: G [G00446389]!, P [P00133804]!, P [P00133805]!). MADAGASCAR. Prov. Mahajanga: Tsingy du Bemara, 9^e Réserve Naturelle, Tsiombivositra, 10 Nov 1932, *J. Leandri* 517 (syntype: P [P00133802]!). MADAGASCAR. Prov. Mahajanga: Trano Passage, *J. Leandri* 264 (P [P00133800], P [P00133802]!). MADAGASCAR. Prov. Mahajanga: Savalika, 11 Dec 1932, *J. Leandri* 341 (P [P00133785]!, P [syntype: P00133786]!). MADAGASCAR. Prov. Mahajanga: Boina, Firingalava, Dec 1898, *H. Perrier de la Bâthie* 777 (syntypes: P [P00133788]!, P [P00133789]!). MADAGASCAR. Prov. Mahajanga: cause d'Ankara, bois rocailleux calcaire de Kamakama, Dec 1901, *H. Perrier de la Bâthie* 9798 (syntype: P [P00154464]!).

Croton antanosiensis var. *pubescens* Radcl.-Sm., Gen. Croton Madag. Comoro 43. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: 44 km Tulear-Ihosy, 12 Nov 1967, *L. Bernardi* 11411 (lectotype, designated here: G [“Hb. G 0044814”]!; isolectotypes: G [“Hb. G 0044804”]!, P [P00154375]!).

Croton boinensis var. *parcelepidotus* Radcl.-Sm., Gen. Croton Madag. Comoro 78. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Ampasimandroro, Maintirano, 12 May 1956, *Service Forestier* 16322-SF (lectotype, designated here: P [P00347747]!; isolectotype: P [P00154435]!).

Type. MADAGASCAR. Prov. Toliara: Bé-Kapaké [Bekopaka], ad. riv. Morondava, s.d., *H. Grévé* 239 (lectotype, designated here: P [P00404488]!; isolectotypes: P [P00133768]!, P [P00133769]!, P [P00133770]!, P [P00133771]!).

Habit and distribution. Large shrubs or small trees; western, central, and southern Madagascar (Fianarantsoa, Mahajanga, Toliara).

64. *Croton guerelae* Leandri, *Adansonia*, sér. 2, 9: 507. 1969 [1970]

Type. MADAGASCAR. Prov. Antananarivo: forêt basse a feuilles persistantes, restes de forêt du Mt. Ambohiby (SE de Tsiroanomandidy), 1600 m, 11-16 Nov 1952, *J. Leandri et al.* 1790 (lectotype, designated here: P [P00312376]!; isolectotypes: K [K001044845]!, P [P00404478]!, P [P00404479]!).

Habit and distribution. Shrubs; central Madagascar (Antananarivo, Toamasina).

65. *Croton heteranthus* Aug.DC., Bull. Herb. Boissier, sér. 2, 1: 566. 1901

Croton ivohibensis var. *furfuraceus* Radcl.-Sm., Gen. Croton Madag. Comoro 149. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Sous-Préfecture d'Andapa, Bealampona, Befingotra, Réserve Anjanaribe-Sud on RN Andapa-Bealanana, Antsahanifelana, near Ampiferantany, 14°47'45"S, 49°27'54"E, 22 May 1995, *D. Ravelonarivo & R. Rabesonina* 816 (holotype: K!; isotype: MO!).

Croton scorpiotogyne Radcl.-Sm., Gen. Croton Madag. Comoro 166. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Ambohihalanana Ct., Antalaha Distr., 15 Dec 1956, *Réserves Naturelles 8059-RN* (holotype: P [P00133301!]).

Type. MADAGASCAR. Prov. Toamasina: Maroa [Maroantsetra], forêts à l'intérieur de la baie d'Antongil, 1897, *A. Mocquerys* 228 (holotype: G [G00018162!]; isotype: Z [Z-000015980]).

Habit and distribution. Large shrubs or small trees; northeastern Madagascar (Antsiranana, Toamasina).

66. *Croton hildebrandtii* Baill., Bull. Mens. Soc. Linn. Paris 2: 847. 1890

Croton heterochrous Baill., Bull. Mens. Soc. Linn. Paris 2: 862. 1890, nom. illeg. non *Croton heterochrous* Müll.Arg. 1865.

Croton belintae Leandri, Cat. Pl. Madag., Euphorb.: 30. 1935, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Vavatobé, Belinta, Feb 1880, *J.M. Hildebrandt* 3326 (lectotype, designated here: P [P00127506!]; isolectotypes: G [G00018184!], G [G00018185!], JE [JE00015890], JE [JE00015891!], K [K001040370!], M [M-0110366], P [P00127507!], P [P00133155!], P [P00133156!]).

Type. MADAGASCAR. Prov. Antsiranana: Pasandava-bai [Bay], Kisimani, Jun 1879, *J.M. Hildebrandt* 3013 (lectotype, designated here: G [G00075617!]; isolectotypes: G [G00075618!], G [G00018186!], JE [JE00000063!], K [K000347497!], M [M0110367!], P [P00133157!], P [P00133158!], P [P00133159!]).

Habit and distribution. Shrubs; northern and northwestern Madagascar (Antsiranana, Mahajanga).

Notes. The type of *Croton belintae* differs from the typically lepidote plants of *C. hildebrandtii* only in the presence of prominent porrect rays emerging from the center of the lepidote scales, which gives the plant a more fuzzy-pubescent appearance. In all other characters, however, such as leaf shape, petiolar glands, and the small flowers with somewhat recurved pedicels, they are identical. We therefore treat *C. belintae* as a synonym of the earlier name *C. hildebrandtii*.

67. *Croton hovarum* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 40. 1939

Croton rubricapitirupis Leandri, Adansonia, sér. 2, 13: 173. 1973, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Ambatomenaloha, à l'W d'Itremo, 20 Jan 1955, *R. Capuron 11580* (lectotype, designated here: P [P00380442]!; isolectotypes: P [P00154295]!, P [P00154296]!, P [P00154297]!, TEF [TEF000185]).

Croton anisatus var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro 14. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatondrazaka Distr., Ambatosoratra Canton, 26 Aug 1959, *Réserves Naturelles 10857* (holotype: P [P00133189]!).

Croton cassinoides var. *alaotrensis* Radcl.-Sm., Gen. Croton Madag. Comoro 10. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatondrazaka Distr., Ambatosoratra Canton, near the shore of Lac Alaotra, 16 Oct 1958, *Réserves Naturelles 9633-RN* (holotype: P [P00131518]!).

Croton greveanus var. *ambositrensis* Leandri ex Radcl.-Sm., Gen. Croton Madag. Comoro 39. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Andina, environs d'Ambositra, Dec 1921, *H. Perrier de la Bathie 18606* (holotype: P [P00133790]!).

Croton hovarum var. *lepidotus* Radcl.-Sm., Gen. Croton Madag. Comoro 179. 2016, **syn. nov.**

Type. MADAGASCAR. sin. loc., Oct 1881, *R. Baron 678* (holotype: K [not seen]; isotype: P [P00133165]!).

Croton hovarum var. *subglaber* Radcl.-Sm., Gen. Croton Madag. Comoro 179. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: RN 5, Ambalavao Distr., Sendrisoa Canton, 12 Nov 1953, *Réserves Naturelles 5871* (lectotype, designated here: P [P00133188]!; isolectotype: P [P00133187]!).

Croton ivohibensis Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 37. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: chaîne du Vohibory, à l'ouest d'Ivohibe, 1000–1300 m, 1 Nov 1924, *H. Humbert 3051* (lectotype, designated here: P [P00133264]!; isolectotypes: G [G00018157]!, K [K001040387]!, P [P00133263]!, P [P00133265]!, TAN [TAN000535]!).

Croton ivohibensis var. *lepidotus* Radcl.-Sm., Gen. Croton Madag. Comoro 149. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Réserve Naturelle V, Antaniloaha Canton, Ivohibe District, 29 Nov 1951, *Réserves Naturelles 35-29 RN* (lectotype, designated here: P [P00133632]!; isolectotype: P00133631!).

Type. MADAGASCAR. Prov. Antananarivo: Imerina, Ifanangoavana, Jan 1881, *J.M. Hildebrandt 3811* (lectotype, designated here: P [P00133177]!; isolectotypes: G [G00446390]!, G [G00446405]!, JE [JE00015925]!, K [K001040345]!, M [M0110359]!, P [P00133176]!). MADAGASCAR. sin. loc., s.d., *R. Baron 675* (syntype: P [P00133164]!), *Baron 678* (syntypes: K [K001040346]!, P [P00133165]), *R. Baron*

3151 (syntypes: K [K001040347]!, P [P00133166], P [P00133167]!). MADAGASCAR. Prov. Antananarivo: 20 km E de Tananarive, sur la route de Tamatave, 30 Oct 1928, *R. Decary* 6813 (syntypes: P [P00133171]!, G [G00018161]!, S [S07-14579]!), *ibid.* loc.. 30 Sep 1928, *R. Decary* 6834 (syntypes: P [P00133172]!; MO [5598313]!). MADAGASCAR. Prov. Antananarivo: au Nord d'Ankazobe, 9 Mar 1930, *Decary* 7292 (syntypes: P [P00133173], GB [GB-0047692]!), *ibid.* loc., 11 Mar 1930, *R. Decary* 7380 (syntypes: P [P00133174], MO [1602793]!). MADAGASCAR. Prov. Antananarivo: Manankazo, au NE d'Ankazobe, Nov 1913, *H. Perrier de la Bâthie* 9867 (syntypes: P [P0013383]!, P [P0013384]!, P [P0013385]!), *ibid.* loc., *H. Perrier de la Bâthie* 9877 (P [P00133186]!). MADAGASCAR. Prov. Toamasina: Andovoranto, Moramanga, bord de la Sahamarirana entre Ampasimpotsy et Bevalanirano, 24 Oct 1912, *R. Viguier & H. Humbert* 989 (syntypes: P [P00422391]!, P [P00422392]!, K [K001040344]!). MADAGASCAR. Prov. Fianarantsoa: Vakinankaratra, Ambatolampy, bois entre Tsinjoarivo et Ambohimasina, 2 Oct 1912, *R. Viguier & H. Humbert* 1924 (syntypes: P [P00133190]!, P [P00133191]!).

Habit and distribution. Shrubs; central upland Madagascar (Antananarivo, Fianarantsoa, Toamasina).

Notes. Leandri (1973a) distinguished *Croton rubricapitirupis* from *C. hovarum* almost exclusively by the sparser, lepidote pubescence on the leaf undersides of *C. rubricapitirupis*. *Croton hovarum* is quite variable in leaf size and degree of indumentum, and we do not consider this a sufficient distinction at the species level. In its monopodial branching, large accrescent female calyx, and finely crenate to serrate leaf margins, *C. hovarum* is a readily recognizable species in upland Madagascar. The syntype *Viguier & Humbert* 989 corresponds to *C. hypochalibaeus*.

68. *Croton humbertii* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 22. 1939, as '*humberti*'

Croton ivohibensis var. *alaotrensis* Radcl.-Sm., Gen. Croton Madag. Comoro 148. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Befody – forêt de l'Est, Ambatondrazaka, 29 Aug 1952, *Service de Eaux et de Forêts de Madagascar* 4052-SF (holotype: P [P00133207]!).

Type. MADAGASCAR. Prov. Toamasina: forêt d'Analamazaotra, Dec 1932, *J. Leandri* 709 (lectotype, designated here: P [P00133198]!; isolectotypes: P [P00133197]!, P [P00133199]). MADAGASCAR. Prov. Toamasina: forêt d'Analamazaotra, 1000m, 19 Oct 1912, *R. Viguier & H. Humbert* 805 (syntypes: P [P00133209]!, P [P00133210]!, B [B100153963]!), *ibid.* loc., 21 Oct 1912, *R. Viguier & H. Humbert* 830 (G [G00018160]!, P [P00133210]!, P [P00133211]!, P [P00133212]), *ibid.* loc., Feb 1912, *H. Perrier de la Bâthie* 9739 (syntypes: P [P00133200]!, P [P00133201]!, P [P00133202]!).

Habit and distribution. Shrubs; eastern montane Madagascar (Toamasina).

69. *Croton humblotii* Baill., Bull. Mens. Soc. Linn. Paris 2: 846. 1890

Croton humblotii var. *anjuanensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 44. 1939, **syn. nov.**

Type. UNION OF THE COMOROS: Anjouan, Apr 1905, *Lavanchie s.n.* (holotype: P [P00154408]!).

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: forêt de Combani, 10 Oct 1884, *L. Humblot 1298* (lectotype, designated here: P [P00196068]!; isolectotypes: K [K000347496]!, K [K001040343]!, LD [LD1210694], LD [LD1210214], LG [LG000009002795]), P [P00196069], P [P00196070].

Habit and distribution. Shrubs or trees; Comoro Islands, occurring on Mayotte and the three islands of the Union of the Comoros (Anjouan, Grande Comore, and Mohéli).

70. *Croton hypochalibaeus* Baill., Bull. Mens. Soc. Linn. Paris 2: 862. 1890, as ‘*hypochalibaeum*’

Croton squamiger var. *acutifolius* Müll.Arg. in A.P.de Candolle, Prodr. 15(2): 523. 1866, **syn. nov.**

Type. MADAGASCAR. in sylvis ins. Madag., s.d., *W. Bojer s.n.* (holotype: P [P00133274]!, isotype: M [M0110356]!).

Croton alceicornu Radcl.-Sm., Gen. Croton Madag. Comoro 70. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatovy, 18°51'34"S, 48°18'25"E, 3 Mar 1997, *P. Rakotomalaza et al. 1220* (holotype: K!; isotype: MO!).

Croton antanosiensis var. *fianarantsoae* Radcl.-Sm., Gen. Croton Madag. Comoro 42. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Ranomafana National Park, 7 km S of the National Road 25 W of Ranomafana, 21°15'30"S, 47°25'00"E, 31 Mar 1993, *D. Turk et al. 378* (holotype: K!; isotype: G [G00414720]!, MO!, P [P00418629]!).

Croton oligostemon Radcl.-Sm., Gen. Croton Madag. Comoro 45. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Analamazava, Binara Range, SW of Daraina (Vohemar), 13°15'S, 49°38'E, 26 Apr 1990, *D. Meyers 90* (holotype: K!; isotypes G00414721!, MO!, P [P00433104]!).

Type. MADAGASCAR. sin. loc., s.d., *R. Baron 5635* (lectotype, designated by Kainulainen et al. 2016, pg. 344: K [K001040371]!; isolectotypes: P [P00133213]!, P [P00133661]!).

Habit and distribution. Shrubs; montane forests of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Toamasina, Toliara).

Notes. Leandri (1939) considered *Croton hypochalibaeus* to be a synonym of *C. noronhae*, whereas Radcliffe-Smith (2016) considered it to be a synonym of *C. jennyanus*. *Croton hypochalibaeus* was accepted by Kainulainen et al. (2016), based on a

number of distinguishing morphological and ecological criteria. It is one of the most wide-ranging *Croton* species in Madagascar.

71. *Croton ibosianus* Leandri, *Adansonia*, sér. 2, 9: 508. 1970, as ‘*ibosiana*’

Croton barorum var. *mangokyensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 68. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Vallée d’Ihosa, bassin du Mangoky, 800-1000 m, 29-30 Oct 1924, *H. Humbert* 2992 (lectotype, designated here: P [P00301485]!; isolectotypes: P [P00404482]!, P [P00127484]!).

Croton bathianus var. *ibosianus* Radcl.-Sm., Gen. Croton Madag. Comoro 114. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: environs d’Ihosa, Mar 1934, *H. Humbert* 14445 (holotype: P [P00127476]!).

Type. MADAGASCAR. Prov. Fianarantsoa: environs d’Ihosa, Dec 1963, *J. Bosser* 18722 (lectotype, designated here: P [P00328080]!; isolectotypes: P [P00133216]!, TAN!).

Habit and distribution. Shrubs; south-central Madagascar (Fianarantsoa).

72. *Croton incisus* Baill., *Adansonia* 1: 159. 1861, as ‘*incisum*’

Oxydectes incisa (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton incisus* Baill.

Croton incisus var. *minor* Leandri, Notul. Syst. (Paris) 13: 183. 1948, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Reserve Naturelle de Betampona, près de Tamatave; 450 m, 19 Feb 1938, *H.J. Lam & B. Meeuse* 6014 (holotype: P [P00133221]!; isotypes: G [G00446382]!, K!, L, S!).

Type. MADAGASCAR. sin. loc., s.d., *L.M.A. Du Petit-Thouars* s.n. (holotype: P [P00389622]!).

Habit and distribution. Shrubs; eastern lowland Madagascar (Toamasina).

Notes. Some indices, such as Govaerts et al. (2000), have listed Baillon (1891b) as the publication in which *C. incisus* was described; however, the correct citation is Baillon (1861).

73. *Croton indrisilvae* Kainul., B.W.van Ee & P.E.Berry, *Candollea* 71: 338. 2016 [23 Nov 2016]

Croton commiphoroides Radcl.-Sm., Gen. Croton Madag. Comoro 21. 2016. [23 Dec 2016], **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Périnet-Analamazaotra, 8-9 Aug 1961, *Service Forestier* 20317 (holotype: P [P00133230]!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga district, Analamazaotra National Park, on trail E of visitor center, 18°56'45"S, 48°25'33"E, 975 m, 11 Aug 2015, *B. van Ee, P.E. Berry & H. Razafindraibe 2175* (holotype: MICH [MICH1513201]!; isotypes: G, MO, TAN).

Habit and distribution. Small shrubs; eastern montane Madagascar (Toamasina - Andasibe area).

74. *Croton inops* Baill., Bull. Mens. Soc. Linn. Paris 2: 864. 1890

Type. MADAGASCAR. Prov. Toliara: pays arides des Antandroi, Fort Dauphin, Jun-Jul, received Sep 1890, *G.F. Scott-Elliot 2986* (lectotype, designated here: P [P00133237]!; isolectotype: K [K000422592]!).

Habit and distribution. Small shrubs; southern Madagascar (Toliara).

75. *Croton isalensis* (Leandri) Leandri, *Adansonia*, sér. 2, 12: 71. 1972

Croton brevispicatus var. *isalensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 28. 1939.

Type. MADAGASCAR. Prov. Fianarantsoa: Isalo, 1910, *H. Perrier de la Bâthie 9788* (lectotype, designated by Leandri 1972a, pg. 71: P [P00389628]!). MADAGASCAR. Prov. Fianarantsoa: Isalo, 900 m, Oct 1924, *H. Perrier de la Bâthie 16607* (syntypes: K [K001040354]!, P [P00133240]!). MADAGASCAR. Prov. Toliara: plateaux et vallées de l'Isalo, gorges de la Sakamarekely et de la Sambalinieto, 500–1000 m, 19–25 Oct 1924, *H. Humbert 2849* (syntypes: G [G00446377]!, G [G00446378]!, G [G00446379]!, K!, P [P00389626]!, P [P00389627]!, K [K001040353]! TAN [TAN000526]!).

Type. Based on *Croton brevispicatus* var. *isalensis* Leandri

Habit and distribution. Shrubs; southern Madagascar (Fianarantsoa, Toliara).

Notes. In his publication elevating *Croton brevispicatus* var. *isalensis* to *C. isalensis*, Leandri (1972a) called the *Perrier de la Bâthie 9788* specimen at P the holotype. We interpret this as a lectotypification of the taxon, and given that there appears to only be a single duplicate of *Perrier de la Bâthie 9788* at P there is no need for a second-step lectotypification.

76. *Croton isomonensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 48. 1939

Type. MADAGASCAR. Prov. Toliara: vallée de la Manambolo, rive droite (basin du Mandrare) aux environs d'Isomono (confluent de la Sakamalia), Mont Morahariva (Mahamena), 1000–1400 m, Dec 1933, *H. Humbert 13247* (lectotype, designated here: P [P00133243]!; isolectotypes: G [G00018158]!, K [K001040341]!, P [P00133244]!,

TAN [TAN000534]!). MADAGASCAR. Prov. Toliara: vallée de la Sakamalio, affluent de la Manambolo (basin du Mandrare), 900-1100 m, Dec 1933, *H. Humbert 13367* (syntypes: P [P00133245]!, P [P00133246]!). MADAGASCAR. Prov. Toliara: bassin de reception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka au Vatazo (S d'Imonty), 900-950 m, Feb 1934, *H. Humbert 14076* (syntypes: P [P00133249]!, P [P00133250]!). MADAGASCAR. Prov. Toliara: bassin de reception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka entre Ampahiso et Mahamavo, 800 m, Jan-Feb.1934, *H. Humbert 13768* (syntype: G [G00018159]!).

Habit and distribution. Large shrubs to small trees; southeastern Madagascar (Toliara).

Notes. Leandri (1939) cited four Humbert collections as syntypes of *Croton isomonensis*: 13247, 13367, 14070, and 13768. We have not located a *Humbert 14070* specimen, but the *Humbert 14076* collection has the verbatim collection locality as given in Leandri (1939) for *Humbert 14070*. We surmise that the '14070' in Leandri (1939) is a typographic error for '14076.'

77. *Croton jennyanus* Gris ex Baill., *Adansonia* 1: 160. 1861, as '*jenny anum*'

Croton squamiger Baill., *Adansonia* 1: 168. 1861, as '*squamigerum*'.

Type. MADAGASCAR. Prov. Antsiranana: sin. loc., s.d., *J.M.C. Richard 576* (lectotype, designated here: P [P00133578]!; isolectotype: P [P00133579]!). MADAGASCAR. Prov. Antsiranana: Diégo-Suarès et baie de Rigny, 1837, *J.M.C. Richard 176* (syntype: P [P00133577]!). MADAGASCAR. Prov. Antsiranana: Cap d'Ambre, 1847-1852, *L.H. Boivin 2658* (syntype: P [P00133273]!).

Croton squamiger var. *obtusifolius* Müll.Arg. in A.P.de Candolle, Prodr. 15(2): 523. 1866, nom. inval.

Type. Based on *Croton squamiger* Baill.

Oxydectes jennyana (Gris ex Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton jennyanus* Gris ex Baill.

Oxydectes squamigera (Baill.) Kuntze, Revis. Gen. Pl. 2: 613. 1891.

Type. Based on *Croton squamiger* Baill.

Type. MADAGASCAR. Prov. Antsiranana [Diana Region]: vers les bas-fonds humides, lorsqu'on s'élève par les torrents au dessus des montagnes qui se trouvent au nord du port Lugwata [Diego Suarez], 1833, *J.P. Goudot s.n.* (holotype: G [G00434419]!; isotypes: P [P00133278]!, P [P00154519]!).

Habit and distribution. Shrubs; northern and western Madagascar (Antsiranana, Mahajanga).

Notes. We follow here the precedent of Leandri (1939) and Radcliffe-Smith (2016) in treating *Croton squamiger* as a synonym of *C. jennyanus*, but we differ in treating *C. hypochalibaeus* as a distinct, more highland species rather than as another

synonym of *C. jennyanus* (see Kainulainen et al., 2016). According to our interpretation, *C. jennyanus* is restricted to lower elevations in northern Madagascar (Montagne des Français, Sahafary, Daraina, Ankarana), as well as in far midwestern Madagascar on or near tsingy formations (Bemaraha).

Concerning the type of *Croton squamiger*, three other sheets of Boivin 2658 correspond to *C. brevispicatus*, so this is clearly a mixed collection. In the description of *C. squamiger*, Baillon (1861) divided the species into two infraspecific taxa, a and b. These were subsequently named by Müller (1866) as *C. squamigerus* var. *obtusifolius* (the typical variety) and *C. squamigerus* var. *acutifolius*, respectively. The latter has been recognized here to be synonymous with *C. hypochalibaeus*.

We have corrected the termination of the specific epithet to “*squamiger*” [masc. gender, Adj. group A nom., see Stearn (1992: 91) and Art. 23.5 and Art. 60.9 Ex. 24 (ICN 2012; *Croton ciliato-glanduliferum* Ortega corrected to *C. ciliatoglandulifer*).

Radcliffe-Smith (2016) listed *Croton jennyanus* as being present in the Comoros Archipelago. The three collections he cited [*Pascal* 928 (K, P) from Mayotte, and *Floret* 1241 (P) and 1249 (P) from Mohéli] all correspond to *C. humblotii*.

78. *Croton kimosorum* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 29. 1939

Croton kimosorum var. *pubescens* Radcl.-Sm., Gen. Croton Madag. Comoro 73. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: NW of Tôlañaro, Andohahela Réserve Intégrale, 24°57'S, 46°39'E, 23 Dec 1993, *S. Malcomber* 2642 (holotype: K!; isotype: MO!).

Type. MADAGASCAR. Prov. Toliara: vallé de la Sakamalio, affluent de la Manambolo (basin du Mandrare), 500–800 m, Dec 1933, *H. Humbert* 13320 (holotype: P [P00133294]!; isotypes: G [G00018156]!, K [K001040384]!, TAN [TAN000536]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

79. *Croton lasiopyrus* Baill., Bull. Mens. Soc. Linn. Paris 2: 926. 1891

Type. MADAGASCAR: “Central Madagascar”, Oct 1882, *R. Baron* 1951 (lectotype, designated by Kainulainen et al. 2016, pg. 350: P [P00133406]!, isoelectotypes: K [K001040378]!, P [P00133407]!). MADAGASCAR: “Central Madagascar”, Oct 1882, *R. Baron* 2114 (syntypes: K [K001040377]!, P [P00133408]!); “Central Madagascar”, s.d., *R. Baron* 4078 (K [K001040376]!). MADAGASCAR. Prov. Toliara: Fort-Dauphin, s.d., *G.F. Scott-Elliot* 1557 (syntype: P [P00133052 packet in upper right]!).

Habit and distribution. Shrubs; eastern montane forests (Antananarivo, Toamasina).

Notes. See the note above under *Croton cassinioides* and its synonym *C. delphinianus* regarding the *Scott-Elliot* 1557 specimen (P00133052, upper right), which was

also cited by Baillon (1891a) as a syntype of *C. lasiopyrus*. *Croton cassinioides* and *C. lasiopyrus* are sufficiently different that they are not easily confused; the former has smaller (1.5–6 × 0.7–3 cm) elliptic leaves with dentate to subentire margins and grows in littoral zones near sea level, while the latter has larger (4–15.5 × 2.5–7 cm) obovate leaves with entire margins and grows in moist montane forests.

80. *Croton lichenisilvae* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 62. 1939

Croton lichenisilvae var. *oligostemon* Radcl.-Sm., Gen. Croton Madag. Comoro 198. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Anony, Sihanaka, 3 Sep 1937, *Herb. Jard. Bot. Tan.* 2953 (holotype: P [P00131512]!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, environs d'Analamazaotra, s.d., 1000 m, *H. Perrier de la Bâthie* 9637 (lectotype, designated here: P [P00389499]!; islectotype: P [P00133451]!).

Habit and distribution. Shrubs; eastern montane Madagascar (Toamasina).

81. *Croton loucoubensis* Baill., Adansonia 1: 155. 1861, as 'loucoubense'

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

Type. Based on *Croton loucoubensis* Baill.

Croton adenophoroides Radcl.-Sm., Gen. Croton Madag. Comoro 117. 2016.

Type. MADAGASCAR. Prov. Antsiranana: Besinkara, Ambalafary, Andvakena: premier cours d'eau sur le chemin de Bekolosy, 14°04'S, 48°17'E, 500 m, 12 Nov 1994, *L. Gautier & P. Derleth* 2529 (holotype: K!; isotypes: G!, MO!, P [P00433174]!).

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Nossibé, forêt de Loucoubé, Mar 1851, *L.H. Boivin s.n.* (lectotype, designated by Kainulainen et al. 2017b, pg. 390: P [P00133453]!). MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Jun 1848, *L.H. Boivin* 3382 (syntype: P [P00133452]!).

Habit and distribution. Large shrubs or small trees; northern Madagascar (Antsiranana).

Notes. Leandri (1939) treated *Croton loucoubensis* as a synonym of *C. adenophorus*, but his concept of *C. adenophorus*, as shown in his key and description, conforms to the type of *C. loucoubensis* as treated here. The syntype of *C. loucoubensis* from Mayotte is sterile and cannot definitively be placed in this species; it could also potentially belong to *C. mayottae*.

82. *Croton macrobuxus* Baill., Bull. Mens. Soc. Linn. Paris 2: 863. 1890

Croton sambiranensis Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 41. 1939.

Type. MADAGASCAR. Prov. Antsiranana: Haut Sambirano, 500 m, Dec 1912, *H. Perrier de la Bâthie* 9699 (lectotype, designated here: P [P00133571]!; isolectotypes: P [P00133572]!, P [P00404491]!).

Croton macrobuxus var. *dolichobotrys* Radcl.-Sm., Gen. Croton Madag. Comoro 176. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatovy, NE of Moramanga, 18°51'07"S, 48°18'26"E, 28 Feb 1998, *G. McPherson* 17500 (holotype: K; isotype: MO!).

Croton macrobuxus var. *glandulifer* Radcl.-Sm., Gen. Croton Madag. Comoro 176. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatovy, 18°51'25"S, 48°17'50"E, 28 Feb 1997, *P. Rakotomalaza et al.* 1194 (holotype: K; isotype: MO, P [P00433501]!).

Croton macrobuxus var. *subfoliaceus* Radcl.-Sm., Gen. Croton Madag. Comoro 177. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Torotorofotsy R., Berano, 15 air-km NE of Moramanga, 11 km E of Antanambao, between Ambatovy-South & Analamay-East, 18°50'32"S, 48°19'55"E, 20 Feb 1997, *P. Rakotomalaza*, *G. Razafimanantsoa* & *F. Andriatsiferana* 1149 (holotype: MO!).

Croton macrobuxus var. *substrigosus* Radcl.-Sm., Gen. Croton Madag. Comoro 177. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antananarivo: Sambaina-Manjakandriana, Ankato-hazo, 29 Oct 1968, *R. Razafindrambao* H534R (holotype: P [P00154348]!).

Croton nitidulus var. *microphyllus* Radcl.-Sm., Gen. Croton Madag. Comoro 173. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Reserve Naturelle Marojejy, along the trail to the summit of Marojejy Est, 14°26'S, 49°15'E, 10 Oct 1988, *J. Miller et al.* 3524 (holotype: K!; isotype: MO!).

Croton nitidulus var. *pubescens* Radcl.-Sm., Gen. Croton Madag. Comoro 173. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Marojejy, N d'Andapa, 14°29'S, 49°38'E, coll. 21–22 Jan 1994, *F. Rasoavimbahoaka et al.* 30 (holotype: K!; isotype: MO!).

Type. MADAGASCAR. Madag. Centr., s.d., *R. Baron* 3063 (lectotype, designated here: K [K001040373]!; isolectotype: P [P00133472]!).

Habit and distribution. Shrubs; upland forests of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

Notes. Both *Croton nitidulus* var. *microphyllus* and *C. nitidulus* var. *pubescens* from high elevations in the Marojejy massif are smaller-leaved plants than most other specimens of *C. macrobuxus*. They should be studied in further detail to determine if they should be recognized as a distinct, related species.

83. *Croton maevaranensis* Leandri, *Adansonia*, sér. 2, 9: 501. 1970

Type. MADAGASCAR. Prov. Antsiranana: Massif de l'Ambohimirahavavy, rebord Sud du plateau de Marofamano, 6 Feb 1951, *Service des Eaux et Forêts de Madagascar* 984-SF (lectotype, designated here: P [P00389625]!; isolectotypes: K [K000422594]!, MO [sheet #04861162], P [P00389623]!, P [P00389624]!, TAN!, TEF [TEF000186]!).

Habit and distribution. Trees; northern and northwestern Madagascar (Antsiranana, Mahajanga).

84. *Croton manampetsae* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 25. 1939

Croton manampetsae var. *angustifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 27. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beza Mahafaly Reserve, near Betioky, 23°41'S, 44°35'E, 28 Oct 1987, *P.B. Phillipson* 2473 (holotype: K; isotypes: MO, P [P00133494]!).

Croton manampetsae var. *chaetogyne* Radcl.-Sm., Gen. *Croton* Madag. Comoro 27. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Fort Dauphin, Ranopiso, Manatalinjo, Réserve Naturelle Intégrale d'Andohahela, 24°49'S, 46°37'E, 26-30 Oct 1994, *S. Eboroke* 875 (holotype: K; isotypes: MO, P [P00433495]!).

Type. MADAGASCAR. Prov. Toliara: Lac Manampetsa, Apr 1933, *H. Perrier de la Bâthie* 19087 (lectotype, designated here: P [P00133491]!; isolectotypes: K [K001040386]!, P [P00133492]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. Except for *Croton manampetsae* var. *lepidotus* (see *Incertae Sedis* section), the varieties recognized by Radcliffe-Smith (2016) appear to be inconsequential forms of the same species, with minor variations in pubescence and leaf shape.

85. *Croton mauritianus* Lam., *Encycl.* 2: 206. 1786

Halecus mauritianus (Lam.) Raf., *Sylva Tellur.*: 62. 1838.

Type: Based on *Croton mauritianus* Lam.

Klotzschiphytum mauritianum (Lam.) Baill., *Étude Euphorb.*: 383. 1858.

Type: Based on *Croton mauritianus* Lam.

Oxydectes mauritiana (Lam.) Kuntze, *Revis. Gen. Pl.* 2: 612. 1891.

Type: Based on *Croton mauritianus* Lam.

Type. RÉUNION [FRENCH OVERSEAS DEPARTMENT]: Île de Bourbon, s.d., *P. Comerson* s.n. (holotype: P-LA [P00382069]!; isotypes: G-DC [G00311200]!),

G [G00446393]!, G [G00446394]!, MPU [MPU014846]!, MPU [MPU014847]!, MPU [MPU014848]!, P [P00121732]!, P [P00404317]!, P-JU Catal. 16377!, P [P00404321]!, P [P00404316]!, P [P00404318]!; possible isotypes, K [K001040358]!, P [P00404319]!, P [P00404320]!).

Habit and distribution. Large shrubs or small trees; restricted to the island of Réunion.

Notes. Lamarck clearly attributed this species to the Île de Bourbon, the former name of Réunion, so it is unclear why he named it “mauritanus.” At the time of Lamarck's publication, both Réunion (Île de Bourbon) and Mauritius (Île de France) were occupied by the French, and Réunion was administered out of Port Louis, Mauritius. So perhaps Lamarck used the name in a general sense for the islands administered out of Mauritius.

Croton mauritanus Lam. is the type of *Croton* sect. *Klotzschiphytum* Baill. (Baillon, 1861), which is one of the few described sections of *Croton* with an Old World species as its type.

86. *Croton mavoravina* Leandri, *Ann. Mus. Colon. Marseille, sér. 5*, 7(1): 25. 1939

Croton capuronii Leandri, *Bull. Soc. Bot. France* 103: 604. 1957 [‘1956’].

Type. MADAGASCAR. Prov. Toliara: Anosy Region: environs de Bevilany, route Ambovombe-Fort Dauphin, 23 Sep 1953, *R. Capuron 8493bis* (lectotype, designated here: P [P00312141]!; isolectotype: P [P00347487]!). MADAGASCAR. Prov. Toliara: environs de Fort Dauphin, près de Bevilany, 14 Sep 1928, *H. Humbert & C.F. Swingle 5673* (syntypes: G, K, P [P00133508]!).

Croton mavoravina var. *gracilis* Radcl.-Sm., *Gen. Croton Madag. Comoro* 31. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beza Mahafaly Reserve near Betioky, 23°40'S, 44°35'E, 5 Jan 1988, *P.B. Phillipson 2785* (holotype: K; isotypes: MO, P [P00133515]!).

Croton mavoravina var. *gymnolepis* Radcl.-Sm., *Gen. Croton Madag. Comoro* 31. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: District d'Amboasary, Canton de Tranomaro, Ambatomika, 25 May 1957, *G. Cours 5221* (holotype: P [P00133507]!).

Croton mavoravina var. *imanombensis* Radcl.-Sm., *Gen. Croton Madag. Comoro* 32. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Imanombo, Nov 1952, *J.M. Bosser 3837* (holotype: P [P00133495]!).

Croton mavoravina var. *rotundifolius* Radcl.-Sm., *Gen. Croton Madag. Comoro* 32. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Beza Mahafaly Reserve near Betioky, hills E of the Sakamena River, valley of the Ambinda stream, 23°40'S, 44°39'E, 26 Oct 1987, *P.B. Phillipson 2450* (holotype: K; isotypes: MO, P [P00133513]!).

Type. MADAGASCAR. Prov. Toliara: de Tsivory à Anadabolava, Mandrare moyen, 300-400 m, Dec 1933, *H. Humbert 12319* (lectotype, designated here: P [P00312342]!; isolectotype: P [P00133510]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. A fourth variety of *Croton mavoravina* that was described by Radcliffe-Smith (2016) as *C. mavoravina* var. *thysanolepis* is not part of this species at all, but rather is a synonym of *C. crossolepis*.

87. *Croton mayottae* P.E.Berry & Kainul., *Candollea* 72: 392. 2017

Croton regeneratrix var. *mayottensis* Radcl.-Sm., Gen. Croton Madag. Comoro 202. 2016.

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Rassi Maoussi, 30 m, 24 Apr 997, *O. Pascal 915* (holotype: K!; isotypes: BR, G!, K, MAO!, MO!, P [P00144592]!, WAG).

Type. MAYOTTE [FRENCH OVERSEAS DEPARTMENT]: Grande-Terre, Chiconi, village, 16 Jan 2001, *F. Barthelat, M'Changama & A.B. Sifary 225* (holotype: P [P00229211]!; isotypes: G!, K!, MAO!, MO!).

Habit and distribution. Shrubs; endemic to the island of Mayotte in the Comoro Islands.

88. *Croton menabeensis* Leandri, *Adansonia*, sér. 2, 12: 68. 1972

Croton subaemulans var. *minor* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 82. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: cause d'Ankara, Kamakama, Dec 1900, *H. Perrier de la Bâthie 9814* (lectotype, designated here: P [P00133377]!; isolectotype: P [P00133376]!). MADAGASCAR. Prov. Mahajanga: embouchure de la Soahanina, Tsiampihy, 15 Oct 1932, *J. Leandri 298* (syntypes: K [K001040361]!, P [P00133370]!).

Croton delicatulus Radcl.-Sm., Gen. Croton Madag. Comoro 20. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: station forestière d'Ampijoroa, ca. 3 km N d'Andranofasika, 16°20'S, 46°51'E, 8 Apr 1984, *L. Dorr & L. Koenders 2962* (holotype: P [P00131505]!; isotypes: K!, MO!).

Croton neoholstiifolius Radcl.-Sm., Gen. Croton Madag. Comoro 120. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Tsingy de Bemaraha, Antsalova-Tsiandro Berano, 18°39'S, 44°44'E, 24 Nov 1992, *J. Labat, T. Deroin, R. Edmond, H. Rabarion & O. Laivao 2153* (holotype: K!; isotype: P [P05606030]!).

Type. MADAGASCAR. Prov. Mahajanga: Antsingy, vers Andobo (E d'Antsalova), vers Tsiandro, 300 m, 5-8 Feb 1960, *J. Leandri & P. Saboureaux 3021bis* (lectotype, designated here: P [P00389507]!; isolectotype: P [P00132918]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga, Toliara).

89. *Croton menarandrae* Leandri, *Adansonia*, sér. 2, 10: 189. 1970

Croton menarandrae var. *pubescens* Radcl.-Sm., Gen. *Croton* Madag. Comoro 87. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Environs d'Ampandrandava, entre Bekily et Tsivory, Oct 1942, *A. Seyrig 139bis* (holotype: P [P00154452]!).

Type. MADAGASCAR. Prov. Toliara: Berge Menarandra, Ampanihy, 25 Sep 1953, *Service Forestier 8273* (lectotype, designated here: P [P00347525]!; isolectotypes: P [P00132921]!, TEF [TEF000187]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

90. *Croton meridionalis* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 59. 1939

Croton sublinearis Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 60. 1939.

Type. MADAGASCAR. Prov. Toliara: Lahimanara, env. d'Ambovombe, 8 Jun 1931, *R. Decary 8991* (holotype: P [P00133597]!; isotypes: G [G00018136]!, K [K001040363]!, S [S07-16870], TAN).

Croton tranomarensis Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 60. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Anosy Region, Tranomaro, au NE d'Ambovombe, 19 Jun 1931, *R. Decary 9022* (lectotype, designated here: P [P00133389]!; isolectotypes: G [G00018135]!, K [K001040392]!, S [S07-16871], TAN [TAN000544]).

Croton meridionalis var. *pseudolepidotus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 194. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: 47–49 km SE of Ihosy on the road to Ivo-hibe, 5 Nov 1967, *L. Bernardi 11179* (holotype: K!; isotypes: G!, P [P00154376]!).

Type. MADAGASCAR. Prov. Toliara: bassin supérieur du Mandrare (Sud-Est), vallée de la Manombolo, 300–400 m, 23–24 Nov 1928, *H. Humbert 6798* (lectotype, designated here: P [P00132930]!; isolectotypes: G [G00018153]!, P [P00132929]!). MADAGASCAR. Prov. Toliara: plateaux et vallées de l'Isalo, environs de Fanjahira 300–600 m, 9–12 Oct 1924, *H. Humbert 2737* (syntype: P [P00132928]!). MADAGASCAR. Prov. Toliara: Vallée de l'Onilahy, aux environs de Tongobory, 100–200 m, 1–8 Oct 1924, *H. Humbert 2737* (syntypes: G [G00018154]!, P [P00132927]!).

Habit and distribution. Shrubs; southern Madagascar (Fianarantsoa, Toliara).

Notes. Most individuals of this species have pairs of falcate, foliaceous, clasping stipules and stellate pubescence. Plants with similar stipules, but usually broader and more silvery-lepidote lower leaf surfaces were described under *Croton meridionalis* var. *latifolius* and *C. meridionalis* var. *stipularis*, which may represent a different species (see *Incertae Sedis*).

91. *Croton miarensis* Leandri, *Adansonia*, sér. 2, 9: 504. 1970

Croton peltieri Leandri, *Adansonia*, sér. 2, 10: 184. 1970, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Lac Manampetsa ("Tsimanampetsotsa"), 23 Oct 1940, *R. Decary 16060* (lectotype, designated here: P [P00338571]!; isolectotypes: P [P00154280]!, P [P00154281]!).

Croton peltieri var. *hazofotsiensis* Radcl.-Sm., Gen. *Croton* Madag. Comoro 74. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Hazofotsy Reserve 11, 28 Apr 1971, *A. Richard 123* (holotype: K!).

Croton miarensis var. *monadenius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 76. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Cap Sainte-Marie et environs Nord du Cap, 17 Dec 1968, *Service Forestier 28552-SF* (lectotype, designated here: P [P00154277]!; isolectotype: P [P00154276]!).

Type. MADAGASCAR. Prov. Toliara: Miari, Nov 1956, *J. Bossier 10492* (holotype: P [P00312379]!, isotype TAN!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. This is a very distinctive species from southern Madagascar with silvery, ovate, long-petiolate leaves that usually have a single acropetiole gland. It is also very unusual in having 1- or 2-locular capsules, and the branching is strongly dichotomous. All of the taxa placed here in synonymy share these features.

92. *Croton milanjensis* Leandri, *Adansonia*, sér. 2, 12: 66. 1972

Type. MADAGASCAR. Prov. Mahajanga: Milanja, près de Soalala, 18 Nov 1954, *Conservation de Réserves Naturelles 6863RN* (holotype: P [P00389506]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

93. *Croton minimarginiglandulosus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 18. 2016.

Croton fianarantsoae var. *ambremontanus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 153. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: National Park of Montagne d'Ambre, path from station to Bianamalao, 12°32'S, 49°10'E, 1120 m, 4 Jun 1989, *B. Du Puy, D. Du Puy, & G. Guy 218* (holotype: K!; isotype: P [P00060699]!).

Croton ivohibensis var. *aesculops* Radcl.-Sm., Gen. *Croton* Madag. Comoro 148. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Reserve Spéciale d'Ankarana, 12°54'43"S, 49°06'39"E, 19 Feb 1994, *M. Andrianarisata et al.* 43 (holotype: K!; isotypes: MO!, P [P00433266]!).

Croton ivohibensis var. *ankaranaensis* Radcl.-Sm., Gen. Croton Madag. Comoro 148. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Reserve Naturelle Intégrale d'Ankarana, 12°51'S, 49°05'E, 18 May 1987, *M. Nicoll & J.P. Abraham* 684 (holotype: K!; isotypes: MICH [MICH1514788]!, MO!, P [P00133271]!).

Croton thouarsianus var. *macrocalyx* Radcl.-Sm., Gen. Croton Madag. Comoro 183. 2016, **syn. nov.**

Type. MADAGASCAR. Antsiranana: Ankarana Reserve, Tsingy area, 12°54'42"S, 49°06'42"E, 22 May 1993, *C.C.H. Jongkind & S. Rapanarivo* 960 (holotype: K!; isotypes: MICH [MICH1514787]!, MO!, P [P00433151]!).

Type. MADAGASCAR. Prov. Antsiranana: au sud d'Antsiranana, près de Joffreville dans le Parc National de Montagne d'Ambre, 12°27'S, 49°13'E, 3–10 Aug 1993, *O. Andriantoanina & Rocseohclher* 283 (holotype: K!; isotype: MO!).

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

Notes. This species is restricted to Montagne d'Ambre and tsingy habitats in the Ankarana Special Reserve. It has somewhat anisophyllous terminal leaves like *C. thouarsianus*, but the calyx of the pistillate flowers is much larger and more accrescent in fruit, with a long pedicel. Plants vary considerably in pubescence, with some hirsute stems in the type of *C. thouarsianus* var. *macrocalyx*. Quoting from Radcliffe-Smith (2016), “The admittedly rather cumbersome name, of 10 syllables & 24 letters, can be justified on the grounds of the distinctive minute ogivaliform marginal glands to be found on the otherwise entire leaf-margins of this species. The name is not occupied in the genus.” No surprise there!

94. *Croton mocquersii* Aug.DC., Bull. Herb. Boissier, sér. 2, 1: 565. 1901, as ‘*moquersii*’

Type. MADAGASCAR. Prov. Toamasina: Maroa [Maroantsetra], forêts à l'intérieur de la baie d'Antongil, 1897, *A. Mocquers* 256 (holotype: G [G00018152]!; isotype: Z [Z-000015988]!).

Habit and distribution. Shrubs or small trees; eastern lowland Madagascar (Antsiranana, Toamasina).

95. *Croton mongue* Baill., Adansonia 1: 158. 1861

Oxydectes mongue (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton mongue* Baill.

Croton oreades Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 72. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Analamazaotra, 800 m, Dec, *H. Perrier de la Bâthie* 5287 (lectotype, designated here: P [P00389513]!; isolectotypes: P [P00389512]!, P [P00389514]!). MADAGASCAR. Prov. Fianarantsoa: haute vallée de la Rienana, province de Farafangana, 3 Oct 1926, *R. Decary* 5563 (syntypes: K [K001040348]!, P [P00133687]!). MADAGASCAR. Prov. Fianarantsoa: Sud-Est de Fianarantsoa, 1000-1200 m, 27 Oct 1926, *R. Decary* 5842 (syntypes: P [P00133688]!, S [S07-17117]!).

Croton oreades var. *occidentalis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 73. 1939, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: plateau de Miangaka [Marangaka, Ankaizina], 1000 m, Dec 1922, *H. Perrier de la Bâthie* 15130 (lectotype, designated here: P [P00133691]!; isolectotype: P [P00133690]!).

Croton mongue var. *vatambensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 72. 1939.

Type. MADAGASCAR. Prov. Toliara: Vatambe, Fort-Dauphin, 7 Sep 1932, *R. Decary* 10601 (holotype: P [P00132950]!, isotypes: K [K001040389]!, TAN [TAN000537]!).

Croton mongue var. *borealis* Radcl.-Sm., Gen. Croton Madag. Comoro 131. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Réserve Naturelle Intégrale no. 12 de Marojejy, le long d'un affluent de la rivière Manantenina, 11 km NW de village Manantenina, 14°26'S, 49°44'E, 1220 m, 27 Oct 1996, *P.J. Rakotomalaza, N. Messmer & D. Ravelonarivo* 793 (holotype: K!; isotypes: MO!, P [P00433430]!).

Croton oreades var. *borealis* Radcl.-Sm., Gen. Croton Madag. Comoro 132. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Mahajanga: Befandriana-Nord, Matsoandakana, Réserve Spéciale Anjanaharibe-Sud, village d'Anjiamazava, suivant la route Nationale d'Andapa-Bealanana, piste vers le Nord approchant le sommet de Bevitsika, 14°42'S, 49°27'E, 1100 m, 14 Dec 1994, *D. Ravelonarivo & R. Rabesonina* 551 (holotype: K!; isotype: MO!).

Croton oreades var. *craspedadenius* Radcl.-Sm., Gen. Croton Madag. Comoro 132. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Andapa, Ambalamanasy II, Andasibe Kobahina, suivant la piste entre Andasibe Kobahina et Andranovola, dans la Réserve Naturelle Intégrale de Marojejy, 14°31'S, 49°38'E, 603 m, 1-3 Feb 1994, *F. Ras-oavimbahoaka et al.* 86 (holotype: K!; isotypes: MO!, P [P00433034]!).

Croton oreades var. *periphoradenius* Radcl.-Sm., Gen. Croton Madag. Comoro 133. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Ampamaherana, 29 Sep 1949, *Service Forestier* 2033-SF (holotype: P [P00132967]!).

Type. MADAGASCAR. sin. loc., s.d., *L.A. Chapelier s.n.* (lectotype, designated here: P [P00132944]!; isolectotype: P [P00132945]!).

Habit and distribution. Trees; montane forests of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

Notes. It is surprising to us that neither Leandri (1939) nor Radcliffe-Smith (2016) realized that *Croton oreades* is not distinct from *C. mongue*. This is the largest tree species among Malagasy *Croton*, and it is widespread in moist, montane forests.

96. *Croton multicostatus* Müll.Arg., *Linnaea* 34: 79 (1865)

Oxydectes multicostata (Müll.Arg.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type: Based on *Croton multicostatus* Müll.Arg.

Croton vernicosus Baker in J. Linn. Soc., Bot. 22: 519. 1887.

Type. MADAGASCAR. sin. loc., s.d., *R. Baron* 4935 (lectotype, designated here: K [K000347500]!), isolectotype: K [K000347498]!).

Croton sclerodorus Baill., Bull. Mens. Soc. Linn. Paris 2: 968. 1891, as ‘*sclerodorum*’.

Type. Madagascar. sin. loc., s.d., *R. Baron* 4735 (holotype: P [P00133318]!).

Type. MADAGASCAR. Prov. Toliara: Fort Dauphin, no collector indicated, (holotype: P-JU [Catalogue # 16338]!; isotype: *Madagascar j. maur.* No. 39, P-LA [P00382066]!).

Habit and distribution. Large shrubs or small trees; southeastern Madagascar (Toliara, possibly also in Fianarantsoa).

Notes. See Berry and Van Ee (2011) for a discussion of how Müller (1865) mistook the type locality of *Croton multicostatus* for the Caribbean (Hispaniola) rather than for Madagascar. In that paper, we attributed both the P-JU and P-LA sheets as being a Philibert Commerson collection, but more likely these were collected by Franz Wilhelm Sieber, who visited Madagascar between 1822 and 1825, and included them under his series “j. maur.”, as indicated on the P-LA sheet.

97. *Croton muricatus* Vahl in E.F.Geiseler, *Croton. Monogr.*: 47. 1807

Oxydectes muricata (Vahl) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton muricatus* Vahl in E.F.Geiseler

Croton denisii Leandri, Bull. Mus. Natl. Hist. Nat., sér. 2, 3: 367. 1931, as ‘*denisi*’, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Behara, 9 Jul 1926, *R. Decary* 4320 (holotype: P [P00389632]!).

Croton bastardii var. *meridionalis* Radcl.-Sm., Gen. Croton Madag. Comoro 204. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Antanimora, Dec 1959, *J. Bosser* 13913 (holotype: P [P00133042]!; isotype: [P00133041]!).

Croton decaryi var. *subglaber* Radcl.-Sm., Gen. Croton Madag. Comoro 124. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Antanimora, Dec 1959, *J. Bosser* 13913 (holotype: P [P00133041]!; isotype: P [P00133042]!).

Type. MADAGASCAR. sin. loc., s.d., *P. Commerson* s.n. (holotype: P-JU [Catal. # 16373]!), isotype: P [P00312343]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. Different sheets of the same collection were designated as types of *Croton bastardii* var. *meridionalis* and *C. decaryi* var. *subglaber* by Radcliffe-Smith (2016). Both clearly belong to the Adenophorus Group and are placed here in synonymy.

98. *Croton myriaster* Baker, J. Bot. 20: 268. 1882

Croton calomeris Baill., Bull. Mens. Soc. Linn. Paris 2: 860. 1890.

Type. MADAGASCAR. Madag. centr., s.d., *R. Baron* 5929 (lectotype, designated here: P [P00132997]!; isolecotypes: K [K001040364]!, P [P00132998]!).

Croton myriaster var. *austromadecassus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 58. 1939, as '*austromadecassa*'.

Type. MADAGASCAR. Prov. Fianarantsoa: Pic d'Ivohibe (Bara), 1500-2000 m, 5-11 Nov 1924, *Humbert* 3198 (lectotype, designated here: P [P00224708]!; isolecotypes: P [P00338294]!, TAN [TAN000538]!). MADAGASCAR. Prov. Fianarantsoa: Befotaka (Prov. de Farafangana), 20 Aug 1926, *R. Decary* 5147 (syntype: P [P00133001]!). MADAGASCAR. Prov. Fianarantsoa: Massif d'Andringitra, 1700 m, Sep 1911, *H. Perrier de la Bâthie* 9762 (syntype: P [P00133016]!). MADAGASCAR. Prov. Fianarantsoa: haute vallée de la Rienana (Bassin du Matitanana), 1000-1400 m, 18-22 Nov 1924, *H. Humbert* 3624 (syntype: P [P00133005]!). MADAGASCAR. Prov. Toliara: Massif du Beampingaratra, vallée de la Maloto, 800-1500 m, 31 Oct-1 Nov 1938, *H. Humbert* 6328 (syntypes: P [P00133008]!, US [US01050275]!). MADAGASCAR. Prov. Toliara: Massif de l'Andohahela, 1800-1979 m, 21-22 Oct 1928, *H. Humbert* 6213 (syntype: P [P00133007]!). MADAGASCAR. Prov. Fianarantsoa: Massif de l'Ikongo (Prov. de Farafangana), 17 Oct 1926, *R. Decary* 5692 (syntype: P [P00133002]!). MADAGASCAR. Prov. Fianarantsoa: Massif de l'Ikongo (Prov. de Farafangana), 17 Oct 1926, *R. Decary* 5779 (syntype: P [P00133003]!).

Croton regeneratrix var. *ranomafanae* Radcl.-Sm., Gen. Croton Madag. Comoro 202. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: W of Ranomafana, Parc National Ranomafana, 21°16'S, 47°28'E, 900-1100 m, 8-10 Sep 1992, *S. Malcomber & R. Rakoto* 1551 (holotype: K!; isotype: MO!).

Type. MADAGASCAR. sin. loc., s.d., *R. Baron* 223 (lectotype, designated here: K [K000422585]!; isolecotypes: [K000422584]!; P [P00132995]!).

Habit and distribution. Trees; montane forests of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

99. *Croton nitidulus* Baker, J. Linn. Soc., Bot. 20: 253. 1883

Croton microprunus Baill., Bull. Mens. Soc. Linn. Paris 2: 861. 1890.

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Didy, 14 Aug 1889, *L.D.M. Catat 1812* (holotype: P [P00132942]!).

Croton macrochlamys Baill., Bull. Mens. Soc. Linn. Paris 2: 863. 1890.

Type. MADAGASCAR. sin. loc., s.d., *R. Baron 4074* (holotype: K [K001040393]!).

Croton fuscirameus Baill., Bull. Mens. Soc. Linn. Paris 2: 927. 1891.

Type. MADAGASCAR. “Central Madagascar, received Dec 1883, *R. Baron 2988* (lectotype, designated here: K [K001040379]!; isolectotype: P [P00154398]!).

Croton nitidulus var. *meridionalis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 39. 1939.

Type. MADAGASCAR. Prov. Fianarantsoa: Chaîne du Vohibory, à l'Ouest d'Ivohibe, 1000–1300 m, 1 Nov 1924, *H. Humbert 3051bis* (lectotype, designated here: P [P00133622]!; isolectotypes: G [G00446406]!), K [K001040388, K001040390]!).

MADAGASCAR. Prov. Fianarantsoa: haute vallée de l'Iantara, bassin du Manampatra, 500–800 m, 16–17 Nov 1924, *H. Humbert 3433* (syntype: P [P00133623]!).

Croton nitidulus var. *parvifolius* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 39. 1939, as '*parvifolia*'.

Type. MADAGASCAR. Prov. Antsiranana: Analamahitso (haut Bemarivo), 1000 m, Aug 1907, *H. Perrier de la Bâthie 9534* (holotype: P [P00133648]!).

Croton nitidulus var. *spatulatus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 40. 1939, as '*spatulata*'.

Type. MADAGASCAR. Prov. Toamasina: Bassin de l'Onive, Mangoro, forêt d'Andasibe, 1000 m, Nov 1911, *H. Perrier de la Bâthie 9659* (lectotype, designated here: P [P00133626]!; isolectotypes: P [P00133627]!, P [P00133628]!).

Croton nitidulus var. *fuscirameus* (Baill.) Radcl.-Sm., Gen. Croton Madag. Comoro 171. 2016.

Type. Based on *Croton fuscirameus* Baill.

Croton bracteatus subsp. *manongarivensis* Radcl.-Sm., Gen. Croton Madag. Comoro 137. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Manongarivo Massif, above Ambodisa-koana, E of Ankaramy, 14°05'S, 48°20'E, 17 Oct 1994, *G. McPherson & H. van der Werff 16377* (holotype: K!; isotype: MO!).

Croton nitidulus subsp. *angustiglans* Radcl.-Sm., Gen. Croton Madag. Comoro 170. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Route d'Anjiroro-Moramanga (M28), Nov 1938, *G. Cours 813* (holotype: P [P00148095]!).

Croton nitidulus subsp. *bekolosiensis* Radcl.-Sm., Gen. Croton Madag. Comoro 170. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antsiranana: Réserve Spéciale de Manongarivo, R. Bekolosy, 1180 m, 14°02'S, 48°18'E, 16 May 1995, *L. Gautier & C. Chatelain LG2681* (holotype: K!; isotype: G!).

Type. MADAGASCAR. Madag. Centr., s.d., *R. Baron 1302* (lectotype, designated here: K [K000347491]!; isoelectotype: P [P00133607]!). MADAGASCAR. Madag. Centr., s.d., *R. Baron 1349* (syntypes: K [K000347490]!, P [P00133610]!, P [P00133611]!).

Habit and distribution. Shrubs; montane forests of eastern and central Madagascar (Antsiranana, Antananarivo, Fianarantsoa, Toamasina, Toliara).

100. *Croton nobilis* Baill., *Adansonia* 1: 148. 1861, as ‘*nobile*’

Oxydectes nobilis (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton nobilis* Baill.

Type. MADAGASCAR. sin. loc., s.d., *L.M.A. Dupetit-Thouars s.n.* (lectotype, designated here: P [P00133651]!; isoelectotypes: P [P00133652]!, P [P00312353]!). MADAGASCAR. Prov. Toliara: Anosy Region, southern slopes of Col de Maningotry, road to Ranomafana, 150 m, 16 Feb 2009, *B. van Ee, P.E. Berry, B.L. Dorsey & H. Razanatsoa 938* (epitype, designated here: MICH [MICH1514784]!; additional duplicates: MO, P, TAN).

Habit and distribution. Trees; submontane moist forests of southeastern Madagascar (Toliara).

Notes. The existing syntypes of *Croton nobilis* at P are all large-leaved (most around 18 × 7 cm), sterile branches. They are consistent with oversized sucker shoots that can sometimes be found on basal growth or regrowth of cut trees. The leaves on these specimens also resemble sucker leaves of *C. chrysodaphne*, which comes from eastern coastal Madagascar. However, Baillon (1861) clearly stated in the protologue that the staminate flowers of *C. nobilis* have five petals (the normal state in *Croton*), whereas *C. chrysodaphne* usually has ten (Berry et al. 2011). Also, the pistillate sepals of *C. chrysodaphne* are described by Baillon (1861) as being oblong and entire, whereas those of *C. nobilis* are broad, squat, and reduplicate (Berry, pers. obs.). The lectotype chosen here contains a packet labeled “Flores,” with only a small fragment of an inflorescence with an irregularly flattened and straight rachis, but lacking any recognizable floral parts that can be reconstructed. The inflorescences of *C. chrysodaphne* tend to be more slender, subterete, and curved, and this fragment does not fit that profile. Finally, Du Petit-Thouars spent six months in the Fort Dauphin area between 1792 and 1793 (Dorr 1997), so this would be consistent with the limited localities where *C. nobilis* occurs to the northwest of Fort Dauphin. We therefore conclude that the Dupetit-Thouars collections are consistent with the tree species that has subsequently been collected in moist, mid-elevation forests in the area that is now part of Andohahela National Park, named *C. nobilis*. To stabilize better this concept of *C. nobilis*, we designate here a modern epitype that has also been photographed *in situ* (viz., Fig. 1B) and sequenced for molecular phylogenetic studies (Haber et al. 2017).

101. *Croton noronhae* Baill., *Adansonia* 1: 162. 1861

Oxydectes noronhae (Baill.) Kuntze, Revis. Gen. Pl. 2: 612. 1891.

Type. Based on *Croton noronhae* Baill.

Type. MADAGASCAR. Prov. Toamasina: Côte est, s.d., *L.A. Chapelier s.n.* (lecto-type, designated here: P [P00133669]!; isolectotypes: MPU [MPU014849]!, P [P00133668]!). MADAGASCAR. Prov. Toamasina: Foulpointe, *F. Noronha s.n.* (syntypes: G [G00018150]!, G-DC [G00311743]; ibid. loc., *W. Bojer s.n.* (syntypes: K [K001040398]!, P [P00133664]!). MADAGASCAR. sin. loc., *L.M.A. Du Petit-Thouars s.n.* (syntypes: P [P00133680]!, P [P00133681]!).

Habit and distribution. Shrubs; eastern coastal Madagascar (Fianarantsoa, Toamasina).

Notes. A *Bojer s.n.* specimen at G-DC (G00311742) has a label that states “Insula Mauritius, M. Bojer 1833,” and is indicated as a type. The only Bojer specimen cited in the protologue of *Croton noronhae* (Baillon 1861) is identified as being from Foulpointe, Madagascar, and is cited from P (“h. Mus.”). Although the Geneva specimen appears to be correctly identified as *C. noronhae*, that species is not known from Mauritius. Perhaps it was from a plant native to Madagascar that was cultivated in Mauritius, as was the case with the type of *C. anisatus*.

102. *Croton nudatus* Baill., *Adansonia* 1: 168. 1861, as ‘*nudatum*’

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

Type. Based on *Croton nudatus* Baill.

Croton boivinanus var. *brevifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 12. 2016.

Type. MADAGASCAR. Prov. Antsiranana: Fivonandra Antsiranana II, 79 km au Sud d’Antsiranana par route RN6, et 15 km à l’Est de l’ancien chantier du Colas à Marotaolana, Campement à l’Est du village d’Ampantsona, 12°51'20"S, 49°18'10"E, 394–551 m, 3–6 Jun 1997, *O. Andrianantoanina & R. Bezara* 1068 (holotype: K!; isotypes: G!, MO!, P [P00433267]!).

Croton hirsutissimus Radcl.-Sm., Gen. Croton Madag. Comoro 99. 2016.

Type. MADAGASCAR. Prov. Antsiranana: versant Est du Massif de l’Ankerana (partie S du Massif de Mafokovo, au N de Vohémar), 50–400 m, 17 Dec 1966, *Service Forestier 27363-SF* (holotype: P [P00154439]!).

Croton menabeensis var. *furfuraceus* Radcl.-Sm., Gen. Croton Madag. Comoro 101. 2016.

Type. MADAGASCAR. Prov. Mahajanga: Sofia Region, Antsohihy District, Antsatanana, Bora, 17 Jul 1970, *Service Forestier 30011* (holotype: P [P00154438]!).

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Baie de Diego-Suarès, Dec 1848, *L.H. Boivin* 2659 (holotype: P [P00389498]!). MADAGASCAR. Prov. Antsiranana:

Diana Region, Antsiranana II, Orangea, road going uphill from military checkpoint at entrance to Orangea, 12°14'08"S, 49°21'40"E, 50 m, 25 Oct 2009, *B. van Ee, P.E. Berry, K.J. Wurdack, E.A. Haber & H. Razafindraibe 1081* (epitype, designated by Kainulainen et al. 2017b, pg. 374: MICH [MICH1517189]!; additional duplicate: TAN).

Habit and distribution. Shrubs; northern and western Madagascar (Antsiranana, Mahajanga).

103. *Croton orangeae* Kainul. & P.E.Berry, *Candollea* 72: 394. 2017

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Ramena, Ankorikakely, Baie des Sakalava, 12°16'40"S, 49°23'01"E, 25 m, 9 Dec 2004, *J. Razafitsalama et al. 692* (holotype: MICH [MICH1517188]!; isotypes: CNARP, MO!, P [P05484901]!, TAN).

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

104. *Croton plurispicatus* P.E.Berry, Kainul. & B.W.van Ee, *Candollea* 71: 342. 2016

Type. MADAGASCAR. Prov. Toamasina. Alaotra-Mangoro Region: Moramanga District, in primary moist montane forest along road heading south from highway Route Nationale 2 towards Lakato, ca 9.8 km south by line-of-sight from RN 2, 19°03'05"S, 48°21'32"E, 1030-1060 m, 13 Aug 2015, *B. van Ee, P.E. Berry & H. Razafindraibe 2198* (holotype: MICH [MICH1513198]!; isotypes: MAPRI, MO!, MICH [MICH1513199]!, P! TAN!).

Habit and distribution. Large shrubs or small trees; montane forests of eastern Madagascar (Toamasina).

105. *Croton promunturii* Leandri, *Adansonia*, sér. 2, 10: 187. 1970

Type. MADAGASCAR. Prov. Toliara: Cap Sainte Marie, 1-150 m, 5-7 Mar 1955, *H. Humbert & R. Capuron 29220* (lectotype, designated here: P [P00312372]!; isolectotypes: K [K000422596]!, P [P00389510], P [P00389511]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

106. *Croton radiatus* P.E.Berry & Kainul., *Candollea* 71: 339. 2016 [23 Nov 2016]

Croton dasygyne Radcl.-Sm., Gen. *Croton* Madag. Comoro 19. 2016 [23 Dec 2016], **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Chutes du Maningory, Lac Alaotra, s.d., *Herb. Jard. Bot. Tan. 3769 (S-39)* (holotype: P [P00131514]!).

Type. MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region, Moramanga District, Commune Ambohibary, Fokontany Ampitambe, forêt Sahaevo, 18°49'59"S, 48°17'47"E, 1118 m, 11 Dec 2006, *J. Razanatsoa & T. Marcellin* 279 (holotype: MICH [MICH1458525]!; isotypes: MO!, TAN!).

Habit and distribution. Shrubs; eastern montane forests of Madagascar (Toamasina).

107. *Croton rakotoniainii* Leandri, *Adansonia*, sér. 2, 13: 295. 1973, as '*rakotonianii*'

Type. MADAGASCAR. Prov. Antsiranana: Ampitambarimena, Antalaha, 14 Mar 1955, *Réserves Naturelles de Madagascar (Rakotoniaina)* 7057 (lectotype, designated here: P [P00312373]!; isolectotypes: G [G00190674]!, K [K000422597]!, MO [sheet #04861160]), P [P00404493]!, P [P00404494]!).

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

Notes. The lectotype was annotated in Leandri's hand as "*Croton rakotoniainii*", which is in accord with the collector's actual surname, so the spelling is corrected here from the variant it was published as.

108. *Croton regeneratrix* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 62. 1939

Croton regeneratrix var. *perrierianus* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 64. 1939, as '*perrieriensis*'.

Type. MADAGASCAR. Prov. Antananarivo: planté près d'Ambatolampy, provenant de l'Ankaratra, May 1921, *H. Perrier de la Bâthie* 13769 (lectotype, designated here: P [P00133537]!; isolectotype: P [P00133538]!).

Type. Madagascar. Prov. Fianarantsoa: versant nord du Pic d'Ivohibe, 1200–1400 m, 28 Sep 1926, *R. Decary* 5708 (lectotype, designated here: P [P00133532]!; isolectotypes: K [K000422586]!, P [P00394468]).

Habit and distribution. Trees; montane forests of central Madagascar (Antananarivo, Fianarantsoa).

109. *Croton sahafariensis* Kainul. & P.E.Berry, *Candollea* 72: 395. 2017

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, 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 Oct 2009, *B. van Ee, P.E. Berry, K.J. Wurdack, E.A. Haber, H. Razafindraibe & L.J. Razafitsalama* 1089 (holotype: MICH [MICH1517187]!; isotypes: P!, TAN).

Habit and distribution. Shrubs; northern Madagascar (Antsiranana).

110. *Croton sakamaliensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 54. 1939

Croton sakamaliensis var. *microphyllus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 55. 1939, as '*microphylla*'.

Type. MADAGASCAR. Prov. Toliara: vallée de la Manambolo, rive gauche (Bassin du Mandrare) aux environs d'Isomono (confluent de la Sakamalio), Monts Kotriha et Isomonobe, 400-600 m, Dec.1933-Jan 1934, *H. Humbert 12826* (lectotype, designated here: P [P00133552]!; isolectotypes: K [K001040361]!, P [P00133551]!, P [P00133553]!).

Type. MADAGASCAR. Prov. Toliara: Vallée de Sakamalio, affluent de la Manambolo (Bassin du Mandrare), 500-800 m, Dec 1933, *H. Humbert 13322* (lectotype, designated here: P [P00389497]!; isolectotype: P [P00133549]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

111. *Croton salviformis* Baill., Bull. Mens. Soc. Linn. Paris 2: 926. 1891

Croton salviformis var. *rufopunctatus* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 57. 1939, as '*rufopunctata*'.

Type. MADAGASCAR. Prov. Toliara: Atsimo-Andrefana Region, du lac Manampetsa au delta de la Linta (côte Sud-Ouest), au N d'Itampolo, 1-10 m, 24-28 Aug 1928, *H. Humbert & C.W. Swingle 5380* (lectotype, designated here: P [P00133569]!; isolectotype: TAN [TAN000541]!). MADAGASCAR. Prov. Toliara: Atsimo-Andrefana Region, du lac Manampetsa au delta de la Linta, 1-10 m, 17-24 Aug 1928, *H. Humbert & C.W. Swingle 5297* (syntypes: G [G00446401]!, K [K001040367]!, P [P00133567]!, P [P00133568]!).

Type. MADAGASCAR. Prov. Toliara: Anosy Region, Fort-Dauphin, s.d., *G.F. Scott-Elliot 2990* (holotype: P [P00133566]!, isotype: K [K000422583]!).

Habit and distribution. Shrubs; southern Madagascar (Toliara).

112. *Croton scoriarum* Leandri, Adansonia, sér. 2, 12: 68. 1972

Croton bathianus var. *ambatondrazakae* Radcl.-Sm., Gen. Croton Madag. Comoro 114. 2016.

Type. MADAGASCAR. Prov. Toamasina: Menaloha (G-3), Distr. d'Ambatondrazaka, Nov 1937, *G. Cours 587* (holotype: P [P00127483]!).

Type. MADAGASCAR. Prov. Antsiranana-Mahajanga border: Centre, au lieu dit Analankeboka, à l'Ouest de Bealanana, 20 Nov 1966, *Service Forestier 27107-SF* (lectotype,

designated by Kainulainen et al. 2017b, pg. 398: P [P00706283]!; isoelectotypes: K [K000895678]!, P [P00706284]!, TEF [TEF000183]!).

Habit and distribution. Shrubs or small trees; northern and central Madagascar (Antsiranana, Mahajanga, Toamasina).

113. *Croton stanneus* Baill., Bull. Mens. Soc. Linn. Paris 2: 850. 1890, as ‘*stanneum*’

Croton perrieri Leandri, Bull. Mus. Natl. Hist. Nat., sér. 2, 3: 369. 1931.

Type. MADAGASCAR. Prov. Mahajanga: Le Berizoka [Beritsoka], Oct 1897, *H. Perrier de la Bâthie* 353 (lectotype, designated by Kainulainen et al. 2017b, pg. 378: P [P00404485]!; isoelectotypes: K [K001040360]!, P [P00404484], P [P00404486]!, P [P00404487]!).

Croton baldauffii Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 55. 1939, as ‘*baldauffi*’.

Type. MADAGASCAR. Prov. Toliara: forêt de Besomaty, entre le Fiherenana et l’Isahena (Mangoky), 750–800 m, Oct 1933, *H. Humbert* 11249 (lectotype, designated by Kainulainen et al. 2017b, pg. 378: P [P00301487]!; isoelectotype: P [P00127468]!).

Croton ikopae Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 83. 1939.

Type. MADAGASCAR. Prov. Antananarivo: Analamanga Region, vallée de l’Ikopa, au NW d’Ankazobe, 15 Mar 1930, *R. Decary* 7554 (lectotype, designated by Kainulainen et al. 2017b, pg. 378: P [P00154394]!; isoelectotypes: K [K001040362]!, P [P00154395]!, P [P00154396]!, P [P00154397]!).

Croton crocodilorum var. *platyaster* Radcl.-Sm., Gen. Croton Madag. Comoro 112. 2016.

Type. MADAGASCAR. Prov. Toliara: forêt du Zombitsy, près de Sakaraha, Mar 1960, *M. Keraudren* 510 (holotype: P [P00154485]!).

Croton parvifructus Radcl.-Sm., Gen. Croton Madag. Comoro 122. 2016.

Type. MADAGASCAR. Prov. Toliara: Forêt de Zombitsy, au NE de Sakaraha (150 km NE Tuléar), 600–800 m, 2 Nov 1960, *J. Leandri* & *J. Ratoto* 3605 (holotype: P [P00132992]!).

Croton stanneus var. *hirsutus* Radcl.-Sm., Gen. Croton Madag. Comoro 64. 2016.

Type. MADAGASCAR. Prov. Fianarantsoa. Andranovola, near Lomanosiny, Antambohobe Canton, Ivohibe District, 13 Aug 1967, *Service Forestier* 26381 (holotype: P [P00133592]!).

Type. MADAGASCAR. “Madag. centr.”, received Nov 1885, *R. Baron* 3382 (holotype: K [K001040368]!, isotype: P [P00133580]!).

Habit and distribution. Shrubs to small trees; across most of Madagascar (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara).

Notes. See Kainulainen et al. (2017b) for a discussion on the morphological variation and recircumscription of this widespread species.

114. *Croton submetallicus* Baill., Bull. Mens. Soc. Linn. Paris 2: 966. 1891, as ‘*submetallicum*’

Croton chapelieri var. *longepetiolata* Radcl.-Sm., Gen. Croton Madag. Comoro 152. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: W of Vavatenina, Réserve Naturelle Intégrale Zahamena, Amboditamena Forest, 17°44'S, 49°00'E, 15–20 Sep 1993, S. Malcomber B. Rasolondraibe, L.M. Randrianjanaka & J.P. Abraham 2511 (holotype: K!; isotypes: MO [MO-2990285]!, P [P00433109]!).

Croton fianarantsoae var. *obovalifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 155. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: W of Ranomafana, 21°16'S, 47°28'E, 8–10 Sep 1992, S. Malcomber & R. Rakoto 1550 (holotype: K; isotypes: MO, P [P00422460]!).

Croton nitidulus var. *acuminatus* Radcl.-Sm., Gen. Croton Madag. Comoro 169. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Itinéraire de Didy à Brickaville (forêt orientale), reçu Apr 1954, G. Cours 4871 (lectotype, designated here: P [P00133641]!; isolectotypes: P [P00133639]!, P [P00133640]!, P [P00133642]!).

Croton nitidulus var. *cinereus* Radcl.-Sm., Gen. Croton Madag. Comoro 170. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Ambatovy, 18°51'34"S, 48°18'25"E, 3 Mar 1997, P. Rakotomalaza et al. 1217 (holotype: K!; isotype: MO!).

Croton nitidulus var. *hypopoliotes* Radcl.-Sm., Gen. Croton Madag. Comoro 172. 2016, **syn. nov.**

Type. MADAGASCAR. “Central Madagascar”, received Dec 1883, R. Baron s.n. (holotype: K!).

Croton nitidulus var. *macrophyllus* Radcl.-Sm., Gen. Croton Madag. Comoro 172. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: Itinéraire de Didy à Brickaville (forêt orientale), s.d., G. Cours 4660 (lectotype, designated here: P [P00133616]!; isolectotypes: P [P00133615]!, P [P00133617]!).

Croton submetallicus var. *tomentosus* Radcl.-Sm., Gen. Croton Madag. Comoro 58. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toamasina: forêt de l’Analamazaotra, reçu 3 Dec 1934, E. Ursch 21 (holotype: P [P00133354]!).

Type. MADAGASCAR. sin. loc., s.d., R. Baron 5286 (lectotype, designated here: K [K000422582]!; isolectotypes: K [K000422581]!, P [P00133327]!). MADAGASCAR. Prov. Toamasina: Alaotra-Mangoro Region. Forest W of Eulophiella Hotel, south of RN 2 and Andasibe, 18°59'08"S, 48°25'55"E, 900 m, 15 Aug 2015, B. van Ee, P.E. Berry & H. Razafindraibe 2222 (epitype, designated here: MICH [MICH1514786]!; additional duplicates: G, K, MO, P, TAN, US).

Habit and distribution. Shrubs or trees; eastern montane forests of Madagascar (Fianarantsoa, Toamasina).

Notes. The type of *Croton submetallicus* is deficient for characterizing this species properly; it lacks pistillate flowers, which are very diagnostic. Therefore we are designating an epitype that is well distributed, has photographs in Tropicos®, and is also sampled molecularly. The only other described species name that could be applied here is *C. macrochlamys*, but it has a very poor type specimen, and we are treating it here as a synonym of *C. nitidulus* because of its smaller leaf size.

For *Croton nitidulus* var. *acuminatus*, Radcliffe-Smith (2016) designated *Cours* 4871 at P as the holotype, but there are four nearly identical specimens of this collection at P, so we selected one of them here as lectotype. Likewise, for *C. nitidulus* var. *macrophyllus*, Radcliffe-Smith (2016) designated *Cours* 4660 at P as the holotype, but since there are three duplicates of that collection there, we selected one of them as the lectotype.

115. *Croton tanalorum* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 38. 1939

Type. MADAGASCAR. Prov. Fianarantsoa: Ifandana (Prov. de Farafangana), 8 Sep 1926, *R. Decary* 5070 (holotype: P [P00133355]!; isotypes: K [K001044840]!, TAN [TAN000543]!).

Habit and distribution. Shrubs; eastern montane forests of Madagascar (Fianarantsoa).

116. *Croton tardeflorens* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 50. 1939

Type. MADAGASCAR. Prov. Mahajanga: Ménabé, Tsingy du Bemaraha (9^e Réserve), Feb 1933, *J. Leandri* 941 (lectotype, designated here: P [P00133358]!; isolectotypes: K [K001040355]!, P [P00133359]!, P [P00133360]!). MADAGASCAR. Prov. Mahajanga: Boïna, bords du Jabohazo près du Mont Tsitondroina, Dec 1902, *H. Perrier de la Bâthie* 9799 (syntypes: P [P00133361]!, P [P00133362]!, P [P00133363]!).

Habit and distribution. Shrubs; western Madagascar (Mahajanga).

117. *Croton thouarsianus* Baill., Adansonia 1: 167. 1861, as ‘*thuarsianum*’

Oxydectes thouarsiana (Baill.) Kuntze, Revis. Gen. Pl. 2: 613. 1891.

Type. Based on *Croton thouarsianus* Baill.

Croton mocquersii var. *meridionalis* Radcl.-Sm. Radcl.-Sm., Gen. Croton Madag. Comoro 160. 2016, **syn. nov.**

Type. MADAGASCAR. Toliara Province: Réserve Naturelle Intégrale # 11, Andohahela, à proximité d'Eminiminy, 24°40'S, 46°48'E, 13–25 Jan 1993, *B. Randriamampionona* 77 (holotype: K!; isotypes: MO!, P [P00433050]!).

Croton thouarsianus var. *robustior* Radcl.-Sm., Gen. Croton Madag. Comoro 183. 2016, **syn. nov.**

Type. MADAGASCAR. Toliara Province: Préfecture de Fort Dauphin, Forêt d'Analava, Manantenina, côte Est, 1 Nov 1990, *N. Dumetz 1378* (holotype: K!; isotype: MO!).

Type. MADAGASCAR: sin. loc., s.d., *L.M.A. Du Petit-Thouars s.n.* (lectotype, designated here: P [P00389504]!; islectotype: P [P00389505]!).

Habit and distribution. Shrubs; southeastern Madagascar (Toliara).

118. *Croton tiliifolius* Lam., Encycl. 2: 206. 1786, as '*tiliaefolium*'

Oxydectes tiliifolia (Lam.) Kuntze, Revis. Gen. Pl. 2: 613. 1891.

Type. Based on *Croton tiliifolius* Lam.

Type. MAURITIUS. collector unknown [likely *P. Commerson s.n.*] (holotype: P-LA [P00382046]!). MAURITIUS. s.d., *P. Commerson s.n.* (likely original material or isotype: P [P00121778]!).

Habit and distribution. Trees; Mauritius.

Notes. Lamarck (1786) stated in his protologue that *Croton tiliifolius* is found on the islands of Mauritius and Réunion (Isles de France et de Bourbon), but we have no evidence to support its native presence on Réunion. Lamarck (1786) cited a Commerson herbarium specimen from Mauritius, and that corresponds well to the specimen in the general herbarium at P [P00121778], whereas the specimen in the Lamarck Herbarium does not list a collector or locality.

119. *Croton toliarensis* B.W.van Ee & Kainul., nom. nov.

urn:lsid:ipni.org:names:77167303-1

Croton tranomarensis var. *rosmarinifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 196. 2016.

Type. MADAGASCAR. Prov. Toliara: 38 km SW of Ampanihy, on road to Androka, 24°50'S, 44°25'E, 5 Feb 1990, *P.B. Phillipson J.-N. Labat, D. Du Puy & B. Du Puy 3434* (holotype: K! isotypes: DAV!, G!, MO!, P [P00433298]!).

Type. Based on *Croton tranomarensis* var. *rosmarinifolius* Radcl.-Sm.

Habit and distribution. Shrubs; southern Madagascar (Toliara).

Notes. The specific epithet "*rosmarinifolius*" is previously occupied in *Croton* (*Croton rosmarinifolius* Salisb. (1796), which is itself an illegitimate replacement name for *C. cascarilla* (L.) L.), hence the new name coined here. In both this species as well as the similar *C. chlaenacomes*, the leaf margins often become revolute when the plant

is undergoing drought stress; that is most likely what caused the strongly inrolled margins on the type of *C. tranomarensis* var. *rosmarinifolius*.

120. *Croton trichotomus* Geiseler, *Croton*. Monogr.: 50. 1807

Croton pulchellus Baill., *Adansonia* 1: 161. 1861, as '*pulchellum*'.

Type. MADAGASCAR. sin. loc., s.d., *J. Martin s.n.* (holotype: G [G00446399]!; isotype: P [P00133530]!).

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

Type. Based on *Croton pulchellus* Baill.

Oxydectes trichotoma (Geiseler) Kuntze, *Revis. Gen. Pl.* 2: 613. 1891.

Type. Based on *Croton trichotomus* Geiseler

Croton trichotomus var. *pulchellus* (Baill.) Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 50. 1939.

Type. Based on *Croton pulchellus* Baill.

Croton remotiflorus Radcl.-Sm., *Gen. Croton Madag. Comoro* 48. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Toliara: Réserve Intégrale # 11, Andohahela, vicinity of Eminiminy, 24°40'S, 46°48'E, 4–24 May 1993, *B. Randriamampionona* 385 (holotype: K!; isotypes: DAV!, G [G00414974]!, MICH!, MO!).

Croton antanosiensis var. *ambohibyi* Leandri ex Radcl.-Sm., *Gen. Croton Madag. Comoro* 42. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Antananarivo: Mont Ambohiby, SE de Tsiroanomandidy, 1600 m, 11–16 Nov 1952, *J. Leandri*, *R. Capuron* & *A. Razafindrakoto* 1775 (lectotype, designated here: P [P00154305]!; isolectotypes: P [P00154302]!, P [P00154303]!, P [P00154304]!).

Croton isomonensis var. *microcarpus* Radcl.-Sm., *Gen. Croton Madag. Comoro* 50. 2016, **syn. nov.**

Type. MADAGASCAR. Prov. Fianarantsoa: Antambohobe Canton, Ivohibe Distr., 6 Mar 1962, *Réserves Naturelles* 12150-RN (holotype: P [P00154428]!).

Type. MADAGASCAR. "*Madagascar f. maut.*, N° 38" (lectotype, designated here: P-LA [P00382065]!).

Habit and distribution. Shrubs; mainly an eastern coastal species of Madagascar in Toamasina and Toliara Provinces, as far south as the Fort Dauphin area, but also recorded from Antananarivo and Fianarantsoa Provinces in upland forests (as *C. antanosiensis* var. *ambohibyi* and *C. isomonensis* var. *microcarpus*).

Notes. In the protologue of *Croton trichotomus*, Geiseler (1807) listed two different elements, *C. trichotomus* from Madagascar and *C. punctatus* from the Caribbean. We choose here as lectotype the collection in P-LA that Leandri (1939) attributes to P. Commerson. There is no sheet in P-JU that matches the plant of *C. trichotomus* on the P-LA sheet, but P-JU Catal. 16347 is a mixed collection that bears a label on the left-hand specimen [P00674048] that states, possibly in Geiseler's hand, [*Croton*]

“punctatum Jacq.” followed below by “trichotomum Geiseler, *Crot. Monogr.*” However, this is a completely different plant from the one represented on the P-LA sheet, instead belonging to the Caribbean *C. flavens* L.

In our view, *Croton trichotomus* is primarily a littoral species of the eastern coast, but it also occurs in a number of more inland and higher elevation situations, which is an exception among Malagasy *Croton* species.

For *Croton antanosiensis* var. *ambohibyi*, Radcliffe-Smith (2016) designated *Leandri et al. 1775* at P as the holotype, but since there are four sheets of this number at P, we select one of them as lectotype.

121. *Croton tsiampiensis* Leandri, *Ann. Mus. Colon. Marseille*, sér. 5, 7(1): 79. 1939

Croton tsiampiensis var. *ankaranensis* Radcl.-Sm., Gen. *Croton* Madag. Comoro 110. 2016.

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, Massif de l'Ankarana, 4 Nov 1990, *M. Bardot-Vaucoulon 224* (holotype: P00123707!).

Croton tsiampiensis var. *macrophyllus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 110. 2016.

Type. MADAGASCAR. Prov. Mahajanga: Reserve Naturelle Bemaraha, Ambodiriana, ca. 9 km E of Antsalova, 18°39'S, 44°43'E, 100–125 m, 13–15 Dec 1990, *L. Gillespie 4139* (holotype: K!; isotype: MO!).

Croton tsiampiensis var. *microphyllus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 111. 2016.

Type. MADAGASCAR. Prov. Antsiranana: Diana Region, P.K. 10 de la route Diego Suarez-Orangea, 13 Dec 1963, *Service Forestier 22956* (holotype: P00123706!).

Type. MADAGASCAR. Prov. Mahajanga: Tsiampihy, près de l'embouchure de la Soahana, 15 Oct 1932, *J. Leandri 311* (lectotype, designated by Kainulainen et al. 2017b, pg. 399: P [P00389521]!; isolectotype: P [P00133302]!).

Habit and distribution. Shrubs; northern and western Madagascar (Antsiranana, Mahajanga).

122. *Croton ustulatus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 28. 2016

Type. MADAGASCAR. Prov. Toliara: 8–16 km E of Tuléar (Toliara) on road to Tananarive (Antananarivo), 50 m, 7 Feb 1975, *T. Croat 30998* (holotype: K!; isotypes: MO!, P [P00433216]!).

Habit and distribution. Shrubs; southwestern Madagascar (Toliara).

123. *Croton vauhanii* Croizat, *Trop. Woods* 77: 14. 1944

Type. MAURITIUS. Perrier, near the Mare aux Vacoas, 500 m, 12 May 1938, *R.E. Vaughan MAU accession number 863* (holotype: A [A00047560]; isotype: WIS

[WIS00000605MAD]). MAURITIUS. [in flower] 14 Feb 1934, *R.E. Vaughan* MAU accession number 863 (paratype: K [K000422600]!). MAURITIUS. [in fruit] 1 Apr 1934, *R.E. Vaughan* MAU accession number 863 (paratype: K [K000422600]!), MAU, MAU).

Habit and distribution. Shrubs; Mauritius.

Notes. Croizat (1944) referenced collector information for characteristics of *C. vaughanii* that are not observable on the holotype at A (“*fide collectoris*”), and the holotype is accompanied by a copy of field notes referencing that the species drops its leaves in November and December, and that flowering takes place immediately afterward. According to information in the Mauritius Herbarium (MAU) database, in this case “863” is the accession number rather than the collection number. Given this, the sheets at K and MAU with the accession number 863 are not a part of the same gathering as the holotype at A and therefore are not syntypes. Even though Croizat (1944) did not explicitly refer to the “*Vaughan 863*” collections at K and MAU, we interpret them as being paratypes. Furthermore, the sheet at K labeled with the barcode K000422600 represents material from two gatherings on different dates and should be considered two distinct specimens.

Croton vaughanii is listed by the IUCN as Critically Endangered (Strahm 1998), and is known from only a single individual according to information on the label of *Haevermans et al.* 558 (P [P00696110]), making it one of the rarest of all *Croton* species.

124. *Croton vatomandrensis* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 71. 1939

Type. MADAGASCAR. Prov. Toamasina: environs de Vatomandry, près de lagunes, Nov 1921, *H. Perrier de la Bâthie* 14084 (lectotype, designated by Kainulainen et al. 2017a, pg. 39: P [P00248926]!; isolectotypes: P [P00154409]!, P [P00154410]!).

Habit and distribution. Shrubs or small trees; eastern littoral forests of Madagascar (Fianarantsoa, Toamasina).

Incertae Sedis

This section includes 22 taxa described by Radcliffe-Smith (2016) and three by Leandri (1939) for which we have not yet been able to determine if they are worthy of recognition; they will require further evaluation to decide whether they should be considered synonyms of earlier-described taxa, or if in some cases they are actually distinct species rather than mere varieties of existing species.

***Croton ankarensis* var. *ankarafantsikae* Radcl.-Sm., Gen. *Croton* Madag. Comoro 139. 2016**

Type. MADAGASCAR. Prov. Mahajanga: Ampijoroa, Ankarafantsika, 26 Oct 1970, *A. Richard* 476 (holotype: K!).

Notes. It is uncertain what this variety is, but probably does not belong to *Croton ankarensis*.

***Croton bastardii* var. *bongolavae* Radcl.-Sm., Gen. *Croton* Madag. Comoro 204. 2016**

Type. MADAGASCAR. Prov. Mahajanga: Bongolava Hills, Port Bergé, 15°40'S, 47°30'E, 23 Nov 1987, *E. Bisset* 38 (holotype: K!).

Notes. It is uncertain what this is, but it is probably not a member of *Croton bastardii*.

***Croton bemarkanus* var. *parvistipulatus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 209. 2016**

Type. MADAGASCAR. Prov. Toliara: 45 km N of Tulear on Morombe road E of junction to Manombo, 23°01'S, 43°36'E, 14 Dec 1988, *P.B. Phillipson* 2884 (holotype: K!; isotype: MO!).

Notes. *Croton bemarkanus* is restricted to tsingy habitats in Antsiranana and Mahajanga Provinces and has entire leaves and elongate stipules. This variety does not fit the species at all and requires further study to determine its affinities.

***Croton betiokensis* var. *haplostylis* Radcl.-Sm., Gen. *Croton* Madag. Comoro 102. 2016**

Type. MADAGASCAR. Prov. Fianarantsoa: Ihosy-Ivohibe, 21 Dec 1965, *J. Peltier* & *M. Peltier* 5534 (holotype: P [P00154466]!).

Notes. This is a very scrappy specimen, making it difficult to determine what it may be. It does not appear to belong to *Croton betiokensis*, which is confined to southern Toliara Province.

***Croton catatii* var. *schizolepis* Radcl.-Sm., Gen. *Croton* Madag. Comoro 44. 2016**

Type. MADAGASCAR. Prov. Toliara: 45 km NE of Morondava on Beroboka road, 20°03'S, 44°37'E, 7/8 Dec 1990, *L. Gillespie* 4117 (holotype: K!; isotype: MO!).

Notes. This variety has much smaller leaves than typical *Croton catatii* and is only a small shrub, so it is not clear yet whether it fits within another species or of it may represent an undescribed species.

***Croton daphniphylloides* var. *stellatipilus* Radcl.-Sm., Gen. Croton Madag. Comoro 165. 2016**

Type. MADAGASCAR. Prov. Antsiranana: Marojejy, N of Mandena, 14°29'S, 49°49'E, 22 Apr 1993, *A. Randrianasolo* 322 (holotype: K!; isotype MO!).

Notes. It is unlikely this belongs to *C. chapelieri* (in which *C. daphniphylloides* is treated here as a synonym); it occurs in the Marojejy Reserve at 500 m elevation and is a 8 m tall tree, whereas *C. chapelieri* is confined to the eastern littoral zone near sea level. It could also be a northern form of *C. submetallicus*, with more acute leaves and lacking the submetallic leaf undersides of that species.

***Croton daphniphylloides* var. *triplinervius* Radcl.-Sm., Gen. Croton Madag. Comoro 165. 2016**

Type. MADAGASCAR. Prov. Antsiranana: Mt. Anjenabe, vallée inférieure de l'Androranga, affluent de la Bemarivo aux environs d' Antongondriha, 3-7 Nov 1950, *H. Humbert & R. Capuron* 24021 (holotype: K!; isotypes: MO!, P [P00433396!]).

Notes. Radcliffe-Smith (2016) erroneously cited the type collection number as 24041, which is a *Wielandia*. This may be the same entity as *C. daphniphylloides* var. *stellatipilus*.

***Croton elaeagni* var. *argyrocarpos* Radcl.-Sm., Gen. Croton Madag. Comoro 90. 2016**

Type. MADAGASCAR. [Prov. Antananarivo?]: environs d'Ambohikely, s.d. [1952-1955], *J. Dequaire* 27466 (holotype: P [P00154267!]).

Notes. This does not appear to belong to *C. elaeagni*, and its placement is uncertain.

***Croton elaeagni* var. *brevipedicellatus* Radcl.-Sm., Gen. Croton Madag. Comoro 90. 2016**

Type. MADAGASCAR. [Prov. Antananarivo?]: environs d'Ambohikely, s.d. [1952-1955], *J. Dequaire* 27460 (holotype: P [P00154282!]).

Notes. This may be the same as the preceding variety.

***Croton fianarantsoae* var. *petiolaris* Radcl.-Sm., Gen. *Croton* Madag. Comoro 155. 2016**

Type. MADAGASCAR. Prov. Antsiranana: Andapa, Andrakata, Analamboahangy Marojejy RNI, aux environs de Manenobasy, 14°35'16"S, 49°41'20"E, 1171 m, 18-24 Jan 1995, *F. Rasoavimbahoaka* 488 (holotype: MO; isotypes: P [P00433385]!, TAN).

Notes. This may correspond to *Croton submetallicus*, but the leaves are acuminate and not submetallic on the undersides, and it occurs well north of the known distribution of that species.

***Croton hovarum* var. *hirsutifructus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 178. 2016**

Type. MADAGASCAR. Prov. Toamasina: Valoala Triangulation Point, 17°25'S, 48°15'E, 6 Jan 1945, *A.M. Homolle* 2193 (holotype: P [P00133178]!).

Notes. This is a fruiting specimen with small pistillate sepals and rusty stellate pubescence that is probably not *C. hovarum*, but it cannot be placed yet in another species.

***Croton ivohibensis* var. *integrifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 149. 2016**

Type. MADAGASCAR. Prov. Toliara: bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, Mt Apiky au dessus de Mahamava, 800-900 m, Jan-Feb 1934, *H. Humbert* 13821 (lectotype, designated here: P [P00133268]!; isolectotypes: P [P00133269]!, P [P00133270]!).

Notes. This is likely an undescribed species from the lower end of evergreen forests in southeastern Toliara Province. The pistillate flowers have a very long pedicel, and the calyx is very well developed. It is likely the same as *C. nitidulus* var. *eglandulosus* and *C. thouarsianus* var. *angustifolius* (see below).

***Croton ivohibensis* var. *macrocalyx* Radcl.-Sm., Gen. *Croton* Madag. Comoro 150. 2016**

Type. MADAGASCAR. sin. loc., received Jan 1892, *R. Baron* 6134 (holotype: K!; isotype: P [P00154509]!).

Notes. This could be a form of *Croton hovarum*, but the leaves seem too coarsely serrate for that species, and not knowing where the specimen came from, hinders our ability to place it.

***Croton ivohibensis* var. *polygynus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 150. 2016**

Type. MADAGASCAR. Prov. Toamasina: Lac Alaotra, *Herb. Jard. Bot. Tan.* 3777 (holotype: P [P00133298]!).

Notes. This is an interesting specimen that bears some resemblance to *Croton tanalorum*. Additional material is needed to assess this further. Another specimen of it is *Cours* 631 (P [P00133297]).

***Croton ivohibensis* var. *verticillatus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 151. 2016**

Type. MADAGASCAR. Prov. Fianarantsoa: Reserve Speciale de Pic d' Ivohibe, Marovitsika Forest, 22°28'49"S, 46°56'49"E, 850 m, 17 Oct 2000, *P. Hoffmann et al.* 223 (holotype: K; isotype: MO!).

Notes. This does not appear to belong to *Croton hovarum* (where we include *C. ivohibensis*), and it needs further study to determine its affinities.

***Croton lapiazicola* var. *longibracteatus* Leandri, *Ann. Mus. Colon. Marseille, sér.* 5, 7(1): 42. 1939, as '*longibracteata*'**

Type. MADAGASCAR. Prov. Mahajanga: bassin supérieur du Bemarivo (Boina), 800 m, Sep 1907, *H. Perrier de la Bâthie* 9550 (lectotype, designated here: P [P00133404]!; isolectotypes: P [P00133403]!, P [P00133405]!).

Notes. The type is somewhat similar to *Croton ericius*, but the leaves are much narrower and it is less hirsute than that species.

***Croton manampetsae* var. *lepidotus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 27. 2016**

Type. MADAGASCAR. Prov. Toliara: environs de Tuléar (Toliara), 30 km Tulear-Tanana-rive, Mar 1960, *M. Keraudren* 541 (holotype: P [P00133295]!).

Notes. This variety differ from *Croton manampetsae* in that the leaves are mostly alternate (vs. opposite) and in the lepidote indumentum on the abaxial side of the leaves (vs. stellate trichomes). It will likely be described as a distinct species.

***Croton meridionalis* var. *latifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 193. 2016**

Type. MADAGASCAR. Prov. Toliara: haute vallée du Mandrare près d'Andetra (Andotsy), 26 Nov 1928, *H. Humbert* 6849 (holotype: G!; isotypes: K, P [P00418562]!).

Notes. This plant is similar to *C. meridionalis*, except that it has considerably wider leaves that are silvery-lepidote on the lower surface and turn dark blackish green on the upper surface when dried. Further study is needed to determine if it should be recognized as a distinct species.

***Croton meridionalis* var. *stipularis* Radcl.-Sm., Gen. *Croton* Madag. Comoro 194. 2016**

Type. MADAGASCAR. Prov. Toliara: 45 km N of Tulear (Toliara) on road to Morombe E of junction to Manombo, 23°01'S, 43°36'E, 14 Dec 1988, *P.B. Phillipson* 2885 (holotype: K!; isotypes: DAV!, MO!, P [P00123724]!).

Notes. This is likely the same as the preceding variety.

***Croton nitidulus* var. *eglandulosus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 171. 2016**

Type. MADAGASCAR. Prov. Toliara: bassin de réception de la Mananara, affluent du Mandrare, entre Andohahela et Elakelaka, Mt. Apiky au-dessus de Mahamavo, Jan-Feb 1934, *H. Humbert* 13848 (lectotype, designated here: P [P00133646]!; isolectotypes: G!, P [P00133647]!).

Notes. This is probably the same undescribed species as *Croton ivohibensis* var. *integrifolius* and *C. thouarsianus* var. *angustifolius*.

***Croton rubricapitirupis* var. *macrophyllus* Radcl.-Sm., Gen. *Croton* Madag. Comoro 158. 2016**

Type. MADAGASCAR. Prov. Antsiranana: Andapa, pentes occidentales du Massif de Marojejy (Nord- Est), Bassin de la Lokoho, à l'Est d' Ambalamanasy II, 500-800 m, 28 Nov-6 Dec 1948, *H. Humbert* & *R. Capuron* 22126 (holotype: K; isotypes: P [P00433398]!, P [P00433399]!).

Notes. The type of this variety is a large-leaved shrub with a very large, foliaceous pistillate calyx on a long pedicel. It may represent an undescribed species.

***Croton thouarsianus* var. *angustifolius* Radcl.-Sm., Gen. *Croton* Madag. Comoro 183. 2016**

Type. MADAGASCAR. Toliara Province: NW of Tolanaro, Reserve Naturelle Intégrale # 11 (Andohahela), NW of Eminiminy, beside River Itrotroky, 24°38'S, 46°46'E, 6–13 Feb 1993, *S. Malcomber et al.* 2159 (holotype: K!; isotypes: G!, MO!).

Notes. This is probably the same undescribed species as *Croton ivohibensis* var. *integrifolius* and *C. nitidulus* var. *eglandulosus*.

***Croton thouarsianus* var. *longifolius* Radcl.-Sm., Gen. Croton Madag. Comoro 183. 2016**

Type. MADAGASCAR. Prov. Fianarantsoa: Réserve Speciale de Manombo, 23°01'43"S, 47°43'51"E, 26 Oct 2000, *P. Hoffmann et al.* 270A (holotype: K!; isotypes: BR, G, MO).

Notes. This is probably an undescribed species from the inland area of the Manombo Reserve in Fianarantsoa Province close to the coast, but not related to *Croton thouarsianus*.

***Croton tranomarensis* var. *isomoni* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 61. 1939**

Type. MADAGASCAR. Prov. Toliara: Anosy Region, vallée de la Manombolo, rive droite (basin du Mandrare) aux environs d'Isomono (confluent de la Sakamalio), mont Morahariva, 1000–1200 m, Oct 1933, *H. Humbert* 13105 (lectotype, designated here: P [P00133393]!; isolectotypes: G [G00446403]!, P [P00133391]!, P [P00133392]!; K [K001040390]!, TAN [TAN000546]).

Notes. The leaves of these specimens are too small to conform to *Croton meridionalis*, and Radcliffe-Smith (2016) also expressed doubt that it belonged there but did not know where else to place it.

***Croton tranomarensis* var. *minor* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 61. 1939**

Type. MADAGASCAR. Prov. Toliara: Anosy Region, Ambovombe, Behara, 9 Jan 1931, *R. Decary* 8370 (holotype: P [P00133390]!; isotypes: K [K001040391]!, TAN [TAN000545]).

Notes. The leaves of the type of this variety are too small to conform to *Croton meridionalis* (for which *C. tranomarensis* is a synonym). Radcliffe-Smith (2016) expressed doubt that it belonged here, but he did not know where else to place it other than to suggest that it may be close to *C. salviformis* (presumably because of the small leaves and venose pistillate sepals). However, the holotype appears to have entirely pistillate inflorescences, suggesting that the plants may be dioecious. If so, it may correspond to an apparently undescribed species that we have also found south of Ranopiso at Mt. Vohitsiandriana in Toliara Province.

“Names” not validly published

Croton ambovombensis var. *lepidotus* Radcl.-Sm., Gen. Croton Madag. Comoro 192. 2016, nom. inval. (Art. 40.7). This designation is not validly published because Radcliffe-Smith (2016) cited both the G specimen and the P specimen (based on the collection: Madagascar. Prov. Toliara: 6 km N de Faux Cap, Apr 1972, *P. Morat* 3952 (G, K, P [P00154467]!) as the holotype, in contravention to Article 40.7 of the ICN (McNeill et al. 2012). Had it been validly published, it would have been placed in the Incertae Sedis section. This collection is of a linear-leaved plant with long virgate stems that lacks the orangeish stellate indumentum and strongly divaricate branching pattern of *C. ambovombensis*.

Croton arenicola f. *pubescens* Leandri, Ann. Mus. Colon. Marseille, sér. 5, 7(1): 58. 1939, nom. inval. Protologue lacking Latin description or diagnosis (McNeill et al. 2012; Art. 39.1). = *Croton toliarensis* B.W.van Ee & Kainul.

Croton leandrii var. *pubescens* Radcl.-Sm., Gen. Croton Madag. Comoro 188. 2016, nom. inval. (Art. 40.6). Leandri (1939, pg. 58) published "*Croton arenicola* f. *pubescens* Leandri," but as seen in the preceding paragraph, it was not validly published. Radcliffe-Smith (2016, pg. 188) later attempted to transfer it as "*Croton leandrii* var. *pubescens* (Leandri) Radcl.-Sm." Given that the intended basionym is not a validly published name, Radcliffe-Smith's new combination at a different rank is also invalid. Radcliffe-Smith (2016, pg. 188) did include a short diagnosis, which would have qualified as a new name if he had designated a holotype, but since he called the *Decary* 9031 (K) specimen the "lectotype," Art. 40.6 is not satisfied for valid publication of that name.

Excluded taxa

***Croton haumanianus* J. Léonard, Bull. Agric. Congo Belge 48: 79. 1957**

Type. DEMOCRATIC REPUBLIC OF THE CONGO: Yaosuka [Yangambi], 26 Sep 1947, *J. Léonard* 1448 (holotype: BR [BR00000889422]; isotypes: K [K000347428], YBI [YBI159606671]).

Notes. *Croton haumanianus* is known from Madagascar from a single collection, *Bosser* 17019 (P [P00133154]!, TAN), from the Station d'Essais "Caroline," Ilaka-Est [Toamasina Province, south of Vatoman-dry]. According to Schmelzer (2007), *C. haumanianus* is commonly used as a shade plant in coffee and cacao plantations, which is likely the context of this report from Madagascar. No additional information is known as to whether this species has persisted in Madagascar.

***Croton macrostachyus* Hochst. ex Delile, Voy. Abyssinie 3: 158. 1848**

Oxydectes macrostachya (Hochst. ex Delile) Kuntze, Revis. Gen. Pl. 2: 610. 1891.

Type. Based on *Croton macrostachyus* Hochst. ex Delile

Type. [ETHIOPIA] Abyssinicum: prope Djeladjeranne, 10 Aug 1840, *W.P. Schimper 1665* (syntypes: BR [BR0000008252005], K [K000347438], K [K000347439], M [M0110345], M [M0110346], MO [1905790], MPU [MPU007279], P [P00540347], P [P00540348], P [P00540349]; possible isosyntype: MPU [MPU007276]). [ETHIOPIA]: in regione inferiori septentrionali montis Scholoda, 20 Jun 1837, *W.P. Schimper 196* (syntypes: BR [BR0000008252012], BR [BR0000008367969], HBG [HBG516429], HBG [HBG516430], K [K000347440], MPU [MPU007275], NY [NY00688543], S [S07-16861]).

Notes. Radcliffe-Smith (1996) gave the range of *C. macrostachyus* as “throughout tropical Africa from Guinée eastwards to Ethiopia and southwards to Angola and Mozambique; also in Madagascar.” However, unlike for Malawi, Mozambique, Zambia, and Zimbabwe, he did not cite any specific specimens for Madagascar. *Gentry 11408* (MO, P [P00433498]) from Ankaratra, Antananarivo Province, Madagascar, was determined by Gentry as *C. macrostachyus*, but it is actually a specimen of the native *C. goudotii* Baill.

***Croton sonorae* Torr., Rep. U.S. Mex. Bound. 2(1): 194. 1859**

Croton furcellatus Baill., Bull. Mens. Soc. Linn. Paris 2: 967. 1891.

Type. MEXICO. Estado Sonora: [Ravines and mesas about] Guaymas, 1887, *E.W. Palmer 180* (holotype: P [P00404489]!; isotypes: GH [GH00303156]!, K [K000476756]!, US [00851399]!, US [00851400]!).

Type. MEXICO. Estado Sonora: Sierra de Nayos [Nariz], Jul 1855, *A.C.V. Schott III. 17* (holotype: NY [NY00246490]!; isotype: F [F0093623F]!).

Notes. Due to mislabeled herbarium specimens, Baillon (1891a) described *Croton furcellatus* as coming from Madagascar, thinking that the type specimen had been collected by Scott-Elliot in southern Madagascar. As pointed out by Humbert (1948), Perrier de la Bâthie (1948), and Arènes (1948), a shipment of plants collected in 1887 by Edward Palmer in Mexico was sent from K to P in 1890 and was mislabeled as being Scott-Elliot collections from Madagascar. The only *Croton* among these, # 180, is a collection of *C. sonorae* Torr. from Guaymas, Sonora, Mexico (Watson 1889).

***Croton tiglium* L., Sp. Pl. 2: 1004. 1753**

Kurkas tiglium (L.) Raf., Sylva Tellur.: 62. 1838.

Type. Based on *Croton tiglium* L.

Tiglium officinale Klotzsch, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 418. 1843.

Type. Based on *Croton tiglium* L.

Croton officinalis (Klotzsch) Alston in H. Trimen, Handb. Fl. Ceylon 64 (Suppl.): 264. 1931, nom. superfl.

Type. Based on *Croton tiglium* L.

Oxydectes tiglium (L.) Kuntze, Revis. Gen. Pl. 2: 614. 1891.

Type. Based on *Croton tiglium* L.

Type. SRI LANKA. (lectotype, first-step designated by Chakrabarty and Balakrishnan 1997, pg. 72, second-step designated by Philcox 1997, pg. 94: Herb. Hermann 2: 6, No. 343; left-hand specimen BM-SL [BM 000621512!]).

Notes. There is an early collection of this species from Madagascar, namely *Boivin s.n.* (G), from the côte orientale de Madagascar, 1846-1852, but it has not been recorded since.

***Lobanilia luteobrunnea* (Baker) Radcl.-Sm., Kew Bull. 44: 338 (1989)**

Croton luteobrunneus Baker, J. Linn. Soc., Bot. 20: 254. 1883, as '*luteo-brunneum*.'

Type. MADAGASCAR. sin. loc., s.d., *R. Baron* 1770 (holotype: K [K000431062!]).

Type. Based on *Croton luteobrunneum* Baker

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The systematic position of *Dryopteris blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins within the genus *Dryopteris* Adans.

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Abstract

Dryopteris blanfordii (C.Hope) C.Chr. is a member of the Dryopteridaceae, growing in high altitude *Picea* or *Abies* forests (2900–3500 m) in China and India. Phylogenetic relationships between *D. blanfordii* subsp. *nigrosquamosa* and closely related species of *Dryopteris* were investigated using a combined analysis of multiple molecular data sets (the protein-coding region of *rbcL* and *matK* genes and intergenic spacers *psbA-trnH*, *trnP-petG*, *rps4-trnS*, *trnL-trnF* and *rbcL-accD*). An assumption about the position of *D. blanfordii* subsp. *nigrosquamosa* within *Dryopteris* was made by using the Maximum Likelihood and Bayesian Inference approach and chloroplast marker sequences of *Dryopteris* species from GenBank. The results demonstrated that Asian taxa *D. blanfordii* subsp. *nigrosquamosa* and *D. laeta* as well as two American species *D. arguta* and *D. marginalis* belong to the same clade, all four of them being part of *Dryopteris* section *Dryopteris*.

Keywords

chloroplast genome markers, Dryopteridaceae, *Dryopteris blanfordii* subsp. *nigrosquamosa*, phylogeny

Introduction

Dryopteris is a large fern genus of some 225–230 species belonging to the Dryopteridaceae (Fraser-Jenkins 1986, Kramer 1990, Zhang et al. 2012). *Dryopteris blanfordii* (C.Hope) C.Ch. grows in *Picea* or *Abies* forests at 2900–3500 m in China (Gansu, Sichuan, Xizang, Yunnan), Afghanistan, India, Kashmir, Nepal and Pakistan (Zhang et al. 2013). It is divided into two subspecies, subsp. *nigrosquamosa* (Ching) Fraser-Jenkins and subsp. *blanfordii*. *Dryopteris blanfordii* subsp. *nigrosquamosa* is abundant in India (the Kashmir valley) (Mir et al. 2014, Mir et al. 2015), China (Gansu, Sichuan, Xizang, Yunnan) and Nepal (Zhang et al. 2013).

The current taxonomy and infrageneric position of *D. blanfordii* are still unresolved. More than a quarter of a century ago, Fraser-Jenkins (1986) divided *Dryopteris* into several sections based on the comparison of macro- and micro-morphological traits. He established Sect. *Remotae* with a single species (*D. blanfordii*) in the Indian subcontinent and with two European species (*Dryopteris remota* Hayek. and *D. corleyi* Fraser-Jenk.). Fraser-Jenkins suggested that all species from Sect. *Remotae* are allopolyploids resulting from hybridization between species from different sections (such as sect. *Fibrillosae*, sect. *Lophodium* or sect. *Marginatae*) (Fraser-Jenkins 1986).

In a recent study, a phylogeny including 100 species of *Dryopteris* was reconstructed and 13 phylogenetic clades (or major evolutionary lineages) were identified using DNA sequences of four plastid loci (*rbcL* gene, *rps4-trnS* spacer, *trnL* intron and *trnL-F* spacer) (Zhang et al. 2012). Two of the three species, previously placed in Sect. *Remotae*, were identified in this study as members of other clades, namely clade Aemulae (*D. corleyi*) and clade Lophodium (*D. remota*) (Zhang et al. 2012). Similar results were demonstrated by Sessa et al. (2012a, 2012b), where seven plastid loci (*rbcL*, *psbA-trnH*, *trnP-petG*, *rps4-trnS*, *trnL-F*, *trnG-trnR* and *rbcL-accD*) and a single nuclear marker *pgiC* were used to analyse 97 *Dryopteris* species. The data of these phylogenies, although valuable, were far from complete and the taxonomic position of *D. blanfordii* subsp. *nigrosquamosa* remained unclear.

Material and methods

Plant material

To examine the morphology of *D. blanfordii* subsp. *nigrosquamosa*, adult plants from the Botanical Garden of Moscow State University were used. The parent plant of *Dryopteris blanfordii* (C.Hope) C.Ch. subsp. *nigrosquamosa* (Ching) Fraser-Jenk was collected in 2003 in Uttar Pradesh State, India, at 3000 m. Spores of the specimen were germinated under artificial conditions in the greenhouse complex of MSU Botanical Garden. Subsequently, developed sporophytes were transplanted to the outdoor section of the Botanical Garden. The adult specimens were used for DNA sampling. The voucher specimen was deposited at Herbarium MW. Reference morphological char-

acters for *D. blanfordii* subsp. *nigrosquamosa* were scored from a type specimen (PE 00133945, locality: Tibet) and from descriptions of *Dryopteris blanfordii* (C.Hope) C.Chr. subsp. *nigrosquamosa* (Zhang et al. 2013, Mir et al. 2014, Mir et al. 2015).

Chloroplast markers sequencing and assembling

The chloroplast marker sequences of *D. blanfordii* subsp. *nigrosquamosa* were obtained during a large project on Polypodiales chloroplast genome sequencing. Sequencing data were generated using Illumina MiSeq high-throughput sequencing platform. For sample preparation, adult living plants were taken from the collection of the MSU Botanical Garden. The cpDNA fraction was extracted from 2.6 g (fresh weight) of fronds using a slightly modified cpDNA extraction protocol (Shi et al. 2012, Vieira et al. 2014). The purification of DNA was carried out using a protocol designed by the authors (Krinitsina et al. 2015). TruSeq protocol (NEBNext® DNA Library Prep Master Mix Set for Illumina, E6040, NEB reagents) was used for preparing the libraries. Pare end (PE) sequences (2×300bp) with a double number of each library reads about 1.2–1.97M were made. After quality trimming by Trimmomatic (Bolger et al. 2014), reads were filtered using 13 complete and five partial fern chloroplast genome sequences from RefSeq database and Bowtie2 (Langmead and Salzberg 2012). Then two sets of contigs were produced for both filtered and unfiltered sets of reads using Velvet Assembler (Zerbino and Birney 2008) and MIRA4 (Chevreux et al. 2004). Assembled contigs and scaffolds were used for assembling the complete chloroplast genome (the data are not presented in this paper) and for extracting target chloroplast markers, namely *rbcL*, *matK* genes and intergenic spacers *psbA-trnH*, *trnP-petG*, *rps4-trnS*, *trnL-trnF* and *rbcL-accD*.

Dryopteris blanfordii subsp. *nigrosquamosa* phylogenetic analysis

To determine the phylogenetic position of *D. blanfordii* subsp. *nigrosquamosa*, a phylogenetic analysis using sequences published in GenBank was performed. The GenBank accession numbers of sequences of *Dryopteris* species included in this study are listed in Appendix 1. Sequence alignment was conducted using Muscle algorithm and MEGA6.0 software package (www.megasoftware.net, Tamura et al. 2013). Phylogenetic analyses were performed using the Maximum Likelihood (ML) method at MEGA 6.0 (Tamura et al. 2013) and Bayesian Inference (BI) in BEAST (Bouckaert et al. 2014). A combined matrix including *matK* and *rbcL* gene and five intergenic spacers (*psbA-trnH*, *rps4-trnS*, *trnL-trnF*, *trnP-petG* and *rbcL-accD*) of 84 *Dryopteris* species (including *D. blanfordii* subsp. *nigrosquamosa*) was analysed.

A bootstrapping of 1000 replicates for ML analysis was processed to estimate the confidence probabilities on each branch of the phylogenetic trees constructed. The initial tree (ML) for heuristic search was obtained by applying the Neighbour-Joining

method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood approach (Lindsay 1988, Tamura et al. 2013). All positions containing gaps and missing data were eliminated.

Bayesian analyses were run for 20,000,000 generations with four MCMC chains in two independent runs. The first 2,000,000 samples from each run were discarded as burn-in. Convergence was assessed by comparing the standard deviation of split frequencies between different runs (MCMC Trace Analysis Tool (Tracer) version v1.6.0 (Rambaut et al. 2014). For ML and BI analyses, optimal models of molecular evolution for combined matrices were identified using jModelTest2 (Darriba et al. 2012) through Bayesian Information Criterion (BIC).

Results

Dryopteris blanfordii subsp. *nigrosquamosa* phylogenetic position

Seven marker regions of the assembled cp genome were used for determining phylogenetic relationships between *D. blanfordii* subsp. *nigrosquamosa* and other *Dryopteris* species, i.e. protein-coding regions of *rbcL* and *matK* genes and intergenic spacers *psbA-trnH*, *trnP-petG*, *rps4-trnS*, *trnL-trnF* and *rbcL-accD*. These markers were assembled into a single data matrix consisting of 3734 total bases. The optimal model of molecular evolution for combined matrices was TPM1uf+G+I with BIC = 36592.7258. The phylogenetic tree is shown in Fig. 2. The analysis demonstrated close relationships between *D. blanfordii* subsp. *nigrosquamosa*, *D. laeta*, *D. marginalis* and *D. arguta*. The clades containing *D. blanfordii* subsp. *nigrosquamosa* were well-supported ($\geq 80\%$ bootstrap support). *Dryopteris blanfordii* subsp. *nigrosquamosa* is close to *D. laeta* (bootstrap=100/PP=100%), *D. arguta* (bootstrap=87/PP=99.6%) and *D. marginalis* (bootstrap=96/PP=100%). The results of Bayesian Inference analysis based on the combined matrix were highly congruent with the strict consensus tree from ML analysis. The clade that included *D. arguta*, *D. marginalis*, *D. laeta* and *D. blanfordii* subsp. *nigrosquamosa* in the combined matrix of seven markers had the posterior probability (PP) value of 100%.

Morphological characters of *D. blanfordii* subsp. *nigrosquamosa* and closely related species.

The adult specimens of *D. blanfordii* analysed in the present work have 55–57×30–35 cm fronds. The frond dissection is 2-pinnate with symmetrical pinnae and pinnules (Fig. 1A). The rachises and petioles are fibrillose and have dense basal scales. The scales on the petioles are dark-brown basally and light-brown at the apex (Fig. 1 B and C). The costa and rachises are slightly grooved adaxially (Fig. 1D) and rounded abaxially (Fig. 1E).



Figure 1. *Dryopteris blanfordii* subsp. *nigrosquamosa* morphology. **A** Frond of mature plants **B** Petiole covered with scales **C** Petiole scale **D** Adaxial surface of rachis and costa **E** Abaxial surface of rachis and costa.

Two closely related species, namely *D. arguta* and *D. marginalis*, are native to North America. *Dryopteris marginalis* is evergreen and has tawny or cinnamon-coloured scales, lanceolate and coriaceous laminae, with sori mostly at margins of ultimate pinnules' segments (Table 1). *Dryopteris arguta* is winter green, having grassy-green to yellow-green, ovate-lanceolate, herbaceous, glandular laminae; the basal basis-copic pinnule and basal acroscopic pinnule are $\pm$ equal; its pinnule margins are serrate with spreading, spinelike teeth; the sori are medial. Both North American species have longer stipes ($1/4$ – $1/3$ length of leaf), 1-pinnate-pinnatifid to 2-pinnate-pinnatifid fronds (Montgomery and Wagner 1993).

Table 1. Morphological characters of four species of *Dryopteris*: *D. blanfordii* subsp. *nigrosquamosa*, *D. laeta*, *D. marginalis* and *D. arguta* according to Montgomery and Wagner (1993), Mir et al. (2014), Mir et al. (2015).

Species	<i>D. blanfordii</i> subsp. <i>nigrosquamosa</i>	<i>D. laeta</i>	<i>D. marginalis</i>	<i>D. arguta</i>
Natural range	Southeast Tibet, Western China, Nepal, India (Kashmir)	North China, Eastern Siberia, North Korea and North Japan	Eastern North America	From British Columbia to Baja California
Seasonality	semi-evergreen	deciduous	evergreen	winter green
Rhizomes	erect	creeping	ascending to erect	short-creeping
Scale colour	light brown with black veins	pale brown	tawny to cinnamon	light brown
Lamina length (cm)	40–75	25–50	25–50 (75)	25–90
Lamina division	2-pinnate to 3-pinnate-pinnatifid	3-pinnate-pinnatifid	1-pinnate-pinnatifid to 2-pinnate-pinnatifid	2-pinnate-pinnatifid
Lamina colour and texture	glaucous green, coriaceous	green, herbaceous to thinly papyraceous	green, coriaceous	green to yellow-green, herbaceous, glandular
Lamina shape	lanceolate to oblong-lanceolate	ovate-oblong or deltoid-ovate	ovate-lanceolate	ovate-lanceolate
Stipe length	1/5–1/4 of rachis length	1/3 to 1/2 of rachis length	1/4 to 1/3 of rachis length	1/4 to 1/3 of rachis length
Sori arrangement	in 1 row at each side of midvein, inframedial	in 2 rows at each side of midvein	in 1 row at each side of midvein, intramarginal at margins of segments	in 1 row at each side of midvein, medial

Dryopteris laeta is characterised by a long stipe (length roughly equal to blade length) with very few lanceolate scales; deciduous, ovate-oblong or deltoid-ovate, 3-pinnate-pinnatifid, 25–50×15–40cm, herbaceous to thinly papyraceous laminae; pinnules with toothed margins ending in an acute apex; sori in 1 or 2 rows on each side of pinnule costa; indusia orbicular-reniform, membranaceous, margin eroded (Zhang et al. 2013). The main morphological characters of these four species of *Dryopteris* are presented in the table below.

Discussion

The data obtained in this study allowed us to suggest a more accurate view of the taxonomic position of *D. blanfordii* subsp. *nigrosquamosa*. Our results demonstrated that *D. laeta* and *D. blanfordii* subsp. *nigrosquamosa* belong to the same clade as *D. arguta* and *D. marginalis*. According to the classification system of the genus *Dryopteris* by Fraser-Jenkins (1986), *D. arguta* and *D. marginalis* belong to sect. *Pallidae*, while *D. blanfordii* belongs to sect. *Remotae*. More recent classifications divide the genus *Dryopteris* into either five (Sessa et al. 2012b) or 13 different clades (Zhang et al. 2012). We have concluded that *D. blanfordii* subsp. *nigrosquamosa* together with *D. laeta*, *D. arguta* and *D. marginalis* belong to the *Dryopteris* clade following Zhang et al. (2012) or clade I according

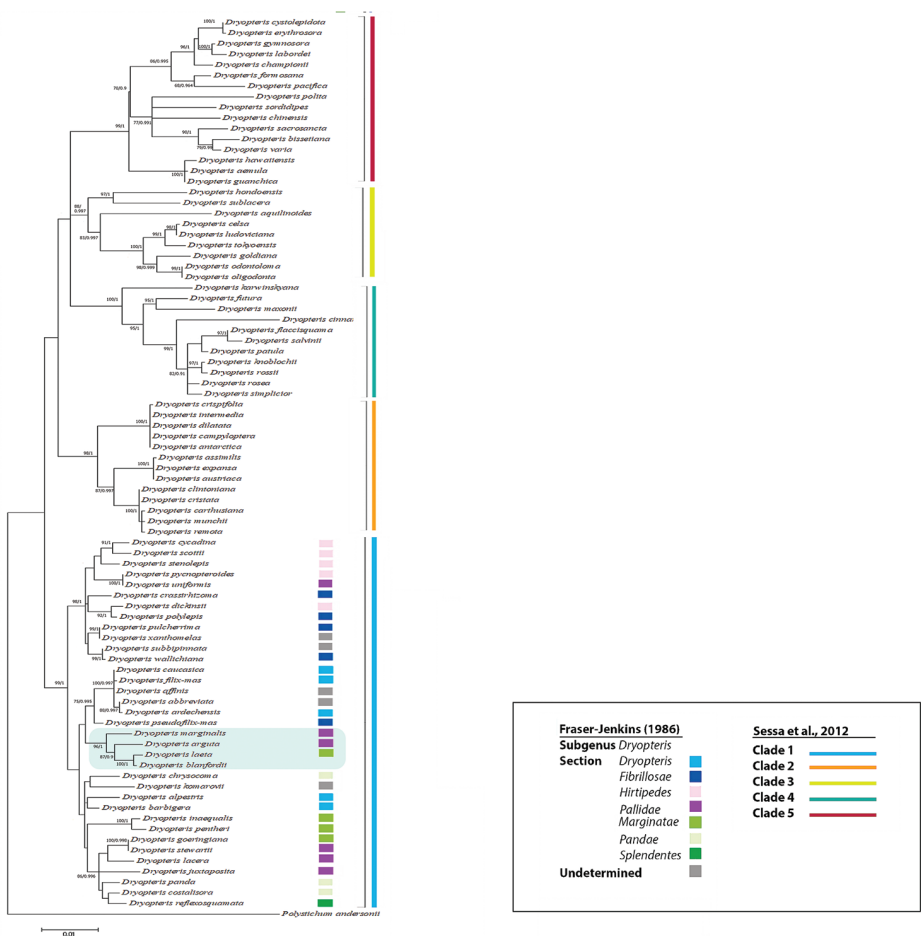


Figure 2. Topology from ML and BI analyses of *Dryopteris* species using six marker regions consisting of 3734 total bases (*psbA-trnH*, *rbcL-accD*, *rbcL*, *trnL-trnE*, *trnP-petG*, *rps4-trnS* and *matK*). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Bootstrap values are specified at the branch nodes (cut off >50%) / Bayesian PP. *Dryopteris blanfordii* subsp. *nigrosquamosa* and closely related species are marked with a blue rectangle.

to Sessa et al. (2012b). *Dryopteris arguta* and *D. marginalis* are closely related American species (from western and eastern parts of North America respectively) and the *D. laeta* specimen is from a population located in Iwaizumi (Iwate prefecture, Japan). According to some recent studies (Widén et al. 2015), *Dryopteris goeringiana* (Kunze) Koidz. is a synonym of *D. laeta*, growing in Japan. Our analyses rather showed that *D. goeringiana* proves to be related to *Dryopteris stewartii* Fraser-Jenk., *Dryopteris lacera* (Thunb.) Kunze and *Dryopteris sieboldii* (Van Houtte ex Mett.) Kuntze (Fig. 2), which agrees with the data of other authors (Sessa et al. 2012b). At the same time, *D. laeta* from Japan does not belong to this group of *Dryopteris* species (Ebihara 2011, Zhang et al. 2012) (Fig. 2). The relationship between species from Europe, Central America and Asia may indicate that a

long-distance dispersal event occurred. Unfortunately, it is impossible to indicate where the ancestor of these species might have originated.

Dryopteris arguta, *D. marginalis*, *D. laeta* and *D. blanfordii* subsp. *nigrosquamosa* differ from each other in many morphological characters (Table 1), but share the structure of segments of second and third orders. The second order segments (pinnules) are short- or very short-stalked (1–5(10) mm). The distal part of the pinnule is attenuated and elongated, with its distal third alate and lacking sori. The basal basiscopic to acroscopic pinnulae length ratio is 1–1.5. The third order segments, when present, are isomorphic. Pinnules are serrate, ending with more or less prominent spiny teeth.

Conclusion

The relationship of *D. blanfordii* subsp. *nigrosquamosa* within the *Dryopteris* genus was defined using phylogenetic analyses based on chloroplast markers. Our results demonstrate that Asian species *D. blanfordii* subsp. *nigrosquamosa* and *D. laeta* belong to the same clade as two North American species *D. arguta* and *D. marginalis*, with all four species being part of the *Dryopteris* section *Dryopteris*.

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Appendix I

GenBank accession numbers of marker sequences of *Dryopteris* species included in the study. All sequences of *D. blanfordii* subsp. *nigrosquamosa* were newly generated in this study.

Species	<i>matK</i> GenBank accession/ voucher or isolate	<i>psbA-trnH</i> GenBank accession / voucher or isolate	<i>rbcL-accD</i> GenBank accession / voucher or isolate	<i>rps4-trnS</i> GenBank accession / voucher or isolate	<i>trnL-trnF</i> GenBank accession / voucher or isolate	<i>trnP-petG</i> GenBank accession / voucher or isolate	<i>rbcL</i> GenBank accession / voucher or isolate
<i>Dryopteris abbreviata</i> Kuntze		<i>JN189448.1/</i> isolate E335	<i>JN189664.1/</i> isolate E335	<i>JN189231.1/</i> isolate E335	<i>JN189126.1/</i> -	<i>JN189342.1/</i> isolate E335	<i>JN189557.1/</i> isolate E335
<i>Dryopteris aemula</i> (Ait.) Kuntze		<i>JN189407.1/</i> isolate E113	<i>JN189625.1/</i> isolate E113	<i>JN189189.1/</i> isolate E113	<i>AY268816.1/</i> -	<i>JN189301.1/</i> isolate E113	<i>AY268881.1/</i> -
<i>Dryopteris affinis</i> (Lowe) Fraser-Jenk.		<i>JN189408.1/</i> isolate E114	<i>JN189626.1/</i> isolate E114	<i>JN189190.1/</i> isolate E114	<i>AY268780.1/</i> -	<i>JN189302.1/</i> isolate E114	<i>AY268849.1/</i> -
<i>Dryopteris alpestris</i> Tagawa ex Ching & S.K.Wu	JQ941627.1/ Heng 32147 (UC)	<i>JN189428.1/</i> isolate E314	<i>JN189645.1/</i> isolate E314	<i>JN189210.1/</i> isolate E314	<i>JX535868.1/</i> Xiaohua Jin & Liang Zhang 11103 (CDBI)	<i>JN189322.1/</i> isolate E314	<i>JX535858.1/</i> Xiaohua Jin & Liang Zhang 11103 (CDBI)
<i>Dryopteris antarctica</i> (Baker) C.Chr.	JQ941648.1/ Hennequin 2009- R109 (REU)	<i>JN189467.1/</i> isolate E378	<i>JN189682.1/</i> isolate E378	<i>JN189250.1/</i> isolate E378	<i>JN189141.1/</i> isolate E378	<i>JN189356.1/</i> isolate E378	<i>JN189577.1/</i> isolate E378
<i>Dryopteris aquilinoides</i> (Desv.) C.Chr.	JQ941617.1/ Kessler 13855 (UC)	<i>JN189429.1/</i> isolate E315	<i>JN189646.1/</i> isolate E315	<i>JN189211.1/</i> isolate E315	<i>JN189106.1/</i> isolate E315 AY268803.1/ Ranker 1536	<i>JN189323.1/</i> isolate E315	<i>JN189537.1/</i> isolate E315 AY268868.1/ -
<i>Dryopteris arguta</i> (Kaulf.) Maxon	JQ941647.1/ EBS 35 (WIS) JQ941660.1/ EBS 36 (WIS)	<i>JN189400.1/</i> isolate E069	<i>JN189619.1/</i> isolate E069	<i>JQ366838.1/</i> EBS 36 (WIS)	<i>AY278397.1/</i> -	<i>JN189294.1/</i> isolate E069	<i>JN189509.1/</i> isolate E069 JQ935258.1/ EBS 36 (WIS)
<i>Dryopteris ardechenensis</i> Fraser-Jenk.		<i>JN189487.1/</i> isolate NH56	<i>JN189702.1/</i> isolate NH56	<i>JN189271.1/</i> isolate NH56	<i>AY268817.1/</i> -	<i>JN189377.1/</i> isolate NH56	<i>JN189596.1/</i> isolate NH56
<i>Dryopteris assimilis</i> S.Walker	JQ941622.1/ Skvortsov 1.VIII.1982 (NY)	<i>JN189409.1/</i> isolate E117	<i>JN189627.1/</i> isolate E117	<i>JN189191.1/</i> isolate E117	<i>JN189086.1/</i> isolate E117	<i>JN189303.1/</i> isolate E117	<i>JN189517.1/</i> isolate E117

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<i>Dryopteris austriaca</i> (Jacq.) Woy. ex Schinz & Thell.	JQ941637.1/ Degn 25 (NY)	JN189410.1/ isolate E119	JN189628.1/ isolate E119	JN189192.1/ isolate E119	JN189087.1/ isolate E119	JN189304.1/ isolate E119	JN189518.1/ isolate E119
<i>Dryopteris barbigera</i> (Moore) Kuntze		JN189431.1/ isolate E317	JN189647.1/ isolate E317	JN189213.1/ UC<USA-CA> Miehe 94-191- 14	JN189108.1/ isolate E317	JN189325.1/ isolate E317	JN189539.1/ UC<USA-CA> Miehe 94-191- 14
<i>Dryopteris bissetiana</i> (Baker) C.Chr.		AB575740.1/ TNS:763335	JN189693.1/ isolate NH28	DQ191829.1/ SG Lu/C75 JN189261.1/ isolate NH28	AY268796.1/ R. Moran, COLO	JN189367.1/ isolate NH28	AY268862.1/ -
<i>Dryopteris campyloptera</i> (Kunze) Clarkson	JQ941638.1/ EBS 22 (WIS) JQ941619.1/ EBS 19 (WIS)	JN189395.1/ isolate E058	JN189614.1/ isolate E058	JQ936819.1/ EBS 19 (WIS)	AY268801.1/ WJ Cody 23484 FR731970.1/ isolate A183	JN189289.1/ isolate E058	JQ935255.1/ EBS 19 (WIS) AY268866.1/ -
<i>Dryopteris carthusiana</i> (Vill.) H.P.Fuchs	JQ941634.1/ EBS 42 (WIS) JQ941655.1/ EBS 43 (WIS) JQ941653.1/ EBS 7 (WIS) JQ941640.1/ EBS 41 (WIS)	JN189402.1/ isolate E075	JN189621.1/ isolate E075	JN189184.1/ isolate E075 JQ936839.1/ EBS 42 (WIS)	AY268777.1/ GW Argus 9327, COLO	JN189296.1/ isolate E075 JQ683076.1/ EBS 43 (WIS) JQ683064.1/ EBS 7 (WIS)	JN189511.1/ isolate E075 JQ935266.1/ EBS 7 (WIS) JQ935272.1/ EBS 43 (WIS)
<i>Dryopteris caucasica</i> (A.Braun) Fraser-Jenk. & Corley	JQ941604.1/ Christenhusz 4309 (UC)	JN189432.1/ isolate E318	JN189648.1/ isolate E318	JN189214.1/ isolate E318	JN189109.1/ isolate E318	JN189326.1/ isolate E318	JN189540.1/ isolate E318
<i>Dryopteris calsa</i> (W.Palmer) Small	JQ941652.1/ EBS 27 (WIS) JQ941658.1/ Price 94-2 (NY)	JQ936652.1/ Price 94-2 (NY)	JN189609.1/ isolate E043	JN189175.1/ isolate E043 JQ936822.1/ EBS 49 (WIS)	JN105314.1/ EBS49 (WIS)	JQ683075.1/ Price 94-2 (NY)	JQ935249.1/ EBS 49 (WIS)

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<i>Dryopteris championii</i> (Benth.) C.Chr.		<i>JN189480.1/</i> isolate NH31 AB575742.1/ TNS:764357	<i>JN189694.1/</i> isolate NH31	<i>DQ151856.1/</i> SG Lu/M3	<i>AY268797.1/</i> R. Moran, COLO KC896581.1/ isolate CHA 1419	<i>JN189368.1/</i> isolate NH31	<i>AY268863.1/</i> - KC896547.1/ isolate CHA 1419
<i>Dryopteris chinensis</i> Koidz.		<i>AB575743.1/</i> TNS:763933	<i>JN189649.1/</i> isolate E319	<i>JN189215.1/</i> isolate E319 JX35819.1/ Liang Zhang & Zhangming Zhu 1114 (CDBI)	<i>JX535872.1/</i> Liang Zhang & Zhangming Zhu 1114 (CDBI)	<i>JN189327.1/</i> isolate E319	<i>AB575119.1/</i> TNS:763933
<i>Dryopteris chrysocoma</i> (Christ) C.Chr.		<i>JN189434.1/</i> isolate E320	<i>JN189650.1/</i> isolate E320	<i>JN189216.1/</i> isolate E320 DQ191832.1/ SG Lu/C76	<i>DQ514495.1/</i> LJM079	<i>JN189328.1/</i> isolate E320	<i>DQ508773.1/</i> -
<i>Dryopteris cinnamomea</i> C.Chr.		<i>JN189420.1/</i> isolate E279	<i>JN189638.1/</i> isolate E279	<i>JN189202.1/</i> isolate E279	<i>AY278398.1/</i> - FR731991.1/ A190	<i>JN189314.1/</i> isolate E279	<i>JN189528.1/</i> isolate E279
<i>Dryopteris clintoniana</i> (D.C.Eaton) Dowell	JQ941605.1/ EBS 16 (WIS) JQ941626.1/ EBS 8 (WIS)	<i>JQ936651.1/</i> EBS 8 (WIS) JN189389.1/ isolate E020	<i>JN189608.1/</i> isolate E020	<i>JN189174.1/</i> isolate E020 JQ936813.1/ EBS 8 (WIS)	<i>JQ683004.1/</i> EBS 8 (WIS)	<i>JN189283.1/</i> isolate E020	<i>JQ935247.1/</i> EBS 8 (WIS) KF186502.1/ OAC 96815
<i>Dryopteris crispifolia</i> Rasbach, Reichst. & G.Vida	<i>JQ941650.1/</i> BPSE	<i>JN189488.1/</i> isolate NH58	<i>JN189703.1/</i> isolate NH58	<i>JN189272.1/</i> isolate NH58	<i>AY268819.1/</i> -	<i>JN189378.1/</i> isolate NH58	<i>AY268884.1/</i> -
<i>Dryopteris costalisora</i> Tagawa		<i>JN189493.1/</i> isolate NH85	<i>JN189710.1/</i> isolate NH85	<i>JN189278.1/</i> isolate NH85	<i>JN189170.1/</i> isolate NH85	<i>JN189384.1/</i> isolate NH85	<i>JN189603.1/</i> isolate NH85

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<i>Dryopteris crassirhizoma</i> Nakai		<i>AB575746.1</i> / TNS:764333	<i>JN189651.1</i> / isolate E321	<i>JN189217.1</i> / isolate E321	<i>AY268805.1</i> / - <i>AY278399.1</i> / -	<i>JN189329.1</i> / isolate E321	<i>JN189543.1</i> / isolate E321 <i>AY268870.1</i> / - <i>KC896537.1</i> / isolate CRA 176
<i>Dryopteris cristata</i> (L.) A.Gray	<i>JQ941613.1</i> / EBS 58 (WIS) <i>JQ941608.1</i> / EBS 68 (WIS) <i>JQ941614.1</i> / Montgomery 07- 99 (NY) <i>JQ941609.1</i> / Leoschke 2119 (NY) <i>JQ941621.1</i> / ESB 26 (WIS)	<i>JQ936659.1</i> / EBS 68 (WIS) <i>JQ936654.1</i> / Leoschke 21119 (NY)	<i>JQ947928.1</i> / EBS 58 (WIS)	<i>JQ936835.1</i> / Montgomery 07-99 (NY)	<i>JQ682997.1</i> / EBS 68 (WIS)	<i>JN189330.1</i> / isolate E322 <i>JQ683056.1</i> / Montgomery 07-99 (NY) <i>JN189299.1</i> / isolate E089 <i>JQ683055.1</i> / ESB 26 (WIS) <i>JQ683065.1</i> / EBS 68 (WIS) <i>JQ683070.1</i> / EBS 58 (WIS) <i>JQ683073.1</i> / EBS 52 (WIS) <i>JQ683078.1</i> / Leoschke 2119 (NY)	<i>JQ935251.1</i> / Montgomery 07-99 (NY) <i>KF186503.1</i> / OAC 96818

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<i>Dryopteris cycadina</i> (Franch. & Sav.) C.Chr.		<i>JN189436.1/</i> isolate E322	<i>JN189652.1/</i> isolate E322	<i>JN189218.1/</i> isolate E322 DQ191835.1/ SG Lu/C38	<i>JN189113.1/</i> isolate E322 AY278400.1/ -	<i>JN189330.1/</i> UC<USA-CA> RBCTW-078	<i>JN189544.1/</i> isolate E322 EF463127.1/ - AY587115.1/ -
<i>Dryopteris cystolepidota</i> (Miq.) C.Chr.		<i>JN189485.1/</i> isolate NH52	<i>JN189699.1/</i> isolate NH52	<i>JN189268.1/</i> isolate NH52	<i>AY268813.1/</i> -	<i>JN189374.1/</i> isolate NH52	<i>JN189593.1/</i> isolate NH52 AY268878.1/ -
<i>Dryopteris dilatata</i> (Hoffm.) A.Gray	JQ941646.1/ Hennequin 2010- B1 (P) JQ941599.1/ Schuettpeiz 535 (DUKE) JQ941645.1/ Camoletto 2021 (NY)	<i>JN189465.1/</i> isolate E375 JQ936648.1/ Schuettpeiz 535 (DUKE) JQ936650.1/ Camoletto 2021 (NY)	<i>JN189680.1/</i> isolate E375	<i>JQ93684.1/</i> Schuettpeiz 535 (DUKE)	<i>JQ683001.1/</i> Schuettpeiz 535 (DUKE) AY268779.1/ Kasnoborov 679, COLO	<i>JN189354.1/</i> isolate E375	<i>JN189575.1/</i> - AY268848.1/ - JQ935276.1/ Schuettpeiz 535 (DUKE)
<i>Dryopteris dickinsii</i> (Franch. & Sav.) C.Chr.		<i>JN189489.1/</i> isolate NH59	<i>JN189704.1/</i> isolate NH59	<i>JN189273.1/</i> isolate NH59 DQ191839.1/ SG Lu/QC3	<i>JX535875.1/</i> K. Ohora s.n.; VS766491 (TNS) AY268820.1/ -	<i>JN189379.1/</i> isolate NH59	<i>JN189598.1/</i> isolate NH59 AB575125.1/ TNS:766491 DDU05622.1/ -
<i>Dryopteris dehuensis</i> Ching & K. H. Shing				DQ191838.1/ SG Lu/O9			

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<i>Dryopteris erythrosora</i> (D. C. Eat.) O. Kuntze		<i>KM208819.1/</i> - PSMT3776/ - EF590692.1/ NMINH 06- 8357	<i>JN189687.1/</i> isolate NH13	<i>JN189255.1/</i> isolate NH13 DQ191840.1/ SG Lu/B33	<i>AY268787.1/</i> Geiger 94, COLO	<i>JN189361.1/</i> isolate NH13	<i>AY268852.1/</i> - <i>AB232392.1/</i> Tsutsumi CT1001 AY587111.1/ - KC896551.1/ isolate ERY 2006899
<i>Dryopteris expansa</i> (C. Presl) Fraser-Jenk. & Jermy	JQ941606.1/ EBS 37 (WIS) JQ941612.1/ EBS 40 (WIS) JQ941633.1/ EBS 30 (WIS) JQ941610.1/ EBS 33 (WIS)	<i>AB575750.1/</i> TNS:765180	<i>JN189616.1/</i> isolate E064	<i>JN189180.1/</i> isolate E064 KF020383.1/ Nelson 7921	<i>AY268775.1/</i> Nelson 7921	<i>JN189291.1/</i> isolate E064	<i>JQ935275.1/</i> EBS 37 (WIS) EF463179.1/ Christenhusz 4263 (TUR) AB575127.1/ TNS:765180 AB908270.1/ -
<i>Dryopteris filix-mas</i> (L.) Schott	JQ941618.1/ EBS 38 (WIS) JQ941611.1/ EBS 32 (WIS)	<i>JN189398.1/</i> isolate E066	<i>JN189617.1/</i> isolate E066	<i>JN189181.1/</i> isolate E066	<i>FR731980.1/</i> isolate A213	<i>JQ683060.1/</i> EBS 38 (WIS)	<i>JN189507.1/</i> isolate E066 JQ935265.1/ EBS 38 (WIS) KM114199.1/ Lehtonen 725 (TUR) JF832067.1/ -
<i>Dryopteris flaccisquama</i> A.Rojas		<i>JN189411.1/</i> isolate E236	<i>JN189629.1/</i> isolate E236	<i>JN189193.1/</i> isolate E236	<i>JN189088.1/</i> isolate E236	<i>JN189305.1/</i> isolate E236	<i>JN189519.1/</i> -

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<i>Dryopteris fragrans</i> (L.) Schott	JQ941603.1/ EBS 47 (WIS)	JN189403.1/ isolate E081		JN189185.1/ isolate E081	AY268800.1/ Kelso 83-221	JQ683049.1/ EBS 53 (WIS) JN189297.1/ isolate E081	AB575129.1/ TNS:743728 JN189512.1 / isolate E081 JQ935274.1/ EBS 53 (WIS) AY268865.1/ -
<i>Dryopteris formosana</i> (Christ) C.Chr.		AB575751.1/ TNS:763153	JN189653.1/ isolate E323	JN189219.1/ isolate E323	AY268793.1/ R. Moran, COLO	JN189331.1/ isolate E323	JN189545.1/ - AB575128.1/ TNS:763153 AY268857.1/ -
<i>Dryopteris fuscipes</i> C.Chr.		AB575752.1/ TNS:762541		DQ191841.1/ SG Lu/M2	KC896583.1/ FUS 1058		AB575130.1/ TNS:762541 KC896549.1 \ isolate FUS 1058
<i>Dryopteris future</i> A.R.Sm.		JN189426.1/ isolate E299	JN189643.1/ isolate E299	JN189208.1/ isolate E299	JN189103.1/ isolate E299	JN189320.1/ isolate E299	JN189534.1/ -
<i>Dryopteris goldiana</i> (Hook.) A.Gray		JN189396.1/ isolate E063	JN189615.1/ isolate E063	JN189179.1/ -	FR731984.1/ isolate A202	JN189290.1/ isolate E063	AF537228.1/ -

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<i>Dryopteris goeringiana</i> (G. Kze.) Koidz.		<i>JN189474.1</i> / isolate NH16	<i>JN189688.1</i> / isolate NH16	<i>JN189256.1</i> / -	<i>AY268790.1</i> / - AF515241.1/ -	<i>JN189362.1</i> / isolate NH16	<i>AY268855.1</i> / R. Moran; COLO», cultivated in NY botanical garden KC896541.1/ isolate GOE 080368
<i>Dryopteris gymnosora</i> (Mak.) C. Chr.		<i>JN189438.1</i> / isolate E324	<i>JN189654.1</i> / isolate E324	<i>JN189220.1</i> / isolate E324 JX535824.1/ -	<i>JN189115.1</i> / isolate E324 JX535877.1/ -	<i>JN189332.1</i> / isolate E324	<i>AB575132.1</i> / TNS:763325
<i>Dryopteris guanchica</i> Gibby & Jermy		<i>JN189463.1</i> / isolate E373	<i>JN189678.1</i> / isolate E373	<i>JN189246.1</i> / -	<i>FR731992.1</i> / isolate A207	<i>JN189352.1</i> / isolate E373	<i>JN189573.1</i> / isolate E373
<i>Dryopteris hauwaiensis</i> (Hillebr.) Robinson		<i>JN189470.1</i> / isolate MA85	<i>JN189685.1</i> / isolate MA85	<i>JN189253.1</i> / isolate MA85	<i>JN189144.1</i> / isolate MA85 <i>AY268784.1</i> / Geiger 7/4, COLO	<i>JN189359.1</i> / isolate MA85	<i>AY268840.1</i> / -
<i>Dryopteris bondoensis</i> Koidz.		<i>AB575761.1</i> / TNS:764343	<i>JN189689.1</i> / isolate NH17	<i>JN189257.1</i> / isolate NH17	<i>AY268791.1</i> / R. Moran, COLO	<i>JN189363.1</i> / isolate NH17	<i>JN189583.1</i> / isolate NH17 AB575139.1/ TNS:764343
<i>Dryopteris inaequalis</i> (Schlecht.) Kuntze		<i>JN189440.1</i> / isolate E326	<i>JN189655.1</i> / isolate E326	<i>JN189222.1</i> / isolate E326	<i>JN189117.1</i> / isolate E326	<i>JN189333.1</i> / isolate E326	<i>JN189548.1</i> / isolate E326

Species	<i>matK</i> GenBank accession/ voucher or isolate	<i>psbA-trnH</i> GenBank accession / voucher or isolate	<i>rbcl-accD</i> GenBank accession / voucher or isolate	<i>rps4-trnS</i> GenBank accession / voucher or isolate	<i>trnL-trnF</i> GenBank accession / voucher or isolate	<i>trnP-petG</i> GenBank accession / voucher or isolate	<i>rbcl</i> GenBank accession / voucher or isolate
<i>Dryopteris intermedia</i> (Willd.) A.Gray	JQ941657.1/ EBS 63 (WIS) JQ941659.1/ EBS 44 (WIS) JQ941642.1/ EBS 69 (WIS) JQ941663.1/ EBS 13 (WIS) JQ941624.1/ ESB 15 (WIS) JQ941630.1/ EBS 18 (WIS)	<i>JQ936670.1</i> / EBS 63 (WIS)	<i>JN189613.1</i> / isolate E056	<i>JN189178.1</i> / isolate E056	<i>FR731994.1</i> / Alanko 96215 (H:1695737) FR731993.1/ isolate A141	<i>JN189288.1</i> / isolate E056	<i>AB575143.1</i> / TNS:766638
<i>Dryopteris juxtaposita</i> Christ		<i>JN189441.1</i> / isolate E327	<i>JN189656.1</i> / isolate E327	<i>JN189223.1</i> / isolate E327 DQ191848.1/ SG Lu/66	<i>JN189118.1</i> / isolate E327 AY268810.1/ -	<i>JN189334.1</i> / isolate E327	<i>JN189549.1</i> / isolate E327 AY268875.1/ -
<i>Dryopteris karwinskiana</i> (Mett.) Kuntze		<i>JN189413.1</i> / isolate E241	<i>JN189631.1</i> / isolate E241	<i>JN189195.1</i> / isolate E241	<i>JN189090.1</i> / isolate E241	<i>JN189307.1</i> / isolate E241	<i>JN189521.1</i> / isolate E241
<i>Dryopteris komarovii</i> Kossinsky		<i>JN189442.1</i> / isolate E328	<i>JN189657.1</i> / isolate E328	<i>JN189224.1</i> / isolate E328	<i>JN189119.1</i> / isolate E328	<i>JN189335.1</i> / isolate E328	<i>JN189550.1</i> / -
<i>Dryopteris knoblochii</i> A. R. Sm.		<i>JN189414.1</i> / isolate E242	<i>JN189632.1</i> / isolate E242	<i>JN189196.1</i> / isolate E242	<i>JN189091.1</i> / isolate E242	<i>JN189308.1</i> / isolate E242	<i>JN189522.1</i> / -
<i>Dryopteris kobayashii</i> Kitag.							AB908374.1/ haplotype: Type 6
<i>Dryopteris labordei</i> (Christ) C.Chr.		<i>JN189492.1</i> / isolate NH84	<i>JN189709.1</i> / isolate NH84	<i>JN189277.1</i> / isolate NH84	<i>JN189169.1</i> / isolate NH84	<i>JN189383.1</i> / isolate NH84	<i>JN189602.1</i> / isolate NH84 EF463128.1/ -

Species	<i>matK</i> GenBank accession/ voucher or isolate	<i>psbA-trnH</i> GenBank accession / voucher or isolate	<i>rbcl-accD</i> GenBank accession / voucher or isolate	<i>rps4-trnS</i> GenBank accession / voucher or isolate	<i>trnL-trnF</i> GenBank accession / voucher or isolate	<i>trnP-petG</i> GenBank accession / voucher or isolate	<i>rbcl</i> GenBank accession / voucher or isolate
<i>Dryopteris lacera</i> (Thunb.) Krze.		<i>AB575770.1/</i> TNS:774850	<i>JN189691.1/</i> isolate NH23	<i>JN189259.1/</i> isolate NH23 DQ191851.1/ SG Lu/QC36	<i>AY268794.1/</i> R. Moran, COLO KC896572.1/ isolate LAC 1027	<i>JN189365.1/</i> isolate NH23	<i>JN189585.1/</i> isolate NH23 KC896538.1/ isolate LAC 1027
<i>Dryopteris ludoviciana</i> (Kze.) Small	JQ941656.1/ EBSlud2 (WIS) JQ941628.1/ EBSlud3 (WIS) JQ941639.1/ EBSlud4 (WIS) JQ941654.1/ EBS 48.A (WIS)	<i>JQ936667.1/</i> EBSlud2 (WIS)	<i>JQ947929.1/</i> EBSlud4 (WIS)	<i>JN189186.1/</i> isolate E082 JQ936837.1/ EBS 48 (WIS)	<i>JQ682979.1/</i> EBSlud2 (WIS)	<i>JN189298.1/</i> isolate E082	<i>JQ935277.1/</i> EBSlud3 (WIS) JQ935273.1/ EBS 48 (WIS)
<i>Dryopteris marginalis</i> (L.) A.Gray	JQ941607.1/ EBS 17 (WIS)	<i>JN189393.1/</i> isolate E055	<i>JN189612.1/</i> isolate E055	<i>JN189177.1/</i> isolate E055	<i>FR731986.1/</i> isolate A203	<i>JN189287.1/</i> isolate E055	<i>EF463181.1/</i> - KF186511.1/ OAC 96835
<i>Dryopteris maxonii</i> Underw. & C.Chr.		<i>JN189421.1/</i> isolate E284 AB575774.1/ TNS:776976	<i>JN189639.1/</i> isolate E284	<i>JN189203.1/</i> isolate E284	<i>JN189098.1/</i> isolate E284	<i>JN189315.1/</i> isolate E284	<i>JN189529.1/</i> isolate E284 AB575152.1/ 776976
<i>Dryopteris medioxima</i> Koidz.				<i>JN189209.1/</i> - JQ936827.1/ Hoshizaki (UC)	<i>AY268822.1/</i> -	<i>JN189321.1/</i> WIS EBS54	<i>JN189535.1/</i> isolate E311
<i>Dryopteris munchii</i> A.R.Sm.	JQ941632.1/ EBS 54 (WIS)	<i>JN189427.1/</i> isolate E311	<i>JN189644.1/</i> isolate E311	<i>JN189265.1/</i> - DQ191859.1/ -	<i>AY268807.1/</i> -	<i>JN189371.1/</i> isolate NH46	<i>JN189590.1/</i> isolate NH46 AY268872.1/ -
<i>Dryopteris odontoloma</i> (Moore) C. Chr.		<i>JN189483.1/</i> isolate NH46	<i>JN189696.1/</i> isolate NH46				

Species	<i>matK</i> GenBank accession/ voucher or isolate	<i>psbA-trnH</i> GenBank accession / voucher or isolate	<i>rbcl-accD</i> GenBank accession / voucher or isolate	<i>rps4-trnS</i> GenBank accession / voucher or isolate	<i>trnL-trnF</i> GenBank accession / voucher or isolate	<i>trnP-petG</i> GenBank accession / voucher or isolate	<i>rbcl</i> GenBank accession / voucher or isolate
<i>Dryopteris oligodonta</i> (Desv.) Pichi-Serm.	JQ941643.1/ voucher Hennequin 2010- C11 (P)	<i>JN189464.1/</i> isolate E374	<i>JN189679.1/</i> isolate E374	<i>JN189247.1/</i> isolate E374	<i>FR731987.1/</i> isolate A156	<i>JN189353.1/</i> isolate E374	<i>JN189574.1/</i> isolate E374
<i>Dryopteris pacifica</i> (Nakai) Tag.		<i>AB575778.1/</i> TNS:763312	<i>JN189700.1/</i> isolate NH53	<i>JN189269.1/</i> isolate NH53 DQ191860.1/ - JX535838.1/ -	<i>JX535891.1/</i> - KC896588.1/ isolate PAC 487 AY268814.1/ -	<i>JN189375.1/</i> isolate NH53	<i>JN189594.1/</i> - AB575157.1/ TNS:763312
<i>Dryopteris panda</i> (C. B. Cl.) C. Chr.		<i>JN189443.1/</i> isolate E329	<i>JN189658.1/</i> isolate E329	<i>JN189225.1/</i> - DQ191861.1/ -	<i>JN189120.1/</i> isolate E329	<i>JN189336.1/</i> isolate E329	<i>JN189551.1/</i> -
<i>Dryopteris patula</i> (Sw.) Underw.		<i>JN189391.1/</i> isolate E047	<i>JN189610.1/</i> isolate E047	<i>KJ464668.1/</i> isolate MS1104	<i>AY268823.1/</i> -	<i>JN189285.1/</i> isolate E047	<i>KJ464427.1/</i> - AY268888.1 -
<i>Dryopteris pentheri</i> (Krasser) C. Chr.		<i>JN189466.1/</i> isolate E377	<i>JN189681.1/</i> isolate E377	<i>JN189249.1/</i> isolate E377	<i>JN189140.1/</i> isolate E377	<i>JN189355.1/</i> isolate E377	<i>KF992481.1/</i> -
<i>Dryopteris polita</i> Rosenst.	KJ196593.1/ S.Y. Dong 718	<i>AB575779.1/</i> TNS:763901	<i>JN189713.1/</i> isolate NH92	<i>JN189281.1/</i> isolate NH92	<i>KJ196700.1/</i> S.Y. Dong 718	<i>JN189387.1/</i> isolate NH92	<i>AB575158.1/</i> TNS:763901
<i>Dryopteris polyplepis</i> (Franch. & Sav.) C. Chr.		<i>AB575780.1/</i> TNS:764340	<i>JN189695.1/</i> isolate NH33	<i>JN189263.1/</i> isolate NH33	<i>AY268798.1/</i> R. Moran, COLO	<i>JN189369.1/</i> isolate NH33	<i>AB575159.1/</i> TNS:764340
<i>Dryopteris pseudofilix-mas</i> (Fée) Rothm.		<i>JN189415.1/</i> isolate E259	<i>JN189633.1/</i> isolate E259	<i>JN189197.1/</i> isolate E259	<i>AY278404.1/</i> -	<i>JN189309.1/</i> isolate E259	<i>JN189523.1/</i> -
<i>Dryopteris pulcherrima</i> Ching		<i>JN189406.1/</i> isolate E108	<i>JN189624.1/</i> isolate E108	<i>JN189188.1/</i> isolate E108	<i>JN189083.1/</i> isolate E108 AY268811.1/ -	<i>JN189300.1/</i> isolate E108	<i>JN189515.1/</i> isolate E108

Species	<i>matK</i> GenBank accession/ voucher or isolate	<i>psbA-trnH</i> GenBank accession / voucher or isolate	<i>rbcl-accD</i> GenBank accession / voucher or isolate	<i>rps4-trnS</i> GenBank accession / voucher or isolate	<i>trnL-trnF</i> GenBank accession / voucher or isolate	<i>trnP-petG</i> GenBank accession / voucher or isolate	<i>rbcl</i> GenBank accession / voucher or isolate
<i>Dryopteris pycnopteroides</i> (Christ) C. Chr.		AB575781.1/ TNS:764373	JN189690.1/ isolate NH22	JN189258.1/ isolate NH22 DQ191868.1/ SG Lu/C79	AY268799.1/ R. Moran, COLO	JN189364.1/ isolate NH22	AB575160.1/ TNS:764373 AY587114.1/ -
<i>Dryopteris remota</i> Hayata	JQ941635.1/ Schuertpelz 528 (DUKE) JQ941616.1/ Moran.A (COLO)	JQ936655.1/ Moran (COLO)	JN189640.1/ isolate E285	JN189204.1/ Isolate E285 JQ936826.1/ Moran (COLO)	JQ682983.1/ Moran (COLO) AY268792.1/ R. Moran, COLO	JN189316.1/ isolate E285 JQ683062.1/ Moran (COLO)	AY268858.1/ - JQ935253.1/ Moran (COLO)
<i>Dryopteris reflexosquamata</i> Hayata		JN189494.1/ isolate NH86	JN189711.1/ isolate NH86	JN189279.1/ isolate NH86	JN189171.1/ isolate NH86	JN189385.1/ isolate NH86	JN189604.1/ isolate NH86
<i>Dryopteris rosea</i> (E.Fourn.) Mickel & Beitel		JN189416.1/ isolate E260	JN189634.1/ isolate E260	JN189198.1/ isolate E260	JN189093.1/ isolate E260	JN189310.1/ isolate E260	JN189524.1/ -
<i>Dryopteris rossii</i> C. Chr.		JN189423.1/ isolate E286	JN189641.1/ isolate E286	JN189205.1/ isolate E286	JN189100.1/ isolate E286	JN189317.1/ isolate E286	JN189531.1/ isolate E286
<i>Dryopteris sacrosancta</i> Koidz.		AB575784.1/ TNS:764377	JN189698.1/ isolate NH51	JX535843.1/ cult. Tsukuba Botanical Garden; VS764377 (TNS) JN189267.1/ AFSSE	JX535896.1/ cult. Tsukuba Botanical Garden; VS764377 (TNS) AY268812.1/ -	JN189373.1/ isolate NH51	AY268877.1/ - AB575163.1/ TNS:764377
<i>Dryopteris salvinii</i> (Bak.) Kuntze		JN189418.1/ isolate E264	JN189636.1/ isolate E264	JN189200.1/ isolate E264	JN189095.1/ isolate E264	JN189312.1/ isolate E264	JN189526.1/ isolate E264
<i>Dryopteris scottii</i> (Bedd.) Ching	JQ941623.1/ voucher RBC 202 (UC)	JN189444.1/ isolate E330	JN189659.1/ isolate E330	JN189226.1/ isolate E330 DQ191872.1/ SG Lu/B31	JX535898.1/ Hai He 4 (CTC) DQ514498.1/ MMO03-313	JN189337.1/ isolate E330	JX535863.1/ - DQ508775.1/ -

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<i>Dryopteris simplicior</i> Mickel & Beitel		<i>JN189419.1/</i> isolate E265	<i>JN189637.1/</i> isolate E265	<i>JN189201.1/</i> isolate E265	<i>JN189096.1/</i> isolate E265	<i>JN189313.1/</i> isolate E265	<i>JN189527.1/</i> isolate E265
<i>Dryopteris sordidipes</i> Tagawa		<i>JN189495.1/</i> isolate NH88 AB575793.1/ TNS:763050	<i>JN189712.1/</i> isolate NH88	<i>JN189280.1/</i> isolate NH88 JX535848.1/ S. Tagane & K. Fuse TF009; VS763050 (TNS)	<i>JX535902.1/</i> S. Tagane & K. Fuse TF009; VS763050 (TNS)	<i>JN189386.1/</i> isolate NH88	<i>AB575172.1/</i> TNS:763050
<i>Dryopteris stenolepis</i> (Baker) C.Chr.		<i>JN189445.1/</i> isolate E331	<i>JN189660.1/</i> isolate E331	<i>JN189227.1/</i> isolate E331 DQ191877.1/ SG Lu/B28	<i>JN189122.1/</i> isolate E331 AY268824.1/ -	<i>JN189338.1/</i> isolate E331	<i>AY268889.1/</i> -
<i>Dryopteris stewartii</i> Fraser-Jenk.		<i>JN189478.1/</i> isolate NH26	<i>JN189692.1/</i> isolate NH26	<i>JN189260.1/</i> isolate NH26	<i>AY278405.1/</i> -	<i>JN189366.1/</i> isolate NH26	<i>JN189586.1/</i> isolate NH26
<i>Dryopteris subbipinnata</i> W.H. Wagner & R.W.Hobdy		<i>JN189469.1/</i> isolate MA116	<i>JN189684.1/</i> isolate MA116	<i>JN189252.1/</i> isolate MA116	<i>AY268765.1/</i> Oppenheimer H50074, COLO	<i>JN189358.1/</i> isolate MA116	<i>JN189579.1/</i> isolate MA116
<i>Dryopteris sublucena</i> Christ		<i>JN189446.1/</i> isolate E332	<i>JN189661.1/</i> isolate E332	<i>JN189228.1/</i> isolate E332 DQ191878.1/ SG Lu/59	<i>JN189123.1/</i> isolate E332 AY268788.1/ Geiger 95, COLO DQ514501.1/ LJM080	<i>JN189339.1/</i> isolate E332	<i>JN189554.1/</i> isolate E332
<i>Dryopteris tokyoensis</i> (Matsum.) C.Chr.	JQ941651.1/ voucher Moran.B (COLO)	<i>AB575795.1/</i> TNS:766452	<i>JN189683.1/</i> isolate JGrok	<i>JN189251.1/</i> isolate JGrok	<i>AY268795.1/</i> R. Moran, COLO	<i>JN189357.1/</i> isolate JGrok	<i>AB575174.1/</i> TNS:766452
<i>Dryopteris uniformis</i> Makino		<i>AB575797.1/</i> TNS:774834	<i>JN189662.1/</i> isolate E333	<i>DQ191883.1/</i> -	<i>AY268806.1/</i> -	<i>JN189340.1/</i> isolate E333	<i>JN189555.1/</i> isolate E333

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<i>Dryopteris varia</i> (L.) Kuntze		<i>AB575798.1/</i> TNS:763911	<i>JN189663.1/</i> isolate E334	<i>JN189230.1/</i> - JX535852.1/	<i>AY736355.1/</i> -	<i>JN189341.1/</i> isolate E334	<i>AB575178.1/</i> TNS:763911
<i>Dryopteris wallichiana</i> (Spreng.) Hyl.		<i>JN189388.1/</i> -	<i>JN189607.1/</i> isolate E001	<i>DQ191884.1/</i> -	<i>AY268761.1/</i> -	<i>JN189282.1/</i> isolate E001	<i>AY268826.1/</i> -
<i>Dryopteris xanthomelas</i> (Christ) C.Chr.		<i>JN189449.1/</i> -	<i>JN189665.1/</i> isolate E337	<i>JN189232.1/</i> -	<i>JN189127.1/</i> -	<i>JN189343.1/</i> isolate E337	<i>JN189558.1/</i> isolate E337
<i>Dryopteris blanfordii</i> (C.Hope) C.Chr. subsp. <i>nigrosquamosa</i> (Ching) Fraser-jenk.	KT876448.1/ -	<i>KT876440.1/</i> -	<i>KT876441.1/</i> -	<i>KT876442.1/</i> -	<i>KT876443.1/</i> -	<i>KT876444.1/</i> -	<i>KT876447.1/</i> -
<i>Polystichum andersonii</i> Hopkins	JQ941662.1/ EBS 39 (WIS)	<i>JN189401.1/</i> isolate E073	<i>JN189620.1/</i> isolate E073	<i>JN189183.1/</i> isolate E073	<i>JN189078.1/</i> isolate E073	<i>JN189295.1/</i> isolate E073	<i>JN189510.1/</i> isolate E073

Vascular flora of Kenya, based on the Flora of Tropical East Africa

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Abstract

Kenya, an African country with major higher plant diversity, has a corresponding diversity of plant associations, because of the wide geographic distribution, diverse climatic conditions and soil types. In this article, all vascular plants of Kenya were counted based on the completed "Flora of Tropical East Africa (FTEA)", and all families and genera were revised using recent molecular systematics research, forming a "Synoptic List of Families and Genera of Kenyan Vascular Plants (SLFGKVP)". In total, there are 225 families, 1538 genera and 6293 indigenous species and 62 families, 302 genera and 588 exotic species in Kenya. The Fabaceae with 98 genera and 576 Species is the largest family. Two of the seven plant distribution regions of Kenya, K4 and K7 are the most species-richest areas with regard to both total and endemic species, with 3375 and 3191 total species and 174 and 185 endemic species in K4 and K7 respectively. While, K3 and K5 have the highest density of both total and endemic species. K1 has the lowest density of total species, and K2 has the lowest density of endemic species.

Keywords

East Africa, Kenya, FTEA, vascular plants, molecular systematics, diversity

Introduction

The Republic of Kenya (Fig. 1) lies in the equatorial zone of eastern part of Africa continent, between latitudes 4°N and 4°S and between longitudes 34°E and 42°E. It is bordered by Tanzania to the south, Uganda to the west, Ethiopia to the north, Sudan to the north-west, Somalia to the east, and the Indian Ocean to the south-east (Orodho 2006). Kenya covers a total area of 582,646 km², including 569,253 km² land area and 13,393 km² water area. The equator runs through the central part of Kenya, intersecting the Great Rift Valley, forming the famous "East Africa Cross". Mt. Kenya is the largest ancient extinct volcano in Great Rift Valley areas. It is the highest mountain of Kenya and the second highest in Africa with a height of 5,199 m a.s.l. (the first one being Mt. Kilimanjaro, 5,892 m a.s.l.) (Ojany and Ogendo 1973, Speck 1982, Sombroek et al. 1982, MU 2009).

According to the early administrative division of Kenya, seven plant distribution regions (K1–K7) had been divided by "Flora of Tropical East Africa" (hereafter FTEA) (FTEA editors 1952–2012) (Fig. 1). K1 represents the "Northern Frontier Province" which is located in the northern part of Kenya. K2 represents the "Turkana Province" which is located in the northwest part of Kenya. K3 represents the "Rift Valley Province" which is located in western part of Kenya. K4 represents the "Central Province" which is located in central part of Kenya. K5 represents the "Nyanza Province" which is located in southwest part of Kenya. K6 represents the "Masai Province" which is located in southern part of Kenya. K7 represents the "Coast Province" which is located along the coastal area of Kenya (Polhill 1988).

The soils of Kenya are diverse ranging from the coral types on the coastal areas to the alluvial, swampy, and black cotton soils along river valleys and plains, to abundant volcanic soils on the high mountain regions (Orodho 2006). Climatically Kenya is considered part of the tropical monsoon area belonging to the tropical savanna climate region, and the annual maximum temperature is from 22 to 26 °C, and annual minimum is from 10 to 14 °C (Gao 2004). Rainfall patterns varies with different seasons around the year, that is, most parts experience high rainfall from March to June and October to December, and the rest are dry spells. Annual rainfall from the southwest to the northeast decreasing from 2000 mm to 250 mm (Gao 2004, Orodho 2006).

Topography, climatic conditions, soil types and human activity, all have a great impact on the vegetation types in Kenya. Three main types and several sub-types of Kenyan vegetation had been recognized by Edwards (1940): i) Forest types, subdividing into mountain forest, thorn forest, and mangrove forest; ii) Grasslands (including parkland or savannah grasslands), subdividing into mountain grassland, high moisture savannah, *Acacia*-tall grass savannah and open grassland (tall grass); iii) Semi-arid grasslands, subdividing into *Acacia*-desert grass savannah and open grassland (desert grass), and desert shrub-desert grass. In recent years, researchers from University of Copenhagen and The World Agroforestry Centre constructed the Potential Natural Vegetation of eight countries from eastern and southern Africa (VECEA team 2015).

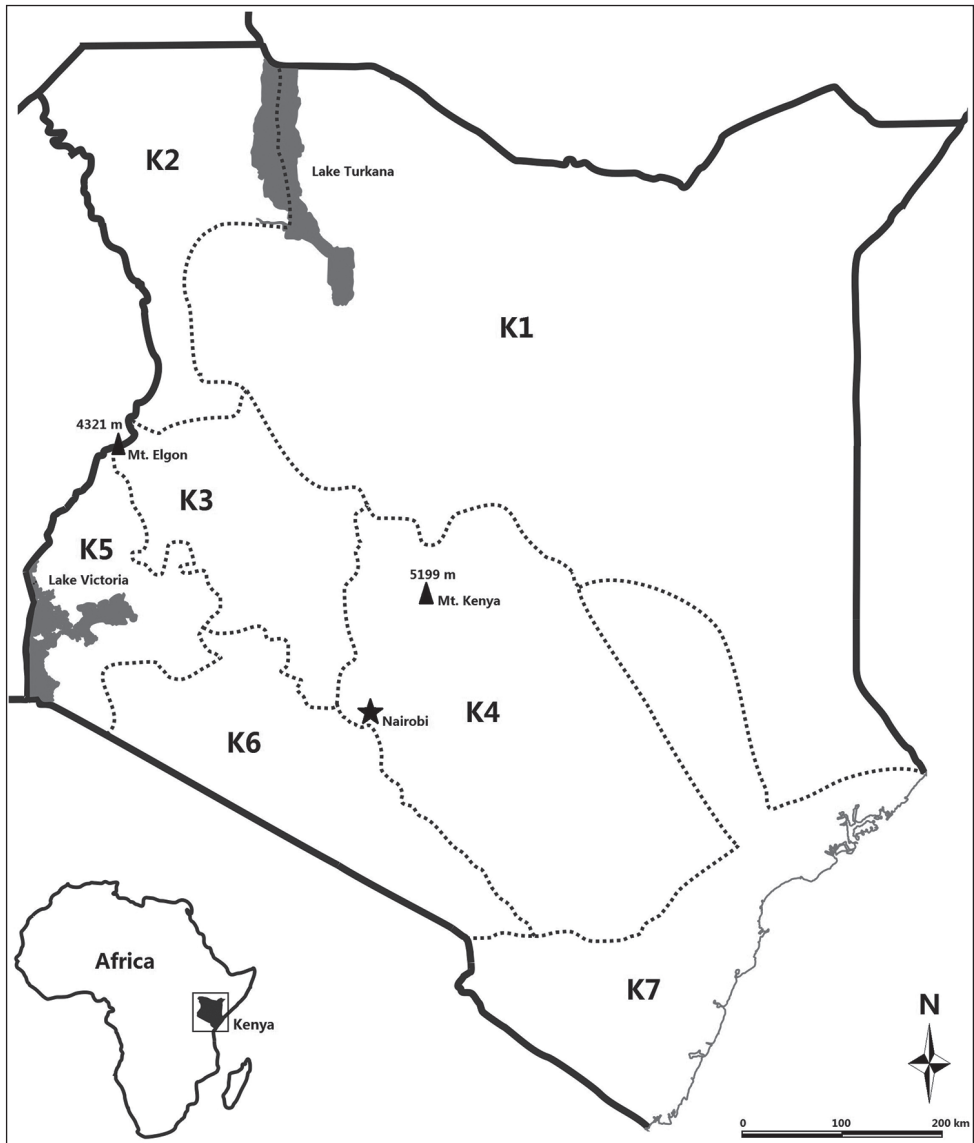


Figure 1. Kenya and its location. **K1–K7** indicates plant distribution regions in "Flora of Tropical East Africa" (FTEA editors 1952–2012).

The diverse vegetation types of Kenya include numerous indigenous plant species, many of which are endemic, such as *Dendrosenecio keniensis* (Asteraceae) in K4 (Mt. Kenya), *Impatiens fischeri* (Balsaminaceae) in K3 and K4, *Habenaria keniensis* (Orchidaceae) in K3, K4 and K5, and the recently published species *Sedum keniense* (Crasulaceae) in K4 (Mt. Kenya) (Zhou et al. 2016a). Over the years, botanists from all over the world have studied Kenyan plants and accumulated a series of monographs. In 1961, Dale I.R. and Greenway P.J. published "Kenya Trees and Shrubs", which recorded

about 1000 trees and shrubs of Kenya (Dale and Greenway 1961), and Beentje H.J. republished this book in 1994 reviewing some species and adding lianas (Beentje 1994). In 1974, Agnew A.D.Q. published "Upland Kenya Wild Flowers" and republished it in 1994, recording over 3000 herbs and ferns of Kenyan upland areas; the third edition of which was published in 2013, with the addition of grasses and sedges (Agnew 1974, 2013, Agnew and Agnew 1994). Other books on Kenya plants include, "The wild flowers of Kenya" (Blundell, 1982), "An illustrated manual of Kenya Grasses" (Ibrahim and Kabuye 1987), "The beautiful plants of Kenya" (Karmali 1988), "Orchids of Kenya" (Stewart 2003), "Useful trees and shrubs for Kenya" (Maundu and Tengnas 2005), "Common plants of Kenya" (Wang et al. 2016), and some other books with a broader coverage of whole east Africa, such as "Collins guide to the wild flowers of East Africa" (Blundell 1987), "Field Guide to Acacias of East Africa" (Dharani 2006), "Medicinal Plants of East Africa, 3rd Edition" (Kokwaro 2009), "Medicinal Plants of East Africa-An Illustrated Guide" (Dharani and Yenesew 2010), "Field Guide to Common Trees and Shrubs of East Africa, 2nd Edition" (Dharani 2011). "Flora of Tropical Africa" was the first flora record of Kenya plants, which included 13000 plants of tropical Africa and divided into 10 volumes (Daniel et al. 1868–1933). "Flora of Tropical East Africa (FTEA)" covers plants from Uganda, Kenya and Tanzania, which has been edited several times since 1952 and completed in 2012. To date, FTEA records c.125000 plant species from the three countries. Shortcomings of FTEA on Kenya plants are that: i) taxa are still under-represented; ii) New families, genera and taxa have not been reviewed and recorded; iii) Families have not been arranged using the recent available botanical systems.

Plant systematics has been one of the hottest research areas in botanical studies (Singh 2010, Simpson 2010). In the early years, some plants systems were published based on morphological characteristics, such as Ching's system on ferns (Ching 1978a, b), Cheng's system about gymnosperms (Cheng and Fu 1978), and Takhtanjan's system, Cronquist's system and Engler's system about angiosperms (Yang et al. 2004, Liu et al. 2015). Lycophytes had been separated from ferns according to recent molecular systematics evidences, and was positioned as the sister group to Euphyllophytes (including Spermatophytes and Monilophytes) (Pryer et al. 2004, Liu et al. 2009). Smith et al. (2006) proposed a new classification system on Monilophytes, dividing ferns into 4 classes, 10 orders and 37 families, and later some new families were established and new classification system was proposed (Christenhusz et al. 2011b, Liu et al. 2013, Zhang and Zhang 2015). Recently, the Pteridophyte Phylogeny Group proposed a community-derived classification on extant lycophytes and ferns, including 2 classes, 14 orders and 51 families (PPG I 2016). Based on branch taxonomy and molecular systematics results, the Angiosperm Phylogeny Group (APG) proposed a new classification, refined over four publications (APG 1998, APG II 2003, APG III 2009, APG IV 2016). Compared with the APG III system, the APG IV system proposed two additional informal major clades, namely superrosids and superasterids, and recognized 5 new orders, namely Boraginales, Dilleniales, Icaciniales, Metteniuales and Vahliales, resulting in a total of 64 orders and 416 families of Angiosperms (APG IV 2016).

This article summarizes families and genera of Kenya plants based on FTEA, and combined with other recent molecular systematic research. Our goal was to answer the following questions: i) What is the total number of plant species found in Kenya? ii) Which families and genera are the largest? iii) Which part in Kenya contains the highest plant species richness, and iv) What measures can be carried out so as to protect and conserve the Kenyan plants?

Data and methods

All information is sourced from the FTEA, since it has recorded over 12500 vascular plants of Uganda (U1–U4), Kenya (K1–K7) and Tanzania (T1–T8), including some planted and naturalized species. Each family has been published in one volume, although some big families with 2–4 volumes also have been done, such as Leguminosae (4 volumes), Poaceae (3 volumes), Rubiaceae (3 volumes) and Compositae (3 volumes). Except for some exotic plants, FTEA has described each species, the distribution regions, and characteristic habitat. and recorded the voucher specimens.

Here, we conducted a census of all Kenyan species recorded by FTEA, gathering distribution information on endemic plants, exotic plants and naturalized species. We then reviewed the families and genera of all the species based on recent systematic research, creating a "Synoptic List of Families and Genera of Kenyan Vascular Plants (SLFGKVP)" (see Supplementary material 1). Families of Lycophytes and monilophytes are revised by PPG I system (PPG I 2016), families of gymnosperms are revised the system advocated by Christenhusz et al. (2011a), and families of angiosperms are revised by APG IV system (APG IV 2016). We analyzed the largest families and genera, as well as the number of endemic and exotic species of Kenya plants. We also compared total and endemic species number, and species density among different regions (K1–K7) of Kenya.

Results

Families, genera and species of indigenous plants

A total of 6293 Kenyan indigenous vascular plants were recorded by FTEA, representing 225 families and 1538 genera, of which 95.5% are angiosperms, 4.0% are monilophytes, 0.37% are Lycophytes and a very small percentage are gymnosperms. Three families, 5 genera and 23 species belong to lycophytes; 27 families, 87 genera and 252 species belong to monilophytes; 3 families, 3 genera and 5 species belong to gymnosperms; 192 families, 1443 genera and 6013 species belong to angiosperms. Based on new systematic systems, the families number of SLFGKVP decrease to 224, including 3 families of Lycophytes, 28 families of monilophytes, 3 families of gymnosperms and 190 families of angiosperms. Because we fully accepted FTEA's treatment on synonyms, the genera and species number kept the same.

The top three species-rich families of Kenyan indigenous vascular plants are Fabaceae, Poaceae and Asteraceae, which contain 576, 565 and 403 species, respectively. The top three species-rich genera are *Euphorbia* (Euphorbiaceae), *Cyperus* (Cyperaceae) and *Crotalaria* (Fabaceae), which contain 95, 94 and 93 species, respectively. The most species-rich family and genus of monilophytes are Aspleniaceae and *Asplenium* with 51 species (Table 1).

Endemism

There is no endemic family in Kenya, but there is one endemic genus, which is *Dibrachionostylus*, a monotypic genus of Rubiaceae restricted to K4. The genus has only one species, *D. kaessneri* and is closely related to *Hedythyrus* and *Agathisanthemum* (Verdcourt 1976).

In total, 467 endemic species including unnamed ones were recorded in FTEA. The endemic taxa of Lycophytes are mainly in *Isoetes* (Isoetaceae), 3 species out of 4 in this genus in Kenya being endemic. *Lycopodium aberdaricum* is also an endemic lycophyte only found in K3 and K4. There are only 4 endemic species in monilophytes and 3 belong to Marsileaceae. Another unnamed species of *Asplenium* (Aspleniaceae) recorded as endemic. There are no endemic gymnosperms. However, in angiosperms, 459 species are endemic, with the top contributing families for endemics the Euphorbiaceae (50 endemic species), Fabaceae (40 endemic species) and Acanthaceae (33 endemic species) (Table 2). There are 12 families with more than 10 endemic species, with the endemic ones in Asphodelaceae contributing 38.33% of the total species in that family (Table 2).

Exotic plants of Kenya

A total number of 588 exotic plants including 212 naturalized species of Kenya were recorded in FTEA, which belong to 62 families and 302 genera. The top 10 exotic families and their species number are shown in Table 3. Myrtaceae, Fabaceae, Asteraceae and Solanaceae are the 4 largest families which have more than 40 exotic species, and *Eucalyptus* (Myrtaceae) is the largest exotic genus with 99 exotic species.

Distribution patterns

The total number of indigenous and endemic species within each distribution region was counted (Fig. 2). Because species in gymnosperms are few, there is no significant uniformity (Fig. 2c). The results of Lycophytes (Fig. 2a), monilophytes (Fig. 2b), angiosperms (Fig. 2d) and the total species (Fig. 2e; Table 4) had similar patterns among seven regions and showed that K4 and K7 are the two most species-rich regions with regard to both total and endemic species. If the areas of different regions were taken into account, K3 and K5 have the highest density of total vascular plants, with ca. 776 species/10000 km² in K3 and ca. 768 species/10000 km² in K5. K3 and K7 have the

Table 1. The 13 largest families with more than 100 species, and the 12 largest genera with more than 50 species.

Family	Genera	Species	Genus	Species
Fabaceae	98	576	<i>Euphorbia</i> L. (Euphorbiaceae)	95
Poaceae	137	565	<i>Cyperus</i> L. (Cyperaceae)	94
Asteraceae	99	403	<i>Crotalaria</i> L. (Fabaceae)	93
Acanthaceae	42	279	<i>Indigofera</i> L. (Fabaceae)	70
Cyperaceae	29	274	<i>Ipomoea</i> L. (Convolvulaceae)	57
Rubiaceae	74	265	<i>Aloe</i> L. (Asphodelaceae)	55
Orchidaceae	47	243	<i>Plectranthus</i> L'Hér. (Lamiaceae)	54
Apocynaceae	70	235	<i>Justicia</i> L. (Acanthaceae)	54
Euphorbiaceae	29	219	<i>Vernonia</i> Schreb. (Asteraceae)	52
Malvaceae	40	219	<i>Asplenium</i> L. (Aspleniaceae)	51
Lamiaceae	32	206	<i>Commiphora</i> Jacq. (Burseraceae)	51
Convolvulaceae	20	118	<i>Eragrostis</i> Wolf (Poaceae)	50
Asparagaceae	13	104		

Table 2. The number of endemic plant species and total species of the top 12 families.

	Endemic species	Species in family	Endemism in family
Euphorbiaceae	50	219	22.83%
Fabaceae	40	576	6.94%
Acanthaceae	33	279	11.82%
Rubiaceae	29	265	10.94%
Asteraceae	29	403	7.19%
Asphodelaceae	23	60	38.33%
Apocynaceae	23	235	9.78%
Poaceae	18	565	3.19%
Lamiaceae	15	206	7.28%
Cyperaceae	12	274	4.38%
Vitaceae	12	63	19.05%
Cucurbitaceae	10	80	12.50%

Table 3. The number of exotic plant species of the top ten families in Kenya.

Family	Exotic species
Myrtaceae	133
Fabaceae	54
Asteraceae	44
Solanaceae	42
Bignoniaceae	25
Euphorbiaceae	25
Lamiaceae	24
Amaryllidaceae	22
Apocynaceae	19
Malvaceae	18

Table 4. The number and density of total and endemic species in K1–K7 regions in Kenya.

Regions	Area/10000 km ²	Total species	Endemic species	Density of total species	Density of endemic species
K1	26.79	2302	161	85.93	6.01
K2	4.55	1350	16	296.70	3.52
K3	3.7	2871	90	775.95	24.32
K4	9.29	3375	175	363.29	18.84
K5	2.72	2090	20	768.38	7.35
K6	4.44	2108	50	474.77	11.26
K7	6.77	3191	185	471.34	27.33

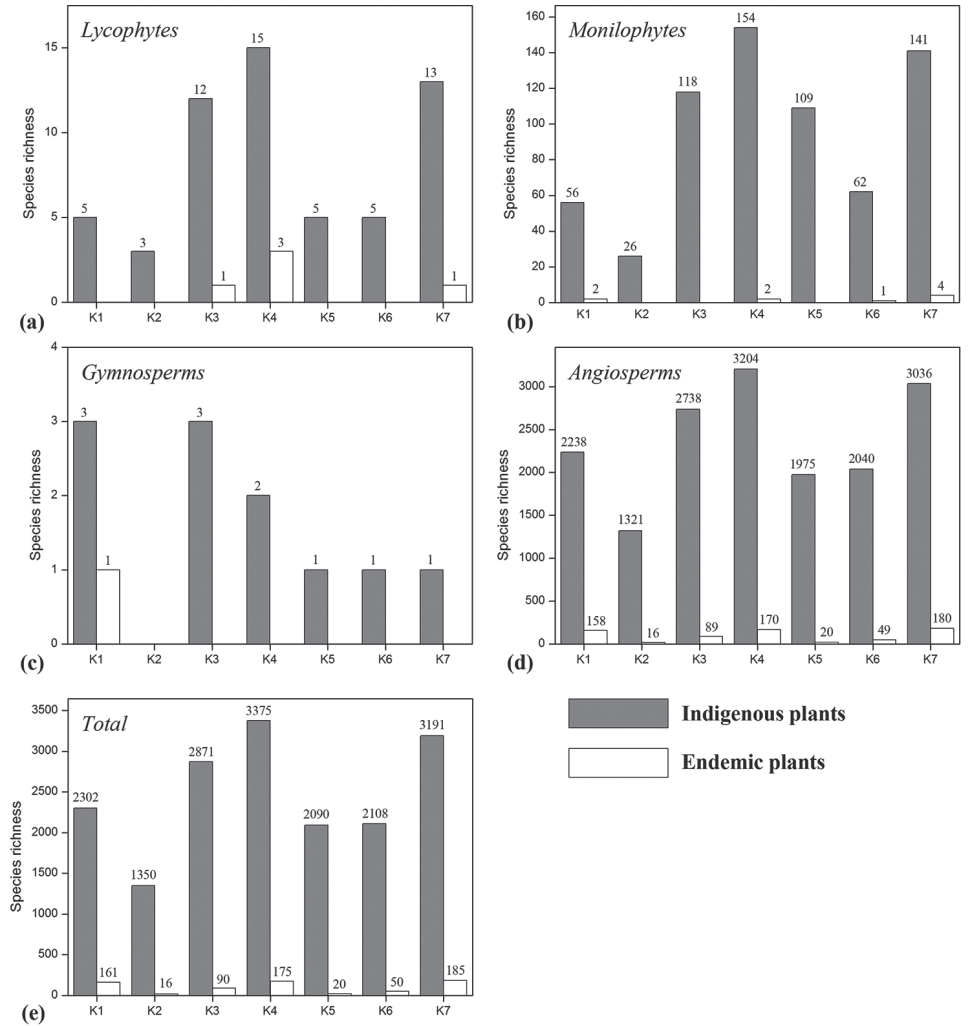


Figure 2. Lycophytes (a), monilophytes (b), gymnosperms (c), angiosperms (d) and total (e) species richness of indigenous (grey bars) and endemic (white bars) vascular plants in K1–K7 regions of Kenya.

highest density of endemic vascular plants, with ca. 24 species/10000 km² in K3 and ca. 27 species/10000 km² in K7. In contrast, K1 has the lowest density of total species (ca. 86 species/10000 km²) and K2 has the lowest density of endemic species (ca. 4 species/10000 km²) (Table 4).

Discussion

The diversity of Kenya vascular plants

Kenya has many unique geographical features resulting in the great diversity of plants. FTEA has recorded 6881 vascular plants in Kenya (including 588 exotic species), although the total species number is estimated to be 7000 to 8000 or more. The number of species is still increasing because of new records, new species, new cultivated and invasive plants. Recently, researchers from China and Kenya have found several new species from Kenya, such as *Sedum keniense* (Crassulaceae) (Zhou et al. 2016a), *Zehneria subcoraicea* (Cucurbitaceae) (Zhou et al. 2016b), *Z. longiflora* (Cucurbitaceae) (Wei et al. 2017), *Cissampelos keniensis* (Menispermaceae) (Zhou et al. 2017) and *Adenia angulosa* (Ngumbau et al. 2017).

The top three species-rich families of Kenya are Fabaceae, Poaceae and Asteraceae, which are also the largest families in the world, having 745 genera/19560 species, 707 genera/11337 species and 1620 genera/23600 species respectively (Stevens 2012). The proportion of Kenyan plants within the top total species in the world in these families is very small, though the endemism in them is relatively high (Table 1, 2).

Totally, 3375 indigenous vascular plants have been found in K4 (Fig. 2e; Table 4). The main vegetation types of K4 is Afromontane rain forest, Afromontane moist transitional forest, Dry *Combretum* wooded grassland and *Acacia-Commiphora* deciduous bushland-thicket (VECEA team 2015). The two most species-rich areas of K4 are Mt. Kenya and its neighboring Aberdare Ranges (Fig. 1). Montane forest vegetation as well as the unique Afroalpine vegetation also have high plant diversity and special species (Mittermeier et al. 2004, 2011, Gehrke and Linder 2014), such as *Vitex keniensis* (Lamiaceae), *Impatiens fischeri* (Balsaminaceae), *Cyphostemma grahamii* (Vataceae), *Ranunculus keniensis* (Ranunculaceae), *Dendrosenecio keniensis* (Asteraceae), *Lobelia deckenii* (Campanulaceae) (Young 1985, Bussmann 1995). There is also an endemic genus, *Dibrachionostylus* (Rubiaceae), recorded in K4 (Verdcourt 1976). There are at least 774 species, subspecies and varieties of vascular plants within the Aberdare Ranges, belonging to 213 genera, 128 families (Schmitt 1991). About 880 species, subspecies and varieties belonging to 479 genera and 146 families from Mt. Kenya below 3200 m altitude were recorded by Beentje (1991) and Bussman (1994), and a recent research results showed that more than 1500 vascular species are growing in this area, representing over 20% of total plants in Kenya (Zhou 2017). The Coastal Forests of Eastern Africa is one of the two diversity hotpots in east Africa, which is expanded to Somalia and Mozambique (Mittermeier et al. 2004, 2011). In our study, we recognise 3191 indigenous plants and 185 endemic plants in K7 (Fig. 2e; Table 4). K7 is located in the coastal areas of Kenya (Fig. 1) and has highest density of

endemic plants with ca. 27 species/10000 km², though the density of total indigenous plants is not very high with ca. 471 species/1000 km² (Table 4). The two main vegetation types of K7 are *Acacia-Commiphora* deciduous bush land-thicket and Coastal mosaic (VECEA team 2015). A number of tropical coastal plants are living here, such as *Ceriops tagal* and *Bruguiera gymnorhiza* (Rhizophoraceae), *Sonneratia alba* (Lythraceae), *Xylocarpus granatum* (Meliaceae) and *Lumnitzera racemosa* (Combretaceae) (Dharani 2011).

Flora of Kenya

To date, there is no known regional flora within Kenya. "Flora of Tropical Africa", "Flora of East Tropical Africa" and other floras all have a long publication history. However, some information in them is not accurate, and a lot of species are still unnamed. In recent years, many new species, new records and new taxonomic treatments have been found and proposed. A series of surveys on plant resources at some biodiversity hotspots of Kenya have been carried out. Numerous plant checklists covering different regions of Kenya have been published, such as Mt. Elgon (Tweedie 1976), Mt. Nyiru (Bytebier and Bussmann 2000), Taita hills (Thijs et al. 2013), Nandi Forests (Girma et al. 2015). Therefore, an up-to-date and comprehensive flora (i.e. "Flora of Kenya") is urgently needed, as this will further promote further botanical studies and help action conservation measures to protect the plant diversity in Kenya. At present, Chinese researchers are actively involved in the preparation of a new Flora of Kenya, and contributing their skills to help the Kenyan people determine exactly what plants live in Kenya, to enable better protection for them, and to develop and utilize where practical the extremely high diversity of Kenyan plants.

Conservation of plant diversity in Kenya

Due to human disturbance and destruction, exotic plant invasion, climate change, deterioration of ecological environment and other factors, the plant diversity of Kenya is also facing severe pressures (FAO 1981, Barnes 1990, Bussmann 1996, Gathaara 1999). For example, at the foot of Mt. Kenya, a large area of the original forest was cut down for plantations of *Cupressus lusitanica*, *Pinus patula* and *Eucalyptus* spp. for timber and also some cultivations of crops such as banana (*Musa* spp.), potato (*Solanum tuberosum*) and maize (*Zea mays*) (Bussmann 1996, Gathaara 1999). K3, K4, K5 and K7 have high plant diversity and high density of total and endemic plants. Consideration of better protection measures of a representation of these distribution regions is urgently needed.

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Supplementary material I

The Synoptic List of Families and Genera of Kenyan Vascular Plants (SLFGKVP)

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Data type: species data

Explanation note: There are 6293 indigenous and 588 exotic vascular plants of Kenya in total, which belong to 1752 genera and 223 families. Families of Lycophytes and monilophytes are arranged by PPG I system (PPG I 2016), families of gymnosperms are arranged by Christenhusz gymnosperms system (Christenhusz et al. 2011a), and families of angiosperms are arranged by APG IV system (APG IV 2016).

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