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A revision of *Xylopia* L. (Annonaceae): the species of Madagascar and the Mascarene islands

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ABSTRACT

We recognize 30 species of the pantropical genus *Xylopia* L. from Madagascar and an additional three species from the Mascarene Islands. Of the six sections of the genus, three are represented in the region: sect. *Xylopia*, sect. *Verdcourtia*, and sect. *Stenoxylopia*. All species are endemic, and many are microendemics of conservation concern. The greatest species richness occurs in humid forests below 1000 m. Taxonomic review supports the hypothesis that the genus dispersed to Madagascar from continental Africa five times. Ten new species are described: *Xylopia anomala* D.M.Johnson & N.A.Murray, sp. nov., *X. australis* D.M.Johnson & N.A.Murray, sp. nov., *X. galokothamna* D.M.Johnson & N.A.Murray, sp. nov., *X. lokobensis* D.M.Johnson & N.A.Murray, sp. nov., *X. lokobensis* D.M.Johnson & N.A.Murray, sp. nov., *X. navelonarivoi* D.M.Johnson & N.A.Murray, sp. nov., *X. marojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. navelonarivoi* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., *N. ceripsila* D.M.Johnson & N.A.Murray, sp. nov., *X. navelonarivoi* D.M.Johnson & N.A.Murray, sp. nov., *X. navelonarivoi* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., *M. celevophylla* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., and *X. sclerophylla* D.M.Johnson & N.A.Murray, sp. nov. An identification key, technical descriptions, illustrations, and distribution maps are provided.

RÉSUMÉ

Révision du genre Xylopia L. (Annonaceae): les espèces de Madagascar et des îles Mascareignes.

Nous reconnaissons 30 espèces du genre pantropical *Xylopia* L. qui viennent de Madagascar et trois espèces additionnelles des Mascareignes. Des six sections du genre, trois sont représentées dans la région : sect. *Xylopia*, sect. *Verdcourtia*, et sect. *Stenoxylopia*. Toutes les espèces sont endémiques, et beaucoup sont des espèces micro-endémiques dont l'état de conservation est préoccupant. La plus grande richesse spécifique se trouve dans les forêts humides en dessous de 1000 m. La révision taxonomique soutient l'hypothèse que le genre s'est dispersé à Madagascar depuis l'Afrique continentale cinq fois. Dix nouvelles espèces sont décrites : *Xylopia anomala* D.M.Johnson & N.A.Murray, sp. nov., *X. australis* D.M.Johnson & N.A.Murray, sp. nov., *X. carinata* D.M.Johnson & N.A.Murray, sp. nov., *X. galokothamna* D.M.Johnson & N.A.Murray, sp. nov., *X. lokobensis* D.M.Johnson & N.A.Murray, sp. nov., *X. narojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. narojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. narojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., *X. narojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. narojejyana* D.M.Johnson & N.A.Murray, sp. nov., *X. retusa* D.M.Johnson & N.A.Murray, sp. nov., *X. tetusa* D.M.Johnson & N.A.Murray, sp. nov., *B. tetus* determination, des descriptions techni

KEY WORDS *Xylopia*, pantropical Annonaceae, Madagascar, Mascarene, islands, long-distance dispersal, bird/lemur dispersal, microendemism, conservation, lectotypification, new species.

MOTS CLÉS Xylopia, Annonaceae pantropicales, Madagascar, Mascareignes, dispersion à longuedistance, dispersion par oiseaux/ lémuriens, micro-endémisme, conservation, lectotypification, espèces nouvelles.

INTRODUCTION

Within the early-divergent angiosperm family Annonaceae the genus *Xylopia* L. is unique in its pantropical distribution and, with nearly 200 species of trees, shrubs, and lianas, is the second largest genus in the family. The plants bear distinctive fruits composed of clusters of monocarps that dehisce when ripe, displaying the seeds against an endocarp of contrasting color (Johnson & Murray 2018). Twenty-five endemic species had previously been described from the floras of Madagascar and the Mascarene Islands of La Réunion and Mauritius (Cavaco & Keraudren 1958; Keraudren-Aymonin 1980; Callmander *et al.* 2009), many from only one or two collections.

Xylopia arose in continental Africa and diversified into six evolutionary lines that we recognize as sections (Stull *et al.* 2017, Johnson & Murray 2018). A sample of 19 accessions from Madagascar and the island of Mauritius analyzed in the Stull *et al.* (2017) study showed the Madascar and Mascarene samples to represent three of the five evolutionary lines present in Africa, and the evidence that there have been at least five separate colonizations of the islands from Africa. Eight of the 19 Madagascar accessions could not be identified as a known species at that time. In order to clarify the taxonomy of the Madagascar and Mascarene species of *Xylopia*, we conducted the following revisionary study.

TAXONOMIC HISTORY

Aublet (1775), in concluding his description of "Waria zeylanica" for French Guiana, reported that the species was also found on the Isle de France [Mauritius], where two variants were distinguished by local people as the "bois blanc à grande feuille" and the "bois blanc à petite feuille". He reported that the two species occurred in abundance in the ravines and forests of the island at the base of the mountains near Port Louis and Moka. With this brief account he provided the first published record of Xylopia from the Madagascar and Mascarene region. Lamarck (1785) cited Aublet's report in his description of Uvaria aromatica Lam., which, according to his description, encompassed plants from Africa and South America as well, and in 1786 he described two species of "Anona", A. grandiflora Lam. and A. amplexicaulis Lam., the former reported from Madagascar and l'Isle de Bourbon [La Réunion] and the latter from l'Isle de France (Mauritius) and Madagascar, in both cases on the basis of collections and observations of Commerson. Persoon (1806) distinguished the Réunion and Madagascar plants of A. grandiflora, recognizing the latter as A. grandiflora * [= var.] *madagascariensis* Pers.

In 1817 Dunal, in the first monograph of Annonaceae, provided illustrations of *A. grandiflora* and *A. amplexicaulis*, rejected Persoon's variety, and maintained the link of Aublet's plants to *Uvaria aromatica*, which he transferred to the genus *Unona* L.f. In 1837, Bojer enumerated four species of Annonaceae indigenous to the island of Mauritius: *Annona amplexicaulis* Lam., *A. grandiflora* Lam., *A. pyriformis* Bojer, and *Unona aromatica* (Lam.) Dunal, the latter continuing to be based on the report of Aublet.

The generic concept of Xylopia was clarified during the first half of the 19th century, and Baillon (1864) worked from this improved understanding to review the known African species of Xylopia, including plants from Madagascar and the Mascarene islands (summarized in Johnson & Murray 2018). He pointed out that Annona grandiflora and A. amplexicaulis had numerous ovules in each carpel, and that their carpels were not fused at the base but were surrounded by a cuplike sac. He stressed that these characteristics were discordant with Annona but much like those of Xylopia, and accordingly moved them to the latter genus, although he segregated them in a distinct section he named Pseudanona. He renamed Annona grandiflora as Xylopia lamarckii Baill. because the epithet grandiflora was preoccupied in Xylopia, described two new species from Madagascar, X. buxifolia Baill. and X. lastelliana Baill., and described one additional species, X. richardii Boivin ex Baill., from the island of La Réunion. By Baillon's accounting, there were now four Xylopia species known from Madagascar (X. amplexicaulis (Lam.) Baill., X. buxifolia, X. lamarckii, and X. lastelliana), one from Mauritius (X. lamarckii), and two from La Réunion (X. lamarckii and X. richardii). Baker (1877) did not accept Baillon's transfer of A. grandiflora and A. amplexicaulis to Xylopia, but validly published the name An[n]ona pyriformis Bojer ex Baker. In 1882 Baillon described Xylopia humblotiana Baill. from eastern Madagascar. At the beginning of the 20th century Safford (1913) chose to stress the distinctive large fleshy petals of X. lamarckii and X. amplexicaulis in raising Xylopia section *Pseudanona* to the level of a distinct genus.

As the 20th century began Xylopia did not appear to be diverse within the Madagascar and Mascarene region, particularly in comparison to the number of Xylopia species enumerated in the monograph of African Annonaceae that had been published by Engler & Diels (1901). The collections and explorations of Perrier de la Bâthie in the early 1900s, however, led to the description of seven new Xylopia species from Madagascar by Diels (1925), who also provided a key to the species known from the island. Additional Madagascar Xylopia species were recognized by Ghesquière in the 1930s but were not published until the researches of Cavaco & Keraudren (1956, 1957; Cavaco 1957) in preparation for the Flore de Madagascar et des Comores treatment of the Annonaceae (Cavaco & Keraudren 1958). These authors more than doubled the list of Xylopia species for Madagascar, recognizing 23 species, many based on the collections made by R. Capuron during the 1950s. Pseudanona was maintained at the generic level by Fries (1959) and Hutchinson (1964), but was returned to synonymy under *Xylopia* by Keraudren-Aymonin (1980).

Comprehensive study of Annonaceae systematics has supported the inclusion of *Pseudanona* in *Xylopia* (Walker 1972b; Stull *et al.* 2017), and established the monophyly of the genus (Chatrou *et al.* 2012). Intensive collecting over the last 40 years has expanded knowledge of diversity on Madagascar for many plant groups, including *Xylopia*. Collecting in the Galoka Mountain massif led to the recognition of the first new *Xylopia* species since Cavaco and Keraudren's flora treatment, *X. kalabenonensis* D.M.Johnson, Deroin, & Callmander (Callmander *et al.* 2009). Phylogenetic study of *Xylopia* allowed us to classify the species of the genus into six sections: sect. *Neoxylopia* Engl. & Diels (continental Africa), sect. *Rugosperma* D.M. Johnson & N.A. Murray (Asia), sect. *Ancistropetala* (Engl. & Diels) D.M. Johnson & N.A. Murray (continental Africa), sect. *Xylopia* (tropical America, continental Africa, Madagascar, Mascarene Islands), and sect. *Stenoxylopia* Engl. & Diels (continental Africa, Madagascar, and Australasia) (Stull *et al.* 2017), with the sixth, sect. *Verdcourtia D.M.* Johnson & N.A. Murray (East Africa, Madagascar), characterized and separated from sect. *Stenoxylopia* more recently (Johnson & Murray 2018).

METHODS

We studied *c.* 370 collections of *Xylopia* from Madagascar, Mauritius, and La Réunion from the following herbaria: A, B, BM, BR, CAS, DSM, EA, F, G, GH, K, L, M, MAU, MO, NY, OWU, P, PRE, RSA, SING, US, and WAG. These specimens have been examined on loan or from digital images. All measurements of plant parts, unless otherwise indicated, are based on dried herbarium specimens. Measurements of fine details of indument, flower parts, and seeds were made using an ocular micrometer mounted on a stereomicroscope and measuring to the nearest 0.1 mm. Publication dates, when unclear, were obtained from the Taxonomic Literature II (TL-II) series (Stafleu & Cowan 1976 and succeeding volumes). Standard forms of author names follow Brummitt & Powell (1992). Specimen citations are organized alphabetically by Province name, and then alphabetically by principal collector.

The distribution maps are based on herbarium specimen data. In cases where latitude and longitude coordinates were not provided on the specimen label we determined the coordinates from published maps and consultation of online gazetteers. Coordinates were assembled in an Excel spreadsheet for each species, and imported into ArcGIS to produce the final maps. A summary map of species diversity per $0.5 \times 0.5^{\circ}$ grid cell was produced using the individual species maps in ArcGIS. The individual species maps were also used to calculate Extent of Occurrence (EOO) and Area of Occupancy (AOO), following IUCN Red List guidelines (IUCN Species Survival Commission 2012). For the AOO calculations a grid cell size of 2×2 km was used.

MORPHOLOGY

On Madagascar, Mauritius, and La Réunion *Xylopia* species are most commonly small to midsized trees. Sixteen of the 33 species reach 15-25 meters; the tallest species, *X. beananensis* Cavaco & Keraudren and *X. fananehanensis* Cavaco & Keraudren, reach 30 meters. The remainder of species are treelets and shrubs (Fig. 1A) with the possible exception of *Xylopia lamarckii*, which is often described as a subscandent treelet or shrub although it does not seem to have specialized climbing structures. Trunk diameter is also generally smaller than elsewhere in the distribution of the genus, with only ten species reaching a d.b.h. of 30 cm or more; the maximum diameter reported was 55 cm for one specimen of *X. lastelliana*. At least half of the species are known to produce a distinctive branching pattern with two equal branches emerging from collateral buds of a single leaf axil (Fig. 1B), a characteristic of many Old World *Xylopia* species, primarily in sects. *Verdcourtia* and *Stenoxylopia* (Johnson *et al.* 1999, 2017; Johnson 2003; Johnson & Murray 2018). The Mauritian species *X. amplexicaulis* is notable for the erect orientation of its branches; *Xylopia* species typically have the horizontal branching from the main trunk typical of Annonaceae.

Most species are evergreen, but *X. sericolampra* Diels and *X. bemarivensis* Diels of the northern dry forests of Madagascar drop their leaves for part of the year. The leaf blades are chartaceous to coriaceous, commonly elliptic to oblong, and small to medium-sized with short petioles. The leaves of *X. retusa*, sp. nov., reaching at most 3.6 cm in length, are among the smallest in the entire family. The leaf blade margins can be flat, slightly recurved, or even strongly revolute. The secondary veins of most species are weakly brochidodromous near the margin; in *X. australis*, sp. nov., they may join to form a distinct intramarginal vein.

Many species have short, often appressed hairs on one or both leaf surfaces when young. The hairs are persistent and still conspicuous at leaf maturity in *X. bemarivensis, X. capuronii* Cavaco & Keraudren, *X. ghesquiereana* Cavaco & Keraudren, *X. kalabenonensis*, and *X. lastelliana. Xylopia buxifolia* and *X. lamii* Cavaco & Keraudren were reported by Kramer (1969) to have papillae on the abaxial leaf surfaces; these are visible at high magnification under a dissecting microscope, and may be present in other species as well.

Inflorescences, as is characteristic of the genus, arise from the leaf axils and consist typically of 1-2 flowers in Madagascar and Mascarene species, rarely up to eight flowers in X. ambanjensis. Inflorescences in X. flexuosa Diels are sometimes borne on tubercles arising from older leafless branches; in the specimen Randrianjanaka et al. 566 one of these bears 14 flower buds. Inflorescences consisting of more than one flower may arise from a common peduncle or from the axil on separate pedicels. In X. anomala, sp. nov., the pedicels are clustered at the peduncle apex, giving a corymb-like appearance. The indument of the peduncle, pedicels, bracts, and abaxial surfaces of the sepals is usually uniform. The peduncle lacks bracts, but the pedicels bear 1-4 small bracts, which may be persistent or caducous. Buds vary in shape from ovoid to linear, commonly lanceolate, and are acute to obtuse at the apex.

The sepals are always much shorter than the petals, partially connate, and coriaceous in texture. In bud the petals are erect with the outer whorl of petals pressed together in bud around the inner petals. The outer petals retain a short ridge on the adaxial apex where the petals met in bud, and there is sometimes a slight ridge extending along the entire length of the petals abaxially (Fig. 1G-I). The inner petals are ridged or keeled on both surfaces except for the concave base of the adaxial surface, which surTABLE 1. — Seed dispersal-related traits of the fruits and seeds of Madagascar and Mascarene *Xylopia* species. Species marked with * have monocarp dehiscence documented in the form of a dehisced monocarp present on a herbarium specimen, a photograph of known identity, or a verbal description of fruit dehiscence on the label. Known endocarp color indicates that the fruit is dehiscent.

Species	Aril	Endocarp color	Sarcotesta	Seed width (mm)
X. ambanjensis Cavaco & Keraudren*	Absent	Red	Unknown	6.7-8.3
X. amplexicaulis (Lam.) Baill.*	Present	Red	Absent	4-5
X. anomala, sp. nov.	Absent	Unknown	Unknown	9-15.6
X. australis, sp. nov.	Absent	Unknown	Unknown	9-10.3
X. beananensis Cavaco & Keraudren*	Present	Red	Absent	3.7-5.2
X. bemarivensis Diels*	Absent	Red	Orange	7.6-10
X. buxifolia Baill.*	Absent	Red	Green	5.5-6.9
X. capuronii Cavaco & Keraudren	Absent	Unknown	Unknown	9-10.1
X. carinata, sp. nov.	Unknown	Unknown	Unknown	Unknown
X. danguyella Ghesg. ex Cavaco & Keraudren	Absent	Unknown	Unknown	c. 10.4
X. dielsii Cavaco & Keraudren*	Absent	Unknown	Yellow?	c. 5.2
X. fananehanensis Cavaco & Keraudren	Absent	Unknown	Unknown	6.5-8.4
X. flexuosa Diels*	Present	Unknown	Absent	4.4-4.5
<i>X. galokothamna</i> , sp. nov.	Absent	Unknown	Unknown	9.2-13.3
X. ghesquiereana Cavaco & Keraudren	Unknown	Unknown	Unknown	Unknown
X. humbertii Ghesq. ex Cavaco & Keraudren	Unknown	Unknown	Unknown	Unknown
X. humblotiana Baill.*	Present	Red	Absent	4.6-5.6
X. kalabenonensis D.M.Johnson, Deroin, & Callmander	Absent	Unknown	Unknown	4.3-4.8
X. lamarckii Baill.	Unknown	Unknown	Unknown	Unknown
X. lamii Cavaco & Keraudren*	Absent	Red	Light green	8.2-8.6
X. lastelliana Baill.*	Absent	Pinkish red	Present	8.8-12
X. lemurica Diels*	Absent	Pinkish red	Yellow-green	5.4-7.4
X. lokobensis, sp. nov.*	Absent	Red	Unknown	6.9-8
X. longirostra, sp. nov.	Absent	Unknown	Unknown	10.7-11.4
X. madagascariensis Cavaco & Keraudren*	Absent	Red	Absent	4.2-4.6
X. marojejyana, sp. nov.	Absent	Unknown	Unknown	с. б
X. perrieri Diels*	Absent	Rose, orange-red	Light green	9.6-10.9
X. ravelonarivoi, sp. nov.*	Present	Unknown	Absent	2.9-4.6
X. retusa, sp. nov.*	Absent	Red	Orange	7.9-8.7
<i>X. richardii</i> Boivin ex Baill.*	Present	Unknown	Absent	5.1-7.0
X. sahafariensis Cavaco & Keraudren	Unknown	Unknown	Unknown	Unknown
X. sclerophylla, sp. nov.*	Absent	Pink	Green	8.2-8.7
X. sericolampra Diels	Unknown	Unknown	Unknown	12-13.9

rounds the androecium and carpels. The petals of both whorls are usually covered with fine hairs on one or both surfaces; the basal concavity of the inner petals is usually glabrous. The base of the adaxial surface of the inner petals sometimes bears a transverse thickening just above the basal concavity (Fig. 17I).

Petal position at anthesis is variable, and in many cases with herbarium material not clearly discernible. In *X. lastelliana* the outer petals are erect and the inner petals bend outward in the gaps between them (Fig. 1C), in *X. kalabenonensis* the outer petals are spreading and the inner petals are erect, and in *X. richardii* the petals of both whorls are pinched together at the base, with the stigmas exserted through the small aperture thus produced (Fig. 1F).

The largest outer petals are present in *X. lamarckii* and *X. amplexicaulis*, the former with petals reaching a length of 55 mm and a width of 28 mm (Fig. 1H-I). The shortest petals are found in *X. sahafariensis* Cavaco & Keraudren, which can have outer petals as short as 5.6 mm; those of *X. anomala*, sp. nov., are never over 9 mm in length. Petal coloration typical of *Xylopia* species elsewhere prevails in the Madagascar and Mascarene species: cream colored to pale yellow but often marked with red or purple toward the base. The most unusual color feature in Madagascar species is the distinct red coloration on the abaxial base of the

outer petals, giving a bicolored "candy corn" effect to the maturing buds of *X. lemurica* and *X. perrieri* Diels (Fig. 1D).

The inner petals are usually distinctly shorter and narrower than the outer petals. Those of *X. buxifolia* and *X. lemurica* are almost needlelike, with a midpoint width of 1 mm or less. In a few species of section *Xylopia* the inner petals are compressed laterally and bladelike. The inner petals of *X. australis*, sp. nov., have unique longitudinal corrugations on the adaxial surface.

The flowers have c. 50 to 400 stamens; the outermost and innermost stamens are staminodial. Outer staminodes are absent in X. humbertii Ghesq. ex Cavaco & Keraudren and sometimes absent in X. sahafariensis; inner staminodes are absent in X. richardii and X. sahafariensis. Stamens have the typical annonaceous morphology, with a shieldshaped anther connective apex and a short filament, and the stamens themselves are packed tightly together in bud; X. sahafariensis and X. sericolampra vary in having only a rudimentary anther connective apex that is barely visible above the tops of the anther thecae, as is typical in sect. Verdcourtia. The stamens vary in length from 0.8 mm long in X. retusa, sp. nov., and X. sahafariensis to 2 mm long in X. galokothamna, sp. nov. The connective apex may have papillae or short hairs. Number of anther locelli per anther ranges from 4 locelli in some stamens of X. anomala,

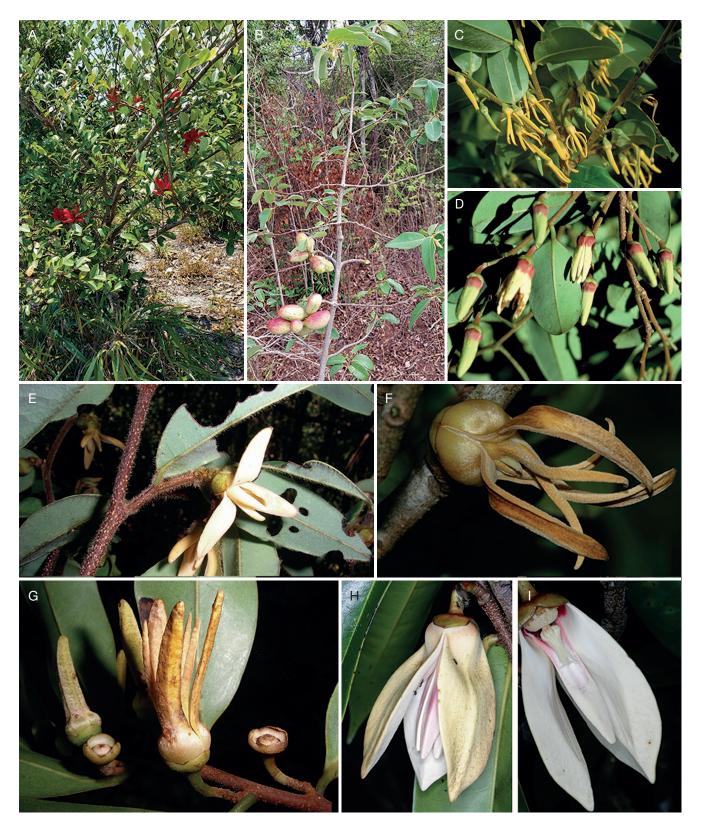


Fig. 1. — Aspects of *Xylopia* L. vegetative and floral morphology: **A**, shrub habit of *X. humblotiana* Baill.; **B**, habit of *X. bemarivensis* Diels, showing several nodes with both collateral buds forming shoots, creating pseudo-opposite branches; **C**, flowers of *X. lastelliana* Baill., showing inner petals bent outward through the gaps between outer petals (*Schatz & Modeste 2877*); **D**, flowers of *X. perrieri* Diels showing conspicuous red coloration at the bases of the outer petals (*Schatz & O'Connor 2964*); **E**, spreading outer petals and erect inner petals of *X. kalabenonensis* D.M.Johnson, Deroin, & Callmander (*Razafitsalama et al. 1041*); **F**, flower of *X. richardili* Boivin ex Baill., with stigmas emerging in the center amidst the inner petals; **G**, inflorescences of *X. beananensis* Cavaco & Keraudren, showing a bud, two flowers of flower, including stamens, and stigmas fallen so that the staminal cone is visible, and one open flower (*Buerki 14*); **H**, open flower of *X. lamarckii* Baill.; **I**, open flower of *X. lamarckii* and one inner petal removed to show interior of flower, including stamens and stigmas. Photos: **A**, M. C. Andriamahay; **B**, F. Rakotaris, **C**, D, G. E. Schatz; **E**, J. Razafitsalama; **F**, **H**, **I**, C. Kaiser-Bunbury; **G**, M. W. Callmander. **A**, **B**, used under the terms of the Creative Commons license for Tropicos, the botanical information system at the Missouri Botanical Garden.

sp. nov., to 16 locelli in stamens of *X. ambanjensis*. Outer staminodes are often longer and wider than the fertile stamens, while the inner staminodes are more similar to fertile stamens in shape and size, and often adhere to the bases of the stigmas.

A staminal cone is present in most Madagascar and Mascarene species of *Xylopia*. The filament bases from which it is formed are only loosely connate in *X. anomala*, sp. nov., but in other species it is a solid conical or dome-shaped structure (Fig. 1G). The cone conceals at least the lower half of the ovaries and often the ovaries in their entirety, with only the stigmas exserted through the aperture at the top. The rim of the cone is irregularly laciniate in sect. *Stenoxylopia*, and in sect. *Xylopia* it is even or nearly so (Fig. 1G). The cone is absent in *X. sahafariensis* and rudimentary in *X. sericolampra*, both of sect. *Verdcourtia*.

No Madagascar species were examined in the pollen survey of Annonaceae by Walker (1971), but Walker (1972b) described the pollen of *X. amplexicaulis* under the genus *Pseudanona*. He found that the pollen was shed in tetragonal tetrads such as those found in other species of *Xylopia*, and that the exine was reduced with slight pitting. Le Thomas (1980, 1981) included material of *X. lamarckii* and *X. amplexicaulis* in her survey of African Annonaceae pollen exine ultrastructure, and reported that the pollen was shed in tetrads, and that fractured exines of all species studied with Transmission Electron Microscopy showed a continuous tectum and coarse, often clustered, infratectal granules.

Carpel number ranges from the single carpel of Xylopia sericolampra up to 27 carpels in X. richardii. The carpels are tightly packed together within the staminal cone and it is often difficult to count them, which accounts, along with the extreme paucity of material for study, for the species descriptions in which there are higher monocarp numbers than carpel numbers. The carpels consist of a short oblong ovary with an elongate stigma that may be either filiform or clavate. A point of articulation between ovary and stigma is usually visible, but in X. sahafariensis and X. sericolampra the articulation is absent so that the point of transition is not apparent externally. The stigmas, which may be glabrous or hairy, are often connivent and fall as a unit at the end of anthesis; in X. flexuosa they are so tightly pressed together that there appears to be only a single pyramidal stigma present. Ovules vary in number from 2 to 9 per carpel and usually appear to be interdigitated to form a single row.

As the fruit ripens the pedicel elongates and thickens, and the torus enlarges. The monocarps are usually somewhat oblong, sessile to short-stipitate, and rounded to acute at the apex (Fig. 2). Pericarp thickness varies from 0.3 mm in *X. ravelonarivoi*, sp. nov., to 7 mm in *X. danguyella*. Where known, all monocarps are dehiscent. In Malagasy and Mascarene species, however, monocarp dehiscence could only be positively documented for 18 species (Table 1). This is worth noting because dehiscence determines whether the seed or the fruit will be presented as the diaspore, and dispersal mechanisms of *Xylopia* in the region remain virtually unknown.

The seeds range in number per monocarp from 3 in X. sericolampra to c. 9 in X. anomala, sp. nov., and are arranged in one or two rows with the long axis of the seed parallel, oblique, or perpendicular to the long axis of the monocarp. The seeds have the hard seed coat and ruminate endosperm that are universal in the family Annonaceae, are roughly ellipsoid, and range in length from 5.6 mm in X. ravelonarivoi, sp. nov., to nearly 20 mm in X. longirostra, sp. nov. In species of section Xylopia the seeds bear bilobed arils around the micropyle, although the two lobes may expand in width so that the individual lobes are no longer easily distinguishable (Fig. 2F). In some species of sect. Stenoxylopia, such as X. buxifolia, a hard donut-shaped ring of undetermined developmental origin (referred to as a "raised collar" in Stull et al. 2017) forms around the micropyle (Fig. 17C, D). In sect. Stenoxylopia the seeds can form an orange or yellow to green sarcotesta, but the sarcotesta can be difficult or impossible to discern in dried specimens so for a number of species its presence or absence is not known. Photographs of freshly-dehisced monocarps show the presence of orange sarcotestas in X. retusa, sp. nov., (Fig. 2A), X. bemarivensis (Fig. 2D), and a species that is possibly X. carinata, sp. nov., (Fig. 2C), and yellow-green sarcotestas in X. buxifolia, X. lemurica, X. perrieri (Fig. 2B), and X. sclerophylla, sp. nov., (Fig. 2G, H) are known from either photographs or label descriptions. Endosperm ruminations are platelike in quadrants in X. perrieri in the most common Annonaceae pattern, but in *X. bemarivensis* the plates are more triangular and 6-7 are visible in a plane of section rather than only 4, and in X. beananensis and X. humblotiana the ruminations are narrowly oblong and irregular in position.

A chromosome number of 2n =16 was reported by Morawetz & Le Thomas (1988) for *X. lemurica*. The base number of 8 is consistent with that known for other *Xylopia* species (Walker 1972a), but the low elevation provenance of the voucher collections, which could not be located, suggests that the cytological material came from a different species.

PHYLOGENY AND CLASSIFICATION OF MADA-GASCAR AND MASCARENE *XYLOPIA* SPECIES

A phylogenetic framework and infrageneric classification of *Xylopia* were laid out in Thomas *et al.* (2015), Stull *et al.* (2017), and Johnson & Murray (2018). Only a representative sample of species was included in those analyses, but this framework has allowed us to place the remaining Malagasy and Mascarene species on the basis of morphology. As many species are still incompletely known, placements are tentative.

Represented on Madagascar and the Mascarene Islands are the Xylopia clade and Stenoxylopia clade sister groups. Species of these clades are placed in three formal taxonomic sections of *Xylopia*. Subclades present in the region are informally defined below.



Fig. 2. — Fruits and seeds of Madagascar *Xylopia* L. species: **A**, fruits of *X. retusa*, sp. nov., showing at left a dehiscent monocarp with one seed covered by an orange sarcotesta (*Rabenantoandro et al. 1249*); **B**, fruit of *X. perrieri* Diels, one monocarp dehiscing to reveal barely visible seed with light green sarcotesta (*Antilahimena 7187*); **C**, dehiscing monocarps of a *Xylopia* sp., possibly *X. carinata*, sp. nov., with orange sarcotesta of seeds visible; **D**, fruit of *X. bernarivensis* Diels, with one dehiscing monocarp and seed with orange sarcotesta visible (*Ranirison PR 808*); **E**, immature fruit of *X. flexuosa* Diels, showing the elongate monocarp characteristic of species in sect. *Xylopia* (*Rakotovao 4687*); **F**, fruit of *X. humblotiana* Baill, with one dehisced monocarp and black seeds with white arils visible (*Rakotovao 4886*); **G**, fruits of *X. sclerophylla*, sp. nov.; monocarp at lower right is probably recently dehisced because green sarcotesta of seed is fully intact (*Nusbaumer LN 943*); **H**, dehisced monocarp of *X. sclerophylla*, sp. nov., at a slightly later stage, showing the sarcotesta collapsing and losing its color (*Nusbaumer LN 943*). Photos: **A**, P. P. Lowry II; **B**, P. Antilahimena; **C**, J. Tan; **D**, P. Ranirison (© Conservatoire et Jardin botaniques de la Ville de Genève); **A**, **B**, **D**, **E**, **F**, used under the terms of the creative Commons license for Tropicos, the botanical information system at the Missouri Botanical Garden; **C**, used under the terms of the the Creative Commons license for iNaturalist.

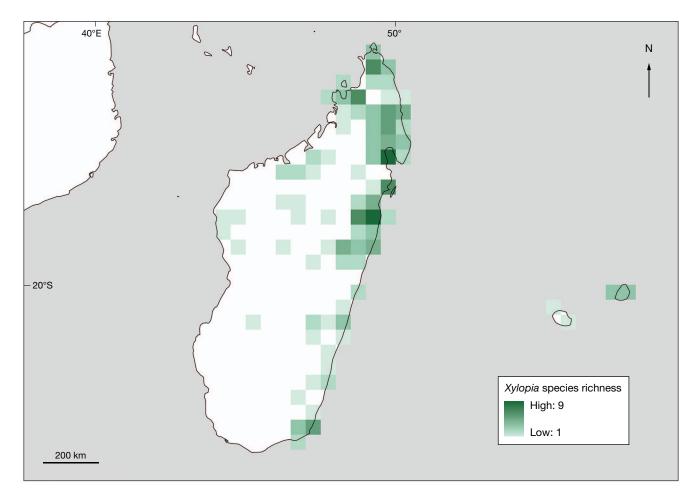


Fig. 3. – Species richness map for Xylopia L. on Madagascar and the Mascarene Islands, plotted by 0.5° × 0.5° grid squares.

Xylopia Clade

Section Xylopia

Nodes with a single axillary branch; anther connective apex shield-shaped, overhanging the anther thecae; staminal cone present, completely concealing the ovaries; seeds with a fleshy bilobed aril; seed coat smooth, sarcotesta present or absent.

Subclade 1. As described for the section but sarcotesta always absent. *Xylopia amplexicaulis, X. beananensis, X. flexuosa, X. humblotiana, X. lamarckii, X. madagascariensis, X. ravelona-rivoi,* **sp. nov.** (*X. humblotiana in* Stull *et al.* 2017), *X. richardii.*

STENOXYLOPIA CLADE

Section Verdcourtia

Nodes with 1-3 axillary branches; anther connective apex rudimentary, not overhanging anther thecae; staminal cone surrounding only the bases of ovaries; seeds with cupular aril and lacking a sarcotesta. *Xylopia sahafariensis* (*X.* sp. aff. *sahafariensis in* Stull *et al.* 2017), *X. sericolampra*.

Section Stenoxylopia

Nodes with 1-3 axillary branches; anther connective apex shieldshaped, overhanging anther thecae; staminal cone partially to completely concealing ovaries; seeds not arillate, sarcotesta present. Subclade 1. Outer petals spreading and inner petals erect at anthesis in many species; stigmas clavate; sarcotesta orange in one species, otherwise unknown. *Xylopia anomala*, **sp. nov.**, *X. australis*, **sp. nov.**, *X. capuronii*, *X. carinata*, **sp. nov.**, *X. danguyella* (X. sp. aff. fananehanensis [4] in Stull et al. 2017), *X. dielsii*, *X. fananehanensis* (X. sp. aff. fananehanensis [1] in Stull et al. 2017), *X. galokothamna*, **sp. nov.**, (X. sp. aff. fananehanensis [2] in Stull et al. 2017), *X. ghesquiereana*, *X. humbertii*, *X. kalabenonensis*, *X. lokobensis*, **sp. nov.**, (X. sp. aff. fananehanensis [3] in Stull et al. 2017), *X. marojejyana*, **sp. nov.**, *X. retusa*, **sp. nov.** (X. sp. aff. buxifolia in Stull et al. 2017).

Subclade 4. Outer petals spreading and inner petals erect at anthesis; stigmas filiform; sarcotesta orange. *Xylopia bemarivensis*.

Subclade 7. Petals of both whorls loosely spreading at anthesis; stigmas filiform; sarcotesta (where known) pale green to yellow-green. *Xylopia ambanjensis, X. buxifolia, X. lamii, X. lastelliana, X. lemurica* (includes also *X. pseudolemurica in* Stull *et al.* 2017), *X. longirostra,* sp. nov., *X. perrieri, X. sclerophylla,* sp. nov., (*X.* sp. aff. *lastelliana in* Stull *et al.* 2017).

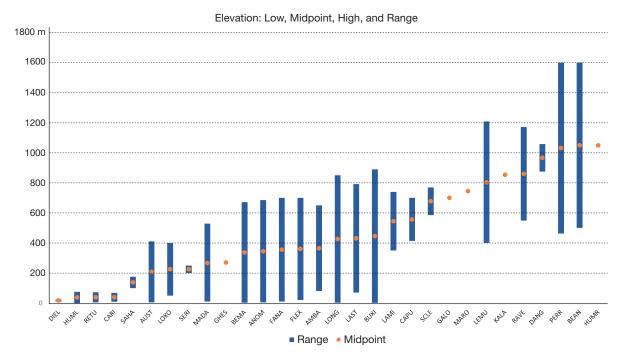


Fig. 4. — Elevational ranges in meters for the 30 Madagascar Xylopia L. species, with midpoint value indicated by an orange dot. Individual species are indicated by the first four letters of the specific epithet in all capital letters, except for combinations HUML and HUMR used to distinguish X. humblotiana Baill. and X. humblertii Ghesq. ex Cavaco & Keraudren, respectively.

BIOGEOGRAPHY

All Madagascar and Mascarene *Xylopia* species are endemics to the islands. *Xylopia richardii* occurs on La Réunion and Mauritius, *X. amplexicaulis* and *X. lamarckii* are endemic to Mauritius, and the remaining species are endemic to Madagascar. Many can be categorized as "microendemics" (Wilmé *et al.* 2006; Vences *et al.* 2009). Within Madagascar, endemism is highest in the north and east, with seven species restricted to Antsiranana Province, six to Toamasina Province, two to Mahajanga Province, and one to Toliara Province; Fianarantsoa and Antananarivo Provinces have no endemic species.

Phylogenetic study of *Xylopia* provided evidence that *Xylopia* diversity in Madagascar and the Mascarene Islands resulted from a minimum of five separate dispersals from Africa (Stull *et al.* 2017). One colonization took place from within the Xylopia clade of the genus, which was estimated to have split from its sister Stenoxylopia clade *c.* 23 My (Thomas *et al.* 2015). Most species of the clade occur in tropical America; continental Africa is represented by one species (*X. aethiopica* (Dunal) A. Rich.), and Madagascar and the Mascarene Islands form a secondary center: Madagascar has five species, and the Mascarene Islands support three additional species. Ancestral area reconstruction showed a greater probability that the Madagascar and Mascarene taxa are the result of dispersals from Africa rather than *X. aethiopica* deriving from a Madagascar or Mascarene ancestor (Stull *et al.* 2017).

Xylopia is the only genus of Annonaceae indigenous to Mauritius or La Réunion. And although the Xylopia clade contributes only one-sixth of contemporary *Xylopia* diversity on Madagascar, it is the only clade to have reached the Mascarene Islands. Of the Madagascar species in this clade, *Xylopia flexuosa* exhibits a trend toward larger and thicker petals that reaches an extreme expression in the two Mauritian species *X. amplexicaulis* and *X. lamarckii*. The third Mascarene species, *X. richardii*, is more similar to species on Madagascar, for example *X. beananensis*, than to the other two Mascarene species, implying two separate dispersal events between the islands.

Four other *Xylopia* colonizations of Madagascar from Africa occurred within the Stenoxylopia clade. The phylogeny of the East African and Madagascar species of section *Verdcourtia* indicated a unique dispersal to Madagascar, as *X. sahafariensis* from Madagascar is nested within the African species of the section. Section *Stenoxylopia* subclade 1, composed of exclusively Madagascar species, represents a second dispersal. Subclade 4, arising between two African subclades, consists solely of the Madagascar species *X. bemarivensis*. The fourth dispersal occurred within the crown group of the Stenoxylopia clade, subclades 5-7, which includes species from both African and Madagascar (Johnson & Murray 2018).

Xylopia section *Stenoxylopia* extends through the tropical forests of Africa eastward as far as Fiji, and Asian origins of Madagascar taxa have been posited for several plant groups (Schatz 1996, Renner *et al.* 2010, Daly *et al.* 2015, Yang *et al.* 2017). Morley (2018) summarized a role for the "Kohistan-Ladakh Island Arc", between India, Africa, and Europe to explain biotic connections between the tropical London Clay flora (age *c.* 51 My) and South Asian fossil deposits. The Xylopia clades represented on Madagascar, however, diverged at about 23 My (Thomas *et al.* 2015), which post-dates this connection. In addition, ancestral area reconstruction of Madagascar clades provided evidence for an origin in Africa rather than Asia, and *Xylopia* aril types in Asia, which have been predictive of phylogenetic relationships,

are unknown outside that region (Stull *et al.* 2017). Variation in climatic conditions in South and Southeast Asia from the early Miocene onward (Morley 2018), would, however, have permitted intermittent migration of *Xylopia* eastward, with the genus ultimately reaching New Caledonia and Fiji by long-distance dispersal (Johnson *et al.* 2013). In conclusion, Madagascar may have played a role in the dispersal of the Stenoxylopia clade into Asia, but there is no current evidence, morphological, fossil, or molecular, to suggest that the sect. *Stenoxylopia* species of Madagascar are derived from an Asian progenitor.

ECOLOGY

On Madagascar *Xylopia* is most common in lower elevation evergreen humid forests, a pattern typical for the genus and the family, but several species also occur in drier deciduous to semi-deciduous forests of the northwest (Fig. 3). Species richness peaks coincide with areas of micro-endemism, and are greatest in Antsiranana and Toamasina Provinces. Together these provinces contain 27 species, 90% of the Madagascar total. Species occurring outside this area include *X. humbertii* and *X. sericolampra* from Mahajanga Province and *X. australis*, sp. nov., from Toliara Province. The only species to occur in all six Madagascar Provinces is *X. perrieri*.

The distribution of the genus extends from sea level to 1600 meters. The elevational ranges of the 30 Madagascar *Xylopia* species, rank-ordered by midpoint elevation from lowest to highest, are shown in Figure 4. Twenty species occur below 500 m, 19 between 500 and 1000 m, and six above 1000 m. The only species exceeding an elevation of 1500 meters, *X. beananensis* and *X. perrieri*, also occupy the greatest elevational amplitudes and are two of the most widespread species on the island. There is a steady turnover in species with increase in elevation. Above 1300 meters, cited as a transition from humid montane forest to sclerophyllous montane forest (White 1983, World Wildlife Fund "Eastern Madagascar", https://www.worldwildlife. org/ecoregions/at0117#), only *X. beananensis* and *X. perrieri* are present and even those species have an elevational range midpoint, *c.* 1000 meters, below that transition zone.

Xylopia species richness is highest, with 8-9 species per $0.5^{\circ} \times 0.5^{\circ}$ grid cell, near the Baie d'Antongil, Soanierana-Ivongo, and Toamasina, areas where annual precipitation averages well over 3000 mm (Fig. 3). *Xylopia* does not occur in areas where annual precipitation is below 1000 mm. The distribution of the palm family on Madagascar, mapped by Rakotoarinivo *et al.* (2013) closely matches that of *Xylopia*. Those authors acknowledged a link to high precipitation and evapotranspiration but concluded that the best fit of the palm diversity pattern was to annual precipitation at the end of the last glacial maximum, *c.* 21 000 years ago, rather than to modern annual precipitation.

In the humid forests of eastern Madagascar canopy height is lower than in many tropical lowland forests but can exceed 30 m at elevations below 800 m and ranges from 20 to 25 meters at elevations above 800 m ("Eastern Madagascar", https://www. worldwildlife.org/ecoregions/at0117). Two species, *Xylopia beananensis*, a middle elevation species, and *X. fananehanensis*, a lowland species, are recorded as reaching a height of 30 meters and form part of the canopy. Most *Xylopia* species, however, have maximum heights of 15-25 meters and are thus sub-canopy species at lower elevations but may form part of the canopy at higher elevations.

The humid forest habitat has a mix of microendemic and more widespread species of Xylopia. For example, Xylopia perrieri is a relatively widespread species, suggesting a continuity of habitat throughout its range, perhaps including secondary growth areas. Xylopia australis, sp. nov., occurs only in a limited area of southeastern Madagascar, in a region known as a center of plant endemism (Razakamalala et al. 2011). The littoral forests of eastern Madagascar are a special category of humid lowland evergreen forest, which were inventoried by Consiglio et al. (2006) using remote-sensing and targeted collecting. The *Xylopia* flora of this forest again includes a mixture of widely distributed species (X. bemarivensis, X. buxifolia, X. humblotiana, X. lastelliana) and a group of microendemics (X. australis, sp. nov., X. carinata, sp. nov., X. dielsii, X. longirostra, sp. nov., X. retusa, sp. nov.). For the most part, however, we did not find that the narrow endemics of humid forests were associated with particular habitats or centers of endemism.

While *Xylopia* is absent from the driest areas of Madagascar, there are four species in the deciduous and semi-deciduous forests from sea level to 671 meters in western and northwestern Madagascar. One of these, *X. bemarivensis*, occurs on a variety of soil substrates and has the widest geographic distribution of any Madagascar *Xylopia* species; the other three species, *X. ambanjensis*, *X. sahafariensis*, and *X. sericolampra*, have restricted distributions, the latter two known from only three localities each.

Because so little of the original vegetation of the Mascarene Islands remains it is difficult to interpret the historical distribution and habitats of the species that occur there. We do, however, have documentation that some Mauritian Xylopia may have been more common in the past. Aublet (1775), who visited Mauritius in 1754, reported that the "bois blanc à grande feuille" (presumably X. lamarckii) and the "bois blanc à petite feuille" (presumably X. richardii), occurred in abundance in the ravines and forests at the bases of mountains near Port Louis and Moka. Our current understanding from study of herbarium material is that Xylopia grows in low heath forests and thickets from 150 to 780 m on both islands. Xylopia amplexicaulis and X. richardii are small trees, while X. lamarckii is most often described as a scrambling or sub-scandent shrub. Sideroxylon (Sapotaceae) is a frequently mentioned associate for all three *Xylopia* species, but in contrast to Sideroxylon, the Xylopia species are now rare.

REPRODUCTIVE BIOLOGY

Flowering and fruiting phenology of *Xylopia* are remarkably uniform across phylogenetic groups, habitats, and elevations in the region. Flowering for most species commences in October and ends in March. The most notable exception to this pattern is found in *X. flexuosa*, with specimens with flowers collected in May, July, September, and October. In distribution and habitat the species does not appear to be unique – it is found in lowland humid forests from Antalaha to Taolagnaro along the eastern coast, as are a number of other species. Gauging the timing of fruit maturity for *Xylopia* is more difficult from available herbarium material, but maturing fruits are known to occur from May to August for many species. In a particular site, however, there may be evidence of phenological separation between species. In Ranomafana National Park, for example, *X. lemurica* has been collected in fruit in January, while *X. perrieri* has been collected in fruit in July, November, and December. A species from this site identified as *X. buxifolia*, but which most likely represents *X. lemurica* or *X. perrieri*, was documented, over a 12-year period, to produce mature fruits beginning in January and lasting an average of three months (Dunham *et al.* 2018).

Floral visitors have only been observed for *X. lamarckii* (Kaiser 2006, Kaiser-Bunbury *et al.* 2009) on Mauritius: two non-native generalist visitors, an ant and a chrysomelid beetle, were found and no fruiting was observed. Otherwise, pollination biology of Malagasy and Mascarene *Xylopia* species is unknown. Floral traits and the limited pollinator observations available throughout the range of the genus are generally consistent with a small beetle pollination system, posited by Saunders (2012) as ancestral in the Annonaceae. The floral morphology of the Malagasy and Mascarene species accords well with this pollination syndrome. While enforced outcrossing is common among Annonaceae, a study by Ratnayake *et al.* (2007) documents self-compatibility in the Sri Lankan *X. championii*, so the possibility that some form of autogamy occurs in the Malagasy and Mascarene species should be considered.

The colors documented for the ripe dehisced fruits and seeds of Xylopia are contrasting shades of red, orange, green, black, and white (Table 1; Fig. 2). This coloration suggests birds or primates with trichromatic vision as significant seed dispersers, as they are in West and Central Africa (summarized in Johnson & Murray 2018). In the Madagascar and Mascarene region, however, as many ecologists have noted, frugivorous birds are in short supply. Razafindratsima (2014) listed 25 bird species as possible seed dispersers in Madagascar, but only one of these has so far been reported as feeding on Xylopia fruits, the Madagascar blue pigeon (Alectroenas madagascariensis) feeding on the fruits of X. anomala, sp. nov., (Martial 306). There may be additional bird species with the potential to act as dispersers of *Xylopia*, as evidenced by reports of several species of vanga shrikes (Vangidae) feeding on the red arils in the dehiscent fruits of Commiphora (Burseraceae) (Gardner & Jasper 2018).

Feeding by lemurs, the only primates in the region, has also been reported. Birkinshaw (2001) identified a species described here as *X. lokobensis*, sp. nov., as "associated with black lemur [*Eulemur macaco*] seed dispersal". Andriamampianina (2013) reported the fruits of *X. buxifolia* to be an important component of the diet of *Varecia variegata*, and Joromampionona Andriamadijaona (2013) documented that seeds of *X. buxifolia* passed intact and viable through the gut of both *V. variegata* and *Eulemur rufifrons*. Razafindratsima (2015) found that *Eulemur rubriventer* fed on fruits of a *Xylopia* species (probably *X. lemurica* or *X. perrieri*), but concluded that it did not appear to disperse the seeds. Some lemur species are clearly seed predators (Hemingway 1996, Powzyk 1997), so it is not possible to interpret feeding data as indicating dispersal without detailed documentation of seed handling by the particular lemur species involved. Ambiguous feeding reports include *Propithecus tattersalli* feeding on the seeds of *X. bemarivensis* (*Meyers 92*) and an unspecified lemur species feeding on the seeds of *X. sclerophylla*, sp. nov., (*Nusbaumer LN 943*). The plants offering potential attractants and rewards to these lemurs included three species with green sarcotestas (Fig. 2B, G-H), one with orange (Fig. 2D), and one of unknown color (a similar species has orange) (Table 1). There are no reports of visits to black seeds with small white arils.

All of these seed colors, shown against the red to rose colored endocarp of the fruit, provide effective visual cues for animals with trichromatic color vision foraging during daylight hours. Two of the best documented cases of lemur dispersal involve species with polymorphic trichromatic vision (Tan & Li 1999; Jacobs et al. 2019). However, many lemur species are nocturnal, feeding upon fruits that remain green at maturity (Génin & Rambeloarivony 2018). Lemurs may benefit from loss of trichromatic vision (Jacobs et al. 2019), the animals using luminescence cues for enhanced feeding under low light conditions. Two lemurs with dichromatic color vision, Eulemur rubriventer and *E. rufifrons*, both feed on xylopias with light green sarcotestas. The seed color of those plants may enhance cues for frugivores with dichromatic vision. We conclude that lemurs may have an unknown or evolving role in Xylopia dispersal or may not be significant dispersers of many species of the plants.

Compounding the problem of understanding *Xylopia* dispersal is the fact that the fruits of many species are still poorly known, for example some species may have indehiscent fruits, or attractants other than color (Table 1). And unlike the African forests where dispersal has been best studied, in this region most *Xylopia* species appear to be rare and may not provide a significant resource for dispersers.

That some *Xylopia* species represent "orphaned' Malagasy plant lineages/large seeded taxa, bereft of their dispersers" (Federman *et al.* 2016) is an open possibility. Giant lemurs or birds such as elephant birds (Dransfield & Beentje 1995), with the ability to handle large seeds, are now extinct. An alternative hypothesis is that *Xylopia*, in its multiple dispersals to the islands, lacked local pollination and dispersal services. With the additional isolating mechanisms of extreme topography and the effects of glaciation, it is easy to imagine the rapid speciation often seen in island floras operating to produce the exceptional diversity of the region (33 species in the region, versus 45 species for continental Africa)

ETHNOBIOLOGY

Riondato *et al.* (2019) recently reported the results of an ethnobotanical and phytochemical survey of plants used for medicine by people living in the vicinity of the Maromizaha New Protected Area in southern Toamasina Province. A plant identified as *Xylopia lemurica* was found to have the greatest number of uses of any plant in the survey, with decoctions of the leaves being used to treat fatigue, malaria, menstrual pain, food poisoning, stomach ache, and spider bite. Analysis of the

leaves showed high Total Phenolic Content and Antioxidant Activity values, as well as the presence of constituents representing all compound classes in the screening protocol, for example catechins and flavonols. This is in keeping with the human uses of the large number of bioactive compounds revealed in *Xylopia* leaf analyses elsewhere (see Johnson & Murray 2018 for Africa).

CONSERVATION ASSESSMENTS

IUCN conservation assessments have been published for five species: *X. amplexicaulis* (Page 1998a), *X. flexuosa* (Lantoarisoa 2015), *X. kalabenonensis* (Callmander *et al.* 2009), *X. lamarckii* (Page 1998b), and *X. richardii* (Page 1998c). The data presented in this revision are consistent with these prior assessments, except that of *X. flexuosa*, a species that has been misidentified and is now known from 12 localities rather than the three reported by Lantoarisoa, so its status may be somewhat less critical than previously understood; the data are discussed under that species.

Given the extreme endemism of the Madagascar and Mascarene *Xylopia* species, we have quantified distributions for each of the 33 species following IUCN guidelines (IUCN Species Survival Commission 2012) for determining the EOO and the AOO (Table 2). EOO ranges from zero (for species known from a single locality) to 192983 km² for *X. beananensis*. The AOO values range from 4 km² for single-locality species to 240 km² for *X. humblotiana*. [For scale, the capital city of Antananarivo has an area of 86.4 km², and 29 of the 33 *Xylopia* species treated here have an AOO smaller than the area of that city.]

These statistics are based on cumulative distribution records compiled over more than two centuries of botanical collecting. Four species are known from single collections: *Xylopia humbertii* from 1937, *X. ghesquiereana* from 1950, *X. marojejyana*, sp. nov., from 1989, and *X. kalabenonensis* from 2006. We argue that these species merit the highest priority for field assessment and give them all a preliminary conservation assessment of Critically Endangered on the basis of the IUCN D Criterion.

Twenty-two species are known from two to 12 localities, and have EOO values of 144-7118 km² and AOO values of 8-48 km². As discussed in more detail under individual species, some are known from recent (post-2000) collections and some are known to occur within areas under conservation protection. Again using the IUCN D Criterion, we have classified all of these species as Critically Endangered or Endangered (Table 2), but each of them requires more intensive field study. The remaining seven species are known from 16-60 localities, have EOOs from 38756 to 192983 km² and AOOs from 64 to 240 km². All of these species fit various B, C, and D criteria but lack sufficient data on other criteria in these categories to assign a conservation assessment and are characterized as Data Deficient. We give what insight we have under each species, however further analyses by biologists with extensive field experience in the forests of Madagascar is needed. Many if not all of the Data Deficient species are certainly at risk.

TAXONOMIC TREATMENT

Genus Xylopia L.

Systema Naturae, ed. 10, 2: 1250 [+1378] (1759), nom. conserv. — *Xylopicrum* P. Browne, *The Civil and Natural History of Jamaica* 250-251 + t. 5, fig. 2 (1756). — *Xylopicron*, orth. mut., Adans., *Familles des Plantes* 2: 365 (1763). — Type species: *Xylopia muricata* L., typ. conserv.

- Unona L. f., Supplementum Plantarum 270 (1782). Bulliarda Neck., Elementa Botanica 2: 321 (1790), nom. superfl., non DC. (1801). — Type species: Unona discreta L. f.
- *Krockeria* Neck., *Elementa Botanica* 2: 317-318 (1790). Type species: *Unona concolor* Willd. (lecto-, designated by Johnson & Murray, *PhytoKeys* 97: 32 [2018]).
- Coelocline A. DC., Mémoires de la Société de Physique et d'Histoire naturelle de Genève 5: 208-209 (1832). — Type species: Coelocline acutiflora (Dunal) A. DC.
- Parartabotrys Miq., Flora van Nederlandsch Indië, Eerste bijvoegsel 3: 374 (1861). — Type species: Parartabotrys sumatranus Miq.
- Pseudanona (Baill.) Saff., Journal of the Washington Academy of Sciences 3: 17 (1913), as "Pseudannona". — Xylopia section Pseudanona Baill., Adansonia; Recueil d'Observations botaniques 4: 141-142 (1864). — Type species: Pseudanona amplexicaulis (Lam.) Saff. (lecto-, designated by Safford [1913: 18]).

DESCRIPTION

Trees or shrubs, evergreen or sometimes deciduous, with spiral branching from the main trunk axis.

Indument of simple hairs.

Twigs persistently pubescent to glabrate, sparsely lenticellate, longitudinally wrinkled; nodes with one, or in many species with two-three collateral axillary branches.

Leaves with simple entire blades, chartaceous to coriaceous, base symmetrical, sometimes decurrent on petiole, margins flat, recurved, or revolute, midrib impressed to slightly raised adaxially, raised abaxially, secondary veins distinctly to weakly brochidodromous, petiole short, sub-terete, canaliculate, or flattened.

Inflorescences axillary, occasionally arising from the leafless portions of branches, 1-14-flowered in Madagascar and Mascarene species; peduncles 1-several per leaf axil or absent, pedicels 1-several per peduncle, or arising separately from axil, with 1-4 small caducous to persistent bracts; buds ovoid to linear, obtuse to acute, occasionally falciform.

Flowers bisexual.

Sepals 3, connate at least at the base to form a cuplike calyx much shorter than the petals.

Petals 6, in two series of three, valvate, free; outer petals ovate to linear, flattened to a concave base adaxially, flat but sometimes with a longitudinal ridge abaxially; inner petals slightly shorter and narrower than outer petals, ovate to linear, keeled on both surfaces but becoming concave at the base adaxially and flat at the base abaxially, often narrowed into a short claw.

Stamens 50-400; fertile stamens clavate to oblong, anther connective apex shield-shaped, hemispherical, capitate, or conical, often overhanging anther thecae, rarely rudimentary and not overhanging anther thecae, pubescent or papillate, rarely glabrous, anthers transversely septate, filament much shorter than anther, articulated with the staminal cone; outer staminodes present, oblong to clavate, apex obtuse to obliquely truncate, rarely absent; inner staminodes present, often adhering to the bases of the stigmas, usually shorter than outer staminodes, clavate to oblong, apex rounded, rarely absent; filament bases connate into a staminal cone that partially or completely encloses the ovaries, the rim even or irregularly laciniate, staminal cone rudimentary to absent in a few species.

Carpels separate; ovaries oblong or ovoid, stigmas free or loosely connivent, longer than the ovaries (in Malagasy and Mascarene species).

Torus flat or slightly concave.

Fruits consisting of elongate dehiscent monocarps (dehiscence undocumented for several Malagasy species), these often with a green to red exterior and red endocarp; monocarps sometimes torulose, short-stipitate to sessile.

Seeds up to 9 per monocarp in Madagascar species, attached laterally in one or two rows, ellipsoid, smooth or rugose, the hard brown to black inner layer of the seed coat sometimes covered by a light green or orange sarcotesta, perichalazal ring raised or not visible externally, endosperm ruminations platelike to spinelike, an aril forming fleshy lobes or rings around the micropyle in some species.

Notes

A pantropical genus of nearly 200 species, represented on Madagascar by 30 endemic species and on the Mascarene Islands by three endemic species. Three of the six sections of *Xylopia* are represented in the region: sect. *Xylopia* (species 1-8), sect. *Verdcourtia* (species 9-10), and *sect. Stenoxylopia* (species 11-33). Species are listed alphabetically within each section.

Keys to the species of *Xylopia* L. from Madagascar and the Mascarene Islands

Notes: Vegetative characters are emphasized in the keys because flowers of two species and fruits of four species remain unknown. Reference to the elevational ranges of species in Figure 4 and seed data in Table 1 may be useful aids to identification. As in the species descriptions, the leaf blade dimensions pertain to the larger leaves on a specimen.

KEY TO THE MASCARENE ISLAND SPECIES OF XYLOPIA

1.	Leaf blades 4.4-8.8 cm long, 2.6-3.7 cm wide; outer petals 19-37 mm long, 3.5-5 mm wide at midpoint <i>X. richardii</i> Boivin ex Baill.
—	Leaf blades 9.7-23.5 cm long, 5.5-8.4 cm wide; outer petals 31-55 mm long, 11-28 mm wide at midpoint 2
	Leaf blades cordate-auriculate at the base, lobes clasping the stem
	Key to the Malagasy species of <i>Xylopia</i>
	Hairs on young twigs, petioles, and pedicels erect or loosely spreading
2.	Leaf blades with margins flat or slightly recurved; outer petals 1.0-1.8 mm wide at midpoint
	Leaf blades densely sericeous abaxially, the hairs silvery, apex acuminate or sometimes acute; inflorescences 1-4-flowered
	Leaf blades pubescent abaxially, the hairs brown and dull, apex obtuse, rounded, or retuse, rarely acute; inflo- rescences always 1-flowered
4.	Twigs sparsely covered with persistent erect brown hairs 0.2-0.3 mm long; leaf blades lanceolate to elliptic, obtuse or rarely acute; pedicels 4.3-7.1 mm long; pericarp 0.6-1.2 mm thick, sarcotesta orange
	Twigs densely covered with persistent erect ferruginous hairs 0.3-1.2 mm long; leaf blades ovate to elliptic, retuse and sometimes truncate; pedicels 2.9-4 mm long; pericarp 3.0-3.1 mm thick; sarcotesta pale green

5.	Leaves strongly revolute, pubescence of twigs, leaves, inflorescences, and monocarps dull red; petiole 5-10 mm long
6.	Leaf blades small, < 6 cm long AND < 3 cm wide
7.	Leaf blades acute to acuminate at the apex
8.	Leaf blades glabrous or with a few scattered hairs abaxially <i>X. humbertii</i> Ghesq. ex Cavaco & Keraudren Leaf blades appressed-pubescent abaxially
9.	Leaf blades with appressed hairs that are longer and more spreading along midrib and margins, abruptly sharp- acuminate; outer petals linear, 0.7-1.4 mm wide at midpoint
	Base of leaf blade cuneate, inner petals straight and needle-like X. lemurica Diels Base of leaf blade broadly cuneate to rounded, inner petals narrowly sinuous X. ghesquiereana Cavaco & Keraudren
11. —	Petiole 5.5-8 mm long; pedicels 2.5-3.2 mm long; anther connective apex rudimentary, not overhanging anther thecae; carpels 2-3
12.	Leaves sparsely appressed-pubescent abaxially; axillary branches always one per node; monocarps narrowly ob- long to cylindrical, 0.7-1.1 cm wide
13.	Leaf blades sericeous abaxially, the hairs silvery abaxially
	<i>X. sclerophylla</i> D.M.Johnson & N.A.Murray, sp. nov. Leaf blades appressed-pubescent the hairs dull colored, or glabrous abaxially
14. 	Leaf blades narrowly oblong, elliptic, oblanceolate, or linear-lanceolate, length to width ratio > 3:1, apex always retuse
15.	Outer petals linear to linear-lanceolate, 1.0-1.8 mm wide at midpoint
	Leaf blades truncate or rounded at base; monocarp 1, conspicuously veined longitudinally, pyriform, oblong, or ovoid
17.	Leaf blades widest at or proximal to the midpoint; monocarps oblong to pyriform, 1.3-2.1 cm wide
	<i>X. perrieri</i> Diels Leaf blades widest at or distal to the midpoint; monocarps narrowly oblong to clavate, 0.8-1.2 cm wide 18
18.	Pedicels and sepals densely pubescent; outer petals lanceolate; pedicel of fruit 13-19 mm long
	Pedicels and sepals sparsely appressed-pubescent; outer petals narrowly oblong; pedicel of fruit 8-11 mm long <i>X. humblotiana</i> Baill.
19. 	Leaf blade length to width ratio > 3.5:120Leaf blade length to width ratio < 3.5:1, often much less
20.	

21.	Monocarps densely lenticellate, ovoid to ellipsoid, 2.3-2.6 cm wide, leaf acumen forming ¼-1/5 of leaf blade length; littoral forests and nearby hills of eastern Madagascar
	<i>X. longirostra</i> D.M.Johnson & N.A.Murray, sp. nov. Monocarps sparsely lenticellate, oblong to obovoid, 1.3-1.8 cm wide; leaf acumen forming ¹ / ₆₋ / ₈ of leaf blade length; dry forests of northern Madagascar
22.	Bark of leafy twigs exfoliating, leaf blade long-decurrent on petiole
	<i>X. marojejyana</i> D.M.Johnson & N.A.Murray, sp. nov. Bark of leafy twigs smooth or with occasional flaking patches, leaf blade short-decurrent or not decurrent on petiole
23.	Pedicellar bracts 2, one attached at midpoint and often caducous, the other immediately subtending the sepals
_	and persistent24Pedicellar bracts 2-4, attached at various points but never immediately subtending the sepals27
24. —	Sepals < 4 mm long
25.	Leaf blades 8.7-15 cm long, 2.9-6.5 cm wide, anther connective apex shield-shaped, overhanging anther the- cae
—	Leaf blades 4.9-8.6 cm long, 1.5-3.3 mm wide, anther connective apex rudimentary, not overhanging anther thecae
26.	Outer petals with a distinct longitudinal ridge on the abaxial surface, 2.9-3.7 mm wide at midpoint; leaf blades slightly revolute at margins, sharply acuminate, midrib distinctly impressed adaxially; eastern Madagascar
_	<i>X. carinata</i> D.M.Johnson & N.A.Murray, sp. nov. Outer petals flat or with an indistinct longitudinal ridge on the abaxial surface, 1.8-3 mm wide at midpoint; leaf blades flat at margins, obtuse or blunt-acuminate, midrib flat adaxially; northwestern Madagascar
27.	Leaf blades > 5.5 cm wide; flowers up to 5 per inflorescence; outer petals ovate, 8.6-9 mm long, monocarps
	densely lenticellate
28.	Leaf blades truncate or rarely rounded at the base, not decurrent on petiole; emerging shoots densely covered with silvery hairs; anther connective apex rudimentary, not overhanging anther thecae; monocarp strongly marked with longitudinal veins when dried
29.	Leaf blades appressed-pubescent abaxially, with longer hairs present along the midrib and margins; outer petals 0.7-1.4 mm wide at midpoint
	Leaf blades glabrous to nearly so or, if appressed-pubescent, then hairs all of equal length; outer petals 1.2- 5.5 mm wide at midpoint
30. 	Leaf apex obtuse, rounded, retuse, or emarginate
31.	Pedicels and sepals densely pubescent; outer petals lanceolate; pedicel of fruit 13-19 mm long; elevations above 500 meters
	Pedicels and sepals sparsely appressed-pubescent; outer petals narrowly oblong; pedicel of fruit 8-11 mm long; elevations of 50 meters or less
	Outer petals 12.6-14.6 mm long; stamens <i>c.</i> 80
	Seeds not arillate; staminal cone 1.0-2.4 mm in diameter, 0.6-1.8 mm high, slightly wider than high, rim ir- regularly laciniate
34.	Bracts on pedicel persistent, even into the fruiting stage; flowers often arising from tubercles on leafless growth
	Bracts on pedicel caducous; flowers borne on leafy twigs

35.	Leaf blades 6.5-12.7 cm long, 2.5-4.8 cm wide	e X. beananensis Cavaco & Keraudren
	Leaf blades 5.2-6.6 cm long, 1.8-2.7 cm wide	X. madagascariensis Cavaco & Keraudren

I. Xylopia L. section Xylopia

Xylopia section *Pseudanona* Baill., *Adansonia; Recueil d'Observations botaniques* 4: 141, 142 (1864). — Type: *Pseudanona amplexicaulis* (Lam.) Saff. (lectotype designated by Safford [1913: 18]).

Xylopia section *Habzelia* Engl. & Diels, *Monographien Afrikanischer Pflanzen-Familien und Gattungen* 6: 58 (1901). — Type: *Xylopia aethiopica* (Dunal) A. Rich. (lectotype designated in Stull *et al.* [2017: 221]).

TYPE SPECIES. — As for the genus, *X. muricata* L.

Description (for species of the section from Madagascar and the Mascarene Islands)

Nodes with a branch from a single axillary bud; outer and inner petals linear to ovate, similar in length, or the inner petals shorter and narrower; inner petals sometimes laterally compressed, with margins curved inward at base but of uniform texture, lacking differentiated fleshy basal margins; anther connective apex shield-shaped, overhanging the anther thecae; staminal cone present, completely concealing the ovaries, rim even; carpels 7-27, the stigmas connivent, smooth; seed coat smooth, rarely slightly pitted and wrinkled, sarcotesta absent in Malagasy and Mascarene species; aril bilobed, fleshy.

Notes

Eight species of this section occur on Madagascar and the Mascarene Islands. Species of sect. *Xylopia* are the only Annonaceae represented on the islands of La Réunion and Mauritius. The section also includes all tropical American species and the single African species *X. aethiopica*.

1. *Xylopia amplexicaulis* (Lam.) Baill. (Figs 5; 6A)

Adansonia; Recueil d'Observations botaniques 4: 142 (1864). — An[n]ona amplexicaulis Lam., Encyclopédie méthodique, Botanique 2 (1): 127 (1786). — Pseudannona amplexicaulis (Lam.) Saff., Journal of the Washington Academy of Sciences 3: 18 (1913). — Type: Mauritius. "Madagascar", s. d. (fl.), Commerson s. n. (lecto-, here designated, P[P030364]!).

MATERIAL EXAMINED. — Mauritius. Without definite locality, s.d. (fl.), *Ayres 11* (MAU[MAU0000966]); without definite locality, s. d. (fl.) [presented in 1863], *herb. Blackburn s. n.* (K); Pér[r] ier (reserve), s. d. (fl., in spirit collection only, see Fig. 5), *Bosser*

21824 (P[P01954053]); upland forests, without definite locality, s. d. (st.), Bouton 10 (MAU[MAU0000986]); Île de France, without specific locality, Commerson s. n. (B fragment, FI-W, G[G197204/2, G197204/1], MPU[2 sheets], P[P030363, P01954064, P01954065, Drake Herb. ex Herb. Richard, P01954066]); Crown Land Perrier in the National Reserves, 21.III.1950 (fl.), Duljeet F. D. 77 (MAU[MAU0000961, MAU0000962]); without definite locality, Herbier du Petit-Thouars s. n. (P[P01954067]); Gaulettes serrées, 20°12'40"S, 57°38'23"E, 8.XII.1998 (st.), Florens et al. 22975 (MAU[MAU0000982]); without definite locality, 1858 (fl.), Grey s. n. (K); Perrier Nature Reserve, 5.III.1974 (fl.), Guého 16133 (MAU[MAU0000984, MAU00000985]); Perrier Nature Reserve, near Mare aux Vacoas, 1800 ft, 3.II.1973 (fl.), Lorence M57 (MO); Perrier Nature Reserve, 14.III.1975 (fr.), Lorence 1180 (MAU[MAU0000988, spirit collection only]); Bel Ombre forest reserve, 200-400 m, 16.II.1979 (buds), Lorence & Lecordier 2405 (K n.v., MAU[MAU0000983], MO); Perrier Nature Reserve, near Mare aux Vacoas, 600 m, 14.III.1979 (fl.), Lorence 2535 (K n.v., MO, P); Grand Port, s. d. (fl.), Wallich s. n. (BM).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Xylopia amplexicaulis is restricted to the island of Mauritius (Fig. 7), where it occurs in forests and thickets, sometimes along streams and sometimes in habitats dominated by Sideroxylon species, at elevations of 200-600 m. Baker (1877) reported it as occurring in mountain woods at Nouvelle Découverte and La Savanne, but no specimens from these localities have been seen; C. Baider (personal communication) lists the localities where the plant has most recently been observed and photographed as Perrier, Bel Ombre, Gaulettes Serrées, Mt. Lion, Brise Fer, Mare Longue/Machabe, and Florin. Specimens with flowers have been collected in February and March and with fruits in March. The species was initially assessed as Endangered by Page (1998a), and is currently listed as Critically Endangered on the IUCN Red List. In 1998 it was only known from 20 mature trees distributed across three localities on the island. Our EOO and AOO estimates of 334 km² and 16 km², respectively (Table 2), support the assessments.

Description

Tree up 5 m tall; d.b.h. 6 cm.

Twigs glabrous or sparsely appressed-pubescent, the hairs 0.1-0.2 mm long, but soon glabrate; number of axillary branches per node unknown.

Leaves with larger blades 9.7-13.4 cm long, 5.5-7.0 cm wide, subcoriaceous, discolorous, dull green to brown adaxially, tan and occasionally somewhat glaucous abaxially, ovate to lanceolate, apex acute, obtuse, rounded, or emarginate, base cordate-auriculate with the *c*. 1 cm long lobes clasping the

TABLE 2. — Preliminary and published conservation assessments for Madagascar and Mascarene *Xylopia* species. Abbreviations: **CR**, Critically Endangered; **D**, based on IUCN Criterion D; **DD**, Data Deficient; **EN**, Endangered; **VU**, Vulnerable. Sources: **1**, Page 1998a; **2**, Lantoarisoa 2015; **3**, Callmander *et al.* 2009; **4**, Page 1998b; **5**, Page 1998c. *, See Discussion under *X. flexuosa* Diels.

Species	Status	EOO (km²)	AOO (km²)	Localities
X. ambanjensis Cavaco & Keraudren	EN (D)	5498	48	12
X. amplexicaulis (Lam.) Baill.	CR₁	334	16	4
X. anomala, sp. nov.	EN (D)	3468	24	6
X. australis, sp. nov.	EN (D)	185	24	6
X. beananensis Cavaco & Keraudren	DD`́	192983	80	20
X. bemarivensis Diels	DD	171046	172	43
X. <i>buxifolia</i> Baill.	DD	149436	96	24
X. capuronii Cavaco & Keraudren	CR (D)	3846	16	4
X. carinata, sp. nov.	EN (D)	1110	8	2
X. danguyella Ghesg. ex Cavaco & Keraudren	EN (D)	2191	28	7
X. dielsii Cavaco & Keraudren	EN (D)	461	12	3
X. fananehanensis Cavaco & Keraudren	EN (D)	1510	24	6
X. flexuosa Diels*	EN ₂	41 558	48	12
K. galokothamna, sp. nov.	EN (D)	5	8	2
X. ghesquiereana Cavaco & Keraudren	CR (D)	0	4	1
K. humbertii Ghesg. ex Cavaco & Keraudren	CR (D)	0	4	1
K. humblotiana Baill.	DD`´	41 472	240	60
K. kalabenonensis D.M.Johnson, Deroin, & Callmander	CR ₃	0	4	1
K. lamarckii Baill.	CR₄	270	32	8
K. lamii Cavaco & Keraudren	EN (D)	6316	24	6
X. lastelliana Baill.	DD`́	124820	72	18
K. lemurica Diels	DD	38756	68	17
K. lokobensis, sp. nov.	EN (D)	144	8	2
K. longirostra, sp. nov.	EN (D)	5003	24	6
K. madagascariensis Cavaco & Keraudren	EN (D)	3780	24	6
K. marojejyana, sp. nov.	CR (D)	0	4	1
X. perrieri Diels	DD`´	50587	120	30
<i>. ravelonarivoi</i> , sp. nov.	EN (D)	7118	40	10
<i>K. retusa</i> , sp. nov.	EN (D)	1751	32	8
<i>K. richardii</i> Boivin ex Baill.	VU ₅	558	36	9
X. sahafariensis Cavaco & Keraudren	EN (D)	853	12	3
X. sclerophylla, sp. nov.	EN (D)	859	20	5
X. sericolampra Diels	EN (D)	1940	12	3

stem, margin flat, not revolute, glabrous on both surfaces; midrib concolorous with blade adaxially, secondary veins weakly brochidodromous, 13-15 per side, diverging at 65-70° from midrib, these and higher-order veins slightly raised and forming a conspicuous reticulum on both surfaces; petiole 0-2 mm long, broad and flattened, wrinkled, glabrous.

Inflorescences axillary, 1-2-flowered, if more than one flower then peduncle present, sparsely appressed-pubescent except for distal half of peduncle, which is glabrous and sometimes glaucous; peduncle *c*. 3.4 mm long; pedicels 1-2 per peduncle, 7-15 mm long, 2-2.2 mm thick; bracts 3-4, on proximal half of pedicel, caducous or occasionally with distal bract persistent, distal bract 1.7-4 mm long, semicircular; buds oblong, apex obtuse.

Sepals erect to slightly spreading at anthesis, *c*. ¼-connate, 5-8 mm long, 6.5-7 mm wide, coriaceous, broadly triangular and concave, apex acute, sparsely pubescent abaxially.

Petals creamy white, wine-colored with a white patch at the base adaxially and with a pink to purple tinge on the outer petals abaxially *in vivo*; outer petals possibly erect at anthesis, fleshy, 31-45 mm long, 10-14 mm wide at base, 14-15 mm wide at midpoint, fleshy, oblong, flat, apex obtuse, keeled on apical ¼-¼ but becoming concave toward the base adaxially, densely but finely appressed-pubescent abaxially; inner petals with position at anthesis unknown, *c*. 26 mm long, *c*. 4 mm wide at base and midpoint, fleshy, lanceolate, laterally compressed, apex acute, base concave with undifferentiated margin, indument not determinable.

Stamens c. 400; fertile stamens 0.9-1.2 mm long, narrowly oblong, anther connective apex 0.1-0.2 mm long, depressed-globose to bluntly conical, slightly overhanging anther thecae, papillate, anthers 13-14-locellate, filament 0.3-0.4 mm long; outer staminodes 0.8-1.0 mm long, oblong, apex truncate to rounded; inner staminodes c. 0.9 mm long, oblong to quadrate, apex truncate; staminal cone c. 3.5 mm in diameter, c. 0.9 mm high, completely concealing the ovaries, rim even.

Carpels c. 25; ovaries 0.9-1.3 mm long, lanceolate-oblong, glabrous, stigmas loosely appressed, c. 1 mm long, filiform, glabrous.

Fruit of *c*. 17 monocarps borne on a pedicel 25-30 mm long, glabrate; torus *c*. 10.5 mm in diameter, *c*. 9 mm high, depressed-globose; monocarps with light yellow faintly glaucous

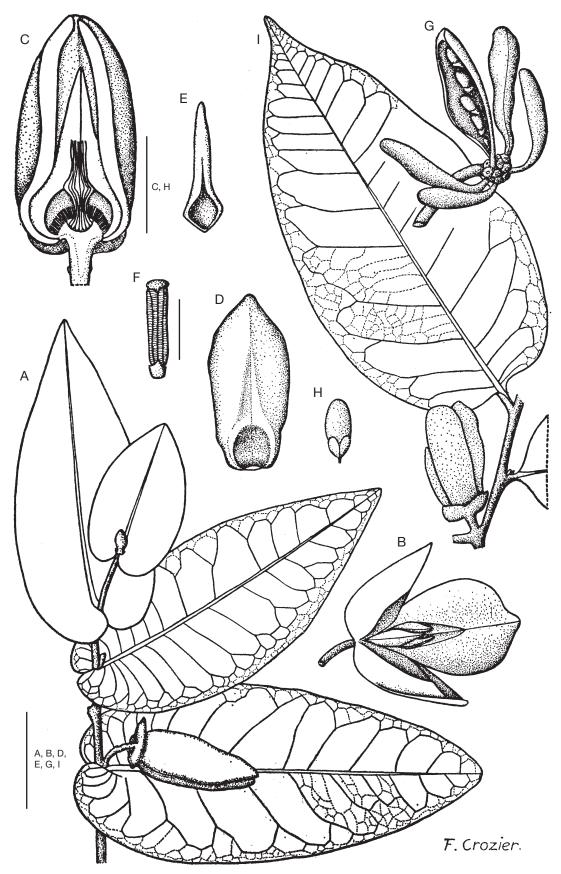


Fig. 5. – *Xylopia amplexicaulis* (Lam.) Baill. and *X. lamarckii* Baill. A-H, *X. amplexicaulis*: A, habit; B, C, flower, longitudinal section showing carpels, staminal cone, inner petals, and outer petals; D, outer petal, adaxial view; E, inner petal, adaxial view; F, stamen, abaxial view; G, fruit; H, seed, side view; I, *X. lamarckii*, habit. Flowers and fruits are based on fluid-preserved specimens, and the sizes are larger than indicated in the species descriptions. A, From *Commerson s. n.* (P); B-F, from *Bosser 21824* (P, spirit collection and photograph); G, H, from *Lorence 1180* (MAU, spirit collection); I, from *Commerson s. n.* (P). Figure reproduced from Keraudren-Aymonin 1980, re-used with permission of T. Mourier, Service Editions, Mission culture scientifique et technique, Institut de recherche pour le développement (IRD), Montpellier. Scale bars: A, B, D, E, G, I, 3 cm; C, H, 2 cm; F, 1 mm.

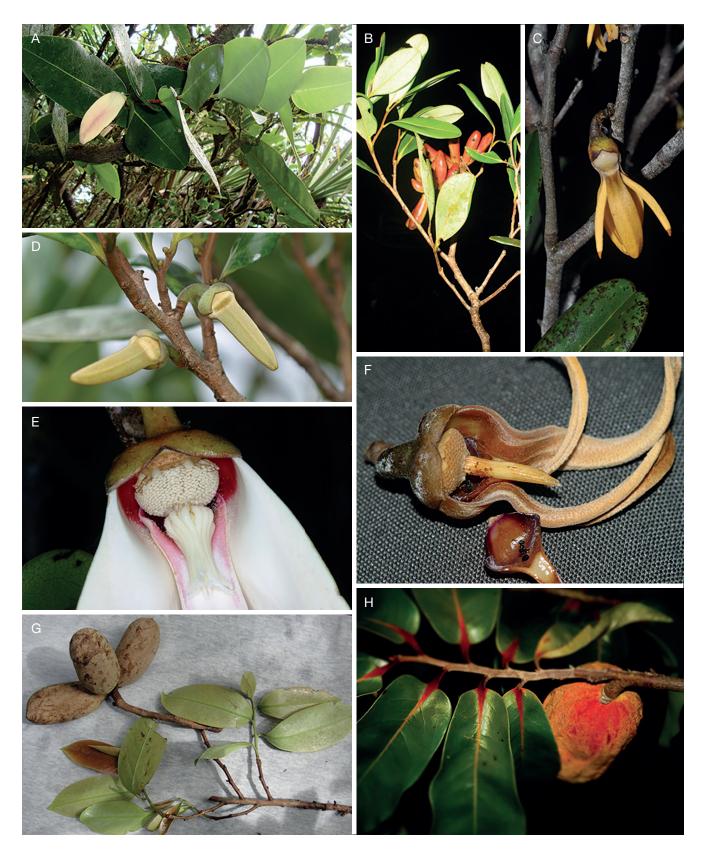


Fig. 6. — **A**, Shoot of *X. amplexicaulis* (Lam.) Baill., showing flower bud at left and clasping leaf bases visible at several nodes; **B**, branch of *X. ravelonarivoi*, sp. nov., with fruit (*Ravelonarivo 4171*); **C**, flower of *X. humblotiana* Baill., side view (*Schatz 4475*); **D**, buds of *X. richardii* Boivin ex Baill.; **E**, close-up of flower interior of *X. lamarckii* Baill., showing red coloration at bases of petals, and the stamens and stigmas; outer staminodes are visible along the edge of the androecium; **F**, flower of *X. richardii* at anthesis, one outer petal and one inner petal removed, so that androecium and stigmas are visible; **G**, leaves and fruit of *X. sanomala*, sp. nov., (*Rakotonirina 48*); **H**, leaves and fruit of *X. sericolampra* Diels. Photos: **A**, Carlos Magdalena; **B**, D. Ravelonarivo; **C**, G. E. Schatz; **D-F**, C. Kaiser-Bunbury; **G**, C. Birkinshaw; **H**, R. N. Rabarijaona. **B**, **C**, **G**, used under the terms of the Creative Commons license for Tropicos, the botanical information system at the Missouri Botanical Garden; **H**, used under the terms of the the Creative Commons license for iNaturalist.

exterior and bright red endocarp *in vivo*, 2-4.5 cm long, 0.6-1 cm wide and thick, clavate to fusiform, not torulose, apex obtuse, base gradually contracted into a stipe 8.8-10 mm long, 1.7-3.4 mm thick, smooth, glabrous; pericarp thin, leathery.

Seeds up to 6 per monocarp, in a single row, oblique to parallel to long axis, 10-12 mm long, 4-5 mm wide, narrowly ellipsoid, circular in cross-section, black, smooth, shiny, perichalazal ring not evident; sarcotesta absent; aril translucent white *in vivo*, bilobed, lobes *c*. 3.8 mm long and wide, fleshy, semicircular.

Notes

The flowers of *X. amplexicaulis*, with their broad and thick outer petals, are among the largest in the entire genus, and were the basis for the original placement of the plant in the genus *Annona* by Lamarck, and the recognition of section *Pseudanona* by Baillon and later a genus of the same name by Safford. The auriculate clasping leaf bases are unique in the genus and unusual among Annonaceae. *Xylopia lamarckii*, also endemic to Mauritius, has similar flowers but a distinctly petiolate leaf with a rounded base. Labels of the collections made by D. Lorence indicate that the branches are erect, forming a compact crown; such a growth habit is unusual within both the genus and family.

Two collections of *Xylopia amplexicaulis* in the Lamarck herbarium with handwritten labels state that they were collected by Commerson: one from Isle de France, the other from Madagascar. This agrees with the provenance information given in Lamarck's protologue: "Cette plante croît à l'Isle de France & à Madagascar, où Commerson l'a observée". Commerson apparently collected mostly around Taolagnaro (Fort Dauphin) during his brief visit to Madagascar (Morel 2012), and, as noted above, the plant has never been collected or reported from Madagascar subsequently. This provenance is regarded as a labeling error.

It is unclear whether the two locality labelings represent different collections, or the mis-labeling of some duplicates, but in either case, and to avoid future difficulties, a lectotype is designated above. Lamarck's diagnosis states "Anona foliis cordato-oblongis acutis distichis amplexicaulibus". The leaves of the specimen marked as collected from "isle de france" have distinctly acute apices in addition to the cordate bases, while the leaves of the specimen marked as collected from "Madagascar" have cordate bases but rounded apices. Lamarck's description carefully describes the sepals and petals of the flowers, which are only present on the "Madagascar" specimen. This is also the more complete specimen, and is designated as the lectotype. There is uncertainty as to whether other collections are duplicates and thus isolectotypes, and they are therefore not listed as types.

2. *Xylopia beananensis* Cavaco & Keraudren (Figs 1G; 8J-P)

Bulletin de la Société botanique de France 103: 275 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est"], bassin de la Rantabe, environs de Beanana, 650 m, 25.II.1954 (fl., fr.), *Capuron 9077* (holo-, P[P030365]!; iso-, P[P030366, P030367, P00697844]!; TEF, photo!; WAG!).

MATERIAL EXAMINED. — Madagascar. Prov. Antananarivo. Centre, forêt d'Ambotantely, sur le Tampoketsa d'Ankazobe, 1600 m, 27.II.1966 (fl.), *Capuron 24569 SF* (K n.v., P[P01954040, P01954041, P01954042]); 3.0 km NW of Ambohitsaratelo-Bebao (NW of Tsiroanomandidy), 1100-1200 m, 16.I.1985 (fr.), *Dorr et al. 3588* (BR, G, MO, NY, P[P01954044, P01954045], US, WAG).

Prov. Antsiranana. Réserve naturelle intégrale de Tsaratanana, slopes W of River Antsahamanara, Fir. Marolana, Fiv. Ambanja, 14°02'06"S, 48°47'08"E, 1408 m, 28.XI.2000 (buds), Antilahimena et al. 667 (OWU, P[P02034675]); Diana Region, Anketrabe-Belinta, Ambilobe, Beramanja, Camp Bilahy, 13°35'09"S, 48°43'34"E, 963 m, 22.II.2005 (fl.), Buerki et al. 14 (MO); Ambilobe, Beramanja, Anketrabe, forêt de Kalabenono, 13°38'31"S, 48°40'25"E, 700 m, 25.XI.2006 (fr.), Callmander et al. 598 (K n.v., P[P01954043]); East (Nord), environs sud de Tsaratanana, entre Nosiarina et Antsirabe-Nord (route Sambava-Vohémar), 1.IV.1967 (fl.), Capuron 27657 SF (P[P01954055, P01954056, P01954057, P01954058]); SW of Andapa, near SW edge of Anjanaharibé-Sud Reserve, 14°48'15"E, 49°26'45"E, 1000-1100 m, 6.VIII.1997 (fr.), McPherson 17267 (K n. v., MO, WAG); Sava Region, Sava, Andapa, Anjialavabe, Ankiakabe, forêt dense humide de moyenne altitude d'Antsahaberaoka, située à 11 km au NW d'Anjialavabe, 14°09'53"S, 49°22'52"E, 1002 m, 24.II.2007 (fr.), Rakotovao et al. 3717 (MO); Marotolana à 7 km est de Beangona-Ambevy, 14°01'54"S, 48°47'01"E, 700-1300 m, 26.XI.2000 (fl.), Ratovoson et al. 342 (P[P01954032]).

Prov. Fianarantsoa. Fianarantsoa, Iakora, Begogo, Bekora, forêt de Sahalava au S de village du Androizaha, 23°32'26"S, 46°32'00"E, 1260 m, 29.I.2005 (fr.), *Andrianjafy et al. 800* (MO).

Prov. Mahajanga. Sous-Préfecture de Befandriana-Nord, commune rurale de Matsoandakana, Quartier de Belalona, Sud-Ouest d'Andapa, Réserve Spéciale Anjanaharibe-Sud, village d'Anjiamazava, suivant la route Nationale d'Andapa-Bealanana, piste vers Nord approchant le sommet de Bevitsika, 14°42'S, 49°27'E, 1100 m, 14.XII.1994 (fr.), *Ravelonarivo & Rabesonina 569* (OWU, P[P01954033]).

Prov. Toamasina. Alaotra Mangoro, Moramanga, Ambatovola, Fanovana, forêt de Vohimana, 18°55'13"S, 48°30'49"E, s. d. (fr.), Andriatsiferana 2590 (Kn.v., MO, P[P00909316]); Alaotra-Mangoro Region, Fivondronana Moramanga, Commune Andasibe, Fokontany Beravo, Ambatovy forest, 18°48'28"S, 48°18'43"E, 1100 m, 26.I.2005 (fr.), Antilahimena et al. 3247 (K n.v., MO, P[P01954034]); Alaotra-Mangoro Region, Fivondronana Moramanga, Commune Andasibe, Fokontany Beravo, Ambatovy forest, near Berano village, 18°50'17"S, 48°19'42"E, 1025 m, 11.II.2005 (fr.), Antilahimena et al. 3377 (K n.v., MO, P[P01954031]); Moramanga, Andasibe, Menlamba, near Behontsa village, Ambatovy forest, 18°51'59"S, 48°19'09"E, 1045 m, 8.III.2005 (fr.), Antilahimena et al. 3623 (K n. v., P[P01954035]); Toamasina, Moramanga, Commune Ambohibary, Fokontany Ampitambe, 18°51'02"S, 48°17'24"E, 1080 m, 9.II.2007 (fr.), *Antilahimena & Edmond 5244* (P[P06901360]); au-dessus d'Andratambe, alt. 500 m, bassin inférieur de la Vohilava, affluent rive gauche de la Rantabe, III.1954 (large buds, fr.), Capuron 9159 (OWU, P[P01757050, P01954037, P01954038]); Alaotra-Mangoro Region, District Moramanga, Commune Ambohibary, Fokontany Ampitambe, Ambatovy, NE de Moramanga, environ 22 km de Moramanga, 18°51'31"S, 48°19'03"E, 1121 m, 19.II.2005 (fr.), Rakotovao et al. 1232 (MO); Alaotra-Mangoro Region, Analamay, Ambatovy, Fokontany Ampitambe, Firaisina Ambohibary, Fivondronana Moramanga, 18°50'52"S, 48°18'31"E, 1148 m, 10.II.2005 (fr.), Razafindraibe & Antilahimena 101 (OWU); Alaotra-Mangoro Region, Torotorofotsy forest, Fokontany Ampitambe, Ambatovy, commune rurale Ambohibary, district Moramanga, 18°51'48"S, 48°20'33"E, 958 m, 13.I.2005 (fr.), Razanatsoa 27 (K); forêt Tsiazonomby, Dist. Moramanga, Canton Anosibe, 26.VI.1952 (old fls,



FIG. 7. - Distributions of Xylopia amplexicaulis (Lam.) Baill., X. lamarckii Baill., and X. richardii Boivin ex Baill. on the islands of La Réunion and Mauritius.

fr.), Service Forestier (Stanislas) 6123 SF (P[P01954049, P01954050 (fruit), P01954051]); Antetezampandrana, Toby Comexfo P. K. 45 route Moramanga-Anosibe, District Moramanga, Canton Moramanga, 23.I.1969 (buds), Service Forestier 26848 SF (P[P01954039]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia beananensis* occurs in humid lowland to lower montane forests of northern, central, and southern Madagascar at elevations from 500 to 1600 meters (Fig. 28). Specimens with enlarging buds have been collected in January, March, and August, with open flowers in February, April, and November, and with floral remnants in June. Specimens with mature fruits have been collected from November to March and with immature fruits in August. We have given this species a preliminary conservation assessment of Data Deficient, but its large EOO, at 192983 km² the largest for any Madagascar *Xylopia* species (Table 2), suggests that it is not of immediate conservation concern.

LOCAL NAMES. — Hazoambo (Antilahimena et al. 337, Razafindraibe & Antilahimena 101), rotry (Ravelonarivo & Rabesonina 569).

DESCRIPTION Tree up to 30 m tall; d.b.h. up to 42 cm.

Twigs finely appressed-pubescent, the hairs 0.1-0.2 mm long, becoming glabrate; nodes with one axillary branch.

Leaves with larger blades 6.5-10.8 cm long, 2.5-4.8 cm wide, coriaceous, discolorous, olive-green and shining adaxially, tan to rusty abaxially, broadly lanceolate, oblong-lanceolate, elliptic, or rarely obovate, apex acute to acuminate, the acumen 5-15 mm long, base broadly cuneate and short-decurrent on petiole, margins somewhat revolute, glabrous adaxially, sparsely appressed-pubescent

to glabrous abaxially; midrib red toward the base adaxially, secondary veins weakly brochidodromous, 10-14 per side, diverging at 45-70° from midrib, these and higher-order veins slightly raised and forming a conspicuous reticulum on both surfaces; petiole 3.5-8 mm long, flattened, winged along margins, longitudinally wrinkled, glabrous.

Inflorescences axillary or from the axils of fallen leaves, 1-4-flowered, pedunculate or not, pubescent; peduncle 1.1-2 mm long or absent; pedicels 2-4 per peduncle or arising separately from leaf axil, often recurved, 5.3-7.6(-11) mm long, 1.0-1.3 mm thick; bracts 2-4, spaced evenly along pedicel, caducous, only scars seen; buds lanceolate, apex obtuse.

Sepals wide-spreading at anthesis, ½-½-connate, 2.7-3 mm long, 2.8-4.7 mm wide, coriaceous, semicircular, apex rounded or occasionally apiculate, pubescent abaxially.

Petals white to dull yellow, with the inner petals tinted red at the base *in vivo*; outer petals slightly spreading at anthesis, 17-18 mm long, 4-5 mm wide at base, 2.5-3 mm wide at midpoint, fleshy, lanceolate, keeled only at tip adaxially, with a faint keel abaxially, apex obtuse, densely puberulent except for the glabrous base adaxially, appressed-pubescent abaxially; inner petals slightly spreading at anthesis, 13.5-16.9 mm long, 3.5-3.9 mm wide at base, *c*. 1.2 mm wide at midpoint, fleshy, linear, keeled on both surfaces, apex acute, base concave with undifferentiated margins, densely puberulent except for the glabrous base on both surfaces.

Stamens 150-200; fertile stamens *c*. 1.5 mm long, narrowly oblong, anther connective apex *c*. 0.2 mm long, shield-shaped, slightly overhanging anther thecae, papillate, anthers 11-12-locellate, filament 0.5-0.6 mm long; outer staminodes 1.4-1.5 mm long, clavate, apex rounded; inner staminodes *c*. 1.1 mm long, oblong, apex truncate; staminal cone 2.8-3.2 mm diameter, 1.3-1.4 mm high, completely concealing the ovaries, rim irregularly laciniate.

Carpels *c.* 15; ovaries *c.* 0.7 mm long, ovoid, densely rusty appressed-pubescent, stigmas connivent, *c.* 3.3 mm long, filiform, glabrous.

Fruit of up to 15 monocarps borne on a pedicel 12-20 mm long, 2.5-3.5 mm thick, sparsely pubescent; torus 6.5-10 mm in diameter, 4-6 mm high, depressed-globose; monocarps with bright pink-red to red exterior and red endocarp *in vivo*, 2.4-4.8 cm long, 0.7-1.1 cm wide, 0.7-0.8 cm thick, narrow-ly oblong, often slightly torulose, apex obtuse, sometimes with a beak 2-5 mm long, base sessile, obliquely wrinkled, sparsely pubescent to glabrate; pericarp 0.6-2 mm thick.

Seeds up to 5 per monocarp, in a single row, oblique to parallel to long axis, 7.1-8.3 mm long, 3.7-5.2 mm wide, 3.5-4.5 mm thick, oblong-ellipsoid, circular to broadly elliptic in cross-section, brownish black to black, smooth or slightly pitted and wrinkled, shiny, perichalazal ring inconspicuous to slightly raised; sarcotesta absent; aril white *in vivo*, whitish orange when dried, bilobed, lobes 1.2-3.0 mm long, 3.1-4.7 mm wide, papery to fleshy, with ruffled margins.

Notes

Xylopia beananensis is distinguished by its coriaceous broadly lanceolate to elliptic leaves with a prominent vein reticulum on both surfaces, the well-developed staminal cone, and the strongly wrinkled and narrowly oblong monocarps with seeds lying nearly parallel to the long axis. It is most similar to *X. flexuosa*, but differs in the flattened petioles, shorter pedicels with caducous bracts, and shorter petals. One collection (*Antilahimena et al. 3377*) reports the bark to be white. Precocious growth from the axillary vegetative bud superposed above inflorescences is an odd feature of some specimens.

At the time of the floristic treatment of Cavaco & Keraudren (1958) this species was only known from the basin of the Rantabe River in what is now northern Toamasina Province, but more recent collections show that it occurs up to 1600 meters from Antsiranana Province in the north south to Fianarantsoa Province. It is one of several relatively widespread mid-elevation *Xylopia* species on the island, including *X. lemurica* and *X. perrieri*, which do not occur below 400 meters.

Of all species of sect. *Xylopia* from the region, *X. beananensis* bears the closest resemblance, in habit, foliage, flowers, and fruits, to *X. aethiopica*, the single species of the section that occurs in Africa.

3. *Xylopia flexuosa* Diels (Figs 2E; 8Q-X)

Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 350 (1925). — Type: Madagascar. Prov. Toamasina ["Madagascaria orientalis"], Beforona, 700 m, X.1921 (fl., fr.), Perrier de la Bâthie 14057 (holo-, P[P030388]!; iso-, P[P030389]!).

Xylopia flexuosa var. *latiflora* Ghesq. ex Cavaco & Keraudren, *Bulletin du Jardin botanique de l'État à Bruxelles* 27: 88 (1957). — Type: Madagascar. Prov. Fianarantsoa ["Est"], Pointe de Farafangana, 5.X.1926 (fl., immature fr.), *Decary 5570* (holo-, P[P030390]!; iso-, K[K001208445]!, P[P030391]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana. Forêt Betafonanana-Maromandia–Antalaha, 18.XI.1956 (fr.), *Service Forestier 12450* (P[P00524380]).

Prov. Fianarantsoa. Atsimo-Atsinanana Region, Vangaindrano, Vohipaho, forêt d'Ankarabolava, 23°21'51"S, 47°29'48"E, 72 m, 17.IX.2009 (buds), *Andriamihajarivo et al.* 1678 (MO); Péninsule de Farafangana, 1.IX.1926 (fr.), *Decary 5088* (P[P00524379, P01986967, P01986968]); bassin de Mananjary, Mt. Vatovavy, VII.1911 (fl.), *Perrier 4973* (B, P[P01986954, P01986970]); Commune Farafangana, District Vondrozo, Anivotany, 9 km from Madiorano to Vohibe (RN 27), 22°47'28.9"S, 47°11'52.5"E, 583 m, 22.X.2006 (fl., fr.), *Ranarivelo et al. RTI 340* (K); Antseromana, Fort-Carnot, 18.X.1954 (st.), *Service Forestier 14512* (P[P01986956]).

Prov. Toamasina. Fivondronana Vavatenina, Commune Ambodimangavalo, Fokontany Manakambahiny I, Rivière d'Ihofika, près du campement Andranofantsona, 17°39'07"S, 48°58'14"E, 550-600 m, 25.X.2002 (fl.), *Andrianjafy et al.* 325 (MO, P[P01986955]); Analanjirofo Region, Soanierana Ivongo, Manopana, Fokontany Tanambao Ambodimanga, Andranomintina, 16°47'03"S, 49°41'26"E, 23 m, 31.V.2010 (fl.), *Lehavana & Fotsy* 735 (MO); Tamatave District, R. N. I., 20.X.1951 (fl.), *Rakotoniama* 3231 RN (P[P00169374, P01986953]); Parc national de Zahamena, 17°39'07"S, 48°58'14"E, 650 m, 14.VIII.2000 (flower buds), *Randrianjanaka et al.* 566 (P[P01986969]); District Tamatave, R. N. I., 18.IV.1952 (fr.), *Réserves Naturelles* 3681 (P[P01986957]).

Prov. Toliara. Anosy Region, District Taolagnaro, Commune Rurale de Mahatalaky, Fokontany Sainte Luce, forêt littorale d'Analavinaky, située à l'Ouest du village d'Ambandrika, 24°46'30"S, 47°09'00"E, 21 m, 24.XI.2009 (fr.), *Rakotovao 4687* (MO); Taolanaro, près du village d'Amboahangy, Tsitongambarika, Androkabe, Antamponandakato, Commune Rurale Iaboakoho, 24°55'42"S, 47°15'61"E, 17.X.2013 (fl., fr.), *Rapanarivo et al. RS 918* (P[P01031663]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia flexuosa* occurs in east-central Madagascar, in humid forests at elevations from 21 to 700 meters (Fig. 28); the elevational range of 500-999 m given by Lantoarisoa (2015) may be based on misidentified specimens. Specimens with flowers have been collected in May, July, September, and October, and those with fruits from April, September, October, and November. This species was given a preliminary conservation assessment of Endangered by Lantoarisoa (2015) on the basis of EOO estimated at 11 904 km² and an AOO of 27 km². We suggest that this estimate be reconsidered, given our EOO estimate of 41 558 km² and AOO estimate of 48 km².

LOCAL NAMES. — Fotsivavo (*Decary 5088*), havoka (*Rakotomania 3231RN*), hazoambo (*Andrianjafy et al. 325*), hazoamboay (*Andrianjanaka 566*), malaohazo (*Andrianjafy et al. 325*), morangavavy (*Service Forestier 12450*).

DESCRIPTION

Tree or shrub up to 10 m tall; d.b.h. up to 20 cm.

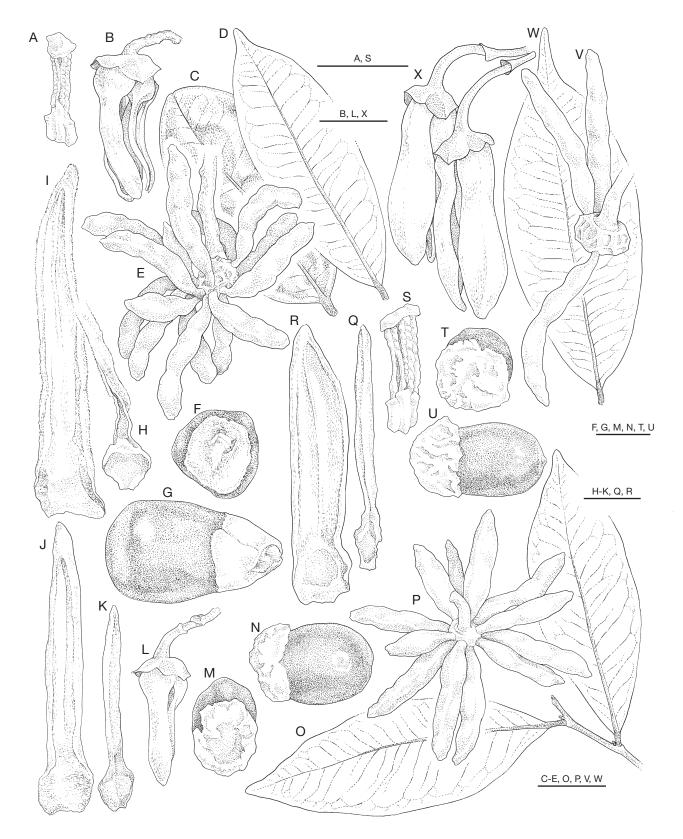


Fig. 8. — *Xylopia richardii* Boivin ex Baill., *X. beananensis* Cavaco & Keraudren, and *X. flexuosa* Diels. **A-I**, *X. richardii*: **A**, stamen, abaxial view; **B**, flower bud, side view; **C**, **D**, leaves; **E**, fruit; **F**, seed, view of micropylar end; **G**, seed, side view; **H**, basal half of inner petal, adaxial surface; **I**, outer petal, adaxial surface; **K**, inner petal, adaxial surface; **L**, flower bud, side view; **M**, seed, view of micropylar end; **N**, seed, side view; **O**, leaves; **P**, fruit. **Q-X**, *X. flexuosa*: **Q**, inner petal, adaxial surface; **R**, outer petal, adaxial surface; **S**, stamen, abaxial view; **T**, seed, view of micropylar end; **N**, seed, side view; **U**, seed, side view; **V**, fruit; **W**, leaf; **X**, flowers, side view. **A**, **C**, **H**, **I**, from *Friedmann* 3037 (MAU); **B**, from *Florens et al.* 24082 (MAU); **D**, from *Bernardi* 15071 (NY); **E**-**G**, from *Lorence R* 41 (MO); **J**-**L**, from isotype specimen at TAN; **M**, **N**, **P**, from *Ravelonarivo* & *Rabesonina* 569 (OWU); **O**, from *Dorr* 3588 (NY); **Q-S**, from *Perrier de la Bâthie* 4973 (B); **T-V**, from *Service des Eaux et Forêts de Madagascar* 12450 SF (P); **W**, **X**, from *Decary* 5570 (P). Scale bars: A, S, 1 mm; B, L, X, 1 cm; C-E, O, P, V, W, 2 cm; F, G, M, N, T, U, 3 mm; H-K, Q, R, 5 mm.

Twigs glabrous to sparsely pubescent, the hairs 0.1-0.2 mm long; nodes with one axillary branch.

Leaves with larger blades 7.9-12.7 cm long, 2.8-4.8 cm wide, subcoriaceous to coriaceous, concolorous or slightly discolorous, grayish to blackish green adaxially, slightly brownish green abaxially, elliptic, elliptic-oblanceolate, oblong, or oblong-oblanceolate, apex acuminate, the acumen 8-20 mm long, base cuneate to broadly cuneate and short-decurrent on the petiole, margin flat, not revolute, glabrous adaxially, glabrous or sparsely appressed-pubescent but soon glabrate abaxially; midrib orange to red adaxially, secondary veins weakly brochidodromous, 12-17 per side, diverging at 60-80° from midrib, these and higher-order veins slightly raised and forming a conspicuous reticulum on both surfaces; petiole 2-7 mm long, semi-terete, transversely and longitudinally wrinkled, glabrous.

Inflorescences arising from the axils of fallen leaves, 1-14-flowered, occasionally persistent and forming tubercles on older branches, pedunculate, sparsely pubescent; peduncle 3-8 mm long; pedicels up to 3 per peduncle, 9-18 mm long, 1.0-1.3 mm thick; bracts 2, one attached just distal to the pedicel base and the other just proximal to the pedicel midpoint, persistent, 1-1.8 mm long, ovate to nearly circular; buds oblong, apex obtuse, sometimes slightly falciform.

Sepals somewhat spreading at anthesis, ½-connate, 2-3.5 mm long, 2.7-4.4 mm wide, coriaceous, broadly ovate to semicircular, apex broadly acute, sparsely pubescent abaxially.

Petals white, yellow, or greenish yellow, red on the inner base *in vivo*; outer petals with position at anthesis unknown, but separating first at the base and moving apically, (13.5-)18-28 mm long, 2.5-5.5 mm wide at base, 3.2-5.4 mm wide at midpoint, fleshy, narrowly oblong or slightly panduriform, flat, apex obtuse, finely puberulent adaxially, densely appressed-pubescent abaxially; inner petals with position at anthesis not determinable, 18-23 mm long, 2.5-4 mm wide at base, 1-2.8 mm wide at midpoint, fleshy, linear, laterally compressed and sharply keeled abaxially, apex acute, base concave with undifferentiated but somewhat bilobed margins, finely puberulent on both surfaces except for glabrous concavity.

Stamens *c*. 200; fertile stamens 1-1.7 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm high, shield-shaped to capitate, overhanging anther thecae, puberulent or papillate, anthers *c*. 11-locellate, filament 0.2-0.4 mm long; outer staminodes 1.2-1.5 mm long, oblong to clavate, apex obtuse; inner staminodes 0.9-1.1 mm long, oblong, apex truncate; staminal cone 2.7-3.9 mm in diameter, 0.9-1.7 mm high, completely concealing the ovaries, rim slightly uneven.

Carpels 17-25; ovaries *c*. 1.6 mm long, oblong, pubescent along the edges but otherwise glabrous, stigmas white *in vivo*, connivent into a pyramidal mass but with the apices separated, 2.2-2.5 mm long, filiform, apices pilose.

Fruit of up to 28 monocarps borne on a pedicel 13-20 mm long, 2.2-5 mm thick, glabrate; torus 11-17 mm in diameter, 7-8 mm high, depressed-globose; monocarps red *in vivo*, 3.7-6.3 cm long, 0.6-0.8 cm wide, *c*. 0.7 cm thick, narrowly oblong, weakly torulose, apex with a blunt beak 1.5-2 mm long, base slightly contracted into a stipe 4.5-6 mm long, 3.5-4.1 mm thick, obliquely wrinkled, glabrate or sparsely pubescent; pericarp *c*. 0.8 mm thick.

Seeds up to 5 per monocarp, in a single row, lying oblique to parallel to long axis, 7.6-8.6 mm long, 4.4-4.5 mm wide, 3.9-4.2 mm thick, oblong-ellipsoid, circular to broadly elliptic in cross-section, brownish black, smooth, shiny, perichalazal ring slightly elevated and sometimes forming a small umbo at the chalazal end; sarcotesta absent; aril white *in vivo*, light orange-brown when dried, bilobed, lobes 2.8-3.6 mm long, 4-4.8 mm wide, fleshy with ruffled margins.

Notes

Xylopia flexuosa was named by Diels for the conspicuously flexuous younger branches of the type specimen. The plants are similar to *X. beananensis*, but may be distinguished by long-acuminate leaves with semi-terete petioles, longer flower pedicels with persistent bracts, and laterally compressed inner petals. The variety *X. flexuosa* var. *latiflora* is not recognized here. It is qualitatively similar to the nominate variety, differing only in the slightly wider outer petals and the better-developed tubercle-like inflorescence base, which may produce a larger number of flowers. In floral morphology *X. flexuosa* is the Madagascar species most similar to the Mascarene species *X. amplexicaulis* and *X. lamarckii*.

4. *Xylopia humblotiana* Baill. (Figs 1A; 2C, F; 9G-M)

Bulletin mensuel de la Société linnéenne de Paris 1: 340 (1882). — Type: Madagascar. Prov. Toamasina, ad lacum Nossibé, IV.1882 (fl., fr.), Humblot 117 (holo-, P[P030398]!; iso-, K[K000199050]!, P[P030399]!).

Xylopia platynema Diels, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 351 (1925). — Type: Madagascar. Prov. Toamasina ["Madagascaria orientalis"], forêt littorale orientale pres d'Ambilo, II.1924 (fl., fr.), Perrier de la Bâthie 15998 (holo-, P[P00524382]!, iso-, P[P00608328]!).

MATERIAL EXAMINED. — **Madagascar**. Prov. Antsiranana. Parc national de Masoala, Andranomaintiny, Fok. Sahamalaza, Fir. Vinanivao, 15°49'S, 50°18'E, 0-41 m, 21.II.1996 (fl.), *Aridy & Moïse 168* (MO); sur la piste de Beankoraka vers Vinanivao, Firaisana Vinanivao, Masoala, 15°57'S, 50°12'E, 10-60 m, 17.XI.1994 (fr.), *Rabe 154* (MO); forêt littorale Ambodiletry, Beankoraka, Parc national de Masoala, 15°59'17"S, 50°13'00"E, 0 m, 12.XI.1994 (fr.), *Rahajasoa et al.* 844 (MO); Sava Region, forêt d'Antsoha, Fokontany Sahafary, Firaisana Ambohitralanana, Fivondronana Antalaha, 15°16'12"S, 50°23'14"E, 50 m, 1.X.1997 (fl.), *Ravololonanahary 110* (OWU); 5.8 km S of Lokoho River along coastal road between Sambava and Antalaha, 6.8 km S of Farahanana, 14°29'S, 50°10'E, 50 m, 15.X.1988 (fl., fr.), *Schatz 2381* (K n.v., MO); Masoala National Park, 2 km W of Camp Est, 15°16'23"E, 50°27'24"E, 5 m, 23.I.1999 (bud, fr.), *Schatz et al. 3776* (MO).

Prov. Fianarantsoa. Route Farafangana-Vangaindrano, XII.1963 (fl.), Bosser 18678 (K n.v., MO); Fiv. Nosy Varika, Fir. Ambahy, littoral forest on sand of Ambahy, 20°46'20"S, 48°28'39"E, 13 m, 7.XII.2002 (fl.), Koopman et al. 135 (OWU); Vatovavy Fitovinany, Manakara, Andosy, Lohokola Forest, 21°43'38"S, 48°11'19"E, 22 m, 28.I.2009 (fr.), Letsara et al. LRK 824 (CAS); Farafangana, Mahabo Mananivo, Nosiala, 23°11'10"S, 47°43'02"E, 30 m, 5.VIII.2004 (immature fr.), Ludovic et al. 883 (MO); Préfecture Farafangana, Commune rurale Mahabo Mananivo, Fokontany Mahabo, 23°11'19"S, 47°41'16"E, 12 m, 28.IX.2004 (immature fr.), Ludovic et al. 914 (MO); S of Farafangana, near village of Mahabo, 23°10'36"S, 47°42'01"E, 3.XI.2001 (fr.), McPherson & Rabenantoandro 18316 (K n.v., MO); Fivondronana Nosy Varika, Firaisana Ambahy, Rokontany Ambahy, forêt d'Andohan'İ Martin, 20°48'07"S, 48°38'56"E, 9 m, 15.II.2004 (fl., fr.), Rabehevitra et al. 871 (MO, P[P02090396]); Fivondronana: Farafangana, Fokontany: Manombo, forêt littorale sur sable de Manombo, 23°04'13"S, 47°45'45"E, 20 m, 12.XI.2001 (fl.), Rabenantoandro et al. 747 (MO); Fokontany Mahabo, commune rurale Mahabo-Mananivo, Fivondronana Farafangana, 23°10'12"S, 47°41'54"E, 5.II. 2001 (fr.), Rabevohitra & Rabenantoandro 3792 (MO); Fokontany Mahabo, commune rurale Mahabo-Mananivo, Fivondronana Farafangana, 23°10'12"S, 47°41'54"E, 5.II.2001 (fl., fr.), *Rabevohitra & Rabenantoandro 3793* (MO); Fivondronana, Nosy Varika, Firaisana et Fokontany: Ambahy, 20°46'15"S, 48°28'48"É, 21.III.2003 (fl.), Rabevohitra et al. 4608 (K n.v., MO, NY); Fivondronana, Nosy Varika, Firaisana et Fokontany: Ambahy, 20°46'15"S, 48°28'48"E, 21.III.2003 (fr.), Rabevohitra et al. 4635 (MO); Fivondronana: Nosy Varika, Commune rurale: Ambahy, Fokontany: Ambahy, forêt d'Ambahy à 500 m à l'Est du Fokontany, 20°46'57"S, 48°28'54"E, 17.XI.2003 (fl.), Rabevohitra et al. 4789 (Kn.v., NY); Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, forêt de Nankinana, 20°22'22"S, 48°33'56"E, 13 m, 17.IV.2004 (fl.), Ranaivojaona et al. 618 (MO, OWU); Fivondronana Mananjary, Firaisana Ankatafana, Fokontany Marohita, 21°28'29"S, 48°16'51"É, 13 m, 3.X.2004 (immature fr.), Ranaivojaona et al. 924 (K n v., MO); Farafangana, Mahabo-Mananivo, Mahabo, 23°11'13"S, 47°42'27"E, 22 m, 26.VIII.2003 (immature fr.), Razakamalala & Rabehevitra 700 (MO); Fivondronana: Mahanoro, Commune rurale: Ambodibonara, Fokontany: Ambalavontaka, forêt littorale sur sables de Nakinà, 20°21'06"Ś, 48°36'48"E, 41 m, 8.XI.2003 (fr.), Razakamalala et al. 838 (MO, OWU); Fivondronana, Nosy Varika, Firaisana: Ambahy, Fokontany: Ambahy, forêt d'Ambahy, 20°47'49"S, 48°28'58"E, 10 m, 23.IV.2004 (fl.), Razakamalala et al. 1175 (MO, OWU, P[P06901350]).

Prov. Toamasina. Près Fénérive, XI.1906 (fl., immature fr.), d'Alleizette s. n. (L); Station forestière de Tampolo, Fénérive-Est, Parcelle A1, 17°17'00"S, 49°23'30"E, 10 m, 3.X.2004 (fr.), Andriambololonera & Lehavana 25 (OWU, P[P00909322]); Fivondronana Sainte Marie, Firaisana Lokintsy, Fokontany Sahasifotra, 16°51'09"S, 49°57'13"E, 19 m, 9.X.2003 (immature fr.), Andrianarivelo et al. 88 (MO); Tamatave, III.1891 (fl.), Baron 5997 (K); Toamasina, 0-2 km E of Andavakimenarana (location of ferry to cross Pangalanes on road to Brickaville-Ambila), Tamatave, 18°52'34"S, 49°08'12"E, 1-10 m, 14-16.II.1999 (fl.), Birkinshaw et al. 560 (K n.v., MO); Est: forêt sublittorale, à Tampolo, au Nord de Fénérive, 9.III.1965 (fl.), Capuron 24044 SF (K n.v., BR); Tamatave, Ankarefo (canal des Pangalanes), 14.XII.1966 (bud, immature fr.), Capuron SF 26227 (K n.v., OWU); Prov. Tamatave, along Route #5 between Tamatave and Fenerive at World Wildlife Fund Aye-Aye Preserve, near PK 83, more than 50 m, 27.II.1975 (fr.), Croat 32529 (MO); E coast of Madagascar, Ambila-Lemaitso, c. 103 km S of Toamasina, 18°51'S, 49°08'E, 21.XI.1997 (fr.), Davis 1121 (G, K n.v., MO); Prov. Tamatave, Station Forestière de Tampolo, 10 km N of Fenerive, 29.XI.1985 (fr.), Dorr et al. 4397 (K n.v., MO, PRE, WAG); Prov. Tamatave, south side of ferry-crossing on road from Brickaville to Ambila Lemaitso, 11.XII.1985 (fr.), Dorr et al. 4479 (K n. v., MO, PRE); Prov. Tamatave, Ambila-Lemaitso, second lake S of road-junction for Andevoranto and Brickaville, 20.I.1986 (fr.), Dorr et al. 4593 (Kn.v., MO, PRE); along coast at Ambila-Lemaitso, 18°49'S, 49°09'E, 15.XI.1989 (fr.), Keating & Miller 2255 (K n.v., MO); Ambila-Lemaitso, E of Brickaville, Old Station Forestière, c. 5 km S of town, 18°54'S, 49°07'E, 10 m, 17.I.1999 (fl., fr.), Lowry & Miller 5138A (MO); Vohibola, forest N of Pangalane Hotel, N shore of Lac Ampitabe, c. 2 km W of Andranokoditra, 18°35'46"S, 49°14'06"E, 2-5 m, 9.II.2003 (fr.), Lowry et al. 6030 (MO, OWU); Vohibola, forest N to NNW of village of Andranokoditra, N of Lac Ampitabe, 18°33'34"S, 49°15'01"Ĕ, 5 m, 12.II.2003 (fl.), Lowry et al. 6090 (Kn.v., MO, OWU); Préfecture Mahanoro, S. P. Masomeloka, Comm. Ambodibonara, Fok. Ambalavontaka, 20°21'44"S, 48°37'05"E, 23 m, 11.II.2004 (fr.), Ludovic & Rabehevit[r]a 552 (MO); Toamasina, Ile Sainte-Marie, Lokintsy, forêt d'Ambohidena, 16°51'11"S, 49°57'10"E, 10 m, 13.V.2003 (fr.), McPherson et al. 18900 (MO); Analanjirofo Region, Pointe ? Larree, District de Soanierana-Ivongo, la commune Antanifotsy, Fokontany Manjato, 16°46'06"S, 49°42'38"E, XI.2008 (fr.), Nikolov 1774 (MO, P[P00982779, P01061922]); Brickaville District, Hotel Pangalan on Lake Ampitabe, W of Andranokoditra, 18°35'S, 49°14'E, 9.I.2003 (fr.), Pell et al. 617 (MO, NY); Maroantsetra, Tampolo, Péninsule Masoala, 15°43'S, 49°57'E, 20-50 m, 5.XI.2001 (fl.), Poncy et al. 1594 (MO); Maroantsetra, Tampolo, Péninsule Masoala, 15°43'S, 49°57'E, 0-10 m, 5.XI.2001 (fr.), Poncy et al. 1597 (K n.v., MO); Fivondronana: Sainte Marie, Firaisana: Lokintsy, Fokontany: Ambohidena, forêt littorale sur sable non consolidé d'Ambohidena, 16°51'11"S, 49°57'10"E, 1.VI.2004 (fl.), Rabehevitra & Poity 1205 (MO, OWU, P[P01954138]); Fivondronana: Soanierana Ivongo, Firaisana: Manompana, Fokontany: Antanambaon 'Ambodimanga, forêt d'Andakibe, 16°47'01"S, 49°44'23"E, 3 m, 4.X.2003 (fr.), Rabehevitra et al. 579 (MO, OWU, P[P01986989]); Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, forêt de Nankinana, 20°21'15"S, 48°36'26"E, 18 m, 10.II.2004 (fl.), Rabehevitra et al. 782 (MO, OWU, P[P06901351]); Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, forêt de Antaimby, 20°22'21"S, 48°33'15"E, 16 m, 12.II.2004 (fl.), Rabehevitra et al. 825 (MO, OWU, P[P06901352]); Fivondronana, Soanierana-Ivongo, Commune Rurale: Manompana, forêt d'Antanambao-Ambodimanga, 16°46'24"S, 49°42'51"E, 30.I.2003 (fl., fr.), Rabevohitra et al. 4306 (MO, NY); Fivondronana Soanierana-Ivongo, village d'Andrangazaha, Bureau Dette Nature Andrangazaha, 16°52'02"S, 49°40'52"E, 29.I.2004 (buds), Rabevohitra & Rakotomamonjy 4874 (MO); Fivondronana: Sainte Marie, Firaisana: Lokintsy, Fokontany: Ambohidena, forêt d'Ambohidena, 16°51'11"S, 49°57'18"E, 8.II.2004 (fr.), Rabevohitra et al. 4986 (MO, OWU); Toamasina, Parc national de Masoala, Antalavia, 15°47'00"S, 50°02'00"E, 0 m, 27.XI.1994 (st.), Rahajasoa et al. 1066 (MO); District Fenerive-Est, Station forestière de Tampolo, 10 km Nord de Fenerive-Est, 17°16'52"S, 49°24'44"E, 0-150 m, 24.I.1995 (fr.), Raholivelo et al. 251 (MO); Brickaville, Ambinaninony, Andranokoditra, Vohibola, 18°33'35"S, 49°15'05"E, 0-10 m, 26.X.2002 (fr.), Ranaivojaona et al. 448 (K n.v., MO); Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, forêt de littoral d'Ampanamara (Antaimby Kely), 20°22'48"S, 48°33'23"E, 13 m, 12.VI.2004 (fr.), Ranaivojaona et al. 755 (MO, OWU); Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, forêt de littorale d'Analamalotra (Antaimby Kely), 20°22'57"S, 48°33'13"E, 13 m, 28.IX.2004 (fr.), Ranaivojaona et al. 843 (MO, OWU, P[P01954137]); Fivondronana Mahanoro, Firaisana Ambodibonara, Fokontany Ambalavontaka, forêt littorale de Nankinana, 20°21'30"S, 48°36'50"E, 8 m, 30.IX.2004 (immature fr.), Ranaivojaona et al. 893 (MO, P[P00982781]); Fivondronana Brickaville, S of Ambila, 18°54'S, 49°07'E, 0-10 m, 4.VIII.1996 (fl., immature fr.), Randrianasolo 478 (MO); Analanjirofo Region, Fivondronana: Fénérive-Est, Fokontany Ambodimanga, Tampolo, 17°17'05"S, 49°23'16"E, 0-10 m, 13.I.2001 (fr.), Razafitsalama 101 (K n.v., MO, P[P00903556]); Analanjirofo Region, Commune Manompana, Fokontany Antanambao-Ambodimanga, 16°48'07"S, 49°44'32"E, 6-16 m, 22-29.IX.2010 (fr.), *Razanatsoa et al. 523* (MO); Andevoranto-Ambila Lemaitso Road, *c.* 3-6 km NNE of Andevoranto, 18°53'50"S, 49°07'40"E, 30 m, 2.II.2006 (fl.), *Rogers & Antilahimena 1007* (MO[2 sheets], OWU, P[P02005890]); Prov. Toamasina, 6-10 km S of Ambila-Lemaitso, 18°51'S, 49°08'E, 0-20 m, 6.III.1988 (fl.), *Schatz et al. 1952* (BR, K n.v., MO, WAG); Ampanihy, littoral forest on Ile Ste. Marie, 16°54'51"S, 49°55'46"E, 10 m, 18.I.2006 (fr.), *Tosh et al. JT214* (K n.v., MO, P[P01954126]); Tampina, I.1935 (fl., fr.), *Ürsch 44* (L).

Prov. Toliara. Forêt de Bemangidy, au N de Mahatalaky (Fort-Dauphin), 1-2.II.1963 (st.), Capuron 22335-SF (K); Fort Dauphin, Roubara, s. d. (fl.) [Recd. 1891], Cloisel 142 (BM); Préfecture de Tôlanaro, forêt sur la route de Ste. Luce, partie Sud, 24°46'S, 47°09'E, 0-10 m, 23.III.1989 (fr.), Dumetz et al. 633 (K n.v., MO); N of Tolanaro, Mandena, 24°58'S, 46°59'E, 40 m, 9.XII.1991 (fl., fr.), Malcomber & Leeuwenberg 1176 (K n.v., MO); Fort Dauphin (Tôlanaro) region, near area called Mandena, beyond QIT camp, 24°57'S, 47°00'E, 20 m, 4.XI.1989 (fl., fr.), McPherson 14371 (K n.v., MO); Fort Dauphin (Tôlanaro) region, NE of town in forest called Mandena, beyond QIT camp, 24°57'S, 47°00'E, 20 m, 13.I.1990 (fr.), McPherson et al. 14776 (K n.v., MO), 14777 (K n.v., MO, RSA); Fort Dauphin (Tôlanaro) region, NE of town in forest called Mandena, in area called Botanical Garden, 24°57'S, 47°00'E, 10 m, 24.I.1990 (fl., fr.), McPherson et al. 14878 (K n.v., MO); forêt littorale sur sable à Mandena, Ampasy, Tolagnaro, 24°57'06"S, 47°00'06"E, 0-10 m, 20.XII.2000 (fl.), Rabenantoandro et al. 402 (K n.v., NY); Préfecture de Tôlanaro (Fort Dauphin), Mandena, 24°57'S, 47°02'E, 26.I.1990 (fl.), Rabevohitra 2204 (K n.v., MO); Anosy Region, Taolagnaro, sentier reliant Ampasy et Iaboakoho (village), 24°34'56"S, 47°09'01"E, 24 m, 29.XI.2009 (fr.), Rakotovao 4886 (MO); Anosy Region, District Taolagnaro, Commune rurale de Iaboakoho, Fokontany de Iaboakoho, 24°34'58"S, 47°09'01"E, 25 m, 25-30.XI.2009 (fr.), Rakotovao & Alvarez 4776 (MO); Anosy Region, Fivondronana Fort-Dauphin, Firaisana et Fokontany Ampasy-Nahampoana, 24°57'S, 47°00'E, 8.I.2002 (fr.), Randriatafika 336 (MO); Anosy Region, Fort Dauphin, Mahatalaky Sainte Luce, S11 - 3.1 km au nord d'Ambandrika, 24°44'26"S, 47°10'38"E, 20 m, 21.XI.2011 (fr.), Ratovoson 1689 (MO); Anosy Region, Iabakoho, fkt Ambanihazo, 24°39'53"S, 47°12'58"E, 13 m, 22.XI.2011 (immature fr.), Razakamalala et al. 6651 (MO); Fort Dauphin, South Madagascar, X.1889 (fr.), Scott-Elliot s. n. (K); Mandena, Fort Dauphin, 5.XII.1952 (fr.), Service Forestier 7008 SF (OWU). Province unknown. "Uvaria Diclinis Madagascar", no specific locality or date, Unknown Collector s. n. (BM[BM000511083]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia humblotiana* occurs in littoral and sublittoral forests on sandy soil along the full length of the eastern Madagascar coast at elevations below 50 meters (Fig. 29). *Asteropeia multifolia* and a species of *Homalium* were listed as associates at one site, species of *Brochoneura*, *Sarcolaena*, and *Intsia* at another. Specimens with flowers have been collected from October to April, and in June and August, with the greatest number of collections from January, February, and November. Specimens with fruits have been collected from September to March and in May and June, with the greatest number of collections from November. *Xylopia humblotiana* has the largest AOO of any Madagascar species (240 km²) but its relatively small EOO (41 472 km²) reflects the narrow coastal distribution (Table 2) in endangered littoral forest habitats.

LOCAL NAMES. — Fotsivavo (*Randriatafika 336, Ratovoson 1689*), hazoambo (multiple reports), hazoambo kely ravina (*Rabevohitra et al. 4306*), moranga (*Rabevohitra & Rabenantoandro 3792, Rabevohitra & Rabenantoandro 3793, Schatz et al. 3776*), movangavato (*Aridy & Moïse 168*), ombavy (*McPherson & Rabenantoandro 18316*), ramiavina (*Ludovic & Rabehevit*[*r*]*a 552*), ramiavo (*Rabevohitra et al. 4608*), rombavy (*Ludovic et al. 883, Ludovic et al. 914*).

DESCRIPTION

Shrub or tree up to 15 m tall, commonly 2.5-7 m tall; d.b.h. up to 30 cm.

Twigs short-appressed-pubescent, the hairs 0.1-0.4 mm long, becoming glabrate; nodes with one axillary branch.

Leaves with larger blades 4.9-7.0 cm long, 2.2-3.9 cm wide, coriaceous, discolorous, gray to olive-gray adaxially, tan-colored abaxially, elliptic, oblanceolate, or obovate, rarely oblong, apex obtuse, rounded, retuse, or emarginate, base cuneate, often short-decurrent on petiole, margin flat or slightly recurved, glabrous on both surfaces; midrib often somewhat darkened toward base adaxially, secondary veins weakly brochidodromous, 8-13 per side, diverging at 45-70° from midrib, these and higher-order veins raised and forming a conspicuous reticulum on both surfaces; petiole 2.5-7 mm long, semi-terete, transversely wrinkled, glabrous.

Inflorescences axillary, sometimes from the axils of fallen leaves, 1-4-flowered, pedunculate, sparsely appressed-pubescent; peduncle 1.4-4 mm long; pedicels up to 4 per peduncle, 4.6-10.9 mm long, 0.9-1.3 mm thick; bracts 2, one near base of the pedicel and the other near the apex, caducous, distal bract 1.3-1.8 mm long, broadly ovate, sometimes bilobed; buds narrowly oblong, apex acute to obtuse.

Sepals erect to slightly spreading at anthesis, ¹/₄-¹/₂-connate, 1.4-3.4 mm long, 2.8-3.8 mm wide, coriaceous, semicircular to broadly triangular, apex acute, appressed-pubescent abaxially.

Petals white, yellow, or pale orange with a red to purple mark on the inner base *in vivo*; outer petals slightly spreading at anthesis, 15.8-19.0 mm long, 3.2-4.3 mm wide at base, 1.4-4.1 mm wide at midpoint, coriaceous, narrowly oblong, flat, apex obtuse, densely pubescent except for glabrous base adaxially, densely sericeous-pubescent except for glabrous area toward margins at base abaxially; inner petals slightly spreading at anthesis, 14.6-17.3 mm long, 2.2-2.7 mm wide at base, 1.0-1.5 mm wide at midpoint, coriaceous, linear, keeled on both surfaces, apex acute, base concave with undifferentiated margin, densely pubescent on both surfaces except for glabrous base.

Stamens 200-240; fertile stamens 1.2-1.7 mm long, narrowly oblong to clavate, anther connective apex *c*. 0.2 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 9-12-locellate, filament 0.4-0.6 mm long; outer staminodes 1.7-1.9 mm long, broadly clavate, apex obtuse to truncate; inner staminodes 0.8-1.1 mm long, clavate, apex rounded; staminal cone 1.6-2.6 mm in diameter, 0.8-1.2 mm high, completely concealing the ovaries, rim even or slightly irregular.

Carpels 7-14; ovaries *c*. 1.2 mm long, oblong, densely pubescent, stigmas connivent, (2.4-) 3.8-4.5 mm long, filiform, verrucose, with a few hairs at the apices.

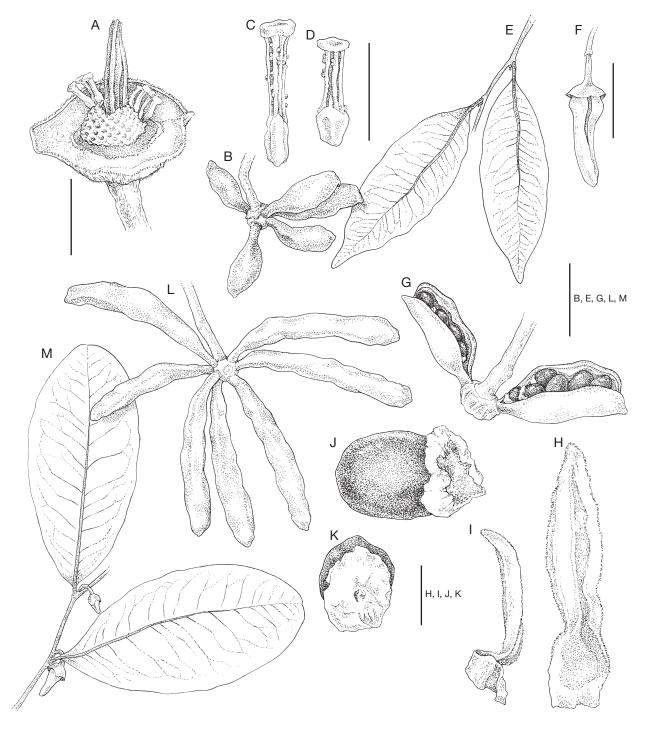


FIG. 9. – *Xylopia madagascariensis* Cavaco & Keraudren and *X. humblotiana* Baill.. **A-F**, *X. madagascariensis*; **A**, flower with petals and most stamens removed, showing stigmas and staminal cone; **B**, fruit; **C**, **D**, Stamens, abaxial view; **E**, leaves; **F**, flower bud, side view. **G-M**, *X. humblotiana*; **G**, fruit with dehiscing monocarps; **H**, outer petal, adaxial surface; **I**, inner petal, side view; **J**, seed, view from side; **K**, seed, view from micropylar end; **L**, fruit, showing more elongate monocarps; **M**, habit, with leaves and flower buds; **A-F**, from *Schatz & Modeste 3095* (MO); **G**, **J**, **K**, from *Lowry & Miller 5138A* (MO); **H**, **I**, from *McPherson et al. 14777* (MO); **L**, **M**, from *Schatz et al. 3776* (MO). Scale bars: A, H-K, 3 mm; B, E, G, L, M, 2 cm; C, D, 1 mm; F, 1 cm.

Fruit of up to 11 monocarps borne on a pedicel 8-11 mm long, 3-5 mm thick, glabrate; torus 7.5-12 mm in diameter, 6-7.5 mm high, globose to depressed-globose; monocarps with greenish red to bright scarlet exterior and red endocarp *in vivo*, 3.0-6.1 cm long, 0.8-1.2 cm wide, 0.6-0.9 cm thick, narrowly oblong to clavate, not torulose or rarely slightly torulose, apex obtuse to rounded, base tapered gradually,

sometimes contracted into a stipe 2-3 mm long, 3.5-4.5 mm thick, vertucose, smooth or sometimes obliquely wrinkled, glabrate; pericarp 0.8-1.3 mm thick.

Seeds up to 6 per monocarp, in a single row, parallel or oblique to long axis, 7.5-9.5 mm long, 4.6-5.6 mm wide, 3.4-3.9 mm thick, ellipsoid to oblong-ellipsoid, elliptic in cross-section,

black, smooth or slightly wrinkled, shiny, perichalazal ring not evident; sarcotesta absent; aril white *in vivo*, dull white when dried, bilobed, lobes 1.9-3.3 mm long, 2.5-3.5 mm wide, papery to fleshy, smooth or wrinkled.

Notes

Xylopia humblotiana is the most frequently collected *Xylopia* species on Madagascar. Its small stature, abundant flowers open on the same branch at once, and clusters of bright red monocarps make it a conspicuous plant in the littoral and sublittoral forests where it is found. It differs from the higherelevation *X. ravelonarivoi*, sp. nov., in the nearly glabrous pedicels and sepals, the shorter sepals, the oblong shape of the longer outer petals, the smooth rather than strongly wrinkled monocarps, and the larger seeds. It is distinguishable from *X. madagascariensis* by the obtuse to rounded, rather than acute to acuminate, leaf apices and the longer monocarps.

The label of *Schatz 2381* describes the floral fragrance as "extremely spicy menthol fragrant", but nothing is known of the pollination biology of the species.

5. *Xylopia lamarckii* Baill. (Figs 1H-I; 5; 6E; 10)

Adansonia; Recueil d'Observations botaniques 4: 142, 143 (1864). — An[n]ona grandiflora Lam., Encyclopédie méthodique, Botanique 2 (1): 126, 127 (1786). — Pseudanona ["Pseudannona"] grandiflora (Lam.) Saff., Journal of the Washington Academy of Sciences 3: 18 (1913). — Xylopia grandiflora (Lam.) Ghesq. ex Cavaco & Keraudren, Flore de Madagascar et des Comores, Annonacées, vol. 78: 26 (1958), non A.St.-Hil. (1825). — Type: "Isle de Bourbon", s. d. (fl.), Commerson s. n. (lecto-, P[P0034246]!; isolecto-, P[P0034247]!).

- ? An[n] ona grandiflora * madagascariensis Pers., Synopsis Plantarum seu Enchiridium Botanicum 2 (1): 95 (1806). — Type: Hab. in ins. Madagasc., herb. Juss[ieu] (not found).
- Annona pyriformis Bojer ex Baker, Flora of Mauritius and the Seychelles 3 (1877). — Type: Mauritius. Without definite locality, Bojer s. n. (not found).

MATERIAL EXAMINED. — Mauritius. "Dans l'infonumene delaplace de Hollandois au Pon du P. E. habitation du Prahy" [?], 29.IX.1754 (fl.), Aublet s. n. (BM); Moka (Vuillemin), 15.I.1924 (old fl.), Bijoux s. n. (P[P01987045]); native of mountain woods of Nouvelle Decouverte, s. d. (fl.) [presented 17.VII.1863], Black*burn herb. [ex Bojer?]* (K); in campis sylvestribus insula Mauritii, s. d. (st.), *ex herb. Bojer[er]*, (BM); "isle de france", without definite locality, s. d. (st.), Commerson s. n. (P[P030400]); Grand Bassin, 31.I.1933 (st.), Duhamel 16139 (MAU); Crown Land Perrier, s. d. (bud), Duljeet 16140 (MAU); Ripailles, II.1862 (fl.), Dupont [coll. Ayres?] s. n. (K); Ravine Cascade, 500 ft, V.1971 (st.), Friedmann 1202 (P[P01987041]); without definite locality, s. d. (fl., st.), Herb. Du Petit-Thouars s. n. (P[P01987042, P01987048]); "Ile de France", s. d. (fl.), Herb. E. Drake (ex Herbarium Richard) s. n. (P[P01987044]); without definite locality, s. d., Herb. R. Botanic Gardens Pamplemousse (st., collector unknown) 14, (st., Bouton) 15, (st., Bijoux) 16, (old fl., Bijoux) 17, (all MAU); Pétrin Nature Reserve (S. W.), 2000 feet, 6.I.1973 (fl.), Lorence M23 (MO, WAG); Pétrin Nature Reserve, 12.XII.1978 (fl.), Lorence 2124 (K n.v., MAU, MO, P[P01987040], US); Perrier Nature Preserve near Mare aux Vacoas, 600 m, 28.XII.1978 (fl.), Lorence 2225 (K n.v., MAU, MO, P[P01987046]); Gaulettes Serrées, 400-450 m, 19.V.1979 (st.), *Lorence et al. 2635* (MAU); Brise Fer, west edge of Central Plateau, 600 m, 1.VI.1979 (st.), Lorence s. n. (MAU); Petrín Nature Reserve, 24.II.1972 (fl.), *Owadally 15115* (MAU); Perrier Nature Reserve, 17.II.1971 (fl.), *Vaughan 15228* (MAU); La Villebague, s. d. (buds), *Wallich s. n.* (BM); Grand Port, s. d. (fl.), *Wallich s. n.* (BM); without definite locality, s. d. (fl.), *collector unknown, ex herb. Lambert* (BM, 2 sheets).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Endemic to the island of Mauritius, *Xylopia lamarckii* occurs in thickets and in the upland heath and dwarf forest of *Philippia* and *Phylica* over laterite, sometimes with emergent *Sideroxylon* and *Calophyllum* (Kaiser 2006), at elevations of 150-700 meters (Fig. 7). Specimens with flowers have been collected from December to February. *Xylopia lamarckii* was given a status of Critically Endangered by Page (1998b), who estimated the population at that time as 250 individuals. Our EOO and AOO calculations of 270 km² and 32 km², respectively, support that status, as does the lack of effective pollinators described below.

LOCAL NAME. — Bois blanc (Aublet s. n.).

Description

Treelet or shrub up to 4 m tall, often sprawling or subscandent; d.b.h. up to 2 cm.

Twigs sparsely appressed-public expressed public expression of the state of the s

Leaves with larger blades 11.5-23.5 cm long, 6.2-8.4 cm wide, chartaceous, discolorous, olive-gray adaxially, dull orange-brown and occasionally somewhat glaucous abaxially, lanceolate to ovate, apex acute to acuminate, the acumen 8-26 mm long, base rounded to truncate, occasionally subcordate, not decurrent, margin flat, not revolute, glabrous adaxially, sparsely pubescent on the midrib but otherwise glabrous abaxially; midrib light brown toward the base adaxially, secondary veins weakly brochidodromous, 12-20 per side, diverging at 60-70° from midrib, these and higher-order veins slightly raised and forming a conspicuous reticulum on both surfaces; petiole 3-6 mm long, semi-terete, transversely wrinkled, sparsely pubescent to glabrate.

Inflorescences axillary, 1-flowered, not pedunculate, appressedpubescent; pedicels 8-13 mm long, 2-2.6 mm thick; bracts 2-3, one attached near the pedicel midpoint and the others near the pedicel base, caducous; buds oblong to obovoid, apex obtuse, occasionally slightly falciform.

Sepals spreading at anthesis, ¹/₅-¹/₂-connate, 4.5-10 mm long, 6.5-12 mm wide, coriaceous, broadly triangular-ovate, apex acute to obtuse, appressed-pubescent abaxially.

Petals creamy white, sometimes flushed with rose, with a purple spot at the base adaxially *in vivo*; outer petals slightly spreading at anthesis, 32-55 mm long, 5-12.5 mm wide at base, 11-28 mm wide at midpoint, fleshy, lanceolate, oblong, or oblanceolate, flattened toward the base adaxially, apex obtuse, densely puberulent on apical half and along margins to the base adaxially, uniformly appressed-pubescent abaxially; inner petals slightly spreading at anthesis, 29-41 mm long,

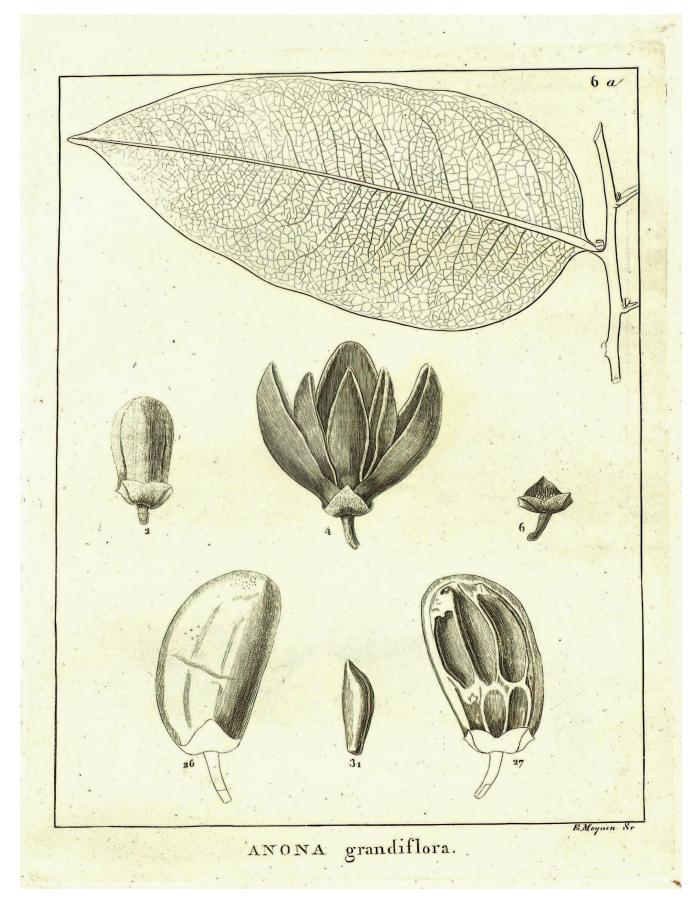


Fig. 10. – Plate 6A from Dunal (1817), showing the only fruit and seed details known for *Xylopia lamarckii* Baill.

c. 4.7 mm wide at base, 3-10 mm wide at midpoint, fleshy, narrowly oblong, laterally compressed, keeled at apex adaxially, sharply keeled abaxially, apex acute, base deeply concave with undifferentiated margin, densely puberulent at apex but glabrous toward base adaxially, thinly appressed-pubescent at apex and along keel abaxially.

Stamens *c*. 300; fertile stamens 1.3-1.9 mm long, narrowly oblong, anther connective apex *c*. 0.2 mm long, capitate or shield-shaped, overhanging the anther thecae, papillate, anthers 10-12-locellate, filament 0.4-0.5 mm long; outer staminodes 1.3-1.6 mm long, clavate, apex truncate; inner staminodes *c*. 1.2 mm long, oblong, quadrate, or clavate, apex truncate; staminal cone 5-6 mm in diameter, 1.5-4 mm high, completely concealing the ovaries, rim even.

Carpels *c*. 20; ovaries *c*. 1.5 mm long, narrowly oblong, tomentose, stigmas basally connivent with the tips free, 9.5-11 mm long, filiform, glabrous or with a few scattered hairs.

Fruit (ex Keraudren-Aymonin 1980) "Fruit mal connu, à monocarpes d'environ 3.5×0.8 cm, glabres.

Seeds (Keraudren-Aymonin 1980) "Graines arillées, longues de 11-12 mm".

Notes

The large broad fleshy petals of *Xylopia lamarckii* sets it apart from all other Xylopia species of the Madagascar and Mascarene region with the exception of the Mauritian species *X. amplexicaulis*, from which it is distinguished by the distinctly petiolate leaves that are rounded to truncate at the base. The distinctive floral structure led to the initial description of both species in the genus *Annona* by Lamarck (1786), and was the basis for segregating them in a new section *Pseudanona* when Baillon (1864) transferred them from *Annona* to *Xylopia*. Additional floral characters that place both species securely in *Xylopia* include axillary inflorescences, septate anthers, and a well-developed staminal cone surrounding the ovaries. The phylogenetic analysis of Stull *et al.* (2017) showed *X. lamarckii* nested well within the Xylopia clade on the basis of molecular data.

Apart from the nature of the leaf base, *X. lamarckii* and *X. amplexicaulis* are similar, and in fact some specimens of *X. lamarckii* have a relatively short petiole and a subcordate base of the leaf blade. Both species have been reported from Nouvelle Découverte (Bojer 1837), the Perrier Nature Preserve near Mare aux Vacoas, Grand Port, and Gaulettes Serrées. As indicated by the report of Aublet (1775), *X. lamarckii* was also once common in the vicinity of Port Louis and Moka.

As part of a larger study of pollinator webs in Black River Gorges National Park in Mauritius, Kaiser (2006, Kaiser-Bunbury *et al.* 2009) examined floral phenology and floral visitors for *Xylopia lamarckii*. He documented the narrow flowering period from December to January, and noted that fruit set was not observed. Floral visitors included only one species of ant and one species of Chrysomelid beetle, both introduced and both found on flowers of a wide range of species at the study site. The flowers have a fruity-spicy odor (*Lorence 2225*). The habitat in the pollinator study site was dwarf forest dominated by *Erica* and *Phylica* spp., with emergent *Sideroxylon* and *Calophyllum* spp., an endangered habitat on the island.

The provenance of the type material of *Annona grandiflora* Lamarck is uncertain. Lamarck (1786) cited the Commerson collections he examined as having come from Madagascar and La Réunion ("isle de Bourbon"). Specimens at P collected by Commerson are labeled as coming from La Réunion and Mauritius ("isle de france"). Because *X. lamarckii* has never been collected again from either La Réunion or Madagascar, those attributions are set aside as labeling errors, as has been concluded previously (Cavaco & Keraudren 1958, Keraudren-Aymonin 1980).

Lamarck (1786) described the fruit and seeds: "Le fruit est médiocre, ovoïde, à écorce glabre, légérement ponctuée ou chagrinée. Il contient des semences oblongues, pointues, tranchantes du côte intérieur, avec deux faces applaties, convexes & plus épaisses sur leur dos ; ces semences sont disposées en petit nombre dans la longueur du fruit, & enveloppées d'une pulpe médiocre". Dunal (1817; Fig. 10[26, 27]) illustrated a single sessile ovoid monocarp, with the calyx persistent around its base, and a longitudinal section of the fruit showing five depressions in which the seeds sat. The seed illustrated (Fig. 10[31]) is narrowly obovoid, smooth, truncate at one end and pointed at the other. He did not, however, identify the source material for the drawings. It is possible that the dimensions given by Keraudren-Aymonin (1980) for the fruit, "d'environ 3.5×0.8 cm", and for the seed, "longues de 11-12 mm", were estimated from this drawing. Fruits and seeds are not attached to any of the specimens we examined.

The name An[n] ona grandiflora * madagascariensis of Persoon was based on a specimen in the Jussieu Herbarium that we have not located. The name is listed as a synonym of X. lamarckii because past authors (Dunal 1817, Keraudren-Aymonin 1980) have attributed it that way, but we were not able to confirm the identification. The short diagnosis, "fol. ovatis coriaceis integerrimis lucidis", does not provide adequate details for confirmation.

Baker (1877) gave a brief, but validating, description of *Annona pyriformis*, a *nomen nudum* listed by Bojer (1837). With the exception of the statement that the inner and outer petals are subequal, the description conforms to that of *X. lamarckii*, and Keraudren-Aymonin (1980) placed the name in synonymy. Type material has not been found, although a specimen at BM, BM000510673, is stated on the label as having come from the Bojer herbarium. The only plant name given on the label, however, is "*Anona grandiflora* DC. Prod." This specimen does not seem supportable as a lectotype of *A. pyriformis* without additional information.

The specimens from the Lambert Herbarium now at BM have no indication of the collector, but according to Miller (1970) there were specimens in the Lambert Herbarium collected in Mauritius by Colebrooke, Hardwicke, Hilsenberg (part of Sieber collection), and A. Michaux. Both specimens have the name "*Michelia rufinervis* Decand. Syst." Written in faint pencil at the bottom; this name was based on a specimen collected from a cultivated plant in Mauritius by Commerson (Candolle 1817).

6. *Xylopia madagascariensis* Cavaco & Keraudren (Fig. 9A-F)

Bulletin de la Société botanique de France 103: 276 (1956). — Type: **Madagascar. Prov. Toamasina** ["Domaine de l'Est"], Vohimarangitra, environs de Tamatave [= Betampona, 17°55'S, 49°13'E], 22.II.1950 (fl.), *Réserves Naturelles de Madagascar 2440* (holo-, P[P030410]!; iso-, K[K000199049]!, P[P030411, P030412]!).

MATERIAL EXAMINED. — **Madagascar. Prov. Antsiranana.** Sava Region, Sambava, Anjangoveratra, forêt de Tsihomanaomby, 14°06'S, 50°02'E, 17.II.2013 (fl. buds, fr.), *Martial et al. 34* (MO, OWU).

Prov. Toamasina. Canton Ambodiriana, Tamatave District, 9.II.1962 (fr.), *Momohizaza 11999 RN* (P[P01987141]); R. N. I. Tamatave, 24.III.1951 (fr.), *Rakotoniama 2861 RN* (P[P01987142, P01987143]); Antsinanana, District Toamasina II, Commune Rurale Sahambala, Fokontany Sahavongo, village le plus proche Sahavongo, Iambeau de forêt d'Ambavadilagna, 18°01'16"S, 49°05'42"E, 529 m, 5.II.2017 (fl., fr.), *Ralaijaona et al. 74* (MO); Masoala Peninsula, flat coastal sand forest just N of Tampolo, approximately 11 km S of Ambanizana, 15°43'S, 49°57-58'E, 0-5 m, 26.XII.1990 (fl., fr.), *Schatz & Modeste 3095* (G, K n.v., MO, P[P01954052], WAG); Faranharoina-Maroantsetra, 8.III.1955 (fr.), *Service Forestier 12977* (BR, K n.v., P[P06901365]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia* madagascariensis occurs in eastern Madagascar, in humid forest near the coast, at elevations from 0-5 meters up to 529 m (Fig. 29). The specimens with flowers were collected in February and December, and with fruits in February, March, and December. With an EOO and AOO estimated as 3780 km² and 24 km², respectively, the species is given a preliminary conservation assessment of Endangered.

LOCAL NAMES. — Hazoambo (*Momohizaza 11999 RN, Ralaijaona et al. 74*), hazoambolahy (*Rakotoniama 2861 RN*), moranga (*Martial et al. 34*).

Description

Tree up to 16 m tall; d.b.h. up to 28 cm.

Twigs sparsely appressed-pubescent, the hairs 0.1-0.4 mm long, becoming glabrate; nodes with a single axillary branch.

Leaves with larger blades 5.2-6.6 cm long, 1.8-2.7 cm wide, subcoriaceous, slightly discolorous, dull gray to gray-green adaxially, tan to reddish brown abaxially, lanceolate to elliptic, apex blunt-acuminate, the acumen 4.5-11 mm long, base broadly cuneate, short-decurrent on petiole, margins flat or slightly revolute, glabrous adaxially, sparsely sericeous abaxially; midrib red toward the base adaxially, secondary veins brochidodromous, 11-13 per side, diverging at 60-70° from midrib, these and higher-order veins raised and forming a conspicuous reticulum on both surfaces; petiole 3.3-6 mm long, semi-terete, transversely and longitudinally wrinkled, glabrous to sparsely pubescent.

Inflorescences axillary or from the axils of fallen leaves, 2-4-flowered, pedunculate, appressed-pubescent; peduncle 1.8-2.2 mm long; pedicels 2-4 per peduncle, 5.5-9 mm long, 0.8-1.0 mm thick; bracts 2-3, attached proximal to the pedicel midpoint, caducous, 0.5-0.7 mm long, semicircular; buds narrowly oblong, apex obtuse.

Sepals slightly spreading at anthesis, ½-connate, 2.3-2.5 mm long, 4.0-4.3 mm wide, coriaceous, semicircular, apex broadly acute to rounded, appressed-pubescent abaxially.

Petals dull yellow to orange, with the outer petals whitish at the base and the inner petals red-tinted at the base *in vivo*; outer petals spreading at anthesis, 16-18 mm long, 3.5-3.9 mm wide at base, 2.3-2.8 mm wide at midpoint, coriaceous to slightly fleshy, narrowly oblong, flat, apex obtuse, appressed-pubescent except for the glabrous base adaxially, velutinous abaxially; inner petals possibly erect and somewhat connivent at anthesis, 14-20 mm long, 2.9-3.0 mm wide at base, 0.8-1.1 mm wide at midpoint, fleshy, linear, laterally compressed, weakly keeled on upper $\frac{2}{3}$ adaxially, strongly keeled abaxially, apex obtuse to acute, base concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces.

Stamens *c*. 140; fertile stamens 1.2-1.6 mm long, narrowly oblong, anther connective apex 0.1-0.2 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 9-14-locellate, filament 0.5-0.6 mm long; outer staminodes *c*. 1.5 mm long, clavate, apex rounded; inner staminodes *c*. 1 mm long, clavate, apex truncate; staminal cone 2.0-2.6 mm in diameter, 1.0-1.4 mm high, completely concealing the ovaries, rim even.

Carpels *c*. 15; ovaries *c*. 1 mm long, narrowly oblong, sericeous, stigmas connivent, 2.2-2.9 mm long, filiform, smooth, glabrous.

Fruit of up to 10 monocarps, borne on a pedicel 8-14 mm long, 2.0-3.5 mm thick, glabrate; torus 4.7-8.0 mm in diameter, 3.5-5.5 mm high, depressed-globose to globose; monocarps with red exterior and red endocarp *in vivo*, 2-3.7 cm long, 0.8-1.1 cm wide, 0.7-0.8 cm thick, oblong to narrowly cylindrical, not torulose, apex rounded or obtuse, base sessile or contracted into a stipe 2-3 mm long, *c*. 3 mm thick, verrucose, smooth or faintly wrinkled, glabrate or bearing a few sparse hairs; pericarp *c*. 1.5 mm thick.

Seeds up to 3 per monocarp, in a single row, oblique or perpendicular to long axis, 6-8.6 mm long, 4.2-4.6 mm wide, *c.* 3.8 mm thick, oblong, broadly elliptic in cross-section, black, smooth, shiny, perichalazal ring slightly raised; sarcotesta absent; aril white *in vivo*, whitish orange to dull orange when dried, bilobed, lobes *c.* 2.2 mm long, 3-3.4 mm wide, papery, smooth to somewhat wrinkled.

Notes

Xylopia madagascariensis is very similar to *X. humblotiana*, but differs consistently in the proportionally narrower leaves that

are acuminate rather than obtuse to rounded. In addition, its leaves are sparsely appressed-pubescent abaxially rather than glabrous. In the limited sample available, the inner petals are wider at the base and narrower at the midpoint than in X. humblotiana. The monocarps average smaller with fewer seeds, which are oblique to perpendicular to the long axis of the monocarp rather than parallel. Although little habitat information is given on the labels for any of the specimens of X. madagascariensis, it seems to frequent a wider range of forest habitats and elevations than the littoral forests on sand where X. humblotiana occurs. The specimen Randriatafika 16 (MO), from Fianarantsoa Province (forêt dense humide de l'Est d'Andranobetokana, Ampasimadinika, Marofototra, Mananjary, 20°49'51"S, 48°05'00"E, 16-21.I.1999 [fl.]) resembles X. madagascariensis, but the bracts and pedicels are less pubescent and the petals shorter (but only large buds on the specimen). It was collected to the south of the main range of X. madagascariensis, and additional collections from the area would be helpful in determining its status.

7. *Xylopia ravelonarivoi* D.M.Johnson & N.A.Murray, sp. nov. (Figs 6B; 11)

Species resembling *Xylopia humblotiana* Baill. in its small blunt coriaceous leaves, obtuse petals, and narrowly oblong monocarps, but differing in the tree habit, more strongly decurrent leaf bases, densely pubescent pedicels and sepals, lanceolate outer petals, and more strongly wrinkled monocarps borne on pedicels 13-19 mm long and 1.6-3.7 mm thick.

TYPE. — **Madagascar**. Prov. Toamasina, Antsimanana Region: Brickaville, Maroseranana, Ambodilendemy, suivant la rivière d'Andrangato, 18°26'05"S, 48°46'51"E, 658 m, 14.III.2011 (fl.), *Ravelonarivo et al. 3641* (holo-, MO!).

PARATYPES. — Madagascar. Prov. Antsiranana, Sava Region, Diego, Sambava, Anjangoveratra, Anamboafo, forêt de Makirovana-Beraharaha, 14°09'07"S, 49°57'13"E, 549 m, 6.III.2014 (fl.), *Martial et al. 548* (MO); Sava Region, Sambava, Anjangoveratra, Anamboafo, forêt de Belalitra, Makirovana, 14°09'14"S, 49°58'09"E, 585 m, 8.III.2014 (fl.), *Rakotonirina et al. 537* (MO); Marojejy RNI, Analamboahangy, Andrakata, Andapa, aux environs de Manenobasy, 14°35'16"S, 49°41'20"E, 1171 m, 18-24.I.1995 (fr.), *Rasoavimbahoaka 509* (MO, P[P01954048]); Andrakata Canton, Andapa District [14°37'S, 49°43'E], 13.VIII.1957 (fr.), *Safy 9089 RN* (P[P01954046]).

Prov. Mahajanga, Ruisseau Ambatoharanana Andranomena commune rurale de Matsoandakana, district de Befandrina Nord, 15°08'16"S, 49°21'02"E, 1045 m, 12.II.2008 (fr.), Bernard et al. 778 (K, MO). Prov. Toamasina, Fivondronana Maroantsetra, Commune Ambinanitelo, Fokontany Marovovonana, Ankiriandro Mountain, 15°17'37"S, 49°33'10"E, 640 m, 10.I.2003 (fr.), Antilahimena et al. 1683 (K, P[P01954047]); Analanjirofo Region, Fivondronana Vavatenina, Commune Ambodimangavalo, à 3 km à l'Ouest du village Ambatoharanana, dans le Parc national de Zahamena, le long de la piste vers Antevibe, 17°33'54"S, 48°53'18"E, 875 m, 29.IV.2003 (fr.), Rakotonandrasana 676 (OWU); Toamasina sous-préfecture, Vavatenina, commune: Ambodimangavelo, Moango, dans l'Aire protégée de Zahamena, 17°33'32"S, 48°53'55"E, 800 m, 4.V.2003 (immature fr.), Rakotondrajaona et al. 281 (K, MO); Antsinanana Region, Vohimanana, Dist. Brickaville, Com. Maroseranana, Fkt. Ambatolampy, 18°23'27"S, 48°48'11"E, 846 m, 23.I.2012 (fr.), Ravelonarivo et al. 4171 (MO).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia ravelonarivoi*, sp. nov., occurs in humid lowland and lower montane forest on ridges and slopes in northeastern Madagascar at elevations from 549 to 1171 meters.Specimens have been collected with flowers in March and with fruits in January, February, April, and May. With an EOO and AOO estimated as 7118 km² and 40 km², respectively, the species is given a preliminary conservation assessment of Endangered. It is documented by two collections from within the protected area of Zahamena National Park and one collection from the Marojejy Reserve.

LOCAL NAMES. — Hazoambo (*Rakotondrajaona et al. 281*), hazoambo boriboriravina (*Rakotonandrasana 676*), moranga (*Martial et al. 548*), morango (*Rakotonirina et al. 537*).

DESCRIPTION

Tree up to 15 m tall, or rarely a shrub up to 8 m; d.b.h. up to 30 cm.

Twigs densely appressed-pubescent, the hairs 0.1-0.3 mm long, eventually glabrate; nodes with one axillary branch.

Leaves with larger blades 5.0-7.2 cm long, 2.0-3.4 cm wide, subcoriaceous to coriaceous, discolorous, dark brown to gray and often shiny adaxially, light brown and dull abaxially, obovate, oblanceolate, elliptic, or elliptic-oblong, apex obtuse, rounded, retuse, or emarginate, base cuneate, decurrent on petiole, margin slightly recurved or revolute, glabrous adaxially, sparsely appressed-pubescent, especially along midrib, abaxially, midrib dull red to brown, darkening toward base adaxially, secondary veins weakly brochidodromous, 8-11 per side, diverging at 50-70° from midrib, these and higher-order veins raised and forming a conspicuous reticulum on both surfaces; petiole 1.5-7 mm long, shallowly canaliculate or a little flattened, smooth or faintly wrinkled, glabrous or with a few hairs.

Inflorescences axillary from the axils of fallen leaves, 1-3-flowered, pedunculate, densely appressed-pubescent; peduncle 1.7-1.8 mm long; pedicels up to 3 per peduncle, 4.8-9.7 mm long, 1.0-1.2 mm thick; bracts 2, one near base of the pedicel and the other near midpoint, caducous, only scars seen; buds lanceolate, apex obtuse.

Sepals spreading at anthesis, ¹/₄-¹/₂-connate, 1.4-3.6 mm long, 3.5-4 mm wide, coriaceous, broadly triangular, apex acute or rarely obtuse, appressed-pubescent abaxially.

Petals greenish white *in vivo*; outer petals slightly spreading at anthesis, 10.0-12.2 mm long, 2.7-4.5 mm wide at base, 2.4-3.0 mm wide at midpoint, fleshy, lanceolate, keeled at the apex but otherwise flat adaxially, flat abaxially, apex obtuse, densely pubescent except for glabrous base adaxially, densely appressed-pubescent abaxially; inner petals slightly spreading at anthesis, 10.5-10.9 mm long, 2.2-3.0 mm wide at base, 0.9-1.2 mm wide at midpoint, fleshy, linear-subulate, keeled on both surfaces, apex acute, concave with undifferentiated margin, densely pubescent on both surfaces except for glabrous base, with a band of papillae across widest point adaxially.

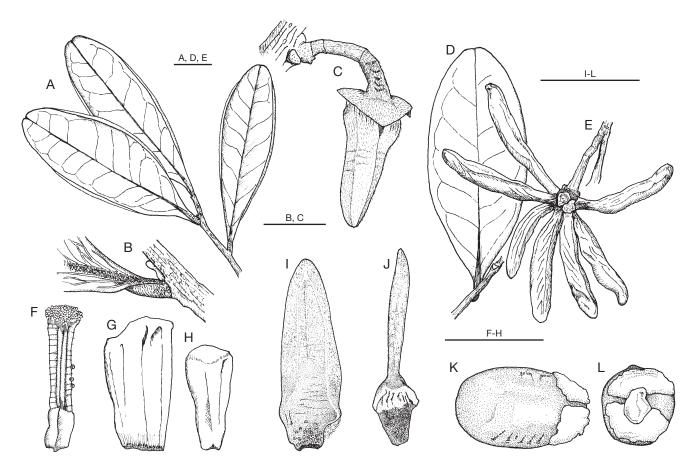


FIG. 11. – *Xylopia ravelonarivoi*, sp. nov.: **A**, habit; **B**, leaf base, oblique adaxial view to show decurrence of leaf blade on petiole; **C**, flower bud, side view; **D**, leaf; **E**, fruit; **F**, fertile stamen, abaxial view; **G**, outer staminode, abaxial view; **H**, adaxial staminode, abaxial view; **I**, outer petal, adaxial view; **J**, inner petal, adaxial view; **K**, seed, side view; **L**, seed, view of micropylar end. **A**, from *Rakotondrajaona et al.* 281 (MO); **B**, **D**, **E**, **K**, **L**, from *Ravelonarivo et al.* 4171 (MO); **C**, **F**-J, from *Ravelonarivo et al.* 3641 (MO). Scale bars: A, D, E, 1 cm; B, C, I-L, 5 mm; F-H, 1 mm.

Stamens *c*. 250; fertile stamens 1.1-1.4 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm long, shield-shaped to capitate, overhanging anther thecae, minutely papillate, anthers 7-9-locellate, filament 0.4-0.6 mm long; outer staminodes *c*. 1.3 mm long, oblong to clavate, apex truncate or rounded; inner staminodes 1.0-1.1 mm long, clavate, apex truncate; staminal cone 2.2-2.6 mm in diameter, 1.0-1.5 mm high, completely concealing the ovaries, rim even.

Carpels 10-13; ovaries 1.0-1.1 mm long, narrowly oblong, pubescent, stigmas connivent, 1.8-2.2 mm long, filiform, glabrous or with a few apical hairs.

Fruit of up to 13 monocarps borne on a pedicel 13-19 mm long, 1.6-3.7 mm thick, glabrate or with a few scattered hairs; torus 5-12 mm in diameter, 3.5-9 mm high, depressed-globose; monocarps with red exterior *in vivo*, 2.2-4.5 cm long, 0.5-0.9 cm wide, 0.5-0.8 cm thick, narrowly oblong, often slightly torulose, apex obtuse to rounded, sometimes slightly beaked, base tapered gradually, sometimes forming a stipe *c*. 4 mm long, 3 mm thick, obliquely wrinkled, shiny, glabrate; pericarp 0.3-0.8 mm thick.

Seeds up to 5 per monocarp, in a single row, nearly parallel to long axis, 5.6-7.8 mm long, 2.9-4.6 mm wide, 3.3-4.0 mm

thick, broadly ellipsoid to oblong, elliptic in cross-section, dark brown to black, smooth or slightly wrinkled and pitted, shiny, perichalazal ring slightly raised; sarcotesta absent; aril white *in vivo*, white to amber-colored when dried, bilobed, lobes 2.0-2.5 mm long, 3.0-3.6 mm wide, fleshy, surface wrinkled.

Notes

Xylopia ravelonarivoi, sp. nov., is similar to X. humblotiana but differs in a number of characters that, together with the ecological differences, distinguish the two species. It is usually a tree up to 15 m tall, rather than a shrub or treelet. The leaves have a more decurrent base, such that the demarcation between blade and petiole is indistinct (Fig. 11B). The pedicels and sepals are densely pubescent. The sepals are longer, and the outer petals are lanceolate rather than oblong; the latter character is also expressed in the buds that are lanceolate rather than oblong as in X. humblotiana. The monocarps of this species are obliquely wrinkled, while those of X. humblotiana are usually smooth. There is a sharp difference in elevation range between the two species: X. ravelonarivoi, sp. nov., grows at elevations from 550 to 1170 m and X. humblotiana from sea level to 50 m. Xylopia madagascariensis also has monocarp and leaf sizes similar to those of X. ravelonarivoi, sp. nov., but its leaves are bluntacuminate rather than obtuse to rounded and its monocarps are smooth and finely verrucose rather than strongly wrinkled. In addition, *X. madagascariensis* reaches its upper elevational limit at just over 500 meters, while the lower elevational limit for *X. ravelonarivoi*, sp. nov., is *c.* 550 meters.

The specimen *Rakotondrajaona et al. 281* was the source of molecular data used in the phylogenetic analysis of *Xylopia* by Stull *et al.* (2017), where it was identified as *X. humblotiana*; the seed illustrated in Figure 4H of that work is, however, correctly identified as *X. humblotiana*.

The species is named for Désiré Ravelonarivo, the collector of the type specimen, who has contributed to a clearer understanding of *Xylopia* diversity on Madagascar by making 16 critical *Xylopia* collections representing six species.

8. *Xylopia richardii* Boivin ex Baill. (Figs 1F; 6D, F; 8A-I)

Adansonia; Recueil d'Observations botaniques 4: 145, 146 (1864). — *Xylopicrum richardii* (Boiv. ex Baill.) Kuntze, *Revisio generum plan tarum*, Pars 1: 8 (1891). — Type: La Réunion. Île Bourbon, Montagne de St. Denis, s. d. (fl., fr.), *Richard s. n.* [687?] (lecto-, here designated, P[P030420, as to Richard specimen on lower portion of sheet only]!; isolecto-, K[K001208416]!, P[P030419]!).

MATERIAL EXAMINED. — Mauritius. Macchabée ["Macabé"], 550 m, 4.II.1976 (fl.), Argent MAU 19684 (K n.v., MAU); "Ile de France", without definite locality, Aublet s. n. (BM); Nouvelle Découverte, high levels, 1907 (fr.), Bijoux s. n. (L[L0191349]); upland forests, s. d. (immature fr.), Bijoux MAU 21 (MAU); without definite locality, Bijoux MAU22 (MAU); in sylvis ins. Mauritii, s. d. (fl., fr.), Bojer? s. n. (K, see below); without definite locality, s. d. (old fl.), MAU 18, 19, 20, 3060 (MAU); Crown Land Perrier, 14.II.1950 (fl., fr.), Duljeet F. D. N055 (MAU); Piton Savanne, 6.XII.1995 (st.), Florens 22735 (MAU); east of Bassin Blanc, 26.I.2000 (fl., fr.), Florens et al. 24082 (MAU); valley of Cascade 500 pieds, 600 m, 31.V.1975 (st.), Lorence 1274 (MAU 17645); valley of Cascade 500 pieds, 600 m, 17.I.1976 (immature fr.), Lorence 1612 (K n.v., MAU 17671); Crown Land Macabé, 22.I.1977 (fl.), Owadally MAU 18435 (MAU); without definite locality, Rivals MAU 2795 (MAU); Pétrin CMA, 20°24'29.0"S, 57°28'20.0"E, 11.IV.2007 (fr.), *Seepaul et al. SB013* (K); forest near Le Peracheret, 2100 ft, 7.II.1927 (fl.), *Vaughan 434* (K).

La Réunion. Pointe de Grands Bois, VI.1905 (bud, immature fr.), d'Alleizette s. n. (L [L0191348]); regione St-Philippe, parte australi insulae, Mare Longue, 400-780 m, 14.I.1975 (fl., immature fr.), Bernardi 15071 (Å, BM, K n.v., L [L0192019], MICH, MO, NY, P[P01954004, P01954021, P06901366], SING); Mare Longue, St. Philippe, II.1971 (fl.), Bosser 20651 (P[P01954005, P01954013]); forêt du Brulé du Baril, St. Philippe, 350 m, 19.I.1972 (fl.), Cadet 3498 (P[P01954016]); Mare Longue (St. Philippe), 22.II.1971 (fr.), Friedmann 1041 (P[P01954008, P01954012]); Marelongue (St. Philippe), 400 m, III.1973 (fr.), Friedmann 2166 (K, P[P01954027, P01954028, P01954029, P01954030]); Mare Longue, St. Philippe, I.1977 (fl.), Friedmann 3037 (K n.v., MAU, P[P01954010, P01954011, P01954019, P01954020, P01954023]); Mare Longue, 19.III.1981 (fl., fr.), Lecordier GL 6 (MAU); Mare Longue forest, Réserve Biologique, alt. 150-200 m, 29.III.1973 (fr.), Lorence R41 (EA, K n.v., MAU 15651, MO, P[P01954006]); versant de la propriété de Villeneuve, Rivière de Marsonina, III.1944 (fr.), *Rivals* 51 (P[P01954018]).

Provenance uncertain. "Madag.[ascar] – Côte Est, env. de Tamatave." XI.1906 (fl. buds), *d'Alleizette* 111 (L[L0196007]); *Herb. Du Petit-Thouars s. n.* (P[P030420, upper right specimen]); *Herb. Du Petit-Thouars s. n.* (P[P030421]). DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia richardii* is endemic to the islands of Mauritius and La Réunion, where it grows in upland thickets and humid evergreen forest with a *Sideroxylon* species as the dominant in the canopy, at elevations of 150-780 meters (Fig. 7).

LOCAL NAMES. — Bois de banane (*Bernardi 15071, Bosser 20651, Cadet 3498*), pigeon wood (*Florens et al. 24082*).Specimens with flowers and with fruits have been collected from January to March; one specimen collected in June had flower buds and immature fruits. Page (1998c) gave *Xylopia richardii* an IUCN conservation assessment of Vulnerable. Our EOO and AOO calculations of 558 km² and 36 km², respectively (Table 2), support that assessment. The species is present in some protected areas on both islands.

DESCRIPTION

Tree or shrub up to 13 m tall; d.b.h. up to 30 cm.

Twigs appressed-public public public of the hairs 0.1-0.3 mm long, soon glabrate; nodes with one axillary branch.

Leaves with larger blades 4.4-8.8 cm long, 2.6-3.7 cm wide, coriaceous, discolorous, grayish green to olive gray adaxially, reddish brown to orange-brown abaxially, or concolorous, elliptic, oblong, or oblanceolate, apex obtuse, rounded, emarginate, or acuminate, the acumen 2-7 mm long, base cuneate to broadly cuneate, short-decurrent on petiole, margin often revolute, glabrous on both surfaces; midrib reddened or green adaxially, secondary veins weakly brochidodromous, 9-16 per side, diverging at 55-75° from midrib, these and higher-order veins plane or slightly raised adaxially, slightly raised and forming a conspicuous reticulum abaxially; petiole 2.2-7 mm long, semi-terete, smooth to longitudinally wrinkled, glabrous or with a few appressed hairs.

Inflorescences axillary or from the axils of fallen leaves, 1(-2)-flowered, not pedunculate, appressed-pubescent; pedicels often recurved, 7-13 mm long, 1.8-2 mm thick; bracts 3-4, attached at or proximal to the pedicel midpoint, caducous even with smallest buds seen; buds lanceolate to linear-lanceolate, apex acute to obtuse, rarely a little falciform.

Sepals erect to spreading at anthesis, ¹/₄-¹/₃-connate, 2.7-3.8 mm long, 4.7-6.0 mm wide, coriaceous, broadly ovate, apex obtuse, appressed-pubescent abaxially.

Petals pale yellow *in vivo*; outer petals with position at anthesis unknown, 19-37 mm long, 5.8-7.2 mm wide at base, 3.5-5 mm wide at midpoint, fleshy, lanceolate to linear-lanceolate, flat on both surfaces, apex acute, base slightly concave, densely dusty-puberulent except for the glabrous basal concavity adaxially, densely sericeous abaxially; inner petals with position at anthesis unknown, 18-25 mm long, 3.5-4.5 mm wide at base, 1.1-1.5 mm wide at midpoint, fleshy, linear, keeled on the apical ¼ adaxially, keeled abaxially, apex acute, base deeply concave with undifferentiated margins, laterally compressed, densely dusty-puberulent except for the mostly glabrous basal concavity adaxially, densely puberulent except for glabrous base abaxially. Stamens (150-)250-300; fertile stamens 1.4-1.7 mm long, narrowly oblong, anther connective apex 0.2-0.4 mm long, shield-shaped to capitate, overhanging anther thecae, papillate, anthers 10-13-locellate, filament 0.3-0.4 mm long; outer staminodes 1-1.5 mm long, oblong, apex truncate; inner staminodes absent; staminal cone 2.5-4.5 mm in diameter, 0.5-1.8 mm high, concealing all but the apices of the ovaries, rim even or slightly irregular.

Carpels 20-27; ovaries 1-1.5 mm long, narrowly oblong, pubescent, stigmas loosely connivent, 6.6-7.0 mm long, filiform, pilose at apices.

Fruit of up to 24 monocarps borne on a pedicel 15-22 mm long, 3-6 mm thick, glabrate or with a few scattered hairs; torus 5-19 mm in diameter, 4-9 mm high, depressed-globose; monocarps with a reddish green exterior and red endocarp *in vivo*, 2.5-4.8 cm long, 0.6-0.9 cm wide, 0.7-0.9 cm thick, narrowly oblong, slightly torulose, apex obtuse or with a blunt beak 1-3 mm long, base sessile or slightly contracted into a stipe 3-9 mm long, 2.5-4.1 mm thick, sometimes verrucose, longitudinally wrinkled, glabrate or sparsely pubescent; pericarp 1.1-1.4 mm thick.

Seeds up to 6 per monocarp, in a single row, oblique to long axis, 9.1-10 mm long, 5.2-6.1 mm wide, 5.1-7 mm thick, oblong-ellipsoid, flattened-elliptic to circular in cross-section, dark brown, smooth or faintly wrinkled, shiny, perichalazal ring forming a faint ridge; sarcotesta absent; aril whitish to pink *in vivo*, amber-colored with white flecks when dried, bilobed, lobes 2.1-3.5 mm long, 4.0-5.9 mm wide, fleshy, smooth to wrinkled.

Notes

Xylopia richardii differs from the other Mauritian species of *Xylopia* in the much smaller leaves (not exceeding 8.8 cm in length) and the smaller flowers with the outer petals lanceolate to linear-lanceolate and reaching a length of only 37 mm. There are slight differences between *X. richardii* specimens from Mauritius and those from La Réunion: those from Mauritius tend to have oblanceolate and emarginate leaves and shorter petals, while specimens from La Réunion have more elliptic and acuminate leaves and longer petals. There may, however, be variation in the leaf shape even on the same specimen, for example sheets of *Bosser 20651* (P01954005) and *Friedmann 3037* (P01954011) at P show both morphologies.

The specimen *d'Alleizette 111* (L), was originally identified as *Xylopia flexuosa* Diels and its provenance was given as "Madag.[ascar]-Côte Est, env. de Tamatave". It bears the leaf and bud characters of *X. richardii*, but this species has never been collected on Madagascar. The same collector made a collection of *Xylopia richardii* in June 1905 from La Réunion (see above), so it is possible that this represents a labeling error.

The original description by Baillon was based on specimens collected by Richard and Du Petit-Thouars. Richard's specimen with the label giving the name as "*Xylopia richardi* Bvn."

is designated here as the lectotype. The lectotype specimen is mounted on the same sheet as a collection of X. richardii with fruits from the Herb. Du Petit-Thouars. A second collection by Richard, identical in the size and shape of the leaves and the degree of maturation of flowers and fruits, is considered to be an isolectotype; a label on the sheet gives the name as "Xylopia richardiana H. Bn." and the specimen is identified as having been a part of the Drake Herbarium, which was acquired by P in 1913 (Stafleu & Cowan 1976). A second specimen from the Herb. Du Petit-Thouars (P030421) that has only flowers and leaves with more acute apices than on any of the other specimens, was specifically mentioned by Baillon in the protologue: "Stirpis hujusce formam alteram ß, foliis apice angustioribus elongatis acuminatis, dignitati specificae, ut mihi videtur, non sat aequalem, in herbario Thouarsiano nuperrime detexi".

II. *Xylopia* section *Verdcourtia* D.M.Johnson & N.A.Murray

PhytoKeys 97: 88, 89 (2018). — Type: *Xylopia mwasumbii* D.M.Johnson.

DESCRIPTION

Nodes with branches from 2-3 axillary buds; outer and inner petals lanceolate, similar in length; inner petals flat at the base and lacking differentiated fleshy basal margins; anther connective apex rudimentary, not overhanging the anther thecae, staminal cone rudimentary, surrounding only the bases of the ovaries and rim laciniate, or cone absent; carpels 1-5, the stigmas sometimes thickened and falciform; seed (where known) bearing a cupular aril surrounding the base; seed coat smooth, sarcotesta absent. Three species in East Africa and two species on Madagascar, all at low elevations.

Notes

Xylopia section *Verdcourtia* is characterized by a rudimentary anther connective apex, which does not overhang the anther thecae, a rudimentary or absent staminal cone, and a smooth fleshy white cupular aril (Johnson & Murray 2018). Two Madagascar *Xylopia* species, *X. sahafariensis* and *X. sericolampra*, have this unusual androecium and are classified in the section even though their seeds are imperfectly known. An accession of *X. sahafariensis* was nested in a subclade with section members *X. mwasumbii* and *X. lukei* from East Africa in the molecular phylogeny of Stull *et al.* (2017).

9. *Xylopia sahafariensis* Cavaco & Keraudren (Fig. 12)

Bulletin de la Société botanique de France 103: 277 (1956). — Type: **Madagascar. Prov. Antsiranana** ["Domaine de l'Ouest"], bassin de la Saharaina, forêt de Sahafary (au S.-E. de Diégo-Suarez), 23.X.1956 (fl.), *Capuron 11370* (holo-, P[P030422]!; iso-, OWU!, P[P030423, P030424, P00800918]!; TEF[photo]!). MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana, Vohemar, Maromokotra, Ankijomantsina, 3 km au S d'Ankijomantsina, 13°07'40"S, 49°27'53"E, 100 m, 30.X.2005 (fl.), *Ratovoson et al. 1036* (MO, P[P01954022]); Ampisikina (Ampisikinana), Soatanana, Ambarilao, forêt d'Ampondrabe, 12°57'39"S, 49°42'31"E, 175 m, 5.XI.2005 (fl.), *Ratovoson et al. 1067* (MO, P[P06901369]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia* sahafariensis occurs only in northeastern Madagascar, in dry deciduous forest at elevations of 100 and 175 m (Fig. 30). Specimens with flowers have been collected in late October and early November. With an EOO and AOO estimated as 853 km² and 12 km², respectively, it has a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Taimbarika (*Ratovoson et al. 1036*).

DESCRIPTION

Tree up to 12 m tall; d.b.h. up to 12 cm.

Twigs glabrous or sparsely pubescent, the hairs 0.2-0.3 mm long, soon glabrate; nodes with one or two axillary branches.

Leaves with larger blades 4.9-8.6 cm long, 1.5-3.3 cm wide, chartaceous to subcoriaceous, slightly discolorous, somewhat shining and greenish gray adaxially, dull and light brown abaxially, lanceolate, apex acuminate, the acumen gradual, short, and blunt, attenuate to an obtuse tip, base broadly cuneate to obliquely rounded, short-decurrent on petiole, margin flat, not revolute, glabrous adaxially, glabrous to sparsely appressed-pubescent abaxially; midrib concolorous or light orange-brown toward the base adaxially, secondary veins weakly brochidodromous, 10-13 per side, diverging at 45-75° from midrib, these and higher-order veins slightly raised on both surfaces, sometimes forming a conspicuous reticulum; petiole 5.5-8 mm long, flattened and ribbonlike to shallowly canaliculate adaxially, longitudinally or transversely wrinkled, glabrous or with a few hairs.

Inflorescences axillary or from the axils of fallen leaves, 1-2-flowered, pedicels arising separately from leaf axil, sparsely pubescent; peduncle absent; pedicels 2.5-3.2 mm long; 0.6-0.8 mm thick; bracts 2, one bract at or just proximal to the pedicel midpoint and the other subtending the sepals, persistent, 0.8-1.8 mm long, broadly ovate to semicircular; buds lanceolate, apex obtuse.

Sepals slightly spreading at anthesis, ¹/₂-¹/₂-connate, 1.4-2.3 mm long, 1.7-3.2 mm wide, coriaceous, broadly ovate to semicircular, apex acute to obtuse, appressed-pubescent abaxially.

Petals yellow *in vivo*; outer petals spreading at anthesis, 5.6-9.6 (-12 ex protologue) mm long, 2.5-3.4 (-4 ex protologue) mm wide at base, 1.1-2.4 mm wide at midpoint, fleshy, lanceolate, keeled only at apex adaxially, with a faint longitudinal ridge abaxially, apex obtuse, puberulent adaxially, appressed-pubescent abaxially; inner petals probably erect with the apices curved outward at anthesis, 5.3-7 (-10 ex protologue) mm long, 1.6 (-3 ex protologue) mm wide at base, 0.6-1.0 mm wide at midpoint, fleshy, lanceolate to linear-lanceolate, weakly keeled toward apex adaxially, slightly keeled abaxially, apex obtuse, base concave with undifferentiated margin, puberulent on both surfaces.

Stamens 80-120; fertile stamens 0.8-1.0 mm long, narrowly oblong, anther connective apex *c*. 0.1 mm long, truncate, oblong, or bifid, rudimentary, not overhanging anther thecae, glabrous, anthers 9-11-locellate, filament 0.4-0.5 mm long; outer staminodes present or absent, if absent then outermost stamens sometimes with reduced anthers, same length as the fertile stamens, oblong, apex truncate to rounded; inner staminodes absent; staminal cone absent.

Carpels 2-3, *c*. 2.5 mm long, ovary and stigma merging imperceptibly, oblong to obovoid, glabrous, stigmas linear or slightly spatulate, smooth.

Fruits and seeds unknown.

Notes

The flowers of *Xylopia sahafariensis* are superficially similar to those of *X. bemarivensis*, but the reduced anther connective apices, glabrous carpels, and absence of a staminal cone place it in section *Verdcourtia*. *Xylopia sahafariensis* and *X. sericolampra* are the only species of section *Verdcourtia* occurring outside of East Africa. All known species in the section are restricted to dry coastal forests.

The type specimen has slightly longer and more abundant hairs on the petals, and the petals, especially the inner ones, are narrower toward the apex, but otherwise the three specimens agree well.

10. *Xylopia sericolampra* Diels (Figs 6H; 13)

Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 353 (1925). — Type: Madagascar. Prov. Mahajanga ["Madagascaria occidentalis"], Boina, Bongolava, in silvis sabulosis aridis, X.1907 (fl.), Perrier de la Bâthie 4966 (holo-, B!; iso-, P[P030425, P00364248]!).

MATERIAL EXAMINED. — **Madagascar**. Prov. Mahajanga. Canton Tsaramandroso, District A[mba] to Boina, Antongomlilanivy de Ankarafantsika, 5.X.1948 (fl.), *Réserves Naturelles* [*Ramamanjisoa*] 1665 *RN* (K n.v., OWU, P[P01953995, P01953996, P02133042]); R. N. 7, Canton Tsaramandroso, District Ambato-Boeni, 10.XI.1952 (fl.), *Ramamanjisoa* 4737 *RN* (K, P[P01953991, P01953992, P02133041]); Ampijoroa, Ankarafantsika, J. Botanique, on gentle slope 1 mi from lake, 26.VII.1970 (buds), *Richard* 429 (K); Without definite locality, s. d. (fr.), *Service Forestier 114 SF* (P[P00524384, P01953990]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia sericolampra* is known only from a small area of dry forest on sand in northwestern Madagascar (Fig. 30). Specimens with flowers have been collected in October and November; the one specimen with fruits is undated. Several iNaturalist postings from the vicinity of Sofia show new flushes of leafy shoots and flowers appearing in late September and November, and an apparently mature fruit in January (Fig. 6H). In the September photographs the leaves of the previous growing season are still present, but in the November photographs they have been shed from the plant. With an EOO and AOO estimated as 859 km² and 20 km², respectively, it is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Lompingo (*Réserves Naturelles* [*Ramamanjisoa*] 1665 *RN*). According to Baron (1890), this name is also given to a species of *Diospyros*.

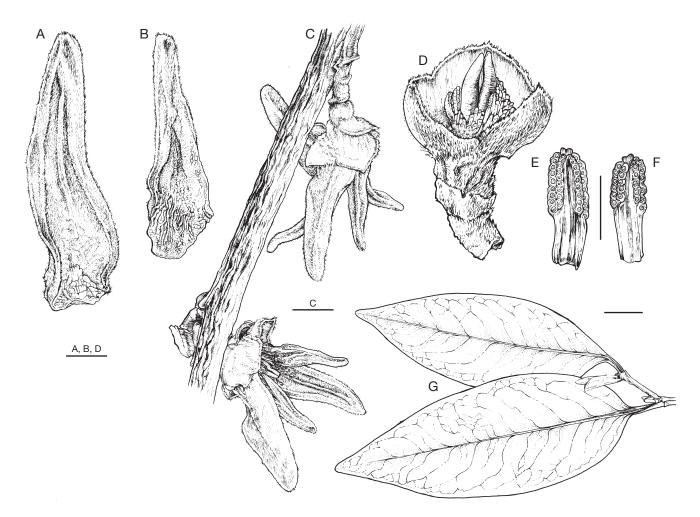


Fig. 12. – *Xylopia sahafariensis* Cavaco & Keraudren: **A**, outer petal, adaxial surface; **B**, inner petal, adaxial surface; **C**, inflorescences; **D**, flower with petals and stamens removed to show staminal cone and carpels; **E**, **F**, stamens, abaxial view; **G**, habit. All from *Ratovoson et al.* 1067 (MO). Scale bars: A, B, D, 1 mm; C, 2 mm; E, F, 0.5 mm; G, 1 cm.

DESCRIPTION Shrub up to 4 m tall.

Twigs short silvery appressed-pubescent, the hairs 0.1-0.2 mm long, eventually glabrate; nodes with one axillary branch.

Leaves with larger blades 4.7-7.2 cm long, 2.0-3.0 cm wide, subcoriaceous, discolorous, gray to brown and shiny adaxially, dull grayish tan abaxially, oblanceolate to narrowly elliptic, apex obtuse to rounded, sometimes slightly emarginate, base truncate or sometimes rounded, margin flat to slightly revolute, glabrous adaxially, sparsely and finely appressed-pubescent abaxially; midrib pinkish brown toward the base adaxially, secondary veins weakly brochidodromous, 9-14 per side, diverging at 45-60° from midrib, these and higher-order veins plane and indistinct on both surfaces; petiole 1.8-3.5 mm long, semi-terete, longitudinally wrinkled, glabrate or with a few sparse hairs.

Inflorescences arising from axils of the first 3-4 bracts of newly expanding shoots, 1-flowered, not pedunculate, densely sericeous; pedicels 1.7-3.2 mm long, *c*. 1.0 mm thick; bracts 3-4, evenly spaced on pedicel, proximal bracts usually caducous,

distal bract 2.3-4 mm long, orbicular to reniform; buds lanceolate, apex obtuse, sometimes slightly falciform.

Sepals slightly spreading at anthesis, ¹/₄-²/₃-connate, 3.0-4.2 mm long, 2.9-4 mm wide, coriaceous, broadly ovate, apex acute or apiculate, densely sericeous abaxially.

Petals yellow *in vivo*; outer petals spreading at anthesis, 13.9-17.4 mm long, 2.4-2.9 mm wide at base, 1.0-1.6 mm wide at midpoint, coriaceous, linear-lanceolate, flat, apex acute, densely puberulent except at base adaxially, densely sericeous abaxially; inner petals more or less spreading at anthesis, 10-15.8 mm long, 1.5-2.2 mm wide at base, 0.7-0.8 mm wide at midpoint, slightly fleshy, linear, faintly keeled on both surfaces, apex acute, base concave with undifferentiated margin, thinly puberulent except at base adaxially, more densely puberulent but sparse toward base abaxially.

Stamens *c*. 100; fertile stamens 1.2-1.3 mm long, narrowly oblong, anther connective apex *c*. 0.1 mm long, conical or slightly bifid, rudimentary, not overhanging anther thecae, glabrous, anthers *c*. 10-locellate, filament 0.5-0.6 mm long; outer stami-

nodes (loose in packet) *c*. 1.4 mm long, clavate, apex obtuse; inner staminodes (loose in packet) *c*. 1.0 mm long, oblong, apex obliquely truncate; staminal cone rudimentary or absent.

Carpel 1, *c*. 1.7 mm long, lanceolate; ovary and stigma continuous, apex obtuse, pilose.

Fruit a single monocarp borne on a pedicel 3 mm long, 3.5 mm thick, pubescent; torus *c*. 4.2 mm in diameter, not expanded; monocarp with peach-colored exterior *in vivo*, 2.5-4.8 cm long, 2.0-2.5 cm wide, 1.9-2.5 cm thick, pyriform, oblong, or ovoid, not torulose, apex rounded, base sessile, rounded or slightly tapered, smooth or slightly wrinkled, surface marked by a pattern of raised longitudinal veins, pubescent; pericarp *c*. 3.4 mm thick.

Seeds c. 3 per monocarp, in a single row, lying perpendicular to long axis, c. 15.4 mm long, 12-13.9 mm wide, 8.8-9 mm thick, ellipsoid, irregularly elliptic in cross-section, light brown, smooth, dull, perichalazal ring not elevated; sarcotesta presence or absence undeterminable; aril absent, micropylar end of seed marked by a light brown smooth area.

Notes

Xylopia sericolampra is distinguished from other Madagascar species by the combination of silvery indument of the new shoots and inflorescences, the shiny leaves with blunt apices and truncate bases, and the remarkable single ovoid monocarp with raised venation on its surface. The raised monocarp venation is shared with *X. mwasumbii* of coastal Tanzania, but the latter has flattened rather than ovoid monocarps. *Xylopia sericolampra* differs from the second Madagascar species of section *Verdcourtia*, *X. sahafariensis*, the fruits of which are unknown, by its longer and narrower petals, truncate leaf bases, and indument of silver hairs on the young growth. Its inflorescences appear with the expansion of the new vegetative shoots, which are enclosed by overlapping conduplicate leaves. The label of the type specimen reports the bark to be black.

III. Xylopia section Stenoxylopia Engl. & Diels

Monographien Afrikanischer Pflanzen-Familien und Gattungen 6: 59 (1901). — Type: Xylopia odoratissima Welw. ex Oliv. (lecto-, designated in Stull et al. [2017: 221]).

DESCRIPTION

Nodes with branches from one to three axillary buds; outer petals lanceolate to linear, rarely ovate; inner petals lanceolate to linear, rarely ovate, fleshy basal margins absent in Malagasy species; anther connective apex shield-shaped to capitate, overhanging anther thecae; staminal cone rudimentary to well-developed, partially to completely concealing the ovaries, rim even to irregularly laciniate; carpels 3-9 in Malagasy species, the stigmas connivent, smooth; arils absent; seed coat smooth, rarely slightly papillate, pitted, or wrinkled, sarcotesta present, in Malagasy species either orange to red or light green to yellow-green. This section is represented by 34 species in tropical Africa (Johnson & Murray 2018), 23 species on Madagascar, and *c*. 40 species in Southeast Asia.

Notes

Many of the sect. *Stenoxylopia* species from Madagascar are still imperfectly known: for example, *X. carinata*, sp. nov., *X. ghesquiereana*, and *X. humbertii* are unknown in fruit, and *X. longirostra*, sp. nov., and *X. marojejyana*, sp. nov., are unknown in flower. Some assignments of the Madagascar sect. *Stenoxylopia* species to the three subclade groups in the Phylogeny section were thus provisional. Given the tentative nature of the subclade classifications the species of the section appear alphabetically in the following account.

11. *Xylopia ambanjensis* Cavaco & Keraudren (Fig. 14L-P)

Bulletin de la Société botanique de France 103: 275, 276 (1956). — Type: **Madagascar. Prov. Antsiranana** ["Domaine du Sambirano"], Anaborano-Ambanja, 18.IX.1951 (fl.), *Service Forestier 3878* (holo-, P[P030362]!; iso-, TEF[photo]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana. Ampasindava, forêt de Betsitsika, 13°45'38"S, 47°59'27"E, 21.I.2009 (fr.), Ammann et al. MYA 304 (K n.v., MO); Sava Region, Vohemar, Ampisikina, Ambararatamisakana, sur flanc rocheux du sommet d'Antseramborona, 12°57'10"S, 49°36'52"E, 510 m, 29.IX.2013 (fr.), Andriamiarinoro et al. 369 (MO, P[P01047533]); Ambobaka, on savoka, Fiv. Ambanja, 13°44'54"S, 48°31'59"E, 200 m, 8.IV.2000 (fr.), Antilahimena et al. 455 (MO, P[P01954132]); Réserve spéciale de Manongarivo, Ambongomirahavavy (13°59'S, 48°17'E), confluence Manongarivo/Marofotrotro, 100 m, 29.IX.1996 (fl.), Gautier et al. LG 3160 (K, P[P01954145]); Réserve spéciale de Manongarivo, Ambahatra, cours supérieur (13°59'S, 48°26'E), 650 m, 9.VI.2000 (fr.), Gautier et al. LG 3774 (Kn.v., MO, P[P01954153]); Diana, Antsiranana II, Anjakely, Andrafiamena, Ampantsona Forest, 12°54'49"S, 49°17'24"E, 494 m, 18.VI.2007 (fr.), Letsara & Jaomora LRK 238 (CAS); Diana Region, Ambilobe, Beramanja, Anketrabe Belinta, forêt de Galoko, 13°35'17"S, 48°42'49"E, 325 m, 2.X.2013 (fl.), Manjato et al. 433B (OWU, P[P01060835]); Antsiranana (Diego Suarez) region, c. 80 road-km S of city, in Réserve spéciale Ankarana, 12°52'S, 49°14'E, 320 m, 23.XI.1989 (fl. buds), McPherson 14522 (K n.v., MO); Daraina, forêt de Bekaraoka, 13°06'38"S, 49°42'29"E, 261 m, 12.II.2004 (fr.), Nusbaumer & Ranirison LN 1160 (G, K n.v., P[P06774748]); Fiv. Ambanja, Fir. Ambodimanga-Ramena, Fkt. Antsahabe, Village Mandrizavona, rivière d'Antsahasoa, 13°47'31"S, 48°45'26"E, 460 m, 12.IV.2000 (fr.), Rabenantoandro et al. 166 (Kn.v., MO, P[P01954146]); Antsiranana, Fiv. Ambanja, Domaine de Sambirano, village de Benavony, Bekaka, à 6 km au SE d'Ambanja, 13°43'32"S, 48°28'48"E, 80 m, 15.V.1988 (fr.), Randrianaivo et al. 233 (MO, P[P01954147]); Daraina, forêt de Bekaraoka, partie nord, 13°07'03"S, 49°42'41"E, 360 m, 12.II.2004 (fr.), Ranirison & Nusbaumer PR 438 (G, K n. v., P[P06774747]); Marotongoza, district de Nossy Bé, 13.III.1957 (st.), Réserves Naturelles 9400 (B, K n.v., P[P01954151, P01954152]); Manisakaomby, Latsory, Ankaramy Canton, Analalava District, 14.V.1959 (st.), Service Forestier 32 33 R 362 (K, P[P01954148]); Ambanja, Béamfrangibé Marotovy, 16-30.III.1951 (fr.), Service Forestier 2958 SF (P[P01954150]); Benavony-Ambanja, 8.IV.1953 (fr.), Service Forestier 7247 (P[P02008537, P01954130, P01954131]); Station forestière de Sakaramy-Diego, 17.XII.1953 (fl. buds), Service Forestier 7962 (P[P02005956]); Forêt d'Ambre, Diégo, 18.VI.1954 (st.), Service Forestier 10284 (P[P02008536]).

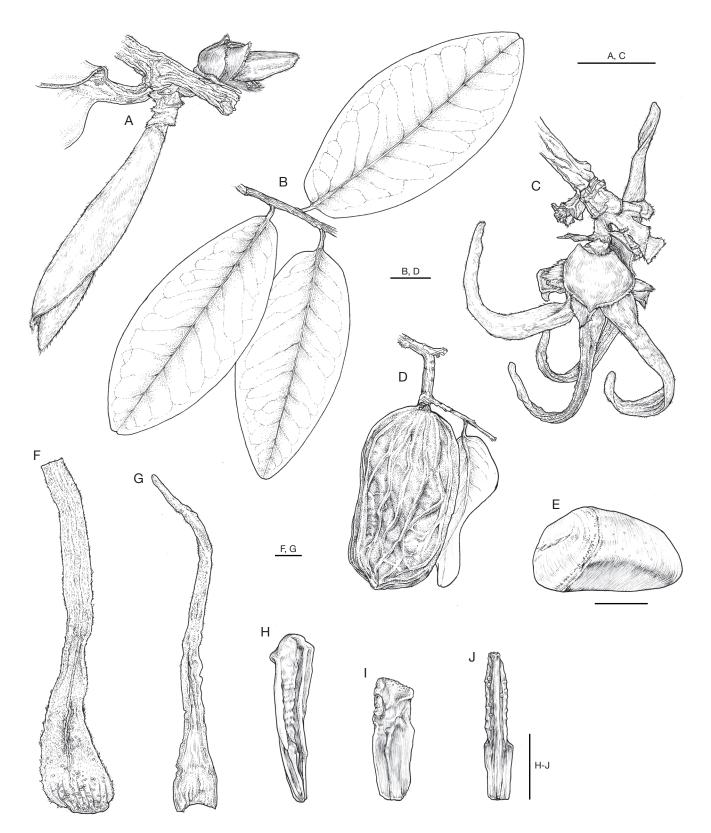


Fig. 13. – *Xylopia sericolampra* Diels: **A**, side views of expanding shoot and flower bud; **B**, leaf habit; **C**, flower, side view; **D**, monocarp, side view; **E**, seed, view from above; **F**, adaxial view of outer petal (apex not shown); **G**, adaxial view of inner petal; **H**, **I**, staminodes; **J**, fertile stamen. **A**, **C**, from *Perrier de la Bâthie 4966* (P); **B**, from *Richard 429* (K); **D**, **E**, from *Service Forestier 114* (P); **F**-**J**, from *Perrier de la Bâthie 4966* (B). Scale bars: A, C, E, 5 mm; B, D, 1 cm; F, G, 1 mm; H-J, 0.5 mm.

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia ambanjensis* is restricted to a small area of northern Madagascar, usually in dry deciduous forest but occasionally in humid evergreen

forest (D'Amico & Gautier 2000), often on rocky or sandy sites, at elevations from 80 to 650 meters (Fig. 28). Specimens with expanding flower buds have been collected in November and December,

specimens with flowers in September and October, and specimens with fruits from January to June and in September. With an EOO and AOO of 5498 km² and 48 km², respectively, and documented from 12 localities, *X. ambanjensis* is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAMES. — Fotsiavadika (*Andriamiarinoro et al. 369*), hazoambo (*Réserves Naturelles 9400, Service Forestier 2958 SF*), mampahy (*Gautier LG 3160*), moranga (*Randrianaivo et al. 233, Service Forestier 7247*), morango (*Antilahimena et al. 455*).

DESCRIPTION

Tree up to 25 m tall, rarely a shrub; d.b.h. up to 20 cm.

Twigs sparsely appressed-pubescent, the hairs 0.1-0.3 mm long, soon glabrate; nodes with one or occasionally two axillary branches.

Leaves with larger blades 6.4-8.8 cm long, 1.5-2.2 cm wide, chartaceous, discolorous, greenish gray and shiny adaxially, brown and dull abaxially, narrowly lanceolate, apex gradually acuminate, the acumen 9-12 mm long, occasionally acute, base cuneate, short-decurrent on petiole, margin flat or slightly recurved, glabrous adaxially, finely appressed-pubescent but eventually glabrate abaxially; midrib darkening toward base adaxially, secondary veins brochidodromous, 13-17 per side, diverging at 45-70° from midrib, these and higher-order veins indistinct, plane adaxially, very slightly raised abaxially; petiole 3.8-6 mm long, shallowly canaliculate, faintly wrinkled, glabrate.

Inflorescences axillary, 1-8-flowered, the inflorescence axis sometimes becoming leafy, pedunculate or not, sparsely appressed-pubescent; peduncle 1-2.5 mm long, or absent; pedicels two per peduncle or arising separately from leaf axil, 4.2-6.4 mm long, 0.5-0.6 mm thick; bracts 2, spaced evenly along the length of the pedicel, caducous or distal bract often persistent, 1.1-1.7 mm long, ovate; buds lanceolate, apex obtuse.

Sepals slightly spreading at anthesis, ¹/₃-connate, 1.3-1.6 mm long, 1.9-2.3 mm wide, subcoriaceous, triangular to semicircular, apex acute to obtuse, appressed-pubescent abaxially.

Petals yellow-green, red at base *in vivo*; outer petals spreading at anthesis, 10.9-12.1 mm long, 1.9-2.1 mm wide at base, 1.0-1.3 mm wide at midpoint, slightly fleshy, lanceolate, keeled at apex adaxally, keeled abaxially, apex obtuse, puberulent adaxially, appressed-pubescent abaxially; inner petals slightly spreading at anthesis, 8.4-8.8 mm long, 1.8-2.2 mm wide at base, 0.6-0.7 mm wide at midpoint, slightly fleshy, linear-subulate, keeled on apical ¼-½ adaxially, keeled abaxially, apex acute, base concave with undifferentiated margin and long claw, puberulent but becoming glabrous toward the base on both surfaces.

Stamens *c*. 100; fertile stamens 1.3-1.4 mm long, narrowly oblong, anther connective apex 0.2-0.4 mm long, shield-shaped, overhanging anther thecae, minutely papillate, anthers 14-16-locellate, filament 0.4-0.5 mm long; outer staminodes 1.3-1.4 mm long, oblong to clavate, apex obtuse to truncate; inner staminodes 0.8-1.0 mm long, oblong, apex rounded to truncate; staminal cone 1.2-1.4 mm in diameter, *c*. 0.8 mm high, concealing lower half of ovaries, rim irregularly laciniate.

Carpels *c*. 5; ovaries *c*. 1 mm long, oblong, pubescent, stigmas loosely connivent, *c*. 2.5 mm long, filiform, setose at apex.

Fruit of up to 5 monocarps borne on a pedicel 3.5-12 mm long, 1.5-4.5 mm thick, glabrate or with a few hairs; torus 3-8 mm in diameter, 2-6 mm high, globose to depressed-globose; monocarps with yellowish, greenish, or blackish red exterior and red endocarp *in vivo*, 2.3-3.1 cm long, 1.5-1.8 cm wide, 1.3-1.5 cm thick, oblong to obovoid, not torulose, apex rounded, base sessile or contracted into a stipe 2-3 mm long, 5-7 mm thick, finely verrucose, rugose, sparsely lenticellate, dull, frequently with a pronounced abaxial ridge, glabrate; pericarp 2-4 mm thick.

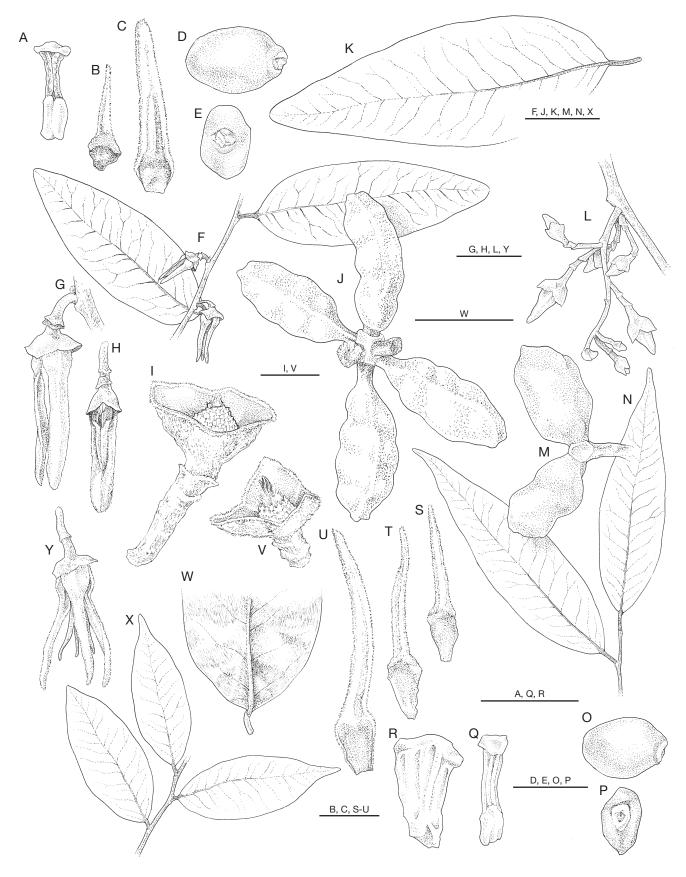
Seeds up to 6 per monocarp, in two rows, perpendicular to oblique to long axis, 9.9-11.6 mm long, 6.7-8.3 mm wide, 4-6.1 mm thick, broadly ellipsoid, elliptic, semicircular, or wedge-shaped in cross-section, brown, smooth, dull, perichalazal ring faintly or not evident; presence of sarcotesta not determined; aril absent.

Notes

Xylopia ambanjensis is readily separated from most Madagascar *Xylopia* species by the narrow leaves with gradually acuminate apices. It is most similar to *X. longirostra*, sp. nov., but that species has leaves with a proportionately longer acumen and its monocarps are much larger and lenticellate. *Xylopia ambanjensis* also resembles *X. lastelliana*, but lacks the sericeous indument of the leaves and twigs and has smaller monocarps that are somewhat wrinkled but not strongly lenticellate. An odd characteristic of *X. ambanjensis* seen in several specimens is that one branch of the inflorescence may continue to grow out as a leafy shoot. The shoot is usually not persistent, but leaves a stub that remains visible on the pedicel of the fruit.

Xylopia ambanjensis overlaps in distribution and habitat with several other northern dry forest species in Madagascar. The cuneate leaf base distinguishes it from *X. bemarivensis*, *X. sahafariensis*, and *X. sericolampra*, and the larger and gradually acuminate leaves distinguish it from *X. sclerophylla*, sp. nov. The specimen *Service Forestier 5539* (P[P01989232]) from Sakaramy – Diego, 12.VIII.1952 (fr.), has twigs and foliage typical in appearance for *X. ambanjensis*, but the monocarps on the specimen are distinctly stipitate with strong oblique wrinkles, a fruit morphology that was not seen on any other specimens.

Fig. 14. — Xylopia bemarivensis Diels, X. ambanjensis, and X. lastelliana Baill. A-K, X. bemarivensis: A, stamen, abaxial view; B, inner petal, adaxial surface; C, outer petal, adaxial surface; D, seed, side view; E, seed, view of micropylar end; F, habit; G, flower, side view; H, bud, side view with one outer petal removed to show inner petals; I, flower with petals, stamens, and stigmas removed to show staminal cone; J, fruit; K, leaf. L-P, X. ambanjensis: L, inflorescence; M, fruit; N, leaves; O, seed, side view; P, seed, view from micropylar end. Q-Y, X. lastelliana: Q, stamen, abaxial view; R, outer staminode, abaxial view; S, T, inner petals adaxial surface; U, outer petal, adaxial surface; V, flower with petals and stamens removed to show stigmas and staminal cone; W, leaf base abaxial surface;



showing indument; X, leaves; Y, flower, side view. A, B, from Rabenantoandro et al. 1035 (OWU); C, H, from McPherson 18833 (OWU); D, E, from Rabehevitra et al. 1009 (OWU); F, G, I, J, from Randriambololona et al. 48 (MO); K, from Andrianantoanina et al. 848 (OWU); L, from McPherson 14522 (MO); M-P, from Gautier et al. LG 3774 (MO); Q-Y, from Schatz & Modeste 3086; Q-V, Y, from WAG sheet; W, X, from MO sheet. Scale bars: A, Q, R, 1 mm; B, C, S-U, 3 mm; D, E, O, P, W, 1 cm; F, J, K, M, N, X, 2 cm; G, H, L, Y, 5 mm: I, V, 2 mm.

In the phylogenetic study of Stull *et al.* (2017) an accession of *X. ambanjensis, Ammann et al. MYA 304*, was part of a subclade with the Madagascar species *X. buxifolia* and *X. lemurica*, but with weak branch support. This subclade includes all Madagascar species known to have a green sarcotesta on the seed, but the label of *Rabenantoandro et al. 166* describes the seed of *X. ambanjensis* as having an "arille de couleur rouge". No aril was seen on the seeds of this species, however, so it is not possible to decide if the red color is a reference to the red endocarp in which the seeds are embedded, or to a sarcotesta.

12. *Xylopia anomala* D.M.Johnson & N.A.Murray, sp. nov. (Figs 6G; 15A-K)

Belonging the Madagascar group of *Xylopia* species having short broad petals and clavate stigmas, but distinguished from the others by the chartaceous leaves lacking a pronounced vein reticulum, the flowers up to 5 per inflorescence and forming a short corymb-like inflorescence, the obtuse outer petals 8.6-9.0 mm long and 2.5-4.1 wide at base, the stamens only 4-7-locellate, the staminal cone with filament bases only loosely connate, and the densely lenticellate monocarps up to 7.3 cm long and 3.2 cm thick.

TYPE. — **Madagascar. Prov. Antsiranana**, Sava Region, Anjangoveratra, Antanandava, Makirovana, 14°10'01"S, 49°57'12"E, 685 m, 4.V.2010 (fl.), *Razakamalala et al. 5422* (holo-, MO!).

PARATYPES. — Madagascar. Prov. Antsiranana, Sava Region, Vohemar, Antsirabe-Nord, Antanambaon'Isokitra, forêt de Tsihomanaomby, au sud-est du village Antanambaon'Isokitra, 14°06'S, 50°02'E, 30.XI.2013 (fr.), *Martial et al. 306* (OWU, P[P00982778]); Sava Region, Vohemar, Antsirabe Nord, Andravinambo, forêt d'Antsolatra, 14°06'45"S, 49°57'44"E, 387 m, 27.II.2013 (fr.), *Rakotonirina et al. 48* (OWU, P[P01030032]); Sava Region, Sambava, Marogaona, Ambodivapaza, forêt de Farahangitra, 14°08'09"S, 49°54'43"E, 322 m, 11.IV.2013 (fl.), *Rakotonirina et al. 105* (OWU, P[P01047882]); Sava Region, Sava, Andapa, Ambodivohitra, forêt Gelose à 1.5 km E du village de Marovato, 710 m, 14°34'40"S, 49°38'32"E, 16.II.2006 (buds), *Rakotovao et al. 2680* (MO, OWU, P[P01954121]).

Prov. Toamasina, Masoala Peninsula, coastal trail leading S from Ambanizana, 0-10 m, 10.XII.1990 (fr.), *Schatz & Modeste 3042* (K, MO, P[P01966122]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia anomala*, sp. nov., is restricted to northeastern Madagascar, occurring in humid forest at elevations from near sea level up to nearly 700 meters (Fig. 28); one collection label mentions a blackish soil substrate and another sand. Specimens with large buds or flowers have been collected in February, April, and May, and with fruits in February, November, and December. The label of *Martial et al. 306* reports the fruit to be consumed by the Madagascar blue pigeon, *Alectroenas madagascariensis*. With an EOO and AOO estimated as 3468 km² and 24 km², respectively, *Xylopia anomala*, sp. nov., is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Moranga (*Rakotonirina et al. 48, Martial et al. 306*).

DESCRIPTION

Tree up to 16 m tall; d.b.h. up to 12 cm.

Twigs finely appressed-pubescent, the hairs 0.1-0.3 mm long, at length glabrate; nodes with one or sometimes two axillary branches.

Leaves with larger blades 14.0-19.0 cm long, 5.3-6.5 cm wide, chartaceous, slightly discolorous, dull green adaxially, brown to orange-brown abaxially, elliptic, oblong, or oblanceolate, apex obtuse, acute, or acuminate, the acumen 18-22 mm long, base cuneate, decurrent on petiole, margin flat, not revolute, glabrous adaxially, glabrous or with a few scattered hairs along the midrib abaxially; midrib dull yellow or blackish brown toward base adaxially, secondary veins weakly brochidodromous, 8-15 per side, diverging at 40-70° from midrib, these and higher-order veins plane to raised adaxially, raised abaxially; petiole 4.5-13 mm long, semi-terete, smooth, sparsely pubescent.

Inflorescences axillary, 2-5-flowered, corymb-like, pedunculate, pubescent; peduncles 2-3 mm long; pedicels 2-5 per peduncle, 5.4-6.2 mm long, 1.1-1.4 mm thick; bracts 3, evenly spaced along pedicel, caducous or distal bract persistent, 1.7-3.3 mm long, ovate to broadly ovate; buds oblong, apex rounded.

Sepals slightly spreading at anthesis, ¹/₄-¹/₃-connate, 3.6-5 mm long, 3.7-4.8 mm wide, subcoriaceous, broadly ovate to triangular, apex obtuse, pubescent abaxially.

Petals light yellow *in vivo*; outer petals erect (?) at anthesis, 8.6-9.0 mm long, 2.5-4.1 mm wide at base, 4.9-6.8 mm wide at midpoint, fleshy, ovate, concave, keeled at the apex adaxially, flat or slightly ridged abaxially, apex obtuse, densely pubescent except for the glabrous base adaxially, pubescent abaxially; inner petals erect and possibly connivent at base at anthesis, 8.2-9.0 mm long, 2.5-3.3 mm wide at base, 2.5-2.7 mm wide at midpoint, fleshy, lanceolate-oblong, keeled at the apex adaxially, keeled abaxially, apex broadly acute to obtuse, base shallowly concave into a short claw, with undifferentiated margin but with a transverse thickening above the concavity, densely hairy except for the glabrous base on both surfaces.

Stamens *c*. 100; fertile stamens 1.4-1.7 mm long, narrowly oblong or slightly clavate, anther connective apex 0.1-0.3 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 4-7-locellate, filament 0.4-0.6 mm long; outer staminodes 1.8-2.0 mm long, oblong to clavate, apex rounded to truncate; inner staminodes 1.1-1.4 mm long, oblong to clavate, apex truncate; staminal cone 1.6-2.4 mm in diameter, 0.7-1.0 mm high, concealing only the bases of the ovaries, rim irregularly laciniate.

Carpels *c*. 5; ovaries 1-1.4 mm long, narrowly oblong, densely pubescent, stigmas loosely connivent, 1.5-1.9 mm long, clavate and somewhat falciform, glabrous or with a few hairs at the apex.

Fruit of up to 4 monocarps borne on a pedicel 10-12 mm long, 5-6 mm thick, sparsely pubescent to glabrate; torus 11-15 mm in diameter, *c*. 7 mm high, depressed-globose; monocarps with light brown exterior *in vivo*, 5.8-7.3 cm long, 1.9-2.6 cm wide, 1.3-3.2 cm thick, oblong to oblanceolate,

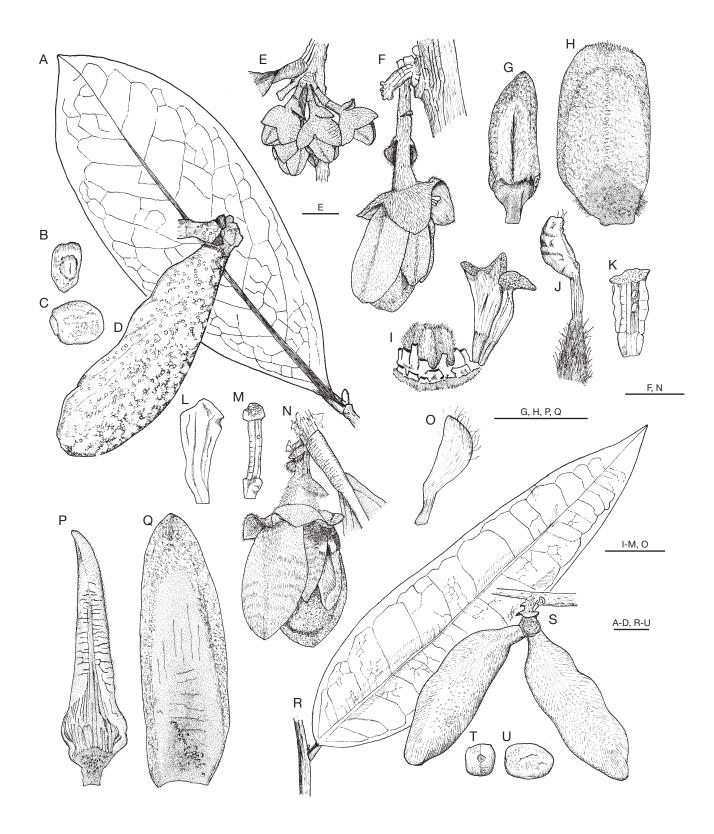


Fig. 15. – Xylopia anomala, sp. nov. and X. australis, sp. nov.: A-K, X. anomala, sp. nov.; A, habit; B, seed, view from micropylar end; C, seed, side view; D, fruit; E, inflorescence; F, inflorescence with mature flower; G, inner petal, adaxial view; H, outer petal, adaxial view; I, staminal cone, ovaries, and outer staminodes; J, carpel; K, fertile stamen, abaxial view; L-U, X. australis, sp. nov.: L, outer staminode, abaxial view; M, fertile stamen, abaxial view; N, inflorescence; O, stigma; P, inner petal, adaxial view; Q, outer petal, adaxial view; R, habit; S, fruit; T, seed, view from micropylar end; U, seed, side view. A, from *Rakotonirina 48* (OWU); B-D, from Schatz & Modeste 3042 (MO); E, from *Rakotovao et al. 2680* (MO); F-I, K, from *Razakamalala et al. 5422* (MO); J, from *Rakotovao et al. 2680* (OWU); L, M, O-Q, from Schatz 2641 (MO); N, from *Rakotovao et al. 4575* (MO); R-U, from *Razakamalala et al. 2414* (MO). Scale bars: A-D, R-U, 1 cm; E, F, G, H, N, P, Q, 5 mm; I-M, O, 1 mm.

not torulose, apex obtuse, sometimes contracted into a short beak *c*. 3.5 mm long, base narrowed, sessile or contracted into a stipe *c*. 2 mm long, 8 mm thick, smooth, densely lenticellate, dull, glabrate or with scattered patches of pubescence; pericarp 1.5-2 mm thick.

Seeds *c*. 9 per monocarp, in two rows, perpendicular to long axis, 13.3-17.2 mm long, 9.0-15.6 mm wide, 6.7-9.1 mm thick, ellipsoid to nearly globose, wedge-shaped to elliptic in cross-section, brown, smooth, dull, perichalazal ring visible but not elevated; sarcotesta color *in vivo* unknown, visible as white crusty patches on dried seeds; aril absent.

Notes

The first impression of *Xylopia anomala*, sp. nov., both in flower and in fruit, is that it is not a *Xylopia* at all. The leaves are large, papery, and broad, the flower buds are rounded rather than pointed, and the inflorescences are corymb-like. Densely lenticellate oblong woody monocarps are unique among Madagascar *Xylopia* species, and rare in the genus, although this fruit morphology is known in species such as *X. hypolampra* in Africa (Johnson & Murray 2018) and *X. ngii* in Asia (Johnson & Murray 2015). Unusual features of the plant extend to the androecium: the stamens have a low number of anther locelli, 4-7, and are borne on a staminal cone in which the stamen filaments are only loosely connate (Fig. 15I). The number of characters unusual for the genus suggested the specific epithet.

The short, broad, and thick petals, together with the clavate stigmas, place this species in the subclade of the Stenoxylopia clade with species such as *X. danguyella* and *X. fananehanensis*, but without any close resemblance to other species within that group.

13. *Xylopia australis* D. M.Johnson & N. A.Murray, sp. nov. (Figs 15L-U; 16A, G)

One of a group of *Xylopia* species in Madagascar with short broad petals and clavate stigmas, distinguished by the strongly raised reticulation of the leaves, the secondary veins often joining to form a sinuous intramarginal vein, the narrowly oblong or elliptic-oblong to lanceolate shape of the leaf blades, the corrugated adaxial surface of the inner petals, and the oblong glaucous and glabrate monocarps.

TYPE. — **Madagascar. Prov. Toliara**, Préfecture de Taolagnaro ["Tôlanaro"] (Fort-Dauphin), Petriky forest, *c*. 15 km WSW of Taolagnaro ["Tôlanaro"] (Fort Dauphin), 25°04'S, 46°51'E, 0-10 m, 9.III.1989 (fl.), *Schatz et al. 2641* (holo-, MO!; iso-, BR!; K!; WAG!).

PARATYPES. — Madagascar. Prov. Toliara, forêt de Vinanibe près Fort-Dauphin, 5-50 m, 2.IV.1947 (fl.), *Humbert 20767* (P); Région de l'Anosy, Bemangidy Forest, c. 3 km W of Antsotso, along RN 12a, 65 km N of Ft. Dauphin, E of Ivohibe peak, 24°35'02"S, 47°12'44"E, 100-250 m, 7.II. 2006 (fl.), *Lowry et al.* 6669 (MO); Anosy Region, ouest du village Malana, vers sommet entre Andohavola et Tanimena, FKT: Farafara Vatambe, CR: Mahatalaky, Dist.: Taolagnaro, Rég.: Anosy, 24°51'22"S, 47°00'27"E, 411 m, 16.XI.2009 (fl., fr.), *Rakotovao et al.* 4575 (MO); Fiv. Fort Dauphin, Com. Ampasinampoa, Fkt. Analambendrana à 4 km (vol d'oiseau) à l'ouest d'Ampasinapoa, 24°59'06"S, 46°57'37"E, 400 m, 24.XI.2002 (fr.), *Randrianaivo et al. 838* (MO); Anosy Region, Fort-Dauphin, Iaboko, Antsotso, Forêt Ivohibe, 24°34'14"S, 47°12'04"E, 265 m, 28.XI.2005 (fr.), *Razakamalala et al. 2414* (MO, P[P06901342]); Anosy Region, Taolagnaro, Iaboko, Antsotso Avaratra, 24°34'16"S, 47°12'06"E, 271 m, 8.XII.2007 (fr.), *Razakamalala et al. 3797* (MO, P[P06490487]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia australis*, sp. nov., is restricted to a small area in southeastern Madagascar, where it occurs in humid forest, sometimes on forested dunes or sand, at elevations from sea level to *c*. 400 m (Fig. 28). Specimens with flowers have been collected from February to April and in November, and with fruits in November and December. With its small EOO and AOO values, 185 km² and 24 km², respectively, *X. australis*, sp. nov., is given a preliminary conservation assessment of Endangered (Table 2). Several of the collections come from the general area of the Tsitongambarika forest, an area of high endemism (Razakamalala *et al.* 2011), which was designated as a protected area in 2015. The forests there are tropical in structure (Goodman *et al.* 1997) but lie south of the Tropic of Capricorn.

LOCAL NAME. — Ovaria (*Rakotovao et al. 4575*).

DESCRIPTION

Tree or shrub up to 8 m tall; d.b.h. up to 10 cm.

Twigs glabrous to sparsely pubescent, the hairs 0.2-0.4 mm long, soon glabrate; nodes with a single axillary branch.

Leaves with larger blades 8.7-17.2 cm long, 2.2-4.4 cm wide, subcoriaceous, discolorous, light gray to grayish green adaxially, orange-brown to brown abaxially, or concolorous, narrowly oblong or elliptic-oblong to lanceolate, apex acute to acuminate, the acumen 4-20 mm long, base rounded to broadly cuneate, short-decurrent on petiole, margin slightly revolute, glabrous adaxially, sparsely and finely appressedpubescent abaxially, the hairs sometimes restricted to the midrib; midrib pale yellow to brown or concolorous with blade adaxially, secondary veins distinctly brochidodromous, forming a wavy intramarginal vein, 14-17 per side, diverging at 60-90° from midrib, these and higher-order veins strongly raised and forming a conspicuous reticulum on both surfaces; petiole 2-9 mm long, shallowly canaliculate to semi-terete, transversely wrinkled and longitudinally striate, glabrous to sparsely pubescent.

Inflorescences axillary, 1-flowered, not pedunculate, sparsely appressed-pubescent; pedicels 4.7-6.5 mm long, 1.1-1.6 mm thick; bracts 3, evenly spaced along pedicel, caducous or persistent, 2.3-2.7 mm long, triangular; buds ovoid to oblong, apex obtuse.

Sepals somewhat spreading at anthesis, 1/4-1/3-connate, 3-4.7 mm long, 3.9-4.5 mm wide, coriaceous, broadly triangular, apex acute, appressed-pubescent abaxially.

Petals pale yellow to creamy white, the inner petals also red at the base *in vivo*; outer petals spreading at anthesis, 11-18.8 mm long, 3-5.9 mm wide at base, 4.9-5.7 mm wide at midpoint, fleshy, oblong-lanceolate to oblong-ovate, flattened and some-

what concave but keeled at apex adaxially, not keeled abaxially, apex obtuse, pubescent toward apex and glabrous toward base adaxially, appressed-pubescent abaxially; inner petals erect at anthesis, 13.1-15.2 mm long, 2.5-3.9 mm wide at base, 2.0-2.4 mm wide at midpoint, fleshy, lanceolate, keeled at apex, flat and corrugated in center adaxially, keeled abaxially, apex acute, base shallowly concave with undifferentiated margin, puberulent on distal ¹/₄ on both surfaces.

Stamens 200-250; fertile stamens 1.4-1.8 mm long, narrowly oblong, anther connective apex 0.2-0.4 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 7-11-locellate, filament 0.3-0.4 mm long; outer staminodes 1.4-1.7 mm long, oblong, apex obtuse; inner staminodes 1.4-1.7 mm long, clavate to oblong, apex obtuse; staminal cone 2.7-3.1 mm in diameter, 1.6-2.0 mm high, completely concealing the ovaries, rim irregularly laciniate.

Carpels 5-7; ovaries *c*. 1.3 mm long, narrowly oblong, pubescent, stigmas free or loosely connivent, 2.6-2.9 mm long, clavate and somewhat falciform, sparsely pilose.

Fruit of up to 5 monocarps borne on a pedicel 4.5-7.3 mm long, 2.5-3.3 mm thick, pubescent; torus 4.7-5.7 mm in diameter, 4.5-5.0 mm high, ovoid to globose; monocarps with glaucous-green exterior *in vivo*, 2.9-5.3 cm long, 1.3-2.0 cm wide, 1.2-2.0 cm thick, ovoid to oblong, sometimes weakly torulose, apex rounded or with a blunt beak 2-4 mm long, base sessile or contracted into a stipe 3-5 mm long, 4-6 mm thick, finely verrucose and wrinkled, with a glaucous bloom, dull to slightly shiny, glabrate; pericarp 0.4-1 mm thick.

Seeds up to 4 per monocarp, in a single row, lying oblique to nearly perpendicular to long axis, 12-14.4 mm long, 9-10.3 mm wide, *c*. 9.5 mm thick, ellipsoid to broadly ellipsoid, somewhat quadrangular in cross-section, light brown, wrinkled and pitted, dull, perichalazal ring visible as a slightly raised line; sarcotesta not detected; aril absent.

Notes

Xylopia australis, sp. nov., is readily identifiable by its relatively large, but narrow, long-acuminate subcoriaceous leaves, with the higher-order venation raised and forming a conspicuous reticulum on both surfaces. The secondary veins frequently unite to form a wavy intramarginal vein. The corrugated surfaces of the inner petals and the glaucous monocarps are unique characters among Madagascar *Xylopia* species. This southern distribution of the species in Madagascar is the basis for the specific epithet.

The collection *Lam & Meeuse 6013* (L, WAG), Tamatave, Rés. Nat. Betampona, 450 m, 19.XII.1938 (fr.), bears monocarps that resemble those of *X. australis*, sp. nov., in the blunt apex, the glabrate surface, and the small number of large seeds. The leaves differ from those of *X. australis*, sp. nov., in being elliptic to obovate, smaller (up to 9.4 cm long), and chartaceous in texture. The monocarps are distinctly stipitate, with a flat truncate apical beak. It has not been re-collected, despite recent plant inventory efforts in the Betampona Reserve.

14. *Xylopia bemarivensis* Diels (Figs 1B; 2D; 14A-K; 16B)

Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 352 (1925). — Type: Madagascar. Prov. Mahajanga ["Madagascaria occidentalis"], Boina: ad rivum Bemarivo superiorem, III.1907 (fr.), Perrier de la Bâthie 4945 (holo-, B!; iso-, P[P00524385]!).

Xylopia decidua Diels, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 353 (1925). — Type: Madagascar. Prov. Mahajanga ["Madagascaria occidentalis"], Boina, bois sablonneux, environs du Mt. Tsitondraina [Tsitondroina], XII.1900 (fl., fr.), Perrier de la Bâthie 1167 (holo-, B!; iso-, P[P030368, P030369]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana, Réserve spéciale d'Ankarana, à 10 km à l'Est du village de Matsaborimanga (Campement des Anglais), 12°54'59"S, 49°06'24"E, 180 m, 9.VI.1995 (fr.), Andrianantoanina et al. 848 (OWU); Ambilobe, Mahamasina, Réserve spéciale d'Ankarana, 12°57'49"S, 49°07'28"E, 100 m, 5.XI.1997 (fr.), Bardot-Vaucoulon 915 (Kn.v.; MO; P[P00309729, P00309730]); Ambilobe, Ambondromihefy, Réserve spéciale d'Ankarana, Mahoro, sentier botanique partie nord est en direction d'Ambalihatsara, 12°51'21"S, 49°13'45"E, 300 m, 22.I.2003 (fl.), Bardot-Vaucoulon et al. 1263 (MO, P[P00455560]); Vovo Village District, c. 6 km from Diego Suarez on Diego Suarez-Vovo village road, and c. 1.5 km S of beach on Indian Ocean, 12°19'05"S, 49°23'07"E, 85 m, 21.IV.1993 (fl., fr.), Harder et al. 1658 (MO, WAG); Diana Region, Ambilobe, Ambakirano, Behefaka, Anjahana, 13°21'56"S, 49°10'04"E, 151 m, 5.VI.2005 (fr.), Hong-Wa 303 (MO, P[P01953785]); Ampasindava, forêt d'Andranomatavy, 13°39'59"S, 47°59'24"E, 285 m, 25.XI.2009 (bud, fr.), Madiomanana et al. MAD 267 (K n.v., MO, P[P0175075]); Sava Region, Sous-préfecture Vohemar, Commune Nosibe, Fokontany Anjiabe, Village Anaborano, 13°04'06"S, 49°54'27"E, 49 m, 7.XII.2004 (fr.), Manjakahery & Sola 72 (MO); 40 km N of Vohemar, near N end of Lac Sahaka, Fir.: Nosibe, Fkt.: Anjiabe, 13°04'45"S, 49°54'17"E, 20 m, 3.XI.2002 (buds), McPherson 18833 (OWU); Analamazava, part of Binara Range, SW of Daraina (Vohemar), 13°15'S, 49°38'E, 200-1180 m, 26.IV.2000 (fr.), Meyers 92 (OWU; P[P02005891]); sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt d'Antsaharaingy, 12°55'N, 49°40'E, 50 m, 28.II.2005 (fl.), Nusbaumer & Ranirison LN 1509 (G, K n.v., MO); Fivondronana: Vohémar, Firaisana: Tsarabaria, Fokontany: Manakana, 13°43'06"S, 50°05'52"E, 15.VII.2003 (fr.), Rabehevitra et al. 358 (MO, OWU, P[P02133052]); Fivondronana: Vohémar, Firaisana: Nosy be, Fokontany: Anjiabe, 13°04'43"S, 49°54'04"E, 11.V.2004 (fr.), Rabehevitra et al. 938 (OWU, P[P01954139]); Fivondronana: Vohémar, Firaisana: Tsarabaria, Fokontany: Manakana, 13°42'46"S, 50°05'25"E, 3 m, 18.V.2004 (fr.), Rabehevitra et al. 1009 (MO, OWU, P[P01954128]); Fiv.: Vohémar, Fir.: Tsarabaria, Fok.: Manakana, 13°42'58"S, 50°05'37"E, 3 m, 24.X.2002 (fl.), Rabenantoandro et al. 1035 (MO, OWU); Fivondronana: Vohémar, Firaisana: Nosibe, Fokontany: Anjiabe, 13°04'43"S, 49°54'04"E, 10 m, 23.II.2003 (fl., fr.), Rabenantoandro et al. 1318 (MO, OWU, P[P06901368]); Fivondronana: Vohémar, Firaisana: Tsarabaria, Fokontany: Manakana, 13°42'49"S, 50°05'13"E, 5 m, 1.III.2003 (bud, fr.), Rabenantoandro et al. 1380 (MO, K n.v., OWU, P[P01987003]); Diana Region, Diana, Ambolobozobe, Ambovomavo, à 1 km W du village d'Ambolobozobe, 12°31'13"S, 49°31'21"E, 24.XI.2007 (fr.), Rakotonandrasana 1217 (OWU, P[P02090377]); Vohemar, Maromokotra, Antsiranana, forêt d'Andavaposa, à 5 km au Sud du village d'Antsaharaingy, 12°54'05"S, 49°38'45"E, 36 m, 11.XI.2005 (fr.), Rakotondrafara et al. 430 (MO); Montagne d'Ambre, versants ouest, 12°35'12"S, 49°05'52"E, 671 m, 25.I.2012 (fl., fr.), Ramandimbimanana & Randimbiarison SDR 318 (K n.v., MO); Diana Region, Antsiranana II, Ankarongana, 12°36'18"S, 49°26'34"E, 258 m, 7.XI.2006 (fr.), Ranaivojaona et al. 1527 (OWU, P[P02090430, P02090431]); Diana Region,

Antsiranana II, Ankarongana, Sahafary, 12°36'18"S, 49°26'34"E, 258 m, 4.XII.2006 (fl., fr.), Ranaivojaona et al. 1651 (MO); Fivondronana: Diego II, Commune: Mahavanona, Montagne des francais, forêt d'Ampitiliantsambo, à 3 heures de marche à pied, à l'Est d'Andranomanitra, 12°23'13"S, 49°23'04"E, 205 m, 14.I.2005 (fl., fr.), Randrianaivo et al. 1155 (K n.v., MO, P[P02133047]); Sava Region, Sous-préfecture Vohemar, Commune Nosibe, Fokontany Anjiabe, Village Anabovano, Campement Andrainginalo, 10 km à l'Est d'Anaborano, 13°04'09"S, 49°54'08"E, 18 m, 11.X.2004 (bud, fr.), Randrianarivelo et al. 159 (K n.v., MO); Diana Region, Sous préfecture Antsiranana II, Commune Mahavanona, Fokontany Andranomanitra, 12°22'05"S, 49°19'37"E, 382 m, 8.II.2005 (fl.), Randrianarivelo et al. 219 (Kn.v., MO); Réserve Spéciale d'Ankarana, sur le Tsingy près de la grotte de chauve-souris et aux alentours, 12°54'43"S, 49°06'39"E, 180 m, 20.II.1994 (fl., fr.), Randrianambolona et al. 48 (MO); sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt d'Antsahabe, 13°13'N, 49°33'E, 345 m, 4.V.2004 (fr.), Ranirison PR 808 (G, K n.v., MO); sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt d'Ankaramy, 13°18'N, 49°40'E, 24.II.2004 (fl.), Ranirison & Nusbaumer PR 475 (G, K n.v., MO); Andrafiabe, Ambolobozobe, 1 km au Nord est d'Ambolobozobe, forêt d'Ampanasagna, 12°31'01"S, 49°32'14"E, 50 m, 1.II.2005 (fl.), Ratovoson et al. 864 (K n.v., MO); Vohemar, Maromokotra, Ankijomantsina, 3 km au Sud d'Ankijomantsina, 13°07'40"S, 49°27'53"E, 100 m, 30.X.2005 (fr.), Ratovoson et al. 1045 (MO, P[P01953997]); Diana Region, Sadjoavato, forêt de Sahafary, 12°36'26"S, 49°26'43"E, 280 m, 8.I.2007 (fl.), Ratovoson et al. 1180 (MO, OWU, P[P01954133]); Ambobaka, 300 m Sud du pont Antomboka, Commune Ambodimanga Ramena, Fivondronana Ambanja, 13°45'12"S, 48°31'19"E, 41 m, 4.XII.2000 (fr.), Razakamalala et al. 49 (MO); Diana Region, Commune Sadjoavato, Fok. Saharenana, forêt d'Andranomadiro SW of Sahafary, 12°36'18"E, 49°26'35"E, 300 m, 14.II.2005 (fr.), Schatz et al. 4271 (MO); Benavone, Ambanja, Service Forestier 10275 (OWU).

Prov. Mahajanga. Maevatanana, Antsiafabositra, Bemanevika, 17°13'28"E, 46°59'37"E, 350 m, 7.V.2005 (fr.), Andrianjafy et al. 1003 (MO, P[P01953993]); Beanka, partie centrale, Antsinginarefy, 17°57'23"S, 44°28'06"E, 329 m, 11.II.2012 (fr.), Bolliger et al. RFB 212 (MO); forêt d'Amparihymikimbo, auprès de l'embouchure de la Mafaika (E de la Baie de Narinda), 28.V.1958 (fr.), Capuron 18540-SF(K); forêt d'Ambondro-Ampasy (Exploitation Loyseau), Canton d'Antonibe, District d'Analalava, 29.X-3.XII.1958 (fl.), Capuron 18798-SF (K); Ambongo, sables, près de Benetsy (riv. g. de la basse Mahevavy), 21.XI.1965 (fl.), Capuron 24263-SF (K); Station forestière d'Ampijoroa, c. 3 km N d'Andranofasika, 16°20'S, 46°51'E, 12.IV.1984 (fr.), Dorr & Koenders 3012 (GH, K n.v., MO, WAG); région Melaky, Beanka, partie sud, 18°01'59"S, 44°28'33"E, 230 m, 7.XII.2012 (fr.), Gautier et al. LG 5964 (K n.v., MO); forêt de Tsiampihy, de Besaraha, de Bemiha et de Soahanina, Leandri et al. 2229 (OWU); Melaky Region, Maintirano, Belitsaka, Ambinda, 18°02'38"S, 44°28'56"E, 232 m, 20.X.2009 (fl.), Letsara et al. LRK 898 (CAS, MO, P[P00722348]); Boriziny (Port-Berg.), Bongolava, on Bongolava mountain, 3 km bifurcation from Port-Bergé, 15°36'49"S, 47°35'21"E, 215 m, 18.III.2010 (fr.), Rajaovelona & Rakotonasolo RJL 166 (K); Station Forestière d'Ampijoroa, piste vers Jardin botanique A[mpijoroa], 16°18'40"S, 46°48'00"E, 200 m, 9.III.1996 (fr.), Rakotomalaza et al. 636 (K n.v., MO, NY); Sofia Region, Boriziny, Port-Bergé, Tsingingia, Marosely, 18 km au Sud Boriziny, 15°38'58"S, 47°35'03"E, 217 m, 16.XI.2004 (fl., fr.), Ramananjanahary 121 (K n.v., MO); Sofia Region, Boriziny, Port-Bergé, Tsingingia, Andranomena II, 15°34'00"S, 47°29'55"E, 115 m, 27.XI.2004 (fl., fr.), *Ramanan*janahary 151 (MO, P[P01954134]); Faritany Mahajanga, Fivondronana Port-Bergé, Bongolava, 17°38'58"S, 47°35'03"Ĕ, 217 m, 17.XI.2004 (buds, immature fr.), Razakamalala et al. 1743 (MO, P[P00903552]); Faritany: Mahajanga, Fivondronana: Port-Bergé, Mampikony, Bongolava, Betaramahamay, forêt sèche sur sable d'Ambohimanga, 15°57'05"S, 47°26'09"E, 232 m, 6.XII.2004 (fl., fr.), *Razakamalala et al. 1834* (A, MO); Bevazaha, canton Tsaramandroso, district Ambato Boeni, 28.XI.1951 (fl.), *Réserves Naturelles 3338* (K as "338", MO, OWU); Ampijoroa, Marovoay, 16.XII.1953 (fl.), *Service Forestier 8066* (K n.v., OWU); forêt Katsijy, Kandreho, Maevatanana, 12.XI.1953 (fr.), *Service Forestier 8073* (OWU); Ampijoroa, Marovoay, 17.XII.1953 (fl., fr.), Service Forestier 8103 (OWU); forêt Mafaijijo, Maintirano, 28.II.1956 (fl.), *Service Forestier 12646* (OWU); Andrianonakanga, Sitampihy, Ambato Boini, 26.IV.1955 (fr.), *Service Forestier 14921* (OWU); Jardin botanique d'Ampijoroa, Ampijoroa, Fokontany Andranofasika, Fivondronana Marovoay, 16°18'S, 46°49'E, 200 m, 25.I.1992 (fr.), *Service Forestier (Comtet) SF 34395* (K n.v., MO).

Prov. Toliara. Atsimo-Andrefana Region, Beroroha à 4 km avant Antsoa, 21°15'43"S, 45°10'04"E, 461 m, 3.XII.2010 (buds, immature fr.), *Andriantiana et al. 1011* (MO); Atsimo-Andrefana Region, Makay Massif, Lake Anosilahy, 21°20'31"S, 45°10'57"E, 415 m, 27.XI.2010 (fl., fr.), *Phillipson et al. 6251* (MO); Atsimo-Andrefana Region, forêt d'Anosilamy, Fokontany Beronono, Commune Beronono, 21°20'30"S, 45°10'53"E, 448 m, 13.I.2010 (fr.), *Razakamalala et al. 5146* (MO, P[P02090409]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Xylopia bemarivensis occurs in northern and western Madagascar, in dry deciduous forest, semi-deciduous forest, and rarely littoral forest on brown or white sand, rarely on clay soils, at elevations from sea level to nearly 700 meters (Fig. 28). Its distribution is discontinuous (Fig. 28), reflecting an actual discontinuity in this vegetation type (Moat & Smith 2007); specimens from the two areas are very similar. Occurring south of 21°S latitude, X. bemarivensis extends further into the dry forests of southwestern Madagascar than any other Xylopia.Specimens with flowers have been collected from October to February and in April, and with fruits from October to June. Seeds were reported to be eaten by the lemur Propithecus tattersalli (Meyers 92), but no additional details were given. Xylopia bemarivensis has the second largest EOO and AOO of any Madagascar Xylopia species, 171046 km² and 172 km², respectively. One of the least likely Xylopia species in Madagascar to be of conservation concern, X. bemarivensis is nevertheless given a preliminary conservation assessment of Data Deficient because we have no information about habitat alteration or population structure or size.

LOCAL NAMES. — Azoambo (*Bardot-Vaucoulon 915*), fandriambarika (*Ramananjanahary 121*), fandribarika (*Réserves Naturelles 3338*), fotsiavadika (*Andrianantoanina et al. 848*), fotsimavo (*Bardot-Vaucoulon et al. 1263*), hazoambo (*Rakotondrafara et al. 430, Service Forestier* (*Comtet*) SF 34395), hazoambolahy (*Hong-Wa 303*), hazomavo (*Randrianarivelo et al. 159*), marohefaka (*Manjakahery & Sola 72*), moranga (*Ratovoson et al. 1045*).

DESCRIPTION

Tree or shrub up to 20 m tall; d.b.h. up to 22 cm.

Twigs short erect-pubescent, the hairs 0.2-0.3 mm long, eventually glabrate; nodes with one or occasionally two axillary branches.

Leaves with larger blades 4.0-9.8 cm long, 1.9-3.4 cm wide, chartaceous, concolorous or slightly paler abaxially, narrowly to broadly lanceolate, oblong, or elliptic, apex obtuse to rounded or occasionally acute, base broadly cuneate to obliquely rounded or subcordate, short-decurrent on petiole, margin flat, not revolute, pubescent, sometimes with hairs only along the midrib or glabrate adaxially, pubescent abaxially; midrib concolorous adaxially, secondary veins weakly brochidodromous, 9-16 per side, diverging at 45-80° from



Fig. 16. – **A**, Fruit of *X. australis*, sp. nov. (*Rakotovao 4575*); **B**, flower of *X. bemarivensis* Diels (*Nusbaumer 8139*); **C**, flower bud of *X. galokothamna*, sp. nov. (*Ratovoson 2065*); **D**, fruit of *X. galokothamna*, sp. nov. (*Ratovoson 2065*); **E**, fruit of plant resembling *X. galokothamna*, sp. nov., but with different pericarp pattern (see text) (*Buerki 20*); **F**, monocarps and leafy shoots of *X. lastelliana* Baill. (*Rakotovao 4603*); **G**, flowers of *X. australis*, sp. nov. (*Schatz 2641*); **H**, monocarps of *X. kalabenonensis* D.M.Johnson, Deroin, & Callmander (*Razafitsalama et al. 1041*). Photos: **A**, **F**, C. Rakotovao; **B**, L. Nusbaumer; **C**, **D**, F. Ratovoson; **E**, M. W. Callmander; **G**, G. E. Schatz; **H**, J. Razafitsalama. **A**, **C**-**H**, used under the terms of the Creative Commons license for Tropicos, the botanical information system at the Missouri Botanical Garden; **B**, L. Nusbaumer (© Conservatoire et Jardin botaniques de la Ville de Genève).

midrib, plane adaxially, slightly raised abaxially, higher-order veins indistinct to slightly raised on both surfaces; petiole 4.5-7 mm long, flat, smooth, pubescent.

Inflorescences axillary or from the axils of fallen leaves on new flushes of growth, 1-flowered, not pedunculate, densely erect-pubescent; pedicels often obliquely bent near midpoint, 4.3-7.1 mm long, 0.5-1.0 mm thick; bracts 2, proximal bract attached near midpoint of pedicel and usually caducous, distal bract subtending sepals and persistent, 1.8-2.0 mm long, ovate to semicircular; buds narrowly oblong, apex obtuse.

Sepals spreading at anthesis, ¹/₃-¹/₂-connate, 1.7-2.3 mm long, 2.4-2.8 mm wide, coriaceous, semicircular, apex broadly acute to obtuse, sericeous to tomentose abaxially.

Petals white, cream-colored, or yellow, the inner petals also with a red blotch at the base *in vivo*; outer petals spreading at anthesis, 9.7-12.2 mm long, 2.0-3.3 mm wide at base, 1.2-1.8 mm wide at midpoint, coriaceous, narrowly lanceolate to lanceolate, keeled at apex adaxially, flat or faintly ridged abaxially, apex acute, densely puberulent except for glabrous base adaxially, densely sericeous except for glabrous base abaxially; inner petals more or less erect at anthesis, 7.3-8.9 mm long, 1.6-2.4 mm wide at base, 0.7-1.0 mm wide at midpoint, coriaceous, linear-subulate, keeled on upper ²/₃ adaxially, keeled abaxially, apex acute, base concave with an undifferentiated margin, puberulent on both surfaces except for the sharply glabrous base.

Stamens 100-120; fertile stamens 1.1-1.3 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm long, shield-shaped to capitate, overhanging anther thecae, glabrous, anthers 9-11-locellate, filament 0.2-0.6 mm long; outer staminodes *c*. 1.1 mm long, oblong or broadly clavate, apex truncate; inner staminodes 0.9-1.1 mm long, oblong or clavate, apex truncate; staminal cone 1.3-2.0 mm in diameter, *c*. 0.8 mm high, completely concealing the ovaries, rim even or slightly laciniate.

Carpels 3-5; ovaries *c*. 0.6 mm long, oblong, pubescent, stigmas loosely connivent, 1.4-1.8 mm long, filiform, with a few hairs at the apices.

Fruit of up to 9 monocarps borne on a pedicel 6-9 mm long, 4.2-5 mm thick, glabrate; torus 7-11 mm in diameter, 6-7 mm high, globose to depressed-globose; monocarps with reddish green or purplish green to red exterior and red endocarp *in vivo*, 2.8-4.6 cm long, 1.3-2.0 cm wide, 1.3-1.6 cm thick, ellipsoid to oblong, weakly torulose, apex obtuse to rounded, base usually contracted into a stipe 3-5 mm long, 3-6 mm thick, verrucose, longitudinally wrinkled, sometimes also with a ridge along the abaxial surface, glabrate; pericarp 0.6-1.2 mm thick.

Seeds up to 7 per monocarp, in two rows, perpendicular to long axis, 9.7-14 mm long, 7.6-10 mm wide, 6.0-6.6 mm

thick, obovoid, oblong, or ellipsoid, irregularly elliptic in cross-section, brown to dark brown, smooth, dull, perichalazal ring not elevated; sarcotesta orange to red *in vivo*, sometimes visible as a white crust on dried seeds; aril absent.

Notes

Xylopia bemarivensis is distinctive among Madagascar species of the genus for its pubescent twigs, thin-textured hairy leaves blunt at the apex and rounded at the base, one-flowered inflorescences with relatively long pedicels, and orange seeds. The only sympatric species of *Xylopia* in these dry forests is *X. sericolampra*, which has subcoriaceous leaves that are truncate at the base, silvery appressed hairs on the buds and perianth, flowers that emerge from leafless branches, and single pear-shaped monocarps.

There is variation in flower color, with mature flowers varying from yellow-green on some specimens to white on others. Petal length is also variable, but in this case petal length can be variable within a single plant: the outer petals on the specimen *Service Forestier 8066 SF* range in length from 9.9 to 12.1 mm, or nearly the full range of variation seen for the species. The flowers are reported by many collectors to be fragrant, on the label of *Gautier et al. LG 5964* as having an "odeur citronnée."

On the basis of its orange to red sarcotesta and thin pubescent leaves, *Xylopia bemarivensis* seems allied to the *Xylopia odoratissima* subgroup of section *Stenoxylopia* distributed across eastern and southern Africa (Johnson & Murray 2018).

15. *Xylopia buxifolia* Baill. (Fig. 17A-K)

Adansonia; Recueil d'Observations botaniques 4: 143 (1864). — Type: **Madagascar**. Without definite locality, *Du Petit-Thouars s. n.* (holo-, P[P030370]!; iso-, P[P030371]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana, Vallée de la Lokoho, près de Ambalavoniho [14.5667°S, 49.7333°E], 75-300 m, 9-10.I.1949 (fr.), Humbert & Cours 22831 (OWU, P[P01757073]); sous-préfecture: Antsiranana II, Commune: Antsalaka, Fokontany: Antsalaka Morafeno, Ampanihy, à 5 km à l'Ouest du village Antsalaka Morafeno, 12°36'22"S, 49°13'33"E, 717 m, 13.XII.2004 (fl.), Rakotondrafara et al. 280 (MO); Sous-Préfecture d'Andapa, Commune Rurale d'Andapa, Forêt Domaniale de Masiaposa, 14°39'20"S, 49°42'20"E, 890 m, 10.XI.1995 (fr.), Ravelonarivo & Lowry 887 (K n.v., MO, OWU); Réserve Spéciale #5, Manongarivo, 30 km SE of Ankaramy, western slopes of Antsatrotro, 14°08'S, 48°21'E, 550 m, 23-25.III.1991 (fl.), Schatz 3220 (K n.v., MO). Prov. Fianarantsoa. Fivondronana: Mahanoro, Firaisana: Ambodibonara, Fokontany: Ambalavontaka, 20°23'26"S, 48°32'43"E, 10 m, 20.IV.2004 (fr.), Ranaivojaona et al. 645 (OWU, P[P01953922]); Manampona, Mananjary, 7.I.1952 (fl.), Service Forestier 5613 SF (P[P01953971]); F. Manampano, Canton Mananjary, Dist. Mananjary, au bord du canal d'Ampangalana, 10 m, 27.VIII.1963 (fr.), Service Forestier 21337 SF (P[P01953944, P02133050]). Prov. Toamasina. Ampasimbe Onibe, Andranotsara, Station Forestière Mahatwara, 17°38'16"-17°38"21"S, 49°29'02"-17°29'11"E, 5-10 m, 24.IX.2002 (fr.), Andriamihajarivo et al. 72 (MO[2 sheets]);

Ampanotoamaizina, 12.XI.1966 (fr.), *Boiteau 505* (K); à Ambila-Lemaitso, 8-10.VIII.1957 (immature fr.), *Capuron 18057-SF* (K); environs de la Baie d'Antongil, W. d'Anandrovola, 100-150 m,

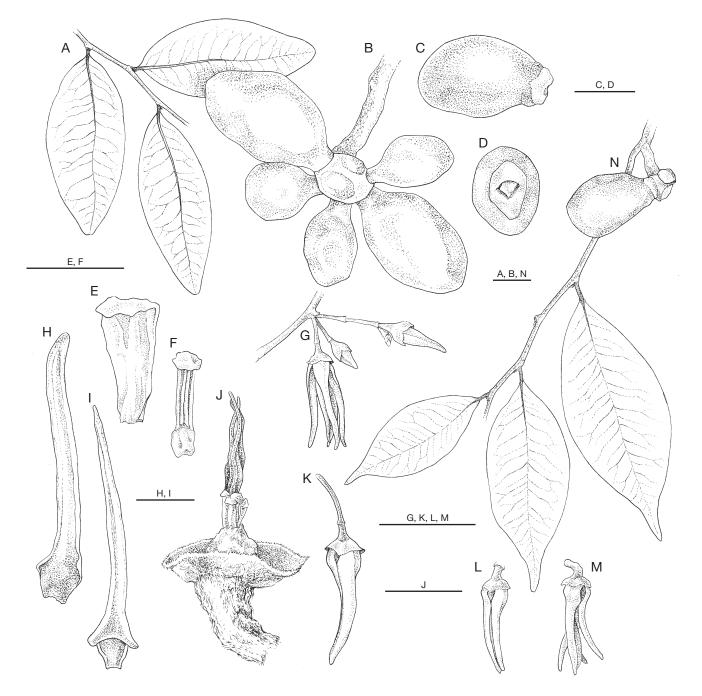


Fig. 17. – Xylopia buxifolia Baill. and X. lemurica Diels. A-K, X. buxifolia; A, leaves; B, fruit; C, seed, side view; D, seed, view of micropylar end; E, outer staminode; F, fertile stamen; G, inflorescence; H, outer petal, adaxial surface; I, inner petal, adaxial surface; J, flower with petals and most of stamens removed to show staminal cone and stigmas; K, bud, side view; L-N, X. lemurica; L, flower bud, side view; M, open flower, side view; N, habit. A-K, from Schatz & Carlson 2861; A, WAG; E, F, H-K, MO, sheet 1 of 2; B-D, G, MO sheet 2 of 2; L-N, from Perrier de la Bâthie 4975 (P). Scale bars: A, B, G, K-N, 1 cm; C, D, 5 mm; E, F, 1 mm; H, I, 3 mm; J, 2 mm.

11.IX.1957 (fr.), *Capuron 18234 SF* (K, P[P01953920]); Toamasina II, Foulpointe, Morarano, Analalava, forêt d'Analalava à 6 km Sud-Ouest de Foulpointe, 17°42'19"S, 49°27'28"E, 50 m, 13.X.2004 (fr.), *Lehavana et al. 142* (K n.v., MO, P[P01953964]); Tamatave, Tampina, Rés. For. Chemins de Fer, 5 m, 21.XII.1938 (fl.), *Lam & Meeuse 6053* (K n.v., L, WAG); environs d'Ambila-Lemaitso, 14.XI.1986 (fr.), Le Thomas 112 (P[P01953984, P01953985]); Toamasina, Ambila-Lemaitso, E of Brickaville, Old Station Forestière, c. 5 km S of town, 18°54'S, 49°07'E, 10 m, 17.I.1999 (fr.), *Lowry & Miller 5138* (K n.v., MO, P[P01953987]); Toamasina, District: Fénérive-Est, Canton: Ampasina, Tampolo, Station forestière de Tampolo, 17°16'52"S, 49°24'33"E, 0-10 m, 2.VII.2001 (fr.), *Ludovic et al. 106* (K n.v., MO, P[P01953968]); Toamasina, Fivondronana: Toamasina II, Firaisana: Ampasimbe, Fokontany: Mahatsara, station forestière de Mahatsara, 17°38'13"S, 49°29'03"E, 2 m, 7.VII.2001 (fr.), *Ludovic et al. 118* (MO, NY, P[P01953979]); Toamasina, Toamasina Dist., vicinity of entrance to Mahatsara Forest Reserve, 1.5 km E of National Highway 5, 9.4 km N of Mahavelona village (Foulpointe), 17°38'S, 49°30'E, 8 m, 24-27.II.1992 (fr.), *Noyes et al. 944* (K n.v., MO, P[P01953958]); près de Tamatave, s. d. (fr.), *Perrier de la Bâthie 14912* (P[P01953941, P01953942, P01953960]); Maroantsetra, Tampolo, Péninsule Masoala, 15°43'S, 49°57'E, 20-50 m, 5.XI.2001 (fr.), *Poncy et al. 1593* (K n.v., MO, P[P00373122]); Toamasina, Fivondronana: Mahanoro, Firaisana:

Ambodibonara, Fokontany: Ambalavontaka, forêt de Nankinana, 20°22'21"S, 48°33'15"E, 41 m, 8.XI.2003 (fl.), Rabehevitra et al. 682 (OWU, P[P01986993]); Toamasina, Fiv. Fénérive Est, Fir. Ampasimanigoro, Fkt. Tampolo, forêt littorale sur sable de Tampolo, 17°17'22"S, 49°24'31"E, 10 m, 30.VI.2001 (fr.), Rabenantoandro et al. 544 (MO, NY, P[P01986995]); Toamasina, Fiv. Soanierana-Ivongo, Fkt. Antanambao-Ambodimanga, forêt littorale sur sable d'Antanambao 16°47'27"S, 49°43'22"E, 5 m, 31.I.2003 (fl.), Rabenantoandro et al. 1184 (Kn.v., MO, NY, P[P01953921]); Toamasina, Soanierana-Ivongo, Antanambao-Ambodimanga, 16°46'08"S, 49°43'53"E, 18.V.2003 (immature fr.), Rabenantoandro et al. 1511 (MO, P[P01071823]); region Analanjirofo, Fénérive-Est, Station forestière Tampolo, 17°16'31"S, 49°24'13"E, 10 m, 20.VI.2009 (fr.), Rakotonasolo et al. RNF 1328 (K); Toamasina, Tampolo (Masoala), Ambanizana, Anjahana, Maroantsetra, forêt de Tampolo, 15°43'45"S, 49°57'38"E, 10 m, 16.X.2001 (fr.), Randrianaivo 680 (MO, NY, P[P01986989]); Toamasina, Tampolo (Masoala), Ambanizana, Anjahana, Maroantsetra, forêt littorale de Tampolo, 15°43'45"S, 49°57'38"E, 10 m, 18.X.2001 (fr.), Randrianaivo 705 (MO, NY, P[P01953957]); District Toamasina II, Commune Rurale Ambodiriana, Fokontany Fontsimavo, village le plus proche Marinidrano, forêt de Vohidakatra, 17°56'41"S, 49°12'34"E, 294 m, 14.XI.2016 (fl.), Rasoanindriana et al. 15 (OWU); Toamasina, Nosy Mangabe, a 520 hectare island in the Bay of Antongil, 5 km S of Maroansetra, 15°30'S, 49°46'E, 200 m, 13-17.XII.1989 (fl., fr.), Schatz & Carlson 2861 (BR, DSM, G, K n.v., MO[2 sheets], NY, WAG); Tampolo-Fénérive, 3.I.1955 (fl.), Service Forestier 12497 SF (K n.v., P[P01953948]); Tampolo, Ampasina, Fénérive, 21.III.1957 (fr.), Service Forestier 16891 SF (P[P01953965, P01953966]); Toamasina, Masoala Peninsula, S of village of Ambanizana in the Andranobe River Watershed, 15°40'24"S, 49°57'51"E, 110-260 m, 29.XII.1994 (fl.), Vasey & Behasy 232 (MO); Toamasina, Masoala Peninsula, S of village of Ambanizana in the Andranobe River Watershed, 15°40'24"S, 49°57'51"E, 110-260 m, 20.XII.1994 (fl.), Vasey & Behasy 241 (MO); Toamasina, Masoala Peninsula, S of village of Ambanizana in the Andranobe River Watershed, 15°40'24"S, 49°57'51"E, 110-260 m, 22.XII.1994 (fl.), Vasey & Velo 269 (K n.v., MO).

Prov. Toliara. Fort Dauphin (Tôlanaro) region, *c*. 115 road km N of town, *c*. 5 km NW of Manantenina, in Forêt d'Analalava, 24°13'S, 47°21'E, 40 m, 29.X.1989 (fr.), *McPherson 14285* (K n.v., MO); Taolagnaro, Région Anosy, Commune Bevoay, Mahatalaky, Sainte Luce, 24°48'46"S, 47°09'25"E, 5 m, 9.XI.2006 (fr.), *Ramison 26* (MO[2 sheets], P[P06490489]); Taolagnaro, Région Anosy, Commune Bevoay, Fokontany Fenoambany, 24°29'45"S, 47°05'52"E, 382 m, 17.XI.2009 (fr.), *Razakamalala et al. 4639* (MO, OWU); Mandena, Fort Dauphin, 5.XII.1952 (fl.), *Service Forestier 7418* (P[P01757072, P01953863]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Xylopia buxifolia is a common component of lowland humid forests in eastern Madagascar, often occurring in littoral forests on sand, at elevations from sea level to 300 meters (Fig. 28); there are scattered specimens from higher elevations (500-900 meters) in northern and northeastern Madagascar. It is a medium-sized or occasionally emergent (Andriamampianina 2013) tree; a narrow crown diameter of 5-6 m for trees 21-26 m tall was reported on the labels of Vasey & Behasy 232 and Vasey & Velo 269. In sandy littoral forest habitats it may occur together with species of Brochoneura (Ludovic 106). Andriamampianina (2013) listed as additional associates Ocotea grayi, Protium madagascariensis, Ravenala madagascariensis, Rinorea arborescens, Tambourissa purpurea, and Trilepisium madagascariense at a field site in Fianarantsoa Province. Specimens with flowers have been collected in January, March, November, and December, and those with fruits from all months of the year; Andriamampianina (2013) reports flowering from November to February and fruiting from January to April at the Fianarantsoa site. With an EOO and AOO of 149 436 km² and 92 km², respectively, X. buxifolia is given a preliminary conservation assessment of Data Deficient, but does not appear to be of immediate conservation concern. Although individual local populations may be threatened, plots at three field sites showed the presence of both mature and regenerating individuals of *X. buxifolia* (Andriamampianina 2013).

LOCAL NAMES. — Fotsy vavo (*Ramison 26*), hazoambo (*Ludovic et al. 118*, *Noyes et al. 944*, *Rabenantoandro et al. 1511*), hazoambo mena (*Ludovic et al. 106*), hazoambo madinidravina (*Rabenantoandro et al. 1184*), ombavy (*Ludovic et al. 118*), ramiavona (*Service Forestier 5613 SF*).

DESCRIPTION

Tree up to 26 m tall, rarely a rounded shrub up to 5 m tall; d.b.h. up to 40 cm.

Twigs red-brown or orange-brown pubescent, the hairs 0.1-0.4 mm long, eventually glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 2.8-5.7 cm long, 1.2-2.7 cm wide, chartaceous to subcoriaceous, slightly discolorous, purplish green to light olive-brown and often somewhat shiny adaxially, dull and tan abaxially, elliptic, obovate, oblanceoleate, or occasionally lanceolate, apex obtuse to rounded and usually retuse or emarginate, base cuneate to broadly cuneate and occasionally short-decurrent on petiole, margin flat or slightly revolute, glabrous or with a few hairs along the midrib adaxially, secondary veins weakly brochidodromous to camptodromous, 7-13 per side, diverging at 45-60° from midrib, these and higher-order veins indistinct to slightly raised abaxially; petiole 2-4 mm long, shallowly canaliculate, longitudinally wrinkled, sparsely appressed-pubescent.

Inflorescences axillary, rarely supra-axillary, commonly from axils of fallen leaves, 1-4-flowered, pedunculate, pubescent; peduncle 1.2-2 mm long; pedicels 2-4 per peduncle, 4.5-6.8 mm long, 0.5-1.0 mm thick; bracts 2-3, spaced evenly along pedicel, caducous or the distal bract sometimes persistent, 0.5-1.3 mm long, ovate; buds lanceolate, apex acute.

Sepals erect to slightly spreading at anthesis, ½-½-connate, 1.9-2.6 mm long, 1.9-2.4 mm wide, coriaceous, broadly ovate, apex acute, sparsely appressed-pubescent abaxially.

Petals pale yellow, sometimes with a red blotch at the base *in vivo*; outer petals slightly spreading at anthesis (ex photographs of *Schatz et al. 2861*), 9.8-16.1 mm long, 2.3-2.8 mm wide at base, 1.2-1.8 mm wide at midpoint, fleshy, linear to linear-lanceolate, keeled only at apex adaxially, keeled abaxially, apex obtuse, puberulent except for the glabrous base adaxially, sparsely appressed-pubescent or puberulent abaxially; inner petals slightly spreading at anthesis, 8.5-14.8 mm long, 1.5-1.8 mm wide at base, 0.7-0.8 mm wide at midpoint, fleshy, linear, longitudinally keeled adaxially, with a slight longitudinal keel abaxially, apex acute, base concave into a short claw, margin undifferentiated but with a transverse bilobed thickening at the widest point, puberulent except for the glabrous claw adaxially, pubescent except for the glabrous basal lobes abaxially.

Stamens 100-120; fertile stamens 0.9-1.3 mm long, narrowly oblong, anther connective apex *c*. 0.2 mm long, capitate or shield-shaped, overhanging anther thecae, papillate, anthers 8-11-locellate, filament 0.2-0.4 mm long; outer staminodes 0.9-1.0 mm long, broadly clavate to obtriangular, apex rounded, truncate, or slightly emarginate; inner staminodes 0.8-0.9 mm long, oblong to clavate, apex truncate to slightly emarginate; staminal cone 1.1-1.4 mm in diameter, 0.6-0.7 mm high, completely concealing the ovaries, rim irregularly laciniate.

Carpels 6-8; ovaries *c*. 1 mm long, narrowly oblong, sericeous, stigmas connivent, 1.9-3.3 mm long, filiform, glabrous to sparsely pubescent.

Fruit of up to 7 monocarps borne on a pedicel 5-13 mm long, 3.5-5 mm thick, sparsely pubescent to glabrate; torus 8-14 mm in diameter, 6.3-9 mm high, depressed-globose; monocarps with greenish red, brownish red, red, or orange exterior and red endocarp *in vivo*, 2.3-4.0 cm long, 1.4-2.3 cm wide, 1.0-2.2 cm thick, oblong to ovoid, not torulose, apex rounded, obtuse, or truncate, base sessile or contracted into a stipe 2-4 mm long, 5-10 mm thick, finely verrucose, obliquely wrinkled, dull to somewhat shiny, sometimes lenticellate, occasionally longitudinally ridged, glabrate; pericarp 0.8-1.5 mm thick.

Seeds up to 8 per monocarp, in two rows, perpendicular to long axis, (7-) 8.5-12.6 mm long, 5.5-6.9 mm wide, 3.5-6.5 mm thick, oblong to ellipsoid but slightly narrowed toward the micropylar end and expanded into a hard donut-shaped ring, elliptic to wedge-shaped in cross-section, light brown, smooth, dull, perichalazal ring visible as a faint ridge; sarcotesta green *in vivo*; aril absent.

Notes

Among Madagascar *Xylopia* species with small but broad leaves *X. buxifolia* is most similar to *X. lamii* and *X. lemurica* in the needle-like inner petals and the relatively small but broad and blunt monocarps. It shares with *X. lamii* the obtuse to rounded and emarginate leaf apex, and the thick fruit pericarp, but it lacks the denser and more persistent reddish-brown indument of the twigs, abaxial leaf surfaces, and inflorescences of that species. The blunt leaf apex, in addition to the finer shorter hairs of twigs and leaves, distinguish it from *X. lemurica*, which has a pronounced leaf acumen and longer hairs on the twigs and abaxial leaf surfaces.

There is, however, ecological and morphological variability within *X. buxifolia* as circumscribed here, and with closer field and laboratory study it is likely to prove to be a complex of species rather than a single variable one. For example, on the collection *Service Forestier 12497 SF* from Tampolo-Fénérive many of the leaves are acute at the apex and lanceolate to elliptic and conspicuously appressed-pubescent abaxially, but the norm for this region is obovate leaves with rounded and emarginate apices and with fine sparse appressed hairs on the abaxial surface. In the Masoala Peninsula region the leaves, while still obtuse and notched at the apex, are often larger and more lanceolate. Several specimens from Antsiranana Province, all collected from elevations above 500 meters, have subcoriaceous to coriaceous leaves that are more lanceolate and taper toward the apex while still being notched at the tip, as well as denser pubescence on the twigs and inflorescences. The single fruiting collection among these higher elevation specimens has a distinct stipe on the glabrate and wrinkled monocarps and its seeds lack the donut-shaped ring on the base of the seed, which is a consistent feature across the lowland specimens.

No locality is given on the label for the type specimen. According to Lasègue (1845), Du Petit-Thouars spent six months in Madagascar. A number of his plant descriptions were based on plant collections from Foulpointe (Mahavelona) made in 1794-1795 (Du Petit-Thouars 1804), so it is likely that the specimen was collected from that general region.

16. *Xylopia capuronii* Cavaco & Keraudren (Fig. 18A-D)

Bulletin de la Société botanique de France 103: 274 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est'], forêt orientale, bassin de l'Anketrabe, affluent r. g. de la Rantabe, au N de Sahajinja, vers 700 m d'alt., 6.III.1954 (fl.), *Capuron 9110* (holo-, P[P030372]!; iso-, P[P00697845, P030373, P030374, P030375]!, TEF[photo]!, WAG!).

MATERIAL EXAMINED. — **Madagascar. Prov. Toamasina**. Forêt orientale, environs de la baie d'Antongil, bassin de la Fananehana, massif de l'Androrona [*c.* 15°51'S, 49°30'15"SE], vers 700 m d'altitude, II.1954 (fl. bud, fr.), *Capuron 8997* (P[P01986985, P01986986, P01987227, P01987228, P01987229]); Antsinanana, Ambodiriana, Andrantambe, Rendrirendry, Betampona RNI, 17°55'27"S, 49°11'59"E, 414 m, 10.IV.2010 (buds), *Razakamalala et al. 5372* (to be distributed to MO, P, TAN); forêt Tsikambolozatsy-Mananara, village Ankarany, Canton Antsirabe, Dist. Mandritsara, 13.IV.1956 (st.), *sine coll. 107-R-301* (P[P01986987, P01986988]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia capuronii* occurs in humid lowland forest at elevations of 414-700 m in northeastern to eastern Madagascar (Fig. 28). Specimens with flowers or buds have been collected from February to April, and with fruits in February. A preliminary conservation assessment of Critically Endangered is assigned, based on IUCN Criterion D. The species has EOO and AOO values of 3846 km² and 16 km², respectively. The type locality appears to fall within the boundaries of the Makira Natural Park, but the species has not been re-collected there since 1956; the more recent collection from the Betampona Reserve both extends the known distribution of *X. capuronii* significantly southward and indicates another population within a protected area.

LOCAL NAME. — Hazoambomena (Tsimihety, 107-R-301).

DESCRIPTION

Tree up to 15 m tall; d.b.h. up to 45 cm.

Twigs densely pubescent with persistent erect dull red hairs, the hairs 0.4-0.6 mm long; nodes with a single axillary branch.

Leaves with larger blades 9.8-14.5 cm long, 2.5-4.5 cm wide, coriaceous to subcoriaceous, slightly discolorous, olive gray and shiny adaxially, brownish gray and dull abaxially, narrowly oblong to elliptic, apex acuminate, the acumen 5-9 mm long, base broadly cuneate, not decurrent on petiole, margin revolute, glabrous except for the pubescent midrib adaxially, densely dull red erect-pubescent abaxially, especially pronounced on the midrib and margins *in vivo*; midrib darkened abaxially; secondary veins weakly brochidodromous, 12-16 per side, diverging at 50-80° from midrib, these and higher-order veins forming a slightly raised reticulum on both surfaces; petiole 5-10 mm long, canaliculate, slightly wrinkled, densely dull red erect-pubescent.

Inflorescences axillary, 1-2-flowered, arising from axils on separate pedicels, densely covered with dull red hairs; pedicels 5-8 mm long, 1.6-2 mm thick; bract 1, subtending the sepals, persistent or caducous, 4.2-4.5 mm long, broadly ovate; buds ovoid, apex obtuse to short-acuminate.

Sepals erect or slightly spreading, *c.* ¹/₃-connate, 5-6 mm long, 6-7 mm wide, coriaceous, broadly ovate, apex obtuse, densely dull red-pubescent abaxially.

Petals with color *in vivo* and position at anthesis unknown; outer petals 11-13 mm long, 6.1-7.2 mm wide at the base, 3.3-4.4 mm wide at midpoint, fleshy, lanceolate, apex acute, covered with short appressed hairs and dense glandular punctations except for the glabrous base adaxially, appressed-pubescent abaxially; inner petals 10-10.5 mm long, 5-6.1 mm wide at base, 1.7-2.2 mm wide at midpoint, fleshy, lanceolate, somewhat subulate, puberulent on both surfaces.

Stamens numerous; staminal cone concealing the lower half of the ovaries.

Carpels *c*. 18; ovaries *c*. 1 mm long, narrowly ellipsoid, covered with long sparse white hairs, stigmas loosely connivent, 3 mm long, covered with long white tangled ascending hairs.

Fruit of up to 9 monocarps borne on a pedicel 10-11 mm long, *c*. 5 mm thick, pubescent; torus *c*. 10 mm in diameter, *c*. 7 mm high, irregularly depressed-globose; monocarps with color *in vivo* unknown, 2.3-3.1 cm long, 1.5-1.9 cm wide, 1.3-1.8 cm thick, oblong, obovoid, or pyriform, sometimes slightly torulose, apex rounded, base sessile but gradually narrowed to point of attachment, obliquely wrinkled, dull, sparsely dull red pubescent; pericarp *c*. 1.5 mm thick.

Seeds up to 6 per monocarp, in two rows, oblique to nearly perpendicular to long axis, 12.4-14 mm long, 9-10.1 mm wide, 6-6.9 mm thick, flattened-ellipsoid, narrowly elliptic in cross-section, brown or olive-colored, finely pitted, dull or slightly shiny, perichalazal ring visible but not raised; presence of sarcotesta undetermined; aril absent.

Notes

Xylopia capuronii may be separated from other Madagascar species by the conspicuous dull red indument on all parts, as well as the coriaceous to subcoriaceous narrowly oblong to elliptic leaves with revolute margins. In the short broad petals, and the short-stipitate to sessile and slightly compressed monocarps it is most similar to *X. lokobensis*, sp. nov., which has thinner leaves with flat margins, and a yellowish brown rather than dull red indument.

17. *Xylopia carinata* D.M.Johnson & N.A.Murray, sp. nov. (Fig. 19J-Q)

Species resembling *X. capuronii* and *X. lokobensis*, sp. nov., in the subcoriaceous leaves, sepals exceeding 4 mm in length, and broad acute outer petals, but differing from the former in the recurved rather than strongly revolute leaf margins and the sparse yellow-brown rather than dense dull red indument of the twigs and leaves, from the latter in the longer pubescence of the twigs and the recurved rather than flat leaf margins, and from both species in the more pronounced keel on the abaxial surface of the outer petals.

TYPE. — **Madagascar. Prov. Toamasina** ["Est"], sur sables de Mangalimaso à l'ouest de Foulpointe, 29.X.1963 (fl.), *Capuron 22777-SF* (holo-, P[P00524381]!; iso-, A!, K![K001208446, K001208447]).

PARATYPE. — Madagascar. Prov. Antsiranana ["Est (Nord)"], forêt d'Analamateza, au Sud d'Antsirabe-Nord, 25-27.III.1967 (fl.), *Capuron 27564-SF* (P[P01585923, P01585924]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia carinata*, sp. nov., is known from only two collections, both from northeastern Madagascar in humid forest at elevations up to 200 meters, one collection on sand (Fig. 28). It is possible that *X. carinata*, sp. nov., is a habitat specialist, as the type specimen was collected from sublittoral forest on sand, to which a number of other Madagascar *Xylopia* species appear to be restricted, but the paratype specimen label does not give any habitat information and was collected some distance inland. The collections, both with flowers only, were collected in March and in October. The AOO of 8 km² and its known occurrence at only two localities make this a species of conservation concern, and it is given a preliminary assessment of Endangered (Table 2).

DESCRIPTION Tree up to 20 m tall.

Twigs yellowish brown-pubescent, the hairs 0.1-0.5 mm long, eventually glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 7.5-9.7 cm long, 2.6-4.0 cm wide, subcoriaceous, discolorous, olive-gray to dark brown adaxially, brown abaxially, oblong to oblong-elliptic, apex acute to acuminate, the acumen 5-8 mm long, base broadly cuneate to rounded, short-decurrent on petiole, margin recurved, pubescent along midrib but otherwise glabrous adaxially, sparsely appressed-pubescent, hairs densest on the midrib abaxially; midrib concolorous or darkened toward base adaxially, secondary veins brochidodromous, 11-15 per side, diverging at 60-70° from midrib, these and higher-order veins slightly raised to indistinct on both surfaces; petiole 4-8 mm long, canaliculate to semi-terete, wrinkled, pubescent.



Fig. 18. – Plate showing illustration of Xylopia capuronii Cavaco & Keraudren (A-D), reproduced from Cavaco & Keraudren (1958).

Inflorescences axillary or from axils of fallen leaves, occasionally pseudoterminal from the abortion of the terminal bud, 1-2-flowered, not pedunculate, yellowish brown-pubescent; pedicels 2.5-12.1 mm long, 1.0-1.8 mm thick; bracts 2, one attached near pedicel midpoint and caducous, the other just proximal to the sepals and persistent, 3.3-4.9 mm long, broadly ovate to semicircular; buds lanceolate, apex acute.

Sepals erect to spreading at anthesis, ¹/₄-¹/₃-connate, 4.5-5.5 mm long, 4.6-6 mm wide, coriaceous to slightly fleshy, broadly ovate, apex acute to obtuse, densely brown-pubescent abaxially.

Petals yellowish *in vivo*; outer petals probably slightly spreading at anthesis, 16-25 mm long, 5.2-6.0 mm wide at base, 2.9-3.7 mm wide at midpoint, slightly fleshy, lanceolate, keeled on apical ½ but otherwise flat adaxially, keeled abaxially, apex acute to obtuse, densely puberulent except for the glabrous base adaxially, velutinous abaxially; inner petals probably with apices spreading at anthesis, 10.2-17 mm long, 3-4.3 mm wide at base, 1.2-1.7 mm wide at midpoint, slightly fleshy, lanceolate, keeled on apical ½ adaxially, sharply keeled abaxially, apex acute, base concave with undifferentiated or slightly thickened margin, densely puberulent except for glabrous base on both surfaces.

Stamens 120-200; fertile stamens 1.3-1.8 mm long, narrowly oblong, anther connective apex *c*. 0.4 mm long, hemispherical, overhanging anther thecae, long-papillate, anthers 7-9-locellate, filament 0.2-0.5 mm long; outer staminodes 1.7-1.8 mm long, clavate, apex obtuse, truncate, or emarginate; inner staminodes 1.4-1.7 mm long, narrowly oblong, apex truncate to obtuse; staminal cone 1.3-3.0 mm in diameter, 0.8-1.3 mm high, concealing all but apical ¹/₃ of ovaries, rim irregularly laciniate.

Carpels 6-17; ovaries *c*. 0.8-1.8 mm long, narrowly oblong, pubescent, stigmas connivent, 2.4-3.2 mm long, narrowly clavate, glabrous or hairy at the apices.

Fruits and seeds unknown.

Notes

The keel on the abaxial surface of the outer petals, for which *Xylopia carinata*, sp. nov., is named, is conspicuous in both of the collections. In the type collection some flowers arise at the proximal nodes of an expanding axillary shoot from which the subtending leaves have precociously fallen, giving the appearance of a multi-flowered inflorescence. *Xylopia carinata*, sp. nov., is a member of the group of Madagascar *Xylopia* species with clavate stigmas, and, as noted in the diagnosis, is most similar to *X. capuronii* and *X. lokobensis*, sp. nov. The type specimen was determined by Keraudren as *X. ghesquiereana*, but it does not have the linear petals and barbate leaf midrib and leaf margins found in that species.

Fruits and seeds are not known for this species. However, two *Xylopia* collections with fruits, *Capuron 18178 SF* (P[P01986948, P01986949]) from Rantolava, NW de Tampolo – Fénérive, 1.IX.1957, and *Service Forestier 15268-SF* (P[P01986952]), Manakara, 27.VIII.1955, are tentatively placed here, as the leaves, while more chartaceous, are similar in size and indument to those of *X. carinata*, sp. nov., and the specimens were both collected from coastal locations in the general area of the type locality. The collection *Service Forestier 15268-SF* is further noteworthy in including a mass of monocarps that have dehisced. The monocarps of both specimens are ellipsoid and sparsely pubescent. A photograph posted on iNaturalist in 2017, taken in the Analalava Nature Preserve near the type locality, shows a similar mass of dehisced monocarps, as well as an orange sarcotesta on the seeds (Fig. 2C).

18. *Xylopia danguyella* Ghesq. ex Cavaco & Keraudren (Fig. 20D-H)

Bulletin du Muséum national d'Histoire naturelle (Paris), Série 2, 29: 351 (1957). — Type: Madagascar. Prov. Toamasina ["Centre"], forêt d'Analamazaotra, I.1919 (fr.), Ramanantoavolana (Thouvenot) 94 (lecto-, here designated, P[P030380]!; iso-, P[P030377, P030378]!).

MATERIAL EXAMINED. — **Madagascar. Prov. Antsiranana.** Préfecture d'Antalaha, Sous-Préfecture d'Andapa, Commune rurale de Bealampona, village de Mandritsarahely, Sud-Ouest d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, suivant la piste vers Ranomafana, 5.5 km Sud-Ouest de Befingotra, 14°45'03"S, 49°30'03"E, 875 m, 18.X.1994 (fr.), *Ravelonarivo et al. 460* (MO, OWU).

Prov. Toamasina. Alaotra-Mangoro Region, Moramanga, Ambatovy, Andasibe, Menalamba, Analamay forest, 18°47'48"S, 48°26'26"E, 1058 m, 11.X.2005 (fr.), *Antilahimena et al. 3940* (K n.v., MO, P[P01986964]); Est (confins du Centre, base du rocher de l'Andriandavibe entre Périnet et Anevoke, 21.XII.1965 (buds), *Capuron 24356 SF* (A, K n.v., P[P00524376]); forêt d'Analamazaotra, s. d. (fl.), *Louvel 220* (P[P030381]); Fivondronana: Ambatondrazaka, Commune: Antanandava, 1 km à l'Ouest du Parc national de Zahamena, 17°30'25"S, 48°46'04"E, 860 m, 5.XII.2002 (fr.), *Rakotondrajaona et al. 261* (P[P01986982]); Perinet, s. d. (fr.), *Service Forestier 2630* (P[P01986962]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia danguyella* is restricted to eastern Madagascar, in humid lower montane forest at elevations from 800 to 1050 meters (Fig. 28). A specimen with flower buds was collected in December, and specimens with fruits have been collected in January, October, and December. With an EOO and AOO estimated as 2191 km² and 28 km², respectively, *X. danguyella* is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAMES. — Fontsimavo (*Ramanantoavolana (Thouvenot) 94*), hazoambo (*Antilahimena et al. 3940*), hazoamboa (*Louvel 220*).

DESCRIPTION

Tree up to 25 m tall; d.b.h. up to 30 cm.

Twigs densely brown-pubescent, the hairs 0.2-0.4 mm long, becoming glabrate; nodes with one or occasionally two axillary branches.

Leaves with larger blades 8.7-15.0 cm long, 2.9-6.0 cm wide, coriaceous to subcoriaceous, discolorous, brownish or purplish black adaxially, brown abaxially, oblong to lanceo-

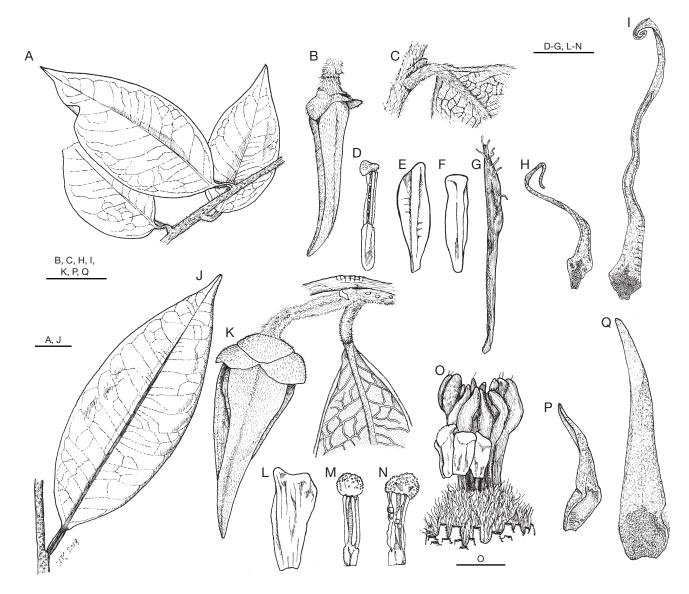


FIG. 19. — *Xylopia ghesquiereana* Cavaco & Keraudren and *X. carinata*, sp. nov.: **A-I**, *X. ghesquiereana*; **A**, habit; **B**, flower bud, side view; **C**, close-up of leaf base; **D**, fertile stamen; **E**, outer staminode, abaxial view; **F**, inner staminode, abaxial view; **G**, stigma, side view; **H**, inner petal, adaxial view, slightly oblique; **I**, outer petal, adaxial view; **J-Q**, *X. carinata*, sp. nov.; **J**, leaf, adaxial view of flower bud and abaxial view of leaf base; **L**, outer staminode, abaxial view; **M**, **N**, fertile stamens, abaxial view; **O**, stigmas, with inner staminodes adhering at the base, apical portions of ovaries, and rim of staminal cone, all in side view; **P**, inner petal, oblique view of adaxial surface; **Q**, outer petal, adaxial view. **A-I**, from *R. N. 5440 bis* (P); **J**, **K**, **M**, **P**, **Q**, from *Capuron 22777* (P); **L**, **N**, **O**, from *Capuron 22777* (A). Scale bars: A, J, 1 cm; B, C, H, I, K, P, Q, 5 mm; D-G, L-O, 1 mm.

late, ovate-oblong, or elliptic, apex acuminate, the acumen 4-12 mm long, base obliquely rounded to broadly cuneate, short-decurrent on petiole, margin slightly recurved, glabrous adaxially, sparsely appressed-pubescent to glabrate abaxially; midrib usually darkened toward base adaxially, secondary veins brochidodromous and somewhat arcuate, 11-17 per side, diverging at 60-70° from midrib, these and higher-order veins indistinct to slightly raised adaxially, raised and forming a conspicuous reticulum abaxially; petiole 4-8 mm long, semi-terete, longitudinally wrinkled, pubescent.

Inflorescences axillary or from the axils of fallen leaves, 1-3-flowered, pedunculate or not, densely brown-pubescent; peduncle 1 mm long or pedicels arising separately from leaf axil; pedicels 2 per peduncle, 3.5-7.5 mm long, 1.0-1.8 mm

thick; bracts 2, one bract near midpoint and the other just proximal to the sepals, caducous or persistent, 1.8-2.2 mm long, semicircular; buds lanceolate, apex obtuse.

Sepals slightly spreading at anthesis, *c*. ¹/₃-connate, 2.1-2.9 mm long, 2.7-3.2 mm wide, coriaceous, broadly triangular, apex acute to rounded, densely brown-pubescent abaxially.

Petals with color *in vivo* unknown; outer petals with position at anthesis unknown, 13.0-13.7 mm long, 3.1-3.9 mm wide at base, *c*. 2.5 mm wide at midpoint, slightly fleshy, lanceolate, flat adaxially, weakly keeled abaxially, apex obtuse, densely gray-puberulous except for the glabrous base adaxially, densely brown-pubescent abaxially; inner petals with position at anthesis unknown, 10.6-11.3 mm long, 2.7-3.2 mm wide at

base, *c*. 1.5 mm wide at midpoint, slightly fleshy, lanceolatesubulate, slightly keeled on both surfaces, apex acute, base concave with undifferentiated margin, densely gray-puberulent except for glabrous base on both surfaces.

Stamens 50-60; fertile stamens 1.3-1.4 mm long, narrowly oblong, anther connective apex *c*. 0.3 mm long, shield-shaped to capitate, overhanging anther thecae, papillate, anthers 8-11-locellate, filament *c*. 0.4 mm long; outer staminodes 1.5-1.7 mm long, clavate, apex obtuse to rounded; inner staminodes 1.3-1.5 mm long, oblong-clavate, apex rounded; staminal cone 1.3-1.9 mm in diameter, 0.8-1.0 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels *c*. 6; ovaries *c*. 1 mm long, oblong, densely pubescent, stigmas connivent, *c*. 3.3 mm long, filiform, uniformly pilose.

Fruit of up to 11 monocarps borne on a pedicel 6-11 mm long, *c*. 5 mm thick, glabrate; torus 13-14 mm in diameter, 11-12 mm high, depressed-globose to pyramidal; monocarps with green exterior *in vivo*, 4.2-6.5 cm long, 2.3-3.3 cm wide, 1.9-3.2 cm thick, oblong, not torulose, apex rounded, base sessile or sometimes contracted into a stipe 3 mm long, 11 mm thick, slightly wrinkled, lenticellate, glabrate or with scattered brown pubescence; pericarp 6-7 mm thick.

Seeds *c*. 8 per monocarp, in two rows, lying more or less perpendicular to long axis, *c*. 17.2 mm long, *c*. 10.4 mm wide, *c*. 7.5 mm thick, oblong-ellipsoid, broadly elliptic in crosssection, brown, smooth, dull, perichalazal ring not evident; presence of sarcotesta not determinable; aril absent.

Notes

Xylopia danguyella is readily distinguished from other lower montane *Xylopia* species in eastern Madagascar by the much larger and more leathery leaves. The flowers are relatively small, the outer petals reaching a length of 13.7 mm, and have only 50-60 stamens, the lowest number of any Madagascar species. The monocarps, attaining a length of 5.5 cm, are some of the largest of any Madagascar *Xylopia* species, exceeded only by those of *X. anomala*, sp. nov.

The specimen *Louvel 220* at P was marked as the holotype, and indeed matches the description in the protologue more closely than does *Thouvenot 94*. Nonetheless, *Thouvenot 94* is cited as the type in the protologue and that designation must be accepted. No sheet of *Thouvenot 94* was designated as the holotype, however, so a lectotype has been designated here.

19. *Xylopia dielsii* Cavaco & Keraudren (Fig. 21G-K)

Bulletin de la Société botanique de France 103: 277 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est"], forêt de Tampolo, au nord de Fénérive, XI.1953 (fl.), *Capuron* 8627 (holo-, P[P030383]!; iso-, OWU!, P[P030384, P030385]!, TEF[photo]!). MATERIAL EXAMINED. — **Madagascar. Prov. Toamasina**. Atsinanana Region, Mahavelona/Foulpointe, Morarano, Analalava, 17°42'35"S, 49°27'02"E, 24 m, 14.II.2008 (fr.), *Andriamiarinoro 124* (OWU, P[P00847930]); Soanierana Ivongo, 27.XII.1949 (fl.), *Service Forestier 2380* (P[P01986980]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia dielsii* is restricted to the coast of a small area of northeastern Madagascar (Fig. 28). It seems to be yet another microendemic species of the littoral and sublittoral humid forest on sand that occurs along the eastern Madagascar coast. Specimens with flowers have been collected in November and December, and with fruits in February. Known from only three localities, and with an EOO and AOO of 461 km² and 12 km², respectively, *X. dielsii* is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Hazoambo (Andriamiarinoro 124, Service Forestier 2380).

DESCRIPTION Tree up to 15 m tall.

Twigs glabrous or with a few fine hairs < 0.1 mm long; nodes with one or often two axillary branches.

Leaves with larger blades 5.9-10.9 cm long, 2.8-4.3 cm wide, chartaceous, drying gray to black on both surfaces, shiny adaxially, dull abaxially, obovate, oblanceolate, or oblong-obovate, apex cuspidate to acuminate, the acumen 4-6 mm long, base rounded to broadly cuneate, short-decurrent on petiole, margin flat, not revolute, glabrous on both surfaces; midrib paler toward base adaxially, secondary veins weakly brochidodromous and somewhat arcuate, 11-16 per side, diverging at 50-90° from midrib, these and higher-order veins strongly raised and forming a conspicuous reticulum on both surfaces; petiole 8-14 mm long, narrowly but deeply canaliculate, slightly wrinkled, glabrous or with a few hairs.

Inflorescences axillary, 1-2-flowered, not pedunculate, glabrous; pedicels arising separately from the axil, 5.7-10.5 mm long, 0.9-1.2 mm thick; bracts 3, one near the pedicel base, one just proximal to the pedicel midpoint, and one just distal to the pedicel midpoint, usually persistent or sometimes the lower bracts caducous, 0.8-1.7 mm long, ovate to triangular; buds linear-lanceolate, apex obtuse.

Sepals spreading at anthesis, *c*. ¹/₄-connate, 1.4-1.8 mm long, 1.9-2.1 mm wide, coriaceous, semicircular, apex acute to rounded, ciliate near margin but otherwise glabrous abaxially.

Petals with color *in vivo* unknown; outer petals with position at anthesis unknown, 14.5-20 mm long, 2.7-3.7 mm wide at base, 1.2-1.5 mm wide at midpoint, slightly fleshy, lanceolate, flat adaxially, weakly keeled abaxially, apex obtuse, densely puberulent except for the glabrous base adaxially, densely pubescent abaxially; inner petals with position at anthesis unknown, 11.8-18.4 mm long, 1.8-2.5 mm wide at base, 0.5-0.7 mm wide at midpoint, slightly fleshy, linear, slightly keeled on apical ½ adaxially, slightly keeled abaxially, apex acute, base concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces.



Fig. 20. – Plate including illustration of Xylopia danguyella Ghesq. ex Cavaco & Keraudren (D-H), reproduced from Cavaco & Keraudren (1958).

Stamens 80-160; fertile stamens 1.1-1.3 mm long, narrowly oblong, anther connective apex *c*. 0.2 mm long, hemispherical, overhanging anther thecae, long-papillate, anthers 7-9-locellate, filament 0.4-0.5 mm long; outer staminodes 1.3-1.6 mm long, clavate, apex obtuse; inner staminodes sometimes with reduced anther thecae, 1.1-1.2 mm long, oblong, apex rounded to truncate; staminal cone 1.3-1.5 mm in diameter, 0.6-1.1 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 5-6; ovaries *c*. 1 mm long, oblong, densely pubescent, stigmas loosely connivent, 2.3-2.5 mm long, clavate to narrowly oblong, glabrous or with a few hairs at the tips.

Fruit of up to 7 monocarps borne on a pedicel 13-20 mm long, *c*. 2 mm thick, glabrous; torus *c*. 4.6 mm in diameter, *c*. 4.1 mm high, globose; monocarps with yellowish violet exterior *in vivo*, endocarp color unknown, 4.3-4.6 cm long, *c*. 1.1 cm wide, *c*. 0.8 cm thick, narrowly oblong, slightly falciform and torulose, apex obtuse, formed into beak 2-3 mm long, base contracted into a stipe 11-15 mm long, 3.7-4 mm thick, strongly and obliquely wrinkled, shiny, glabrate; pericarp *c*. 0.5 mm thick.

Seeds up to 3 per monocarp, in a single row, oblique to long axis, 8.8-11.8 mm long, *c*. 5.2 mm wide and thick, narrowly ellipsoid, circular in cross-section, light brown, smooth, dull, perichalazal ring not evident; presence of sarcotesta undeterminable; aril absent.

Notes

Xylopia dielsii is a distinctive species, standing apart from others in Madagascar in its virtual lack of hairs on the vegetative parts, the long deeply canaliculate petioles, and the relatively long pedicels.

The vegetative features of Andriamiarinoro 124 accord well with the type collection, but its fruit, which is narrowly oblong and over 4 cm in length but only about 1 cm wide and glabrous, does not agree with the protologue description of the fruit of X. dielsii, which is given as "Fructus obovoideus 3 cm. longus 2 cm. latus pilosus." A fruit of the latter description has not been found among the herbarium material of this species. Neither does the fruit of Andriamiarinoro 124 match the fruit description of *X. dielsii* given by Cavaco & Keraudren (1958): "Fruit volumineux, oblong-ovoïde, de 9.5 cm. de long et de 6 cm. de large, noir à l'état sec", which seems to be based on the separate fruit collection of the paratype Capuron 8860 from "Haut bassin de la Sahafihitra (massif du Beanjada, au nord de la presqu'île Masoala) vers 800 m d'alt." We have determined, however, that this latter specimen is an *Isolona*, possibly I. perrieri Diels (see Couvreur 2008).

20. *Xylopia fananehanensis* Cavaco & Keraudren (Fig. 22A-F)

Bulletin de la Société botanique de France 103: 276 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est"], bassin de la Fananehana, environs du village d'Aditavolo, vers 300 m d'alt., 30.I.1954 (fl.), *Capuron 8960* (holo-, P[P030386]!; iso-, P[P00364245, P030387], TEF[photo]!).

MATERIAL EXAMINED. — **Madagascar. Prov. Toamasina.** Environs de la baie d'Antongil, forêt d'Antandrokolaka, entre Aditavolo (bassin de la Fananehana) et Morafuro (bassin de la Rantabe), vers 700 m alt., 16.II.1954 (fl., fr.), *Capuron 9038 SF* (OWU, P[P00524378, P01986973, P02133039]); environs de la baie d'Antongil: bassin de la Manonga (affluent rive gauche de la Rantabe), aux environs de la Sahajinja, 5.III.1954 (fl.), *Capuron 9103-SF* (P[P01986972, P01986977, P02133040]); environs de Vohilava, bassin de la Vohilava, III.1954 (fl.), *Capuron 9145 SF* (P[P01986974, P01986975, P01986976, P01986978, P01986979]); Maroantsetra, Tampolo, Péninsule Masoala, 15°43'S, 49°57'E, 100-200 m, 4.XI.2001 (fr.), *Poncy 1587* (MO, P[P00373115]); Tampolo (Masoala), Ambanizana, Ajahana, Maroantsetra, forêt de Tampolo, 15°43'45"S, 49°57'38"E, 10 m, 16.X.2001 (fr.), *Randrianaivo 681* (MO, OWU).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia fananehanensis* occurs in northeastern Madagascar, in small river drainages emptying into Antongil Bay, at elevations from 10 to 700 meters (Fig. 28). The specimens with flowers were collected from January to March, and those with fruits in February, October, and November. With an EOO and AOO estimated as 1510 km² and 24 km², respectively, *X. fananehanensis* is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Hazoambo (*Capuron 9038 SF, Capuron 9103-SF*).

DESCRIPTION

Tree up to 30 m tall; d.b.h. up to 40 cm.

Twigs sparsely pubescent, the hairs 0.1-0.2 mm long, soon glabrate; nodes with one axillary branch.

Leaves with larger blades 6.4-10.5 cm long, 3.0-3.5 cm wide, subcoriaceous, slightly discolorous, shiny brownish olive to brown adaxially, dull tan to brown abaxially, elliptic to elliptic-oblong, apex acuminate, the acumen 7-8 mm long, base cuneate, short-decurrent on petiole, margin flat or slightly recurved, glabrous or with a few hairs along the midrib on both surfaces; midrib brown or darkened toward base adaxially, secondary veins brochidodromous and somewhat arcuate, 10-15 per side, diverging at 50-70° from midrib, these and higher-order veins raised and forming a conspicuous reticulum on both surfaces; petiole 7-11 mm long, shallowly canaliculate, faintly wrinkled, sparsely pubescent.

Inflorescences axillary, 1-flowered, not pedunculate, rustypubescent to glabrate, lenticellate on basal half; pedicels 6-8.7 mm long, 0.9-1.3 mm thick; bracts 3, all attached near or just distal to pedicel midpoint, caducous or distal bract sometimes persistent, 2.2-2.4 mm long, broadly ovate; buds linear-lanceolate, apex acute, slightly falciform.

Sepals slightly spreading at anthesis, *c*. ¹/₃-connate, 2.7-3.3 mm long, 3.0-3.2 mm wide, coriaceous, broadly triangular, apex acute to obtuse, rusty-pubescent abaxially.

Petals with color *in vivo* unknown; outer petals possibly slightly spreading at anthesis, 18.1-22.7 mm long, 3.1-3.3 mm wide

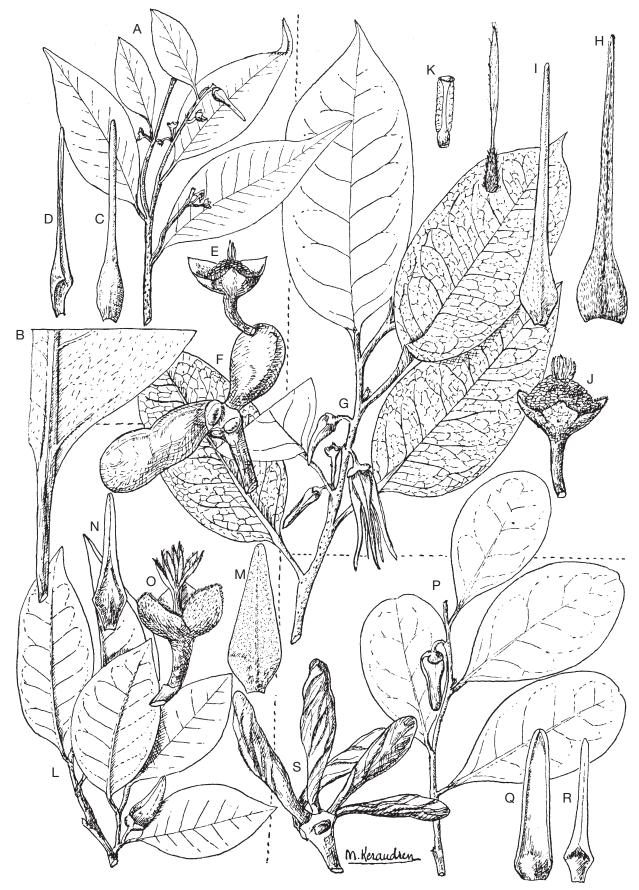


FIG. 21. — Plate including illustrations of Xylopia dielsii Cavaco & Keraudren (G-K) and X. humbertii Ghesq. ex Cavaco & Keraudren (L-O), reproduced from Cavaco & Keraudren (1958).

at base, 1.8-2.1 mm wide at midpoint, slightly fleshy, linearlanceolate, flat but becoming weakly keeled toward apex adaxially, weakly keeled abaxially, apex acute, densely yellowish gray puberulent except for the glabrous base adaxially, densely golden brown-pubescent abaxially; inner petals with position at anthesis unknown, 9.7-13 mm long, 2-2.6 mm wide at base, 0.5-0.7 mm wide at midpoint, slightly fleshy, acicular, slightly keeled except at the base on both surfaces, apex acute, base shallowly concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces.

Stamens 90-120; fertile stamens 1.4-1.7 mm long, narrowly oblong, anther connective apex 0.3-0.4 mm long, capitate, overhanging anther thecae, long-papillate to pubescent, anthers 11-13-locellate, filament 0.3-0.6 mm long; outer staminodes 1.5-1.9 mm long, clavate to narrowly oblong, apex rounded; inner staminodes 1.4-1.5 mm long, narrowly oblong, apex obliquely truncate; staminal cone *c*. 1.7 mm in diameter, *c*. 1.0 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 4-6; ovaries *c*. 1.2 mm long, narrowly oblong, pubescent, stigmas loosely connivent, 1.4-1.7 mm long, clubshaped, with a few hairs at the apex.

Fruit of up to 6 monocarps borne on a pedicel 11-14 mm long, 5-6 mm thick, sparsely appressed-pubescent to glabrate; torus 11-13 mm in diameter, 7-10 mm high, irregularly globose to pyramidal; monocarps with red exterior *in vivo*, 2.5-3.9 cm long, 2.0-2.5 cm wide, 2.0-2.3 cm thick, obovoid or ellipsoid, not torulose, apex rounded to truncate, base sessile, slightly verrucose and wrinkled, dull, brown-pubescent; pericarp 2.8-4 mm thick.

Seeds up to 6 per monocarp, in two rows, perpendicular to long axis, 10.5-12.3 mm long, 6.5-8.4 mm wide, 5.5-6.8 mm thick, ellipsoid, broadly elliptic to wedge-shaped in cross-section, brown, smooth, dull, perichalazal ring not or only slightly evident; presence of sarcotesta undeterminable; aril absent.

Notes

Xylopia fananehanensis is easily distinguished from other Madagascar species of *Xylopia* by the combination of the conspicuous raised vein reticulum on the adaxial leaf surface, long pedicels ringed by multiple bract scars, narrow petals with the two whorls dissimilar in length, and relatively long and slender petioles. It reaches a greater height than most Madagascar *Xylopia* species, up to 30 meters.

Of the four accessions identified as "*Xylopia* sp. aff. *fananehanensis*" in the phylogenetic analysis of Stull *et al.* (2017), only one, *Randrianaivo* 681, has proved to actually be this species. All four accessions clustered together in the molecular analysis, however, suggesting a phylogenetic relationship among the species represented, i.e. *X. danguyella*, *X. fananehanensis*, *X. galokothamna*, sp. nov., and *X. lokobensis*, sp. nov. They have in common medium-sized subcoriaceous to coriaceous leaves and relatively thick sessile to sub-sessile monocarps. One sheet of *Poncy 1565* at P[P00373086] is identifiable as *X. fananehanensis*, but it is not the same species as in the other P duplicate [P00373087] of this collection or the sheet of this collection at MO, both of which resemble *X. lemurica*. The label identification of the collection as *X. buxifolia* Baill, which the MO sheet resembles, suggests that the P00373086 sheet is a possible duplicate of *Poncy 1587* that received the wrong label.

21. *Xylopia galokothamna* D.M.Johnson & N.A.Murray, sp. nov. (Figs 16C, D; 23F-L, N)

Xylopia species belonging to the Madagascar group with relatively broad outer petals and clavate stigmas, but distinguishable from the other species of the group by the shrub habit, cuneate to broadly cuneate leaf bases, stamens 1.5-2.0 mm long borne on a staminal cone *c*. 1.8 mm high, monocarps with a beak 1.5-3 mm long and stipe 4-5 mm long and 2.8-4.8 mm thick, and ovoid seeds 11.8-13.3 mm wide.

TYPE. — **Madagascar. Prov. Antsiranana**, Diana Region, Ambilobe, Beramanja, Anketrabe, forêt de Kalabenono, Ambatoharanana, 13°38'46"S, 48°40'30"E, 706 m, 24.XI.2006 (fl., fr.), *Callmander et al. 585* (holo-, P[P01986966]!; iso-, MO!, OWU!).

PARATYPE. — **Madagascar. Prov. Antsiranana**, Diana Region, Ambilobe, Beramanja, Ambatoharanana, Anketrabe belinta, Kalobinono Manongarivo, 5 km au sud de Belinta, 13°38'40"S, 48°40'26"E, 700 m, 28.IX.2013 (fr.), *Ratovoson 2065* (MO, P[P01044912]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Like *X. kalabenonensis*, this is a new species revealed by recent collecting efforts in the Galoka Mountain chain of northwestern Madagascar (Callmander *et al.* 2009). *Xylopia galokothamna*, sp. nov., is known from a single locality in humid forest at *c.* 700 m elevation (Fig. 29). The specimen with flowers was collected in November, the specimens with fruits in September and November. The small EOO and AOO values, 5 km² and 8 km², respectively, lead to a preliminary conservation assessment of Endangered (Table 2).

DESCRIPTION Shrub up to 6 m tall.

Twigs sparsely appressed-pubescent, the hairs 0.1-0.3 mm long, soon glabrate; nodes with one axillary branch.

Leaves with larger blades 10.4-14.0 cm long, 3.7-5.0 cm wide, subcoriaceous, concolorous or slightly discolorous and brownish green adaxially, reddish brown abaxially, elliptic to oblong-elliptic, apex acuminate, the acumen 5-9 mm long, base cuneate to broadly cuneate, decurrent on petiole, margin flat or slightly recurved, glabrous but densely verrucose adaxially, sparsely appressed-pubescent and soon glabrate abaxially; midrib darkened toward base adaxially, secondary veins brochidodromous, 15-18 per side, diverging at 60-90° from midrib, these and higher-order veins slightly raised or indistinct adaxially; raised and distinct abaxially; petiole 4-8 mm long, canaliculate, wrinkled, sparsely pubescent to glabrate.

Inflorescences axillary, 1-flowered, not pedunculate, densely pubescent; pedicels 2.0-4.5 mm long, 1.6-2.0 mm thick;

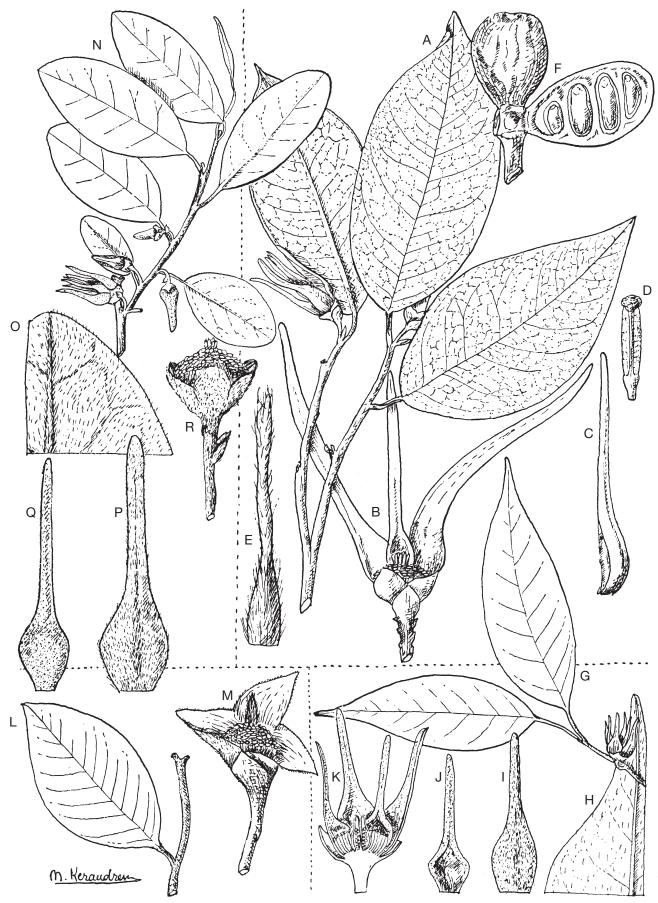


Fig. 22. – Plate including illustration of Xylopia fananehanensis Cavaco & Keraudren (A-F), reproduced from Cavaco & Keraudren (1958).

bracts not seen; buds linear-lanceolate, apex acute, slightly falciform (Fig. 16C).

Sepals spreading at anthesis, *c*. ¹/₃-connate, 2.3-3.5 mm long, 3.8-4.5 mm wide, coriaceous, broadly triangular, apex acute, densely pubescent abaxially.

Petals yellow *in vivo*; outer petals slightly spreading at anthesis, *c.* 18 mm long, 4.4-5.9 mm wide at base, 2.7-3.0 mm wide at midpoint, slightly fleshy, linear-lanceolate, keeled on apical ¼ but otherwise flat adaxially, weakly keeled abaxially, apex obtuse, densely puberulent except for the glabrous base adaxially, densely appressed-pubescent abaxially; inner petals with apices spreading at anthesis, 11.4-12.8 mm long, 3.3-3.5 mm wide at base, *c.* 1.3 mm wide at midpoint, slightly fleshy, linear-lanceolate, keeled on apical ½ adaxially, keeled abaxially, apex acute, base concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces, with a band of papillae across widest point adaxially.

Stamens *c.* 170; fertile stamens 1.5-2.0 mm long, narrowly oblong, anther connective apex 0.3-0.4 mm long, capitate to slightly conical, overhanging anther thecae, papillate, anthers 12-14-locellate, filament 0.5-0.7 mm long; outer staminodes 1.6-2.6 mm long, clavate or narrowly oblong, apex obtuse; inner staminodes 1.1-1.4 mm long, oblong, apex rounded; staminal cone *c.* 2.4 mm in diameter, *c.* 1.8 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 5-7; ovaries < 2 mm long, oblong, pubescent, stigmas connivent, 2.8-3.2 mm long, narrowly clavate, with a few hairs.

Fruit of up to 3 monocarps borne on a pedicel 5-8 mm long, 3-3.7 mm thick, sparsely pubescent; torus 5-6 mm in diameter, 4.5-5 mm high, ovoid; monocarps with yellow exterior *in vivo*, 2.9-5.1 cm long, 2.0-2.8 cm wide, (0.7-) 1.4-2.4 cm thick, oblong or ovoid, not torulose to slightly torulose, apex rounded to a broad beak 1.5-3 mm long, base contracted into a stipe 4-5 mm long, 2.8-4.8 mm thick, verrucose, obliquely wrinkled and with a narrow ridge encircling the monocarp lengthwise, dull, finely pubescent; pericarp 1.0-2.0 mm thick.

Seeds up to 5 per monocarp, in a single row, oblique to perpendicular to long axis, 14.1-16.2 mm long, 11.8-13.3 mm wide, 8.6-11.2 mm thick, ovoid, sometimes slightly flattened, broadly elliptic to semicircular in cross-section, light yellowbrown, smooth, dull, perichalazal ring visible as a flat darkened band; presence of sarcotesta not determinable; aril absent.

Notes

Xylopia galokothamna, sp. nov., is one of the few Madagascar *Xylopia* species with a shrub habit. It is part of the species group with clavate stigmas and often relatively broad petals, and within that group stands out by the combination of short thick flower pedicels, distinct beak and stipe on the fruits, and the broad seeds. It occurs in the same gen-

eral region of Madagascar as *X. lokobensis*, sp. nov., but leaf shape, pedicel length, and habit distinguish the two species. The type specimen was one of several identified as *"Xylopia* sp. aff. *fananehanensis"* in Stull *et al.* (2017) that are recognized in this work as distinct species.

The type and paratype collections have monocarps that are finely pubescent, with a pericarp 1-2 mm thick. Three additional specimens collected from the same general area of the Galoka Mountains have in common the shrub habit, relatively large seeds, and a broad beak and stipe of the monocarps: Buerki et al. 20 (MO), Diana Region, Chaîne Galoka, Mont Galoka, Anketrabe-Belinta, Ambilobe, Beramanja, Camp Bilahy, 13°35'20"S, 48°43'42"E, 928 m, 23.II.2005 (fr.); Callmander et al. 720 (MO), Ambanja, commune Beramanja, 13°38'40"S, 48°40'09"E, 518 m, 22.XI.2007 (fr.); Rakotovao et al. 3823 (MO). Ambilobe, Beramanja, Anketrabe, village le plus proche Antanambao Belinta, 1007 m, 13°39'10"S, 48°40'29"E, 28.XI.2007 (fr.). All of these specimens, however, have monocarps that are glabrous, more elongate (up to 7 cm long), and strongly torulose (Figs 16E, 23M), with the pericarp only 0.2-0.7 mm thick; the labels of all three specimens indicate that the monocarps are tinged with red and the label of Buerki 20 describes the seeds as orange. The leaves of these specimens are more lanceolate, glabrous to glabrate, and lack the verrucose adaxial surface. Given the degree of disparity in the fruit, and to a lesser extent the vegetative features, we exclude these specimens as paratypes of X. galokothamna, sp. nov., but draw attention to the similarities and the fact that additional collections are needed to resolve their status.

22. *Xylopia ghesquiereana* Cavaco & Keraudren (Fig. 19A-I)

Bulletin du Jardin botanique de l'État à Bruxelles 27: 87 (1957). — Type: Madagascar. Prov. Toamasina ["Est"], Vohimarangitra (district de Tamatave) [= Betampona, 17°55'S, 49°13'E], 22.II.1950 (fl.), Réserves Naturelles R N 2440 bis (holo-, P[P030392]!; iso-, P[P030393, P030394]!).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia ghesquiereana* is known only from the type locality in east-central Madagascar (Fig. 29). The type specimen with flowers was collected in February. In light of the fact that the species is only known from a single collection made in 1950 it is given a preliminary conservation assessment of Critically Endangered (Table 2).

LOCAL NAME. — Hazoambomena.

DESCRIPTION **Tree**.

Twigs densely brown-tomentose, the hairs 0.4-0.6 mm long, at length glabrate; nodes with two axillary branches.

Leaves with larger blades 4.6-5.8 cm long, 2.1-2.5 cm wide, subcoriaceous, slightly discolorous, dark purple brown adaxially, brown abaxially, elliptic to elliptic-ovate or obovate, apex acuminate, the acumen 6-8 mm long, base broadly cuneate

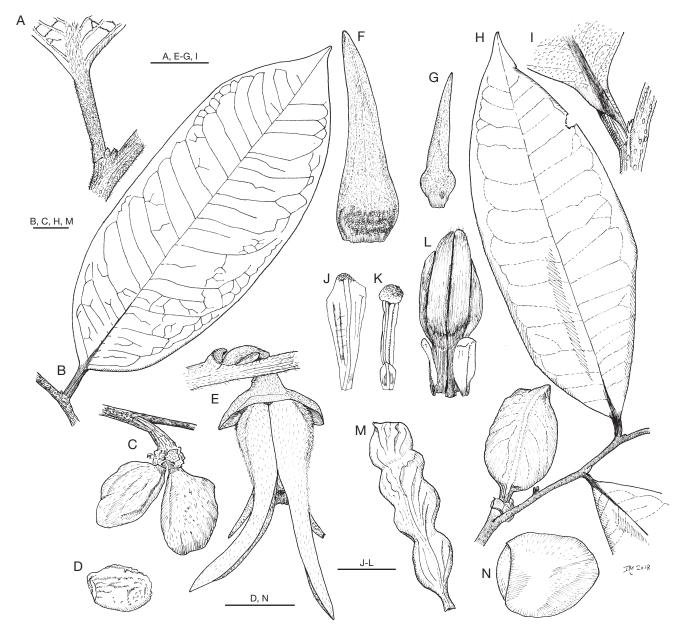


Fig. 23. – Xylopia lokobensis, sp. nov., and X. galokothamna, sp. nov. A-E, X. lokobensis, sp. nov.: A, petiole and base of leaf blade; B, leaf; C, fruit, side view; D, seed, side view; E, flower, side view. F-N, X. galokothamna, sp. nov.: F, outer petal, adaxial view; G, inner petal, adaxial view; H, habit, with fruit; I, petiole and base of leaf blade; J, outer staminode, abaxial view; K, fertile stamen, abaxial view; L, stigmas with adhering inner staminodes, side view; M, monocarp; N, seed, side view. A, D, E, from Antilahimena 340 (P); B, from Antilahimena 340 (MO); C, from Birkinshaw 186 (OWU); F, G, J, K, L, from Callmander et al. 585 (P); I, from Callmander et al. 585 (OWU); M, from Buerki et al. 20 (MO). Scale bars: A, E-G, I, 5 mm; B-D, H, M, N, 1 cm; J-L, 1 mm.

to rounded, short-decurrent on petiole, margin slightly recurved, densely pubescent along midrib but otherwise glabrous adaxially, barbate along midrib and margins but otherwise sparsely appressed-pubescent to glabrate abaxially; midrib concolorous with or slightly paler than rest of blade toward base adaxially, secondary veins weakly brochidodromous, 10-12 per side, diverging at 50-70° from midrib, these and higher-order veins slightly raised and forming a conspicuous reticulum on both surfaces; petiole 4.5-5 mm long, shallowly canaliculate, smooth, densely pubescent.

Inflorescences axillary, 1-flowered, not pedunculate, pubescent; pedicels 2.9-5.5 mm long, 0.9-1.3 mm thick; bracts 2, one attached near pedicel base and the other just proximal to the sepals, lower bract caducous, distal bract often persistent, 1.5-2.0 mm long, broadly ovate to nearly circular; buds linear, apex acute, slightly falciform.

Sepals spreading to slightly recurved at anthesis, ¹/₃-1/₃-connate, 2.3-2.8 mm long, 2.2-2.8 mm wide, coriaceous, slightly fleshy at base, triangular, apex acute to obtuse, densely pubescent abaxially.

Petals with color *in vivo* unknown; outer petals with position at anthesis unknown, possibly curved outward, 21-28 mm long, 2.9-3.2 mm wide at base, *c*. 1.2 mm wide at midpoint, fleshy,

linear, sinuous, keeled only at the apex adaxially, weakly keeled abaxially, apex acute to obtuse, densely puberulent except for glabrous base adaxially, densely sericeous abaxially; inner petals with position at anthesis unknown, possibly erect, *c*. 18 mm long, 2.3-2.5 mm wide at base, 0.7-1.0 mm wide at midpoint, fleshy, linear, sinuous, keeled except for the base on both surfaces, apex acute to obtuse, base concave with undifferentiated margin, puberulent except for the glabrous base on both surfaces.

Stamens *c.* 140; fertile stamens 1.5-1.8 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm long, hemispherical to capitate, slightly overhanging the anther thecae, papillate, anthers 13-14-locellate, filament 0.5-0.7 mm long; outer staminodes 1.6-1.9 mm long, oblong, apex obtuse to rounded; inner staminodes 1.5-1.7 mm long, oblong to clavate, apex truncate to rounded; staminal cone 1.4-1.8 mm in diameter, 0.8-1.4 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 5-7; ovaries *c*. 1.6 mm long, oblong, densely pubescent along the edges, stigmas connivent, 3.0-3.4 mm long, narrowly clavate, pubescent.

Fruits and seeds unknown.

Notes

Xylopia ghesquiereana is a morphologically isolated species. The sharply short-acuminate leaves with pronounced hairs along the midrib resemble those of *X. lemurica*, but the leaves of *X. ghesquiereana* are proportionately broader. The relatively long stamens with long filaments also distinguish *X. ghesquiereana* from *X. lemurica*. The pedicels of the flowers are relatively short, and densely covered with a brown tomentum. The sepals spread widely and are somewhat recurved at the apices. The petals are the longest of any Madagascar species, only approached by those of *X. fananehanensis*, which lacks hairs on the leaves and has a much longer pedicel.

In the original description Cavaco and Keraudren compared *X. ghesquiereana* to *X. madagascariensis*, distinguishing it from the latter by the tan tomentum of its young branches and petioles, the presence of hairs on the leaf midrib, the shorter pedicel, the persistent bract subtending the calyx, the large calyx, composed of 3 equal lobes that are not erect, and by absence of punctate glands on the style. The type specimens of both species came from the same locality and superficially resemble each other in leaf size and shape, but *X. madagascariensis* is more similar in flower, fruit, and seed morphology to *X. humblotiana* of sect. *Xylopia*.

23. *Xylopia humbertii* Ghesq. ex Cavaco & Keraudren (Fig. 21L-O)

Bulletin du Jardin botanique de l'État à Bruxelles 27: 87 (1957). — Type: Madagascar. Prov. Mahajanga ["Centre"], entre Mandritsara et Andilamena, 900-1200 m, XI.1937 (fl.), *Humbert 17980* (holo-, P[P030395]!; iso-, P[P030396, P030397, one without bar code]!). DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia humbertii* is known only from its type, which was collected in east-central Madagascar at an elevation of 900-1200 m with flowers in early November (Fig. 29). The habitat is described as forest remains and secondary growth (*savoka*) of the eastern slope, on lateritic soil derived from gneiss. The type locality appears to fall within the boundaries of Marotandrano National Park. The species has not been re-collected since 1937 and should be regarded as of high conservation concern; it is given a preliminary conservation assessment of Critically Endangered (Table 2).

DESCRIPTION Small tree.

Twigs glabrous or with a few scattered appressed hairs, the hairs 0.1-0.2 mm long, but soon glabrate; nodes with one axillary branch.

Leaves with larger blades 5.2-6.3 cm long, 2.2-2.8 cm wide, subcoriaceous to coriaceous and somewhat conduplicate, discolorous, shiny and olive gray to blue gray adaxially, dull and light brown abaxially, elliptic, apex acute to blunt-acuminate, the acumen 3-5 mm long, base cuneate and decurrent on petiole, margin slightly recurved, glabrous on both surfaces, rarely with a few scattered hairs abaxially; midrib concolorous with blade or dark red toward base adaxially, secondary veins weakly brochidodromous, 11-12 per side, diverging at 70-80° from midrib, slightly raised adaxially, raised abaxially; higher-order veins indistinct adaxially, raised abaxially; petiole 4-5 mm long, semi-terete, faintly wrinkled, glabrate or with a few hairs.

Inflorescences axillary, 1-flowered, not pedunculate, pubescent; pedicels strongly recurved, 3.8-4.3 mm long, 0.9-1.1 mm thick; bracts 2, both attached proximal to pedicel midpoint, caducous, *c*. 0.5 mm long, semicircular; buds lanceolate, apex obtuse.

Sepals spreading at anthesis, ¹/3-connate, 1.9-3.0 mm long, 2.5-3.0 mm wide, coriaceous, semicircular, apex acute, pubescent abaxially.

Petals white *in vivo*; outer petal position at anthesis unknown, 12.6-14.6 mm long, 3.1-3.7 mm wide at base, 2.1-2.5 mm wide at midpoint, coriaceous to fleshy, lanceolate, with a faint ridge at apex adaxially, faintly ridged abaxially, apex obtuse, shallowly concave adaxially, densely puberulent except for glabrous base adaxially, densely pubescent except for a glabrous patch at base abaxially; inner petals with position at anthesis unknown, 10.6-12.3 mm long, 2.7-3.1 mm wide at base, 1.1-1.4 mm wide at midpoint, coriaceous, linear-lanceolate, keeled on apical ¼-⅓ adaxially, keeled abaxially, apex acute, base concave with undifferentiated margin, densely puberulent at apex and along margins adaxially, puberulent except for glabrous base abaxially.

Stamens *c*. 80; fertile stamens 1.5-1.9 mm long, narrowly oblong, anther connective apex 0.4-0.5 mm long, capitate, overhanging the anther thecae, papillate, anthers 9-13-locellate, filament 0.4-0.7 mm long; outer staminodes absent;

inner staminodes 1.0-1.4 mm long, oblong, apex truncate to obtuse; staminal cone 1.4-2.0 mm in diameter, 0.6-1.3 mm high, concealing all but apices of the ovaries, rim irregularly laciniate.

Carpels 5-6; ovaries *c*. 1.1 mm long, oblong, pubescent, stigmas loosely connivent, 2.9-3.2 mm long, falciform-lanceolate, pilose at apices.

Fruits and seeds unknown.

Notes

The combination of glabrate subcoriaceous leaves and relatively short broad buds and outer petals distinguishes *X. humbertii* from other Madagascar species. It most closely resembles *X. perrieri*, another species from higher elevations, but the latter has densely appressed-pubescent lower leaf surfaces and longer pedicels. The twigs in *X. humbertii* are initially reddish brown with the epidermis soon exfoliating, and densely marked with protuberant white lenticels.

Two specimens from the Montagne d'Ambre region of extreme northern Madagascar, *Capuron 20051 SF* [P01986981] and Ursch 245 [P01986961], resemble X. humbertii in the tendency for the subcoriaceous leaves to be conduplicate and thus longitudinally folded when pressed. These specimens may represent a distinct species, differing from the type material of X. humbertii in the more densely pubescent young twigs, the slightly larger leaves, and the more acute angle of the secondary veins (45-50°). Capuron 20051 SF has, in addition to immature fruits, an old flower receptacle, which shows the sepals c. 4.3 mm wide, i.e. wider than in the type material of X. humbertii. The specimen Ursch 245, annotated by Ghesquière as Xylopia danguyella Ghesq. in 1938 and identified as that species by Cavaco & Keraudren (1958), bears nearly mature monocarps, which are 3.9-4.9 cm long, c. 1.7 cm wide, and 1.5-1.6 cm thick, oblong, with a short broad beak 2.5-4.5 mm long and a short stipe 8-9.5 mm long and 4-5 mm thick. The monocarps are obliquely wrinkled, strongly verrucose between the wrinkles, and contain up to 8 seeds arranged in a single row. This monocarp morphology is different from that of X. danguyella, but similar to that of Capuron 20051 SF.

24. *Xylopia kalabenonensis* D.M.Johnson, Deroin & Callmander (Figs 1E; 16H)

Candollea 64 (2): 183-187 (2009). — Type: Madagascar. Prov. Antsiranana, Préfecture d'Ambilobe, commune de Beramanja, Anketrabe, forêt de Kalabenono, chaîne du Galoka, 7 km au SE d'Anketrabe, 13°38'23"S, 48°40'06"E, 854 m, 18.XI.2006 (fl., fr.), *Razafitsalama et al. 1041* (holo-, MO!; iso-, G!, OWU!, P n. v.).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia kalabenonensis* is only known on the rocky sandstone areas of the Kalabenono massif of northern Madagascar, where it occurs in subhumid to humid forest at *c*. 850 m. The single specimen, with both flowers and fruits, was collected in November. The previous

conservation assessment of Critically Endangered, based on its AOO of only 9 km² encompassing a single known population occurring outside any protected area (Callmander *et al.* 2009), has not changed.

DESCRIPTION **Shrub** 6 m tall; d.b.h. 8 cm.

Twigs densely hispid, with persistent pale brown hairs 1.2-2 mm long; nodes with one or occasionally two axillary branches.

Leaves with larger blades 8.4-9.0 cm long, 2.8-2.9 cm wide, subcoriaceous, discolorous, greenish gray adaxially, light brown abaxially, oblong, apex acuminate, the acumen 6-8 mm long, base rounded, not decurrent, margin slightly revolute, glabrous except for dense erect hairs on the midrib adaxially, erect-hairy abaxially; midrib darker than blade adaxially, secondary veins irregularly brochidodromous, 12-13 per side, diverging at 70-90° from midrib, these and higher-order veins indistinct adaxially, raised and conspicuous abaxially; petiole 3-4 mm long, semi-terete, smooth, densely hispid.

Inflorescences axillary, 1-flowered, not pedunculate, densely hispid; pedicels 7-7.5 mm long, 1.2-1.3 mm thick; bract 1, attached distal to the midpoint, persistent, 3-3.6 mm long, triangular to ovate; buds oblong, apex obtuse.

Sepals slightly spreading at anthesis, ½-connate, 4.0-4.5 mm long, 4.0-4.7 mm wide, coriaceous, ovate, apex acute, hispid abaxially.

Petals white to cream-colored *in vivo*; outer petals spreading at anthesis, 11.5-13 mm long, 3.5-4.5 mm wide at the base, 3.3-4 mm wide at midpoint, fleshy, lanceolate-oblong, weakly keeled on apical ¹/₄ adaxially, flat abaxially, apex obtuse, densely puberulent except for the glabrous base adaxially, densely silvery sericeous abaxially; inner petals erect at anthesis, 8-10.1 mm long, 3.3-3.4 mm wide at base, 1.9-2.0 mm wide at midpoint, fleshy, lanceolate, weakly keeled on apical ¹/₃ adaxially, keeled abaxially, apex acute, base shallowly concave with undifferentiated margin, sparsely puberulent but becoming glabrous toward the base adaxially, pubescent except for the glabrous base abaxially.

Stamens *c*. 300; fertile stamens *c*. 2 mm long, clavate to narrowly oblong, anther connective apex 0.2-0.3 mm long, hemispherical, overhanging anther thecae, papillate or with a few hairs, anthers 11-14-locellate, filament 0.4-0.5 mm long; outer staminodes 2-2.2 mm long, clavate to narrowly oblong, apex obtuse; inner staminodes 1.2-1.4 mm long, oblong to clavate, apex obtuse; staminal cone 2.4-2.8 mm in diameter, 1.4-2 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels *c.* 8; ovaries 1-1.4 mm long, narrowly oblong, sparsely pilose, stigmas connivent, 3.2-3.3 mm long, clavate, pilose at the apices.

Fruit of up to 5 monocarps borne on a pedicel 5-7 mm long, *c*. 3.5 mm thick, pubescent; torus 5-6 mm in diameter, *c*. 5 mm high, short-cylindrical; monocarps with red exterior *in vivo*, 3-3.5 cm long, 1.5-2 cm wide, 1.8-2 cm thick, oblong, slightly torulose, apex rounded to obtuse, base sessile, faintly wrinkled, slightly shiny, hispid; pericarp *c*. 0.4 mm thick.

Seeds [ex Callmander *et al.* 2009] up to 5 per monocarp, in two rows, oblique to long axis, 7-7.6 mm long, 4.3-4.8 mm wide, 3.8-4.1 mm thick, ellipsoid, elliptic to somewhat wedge-shaped in cross-section, light brown, smooth, dull, perichalazal ring not evident; presence of sarcotesta undeterminable; aril absent.

Notes

Xylopia kalabenonensis belongs to the group of Madagascar species with clavate stigmas and relatively broad petals. It resembles *Xylopia capuronii* in its densely pubescent twigs and pedicels, but the hairs are pale brown and straight instead of dull red and twisted. The leaf blades are only slightly revolute rather than strongly revolute, and the outer petals are longer and narrower. The petal orientation at anthesis, with the outer petals wide spreading and the inner petals erect, is similar to that of *X. australis*, sp. nov., which is also a member of the species group within sect. *Stenoxylopia* with clavata stigmas.

As noted in Callmander *et al.* (2009), another specimen collected from the same mountain (*Razafitsalama et al.* 1055 (MO, OWU), Ambilobe, Beramanja, Anketrabe, forêt de Kalabenono, sur la chaine Galoko, 7 km au Sud-Est d'Anketrabe, 13°88'23"S, 48°40'06"E, 854 m, 18.XI.2006) differs in several ways from the new species: the indument is shorter (hairs 0.5-0.9 mm long) and more lax, the leaf is lanceolate, cuneate at the base, slightly longer, and has flat rather than revolute margins, the inflorescences are sometimes 2-flowered, with slightly shorter (3-5 mm) pedicels, and the staminal cone is smaller (1.7 mm in diameter). As this specimen lacks mature flowers or fruits, additional material will be needed to determine its status.

25. *Xylopia lamii* Cavaco & Keraudren (Fig. 24F-J)

Bulletin de la Société botanique de France 103: 275 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est"], bassin de la Manonga, affluent de la Rantabe, aux environs de Sahajinja, 700 m, 3.III.1954 (fl.), *Capuron 9087* (holo-, P[P030401]!; iso-, OWU!, P[P030402, P030403]!, WAG!).

MATERIAL EXAMINED. — **Madagascar**. Prov. Toamasina. Limite W de la R. N. No 1 Betampona, 1200 m [see below], 22.I.1950 (fr.), *Cours 2519* (P[P01987039, P02005961]); itinéraire de Didy à Brickaville, s. d. (fr.), *Cours 4798* (P[P01987017]); Soanierana– Andasibé, 350 m, 13.XII.1938 (buds), *Lam & Meeuse 5971* (K n.v., L, WAG); R. N. I. Tamatave, 22.IX.1955 (fr.), *Marten 7580-RN* (OWU, P[P01987018]); District Toamasina II, Commune Rurale Sahambala, Fokontany Sahavongo, village le plus proche Ambodirafiahely, forêt d'Andromasina, 18°01'26"S, 49°05'44"E, 565 m, 2.II.2017 (fr.), *Rakotonirina et al. 38* (MO); Ambodimangavalo, Ambatoharanana, sur pente sur piste entre Moango et Antanamarina à 3 km du village d'Antanamarina, 17°33'57"S, 48°53'58"E, 740 m, 27.X.2000 (fr.), *Randrianjanaka et al. 591* (P[P01987019]. DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia lamii* occurs in east-central Madagascar, in humid forest from 350 to 740 meters (Fig. 29). An elevation of 1200 meters was reported on the label of *Cours 2519*, which was collected along the western boundary of the Betampona Reserve. However, Ghulam *et al.* (2015), determined the elevational range of the Reserve to be 2-580 meters. The type specimen with flowers was collected in March and an additional specimen with flower buds was collected in December; collections with fruits have been gathered in January, February, September, and October. With an EOO value of 6316 km² and an AOO value of 24 km², *X. lamii* is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAMES. — Hazoambo (*Cours 2519, Lam & Meeuse 5971*), hazoambohay (*Randrianjanaka et al. 591*).

Description

Tree up to 20 m tall; d.b.h. up to 20 cm.

Twigs erect ferruginous-pubescent, the hairs 0.3-1.2 mm long, at length glabrate or pubescence persistent only in strips; nodes with one axillary branch.

Leaves with larger blades 4.1-5.6 cm long, 2.0-2.8 cm wide, chartaceous to subcoriaceous, discolorous, gray to dark brown adaxially, orange-tan to light brown abaxially, ovate to elliptic, apex rounded to truncate and often retuse, base broadly cuneate to rounded, short-decurrent on petiole, margin flat or slightly recurved, glabrous except for dense erect ferruginous pubescence on midrib adaxially, thinly appressed ferruginous-pubescent, hairs denser and longer on midrib, margins, and base, often with a tuft of hairs at the apex, abaxially; midrib concolorous with blade adaxially, secondary veins weakly brochidodromous, 9-11 per side, diverging at 50-70° from midrib, these and higher-order veins slightly raised on both surfaces; petiole 1.8-3.5 mm long, semi-terete to shallowly canaliculate, faintly wrinkled, densely ferruginous-pubescent.

Inflorescences axillary, 1-flowered, not pedunculate, densely ferruginous-pubescent; pedicels 2.9-4 mm long, 0.8-1 mm thick; bracts 2, both attached near pedicel midpoint, caducous or occasionally persistent, 1.4-1.9 mm long, ovate; buds linear, apex acute.

Sepals spreading at anthesis, ¹/₄-¹/₂-connate, 2.1-2.2 mm long, 1.9-2.3 mm wide, coriaceous, triangular to ovate, apex acute to obtuse, appressed ferruginous-pubescent abaxially.

Petals green-yellow *in vivo*; outer petals with position at anthesis unknown, 12.0-14.5 mm long, 2.6-2.8 wide at base, 1.0-1.5 mm wide at midpoint, slightly fleshy, linear, keeled at the apex but otherwise flattened adaxially, faintly keeled abaxially, apex acute to obtuse, sparsely puberulent adaxially, appressed-pubescent abaxially; inner petals with position at anthesis unknown, 11.7-11.8 mm long, 2.2-2.3 mm wide at base, 0.7-0.8 mm wide at midpoint, slightly fleshy, linear, keeled except at base on both surfaces, apex acute, base concave with undifferentiated margin but with a bilobed thickening at the widest point, puberulent except for glabrous base on both surfaces.

Stamens 70-80; fertile stamens 1.1-1.2 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm long, hemispherical to capitate, overhanging anther thecae, papillate, anthers 8-10-locellate, filament 0.3-0.4 mm long; outer staminodes *c*. 1.5 mm long, clavate, apex obtuse to rounded; inner staminodes *c*. 1.1 mm long, clavate, apex rounded; staminal cone 1-1.2 mm in diameter, *c*. 0.7 mm high, concealing all but apical $\frac{1}{3}$ of the ovaries, rim irregularly laciniate.

Carpels 4-6; ovaries *c*. 1 mm long, narrowly oblong, pubescent, stigmas connivent, 3.0-3.1 mm long, filiform, pubescent at the apices.

Fruit of up to 5 monocarps borne on a pedicel 8-10 mm long, 5-6 mm thick, sparsely pubescent to glabrate; torus 12-22 mm in diameter, 9-15 mm high, depressed-globose to pyramidal; monocarps with red and yellow exterior and red endocarp *in vivo*, 2.7-5 cm long, 2.0-2.5 cm wide, 2.2-2.5 cm thick, obovoid, ellipsoid, or oblong, not torulose, apex rounded, base sessile or contracted into a stipe 2 mm long, 8 mm wide, finely wrinkled and verrucose, sometimes with a slightly raised longitudinal ridge, sparsely lenticellate, shiny to dull, glabrate; pericarp 3.0-3.1 mm thick.

Seeds up to 8 per monocarp, in two rows, perpendicular to long axis, 13.0-14.1 mm long, 8.0-8.6 mm wide, 6.1-6.8 mm thick, oblong, elliptic in cross-section, brown, slightly rough and wrinkled, dull, perichalazal ring indistinct, forming a slight ridge on antiraphal side; sarcotesta light green *in vivo*; aril absent.

Notes

Xylopia lamii has distinctive persistent erect ferruginous indument on the twigs, leaves, pedicels, and sepals, and pubescent leaves that are retuse at the apex. It shares with *Xylopia buxifolia* and *X. lemurica* the characters of short sepals and narrow acute inner petals. It appears to occupy an elevational zone in between those two species, but little is known concerning its habitat.

Kramer (1969), in a survey of leaf and floral anatomy in *Xylopia* and related genera, reported that *X. lamii* was one of two species, along with *X. buxifolia*, to have papillae on the abaxial leaf epidermis, a feature not seen in any other *Xylopia* species he surveyed.

26. *Xylopia lastelliana* Baill. (Figs 1C; 14Q-Y; 16F)

Adansonia; Recueil d'Observations botaniques 4: 144 (1864). — Type: Madagascar. Without definite locality, 1841 (fl.), *Lastelle s. n.* (holo-, P[P030304]!).

Xylopia lastelliana var. acuta Ghesq. ex Cavaco & Keraudren, Bulletin du Jardin botanique de l'État à Bruxelles 27: 88 (1957). — Type: Madagascar. Prov. Antsiranana ["Est"], Antalaha, IX.1912 (fl.), Perrier de la Bâthie 4940 (holo-, P[P030405]!; iso-, B!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana. Parc national de Masoala, c. 1.0-1.5 km E of campsite at Ambatoledama, 720-792 m, 14.XII.1998 (fl., fr.), *Flores & Andriantiana 72* (A, K n.v., MO); Marosena, Ampanavohana, 2.I.1955 (fl.), *Réserves Naturelles de Madagascar 6953* (OWU, P[P01987013, P01987014, P01987015, P02133044, P02133045, P02133046]); Sarahandrano-Antalaha, 8.IX.1958 (fr.), *Service Forestier 19181* (K).

Prov. Fianarantsoa. Bassin de Mananjary, entre Vatovavy et Mananjary, VIII.1911 (fl.), *Perrier de la Bâthie 4944* (B, P[P01987033, P01987034]).

Prov. Toamasina. Environs de la Baie d'Antongil colline d'Ambodiatafana, au NW de l'embouchure de la Rantabe, 12.IX.1957 (fr.), Capuron 18258 SF (BR, K n.v., P[P01986998, P01986999]); Fivondronana: Ambodiriana, Firaisina: Fontsimavo, Réserve naturelle intégrale de Betampona, 17°54'46"S, 49°12'20"E, 427 m, 20.XI.2001 (bud, fr.), Rabehevitra et al. 24 (MO, P[P06839267]), 20.XI.2001 (fl.), Rabehevitra et al. 25 (MO, P[P06839285]); Atsinanana Region, Atsinanana, Vatomandry, Ambalabe, Sahanionaka, route Vodiriana–Ambalabe, 19°11'31"S, 48°34'40"E, 305 m, 19.IX.2011 (fr.), Rakotoarivelo et al. 558 (MO, P[P00903563]); Analanjirofo Region, Masoala Parc national, Ambatolaidama, Mahalevona, Maroantsetra, 15°17'21"S, 50°00'08"E, 0-1000 m, 1.X.1997 (fr.), Ranaivojaona et al. 173 (MO, OWU, P[P01986997]); Atsinanana Region, Commune: Ambodiriana, Fokontany: Fontsimavo (Fotsimavo by map) (Andrantabe), Andrendrirendry, Réserve naturelle intégrale de Betampona, 17°55'46"S, 49°12'14"E, 341 m, 20.XI.2001 (fr.), Razafitsalama 119 (MO, P[P00903551]); Atsinanana Region, Atsinanana, Vatomandry, Ambalabe, Ambinanindrano II, forêt de Vohibe, 19°10'17"S, 48°32'05"E, 548 m, 16.VIII.2014 (fr.), Razanatsima et al. 1320 (MO, P); Masoala Peninsula just S of Ambanizana along coastal trail and just E of Ambanizana, 15°38'S, 49°58'E, 70 m, 21.XII.1989 (fl.), Schatz & Modeste 2877 (BR, K n.v., MO, P[P01987012], WAG); Masoala Peninsula, "South Trail" (S of Androka River), climbing hills SE of Ambanizana, 15°38'S, 49°59'E, 250 m, 24.XII.1990 (fl.), Schatz & Modeste 3086 (G, K n.v., MO, PRE, WAG); F. Amelamena, Vohilengo, Soanierana-Ivongo, 23.VII.1954 (fr.), Service Forestier 11062 (OWU, P[P01987000, P01987001, P01987002]); Ampasina, District Fénérive-Est, s. d. (fl.), Service Forestier 19155 (K).

Prov. Toliara. Commune rurale Mahatalaky, Fokontany Tsialagna, village proche Tsialagna, 24°43'01"S, 47°00'39"E, 190 m, 19.XI.2009 (fl. buds, fr.), *Rakotovao et al. 4603* (MO); Anosy Region, District Fort-Dauphin, Commune Ranomafana, Fokontany Magatsika, forêt Tsirandrany, 24°35'06"S, 47°02'14"E, 669 m, 21.XI.2009 (fr.), *Razakamalala 4755* (MO).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Restricted to humid evergreen forests and occasionally littoral forests of northeastern Madagascar, *Xylopia lastelliana* usually occurs at elevations from 70 up to nearly 800 meters (Fig. 29); two atypical specimens, discussed below, were collected at *c*. 1300 meters. Specimens with flowers have been collected in January, August, November, and December, and with fruits in February and from July to December. *Xylopia lastelliana* has the fourth largest EOO of any Madagascar species, 124 820 km², but a relatively small AOO of 72 km², and is given a preliminary conservation assessment of Data Deficient (Table 2).

LOCAL NAMES. — Hazoambo (*Rakotoarivelo et al. 558, Razafitsalama 119*), moranga (*Schatz & Modeste 2877, 3086*).

DESCRIPTION

Tree up to 25 m tall; d.b.h. up to 55 cm.

Twigs densely sericeous, the hairs 0.4-1.0 mm long, eventually glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 3.5-6.7 cm long, 1.1-2.5 cm wide, subcoriaceous or chartaceous, concolorous, lanceolate, ovate,

or elliptic, apex acuminate, the acumen 7-10 mm long, to acute, base cuneate to rounded, sometimes oblique, decurrent on petiole, margin flat, not revolute, glabrous or with a few hairs on the midrib adaxially, sericeous abaxially with silvery hairs; midrib slightly darkened toward base adaxially, secondary veins weakly brochidodromous, 8-13 per side, diverging at 50-60° from midrib, these and higher-order veins indistinct to slightly raised on both surfaces; petiole 1.5-3.5 mm long, shallowly canaliculate, smooth or slightly wrinkled, pubescent.

Inflorescences axillary, 1-4-flowered, pedunculate or not, densely rusty-pubescent; peduncle 0.6-5 mm long; pedicels 2 per peduncle or arising separately from leaf axil, 3.5-6.8 mm long, 0.6-1.0 mm thick; bracts 2, one attached near the pedicel midpoint and the other just proximal to the sepals, caducous or the distal bract sometimes persistent, 1.2-1.9 mm long, broadly ovate; buds lanceolate, apex acute, sometimes slightly falciform.

Sepals spreading at anthesis, ¹/₅-¹/₂-connate, 1.8-2.5 mm long, 2.0-2.5 mm wide, coriaceous, ovate to broadly triangular, apex acute, densely sericeous abaxially.

Petals yellow, cream-colored, or amber colored and the inner petals tinged with red at the base *in vivo*; outer petals erect at anthesis, 9.5-15.5 mm long, 2.0-3.3 mm wide at base, 1.0-1.7 mm wide at midpoint, coriaceous or slightly fleshy, linear to linear-lanceolate, flat adaxially, faintly keeled abaxially, apex obtuse, pubescent except for glabrous concave base adaxially, sericeous abaxially; inner petals bent or curved outward at anthesis, 8.5-11.2 mm long, 1.4-2.7 mm wide at base, 0.5-0.8 mm wide at midpoint, coriaceous or slightly fleshy, linear-subulate, keeled on both surfaces, apex obtuse, base concave with undifferentiated margin, densely puberulent except for the glabrous base on both surfaces.

Stamens c. 75; fertile stamens 0.8-1.2 mm long, narrowly oblong, anther connective apex 0.1-0.2 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 7-10-locellate, filament 0.2-0.3 mm long; outer staminodes 1.0-1.2 mm long, narrowly oblong to clavate, apex obtuse to rounded; inner staminodes 0.7-0.8 mm long, clavate, apex truncate or slightly emarginate; staminal cone 0.9-1.5 mm in diameter, 0.7-1.0 mm high, concealing the basal half of the ovaries, rim irregularly laciniate.

Carpels 3-5; ovaries *c*. 0.8 mm long, oblong, densely sericeous, stigmas connivent, 1.6-2.5 mm long, filiform, glabrous or occasionally pubescent.

Fruit of up to 6 monocarps borne on a pedicel 6-8 mm long, 4-5 mm thick, glabrate; torus 10-18 mm in diameter, 12-14 mm high, depressed-globose to pyramidal; monocarps with greenish red, red, or brown exterior and pinkish red endocarp *in vivo*, 2.3-4.1 cm long, 1.8-2.5 cm wide, 1.8-2.7 cm thick, ellipsoid to ovoid, not torulose, apex rounded, base sessile or occasionally contracted into a stipe *c*. 4 mm long and 8 mm thick, sometimes faintly verrucose, slightly wrinkled, dull, lenticellate, glabrate; pericarp 1.4-1.8 mm thick.

Seeds up to 8 per monocarp, in two slightly overlapping rows, perpendicular to long axis, 10.8-15.2 mm long, 8.8-12.0 mm wide, 3.9-5.9 mm thick, oblong to nearly circular and narrowed into a short neck around the micropyle, narrowly oblong in cross-section, brown to reddish brown, smooth or slightly wrinkled, dull or slightly shiny, perichalazal ring sometimes slightly raised; sarcotesta color *in vivo* unknown, but sometimes visible as white crust on dried seeds; aril absent.

Notes

Xylopia lastelliana is readily distinguished from most other Madagascar species of *Xylopia* by the densely and persistently sericeous abaxial leaf surfaces, the hairs most persistent along the midrib. Only *X. sclerophylla*, sp. nov., has similar leaf indument, and its leaves are smaller, acute to more often obtuse at the apex rather than acute to acuminate, and its monocarps are longitudinally ridged and only sparsely lenticellate. The monocarps of *X. lastelliana* are large and thick-walled, containing somewhat flattened seeds narrowed to a donutshaped ring around the micropyle similar to that seen in the seeds of *X. buxifolia*.

The variety distinguished by Cavaco and Keraudren, *X. lastelliana* var. *acuta*, merges imperceptibly into the nominate variety and is not recognized here; there is variation in shape of the leaf apex even on the same specimen in this species. Some specimens previously determined by Keraudren as *X. lastelliana*, however, are here segregated as *Xylopia sclerophylla*, sp. nov., which has leaves that are consistently less sericeous and more coriaceous, and monocarps with a thinner pericarp.

Two collections from the Maevarano River region of northwestern Madagascar, Capuron 3004 (OWU, P[P01989230]), Gorges de la Maevarano [c. 14°38'S, 48°17'E], 1350 m, 12.II.1950 (fr.), and Humbert & Capuron 25381 (OWU, P[P02034869]), Montagnes au Nord de Mangindrano (Haute Maevarano), jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga: Centre Nord), vallon d'Ambatohafo [14°10'S, 48°58'E], 1350 m, 19.I.-12.II.1951 (fr.), while having leaves resembling those of X. lastelliana in shape and indument, are distant from other localities for the species and were collected from much higher elevations. Neither collection has flowers. The leaves are toward the small end of the range for X. lastelliana, 4.2-4.6 cm long and 1.5-1.6 cm wide. The monocarps are more oblong than ovoid or ellipsoid, c. 4.6 cm long, 2.7 cm wide, and 2.4 cm thick, wrinkled, and lacking lenticels, and have an even thicker pericarp (c. 2.6 mm), and the seeds do not have the donut-shaped ring around the micropyle seen in the seeds of X. lastelliana elsewhere. Similarly, the specimen Gautier et al. LG 3161 (K, P[P01954149]), from Réserve Spéciale de Manongarivo, Ambongomirahavavy (13°59'S, 48°17'E), confluence Manongarivo/Marofotrotro, 100 m, 29.IX.1996 (buds, immature fr.), has a silvery indument similar to that seen in *X. lastelliana*, and is from a tree 25 m tall with a d.b.h. of 40 cm, but its monocarps are smaller than those in both the Maevarano and eastern lowland material.

No locality is given in the protologue or on the label of the type specimen of *X. lastelliana* collected by de Lastelle,



Fig. 24. – Plate including illustration of Xylopia Iamii Cavaco & Keraudren (F-J), reproduced from Cavaco & Keraudren (1958).

but given that de Lastelle made his home in Tamatave (now Toamasina; Ellis 1859) it is likely that the specimen came from the vicinity of that city.

27. *Xylopia lemurica* Diels (Fig. 17L-N)

Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 350 (1925). — Type: Madagascar. Prov. Toamasina ["Madagascaria centralis"], Analamazaotra, in silvis, 800 m, II.1912 (fl., fr.), *Perrier de la Bâthie 4975* (lecto-, here designated, P[P030406]!; isolecto-, B [B100153146]!).

- Xylopia pseudolemurica Cavaco & Keraudren, Bulletin de la Société botanique de France 103: 276 (1956). — Type: Madagascar. Prov. Antsiranana, Massif de l'Ambohitsitondroina de Mahalevona, nord de la presqu'île de Masoala, vers 400 m d'alt., 28.XI.1953 (fl.), Capuron 8674 (lecto-, here designated, P[P030416]!; iso-, OWU!, P[P030417, P030418]).
- Xylopia microphylla Cavaco & Keraudren, Bulletin de la Société botanique de France 103: 277 (1956). — Type: Madagascar. Prov. Toamasina ["Domaine de l'Est"], massif du Beanjada, N de la presqu'île Masoala, vers 1000 m d'alt., 28.XII.1953 (fl.), Capuron 8815 (holo-, P[P030407]!; iso-, P[P030408, P030409]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana. SW of Andapa, near SW edge of Anjanaharibé-Sud Reserve, 14°48'15"S, 49°26'45"E, 1000-1100 m, 6.VIII.1997 (fr.), *McPherson 17265* (MO); Marombihy, Mandena, Parc national de Marojejy, le long d'un affluent de la rivière Manantenina, 11 km du village Manantenina, 14°26.2'S, 49°44.5'E, 1200 m, 1.XI.1996 (fl., fr.), *Messmer et al. NM 312* (G, MO); Préfecture d'Antalaha, Sous-Préfecture d'Andapa, Commune rurale de Bealampona, Quartier de Befingotra, Sud Ouest d'Andapa, Réserve spéciale d'Anjanaharibe-Sud, suivant la route nationale d'Andapa-Bealanana, environ d'Ampiferantany, 14°47'45"S, 49°27'45"E, 1020 m, 3.VII.1995 (immature fr.), *Ravelonarivo & Remainty 829* (MO, OWU, P[P01954125]).

Prov. Fianarantsoa. Řanomafana National Park, parcelle 3, S of National Road 25 at 7 km W of Ranomafana, Talatakely trail system, 21°15'30"S, 47°25'00"E, 950-1150 m, 8.XII.1992 (fl.), *Turk & Radriamanatena 202* (MO); Ranomafana National Park, parcelle 3, S of National Road 25 at 7 km W of Ranomafana, Talatakely trail system, 21°15'30"S, 47°25'00"E, 950-1150 m, 26.I.1993 (fl., fr.), *Turk & Solo 262* (MO, OWU).

Prov. Mahajanga. Sous-Préfecture de Befandriana-Nord, commune rurale de Matsoandakana, Quartier de la Belalona, Sud-Ouest d'Andapa, 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.XII.1994 (fl.), *Ravelonarivo & Rabesonina 549* (OWU).

Prov. Toamasina. Fivondronana: Moramanga, Commune: Andasibe, Fokontany: Menalamba, Ambatovy Forest, 18°50'13"S, 48°19'19"E, 1130 m, 17.I.2005 (fl., fr.), *Antilahimena et al. 3208* (K n.v., MO, P[P02006079]); Fivondronana: Moramanga, Commune: Andasibe, Fokontany: Berano, Ambatovy Forest, 18°48'29"S, 48°18'45"E, 1120 m, 26.I.2005 (fl.), *Antilahimena et al. 3243* (MO, OWU); Fivondronana: Moramanga, Commune: Andasibe, Fokontany: Berano, Ambatovy Forest, 18°49'14"S, 48°20'07"E, 1110 m, 3.II.2005 (fl., fr.), *Antilahimena et al. 3265A* (MO, P[P06901344]); Alaotra-Mangoro Region, Moramanga, Commune Ambohibary, Fokontany Ampitambe, 18°51'02" S, 48°17'24"E, 1080 m, 9.II.2007 (fl.), *Antilahimena & Edmond 5245* (K n.v., MO, P[P06901346]); Phelps Dodge project site, *c.* 15 aire-km NE of Moramanga, *c.* 11 km E of Antanambao, between Ambatovy-South and Analamay-East, Torotorofotsy River, Berano, 18°50'32"S, 48°19'55"E, 1000 m, 18.II.1997 (fr.), Andriatsiferana et al. 2184 (MO, P[P02006077], WAG); Alaotra Mangoro, Moramanga, Ambohibary, Ampitambe, Ambatovy, 18°49'S, 48°18'E, s. d. (immature fr.), Andriatsiferana et al. 2489 (MO); ouest du village d'Antanandava (P. K. 45 de la route Moramanga-Anosibe, XI.1968 (fr.), Capuron 28412-SF (K); Phelps Dodge project site, c. 15 aire-km NE of Moramanga, c. 11 km E of Antanambao, between Ambatovy-South and Analamay-East, Torotorofotsy River, Berano, 18°50'32"S, 48°19'55"E, 1000 m, 20.II.1997 (fl.), Rakotomalaza et al. 1145 (MO); Vatomandry, Ambalabe, Ambinaninandro II, direction sud ouest de Toby Foara, 19°09'36"S, 48°34'44"E, 636 m, 20.I.2006 (fl.), Razanatsima & Honoré 82 (K n.v., MO); Fiv. Moramanga, Ambatovy, Sahavaharina Forest, 18°51'32"S, 48°20'44"E, 975 m, 3.II.2006 (fl.), Rogers & Antilahimena 1019 (OWU).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Xylopia lemurica occurs in eastern Madagascar, from Antsiranana Province south to Fianarantsoa Province in humid forests along the eastern slope at elevations of 400-1150 meters, most commonly from over 1000 m (Fig. 29). This species is one of several, also including X. beananensis, X. danguyella, and X. perrieri, that frequent lower montane forests. The labels of the two Turk collections from Ranomafana describe the habitat as humid montane forest characterized by trees of Weinmannia spp., Monimiaceae (Tambourissa, Decarydendron, Ephippiandra), Lauraceae (primarily species of Ocotea and Cryptocarya), with Psychotria spp., Oncostemum spp., and Cyathea spp. abundant in the understory, a similar list of associates as given for Xylopia perrieri at the same site. The MO sheet of *Turk & Solo 262* shows three spiny galls, which appear to have developed from flowers. Similar "flower galls" occur in some African species, such as X. mwasumbii (Johnson et al. 1999). Specimens with flowers have been collected from November to February, and with fruits in July, August, and from November to February. With an EOO value of 38756 km² and an AOO value of 64 km², the species has a relatively large range but is seemingly uncommon throughout, and is given a preliminary conservation assessment of Data Deficient.

LOCAL NAMES. — Fotsimavo (*Perrier de la Bâthie 4975*), hazoambo (six collections), ramiavona (*Turk & Radriamanatena 202, Turk & Solo 262*).

DESCRIPTION

Tree up to 17 m tall; d.b.h. up to 27 cm.

Twigs finely appressed-pubescent, the hairs 0.1-0.8 mm long, becoming glabrate; twigs often branching with expansion of new growth, nodes with one or frequently two axillary branches.

Leaves with larger blades 3.5-8.3 cm long, 1.4-2.8 cm wide, chartaceous to subcoriaceous, discolorous, purplish brown adaxially, brown abaxially, elliptic to lanceolate, apex acuminate, the acumen 3-11 mm long and often bent to the side when pressed, base cuneate and short-decurrent on petiole, margin flat, not revolute, glabrous except for erect hairs on midrib adaxially, sparsely appressed-pubescent with the hairs longest, densest, and most persistent on the midrib and margin abaxially; midrib light brown toward base adaxially, secondary veins irregularly brochidodromous, 11-15 per side, diverging at 50-60° from midrib, these and higher-order veins indistinct to slightly raised adaxially, raised and forming a fine reticulum abaxially; petiole 1.5-6 mm long, shallowly canaliculate, longitudinally wrinkled, sparsely pubescent to glabrate.

Inflorescences axillary, 1-2-flowered, pedunculate or pedicels arising separately from leaf axil, densely fine-pubescent; peduncle 0.8-2 mm long; pedicels 2 per peduncle, 3.1-9.3 mm long, 0.5-0.8 mm thick; bracts 2-3, 2 attached near midpoint and sometimes a third just above the pedicel base, caducous or rarely persistent, 1-2 mm long, broadly ovate to semicircular; buds linear-subulate to linear-lanceolate, apex obtuse, occasionally falciform.

Sepals spreading at anthesis, ¹/₅-¹/₂-connate, 1.5-2.7 mm long, 1.8-2.6 mm wide, coriaceous, triangular, apex acute, pubescent abaxially.

Petals yellow, red to maroon at base on both surfaces *in vivo*; outer petals erect or slightly curved outward at anthesis, 10.2-20.3 mm long, 1.9-3.3 mm wide at base, 0.7-1.4 mm wide at midpoint, fleshy, linear, flat or slightly concave adaxially, keeled except at the base abaxially, apex obtuse, puberulent adaxially, sericeous abaxially; inner petals perhaps slightly curved outward at anthesis, 8.3-18 cm long, 1.6-2.4 mm wide at base, 0.6-1.0 mm wide at midpoint, fleshy, linear, keeled except at the base adaxially, keeled to the base abaxially, apex acute to obtuse, base deeply concave with undifferentiated margin but somewhat bilobed at widest point, puberulent only along keel adaxially, puberulent abaxially.

Stamens 120-160; fertile stamens 0.8-1.2 mm long, oblong, anther connective apex 0.2-0.3 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 6-8-locellate, filament 0.2-0.5 mm long; outer staminodes 1.0-1.1 mm long, oblong, apex rounded or truncate; inner staminodes 0.7-0.8 mm long, oblong or broadly clavate, apex rounded, truncate, or umbonate; staminal cone 1.1-1.9 mm in diameter, 0.6-1.1 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 6-9; ovaries 1-1.2 mm long, narrowly oblong, densely pubescent, stigmas loosely connivent, 2.2-2.7 mm long, filiform, sparsely pubescent.

Fruit of up to 7 monocarps borne on a pedicel 6-15 mm long, 2.1-6 mm thick, glabrate; torus 7-12 mm in diameter, 4-8 mm high, depressed-globose; monocarps with a pink to red exterior and pinkish red endocarp *in vivo*, 1.5-2.9 cm long, 1.1-1.5 cm wide, 1.2-1.4 cm thick, ellipsoid, oblong, or obovoid, slightly torulose, apex obtuse to rounded, base sessile, slightly narrowed, smooth, longitudinally wrinkled, dull, with a longitudinal adaxial ridge, glabrate; pericarp 0.7-1.5 mm thick.

Seeds up to 6 per monocarp, in two rows or sometimes a single irregular row, perpendicular to long axis, 8.5-10.3 mm long, 5.4-7.4 mm wide, 4.5-5.8 mm thick, ellipsoid to oblong-ellipsoid, slightly thickened around the micropyle, semicircular to wedge-shaped in cross-section, brown to light brown, smooth, dull, perichalazal ring forming a slight ridge on antiraphal side; sarcotesta yellow-green *in vivo*; aril absent.

Notes

Xylopia lemurica may be distinguished by the relatively small elliptic to lanceolate and usually abruptly acuminate leaves, the needle-like inner petals, and the relatively small blunt sessile and torulose monocarps often marked by an adaxial ridge. The hairs along the leaf margins and abaxial midrib tend to be both longer and more persistent than on the rest of the leaf. *Xylopia perrieri*, which occurs in many of the same lower montane sites (both were described from the same type locality, Analamazaotra), may be distinguished by the obtuse leaves with denser persistent abaxial pubescence of uniform length, the broader petals, and larger and shinier monocarps with larger seeds. In the linear sparsely pubescent petals and shape of the monocarps *X. lemurica* more closely resembles *X. buxifolia*, but the sharp leaf acumen of *X. lemurica* will distinguish the two.

Cavaco & Keraudren (1956) distinguished Xylopia pseudolemurica from X. lemurica on the basis of the color of the indument on the young branches and petioles ("chamois-clair"), by the larger fawn-velutinous calyx, and the longer petals. *Xylopia microphylla* was distinguished from *X. lemurica*, in the same publication, by its leaves densely publication with silvery hairs, and from X. pseudolemurica by its smaller leaves, and the calyx smaller and lacking the fawn-colored hairs. With additional collections it is now possible to see that all of these characters represent extremes of variation. Two collections from Ranomafana National Park illustrate the situation. The specimen Turk & Radriamanatena 202 bears flowers with sepals c. 2.7 mm long but outer petals only c. 11.5 mm in length, thus not in keeping with the combination of characteristics used by Cavaco and Keraudren to separate X. lemurica and X. pseudolemurica, and has a relatively coarse sericeous indument on the leaves and twigs of silvery hairs 0.7-0.8 mm long, which seems to be quickly lost. The specimen Turk & Solo 262, in contrast, has flowers with sepals c. 1.9 mm long and outer petals 16.5-19 mm long, and finer pubescence (hairs only 0.2-0.3 mm long) on the twigs and leaves. The type specimen of X. lemurica does, in fact, have relatively short hairs and short petals compared to the type specimen of X. pseudolemurica.

Neither the P sheet nor the B sheet of *Perrier de la Bâthie* 4975, the type collection of *Xylopia lemurica* Diels, is identified as the holotype. Both bear drawings of floral details, presumably by Diels. The P sheet is the more ample material, and shows a greater study with respect to the detail drawings attached, and is chosen as the lectotype.

The type information given in the protologue for *Xylopia* pseudolemurica is "Domaine de l'Est: nord de Tamatave, Service Forestier 7888 (type)." A second collection is also listed: "Domaine de l'Est : [...] massif de l'Ambohitsitondroina de Mahalevona, *Capuron 8674*." The type locality and number appear to have been an error, as this information has been crossed out on the holotype sheet and the collection details for the *Capuron 8674* specimen substituted. A note has also been glued to the sheet, stamped with "Service des Eaux et Forets, Madagascar", stating that the sheet cannot be 7888 *SF*. The specimen *Capuron 8674* is therefore understood to

be the type of this name, but the sheet P030416 is designated here as the lectotype to avoid future confusion.

A chromosome number of 2n=16 was reported for this species by Morawetz & Le Thomas (1988) but the voucher collections, *Le Thomas 15* and *Le Thomas 20*, have not been traced. Given the low elevation provenance of the collections, however, it is likely that the collections do not represent this species.

28. *Xylopia lokobensis* D.M.Johnson & N.A.Murray, sp. nov. (Fig. 23A-E)

In the relatively broad flowers with sepals exceeding 4 mm in length and the short obliquely oblong monocarps, *Xylopia lokobensis*, sp. nov., is most similar to *X. capuronii*, but it is distinguishable by the sparse yellowish brown indument on the twigs, leaves, and monocarps, the oblong leaf blades with flat margins, the broad leaf acumen 4-10 mm long, and the outer petals 13-19 mm long. *Xylopia capuronii*, in contrast, has dense dull red indument on the twigs, leaves, and monocarps, narrowly oblong to elliptic leaf blades with strongly revolute margins, a narrow leaf acumen 5-9 mm long, and outer petals 11-13 mm long.

TYPE. — **Madagascar. Prov. Antsiranana**, Fivondronana Nosy-Be, Lokobe Réserve intégrale, Ampasindava, 13°24'44"S, 48°18'53"E, 300 m, 7.XII.1996 (fl., fr.), *Antilahimena 340* (holo-, P[P01986965]!; iso-, MO!).

PARATYPES. — Madagascar. Prov. Antsiranana, Réserve naturelle intégrale No. 6 – Lokobe, south side of the reserve ("Study Site" for the Black Lemur Forestry Project), 5 km SE of Hell Ville, Nossi Be, 13°25'S, 48°18'E, 50 m, 24.XI.1992 (fl., fr.), *Birkinshaw 186* (MO n. v., OWU, P[P01986963]); région Diana, Ampasindava, forêt de Bongomihirahavavy, 13°45'34"S, 48°05'54"E, 400 m, 2.XII.2012 (fr.), *Gautier LG 6068* (G, n. v., P[P00982774]).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia lokobensis*, sp. nov., occurs in northwestern Madagascar, on Nosy-Be island and the nearby Ampasindava peninsula, in humid forest at elevations from 50 to 400 m (Fig. 29). Specimens with both flowers and fruits were collected in November and December. With an EOO value of 144 km² and an AOO of 8 km² the species is given a preliminary conservation assessment of Endangered. One of its known populations, however, lies within the protected Lokobe Reserve.

LOCAL NAMES. — Hazoabo, moranga (Antilahimena 340).

Description

Tree up to 18 m tall; d.b.h. up to 8 cm.

Twigs densely yellowish brown-pubescent, the hairs 0.2-0.5 mm long, eventually glabrate; nodes with one axillary branch.

Leaves with larger blades 8.0-13.4 cm long, 2.7-4.8 cm wide, subcoriaceous, discolorous, dark brown to olive-gray adaxially, brown abaxially, oblong, apex obtuse to short-acuminate, the acumen 4-10 mm long, base broadly cuneate to rounded, short-decurrent on petiole, margin flat, not revolute, glabrous except for the pubescent midrib adaxially, appressed-pubescent abaxially; midrib often darkened adaxially, secondary veins irregularly brochidodromous, 14-20 per side, diverging at

60-80° from midrib, these and higher-order veins slightly raised on both surfaces; petiole 5-10 mm long, shallowly canaliculate, smooth, pubescent.

Inflorescences axillary, 1-flowered, not pedunculate, yellowish brown-pubescent; pedicels 6-8.3 mm long, 1.2-1.4 mm thick; bracts 2, one near midpoint, one just proximal to the sepals, caducous or somewhat persistent, 3-3.8 mm long, semicircular; buds broadly lanceolate, apex obtuse, slightly falciform.

Sepals somewhat spreading at anthesis, ¹/₄-¹/₃-connate, 4.2-4.6 mm long, 5.0-5.2 mm wide, coriaceous to slightly fleshy, broadly ovate to triangular, apex broadly acute to obtuse, pubescent abaxially.

Petals light green in bud *in vivo*; outer petals slightly spreading at anthesis, 13-19 mm long, 3.5-6 mm wide at base, 1.8-3 mm wide at midpoint, fleshy, lanceolate, keeled on apical ¹/₄ but otherwise flat adaxially, slightly keeled abaxially, apex obtuse to acute, densely puberulent except for the glabrous base adaxially, densely appressed-pubescent abaxially; inner petals probably slightly spreading at anthesis, 8.3-13 mm long, *c.* 2.8 mm wide at base, *c.* 1.3 mm wide at midpoint, slightly fleshy, lanceolate, keeled except for the concave base adaxially, keeled abaxially, apex acute to obtuse, base concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces.

Stamens and carpels not examined.

Fruit of up to 5 monocarps borne on a pedicel 9-11 mm long, 4-7 mm thick, glabrate; torus 9-17 mm in diameter, 8-10 mm high, irregularly globose; monocarps with green exterior and red endocarp *in vivo*, 2.4-3.0 cm long, 1.4-2.3 cm wide, 1.4-1.6 cm thick, obliquely oblong, occasionally slightly torulose, apex rounded to obtuse, base sessile or contracted into a stipe 2-3 mm long, 4-8 mm thick, finely verrucose, obliquely wrinkled, dull, finely tomentose; pericarp 0.6-1.7 mm thick.

Seeds up to 4 per monocarp, in two rows, oblique to perpendicular to long axis, 9.5-12.6 mm long, 5.6-8 mm wide, 4.5-6.5 mm thick, oblong-ellipsoid to obovoid, wedge-shaped, broadly elliptic, or semicircular in cross-section, brown, smooth to slightly wrinkled and pitted, dull, perichalazal ring not evident; sarcotesta color *in vivo* not determined; aril absent.

Notes

Xylopia lokobensis, sp. nov., belongs to the group of sect. *Stenoxylopia* species with clavate stigmas, and is one of several species with medium-sized leaves, moderately large flowers and subsessile oblong monocarps. The species has a tendency for the midrib and secondary veins to be darkened on the adaxial surface. Two of the three collectors of this species remarked on the strong aroma of the foliage, a characteristic not noted for other Madagascar *Xylopia* species. *Xylopia lokobensis*, sp. nov., may distinguished from *X. galokothamna*, sp. nov., which

occurs in the same general region of Madagascar, by the tree rather than shrub habit, the leaf blade short-decurrent on a longer petiole (cf. Fig. 23A, I), and the absence of both beak and stipe on the monocarps.

Xylopia lokobensis, sp. nov., was identified as *Xylopia* sp. in Birkinshaw (2001), where it was listed as a minor food source for the Black Lemur (*Eulemur macaco macaco*). *Xylopia lokobensis*, sp. nov., is one of the few large-fruited Madagascar *Xylopia* species for which monocarp dehiscence and red endocarp color have been documented, but color of the sarcotesta covering the seed has not been reported. The specimen *Birkinshaw 186* was included in the molecular phylogenetic analysis of Stull *et al.* (2017), where it was one of four accessions identified as *Xylopia* sp. aff. *fananehanensis*, which, although they are recognized in this treatment as four distinct species, formed part of a single subclade in the phylogenetic analysis.

29. *Xylopia longirostra* D.M.Johnson & N.A.Murray, sp. nov. (Fig. 25A-E)

Species resembling *Xylopia ambanjensis* and *X. lastelliana* in the lanceolate leaves under 9 cm long with acuminate apices, but differing from both in the leaf acumen forming 1/4-1/5 rather than 1/6-1/8 of the leaf length. It additionally differs from *X. ambanjensis* in the subcoriaceous rather than chartaceous leaves, the absence of persistent hairs along the leaf margins, and the mature monocarps larger, 3.8-5 cm long, and more prominently lenticellate. From *X. lastelliana* it differs in the sparsely appressed-pubescent rather than densely sericeous abaxial leaf surfaces.

TYPE. — Madagascar. Prov. Toamasina, Vohibola, forest N to NNW of village of Andranokoditra, N of Lac Ampitabe, 18°33'34"S, 49°15'17"E, 5 m, 12.II.2003 (fr.), *Lowry et al. 6064* (holo-, MO!; iso-, OWU!, P[P01987028]!).

PARATYPES. — Madagascar. Prov. Toamasina, Analanjirofo Region, Vavatenina, Sahatavy, Sahalangina, forêt d'Anjirobe, 17°28'02"S, 48°54'23"E, 550 m, 26.X.2000 (buds), Andrianjafy et al. 120 (MO); à Ambila-Lemaitso, 14.XII.1967 (fr.), Capuron 28035 SF (K, P[P01987026]; Foulpointe, 22.I.1973 (st.), Debray 1974 (P[P02034676, P02034677]); Fivondronana: Brickaville, Firaisana: Ambinaninony, Fokontany: Andranokoditra, forêt littorale sur sable du label Conservation Biodiversité Développements (CBD) à Vohibola, 18°34'50"S, 49°15'16"E, 10 m, 8.XII.2001 (fr.), Rabenantoandro et al. 854 (K, MO, P[P01987029]); Analanjirofo Region, Fivondronana Vavatenina, Commune Ambodimangavalo, limite du Parc national de Zahamena, 17°33'41"S, 48°54'14"E, 850 m, 2.V.2003 (immature fr.), Rakotonandrasana et al. 682 (OWU, P[P01954127]); Fivondronana: Brickaville, Firaisana: Ambinaninony, Fokontany: Andranonkoditra, forêt littorale de Vohibola, 18°33'55"S, 49°15'22"E, 3 m, 24.X.2002 (fr.), Razakamalala 266 (K, MO, NY).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — Five of the seven collections of *X. longirostra*, sp. nov., were made in the Vohibola coastal littoral forest area of east-central Madagascar, where the species occurs with *X. retusa*, sp. nov., another near-endemic to the area and two more widespread *Xylopia* species, *X. buxifolia* and *X. humblotiana*. Two incomplete specimens of *X. longirostra*, sp. nov., have also been collected from humid forest on low summits inland at elevations of 550 and 850 meters (Fig. 29). A specimen with flower buds was collected in October, and the specimens with fruits were collected in February, May (immature), October, and December. The EOO of 5003 $\rm km^2$ and AOO of 24 $\rm km^2$ lead to a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Ankahatra madinika lava ravina (*Rakotonandrasana* 682), hazoambo (*Andrianjafy et al. 120*).

DESCRIPTION

Tree up to 12 m tall; d.b.h. up to 20 cm.

Twigs glabrous or sparsely pubescent, the hairs 0.1-0.4 mm long, soon glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 4.9-7.0 cm long, 1.3-1.7 cm wide, subcoriaceous, slightly discolorous, brown-olive adaxially, light brown abaxially, lanceolate to oblong-lanceolate, apex acuminate, the acumen 9-16 mm long, base cuneate, short-decurrent on petiole, margin slightly recurved, glabrous adaxially, sparsely appressed-pubescent abaxially; midrib reddened toward base adaxially, secondary veins weakly brochidodromous, 11-13 per side, diverging at 50-70° from midrib, these and higher-order veins slightly raised on both surfaces; petiole 3-5.5 mm long, canaliculate, slightly wrinkled, glabrate or with a few hairs.

Inflorescences axillary from the axils of newly expanding shoots, 1-flowered, not pedunculate, sparsely pubescent; pedicels [probably not fully elongated] 1.8-2.5 mm long, *c*. 0.7 mm thick; bracts 2, both attached near the pedicel midpoint, persistent [but flowers immature], 0.9-1.2 mm long, broadly ovate to semicircular; buds lanceolate, apex acute.

Sepals with position at anthesis unknown, ¹/₅-¹/₃-connate, *c*. 1.3 mm long, *c*. 1.6 mm wide, coriaceous, ovate to broadly triangular, apex acute, margins ciliate and with a few sparse hairs abaxially.

Petals, stamens, and carpels unknown.

Fruit of up to 4 monocarps borne on a pedicel 4-7 mm long, 3.5-4.5 mm thick, glabrate; torus 5.5-10 mm in diameter, 6-7 mm high, depressed-globose; monocarps with orange yellow to red exterior *in vivo*, 3.8-5.0 cm long, 2.3-2.4 cm wide, 2.3-2.6 cm thick, ellipsoid to ovoid, not torulose, apex rounded, base sessile or occasionally contracted into a stipe 3.5-4 mm long, 5.5-9 mm thick, verrucose, longitudinally wrinkled, conspicuously marked with raised lenticels, dull, glabrate; pericarp *c*. 2.1 mm thick.

Seeds c. 10 per monocarp, in two rows, perpendicular to long axis, 18.7-19.6 mm long, 10.7-11.4 mm wide, 8.5-9.2 mm thick, oblong-ellipsoid, broadly wedge-shaped in cross-section, chestnut brown, smooth, slightly shiny, perichalazal ring not evident; presennce of sarcotesta undeterminable; aril absent.

Notes

Xylopia longirostra, sp. nov., has relatively small narrow leaves similar to those of *X. ambanjensis*, but the leaves are subco-

riaceous and shiny adaxially and, as indicated by the specific epithet, have an acumen forming a greater proportion of the total blade length, about 1/4-1/5 rather than 1/6-1/8. The leaves are also less hairy than those of X. ambanjensis, lacking the persistent hairs along the midrib and leaf margins. The monocarps of X. longirostra, sp. nov., are prominently lenticellate and much larger than those of X. ambanjensis, with seeds over 18 mm long. The lenticels are often prominent on the twigs as well, giving them a bumpy appearance. Another character that X. longirostra, sp. nov., and X. ambanjensis have in common is that the leaf acumen is wrapped around itself early in development and sometimes remains that way in mature leaves (Fig. 25B). Xylopia lastelliana resembles X. longirostra, sp. nov., in its leaf shape and fruit morphology, and occurs in similar localities in a comparable range of elevations. Xylopia longirostra, sp. nov., is readily distinguished from X. lastelliana, however, by the absence of sericeous leaf indument on the leaves as well as by the longer and more abrupt leaf acumen.

The specimens *Andrianjafy et al. 120* and *Rakotonandrasana* 682 were collected some distance from the coast and slightly north of the forests where the other specimens were collected, but the leaves are identical in shape and texture. One of these specimens has only flower buds, while the other has only immature fruits, which limits additional comparisons.

30. *Xylopia marojejyana* D. M.Johnson & N. A.Murray, sp. nov. (Fig. 25F-H)

Species resembling *Xylopia humbertii* in its elliptic subcoriaceous leaves with the blades decurrent on the petiole, but differing in the exfoliating bark of the twigs, the leaf blades 5.8-7.3 cm long and 3.1-3.3 cm wide with a narrow sharp-pointed acumen 7-10 mm long, and the conspicuous reticulum formed by the secondary and higher-order veins on the adaxial blade surface. *Xylopia humbertii*, in contrast, lacks exfoliating bark on the twigs, has leaves 5.2-6.3 cm long and 2.2-2.8 cm wide with a blunt acumen 3-5 mm long, and the secondary and higher-veins only slightly raised and not conspicuous on the adaxial blade surface. The monocarps of *X. marojejyana*, sp. nov., which are oblong, short-stipitate, and 4.0-4.9 cm long and 2.0-2.3 cm wide with strong oblique wrinkles, will distinguish it from many other Malagasy *Xylopia* species.

TYPE. — Madagascar. Prov. Antsiranana, Réserve naturelle de Marojejy, western slopes of Mt. Beondroka, 14°27'S, 49°47'E, 660-830 m, 23-24.X.1989 (fr.), *Miller & Randrianasolo 4423* (holo-, MO).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia marojejyana*, sp. nov., is known only from the Réserve Naturelle de Marojejy, where it was collected from the forested slopes of Mount Beondroka at an elevation of 660-830 meters (Fig. 29). The Marojejy massif area has been documented as a center of plant microendemism, with endemic species from many different families represented. Most of the endemics, however, are typical of higher elevation vegetation, for example *Weinmannia* in the Cunoniaceae (Bradford & Miller 2001). The type specimen with fruit only was collected in October. It has not been re-collected in 30 years. We give it a preliminary conservation assessment of Critically Endangered.

DESCRIPTION Tree 10 m tall. Twigs glabrous, with exfoliating bark; nodes with one axillary branch.

Leaves with larger blades 5.8-7.3 cm long, 3.1-3.3 cm wide, subcoriaceous, slightly discolorous, dark brown adaxially, dull reddish brown abaxially, broadly elliptic, apex acuminate, the acumen 7-10 mm long, base cuneate and long-decurrent on the petiole, margin flat, not revolute, glabrous on both surfaces; midrib concolorous with rest of blade adaxially, secondary veins weakly brochidodromous, 15-16 per side, diverging at *c*. 60° from midrib, these and higher-order veins raised and forming a conspicuous reticulum adaxially, but only slightly raised and less distinct abaxially; petiole 4-5 mm long, canaliculate, wrinkled, glabrous.

Inflorescences and flowers unknown.

Fruit of 4 monocarps borne on a pedicel c. 10 mm long, *c*. 4 mm thick, glabrous; torus *c*. 10 mm in diameter, *c*. 5 mm high, depressed-globose; monocarps with green exterior *in vivo*, 4.0-4.9 cm long, 2.0-2.3 cm wide, 1.4-1.8 cm thick, oblong to obovoid, not torulose, apex rounded, base contracted into a stipe 3-4 mm long, 4-7 mm thick, finely verrucose, strongly and obliquely wrinkled, with scattered lenticellate patches, slightly shiny, glabrous; pericarp *c*. 1.7 mm thick.

Seeds *c*. 6 per monocarp, in a single irregular row, oblique to perpendicular to long axis, *c*. 12 mm long, 6 mm wide, ellipsoid, wedge-shaped in cross-section, light brown, smooth, dull, perichalazal ring not evident; presence of sarcotesta undeterminable; aril absent.

Notes

Xylopia marojejyana, sp. nov., is superficially similar to *Xylopia lemurica*, which occurs in nearby sites, but differs in the completely glabrous twigs with exfoliating bark and glabrous broader leaf blades with a pronounced raised vein reticulum on the adaxial surface. The monocarps differ from those of *X. lemurica* in being thicker, more strongly wrinkled, and having short broad stipes. It is also similar to *X. humbertii*, sharing the shiny subcoriaceous glabrous leaves. The type collection of *X. humbertii* has only flowers and that of *X. marojejyana*, sp. nov., only fruits, preventing more detailed comparison, but the vegetative features are sufficiently different to separate the two species.

31. *Xylopia perrieri* Diels (Figs 1D; 2B; 26)

Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 351 (1925). — Type: Madagascar. Prov. Toamasina ["Madagascaria orientalis"], forêt d'Analamazaotra [c. 18°56'S, 48°25'E], 800 m, XII (fl.), Perrier de la Bâthie 4936 (holo-, P[P030413]!; iso-, P[P030414, P030415]!).

MATERIAL EXAMINED. — Madagascar. Prov. Antananarivo. Centre, Forêt d'Ambohitantely, sur le Tampoketsa d'Ankazobe

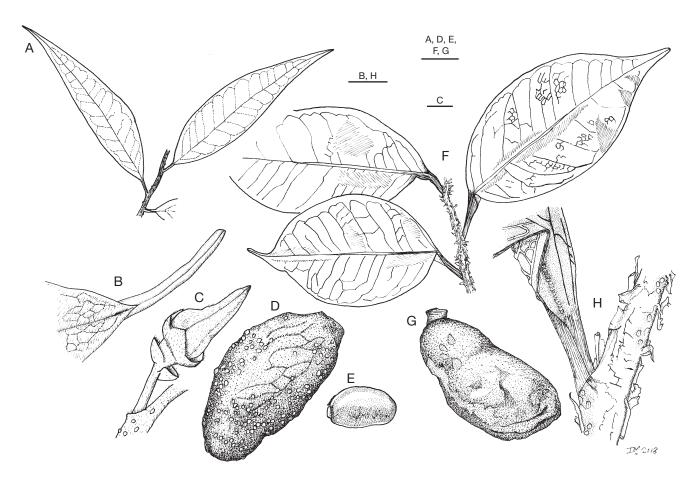


FIG. 25. — Xylopia longirostra, sp. nov., and X. marojejyana, sp. nov. A-E, X. longirostra, sp. nov.: A, habit; B, close-up of rolled apex of developing leaf; C, immature flower bud, side view; D, monocarp, side view; E, seed, side view. F-H, X. marojejyana, sp. nov.: F, habit; G, monocarp, adaxial view; H, petiole and twig, side view. A, D, E, from Lowry et al. 6064 (OWU); B, from Razakamalala 266 (NY); C, from Andrianjafy et al. 120 (MO); F-H, based on Miller & Randrianasolo 4423 (MO). Scale bars: A, D-G, 1 cm; B, H, 2 mm; C, 1 mm.

[18.161°S, 47.302°E], 1600 m, 12.II.1959 (fl.), *Capuron 20165 SF* (P[P00169371]); Bongolava ouest de Tsiroanomandidy, VII.1974 (fr.), *Morat 4640* (P[P01987127, P01987128, P01987129]).

Prov. Antsiranana. Sava, Andapa, Marojejy, Marojejy National Park, trail between camp 2 and 3, 14°26'S, 49°43'E, 10.XII.2005 (fr.), *Ranarivelo & Ravelonarivo RHS 752* (CAS, K, MO); au nord d'Andapa, dans la Réserve naturelle intégrale de Marojejy, aux environs du sommet d'Ambatosoratra, 14°32'S, 49°42'E, 1583 m, 17-24. VI.1994 (fr.), *Ravelonarivo 259* (MO); Sous-Préfecture d'Andapa, Commune Rurale d'Andapa, Quartier d'Andasibe, Réserve Spéciale d'Anjanaharibe-Sud, environ de Matsaborimaina, suivant la limite, 14°41'20"S, 49°32'30"E, 867 m, 1.IX.1995 (fr.), *Ravelonarivo & Rabesonina 845* (MO, OWU); SW d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, 14°46'15"S, 49°28'E, 1161-1424 m, 21.III.-7.IV.1994 (fr.), *Ravelonarivo et al. 99* (MO); Sava, Andapa, Doany, Anjialavahely, Antsahabalika situé à 10 km vol d'oiseau au Nord d'Anjialava, 14°13'29"S, 49°23'00"E, 1293 m, 27.II.2006 (fl., fr.), *Ravelonarivo et al. 1659* (K n.v., MO).

Prov. Fianarantsoa. Parc national Ranomafana, near Vohipara, 37.5 km due NE (BRG 46°) of Fianarantsoa, 21°13'33.6"S, 47°22'12.54"E, 1000 m, 4.XI.1997 (fr.), *Davis 1058* (K n.v., MO); Fianarantsoa, 7 km W of Ranomafana, just S of Namorona River, the Duke University Primate Center study site, 21°16'S, 47°25'E, 1000 m, 5.XII.1988 (fr.), *Schatz & Miller 2456* (BR, K n.v., MO, P[P01987121], WAG); vicinity of Ranomafana National Park, near Sahavondronana along road 45, 21°16'S, 47°21'E, 1200 m, 26.VII.1994 (fr.), *Turk & Marolahy 592* (MO); Ranomafana National Park, parcelle 3, S of National Road 25 at 7 km W of Ranomafana, Valohoaka

trail system, 21°18'S, 47°26'E, 1100-1250 m, 19-21.XI.1992 (fl., fr.), *Turk et al. 171* (MO).

Prov. Mahajanga. Forêt domaniale à Anjiamazava, versant ouest de la Réserve Spéciale d'Anjanaharibe-Sud, Manandriana, Matsoandakana, Befandriana-nord, Mahajanga, 14°48'S, 49°27.20'E, 961 m, 3-7.II.1997 (fl.), Ravelonarivo et al. 1067 (K n.v., MO, OWU). Prov. Toamasina. Alaotra-Mangoro Region, Ambatovy, 18°48'16"S, 48°19'54"E, 1133 m, 26.XI.2006 (fr.), Andriantiana 394 (MO); Alaotra Mangoro, Moramanga, Ambohibary, Ampitambe, Antsatsaka forest, 18°48'34"S, 48°16'48"E, 1076 m, 15.V.2009 (immature fr.), Antilahimena et al. 7088 (K n.v., MO); Alaotra-Mangoro Region, Moramanga, Ambohibary, Ambadidifanatsy forest, Ambatovy, 18°51'38"Š, 48°16'22"E, 966 m, 28.XI.2009 (fr.), Antilahimena et al. 7187 (MO, OWU); 1 km NE of Ankosy, 2 km outside limit of RNI Zahamena, 17°28'28"S, 48°44'12'É, 880 m, 21.I.2000 (fl.), Birkinshaw et al. 636 (GH, P[P02006076]); ouest du village d'Antanandava (P. K. 45 de la route Moramanga-Anosibe), XI.1968 (st.), Capuron 28450-SF (K); East Coast, Betampona Réserve naturelle intégrale, 40 km NW of Toamasina, 17°31'S, 49°07'E, 275-650 m, 28.IX.1993 (fr.), Lewis & Razafimandimbison 660 (MO, P[P01987125], WAG); Alaotra-Mangoro Region, Ambohilero Forêt Classée, 17°59'33"S, 48°35'51"E, 1200 m, 30.IX.2005 (fr.), Lowry et al. 6624 (K n.v., MO, P[P06774749]); Manerinerina sur le Tampoketsa entre l'Ikopa et la Betsiboka, XII.1924 (fl., fr.), Perrier de la *Bâthie 16745* (P[P00169370, P01987119]); Vohimenakely, Ambodirakauna, Ambodisaina, SE du village Ambodisaina, 17°17'25"S, 48°40'30"E, 850 m, 10.XII.2001 (fr.), Rakotondrafara et al. 95 (A, MO, P[P01986990]); Ambatondrazaka, Manakambahiny

Est., Sahamalaza, Andrarangabe, 17°43'30"S, 48°46'14"E, 950 m, 4.III.2001 (fl.), Rakotondrajaona et al. 154 (GH, P[P02006074); Toamasina, dans la partie nord-ouest de la Réserve naturelle intégrale de Zahamena, à 1 km au sud-ouest du village d'Antenina, Commune d'Imerimandroso, Ambatondrazaka, 17°30'28"S, 48°46'00"E, 910 m, 15.VIII.1994 (fr.), Randrianjanaka & Zafy 199 (K n.v., MO, OWU); Alaotra-Mangoro Region, Moramanga, Andasibe, Andasifahatelo, Ambatoaranana, Corridor Forestier Analamay Mantadia, 18°47'59"S, 48°24'29"S, 1041 m, 25.IV.2012 (immature fr.), Rasoazanany & Tafita 143 (MO, P[P00903560]); Fivondronana, Ambatondrazaka, Firaisana, Antanandava, Ankosy, Ambarikely (3 km à l'Est d'Ankosy et à 2:30 de marche à l'Ouest d'Antenina), Limite du Parc national de Zahamena, 17°29'S, 48°43'E, 800-850 m, 3.VIII.2003 (fr.), Ratovoson et al. 725 (MO); Alaotra-Mangoro Region, commune rurale d'Andasibe, Fokontany de Menalamba, Marohonkona, Site 2 Ambatovy, 18°50'45"S, 48°18'49"E, 1062 m, 7.VI.2007 (fr.), *Ravelonarivo 2514* (MO); Moramanga, Andasibe, Menlamba, en-tre Analamay and Ambatovy, 18°49'47"S, 48°18'41"E, 1224 m, 23.XI.2005 (fr.), Razafindraibe et al. 126 (MO); Alaotra Mangoro, Moramanga, Lakato, village Manasamena, 19°04'02"S, 48°22'02"E, 1041 m, 19.IX.2007 (fr.), Razanatsima et al. 376 (K n.v., MO); Analamazaotra, 1919 (immature fr.), Thouvenot 94 bis (P).

Prov. Toliara. Reserve No. 11, Andohahela, parcel 1, along trail to Eminyminy, *c*. 10 km NNE of Hazoambo, 24°45'S, 46°51'E, 600 m, 13.II.1990 (fl.), *Schatz & O'Connor 2964* (G, K n.v., MO, P[P01954118], PRE, WAG).

Province unknown. Central Madagascar, without definite locality, *Baron 1632* (BM, K n.v.).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia perrieri* occurs in scattered localities from northern to southeastern Madagascar in humid forests from 600 to 1600 m (Fig. 30). Associates include species of *Weinmannia* (Cunoniaceae), Monimiaceae, and Lauraceae in the canopy, as well as species of *Psychotria, Oncostemum*, and *Cyathea* in the understory. Specimens with flowers have been collected in January, February, March, October, and November, and with fruits in all months of the year. *Xylopia perrieri* was calculated to have an EOO of 50587 km² and an AOO of 120 km². Known from 30 localities, this species has the third largest EOO and AOO sizes of any Madagascar species. Although not of highest conservation concern, this species grows in mid-elevation forests that are vulnerable to development pressures and in-country assessment is needed. We have given it a preliminary conservation assessment of Data Deficient (Table 2).

LOCAL NAMES. — Fontsimavo (*Thouvenot 94 bis*), hazoambo (multiple collections), ramiavona (*Turk & Marolavy 592*, *Turk et al. 171*).

DESCRIPTION

Tree up to 20(-25) m tall; d.b.h. up to 30(-40) cm.

Twigs pubescent, the hairs 0.1-0.7 mm long, eventually glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 2.4-5.9 cm long, 1.5-2.1 cm wide, chartaceous to subcoriaceous, slightly discolorous, green to purplish brown adaxially, light brown abaxially, elliptic to lanceolate, occasionally ovate, apex obtuse, emarginate, or occasionally with a blunt acumen 2.5-5 mm long, base cuneate to broadly cuneate and decurrent on petiole, margin flat, not revolute, glabrous except for the pubescent midrib adaxially, uniformly appressed-pubescent abaxially; midrib with age darkened adaxially, second-ary veins weakly brochidodromous, 9-14 per side, diverging at 50-80° from midrib, these and higher-order veins forming a conspicuous reticulum on both surfaces; petiole 1.3-4.5 mm long, shallowly canaliculate or flattened, smooth, pubescent.

Inflorescences axillary, 1(-3)-flowered, pedunculate or pedicels arising separately from leaf axil, appressed-pubescent; peduncle *c*. 0.8 mm long; pedicels 2 per peduncle, 3.6-6.8 (8-11.3) mm long, 0.8-1.0 mm thick; bracts 2(-4), attached near midpoint of pedicel, caducous or the distal bract sometimes persistent, 1.5-1.8 mm long, ovate; buds lanceolate, apex obtuse.

Sepals slightly spreading at anthesis, ¹/₂-¹/₂-connate, 1.8-2.9 mm long, 2.6-2.7 mm wide, coriaceous, semicircular to triangular, apex broadly acute to apiculate, sparsely pubescent abaxially.

Petals yellowish-white, red at the base *in vivo*; outer petals more or less erect at anthesis, 10-16.4 mm long, 2.6-3.7 mm wide at base, 2.0-2.7 mm wide at midpoint, coriaceous, lanceolate, flat, apex obtuse, pubescent except for glabrous basal concavity adaxially, pubescent abaxially; inner petals more or less erect at anthesis, 8-13.7 mm long, 2.0-2.5 mm wide at base, 1.3-1.7 mm wide at midpoint, coriaceous, lanceolate, keeled on apical ¼-⅓ adaxially, keeled abaxially, apex acute, base concave with undifferentiated margin, puberulent except for glabrous base adaxially, puberulent abaxially.

Stamens *c*. 180; fertile stamens 1.2-1.4 mm long, narrowly oblong to clavate, anther connective apex 0.2-0.3 mm long, shield-shaped, overhanging anther thecae, papillate, anthers 10-11-locellate, filament *c*. 0.4 mm long; outer staminodes 1.0-1.2 mm long, clavate, apex obtuse; inner staminodes 1.1-1.2 mm long, clavate, apex rounded; staminal cone 1.7-2.1 mm in diameter, 0.7-1.0 mm high, partially to completely concealing the ovaries, rim irregularly laciniate.

Carpels 7-11; ovaries 1.2-1.4 mm long, oblong, pubescent, stigmas loosely connivent, 3.7-4.5 mm long, filiform, glabrous to pilose.

Fruit of up to 8 monocarps borne on a pedicel 6-12 mm long, 2.5-6 mm thick, glabrate; torus 4.9-20 mm in diameter, 3.8-10 mm high, irregularly depressed-globose; monocarps with yellowish red to reddish green exterior and rose-colored to orange-red endocarp *in vivo*, 1.9-4.2 cm long, 1.3-2.1 cm wide, 1.4-1.9 cm thick, oblong to pyriform, often weakly torulose, apex rounded, base sessile or contracted into a stipe 3-6 mm long, 4-6 mm thick, verrucose, longitudinally or obliquely wrinkled, usually shiny, glabrate; pericarp 0.4-1.8 mm thick.

Seeds up to 7 per monocarp, in two rows, sometimes interdigitated to form a single row, more or less perpendicular to long axis, 12.2-14.4 mm long, 8.5-10.9 mm wide, 5.6-6.9 mm thick, ovoid, semicircular to wedge-shaped in cross-section, light brown to reddish brown, smooth, dull or slightly shiny, perichalazal ring not evident; sarcotesta waxy, light green *in vivo*; aril absent.

Notes

Xylopia perrieri may be recognized by its small leaves, which are usually densely appressed-pubescent abaxially, obtuse flower buds, lanceolate petals strongly marked with red at the base, and oblong shiny monocarps. The buds and flowers most resemble those of *X. humbertii*, but the leaves of *X. humbertii*

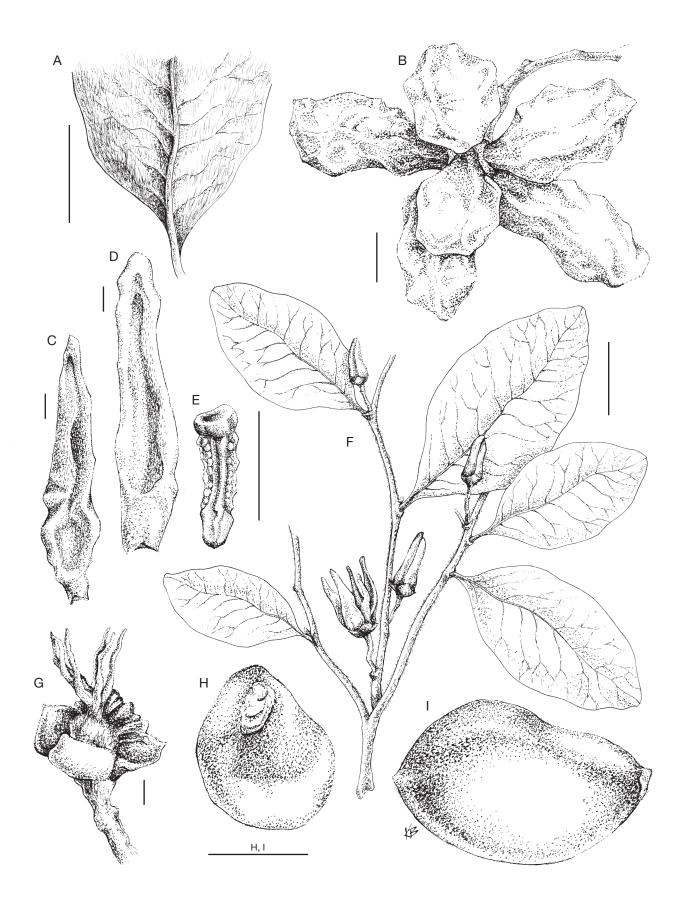


FIG. 26. — *Xylopia perrieri* Diels: **A**, abaxial surface of leaf base, showing indument; **B**, fruit; **C**, inner petal, adaxial view; **D**, outer petal, adaxial view; **E**, stamen, abaxial view; **F**, habit; **G**, calyx and gynoecium, lateral view; **H**, seed, view from micropylar end; **I**, seed, lateral view. **A**, **C**-**G**, from *Ravelonarivo et al. 1067* (OWU); **B**, **H**, **I**, from *Schatz & Miller 2456* (MO). Scale bars: A, B, F, 1 cm; C-E, G, 1 mm; H, I, 5 mm.

are glabrous. *Xylopia perrieri* also resembles *X. buxifolia*, but the latter species has acute rather than obtuse flower buds, linear rather than lanceolate petals, and leaves usually widest at or distal to the midpoint. The seeds of *X. perrieri* lack the donut-shaped thickening around the micropyle usually present on the seeds of *X. buxifolia*. Collections of *X. perrieri* come from elevations of 600-1600 m, while those of *X. buxifolia* are from elevations below 500 meters, rarely reaching 900 meters. *Xylopia perrieri* is sympatric with *X. lemurica* in some localities, for example Ranomafana National Park, but lacks the abruptly acuminate leaves, longer and more persistent hairs of the leaf midrib and margins, and needle-like inner petals found in that species.

Xylopia perrieri is remarkably uniform in morphology throughout its range. The specimen Schatz & O'Connor 2964 from Toliara Province varies from other collections in its longer pedicels, some reaching over 11 mm in length, and in bearing 3-4 bracts rather than the usual 2 on these longer pedicels. The collection is identical to others of the species, however, in its other floral features, including the bicolored outer petals described by most collectors (Fig. 1D).

Several Xylopia specimens from elevations between 400 and 1000 meters from Toamasina Province resemble X. perrieri in leaf form but have monocarps that are not wrinkled or torulose but instead are finely verrucose and have a longitudinal ridge down one side of the monocarp: Capuron 28155-SF(K n.v., P), Est, à l'Est de Marozevo (Beforona), 23.I.1968 (fr.); Poncy et al. 1565 (K, MO, P[P00373087]), Maroantsetra, Tampolo, Péninsule Masoala, entre Ambodiforaha et Laotrozo, 15°42'17"S, 49°58'43"E, 400-450 m, 2.XI.2001 (buds, fr.); Ravelonarivo et al. 4148 (MO); Atsinanana Region, Vohimanana, Dist. Brickaville, Com. Maroseranana, Fkt. Ambatolampy, 18°23'36"S, 48°48'38"E, 942 m, 23.I.2012 (fr.). Two specimens from the same area and with the same fruit morphology also have immature flower buds, which are more acute than is typical for X. perrieri: Randrianjanaka & Arnaud 9 (G, K, MO, P[P01987123]), Toamasina, Réserve naturelle intégrale 3, Zahamena, au NW du village Andratanantsoitra, 17°43'S, 48°59'E, 700 m, 9-14.XII.1993 (fl. buds, fr.); Rasoanindriana 385 (OWU), District Toamasina II, Commune Rurale de Sahambala, Fokontany de Sahavongo, village de Sahavongo, forêt d'Andasibe, 18°01'39"S 49°07'16"E, 648 m, 24.XI.2017 (buds, fr.). Also problematic is the specimen Razafitsalama & Torze 1149 (K, MO), Ambilobe, Beramanja, Anketrabe, forêt de Kalabenono, sur la chaîne Galoko, 7 km au SE d'Anketrabe, 13°39'09"S, 48°40'35"E, 795 m, 25.XI.2006 (fr.). The leaf blades of the specimen fit those of X. perrieri in both shape and indument although they are somewhat large for the species, and the monocarps are torulose and have the same shiny wrinkled surface. However, the specimen did not cluster with the accession of X. perrieri included in our molecular analysis (Stull et al. 2017). Additional field observations are needed to determine the status of all these specimens.

The type and other specimens of this species at P collected by Perrier de la Bâthie were annotated in 1934 by Ghesquière with the name *Xylopia lastelliana* var. *perrieri* (Diels) Ghesq. As far as we can determine, this combination was never published.

32. *Xylopia retusa* D.M.Johnson & N.A.Murray, sp. nov. (Figs 2A; 27L-R)

Xylopia species resembling *X. buxifolia* in the small leaves having retuse to emarginate apices, but differing in the leaves proportionally narrower, 0.6-1.1 versus 1.2-2.7 cm wide, the densely sericeous petals with the apices of the inner petals strongly bent outward at anthesis, the stigmas *c.* 0.8 mm long and oblong versus 1.9-3.3 mm long and filiform, the monocarps 3.2 cm long or shorter that are obliquely wrinkled and have a broad beak at the apex, and the orange sarcotesta of the seeds.

TYPE. — Madagascar. Prov. Toamasina, Fivondronana Sainte Marie, Firaisana Lokintsy, Fokontany Ambohidena, 16°51'11"S, 49°57'18"E, 18.II.2004 (fl.), *Rabevohitra et al. 5073* (holo-, MO!; iso-, OWU!).

PARATYPES. — Madagascar. Prov. Toamasina, Antsinanana Region, Mahavelona Foulpointe, sur la piste des lémuriens, 17°42'21"S, 49°27'21"E, 72 m, 8.X.2011 (fr.), Andriamiarinoro & Amosa 256 (MO, P[P01197860]); Est: forêt sublittorale, sur sables, à Ambila-Lemaitso, 14.XII.1967 (fr.), Capuron 28028 SF (K, OWU); Est: partie méridionale de la forêt de Vohibola (Tampina), au lieu-dit Ankany ny nofy, 17.XII.1967 (fr.), Capuron 28060_SF (AAU, B); Pref. Brickaville, Com. Amboniaonana, Fok. Andranokoditra, 18°35'53"-18°34'20"S, 49°14'42"-49°14'54"E, 53 m, 7.I.2003 (fr.), Ludovic & Rakotoarivony 212 (MO, OWU); Fivondronana: Brickaville, Firaisana: Ambinaninony, Fokontany: Andranonkoditra, forêt littorale sur sable du label Conservation Biodiversité Développements (CBD) à Vohibola, 18°34'50"S, 49°15'16"E, 10 m, 8.XII.2001 (fr.), Rabenantoandro et al. 855 (MO[2 sheets]); Fivondronana Brickaville, Firaisana Ambinaninony, Fokontany Andranokoditra, 18°35'32"S, 49°14'02"E, 5 m, 11.II.2003 (fr.), Rabenantoandro et al. 1244 (MO, OWU, P[P01986994]); Fivondronana Brickaville, Firaisana Ambinaninony, Fokontany Andranokoditra, 18°35'32"S, 49°14'02"E, 5 m, 11.II.2003 (fr.), Rabenantoandro et al. 1249 (K, MO, OWU, P[P01986991]); Toamasina District, Analalava forest, far southwest corner of the forest occurring north of the road from Foulpointe to Sahamamy, 17°42'28"S, 49°27'04"E, 17.VI.2005 (fr.), Skema et al. 73 (MO).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia retusa*, sp. nov., is restricted to central-eastern Madagascar, in littoral forests on sandy soil near the coast at elevations from sea level up to 70 meters (Fig. 30). The specimen with flowers was collected in February, those with fruits have been collected in January, February, June, October, and December. *Xylopia retusa*, sp. nov., was estimated to have an EOO of 1751 km² and an AOO of 32 km², and is given a preliminary conservation assessment of Endangered (Table 2).

LOCAL NAME. — Hazoambo (Andriamiarinoro & Amosa 256, Skema et al. 73).

DESCRIPTION

Tree up to 12 m tall; d.b.h. up to 18 cm.

Twigs finely pubescent, the hairs 0.1-0.2 mm long, soon glabrate; nodes with one or often two axillary branches.

Leaves with larger blades 2.4-3.6 cm long, 0.6-1.1 cm wide, chartaceous to subcoriaceous, slightly discolorous, pale graygreen adaxially, dull brown abaxially, elliptic, narrowly oblong, oblanceolate, or linear-lanceolate, apex rounded and retuse to emarginate, base cuneate, short-decurrent on petiole, margin

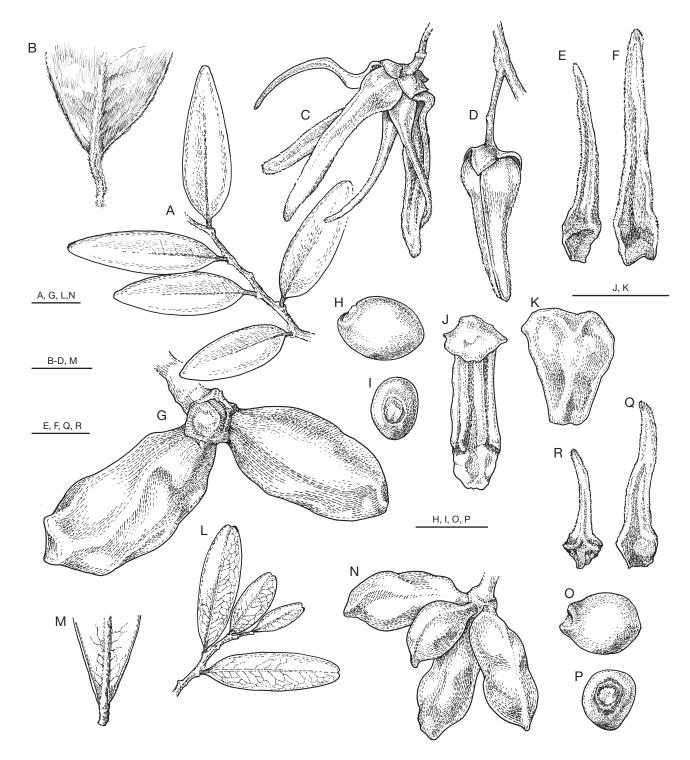


Fig. 27. – Xylopia sclerophylla, sp. nov., and X. retusa, sp. nov. A-K, X. sclerophylla, sp. nov.: A, leaves; B, leaf base, lower surface; C, flower, side view; D, flower bud, side view; E, inner petal, adaxial surface; F, outer petal, adaxial surface; G, monocarps; H, seed, side view; I, seed, view of micropylar end; J, stamen, abaxial view; K, outer staminode, abaxial view. L-R, X. retusa, sp. nov.: L, leaves; M, leaf base, abaxial surface; N, monocarps; O, seed, side view; P, seed, view of micropylar end; Q, outer petal, adaxial surface; R, inner petal, adaxial surface. A-K, from *Capuron 20041_SF* (OWU); L-N, from *Capuron 28060_SF* (B); O, P, from *Ludovic & Rakotoarivony 212* (OWU); Q, R, from *Rabevohitra et al. 5073* (OWU). Scale bars: A, G-I, L, N-P, 1 cm; B-D, M, 5 mm; E, F, Q, R, 3 mm; J, K, 1 mm.

slightly revolute, glabrous adaxially, sparsely appressed-pubescent abaxially, a tuft of hairs often visible in the apical notch; midrib concolorous with blade adaxially, secondary veins weakly brochidodromous, 9-11 per side, diverging at 50-70° from midrib, these and higher-order veins indistinct to slightly raised on both surfaces; petiole 0.8-2 mm long, semi-terete, smooth, with a few scattered hairs.

Inflorescences axillary, 1-flowered, not pedunculate, pubescent; pedicels 5-6.3 mm long, 0.5-0.7 mm thick; bracts 3, one attached just distal to the pedicel base and the other 2 on the distal ^{1/3} of the pedicel, caducous or sometimes persistent, 1-1.5 mm long, semicircular to triangular; buds lanceolate, apex obtuse.

Sepals slightly spreading at anthesis, ¹/₅-¹/₂-connate, 1.6-2.4 mm long, 2.0-2.2 mm wide, coriaceous, broadly ovate, triangular, or semicircular, apex obtuse to rounded, appressedpubescent abaxially.

Petals yellow to yellowish orange *in vivo*; outer petals erect at anthesis, 9.3-11.4 mm long, 1.7-2.2 mm wide at base, 0.7-1.0 mm wide at midpoint, coriaceous, linear, keeled from midpoint to apex adaxially, keeled abaxially, apex obtuse, densely puberulent except for the glabrous base adaxially, sericeous abaxially; inner petals erect with the apices sharply bent outward at anthesis, 6.0-7.5 mm long, 1.9-2.6 mm wide at base, 0.5-0.7 mm wide at midpoint, coriaceous, long-subulate, keeled adaxially except for concave base, slightly keeled abaxially, apex acute, base concave with undifferentiated margin but transversely thickened at the widest point, puberulent on both surfaces except for the glabrous base.

Stamens *c.* 120; fertile stamens 0.8-1.1 mm long, narrowly oblong, anther connective apex 0.1-0.2 mm long, capitate to depressed-globose, overhanging anther thecae, papillate, anthers 7-8-locellate, filament 0.2-0.3 mm long; outer staminodes *c.* 1.0 mm long, clavate, apex obliquely truncate; inner staminodes *c.* 1.0 mm long, clavate, apex truncate-emarginate; staminal cone 1.2-1.4 mm in diameter, 0.4-0.5 mm high, completely concealing the ovaries, rim even.

Carpels 2-3; ovaries 0.4-0.5 mm long, oblong, pubescent, stigmas connivent, *c*. 0.8 mm long, narrowly oblong, glabrous or with a few hairs.

Fruit of up to 5 monocarps borne on a pedicel 8-12 mm long, 3-3.5 mm thick, glabrate; torus 5.5-8 mm in diameter, 5.7-7 mm high, depressed-globose to globose; monocarps with greenish red exterior and red endocarp *in vivo*, 2.4-3.2 cm long, 1.2-1.6 cm wide, 1.2-1.5 cm thick, oblong, sometimes slightly torulose, apex rounded to a broad beak 1-2 mm long, base contracted into a stipe 1-4 mm long, 4-5 mm thick, verrucose, obliquely wrinkled, usually with a prominent longitudinal ridge abaxially, dull, glabrate; pericarp *c*. 1 mm thick.

Seeds up to 4 per monocarp, in a single row, perpendicular to long axis, 10-11.7 mm long, 7.9-8.7 mm wide, 4.8-7.0 mm thick, ellipsoid to broadly ellipsoid, flattened-elliptic or semicircular in cross-section, light brown, smooth, dull, perichalazal ring not evident; sarcotesta orange *in vivo*; aril absent.

Notes

The small leaves of *X. retusa*, sp. nov., which are retuse to emarginate at the apex, resemble those of *X. buxifolia*, which occurs in some of the same habitats and localities. This appears to represent a convergence, as *X. retusa*, sp. nov., by virtue of its

pubescent petals with the apices of the inner petals bent strongly outward and the orange sarcotesta of the seeds, most closely resembles *X. arenaria* of eastern Africa. Additional features of *X. retusa*, sp. nov., distinguishing it from *X. buxifolia* include the narrowness of the leaves, the outer petals densely sericeous rather than sparsely so (and not turning black when dried), and the smaller and somewhat beaked monocarps usually marked by strong oblique wrinkles on the surface. The short stigmas that barely exceed the tops of the stamens are also unusual.

33. *Xylopia sclerophylla* D.M.Johnson & N.A.Murray, sp. nov. (Figs 2G, H; 27A-K)

In its sericeous abaxial leaf surfaces most similar to *Xylopia lastelliana*, but differing in the leaves that are subcoriaceous with slightly revolute margins, 2.9-3.9 cm long and 0.9-1.2 cm wide, and obtuse to rarely acute at the apex, as well as monocarps that are longitudinally ridged, while the leaves of *X. lastelliana* are usually chartaceous, rarely subcoriaceous, have flat margins, are 3.5-6.7 cm long and 1.1-2.5 cm wide, and have acute to acuminate apices; the monocarps of *X. lastelliana* lack longitudinal ridges.

TYPE. — **Madagascar**. Prov. Antsiranana ["Centre (Nord)"], Massif de la Montagne d'Ambre, rive droite de la Rivière des Makis entre la Station des Roussettes et la grande cascade, 18-20.XI.1958 (fl., fr.), *Capuron 20041 SF* (holo-, BR!; iso-, K[K001208409]!, OWU!).

PARATYPES. — **Madagascar. Prov. Antsiranana**, Sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt d'Ansahabe, 13°13'S, 49°33'E, 585 m, 13.I.2004 (fr.), *Nusbaumer LN 943* (G, K, MO, P[P06774750]); sous-préfecture de Vohemar, commune rurale de Daraina, forêt de Binara (13°15'S, 49°37'E, 600 m, 11.XI.2005 (fr.), *Nusbaumer & Ranirison LN 1693* (G, P[P06901367]); sous-préfecture de Vohemar, commune rurale de Daraina, forêt de Binara, 13°15'S, 49°37'E, 702 m, 6.XII.2005 (fr.), *Nusbaumer & Ranirison LN 2328* (G); Montagne d'Ambre, partie nord, 12°29'13"S, 49°10'28"E, 770 m, 19.XII.2011 (fr.), *Ramandimbimanana & Randimbiarison SDR 186* (MO); Vohemar, Daraina, Daraina, forêt sur montagne, au sud d'Antampon'Ambilodambo, 13°09'28"S, 49°38'20"E, 681 m, 18.XI.2005 (fr.), *Razafitsalama et al. 851* (MO).

DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS. — *Xylopia sclerophylla*, sp. nov., is known only from northern Madagascar, where it occurs in humid evergreen forests at elevations of 585-770 m (Fig. 30). The specimen with flowers was gathered in November, those with fruits from November to January. With an EOO of 859 km² and an AOO of 20 km², this species is given a preliminary conservation assessment of Endangered (Table 2).

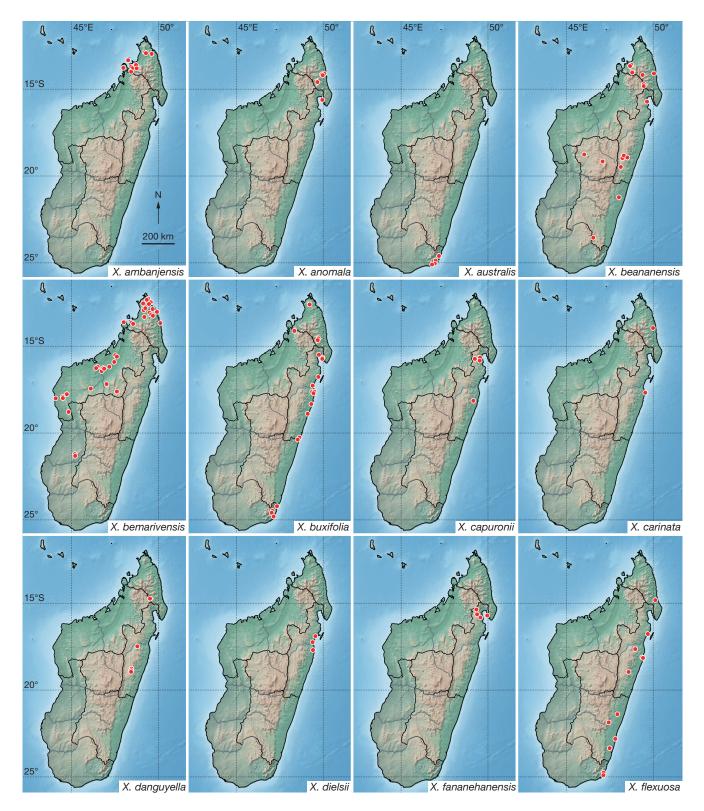
LOCAL NAME. — Hazoambo (*Capuron 20041 SF*).

DESCRIPTION

Tree up to 16 m tall; d.b.h. up to 22 cm.

Twigs densely pubescent, the hairs 0.2-0.6 mm long, at length glabrate; nodes with one or occasionally two axillary branches.

Leaves with larger blades 2.9-3.9 cm long, 0.9-1.2 cm wide, subcoriaceous, concolorous or slightly discolorous and then purplish brown adaxially, light brown abaxially, lanceolate to oblong-lanceolate, apex acute to obtuse, base cuneate and short-decurrent on the petiole, margin slightly revolute,



glabrous or with hairs on the midrib adaxially, densely and finely sericeous abaxially; midrib slightly darkened adaxially, secondary veins weakly brochidodromous, 8-11 per side, diverging at 50-75° from midrib, these and higher-order veins raised adaxially, slightly raised but indistinct abaxially; petiole 2-3 mm long, shallowly canaliculate, smooth, pubescent. **Inflorescences** axillary, 1-2-flowered, pedunculate or not, densely sericeous-pubescent; peduncle 0.9-1.0 mm long; pedicels 2 per peduncle or arising separately from leaf axil, 4.2-6.8 mm long, 0.5-0.7 mm thick; bracts 2, one attached near midpoint and the other just proximal to the sepals, usually caducous, 1.6-1.8 mm long, ovate; buds linear-lanceolate, apex obtuse.

Sepals spreading at anthesis, ¹/₈-¹/₄-connate, 1.1-1.8 mm long, 2.0-2.3 mm wide, coriaceous, broadly triangular to nearly semicircular, apex acute, densely sericeous abaxially.

Petals with color *in vivo* unknown; outer petals erect at anthesis, 12.7-14.5 mm long, 2.6-3.3 mm wide at base, 1.2-1.7 mm wide at midpoint, subcoriaceous, linear to linear-lanceolate, keeled only at the apex adaxially, indistinctly keeled abaxially, apex obtuse, pubescent except for glabrous concave base adaxially, sericeous abaxially; inner petals curved outward from the base with the apices curved inward at anthesis, 10.5-12.7 mm long, 1.9-2.7 mm wide at base, 0.8-0.9 mm wide at midpoint, subcoriaceous, linear-subulate, keeled on both surfaces except for the adaxial basal concavity, apex obtuse, base concave with undifferentiated margin, densely puberulent except for glabrous base on both surfaces.

Stamens *c*. 100; fertile stamens 0.9-1.1 mm long, narrowly oblong, anther connective apex 0.2-0.3 mm long, depressed-globose, overhanging anther thecae, papillate, anthers 6-8-locellate, filament 0.3-0.4 mm long; outer staminodes 1.1-1.2 mm long, oblong to clavate, apex rounded to truncate; inner staminodes *c*. 0.8 mm long, oblong to clavate, apex truncate; staminal cone 1.3-1.5 mm in diameter, 0.5-0.8 mm high, concealing all but the apices of the ovaries, rim irregularly laciniate.

Carpels 4-6; ovaries *c*. 0.9 mm long, narrowly oblong, densely pubescent, stigmas connivent, 1.7-1.8 mm long, narrowly oblong, pubescent at apices.

Fruit of up to 8 monocarps borne on a pedicel 6-8 mm long, 2.5-5.5 mm thick, glabrate; torus 7-15 mm in diameter, 4.5-9 mm high, depressed-globose; monocarps with green to red exterior and pink endocarp *in vivo*, 2.3-3.9 cm long, 1.4-2.4 cm wide, 1.2-2.1 cm thick, ellipsoid, ovoid, or oblong, not torulose, apex obtuse to rounded, base sessile or contracted into a stipe 1-2 mm long, 5-6.5 mm thick, somewhat verrucose, weakly wrinkled, occasionally lenticellate, ridged longitudinally, glabrate; pericarp 2.1-2.3 mm thick.

Seeds up to 4 per monocarp, in a single irregular row, perpendicular to long axis, 12-13 mm long, 8.2-8.7 mm wide, 5.8-7.3 mm thick, oblong to ellipsoid, ovate to semicircular in cross-section, brown to light brown, smooth, dull, perichalazal ring faintly visible but not elevated; sarcotesta pale green to green-yellow *in vivo*; aril absent.

Notes

Xylopia retusa, sp. nov., and *X. sclerophylla*, sp. nov., have the smallest leaves of any Madagascar *Xylopia* species, but the

subcoriaceous leaves of *X. sclerophylla*, sp. nov., are thicker. The monocarps have a thicker pericarp and are rounded at the apex, and the seeds have a green rather than orange sarcotesta. *Xylopia sclerophylla*, sp. nov., also resembles *X. lastelliana* in the sericeous indument of the abaxial leaf surfaces, but its leaves are consistently much smaller and thicker and are obtuse to occasionally acute rather than acuminate. The inland upland habitat also sets it apart from these two more coastal species.

The label of *Nusbaumer LN 943* reports that lemurs eat the fruits, but no details were given as to the species of lemur eating the fruits or the part of the fruit eaten by the animals.

EXCLUDED SPECIES FROM MADAGASCAR FORMERLY PLACED IN *UNONA* AND *XYLOPIA*

- Unona ambongensis Baill., Adansonia; Recueil d'Observations botaniques 8: 350-351 (1868). — Uvaria ambongensis (Baill.) Diels, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 337 (1925).
- Unona boivinii (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). — Monanthotaxis boivinii (Baill.) Verdc., Kew Bulletin 25 (1): 24 (1971).
- Unona boivinii var. pervillei (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). Monanthotaxis boivinii (Baill.) Verdc. Kew Bulletin 25 (1): 24 (1971).
- Unona chapelieri (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 338 (1882). — Fenerivia chapelieri (Baill.) R.M.K.Saunders, Taxon 60 (5): 1412 (2011).
- Unona furfuracea A.DC, Mémoires de la Société de Physique et d'Histoire naturelle de Genève 5: 205 (1832). — Uvaria furfuracea (A.DC) Walp., Repertorium Botanicae Systematicae 1: 79 (1842).
- Unona gerrardii Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 540 (1885). — Ambavia gerrardii (Baill.) Le Thomas, Comptes rendus hebdomadaires des Séances de l'Académie des Sciences. Série D, Sciences naturelles 274 (11): 1655 (1972).
- Unona glaucocarpa (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). — Monanthotaxis glaucocarpa (Baill.) Verdc., Kew Bulletin 25 (1): 26 (1971).
- Unona greveana Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). Bygrave (2000) suggested that this species should be placed in *Sphaerocoryne*, but did not effectively or validly publish the combination, invoking Article 29 of ICN (see Turland *et al.* 2018).
- Unona lucens (Baker) Drake in Grandid., Histoire physique, naturelle et politique de Madagascar 30: Histoire naturelle des Plantes 1: 14 (1903) ["1902"]. — Fenerivia chapelieri (Baill.) R.M.K.Saunders, Taxon 60 (5): 1412 (2011).
- *Unona lucida* Bojer, *Hortus mauritianus* 6 (1837), non Dunal (1817). In making the combination *Guatteria lucida*, Bojer identified the basionym as "Unona lucida. Sweet. Hort. Brit.", but the name was listed by Sweet (1830) as *Uvaria lucida* Bojer All names were *nomina nuda*. The name *Uvaria lucida* Bojer was eventually published by Bentham (1862).
- Unona macrocarpa (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882), non Dunal (1817). — This name

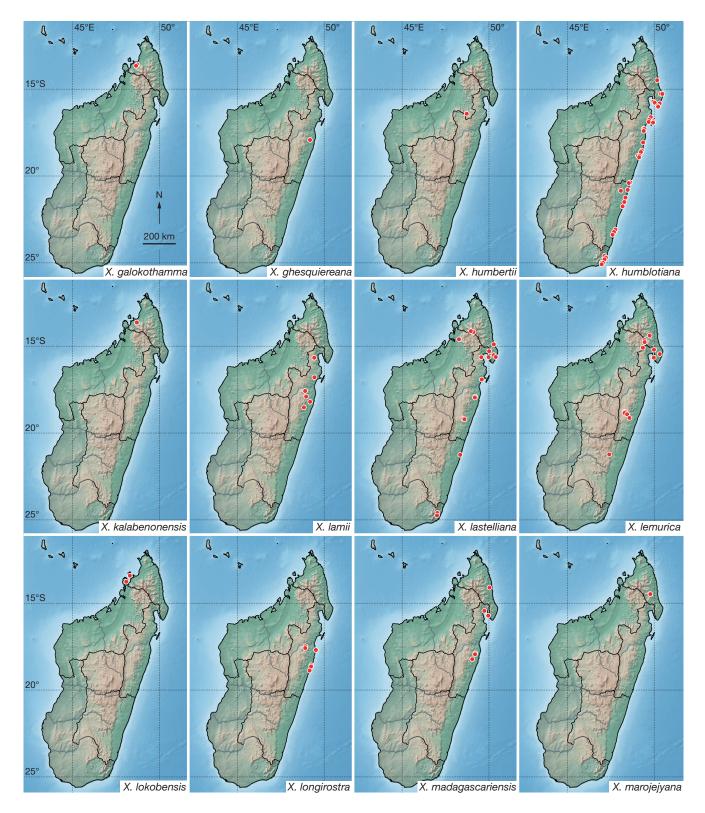


Fig. 29. — Distributions of Xylopia galokothamna, sp. nov., X. ghesquiereana Cavaco & Keraudren, X. humbertii Ghesq. ex Cavaco & Keraudren, X. humblotiana Baill., X. kalabenonensis D.M.Johnson, Deroin, & Callmander, X. lamii Cavaco & Keraudren, X. lastelliana Baill., X. lemurica Diels, X. lokobensis, sp. nov., X. longirostra, sp. nov., X. madagascariensis Cavaco & Keraudren, and X. marojejyana, sp. nov., on Madagascar.

was listed as a taxonomic synonym of *Popowia maritima* by Cavaco & Keraudren (1958), on which the name *Unona maritima* (see below) is based.

Unona marenteria Dunal, Monographie de la Famille des Anonacées. 101 (1817). — Uvaria marenteria (Dunal) Baill., Adansonia; Recueil d'Observations botaniques 8: 304 (1868).

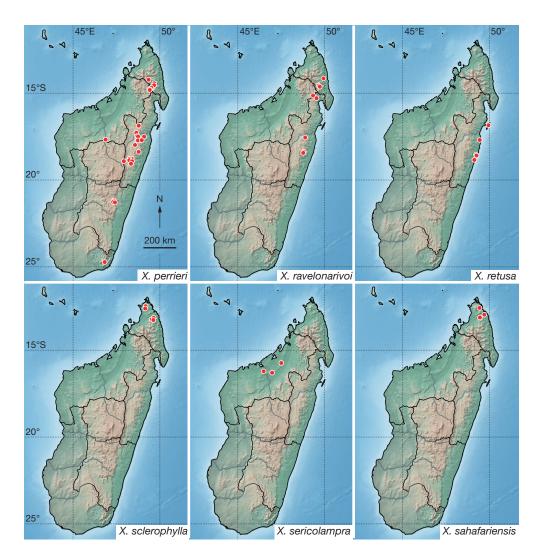


FIG. 30. — Distributions of Xylopia perrieri Diels, X. ravelonarivoi, sp. nov., X. retusa, sp. nov., X. sclerophylla, sp. nov., X. sericolampra Diels and X. sahafariensis Cavaco & Keraudren on Madagascar.

- Unona maritima (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). — Bygrave (2000) suggested that this species should be placed in Sphaerocoryne, but did not effectively or validly publish the combination, invoking Article 29 of ICN (see Turland *et al.* 2018).
- Unona pilosa (Boivin ex Baill.), Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). — Monanthotaxis pilosa (Boivin ex Baill.) Verdc., Kew Bulletin 25 (1): 28 (1971).
- Unona richardiana (Baill.) Baill., Bulletin mensuel de la Société linnéenne de Paris 1: 339 (1882). — Fenerivia richardiana (Baill.) R.M.K.Saunders, Taxon 60 (5): 1414 (2011).
- Xylopia decaryana Cavaco & Keraudren, Bulletin de la Société botanique de France 103: 275 (1956). — Artabotrys scytophyllus (Diels) Cavaco & Keraudren, Bulletin du Jardin botanique de l'État à Bruxelles 27: 74 (1957).

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