Taxonomy and biogeography of the New Caledonian species of *Xylopia* L. (Annonaceae)

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**ABSTRACT**

A taxonomic review of the New Caledonian representatives of the pantropical tree genus *Xylopia* L. (Annonaceae) is presented based on museum study of 157 collections. Distinctions are clarified among the four endemic species, two of them previously undescribed in flower and two others described in the literature from only the type collections. A key and species descriptions are presented. *Xylopia pancheri* Baill., the most frequently collected species, occurs in maquis environments with ultramafic rocks in the central and southern regions of the island, as well as on the Île des Pins. *Xylopia vieillardii* Baill. is widespread in low elevation humid forests but the remaining two species, *X. dibaccata* Däniker and *X. pallescens* Baill., have restricted distributions and their ecology is still incompletely known. *Xylopia pancheri* shares similarities with the endemic Fijian species *X. degeneri* A.C.Sm. and *X. vitiensis* A.C.Sm.; the remaining three species share more traits with the Fijian endemic *X. pacifica* A.C.Sm.

**KEY WORDS**  
Annonaceae,  
*Xylopia*,  
New Caledonia,  
endemism,  
biogeography,  
seed dispersal.
INTRODUCTION

*Xylopia* L., a pantropical genus of about 200 species of Annonaceae, occurs across the Australasian region, including New Caledonia. The genus is readily distinguished from other members of its family by the combination of axillary inflorescences, relatively narrow petals, septate anther locules, and dehiscent monocarps bearing seeds that have fleshy appendages or seed coats. Seeds of *Xylopia*, typically displayed against a red exocarp and offering a lipid-rich food reward, exhibit a strong syndrome of features promoting bird dispersal.

*Xylopia vieillardii* Baill. was described from New Caledonia by Baillon (1868) on the basis of a single fruiting collection. Baillon later (1874) described *X. pancheri* Däniker and *X. pallescens* Baill., the former from one flowering collection and the latter from a single fruiting collection. Däniker (1931) described a fourth species, *Xylopia dibaccata* Däniker, from a single specimen bearing both flowers and fruits. The four species were reviewed briefly by Guillaumin (1932, 1948), who provided a brief diagnostic key, but two of the species were still only known from their type specimens at the time of those publications; the species were thus still incompletely known morphologically, and nothing had been published about their ecology.

Since the time of Guillaumin’s publications additional *Xylopia* collections have been made on New Caledonia; Guillaumin’s key is no longer adequate for their identification, and many *Xylopia* specimens have lain undetermined to species or even genus in various museum collections. In order to review the taxonomy and ecology of *Xylopia* species occurring on New Caledonia we assembled 157 collections from 14 herbaria (A, BISH, BM, BR, GH, K, L, MO, NOU, NY, OWU, P, US, and WAG; acronyms from Holmgren et al. 1990) for study. A key to the species is provided, as are lists of material examined, descriptions, and remarks on distribution and ecology for each species, based on herbarium specimens as well as field observations using the NC-PIPPN database (New Caledonian Plant and Inventory Permanent Plot Network) (Ibanez et al. 2013). IUCN status is also given, using a 3 × 3 km grid to calculate area of occupancy (AOO), and a 2 × 2 km grid to calculate number of sub-populations (following Swenson & Munzinger 2009). An identification list of specimens is provided in an Appendix.
KEY TO SPECIES OF *XYLOPIA* L. ON NEW CALEDONIA

1. Outer petals 12-33 mm long; staminal cone 2-3.5 mm in diameter; monocarps 2.8-5.6 cm long, narrowly oblong to oblanceolate, torulose; seeds lacking a corky aril encircling the micropyle ................................................................. 1. *X. pancheri* Baill.
   — Outer petals 4-9 mm long; staminal cone 2 mm or less in diameter; monocarps less than 3.6 cm long, ellipsoid to nearly spherical; seeds bearing a corky aril encircling the micropyle ........................................................................ 2

2. Lamina of larger leaves 1.9-2.3 cm wide; lamina densely papillate and glaucous below ................................................................. 4. *X. pallescens* Baill.
   — Lamina of larger leaves 2.8-4.6 cm wide or wider; lamina discolored but neither papillate nor glaucous nor below ................................................................. 3

3. Lamina of larger leaves 8.1-12 cm long, dull above, usually acute at the apex; pedicel, bracts, and calyx gray- or yellow-pubescent, or glabrate; monocarps drying brown with white lenticels, the stipe 1.2-3.5 mm long ................................. 2. *X. vieillardii* Baill.
   — Lamina of larger leaves 6.2-9.7 (-11.6) cm long, shiny above, obtuse, rounded, or retuse at the apex; pedicel, bracts, and calyx rusty-pubescent; monocarps reddish to blackish brown, not lenticellate, the stipe 5-6 mm long ................................. 3. *X. dibaccata* Däniker

SYSTEMATICS

Genus *Xylopia* L.


DISTRIBUTION. — A pantropical genus of about 200 species, in the Neotropics distributed from southern Mexico and Cuba south through Central America and Jamaica to Bolivia, Paraguay, and southern Brazil. Occurs widely in sub-Saharan Africa, Madagascar, and the Mascarene Islands. In Asia distributed from southern India and Sri Lanka across southeastern Asia and into southern China, and then south and east across the Malesian region to northern Australia, New Caledonia, and Fiji.

DESCRIPTION

Trees or shrubs with an indument of simple hairs; some species with two axillary branches (double-branching). Leaves distichous, often somewhat coriaceous, simple, entire. Inflorescences axillary, occasionally from the trunk or older branches, few-flowered, axes bearing small bracts. Flowers bisexual, buds elongate; sepals 3, connate at least at the base so that a cuplike calyx shorter than the petals is formed; petals 6 in 2 whors, free, usually much longer than wide, inner petals slightly shorter and narrower, both whors somewhat concave at base; stamens numerous, anthers transversely separte, with a polyad of 4-16 pollen grains held in each locule; apex of connective truncate, rarely apiculate or absent; filaments connate at base to form a pyramidal or dome-shaped cone that encloses the ovaries, the free part of the filament shorter than the anther; innermost and sometimes outermost stamens slightly broader and staminodial; carpels few to numerous, seated within the staminal cone with only the stigmas emergent, ovaries pubescent with ovules laterally attached in one or two rows, stigmas filiform to lanceolate, often connivent. Monocarps free, dehiscent abaxially with a fleshy red endocarp, stipitate or not; seeds attached laterally in one or two rows, ellipsoid to oblong. Seeds have an aril or a sarcotesta, a fleshy seed coat. Arils fibrous, corky, or fleshy and colored, white, yellow, orange, or red. Sarcotesta blue-gray, orange, or lime-green. Endosperm ruminations plate-like in four rows, or irregularly spiniform.

1. *Xylopia pancheri* Baill.

(Figs 11-M; 2)

*Adansonia* 11: 177, 178 (1873-1876) [date 4 mars 1874 is printed at bottom of p. 177. According to Stafleu & Cowan (1976), the fascicles of Volume 11 appeared at irregular intervals]. — Type: New Caledonia, without definite locality, *Pancher s.n.* (holo-, P, not located). New

**Distribution and phenology.** — \textit{Xylopia pantheri} occurs in open or dense \textit{maquis} on ultramafic soils, primarily over peridotite, at elevations below 400 meters. It is most abundant in the Grand Massif area of southern New Caledonia and is the only \textit{Xylopia} species to occur on the Île des Pins (Fig. 2). Collections with flowers have been made in all months except April and August, but are most frequent from December and January. Collections with fruits have been made from all months except April, June, and September. The seeds are blue-gray in \textit{vivo}, displayed against a scarlet endocarp.

Fig. 1. — The New Caledonian species of *Xylopia* L.: **A, B**, *X. pallescens* Baill.; **A**, habit with fruit; **B**, habit with flowers; **C-H**, *X. vieillardii* Baill.; **C**, carpels and surrounding staminal cone with a few stamens still attached; **D**, fruit; **E**, leaves; **F**, seed, view from micropylar end; **G**, seed, side view; **H**, flowers; **I-M**, *X. pan cheri* Baill.; **I**, habit; **J**, fruit; **K**, stigmas, stamens, and sepals, side view; **L**, seed, view from micropylar end; **M**, seed, side view; **N-O**, *X. dibaccata* Däniker; **N**, habit with young fruit; **O**, habit with flowers; **A, B**, Veillon 4730 (OWU); **C**, McPherson 6281 (MO); **D, E**, McPherson 6330 (MO); **F, G**, Brinon 1130 (NOU); **H**, from Sarlin 322 (P00507339); **I, McPherson** 3575 (MO); **J, McPherson** 5976 (MO); **K-M**, MacKee 29715 (P00507360); **N, Munzinger & McPherson** 2526 (NOU); **O, McPherson** 5397 (MO). Scale bars: **A, B, D-J, L-O, 1 cm; C, K, 3 mm. Drawing by Kate Ball. 

**Description**

Shrub to 6 m tall, bark brown-gray, rough. Twigs dark red-brown to gray, initially appressed golden-pubescent with hairs 0.2-0.4 mm long, soon sparsely pubescent to glabrate, eventually lenticellate. Lamina of larger leaves 5.9-12.5 cm long, 2.4-5.9 cm wide, leaf olive-green to dark purple-brown mottled above, rusty to pale brown below, coriaceous to subcoriaceous, lanceolate to lanceolate-ovate, elliptic, or oblong, cuneate to rounded and slightly decurrent on petiole at the base, obtuse to acute, rarely rounded or retuse, at the apex, glabrous above, sparsely appressed-pubescent with pale hairs below; midrib slightly raised or plane above, raised and strongly keeled below; secondary veins 8-14 per side, at midpoint of leaf diverging at 55-70° from the midrib, brochidodromous, slightly raised above and below; higher-order veins slightly raised and forming a reticulum. Petiole 4-10 (-15) mm long, shallowly canaliculate in cross-section, longitudinally wrinkled, sparsely pubescent to glabrate. Inflorescences of 1-3 (6) flowers, axillary or sometimes from the axils of fallen leaves; pedicels 3.5-10 mm long arising from a common peduncle 2 mm long that appears to be derived from connation of the bases of the pedicels, commonly bent and articulating at the penultimate bract, densely pubescent; bracts 1-3, the uppermost 1.7-2.5 mm long, clasping the pedicel, ovate, apex obtuse to retuse, pubescent. Buds conical or oblong, occasionally falcate or uncinate. Sepals ½-⅓ connate, 3.0-5.0 mm long, 3.2-5.6 mm wide, broadly ovate to triangular, cuspidate to apiculate at apex, pubescent externally, glabrous internally. Petals white and fleshy in vivo; outer petals 12-33 mm long, 2.7-5.5 mm wide, ligulate, obtuse at apex, keeled externally, becoming concave at base.
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Fig. 2. — Distribution of *Xylopia pancheri* Baill. on New Caledonia and the Île des Pins. Ultramafic substrates are shown in grey, except for serpentinites, which are shown in black. Localities marked with open squares indicate sight records only.

on inner surface, appressed-pubescent on both surfaces except for a small glabrous patch at the base internally; inner petals 10-23 mm long, 2.0-2.4 mm wide at midpoint, widening to 2.5-3.5 mm at the base, linear, acute at apex, keeled on both surfaces but becoming deeply concave at base on inner surface, appressed-pubescent except for a glabrous basal patch on both surfaces. Stamens 125-150; fertile stamens 1.1-1.7 mm long, quadrate, oblong, or clavate; anthers septate at anthesis, with 5-9 locules; apex of connective 0.2-0.3 mm long, dome-shaped, overhanging anther thecae, long-papillate; filament ¼-½ length of stamen; innermost stamens staminodial, c. 8, 1.2-1.4 mm long, pentagonal or quadrate; staminal cone well-developed, 2.0-3.5 mm in diameter, 1.1-2.2 mm high. Carpels 5-8; ovaries 1.1-1.3 mm long, pressed together, narrowly oblong, golden-tomentose, the hairs 0.4-0.7 mm long; stigmas initially pressed together but spreading apart at anthesis, 2.0-3.1 mm long, linear, obtuse at the apex, glabrous but somewhat papillate. Torus of flower 3.1-3.6 mm in diameter, glabrous except for hairs on carpellate portion. Fruit of up to 7 monocarps borne on a pedicel 10-16 mm long, 3-6 mm thick, red-brown to gray, pubescent; torus of fruit 4-7 mm in diameter, 3-5 mm high, subglobose to hemispherical; monocarps green, dehiscing to reveal a red endocarp *in vivo*, 2.8-5.6 cm long, 0.8-1.5 cm wide, 0.6-1.1 cm thick, narrowly oblong to oblanceolate, torulose and somewhat falcate, finely
verrucose and obliquely wrinkled, glabrate, contracted into a stipe 2-9 (-12) mm long and 2-5 mm thick; apex forming a flattened beak 2-5 mm long; pericarp 1.0-1.2 mm thick. Seeds in a single row, commonly 4-5 per monocarp, rarely up to 8, with a gray-blue sarcotesta *in vivo* but drying brownish gray, lying oblique to long axis of monocarp in a single row, 9.7-12 mm long, 4-6.4 mm wide, 3.5-4.2 mm thick, ovoid to obovoid, ovate-oblong in cross-section, smooth, narrowed to a short beak around the micropyle 1 mm long and 1.5-2 mm wide; aril absent.

**Remarks**

This species is by far the most frequently collected species of Xylopia on New Caledonia, comprising nearly two-thirds of the 157 collections available for study. This may be in part due to the showy flowers, which are also strongly fragrant: several collectors compared the fragrance to that of *Gardenia* J.Ellis. The species stands apart from other New Caledonian Xylopia species by virtue of these large flowers plus the elongate monocarps and the absence of a corky ring on the seed.

The major variation in floral morphology is in the length of the petals, which can vary from 12-33 mm in the outer petals and 10-23 mm in the inner petals. This appears to be variation in mature flowers rather than variation in developmental stage. Similarly there is variation in leaf size: the specimen Schmid 2737 from the Rivière Bleue stands out because of its exceptionally large oblong leaves (12.5 cm long, 5.9 cm wide), but other specimens from the same general geographic area do not exhibit this characteristic: the largest leaf of Koyama & Setoguchi 8211 is, for example, only 7.9 cm long and 3.5 cm wide.

On the basis of field study of tree architecture by Veillon (1976), Hallé (2004) reported Xylopia *pancheri* to exhibit Petit’s Model of tree architecture, in which inflorescences are formed by the terminal bud and continued lateral branch growth is thus sympodial. All Xylopia *pancheri* material we have seen, however, exhibits axillary inflorescences and the trees thus must have Roux’s model with spiral trunk phyllotaxis, as occurs in other Xylopia species (Johnson 2003). In addition, Veillon (pers. comm.) reports that further study of the voucher specimen, on which he based his work, appears to be the following species, *X. vieillardii*, and he confirms that it has the Petit’s Model type architecture, as illustrated by Hallé (2004). The voucher specimen, *MacKee 26143*, is in fact a mixed collection: sheet 012298 at NOU is *X. pancheri*, and sheet 012347 at NOU is *X. vieillardii*, as is sheet 6244063 at MO. Further field study of architecture of New Caledonian Xylopia species is needed, to both confirm this difference in architecture pattern from other members of the genus and verify the identity of the species under study.

The type specimen of *Xylopia pancheri*, *Pancher s. n.*, was not located. The only Pancher specimen of *Xylopia* examined, *Pancher 640*, bears only a young fruit: Baillon’s protologue for *X. pancheri* describes the long petals and other floral parts in detail, and thus does not seem to pertain to this specimen. However, the description clearly applies to this species and not others. In the interest of nomenclatural stability, the specimen *Balansa 1175* has been designated as a neotype. This is the only other collection of *X. pancheri* cited by Guillaumin (1911) in addition to the type, and the label of sheet P00507380 at P bears a determination in Baillon’s hand. The specimen *Balansa 3529*, identified by Guillaumin (1932) as *X. pancheri*, is a mixed collection: a packet on one of the three sheets contains flower parts of *X. pancheri*, but the fruiting specimens on all three sheets are *X. dibaccata*.

Guillaumin (1911) reports the vernacular name “namanigo” for a species of Xylopia, but no subsequent collectors have confirmed the local use of this name for *X. pancheri* or any other species.

2. **Xylopia vieillardii** Baill.  
(Figs 1C-H; 3)

**Distribution and phenology.** — *Xylopia vieillardii* occurs widely over the island at elevations of 50-750 meters, most commonly between 150 and 500 meters, in moist forests over metamorphic rocks, usually schist. Most of the collections come from the non-ultramafic basement terranes. Only in the southern part of the island does it occur on ultramafic sites, and there only at the bases of slopes where there is accumulation of nutrients washed down by rain from higher up. Specimens with flowers have been collected from October through February, while those with fruits have been gathered in January, February, April, August, November, and December. The seeds are grayish green *in vivo*, the exposed endocarp reddish-pink to dark purple. One of the authors has observed the Red-Crowned Parakeet (*Cyanoramphus saisseti*) feeding on the fruits of *X. vieillardii*. In general, parrots and parakeets are seed predators (see e.g., Villaseñor-Sánchez *et al*. 2010); seed dispersal by this bird species would probably be accidental.

**Conservation status.** — *Xylopia vieillardii* shows an EOO of 8382 km² and an AOO of 261 km² comprising 18 sub-populations, with five included in protected areas: Aoupinié Special Fauna Reserve, Parc des Grandes Fougères, Thy, Chutes de la Madeleine, Forêt Nord. The plant is abundant in these localities. *Xylopia vieillardii* is assigned a preliminary status of Least Concern.


**Description**

Tree up to 16 m tall, occasionally a shrub 3-6 m tall; double-branching occasional. Twigs light gray to mottled reddish brown, initially appressed brown-pubescent, the hairs 0.1-0.3 mm long, later glabrate, usually conspicuously and densely lenticellate. Lamina of larger leaves 8.1-12 cm long, 2.6-4.4 cm wide, dull olive-green to brown-purple above when dry, paler and light to medium brown below, coriaceous to subcoriaceous, elliptic, oblong, or lanceolate-elliptic, rounded and short-decurrent at the base, acute, occasionally rounded, at the apex, glabrous above, sparsely appressed-pubescent below; midrib plane above, raised below; secondary veins 9-16 per side, at midpoint of leaf diverging at 55-75° from the midrib, brochidodromous, these and higher order veins raised and forming a prominent reticulum on both surfaces. Petiole 3-9 mm long, somewhat flattened, wrinkled, sparsely pubescent to glabrate. Inflorescences of 1-4 flowers, axillary or sometimes from the axils of fallen leaves; pedicels fascicled, (0.8) 3-5.5 mm long, straight, densely yellow- to gray-pubescent to glabrate; bracts 1-3, the uppermost 0.7-1.4 mm long, 0.8-1.6 mm wide, clasping the pedicel, ovate, apex obtuse to retuse or acute, yellow- to gray-pubescent to glabrate. Buds conical. Sepals ½-3/5 connate, 0.8-2.5 mm long, 1.7-2.5 mm wide, broadly triangular, broadly acute at the apex, yellow- to gray-pubescent to glabrate externally, with a strip of hairs traversing the base but otherwise glabrous internally. Outer petals white to greenish or yellowish white, fleshy, 4.4-7.6 mm long, 2.0-2.5 mm wide, lanceolate, acute at apex, slightly keeled on outer surface but concave at base on inner surface, densely appressed-pubescent on both surfaces; inner petals white *in vivo*, fleshy, 3.5-6.8 mm long, 1.3-1.8 mm wide, linear-lanceolate, acute at apex, slightly keeled on exterior, becoming concave at base on inner surface, densely pubescent on both surfaces. Stamens 60-85; fertile stamens 0.5-1 mm long, quadrate, oblong, or clavate; anthers sepalate at anthesis, with 4-6 locules; apex of connective 0.1-0.2 mm long, dome-shaped, overhanging anther thecae, puberulent; filament 2/3-2/3 length of most stamens; innermost stamens staminodial, c. 5 or fewer, 0.9-1 mm long, quadrate; staminal cone well-developed, 1.2-1.6 mm in diameter, 0.9-1.1 mm high. Carpels 2-4; ovaries 0.7-1 mm long, pressed together, narrowly oblong, golden-tomentose; stigmas loosely appressed, slightly spreading toward apex, 2-2.9 mm long, filiform but tortuous and tentacle-like, glabrous, apex acute. Torus of flower 1.4-2.6 mm in diameter, glabrous except for hairs on carpellate portion. Fruit of up to 4 monocarps borne on a pedicel 3-9 mm long, 1.2-3.2 mm thick, mottled red-brown to gray-brown, sparsely pubescent; torus of fruit 2.2-6.2 mm in diameter, 2.5-5 mm high, subglobose, globose, or hemispherical; monocarps green speckled with...
Remarks

This species has some amount of variability in its leaf size and shape: in some specimens the leaves are broadly elliptic and obtuse, while in others the leaves are lanceolate and nearly acuminate. The dense clusters of short-petaled flowers with acute petals lacking brown hairs, plus the densely lenticellate monocars, serve to distinguish this species from the rarer X. dibaccata and X. pallescens.

Sarlin (1954) reports the vernacular name “ébène” (ebony) for Xylopia vieillardii, but no subsequent collectors, nor the field experience of JM in New Caledonia, have confirmed the local use of this name, which is often applied instead to species of Diospyros (Ebenaceae) in other parts of the world.
3. *Xylopia dibaccata* Däniker


**Distribution and Phenology.** This species occurs at scattered locations on the island, but always associated with serpentinites, i.e. in areas of relatively more metamorphosed and hydrothermally altered ultramafic geology. It is found in sclerophyll forest at elevations of 50-200 meters but does not seem common anywhere within its range. Specimens with flowers have been collected from November through February, and those with fruits in February, March, October, November, and December. Colors of seeds and fruits *in vivo* are not known.

**Conservation Status.** *Xylopia dibaccata* shows an EOO of 7556 km² and an AOO of 81 km². There are nine sub-populations, and none of them is included in a protected area. Two of these are in areas with mining activity with future impact on vegetation. As the plant is restricted to serpentinites, the calculated EOO is a gross overestimate. The plant is never abundant, even in the localities known. *Xylopia dibaccata* is assigned a preliminary status of Vulnerable (VU: A3cd, B1ab(i, ii, iii)2ab(i, ii, iii)).


**Description.** Tree or shrub up to 9 m tall; double-branching occasional. Twigs light gray to brown, initially densely appressed golden-pubescent, the hairs 0.1-0.2 mm long, but soon glabrate, lenticellate. Lamina of larger leaves 6.2-9.7 (-11.6) cm long, 2.8-4.6 (-5.4) cm wide, shiny olive-green to brown above, dull, pale brown below, coriaceous, elliptic, elliptic-oblong, or elliptic-oblanceolate, broadly cuneate to rounded and slightly decurrent on petiole at the base, obtuse, rounded, or retuse at the apex, glabrous above, sparsely appressed-pubescent to glabrate below; midrib slightly raised or impressed to plane above, plane to slightly raised below; secondary veins 8-13 per side, at midpoint of leaf diverging at 45-70° from the midrib, irregularly brochidodromous, these and higher-order veins raised and forming a prominent reticulum on both surfaces. Petiole 3.7 mm long, shallowly canaliculate adaxially, longitudinally wrinkled, sparsely pubescent to glabrate. Inflorescences of 1-3 flowers, axillary or from the axils of fallen leaves; pedicels 1.8-4 mm long, 1-1.5 mm thick, straight, rusty-pubescent; bracts usually 2, the uppermost 0.8-2 mm long, clasping the pedicel, crescent-shaped or semicircular, apex rounded, rusty-pubescent. Buds conical. Sepals ¼-½ connate, 1.8-3 mm long, 2-3.2 mm wide, broadly ovate to triangular, rounded at the apex, rusty-pubescent externally, with a strip of hairs traversing the base but otherwise glabrous internally. Outer petals fleshy, 6.1-9 mm long, 2.5-3.3 mm wide, lanceolate to narrowly ovate or oblong-lanceolate, acute to obtuse at apex, slightly keeled on both surfaces but concave at base on inner surface, appressed-pubescent inside and externally; inner petals fleshy, 6.5-7.0 mm long, 1.5-1.9 mm wide, linear-lanceolate, acute at apex, keeled and pubescent externally, flat and pubescent on inner surface except for the deeply concave and glabrous base. Stamens c. 100; fertile stamens 0.5-1.1 mm long, quadrangular, oblong, or clavate; anthers sepaete at anthesis, with 4-7 locules; apex of connective dome-shaped to flattened, overhanging anther thecae, papillate; filament ¼-½ length of most stamens; innermost stamens staminodial, c. 5, 0.5-0.8 mm long, pentagonal or quadrate; staminal cone evident, 1.5-2 mm in diameter, 0.5-0.9 mm high. Carpels 4-6; ovaries 0.5-1 mm long, pressed together, oblong, golden-tomentose; stigmas loosely...
**Taxonomy and biogeography of the New Caledonian species of Xylopia (Annonaceae)**

** Remarks**

*Xylopia dibaccata* closely resembles *X. vieillardi* in its short broad monocarps and conical flower buds and is difficult to distinguish from it, a task made further difficult by the limited number of specimens available for study. It appears to be a species of slightly lower elevations restricted to serpentinite sites. The shiny upper surface of the leaf and the rusty pubescence of the pedicels, bracts, and calyx seem to be consistent differences between the two species; in addition, *X. dibaccata* tends to have only 1-2 flowers per inflorescence, while *X. vieillardi* commonly has 3-4. No specimens with dehisced monocarps have been seen. The specimen Guillaumin & Baumann-Bodenheim 12128 (A,
NY) (Vallée supérieure de la rivière Voh, 250 m, 12.IV.1951), both sheets of which are sterile, may represent this species.

4. Xylopia pallescens Baill. (Figs 1A, B; 5)

Adansonia 11: 178 (1873-1876) [date 4 mars 1874 is printed at bottom of p. 177. According to Stafleu and Cowan (1976), the fascicles of Volume 11 appeared at irregular intervals]. — Type: “Oritur in Austro-Caledoniae collibus ferrugineis ad orientem ‘Messoncoué, prope Port Bouquet’”, XII.1869, Balansa 1776 (holo-, P[P00507382]!; iso-, P[P00507383]!).

Distribution and phenology. — Xylopia pallescens is confined to slopes and stream edges in a small area of ultramafic soils on the eastern coast at elevations of 100-400 m (Fig. 5). One collector mentioned Anartucaria rulei as a dominant associate. Flowers have been collected in November and December, and fruits in May, November, and December. Colors of mature seeds and fruit endocarp in vivo are not known.

Conservation status. — Xylopia pallescens shows an EOO of 1336 km² and an AOO of 90 km²; it has six sub-populations, none of them included in a protected area. In addition, all populations are in or near mining concessions, several of which are being actively mined. Some isolated populations of the west coast are also potentially threatened by fire, as they occur in areas where fire control access is limited; fire tolerance of the species is assigned a preliminary status of “Endangered” (EN: A1cd, B1ab(i, iii)2ab(i, iii)).


Description

Shrub up to 4 m tall; double-branching occasional. Twigs gray to red-brown, initially appressed-pubescent, the hairs 0.2 mm long or less, eventually glabrate, lenticellate. Lamina of larger leaves 5.3-8 cm long, 1.9-2.3 cm wide, olive-green to brown-green above, light brown-green below, coriaceous to subcoriaceous, narrowly elliptic to oblong, cuneate to acute at the base, occasionally decurrent on petiole, rounded or rarely acute to obtuse, occasionally re-cuse, at the apex, glabrous above, glaucescent below from dense papillae, sparsely appressed-pubescent below; midrib raised and keeled below, slightly raised above; secondary veins 10-16 per side, at midpoint of leaf diverging at 50-65° from the midrib, weakly brochidodromous, slightly raised above and below; higher-order veins slightly raised and forming a reticulum. Petiole 2-4.5 mm long, wrinkled, sparsely appressed-pubescent to glabrate. Inflorescences of 1-2 flowers, axillary or sometimes from the axils of fallen leaves; pedicels 1.5-2.5 mm long, curved downward, densely pubescent; bracts 1-3, the uppermost 0.6-1.3 mm long, clasping the pedicel, ovate, apex obtuse to retuse or acute, pubescent. Buds ovoid. Sepals ½-1½ connate, 1.2-1.7 mm long, 1.5-2.2 mm wide, broadly triangular, apex rounded, pubescent externally, glabrous internally. Outer petals white to yellow-white, fleshy, 4-6 mm long, 2-2.7 mm wide, narrowly ovate, acute to obtuse at apex, slightly keeled on outer surface, concave on inner surface, densely appressed-pubescent on both surfaces; inner petals white, fleshy, 3.1-4.4 mm long, 1.1-1.8 mm wide, lanceolate, acute at the apex, slightly keeled on exterior, becoming concave at base on inner surface, densely pubescent on both surfaces. Stamens 70-80; fertile stamens 0.5-1 mm long, quadrate, oblong, or clavate; anthers septate at anthesis, with 4-6 locules; apex of connective 0.2-0.4 mm long, dome-shaped, overhanging another thecae, minutely papillate; filament ½-⅔ length of most stamens; innermost stamens staminodial, c. 6, 0.7-9 mm long, quadrate; staminal cone evident, 1.1-1.4 mm in diameter, 0.7-0.9 mm high. Carpels 2-3; ovaries 0.5-0.7 mm long, pressed together, oblong, golden-tomentose; stigmas appressed along their length, sometimes slightly spreading toward the apex, 1.8-2.4 mm long, trowel-shaped, i. e. distinctly narrowed in the basal ⅓, apex rounded, glabrous. Torus of flower 1-1.5 mm in diameter, glabrous except for hairs...
on carpellate portion. Fruit of up to 4 monocarps on a pedicel 6-8.5 mm long, 1.2-2.4 mm thick, red-brown to gray-brown sparsely pubescent; torus of fruit 2.3-4.5 mm in diameter, 2-4.3 mm high, subglobose or hemispherical; monocarps green to reddish green-brown in vivo, 1.2-2 cm long, 0.7-1.4 cm wide, 0.3-0.5 cm thick, obovate, finely verrucose and finely obliquely wrinkled, sparsely pubescent to glabrous, contracted into a stipe 1.5-3.5 mm long and 2.5-4.5 mm thick; apex obtuse. Seeds 1-2 per monocarp, lying oblique to long axis of monocarp, 9-11 mm long, 6.2-7.8 mm wide, 4.9-5.7 mm thick [seeds immature], with a corky ring around the micropyle.

REMARKS
This species resembles X. vieillardii and X. dibaccata in having small flowers and short broad monocarps, but stands apart from both of them in several features: the leaves are relatively narrow, with a lower surface that is distinctly glaucescent from the presence of dense papillae, the flower pedicels are recurved, and the stigmas are shorter and broader.

DISCUSSION
Because of its high biological diversity and endemism, the island of New Caledonia has been of particular interest in biogeography. The large number of putatively relict taxa present there has suggested that the biota of the island is ancient (Morat 1993; Lowry 1998). It is increasingly acknowledged, however, that all of New Caledonia was under water from the late Cretaceous until the early Eocene (Pelletier 2006; Grandcolas et al. 2008; Heads 2008; Pillon et al. 2010; Morat et al. 2012); the ultramafic (high magnesium) geology for which the island is noted (Jaffré 1974; Brooks 1987) emerged during the late Eocene (Aitchison et al. 1995). Because of the evidence for prolonged submergence of the island, Grandcolas et al. (2008) argued that the biota of New Caledonia assembled entirely by long-distance dispersal; these authors thus characterized New Caledonia as a “Darwinian” island. Intermediate biogeographic scenarios have also been posited. Ladiges & Cantrill (2007) stressed that some geological evidence supports the idea of the survival of the regional biota on ancient neighboring land masses, now submerged, and that the ancient biota hypothesis should not yet be abandoned; Heads (2008) emphasized a possible role for island terranes tectonically accreted to New Caledonia as bearing additions to the island biodiversity.

Grandcolas et al. (2008) suggested that “work on estimating the time of origin of groups that may represent pre-Oligocene relicts should be continued to confirm or falsify the Darwinian nature of New Caledonia” and that “efforts to understand the adaptive significance of New Caledonian evolutionary novelties must be sought by documenting whether taxa diversified into so-called vacant niches.” Magnoliid angiosperms in the New Caledonian flora offer a large pool of pre-Oligocene relict candidates; if there are multiple species of a genus or family present, they offer an opportunity to examine diversification into vacant niches. Xylopia is thus of interest on both counts. A recent estimate of the divergence time of Xylopia from its sister genus Artabotrys places this divergence in the mid-Paleocene to mid-Eocene (Couvreur et al. 2010); this estimate, while based on a small sampling of Xylopia taxa and thus somewhat preliminary, allows the possibility that the New Caledonian Xylopia species could represent pre-Oligocene relicts. Furthermore, our study suggests that the New Caledonian species of Xylopia arose from two different ancestors within the genus. Xylopia pancheri has long strap-shaped petals, elongate monocarps bearing 4-8 seeds in a single row, and seeds that lack a corky ring encircling the micropyle. Xylopia vieillardii, X. dibaccata, and X. pallescens, in contrast, all have relatively short broad petals, short ovoid monocarps with 1-4 seeds, and seeds that bear a conspicuous corky ring encircling the micropyle. The three species share these floral and fruit characteristics with Xylopia pacifica A.C.Sm. from Fiji, Xylopia papuana Diels in New Guinea and the Solomon Islands, and the recently described X. monosperma Jessup from northern Australia (Jessup et al. 2011).
sup 2007). Estimates for the divergence times of all these species are needed; recent analysis of the
genus Meiogyne (Thomas et al. 2012) revealed very recent divergence times (late Miocene/Pliocene) for the two New Caledonian species sampled.

*Xylopia* species distribution on New Caledonia is inconclusive with respect to both the ancient biota and “Darwinian island” hypotheses. *Xylopia vieillardii* is largely confined to the non-ultramafic basement terranes of the island (Fig. 3) and has a distribution similar to that of the archaic angiosperm *Amborella trichopoda* (Heads 2008). In contrast, *X. pancheri*, *X. dibaccata*, and *X. pallescens* are all associated in some way with ultramafic habitats, suggesting more recent long-distance dispersal and divergence. Crisp et al. (2009) recently argued that there is a considerable degree of phylogenetic “constraint” to the ability to diverge and colonize new habitats, with more primitive groups such as magnoliid angiosperms (which include Annonaceae) less equipped for long-distance dispersal and establishment. The absence of Annonaceae from the re-forestation floras of three volcanic islands, Tuluman Island, Papua New Guinea (Kisokau et al. 1984), Anak Krakatau, Indonesia (Partomihardjo et al. 1992), and Long Island, Papua New Guinea (Harrison et al. 2001), certainly supports this view. Whittaker & Jones (1994) observed that Anak Krakatau was within range of effective dispersal of plants by birds and fruit bats from both Sumatra and Java, and Whittaker et al. (1997) identified Annonaceae as a family underrepresented on the island given its diversity levels in these nearby source areas. This suggests that this family should not be well represented in areas where only long-distance dispersal can provide the biota, and yet at least two of the New Caledonian *Xylopia* species, *X. pancheri* and *X. vieillardii*, are known to exhibit the characteristic ornithochory features of *Xylopia*, i.e. large fleshy-coated seeds displayed against a bright red endocarp, and occur in an area where frugivores such as fruit pigeons both feed on fruit and travel between islands, e.g., *Ducula pacifica* Gmelin (Gibbs et al. 2001); however, such hypotheses must be weighed against seed retention times of these birds, which so far have proven to be relatively short, e.g., 19 to 330 minutes in the New Zealand pigeon, *Hemiphaga novaeseelandiae* Gmelin (Wotton et al. 2008) and 55-207 minutes in the New Caledonian endemic *Ducula goliath* Gray (Munzinger, unpublished data).

Successful germination and seedling establishment may present greater obstacles than seed dispersal per se to population establishment of Annonaceae in open habitats. Seeds of Annonaceae have shown slow germination in research trials. Ng and Mat Asri Ngah Sanah (1991) reported germination data for 14 species of Annonaceae, and germination percentages were mostly below 50% and times to germination of over 60 days were frequent. Similarly, Garwood (1995), in a study of seed germination and seedling development of 15 Panamanian Annonaceae species, found that at least six weeks was required for germination of most species studied. Throughout the tropics, Annonaceae are plants of moist lowland forests. We speculate that these attributes taken together dictate that Annonaceae will not be effective colonizers of new habitats until a framework forest has been established on a site. Germination and establishment studies of New Caledonian Annonaceae would provide empirical data to further test this idea.

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APPENDIX

Identification index to Xylopia specimens from New Caledonia; Abbreviations: DIBA, X. dibaccata; PANC, X. pancheri; PALL, X. pallerescens; VIEI, X. vieillardii.

Balansa
1175: X. pancheri;
1776: PALL;
3529: DIBA, PANC (mixed collection).

Bamps P
5869, 5881: VIEI;
5994, 6021, 6049: PANC.

Barrabé et al. 273: VIEI.

Barrière 156: PANC.

Baumann-Bodenheim 13792, 13824, 13857B, 15562: PANC.

Bernardi 10183: VIEI.

Blanchon 598, 599, 648, 749, 1171, 1305, 1305 bis: PANC.

Brinon 1130: VIEI.

Buchholz 1652: PANC.

Cayrol 32: PANC.

Cribs 1299 [Bernier on printed label] 1551: PANC.

Dagostini & Rigault 1331: PANC.

Däniker 1281: DIBA.

Franc 688, 1581 Série A, 1631 Série A, 1825, 2440: PANC.

Gentry & McPherson 34621: PANC.

Green 1826: PANC.

Guillaumin A. 8011: VIEI.
Veillon
1049, 1399: PANC;
1867, 4730: PALL;
6477, 6999, 7613: VIEI;
6980, 8148: DIBA.

Vieillard
95: VIEI (type);
2284: PANC.

Virot
91, 365, 368, 373: PANC.

Morat P
5310: DIBA;
5580, 7297: PANC.

Munzinger J. 1022: PALL.

Munzinger J. & G. McPherson 2526: DIBA.

Munzinger J. & Rigault 2678: VIEI.

Munzinger J. & Barrabé 4109: PANC.

Munzinger J. et al.
4171, 4690: DIBA;
4192: PANC;
4413: PALL;
5896, 6335: VIEI.

Pancher 640: PANC.

Pusset 55: PANC;

Pusset-Chauvière 490: DIBA.

Raoul s.n.: PANC.

Raynal & Schmid 16630: PANC.

Sarasin 372: PANC.

Sarlin 231, 322: VIEI.

Schmid 2055, 2640, 2737, 4904, (coll. Favier)
5194: PANC;

Schodde 5295: VIEI.

Sévenet 402, 425: PANC.

Stauffer & Blanchon 5739: PANC.

Suprin
166: PANC;
1219: VIEI.

Thorne 28484: PANC.