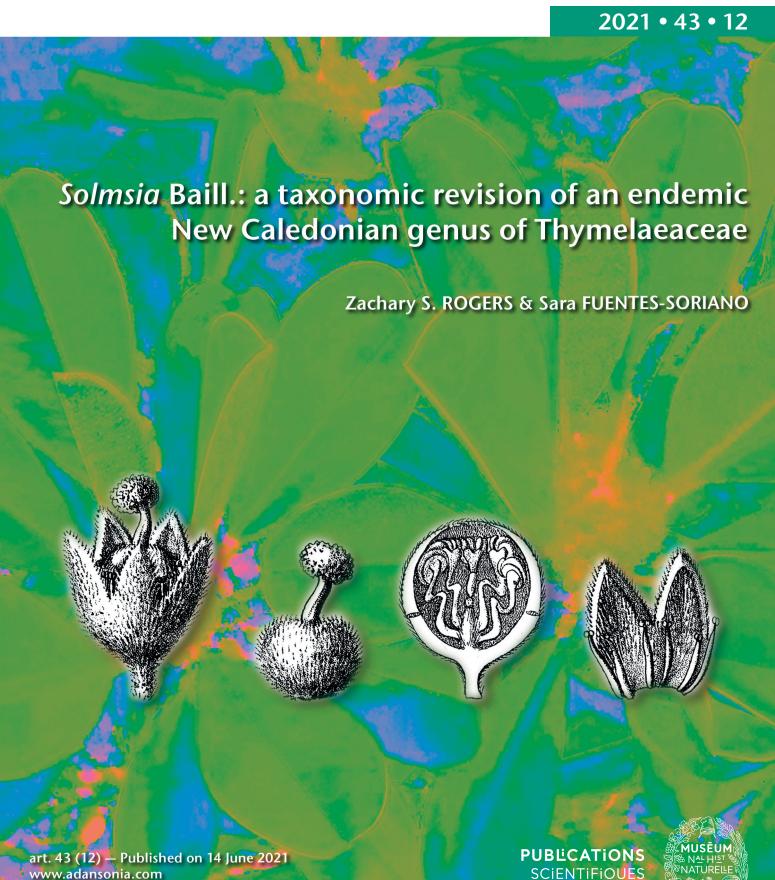
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Solmsia Baill.: a taxonomic revision of an endemic New Caledonian genus of Thymelaeaceae

Zachary S. ROGERS Sara FUENTES-SORIANO

New Mexico State University, Department of Animal & Range Sciences, Herbarium, Box 30003, MSC 3-I Las Cruces, New Mexico, 88003-8003 (United States) zrogers@nmsu.edu (corresponding author) sfuensor@nmsu.edu

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ABSTRACT

The endemic New Caledonian Solmsia Baill. (Thymelaeaceae Juss.: Octolepidoideae Gilg) was founded in 1871 on two species, S. calophylla Baill. and S. chrysophylla Baill. Over the past 150 years, the genus has received little attention taxonomically or otherwise. New morphological, ecological and distribution information gathered from 484 herbarium specimens indicate that the two currently recognized species (evaluated as morphogroups) exhibit continuous, overlapping variation based on statistical multivariate analyses. Both partially sympatric morphogroups are treated here as conspecific under S. calophylla, the lectotype of the genus, and formal recognition of either group at any infraspecific rank is deemed unnecessary. The recircumscribed, single species is completely restricted to Grande Terre, where it occurs in maquis vegetation on ultramafic rocks (peridotite and serpentinite) and some form of ferrallitic soil (ferralsols/oxisols). Lectotypes, selected from a total of c. 55 sheets representing probable or possible syntypes, are designated for both of Baillon's binomials. Full descriptions are provided for the genus and species, accompanied by illustrations, photographs, a distribution map, and a preliminary IUCN conservation assessment of Near Threatened (NT). Morphological and biogeographical relationships of Solmsia are discussed in the phylogenetic context of other Octolepidoideae, a basal subfamily of Thymelaeaceae, along with the closely related, but massively disjunct, Guayana Shield-centered Tepuianthus Maguire & Steyerm. (formerly Tepuianthaceae Maguire & Steyerm.). Dehiscence and capsule size at maturity are also confirmed and documented, respectively, for the first time in the closely related, Deltaria Steenis, another poorly known New Caledonian monospecific endemic genus.

KEY WORDS
Thymelaeaceae,
Deltaria,
Lethedon,
Octolepidoideae,
New Caledonia,
Grande Terre,
morphometric analysis,
ecology,
ultramafic substrate,
IUCN Red List,
lectotypification.

RÉSUMÉ

Solmsia Baill. : une révision taxonomique d'un genre néo-calédonien endémique de Thymelaeaceae. Le genre endémique Solmsia Baill. (Thymelaeaceae Juss.: Octolepidoideae Gilg) a été fondé, en 1871, sur deux espèces S. calophylla Baill. et S. chrysophylla Baill. Au cours des derniers 150 ans, le genre à reçu peu d'attention qu'elle soit taxonomique ou autre. De nouvelles informations morphologiques, écologiques et de répartition, recueillies sur 484 échantillons d'herbiers indiquent que les deux espèces actuellement reconnues (considérées comme des morphogroupes) montrent une variation continue, chevauchante, dans des analyses statistiques multivariées. Ces deux morphogroupes partiellement sympatriques sont traités ici comme conspécifiques sous le nom S. callophylla, le lectotype du genre, et la reconnaissance formelle de l'un ou de l'autre de ces groupes, à quelque rang infraspécifique que ce soit, est jugée inutile. L'espèce unique, recirconscrite, est entièrement restreinte à Grande Terre, ou elle se rencontre de la végétation de maquis sur roches ultramafiques (péridotite et serpentine) et sur certaines formes de sols ferrallitiques (ferralsols/oxisols). Des lectotypes, sélectionnés parmi environ 55 parts représentant des syntypes probables ou possibles, sont désignés pour les deux binômes de Baillon. Des descriptions complètes sont données pour le genre et les espèces, accompagnées d'illustrations, de photographies, d'une carte de répartition, et d'un statut UICN de conservation préliminaire de niveau quasi menacé (NT). Les relations morphologiques et biogéographiques de Solmsia sont discutées dans le contexte phylogénétique des autres Octolepidoideae, une sous-famille basale des Thymelaeaceae, ainsi qu'avec le genre Tepuianthus Maguire & Steyerm. (antérieurement Tepuianthaceae Maguire & Steyerm.) étroitement lié mais notablement disjoint car centré sur le plateau des Guyanes. La déhiscence et la taille des capsules matures sont aussi, et respectivement, confirmées et documentées pour la première fois dans le genre étroitement apparenté, Deltaria Steenis, un autre genre monospécifique, peu connu et endémique de Nouvelle Calédonie.

MOTS CLÉS
Thymelaeaceae,
Deltaria,
Lethedon,
Octolepidoideae,
Nouvelle-Calédonie,
Grande Terre,
analyse morphométrique,
écologie,
substrat ultramafique,
liste rouge de l'UICN,
lectotypification.

INTRODUCTION

Solmsia Baill. is a small, functionally dioecious genus of shrubs and small trees endemic to the Grande Terre of New Caledonia. The genus is relatively common in the low (c. 1-5 m tall), usually shrubby, "maquis" (scrub) vegetation that grows on ultramafic substrates (also termed ultrabasic when especially rich in magnesium) that produce nutrient poor soils, which are iron rich, and frequently contain large quantities of magnesium, olivine and heavy metals, such as nickel and chromium (Mueller-Dombois & Fosberg 1998; Read et al. 2006). These ultramafic areas cover less than one-third of New Caledonia's surface area (c. 5500 km²), and yet hold a disproportionally large, edaphically-adapted flora (c. 1218) of 3370 total New Caledonian spp.), which displays high rates of plant endemism (c. 97% of 1218 ultramafic spp. are endemic to substrate) across many plant families (Morat et al. 2012; Isnard et al. 2016). Thymelaeaceae are no exception, with 14 of the c. 15 New Caledonian species endemic to the French overseas collectivity (Rogers 2009-onwards). Besides Solmsia, three other genera of the family occur there (Deltaria Steenis, *Lethedon* Biehler, *Wikstroemia* Endl.).

Historically, *Solmsia* is a very poorly studied genus in all respects. In terms of taxonomy, its familial placement and species diversity have been rather unstable dating all the way back to the foundation of the genus on two concurrently described species, *S. calophylla* and *S. chrysophylla* (Baillon 1871). Over the last 150 years, *Solmsia* has most often been ascribed to one of several malvaceous families, while the number of its constituent species has usually been cited as

either one or two, depending on the author and era (Table 1). The majority of taxonomists have recognized Baillon's two original species as distinct, but in some cases the distinctiveness of the two was questioned, including by Baillon himself only a couple years after his original 1871 protologue (e.g., Baillon 1873; Warburg 1893; Berry & Rogers 2005). More infrequently in the literature, a single species, *S. calophylla*, has been accepted, with *S. chrysophylla* treated as its sole variety (e.g., Guillaumin 1909, 1911; Guillaumin *et al.* 1965). Guillaumin (1948), in the last quasi-comprehensive evaluation of *Solmsia*, only accepted *S. calophylla*, without recognizing any infraspecific taxa (no supporting specimens were cited in the treatment).

It is historically interesting to note that Guillaumin, the most prolific researcher to study New Caledonian Thymelaeaceae, was actually one of the last taxonomists to accept the very close affinity of Solmsia with Lethedon, as well as, to recognize their correct family assignment. In his publications, Lethedon was retained in Ternstroemiaceae Mirb. ex DC. [= Pentaphylacaceae Engl., Ericales, APG 2016] until Guillaumin (1964), before it was finally treated along with Solmsia properly as Thymelaeaceae in Guillaumin et al. (1965). During the later stages of his career, Guillaumin began to formally recognize his var. chrysophylla again, returning to his earlier taxonomic opinion held in Guillaumin (1911), as evidenced by his herbarium specimen annotations from the 1950-1960s. Most authors since Guillaumin et al. (1965) have reversed course recognizing S. calophylla and S. chrysophylla as two distinct species (e.g., Jaffré et al. 2001; Herber 2003; Rogers 2005; Morat et al. 2012; Munzinger et al. 2016; see

TABLE 1. — A summary of the taxonomic history of Solmsia Baill, since the genus was founded by Baillon in 1871, including its various group assignments and species diversity figures mentioned in relevant literature. Format of suprageneric rank assignments: FAMILY: Subfamily/Tribe. See the References section for complete citations.

Citing publication	Suprageneric rank(s)	Number of species (infraspecific taxa)
Baillon (1871)	TILIACEAE	2
Baillon (1873)	TILIACEAE/Prockieae	2 or 3 (unless all varieties of one species)
Baillon (1888)	THYMELAEACEAE	not mentioned
Warburg (1893)	FLACOURTIACEAE/Bembicieae	2 (hardly different from each other)
Van Tieghem (1893)	TILIACEAE/Solmsieae	2
Schlechter (1906)	GONYSTYLACEAE	2
Guillaumin (1909)	TILIACEAE	1 (with var. chrysophylla recognized)
Guillaumin (1911)	TILIACEAE	1 (with var. chrysophylla recognized)
Domke (1934)	THYMELAEACEAE: Aquilarioideae/Solmsieae	not mentioned
Edlin (1935)	SCYTOPETALACEAE	not mentioned
Guillaumin (1948)	GONYSTYLACEAE	1 (no infraspecific taxa recognized)
Metcalfe & Chalk (1950)	THYMELAEACEAE (excl. GONYSTYLACAE)	not mentioned
Dehay (1956)	THYMELAEACEAE	1 (no infraspecific taxa recognized)
Steenis (1959)	THYMELAEACEAE: Aquilarioideae	not mentioned
Ding Hou (1960)	THYMELAEACEAE: Aquilarioideae	not mentioned
Guillaumin (1964)	TERNSTROEMIACEAE	not mentioned
Guillaumin <i>et al.</i> (1965)	THYMELAEACEAE (incl. GONYSTYLACEAE)	1 (with var. chrysophylla recognized)
Jaffré (1974)	GONYSTYLACEAE	not mentioned
Airy Shaw (1978)	THYMELAEACEAE: Gonystyloideae	not mentioned
Metcalfe & Chalk (1979, 1983)	THYMELAEACEAE (incl. GONYSTYLACEAE)	not mentioned
Weberling & Herkommer (1989)	THYMELAEACEAE: Aquilarioideae/Solmsieae	2
Jaffré <i>et al.</i> (2001)	THYMELAEACEAE	2
Herber (2002, 2003)	THYMELAEACEAE: Octolepidoideae/"Octolepis Group"	2
Rogers (2005)	THYMELAEACEAE: Octolepidoideae	2
Berry & Rogers (2005)	THYMELAEACEAE: Octolepidoideae	1 or 2
Rogers (2009-onwards)	THYMELAEACEAE: Octolepidoideae	1
Morat et al. (2012)	THYMELAEACEAE	2
TPL (2013)	THYMELAEACEAE	2
Schlessman et al. (2014)	THYMELAEACEAE	2
Munzinger et al. (2016)	THYMELAEACEAE	2
WFO (2020)	THYMELAEACEAE	2

Table 1). Albeit most of these recent publications represent area checklists or only brief mentions of the diversity of the genus in a general sense.

Due to the ambiguous status of Baillon's two published Solmsia binomials, the names have been applied inconsistently to specimens in herbaria over the decades, with contradictions even visible in Baillon's own handwritten annotations on a few mixed collections (e.g., Pancher s.n., P06622220!) representing some of the many syntypes used in his descriptions of the two species.

The phylogenetic position of Solmsia in Thymelaeaceae Juss.: Octolepidoideae Gilg is now well-supported based on molecular data (Beaumont et al. 2009; Wurdack et al. unpublished data) and morphological studies (Herber 2002, 2003). However, two important unanswered questions remain. First, what is the relationship of the genus to other members of Octolepidoideae and putative relatives? Second, how many taxa are actually present in *Solmsia*? Clearly, a comprehensive, modern taxonomic revision is needed to address these issues given the confounding morphological variation on display in specimens of Solmsia. The specific goals of this study were to delimit species using morphological and ecological criteria, determine whether or not infraspecific taxa should be recognized, clarify the type material of both of Baillon's binomials, and provide an IUCN conservation assessment of the resulting taxa.

DIVERSITY, ECOLOGY, MORPHOLOGY AND CLASSIFICATION OF SOLMSIA WITHIN OCTOLEPIDOIDEAE

Molecular evidence (e.g., Wurdack & Horn 2001; Wurdack et al. unpublished data) and morphology (e.g., Herber 2002, 2003; Horn 2004; Berry & Rogers 2005) elucidate a close phylogenetic relationship of Solmsia with Deltaria and Lethedon, the three genera together representing the New Caledonian part of the basal subfamily Octolepidoideae (c. 54 total spp. in eight genera) that occurs discontinuously in tropical Western and Central Africa, Madagascar, Southeast Asia, Northern Australia, and through parts of Melanesia to Fiji (Rogers 2009-onwards). Octolepidoideae (sensu Herber 2003) have been further subdivided morphologically into two informal taxonomic groups, i.e., the "Octolepis Group" (5 genera, c. 21 spp.) and the "Gonystylus Group" (3 genera, c. 33 spp.) (diversity statistics from Rogers 2009-onwards). Solmsia, Deltaria and Lethedon are further classified into the Octolepis Group, along with *Octolepis* Oliv., an Afro-Malagasy genus (6 spp., 5 of those Malagasy endemics and 1 widespread African endemic, Rogers 2005), and Arnhemia Airy Shaw, a monospecific genus narrowly endemic to Arnhem Land in the Northern Territory of Australia (Rye 1990). Steenis (1959) considered Solmsia to be a morphological intermediate between Deltaria and Lethedon, but Solmsia also shares some features with Octolepis and Arnhemia, as well as with the three genera of the Gonystylus Group, especially Gony-

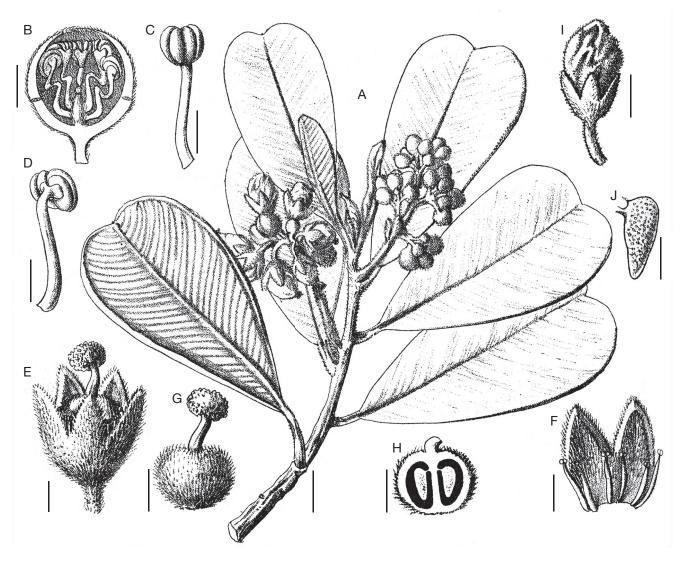


Fig. 1. — Solmsia Baill.: **A**, branch from pistillate plant, with immature fruits and unopened floral buds; **B**, staminate floral bud, showing S-shaped, folded filaments; **C**, **D**, stamen; **E**, pistillate flower; **F**, sepals and several associated staminodia removed from a pistillate flower; **G**, gynoecium; **H**, ovary, longitudinal section; **I**, very immature loculicidal capsule; **J**, immature seed. Modified from plate of figures originally published in Schlechter (1906). All illustrated parts based upon a mixture of specimens gathered from staminate and pistillate plants collected under *F. R. R. Schlechter* 15138 (BM!, G!, K!, L!, P!, Z!). Scale bars: A, 6 mm; B, 1 mm; C, D, 0.5 mm; E-H, 1 mm; I, 3 mm; J, 2 mm.

stylus Teijsm. & Binn. A preliminary molecular phylogenetic analysis (Wurdack et al., unpublished data) indicated that Solmsia was probably most closely related to Octolepis and Lethedon, an evolutionary hypothesis that does have a decent amount of morphological support (Rogers 2005), including a few anatomical features such as the shared incurved fold of the palisade exotegmen occurring in the chalazal region of the seed coat (Horn et al. unpublished ms.).

Comparing *Solmsia* to the other two New Caledonian genera of the Octolepis Group, *Deltaria* contains a single species, *D. brachyblastophora* Steenis, endemic to a couple ultramafic sites in the extreme northwestern subcoastal region of Grande Terre (around Kaala-Gomen and Koumac), and the rare genus is still known only in the herbarium from 13 collections (Rogers 2009-onwards). The more diverse *Lethedon*, composed of *c*. 12 accepted, currently described species (Rogers, in prep.), is nearly endemic to New Caledonia, with a single disjunct

species endemic to the rainforests of Queensland, Australia. Ecologically speaking, as with *Solmsia* and *Deltaria*, a few New Caledonian species of *Lethedon* are similarly restricted to maquis vegetation on ultramafics (e.g., *L. cordatoretusa* Aymonin, *L. thornei* (Guillaumin) Aymonin).

Solmsia (Fig. 1) is easily distinguished from Lethedon and Deltaria, by its Calophyllum-like leaf venation, which is formed by many thin ± parallel veins that terminate in a thick fibrous marginal vein (vs brochidodromous and lacking a marginal vein in the other two), and by its pedunculate, branched inflorescence (vs solitary-flowered or fasciculate in Lethedon; vs flowers borne racemosely on woody "brachyblast" axes in Deltaria, Steenis 1959). The distinctive spur-like inflorescences of Deltaria are rare in the family and comparable to those found in the single African species of Octolepis (classified as sect. Octolepis, Rogers 2005; see also illustrations and photos in Weberling & Herkommer 1989: pl. 4, figs 5-6, pl. 5,

fig. 1). Moreover, Weberling & Herkommer (1989) investigated and described the inflorescence structures of Solmsia, Octolepis, and the three genera of the Gonystylus Group in great detail (Lethedon, Deltaria and Arnhemia not analyzed). Flowers of Solmsia are most morphologically similar to those of *Deltaria*, but differ by the S-shaped filaments folded in bud (Fig. 1B, vs straight), and normally 4-merous, less often 3- or 5-merous condition (vs 3-merous). Herber (2003) noted that stamens with ± peltate anthers are shared between Solmsia (Fig. 1C, D), Lethedon and the Australian Arnhemia, but the extrorse, basally reflexed anthers in *Deltaria* were equated to the horseshoe-shaped anthers present in the three genera of the Gonystylus Group. The androecium of Octolepis is the exception in the subfamily with its introrse, basifixed anthers (Rogers 2005). Fruits of *Deltaria*, confirmed here for the first time as truly dehiscent capsules after attaining a size of c. 1.4-1.8 × 0.5-0.6 cm (based on dried material, e.g., *Dagostini* et al. 816, P06622094!), are markedly different compared to the capsules found in Solmsia and Lethedon because of their elongated, trigonous shape (vs obovoid or obpyramidal in Solmsia) and smaller number of locules (3 vs usually 4-12, but rarely 3-locular in *Solmsia*).

An interesting character to track in Thymelaeaceae is the incidence of dioecy, or at least partial dioecy (most often gynodioecy), which has been reported in c. 14 genera in the family, and more prevalently in Thymelaeoideae Burnett (recorded in nine of its 41 genera, Rogers 2009-onwards). Besides the functional dioecy present in Solmsia, Lethedon, and Deltaria (pers. obs.; see also Schlessman et al. 2014), only one other genus of Octolepidoideae exhibits the condition, Octolepis, and then only in one of its two sections (sect. Dioicae Z. S. Rogers, i.e., the Malagasy section, Rogers 2005).

Comparing Solmsia to members of the completely monoecious Gonystylus Group, Ding Hou (1960) noted similarities in leaf venation and texture found in Solmsia and Gonystylus (SE Asia through Melanesia, c. 31 spp.; Tawan 2004; Rogers 2009-onwards), while further pointing out that the different leaf morphology present in Lethedon and Deltaria was more similar to that of the Bornean Amyxa Tiegh., and its sole species, A. pluricornis (Radlk.) Domke.

Anatomically, secretory cavities and mucilaginous cells are present in the leaves of Solmsia (Domke 1934; Metcalfe & Chalk 1950; Dehay 1956) and in Octolepidoideae in general (Stevens 2001-onwards). These glands are usually visible as translucent punctations that turn black on dried herbarium material of Solmsia and in closely related genera such as Deltaria and Lethedon (pers. obs.), becoming particularly conspicuous in members of the Gonystylus Group (i.e., Gonystylus, Amyxa and Aëtoxylon (Airy Shaw) Airy Shaw). Regarding wood anatomy, as in all Octolepidoideae, intraxylary phloem is absent in Solmsia, whereas its presence in young wood is almost universal across Thymelaeoideae (Metcalfe & Chalk 1950; Herber 2002, 2003).

Unlike the common crotonoid pollen found throughout Thymelaeoideae (c. 915 spp., Rogers 2009-onwards), Octolepidoideae pollen grains show strikingly diverse palynological features, which led Herber (2002) to provide a helpful taxonomic classification based on characteristics of the sexine (especially ornamentation) and the basal layer, i.e., the inner and non-sculptured part of the exine (= nexine sensu Erdtman 1952). Solmsia pollen is categorized as morphological "Type I" and distinguished by the presence of a basal layer with pending rods that intrude into the intine, which may be a palynological condition unique within the angiosperms (Nowicke et al. 1985; Herber 2003). In the Octolepis Group, Type I pollen is shared with one other member, the Australian Arnhemia, and the two also exhibit nearly identical ranges in pollen grain sizes, which are the smallest reported in Octolepidoideae thus far (i.e., 27-39 vs 28-36 µm diam., respectively). Pollen Type I is also found in all three genera of the Gonystylus Group (Herber 2002). For comparison, Herber (2002) provided pollen size ranges of 40-72 µm in diam. for the Gonystylus Group, but only three of the c. 31 species of the genus *Gonystylus* were surveyed. The remaining members of Octolepidoideae have different palynological types, or in the case of Deltaria, a distinct subtype, summarized as follows: Lethedon (type II, inward facing rods of type I absent), Octolepis (type III, reticulate exine) and Deltaria (subtype III.A, microreticulate exine).

Unfortunately, no chromosome numbers have been published for Solmsia or other Octolepidoideae. Phytochemistry studies are sparse for the subfamily, mainly coming from thesis reports for Gonystylus (Tawan 1989), but within the Octolepis Group the closely related Lethedon was found to have gynocardin (a cyclopentenoid cyanogenic glycoside) in the seeds of four species (Spencer & Seigler 1985), homoeriodictyol (a trihydroxyflavanone) in the leaves of L. thornei (Paris & Nothis 1970, voucher misidentified as L. cernua (Baill.) Kosterm.), and five 7-methoxy-flavone 5-O-glycosides in L. tannensis Biehler leaves (Zahir et al. 1999).

BIOGEOGRAPHIC CONNECTIONS AND RELATIONSHIPS AMONG SOLMSIA, OTHER OCTOLEPIDOIDEAE AND THE Guayana Shield-centered genus Tepuianthus An interesting biogeographical link has been found between the ± paleotropical Octolepidoideae and neotropical Tepuianthus Maguire & Steyerm. (formerly Tepuianthaceae Maguire & Steyerm., 6 spp. endemic to the sandstone tepuis and adjacent lowland savannas on sands and quartzite in Venezuela, Brazil, and Colombia), based on molecular, morphological and ecological data (Wurdack & Horn 2001; Horn 2004; Berry & Rogers 2005; Rogers et al. 2005; Rogers 2010; Wurdack et al., unpublished data). Wurdack & Horn (2001) were first to recommend placing Tepuianthus in its own new basal subfamily within Thymelaeaceae, using 18S rDNA, atpB and rbcL molecular markers. Tepuianthaceae was retained most notably by Kubitzki (2003), while Berry & Rogers (2005) upheld the family for historical reasons. The name "Tepuianthoideae" remains invalidly published, but *Tepuianthus* has been treated as a basal member of Thymelaeaceae by Rogers (2009-onwards, 2010) and Stevens (2001-onwards).

Solmsia is strikingly similar to Tepuianthus with respect to gross vegetative morphology – e.g., bark peels off in strips, leaves are thick, tough, apically emarginate, with a Calo-

phyllum-like venation pattern, adaxially nitid, and (at least initially) abaxially densely pubescent with golden-whitish, simple trichomes (Berry & Rogers 2005). Anatomically, the two genera, plus the remaining Octolepidoideae, also share similar stem and leaf features such as their lack of intraxylary phloem (Herber 2002, 2003), mucilaginous epidermis, and obconically-projecting epidermal cells (Horn et al. unpublished ms.). Furthermore, numerous additional similarities exist between Solmsia and Tepuianthus with respect to their sexual systems (frequently at least partial functional dioecy), inflorescence structures (± cymose and relatively few-flowered), flowers (e.g., sepals fused to form a very short calyx tube, ovary usually 3-carpellate), fruits (e.g., loculicidally dehiscent capsules) and seeds (Berry & Rogers 2005; pers. obs.).

Tepuianthus has several obvious floral differences distinguishing it from Solmsia - the presence of (2) 3 paired bifid styles, a well-developed corolla, which is composed of five clawed, yellow petals in addition to another separate whorl of fleshy extrastaminal scales (Maguire & Steyermark 1981; Horn 2004; described as a "nectary disk of 5-10 discrete glands" in Berry & Rogers 2005), and introrse stamens (recall that *Octolepis* is the only genus with introrse stamens in the Octolepis Group of Octolepidoideae). In Thymelaeaceae, a true corolla whorl is absent (a somewhat contentious point), but the flowers in some genera possess a series of petaloid organs, derived from sepals or in some genera possibly emanating from androecia, based on shared vasculature traces (cf. Heinig 1951; Stevens 2001-onwards). Within the Octolepis Group, these structures are absent in Solmsia, Deltaria and Arnhemia (Herber 2003), present and scale-like in Lethedon and Octolepis sect. Octolepis (1 African species), and more petaloid in Octolepis sect. Dioicae (5 Malagasy species) (Rogers 2005), while in the three genera of the Gonystylus Group these petaloid organs, if truly homologous, are always present, and in Gonystylus, in particular, are much more numerous in some species (c. 8-65, Tawan 2004). Contrary to statements made by Herber (2003) and Bernardello (2007) that nectaries are always missing in Octolepidoideae flowers, petaloid organs possessing "nectary stomata" have been reported in the flowers of the monospecific Aëtoxylon and in six species of Gonystylus (Tawan 1989). The scale-like petaloid organs found in Lethedon (pers. obs.) are expected to similarly produce some form of nectar. Domke (1934), Heinig (1951) and Herber (2003) provided useful analyses and summaries of various interpretations of the floral whorls in Thymelaeaceae. See Stevens (2001-onwards) for speculation related to the homology of these diverse, perplexing petaloid floral organs.

Solmsia and Tepuianthus show similar ecological and habit characteristics in that both are shrubs or smaller-sized trees, and usually occur in vegetation exposed to high light levels on well-drained, nutrient poor soils (Horn et al., unpublished ms.; pers. obs.). On the other hand, many morphological traits have evolved in parallel between Solmsia, which grows entirely on ultramafic substrates, and Tepuianthus, which is restricted to sandstone/quartzite (populations of the two are currently separated by a geographical disjunction of c. 13 500 air-km).

Other close phylogenetic relationships are found among isolated SE Asian/Melanesian/Australasian groups and Guayana Shield-centered genera, for instance *Ploiarium* Korth. with *Archytaea* Mart. [Bonnetiaceae Nakai], *Tetramerista* Miq. with *Pentamerista* Maguire [Tetrameristaceae Hutchinson], and Old World Dipterocarpaceae Blume with *Pakaraimaea* Maguire & P. S. Ashton [near Cistaceae Juss.] and *Pseudomonotes* A.C. Londoño, E. Alvarez D. & Forero [Dipterocarpaceae: Monotoideae Gilg]) (Berry & Rogers 2005; current classification details fide APG 2016).

Additional formally published molecular analyses with better sampling and stronger supported internal nodes are needed to clarify *Solmsia*'s exact position in the subfamily, confirm relationships among the eight genera classified in Herber's two morphologically-based informal Groups, and to elucidate how *Tepuianthus* fits in phylogenetically as a basal lineage of Thymelaeaceae, which is itself an unresolved basal lineage of Malvales (Stevens 2001-onwards; APG 2016).

MATERIAL AND METHODS

A total of 170 available collections (484 herbarium sheets) of Solmsia were examined from 25 herbaria (acronyms following Thiers 2020): A, BISH, BM, BRI, CANB, DUKE, F, FI, G, GH, K, L, MARS, MEL, MO, NOU, NSW, NY, P, PTBG, RSA, U, US, WU, Z. Physical specimens were studied in nearly all cases except for a few digital photos used in lieu of several unloanable sheets deposited in FI, L, MARS, MEL, U and WU. Additional information was gathered from online digital photos of living plants (e.g., https://www.endemia. nc/, https://www.tropicos.org, https://www.inaturalist.org/) to document morphological details that do not preserve well on dried specimens (e.g., colors, growth form specifics), and also to determine finer-scale pertinent ecological information infrequently or imprecisely reported on herbarium labels (e.g., specific habitat details, degree of sun exposure, slope/ drainage, species associations).

All of the amassed materials were first evaluated morphologically to determine the amount of variation present in the specimens, and to identify any patterns of discontinuous variation signaling potential taxonomically useful characters. Sixty-five characters related to all major plant organs were selected for more detailed observation (e.g., stems, leaves, inflorescences, flowers of both sexes, fruits, seeds). Morphometric variation was measured for larger organs using either a digital caliper or *ImageJ* software (Schneider et al. 2012), while smaller features were quantified using a dissecting scope with an ocular micrometer. Qualitative character variation was divided into appropriate discrete character states (e.g., indument density, leaf texture and thickness, blade apex shape). The specimens of functionally staminate and pistillate plants were treated separately initially, but were found to only differ by features resulting from the degree of androecium or gynoecium development (e.g., organ size and shape, see descriptions for variation), and thus observations from both sexes were pooled for subsequent analyses. Data visualization

and morphometric statistical analyses were carried out using JMP°, Version 15 (SAS Institute Inc., Cary, NC, 1989-2019). Measurements were standardized *a priori* in the software for the multivariate principal component analysis (PCA) and the hierarchical cluster analysis. The PCA was run using the default settings, while the clustering was carried out using Ward's distance method.

Herbarium labels of nearly all examined collections lacked geographic coordinates at the start of the study, so latitudes and longitudes were assigned post-facto using The New Caledonia and Wallis and Futuna Gazetteer (USDMATC 1974) as a primary reference. Google Earth Pro and other online resources served as secondary sources to identify place names and determine suitable coordinates. Modern administrative divisions of New Caledonia were added based on polygons within a GIS data layer imported into Google Earth. Whenever possible, missing elevations, or more general elevational ranges, were added post-facto using the digital elevation model included in Google Earth. Post-facto coordinates and elevations are surrounded by square brackets in the text. The prerequisite georeferencing step allowed for a more complete analysis of distributional, elevational and ecological data, aimed at identifying any potential biotic or abiotic factors affecting morphology within and among populations of Solmsia, considerations that are especially important in the event of infraspecific variation. To that end, seven ecological characters were explored to identity similarities and differences between specimens and populations (e.g., rock/ soil associations, specific maquis type/subtype, slope/aspect, phenology). Most of these parameters were determined or confirmed by superimposing the geographic distribution over available data layers (e.g., geology, pedology, vegetation, precipitation, mining areas) gathered from standard paper and digital atlases (e.g., ORSTOM 1981; Bonvallot et al. 2012) and imported into Google Earth Pro using the 'Image Overlay' option. Supplemental information regarding climate, characterizations of maquis types and subtypes, soil descriptions, geological history, etc. were taken from summaries provided in Mueller-Dombois & Fosberg (1998) and Isnard et al. (2016, and references therein). Ecological variation was broken down into qualitative characters and mapped on top of the morphometric data in the JMP software.

The taxonomic species concept and criteria follows Rogers (2004), while infraspecific variation was evaluated in the context of long established, albeit sometimes historically inconsistently applied, standards and methods as outlined in Stuessy (1994, 2012) and Stuessy et al. (2014). The rationale supporting the recognition of the taxonomic units at the rank of species and below are explicitly stated as recommended by Hamilton & Reichard (1992). Typification methodology follows current taxonomic usage and standard nomenclatural practices (Turland et al. 2018), with additional considerations regarding type selection summarized in Rogers & Spencer (2006).

The distribution map was created using the free, online tool SimpleMappr (Shorthouse 2010, https://www.simplemappr.net).

Conservation assessment was based on IUCN categories, criteria and recommendations (IUCN 2012, 2019). Calculations of the Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using the online GeoCAT tool (Bachman et al. 2011, http://geocat.kew.org/). Populations occurring within New Caledonia's protected area network were identified using GIS data layers and associated information available via The World Database on Protected Areas (UNEP-WCMC 2020, https://www.protectedplanet.net).

Complete collection data and digital photographs of Solmsia herbarium vouchers (including types), are available on Tropicos (https://www.tropicos.org) and the Muséum national d'Histoire naturelle database (https://science.mnhn.fr/all/search).

RESULTS AND DISCUSSION

Morphological and ecological observations were made for 170 available collections of *Solmsia*, a quantity representing an eight-fold increase in the amount of herbarium material available at the time of the last significant treatment (Guillaumin 1948), which was itself only a synoptical account that lacked detailed information, species descriptions and specimen vouchers. The examined modern collections document a broader range of morphological variation and voucher a much wider geographic distribution of the genus on Grande Terre.

ANALYSIS OF MORPHOLOGICAL CHARACTERS

During the preliminary evaluation, many of the 65 investigated morphological characters showed promise as taxonomically useful to distinguish between groups of Solmsia specimens, but nearly all of those were abandoned soon afterwards as they exhibited continuous variation, which overlapped throughout most, and sometimes all, of their quantitative ranges and qualitative states – e.g., plant height, internode length of distal branches, general branching pattern, branch pubescence, degree of leaf persistence, leaf blade thickness and texture, petiole pubescence, inflorescence structure, number of flowers per distal inflorescence cluster, peduncle/pedicel lengths, number and size of sepals, differences in floral structure between sexes, fruit size and shape, number of carpels, seed size and shape, etc. (see descriptions for specific ranges of variation in the referenced characters). Moreover, all features related to flowers, fruits, and seeds were homogenous in Solmsia material. Reproductive organs were therefore treated as taxonomically unimportant in subsequent analyses.

Only a few characters, all vegetative, displayed more consistent patterns of variation that were used to presort the material into two, albeit somewhat overlapping, groups, which were classified as Morphogroups A and B. Morphogroup A roughly corresponded to what Baillon (1871) originally described as Solmsia calophylla, and was characterized qualitatively by its overall less densely pubescent appearance compared to Morphogroup B, which approximated Baillon's simultaneously published S. chrysophylla. Morphogroup A tended to have larger leaves with blades that were more strongly retuse at the apex and abaxially glabrescent, thus allowing the distinctive Calo*phyllum*-like venation pattern to show through prominently, whereas Morphogroup B tended toward smaller leaves, with

Table 2. — The 42 herbarium sheets of *Solmsia* Baill. measured for the morphometric analyses, selected from a total of 170 examined collections. Morphogroups: **A**, "calophylla form"; **B**, "chrysophylla form". An asterisk (*) appearing after the morphogroup designation denotes the presence of some intermediate leaf morphological variation as discussed in the text.

Voucher collection	Herbarium	Morphogroup
Aubréville & Heiné 252	P	Α
Balansa 262 (lectotype of S. chrysophylla)	Р	В
Balansa 263 (lectotype of S. calophylla)	Р	Α
Balansa 1191a (syntype of S. chrysophylla) Baumann-Bodenheim 8123	P P	B B
Bernardi 9326	P	А
Blanchon 394	P	A
Bradford & Hopkins 626	P	A
Bruy & Munzinger 528	P	A
Fallen et al. 117	MO	В
Guillaumin 8388	Z (sheet 1 of 2)	Ā
Guillaumin 8388	Z (sheet 2 of 2)	Α*
Guillaumin & Baumann-Bodenheim 11594	` P ´	Α
Guillaumin & Baumann-Bodenheim 11611	Р	В
Guillaumin 12406	Р	B*
Hürlimann 524	Р	Α
Jaffré 2881	Р	В
Koyama & Setoguchi 8212	A	A*
Lowry et al. 7210	MO	Α
Lowry et al. 7222	МО	В
MacKee 10103 MacKee 20233	P MO	B B
MacKee 20233 MacKee 20293	MO P	А
MacKee 20293 MacKee 25117	MO	A B*
MacKee 29572	P	В
MacKee 29640	MO	A
MacKee 37962	P	В
McMillan 5135	Р	A
McMillan 5196	A	В
McPherson 2334	MO	B*
McPherson 3008	MO	A*
McPherson 3609	Р	A*
McPherson 3610	MO	A*
McPherson 5511	MO	A*
McPherson 5819	MO	B*
McPherson & Mouly 19221	MO	B*
Morat 5944	Р.	В
Mueller-Dombois 81081403	BISH	A
Pillon et al. 318	MO	B*
Sarasin 636	Z	В
Thorne 28584 Wilson 7024	RSA MEL	A A
VVIISUIT /UZ4	IVIEL	А

TABLE 3. — The six quantitative leaf characters measured for the morphometric multivariate analyses, with summary statistics, and the code adopted for the principal component analysis (**PCA**).

		Mean ± St		
No.	Organ: Character	Morpho- group A	Morpho- group B	Code for PCA
	Petiole:			
1	Length	1.75 ± 0.45	0.84 ± 0.26	PL
	Leaf blade:			
2	Perimeter	13.88 ± 4.30	9.18 ± 2.98	Lper
3	Length	5.53 ± 1.75	4.22 ± 1.30	LĹ
4	Distal width	1.79 ± 0.63	0.99 ± 0.41	Dw
5	Medial widh	2.78 ± 0.88	1.58 ± 0.56	Mw
6	Proximal width	2.91 ± 0.84	1.65 ± 0.57	Pw

blades that were slightly emarginate to rounded apically and so densely abaxially velutinous that the persistent trichomes almost completely obscured the same underlying distinctive venation pattern more visible in Morphogroup A. Despite the vegetative morphological tendencies for specimens to sort into one morphogroup, numerous herbarium specimens and photos documented intermediates in features previously reported as diagnostic in the protologues (Baillon 1871) and subsequent taxonomic literature. Most notably, Guillaumin (1909) decided that material of Solmsia chrysophylla should be formally recognized as a variety of S. calophylla because he found that the only real differences between Baillon's two species were that the leaves were larger in S. calophylla, reporting c. 7-9 \times 4.5 vs 5 \times 1.5-2 cm, and remarking that the petioles were longer, citing c. 2 vs 0.5-1 cm. In fact, these ranges were stated verbatim in Baillon's original descriptions, suggesting that Guillaumin based his taxonomic decision entirely on the variation reported in the protologues, rather than on a study of the wider amount of variation present in the 20 collections of Solmsia that he specifically cited at the time (Guillaumin 1909, 1911).

To more rigorously investigate the variation present in the 170 available collections of Solmsia, a representative subset of 42 fertile, good quality herbarium sheets (25% sample) were selected for a morphometric statistical analysis (Table 2). Sampled collections were chosen from both morphogroups equally and taken from localities occurring throughout the ecological and distributional ranges of each group (Fig. 2). Several specimens of each morphogroup showing intermediate variation were also included in the sampling for reference. From each sheet, 10 representative leaves were measured for six characters, generating a total of 420 measurements related to leaf blade size and petiole length, which were then analyzed statistically in JMP (characters and summary statistics, Table 3). Boxand-whisker plots of all six individual leaf characters (Fig. 3) showed continuous, overlapping variation in Morphogroups A ("calophylla form") and B ("chrysophylla form"). A plot of three selected leaf characters together (blade length vs blade distal width vs petiole length) displayed similar overlapping size ranges for both morphogroups (Fig. 4). The statistical results confirmed the preliminary observations that leaves of Solmsia are quite variable and that Morphogroup A ("calophylla form") tended overall to have longer, wider blades and longer petioles.

In the PCA analysis, when measurements for all 420 leaves were included, 15 of the largest leaves were distant outliers and skewed the main cluster of data points: *Guillaumin 8388* (Z!, 5 leaves on sheet 1 of 2), *Guillaumin 12406* (P!, 9 leaves), *MacKee 25117* (MO!, 1 leaf). After those extreme measurements were excluded from the data set, the PCA was re-run with Components 1 and 2 plotted on their respective x-y axes (Fig. 5). Morphogroups A and B did not separate in multivariate space, showing a good deal of overlap across both axes. Over 94% of the variation was explained on the first two principal components, 88% and 6%, respectively (Table 4). Each of the five leaf blade characters contributed roughly equally to the variation on Component 1 (loadings: 0.396-0.422), while petiole length accounted for the majority

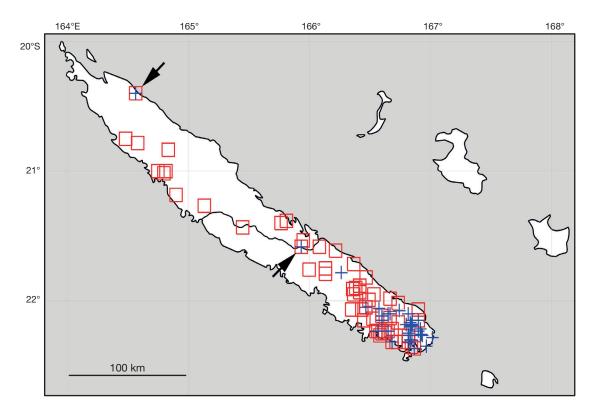


Fig. 2. — Distribution of Solmsia Baill. in New Caledonia. Morphogroups: **A**, "calophylla form" (+); **B**, "chrysophylla form" (□). The two arrows indicate doubtful sympatric populations of both morphogroups based on questionably labeled Vieillard material collected in the mid-1800s: upper arrow denotes the Pouébo locality (non-ultramafic substrate) where both morphogroups were likely erroneously reported on the label of E. Vieillard 254 (P00239877!); lower arrow denotes the "Kanala" [= Canala] locality where several ambiguously labeled sheets of Morphogroup A were supposedly collected (e.g., Vieillard 145, "145=146" and "147"). See Results and discussion section for more details.

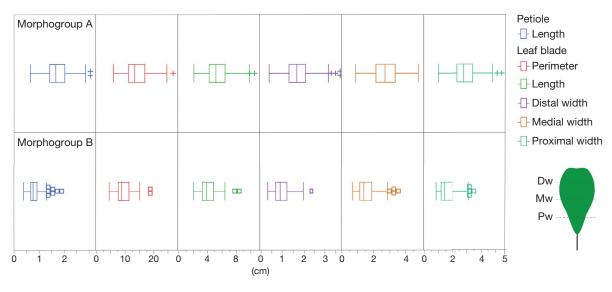


Fig. 3. — Morphometric variation in six leaf characters measured for 420 leaves sampled from 42 herbarium sheets of Solmsia (data classified into Morphogroups A, "calophylla form"; and B, "chrysophylla form"). Leaf sketch illustrates where the three widths were measured on the blade. Abbreviations: Dw, distal width; Mw, medial width; Pw, proximal width.

of the recovered variation on Component 2 (loading: 0.724) (Table 5). A hierarchical cluster analysis was also conducted, and as expected again results provided no resolution (data not shown, available upon request). A few of the qualitative morphological characters considered taxonomically important by Baillon and Guillaumin (e.g., persistence of abaxial leaf indument, blade apex shape) were mapped onto the results of the univariate and multivariate analyses, but these additional

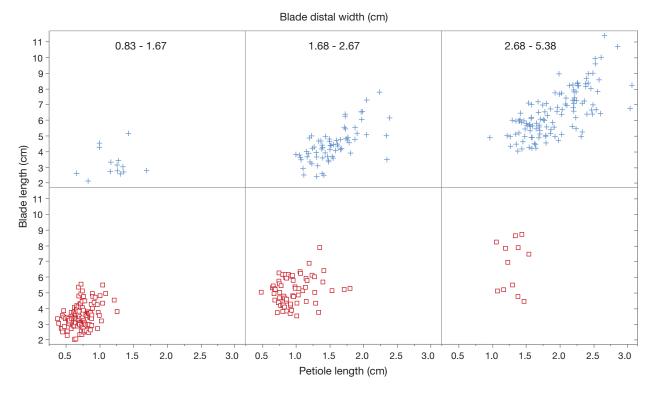


Fig. 4. — Visualization of morphometric data in three selected leaf characters measured for 420 leaves of *Solmsia* Baill. (blade length vs blade distal width vs petiole length). Size variation for blade width and petiole length are summarized into three successively larger categories, with the data points classified into Morphogroups **A** ("calophylla form", +) and **B** ("chrysophylla form", □).

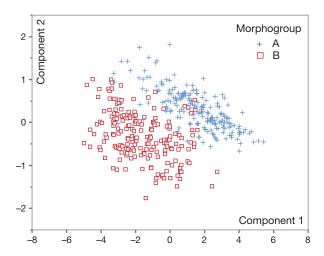


Fig. 5. — Leaf variation of all six morphometric characters recovered by the Principal Component Analysis (94% of the total variation is contained within the first two components), with the data points classified into Morphogroups A ("calophylla form", +) and B ("chrysophylla form", □). Fifteen of the large-leaved outliers were excluded from the plot to reduce skewing of the main cloud of points. 405 measured leaved are plotted, taken from 42 sampled herbarium specimens.

characters also failed to resolve any coherent, distinct groupings, with or without the intermediates included.

Moreover, the possibility that specimens from multiple plants (or even different populations) are mixed together under a single collection number, and thus misrepresenting the actual amount of variation possible in an individual plant, can be ruled out thanks mostly to the efforts of a few skilled collectors that carefully documented variation within and between individuals, including capturing intermediate forms together on a single larger, well-preserved branch – e.g., *McPherson 2334* (MO!, NOU!), *McPherson 3609* and *3610* (both MO!, NOU!, P!, PTBG!), *McPherson 5511* (MO!), *McPherson 5819* (BRI!, MO!, NOU!, P!, PTBG!), *McPherson et al. 19221* (MO!, NOU!, P!), etc. (see documenting images at www.tropicos.org and https://science.mnhn.fr/all/search).

Additionally, the practice of mixing individual plants, especially in a woody, obviously dioecious, often-locally common group like Solmsia, is a poor collecting practice that continues to be perpetuated by many contemporary collectors. Besides ensuring that different plants receive unique collection numbers, it would be especially helpful in the future for collectors of Solmsia (and other dioecious Thymelaeaceae genera like Lethedon, also occurring in New Caledonia) to indicate in their field notes and on labels where the branches for specimens were pruned from the plant (e.g., basal vs plagiotropic/lateral vs orthotropic/crown shoots). Photographers of living plants should be aware of these important distinctions as well, and make every attempt to adequately document similarities and differences within an individual, always including something in-frame for scale, capturing any (micro)habitat features affecting photographed individuals, and avoiding mixtures of different sexed plants together when labeling and posting images. Pressing at least one herbarium voucher per photographed plant (fertile if possible) would help in this regard and greatly increase the scientific value of images, which are

TABLE 4. — Principal component loadings across the first three principal components, which together accounted for c. 97% of the total variation measured in the combined six leaf characters.

		Initial Eigen value	es
Component	Total	% of variance	Cumulative %
1	5.278	87.969	87.969
2	0.367	6.108	94.077
3	0.170	2.838	96.915

rapidly becoming one of the most popular methods of online documentation on biodiversity portals like iNaturalist.

Analysis of ecological and distributional characters Using results from the morphometric analyses of the 42 selected specimens, several ecological characters (e.g., elevation, phenology, substrate, vegetation type) were mapped over the variation patterns and failed to discern any cohesive, distinct groupings.

Extending the evaluation to include all 170 examined collections together, both Morphogroups A ("calophylla form") and B ("chrysophylla form") completely overlapped at elevations from near sea level up to 1000 m (most specimens collected between 100-600 m), and showed two similar peaks of flowering activity in March and July (i.e., during the second halves of two of the four intervening wet seasons of New Caledonia, Mueller-Dombois & Fosberg 1998).

Regarding distributional data, Morphogroups A and B are mostly sympatric geographically, and both are edaphically restricted to the ultramafic substrates and maquis vegetation of Grande Terre (Fig. 2). Most populations of the two morphogroups together are found in the large ultramafic section ("maquis minier") located in the southern-third of the island (Massif du Sud), with 90% (153 collections) of the total examined collections found below 21°30'S latitude. Collections of Morphogroup B (102) accounted for 60% of the study material. Morphogroup A ("calophylla form") has a comparatively smaller range, with most populations falling inside the southern zone of the much more broadly distributed Morphogroup B. All but two localities of Morphogroup A occur south of c. 21°45'S latitude, yielding a distributional centroid located in the greater Plaine des Lacs region; the two exceptions, both very disjunct populations located much further north, are each based on a single Vieillard collection made in the mid-1800s that are of highly questionable positional accuracy given the well-known irregular labeling and numbering problems present in Vieillard's herbarium material as discussed in Guillaumin (1942) and Morat (2010).

The two anomalous populations in Morphogroup A (arrowed in Fig. 2) require further comment as they both vouchered by specimens of probable syntype status, and their accuracy is an important consideration that has some effect on specific values related to the conservation assessment presented in a later section within the taxonomic treatment. The label of Vieillard 254 (P00239877!) mentions the mountains of Pouébo (c. 20°24'S, 164°34'E; upper arrowed locality) and the sheet bears fertile branches belonging to both morpho-

TABLE 5. — Leaf character loadings on the first two principal components.

	Component		
Character	1	2	
Lper	0.421	-0.34	
PL	0.377	0.724	
LL	0.396	-0.58	
Dw	0.415	0.091	
Mw	0.422	0.058	
Pw	0.416	0.092	

groups, while labels of Vieillard 147 (GH!, K!, P[5 sheets]!) cite the mountains of Canala (c. 21°31'S, 165°57'E; lower arrowed locality). The vicinity of Pouébo, located on the NE coast, is almost certainly incorrect as the substrate in that region of Grande Terre is not ultramafic, instead composed of haplic regosols associated with ferralic cambisols (Fritsch in Bonvallot et al. 2012), derived from a complex metamorphic assemblage of siliceous glaucophane/blue and eclogite/ green schists (Mueller-Dombois & Fosberg 1998; Isnard et al. 2016). Additional evidence suggesting an erroneous Pouébo labeling on *Vieillard 254* is that no other *Solmsia* collections, of either morphogroup, have been made within the relatively well collected region since that one and only attribution on the label (dated 1855-1860). For reference, the next closest population of either morphogroup to Pouébo, is vouchered by two collections made on ultramafic substrate at Mont Ouazangou, a site located on the opposing NW coast and situated *c*. 40 air-km to the south of Pouébo. The caveat is that both of those vouchers would best be classified as Morphogroup B, but one of those collections (MacKee 25117, BM!, CANB!, K!, L!, MO!, NOU!, P!) has larger leaves exhibiting tendencies towards Morphogroup A (cf. MacKee 37962, NOU!, P!). On the other hand, the closest exemplar population of Morphogroup A to Pouébo is that aforementioned second questionable disjunct locality at Canala (Vieillard 147), which is in a subcoastal region located c. 190 air-km to the southwest. Unlike the obvious substrate mismatch at Pouébo, parts of the Canala region overlie patches of ultramafic substrate. The problematic issue with Canala is that although both morphogroups have been recorded in that area, only Morphogroup B has been collected more than once, where it has actually been well vouchered by modern collections made as recently as the 1980s. Nevertheless, given the mosaic of substrates present in the relatively large Canala region, it remains quite plausible that the locality for the Morphogroup A specimen is also an error that was introduced early in the history of the specimens when they became associated with the wrong Vieillard label (Guillaumin 1942; Morat 2010). If one of these scenarios is the case, those specimens of Morphogroup A were most likely instead collected much further to the south, possibly somewhere in the vicinity of Mont-Dore in the SW of Grande Terre, a historical collecting locality prominently mentioned on Vieillard sheets with adjacent numbering that bear specimens belonging to Morphogroup A (labels numbered variously as "145", "145, 146", or "145=146"). The area around Mont-Dore obviously fits better within the core distribution



Fig. 6. — Solmsia calophylla Baill. (photos **A-D** belong to plants of Morphogroup A, "calophylla form"; photo **E** belongs to a plant of Morphogroup B, "chrysophylla form"): **A**, **B**, habit and vegetative features at La Madeleine (photos: B. Henry, 23.VIII.2009); **C**, habit at Forêt Cachée (photo: B. Henry, 5.II.2012); **D**, branches with immature fruits (photo: B. Suprin, locality and date unavailable); **E**, branch, Barrage de Dumbéa (photo: C. Davidson, 11.XI.2007, based on *Munzinger et al.* 4666, NOU!, P!). Photos **A-D** downloaded from https://endemia.nc/, copyright of the photographers, and covered under Creative Commons Attribution-Non Commercial 4.0 International Public License (CC BY-NC 4.0), viewable at: https://creativecommons.org/licenses/by-nc/4.0/legalcode [accessed 24.X.2020]. Photo **E** kindly provided with compliments of the photographer.

of Morphogroup A (below 22°05'S latitude, Fig. 2). The problems associated with specific Vieillard collections, many representing probable syntypes, are further discussed in the typification section of the taxonomic treatment.

Returning to the subject of geographic sympatry, even if one were to exclude the two ambiguous co-occurrences of both morphogroups at Canala and Pouébo, there are still at least seven other examples where both forms occur at the same general locality, and in those cases the two are frequently recorded on the same substrate, with the same kind of habit described at the same height, and sometimes even gathered on the same day (including the lectotypes designated in this study for both Solmsia binomials) — e.g., Baie de Prony and environs, Balansa 262 (P[3 sheets]!; lectotype collection of S. chrysophylla), etc. vs Balansa 263 (A!, NY!, P[2 sheets]!; lectotype collection of S. calophylla), etc.; Col de Mouirange, MacKee 20233 (BM!, CANB!, G!, K!, L!, MA!, MO!, NOU!, NY!, P!, Z!) vs Pillon et al. 318 (MO!, NOU!); near La Capture, Plaine des Lacs, Lowry et al. 7210 vs 7222 (both MO!, P!); several places along the route de Yaté, MacKee 29640 (BM!, CANB!,

G!, K!, L!, MO!, P!, Z!), etc. vs Sarasin 636 (Z!), etc.; Rivière des Pirogues, upper valley, Guillaumin & Baumann-Bodenheim 11594 (A!, NY!, P!, Z!) vs 11611 (P!, Z!); Montagne des Sources, Baas-Becking 5966 (G!, Z!) vs Bernardi 12483 (G!, K!, P!, Z!); around Mont Dzumac, Aubréville 252 (P!) vs Stone 14805 (BISH!), Virot 171 (A!, P!), etc. (see documenting images at www.tropicos.org and https://science.mnhn.fr/all/search).

Ecologically, however, within the core zone of morphogroup sympatry (i.e., the ultramafic maquis in the southern half of the Massif du Sud), the plants of Morphogroups A and B are usually (but not always) associated with different kinds of habitats, which arise from their own local soils, geology and derived vegetation types. Both morphogroups occur predominantly on widespread "ferritic ferralitic" soils (Latham et al. 1978; Jaffré et al. in Bonvallot et al. 2012), which are also known as ferralsols/oxisols (Read et al. 2006; Fritsch in Bonvallot et al. 2012). Within the ferralsol soil group, on Grande Terre there is significant variation with respect to depth (up to 30 m), pH (3.25-6), magnesium concentrations, and in available quantities of manganese, nickel, etc. (Isnard

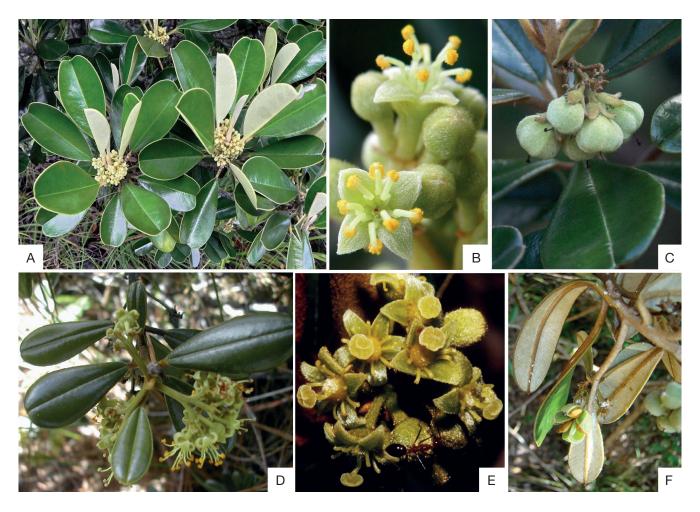


Fig. 7. — Solmsia calophylla Baill. (photos A, B belong to plants of Morphogroup A, "calophylla form"; photos C, D, F belong to plants of Morphogroup B, "chrysophylla form"; photo E lacks vegetative material and locality details and thus cannot be placed in either morphogroup): A, B, branches with inflorescences of a staminate plant at Forêt Cachée (photos: B. Henry, 5.II.2012); C, immature loculicidal capsules at Dumbéa Nord (photo: G. Gâteblé, 1.IX.2005); D, flowering branch from a staminate plant at Col de Plum (photo: G. Gâteblé, 15.II.2006); E, flowers of pistillate plant with an ant visitor (photo: B. Suprin, locality and date unavailable); F, branch with one mature, 4-carpellate capsule (with three seeds visible) at Barrage de Dumbéa (photo: C. Davidson, 11.XI.2007, based on Munzinger et al. 4666, NOUI, P!). Photos A-E downloaded from https://endemia.nc/, copyright of the photographer, and covered under Creative Commons Attribution-NonCommercial 4.0 International Public License (CC BY-NC 4.0), viewable at: https://creativecommons.org/licenses/by-nc/4.0/legalcode [accessed 24.X.2020]. Photo F kindly provided with compliments of the photographer.

et al. 2016). In addition, particle size varies from ultrafine to very coarse (e.g., clay \rightarrow gravel \rightarrow larger rock fragments) depending on the extent and kind of weathering, and along with slope/aspect variation greatly influence how well soils drain (Mueller-Dombois & Fosberg 1998).

Differences in these interrelated variables in New Caledonia give rise to four ferralsol subtypes, namely eroded ferralsols, colluvial ferralsols, gravelly or indurated ferralsols and hydromorphic colluvio-alluvial ferralsols (Isnard et al. 2016), which are each associated with a particular maquis vegetation structure and plant community assemblage. Areas with different soil and maquis subtypes are frequently adjacent to one another, intergrade, and thus have some climatological, compositional and ecological overlaps. For many examined Solmsia collections, it was difficult to determine this useful information with certainty because herbarium label data, post-facto assigned coordinates, and available maps proved too imprecise. Finer-scale observations and photographs documenting habitat/edaphic differences (made at the time of collection) would alleviate many of these limitations, especially for larger, more taxonomically complex groups of Thymelaeaceae occurring in New Caledonia like the closely related Lethedon (Rogers work in progress).

With these caveats in mind, plants of the more widely distributed Morphogroup B ("chrysophylla form") are generally found in more open vegetation growing on upland, well-drained and eroded slopes of ferralsols, while those of Morphogroup A ("calophylla form") are associated with more closed/forest vegetation occurring in low lying, poorly drained areas found along water sources, as observed in the denser population clusters in the vicinities of Lac Yaté, Plaine des Lacs, Creek Pernod, Rivière Madeleine and Grand Lac (Fig. 2). These zones overlie fluvio-lacustrine and cuirasse formations, which develop where sediments build up partly due to the result of flowing waters of rivers, lakes, and within deltas, and lead to loose, weathered gravels, i.e., alluvial and colluvial hydromorphic substrates (Mueller-Dombois & Fosberg 1998; Maurizot & Vendé-Leclerc in Bonvallot et al. 2012).

In the absence of fire and wind, the maquis vegetation around these water sources often follow the familiar succession pattern from the three more exposed forms of maquis vegetation (i.e., "bushy", "shrubby to bushy", and "lignoherbaceous") to a low (rain)forest with more shrubs and small trees (for examples see photos provided in Isnard et al. 2016, fig. 2). Compared to open maquis on nutrient-poor eroded ferralsols, maquis with more tree cover results in large improvements in soil fertility, water availability, and added protection from wind and extreme sun. For instance, ultramafic forests compared to adjacent ultramafic maguis (at four ferralsol sites where both morphogroups co-occur) were found to have about twice as much nitrogen, phosphorus, potassium and magnesium, seven times as much calcium, and lower amounts of iron (Read et al. 2006; Isnard et al. 2016, and references therein). Plants of Morphogroup A ("calophylla form") tend to grow under less environmental stress and have larger, less sclerophyllous leaves that lose their initially dense abaxial velutinous pubescence, while at the same time do not require the densely branched, more compact habit often seen in the most exposed plants of Morphogroup B ("chrysophylla form").

Some populations growing in areas where maquis vegetation and soil subtypes intergrade show an intermediate morphology between the two morphogroups. These forms may be located inside and outside of the sympatric zones of the exemplar morphogroups. In general, populations of Morphogroup B growing in the relatively small isolated pockets of ultramafic substrate moving northwards along Grande Terre are more homogenous morphologically and ecologically, but individuals within a population may show tendencies toward Morphogroup A, even seen at the most northern distribution point for the genus, i.e., Mont Ouazangou, western slope, c. 20°45'S, 164°29'E (MacKee 25117 vs 37962, same site but the latter at higher elevation and probably more exposed and upland from one of the many watercourses on the mountain).

Circumscription of Solmsia based on the combined analyses of variation

The morphological characters observed in *Solmsia* collections show continuous, overlapping quantitative variation as evidenced by the morphometric analyses (Figs 3-5). Intermediate states in all qualitative characters are also well documented by numerous herbarium vouchers (see aforementioned links to online images of specific supporting specimens). Perhaps the most consistent morphological distinction between Morphogroup A (Figs 6; 7A, B) and Morphogroup B (Fig. 7C, D, F) is the degree to which trichomes emanating from the abaxial surfaces of the leaf blades persist as leaves mature. However, that pubescence feature is itself also rather labile in some examined collections within and among populations of either morphogroup. The morphogroups are geographically sympatric, and include at least seven sites where populations of the two co-occur. All available evidence suggests that plants showing morphological characteristics of Morphogroup A ("calophylla form") tend to grow in lower lying areas with

more available moisture, tree cover, and thus individuals are afforded more protection from the sun and wind than plants of Morphogroup B. Populations of Morphogroup A are restricted to the southern part of Grande Terre in areas generally associated with fluvio-lacustrine deposits around the Plaine des Lacs region and in alluvial river valleys that yield much richer soils compared to substrates supporting populations of Morphogroup B (Fritsch in Bonvallot *et al.* 2012; Maurizot & Vendé-Leclerc *in* Bonvallot *et al.* 2012).

Considering the combined data gathered from morphological, distributional, and ecological characters, the final taxonomic decision reached in this study is to treat the two partially sympatric morphogroups as two minor forms within a single species. Moreover, formal recognition of either one at an infraspecific rank is unwarranted following standard criteria summarized in Stuessy *et al.* (2014). Observed variation in *Solmsia* populations appears to be caused mostly by ecological differences found at the local level. Genetic differences among individuals and between populations are expected to be minor, and thus any natural hybrids would be expected to show total fertility. In the following taxonomic treatment, Baillon's two binomials are synonymized under *S. calophylla*, the designated lectotype of the species and the better known name.

TAXONOMIC TREATMENT

Family THYMELAEACEAE Juss. Subfamily OCTOLEPIDOIDEAE Gilg

Genus Solmsia Baill.

Adansonia, Recueil d'Observations botaniques 10: 37, 38 (Baillon 1871) [12.VI.1871]. — Type: Solmsia calophylla Baill. — Lectotype designated [as "Leitart"] by Domke (1934: 117).

ETYMOLOGY. — Baillon chose the name *Solmsia* in honor of Hermann [Maximilian Carl Ludwig Friedrich zu] Solms-Laubach (1842-1915), a German botanist who published research on Chloranthaceae R. Br. ex Sims, Lennoaceae Solms, and several parasitic plant groups, but who himself never visited New Caledonia.

DESCRIPTION

Shrubs, rarely treelets or small trees; intraxylary phloem absent; plants functionally dioecious, most vegetative structures (e.g., young branches, petioles, abaxial surface of leaf blades) and many reproductive structures (e.g., buds, pedicels, sepals, fruit pericarp) densely velutinous; pubescence tan-golden or whitish; trichomes simple, very short, erect, soft.

Leaves

Simple, exstipulate and entire (all three family characters), phyllotaxy spiral, alternate (sometimes appearing subopposite when leaves crowded at distal tips of branches), petiolate, conduplicately folded in bud; epidermis with secretory cavities and mucilaginous cells, densely punctate; punctations usually translucent when fresh and blackish when dry; leaf blade obcordate or obovate, size variable (even on the same

branch), very thick, tough and fibrous, texture coriaceous; surfaces discolorous, adaxial surface glabrous, shiny, abaxial surface initially densely velutinous, trichomes persisting and remaining dense ("chrysophylla form") or becoming glabrescent ("calophylla form"); apex usually somewhat emarginate and terminated with a mucronate tip formed by a short extension of the distal end of the midrib; venation penninerved, Calophyllum-like, veins numerous, all equally thin, diverging from midrib at relatively wide angles then running ± straight and parallel to each other before finally joining with a distinct fibrous marginal nerve that outlines the blade.

Inflorescences

Axillary or pseudoterminal, congested or lax, pedunculate [cf. thyrsoid and analysis in Weberling & Herkommer 1989]; peduncles of variable lengths (up to 2.1 cm long), borne near the distal tips of the branches and usually in the axils of small leaves, terminus of peduncle usually branched into a few shorter secondary axes; secondary inflorescence axes of variable lengths (up to 1.1 cm long), each cluster apparently cymose and terminated with c. 5(-10) shortly pedicellate flowers.

Flowers

Unisexual (functionally), (3)4(5)-merous, staminate and pistillate flowers of similar shape and size, relatively small, pubescent; calyx fused proximally into a very short cupuliform or subcampanulate tube, with the distal part divided into (3)4(5) distinct sepals of \pm uniform shape and size, those slightly longer than fused portion of tube, calyx persistent through fruiting; sepals valvate, subtriangular or ovate-triangular, small, velutinous on both surfaces; petaloid scales absent; androecium diplostemonous, glabrous, persistent in fruit, in pistillate flowers with sterile anthers and shorter staminodial filaments, otherwise similar in flowers of both sexes.

Staminate flowers. With (6)8(10) fertile stamens, all free; filaments slightly extending beyond the sepals, S-shaped and folded in bud (and retaining shape after anthesis), inserted in a ring surrounding a small pistillode; fertile anthers extrorse, ± peltate; pistillode (3)4(5)-locular; rudimentary ovary often with minute ovules; stylode reduced, apex minutely capitate with a rudimentary stigmatic surface.

Pistillate flowers. With (6)8(10) staminodia, all free, usually about half as long as sepals and fertile stamens in staminate flowers; sterile anthers minute; gynoecium (3)4(5)-locular; ovary densely tomentose-sericeous, sessile; carpels uniovulate; ovules anatropous, pendulous; subgynoecial disc absent; style terminal, short, slightly longer than sepals, relatively thick, straight in bud, persistent in fruit; stigma capitate, well-developed.

Fruits

Loculicidal capsules, (3)4(5)-carpellate, obovoid or obpyramidal; pericarp densely velutinous; fruit valves inwardly partitioned (with a septum) at the middle.

Seeds

Compressed laterally, seed coat crustaceous and black, covered with a thin transparent or translucent orange-yellow membrane, outer epidermis of membrane pubescent; chalazal end with a horn-shaped arillate appendage [for illustrated seed and comparisons with several species in other closely related genera of Thymelaeaceae, see Domke 1934: pl. 5, fig. 43b]; endosperm abundant; embryo axile, with flattened, narrow cotyledons, hypocotyl short.

Solmsia calophylla Baill. (Figs 1; 6; 7)

Adansonia, Recueil d'Observations botaniques 10: 38 (Baillon 1871) [12.VI.1871]. — Lectotype (designated here by Rogers): New Caledonia. Grande Terre, Province du Sud, Mont-Dore Commune, "Collines ferrugineuses de la Baie du Prony", [general area: c. 22°19'S, 166°50'E], IX.1868, imm. fr., fr., B. Balansa 263 (lecto-, P[P00239783]!, Fig. 8; isolecto-, A[A01005249]!, NY[NY03101927]!, P[P06622659]!) [residual syntypes (probable and possible) indicated in Specimens examined section].

Solmsia chrysophylla Baill., Adansonia, Recueil d'Observations botaniques 10: 38, 39 (Baillon 1871) [12.VI.1871]. — Solmsia calophylla Baill. var. chrysophylla (Baill.) Guillaumin, Notulae Systematicae 1: 108, 109 (Guillaumin 1909) [20.XII.1909]. — Lectotype (designated here by Rogers): New Caledonia. Grande Terre, Province du Sud, Mont-Dore Commune, "Collines ferrugineuses de la Baie du Prony", [general area: c. 22°19'S, 166°50'E], IX.1868, fl. bud, fr., B. Balansa 262 (lecto-, P[P06622241]!, Fig. 9; isolecto-, P[P00239812]!, P[P06622240]!), syn. nov. [residual syntypes (probable and possible) indicated in Specimens examined section].

DISTRIBUTION, PHENOLOGY AND ECOLOGY. — Solmsia calophylla is endemic to the Grande Terre of New Caledonia (Fig. 2), where it is restricted to the "maquis" zone, a diverse vegetation type associated with ultramafic substrates most common in the southern quarter of the island (Massif du Sud), but also with numerous relatively small subcoastal outcrops distributed sporadically northwards along the NW coast. The maquis, comprising less than one-third of New Caledonia (c. 5500 km²), is composed of low, shrubby vegetation that grows on several different variants of ferralsols (also known as oxisols), which are relatively nutrient poor and often rich in heavy metals, especially nickel (region locally known as "maquis minier") (ORSTOM 1981; L'Huillier et al. 2010; Isnard et al. 2016). Most populations occur in the southern half of the expansive Massif du Sud region. Disjunct ultramafic outcrops host populations at several sites (running from S to N): Massif Mé Maoya, Massif du Boulinda, Plateau de Tiéa, Massif de Koniambo, Mont Oua Tilou, Massif de Taom/Mont Ouazangou.

Solmsia calophylla occurs from near sea level up to 1000 m elevation, but most herbarium collections were made from within the elevation range of 100 to 600 m. The highest known populations are found around Montagne des Sources, Massif du Humboldt, Col de Vulcain, Mont Koniambo and Mont Taom. The species is locally common at some sites, particularly in the south, and plants have adapted to a wide variety of habitats. Populations occur in several different subtypes of maquis, ranging from the more widespread, open, eroded upland maquis, where plants are exposed to higher light levels, winds, and poorer-quality soils (Morphogroup B, "chrysophylla form"), to the hydromorphic maquis associated with low-lying watercourses on colluvio-alluvial substrates that yield a more protected, low forest maquis vegetation, with much richer soils (Morphogroup A, "calophylla form"). For more specific ecological details and edaphic associations see the corresponding subsection

above within the Results and discussion text.

Flowering and fruiting may take place year round, and sometimes the same plant will have floral buds and mature, dehisced fruits simultaneously present on a single branch. New Caledonia's climate has been classified into four seasons (Mueller-Dombois & Fosberg 1998), and rain received during the two intervening wetter seasons significantly impact flowering activity in *Solmsia*. The most frequent month for flowering recorded by far is March, near the end of the warm, rainy season (perhaps due to collection bias), followed by a second less prolific peak in July during the middle of a season of moderate precipitation. The most commonly reported fruiting period for *S. calophylla* is June through November.

Flowers were reported as fragrant on the labels of five collections (all staminate). Pistillate plants in flower are frequented by ants (*MacKee 43461*, MO!, NOU!, P!; also see a separate visitation event in photo, Fig. 7E). It would appear that pollen is the reward because flowers of both sexes lack potentially nectar-producing organs such as petaloid organs and a subgynoecial disk. Ant visitors have also been observed carrying seeds away from the parent plant in the closely related *Lethedon* on Grande Terre (J. Munzinger, pers. comm.). Besides the possibilities of intentional or unintentional pollination, it seems likely that ants in both genera are drawn to the thin, outer epidermis of the seeds that include a semi-fleshy arillate appendage at one end (Fig. 7F).

VERNACULAR NAME. — The name "Mouoguéporo" (Bourail) has been applied to *Solmsia calophylla* var. *chrysophylla* (fide Guillaumin 1911). No specimen vouchers documenting that local name or any other common name for *Solmsia* have been located in herbaria or literature.

USES. — No uses have been reported for *Solmsia calophylla*, but the species would make an attractive ornamental if brought into cultivation (Figs 6; 7), especially in regards to those individuals with persistent golden velutinous pubescence on their abaxial leaf surfaces (i.e., Morphogroup B, "chrysophylla form").

SPECIMENS EXAMINED [crosses (+): Morphogroup A, "calophylla form"; squares (□): Morphogroup B, "chrysophylla form"; asterisks (*): morphological intermediates]. — New Caledonia. Grande Terre, Province du Nord, Canala, [sheets variously annotated: "Kanala, Mt. Dore" or "Kanala, etc."], [Canala: c. 21°31'S, 165°57'E], 1861-1867, fl. bud, fl., imm. fr., E. Vieillard "145, 146" (F!, G!, GH!, K!, P[4 sheets]!, Z!) [possible residual syntypes of Solmsia chrysophylla] [□]; [sheet annotated: "Montagnes ferrug. Kanala 8" [final letter or number illegible], [Canala: c. 21°31'S, 165°57'E], 1861-1867, fl., E. Vieillard "145=146" (P!) [possible residual syntype of Solmsia calophylla (upper-right branch), and possible residual syntypes of *Solmsia chrysophylla* (two left-hand branches)] [+ and _]; [sheets annotated: "Bois des Montagnes Kanala"], [Canala: c. 21°31'S, 165°57'E], 1855-1860, fl. bud, E. Vieillard 146 (P[3 sheets]!, Z!) [possible residual syntypes of Solmsia chrysophyl-*[a]* [□]; [sheet annotated: "Bois des Montagnes Kanala", but locality questionably within distribution of Morphogroup A, possibly instead collected near Mont-Dore, see Results and discussion section], [Canala: c. 21°31'S, 165°57'E], 1855-1860 [a few sheets with typewritten labels dated 1861-1867], fl., imm. fr., E. Vieillard 147 (GH!, K!, P[5 sheets]!) [probable residual syntypes of Solmsia calophylla] [+]; Canala, dans les terrains ferrugineux, [21°31'S, 165°57'E], XI.1869, fl., imm. fr., fr., B. Balansa 1905 (G!, P[4 sheets]!) [possible residual syntypes of *Solmsia chrysophylla*] []; Canala, [21°31'S, 165°57'E], 20.ÎI.1912, fl. bud, fl., F. Sarasin 553 (Z!) [□]. — Kaala-Gomen, Mont Ouazangou, pente ouest, maquis sur terrains, 300-500 m, [20°45'S, 164°29'E], 4.III.1972, fl., H. S. MacKee 25117 (BM!, CANB!, K!, L!, MO!, NOU!, P!) [and *]; Koniambo, maquis ligno-arbustif, Relevé TK1, [21°01'S, 164°44'23"E], 19.IX.2003, fl. bud, fl., J. Fambart-Tinel & F. Roumagnac 40 (NOU!, P!) []; Mont Ouazangou, pente ouest, maquis, pente rocheuse serpentineuse, 700 m, [20°45'S, 164°29'E], 26. III.1980, fl., *H. S. MacKee 37962* (L!, NOU!, P!) [□]; Mont Taom (contrefort nord-ouest), maquis, terrain serpentineux, 900 m, [20°47'S, 164°35'E], 8.II.1980, fl., H. S. Mackee 37842 (CANB!, G!, K!, L!, MO!, NOU!, P!) [□]. — Koné, Koniambo, Koné, [21°01'S, 164°48'E], 18.I.1925, fr., A. U. Däniker 958 (Z!) []; Massif de Koniambo, south of Voh, 750 m, [21°00'S, 164°49'E], 6.I.1983, fl. bud, *G. McPherson 5300* (MO!) [□]; Massif de Koniambo, rocky hillside with maquis, 650 m, [21°00'S, 164°45'E], 25.III.1987, fl., K. L. Wilson 7153 (NSW!) [□]; Pouembout, Tiéa (plateau), maquis dégradé, terrain serpentineux altéré, 350-450 m, [21°11'S, 164°54'E], 27.XII.1974, fl. bud, fl., H. S. MacKee 29572 (G!, K!, L!, MA, MO!, P!) [□]. — Kouaoua, Kouaoua mine SLN, [21°23'00"S, 165°48'40"E], 14.II.1978, fl. bud, fl., P. Cabalion 405 (MO!, P!) [□]; Kouaoua, Ouaseoua, maquis dégradé, alluvions serpentineuses, 30 m, [21°24'S, 165°46'E], 29.III.1977, fl. bud, fl., *H. S. MacKee 32967* (NOU!, P!) [\square]. — Pouébo?, [sheet annotated: "Montagnes de Pouébo" and bearing specimens belonging to both morphogroups, the locality is doubtful for both groups because the site is an extremely disjunct northern population that overlies non-ultramafic substrate, see Results and discussion section], [Pouébo: c. 20°24'S, 164°34'E], 1855-1860, fl., E. Vieillard 254 (P!) [possible residual syntypes of Solmsia calophylla (three leftmost branches), and possible residual syntype of Ŝolmsia chrys*ophylla* (rightmost branch)] [+ and □]. — Poya (northern), Massif du Boulinda, 500 m, [21°16′S, 165°08′E], 28.VIII.1987, fl., imm. fr., T. Jaffré 2881 (MO!, NOU!, NSW!, P!) []; Massif du Boulinda, maquis, 400 m, [21°16'S, 165°08'E], 23.II.1978, fl. bud, fl., fr., P. Morat 5944 (NOU!, P!) []; Massif du Boulinda, route de la mine St-Louis, au niveau du petit creek, en maquis minier, [21°16'S, 165°08'E], 22.II.1978, fl. bud, fl., fr., B. Suprin 251 (NOU!) [□]. — Voh, Oua Tilou, sur serpentine, 800 m, [20°51'57"S, 164°51'28"E], 14.IV.1951, st., A. Guillaumin 12406 (G!, P!, Z!) [1]. — Province du Nord/Sud, Bourail, crest to N of Col des Roussettes, between upper valley of Houaïlou and Azareu (spur of Mé Maoya Massif), 700 m, [21°26'S, 165°27'E], 22.I.1963, fl. bud, fl., H. S. MacKee 10103 (K!, L!, P!) [□]; entre Thio et Houaïlou, 1910, st., M. Fetscherin s.n. (P!) [□]. — Province du Sud, Boulouparis, Col de Vulcain, serpentine scrub, 900 m, [21°54'S, 166°23'E], 11.XI.1950, imm. fr., M. G. Baumann-Bodenheim 8123 (K!, P!, Z!) [□]; Bwa Bwi, contrefort Sud-Est, maquis arbustif, substrat ultramafique, 890 m, 21°46'40.8"S, 166°17'57.3"E, 23.XI.2016, imm. fr., *D. Bruy & J. Munzinger 528* (MPU, NOU, P!) [+]; contrefort Nord du Koungouhaou Nord, sous la Concession Byzance Red, maquis haut, [21°47'30"S, 166°08'00"E], 12.I.2005, fl. bud, J. Munzinger & G. Dagostini 2634 (MO!, NOU!) []; La Ouaménie, terre ferrugineuse, 600 m, VIII.1881, fl., imm. fr., A. *Brousmiche s.n.* (P!) [□ and *]; Massif du Humboldt, growing in low forest, 800 m, [21°53'S, 166°25'E], 14.XI.1982, imm. fr., fr., W. G. Ziarnik 75 (BRI!, MO!, NOU!) [1]; bassin de la Tontouta, route du Humboldt, maquis dominé par Gynostoma chamaecyparis, sol érodé sur péridotites serpentinisées, [22°00'S, 166°09'E], 21.III.1996, fl., *T. Jaffré et al. 3301* (NOU!, P!) []; Mine Galliéni, at upper end of Tontouta River valley, partially disturbed maquis, near remnant forest, 740 m, 21°54'32"S, 166°21'30"E, 24.IX.1998, imm. fr., P. Lowry 5085 (MO!, NOU!, P!) [□]; Mont Do, upper region towards top, depauperate bush and heath on E slope, rather dense and humid Araucaria montana forest on W slope, serpentine and peridotite, 700-1014 m, [21°45'S, 166°00'E], 28.XI.1966, imm. fr., F. Ehrendorfer 6600-138.11 (W, WU!) [□]; Mount Gouavi, south slope, above the lower Tontouta Valley, 400 m, 21°56'S, 166°12'E, 10.II.1991, fl. buds, A. M. Buchanan 11945 (HO, MEL!) []. — Boulouparis/Païta, bord de la Rivière du Humboldt, [21°57] 166°22'E], 15.XII.1964, fl. bud, J. P. Blanchon 1310 (NOU!) [n]. — Dumbéa, Dumbéa, [22°09'S, 166°27'E], 1910, fl. bud, A. *D'Alleizette 507* (P!) [□]; bord de la Dumbéa, [22°09'S, 166°27'E], 1911, fl. bud, *I. Franc 27* (G!, P!) [□]; North Dumbéa Valley, between 1st and 4th bunkers of abandoned mine, 400-800 m, 13. XI.1955, fr., H. S. MacKee 3350 (K!, P!, US!) []; Barrage de



 $\label{eq:Fig. 8.} \textbf{Fig. 8.} - \textbf{Lectotype of Solmsia calophylla Baill. designated in this study (\textit{B. Balansa 263}, P00239783!)}. \\ \textbf{Scale bar: 4 cm.}$

Dumbéa, 110 m, [22°08'15"S, 166°31'30"E], 11.XI.2007, fr., J. Munzinger et al. 4666 (NOU!, P!) [□]; Mine Werguin (haute Dumbéa), 200 m, [22°09'S, 166°27'E], 30.IX.1939, fl. bud, fl., R. Virot 212bis (A!, P!) []; Montagne des Sources, [22°07'S, 166°36'E], 24.I.1950, fl. bud, *L. Baas-Becking 5966* (G!, Z!) [□]; Montagne des Sources, 900-1000 m, [22°07'S, 166°36'E], 1. IV.1968, fl. bud, L. Bernardi 12483 (G!, K!, L!, P!, Z!) [+]; Montagne des Sources, mountain plateau, evergreen forest with Araucaria on peridotite, bush and pioneer vegetation on wind exposed slopes and ridges, 600-750 m, [22°07'S, 166°36'E], 30.XI.1966, imm. fr., *F. Ehrendorfer 6600-146.32* (W, WU!) [+]; Montagne des Sources, middle pt, [22°07'S, 166°36'E], 14.VIII.1981, fl., imm. fr., B. C. Stone 14949 (NOU!) [+]; road to Montagne des Sources, c. 20 km from Nouméa, maquis scrub vegation, secondary growth, 200 m, [22°13'S, 166°36'E], 23.VI.1977, fl., imm. fr., M. Fallen et al. 117 (BISH!, L!, MO!, NOU!, P!) []; road from Nouméa to Montagne des Sources, 14 miles [= 22.5 km] from Nouméa, serpentine area, 60-90 m, 1.VIII.1952, imm. fr., C. McMillan 5196 (A!, L!, P!) [□]; c. 15 km N of Nouméa, on road to Montagne des Sources, in the major watershed area for the island, 350 m, 14.VIII.1981, imm. fr., *D. Mueller-Dombois 81081403* (BISH!) [+]; versant W de la crête S du Pic Buse, forêt mésophile sur serpentine, 570 m, [22°09'S, 166°35'30"E], 30.XII.1950, st., H. Hürlimann 524 (A!, NY!, P!, Z!) [+]; pentes sud du Pic Buse (Haute Boulari), 600 m, [22°09'S, 166°35'30"E], 18.VI.1939, fl. bud, R. Virot 101bis (A!, P[2 sheets]!) [+]. — Dumbéa?, road to Montagne des Sources, 800 m, [22°07'S, 166°36'E], 13.III.1955, fl. bud, fl., H. S. MacKee 2206 (US!) [+]. — Mont-Dore, Baie de Prony, collines ferrugineuses, [22°19'S, 166°50'E], IX.1868, fl. bud, fr., B. Balansa 262 (P[3 sheets]! [lectotype collection of S. chrysophylla] [□]; Baie de Prony, collines ferrugineuses, [22°19'S, 166°50'E], IX.1868, imm. fr., fr., B. Balansa 263 (A!, NY!, P[2 sheets]!) [lectotype collection of S. calophylla] [+]; à l'ouest de la Baie des Pirogues, pente raide et rocailleuse, maquis serpentineux bas et épars, 100 m, [22°19'S, 166°41'E], 16.XII.1950, fl. bud, imm. fr., *Ĥ. Hürlimann 361* (A!, NY!, P!, RSA!, Z!) [□]; Rivière des Pirogues, W side, near Baie des Pirogues, mangrove swamp and nearby cliffs and beaches, [22°19'S, 166°41'E], 23.V.1977, fl., L. J. Musselman et al. 5355 (NOU!) []; between the N'Go Bay [= Baie Ngo] and Touaourou, [22°18'10"S, 166°43'E], 1903, fl. bud, O. Rorhdorf 141 (Z!) [□]; between the N'Go Bay [= Baie Ngo] and Touaourou, [22°18'10"S, 166°43'E], VIII.1903-XII.1903, fr., O. Rorhdorf 191 (Z!) [+]; Baie du Carénage, surrounding hillsides, serpentine area, 60-90 m, [22°18'10"S, 166°50'50"E], 22.VII.1952, fl., imm. fr., C. McMillan 5135 (A!, K!, L!, P!) [+]; Col de Mouirange, avant le Col, sur la route à Yaté, la forêt mésophile sur serpentine, 200 m, [22°13'30"S, 166°39'15"E], 26.I.1951, fr., H. Hürlimann 751 (A!, NY!, P!, Z!) [□]; Col de Mouirange, route de Yaté, maquis sur terrain serpentineux, 200 m, [22°12'30"S, 166°40'45"E], 31.I.1969, fl. bud, fl., H. S. MacKee 20233 (BM!, CANB!, G!, K!, L!, MA, MO!, NOU!, NY!, P!, Z!) [□]; along Nouméa road, along creek, c. 1 km E of Col de Mouirange, low forest, 150 m, [22°12'15"S, 166°42'00"E], 16.III.1981, fl. bud, G. McPherson 3597 (MO!, P!) [+]; Col de Mouirange, formation paraforestière, ultramafique, [22°12'30"S, 166°40'45"E], 4.III.2006, fl. bud, fl., Y. Pillon et al. *318* (MO!, NOU!) [□]; Col de Plum (Mont-Dore), sur serpentine, 200 m, [22°15'S, 166°36'E], 22.VIII.1950, st., M. G. Baumann-Bodenheim 5613 (Z!) [□]; Col de Plum, on RT2, along the trail leading to the peak Gué Xi, vegetation is maquis minier, dominated by Soulamea pancheri, Solmsia calophylla, Codia spp., and Hibbertia spp., soil is red-brown ultrabasic laterite, 100-450 m, 22°14'48"S, 166°37'26"E, 12.XII.2000, fl. bud, fl., J. W. Horn *3519* (DUKE!) [□]; La Coulée, [22°14'S, 166°34'E], 12.III.1950, fl., L. Baas-Becking 6004 (Z!) []; Haute Boulari, ravin boisé, terrain serpentineux, 500 m, [22°09'10"S, 166°35'30"E], 28.VI.1978, imm. fr., H. S. MacKee 35307 (K!, L!, MO!, NOU!, P!) [+]; La Coulée River (Boulari) Valley, 75 m, [22°14'S, 166°34'E], 10. IX.1983, imm. fr., *G. McPherson 5776* (MO!) [□ and *]; La Coulée

Valley, NE of Nouméa, secondary scrub near river, [22°14'S, 166°34'E], 30.IX.1983, fr., G. McPherson 5819 (BRI!, MO!, NOU!, P!, PTBG!) [□ and *]; au-dessus de l'Hôtel des Brugerès, à la Coulée Boulari, collines serpentineuses, 200 m, [22°14'S, 166°34'E], V.1938, fr., R. Virot s.n. (A!, P!) [□]; Mont-Dore, scrubby woods on serpentine along Rivière La Coulée, 6.5 km upstream from La Coulée, [22°16'S, 166°35'E], 4.VIII.1968, fl. bud, fl., G. L. Webster & R. Hildreth 14535 (BISH!, GH!, NOU!, NSW!, P!) []; Prony, île Casy, 0-40 m, [22°21'15"S, 166°50'35"E], 15.IV.1974, fl. bud, fl., H. S. MacKee 28501 (P!) []; Les Dalmates, route Nouméa-Yaté, terrain serpentineux, maquis dégradé, 150 m, [22°13'S, 166°41'E], 8.III.1969, fl., H. S. MacKee 20271 (BM!, CANB!, G[2 sheets]!, K!, L!, MA, MO!, NOU!, NY!, P!, Z!) and *]; sur le versant Est du Mont-Dore, forêt à Araucaria, 500 m, [22°16'S, 166°35'E], 21.III.1951, st., A. Guillaumin & M. G. Baumann-Bodenheim 11345 (P!, Z!) [□]; secteur du Mont-Dore, [22°16'S, 166°35'E], 4.I.1978, fl. bud, fl., imm. fr., T. Jaffré 2130 (MO!, NOU!, P!) [□]; Mt D'or [= Mont-Dore], [22°19'S, 166°47'E], 1860, imm. fr., J. A. Pancher s.n. (P[2 sheets]!) [possible residual syntypes of *Solmsia chrysophylla*] [□]; Mont-Dore [one duplicate, P06622211, with the Mont-Dore deleted and replaced with "Kanala" (= Canala)], [Mont-Dore: c. $22^{\circ}19$ 'S, $166^{\circ}47$ 'E], [most sheets dated 1855-1860, but with a few alternatively dated 1861, or 1861-1867], fl. bud, fl., fr., E. Vieillard 145 (P[5 sheets]!) [possible residual syntypes of Solmsia chrysophylla, except the small lower-middle branch on P06622209, which is a possible residual syntype of *Solmsia calophylla*] [+ and □]; c. 2 km NW of RT2 and Mont-Dore Road, 19.VII.1977, fl., imm. fr., T. Whaite & J. Whaite *3643* (NSW!) [□]; Val des Pins supérieur, Pic du Pin, [22°15'00"S, 166°48'58"E], 1.IV.1951, fl. bud, fl., A. Guillaumin & M. G. Baumann-Bodenheim 11924 (L!, P!, Z!) [+]; Plaine du Lac en 8, route du Carénage, serpentines, sol à tendance hydromorphe, [22°18'S, 166°50'E], 1964, fr., J. P. Blanchon 1168 (L!, NOU!, P!) [+]; Plaine des Lacs, La Capture, S of Chutes de la Madeleine, c. 6 km from turnoff to entrance of reserve, maquis along creek, just W of road, 280 m, 22°16'01"S, 166°49'19"E, 24.I.2010, fl. bud, fr., P. Lowry et al. 7210 (MO!, P!) [+]; Plaine des Lacs, partially degraded remnant forest and adjacent maquis W of Camp Penamax, ultramafic substrate, 210 m, 22°16'15"S, 166°49'10"E, 24.I.2010, fl. bud, fl., P. Lowry et al. 7222 (MO!, P!) []; Port-Boisé, [22°21'S, 166°58'E], 6.VI.1977, imm. fr., J. Pusset 17 (NOU!) [+]; Port-Boisé, [22°21'S, 166°58'E], 16.VII.1977, B. Suprin 170 (NOU!) [+]; vallée de la Poueta Koure, sur serpentine, [22°19'S, 166°43'E], 19.II.1951, st., M. G. Baumann-Bodenheim 10665 (NY!, P!, Z!) []; vallée supérieure de la Poueta Koure, forêt sur serpentine, 200 m, [22°19'S, 166°43'E], 10.V.1951, fl. bud, A. Guillaumin & M. G. Baumann-Bodenheim 13216 (A!, L!, Z!) [□]; 5 km au NW de Prony, sur serpentine, 400 m, [22°19'S, 166°49'E], 17.IX.1950, imm. fr., L. Baas-Becking 6081 (L!, P!, Z!) [+]; Prony, terrain ferrugineux, Plateau Ouest, 100 m, [22°19'S, 166°49'E], VIII.1903, fl., fr., L. Cribs 1545 (P!) [+]; Prony, terrain ferrugineux, [22°19'S, 166°49'E], XI.1903, fl., fr., *L. Cribs* 1615 (P[2 sheets]!) [□]; Prony, localité Bergerie, terrain ferrugineux, 3 m, [22°19'S, 166°49'E], XII.1903, fl. bud, imm. fr., *L. Cribs 1728* (P[2 sheets]!) [□]; Prony, serpentine, [22°19'S, 166°49'E], 5.II.1926, fl. bud, fl., A. U. Däniker 2792 (P!, Z!) [+]; Prony, littoral, lieux arides, [22°19'S, 166°49'E], I.1907-II.1914, fl. bud, fl., I. Franc 230A (A!, BRI!, G!, MEL!, NY!, P[2 sheets]!, Z!) [\square]; Prony, littoral, [22°19'S, 166°49'E], I.1914, fl. bud, fl., I. Franc 232 (A!, BRI!, NY!, P!, Z!) [+]; Prony, terrains arides, [22°19'S, 166°49'E], I.1907, fl. bud, fl., I. Franc 232A (P[2 sheets]!) [+]; Prony, du littoral, I.1914, fl. bud, fl., I. Franc 234 (G!, NY!) [+]; Prony, lande et vallées, [22°19'S, 166°49'E], II.1914, fl. bud, *I. Franc 1724A* (A!, G!, K!, P!) []; route de Prony, [22°19'S, 166°49'E], 24.XII.1977, fl. bud, T. Jaffré 2104 (NOU!) [n]; Prony, zone maritime, [22°19'S, 166°49'E], 1900-1910, imm. fr., A.-J. Le Rat 1721 (P!) [+]; Prony, [22°19'S, 166°49'E], 1900-1910, fl. bud, imm. fr., A.-J. Le Rat 220 (A!, P!) [□]; c. 10 km E from the junction of Rivière Bleue along Rt. 2, roadside forest on



 $\label{eq:Fig. 9.} \textbf{Fig. 9.} - \textbf{Lectotype of } \textit{Solmsia chrysophylla Baill.} \ [= S. \ \textit{calophylla Baill.}] \ designated in this study (\textit{B. Balansa 262}, P06622241!). \ Scale \ bar: 4 \ cm.$

ridge, [22°18'S, 166°50'E], 1.III.1992, fl. bud, fl., H. Koyama & H. Setoguchi 8212 (A!) [+]; dans la vallée supérieure de la Rivière des Pirogues, maquis serpentineux, [22°19'S, 166°41'E], 29.III.1951, fl. bud, A. Guillaumin & M. G. Baumann-Bodenheim 11527 (Z!) [n]; ibid., st., A. Guillaumin & M. G. Baumann-Bodenheim 11594 (A!, NY!, P!, Z!) [+]; ibid., fl. bud, fl., A. Guillaumin & M. G. Baumann-Bodenheim 11611 (L!, P!, Z!) []; ibid., st., A. Guillaumin & M. G. Baumann-Bodenheim 11613 (P!, Z!) [+]; Rivière des Pirogues, [22°19'S, 166°41'E], 24.X.1923, fr., C. T. White 2241 (A!, BM!, BRI!, P!) [+]; au NE de St. Louis, collines argilo-ferrugineuses, [22°12'54"S, 166°34'19"E], 15.I.1869, fl. bud, fr., *B. Balansa 1191* (A!, BM!, G!, K!, NY!, P[4 sheets]!, Z!) [possible residual syntypes of Solmsia chrysophylla []. — Païta, Mont Dzumac, [22°03'S, 166°28'E], 8.VII.1965, st., A. Aubréville & Heine 252 (P!) [+]; Mont Dzumac, pentes, [22°03'S, 166°28'E], VII.1906, fl. bud, *I. Franc 230* (P!) []; Mont Dzumac, [22°03'S, 166°28'E], I.1906, fl. bud, *I. Franc 230[B]* (FI!) []; Mont Dzumac, pentes, [22°03'S, 166°28'E], II.1906, fl., *I. Franc 230[C]* (FI!) [□]; Mont Dzumac, pentes, Couvelée, 500 m, [22°03'S, 166°28'E], 15. VIII.1930, fl. bud, fl., imm. fr., *I. Franc 2481* (A!, BM!, BRI!, L!, NSW!, NY!, P!, US!, Z!) []; Mont Dzumac, lower slopes, 600 m, [22°03'S, 166°28'E], 9.VIII.1971, fl. bud, B. C. Stone 14805 (BISH!) [□]; Dzumac, sentier, 600 m, [22°03'S, 166°28'E], 4. IX.1940, fl. bud, imm. fr., R. Virot 171 (A!, P!) [□]; Mont Mou, [22°04'S, 166°21'E], VII.1906, fl., *I. Franc 231* (NY!, P!) [□]; Mont Mou, 30 km NW of Nouméa, in macchia in rainforest on ultrabasic soil, common in scrub vegetation, 500 m, [22°04'S, 166°21'E], 8.VIII.1981, st., D. Mueller-Dombois 81080805 (BISH!) [and *]; Mont Ni, sur les pentes, collines argilo-ferrugineuses, [21°56'S, 166°25'E], 9.III.1869, fl., B. Balansa 1191a (P!) [possible residual syntype of *Solmsia chrysophylla*] []; above a tributary of the Rivière Ni, forested slopes, 820-950 m, 21°59'30"S, 166°29'32"E, 11.XI.2003, imm. fr., fr., G. McPherson & A. Mouly 19221 (MO!, NOU!, P!) [□ and *]. — Païta/Dumbéa, Mts. Kouvele [= Couvelée] moyens, forêt mésophile sur serpentine, [22°04'S, 166°26'E], 9.V.1951, st., A. Guillaumin & M. G. Baumann-Boden*heim 13106* (P!, RSA!, Z!) [□]. — Thio, Col de Petchicara, [21°35'S, 166°05'E], 3.XII.1986, fl. bud, T. Jaffré 2762 (MO!, NOU!, P!) [n]; Riv. Koum, [21°43'S, 166°22'E], [no date], *J. Munzinger 1012* (MO!, P!) [□]; Mont Ninga, fourré maquis, 1000 m, [21°45'S, 166°08'E], 19.VI.1975, imm. fr., *M. Schmid 5349* (NOU!) [□]; auf den Hügeln am Ngoye [= on the hills at Ngoye], 50 m, [21°49'10"S, 166°28'10"E], 29.XI.1902, imm. fr., F. R. R. Rudolf Schlechter 15138 (BM!, G!, K!, L!, P!, Z!) []; à l'embouchure du Tio [= Thio], base des montagnes ferrugineuses, [21°36'46"S, 166°13'00"E], V.1872, fl., B. Balansa 3453 (A!, BM!, G!, K!, NY!, P[3 sheets]!, Z!) []. — Yaté, Plaine du Bidou Rouge (Plaine des Lacs), 150 m, [22°16'S, 166°55'E], VIII.1947, fr., *J. Bernier 166* (P!) [+]; c. 3 km NW of the Chute de la Madeleine, on Nouméa road, woodland in valley, growing with Agathis ovata and Gynostoma deplancheanum, on ultrabasic rocks, 22°12'S, 166°50'E, 17.III.1987, fl., K. L. Wilson 7024 (AD, MEL!, NSW!, NOU) [+]; Creek Pernod, ravin au Sud du creek, Plaine des Lacs, sur serpentine, [22°11'30"S, 166°50'30"E], 16.XI.1950, imm. fr., fr., A. Guillaumin 8388 (G!, NY!, P!, RSA, Z[2 sheets]!) [+]; Creek Pernod, Plaine des Lacs, route de Yaté, 150 m, [22°10′50"S, 166°50′34"E], 6.III.1966, fl. bud, fl., H. S. MacKee 14480 (CANB!, G!, K!, L!, MA, MO!, NOU!, NY!, P!, U!, Z!) [+]; Creek Pernod, route de Yaté, maquis "carapace de fer", 200 m, [22°10'50"S, 166°50'34"E], 23.II.1983, fl. bud, fl., *H. S. MacKee 41264* (MO!, NOU!, P!) [+]; Creek Pernod, 2.5 km N of creek, serpentine, [22°11'S, 166°51'E], 11.V.1977, fl., L. J. Musselman et al. 5099 (NOU!) [+]; Creek Pernod, 2.3 km S of Route 2 bridge, [22°11'27"S, 166°50'30"E], 12.V.1977, fl., L. J. Musselman et al. 5129 (NOU!) [+]; Creek Pernod, maquis, cuirasse ferrallitique, [22°10'50"S, 166°50'34"E], 4.III.2006, fl., Y. Pillon et al. 313 (MO!, NOU!) [+]; Goro-Cascade, [22°17'30"S, 167°00'45"E], 20.IX.1978, imm. fr., B. Suprin 428 (NOU!) [+]; Plaine des Lacs, NE of Grand Lac, low forest remnant,

300 m, [22°15'30"S, 166°55'30"E], 31.VIII.1980, imm. fr., G. McPherson 3008 (MO!, NOU!) [+ and *]; Plaine des Lacs, E of Grand Lac, low forest remnants, [22°16'S, 166°56'E], 20.II.1983, fl. bud, fl., G. McPherson 5511 (MO!) [+ and *]; Plaine des Lacs, E of Grand Lac, c. 3 km along road to Haut Kuebini, low forest, 300 m, [22°16'S, 166°55'E], 4.XI.1982, st., W. G. Ziarnik 49 (BRI!, NOU!) [+]; route forestier de Mamié, maquis, [22°04'S, 166°54'E], 27.VII.1965, fl. bud, imm. fr., M. Schmid 498 (NOU!, P!) [□]; Marais Kiki, colline entre les deux lacs, sur serpentine, 300 m, [22°09'30"S, 166°49'50"E], 26.IX.1950, st., M. G. Baumann-Bodenheim 6197 (K!, P!, Z!) [+]; ibid., [22°11'S, 166°48'E], 26.IX.1950, fl., M. G. Baumann-Bodenheim 6231 (P!, Z!) [+]; ibid., [22°09'30"S, 166°49'50"E], 26.IX.1950, fr., M. G. Baumann-Bodenheim 6251 (A!, NY!, P!, Z!) [+]; Marais Kiki, route de Yaté, maquis haut, terrain serpentineux altéré, 200 m, [22°09'20"S, 166°49'50"E], 8.IX.1985, imm. fr., fr., H. S. MacKee 42795 (NOU!, P!) [+]; Mont Kouakoué, maquis passant à fourré, 800 m, [21°57'S, 166°32'E], 18.XI.1972, fl. bud, *M. Schmid 4291* (NOU!, P!) [□]; Col de Ouénarou, route de Yaté, terrain serpentineux, maquis dégradé, 150 m, [22°10'S, 166°44'E], 19.III.1969, fl. bud, fl., H. S. MacKee 20293 (CANB!, K!, L!, MO!, NOU!, P!) [+]; along Nouméa-Yaté road, c. 5 km E of Ouénarou (the turn-off towards the Rivière Bleue Reserve), maquis vegetation, [160 m], [22°10'08"S, 166°44'35"E], 20.I.1980, fl. bud, fl., G. McPherson 2334 (MO!, NOU!) [+ and *]; along Nouméa-Yaté road, c. 5 km W of Ouénarou, [22°10'S, 166°44'E], 21.III.1981, fl. bud, fl., G. McPherson 3609 (MO!, NOU!, P!, PTBG!) [+ and *]; ibid., fl. bud, fl., G. McPherson 3610 (MO!, NOU!, P!, PTBG!) [+ and *]; basse vallée de la Ouinne, 0-20 m, [21°59'S, 166°40'E], 3.VIII.1973, fl. bud, imm. fr., fr., H. S. MacKee 27132 (NOU!, P!) [□]; Plaine des Lacs, fork of the road to Yaté, the left road leading back northward to 22 km station, [22°16'S, 166°55'E], 27.XI.1947, imm. fr., J. T. Buchholz 1430 (A!, NY!, US!) [+]; Plaine des Lacs, route de Prony, [22°16'S, 166°55'E], 12.VIII.1977, imm. fr., *T. Jaffré 1900* (NOU!, P!) [+]; Plaine des Lacs, 200 m, [22°16'S, 166°55'E], 29.III.1912, fl., F. Sarasin 712 (Z!) [+]; basse Pourina, forêt galerie, terrain serpentineux, 10 m, [22°01'S, 166°44'E], 7.XI.1979, fl. bud, H. S. MacKee 37554 (K!, L!, MO!, NOU!, P!) [□]; Plaine des Lacs, haute Rivière Blanche, forêt des Électriques, forêt humide en vallée, terrain serpentineux, 200 m, [22°16'S, 166°55'E], 27.VII.1996, fr., H. S. MacKee 15365 (K!, L!, P!) [+]; Rivière Blanche, galerie forestière en bordure de marais, [22°08'S, 166°40'E], 1965, fl., *J.-M.* Veillon 77 (NOU!, P!) [□]; Rivière Bleue, maquis, 150 m, [22°06'S, 166°40'E], 1.VII.1965, imm. fr., L. Bernardi 9326 (G!, K!, L!, P!, Z!) [+]; Haute Rivière Bleue, forêt avant le pont, sol alluvionnaire grossier, [22°06'S, 166°49'E], 4.IX.1963, fr., J. P. Blanchon 394 (NOU!, P!) [+]; Parc Rivière Bleue, maquis near road just beyond where road crosses river (heading upstream), dense vegetation with trees and shrubs 3-8 m tall, porous-rocky, red soil, 230 m, [22°06'S, 166°39'E], 11.IV.1996, fl. bud, fl., J. C. Bradford & H. F. Hopkins 626 (MO!, NOU!, P!) [+]; Rivière Bleue, maquis, 150 m, 1.VI.1994, fl. bud, J.-C. Pintaud 36 (P!) [+]; près du pont de la route à Yaté sur la Rivière des Lacs, maquis serpentineux, [22°09'S, 166°51'E], 5.X.1950, imm. fr., A. Guillaumin & M. G. Baumann-Bodenheim 6483 (A!, G!, NY!, P!, Z!) [+]; à l'ouest du pont de la route à Yaté sur la Rivière des Lacs, maquis serpentineux, [22°09'S, 166°51'E], 6.X.1950, fr., A. Guillaumin & M. G. Baumann-Bodenheim 6620 (L!, P!, RSA!, Z!) [+]; Riviére des Lacs, 5 km en aval de la Chute, maquis, terrain serpentineux, 200 m, [22°09'S, 166°51'E], 1. III.1987, fl. bud, fl., H. S. MacKee 43461 (MO!, NOU!, P!) [+]; Plaine des Lacs, serpentine slope, 6 km E of road parallelling Rivière des Lacs, 300 m, [22°13'S, 166°55'E], 2.VIII.1968, imm. fr., G. L. Webster & R. Hildreth 14479 (GH!, NOU!, P!) [+]; Pont de la Rivière Madeleine (Nouméa-Yaté), maquis-fourré en bordure de la rivière, 150 m, 22°10'S, 166°50'E, 20.XII.1977, fr., P. Bamps 6015 (BM!, NOU!, P!) [+]; sur la route à Yaté au PK 40, maquis serpentineux, 300 m, [22°09'S, 166°46'E], 21.II.1951, fl. bud, fl., A. Guillaumin & M. G. Baumann-Bodenheim 10747 (L!, Z!) [+];

route de Yaté, 44 km from Nouméa, maquis, [22°10'S, 166°48'E], 5.XI.1959, fl. bud, R. F. Thorne 28584 (RSA!) [+]; Yaté, [22°09'S, 166°54'E], 27.VII.1965, imm. fr., A. Aubréville 284 (P[2 sheets]!) [+]; Yaté, Plateau au sud du village, maquis sur terrain serpentineux altéré, 300 m, [22°09'40"S, 166°54'40"E], 19.I.1975, fl. bud, fl., H. S. MacKee 29640 (BM!, CANB!, G!, K!, L!, MO!, P!, Z!) [+]; Yaté [probably Lac de Yaté], 150 m, [22°10'S, 166°53'E], 20. IV.1987, fl., H. S. MacKee 43506 (NOU!, P!) [+]; Yaté [probably village], [22°09'15"S, 166°54'40"E], 19.III.1912, fl., F. Sarasin 636 (Z!) [□]. — Province and Commune unassignable, "D", [no date], st., A.-J. Le Rat 699 (P!) []; "Lre Western Track, maquis" 240 m, 22.III.1982, fl., *H. Brinon 1225* (NOU!) [\square]; "Panlaithe" or "Panlaitche" [E. Caldwell worked with E. Vieillard on the West Coast of New Caledonia in 1868, and Mrs. E. Caldwell sent his collections to K – fide Morat 2010], 1868, fl., E. Caldwell s.n. (K!) [1]; [no specific locality], 27.X.1977, st., *J. Bourret 1384* (NOU!) [no specific locality], 186_ [final digit of year missing], fl. bud, E. Deplanche 284 [or 384:] (P!) [probable residual syntype of Solmsia calophylla] [+]; [no specific locality and no date], fl. bud, A.-J. Le Rat 1108 (P!) [□]; [no specific locality, "Donné par M. Pancher, 1870"], imm. fr., J. A. Pancher s.n. (P!) [probable residual syntype of Solmsia calophylla (uppermost branch), and possible residuals syntypes of Solmsia chrysophylla (two lower branches)] [+ and []; [no specific locality], 186_ [final digit of year missing], imm. fr., Petit 144 (P!) [possible residual syntype of Solmsia calophylla] []; [no specific locality and no date], st., Pennel 119 (MARS[2 sheets]!) []; [no specific locality and no date], st., Pen*nel 428* (MARS!) [□].

DESCRIPTION

Shrubs (0.75-)1-4(-5) m tall, rarely treelets or small trees (0.5-)1-5(-6) m tall, dbh c. 10 cm (at 3 m) to 30 cm (at 5 m), branching dense or lax, ± arcuate with a candelabra-like growth form; bark on older branches greyish or reddish brown, on dried material longitudinally striate and sometimes also transversely fissured/cracked; branches densely velutinous; pubescence tan-golden; trichomes very short; leaf scars on older stems conspicuous, subcircular, discolorous compared to surrounding stem.

Alternate, usually only persisting near the distal tips of the branches, when internodes short sometimes giving a subopposite appearance, total leaf length (2.7-)3.5-11.5(-16) cm, smaller leaves usually associated with inflorescences, more proximal leaves generally larger, all leaves densely punctate; punctations usually translucent when fresh and blackish when dry, often obscured abaxially when densely velutinous ("chrysophylla form"); petioles (0.4-)0.7-2.5(-3.1) cm long, c. 1.5-2 mm in diam., longitudinally striate, robust, densely velutinous, pubescence initially tan-golden (darker brown on older petioles when dry), adaxially grooved, groove deeper near base of leaf blade; leaf blade obcordate or obovate, $(2.2-)3-9(-13) \times (0.8-)1.2-$ 5(-6) cm, blade length/width ratio c. 1.5-3.5(-4.5): 1, very thick, tough and fibrous, texture coriaceous; adaxial surface glabrous, very shiny, ± smooth or rugulose when fresh, more rugose when dry, darker green (or darker brown when dry) compared to abaxial surface; abaxial surface initially densely velutinous (Fig. 6B), remaining denser in "chrysophylla form" (Fig. 7F), usually becoming glabrescent in "calophylla form"; pubescence tan-golden or whitish; trichomes simple, very short, erect, soft; base cuneate or less often shortly attenuate-cuneate, more attenuated when margin more strongly revolute near base of blade; apex emarginate, retuse, or rounded; distal mucro c. 0.05(-0.1) mm long, relatively thick, formed by a short extension of the distal end of the midrib; margin usually slightly revolute, generally more obvious near base of leaf blade and after drying; midrib adaxially deeply grooved, abaxially very prominent and thick (c. 1.5-2 mm in diam. at midpoint of blade), longitudinally striate, densely velutinous; venation Calophyllum-like, c. 40-80(-100) vein pairs per side, adaxially generally invisible or usually only perceptible as rugulose folds, abaxially raised slightly and visible except when almost completely obscured by the dense velutinous pubescence ("chrysophylla form"), secondary veins diverging from midrib at an angle of (40-)60-70°, marginal nerve c. 0.05 mm from blade edge, vein course more arcuate in distal 1/4 of the blade; fine venation absent or inconspicuous.

Inflorescences

Similar in staminate and pistillate material (Fig. 7D vs 7C, respectively); bracts absent or minute early caducous; peduncles 0.4-2.1 cm long; secondary inflorescence axes 1.5-11 mm long; floral clusters c. 5(-10)-flowered.

Flowers

Greenish-yellow, globose in bud, fragrant (x 5 reports on labels), densely velutinous, trichomes tan-golden or whitish; pedicels similar in staminate and pistillate flowers, longitudinally striate, densely velutinous, pubescence tan-golden, 1.8-2.5(-4.5) mm long (staminate pedicels), 1.5-2.5(-3) mm long (pistillate pedicels), and up to c. 3.5 mm long (fruiting pedicels); calyx similar in staminate and pistillate flowers, greenish-yellow; tube very short cupuliform or subcampanulate, c. 1-1.5 mm long; sepals subtriangular or ovate-triangular, c. 2×1.5 -1.8 mm (staminate sepals), $2-2.5 \times 1.5-2$ mm (pistillate sepals), eventually reflexed or recurved in later anthesis, adaxially velutinous, often denser in distal half and especially near their somewhat thickened margins, densely velutinous abaxially, apex acute.

Staminate flowers. With (6)8(10) fertile stamens; filaments light green, (1.2-)1.5-2 mm long, c. 0.2 mm wide, effects of compression and folding in S-shape in bud still visible during later anthesis (Fig. 7B); fertile anthers yellow-orange, c. 0.5- 0.6×0.5 -0.6 mm (dry); pistillode minute, with all of the requisite parts but those greatly reduced in size.

Pistillate flowers. With (6)8(10) staminodia; staminodial filaments light green, 1-1.2(-1.4) mm long, c. 0.1-0.15 mm wide, distal portion generally recurved away from center of flower (Fig. 7E); sterile anthers punctate-subglobose, c. 0.1-0.15 in diam.; ovary greenish, \pm subglobose, (1-)1.5-1.8 \times (1.2-)1.5-2.2 mm, densely tomentose-sericeous, pubescence tan-golden or whitish; style 0.8-1 × 0.2-0.3 mm, glabrous, extending c. 0.05-0.1 mm beyond sepals; stigma discoid to subglobose, 0.5-0.6 × 0.7-0.9 mm, densely papillate, lobed (Fig. 7E).

Fruits

Greenish-yellow, obovoid or obpyramidal, $8-10 \times 6.5-8.5$ mm; base of undehisced fruit attenuated for c. 1-1.5 mm and subtended by the persistent (non-accrescent) calyx; apex of undehisced fruit depressed, slightly retuse to emarginate (Fig. 7C); pericarp densely velutinous, pubescence tan-golden, persistent; persistent stamens, staminodia, style and stigma turning black (fresh or dry), remaining attached even after fruit valve dehiscence; dehisced fruit valves c. $6-8.5 \times 5.5-6.5$ mm.

Seeds

Black, c. 5.8-6.5 × 2 mm, covered with a thin transparent or translucent orange-yellow membrane (Fig. 7F), outer epidermis of membrane \pm villous, trichomes orange-yellow, up to c. 1 mm long.

CONSERVATION ASSESSMENT

Solmsia calophylla is assigned a preliminary conservation assessment of Near Threatened, NT (IUCN 2012). Using GeoCAT (Bachman et al. 2011; http://geocat.kew.org/), and considering the aggregate populations of both morphogroups of S. calophylla, the Extent of Occurrence (EOO) is 14008 km² (Vulnerable, VU) and the Area of Occupancy is 296 km² (Endangered, EN), based on the recommended standard 2 × 2 km grid cell size (IUCN 2019). The values of EOO and AOO qualify the species as VU using the primary Criteria B1 and B2, respectively, but the necessary subcriteria for B1 and/ or B2 are not met because S. calophylla is relatively widespread with plenty of suitable habitats, i.e., the habitat of the species is not severely fragmented, it occurs at many more sites than the 10 location maximum threshold, and there have been no extreme fluctuations detected in EOO, AOO, number of locations or subpopulations, or in the number of mature individuals (when analyzed in aggregate or as discrete morphogroups). Due to the preferences of S. calophylla to grow on ultramafics, many populations, occur within the "maquis minier", a mining zone especially focused in the southern part of the island, and although maquis land is unsuitable for agriculture, it does occasionally become degraded by fires (Jaffré in ORSTOM 1981; Isnard et al. 2016). Populations of both morphogroups are well represented within New Caledonia's protected area network, with plants already recorded inside at least 10 reserves and parks: Mont Do Special Fauna and Flora Reserve, Pic Ningua Special Botanical Reserve, Mont Humboldt Special Botanical Reserve, Mont Mou Special Botanical Reserve, Montagne des Sources Strict Nature Reserve, Parc Territorial de la Rivière Bleue, Les Lacs du Grand Sud Néo-Calédonien, Forêt Cachée Special Botanical Reserve, Pic du Pin Special Botanical Reserve, and Zone côtière Ouest Parc Provincial (UNEP-WCMC 2020). The preliminary conservation assessment of NT assigned to S. calophylla should be reevaluated periodically as stipulated by the IUCN, especially as nickel mining activities further encroach into suitable habitat of the species (see also L'Huillier et al. 2010).

Evaluating the conservation status of either informally recognized morphogroup (A-B) discretely proves problematic because of the ambiguous localities at Pouébo (for both

morphogroups) and Canala (for Morphogroup A), which were each vouchered by a single herbarium collection made in the mid-1800s by Vieillard, a collector well-known for using confusing "irrational" labeling and numbering (Morat 2010). Nevertheless, while it is true that analyzing Morphogroup A and B separately produce smaller values in important measures such as EOO and AOO for the two groups (especially for the EOO of Morphogroup A if the Pouébo locality is excluded from the distribution), the earlier unsatisfied subcriteria B1 and/or B2 mentioned before for the aggregate populations of the entire species still are not met for each morphogroup individually, and thus a level of threat higher than NT cannot be justified for either one.

Typifications

Baillon (1871) simultaneously published a composite genus description for *Solmsia*, along with detailed descriptions of its two constituent species, *S. calophylla* and *S. chrysophylla*, in a short article that appeared in volume 10 of his periodical *Adansonia*, *Recueil d'Observations botaniques* (dated 12 June 1871). The generic description included a mixture of comprehensive observations gathered from vegetative, flowering, and fruiting materials (including seeds). Domke (1934) effectively lectotypified *Solmsia*, by designating *S. calophylla* as its "Leitart." The untypified status of the two binomials has never been addressed until the present study.

Baillon did not cite collection information for either species in the protologue, and only provided a very brief and similar general provenance for both. For *Solmsia calophylla*, the protologue locality was cited as "In sylvis montium Novae-Caledoniae", the habit was noted as "arbor media", and the flowers and fruits were described, whereas for *S. chrysophylla*, the locality was cited as "In montuosis Novae-Caledoniae", the habit was given as "Arbor parva?", and the inflorescences were generally described, without a specific description of the flowers or fruits.

In the introduction of the protologue article, Baillon (1871: 34, 37) specified that he obtained a fair amount of material to use in the genus and species descriptions from multiple sources via the statements "[...] de plusieurs explorateurs de la Nouvelle-Calédonie [...] La plupart de ceux auxquels nous avons eu recours nous ont remis [...] une autre plante qui paraît être bien commune dans le pays, car il n'y a pas de collection où elle n'abonde" [i.e., from several explorers who sent material of *Solmsia* along with specimens of another relatively widespread and closely related species endemic to New Caledonia — i.e., *Lethedon tannensis*].

Particularly regarding original source material used for his second new species, *Solmsia chrysophylla*, Baillon (1871: 37) alluded to multiple collections gathered by those same unnamed botanical explorers who had provided him with material for the protologue description of *S. calophylla*, via the passage "Dans une autre Espèce [= *S. chrysophylla*], également abondante dans les collections, [...]" [i.e., in the other species (= *S. chrysophylla*), equally abundant in the collections [...]].

Determining the identities of Baillon's "de plusieurs explorateurs de la Nouvelle-Calédonie" and identifying their

collections that served as original material for the Solmsia species is simplified by the fact that only a few botanists, mostly French in origin, had collected plant specimens from New Caledonia by mid-1871 (Guillaumin 1911; Morat 2010), and even fewer still visited the regions of the Grande Terre where Solmsia occurs.

Considering published itinerary information taken together with the material deposited in the P herbarium, Baillon's home herbarium, there were four significant botanists who collected potential syntype specimens: Eugène Vieillard (coll. 1855-1867, used "numérotation spéciale et irrationnelle" [= special and irrational specimen numbering]), Jean Armand Pancher (coll. 1857-1869, also used special and irrational specimen numbering), Émile Deplanche (coll. 1855-1860 and 1861-1867, used "particulière" [i.e., peculiar/irregular] specimen numbering), and Benjamin Balansa (coll. 1868-1872) (parenthetical information fide Morat 2010). It is interesting historically to note that material of Solmsia, a relatively common and widespread plant, was not collected by the 18th century explorers, including the first Europeans to visit New Caledonia, i.e., The Forsters and W. Anderson (coll. 1774), who accompanied Captain James Cook on his second voyage on the H.M.S. Resolution, and J. Labillardière (coll. 1793), another prolific early visitor who led the second expedition to New Caledonia as part of a mission to find out what happened to the lost French expedition led by Lapérouse.

The confusing and often inconsistent labeling and specimen numbering systems present on Vieillard, Pancher and Deplanche duplicates, widely distributed to many herbaria around the world, are problematic on the examined potential syntype sheets of *Solmsia* at P. For instance, individual Vieillard sheets often contain multiple specimens belonging to both morphogroups, while some identically numbered sheets may bear more than one label (or specimen) that frequently includes at least two contradictory localities (e.g., "Kanala" vs "Kanala, Mt. Dore" vs "Kanala, etc." vs "Mont-Dore" vs "Mont-Dore[deleted anonymously, and replaced with] Kanala"), or dates (e.g., labels typewritten as "1855-1860" vs "1861-1867", and sometimes with a second handwritten year that falls outside of the year range printed on the typewritten label). One specific worst-case example of Solmsia labels with these kinds of discrepancies besides other irregularities in collection numbering is observable in the Vieillard "duplicates" with numbers variously handwritten as "145, 146", "145=146", or simply either "145" or "146" that may be present on one or more labels attached to an individual sheet. In some instances, a sheet with a single number may have two or more affixed specimens belonging to the two different morphogroups, or conversely a sheet numbered with two different numbers, e.g., containing both "145" and "146", may only bear a single affixed branch. Regarding the examined Pancher material, one unnumbered sheet (P06622220!) was nicely annotated by Baillon as S. calophylla and with its partial place of publication (as "Solmsia calophylla H. Bn in Adans. X. 38."), but only the uppermost branch of the three branches affixed to this particular sheet corresponds taxonomically to his S. calophylla. In fact, it is certainly possible that the two lowermost branches on P06622220 may actually represent syntype material of Baillon's S. chrysophylla, which coincidentally also first appeared on the same protologue page (Baillon 1871: 38) as S. calophylla. It is not clear if Baillon missed that the specimens were mixed from different collections, or if the mistake was introduced after the protologues were published, perhaps during the mounting process. Regardless, the dubiously determined, mixed, mostly sterile nature of these Pancher specimens make them undesirable choices as lectotypes for either binomial.

The fourth New Caledonian explorer, Benjamin Balansa, collected several Solmsia collections that do not suffer from the kinds of problems plaguing the specimens of the three other botanists. Balansa assigned handwritten unique collection numbers to his material following a standard numerical format. In addition, Balansa's collections are usually larger, more fertile, and contain more detailed label information, such as descriptions of habitat and habit, and clearly specified collection dates. Given these advantages, two Balansa collections at P, coincidentally with adjacent collection numbers, 263 and 262, are the most suitable choices for the lectotype collections of Baillon's S. calophylla and S. chrysophylla, respectively. Moreover, both collections bear almost identical labels handwritten by Balansa citing the exact same locality ("Collines ferrugineuses de la Baie du Prony"), habit/height description ("Arbrisseau de 2 mètres de hauteur"), and date ("Septembre 1868"), which again illustrate the similarities related to habit, ecology and distribution found in Morphogroups A and B.

Specifically regarding the lectotypification of Solmsia calophylla, both P sheets of Balansa 263 (P00239783!, P06622659!), each bear a single, large nice quality fruiting branch that closely matches the morphology described in the protologue (Baillon 1871). Sheet P00239783 (Fig. 8) is designated as the lectotype because it is the only duplicate of the two that includes the species annotation in Baillon's handwriting (as "Solmsia calophylla H. Bn", but without date of determination and protologue publication details). Two labels are affixed to the sheet. The first label includes Balansa's handwritten inscription: "263. Arbrisseau de 2 mètres de hauteur. Collines ferrugineuses de la Baie du Prony (Nlle Calédonie). Septembre 1868", whereas the second label was typewritten as "HERB. MUS. PARIS. NOUVELLE CALÉDONIE. M. BALANSA, 1868-1870." Baillon did not mention some of Balansa's specific label details in his protologue, possibly because Baillon had examined so much material belonging to his new species, or perhaps he may have been aware of numbering/labeling problems so prevalent in Vieillard material. A third possibility is that he primarily studied the ample fruiting specimen affixed to the sheet designated here as an isolectotype (P06622659), which bears minimal inscriptions on its two labels (viz a handwritten collection number by Balansa on one label, and an anonymous handwritten mention of Nouvelle-Calédonie on the second label).

For Solmsia chrysophylla, all three sheets (P00239812!, P06622240!, P06622241!) of the designated lectotype collection, Balansa 262, have large, nice quality, fertile specimens, complete with many mature, dehisced fruits and floral buds, and with all branches closely matching the morphology de-

scribed in the protologue (Baillon 1871). Sheet P06622241 (Fig. 9) is specifically chosen as the lectotype because it is the only one of the three duplicates to include the species annotation in Baillon's handwriting (as "Solmsia chrysophylla H. Bn", but without date of determination and protologue publication details). Sheet P00239812 is the only one of the three sheets to include specific information relating to locality, plant height, habitat, and date of collection, via a label with Balansa's handwritten inscription: "262. Arbrisseau de 2 mètres de hauteur. Collines ferrugineuses de la Baie du Prony. Septembre 1868. B. Balansa." The second label is the same kind of "HERB. MUS. PARIS" typewritten label that was affixed to the lectotype designated for S. calophylla (Balansa 263). Finally, isolectotype sheet P06622240 bears minimal inscriptions on its two labels, most notably Balansa's handwritten collection number "262", but it also contains a single large fruiting branch affixed to the sheet that is undoubtedly duplicate material of the lectotype sheet.

Counting the lectotypes and isolectotypes of *Solmsia calophylla* and *S. chrysophylla*, a total of *c*. 55 sheets (representing *c*. 15 different collections) were identified as either probable or possible syntype material of Baillon's two binomials (*c*. 30% of the sheets are deposited in other herbaria besides P and those are thus regarded as isosyntypes). All residual syntype information is indicated inside square brackets immediately after the relevant repository information cited in the Specimens examined section (exsiccatae details including barcode/accession numbers and the images of the syntypes are posted at https://www.tropicos.org/ and https://science.mnhn.fr/all/search).

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