

## A MONOGRAPHIC REVISION OF *RETROPHYLLUM* (PODOCARPACEAE)

R. R. MILL

The living species of the genus *Retrophyllum* C.N. Page (Podocarpaceae) are revised. A key to the six species recognised is given. *Retrophyllum filicifolium* (N.E.Gray) R.R.Mill *comb. nov.* from New Guinea and the Moluccas is recognised as a species distinct from *R. vitiense* (Seemann) C.N. Page, which is restricted to material from Fiji and the Solomon Islands. Additional characters are given by which to separate *Retrophyllum piresii* (Silba) C.N. Page (Brazil) from *R. rospigliosii* (Pilg.) C.N. Page (Andes). The six species fall into three species-pairs that differ in reproductive characters: one pair in Papuaia and Melanesia, a second on New Caledonia and a third in South America. In the New Caledonian species-pair, the adult leaves are flattened in four ranks with only minimal heterofacial twisting, whereas in the species-pair inhabiting Fiji, New Guinea and neighbouring areas, as well as the pair inhabiting South America, the adult leaves are arranged in two ranks with significant heterofacial twisting. The names *Podocarpus filicifolius* N.E.Gray and *Nageia minor* Carrière, respectively the basionyms of *Retrophyllum filicifolium* and *R. minus*, are lectotypified, and the typification of *Nageia minor* comprehensively discussed in an appendix. Adult female epitypes are additionally designated for *Podocarpus filicifolius*, which was originally based on juvenile foliage of *Retrophyllum* mixed with a detached seed of *Nageia wallichiana*, and for *Nageia minor*, which Carrière described on the basis of sterile material. Two other appendices provide a list of accepted names and synonyms, and a list of exsiccatae. Illustrations and distribution maps are provided for each species.

*Keywords.* Colour profiles, *Decussocarpus*, epitype, Fiji (island), ImageJ, lectotype, Malesia, *Nageia*, New Caledonia, new combination, New Guinea, Papuaia, *Podocarpus* sect. *Polypodiopsis*, South America.

### INTRODUCTION

The genus *Retrophyllum* C.N. Page was erected by Page (1989 [‘1988’]) for a small group of species in the family Podocarpaceae. This group has been recognised as distinct ever since Bertrand (1874) used the name *Podocarpus* sect. *Polypodiopsis* C.E.Bertr. for two species that were then known as *Podocarpus vitiensis* Seem. and *P. minor* (Carrière) Parl. A similar concept was followed by Wasscher (1941), Buchholz & Gray (1948) and Gray (1962), among others. This sectional name appeared to be based on an earlier name, *Polypodiopsis* Carrière, but that name, and the name *Polypodiopsis muelleri* Carrière, were proposed for rejection by Mill & Weston (2004)

Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, UK.  
E-mail: [r.mill@rbge.ac.uk](mailto:r.mill@rbge.ac.uk)

on the grounds that the names are ambiguous and could refer to a species of a genus of Proteaceae, such as *Beauprea* Brongn. & Gris. These two nomenclatural proposals were subsequently approved (Barrie, 2006). By the time of Gray (1962), *Podocarpus* sect. *Polypodiopsis* comprised six named species, *P. rospigliosii* Pilg. having been described by Pilger (1923), *P. comptonii* J.Buchholz and *P. palustris* J.Buchholz by Buchholz (1949) and *P. filicifolius* N.E.Gray by Gray (1962). Shortly afterwards, de Laubenfels (1968) published a short note pointing out that the material Gray (1962) had used to describe her new species *Podocarpus filicifolius* was a mixture of juvenile foliage of what he regarded as *Podocarpus vitiensis* Seem. and detached fruits of what he called *P. blumei* Endl. [= *Nageia wallichiana* (C.Presl) Kuntze], and therefore he regarded *Podocarpus filicifolius* as a synonym of *P. vitiensis* [= *Retrophyllum vitiense*].

More recently, authors have realised that *Podocarpus* L'Hér. ex Pers. as conceived by Buchholz & Gray (1948) and earlier workers is heterogeneous, and have split it into numerous smaller genera. De Laubenfels (1969) erected the genus *Decussocarpus* de Laub., with three sections: *Decussocarpus* sect. *Decussocarpus* corresponded to *Podocarpus* sect. *Polypodiopsis*, *D.* sect. *Dammaroides* (Bennett) de Laub. to *P.* sect. *Nageia* (Gaertn.) Endl. and *D.* sect. *Afrocarpus* (J. Buchholz & N.E.Gray) de Laub. to *P.* sect. *Afrocarpus* J.Buchholz. *Decussocarpus* sect. *Decussocarpus* had four species: *D. vitiensis* (Seem.) de Laub., *D. minor* (Carrière) de Laub. and *D. comptonii* (J.Buchholz) de Laub. in the South Pacific, and *D. rospigliosii* (Pilg.) de Laub. in tropical South America. To these was subsequently added *Decussocarpus piresii* Silba, a close ally of *D. rospigliosii* that was rather unsatisfactorily described from Brazil (Silba, 1983). Later, on account of a change in the rules of the *International Code of Botanical Nomenclature*, the generic name *Nageia* Gaertn. had to be adopted for *Decussocarpus*, and de Laubenfels (1987) then referred to the three sections as *Nageia* sect. *Nageia* (= *Decussocarpus* sect. *Dammaroides*), *N.* sect. *Polypodiopsis* (C.E.Bertr.) de Laub. (= *D.* sect. *Decussocarpus*) and *N.* sect. *Afrocarpus* (J.Buchholz & N.E.Gray) de Laub. (= *D.* sect. *Afrocarpus*). De Laubenfels (1987) accepted five species in *Nageia* sect. *Polypodiopsis*, namely *Nageia vitiensis* (Seem.) O. Kuntze, *N. comptonii* (J.Buchholz) de Laub., *N. minor* Carr., *N. rospigliosii* (Pilg.) de Laub. and *N. piresii* (Silba) de Laub. In both that paper and his earlier one, he regarded *Podocarpus filicifolius* as a synonym of *Nageia/Decussocarpus vitiensis* and *Podocarpus palustris* as a synonym of *N./D. minor*.

Page (1989) decided that the three sections of *Nageia* as delimited by de Laubenfels (1987) were each worthy of independent generic status. For *Nageia* sect. *Polypodiopsis*, he had to propose the name *Retrophyllum* C.N. Page, because *Decussocarpus* de Laub. had been declared illegitimate and was (and still is) unavailable for use. *Retrophyllum* as delimited by Page (1989) had five species, corresponding to those recognised under *Nageia* by de Laubenfels (1987): *Retrophyllum vitiensis* (Seem.) C.N. Page on Fiji (the New Guinea etc. distribution was not accounted for), *R. comptonii* (J.Buchholz) C.N. Page and *R. minus* (Carrière) C.N. Page (by Page mis-spelled 'minor') on New Caledonia, and 'at least two' – *R. rospigliosii* (Pilg.) C.N. Page and *R. piresii* (Silba) C.N. Page – in tropical South America. Once again, Page (1989) included *Podocarpus palustris* under *Retrophyllum minus*, but unlike de Laubenfels (1969, 1987) he did not

account for *Podocarpus filicifolius* nor cite Gray's 1962 paper in his bibliography. The possibility that there might be more than two species of *Retrophyllum* in South America was repeated in Page's later treatment of Podocarpaceae for *The Families and Genera of Vascular Plants* (Page, 1990), but the reason for this opinion was unexplained in both works.

As well as these five extant taxa, two Australasian fossils have been assigned to *Retrophyllum* as well as an undescribed fossil species from Argentina that is known from leafy branches bearing attached pollen cones (Wilf, 2012; Wilf *et al.*, 2012, 2014; Merkhofer *et al.*, 2015). A fourth fossil species may also belong to *Retrophyllum*, although the necessary combination has not yet been made. The Miocene fossil *Retrophyllum vulcanense* M.Pole is known from St. Bathans and Mata Creek in Otago, New Zealand (Pole, 1992, 1997; Hill & Brodribb, 1999; Pole, 2007), while *R. australe* R.S.Hill & Merrifield from West Dale in Western Australia is slightly older, of Middle Eocene or Oligocene age (Hill & Merrifield, 1993; Hill & Brodribb, 1999). Both these appear to be unequivocal members of *Retrophyllum*. However, on account of some morphological differences, *Decussocarpus maslinensis* D.T.Blackburn from South Australia (Blackburn, 1981) was later transferred to the extinct genus *Willungia* R.S.Hill & M.Pole as *W. maslinensis* (D.T.Blackburn) R.S.Hill & M.Pole ex R.R.Mill & R.S.Hill (Hill & Pole, 1992; Mill & Hill, 2004). Rather more contentious is *Decussocarpus araucoensis* (E.W.Berry) D.R.Greenw., an Eocene fossil from Coronel, Chile (Berry, 1922; Greenwood, 1987). This may well also belong to *Retrophyllum* but, unlike the other fossil species, it has not yet been compared with similar, *Retrophyllum*-like fossils that were described by Hill & Pole (1992) as the new fossil-genera *Smithtonia* R.S.Hill & M.Pole and *Willungia*. Until that is done, assignment of '*Decussocarpus araucoensis*' to *Retrophyllum* should not be made, even though its current name is nomenclaturally incorrect because of the illegitimacy of *Decussocarpus* and should not be used. '*Decussocarpus araucoensis*' was first described as a species of *Araucaria* Juss. by Berry (1922) but was transferred to *Podocarpus* by Florin (1940), who commented that it was near to *P. rospigliosii* (i.e. *Retrophyllum rospigliosii*). Hill & Pole (1992), based only on an examination of albeit excellent quality photographs in Florin's 1940 paper, considered that "probably some, but not all, of the specimens illustrated by Florin belong to this genus" [*Retrophyllum*]. More recently, Hill & Brodribb (1999: 667) repeated this assertion but were more definite in a footnote to a table in the same paper (Hill & Brodribb, 1999: 662), in which they wrote, "Hill & Pole (1992) considered this species to belong to *Retrophyllum*, but they did not formally transfer it to that genus".

In recent molecular phylogenetic studies, *Retrophyllum* in its traditional sense appears close to *Afrocarpus* and *Nageia*, the three genera forming a monophyletic subclade that is sister to *Podocarpus* (Conran *et al.*, 2000; Sinclair *et al.*, 2002; Biffin *et al.*, 2011, 2012; Knopf *et al.*, 2012). Only the studies by Sinclair *et al.* (2002), Herbert *et al.* (2002) and Biffin *et al.* (2011, 2012) used species from all three informal groups A (South Pacific), B (New Caledonia) and C (South America) here recognised within *Retrophyllum*. Those by Sinclair *et al.* (2002) and Herbert *et al.* (2002) remain the most comprehensive in their sampling; Conran *et al.* (2000) sampled only the two species

of group B, while Knopf *et al.* (2012) sampled only species from New Caledonia and South America (i.e. groups B and C) and Biffin *et al.* (2011, 2012) sampled only three of the six species treated here (one from each group). Herbert *et al.* (2002) sampled the same four species as Sinclair *et al.* (2002), i.e. excluding *Retrophyllum piresii*, for which DNA could not be obtained, and *R. filicifolium* (N.E.Gray) R.R.Mill, which at that time was not recognised as distinct from *R. vitiense*. Their results strongly supported the monophyly of *Retrophyllum*, despite the large disparities in morphology between the three morphological groups. For that reason, despite the large morphological differences, some of which appear to be quite fundamental, the genus is retained in its traditional circumscription in this paper. Herbert *et al.* (2002) additionally used random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism to assist in separation of the two New Caledonian species *Retrophyllum comptonii* and *R. minus*.

*Retrophyllum* has been placed controversially by Bobrov & Kostrikin (2000) and Melikian & Bobrov (2000) in Nageiaceae, in the order *Cephalotaxales*. Although a relationship with *Nageia* is suggested by other evidence (including molecular data: Conran *et al.*, 2000; Sinclair *et al.*, 2002; Biffin *et al.*, 2011, 2012; Knopf *et al.*, 2012), a removal from Podocarpaceae (even in a broad sense) is not, nor is its removal to a different order. Salter (2004) has pointed out that Bobrov & Melikian's removal of *Retrophyllum* to *Cephalotaxales* was based on a misinterpretation of the tissue layers of the mature seeds; they interpreted the seeds of *Retrophyllum* and *Nageia* as possessing two integuments, rather than a single integument and an epimatium.

#### TAXONOMIC PROBLEMS

Although a small group, the genus has been the subject of some debate. Four principal problems are addressed in this revision:

- the status of the genus and whether its widely disjunct species form a monophyletic group.
- species limits within *Retrophyllum vitiense*.
- identification of the two New Caledonian species *Retrophyllum minus* and *R. comptonii*, which can be very difficult to separate in the herbarium.
- whether *Retrophyllum piresii* is taxonomically distinguishable from *R. rospigliosii*, and if so at what rank.

#### *Limits of the genus*

*Retrophyllum* in the sense as originally defined by Page (1989, 1990) appears to be a morphologically unnatural genus that has been held together by the single character of heterofacially flattened shoots, which has been regarded as unique within Podocarpaceae. Although this is true for the extant genera of the family, two extinct genera with heterofacially flattened shoots (*Smithtonia* and *Willungia*) have since been described (Hill & Pole, 1992), demonstrating that the character has evolved more

than once in the family in the past. In fact, the six living species recognised here fall into three natural groups, here denoted Groups A, B and C, that are geographically separated today, although in each of them the mechanism whereby the ‘retrophyllous’ leaf arrangement is achieved is similar. The Southwest Pacific species divide into those with distichous leaves in both adult and juvenile phases (Group A: Fiji, Papuasia) and those with 4-ranked leaves in the adult phase but distichous ones in the juvenile state (Group B: New Caledonia). The South American species-pair (Group C) also has distichous leaves in both adult non-reproductive and juvenile phases, but on reproductive shoots the leaves are not ‘retrophyllous’. In all three groups, some degree of internode torsion appears to be involved in bringing the leaves into one plane, just as it is in *Amentotaxus* Pilg. of Taxaceae (Tomlinson & Zacharias, 2001); this results in a characteristic zigzag pattern of decurrent leaf bases along the twigs that is particularly noticeable in twigs of the penultimate order and is especially pronounced in Group C. Each of the three Groups A, B and C possesses unique combinations of characters of male and female reproductive organs, the degree of importance of which is such that, on the basis of morphology alone, each group could probably be segregated at generic rank, as has been done for other small genera of Podocarpaceae such as *Lepidothamnus* Phil., *Lagarostrobos* Quinn and *Manoao* Molloy. Furthermore, in the two groups for which seedlings are known (Groups B and C), these are totally different in their morphology; seedlings of Group B have epigeal germination, about 10 ‘cotyledons’ arranged decussately on a naked axis with very short internodes between them, and decussate phyllotaxis of the first few foliage shoots, while *Retrophyllum rospigliosii* of Group C has apparently hypogeal germination with no visible cotyledons, and spiral phyllotaxis of the initial foliage shoots, which are separated by relatively long internodes along an axis clad with leaves. Nevertheless, the three groups always form a monophyletic clade in molecular phylogenetic studies (e.g. Conran *et al.*, 2000; Sinclair *et al.*, 2002). For that reason, the decision has been made to retain the present generic limits but to recognise three informal geographically defined Groups A, B and C within the genus, as outlined above and defined in detail below.

#### *Group A species*

Group A comprises the species occurring in the Southwest Pacific exclusive of New Caledonia. Most authorities have recognised only one species of *Retrophyllum* in this area, *R. vitiense*, with a range extending from Fiji through the Solomon Islands to New Guinea and the Moluccas (e.g. Eckenwalder, 2009; Farjon, 2010). Seemann (1862, 1863) provided the first descriptions of *Retrophyllum vitiense* (as *Podocarpus vitiensis*), based on material from Fiji collected by himself. Pilger (1903) also knew the species only from Fiji, citing Seemann’s collection and one other. Wasscher (1941) was the first author to realise that a species of *Podocarpus* sect. *Polypodiopsis* [i.e. *Retrophyllum*] also grew in New Guinea and adjacent islands. Under what he regarded as *Podocarpus vitiensis*, he cited two specimens from the south-eastern part of New Guinea and one from New Ireland in the Bismarck Archipelago and gave a very full

description (as is typical of his work) that was based on those three specimens and one female specimen from Fiji. Therefore, although he was the first to describe male material of what is here treated as *Retrophyllum filicifolium*, he did not see female material of the New Guinea plant. Since then, much more material of *Retrophyllum* has been collected from New Guinea, and it is now known from both the eastern half of the island (Papua New Guinea) and the western half (West Papua and Papua). Netta Gray, in her revision of the Pacific members of *Podocarpus* sect. *Polypodiopsis* [i.e. *Retrophyllum*], also regarded *Podocarpus vitiensis* (= *Retrophyllum vitiense*) as occurring in Fiji, the Solomon Islands and New Guinea, but she also described a new species, *Podocarpus filicifolius* N.E.Gray, from Morotai in the Moluccas, just west of New Guinea (Gray, 1962). This she separated from *Podocarpus vitiensis* on the basis of “the spreading scale leaves, thinner foliage leaves, the distinct receptacle 7 mm long supporting the seeds, and the spherical seeds” and used the last of those supposed differences (spherical seeds) to distinguish *Podocarpus filicifolius* from *P. vitiensis*. She also rather perceptively commented that the New Guinea specimens (all of them were by her included under *Podocarpus vitiensis*) “may still prove to represent a separate species”, but the immature ovules that she had seen were pear-shaped, as in Fijian *Podocarpus vitiensis*, and so she did not segregate them. De Laubenfels (1968) discovered that Gray’s *Podocarpus filicifolius* was in fact based on a loose female cone of *Nageia wallichiana* (C.Presl) Kuntze and juvenile foliage of what he regarded in his paper as *Podocarpus vitiensis*. Consequently, most of the alleged differences that Gray had proposed between her new species and the Fijian *Podocarpus vitiensis* become irrelevant, and de Laubenfels (1968) therefore synonymised Gray’s species with the latter. That remained his stance when in the following year he segregated the genus *Decussocarpus* from *Podocarpus* and regarded *Podocarpus filicifolius* as a synonym of *D. vitiensis* (de Laubenfels, 1969). Until now, no one has revisited Gray’s comment that New Guinea material might be taxonomically separable from Fijian *Retrophyllum vitiense*, possibly because Gray’s taxon from Morotai was founded on mixed material. Nevertheless, examination of ample material demonstrates that there are numerous other differences, not observed by either Gray or de Laubenfels, between the New Guinea plants that have been hitherto included in *Retrophyllum vitiense* and the Fijian ones, and that the material from mainland New Guinea agrees with that from Morotai (excluding the foreign cone material). Accordingly, Gray’s name is here reinstated and applied in an emended sense to encompass all plants of *Retrophyllum* seen from New Guinea and the Moluccas. Because Gray’s type material is deemed insufficient, consisting as it does of juvenile leaves belonging to *Retrophyllum* plus a cone that does not belong to the genus, an epitype is designated in this paper to fix the application of the name with regard to the characters of adult foliage and female cones. Gray’s protologue of *Podocarpus filicifolius* is here emended to exclude all mention of female cone characteristics, specifically all the text in the Latin diagnosis after “strobilis masculis ignotis”, everything after “foliage leaves” in the paragraph beginning “This tree differs from *Podocarpus vitiensis* in...”, the last sentence of the paragraph on p. 71 beginning “The female strobili”, and the supposed difference in seed shape in couplet C

of the key to species (p. 71). The description given here provides full details of the male and genuine female cones of *Retrophyllum filicifolium* – the female being here described for the first time although, as mentioned above, Wasscher (1941) had already described the male cones.

#### *Group B species*

Three taxa belonging to *Retrophyllum* have been described from New Caledonia, but until 1949 only one of them was known: *Podocarpus minor* Carrière, now known as *Retrophyllum minus*. Carrière (1867: 641) in his protologue said that this grew “au sommet de très-hautes montagnes, où il fut découvert par un jardinier anglais nommé Richard”, but the only actual specimen cited, *Vieillard* 1275, was from a low-lying locality (Lac Arnaud in the Plaine des Lacs) in the south of the island. From the very start, therefore, *Retrophyllum minus* seems to have been used to apply to all *Retrophyllum* of the island. The discoverer of the high-altitude plant mentioned in Carrière’s protologue was most likely to have been N. Richards, who along with W. H. Duncan was a collector in New Caledonia for Ferdinand von Mueller (Morat, 2010). Richards collected *Araucaria biramulata* J.Buchholz “on open stony land of a very high mountain” in or before 1862 (Richards 3, P, barcoded P00190084, originally named *Araucaria cookii* R.Br.). However, no specimen of *Retrophyllum* collected by him in New Caledonia has been traced at P by me, and none was cited by Guillaumin (1911), who did, however, include three specimens of *Araucaria* collected by him. *Nageia minor* is therefore based purely on the single specimen cited, *Vieillard*’s collection from low land in the south, as discussed in Appendix I of this paper. However, much of what is now recognised as the distinct species *Retrophyllum comptonii* was originally named *Podocarpus minor* in herbaria. Indeed, when Brongniart & Gris (1869) published the first description of the female cones of what they called *Podocarpus minor*, that description was based on two then newly collected specimens: *Balansa* 186 from Prony, which is *Retrophyllum minus*, and *Balansa* 1381 from woods near Téné and Bourail, which belongs to what we now know as *R. comptonii*. Brongniart & Gris’s description of the albumen and embryo of *Podocarpus minor* could only have been based on the seed of *Balansa* 1381, and so this part of their description of *P. minor* applies only to *Retrophyllum comptonii* in today’s taxonomy of the group. Seed colour, which varies from red to whitish-grey and has been used to separate taxa within the group (notably *Podocarpus palustris*), was not mentioned by Brongniart & Gris. However, an early collection of *Retrophyllum minus* by Pancher (s.n., labelled *Vieillard* 1275; see discussion, Appendix I) from Prony described the fruit as red, although only very young seed cones, not long past receptivity, are present on the sheet.

Buchholz (1949) described three new species of *Podocarpus* sensu lato from New Caledonia, the first two of which, *P. comptonii* J.Buchholz and *P. palustris* J.Buchholz, belong to *Retrophyllum* (the third, *Podocarpus sylvestris* J.Buchholz, does belong to *Podocarpus* as currently circumscribed: de Laubenfels, 1972). Both *Podocarpus comptonii* and *P. palustris* were distinguished by him from *P. minor* [*Retrophyllum*

*minus*], for which, however, he provided no comparable description. *Podocarpus comptonii* was separated by its habit (a tall tree), its thinner adult leaves with midrib less than one quarter the width of the lamina, and by differences in female seed shape and wood colour. *Podocarpus palustris* was described as being amphibious and was distinguished from *P. minor* by: (1) the large caudices (trunks enlarged below: an adaptation to the amphibious habit); (2) the whitish wood of lower density (0.3); (3) the thicker, shorter, strongly reflexed seeds; (4) the smaller bracts on the female peduncle; (5) the smaller receptacle only 2 mm long; (6) the beak of what he called the ‘nut’ [i.e. the seed proper, only visible by dissection of a cone] shorter, more broadly conical and recurved; (7) the leaves broader than usual for *P. minor* relative to the length, with the margins less thick in the dried state, and deciduous on the branches of the current year, the individual leaves (called by Buchholz ‘leaflets’) 2–6 × 1–3 mm. The seeds of *Podocarpus comptonii* were stated to be red, while those of *P. palustris* were described as having a grey epimatium when ripe, thereby distinguishing it from the red epimatium of *P. minor* (and *P. comptonii* as described in its protologue). Buchholz (1949) noted that both species sometimes grew at the same locality (e.g. 22 km Station) while maintaining their character differences.

The description of these two new species by Buchholz (1949) brought a deal of confusion into the taxonomy of New Caledonian *Retrophyllum* that is still not satisfactorily resolved. There are two separate problems: the distinction between *Retrophyllum minus* and *R. comptonii*, and whether or not *Podocarpus palustris* is a distinct taxon.

Over most of the island, there is no problem over species separation of *Retrophyllum comptonii* and *R. minus*, because *R. comptonii* is the only one present, but in the south both species can occur sympatrically, along with the taxon *Podocarpus palustris* if that is regarded as distinct from *R. minus*. Of the various differential characters cited by Buchholz (1949) to distinguish *Retrophyllum comptonii* and *R. minus*, the width of the midrib (or ‘central band’ of de Laubenfels, 1969) is the one that has more often been used (e.g. de Laubenfels, 1969, 1972). Herbert *et al.* (2002: 176), however, commented that this character was “exceedingly difficult to interpret” and that it was therefore “a poor arbiter where there is uncertainty over identifications” but provided no alternative morphological means of separating the two species. They did, however, find that the use of RAPD provided reliable molecular markers that could be employed to separate them. Gray (1962) had separated them on the basis of habit (large trees in *Retrophyllum comptonii*, small trees or shrubs in *R. minus*), foliage mostly flattened (*R. comptonii*) versus rarely flattened (*R. minus*) and twigs pinnately leaved (*R. comptonii*) versus foliage mostly decussate (*R. minus*). Farjon (2010) attempted to get round the problem by keying out *Retrophyllum minus* first on the basis of specimens of it being ‘shrubs or small, dwarfed trees’ as compared with the other four species, all of which he considered to be ‘potentially tall trees’, by the foliage branches of *R. minus* being ‘ascending or spreading’ versus ‘spreading or more or less pendulous’ in *R. comptonii* and the other species, and by the leaf apex ‘always obtuse’ versus ‘acute, apiculate or some obtuse’. The habit/stature characters used by both these authors are difficult or impossible to

interpret correctly from herbarium specimens unless these are accompanied by detailed notes on habit, which is rarely the case; additionally, although *Retrophyllum minus* is normally short in stature (0.9–3.5 m), it can occasionally reach a height of 8 m, thereby causing confusion with *R. comptonii* (2.5–30 m).

No one since Gray (1962) has tackled the issue of *Podocarpus palustris*, which later workers such as de Laubenfels (1969, 1972), Gaussen (1976) and Farjon (2010) have all regarded simply as a synonym of *Retrophyllum minus*. Before Buchholz's work, Bernier (in sched., P) had differentiated two informal taxa within *Podocarpus minor* in southern New Caledonia: 'type sylvestre' and 'type lacustre', corresponding to *P. minor* sensu stricto (? and also southern, lowland plants of what Buchholz recognised as *P. comptonii*) and what Buchholz subsequently described as *P. palustris*. Most of Bernier's collections are labelled 'type lacustre' (Bernier 245, 246, 247, 248, 249, 250, 251; s.n. 7 iii 1948); of those seen, only Bernier 269 and 270 from Forêt Walker and Bernier 271 from Montagne des Sources are labelled 'type sylvestre'. All of these have been determined for this revision as *Retrophyllum comptonii*. Bernier 271 was collected at an altitude of 900–1000 m at Montagne des Sources and is obviously that species. Bernier 269 and 270, however, were collected at only 200 m at Forêt Walker. Buchholz & Gray determined three sheets of *Podocarpus comptonii* at P as being possibly a new form or variety of *Podocarpus comptonii*; these were Bernier 203 (Forêt du Mois de mai), Buchholz 1350 (Walker's place) and Buchholz 1697 (Walker's place).

It is clear from *determinavit* slips (e.g. on Viro 658 at A, in 1953) that Gray originally intended to retain *Podocarpus palustris* as distinct from *P. minor*. However, that was not the case in her published revision (Gray, 1962). In that work, Gray justified her synonymisation of *Podocarpus palustris* with *P. minor* by saying that "Dr Buchholz (*ms. data*) believed there to be a related species *Podocarpus palustris* which he described, but the differences he listed do not fall outside the normal range of variation in *P. minor*, and the difference in wood density is no more than expected from the slightly different ecological habitats". Other apparent differences between *Podocarpus minor* and *P. palustris* can be found when herbarium material is examined. However, insufficient is known about the variation or constancy of these differences, and in this revision *Podocarpus palustris* is therefore regarded as a synonym of *Retrophyllum minus*.

#### Group C species

Until 1983, only one species of *Retrophyllum* was considered to grow in South America. This was *Retrophyllum rospigliosii*, first described as *Podocarpus rospigliosii* by Pilger (1923) based on a collection from Peru bearing very young male cones. Female cones were apparently unknown until they were described, from Venezuelan material, by Schnee (1944). The species is now known to be widespread along the northern Andes chain, occurring in Bolivia, Peru, Colombia, Ecuador and Venezuela, where it reaches its northernmost limit in the state of Trujillo, whence it has been recently collected (Dorr *et al.*, 2000; Hokche *et al.*, 2008). Paradoxically, it is now the case that female cones have been much more often collected than mature male ones, and there is some

variation in female cone shape, which might have led Page (1989, 1990) to suggest that there could be more than two species of *Retrophyllum* in South America. However, *Retrophyllum rospigliosii* is not divided here. Regional treatments of the species have been provided by Schnee (1944), Buchholz & Gray (1957) and de Laubenfels (1982) for Venezuela, Torres-Romero (1988) for Colombia and de Laubenfels (1994) for Peru.

The second South American species of *Retrophyllum* is *R. piresii*, first described as *Decussocarpus piresii* by Silba (1983). This is apparently a narrow endemic to the Serra Pacaás Novos in Rondônia, Brazil, and remains very poorly known from the type (a female specimen with ripe cones, represented in several herbaria) and two other wild-collected specimens as well as one of cultivated material. No male material appears to have been collected so far. As noted in the species account, there have been records of *Retrophyllum piresii* from similar habitats in Bolivia and Peru, but these cannot be confirmed at present. There is little published taxonomic information about the species apart from the protologue, a short treatment by Secco *et al.* (2009) and a more detailed one by Farjon (2010), who said that it should be provisionally kept distinct from *Retrophyllum rospigliosii*, a decision accepted here for reasons given later.

Graham (2008) documented the discovery of an unidentified *Retrophyllum* species from humid lowland swamp forest at Madre Selva Biological Station near Iquitos, Peru. Two male trees (nicknamed ‘Lonely George’ and ‘Lonely John’: Graham, 2012) were found but at that time no females, and so the field botanists could not determine whether it was a new species, although it appeared to be different from *Retrophyllum rospigliosii*. The photograph published in Graham (2008) shows a tree with leaves similar to those of *Retrophyllum piresii* in their elliptic outline. The pollen cones are borne very profusely in the leaf axils; they are brown and about twice the length of the leaves. One female tree has since been found, as well as at least 20 seedlings and other mature trees, all over 100 ft [c.30 m] tall (Graham, 2012). However, no herbarium material of this enigmatic taxon has been seen, and it is not known whether any exists. Cones from the single known female tree need to be collected to determine whether this taxon is conspecific with Brazilian *Retrophyllum piresii* or represents a third South American species of the genus.

In the Paris herbarium, there is also an undetermined specimen (10 xii 1875, *Mosén* 4393) from Sao Paulo, Brazil, labelled simply ‘*Podocarpus*’. Superficially it looks rather like a juvenile *Retrophyllum*, but closer examination reveals that it has net-veined, angiospermous leaves that have apiculate tips. Lindman (1898: 25) identified the Stockholm duplicate of this number as sterile material of *Holocalyx balansae* Micheli (Fabaceae); for a recent revision of that genus see Mansano & Vianno Filho (2010), although it does not cite the Mosén material.

## MATERIALS AND METHODS

This revision is based on examination of selected specimens from the herbaria (using standard codes according to Thiers, continuously updated) A, B (types), BM, E, GH, K and NY, as well as specimen images in the following online repositories and databases:

COL (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 2004 and continuously updated, accessed 8 February 2013; Herbario Nacional Colombiano, no date, accessed 5 February 2015 etc.), JSTOR Global Plants (no date, accessed 3 September 2014 etc.: some types), L, MG (one isotype), MO (types), P, PNGplants (Conn et al., 2004 onwards, accessed 18 December 2014), R (one isotype), RB (JBRJ, no date, accessed 15 April 2014: one isotype), S (Krypto-S, no date, accessed July 2014 etc.: some types) and UDBC. Additional material at COL and UDBC was photographed for this research. The databases of COL, K (Kew, no date, accessed 3 September 2014 etc.), MEDEL, MO (TROPICOS), NOU (Herbier du centre IRD de Nouméa, no date, accessed 21 and 22 July 2014), S (Krypto-S, no date), WU (Vienna Herbaria) and Z (Zürich Herbaria, no date, accessed July 2014) were also consulted (that of MEDEL can no longer be found on the Internet so is not cited). Database records (indicated in specimen citations by the suffix ‘-database’) have been included only where there is no doubt as to correctness of identification, particularly if no duplicates of the specimen concerned have been examined either physically or as images. In specimen citations, the suffix ‘-photo’ denotes a photograph of a specimen, either mounted on a herbarium sheet (as in the case of much of Buchholz’s material) or taken by a colleague, while the suffix ‘-image’ indicates a digital image in an online repository.

Herbarium specimens were examined using a stereo dissecting microscope and Leitz  $\times 6$  or  $\times 8$  loupes and photographed using a Panasonic Lumix TZ30 digital camera. Measurements were all made on dried material; when fresh, some organs can be larger, especially female cones, but in *Retrophyllum* there is not the same degree of lengthening of pollen cones with age as there is in genera such as *Podocarpus*. Some measurements were made on calibrated images using ImageJ version 1.49d (Rasband, 2014); calibration of Paris database images lacking scales was performed using the barcode label, measuring  $50 \times 20$  mm, as a datum basis. Line drawings are provided for taxa that have not been previously illustrated or for which the known published illustrations are in some way unsatisfactory. Microsporophylls and microsporangia were, when possible, rehydrated for drawing by the artist. Where a species has been previously satisfactorily illustrated, an iconography is given listing known published illustrations of good quality and correctly identified.

References to Articles of the *International Code of Nomenclature* refer, unless stated otherwise, to the current Melbourne version (McNeill et al., 2012).

For each species, as part of the distribution summary, the Level 3 and 4 country names and codes of the Taxonomic Databases Working Group (TDWG) are listed according to Brummitt (2001). The names of World Wide Fund for Nature Bioregions and Ecoregions follow the schemes published for Latin America and the Caribbean by Dinerstein et al. (1995) and for the Indo-Pacific by Wikramanayake et al. (2002). Assignments to ecoregions were done using the Worldwide Fund for Nature’s ecoregion map available at Wildfinder (no date).

In specimen citations, country names are in SMALL CAPITALS, first-order subdivisions of countries (divisions in Fiji; provinces in Solomon Islands, Indonesia, Papua New

Guinea, New Caledonia and Ecuador; states in Brazil and Venezuela; departments in Bolivia and Colombia; and regions [formerly provinces, until 2002] in Peru) in **Bold** and second-order subdivisions of countries (provinces in Fiji, Papua New Guinea, Bolivia and Peru; regencies in Indonesia; districts in Papua New Guinea; communes in New Caledonia; municipalities in Brazil, Colombia and Venezuela; and cantons in Ecuador) in **Bold Italic**. Solomon Islands has no second-order administrative divisions. Some countries also have third-order divisions (e.g. districts in Peru and municipalities in Bolivia); where known, these are indicated in *italic*. Assignment to communes in New Caledonia follows the database of NOU (Herbier du Centre IRD de Nouméa, no date). Some peaks in New Caledonia are at the boundary between two or more communes (e.g. Mt. Dzumac: Dumbéa and Païta), so some records are assigned to one commune and some to another. For Fiji, it has seemed helpful also to indicate the main islands in **BOLD SMALL CAPITALS**, because the first-order administrative divisions sometimes divide islands or are divided between islands.

The paper includes a list of accepted names and synonyms (Appendix II) and a list of exsiccatae (Appendix III). Collectors' initials are given in Appendix III but not in the specimen citations unless omitting them would create ambiguity (e.g. *A. C. Smith*, *D. Smith* and *D. N. Smith*). The New Caledonian collector *H. S. MacKee* spelled his surname in earlier collections as *McKee*; all specimen listings have been standardised as the more frequent *MacKee*, following Morat (2010), although his wife Margaret styled herself *McKee* (cf. *McKee*, 1972, cited elsewhere in this paper). In Appendix II, specimens collected by one person but numbered in another person's series are listed twice for cross-referencing, under both the name of the actual collector and that of the person whose number sequence was used. This situation is most common with *MacKee*, in whose collection number series are specimens collected by numerous other individuals, but is also found in other numbering series, such as that of *Vieillard*, which includes material collected by *Pancher* and probably also *Deplanche*.

Maps are provided for all species. These were generated in ArcGis version 9.3 (ESRI, 2008) after geospatial coordinates had been added for specimens lacking such information. The main sources of geographical coordinates were GeoNames (no date) and Fuzzy Gazetteer (no date), as well as, for New Caledonia, the gazetteer coordinates in many specimen records in the database VIROT (Herbier du Centre IRD de Nouméa, no date; cited in square brackets after the locality). Phytogeography is indicated according to the scheme of *Takhtajan* (1986).

Version 3.1 (second edition) of the categories and criteria of the International Union for the Conservation of Nature (IUCN, 2012) and version 10.1 of the guidelines for applying these (IUCN Standards and Petitions Subcommittee, 2013) were used to make the provisional conservation assessments for certain taxa treated in this paper.

As part of the process for the lectotypification of the name *Nageia minor* *Carrière*, basionym of *Retrophyllum minus* (Appendix I), colour profiling was performed on the digital images of certain collections of *R. minus* at P using the image-processing and -analysis program *ImageJ* (Rasband, 2014). These included all those numbered *Vieillard* 1275 (the 'type material'), as well as collections by *Pancher* and *Deplanche*

(Appendix table 1). The original images were assumed to have been made using identical exposures, and no alterations were made to the original files. The colour profiles of portions of leaf measuring approximately  $20 \times 20$  pixels (px, equivalent to  $c.1.7 \times 1.7$  mm on all the Paris specimens analysed, after calibration at 11.7 px/mm), as well as of a transverse line across the middle of that leaf, were generated using the ImageJ tool *Analyze – Tools – Colour Profiler*, which determines the proportions of red (R), green (G) and blue (B) in the image and provides a plot of intensity for each of the channels as well as tabulating the results (Ross, 2007). Profiles were generated for several leaves on each specimen on each sheet; usually one profile was generated per leaf, but on very small fragments with few leaves, or single leaves, separate profiles were generated for areas  $c.20 \times 20$  px at the base and apex of the leaf. Areas of obvious discoloration or damage of the leaf surface were avoided whenever possible. The profile values given in Appendix table 1 relate to  $20 \times 20$  px areas; those from the transverse lines showed slightly more variation, related to the often greater changes in topography of the dried leaf across the line. The profile values and corresponding plots allowed the accurate assignment of specimen fragments to the different elements that make up the mixed gatherings numbered *Vieillard* 1275, as well as ones by Deplanche and Pancher.

#### TAXONOMY

**Retrophyllum** C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45(2): 379 (22 Feb. 1989 [‘1988’]). – *Podocarpus* L’Hér. ex Pers. sect. *Polypodiopsis* C.E.Bertr., Ann. Sci. Nat., Bot. Sér. 5, 20: 65 (1874; see comments). – *Nageia* Gaertn. sect. *Polypodiopsis* (C.E.Bertr.) de Laub., Blumea 32: 210 (3 Feb. 1987). – [*Decussocarpus* de Laub., J. Arnold Arbor. 50: 340 (1969) sect. *Decussocarpus* (op. cit. p. 341), now a nom. illegit. (Art. 52) although legitimate when published.] – Type: *Retrophyllum vitiense* (Seem.) C.N. Page, based on *Podocarpus vitiensis* Seem.; the latter name is also the type of *Decussocarpus* de Laub. and of *Podocarpus* sect. *Polypodiopsis* C.E.Bertr. (non *Polypodiopsis* Carrière).

?[*Polypodiopsis* Carrière, Traité Gén. Conif. ed. 2: 710 (1867), nom. utique rej. (see comments)]. – Type: *Polypodiopsis muelleri* Carrière, loc. cit. (type specimen not indicated).

*Nomenclatural note.* *Polypodiopsis* Carrière, typified by *P. muelleri* Carrière from New Caledonia, may be synonymous with *Retrophyllum*, or it could be a member of the Proteaceae, such as *Beauprea balansae* Brongn. & Gris, as was suggested by Hutchinson (1920). *Polypodiopsis* Carrière, an earlier homonym of the fern genus *Polypodiopsis* E.B.Copel., is now a *nomen rejiciendum* and cannot be used at genus rank (Mill & Weston, 2004; Brummitt, 2006 [‘2005’]; Barrie, 2006). However, when Bertrand (1874) apparently reduced Carrière’s name to *Podocarpus* sect. *Polypodiopsis*, he designated a different name, *Podocarpus vitiensis* (now *Retrophyllum vitiense*), as type of the section, the name of which should therefore be attributed to Bertrand, not Carrière.

*Etymology.* *Retrophyllum* is derived from Latin, *retro* ('backwards'), and Greek, *phyllon*, Latinised as *phyllum* ('leaf'), on account of the orientation of the leaves, which are twisted so that along one side of the stem axis all the abaxial surfaces face uppermost, while along the other side of the axis all the adaxial surfaces are turned uppermost. The gender is neuter.

Trees or shrubs; dioecious. *Trunk* buttressed or not. *Bark* exfoliating in short vertical strips or small pieces (Pacific species: Groups A and B), or as large plates (South America: Group C). *Vegetative shoots* dimorphic with either both foliage and scale leaves or only scale leaves (Groups A and B) or monomorphic with foliage leaves only (Group C), heterofacially flattened at least in juvenile phase, in adult phase sometimes not fully so (New Caledonian species: Group B). *Terminal buds* developed on shoots, these either protected in some way (Groups A and B) or naked (Group C); bud scales present (Fiji and Malesia: Group A) or absent (Groups B and C). *Leaves of juvenile phase* always  $\pm$  distichous, heterofacially turned at base so that all leaves along one side of the axis present their abaxial surface to the light and all those along the other side present the adaxial surface; those of adult phase either distichous and flattened in 2 ranks (Groups A and C) or wholly or partly in 4 ranks that show only minimal heterofacial turning (Group B). *Adult leaves* subsessile with bases decurrent and  $\pm$  crossing over to a departure point on the opposite side and so creating a  $\pm$  zigzag pattern along the branch (all groups, but particularly prominent in Group C); blades bifacially flattened, coriaceous, relatively thin (Groups A and C) or thick to very thick (Group B), with or without a visible midrib; resin canals 1 median below the vascular bundle (Groups A and B) or (1)3(5) below the vascular bundle plus 2–6 lateral bundles around the leaf margin (Group C); transfusion tissue present; accessory transfusion tissue absent. *Pollen cones* usually lateral but sometimes terminal in *Retrophyllum vitiense*, 1–8 together, potentially arranged in racemose inflorescences (Groups A and C) or groups (Group B) borne on a common peduncle; individual pollen cones  $\pm$  pedicellate (Groups A and C) or sessile (Group B), cylindrical, ellipsoid or ovoid; microsporophylls imbricate, decussate (Group B: appearing spirally arranged) or spirally arranged (Groups A and C), triangular or ovate (Groups A and B) or lanceolate (Group C). Pollen 2-saccate. *Female cones* borne on current growth, as part of specialised reproductive shoots (Groups A and C) or terminating foliage shoots (Group B); cones sylleptic (Groups A and C) or proleptic (Group B), pedunculate; peduncle broadened distally (Group C) or not (Groups A and B), in the vegetative portion bearing adpressed scales (Group A) or spreading bracts (Groups B and C); carpophore absent; cone axis with either 1 or 2 (Group B) or 6–8 (Groups A and C) sterile bracts below the fertile bract; fertile bract free from the epimatium (Groups A and B) or with its basal half firmly adnate to it (Group C), distally navicular (Group C) or flat (Groups A and B). *Prophylls* absent. *Receptacle* vestigial, formed from the fertile bract and sometimes the last sterile bract (Groups A and C) or from 1 or 2 peduncle bracts plus the last sterile bract and fertile bract (Group B), cylindrical (Groups A and C) or obovoid (Group B). *Ovule* inverted. *Epimatium* present. *Seed* distally crested or not, with a beak at the micropylar end (Groups A and

B) or lacking a beak (Group C). *Germination* epigeal (Group B) or hypogeal (Group C). Seedling phyllotaxis decussate (Group B), spiral (Group C) or currently unknown (Group A).

*Present diversity and distribution.* Six living species in three very distinct morphological lineages occurring respectively in: (A) Fiji, Solomons and eastern Malesia west to the island of Morotai in the Moluccas; (B) New Caledonia; and (C) tropical South America (eastern slopes of the Andes and extending into the Amazon Basin in Brazil).

*Past diversity and distribution.* Two (or more?) fossil species have also been included in the genus as traditionally circumscribed: †Australasia (New Zealand, Western Australia and Tasmania [undescribed material]) and southern South America (Argentina and ?Chile). There is apparently no record of the genus having occurred in Antarctica, which might be expected given the disjunct distribution of the living and known fossil species between the Australasia/Southwest Pacific area and South America.

*Chromosome number and genomics.* Diploid chromosome number:  $2n = 20$  (3 species cytologically known, from Groups A and B only). The karyotype of all known species comprises 10 pairs of metacentric chromosomes. The genome size is known only for *Retrophyllum rospigliosii* (of which the chromosome number is not yet known); at 12 pg, it is small for conifers but average within the Podocarpaceae, most species of which have small genome sizes of 8–18 pg, with only *Falcatifolium* (22 pg in *F. taxoides*) and *Manoao colensoi* (28 pg) being larger within the family (Zonneveld, 2012). Vieira *et al.* (2016) have very recently published the complete plastome sequence of *Retrophyllum piresii*, based on material cultivated at the Museu Paraense Emílio Goeldi in Belém; I have seen herbarium material of this plant as well as photographs kindly sent by Chad Husby, and have verified the identification.

#### *Key to species*

- 1a. Vegetative shoots monomorphic, scale leaves absent; buds naked; female reproductive shoots subtended by a bract or by a modified (reduced) foliage leaf; female cones with the base of the fertile scale firmly adnate to the epimatium and with a navicular tip; bark exfoliating in large plates (Group C: South America) \_\_\_\_\_ 2
- 1b. Vegetative shoots dimorphic, scale leaves present; buds protected, either by true bud scales or by modified leaves; female reproductive shoots subtended by a normal foliage leaf; female cones with the fertile scale free from the epimatium and not navicular; bark exfoliating in short vertical strips or small pieces (Malesia, Papuasias and New Caledonia) \_\_\_\_\_ 3
- 2a. Peduncle of female cone bearing reduced leaves; foliage leaves lanceolate, acute to acuminate and frequently abruptly narrowed just below apex; adult shoots ± alternate (widespread from Venezuela to Peru) \_\_\_\_\_ **5. *R. rospigliosii***

- 2b. Peduncle of female cone bearing small bracts; foliage leaves elliptic, obtuse, never abruptly narrowed below the tip; adult shoots opposite (one definite locality in Brazil) \_\_\_\_\_ **6. *R. piresii***
- 3a. Female cones borne on specialised reproductive shoots that are either lateral or terminal; ultimate adult foliage shoots pendulous with leaves in 2 ranks; adult leaves with an evident midvein; buds protected by true bud scales (Group A: Malesia, Fiji, Solomons) \_\_\_\_\_ 4
- 3b. Female cones terminal at ends of ordinary foliage shoots; ultimate adult foliage shoots erect or suberect with at least some leaves in 4 ranks; adult leaves with no visible midvein; buds protected by very reduced leaves, lacking true bud scales (Group B: New Caledonia) \_\_\_\_\_ 5
- 4a. Leaves broadest near base; microsporophylls 44–80 in 11–20 whorls; female cone axis with 6–8 sterile scales that persist at least until the resting phase (Fiji and Solomons) \_\_\_\_\_ **1. *R. vitiense***
- 4b. Leaves broadest near middle; microsporophylls 20–32 in 5–8 whorls; female cone axis with 4 sterile scales that are very quickly caducous, only present during the youngest stages (New Guinea, Moluccas) \_\_\_\_\_ **2. *R. filicifolium***
- 5a. Adult leaves with the raised central area narrower than the marginal area; some adult leaves on ultimate shoots in 2 ranks, those towards shoot tips normally in 4 ranks; habit variable from shrub to tall tree; not aquatic \_\_\_\_\_ **3. *R. comptonii***
- 5b. Adult leaves with the raised central area broader than or at least equalling the marginal area; all adult leaves on ultimate shoots in 4 ranks; aquatic shrub or ‘treelet’ with trunk rapidly tapering from a wide base \_\_\_\_\_ **4. *R. minus***

### *Species descriptions*

**Group A.** Bark exfoliating in short strips or small pieces. Vegetative adult shoots dimorphic. Terminal buds protected by bud scales. Leaves heterofacially flattened in both juvenile and adult phases. Adult leaves distichous in 2 ranks, relatively thin. Resin canal 1, positioned below vascular bundle. Pollen cones in racemose inflorescences subtended by scale-like bracts (or sometimes terminal and apparently solitary, as in the type of *Retrophyllum vitiense*), the raceme branches if present alternate or spiral, individual cones pedicellate, subtended by smaller scale-like bracts. Female cones on specialised lateral reproductive shoots, sylleptic; peduncle not broadened distally, in its vegetative portion bearing subadpressed scales. Cone axis with 4–8 sterile bracts. Fertile bract free from epimatium, flat. Receptacle vestigial, formed from the fertile bract and distal part of peduncle which may be slightly swollen, cylindrical or obovoid. Seed beaked at micropylar end. Details of germination and seedlings not known.

- 1. *Retrophyllum vitiense*** (Seem.) C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45(2): 380 publ. (22 Feb. 1989 [‘1988’]). – *Podocarpus vitiensis* Seem., Bonplandia 10: 366

(25 Dec. 1862) & J. Bot. 1: 33, t. 2 (1863). – *Nageia vitiensis* (Seem.) Kuntze, Revis. Gen. Pl. 2: 800 (1891). – *Decussocarpus vitiensis* (Seem.) de Laub., J. Arnold Arbor. 50: 342 (1969). – Lectotype (Farjon, 2010: 942 & 943): Fiji, *Seemann* 576, sheet 2/2 (lecto K, isolectos BM [2 sheets], E, GH–image, S–images). **Fig. 1D**.

?[*Torreya bogotensis* Linden ex K.Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 14(25): 199 (1871), nom. utique rejic.: Mill, 2010; Brummitt, 2011].

*Note on typification.* Gray (1962: 73) indicated that the Kew example of *Seemann* 576 was the ‘holotype’ of *Podocarpus vitiensis* (basionym of *Retrophyllum vitiense*), with an isotype (not so indicated) at GH. This was incorrect because, as was noted by Smith (1979), *Seemann* (1862: 366; 1863: 33) cited two syntypes in both the original protologue and in another publication the following year; the first of these was collected by W.G. Milne on the voyage of HMS *Herald*, and the second was *Seemann* 576. (Smith, 1979: 101 in fact cites two Milne collections of this species, both unlocalised, one without number and the other *Milne* 33). However, de Laubenfels (1969: 344) repeated the designation of *Seemann* 576 at K as ‘holotype’ of *Podocarpus vitiensis*, with specimens at A and BM indicated as ‘isotypes’. These specimens should be regarded as lectotype (K) and isolectotypes (A, BM, GH) respectively, following Smith (1979: 100) and the more precise lectotypification by Farjon (2010). The choice of a Kew specimen as lectotype by both the above authors is difficult to understand, because it is one of the two BM sheets, not either of the K sheets, that bears *Seemann*’s drawings that were used in his two publications (1863, 1868). However, there is no controversy over the identity of any of these sheets, and Farjon’s recent designation, which supersedes the earlier ones by de Laubenfels (1969: 342) and Smith (1979: 100), must therefore stand. Both latter authors independently chose *Seemann* 576 at K but without realising that there are two sheets of that number at K, one of them (annotated ‘1/2’, i.e. sheet 1 of 2) being a seedling and the other (‘2/2’) a branch from a young tree, and they could not have come from the same plant. Sheet ‘1/2’ at Kew is therefore not an isolectotype.

*Iconography.* *Seemann*, J. Bot. 1: t. 2 (1863).

*Etymology.* Derived from Viti, alternative name for Fiji.

*Vernacular names.* *ailumu* (Solomon Is., Kwara’ae language: *Mauriasi et al.* BSIP 17025 in sched., K, L); *dakua salusalu* (Fiji: Parham, 1964, 1972; *Damanu* R10 in sched., K), *ndakua salusalu* or *salu-salu* (Fiji: Mead, 1928; Smith, 1979); *ngapiru* [Vanikoro (Solomon Is.: Nambalua – *Piaito* BSIP 7061 in sched., L); *?kau solo* (Fiji: *Seemann*, 1862, 1863, 1868); *tau solo* (Fiji: *Seemann*, 1868, possibly a misprint for *kau solo*). *Seemann*’s use (1862 etc.) of the name *kau solo* in fact refers to *Dacrycarpus imbricatus* var. *patulus*, according to Smith (1979), who also said that the most frequently used name for *Retrophyllum vitiense* is *ndakuua salusalu*.

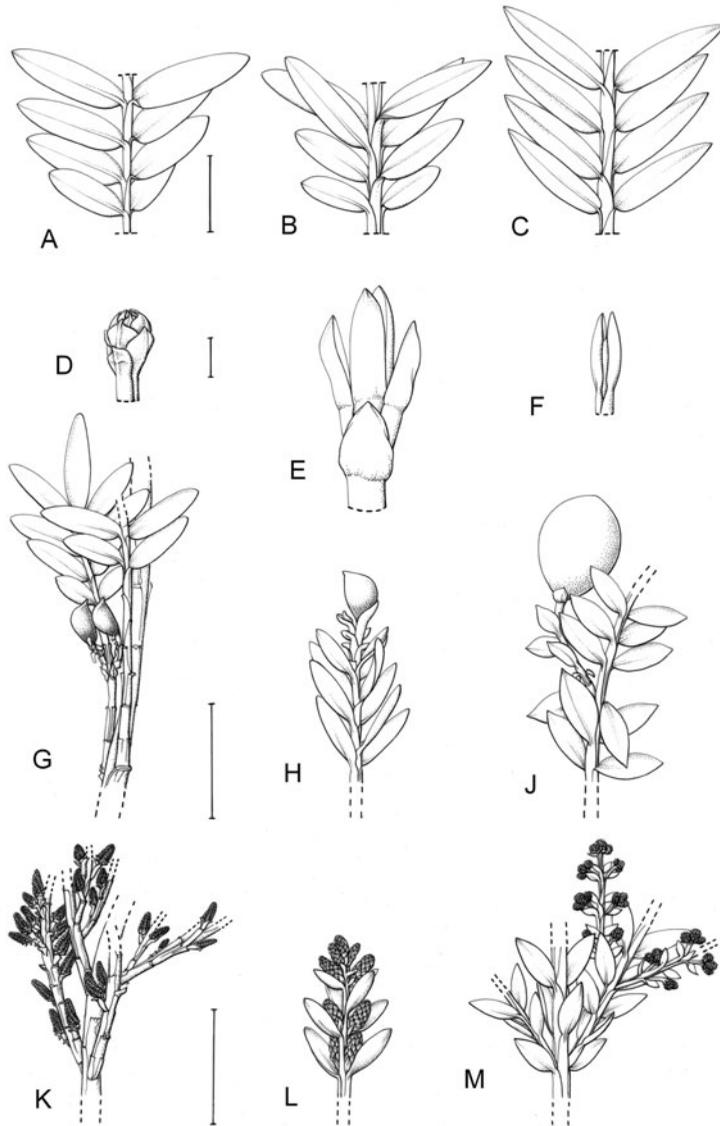


FIG. 1. *Retrophyllum* species, comparative drawings. A–C, Leaf arrangements  $\times 2$ . A, *Retrophyllum filicifolium* (Group A) (Woods 345). B, *R. comptonii* (Group B) (Gardner *et al.* TNCA 5045). C, *R. rospigliosii* (Group C) (Wright 247). D–F, Terminal bud or equivalent,  $\times 15$ . D, *Retrophyllum vitiense* (Group A) (Smith 7076). E, *R. comptonii* (Group B) (Gardner *et al.* TNCA 2036). F, *R. rospigliosii* (Group C) (García-Barriga 27584). G–J, Female cones,  $\times 1.5$ . G, *Retrophyllum filicifolium* (Group A) (Woods 345). H, *R. comptonii* (Group B) (Gardner *et al.* 256). J, *R. rospigliosii* (Group C) (Bunting 4939). K–M, Male cones  $\times 1.5$ . K, *Retrophyllum filicifolium* (Group A) (Carr 14160). L, *R. minus* (Group B) (McMillan 5139). M, *R. rospigliosii* (Group C) (R.T. Pennington 1433). Scale bars: A–C, 1 cm; D–F, 1 mm; G, H, J–M, 2 cm. Drawn by Claire Banks.

*Distinguishing features.* *Retrophyllum vitiense* is most closely allied to *R. filicifolium* (N.E.Gray) R.R.Mill (see below) from New Guinea and the Moluccas. Both have  $\pm$  flat, distichous adult leaves, female cones borne laterally near the base of an ultimate foliage shoot, and dimorphic shoots bearing either foliage leaves or small decussate scale leaves. The dimorphic shoots separate both these species from the two South American species of *Retrophyllum*, which have monomorphic shoots. The flat, distichous, non-imbricate adult leaves and lateral female cones separate the two Papuan species from the New Caledonian species *Retrophyllum comptonii* and *R. minus*, both of which have terminal female cones and adult leaves more or less in 4 ranks and  $\pm$  imbricate (although juvenile and transitional shoots are distichous). Vegetative material of *Retrophyllum vitiense* is best separated from its nearest ally *R. filicifolium* by its tapered leaves widest close to the base, not near the middle. For differences in reproductive characters between these two species, see under *Retrophyllum filicifolium*.

Tree, 15–47 m, dbh 25–450 cm. *Trunk* sometimes spur-buttressed at base on large trees, bole straight and when adult unbranched except near top. *Bark* smooth, finally with faint vertical fissures, flaking into small longitudinal crumbly pieces, fissured, greyish-brown or (Solomons) dark brown, whiter in mature trees; inner bark yellowish-brown or (Solomons) reddish-brown; wood cream-coloured. *Crown* compact but much branched, pyramidal and finally rounded, with pendulous branchlets and twigs. *Buds* ovoid or obovoid; bud scales present, in 2 series, decussate, all equal, ovate and keeled, acute, brownish with narrow paler entire margin, initially persistent but later slowly caducous, not leaving scars. Ultimate *juvenile shoots* alternate, subopposite or opposite, 130–280 mm, with 23–72 (usually 35–60) pairs of foliage leaves, occasionally biramulate. *Juvenile foliage leaves* 4–11 mm apart, opposite-distichous, heterofacially turned at base, diverging at 60–80°, shortly petiolate, the petiole 0.2–0.5(–1.5) mm, lamina lanceolate or narrowly lanceolate, those near middle of branchlet 18–35  $\times$  (3.8–)4–6(–7) mm. *Adult trees* with dimorphic shoots, most shoots bearing foliage leaves but leader shoots bearing scale leaves; shoot flattening heterofacial with the decurrent leaf bases running straight down the internodes. *Primary adult branches* opposite-decussate or alternate. *Penultimate adult branches* erecto-patent with respect to subtending branch (although topographically deflexed-patent), straight or slightly curved with flexuous internodes, alternately bearing axillary decussate lateral foliage shoots and decussate ovate to orbicular bracts c.2 mm. *Ultimate adult foliage shoots* (70–)100–230 mm with (7–)11–60 pairs of leaves, straight or curved with slightly flexuous internodes. *Leaf scars* absent. *Adult foliage leaves* 4–8 mm apart, opposite-distichous, not imbricate, heterofacially twisted, shortly petiolate; petiole decurrent straight along length of internode, free part 0.2–1.7 mm; lamina of most leaves spreading but not forming a shallow ‘V’ along branch, widely erecto-patent, diverging at 45–70(–80)°, deep green, narrowly lanceolate to lanceolate (widest just above the base), those near middle of branchlets (12–)16–27(–32)  $\times$  3.2–6(–7) mm but lowest ones shorter and more ovate, all straight, coriaceous but relatively thin and flexible; margin not thickened, narrowly hyaline; surfaces equally amphistomatic, lacking a

raised central area but with longitudinal vein-like striae between the rows of stomata; midrib evident, raised beneath, obscure throughout or at least distally above; apex subacute or obtuse, never mucronate; base rounded, obtuse or cuneate.

*Pollen cones* terminal or lateral, subtended by a bract, foliage leaf or (when terminal) pair of foliage leaves, solitary or 1–3 together, occasionally in a compound ‘inflorescence’ of 2 pairs of cones and a terminal cone, the individual cones when more than one present each subtended by a bract and shortly pedicellate; cones linear-cylindrical to narrowly cylindrical when terminal, cylindrical to ovoid when lateral; *microsporophylls* 44–80 per cone, in 11–15(–20) whorls; lamina triangular to ovate or somewhat wedge-shaped with buff-coloured scarious margin; *microsporangia* reniform, equalling the microsporophyll; *pollen* with hyaline body and whitish to hyaline sacci.

*Female cones* lateral, arising from near the base of an ultimate foliage shoot, 1 or 2 per shoot, pedunculate. *Peduncle* unbranched (bearing 1 cone axis) or forked at apex (bearing 2 cone axes), 2–12 mm, equalling or shorter than cone, longer than vestigial receptacle, erect or erecto-patent when young, with 3–5 pairs of bracts below the cone axis; distal part of peduncle not shed with cone. *Peduncle bracts* adpressed or subadpressed, ovate, c.1 × 0.5 mm, scarious-margined. *Cone axis* formed of 6–8 sterile bracts and 1 or 2 fertile bracts. *Sterile bracts* persisting till resting phase and then slowly caducous, narrowly ovate or ovate-elliptic, subacute, larger than peduncle bracts, at first horizontally spreading, later deflexed and finally caducous. *Receptacle* cylindrical. *Fertile bract* initially erect and longer than the epimatium, free from the epimatium and last sterile bract, with a narrowly wedge-shaped, prominently keeled proximal portion and free, ovate-elliptic, acute, non-keeled distal portion. *Cones* obovoid or pyriform, 15–23 × 10–12 mm; epimatium initially blackish-violet, later turning bright magenta and finally becoming bluish-red when ripe, not crested, with a conical, slightly hooked beak at micropylar end; micropylar beak with two short prongs that point ± vertically downwards towards the last sterile bract.

*Taxonomic notes.* Seemann was convinced that he was dealing with a new genus allied to *Podocarpus* (see Seemann, 1863: 33 as well as his annotation on the type, and Wasscher, 1941: 424), although he nevertheless provisionally placed the species in *Podocarpus*. His perceptive taxonomic insight has since proved to be correct, because there is no doubt that *Retrophyllum*, in whatever sense it is defined, is distinct from *Podocarpus*.

*Podocarpus filicifolius* N.E.Gray, based on material from Morotai in the Moluccas, has usually been regarded as a synonym of this species, but examination of ample material both from Fiji and from New Guinea and Morotai has demonstrated that the plants from the latter areas are taxonomically distinct from Fijian material. They are treated below as *Retrophyllum filicifolium*.

Seeds of a fossil species allegedly closely allied to *Retrophyllum vitiense* were found in Pliocene beds in New Zealand by Evans (1937: 192, note; quoted by Florin, 1940: 47). The fossil was not named, and the only other New Zealand fossil that has been definitely assigned to *Retrophyllum* is the Miocene species *R. vulcanense* M.Pole (Pole,

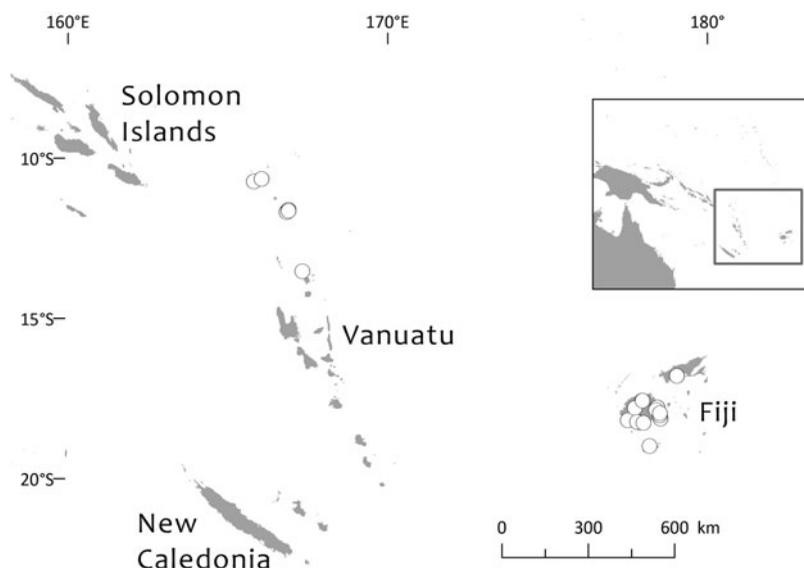


FIG. 2. Global distribution of *Retrophyllum vitiense*.

1992). The possibility that Evans's seeds may have belonged to an extinct allied genus, such as *Smithtonia* or *Willungia*, should not be discounted.

*Nomenclatural notes.* Page (1989) used Seemann (1863) as the basionym reference, being presumably unaware of the earlier *Bonplandia* one (Seemann, 1862).

Linden [1869, *nomen nudum* (see Mill, 2010); in Thurber (1870, *nomen nudum*); Linden ex K. Koch (1871)], described *Torreya bogotensis* from Bogotá, Colombia; this was considered to be synonymous with *Podocarpus vitiensis* (*Retrophyllum vitiense*) by Bertrand (1874), but this is surely incorrect. If it really is a *Retrophyllum* at all (and there is some doubt), it is far more likely to be *R. rospigiosii*, which grows in Colombia. Linden's name was proposed for rejection under Art. 56 of the ICBN (McNeill *et al.*, 2006) by Mill (2010), and this was unanimously recommended by the Nomenclature Committee for Vascular Plants (Brummitt, 2011). Reveal (2012) considered that the 1869 French description by Linden validated the name but Mill (2010) did not, and Brummitt (2011) reported that even the more detailed descriptive matter given by Koch (1871) was "just sufficient to validate the name".

*Phenology.* Fl. Mar–Dec; fr. Jun–Feb (Smith, 1979: 99).

*Distribution.* Southwest Pacific: Solomon Is. (Santa Cruz group), Vanuatu (only Banks Islands, Prov. Torba: absent from the main archipelago), Fiji. The Santa Cruz group (Solomons) and Banks Islands (Vanuatu) are adjacent. TDWG: 60 FIJ SCZ VAN.

*Map:* Fig. 2.

*Specimens seen and other records.* FIJ. Unloc., vii 1860, Seemann 576 (K, 2 sheets annotated '1/2' and '2/2', sheet '2/2' being lecto); isolecto BM–2 sheets, E, S–database; 2nd Seemann collection at

S (S–database) without collector’s number may be another isolectotype, as may a third “fragment ex Berlin” that lacks any information regarding collector or locality). Unloc., no date, *Graeffe* s.n. (BM, K). ‘Albizzi Levu’: otherwise unloc., *Graeffe* (K: Graeffe’s locality has not been traced). Unloc., *anon.* (Department of Agriculture, Fiji) 5536 (L–image). Unloc., 300 m, 10 v 1962, *Damanu* L12 (K–database). **VITI LEVU: Western:** Nausori Highland intermediate montane zone, 1900 ft [579 m], 8 iii 1962, *Damanu* NH15 (K). **Ba:** Nandarivatu, seedlings, 2800 ft [853 m], 21 ii 1927, *Mead* 1964 (K). Nandarivatu, 2800 ft [853 m], 26 ii 1927, *Mead* 1974 (K); *ibid.*, 840 m, 9 iii 1927, *Mead* 1982 (K–database). Nandarivatu, valley of the Sigatoka river, Colo-north (= Tholo North), 800 m, 17 xi 1927, *Gillespie* 3865 (K); *ibid.*, 900 m, 17 xi 1927, *Gillespie* 3865 (NY; note altitude discrepancy cf. K sheet). Nandarivatu, 2700 ft [823 m], v 1947, *d’Espeissis* 1460 (E, 2 sheets). Mt. Lomalagi (Nandarivatu), 3000 ft [914 m], 6 viii 1946, *Vaughan* 3254 (BM). Nandarivatu, 2700 ft [823 m], ix 1907, *Gibbs* 674 (BM). Nandarivatu, Easter [2–5 iv] 1926, *Teulon* s.n., comm. (*J.D. & B.H.*) *Tothill* 844 (K). Tholo North, vicinity of Nandarivatu, 750–900 m, Nauwanga, 4 ii–26 iii 1941, *Degener* 14483 (A, L–image, NY, S–database), 11484 (S–database). Tholo North, vicinity of Nandarivatu, 4 ii–26 iii 1941, *Degener* 14496 (NY). Mba, Tavua, 2.5 miles (by road) W of Nandarivatu, 2800 ft [853 m], 15 vii 1968, *Webster & Hildreth* 14270 with *I. Kuruvoli* (GH). Mba, Mandrongo, Nausori Highlands, W slopes of Mt. Mandrongo [Mangondro], 2000 ft [610 m; but the summit is only c.547 m *vide* GeoNames], 16 vii 1968, *Webster & Hildreth* 14277 with *I. Kuruvoli* (GH). **Central: Serua:** Naboutini, 4 vii 1962, *Damanu* R10 (K); *ibid.*, 240 m, 5 xii 1962, *Damanu* R15 (K–database); *ibid.*, 150 m, 28 iii 1963, *Damanu* R32 (K–database). Galoa, c.500 ft [152 m], 27 vii 1962, *Damanu* G7 (K). Near Korovisilou, Serua, 300 ft [91 m], 2 vii 1973, *de Laubenfels* P 508 (A, L–image); Korovisilou, 900 m, 12 xii 1968, *Redrod* K110 (K–database). Road to Nambukilevu from Namboutini, c.1000 ft [305 m], 1 xi 1964, *de Laubenfels* P 309 (A). **Tailevu:** hills east of Wainimbuka River, in vicinity of Ndakuivuna, 100–200 m, 15–27 iv 1953, *A.C. Smith* 7076 (GH, L–image, NY, S–database, K–database). **Tailevu INaitasiri:** Upper Rewa River valley, 3 vi 1992, *Cox* 1360 (NY, BRY–database). **Naitasiri:** Navolau, 17°52’S 178°24’E, 50 m, vi 1936, *Peni* 636 (K–database). **KADAVU: Eastern: Kadavu:** Kadavu Naikorokoro, 18°59’S 178°12’E, 240 m, 12 ix 1962, *Damanu* KU22 (K–database). Navutulevu, 18°14’S 177°48’E, 90 m, 4 vi 1962, *Damanu* NL10 (K–database). **VANUA LEVU: Northern: Cakaudrove:** Thakaudrove, Yanawai River region, Mount Kasi, 300–430 m, 10–11 v 1934, *A.C. Smith* 1796 (GH, NY, K–database, S–database). **Macuata:** Labasa Sarava, 18°02’S 178°31’E, 300 m, 10 v 1962, *Damanu* L10 (K–database). **VANUATU. Torba: Banks Islands:** Ureparapara, near Lehali village, 13°32’S 167°20’E, 300 m, 6 ix 1982, *Hammer* s.n. (K–database). **SOLOMON ISLANDS: Temotu: Santa Cruz I.:** N.E. Santa Cruz, Carlisle Bay area, 900 ft [274 m], 22 x 1969, *Mauriasi et al.* BSIP 17025 (K, L–image). **Ndeni I.:** Graciosa Bay, 130 m, 11 xi 1969, *Mauriasi et al.* BSIP 17794 (K–database, L–image). **Vanikoro I.:** Lawrence River, 22 iii 1963, *Whitmore* BSIP 1580 (K–database, L–image); Vanikolo, 11°37’S 166°54’E, iii 1965, *Piaito* BSIP 7061 (K–database, L–image); nr Lemon River [11°39’S 166°54’E], 27 xi 1945, *Walker* BSIP 212 (A, K–database). **FIJI (CULTIVATED).** Agr. exp. Garden, Naduruloulou, 215 i 1949, *Lam* 6932 (L–image). **AUSTRALIA (CULTIVATED).** **New South Wales:** Botanic Gardens, Sydney, viii 1908, *Boorman* s.n. (A). **JAVA (CULTIVATED).** Jardin Botanique de Tjiboudas, viii 1959, *Schnell* 10647 (2 sheets, P–images).

**Bioregions:** Oceania; New Guinea & Melanesia (only the Santa Cruz and Vanuatu populations). **Ecoregions:** OC0105 Fiji tropical moist forests, AA0126 Vanuatu rain forests.

**Ecology:** Dense lowland wet zone rain forest, montane rain forest or ridge forest, where it typically grows as scattered trees on slopes and in gullies in areas with rainfall of approximately 5000 mm per annum; 50–915 m. According to Mead (1928),

this rain forest develops on the southeastern or ‘weather’ sides of the mountains. Associates include species of *Agathis* Salisb., *Calophyllum vitiense* Turrill, *Gironniera celtidifolia* Gaudich. (in the understorey), *Parinari insularum* A.Gray, *Semecarpus vitiensis* (A.Gray) Engl. and *Pagiantha thurstonii* (Horne ex Baker) A.C.Sm. (Keppel, 2005; Mead, 1928, gives additional rain forest components). It can form a unique community in which it and *Calophyllum vitiense* are codominant (Keppel *et al.*, 2011).

*Chromosome number*:  $2n = 20$  (Hair & Beuzenberg, 1958, as *Podocarpus vitiensis*).

*Phytochemistry*. The wood of *Retrophyllum vitiense* contains podocarpic acid, totarol, 19-hydroxytotarol and  $4\beta$ -carboxy-19-nortotarol (Cambie *et al.*, 1983), a unique combination of phenolics among the 10 species of Podocarpaceae studied.

*Plant–animal interactions*. The beetle *Xyleborus rameus* Schedl is known to bore into the seeds of *Retrophyllum vitiense* in Fiji (Greenwood, 1977). The drywood termite *Cryptotermes domesticus* (Haviland) is known to attack timber of *Retrophyllum vitiense* in Fiji (Gray, 1974).

*IUCN conservation assessment* (global: IUCN 3.1). The most recent assessments are as LC (Farjon, 2010: 943; Thomas, 2013), but these both referred to the species in a wide sense, including what is here recognised as the separate species *Retrophyllum filicifolium*. Doyle (1999), using an earlier IUCN grading system, evaluated the species as circumscribed here as LRlc on both Fiji and the Solomon Islands, also equivalent to IUCN 3.1: LC. Therefore it is considered that an assessment of LC is appropriate for the species as more narrowly circumscribed here, although it should be noted that Farjon commented that, in the wider geographical area of his circumscription, the species was subject to logging throughout its range.

*Uses*. *Retrophyllum vitiense* is one of the most highly prized timber trees of Fiji, being used for high-quality furniture, etc. and for flooring, exterior work and construction (*Damanu* 15 in sched., K). Mead (1928) commented that in his time it was one of the commonest and most important timber trees of Fiji. He also mentioned its use in boat-building. However, use of the species today should be avoided, because most imports are from non-sustainable forests (Rainforest Information Centre, no date, accessed 16 September 2015). Moreover, the wood is not very decay-resistant and is therefore unsuitable for use in some situations, such as ground contact (Osborne, 1967). The resin is inflammable and is used by Fijians to start fires (*Degener* 14483 in sched., A, NY and Degener & Degener, 1953).

**2. *Retrophyllum filicifolium*** (N.E.Gray) R.R.Mill, **comb. nov.** – *Podocarpus filicifolius* N.E.Gray, J. Arnold Arbor. 43: 74 (15 Jan. 1962) quoad descr. foliorum tantum. – Lectotype designated here: Moluccas, Morotai, “tree, 15 m”, 1949, *A. Kostermans* s.n. (lecto L, foliage shoots only – image, originally determined by van Steenis as *Podocarpus vitiensis* Seem.; isolecto A, K). The lectotype specimen at L is a mixture of juvenile foliage of *Retrophyllum filicifolium* and detached fruits of *Nageia wallichiana*; the latter are here excluded as a result of lectotypification by the foliage

element. The isoelectotypes cited comprise foliage only. Epitype designated here: New Guinea, Northern District, ridge above Doma, 1500 m, 14 xi 1962, *P.J.B. Woods* 345 (epi E, barcode E00094518: comprising adult foliage, several attached young female cones, one attached older female cone and another in packet; isoepe K–database). **Figs 1A, G, K, 3A–J.**

*Podocarpus vitiensis* sensu Wasscher (1941: 425–427), Gray (1962: 72–74), p.p. quoad pl. novoguineensis, non Seemann (1862).

*Decussocarpus vitiensis* sensu de Laubenfels (1969: 342) p.p. excl. typ., quoad syn. *Podocarpus filicifolius* N.E.Gray (p.p.).

*Nageia vitiensis* (Seem.) Kuntze sensu de Laubenfels (1988: 394–395) p.p. excl. typ., quoad syn. *Podocarpus filicifolius* N.E.Gray (p.p.).

*Nageia vitiensis* sensu Takeuchi (2010: 20) non (Seem.) Kuntze (1891).

*Retrophyllum vitiense* sensu Li (2007: 346), Abdillahi *et al.* (2010: 7) p.p. quoad pl. novoguineensis.

*Etymology:* *filicifolium*, Latin from *filix*, ‘a fern’, and *folium*, ‘a leaf’. “The name refers to the fern-like appearance of the pinnately leaved twigs, reminiscent of the royal fern, *Osmunda regalis*” (Gray, 1962: 74).

*Vernacular names:* *lehil* (New Britain: *Frodin* NGF 26292), *moegò* (New Guinea – Wissel Lakes, Kapaukoe language, *Vink & Schram* BW8730 as *Retrophyllum vitiense*).

*Distinguishing features.* *Retrophyllum filicifolium* has for long been confused with and included within *R. vitiense*, as explained in the *Taxonomic Problems* section of this paper. Male material of *Retrophyllum filicifolium* can be distinguished from *R. vitiense* by its pollen cones with fewer microsporophylls (typically 20–32 in 5–8 whorls as opposed to 44–80 in 11–20 whorls). Terminal pollen cones, which occur in some examples of *Retrophyllum vitiense*, including its type specimen, have not so far been observed in *R. filicifolium*. Material with young female cones can be separated from *Retrophyllum vitiense* by the fewer sterile bracts on the female cone axis (about 4, not 6–8) that are ephemeral and quickly caducous, not persisting till the cones reach resting phase, by the fertile bract with the proximal half lacking a keel, and by the obovoid, not cylindrical, receptacle. The ripe cones also appear to be slightly larger on the basis of the few that have been seen, being c.26 × 17 mm rather than 15–23 × 10–12 mm, although this may not hold when additional material is examined. Vegetative differences include the more quickly caducous bud scales that leave pale scars on the branchlet, the typically shorter juvenile and adult ultimate foliage shoots with fewer pairs of leaves (although there is overlap) and especially the broadest point of both adult and juvenile leaves being near the middle of the lamina rather than towards the base as in *Retrophyllum vitiense*. There is no geographical overlap between the two species, so if the provenance is known, identification is automatic.

Tree, 27–60 m, dbh 50–130 cm. *Trunk* sometimes spur-buttressed at base, when adult unbranched except near top. *Bark* smooth, flaking, fissured, dark brown or blackish on mature trees, light or medium brown on juveniles; inner bark reddish-brown, salmon or

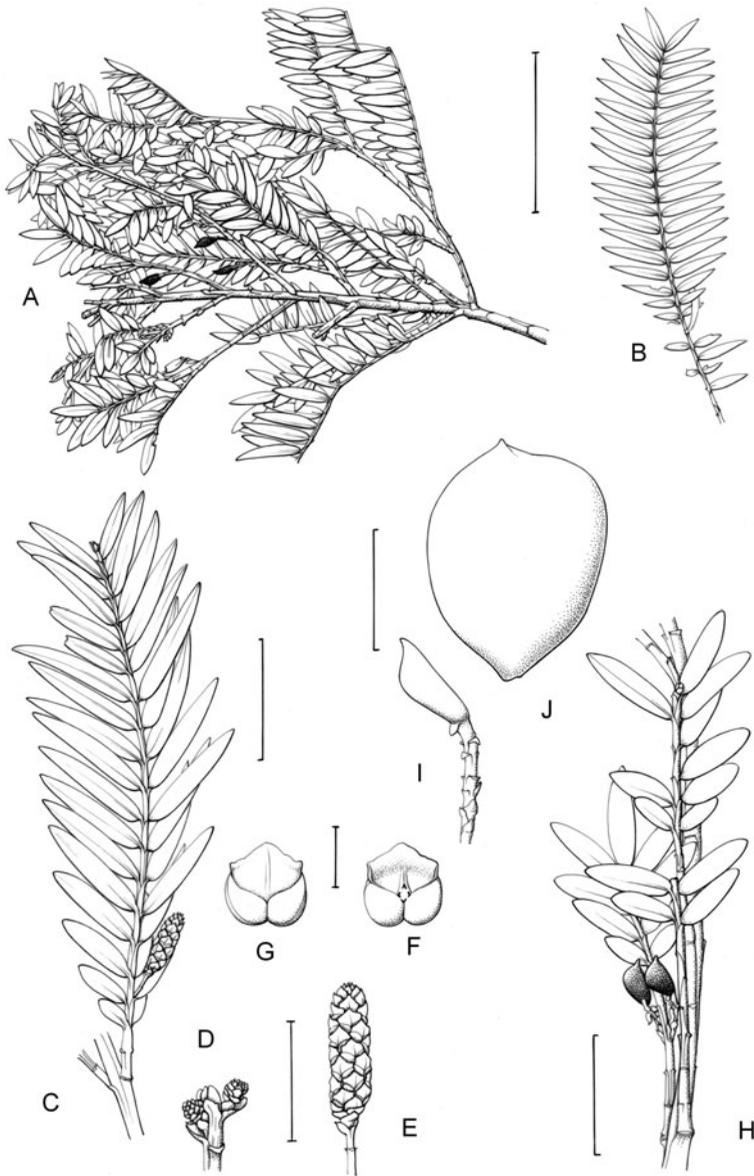


FIG. 3. *Retrophyllum filicifolium*. A, Branching arrangement (*Woods* 345). B, Juvenile foliage shoot (*Woods* 241). C, Adult male shoot (*Carr* 15666). D, Young male cones (*Carr* 15666). E, Mature male cone (*Carr* 15666). F, Microsporophyll and microsporangia, adaxial view (*Carr* 15666). G, Microsporophyll and microsporangia, abaxial view (*Carr* 15666). H, Adult female branch (*Woods* 345). I, Young female cone (*Woods* 345). J, Mature female cone (*Woods* 345). Magnifications: A, B,  $\times 0.67$ ; C, H,  $\times 1.5$ ; D, E, I, J,  $\times 3$ ; F, G  $\times 15$ . Scale bars: A, B, 6 cm; C, H, 2 cm; D, E, I, J, 1 cm; F, G, 1 mm. Drawn by Claire Banks.

pink; wood pale orange, straw-coloured, yellow or white. *Crown* not widely spreading. *Terminal buds* on primary branches globose or ovoid; bud scales present, in 4 series, decussate, the lowest pair longer and slightly wider than the other three pairs, all ovate or ovate-rhombic and slightly keeled, acute, brownish with very narrow paler entire margin, caducous, leaving cream, transversely narrowly rhombic scars much paler than the branchlet; those on foliage shoots usually remaining dormant, ovoid. *Ultimate juvenile shoots* alternate, subopposite or opposite, 65–210 mm, with 7–35 (usually 11–20) pairs of foliage leaves, occasionally biramulate or sending off a lateral scale-bearing shoot. *Juvenile foliage leaves* 4–7 mm apart, opposite-distichous, heterofacially turned at base, diverging at 60–85°, shortly petiolate, the petiole 0.2–1 mm, lamina lanceolate or narrowly lanceolate with the lowest ones elliptic, oblong-elliptic, ovate or narrowly ovate and considerably smaller, those near middle of branchlet 18–40 × 4.2–6 mm, the apex often indistinctly mucronate. *Adult* (and juvenile) *trees* with dimorphic shoots, most shoots bearing foliage shoots but leaders bearing scale leaves; shoot flattening heterofacial with the decurrent bases running straight down the internodes. *Primary adult branches* not observed. *Penultimate adult branches* erecto-patent to widely patent with respect to subtending branch, straight or slightly curved, bearing opposite-decussate axillary lateral foliage shoots interspersed with remote pairs of decussate subadpressed to spreading ovate scales. *Ultimate adult foliage shoots* 20–90 (–120) mm with 4–18(–25) pairs of leaves, straight or curved, internodes slightly flexuous. *Leaf scars* absent. *Adult foliage leaves* 2–7 mm apart, opposite-distichous, pectinate, not imbricate, heterofacially twisted, sessile to shortly petiolate; petiole decurrent straight along whole length of internode, free part 0.2–1.5(–2) mm; lamina spreading and at least sometimes forming a shallow ‘V’ along the branchlet (cf. label of epitype), widely erecto-patent, diverging at (45–)50–80(–90)°, mid to deep green, narrowly elliptic to elliptic or oblong (widest just below the middle), those near middle of branchlets 7–25(–30) × 3–4.5(–5) mm but lowest ones shorter, all straight, coriaceous and moderately thick; margin not thickened, very narrowly hyaline; abaxial surface flat to ± convex, adaxial surface ± flat, both equally amphistomatic, lacking a raised central area but with vein-like striae alternating with the stomatal rows; midrib evident, raised beneath but obscure throughout or at least distally above; apex subacute, obtuse or sometimes broadly rounded, usually not mucronate, the base rounded, obtuse or cuneate.

*Pollen cones* terminal on lateral shoots arising just above bud scales of previous season, subtended by a bract, 1–several together in groups that sometimes form a raceme-like inflorescence, ellipsoid or ovoid; *microsporophylls* 20–32(–40) per cone, in 5–8(–10) whorls; lamina triangular to ovate with buff-coloured scarious margin; *microsporangia* reniform; *pollen* hyaline.

*Female cones* borne laterally from near the base of an ultimate foliage shoot of the previous year’s growth, the reproductive shoot subtended by a bract. *Peduncle* 5–10 mm, equalling or shorter than unripe cone and always shorter than ripe cone, longer than vestigial receptacle, erect or erecto-patent when young, becoming pendulous, with 3–5 pairs of bracts below the cone axis. *Peduncle bracts* adpressed or subadpressed,

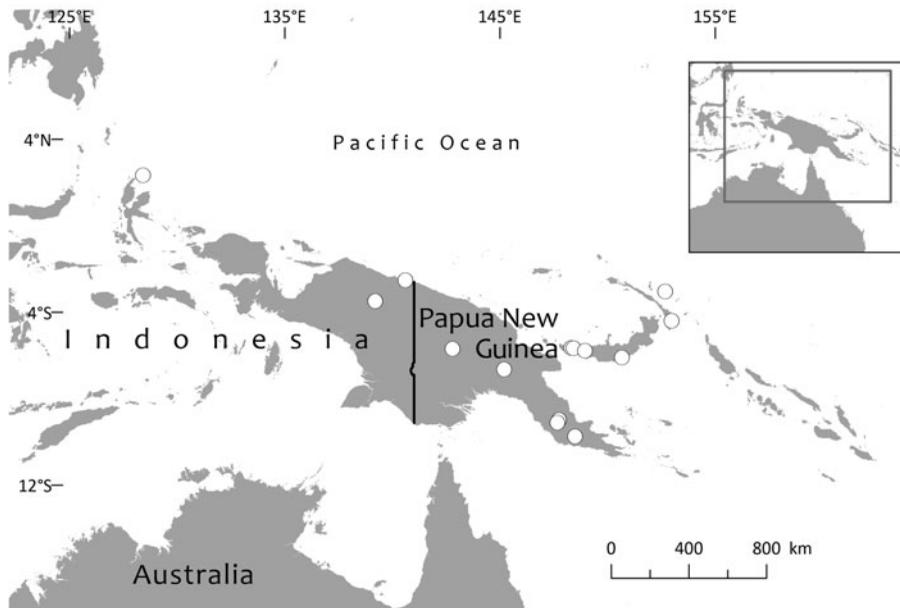


FIG. 4. Global distribution of *Retrophyllum filicifolium*.

ovate to ovate-rhombic, c.  $1.5 \times 0.3\text{--}0.5$  mm, very narrowly scarious-margined. *Cone axis* formed of c.4 sterile bracts and 1 or 2 fertile bracts. *Sterile bracts* ephemeral, present at receptivity but then quickly caducous, elliptic, obtuse to rounded, larger than peduncle bracts, at first spreading but soon becoming deflexed and falling. *Receptacle* obovoid, purplish-brown, glaucous. *Fertile bract* initially erect, its proximal half fused to the epimatium and lacking a keel. *Cones* obovoid or pyriform, c.  $26 \times 17$  mm; epimatium green when young becoming red when ripe, glaucous when unripe, not crested, with conical, slightly hooked beak at micropylar end.

*Distribution.* Malesia: Moluccas (Morotai: type locality of *Podocarpus filicifolius*), New Guinea, Bismarck Archipelago (New Ireland, New Britain). Morotai marks not only the westernmost limit of this species, but also of the genus *Retrophyllum* in Asia. TDWG: 42 MOL 43 BIS NWG-IJ NWG-PN. *Map:* Fig. 4.

*Specimens seen and other records.* INDONESIA. **North Maluku: Morotai Island Regency:** Morotai, without detailed locality, 1949, tree, 15 m, *Kostermans* s.n. (lecto L-image, excl. fruits of *Nageia wallichiana* in packet; isolecto A, K). **Papua: Jayapura:** Dist. Hollandia, Cycloop Mountains, 1220 m, 28 vi 1961, *van Royen & Sleumer* 6073 (A, K, L-image, P-image). Res. Hollandia, Cycloop Mts (Ifar-Ormu), 1100 m, 2 xi 1954, *Versteegh* B.W. 913 (A, CANB-n.v., K, L-2 sheets, images). **Paniai:** Wissel Lake Region, slope and summit of Mt. Barara, 4 ix 1939, *Eyma* 5155 (L-image). Motito, Wissel Lakes, 1800 m, 18 v 1960, *Vink & Schram* BW 8730 (CANB-n.v., L-image, collection date wrongly entered in database as '18 vi'). **Wamena:** 6 km SW of Bernhard Camp, Idenburg River, 1200 m, ii 1939, *Brass* 12787 (A, BM, K-database, L-image); *ibid.*, juvenile foliage of no. 12787, from a plant 4 m high, 1200 m, ii 1939, *Brass* 12787a (A, L-image). 6 km SW of Bernhard Camp, Idenburg [Taritatu] River, 1200 m, 17 ii 1939, *Brass & Versteegh*

12534 (A, L–image). *ibid.*, “further material of no. 12787,” 1200 m, ii 1939, *Brass* 12912 (A, L–image). PAPUA NEW GUINEA. **Northern [Oro] (border with Central)**: ridge above Doma, 1500 m, 14 xi 1962, *Woods* 345 (epitype E, isoeptype K–database); near Doma village, 900–1500 m, 2 xi 1962, *Woods* 241 (E). **Northern [Oro]: Sohe**: Lala River, c.5000 ft [1524 m], 20 ii 1936, *Carr* 15666 (BM–2 sheets, CANB–n.v., L–image, NY, S–database). Alola, c.6000 ft [1829 m], 3 i 1936, *Carr* 14160 (A, BM–2 sheets, L–image, NY). **Eastern Highlands: Lufa**: Herowana, Crater Mt. WMA, N of airstrip, 6°39′3″S 145°11′30″E, 21 xi 2005, *Kuria* LAE 87216 & *Oliver* (LAE–n.v., NSW–n.v.). **Hela: Koroba-Kopiago**: Southern Highlands, c. 6 miles [9.5 km] E of Koroba station, 5°42′S 142°48′E, c.80 ft. [24.5 m] tall, 26 viii 1961, *Pullen* 2840 (LAE 96292–n.v.: de Laubenfels, 1969: 343). **West New Britain: Talasea**: NE slope of Mt. Tangis, SW of Airagilpua, Talasea, 5°40′S 148°25′E, 3500 ft [1067 m], 17 xi 1965, *Frodin* NGF 26292 (A, CANB–n.v., L–image, NY). Mt. Tangis, NW slope, Talasea, 5°39′S 148°18′E, 2400 ft [732 m], 30 v 1966, *Frodin* NGF 26917 (A, CANB–n.v., L–image, NY). **Kandrian**: Umai River, Fullerborn Harbour, 6°06′S 150°40′E, 100 ft. [30.5 m], 5 iii 1965, *Hammermaster & Sayers* NGF 21842 (L–2 sheets, images); 7 miles SE of Benim village, Waria subdist., Kandrian dist., 1000 ft [305 m], 5°47′S 148°57′E, 23 iii 1966, *Henty & Frodin* NGF 27359 (A, CANB–n.v., K, L–image, NY). **New Ireland: Namatanai**: Namatanai subprovince, Hans Meyer Range, 4°24′S 152°58′E, c.8 km (map distance) WNW of Taron on E coast, 1350 m, 29 x 1975, *Sands* 2381 *et al.* (A, CANB–n.v., K–database, L–image). Northern Hans Meyer Range, 70 km SE of Namatanai, 850 m, 3°03′S 152°40′E, 1 xi 1984, *Gideon & Obedi* LAE 77181 (BISH–n.v., CANB–n.v., E, K–database, L–image).

*Bioregions*: Wallacea; New Guinea & Melanesia. *Ecoregions*: AA106 Halmahera Rain Forests, AA0112 New Britain–New Ireland Montane Rain Forests, AA0116 Northern New Guinea Montane Rain Forests.

*Ecology*. According to field notes on specimen labels, *Retrophyllum filicifolium* is a typical species of tall primary montane rain forest or ridge forest, associated with *Dacrycarpus* (Endl.) de Laub., emergent palms such as *Gulubia* Becc. and other trees including *Agathis*, *Podocarpus* L’Hér. ex Pers., *Serianthes* Benth., *Syzygium* R.Br. ex Gaertn., *Casuarina rumphiana* Miq., and sometimes in shade among bamboos. It occurs at altitudes of 300–1800 m, mostly between 900 and 1500 m. It would seem to occur chiefly at higher altitudes than *Retrophyllum vitiense* which, in Fiji and the Solomon Islands, grows mainly between 100 and 900 m.

*Provisional IUCN conservation assessment*: LC. This species is here reinstated for the first time after a lapse of more than 40 years (when it was synonymised with *Podocarpus vitiensis* by de Laubenfels, 1968), and there has therefore been no previous conservation assessment for it as a separate species. The species appears to be widespread on New Guinea, and it is therefore regarded as Least Concern, although it is, or has been, subjected to logging.

*Uses*. None have been recorded. However, they are likely to be similar to those of *Retrophyllum vitiense*.

**Group B.** Bark exfoliating in short strips or pieces. Vegetative shoots dimorphic. Terminal buds protected by reduced foliage leaves; true bud scales absent. Leaves heterofacially flattened in both juvenile and adult phases. Adult leaves in 4 ranks, thick to very thick; juvenile ones distichous. Resin canal 1, situated below vascular bundle.

Pollen cones in groups at branch tips, on a common peduncle (sometimes  $\pm$  sessile), individual cones sessile, subtended by scale-like bracts and the lower ones in the group axillary to leaves; microsporophylls decussate (appearing spirally arranged), triangular or ovate. Female cones terminating ordinary foliage shoots, proleptic; peduncle not broadened distally, in its vegetative portion bearing spreading bracts; cone axis with 1 or 2 sterile bracts below fertile bract. Fertile bract free from epimatium, flat. Receptacle formed from 1 or 2 peduncle bracts plus the last sterile bract and the fertile bract, obovoid. Seed beaked at micropylar end. Germination epigeal. Seedling phyllotaxis decussate. – New Caledonia.

**3. *Retrophyllum comptonii*** (J.Buchholz) C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45(2): 380 (22 Feb. 1989 [‘1988’]). – *Podocarpus comptonii* J.Buchholz, Bull. Mus. Hist. Nat. Paris sér. 2, 21: 284 (30 Jul. 1949). – *Decussocarpus comptonii* (J.Buchholz) de Laub., J. Arnold Arbor. 50: 344 (15 Jul. 1969). – *Nageia comptonii* (J. Buchholz) de Laub., Blumea 32(1): 211 (3 Feb. 1987). – Type: New Caledonia, Mt. Mou, *J. Buchholz* 1684 (holo ILL–image, photos A, P; iso ILL–image, K–image, MO, NY, S–image [S-C-1294]). Paratypes Mt. Mou, *Buchholz* 1085 (ILL–image; isoparatypes elsewhere as cited below); Mt. Mou, *Buchholz* 1449 (ILL–image; isoparatypes elsewhere as cited below); Mt. Humboldt, *Buchholz* 1697 (ILL–image), 1697a and 1697s. **Fig. 1B, E, H.**

*Iconography.* De Laubenfels, Fl. Nouv. Caléd. 4: 51, pl. 11 f. 1–8 (1972), as *Decussocarpus comptonii*.

*Etymology.* This species is named after Robert Harold Compton (1886–1979), Cambridge botanist who, after the First World War, became director of Kirstenbosch Botanical Garden (South Africa) in 1919. Compton collected *Retrophyllum comptonii* several times during a field expedition to New Caledonia in 1914, although he was not the first to do so; a much earlier collection by Vieillard has been seen.

*Vernacular names:* *palissandre* (Chevalier, 1957: 114; Suprin, 2011b).

*Distinguishing features.* *Retrophyllum comptonii* in most of its wide range has the capacity to become a tall tree up to at least 30 m, although in the far south of the island it tends to be much shorter. It is rarely if ever an aquatic. The adult foliage is mostly opposite decussate, with only the leaves in the upper part of the tree in 4 ranks. The adult leaves have a raised central area that is always narrower than the leaf margins and when dried is marked either by two (not three) parallel ridges or longitudinal wrinkles. The surface of the seed is scalloped and ridged, these low and not prominent.

Tree or shrub, 2.5–30 m tall, 12–80 cm dbh. *Trunk* apparently not buttressed, the bole straight and lacking branches for 10 m or more in large trees. *Bark* smooth when young,  $\pm$  rough on older trees, peeling in short vertical strips or ragged pieces, fissured, dark grey, greyish-brown, tan or reddish-brown; inner bark brownish; wood cream or whitish. *Crown* pyramidal, finally rounded. *Buds* ovoid, protected by very reduced foliage leaves; true bud scales absent. *Juvenile shoots* with 1 or 2 very small leaves at

base and 22–35 pairs of foliage leaves in up to 3 growth increments. *Juvenile leaves* 5–7 mm apart, opposite, distichous and pectinate, heterofacially turned at base, diverging at 55–65°, sessile or subsessile, lamina narrowly lanceolate or linear-lanceolate, 20–35 × c.2.5 mm on seedlings, somewhat smaller on older saplings, gradually tapered to a subacute, narrow and frequently slightly mucronate tip. *Adult trees* with dimorphic shoots, most shoots bearing foliage leaves but a few leader shoots bearing scale leaves and these either emitting lateral foliage shoots or terminating in foliage shoots; shoot flattening fully heterofacial on juvenile and transitional shoots but only partly so on adult branches. *Primary adult branches* irregularly arranged, divaricate or widely spreading, opposite, alternate or in whorls of 3. *Penultimate adult branchlets* erecto-patent to divaricate, ± curved, initially clad with distant, alternate, small, elliptic-ovate subadpressed scales with decurrent bases, their free laminae finally deciduous. *Ultimate adult foliage shoots* ± clustered at tips of penultimate branches, erecto-patent to suberect, flexuous, 40–70 mm with 8–15 pairs of leaves, subtended by 1 or 2 pairs of very reduced scale-like foliage leaves. *Leaf scars* absent. Lowest true *adult foliage leaves* smaller and relatively broader than the others; adult leaves in 4 ranks or some (on transitional shoots) opposite-decussate and distichous, crowded, 3–4 mm apart, sessile with partly twisted bases, most showing heterofacial twisting, scarcely or not imbricate, erecto-patent to suberect, mid to dark green; lamina of leaves in middle of shoot elliptic, oblong-elliptic, narrowly lanceolate or lanceolate, 6–15 × 2–5 mm, straight, thick and coriaceous; margin not thickened, narrowly hyaline; surfaces unequally amphistomatic, with more stomata on adaxial surface; midrib not visible on either surface but both surfaces with a raised, narrowly elliptic central area narrower than the margins and either longitudinally wrinkled or marked by two parallel ridges when dried; apex obtuse or broadly rounded; base obtuse or cuneate.

*Pollen cones* lateral (axillary) or terminal on lateral shoots of current growth, subtended by a leaf or scale-leaf, 1–5 together, pedunculate (individual cones sessile when > 1 together); peduncle shorter than cone(s), erecto-patent, bearing 1 pair of ± adpressed scales; peduncle scales greenish, keeled, ovate with decurrent base, acute, with very narrow, buff scarious margin; cones ellipsoid or ovoid, 4–6(–12) × 2.5–3 mm, straight, reddish, or greenish with a pink tinge; *microsporophylls* decussate but appearing spirally arranged, 16–20(–28) per cone in 4 or 5 short/3 or 4 long ‘spirals’; lamina greenish sometimes tinged pink or red, broadly triangular or deltate and abruptly narrowed to an acute, apiculate apex, with very narrow whitish hyaline margin, longer than the microsporangia; *microsporangia* pinkish, elliptic; *pollen* white or cream.

*Female cones* terminal on lateral foliage shoots of current growth, shortly pedunculate. *Peduncle* in line with shoot or erecto-patent, shorter than remainder of cone but longer than receptacle, bearing 1 (occasionally 2) cone(s), bearing 8–10 bracts in 4 or 5 decussate pairs; distal part of peduncle shed with cone. *Peduncle bracts* light green turning brownish green, not keeled but convex abaxially, elliptic or ovate-elliptic, 1.5–4 × c.1–1.5 mm, subacute to obtuse. *Proximal sterile bracts* (cone axis) absent other than the one subtending the fertile bract. *Cone* subtended by a non-

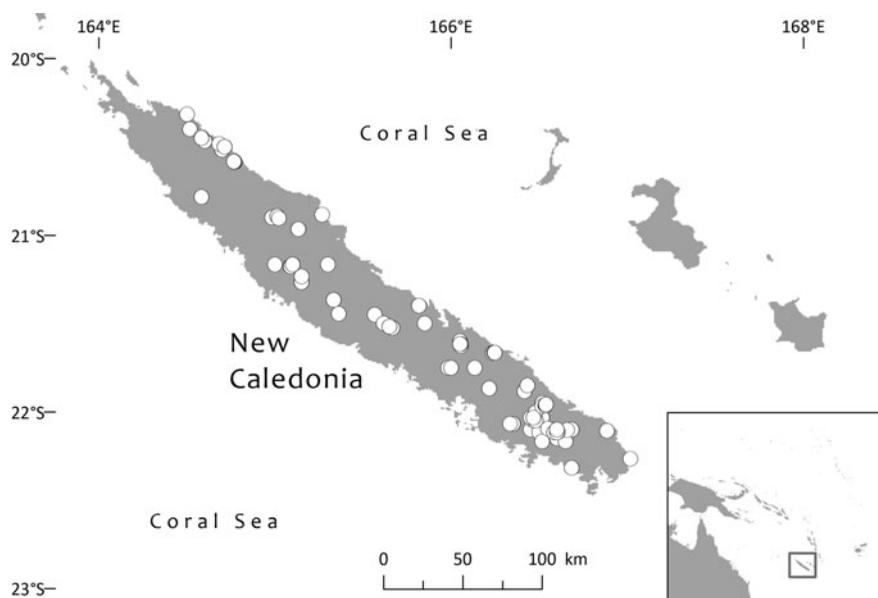


FIG. 5. Global distribution of *Retrophyllum comptonii*.

fleshy receptacle formed from 1 or 2 peduncle bracts plus either one sterile and one fertile bracts or two fertile (or part-fertile) bracts. *Receptacle* narrowly obovoid or narrowly pyriform, light green at first becoming orange. *Sterile bract* normally 1, light green becoming pale orange, stiffly spreading to erecto-patent, elliptic to ovate-elliptic, obtuse, with scarious margin. *Fertile bract* light green becoming pale orange, initially erect, with median longitudinal groove, wholly free from epimatium, with reflexed, ovate free tip with acute apex. *Cones* pyriform, 20–25 × 13–20 mm; epimatium green becoming scarlet or deep red when ripe (occasionally blue-black, *fide* Munzinger *et al.* 1680 in sched., P), with short conical apical crest; seed beaked at micropylar end, the beak usually straight, occasionally curved. Seed surface with two ridges leading to the micropylar beak, not porous and not adapted to water dispersal.

*Germination* epigeal. *Seedlings* with two brown, erect, soon deciduous cataphylls that envelop the base of the stem and have greenish linear lanceolate tips that protect the first leaves; initial leaves of main axis cotyledon-like, c.6 pairs, separated by short, naked internodes, widely spreading and the lowest pair becoming recurved, their blades linear, 21–28 × 1.5–2 mm, longer than the leaves on the initial branchlets, basally not twisted, opposite-decussate, amphistomatic.

*Distribution.* New Caledonia (throughout the island except the northern half of the western coast). TDWG: 60 NWC. *Map:* Fig. 5.

*Specimens seen and other records.* NEW CALEDONIA. Unloc., *Baudouin* 542 (P-image); unloc., no date, *Bernier* s.n. (P-image, barcode P00188269); unloc., *Pancher* s.n. (P-image, barcode P00188209); unloc., *Sarlin* 228 (P-image) and 238 (P-image); collection details obscured, *Bernier*

268 (K–database, P–image, possibly a composite sheet of up to three separate gatherings?; *Bernier* 269 is from Plaine des Lacs); **Province Nord: Hienghène:** Contrefort est du Mt. Panié, 1000–1400 m, 10 ix 1966, *MacKee* 15594 (P–image); *ibid.*, 800 m, 10 ix 1966, *MacKee* 15639 (P–image, seedlings); Mont Panié [20°35'S 164°46'E], 700–900 m, 19 ix 1966, *Schmid* 1422 (NOU–database). Mont Panié, 800 m, 3 viii 1978, *MacKee* 35577 (P–image); Mt. Panié, c.20 air-km NW of Hienghène, 950 m, 6 xii 1979, *McPherson* 2191 (MO–database, P–image, NOU–database); Mont Panié [20°35'S 164°46'E], 950 m, 3 iii 1983, *Lauri* 45 (NOU–database). Mt. Panié, above Haut Coulna, on SW slopes, 20°36'82[sic]''S 164°44'40''E, 1060–1250 m, 30 x 1999, *McPherson & van der Werff* 17834 (P–image, NOU–database); Mt. Panié, NE slopes on summit route via eastern trail, 20°35'00''S 164°46'14''E, 1158 m, 7 xii 2002, *Gardner et al.*, *Third New Caledonia Araucaria Exped. (TNCA)* 5045 (E). **Kaala-Gomen:** Mont Taom (Crête Ouest), 900 m, 24 iv 1982, *MacKee* 40376 (MO–database, P–image, NOU–database), 40377 (P–image). **Kouaoua:** décharge Montmartre, 750 m, 14 ii 1978, *Veillon* 3514 (P–image, NOU–database, Z–database). **Poindimié:** Wagap, *Veillard* 3264 [p.p.] (P–image, original label bearing manuscript name “*Podocarpus Guillauii*”). Sommet du Mt. Grandie (Haute Amoa), 900–960 m, 14 v 1968, *MacKee* 18807 (NOU–database, P–images, 2 sheets), 18808 (NOU–database, P–image); massif de Grandie, pente SE, c.700 m, 31 iii 1988, *Veillon* 6783 (P–image, NOU–database). Dans une cuvette au massif du Tchinguou, c.1250 m, 18 iv 1951, *Hürlimann* 1220 (P–image, Z–database); Massif de Tchinguou, 750 m, 13 xii 1983, *Morat* 7621 (P–image); Massif de Tchinguou, 20°53'36''S 165°00'42''E, 1160–1175 m, 1 iv 2001, *McPherson & Munzinger* 18100 (P–image, MO–database, NOU–database); *ibid.*, 20°54'15''S 165°01'19''E, 760–850 m, 5 iv 2001, *McPherson & Munzinger* 18149 (MO–database). **Pouébo:** Bois du montagne à Balade, 1855–1860, *Veillard* 1265 (P–image). Mont Colnett [20°29'S 164°41'E], c.1000 m, 1 x 1997, *Suprin* 2628 (NOU–database); sur la crête SW du Mt. Colnett, c.1200 m, 12 ix 1951, *Hürlimann* 1964 (P–image, S–database), 1966 (P–image, Z–database); Mont Colnett (pente est), 1100 m, xi 1981, *Nasi* s.n. (*MacKee* 39997) (P–image); *ibid.*, 1100 m, xi 1981, *Nasi* (*MacKee* 40011) (P–image); Mt. Colnett, E slopes, 20°30'00''S 164°42'52''E, 1000 m, 29 x 2003, *McPherson* 19070 *et al.* (P–image, MO–database); *ibid.*, 1000 m, 29 x 2003, *McPherson* 19073 *et al.* (P–image, MO–database, S–database). ‘Ignambi, 18 iii 1914’, *Compton* 608 (S–database under *Retrophyllum minus*, 3 accessions in spirit coll., nos. S-A-3669, S-A-3681, S-A-3684; the locality, date [only given for S-A-3681] or collection number of all must be wrong because Compton collected at Mt. Mou in the S of the island on that date, see *Compton* 607 below); Ignambi, > 3500 ft [1067 m], 30 vii 1914, *Compton* 1524 (A–photo, BM, K); Ignambi, *Compton* 1527 (S–database under *R. minus*); Ignambi, 3000 ft [914 m], 1 viii 1914, *Compton* 1587 (BM, A–photo); am Gipfel des Ignambi, 4 vi 1925, *Däniker* 2901a (Z–database); en montant vers le sommet de l’Ignambi, c.1250 m, 17 viii 1951, *Hürlimann* 1842 (P–image, Z–database); sur la crête du massif Ignambi le long de la route de Gomen, c.1170 m, 25 viii 1951, *Hürlimann* 1832 (P–image, Z–database); summit of Ignambi, on trail from Oubatche to Gomen, c.1000 m, 12 vi 1956, *Foster* 160 (P–image); near top of Mt. Ignambi, c.10 km S of Panébo, c.1300 m, 7 xii 1963, *Green* 1783 (A); Mont Ignambi, 1100–1200 m, 19 viii 1965, *Bernardi* 10347 (L–image, P–image, Z–database); E slopes of Mont Ignambi, 20°26'39''S 164°34'58''E, 1200 m, 6 iii 1999, *Cretinon & Gardner*, *ICCP New Caledonia Exped. (1999)*: 73 (E); Ignambi [20°27'S 164°35'E], 1250–1300 m, 2 v 2002, *Lowry* 5747 (MO–database, NOU–database). **Pouembout:** Kopéto [21°10'S 165°00'E], 940 m, 8 viii 2006, *Rigault & Barrière* s.n. (*Barrabé* 365) (NOU–database). Ad montem Paéoua metalliferum, 900 m, 13 viii 1965, *Bernardi* 10131 (K, L–image, P–image, Z–database); *ibid.*, 900–950 m, 13 viii 1965, *Bernardi* 10149 (K–database, L–image, P–image, S–database, Z–database); Mt. Paéoua, 900–1100 m, 4 vii 1967, *MacKee* 17032 (P–image), 17056 (K, NOU–image, P–image, Z–database); Mt. Paéoua, c.1100 m, 16 x 1986, *Veillon* 6062 (P–image, NOU–database); Paéoua, 21°10'36.0''S 165°05'14.2''E, 1077 m, 5 xii 2005, *Gardner et al.* 256 (E). **Poya (N):** Mt. Boulinda, c.1102 m, 26 iv 1965, *Veillon* 120 (P–image, NOU–database; P sheet has ‘Blanchon’ blacked out and ‘Veillon’ substituted below, with Blanchon’s initials J.P. remaining; Veillon’s are J.M.). Boulinda

[21°14'S 165°09'E], 1102 m, 26 iv 1965, *Veillon* 122 (NOU-database). Mont Boulinda, c.1200 m, 28 iv 1965, *Schmid* 137 (P-image); Mt. Boulinda, pente nord, 1150–1300 m, 28 viii 1967, *MacKee* 17354 (P-image), 17357 (NOU-database, P-image, Z-database), 17358 (P-image). Monte Boulinda, 450–900 m, 12–15 iv 1968, *Bernardi* 12754 (K, P-image, Z-database); Massif de Boulinda, N of Poya, c.850 m, 28 viii 1981, *McPherson* 4121 (GH, P-image, MO-database, NOU-database, Z-database). Aoupinié [21°10'S 165°18'E], 1000 m, 16 ix 1981, *Suprin* 1407 (NOU-database). **Province Sud: Bouloupari:** Dent du St Vincent, vii 1909, *Le Rat* 71 (P-image, seedlings, also duplicate without locality details, P-image). Mont Do, 1000 m, 28 xi 1966, *Veillon* 949 (P-image, NOU-database); c.15 km towards NW, Mont Do, upper region towards top, 700–1014 m, 28 xi 1966, *Ehrendorfer* 6600-138-38 (WU-image). Mont Do [21°45'S 165°59'E], 1000 m, 24 v 1977, *Musselman* 5415 (NOU-database). **Bourail:** au-dessus de Téné, près de Bourail, 18 iii 1869, *Balansa* 1381 (P-image); duplicate without locality information, P-image). Pente boisée d'un contrefort du massif Mé Maoya (Haute Houaïlou), 800–900 m, 28 xii 1962, *MacKee* 9886 (CANB-database, L-image, P-image, K-database). Poya, Mé Maoya Massif, southern edge of Këiyoyimê in disused mine, 21°26'37.8''S 165°21'43.5''E, 1012 m, 2 xi 2008, *Hollingsworth et al.* 194 (E, P-image). Mé Aoui, 850 m, 18 vi 1981, *Cherrier* (*MacKee* 39235) (NOU-database, P-image). **Canala:** Crête Mt. Nakada, 21°37'S 166°03'E, 1050 m, 6 x 1977, *MacKee* 33961 (MO-database, NOU-database). Near Prokoméo radio tower, NW of Canala, 21°30'S 165°51'E, 700 m, 3 ii 1983, *McPherson* 5477 (MO-database). Mt. Nakada, 21°37'35''S 166°03'22''E, 800–900 m, 17 iv 2001, *McPherson & Munzinger* 18254 (P-image, MO-database); *ibid.*, 21°37'82 [sic]'S 166°03'35''E, 780 m, 18 iv 2001, *Munzinger* 764 & *McPherson* (P-image). **Dumbéa:** Mt. Dzumac, 1000 m, 28 iv 1951, *Guillaumin & Baumann-Bodenheim* 12717 (Z-database), 12725 (P-image, Z-database), 12727 (P-image, Z-database); N face of Mt. Dzumac, c.1000 m, 27 ix 1963, *Green* 1216 (A, K-database, NOU-image). Pic de Kouwehé [Couvélé], 700–1000 m, 4 ix 1882, *Brousmiche* 697 (P-image). Au fond de la vallée derrière la mine Sunshine, c.730 m, 15 iii 1951, *Hürlimann* 1062 (P-image, K-database, Z-database). Near Pic du Rocher, on mountain crest along trail to Pic du Rocher, Plateau Montagne des Sources, nr Pic du Rocher, 950 m, 15 x 1947, *Buchholz* 1222 (NY, P-image, K-database, S-database; photo of trees in situ, A). Un vallon au dessous de la route vers la Montagne des Sources au Pic Buse, c.530 m, 11 vii 1951, *Hürlimann* 1573 (P-image, Z-database). Mont Dzumac, 900 m, 25 vii 1981, *McPherson* 3958 (NOU-database). Mont Dzumac [22°02'S 166°28'E], 880 m, 5 i 1982, *Suprin* 1612 (NOU-database, 2 sheets); *ibid.*, 1050 m, 4 v 1982, *Suprin* 1830 (K-database, NOU-database). Mont Dzumac, '0 m' [sic: from map, must be c.600 m], 11 ix 1984, *Jaffré* 2585 (NOU-database, 2 sheets). **Le Mont-Dore:** Thy [22°10'S 166°31'E], 980 m, 19 x 1982, *Brinon* 1359 (NOU-database). Mont Koghis, [22°10'S 166°31'E], 1000 m, 26 x 1982, *Zlarnik* 30 (NOU-database). Inland from Baie des Pirogues, 16 x 1923, *White* 2120 (A, 2 sheets; S-database). **Moindou:** Mé Ori, 900–1000 m, 3 xii 1969, *MacKee* 21219 (P-image, K-database, MO-database, NOU-database, Z-database). Along old lumber road to top of Mt. Mé Ori, above Katrikoin, 21°31'S 165°39'E, 8 ix 1980, *McPherson* 3066 (MO-database, 2 sheets). Bourail, E slopes and summit area of Mé Ori (ascent starting from Katrikoin), 21°31'31.7''S 165°39'56.4''E, 31 x 2008, *Hollingsworth et al.* 153 (E, P-image). Me Adeo pente O, c.750 m, 24 iii 1988, *Veillon* 6747 (P-image, NOU-database). **Païta:** Mont Humboldt, 1400 m, 16 ix 1902, *Schlechter* 15331 (A-photo of BM sheet, BM, E, K-2 sheets, L-image [currently as *R. minus*, May 2015], P-image, S-database, Z-database); *ibid.*, 1400 m, *Schlechter* 15332 (P-image); Mt. Humboldt, 1200–1300 m, *Buchholz* 1578 (A-photo, seed; NY, S-database); Mt. Humboldt, 1400 m, 20 ix 1951, *Baumann-Bodenheim* 15393 (P-image, Z-database); *ibid.*, 1400 m, 20 ix 1951, *Baumann-Bodenheim* 15411 (P-image, Z-database); Mt. Humboldt, c.1100 m, xi 1973, *Schmid* 4838 (P-image, NOU-database); Mont Humboldt, Réserve Spéciale Botanique, 29 xi 2005, *Gardner et al.* 108 (E); Mont Humboldt [21°53'S 166°24'E], 1380 m, 2 xii 2009, *Grignon et al.* 559 (NOU-database). Mt. Dzumac, 800 m, 1 xii 1957, *de Laubenfels* P153 (S-database); Mont Dzumac, [22°02'S 166°27'E], 950 m, 6 xii 1964, *Blanchon* 1246 (NOU-database); Mt. Dzumac, 760 m, 29 xi 1964, *de Laubenfels* P 415

(K); Mt. Dzumac, 8 vii 1965, *Aubréville & Heine* 229 (P-image); Mont Dzumac, 22°06'–22°08'S 166°27'–166°32'E, 800–900 m, 8 vii 1965, *Bernardi* 9520 (P-image). Crête entre Mt. Dzumac et Mt. Ouin, c.1000 m, 22 xii 1962, *Barets* 8 (P-image); *ibid.*, 900 m, 11 x 1967, *MacKee* 17670 (P-image); *ibid.*, 900 m, 17 iv 1968, *MacKee* 18694 (P-image, seedlings); *ibid.*, 900 m, 7 vii 1969, *MacKee* 20244 (P-image); *ibid.*, 6 i 1982, *MacKee* 40185 (P-image, K-database, NOU-database, Z-database). Haute Ouinné, côte orientale, 750 m, 18 i 1948, *Bernier* 267 (P-image); Ouinné sup., 700 m, 29 iv 1951, *Guillaumin & Baumann-Bodenheim* 12815 (P-image, Z-database), 12843 (P-image, Z-database), 12861 (P-image, Z-database); *ibid.*, 900 m, 30 iv 1951, *Guillaumin & Baumann-Bodenheim* 12910 (Z-database), 12960 (P-image). Monts Dzumac and down to the Rivière Ouinné, 800 m, 22°02'54"S 166°28'47"E, 9 iii 1999, *Cretinon & Gardner, ICCP New Caledonia Exped. 1999*: 90 (E); Monts Dzumac road down to the Rivière Ouinné, 800 m, 22°02'54"S 166°28'47"E, 3 vi 2001, *Gardner et al., New Caledonia Araucaria Exped. 2001*: 1026 (E, 2 sheets). Mont Mou, 1861–1867, *Vieillard* 3064 (GH, P-image, original labels of both sheets bearing manuscript name “*Podocarpus Guillainii*”); sommet du Mont Mou, 1866, *Vieillard* 3264 [p.p.] (P-image, with manuscript name “*Podocarpus Guillainii*”). Mt. Mou, 1910–11, *Godefroy* s.n. (P-image); Mont Mou, 3500 ft [1067 m], 18 iii 1914, *Compton* 607 (BM, A-photo; *Compton* 608, at S and said to be collected from Ignambi, could not have been collected on 18 iii 1914 as the S database record says); summit of Mt. Mou, 3500 ft [1067 m], x 1923, *White* 2033 (E, P-image, K-database); Gipfelcrête des Mt. Mou, 21 ii 1926, *Däniker* 2902 (P-image, Z-database); crête sommitale du Mont Mou, c.1150 m, 19 vi 1938, *Viroit* s.n. (A, P-image); *ibid.*, c.1100 m, 4 ix 1938, *Viroit* 38 (A, P-image); crête sommitale du Mont Mou, 1150 m, 19 ii 1939, *Résineux* no. 8, coll. *Viroit* (A, P-image); Mont Mou, 1100 m, 28 ix 1947, *Buchholz* 1085 (paratypes ILL–2 sheets, images; isoparatypes A-photo, GOET-image, NY, P-image, K-database, S-database); Mt. Mou, 1100 m, 4 xii 1947, *Buchholz* 1447 (A-photo), 1449 (paratype ILL-image, isoparatypes A-photo [seed kernel]), K, NY, P-image, S-database: paratype and isoparatypes of *Podocarpus comptonii*); Mont Mou, 1100 m, 4 xii 1947, *Buchholz* 1452 (K-database, NY, S-database); Mt. Mou, 1100 m, 9 ii 1948, *Buchholz* 1684 (holo ILL-image, A and P-photos of holotype, iso ILL-image, K-image, MO, NY, S-image); Mt. Mou, 1100 m, 9 ii 1948, *Buchholz* 1684s (small seedlings, ILL-image, P-image); Mt. Mou, 1100 m, 5 vi 1948, *Buchholz* 1791 (NY, S-database); Mont Mou, Pic des Mousses, 1000–1100 m, 23 i 1949, *Skottsberg* 202 (P-image); Mont Mou, Pic des Mousses, 23 i 1949, *Selling* 202 (S-database); Mont Mou, 1000 m, 22 xi 1949, *MacDaniels* 2323 (P-1041) (NY-database). Mt. Mou, 1200 m, 23 viii 1950, *Baumann-Bodenheim* 5654B (Z-database); Mt. Mou, 1200 m, 13 iii 1951, *Guillaumin & Baumann-Bodenheim* 11257 (P-image, Z-database); *ibid.*, 1200 m, 13 iii 1951, *Guillaumin & Baumann-Bodenheim* 11261 (P-image, Z-database), 11282 (P-image, Z-database), 11299 (P-image, Z-database), 11301 (P-image, Z-database); Mount Mou, c.20 miles NW of Nouméa and c.5 miles N. of Païta, 26 vi 1952, *McMillan* 5015 (P-image); Mt. Mou, below N. summit, 1100 m, 25 xi 1955, *MacKee* 3516 (A, E, P-image); sommet du Mont Mou, *Blanchon* 341 (P-image); Mont Mou, 1200 m, 9 x 1957, *de Laubenfels* P129 (S-database, spirit coll.; SBT-n.v., cited by *de Laubenfels*, 1969: 345); *ibid.*, 9 ix 1960, *Erdtman* s.n. (3 collections, S-database); Mt. Mou (c.25 km N of Nouméa), c.1200 m, 7 x 1963, *Green* 1268 (A, K-database, NOU-database); Mt. Mou, 1140 m, 18 xi 1964, *de Laubenfels* P 360 (A); *ibid.*, juvenile, 1140 m, 18 xi 1964, *de Laubenfels* P 361 (A); Mont Mou, 28 v 1965, *Boisseau* (hb. *MacKee* 12725) (P-image); Mont Mou, 22°03'–22°04'S 166°19'–166°22'E, 30 vii 1965, *Bernardi* 9879 (L-image, P-image, Z-database); Mt. Mou, along trail starting near Sanatorium c.7 air-km NNW of Païta, 1100 m, 8 ix 1979, *McPherson* 1867 (P-image, MO-database, NOU-database); Mt. Mou, along trail from near Sanatorium to summit, 1150 m, 8 viii 1981, *McPherson* 4020 (P-image, K-database, MO-database, NOU-database); Mont Mou, close to summit on N ridge slope, 1000 m, 22°04'S 166°20'E, 27 v 2001, *Gardner et al., New Caledonia Araucaria Exped. 2001*: 1014 (E). **Poya (S)**: Contrefort Ouest du Mé Maoya au dessus de la Mine Emma, 1350 m, 11 vii 1965, *Corbasson* (hb. *MacKee* 13037) (P-image,

K-database); *ibid.*, 1400–1450 m, 2 x 1965, *MacKee* 13492 (K, P-image); **Thio**: Mont Poueari (SE Thio) [21°40'S 166°14'E], 1140 m, 13 x 1994, *Suprin* (hb. *MacKee* 46368) (P-image, NOU-database). Forêt de Sailles, 21°39'58''S 166°14'49''E, 1100 m, 12 iv 2001, *Munzinger* 1200, *Suprin & Carriconde* (P-image, det. *Suprin* incorrectly as *Prumnopitys ferruginoides*); *ibid.*, forêt au bas du col juste avant le mont Pwénari, 21°39'58''S 166°14'49''E, 1200 m, 8 xii 2001, *Munzinger* 1307, *Suprin & Carriconde* (MO-n.v., P-image, NOU-database). Forêt de Sailles vers Thio, parcelle 3 no. 25909, 21°39'56''S 166°14'38''E, 849 m, 18 xi 2009, *Grignon et al.* 584 (P-image, NOU-database). Mont Ninga [21°45'S 166°08'E], 19 vi 1975, *Sévenet* 958 (NOU-database). Pic de Na Kado, *Brousmiche* s.n. (P-image, named as *Decussocarpus minor* (Carr.) de Laub. by de Laubenfels). Mt. Nekandi, 1200–1300 m, 7 xi 1967, *MacKee* 17908 (P-image). Nékando [21°51'S 166°26'E], 1100 m, 28 xi 1983, *Veillon* 5659 (NOU-database). **Yaté**: Montagne des Sources, Pic des Conifères et Campement “Bernier”, 900–1000 m, x 1947, *Bernier* 271 (P-image and duplicate without locality information, P-image). Montagne des Sources, 850 m, 9 vii 1949, *Selling* 208 (S-database); au dessous du Camp Bernier à la Montagne des Sources, c.800 m, 21 ii 1951, *Hürlimann* 931 (NY, P-image, Z-database); Montagne des Sources, 22°05'–22°09' S 166°32'–166°38' E, 6 vii 1965, *Bernardi* 9445 (L-image, P-image, Z-database); *ibid.*, 8 ix 1960, *Erdtman & Chevalier* s.n. (S-database); *ibid.*, 8 ix 1960, *Erdtman* s.n. (3 sheets, S-database); Montagne des Sources [22°07'S 166°35'E], 600 m, 6 vii 1965, *Veillon* 281 (NOU-database). Crête sommet Montagne des Sources, 22°07'S 166°36'E, 900 m, 7 x 1969, *MacKee* 20928 (NOU-database). Montagne des Sources [22°07'S 166°35'E], 850 m, 24 i 1982, *Suprin* 1636 (NOU-database). Montagne des Sources, Parc Territorial de la Rivière Bleue, highest summit area to which trail leads, 22°06'52.06''S 166°36'19.68''E, 1011 m, 11 xii 2002, *Gardner et al.*, *Third New Caledonia Araucaria Exped. (TNCA)* 2036 (E). Forêt du Mois de mai, 150 m, viii 1947, *Bernier* 203 (P–3 sheets, images, one juvenile and lacking locality or date); Forest du Mois de mai, Plaine des Lacs near Walker's place, 4 xi 1947, *Buchholz* 1350 (K-database, P-image, NY, S-database); Plaine des Lacs, Mois de mai, 4 xi 1947, *Buchholz* 1350a (NY, S-database); Forêt Walker, Haute Yaté, Plaine des Lacs, c.200 m, 6 xi 1947, *Bernier* 269 (P-image, seedlings); *ibid.*, same details, *Bernier* 270 (P-image); Mois de mai forest, Plaine des Lacs, 160–200 m, 6 xi 1947, *Buchholz* 1359 (A, P-image, S-database), 1359a (P-image, MO-database, S-database); Forest du Mois de mai, 180–250 m, 13 ii 1948, *Buchholz* 1697 (A-photo, seed kernel; ILL-image, K, NY, S-database; paratype and isoparatypes), 1697a (S-database), 1697s (ILL-image, NY); forest du Mois de mai near Walker's place, Plaine des Lacs, 180–200 m, no date, *Buchholz* 1697 (P-image, isoparatype, label details differ slightly from others of this number); forêt “Mois de mai” (Riv. blanche), 13 vii 1951, *Baumann-Bodenheim* 14057 (P-image, Z-database); *ibid.*, 14 viii 1951, *Baumann-Bodenheim* 15178 (NY, P-image, Z–2 sheets, database); *ibid.*, 14 viii 1951, *Baumann-Bodenheim* 15197 (P-image, Z-database); Rivière Blanche, 200 m, 24 vii 1954, *H.D. Ingle* I. 66 (L-image, MEL-n.v.); Mois de mai, 300 m, 22°07'S 166°39'E, 15–29 iii 1987, *Watt* 519 (NY-image, juvenile, fragment). Parc Territorial de la Rivière Bleue, Mois de mai, 22°07'11.2''S 166°39'36.8''E, 230 m, 27 xi 2005, *Gardner et al.* 68 (E). [Forêt] des Electriques (Rivière blanche sup.), [c.350 m], 17 vii 1958, *Hürlimann* 3173 (Z-database, 2 sheets); Rivière Bleue, 5 viii 1951, *Baumann-Bodenheim* 15028 (NY, P-image, Z–2 sheets, database); Rivière Bleue [22°06'S 166°38'E, c.200 m], 4 viii 1963, *Blanchon* 399 (NOU-database, det. *Blanchon*, needs confirmation); forêt de la Rivière Bleue, 150 m, 1 vi 1994, *Pintaud* 51 (juv., P-image); Plaines des Lacs, sources de la Kuébini, 24 vi 1980, *Cherrier* (hb. *MacKee* 39255) (P-image); margin of Rivière Bleue at Pont Germain, 22°06'05.2''S 166°39'28.9''E, 111 m, 27 xi 2005, *Gardner et al.* 85 (E). Kouakoué, piste Haute Ouinni, 22 ix 1977, *Veillon* 3305 (P-image, NOU-database); Kouakoué [21°58'S 166°31'E], 1300 m, 22 ix 1977, *Morat* 5676 (NOU-database). Haute Yaté, Rivière Bleue, 200 m, 1 x 1981, *MacKee* 39724 (A, E, NOU-database, P-image); Mt. Kouakoué, 21°57'29''S 166°32'20''E, 26 xi 2002, *Munzinger* 1661, *Tronchet et al.* (P-image, NOU-database); Mt. Kouakoué, 21°57'31''S 166°32'11''E, 26 xi 2002, *Munzinger* 1680, *Tronchet et al.* (P-image, NOU-database); Kouakoué, along trail SW of

camp, 21°57'49''S 166°32'07''E, 12 v 2006, *Lowry II et al.* 6821 (P–image, MO–database, NOU–database); Kouakoué [21°57'S 166°31'E], 950 m, 3 xi 2009, *Grignon et al.* 470 (NOU–database). Forested slopes above a tributary of the Rivière Ni, 22°00'17''S 166°28'42''E, 950–1000 m, 10 xi 2003, *McPherson 19209 & Mouly* (P–image, MO–database). Mamié, between Ointapoin and Tiova, 22°06'23.8''S 166°53'03''E, 552 m, 27 x 2008, *Hollingsworth et al.* 90 (E, P–image).

USA (CULTIVATED). **Georgia:** Atlanta Botanical Garden, Fuqua Conservatory, 16 xii 2009, *Silba B-640* (accession 9040015/1996-0015, coll. *A. Watt* in New Caledonia) (NY–image).

A specimen collected by Bernard Suprin (in herb. *MacKee*, no. 46368, P, barcoded P001655140) very closely resembles *Retrophyllum minus* (treated below) in branching pattern but is from a high-altitude locality in the north of New Caledonia and belongs to *R. comptonii*, with which it agrees in leaf characters. *Vieillard 1265* from Balade (extreme NE New Caledonia) also has to belong to *Retrophyllum comptonii* on geographical and habitat grounds, although it was determined as *Podocarpus minor* Parl. by Guillaumin in 1943 – this was 6 years before *Podocarpus comptonii* (now *Retrophyllum comptonii*) was segregated from *P. minor* (now *R. minus*). The later annotation slip “= *Nageia minor* Carrière cf. de Laubenfels, *Blumea* 32: 211, 1987” is misleading and represents an uncritical up-dating of the nomenclature on the 1943 *determinavit* slip rather than a new determination; this is also a feature of several other specimens in the P herbarium. The specimen not unexpectedly has the characteristics of *Retrophyllum comptonii*. On the other hand, a specimen from Port Boisé (Le Mont-Dore) that de Laubenfels in 1972 determined as *Decussocarpus comptonii* has in this revision been reassigned to *Retrophyllum minus*, along with others from the same locality that had previously been identified as *Decussocarpus minor*. Gray (1962: 75) cited an example of *Vieillard 1275* from Mt. Mou at P under *Podocarpus comptonii*, but I have not seen such a specimen and it is not among those imaged in the P database: all examples of *Vieillard 1275* that I have seen are from low-lying localities and are *Retrophyllum minus*. It is possible that the specimen Gray (1962) cited is the one now barcoded P00188118, which is an unnumbered Pancher collection but was given the number *Vieillard 1275* and mentions Mt. Mou among several collecting localities, which may not all relate to that number.

*Veillon 2962* from Ouégoa is currently determined at P as *Decussocarpus comptonii*, but the corresponding sheet at NOU is indicated as having been identified as *Falcatifolium taxoides* (Brongniart & Gris) de Laub. by Veillon on the date of collection. After examining images of both sheets, on account of its leaf and pollen cone morphology I concur with Veillon's determination.

*Bioregion:* New Guinea & Melanesia. *Ecoregion:* AA0113 New Caledonia Rain Forest.

*Ecology.* Dense humid rain forest, moss forest or dry montane forests on mountain slopes and by rocky riverbanks; chiefly on ultrabasic rocks but also occurring on gneiss (Mt. Ignambi, Mt. Colnett) and limestone (Mt. Panié); 150–1600 m. The lower altitudinal range was given as 600 m by Farjon (2010), even though de Laubenfels (1972) had cited numerous collections from locations such as Mois de mai that are at much lower altitudes; more recent collections from as low as 150 m in

the Plaine des Lacs area have also been made, and the species descends to near sea level at Baie des Pirogues in the extreme south of Grande Terre. In these low-lying locations, the species grows together with *Retrophyllum minus* and some individuals are very difficult to separate from it. Indeed, it is possible that some plants of *Retrophyllum minus*, including the epitype collection, with female cones maroon-red or greenish red, are in fact fertile hybrids between *R. comptonii* and the lacustrine form of *R. minus*, equivalent to Buchholz's *Podocarpus palustris*, although there is as yet no evidence to support this hypothesis other than their intermediate morphology. Associates of *Retrophyllum comptonii* in its more typical montane forest habitats include other gymnosperm trees such as *Acropyle pancheri* Pilg., *Araucaria humboldtensis* J.Buchholz, *A. laubenfelsii* Corbasson, *A. montana* Brongn. & Gris, *A. muelleri* (Carrière) Brongn. & Gris, *Austrotaxus spicata* Compton, *Falcatifolium taxoides* (Brongn. & Gris) de Laub., *Podocarpus sylvestris* J.Buchholz and various angiosperm trees such as species of *Nothofagus* Blume.

Little or nothing is known about the dispersal of this species. The attractively coloured red ripe female cones suggest an adaptation to dispersal by vertebrates such as birds, as postulated by Farjon (2010), although the flesh has been described as tasteless (*McPherson* 2191 in sched.). Pigeons such as *Ducula goliath* (Gray), the New Caledonian Imperial Pigeon, might act as dispersers, although no fruits of Podocarpaceae were recorded in the diet of that species in one limited study in the months of March and April (Barre *et al.*, 2003).

*Chromosome number*:  $2n = 20$  (Hair & Beuzenberg, 1958, as *Podocarpus comptonii*).

*Phytochemistry*. Cambie *et al.* (1984) recorded the presence of the phenolics totarol and 19-hydroxytotarol in the wood of *Retrophyllum comptonii*. These were the only two phenolic compounds isolated; podocarpic acid and 4 $\beta$ -carboxy-9-nortotarol were both absent, in contrast to their earlier report on *Retrophyllum vitiense* (Cambie *et al.*, 1983).

*Mycological associations*. The ascomycete fungus *Caliciopsis podocarpi* Huguenin was first described from two specimens; the host of the holotype was *Retrophyllum minus* and that of the other collection was *R. comptonii* (Huguenin, 1969: 300). This was the first instance of *Caliciopsis* Peck occurring on *Retrophyllum* or indeed any member of 'Podocarpus sensu lato' (in the sense of Buchholz & Gray, 1948), although the genus was later recorded from *Podocarpus nubigenus* (Butin, 1970).

*IUCN conservation assessment*: LC (Farjon, 2010: 938; Jaffré *et al.*, 2010: 1489; Thomas, 2010a). The species is one of the most widespread of all New Caledonia's conifers, occurring throughout the island.

*Uses*. According to Farjon (2010), the species has been extensively logged, especially at lower altitudes, for its high-quality wood used locally for flooring, furniture and similar purposes.

**4. *Retrophyllum minus*** (Carrière) C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45(2): 380 (22 Feb. 1989 [‘1988’], ‘minor’). – *Nageia minor* Carrière, Traité Gén. Conif. ed. 2, 2: 641 (15 Jan. 1867). – *Podocarpus minor* (Carrière) Parl. in A. DC., Prodr. 16(2): 509 (1868). – *Decussocarpus minor* (Carrière) de Laub., J. Arnold Arbor. 50: 352 (15 Jul. 1969). – Type citation: [New Caledonia] “Habite dans la Nouvelle-Calédonie, au sommet de très-hautes montagnes, où il fut découvert par un jardinier anglais nommé Richard. – D’après M. Vieillard (herbier de la Nouvelle Calédonie no. 1275 – in Herb. Mus. Par.) on le trouve aussi au bord du lac Arnaud.” – Lectotype designated here: New Caledonia, Yaté, “bord du Lac Arnaud”, Vieillard 1275 (P: sheet barcoded P00118110, top left sterile specimen, here designated 110-A: see Appendix I). Isolectotypes (all Vieillard 1275, P): sheet barcoded P00188109, sterile specimens at top centre right here designated 109-C and at bottom right here designated 109-G; sheet barcoded P00188110, unbranched sterile specimen c.26 cm long at right here designated 110-C and shoot in packet with c.9 larger leaves here designated 110-G. Epitype designated here: New Caledonia, “from banks of River des Lacs [sic] at site of former village below mine excavations of Madeliene [sic] mine Plaine des Lacs, 140 m or probably less. Tree 2–3 m high; wood sample with wood yellowish density near 0.5. Seeds maroon red, elongated pear-shaped, larger than coll. made of var. at 22 km Sta.”, 22 ii 1948, J.T. Buchholz 1729 (epi NY, isoepi ILL–n.v. [photos A, P], K, MO–n.v. [fide TROPICOS database], S–database). – For full details of the very difficult and complex typification of this name, see Appendix I.

**Fig. 1L.**

[*Podocarpus minor* (Carrière) Parl. var. *palustris* J.Buchholz, in sched. Buchholz 1421, nom. nud.]. – *Podocarpus palustris* J.Buchholz, Bull. Mus. Natl. Hist. Nat. (Paris) sér. 2, 21: 284 (1949). – Type: New Caledonia, “Small tree growing in water, with stems flaring at base, dark gray bark, brownish beneath. 2–3 m high, some stems 40–50 cm in diameter at water line. Wood white soft of density about 0.3. Trees subject to flooding at times the leaves becoming covered with ferruginous [sic] silt. Seeds smaller than in species coll. on Rio des Lacs”, 27 xi 1947, J. Buchholz 1421 (holo ILL–image barcoded ILL00010021, iso ILL–2 sheets–images barcoded ILL00010019 and ILL00010020, A–photo, K, MO–image (stamped 1712087), NY, P–image barcoded P00188158, RSA–image, S–image, TEX–image barcoded 00370048, WIS–image barcoded 0057120).

*Iconography.* De Laubenfels, Fl. Nouv. Caléd. 4: 51, pl. 11 f. 9–15 (1972), as *Decussocarpus minor*.

*Etymology.* *Retrophyllum minus* was originally described by Carrière (1867) in the genus *Nageia* as *N. minor* Carrière. The other six species that he enumerated in that genus all had leaves measuring 40–160 mm in length, whereas he gave the length of the leaves of *Nageia minor* as 12–17 mm. The epithet *minor* (Latin for ‘smaller’; *minus* when neuter) therefore most probably alludes to the much smaller leaves of *Retrophyllum minus* compared with the leaves of the other six *Nageia* species, although there are no clues in his protologue as to why the epithet was chosen. Although less likely, it might also refer to the smaller stature of *Retrophyllum minus* compared with those six *Nageia* species, for which Carrière only gave actual height details for two. The

epithet has nothing whatever to do with *Retrophyllum minus* being the smallest species in the genus *Retrophyllum*, as stated by Farjon (2010: 938) and implied also by Gray (1962: 76), because, with the exception of *R. vitiense* (1863), of which Carrière was apparently unaware as he gave no treatment of it under any genus, all other species of *Retrophyllum* were first described between 1923 and 1983, long after Carrière described *Nageia minor*. Buchholz's epithet *palustris* alludes to the fact that the species is very frequently aquatic.

*Vernacular name:* *bois bouchon* (Jaffré, 1988; Suprin, 2011a) – French for ‘cork wood’, referring to the very light, corky texture of the wood (an adaptation to its aquatic habitat).

*Distinguishing features.* *Retrophyllum minus* is a low shrub or small tree that is typically aquatic. The adult foliage is all in 4 ranks. The very thick adult leaves have a raised central area that when dried is marked by longitudinal wrinkles or by three (not two) ridges, and is typically wider than the leaf margins, although this is variable and plants with a narrower central area can be confused with *Retrophyllum comptonii* unless other characters are also examined. The seed surface is rough, porous and very buoyant, an adaptation to the aquatic habitat.

Small tree or shrub, frequently aquatic, normally 0.9–3.5 m tall but rarely attaining 8 m; 20–50 cm diam. at water-line. *Trunk* rapidly tapering from a wide, buttressed base, sometimes split from near base. *Bark* rough when old, peeling in short vertical strips or ragged pieces, fissured, dark grey, greyish brown or tan (colour often masked by ferruginous silt); inner bark brownish or reddish-brown; wood cream or whitish, very light. *Crown* open, irregular. *Buds* shortly ovoid to shortly ellipsoid, protected by very reduced foliage leaves; true bud scales absent. *Primary branches* irregularly arranged, divaricate, widely spreading or ascending; foliage branches clustered at tips of branches, erecto-patent to erect, straight, curved or flexuous. *Shoots* dimorphic but appearing mostly monomorphic, with only occasional scale-bearing shoots that soon pass into foliage shoots. *Shoot flattening* heterofacial on juvenile shoots but adult shoots  $\pm$  lacking flattening. *Juvenile foliage shoots* with (1–)2–4 small leaves at base and 17–35 pairs of foliage leaves in 2–3 growth increments. *Juvenile leaves* (3.5–)4.5–6(–7.5) mm apart, opposite, distichous and pectinate, heterofacially turned at base, diverging at (40–)50–60(–70)°, sessile or subsessile, lamina narrowly lanceolate, linear-lanceolate or lanceolate-elliptic, 25–33  $\times$  2.8–4 mm, gradually tapered to a narrow, obtuse tip. *Adult foliage shoots* subtended by 1–3 pairs of very reduced scale-like foliage leaves, the lowest true foliage leaves smaller and relatively broader than the others; leaves opposite-decussate in 4 ranks, crowded, sessile with bases not twisted and all with abaxial surfaces outermost, the upper leaves of each shoot partially imbricate, erecto-patent to erect, either yellow- to mid-green or grey-green; lamina of leaves in middle of shoot narrowly elliptic, elliptic, narrowly lanceolate-elliptic, lanceolate-elliptic or narrowly lanceolate, straight, very thick and coriaceous; margin thickened, extremely narrowly hyaline; midrib not visible on either surface but both surfaces with a raised elliptic central area as wide as or wider than the margins and either longitudinally wrinkled

or marked by three longitudinal lines when dried; apex obtuse, broadly rounded or occasionally subacute; base cuneate or shortly attenuate.

*Pollen cones* lateral (axillary) or terminal on lateral shoots of current growth, subtended by a leaf or scale-leaf, 1–7 together, pedunculate (individual cones sessile when > 1 together); peduncle shorter than cone(s), erecto-patent, bearing 1–3 decussate pairs of spreading scales; peduncle scales green or grey-green, not keeled, ovate or ovate-lanceolate with  $\pm$  long decurrent base and  $\pm$  patent free part, subacute, with or without a narrow scarious margin; cones ellipsoid, ovoid or subglobose, 4–8  $\times$  2–3 mm, straight; *microsporophylls* decussate but appearing spirally arranged, 24–40 per cone, the lamina green,  $\pm$  heavily tinged violet, broadly triangular, deltate or triangular-ovate, abruptly narrowed to an acute, apiculate apex, with extremely narrow whitish hyaline margin, shorter than the microsporangia; *microsporangia* free, pinkish, elliptic or semicircular, stomium longitudinal, abaxial; *pollen* white to hyaline.

*Female cones* terminal on lateral foliage shoots of current growth, shortly pedunculate. *Peduncle* in line with shoot or erecto-patent, shorter than remainder of cone but longer or shorter than receptacle, bearing either 8–10 or 4 bracts in 4–5 or 2 decussate pairs respectively; distal part of peduncle shed with cone. *Peduncle bracts* light green or grey-green, keeled, elliptic, ovate-elliptic or ovate-rhombic, subacute to obtuse. *Cone* subtended by a non-fleshy to slightly fleshy receptacle formed from 1 or 2 peduncle bracts plus the sterile and fertile bracts. *Receptacle* narrowly obovoid, narrowly pyriform, narrowly obconical or cylindrical, light green or greyish-violet. *Sterile bract* normally 1, stiffly spreading to erecto-patent, oblong-elliptic, ovate-elliptic or elliptic, obtuse or subacute, with very narrow scarious margin. *Fertile bract* light green or greyish-violet, initially erect, with median longitudinal groove, wholly free from epimatium, with spreading, ovate free tip with acute apex. *Cone* obovoid (sometimes shortly so), ellipsoid or pyriform; epimatium either green at first, then blushing red and finally maroon-red when ripe, or grey-green and not turning red, with a shortly conical (sometimes indistinct) apical crest; seed beaked at micropylar end, the beak straight or curved. *Seed* with rugulose, porous texture, adapted to floating in water. *Germination* epigeal. *Seedlings*: initial leaves of main axis c.5 pairs, linear, 15–18  $\times$  c.1.5 mm excluding decurrent base, basally not twisted, opposite-decussate in a spiral arrangement, amphistomatic, separated by short, naked internodes, the youngest ones narrowly linear, apiculate and 23–31  $\times$  1.5–2.2 mm, older ones becoming opposite in one plane, linear-elliptic or narrowly elliptic, shorter (11–20  $\times$  1.9–3.0 mm) and bluntly mucronate at tip.

*Taxonomy.* *Retrophyllum minus* is a variable species. Some states, including the type, have ascending branches, leaves yellow- to mid-green when fresh, and female cones initially green turning red or finally maroon, as in *Retrophyllum comptonii*. Other states, including virtually all the aquatic material assigned by Buchholz to *Podocarpus palustris* and collected since, have more widely divaricate or patent branches, leaves grey-green, and female cones that are grey-green or whitish and apparently not turning red when ripe. Such plants also appear to have more microsporophylls per pollen cone

(30–40) compared with plants at the other end of the spectrum of variation, which have only about 25 microsporophylls per cone. The plants with almost white, extremely glaucous ripe female cones are very distinct and easily recognisable in the field as belonging to *Retrophyllum minus*. This is not the case with the state having pinkish-green to red ripe cones, which often shows *Retrophyllum comptonii*-like characteristics. The variation within the species clearly influenced Buchholz to describe one extreme, that with cones not turning red when ripe, as *Podocarpus palustris*. Plants assignable to this and to typical *Retrophyllum minus* often occur together at the same site, however. The two states appear to be very distinct, especially when reproductive organs are present, and the fact that many of the distinguishing features are reproductive rather than vegetative also makes the case for recognising varieties within the species stronger than it might otherwise be. Matters are complicated, however, by the occurrence of low-altitude populations of *Retrophyllum comptonii* sympatrically with *R. minus* in the Plaine des Lacs area, and it is therefore possible that hybridisation may occur. Indeed, as mentioned under *Retrophyllum comptonii*, the morphological characters of ‘typical’ *Retrophyllum minus* (i.e. including its type material) are intermediate between those of *Podocarpus palustris* and *Retrophyllum comptonii*, and a hybrid origin of those populations of *R. minus* agreeing with its type therefore needs testing. For this reason, varieties are not here recognised within the species.

Material from the Port Boisé area (hb. *MacKee* 19303, 19304, 19305) was determined at Paris as both *Decussocarpus minor* and *D. comptonii* by de Laubenfels in 1972. All three sheets seem identical in foliage characters and are more similar to *Retrophyllum comptonii* than they are to *R. minus*. However, plants from the same population were analysed using RAPD by Herbert *et al.* (2002), who found that the Rivière Trou Bleu population, coded by them as RTB, grouped with *Retrophyllum minus*, not *R. comptonii*, using this technique. Hence, all the specimens from this locality are here assigned to *Retrophyllum minus*.

*Distribution.* New Caledonia (Grande Terre, Province Sud: Prony, Baie du Sud, Lac en Huit, Rivière des Lacs, Plaine des Lacs). *Map:* Fig. 6.

In the Rivière des Lacs area *Retrophyllum minus* coexists with plants that are assignable to *Retrophyllum comptonii* and as noted above some plants possess characters intermediate between the two species, suggestive of hybridisation. Most of the area of the two lakes forming Lac en Huit, one of the classic localities for *Retrophyllum minus*, is in Yaté commune, but the southern third of the eastern lake is in Le Mont-Dore, as well as the RM9 road (‘Route de l’Aérodrome’) along the south side of both lakes and all of the CR7 road (‘Route du Déversoir’ – the Nouméa–Yaté main road). Records from this area have therefore been assigned to one or other commune, or an unassignable boundary zone, depending on field notes and their accuracy. The whole of Grand Lac (Lac Arnaud) is in Yaté.

*Specimens seen and other records.* NEW CALEDONIA. Unloc., *Le Rat* 253A (S–database). Unloc., no date, *Petit* 138 (P–image); *Bernier* 245/1 (seedlings; P–image, barcode P00188175); *Bernier* 245/4 (P–image, barcode P00188172); *Aubréville & Heine* 241 (P–image); unloc.,

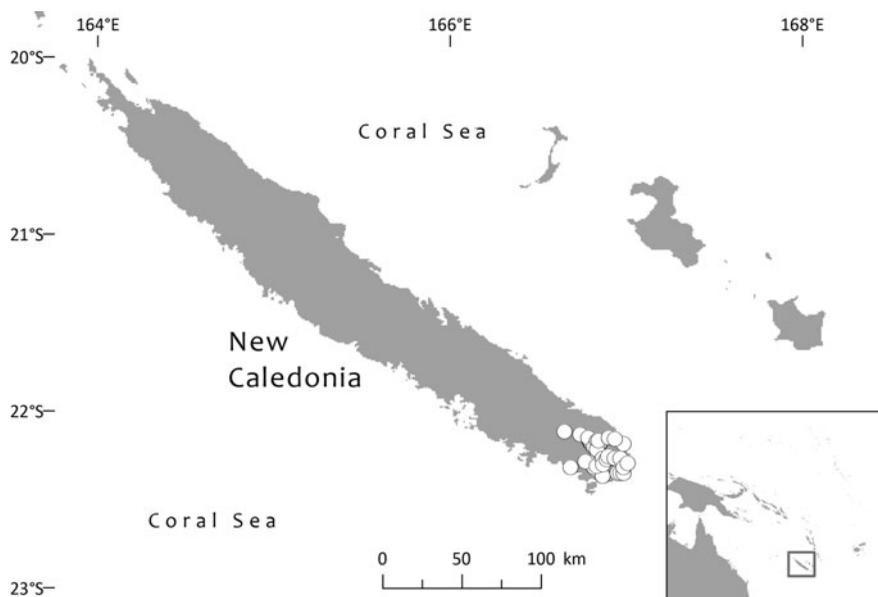


FIG. 6. Global distribution of *Retrophyllum minus*.

1950–1951, *Baumann-Bodenheim* 6378 (P–image, juvenile and adult); unloc., 1861, *Deplanche* 170 (P–image); unloc., 1863, *Deplanche* 170 (P–image, central area of leaf rather narrow and transitional to *R. comptonii* but determined in 1950 as *Podocarpus minor* by Buchholz & Gray; A–photo). Without definite locality, “Hauteur un mètre sur les plateaux couverts du marais fort arides. 8 m sur les flancs escarpées des Montagnes du même sol, fruit rouge,” *Pancher* (*Vieillard* 1275) (BM–also seemingly (re?)numbered *Hance* 17247, K). **Province Sud: Le Mont-Dore:** Baie du Sud, 1861–1867, *Vieillard* 1275 (A, GH, K–2 sheets, P–2 sheets, images and also A–photos). Prony, without date, *Franc* 207 (BM [photo A], GH, K: note discrepancy in numbering and dating of other sheets, see below). Bords d’un torrent situé au fond de la Baie de Prony, ix 1868, *Balansa* 186 (2 sheets, P–images). Prony, Baie de Kué, 3 m, x 1903, *Cribs* 1493 (P–image, K–database); Prony, *Le Rat* 149 (P–image). Prony, x 1913, *Franc* 207 (P–image); *ibid.*, x 1913, *Franc* 207 (Série A) (2 sheets, P–images); *ibid.*, i 1914, *Franc* 207 (A); Prony, undated, *Franc* 207 (Série A) (A); Prony, 100 m, *Pancher* s.n. (P–image: label bears manuscript names ‘*Podocarpus nana* Parl.’, ‘*Dacrydium austrocaledonicum* Vieillard’ and ‘*Podocarpus Guillainii* Vieillard’, as well as the inscription “C’est la même plant que *Vieillard* 1275”, the first five words of which are in different handwriting to the rest of the label, which also gives locality information for specimens collected at Cougui 800 m and Mt. Mou 1200 m that are, from the altitudes, assignable to *Retrophyllum comptonii*). Prony, where road crosses the Rivière Bleue, very close to the river margin, 50 m, 22°18′35″S 166°49′55″E, 28 iii 1999, *Cretinon & Gardner*, *ICCP New Caledonia Exped.* 1999: 17 (E). Rivière des Pirogues, 31 x 1923, *White* 2261 (E, K, P–image). Le Carénage, just above sea, 8 iv 1955, *MacKee* 2373 (E, L–image, P–image); c.5 miles from Baie du Carénage, on road between Baie du Carénage and highway from Nouméa to Yaté, 600 ft [183 m], 22 vii 1952, *McMillan* 5139 (A, E, K, L–image, P–image). Port Boisé, embouchure du Port Boisé, vallée de Koué, 100 m, 28 ii 1976, *Viratelle* (hb. *MacKee* 32355) (P–image). Port Boisé, embouchure du ruisseau Trou Bleu, 20 viii 1968, *Lavoix* (hb. *MacKee* 19303 & 19304, both det. de Laubenfels as *Decussocarpus minor*) (P–images, 19303 also

NOU–database, 19304 also K–database); *ibid.*, *Lavoix* (hb. *MacKee* 19305, det. as *D. comptonii* or *R. comptonii*) (P–image, K–database, NOU–database). Port Boisé, Rivière Trou Bleue, *Cretinon & Gardner, ICCP New Caledonia Exped. 1999*: 50 (E; also specimen collected 25 iv 2001 from E cultivated accession 19990384C, E); *ibid.*, 1 iii 1999, *Cretinon & Gardner, ICCP New Caledonia Exped. 1999*: 50A (E, seedling). Lac en Huit [22°16'S 166°52'E], 7 x 1957, *de Laubenfels* P115 (SBT–n.v., *fide* de Laubenfels, 1969: 345; S–database); *ibid.*, 19 v 1977, *Musselman* 5280 (NOU–database). Rivière Bleue, route de Prony [22°17'S 166°46'E], xi 2007, *Munzinger* 4830 (NOU–database). **Le Mont-Dore / Yaté boundary**: Plaine des Lacs, 22°14'–22°16'S 166°50'–166°57'E, ad ripam lacus “en 8” (Lac en Huit) dicti, 250 m, 3 vii 1965, *Bernardi* 9369 (L–image, P–image, Z–database); along banks of La Madeleine (Rivière des Lacs), S of Nouméa–Yaté road, edge of Lac en Huit, c.250 m, 30 viii 1980, *McPherson* 2996 (P–image); Lac en Huit, 150 m, 15 xi 1955, *MacKee* 3382 (A, L–image, P–image). **Yaté**: Bords du lac Arnaud, 1855–1860, *Vieillard* 1275 p.p. (lectotype and isolectotypes as specified above and in Appendix I, P–images); *ibid.*, *Vieillard* 1275 p.p. (non-lectotype material as specified in Appendix I, P–image). Grand Lac (Plaine des Lacs), 250 m, 30 iii 1942, *Viroit* 658 (A, P–2 sheets, images); western margin of Grand Lac, 22°15'52''S 166°54'30''E, 250 m, 1 iii 1999, *Cretinon & Gardner, ICCP New Caledonia Exped. 1999*: 44 (E). Plaine des Lacs, Lac en Huit, au niveau du déversoir (berge du lac), 250 m, 8 i 1987, *Jérémie & Tirel* 1572 (P–image). Lac en Huit, 22°16'16.0''S 166°53'13.5''E, 256 m, 24 xi 2005, *Gardner et al.* 02 (E). Lac en Huit, northern shore-line of second lake, 22°15'20.3''S 166°53'51''E, 241 m, 24 xi 2005, *Gardner et al.* 04 (E). Plaine des Lacs, prior to 19 xii 1889 (date of receipt at P), *Raoul* s.n. (P–image); Plaine des Lacs, *Le Rat* 607 (BM and photo of this sheet A; P–image), 751 (P–image), 1040 (P–image); Bord des rivières de la Plaine des Lacs, ix 1905, *Le Rat* 2587 (P–image). Plaine des Lacs, bords de la rivière Pouéné, ix 1905, *Le Rat* 2621 (2 sheets, P–images, one without locality information). Plaine des Lacs, 22 km [station], c.750 m, viii 1947, *Bernier* 204 (P–image); 22 km station, 31 x 1947, *Bernier* 245/3 (female, P–image, barcode P00188173); Plaine des Lacs, 22 km Station, 4 xi 1947, *Buchholz* 1347 (paratypes of *Podocarpus palustris* ILL, 2 sheets (ILL00010017 and ILL00010018)–images, isoparatypes of *Podocarpus palustris* K, NY, P–image, RSA–image, S–database; photo of trees in situ, A); *ibid.*, same date, *Buchholz* 1348 (paratype of *Podocarpus palustris* ILL–image (ILL00010016), isoparatypes of *Podocarpus palustris* GOET–image, K, NY, P–image, RSA–image, S–database, WIS–image); *ibid.*, 22 xi 1947, *Buchholz* 1421 (holotype of *Podocarpus palustris* ILL–image (ILL00010021), isotypes of *Podocarpus palustris* ILL–images (ILL00010019, ILL00010020), K, MO–image, NY, P–image, RSA–image, S–image, TEX–image; photo of seeds, A); *Buchholz* 1474 (paratypes of *Podocarpus palustris* ILL–2 sheets (ILL00010015 and ILL00010022)–images [photo of latter specimen at A], isoparatype of *Podocarpus palustris* S–database (photo)); *ibid.*, 14 ii 1948, *Buchholz* 1705 (K, seedling, P–image, 2 seedlings; S–database). Guépyville, radier du 22 km, 150 m, 27 v 1948, *Bernier* 251 (P–image, K–database). Route de Yaté, km 22, viii 1949, *Sarlin* 73 (P–image). Route Bon Secour, 22 km ck., R[ivière] Blanche, 200 m, 19 vii 1954, *Ingle* I.44 (L–image, MEL–n.v.). 22 km station, 10 vii 1957, *de Laubenfels* P112 (SBT–n.v., *fide* de Laubenfels, 1969: 347; S–database). Plaine des Lacs, Mine Madeleine, 140 m or less, 22 ii 1948, *Buchholz* 1729 (epitype NY, designated here; isoepitype ILL–n.v. [photos A, P; A example with somewhat different text on label from others], K, MO–n.v. [*fide* TROPICOS], S–database). Plaine des Lacs, on road from Nouméa to Yaté, 10 vii 1956, “this specimen is from same tree as that from which Buchholz obtained his type”, *Foster* 200 (topotype of *Podocarpus palustris*, P–image). Plaine des Lacs, village Anna Madeleine, delta du *Dacrydium* n.sp., 230 m, 7 iii 1948, *Bernier* 246 (P–image); *ibid.*, juvenile, 7 iii 1948, *Bernier* s.n. (P–image); *ibid.*, 6 vi 1948, *Bernier* 249 (P–image, K–database, Z–database). Madeleine, Plaine des Lacs, 30 iii 1951, *Guillaumin & Baumann-Bodenheim* 11749 (P–image, Z–database); *ibid.*, 30 iii 1951, *Guillaumin & Baumann-Bodenheim* 11811 (P–image, Z–database). Plaine des Lacs, Rivière des Lacs, la Chute, 239 m, 13 iii 1964, *Stauffer & Blanchon* 5807 (L–image, P–image, K–database, NOU–database, Z–database);

Plaine des Lacs – Bords du lac de Yaté (sous ligne haute tension après riv. Madeleine) – la Chute, 13 iii 1964, *Blanchon* 736 (P–image, NOU–database). Along banks of La Madeleine (Rivière des Lacs), S of Nouméa–Yaté road, near bridge, 23 xi 1979, *McPherson* 2132 (P–image, K–database, NOU–database); *ibid.*, beside Chute de la Madeleine [22°13'S 166°50'E], 29 v 1980, *McPherson* 2748 (P–image, NOU–database); riverbanks below Chutes de la Madeleine, 10 viii 1981, *Stone* 14836 (P–image). Rivière des Lacs (rive droite) 5 km en Aval de la Chute, 200 m, 29 vi 1986, *MacKee* 43169 (CANB–database, P–image, K–database, NOU–database, Z–database). Forêt “Mois de mai”, Riv. blanche, 22 vii 1951, *Baumann-Bodenheim* 13923 (P–image, Z–database). Serpentine area, Rivière Blanche c.30 miles E of Nouméa on road to Yaté, Plaine des Lacs, 600 ft [183 m], 21 vii 1952, *McMillan* 5120 (A, E, L–image, P–image, K–database). Ex-radier Anna-Mad.[eleine] (locality given on composite label on sheet 245/4), *Bernier* 245/2 (male; P–image, P00188174). Plaine des Lacs, Anna Madeleine, 150 m, 22 i 1967, *Aymard* (hb. *MacKee* 16325) (P–image). Anna-Madeleine, rivière [22°09'S 166°54'E], 100 m, 23 xi 1979, *Hartley* 15064 (CANB–database, L–image, NOU–database). La Madeleine, 8 xii 1981, *Dickison* 223 (NOU–database). Rivière des Lacs (La Madeleine) en amont des chutes, 20 ix 2007, *Dagostini et al.* 1340 (P–image, NOU–database); Trois Bras [22°09'S 166°54'E, c.320 m], 18 ix 1980, *Suprin* 693 (NOU–database). Near bridge over ‘River des Lacs’ [sic] on road to Yaté, 21–22 ii 1948, *Buchholz* 1719 (P–image, packet only, its contents not visible; seeds similar to *Buchholz* 1729, *fide* label); Plaine des Lacs, Campement 22, 5 vii 1949, *Selling* 78 (S–database); Plaine des Lacs, i 1914, *Franc* 207 (Z–database: specimens seen of this number have all been from a different locality, Prony); Plaine des Lacs, Rivière des Lacs, 6 x 1924, *Däniker* 228 (Z–database); *ibid.*, 11 x 1924, *Däniker* 228 (P–image, Z–database); Plaine des Lacs, 8 ii 1926, *Däniker* 228a (Z–database); Plaine des Lacs, Rivière des Lacs, Plaine des Lacs, rades de la Rivière des Lacs, c.100 m, 6 vi 1948, *Bernier* 250 (P–image); Plaine des Lacs, c.250 m, 14 xii 1949, *MacDaniels* 2544 (GH); Vallée des Lacs, 5 x 1950, *Guillaumin & Baumann-Bodenheim* 6511 (Z–database, 2 sheets); *ibid.*, pont, 3 x 1950, *Guillaumin & Baumann-Bodenheim* 6580 (P–image, Z–database, 2 sheets); *ibid.*, 5 x 1950, *Guillaumin & Baumann-Bodenheim* 6582 (P–image, juvenile; Z–database); *ibid.*, 5 x 1950, *Guillaumin & Baumann-Bodenheim* 6594 (P–image; Z–database, 2 sheets); *ibid.*, 7 x 1950, *Guillaumin & Baumann-Bodenheim* 6766 (P–image, Z–database). Rivière des lacs, route de Yaté, c.100 m, *Bernier* 245/2 (P–image). Plaine des Lacs, route de Yaté, near new bridge over Madeleine River, 5 xi 1959, *Thorne* 28565 (L–image, P–image). Bassin de la Rivière Yaté, Laverie Lafleur du 22ème km, 19 viii 1957, *Service des Eaux et Forêts, Nouméa* 225 (S–database); au bord de la Rivière des Lacs, au S du pont, 150 m, 9 vii 1958, *Hürlimann* 3113 (Z–database); Rivière des Lacs, 22°10'50"S 166°50'56"E, 200 m, 1 iii 1999, *Cretinon & Gardner, ICCP New Caledonia Expedition 1999*: 26 (E). Plaine des Lacs, bords de la Riv. à Chute, 25 vi 1963, *Blanchon* 208 (P–image, NOU–database); Plaine des Lacs, 29 vi 1965, *Aubrèville & Heine* 130 (P–image); Tournée des Lacs, 3 vii 1965, *Aubrèville & Heine* 170 (P–image). Süd-Bai, zwischen der Bai N'Go und Touaourou, viii–xii 1903, *Rohrdorf* 178 (Z–database); Touaourou, 350 m, x 1903, *Cribs* 1752 (P–image; highest altitude known for this species). Vallée de Toémo (entre Goro et Port-Boisé), 30 m, 4 v 1990, *Cherrier* (hb. *MacKee* 44895) (P–image, NOU–database as *Retrophyllum comptonii*). Bord de la Kuébini, 14 ii 1984, *Lauri & Gay* 165 (P–image, NOU–database). Rivière des Kaoris, Baie des Requins, 30 m, 7 iii 1948, *Bernier* 247 (P–image). Cascade de N'Goro, 50 m, 7 v 1948, *Bernier* 248 (2 sheets, P–images). Marais Kiki, 28 ix 1950, *Baumann-Bodenheim* 6370 (Z–database, 2 sheets); Marais Kiki, Plaine des Lacs, 150 m, 22 x 1954, *MacKee* 1118 (A, E); *ibid.*, *MacKee* 1119 (E, P–image); bassin de la Rivière Yaté, Marais “Kiki”, 19 viii 1957, *Service des Eaux & Forêts, Nouméa* 226 (S–database, spirit coll.); au bord du Marais Kiki, 148 m, 17 vii 1958, *Hürlimann* 3157 (Z–database). Near forks of Yaté river, 3 xii 1957, *de Laubenfels* P160 (SBT–s.n., *fide* de Laubenfels, 1969: 347; S–database). Along Riv. des Lacs near beginning of Route du Carénage, 22°10'S 166°50'E, 150 m, 11 xii 1973, *Webster* 19205 (GH, P–image, NOU–database). Carénage – Creek Pernod [22°12'S 166°49'E, c.190 m], 1 xii 1964, *Blanchon* 1160

(P–image, NOU–database). Plaine des Lacs, Crique Pernod, 16 xi 1950, *Guillaumin* 8339 (P–image, S–database, Z–database); *ibid.*, 16 xi 1950, *Guillaumin* 8345 (P–image, Z–database). Plaine des Lacs–Carénage road at crossing of Creek Pernod, 200 m, 15 xi 1955, *MacKee* 3377 (A, L–image, P–image; E, dated 15 xi 1953). Rivière des Lacs, near the junction with the Pernod Rau., c.160–170 m, 24 ix 1963, *Green* 1187 (A, P–image, K–database); Creek Pernod [22°12'S 166°49'E], 15 i 1970, *Jaffré* 352 (P–image, NOU–database); along road to Plaine des Lacs, at crossing of Creek Pernod, 22°11'01''S 166°50'39''E, 5 xii 1996, *Lowry II et al.* 4683 (MO–database, P–image, mis-determined as *Decussocarpus comptonii*); Pernod Creek, 4 xi 1984, *Page* 22031 (E = no. 22032 at ORSTOM); *ibid.*, *Page* 22034 (E = no. 22032 at ORSTOM: some larger leaves lanceolate); *ibid.*, *Page* 22033 (E); *ibid.*, *Page* 22030 (E). Rivière des Lacs, 100 m before the fork in the river which divides into Creek Pernod, 22°10'45''S 166°50'50''E, 130 m, 29 xi 2002, *Gardner et al.*, *Third New Caledonia Araucaria Exped.* TNCA 5000 (E); *ibid.*, *Gardner et al.*, *Third New Caledonia Araucaria Exped.* TNCA 5001 (E). Lake Suprin, 22°17.247'S 166°59.504'E, 238 m (Hope, 2015); Lake Boulet, 22°16.973'S 166°58.587'E, 222 m (Hope, 2015).

USA (CULTIVATED). **Florida: Miami:** Montgomery Botanical Center (Coral Gables), cultivated in nursery, 20 xii 2009, *J. Silba* B-654 (NY–image).

*Bioregion:* New Guinea & Melanesia. *Ecoregion:* AA0113 New Caledonia Rain Forest.

*Ecology.* *Retrophyllum minus* as delimited here, and by de Laubenfels (1972), is exclusively a low-altitude species. It grows along lake and shallow river margins in areas subject to seasonal flooding, from near sea level up to 350 m but typically below 170(–250) m, very often as a swamp tree. The observation in the protologue, “Habite dans la Nouvelle-Calédonie, au sommet de très-hautes montagnes...” presumably applies to material of *Retrophyllum comptonii*, which does inhabit mountain summit habitats as well as lowlands. Before the separation of *Podocarpus comptonii* from *P. minor* by Buchholz (1949), the name *Podocarpus minor* was applied indiscriminately to New Caledonian plants of *Retrophyllum* from both lowland swamps and high mountains. *Retrophyllum minus* grows in single-species stands or with other tall shrubs, such as *Dacrydium araucarioides* Brongn. & Gris. *Retrophyllum comptonii* also occurs at some localities, especially in the Plaine des Lacs. Plants from lowland swamp habitats (true *Podocarpus minor*, = *Retrophyllum minus*) were often given the informal designation “type lacustre”, especially on labels of specimens collected by Bernier, while plants later segregated as *Podocarpus comptonii* (= *Retrophyllum comptonii*) were labelled “type sylvestre”. This species has been regarded as a rheophyte by van Steenis (1981: 168), and its seeds float, aided by their porous epimatium (Carlquist, 1974: 223). Jaffré (1988) described an association in which the two dominant species were *Retrophyllum minus* and *Dacrydium guillauminii* J.Buchholz, which are otherwise two of the rarest plant species of New Caledonia. *Retrophyllum minus* was, according to Jaffré (1988), found on unstable soil in small coves in the 1- to 5-m-wide alluvial zone along the riverbanks. Other associates include *Cloezia aquarum* (Guillaumin) J.W.Dawson, *Homalium kanaliense* Briq., *Melaleuca brongniartii* F.Muell., *Neocallitropsis pancheri* (Carrière) de Laub., *Pancheria communis* Baker f. and *Xanthostemon aurantiacus* Schltr. Fruiting periods of *Retrophyllum minus* tend to coincide with periods of high water levels (Cornu *et al.*, 2001).

Analysis of late Quaternary sediment cores from Lac Xere Wapo in the eastern Plaine des Lacs region has revealed the presence of *Retrophyllum minus* pollen and wood as far back as 120,000 years ago, but that there have been some marked fluctuations in abundance; the species was abundant in the earliest zone, XW-4 (120,000–90,000 years ago), but there was an abrupt rise and fall in abundance in zone XW-3 (90,000–80,000 years ago) and a dramatic decline in zone XW-2 (80,000–45,000 years ago) that is countered by a rise in *Araucaria* pollen. In the most recent zone (XW-1, 45,000 years ago to present), *Retrophyllum* again becomes one of the dominant species but *Dacrydium* is the most dominant (Stevenson & Hope, 2005).

*Chromosome number*:  $2n = 20$  (Hair & Beuzenberg, 1958, two separate counts as *Podocarpus minor* and *P. palustris*).

*Mycological associations*. See under *Retrophyllum comptonii*.

*Conservation status*: EN B1ab(iii,v)+2ab(iii,v); C2a(i) (Thomas, 2010b). At the Madeleine site, which has been subjected to much trampling by the public, who have used the rare trees as diving platforms (Province Sud, 2012), there has been extensive planting since 1999 of *Retrophyllum minus* (1200 trees: Province Sud, 2012) and other rare gymnosperms, such as its associates *Dacrydium guillauminii* and *Neocallitropsis pancheri*. Germination success of *Retrophyllum minus* there has been very good (Cornu *et al.*, 2001; Province Sud, 2012).

*Uses*. No uses of *Retrophyllum minus* are reported in recent literature. Sebert (1874), however, commented that, among the New Caledonian Podocarpaceae, *Podocarpus minor* was “l’espèce la plus intéressante sous le rapport industriel”; this opinion of course also embraced *Retrophyllum comptonii*, which at that time was included in a broad concept of *Podocarpus minor* as previously stated.

**Group C.** Bark exfoliating as large plates. Vegetative shoots monomorphic. Terminal buds naked. Adult leaves distichous and heterofacially flattened in 2 ranks, relatively thin. Resin canals (1)3(5) median plus 2–6 lateral ones round leaf margin. Pollen cones in racemose inflorescences subtended by leaves, the raceme branches opposite, individual cones  $\pm$  pedicellate, subtended by leaf-like bracts; microsporophylls spirally arranged, lanceolate. Female cones borne on specialised lateral reproductive shoots, sylleptic; peduncle broadened distally, in its vegetative portion bearing small spreading bracts that may or may not resemble reduced leaves; cone axis with 6–8 sterile bracts below fertile bract. Fertile bract with its basal half firmly adnate to epimatium, navicular. Receptacle formed from fertile bract and last sterile bract, cylindrical. Seed not beaked at micropylar end. Germination hypogeal. Seedling phyllotaxis spiral. – South America.

**5. *Retrophyllum rospigliosii*** (Pilg.) C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 380 (22 Feb. 1989 [‘1988’]). – *Podocarpus rospigliosii* Pilg., Notizbl. Bot. Gart. Berlin 8: 273 (1 Feb. 1923). – *Decussocarpus rospigliosii* (Pilg.) de Laub., J. Arnold Arbor. 50:

347 (15 Jul. 1969). – *Nageia rospigliosii* (Pilg.) de Laub., *Blumea* 32(1): 211 (3 Feb. 1987). – Type: Peru, Oxapampa, *N. Esposto* 556 (holo B–extant, images seen; photos of holo at A, F [negative #11579, and a second duplicate photo of the B holotype mounted on a herbarium sheet], GH, NY); iso S (2 sheets: SBT W 430–image, S–Regnell 7799–image, both fragments ex Berlin) and S spirit collection–database). Farjon (2010: 941) indicated that the holotype was at USM (Universidad Nacional Mayor de San Marcos, Peru) but, if there is a duplicate there, it is highly improbable that Pilger saw it and, if it exists, it will be another isotype. **Figs 1C, F, J, M, 7A–H, 9D, E.**

?*Torreyia bogotensis* [Linden, Cat. n. 25 (1870) et ex Thurb. in Bull. Torrey Bot. Club 1: 7 (1870) nom. inval.]; Linden ex K. Koch, *Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* 14(25): 199 (1871), nom. utique rej. (Mill, 2010; Brummitt, 2011: 1207). – Type not indicated.

*Podocarpus montanus* sensu Knuth in Fedde, *Repert. Spec. Nov. Regni Veg. Beih.* 43: 95 (1926) non (Humb. & Bonpl. ex Willd.) Lodd. (1836).

*Etymology.* *Podocarpus rospigliosii* is named after Dr Carlos Rospigliosi Vigil, who led the first expedition sent out in May 1918 by the newly founded Museo de Historia Natural in Lima, of which Rospigliosi was the inaugural director, and in which both Nicolás Esposto (collector of the type of *P. rospigliosii*) and Rospigliosi participated. In 1922, Rospigliosi sent specimens of *Podocarpus rospigliosii* to Pilger in Berlin, who described it as new some months later.

*Vernacular names:* *pino*, *pino hayuelo*, *pino de montaña*, *pino colombiano* (Colombia: Villamizar & Suevara 63, UDBC), *pino hembra* (Colombia, Santander: Cardenas & Oliveros 198, COL–database), *chaquiro crespo* and *chaquiro colorado* (Colombia: Vásquez Correa, 2010), *pino negro* (Colombia: Villamizar & Suevara 63, UDBC), *diablo fuerte* (Cajamarca, Peru: Vicuña-Miñano & León, 2003), *pino romerón*, *pino silvestre* (throughout Colombia); *pino de Pacho* (Cundinamarca, Colombia); *romerillo macho* (Becerra-Montalvo & Zevallos-Pollito, 2014), *romerillo blanco*, *diablo fuerte*, *alcumano*, *ulcumano*, *utcumanu* (NW Peru: Vicuña-Miñano & León, 2003; Vicuña-Miñano, 2005), *pino criollo* (Mérida, Venezuela: Aranguren & Márquez, 2011). Some of the above, such as *diablo fuerte* and *ulcumano*, are shared with other species of Podocarpaceae.

*Distinguishing features.* *Retrophyllum rospigliosii* is distinguishable from the only other currently known South American species of its genus, *R. piresii*, by its more lanceolate leaves that are acute to shortly acuminate and frequently abruptly narrowed just below the tip, and by its more shortly ellipsoid to subglobose female cones that are narrowed at the base. The foliage shoots are at all stages arranged  $\pm$  alternately, whereas in *Retrophyllum piresii* the adult shoots (the only state known) are opposite. The peduncle of the female cone bears reduced leaves, not scales as in *Retrophyllum piresii*. Several of these characters were not noted when the original description of *Retrophyllum piresii* was drawn up and serve as additional justification for the recognition of two separate species. Eckenwalder (2009), however, reduced *Retrophyllum piresii* to synonymy within

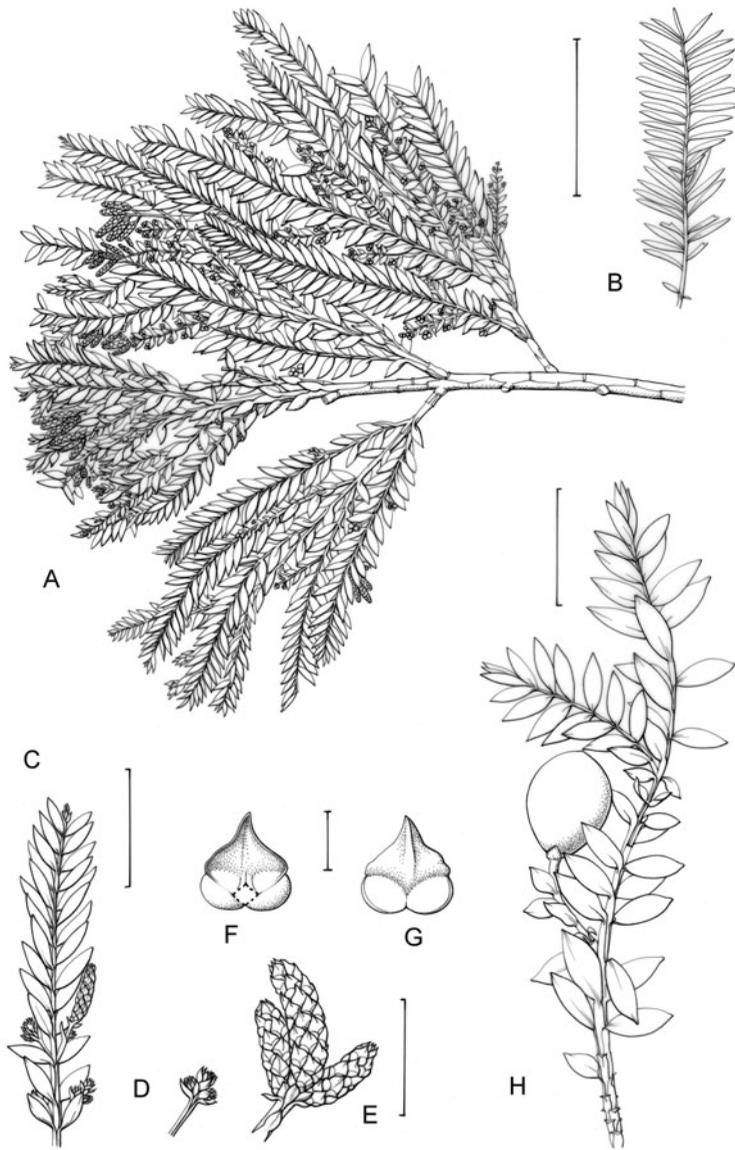


FIG. 7. *Retrophyllum rospigliosii*. A, Branching arrangement (Pennington 1433). B, Juvenile foliage shoot (Roldán *et al.* 3168). C, Adult male shoot (Pennington 1433). D, Young male cones (Pennington 1433). E, Mature male cone (Pennington 1433). F, Microsporophyll and microsporangia, adaxial view (Carr 15666). G, Microsporophyll and microsporangia, abaxial view (Pennington 1433). H, Adult female branch (Bunting 4939). Magnifications: A, B,  $\times 0.67$ ; C, H,  $\times 1.5$ ; D, E,  $\times 3$ ; F, G,  $\times 15$ . Scale bars: A, B, 6 cm; C, H, 2 cm; D, E, 1 cm; F, G, 1 mm. Drawn by Claire Banks.

*R. rospigliosii* on the grounds that, in his opinion, the specimen known to him fell within the range of variation of the latter species. *Retrophyllum rospigliosii* can be distinguished from the Fijian *R. vitiense* and the New Guinea *R. filicifolium* (the only other species in the genus that have all leaves not imbricate) by its bark exfoliating in large plates (not small pieces), the naked buds (in *R. vitiense* and *R. filicifolium* protected by bud scales), the foliage shoots lacking scale leaves, the blade of the microsporophyll longer than the microsporangia (not equalling or shorter than them), the more acute female cone peduncle bracts that lack even a narrow scarious margin, the much more pronounced zigzag arrangement of the decurrent leaf bases (which in fresh material are bright green and contrast strongly with the brownish colour of the rest of the branchlet) and the ellipsoid to subglobose (not obovoid) female cones. *Pumnopitys montana* (Humb. & Bonpl. ex Willd.) de Laub., which has in the past been confused at least once with *Retrophyllum rospigliosii* (Knuth, 1926: see synonymy), has spirally arranged leaves that appear alternate-distichous and the shoot flattening is homofacial, not heterofacial, so that the leaves along both sides of the shoots are turned with their abaxial surfaces uppermost; the laminas are also almost all obovate, rather than lanceolate as in *R. rospigliosii*.

Evergreen tree 20–45 m; dbh to 250 cm (Vicuña-Miñano & León, 2003). *Trunk* of mature trees buttressed at base, unbranched for up to 28 m although branching in young trees begins at c.3 m. *Bark* of trunk smooth, bluish-black, exfoliating in large plates; wood reddish-yellow. *Crown* ovoid or umbrella-shaped, much branched. *Branchlets* of last two orders erecto-patent, straight or slightly curved; ultimate branchlets usually alternate, adult ones 25–140(–210) mm with 5–32(–50) pairs of leaves, juvenile ones up to 270 mm (perhaps more) with up to at least 40 pairs of leaves. *Leaf scars* absent. *Buds* naked. *Leaves* on last two orders of branching all of one type (scale leaves absent). Leaves on penultimate axes soon caducous except when subtending branch bases or when branch does not develop further branching, arranged in 2 stepped opposite-distichous parallel ranks; decurrent bases crossing over to opposite side of branchlet and forming a green zigzag pattern that contrasts strongly with the dark brown bark when fresh; lamina larger than those of ultimate shoots, ± ovate-elliptic. *Juvenile leaves* of ultimate shoots unequally amphistomatic, 4–5 mm apart, opposite-distichous, pectinate, subsessile; lamina horizontally spreading, mid to deep green, narrowly lanceolate or lanceolate, 15–23 × 3–6 mm, straight, coriaceous, initially dorsally keeled when unfolding but both surfaces becoming flat, with vein-like striae between rows of stomata, midrib slightly raised on both surfaces, apex subacute or obtuse, base obtuse. *Adult leaves* equally or unequally amphistomatic, 3–5 mm apart throughout on most foliage shoots but up to 10 mm apart on leader shoots and sometimes in lower 1/3 of foliage shoots, opposite-distichous, pectinate, not imbricate, subsessile (free part of petiole 0.3–0.5 mm); lamina spreading and forming a shallow ‘V’ along branch, erecto-patent, diverging at 45–60(–70)°, mid to deep green, elliptic, lanceolate, ovate, ovate-elliptic, obovate-elliptic or obovate, 7–14 × 3–5 mm, straight, thinly coriaceous, the margin only slightly thickened, both surfaces flat with vein-like striae alternating with the stomatal rows, midrib only slightly

raised but distinct on both surfaces, the blade frequently (but not always) abruptly narrowed distally below the acute or shortly blunt-acuminate apex that is never mucronate, the base obtuse or cuneate, the petiole decurrent along the whole length of the internode.

*Pollen cones* subtended by a foliage leaf, lateral in leaf axils of current growth, solitary or in groups or primary clusters of up to 3, often with an opposite pair of cones below; common peduncle present when cones in clusters but otherwise absent, individual cones shortly pedicellate and subtended by a pair of bracteoles; *peduncle* (when present) with 4–6 decussate, ovate, acute scales; *cones* greenish brown when young turning pinkish brown, ovoid when young becoming cylindrical, straight or curved from base, 8–12 mm when shedding pollen; *microsporophylls* 28–36, decussate in 7–9 whorls of 4, lamina longer than microsporangia, triangular-lanceolate, narrowly lanceolate or lanceolate, with entire or finely crenulate whitish hyaline scarious margin, the apex acute and incurved; *microsporangia* reniform; *pollen* snow-white or cream.

*Female cones* borne on current year's growth, terminal on specialised lateral reproductive shoots bearing reduced, ovate, acute leaves. *Peduncle* deflexed-patent to pendulous, its lower portion bearing 1 or 2 pairs of ovate-elliptic, leaf-like peduncle bracts and passing into the cone axis which bears 3 or 4 pairs of decussate, elliptic to obovate leaf-like sterile bracts (sometimes with interspersed small scales) with acute apex and glaucous on adaxial surfaces; apical part of cone axis (above last pair of sterile bracts) forming an indistinct cylindrical receptacle that becomes violet when ripe and is often shed with the cone together with the fertile bract. *Fertile bract* initially erect, with its basal part adnate to epimatium, distal part navicular and free. *Female cone* shortly ellipsoid to subglobose, 16–30 × 12–18 mm (the seed proper c.15 × 11 mm); *epimatium* violet and ± glaucous especially when not fully ripe, somewhat asymmetrical with the adaxial side rather more convex than the abaxial, with a narrowed base and very short conical distal crest that sometimes breaks off and with a straight, conical beak at micropylar end; micropylar beak with two short prongs that point slightly obliquely (towards the abaxial side) downwards towards the last sterile bract; cone resiniferous within; seed proper rounded at the distal end, narrowed to a conical spine at the micropylar end.

*Germination* apparently hypogeal (first foliage shoot emerging at soil level, cotyledons not visible). *Seedlings* with alternate-spiral phyllotaxis, the main axis with relatively long internodes and rather widely spaced, alternate-spiral leaves similar to those of the foliage shoots; foliage shoots with 12–25 pairs of leaves (the lower ones with fewer pairs than the upper), the leaves in 4 ranks (2 sets of 2) that are flattened distichously to form a shallow 'V' along the shoot with the largest leaves near the middle of the shoot.

*Notes.* Adult foliage shoot length (and consequently number of leaves) is very variable, being dependent at least partly on position on the tree and reproductive condition; individual ultimate foliage shoots in the upper or fertile regions of the tree are much shorter than those lower down (which also have longer leaves than those higher up). *Neill & Salinas* 7202 and *Morales et al.* 867, both from Ecuador, are atypical in having

adult foliage leaves diverging from the axis mostly at angles greater than 65°, with many almost at a right angle especially in the former specimen. The adult foliage shoots of *Neill & Salinas* 7202 are also unusually long (to > 20 cm, with up to 50 pairs of leaves), whereas those of *Morales et al.* 867 are much shorter. The habitat and altitude (tropical forest at 600–675 m) of these two gatherings are also atypical for *Retrophyllum rospigliosii*. The habitat and foliage angle of both specimens are more characteristic of *Retrophyllum piresii*, which has not been recorded from Ecuador. However, *Neill & Salinas* 7202 has the alternate branching and lanceolate, acute leaves that are typical of *Retrophyllum rospigliosii* and consequently it is assumed to be a slightly divergent form of that species. In *Morales et al.* 867 most branches are opposite as in *Retrophyllum piresii*, but a few are alternate. Another specimen [PERU. **Puno**: Río Candamo, fila at mouth of Río Guacamayo, ridge top forest with cloud forest aspects, 13°30'S 69°50'W, 870 m, 28 v 1992, *Gentry et al.* 77310 (MO)] is also problematic. It is again from a rather low altitude for *Retrophyllum rospigliosii*, and the branches are opposite as in *R. piresii*. Unfortunately, it is sterile so it is not known whether it would have the distinctive long ellipsoid female cones that are so characteristic of *Retrophyllum piresii*. It was determined as the latter species [on the field label, as *Nageia piresii* (Silba) de Laub.] by de Laubenfels in 1994, which remains the current determination, but its true status remains uncertain.

*Distribution.* Northern and Western South America. W Venezuela (Táchira, Mérida, Trujillo), E Colombia (Antioquia, Cundinamarca, Magdalena, Norte de Santander, Santander del Sur), Ecuador (Napo, one collection; also see Jørgensen & León-Jáñez, 1999), NW & C Peru (Gray & Buchholz, 1948: 120; Torres-Romero, 1988; Brako & Zarucchi, 1993: 2; Vicuña-Miñano, 2005: 286), NE Bolivia (Dpto. La Paz: Prov. Bautista Saavedra and Prov. Franz Tamayo, 3 collections: Zenteno-Ruiz, 2007 and more recently collected specimens cited below). Andean Region (Northern Andean Province). TDWG: 82 VEN 83 BOL CLM ECU PER. *Map*: Fig. 8.

*Specimens seen and other records.* VENEZUELA. **Mérida**: otherwise unloc., 7000 ft [2135 m], 1846, *Funck & Schlim* 1208 (P–image); 1928, *Pittier* 12756 (S–database); [distributed] 1959, *Bernardi* s.n. (K). **Campo Elias**: Los Quebraditos, above Jaji, 2590 m, 21 iv 1944, *Steyermark* 55999 (K, MO, NY, S–database). Bosque de San Eusebio, 2100–2400 m, 30 x 1962, *Ruiz Terán* 1148 (K). **La Azulita**: Environs de La Carbonera, 2000–2500 m, ix 1952, *Humbert* 25588 (NY–database, previously determined as *Podocarpus harmsianus* and *Prumnopitys harmsiana*). La Carbonera, 2250 m, 30 i 1953, *Bernardi* 335 (NY); La Carbonera [sic], 15 km NW of Ejido, 2200 m, 19 vi 1953, *Little Jr.* 15245 (NY–database). La Carbonera, ± 25 km W. of Mérida, 2400 m, 22 iv 1965, *Breteler* 4495 (COL–photo, MO, NY, RB–image, S–database). La Carbonera, 17 ii 1972, *Dobson* 1277 (CONN–database). La Carbonera, 2400 m, 6 i 1980, *de Laubenfels* 754 (A, male and bark; K–database, L–image, male and bark); *ibid.*, 2400 m, 6 i 1980, *de Laubenfels* 755 (A, K–database, L–image); *ibid.*, 2400 m, 6 i 1980, *de Laubenfels* 756 (A, L–image, female; K–database); La Azulita road, 50 km from Mérida, 1700 m, 11 iii 1980, *Sobel & Strudwick* 2130 (NY). Río Capaz, Via Azulita, 20 vii 1951, *Curran* 2147 (NY). **Libertador**: Environs de Mérida, 1600–2200 m, 14 ix 1952, *Humbert* 26148 (P–image, seedlings). **Santos Marquina**: La Mucuy, 18 x 1955, *García-Barriga* 15490 (COL–image and photos). **Táchira**: **Jáuregui**: Savana Grande between La Grita and Yeguines, 1911, *Jahn* 99 (S–database). **Junín**: Municipio Delicias, Caserío Villa Páez y sus alrededores, 1900–2300 m, 6 iii 1962, *Ruiz Terán* 918 (K, MO). Entre



FIG. 8. Global distribution of *Retrophyllum rospigliosii*.

Villa Páez y Betania, cerca de la frontera de Colombia, 2000–2400 m, 15 xi 1975, *Bunting* 4898 (NY); *ibid.*, 2050–2350 m, 11 x 1976, *Bunting* 4939 (NY, K–database); faldas debajo del Páramo de Tamá, cerca de la frontera Colombo-Venezolana, arriba de Betania y Tamá, cerca de la Quebrada Buena Vista, 2300–2450 m, 22–24 v 1967, *Steyermark et al.* 98706 (S–database); **Trujillo: Boconó:** P. N. Guaramacal, alrededores de la Laguna de los Cedros, 1830 m, 9 i 2004, *Stergios et al.* 20755 (E, F–n.v., MER–n.v., MERF–n.v., MO–n.v., PORT–n.v., NY–n.v., US–database (barcode 00772960)–n.v., VEN–n.v.).

**COLOMBIA.** Unloc., 1828–1890, Hb. *Triana* 665 (BM). **Cundinamarca** [Prov. Gualivá]: **Albán:** Albán, 1962, *Goitia* s.n. (UDBC 10797–image and photos). Vereda Santa Ana, finca San Pablo, 1800 m, 1 ix 1985, *Schmidt-Mumm* 324 (COL–photo). **San Francisco:** Cordillera Oriental, Finca « El Carmero » El Tablazo entre Subachoque y San Francisco, 1900–2100 m, 26 i 1944, *García-Barriga* 11038 (COL–photo, MA–n.v.); *ibid.*, 26 i 1944, *García-Barriga* 11041 (COL–image). Vereda “San Miguel”, 2100 m, 18 iv 1983, *Barrera* 50 (COL–photo). **Sasaima:** Estación San Bernardo, entre Sasaima y Albán, 1700–1800 m, 2–5 viii 1945, *Dugand & Jaramillo* 3962 (COL–photo). Sasaima, vereda San Bernardo, carretera a Villeta, entre los kilómetros 66–70, 1860 m, 30 vi 1945, *García-Barriga* 11586 (COL–photo). Sasaima, vereda de Apocentos (antigua hacienda de Apocentos), 10–12 vii 1960, *García-Barriga* 17259 (NY, COL–photo). Sasaima, San Bernardo, quebrada La María y Río Dulce, 1750–1950 m, 20–30 xi 1962, *García-Barriga* 17584 (NY). Sasaima, San Bernardo, quebrada La María y Río Dulce, 1750–1950 m, 20–30 xi 1962, *García-Barriga* 17585 (BM, COL–photo). Sasaima, Vereda San Bernardo, orillas del Río Dulce, 1780 m, 31 xii 1962, *García-Barriga* 18014 (COL–image and photos). Sasaima, Hacienda San Pablo, 1800–1900 m, 1949, *Schneider* 905 (S–database). Sasaima, Vereda las Mercedes, 1200 m, *García-Barriga* 20159 (COL–n.v.). Sasaima, Vereda de Guane, entre los ríos Gualibá y Guane, Finca La Concepción, 8–11 i 1974, *García-Barriga* 20468 (COL–image). **Vergara:** Mpio. de San Francisco [sic], Vergara, 2 ii 1981, *Barrera* 45 (COL–photo), 46 (COL–photo). [Prov. Guavio] **Guasca:** Guasca, i 1936, *Pérez-Arbeláez* 4798 (COL–photo). [Prov. Rionegro] **Pacho:**

Mpio. Pacho, otherwise unloc., 2000 m, ix 1962, *Goitia* s.n. (UDBC 2060–images and photos); *ibid.*, 1965, *Mahecha* s.n. (UDBC 5436–image and photos). Pacho, 18 x 1934, *Pérez-Arbeláez* 3150 (COL–2 sheets, photos). Pacho, Vereda Patasía, Hacienda Patasía, 1650–1820 m, 4 viii 1947, *García-Barriga* 12492 (COL–photo, K, NY). Pacho, Hacienda de Patasía, 1800 m, 21 vi 1948, *Uribe Uribe* 1734 (COL–photo). Pacho, 1859 m, 1 vi 1944, *Bohorquez R.* 475 (COL–photo). [Prov. Tequendamá] **Tena:** Laguna de Pedro Palo, finca La Laguna, por carretable desde Patio Bonito, 7 iii 1988, *Franco et al.* 2430 (COL–photo). [Prov. Ubaté] **Ubaté:** Mpio. Ubaté, without precise locality, *Mahecha* s.n. (UDBC 11190–image and photos). **Antioquia:** [Subreg. Norte] **Angostura:** Vereda El Guásimo, Finca El Guásimo, 2312 m, 10 viii 2007, *A.M. Vásquez* 3 (MEDEL–database). [Subreg. Oriente] **Guatapé:** Vereda Santa Rita, Finca Vertedero (Empresas Publicas de Medellín), 1967 m, 22 viii 2007, *A.M. Vásquez* 5 (MEDEL–database). [Subreg. Suroeste] **Fredonia:** Fredonia, 1850 m, 2 viii 1930, *Archer* 541 (US–n.v., photo NY; PH–database, S–database; seed separate, with *Soukup* 1801 from Peru, see below). **Jardín:** Vereda El Salado, Río Docató, Finca Las Manguitas, 5°33.1'N 75°53.0'W, 1500 m, 11 iv 1990, *Betancur et al.* 1817 (COL–photo, MO, NY). [Subreg. Valle de Aburra] **Envigado:** Vereda Santa Catalina, 2050 m, 7 viii 2007, *Vélez-Puerta* 1999 (MEDEL–database). **Medellín:** El Poblado, Carrera 49, primera entrada a EAFIT, 1530 m, 14 xii 2005, *Vélez* 6946 (MEDEL–3 sheets, database). **Huila:** [Subreg. Subsur] **Acevedo:** Parque Nacional Natural Cueva de los Guácharos, centro de potrero de Leonidas, 2090 m, 11 ix 1979, *Henaó* 237 (COL–photo). **Magdalena:** **Santa Marta:** Sierra Nevada de Santa Marta, Cerro San Lorenzo, 1850 m, 11 vii 1968, *Villamizar & Guevara* 63 (UDBC 2223–image and photos); *ibid.*, 2100 m, 11 ix 1965, *Espinal-T. & Delgado-F.* 1790 (COL–photo). **Quindío:** **Salento:** Barsinal, 1970 m, i 1853, *Triana* 1800 (BM). **Pereira:** **Acosta:** Parque Regional Natural Ucumari, Sectores La Pastora y Los Chorros, 2200 m, 9 ii 2000, *Roldán et al.* 3168 (MO). **Risaralda:** **Santa Rosa de Cabal:** Vereda La Suiza, Sector Riobarbo, Finca Lisbrán, 1841 m, 10 xii 2007, *Rodríguez-C. et al.* 505 (COL–image). **Norte de Santander:** [Subreg. Occidente] **Abrego:** Línea divisoria entre los Deptos. Santander del Norte y Cesar, entre Abrego y Las Jurisdicciones (Cerro de Croque), 3440–3750 m, 22–23 v 1969, *García-Barriga & Jaramillo-Mejía* 19866 (MA–n.v., NY, COL–photo; assigned to Norte de Santander by Torres-Romero, 1988, and Vargas Rincón, 2011). [Subreg. Sur-oriente] **Toledo:** Hoya de Samaria, 2000–2100 m, 29, 30 x 1941, *Cuatrecasas et al.* 12768 (COL–photo; cited by Vargas Rincón, 2011, as *Decussocarpus rospigliosii*). **Santander del Sur:** [Prov. Comunera] **Gámbita:** Vereda de Gausa, margen izquierdo carretera, 2070 m, 28 vi 1999, *Cardenas & Oliveros* 198 (COL–image). [Prov. Soto] **Piedecuesta:** Piedecuesta, Cristales en bosque, 2100 m, 15 xi 1989, *Roncancio* 23 (UDBC 2915–image and photos); *ibid.*, 12 xii 1989, *Roncancio* 024 (COL–photo). **Tona:** Tona, 2295 m, 20 xi 1989, *Roncancio* 055 (COL–photo); Tona, Vereda Guarumales, finca La Plazuela, 7°09'00"N 72°59'29"W, 2288 m, 13 xi 2003, *Quirós Quirós* 75 (COL–2 sheets, image and photos).

ECUADOR. **Napo:** **El Chaco:** 4 km al E de Lumbaqui, 1 km al E del puente sobre Río Aguarico, arriba del Río Aguarico, 0°05'N 77°20'W, 600 m, 5 viii 1986, *Neill & Salinas* 7202 (NY, K–database, MO–database; atypical, see comments). **Sucumbios:** **Gonzalo Pizarro:** Lumbaqui, derecho de Vi OCP, 0°04'16"N 77°18'00"W, 675 m, 29 v 2002, *Morales et al.* 867 (MO, atypical, see above). **Zamora-Chinchipe:** **Chinchipe:** Parque Nacional Podocarpus, La Esmeralda (Coperativa San Francisco de Numbala Alto), 4°22'S 79°03'W, 2250 m, i 1995, *Palacios & Tirado* 13026 (MO). Región de la Cordillera del Cóndor, sector sur, Parroquia San Francisco de Vergel, Cuenca alta del Río Vergel, Pica Sangola, 4°44'09"S 78°56'59"W, 2200 m, 16 iii 2005, *Quizhpe et al.* 1092 (MO); *ibid.*, cerca a La Canela, Sendero a Las Palmas, 4°35'44"S 78°59'08"W, 2190 m, 5 iii 2007, *Quizhpe & Wisum* 2461 (MO–database). Road south of Podocarpus National Park and Tapichalaca Reserve, c.4 km N of Valladolid, Río Valladolid, upper Río Chinchipe watershed, 4°30'43"S 79°07'24"W, 2150 m, 3 xii 2006, *Neill & Jost* 15337 (MO–database). **Palanda:** Camino paralelo a quebrada Flor Amarilla, cruce sobre la quebrada San Francisco, limite con el Parque

Nacional Podocarpus, 4°00'00''S 79°13'00''W, 1900–2200 m, i 1995, *Palacios & Tirado* 13159 (MO–database).

**PERU. Cajamarca: San Ignacio:** *Chirinos:* La Palma, 10 km NW de Chirinos, 5°25'S 78°53'W, 1780 m, 5 ii 1988, *Gentry et al.* 61207 (MO). *Huarango:* El Triunfo-Convento, 5°13'S 78°40'W, 1000–1400 m, 30 vi 1996, *Campos & Rodríguez* 2825 (MO). *San José de Lurdes:* Buenos Aires, 4°55'S 78°51'W, 1870 m, 28 x 1995, *R. Vásquez & Jaramillo* 20459 (MO). **Pasco: Oxapampa: Huancabamba:** Parque Nacional Yanachaga-Chemillén, Parcela Permanente 1 ha Oso Playa, 10°17'58''S 75°36'35''W, 2200 m, 31 xi [sic] 2006, *Monteagudo et al.* 12942 (MO–image); *ibid.*, 2200 m, same date [with same error!], *Monteagudo et al.* 12986 (MO–image); *ibid.*, 3 xi 2006, *Monteagudo et al.* 13078 (MO–image); *ibid.*, 6 xi 2006, *Monteagudo et al.* 13230 (MO–image); *ibid.*, árbol no. 403, 11 xi 2006, *Monteagudo et al.* 13353 (MO–image, NY–database). Parque Nacional Yanachaga-Chemillén, remediación de parcela Oso-Playa 1.0 ha, 10°17'58''S 75°36'56''W, 2200 m, 20 vi 2008, *Monteagudo et al.* 16407 (MO–database). *Oxapampa:* Oxapampa, *Esposito* 556 (holo B–image, iso GH–image, NY–image, fragment of holo S). Oxapampa, otherwise unloc., viii 1942, *Soukup* 1801 (US–n.v.; image NY; sterile shoot; loose seed is annotated, “this seed belongs in packet with *W.A. Archer* 541, Fredonia, Colombia”); S–database). Oxapampa, *R.T. Pennington* 1422 (E); *ibid.*, *R.T. Pennington* 1426 (E); *ibid.*, *R.T. Pennington* 1427 (E); *ibid.*, *R.T. Pennington* 1431 (E); *ibid.*, *R.T. Pennington* 1433 (E). *Chorobamba,* 10°33'S 75°33'W, 1700 m, 5 vii 1985, *D.N. Smith & Brack* E. 7634 (NY, F–image, MO–n.v.; cultivated). *Palcazú:* Comunidad Nativa Santa Rosa de Palcazú, sector Santo Domingo, 10°26'50''S 75°03'25''W, 470 m, 13 x 2008, *Huamán et al.* 313 (MO–database, cultivated). *Chontabamba:* 2 de Mayo, Hacienda La Victoria, 10°35'S 75°28'W, 1890 m, 28 v 1982, *D. Smith et al.* 1752 (NY). *Villa Rica,* viii 1955, *Soukup* 4401 (GH). *Villa Rica,* 10°43'S 75°16'W, Chacras above town, 1500 m, 21 xi 1998, *Daza & T.D. Pennington* 16464 (E). Centro Bocaz, camino y trocha a Purus, 10°38'S 75°11'W, 1590 m, 19 ix 2003, *Perea* 381 *et al.* (NY–database). Base of road towards Pajonal/Villa Rica, near Oxapampa, 10°38'05''S 75°20'16''W, 2093 m, 17 ix 2001, *Weigend* 5795 *et al.* (NY–database). **Junín: Junín:** *Junín:* Caserío de Pampas Raimondi, 11°05'S 76°0'W, 2040 m, 23 xi 1973, *Espejo* 29ELE (K–database). **Ucayali: Coronel Portillo: Iparia:** falda dentro las cuencas del Río Ariapo y Río Iparia, afluentes del Río Ucuyali, Reserva Comunal el Sira, 1550–1600 m, 9°27.85'S 74°33.95'W, 1 xi 2009, *Graham* 5179 (E, MOL–image).

**BOLIVIA. La Paz: Franz Tamayo:** Parque Nacional Madidi (ANMI), Sector Macheineo, Camino viejo de la carretera de Mohima a Pata, 14°39'18''S 68°34'30''W, 1873 m, 27 v 2011, *Gardner et al.* (2011): 30 (E). Parque Nacional Madidi (ANMI), Camino hacia el Río Tuichi, 14°36'52''S 68°33'53''W, 1811 m, 29 v 2011, *Gardner et al.* (2011): 37 (E). Parque Nacional Madidi (ANMI), Santa Cruz de Valle Ameno, 14°38'23''S 68°31'30''W, 1605 m, cultivated, 29 v 2011, *Gardner et al.* (2001): 38 (E). **Santa Cruz: Andrés Ibáñez:** “Western slopes of the Andes”, in swampy places about Santa Cruz, 0°–40°S, vii 1860, *Pearce* s.n. (BM).

**COLOMBIA (cultivated). Cundinamarca: Bogotá:** Bogotá, Parque de La Independencia; jardines y parques, 2620 m, 20 iii – 20 iv 1946, *Duque-Jaramillo* 2964 (COL–photo); *ibid.*, *Duque-Jaramillo* 3108 (COL–photo, NY). Santafé de Bogotá, Parque Nacional, 2650 m, i 1963, *Goitia* UDBC 2129 (UDBC–image and photos). Avenida de los Cerros Orientales, 2700 m, 1 xi 1973, *Mahecha* 1391 (UDBC 5985) (UDBC–image and photos). Bogotá, D.E. Calle 74 con carrera 11, 8 vii 1979, *E. Forero & J. Forero* G. 6207 (NY, COL–photo). [Prov. Sabana Occidente] **Subachoque:** Vereda Casablanca, finca “California”, 2700 m, plantada junto a una cerca, como ornamental, 12 vi 2003, *Hernández Schmidt* 1190 (COL–photo). Vereda Tobal, 2800 m, cultivada en un jardín, 9 xi 2003, *Hernández Schmidt* 1384 (COL–photo). **Quindío: Calarcá** (introduced): Jardín Botánico del Quindío, Sede principal, Sector del Sendero de los Caobos, 1490 m, 1 iv 1999, *Matallana Tobón* 523 (COL–photo). **Armenia** (introduced): City of Armenia, Parque Aborigen, 1550 m, planted as an ornamental, 7 x 1993, *Wright* 047 (E–3 sheets).

PERU (CULTIVATED). **Lima:** Lima, botanic garden, *Asplund* s.n. (S-database); *ibid.*, 1940, *Asplund* 12027 (S-database).

SCOTLAND. **Midlothian:** (Cultivated, origin Venezuela, cuttings from Arnold Arboretum via J. Silba). Royal Botanic Garden Edinburgh, accession 19951955\*A, *Frachon* 1337 (E). (Cultivated, origin Colombia, *R. Nicholson* 348/92). Royal Botanic Garden Edinburgh, accession 20001721\*A, *Frachon* 1340 (E).

*Bioregions:* Northern Andes, Central Andes. *Ecoregions:* NT0105 Bolivian Yungas, NT0109 Cauca Valley Montane Forests, NT0118 Cordillera Oriental Montane Forests, NT0121 Eastern Cordillera Real Montane Forests, NT0136 Magdalena Valley Montane Forests (in which it and *Podocarpus oleifolius* D. Don are two of the most dominant trees), NT0153 Peruvian Yungas, NT0159 Santa Marta Montane Forests, NT0175 Venezuelan Andes Montane Forests (where again it is one of the most dominant trees along with *Prumnopitys montana* and *Podocarpus oleifolius* together with assorted dicot trees).

*Ecology.* Montane forests, cloud forest; (600–)1500–3750 m (generally at higher altitudes than *Retrophyllum piresii*; the three records from below 1000 m relate to the three atypical specimens from Ecuador and Peru discussed above, all of which have some features of *Retrophyllum piresii*). *Retrophyllum rospigiosii* grows best on slightly sloping ground, fertile river beds and small depressions, on wet, deep, fertile acid clay or clay/sand soils with good to slow drainage; it is not tolerant of either swampy or drought conditions. It requires constant humidity and cloudy conditions with an annual rainfall of 1500–2500 mm and an annual average temperature of 10–18°C (Nieto & Rodriguez, 2003). It plays an important role in intercepting rainfall: a *Retrophyllum rospigiosii* plantation at La Mucuy (Mérida, Venezuela) intercepted 42% of precipitation, almost the same percentage as the 45% intercepted by nearby montane cloud forest (Ataroff, 2002). The seeds of *Retrophyllum rospigiosii* are recalcitrant, with a viability in storage at 12°C of 3–6 months but with a drastic drop in viability after 4 months (Ceballos-Freire & López-Ríos, 2007).

In Cajamarca, Peru, *Retrophyllum rospigiosii* occurs in undisturbed and fragmented primary forest together with *Cecropia polystachya* Trécul, *Cinnamomum triplinerve* (Ruiz & Pav.) Kosterm., *Heliocarpus americanus* L., *Ladenbergia magnifolia* (Ruiz & Pav.) Klotzsch, *Otoba parvifolia* (Markr.) A.H.Gentry, *Piptocoma discolor* (Kunth) Pruski, *Ruagea insignis* (C.DC.) T.D.Penn., *Virola calophylla* Warb., etc. (Vicuña-Miñano & León, 2003).

*Phytochemistry.* Ninety-one compounds have been isolated and identified from the essential oil of the ‘fruits’ of *Retrophyllum rospigiosii* (Quijano-Celis *et al.*, 2010). The essential oil from the leaves yielded 68 compounds (Quijano-Celis *et al.*, 2013). In both cases, limonene (38% in ‘fruits’, 43% in leaves) and  $\alpha$ -pinene (16% in ‘fruits’, 18% in leaves) comprised the largest fractions. *Retrophyllum rospigiosii* contains several norditerpene dilactones that were previously known only in *Podocarpus* and/or *Nageia*, including nagilactones E, F and G,  $\beta$ -sitosterol and a derivative of the latter (Amaro-Luis & Carroz, 1988), as well as a unique compound, rospiglioside (Amaro Luis

*et al.*, 2006). As well as rospiglioside, Amaro Luis *et al.* (2006) isolated ferruginol, sugiol, sugiol acetate, totarol, totarol acetate, 4 $\beta$ -carboxy-19-nortotarol and 16-hydroxy-4 $\beta$ -carboxy-19-nortotarol from the leaves of *Retrophyllum rospigliosii*, but the phenolics of the wood do not appear to have been studied. Its biflavones are similar to those found elsewhere in Podocarpaceae and include sciadopitysin, podocarpusflavone A, podocarpusflavone B, amentoflavone, 7,4',7'',4'''-tetra-*O*-methyl-amentoflavone, 7,4',7''-tri-*O*-methyl-amentoflavone, 7,7''-di-*O*-methyl-amentoflavone, sequoiaflavone and heveaflavone (Chaabi *et al.*, 2007; Amaro-Luis *et al.*, 2008). The biflavones act as phosphodiesterase inhibitors and may therefore have potential as therapeutic drugs for a wide variety of medical conditions (Rahimi *et al.*, 2010 and work cited therein). However, the biflavones and other compounds of *Retrophyllum rospigliosii* assayed were found to lack any antimycotic activity against three pathogenic fungi (Niño *et al.*, 2007).

*Plant–animal interactions.* In Colombia, the seeds of *Retrophyllum rospigliosii* are eaten by the endangered yellow-eared parrot or *loro orejiamarillo*, *Ognorhynchus icterotis* (Massena & Souanc) (Botero-Delgado & Páez, 2011). Whether this activity effects dispersal is not known.

*Retrophyllum rospigliosii* is the one of the hosts of at least three members of the wood-boring beetle family Scolytidae, namely *Araptus impensus* (Wood), *Platypus secus* Wood (Wood & Bright, 1992, as *Podocarpus 'raspigliosii'*) and *Thamnophthorus impensus* Wood (Schedl, 1965). Some of the paratypes of *Platypus secus* were collected from *Retrophyllum rospigliosii* logs at the beetle's type locality in La Carbonera Experimental Forest, Mérida, Venezuela (Wood, 1971, as *Podocarpus 'raspigliosii'*).

*Mycological associations.* *Retrophyllum rospigliosii* is the only known host of *Tripospora venezuelensis* E.Müll. (Coryneliales), which is known only from the type collection from Mérida, Venezuela (Müller & Dennis, 1965; Benny *et al.*, 1985). The mycorrhiza of *Retrophyllum rospigliosii* have been investigated by Furman (1970) and Guerrero Forero & Hodson de Jaramillo (1988). The latter team found that *Retrophyllum rospigliosii* had a mixture of vesicular arbuscular mycorrhiza that included several species of *Acaulospora* Gerdemann & Trappe (Acaulosporaceae) and *Glomus* Tul. & C.Tul. (Glomeraceae).

*Conservation status (global):* VU (A2acd) (Gardner & Thomas, 2013). Logging of this valuable timber tree has reduced or fragmented most of the formerly rather extensive stands of this species. Whole mountainsides of the species in Peru were clear-felled in the 1980s for timber, and the species is there now reduced to scattered individuals (M. Gardner, Royal Botanic Garden Edinburgh, pers. comm., 7 Feb. 2012). Yaguana *et al.* (2012) have commented that the forest at Numbala (Ecuador), at the edge of Podocarpus National Park, is one of the last remnants of its type. *Retrophyllum rospigliosii* is regarded as NT in Colombia (Barragan Bedoya & Valdés Torres, 2011).

*Uses.* The fruits are reported as edible (Gray & Buchholz, 1948; Buchholz & Gray, 1957; and several specimen labels). The tree is often cultivated in gardens and parks in

Colombia (Nieto & Rodriguez, 2003) and Peru (Brako & Zarucchi, 1993), and is used in forestry in Colombia (Nieto & Rodriguez, 2003, who also give details of recommended practices for seed harvesting and silviculture) as well as in Venezuela (*Ruiz Terán* 918 in sched., K, MO). The wood is of very good quality and is widely used in construction in Venezuela and Colombia. It is easily worked and is used to make furniture, boxes, cabinets, veneer, pencils, paper pulp and other items (Nieto & Rodriguez, 2003). It is also used to make handcrafted decorative objects (Feuillet Hurtado *et al.*, 2011). Its characteristics have been described recently by Vásquez Correa & Alcántara Vara (2009) and Vásquez Correa *et al.* (2010). The logging cycle for the species was estimated at 109 years by Becerra-Montalvo & Zevallos-Pollito (2014).

**6. *Retrophyllum piresii*** (Silba) C.N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 380 (22 Feb. 1989 [‘1988’]). – *Decussocarpus piresii* Silba, Phytologia 54: 461, t. 1 (10 Dec. 1983). – *Nageia piresii* (Silba) de Laub., Blumea 32(1): 211 (3 Feb. 1987). – Type: Brazil: Território de Rondônia, Serra Pacas Novos, Seringal S. Luiz, 50 km east of Rio Pacas Novos, 14 viii 1976, *N.A. Rosa, J.M. Pires, W. Rodrigues, S. Barros* 856 [misprinted in protologue as ‘*Rosa & Pires* 586’] (holo US, iso K–database, L–image, MG–image, MO, NY, R–2 sheets, images, RB–image). **Fig. 9 A–C.**

*Etymology.* *Retrophyllum piresii* is named after João Murça Pires (1917–1994), Brazilian botanist, who published (with C. Mainieri) a revision of *Podocarpus* in Brazil (*Silvic. Sao Paulo* 8: 1–24, 1973) and who was one of those who collected both the type and the only two other currently known specimens of wild origin, made a few days earlier and on the same day.

*Vernacular name:* *pinheiro-da-amazônia* (Secco *et al.*, 2009).

*Distinguishing features.* This species shares many characters with its South American congener *Retrophyllum rospigliosii* but, as was noted in the protologue, it can be distinguished by its elliptic (not lanceolate) leaves with  $\pm$  parallel sides, and the more ellipsoid female cones that are not narrowed at the base. Additional characters not described by Silba that distinguish it from *Retrophyllum rospigliosii* are the bracts on the female peduncle all very reduced and scale-like (not foliar), the obtuse leaf apices (misleadingly described in the protologue as ‘bluntly acute’) and the leaves never abruptly narrowed just below the apex (normally so in *Retrophyllum rospigliosii*). The opposite branching with leaves on penultimate branches opposite and not forming stepped ranks also separates *Retrophyllum piresii* from the vast majority of specimens of *R. rospigliosii*, although a few specimens of the latter approach *R. piresii* in these features, as noted above. Further differences may become apparent when more material is collected (male and juvenile collections of *Retrophyllum piresii* are particularly desirable to complete the description). The two species also appear to be ecologically separated, with *Retrophyllum piresii* inhabiting lowland swamp forest at altitudes of less than 1000 m and *R. rospigliosii* normally occurring in montane and cloud forests, nearly always above 1500 m, although there are one or two low-altitude records as discussed under that species.

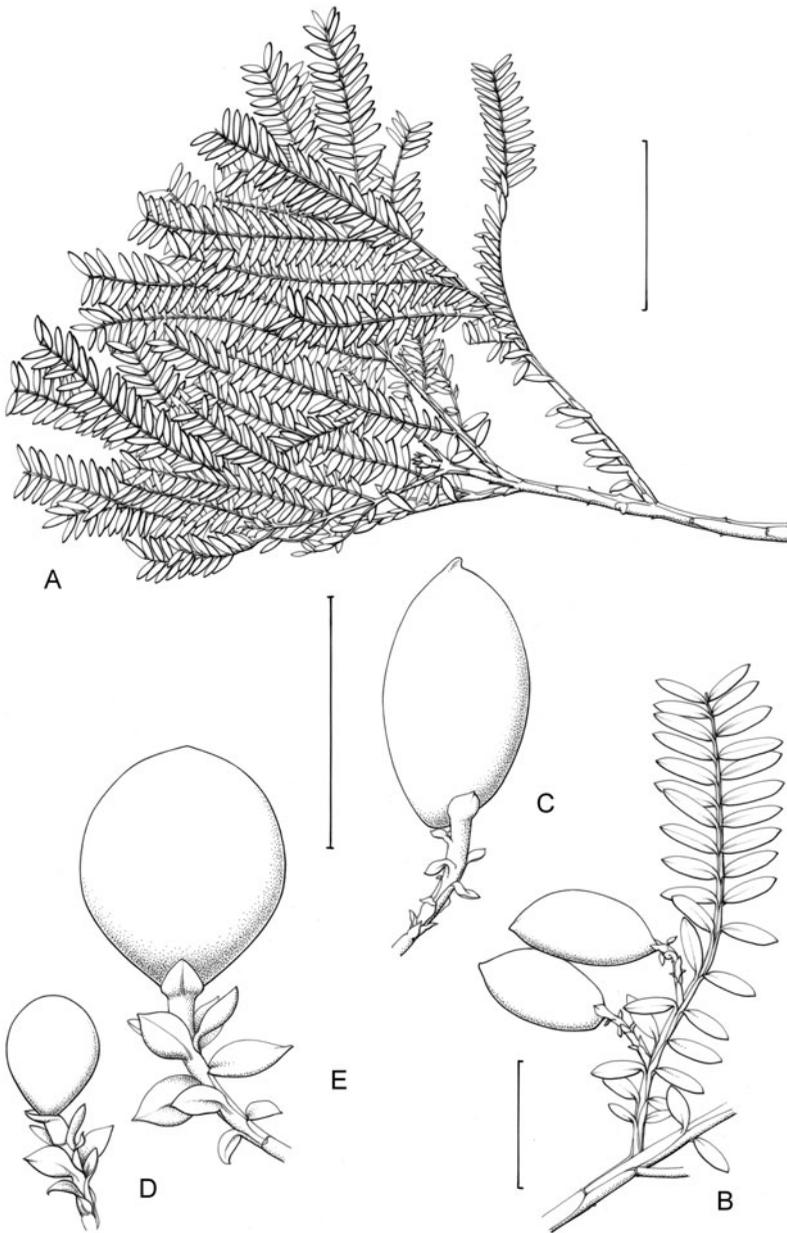


FIG. 9. *Retrophyllum piresii*. A, Branching arrangement (Rosa *et al.* 856). B, Adult female branch (Rosa *et al.* 856). C, Mature female cone (Rosa *et al.* 856). *Retrophyllum rospigliosii*. D, Young female cone (Vasquez *et al.* 20459). E, Mature female cone (Bunting 4939). Magnifications: A, B,  $\times 0.67$ ; C,  $\times 1.5$ ; D, E,  $\times 3$ . Scale bars: A, 6 cm; B, 2 cm; C, D, E, 2 cm. Drawn by Claire Banks.

Evergreen tree c.30 m tall and up to 2.5 m dbh, adult tree branching at c.15 m above base. *Trunk* (*vide* Farjon, 2010) straight and erect, in large trees lacking branches for 15 m or more. *Bark* (imperfectly known) medium to dark brown outside, purplish to dark brown inside, smooth on branchlets; wood reddish brown. *Crown* rounded (*vide* Farjon, 2010: 940). *Branchlets* of last two orders erecto-patent, slightly curved; ultimate branchlets usually opposite, 50–130 mm with 24–38 pairs of leaves, penultimate ones 180–210 mm. *Leaf scars* absent. *Buds* obconical, naked. Leaves on last two orders of branching all of one type (scale-leaves absent). *Leaves* on penultimate axes normally soon caducous although persistent when subtending branch bases and when axis has not developed further branching, opposite and spreading or orientated so that both leaves of each pair are suberect, not forming stepped ranks. *Juvenile foliage* not known. *Adult foliage leaves* unequally amphistomatic, 4–5 mm apart, opposite-distichous, pectinate, not imbricate, subsessile (petiole 0.2–0.5 mm); lamina spreading and forming a shallow ‘V’ along branch, erecto-patent, diverging at 65–80°, mid to deep green, elliptic, oblong-elliptic or obovate-elliptic (never lanceolate), 9.5–11 × 2–2.5 mm in middle of shoot and 5–6 × 1.7–2.5 mm near base, straight, thinly coriaceous, the margin only slightly thickened, both surfaces flat with vein-like striae alternating with the stomatal rows, midrib only slightly raised on both surfaces or not at all, sometimes obscure distally on abaxial surface, the apex obtuse and the blade never abruptly narrowed below it, usually with an indistinct mucro, the base obtuse, the petiole decurrent along the whole length of the internode. *Pollen cones* unknown. *Female cones* borne on previous year’s growth, terminal on specialised lateral shoots bearing very reduced scale-leaves or bracts. *Peduncle* c.15–16 mm, about 2/3 length of cone, deflexed-patent to pendulous, its lower portion bearing at least 3 pairs of decussate scale-like, shortly ovate or elliptic bracts, its apical part together with the fertile bract forming an indistinct, cylindrical receptacle that is shed with the cone. *Fertile bract* with basal part adnate to epimatium, distal part free and navicular. *Female cone* with epimatium pecan-brown turning reddish when mature, 19–22 × 11–14 mm, distinctly ellipsoid with a shortly conical distal crest, not narrowed at the base, the seed proper slightly smaller.

*Taxonomic notes.* Silba’s protologue, and later description (Silba, 1986: 78), are both very brief and give little detail concerning many aspects of its morphology, but no other taxonomic account of this species appears to have been published until now except that of Farjon (2010), which added some details of trunk and habit. Further collections of the species from the type locality are badly needed, particularly of the unknown juvenile stages and male cones.

*Distribution.* W Brazil (SW Rondônia: Serra dos Pacaás Novos), near the border with lowland NE Bolivia. More recently recorded from Bolivia and Peru in similar habitats (D.J. de Laubenfels, pers. comm., 24 October 2005). These records require confirmation; one problematic sterile specimen, determined as *Retrophyllum piresii* by de Laubenfels, is discussed above under *R. rospigliosii*. For the time being, the species



FIG. 10. Global distribution of *Retrophyllum piresii*.

is regarded as endemic to Brazil and known from the two wild gatherings (both female) and one sterile cultivated collection cited here. *Map:* Fig. 10.

*Specimens seen.* BRAZIL. **Rondônia:** *Guajará-Mirim:* Serra Pacaás Novos, Seringal S. Luiz, 50 km E of Rio Pacas Novos, 14 viii 1976, *Rosa et al.* 856 (holo US, iso K, L–image, MG–image, MO, NY, R–image, RB–image); Serra Pacas Novos, 11°13'S 63°35'W, 250 m, 14 viii 1976, *Rosa et al.* 856 (iso INPA–image with different label information as indicated). Serra dos Pacos [sic] Novos, 30 min. de vôo de helicóptero de S. Luz–Rio Pacos Novos, 11°15'S 23°50'W [sic: presumably an error for 63°50'W], 7 viii 1976, *Pires* 850 & *Rosa* (RB–2 sheets both numbered RB253293, images). Região do rio Pacaas Novos, Projeto RADAM/BRASIL, ponto 15 à 250–300 m de altitude, 11°13'S e 63°35'W, 14 viii 1976, *Rodrigues et al.* 9646 (INPA–2 sheets, images; female; third collector listed as 'S.N. Rosas' but probably a misprint for *N. Rosa*). BRAZIL (CULTIVATED). **Pará:** *Belém:* Belém, Museu Emilio Goeldi, Parque Zoobotânico Emilio Goeldi, procedente de Rondônia, 30 x 2008, *Kinupp* 3426 (RB–image; also photos of living plant).

*Bioregion.* Amazonia. *Ecoregion:* NT0135 Madeira–Tapajós moist forests; perhaps also in NT0166 Southwest Amazon moist forests.

*Ecology.* Lowland tropical swamp forest; 250–300 m.

*Phenology.* Reputedly fertile in January (de Oliveira, 2012).

*Conservation status* (global, IUCN 3.1): DD (two independent assessments: de Oliveira, 2012; Gardner, 2013). The only confirmed locality from which wild material has been gathered is within a National Park. Insufficient is known about the extent and

area of occurrence, or of potential threats, to award an assessment other than DD and this will not change until further research can be done on the species in the field. The species is in cultivation (see cited specimens).

*Uses.* None have been reported although it is likely to have wood of high quality similar to that of *R. rospigliosii*.

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## APPENDIX I

### *Typification of Nageia minor* Carrière (*basionym* of *Retrophyllum minus*)

As noted by Farjon (2010: 939), typification of *Retrophyllum minus* is difficult. First of all, the protologue (Carrière, 1867: 641) clearly implies that the basionym, *Nageia minor*, as conceived by Carrière, was intended to be based primarily on material from the summits of high mountains,

but that “according to Vieillard ... it is also found on the banks of lac Arnaud”. Clearly, Carrière (1867), Parlatore (1868) and other contemporary workers believed that there was only one *Retrophyllum* species on New Caledonia, the one based on *Nageia minor* that we now know as *R. minus*. As late as the 1920s, Compton (1922) referred to material from Mt. Mou (Compton 607) as *Nageia minor*, saying that his specimens “match the type perfectly” but were collected from a tree 40–50 ft in height at an altitude of 3500 ft. No specimens from high altitude were, however, cited by Carrière (1867) in support of his statement that it had been collected at altitude by an ‘English gardener called Richard’ [= N. Richards, collector for F. von Mueller; see main paper]. We have to accept, as Compton (1922) did, that the type of *Nageia minor* is to be found among the material numbered Vieillard 1275. High-altitude material of New Caledonian *Retrophyllum* was finally separated from the low-altitude Vieillard collection as *Podocarpus comptonii* by Buchholz (1949) and is now known as *Retrophyllum comptonii*. The latter, as mentioned in the introduction and relevant species account in the present paper, also descends to low altitudes in the south of the island and sometimes occurs sympatrically with *R. minus*.

Typification of *Nageia minor*, the basionym of *Retrophyllum minus*, is complicated by the existence of several different collections, made from two different localities (‘lac Arnaud’ and ‘Baie du Sud’) and in two time periods (1855–1860 and 1861–1867), all numbered Vieillard 1275. Buchholz (in sched., P00188111), indicates a selection of fragments labelled ‘bord du lac Arnaud’ as representing the ‘type specimen’, and sheet P0018111 at Paris is designated ‘holotype’ of *Nageia minor* in the Paris Herbarium database. Subsequently, Gray (1962: 77) stated that Vieillard 1275 from “borders of Lac Arnaud” was the ‘holotype’ of *Nageia minor*, so agreeing with her late coworker’s annotation. On the other hand, Farjon (2010: 938) stated that the ‘holotype’ of the name was a collection of Vieillard 1275 at P from Baie du Sud.

Of the seven sheets at P listed below that bear specimens numbered Vieillard 1275, two sheets (with barcodes P00188106 and P00188107) give the locality only as Baie du Sud and three (barcoded P00181108–110) are labelled only ‘lac Arnaud’, while the remaining two (barcoded P00181111 and P00197538) bear labels indicating both localities. Because there are multiple collections and for other reasons, there cannot be a ‘holotype’ but rather a number of syntypes. Therefore, both indications by Gray (1962) and Farjon (2010) are incorrect. Because at least six different gatherings (probably more), belonging to two different genera, have been numbered Vieillard 1275 (see below), lectotypification is necessary to fix the application of the names *Nageia minor* and *Retrophyllum minus*. Because several of the sheets comprise mixed gatherings, lectotypification has by necessity been a two-stage process. First of all, conventional taxonomic and nomenclatural deductive methods were used to eliminate entire sheets that for a variety of reasons are unsuitable for selecting the actual lectotype (although some bear isoelectotypes). These enabled the choice of lectotype to be narrowed down to one particular sheet out of the seven. Then, similar methodology in combination with colour profiling using ImageJ (Rasband, 2014) was used to select the actual lectotype specimen on that sheet and its isoelectotypes on others. Finally, because the resulting lectotype and isoelectotypes are all sterile, an epitype is designated to further fix the application of the name.

*Selection of the lectotype sheet.* Élie-Abel Carrière (1818–1896) was a horticulturist at Paris, and there is no trace of a personal herbarium. Williams (2004) believed that he relied on the collections in the Muséum d’Histoire Naturelle, i.e. the herbarium P. There is no evidence that he consulted herbaria elsewhere in connection with his research on gymnosperms. The protologue in fact gives two clues that Paris material formed the basis of his new species *Nageia minor*: the synonym “*PODOCARPUS Spec. in herb. Mus. Paris.*” and the indication of the specimen, “D’après M. Vieillard (herbier de la Nouvelle-Calédonie n° 1275–in *Herb. Mus. Par.*)...” Therefore the lectotype must be selected only from among the Paris examples of Vieillard 1275. Seven exist, now barcoded P00188106, P00188107, P00188108, P00188109, P00188110, P00188111 and P00197538. Details of these follow, after a discussion of the elements in Carrière’s protologue

that are helpful to the task of selecting the choice of lectotype. Individual elements on sheets are designated by adding a suffix letter to the last three digits of the Paris herbarium barcode, e.g. 106-A (also see [Appendix table 1](#), which gives the position of each element on each sheet). It is also important to know some facts about Vieillard's collections and how they were numbered, although it is equally important to remember that Carrière was most probably unaware of these.

Eugène Vieillard (1819–1896) was a French doctor, naturalist and explorer who was a contemporary of both Émile Deplanche (1824–1874) and Jean Armand Isidore Pancher (1814–1877), two other French doctor–naturalists. All three collected on New Caledonia. Morat (2010) gives biographies and details of their collections. The relationship between Vieillard and Deplanche seems to have been particularly close; they published together concerning New Caledonia (Vieillard & Deplanche, 1863). Vieillard's numbers refer to *taxa*, not specimens, so the same number was used for different collections made at different times. The two time periods that appear on Vieillard's printed labels, 1855–1860 and 1861–1867, correspond exactly with Deplanche's two sojourns on the island as given in Morat (2010); indeed, Guillaumin (1911) seems to imply that both collected together during both those periods on the island. Deplanche sometimes used his own number but sometimes a Vieillard number. Deplanche also at times seems to have given material to Vieillard, who would then give this a different number in his own system (de Kok & Mabberley, 1999). These and many other aspects of the hazards associated with specimens collected by Vieillard and/or Deplanche, and their typification, have been carefully set out by Hopkins & Bradford (2009).

Possibly the most important pieces of information in Carrière's protologue of *Nageia minor* are:

- the fact that he cited only material from lac Arnaud, which would seem to rule out sheets P00188106 and P00188107, both of which bear labels giving the locality as Baie du Sud, as well as sheets such as P001880111 that bear more than one collection from different localities (sheet P00188011 not only has Vieillard's collections numbered 1275 from both lac Arnaud and Baie du Sud, but also another gathering numbered *Deplanche* 170, discussed later). However, Farjon (2010) placed less importance on the locality information than on the appearance and reproductive state of the specimens, restricting candidates for the type to specimens that were either male or sterile. Vieillard's locality information on the labels is known to be unreliable (de Kok & Mabberley, 1999), so Farjon was perhaps acting wisely in putting more importance on morphology. However, it is important to recognise the fact that Vieillard did not describe *Nageia minor* – Carrière did. Carrière may not have known about the unreliability of Vieillard's locality information, so it seems better to emphasise the importance of the fact that he gave the locality as lac Arnaud and no other.
- the indication of the previous determination of the material he saw: *Podocarpus Spec. in herb. Mus. Paris*. This rules out sheet P00188109, on which the only determination in Carrière's time was *Dacrydium*, a completely different genus of Podocarpaceae. It was first realised not to be that genus by Guillaumin, who in 1943 determined that particular sheet as *Podocarpus minor*. It also rules out all sheets that were not in the P herbarium in Carrière's time. Many of Vieillard's collections now in P were formerly housed at CN (the herbarium of the Université de Caen; Vieillard was director of the Jardin botanique du Caen, 1871–1895), and were transferred to P only in the 1970s. Consultation of the P herbarium database, which gives the origins of all sheets transferred from other sources, shows that none of the sheets discussed here originated from CN but the database and/or labels on the sheets themselves do indicate that some were indeed incorporated into the P herbarium from other sources after 1867 (the date of publication of Carrière's *Traité des Conifères*) and so have to be rejected as lectotype choices.
- the locality being given as in the protologue “au bord du lac Arnaud” and the word “Arbuste” at the beginning of the description: both these texts are found on the labels of specimens now

APPENDIX TABLE 1. New Caledonian collections of *Retrophyllum minus* made by Vieillard, Deplanche and Pancher in the Paris Herbarium, with details of leaf dimensions, reproductive state and colour profiling values obtained using ImageJ. Specimen codes are formed by adding a suffix letter to the last three digits of the P barcode. Colour profile values: mean % red (R), green (G) and blue (B) of 20 × 20 px (c.1.7 × 1.7 mm) squares: for each set of analyses the highest and lowest mean values are shown as a range. The material can be inferred as belonging to nine different collections, six (1–6) by Vieillard and three (I–III) by Deplanche or Pancher, as detailed in the last column

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188106</b> <i>Baie du Sud 1861–67</i> Label shared by whole sheet	Lower	106-A	Erect or suberect 2 or 3 orders alternate	Sterile	12–18	2.5–4.2	37.72–53.21	23.87–35.52	22.90–32.42	1
<b>P00188106</b> <i>Baie du Sud 1861–67</i> Label shared by whole sheet	Upper	106-B	Erect or suberect 3 orders opposite	Male, cones fairly abundant	(5)7.8–11.5	(2.4)2.7–3.4	36.23–42.64	23.17–29.52	24.88–27.46	1
<b>P00188107</b> <i>Baie de Sud 1861–67</i> Label shared with whole sheet	Bottom left	107-A	Erect unbranched shoot	Sterile	(6.7, lower) 11–20.5	(2.6, lower) 3.2–3.9	58.23–73.81	45.27–63.90	34.01–50.81	2
<b>P00188107</b> <i>Baie du Sud 1861–67</i> Label shared with whole sheet	Bottom right	107-B	Erect or suberect 2 orders opposite or single	Male (very few)	9.7–16.6	2.5–4.1	67.17–75.68	52.88–63.02	35.33–46.88	2
<b>P00188107</b> <i>Baie du Sud 1861–67</i> Label shared with whole sheet	Centre	107-C	Very small fragment, five leaves and short portion of shoot	Sterile	12.8–15.7	3.2–3.5	67.07–71.84	52.36–58.39	34.95–42.80	2
<b>P00188107</b> <i>Baie du Sud 1861–67</i> Label shared with whole sheet	Centre, above 107-C	107-D	Single detached leaf	n/a	10.6	3.0	61.46–68.61	50.31–56.79	39.31–42.55	2
<b>P00188108</b> <i>Arbuste; bord du lac Arnaud 1855–60</i>	Only	108-A	Erect or suberect dense bushy opposite or alternate 3 orders	Male (very few)	12.0–19.4	3.7–4.8	96.19– 104.88	82.24–89.59	53.95–64.65	3

APPENDIX TABLE 1. (Continued)

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Top far left	109-A	Erect or suberect 3 orders opposite or alternate	Male (evident at most branch tips)	8.9–16.0	2.3–4.1	83.17–105.34	73.51–93.89	55.09–73.66	3
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Top centre left	109-B	Erect or suberect 2 orders opposite	Sterile	10.9–13.6	3.2–4.4	(60.01) 69.54–86.39	(57.50)61.04– 82.71	(40.00)41.15– 70.61	4
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Top centre right	109-C	Single shoot fragment	Sterile	13.1–17.3	2.6–3.2	71.11–82.42	62.56–74.53	43.42–58.77	5
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Top far right	109-D	Erect or suberect 3 orders opposite	Apparently sterile	5.0–13.1	2.1–3.6	(63.44)74.22– 97.89	(64.07) 72.25–90.75	(51.51) 57.97–75.72	4
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Bottom left	109-E	Erect or suberect 3 orders opposite or alternate	Male, abundant	7.8–11.7	2.9–3.7	64.19–80.23	63.92–75.90	53.94–64.39	6
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Bottom centre	109-F	Erect or suberect 3 orders mostly alternate	Apparently sterile	13.0–18.5	2.7–4.3	94.43–105.76	79.14–93.22	53.13–63.55	3
<b>P00188109</b> <i>Dacrydium lac Arnaud</i> Label shared with whole sheet	Bottom right	109-G	Single shoot	Sterile	18.2–22.8	3.6–4.7 (–7)	70.65–82.18	64.57–77.82	49.13–66.54	5
<b>P00188110</b> <i>Arbuste – bord du Lac Arnaud 1855–60</i> Label shared with whole sheet	Top left	110-A	Erect 3 orders sparse	Sterile	12.0–17.1	2.7–4.1	69.48–83.50	65.63–79.42	51.86–67.44	5

APPENDIX TABLE 1. (Continued)

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Top centre	110-B	Suberect 2 orders	Male (very few)	13.8–18.5	3.4–4.2	87.06–101.60	79.85–94.74	62.26–71.97 (–79.62)	3
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Right	110-C	Single, long unbranched shoot 26 cm long	Sterile	21.2–24.4	4.0–4.6	78.61–91.76	71.39–83.77	52.84–70.96	5
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Bottom left	110-D	Single, short unbranched shoot 9.1 cm long	Sterile	(9.9–)13.3– 21.1	2.8–4.2	90.31–110.05	77.15–95.35	51.40–69.72	3
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Bottom centre	110-E	Erect or suberect 3 orders, small dark leaves	Male, abundant cones	6.0–12.8 (–15)	2.2–3.9	(67.49–)75.79– 84.75	(60.14)72.01– 76.12	(41.88)54.24– 61.40	6
		110-E				n/a	n/a	<i>Cones</i> 67.07–82.31	57.84–74.76	40.56–60.97
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Packet	110-F	Single, short unbranched shoot fragment with c.14 visible small, rather obovate, darker leaves	Sterile	4.7–7.7	2.3–3.1	71.41–87.33	61.76–80.60	41.17–61.77	6

APPENDIX TABLE 1. (Continued)

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Packet	110-G	Short, apical portion of shoot with c.9 longer, lanceolate, slightly paler leaves	Sterile	11.1–14.4	2.6–3.5	78.24–96.08	72.38–88.23	56.65–65.95	5
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Packet	110-H	Detached cone fragment	Male	n/a	n/a	64.96–73.03	66.92–75.13	49.87–62.19	6
<b>P00188110</b> <i>bord du Lac Arnaud</i> 1855–60 Label shared with whole sheet	Packet	110-J	Single leaf	n/a	11.2	3.5	92.14–100.70	82.87–88.62	60.13–66.38	3
<b>P00188111</b> <i>Baie du Sud</i> 1861–67 Label shared with 111-B	Top left, below packet	111-A	Erect or suberect 2 orders	Sterile	8.5–15.1	2.4–3.6	87.32–105.23	73.81–95.67	44.73–71.30	3
<b>P00188111</b> <i>Baie du Sud</i> 1861–67 Label shared with 111-A	Top left above label	111-B	Erect or suberect 2 orders	Sterile	(8–)11.1– 12.1	(2–)2.7–4.2	(69.89) 75.51–83.20	64.31–78.21	(42.80) 44.17–59.86	4
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, single leaf	111-C	Single leaf	n/a	11.5	3.4	93.50–96.24	84.73–86.73	60.28–64.07	3

APPENDIX TABLE 1. (Continued)

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, 4th from right	<i>111-D</i>	Unbranched shoot fragment	Male (evident at branch tip)	12.2–18.0	(2.4–)3.1– 3.9	96.79–104.63	83.68–88.64	57.09–62.30	3
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, 3rd from right	<i>111-E</i>	Unbranched shoot fragment	Sterile	10.5–17.4	2.0–3.7	74.73–85.32	69.26–80.67	50.90–61.64	4
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, 2nd from right	<i>111-F</i>	Branched shoot fragment, 2 orders	Sterile	8.7–16.3	3.0–4.4	92.01–98.19	78.28–86.06	50.50–64.29	3
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, far right	<i>111-G</i>	Unbranched shoot fragment	Sterile	10.6–16.2	2.5–3.3	96.67–103.06	81.92–90.61	55.97–62.46	3
<b>P00188111</b> <i>Arbuste – bord du lac</i> <i>Arnaud</i> Label shared with 111-D, E, F, G, H	Top right, middle centre near top left corner of label	<i>111-H</i>	Very short fragment of twig with 3 attached leaves and 2 detached leaves adjacent	Sterile	14.2–17.4	3.4–3.7	86.18–108.00	73.59–96.03	52.41–73.91	3
<b>P00188111</b> <i>Deplanche 170</i>	Bottom centre	<i>111-J</i>	Erect or suberect 3 orders	Male (few)	12.9–16.9	2.9–4.1	80.58–106.35	67.39–89.92	48.33–64.17	I
<b>P00188146</b> <i>Deplanche 170</i>	Left	<i>146-A</i>	Erect or suberect 2 orders	Male (few)	15.0–17.9	3.6–4.3	59.44–65.43 (79.87)	48.02–57.50 (68.96)	27.42–40.75 (46.53)	II

APPENDIX TABLE 1. (Continued)

Barcode, locality/year, label details	Specimen location	Specimen code	Branching	Reproductive state	Leaf length (mm)	Leaf width (mm)	Colour profiling values			Collection (inferred)
							Mean R	Mean G	Mean B	
<b>P00188146</b> <i>Deplanche 170</i>	Right	<i>146-B</i>	Erect or suberect 2 orders, small fragment	Male (few)	10.3–15.9 (19.3)	3.1–4.2	57.89–71.91	(43.39)52.64– 60.58	25.77–42.99	II
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Top left	<i>118-A</i>	Short fragment with opposite side branches	Sterile	14.0–16.9	3.9–4.3	51.53–59.22	37.02–48.26	30.77–40.12	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Top centre	<i>118-B</i>	Short fragment	Female, very young	9.7–16.4	3.0–3.7	48.72–58.53	32.40–48.35	27.45–40.94	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Top right	<i>118-C</i>	Erect or suberect somewhat bushy short fragment of 4 branchlets 2 orders	Female, very young	13.4–17.3	3.1–4.4	42.29–73.74	27.03–58.90	27.18–44.70	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Middle left	<i>118-D</i>	Small fragment, unbranched	Sterile	15.2–17.9	2.8–3.7	60.90–66.67	46.96–53.88	33.74–40.03	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Lower left, excl. fragment next to packet	<i>118-E</i>	Branched shoot, branches erect or suberect 2 orders	Female, very young	14.1–19.4	3.5–4.1	62.29–73.21	47.94–60.64	33.19–45.51	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Lower left, very small fragment next to packet	<i>118-F</i>	Very small fragment of few leaves	Sterile	10.8–14.3	3.5–4.1	60.14–74.07	44.36–61.06	31.13–45.33	III
<b>P00188118</b> <i>Pancher s.n. with number Vieillard 1275</i>	Middle right, above packet	<i>118-G</i>	Short fragment, unbranched	Sterile	15.0–20.0	3.7–4.4	59.72–73.57	47.17–60.74	34.53–49.15	III

mounted on sheets P00188108, P00188110 and P00188111, but not on P00188109, whose label simply reads “lac Arnaud”. This provides a second reason for excluding sheet P00188109. ‘Arbuste’ is also absent from the labels of specimens collected from Baie du Sud, viz. sheets P00188106 and P00188107.

- the fact that Carrière described only vegetative characters, implying that he did not see either male or female material, or at least that if sexual material was present on whatever sheet(s) (or specimens) he saw, it must have been easily overlooked because of scarcity, small size or both: sheets P00188109 and P00188110 in their present states both include, among several specimens, at least one collection that bears abundant male cones. However, it is possible that at least some of the specimens on both these sheets might not have been present when Carrière examined them. Indeed, the present constitution of at least some of the sheets definitely post-dates his time: the fragments on the sheet now barcoded P00188111 were removed for photography when sent on loan to Buchholz. There is evidence that some damage occurred during or subsequent to this procedure: at the time of photography, the left-hand side branch of *Deplanche* 170 (here designated *111-J* for reference purposes) was longer and possessed a secondary side branch arising from its left side just above the one coming off from the right, and the side branch coming off just below the apex of the specimen here designated *111-F* (top right, *Vieillard* 1275 from lac Arnaud, second from right) was longer; the missing portion is most probably the shoot tip now mounted immediately to the right (here designated *111-G*). The two twigs now mounted above the *Vieillard* 1275 ‘Baie du Sud 1861–67’ label (*111-A*, *111-B*) have both suffered considerable damage, and it is possible that the packet contains some of the detached portions.
- the leaf measurements, which Carrière gave as 12–17 × 4–5 mm.
- the leaf features: very regularly oval-elliptic, flat.
- the branching habit: Carrière’s description allows for some variation in branching density (“Rameaux et ramules opposés, plus rarement épars” and in leaf density (“plus rarement épars”), suggesting that the material he had to hand comprised more than one shoot. Plants were described as having erect or suberect branches, the secondary branches and branchlets opposite, more rarely scattered, short. This would seem to rule out sheet P00188108, which consists of a single piece comprising just two side branches, although from the point of view of him overlooking the male cones, which are very few on this specimen, this would perhaps actually be the best choice for lectotype. He described the branches as “dressées ou subdressées” (erect or suberect), a character that is most applicable to the shoots mounted on sheets P118109 and P118110.

The seven sheets are as follows.

1. *Barcode P00188106*. Left-hand label: VIEILLARD, HERB. DE LA NOUVELLE CALÉDONIE. / No. 1275. / *Podocarpus nana*, Parl. / Baie du Sud. / 1861–67. Right-hand label: HERB. MUS. PARIS. / *Podocarpus minor* Parlat. / NOUVELLE-CALÉDONIE. / M. VIEILLARD, 1861–1867. – Two specimens, the upper one (*106-A*) male, the lower one (*106-B*) apparently sterile, with small leaves, many of which, on both specimens, have conspicuous paler margins. Because Carrière gave the locality as ‘lac Arnaud’, the indication ‘Baie du Sud’ would seem to exclude this sheet automatically, but there are also other reasons for doing so, as explained later.
2. *Barcode P00188107*. Left-hand label: VIEILLARD, HERB. de la Nouvelle Calédonie. / No. 1275. / *Podocarpus* [*nana* stroked out] *minor* Parl. / Baie du Sud. / 1861–67. Right-hand label: HERBIER E. DRAKE. [Otherwise blank]. – Two specimens, the left-hand one (*107-A*) sterile, the right-hand one (*107-B*) virtually so but with a single, easily overlooked male cone at the tip of one branch. Leaves of the male specimen larger than in P00188106. – The Drake Herbarium was not gifted to the Paris Herbarium until 1913, 9 years after

Drake's death (Staffleu & Cowan, 1976). Therefore, this sheet would not have been available to Carrière before the publication of his 1867 work. For this reason, as well as the facts that Vieillard's label gives the collection period as 1861–1867 and locality as Baie du Sud rather than lac Arnaud, this sheet must be ruled out for lectotypification purposes.

3. *Barcode P00188108*. Left-hand label: VIEILLARD, HERB. de la Nouvelle Calédonie. / No. 1275. / Arbuste; bord du lac Arnaud. / 1855–1860. Right-hand: HERBIER de l'EXPOSITION COLONIALE / Ministère de la Marine. / *Podocarpus minor* Parl. / N<sup>lle</sup> CALÉDONIE. / M. Vieillard 1862. / Catal. No. 1275. – A single specimen (108-A) that bears a couple of male cones at the tip of one its branches, which could easily have been overlooked by Carrière. Leaves very similar in shape and size to the male specimen of P00118107 and giving the impression that they were once part of the same gathering. Clearly the right-hand label on this sheet was added later, because Parlatore did not describe *Podocarpus minor* until 1868. Above the right-hand 'original' label is a third one that reads HERB. MUS. PARIS. / Herbiers des Colonies françaises donnés par le MINISTÈRE DES COLONIES. / 29 septembre 1894. This would suggest that this sheet did not become part of the P herbarium until 1894, long after Carrière had published *Nageia minor*, and therefore, like P00188107, it must be excluded for lectotypification purposes even though the specimen is clearly a duplicate of the one Carrière mentioned from lac Arnaud and is designated 'isotype' in the Paris Herbarium database. The sheet bears later annotations by Buchholz & Gray in 1950 [*Podocarpus minor* (Carr.) Parl. type collection] and de Laubenfels in 1972.
4. *Barcode P00188109*. Label: handwritten, "1275 / Dacrydium / lac Arnaud" (the word 'Arnaud' appears more like 'Afnaud' or 'Abnaud', with what is presumed to be the 'r' quite unlike the 'r' of 'Dacrydium'). Seven small pieces of shoot ('109-A' to '109-G'), the top left ('109-A') and bottom left ('109-E') ones obviously male (cones particularly numerous on 109-E), the other five shoots all apparently sterile and some fragmentary. There is a later determination slip by Guillaumin in 1943 (*Podocarpus minor*) and a typewritten one attributed to de Laubenfels in 1972 (*Decussocarpus minor*, with a second identically typed 'fide slip' above it labelled *Nageia minor*, and with a reference to de Laubenfels in *Blumea* 32: 211, 1987) but there is no evidence that Buchholz saw the sheet. It is possible that Carrière could have seen this sheet, or at least the sheet lacks evidence that he could not have done. However, the handwritten label lacks the word 'Arbuste', found on the labels of some specimens on P00188108, P00188110, P00188111 and P00197538, and the genus assignation 'Dacrydium' was not mentioned by Carrière in the protologue, which assigned the specimen he saw to *Podocarpus*. Therefore the sheet must be excluded for lectotypification purposes even though it is currently labelled 'isotype' in the P Herbarium database.
5. *Barcode P00188110*. Label: design similar to P00188108 but the original text reads "VIEILLARD, Herb. de la Nouvelle Calédonie. / arbuste – bord du Lac Arnaud". / 1855–1860". There is a determination in different handwriting: "*Podocarpus minor* Parl. (nommé par M. Parlatore." This determination obviously dates from after Parlatore's 1868 publication as well as that of Carrière's of the previous year, but the original label does not preclude it from being considered for typification purposes. – Five shoots (110-A to 110-E) of various sizes, the bottom-centre one (110-E) bearing numerous male cones, the top centre one (110-B) also male but with very few cones, the others either sterile (110-A, 110-C) or possibly bearing very young female cones (110-D). Also a packet containing two small shoot fragments, one bearing c.14 small leaves (110-F) and the other c.9 larger ones (110-G) as well as a detached pollen cone fragment (110-H) and a single leaf (110-J). Again there are later determination labels by Guillaumin in 1943 and de Laubenfels in 1972, but not one by Buchholz. The sheet is currently designated 'isotype' in the Paris Herbarium database.

6. *Barcode P00188111*. This sheet bears three different collections as follows: (Top left) Label: reads VIEILLARD, Herb. de la Nouvelle Calédonie. / *Podocarpus nana* [sic] Parl. / Baie du Sud. / 1861–1867. – Two sterile shoot fragments here designated *111-A* and *111-B*. (Top right) Label: very similar to that described in paragraph 1 above, but with minor differences: VIEILLARD, HERB. de la Nouvelle Calédonie. / No. 1275. / arbuste – bord du lac Arnaud. / 1855–1860. Someone else has added a later determination, *Nageia minor* Carr. – Four shoot fragments (one male: *111-D*; others sterile: *111-E*, *111-F*, *111-G*) and a few more or less detached leaves (*111-C*, *111-H*). (Bottom left: *111-J*). Label: *Dammara* [stroked out] / 170 (in pencil) / *Podocarpus* § *Nageia*. Also label at bottom right of whole sheet, which clearly pertains to this gathering: HERB. MUS. PARIS. / *Nageia minor*, Carr. / *Podocarpus minor* Parl. / Prodr. t. XVI. p. 509 / No. 170 / Nouvelle Calédonie – M. Deplanche. 1861. – This is male material of a different collection, apparently made by Deplanche. (Packet, top left of sheet) – this contains mixed contents of by now probably in part unidentifiable origin; for example, the detached male cone could have come from either the top right example of *Vieillard* 1275, *111-D* or from *Deplanche* 170, *111-J*. From the prominence of the larger specimen at bottom centre and the two labels at bottom left and bottom right, this sheet appears to have originally comprised *Deplanche* 170 as either the only or the principal specimen. This example of *Deplanche* 170 was collected in 1861, the two *Vieillard* collections in 1855–60 and 1861–67. Because of this, it is likely that both the *Vieillard* collections, occupying much smaller areas in the upper part of the sheet, could have been added to the sheet later. Buchholz in October 1948 added a long annotation label below the top right specimen, saying, “This is the *type specimen* of *Nageia minor* Carr., now known as *Podocarpus minor* (Carr.) Parl. It was the only specimen of those of *Vieillard* bearing No. 1275 specifically listed accompanied by the note ‘bord du lac Arnaud’. Also the dates given 1855–1860 indicate that this may be his earliest collection of this entity.” Perhaps on account of this, this sheet is the one currently designated ‘holotype’ of *Nageia minor* in the Paris Herbarium database. However, sheet P00188111 comprises material collected at three different localities by two different collectors, and the earliest-mounted appears to have been the *Deplanche* specimen, whereas *Carrière* only specifically cited *Vieillard* as collector and lac Arnaud as locality. If *Carrière* had seen this sheet, in its present composition, he would surely have listed Baie du Sud as another locality in the protologue, but he did not. Furthermore, one of the *Vieillard* collections (that of 1861–67) would not have been available to him. All this indicates, therefore, that, contrary to Buchholz’s annotation, the whole sheet should be excluded for lectotypification purposes. The specimen collected by *Deplanche* is discussed later.
7. *Barcode P00197538*. Two labels at bottom of sheet. Left hand label: VIEILLARD, HERB. de la Nouvelle Calédonie. / No. 1275. / Arbuste; bord du lac Arnaud. / 1855–60. Right-hand label: VIEILLARD, HERB. de la Nouvelle Calédonie. / No. 1275. / *Podocarpus nana* (Parlat.) / baie du Sud. / 1861–67. – Two specimens of different *Podocarpus* species, the top left specimen determined as *P. sylvestris* J.Buchholz by R. D. Hoogland in 1992 and the bottom right specimen determined as *P. longefoliolatus* Pilg. by both Guillaumin in 1943 (also see Guillaumin, 1944, who cites examples of *Vieillard* 1275 under *Podocarpus longefoliolatus* from both Baie du Sud and Wagap, but none of *P. minor*) and Hoogland in 1992. It is most likely that the right-hand label applies to the lower-right specimen and the left-hand label to the top-left specimen. This sheet obviously has to be rejected as neither specimen belongs to *Retrophyllum*.

Of the seven sheets listed above, five can be ruled out for lectotypification purposes for the reasons given, and the choice therefore lies between those barcoded P00188106 and P00188110. Farjon (2010) mentioned that neither of the toponyms ‘lac Arnaud’ and ‘Baie du Sud’ was in current use and that they might have been written by someone who was not the collector. This

may be true of the printed labels but one sheet of *Retrophyllum minus* at Paris (P00188109) bears an older handwritten label giving the toponym 'lac Arnaud'. Study of a geological work contemporary with Carrière's *Traité de Conifères*, by Garnier (1867), shows that in his time the name Lac Arnaud was used for the larger of the two principal lakes of the Plaine des Lacs, now called Grand Lac, while the other lake, currently known as Lac en Huit, was in Garnier's work called Lac Latour. 'Baie du Sud' is the Baie de Prony (Lapie, 1928; McKee, 1972). The two localities are therefore geographically close but not identical, and are today in different communes: Grand Lac (Lac Arnaud) is in Yaté while Baie de Prony (Baie du Sud) is in Le Mont-Dore. Because Carrière only cited, very specifically, material collected "au bord du lac Arnaud", typification must be based on material from that locality alone, rather than from Baie du Sud, the locality of the 'holotype' as given by Farjon (2010). Not only that, but examination of the contemporary botanical literature reveals that no material of the 1861–67 Baie du Sud gathering could possibly have been available to Carrière when preparing his *Traité Général des Conifères*, which was published on 15 January 1867. It was not cited by Parlatore (1868), who cited only one specimen, that from lac Arnaud. More importantly, Brongniart & Gris, who worked at Paris, state (Brongniart & Gris, 1869: 326 and 1871: 342) that [in translation] "M. Balansa gives us complete knowledge of another species of *Podocarpus* ... belonging to the section *Nageia*, and which, for many years, had only been represented in our herbaria by *two poor specimens*, bearing at the top of their short branches small groups of *rather poorly developed* male spikes" [bold italic emphasis mine]. They cite these two specimens as 'Deplanche 1861' and Vieillard "ad ripas lacus Arnaud dicti n° 1275". Consequently, even by 1869 the 1861–67 Baie du Sud collection was not known to Brongniart & Gris, and one must therefore assume that Carrière could not possibly have seen it before publication of *Traité des Conifères* in 1867. Hence, all sheets bearing Vieillard '1861–67' labels must be excluded for lectotypification purposes. This means that sheet P00188106 must be regarded as unsuitable.

Therefore, out of the seven sheets, only one, P00118110, is suitable for lectotypification purposes. The lectotype must therefore be chosen from among the specimens on this sheet. However, at least one of the shoots now mounted on this sheet bears numerous male cones that it would have been difficult for Carrière to overlook if it had been present on the sheet in his time. Farjon (2010) considered both male and sterile material when attempting to typify the species. However, I consider that male material should be excluded, for two reasons.

1. Carrière described only vegetative characters. He may have overlooked the male cones on some specimens because of their paucity, but other material now mounted on the same sheets bears abundant cones that could not have been overlooked, as in the case of the sheet here chosen for lectotypification. Male cones were first described by Parlatore (1868), but still on the basis of the poorly developed ones on the lac Arnaud gathering of Vieillard 1275. As mentioned above, the Baie du Sud 1861–67 gathering numbered Vieillard 1275, which has more abundant, better developed male cones, was not known either to Carrière (1867) or Brongniart & Gris (1869, 1871).
2. Farjon (2010: 939) wrote that "the sterile/male shoots all seem to have been gathered from the same plant". However, careful examination of the material on the six Paris sheets of Vieillard 1275 that belong to *Retrophyllum minus*, and indeed of the one sheet from which I have deduced the lectotype must be chosen, shows that this is not true. The male specimens currently found among some collections of Vieillard 1275 (supposedly) from lac Arnaud, i.e. specimens 108-A, 109-A, 109-E, 110-B, 110-E and 111-D, actually fall into two distinct groups, here regarded as different collections from different plants. Specimens 109-E and 110-E have small dark leaves (much smaller than the 12–17 mm mentioned in the protologue) and abundant cones, while specimens 108-A, 109-A, 110-B and 111-D have larger, paler leaves and mostly very few cones. Unfortunately, analysis of the colour profiles generated by ImageJ reveals that these latter four specimens are identical in

their profile characteristics to *Deplanche* 170 (here designated P00118111 specimen *111-J*: [Appendix table 1](#)), which also bears few male cones. Therefore it is possible that either: i, all these shoots may actually be duplicates of *Deplanche* 170 *111-J*; or ii, *Deplanche* 170 *111-J* and the male specimens numbered *Vieillard* 1275 *108-A*, *109-A*, *110-B* and *111-D* were collected at the same time from the same plant but numbered separately by Deplanche (as 170) and Vieillard (as 1275). (Hopkins & Bradford, 2009, describe a similar practice by the two collectors in gatherings of the genus *Pancheria* Brongn. & Gris). Therefore they, and similar sterile specimens (*109-F*, *110-D*, *111-A*, *111-C*, *111-F*, *111-G* and *111-H*), are all considered unsafe for lectotypification purposes, partly because Vieillard may not have collected them and partly because Carrière could not have seen either gathering numbered *Deplanche* 170, as discussed later.

Among the material currently mounted on sheet P00188110, the fragment at top left (here designated *110-A*) has leaves measuring 12–17 mm long, exactly the range given in the protologue, and it is sterile. This fragment is accordingly here designated lectotype of *Nageia minor* and therefore of *Podocarpus minor*, *Decussocarpus minor* and *Retrophyllum minus*. Its colour profile is shown in [Fig. 11L](#), M. It is curious that another specimen now mounted on this sheet and (by analysis of its colour profile characteristics: data not shown) clearly part of the same gathering, *110-C*, has leaves measuring 21–24 mm, well outside the range quoted in the protologue. However, similar objections can be raised about any of the sheets numbered *Vieillard* 1275 in their current states (except P00118108, which comprises only one specimen), and it can only be assumed that their current compositions post-date Carrière's examination of the material.

The following three specimens at P match *110-A* in their colour profile characteristics and in their morphology: *109-C*, *109-G* and *110-C*. These four specimens match most closely the characters as given in the protologue and are selected as lectotype (*110-A*) and isolectotypes (*109-C*, *109-G* and *110-C*). These four specimens are the only ones here considered to be suitable as lectotypes. All other specimens numbered *Vieillard* 1275, whether labelled from lac Arnaud or Baie du Sud, are not regarded as type material, because morphologically they show evidence of having been collected from plants other than the one from which the lectotype was gathered.

*Material collected by Deplanche.* Vieillard and Deplanche collected much material at the same time in the field. The collection referred to by Brongniart & Gris (1869, 1871) as '*Deplanche* 1861' is clearly the specimen in the Paris herbarium (P) numbered *Deplanche* 170. This collection, according to its printed label, was made in 1861 and is mounted on the sheet barcoded P00188111, which now also bears two fragmentary assemblages numbered *Vieillard* 1275, as discussed above. The first mention of *Deplanche* 170 in the literature is by Brongniart & Gris (1869), who mention it as one of the only two collections of *Podocarpus minor* known to them. As mentioned earlier, Carrière (1867) did not cite it; therefore we must assume that it became available for consultation sometime between 1867 and 1869. If that is so, Carrière could not have seen it before publication of *Nageia minor*.

B channel clearly separated from the other two. Leaves rather rough. L & M, *Vieillard* 1275 *110-A*, chosen as lectotype and with profiles typical of *Vieillard* 1275 gathering 5. Channel separation similar to J & K but leaves much smoother. N & O, *Vieillard* 1275 *110-E*, typical of gathering 6 with small dark leaves and abundant male cones. R & G channels close but separate. Rough texture. P & Q, *Deplanche* 170 *146-A*. All channel values low but channels all separated clearly, G closer to R than B. Compare with G & H – the profiles are different. R & S, *Pancher* s.n. with number '*Vieillard* 1275'. G channel closer to B than to R but all separated. The profiles do not match any of the *Vieillard* 1275 gatherings and this is a unique, female gathering by Pancher.

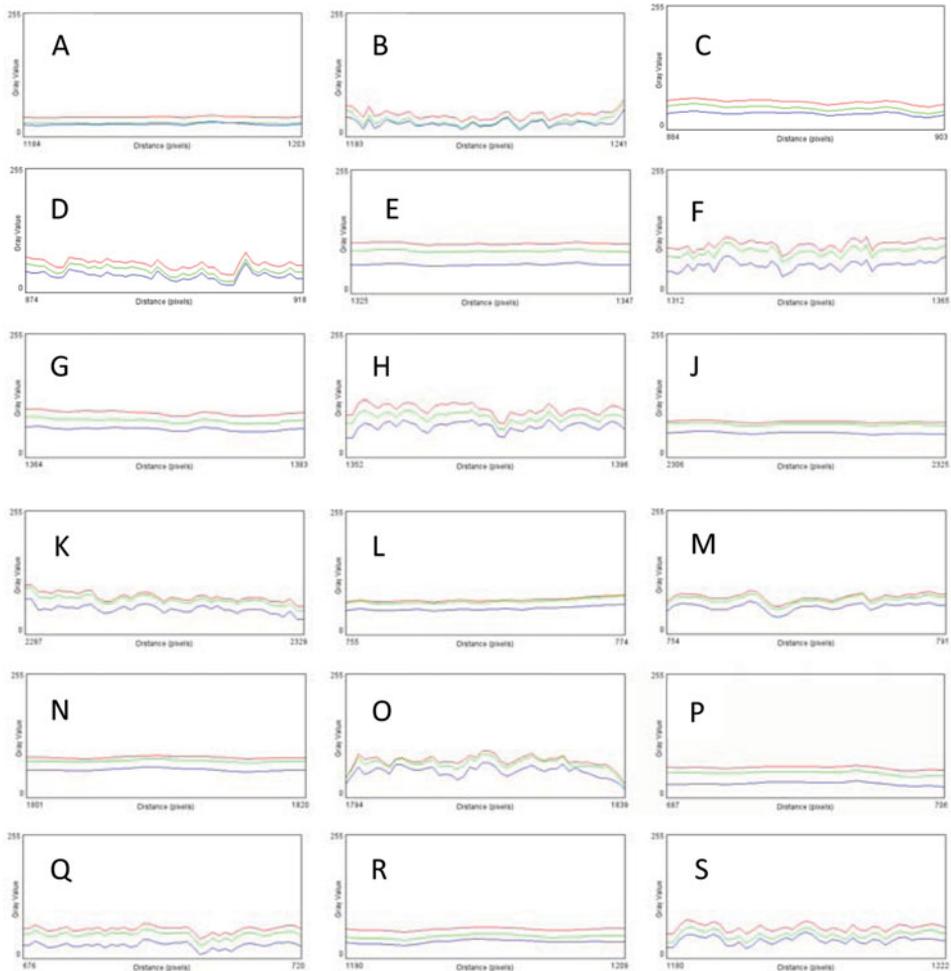


FIG. 11. (Colour online) ImageJ colour profiles of *Retrophyllum minus* leaves. Lines represent colour channels, always from top to bottom: red (R), green (G), blue (B). A, C, E, G, J, L, N, P, R,  $20 \times 20$  px squares; B, D, F, H, K, M, O, Q, S, transverse lines across leaves at midpoint. A & B, *Vieillard 1275 106-A*, Baie de Sud. R channel separate from G and B, which are very close together. A unique profile not found in any other gathering, indicating that this gathering from Baie de Sud ('1' in the last column of [Appendix table 1](#)) is different not only all from the lac Arnaud gatherings of *Vieillard 1275* but also from the other gathering from Baie de Sud. C & D, *Vieillard 1275 107-A*, Baie de Sud. The three channels are all separate from one another. This profile (gathering '2', [Appendix table 1](#)) is similar to *Vieillard 1275* gathering 3 (E, F) and to *Deplanche 170 111-J* (G, H). E & F, *Vieillard 1275 108-A*. All three channels well separated, the B even more so than the R and G. Leaves rough textured (many irregularities in the lines in Fig. 11B). G & H, *Deplanche 170 111-J*. Profiles E–H are typical of *Vieillard 1275* gathering 3 from lac Arnaud and *Deplanche 170* gathering I. They are also very similar to *Vieillard 1275 107-A* and *107-B* ('Baie de Sud', gathering 2), indicating that the three gatherings, or at least the two from lac Arnaud, were most likely made from the same plant at the same time. J & K, *Vieillard 1275 111-E*, typical of gathering 4. R and G channels scarcely separated and sometimes merging;

A second example of *Deplanche* 170 exists at P, namely the sheet barcoded P00188146. According to its printed label, this was collected in 1863, but another label indicates that it was not donated to the P herbarium until 29 September 1894, long after Brongniart & Gris (1869, 1871) published their note. Because the two collections were made in different years, it seems that, like Vieillard, Deplanche may have used the number 170 as a catalogue number rather than a field collection number. (In fact, the number *Deplanche* 170 has also been used for a collection of *Parasitaxus usta* (Vieill.) de Laub. from Pic de Pouébo in the north of New Caledonia, corresponding to *Vieillard* 1269 of that species from the same locality: Gray, 1960, as *Podocarpus ustus*.) Obviously Carrière could not have seen this sheet. Colour profile analysis of the leaves of the two sheets numbered *Deplanche* 170 (Appendix table 1; Fig. 11G, H, P, Q) reveals that they represent collections from two different plants and that the two shoots on the sheet barcoded P00188146 (Fig. 11P, Q) both came from the same plant. As noted above, the colour profiles of the leaves on *Deplanche* 170 111-J (Fig. 11G, H) on the other sheet (P00188111) are identical to 111-A, C, D, F, G, H on the same sheet that are assumed to have been collected by Vieillard, almost certainly from the same plant.

*Alleged female specimens of Vieillard 1275.* Farjon (2010) also claimed that male and female shoots, on different sheets, had been given the number *Vieillard* 1275. It is not clear from his work what was the basis for this statement; de Laubenfels (1972) indicated that *Vieillard* 1275 from both lac Arnaud and Baie du Sud was male, and cited no female material under the number. Likewise, I have not seen any female material numbered *Vieillard* 1275 in the Paris Herbarium that genuinely belongs to any one of the specimens in that assemblage of gatherings. Farjon (2010) mentioned a sheet at K numbered '*Pancher* 1275' that was female and, implicitly at least, regarded it as belonging to *Vieillard* 1275. Pancher typically did not give numbers to his specimens. However, de Laubenfels (1972) cites a female specimen of *Retrophyllum minus* at P collected by Pancher in 1864 at Prony, which is on Baie du Sud. One of the labels on this sheet (now barcoded P00188118, and comprising seven mostly small fragments) is headed '*Vieillard* 1275', but a later curator has pencilled before that number, "C'est la même plant que". There are two possible interpretations of this comment: (1) whoever wrote it was indicating that it was not being regarded as part of *Vieillard* 1275; and (2) it was meant to indicate that it was a duplicate of *Vieillard* 1275 in Pancher's herbarium (apparently, Pancher did 'appropriate' specimens from both Vieillard and Deplanche, according to letters of Deplanche mentioned by Hopkins & Bradford, 2009). Careful examination of the Paris example of the Pancher collection reveals that all seven fragments on it are homogeneous other than three being female and the others sterile (sometimes on account of being such small pieces). Image analysis of the colour profiles of the various fragments supports both the homogeneity of the fragments forming this collection (Appendix table 1; Fig. 11R, S) and that it is a unique gathering, by Pancher, unconnected with *Vieillard* 1275; this is also supported by the fact that three of the fragments are female, whereas only male material has been seen among the fertile specimens on the Paris sheets of *Vieillard* 1275.

*Epitype designation.* Because *Vieillard* 1275 is a mixture of sterile and male material and all of the male material has had to be excluded for typification purposes for the reasons given above, an epitype is designated here to fix the application of the name in relation to *Podocarpus palustris* so that the latter name might be used correctly if in future it were segregated from *Retrophyllum minus* at any rank. Because Buchholz distinguished *Podocarpus palustris* from *P. minor* on the basis of female sexual characters rather than male ones, his specimen *Buchholz* 1729, on whose labels he sets out the differences he perceived, is here chosen as epitype of *Nageia minor* and therefore also of *Podocarpus minor* and *Retrophyllum minus*. Unfortunately, the labels on the NY and P duplicates of *Buchholz* 1729 do not give as much information on the seed characters

as that on a photograph at A of what is here assumed to be the example at ILL. This label reads “This specimen shows the seeds [of *Podocarpus minor*] not previously described. They are deep maroon red, crested, having kernels with straight point. The cone bearing two seeds at left below are rare, not present in any duplicate of this collection. The leaf anatomy of this collection agrees with the Vieillard types. They have wide midveins (not visible externally) and similar loaf-like sclereids”. The locality information (“Plaine des Lacs, along Riv. des Lacs a western tributary of Yate river”) is, however, abbreviated on this label compared with those of the NY duplicate specimen and the photographs of the ILL specimen and dissected seeds at P, and there is no date. Consequently, the NY specimen, whose label is dated and gives a more precise locality, is here designated as epitype. *Buchholz* 1729 was the only collection made by him of *Podocarpus minor* sensu stricto, as opposed to *P. palustris*, according to a list of his collections posthumously published (*Buchholz*, 1955), although, with respect to *P. palustris* at least, that list is incomplete because it does not list the holotype and paratypes of *P. palustris* that are duplicated at Paris, nor does it include the photograph and fragment of *Buchholz* 1719, another specimen of *P. minor* sensu stricto.

## APPENDIX II

*List of accepted names and synonyms*

- Decussocarpus* de Laub. sect. *Decussocarpus* – **Retrophyllum** C.N. Page  
*Decussocarpus comptonii* (J.Buchholz) de Laub. – 3  
*Decussocarpus minor* (Carrière) de Laub. – 4  
*Decussocarpus piresii* Silba – 6  
*Decussocarpus rospigliosii* (Pilg.) de Laub. – 5  
*Decussocarpus vitiensis* (Seem.) de Laub. – 1  
*Nageia* Gaertn. sect. *Polypodiopsis* (C.E.Bertr.) de Laub. – **Retrophyllum** C.N. Page  
*Nageia comptonii* (J. Buchholz) de Laub. – 3  
*Nageia minor* Carrière – 4  
*Nageia piresii* (Silba) de Laub. – 6  
*Nageia rospigliosii* (Pilg.) de Laub. – 5  
*Nageia vitiensis* (Seem.) Kuntze – 1  
*Podocarpus* L’Hér. ex Pers. sect. *Polypodiopsis* C.E.Bertr. – **Retrophyllum** C.N. Page  
*Podocarpus comptonii* J.Buchholz – 3  
*Podocarpus filicifolius* N.E.Gray – 2  
*Podocarpus minor* (Carrière) Parl. – 4  
*Podocarpus montanus* sensu Knuth (1926: 95) non (Humb. & Bonpl. ex Willd.) Lodd. – 5  
*Podocarpus palustris* J.Buchholz – 4  
*Podocarpus rospigliosii* Pilg. – 5  
*Podocarpus vitiensis* Seem. – 1  
**Retrophyllum** C.N. Page  
**Retrophyllum comptonii** (J.Buchholz) C.N. Page – 3  
**Retrophyllum filicifolium** (N.E.Gray) R.R.Mill, comb. nov. – 2  
**Retrophyllum minus** (Carrière) C.N. Page – 4  
**Retrophyllum piresii** (Silba) C.N. Page – 6  
**Retrophyllum rospigliosii** (Pilg.) C.N. Page – 5  
**Retrophyllum vitiense** (Seem.) C.N. Page – 1  
[*Torreya bogotensis* Linden ex K.Koch, nom. utique rejic.] – ?1 or ?5

## APPENDIX III

*List of exsiccatae*

- anon.* 5536 (Department of Agriculture, Fiji) – 1; *Archer, W.A.* 541 – 5; *Asplund, E.* s.n. (no date; Lima botanic garden) – 5; 12027 – 5; *Aubréville, A. & Heine, H.* 130 – 4; 170 – 4; 229 – 3; 241 – 4; *Aymard, R.* (*MacKee* 16325) – 4
- Balansa, B.* 186 – 4; 1381 – 3; *Barets, R.* 8 – 3; *Barrabé, L.* 365 (*Rigault, F. & Barrière, R.* s.n.) – 3; *Barrera, E.* 45 – 5; 46 – 5; 50 – 5; *Baudouin, A.* 542 – 3; *Baumann-Bodenheim, M.G.* 5654B – 3; 6370 – 4; 6378 – 4; 6580 – 4 (juvenile; adult specimen numbered *Guillaumin & Bodenheim* 6580, q.v.); 13923 – 4; 14057 – 3; 15028 – 3; 15178 – 3; 15197 – 3; 15393 – 3; 15411 – 3; *Baumann-Bodenheim, M.G.* see also *Guillaumin & Baumann-Bodenheim* with same numbering sequence; *Bernardi, L.* 335 – 5; 1959 – 5; 9369 – 4; 9445 – 3; 9520 – 3; 9879 – 3; 10131 – 3; 10149 – 3; 10347 – 3; 12754 – 3; *Bernier, J.* s.n. (barcode P00188269) – 3; s.n. (7 iii 1948) – 4; 203 (2 sheets) – 3; 204 – 4; 245 (all 4 sheets) – 4; 246 – 4; 247 – 4; 248 – 4; 249 – 4; 250 – 4; 251 – 4; 267 – 3; 268 – 3; 269 – 3; 270 – 3; 271 – 3; *Betancur, J. et al.* 1817 – 5; *Blanchon, J.P.* 208 – 4; 341 – 3; 399 – 3? (confirmation needed); 736 – 4; 1160 – 4; 1246 – 3; *Bohorquez R., P.* 475 – 5; *Boisseau, P.* (*MacKee* 12725) – 3; *Boorman, J.R.* s.n. – 1; *Brass, L.J.* 12787 – 2; 12787a – 2; 12912 – 2; *Brass, L.J. & Versteegh, C.* 12534 – 2; *Breteler, F.J.* 4495 – 5; *Brinon, H.* 1359 – 3; *Brousriche, E.* s.n. (Pic de Na Kado) – 3; 697 – 3; *Buchholz, J.T.* 1085 – 3 (paratype and isoparatypes); 1222 – 3; 1347 – 4 (paratype & isoparatypes, *Podocarpus palustris*); 1348 – 4 (paratype & isoparatypes, *Podocarpus palustris*); 1350 – 3; 1350a – 3; 1359 – 3; 1359a – 3; 1421 – 4 (holotype of *Podocarpus palustris* ILL, isotypes of *Podocarpus palustris* A–photo, ILL–2 sheets, K, MO, NY, P, RSA, S, TEX, WIS); 1447 – 3 (paratype); 1449 – 3 (paratype and isoparatypes); 1452 – 3; 1474 – 4 (paratypes of *Podocarpus palustris*, ILL00010015, ILL00010022 [photo of latter, A], isoparatype of *Podocarpus palustris*, S); 1578 – 3; 1648 – 3; 1684 – 3 (holotype ILL with photos at A and P, isotypes K, MO, NY, S); 1684s – 3; 1697 – 3 (paratype and isoparatypes); 1697a – 3 (paratype and isoparatypes); 1697s – 3 (paratype and isoparatypes); 1705 – 4; 1719 – 4; 1729 – 4 (epitype); 1791 – 3; *Bunting, G.S.* 4898 – 5; 4939 – 5
- Campos, J. & Rodríguez, E.* 2825 – 5; *Cardenas, C.d.l.A. & Oliveros, S.E.* 198 – 5; *Carr, C.E.* 14160 – 2; 15666 – 2; *Cherrier, J.-F.* (*MacKee* 39235) – 3; (*MacKee* 39255) – 3; (*MacKee* 44895) – 4; *Compton, R.H.* 607 – 3; 608 – 3; 1524 – 3; 1527 – 3; 1587 – 3; *Corbasson, M.* (*MacKee* 13037) – 3; *Cox, P.A.* 1360 – 1; *Cretinon, L. & Gardner, M.F., ICCP New Caledonia Exped. (1999)* 17 – 4; 26 – 4; 44 – 4; 50 – 4; 50A – 4; 73 – 3; 90 – 3; *Cribs, L.* 1493 – 4; 1752 – 4; *Cuatrecasas, J., Schultes, R.E. & Smith, E.* 12768 – 5; *Curran, H.M.* 2147 – 5
- Dagostini, G. et al.* 1340 – 4; *Damanu, E.* G7 – 1; KU22 – 1; L10 – 1; L12 – 1; NH15 – 1; NL10 – 1; R10 – 1; R15 – 1; R32 – 1; *Däniker, A. U.* 228 (6 x 1924) – 4; 228 (11 x 1924) – 4; 228a – 4; 2901a – 3; 2902 – 3; *Daza, A. & Pennington, T.D.* 16464 – 5; *de Laubenfels, D.J.* s.n. (3 xii 1957) – 4; P 112 – 4; P 115 – 4; P 129 – 3; P 153 – 3; P 160 – 4; P 309 – 1; P 360 – 3; P 361 – 3; P 415 – 3; P 508 – 1; 754 – 5; 755 – 5; 756 – 5; *Degener, O.* 14483 – 1; 14484 – 1; 14496 – 1; *Deplanche, É.* 170 (1861) – 4; 170 (1863) – 4 (transitional to 3); *d'Espeissis, J.C.* 1460 – 1; *Dickison, W.C.* 223 – 4; *Dobson, F.H.* III 1277 – 5; *Dugand, A. & Jaramillo, R.* 3962 – 5; *Duque-Jaramillo, J.M.* 2964 – 5; 3108 – 5
- Ehrendorfer, F.* 6600-138-38 – 3; *Erdtman, H.* s.n. (8 ix 1960) – 3; s.n. (9 ix 1960) – 3; *Erdtman, H. & Chevalier, L.* s.n. (8 ix 1960) – 3; *Espejo, E.L.* 29ELE – 5; *Espinal-T., S. & Delgado-F., A.* 1790 – 5; *Esposto, N.* 556 – 5 (holotype B, fragment S, isotypes GH, NY); *Eyma, P.J.* 5155 – 2
- Forero, E. & Forero G., J.* 6207 – 5; *Foster, A.S.* 160 – 3; 200 – 4 (topotype, *Podocarpus palustris*); *Frachon, N.* 1337 – 5; 1340 – 5; *Franc, I.* 207 (i 1914, Plaine des Lacs) – 4; 207 (no date, Prony) – 4; 207 (x 1913, Prony) – 4; 207 (i 1914, Prony) – 4; 207 (Série A, no date, Prony) – 4; 207 (Série A, x 1913, Prony) – 4; *Franco, P., Jaramillo, R. & Uribe, J.* 2430 – 5; *Frodin, D.G.* NGF 26292 – 2; 26917 – 2; *Funck, N. & Schlim, L.J.* 1208 – 5

- García-Barriga, H.* 11038 – 5; 11041 – 5; 11586 – 5; 12492 – 5; 15490 – 5; 17259 – 5; 17584 – 5; 17585 – 5; 18014 – 5; 20159 – 3; 20468 – 5; *García-Barriga, H. & Jaramillo-Mejía, R.* 19866 – 5; *Gardner, M.F. et al., New Caledonia Exped. 2001* 1014 – 3; 1026 – 3; *Gardner, M.F. et al., Third New Caledonia Araucaria Exped.* TNCA 2036 – 3; TNCA 5000 – 4; TNCA 5001 – 4; TNCA 5045 – 3; *Gardner, M.F., Gaudeul, M. & Hollingsworth, P.M.* 02 – 4; 04 – 4; 68 – 3; 85 – 3; 108 – 3; 246 – 3; 256 – 3; *Gardner, M.F., Nieto, E., Alanes, D. & Zenteno, F. (2011)* 30 – 5; 37 – 5; 38 – 5; *Gentry, A., Diaz, C. & Blaney, C.* 61207 – 5; 77310 – 25 (see notes under that species); *Gibbs, L.S.* 674 – 1; *Gideon, O. & Obedi, S.* LAE 77181 – 2; *Gillespie, J.W.* 3865 – 1; *Godefroy, C.\** s.n. – 3; *Goitia, D.* s.n. (UDBC 2060) – 5; (UDBC 2129) – 5; (UDBC 10797) – 5; *Graeffe, E.O.* s.n. (unloc.) – 1; s.n. ('Albizzi Levu') – 1; *Graham, J.G.* 5179 – 5; *Green, P.S.* 1187 – 4; 1216 – 3; 1268 – 3; 1783 – 3; *Grignon, C. et al.* 470 – 3; 559 – 3; 584 – 3; *Guillaumin, A.* 8339 – 4; 8345 – 4; *Guillaumin, A.* see also *Baumann-Bodenheim*, and *Guillaumin & Baumann-Bodenheim*, both with same number sequence; *Guillaumin, A. & Baumann-Bodenheim, M.G.* 6511 – 4; 6580 (adult) – 4 [see also *Baumann-Bodenheim* 6580, juvenile]; 6582 – 4; 6594 – 4; 6766 – 4; 11257 – 3; 11261 – 3; 11282 – 3; 11299 – 3; 11301 – 3; 11749 – 4; 11811 – 4; 12717 – 3; 12725 – 3; 12727 – 3; 12815 – 3; 12843 – 3; 12861 – 3; 12910 – 3; 12960 – 3
- Hammer, P.* s.n. – 1; *Hammermaster, E. & Sayers, D.* NGF 21842 – 2; *Hance, H.F.* 17247 (BM, = *Vieillard* 1275) – 4; *Hartley, T.G.* 15064 – 4; *Henao, J.E.* 237 – 5; *Henty, E.E. & Frodin, D.G.* NGF 27359 – 2; *Hernández Schmidt, M.* 1190 – 5; 1384 – 5; *Hollingsworth, P.M. et al.* 2008: 90 – 3; 153 – 3; 194 – 3; *Huamán, M., Mateo, J.L., Rojas T, C. & Hurtado, D.* 313 – 5; *Humbert, H.* 25588 – 5 (not *Prumnopitys harmsiana* or *Podocarpus harmsianus*); 26148 – 5; *Hürlimann, H.* 931 – 3; 1062 – 3; 1220 – 3; 1573 – 3; 1832 – 3; 1842 – 3; 1964 – 3; 1966 – 3; 3113 – 4; 3157 – 4; 3173 – 3
- Ingle, H.D.* I.44 – 4; I.66 – 3
- Jaffré, T.* 352 – 4; 2585 – 3; *Jahn, A.* 99 – 5; *Jérémie, J. & Tirel, C.* 1572 – 4
- Kinupp, V.F.* 3426 – 6; *Kostermans, A.* s.n. (Morotai, 1949) – 2 (lecto L, foliage only; isolecto A, K); *Kostermans* s.n. (Morotai, 1949) p.p. (L, detached fruits) – *Nageia wallichiana* (C.Presl) Kuntze; *Kuria, T.* 87216 & *Oliver, P.* – 2
- Lam, H.J.* 6932 – 1; *Lauri, P.E.* 45 – 3; *Lauri, P.E. & Gay, H.* 165 – 4; *Lavoix, L. (MacKee 19303)* – 4; (*MacKee 19304*) – 4; (*MacKee 19305*) – 4; *Le Rat, A.* 71 – 3; 149 – 4; 253A – 4; 607 – 4; 751 – 4; 1040 – 4; 2587 – 4; 2621 – 4; *Little Jr., E.L.* 15245 – 5; *Lowry, P.P. II* 5747 – 3; *Lowry, P.P. II et al.* 4683 – 4; 6821 – 3
- MacDaniels, L.H.* 2323 (P-1041) – 3; 2544 – 4; *MacKee, H.S.* (a.k.a. *McKee*) 1118 – 4; 1119 – 4; 2373 – 4; 3377 – 4; 3382 – 4; 3516 – 3; 9886 – 3; 12725 (coll. *P. Boisseau*) – 3; 13037 (coll. *M. Corbasson*) – 3; 13492 – 3; 15594 – 3; 15639 – 3; 16325 (coll. *R. Aymard*) – 4; 17032 – 3; 17056 – 3; 17354 – 3; 17357 – 3; 17358 – 3; 17670 – 3; 17908 – 3; 18694 – 3; 18807 – 3; 18808 – 3; 19303 (coll. *L. Lavoix*) – 4; 19304 (coll. *L. Lavoix*) – 4; 19305 (coll. *L. Lavoix*) – 4; 20244 – 3; 20928 – 3; 21219 – 3; 32355 (coll. *L. Viratelle*) – 4; 33961 – 3; 39997 (coll. *R. Nasi*) – 3; 35577 – 3; 39235 – 3; 39255 (coll. *J.-F. Cherrier*) – 3; 39724 – 3; 40011 (coll. *R. Nasi*) – 3; 40185 – 3; 40376 – 3; 40377 – 3; 43169 – 4; 44895 (coll. *J.-F. Cherrier*) – 4; 46368 (coll. *B. Suprin*) – 3; *Mahecha, S.* s.n. (UDBC 5436) – 5; s.n. (UDBC 11190) – 5; 1391 (UDBC 5985) – 5; *Matallana Tobón, G.* 523 – 5; *Mauriasi, R. et al.* BSIP 17025 – 1; 17794 – 1; *McKee, H.S.* (see *MacKee*); *McMillan, C.* 5015 – 3; 5120 – 4; 5139 – 4; *McPherson, G.D.* 1867 – 3; 2132 – 4; 2191 – 3; 2748 – 4; 2996 – 4; 3066 – 3; 3958 – 3; 4020 – 3; 4121 – 3; 5477 – 3; *McPherson, G.* 19209 & *Mouly, A.* – 3; *McPherson, G. & Munzinger, J.* 18100 – 3; 18149 – 1; 18254 – 3; *McPherson, G. & van der Werff, H.* 17834 – 3; *McPherson, G., Swenson, U. & Mouly, A.* 19070

\* Assignment of initial follows Muséum national d'histoire naturelle (no date, accessed 3 February 2015); this gives C. Godefroy for the collector in New Caledonia and A. Godefroy for the Indo-Chinese collector named Godefroy. Morat (2010) failed to indicate Godefroy's initial(s) in his list of New Caledonian plant collectors.

- 3; 19073 – 3; Mead, J.P. 1964 – 1; 1974 – 1; 1982 – 1; Monteagudo, A., Peña, A., Francis, R. & Mateo, J.L. 13230 – 5; 13353 – 5; Monteagudo, A., Peña, A., Mateo, J.L. & Francis, R. 12942 – 5; 12986 – 5; 13078 – 5; 16407 – 5; Morales, C., Suárez, D. & Endara, S. 867 – 5; Morat, P. 5676 – 3; 7621 – 3; Mosén, H. 4393 – *Holocalyx balansae* Micheli (Fabaceae), fide Lindman (1898); Munzinger, J. 4830 – 4; Munzinger, J. & McPherson, G. 764 – 3; Munzinger, J. 1200, Suprin, B. & Carriconde, F. – 3; 1307, Suprin & Carriconde – 3; Munzinger, J. 1661, Tronchet, F., Le Borgne, T. & Oddi, A. – 3; 1680 – 3; Musselman, L.J. 5280 – 4; 5415 – 3
- Nasi, R. s.n. (MacKee 39997) – 3; (MacKee 40011) – 3; Neill, D. & Jost, L. 15337 – 5; Neill, D. & Salinas, J. 7202 – 5 (atypical); Nicholson, R. 348/92 (wild collection source of Frachon 1340) – 5
- Page, C.N. 22030 – 4; 22031 – 4; 22032 – 4; 22033 – 4; 22034 – 4; 22041 – 3; Palacios, W. & Tirado, M. 13026 – 5; 13159 – 5; Pancher, J.A.I. s.n. (barcode P00188209) – 3; s.n. (unloc.) – 4; s.n. (“C’est la même plant que Vieillard 1275”, material from Prony) – 4; s.n. (“C’est la même plant que Vieillard 1275”, high-altitude material from Cougui and Mt. Mou) – 3; Pearce, R. s.n. (vii 1860) – 5; Peni, T. 636 – 1; Pennington, R.T. 1422 – 5; 1426 – 5; 1427 – 5; 1431 – 5; 1433 – 5; Perea, J. 381, Mateo, C., Francis, R. & Ortiz, G. – 5; Pérez-Arbeláez, E. 3150 – 5; 4798 – 5; Petit, G. 138 – 4; Piao, W. BSIP 7061 – 1; Pintaud, J.C. 51 – 3; Pires, M. & Rosa, N. 850 – 6; Pittier, H. 12756 – 5; Pullen, R. 2840 (LAE 96292) – 2
- Quirós Quirós, B. 75 – 5; Quizhpe, W., Medina, B., Aguirre, C. & Prado, M. 1092 – 5; Quizhpe, W. & Wisum, A. 2461 – 5
- Raoul, N. s.n., no date (Plaine des Lacs, barcode P00188116) – 4; Redrodro, M. K110 – 1; Résineux no. 8, coll. R. Virot – 3; Rigault, F. & Barrière, R. s.n. (Barrabe, L. 365) – 3; Rodrigues, W., Pires, J.M. & ‘Rosas, S.N.’ [sic = Rosa, N.?] 9646 – 6; Rodríguez-C., Á., Sarmiento, H. & Cruz, P. 505 – 5; Rohrdorf, O. 178 – 4; Roldán, F.J. et al. 3168 – 5; Roncancio, D. 23 – 5; 024 – 5; 055 – 5; Rosa, N.A. et al. 856 – 6 (holotype US, isotypes K, L, MG, MO, NY, R, RB; protologue has number misprinted ‘Rosa & Pires 586’); 856 – 6 (iso INPA, information on label differs from other sheets); Ruiz Terán, L. 918 – 5; 1148 – 5
- Sands, M.J.S. 2381 et al. – 2; Sarlin, P. 73 – 4; 228 – 3; 238 – 3; Schlechter, R.F.R. 15331 – 3; 15332 – 3; Schmid, R. 137 – 3; 1422 (wrongly in NOU-database as ‘M. Schmid’) – 3; 4838 (wrongly in NOU-database as ‘M. Schmid’) – 3; Schmidt-Mumm, U. 324 – 5; Schneider, M. 905 – 5; Schnell, R. 10647 – 1; Seemann, B. 576 sheet 1/2 – 1; Seemann 576 sheet 2/2 – 1 (lectotype K, isolecto BM–2 sheets, E, S); Selling, O.H. 78 – 4; 202 – 3; 208 – 3; Service des Eaux et Forêts, Nouméa 225 – 4; 226 – 4; Sévenet, T. 958 – 3; Silba, J. B-640 – 3; B-654 – 4; Skottsberg, C. 202 – 3; Smith, A.C. 1796 – 1; 7076 – 1; Smith, D.N. & Brack, W. E. 7634 – 5; Smith, D., Brack, W. & Palomino, J. 1752 – 5; Sobel, G.L. & Strudwick, J. 2130 – 5; Soukup, J. 1801 – 5 (but loose seed in packet, NY, belongs to Archer 541); 4401 – 5; Stauffer, H.U. & Blanchon, J.P. 5807 – 4; Stergios, B.G., Caracas, R. & Zambrano, L. s.n. – 5; 20755 – 5; Steyermark, J.A. 55999 – 5; 98706 et al. – 5; Stone, B.C. 14836 – 4; Suprin, B. 693 – 4; 1407 – 3; 1612 – 3; 1636 – 3; 1830 – 3; 2628 – 3; s.n. (MacKee 46368) – 3
- Terán, L. Ruiz see Ruiz Terán, L.; Teulon, W. s.n. (J.H. & B.H. Tothill 844) – 1; Thorne, R. 28565 – 4; Tothill, Mr & Mrs. (J.D. & B.H.) 844 (coll. W. Teulon) – 1; Triana, J.J. 665 – 5; 1800 – 5
- Uribe Uribe, L. 1734 – 5
- van Royen, P. & Sleumer, H. 6073 – 2; Vásquez, A.M. 3 – 5; 5 – 5; Vásquez, R. & Jaramillo, N. 20459 – 5; Vaughan, J.H. 3254 – 1; Veillon, J.M. 120 – 3; 122 – 3; 281 – 3; 949 – 3; 2962 – *Falcatifolium taxoides* (Brongn. & Gris) de Laub.; 3305 – 3; 3514 – 3; 5659 – 3; 6062 – 3; 6747 – 3; 6783 – 3; Vélez, J.G. 6946 – 5; Vélez-Puerta, J.M. 1999 – 5; Versteegh, C. B.W. 913 – 2; Vieillard, E. 1265 – 3; 1275 (unloc., coll. Pancher) – 4; 1275 (Baie du Sud, 1861–1867) – 4; 1275 (BM, also numbered Hance 17247) – 4; 1275 (lac Arnaud, 1855–1860) – 4 (lectotype and 4

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isolectotypes, P, plus other non-type material as indicated in Appendix I); 3064 – 3; 3264 p.p. (Mont Mou) – 3; 3264 p.p. (Wagap) – 3; *Villamizar, H. & Guevara, F.* 63 (UDBC 2223) – 5; *Vink, W. & Schram, F.A.W.* BW 8730 – 2; *Viratelle, L.* (*MacKee* 32355) – 4; *Virost, R.* s.n. (19 vi 1938) – 3; 38 – 3; 658 – 4; *Résineux no.* 8 – 3  
*Walker, F.S.* BSIP 212 – 1; *Watt, A.* 519 – 3; *Webster, G.L.* 19205 – 4; *Webster, G.L. & Hildreth, R.* (with *Kuruvoli, I.*) 14270 – 1; 14277 – 1; *Weigend, M., Diané, N., Gottschling, M., Hilger H. & Skrabal, J.* 5795 – 5; *White, C.T.* 2033 – 3; 2120 – 3; 2261 – 4; *Whitmore, T.* BSIP 1580 – 1; *Woods, P.J.B.* 241 – 2; 345 – 2 (epitype E, isoepitype K); *Wright, J.A.* 047 – 5  
*Zlarnik, W.G.* 30 – 3