



# Relict lineages with extreme ecology and physiology: metal hyperaccumulation on ultramafic substrates in New Caledonian Alseuosmineae (Asterales)

Karine Gotty, Gael J. Kergoat, Pierre Jouannais, Vanessa Invernón, Sylvain Merlot, Yohan Pillon

## ► To cite this version:

Karine Gotty, Gael J. Kergoat, Pierre Jouannais, Vanessa Invernón, Sylvain Merlot, et al.. Relict lineages with extreme ecology and physiology: metal hyperaccumulation on ultramafic substrates in New Caledonian Alseuosmineae (Asterales). *Plant ecology & diversity*, 2022, 15 (5-6), pp.227-242. 10.1080/17550874.2022.2093290 . hal-03777188

HAL Id: hal-03777188

<https://hal.science/hal-03777188>

Submitted on 14 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

1   **Relict lineages with extreme ecology and physiology: metal**  
2   **hyperaccumulation on ultramafic substrates in New Caledonian**  
3   **Alseuosmineae (Asterales)**

4  
5   Karine Gotty<sup>1</sup>, Gael J. Kergoat<sup>2</sup>, Pierre Jouannais<sup>3</sup>, Vanessa Invernon<sup>4</sup>, Sylvain Merlot<sup>3</sup>, Yohan  
6   Pillon<sup>1</sup>

7  
8   <sup>1</sup>Laboratoire des Symbioses Tropicales et Méditerranéennes (LSTM), IRD, INRAE, CIRAD,  
9   Institut Agro, Univ. Montpellier, Montpellier, France

10   <sup>2</sup>CBGP, INRAE, CIRAD, IRD, Institut Agro, Montpellier, France

11   <sup>3</sup>Université Paris-Saclay, CEA, CNRS, Institute for Integrative Biology of the Cell (I2BC),  
12   91198, Gif-sur-Yvette, France

13   <sup>4</sup>Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire  
14   naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, Paris, France

15

16

17   Special Issue ‘The Ecology and Evolution of Plants in Extreme Environments’

18

19

20   Word count: 6054

21

22

23    **Abstract**

24

25    **Background:** Relict lineages are an important component of the biodiversity, but it is unclear  
26    under what circumstances these groups persist. A potential example of such a group is the  
27    Alseuosmineae (Asterales) of Oceania. This clade contains the three small families-  
28    Alseuosmiaceae, Argophyllaceae and Phellinaceae. The clade has highest diversity in New  
29    Caledonia, where there are extensive ultramafic substrates, creating an extreme edaphic  
30    environment.

31

32    **Aims:** Using several lines of evidence we aimed to show that Alseuosmineae qualify as a relict  
33    lineage, with specialized adaptations for ultramafic substrates.

34

35    **Methods:** Molecular phylogenetics and dating analyses were carried out on representatives  
36    from all Alseuosmineae genera. Metal concentration in 33 out of 44 Alseuosmineae species  
37    was measured in herbarium specimens with XRF spectrometry.

38

39    **Results:** Dating analyses indicated that Alseuosmineae began diversifying about 75-80 million  
40    years ago, and had much slower net diversification rates than other Asterales groups. One-third  
41    of the species occur on ultramafic substrates in New Caledonia. Six are categorised as nickel  
42    hyperaccumulators, and two as manganese hyperaccumulators.

43

44    **Conclusions:** Extinction was probably paramount in the history of Alseuosmineae, especially  
45    for continental species. We postulate that their adaptation to ultramafic substrates and metal  
46    accumulation may have contributed to their survival until today.

47

48 **Keywords**

49 Australia, island biogeography, molecular dating, refugium, serpentine

50

51    **Introduction**

52    Relicts are ‘species or a group of species remaining from a large group that is mainly extinct’  
53    (Grandcolas et al. 2014). The use of the term ‘relicts’ in evolutionary biology is ancient, as  
54    Wallace (1880 p. 296) stated regarding the flora of Saint Helena: ‘*For, on the theory of  
55    evolution, nothing can be more certain than that groups now broken up and detached were  
56    once continuous, and that fragmentary groups and isolated forms are but the relics of once  
57    widespread types, which have been preserved in a few localities where the physical conditions  
58    were especially favourable, or where organic competition was less severe.*’ Stebbins (1950)  
59    discussed the morphological features of Ranales, a group once thought to include ‘primitive’  
60    living angiosperms. He wrote (p.8): ‘*the group includes a high proportion of species which on  
61    the basis of all characteristics must be placed not only in monotypic genera but even  
62    monogeneric or digeneric families. They are obviously relict types of which the close relatives  
63    have long since become extinct.*’ He (p.8) also noticed that ‘*the genera and species are at  
64    present strongly concentrated in eastern Asia and Australasia*’, an idea that re-emerged later  
65    (Morley 2001) when molecular phylogenetics shed new light on the true earliest diverging  
66    lineages within angiosperms. The term ‘relict’ was also extensively used by Carlquist (1965,  
67    1974) regarding island biology, particularly in the context of ‘continental’ islands. Related  
68    concepts in paleobiology include ‘bradytelic lineages’ – lineages with little morphological  
69    diversity, low rates of morphological change and low taxonomic diversity (Eldredge 1979), and  
70    ‘dead clades walking’ – clades that survived extinction events only to become marginal or  
71    eventually disappearing (Jablonski 2001). Importantly, species belonging to relict lineages may  
72    be considered to have more values in conservation biology than species from larger and more  
73    recent radiations, as they represent the sole survivors of groups with unique traits (Vane-Wright  
74    et al. 1991).

75        The biodiversity hotspot of New Caledonia in the Southwest Pacific is well known for  
76        being home to *Amborella* Baill., the sister group to all other extant angiosperms (Poncet et al.  
77        2019). The term ‘relict’ was already present in the work of the earlier scholars of the New  
78        Caledonian biota: Virot (1956, p.354), Holloway (1979, p.58, p.79), and many vascular plant  
79        lineages there could qualify as relicts (Pillon et al. 2017). One such group is the  
80        Alseuosmiaceae–Argophyllaceae–Phellinaceae (APA clade = suborder Alseuosmineae), with  
81        ca. 44 species within the species-rich order Asterales (ca. 28000 spp. Christenhusz and Byng  
82        2016). The existence and affinities of the APA clade were not suspected before the advent of  
83        molecular phylogenetic studies (Kårehed et al. 1999). The genera now included in these three  
84        families have been historically placed in various families, including Aquifoliaceae,  
85        Caprifoliaceae, Escalloniaceae, or Saxifragaceae, that are quite distantly related (Angiosperm  
86        Phylogeny Group IV, 2016). A later molecular phylogenetic study indicated that the enigmatic  
87        and unplaced genus *Platyspermation* Guillaumin, originally described in Myrtaceae  
88        (Guillaumin 1950), was sister to Alseuosmiaceae (Lundberg and Bremer 2003), where it is now  
89        included. The APA clade now includes 7-8 genera and ca. 44 species (Table 1) from eastern  
90        Australia, Lord Howe Island, New Caledonia, New Guinea, New Zealand, and Rapa Iti (Figure  
91        1).

92        Similarly to most Asterales (see the review of Martínez-Millán 2010), the fossil record of  
93        Alseuosmineae is sparse, consisting either of very recent fossils from the Quaternary or of three  
94        well-assigned fossils from the Early Miocene of New Zealand (Conran et al. 2014; Pole 2008,  
95        2010; see also Shepherd et al. 2020).

96

97

98

99

100      **Table 1.** List of species in the Alseuosmineae with their natural distribution. Intraspecific and  
101      hybrid taxa are not shown. Underlined: restricted to ultramafic substrates of New Caledonia,  
102      Dotted underlined: occurring on ultramafic and other substrates in New Caledonia.  
103

Alseuosmiaceae Airy Shaw

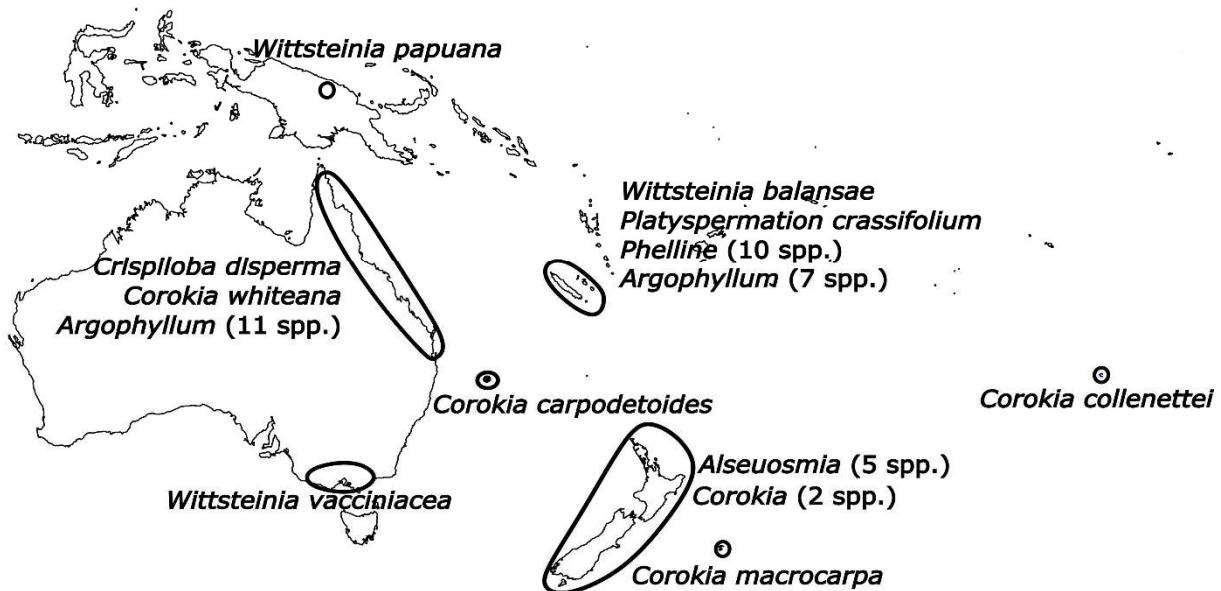
- Alseuosmia banksii* A.Cunn. – New Zealand  
*Alseuosmia macrophylla* A.Cunn. – New Zealand  
*Alseuosmia pusilla* Colenso – New Zealand  
*Alseuosmia quercifolia* A.Cunn. – New Zealand  
*Alseuosmia turneri* R.O.Gardner – New Zealand  
*Crispiloba disperma* (S. Moore) Steenis – Australia  
*Platyspermation crassifolium* Guillaumin – New Caledonia  
*Wittsteinia (= Periomphale) balansae* (Baill.) Steenis – New Caledonia  
*Wittsteinia papuana* (Steenis) Steenis – New Guinea  
*Wittsteinia vacciniacea* F.Muell. – Australia

Argophyllaceae (Engl.) Takht.

- Argophyllum cryptophlebum* Zemann – Australia  
*Argophyllum curtum* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum ferrugineum* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum heterodontum* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum iridescent* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum jagonis* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum lejourdanii* F.Muell. – Australia  
*Argophyllum loxotrichum* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum nullumense* R.T.Baker – Australia  
*Argophyllum palumense* A.R.Bean & P.I.Forst. – Australia  
*Argophyllum verae* P.I.Forst. – Australia  
*Argophyllum brevipetalum* Guillaumin – New Caledonia  
*Argophyllum ellipticum* Labill. – New Caledonia  
*Argophyllum grunowii* Zahlbr. – New Caledonia  
*Argophyllum montanum* Schltr. – New Caledonia  
*Argophyllum nitidum* J.R.Forst. & G.Forst. – New Caledonia  
*Argophyllum vernicosum* Däniker – New Caledonia  
*Argophyllum riparium* Pillon & Hequet – New Caledonia  
*Corokia buddleioides* A. Cunn. – New Zealand  
*Corokia cotoneaster* Raoul – New Zealand  
*Corokia macrocarpa* Kirk – Chatham Islands  
*Corokia carpodetoides* (F.Muell.) L.S.Sm. – Lord Howe Island  
*Corokia collenettei* L.Riley – Rapa Iti  
*Corokia whiteana* L.S.Sm. – Australia

Phellinaceae (Loes.) Takht.

- Phelline barrierei* Barriera & Schlüssel – New Caledonia  
*Phelline billardierei* Pancher ex Loes. – New Caledonia  
*Phelline brachyphylla* Baill. – New Caledonia  
*Phelline comosa* Labill. – New Caledonia  
*Phelline dumbeensis* Guillaumin – New Caledonia  
*Phelline erubescens* Baill. – New Caledonia  
*Phelline gracilior* (Loes.) Barriera – New Caledonia  
*Phelline indivisa* (Baill.) Harms & Loes. – New Caledonia  
*Phelline lucida* Vieill. ex Baill. – New Caledonia  
*Phelline macrophylla* Baill. – New Caledonia



104

105 **Figure 1.** Distribution of Alseuosmineae (Asterales) in Oceania.  
 106

107 The APA clade is most diversified in New Caledonia, with four genera (three endemic)  
 108 and 19 species (all endemic). This archipelago is also well-known for the extent of ultramafic  
 109 rocks that have shaped its flora (Isnard et al. 2016) and filtered some plant families (Pillon et  
 110 al. 2010). Ultramafic rocks are composed of minerals high in magnesium and metals including  
 111 nickel. These rocks weather to produce soils with extremely low Ca/Mg molar ratios and high  
 112 concentrations of metals available to plants (Kazakou et al. 2008; Proctor 2003). Some of the  
 113 specialised physiological adaptations of plants to ultramafic substrates are metal tolerance and  
 114 hyperaccumulation. New Caledonia is one of the world's major biodiversity hotspots for metal  
 115 hyperaccumulating plant species (Reeves et al. 2018). Within the APA clade Ni  
 116 hyperaccumulation was first reported in *Argophyllum* J.R.Forst. & G.Forst. (Jaffré 1980). More  
 117 recently a systematic screening of the herbarium of New Caledonia has also revealed Ni  
 118 hyperaccumulation in *Phelline* Labill. and manganese hyperaccumulation in *Platyspermation*  
 119 (Gei et al. 2020).

120 Relict lineages have often been studied with two approaches, (*i*) through the  
121 reconstruction of ancestral characters, or (*ii*) through the reconstruction of ancestral areas in  
122 biogeography, often with the wrong assumption that they have conserved ancestral characters.  
123 Few of these studies have considered the particular ecological settings where relicts are more  
124 likely to be found. Interpretations of the habitat conditions of the early diverging angiosperms  
125 suggested a preference for shady, wet, and disturbed habitats (Feild et al. 2004), or tropical  
126 montane cloud forests (Pouteau et al. 2020). Relicts within crown clades of angiosperms (*i.e.*,  
127 Eudicots and Monocots) have been comparatively less studied, but preferences for humid  
128 subtropical/warm-temperate forests have also been found in 133 relict genera of East Asia  
129 (Tang et al. 2018). Most studies have therefore focused on climatic preferences and have  
130 emphasized the importance of Pleistocene glacial refugia (Cao et al. 2016; Pouteau et al. 2015).  
131 In contrast, other authors (*e.g.*, Parsons 2005) have suggested that relict lineages are more likely  
132 to survive in harsh or fluctuating environments where the presence of predators or competitors  
133 is less likely and reduces negative interspecific interactions. Alseuosmineae are therefore an  
134 interesting model to investigate the ecological niches of relicts through analyses of plant-soil  
135 interactions.

136 Alseuosmineae have been the subject of several recent taxonomic reviews that have  
137 clarified species limits, particularly in the genera *Alseuosmia* A.Cunn. (Shepherd et al. 2020),  
138 *Argophyllum* (Bean and Forster 2018; Pillon and Hequet 2021) and *Phelline* (Barriera 2017,  
139 2020). The first aim of this study is to demonstrate that Alseuosmineae qualify as a relict  
140 lineage. We use molecular phylogenetics and molecular dating analyses to reconstruct the  
141 evolutionary history of the group. Particular attention is given to the New Caledonian endemic  
142 genus *Periomphale* Baill. (sometimes included in *Wittsteinia* F.Muell.), which has never been  
143 included in any molecular phylogenetic study. We also characterise edaphic preferences for

144 New Caledonian Alseuosmineae and determine their metal concentration with novel  
145 measurements to measure the frequency of metal (hyper)accumulation in the group.

146

147 **Material and methods**

148

149 **DNA extraction and sequencing**

150 Silica-dried leaf material of *Periomphale balansae* Baill. was obtained from the Herbarium of  
151 New Caledonia (NOU, Bruy et al. 2022) (herbarium code according to Thiers 2021). Total  
152 genomic DNA was extracted following a modified cetyltrimethylammonium bromide (CTAB)  
153 protocol (Doyle and Doyle 1987).

154 Three plastid genes were amplified by PCR. The ATP synthase subunit beta (*atpB*) was  
155 amplified in two fragments with the primers rbcL1pro from Mast et al. (2005), S1494R, S611  
156 from Hoot et al.(1995) and S766RProt modified from Hoot et al. (1995). The NADH  
157 dehydrogenase F (*ndhF*) was amplified in two fragments with primers -52pro, 972Rpro,  
158 972Fgre and 2100Rgre from Mast et al. (2008). The ribulose bisphosphate carboxylase large  
159 chain (*rbcL*) was amplified using primers rbcL1F of Fay et al. (1997) and rbcL889R from  
160 Vidal-Russell and Nickrent (2008). The PCR amplification program consisted of 5 min of initial  
161 denaturation at 80 °C, followed by 30 cycles of 1 min denaturation at 95 °C, 1 min of annealing  
162 at 50 °C, 1.5 min elongation at 65 °C, and a final hold of 4 min at 65 °C. Purification and  
163 bidirectional sequencing were carried out by an external service (Genoscreen, Lille, France) on  
164 an automated sequencer using BigDye Terminator V3.1 Cycle sequencing kit. The resulting  
165 sequences were deposited in GenBank (see Table S1 for the corresponding accession numbers).

166

167 **Molecular dataset**

168 To establish the phylogenetic placement of *Periomphale balansae* we used GenBank to  
169 assemble a molecular dataset consisting of the three sequenced plastid genes. We included 10  
170 members of the APA clade, with at least one representative of all Alseuosmineae genera.  
171 Species in Alseuosmiaceae included *Alseuosmia macrophylla*, *Crispiloba disperma*,  
172 *Platyspermation crassifolium*, and *Wittsteinia vacciniacea*. Species in Argophyllaceae included  
173 *Argophyllum cryptophlebum*, *Argophyllum nullumense*, and *Corokia cotoneaster*. Species in  
174 Phellinaceae included *Phelline billardierei*, *Phelline comosa*, and *Phelline lucida*. For outgroup  
175 selection, we included *Stylium graminifolium* in the Stylidiaceae family. Phylogenetically,  
176 Stylidiaceae is sister to Alseuosmineae (Ramírez-Barahona et al. 2020). As a more distinct  
177 outgroup (see also Ramírez-Barahona et al. 2020) we selected *Menyanthes trifoliata*, a member  
178 of the Menyanthaceae family. GenBank accession numbers and voucher information for all  
179 corresponding sequences are presented in the Appendix.

180 The sequences of the three plastid gene fragments were slightly variable in length. Their  
181 alignment was accomplished using MAFFT v7 (Katoh and Standley 2013) with default option  
182 settings. For all gene fragments, we used Mesquite v3.61 (Maddison and Maddison 2019) to  
183 check the coding frame for possible errors or stop codons. The combination of the three gene  
184 fragments resulted in a combined matrix of 13 specimens and 5030 aligned characters (with ca.  
185 16% of missing data).

186

### 187 ***Phylogenetic inference***

188 Phylogenetic analyses were conducted using both Bayesian inference (BI) and maximum  
189 likelihood (ML). For both analytical approaches, partitioned analyses were implemented to  
190 improve phylogenetic accuracy (Nylander et al. 2004). The dataset was divided a priori into  
191 nine partitions, with three partitions (one per codon position) defined for each chloroplastic

192 gene fragment. The best partitioning schemes and models were determined using ModelFinder  
193 (Kalyaanamoorthy et al. 2017) with default settings.

194 Bayesian inference analyses were performed with BEAST v1.10.4 (Suchard et al. 2018).  
195 The BI partitioned analyses consisted of 50 million generations of MCMC with the parameters  
196 and trees sampled every 5000 generations. A maximum credibility tree was further generated  
197 with TreeAnnotator v1.10.4 (Suchard et al. 2018), after removing the first 25% of topologies  
198 as burn-in. Convergence of runs was assessed by examining the ESS of parameters under Tracer  
199 v.1.7, using the recommended threshold of 200 (Drummond et al. 2006). Support of nodes for  
200 the BEAST analyses was provided by clade posterior probabilities (PP), as directly estimated  
201 from the majority-rule consensus topology. Nodes supported by  $PP \geq 0.95$  were considered  
202 strongly supported following Erixon et al. (2003).

203 Maximum likelihood analyses were conducted with IQ-TREE v2 (Minh et al. 2020).  
204 The best-score ML tree was obtained using a heuristic search implementing 500 random-  
205 addition replicates with the following settings: random-starting tree, hill-climbing nearest  
206 neighbour interchange (NNI) search (*-allnni* option), perturbation strength of 0.2 (*-pers 0.2*  
207 option), partition-resampling strategy (*--sampling GENE* option), best partition scheme  
208 allowing the merging of partitions (*-m MFP+MERGE* option). Support of nodes for the IQ-  
209 TREE 2 analyses was assessed using 1000 replicates for both ultrafast bootstraps (Minh et al.  
210 2013) and SH-like approximate likelihood ratio tests (SH-aLRT; Guindon et al. 2010). Nodes  
211 supported by ultrafast bootstrap values (uBV)  $\geq 95\%$  and SH-aLRT values  $\geq 80\%$  were  
212 considered as strongly supported following authors' recommendations.

213

#### 214 ***Molecular dating***

215 Molecular dating analyses were carried out using Bayesian relaxed clocks as implemented in  
216 BEAST v1.10.4 (Suchard et al. 2018). First, we implemented primary fossil calibrations relying

217 on the three Alseuosmineae fossils. The first is a dispersed leaf cuticle assigned to the genus  
218 *Argophyllum* (see Pole 2008 for a complete description), from the Early Miocene of Central  
219 Otago in New Zealand (fluvial-lacustrine Manuherikia Group). This formation is from the  
220 Altonian stage of New Zealand dated at 15.9-19.0 Million years ago (Ma). As a conservative  
221 estimate, we used the youngest age estimated for this formation (15.9 Ma) to set a minimum  
222 age. Since our sampling for the genus *Argophyllum* is not comprehensive and because we  
223 cannot exclude the possibility that this Miocene cuticle is sister to all extant *Argophyllum*  
224 species, we used this as a stem calibration. The second calibration is based on a dispersed leaf  
225 fossil cuticle assigned to the genus *Phelline* (see Pole 2010 for a complete description) also  
226 found in the fluvial-lacustrine Manuherikia Group. Similarly to the *Argophyllum* fossil, we used  
227 this fossil for stem calibration with a minimum age of 15.9 Ma. The third fossil is a compression  
228 fossil (flower) assigned to the genus *Alseuosmia* (see Conran et al. 2014) from the Early  
229 Miocene of the Foulden Hills Diatomite Formation of New Zealand (Foulden Maar locality).  
230 This formation is from the Early Miocene (16.0-23.0 Ma) and was also radiometrically dated  
231 at *ca.* 23 Ma (Lindqvist and Lee 2009). This age corresponds to the age of the Aquitanian stage  
232 (20.44-23.03 Ma; Walker et al. 2018). To be conservative we set a minimum age for the stem  
233 of *Alseuosmia* at 20.44 Ma. For the three calibrated nodes and the root we also set a maximum  
234 age which was conservatively based on the lowest boundary of the 95% HPD of the age of the  
235 MRCA of Asterales (*i.e.*, 114.93 Ma) from the study of Ramírez-Barahona et al. (2020).

236 In a complementary way we relied on secondary calibrations derived from the study of  
237 Ramírez-Barahona et al. (2020) who analysed a multi-marker molecular dataset of 1209 taxa  
238 encompassing all 435 currently recognized plant families. In this study, up to 238 fossil  
239 calibrations were used to infer divergence time estimates within angiosperms. Importantly their  
240 sampling includes 49 Asterales representatives, of which six belong to the APA clade. Based  
241 on the taxa shared between our dataset and theirs, we were able to set secondary calibrations

242 for six nodes. We relied on ages estimated with the relaxed calibration dating strategy with the  
243 complete fossil set: (i) MRCA of sampled Alseuosmiaceae (median age of 23.40 Ma; 95%  
244 highest posterior densities, HPD: 5.05-45.53 Ma), (ii) MRCA of sampled Argophyllaceae  
245 (median age of 18.75 Ma; 95% HPD: 5.45-34.50 Ma), (iii) MRCA of sampled Phellinaceae  
246 (median age of 12.60 Ma; 95% HPD: 3.27-26.59 Ma), (iv) MRCA of sampled [Argophyllaceae  
247 + Phellinaceae] (median age of 71.81 Ma; 95% HPD: 36.52-95.02 Ma), (v) MRCA of sampled  
248 Alseuosmineae (median age of 81.07 Ma; 95% HPD: 48.18-102.23 Ma), and (vi) MRCA of  
249 [Alseuosmineae + *Stylium graminifolium*] (median age of 92.58 Ma; 95% HPD: 79.75-105.03  
250 Ma). The corresponding calibrations were enforced using truncated normal distributions with  
251 minimum and maximum ages reflecting the 95% HPD, and a standard deviation of 10 Ma.

252 For both analyses, the tree model was set to a birth-death speciation process (Gernhard  
253 2008) to account more accurately for extinct and missing lineages. The other settings for the  
254 BEAST analyses were similar to the settings used for the phylogenetic analysis carried out  
255 beforehand (50 million generations of MCMC with the parameters and trees sampled every  
256 5000 generations).

257 Net diversification rates were calculated based on the results of both dating analyses using the  
258 equation #4 from Magallón and Sanderson (2001), and time to net speciation events with  
259 equation #3. We compared diversification rates obtained here for Alseuosmineae with those  
260 calculated for total Asterales, Asteraceae and Campanulaceae using crown ages from Ramírez-  
261 Barahona et al. (2020) and estimates of species numbers from Christenhusz and Byng (2016).

262

### 263 ***Ecology and metal measurements***

264 Edaphic preferences of New Caledonian Alseuosmineae were obtained from the literature  
265 including: Tirel and Jérémie (1996), Barriera (2020), and Pillon and Hequet (2021).  
266 Additionally, information was obtained from descriptions on herbarium specimens labels from

267 the herbarium of New Caledonia (NOU) and the herbarium of Muséum national d'Histoire  
268 naturelle (P).

269 We used a Niton XL3T 950 GOLDD™ + handheld XRF analyzer (Thermo Fisher  
270 Scientific, Waltham, Massachusetts, USA) to screen herbarium specimens (see Belloeil et al.  
271 2021; van der Ent et al. 2019; Invernón et al. 2021) at herbarium P. Each herbarium specimen  
272 was placed on 2 mm titanium foil (#269489, Sigma-Aldrich, Saint Louis, Missouri, USA) and  
273 X-ray fluorescent spectra were recorded in the soil mode for 30 sec. using the main filter. The  
274 analysis of spectra by the proprietary XRF quantification software (ver. HH-XRF\_8.4G)  
275 provided an estimated concentration in  $\mu\text{g.g}^{-1}$  for Mn and Ni, the two elements that are the focus  
276 of this study. Up to ten specimens for each species were screened, to cover as broadly as  
277 possible the distribution and substrate types of each species (Table S1).

278 Because this type of XRF measurements tend to overestimate Mn concentrations  
279 (Belloeil et al. 2021, Gei et al. 2020), some analyses were validated with Microwave Plasma-  
280 Atomic Emission Spectroscopy (MP-AES). On a few selected herbarium specimens, one leaf  
281 was removed and more than 100 mg was ground to powder in a high-speed benchtop  
282 homogenizer (FastPrep®-24, MP Biomedicals, Solon, USA). The plant samples were analysed  
283 at the Service d'Analyses Multi-Élémentaires (INRAE, Montpellier, France) where they were  
284 digested in  $\text{HNO}_3$  (65%) and  $\text{H}_2\text{O}_2$  (30%) before MP-AES analysis (Chay and Mari 2017). The  
285 data were deposited in TRY Plant Trait Database (Kattge et al. 2020)

286

## 287 **Results**

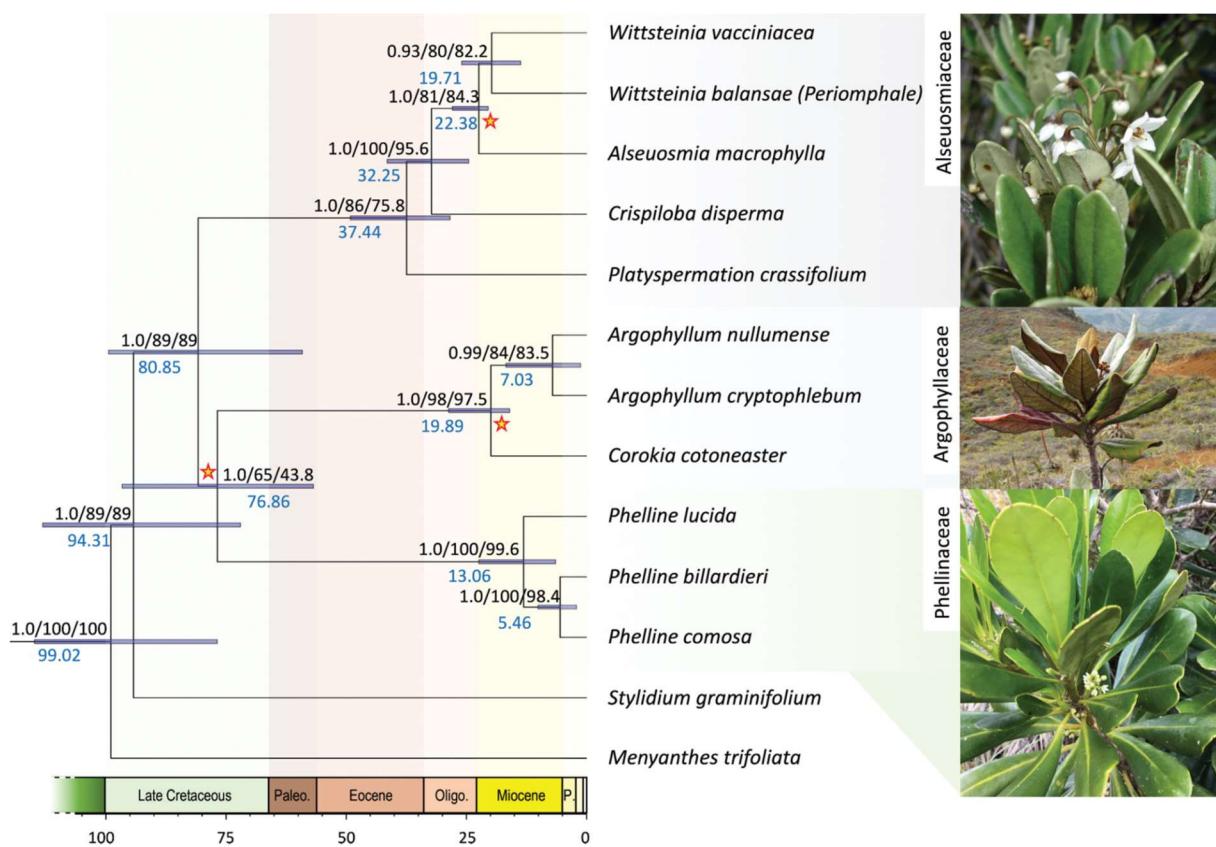
288

### 289 *Phylogenetic inference*

290 In our Bayesian phylogenetic analysis of Alseuosmineae, all parameters showed ESS values  
291  $\geq 200$  for the BEAST analysis. Partitioned phylogenetic analyses yielded identical topologies

292 under BI and ML (Figure 2). Node support was high under BI with 12 nodes out of 13 with PP  
 293  $\geq 0.95$ , whereas under ML, only four nodes were well supported with uBV  $\geq 95\%$  and SH-aLRT  
 294  $\geq 80\%$ . The suborder Alseuosmineae was resolved as monophyletic (PP of 1.0, uBV and SH-  
 295 aLRT of 89%). Monophyly was also observed for the sampled representatives of  
 296 Alseuosmiaceae (PP of 1.0, uBV of 100%, SH-aLRT of 95.6%), Argophyllaceae (PP of 1.0,  
 297 uBV of 98%, SH-aLRT of 97.8%), and Phellinaceae (PP of 1.0, uBV of 100%, SH-aLRT of  
 298 99.6%). Argophyllaceae and Phellinaceae were recovered as sister lineages with either a high  
 299 support under BI (PP of 1.0) but a weak/moderate support under ML (uBV of 65%, SH-aLRT  
 300 of 43.8%). *Periomphale balansae* was placed as sister to *Wittsteinia vacciniacea* with moderate  
 301 support (PP of 0.93, uBV of 80%, SH-aLRT of 82.2%).

302



303

304 **Figure 2.** Dated phylogeny resulting from Bayesian evolutionary analysis sampling trees  
 305 (BEAST) analyses based on primary fossil calibrations [FOSS] (topology identical to the best-  
 306 fit ML tree). Support values at nodes refer to posterior probabilities (PP), ultrafast bootstrap  
 307 values (uBV) and SH-like approximate likelihood ratio tests (SH-aLRT), in that order. Median

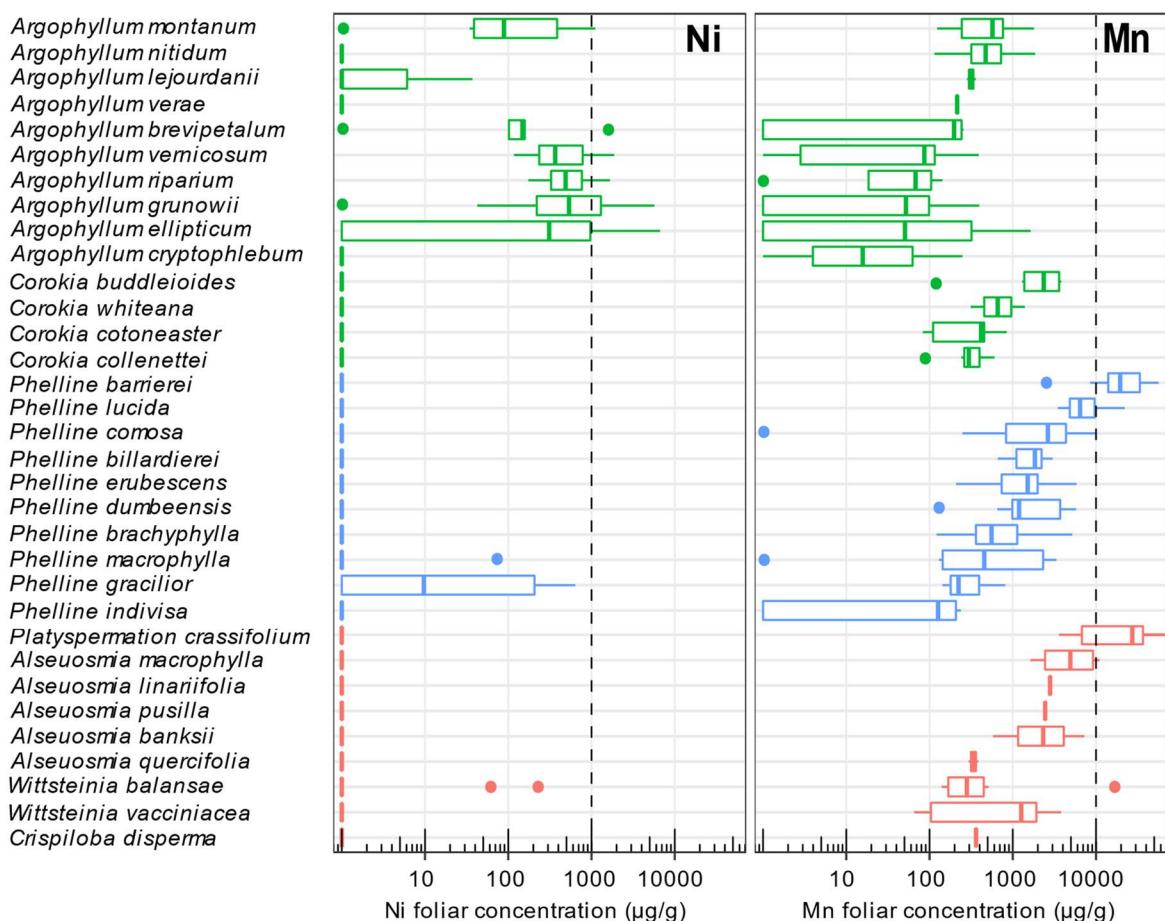
308 ages are also provided on nodes just below the support values. The three fossil constraints are  
309 highlighted with stars. Horizontal bars on nodes represent 95% Highest Posterior Density  
310 (HPD) of age estimates. Time scale (horizontal) in Ma (Paleo.: Paleocene, Oligo: Oligocene,  
311 P: Pliocene). Example plant species photos on the right (from top to bottom): *Platyspermation*  
312 *crassifolium*, *Argophyllum ellipticum*, *Phelline barrierei*.  
313

314 **Molecular dating**

315 In our dating analyses of Alseuosmineae, all parameters showed ESS values  $\geq 200$  for all  
316 BEAST analyses. The results of both analyses yielded dating estimates that were largely  
317 overlapping (see Figure 2 for the analysis based on fossil calibrations [FOSS] and Figure S1  
318 for the analysis relying on secondary calibrations based on the study of Ramírez-Barahona et  
319 al. (2020) [R2020]), with slightly older ages for the fossil-constrained analysis [FOSS]. Age  
320 estimates for the suborder Alseuosmineae suggested an origin between the Late Cretaceous and  
321 the Paleocene (median age 80.85 Ma, 95% HPD: 59.14-99.48 Ma [FOSS]; median age 75.27  
322 Ma, 95% HPD: 64.17-86.96 Ma [R2020]). The median age for the MRCA of Argophyllaceae  
323 + Phellinaceae was estimated at about 71-76 Ma (median age 76.86 Ma, 95% HPD: 56.84-  
324 96.67 Ma [FOSS]; median age 71.84 Ma, 95% HPD: 60.58-83.16 Ma [R2020]). The age  
325 estimates for the MRCA of the sampled representatives of Alseuosmiaceae, Argophyllaceae,  
326 and Phellinaceae were significantly younger: (i) for Alseuosmiaceae: median age 37.44 Ma,  
327 95% HPD: 28.39-49.14 Ma [FOSS]; median age 29.13 Ma, 95% HPD: 20.46-38.24 Ma  
328 [R2020]; (ii) for Argophyllaceae: median age 19.89 Ma, 95% HPD: 15.97-28.67 Ma [FOSS];  
329 median age 15.81 Ma, 95% HPD: 9.21-24.37 Ma [R2020]; and (iii) for Phellinaceae: median  
330 age 13.06 Ma, 95% HPD: 6.41-22.40 Ma [FOSS]; median age 10.99 Ma, 95% HPD: 5.54-17.90  
331 Ma [R2020]. The age of the MRCA of *Periomphale balansae* and *Wittsteinia vacciniacea* was  
332 estimated at about 13-19 Ma (median age 19.71 Ma, 95% HPD: 13.68-25.96 Ma [FOSS];  
333 median age 12.90 Ma, 95% HPD: 7.28-19.39 Ma [R2020]). Net diversification rates of  
334 Alseuosmineae were estimated to be between 0.038 [FOSS] and 0.041 [R2020], lower than that  
335 of the entire Asterales (0.089), Campanulaceae (0.096), or Asteraceae (0.16).

336 **Leaf metal concentrations**

337 Leaf tissue Ni and Mn concentrations were measured for a total of 249 herbarium specimens  
 338 representing 33 species. In most specimens, Ni was below the level of detection; however, it  
 339 was consistently present in high concentrations in several species of *Argophyllum* from New  
 340 Caledonia (Figure 3).



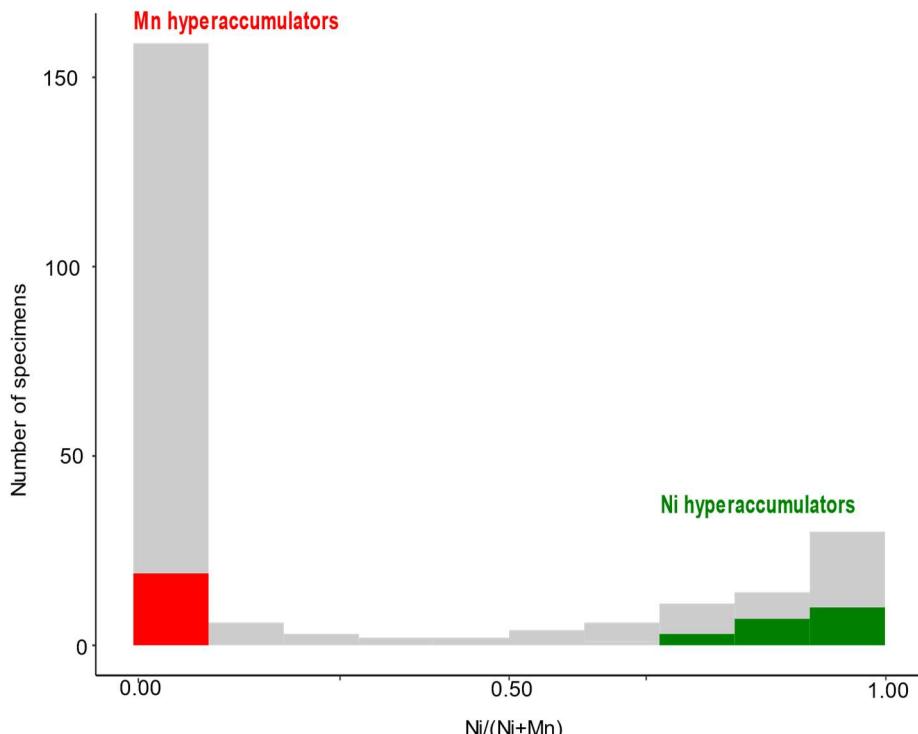
341  
 342 **Figure 3.** Boxplots showing Ni and Mn foliar concentrations ( $\mu\text{g g}^{-1}$ ) measured by X-ray  
 343 fluorescence (XRF) scanning of herbarium specimens from 33 species of Argophyllaceae  
 344 (green), Phellinaceae (blue) and Alseuosmiaceae (red). The dashed lines are the  
 345 hyperaccumulation thresholds of Ni ( $1000 \mu\text{g g}^{-1}$ ) and Mn ( $10,000 \mu\text{g g}^{-1}$ ).  
 346

347 All six *Argophyllum* species occurring on ultramafic substrates had some Ni values exceeding  
 348 the threshold of  $1000 \mu\text{g.g}^{-1}$  (van der Ent et al. 2013) and therefore qualified as Ni  
 349 hyperaccumulators: *A. brevipetalum*, *A. ellipticum*, *A. grunowii* (syn. *A. laxum*, see Pillon &  
 350 Hequet (2021)), *A. montanum*, *A. riparium*, and *A. vernicosum*. Although the median of each of

351 these species was below 1000, one specimen of *A. ellipticum* reached 6700  $\mu\text{g.g}^{-1}$ . Beside the  
352 New Caledonian species of *Argophyllum* cited above, occasional concentrations that were  
353 higher than the average were observed in some specimens of other species collected on  
354 ultramafic substrates from New Caledonia: *Phelline gracilior* (Katépahié: 90 and 640  $\mu\text{g.g}^{-1}$ ,  
355 Koumac: 270  $\mu\text{g.g}^{-1}$ ), *Phelline macrophylla* (Isle of Pines: 70  $\mu\text{g.g}^{-1}$ ) *Periomphale balansae*  
356 (Mount Ninga: 60  $\mu\text{g.g}^{-1}$ , Ongone: 200  $\mu\text{g.g}^{-1}$ ) and *Argophyllum lejourdanii* from Australia on  
357 unknown substrate (Rockingham Bay: 40  $\mu\text{g.g}^{-1}$ ).

358 Mn was above the detection threshold for most specimens and displayed great variation.  
359 Two species endemic to ultramafic substrates of New Caledonia consistently displayed high  
360 Mn concentration: *Phelline barrierei* (2500-57,000  $\mu\text{g.g}^{-1}$ , median = 19,500  $\mu\text{g.g}^{-1}$ , n = 9) and  
361 *Platyspermation crassifolium* (3,600-71,500  $\mu\text{g.g}^{-1}$ , median=28,000  $\mu\text{g.g}^{-1}$ , n=10). Only a few  
362 other specimens of occasionally had Mn values above 10,000  $\mu\text{g.g}^{-1}$ . They were all specimens  
363 collected on ultramafic substrates of New Caledonia: *Periomphale balansae* (Bon Secours:  
364 16,100  $\mu\text{g.g}^{-1}$ ), *Phelline comosa* (Kouaoua: 10,100  $\mu\text{g.g}^{-1}$ ), *Phelline lucida* (Ouenarou: 22,000  
365  $\mu\text{g.g}^{-1}$ , Tchingou: 18,000  $\mu\text{g.g}^{-1}$ , Mont Do: 10,000  $\mu\text{g.g}^{-1}$ ) and one from New Zealand:  
366 *Alseuosmia macrophylla* (Bay of Islands: 11000  $\mu\text{g.g}^{-1}$ ). MP-AES measurements confirmed the  
367 high Mn concentration in both *Phelline barrierei* (11,062 and 19,688  $\mu\text{g.g}^{-1}$ ) and  
368 *Platyspermation crassifolium* (9,615 and 30,068  $\mu\text{g.g}^{-1}$ ), which clearly qualified as Mn  
369 hyperaccumulators.

370 Figure 4 displays Ni/(Ni+Mn) and indicates that most specimens predominantly  
371 accumulated either Ni and/ or Mn but very few accumulated both.



372

373 **Figure 4.** Relation between leaf concentrations of Ni and Mn in Alseuosmineae expressed as  
 374 the distribution of the values of the quotient  $\text{Ni}/(\text{Ni}+\text{Mn})$ . For the purpose of calculation,  
 375 concentrations below the detection limit were assigned the value of zero. Twelve out of 249  
 376 specimens were excluded due to Ni and Mn values below detection levels. Ni  
 377 hyperaccumulators are shown in green, and Mn hyperaccumulators in red.  
 378

## 379 Discussion

380

### 381 *Generic concepts in Alseuosmiaceae*

382 Alseuosmiaceae genera have a tumultuous taxonomic history because of the difficulty in  
 383 placing them in or near well-established families. Cunningham (1838) described the genus  
 384 *Alseuosmia* from New Zealand with eight species, which he did not place in any family but  
 385 suggested affinities with Caprifoliaceae, Cornaceae, and Loranthaceae. Von Mueller (1860)  
 386 described the genus and species *Wittsteinia vacciniacea* that he placed in Vaccinieae  
 387 (Ericaceae) based on material from Australia. Studying specimens from New Caledonia,  
 388 Baillon (1888) described the genus *Periomphale* and the two species *Periomphale balansae*  
 389 and *Periomphale pancheri* that he placed in Gesneriaceae. Later, Gilg and Schlechter (in

390 Schlechter 1906) described the genera and species *Memecylanthus neocaledonicus* and  
391 *Pachydiscus gaultherioides* from New Caledonia. They placed these species in Caprifoliaceae,  
392 noting affinities with *Alseuosmia* as well.

393 Airy Shaw (1965) established the family Alseuosmiaceae to accommodate *Alseuosmia*,  
394 *Memecylanthus*, and *Periomphale* (including *Pachydiscus*). Based on a specimen collected in  
395 New Guinea, van Steenis (1978) described *Periomphale papuana*, and also included  
396 *Memecylanthus* in *Periomphale*. Later, van Steenis (1984a) established the connection between  
397 *Wittsteinia* and *Alseuosmia* + *Periomphale*. The close similarities between *Wittsteinia* and  
398 *Periomphale* prompted him to treat them as the single genus *Wittsteinia* (the oldest name),  
399 encompassing all three species. He also added a genus to the family – *Crispiloba* Steenis, based  
400 on a species originally described in the genus *Randia* (Rubiaceae) from Australia (Queensland).  
401 Later, Tirel (1996) disagreed with some of the morphological observations by van Steenis  
402 (1984b) and re-established the genus *Periomphale* with a single species from New Caledonia.

403 Our phylogenetic analysis recovered *Periomphale balansae* as sister taxon to *Wittsteinia*  
404 *vacciniacea*, with reasonable support (PP of 0.93, uBV of 80%, SH-aLRT of 82.2%). A broad  
405 concept for *Wittsteinia* thus seems preferable for several reasons. A monotypic *Periomphale*  
406 bears little phylogenetic information. The fact that van Steenis originally described *Wittsteinia*  
407 *papuana* in the genus *Periomphale*, then thought to be restricted to New Caledonia, is a clear  
408 indication that the plants from the two regions are sufficiently similar to be congeneric.  
409 *Wittsteinia* in its broad sense is a strong indicator of the biogeographical affinities between  
410 Eastern Australia, New Caledonia, and New Guinea, with similar distributions observed in  
411 *Sphenostemon* (Paracryphiaceae, Dickison and Lundberg 2016) or *Dubouzetia*  
412 (Elaeocarpaceae, Coode 2004).

413 Guillaumin (1950) originally described *Platyspermation* in Myrtaceae, but the genus  
414 has always been difficult to place by most authors. Only molecular phylogenetics (Lundberg

415 and Bremer 2003) firmly placed the genus as sister to the family Alseuosmiaceae where it has  
416 generally been placed ever since. It is interesting to note that van Steenis, who investigated  
417 thoroughly Alseuosmiaceae, also published a note on *Platyspermation* (van Steenis 1982), and  
418 considered it as allied to *Carpodetus* (Rousseaceae, also in Asterales), but did not mention at  
419 all Alseuosmiaceae. Synapomorphies uniting Alseuosmiaceae, including *Platyspermation*,  
420 remain to be found, but most of these plants have been little investigated. The family name  
421 Platyspermataceae Doweld is available if this assemblage is judged too heterogeneous in the  
422 future. However, considering their recent divergence (median age of either 29 Ma [R2020] or  
423 37 Ma [FOSS]), segregating Platyspermataceae from Alseuosmiaceae would make these  
424 families much younger than the average age of other angiosperm families (Ramírez-Barahona  
425 et al. 2020).

426

#### 427 *Alseuosmineae, a relict lineage within Asterales*

428 Alseuosmineae display several features of relict lineages. Phellinaceae are monogeneric,  
429 Argophyllaceae digeneric, and Alseuosmiaceae consists of only four genera. The results of our  
430 dating analyses indicate that Alseuosmineae are slightly older than the phylogenetically related  
431 Campanulaceae (median age of 73.3 Ma for the Campanulaceae in Ramírez-Barahona et al.  
432 2020) and yet has much lower species richness (44 vs. 2300 species). Indeed, Alseuosmineae  
433 have net diversification rates half that of Asterales or Campanulaceae, and one quarter that of  
434 Asteraceae. Using equation (3) of Magallon Sanderson (2001), we estimated that net speciation  
435 events occurred on average every 17-18 Ma. The age of the genus *Phelline* is likely  
436 underestimated here because of incomplete species sampling, but for other non-monotypic  
437 genera (i.e., *Alseuosmia*, *Argophyllum*, *Corokia* and *Wittsteinia*), their stem-age fixes an upper  
438 bound to their crown age at no more than 22 Ma [FOSS]. A similar result was found in a recent  
439 study focused on *Argophyllum* and *Corokia* (Maurin and Smissen 2022), where the authors

440 inferred a median age of 18.0 Ma for the Argophyllaceae. With a complete species-level  
441 sampling, it can be expected that the phylogenetic tree of the Alseuosmineae families and  
442 genera would have a typical broom-and-handle shape with most speciation events being  
443 younger than 22 Ma. Such tree shapes suggest high extinction rates (Condamine et al. 2015)  
444 associated with the extinction of early branching lineages, likely in relation to the impact of the  
445 Cretaceous-Paleogene (K-Pg) mass extinction (see Vajda and McLoughlin 2007 for the  
446 corresponding floristic turnover in New Zealand). In addition, other well-documented events  
447 could have further increased extinction rates in Alseuosmineae ~~the played an important role,~~  
448 ~~noticeably~~, notably the Eocene drowning of New Caledonia until its re-emergence 25-34 Ma  
449 (e.g., Cluzel et al. 2012, Giribet and Baker 2019), and the likely partial inundation of New  
450 Zealand during the Oligocene marine transgression *ca.* 23-25 Ma (Wallis and Jorge 2018). High  
451 extinction rather than low speciation rate is thus more likely to explain why Alseuosmineae  
452 have much lower net diversification rates than related plant groups.

453 There is also fossil evidence for geographical extinction in Alseuosmineae. Leaf cuticle  
454 from New Zealand has been attributed to the New Caledonian endemic *Phelline* (Pole 2010),  
455 and to *Argophyllum*, now restricted to eastern Australia and New Caledonia (Pole 2008). No  
456 fossils attributed to Alseuosmineae have yet been described outside their current range.

457 Alseuosmineae display an excess of representation on islands. Only a third of the species  
458 are now restricted to former Sahul (14 in mainland Australia, and one in New Guinea).  
459 *Wittsteinia papuana* is known from a single collection in New Guinea (van Steenis 1978). The  
460 eleven species of Australian *Argophyllum*, *Corokia whiteana*, and *Crispiloba disperma* each  
461 have relatively narrow distributions in north-east Australia (Queensland), while *Wittsteinia*  
462 *vacciniacea* has a restricted range in south-west Australia (Victoria). Most of the  
463 Alseuosmineae diversity is restricted to islands: Chatham Islands (1), Lord Howe Island (1)  
464 New Caledonia (19), New Zealand (7), and Rapa Iti (1). The occurrence of Alseuosmineae on

465 isolated volcanic islands (Lord Howe Island, Rapa Iti) is also an indication of good dispersal  
466 ability, assisted by birds, wind, or other means. Thus, the current range of Alseuosmineae is  
467 more in line with an ongoing, long-term decline on continental Sahul, with islands likely  
468 serving as (climatic) refugia.

469

470 ***Metal accumulation patterns***

471 Our results confirm previous observations reporting that all six New Caledonian *Argophyllum*  
472 species occurring on ultramafic substrates can be considered Ni hyperaccumulators (Jaffré  
473 1977, Pillon and Hequet 2021). Gei et al. (2020) measured a Ni concentration of 2150 µg.g<sup>-1</sup> in  
474 one specimen at herbarium NOU identified as *Phelline wagapensis* (MacKee 16846,  
475 Katépahié). Measurement of the duplicate specimen at P shows a lower concentration of 640  
476 µg.g<sup>-1</sup>, with the specimen being identified as *Phelline gracilior*, while *Phelline wagapensis* is  
477 now treated as a synonym of *Phelline erubescens* (Barriera 2020). Therefore, we consider that  
478 the occurrence of Ni hyperaccumulation in the genus *Phelline* requires further validation.

479 Two species of Alseuosmineae qualify as Mn hyperaccumulators. We validated the  
480 measurements of Gei et al. (2020) for *Platyspermation crassifolium* with new and more reliable  
481 MP-AES measurements confirming that its Mn concentration exceeds 10,000 µg.g<sup>-1</sup>. We also  
482 discovered another previously undetected Mn hyperaccumulator, *Phelline barrierei*, based on  
483 MP-AES measurements. In several other species including *Alseuosmia macrophylla*,  
484 *Periomphale balansae*, *Phelline comosa*, and *Phelline lucida*, a few specimens have XRF  
485 measurements exceeding 10,000 µg.g<sup>-1</sup> (up to 22,000 µg.g<sup>-1</sup>). However, considering that XRF  
486 spectrometer tends to overestimate high Mn values by a factor of ca. 3.5 (Belloeil et al. 2021)  
487 and that high values were observed only in a minority of specimens for each species, we regard  
488 Mn hyperaccumulation in these species as doubtful, with currently available data.

489 Both Mn and Ni hyperaccumulation evolved independently on ultramafic substrates of New  
490 Caledonia. Within Alseuosmineae, these two metal accumulation physiological pathways seem  
491 to exclude each other as specimens could display either high Ni concentration or high Mn  
492 concentration, but never both. This cannot simply be explained by ecological differences  
493 because the Ni hyperaccumulator *Argophyllum ellipticum* is observed in the same locations as  
494 the Mn hyperaccumulators *Phelline barrierei* (e.g., in Mount Paeoua) and *Platyspermation*  
495 *crassifolium* (in Mount Humboldt and Mount Kouakoué). A similar pattern has previously been  
496 observed in New Caledonian Cunoniaceae (van der Ent et al. 2022), suggesting that Mn and Ni  
497 accumulation are at least partially distinct strategies implying different molecular,  
498 physiological or anatomical pathways and structures.

499

#### 500 ***Specialised ecology, specialised physiology***

501 Alseuosmineae display a high affinity for ultramafic substrates, with 16 species (36%) in four  
502 genera occurring on ultramafic rocks in New Caledonia, of which 10 are restricted to them.  
503 This recurrent specialization for ultramafic substrates is remarkable considering the extreme  
504 chemical conditions of these soils (Proctor 2003; Kazakou et al. 2008), and their limited  
505 distribution globally, as well as within the entire Alseuosmineae range. They have not been  
506 reported on ultramafic substrates in Eastern Australia (Batianoff et al. 2000, 1991), but this  
507 could be explained by the narrow endemism of most Australian Alseuosmineae species (e.g.,  
508 Bean and Forster 2018). Similarly, despite extensive study and production of species lists,  
509 *Alseuosmia* and *Corokia* spp. have not been recorded on New Zealand ultramafic substrates up  
510 to the present time. *Alseuosmia* is most abundant in the western regions of the North Island  
511 (Shepherd et al. 2020), while the largest ultramafic outcrops are in the southwest of the South  
512 Island (van der Ent et al. 2015).

513 It is even more remarkable that metal hyperaccumulation occurs multiple times in  
514 Alseuosmineae. Fourteen percent of Alseuosmineae species are Ni hyperaccumulators, while  
515 only 0.18% of angiosperm species have this property according to the global inventory of metal  
516 hyperaccumulators (Reeves et al. 2018). Similarly, Mn hyperaccumulating species represent  
517 4.5% of Alseuosmineae and only 0.014% of angiosperms. It seems likely that Alseuosmineae  
518 possess some exaptation to adapt to ultramafic substrates and to become metal  
519 hyperaccumulators.

520 A lineage with a similar history may be *Oncotheca* Baill. This genus comprising two  
521 species endemic to New Caledonia is almost restricted to ultramafic substrates, with one species  
522 being a Ni hyperaccumulator (Jaffré 1980, Jaffré et al. 2013). This genus is the sole  
523 representative of the family Oncothecaceae and possibly of the order Oncothecales, a lineage  
524 of ca. 120 Ma (Zhang et al. 2020). The double insularity of New Caledonia (geographical and  
525 ecological) has probably played a role in the persistence of such relict lineages. This may have  
526 allowed them to escape competition from more successful groups, including the related  
527 Asteraceae that are under-represented in New Caledonia (Pillon et al. 2010).

528 There are several lines of evidence that New Caledonia fits in the ‘Old Climatically  
529 Buffered Infertile Landscapes’ (OCBILs; Pillon et al. 2021). When he introduced the OCBIL  
530 theory, Hopper (2009) made several predictions, which included the persistence of old lineages  
531 and nutritional specialisation. Alseuosmineae is a lineage where both features of an ancient,  
532 relictual lineage and edaphic specialisation are combined. Cuba is the other area in the world  
533 where metal hyperaccumulators are particularly diverse (Belloeil et al. 2021, Reeves et al. 1996,  
534 1999). There, the greatest numbers of hyperaccumulators are found in the older ultramafic  
535 terranes of the West and particularly the East that have been exposed for 10-30 Ma (Reeves et  
536 al. 1996, 1999). This age is close to the emergence of New Caledonian substrates which  
537 occurred sometimes between 25 and 34 Ma (Pillon et al. 2021). This suggests that the age of

538 ultramafic terrane (and possibly its stability) is an important factor for metal hyperaccumulation  
539 to originate.

540

## 541 **Conclusions**

542 Alseuosmineae is a relict lineage with low net diversification rates that can probably be  
543 explained by high extinction rates, geographical extinction, and narrow distributions  
544 particularly on continents, in spite of dispersal abilities. Future phylogenetic studies should  
545 consider sampling all species in order to estimate extinction rates throughout the history of this  
546 lineage. Island refugia may have played an important role in the persistence of the diversity of  
547 Alseuosmineae. Alseuosmineae display recurrent specialization for ultramafic substrates in  
548 New Caledonia with multiple independent evolution of rare physiological syndromes: Ni and  
549 Mn hyperaccumulation. Many more studies, on metallophytes or other lineages will be  
550 necessary to determine whether relict lineages are more often generalists or specialists, and to  
551 provide more detailed understanding of their diversification through time and their relative  
552 niche breadth.

553

## 554 **Acknowledgements**

555 We thank David Bruy, Jérôme Munzinger and herbarium NOU for providing leaf material of  
556 *Wittsteinia balansae*, Sandrine Isnard for sharing raw data on *Phelline* metal content. We thank  
557 Florian Jabbour, Myriam Gaudeul and the staff of herbarium P for granting access to their  
558 collections for XRF screening and for sampling leaf material. We thank Sandrine Chay  
559 (Biochimie & Physiologie Moléculaires des Plantes) for access to laboratory and help with MP-  
560 AES analysis. We also thank the “Les Herbonautes” community for their help with the “Fan de  
561 metal” mission (<http://lesherbonautes.mnhn.fr/missions/13907009>). The MNHN gives access  
562 to the collections in the framework of the RECOLNAT national Research Infrastructure (ANR-

563 11-INBS-0004). We are grateful to three anonymous reviewers and the coordinating guest  
564 editor, Xavier Picó, for constructive comments on a previous version of the manuscript.

565

566 **Disclosure statement**

567 No potential conflict of interest was reported by the authors.

568

569 **Funding**

570 This work was supported by the CNRS MITI X-Life program (X-TreM project to SM; Centre  
571 Nationale de la Recherche Scientifique).

572

573 **Notes on contributors**

574 Karine Gotty works on genetic and chemical diversity of plants.

575 Gael J. Kergoat is an evolutionary biologist whose fields of expertise include biogeography,  
576 ecology, molecular dating, and phylogenetics.

577 Pierre Jouannais is currently conducting a PhD on the Prospective Life-Cycle Assessment of  
578 microalgae-based solutions for aquaculture.

579 Vanessa Invernon is the collections manager of MNHN Paris herbarium (P & PC), and has  
580 interest in new uses of natural history collections.

581 Sylvain Merlot is studying the molecular basis of metal hyperaccumulation in plants.

582 Yohan Pillon is a botanist with interests in island systems and metal accumulating plants.

583 **ORCID**

584 Karine Gotty <http://orcid.org/0000-0002-1465-5644>

585 Gael J. Kergoat <http://orcid.org/0000-0002-8284-6215>

586 Pierre Jouannais <http://orcid.org/0000-0002-9342-6099>

587 Vanessa Invernon <http://orcid.org/0000-0002-2037-6158>

588 Sylvain Merlot <http://orcid.org/0000-0002-9352-1184>

589 Yohan Pillon <http://orcid.org/0000-0003-1760-329X>

590

591 **References**

592 Airy Shaw HK. 1965. Diagnoses of new families, new names, etc. for the seventh edition of  
593 Willis's "dictionary." Kew Bulletin 18:249–273.

594 Baillon H. 1888. Observations sur les Gesneriacées. Bulletin mensuel de la Société linnéenne  
595 de Paris 1:731–736.

596 Barriera G. 2017. Novitates neocaledonicae. VIII. Taxonomie et nomenclature du genre  
597 *Phelline* (Phellinaceae) avec la description de la nouvelle espèce *Phelline barrierei*.  
598 Candollea 72:361–370.

599 Barriera G. 2020. Phellinaceae. In Flore de la Nouvelle-Calédonie. pp. 234-295. Faune et Flore  
600 Tropicales. Publications scientifiques du Muséum; IRD, Paris, Marseille.

601 Batianoff GN, Specht CD, Reeves RD. 1991. The serpentine flora of the humid subtropics of  
602 Eastern Australia. Proceedings of the Royal Society of Queensland 101:137–157.

603 Batianoff GN, Neldner VJ, Singh S. 2000. Vascular plant census and floristic analysis of  
604 serpentine landscapes in central Queensland. Proceedings of the Royal Society of  
605 Queensland 109:1–30.

606 Bean AR, Forster PI. 2018. A taxonomic revision of *Argophyllum* J.R.Forst. & G.Forst.  
607 (Argophyllaceae) in Australia. Austrobaileya 10:207–235.

608 Belloeil C, Jouannais P, Malfaisan C, Reyes Fernández R, Lopez S, Navarrete Gutierrez DM,  
609 Maeder-Pras S, Villanueva P, Tisserand R, Gallopin M, et al. 2021. The X-ray  
610 fluorescence screening of multiple elements in herbarium specimens from the  
611 Neotropical region reveals new records of metal accumulation in plants. Metallomics  
612 13:mfab045.

- 613 Bruy D, Barrabé L, Birnbaum P, Dagostini G, Donnat M, Fambart-Tinel J, Girardi J, Hequet V,  
614 Isnard S, Jaffré T, et al. 2022. L'Herbier de Nouvelle-Calédonie. UMR AMAP. IRD, CIRAD,  
615 CNRS, INRAE, Univ. Montpellier, Nouméa. DOI: [https://doi.org/10.23708/HERBIER-  
616 NOUVELLE-CALEDONIE](https://doi.org/10.23708/HERBIER-NOUVELLE-CALEDONIE)
- 617 Cao Y-N, Comes HP, Sakaguchi S, Chen L-Y, Qiu Y-X. 2016. Evolution of East Asia's Arcto-  
618 Tertiary relict *Euptelea* (Eupteleaceae) shaped by Late Neogene vicariance and  
619 Quaternary climate change. BMC Evolutionary Biology 16:66. doi:10.1186/s12862-  
620 016-0636-x.
- 621 Carlquist S. 1965. Island life. American Museum of Natural History, New York.
- 622 Carlquist S. 1974. Island Biology. Columbia University Press, New York.
- 623 Chay S, Mari S. 2017. High throughput multi-elemental profiling of plant samples with the  
624 4200 MP-AES. Agilent Technologies Eds.
- 625 Christenhusz MJM, Byng JW. 2016. The number of known plants species in the world and its  
626 annual increase. Phytotaxa 261:201–217. doi:10.11646/ phytotaxa.261.3.1.
- 627 Cluzel D, Maurizot P, Collot J, Sevin B. 2012. An outline of the geology of New Caledonia; from  
628 Permian–Mesozoic Southeast Gondwanaland active margin to Cenozoic obduction  
629 and supergene evolution. Episodes 35:72–86. doi:10.18814/epiiugs/2012/v35i1/007.
- 630 Condamine FL, Nagalingum NS, Marshall CR, Morlon H. 2015. Origin and diversification of  
631 living cycads: a cautionary tale on the impact of the branching process prior in Bayesian  
632 molecular dating. BMC Evolutionary Biology 15:65. doi:10.1186/s12862-015-0347-8.
- 633 Conran JG, Lee WG, Lee DE, Bannister JM, Kaulfuss U. 2014. Reproductive niche conservatism  
634 in the isolated New Zealand flora over 23 million years. Biology Letters 10:20140647.  
635 doi:10.1098/rsbl.2014.0647.

- 636 Coode MJE. 2004. Elaeocarpaceae. In *The families and genera of vascular plants* (volume 6). K  
637 Kubitzki (ed.), pp. 135–144. Springer, Berlin.
- 638 Cunningham A. 1838. 9. Genus *Corneis* affine. *Alseuosmia*. Annals of Natural History 2:209–  
639 210.
- 640 Dickison WC, Lundberg J. 2016. Paracryphiaceae. In *The Families and Genera of Vascular  
641 Plants* Vol 14. JW Kadereit and V Bittrich (eds.), pp. 281–285. Springer International  
642 Publishing, Switzerland.
- 643 Doyle JJ, Doyle JL. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf  
644 tissue. *Phytochemical Bulletin* 19:11–15.
- 645 Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with  
646 confidence. *PLOS Biology* 4:e88. doi:10.1371/journal.pbio.0040088.
- 647 Eldredge N. 1979. Alternative approaches to evolutionary theory. *Bulletin of the Carnegie  
648 Museum of Natural History* 13:7–19.
- 649 van der Ent A, Baker AJM, Reeves RD, Pollard AJ, Schat H. 2013. Hyperaccumulators of metal  
650 and metalloid trace elements: facts and fiction. *Plant and Soil* 362:319–334.  
651 doi:10.1007/s11104-012-1287-3.
- 652 van der Ent A, Jaffré T, L’Huillier L, Gibson N, Reeves RD. 2015. The flora of ultramafic soils in  
653 the Australia–Pacific Region: state of knowledge and research priorities. *Aust J Bot*  
654 63:173–190.
- 655 van der Ent A, Echevarria G, Pollard AJ, Erskine PD. 2019. X-Ray fluorescence ionomics of  
656 herbarium collections. *Scientific Reports* 9:4746. doi:10.1038/s41598-019-40050-6.
- 657 van der Ent A, Pillon Y, Fogliani B, Gei V, Jaffré T, Erskine PD, Echevarria G, Spiers KM, Paul  
658 ALD, Isnard S. 2022. Contrasting nickel and manganese accumulation and localization

- 659           in New Caledonian Cunoniaceae. *Plant Soil* 475:515–534. doi:10.1007/s11104-022-  
660           053883
- 661       Erixon P, Svensson B, Britton T, Oxelman B. 2003. Reliability of bayesian posterior  
662           probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology* 52:665–  
663           673. doi:10.1080/10635150390235485.
- 664       Fay M, Witherup S, Chase M. 1997. Taxonomic Affinities of *Medusagyne oppositifolia*  
665           (Medusagynaceae). *Kew Bulletin* 52:111–120. doi:10.2307/4117844.
- 666       Feild T, Arens N, Doyle J, Dawson T, Donoghue M. 2004. Dark and disturbed: A new image of  
667           early angiosperm ecology. *Paleobiology* 30:82–107. doi:10.1666/0094-985  
668           8373(2004)030<0082:DADANI>2.0.CO;2.
- 669       Gei V, Isnard S, Erskine PD, Echevarria G, Fogliani B, Jaffré T, van der Ent A. 2020. A systematic  
670           assessment of the occurrence of trace element hyperaccumulation in the flora of New  
671           Caledonia. *Botanical Journal of the Linnean Society* 194:1–22.  
672           doi:10.1093/botlinnean/boaa029.
- 673       Gernhard T. 2008. The conditioned reconstructed process. *Journal of Theoretical Biology*  
674           253:769–778. doi:10.1016/j.jtbi.2008.04.005.
- 675       Giribet G, Baker CM. 2019. Further discussion on the Eocene drowning of New Caledonia:  
676           Discordances from the point of view of zoology. *J Biogeogr* 46:1912–1918.  
677           doi:10.1111/jbi.13635.
- 678       Grandcolas P, Nattier R, Trewick S. 2014. Relict species: a relict concept? *Trends in Ecology &*  
679           *Evolution* 29:655–663. doi:10.1016/j.tree.2014.10.002.
- 680       Guillaumin A. 1950. Plantae Neocaledonicae a C. Skottsberg a. 1949 lectae. *Acta Horti  
681           gothoburgensis* 18:247–265.

- 682 Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New algorithms  
683 and methods to estimate Maximum-Likelihood phylogenies: assessing the  
684 performance of PhyML 3.0. Systematic Biology 59:307–321.  
685 doi:10.1093/sysbio/syq010.
- 686 Holloway JD. 1979. A survey of the lepidoptera, biogeography, and ecology of New Caledonia.  
687 W. Junk, The Hague ; Boston.
- 688 Hoot SB, Culham A, Crane PR. 1995. The utility of *atpB* gene sequences in resolving  
689 phylogenetic relationships: comparison with *rbcL* and 18S ribosomal DNA sequences  
690 in the Lardizabalaceae. Annals of the Missouri Botanical Garden 82:194–207.  
691 doi:10.2307/2399877.
- 692 Hopper SD. 2009. OCBIL theory: towards an integrated understanding of the evolution,  
693 ecology and conservation of biodiversity on old-climatically buffered, infertile  
694 landscapes. Plant and Soil 322:49–86.
- 695 Invernón VR, Tisserand R, Jouannais P, Navarrete Gutiérrez DM, Muller S, Pillon Y, Echevarria  
696 G, Merlot S. 2021. La découverte de nouvelles espèces végétales hyperaccumulatrices  
697 de métaux dans les herbiers. In R. Pellens, Les collections naturalistes dans la science  
698 du XXIe siècle: Une ressource durable pour une science ouverte. pp. 85–100. ISTE  
699 Editions Ltd, London.
- 700 Isnard S, L'Huillier L, Rigault F, Jaffré T. 2016. How did the ultramafic soils shape the flora of  
701 the New Caledonian hotspot? Plant and Soil 403:53–76. doi:10.1007/s11104-016-  
702 2910-5.
- 703 Jablonski D. 2001. Lessons from the past: Evolutionary impacts of mass extinctions. PNAS  
704 98:5393–5398. doi:10.1073/pnas.101092598.

- 705 Jaffré T. 1977. Composition chimique élémentaire des tissus foliaires des espèces végétales  
706 colonisatrices des anciennes mines de nickel en Nouvelle-Calédonie. Cahiers ORSTOM,  
707 série Biologie 12:323–330.
- 708 Jaffré T. 1980. Etude écologique du peuplement végétal des sols dérivés de roches  
709 ultrabasiques en Nouvelle-Calédonie. ORSTOM, Paris.
- 710 Jaffré T, Pillon Y, Thomine S, Merlot S. 2013. The metal hyperaccumulators from New  
711 Caledonia can broaden our understanding of nickel accumulation in plants. *Frontiers*  
712 in Plant Science
- 713 Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017. ModelFinder: fast  
714 model selection for accurate phylogenetic estimates. *Nat Methods* 14:587–589.  
715 doi:10.1038/nmeth.4285.
- 716 Kårehed J, Lundberg J, Bremer B, Bremer K. 1999. Evolution of the Australasian families  
717 Alseuosmiaceae, Argophyllaceae, and Phellinaceae. *Systematic Botany* 24:660–682.  
718 doi:10.2307/2419649.
- 719 Katoh K, Standley DM. 2013. MAFFT Multiple Sequence Alignment Software Version 7:  
720 Improvements in Performance and Usability. *Molecular Biology and Evolution* 30:772–  
721 780. doi:10.1093/molbev/mst010.
- 722 Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA,  
723 Aakala T, Abedi M, et al. 2020. TRY plant trait database – enhanced coverage and open  
724 access. *Global Change Biology* 26:119–188. doi:10.1111/gcb.14904
- 725 Kazakou E, Dimitrakopoulos PG, Baker AJM, Reeves RD, Troumbis AY. 2008. Hypotheses,  
726 mechanisms and trade-offs of tolerance and adaptation to serpentine soils: from  
727 species to ecosystem level. *Biological Reviews* 83:495–508. doi:10.1111/j.1469-  
728 185X.2008.00051.x.

- 729 Lindqvist JK, Lee DE. 2009. High-frequency paleoclimate signals from Foulden Maar, Waipiata  
730 Volcanic Field, southern New Zealand: An Early Miocene varved lacustrine diatomite  
731 deposit. *Sedimentary Geology* 222:98–110. doi:10.1016/j.sedgeo.2009.07.009.
- 732 Lundberg J, Bremer K. 2003. A phylogenetic study of the order Asterales using one  
733 morphological and three molecular data sets. *International Journal of Plant Science*  
734 164:553–578. doi:10.1086/374829.
- 735 Maddison WP, Maddison DR. 2019. Mesquite: a modular system for evolutionary analysis.  
736 Version 3.61. as found on the website (<https://www.mesquiteproject.org/>).
- 737 Magallón S, Sanderson MJ. 2001. Absolute diversification rates in angiosperm clades.  
738 *Evolution* 55:1762–1780. doi:10.1111/j.0014-3820.2001.tb00826.x.
- 739 Martínez-Millán M. 2010. Fossil record and age of the Asteridae. *Bot Rev* 76:83–135.  
740 doi:10.1007/s12229-010-9040-1.
- 741 Mast AR, Jones EH, Haverty SP. 2005. An assessment of old and new DNA sequence evidence  
742 for the paraphyly of *Banksia* with respect to *Dryandra* (Proteaceae). *Australian*  
743 *Systematic Botany* 18:75. doi:10.1071/SB04015.
- 744 Mast AR, Willis CL, Jones EH, Downs KM, Weston PH. 2008. A smaller *Macadamia* from a more  
745 vagile tribe: inference of phylogenetic relationships, divergence times, and diaspora  
746 evolution in *Macadamia* and relatives (tribe Macadamieae; Proteaceae). *American*  
747 *Journal of Botany* 95:843–870. doi:10.3732/ajb.0700006.
- 748 Maurin KJL, Smissen RD. 2022. A dated phylogeny of Argophyllaceae (Asterales) is consistent  
749 with spread by long-distance dispersal. *New Zealand Journal of Botany* 60:27-44.  
750 doi:10.1080/0028825X.2021.1905671.

- 751 Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast approximation for phylogenetic  
752 bootstrap. Molecular Biology and Evolution 30:1188–1195.  
753 doi:10.1093/molbev/mst024.
- 754 Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R.  
755 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the  
756 genomic era. Molecular Biology and Evolution 37:1530–1534.  
757 doi:10.1093/molbev/msaa015.
- 758 Morley RJ. 2001. Why are there so many primitive angiosperms in the rain forests of Asia-  
759 Australasia? In Faunal and floral migrations and evolution in SE Asia-Australasia. I  
760 Metcalfe, JMB Smith, M Morwood, and I Davidson (eds.), pp. 185–199. A.A. Balkema  
761 publishers, Lisse.
- 762 Mueller F von. 1860. Vaccineae. *Wittsteinia*. Fragmenta phytographiae Australiae 2:136–137.
- 763 Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey J. 2004. Bayesian Phylogenetic  
764 Analysis of Combined Data. Systematic Biology 53:47–67.  
765 doi:10.1080/10635150490264699.
- 766 Parsons PA. 2005. Environments and evolution: interactions between stress, resource  
767 inadequacy and energetic efficiency. Biological Reviews 80:589–610. doi:10.1017/  
768 S1464793105006822.
- 769 Pillon Y, Hequet V. 2021. A new species of *Argophyllum* (Argophyllaceae) with notes on the  
770 species from New Caledonia and nickel hyperaccumulation. Plants 10:701.  
771 doi:10.3390/plants10040701.
- 772 Pillon Y, Munzinger J, Amir H, Lebrun M. 2010. Ultramafic soils and species sorting in the flora  
773 of New Caledonia. Journal of Ecology 98:1108–1116. doi:10.1111/j.1365-  
774 2745.2010.01689.x.

- 775 Pillon Y, Barrabé L, Buerki S. 2017. How many genera of vascular plants are endemic to New  
776 Caledonia? A critical review based on phylogenetic evidence. *Botanical Journal of the  
777 Linnean Society* 183:177–198. doi:10.1093/botlinnean/bow001.
- 778 Pillon Y, Jaffré T, Birnbaum P, Bruy D, Cluzel D, Ducousoo M, Fogliani B, Ibanez T, Jourdan H,  
779 Lagarde L, et al. 2021. Infertile landscapes on an old oceanic island: the biodiversity  
780 hotspot of New Caledonia. *Biological Journal of the Linnean Society* 133:317–341.  
781 doi:10.1093/biolinnean/blaa146.
- 782 Pole M. 2008. Dispersed leaf cuticle from the Early Miocene of southern New Zealand.  
783 *Palaeontologia Electronica* 11:1–117.
- 784 Pole M. 2010. Was New Zealand a primary source for the New Caledonian flora? *Alcheringa*  
785 34:61–74. doi:10.1080/03115510903343477.
- 786 Poncet V, Birnbaum P, Burtet-Sarramegna V, de Kochko A, Fogliani B, Gâteblé G, Isnard S,  
787 Jaffré T, Job D, Munoz F, et al. 2019. *Amborella* — bearing witness to the past? *Annual  
788 Plant Reviews online* 3:1–41.
- 789 Pouteau R, Trueba S, Feild TS, Isnard S. 2015. New Caledonia: a Pleistocene refugium for rain  
790 forest lineages of relict angiosperms. *Journal of Biogeography* 42:2062–2077.  
791 doi:10.1111/jbi.12581.
- 792 Pouteau R, Trueba S, Isnard S. 2020. Retracing the contours of the early angiosperm  
793 environmental niche. *Annals of Botany* 125:49–57. doi:10.1093/aob/mcz131.
- 794 Proctor J. 2003. Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far  
795 East. *Perspectives in Plant Ecology, Evolution and Systematics* 6:105–124.  
796 doi:10.1078/1433-8319-00045.

- 797 Ramírez-Barahona S, Sauquet H, Magallón S. 2020. The delayed and geographically  
798 heterogeneous diversification of flowering plant families. *Nat Ecol Evol* 4:1232–1238.  
799 doi:10.1038/s41559-020-1241-3.
- 800 Reeves RD, Baker AJM, Borhidi A, Berazain R. 1996. Nickel accumulating plants from the  
801 ancient serpentine soils of Cuba. *New Phytologist* 133:217–224. doi:10.1111/j.1469-  
802 8137.1996.tb01888.x.
- 803 Reeves RD, Baker AJM, Borhidi A, Berazaín R. 1999. Nickel hyperaccumulation in the  
804 serpentine flora of Cuba. *Annals of Botany* 83:29–38. doi:10.1006/anbo.1998.0786.
- 805 Reeves RD, Baker AJM, Jaffré T, Erskine PD, Echevarria G, van der Ent A. 2018. A global  
806 database for plants that hyperaccumulate metal and metalloid trace elements. *New  
807 Phytologist* 218:407–411. doi:10.1111/nph.14907.
- 808 Schlechter R. 1906. Beiträge zur Kenntnis der Flora von Neu-Kaledonien. *Botanische  
809 Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 39:1–274.
- 810 Shepherd LD, Lange PJ de, Townsend A, Perrie LR. 2020. A biological and ecological review of  
811 the endemic New Zealand genus *Alseuosmia* (toropapa; Alseuosmiaceae). *New  
812 Zealand Journal of Botany* 58:2–18. doi:10.1080/0028825X.2019.1659376.
- 813 Stebbins GL. 1950. Variation and Evolution in Plants. Columbia University Press, New York and  
814 London.
- 815 van Steenis CGGJ. 1978. Miscellaneous botanical notes XXV. *Blumea* 24:479–484.
- 816 van Steenis CGGJ. 1982. Preliminary note on the taxonomic disposition of *Platyspermation*  
817 Guillaumin (Myrtaceae) from New Caledonia. *Reinwardtia* 10:24–25.
- 818 van Steenis CGGJ. 1984a. A synopsis of Alseuosmiaceae in New Zealand, New Caledonia,  
819 Australia, and New Guinea. *Blumea* 29:387–394.
- 820 van Steenis CGGJ. 1984b. Alseuosmiaceae. In *Flora Malesiana* vol 10. pp. 335–336.

- 821 Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A. 2018. Bayesian  
822 phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* 4  
823 (1):vey016.
- 824 Tang C, Matsui T, Ohashi H, Dong Y-F, Momohara A, Herrando-Moraira S, Qian S, Yang Y,  
825 Ohsawa M, Luu HT, et al. 2018. Identifying long-term stable refugia for relict plant  
826 species in East Asia. *Nature Communications* 9:1–14. doi:10.1038/s41467-017-02088-  
827 w.
- 828 Thiers B. 2021. Index Herbariorum -A global directory of public herbaria and associated staff.  
829 New York Botanical Garden's Virtual Herbarium. as found on the website  
830 (<http://sweetgum.nybg.org/science/ih/>).
- 831 Tirel C. 1996. Rétablissement de *Periomphale* Baill. (Alseuosmiaceae), genre endémique de  
832 Nouvelle-Calédonie. *Adansonia* 18:155–160.
- 833 Tirel C, Jérémie J. 1996. Alseuosmiaceae. In *Flore de la Nouvelle-Calédonie et Dépendances*  
834 vol 20. P Morat (ed.), pp. 100–106. Muséum National d'Histoire Naturelle, Paris.
- 835 Vajda V, McLoughlin S. 2007. Extinction and recovery patterns of the vegetation across the  
836 Cretaceous–Palaeogene boundary — a tool for unravelling the causes of the end-  
837 Permian mass-extinction. *Review of Palaeobotany and Palynology* 144:99–112.  
838 doi:10.1016/j.revpalbo.2005.09.007.
- 839 Vane-Wright RI, Humphries CJ, Williams PH. 1991. What to protect?—Systematics and the  
840 agony of choice. *Biological Conservation* 55:235–254. DOI:  
841 [https://doi.org/10.1016/0006-3207\(91\)90030-D](https://doi.org/10.1016/0006-3207(91)90030-D)
- 842 Vidal-Russell R, Nickrent DL. 2008. The first mistletoes: Origins of aerial parasitism in  
843 Santalales. *Molecular Phylogenetics and Evolution* 47:523–537.  
844 doi :10.1016/j.ympev.2008.01.016

- 845 Virot R. 1956. La végétation canaque. Faculté des Sciences de l'université de Paris, Paris.
- 846 Walker JD, Geissman JW, Bowring SA, Babcock LE. 2018. GSA Geologic Time Scale v. 5.0.
- 847 Geological Society of America.
- 848 Wallace, AR, 1880. Island life, or, The phenomena and causes of insular faunas and floras:
- 849 including a revision and attempted solution of the problem of geological climates.
- 850 Macmillan (London).
- 851 Wallis GP, Jorge F. 2018. Going under down under? Lineage ages argue for extensive survival
- 852 of the Oligocene marine transgression on Zealandia. *Molecular Ecology* 27:4368–4396.
- 853 doi : 10.1111/mec.14875
- 854 Zhang C, Zhang T, Luebert F, Xiang Y, Huang C-H, Hu Y, Rees M, Frohlich MW, Qi J, Weigend
- 855 M, et al. 2020. Asterid phylogenomics/phylotranscriptomics uncover morphological
- 856 evolutionary histories and support phylogenetic placement for numerous whole-
- 857 genome duplications. *Mol Biol Evol* 37:3188–3210. doi:10.1093/molbev/msaa160.
- 858
- 859

860 **Appendix** List of taxa, voucher specimen (herbarium), and GenBank accession numbers for  
861 *atpB*, *ndhF* and *rbcL*. Herbarium acronyms follow Thiers (2021).

862

863 *Alseuosmia macrophylla* A. Cunn., Morgan 2141 (WS), AJ236198, \_,\_; Mackinder s.n.  
864 (UPS), \_, AJ238334, X87377; *Crispiloba disperma* (S.Moore) Steen., Telford 10654 (CBG),  
865 AJ318968, AJ238338, X87382; *Platyspermation crassifolium* Guillaumin, Stauffer &  
866 Blanchon 5710 (UC), AJ419689, AJ496220, AJ419700; *Wittsteinia balansae* (Baill.) Steenis,  
867 Munzinger 4583 (NOU), OL794665, OL794664, OL794663; *Wittsteinia vacciniacea* F.  
868 Muell., Carroll 452 (CBG), AJ318985& AJ318986, AJ238345, X87399; *Argophyllum*  
869 *cryptophlebum* Zemann, Harrington JD04 (ATH), \_, \_, KF496493; *Argophyllum nullumense*  
870 R.T.Baker, Telford 3762 (CBG), AJ318965, \_, \_; Telford 5462 (CBG), \_, AJ238335, X87379;  
871 *Corokia cotoneaster* Raoul, Chase 2752 (K), AJ235445, \_, L11221; Taylor 2623 (CBG), \_,  
872 AJ238337, \_; *Phelline billardierei* Pancher ex Loes., M. van Balgooy 7013 (L),\_, AJ238341,  
873 AJ238346; *Phelline comosa* Labill., Savolainen pco1 (G), AJ235557, \_, X69748; Ziesing 289  
874 (CBG), \_, AJ238342, \_; *Phelline lucida* Vieill. ex Baill., M. van Balgooy 7034 (L), \_,  
875 AJ238343, AJ238347; *Menyanthes trifoliata* L., Chase 3501 (K), AJ235533, L39388, L14006;  
876 *Stylium graminifolium* Sw. ex Willd., Cosner 174 (OS), AJ236201, AF130188, L18790.

877

878

Table S1 Ni and Mn foliar concentrations ( $\mu\text{g.g}^{-1}$ ) measured by X-ray fluorescence (XRF) scanning of Alseuosmineae herbarium specimens from 33 species. See:

<https://science.mnhn.fr/institution/mnhn/collection/p/item/search> [insert barcode]. LOD= limit of detection

Family	Genus	Species	Barcode	Origin	Ni concentration	Ni Error	Mn concentration	Mn Error
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183557	New Caledonia	< LOD	$\pm 70$	512	$\pm 90$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183532	New Caledonia	< LOD	$\pm 80$	16,064	$\pm 400$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183593	New Caledonia	< LOD	$\pm 70$	146	$\pm 70$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00217144	New Caledonia	< LOD	$\pm 40$	139	$\pm 40$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183595	New Caledonia	< LOD	$\pm 50$	339	$\pm 60$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183596	New Caledonia	58	$\pm 40$	294	$\pm 70$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183543	New Caledonia	< LOD	$\pm 70$	143	$\pm 70$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00354302	New Caledonia	< LOD	$\pm 70$	250	$\pm 80$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183524	New Caledonia	< LOD	$\pm 70$	266	$\pm 80$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183586	New Caledonia	217	$\pm 50$	491	$\pm 90$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518558	New Caledonia	< LOD	$\pm 60$	1,264	$\pm 110$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518557	Australia	< LOD	$\pm 60$	1,921	$\pm 130$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P00760352	Australia	< LOD	$\pm 20$	103	$\pm 30$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518559	Australia	< LOD	$\pm 50$	3,809	$\pm 140$
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P06775815	Australia	< LOD	$\pm 20$	64	$\pm 30$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233471	Australia	< LOD	$\pm 60$	579	$\pm 80$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233470	New Zealand	< LOD	$\pm 80$	2,323	$\pm 160$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233469	New Zealand	< LOD	$\pm 50$	7,247	$\pm 200$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>linariifolia</i>	P04233472	New Zealand	< LOD	$\pm 60$	2,894	$\pm 150$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>linariifolia</i>	P04233473	New Zealand	< LOD	$\pm 60$	2,724	$\pm 150$
Alseuosmiaceae	<i>Alseuosmia</i>	<i>macrophylla</i>	P04233476	New Zealand	< LOD	$\pm 70$	11,054	$\pm 290$

Alseuosmiaceae	<i>Alseuosmia</i>	<i>macrophylla</i>	P04233474	New Zealand	< LOD	±70	1,627	±130
Alseuosmiaceae	<i>Alseuosmia</i>	<i>macrophylla</i>	P04233475	New Zealand	< LOD	±70	8,659	±270
Alseuosmiaceae	<i>Alseuosmia</i>	<i>macrophylla</i>	P03616801	New Zealand	< LOD	±60	2,796	±150
Alseuosmiaceae	<i>Alseuosmia</i>	<i>pusilla</i>	P04233477	New Zealand	< LOD	±60	2,451	±140
Alseuosmiaceae	<i>Alseuosmia</i>	<i>quercifolia</i>	P04233478	New Zealand	< LOD	±70	385	±90
Alseuosmiaceae	<i>Alseuosmia</i>	<i>quercifolia</i>	P04233479	New Zealand	< LOD	±70	294	±90
Alseuosmiaceae	<i>Crispiloba</i>	<i>disperma</i>	P03790607	New Zealand	< LOD	±70	361	±80
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P00354799	Australia	< LOD	±50	35,235	±420
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P00244019	New Caledonia	< LOD	±30	5,036	±120
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P03021199	New Caledonia	< LOD	±30	3,595	±110
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P00244016	New Caledonia	< LOD	±30	21,217	±250
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P04284510	New Caledonia	< LOD	±50	8,599	±230
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P00244010	New Caledonia	< LOD	±50	39,269	±430
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P01073596	New Caledonia	< LOD	±50	6,253	±170
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P06899934	New Caledonia	< LOD	±50	37,157	±460
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P00244020	New Caledonia	< LOD	±40	35,133	±410
Alseuosmiaceae	<i>Platyspermation</i>	<i>crassifolium</i>	P04393181	New Caledonia	< LOD	±30	71,495	±460
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P04552544	New Caledonia	< LOD	±60	3,825	±160
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P04552545	New Zealand	< LOD	±50	110	±50
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P04552543	Chatham Islands	< LOD	±50	1,294	±100
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P04552542	New Zealand	< LOD	±60	3,363	±160
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P05490160	New Zealand	< LOD	±60	3,690	±160
Argophyllaceae	<i>Corokia</i>	<i>buddleiodes</i>	P04552556	New Zealand	< LOD	±40	1,647	±90
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P06805432	New Zealand	< LOD	±40	603	±70
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P06805434	Rapa Iti	< LOD	±50	261	±60
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P04552549	Rapa Iti	< LOD	±50	239	±60
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P06805433	Rapa Iti	< LOD	±60	390	±70

Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P04352024	Rapa Iti	< LOD	±50	296	±60
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P04352025	Rapa Iti	< LOD	±40	292	±60
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P04552547	Rapa Iti	< LOD	±50	576	±70
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P04552546	Rapa Iti	< LOD	±40	85	±50
Argophyllaceae	<i>Corokia</i>	<i>collenettei</i>	P06805435	Rapa Iti	< LOD	±40	397	±60
Argophyllaceae	<i>Corokia</i>	<i>cotoneaster</i>	P04552539	Rapa Iti	< LOD	±50	845	±90
Argophyllaceae	<i>Corokia</i>	<i>cotoneaster</i>	P04552541	New Zealand	< LOD	±70	109	±70
Argophyllaceae	<i>Corokia</i>	<i>cotoneaster</i>	P04552540	New Zealand	< LOD	±60	416	±80
Argophyllaceae	<i>Corokia</i>	<i>cotoneaster</i>	P06234105	New Zealand	< LOD	±30	82	±40
Argophyllaceae	<i>Corokia</i>	<i>cotoneaster</i>	P05490161	New Zealand	< LOD	±40	453	±60
Argophyllaceae	<i>Corokia</i>	<i>whiteana</i>	P04552538	New Zealand	< LOD	±70	311	±80
Argophyllaceae	<i>Corokia</i>	<i>whiteana</i>	P04352022	Australia	< LOD	±50	1,396	±90
Argophyllaceae	<i>Argophyllum</i>	<i>brevipetalum</i>	P03609438	Australia	101	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>brevipetalum</i>	P03609387	New Caledonia	157	±20	196	±30
Argophyllaceae	<i>Argophyllum</i>	<i>brevipetalum</i>	P03609387	New Caledonia	147	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>brevipetalum</i>	P04351395	New Caledonia	0	±20	255	±30
Argophyllaceae	<i>Argophyllum</i>	<i>brevipetalum</i>	P06234113	New Caledonia	1676	±30	242	±40
Argophyllaceae	<i>Argophyllum</i>	<i>cryptophlebum</i>	P03616518	New Caledonia	0	±30	0	±60
Argophyllaceae	<i>Argophyllum</i>	<i>cryptophlebum</i>	P03616526	Australia	0	±30	248	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P00354794	Australia	309	±10	50	±20
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P03609437	New Caledonia	967	±20	0	±20
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P03609439	New Caledonia	3223	±40	319	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P03609379	New Caledonia	0	±20	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P03609379	New Caledonia	0	±200	0	±500
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P03609382	New Caledonia	2253	±50	533	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P04284932	New Caledonia	608	±20	318	±30
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P04445120	New Caledonia	118	±20	107	±30
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P04445187	New Caledonia	0	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P04445188	New Caledonia	0	±20	637	±40

Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P06234110	New Caledonia	433	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P06234114	New Caledonia	0	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>ellipticum</i>	P04445184	New Caledonia	6670	±50	1,641	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00354673	New Caledonia	1351	±30	124	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537619	New Caledonia	207	±20	74	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351389	New Caledonia	587	±30	66	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351394	New Caledonia	1280	±20	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351404	New Caledonia	782	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284933	New Caledonia	347	±20	63	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445164	New Caledonia	896	±20	397	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445166	New Caledonia	2778	±40	135	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445180	New Caledonia	178	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537622	New Caledonia	3879	±40	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609383	New Caledonia	2649	±30	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609384	New Caledonia	1238	±30	95	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609385	New Caledonia	5694	±50	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609286	New Caledonia	41	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609287	New Caledonia	1581	±20	80	±20
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284938	New Caledonia	0	±20	56	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284939	New Caledonia	489	±20	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284517	New Caledonia	373	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445152	New Caledonia	229	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445157	New Caledonia	73	±20	279	±35
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445160	New Caledonia	0	±20	135	±30

Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00217129	New Caledonia	167	$\pm 20$	115	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609314	New Caledonia	320	$\pm 20$	103	$\pm 35$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351401	New Caledonia	752	$\pm 20$	89	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284521	New Caledonia	796	$\pm 20$	0	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445128	New Caledonia	461	$\pm 20$	0	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445165	New Caledonia	221	$\pm 20$	176	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445172	New Caledonia	672	$\pm 20$	96	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445174	New Caledonia	1775	$\pm 30$	0	$\pm 50$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P06234106	New Caledonia	133	$\pm 20$	370	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P06234119	New Caledonia	3896	$\pm 40$	0	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00217183	New Caledonia	1534	$\pm 20$	0	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537637	New Caledonia	246	$\pm 20$	0	$\pm 60$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537638	New Caledonia	960	$\pm 30$	57	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609305	New Caledonia	737	$\pm 20$	0	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609307	New Caledonia	485	$\pm 20$	55	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609351	New Caledonia	437	$\pm 20$	0	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351397	New Caledonia	2514	$\pm 30$	380	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445122	New Caledonia	127	$\pm 20$	0	$\pm 50$
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445179	New Caledonia	213	$\pm 20$	48	$\pm 30$
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616523	New Caledonia	0	$\pm 30$	359	$\pm 50$
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616524	Australia	0	$\pm 30$	314	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616525	Australia	36	$\pm 20$	281	$\pm 50$
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609289	Australia	1110	$\pm 30$	212	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609293	New Caledonia	1076	$\pm 20$	539	$\pm 40$
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609294	New Caledonia	34	$\pm 20$	776	$\pm 50$

Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04351398	New Caledonia	511	±20	123	±30
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04284918	New Caledonia	103	±20	721	±50
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04284920	New Caledonia	0	±20	1,802	±60
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04445124	New Caledonia	33	±20	285	±40
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04445145	New Caledonia	50	±20	601	±40
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P04445158	New Caledonia	165	±10	1,488	±40
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P05563751	New Caledonia	75	±20	231	±40
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04351380	New Caledonia	0	±30	437	±40
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04284934	New Caledonia	0	±20	833	±50
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04284935	New Caledonia	0	±20	597	±40
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04445131	New Caledonia	0	±20	1,862	±50
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04445133	New Caledonia	0	±20	113	±30
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P04445173	New Caledonia	0	±30	317	±40
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P05563784	New Caledonia	0	±30	472	±40
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P05563794	New Caledonia	0	±30	723	±50
Argophyllaceae	<i>Argophyllum</i>	<i>nitidum</i>	P06234107	New Caledonia	0	±30	222	±40
Argophyllaceae	<i>Argophyllum</i>	<i>riparium</i>	P03609386	New Caledonia	1667	±30	48	±30
Argophyllaceae	<i>Argophyllum</i>	<i>riparium</i>	P03609388	New Caledonia	591	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>riparium</i>	P04445141	New Caledonia	402	±20	142	±30
Argophyllaceae	<i>Argophyllum</i>	<i>riparium</i>	P06234104	New Caledonia	173	±10	93	±30
Argophyllaceae	<i>Argophyllum</i>	<i>verae</i>	P00709627	New Caledonia	0	±30	214	±40
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04351382	Australia	345	±20	121	±30
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04284916	New Caledonia	132	±10	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04284936	New Caledonia	402	±20	98	±30

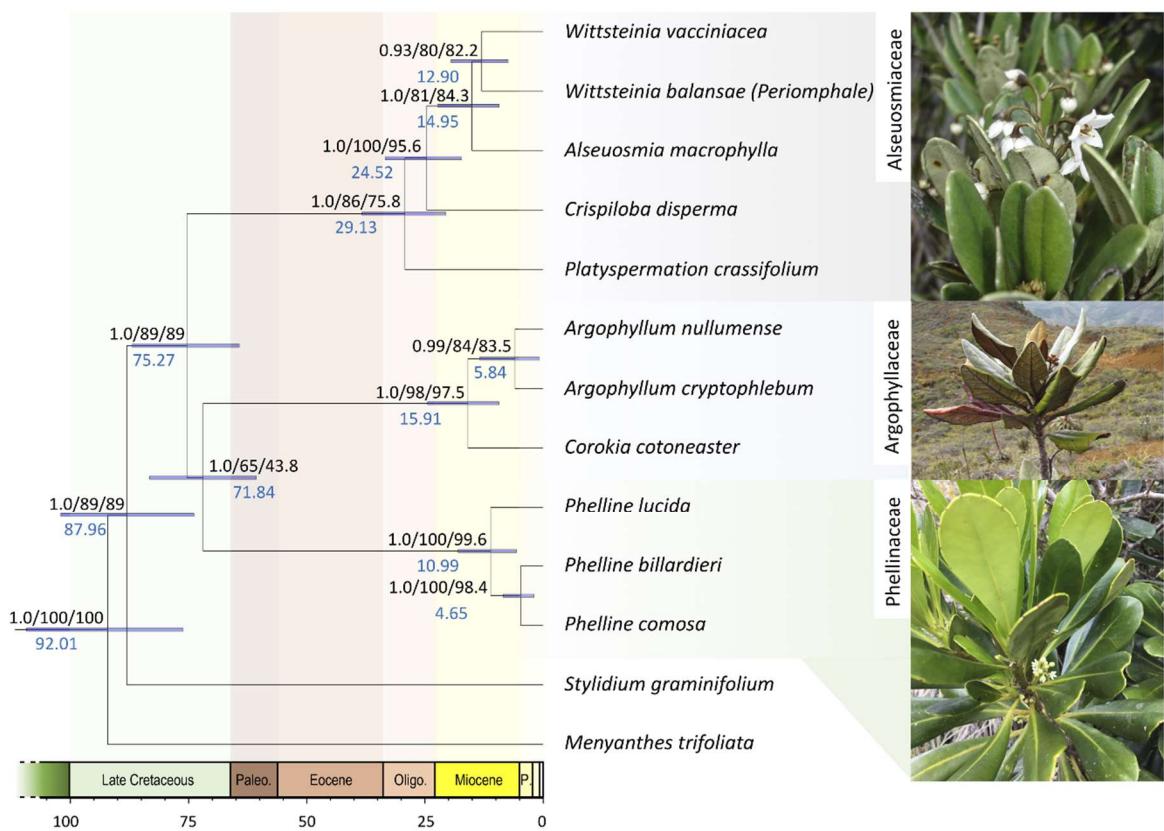
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04445117	New Caledonia	298	±20	376	±40
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04445117	New Caledonia	1023	±20	78	±20
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P04445162	New Caledonia	116	±20	63	±30
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P05563809	New Caledonia	1872	±40	389	±40
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P05563811	New Caledonia	217	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P05563824	New Caledonia	387	±20	94	±30
Argophyllaceae	<i>Argophyllum</i>	<i>vernicosum</i>	P05563829	New Caledonia	977	±30	0	±50
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071784	New Caledonia	< LOD	±50	19,521	±330
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071827	New Caledonia	< LOD	±50	8,496	±220
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00070321	New Caledonia	< LOD	±50	14,215	±260
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071872	New Caledonia	< LOD	±50	44,378	±500
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071874	New Caledonia	< LOD	±60	2,426	±140
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071719	New Caledonia	< LOD	±60	26,176	±420
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00071770	New Caledonia	< LOD	±50	33,615	±430
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00931002	New Caledonia	< LOD	±40	56,793	±450
Phellinaceae	<i>Phelline</i>	<i>barrierei</i>	P00580367	New Caledonia	< LOD	±50	14,026	±260
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071886	New Caledonia	< LOD	±60	2,418	±140
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071638	New Caledonia	< LOD	±70	659	±100
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071728	New Caledonia	< LOD	±60	3,014	±150
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071679	New Caledonia	< LOD	±60	1,846	±120
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071735	New Caledonia	< LOD	±60	1,106	±100
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00070360	New Caledonia	< LOD	±70	2,035	±140
Phellinaceae	<i>Phelline</i>	<i>billardierei</i>	P00071865	New Caledonia	< LOD	±40	1,107	±80
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P06800617	New Caledonia	< LOD	±60	5,201	±190

Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00070316	New Caledonia	< LOD	±70	403	±90
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00071678	New Caledonia	< LOD	±60	1,273	±110
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00071748	New Caledonia	< LOD	±70	121	±70
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00071713	New Caledonia	< LOD	±30	252	±50
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00071814	New Caledonia	< LOD	±70	469	±90
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P06703750	New Caledonia	< LOD	±70	794	±100
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00070315	New Caledonia	< LOD	±50	658	±80
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00071844	New Caledonia	< LOD	±80	347	±90
Phellinaceae	<i>Phelline</i>	<i>brachyphylla</i>	P00931013	New Caledonia	< LOD	±60	2,070	±120
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071824	New Caledonia	< LOD	±50	6,083	±180
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071742	New Caledonia	< LOD	±60	< LOD	±90
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071760	New Caledonia	< LOD	±60	626	±80
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071881	New Caledonia	< LOD	±60	1,947	±120
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P04034829	New Caledonia	< LOD	±60	248	±70
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071834	New Caledonia	< LOD	±60	3,561	±160
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071812	New Caledonia	< LOD	±60	1,954	±120
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00555305	New Caledonia	< LOD	±40	4,563	±140
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071805	New Caledonia	< LOD	±50	10,115	±230
Phellinaceae	<i>Phelline</i>	<i>comosa</i>	P00071672	New Caledonia	< LOD	±40	3,794	±130
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00070452	New Caledonia	< LOD	±70	1,132	±110
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071754	New Caledonia	< LOD	±40	4,378	±150
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071822	New Caledonia	< LOD	±40	123	±50
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071802	New Caledonia	< LOD	±60	650	±90
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071804	New Caledonia	< LOD	±70	945	±110

Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071743	New Caledonia	< LOD	±70	1,171	±110
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071835	New Caledonia	< LOD	±70	4,358	±190
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00070469	New Caledonia	< LOD	±70	1,210	±110
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071807	New Caledonia	< LOD	±70	2,294	±150
Phellinaceae	<i>Phelline</i>	<i>dumbeensis</i>	P00071809	New Caledonia	< LOD	±60	5,771	±200
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071861	New Caledonia	< LOD	±60	241	±70
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P01073019	New Caledonia	< LOD	±60	949	±90
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071860	New Caledonia	< LOD	±60	1,885	±120
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071808	New Caledonia	< LOD	±70	1,639	±130
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071706	New Caledonia	< LOD	±60	1,390	±110
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00070453	New Caledonia	< LOD	±50	2,532	±120
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071684	New Caledonia	< LOD	±60	5,830	±190
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00070456	New Caledonia	< LOD	±50	675	±80
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071692	New Caledonia	< LOD	±50	2,025	±110
Phellinaceae	<i>Phelline</i>	<i>erubescens</i>	P00071781	New Caledonia	< LOD	±60	207	±70
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00555301	New Caledonia	< LOD	±80	227	±80
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00071746	New Caledonia	267.60	±50	167	±60
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00555309	New Caledonia	< LOD	±50	142	±60
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00071777	New Caledonia	< LOD	±60	815	±90
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00071669	New Caledonia	93	±30	218	±50
Phellinaceae	<i>Phelline</i>	<i>gracilior</i>	P00071871	New Caledonia	638	±40	472	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00963295	New Caledonia	< LOD	±50	194	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071820	New Caledonia	< LOD	±20	122	±30
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071668	New Caledonia	< LOD	±70	< LOD	±100

Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00555315	New Caledonia	< LOD	±60	< LOD	±90
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071677	New Caledonia	< LOD	±50	223	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071676	New Caledonia	< LOD	±50	211	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071705	New Caledonia	< LOD	±70	237	±80
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00478189	New Caledonia	< LOD	±30	< LOD	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071726	New Caledonia	< LOD	±40	< LOD	±60
Phellinaceae	<i>Phelline</i>	<i>indivisa</i>	P00071689	New Caledonia	< LOD	±60	130	±60
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071682	New Caledonia	< LOD	±60	4,306	±160
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071773	New Caledonia	< LOD	±40	6,483	±170
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071708	New Caledonia	< LOD	±50	5,293	±170
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00239234	New Caledonia	< LOD	±50	17,956	±280
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071616	New Caledonia	< LOD	±60	8,555	±230
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071661	New Caledonia	< LOD	±60	6,397	±200
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071749	New Caledonia	< LOD	±50	22,115	±360
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071694	New Caledonia	< LOD	±50	3,470	±140
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071619	New Caledonia	< LOD	±60	10,032	±260
Phellinaceae	<i>Phelline</i>	<i>lucida</i>	P00071617	New Caledonia	< LOD	±60	4,699	±180
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071741	New Caledonia	< LOD	±90	2,723	±180
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071778	New Caledonia	< LOD	±70	3,041	±160
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071915	New Caledonia	< LOD	±50	< LOD	±90
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071730	New Caledonia	< LOD	±60	< LOD	±100
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071727	New Caledonia	72	±50	1,428	±120
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P04034864	New Caledonia	< LOD	±60	363	±80
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071830	New Caledonia	< LOD	±60	129	±60

Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071866	New Caledonia	< LOD	±60	3,347	±160
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00071671	New Caledonia	< LOD	±60	195	±70
Phellinaceae	<i>Phelline</i>	<i>macrophylla</i>	P00931006	New Caledonia	< LOD	±60	566	±80



**Figure S1.** Dated phylogeny resulting from the BEAST analyses based on the study of Ramírez-Barahona et al. (2020) [R2020] (topology identical to the best-fit ML tree). Support values at nodes refer to PP, uBV and SH-aLRT, in that order. Median ages are also provided on nodes just below the support values. Horizontal bars on nodes represent 95% HPD of age estimates. Time scale (horizontal) in Ma (Paleo.: Paleocene, Oligo: Oligocene, P: Pliocene). Example plant species photos on the right (from top to bottom): *Platyspermation crassifolium*, *Argophyllum ellipticum*, *Phelline barrierei*.