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

4
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15

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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: Viot (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 *Platyspermatium* 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

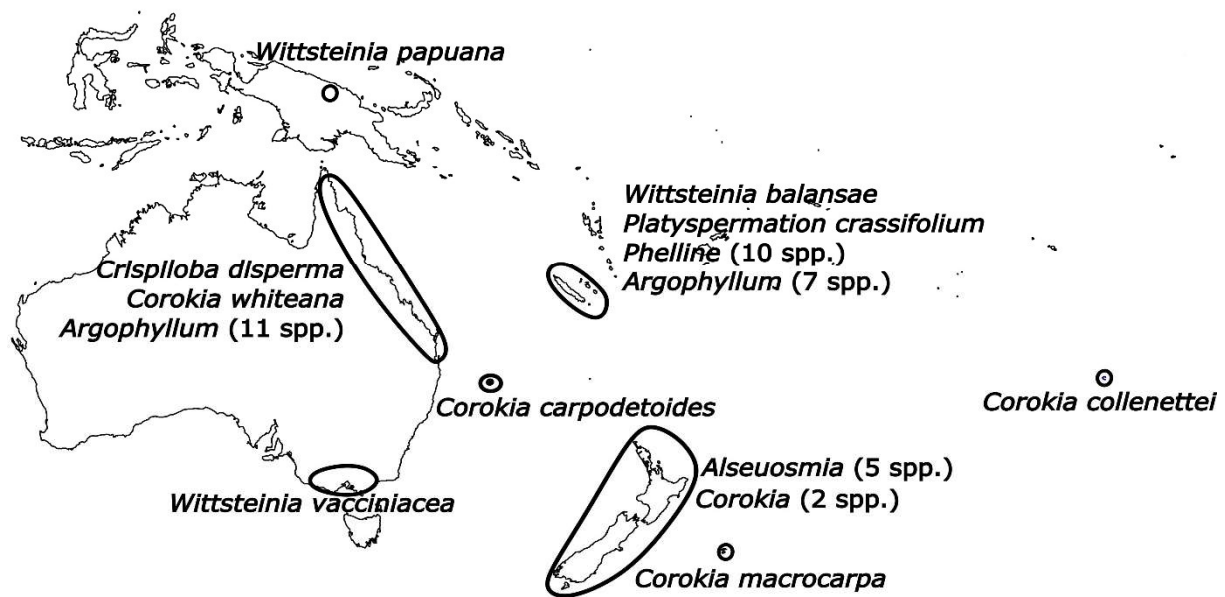
- Alseuosmia banksii* A.Cunn. – New Zealand
Alseuosmia macrophylla A.Cunn. – New Zealand
Alseuosmia pusilla Colenso – New Zealand
Alseuosmia quercifolia A.Cunn. – New Zealand
Alseuosmia turneri R.O.Gardner – New Zealand
Crispiloba disperma (S. Moore) Steenis – Australia
Platyspermation crassifolium Guillaumin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

Argophyllaceae (Engl.) Takht.

- Argophyllum cryptophlebium* 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 iridescens 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 *Platyspermatium*

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 (Poureau 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; Poureau 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 biphosphate 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 *Platyspermatium crassifolium*, and *Wittsteinia vacciniacea*. Species in Argophyllaceae included
173 *Argophyllum cryptophlebium*, *Argophyllum nullumense*, and *Corokia cotoneaster*. Species in
174 Phellinaceae included *Phelline billardierei*, *Phelline comosa*, and *Phelline lucida*. For outgroup
175 selection, we included *Stylidium 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 (Kato 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 + *Stylidium 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 $\mu\text{g}\cdot\text{g}^{-1}$ 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 HNO_3 (65%) and H_2O_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

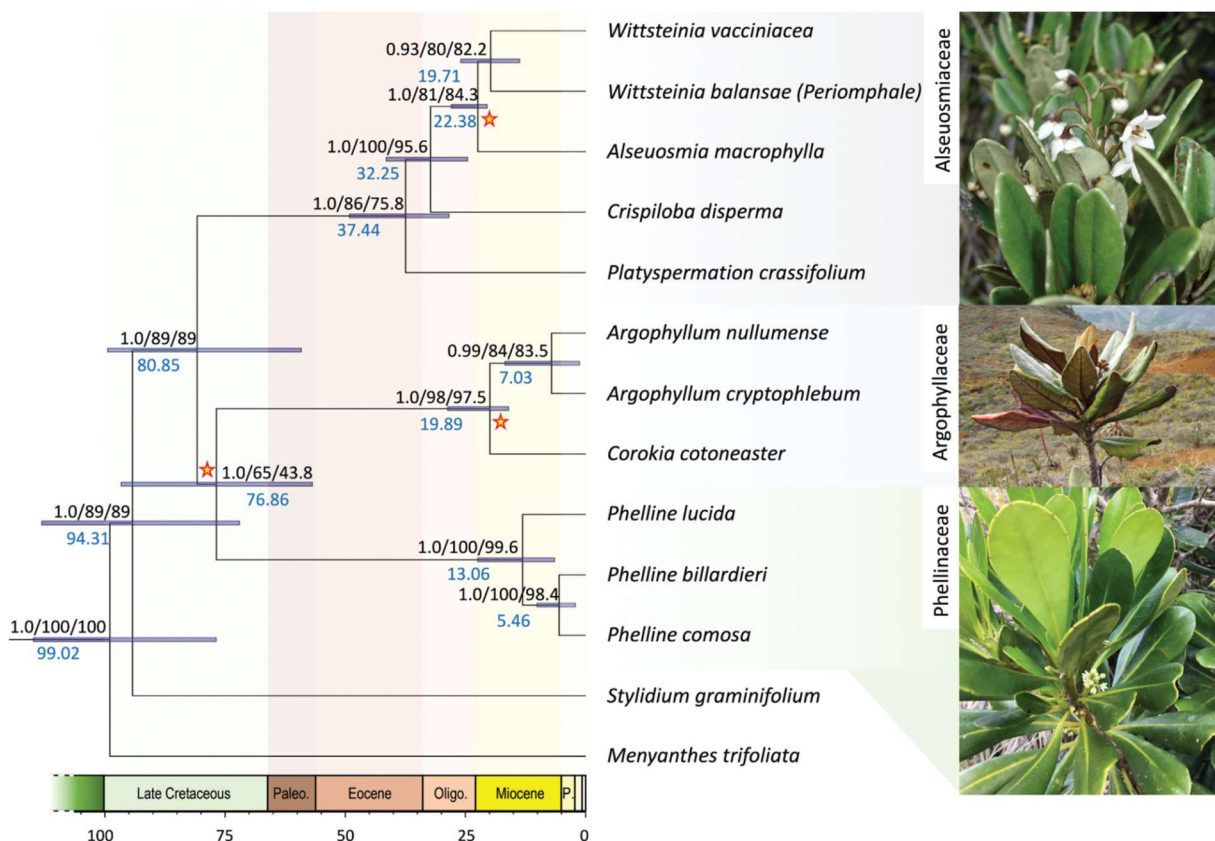
287 **Results**

288

289 *Phylogenetic inference*

290 In our Bayesian phylogenetic analysis of Alseuosmineae, all parameters showed ESS values
291 ≥ 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 ≥ 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



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

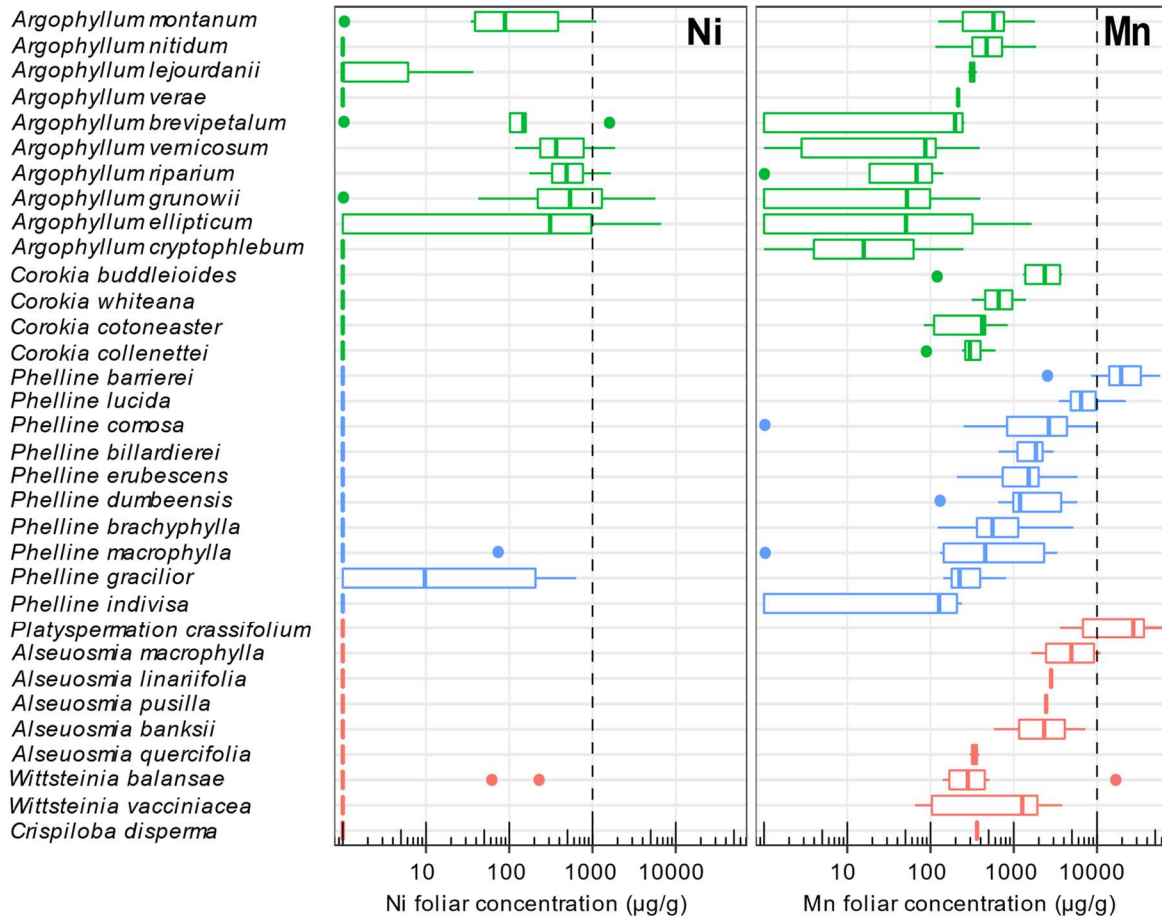
308 ages are also provided on nodes just below the support values. The three fossil constraints are
309 highlighted with stars. Horizontal bars on nodes represent 95% Highest Posterior Density
310 (HPD) of age estimates. Time scale (horizontal) in Ma (Paleo.: Paleocene, Oligo: Oligocene,
311 P: Pliocene).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

314 ***Molecular dating***

315 In our dating analyses of Alseuosmineae, all parameters showed ESS values ≥ 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).



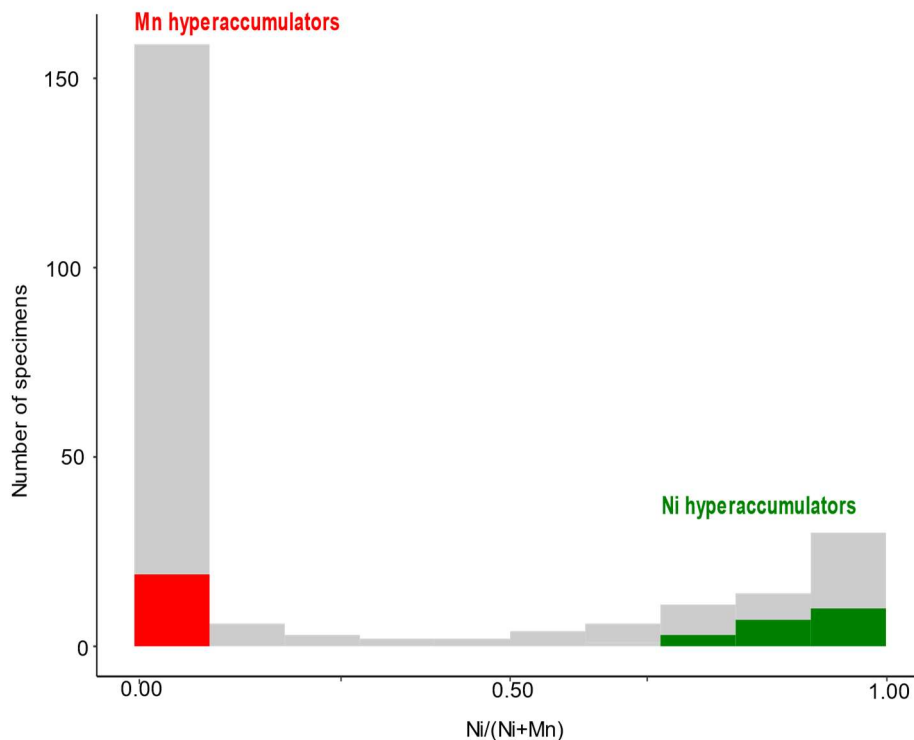
341
 342 **Figure 3.** Boxplots showing Ni and Mn foliar concentrations ($\mu\text{g g}^{-1}$) measured by X-ray
 343 fluorescence (XRF) scanning of herbarium specimens from 33 species of Argophyllaceae
 344 (green), Phellinaceae (blue) and Alseuosmiaceae (red). The dashed lines are the
 345 hyperaccumulation 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 *Platyspermatium 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 *Platyspermatium 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 Ni/(Ni+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 *Platyspermatia* (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 *Platyspermatia*,
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 *Phellina* 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 Smitsen 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 $\mu\text{g}\cdot\text{g}^{-1}$ 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 $\mu\text{g}\cdot\text{g}^{-1}$, 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 $\mu\text{g}\cdot\text{g}^{-1}$. 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 $\mu\text{g}\cdot\text{g}^{-1}$ (up to 22,000 $\mu\text{g}\cdot\text{g}^{-1}$). 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 *Platyspermatium*
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

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565

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568

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572

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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-](https://doi.org/10.23708/HERBIER-NOUVELLE-CALEDONIE)
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, Svennblad 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/botlinnear/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 XXI^e 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 ultrabasiqes 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* 4:279. doi:10.3389/fpls.2013.00279.

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, Havery 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 diaspore
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, Smitsen 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, Ducouso 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 *Platyspermatium*
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 Viot 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.

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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; *Platyspermatium 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 *cryptophlebium* **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 pcol (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 *Stylidium graminifolium* **Sw. ex Willd.**, Cosner 174 (OS), AJ236201, AF130188, L18790.

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878

Table S1 Ni and Mn foliar concentrations ($\mu\text{g}\cdot\text{g}^{-1}$) 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	±70	512	±90
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183532	New Caledonia	< LOD	±80	16,064	±400
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183593	New Caledonia	< LOD	±70	146	±70
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00217144	New Caledonia	< LOD	±40	139	±40
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183595	New Caledonia	< LOD	±50	339	±60
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183596	New Caledonia	58	±40	294	±70
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183543	New Caledonia	< LOD	±70	143	±70
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00354302	New Caledonia	< LOD	±70	250	±80
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183524	New Caledonia	< LOD	±70	266	±80
Alseuosmiaceae	<i>Wittsteinia</i>	<i>balansae</i>	P00183586	New Caledonia	217	±50	491	±90
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518558	New Caledonia	< LOD	±60	1,264	±110
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518557	Australia	< LOD	±60	1,921	±130
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P00760352	Australia	< LOD	±20	103	±30
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P04518559	Australia	< LOD	±50	3,809	±140
Alseuosmiaceae	<i>Wittsteinia</i>	<i>vacciniacea</i>	P06775815	Australia	< LOD	±20	64	±30
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233471	Australia	< LOD	±60	579	±80
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233470	New Zealand	< LOD	±80	2,323	±160
Alseuosmiaceae	<i>Alseuosmia</i>	<i>banksii</i>	P04233469	New Zealand	< LOD	±50	7,247	±200
Alseuosmiaceae	<i>Alseuosmia</i>	<i>linariifolia</i>	P04233472	New Zealand	< LOD	±60	2,894	±150
Alseuosmiaceae	<i>Alseuosmia</i>	<i>linariifolia</i>	P04233473	New Zealand	< LOD	±60	2,724	±150
Alseuosmiaceae	<i>Alseuosmia</i>	<i>macrophylla</i>	P04233476	New Zealand	< LOD	±70	11,054	±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>cryptophlebium</i>	P03616518	New Caledonia	0	±30	0	±60
Argophyllaceae	<i>Argophyllum</i>	<i>cryptophlebium</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	±20	115	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609314	New Caledonia	320	±20	103	±35
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351401	New Caledonia	752	±20	89	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04284521	New Caledonia	796	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445128	New Caledonia	461	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445165	New Caledonia	221	±20	176	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445172	New Caledonia	672	±20	96	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445174	New Caledonia	1775	±30	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P06234106	New Caledonia	133	±20	370	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P06234119	New Caledonia	3896	±40	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00217183	New Caledonia	1534	±20	0	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537637	New Caledonia	246	±20	0	±60
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P00537638	New Caledonia	960	±30	57	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609305	New Caledonia	737	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609307	New Caledonia	485	±20	55	±30
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P03609351	New Caledonia	437	±20	0	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04351397	New Caledonia	2514	±30	380	±40
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445122	New Caledonia	127	±20	0	±50
Argophyllaceae	<i>Argophyllum</i>	<i>grunowii</i>	P04445179	New Caledonia	213	±20	48	±30
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616523	New Caledonia	0	±30	359	±50
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616524	Australia	0	±30	314	±40
Argophyllaceae	<i>Argophyllum</i>	<i>lejourdanii</i>	P03616525	Australia	36	±20	281	±50
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609289	Australia	1110	±30	212	±40
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609293	New Caledonia	1076	±20	539	±40
Argophyllaceae	<i>Argophyllum</i>	<i>montanum</i>	P03609294	New Caledonia	34	±20	776	±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

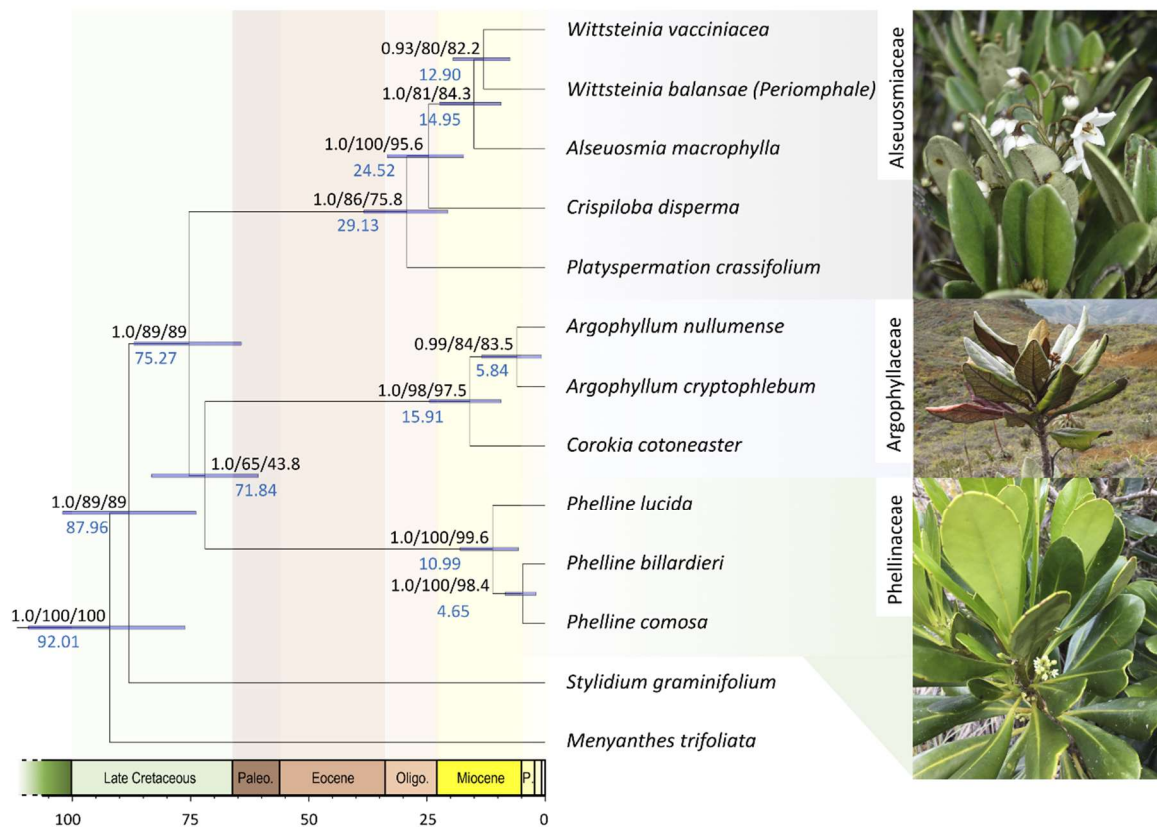


Figure S1. Dated phylogeny resulting from the BEAST analyses based on based on the study of Ramírez-Barahona et al. (2020) [R2020] (topology identical to the best-fit ML tree). Support values at nodes refer to PP, uBV and SH-aLRT, in that order. Median ages are also provided on nodes just below the support 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 barrieriei*.