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## Origins of old lineages in New Caledonia: A geologically informed test of the island-hopping hypothesis

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### ► To cite this version:

Julien Malem, Tony Robillard, Dominique Cluzel, Loïc Bellier, Romain Nattier, et al.. Origins of old lineages in New Caledonia: A geologically informed test of the island-hopping hypothesis. *Journal of Biogeography*, 2023, 50 (9), pp.1587-1601. 10.1111/jbi.14673 . hal-04198375v1

**HAL Id: hal-04198375**

**<https://cnrs.hal.science/hal-04198375v1>**

Submitted on 23 Dec 2023 (v1), last revised 9 Nov 2023 (v2)

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1 **Origins of old lineages in New Caledonia: a geologically-informed test of**  
2 **the island-hopping hypothesis**

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24 **Abstract**

25

26 **Aim:** Although New Caledonia is now considered an oceanic island that emerged ca. 60 Ma,  
27 a few terrestrial clades are significantly older, raising the question of the origin of these  
28 groups. Classically, old lineages on more recent islands are hypothesized to originate through  
29 a process of hopping on now-vanished islands (i.e. island-hopping hypothesis) or other  
30 territories. We aim to test this hypothesis by studying a group of cockroaches with several  
31 lineages found in NC.

32 **Location:** New Caledonia, New Zealand, Australia

33 **Taxon:** Insects: Blattodea

34 **Methods:** We generated a dated phylogeny for blattid cockroaches (Blattidae and  
35 Trypionidae) using Bayesian inference along with fossil calibrations. We reviewed studies on  
36 the paleogeography of the Southwest Pacific region, including hypotheses about the existence  
37 of yet-to-be-discovered past islands, and constructed biogeographic tests accordingly. We  
38 computed ancestral area estimation under different models in *BioGeoBEARS* (DEC,  
39 BAYAREALIKE, DIVALIKE, with or without +J) to test the role of an island-hopping  
40 hypothesis in the establishment of NC blattid fauna.

41 **Results:** We find divergence times older than 60 Ma for two NC clades. We show that these  
42 "old" endemic lineages can partially be explained by indirect dispersal from Australia or New  
43 Zealand through now disappeared islands. Alternative hypotheses suggest multiple  
44 independent colonizations of NC from Antarctica or Australia.

45 **Main conclusions:** Our results indicate that island-hopping may explain the presence of old  
46 groups in NC. The island-hopping hypothesis is nonetheless only supported for a period-area  
47 from which geological evidence is ambiguous. Our work highlights both the fruitful  
48 interactions between geology and biogeography and the underlying difficulties. The multiple  
49 colonization events inferred for NC provide additional insights into the composite nature of  
50 NC biota.

51

52 **Keywords:** relicts, paleoendemics, New Caledonia, paleogeography, historical biogeography,  
53 phylogenetic dating, insects, stepping stones, BioGeoBEARS, competing hypotheses,  
54 vanished islands

55

## 56 ***1. INTRODUCTION***

57

58 Once considered to be of Gondwanan vicariant origin, the biota of New Caledonia (NC) is  
59 now understood as primarily resulting from relatively recent dispersals across the oceans,  
60 following major geological events of emergence and submergence (Grandcolas et al., 2008;  
61 Murienne, 2009; Grandcolas, 2017; Giribet & Baker, 2019). General submersion occurred  
62 across Zealandia—a 4.9 Mkm<sup>2</sup> region of the southwest Pacific Ocean, made up of continental  
63 crust, mostly submerged today, and also known as Tasmantis (e.g. Smith et al., 2007)—  
64 during the Late Cretaceous–Paleocene. This general submersion (reviewed in Maurizot &  
65 Campbell, 2020) argues for a NC biota younger than 60 Myrs. Although marine  
66 sedimentation prevailed during most of the Paleogene, localized and short-lived emersions  
67 occurred before the post-obduction final emersion of NC, which is poorly time-constrained  
68 (30–25 Ma). This final emersion has been previously mentioned in the geological literature  
69 (e.g. Aitchison et al., 1995; Cluzel et al., 2001, 2012; Pelletier, 2007) and therefore taken into  
70 account by biologists to formulate biogeographic scenarios (e.g. Grandcolas et al., 2008;  
71 Nattier et al., 2017). However, the duration of this last event remains uncertain due to the  
72 absence of decisive geological record between -34 and -25 Ma (Maurizot & Campbell, 2020).  
73 Consistent with evidence for a prolonged period of submergence precluding subsistence of a  
74 terrestrial biota, NC is thus commonly seen as an oceanic or Darwinian island (Gillespie &  
75 Roderick, 2002), with its biota perceived to have originated from de novo transoceanic  
76 dispersals, and thus younger than 60 Myrs.

77 This modern view is further supported by several studies relying on phylogenetic dating,  
78 which suggest relatively recent age estimates for NC taxa (Grandcolas et al., 2008; Nattier et  
79 al., 2017; Baker et al., 2020), and by paleontological studies bringing a first view on the past  
80 biota of the island (Garrouste et al., 2021). Nonetheless some terrestrial lineages have been  
81 challenging this view and raised the question of the origin of “old” lineages—i.e. older than  
82 37 Ma, or than 60 Ma to be in line with more recent geological evidence—on younger islands  
83 (Grandcolas et al., 2014; Giribet & Baker, 2019). To decipher the origin of those “old”  
84 lineages, the most frequent explanation is the island-hopping hypothesis (e.g., Gressitt, 1956;  
85 Darlington, 1957; Carlquist, 1965; Heads, 2005, 2008; Ladiges & Cantrill, 2007). A variant  
86 of the stepping-stone dispersal model, this hypothesis involves now vanished islands that  
87 would have served as faunal refugia and stepping stones for colonization, before they  
88 disappeared. The Gondwanan history and hectic regional geological context of NC would  
89 point to this hypothesis. However, this island-hopping scenario is purely narrative in its

90 formulation and has only been tested indirectly, by dating clades with molecular studies to  
91 infer whether they are older than the islands (Nattier et al., 2011, 2017; Grandcolas, 2017;  
92 Magalhaes et al., 2021).

93 In this context, a better understanding of the origin of the NC biota amounts to a better  
94 understanding of the origin of old lineages in NC, be they paleoendemics, relicts or revenant  
95 clades (Gillespie & Roderick, 2002; Sharma & Wheeler, 2013; Grandcolas et al., 2014, 2008;  
96 Grandcolas, 2017; Giribet & Baker, 2019). Some lineages of fig wasps (Cruaud et al., 2012),  
97 harvestmen (Giribet et al., 2012), leaf beetles (Papadopoulou et al., 2013) and moths (Gibbs  
98 & Lee, 2014) have been inferred to have radiated or split from their sister group prior to the  
99 age of submersion and thus identified as old lineages for NC (e.g., Nattier et al., 2017).

100 Different biogeographic events have been suggested to explain this paradoxical situation, but  
101 only *a posteriori*. Instead, we here embrace a hypothesis-driven study using *a priori* the latest  
102 geological context and data about this geologically-complex region, to elucidate the  
103 biogeographic events that might have allowed “old” lineages to colonize NC after its latest  
104 proven emergence (i.e. 60 Ma). Specifically, we test competing biogeographic scenarios that  
105 imply or not island-hopping events according to the geological record and its uncertainties.

106 In contrast with most islands of the Southwest Pacific, NC (as New Zealand) yields a  
107 relatively old geological record, which may be divided into four periods: the Gondwanan  
108 period (Permian to Early Cretaceous), the drifting period (Late Cretaceous to latest  
109 Paleocene), the obduction period (Eocene) and the post-obduction period (Oligocene to  
110 present) (Cluzel et al., 2012). It is now a common practice to include geological history into  
111 biogeographic analyses, but biogeographic models can be further expanded (Ronquist &  
112 Sanmartín, 2011) to strengthen hypothesis-driven research—see for instance Favre et al.  
113 (2015) about the uplift of the Qinghai-Tibetan plateau. Thus, any evidence of now-vanished  
114 islands at different geological times and in the vicinity of NC can be part of biogeographic  
115 analyses, in a geologically-informed test of the island-hopping hypothesis. Here, we adopt a  
116 ‘trans-disciplinary biogeographic’ approach (Antonelli et al., 2018) by summarizing this  
117 evidence to incorporate it into biogeographic models that allow, or disallow, island-hopping  
118 events.

119 To address the knowledge gap about the origin of “old” lineages in NC, we use the  
120 geologically-informed context to formally test the island-hopping hypothesis on two  
121 cockroach families: Blattidae and Tryonicidae. The most recent phylogenetic studies suggest  
122 that these families are sister taxa and that their MRCA would date from the Early Cretaceous,  
123 or alternatively, to the Late Triassic [e.g. 130-140 Ma in Bourguignon et al. (2018) and

124 Evangelista et al. (2019); 230 Ma in Legendre et al. (2015)]. The family Blattidae comprises  
125 53 extant genera with a worldwide distribution (Princis, 1966; Grandcolas, 1996, 1997;  
126 Beccaloni, 2014; Liao et al., 2019), while the family Tryonicidae comprises only two extant  
127 genera known from NC only (genus *Lauraesilpha* Grandcolas, 1997) and from NC and  
128 Australia (genus *Tryonicus* Shaw, 1925). The current dating estimates and their supposed  
129 phylogenetic relationships make them prone to offer at least two additional “old” lineages for  
130 NC, and thus to *a priori* test island-hopping scenarios. We first reconstruct the phylogenetic  
131 relationships of these families and provide updated dating estimates, relying on an improved  
132 taxonomic sampling. If dating estimates of diversification events within NC clades occur  
133 before 60 Ma (i.e. before the latest proven emergence), we expect that the most likely  
134 biogeographic scenarios would involve island hopping events. Thus, we contrast  
135 biogeographic scenarios that allow or disallow island-hopping to decipher the origin of “old”  
136 lineages in NC.

137

## 138 **2. MATERIALS AND METHODS**

139

### 140 **2.1. Taxon & molecular sampling**

141

142 We sampled a total of 126 ingroup terminal taxa considered at the species level (from 42  
143 genera, i.e. 73.4 % of the generic diversity), including 4 representatives of the family  
144 Lamproblattidae, 16 Tryonicidae and 106 Blattidae. All four described Blattidae subfamilies  
145 (i.e. Archiblattinae Kirby, 1904, Blattinae Latreille, 1810, Macrocerinae Roth, 1993 and  
146 Polyzosteriinae Tepper, 1893) were represented by at least one taxon. Subfamilial  
147 delineations within Blattidae were recently revised (Djernæs & Murienne, 2022; Deng et al.,  
148 2023): Macrocerinae was included within Polyzosteriinae, while four additional subfamilies  
149 were erected or revised (Austrostylopyginae Djernæs & Murienne, 2022, Duchailiinae  
150 Roth, 2003, Eurycotiinae McKittrick, 1964 and Hebardinae Deng & Che, 2023). The four  
151 latter subfamilies were also sampled here with at least one taxon. Here, we follow the revised  
152 classification of Djernæs & Murienne (2022) with six subfamilies, although the taxonomy of  
153 these insects needs further investigation. We have chosen taxa according to their geographic  
154 distribution, including 41 taxa endemic to NC and one widespread taxon present in the island.  
155 We sampled as many genera as possible from the two focal families. Because of the very  
156 sparse and controversial fossil record of Blattidae (e.g. Qiu et al., 2020), we chose outgroups  
157 that allowed us to include clades with a robust fossil record. We selected 14 outgroup taxa,

158 comprising 13 Blattodea (4 Blaberoidea, 2 Corydiidae, 1 Cryptocercidae, 6 Termitoidea) and  
159 one Mantodea.

160 We selected three mitochondrial markers [cytochrome c oxidase subunit I (COI), 12S and  
161 16S ribosomal RNAs (12S and 16S)] and two nuclear markers [18S and 28S ribosomal RNAs  
162 (18S and 28S)]. We sequenced most of the molecular sequences analyzed here, using the  
163 primers and PCR experimental conditions described in Legendre et al. (2008). Some  
164 previously published sequences were also retrieved from GenBank. Newly generated  
165 sequences—200 sequences for 55 species—were visually cross-checked using Sequencher  
166 4.0 (Gene Codes, 1999) to assess sequencing quality, and contaminants were checked for  
167 using BLAST. We subsequently excluded poor quality or contaminated sequences from our  
168 final dataset. The complete list of taxa, vouchers and sequences used in this study (including  
169 GenBank accession numbers) is given in Appendix S1.

170

## 171 **2.2. Phylogenetic analyses**

172

173 For each marker, we aligned sequences using MUSCLE (Edgar, 2004) as implemented in  
174 MEGA v.6 (Tamura et al., 2013) with default parameters. Sequences corresponding to the  
175 different 18S amplicons were assembled before alignment, while 28S amplicons were aligned  
176 separately. To check for artifacts or contaminations we ran preliminary analyses for each  
177 marker using IQ-TREE v.1.6 (Trifinopoulos et al., 2016) and we discarded terminals showing  
178 highly incongruent placement for more than one marker. We concatenated alignments for all  
179 markers using SequenceMatrix v.1.7 (Vaidya et al., 2011; resulting final alignment of 3890  
180 bp) and ran PartitionFinder v.1.1 (Lanfear et al., 2012) with the Akaike information criterion  
181 to determine the best-fitting partitioning strategy and substitution models. We recovered three  
182 partitions: one including the markers 12S and 16S, for which a GTR + I + G model was the  
183 most appropriate; a second one comprising the third codon positions for COI, for which GTR  
184 + G (with MrBayes specifications) or a TN93 + G (for BEAST specifications) were the most  
185 appropriate; and a third one, made up of the rest of the data for which the most adequate  
186 models were SYM + I + G (with MrBayes specifications) or TN93 + I + G (with BEAST  
187 specifications). We performed a Bayesian inference (BI) analysis with MrBayes v.3.2.1  
188 (Ronquist & Huelsenbeck, 2003) as implemented through the CIPRES Science gateway  
189 (www.phylo.org) by launching two separate runs with four Markov chains each running for  
190 100 million generations sampled every 10000 generations. We considered convergence was  
191 reached when the average standard deviation of split frequencies was below 0.01 (option

192 *stopval*) and checked that Potential Scale Reduction Factor were close to 1.0 for each  
193 parameter. We then used a 25% burnin proportion before computing a consensus tree (option  
194 *contype=allcompat*). In parallel, we launched an IQ-TREE run with 1000 ultrafast bootstrap  
195 replicates, five partitions (one per marker) and with the best-fit model determined during tree  
196 reconstruction.

197

### 198 **2.3. Divergence time estimates**

199

200 Divergence times were estimated using Bayesian relaxed clocks as implemented in  
201 BEAST v.2.6.5 (Drummond et al., 2012) with an uncorrelated lognormal clock and a birth-  
202 death tree model. Analyses with the partition and models described above failed to converge  
203 and resulted in  $\ll 200$  ESS values for several parameters. We suspected that the high level of  
204 missing data for the partition with the 3<sup>rd</sup> positions of COI only would explain this failure.  
205 Consequently, we chose to use only two partitions, corresponding respectively to  
206 mitochondrial and nuclear data, using the most adequate models as revealed by ModelFinder  
207 (Kalyaanamoorthy et al., 2017) implemented in the IQ-TREE web platform. We recovered a  
208 GTR + I + G model for the mitochondrial data and a TN + I + G model for the nuclear data.  
209 We chose fossils with a strong justification as to their phylogenetic placements to calibrate  
210 the molecular clock (Parham et al., 2012). We used four outgroup calibrations, corresponding  
211 to the following fossil species: “*Gyna*” *obesa* (Piton, 1940), *Cretaholocompsa montesecana*  
212 Martínez-Delclòs, 1993, *Valditermes brenanae* Jarzembowski, 1981, *Archeorhinotermes*  
213 *rossi* Krishna and Grimaldi, 2003, and one ingroup calibration, the blattid *Cretaperiplaneta*  
214 *kaonashi* Qiu et al., 2020 (see Appendix S2 for details on fossil choices, including ages,  
215 authors, calibrated clades and calibration procedures). All calibrations were treated with a  
216 uniform distribution, with the minimum bound being the age of the fossil and a conservative  
217 maximum bound being the age of the Devonian Rhynie chert (412 Myr), except for  
218 *Archeorhinotermes rossi* for which the maximum bound was set at 237 Myr because we can  
219 reasonably assume that no crown-termites existed before the Carnian stage (Evangelista et al.,  
220 2019). Because of its uncertain phylogenetic affinity (see Appendix S2) and its potential  
221 consequences on dating estimates (e.g. Seidel et al., 2021), we tested three calibration  
222 placements for *Cretaperiplaneta kaonashi*, either for stem-Blattidae, crown-Blattidae or  
223 stem-Blattinae, and we also ran an analysis without this calibration. We set a root prior with  
224 an exponential distribution (Mean: 30; Offset: 230) to account for the age interval obtained  
225 by Evangelista et al. (2019) for Dictyoptera in their phylogenomic analysis of Blattodea. We



226 ran analyses for 100 million generations with trees and parameters sampled every 1000  
227 generations. We checked the convergence of parameters using Tracer v.1.7 (Rambaud et al.,  
228 2018) by ensuring ESS of all parameters were > 200. We consequently subsampled the tree  
229 population by resampling every 10000 generations using LogCombiner (Drummond et al.,  
230 2012) and generated a Maximum Clade Credibility consensus tree with median ages with a  
231 burn-in value of 15% using TreeAnnotator (Drummond et al., 2012). Data and script files for  
232 phylogenetic and dating analyses are provided as Supplementary material (Appendix S3).

233

#### 234 **2.4. Historical biogeography**

235

236 We performed historical biogeography analyses using the R package *BioGeoBEARS*  
237 (Matzke, 2014). We pruned outgroups from the consensus dated tree from the BEAST  
238 analysis using the R package *ape* (Paradis & Schliep, 2019). Geographical distributions for  
239 terminal taxa were mostly recovered from collection labels and from the online Cockroach  
240 Species File (Beccaloni, 2014), or from the locality specified by the authors for sequences  
241 uploaded to GenBank. Invasive species were considered to originate from the most probable  
242 geographic area according to the literature (Cornwell, 1968; Tang et al., 2019 and references  
243 herein). These include *Neostylopyga rhombifolia* (Stoll, 1813) of tropical Asian origin, *Blatta*  
244 *orientalis* Linnaeus, 1758 of West Asian origin, the smokybrown cockroach *Periplaneta*  
245 *fuliginosa* Serville, 1838 probably of Asian origin and three *Periplaneta* species, namely *P.*  
246 *americana* (Linnaeus, 1758), *P. australasiae* (Fabricius, 1775) and *P. brunnea* Burmeister,  
247 1838 for which an uncertainty remains regarding their Asian or Afrotropical origin; those  
248 three species were thus coded as present in those two areas.

249 Because our goal focuses on biogeographic events in the vicinity of NC, we coded  
250 biogeographic areas with greater details in the Pacific region. We considered the following  
251 areas: NC, New Caledonia (including Loyalty Islands); NZ, New Zealand; AU, Australia;  
252 NG, New Guinea; IM, Indomalayan region; PA, Palearctic region; AF, sub-saharan Africa;  
253 NT, Neotropical region. We also coded Antarctica (AT) as an area with no terminal taxa. To  
254 model island-hopping routes to NC, we coded two additional areas with no terminal taxa: LH,  
255 “Lord Howe route”, corresponding to landmasses west of NC acting as a possible stepping-  
256 stone for dispersal from Australia and New Guinea, and TK, “Three Kings route”,  
257 corresponding to landmasses located south-east of NC, allowing facilitated dispersal from  
258 New Zealand and Antarctica.

259 We constructed time-stratified paleogeographic models that account for the major global  
260 and regional geological events that could have influenced the distribution of species during  
261 the timeframe of our phylogeny. Larger scale paleogeographic information was derived from  
262 the PALEOMAP atlas for Gplates (Scotese, 2016). Information concerning the evolution of  
263 landmasses in the southwest Pacific region were derived from the most up-to-date literature,  
264 including the paleogeographic review of Maurizot & Campbell (2020), and the work of  
265 Sutherland et al. (2020) regarding the altitudinal changes in Zealandia during the last 60  
266 Myrs. We thus divided NC paleogeography into three major phases (Figure 1):

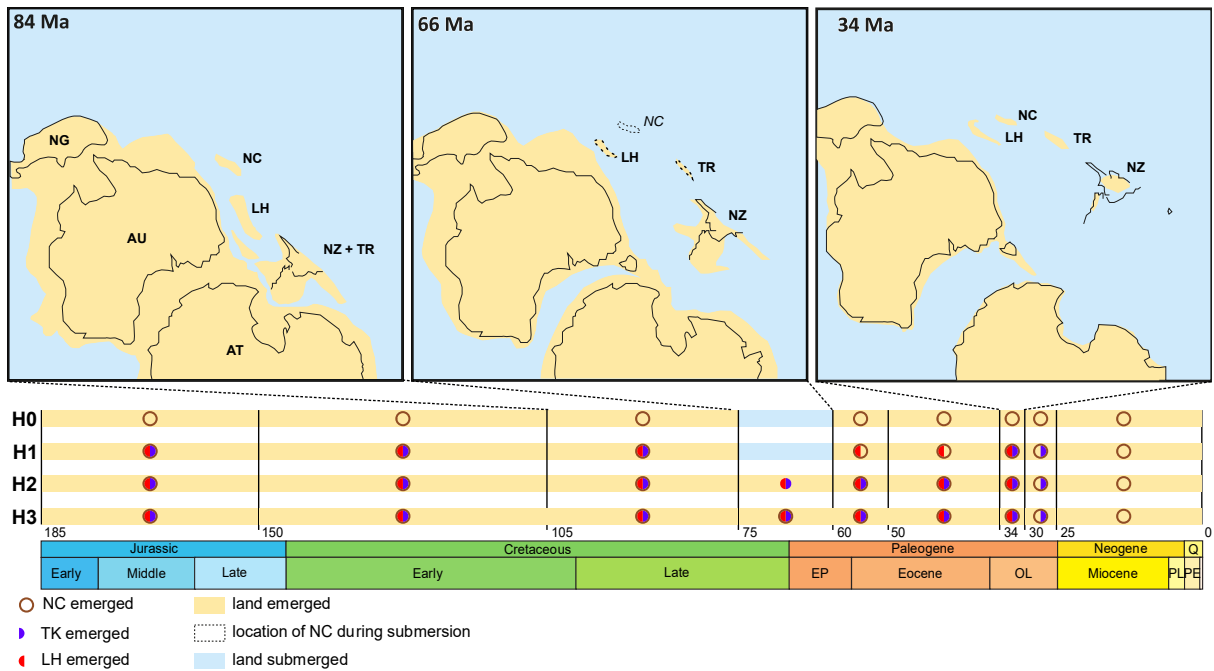
267 A Gondwanan period, ending in the early late Cretaceous, ca 90 Ma, during which proto-  
268 NC was located at the eastern periphery of Gondwana and discontinuously exhibited insular  
269 characteristics (Collignon, 1977; Cluzel & Meffre, 2002; Cluzel et al., 2012). At the end of  
270 this period, proto-New Caledonia was emerged until tectonic processes resulted in  
271 lithospheric thinning and marginal rifting (Cluzel et al., 2012).

272 A general drowning (GD) period, from 75 Ma to 60 Ma, during which thermal subsidence  
273 provoked the almost total drowning of Zealandia, with the exception of parts of New Zealand  
274 (Maurizot & Campbell, 2020). This period is characterized by a uniform cover of pelagic  
275 sediments in the region, indicating a geographically extended submersion as no terrigenous  
276 sediments are recovered for this period (Maurizot et al., 2020a).

277 A period starting with the partial emersion (60 Ma) and ending with the obduction of NC  
278 at 34 Ma. Although marine sedimentation prevailed during this period, small emerged lands  
279 appeared repeatedly, but the precise duration of those emersions remain unknown. Previously  
280 considered to predate any emerged land in the region, this period is thus possibly  
281 characterized by a permanence of land on and in the immediate vicinity of NC, although the  
282 main island would only acquire its current conformation after obduction and subsequent  
283 weathering (Cluzel et al., 2010; Maurizot et al., 2020b; Sevin et al., 2020).

284 Regarding putative colonization routes to/from NC, there is strong evidence for the  
285 presence of lands in Zealandia before the GD period (Maurizot & Campbell, 2020). After the  
286 GD period, there is evidence for the existence of lands west of NC from 50 Ma to 30 Ma  
287 (Maurizot & Campbell, 2020; Sutherland et al., 2020; i.e. our “Lord Howe route”); and  
288 evidence for the existence of lands south of NC from 34 Ma to 25 Ma (Meffre et al., 2006;  
289 Sutherland et al., 2020; i.e. our “Three Kings route”). Information regarding time slices and  
290 associated events is summarized in Table 1, while additional information at a more global  
291 level is presented in Appendix S4.

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**[double column] Figure 1. Timeline of emersion in the Southwest Pacific region according to four biogeographic hypotheses (H0-H3) modeled in *BioGeoBEARS*.** The timeline is divided according to the time slices used in *BioGeoBEARS*, a beige segment indicating that at least one of the three considered landmasses—New Caledonia (NC; brown circle), "Lord Howe route" (LH; red semicircle) or "Three Kings route" (TK; purple semicircle)—is emerged, and a blue segment indicating general drowning of these three landmasses. Antarctica (AT), Australia (AU), New Guinea (NG) and New Zealand (NZ) are considered always emerged. Interpretative maps, modified from Maurizot & Campbell (2020), are given respectively for the immediate pre-drowning period (84 Ma), for the general drowning period (66 Ma), and for the period following the obduction of New Caledonia (34 Ma).

**Table 1. Time slices used in *BioGeoBEARS* analyses and justifying associated events and references.** Emersion of New Caledonia (NC) or proto-NC is indicated following Maurizot & Campbell, 2020.

Time slices (Ma)	Major geological events	References	Emersion of proto-NC / NC
185 – 150	Antarctica, East and West Gondwana joined	Scotese, 2016	Yes (proto-NC)
150 – 105	Separation of East and West Gondwana	Scotese, 2016	Yes (proto-NC)
105 – 75	Separation of Africa and South America	Collignon, 1977; Cluzel & Meffre, 2002; Cluzel et al., 2012	Yes (proto-NC)
75 – 60	General drowning (GD) of Zealandia	Maurizot et al., 2020a; Maurizot & Campbell, 2020	No
60 – 50	First dated emersion of Grande Terre after GD	Cluzel et al., 2010; Maurizot et al., 2020b; Sevin et al., 2020	Possible*

50 – 34	Uplift of eastern Zealandia	Sutherland et al., 2020	Possible*
34 – 30	Emersion of southern Zealandia and likely of NC	Maurizot & Campbell, 2020; Sutherland et al., 2020	Likely
30 – 25	Submersion of “Lord Howe route”	Maurizot & Campbell, 2020; Sutherland et al., 2020	Yes
25 – 0	Submersion of “Three Kings route”	Sutherland et al., 2020	Yes

306 \*Occurrence of small-sized emerged lands at the place of present NC; geological data for the -60 to -34 Ma  
307 period are, however, indecisive.

308

309 To model the paleogeographical events and test the role of potential island-hopping routes,  
310 we used the “areas allowed” matrix implemented in *BioGeoBEARS*. This feature allows the  
311 user to input a binary matrix specifying which areas are authorized or not in the analysis, with  
312 authorized and unauthorized areas indicated by a 1 and a 0, respectively. In the case of a  
313 time-stratified analysis, a matrix is provided for each time slice, thus modeling the  
314 disappearance of areas during one or several user-specified time intervals. We used this  
315 feature to allow or disallow the aforementioned LH and TK routes. We tested three  
316 alternative hypotheses regarding the lands surrounding NC in the past (Figure 1): H0 does not  
317 allow LH and TK routes to be used at any time (i.e. no island hopping), H1 allows LH and  
318 TK routes at times with published geological evidence for emersion, and H2 allows both  
319 routes continuously—including during GD—up to their latest documented drowning,  
320 respectively at 30 and 25 Ma. In addition, and despite geological evidence, we tested a fourth  
321 hypothesis (H3), in which persistence of NC was allowed during GD; H3 also allows LH and  
322 TK routes at this time. We tested these hypotheses using the areas allowed and matrices of  
323 dispersal multipliers implemented in *BioGeoBEARS*. For each hypothesis, we ran analyses  
324 using three biogeographic models implemented in *BioGeoBEARS* (i.e. BAYAREALIKE,  
325 DEC and DIVALIKE; Ree & Smith, 2008; Ronquist & Sanmartín, 2011; Landis et al., 2013)  
326 along with their respective + J derivatives. We used a maximum range size of two areas,  
327 corresponding to the maximum range size coded for terminal taxa, but also ran additional  
328 analyses with a maximum range size of four areas (under H0 and H1, the model that best fit  
329 with current geological evidence) to ensure that range size did not drastically influence the  
330 results. We then performed statistical model comparisons in *BioGeoBEARS* and considered  
331 only the model which yielded the lowest AICc score. R scripts are provided as  
332 Supplementary material (Appendix S5).

333

### 334 3. RESULTS

335

#### 336 3.1. Phylogenetic analyses

337

338 The results of the phylogenetic ML and Bayesian inference are summarized in Appendix  
339 S6. Our analysis recovers the monophyly of the clade Tryonicidae + Blattidae ( $BS_{ML} = 80$ ;  
340  $PP_{BI} = 0.84$ ;  $PP_{BEAST} = 0.86$ ; see Figure 2 for the latter), sister group to a Lamproblattidae +  
341 (Cryptocercidae + Isoptera) clade ( $BS_{ML} = 97$ ;  $PP = 1$ ). We recover three clades in the  
342 ingroup with representatives in NC: one within Tryonicidae and two within Blattidae. Within  
343 Tryonicidae, we recover the monophyly of NC representatives of the family with high  
344 support (i.e. *Lauraesilpha* and *Tryonicus* spp.,  $BS_{ML} = 100$ ;  $PP = 1$ ), sister group to the  
345 Australian *Tryonicus parvus* (Tepper, 1895). The genus *Tryonicus* is thus robustly found  
346 paraphyletic. Within Blattidae, the NC genera *Angustonicus*, *Rothisilpha*, *Pallidionicus*,  
347 *Punctulonicus* and *Pellucidonicus* (all described in Grandcolas (1997)) are monophyletic  
348 (clade P1,  $BS_{ML} = 100$ ;  $PP = 1$ ), whereas other NC representatives (affiliated to the genus  
349 *Maoriblatta* Princis, 1966, clade P2) are paraphyletic—a result weakly supported ( $BS_{ML} =$   
350  $44$ ;  $PP_{BI} = 0.83$ ;  $PP_{BEAST} = 0.64$ )—because of the Australian *Melanozosteria obscura*  
351 (Tepper, 1893).

352 More generally, the six Blattidae subfamilies are not all found monophyletic, but five main  
353 clades can be identified. The two most nested clades are the clades P and PB (for  
354 Polyzosteriinae, and Polyzosteriinae-Blattinae, respectively). In the clade P ( $BS_{ML} = 81$ ;  $PP_{BI}$   
355  $= 0.86$ ;  $PP_{BEAST} = 1$ ), the East Asian genus *Laevifascies* Liao et al., 2019 is sister to a  
356 *Macrocerca* Hanitsch, 1930 + Australasian Polyzosteriinae clade. Among these, the New  
357 Zealand genus *Celatoblatta* Johns, 1966 is sister group to a large clade (P2) made up of NC  
358 genera *Angustonicus*, *Rothisilpha*, *Pallidionicus*, *Punctulonicus* and *Pellucidonicus*, while all  
359 representatives of Polyzosteriini known from Australia form a clade with the NC  
360 representatives of the genus *Maoriblatta* (P1). The clade PB ( $BS_{ML} = 95$ ;  $PP = 1$ ) is made of  
361 Indomalayan/Australasian cockroaches mostly placed in the genus *Dorylaea* Stål, 1877 and  
362 species with reduced or absent wings mostly placed within the genus *Neostylopyga* Shelford,  
363 1911.

364 Sister-group to the clade (P + PB) is clade B ( $PP = 0.86$ ) containing Archiblattinae Kirby,  
365 1904 ( $BS_{ML} = 99$ ;  $PP = 0.94$ ) sister group to a clade comprising sexually dimorphic genera of  
366 old world Blattinae, including the African genera *Deropeltis* Burmeister, 1838 and

367 *Pseudoderopeltis* Krauss, 1890 sister group to a mostly Asiatic group of Blattinae, including  
368 all species of *Periplaneta* Burmeister, 1838.

369 Sister group to (B, (P + PB)) is Eurycotiinae, a Neotropical clade containing *Eurycotis*  
370 Stål, 1874 + *Pelmatosilpha* Dohrn, 1887 ( $BS_{ML} = 100$ ;  $PP = 1$ ). Finally, the clade  
371 Duchailiinae ( $BS_{ML} = 100$ ;  $PP = 1$ ), comprising the genera *Duchailiua* Rehn, 1933 and  
372 *Hebardina* Bei-Bienko, 1938, is sister group to all other Blattidae. Note that the placement of  
373 the Eurycotiinae is not strongly supported ( $PP_{BI} = 0.64$ ) and that Eurycotiinae was found as  
374 sister group to B in the ML and BEAST trees ( $BS = 75$ ;  $PP_{BEAST} = 0.62$ ). This is the only  
375 major discrepancy between the MrBayes/ML and BEAST analyses and it does not affect the  
376 reconstructed biogeographic scenarios for NC lineages, which are either in Tryonicidae or in  
377 the clade P.

378

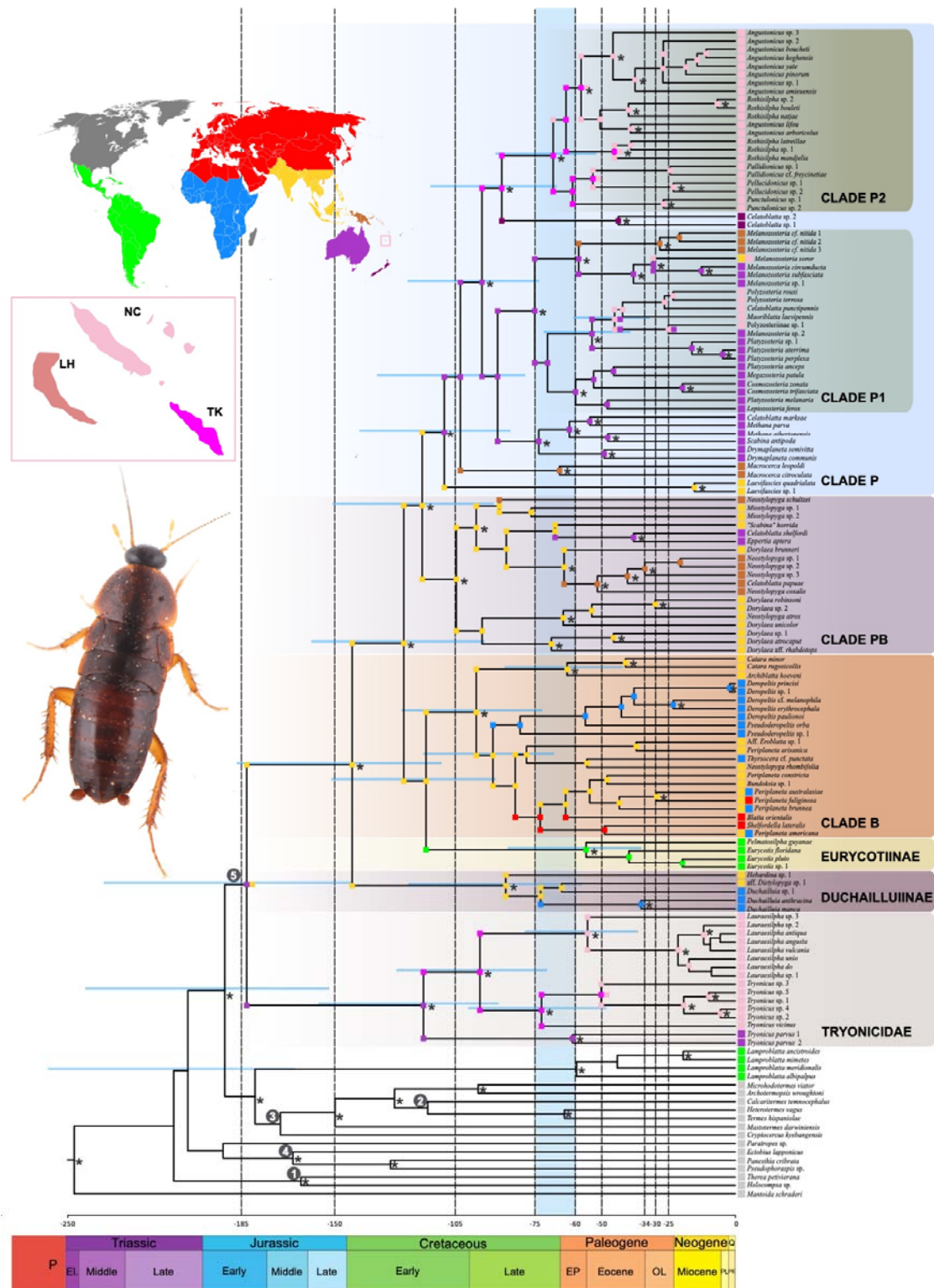
### 379 **3.2. Divergence time estimates and ancestral range estimation**

380

381 The divergence time estimates are presented in Figure 2, along with the BEAST estimated  
382 topology, the 95% credibility intervals for the deepest nodes, and ancestral range estimations  
383 assuming the H2 biogeographic hypothesis under DEC + J model, with *Cretaperiplaneta*  
384 *kaonashi* calibrating stem-Blattidae (age estimates did not differ significantly when this fossil  
385 was removed or used to calibrate another node; see Appendix S7). In brief, H2 favors  
386 biogeographic events that include island-hopping events along the “Three Kings (TK) route”,  
387 contrary to hypotheses H0, H1 and H3. This is also true for DEC models without jump  
388 dispersal events; the number of maximum range size areas (two or four) does not influence  
389 the results either (see Appendix S8). Below, we provide dating estimates for the main clades  
390 and explain the main events under H2 and DEC + J, before highlighting the main  
391 discrepancies with alternative hypotheses (i.e. H0, H1 and H3).

392 We infer an Early Jurassic origin (median age = 183 Ma; 95% HPD = 144–236 Ma) for  
393 the Blattidae + Tryonicidae clade, with a geographic range covering both Australia and Asia.  
394 Following a vicariance event, we recover an Australian origin for Tryonicidae in the Early  
395 Cretaceous (117 Ma; 89–156 Ma). We then recover an island-hopping event (i.e. colonization  
396 of the TK area) followed by three independent colonizations of NC after the re-emersion of  
397 the island at -60 Ma. For Blattidae, we recover an Asian origin around the Late Jurassic /  
398 Early Cretaceous transition (143 Ma; 110–187 Ma). Within Blattidae, two noteworthy  
399 independent colonizations of Africa, in the clade Duchailiinae and within the clade B,  
400 occurred during the Late Cretaceous. We also recover a colonization of the Neotropics in the

401 Early Cretaceous by the Eurycotiinae (116 Ma; 89–151 Ma). In the clade PB (Asian origin;  
402 crown age = 105 Ma; 80–136 Ma), we recover two independent colonizations of New Guinea  
403 and Australia from Asia, both around the K/T transition (64 Ma; 47–86 Ma and 68 Ma; 46–  
404 92 Ma, respectively). Within the clade P (Asian origin, crown age = 109 Ma; 84–141 Ma), we  
405 find an early colonization of Australia during the Cretaceous (103 Ma; 79–134 Ma), rapidly  
406 followed by a colonization of New Guinea by a lineage today represented by the genus  
407 *Macrocerca*. We also recover an island-hopping event through the TK area around the  
408 Early/Late Cretaceous transition (95 Ma; 73–123 Ma) before multiple colonization events of  
409 NC around -60 Ma by members of the clade P2. Colonization of NC by members of the clade  
410 P1 implies a direct dispersal event from Australia in the Eocene (45 Ma; 32–60 Ma).  
411



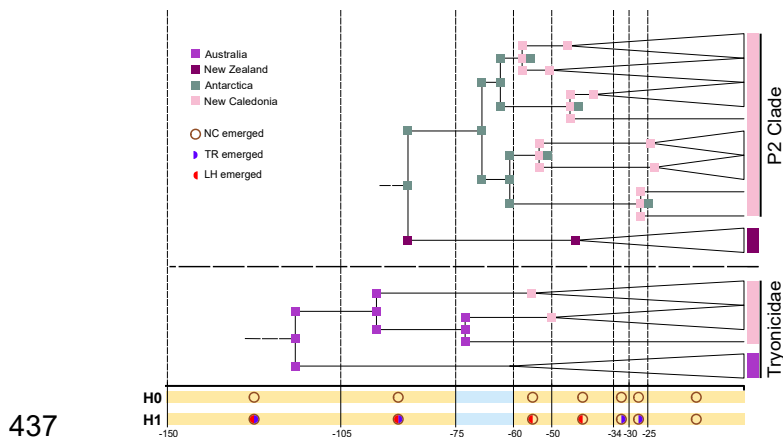
412

413 [double column] Figure 2. Dated molecular phylogeny and biogeographic history of Blattoidea. Time  
 414 tree derived from the Maximum Clade Credibility BEAST consensus tree with median ages, 95%  
 415 credibility interval for major nodes (blue horizontal bars), and most probable ranges recovered by  
 416 *BioGeoBEARS* under a DEC + J model (H2 hypothesis; maximum of two areas; d = 0.0019; e = 0.0013; j =  
 417 0.0679). Geographic ranges for species are indicated left to the taxa names and refer to the colors used in  
 418 the map in the upper left part of the figure. A schematic representation of the positions of vanished



419 landmasses relative to New Caledonia (NC) is given in the pink insert below the global map (LH for ‘Lord  
 420 Howe’ and TK for ‘Three Kings’ routes). Time slices used in the *BioGeoBEARS* analyses are represented  
 421 by vertical dashed lines, with the general drowning period between -75 Ma and -60 Ma highlighted in blue.  
 422 Posterior probabilities (PP) over 0.95 are noted with an asterisk and the five fossil calibrations are also  
 423 depicted: 1 = *Cretaholocompsa montesecana* Martínez-Delclòs, 1993; 2 = *Archeorhinotermes rossi*  
 424 Krishna and Grimaldi, 2003; 3 = *Valditermes brenanae* Jarzembowski, 1981; 4 = “*Gyna*” *obesa* (Piton,  
 425 1940); 5 = *Cretaperiplaneta kaonashi* Qiu et al., 2020. Picture of *Tryonicus* sp. (T. Schubnel©).  
 426

427 The best supported model under H0 (no island hopping) and H1 (island hopping through  
 428 identified areas only) is also DEC + J. Under both hypotheses, this model infers, for  
 429 Tryonicidae, three colonization events of NC from Australia (*contra* through TK route under  
 430 H2). For the clade P2, the model infers multiple colonization events of NC from Antarctica,  
 431 which, at this time, was still part of Gondwana. Those are the main discrepancies with the  
 432 scenario reconstructed under H2 and they are depicted in Figure 3. As for H3, DIVALIKE + J  
 433 and DEC + J have similar supports (AICc of 310.3 and 310.6, respectively). In both cases, a  
 434 single colonization event of NC is inferred before the GD for Tryonicidae and for the clade  
 435 P2 (Appendix S8).  
 436



437  
 438 [single column] **Figure 3. Alternative scenario for the clade P2 (within Polyzosteriinae) (top) and for**  
 439 **Tryonicidae (bottom) according to H0 and H1 hypotheses (DEC + J; maximum range of two areas).**  
 440 H0 does not allow island-hopping, whereas H1 allows island-hopping for geologically-documented periods  
 441 only. Both hypotheses suggest multiple colonization events from Australia (Tryonicidae; bottom) and  
 442 Antarctica (clade P2; top). Terminal branches of the Maximum Clade Credibility BEAST tree are  
 443 collapsed for simplicity. Color codes follow Figures 1 and 2 and are repeated on the top left. Time slices  
 444 are indicated by vertical dashed lines. The horizontal dash line separates the two focal clades.  
 445

446 **4. DISCUSSION**

447

#### 448 **4.1. Towards ‘trans-disciplinary’ biogeography to test the island-hopping hypothesis**

449 Expanding biogeographic models by adding data from other disciplines is an effective way  
450 to strengthen hypothesis-driven research and further move away from narrative biogeography  
451 (Crisp et al., 2011). There have been many calls for this ‘trans-disciplinary’ perspective  
452 (Donoghue & Moore, 2003; Ronquist & Sanmartín, 2011; Antonelli et al., 2018) since the  
453 first statistical approaches of biogeography (Ree et al., 2005), and important conceptual  
454 advances and case studies can be underlined (e.g. trait-dependent biogeography, fossil-based  
455 analyses, biogeographic models including niche modelling or paleoclimatic reconstructions;  
456 Violle et al., 2014; Meseguer et al., 2015; Svenning et al., 2015; Silvestro et al., 2016; Pearse  
457 et al., 2018; Sukumaran & Knowles, 2018; Culshaw et al., 2021). Nonetheless, concrete  
458 applications remain in a minority and it has never been applied to the case of clades older  
459 than the islands they inhabit.

460 The origin of ‘old’ lineages on younger islands is often apparently ‘solved’ by island-  
461 hopping hypotheses, wherein clades are supposed to have evolved through presence in or  
462 dispersal via now-drowned islands (e.g., Carlquist, 1965; Heads, 2005, 2008; Ladiges &  
463 Cantrill, 2007). But, to our knowledge, those hypothetical narratives have never been  
464 formally tested (Grandcolas, 2017), except by dating clades in comparison with island ages  
465 (e.g. Grandcolas et al., 2008; Nattier et al., 2011, 2017; Giribet & Baker, 2019). Here, we  
466 have summarized geological evidence about possible vanished colonization routes so that we  
467 can test the island-hopping hypothesis for a clade of New Caledonian insects. This general  
468 context and the biogeographic models we have built are not restricted to these insects and can  
469 be used for other New Caledonian clades whose ancient origins remain enigmatic (e.g.  
470 Sharma & Giribet, 2012; Papadopoulou et al., 2013; Giribet et al., 2021).

471 Our results support a scenario of island-hopping under some, but not all, circumstances,  
472 through the “Three Kings route”, at the South-East of NC (H2 scenario; Figure 2). Two  
473 clades would have then colonized NC from New Zealand (some endemic Polyzosteriinae)  
474 and, perhaps more surprisingly because of our current understanding of paleocurrents, from  
475 Australia (Tryonicidae). Note that the biogeographic model under this scenario allowed  
476 island-hopping at all times, i.e. even at times for which geological evidence of past vanished  
477 islands is lacking or is very equivocal. This lack of evidence is however not a proof of the  
478 absence of past emerged territories (see for instance Rouillard et al. (2017) about the Fairway  
479 Basin). Conversely, when allowed only at times with geological evidence (H1 scenario)  
480 island-hopping hypothesis was not inferred, NC being colonized directly from Australia or

481 through Antarctica (Figure 3). Also, because of the uncertainties associated to dating results,  
482 a single colonization event of NC for the clade P2 cannot be entirely ruled out, because the  
483 lower bound of the 95% HPD is more recent than the end of the total submersion (Figure 2).  
484 Regardless, we have here built a case about testing island-hopping hypotheses, instead of  
485 merely invoking them, taking part in an ongoing interdisciplinary paradigm between geology  
486 and biogeography (e.g., Landis, 2017; Crews & Esposito, 2020; Feyhl-Buska, 2020; Jöks et  
487 al., 2020; Philippon et al., 2020; Ali & Hedges, 2021; Cornée et al., 2021; Michaux & Ung,  
488 2021; Montes et al., 2021).

489 Such integrative and statistical inferences in biogeography face limitations and difficulties,  
490 notably because of the fragmentary nature of geological information and the difficulty to  
491 interpret geological data to reconstruct paleogeography. On the biological side, extinction  
492 phenomena or poor taxonomic sampling can obfuscate biogeographic interpretations,  
493 especially when the fossil record is lacking (Grandcolas et al., 2014; Barden & Ware, 2017;  
494 Mayr, 2017; Wisniewski et al., 2022). Uncertainties in phylogenetic relationships and in  
495 dating estimates, from calibration procedures to confidence intervals that may overlap with  
496 several time slices, also contribute to becloud biogeographic interpretations. Finally,  
497 biogeographic models also have limitations as they only consider a small number of  
498 biogeographic events, treat dispersal as a time-independent process, while also struggling to  
499 incorporate paleogeographic or diversification-related information that might affect range  
500 evolution; they are also ill-suited to test competing hypotheses that differ in their premises  
501 (Hackel & Sanmartín, 2021). In spite of these caveats, integrative biogeography must be  
502 encouraged and strengthened to help limit overly speculative conclusions (Donoghue &  
503 Moore, 2003; Crisp et al., 2011; Ronquist & Sanmartín, 2011; Antonelli et al., 2018; Ribas et  
504 al., 2022). In the case of the NC biota, geological and biological data could be complemented,  
505 for instance, with paleoclimatic data to further improve the test and robustness of  
506 biogeographic hypotheses.

507

#### 508 **4.2. Paleoendemics in New Caledonia**

509

510 There is a consensus on the mixed origin of the NC biota, especially its endemics. As  
511 previously synthesized (Gillespie & Roderick, 2002; Murienne et al., 2005; Grandcolas et al.,  
512 2008; Sharma & Wheeler, 2013; Giribet & Baker, 2019), these organisms can be classified  
513 into paleoendemics and neoendemics, depending on their ages of divergence and  
514 diversification. While the majority of the New Caledonian biota would fall in the

515 neoendemics group—i.e. groups that diverged from their sister group relatively recently (e.g.  
516 Nattier et al., 2017)—paleoendemics (but not relicts and revenants; Sharma & Wheeler,  
517 2013) inform us more than neoendemics on the general debate about the origin of old taxa in  
518 relatively recent islands.

519 We here identified up to three paleoendemic clades in Tryonicidae and Blattidae  
520 cockroaches that can be added to the relatively short list of New Caledonian paleoendemics,  
521 alongside Troglosironidae or *Zalmoxis* (Giribet & Baker, 2019; Giribet et al., 2021).  
522 Interestingly, these paleoendemics have presumably dispersed from different regions, from  
523 Australia and New Zealand to Antarctica or now vanished islands (e.g. here what we called  
524 the “Three Kings route”), depending on the areas allowed along time in biogeographic  
525 models. This study thus highlights the diversity of the origins of taxa, even within the same  
526 category of endemics.

527 Tryonicidae and the neocaledonian Polyzosteriinae (i.e. genera *Angustonicus*,  
528 *Pallidionicus*, *Pellucidonicus*, *Punctulonicus* and *Rothisilpha*) are particularly remarkable  
529 because their origins is estimated to date back to the Late Cretaceous, before or during the  
530 general submersion. Our results suggest that their history could be misleadingly assumed to  
531 be consistent with a possible vicariant event, had our analyses not incorporated geological  
532 information such as the major and undisputed general drowning period (-75 Ma to -60 Ma).

533 Tryonicidae—found only in Australia and New Caledonia—can also be seen as a relict,  
534 like the harvestman *Troglosiro* (Sharma & Giribet, 2009), because of their much more  
535 diversified and widely distributed sister group (i.e. Blattidae) and because they are at the ‘tip’  
536 of a relatively long branch, a topology congruent with extinction events (Grandcolas et al.,  
537 2014). If they are true relicts, then, by definition, their geographical origin would be hard to  
538 decipher and they would not inform us much about the history of New Caledonia. On the  
539 other hand, they would have value for conservation purposes or to document extinction—  
540 which remains challenging even in modern diversification analyses. As for the clade P2  
541 (*Maoriblatta* and affiliated), they could also correspond to neoendemics given the uncertainty  
542 around their age of origin (ca. 35 Ma as minimal value of the 95% HPD). However, to settle  
543 on their taxonomic and biogeographic status, *Maoriblatta* from New Zealand or Australia  
544 should be added in future analyses. In any case, and maybe even more for relicts in the  
545 southern Hemisphere (Upchurch, 2008), fossil evidence could bring decisive insights and  
546 limit the risk of skewed interpretations (Silvestro et al., 2016; Barden & Ware, 2017; Mayr,  
547 2017; Garrouste et al., 2021).

548

549 **4.3. Difficulties of biogeography in the deep time: extinctions, dispersal ability and areas**  
550 **with no extant representatives**

551

552 Whatever the biogeographic model used to reconstruct the biogeography of these insects,  
553 we inferred multiple colonizations of NC from different origins and following different  
554 biogeographic events. Among these events, jump dispersals have, however, never been  
555 inferred for those clades (Appendix S8), whose dispersal ability is difficult to assess.  
556 Although much of these cockroaches are wingless, several are associated with dead wood—  
557 notably the wood-boring Tryonicidae—or other dead vegetal matter that could facilitate  
558 dispersal across marine barriers. In addition, over such long periods of time, it is difficult to  
559 estimate how rare and (un)likely successful dispersals events are, depending also on  
560 environmental factors such as sea or air currents. For example, long distance dispersals have  
561 been shown in taxa otherwise known to be poor dispersers (e.g. *Leptomymex* ants in Lucky,  
562 2011 or *Nothofagus* trees and shrubs in Cook & Crisp, 2005; but see also Derkarabetian et al.,  
563 2021). Extinctions can also blur biogeographic interpretations, with the effect of generating  
564 discontinuous biogeographic patterns that are difficult to interpret, a point already raised for  
565 New Caledonia (Grandcolas et al., 2014). All this underlines the complex nature of  
566 colonization processes and the difficulty to reconstruct them, especially in very deep time.

567 In this regard, incorporating biogeographic areas with no extant representatives—this  
568 includes, but shall not be restricted to, now vanished islands—into biogeographic analyses is  
569 pivotal. For instance, Antarctica has repeatedly been inferred as a possible colonization route  
570 between Australia and South America (e.g. Cruaud et al., 2011, Vicente et al., 2017). Here, a  
571 passage through Antarctica is inferred in one of the scenarios we tested (for a NC clade  
572 within Polyzosteriinae; Figure 3) but not for the colonization of the Neotropics. Instead, the  
573 neotropical Eurycotiinae, whose position is consistent with previous phylogenetic works  
574 (e.g., Legendre et al., 2015, but *contra* Bourguignon et al., 2018), would have dispersed from  
575 Asia, like the two African clades, during the Cretaceous. We refrain, however, from  
576 discussing further biogeographic implications at the deepest nodes of our phylogeny because  
577 of a few weakly supported nodes, which might impact biogeographic reconstructions (e.g.,  
578 Smith, 2009; Magalhaes et al., 2021). We thus consider that additional data and support are  
579 needed to discuss the early biogeography of those cockroaches. Regardless, counter-intuitive  
580 patterns of range evolution should neither be taken for granted nor be dismissed lightly.  
581 Inferred biogeographic patterns can fit with multiple alternative histories, and the geographic  
582 changes influencing biotic evolution are often very complex. In this regard, the simpler

583 scenario (often the one implying long-distance dispersals) is not necessarily the most  
584 consistent with the geological record, and a better grasp of geologic history can radically alter  
585 biogeographic interpretations (e.g. the influence of translocated Gondwana-derived  
586 landmasses in shaping the Asian biota; Loria & Prendini, 2020; Bolotov et al., 2022).

587

## 588 **ACKNOWLEDGMENTS**

589 We thank H. Jourdan for numerous discussions about the fascinating NC biota and F.  
590 Condamine for fruitful talks, especially regarding *BioGeoBEARS*. The newly generated  
591 molecular data result from various fieldwork expeditions and studies in museum collections,  
592 which involved many people without whom this work would not have been possible. Part of  
593 the specimens was collected during: “Our Planet Reviewed” Guyane-2015 expedition in the  
594 Mitaraka range (APA 973-1), in the core area of the French Guiana Amazonian Park,  
595 organized by the MNHN and Pro-Natura international. The expedition was funded by the  
596 European Regional Development Fund, the Conseil régional de Guyane, the Conseil général  
597 de Guyane, the Direction de l'Environnement, de l'Aménagement et du Logement and by the  
598 Ministère de l'Éducation nationale, de l'Enseignement supérieur et de la Recherche, in  
599 collaboration with the Parc amazonien de Guyane and the Société entomologique Antilles-  
600 Guyane ; ‘Our Planet Reviewed’ expedition in New Caledonia, a MNHN program in  
601 partnership with Conservatoire d’espaces naturels de Nouvelle-Calédonie. The 2017  
602 Katalupaik expedition was funded mainly by the Gouvernement de la Nouvelle-Calédonie,  
603 Province Nord, and Office des Postes et Télécommunications, with in-kind support from  
604 AirCalin and Avis Nouvelle-Calédonie. The expedition operated under permit 60912-2001-  
605 2017/JJC issued by Direction du Développement Économique et de l’Environnement of  
606 Province Nord (APA-NCPS-2016-025). Part of this study was conducted in the framework of  
607 “Our Planet Reviewed Papua-New-Guinea 2012-2013” set up by Pro-Natura International,  
608 MNHN, the Institut de Recherche pour le Développement (IRD) in partnership with the  
609 Royal Belgian Institute of Natural Sciences (RBINS), the New Guinea Binatang Research  
610 Center, the University of Papua New Guinea, and the Divine Word University of Madang and  
611 with core funding of Prince Albert II of Monaco Foundation, the Stavros Niarchos  
612 Foundation, the Total Foundation, the Fondation d’entreprise EDF, the Fonds Pacifique,  
613 Spiecapag, Entrepouse Contracting, the New-Caledonia Government, the Reef Foundation and  
614 the Belgian National Lottery. The IBISCA expert network, the patron for this project, Prof.  
615 R.L. Kitching AM, and all other participants in this collective effort are thanked for their  
616 contribution. We are deeply indebted to O. Pascal for having organized the different “Our

617 Planet Reviewed” expeditions and for having shown us his trust repeatedly by inviting us to  
618 participate. A few samples were also collected during the Project Lengguru 2014, conducted  
619 by the French IRD, the Indonesian Institute of Sciences, the University of Papua, the  
620 University of Cendrawasih, the University of Musamus and the Sorong Fisheries Academy  
621 with corporate sponsorship from COLAS Group, Veolia Water and the Total Foundation. We  
622 are also grateful to J. Constant and C. Paleco for their help during the study of the collections  
623 of the RBINS, funded by the SYNTHESYS European program (BE-TAF-6640); to L.  
624 Anisyutkin for his help during the study of the collections of the Zoological Institute of  
625 Russian Academy of Sciences, Saint-Petersburg, funded by the program ‘Action  
626 Transversale’ of MNHN; to the program “ANR Biodiversité” of the French National Agency  
627 for Research (project BIONEOCAL 2008-2012), to PPF “Etat et structure phylogénétique de  
628 le biodiversité actuelle et fossile” (MNHN), to Action Transversale ‘Biodiversité actuelle et  
629 fossile’ (MNHN), to ATM ‘Emergences’ (MNHN) and to ‘Rapid Assessment Program’  
630 (Conservation International) for supporting fieldwork in French Guiana, Indonesia, New  
631 Caledonia and Philippines; to the National Parks Board of Singapore for delivering permits  
632 N° NP/RP923 for collecting specimens. We thank J. Murienne for sharing some molecular  
633 data before they were published. We also acknowledge help for molecular data acquisition  
634 and are grateful to the ‘Service de Systématique Moléculaire’, UAR 2700 2AD, MNHN,  
635 CNRS, and to the ‘BoEM’ where molecular experimentations were carried out; more  
636 specifically we thank D. Gey, C. Bonillo, G. Colombini, Q. Lefèvre, L. Pindrais and F.  
637 Moreau. This work was presented at the virtual Early Career Biogeographers Conference  
638 held by the International Biogeography Society in October 2021.

639

#### 640 **CONFLICT OF INTEREST STATEMENT**

641 The authors declare no conflicts of interest.

642

#### 643 **DATA AVAILABILITY STATEMENT**

644 The data that support the findings of this study are available in the supplementary material of  
645 this article. Sequence accession numbers for GenBank are in Appendix S1, Alignments and  
646 molecular dating inputs in Appendix S3 and BioGeoBEARS scripts and datasets in  
647 Appendix S5.

648

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1006

1007 **TABLE AND FIGURE CAPTIONS**

1008

1009 **Table 1. Time slices used in *BioGeoBEARS* analyses and justifying associated events and**  
1010 **references.** Emersion of New Caledonia (NC) or proto-NC is indicated following Maurizot  
1011 & Campbell, 2020.

1012

1013 **Figure 1. Timeline of emersion in the Southwest Pacific region according to the four**  
1014 **biogeographic hypotheses (H0-H3) modeled in *BioGeoBEARS*.** The timeline is divided  
1015 according to the time slices used in *BioGeoBEARS*, a beige segment indicating that at least  
1016 one of the three considered landmasses—New Caledonia (NC; brown circle), "Lord Howe  
1017 route" (LH; red semicircle) or "Three Kings route" (TK; purple semicircle)—is emerged, and  
1018 a blue segment indicating general drowning of these three landmasses. Antarctica (AT),  
1019 Australia (AU), New Guinea (NG) and New Zealand (NZ) are considered always emerged.  
1020 Interpretative maps, modified from Maurizot & Campbell (2020) are given respectively for  
1021 the immediate pre-drowning period (84 Ma), for the general drowning period (66 Ma), and  
1022 for the period following the obduction of New Caledonia (34 Ma).

1023

1024 **Figure 2. Dated molecular phylogeny and biogeographic history of Blattoidea.** Timetree  
1025 derived from the Maximum Clade Credibility BEAST consensus tree with median ages, 95%  
1026 credibility interval for major nodes (blue horizontal bars), and most probable ranges  
1027 recovered by *BioGeoBEARS* under a DEC + J model (H2 hypothesis; maximum of two areas;  
1028  $d = 0.0019$ ;  $e = 0.0013$ ;  $j = 0.0679$ ). Geographic ranges for species are indicated left to the  
1029 taxa names and refer to the colors used in the map in the upper left part of the figure. A  
1030 schematic representation of the positions of vanished landmasses relative to New Caledonia  
1031 (NC) is given in the pink insert below the global map (LH for 'Lord Howe' and TK for  
1032 'Three Kings' routes). Time slices used in the *BioGeoBEARS* analyses are represented by  
1033 vertical dashed lines, with the general drowning period between -75 Ma and -60 Ma  
1034 highlighted in blue. Posterior probabilities (PP) over 0.95 are noted with an asterisk and the  
1035 five fossil calibrations are also depicted: 1 = *Cretaholocompsa montesecana* Martínez-  
1036 Delclòs, 1993; 2 = *Archeorhinotermes rossi* Krishna and Grimaldi, 2003; 3 = *Valditermes*  
1037 *brenanae* Jarzembowski, 1981; 4 = "*Gyna*" *obesa* (Piton, 1940); 5 = *Cretaperiplaneta*  
1038 *kaonashi* Qiu et al., 2020. Picture of *Tryonicus* sp. (T. Schubnel©).

1039

1040 **Figure 3. Alternative scenario for Tryonicidae and the clade P2 (within Polyzosteriinae)**  
1041 **according to H0 and H1 hypotheses (DEC + J; maximum range of two areas).** Both  
1042 hypotheses suggest multiple colonization events from Australia (Tryonicidae; bottom) and  
1043 Antarctica (clade P2; top). Terminal branches of the Maximum Clade Credibility BEAST tree  
1044 are collapsed for simplicity. Color codes follow Figures 1 and 2 and are repeated on the top  
1045 left. Time slices are indicated by vertical dashed lines. The horizontal dash line separates the  
1046 two focal clades.  
1047  
1048

1049 **APPENDICES**

1050

1051 **Appendix S1.** Complete list of taxa, vouchers and sequences used in this study (including  
1052 GenBank accession numbers, with newly generated sequences in bold).

1053

1054 **Appendix S2.** Fossil choices and their justifications, including ages, authors and calibrated  
1055 clades.

1056

1057 **Appendix S3.** Data and script files for phylogenetic and dating analyses.

1058

1059 **Appendix S4.** Information regarding time slices and associated events at a global level.

1060

1061 **Appendix S5.** Data and R script files of the different analyses run with *BioGeoBEARS*.

1062

1063 **Appendix S6.** Results of the phylogenetic ML and Bayesian inference on the full dataset.

1064

1065 **Appendix S7.** BEAST dating estimates and 95% credibility intervals for the analyses  
1066 wherein *Cretaperiplaneta kaonashi* is either removed or calibrate different nodes.

1067

1068 **Appendix S8.** Results from the different *BioGeoBEARS* analyses.

1069

1070 **BIOSKETCH**

1071

1072 Our team is broadly interested in the biogeography of South-East Asia and the Pacific, with a  
1073 special interest in the New Caledonian biota. This works represents a chapter of the PhD  
1074 thesis of Julien Malem, who works at the interface between geology and biology to better  
1075 understand the paradoxical occurrence of old lineages on younger islands.

1076

1077 Author contributions: JM, TR, PG and FL conceived the ideas; TR, PG and FL collected  
1078 specimens in the field; FL generated molecular data; JM, DC and LB gathered and  
1079 synthesized geological data; JM, TR and FL analyzed the data with inputs from all authors as  
1080 to their interpretations; JM and FL led the writing with assistance from all authors.