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

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Abstract

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

Location: New Caledonia, New Zealand, Australia.

Taxon: Insects: Blattodea.

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

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

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

KEYWORDS

BioGeoBEARS, competing hypotheses, historical biogeography, insects, New Caledonia, palaeogeography, palaeoendemics, phylogenetic dating, relicts, stepping stones, vanished islands

1 | INTRODUCTION

Once considered to be of Gondwanan vicariant origin, the biota of New Caledonia (NC) is now understood as primarily resulting from relatively recent dispersals across the oceans, following major geological events of emergence and submergence (Giribet & Baker, 2019; Grandcolas, 2017; Grandcolas et al., 2008; Murienne, 2009). General submergence occurred across Zealandia—a 4.9Mkm² region of the southwest Pacific Ocean, made up of continental crust, mostly submerged today, and also known as Tasmantis (e.g., Smith et al., 2007)—during the Late Cretaceous–Palaeocene. This general submergence (reviewed in Maurizot & Campbell, 2020) argues for a NC biota younger than 60Myrs. Although marine sedimentation prevailed during most of the Paleogene, localized and short-lived emersions occurred before the post-obduction final emersion of NC, which is poorly time-constrained (30–25Ma). This final emersion has been previously mentioned in the geological literature (e.g., Aitchison et al., 1995; Cluzel et al., 2001, 2012; Pelletier, 2007) and therefore taken into account by biologists to formulate biogeographical scenarios (e.g., Grandcolas et al., 2008; Nattier et al., 2017). However, the duration of this last event remains uncertain due to the absence of decisive geological record between –34 and –25Ma (Maurizot & Campbell, 2020). Consistent with evidence for a prolonged period of submergence precluding subsistence of a terrestrial biota, NC is thus commonly seen as an oceanic or Darwinian island (Gillespie & Roderick, 2002), with its biota perceived to have originated from de novo transoceanic dispersals, and thus younger than 60Myrs.

This modern view is further supported by several studies relying on phylogenetic dating, which suggest relatively recent age estimates for NC taxa (Baker et al., 2020; Grandcolas et al., 2008; Nattier et al., 2017), and by palaeontological studies bringing a first view on the past biota of the island (Garrouste et al., 2021). Nonetheless, some terrestrial lineages have been challenging this view and raised the question of the origin of ‘old’ lineages—that is, older than 37Ma, or than 60Ma to be in line with more recent geological evidence—on younger islands (Giribet & Baker, 2019; Grandcolas et al., 2014). To decipher the origin of those ‘old’ lineages, the most frequent explanation is the island-hopping hypothesis (e.g., Carlquist, 1965; Darlington, 1957; Gressitt, 1956; Heads, 2005, 2008; Ladiges & Cantrill, 2007). A variant of the stepping-stone dispersal model, this hypothesis involves now vanished islands that would have served as faunal refugia and stepping stones for colonization, before they disappeared. The Gondwanan history and hectic regional geological context of NC would point to this hypothesis. However, this island-hopping scenario is purely narrative in its formulation and has only been tested indirectly, by dating clades with molecular studies to infer whether they are older than the islands (Grandcolas, 2017; Magalhaes et al., 2021; Nattier et al., 2011, 2017).

In this context, a better understanding of the origin of the NC biota amounts to a better understanding of the origin of old lineages in NC, be they palaeoendemics, relicts or revenant clades (Gillespie & Roderick, 2002; Giribet & Baker, 2019; Grandcolas, 2017; Grandcolas et al., 2008, 2014; Sharma & Wheeler, 2013). Some lineages of fig

wasps (Cruaud et al., 2012), harvestmen (Giribet et al., 2012), leaf beetles (Papadopoulou et al., 2013) and moths (Gibbs & Lees, 2014) have been inferred to have radiated or split from their sister group prior to the age of submergence and thus identified as old lineages for NC (e.g., Nattier et al., 2017). Different biogeographical events have been suggested to explain this paradoxical situation, but only a posteriori. Instead, we here embrace a hypothesis-driven study using a priori the latest geological context and data about this geologically complex region, to elucidate the biogeographical events that might have allowed ‘old’ lineages to colonize NC after its latest proven emergence (i.e., 60Ma). Specifically, we test competing biogeographical scenarios that imply or not island-hopping events according to the geological record and its uncertainties.

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

To address the knowledge gap about the origin of ‘old’ lineages in NC, we use the geologically informed context to formally test the island-hopping hypothesis on two cockroach families: Blattidae and Tryonicidae. The most recent phylogenetic studies suggest that these families are sister taxa and that their MRCA would date from the Early Cretaceous, or alternatively, to the Late Triassic (e.g., 130–140Ma in Bourguignon et al., 2018 and Evangelista et al., 2019; 230Ma in Legendre et al., 2015). The family Blattidae comprises 53 extant genera with a worldwide distribution (Princis, 1966; Grandcolas, 1996, 1997; Beccaloni, 2014; Liao et al., 2019), while the family Tryonicidae comprises only two extant genera known from NC only (genus *Lauraesilpha* Grandcolas, 1997) and from NC and Australia (genus *Tryonicus* Shaw, 1925). The current dating estimates and their supposed phylogenetic relationships make them prone to offer at least two additional ‘old’ lineages for NC, and thus to a priori test island-hopping scenarios. We first reconstruct the phylogenetic relationships of these families and provide updated dating estimates, relying on an improved taxonomic sampling. If dating estimates of diversification events within NC clades occur before 60Ma (i.e., before the latest proven emergence), we expect that the most likely biogeographical scenarios would involve island-hopping events. Thus, we contrast biogeographical scenarios that allow or disallow island-hopping to decipher the origin of ‘old’ lineages in NC.

2 | MATERIALS AND METHODS

2.1 | Taxon and molecular sampling

We sampled a total of 126 ingroup terminal taxa considered at the species level (from 42 genera, i.e., 73.4% of the generic diversity), including 4 representatives of the family Lamproblattidae, 16 Tryonicidae and 106 Blattidae. All four described Blattidae subfamilies (i.e. Archiblattinae Kirby, 1904, Blattinae Latreille, 1810, Macrocercinae Roth, 1993 and Polyzosteriinae Tepper, 1893) were represented by at least one taxon. Subfamilial delineations within Blattidae were recently revised (Djernæs & Murienne, 2022; Deng et al., 2023): Macrocercinae was included within Polyzosteriinae, while four additional subfamilies were erected or revised (Austrostylopyginae Djernæs & Murienne, 2022, Duchailuinae Roth, 2003, Eurycotiinae McKittrick, 1964 and Hebardinae Deng et al., 2023). The four latter subfamilies were also sampled here with at least one taxon. Here, we follow the revised classification of Djernæs and Murienne (2022) with six subfamilies, although the taxonomy of these insects needs further investigation. We have chosen taxa according to their geographic distribution, including 41 taxa endemic to NC and one widespread taxon present in the island. We sampled as many genera as possible from the two focal families. Because of the very sparse and controversial fossil record of Blattidae (e.g., Qiu et al., 2020), we chose outgroups that allowed us to include clades with a robust fossil record. We selected 14 outgroup taxa, comprising 13 Blattodea (4 Blaberoidea, 2 Corydiidae, 1 Cryptocercidae, 6 Termitoidea) and one Mantodea.

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

2.2 | Phylogenetic analyses

For each marker, we aligned sequences using MUSCLE (Edgar, 2004) as implemented in MEGA v.6 (Tamura et al., 2013) with default parameters. Sequences corresponding to the different 18S amplicons were assembled before alignment, while 28S amplicons were aligned separately. To check for artefacts or contaminations, we ran preliminary analyses for each marker using IQ-TREE v.1.6 (Trifinopoulos et al., 2016) and we discarded terminals showing highly incongruent placement for more than one marker. We concatenated alignments

for all markers using SequenceMatrix v.1.7 (Vaidya et al., 2011; resulting final alignment of 3890bp) and ran PartitionFinder v.1.1 (Lanfear et al., 2012) with the Akaike information criterion to determine the best-fitting partitioning strategy and substitution models. We recovered three partitions: one including the markers 12S and 16S, for which a GTR+I+G model was the most appropriate; a second one comprising the third codon positions for COI, for which GTR+G (with MrBayes specifications) or a TN93+G (for BEAST specifications) were the most appropriate; and a third one, made up of the rest of the data for which the most adequate models were SYM+I+G (with MrBayes specifications) or TN93+I+G (with BEAST specifications). We performed a Bayesian inference (BI) analysis with MrBayes v.3.2.1 (Ronquist & Huelsenbeck, 2003) as implemented through the CIPRES Science gateway (www.phylo.org) by launching two separate runs with four Markov chains each running for 100 million generations sampled every 10,000 generations. We considered convergence was reached when the average standard deviation of split frequencies was below 0.01 (option *stopval*) and checked that Potential Scale Reduction Factor were close to 1.0 for each parameter. We then used a 25% burn-in proportion before computing a consensus tree (option *contype = allcompat*). In parallel, we launched an IQ-TREE run with 1000 ultrafast bootstrap replicates, five partitions (one per marker) and with the best-fit model determined during tree reconstruction.

2.3 | Divergence time estimates

Divergence times were estimated using Bayesian relaxed clocks as implemented in BEAST v.2.6.5 (Drummond et al., 2012) with an uncorrelated lognormal clock and a birth-death tree model. Analyses with the partition and models described above failed to converge and resulted in $\ll 200$ ESS values for several parameters. We suspected that the high level of missing data for the partition with the 3rd positions of COI only would explain this failure. Consequently, we chose to use only two partitions, corresponding, respectively, to mitochondrial and nuclear data, using the most adequate models as revealed by ModelFinder (Kalyaanamoorthy et al., 2017) implemented in the IQ-TREE web platform. We recovered a GTR+I+G model for the mitochondrial data and a TN+I+G model for the nuclear data. We chose fossils with a strong justification as to their phylogenetic placements to calibrate the molecular clock (Parham et al., 2012). We used four outgroup calibrations, corresponding to the following fossil species: '*Gyna*' *obesa* (Piton, 1940), *Cretaholocompsa montesecana* Martínez-Delclòs, 1993, *Valditermes brenanae* Jarzembowski, 1981, *Archeorhinotermes rossi* Krishna and Grimaldi, 2003, and one ingroup calibration, the blattid *Cretaperiplaneta kaonashi* Qiu et al. (2020) (see Appendix S2 for details on fossil choices, including ages, authors, calibrated clades and calibration procedures). All calibrations were treated with a uniform distribution, with the minimum bound being the age of the fossil and a conservative maximum bound being the age of the Devonian Rhynie chert (412 Myr), except for *Archeorhinotermes*

rossi for which the maximum bound was set at 237 Myr because we can reasonably assume that no crown-termites existed before the Carnian stage (Evangelista et al., 2019). Because of its uncertain phylogenetic affinity (see Appendix S2) and its potential consequences on dating estimates (e.g., Seidel et al., 2021), we tested three calibration placements for *Cretaperiplaneta kaonashi*, for stem-Blattidae, crown-Blattidae or stem-Blattinae, and we also ran an analysis without this calibration. We set a root prior with an exponential distribution (Mean: 30; Offset: 230) to account for the age interval obtained by Evangelista et al. (2019) for Dictyoptera in their phylogenomic analysis of Blattodea. We ran analyses for 100 million generations with trees and parameters sampled every 1000 generations. We checked the convergence of parameters using Tracer v.1.7 (Rambaut et al., 2018) by ensuring ESS of all parameters were >200. We consequently subsampled the tree population by resampling every 10,000 generations using LogCombiner (Drummond et al., 2012) and generated a Maximum Clade Credibility consensus tree with median ages with a burn-in value of 15% using TreeAnnotator (Drummond et al., 2012). Data and script files for phylogenetic and dating analyses are provided as Supplementary material (Appendix S3).

2.4 | Historical biogeography

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

Because our goal focuses on biogeographical events in the vicinity of NC, we coded biogeographical areas with greater details in the Pacific region. We considered the following areas: NC, New Caledonia (including Loyalty Islands); NZ, New Zealand; AU, Australia; NG, New Guinea; IM, Indomalayan region; PA, Paelearctic region; AF, sub-Saharan Africa; NT, Neotropical region. We also coded Antarctica (AT) as an area with no terminal taxa. To model island-hopping routes to NC, we coded two additional areas with no terminal taxa: LH, 'Lord Howe route', corresponding to landmasses west of NC acting as a possible stepping-stone for dispersal from

Australia and New Guinea, and TK, 'Three Kings route', corresponding to landmasses located south-east of NC, allowing facilitated dispersal from New Zealand and Antarctica.

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

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

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

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

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

To model the palaeogeographical events and test the role of potential island-hopping routes, we used the 'areas allowed' matrix implemented in *BioGeoBEARS*. This feature allows the user to input a binary matrix specifying which areas are authorized or not in the analysis, with authorized and unauthorized areas indicated by a 1

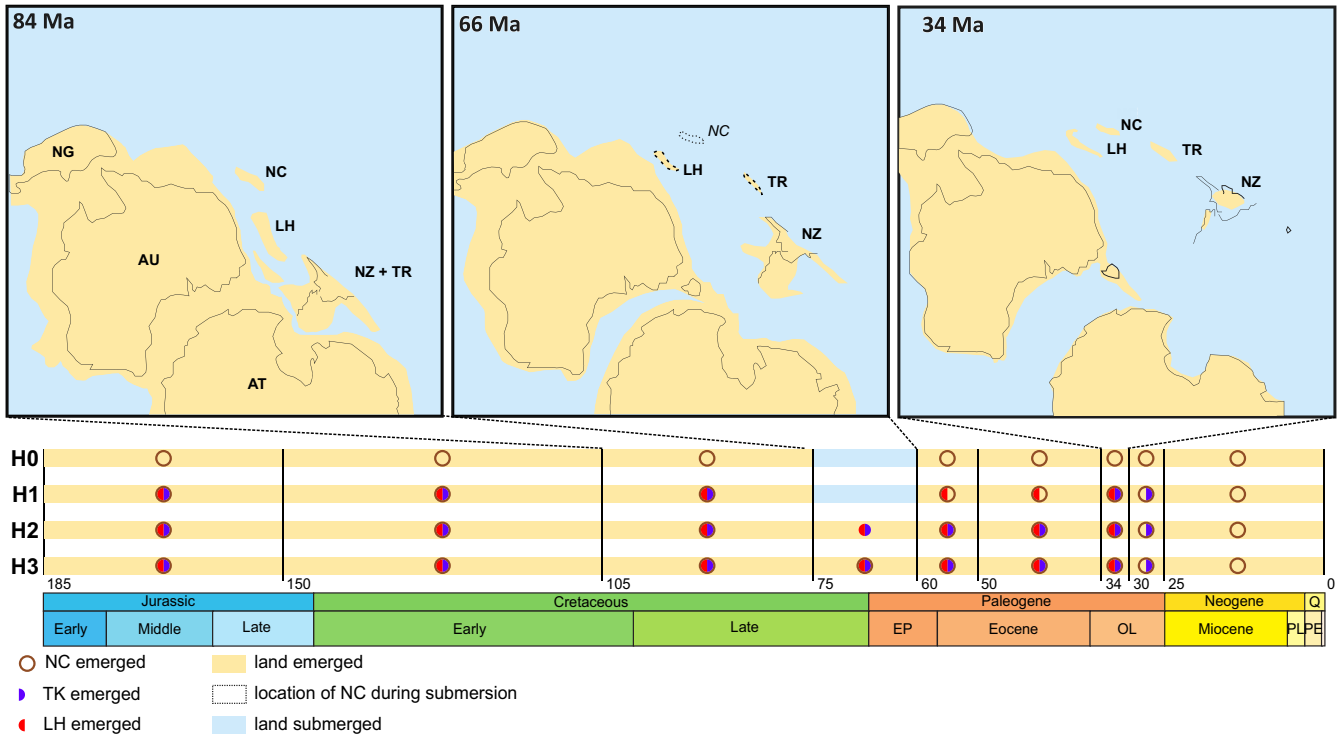


FIGURE 1 Timeline of emersion in the Southwest Pacific region according to the four biogeographical hypotheses (H0–H3) modelled in *BioGeoBEARS*. The timeline is divided according to the time slices used in *BioGeoBEARS*, a beige segment indicating that at least one of the three considered landmasses—New Caledonia (NC; brown circle), ‘Lord Howe route’ (LH; red semicircle) or ‘Three Kings route’ (TK; purple semicircle)—is emersed, 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 emersed. Interpretative maps, modified from Maurizot and 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.

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, Cluzel, et al., 2020; Maurizot & Campbell, 2020	No
60–50	First dated emersion of Grande Terre after GD	Cluzel et al., 2010; Maurizot, Collot, et al., 2020; Sevin et al., 2020	Possible ^a
50–34	Uplift of eastern Zealandia	Sutherland et al., 2020	Possible ^a
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

Note: Emersion of New Caledonia (NC) or proto-NC is indicated following Maurizot and Campbell (2020).

^a Occurrence of small-sized emerged lands at the place of present NC; geological data for the –60 to –34 Ma period are, however, indecisive.

and a 0, respectively. In the case of a time-stratified analysis, a matrix is provided for each time slice, thus modelling the disappearance of areas during one or several user-specified time intervals. We used this feature to allow or disallow the aforementioned LH and TK routes. We tested three alternative hypotheses regarding the lands surrounding NC in the past (Figure 1): H0 does not allow LH and

TK routes to be used at any time (i.e. no island-hopping), H1 allows LH and TK routes at times with published geological evidence for emersion, and H2 allows both routes continuously—including during GD—up to their latest documented drowning, respectively, at 30 and 25 Ma. In addition, and despite geological evidence, we tested a fourth hypothesis (H3), in which persistence of NC was allowed

during GD; H3 also allows LH and TK routes at this time. We tested these hypotheses using the areas allowed and matrices of dispersal multipliers implemented in *BioGeoBEARS*. For each hypothesis, we ran analyses using three biogeographical models implemented in *BioGeoBEARS* (i.e. BAYAREALIKE, DEC and DIVALIKE; Ree & Smith, 2008; Ronquist & Sanmartín, 2011; Landis et al., 2013) along with their respective + J derivatives. We used a maximum range size of two areas, corresponding to the maximum range size coded for terminal taxa, but also ran additional analyses with a maximum range size of four areas (under H0 and H1, the model that best fit with current geological evidence) to ensure that range size did not drastically influence the results. We then performed statistical model comparisons in *BioGeoBEARS* and considered only the model which yielded the lowest AICc score. R scripts are provided as Supplementary material (Appendix S5).

3 | RESULTS

3.1 | Phylogenetic analyses

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

More generally, the six Blattidae subfamilies are not all found monophyletic, but five main clades can be identified. The two most nested clades are the clades P and PB (for Polyzosteriinae and Polyzosteriinae-Blattinae, respectively). In the clade P ($BS_{ML}=81$;

$PP_{BI}=0.86$; $PP_{BEAST}=1$), the East Asian genus *Laevifascies* Liao et al., 2019 is sister to a *Macrocerca* Hanitsch, 1930+ Australasian Polyzosteriinae clade. Among these, the New Zealand genus *Celatoblatta* Johns, 1966 is sister group to a large clade (P2) made up of NC genera *Angustonicus*, *Rothisilpha*, *Pallidionicus*, *Punctulonicus* and *Pellucidonicus*, while all representatives of Polyzosteriini known from Australia form a clade with the NC representatives of the genus *Maoriblatta* (P1). The clade PB ($BS_{ML}=95$; $PP=1$) is made of Indomalayan/Australasian cockroaches mostly placed in the genus *Dorylaea* Stål, 1877 and species with reduced or absent wings mostly placed within the genus *Neostylopyga* Shelford, 1911.

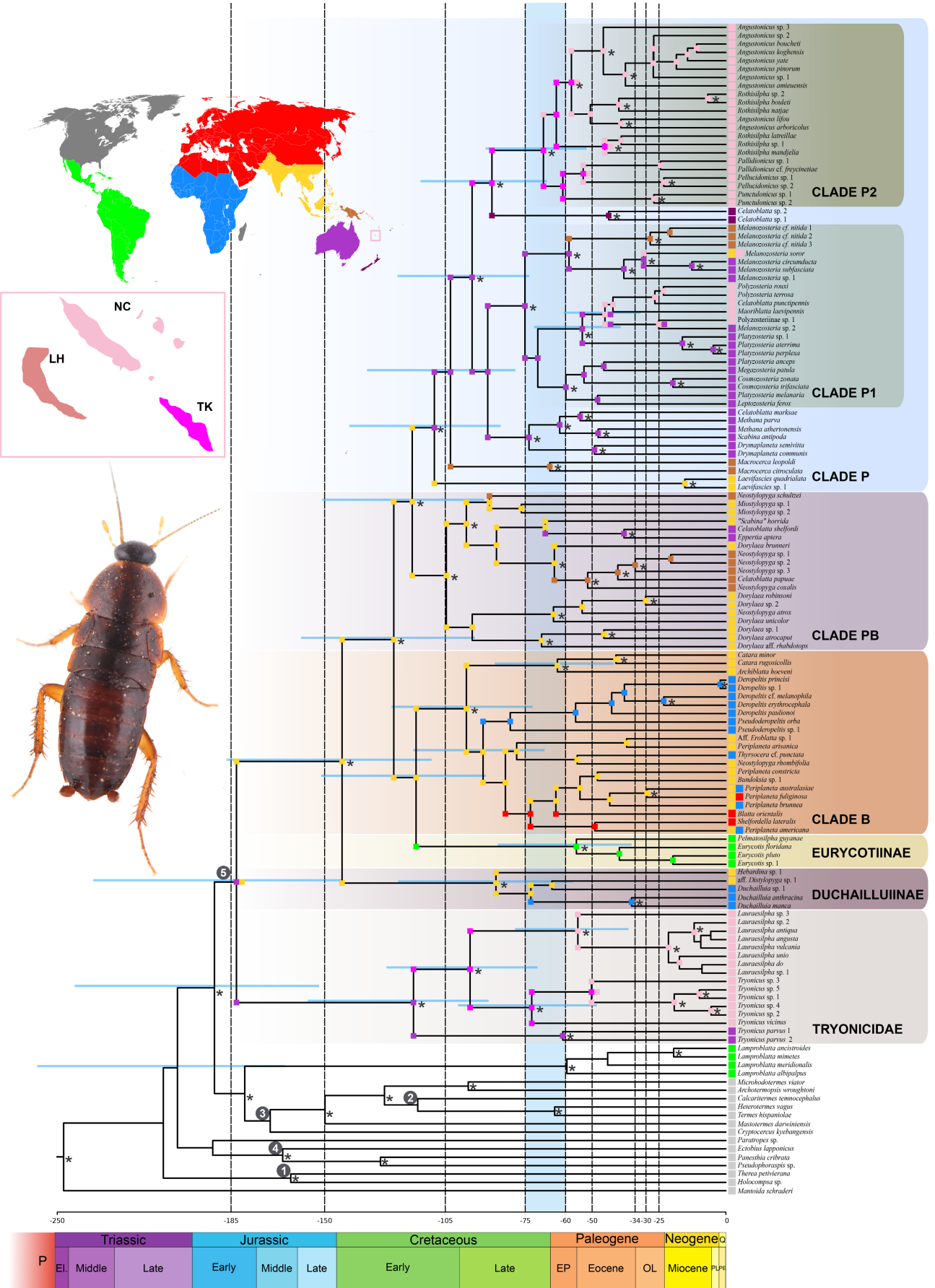
Sister group to the clade (P+PB) is clade B ($PP=0.86$) containing Archiblattinae Kirby, 1904 ($BS_{ML}=99$; $PP=0.94$) sister group to a clade comprising sexually dimorphic genera of old world Blattinae, including the African genera *Deropeltis* Burmeister, 1838 and *Pseudoderopeltis* Krauss, 1890 sister group to a mostly Asiatic group of Blattinae, including all species of *Periplaneta* Burmeister, 1838.

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

3.2 | Divergence time estimates and ancestral range estimation

The divergence time estimates are presented in Figure 2, along with the BEAST estimated topology, the 95% credibility intervals for the deepest nodes, and ancestral range estimations assuming the H2 biogeographical hypothesis under DEC+J model, with *Cretaperiplaneta kaonashi* calibrating stem-Blattidae (age estimates did not differ significantly when this fossil was removed or used to calibrate another node; see Appendix S7). In brief, H2 favours biogeographical events that include island-hopping events along the 'Three Kings (TK) route', contrary to hypotheses H0, H1 and H3. This is also true for DEC models without jump dispersal events; the

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



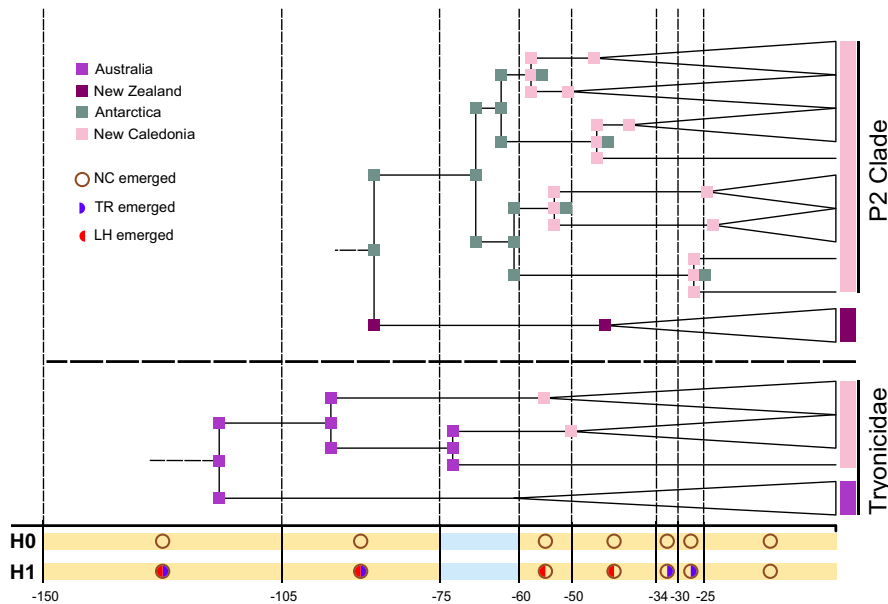


FIGURE 3 Alternative scenario for Tryonicidae and the clade P2 (within Polyzosteriinae) according to H0 and H1 hypotheses (DEC + J; maximum range of two areas). Both hypotheses suggest multiple colonization events from Australia (Tryonicidae; bottom) and Antarctica (clade P2; top). Terminal branches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

number of maximum range size areas (two or four) does not influence the results either (see Appendix S8). Below, we provide dating estimates for the main clades and explain the main events under H2 and DEC + J, before highlighting the main discrepancies with alternative hypotheses (i.e. H0, H1 and H3).

We infer an Early Jurassic origin (median age = 183 Ma; 95% height posterior density [HPD] = 144–236 Ma) for the Blattidae + Tryonicidae clade, with a geographical range covering both Australia and Asia. Following a vicariance event, we recover an Australian origin for Tryonicidae in the Early Cretaceous (117 Ma; 89–156 Ma). We then recover an island-hopping event (i.e. colonization of the TK area) followed by three independent colonizations of NC after the re-emersion of the island at –60 Ma. For Blattidae, we recover an Asian origin around the Late Jurassic/Early Cretaceous transition (143 Ma; 110–187 Ma). Within Blattidae, two noteworthy independent colonizations of Africa, in the clade Duchailuiinae and within the clade B, occurred during the Late Cretaceous. We also recover a colonization of the Neotropics in the Early Cretaceous by the Eurycotiinae (116 Ma; 89–151 Ma). In the clade PB (Asian origin; crown age = 105 Ma; 80–136 Ma), we recover two independent colonizations of New Guinea and Australia from Asia, both around the K/T transition (64 Ma; 47–86 Ma and 68 Ma; 46–92 Ma, respectively). Within the clade P (Asian origin, crown age = 109 Ma; 84–141 Ma), we find an early colonization of Australia during the Cretaceous (103 Ma; 79–134 Ma), rapidly followed by a colonization of New Guinea by a lineage today represented by the genus *Macrocerca*. We also recover an island-hopping event through the TK area around the Early/Late Cretaceous transition (95 Ma; 73–123 Ma) before multiple colonization events of NC around –60 Ma by members of the clade P2. Colonization of NC by members of the clade P1 implies a direct dispersal event from Australia in the Eocene (45 Ma; 32–60 Ma).

The best supported model under H0 (no island-hopping) and H1 (island-hopping through identified areas only) is also DEC + J. Under both hypotheses, this model infers, for Tryonicidae, three

colonization events of NC from Australia (*contra* through TK route under H2). For the clade P2, the model infers multiple colonization events of NC from Antarctica, which, at this time, was still part of Gondwana. Those are the main discrepancies with the scenario reconstructed under H2 and they are depicted in Figure 3. As for H3, DIVALIKE + J and DEC + J have similar supports (AICc of 310.3 and 310.6, respectively). In both cases, a single colonization event of NC is inferred before the GD for Tryonicidae and for the clade P2 (Appendix S8).

4 | DISCUSSION

4.1 | Towards ‘trans-disciplinary’ biogeography to test the island-hopping hypothesis

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

The origin of ‘old’ lineages on younger islands is often apparently ‘solved’ by island-hopping hypotheses, wherein clades are supposed to have evolved through presence in or dispersal via now-drowned

islands (e.g. Carlquist, 1965; Heads, 2005, 2008; Ladiges & Cantrill, 2007). But, to our knowledge, those hypothetical narratives have never been formally tested (Grandcolas, 2017), except by dating clades in comparison with island ages (e.g., Giribet & Baker, 2019; Grandcolas et al., 2008; Nattier et al., 2011, 2017). Here, we have summarized geological evidence about possible vanished colonization routes so that we can test the island-hopping hypothesis for a clade of New Caledonian insects. This general context and the biogeographical models we have built are not restricted to these insects and can be used for other New Caledonian clades whose ancient origins remain enigmatic (e.g., Buckley et al., 2010; Sharma & Giribet, 2009; Papadopoulou et al., 2013; Giribet et al., 2021).

Our results support a scenario of island-hopping under some, but not all, circumstances, through the 'Three Kings route', at the South-East of NC (H2 scenario; Figure 2). Two clades would have then colonized NC from New Zealand (some endemic Polyzosteriinae) and, perhaps more surprisingly because of our current understanding of paleocurrents, from Australia (Tryonicidae). Note that the biogeographical model under this scenario allowed island-hopping at all times, that is, even at times for which geological evidence of past vanished islands is lacking or is very equivocal. This lack of evidence is however not a proof of the absence of past emerged territories (see for instance Rouillard et al. (2017) about the Fairway Basin). Conversely, when allowed only at times with geological evidence (H1 scenario) island-hopping hypothesis was not inferred, NC being colonized directly from Australia or through Antarctica (Figure 3). Also, because of the uncertainties associated with dating results, a single colonization event of NC for the clade P2 cannot be entirely ruled out, because the lower bound of the 95% HPD is more recent than the end of the total submersion (Figure 2). Regardless, we have here built a case about testing island-hopping hypotheses, instead of merely invoking them, taking part in an ongoing interdisciplinary paradigm between geology and biogeography (e.g. Ali & Hedges, 2021; Cornée et al., 2021; Crews & Esposito, 2020; Feyhl-Buska, 2020; Jöks et al., 2021; Landis, 2016; Michaux & Ung, 2021; Montes et al., 2021; Philippon et al., 2020).

Such integrative and statistical inferences in biogeography face limitations and difficulties, notably because of the fragmentary nature of geological information and the difficulty to interpret geological data to reconstruct palaeogeography. On the biological side, extinction phenomena or poor taxonomic sampling can obfuscate biogeographical interpretations, especially when the fossil record is lacking (Barden & Ware, 2017; Grandcolas et al., 2014; Mayr, 2017; Wisniewski et al., 2022). Uncertainties in phylogenetic relationships and in dating estimates, from calibration procedures to confidence intervals that may overlap with several time slices, also contribute to becloud biogeographical interpretations. Finally, biogeographical models also have limitations as they only consider a small number of biogeographic events, treat dispersal as a time-independent process, while also struggling to incorporate paleogeographical or diversification-related information that might affect range evolution; they are also ill-suited to test competing hypotheses that differ in their premises (Hackel & Sanmartín, 2021). In spite of these caveats,

integrative biogeography must be encouraged and strengthened to help limit overly speculative conclusions (Antonelli et al., 2018; Crisp et al., 2011; Donoghue & Moore, 2003; Fritz & Baker, 2022; Ronquist & Sanmartín, 2011). In the case of the NC biota, geological and biological data could be complemented, for instance, with paleoclimatic data to further improve the test and robustness of biogeographical hypotheses.

4.2 | Palaeoendemics in New Caledonia

There is a consensus on the mixed origin of the NC biota, especially its endemics. As previously synthesized (Gillespie & Roderick, 2002; Giribet & Baker, 2019; Grandcolas et al., 2008; Murienne et al., 2005; Sharma & Wheeler, 2013), these organisms can be classified into palaeoendemics and neoendemics, depending on their ages of divergence and diversification. While the majority of the New Caledonian biota would fall in the neoendemics group—that is, groups that diverged from their sister group relatively recently (e.g., Nattier et al., 2017)—palaeoendemics (but not relicts and revenants; Sharma & Wheeler, 2013) inform us more than neoendemics on the general debate about the origin of old taxa in relatively recent islands.

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

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

Tryonicidae—found only in Australia and New Caledonia—can also be seen as a relict, like the harvestman *Trogolosi* (Sharma & Giribet, 2009), because of their much more diversified and widely distributed sister group (i.e., Blattidae) and because they are at the 'tip' of a relatively long branch, a topology congruent with extinction events (Grandcolas et al., 2014). If they are true relicts, then, by definition, their geographical origin would be hard to decipher and they would not inform us much about the history of New Caledonia. On the other hand, they would have value for conservation purposes or to document extinction—which remains challenging even in modern diversification analyses. As for the clade P2 (*Maoriblat*a and affiliated), they could also correspond to neoendemics given the uncertainty around their age of origin (ca. 35 Ma as minimal value of

the 95% HPD). However, to settle on their taxonomic and biogeographical status, *Maoriblatta* from New Zealand or Australia should be added in future analyses. In any case, and maybe even more for relicts in the southern Hemisphere (Upchurch, 2008), fossil evidence could bring decisive insights and limit the risk of skewed interpretations (Barden & Ware, 2017; Garrouste et al., 2021; Mayr, 2017; Silvestro et al., 2016).

4.3 | Difficulties of biogeography in the deep time: Extinctions, dispersal ability and areas with no extant representatives

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

In this regard, incorporating biogeographical areas with no extant representatives—this includes, but shall not be restricted to, now vanished islands—into biogeographical analyses is pivotal. For instance, Antarctica has repeatedly been inferred as a possible colonization route between Australia and South America (e.g., Cruaud et al., 2011; Vicente et al., 2017). Here, a passage through Antarctica is inferred in one of the scenarios we tested (for a NC clade within Polyzosteriinae; Figure 3) but not for the colonization of the Neotropics. Instead, the neotropical Eurycotiinae, whose position is consistent with previous phylogenetic works (e.g. Legendre et al., 2015, but *contra* Bourguignon et al., 2018), would have dispersed from Asia, like the two African clades, during the Cretaceous. We refrain, however, from discussing further biogeographical implications at the deepest nodes of our phylogeny because of a few weakly supported nodes, which might impact biogeographical reconstructions (e.g. Magalhaes et al., 2021; Smith, 2009). We thus consider that additional data and support are needed to discuss the early biogeography of those cockroaches. Regardless, counter-intuitive patterns of range evolution should neither be taken for

granted nor be dismissed lightly. Inferred biogeographical patterns can fit with multiple alternative histories, and the geographical changes influencing biotic evolution are often very complex. In this regard, the simpler scenario (often the one implying long-distance dispersals) is not necessarily the most consistent with the geological record, and a better grasp of geologic history can radically alter biogeographical interpretations (e.g., the influence of translocated Gondwana-derived landmasses in shaping the Asian biota; Loria & Prendini, 2020; Bolotov et al., 2022).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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