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Natália Vicente, Gael G. Kergoat, Jiajia Dong, Karla Yotoko, Frédéric Legendre, et al.. In and out of the Neotropics: historical biogeography of Eneopterinae crickets. *Journal of Biogeography*, 2017, 44 (10), pp.2199-2210. 10.1111/jbi.13026 . mnhn-02520966

HAL Id: mnhn-02520966


<https://mnhn.hal.science/mnhn-02520966v1>

Submitted on 6 Dec 2022

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In and out of the Neotropics: historical biogeography of Eneopterinae crickets

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ABSTRACT

Aim Multiple biogeographical scenarios involving vicariance and different colonization routes can explain disjunct species distributions in the Southern Hemisphere. Here, we tested several alternative hypotheses in Eneopterinae crickets, a diverse subfamily presenting a disjunct worldwide distribution. We inferred a dated phylogeny of Eneopterinae and reconstructed their biogeographical history to unravel the origin of their present-day distribution, focusing on their multiple origins in the Neotropics.

Location Worldwide.

Methods We sampled 62 eneopterine species representing all extant genera. We inferred their phylogenetic relationships through Bayesian and maximum likelihood approaches based on four mitochondrial and three nuclear gene sequences. Divergence time estimates were inferred using Bayesian relaxed clock approaches and primary fossil calibrations. Biogeographical analyses were conducted with the default dispersal–extinction–cladogenesis (DEC) model and a variant model (DEC+J), which accounts for rare-jump dispersal events.

Results Our dating analyses showed that the Eneopterinae is far older than expected and its diversification can be traced back to the Late Cretaceous (*c.* 76 Ma). In this context, the most supported biogeographical scenario (under DEC+J) suggests that the Neotropics were colonized twice independently: first during the break-up of Gondwana, when Antarctica, Australia and South America started separating (compatible with a vicariance event if relying on the result of the DEC model alone); later through a northern recolonization originating from Southeast Asia, likely related to a Holarctic Boreotropical distribution of an eneopterine lineage during the Eocene.

Main conclusions We provided a dated worldwide biogeographical framework for the Eneopterinae crickets. Overall, the subfamily disjunct distribution pattern is better explained by both ancient and recent dispersal events. Whether this could reflect a widespread pattern in insect groups exhibiting a disjunct distribution remains to be investigated by studying other insect lineages. The information gathered here will also help foster new directions for future studies concerning the acoustic innovations of this clade.

Keywords

ancestral area reconstruction, Bayesian relaxed clock, Boreotropical dispersal, crickets, disjunct distribution, dispersal–extinction–cladogenesis, fossil calibration, historical biogeography, Neotropics colonization

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INTRODUCTION

Explaining disjunct distributions among continents is a central goal in biogeography (Lomolino *et al.*, 2010). Major theories regarding biogeographical mechanisms have emerged from debates dealing with the relative importance and interplay of tectonic-driven vicariance resulting from the breakup of Gondwana and long-distance dispersal (LDD) (Raven & Axelrod, 1974; Waters *et al.*, 2000; Heads, 2012; but see Crisp *et al.*, 2011; Gillespie *et al.*, 2012; Waters *et al.*, 2013). Although dispersal and vicariance have been viewed as mutually exclusive, competing, hypotheses in the past, they are now seen as complementary mechanisms to understand the biogeographical history in widespread groups of organisms (e.g. Gamble *et al.*, 2011; Kergoat *et al.*, 2012; Condamine *et al.*, 2013; Rota *et al.*, 2016).

The biogeographical history of the Southern Hemisphere involves either old vicariance events relative to the breakup of Gondwana, LDD among southern continents, or faunal exchanges with the Northern Hemisphere, either through range expansion or regular dispersion. Regarding South America, since the Cretaceous, four main colonization routes, either through dispersion or vicariance, have been hypothesized according to Sanmartín & Ronquist (2004) (Fig. 1). The first is the North America connection (NAC). North American and South American biota were connected at least twice in the past (Hay *et al.*, 1999; Woodburne, 2010). The first connection started during the mid-Cretaceous [100 million years ago (Ma)] at the level of proto-Caribbean islands and remained until Eocene (49 Ma). The second connection started with the process of formation of the Isthmus of Panama during Miocene (15 Ma) (Montes *et al.*, 2015). Here, it is worth underlining that although the consensus hypothesis assumes that the closure of Panama Isthmus and faunal interchange begun 3.5 Ma, recent studies have also demonstrated substantial dispersal of terrestrial organisms much earlier (Bacon *et al.*, 2015). The second is the transatlantic route (TAC). Despite that Africa and South America separated completely around 100 Ma, transatlantic migration is the most supported colonization route for many animal groups in different time periods (e.g. Mayr *et al.*, 2011; Kergoat *et al.*, 2012; Bond *et al.*, 2015). The third is the trans-Antarctic route (TAN). Antarctica connected Australia and South America from late Cretaceous (100.5 Ma) until Eocene (35 Ma), when the Southern Ocean between Tasmania and Antarctica opened. The fourth is the trans-Pacific route (TP). New Zealand separated from Gondwanan landmasses *c.* 80 Ma. However, the TP route is a likely explanation for disjunct distributions between South America and New Zealand sister-group taxa (e.g. Keogh *et al.*, 2008; Sharma & Giribet, 2012; Wei *et al.*, 2015).

In this work, we use the cricket subfamily Eneopterinae as a model system to test hypotheses that might explain diversification and distribution patterns in widespread biota. The *c.* 250 species of Eneopterinae (*sensu* Robillard & Desutter-Grandcolas, 2008) have been extensively studied for the

diversity of their communication signals (e.g. Robillard *et al.*, 2013; ter Hofstede *et al.*, 2015). They exhibit a disjunct distribution throughout the tropics (Fig. 1), which makes them a suitable model for testing alternative routes of colonization of the Southern Hemisphere. For this group, a molecular phylogeny was developed during previous work to test whether the clades distributed in the region of New Caledonia were older than the emergence of the main island in this archipelago (Nattier *et al.*, 2011). Although this study had a more regional focus, its results suggested multiple origins of these insects in the Neotropics.

Here, we infer a new phylogeny of Eneopterinae by expanding the gene and taxonomic sampling. We calibrate the corresponding phylogeny according to a critical review of the fossils available for Grylloidea. Based on the resulting timetree, we perform biogeographical analyses to (1) investigate the hypothesis of multiple colonizations of South America by the Eneopterinae and (2) understand the origin of the extant disjunct distribution of the subfamily.

MATERIALS AND METHODS

Taxon sampling and molecular dataset

In this study, we sampled 62 Eneopterinae species representing all recognized genera, sequenced for three nuclear markers [histone H3 (H3), 18S and 28S ribosomal RNA] and four mitochondrial markers [cytochrome oxidase subunit I (COI), cytochrome b (Cytb), 12S and 16S ribosomal RNA]. In comparison with the most recent molecular phylogeny dealing with Eneopterinae (Nattier *et al.*, 2011), our study increased the sampling of genes and species for the subfamily (seven genes and 62 species versus four genes and 43 species).

For outgroup comparison, we used an approach based on the availability and quality of fossils in Grylloidea provided by the database 'Orthoptera Species File Online' (Cigliano *et al.*, 2017). We selected outgroup species from a recently published phylogeny of crickets (Chintauan-Marquier *et al.*, 2016) containing molecular data for six of the markers we use (H3, 18S, 28S, Cytb, 12S and 16S). For each fossil species that was preselected for calibrating the molecular tree, we sampled two or three species of the corresponding clade in the cricket phylogeny. Using this strategy, we integrated 21 outgroup species encompassing Gryllidae, Gryllotalpidae, Mogoplistidae, Phalangopsidae, Trigoniididae, plus two Acrididae species (Caelifera) to serve as more external outgroups. A complete list of specimens, voucher taxa and GenBank accession numbers, are presented in Appendix S1 in Supporting Information.

Phylogenetic analyses

We used the software MUSCLE (Edgar, 2004) with default parameters, implemented in MEGA 6.0 (Tamura *et al.*, 2013) to align the sequences. With MEGA, we also checked if the protein-coding genes were congruent with codon reading frames. We conducted preliminary maximum likelihood

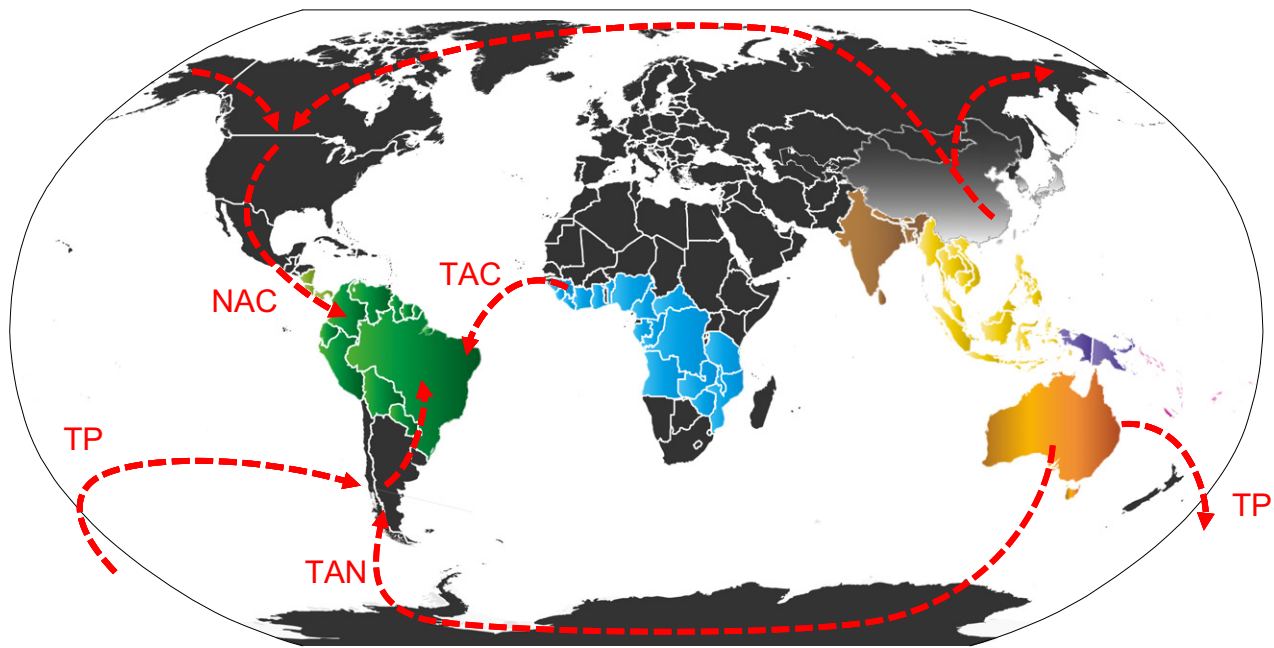


Figure 1 Present-day distribution of Eneopterinae crickets showing the main hypothesized colonization routes towards South America (according to Sanmartín & Ronquist, 2004); symbols: NAC, North America connection; TAC, Transatlantic route; TAN, Trans-Antarctic route; TP, Trans-Pacific route. The colours represent the distribution of the subfamily according to the 10 areas defined for the biogeographical analyses. [Colour figure can be viewed at wileyonlinelibrary.com]

(ML) with rapid bootstrap (BS) analyses (200 replicates) in RAxML 7.4.2. (Stamatakis, 2006) with each gene separately to check for contaminations and artefacts. We concatenated sequences and used PARTITIONFINDER 1.1.1 (Lanfear *et al.*, 2012) with the Bayesian information criterion to infer the best partitioning schemes and substitution models (Ripplinger & Sullivan, 2008). For that, the coding genes were separated according to codon position. A combined ML tree was then obtained with RAxML using 100 replicates (support assessed using 1000 nonparametric BS replicates). A combined Bayesian inference (BI) analysis was carried out using MRBAYES 3.2.3 (Ronquist *et al.*, 2012); eight Markov chains were run simultaneously for 50 million generations, sampled every 1000 generations to ensure independence of samples. We used a conservative burn-in of 12.5 million generations per run after checking for stability on the log-likelihood curves and the split-frequencies of the runs. Support of nodes for MRBAYES analyses was provided by clade posterior probabilities (PP) as directly estimated from the majority-rule consensus topology. A clade with a PP value higher than 0.95 was considered as well supported.

Dating analyses

Bayesian relaxed clock (BCR) analyses were carried out with BEAST 1.8.3 (Drummond *et al.*, 2012) using either uncorrelated lognormal relaxed (UCLN) or random local (RLC; Dornburg *et al.*, 2012) clocks. No reliable fossils were found for a direct calibration for Eneopterinae; the only known fossil records attributed to Eneopterinae (96 Ma *Proecanthus*

anatolicus Sharov and the 122 Ma *Brontogryllus excelsus* Martins-Neto) have uncertain assignment since they rely on incomplete impressions of the tegmen. Therefore, we choose to implement a wide-outgroup approach to calibrate our dating analyses (Sauquet *et al.*, 2012; Strijk *et al.*, 2012) based on fossils that, according to the descriptions, could be reliably addressed (for details about fossil choice, see Appendix S2). As result we set up a total of eight calibration procedures for the BRC analyses (UCLN versus RLC; two or four fossil constraints; uniform or exponential distributions). Four distinct relaxed clocks were specified based on the result of a PARTITIONFINDER analysis (with *beast* option) (Appendix S3). For each calibration procedure, two runs were carried out with 50 million generations and trees sampled every 5000 generations. Based on the result, BEAST .xml files were modified to implement the path-sampling procedure for B_F estimation following the recommendations of Baele *et al.* (2013). We used a conservative burn-in period of 12.5 million generations per run. Post burn-in trees from the two runs (7500 trees for each run) were combined using LOGCOMBINER. Convergence of runs was assessed graphically using the TRACER module of BEAST and by examining the effective sample size (ESS) of parameters. For all dating analyses, $ESS \geq 200$ was obtained for all parameters. Out of the eight calibrations, the one relying on two fossil constraints, UCLN clocks and exponential distributions, has the best harmonic mean ($-66,783.39$) and is significantly recovered as the best-fit calibration procedure in all but one B_F comparisons (Appendix S4). Additional analyses were also carried out using this calibration procedure (UCLN clocks and

exponential distributions) in order to estimate the rates of evolution for each gene of our dataset (Appendix S5).

Historical biogeography

Historical biogeography analyses were carried out using the R package 'BioGeoBears' (Matzke, 2014). This package relies on the LAGRANGE (Ree & Smith, 2008) DEC model. It also implements the model DEC+J that accounts for founder event speciation associated with rare-jump dispersal events (Matzke, 2014). Here, we carried out separate analyses for the DEC and DEC+J models. As a guide tree, we used the dated phylogeny (single consensus tree inferred with LOGCOMBINER) relying on corresponding to the best-fit calibration procedure (two fossil constraints, UCLN clocks and exponential distributions). This tree was further pruned to only include Eneopterinae in order to avoid potential biases resulting from the fact that outgroup taxa were sparsely sampled. We then defined 10 geographical areas after considering the evidence available for historical relationships between relevant geographical areas (Sanmartín *et al.*, 2001; Sanmartín & Ronquist, 2004) and the distribution of Eneopterinae (Fig. 1). The biogeographical regions were Africa, Australia, Central America, India, New Caledonia, New Guinea, Palaearctic, northern South America, Southeast (SE) Asia and Southwest Pacific.

Following the views of several authors (Hines, 2008; Mansion *et al.*, 2008; Nylander *et al.*, 2008), taxa with marginal distribution in an area were not assigned to it. Species ranges were coded by presence-absence and a maximum number of two areas were set for both DEC and DEC+J analyses. Finally, to account for major periods of geological rearrangements, we used time-stratified biogeographical models, with three time slices. The first time slice ($t1$) runs from 80.0 to 65.0 Ma, the second ($t2$) from 65.0 to 30.0 Ma and the last ($t3$) from 30.0 to 0.0 Ma. For each time slice, we provided a matrix of probabilities of dispersion (for details about palaeogeographical model, see Appendix S6), constructed according to the geographical connectivity between areas. To measure connectivity, we considered land bridges between the landmasses that could favour biotic exchange (e.g. Kerguelen Plateau). The rate of dispersion was scaled according to the availability of area connection through time. The factors were as follows (modified from Condamine *et al.*, 2013): (1) adjacent areas: 1.0; (2) areas separated by a minor barrier: 0.7; (3) dispersal between two areas separated by one area: 0.3; (4) LDD: 0.01; (5) dispersal impossible (one area missing): 0. After running both analyses, we used likelihood ratio tests (LRT) to sort between the two competing models (DEC and DEC+J).

RESULTS

Phylogenetic analyses

The complete molecular matrix comprised 3340 base pairs for 83 terminals. Appendix S3 shows the partition scheme of

the substitution model used in our phylogenetic analyses. The separate analyses of each marker showed no major conflict of topology. On the combined dataset, BI (Appendix S7) and ML (Appendix S8) yielded largely congruent topologies, which recovered Eneopterinae as monophyletic with high support (BS: 95; PP: 1; Fig. 2).

Except for Eneopterini, all the currently recognized tribes were retrieved as monophyletic and can be matched to supported clades in our analysis. The subfamily is separated in two main groups, one encompassing the Australian Eurepini (BS: 100; PP: 1) and the other including all remaining tribes: *Eneoptera*, one genus of the polyphyletic Eneopterini (BS: 100; PP: 1) as the sister group of the remaining tribes. The next clade gathered the two genera of Nisitriini (BS: 100; PP: 1), *Paranisitra* and *Nisitrus* as the sister group of the remaining Eneopterinae. Next, Xenogryllini, including *Pseudolebinthus* and *Xenogryllus* (BS: 100; PP: 1), appeared as a sister group of the species rich Lebinthini (BS: 88; PP: 1), including two genera previously classified as Eneopterini, *Ligypterus* and *Ponca*. *Lebinthus* is paraphyletic, as previously found. The other generic relationships were well defined, all genera being monophyletic.

Divergence time estimations

Both calibration procedures yielded comparable timeframes (Appendices S9–S16). Age estimates for Eneopterinae (Fig. 2, Table 1) suggested an origin 76.29 Ma [median age; 95% highest posterior density confidence interval (HPD): 63.28–96.76 for the best-fit calibration procedure]. See Table 1 for the details of molecular dating of the major clades of Eneopterinae. Regarding South America, our results showed that the lineage corresponding to *Eneoptera* branched during late Cretaceous at 70.97 Ma (95% HPD: 58.74–90.06 Ma), with a crown group diverging in early Miocene at 22.26 Ma (95% HPD: 16.25–30.66 Ma). The ancestor of the second Neotropical lineage (*Ligypterus* and *Ponca*) is dated at 40.17 Ma (95% HPD: 30.7–52.92 Ma), but *Ligypterus* began diversifying during the Miocene at 12.73 Ma (95% HPD: 9.29–17.35 Ma).

Historical biogeography

Model selections through LRT significantly supported the DEC+J model ($L = -107.44$) over the DEC model ($L = -116.09$) as the best-fit model for the 'BioGeoBears' historical biogeography analyses. The corresponding inference of ancestral areas evolution (Fig. 2) suggested an origin in Australia for Eneopterinae during the Late Cretaceous (76 Ma). Subsequently one lineage underwent diversification in Australia (Eurepini), whereas the second one colonized the Western Hemisphere via South America. An interesting pattern is then suggested, involving a subsequent colonization of the Old World (Southeast Asia) from the Western Hemisphere *c.* 70 Ma. This dispersal event was followed in the Palaeocene by a colonization of India. During the

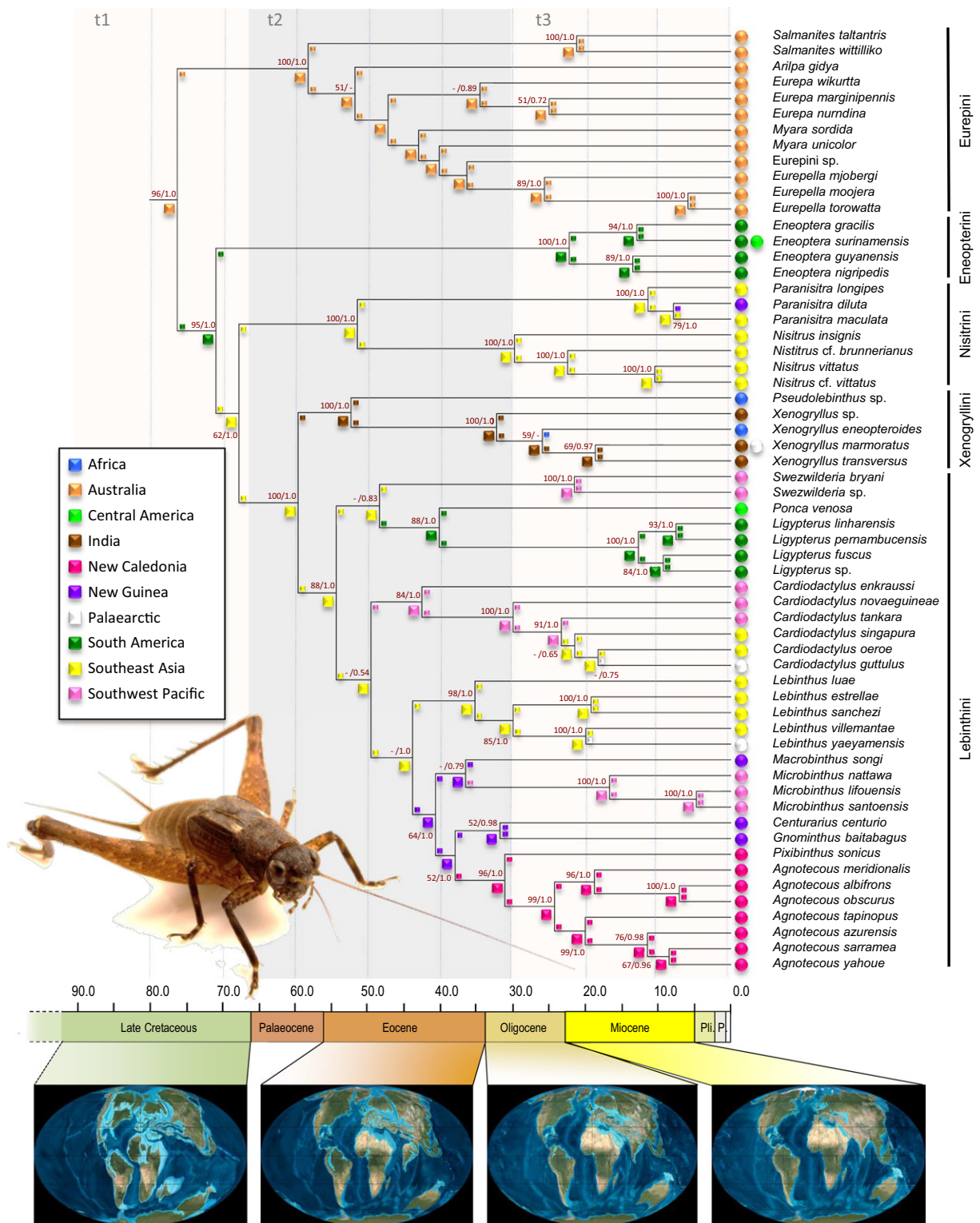


Figure 2 Reconstruction of historical biogeography for Eneopterinae using a stratified dispersal–extinction–cladogenesis (DEC+J) model that accounts for geological history. The top-left box represents the 10 areas implemented in the palaeogeographical model. For each node, a coloured square corresponding to the coloured area in the box represents the inferred area(s) with the highest relative probability in the DEC+J analysis. Present-day distributions of each species are given at the tips by coloured circles corresponding to coloured areas on maps and current tribal assignments are mentioned on the right. The time slices of each palaeogeological period used to measure the dispersal rate are shown. A 5-Ma time scale is placed at the bottom of the chronogram spanning epochs since 90 Ma. Photo: male of *Macrobinthus jharnae*. Palaeogeographical maps reconstructed from Blakey (2008) available at <http://cpgeosystems.com/globaltext2.html>. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 The molecular dating (Ma) of major clades of Eneopterinae. HPD, highest posterior density. The information about clades distributed in South America is presented in grey.

Clade/Taxa	Median age (Ma)	95% HPD (Ma)
Eneopterinae	76.29	63.28–96.76
Eurepini (crown)	58.26	46.93–74.24
<i>Eneoptera</i> (stem)	70.97	58.74–90.06
<i>Eneoptera</i> (crown)	22.26	16.25–30.66
Nisitriini (stem)	67.79	55.88–86.41
Nisitriini (crown)	51.46	40.05–67.15
<i>Paranisitra</i> (crown)	11.40	7.54–16.24
<i>Nisitrus</i> (crown)	29.81	22.07–40.56
Xenogryllini (stem)	59.64	49.22–76.12
Xenogryllini (crown)	52.35	41.97–67.46
<i>Xenogryllus</i> (crown)	32.29	24.68–42.58
Lebinthini <i>sensu lato</i> (crown)	54.38	44.43–69.53
(<i>Swezwilderia</i> (<i>Ligypterus</i> + <i>Ponca</i>)) (crown)	48.42	3.97–62.58
<i>Swezwilderia</i> (crown)	21.55	12.98–32.07
(<i>Ligypterus</i> + <i>Ponca</i>) (crown)	40.17	30.70–52.92
<i>Ligypterus</i> (crown)	12.73	9.29–17.35
Pacific clade of Lebinthini (crown)	49.59	40.14–63.01
<i>Cardiodactylus</i> (crown)	42.57	33.60–55.19
<i>Pixibinthus</i> + <i>Agnotecous</i> (crown)	31.14	24.52–40.69
<i>Agnotecous</i> (crown)	24.28	18.78–31.89

Oligocene, several lineages also reached New Guinea and the southwest Pacific from Southeast Asia. One lineage (now encompassing *Ligypterus* and *Ponca*) went back to the Western Hemisphere at the same period. Colonization of New Caledonia occurred more recently, but shortly after the re-emergence of the Archipelago. Analyses with a DEC model also recovered a quite similar pattern (Appendix S17), noticeably differing by the fact that several vicariance events are inferred using the DEC model (especially at the base of the tree between Australia and South America), contrary to the result of the DEC+J analysis, which exclusively inferred dispersal events.

DISCUSSION

Phylogenetic and systematic account

This study presents the most complete molecular phylogeny of the globally distributed Eneopterinae. The new topology, including more taxa and based on more molecular markers, matches the topology of Nattier *et al.* (2011), including the polyphyly of the Neotropical tribe Eneopterini. The branch leading to the crown of *Eneoptera* diverged very early as the sister group of all other non-Australian Eneopterinae. The two other Neotropical genera, *Ligypterus* and *Ponca*, clustered within the tribe Lebinthini, which is corroborated by the acoustic characteristics shared by these clades (Robillard *et al.*, 2015). *Ligypterus* and *Ponca* are also morphologically similar to Lebinthini. The grouping of Eneopterini (*Eneoptera*, *Ligypterus* and *Ponca*) found earlier when only

morphological data were used for phylogenetic reconstruction (Robillard & Desutter-Grandcolas, 2004a, 2006) appears to be a reconstruction artefact due to weak synapomorphies about details of female wing venation and male genitalia. Therefore, the tribe Eneopterini should be restricted to the genus *Eneoptera* until further notice, while *Ligypterus* and *Ponca* are transferred to Lebinthini, as a Neotropical branch of this tribe (Fig. 2).

Our study positioned *Pseudolebinthus* as the sister genus of *Xenogryllus*, and *Centurarius* and *Gnominthus* within Lebinthini. These genera were recently described and have not been included in a phylogeny. *Centurarius* and *Gnominthus* form a clade located between the paraphyletic *Lebinthus* and the clade (*Agnotecous*, *Pixibinthus*), also found in Anso *et al.* (2016). The genus *Swezwilderia*, previously considered as Eneopterinae *incertae sedis* (Robillard & Desutter-Grandcolas, 2008), is confirmed within the tribe Lebinthini, as suggested by previous studies (Nattier *et al.*, 2011; Chintauan-Marquier *et al.*, 2016). It seems related to the clade (*Ligypterus*+*Ponca*), although this relationship is poorly supported.

Historical biogeography of Eneopterinae

This study is the first attempt to reconstruct a biogeographical scenario for a clade of crickets with a worldwide distribution using modern phylogenetic methods for historical biogeography (Fig. 3a; Appendix S18). Dating analyses suggest that the radiation of Eneopterinae began in the late-mid Cretaceous about 76 Ma (Fig. 2) (95% HPD: 63–96 Ma). This result is much older than the 46 Ma found by the study by Nattier *et al.* (2011), which greatly underestimated the age of the clade by using recent geographical calibration points.

Our ‘BioGeoBears’ historical biogeography analyses suggest that the subfamily originated in Australia during the Late Cretaceous, which was still connected to Antarctica (Fig. 3a). Subsequently one lineage underwent diversification in Australia (Eurepini) (Fig. 3a, orange arrow), whereas the second one colonized South America through the trans-Antarctic route (Fig. 3b, green arrow: genus *Eneoptera*, nowadays distributed in the north of South America). This ‘out-of-Australia pattern’ through the TAN has been also inferred in other insect groups such as colletid bees (Almeida *et al.*, 2012) or fig wasps (Cruaud *et al.*, 2011). In colletid bees, the initial diversification of Australian and South American lineages also occurred in the Late Cretaceous (Almeida *et al.*, 2012), when Antarctica, Australia and South America started breaking up (c. 90 Ma; McLoughlin, 2001; Sanmartín & Ronquist, 2004). As many as 14 trans-Antarctic interchanges were recovered between Australia and South America, suggesting a dynamic pattern in which vicariance events possibly had a pivotal role in explaining the current disjunct ranges of colletid bees (Almeida *et al.*, 2012). As a word of caution, it is also worth highlighting that analyses with the DEC model alone inferred a basal vicariance event between Australia

(a) Late cretaceous (105-66 Ma)

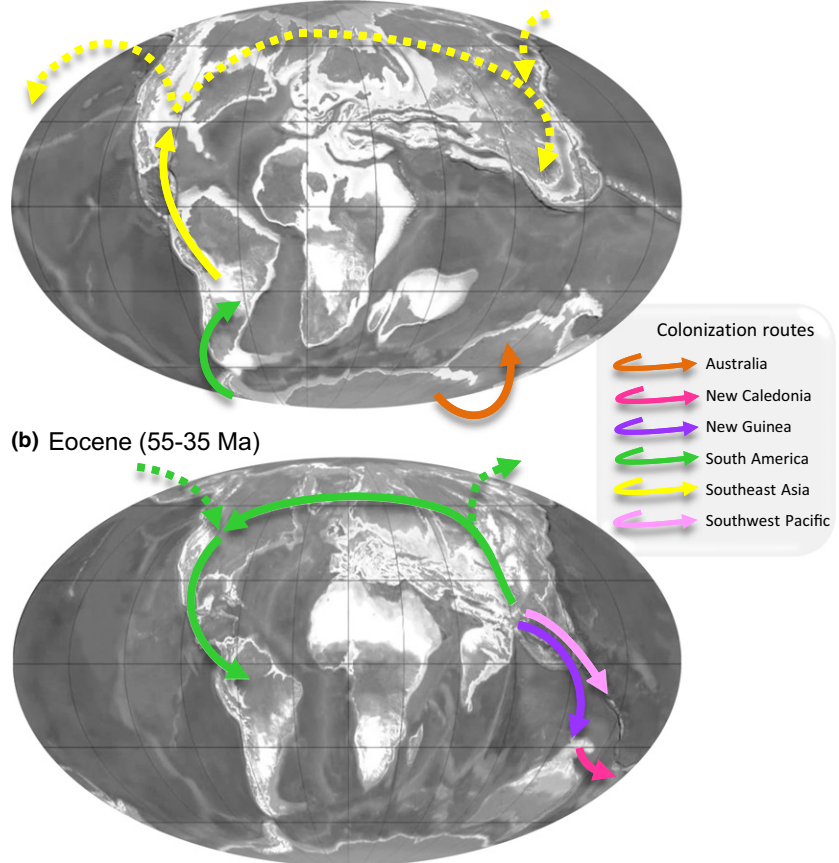


Figure 3 Biogeographical reconstruction for Eneopterinae. (a) Focus on events occurring in the late Cretaceous: divergence of two lineages, one colonizing Australia, the second colonizing the Western Hemisphere through South America. (b) Focus on events occurring during the Eocene: second colonization of South America from the boreotropics, colonization of New Caledonia through New Guinea and newly formed islands of Southwest Pacific and Southeast Asia. Coloured arrows according to the colonized area (colour coding as that in Fig. 2). Dotted arrows represent alternative scenarios as discussed in text. Palaeogeographical maps reconstructed from Blakey (2008) available at <http://cpgeosystems.com/globaltext2.html>. [Colour figure can be viewed at wileyonlinelibrary.com]

(i.e. +Antarctica) and South America, a hypothesis that should not be dismissed because the DEC+J model does not favour widespread ancestors contrary to the DEC model (Matzke, 2014).

The Western Hemisphere (SE Asia, tribe Nisitrini) was, thereafter, colonized during Early Palaeocene (67 Ma), through a northern route of colonization (Fig. 1, North America connection), either through a trans-Atlantic pathway or through the Bering Strait (Fig. 3a, yellow arrows), even if the latter scenario is less likely, as suggested by Sanmartín *et al.* (2001). Our results suggest that the subsequent recolonization of South America by Eneopterinae during the Eocene (40 Ma), corresponding to the lineage (*Ligypterus*+*Ponca*), could have followed the same northern route as the colonization of Asia from South America, but from east to west (Fig. 3b, green arrows). Considering that most of the Holarctic region had a tropical climate during this period (Morley, 2007), both the colonization of SE Asia and later the recolonization of South America may have been greatly facilitated through the likely persistence of northern lineages in the Boreotropical region, which are now extinct. This second colonization event, thus, constitutes a case of parallel Boreotropical migration from north to south (Sanmartín *et al.*, 2001). A large number of plant families support the Boreotropics hypothesis (see the review of Christenhusz & Chase, 2013). Although Boreotropical migration is rarely

investigated in animal groups (but see Hines, 2008; Condamine *et al.*, 2013; Van Damme & Sinev, 2013), we suggest that this large green belt played a crucial role in Eneopterinae dispersal during Eocene as well.

In parallel, the dispersal of ancestral *Swezwilderia* from SE Asia towards islands of the southwest Pacific (Fiji, Samoa) (Fig. 3b; Appendix S18) was probably due to ocean drift, since these islands were not connected to landmasses and were formed only during the Late Eocene-Oligocene (Neall & Trewick, 2008). The biodiversity of islands that were not formed by the fragmentation of continental landmasses depends fundamentally on dispersal. According to Gillespie *et al.* (2012), the major vectors for such LDD in the Pacific are wind, ocean drift and birds. It is likely that wind patterns, storms and oceanic drift may have played important roles in the dispersal of crickets through the Pacific region.

New Caledonia has a complex geological history (Grandcolas *et al.*, 2008). Together with New Zealand, it separated from the Gondwana block very early during the late Cretaceous *c.* 80 Ma (Sanmartín & Ronquist, 2004). From the end of the Cretaceous to the mid-Cenozoic, New Caledonia was, however, under water, emerging only 37 Ma (Grandcolas *et al.*, 2008; Pillon, 2012). New Guinea was a source area of dispersal of crickets to New Caledonia, as also suggested for other groups (Sanmartín & Ronquist, 2004; Pillon, 2012; Swenson *et al.*, 2014). Thus, the ancestor of the endemic

genera *Agnotecous* and *Pixibinthus* arrived in New Caledonia c. 31 Ma, diverging from the New Guinea lineage (*Centuriarus*+*Gnominthus*) and giving rise to a highly diverse group both ecologically and acoustically (Anso *et al.*, 2016).

To summarize, our study provides more statistical support to a scenario where South America was colonized twice through the TAN and NAC (Fig. 1), although a scenario with an initial vicariance is also possible. Extant eneopterines are not found in New Zealand, which is inconsistent with TP, while phylogenetic relationships between African and Neotropical lineages are inconsistent with TAC.

Multiple colonizations of Eneopterinae in South America but lack of diversity

According to the best-fit model (DEC+J), Eneopterinae colonized South America twice independently (Fig. 3). The early divergence of the lineage leading to extant representatives of *Eneoptera* (70 Ma) suggests a history of dispersal from Australia (Antarctica) to South America, through the Drake Passage. However, the hypothesis of an alternative vicariance event associated with a widespread ancestor could not be completely excluded here. Because this lineage now encompasses only a few species that are currently distributed in the northern part of South America, we postulate that this lineage has experienced several episodes of extinction in the past, as suggested by the long branch leading to the crown of the genus. Despite its rather old age, this lineage is poorly diversified compared with other Neotropical cricket lineages (Robillard & Desutter-Grandcolas, 2005). The absence of this lineage in the southern part of South America could be explained by contraction of its distribution due to climatic factors, given that all extant eneopterines live in or near tropical rain forest. However, there is today no explanation of the marginal distribution of this lineage in Central America and its absence in the Caribbean. It is unlikely that the position of *Eneoptera* could be an artefact of long-branch attraction, as it is recovered both in ML and Bayesian analyses.

The northern Andean uplift (c. 23 Ma) marks the beginning of the divergence within *Eneoptera*. This geological event played an important role in the landscape and biota of northern part of South America, including Amazonia (Hoorn *et al.*, 2010). Subsequent influx of sediments into the Amazonian basin created different aquatic environments in the Amazonian landscape. In fact, the pollen records suggest the presence of rain forest combined with grasslands and/or floating meadows (Hoorn *et al.*, 2010). This new environment contributed to increase the local diversity, but the subsequent decline of wetlands isolated populations and resulted in diversification of aquatic invertebrates (Wesselingh *et al.*, 2002), amphibians (Fouquet *et al.*, 2014), mammals (Matauschek *et al.*, 2011) and reptiles (Salas-Gismondi *et al.*, 2015).

The mid-Miocene optimum (17–15 Ma) was an episode marked by a wet period followed by abrupt changes of temperature. These rapid environmental changes may have led

to forest expansions and contractions, isolating forest-adapted species during the contraction periods (Fouquet *et al.*, 2014). Both the northern Andean uplift and the mid-Miocene optimum could have markedly affected *Eneoptera*-related lineages.

Habitat fragmentation and exposure to new environments likely resulted in sister taxa occupying contrasting habitats (Damasceno *et al.*, 2014). Within *Eneoptera*, *E. gracilis*, *E. guyanensis* and *E. nigripedis* occupy restricted forested areas, while *E. surinamensis* presents a wide distribution encompassing open habitats in the entire northern half of South America and part of Central America (Robillard & Desutter-Grandcolas, 2005) (Fig. 1). The forest expansions and retractions induced by Andean uplift and the mid-Miocene climatic optimum probably exposed the species of *Eneoptera* to different habitat conditions, leading to the divergence of a clade adapted to open and secondary habitats.

The second colonization of South America by Eneopterinae occurred c. 48 Ma with the divergence of the clade [*Swezwilderia* (*Ligypterus*+*Ponca*)] from the rest of the Lebinthini. Once in South America, the divergence between *Ligypterus* and *Ponca* matches the uplift of Central Andes (Hoorn *et al.*, 2010). The beginning of the divergence within *Ligypterus* could also be a result of abrupt increase of temperature subsequent to the mid-Miocene climatic optimum (15 Ma), followed by a gradual cooling until 10 Ma (Poulin *et al.*, 2002). Nowadays, this genus is mainly distributed in the southeastern coastal Brazil, but a few species and populations occur in the Amazon forest, in French Guiana and near Manaus, but remain largely unstudied in many locations.

CONCLUSION

In this study, we provided a worldwide-dated biogeographical model for the Eneopterinae crickets. Our results are congruent with general predictions proposed for the evolution of groups with disjunct distributions (Sanmartín & Ronquist, 2004). However, the subsequent patterns, including a widespread distribution along Southeast Asia and Pacific Islands, do not fit with usual Gondwana-group distribution. Instead, it suggests that the current disjunct distribution of these crickets mostly results from dispersal, with a questionable early event that could correspond to either dispersal or vicariance according to the tested biogeographical model. Our results also indicate a Boreotropical dispersal route for Eneopterinae, corroborating suggestions that it was also a corridor for animals. High-frequency songs are a putative acoustic innovation in eneopterines (Robillard & Desutter-Grandcolas, 2004b), which have led to new modalities of communication (ter Hofstede *et al.*, 2015). However, the initial circumstances that promoted their origin have been difficult to pinpoint given the lack of dated phylogenetic and biogeographical information. This study provides a first step towards when and where these acoustic innovations originated and will hopefully foster new directions for future multidisciplinary studies.

ACKNOWLEDGEMENTS

We thank both editors for their handling of the manuscript, and three anonymous referees for their comments and suggestions. We thank A. Nel for his help finding the documentation about fossils, L. Desutter-Grandcolas for her help selecting outgroup species and corresponding DNA sequences used in this study, F. de Assis Ganezo de Mello for providing some of the Neotropical samples, A. Gorochoff for providing some of the Xenogryllini samples and A. Dehne Garcia for his help on the CBGP HPC computational facility. This research was partly funded by CNPq – Brazil, PROTAX [158726/2013-8] and CAPES; PDSE – [BEX 2609/14-2] and benefitted from financial support provided by CNPq and FAPEMIG, Process N. 563360/2010-0, Edital N. 47/2010, SIS-BIOTA Brazil. The laboratory work was carried in the Service de Systématique moléculaire (SSM, UMS 2700 CNRS) of the MNHN: we thank M.C. Boisselier, C. Bonillo, D. Gey and J. Lambourdière for their help in data acquisition. This work was partly supported by agreement no. 2005/67 between the Genoscope (Evry, France) and the MNHN project ‘Macrophylogeny of life’; sequencing was also undertaken in the project @SpeedID proposed by F-BoL, the French Barcode of life initiative and the network ‘Bibliothèque du vivant’ funded by the CNRS, INRA and MNHN. The laboratory procedures were partly realised through Action Transversale du Muséum (ATM-MNHN) ‘Biodiversité actuelle et fossile’ and ATM ‘Barcode’. The samples from Papua New Guinea were obtained in the framework of ‘Our Planet Reviewed Papua-New-Guinea 2012-2013’ set up by Pro-Natura International, MNHN and IRD in partnership with the Royal Belgian Institute of Natural Sciences, the New Guinea Binatang Research Center, the University of Papua New Guinea, and the Divine Word University of Madang and with core funding of Prince Albert II of Monaco Foundation, the Stavros Niarchos Foundation, the Total Foundation, the Fondation d’entreprise EDF, the Fonds Pacifique, Spiecapag, Entrepose Contracting, the New Caledonia Government, the Reef Foundation and the Belgian National Lottery.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Appendix S1** Taxon sampling.
- Appendix S2** Details about fossil calibration.
- Appendix S3** Results of PARTITIONFINDER analyses.
- Appendix S4** Bayes factors.
- Appendix S5** Rates of evolution.
- Appendix S6** Palaeogeographical model.
- Appendix S7** Bayesian inference tree.
- Appendix S8** Maximum likelihood tree.
- Appendices S9–S16** Time trees (alternative calibration procedures).
- Appendix S17** Historical biogeography of Eneopterinae (DEC).
- Appendix S18** Major colonization routes of Eneopterinae.

DATA ACCESSIBILITY

All newly generated sequences were deposited in GenBank (Appendix S1).

Natallia Vicente is a research scientist interested in biodiversity distribution patterns, cryptic species and systematics.

Author contributions: N.V., T.R. initiated the study; N.V., T.R., G.J.K. designed the study; T.R. coordinated permits and collection sites; T.R., N.V., F.L. collected field samples; N.V., T.R., J.D., R.N. produced molecular data; N.V., T.R., J.D., G.J.K. analysed molecular data; N.V., T.R., K.Y. drafted the initial manuscript; N.V., T.R., K.Y., G.J.K., R.N., F.L. contributed to write the article.