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Evolution of Pacific Rim diving beetles sheds light on Amphi-Pacific biogeography

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The origin of biodiversity in the Neotropics predominantly stems either from Gondwana breakup or late dispersal events from the Nearctic region. Here, we investigate the biogeography of a diving beetle clade whose distribution encompasses parts of the Oriental region, the Indo-Australian archipelago (IAA) and the Neotropics. We reconstructed a dated molecular phylogeny, inferred diversification dynamics and estimated ancestral areas under different biogeographic assumptions. For the Oriental region and the IAA, we reveal repeated and complex colonization patterns out of Australia, across the major biogeographic lines in the region (e.g. Wallace's Line). The timing of colonization events across the IAA broadly coincides with the proposed timing of the formation of major geographic features in the region. Our phylogenetic hypothesis recovers Neotropical species nested in two derived clades. We recover an origin of the group in the early Eocene about 55 million yr ago, long after the break-up of Gondwana initiated, but before a complete separation of Australia, Antarctica and the Neotropics. When allowing an old Gondwanan ancestor, we reconstruct an intricate pattern of Gondwanan vicariance and trans-Pacific long-distance dispersal from Australia toward the Neotropics. When restricting the ancestral range to more plausible geological area combinations in the Eocene, we infer an Australian origin with two trans-Pacific long-distance dispersal events toward the Neotropics. Our results support on one hand a potential Gondwanan signature associated with regional extinctions in the Cenozoic and with Antarctica serving as a link between Australia and the Neotropics. On the other hand, they also support a trans-Pacific dispersal of these beetles toward the Andean coast in the Oligocene.

Explaining the origin and distribution of clades across Earth is a major theme of evolutionary biology (Lomolino et al. 2010). Extant ranges of species separated by oceanic barriers were traditionally explained by dispersal events (Darwin 1859, Wallace 1876, Rosen 1978, Nelson and Platnick 1981). After Wegener's theory of plate tectonics (Wegener 1912) gained more and more acceptance in the second half of the 20th century, and the emergence of cladistics, there has been a paradigm shift (Morrone and Crisci 1995). Reconstructing phylogenetic relationships among taxa in a paleogeological context has been a major contribution to the vicariance-dispersal debate. For example, contemporary transoceanic disjunctions could now be explained by separating landmasses that used to be one (Wiley 1988).

The advent and widespread use of molecular phylogenetics also brought the concept of the molecular clock, introducing a timeframe for the evolution of clades across the tree of life (Smith and Peterson 2002). Subsequently, dispersalism has experienced a renaissance as many cases have been found in which inferred divergence times were inconsistent with the proposed timing of continental plate breakup (de Queiroz 2005, Heaney 2007). In this regard, the recent introduction of model based methods of historical biogeography pattern inference represents a major step forward in the vicariance/dispersal debate as these allow the testing of competing hypotheses in a statistical framework (Ree et al. 2005, Ree and Smith 2008, Yu et al. 2010, Landis et al. 2013, Matzke 2013, 2014). However, there are also examples of clades with clear signatures of vicariance that are consistent with molecular clock estimates (Lomolino et al. 2010).

In this context, one striking study system are tropical Amphi-Pacific disjunctions where organisms have ranges in the Neotropical region as well as in the Indo-Australian archipelago (IAA) or beyond (review by Van Damme and Sinev 2013). Such a pattern can be explained by several principle mechanisms, e.g. relics of ancestral Gondwanan or even Pangean distribution (Halling et al. 2008, also in part Van Damme and Sinev 2013); dispersal via a northern route (Beringia) and extinction across east Asia and the Nearctic; and finally long distance dispersal across the Pacific Ocean.

Only a few documented cases of Amphi-Pacific distributed clades have been studied in a phylogenetic context, shedding some light on the biogeographic mechanisms at work.

The Beringian route has been inferred as a colonization pathway out of the Neotropics towards the IAA ca 74 million yr ago (Ma) for Riodinidae butterflies, strikingly with back colonization ca 35 Ma (Espeland et al. 2015). Townsend et al. (2011) suggest a possible Late Palaeocene to Eocene Beringian route to explain the presence of burrowing reptiles in the Dibamidae in south east Asia as well as in the eastern coast of Mexico, similar to the results and timing of Chen et al. (2013) on Asian and Neotropical hinged-teeth snakes.

Van Damme and Sinev (2013, p. 231) suggest that the Amphi-Pacific pattern in some Cladocera Crustacea might be a case of boreotropical migration, organisms formerly widespread in the tropical belt before its regression towards the equator: '*Leydigiopsis* was never present in Africa, Madagascar or south India. In fact, it was widespread in the former tropical belt during the Cenozoic, i.e. the boreotropics that stretched continuously between North America and Europe/Asia until the Oligocene–Miocene. After that time the lineage became fragmented while being pushed southwards, and disjunct between Indochina/Assam and South America.'

Few recent studies have shown Amphi-Pacific clades with divergence time estimates postdating the breakup of Gondwana and then invoke transoceanic long distance dispersal (LDD). In the pantropical fern genus *Diplazium* (Athyriaceae), Wei et al. (2015) suggest one such case to explain an Australian/Neotropical disjunction. The New Caledonian kagu bird and its closest relative, the Neotropical sunbittern are such a case among vertebrates (Hackett et al. 2008). In the notoriously understudied invertebrates, only the Zalmoxidae harvestmen apparently colonized the IAA via LDD from the Neotropics (Sharma and Giribet 2012).

Here, we investigate the evolutionary history of a clade of diving beetles distributed on each side of the Pacific Ocean (Fig. 1). The tribe Hydrotrupini (Coleoptera, Dytiscidae,

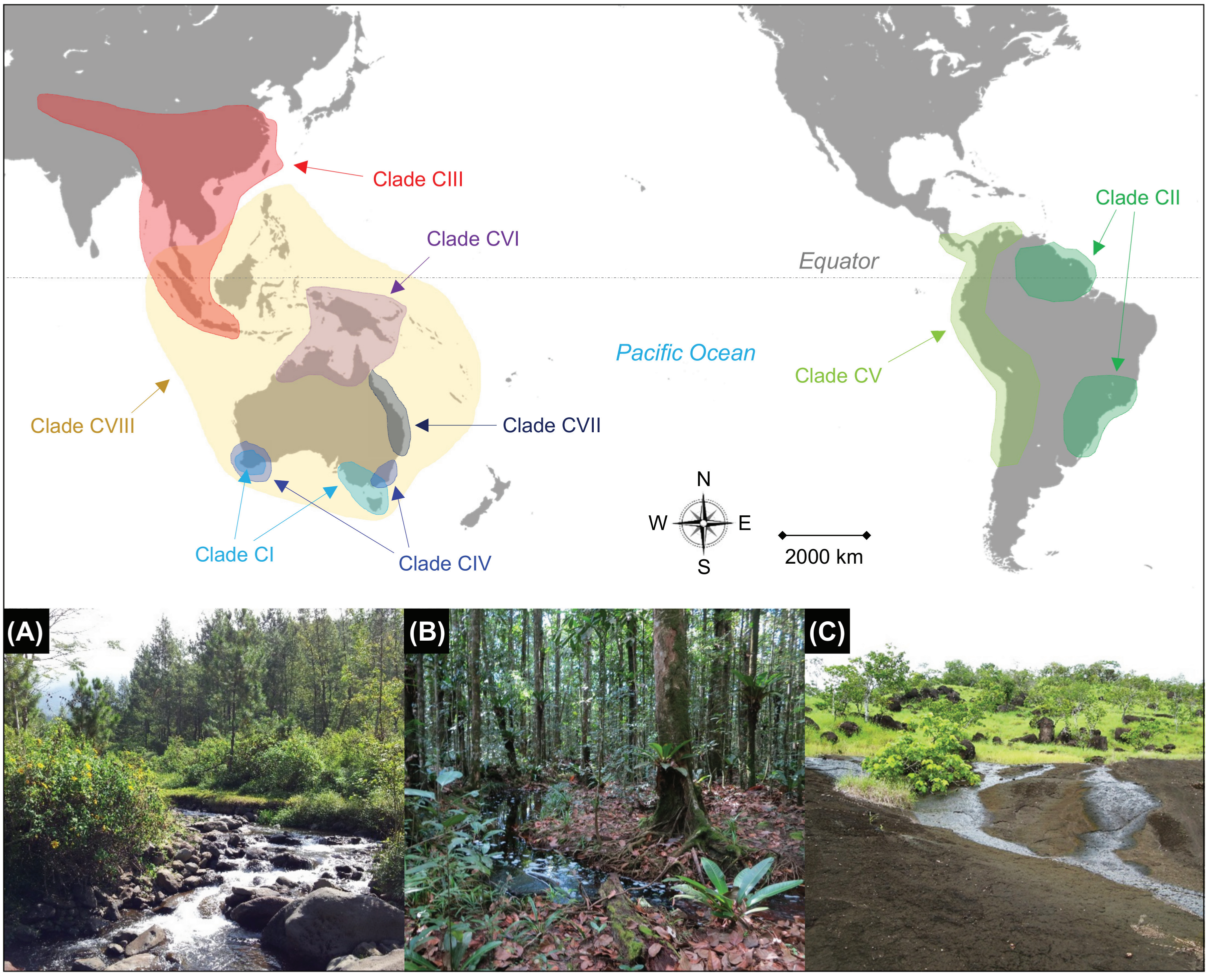

Figure 1. Geographical ranges of the different clades of Platynectini recovered in this study. Map showing the Amphi-Pacific distribution of the different clades found in the tribe Platynectini as inferred from the phylogenetic reconstructions in this study (Fig. 2). The different clades are annotated and colored correspondingly. At the bottom of the figure, the three panels show habitat images. The image in panel (A) shows a typical habitat of *Platynectes* in lotic ecosystems in east Java. In this region, as in most of the IAA (except certain lentic Australian species), *Platynectes* species can be found along river margins in sand banks and where the current is slower. The image in panel (B) shows a typical habitat in Suriname with a small forest stream and dense aquatic vegetation where the beetles dwell. The image in panel (C) shows a typical seepage habitat in Venezuela where certain *Platynectes* diving beetles from clade CII are found in the northern Neotropics.

Agabinae) comprises five genera of aquatic beetles. The largest genus *Platynectes* (ca 50–60 species) has an Amphi-Pacific distribution. Indo-Australian *Platynectes* diving beetles belong to the few truly lotic lineages of the family across that region, although a few Australian species of the genus are lentic. They can be very abundant and their species richness and wide range in the region across major biogeographic lines made them an appealing taxon for biogeographic studies, in particular to test the validity of biogeographic lines for these organisms. A few species are in the east Palearctic, China and some follow the Himalayas west to Kashmir. The genus also comprises Neotropical species predominately on the eastern side of the continent in the Guiana Shield and Brazil. The smaller genera *Agametrus* (7 described spp.), *Andonectes* (14 spp., most of which could be synonyms of one species) and *Leuronectes* (5 spp.) are exclusively Neotropical with a distribution concentrated along the west coast of South America, especially in the Andean region. The Neotropical representatives are less abundant then their Old World counterparts. Most of these Central and South American species occupy stream and creek margins, with a few species restricted to hygropetric seepages. Finally, the genus *Hydrotrupes* has two extant, hygropetric species respectively found in China and the southwest coast of the USA whose relationship with the rest of the subfamily Agabinae are not fully understood. One of the two species was recovered as sister to the *Platynectes* group (all other genera) which was then referred to as Hydrotrupini (Miller and Bergsten 2014).

Here, we aim to 1) reconstruct the phylogenetic relationships of the tribe Hydrotrupini using a comprehensive molecular matrix; 2) infer divergence time estimates using a fossil-based molecular approach; 3) conduct ancestral state estimation to study the biogeography of these beetles specifically in the IAA; 4) test the hypothesis of trans-Pacific LDD using a set of maximum-likelihood model-based approaches; and 5) infer diversification dynamics to test for possible extinction in a Gondwanan setting or if the colonization of a new continental landmass triggered higher diversification rates during the evolution of the group.

Material and methods

Taxon sampling and molecular biology

We assembled a comprehensive dataset with 71 species covering *Agametrus*, *Leuronectes*, *Platynectes* and *Hydrotrupes* across their entire ranges where possible (Supplementary material Appendix 1, Table A1). The rare Hydrotrupini genus *Andonectes* was not available. It was established based on the lack of metacoxal lines which is a highly homoplastic character (Balke et al. 1997) and we suspect *Andonectes* is in fact a clade within *Platynectes* just as we here show is the case for *Agametrus* and *Leuronectes* (see Results). We included representatives of multiple other genera of the subfamily Agabinae as well as *Carabdytes upin* to root the tree (Colymbetinae), based on the most recent phylogenetic hypothesis for the family Dytiscidae (Miller and Bergsten 2014). Total genomic DNA was extracted from whole beetles kept in 96% ethanol using the DNeasy kit (Qiagen, Hilden, Germany). All vouchers were deposited at the Bavarian State Collection of Zoology (ZSM, Munich, Germany). We used the PCR protocols listed in Supplementary material Appendix 1, Table A2 to amplify and sequence the following gene fragments: cytochrome oxidase subunit 1 (Co1, 750 bp), cytochrome b (Cytb, 339 bp), arginine kinase (Ark, 687 bp), histone 3 (H3, 276 bp), histone 4 (H4, 153 bp) and RNA polymerase 2 (Rnp2, 669 bp). The DNA sequences were edited in Geneious R 8.0.5 (Biomatters, <www.geneious.com/>), aligned using Muscle (Edgar 2004) and the reading frames checked in Mesquite 3.0.2 (<http://mesquiteproject.org>). New sequences were deposited in GenBank (accession no. LN998260–LN998639).

Molecular phylogenetics

We used Bayesian inference (BI) to reconstruct phylogenetic relationships using a concatenated dataset. The partitions and corresponding optimal models of substitution were searched with PartitionFinder 1.1.1 (Lanfear et al. 2012) using the ‘kmeans’ algorithm (Frandsen et al. 2015) to partition the entire alignment in subsets without a priori division of the data. This method uses k-means clustering to iteratively divide the alignment in subsets of sites that share similar rates of evolution. The site rates of evolution are calculated using the program Tree Independent Generation of Evolutionary Rates (TIGER, Cummins and McInerney 2011). The Akaike information criterion corrected (AICc) was used to compare the fit of the different models of substitution. The BI analyses were performed using MrBayes 3.2.3 (Ronquist et al. 2012). Two simultaneous and independent runs consisting of eight MCMC (one cold and seven incrementally heated) chains running 30 million generations were used, with a tree sampling every 1000 generations to calculate posterior probabilities (PP). We assessed convergence of the runs by investigating the average standard deviation of split frequencies and effective sample size (ESS) of all parameters in Tracer 1.5 (<http://BEAST.bio.ed.ac.uk/Tracer>). A value of ESS $>$ 200 was acknowledged as a good indicator of convergence. All posterior trees that predated the time needed to reach a log-likelihood plateau were discarded as burn-in, and the remaining samples were summarized to generate a 50% majority rule consensus tree.

We also used IQ-TREE (Nguyen et al. 2015) as implemented on the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at/>) to crosscheck the results of the MrBayes analysis in a maximum likelihood (ML) framework. The concatenated dataset was left unpartitioned and the best-fit model of substitution was searched using the ‘Auto’ function on the IQ-TREE web server based on the AICc. We performed 1000 ultrafast bootstrap replicates (Minh et al. 2013) to investigate nodal support across the topology.

Divergence time estimation

Divergence times were inferred with BEAST 1.8.2 (Drummond et al. 2012). We partitioned the dataset by gene with all substitution models unlinked. The clock models were unlinked except for the mitochondrial genes. The partitions and models of nucleotide substitution were selected under PartitionFinder 1.1.1 (Lanfear et al. 2012) using the 'greedy' algorithm, the 'beast' set of models and the AICc. The molecular clock test was performed in MEGA6 (Tamura et al. 2013) by comparing the ML value of the MrBayes topology with and without the molecular clock constraints under the Tamura–Nei model. The null hypothesis of equal evolutionary rate throughout the tree was rejected at a 5% significance level ($p = 0$). Therefore we used a Bayesian relaxed clock approach as implemented in BEAST 1.8.2. We assigned a lognormal relaxed clock with uncorrelated rates to each clock model. The 'Tree Model' was set to 'Speciation: Birth-Death Process'.

In order to calibrate the tree, we used two fossils of Agabinae. †*Agabus florissantensis* (Wickham 1913) from the Florissant Formation (~ 33.9 Ma) and †*Hydrotrupes prometheus* (Gómez and Damgaard 2014) from Baltic amber were respectively used to constrain the stem of the extant genera *Agabus* and *Hydrotrupes*. The calibrations were not implemented at the crowns as no morphological evidence supports the inclusion of the two fossils within the sampled species groups. The fossil *Hydrotrupes* is however morphologically almost identical to the two extant species and should unambiguously place in the stem line of these (Gómez and Damgaard 2014). Based on stratigraphy (Kosmowska-Ceranowicz and Müller 1985) and K-Ar radiometry (Ritzkowski 1997), Baltic amber is dated from the mid-Lutetian about 44.0 Ma (Engel 2001). We enforced the two minimum constraints with either uniform or exponential distributions going from the age of the fossil to 150 million yr (Myr), an age equivalent to the oldest dytiscid fossil known, †*Palaeodytes gutta* (Ponomarenko 1987). The exponential prior parameters for the *Agabus* and *Hydrotrupes* fossils were respectively as follow; offset = 33.1/43.27 and mean = 31.7/28.92. The runs consisted of 50 million generations sampled every 5000 generations. The convergence of the runs was investigated using ESS, a burn-in of 10% applied after checking the log-likelihood curves and the different runs merged using LogCombiner 1.8.2 (Drummond et al. 2012). The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated afterwards under TreeAnnotator 1.8.2 (Drummond et al. 2012).

Ancestral range estimation

Since *Hydrotrupes* was recovered as sister to Agabini (see Results), we did not include it in the biogeographic or diversification analyses. Instead, we pruned the BEAST chronogram in order to keep only the *Platynectes*-group (all genera within Hydrotrupini except for *Hydrotrupes*). We used BioGeoBEARS (Matzke 2013) as implemented in R to infer the biogeographical history of the *Platynectes*-group across its entire range of distribution. This program implements a parameter describing founder-event speciation (+ j) likely important in oceanic settings (Matzke 2014) and allows the comparison of different models in a statistical framework. We ran and compared different analyses under the DEC (Ree et al. 2005, Ree and Smith 2008) and DIVA (Ronquist 1997) models with or without the + j parameter. The analyses were carried out based on the BEAST maximum clade credibility (MCC) trees from the uniform and exponential prior analyses with outgroups removed. We used the following regions in the analyses: A, Australia; N, New Guinea; O, Oriental; P, Solomons and Vanuatu; T, Neotropics; W, Wallacea. In order to account for the complex assemblage of the Indo-Australian archipelago in the Miocene, we designed two time slices; T1 encompassing the period from the origin of the group about 55 Ma until 20 Ma, and T2 encompassing the remaining 20 Myr when the Asian and Australian plates collided, resulting in a biotic interchange. The dispersal rate (dr) matrices of T1 and T2 were designed based on paleogeographic (Hall 2002, 2012a, b, 2013) evidence. Adjacent areas had a dr = 1.0, areas separated by one area a dr = 0.5, areas separated by two areas a dr = 0.25 and areas separated by a large oceanic barrier a dr = 0.1. Since New Guinea nor the Pacific or Wallacean Islands were yet emerged/present, or each had a reduced proportion of emerged terrains in T1, the dispersal rates toward and from these areas were restricted to 0.1 in this time slice. We constrained the maximum number of ancestral areas at a node to three.

In order to test the origin of the Neotropical biota in the *Platynectes*-group, we used two different biogeographic models. The first model, referred to as 'Gondwanan model', allowed all area combinations except with the Oriental region. Area combinations that included the Oriental region were disallowed in the first time slice as this region belonged to Laurasia, a Pangean fragment that drifted apart from Gondwana more than 150 Ma, an age older than the oldest dytiscid fossil ever found. Although India and Sri Lanka remained attached to Gondwana after this split, they fully detached from Antarctica and Australia between 110 and 120 Ma (Gibbons et al. 2013), an age almost twice older than the origin of the entire subfamily Agabinae as recovered in our dating analyses. In the second biogeographic model referred to as 'constrained model', we disallowed ancestral areas that were implausible with respect to the timeframe and geological arrangement of continental landmasses. As a result, we only allowed combinations of adjacent areas (e.g. Australia + Neotropics was disallowed whereas Australia + New Guinea was allowed).

Diversification analyses

We used the program R with the BEAST MCC tree from which we pruned all outgroups including *Hydrotrupes* (see Results) to investigate the diversification pattern of the *Platynectes*-group in a temporal framework whilst accounting for missing taxon sampling. We were specifically aiming at highlighting potential diversification shifts that might support a Beringian scenario with dispersal followed by extensive regional extinction in the Nearctic and Palearctic.

First, we used the package 'TreePar' (Stadler 2011) to estimate the potential shifts in speciation and extinction rates in the whole phylogeny through the function 'bd.shifts.optim'. This function uses the empirical branching times from the MCC tree as an input and fits several birth-death models including 0 (constant-rate model) to several diversification rate shifts during the lineage evolution. We tested different models ranging from 0 to 3 rate shifts. All the analyses were carried out with the following non-default settings: taxon sampling was set to 71/115 (the extant diversity of the

Platynectes-group in addition to the number of undescribed species included in this study), start = 0, end = 55 and grid = 0.1 Myr for a fine-scale estimation of rate shifts. The missing species were randomly placed in the tree as we have no certainty about their actual placement in the different clades of the tree. We calculated AICc scores and computed likelihood ratio tests (LRT) to select the best-fit between the different models allowing incrementally more shifts during the evolution of the clade.

Second, we used the program Bayesian analysis of macroevolutionary mixture (BAMM) to estimate the dynamics of speciation and extinction rates among and within clades throughout the evolution of the group (Rabosky 2014, Rabosky et al. 2014). We conducted the BAMM analyses with four reversible jump MCMC (Huelsenbeck et al. 2004) running for 10 million generations and sampled every 10 000 generations. We used a prior value for the compound Poisson process of 1.0 therefore the null hypothesis was a constant rate across the phylogeny. Missing taxon sampling was taken into account with a sampling fraction set to 0.62 (71 species out of the 115 described species). As in the 'TreePar' analyses, the missing taxon sampling was randomly distributed in the tree. ESS values calculated using the R package CODA (Plummer et al. 2006) were acknowledged as good indicators of convergence when ESS ≥ 200. The BAMM output files were analyzed using the R package BAMMtools (Rabosky et al. 2014). The fit of the different diversification rate shift models was computed using Bayes Factors. The posterior distribution of the BAMM analysis was used to estimate the best configuration and the 95% credible set of distinct diversification models. To do so, a prior only analysis was run independently in BAMM to provide a simulated prior distribution. We also generated a phylorate and a rate through time (RTT) plot in R.

Results

Phylogenetic relationships

The phylogenetic relationships reconstructed under BI and ML among the subfamily were congruent. The only difference was the branching of three *Agabus* species. We recover *Hydrotrupes* as sister to all Palearctic Agabini. The *Platynectes*-group (Hydrotrupini without *Hydrotrupes*) was monophyletic with moderate to strong support ($BI_{PP} = 0.89$, $ML_{BS} = 99$). However, the genera within the *Platynectes*-group were not monophyletic. *Platynectes* was paraphyletic due to the inclusion of *Agametrus* and *Leuronectes*.

We reveal strong geographic structure, in a succession of clades from different biogeographic regions with an Australian clade (CI, south west and south Australia and Tasmania, Fig. 1) as sister to the rest of the species (Fig. 2). There are two Neotropical clades (CII and CV, Fig. 1). All Neotropical *Platynectes* from the Guiana Shield were in the older clade CII whereas the genera *Agametrus* and *Leuronectes* from the Andes are found mixed in the more recent clade CV (Fig. 1 and 2). Clade CIII is Oriental with some species towards northern China and in the Himalayas (Fig. 1). Clade CIV is in south west and south Australia; clade CV southern Neotropical, clade CVI northern Australia and New Guinea, CVII northern east coast of Australia and CVIII most widely distributed (Fig. 1). It has species in the south east part of the Oriental region such as the Philippines, Peninsula Malaysia, Sumatra and Java, then in Wallacea, New Guinea, Solomon Islands, Vanuatu and across Australia including Tasmania.

Taxonomy

Our results unambiguously support the following nomenclatural acts:

genus *Platynectes* Régimbart, 1879
subgenus *Agametrus* Sharp, 1882, new status
Leuronectes Sharp, 1882, new synonymy

For the tribal classification, we conserve the tribal name Hydrotrupini but only containing the genus *Hydrotrupes*, as the sister of Agabini, and erect the new tribe Platynectini Toussaint & Balke, new tribe for *Platynectes* (and possibly *Andonectes*). Our results also suggest several of the existing subgenera within *Platynectes* are not reciprocally monophyletic. However, realignment of the internal classification of the genus is better left to a comprehensive morphological review and beyond the scope of this paper.

Divergence time estimates

Our BEAST analyses using either uniform or exponential priors to model the distribution of fossil calibrations produced highly congruent results (Fig. 2, 3). The analyses based on uniform priors yielded slightly wider credibility intervals toward the past. Both analyses recover the origin of Platynectini about 50 Ma in the Eocene. The four first clades respectively restricted to Australia, the Neotropics, the Oriental region and Australia have a crown dated from the Miocene (clades CI, CII, CIII and CIV). Neotropical clade CV is found with an origin about the Oligocene–Miocene boundary. Most of the species diversity of the Indo-Australian archipelago is concentrated in clade CVIII, where diversification mainly occurred in the last ca 5 million years.

Ancestral range estimation

Among the different models tested in BioGeoBEARS, the ones including a founder-event speciation parameter (+ j) were significantly supported as a better fit to our data (Table 1). The DEC + j and DIVALIKE + j models had identical log-likelihoods (LnL, Table 1) and supported the same pattern for the constrained analysis (Supplementary material Appendix 1, Fig. A7–A10) but delivered contrasting results in the Gondwanan model (Table 2, Supplementary material Appendix 1, Fig. A3–A6). The analyses conducted on the two different chronograms (uniform versus exponential priors) delivered identical results.

In the constrained model, the analyses recover an origin in Australia followed by a succession of dispersal events towards the Neotropics and Oriental region (Fig. 2, Supplementary material Appendix 1, Fig. A7–A10). A LDD from Australia to the Neotropics is recovered for the clade CII between the

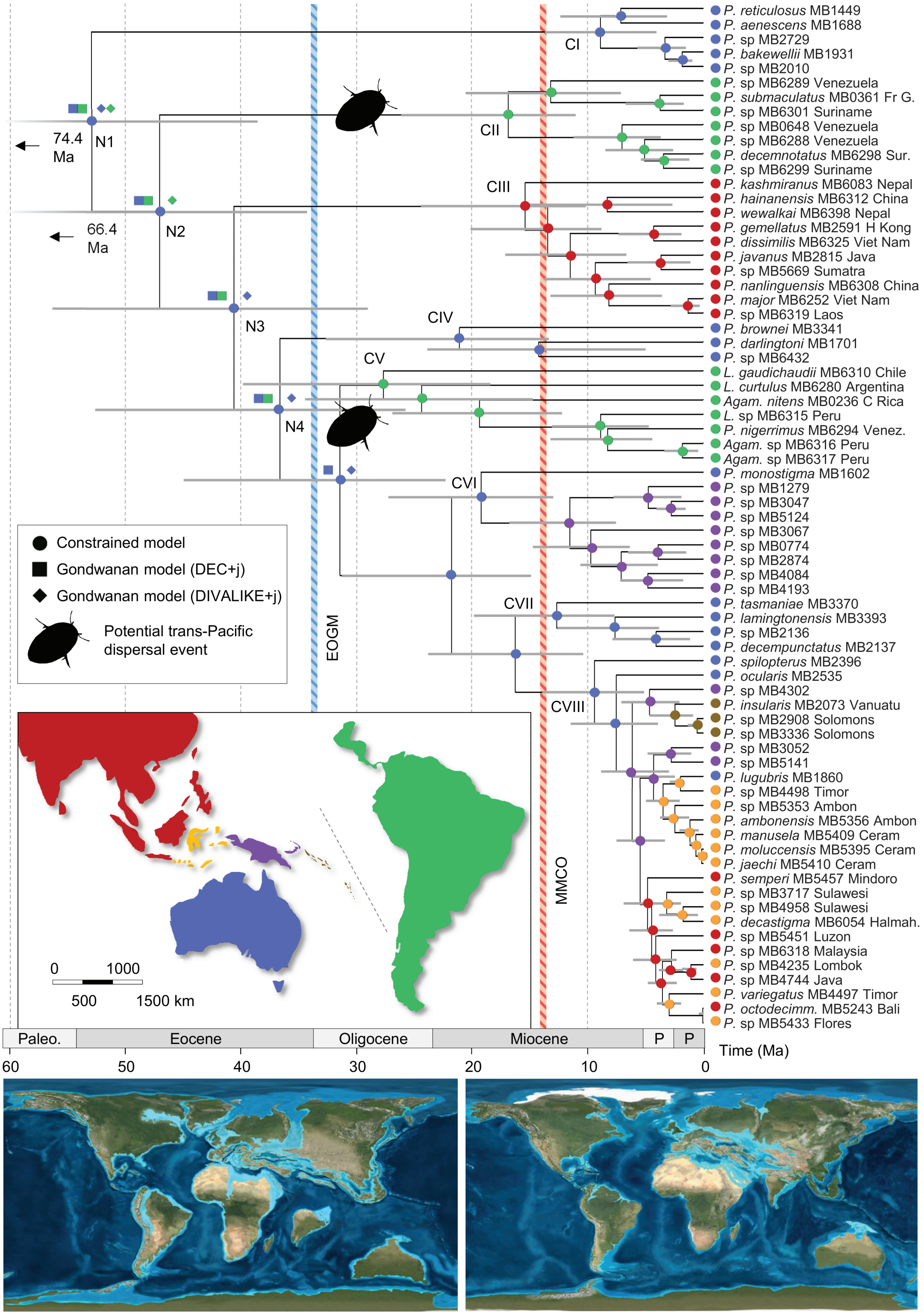

Figure 2. Historical biogeography of Platynectini diving beetles. Chronogram generated in TreeAnnotator based on the BEAST analysis of divergence time inference using exponential priors to model fossil information. The 95% HPD recovered in this analysis are represented as grey bars at each node of the topology. Two colored vertical bars demarcate two major Cenozoic climatic shifts: the Eocene-Oligocene Glacial Maximum (EOGM) and the Mid-Miocene Climatic Optimum (MMCO). Each species of the tribe Platynectini is coded from a biogeographic region corresponding to the map inserted at the bottom left of the figure. The most likely ancestral range (highest relative probability) at each node is shown as recovered from the different BioGeoBEARS analyses (for more details see Supplementary material Appendix 1, Fig. A5, A6, A9, A10). Three symbols are used to show the character state recovered in the different models tested as summarized in the caption inserted on the left side of the figure. At the bottom are presented two paleogeographical reconstructions from Ron Blakey's webpage (<https://www2.nau.edu/rcb7/>). The left one highlights continental assemblages at the Cretaceous–Paleocene (K–P) boundary whereas the right one highlights continental assemblages during the Oligocene.

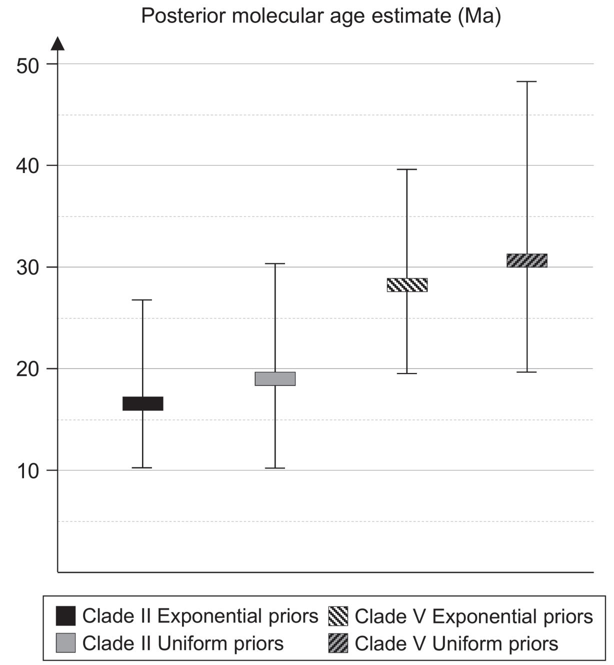

Figure 3. Plots of the divergence time credibility intervals derived from the different BEAST analyses. Detail of the divergence times estimates recovered in the BEAST analyses for the crowns of the two Neotropical clades CII and CV. The boxes indicate the median age estimates recovered when using either exponential or uniform priors to model fossil information in the topology. The 95% HPD are shown using vertical black lines.

late Eocene and the early Miocene. A dispersal event is also recovered during the same timeframe from Australia toward the Oriental region. A second trans-Pacific LDD is recovered for clade CV during the Oligocene. Our estimation suggests that New Guinea was colonized twice from Australia: first in the mid-Miocene, and subsequently in the late Miocene. Some Pacific Islands (the Solomon Islands and Vanuatu) were recently colonized from New Guinea, within the past 5 million years. Wallacean islands such as the Moluccas and Lesser Sunda Islands were colonized during the same period from New Guinea and out of the Oriental region after the latter was colonized by LDD from New Guinea.

In the Gondwanan model, the only differences with the constrained model are restricted to the four first nodes of the backbone annotated N1–N4 in Fig. 2. The DEC + j analysis was favored by the Akaike weights compared to the DIVALIKE + j analysis but since the LnL difference was <2 ($\text{LnL}_{\text{DEC+j}} = -54.10$ vs $\text{LnL}_{\text{DIVALIKE+j}} = -55.89$; Table 2), the hypothesis supported by the DIVALIKE + j model could not be completely ruled out. In the DEC + j model, we recover a combined ancestral area Australia + Neotropics (Fig. 2, Supplementary material Appendix 1, Fig. A3 and A5. This combination is recovered in the three following nodes of the backbone although in the last two the area relative probabilities of the ancestor only slightly differ between Australia and a combination of Australia + Neotropics. The rest of the ancestral areas inferred are identical to the constrained model. As a result, the DEC + j model supports a Gondwanan origin and does not support a long-distance dispersal event toward the Guiana Shield in CII. However, the model supports the second LDD event toward the Andean coast although the area relative probabilities of the ancestor of CV and its sister clade only slightly differ between Australia and a combination of Australia + Neotropics. In the DIVALIKE + j model, we recover a Gondwanan origin Australia + Neotropics at the root followed by a range extinction in Australia. We then infer a LDD event from the Neotropics toward Australia (Supplementary material Appendix 1, Fig. A4 and A6). The LDD event from Australia toward the Andean coast is also supported in this model with a strong relative probability compared to other solutions (Supplementary material Appendix 1, Fig. A6).

Table 1. Results of the BioGeoBEARS analyses assuming a constrained model.

	LnL	np	d	e	j	Akaike weights
DEC	–195.34	2	0.10	0.10	0.00	0.00
DEC + j	–56.80	3	0.00	0.00	0.05	0.50
DIVALIKE	–110.43	2	0.01	0.01	0.00	0.00
DIVALIKE + j	–56.80	3	0.00	0.00	0.05	0.50

Table 2. Results of the BioGeoBEARS analyses assuming a Gondwanan setting.

	LnL	np	d	e	j	Akaike weights
DEC	–183.59	2	0.10	0.10	0.00	0.00
DEC + j	–54.10	3	0.00	0.00	0.04	0.86
DIVALIKE	–82.46	2	0.00	0.00	0.00	0.00
DIVALIKE + j	–55.89	3	0.00	0.00	0.05	0.14

Overall the constrained model strongly supports two LDD events from Australia toward the Guiana Shield and the Andean coast while the Gondwanan model strongly supports a Gondwanan origin of the Guiana Shield species ancestor and supports with moderate to strong support a LDD event from Australia toward the Andean coast (Fig. 2, Supplementary material Appendix 1, Fig. A3–A10). Except for nodes N1–N4, all biogeographic scenarios inferred for the other nodes across the different models are identical (Fig. 2, Supplementary material Appendix 1, Fig. A3–A10).

Diversification analyses

Our TreePar diversification rate analyses conducted in R significantly support a birth-death model with one diversification rate shift as the best model (Table 3). Our likelihood ratio test (LRT) recovered this model as significantly better than the second best model, the Yule model with no diversification rate shift ($\text{LnL}_{\text{BD1shift}} = -227.166$ vs $\text{LnL}_{\text{Yule}} = -231.478$, LRT p-value = 0.035). The best model recovers a shift at the Plio–Pleistocene boundary about 2.7 Ma with an increase in diversification rate. It also recovers a high turnover rate (tr) between the origin of the group and this shift (tr = 0.880) with a diversification rate (dr) three times slower than the one from 2.7 Ma to the present (dr2 = 0.036 vs dr1 = 0.094). Overall our results do not recover an ancient rate shift that could account for post-Beringian dispersal extinction.

The BAMM analyses converged well as indicated by the stationarity of the MCMC and ESS values above 200

Table 3. Results of the TreePar analyses conducted on the BEAST MCC tree.

	LnL	p-value	dr1	tr1	ts1	dr2	tr2	ts2	dr3	tr3	ts3	dr4	tr4
Yule	–231.478	–	0.062	0.695	–	–	–	–	–	–	–	–	–
BD 1 shift	–227.166	0.035	0.094	0.206	2.700	0.036	0.880	–	–	–	–	–	–
BD 2 shifts	–225.928	0.480	0.079	0.335	2.700	0.836	0.000	2.800	0.397	0.850	–	–	–
BD 3 shifts	–224.781	0.574	0.123	0.004	2.700	–0.144	1.168	2.800	0.274	0.000	4.900	0.044	0.689

Note: p-values are derived from LRT between the likelihoods of the Yule model and the first model (BD 1 shift) then between the best model and the next competing model.

(Supplementary material Appendix 1, Fig. A11). We recover four distinct Bayesian credible shift configurations. The three first shift configurations have a unique shift localized at a more or less deeper part of Clade CVII whereas the fourth has no shift at all (Supplementary material Appendix 1, Fig. A12). The first three shift configurations account for more than 90% of the probability of the data with almost identical respective probabilities (~ 30%). The Bayes factors also support a diversification pattern with a unique clade-specific shift of diversification localized in clade CVIII (Fig. 4). Overall, our BAMM analyses do not support a shift in diversification rate earlier in the evolution of the group as expected in the Beringian route scenario (Supplementary material Appendix 1, Fig. A13).

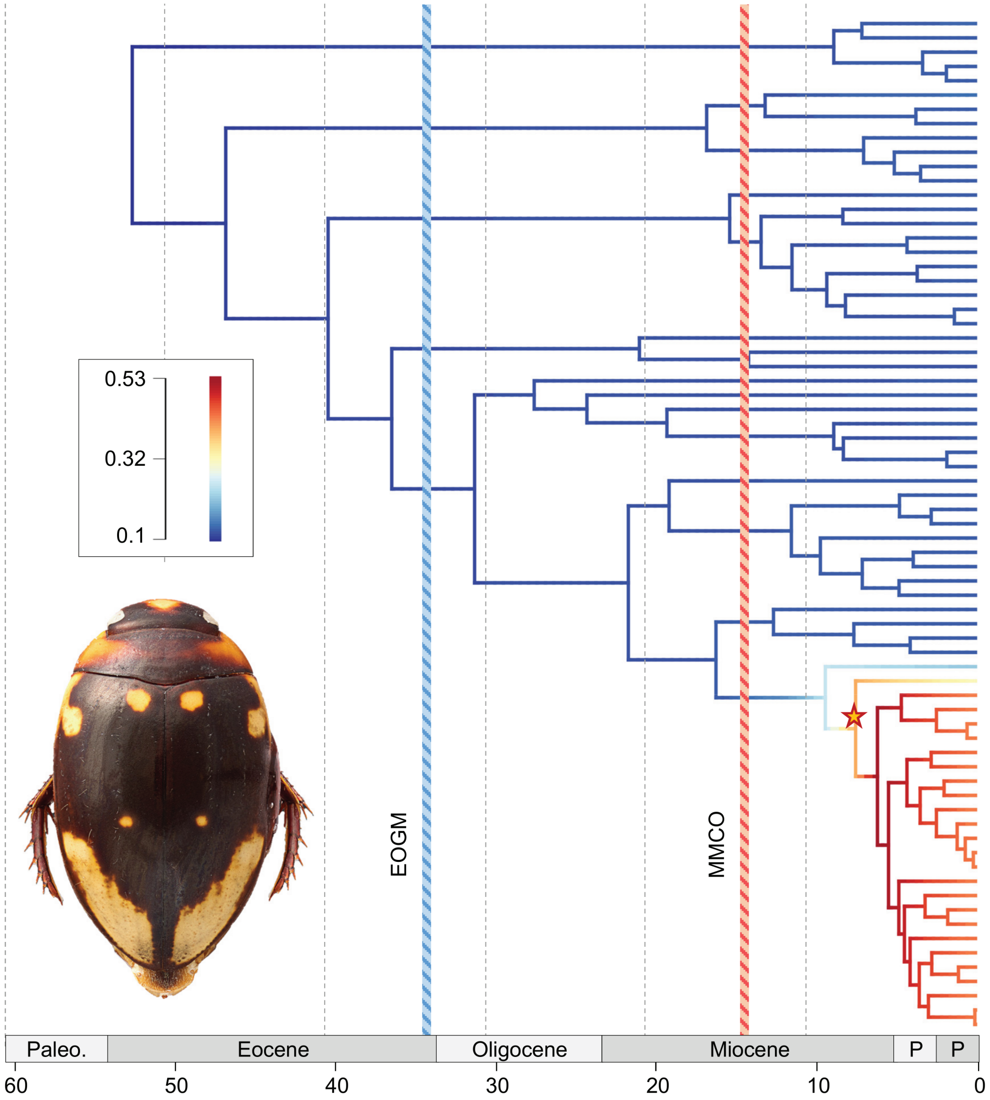

Figure 4. Phylorate of the Platynectini radiation in the Cenozoic. Chronogram of the Platynectini radiation showing the best BAMM diversification rate shift configuration where branches are color-coded according to speciation rates. The unique shift recovered in the BAMM analysis marked by a gold star. Two colored vertical bars demarcate two major Cenozoic climatic shifts: the Eocene-Oligocene Glacial Maximum (EOGM) and the Mid-Miocene Climatic Optimum (MMCO). A picture of an undescribed *Platynectes* species from Venezuela (MB6289 in Fig. 2) is presented at the bottom left of the figure.

Discussion

With our focus on the Indo-Australian region (IAA), we recover a complex biogeographic history broadly reflecting the sequential arrangement of landmasses in the region (Hall 2013, Toussaint et al. 2014). The *Platynectes* of that vast region originated in Australia with repeated subsequent colonization of other areas. The Oriental clade CIII (Fig. 1) is widespread in tropical SE Asia and also temperate parts of China and into the Himalayas, but extends towards the Sunda Islands in the southeast, reaching Java and Sumatra (*P. javanus*, *P.* sp. MB5669). The two Sunda species included in our dataset are recovered in a derived position, reflecting a relatively recent colonization of the IAA out of that clade which had most likely an Australian ancestor in the Eocene. Several clades of insects found in the IAA present a similar and synchronous pattern of out-of-Asia colonization (Müller et al. 2010, Condamine et al. 2013, 2015, Toussaint and Balke 2016) likely taking advantage of the enhanced connectivity in the Quaternary (Voris 2000, de Bruyn et al. 2013, 2014).

In clade CVI, New Guinea was colonized out-of-Australia, in the mid-Miocene, which agrees with the proposed onset of more significant formation of land and altitude in the region of present day New Guinea (Hall 2012a, b, 2013, synopsis in Toussaint et al. 2014). Toussaint et al. (2014, 2015c) also found a similar pattern in *Exocelina* diving beetles (Copelatinae) suggesting this was a time when large-scale environmental change initiated major clade formation and species-level diversification in New Guinea.

Finally, in clade CVIII, New Guinea was again colonized out-of-Australia, at the Miocene–Pliocene boundary when the orogeny of New Guinea was the most dynamic, generating new terrains and vacant habitats (Toussaint et al. 2014). The Solomon Islands were colonized out-of-New Guinea in the Pleistocene when sea-level fluctuations (Miller et al. 2005) resulted in land-bridges connecting most of the islands in this Melanesian archipelago (Mayr and Diamond 2001). Vanuatu was colonized around the same time in clade CVIII. The Moluccas and Timor were colonized out-of-New Guinea and diversified during the past ca 5 Ma. Also slightly more recently, the Philippines were reached possibly out-of-New Guinea, as well as Sulawesi, Peninsula Malaysia, and the Lesser Sunda Islands such as Bali, Lombok, Flores and Sumbawa. This also agrees with the assumption that the Moluccas (i.e. Ambon and Ceram) as well as the Lesser Sunda Islands are of relatively recent origin (e.g. in part Hall 2012b). We also find colonization out of New Guinea towards the west including Peninsula Malaysia and Java, and then back colonization towards the east via the Lesser Sunda Islands up to Timor. This suggests colonization of the Lesser Sunda Islands was from west to east, and the fauna of Timor is the result of two colonizations, from the east and from the west. Major biogeographic lines were thus crossed frequently and seem to have no relevance for these beetles, a pattern already shown in several clades of IAA insects (Condamine et al. 2013, 2015, Tänzler et al. 2014, 2016, Toussaint et al. 2015b, Toussaint and Balke 2016). Also, the IAA was colonized repeatedly and out of different clades, from the west in clade CIII and from the east in CVIII.

The global biogeographic history of the Platynectini is equally complex, with repeated presence of Old World and Neotropical clades across the tree. Clade CII comprising Neotropical species from the Guiana Shield, the Amazon and southeastern Brazil (Fig. 1) has a very long stem that might represent extinction. Yet, our diversification rate analyses do not support a significant rate shift that could match an ancient extinction event. We do however recover a high turnover rate in the Cenozoic before the Plio–Pleistocene boundary that might indicate extinction to some extent. The unfolding of the northern Andes (Gregory-Wodzicki 2000) might have changed local environments in a way to prevent occurrence of *Platynectes* in that region and towards the north west coast of South America, but we suspect that additional sampling might change that picture.

Both analyses from the Gondwanan model recover an ancient Gondwanan origin for this clade (CII) whereas the constrained model analyses recover a LDD origin. We suggest that in the case of clade CII the most likely biogeographical pattern is indeed a Gondwanan origin followed by some regional extinction events. The pattern shown for the first nodes of the phylogeny in the DEC + j reconstruction of the Gondwanan model seems the most parsimonious and is statistically the most supported. Under this scenario, the ancestor of the tribe would have been a widespread taxon occurring in both Australia and the Neotropical region.

The extant distribution in southeast Brazil and then north via Amazonas up to the Guiana Shield would match such an ancestral range. It is likely that this taxon occurred for a long period of time in Antarctica resulting in an ancestral distribution without disjunction. At that time Antarctica had a very similar climate to Australia and the Neotropics which supports this hypothesis. Extinction might have been triggered by climatic disruptions during the Eocene-Oligocene Glacial Maximum (EOGM, Fig. 2). As a result, populations of the ancestral species might have been isolated in some parts of Australia and the Neotropics boosting allopatric speciation in the basal Australian clade CI and in the Neotropical CII. The ancestral area at node N3 is unclear with an Australian, Australian + Neotropics and Neotropics origin suggested by the different models. This ancestral area is however not particularly crucial as the only clade related to this node is the first Oriental radiation. It is likely that this clade was formed when Australia and the Oriental region were getting increasingly closer in the past 30 Myr. Ancestral populations from Australia but independent from populations of the basal clade likely colonized the Oriental region.

All reconstructions recover with moderate to strong support an Australian ancestral origin for the node connecting the Andean clade CV and its sister clade. Our models support a LDD event from Australia to the Andean coastal region in the west of the Neotropics in the Oligocene. The extant range of clade CV, containing exclusively species previously assigned to genera *Leuronectes* and *Agametrus*, would well reflect such an origin by arrival from the west.

The biogeographic history of the Neotropical clades of Platynectini might therefore represent a mix of an ancient Gondwanan widespread distribution shaped by periods of extinction throughout the Cenozoic and a more recent mid-Cenozoic LDD event. Extinction in the Australian region has already been documented (Toussaint et al. 2015a) illustrating the impact of recent climatic changes on diversity assemblages in the region.

Conclusion

Molecular phylogenies permit the testing of biogeographic hypotheses in a comparative manner using the latest biogeographical models and diversification analyses. However, it is paramount to describe a priori the expected patterns under competing biogeographical hypotheses. Without such a theoretical and hypothetico-deductive framework, the use of these methods is mostly descriptive, and therefore less informative with respect to our understanding of biogeographical processes. Using a step-by-step methodology with comparative analyses of phylogenetic inference, divergence times estimation and macroevolution (biogeography and/or diversification dynamics), it should be possible not only to assess the robustness of the results, but also to identify the most likely evolutionary history of focal clades. Here, we show that using a single biogeographical model would likely result in a biased reconstruction of Platynectini evolution. Instead, the use of comparative models in a likelihood framework shows that the early evolution of the group is somehow uncertain. Nevertheless, using this comparative approach we were able to substantiate complex vicariant and dispersal processes in the group, and shed new light on evolutionary mechanisms responsible for Amphi-Pacific disjunct distributions.

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Supplementary material (Appendix ECOG-02195 at <www.ecography.org/appendix/ecog-02195>). Appendix 1.