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Biogeographic mirages? Molecular evidence for dispersal-driven evolution in Hydrobiusini water scavenger beetles

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Abstract. Water beetles of the tribe Hydrobiusini are globally distributed in the northern hemisphere and all austral continents except Antarctica. A remarkable clade also occurs in the Hawaiian Islands. The phylogenetic relationships among genera were recently investigated using a combination of molecules and morphology. Here, we use this phylogenetic framework to address the biogeographic evolution of this group using Bayesian fossil-based divergence times, and model-based maximum likelihood ancestral range estimations. We recover an origin of the tribe in the Cretaceous ca. 100 Ma. Our biogeographic analyses support an origin of the tribe in Laurasia followed by the colonization of Australia. However, a Gondwanan origin of the group cannot be ruled out when considering the fossil record. The timeframe of the tribe's evolution as well as the model-based approach of ancestral range estimation favour a scenario invoking multiple transoceanic dispersal events over a Gondwana vicariance hypothesis. The Hawaiian radiation originated from long-distance dispersal to now-submerged islands, paired with dispersal to new islands as they formed.

Introduction

In the later stages of Earth's geological evolution, the Gondwanan supercontinent progressively fragmented in several major landmasses including Africa, Antarctica, Australia, India, Madagascar, New Caledonia, New Zealand and South America. Starting in the early Jurassic, the block comprising Africa and South America split from East Gondwana (Madagascar-India), though it remained connected to Antarctica until the mid-Cenozoic ~40 million years ago (Ma). However, large water barriers between Africa and South America did not appear before the early Cretaceous ~140 Ma (Seton *et al.*, 2012). India/Madagascar started rifting from Antarctica/Australia around that period of time to migrate northward toward Laurasia. Africa and South America separated from each other in the Cretaceous ~120 Ma with the opening of the Atlantic Ocean. The final separation of India from Madagascar occurred ~90 Ma, while the connection between Antarctica and Australia persisted until the Palaeocene ~60 Ma (Seton *et al.*, 2012). Finally, New Zealand and New Caledonia separated from Australia as early as the late Cretaceous ~80 Ma, although the dating of the split between the two former remains poorly understood (e.g. Schellart *et al.*, 2009).

The contemporary distributions of numerous animal and plant lineages have been offered as examples of Gondwana vicariance. However, the advent of molecular dating has validated only a fraction of these hypothetical Gondwanan relicts (e.g. Gamble *et al.*, 2008; Renner *et al.*, 2010; Thomas *et al.*, 2014; Kim & Farrell, 2015; Mennes *et al.*, 2015; Milner *et al.*, 2015; Andújar *et al.*, 2016; McCulloch *et al.*, 2016; Toussaint *et al.*, 2016, 2017a). As a result, many groups presenting an extant Gondwanan-like distribution have been suggested to be the result of long-distance dispersal rather than ancient vicariance (De Queiroz, 2005).

Water scavenger beetles of the tribe Hydrobiusini (Coleoptera: Hydrophilidae: Hydrophilinae) present such a Gondwanan-like pattern with lineages distributed in several regions that once were part of the supercontinent (Fig. 1). Indeed, the tribe is divided in two major lineages as recovered by Short *et al.* (2017),

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one occurring exclusively in the northern hemisphere, and the other mostly restricted to the southern hemisphere. The latter clade comprises the southwestern Australian endemic *Hybogralius hartmeyeri* Régimbart, 1908, the South African endemic *Limnoxenus sjostedti* Knisch, 1924, the New Caledonian endemic *Limnocyclus puncticeps* Balfour- Browne, 1939, the Argentinian endemic *Hydramara argentina* Knisch, 1925, and several species of the genus *Limnoxenus* Motschoulsky, 1853, found in the Palearctic region, Hawaii, and the Australian region. Previous molecular dating exercises of the family Hydrophilidae found an origin of the tribe in the late Cretaceous (Bloom *et al.*, 2014; Toussaint *et al.*, 2016). Given that the dating and associated credibility intervals of the crown Hydrobiusini do not reject a Gondwanan scenario, there is a need for a proper biogeographic study to investigate the origin of these relict lineages found in the southern hemisphere. A molecular dating framework will also permit the inference of the biogeographic history of the endemic Hawaiian radiation with respect to the geological history of the archipelago (Price & Clague, 2002). In particular, the age estimate of the split between the Hawaiian lineages and their sister group will be of interest to understand if the group colonized present-day subaerial islands or now vanished ones. Indeed, the origin of the Hawaiian biota has been extensively discussed, and is still matter of controversy (e.g. Price & Clague, 2002; Haines *et al.*, 2014). The archipelago was formed as a result of volcanic activity in the Eocene (Carson & Clague, 1995; Price & Clague, 2002). The oldest islands generated through the initial phase of intense volcanism are presently submerged as a result of erosion progressively transforming islands in vanishing atolls that eventually become submerged seamounts (Price & Clague, 2002). The northwest movement of the Pacific plate triggered the formation of multiple islands in the past ~30 Ma. As a result, this systematic geological process formed a linear chain of increasingly younger islands stretching from northwest to southeast. The contemporaneous islands Kauai and Niihau were generated in the past ~5 Ma (Price & Clague, 2002). A majority of Hawaiian clades have an origin younger than this latter age (Price & Clague, 2002), yet the origin of some endemic lineages has been suggested to predate the age of the oldest extant island (e.g. Lapoint *et al.*, 2013; Haines *et al.*, 2014). The evolutionary history of these latter lineages follows a progression rule (Hennig, 1966), whereby the colonization of now-extinct Hawaiian Islands is followed by dispersal toward newly formed volcanic islands as the originally colonized landmasses are submerged. Despite the few examples supporting such a pattern in insects, the estimation of divergence times is often tied to circular biogeographic calibrations, thereby casting doubt on the inferred evolutionary processes. Here we propose to investigate the origin of Hawaiian hydrobiusine beetles in this context as the group is supposedly relatively ancient.

In this study, we use the molecular dataset and phylogenetic framework generated by Short *et al.* (2017) to investigate the origin and evolutionary history of Hydrobiusini water scavenger beetles in order to test the hypothesis of Gondwanan origin in the southern hemisphere clade, and investigate the origin of the radiation endemic to the Hawaiian archipelago.

Materials and methods

Taxon sampling

We used the molecular phylogenetic tree inferred in Short *et al.* (2017) as a starting tree for the dating analyses. The starting tree resulted from a Bayesian inference analysis conducted in MrBayes 3.2 (Ronquist *et al.*, 2012) using a molecular dataset comprising eight genera out of the nine described (Short *et al.* 2017) and a total of 19 species out of the 47 described in the tribe Hydrobiusini (Table S1). The missing species are concentrated in the genera *Ametor* Semenov, 1900 (3 missing species restricted to eastern Palaearctic and Oriental regions), *Hydrobius* Leach, 1815 (4 missing species restricted to the Palaearctic region), *Hydrocassis* Deyrolle & Fairmaire, 1878 (16 missing species restricted to Japan and the Oriental region), and *Limnoxenus* (3 species restricted to Hawaii). The monotypic genera *Hybogralius* d'Orchymont, 1942 (southwestern Australia), *Limnocyclus* (New Caledonia) and *Sperchopsis* LeConte, 1862 (Nearctic) were sampled but the Argentinian monotypic endemic *Hydramara argentina* could not be sampled. However, Short *et al.* (2017) provided an analysis combining DNA and morphology, in which they found this taxon to be nested in a clade comprising *Limnocyclus puncticeps* (New Caledonia) and *Limnoxenus sjostedti* (South Africa). Overall, considering that most missing species are concentrated in deeply nested regions of the tree (Fig. 1 in Short *et al.* 2017) and that we have sampled most of the biogeographic diversity for each genus (except for *Hydramara*), we believe our biogeographic estimation is unlikely to be biased by these missing taxa. We did not use the total-evidence topology of Short *et al.* (2017) because the morphological matrix was too limited to provide meaningful branch length information. Therefore, using a combined matrix (molecules + morphology) in a total-evidence dating analysis would probably induce biases in the branch length optimization of the taxa for which only morphological characters are available. Moreover, total-evidence dating is in its infancy and little is known on the divergence time estimate biases that might result from the assumption of a morphological clock and its implementation in a Bayesian framework (but see Lees, 2016).

Divergence time estimation

Divergence times were estimated using BEAST 1.8.3 (Drummond *et al.*, 2012). The optimal models of substitution were searched under PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) using the '*greedy*' algorithm and the '*beast*' set of models. We used a different partitioning scheme as the one used in the phylogenetic inference analyses to set up a different clock for each gene fragment. The molecular clock test was performed in MEGA6 (Tamura *et al.*, 2013) by comparing the ML value of the MrBayes topology based on the combined dataset 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-value < 0.001).

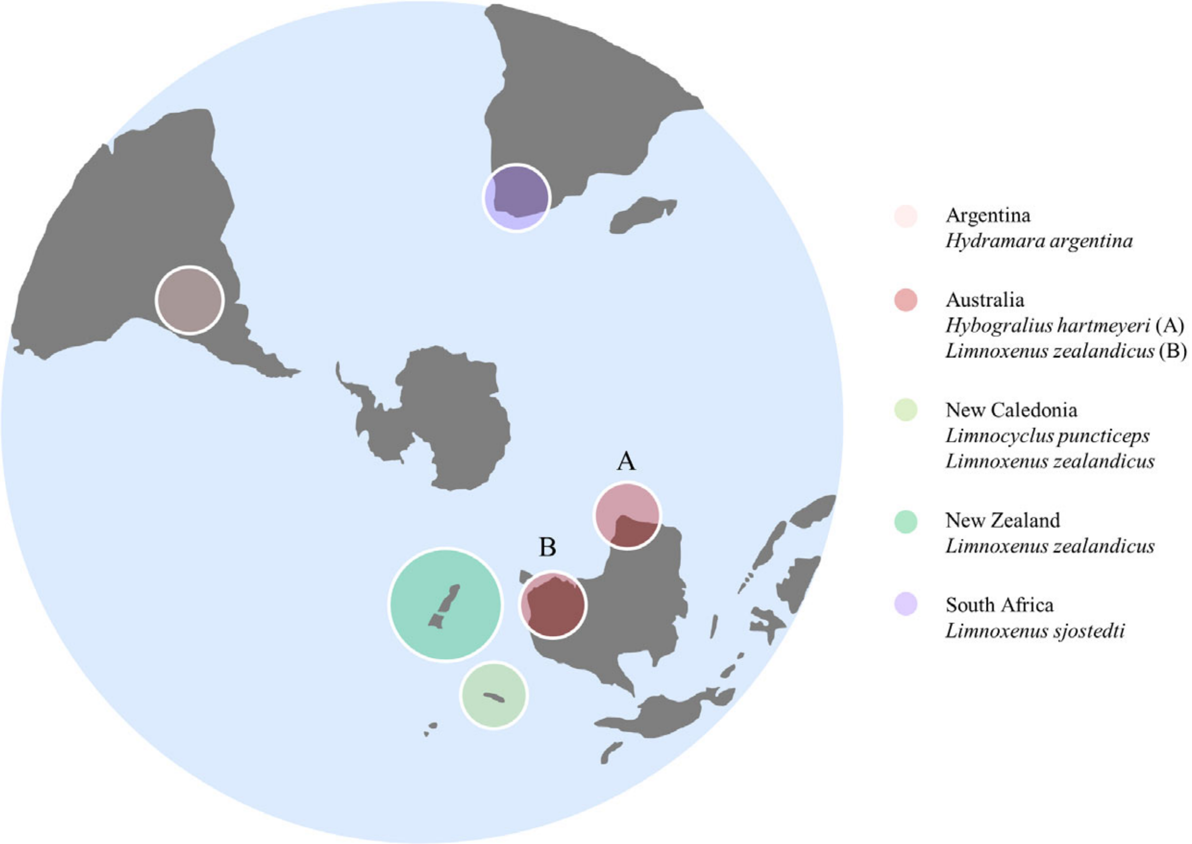

Fig. 1. Distribution of southern hemisphere Hydrobiusini. Geographic map highlighting the distribution of the different hydrobiusine genera occurring in the southern hemisphere and in particular in old Gondwanan landmasses. All species have been sampled in this study except the Argentinian *Hydramara argentina*. [Colour figure can be viewed at wileyonlinelibrary.com].

Therefore, we used a Bayesian relaxed clock approach as implemented in BEAST 1.8.3 (Drummond *et al.*, 2012).

We tested the impact of fossil age prior distributions on posterior estimates by using different prior densities to enforce fossil calibrations under a Yule or a birth death model. Specifically, we used uniform, exponential and lognormal prior distributions. The uniform prior distributions encompassed an interval comprised between the age of the upper (youngest) stratum from which each fossil was described, and the age of the crown Hydrophiloidea of 215 million years (Ma) as recovered in Toussaint *et al.* (2017b). The exponential prior distributions were enforced with 95% of each distribution spanning an interval starting at the age of the upper (youngest) stratum from which each fossil was described, and ending at the age of the crown Hydrophiloidea (215 Ma). Therefore, exponential prior distributions were enforced with soft maxima compared to uniform prior distributions. We also used lognormal prior distributions as these offer the advantage of allowing the mode (maximum probability) for the age of the fossil to be somewhat older than the minimum bound as opposed to uniform (equal probability) and exponential (diminishing probability from the minimum bound) prior distributions. The lognormal prior distributions were enforced with a Mean = 40, a Stdev = 0.50 and an Offset set so that 95% of the distribution would fit the age of the upper (youngest) stratum from which each fossil was described, but not necessarily the age of the crown Hydrophiloidea (215 Ma). In practice, this means that 95% of the lognormal distribution would fit a smaller interval than the one defined in the exponential prior distributions. As lognormal priors necessarily specify a mode different from the minimum age of the fossil stratum, it is often impossible to justify the placement of the mode. In our analysis, we chose to take into account this bias by using the same mean and stdev for each fossil in order to generate similarly shaped prior distributions.

The BEAST analyses consisted of 30 million generations sampled every 3000 generations. The convergence of the runs was investigated using ESS, a burn-in of 10% applied after checking the log-likelihood curves. The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated afterwards under TreeAnnotator 1.8.3 (Drummond *et al.*, 2012). We also performed marginal likelihood estimation using path/stepping stone sampling (Xie *et al.*, 2011) as implemented in BEAST 1.8.3 (Drummond *et al.*, 2012) using the default settings (number of path steps = 100, chain length = 1 000 000, log likelihood sampling = 1000).

Table 1. BEAST median divergence times with 95% credibility intervals and marginal likelihoods.

Analysis	SS MLE	Clade C1	Clade C2	Clade C3	Hawaiian Clade
BD Exp	−24412.40	87.76 (68.58–111.66)	81.94 (62.56–103.90)	66.59 (43.90–90.76)	16.32 (9.40–23.99)
BD LogN	−24411.76	85.50 (66.29–108.28)	81.11 (62.05–102.52)	65.57 (44.14–90.20)	15.86 (9.04–23.30)
BD Uni	−24408.97	102.22 (75.78–135.31)	95.53 (71.11–128.18)	77.89 (49.97–110.19)	19.08 (11.28–29.42)
Yule Exp	−24409.53	88.07 (69.33–110.94)	82.37 (64.94–105.04)	67.00 (44.83–90.97)	16.47 (10.06–24.28)
Yule LogN	−24410.72	88.61 (67.47–108.44)	81.20 (62.95–102.25)	66.36 (44.02–90.65)	16.30 (9.39–23.59)
Yule Uni	−24412.460	102.97 (75.48–136.70)	96.25 (69.92–127.68)	77.66 (48.86–109.76)	19.48 (11.32–29.74)

SS MLE, stepping-stone sampling marginal likelihood estimate; BD, birth-death Tree model; Exp, exponential prior distribution for fossil calibrations; LogN; lognormal prior distribution for fossil calibrations; Uni, uniform prior distribution for fossil calibrations.

Fossil calibration points

We used four fossils to calibrate the phylogeny that were already described in detail and whose placement is justified in Fikáček *et al.* (2010b, 2014) and Bloom *et al.* (2014).

First, we used *Hydrobiomorpha eopalpalis*† Fikáček *et al.*, 2010b, from the Messel pit in Germany, dated from the mid-Eocene about 47 Ma (Mertz & Renne, 2005). Based on morphological characters, this fossil has been unambiguously assigned to the genus *Hydrobiomorpha* Say, 1835, although its placement is uncertain within the genus (Fikáček *et al.*, 2010b). As a result, we used this fossil as a stem calibration for *Hydrobiomorpha*, with an exponential prior distribution to enforce a soft minimum age of 47 Ma (BEAUti settings: Mean = 46.40, Offset = 43.83). We also used a uniform prior distribution (47.0–215.0), and a lognormal prior distribution (Mean = 40.00, stdev = 0.5, Offset = 33.75).

Second, we used *Hydrochara* sp.† Fikáček *et al.*, 2010a, from the same geological formation (Messel pit, Germany, 47 Ma). This fossil was also unambiguously placed in the genus *Hydrochara* Berthold, 1827, although its placement within the genus remains equivocal (Fikáček *et al.*, 2010b). We used this fossil to calibrate the stem of *Hydrochara*. The exponential, uniform and lognormal prior distribution settings were the same as for the *Hydrobiomorpha* fossil.

Third, we used *Hydrobius titan*† Wickham, 1913, described from the Florissant Formation in Colorado (USA, 33.9–37.2 Ma). This fossil represents the extant genus *Sperchopsis* (Bloom *et al.*, 2014; M. Fikáček *et al.*, in preparation). We used this fossil to calibrate the stem of *Sperchopsis* with an exponential prior distribution to enforce a soft minimum age of 33.9 Ma (BEAUti settings: Mean = 49.42, Offset = 32.65). We also used uniform (33.9–215.0) and lognormal (Mean = 40.00, stdev = 0.5, Offset = 20.65) prior distributions.

Finally, we used *Baissalarva hydrobioides*† Fikáček *et al.*, 2014, from the Baissa deposits in the Buryat Republic (Russia, 135–146 Ma). This fossil unambiguously belongs to the tribe Hydrobiusini based on a phylogenetic analysis (Fikáček *et al.*, 2014). Therefore, we used this fossil to calibrate the stem of Hydrobiusini with an exponential prior distribution to enforce a soft minimum age of 135 Ma (BEAUti settings: Mean = 21.83, Offset = 134.45). We also used uniform (135.0–215.0) and lognormal (Mean = 40.00, stdev = 0.5, Offset = 121.8) prior distributions.

We chose not to use †*Limnoxenus olenus* Fikáček *et al.*, 2010b, from the Aix-en-Provence Formation in southern France, which is dated to the Late Oligocene (Late Chattian, 22.5 Ma). This fossil is placed on the stem of *Limnoxenus*, however, as the genus is found paraphyletic due to the inclusion of *Hydramara* (morphology) and *Limnocyclus* (molecular and morphology), we preferred to discard this possible calibration.

The root of the phylogeny was constrained with a relatively uninformative uniform prior with a minimum hard bound of 155 Ma and a hard maximum bound of 215 Ma.

Ancestral range estimation

We inferred the biogeographic history of Hydrobiusini water scavenger beetles across their entire range with BioGeoBEARS (Matzke, 2013) as implemented in R. This program allows estimating historical biogeography patterns under different biogeographic models and also implements a parameter describing founder-event jump speciation (+j). We conducted the analyses under the DEC model (Ree *et al.*, 2005; Ree & Smith, 2008), as well as the likelihood implementation of the DIVA (Ronquist, 1997) and BAYAREA (Landis *et al.*, 2013) models. We used the BEAST Maximum Clade Credibility (MCC) tree with outgroups pruned to perform the analyses. The following regions were used in the analyses: Australia (A), Hawaii (H), Nearctic (N), New Caledonia (C), New Zealand (Z), Oriental region (O), Palaearctic (P), and South Africa (S). The distribution of each taxon was recovered from the literature (Hansen, 1999; Short & Fikáček, 2011; Short *et al.* 2017). To account for the extremely dynamic palaeogeographical events that occurred since the Cretaceous (Seton *et al.*, 2012), we designed four time slices with dispersal rate multipliers/scalers used to downweight dispersal between areas (Figure S1). The first time slice (TS1, 65–100 Ma) runs from the origin of the group until the major breakup of austral landmasses (e.g. Antarctica and Australia). The second time slice (TS2, 37–65 Ma) ends with the submergence of New Caledonia (Schellart *et al.*, 2006; Pelletier, 2007). The third time slice (TS3, 29–37 Ma) ends with the emergence of the first Hawaiian island (Carson & Clague, 1995; Price & Clague, 2002). The last time slice (TS4) extends from 29 Ma to the present. The dispersal rate scaler values were calculated using the following

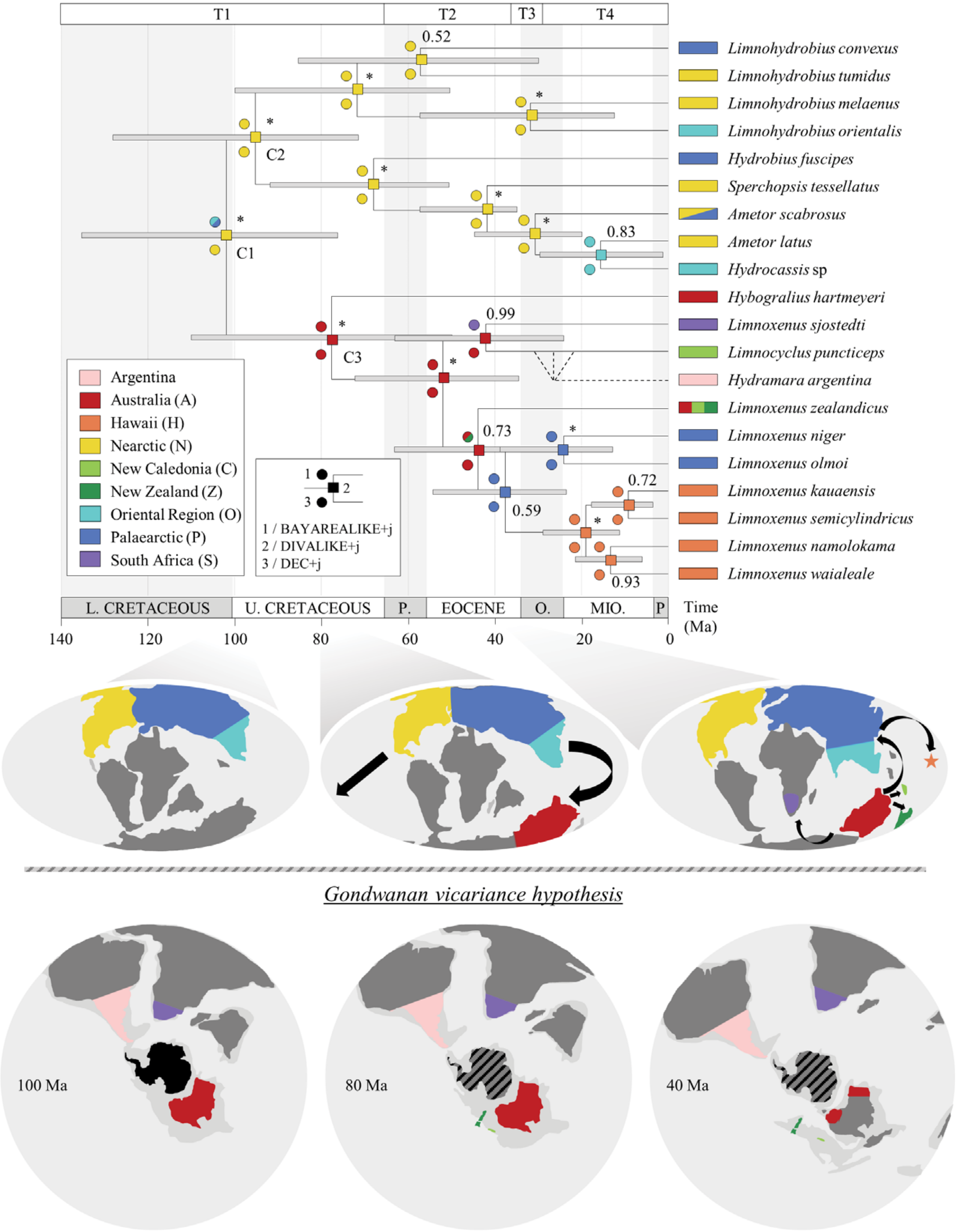

Fig. 2. Legend on next page.

rules; the dispersal rate between adjacent areas is not penalized (dr*1.0), the dispersal rate between areas separated by a small water barrier is slightly penalized (dr*0.75), the dispersal rate between areas separated by another area is moderately penalized (dr*0.50), and the dispersal rate between areas separated by a large water barrier is strongly penalized (dr*0.25). The final four dispersal rate scaler matrices between all possible area combinations were calculated following these rules and taking into account multiple barriers and landmass discontinuities throughout the evolution of the group (Seton *et al.*, 2012). In case of a dispersal rate value becoming zero as a result of several barriers and/or landmass discontinuities (i.e. not applicable to New Caledonia and Hawaii that were forbidden in certain time slices), we chose in a conservative manner to use a dr of 0.1 in order to take into consideration unlikely long-dispersal events. Finally, area combinations were restricted to adjacent areas within each time slice (Figure S1).

Results

All BEAST analyses converged well as indicated by the ESS values of parameters being largely over 200. The analysis conducted with the birth-death model and uniform prior distributions had the best marginal likelihood (Table 1). However, there are only slight differences in the divergence time estimates between the six analyses, with largely overlapping credibility intervals. According to the analysis with the best marginal likelihood (Fig. 2), we recover an origin of the tribe in the early Cretaceous ~102 Ma (95% HPD: 75.78–135.31 Ma). Clade C2 which is presently distributed in the northern hemisphere, has an origin in the late Cretaceous ~96 Ma (95% HPD: 71.11–128.18 Ma) while clade C3 whose current distribution is mostly austral, has an origin ~78 Ma (95% HPD: 49.97–110.19).

All BioGeoBEARS analyses recovered an origin of Hydrobiusini in Laurasia although in different parts of the supercontinent (Figure S2). The DEC and BAYAREALIKE+j models recovered an origin in the Old World with an ancestral range in the Oriental and Palearctic regions. The BAYAREALIKE and DIVALIKE models recovered an origin in an ancestral range comprised of the Nearctic and Palearctic regions. Finally, the DEC+j and DIVALIKE+j analyses recovered an origin in the Nearctic region. The different analyses recovered varying biogeographic patterns depending on the inclusion of the founder event speciation parameter+j. The Akaike weights support the models including the founder speciation event parameter+j over the ones that do not, with significant differences in likelihood scores (Table 2). Although the BAYAREALIKE+j model received the highest Akaike weight (Table 2), the differences in likelihoods in comparison to the DEC+j and DIVALIKE+j models were not significant. These three analyses resulted in highly similar biogeographic patterns except for two nodes in addition to the root (Fig. 2). The DEC+j and DIVALIKE+j models resulted in identical patterns, with an origin in the Nearctic region followed by long distance dispersal (LDD) toward Australia in the late Cretaceous. New Caledonia and South Africa were colonized out of Australia in the past 40 Ma. A LDD event is also recovered between Australia and the Palearctic region in the Eocene, followed by another LDD event from the Palearctic region to Hawaii between the late Eocene and the early Miocene. In the BAYAREALIKE+j model, South Africa is colonized via LDD out of Australia in the Eocene, with subsequently a LDD event from South Africa to New Caledonia. This model also recovers a range expansion in *Limnoxenus* with an ancestral range comprised of both Australia and New Zealand from where the LDD event toward the Palearctic region took place. The less supported models not including the +j parameter recovered patterns exclusively invoking Laurasian range expansions and contractions over the past 100 Ma with very recent LDD events to colonize the austral region out of the Old World (Figure S2).

Discussion

Divergence time estimation and uncertainty

Our BEAST analyses recover an origin of Hydrobiusini at the transition between the early and late Cretaceous. This is in broad agreement with previous studies (Bloom *et al.*, 2014; Toussaint *et al.*, 2016). Bloom *et al.* (2014) and Toussaint *et al.* (2016) used very similar molecular datasets and fossil calibrations but with different BEAST parameters and maximum ages. Bloom *et al.* (2014) recovered an origin of Hydrobiusini ~91/97 Ma (uniform vs. exponential prior distributions), whereas Toussaint *et al.* (2016) recovered an origin of the tribe ~74/88 Ma (uniform vs. exponential prior distributions). Our estimates using exponential and lognormal prior distributions are largely congruent with these previous estimates, whereas our estimates using uniform distribution priors (birth-death and Yule) are older

Fig. 2. Divergence times and historical biogeography of hydrobiusine water scavenger beetles. BEAST chronogram derived from the 'BD Uni' analysis (see Table 1), presenting median ages of the tribe Hydrobiusini. The 95% credibility intervals for each node of the phylogeny are given with horizontal grey bars. Asterisks indicate robust nodal support with a posterior probability PP ≥0.95 as inferred in the MRBayes analysis of the molecular concatenated dataset generated in Short *et al.* (2017). For nodes with lower nodal support, the posterior probability of the MRBayes analysis from Short *et al.* (2017) is given. The higher probability BioGeoBEARS ancestral range estimations of the different models implementing the j parameter are given at each node, and follow the two captions inserted on the left of the figure. Please refer to the supplementary information for the relative probabilities of each node under the different models. Joint present-day and ancestral distributions (two or more areas) are presented with split circles and rectangles. A biogeographic scenario is given underneath the chronogram on three paleomaps representing the placement of landmasses respectively 100, 80 and 40 Ma. At the bottom of the figure, we provide a hypothetical biogeographic scenario implying an ancestral range in Gondwana including Antarctica. Under this scenario, the ancestor was present in Antarctica 100 Ma, and as the Gondwanan supercontinent started to break-up, the ancestors went extinct at some point in Antarctica (dashed grey), resulting in the disjunct distribution observed today. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 2. Results of the BioGeoBEARS analyses.

Model	LnL	N.p.	d	e	j	Ak. W.
DEC	−68.67	2	0.047	0.019	0.000	0.000
DEC+j	−51.66	3	0.006	0.003	0.229	0.324
DIVALIKE	−68.83	2	0.042	0.017	0.000	0.000
DIVALIKE+j	−52.17	3	0.006	0.003	0.191	0.194
BAYAREALIKE	−68.70	2	0.058	0.026	0.000	0.000
BAYAREALIKE+j	−51.26	3	0.006	0.004	0.257	0.482

LnL, log-likelihood of the run; N.p, number of parameters; d, dispersal rate; e, extinction rate; j, jump dispersal rate; Ak. W.; Akaike weight.

(Table 1). This is likely due to the reduced taxon sampling and lack of additional fossils compared to Bloom *et al.* (2014) and Toussaint *et al.* (2016). Nevertheless, the fact that our age estimates are consistent with previous estimates proposed for this group indicate that the main conclusions of our biogeographic analyses (i.e. a non-Gondwanan vicariant origin in the currently mostly southern hemisphere clade C3, and origin of Hawaiian hydrobiusines predating the age of Kauai/Niihau) are robust. Even the large credibility intervals recovered in some analyses for the critical nodes of the phylogeny (Table 1, Fig. 2), do not support a Gondwanan scenario. The oldest credibility age for the origin of clade C3 is ~110 Ma, a period of time postdating the major break-up of Gondwana and most relevant to this study (Seton *et al.*, 2012; Fig. 2). Likewise, the credibility intervals of our estimates for the origin of the Hawaiian radiation do not encompass the age of the oldest subaerial islands Kauai and Niihau.

Historical biogeography of Hydrobiusini water scavenger beetles

Our analyses unambiguously recover an origin of the tribe in Laurasia (Table 2, Fig. 2). A more detailed study taking into account the sister tribe Hydrophilini would help validate or refute this origin. Although there is no published biogeographic study of the tribe Hydrophilini, preliminary results indicate a Gondwanan origin for this slightly older clade (Toussaint *et al.* 2017c). Moreover, Fikáček *et al.* (2014) recently described †*Cretoxenus australis* Fikáček *et al.*, 2014, a fossil found in Australia and dated to the early Cretaceous (112–118 Ma). This fossil was tentatively assigned to the tribe Hydrobiusini, although its placement was uncertain due to a lack of preserved features (Fikáček *et al.*, 2014). Fikáček *et al.* (2014) noted that the fossil shared some features with extant hydrobiusine lineages (e.g. posteriorly projecting mesal portion of the metaventrites), but others (e.g. non-denticulate lateral margins) were not decisive in placing the genus among other genera or even firmly within the tribe. If this fossil was in fact a hydrobiusine representative, it would mean that about ~120 Ma, some ancestors of the tribe were already present in Australia. While this has implications for the origin of the group, it would not dramatically change the biogeographic estimation we recover except in the case of a scenario invoking rampant Cretaceous regional extinction (Fig. 2). Although this hypothesis cannot be completely ruled out, we believe that a dispersal-driven pattern is more plausible as illustrated by the long-distance dispersal colonization of Hawaii. Additionally, our BioGeoBEARS analyses recover very low values for the extinction parameter e (Table 2). If the range of the hydrobiusine ancestor remains relatively unclear, the dating and biogeographic analyses performed in this study clearly reject the hypothesis of old Gondwana vicariance in clade C3 (Fig. 2).

The three analyses excluding the j parameter suggest a very unlikely biogeographic history with most lineage divergence events happening in Laurasia with multiple recent LDD events to colonize the different austral areas. The three best BioGeoBEARS analyses including the j parameter support an Australian origin of this clade following a LDD event from Laurasia. Such a dispersal event is not easily explained considering the large ocean that separated Laurasia from Gondwana ~90 Ma (but see Toussaint *et al.*, 2017b for an example of transoceanic LDD in water beetles). Possible continental dispersal through the Afrotropics followed by regional extinction could be invoked, but we recover very low values of extinction rates in the analyses including the j parameter. The most likely scenario is therefore transoceanic LDD. An Australian origin of the tribe as possibly suggested by †*C. australis*, would be more in line with the presence of the group on the island in the Cretaceous, but would inversely imply a LDD event from Australia toward Laurasia in clade C2.

The DEC + j and DIVALIKE + j models recover an Australian origin of the clade comprising *Limnocyclus*, *Limnoxenus sjostedti* and possibly *Hydramara argentina* (Fig. 2). The BAYAREALIKE + j model recovers a South African origin for this same node. The fact that we could not sample *H. argentina* in this study is problematic and possibly biases our ancestral range estimation. This subclade has a Gondwanan distribution across Argentina, New Caledonia and South Africa. Assuming that *Hydramara* is in fact correctly placed, and considering our age estimates, a Gondwanan vicariant scenario is fully rejected even when considering the upper bound of the credibility intervals. We hypothesize here that Antarctica likely had a role in the present-day distribution of this clade. Regardless of the directionality of the biogeographic pattern, it seems more plausible to assume continental dispersal via Antarctica between these three landmasses and possibly Australia than across oceans. This scenario would imply regional extinction in Antarctica. Here again, the models do not recover a strong signal of extinction. Therefore, direct transoceanic dispersal or via stepping stone in the Kerguelen archipelago cannot be ruled out (Sanmartín & Ronquist, 2004; Fuller *et al.*, 2005; but see Ali & Aitchison, 2009). The presence of hydrobiusines in Antarctica during the Cenozoic would have facilitated dispersal toward southern South America where *Hydramara* is presently distributed, toward South Africa from where *Limnoxenus sjostedti* is endemic, and toward New Caledonia where *Limnocyclus* is endemic. Occupation of Antarctica during this time would have been possible since the continent had a much warmer climate during most the Cenozoic, and only started to experience glaciation after Australia rifted away in the Oligocene (Galeotti *et al.*, 2016; McKay *et al.*, 2016). Several clades with divergence time

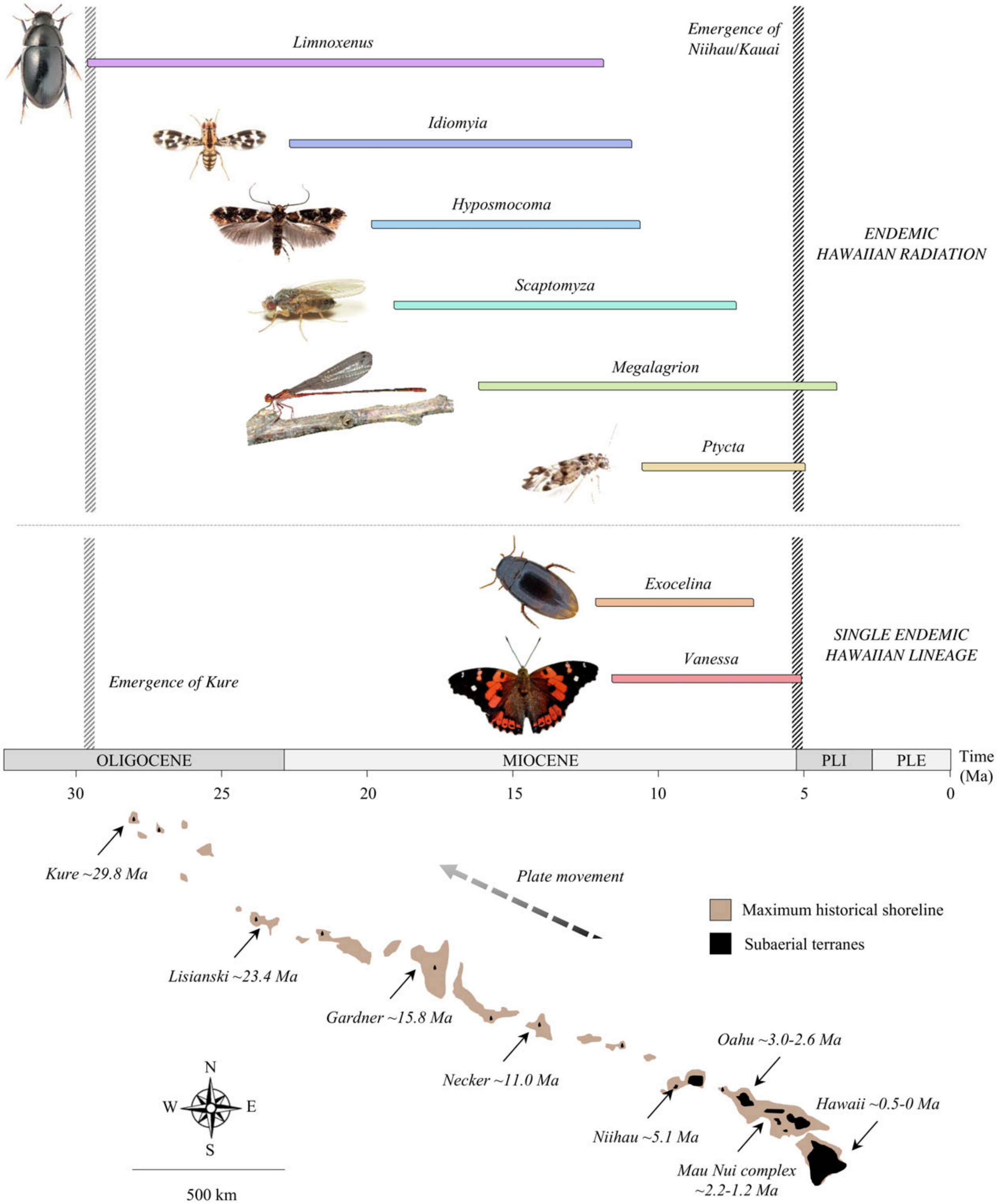

Fig. 3. Summary of endemic Hawaiian lineages whose origin predated the emergence of contemporaneous Hawaiian Islands. The 95% credibility intervals of node divergence times corresponding to the crown of several Hawaiian lineages are presented. The six top lineages are Hawaiian radiations with at least two species, whereas the two bottom ones (*Exocelina* and *Vanessa*) are represented by only one endemic species in the archipelago. Two vertical bars respectively indicate the emergence of the first now-submerged Hawaiian island Kure, as well as the emergence of the oldest contemporaneous islands Kauai and Niihau. At the bottom of the figure is given a geographic reconstruction of the Hawaiian archipelago redrawn from Price & Clague (2002), presenting submerged and subaerial Hawaiian Islands. For submerged islands, the maximum shoreline of the island as reconstructed in Price & Clague (2002) is given. [Colour figure can be viewed at wileyonlinelibrary.com].

estimates inconsistent with the Gondwanan vicariance hypothesis have implied dispersal via Antarctica as a mechanism driving biogeographic patterns (e.g. Winkworth *et al.*, 2015; Givnish *et al.*, 2016).

All preferred analyses recover an origin of *Limnoxenus* (except *L. sjostedti*) in Australia, with the BAYAREALIKE + j analysis recovering a joint range in Australia and New Zealand. From there, ancestors colonized the Palaearctic region most likely via LDD in the Eocene (Fig. 2). The presence of *Limnoxenus* in the Palaearctic region in the late Cenozoic is attested by the fossil *L. olenus* described from southern France in Aix-en-Provence. This fossil was recovered as closely related to the extant Palaearctic species from clade C3 (*L. niger* Gmelin, 1790, and *L. olmoi* Hernando & Fresneda, 1994) as well as *L. sjostedti* and *L. zealandicus* Broun, 1880, by Fikáček *et al.* (2010b), although this relationship was not supported in Short *et al.* (2017). Finally, we infer a LDD event from the Palearctic region toward the Hawaiian archipelago between the late Eocene and early Miocene. This is in line with the early volcanic stage of the orogeny in this string of ephemeral islands. Price & Clague (2002) estimated that the first subaerial terranes in Hawaii emerged as a result of intense volcanism in the Oligocene ~29 Ma (Fig. 3). However, all islands formed in the early stage of the orogeny were later eroded into atolls and eventually were submerged. Our analyses imply that the early colonizing ancestors of Hawaiian Hydrobiusini dispersed to younger islands as the older ones progressively eroded in the Miocene. Examples of dispersal to the Hawaiian Islands prior to the emergence of the current high islands have been found in several other insect groups (Fig. 3), including the bark louse genus *Ptycta* Enderlein, 1925 (ca. 7 Ma, Bess *et al.*, 2014), *Megalagrion* McLachlan, 1883 damselflies (ca. 9 Ma; Jordan *et al.*, 2003), *Idiomyia* Grimshaw, 1901 and *Scaptomyza* Hardy 1849 fruit flies (ca. 10–13 Ma, Lapoint *et al.*, 2013; Katoh *et al.*, 2017), and *Hyposmocoma* Butler, 1881 moths (ca. 15 Ma, Haines *et al.*, 2014). However, some of these studies relied on biogeographic calibrations directly or indirectly derived from radiometric dating of some Hawaiian Islands. Therefore, Hawaiian *Limnoxenus* are, to our knowledge, one of the first groups of insects to be dated from a period of time predating the age of contemporaneous Hawaiian Islands, using external calibrations (i.e. based on the fossil record). Other clades including diving beetles of the genus *Exocelina* Balke, 1998 and brush-footed butterflies of the genus *Vanessa* Fabricius, 1807, each have an endemic species whose divergence from a continental sister lineage predates the formation of Kauai and Niihau based on external calibrations (Wahlberg & Rubinoff, 2011; Toussaint *et al.*, 2015; Fig. 3). However, unlike a multispecies radiation such as in *Limnoxenus*, the existence of a unique species in these two genera and the sister relationship with a widespread clade cannot rule out the hypothesis of an origin in an ancestral range out of Hawaii followed by later dispersal toward the archipelago. In addition to the Hawaiian endemic species sampled in this study, three other *Limnoxenus* species endemic to the archipelago have been described. However, based on Short *et al.* (2017), these species are placed in the two sampled clades recovered in this study. Therefore, the age estimates inferred here are unlikely to substantially change if a larger taxon sampling of Hawaiian species was included.

Conclusion

Although a Gondwanan origin of Hydrobiusini is not recovered in our BioGeoBEARS analyses, it should not be completely ruled out due to the likely incompleteness of the fossil record, sampling of the Argentinean *Hydramara*, and possibly the addition of the sister tribe Hydrophilini. Nevertheless, our dating and biogeographic analyses reject the idea that the break-up of Gondwana drove the vicariant origin of lineages in Hydrobiusini and in particular in clade C3. Instead, it is likely that a more complex suite of biogeographic mechanisms shaped the evolution of the group, and in particular dispersal, range expansion and regional extinction. We hypothesize that Antarctica possibly played a role in facilitating dispersal events between the different regions of the planet where these beetles can be found today. Finally, the Hawaiian radiation likely originated before the formation of the oldest extant subaerial Hawaiian Islands. Despite the rather wide credibility intervals, our results suggest that *Limnoxenus* water beetles count among the very few examples of insect clades having followed a progression rule in the archipelago.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12237

Table S1. Taxon sampling and GenBank accession numbers. Table listing all specimens used in this study and the location of associated data.

Figure S1. Details of the BioGeoBEARS dispersal rate scaler and adjacency matrices. Matrices of dispersal rate scalers and adjacency areas used for the different time slices in the BioGeoBEARS analyses.

Figure S2. Results of the BioGeoBEARS analyses. Detailed outputs of the BioGeoBEARS analyses for the three different models (DEC, DIVALIKE and BAYAREA) with or without the j parameter. The colors and letters correspond to the areas listed in the methods section (see above).

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References

Ali, J.R. & Aitchison, J.C. (2009) Kerguelen Plateau and the Late Cretaceous southern-continent bioconnection hypothesis: tales from a topographical ocean. *Journal of Biogeography*, **36**, 1778–1784.

Andújar, C., Faille, A., Pérez–González, S., Zaballos, J.P., Vogler, A.P. & Ribera, I. (2016) Gondwanian relicts and oceanic dispersal in a cosmopolitan radiation of euedaphic ground beetles. *Molecular Phylogenetics and Evolution*, **99**, 235–246.

Bess, E.C., Catanach, T.A. & Johnson, K.P. (2014) The importance of molecular dating analyses for inferring Hawaiian biogeographical history: a case study with bark lice (Psocidae: *Ptycta*). *Journal of Biogeography*, **41**, 158–167.

Bloom, D.D., Fikáček, M. & Short, A.E. (2014) Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. *PLoS ONE*, **9**, e98430.

Carson, H.L. & Clague, D.A. (1995) Geology and biogeography of the Hawaiian Islands. *Hawaiian Biogeography, Evolution on a Hot Spot Archipelago* (ed. by W.L. Wagner and V.A. Funk), pp. 14–29. Smithsonian Institution Press, Washington, District of Columbia.

De Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution*, **20**, 68–73.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.

Fikáček, M., Wedmann, S. & Schmied, H. (2010a) Diversification of the greater hydrophilines clade of giant water scavenger beetles dated back to the Middle Eocene (Coleoptera: Hydrophilidae: Hydrophilina). *Invertebrate Systematics*, **24**, 9–22.

Fikáček, M., Prokop, J. & Nel, A. (2010b) Fossil water scavenger beetles of the subtribe Hydrobiusina (Coleoptera: Hydrophilidae) from the Late Oligocene locality of Aix-en-Provence (France). *Acta Entomologica Musei Nationalis Pragae*, **50**, 445–458.

Fikáček, M., Prokin, A., Yan, E., Yue, Y., Wang, B., Ren, D. & Beattie, R. (2014) Modern hydrophilid clades present and widespread in the Late Jurassic and Early Cretaceous (Coleoptera: Hydrophiloidea: Hydrophilidae). *Zoological Journal of the Linnean Society*, **170**, 710–734.

Fuller, S., Schwarz, M. & Tierney, S. (2005) Phylogenetics of the allodapine bee genus *Braunsapis*: historical biogeography and long-range dispersal over water. *Journal of Biogeography*, **32**, 2135–2144.

Galeotti, S., DeConto, R., Naish, T. *et al.* (2016) Antarctic Ice Sheet variability across the Eocene–Oligocene boundary climate transition. *Science*, **352**, 76–80.

Gamble, T., Bauer, A.M., Greenbaum, E. & Jackman, T.R. (2008) Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography*, **35**, 88–104.

Givnish, T.J., Spalink, D., Ames, M. *et al.* (2016) Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal. *Journal of Biogeography*, **43**, 1905–1916.

Haines, W.P., Schmitz, P. & Rubinoff, D. (2014) Ancient diversification of *Hyposmocoma* moths in Hawaii. *Nature Communications*, **5**, 3502.

Hansen, M. (1999) *World Catalogue of Insects* Volume 2: Hydrophiloidea (s. str.)(Coleoptera). Apollo Books, Stenstrup.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois.

Jordan, S., Simon, C. & Polhemus, D. (2003) Molecular systematics and adaptive radiation of Hawaii's endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology*, **52**, 89–109.

Katoh, T., Izumitani, H.F., Yamashita, S. & Watada, M. (2017) Multiple origins of Hawaiian drosophilids: phylogeography of *Scaptomyza* Hardy (Diptera: Drosophilidae). *Entomological Science*, **20**, 33–44.

Kim, S.I. & Farrell, B.D. (2015) Phylogeny of world stag beetles (Coleoptera: Lucanidae) reveals a Gondwanan origin of Darwin's stag beetle. *Molecular Phylogenetics and Evolution*, **86**, 35–48.

Landis, M.J., Matzke, N.J., Moore, B.R. & Huelsenbeck, J.P. (2013) Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, **62**, 789–804.

Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.

Lapoint, R.T., O'Grady, P.M. & Whiteman, N.K. (2013) Diversification and dispersal of the Hawaiian Drosophilidae: the evolution of *Scaptomyza*. *Molecular Phylogenetics and Evolution*, **69**, 95–108.

Lees, M.S. (2016) Multiple morphological clocks and total–evidence tip–dating in mammals. *Biology Letters*, **12**, 20160033.

Matzke, N.J. (2013) *BioGeoBEARS: Biogeography with Bayesian (and likelihood) Evolutionary Analysis in R scripts*. R package, version 0.2, 1.

McCulloch, G.A., Wallis, G.P. & Waters, J.M. (2016) A time–calibrated phylogeny of southern hemisphere stoneflies: testing for Gondwanan origins. *Molecular Phylogenetics and Evolution*, **96**, 150–160.

McKay, R.M., Barrett, P.J., Levy, R.S., Naish, T.R., Golledge, N.R. & Pyne, A. (2016) Antarctic Cenozoic climate history from sedimentary records: ANDRILL and beyond. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **374**, 20140301.

Mennes, C.B., Lam, V.K., Rudall, P.J., Lyon, S.P., Graham, S.W., Smets, E.F. & Merckx, V.S. (2015) Ancient Gondwana break-up explains the distribution of the mycoheterotrophic family Corsiaceae (Liliales). *Journal of Biogeography*, **42**, 1123–1136.

Mertz, D.F. & Renne, P.R. (2005) A numerical age for the Messel fossil deposit (UNESCO World Heritage Site derived from 40Ar/39Ar dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg*, **255**, 67.

Milner, M.L., Weston, P.H., Rossetto, M. & Crisp, M.D. (2015) Biogeography of the Gondwanan genus *Lomatia* (Proteaceae): vicariance at continental and intercontinental scales. *Journal of Biogeography*, **42**, 2440–2451.

Pelletier, B. (2007) Geology of the New Caledonia region and its implications for the study of the New Caledonia biodiversity. In: *Compendium of Marine Species of New Caledonia. Dossiers Scientifiques Et Techniques. 117, Seconde Édition* (ed. by C.E. Payri and B. Richer de Forges), 19–32. IRD, Nouméa.

Price, J.P. & Clague, D.A. (2002) How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **269**, 2429–2435.

Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4–14.

Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299–2311.

Renner, S.S., Strijk, J.S., Strasberg, D. & Thébaud, C. (2010) Biogeography of the Monimiaceae (Laurales): a role for East Gondwana and long-distance dispersal, but not West Gondwana. *Journal of Biogeography*, **37**, 1227–1238.

Ronquist, F. (1997) Dispersal–vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.

Ronquist, F., Teslenko, M., van der Mark, P. *et al.* (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event–based models: plant versus animal patterns. *Systematic Biology*, **53**, 216–243.

Schellart, W.P., Lister, G.S. & Toy, V.G. (2006) A Late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: tectonics controlled by subduction and slab rollback processes. *Earth-Science Reviews*, **76**, 191–233.

Schellart, W.P., Kennett, B.L.N., Spakman, W. & Amaru, M. (2009) Plate reconstructions and tomography reveal a fossil lower mantle slab below the Tasman Sea. *Earth and Planetary Science Letters*, **278**, 143–151.

Seton, M., Müller, R.D., Zahirovic, S. *et al.* (2012) Global continental and ocean basin reconstructions since 200Ma. *Earth-Science Reviews*, **113**, 212–270.

Short, A.E.Z. & Fikáček, M. (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). *Acta Entomologica Musei Nationalis Pragae*, **51**, 83–122.

Short, A.E.Z, Cole, J. & Toussaint, E.F.A. (2017) Phylogeny, classification, and evolution of the water scavenger beetle tribe Hydrobiusini inferred from morphology and molecules (Coleoptera: Hydrophilidae: Hydrophilinae). *Systematic Entomology*, in press, https://doi.org/10.1111/syen.12239.

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, **30**, 2725–2729.

Thomas, N., Bruhl, J.J., Ford, A. & Weston, P.H. (2014) Molecular dating of Winteraceae reveals a complex biogeographical history involving both ancient Gondwanan vicariance and long-distance dispersal. *Journal of Biogeography*, **41**, 894–904.

Toussaint, E.F.A., Hendrich, L., Shaverdo, H. & Balke, M. (2015) Mosaic patterns of diversification dynamics following the colonization of Melanesian islands. *Scientific Reports*, **5**, 16016.

Toussaint, E.F.A., Fikáček, M. & Short, A.E.Z. (2016) India–Madagascar vicariance explains cascade beetle biogeography. *Biological Journal of the Linnean Society*, **118**, 982–991.

Toussaint, E.F.A., Hendrich, L., Hájek, J., Michat, M.C., Panjaitan, R., Short, A.E.Z. & Balke, M. (2017a) Evolution of Pacific Rim diving beetles sheds light on Amphi-Pacific biogeography. *Ecography*, **40**, 500–510.

Toussaint, E.F.A., Seidel, M., Arriaga-Varela, E. *et al.* (2017b) The peril of dating beetles. *Systematic Entomology*, **42**, 1–10.

Toussaint, E.F.A., Bloom, D. & Short, A.E.Z. (2017c) Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. *Journal of Biogeography*, in press, https://doi.org/10.1111/jbi.12977.

Xie, W., Lewis, P.O., Fan, Y., Kuo, L. & Chen, M.H. (2011) Improving marginal likelihood estimation for Bayesian phylogenetic model selection. *Systematic Biology*, **60**, 150–160.

Wahlberg, N. & Rubinoff, D. (2011) Vagility across *Vanessa* (Lepidoptera: Nymphalidae): mobility in butterfly species does not inhibit the formation and persistence of isolated sister taxa. *Systematic Entomology*, **36**, 362–370.

Winkworth, R.C., Hennion, F., Prinzing, A. & Wagstaff, S.J. (2015) Explaining the disjunct distributions of austral plants: the roles of Antarctic and direct dispersal routes. *Journal of Biogeography*, **42**, 1197–1209.

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