Syst. Biol. 64(1):3–24, 2015

DOI:10.1093/sysbio/syu067
Advance Access publication August 29, 2014

Unveiling the Diversification Dynamics of Australasian Predaceous Diving Beetles in the Cenozoic

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Received 26 June 2013; reviews returned 18 June 2014; accepted 18 July 2014
Associate Editor: Brian Wiegmann

Abstract.—During the Cenozoic, Australia experienced major climatic shifts that have had dramatic ecological consequences for the modern biota. Mesic tropical ecosystems were progressively restricted to the coasts and replaced by arid-adapted floral and faunal communities. Whilst the role of aridification has been investigated in a wide range of terrestrial lineages, the response of freshwater clades remains poorly investigated. To gain insights into the diversification processes underlying a freshwater radiation, we studied the evolutionary history of the Australasian predaceous diving beetles of the tribe Hydroporini (147 described species). We used an integrative approach including the latest methods in phylogenetics, divergence time estimation, ancestral character state reconstruction, and likelihood-based methods of diversification rate estimation. Phylogenies and dating analyses were reconstructed with molecular data from seven genes (mitochondrial and nuclear) for 117 species (plus 12 outgroups). Robust and well-resolved phylogenies indicate a late Oligocene origin of Australasian Hydroporini. Biogeographic analyses suggest an origin in the East Coast region of Australia, and a dynamic biogeographic scenario implying dispersal events. The group successfully colonized the tropical coastal regions carved by a rampant desertification, and also colonized groundwater ecosystems in Central Australia. Diversification rate analyses suggest that the ongoing aridification of Australia initiated in the Miocene contributed to a major wave of extinctions since the late Pliocene probably attributable to an increasing aridity, range contractions and seasonally disruptions resulting from Quaternary climatic changes. When comparing subterranean and epigean genera, our results show that contrasting mechanisms drove their diversification and therefore current diversity pattern. The Australasian Hydroporini radiation reflects a combination of processes that promoted both diversification, resulting from new ecological opportunities driven by initial aridification, and a subsequent loss of mesic adapted diversity due to increasing aridity. [Australian aridification; diversification; Dytiscidae; Pleistocene extinction; freshwater biota; ground water organisms; Hydroporini.]

Unfolding macroevolutionary processes driving the assemblage of ecological communities across geological timescales is one of the most riveting challenges in biology (Ricklefs 2004). Modern molecular phylogenetic techniques allow the reconstruction of time-calibrated trees to unveil evolutionary radiations in taxonomic groups ranging from insects (Moreau et al. 2006; Hunt et al. 2007; Wiegmann et al. 2011) to tetrapods (Bininda-Emonds et al. 2007; Fritz and Rahbek 2012; Jetz et al. 2012), and from plants (Nagalingum et al. 2011; Soltis et al. 2011; Leslie et al. 2012) to microbial organisms (Morlon et al. 2012). In the last decade, starting from the simple lineages-through-time (LTT) plots (Ricklefs 2007) and the later development of more complex birth–death models to estimate speciation and extinction rates (Stadler 2013), macroevolutionary analyses of phylogenetic trees have made substantial progress to better reveal the tempo and mode of species diversification. A predominant pattern generally inferred in terrestrial radiations is characterized by an early rapid (or even explosive) speciation followed by declining diversification rates (Harmon et al. 2003; McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008; Gavrilets and Losos 2009; Morlon et al. 2012). This common pattern departs from the predictions of constant rate models and is often attributed to the theory of adaptive radiation (Glor 2010). By contrast, radiations of freshwater clades are less well-documented, yet they offer an opportunity to study evolutionary processes because of their ecological specialization, dependency on aquatic resources, often high species richness and relative ease to obtain good species-level coverage even on a continental scale. Very few studies have used macroevolutionary approaches to reveal diversification patterns in freshwater radiations (Day et al. 2013; Morvan et al. 2013). Freshwater clades studied so far exhibit a constant rate of diversification (Day et al. 2013; Morvan et al. 2013). Because too few empirical macroevolutionary case studies have been done to date, this result can be questioned and does not reflect a generality about the tempo and mode of freshwater diversification.

In this context, species-rich and globally distributed clades represent an ideal framework to advance our understanding of the processes governing the dynamics and assembly of biological diversity in freshwater ecosystems over spatio-temporal scales (Derryberry et al. 2011; Condamine et al. 2012; Drummond et al. 2012a). The ongoing development of methods to infer the tempo and mode of diversification at macroevolutionary scales has provided new opportunities to address questions regarding the underlying mechanisms of

geographic range evolution (Ree and Smith 2008; Ronquist and Sanmartín 2011) and among lineage variation in diversification rates (Rabosky 2006; Rabosky and Lovette 2008; FitzJohn et al. 2009; Goldberg et al. 2011; Morlon et al. 2011; Stadler 2011; Etienne et al. 2012). Although those methods are powerful tools, they highly rely on the quality of the taxon sampling (Heath et al. 2008). Ideally, about 80% of species should be included; otherwise diversification models can lead to inaccurate estimates of speciation and extinction rates (Cusimano and Renner 2010; Davis et al. 2013). This is particularly true when a decrease in diversification rates is inferred, a pattern that has been taken as evidence of adaptive radiation (e.g., Harmon et al. 2003; Glor 2010) or diversity-dependent diversification (Phillimore and Price 2008). Assembling such a taxon sampling for freshwater organisms of a species-rich clade would therefore offer a good opportunity to provide reliable estimates of diversification rates and gain insights into the processes shaping contemporary diversity (Day et al. 2013; Morvan et al. 2013).

Here, we study Australasian Hydroporini diving beetles (Coleoptera, Dytiscidae) also known as the "*Necterosoma* group" (Ribera et al. 2008), an endemic radiation of 11 genera distributed across the entire Australian continent and a few neighboring islands such as New Guinea, New Caledonia and Fiji. The 147 extant species occupy various types of lentic and lotic habitats such as well oxygenated rivers (*Barretthydrus*, *Carabhydrus*, *Sekaliporus*), protected embayments and rest pools of slow-flowing streams or standing water pools and saline lakes (*Chostonectes*, *Megaporus*, *Necterosoma*, *Sternopriscus, Tiporus*) but also swamps and peatlands (*Antiporus*, the new genus "*Brancuporus*" in description, *Sternopriscus*) (Watts 1997, 2002; Hendrich 2003, 2008; Hendrich and Watts 2009; Hawlitschek et al. 2011, 2012; Hendrich et al. 2014). Although some previous phylogenetic studies have investigated relationships and divergence times (Leys et al. 2003; Leijs et al. 2012), an accurate and comprehensive phylogenetic framework is still lacking to infer historical biogeography, diversification dynamics, and the processes governing this freshwater radiation.

This group is not only relevant to study a continental-scale Australasian radiation but also to investigate patterns and processes of diversification fostering radiations of two ecologically different lineages. The genera, *Paroster* (47 species) and *Sternopriscus* (29 species), are of particular interest because they represent the most species-rich hypogean and epigean Australian genera, respectively. *Paroster* contains species restricted to calcrete aquifers (underground water) of Western and Central Australia as well as epigean species distributed in mesic habitats of the southern part of the range (Watts and Humphrey 1999–2009; Watts et al. 2008; Hendrich and Fery 2008). Most authors aiming at deciphering the origin of hypogean taxa proposed that these lineages might have colonized underground ecosystems in response to climatic change (e.g., Leys et al. 2003; Faille et al. 2010). For Australian diving beetles, the dominant hypothesis has proposed that the *Paroster* radiation is the result of a groundwater colonization following the onset of Miocene aridification at *ca*. 15 million years ago (Ma) (Leys et al. 2003). At this time, epigean populations might have colonized subterranean aquifers to avoid increasing aridity. As a result, the genus harbors morphological features to specialized underground life including wing-loss, depigmentation and eye reduction. On the other hand, the genus *Sternopriscus*, whilst being characterized by elevated diversity, comprises species that do not show clear ecomorphological disparity (Hawlitschek et al. 2012). The genus is so morphologically homogeneous that many species are only revealed using genitalia and male secondary sexual characters. *Sternopriscus* is mostly distributed in Australian mesic areas such as southeastern, southwestern and northern coasts, and species inhabit a wide variety of lentic and lotic habitats from sea level to high altitudes. Such successful colonization is possible due to flight capacity. The high level of endemism in the southeast and southwest suggests that the arid barrier between these two regions is long-standing. Hypotheses on its origin supposed that the dynamics of biogeographical landscapes and the emergence of allo/parapatric barriers were the main drivers of this radiation (Hawlitschek et al. 2012). In particular, the role of complex climatic disruptions during the Pliocene and especially since the early Quaternary might have played an important role in shaping patterns of diversity and distribution in this radiation. The Quaternary climate changes constitute a period of deep modifications in both climatic regimes and ecological conditions in Australia. This period of time has been marked by global cooling and drying, alteration of rainfall seasonality, especially in Southern Australia, vegetation turnover and local emergence of new high altitude niches (Sniderman et al. 2007, 2009, 2013; Byrne et al. 2008). Rainfall seasonality disruptions which principally occurred in the Pleistocene might be one of the underlying mechanisms triggering diversification dynamics of these aquatic carnivorous beetles. Understanding and defining both radiation patterns is critical in order to understand the deterministic forces that shape the diversification and structure of freshwater community assemblies. Using these two clades that have diversified against a common biogeographic and ecological background, a multidisciplinary and integrative approach at the interface between macroevolution and ecological theory will help in the study of the processes of their radiation.

Here, we use a near-complete species-level coverage of the Australasian Hydroporini to: (i) provide for the first time a robust time-calibrated phylogenetic framework of the group combining nuclear and mitochondrial markers; (ii) investigate the potential effect of aridification on the radiation of the group using the latest methods to infer historical biogeography and diversification rates; (iii) contrast the diversification patterns and processes between the radiations of *Paroster* and *Sternopriscus*; and (iv) compare and discuss our results with previous studies regarding the evolution

of Australasian Hydroporini and also regarding the impact of past climate changes on the Australian fauna in general.

Materials and Methods

Taxon Sampling and Molecular Biology

We included 117 of the 147 described species (≈80%) and all genera of Australasian Hydroporini (Online Appendix 1 available on Dryad http://dx.doi.org/10.5061/dryad.c5g23, Nilsson 2001, 2006; Watts et al. 2008; Watts and Humphrey 2006, 2009; Hendrich 2008; Hendrich and Fery 2008; Hendrich and Watts 2009; Hendrich et al. 2014). Outgroups were 12 species of Bidessini, Hyphydrini, Laccornini, and Vatellini (Appendix 1): the closest tribes to Australasian Hydroporini within Hydroporinae (Ribera et al. 2008). We included several genera for each tribe when possible to improve both phylogenetic resolution and branch length estimation. *Coptotomus* was selected to root the tree since Coptotominae has been found in sister position to the subfamily Hydroporinae (Ribera et al. 2008). Since the genus *Paroster* mainly comprises rare, sometimes monotypic and excessively difficult to sample hypogean species, almost all the sequences used in this study (CO1 and 16S) were recovered from GenBank. In addition to previously sequenced species and in order to improve the placement of the genus in the group, we sequenced mitochondrial and nuclear markers (see below) for four epigean species of *Paroster* diving beetles (Leys and Watts 2008).

Total genomic DNA was extracted from legs, thoracic and head tissues of specimens kept in 96% ethanol using the DNeasy kit (Qiagen, Hilden, Germany). Using standard PCR protocols (Appendix 2) we amplified and then sequenced the following genes: ribosomal 16S (16S, 769 base pairs [bp]), cytochrome oxidase subunit 1 (COI, 741 bp), cytochrome b (CytB, 390 bp), ribosomal 18S (18S, 607 bp), histone 3 (H3, 321 bp), histone 4 (H4, 203 bp), and arginine kinase (ARK, 636 bp). All sequences of the genus *Sternopriscus* were recovered from a recent publication (Hawlitschek et al. 2012.). The DNA sequences were eye corrected under Geneious R6 (Biomatters, http://www.geneious.com/), aligned using Muscle (Edgar 2004) and the reading frames checked under Mesquite 2.75 (http://mesquiteproject.org). The different datasets used to infer phylogenetic relationships were generated under Mesquite. All sequences were deposited in GenBank (accession Nos. HG965576-HG965750).

Phylogeny

We used Bayesian Inference (BI) and Maximum Likelihood (ML) to reconstruct phylogenetic relationships. For each partition (Table 1), the optimal model of substitution was selected under jModeltest 2.1.3 (Darriba et al. 2012) using the Bayesian Information Criterion (BIC). For BI analyses, we used MrBayes 3.2.1 (Ronquist et al. 2012) and partitioning schemes listed in Table 1. Two simultaneous and independent runs consisting of eight Metropolis-coupled Markov chain Monte Carlo (MCMC, one cold and seven incrementally heated) chains and 40 million generations were performed, with a tree sampling every 1000 generations to calculate posterior probabilities (PP). In order to investigate the convergence of the runs we investigated the split frequencies and Effective Sample Size (ESS) of all the parameters, and plotted the log-likelihood of the samples against the number of generations 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 the trees that predated the time needed to reach a log-likelihood plateau were discarded as burn-in, and the remaining samples were used to generate a 50% majority rule consensus tree. The best partitioning scheme was selected according to Bayes Factors (B_F) based on average marginal likelihoods of dual runs estimated using Stepping-stone sampling (Xie et al. 2011). $2\times \ln(B_F)$ scores superior to 10 were considered good indicators of a significantly better partitioning scheme over another (Kass and Raftery 1995). The ML analyses were conducted with

Table 1. Partitioning schemes used for the phylogenetic reconstructions

Partitioning scheme	Details
P1 (NoPart) [1]	Unpartitioned dataset
P2 (ByType) [2]	One partition for the coding genes and one partition for the noncoding genes
P3 (ByGenome) [2]	One partition for the mitochondrial genes and one partition for the nuclear genes
P4 (ByThree) [3]	One partition for the mitochondrial coding genes, one partition for the nuclear coding genes and one partition for the noncoding genes
P5 (ByFour) [4]	One partition per codon position for the coding genes and one partition for the noncoding genes
P6 (BySeven) [7]	One partition per codon position for the mitochondrial genes, one partition per codon position for the nuclear genes and one partition for the noncoding genes
P7 (ByGene) [8]	One partition for each gene
P8 (ByEight) [8]	One partition per codon position for the mitochondrial genes, one partition per codon position for the nuclear genes and one partition for each noncoding gene
P9 (BySixteen) [16]	One partition per codon of each coding gene and one partition for the noncoding genes
P10 (ByMax) [17]	One partition per codon of each coding gene and one partition for each noncoding gene

Notes: The number of partition(s) is given in square brackets for each partitioning scheme.

the best partitioning scheme selected in BI using RAxML (Stamatakis 2006). We performed 1000 *Bootstrap* replicates (BS) to investigate the level of support at each node. A calculated PP >0.95 or a BS >70 was considered to indicate strong support for a given clade (Felsenstein 2004).

Divergence Time Estimation

In order to account for the difficulty of estimating divergence times with confidence, we chose to perform three independent sets of analyses using BEAST 1.7.4 (Drummond et al. 2012b). Prior to this, we tested whether or not the fragments contained in the sequence matrix evolve in a clockwise fashion, using PAUP* (Swofford 2003) to calculate the likelihood with and without enforcing a strict molecular clock. A likelihood ratio test (LRT) was carried out in the same software in order to compare both results, and since the molecular clock hypothesis was not statistically supported (P <0.0001), we used a relaxed clock allowing rate variation among lineages as implemented in BEAST.

First, we used the molecular matrix of the COI gene in combination with different divergence rates calculated for Coleoptera lineages (Balke et al. 2009; Papadopoulou et al. 2010; Andújar et al. 2012). Instead of running several independent analyses with the different rates of evolution calculated in these studies, we used an interval encompassing the different rate values and representative of the idiosyncratic variation of divergence rates within Coleoptera (for recent examples see Tänzler et al. 2014 and Toussaint et al. 2014). First, we used the substitution rate (r = 0.0195; r is the substitutions per site per million years per lineage, subs/s/Myr/l) of *Rhantus* diving beetles calculated by Balke et al. (2009) based on the age of Tahiti. Second, we included the rate of evolution (r = 0.0177 subs/s/Myr/l) of several darkling beetle genera (Tenebrionidae) calculated by Papadopoulou et al. (2010) using the biogeographic history of the Aegean archipelago. Finally, we used the rate of evolution (0.0145 subs/s/Myr/l) inferred from a dated phylogeny of the genus *Carabus* (Carabidae) based on multiple geological and fossil evidence (Andújar et al. 2012). The introduced interval (0.0145–0.0195 subs/s/Myr/l) was used to specify a uniform distribution on the *ucld.mean* (Lower = 0.0145, Upper = 0.0195) therefore taking into account the variation of divergence rates across lineages. The root of the tree was constrained with a Uniform distribution (Lower = 0, Upper = 150) so that the age could not be older than 150 Ma; approximately the age of the oldest dytiscid fossil ever discovered (Ponomarenko 1987). The *Substitution Model* was set accordingly to the jMODELTEST result for the COI dataset, and the *Tree Model* was set to a Yule and a birth–death model in different analyses, each analysis consisting of a 50 million generation run sampled every 1000 generations.

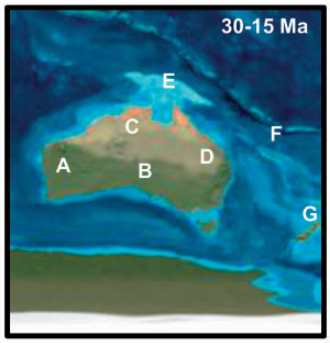
Second, we used the whole molecular dataset (seven genes) and the only unambiguous hydroporine fossil known to calibrate the tree: †*Calicovatellus petrodytes* Miller and Lubkin from the mid-Miocene (see Appendix 3 for more details). Since we included the two extant genera of the tribe Vatellini in the dataset (see Miller 2005 for a revision), but not all the species of the genera, and since the fossil is likely to be sister to the extant genera, we chose in a conservative way to place the calibration point on the stem of the tribe Vatellini based on the "apomorphy-based method" described in Sauquet et al. (2012). The choice of a prior distribution for calibration points is a critical step in dating inference (Ho and Phillips 2009). In order to account for possible biases related to the use of a single calibration point, we carried out different analyses with the Exponential, Lognormal, and Uniform distribution laws as prior for the stem of the tribe Vatellini. We therefore placed a minimum bound on this calibration point with the different priors, so that the 95% confidence interval ranged from 14.8 Ma, the age of the fossil (Woodburne et al. 1990; Miller and Lubkin 2001; towards 150.0 Ma. Parameters for the distribution laws were as follow: Exponential (*Mean* = 36.9, *Offset* = 13.865), Lognormal (Log_{Mean} = 1.44, Log_{Stdev} = 1.7691, *Offset* = 14.669), and *Uniform* (*Lower* = 14.8, *Upper* = 150.0). The tree root was constrained with the same prior as in the first calibration set, and likewise, both Yule and birth–death Tree Models were used in different analyses. The run settings were selected to be the same as the first set of calibration as well, with the best partitioning scheme recovered in phlogenetic analyses.

Third, we carried out a set of analyses based on the molecular matrix of the COI gene and the fossil data to calculate the rate of evolution within the radiation of Australasian Hydroporini. This set of analyses was performed as a cross-validation to check the applicability of the interval of substitution rates (0.0145–0.0195 subs/s/Myr/l) on our data. All settings were the same as the one used to calibrate the MRBAYES topology using the full dataset and the fossil of †*Calicovatellus petrodytes*. We also conducted different analyses using both Yule and birth–death Models.

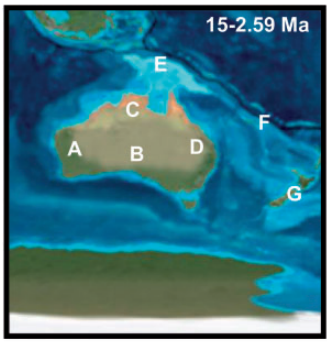
For all analyses, the best BI topology was used to perform dating analyses in order to optimize the search of optimal ages through a minimization of parameter space to explore. The convergence of the runs was investigated using ESS, a conservative burn-in of 25% applied after checking the log-likelihood curves and the different runs merged using LOGCOMBINER 1.7.4 (Drummond et al. 2012b). The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated afterwards under TREEANNOTATOR 1.7.4 (Drummond et al. 2012b). The best analysis was selected based on BF estimates derived from marginal likelihoods of the runs using both the fossil and the CO1 dataset.

ANCESTRAL RANGE RECONSTRUCTION

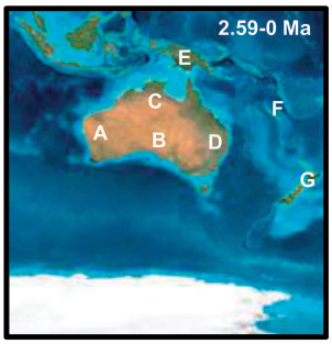
We used the likelihood model Dispersal–Extinction–Cladogenesis (DEC, Ree et al. 2005; Ree and Smith 2008) implemented in LAGRANGE (www.reelab.net/lagrange)



	A	B	C	D	E	F	G
A	-	0.75	0.75	0.5	0.01	0.01	0.01
B		-	0.75	0.75	0.01	0.01	0.01
C			-	0.75	0.01	0.01	0.01
D				-	0.01	0.01	0.01
E					-	0.01	0.01
F						-	0.01
G							-



	A	B	C	D	E	F	G
A	-	0.5	0.25	0.125	0.01	0.01	0.01
B		-	0.5	0.5	0.01	0.01	0.01
C			-	0.5	0.01	0.01	0.01
D				-	0.01	0.01	0.01
E					-	0.01	0.01
F						-	0.01
G							-



	A	B	C	D	E	F	G
A	-	0.25	0.125	0.01	0.01	0.01	0.01
B		-	0.25	0.5	0.01	0.01	0.01
C			-	0.5	0.5	0.01	0.01
D				-	0.125	0.01	0.01
E					-	0.125	0.01
F						-	0.01
G							-

FIGURE 1. Dispersal rate matrices used for biogeographic analyses. Paleogeographical model used for the stratified biogeographical analyses (transitional matrices of dispersal rates between areas) implemented in the Dispersal-Extinction-Cladogenesis model. Maps redrawn from Blakey (2008). A) Pilbara Province + Southwestern Province; B) Paleo Province + Central Australian Province; C) Northern Province + Queensland Province; D) Eastern Province and Tasmanian Province; E, New Guinea; F, New Caledonia + Fiji; G, New Zealand.

to infer ancestral ranges and colonization history of the Australasian members of the tribe Hydroporini. The analyses were carried out based on the different BEAST chronograms with outgroups removed.

The biogeographic regions used in this study were modified from Unmack (2001) to account for present distribution patterns of Australasian Hydroporini (Watts 1997, 2002; Hendrich 2003, 2008; Hendrich and Fery 2008; Hendrich and Watts 2009; Hawlitschek et al. 2011, 2012; and our field notes) (Fig. 1). The seven selected areas yielded a set of $2^7 = 128$ theoretically possible ranges from which we excluded those relying on biological implausibility such as widely disjoint areas. We computed a matrix in which each species was coded as present or absent for each area considered in the analyses (Appendix 1). The choice of temporal constraints and dispersal rates between the discrete distribution ranges was based on paleogeographic and paleoclimatic data (Drexel et al. 1995; Hall 2002, 2011; Hope et al. 2004; Miller 2005; Martin 2006; Byrne et al. 2008, 2011). In order to account for landmass movements and area heterogeneity through time, we defined three time slices spanning the past 30 Ma with the first ranging from 30 Ma to 15 Ma (corresponding to a tropical Australia), the second from 15 Ma to 2.59 Ma (representing the Australian aridification) and the last from 2.59 Ma to present (for the Quaternary climate change) (see Appendix 4 for rationales on the choice of time slices).

Following the principles described in Ree and Smith (2008), we constructed for each time slice a matrix of scaling factors representing dispersal rates between ranges (Fig. 1), and accounting for the geographic position of the areas and their connectivity (biogeographic barriers, ecological corridors). Dispersal rates values were set for each time slice based on paleo-reconstruction evidence (Voris 2000; Hall 2002, 2011; Hope et al. 2004), with long-distance dispersal events

(e.g., Southwestern Australia–New Zealand) authorized with a dispersal rate of 0.01 (in the last time slice, the dispersal rate is fixed to 0.125 instead of 0.01 to account for likely land-connections between New Guinea and Australia).

In order to improve the accuracy and feasibility of the analysis, we enforced all possible combinations of areas at the root and carried out further global likelihood comparisons to select the most likely ancestral area. A difference between potential combinations equal or >2 log-likelihood units was considered significant (Ree et al. 2005; Ree and Smith 2008).

Diversification Analyses

The tempo and mode of diversification were investigated using birth–death methods. We used all chronograms inferred with fossil or rate calibrations for the Australasian Hydroporini, *Paroster* and *Sternopriscus*. Diversification analyses were performed under the R 2.15 software implementing the *ape* ((Paradis et al., 2004)), *diversitree* ((FitzJohn, 2012)), *picante* ((Kembel et al., 2010)), and TreePar ((Stadler, 2011)) packages.

Time-dependent analyses.—First, we used the TreePar approach (Stadler 2011) with the "*bd.shifts.optim*" function allowing the estimation of discrete changes in speciation and extinction rates in possibly incompletely sampled phylogenies. It estimates the maximum likelihood speciation and extinction rates together with the shift times $t = (t_1,t_2,...,t_n)$ in a phylogeny (at the times t, the rates are allowed to change). TreePar analyses were run with: start = 0, end = crown age estimated by dating analyses, grid = 0.1 Myr, sampling fraction = 117/147, 38/47, 27/29 for, respectively, the Australasian Hydroporini, *Paroster*, and *Sternopriscus*, four possible shift times were tested, and posdiv = FALSE to allow the diversification rate to be negative (i.e., allows for periods of declining diversity).

Second, we used the approach of Morlon et al. (2011). Contrary to TreePar, this method has the advantage to take into account the heterogeneity of diversification rates across the tree such that clades may have their own speciation and extinction rates (and their own diversity dynamics), and to estimate continuous variations of rates over time (when discrete in TreePar). Like TreePar, the Morlon et al.'s approach is suitable to potentially infer a declining diversity pattern in which extinction can exceed speciation meaning that diversification rates can be negative (Morlon et al. 2011). We designed four models to be tested: (i) BCSTDCST, speciation and extinction rates are constant; (ii) BVARDCST, speciation rate is exponentially varying and extinction rate is constant; (iii) BCSTDVAR, speciation rate is constant and extinction rate is exponentially varying; and (iv) BVARDVAR, speciation and extinction rates are exponentially varying. The Australasian Hydroporini tree was analyzed as a whole using this approach and missing species were taken into account (stating $f = 117/147$). However, the heterogeneity of diversification rate can mask the phylogenetic signal of some clades for instance recently diversifying clades with short branch lengths vs. ancient clades that diversified early and then experienced slowdown of diversification (Morlon et al. 2011). To identify different evolutionary diversification among genera, we fitted the MEDUSA approach on a genus-level chronogram of which we informed the species richness of each genus in order to find whether rates varied across the tree (Alfaro et al. 2009). Based on the eventual presence of different rates per genus, we subsequently defined subtrees corresponding to each genus recovered by MEDUSA analyses. After isolating these genera and accounting for the missing species in each, we fitted the same diversification models.

Trait-dependent analyses

We assessed the impact of living in subterranean areas (calcrete aquifers) vs. living in epigean areas (surface habitats) by testing the hypothesis of higher diversification rates due to aridification of Australia in the Miocene and the extensive loss of mesic habitats. We used the Binary State Speciation Extinction model (BiSSE; Maddison et al. [2007]) implemented in the *diversitree* package (FitzJohn 2012). We built the likelihood function using "*make.bisse*," that is then optimized by maximum likelihood using "*find.mle.*" Different models were run to test whether speciation, extinction, or transition rates were independent or constrained by the trait. Eight models were built with an increasing complexity starting from the simplest model with no difference in speciation, extinction and transition rates for all character states (three parameters) to the most complex model with speciation, extinction, and transition rates varying independently in each of the character states (six parameters). We also accounted for incomplete taxon sampling (FitzJohn et al. 2009). We estimated posterior density distribution with Bayesian MCMC analyses (10,000 steps) performed with the best-fitting models and the resulting speciation, extinction and dispersal rates.

Diversity-dependent analyses.—We tested the hypothesis that diversity is bounded or at equilibrium meaning that diversity has expanded rapidly in its early stage of diversification and saturates towards the present. We thus explored the effect of diversity on speciation and extinction rates. We used the method of Etienne et al. (2012) implemented in TreePar. The function "*bd.densdep.optim*" was used to fit this model with the following settings for the Australasian Hydroporini, *Paroster* and *Sternopriscus*: discrete = TRUE, the missing species were taken into account (rho = 117/147, 38/47, and 27/29, respectively), an initial carrying capacity (minK) set at 147, 47, and 29, respectively. The final carrying capacity (maxK) was fixed at 1.5× extant diversity of each clade.

Results

Phylogenetic Relationships

The concatenated alignment of 16S, COI, CytB, 18S, H3, H4 and ARK gene fragments comprised 3668 bp for a total of about 37% of missing data in the final matrix and an average gene coverage of 2266 bp. Among the 1287 polymorphic sites, about 30% were contained in the nuclear markers and 70% in the mitochondrial ones. A table highlighting the gene coverage for each genus is available in Appendix 5, and the models of sequence evolution selected by jModelTest for each partition are listed in Appendix 6. All phylogenetic analyses using BI and ML converged well except the BI analysis for partitioning scheme *P8* (*ByEight*) that did not reach convergence even after 40 million generations and was discarded from further comparisons. In accordance with the B_F estimates (Table 2), the partitioning scheme *P6* (*BySeven*) was selected, and the resulting topology is presented in Figure 2 along with values of support for the ML analysis conducted with the partitioning scheme *P6*.

The subfamily Hydroporinae and its tribes were recovered monophyletic with strong support both in BI (PP = 1.0) and ML (BS = 100), except for lower support for Hyphydrini (PP = 1.0/BS = 52) and Australasian Hydroporini (PP = 1.0/BS = 84). Within the latter *Chostonectes* was paraphyletic in the BI analysis and monophyletic in the ML analysis due to the inclusion of *Megaporus* with low support in both analyses (PP = 78/BS = 27). A clade containing *Antiporus*, "*Brancuporus*," *Sekaliporus* and *Tiporus* is recovered as sister of *Chostonectes* + *Megaporus* with high support (PP = 1.0/BS = 100). This first large clade is recovered in a moderately to strongly supported sister position (PP = 1.0/BS = 64) to the rest of the genera nested in a second one (PP = 1.0/BS = 53). Within the latter, *Paroster* is the sister of ([*Necterosoma*] +[*Carabhydrus* + {*Barretthydrus* + *Sternopriscus*}]). The ML and BI analyses were highly congruent with almost 90% of the nodes recovered in both methods and except the possible paraphyly of *Chostonectes*, present no major divergences since the only conflicting nodes involve terminal taxa arrangements.

Divergence Time Estimates

The different types of calibration yielded highly similar results (Table 3), and the choice of distribution as a prior for the fossil calibration had a minor impact on the median ages inferred; the largest discrepancies were in the dating of certain outgroup tribes for which median ages are different even though the credibility intervals are broadly overlapping (Table 3). According to B_F calculations (Appendix 7), the best run under both the Yule Model and the Birth Death Model were based on the rate interval introduced in this study. The result of the analysis based on the rate interval and a birth–death model is presented in Figure 3.

The analysis based on the COI matrix and the fossil yielded an estimated mean rate of evolution for this gene ranging from 0.0175 subs/s/Myr/l (Yule model) to 0.0192 subs/s/Myr/l (birth–death model), and estimated ages highly similar with the ones inferred in the two other sets of calibration. Even though Australasian Hydroporini appear to have originated during the mid- to late Oligocene, the branching pattern and the divergence time estimates shown in Figure 3 suggest that most of the extant diversity in Australia is the result of a diversification that initiated during the late Miocene.

Ancestral Range Reconstruction

Figure 4 shows the result from the ancestral range reconstructions yielded by Lagrange with the same chronogram as in Figure 3. All analyses, based on the other chronograms gave identical results with significant support for the Eastern and Tasmanian Provinces (D) as the most likely ancestral area for the group (Table 4). Only the analysis comprising the chronogram based on a Lognormal prior and a Yule model supported D with a nonsignificant value.

Diversification Analyses

Based on the chronograms of all BEAST analyses, we reconstructed the corresponding lineages-though-time plots for all the Australasian Hydroporini and the genera *Paroster* and *Sternopriscus* separately (Fig. 5). Table 5

Table 2. best-fitting strategies of partitioning for the BI analyses with Bayes Factor (B_F) estimates

	Part.	ESS	SSML	*P1*	*P2*	*P3*	*P4*	*P5*	*P6*	*P7*	*P8*	*P9*	*P10*
P1	1	1935	−50847,80	–	*	*	*	*	*	*	NA	*	*
P2	2	1925	−50058,50	**	–	*	*	*	*	*	NA	*	*
P3	2	2601	−49639,95	**	**	–	*	*	*	*	NA	*	*
P4	3	2550	−49128,49	**	**	**	–	**	*	*	NA	*	*
P5	4	1895	−49019,00	**	**	**	*	–	*	*	NA	*	*
P6	7	2167	−47936,38	**	**	**	**	**	–	**	NA	**	**
P7	7	1242	−48697,14	**	**	**	**	**	*	–	NA	*	*
P8	8	118	NA	NA	NA	NA	NA	NA	NA	NA	–	NA	NA
P9	16	915	−48431,59	**	**	**	**	**	*	**	NA	–	*
P10	17	1442	−48143,71	**	**	**	**	**	**	*	NA	**	–

Notes: Part., number of partitions; ESS, Effective Sample Size; SSML, Stepping-Stone Marginal Likelihood; *, 2*ln(B_F)<1 **, 2*ln(B_F)>10, NA, not available.

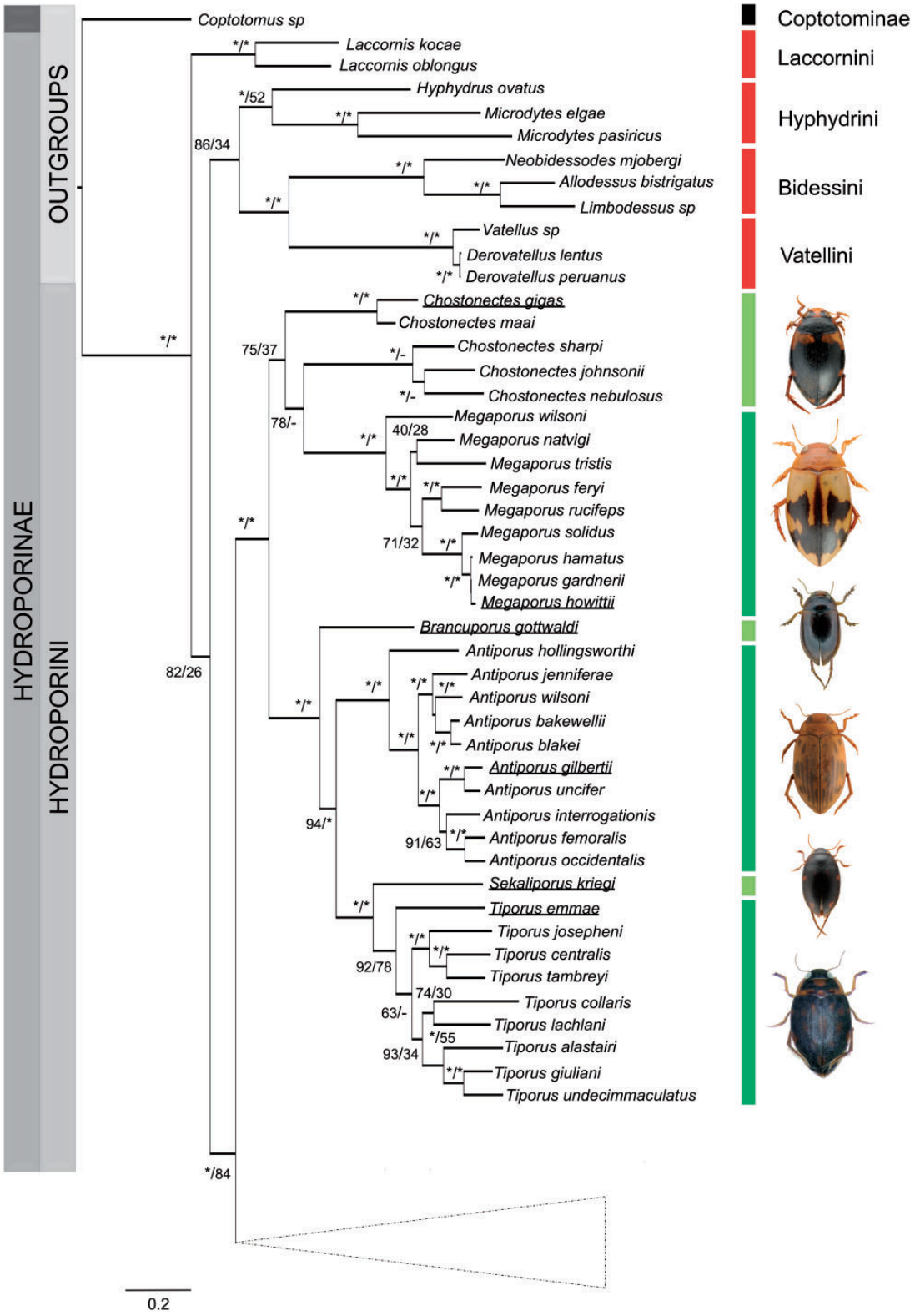


FIGURE 2. Phylogeny of Australasian Hydroporini carnivorous diving beetles. The tree is a 50% majority-rule consensus yielded by the MrBayes analysis based on 16S, 18S, COI, CytB, H3, H4, and ARK. The support of each node is indicated on the topology with respectively the posterior probability (PP) from the BI analysis on the left and the Bootstrap value (BS) from the ML analysis on the right. An asterisk indicates a PP = 1.0 or a BS = 100. The species for which a habitus is displayed have their name underlined.

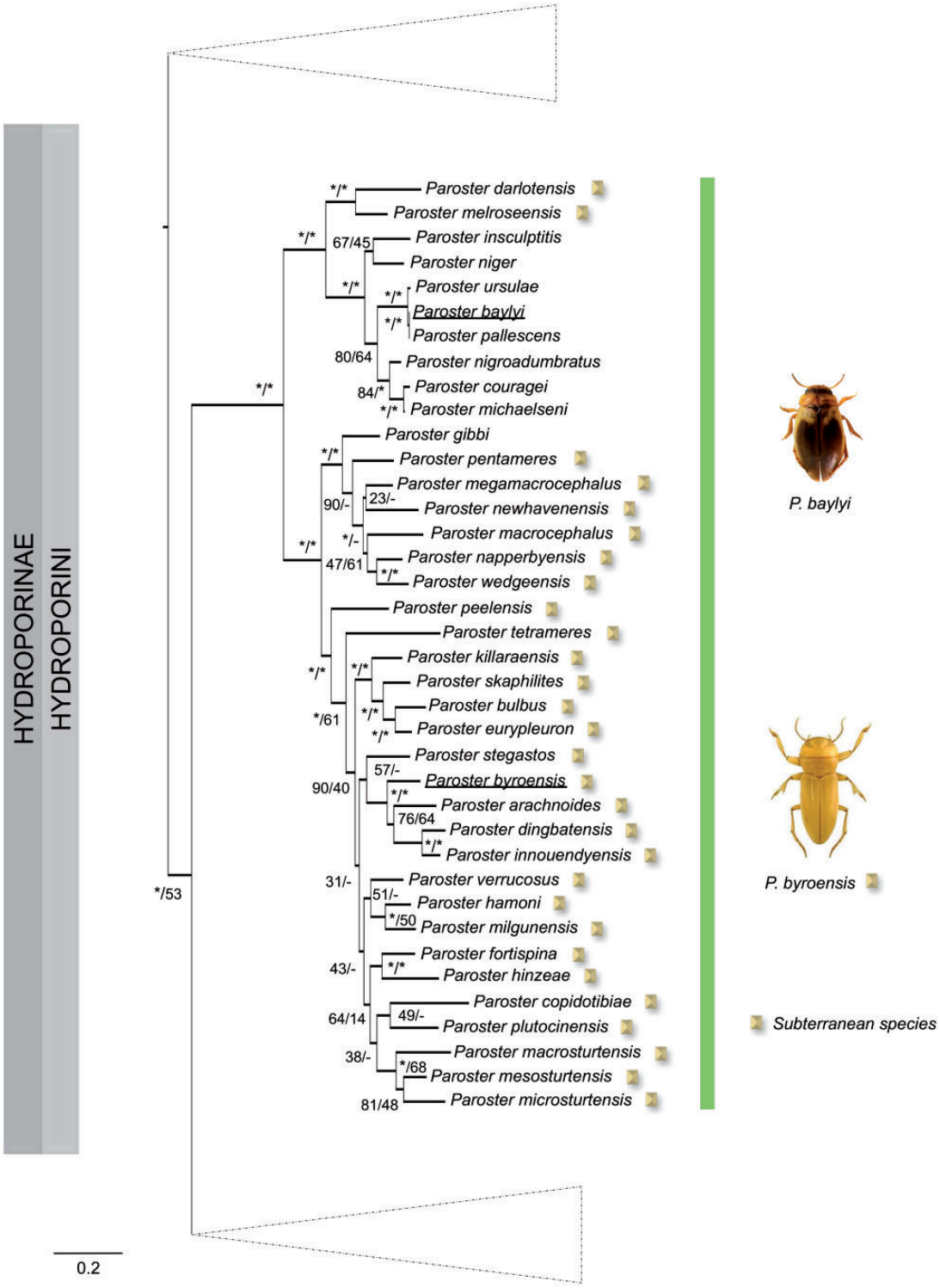


FIGURE 2. Continued.

summarizes the main results of the different analyses conducted on the Australasian Hydroporini and both *Paroster* and *Sternopriscus* genera.

Time-dependent analyses.—For Australasian Hydroporini, TreePar analyses supported a diversification model with varying-rates compared to a constant-rate model (Appendix 8). Interestingly all chronograms (except one that has constant rates) show evidence of recent rate shifts. A rapid initial diversification rate is estimated before the first shift time, which generally occurred in the early Pliocene, and is always followed by a

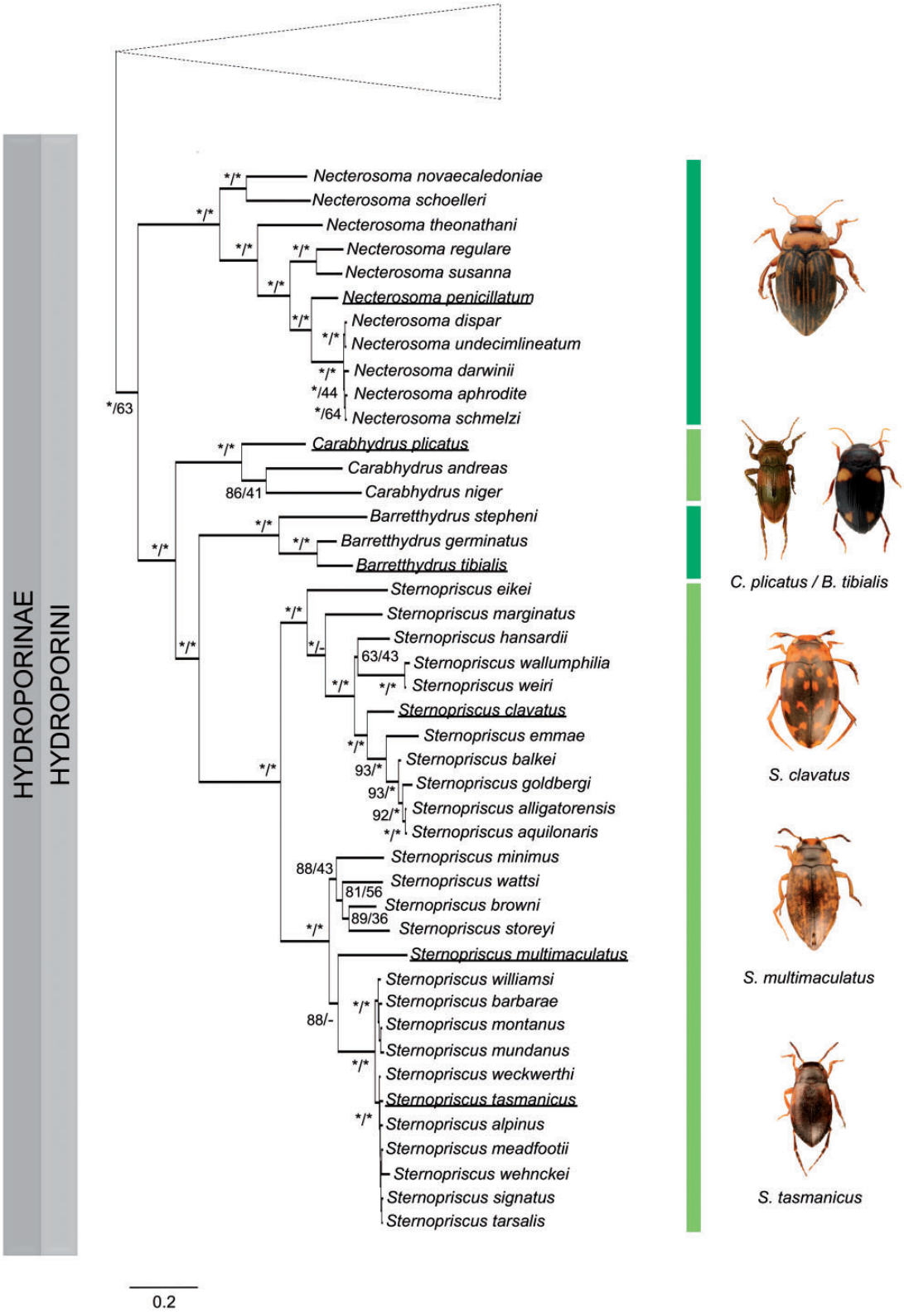


FIGURE 2. Continued.

sharp decrease in diversification rate or a negative diversification rate. The second rate shift occurred in the middle-late Pleistocene. At this period, either a decrease in diversification rate or a negative diversification rate is also recovered. The negative diversification rate at present indicates a declining diversity pattern for the group (extinction rate exceeds speciation rate). The last shift time occurred in the late Pleistocene.

TABLE 3. Median ages and 95% credibility intervals for the different analyses

	Rate *Yule*	Rate *BD*	Fossil *Exp Yule*	Fossil *Exp BD*	Fossil *LogN Yule*	Fossil *LogN BD*	Fossil *Uni Yule*	Fossil *Uni BD*
Root	31.7 (24.3–39.7)	31.7 (24.4–40.0)	32.7 (15.9–68.4)	32.0 (15.8–65.7)	31.5 (18.9–51.7)	31.3 (18.4–57.2)	39.7 (19.4–100.8)	41.9 (19.4–110.2)
Hydroporinae	29.8 (23.6–36.8)	29.6 (23.4–36.9)	30.5 (15.3–63.5)	29.8 (15.4–61.2)	28.0 (17.8–44.2)	28.0 (17.3–49.8)	34.6 (17.6–86.5)	35.5 (18.8–98.7)
Laccornini	17.3 (9.9–25.6)	17.3 (9.7–25.5)	14.8 (5.1–28.8)	15.0 (5.1–29.6)	9.5 (1.6–25.8)	7.0 (2.2–20.0)	9.9 (1.3–30.2)	17.6 (2.5–57.4)
Hyphydrini	23.7 (17.6–30.0)	23.6 (17.5–30.0)	21.6 (11.8–40.0)	22.0 (11.4–41.3)	15.8 (5.2–27.5)	14.2 (5.2–26.7)	17.9 (6.9–44.6)	18.1 (6.3–48.7)
Bidessini	16.0 (11.1–21.4)	15.9 (10.7–21.2)	11.7 (5.7–21.5)	12.0 (5.6–22.7)	9.2 (4.3–14.8)	8.7 (4.0–15.3)	11.6 (4.0–29.3)	11.7 (4.1–28.6)
Vatellini	1.0 (0.4–1.7)	1.0 (0.5–1.7)	2.5 (0.9–4.9)	2.5 (0.8–5.1)	2.2 (0.5–7.9)	2.7 (0.6–9.3)	4.0 (0.7–11.6)	3.9 (0.5–12.8)
Australasian Hydroporini	27.6 (21.8–34.0)	27.5 (21.7–34.0)	27.1 (13.3–56.5)	26.4 (13.4–54.5)	24.1 (14.8–38.0)	23.7 (13.3–43.9)	29.4 (15.3–73.9)	32.5 (16.2–83.9)
Chostonectes+Megaporus	22.6 (17.4–28.4)	22.5 (17.4–28.3)	21.2 (9.9–44.3)	20.8 (9.9–43.0)	17.8 (9.7–28.9)	17.2 (9.1–30.7)	20.4 (8.4–51.2)	23.8 (7.7–61.1)
Megaporus	14.4 (10.3–18.7)	14.3 (10.4–18.7)	11.9 (5.1–25.1)	11.6 (5.2–24.5)	9.4 (4.6–10.3)	10.0 (4.7–16.8)	11.5 (4.4–29.5)	13.0 (4.7–36.4)
*Bra+Ant+Sek+Tip**	22.6 (17.4–28.4)	22.5 (17.4–28.1)	20.0 (9.2–41.6)	19.6 (9.4–40.1)	17.2 (10.1–27.5)	17.2 (8.7–30.6)	20.2 (9.6–52.2)	23.6 (10.6–61.1)
Antiporus	17.4 (12.8–22.7)	17.3 (12.6–22.4)	12.3 (5.3–25.8)	12.0 (5.5–25.0)	11.0 (6.3–17.8)	11.5 (5.7–19.7)	13.0 (6.5–33.9)	13.9 (5.3–36.8)
Sekaliporus+Tiporus	19.5 (14.8–24.7)	19.4 (14.6–24.6)	14.7 (6.8–30.9)	14.4 (6.9–30.2)	11.7 (6.7–19.6)	12.2 (5.9–21.9)	14.2 (6.1–35.8)	16.3 (7.0–44.7)
Tiporus	16.8 (12.5–21.5)	16.6 (12.4–21.3)	12.9 (5.9–27.2)	12.6 (5.8–26.3)	9.7 (5.5–16.2)	10.5 (4.6–18.5)	12.1 (5.2–30.3)	13.5 (5.7–37.9)
Paroster	19.8 (14.9–25.3)	19.7 (14.6–25.2)	14.9 (6.9–31.5)	14.5 (6.9–30.2)	16.4 (8.6–26.1)	15.7 (8.1–27.8)	20.0 (7.7–42.5)	20.7 (9.1–56.5)
Paroster N1	11.8 (8.2–15.7)	11.8 (8.1–15.6)	9.1 (4.5–16.8)	9.2 (4.5–17.7)	9.6 (4.3–17.7)	10.2 (4.5–18.6)	13.5 (4.7–35.2)	12.6 (4.5–37.2)
Paroster N2	13.2 (10.1–17.0)	13.1 (9.8–16.7)	11.4 (6.0–20.7)	11.6 (6.2–22.0)	13.2 (7.0–22.4)	12.8 (6.5–23.2)	16.6 (7.7–42.5)	16.1 (7.4–43.9)
Paroster N3	11.5 (7.9–15.3)	11.4 (7.7–15.4)	7.8 (3.8–14.4)	8.0 (3.8–15.2)	8.9 (3.5–16.7)	8.4 (3.2–17.4)	11.1 (4.0–28.5)	10.5 (3.4–30.0)
Paroster N4	12.5 (9.3–15.9)	12.4 (9.3–15.8)	10.5 (5.6–19.2)	10.7 (5.7–20.4)	11.6 (5.7–19.9)	11.0 (5.6–20.7)	14.6 (6.5–38.1)	14.3 (6.1–38.9)
Necterosoma	16.3 (11.9–21.1)	16.2 (11.7–20.9)	13.9 (5.9–29.5)	13.6 (5.8–28.3)	13.2 (5.1–23.3)	12.5 (5.4–22.1)	15.7 (5.5–39.9)	17.1 (5.3–44.1)
Carabhydrus	12.7 (8.0–17.7)	12.6 (8.1–17.6)	11.8 (4.7–25.2)	11.5 (4.6–24.1)	9.5 (3.2–16.7)	7.9 (2.6–17.7)	11.7 (4.4–30.1)	11.4 (2.5–34.2)
Barretthydrus	11.3 (7.3–15.9)	11.3 (7.3–15.8)	9.2 (3.5–19.7)	8.9 (3.3–18.8)	8.1 (3.6–15.0)	7.2 (1.5–13.9)	8.8 (3.0–22.7)	10.2 (2.3–29.3)
Sternopriscus	18.0 (13.7–22.8)	17.9 (13.4–22.6)	12.6 (5.8–26.6)	12.2 (5.7–25.5)	12.2 (7.1–19.8)	10.9 (5.7–20.2)	13.8 (6.2–34.8)	15.4 (7.2–39.4)
STR clade	1.2 (0.8–1.7)	1.2 (0.8–1.7)	1.7 (0.7–3.6)	1.6 (0.6–3.3)	3.4 (1.4–10.2)	2.6 (0.8–5.7)	3.9 (1.2–11.1)	3.8 (0.8–10.6)

Notes: The 95% confidence intervals are given in brackets; *BD, birth–death Tree Model; Exp, Exponential* distribution; *LogN, Lognormal* distribution; *Uni, Uniform* distribution; *Bra+Ant+Sek+Tip*, Brancuporus+Antiporus+Sekaliporus+Tiporus*; STR clade, *Sternopriscus tarsalis* radiation (Hawlitschek et al. 2012).

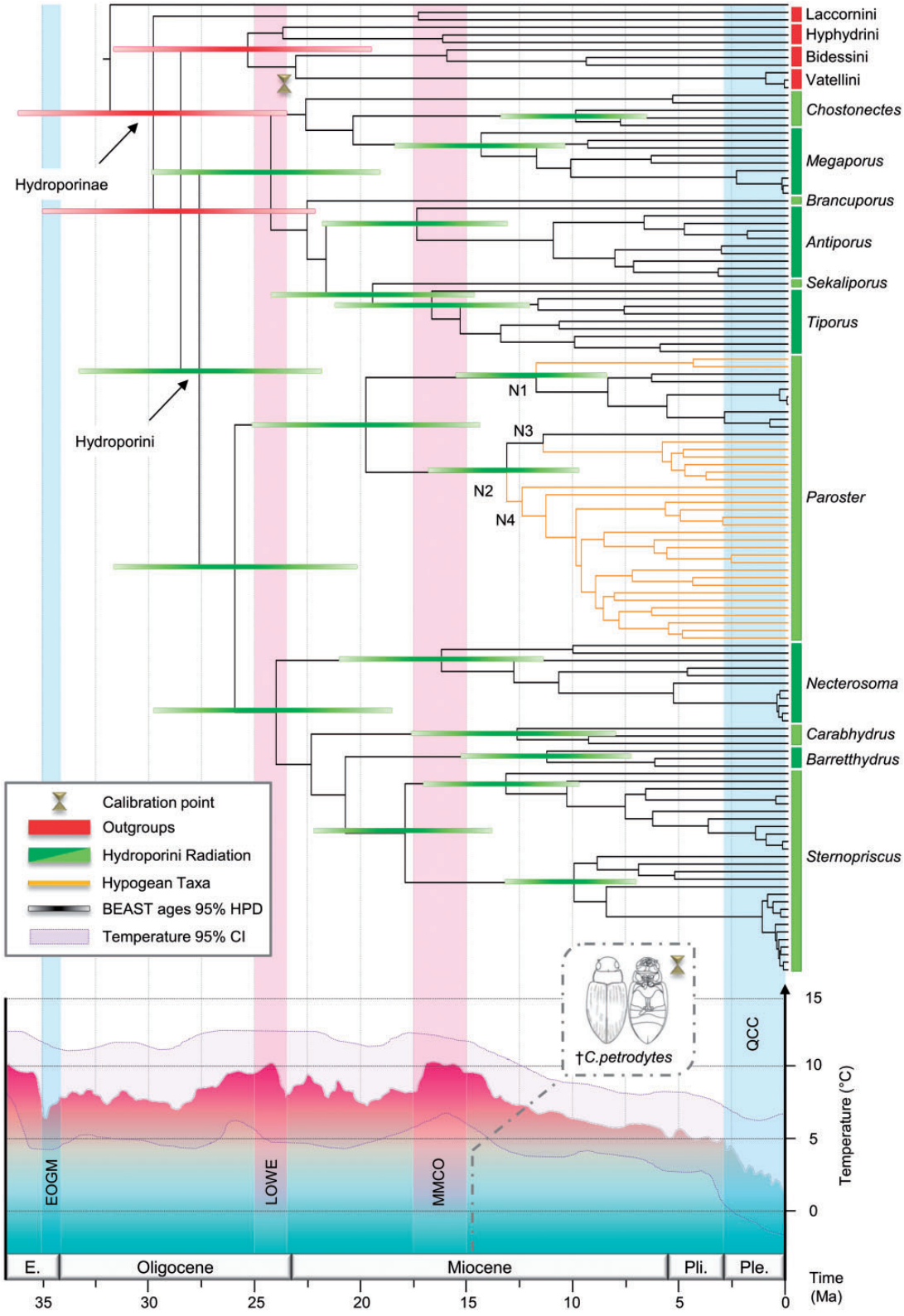


FIGURE 3. Bayesian molecular chronogram of Australian Hydroporini inferred under BEAST. Maximum clade credibility tree from the BEAST analysis. Illustrations on the right highlight the fossil used to calibrate the node indicated by a brownish hourglass. Four vertical bars represent the following major climatic events: Early Oligocene Glacial Maximum (EOGM), Late Oligocene Warming Event (LOWE), Mid-Miocene Climatic Optimum (MMCO) and QCC (Quaternary Climatic Change). A graphic showing the evolution of temperature during the last 37 Ma is presented at the bottom of the figure.

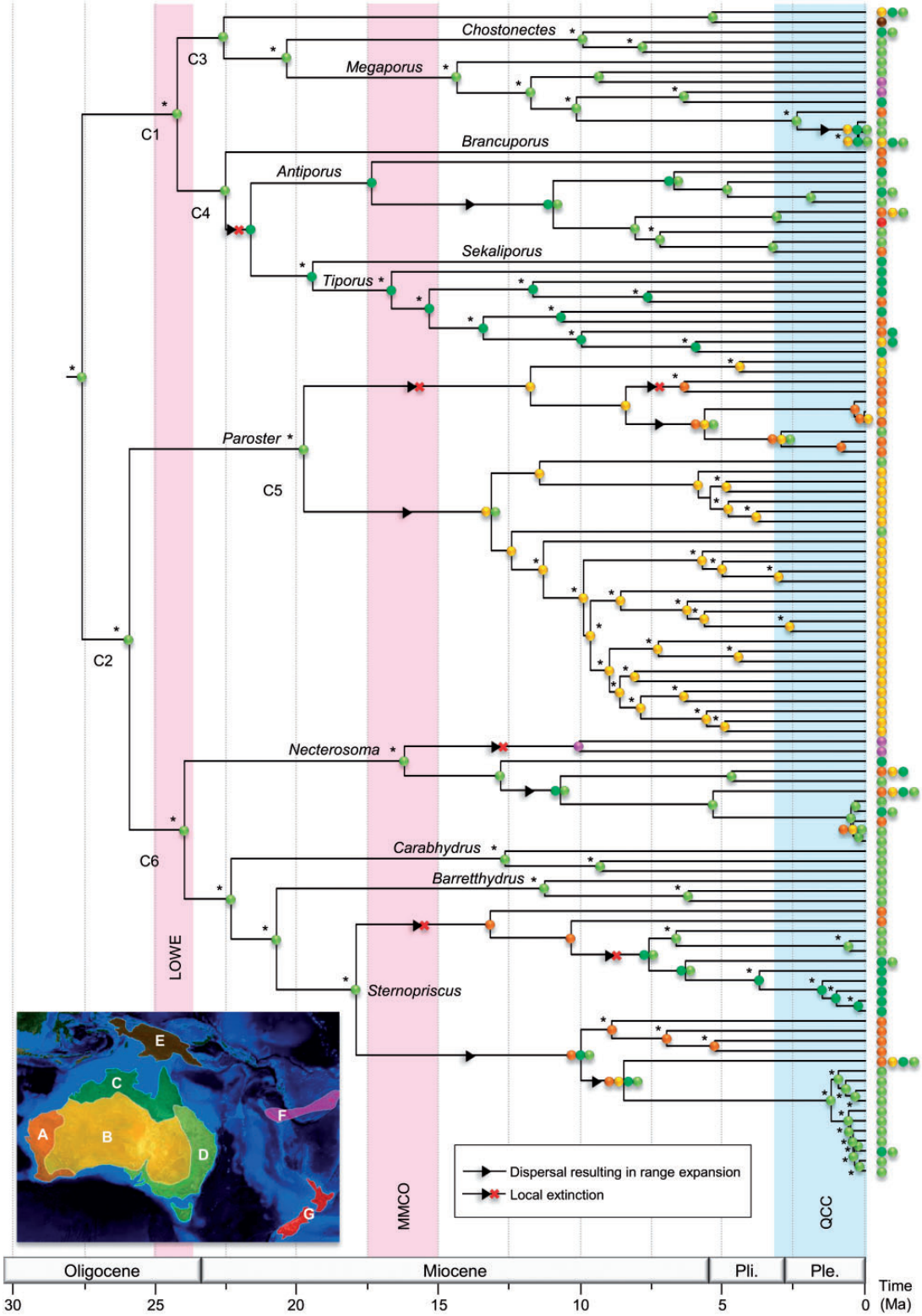


FIGURE 4. Historical biogeography of the Australasian Hydroporini. The bottom-left corner map represents the Australian region delimited in seven biogeographic regions. At the tips of the chronogram, the present-day distribution of the species (Appendix 1) is given. Colored pastilles at each node correspond to the most likely ancestral area recovered by the DEC model, and colored arrows on branches indicate dispersal events. Three vertical bars represent the following major climatic events: Late Oligocene Warming Event (LOWE), Mid-Miocene Climatic Optimum (MMCO) and QCC (Quaternary Climatic Change).

TABLE 4. Best ancestral area at the root using the different BEAST chronograms

Area	Rate *Yule*	Rate *BD*	Fossil *Exp Yule*	Fossil *Exp BD*	Fossil *LogN Yule*	Fossil *LogN BD*	Fossil *Uni Yule*	Fossil *Uni BD*
A	−252.2	−252.1	−253.8	−254.0	−251.9	−251.8	−256.2	−255.9
B	−248.0	−247.7	−249.8	−249.8	−247.3	−247.1	−250.0	−250.2
C	−248.8	−248.8	−248.9	−248.8	−248.9	−248.6	−249.3	−249.1
D	−245.5*	−245.2*	−246.0*	−245.6*	−245.5	−245.0*	−246.6*	−246.6*
E	−261.3	−261.1	−263.2	−263.0	−259.9	−260.1	−265.2	−264.9
F	−278.2	−275.9	−281.2	−281.3	−277.3	−276.0	−283.4	−283.3
G	−275.1	−274.9	−278.2	−279.0	−275.5	−274.4	−280.6	−281.1

Notes: *significantly better likelihood than the second best ancestral area at the root.

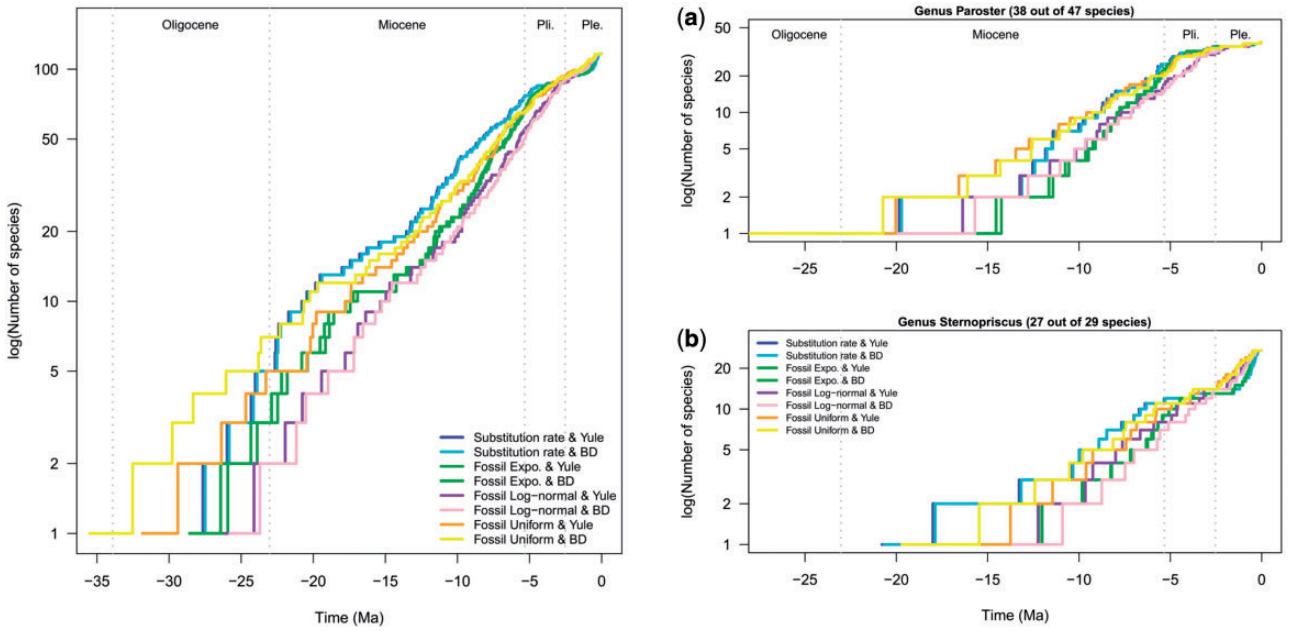


FIGURE 5. Lineages-through-time (LTT) plots for the Australasian Hydroporini and genera *Paroster* (a) and *Sternopriscus* (b). LTT plot on the displays the diversification pattern of all Australasian Hydroporini. The eight BEAST dating analyses are represented each with a different color. Time-scale is indicated spanning the full evolutionary history of the group. On the top, geological periods are indicated (Pli., Pliocene; Ple., Pleistocene).

For all chronograms, the MEDUSA analyses recovered a scenario with no rate change as the best model (Appendix 9), which means that no rate heterogeneity is evidenced among genera within Australasian Hydroporini. Consequently, we analyzed the whole tree with the approach of Morlon et al. (2011). Five out of eight chronograms (calibrated with a substitution rate or with an exponential distribution on the fossil age) were best explained by the BVARDVAR, in which both speciation and extinction rates vary through time (Appendix 10). Specifically, speciation rate increased slightly over time, and extinction rate did not increase until the Pleistocene when extinction exceeded speciation (Appendix 11). The value of the extinction rate at present is very high (around two species lost per lineage per million year, Appendix 10). As a result, a declining diversity scenario is revealed with a maximum of diversity culminating at about 500 species reached in the early Pleistocene (Appendix 12).

To compare diversification processes among the two ecologically-different clades, we analyzed the genera *Paroster* and *Sternopriscus* with both approaches. For *Paroster*, TreePar analyses indicated a scenario with one shift time (Appendix 8). Estimates of diversification rate showed an initial diversification phase with a high diversification rate until the first rate shift occurred in the early mid-Pliocene, and followed by a sharp decrease in diversification rate. With the Morlon et al. (2011)'s approach, the BVARDCST model is recovered for trees calibrated with the substitution rates or with an exponential distribution on the fossil age, and a BCSTDCST for the remaining trees (Appendices 10 and 13). We mostly inferred a damped-increase of species through time of lineages through time (Appendix 14).

For *Sternopriscus*, TreePar analyses provided various results depending on the calibration strategies (Appendix 8). Trees calibrated with the substitution rates or with an exponential distribution on the fossil age gave variable diversification rates with two shift times, whereas trees calibrated with lognormal and uniform distributions gave constant diversification rates. Trees showing shift in rates indicated that the

TABLE 5. Summary of diversification rate inference results

Type of birth–death	Models used	References	Settings	Australasian Hydroporini	*Paroster*	*Sternopriscus*
Time-dependence (rates vary as a function of time and clades)	TreePar (bd.shifts.optim)	Stadler (2011)	5 nested models testing from no rate shift up to 4 rate shifts	7 trees out of 8 show rate shifts in the Plio-Pleistocene (6 have declining diversity, i.e., negative *r*)	All 8 trees show shifts declining diversification rate since the Pliocene	4 trees have constant rates and 4 trees have declining diversification rates in the Pleistocene
	MEDUSA	Alfaro et al. (2009)	1 model estimating rate heterogeneity across clades	No rate shift detected	NA	NA
	Morlon et al.	Morlon et al. (2011)	4 nested models testing whether rates vary or not	5 trees with increase of extinction in the Pliocene, and 3 with constant rates	4 trees with declining speciation rate through time, and 4 with constant rates	6 trees with constant rates, and 2 trees with increase of extinction in the Pliocene
Trait-dependence (rates vary as a function of a character state for a trait)	BiSSE	Maddison et al. (2007); FitzJohn et al. (2009)	8 nested models testing which rates depend or not on the trait	No effect of the trait detected	No effect of the trait detected	NA
Diversity-dependence (rates vary as a function of the number of species)	TreePar (bd.densdep.optim)	Etienne et al. (2012)	1 model estimated the carrying capacity K	Not reached (mean $K = 220$)	Reached at 86% (mean $K = 55$)	Not reached (mean $K = 42$)

Notes: NA, not available.

diversification had an initial period with a medium rate until the first rate shift occurred in the early Pleistocene, and followed by an increase in diversification rate. The second shift time occurred in the middle Pleistocene and followed by a decrease in diversification rate. With the Morlon et al.'s (2011) approach, the BCSTDCST model is generally recovered but for the trees calibrated with substitution rates the BVARDVAR is supported (Appendices 10 and 15). We inferred either a steady accumulation or a recent declining diversity pattern of species through time (Appendix 16).

Trait-dependent analyses.—The BiSSE analyses of diversification suggested that there is no departure from the null model among the six diversification models (Appendix 17). Under these results, there is no difference in speciation, extinction and transition rates in relation to the ecological habitat (epigean vs. subterranean ecology) (Appendix 16). These results are consistent in all chronograms with analyses performed on the whole tree of Australasian Hydroporini and the tree for the genus *Paroster* as well (Appendix 16).

Diversity-dependence analyses.—TreePar analyses indicated that current Australasian Hydroporini diversity is not saturated as the ML estimate is obtained for the maximum carrying capacity at 220 species (Appendix 18). On the contrary, analyses for the genus *Paroster* indicated that the clade is near the equilibrium since the ML estimate gave a carrying capacity at 50 to 60 species, depending on the chronogram (47 species are presently known) (Appendix 18). Analyses of the genus *Sternopriscus* showed that the diversity is not saturated because the ML estimate is obtained for the highest value of the carrying capacity of 44 species (Appendix 18). However, the two rate-calibrated chronograms out of six reached a ML estimate for a carrying capacity equal to the extant number of species.

DISCUSSION

Deciphering biogeographical and diversification processes in the Australasian region has intrigued biologists since Wallace's pioneer works (1860, 1863) and still represents a source of great interest (Lohman et al. 2011 for a review, Carstensen et al. 2012, 2013; de Bruyn et al. 2012, 2013; Müller et al. 2012; Schweizer et al. 2012; Stelbrink et al. 2012; Condamine et al. 2013; Toussaint et al. 2013, 2014; Georges et al. 2014; Tänzler et al. 2014). Yet, the origin and evolution of endemic radiations on continental Australia is far less investigated despite offering a window towards a

better understanding of processes governing diversity dynamics in the region (McGuigan et al. 2000; Bell et al. 2007; Unmack 2010, 2012, 2013; Bowman et al. 2010; Fujita et al. 2010; Byrne et al. 2011; Kayaalp et al. 2013).

Australasian Hydroporini Phylogenetics

The phylogenetic relationships similarly inferred in BI and ML analyses for the Australian Hydroporini are highly congruent with the preliminary work on the family (Dytiscidae) carried out by Ribera et al. (2008). We recover the group monophyletic in all phylogenetic analyses with the highest support as assumed by Leys and Watts (2008) and Ribera et al. (2008). However, the branching pattern shown in Leys and Watts (2008) is incongruent with our inference. For instance, Leys and Watts (2008) recovered the clade (*Necterosoma* + *Paroster*) in a sister-clade to (*Antiporus* + *Brancuporus* + *Chostonectes* + *Megaporus* + *Sekaliporus* + *Tiporus*). This pattern is in contradiction with the one we inferred (Fig. 2), which is instead in agreement with the one recovered by (Ribera et al., 2008): the genus *Paroster* is the sister-clade to the large clade (*Necterosoma*,[*Barretthydrus*,{*Carabhydrus*,(*Sternopriscus*)}]).

Accuracy of Divergence Time Estimation

Dating phylogenies using fossils is a tantalizing concept, yet the methodology and data needed to properly estimate divergence times are paramount despite being sometimes overlooked (Graur and Martin 2004; Near and Sanderson 2004). One could acknowledge four principal sources of error that may lead to fallacious time estimates: (i) improper phylogenetic inference, (ii) misplacement of the fossil in the tree, (iii) wrong dating of the geological strata in which fossils are embedded, and (iv) methodological biases such as inappropriate prior probability distributions, models of sequence evolution and rate heterogeneity among lineages (Drummond et al. 2006; Graur and Martin 2004, Near and Sanderson 2004; Gandolfo et al. 2008; Brandley et al. 2011; Lukoschek et al. 2012).

We investigated some of these potential sources of errors using the most complete molecular dataset ever assembled for a group of Dytiscidae including seven gene fragments, around 80% of the described species, all the extant genera and four tribes representing a large part of the subfamily diversity (Ribera et al. 2008). Molecular dating was based on one of the best preserved specimens of the beetle fossil record that was not preserved in amber (Miller and Lubkin 2001), and we carried out a series of cross-validations to test the robustness of the age estimates using different settings, priors and calibrations (e.g., fossil-based or substitution rate-based dating, Yule model or birth–death process, different distribution laws for the calibrate node prior). Despite the well-known pitfalls of single calibration (Ho and Phillips 2009), our analyses show a close correspondence between the ages of all calibration schemes with overlapping confidence intervals and highly similar median ages whatever the priors or settings we used (Table 3).

All analyses conducted using the BEAST and multiple different priors recovered an Oligocene origin of the group (Fig. 5). In addition, the parallel analysis of cross-validation carried out with the COI dataset and the fossil resulted in rates of evolution congruent with the interval (0.0145–0.0195 subs/s/Myr/l) used to calibrate the tree. Overall, our divergence time estimates are in agreement with the results of Leys et al. (2003) who found a 21.5 Ma-origin for the Australian Hydroporini, an age moderately younger than the median ages we find in this study with different sets of calibration. The ages recovered in Leys et al. (2003, ≈17 Ma) and in Leijs et al. (2012, ≈14 Ma) for the *Paroster* radiation also appear in accordance with our results.

Origins and Biogeography of Australasian Hydroporini

Recent studies addressed the role of Cenozoic climate change on Australian invertebrate diversity and distributions (Sota et al. 2005; Cooper et al. 2011; Hugall and Stanisic 2011; Lucky 2011; Rix and Harvey 2012; Kayaalp et al. 2013), yet empirical studies of the freshwater fauna are either scarce (but see Schultz et al. 2009), focused on fine scales (Ponniah and Hughes 2004; Hawlitschek et al. 2012; Schwentner et al. 2012), or in many cases centered on groundwater-adapted organisms (Cooper et al. 2002, 2007, 2008; Leys et al. 2003; Leys and Watts 2008; Murphy et al. 2009, 2012; Guzik et al. 2012; Leijs et al. 2012). According to our biogeographic reconstructions, the common ancestor of the group most likely originated during the Oligocene in the mesic East coast of Australia whilst luxuriant tropical forests covered the whole region (Martin 2006; Byrne et al. 2008). During the onset of a more arid climate in the early to middle Miocene (Martin 2006; Byrne et al. 2008), two clades derived from the ancestor diversified in the eastern part of the continent and started to colonize the northern area whilst avoiding any westwards colonization (Fig. 4). As the arid zone expanded in central Australia during the middle Miocene around 14 Ma, the ancestors were isolated in mesic and monsoonal coastal ranges of the eastern and northern regions, where these conditions permitted their survival. During this period, a dispersal event occurred toward central Australia and was followed by the origin and diversification of the genus *Paroster* (clade C5, Fig. 4). This radiation likely represents a colonization of groundwater ecosystems which is potentially explained by a combination of modifications of the beetle's ecology via the availability of a new ecological niche, a drying Miocene climate, and a strong morphological adaptation to this new environment (Leys et al. 2003; Leijs et al. 2012).

During this period, the genus *Sternopriscus* (clade nested in C6, Fig. 4) colonized Western Australia (Pilbara) and Southwest Australia twice, a Mediterranean ecosystem with forests and woodlands. A reverse colonization towards the northern and eastern regions occurred during the late Miocene. It is also

during this last timeframe that the colonization of New Caledonian, New Zealand and Fiji archipelagos occurred by long-distance dispersals. Such oversea dispersals have already been highlighted in different diving beetle groups (Balke and Ribera 2004; Monaghan et al. 2006; Balke et al. 2007a, 2007b, 2009; Toussaint et al. 2013). Eventually, several recent dispersals resulting in multiple range expansion especially towards the western regions and the North shaped the extant distribution of the group in Australia. New Guinea and New Zealand therefore appear to have been colonized during the Pleistocene or an even more recent period of time (Balke 1995). The colonization of New Guinea from Eastern or Northern Australia was likely eased by lower sea levels during the Plio-Pleistocene (Voris 2000; Hope et al. 2004; Miller 2005). New Guinea and Australia were connected by a land bridge during this period, whereas today the shallow Torres Strait separates the Australian Cape York Peninsula from Southern New Guinea (Hall 2002, 2011).

Tempo and Mode of Species Diversification

Deciphering an Australasian radiation.—Diversity dynamics in continental Australia have been investigated in previous studies using diversification analyses (e.g., Harmon et al. 2003; Rabosky et al. 2007). However, most of these studies focused on terrestrial vertebrates with few studies investigating the diversification of invertebrates (but see Kayaalp et al. 2013). Here, we provide one of the first empirical studies for Australasian freshwater invertebrate diversity. We found that diversification rates did not remain constant through time (Table 5).

Diversification rates shifted from the early Pliocene (5.332–3.600 Ma) to the middle Pleistocene (0.781–0.126 Ma). Those shifts are associated with negative diversification rates in the last million years resulting in a decline of diversity dynamics of Australasian Hydroporini as recovered in the majority of the analyses (Table 5). This noteworthy pattern is the first empirical evidence for a declining diversity scenario for an invertebrate clade. Previous studies suggested that diversification rate shifted in the middle Miocene as a result of the progressive aridification that began around 15 Ma in Central Australia (Harmon et al. 2003; Rabosky et al. 2007). Although some Australian clades have suffered extinction during periods of environmental changes (Byrne et al. 2011; Sniderman et al. 2013), the pattern for the Australasian Hydroporini provides new insights that such extinction occurred in Australia. The ensuing question is: what can explain this declining diversity scenario? This pattern is attributable to a recent increase in the extinction rate, which exceeds the speciation rate (Table 5). Extinctions might have been fostered by the Quaternary climate change that contributed to increased aridity and perturbed rainfall seasonality in Australia (Sniderman et al. 2007, 2009; Byrne et al. 2008). As a result, freshwater ecosystems may have been quite strongly impacted by the on-going aridification resulting in fewer ecological niches and more geographic contractions.

Contrasting two ecologically different genera.—Variation in diversity dynamics among clades is a famous biological pattern ((Alfaro et al., 2009)). These differences are particularly well illustrated when we look at species richness between sister clades like angiosperms and gymnosperms, or birds and crocodilians. Differences in species richness are often attributable to biological traits or ecological preferences promoting or inhibiting diversification (Rabosky 2009; Wiens 2011). Here, we did not detect significant differences in diversification rates among Australasian Hydroporini genera with MEDUSA (Table 5), but it may be due to the hypothesis of constant-rate over time (Rabosky et al. 2007; Alfaro et al. 2009). Hence, we relaxed this assumption (Morlon et al. 2011) and compared the diversification patterns of the two richest genera that have different ecological features: *Paroster* (47 species), a hypogean-adapted clade that diversified in Central Australia and *Sternopriscus* (29 species), an epigean-adapted clade that diversified in Southeastern and Southwestern Australia (Fig. 4). By applying the same series of diversification analyses, striking differences in diversification processes between the two genera are revealed (Table 5).

Both genera originated in the early Miocene but currently have different species richness, which is explained by different evolutionary scenarios. The genus *Paroster* followed a diversity-dependent pattern characterized by high initial speciation rate that decreased over time. We also estimated a carrying capacity close to the extant species richness meaning that the genus is near equilibrium (Table 5). Given the extent of morphological changes the genus experienced during its evolution, these results are in agreement with the hypothesis of an adaptive radiation of the genus in groundwater ecosystems. Leys et al. (2003) proposed that the ancestor of the genus has colonized groundwater ecosystems as a result of Miocene climate change and has later evolved the morphological traits. The reverse hypothesis states that the clade first evolved the traits that allowed it to colonize the groundwater. Hence, the latter would have conferred a higher speciation rate or a lower extinction rate to this clade. When testing for this, we did not detect any difference in speciation or extinction rates when we applied the BiSSE method. This means that the trait "living in groundwater ecosystem" is not supported as a main driver of diversification (other biological traits may have more contributed). Thus our results support the climatic opportunity in the Miocene (Leys et al. 2003) that would have fostered the diversification of the group. On the contrary, the genus *Sternopriscus* followed a variable-rate diversification featured by recent shifts in diversification rates. The genus has not yet reached its carrying capacity and is still expanding with slowing diversification rate, which is in line with the "damped

increase hypothesis" (Table 5, Cornell 2013). These slower speciation rates recovered by our analyses might be explained by recent evidence showing that southern Australia underwent a major alteration of rainfall seasonality in the Pleistocene, after 1.5 Ma. Sniderman et al. (2009) suggested that early Pleistocene Australia had a dominant summer rainfall system that supported (in upland areas) rainforest and wet sclerophyll forest that was very different to that which occurs today under an altered winter rainfall regime. We hypothesize that these deep macroecological disruptions of seasonality have played a major role in shaping slower speciation rates because many *Sternopriscus* diving beetles are restricted to seasonal aquatic habitats.

Including sufficient species-level sampling within clades is critical for diversification analyses. Our coverage within both examined genera (81% and 93% of described species for *Paroster* and *Sternopriscus*, respectively) falls above the threshold advocated by recent studies (Cusimano and Renner 2010; Davis et al. 2013). Furthermore, our analyses accounted for missing taxon sampling using taxonomic knowledge about the extant diversity of clades. The completeness of DNA matrices is another issue that may bias the inference of diversification patterns. In our study, the overall gene coverage within the group was sufficient for a good phylogenetic resolution and consistent Bayesian-relaxed-clock estimates. In the case of *Paroster*, however, the unknown extant diversity of subterranean species (Guzik et al. 2011) combined with a reduced nuclear dataset compared to other included genera may underestimate the diversification rates, though we believe this is unlikely to change the overall pattern obtained. The results recovered here highlight important differences in diversity dynamics for closely related genera that evolved in different freshwater ecosystems in Australia. Both ecosystems spurred different diversification rates but the groundwater ecosystem fostered an adaptive radiation with a diversity-dependent pattern whereas epigean ecosystems shaped a damped increase diversity pattern.

Conclusion

Using an integrative approach combining DNA sequences, distributional data, the fossil record, and latest methods in phylogenetics and likelihood-based approaches to diversification, we investigated the origin and evolution of Australasian Hydroporini diving beetles. We suggest that the aridification of Australia initiated in the Miocene might have played a cardinal role in shaping the extraordinary radiation of Australasian Hydroporini resulting in a striking diversity of species richness and types of colonized habitats, but also that later climatic adjustment, especially in seasonality of rainfall, contributed to a major wave of recent Pleistocene extinctions. Despite an astonishing adaptation to climate changes that occurred in the past million years, the group presents a boom-then-bust pattern of diversity dynamics, with a declining trajectory of diversity likely shaped by the on-going and increasing desertification that is occurring in Australia, which restricts the availability of suitable habitats and the likelihood of short-range dispersal events. As a result, this Australasian radiation has been influenced by climatic shifts and in particular the Quaternary climatic changes that likely opened new ecological opportunities, and it appears that whilst the climate continued to warm in the region, these beetles may have been the victims of the changes that once led to them thriving.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c5g23 and TreeBASE data repository at http://purl.org/phylo/treebase/phylows/study/TB2:S16016.

Funding

This work, as well as ongoing research on the Australian predaceous water beetle fauna was supported by a grant from the German Science Foundation (DFG) grants BA2152/6-1, 7-1 and 11-1. FLC was funded by the CNRS and an ANR grant ECOEVOBIO-CHEX2011 awarded to his advisor, Hélène Morlon.

Acknowledgments

We want to thank the editor-in-chief Frank Anderson, associate editor Brian Wiegmann as well as two anonymous reviewers, Gael J. Kergoat and Ignacio Ribera for fruitful comments on previous versions of this manuscript. FLC wishes to thank Hélène Morlon for supervision and advice. The Department of Environment and Conservation in Western Australia is acknowledged for giving permission to conduct scientific research in Western Australia (Permit numbers: SF 003017 and NE 002348), and the Parks and Wildlife Commission of the Northern Territory is thanked for giving permission to conduct scientific research in the Northern Territory (Permit Number: 23929 and RK-400/ RK- 660). The Department of Environment and Conservation in New South Wales (Scientific License No. S12040), the Department of Sustainability and Environment in Victoria [Research Permit No. 10003840], and the Department of Primary Industries and Water on Tasmania [Permit No. FA 06487] are acknowledged for giving permission to conduct scientific research in National and State Parks.

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