

Evolutionary history of a secondary terrestrial Australian diving beetle (Coleoptera, Dytiscidae) reveals a lineage of high morphological and ecological plasticity

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Abstract. The evolution of a secondary terrestrial lifestyle in diving beetles (Coleoptera: Dytiscidae) has never been analysed in a phylogenetic framework before. Here we study *Terradessus caecus* Watts, a terrestrial species of the subfamily Hydroporinae endemic to Australia. We infer its phylogenetic placement using Bayesian inference and maximum-likelihood methods based on a multilocus molecular dataset. We also investigate the divergence time estimates of this lineage using a Bayesian relaxed clock approach. Finally, we infer ancestral ecological preferences using a likelihood approach. We recover *T. caecus* nested in the genus *Paroster* Sharp with strong support. Therefore, we establish a synonymy for both species of *Terradessus* with *Paroster*: *Paroster caecus* (Watts) **n.comb.** and *Paroster anophthalmus* (Brancucci & Monteith) **n.comb.** *Paroster* is an endemic Australian genus that has a remarkable number of subterranean species in underground aquifers with highly derived morphologies. Our results highlight one of the most remarkable radiations of aquatic beetles with independent ecological pathways likely linked to palaeoclimatic disruptions in the Neogene. *Paroster caecus* (Watts) **n.comb.** originated from a mid-Miocene split following the onset of an aridification episode that has been ongoing to the present day. The deep changes in ecological communities in association with the drying-out of palaeodrainage systems might have pushed this lineage to colonize a new niche in terrestrial habitats.

Introduction

Most families of adepagan beetles are aquatic, often with strong lineage-idiosyncratic morphological adaptations, for example in whirligig beetles (Gyrinidae; Beutel & Roughley, 2005) and diving beetles (Dytiscidae; Balke, 2005). Among the c. 4300 species of diving beetles (Nilsson, 2015), some lineages have colonized peripheral habitats such as hygropetric rocks (Balke *et al.*, 1997; Ribera *et al.*, 2003) or the transition zone between water and land (e.g. in wet gravel, the so-called interstitial) (Balke, 2005; Jäch & Balke, 2008). Only five species of diving beetles found in the subfamily Hydroporinae have

been reported as secondarily terrestrial, for example, in lacking swimming hairs (Brancucci, 1985a; Brancucci & Hendrich, 2010). This is remarkable, especially considering that reversion to terrestriality is not uncommon, for instance in polyphagan water scavenger beetles whose terrestrial lineages have become, in some instances, very diverse (Bloom *et al.*, 2014). These Hydroporinae beetles have been collected from damp forest leaf litter in Nepal and northern India (*Geodessus besucheti* Brancucci) and southern India (*G. kejvali* Balke & Hendrich), and from rainforests of northeastern Australia (*Terradessus anophthalmus* Brancucci & Monteith and *T. caecus* Watts). *Typhlodessus monteithi* Brancucci was described from a single male collected on Mount Panié on the island of Grande Terre in the New Caledonian archipelago (Brancucci, 1985b; Brancucci & Hendrich, 2010). While *Geodessus* Brancucci resemble related aquatic beetles of the tribe Bidessini (Dytiscidae,

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Hydroporinae), adaptations are more striking in *Terradessus* Watts and *Typhlodessus* Brancucci & Monteith, including small size (around 1.3 mm), depigmentation (*Terradessus*) or near-complete (*Typhlodessus*) loss of eyes, and overall morphology that made it difficult to place them even to tribal level. According to R.A.B. Leschen (personal communication), an undescribed, blind leaf-litter species was discovered in New Zealand and is awaiting description.

Morphologically, *Typhlodessus* is dissimilar to *Terradessus*. The absence of eyes could be a convergent reduction as an adaptation to derived habitats. Both genera undoubtedly belong to Hydroporinae, but their position within this subfamily remains unclear (Watts, 1982; Brancucci & Hendrich, 2010). Watts (1982) placed *Terradessus* in Bidessini because of the small size, fused metacoxal plate and first visible abdominal segment (see Miller, 2001), and simple median lobe of aedeagus. At the same time he noticed similarities with *Paroster* Sharp, a genus in Hydroporini (e.g. strongly reticulate surface).

Both species of the genus *Geodessus* were collected from sifted or washed leaf litter in India and Nepal and were referred to as being terrestrial (see Balke & Hendrich, 1996), but later reported from China in small spring-fed pools in a meadow, in a fully aquatic habitat (Jäch & Ji, 2003); although Brancucci (1985a) established experimentally that *G. besucheti* cannot swim. In contrast to *Typhlodessus* and *Terradessus*, *Geodessus* possess eyes. The life history and habitat of *T. monteithi* remain enigmatic. The lack of eyes is suggestive of an existence hidden from light, where eyesight offers no advantage; the lack of swimming hairs suggests crawling and/or burrowing locomotion. *Typhlodessus monteithi* might inhabit a moist subterranean habitat, which could explain why its morphology differs substantially from other diving beetles.

The larval instars of all so-called terrestrial dytiscids remain unknown. If these were aquatic, the species could conceivably be classified as semiaquatic. Here we obtained fresh specimens of *Terradessus caecus* suitable for DNA sequencing and used our large existing molecular datasets of Australian water beetles (Hendrich *et al.* 2010; Toussaint *et al.*, 2015) to reveal the systematic position of *Terradessus* and its evolutionary history.

Materials and methods

Taxon sampling and molecular biology

We complemented the cytochrome oxidase 1 (*cox1*) database of Australian diving beetles (Hendrich *et al.* 2010) and then the dataset for Australasian Hydroporini (Toussaint *et al.*, 2015) with two specimens of *Terradessus caecus* (Australia: Queensland, Mt Sorrow, plateau, litter berlesate, 760 m a.s.l., 6.xii.2012, 16.078°S 145.433°E, Escalona (18777 QLD Mus)). Total genomic DNA was extracted nondestructively from whole beetles using the DNeasy kit (Qiagen, Hilden, Germany). We used PCR protocols following Toussaint *et al.* (2015) to amplify and then sequence the following gene fragments: cytochrome oxidase subunit 1 (*COI*, 741 bp), cytochrome b (*CytB*, 390 bp), histone 3 (*H3*, 321 bp) and histone 4 (*H4*,

203 bp). We were unable to obtain sequence data for three other gene fragments comprising the molecular dataset: ribosomal 16S (*16S*, 769 bp), ribosomal 18S (*18S*, 607 bp) and arginine kinase (*ARK*, 636 bp). The DNA sequences were corrected under Geneious R8 (Biomatters, <http://www.geneious.com/>), aligned using MUSCLE (Edgar, 2004) and the reading frame checked using MESQUITE 2.75 (<http://mesquiteproject.org>). All sequences were deposited in GenBank (accession # HG965576–HG965750), with *Terradessus* at <http://www.ebi.ac.uk/ena/data/view/LN898122-LN898125>. Sequences for subterranean species were generated by Leijs *et al.* (2012) in Adelaide and were downloaded from GenBank.

Molecular phylogenetics

We used Bayesian inference (BI) and maximum-likelihood (ML) to reconstruct phylogenetic relationships using the dataset of Toussaint *et al.* (2015) complemented with the two specimens of *Terradessus caecus*. The partitions and corresponding optimal models of substitution were searched under PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) using the ‘greedy’ algorithm, either the ‘*mrBayes*’ or ‘*raxml*’ set of models and the Akaike Information Criterion corrected (AICc) to compare the fit of the different models. The BI analyses were performed using MrBayes 3.2.2 (Ronquist *et al.*, 2012). We performed two different analyses; one using the substitution models based on the results of PartitionFinder, and one based on the different partitions recovered in PartitionFinder but using reversible-jump MCMC to explore the entire space of substitution models (Huelsenbeck *et al.*, 2004). For each analysis, we used two simultaneous and independent runs consisting of eight Metropolis-coupled Markov chain Monte Carlo (MCMC, one cold and seven incrementally heated) running 50 million generations, with a tree sampling every 5000 generations to calculate posterior probabilities (PP). In order to check 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 ML analyses were conducted with the best partitioning scheme selected in PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) using RAxML (Stamatakis, 2006). We used the AutoFC option in RAxML to calculate the optimal amount of *Bootstrap* replicates (BS) indicating 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 (Hillis & Bull, 1993; Erixon *et al.*, 2003).

Divergence time estimation

Divergence times were inferred with the BEAST 1.8.2 (Drummond *et al.*, 2012) based on a reduced dataset comprising only

the *Paroster* clade representatives. The partitions and models of nucleotide substitution were selected under PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) using the 'greedy' algorithm, the 'beast' set of models and the AICc. We tested the hypothesis of molecular clock in MEGA 6 (Tamura *et al.* 2013), and because it was significantly rejected ($p < 0.001$), we used a Bayesian relaxed clock allowing rate variation among lineages as implemented in BEAST. In order to calibrate the tree, we used three secondary calibrations derived from Toussaint *et al.* (2015). In this paper, the only unambiguous hydroporine fossil known was used to calibrate a molecular phylogeny of Australasian Hydroporini. This extremely well-preserved fossil †*Calicovatellus petrodytes* (Miller & Lubkin, 2001), found in the Barstow Formation, dated from the Miocene (13.3–19 Ma). It was conservatively enforced as a fossil calibration on the stem of the tribe Vatellini of which the two extant genera were sampled. The authors compared the results of their dating analyses using this fossil with different analyses relying on published rates of molecular evolution. Their results were consistent across dating methods, and therefore the divergence time estimates derived from this study were considered to be robust. Based on the estimates from Toussaint *et al.* (2015), we constrained the *Paroster* node as well as the clades C1 and C2 with a normal distribution encompassing the 95% highest posterior density (HPD) of the median ages recovered when using the fossil calibration. The Tree Model was set to a birth death model. The runs consisted of 10 million generations sampled every 1000 generations. The convergence of the runs was investigated using ESS, a conservative burn-in of 25% applied after checking the log-likelihood curves. The maximum credibility tree, median ages and their 95% HPD were generated afterwards under TreeAnnotator 1.8.2 (Drummond *et al.*, 2012).

Ancestral habitat reconstruction

We used the model Dispersal Extinction Cladogenesis (DEC) as implemented in Lagrange to infer the ancestral habitats in *Paroster* (Ree *et al.*, 2005; Ree & Smith, 2008). We conducted the analyses using the BEAST Maximum Clade Credibility (MCC) tree. The following ecological preferences were used in the analyses: S, aquatic subterranean; E, aquatic epigeal; and T, terrestrial epigeal. The ecological preference of each taxon was recovered from the literature (Leijs *et al.*, 2012; Toussaint *et al.*, 2015). We did not perform a stratified analysis and left the adjacency matrix and dispersal matrix unconstrained (all state combinations allowed and all transition rates equal). Because an ancestral subterranean state associated with parallel regaining of eyes, flight capacity and full pigmentation is a highly unlikely scenario, we constrained the ancestral state of the root to be epigeal (E).

Results

Phylogenetic relationships and taxonomy

The analysis of *cox1* data placed *T. caecus* within Hydroporini (data not shown). A multilocus dataset of *T. caecus* was therefore

integrated and analysed in our existing Hydroporini dataset and placed *T. caecus* with strong support within the genus *Paroster* Sharp (Fig. 1). *Paroster* currently contains 48 species, with more than two-thirds of the species diversity endemic to subterranean habitats (Watts & Humphreys, 2001, 2004; Watts & Leys, 2008; Leijs *et al.*, 2012).

We here transfer *Terradessus caecus* to *Paroster*, with the following taxonomic acts:

Genus *Paroster* Sharp

Paroster Sharp, 1882: 389.

= *Terradessus* Watts, 1982:527, **n.syn.**

Paroster caecus (Watts, 1982), **n.comb.**

Paroster anophthalmus (Brancucci & Monteith, 1997), **n.comb.**

Terradessus anophthalmus is morphologically very similar to *T. caecus* and these two species are very likely to form a monophyletic grouping. As a result, we tentatively transfer *T. anophthalmus* to *Paroster* although future work is needed to investigate this placement in more detail using both morphology and DNA sequences.

Divergence time estimates and ancestral habitat reconstruction

The results of our divergence time estimate and ancestral habitat reconstruction analyses are presented in Fig. 2. We recover the beginning of the initial diversification of *Paroster* in the mid-Miocene, as suggested by Leijs *et al.* (2012). The two subclades C1 and C2 originated about 10 Ma. Our DEC ancestral character state analysis with an enforced epigeal ancestral character state suggests three independent shifts from epigeal to subterranean and one to terrestrial with no secondary reversal from subterranean state to epigeal (Fig. 2).

Discussion

The placement of *Terradessus* in *Paroster* establishes the latter as an ecologically and morphologically very diverse and phenotypically plastic lineage, containing epigeal aquatic, subterranean aquatic as well as terrestrial species. When assuming that the ancestor of *Paroster* was epigeal, our ancestral character state reconstruction suggested multiple transitions to the subterranean habitat. This evolutionary scenario could be explained by larger scale extinction events resulting from the aridification of Australia, which wiped out epigeal fauna and promoted underground radiations, as suggested by Leys *et al.* (2003, 2012) and Toussaint *et al.* (2015). In fact, the stygofauna of Australia is uniquely diverse on a global scale, for example due to wide range and diversity of underground habitats coupled with a comparably long evolutionary history of its colonization (Watts & Humphreys, 2003; Humphreys, 2008; Guzik *et al.*, 2011). The large-scale environmental changes during the Miocene/late Miocene due to global cooling and decreased rainfall had striking effects on Australian aquatic ecosystems and their species. Adaptation to new environments might then

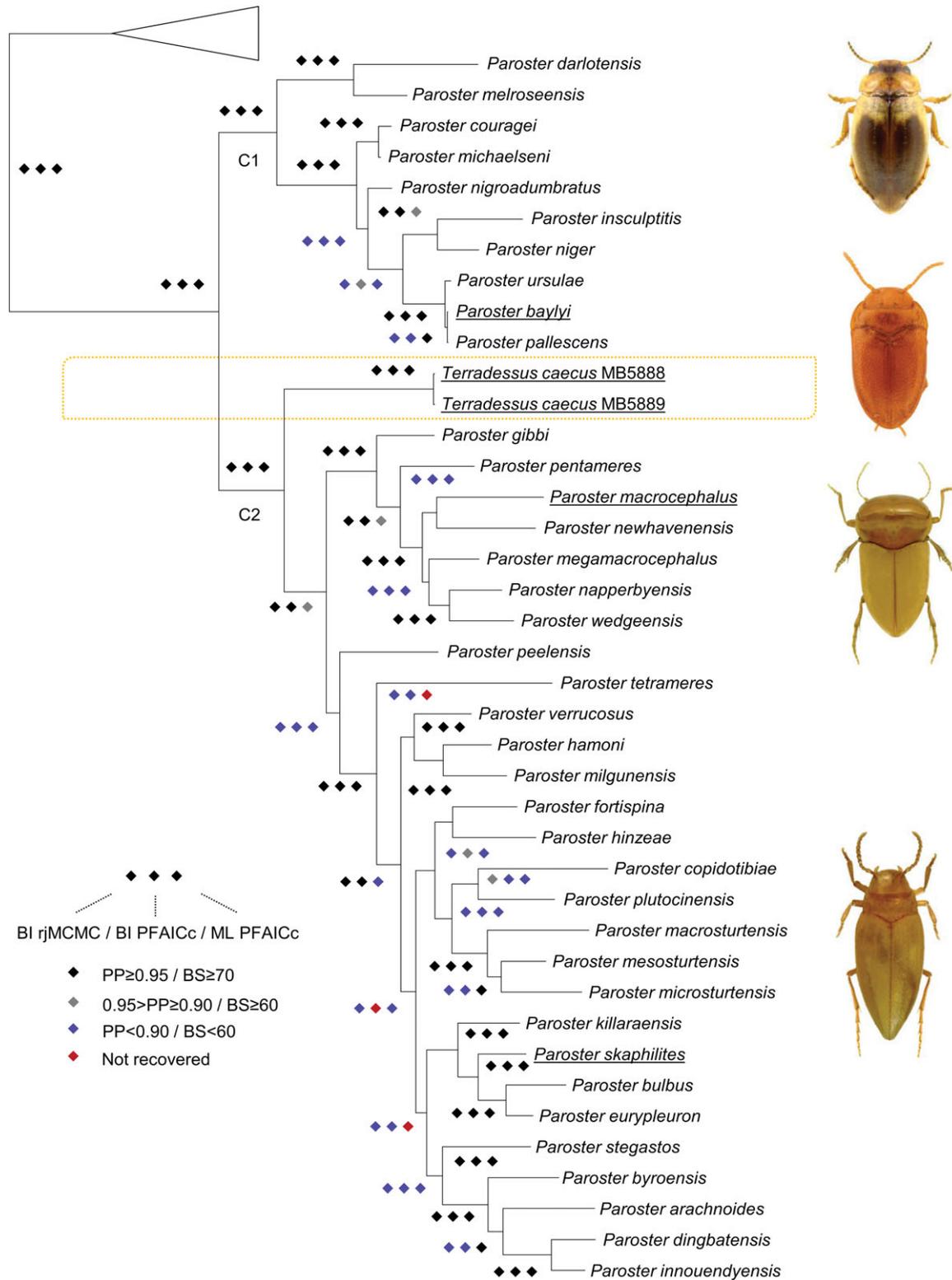


Fig. 1. Phylogenetic relationships in the Australian genus *Paroster*. Maximum clade credibility tree of the Bayesian analysis conducted in MrBayes with nodal support for the three different analyses in Bayesian inference (BI) and maximum-likelihood (ML). The topology shows only the relationships within *Paroster*. Species with underlined names are represented by a beetle picture on the right of the phylogeny in vertical order.

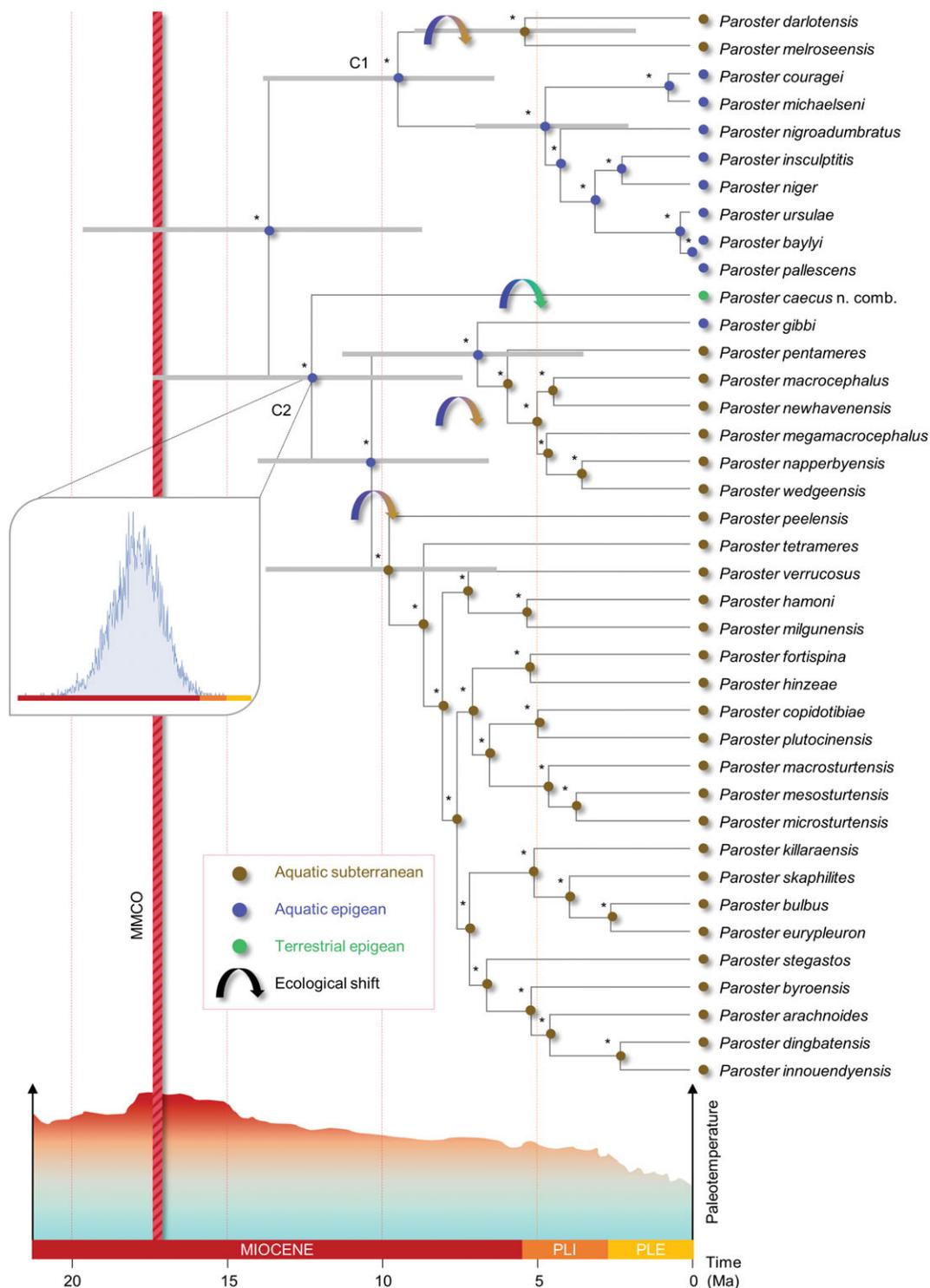


Fig. 2. Divergence time estimates and ancestral habitat reconstruction in the genus *Paroster*. Maximum clade credibility chronogram of the BEAST analysis presenting the median divergence time estimates across *Paroster*. The 95% age posterior distribution of major nodes is highlighted with thick grey horizontal lines. The BEAST posterior distribution of the ages for the node of clade C2 is given in full in a small graph (inset). The results of the Dispersal Extinction Cladogenesis (DEC) analysis are presented with circles at each node of the topology. Shifts in ancestral habitat are presented using arrows as indicated in the inserted caption. Asterisks indicate a relative probability for the character state >90% as estimated in the DEC analysis. At the bottom of the figure, a graph shows the global palaeotemperature in the past 20 Ma. A red vertical line indicates the mid-Miocene climatic optimum (MMCO). [Colour figure available on the online version on Wiley Online Library.]

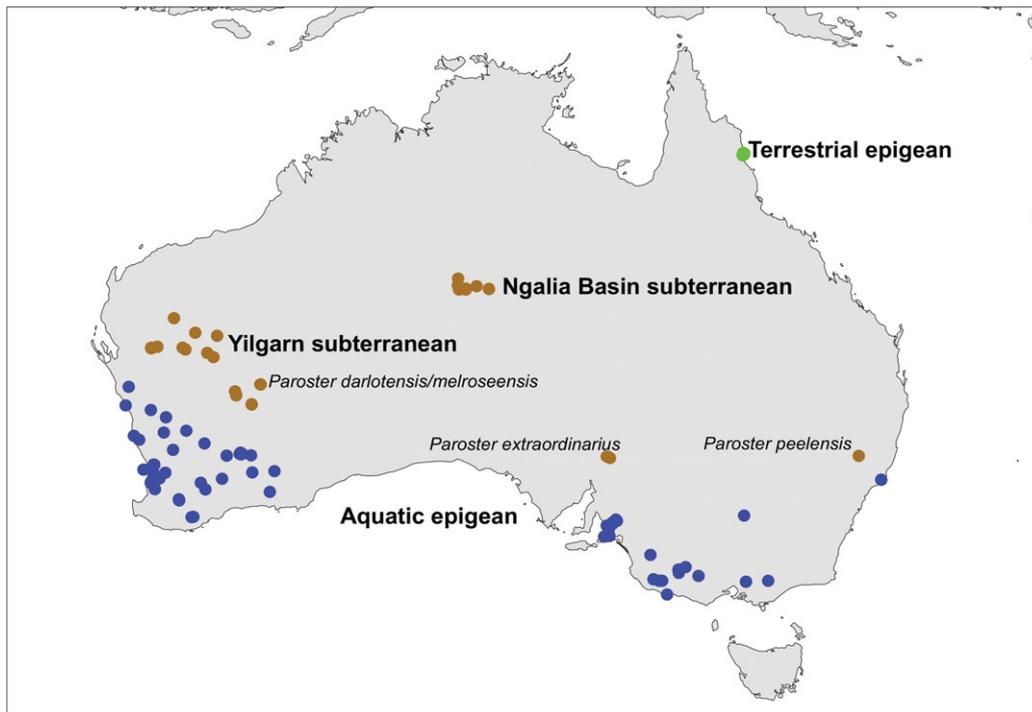


Fig. 3. Geographical range of *Paroster* species. Blue, epigean species; brown, subterranean, where Ngalia and Yilgarn regions both have multiple species; green, terrestrial. [Colour figure available on the online version on Wiley Online Library.]

have caused the phenotypic and ecological diversity seen in *Paroster*, and resulted in their extant distribution patterns.

The extant distribution (Fig. 3) of aquatic epigean *Paroster* reflects their restriction to regions with cool-moderate (mean annual temperature $<20^{\circ}\text{C}$) and winter-wet mesic climates, although two species (*P. michaelsoni* Regimbart and *P. ursulae* Henrich & Fery) extend to the margins of the arid zone in southwestern Australia. A single undescribed species is known from summer rainfall-dominated central New South Wales.

In contrast, the stygobiont radiations ‘Ngalia’ and ‘Yilgarn’ and ‘*P. darlostensis/melroseensis*’ (dm) occur in regions where surface climates are warmer and drier annually (Yilgarn, dm), or at least warmer annually (Ngalia) (Fig. 3). The surface climates in this respect are a proxy for exploring the bioclimatic origins of the lineages and do not directly reflect the conditions to which the underground taxa are exposed to today. The terrestrial *Paroster* species from the Wet Tropics region of northern Queensland inhabit thermal environments similar to those at the warm end of the aquatic epigean range but under moisture regimes substantially wetter, both in summer and annually. This diversity of bioclimatic requirements for the different groups of *Paroster* complicates interpretation of the evolutionary history of the genus, especially when the probability of extinction of ancestral lineages is invoked to explain the present distribution of *Paroster* (Toussaint *et al.*, 2015). Consideration of Australia’s changing climates over the Miocene–Quaternary is informative in relation to understanding scenarios for the evolution of the genus.

Evidence regarding the nature of the climate in the Australian region following the middle Miocene climatic optimum (MMCO, 17–14.5 Ma) (Zachos *et al.*, 2008), suggests that the middle–late Miocene remained warm and was wetter than present, although it was increasingly characterized by the expansion of dry adapted taxa across inland Australia (Hill, 2004; Byrne *et al.*, 2008; Woodhead *et al.*, 2016). It is during this post-MMCO period that the ancestor/s of both the inland stygobiont lineages and the terrestrial species could have occupied much of central and eastern Australia. Extensive and rapid cooling following the MMCO at around 14 Ma (Shevenell *et al.*, 2004) may have contributed to the expansion of ancestral *Paroster* into the mesic Australian inland if we infer this lineage to be a mesotherm-adapted group. Increased precipitation during this period, relative to the present, would have allowed ancestors with similar moisture requirements to the extant aquatic epigean taxa to inhabit inland Australia and widely occupy eastern Australia. However, given the evidence that the middle–late Miocene was still significantly warmer than the present (Pound *et al.*, 2012), it seems unlikely that the ancestral taxa were necessarily bioclimatically (especially thermally) similar to the extant aquatic epigean taxa.

It is conceivable that, like the related hydropterines *Sternopriscus* Sharp, *Megaporus* Brinck, *Antiporus* Sharp and *Necterosoma* Macleay – which all have at least one species widespread across the southern half of the continent, including in inland regions – continentally widespread *Paroster* (now extinct) could have been ancestral to both the aquatic epigean

and terrestrial lineages of *Paroster*. Indeed, the relationships in the phylogeny would suggest a minimum of two principal widespread ancestral taxa: one for the aquatic epigeal taxa (except *P. gibbi* Watts) + *P. melrosensis*/*P. darlotensis*, and one for the remainder of the *Paroster* radiation including terrestrial + *P. gibbi* + Ngalia + *P. peelensis* + Yilgarn. Extinction of such widespread ancestral taxa would reconcile the difficulties of invoking the evolution of aquatic epigeal taxa from either blind terrestrial taxa or stygobionts. It does mean, however, that it is problematic to use evidence from the distribution and bioclimatic requirements of the extant aquatic epigeal taxa to infer evolutionary history in concert with changing Neogene climates, under an assumption of extensive extinction. Hopefully, additional taxon sampling, increasingly robust divergence time estimates and ecological niche modelling studies will help to elucidate the intricate evolution of *Paroster* diving beetles in Australia.

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