







A deep dive into the fossil record of diving beetles (Coleoptera: Dytiscidae): Bayesian inferences elucidate their origin and pulsed diversification at the genus level

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Abstract: Predaceous diving beetles (Dytiscidae) are among the best-known and most extensively studied beetle clades. Their fossil record, however, remains surprisingly sparse and uneven, failing to reflect their broad extant diversity. Consequently, the study of their evolutionary history, leveraging the fossil record, particularly their diversification dynamics, has often been limited. To overcome this issue, we used the Bayesian Brownian bridge model, which is particularly suited for clades with incomplete fossil records. Although primarily designed to estimate clade origination time, the model can also be applied to infer origination and extinction dynamics while accounting for bias due to uneven sampling. Using this model and a curated dataset of fossil

occurrences covering 41 genera and 155 species of Dytiscidae, we estimated the timing of the family's origination and of each genus represented in its fossil record. Our results show an origin of Dytiscidae either during the Late Triassic (c. 220 Ma) or during the Early Jurassic (c. 190 Ma). Although these estimates are consistent with most recent time-calibrated phylogenies, they provide additional clues for an ancient origin of the family. Following their origin, Dytiscidae diversified across the different geological epochs, probably in response to tectonic shifts and climate oscillations.

Key words: Bayesian Brownian bridge, dating, evolution, fossil record, origination.

WITHIN Coleoptera, the family Dytiscidae Leach 1815 (predaceous diving beetles) are the most species-rich aquatic family in the suborder Adephaga, with 4797 described extant species (Nilsson & Hájek 2025). They are found in a wide variety of freshwater habitats, such as streams, stagnant water (e.g. marshes or ponds), and more specialized environments (e.g. water collections in plants, groundwater, thin sheets of water flowing over rocks) (Bergsten & Miller 2016). Adults can range in size from less than 2 mm to over 40 mm, depending on the species (Fig. 1). To breathe, they periodically surface to replenish their air supply located beneath their elytra (Bergsten & Miller 2016; Goczał & Beutel 2023). Adults are capable of flying, which facilitates dispersal between aquatic habitats. Larvae are strictly aquatic and carnivorous, feeding on a variety of invertebrates and sometimes small vertebrates, playing an important role as predators in freshwater ecosystems. Like adults, larvae also rely on

atmospheric oxygen, obtained through a specialized respiratory organ. The pupal stage is the only terrestrial phase in their life cycle, during which they develop outside water, usually in moist soil or leaf litter near the water's edge (Bergsten & Miller 2016). Given their ecological diversity, wide distribution and key role in freshwater ecosystems, understanding the origin of Dytiscidae seems essential to reconstruct the timing and dynamics of their diversification.

The fossil record of Dytiscidae is relatively limited compared with their extensive modern diversity, with only c. 160 species described (Paleobiology Database; PBDB). It includes a subset of living genera, comprising both extinct and extant species. The oldest taxon currently attributed to Dytiscidae is †*Angaragabus jurassicus* Ponomarenko 1963, a larva specimen from the Cheremkhovskaya Formation (Russia) dated to 184.2–174.7 Ma (Fig. 1F). However, the attribution of this fossil to the family is uncertain, and it has been proposed that it may be more closely related to †Liadytidae or Aspidytidae rather than Dytiscidae (Prokin

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et al. 2013; Ponomarenko & Prokin 2015). As such, the oldest unambiguous fossil assigned to Dytiscidae is †*Palaeodytes gutta* Ponomarenko 1987, an adult specimen discovered in Karabastau Formation (Kazakhstan) dated to 165.3–154.8 Ma (Middle–Late Jurassic). A handful of occurrences come from Early Cretaceous lacustrine strata, most notably the Jehol biota of northeastern China (c. 125–121 Ma) (Fig. 1B–E), but diving beetles are conspicuously scarce in Late Cretaceous assemblages, even in well-sampled deposits such as the Kachin amber (c. 99 Ma), with only one species described from this biota (Yang *et al.* 2019). From the Palaeogene onward, their record markedly improves. Overall, most fossil dytiscids derive from lacustrine sediments (e.g. shales, oil shales, tuffaceous mudstones) (Fig. 1B–E), whereas amber inclusions remain rare, limited to a few records from the Kachin (Yang *et al.* 2019), Baltic (Koch & Berendt 1854; Miller 2003; Balke *et al.* 2010; Gómez & Damgaard 2014; Balke & Hendrich 2019; Hendrich & Balke 2020), Saxonian (Balke *et al.* 2019), Mexican (Hájek *et al.* 2025) and Dominican ambers (Miller 2003). Despite this incomplete record, Dytiscidae have been central to many molecular dating efforts aimed at reconstructing their evolutionary timeline.

In molecular dating, Dytiscidae stand out as one of the most studied clades, whether they are included in large-scale phylogenetic analyses (e.g. McKenna *et al.* 2015, 2019; Toussaint *et al.* 2017a; Zhang *et al.* 2018; Baca *et al.* 2021; Cai *et al.* 2022; Cardenas *et al.* 2025) or studied independently (e.g. Ribera *et al.* 2004; Bukontaite *et al.* 2015; Désamoré *et al.* 2018; Balart-García *et al.* 2023). Despite differences stemming from fossil choice and placement, most estimates converge toward a Middle or Late Jurassic origin. Some studies suggested a later, Early Cretaceous origin (e.g. c. 125–130 Ma; McKenna *et al.* 2015; Balart-García *et al.* 2023; but see Toussaint *et al.* 2017a). These last estimations may be due to low taxon sampling: for instance, only two (Cybistrinae and Hydroporinae) out of 11 extant subfamilies are represented in Balart-García *et al.* (2023). Other works, by contrast, consistently support earlier ages, ranging from c. 160–145 Ma (Désamoré *et al.* 2018; McKenna *et al.* 2019) to c. 175–167 Ma (Toussaint *et al.* 2017a; Zhang *et al.* 2018; Baca *et al.* 2021), and up to c. 210 Ma (Cai *et al.* 2022; Cardenas *et al.* 2025). This trend

supports the hypothesis of a putative origin for the family in the Late Triassic to Early Jurassic, despite some uncertainty in precise timing.

All of these previous studies rely on node-dating methods, which infer divergence times by calibrating specific nodes in a phylogenetic tree with fossil evidence. However, node-dating assumes that the phylogenetic placement of the fossils used for calibration is accurate and well-resolved, an assumption that may not hold, particularly for older or fragmentary fossils (e.g. the genera †*Palaeodytes* Ponomarenko 1987, †*Cretodytes* Ponomarenko 1977 and †*Sinoporus* Prokin & Ren 2010 are currently *incertae sedis* within Dytiscidae) (Fig. 1D, E). To date, no tip-dating or total-evidence dating studies (combining both fossil and extant taxa in a single dating analysis) have been conducted for Dytiscidae, preventing a robust estimate of fossil placements within the topology while taking into account their age and morphological transformations (Ronquist *et al.* 2012; Heath *et al.* 2014; Ferreira *et al.* 2024). These limitations in fossil calibration and phylogenetic placement highlight the need for alternative methods that can leverage fossil data more flexibly.

A recently developed approach, the Bayesian Brownian bridge (BBB) model, offers a novel framework for estimating clade ages using only fossil occurrence data and extant species diversity (Silvestro *et al.* 2021). Unlike most traditional dating methods, which require a phylogenetic tree, the BBB model circumvents the need for a dated phylogeny by treating the diversification history of a clade as a stochastic process, specifically, a Brownian motion. This process begins at an unknown point in the past (representing the clade's origin) and is constrained at its endpoint by the known number of extant species. Fossil occurrences act as temporal anchors along this trajectory, helping to refine estimates of origination time. The model has already been successfully applied to various groups such as angiosperms (Silvestro *et al.* 2021), mammals (Carlisle *et al.* 2023), Hymenoptera (Jouault *et al.* 2025), Hemiptera (Boderau *et al.* 2025a) and Scolytinae (Ferreira *et al.* 2026), where it produced robust estimates assessed through extensive simulations, and with most of them aligning with recent dated phylogenetic studies. However, the model can estimate the origination times only for clades that are actually represented in the fossil record, and therefore does not permit the

FIG. 1. Examples of extant and Mesozoic fossil Dytiscidae. A, *Cybister lateralimarginalis* (De Geer 1774) (Cybistrinae). B, †*Liadytiscus latus* Prokin & Ren 2010 (†Liadytiscinae), holotype CNU COL LB 2009031. C, †*Liadroporus elegans* Prokin & Ren 2010 (†Liadytiscinae), holotype CNU COL LB 2009030. D, †*Cretodytes incertus* Prokin *et al.* 2013 (*incertae sedis*), holotype PIN 4626/628. E, †*Sinoporus lineatus* Prokin & Ren 2010 (*incertae sedis*), holotype CNU COL LB 2009104. F, †*Angaragabus jurassicus*, specimen PIN509/4, for which the family-level taxonomic attribution remains uncertain. Scale bars represent 1 mm. Image credits: A, Jules Ferreira; B, C, E, Alexander A. Prokin; from Prokin & Ren (2010) ©Springer Nature, reproduced with permission; D, Alexander A. Prokin from Prokin *et al.* (2013) ©Magnolia Press, reproduced with permission; F, Alexander A. Prokin.



estimation of the origin of the clades that must have existed throughout history but left no identifiable fossils. Given its methodological advantages, the BBB model offers a promising avenue for estimating the origin of Dytiscidae and the diversification of its lineages.

In this study, we apply the BBB model to the dytiscid fossil record to estimate the origin of the family and its constitutive genera represented in the fossil record, but also to highlight key periods during which dytiscid genera expanded. We compare our results with those of previous phylogenetic dating studies, aiming to provide insights into the macroevolutionary history of diving beetles through time. Based on our findings, we propose hypotheses to explain why certain periods may have been particularly beneficial to the origination and diversification of dytiscid lineages.

MATERIAL & METHOD

Fossil data

We compiled all known genus- and species-level fossil occurrences of Dytiscidae from the PBDB (<https://paleobiodb.org/>; accessed on 10 June 2025, using the taxon name 'Dytiscidae' with the following parameters: taxonomic resolution = genus, and the additional output blocks = location, references, and enterer names). The initial dataset from the PBDB consisted of 321 occurrences. We enriched this compilation with further records drawn from the published scientific literature, and supplemented this dataset with additional records from the Palaeoentomology database maintained by the Laboratory of Arthropods, Palaeontological Institute of the Russian Academy of Sciences in Moscow (<http://paleoentomolog.ru/english.html>; accessed on 10 June 2025). Following a thorough review (i.e. removing synonyms, *nomina dubia*, outdated taxonomic combinations and other inconsistencies) and integrating extensive additional data from the literature, the curated fossil dataset comprises 539 genus-level and 249 species-level occurrences for *c.* 160 species (Table S1).

While most taxa in the dataset correspond to formally published and named species, we also included one unnamed but taxonomically distinct genus and species that, although not yet formally described in the literature, can be recognized as a separate entity. Therefore, the fossil species †*Palaeodytes incompletus* Ponomarenko *et al.* 2005 (upper Berriasian, 139.1–137.05 Ma) is here treated as a new undescribed genus, given that it most probably does not belong to the genus †*Palaeodytes* according to Prokin *et al.* (2013).

We did not include the purported oldest fossil attributed to Dytiscidae, †*Angaragabus jurassicus*, in our dataset,

because its assignment to the family is not universally accepted. A detailed re-examination published by Prokin *et al.* (2013) determined that this fossil larva may align more closely with †Liadytidae or Aspdytidae rather than Dytiscidae, even though this hypothesis remains difficult to test. In addition to this species, we also did not include the reported Miocene occurrence of a dytiscid fossil from Australia (McCurry *et al.* 2022), because there was no evaluation conducted for its taxonomic attribution. Finally, we excluded the extinct taxon †*Schistomerus californiense* Palmer 1957, because it is described only from larvae and could potentially belong to other genera known from the adult form of the same locality.

The ages provided by the PBDB, typically based on stratigraphic stages and following the latest International Chronostratigraphic Chart (Cohen *et al.* 2013), were used as a primary reference. However, when recent studies offered improved dating, for example, the U–Pb zircon analysis for the Kachin amber (yielding an age of 98.79 ± 0.62 Ma) (Shi *et al.* 2012), we adopted their revised age estimates for fossils from those localities. For Baltic amber, we retained the age range provided by the PBDB (37.71–33.9 Ma; Aleksandrova & Zaporozhets 2008), which remains highly consistent with the recent study by Ross *et al.* (2025), who established an age of 36–35 Ma for samples from the Upper Blue Earth Formation.

Institutional abbreviations. CNU, Capital Normal University, Beijing, China; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SNHMB, Staatliches Naturhistorisches Museum, Braunschweig, Germany; ZSM, Zoologische Staatssammlung München, Germany.

Dataset construction for Bayesian Brownian bridge analyses

The BBB model does not use fossils as fixed calibration points. Instead, fossil occurrences are treated as a sampled diversity vector through time, which is combined with present-day genus richness to probabilistically infer lineage origination (for extant and extinct clades) and extinction (for extinct clades). The Bayesian framework approximates preservation rate, and the resulting credible intervals explicitly capture uncertainty associated with sparse or unevenly distributed fossil occurrences (Silvestro *et al.* 2021). This enables the model to provide new insights beyond the known temporal placement of known fossils, including estimates of unsampled species inside a clade. The model requires only two input files to run: (1) a specific diversity table over time for each of the studied clades organized in time bins, with the species represented in the fossil record distributed according to their attributed age; and (2) the extant species richness of each studied clade (set to 0 for extinct clades).

To construct the dataset analysed with the BBB model, we retained only one occurrence per species per deposit of different ages to avoid bias caused by multiple occurrences of commonly found taxa in one deposit (e.g. †*Coptotomus balticus* Hendrich & Balke 2020, present in two occurrences from the Baltic amber of Kaliningrad, Russia). For each occurrence, we conservatively assigned the latest age of the associated stratigraphic interval. This helps to reduce the risk of artificially extending ranges toward earlier ages. We acknowledge that this convention may instead bias estimates toward later ages, but we consider this bias more conservative and easier to address than the opposite. We then constructed a specific diversity table over time for each genus, as well as for the entire family Dytiscidae (all species), organized in 1 myr bins with the species represented in the fossil record distributed according to the explanation above (Tables S2, S3). An exception was made for the genus *Platambus* Thomson 1859, given that both species are in the first time bin, which caused a mathematical error in the analyses. Consequently, *Platambus* was excluded. Therefore, the dataset used for our analyses contains 158 occurrences of 155 species distributed in 41 genera (Table S2).

The BBB model leverages extant species richness as an endpoint to infer the historical age of a clade (genus level in the case of this study). To inform this endpoint for Dytiscidae, we relied on the most recent and complete checklist: *A world catalogue of the Family Dytiscidae* (v1.I.2025), compiled by Nilsson & Hájek (2025) and available from the Water Beetles website (<https://www.waterbeetles.eu/>). Extant species richness per genus represented in their fossil record ranges from 1 (genus *Japanolaccophilus* Satô 1972) to 449 species (genus *Copelatus* Erichson 1832). Extinct genera were assigned an extant species richness of 0. The diversity counts are provided in Table S4.

Bayesian Brownian Bridge model applied to genera found in the fossil record of Dytiscidae

We ran the BBB model for 1 000 000 iterations, with samples collected every 1000 iterations and using an exponentially time-increasing rate preservation model (*-q_var 1* option) for the whole family and each of the 41 genera. For all analyses, we performed sensitivity analyses by testing two different settings for the maximum boundary of uniform prior on the root age: (1) 230 Ma, corresponding to the mean divergence time estimates between Dytiscidae and the clade Hygrobiidae + (Amphizoidae + Aspidytidae) in Cardenas *et al.* (2025); and (2) 300 Ma, corresponding to the oldest unambiguous Coleoptera fossil †*Coleopsis archaica* Kirejtshuk, Poschmann & Nel *in*

Kirejtshuk *et al.* 2014. We also assessed the effect of extant diversity on origination time estimates of Dytiscidae by testing three different values for the total number of extant dytiscid species: 4797 (the current number of described species according to Nilsson & Hájek 2025), as well as two other values: 6000 and 8000 species, intended to account for potential under-sampling and undescribed species diversity within the family, following a strategy similar to Jouault *et al.* (2025) and Ferreira *et al.* (2026). Convergence of the MCMC (Markov chain Monte Carlo) chains was evaluated using Tracer v1.7.2 (Rambaut *et al.* 2018), considering good convergence with effective sample sizes (ESS) exceeding 200 after discarding the initial 10% of samples as burn-in. Visualization of the results was performed using custom R scripts (R Core Team 2021) from Boderau *et al.* (2025a) as well as from Silvestro *et al.* (2021). Files used to run the analyses and outputs can be found in Ferreira *et al.* (2025, file S1).

Lineages through time with PyRate

To assess temporal changes in dytiscid genus diversity, we reconstructed a lineages-through-time (LTT) plot using PyRate 3 (Silvestro *et al.* 2014, 2019), based on the estimated origination and extinction times of all genera documented in the fossil record and assessed with PyRate (using the *-ltt 1* option; files and R scripts provided in Ferreira *et al.* 2025, files S2, S3). To obtain the origination and extinction times of those genera with PyRate, we performed analyses at the genus level under the birth-death model with constrained shifts (BDCS) (Silvestro *et al.* 2015) and the reversible jump Markov chain Monte Carlo (RJMCMC) model (*-A 4* option) (Silvestro *et al.* 2019). We used the time-variable Poisson process as a preservation model, which assumes that preservation rates are constant within a predefined time bin, here, geological epochs (*-qShift* option). For the BDCS model, we also used geological epochs as shift constraints (*-fixShift* option). We ran PyRate on 10 randomized datasets (considering age uncertainty in fossil occurrences) for 200 million generations with a sampling every 100 000 generations. All scripts used to run these analyses, and their outputs, are available in Ferreira *et al.* (2025, files S2, S3). All of the 518 genus-level fossil occurrences used in the PyRate analysis are available in Tables S1 and S5.

RESULTS

Timing of origination of Dytiscidae

Table 1 lists the estimated mean origination ages of Dytiscidae obtained using the BBB model, under varying

TABLE 1. Age estimates for the family Dytiscidae using the Bayesian Brownian bridge model.

Extant diversity count	Dytiscidae			
	230 Ma		300 Ma	
	Mean age	95% HPD	Mean age	95% HPD
4797	194.8	225–161.5	218.3	290.9–158.4
6000	190.7	224.9–160	219.1	293.8–158
8000	188.3	220.2–156	220.5	298.9–162

Mean ages and highest posterior densities (HPD) are obtained for two different maximum boundaries of uniform prior on the root age and three different extant diversity counts. They are given in millions of years ago.

assumptions of extant species richness (4797, 6000 and 8000 species) and two different maximum boundaries of uniform prior on the root age (230 and 300 Ma). When the root is constrained to 230 Ma, the mean origination ages are consistent across different diversity values, ranging from 194.8 to 188.3 Ma, with 95% highest posterior density (HPD) intervals spanning *c.* 225 to 156 Ma (Table 1). These results support an Early Jurassic origin of the family. In contrast, when the maximum root age is extended to 300 Ma, the estimated mean ages shift significantly earlier, ranging from 220.5 to 218.3 Ma, while the 95% HPD intervals become wider (e.g. up to *c.* 299 Ma), suggesting greater uncertainty (Table 1). We note that increasing the extant diversity count does not substantially change the ages inferred.

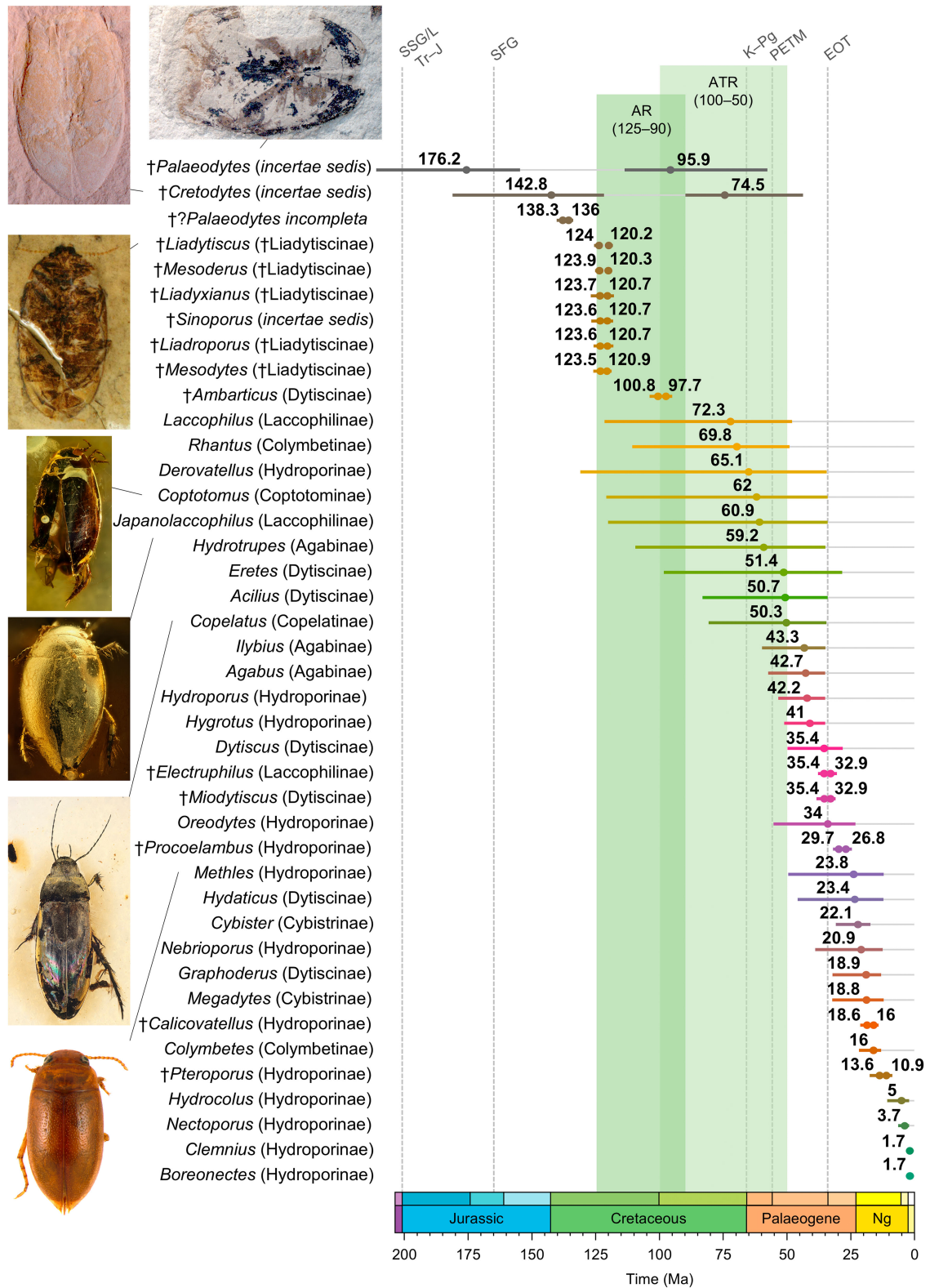
Timing & origination rates of Dytiscidae genera in the fossil record

Hereafter, we describe the origins inferred for the genera of Dytiscidae represented in the fossil record. However, we acknowledge that many genera were probably present in the past but are not represented in the fossil record of

the family. Analyses using the BBB model for each dytiscid genus represented in the fossil record, with the root age constrained to a maximum of 230 Ma (Fig. 2), found that only one genus, †*Palaeodytes*, originated during the Early Jurassic (176.2 Ma; 95% HPD = 211.7–155.1 Ma) (Fig. 2). This was followed by the emergence of nine genera in the Early Cretaceous (especially around the Barremian–Aptian; Figs 2, 3A), accounting for *c.* 22% of those documented in the fossil record (Fig. 2), representing one of the major pulses in genus origination in dytiscid history (Fig. 3). Subsequently, the origination rate dropped significantly during the Early Cretaceous (Figs 2, 3), with only two genera appearing: *Laccophilus* Leach 1815 (72.3 Ma; 95% HPD = 121.9–48 Ma), which is the first inferred origination of an extant genus in Dytiscidae, and *Rhantus* Dejean 1833 (69.8 Ma; 95% HPD = 110.9–49 Ma) (Fig. 2). After the Cretaceous–Palaeogene (K–Pg) extinction event, 18 genera originated during the Palaeogene, representing *c.* 44% of the genera included in this study (Fig. 2). In the Palaeogene, four genera originated during the Paleocene (*c.* 10%), 11 during the Eocene (*c.* 27%), and three during the Oligocene (*c.* 7%). Notably, it was during the Oligocene that three genera went extinct: †*Electruphilus* Balke *et al.* 2019, †*Miodytiscus* Wickham 1911, and †*Procoelambus* Théobald 1937, after the Eocene–Oligocene transition (EOT) (Figs 2, 3). Of these, two, †*Electruphilus* and †*Miodytiscus*, had originated in the Eocene, according to our analyses (Fig. 2). Finally, the Neogene saw the emergence of nine genera, corresponding to *c.* 22% of the total genera represented in the fossil record of Dytiscidae.

When using a *-max_age* prior of 300 Ma, the resulting age estimates and origination rates remained very consistent with those obtained using a *-max_age* prior of 230 Ma (Figs S1, S2). The most notable differences were observed for the genus †*Palaeodytes*, which was also inferred to have originated in the Early Jurassic, but slightly earlier (181.7 Ma; 95% HPD = 232.2–155 Ma), and for †*Cretodytes*, for which the estimated age of origination remained nearly unchanged, although its 95% HPD upper bound increased, from 181.7 Ma under the

FIG. 2. Estimates of origin and extinction of genera represented in the fossil record of Dytiscidae, inferred from the Bayesian Brownian bridge model with a maximum boundary of uniform prior on the root age of 230 Ma. *Abbreviations:* AR, angiosperm radiation; ATR, angiosperm terrestrial revolution; EOT, Eocene–Oligocene transition; K–Pg, Cretaceous–Palaeogene extinction; Ng, Neogene; PETM, Paleocene–Eocene thermal maximum; SFG, start of fragmentation of Gondwana; SSG/L, start of split Gondwana/Laurasia; Tr–J, Triassic–Jurassic extinction. Specimen images, counterclockwise from the top: †*Palaeodytes baissiensis* Prokin *et al.* 2013, holotype PIN 4210/380, †*Cretodytes incertus*, holotype PIN 4626/628, both by Alexander A. Prokin, from Prokin *et al.* (2013) ©Magnolia Press, reproduced with permission; †*Liadytiscus longitibialis* Prokin & Ren 2010, holotype CNU COL LB 2009026, by Alexander A. Prokin, from Prokin & Ren (2010) ©Springer Nature, reproduced with the permission; †*Coptotomus balticus* Hendrich & Balke 2020, holotype, ZSM (no number), by Michael Balke, from Hendrich & Balke (2020) ©Magnolia Press, reproduced with permission; †*Japanolaccophilus beatificus* Balke & Hendrich 2019, holotype, ZSM (no number), by Michael Balke, from Balke & Hendrich (2019) ©Magnolia Press, reproduced with permission; †*Copelatus chiapas* Hájek *et al.* 2025, holotype SNHMB.G 8199 ©Michael Balke, from Hájek *et al.* (2025); *Methles cribratellus* (Fairmaire 1880), ©Jules Ferreira.



230 Ma maximum age to 190.8 Ma with the 300 Ma maximum age (Fig. S1). More generally, the analysis using a *-max_age* prior set to 300 Ma resulted in very

slightly higher upper bounds of the 95% HPD across all genera, with some exceptions towards most recent genera (Fig. S1).

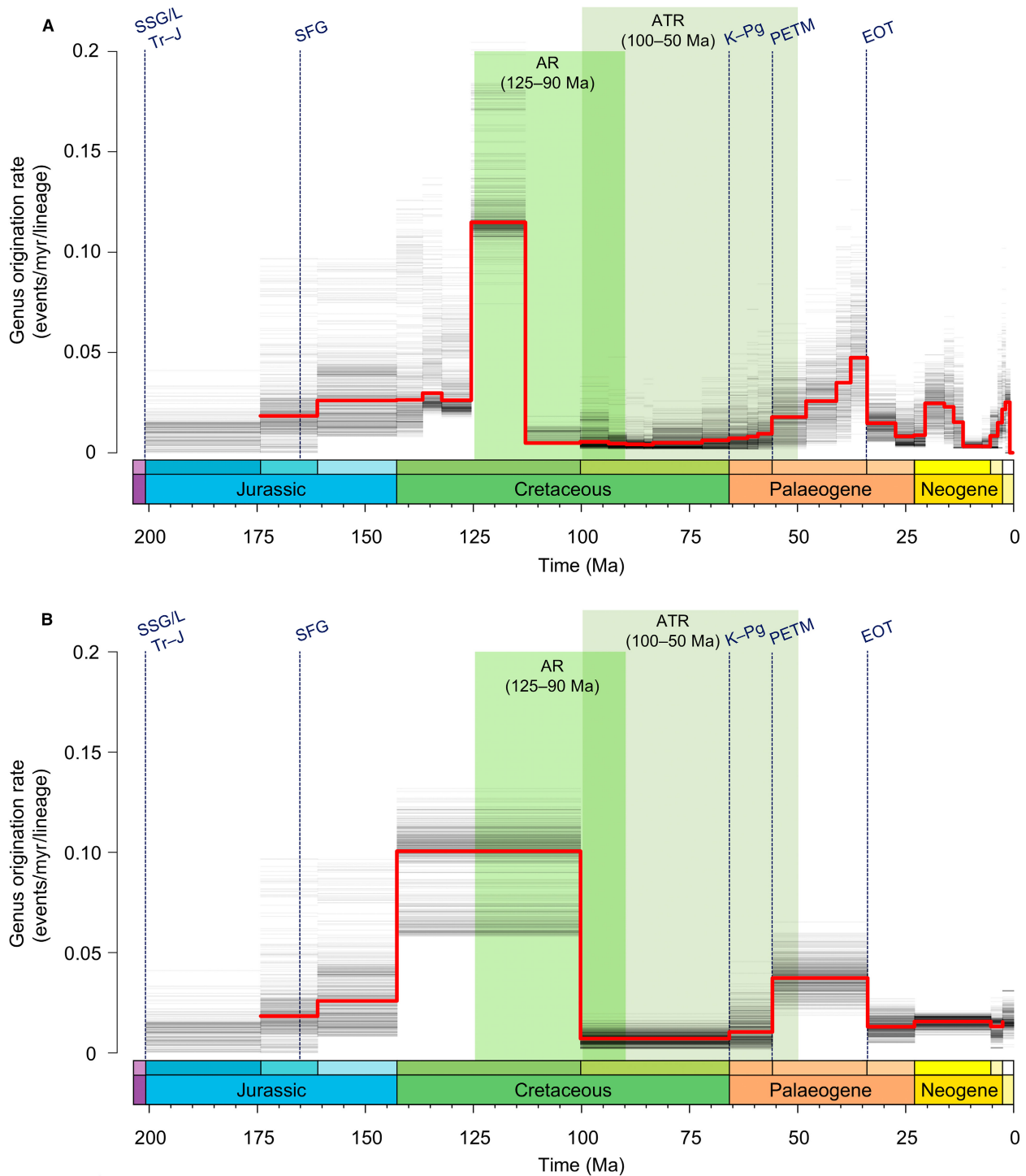


FIG. 3. Genus-level origination rates inferred from the estimated diversity trajectories of the sampled genera in the dytiscid fossil record, with the maximum boundary of uniform prior on the root age set at 230 Ma. A, genus-level origination rate versus geological stage. B, genus-level origination rates versus geological epoch. Black lines represent 1000 posterior samples; red line indicates their median trajectory. *Abbreviations:* AR, angiosperm radiation; ATR, angiosperm terrestrial revolution; EOT, Eocene–Oligocene transition; K–Pg, Cretaceous–Palaeogene extinction; PETM, Paleocene–Eocene thermal maximum; SFG, start of fragmentation of Gondwana; SSG/L, start of split Gondwana/Laurasia; Tr–J, Triassic–Jurassic extinction.

Origination, extinction & diversification rates as inferred under the BDCS model

Results from the BDCS analysis are presented in Figure S3. Due to the scarcity of fossil data for Dytiscidae, these results are difficult to interpret and should be taken cautiously, given that the 95% HPD intervals for origination, extinction and diversification rates per epoch are wide (Fig. S3). Notably, for the diversification rate (Fig. S3C), the only epoch in which the 95% HPD does not overlap zero is the Eocene (56–23.04 Ma). Further discussion on the limitations of using PyRate in this context can be found under [Methodological Limitations & Future Directions](#), below.

DISCUSSION

A Late Triassic or an Early Jurassic origin of Dytiscidae?

Most of our results point toward a Jurassic origin of Dytiscidae, most likely during the Early Jurassic, *c.* 195–188 Ma (95% HPD range = 224.9–156 Ma) (with a *-max_age* prior of 230 Ma; Table 1), which is *c.* 20 myr earlier than several recent phylogenetic dating studies (Toussaint *et al.* 2017a; Désamoré *et al.* 2018; Zhang *et al.* 2018; Baca *et al.* 2021). However, this Jurassic estimation may be due to the constraint on the maximum age in analyses (*i.e.* 230 Ma), as indicated by 95% HPD upper bounds that are close to the constraint. When changing this constraint to a less restrictive one (*i.e.* 300 Ma) the estimated origin is pushed further back, to the end of the Late Triassic, *c.* 220–218 Ma (95% HPD range = 298.9–158 Ma) (Table 1), highlighting the possibility of an earlier diversification of the group. These last results are closer to the *c.* 210 Ma reported by Cai *et al.* (2022) and Cardenas *et al.* (2025), with a slight increase of *c.* 10 myr.

Additionally, our results also show that increasing the maximum root age (to 300 Ma) pushes the divergence point further back in time, yielding ages of *c.* 220 Ma (Table 1), reflecting model sensitivity to the upper age prior, although not visible in genus-level analyses.

Given the inherent uncertainty in deep-time divergence dating, we refrain from strongly favouring one scenario over the other. Both are empirically plausible under current data from the fossil record, BBB model frameworks, and recently dated molecular phylogenies. Future studies incorporating both fossil and extant taxa in integrated phylogenetic approaches, such as tip-dating or total-evidence approaches, will be decisive to resolve these remaining ambiguities.

Identifying major temporal periods in the diversification of Dytiscidae

The Jurassic was undoubtedly a key period for Dytiscidae, which also corresponds to a broader first pulse of the aquatic Dytiscoidea radiation (Beutel *et al.* 2024). The gradual fragmentation of Pangaea, driven by tectonic rifting starting in the Early Jurassic (*c.* 200 Ma), reshaped freshwater habitats by creating extensive epicontinental seas and isolated lakes across the northern and southern hemispheres (Scotese 2021). These habitat changes are likely to have provided new ecological opportunities for aquatic beetles, as supported by fossil evidence from other freshwater invertebrates such as gastropods (Neubauer *et al.* 2022). By the Middle to Late Jurassic (*c.* 170–150 Ma), ongoing continental rifting had generated a patchwork of isolated lacustrine habitats across both Laurasian and Gondwanan landmasses (Scotese 2021) (Fig. 4). In addition, global temperatures began to decline *c.* 180 Ma (Scotese 2016, 2021), which may have also influenced freshwater ecosystems (Fig. 4). While these newly formed freshwater ecosystems probably provided ecological opportunities (Sinitshenkova 2003), the effect on early Dytiscidae remains difficult to evaluate with certainty due to the extremely sparse fossil record of the group during this period, with only one fossil species dating to the Middle–Late Jurassic (†*Palaeodytes gutta*), for which the genus origination is estimated to be *c.* 176 Ma (Early Jurassic) from our results (Fig. 2). Nonetheless, such geographic fragmentation may have promoted episodes of allopatric divergence among aquatic beetle lineages, potentially contributing to the early diversification of Dytiscidae and their aquatic relatives (such as in aquatic beetles at different time scales, *e.g.* Toussaint *et al.* 2016, 2017b; Short *et al.* 2021; or even in Plecoptera, *e.g.* Letsch *et al.* 2021). Therefore, while the Jurassic breakup of Pangaea and/or the cooling of temperatures may not have directly triggered a huge radiation of Dytiscidae, evidence from our results at the genus level, together with those of some dated molecular phylogenies (Désamoré *et al.* 2018; Baca *et al.* 2021; Cardenas *et al.* 2025), supports the idea that their diversification started during this period.

In the Early Cretaceous (143.1–100.5 Ma), the fossil record of Dytiscidae shows a notable pulse of genus origination, with nine genera emerging around the Barremian–Aptian interval (*c.* 126–113 Ma), many of which belong to the extinct subfamily †Liadytiscinae (Figs 1B, C, 2–4). The very beginning of the Early Cretaceous interval corresponds to a global cooling trend, which may have favoured the origination of new dytiscid genera by creating more stable or suitable freshwater thermal regimes (Figs 2–4). It also coincides with major

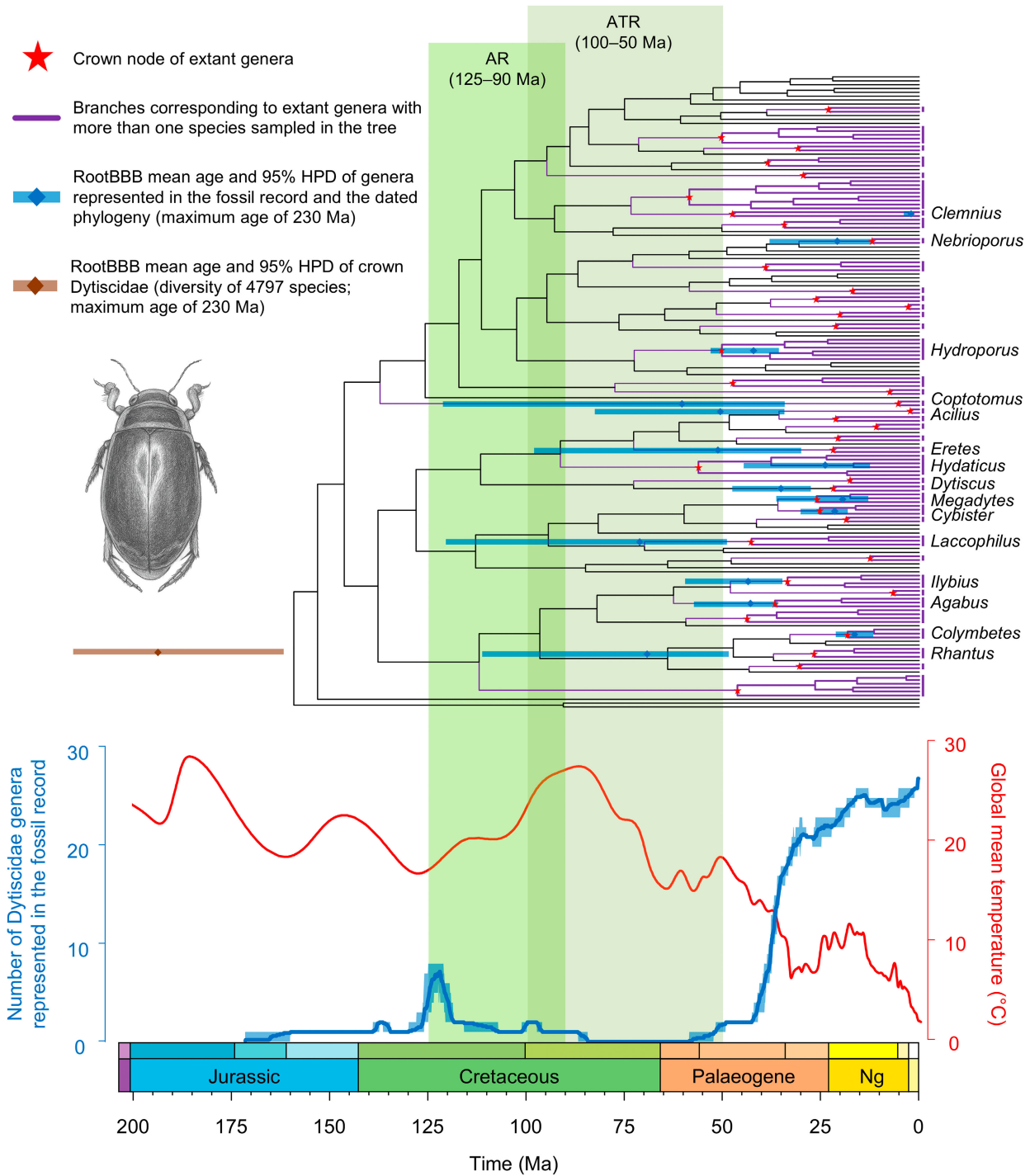


FIG. 4. Dated phylogeny of Dytiscidae from Désamoré *et al.* (2018) shown alongside genus-level diversity estimates using PyRate and fossil occurrences (blue curve, with age uncertainties of fossil occurrences), for direct comparison between molecular divergence times and fossil-based diversification patterns. Global variation in temperature over time is shown as a red curve (Scotese 2016). *Abbreviations:* AR, angiosperm radiation; ATR, angiosperm terrestrial revolution; HPD, highest posterior density; Ng, Neogene. Drawing of male *Dytiscus marginalis* Linnaeus 1758 ©Jules Ferreira.

ecological changes linked to the onset of the angiosperm radiation (AR, 125–90 Ma) (Labandeira 2014), although aquatic habitats were already occupied by horsetails, ferns,

mosses, and other groups before angiosperms appeared, providing structurally complex and productive freshwater environments. Some aquatic angiosperms emerged early

in the radiation, potentially adding to the diversity and biomass of freshwater habitats, but these changes occurred within pre-existing plant-rich aquatic ecosystems (Gomez *et al.* 2015; Du *et al.* 2016; Meseguer *et al.* 2022). As angiosperms started to proliferate, the biomass inputs may, however, have altered freshwater environments by increasing the quantity and diversity of organic matter, such as leaf litter and woody debris, which can serve as resources and habitat substrates for aquatic invertebrates (Sinitshenkova 2003; Mbaka & Schäfer 2016).

During the Late Cretaceous (100.5–66 Ma), fossil occurrences of Dytiscidae are extremely rare, a pattern consistent with the general scarcity of insect fossils from this period, with only two species known (†*Cretodytes latipes* Ponomarenko 1977 and †*Ambarticus myanmaricus* Yang *et al.* 2019). In our analyses, we identified *Laccophilus* (*c.* 72.3 Ma) and *Rhantus* (*c.* 69.8 Ma) as the only genera for which a Late Cretaceous origination is inferred (Figs 2, 4). The apparently low abundance of Dytiscidae fossils during this period may reflect taphonomic and sampling biases rather than a real decline in genus origination (Figs 3A, 4), given that many more genera were most probably present in the past but not yet sampled in the fossil record. That said, the first part of the Late Cretaceous (100.5 to *c.* 75 Ma) is also characterized by a substantial rise in global temperatures, with some of the highest annual temperatures of the entire Mesozoic (Fig. 4) (Scotese 2016). Notably, this interval also coincides with the extinction of three genera in our analyses (†*Palaeodytes*, †*Cretodytes* and †*Ambarticus* Yang *et al.* 2019; Figs 2, 4). While climate factors such as increasing temperatures and environmental instability (Linnert *et al.* 2014) may have contributed to their disappearance, biotic processes are likely to have played an important role. The end of the Late Cretaceous also marks a period during which the dytiscid fauna was becoming rich, and the extinction of these genera may reflect broader faunal turnover, with more ecologically versatile lineages replacing earlier ones. But this period also overlaps with the angiosperm terrestrial revolution (ATR, 100–50 Ma) (Benton *et al.* 2022), a major ecological transformation driven by the diversification and spread of flowering plants. While the ATR is often associated with rapid radiations in other insect groups, such as pollinators (Peris & Condamine 2024), our results suggest that Dytiscidae did not benefit from these environmental changes. Instead, an increase in genus origination occurs later, both after the high temperatures (*i.e.* after *c.* 75 Ma) and during the Paleocene, following the K–Pg boundary. We may hypothesize that there may have been a delayed dytiscid response to angiosperm expansion, in which ecological benefits of flowering-plant-driven habitats, such as novel oviposition sites offered by aquatic monocots, emerged only after the K–Pg ecosystem

restructuring and/or the progressive development of more complex, angiosperm-rich freshwater systems. Supporting this idea, several modern dytiscid lineages lay their eggs on or in plant tissues (Bergsten & Miller 2016; Watanabe 2024). However, testing this hypothesis would require further analysis. An alternative hypothesis would be that Dytiscidae did not benefit from the ATR because freshwater ecosystems were already plant rich before the diversification of flowering plants. Supporting this, fossil evidence indicates that structurally rich aquatic habitats existed well before the Cretaceous: for example, †*Triamyxa* Qvarnström *et al.* 2021 (aquatic genus of Myxophaga suborder) from the Triassic probably occupied fully aquatic environments resembling modern conditions (Qvarnström *et al.* 2021). Similarly, a study on swimming behaviour in *Amphiops* Erichson 1843 (aquatic genus of Hydrophilidae) (Hu *et al.* 2025) suggested that the evolution of the swimming modes in this genus was already driven by specialization for floating aquatic plants, long before the appearance of angiosperms. These examples would then support the idea that freshwater ecosystems already provided suitable ecological opportunities for diving beetles independently of flowering-plant-driven changes.

In the Palaeogene (66–23.04 Ma), following the K–Pg extinction event, there is a noticeable increase in genus origination among Dytiscidae (Figs 2–4), suggesting that the post-extinction recovery phase provided ecological opportunities for diversification or that Dytiscidae may have started to benefit from the ATR. Our estimates of genus origination and origination rates in Dytiscidae genera (Figs 2, 3) are consistent with those reported by Désamóré *et al.* (2018) and Cardenas *et al.* (2025), which are the only phylogenetic dating studies to include multiple representatives per genus within the family. In their work, Désamóré *et al.* (2018) and Cardenas *et al.* (2025) found that all of the sampled extant dytiscid genera, with available crown age estimates, diversified after the K–Pg mass extinction event (Figs 2–4). Furthermore, from our results, a small rise in origination is observed around the Paleocene–Eocene thermal maximum (*c.* 56 Ma), a short (*c.* 200 000 years) but intense interval of global warming (Gingerich 2006; McNerney & Wing 2011) (Figs 2–4). Then, from *c.* 50 Ma onward, global temperatures began a gradual decline throughout the Eocene (Scotese 2016), a trend that appears to correlate with a sustained increase in genus number among Dytiscidae (Figs 2–4). However, this pattern is disrupted at the EOT (*c.* 33.9 Ma), which marks a major climate shift to icehouse conditions (Scotese 2016). These changes led to the contraction of tropical and subtropical ecosystems, including many freshwater habitats (Coxall & Pearson 2007; Liu *et al.* 2009), and correspondingly, genus origination among Dytiscidae temporarily declined (Fig. 3).

The Miocene (23.04–5.333 Ma) exhibits a peak in genus origination rates within Dytiscidae, particularly during the Middle Miocene, a pattern highlighted by both our results and those of Désamoré *et al.* (2018) (Figs 3, 4). This epoch is marked by substantial climate fluctuations and reorganization of terrestrial and freshwater ecosystems (Scotese 2016). The Middle Miocene climatic optimum (*c.* 17–14.5 Ma) represents a warm phase, during which global temperatures temporarily rose (after the icehouse conditions of the Oligocene), leading to the expansion of subtropical and temperate biomes (Zachos *et al.* 2001; Westerhold *et al.* 2020). These warmer conditions may have enhanced the productivity and extent of freshwater habitats, such as lakes, rivers and wetlands, probably providing diverse ecological opportunities for aquatic beetles. Moreover, the Miocene is characterized by the expansion of open landscapes, including prairies, grasslands and steppes (Mannetje 2007). The combination of climate changes, expanding habitat heterogeneity, and changing landscapes probably created a dynamic with more varied and richly structured ecological niches that favoured increased origination rates among Dytiscidae (Figs 3, 4). However, in the Late Miocene (*c.* 14.5–7.246 Ma), global cooling led to drier conditions and shrinking freshwater habitats, which probably caused fewer new genera to appear and some extinctions among Dytiscidae (Figs 3, 4).

From origination estimates to macroevolutionary inferences

Beyond the finer putative correlations described above, the obtained origination estimates enabled us to extract broader evolutionary tendencies for Dytiscidae and to assess their potential biological significance. One emerging signal is that the major pulses of genus origination inferred from our analyses tend to align with intervals of global cooling following a highly warm climate, rather than with warming phases (Figs 2–4). While this may be due to preservation bias, this may also represent a genuine biological signal. This pattern first appears in the Middle Jurassic, when a drop in global temperatures coincides with the earliest genus diversification pulse of the family, and it recurs near the Barremian–Aptian in the Early Cretaceous (Figs 2–4). It becomes especially clear in the Cenozoic, during the Palaeogene, that genus origination rises as global temperatures decline through the Eocene, and the strongest increase during this period occurs before the EOT, a pivotal shift toward cooler icehouse conditions (Figs 2–4). Together, these repeated associations suggest that cooling phases may have promoted the diversification of Dytiscidae (such as seen in some marine clades; *e.g.* Davis *et al.* 2016; Mathes *et al.* 2021). However, the pattern we observe may also

imply that both extremes of temperature may have constrained diversification. When global temperatures were particularly high (*e.g.* during parts of the Late Cretaceous), origination events appear comparatively scarce, and likewise, immediately after the EOT, during the Oligocene, origination rates remain low, probably reflecting conditions that became too cold or too restrictive for substantial diversification (Figs 2–4). From the beginning of the Neogene, global temperatures gradually increased, which appears to disrupt the previous pattern of diversification peaks during cooling periods. But this warming follows an icehouse state rather than a previous warm thermal maximum, suggesting that the effect of temperature on origination may depend on the previous baseline climate context (Figs 2–4). Together, these observations suggest that there may be an intermediate climate window that would favour diversification in Dytiscidae (*e.g.* Vrba 1992). However, because environmental changes are continuous, these putative correlations alone cannot demonstrate causality. Diversification in Dytiscidae is likely to have been driven by a combination of interacting abiotic and biotic factors rather than by single environmental variables acting in isolation. Testing such hypotheses will therefore require more thorough and formal analytical frameworks that integrate phylogenetic information, diversification rates and explicit palaeoenvironmental reconstructions. Environment-dependent diversification models, combined with simulations, could be used to evaluate whether the temporal coincidence between global cooling phases and increased origination exceeds expectations under stochastic or constant-rate scenarios, and to disentangle the relative roles of climate, habitat availability and biotic interactions such as competition or faunal turnover (*e.g.* Condamine *et al.* 2019; Morlon *et al.* 2024). In this context, the divergence time estimates produced here may provide a temporal framework that can serve as a base for proposing a broader range of hypotheses on how multiple, interacting drivers may have shaped the long-term evolutionary trajectory of Dytiscidae.

Methodological limitations & future directions

Estimation of diversification rates from fossil occurrence data using PyRate has become a widely used approach. It relies on modelling fossil occurrences through a birth–death process that explicitly accounts for preservation and sampling biases (Silvestro *et al.* 2014, 2019). However, this method requires relatively rich and continuous fossil occurrence datasets to reliably estimate speciation, extinction and preservation rates (such as done for other insect groups, *e.g.* Condamine *et al.* 2016; Jouault *et al.* 2024;

Peris & Condamine 2024; Boderau *et al.* 2025b; Jouault *et al.* 2025). When fossil records are sparse, uneven, or contain many singletons (taxa with only one occurrence), PyRate's estimates might become unreliable. In the case of Dytiscidae, the fossil dataset has a limited number of taxa and uneven temporal coverage (e.g. the Late Cretaceous). To circumvent these limitations, we used the BBB model implemented in rootBBB, which is better suited to datasets with low sampling density, but is primarily designed to estimate the origin of a clade. The BBB model requires only a number of species distributed across time intervals (identified at the species level), the age of those fossil species, and the extant species richness to estimate clade origination times. Even if the BBB model is not designed to infer diversification patterns, it may be used as such, with genus-level origination rates inferred from the estimated diversity trajectories of the sampled genera of the dataset.

It is also important to note that our analyses are conducted at the genus level, which has both practical and conceptual implications. Although working at this taxonomic rank helps mitigate some issues related to species-level incompleteness in the fossil record and heterogeneity among lineages, it also obscures potential problems of clade monophyly. Genera are not always monophyletic, especially in groups in which taxonomic revisions are ongoing or limited by morphological convergence. In addition, the assignment of fossil material to extant or extinct genera is itself influenced by expertise and taxonomic practice. These biases may distort the apparent temporal ranges and richness of genera in the fossil record, and therefore need to be considered when interpreting our results. Moreover, the definition of genera is inherently subjective and often reflects arbitrary boundaries drawn to represent major morphological shifts. As such, some genera included in our dataset may not correspond to monophyletic lineages, potentially biasing our estimates and the inferred patterns of origination or diversification.

At the same time, it is precisely because fossils are primarily attributed to genera on the sole basis of morphological characters that they constitute a tractable taxonomic unit in palaeontological datasets. Morphological characters enable most fossil specimens (frequently incomplete and lacking molecular data) to be assigned to a genus (either extant or extinct), making genus-level data far more reliable and comparable through deep time than species-level assignments. Although genus boundaries are to some extent subjective and may not always correspond to monophyletic clades, they often capture major and persistent morphological discontinuities that are repeatedly recognizable in the fossil record. In this sense, genera represent a pragmatic compromise between phylogenetic accuracy and fossil identifiability.

Moreover, given the constraints of the fossil record and the lack of detailed phylogenetic placement for many extinct taxa, the genus level remains one of the most operationally consistent units for large-scale macroevolutionary analyses such as those conducted in this study. Furthermore, Dytiscidae represent one of the best-studied beetle groups, with numerous recent phylogenetic studies dedicated to resolving inter-clade and intra-clade relationships (e.g. Baca *et al.* 2021; Bergsten *et al.* 2025; Cardenas *et al.* 2025). These studies therefore provide a robust framework that supports the overall reliability of genus-level analysis in this group, particularly regarding monophyly.

Finally, this study focuses primarily on the timing of dytiscid origination and the diversification patterns of its genera, based mainly on genus origination events observed from the fossil record through our analyses under the BBB model. Extinction dynamics were not explored in detail and are addressed only in brief through the estimated extinction ages of extinct genera studied here (Fig. 2). A more comprehensive understanding of dytiscid evolutionary history, covering turnover rates and extinction patterns, will require dedicated analyses leveraging richer and more continuous fossil records alongside alternative models. In this context, a recent approach demonstrated that phylogeny-based inference of lineage occurrences can significantly enrich occurrence datasets beyond the fossil record. For instance, Brée *et al.* (2022) and Jouault *et al.* (2024) applied birth–death models implemented in PyRate to jointly analyse palaeontological data and neontological data derived from time-calibrated phylogenies. This approach enabled them to infer rates while alleviating the respective limitations of each data type. Adapting such a framework to Dytiscidae could help fill temporal (such as during the Late Cretaceous) as well as taxonomic gaps and yield a more complete picture of their macroevolutionary dynamics. However, it would require phylogenies containing many more terminals and diversity than the ones currently available.

CONCLUSION

Our study provides new evidence supporting an origin of Dytiscidae either during the Late Triassic (c. 220 Ma) or during the Early Jurassic (c. 190 Ma), as inferred from fossil occurrence data analysed using the BBB framework. Both interpretations are consistent with the available empirical data from fossils, BBB model analyses and different recent molecular dating studies. By combining fossil-based age estimates with genus-level diversity patterns, we identified several key periods of increased genus origination in the history of the group, notably during

the first part of the Early Cretaceous, the Palaeogene (mostly Paleocene and Eocene), and the Early–Middle Miocene. These pulses seem to coincide with major environmental shifts such as global temperature changes or tectonic reorganizations, although they are most probably a combination of biotic and abiotic factors. Despite limitations due to the incomplete nature of the fossil record and the lack of detailed extinction analyses, our approach highlights the value of integrating fossil data with probabilistic models to infer the deep-time macroevolutionary dynamics of insect lineages, enabling us to propose hypotheses relative to their diversification. Future work combining fossil and molecular data will be invaluable to refine the evolutionary timeline of Dytiscidae and assess the full extent of their diversification and extinction history.

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Author contributions. **Conceptualization** Jules Ferreira (JF); **Data Curation** JF, Corentin Jouault (CJ); **Formal Analysis** JF; **Funding acquisition** Fabien L. Condamine (FLC), David Peris (DP); **Investigation** JF; **Methodology** JF, CJ, FLC; **Project administration** FLC, DP; **Supervision** FLC, DP; **Validation** CJ, FLC, DP; **Visualization** JF, CJ, FLC, DP; **Writing – Original**

Draft Preparation JF, CJ, FLC, DP; **Writing – Review & Editing** JF, CJ, FLC, DP.

DATA ARCHIVING STATEMENT

Data for this study, including used scripts, prompts and outputs from the rootBBB analyses as well as the BDCS analyses are available in the Dryad digital repository: <https://doi.org/10.5061/dryad.x0k6djj0c>. See [Supporting Information](#) for PBDB dataset.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.70074>):

Figure S1. Estimates of origination and extinction of genera represented in the fossil record of Dytiscidae inferred from the Bayesian Brownian bridge model under rootBBB and with a maximum age of root of 300 Ma.

Figure S2. Genus-level origination rates inferred from the estimated diversity trajectories of the sampled genera in Dytiscidae fossil record with the maximum age of root set at 300 Ma, stratified by geological stage and geological epoch.

Figure S3. Diversification dynamics of Dytiscidae (genus-level analysis) under the BDCS model with PyRate.

Table S1. Database of Dytiscidae fossils used in this study along with their references.

Table S2. Database of Dytiscidae fossil species occurrences used in rootBBB analyses with their age.

Table S3. Specific diversity table over time for each genus, as well as for the entire family Dytiscidae (all species) organized in 1-million-year bins.

Table S4. Specific diversity counts for sampled genera.

Table S5. Database of fossils used in PyRate 3 at the genus-level.

REFERENCES

- Aleksandrova, G. N. and Zaporozhets, N. I. 2008. Palynological characteristics of Upper Cretaceous and Paleogene deposits on the west of the Sambian Peninsula (Kaliningrad region), Part 2. *Stratigraphy and Geological Correlation*, **16**, 528–539. <https://doi.org/10.1134/S0869593808050067>
- Baca, S. M., Gustafson, G. T., Alexander, A. M., Gough, H. M. and Toussaint, E. F. A. 2021. Integrative phylogenomics reveals a Permian origin of Adephaga beetles. *Systematic Entomology*, **46**, 968–990. <https://doi.org/10.1111/syen.12506>
- Balart-García, P., Aristide, L., Bradford, T. M., Beasley-Hall, P. G., Polak, S., Cooper, S. J. B. and Fernández, R. 2023. Parallel and convergent genomic changes underlie independent subterranean colonization across beetles. *Nature Communications*, **14**, 3842. <https://doi.org/10.1038/s41467-023-39603-1>

- Balke, M., Beigel, A. and Hendrich, L. 2010. *Hydroporus carsten-groehni* sp. n. und zwei unbestimmte Hydroporinae aus dem baltischen Bernstein (Dytiscidae: Hydroporinae). *Nachrichtenblatt Bayerischen Entomologen*, **59**, 2–8.
- Balke, M. and Hendrich, L. 2019. †*Japanolaccophilus beatificus* sp. n. from Baltic amber and a key to the Laccophilinae genera of the world (Coleoptera: Laccophilinae). *Zootaxa*, **4567** (1), 176–182. <https://doi.org/10.11646/zootaxa.4567.1.10>
- Balke, M., Toledo, M., Gröhn, C., Rappsilber, I. and Hendrich, L. 2019. *Electruphilus wendeli* gen. n., sp. n.: the first diving beetle recorded from Saxonian (Bitterfeld) amber (Coleoptera: Dytiscidae: Laccophilinae). *Russian Entomological Journal*, **28**, 350–357. <https://doi.org/10.15298/rusentj.28.4.02>
- Benton, M. J., Wilf, P. and Sauquet, H. 2022. The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytologist*, **233**, 2017–2035. <https://doi.org/10.1111/nph.17822>
- Bergsten, J. and Miller, K. B. 2016. *Diving beetles of the world: Systematics and biology of the Dytiscidae*. Johns Hopkins University Press.
- Bergsten, J., Nylander, J. A. A., Ospina, O. E., Lemmon, A. R. and Miller, K. B. 2025. Whole genome shotgun phylogenomics resolve the diving beetle tree of life. *Systematic Entomology*, **50**, 940–974. <https://doi.org/10.1111/syen.12685>
- Beutel, R. G., Xu, C., Jarzembowski, E., Kundrata, R., Boudinot, B. E., McKenna, D. D. and Goczał, J. 2024. The evolutionary history of Coleoptera (Insecta) in the late Palaeozoic and the Mesozoic. *Systematic Entomology*, **49**, 355–388. <https://doi.org/10.1111/syen.12623>
- Boderau, M., Fu, Y., Jiang, H., Guan, S., Peng, A., Nel, A. and Jouault, C. 2025a. Bayesian modelling of the fossil record enlightens the evolutionary history of Hemiptera. *Proceedings of the Royal Society B*, **292**, 20251133. <https://doi.org/10.1098/rspb.2025.1133>
- Boderau, M., Nel, A. and Jouault, C. 2025b. Diversification and extinction of Hemiptera in deep time. *Communications Biology*, **8** (1), 352. <https://doi.org/10.1038/s42003-025-07773-x>
- Brée, B., Condamine, F. L. and Guinot, G. 2022. Combining palaeontological and neontological data shows a delayed diversification burst of carcharhiniform sharks likely mediated by environmental change. *Scientific Reports*, **12**, 21906. <https://doi.org/10.1038/s41598-022-26010-7>
- Bukontaite, R., Ranarilalaitiana, T., Randriamihaja, J. H. and Bergsten, J. 2015. In or out-of-Madagascar? Colonization patterns for large-bodied diving beetles (Coleoptera: Dytiscidae). *PLoS One*, **10**, e0120777. <https://doi.org/10.1371/journal.pone.0120777>
- Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J. F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M. K., Newton, A. F., Leschen, R. A. B., Gimmel, M. L., Lü, L., Engel, M. S., Bouchard, P., Huang, D., Pisani, D. and Donoghue, P. C. J. 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science*, **9**, 211771. <https://doi.org/10.1098/rsos.211771>
- Cardenas, C. R., Gustafson, G. and Toussaint, E. 2025. Global integration of phylogenomic data and fine-scale partitioning strategies refine the evolutionary tree of Adephaga beetles. *Bulletin of the Society of Systematic Biologists*, **4** (1), 1–35. <https://doi.org/10.18061/bssb.v4i1.10345>
- Carlisle, E., Janis, C. M., Pisani, D., Donoghue, P. C. J. and Silvestro, D. 2023. A timescale for placental mammal diversification based on Bayesian modeling of the fossil record. *Current Biology*, **33**, 3073–3082. <https://doi.org/10.1016/j.cub.2023.06.016>
- Cohen, K. M., Finney, S. C., Gibbard, P. L. and Fan, J.-X. 2013. The ICS international chronostratigraphic chart. *Episodes*, **36**, 199–204.
- Condamine, F. L., Clapham, M. E. and Kergoat, G. J. 2016. Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Scientific Reports*, **6**, 19208. <https://doi.org/10.1038/srep19208>
- Condamine, F. L., Rolland, J. and Morlon, H. 2019. Assessing the causes of diversification slowdowns: temperature-dependent and diversity-dependent models receive equivalent support. *Ecology Letters*, **22**, 1900–1912. <https://doi.org/10.1111/ele.13382>
- Coxall, H. K. and Pearson, P. N. 2007. The Eocene–Oligocene transition. 351–387. In Williams, M., Haywood, A. M., Gregory, F. J. and Schmidt, D. N. (eds) *Deep-time perspectives on climate change: Marrying the signal from computer models and biological proxies*. The Micropalaeontological Society, Special Publications. <https://doi.org/10.1144/TMS002.16>
- Davis, K. E., Hill, J., Astrop, T. I. and Wills, M. A. 2016. Global cooling as a driver of diversification in a major marine clade. *Nature Communications*, **7**, 13003. <https://doi.org/10.1038/ncomms13003>
- De Geer, C. 1774. *Mémoires pour servir à l'histoire des insectes*, Vol. 4. Pierre Hesselberg, Stockholm, xii + 456 pp. + 19 pls.
- Dejean, P. F. M. A. 1833. *Catalogue des coléoptères de la collection de M. le Comte Dejean. Livraisons 1 & 2*. Méquignon-Marvis, Paris, 176 pp.
- Désamoré, A., Laenen, B., Miller, K. B. and Bergsten, J. 2018. Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae). *Molecular Ecology*, **27**, 979–993. <https://doi.org/10.1111/mec.14492>
- Du, Z., Wang, Q. and China Phylogeny Consortium. 2016. Phylogenetic tree of vascular plants reveals the origins of aquatic angiosperms. *Journal of Systematics and Evolution*, **54**, 342–348. <https://doi.org/10.1111/jse.12182>
- Erichson, W. F. 1832. *Genera Dyticeorum*. Nietackianis, Berlin, ii + 48 pp.
- Erichson, W. F. 1843. Beitrag zur Insecten-Fauna von Angola, in besondere Beziehung zur geographischen Verbreitung der Insecten in Afrika. *Archiv für Naturgeschichte*, **9**, 199–267.
- Fairmaire, L. 1880. Descriptions de coléoptères nouveaux du nord de l'Afrique. 4. Partie (1). *Annales de la Société Entomologique de France, Serie 5*, **10**, 245–252.
- Ferreira, J., Desutter-Grandcolas, L., Nel, A., Josse, H. and de Campos, L. D. 2024. First 3D reconstruction of the male genitalia of a Cretaceous fossil cricket: diving into the evolutionary history of the Oecanthidae family (Orthoptera: Grylloidea) with the incorporation of new fossils in its phylogeny and a total-evidence dating approach. *Systematic Entomology*, **49**, 429–446. <https://doi.org/10.1111/syen.12625>
- Ferreira, J., Jordal, B. H., Condamine, F. L. and Peris, D. 2026. Multiple dating methods and insights from the fossil record reveal that bark beetles predate the angiosperm terrestrial revolution. *Systematic Biology*, syag015. <https://doi.org/10.1093/sysbio/syag015>

- Ferreira, J., Jouault, C., Condamine, F. L. and Peris, D. 2025. Data from: A deep dive into the fossil record of diving beetles (Coleoptera: Dytiscidae): Bayesian inferences reveal their origin and pulsed diversification at the genus level [dataset]. Dryad. <https://doi.org/10.5061/dryad.x0k6djj0c>
- Gingerich, P. D. 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. *Trends in Ecology & Evolution*, **21**, 246–253. <https://doi.org/10.1016/j.tree.2006.03.006>
- Goczal, J. and Beutel, R. G. 2023. Beetle elytra: evolution, modifications and biological functions. *Biology Letters*, **19**, 20220559. <https://doi.org/10.1098/rsbl.2022.0559>
- Gomez, B., Daviero-Gomez, V., Coiffard, C., Martín-Closas, C. and Dilcher, D. L. 2015. *Montsechia*, an ancient aquatic angiosperm. *Proceedings of the National Academy of Sciences*, **112**, 10985–10988. <https://doi.org/10.1073/pnas.1509241112>
- Gómez, R. A. and Damgaard, A. L. 2014. A rare diving beetle from Baltic amber: *Hydrotrupes prometheus* new species reveals former widespread distribution of the genus (Coleoptera, Dytiscidae). *Journal of Paleontology*, **88**, 814–822. <https://doi.org/10.1666/13-017>
- Hájek, J., Zippel, A., Müller, P., Pankowski, M. G., Hendrich, L. and Balke, M. 2025. *Copelatus* diving beetles (Coleoptera, Dytiscidae) from early Miocene Mexican amber, with description of a new species displaying distinct sexual dimorphism. *Journal of Paleontology*, **98**, 830–837. <https://doi.org/10.1017/jpa.2024.29>
- Heath, T. A., Huelsenbeck, J. P. and Stadler, T. 2014. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences*, **111**, E2957–E2966. <https://doi.org/10.1073/pnas.1319091111>
- Hendrich, L. and Balke, M. 2020. A Baltic amber species of the diving beetle genus *Coptotomus* Say, 1830 (Coleoptera: Dytiscidae: Coptotominae). *Zootaxa*, **4895** (2), 285–290. <https://doi.org/10.11646/zootaxa.4895.2.7>
- Hu, F.-S., Luo, X.-Z., Kuan, K.-C., Beutel, R. G., Chi, K.-J., Liu, H.-C. and Fikáček, M. 2025. Ancient divergent evolution of specialized swimming modes in aquatic beetles. *Proceedings of the Royal Society B*, **292** (2045), 20243093. <https://doi.org/10.1098/rspb.2024.3093>
- Jouault, C., Condamine, F. L., Legendre, F. and Perrichot, V. 2024. The Angiosperm Terrestrial Revolution buffered ants against extinction. *Proceedings of the National Academy of Sciences*, **121**, e2317795121. <https://doi.org/10.1073/pnas.2317795121>
- Jouault, C., Oyama, N., Álvarez-Parra, S., Huang, D., Perrichot, V., Condamine, F. L. and Legendre, F. 2025. The radiation of Hymenoptera illuminated by Bayesian inferences from the fossil record. *Current Biology*, **35**, 2164–2174. <https://doi.org/10.1016/j.cub.2025.03.002>
- Kirejtshuk, A. G., Poschmann, M., Prokop, J., Garrouste, R. and Nel, A. 2014. Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tsherkardocoleidae). *Journal of Systematic Palaeontology*, **12**, 575–600. <https://doi.org/10.1080/14772019.2013.821530>
- Koch, C. L. and Berendt, G. C. 1854. *Die in Bernstein befindlichen organischen Reste der Vorwelt gesammelt in Verbindung mit mehreren bearbeitet und herausgegeben die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Aptereren der Vorwelt*. Nicolai, Berlin, 124 pp.
- Labandeira, C. 2014. Why did terrestrial insect diversity not increase during the angiosperm radiation? Mid-Mesozoic, plant-associated insect lineages harbor clues. 261–299. In Pontarotti, P. (ed.) *Evolutionary biology: Genome evolution, speciation, coevolution and origin of life*. Springer. https://doi.org/10.1007/978-3-319-07623-2_13
- Leach, W. E. 1815. Entomology. 57–172. In Brewster, D. (ed.) *The Edinburgh encyclopaedia*. Vol. 9. Part 1. Baldwin, Edinburgh, 384 pp.
- Letsch, H., Simon, S., Frandsen, P. B., Liu, S., Machida, R., Mayer, C., Misof, B., Niehuis, O., Zhou, X. and Wipfler, B. 2021. Combining molecular datasets with strongly heterogeneous taxon coverage enlightens the peculiar biogeographic history of stoneflies (Insecta: Plecoptera). *Systematic Entomology*, **46**, 952–967. <https://doi.org/10.1111/syen.12505>
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, **1**, Tenth edition (revised) edition. L. Salvii, Holmiae, 824 pp.
- Linnert, C., Robinson, S. A., Lees, J. A., Bown, P. R., Pérez-Rodríguez, I., Petrizzo, M. R., Falzoni, F., Littler, K., Arz, J. A. and Russell, E. E. 2014. Evidence for global cooling in the Late Cretaceous. *Nature Communications*, **5**, 4194. <https://doi.org/10.1038/ncomms5194>
- Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S. R., Leckie, R. M. and Pearson, A. 2009. Global cooling during the Eocene–Oligocene climate transition. *Science*, **323**, 1187–1190. <https://doi.org/10.1126/science.1166368>
- Mannetje, L. 't. 2007. Climate change and grasslands through the ages: an overview. *Grass and Forage Science*, **62**, 113–117. <https://doi.org/10.1111/j.1365-2494.2007.00574.x>
- Mathes, G. H., Kiessling, W. and Steinbauer, M. J. 2021. Deep-time climate legacies affect origination rates of marine genera. *Proceedings of the National Academy of Sciences*, **118** (36), e2105769118. <https://doi.org/10.1073/pnas.2105769118>
- Mbaka, J. G. and Schäfer, R. B. 2016. Effect of small impoundments on leaf litter decomposition in streams. *River Research and Applications*, **32**, 907–913. <https://doi.org/10.1002/rra.2924>
- McCurry, M. R., Cantrill, D. J., Smith, P. M., Beattie, R., Dettmann, M., Baranov, V., Magee, C., Nguyen, J. M. T., Forster, M. A., Hinde, J., Pogsoson, R., Wang, H., Marjo, C. E., Vasconcelos, P. and Frese, M. 2022. A Lagerstätte from Australia provides insight into the nature of Miocene mesic ecosystems. *Science Advances*, **8**, eabm1406. <https://doi.org/10.1126/sciadv.abm1406>
- McInerney, F. A. and Wing, S. L. 2011. The Paleocene–Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual Review of Earth and Planetary Sciences*, **39**, 489–516. <https://doi.org/10.1146/annurev-earth-040610-133431>
- McKenna, D. D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D. J., Donath, A., Escalona, H. E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P. J., Niehuis, O., Peters, R. S., Podsiadlowski, L., Pohl, H., Scully,

- E. D., Yan, E. V., Zhou, X., Ślipiński, A. and Beutel, R. G. 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences*, **116**, 24729–24737. <https://doi.org/10.1073/pnas.1909655116>
- McKenna, D. D., Wild, A. L., Kanda, K., Bellamy, C. L., Beutel, R. G., Caterino, M. S., Farnum, C. W., Hawks, D. C., Ivie, M. A., Jameson, M. L., Leschen, R. A. B., Marvaldi, A. E., McHugh, J. V., Newton, A. F., Robertson, J. A., Thayer, M. K., Whiting, M. F., Lawrence, J. F., Ślipiński, A., Maddison, D. R. and Farrell, B. D. 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, **40**, 835–880. <https://doi.org/10.1111/syen.12132>
- Meseguer, A. S., Carrillo, R., Graham, S. W. and Sanmartín, I. 2022. Macroevolutionary dynamics in the transition of angiosperms to aquatic environments. *New Phytologist*, **235**, 344–355. <https://doi.org/10.1111/nph.18100>
- Miller, K. B. 2003. The unusual occurrence of aquatic beetles in amber, *Copelatus aphrodite* Balke, n. sp. and *C. predaveterus* Miller, n. sp. (Coleoptera: Dytiscidae: Copelatinae). *Proceedings of the Entomological Society of Washington*, **105**, 809–815.
- Morlon, H., Andréoletti, J., Barido-Sottani, J., Lambert, S., Perez-Lamarque, B., Quintero, I., Senderov, V. and Veron, P. 2024. Phylogenetic insights into diversification. *Annual Review of Ecology, Evolution, and Systematics*, **55**, 1–21. <https://doi.org/10.1146/annurev-ecolsys-102722-020508>
- Neubauer, T. A., Harzhauser, M., Hartman, J. H., Silvestro, D., Scotese, C. R., Czaja, A., Vermeij, G. J. and Wilke, T. 2022. Short-term paleogeographic reorganizations and climate events shaped diversification of North American freshwater gastropods over deep time. *Scientific Reports*, **12**, 15572. <https://doi.org/10.1038/s41598-022-19759-4>
- Nilsson, A. N. and Hájek, J. 2025. A world catalogue of the family Dytiscidae, or the diving beetles (Coleoptera, Adephaga) version 1.1.2025. <https://www.waterbeetles.eu> [accessed 24 September 2025]
- Palmer, A. R. 1957. Miocene arthropods from the Mojave Desert, California. *United States Geological Survey Professional Paper*, **294-G**, 237–280.
- Peris, D. and Condamine, F. L. 2024. The angiosperm radiation played a dual role in the diversification of insects and insect pollinators. *Nature Communications*, **15**, 552. <https://doi.org/10.1038/s41467-024-44784-4>
- Ponomarenko, A. G. 1963. Lower Jurassic diving beetles from Angara River. *Paleontologicheskii Zhurnal*, **4**, 128–131. [in Russian with English summary]
- Ponomarenko, A. G. 1977. Podotryad Adephaga [suborder Adephaga]. 17–104. In Arnoldi, L. V., Zherikhin, V. V., Nikritin, L. M. and Ponomarenko, A. G. (eds) *Mezozoiskie zhestkokrylye*. Nauka Publishers, Moscow. Trudy Paleontologicheskogo Instituta [Academy of Sciences of the USSR, Proceedings of the Paleontological Institute 161]. [in Russian]
- Ponomarenko, A. G. 1987. New Mesozoic water beetles (Insecta, Coleoptera) from Asia. *Paleontological Journal*, **21**, 79–92. [Original Russian text published in *Paleontologicheskii Zhurnal*, 1987(2), 83–97.]
- Ponomarenko, A. G., Coram, R. A. and Jarzembowski, E. A. 2005. New beetles (Insecta: Coleoptera) from the Berriasian Purbeck Limestone Group, Dorset, UK. *Cretaceous Research*, **26**, 277–281. <https://doi.org/10.1016/j.cretres.2004.12.002>
- Ponomarenko, A. G. and Prokin, A. A. 2015. Review of paleontological data on the evolution of aquatic beetles (Coleoptera). *Paleontological Journal*, **49**, 1383–1412. <https://doi.org/10.1134/S0031030115130080>
- Prokin, A. A., Petrov, P. N., Wang, B. and Ponomarenko, A. G. 2013. New fossil taxa and notes on the Mesozoic evolution of Liadytidae and Dytiscidae (Coleoptera). *Zootaxa*, **3666**, 137–159. <https://doi.org/10.11646/zootaxa.3666.2.2>
- Prokin, A. A. and Ren, D. 2010. New Mesozoic diving beetles (Coleoptera, Dytiscidae) from China. *Paleontological Journal*, **44**, 526–533. <https://doi.org/10.1134/S0031030110050072>
- Qvarnström, M., Fikáček, M., Wernström, J. V., Huld, S., Beutel, R. G., Arriaga-Varela, E., Ahlberg, P. E. and Niedźwiedzki, G. 2021. Exceptionally preserved beetles in a Triassic coprolite of putative dinosauriform origin. *Current Biology*, **31**, 3374–3381. <https://doi.org/10.1016/j.cub.2021.05.015>
- R Core Team. 2021. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G. and Suchard, M. A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **67**, 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ribera, I., Nilsson, A. N. and Vogler, A. P. 2004. Phylogeny and historical biogeography of Agabinae diving beetles (Coleoptera) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **30**, 545–562. [https://doi.org/10.1016/S1055-7903\(03\)00224-0](https://doi.org/10.1016/S1055-7903(03)00224-0)
- Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D. L. and Rasnitsyn, A. P. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology*, **61**, 973–999. <https://doi.org/10.1093/sysbio/sys058>
- Ross, A. J., Bojarski, B. and Szewo, J. 2025. A critical review of the age of Baltic amber. 69–70. In *Book of abstracts – Fossil insects – Bridging past & present 2025*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.
- Satō, M. 1972. New dytiscid beetles from Japan. *Annotationes Zoologicae Japonenses*, **45**, 49–59.
- Scotese, C. R. 2016. Some thoughts on global climate change: The transition from icehouse to hothouse conditions. PALEO-MAP Project, IL, USA.
- Scotese, C. R. 2021. An atlas of Phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annual Review of Earth and Planetary Sciences*, **49**, 679–728. <https://doi.org/10.1146/annurev-earth-081320-064052>
- Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. and Li, X. 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, **37**, 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>
- Short, A. E. Z., Girón, J. C. and Toussaint, E. F. A. 2021. Evolution and biogeography of acidocerine water scavenger beetles (Coleoptera: Hydrophilidae) shaped by Gondwanan vicariance and Cenozoic isolation of South America. *Systematic Entomology*, **46**, 380–395. <https://doi.org/10.1111/syen.12467>

- Silvestro, D., Bacon, C. D., Ding, W., Zhang, Q., Donoghue, P. C. J., Antonelli, A. and Xing, Y. 2021. Fossil data support a pre-Cretaceous origin of flowering plants. *Nature Ecology & Evolution*, **5**, 449–457. <https://doi.org/10.1038/s41559-020-01387-8>
- Silvestro, D., Cascales-Miñana, B., Bacon, C. D. and Antonelli, A. 2015. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytologist*, **207**, 425–436. <https://doi.org/10.1111/nph.13247>
- Silvestro, D., Salamin, N., Antonelli, A. and Meyer, X. 2019. Improved estimation of macroevolutionary rates from fossil data using a Bayesian framework. *Paleobiology*, **45**, 546–570. <https://doi.org/10.1017/pab.2019.23>
- Silvestro, D., Schnitzler, J., Liow, L. H., Antonelli, A. and Salamin, N. 2014. Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. *Systematic Biology*, **63**, 349–367. <https://doi.org/10.1093/sysbio/syu006>
- Sinitshenkova, N. D. 2003. Main ecological events in aquatic insects history. *Acta Zoologica Cracoviensia*, **46**, 381–392.
- Théobald, N. 1937. Les insectes fossiles des terrains oligocènes de France. *Bulletin Mensuel (Mémoires) de la Société des Sciences de Nancy*, **1**, 1–473.
- Thomson, C. G. 1859. *Skandinaviens Coleoptera, Synoptiskt Bearbetade*, Vol. 1. Lundsbergiska boktryckeriet, Lund.
- Toussaint, E. F. A., Bloom, D. and Short, A. E. Z. 2017b. Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. *Journal of Biogeography*, **44**, 1952–1965. <https://doi.org/10.1111/jbi.12977>
- Toussaint, E. F. A., Fikáček, M. and Short, A. E. Z. 2016. India–Madagascar vicariance explains cascade beetle biogeography. *Biological Journal of the Linnean Society*, **118**, 982–991. <https://doi.org/10.1111/bij.12791>
- Toussaint, E. F. A., Seidel, M., Arriaga-Varela, E., Hájek, J., Král, D., Sekerka, L. and Short, A. E. Z. 2017a. The peril of dating beetles. *Systematic Entomology*, **42**, 1–10. <https://doi.org/10.1111/syen.12198>
- Vrba, E. S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy*, **73**, 1–28. <https://doi.org/10.2307/1381862>
- Watanabe, K. 2024. Review of Dytiscidae (Coleoptera) eggs: focus on Japanese species. *Journal of Insect Conservation*, **29**, 1. <https://doi.org/10.1007/s10841-024-00636-6>
- Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnett, J. S. K., Bohaty, S. M., Vleeschouwer, D. D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretano, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A. and Zachos, J. C. 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science*, **369**, 1383–1387. <https://doi.org/10.1126/science.aba6853>
- Wickham, H. F. 1911. Fossil Coleoptera from Florissant, with descriptions of several new species. *Bulletin of the American Museum of Natural History*, **30**, 53–69.
- Yang, Q., Chen, Z.-Y. and Jia, F.-L. 2019. *Ambarticus myanmarius* gen. et sp. nov., the first diving beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera, Dytiscidae, Dytiscinae). *Cretaceous Research*, **102**, 1–6. <https://doi.org/10.1016/j.cretres.2019.05.005>
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693. <https://doi.org/10.1126/science.1059412>
- Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński, A. and Zhang, P. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, **9**, 205. <https://doi.org/10.1038/s41467-017-02644-4>