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Estimating the drivers of diversification of stoneflies through time and the limits of their fossil record

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Abstract

Deciphering the timing of lineage diversification and extinction has greatly benefited in the last decade from methodological developments in fossil-based analyses. If these advances are increasingly used to study the past dynamics of vertebrates, other taxa such as insects remain relatively neglected. Our understanding of how insect clades waxed and waned or of the impact of major paleoenvironmental changes during their periods of diversification and extinction (mass extinction) are rarely investigated. Here, we compile and analyze the fossil record of Plecoptera (1,742 vetted occurrences) to investigate their genus-level diversification and diversity dynamics using a Bayesian process-based model that incorporates temporal preservation biases. We found that the Permian-Triassic mass extinction has drastically impacted Plecoptera, while the Cretaceous Terrestrial Revolution corresponds with a turnover of plecopteran fauna. We also unveiled three major gaps in the plecopteran fossil record: the Carboniferous-Permian transition, the late Early Cretaceous, and the late Cenomanian to Bartonian, which will need to be further investigated. Based on the life history of extant Plecoptera, we investigate the correlations between their past dynamic and a series of biotic (Red Queen hypothesis) and abiotic (Court Jester hypothesis) factors. These analyses highlight the major role of continental fragmentation in the evolutionary history of stoneflies, which is in line with phylogeny-based biogeographic analyses showing how vicariance drove their diversification. Our study advocates analyzing the fossil record with caution, while attempting to unveil the diversification and extinction periods plus the likely triggers of this past dynamics of diversification.

Key words: Crises, extinctions, fossil record, Plecoptera, PyRate

Documenting the biodiversity dynamics in the deep time of various organisms is among the major goals of evolutionary biologists (Raup and Sepkoski 1982, Alroy et al. 2008, Close et al. 2020). However, despite their huge diversity (Stork 2018), the diversification dynamics of insects remains relatively poorly studied with fossil-based analyses (e.g., Smith and Marcot 2015, Clapham et al. 2016, Condamine et al. 2016, 2020). Yet, the fossil record of several insect lineages is relatively continuous (Schachat and Labandeira 2021) so that it could be integrated into diversification analyses to better understand both the evolutionary history of these organisms and the impact of major environmental changes in the deep time. Among those drivers of diversification, mass extinctions as well as biotic (Red Queen hypothesis) and abiotic (Court Jester hypothesis) factors are regularly invoked (Grimaldi and Engel 2005, Benton 2009, Shachat and Labandeira 2021), and their relative impact can be disentangled with the latest methods used to analyze the fossil record (Silvestro et al. 2019). Those methods take advantage of the full fossil record and can account for its well-known biases (Foote and Miller 2007, Alroy 2016). Benefiting from these methods, one can study a group of insects whose origin goes back to the Permian and address questions related to past diversification dynamics and the likely drivers affecting this diversification.

The order Plecoptera (stoneflies) is of particular interest because today they are considered as bio-indicators of water quality due to their need for well oxygenated and unpolluted freshwater (e.g., Törnblom et al. 2011). The latest molecular dated phylogeny estimated that the order originated ≈265 million years ago (Ma, 95% credibility interval: 236–294 Ma, Letsch et al. 2021). Investigating the diversification dynamics of Plecoptera can provide insights into the impact of three of the Big Five mass extinctions—the Permian-Triassic, Triassic-Jurassic and Cretaceous-Paleogene boundaries (Raup and Sepkoski 1982, Hoyal Cuthill et al. 2020)—and during the Carnian Humid Episode (Ruffell et al. 2016). These events have strongly impacted the diversity dynamics of various organisms (e.g., Hull 2015, Chen and Benton 2012, Benton et al. 2021). For instance, the Permian-Triassic boundary is known as the most important crisis for insects (e.g., Labandeira and Sepkoski 1993, Labandeira 2005), while the Carnian Humid Episode corresponds to a period of climate changes, extinctions and radiations (Dal Corso et al. 2020). We might expect that these events have also impacted the evolutionary history of Plecoptera. Studying Plecoptera can also contribute to better understand the impact of past environmental changes on continental aquatic communities.

In addition to these major events, the diversification of Plecoptera has likely been linked with a series of abiotic (i.e. climate and/or geological changes: see Zwick 2000 for a discussion on the putative effect of the break-up of Gondwana) and biotic factors (e.g. ecological changes and/or diversity dependence). Among the most notable environmental changes, the Cretaceous Terrestrial Revolution (KTR: Lloyd et al. 2008, Benton et al. 2021), along with the rapid diversification of angiosperms, has radically altered ecosystems (Chaboureau et al. 2014) and the diversification of other plant groups (Condamine et al. 2020). Plecoptera have likely been affected by these changes, including some specialized herbivores (Monakov 2003) or predators, whose diets or abilities to detect or pursue preys have likely been disturbed (Fuller and Rand 1990). The replacement of gymnosperms by angiosperms as dominant plant groups in terrestrial environments is indeed often seen as the trigger for major faunal changes in past freshwater ecosystems (e.g., replacement of subfamilies of Chironomidae, extinction of certain groups of Odonata and Plecoptera: Sinitschenkova 2003). Angiosperms tend to produce more biomass from their leaves than gymnosperms, and this biomass is recycled into the soil and freshwater by microorganisms that consume dissolved oxygen in the water, causing eutrophication of water, especially lakes. Such eutrophication is highly deleterious for Plecoptera, adapted to well-oxygenated waters (Gaufin et al. 1974, Sinitschenkova 2003, Malison et al. 2020). However, these hypotheses have never been formally tested, questioning the impact of the angiosperm diversification or of the Cretaceous Terrestrial Revolution on Plecoptera and, more generally, on freshwater communities.

The fossil record of Plecoptera represents currently 322 species distributed in 25 families and two suborders: Antarctoperlaria and Arctoperlaria (Zwick 1973). But, as for extant species (more than 3,500), the number of fossil representatives of each sub-order is largely unequal, with about 10% of extinct species for Antarctoperlaria, while the Arctoperlaria represents 90% of the past diversity (data compiled from http://fossilworks.org; last accessed March 27, 2021; Fochetti and Tierno de Figueroa 2007). The Perlopseina record—a Permian stem group (Martynov 1940, Zwick 2000)—is limited in number, with only three species. Such unbalanced species richness brings the question of the evolutionary drivers underlying the diversification of the two suborders.

As in many insect groups, the number of fossil plecopteran species is likely underestimated because there are less than a handful of people studying them. Moreover, their long evolutionary history and the difficulty to get a rich and continuous fossil record over such a long time inevitably led to a knowledge bias towards certain periods and the virtual absence of fossil for others. Also, the phylogenetic placement of many fossil species at the family level needs to be revised; a task made even more complicated because of the high plasticity of the wing veins of stoneflies. This situation is often ignored, most fossil plecopteran species being described from a single—sometimes partial—specimen (Jouault et al. 2021a). Altogether, these features make any inference drawn from the fossil record sensitive to several paleontological biases, which need to be considered.

Here we study how Plecoptera have waxed and waned through time, analyzing all stoneflies fossil occurrences and modeling preservation rates through time and across taxa. Our analyses not only allow highlighting the periods of radiation and those of decline, but also discussing gaps in the plecopteran fossil record throughout geological times. We further perform analyses to tease apart the factors that may have impacted the diversification or extinction of Plecoptera by studying correlations between their diversification dynamics and different biotic and abiotic variables.

Material and methods

Fossil occurrences and dataset

The fossil record of Plecoptera was compiled from the Paleobiology Database (http://fossilworks.org/, https://paleobiodb.org: last accessed July 10, 2021). The original dataset contained about 430 occurrences and was then corrected and emended. The dataset was cleaned of synonyms, outdated combinations, *nomina dubia* and other erroneous and doubtful records. After correction including data addition from the literature, it is composed of 322 species (130 genera) for 1,742 occurrences resulting from an in-depth study of the entire bibliography of fossil Plecoptera (Supp Table S1 [online only]). The differences between genus level or sub-order occurrence numbers are explained by the systematic placement of some genera that can only be placed confidently in a sub-order but not in a family (Supp Table S2 [online only]). Note that some occurrences of *Plutopteryx beata* Sinitshenkova, 1985 are not included since the species is known from more than 1,400 specimens but 1,000 of them are not labelled as indicated by Sinichenkova (1985: p. 133). Therefore, we only include the labelled specimens, *viz.* 467 specimens (Sinitshenkova 1985: p. 133) to avoid overrepresentation of a genus while not being informative for the whole analysis. We removed the species *Marciperla curta* Lin, 1986 from our dataset. Initially considered as Plecoptera *incertae sedis*, it cannot be placed with certainty in this order (Lin 1986). This taxon is possibly a Plecoptera because of its two cercomeres, but the partial preservation challenges a clear attribution of this species (Lin 1986: fig. 62). It has for instance been considered as a possible Grylloblattodea (Storozhenko 1998: figs. 82-87). To avoid unsupported placement, authors are encouraged to keep some specimens in open nomenclature until additional material is discovered. Similarly, the systematic position of numerous fossil Plecoptera at the subfamily or family level being poorly supported, we refrain from conducting analyses at these taxonomic levels. The complete datasets used for each analysis are available as supplementary data.

Temporal dynamics of origination and extinction rates

Traditionally the past dynamic of lineages was inferred using the fossil record (e.g., Stanley 1979), although recent progress have led to estimate diversification rates from dated phylogenies (e.g., Harvey et al. 1994, Morlon et al. 2011, Rabosky et al. 2013). Numerous issues have arisen regarding the analyses of the fossil record: (1) using discrete time bins, (2) analyzing only first and last appearances of taxa, thus ignoring other occurrences if available while first and last occurrences cannot be assumed to reflect the true times of speciation/origination and extinction (Strauss and Sadler 1989, Marshall 1990), (3) the inability to perform model testing against over-parameterization, which limits models' robustness (Burnham and Anderson 2002), (4) the poor or sole incorporation of extant taxa in the analyses, which in both cases represents only a small fraction of the total diversity that has existed since their origination (e.g., Raup 1986).

To overcome these issues, new methodologies were developed and implemented in PyRate (Silvestro et al. 2014a, 2019). PyRate estimates speciation and extinction rates and their temporal dynamics from fossil occurrence data and has proven to be robust thanks to simulations under a range of potential biases, including violations of the sampling assumptions, variable preservation rates, and incomplete taxon sampling (Silvestro et al. 2014b, 2015a, 2019). Simulation results showed that the dynamics of speciation and extinction rates, including sudden rate changes and mass extinctions, are correctly estimated under a wide range of conditions, such as low levels of preservation (down to 1–3 fossil occurrences per species on average), severely incomplete taxon sampling (up to 80% missing), and high proportion of singletons (exceeding 30% of the taxa in some cases).

We analyzed the plecopteran fossil record using a Bayesian approach, as implemented in PyRate 3.0 (Silvestro et al. 2019), to simultaneously infer (1) the times of speciation (*Ts*) and of extinction (*Te*) for each taxon in the dataset, (2) the temporal dynamics of origination and extinction rates, (3) the preservation rate across taxa, and (4) the preservation rate through time. To model the processes of diversification and preservation, this approach uses as input all fossil occurrences that can be assigned to taxa, in our case fossil genera. All analyses were set with the best-fit preservation process after comparing (*-PPmodeltest* option) the homogeneous Poisson process (*-mHPP* option), the non-homogeneous Poisson process (default option), and the time-variable Poisson process (*-qShift* option). The time-variable Poisson process assumes that preservation (expected number of occurrences *per* lineage *per* Ma) rates are constant within a predefined time frame but may vary over time. In the present study we used a predefined time frame of bins of 10 million years since the Carboniferous. This model is thus appropriate when rates over time are heterogeneous. We also accounted for varying preservation rates across taxa using the Gamma model (*-mG* option), which is with gamma-distributed rate heterogeneity with four rate categories.

We jointly estimated the number of rate shifts as determined by log Bayes factors and the times at which origination and extinction undergo a shift using the reversible jump Markov Chain Monte Carlo (RJMCMC, *-A 4* option; Silvestro et al. 2019) or a birth–death model with constrained shifts (BDCS, Silvestro et al. 2015b). This allowed us to obtain an overview of the general trends of rate variation across a long timescale. Both the preservation and the birth-death processes are modeled in continuous time. Thus, the origination and extinction rates are measured as the number of origination and extinction events per lineage per Ma, while the preservation rate is expressed as expected occurrences per taxon per Ma. We performed two BDCS analyses: one to estimate diversification rates per bin of 10 million years, and the second to estimate diversification rates per geological epochs. The BCDS model is one of the first to be implemented in PyRate, but recent progress suggests that the RJMCMC model provides more robust results (Silvestro et al. 2019). To cross-validate our results we have opted for a multi-model approach. To look for differences in the diversification patterns of the two sub-orders of Plecoptera, we also analyzed two sub-datasets corresponding to the fossil record of the Antarctoperlaria composed of 13 genera for 398 occurrences (Supp Table S3 [online only]) and to the Arctoperlaria composed of 108 genera and 1,242 occurrences (Supp Table S4 [online only]).

For each analysis, we ran PyRate for 10 million MCMC iterations with sampling frequency of 1,000 and combined the posterior samples of the parameters from the 10 randomly replicated datasets after excluding the first 10% of the samples as burnin. These 10 datasets were generated using the *extract.ages* function to randomly resample the age of fossil occurrences within their respective temporal ranges (i.e., resampled ages are randomly drawn between the minimum and the maximum ages of the geological stratum). We monitored chain mixing and effective sample sizes by examining the log files in Tracer 1.7.1 (Rambaut et al. 2018). The parameters are considered convergent when the effective sample size (ESS) is greater than 200. We combined the posterior estimates of the origination and extinction rates across all replicates to generate rate-through-time plots. Thus, we obtained ten posterior estimates of the *Ts* and *Te* for all genera and we estimated the past diversity dynamics by calculating the number of living taxa at every point in time based on the *Ts* and *Te* (*-ltt 1* option). We also looked at the marginal posterior distributions of origination and extinction rates during the largest extinction events documented in geological history. We particularly examined the diversification dynamics at three of the Big Five events: the Permian-Triassic, the Triassic-Jurassic and the Cretaceous-Paleogene boundaries (*sensu* Raup and Sepkoski 1982, Hoyal Cuthill et al. 2020). Shifts of diversification were considered significant when log Bayes factors > 6 with the RJMCMC model, while we considered shifts to be significant with the BDCS model when mean rates in a time bin do not overlap with the 95% CI of the rates of adjacent time bins.

Correlations with biotic and abiotic variables

To propose a global scenario of the evolution of Plecoptera, we focused on biotic (e.g. relative diversity of angiosperms or gymnosperms) and abiotic (e.g. temperature, continental fragmentation) factors, potentially responsible for the phenomena of apparitions or extinctions. Analyses were performed with PyRate 3.0 (Silvestro et al. 2019) using the multivariate birth-death (MBD) model. This model estimates speciation and extinction rates based on several continuous variables over time assuming linear or exponential functions linking temporal variations in birth-death rates to change as a function of one or more variables (Lehtonen et al. 2017). In the MBD model, a correlation parameter is estimated to quantify independently the role of each variable on speciation and extinction. A horseshoe prior (explained in Lehtonen et al. 2017) is used to reduce the correlation parameters around zero, thereby reducing the risk of over-parameterization and the need to test explicit models. The data used for the analyses (*Ts* and *Te* data) are derived from our previous RJMCMC inferences. In this study, we tested five variables that we assume, because of the group's biology, having an impact on their diversification or extinction, namely: (0) intra-clade competition; (1) fluctuation in relative diversity of angiosperms (Silvestro et al. 2015b); (2) fragmentation of continents, which is an index with low values reflecting a continental agglomeration (e.g., Pangea) and high values a continental splitting (Zaffos et al. 2017); (3) fluctuation in relative diversity of gymnosperms (Silvestro et al.

2015b); and (4) average global temperatures over geological time, which was obtained combining the $\delta^{18}O$ data from Prokoph et al. (2008) and Zachos et al. (2008) to encompass the period ranging from the Holocene to the lowermost Carboniferous (Condamine et al., 2019). All the datasets for these five variables are available in the publications cited aside each variable. The MBD analyses were performed over 10 million generations, and visualization of results and convergence parameters was performed on Tracer 1.7.1 (Rambaut et al. 2018). We considered correlation parameters to be significant when the shrinkage weights (ω) > 0.5 and the 95% CI does not overlap with 0.

Results

Global diversification pattern

The net diversification rate (origination minus extinction) corresponds to the number of events per million years per lineage. The phases of diversification are visible when the net diversification rate is superior to 0; oppositely when it is below 0 it indicates periods of decline.

Using the RJMCMC model, Plecoptera seem to diversify (net diversification between 0.3 and 0.6) between ca. 310 Ma and ca. 275 Ma, which corresponds with the period ranging from the middle Pennsylvanian to the middle Cisuralian (Figs. 1-3, 5A,B). Then the speciation and extinction rates drop to reach zero until the Permo-Triassic boundary (between 259-247 Ma) (Figs. 1A), where Plecoptera undergo a strong decline (max. net diversification ≈ -0.25) (Figs. 1-2, 5A,B). The origination (Figs. 2A, B) and the extinction (Figs. 2C, D) seem to increase before the Permo-Triassic boundary, during the Cisuralian and Guadalupian, with the origination stronger than the extinction (Fig. 2) but the dramatic event occurs at the Permo-Triassic boundary with an impressive burst of extinction and no origination (= mass extinction) (Figs. 1-3, 5A,B). After this event, the net diversification, the origination and extinction rates remain relatively constant (≈ 0 or at least <0.2) from the Triassic (ca. 247 Ma) to the Aptian (ca. 125 Ma) (Figs. 1-3, 5A,B). Following this plateau, the fossil record of Plecoptera indicates a period of major decline (max. net diversification ≈ -1.4) extending from the lower Aptian (ca. 125 Ma) to the lower Cenomanian (ca. 100 Ma). This period is the outcome of a feeble speciation and a massive extinction peak (= turnover) (Figs. 1-3, 5A,B). This extinction peak is followed by a period of diversification but differences in diversification rates are recorded between the RJMCMC and the BDCS models (Figs. 1-3, 5A,B; Supp Figs. 1-2 [online only]).

Heterogeneous diversification between the Antarctoperlaria and Arctoperlaria

The fossil record of Antarctoperlaria is very fragmentary while that of Arctoperlaria is much more diverse and somewhat continuous (Supp Table S2 [online only]). Fossil representatives of Antarctoperlaria range only from the Guadalupian to the Aptian-Albian, resulting in a partial modeling of their past dynamic (Figs. 1B-C). Despite their current diversity, there is no fossil Antarctoperlaria in the Late Cretaceous and the Cenozoic. Antarctoperlaria feebly diversified from the Guadalupian to Aptian-Albian without experimenting peaks of strong extinction or diversification (net diversification between 0.01 and 0.05) (Figs. 1B-C).

The oldest Arctoperlaria are nearly contemporaneous with the oldest Antarctoperlaria but their fossil record, more abundant, allows modeling their past dynamic showing a pattern strongly resembling that of the order. They are impacted by the Permo-Triassic crisis (net diversification ≈ -1.5) and suffer a strong decline during the Early Cretaceous (net diversification ≈ -1.25) (Fig. 1C). They diversified slightly during the Middle Triassic (max. net diversification ≈ 0.25) and strongly diversified from the mid-Cretaceous (net diversification between 0.2 and 1.75) until the Priabonian (Fig. 1C). The Carnian Humid Episode, the Triassic-Jurassic events or the subsequent mass extinction events have no real impact on the dynamic of each group since we found no change in net diversification (Figs. 1B-C).

Disparities in preservation rates and deposits

Three gaps are recorded during the evolutionary history of the Plecoptera. To better illustrate these gaps, we used the preservation rates and the number of lineages from the Carboniferous to present. The preservation rate indicates four time-intervals in which the preservation is low (ca. or inferior to 1, Fig. 4A). The first is around the Carboniferous-Permian boundary (preservation rate ≈ 1), the second during the Early and early Middle Triassic (preservation rate ≈ 0), the third extends from the middle of the Late Triassic to the Early Jurassic (preservation rate ≈ 1), and the fourth encompasses the period ranging from the late Early Cretaceous to nowadays (preservation rate between 1.3 and 0) (Fig. 4A). Plotting the diversity dynamic through time, we found three gaps (Fig. 4B), corresponding to the periods where there is no lineage recorded over time. The first encompasses the Carboniferous-Permian transition (Fig. 4B) and ranges from the Kasimovian (ca. 306 Ma) to the Asselian (ca. 295 Ma). The second gap occurs during the lower Cretaceous (ca. 111 Ma) and the mid-Cretaceous (ca. 100 Ma) (Fig. 4B). The third and largest gap extends from the uppermost Cenomanian (ca. 94 Ma) to the Bartonian (ca. 39 Ma) (Fig. 4B).

Correlations with abiotic and biotic variables

The results of the MBD analyses are summarized in Table 1. Shrinkage weights indicate good support ($\omega > 0.8$) for all correlation parameters (G) of origination and extinction rates, except for the ω of extinction depending on the clade's diversity and the ω of the extinction depending on the relative abundance of gymnosperms ($\omega < 0.5$). The effect of a variable is assessed as significant when $\omega > 0.5$ and 95% HPD does not encompass 0.

The variables positively correlated with the origination of Plecoptera are the temperature ($\omega = 0.74$, $G \approx 0.03$) and the fragmentation of continents ($\omega = 0.9$, $G \approx 12.15$) (Table 1;

Fig. 5C). However, only the continental fragmentation is significantly correlated with origination (indicated by a star in Fig. 5C). The variables negatively correlated with the origination of Plecoptera are the relative abundance of gymnosperms ($\omega = 0.63$, $G \approx -1.2$), angiosperms ($\omega = 0.82$, $G \approx -1.6$) and the intra-clade competition ($\omega = 0.9$, $G \approx -2.8$). Only the intra-clade competition is significantly correlated with origination (Table 1; Fig. 5C).

The variables positively correlated with the extinction of Plecoptera are the temperature ($\omega = 0.91$, $G \approx 0.08$) and the fragmentation of continent ($\omega = 0.96$, $G \approx 20.2$), with a significant correlation only for the latter (Table 1; Fig. 5D). The relative abundance of gymnosperms ($\omega = 0.44$, $G \approx -0.09$), angiosperms ($\omega = 0.88$, $G \approx -2.3$) and the intra-clade competition ($\omega = 0.50$, $G \approx -0.39$) are all negatively correlated with the extinction, and none is significantly correlated with extinction (Table 1; Fig. 5D).

Discussion

We analyzed the plecopteran fossil record, comprising >300 species and >1,700 specimen occurrences, using a Bayesian framework to investigate the impact of major crises, biotic and abiotic factors on the diversification dynamics of these insects that now thrive in well-oxygenated waters. We have unveiled different periods of diversification, extinction and turnovers (Figs. 1-3, 5). The first critical period corresponds to the early dynamics of Plecoptera, at the transition between stem-Plecoptera and crown-Plecoptera. The second corresponds to the 'mid'-Cretaceous, a period characterized by the Cretaceous Terrestrial Revolution and the outcomes of Gondwana fragmentation. We then focus on the results of the MBD analyses to contrast the support for the Red Queen and Court Jester hypotheses, i.e. for biotic and abiotic factors, respectively (Fig. 5). Finally, we discuss a few critical gaps in the plecopteran fossil record, leveraging known gaps for insects and new analyses of preservation rate (Fig. 4). Pinpointing these gaps could help guide future efforts that would benefit analyses of plecopteran diversification and, more broadly, aquatic insect communities.

Early dynamics of Plecoptera derived from the fossil record

Chronologically, the first transitional events (from diversification to extinction) occur between the Carboniferous and middle Permian. The stem Plecoptera is uniquely recorded in the Carboniferous (Béthoux et al. 2011, Schubnel et al. 2019). These pre-Pangean faunas, as shown by the fossil record in China and France during the Carboniferous (Béthoux et al. 2011, Schubnel et al. 2019), have likely led to new Pangean faunas developing on the northern continental block, dividing during the Permian (Blakey 2008; Letsch et al. 2021). Our analyses indicate an increase in origination rate around 300 Ma (Figs. 1-2, 5A-B), which can be attributed to this continental re-organization. Because of the relative scarcity of the plecopteran fossil record at this period, a fine understanding of their early diversification is out of reach, but it is certain that this period was critical in their evolution. It is also important to associate this diversification period with the Carboniferous-Permian glaciation and deglaciation events that have substantially reset terrestrial ecosystems (Montañez et al. 2007). These events likely created suitable habitats for Plecoptera, which are known to live in cold waters (particularly in glacier streams). Additionally, this period also coincides with a period of continental agglomeration, while the distribution of Plecoptera would have been restricted (Letsch et al. 2021) because of arid areas in the center of the Pangea (Pardo et al. 2019).

The second remarkable event—and likely the most important of the early dynamics of Plecoptera—is the Permian-Triassic boundary (Figs. 1-2, 5A-B). It corresponds to a general mass extinction event (e.g., Labandeira and Sepkoski 1993, Labandeira 2005; Benton and Newell 2014, Zhao et al. 2021) that we record for Plecoptera as well with a sudden decrease in the net diversification (Fig. 1A). This extinction event is visible when confronting the numerous stoneflies from the Lopingian (Supp Table S2 [online only]) with the lack of stonefly from the Early and the Middle Triassic (Fig. 4) despite several fossil insect deposits, e.g., Brookvale in Australia, Vosges in France, or Tongchuan in China (Zheng et al. 2018). This period would also correspond to the divergence of the two infraorders of the Arctoperlaria (Euholognatha and Systellognatha, Letsch et al. 2021) but we have recorded only a massive extinction and not any increase in origination before the Middle Triassic (Fig. 1; Supp Figs. S1-2). The end-Permian extinction is supposed to be linked to massive volcanic eruptions in Siberia causing drastic changes in ecosystems that have affected most organisms (e.g., Benton and Twitchett 2003, Ogden and Sleep 2012, Burgess and Bowring 2015, Fielding et al. 2019). Temperatures rose by ca. 15°C, a global warming that, combined with volcanic gases resulted in acid rains that have destroyed trees and led to a loss of vegetation cover (Benton 2016). This crisis was unfavorable to life at equatorial latitudes and prevented ecosystem recovery after greenhouse events (Sun et al. 2012). Our results indicate that this dramatic event has strongly affected Plecoptera (Figs. 1A, 5A,B) and most likely the whole aquatic insect communities.

During the Late Triassic, another period has recently gained attention: the Humid Episode of the Carnian, which has mainly affected marine diversity (e.g., Dal Corso et al. 2020). Given the biology of Plecoptera (life in torrent waters), an effect of the paleoenvironmental conditions of the Carnian on their diversification could have been expected. However, we have not detected any change in net diversification during the Carnian (Fig. 1A).

Similarly, we have not detected the Triassic-Jurassic extinction in our analyses (Figs. 1A, 2C-D, 5A-B), suggesting that this crisis may have not been so severe for insects (e.g., Labandeira 2005, Condamine et al. 2016, Nel et al. 2018). Instead, it corresponds with the beginning of the radiation of many extant insect orders that have their oldest known representatives during the Triassic (Montagna et al. 2019). For Plecoptera, this period would correspond to an increase in diversification in Perloidea (Letsch et al. 2021) and to the colonization of the southern hemisphere by Notonemouridae and Antarctoperlaria after a long dispersal on lands, while the continents were still connected (Cui et al. 2019, Letsch et al. 2021). However, these phylogeny-derived hypotheses are not confirmed with our analyses of the fossil record (e.g., stable origination, extinction and net diversification before and after the Triassic-Jurassic boundary) (Figs. 1A, 2). Given that the number of lineages in this period is relatively high (Fig. 4), we would have expected to record these events if they had been impactful. After this period, no significant change in the diversification of the Plecoptera was recorded before the Early Cretaceous (Figs. 1A, 2).

The Cretaceous Terrestrial Revolution and the subsequent diversification of Plecoptera

For Plecoptera, the most dramatic extinction event occurred from the early Aptian (ca. 125 Ma) to the early Cenomanian (ca. 100 Ma; Fig. 1A). This brutal extinction is sometimes recorded at a broader taxonomic scale when studying the complete fossil record of insects (Labandeira 2005) but also tempered in other studies (Labandeira and Sepkoski 1993, Labandeira 2014, Condamine et al. 2016; see also our section on fossil gaps below and how they interfere with diversification analyses of Plecoptera). A few hypotheses have been proposed to explain this major event and, for Plecoptera, both the importance of the KTR and of the fragmentation of Gondwana can be defended. The KTR is characterized by the radiation of the angiosperms, a drastic ecological change that reshuffled the ecosystems (Lloyd et al. 2008, Meredith et al. 2011, Benton et al. 2021) and that translated into biotic turnovers (*sensu* Schachat and Labandeira 2021) with a high extinction and origination in different lineages. We recorded such a turnover at this period for Plecoptera (Figs. 1A, 2). Alternatively or concomitantly, major geological events might have played a strong role in the diversification of Plecoptera, e.g., the fragmentation of the Gondwana or the opening of the Atlantic, which continued into the Late Jurassic and Cretaceous (Daly et al. 1989, Seton et al. 2012). The fragmentation of continents is the only variable tested strongly positively correlated with origination and extinction rates (Figs. 5C, D); we discuss it further in the next section. The fragmentation of continents could have favored the diversification of Antarctoperlaria in the southern hemisphere (Letsch et al. 2021: fig. 4). However, several land masses such as India, Africa or Burmese Block lack evidence for a colonization by Antarctoperlaria at that time (e.g., Jouault et al. 2022). This is rather surprising given that the biome homogeneity in central Gondwana could have facilitated wide dispersion between South America and Africa during the Early Cretaceous (Jouault et al. 2021b, Nel and Jouault 2021) and by extension up to the Burma Terrane (Jouault et al. 2021c). Similarly, Antarctica may have served as an exchange route between Australia and South America when a large expanse of temperate rainforests was present on the continent (Klages et al. 2020) and until the opening of the Drake Passage around 41 Ma (Scher and Martin 2006, Letsch et al. 2021). The availability of new habitats (e.g., in Antarctica) and the colonization of new continental land masses (Letsch et al. 2021) would suggest a phase of plecopteran diversification but we record an extinction during the Early Cretaceous, rather indicating that these opportunities fail to counterbalance extinction events (Figs. 1A, 2, 5A-B).

Interestingly, two shifts in diversification rate, estimated from a molecular phylogeny and located in Nemouridae and Leuctrinae, occurred during the KTR in the late Early Cretaceous (Letsch et al. 2021), further supporting our results derived from the fossil record. These inferred diversification rate shifts suggest that the KTR has generated an increase in the diversification of Nemouridae and Leuctrinae, and additional studies must be conducted to decipher its causes.

The second major event of the Cretaceous period is the Cretaceous-Paleogene (K/Pg) extinction, which corresponds to a series of drastic events leading to the most famous mass extinction with the final demise of non-avian dinosaurs (e.g., Brusatte et al. 2015). The origin of this mass extinction event is far from being consensual, but a combination of biotic and abiotic factors likely led to these dramatic events (e.g., Mitchell et al. 2012, Chiarenza et al. 2020, Condamine et al. 2021). Like for the early Aptian extinction, recorded in our analyses, the impact of K/Pg events does not seem to be strong when analyses are conducted on the insect fossil record at the family or order level (Labandeira and Sepkoski 1993, Labandeira, 2014, Condamine et al. 2016). However, given that the main trigger of the K/Pg extinction is supposed to be, most of the time simplified to, a cataclysm related to the impact of an asteroid (Alvarez et al. 1980), we wonder if this crisis has also affected the Plecoptera. Based on the results detailed above, and the elevated net diversification rate recorded before and after the K/Pg boundary, it appears that this event did not have a significant impact on Plecoptera (Fig. 1A). Like recent results for vertebrate clades, the decline or faunal turnover appears to begin before the impact of the asteroid (Condamine et al. 2021). For Plecoptera, these diversification rate changes occur earlier in the Early Cretaceous (Fig. 2), suggesting that the K/Pg events had a low impact on the clade dynamics. This is corroborated by the moderately high preservation rate of this period, suggesting that drastic events should have been recorded in the fossil record. In addition, a significant shift in diversification rate is recorded at the K/Pg boundary for the Capniidae (Letsch et al. 2021: fig. 2), suggesting that at least this family flourished during this period. According to all these elements, the K/Pg severity on the diversification of Plecoptera appears to be reduced.

How Plecoptera diversified: Red Queen or Court Jester hypotheses?

The diversification dynamics of organisms is often investigated by contrasting the importance of biotic and abiotic drivers, what is commonly known as the Red Queen and Court Jester hypotheses, respectively (Van Valen 1973, Barnosky 2001). Using the plecopteran fossil record, we aimed at deciphering the relative importance of those hypotheses, looking at correlations between a few factors (intra-clade competition, relative abundance of angiosperms and gymnosperms *vs.* temperature variation, continental fragmentation) and the dynamics of Plecoptera over geological time (Figs. 5C-D).

One biotic factor—intra-clade competition—and one abiotic factor—fragmentation of continents—were significantly correlated with the diversification of Plecoptera (Figs. 5C-D). Intra-clade competition was negatively correlated with origination, whereas continental fragmentation was positively correlated with both origination and extinction. The first result indicates that origination decreases when the diversity of Plecoptera increases, suggesting intra-clade competition or diversity dependence (Fig. 5C). This is in line with the life history traits of Plecoptera, whose adults are relatively poor flyers and whose nymphs have specialized ecological requirements (fresh and well-oxygenated waters), resulting in low dispersal rates (Marden and Kramer 1994, Thomas et al. 2000, Zwick 2000, Fochetti and Tierno de Figueroa 2007, McCulloch et al. 2009). Based on these considerations, it is accepted that long-range dispersal capabilities of Plecoptera are reduced. Therefore, when a population or diversity increases locally, competition for resources and particularly for food reaches its climax, limiting speciation by intra-clade competition. This is especially relevant since plecopteran nymphs are represented in all functional feeding groups (e.g., predator, phytophagous, detritivores, etc.) (Tierno de Figueroa and López-Rodríguez 2019) and sometimes change diet according to their developmental stage (Yule 1990). Competition between species may increase depending on the stage of development of the different local populations. Similarly, cases of cannibalism are reported (Yule 1990) and we can imagine a similar behavior in deep time under strong selection and competition pressure. Therefore, reaching suitable ecological niches might be challenging for these insects and competition very disadvantageous.

Continental fragmentation has likely driven both origination and extinction of Plecoptera, likely by promoting allopatric speciation but also by altering previous ecosystems and increasing extinctions (Figs. 5C-D). Our results are congruent with the main distribution of extant stonefly species, which postulates that continental fragmentation is a driver of their diversification and distribution. In fact, previous authors named the two sub-orders after the Antarctica (Antarctoperlaria) and the Arctic (Arctoperlaria) because of the restricted distribution of their constitutive families (Zwick 2000). The only exceptions are the arctoperlarian families, Notonemouridae and Perlidae, which are present and diversified in the southern hemisphere. Therefore, it is considered that Antarctoperlaria originated in Gondwana, while Arctoperlaria originated in Laurasia (Zwick 2000), but a recent biogeographic analysis suggests a more complicated scenario (Letsch et al. 2021). An alternative hypothesis states that the current restricted distribution of Plecoptera suborders could be explained by the disappearance of Antarctoperlaria on Laurasia and of Arctoperlaria on Gondwana (Zwick 2000). In any case, the ancestral plecopteran stock on the Pangea was divided during major geological events of continental fragmentation (Letsch et al. 2021). The link between diversification and continental fragmentation is also strengthened by the limited dispersal abilities of stoneflies letting us assume that vicariance (i.e. the isolation of previously connected ancestral groups as a result of plate tectonics or other geographic barriers) shaped their biogeography and diversification (Zwick 2000). Vicariance and allopatric speciation are driven by historical glaciation, orogenesis, and small-scale population fragmentation (Zwick 2000, Fochetti and Tierno de Figueroa 2007, Fochetti et al. 2009, 2011, Weiss et al. 2011, Theissinger et al. 2013). Continental fragmentation can also affect mountain orogeny and thus habitats for Plecoptera, which often occur in mountain streams (similar observations are made for other freshwater lineages: Hrivniak et al. 2020). Examples of clade radiations in mountains across the globe can testify for the impact of orogenic events in Plecoptera (e.g., Stark and Nelson 1994, Sproul et al. 2015). For instance, the endemic radiation of the genus *Chilenoperla* in the Andes exemplifies the link between mountain building and speciation. *Chilenoperla* diverged in the Eocene (Letsch et al. 2021) when the separation of South America, Antarctica and Australia led to a cooling of the circum-Antarctic zone and to the formation of mountains, like the Andes (Barrett 2003). This synchronicity between the Andean orogeny, which took place during the late Eocene–early Miocene and led to the growth of the Western Cordillera (e.g., Armijo et al. 2015, Riesner et al. 2018, Boschman, 2021), and the diversification of some extant genera like *Chilenoperla* in the region might reflect the strong influence of continental fragmentation on the diversification of Plecoptera. This influence needs to be further examined when significant gaps in the fossil record are filled (see below) or using phylogenetic approaches (Boschman and Condamine 2022). As evidenced by the strong correlation recorded in our MBD analysis, it appears that continental fragmentation, a component of the Court Jester hypothesis, is a major driver of the diversification dynamics of Plecoptera (Figs. 5C-D).

Gaps in Plecoptera fossil record: Where should we look?

As for many extant insect orders, the order Plecoptera has a long evolutionary history that can be traced from the fossil record. Nonetheless, the fossil record has a few gaps that challenge the estimation of evolutionary history of Plecoptera and that should guide future efforts (Fig. 4). Beyond known gaps in the paleo-entomological record (Nel et al. 2018), our analyses inferred preservation rate through time, which allows us to expand our critical analysis of those gaps for Plecoptera (Fig. 4).

The first gap (Fig. 4B), from the Kasimovian (ca. 306 Ma) to the Asselian (ca. 295 Ma), is flanked by the appearance of stem-Plecoptera (Béthoux et al. 2011, Schubnel et al. 2019) and the early diversification of crown-Plecoptera. It makes the transition between stem- and crown-Plecoptera opaque and prevents us from understanding the morphological changes (wing venation, genitalia, etc.) that took place between these lineages. As a result, the early evolutionary history of Plecoptera remains poorly understood. Several fossil deposits could inform us (e.g., Mazon Creek: USA, Wettin: Germany, Avion: France) on this pivotal period for Plecoptera.

A second gap is recorded during the late Early Cretaceous (Fig. 4B), but it may simply reflect the lack of deposits covering this period. Filling this gap might thus be more challenging than the first one. It is nonetheless crucial because it corresponds to the angiosperm diversification. If not filled, this gap may weaken our ability to quantify the impact of angiosperm diversification on Plecoptera. This period also corresponds to a sudden diminution of the net diversification (Fig. 1A) rate and to two major shifts in the plecopteran diversification (Letsch et al. 2021), for the Leuctrinae and Nemouridae, and to some major events in continental fragmentation. Disentangling the relationships between these results and putative driving forces would require a better documentation of the late Early Cretaceous gap.

The third and largest gap extends from the mid-Cretaceous to the end of the Eocene (Fig. 4B) and thus encompasses the K/Pg event. It prevents from a robust quantifying of the impact of this crisis and of the warming events of the Cenozoic (e.g., Paleocene–Eocene Thermal Maximum, Middle Miocene Climatic Optimum). This gap is bewildering because many fossil entomofaunas are known for this time interval from amber deposits, compressions or imprints (Schachat and Labandeira 2020). If the fossil record of Plecoptera trapped in amber is relatively scarce, the imprints or compressions of Plecoptera are generally more abundant. Therefore, the absence of described Plecoptera from the Paleocene of Menat (France) or from the Eocene of the Green River Formation or Florissant (USA) is puzzling, especially since a few fossils are known from these localities (for example in the collection of the Museum of Natural History, University of Colorado). This period also includes a major shift in diversification rate for the Capniidae (Letsch et al. 2021), supposedly around the K/Pg boundary. However, the lack of fossils of this family or other Plecoptera impedes further study.

Overall, our results show the crucial interest in documenting fossil taxa to analyze the evolutionary history of a clade and infer scenarios about periods of diversification or decline. In this study, we analyzed, for the first time, the fossil record of Plecoptera to study their diversification and diversity dynamics in the deep time. Our analysis suggests that the Permian-Triassic crisis had a notable impact on the diversification of the Plecoptera, with a drastic decrease in the number of lineages, whereas the rainy episodes of the Carnian and the Triassic-Jurassic transition did not. A second, major extinction event is also recorded at the end of the Early Cretaceous and may be interpreted as a turnover between ‘pre-angiosperm' Plecoptera and ‘new’ Plecoptera developing in novel ecosystems dominated by angiosperms. We also unveiled three major gaps (i.e. the Carboniferous-Permian transition; the late Early Cretaceous; uppermost Cenomanian to Bartonian) to be filled for a better understanding of the evolutionary history of this insect clade. These gaps in the fossil record are even more troublesome when they overlap with a crisis or when major diversification events are expected to occur.

Supplementary Data

Supplementary data are available at Insect Systematics and Diversity online.

Author Contributions

CJ: Conceptualization, Data curation, Formal analysis, Methodology, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. AN: Investigation, Supervision, Validation, Writing – original draft, Writing – review & editing. FL: Conceptualization, Investigation, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. FLC: Conceptualization, Formal analysis, Methodology, Investigation, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Figure captions

Parameters	**Median**	**95% HPD interval**
λ0	0.093	[2.653E-3, 0.4572]
μ0	3.5749E-3	[3.9487E-5, 0.034]
Gλ0_0	**-2.8479**	**[-4.2277, -1.4515]**
Gλ0_1	-1.6563	[-3.553, 0.1121]
Gλ0_2	**12.1565**	**[7.2823, 16.861]**
Gλ0_3	-1.202	[-3.4144, 0.6472]
Gλ0_4	0.0293	[-0.0069, 0.0736]
Gμ0_0	-0.3878	[-1.7648, 0.5667]
Gμ0_1	-2.3305	[-4.4254, 1.1782E-4]
Gμ0_2	**20.241**	**[15.0017, 25.681]**
Gμ0_3	-0.0861	[-2.768, 2.3462]
Gμ0_4	0.0785	[0.0263, 0.1302]
ωλ0_0	0.9064	[0.6016, 1]
ωλ0_1	0.8175	[0.1295, 1]
ωλ0_2	0.9045	[0.6096, 1]
ωλ0_3	0.6305	[4.6246E-9, 0.9796]
ωλ0_4	0.7362	[0.042, 1]
ωμ0_0	0.4962	[2.7324E-8, 0.9726]
ωμ0_1	0.8763	[0.374, 1]
ωμ0_2	0.9551	[0.8069, 1]
ωμ0_3	0.4886	[5.4705E-8, 0.9707]
ωμ0_4	0.9149	[0.5803, 1]

Table 1. Results of the analyses of correlations between Plecoptera diversification and the variables: clade diversity; Angiosperms; fragmentation(s) of continents; Gymnosperms; temperatures. In bold: correlations with median and 95% HPD not containing 0. λ0 and μ0: baseline rates; Gλ correlation parameters to origination; Gμ correlation parameters to extinctions. ωλ and ωμ statistical support (significant between 0.8–1). Parameter end numbers:

intra-clade competition (0); Angiosperms (1); continental fragmentation (2); Gymnosperms (3); temperatures (4).

Figure 1. Net diversification rate for the entire evolutionary history of Plecoptera. A. From Carboniferous to mid-Eocene; B. Focus on the Carboniferous to Middle Triassic period; C.

Focus on the late Middle Triassic to the late Lower Cretaceous period. The rates are deduced through the analysis of the fossil register at the genus-level, via the RJMCMC model implemented in PyRate. Abbreviation: Pen = Pennsylvanian, Cis= Cisuralian, Gua= Guadalupian, L= Lopingian, ET= Lower Triassic, MT = Middle Triassic, LP= Upper Triassic, EJ= Lower Jurassic, MJ= Middle Jurassic, LJ= Upper Jurassic, EC= Lower Cretaceous, LC= Upper Cretaceous, Pa= Paleocene, Eoc= Eocene.

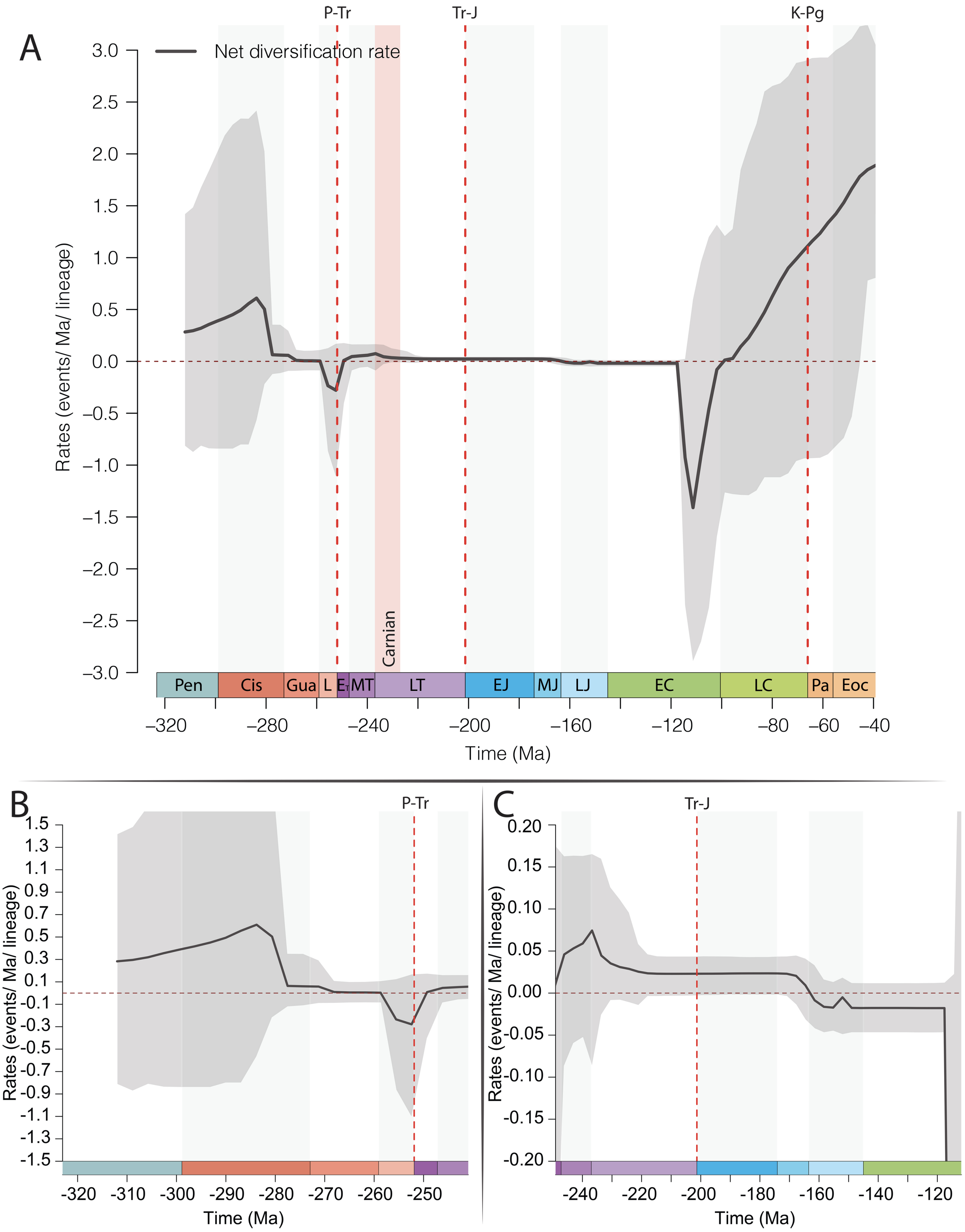

A
Net diversification rate
P-Tr
Tr-J
K-Pg
Carnian
Rates (events/ Ma/ lineage)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
−2.5
−3.0
Pen
Cis
Gua
L
E
MT
LT
EJ
MJ
LJ
EC
LC
Pa
Eoc
−320
−280
−240
−200
−160
−120
−80
−60
−40
Time (Ma)
B
P-Tr
1.5
1.3
1.1
0.9
0.7
0.5
0.3
0.1
-0.1
-0.3
-0.5
-0.7
-0.9
-1.1
-1.3
-1.5
Rates (events/ Ma/ lineage)
-320
-310
-300
-290
-280
-270
-260
-250
Time (Ma)
C
Tr-J
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
Rates (events/ Ma/ lineage)
-240
-220
-200
-180
-160
-140
-120
Time (Ma)

Figure 2. Plecoptera diversification dynamics. A. Origination rate; B. Probability of changes in origination rate; C. Extinction rate; D. Probability of changes in extinction rate. The rates and their changes are deduced through the analysis of the fossil register at the generic level, via the RJMCMC model implemented in PyRate (the colors of the geological time scale correspond to the same periods as in Fig. 1A).

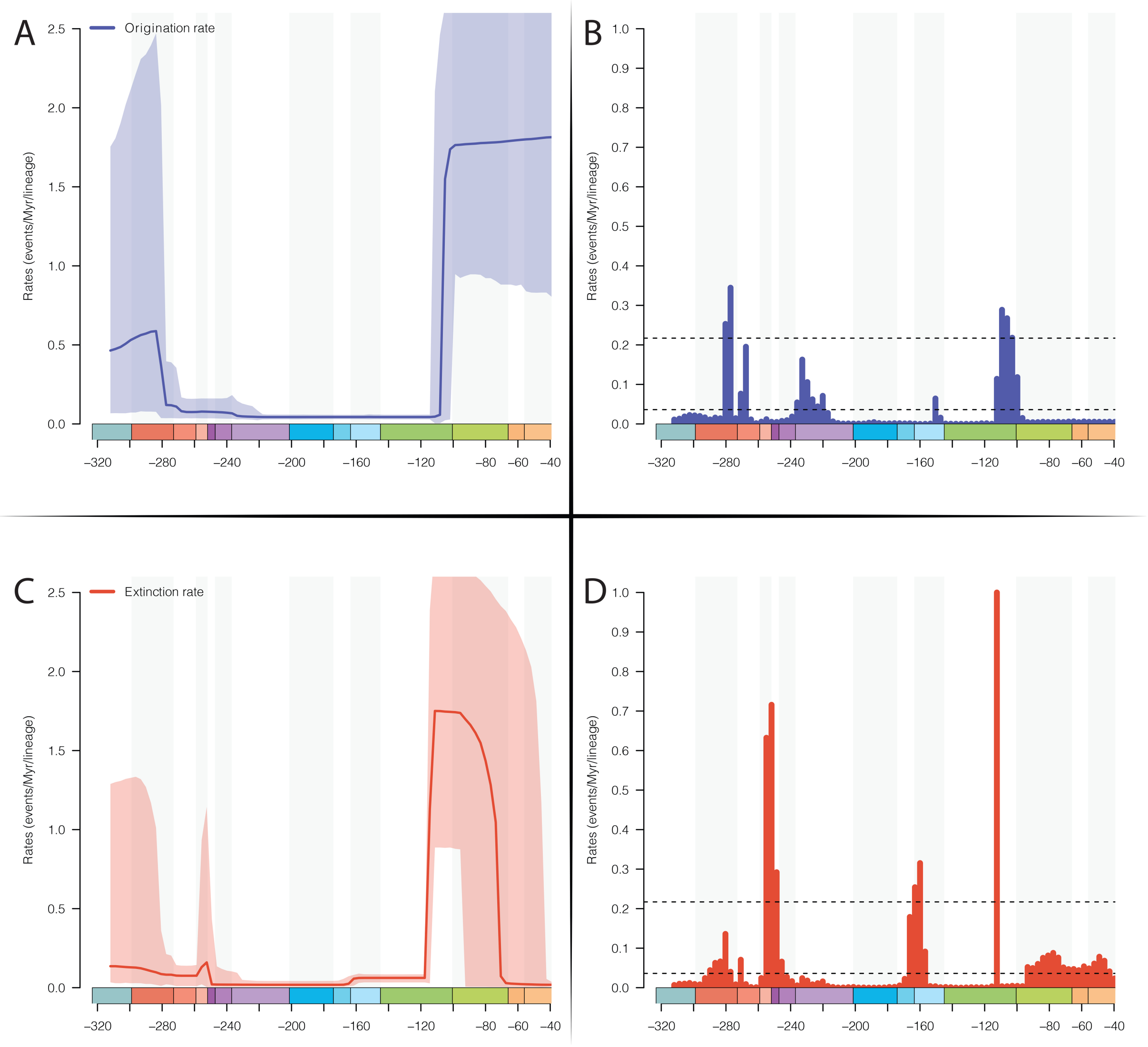


Figure 3. Past dynamic of extant Plecoptera sub-orders. A. Antarctoperlaria from Guadalupian to the Lower Cretaceous; B. Arctoperlaria from Guadalupian to the middle Eocene. The rates are deduced through the analysis of the fossil register at the generic level, via the RJMCMC model implemented in PyRate (the colors of the geological time scale correspond to the same periods as in Fig. 1A).

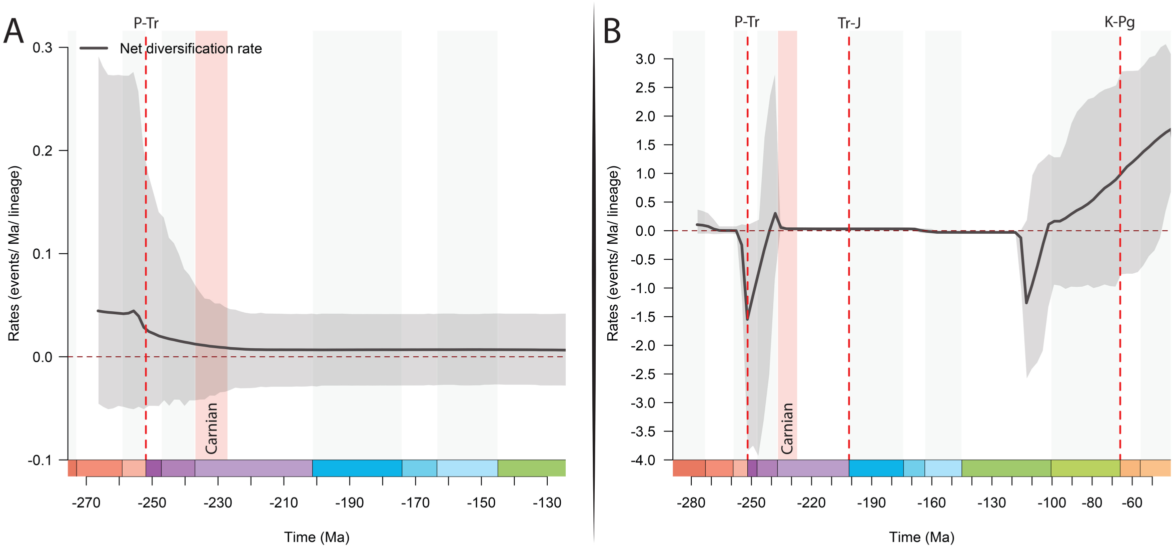


Figure 4. Preservation and gaps throughout Plecoptera fossil record. A. Mean preservation rates (i.e. number of occurrences per species per Myr) and the variations though time (solid lines

indicate mean posterior rates and shaded areas show 95% CI); B. Lineage-thorough-time plots and fossil diversity (solid lines indicate mean posterior rates and shaded areas show 95% CI) (the colors of the geological time scale correspond to the same periods as in Fig. 1A).

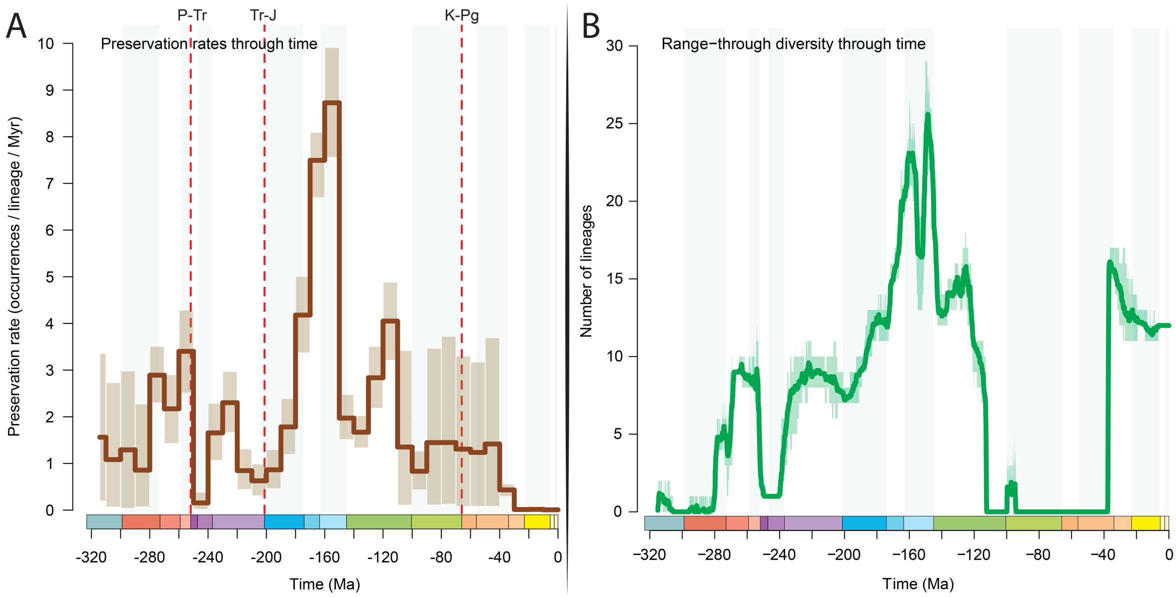
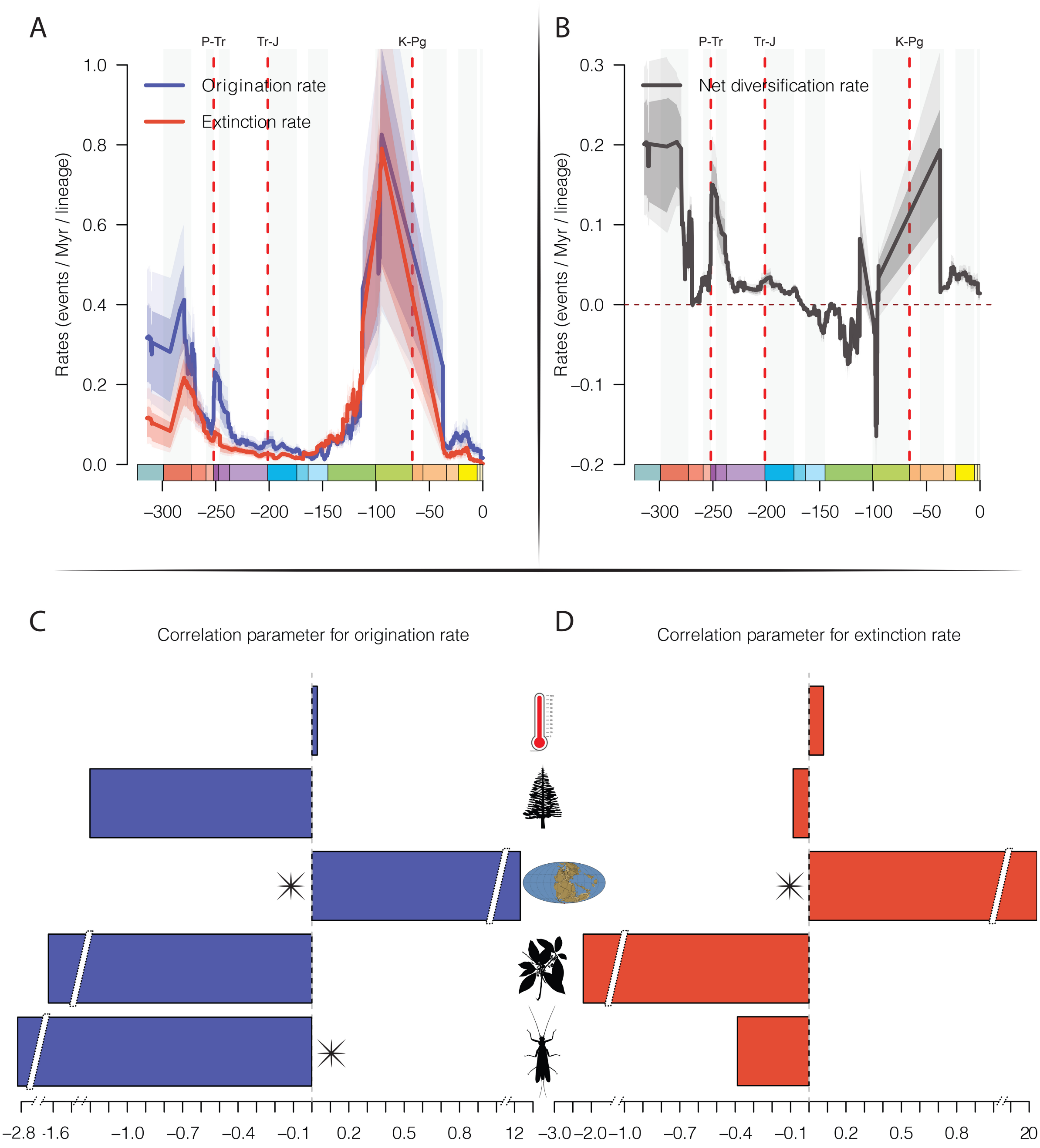


Figure 5. A. Dynamics of speciation and extinction rates through time as estimated with the Bayesian multivariate birth–death model in PyRate, while incorporating the effect of putative factors; B. Dynamic of the net diversification rate through time (solid lines indicate mean posterior rates, whereas the shaded areas show 95% CI); C, D. Bayesian inferences of

correlation parameters on speciation and extinction with abiotic factors like global temperature, and global continental fragmentation; with biotic factors like the relative diversity through time of gymnosperms, and angiosperms; and diversity-dependence factors with the diversity through time of all fossil Plecoptera. The asterisk (*) indicates significant correlation parameter for a given variable (shrinkage weights $(\omega) > 0.5$). Thermometer from CJ; Angiosperms, Gymnosperms and Plecoptera silhouettes from http://phylopic.org/; Triassic world maps pictures of courtesy of Eikeskog1225 (© Wikimedia Commons): https://creativecommons.org/licenses/by-sa/4.0/; the colors of the geological time scale correspond to the same periods as in Fig. 1A.


A
P-Tr
Tr-J
K-Pg
1.0
0.8
0.6
0.4
0.2
0.0
Rates (events / Myr / lineage)
Origination rate
Extinction rate
–300
–250
–200
–150
–100
–50
0
B
P-Tr
Tr-J
K-Pg
0.3
0.2
0.1
0.0
–0.1
–0.2
Rates (events / Myr / lineage)
Net diversification rate
–300
–250
–200
–150
–100
–50
0
C
Correlation parameter for origination rate
D
Correlation parameter for extinction rate
–2.8
-1.6
–1.0
–0.7
–0.4
–0.1
0.2
0.5
0.8
12
–3.0
–2.0
–1.0
–0.7
–0.4
–0.1
0.2
0.5
0.8
20

Supp Table 1. Fossil occurrences of Plecoptera at the genus-level with their status and life span.

Supp Table 2. Fossil record of Plecoptera with their current systematic placement (the systematic proposed here is widely accepted but does not reflect the opinion of the authors).

Supp Table 3. Fossil occurrences of Antarctoperlaria at the genus-level with their status and life span.

Supp Table 4. Fossil occurrences of Arctoperlaria at the genus-level with their status and life span.

Supp Fig. S1. Dynamic of Plecoptera deduced through the analysis of the fossil register at the genus-level, via the BDCS model implemented in PyRate for 10 million years bins.

Supp Fig. S2. Dynamic of Plecoptera deduced through the analysis of the fossil register at the genus-level, via the BDCS model implemented in PyRate for epoch bins.