Distributions of extinction times from fossil ages and tree topologies: the example of some mid-Permian synapsid extinctions

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Abstract

Given a phylogenetic tree of extinct and extant taxa with fossils where the only temporal information stands in the fossil ages, we devise a method to compute the distribution of the extinction time of a given set of taxa under the Fossilized-Birth-Death model.

Our approach differs from the previous ones in that it takes into account the possibility that the taxa or the clade considered may diversify before going extinct, whilst previous methods just rely on the fossil recovery rate to estimate confidence intervals.

We assess and compare our new approach with a standard previous one using simulated data. Results show that our method provides more accurate confidence intervals.

This new approach is applied to the study of the extinction time of three Permo-Carboniferous synapsid taxa (Ophiacodontidae, Edaphosauridae, and Sphenacodontidae) that are thought to have disappeared toward the end of the Cisuralian, or possibly shortly thereafter. The timing of extinctions of these three taxa and of their component lineages supports the idea that a biological crisis occurred in the late Kungurian/early Roadian.

1 Introduction

Reconstructing the history of the diversification of life on Earth has long been one of the main goals of evolutionary biology. In this great enterprise, the fossil record plays a central role because it gives fragmentary but direct evidence of the biodiversity at various times (Carroll, 1988), and even documents spectacular changes in the rates of cladogenesis (evolutionary divergence of a lineage that splits into two lineages, a process that we here equate with speciation), anagenesis, and extinction, that occurred more or less regularly in the history of life. Such changes generated evolutionary radiations (Ronquist *et al.*, 2012; Slater, 2015; Gavryushkina *et al.*, 2016; Brocklehurst, 2017; Ascarrunz *et al.*, 2019) that occur when the diversification of a taxon accelerates significantly, and mass extinction events (Axelrod and Bailey, 1968; Lewin, 1983; Raup and Sepkoski, 1984; Stanley, 1988; MacLeod, 1996; Benton, 2003; Ward *et al.*, 2005; Retallack *et al.*, 2006; Wignall *et al.*, 2009; Bond *et al.*, 2010; Ruta *et al.*, 2011; Sidor *et al.*, 2013; Lucas, 2017; Brocklehurst, 2018), during which the extinction rate of many taxa increases spectacularly, but typically for a short time.

So far, most studies of these phenomena that emphasized the fossil record have used the taxic approach, which consists of counting the number of taxa of a given rank (most frequently, families or genera; more rarely, species) in various time bins and estimating fluctuations in extinction and origination rates (Raup and Sepkoski, 1984; Benton, 1985, 1989; Alroy, 1996; Day *et al.*, 2015a; Brocklehurst, 2018). Several limitations are inherent to this approach.

First, some early studies relied on databases that included many paraphyletic or even polyphyletic taxa and thus confused pseudoextinction with genuine extinction (Patterson and Smith, 1987). Indeed, this was identified by Benton (1989) as one of the main aspects that could be improved in subsequent studies, and subsequent developments proved him right. Some recent analyses using the taxic approach

even include a phylogenetic correction to these biodiversity counts by accounting for ghost lineages (Ruta *et al.*, 2011; Martin *et al.*, 2014; Jouve *et al.*, 2017). Progress has also been made on how to integrate events from various sections into an optimal sequence (Sadler, 2004), and this has been applied to one of the Permian mass extinction events (Day *et al.*, 2015a).

Second, counts of taxa at a given Linnaean nomenclatural level (except for species, if these are conceptualized as an evolutionary lineage) are poor measures of biodiversity (Bertrand *et al.*, 2006; Laurin, 2010), because taxa of a given level share no objective properties (Ereshefsky, 2002) and may include one to many lineages. For this reason, better ways to quantify biodiversity were developed (Faith, 1992).

A third problem of the classical taxic approach is that the known stratigraphic range of taxa typically underestimates their true stratigraphic range (real age of appearance and extinction), a problem that is likely to be especially acute for taxa with a poor fossil record (Strauss and Sadler, 1989). Most recent analyses using the taxic approach still rely on a fairly literal reading of the fossil record to the extent that they use first and last stratigraphic occurrence data as if it were the true stratigraphic range of taxa.

Fourth, counting taxa in time bins can create artefacts. If the time bins are relatively long (like geological periods or stages), the resulting counts may give the impression that origination or extinction events are concentrated at the limits between two consecutive bins, whereas in fact, the diversity of a taxon may have changed more or less gradually throughout the time bin (Day *et al.*, 2015a; Lucas, 2017). When more detailed stratigraphic data are available, it may be possible to assess whether the changes are abrupt or gradual. However, this raises another problem: for taxa that have a sparse fossil record, simple sampling effects may give the false impression that extinctions have been gradual. This is called the "Signor-Lipps effect" because of the landmark study by Signor *et al.* (1982), even though Shaw (1964) described it earlier, according to MacLeod (1996).

To establish a better understanding of the dynamics of fluctuations in biodiversity over time, it is thus useful to assess as accurately as possible the stratigraphic ranges of taxa. Early developments in this field tackled both ends (origination and extinction) of the stratigraphic ranges of taxa (Strauss and Sadler, 1989; Marshall, 1990, 1997; Wagner, 2000). Most recent methodological developments have addressed the problem of taxon origination by inferring how much of the earliest phase of each taxon's history remains hidden from the known fossil record, which may be useful to date the nodes of the Tree of Life (Marshall, 2008; Laurin, 2012; Warnock *et al.*, 2012; Sterli *et al.*, 2013; Warnock *et al.*, 2015; Didier and Laurin, 2020). However, determining when taxa became extinct is also interesting, especially to better understand past biological crises. Mass extinction events have been increasingly studied in the last decades (Benton, 2003; Ward *et al.*, 2005; Retallack *et al.*, 2006; Wignall *et al.*, 2009; Bond *et al.*, 2010; Ruta *et al.*, 2011; Sidor *et al.*, 2013; Lucas, 2017; Brocklehurst, 2018), a trend that is partly fueled by the rising concern about the current anthropogenic biodiversity crisis (Wake and Vredenburg, 2008; Barnosky *et al.*, 2011; Ceballos *et al.*, 2015, 2017). Thus, time is ripe to return to the question of timing of extinction of taxa.

Most of the approaches that addressed this question were derived from the seminal work of Strauss and Sadler (1989), which can provide confidence intervals for the origination and extinction time of a taxon when its fossilization potential is constant in time. Later, Marshall (1994, 1997) and Marjanović and Laurin (2008) extended this work to the case where the fossilization potential varies through time. In the same way, Silvestro *et al.* (2014a,b) consider a model where the fossilization recovery rate follows a PERT distribution (a generalized form of the beta distribution) between the origin and the end of a lineage, which is used in a Bayesian framework with priors defined from a birth-death process, to estimate the speciation and the extinction times. See Laurin (2012), Wang and Marshall (2016) and Marshall (2019) for recent reviews on this topic.

Studies of mass extinction events focus on patterns affecting taxa of various sizes, some of which include many lineages. For such studies, the methodology of Strauss and Sadler (1989) might not be appropriate because it considers each taxon as if it were composed of a single lineage that does not diversify. Thus, the derivative approaches do not take into account the possibility that the considered taxon (whether it is composed of one or more lineages) may have given birth to one or more lineages that left no fossil record before going extinct, possibly well after all lineages documented in the fossil record (Fig. 1). Neglecting this possibility could be justified in the case where the diversification rates are low with regard to the fossil recovery rate. Unfortunately, our previous studies suggest the opposite situation in the datasets considered in Didier *et al.* (2017) and Didier and Laurin (2020). It follows that one could

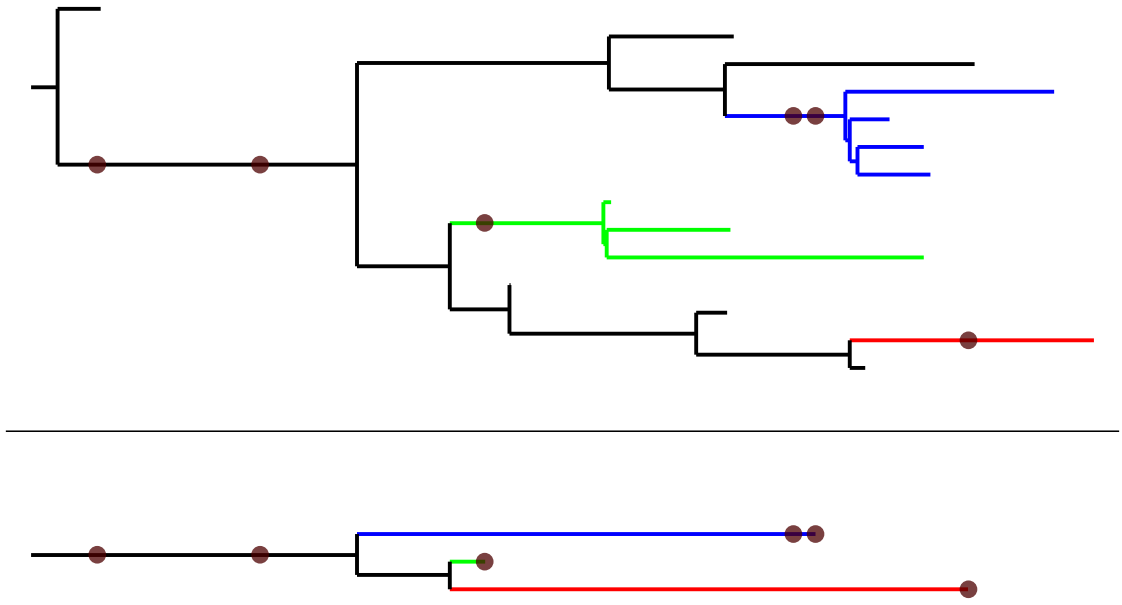

Figure 1: A simulated extinct clade where fossils are figured by brown dots. Top: the whole evolution. Bottom: The part observable from the present time. Note that "blue" and "green" taxa diversifies before going extinct.

expect the extinction times (and the stratigraphic range extensions) provided by Strauss and Sadler (1989) to be inaccurate in some cases. This problem may be minor when estimating the stratigraphic range of a single nominal species, but it is probably more severe when estimating the extinction time of a clade known to have included several species, as in the case of the Permo-Carboniferous taxa (Ophiacodontidae, Edaphosauridae and Sphenacodontidae) studied below. Note that taking into account the diversification process to assess the time of extinction is much more important for a clade that became extinct long ago (i.e., tens of thousands of years ago or more) than for species that became extinct in historical times and for which sighting records are available (Rivadeneira *et al.*, 2009). The timescales involved in this latter case ensure that no speciation (cladogenesis) event may occur before the extinction of the considered species.

To better estimate extinction time by considering additional lineages that may have left no fossil record, the fossilized birth-death model (FBD model) could be used. The FBD model assumes that fossil finds follow a Poisson process, which is also assumed by Strauss and Sadler (1989), but it also models the diversification of taxa as a birth-death process. Given that the parameters that characterize the FBD model include an extinction rate, it should be possible to use this process to estimate the probability distribution of extinction times. So far, the FBD model has been used to date cladogeneses (Stadler and Yang, 2013; Heath *et al.*, 2014; Didier and Laurin, 2020) but not extinction. Evaluating extinction times through the FBD would be very useful to determine the extent to which the Signor-Lipps effect has biased our perspective on mass extinction events. It could also be useful to reassess the reliability and stratigraphic significance of some taxa as index fossils, at least those with a relatively sparse fossil record for which reliable phylogenies exist; such cases are presumably fairly rare in the marine realm, but may be more common in continental biochronology (Steyer, 2000; Day *et al.*, 2013, 2015b). Indeed, stratigraphic correlations of continental strata, at least when relying on vertebrate fossils, often use higher-ranking taxa (nominal genera or families), especially when strata located on different continents are assessed (Rubidge, 2005).

Another concern with the approach of Strauss and Sadler (1989) is that it requires several fossils of a taxon to provide a confidence interval that bounds the corresponding extinction time, which makes it unsuitable for lineages or small clades with a low fossilization rate. Moreover, because it is computed

independently on each extinct taxon (without consideration of its close relatives and the tree structure of this set of lineages), the level of precision provided by the method developed by Strauss and Sadler (1989) depends on the number of fossils present on each terminal branch. This point can be a major issue for datasets where the fossil recovery is low (Section 4). This limitation does not apply to the method we propose, in which the extinction-time distribution of taxa with a single fossil on their terminal branch can be determined, if this branch belongs to a clade with a sufficient number of fossils.

Below, we develop the FBD model to estimate extinction times of taxa that may consist of one to many lineages. Namely, given a dataset that consists of a phylogenetic tree of extant and extinct taxa, with fossils and their ages but without divergence times, we compute the probability that a given set of taxa (known to be extinct at the present time) goes extinct before a time t. The computation of this probability density is a direct extension of the method provided in Didier and Laurin (2020). We also provide an explicit formula for the probability that a given subset of extinct taxa (typically a clade) goes extinct before another one under the FBD model (Appendix B).

Our approach differs conceptually from that of Strauss and Sadler (1989) and subsequent works in the sense that, in our method, the extinction date is the time of a particular event whose distribution can be computed from the parameters of the model. By contrast, in the approach of Strauss and Sadler (1989), the extinction time is a parameter of the model, which has to be estimated or bounded in a confidence interval, and requires a Bayesian framework to obtain posterior distributions.

We adapted the Monte Carlo Markov Chain (MCMC) importance sampling procedure devised by Didier and Laurin (2020) in order to deal with the common case where fossil ages are provided as stratigraphic time intervals and to integrate distributions over the parameters of the model. Our approach allows incorporating phylogenetic uncertainty by estimating the extinction times over a set of trees.

The method presented below, like our previous works in this field, assumes a fairly homogeneous fossilization rate through time. Note that this hypothesis would not be reasonable if we had adopted what Lucas (2017) called the "best sections" analysis, which focuses on a region where a given taxon has a rich fossil record for a given period. Given that the FBD models diversification of clades, and that the clades that we analyze had a fairly cosmopolitan distribution, it would be inappropriate to restrict our analysis on a single fossiliferous sedimentary basin. A recent literature review of Middle Permian amniote-bearing localities (Olroyd and Sidor, 2017) shows that the assumption of a reasonably homogeneous fossilization rate (worldwide) through the studied time interval (Bashkirian-Roadian) is reasonable.

Our approach is first assessed and compared to that of Strauss and Sadler (1989) on simulated datasets. It is then applied to study the extinction of three Permo-Carboniferous taxa: Ophiacodontidae, Edaphosauridae and Sphenacodontidae. Two additional studies, which are not directly related to the extinction time question, are presented in appendices:

- We exploited the simulated data to assess the relevance of the posterior distributions of speciation, extinction and fossilization rates from phylogenetic tree with fossils, which can be obtained from our approach (Appendix C).
- The dataset used here incorporates a significantly larger amount of fossil data from the Paleobiology Database than that of Didier and Laurin (2020) (though it includes only a subset of taxa of this previous dataset). We applied the approach of Didier and Laurin (2020) to compute the divergence time densities and the posterior densities of the speciation, extinction and fossilization rates of this new dataset (Appendix D).

The computation of the extinction time distribution and of its confidence upper bound at a given threshold was implemented as a computer program and as a R package, both available at `https://github.com/gilles-didier/DateFBD`.

2 Empirical example: Permian extinction of Ophiacodontidae, Edaphosauridae and Sphenacodontidae

We illustrate our method with an empirical example from the rich fossil record of Permian synapsids. Synapsida originated in the Carboniferous and experienced a few evolutionary radiations, the first one of which, in the Late Carboniferous and Early Permian, gave rise to taxa that have long been known

as "pelycosaurs" (Romer and Price, 1940; Reisz, 1986; Benson, 2012), but which will be called here "Permo-Carboniferous synapsids". Among these taxa arose the stem lineage of therapsids, probably in the Late Carboniferous (Sidor, 2001; Amson and Laurin, 2011). Therapsids become increasingly common in the Roadian (early Middle Permian) fossil record (Reisz and Laurin, 2002; Abdala *et al.*, 2008), and dominated several ecological niches from the Wordian (mid-Guadalupian) to the end of the Permian (Smith *et al.*, 2012). All other synapsid clades appear to have became extinct before the end of the Guadalupian (Modesto *et al.*, 2011). Therapsida experienced several evolutionary radiations, including one that gave rise to mammals, in the Triassic or in the Jurassic (King and Beck, 2020).

Up to four mass extinction events have been recognized in the Permian fossil record of synapsids (Lucas, 2017), and a brief review of these is relevant to understand the context of the present study and to justify the taxonomic sample. The first may have occurred at the Artinskian/Kungurian boundary (about 282 Ma), or possibly at the Sakmarian/Artinskian boundary (about 290.1 Ma), or it may be a long decline that occurred throughout the Sakmarian and Artinskian (Benton, 1985, 1989; Brocklehurst *et al.*, 2013). This extinction was suggested by early studies (Olson and Vaughn, 1970; Olson, 1982). Benton (1989) included it in his list of major mass extinctions (along with the P/Tr and K/Pg events), and stated that Ophiadocontidae, Edaphosauridae, and Sphenacodontidae were among the taxa that became extinct then. However, Lucas (2017) argued that it was a "non-event" that represents a normal level of faunal turnover and he later asserted that it simply represents the end of his very long-lasting (about 15-20 Ma) Coyotean chronofauna (Lucas, 2018, p. 429), which extends approximately from the late Gzhelian to the late Sakamrian. In any case, it is now clear that Ophiadocontidae, Edaphosauridae, and Sphenacodontidae persisted at least until the Kungurian, which is well after Lucas' Coyotean chronofauna.

The second possible mass extinction event in Permian tetrapods, which we study here, may have occurred near the Kungurian/Roadian stage boundary (Brocklehurst *et al.*, 2013; Lucas, 2017), which is also the Cisuralian (Early Permian)/Guadalupian (Middle Permian) series boundary. It seems plausible that some of the extinctions (among others, those of Ophiadocontidae, Edaphosauridae, and Sphenacodontidae) that had at some point been postulated to have taken place in the Sakmarian and/or Artinskian actually took place toward the end of the Kungurian. The observed stratigraphic range of Ophiadocontidae, Edaphosauridae, and Sphenacodontidae ends shortly before the top of the Kungurian. Sahney and Benton (2008) called this event "Olson's extinction" and considered that it was the first of three Permian crises (they seem to have ignored the possibility of an earlier crisis in the Artinskian, which their data were not designed to reveal). They did not date it very precisely, mentioning only that it had taken place in the Roadian and/or Wordian, but estimated that it "reveals an extended period of low diversity when worldwide two-thirds of terrestrial vertebrate life was lost" (Sahney and Benton, 2008, p. 760). Olroyd and Sidor (2017) suggested, among other hypotheses, that extinction of most Permo-Carboniferous synapsids at the end of the Kungurian could have allowed their non-competitive replacement by therapsids, and this hypothesis is tested indirectly here (see below). Lucas (2018, p. 430) suggested that rather than a single, large crisis, a few events (which he called "Redtankian events", after his Redtankian chronofauna) took place in the Kungurian. Lucas (2018, p. 430) suggested that ophiacodontids became extinct before edaphosaurids, but that both clades were extinct in the early Redtankian. Sphenacodontids became extinct later because they occur in the Littlecrotonian (Lucas, 2017, p. 43). However, this interpretation is based on a literal interpretation of the fossil record; no attempts have been made at assessing confidence intervals for the extinction times of relevant taxa, as far as we know. Our study aims at filling this gap.

The third mass extinction events took place near the end of the Capitanian, the last stage of the Guadalupian (Middle Permian), around the time of the Emeishan volcanism in southern China (Day *et al.*, 2015a; Lucas, 2017). It wiped out the dinocephalians (a fairly large clade of Guadalupian therapsids), although this apparently occurred gradually in the *Tapinocephalus* Assemblage Zone (Day *et al.*, 2015b). Varanopid synapsids also appear to have become extinct then (Modesto *et al.*, 2011); this was the last of the Permo-Carboniferous synapsid clades to become extinct because caseids are not currently known after the Roadian. Maddin *et al.* (2008) assigned a mid-Capitanian age to the caseid *Ennatosaurus tecton*, but more recently, Golubev (2015) assigned a Roadian age to the locality (Moroznitsa) of the holotype. The biodiversity of therocephalians decreased around the same time (Smith *et al.*, 2012). Other therapsid taxa also appear to have been affected by this crisis, which appears to also have influenced the marine realm (Day *et al.*, 2015a). Lucas (2017) argued that parareptiles were also affected by this crisis, but other studies suggests that parareptiles were only affected by background extinctions throughout the

Guadalupian (Ruta *et al.*, 2011; Cisneros *et al.*, 2020). Day *et al.* (2015a) estimated that there was a 74-80% loss of generic richness in amniotes in this crisis, and that it was not as severe as the end-Permian crisis. On the contrary, Lucas (2017) considered that this extinction event was more severe for amniotes than the much better-known end-Permian event and that both may have lasted longer than previously thought. In the seas, goniatitids and most fusulinids disappeared around that time, but ammonoids do not appear to have been strongly affected (Lucas and Shen, 2018, p. 34). Furthermore, Day *et al.* (2015a, p. 6) attributed this extinction to the short-term cooling and darkness induced by the Emieshan volcanism, as well as related acidification.

The fourth and best-known of the Permian mass extinction event took place at the Permian/Triassic boundary. Like most such events, it has been studied mostly in the marine realm (Raup and Sepkoski, 1982; Payne, 2005; Brayard *et al.*, 2009; Forel *et al.*, 2013; Romano *et al.*, 2013), where it is estimated that between 80 and 96% of species were eliminated (Sahney and Benton, 2008), but recent studies have shown a significant crisis in continental vertebrates as well (Benton, 2003; Ward *et al.*, 2005). Thus, Smith *et al.* (2012, p. 47) reported that out of 41 therapsid genera present in the middle of the *Dicynodon* Assemblage Zone, only three survived the End-Permian extinction (not taking into consideration ghost lineages that imply a slightly greater proportion of survivors). The extinctions on land and in the seas seem to have been synchronous (Smith and Botha-Brink, 2014). Lucas (2017) claims that this extinction event lasted longer than previously claimed and occurred in a stepwise manner. In fact, it was once thought that this crisis lasted over the last 10 Ma of the Permian (Erwin, 1990), but that was before the end-Guadalupian crisis was identified.

As can be seen from this very brief review, a recurring question is how long each crisis lasted. In other words, did most taxa become extinct at about the same time (in a few tens of thousand years, possibly a few hundred thousand years), or were the extinctions spread over a few million years? Settling this question ideally requires abundant, well-dated, and geographically-widespread data, as well as appropriate analytical methods to discriminate between genuine gradual extinctions and the Signor-Lipps effect on taxa with a relatively scarce fossil record, as is typically the case for continental vertebrates.

Our dataset is relevant to assess extinction times that span the first and second of the possible tetrapod Permian mass extinction events. Our method is not designed to assess fluctuations in extinction rates; rather, our objective is to obtain a better understanding of the timing of extinction of various taxa to either corroborate or refute previous statements about such events. More specifically, we test the following hypotheses:

1. Many ophiacodontids, edaphosaurids, and sphenacodontids had become extinct well before the end of the Kungurian (which is consistent with a prolonged crisis, or a series of crises, rather than with a single, catastrophic, sudden event at the end of the Kungurian; this can also test the existence of the first of the four crises listed above, near the Artinskian/Kungurian boundary).

2. Ophiadocontidae, Edaphosauridae, and Sphenacodontidae became extinct (gradually or not) by the end of the Kungurian, at the latest (Benton, 1989; Brocklehurst *et al.*, 2013; Lucas, 2017);

3. These three clades became extinct in the following order: Ophiacodontidae, Edaphosauridae, and Sphenacodontidae.

We test the first hypothesis by verifying the proportion of terminal branches (observed nominal species) of these three clades that became extinct before the end of the Kungurian (i.e., more than 95% of their extinction probability is before the end of the Kungurian). A substantial proportion of lineages becoming extinct before the end of the Kungurian would be compatible with a gradual extinction of these clades, even though additional tests will be required to prove this hypothesis. If a high proportion of the early extinctions were concentrated in time (especially around the Artinskian/Kungurian boundary), this would be compatible with (but would not prove) the possibility of a crisis around that time.

We test the second hypothesis by verifying if the extinction-density probability of the three clades is compatible with an extinction of these clades by the end of the Kungurian. Contrary to previous methods, ours considers the extinction times of lineages that have not been preserved in the fossil record but that are very likely to have existed because of the speciation extinction and fossilization rates. The fact that Didier *et al.* (2017, p. 981) estimated that only about 14% of the eupelycosaur lineages (defined as an internode on the tree) had left a fossil record suggests that taking into consideration unobserved lineages

can have a major impact on our estimates of the extinction times of these three large eupelycosaur clades. Hence, these times should be somewhat later than the extinction of the most recent known lineage of each of these clades, and potentially, substantially more recent than the last observed fossil of each of these clades.

The third hypothesis is tested by looking at the peak probability density of extinction time and the end of the 95% confidence interval of the extinction time of all three clades and by computing the probability of a given clade becoming extinct before another clade under the FBD model.

Note that testing hypotheses 1 and 2 above amounts to testing indirectly the suggestion that the replacement of Permo-Carboniferous synapside by therapsids was non-competitive (Olroyd and Sidor, 2017, p. 593) because a literal reading of the fossil record suggests that therapsid diversification accelerated sharply in the Roadian and that this is after the extinction of Ophiacodontidae, Edaphosauridae, and Sphenacodontidae. If this is correct, this replacement was non-competitive. On the contrary, if it seemed plausible that Ophiacodontidae, Edaphosauridae, and Sphenacodontidae became extinct only in the Wordian or later (time at which theraspids were already abundant in most terrestrial assemblages), this replacement may well have been competitive.

Note that these three hypotheses are not mutually exclusive. For instance, these clades could have become extinct gradually by the end of the Kungurian in the order suggested by (Lucas, 2018, p. 430), in which case all three hypotheses would be correct. Alternatively, these three clades might also have become extinct suddenly after the Kungurian and in a different sequence than stipulated by (Lucas, 2018, p. 430), even though this is not what a literal interpretation of their fossil record suggests; in this case, all three hypotheses would be false. But any combination is possible.

Our dataset includes a subset of the taxa represented in the dataset used by Didier and Laurin (2020), from which we simply extracted the smallest clade that includes Ophiacodontidae, Edaphosauridae and Sphenacodontidae. However, we incorporated all the information that we could find about the relevant taxa in the Paleobiology Database (Alroy *et al.*, 2012). Thus, we now have more fossil occurrences than in our previous studies that used this dataset (Didier *et al.*, 2017; Didier and Laurin, 2020). We also updated the geological ages using the recent literature (see below). The 100 trees used here were sampled from the 15 000 000 equiparsimonious trees reported by Didier and Laurin (2020) and pruned to retain the taxa included in this study.

Our method, contrary to those derived from Strauss and Sadler (1989); Marshall (1990, 1997), ideally requires stratigraphic data expressed in absolute age (Ma) rather than height in a section because we model events in time. It could use section height, provided that sedimentation rates were more or less homogeneous in time, but this would be less interesting (evolution happens in geological time, not in strata) and would be meaningless if applied to sections of different basins in which sedimentation rates were not necessarily comparable. In any case, these would still have to be correlated to each other. We thus relied on the literature to convert stratigraphic position of the fossils into approximate ages (represented by age ranges, which our method samples using a flat distribution). We tried to adopt the established consensus, as summarized, for part of the fossiliferous basins in SW USA, by Nelson *et al.* (2013) and the age assignments usually attributed to these formations as summarized (for much of the relevant stratigraphic range) by Lucas (2018, fig. 4), using the most recent geological timescale, as summarized by Lucas and Shen (2018, fig. 9). However, we consider that most of the Pease River and El Reno Groups are Guadalupian, as previously suggested by one of us and as supported by other studies based on various types of evidence (Clapham, 1970; Reisz and Laurin, 2001, 2002; Nelson and Hook, 2005; Foster *et al.*, 2014; Soreghan *et al.*, 2015).

3 Methods

3.1 The FBD model

The FBD model was introduced in Stadler (2010) and has been referred to as the "Fossilized-Birth-Death" model since Heath *et al.* (2014). This model assumes that the diversification process starts with a single lineage at the origin time, which is one of its parameters. Next, each lineage alive evolves independently until its extinction and may be subject during its lifetime to events of speciation (here equated with cladogenesis, which leads to the birth of a new lineage), extinction (which terminates the lineage) or fossilization (which leaves a fossil of the lineage dated at the time of the event) which occur

with respective rates λ, μ and ψ, which are the main parameters of the model. Last, the extant lineages (if any) are sampled at the present time with probability ρ, the last parameter of the model.

Let us recall the probabilities of the following basic events, derived in (Stadler, 2010; Didier *et al.*, 2012, 2017) under the FBD model, which will be used to compute various probability distributions on the observable part of realizations of the FBD process (Fig. 1 here or Didier and Laurin, 2020, fig. 1). The probability $\mathbf{P}(n,t)$ that a single lineage starting at time 0 has n descendants sampled with probability ρ at time $t>0$ without leaving any fossil (i.e., neither from itself nor from any of its descendants) dated between 0 and t is given by

$$\mathbf{P}(0,t) = \frac{\alpha(\beta-(1-\rho)) - \beta(\alpha-(1-\rho))\mathrm{e}^{\omega t}}{\beta-(1-\rho)-(\alpha-(1-\rho))\mathrm{e}^{\omega t}} \text{ and}$$
$$\mathbf{P}(n,t) = \frac{\rho^n(\beta-\alpha)^2\mathrm{e}^{\omega t}\left(1-\mathrm{e}^{\omega t}\right)^{n-1}}{\left(\beta-(1-\rho)-(\alpha-(1-\rho))\mathrm{e}^{\omega t}\right)^{n+1}} \text{ for all } n>0,$$

where $\alpha<\beta$ are the roots of $-\lambda x^2+(\lambda+\mu+\psi)x-\mu=0$, which are always real (if λ is positive) and are equal to

$$\frac{\lambda+\mu+\psi\pm\sqrt{(\lambda+\mu+\psi)^2-4\lambda\mu}}{2\lambda},$$

and where $\omega=-\lambda(\beta-\alpha)$. Note that $\mathbf{P}(0,t)$ is the probability that a lineage alive at time 0 goes extinct before t without leaving any fossil dated between 0 and t.

The probability density $\mathbf{D}(t)$ for a lineage alive at time 0 to go extinct exactly at time t (without leaving any fossil) is basically obtained by deriving $\mathbf{P}(0,t)$ w.r.t. t. We get that

$$\mathbf{D}(t) = \frac{\lambda(\alpha-(1-\rho))(\beta-(1-\rho))(\beta-\alpha)^2\mathrm{e}^{\omega t}}{(\beta-(1-\rho)-(\alpha-(1-\rho))\mathrm{e}^{\omega t})^2}.$$

In the particular case where $\rho=1$, expressions above simplify to

$$\mathbf{P}(0,t) = \frac{\alpha\beta(1-\mathrm{e}^{\omega t})}{\beta-\alpha\mathrm{e}^{\omega t}} \;,\; \mathbf{P}(n,t) = \frac{(\beta-\alpha)^2\mathrm{e}^{\omega t}\left(1-\mathrm{e}^{\omega t}\right)^{n-1}}{\left(\beta-\alpha\mathrm{e}^{\omega t}\right)^{n+1}} \text{ for all } n>0 \text{ and } \mathbf{D}(t) = \frac{\mu(\beta-\alpha)^2\mathrm{e}^{\omega t}}{(\beta-\alpha\mathrm{e}^{\omega t})^2}. \tag{1}$$

3.2 Extinction time distributions

We consider here a dataset consisting of a phylogenetic tree $\mathcal{T}$ of extant and extinct taxa with fossils, which is interpreted as the observable part of a realization of the FBD process, and of the fossil age vector $\mathbf{f}$. We aim to compute the joint probability density of $(\mathcal{T},\mathbf{f})$ and that a particular subset S of taxa of $\mathcal{T}$ goes extinct before a time t under the FBD model. This question makes sense only if the taxa of S all go extinct before the present time. In the empirical example provided below, these subsets consist of three clades, but the method can handle any set (monophyletic or not) of taxa.

This joint probability density can be computed in the exact same way as that of the dataset $(\mathcal{T},\mathbf{f})$ presented in Didier and Laurin (2020). To show this, we adapted figure 3 from Didier and Laurin (2020), which illustrates the fact that, from the Markov property, the probability density of $(\mathcal{T},\mathbf{f})$ can be written as the product of that of the "basic trees" obtained by splitting $\mathcal{T}$ at each fossil find (Fig. 2). The tree of Figure 2 contains only one extinct taxon that goes extinct between f_1, the age of its most recent fossil, and the present time T. The contribution factor of the basic tree starting from time f_1, which is unobservable from f_1 to the present time, is the probability that a lineage alive at f_1 goes extinct before the present time T without leaving any fossil dated between f_1 and T, i.e, $\mathbf{P}(0,T-f_1)$. Computing the joint probability density of the dataset of Figure 2 and that its extinct lineage goes extinct before a given time t (resp. exactly at a given time t) is performed by setting the contribution factor of the basic tree starting from time f_1 to $\mathbf{P}(0,t-f_1)$ (resp. to $\mathbf{D}(t-f_1)$).

More generally, the joint probability density of a dataset $(\mathcal{T},\mathbf{f})$ and that of a subset S of taxa goes extinct before a given time t is obtained by setting, for all taxa $n\in S$, the contribution factor of the unobservable basic tree pending from the leaf n, which starts from time $\ell_{\mathbf{f},n}$, i.e., the age of the most recent fossil of n, to $\mathbf{P}(0,t-\ell_{\mathbf{f},n})$, that is the probability that a lineage alive at $\ell_{\mathbf{f},n}$ goes extinct before t without leaving any fossil dated between $\ell_{\mathbf{f},n}$ and t. The computation of this joint probability density is

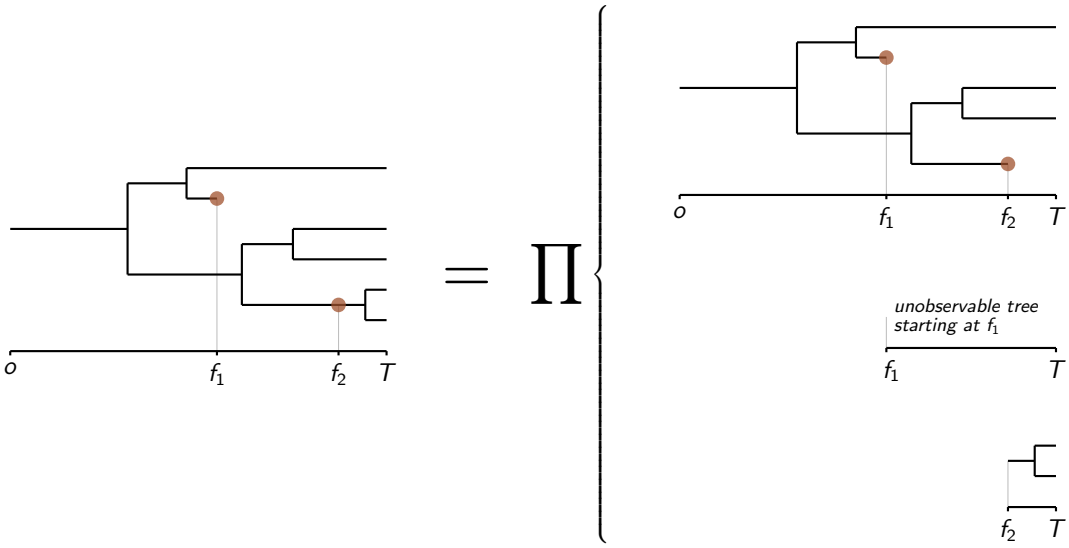

Figure 2: Decomposition of the probability density of a phylogenetic tree of extinct and extant taxa with fossils (figured by brown dots) as the product of the probability densities of "basic trees" by cutting it at each fossils find (adapted from Didier and Laurin, 2020).

thus computed in the very same way and with the same algorithmic complexity as that of the probability density of $(\mathcal{T}, \mathbf{f})$ presented in Didier and Laurin (2020).

The computation presented above allows us to determine the distribution of the extinction time of a subset of taxa in the case where where the tree topology, the fossil ages and the parameters of the FDB model are exactly known, a situation which is unfortunately never met in practice. Namely, the rates of the FBD model are unknown; morphological data of the fossils may be consistent with several topologies and fossil ages are provided as time intervals of plausible ages.

Given a priori probability distributions over the parameters and the data, a standard way to deal with the uncertainty on the model parameters and the data consists in integrating the extinction time distribution over all the possible values of the FBD parameters, of the fossil ages (constrained within confidence intervals) and over all tree topologies included in a population of trees. We implemented the numerical computation of this integration by Monte Carlo Markov Chain (MCMC, see Appendix A).

Note that determining the whole distribution of the extinction time is generally not required. Getting a *confidence upper bound of the extinction date at a given order* (usually 95%), i.e., an upper bound such that the probability to observe an extinction date anterior to it is equal to the order required, provides sufficient information for most purposes. In our framework, this bound is basically the quantile at the order required of the extinction time distribution.

If one is interested in comparing the extinction dates of two given extinct clades (or more generally two subsets of extinct taxa) A and B, it is possible to compute the probability that A goes extinct before B under the FBD model. In Appendix B, we provide an explicit formula for this probability.

4 Simulation study

In order to assess the accuracy of the upper bound of the extinction time corresponding to a given confidence level (here the usual 95%) obtained from the approach of Strauss and Sadler (1989) and that obtained from the method presented here, we simulated the diversification and the fossilization of a clade under the FBD model with five fossilization rates. The simulated data consist of the observable parts of the simulated diversification processes but we also stored the extinction time of all the extinct taxa (including those that are not observable) in order to assess the accuracy of different approaches.

In the simulation case, we have access to the (exact) tree topology, the fossil ages and the model parameters. In this section, we shall assume that both the tree topology and the fossil ages are exactly

known but consider both the upper bounds obtained from the model parameters used to simulate the data, which is the reference method since the extinction ages follow the distributions from which these upper bounds are computed in this case, and the upper bounds obtained without the knowledge of the model parameters, i.e. by dealing with their uncertainty by integrating over all the possible model parameters (by assuming that they follow improper uniform distributions; see the section above and Appendix A).

For each simulation, the "real" extinction times of all the extinct taxa were stored and compared to the upper bounds obtained from each method. Namely, the accuracy of each method is assessed with regard to two features:

1. their percentage of errors, that is the proportion of situations in which the real extinction date is posterior to the upper bound provided and,

2. the average width of the confidence interval, that is the average duration separating the age of the most recent simulated fossil of each taxon from the upper bound of the 95% confidence interval of its estimated extinction time.

The simulations were obtained by running a FDB process with speciation and extinction rates 0.2 and 0.19 respectively during 200 Ma. We considered five fossilization rates: 0.005, 0.01, 0.1, 1 and 5. The simulations were filtered for technical reasons. We kept only those leading to an observable tree of size from 50 to 100 nodes and containing more than 20 fossils.

The three following ways to obtain a 95% confidence upper bound of the extinction date were assessed:

S.S.: the method of Strauss and Sadler (1989),

Ref.: the 95% quantile of the extinction time distribution computed from the parameters used to simulate the data, which is the reference method (unfortunately, this method can not be applied in practice since we do not known the actual rates of speciation, extinction and fossilization in real situations),

Int.: the 95% quantile of the extinction time distribution obtained by integrating uniformly over the speciation, extinction and fossilization rates (numerically estimated from the MCMC procedure presented in Appendix A. For each simulated tree, we discarded the first 10000 iterations; then, we kept 1 iteration out of 10 until getting 5000 sets of rates from which the 95% quantiles associated to all the extinct taxa are computed).

Tables 1 to 3 display the results obtained over 1000 simulated trees for each fossilization rate.

Fossilization rate	Total extinct taxa	% **S.S.** feasible
0.005	20 787	7.42
0.01	25 084	10.19
0.1	35 928	33.83
1	36 088	75.02
5	35 820	93.07

Table 1: Simulated extinct taxa statistics. This table displays the total number of extinct taxa observed over all the simulations and the percentages of extinct taxa on which the computation using the method of Strauss and Sadler (1989) was possible (i.e. those corresponding to terminal branches bearing at least two fossils).

As expected, Table 1 shows that the proportion of extinct taxa on which the method of Strauss and Sadler (1989) can be applied, i.e. those corresponding to terminal branches bearing at least two fossils, may be very low when the fossil recovery rate is small. Within the covered simulation space, this proportion ranges from about 7% when the fossil recovery rate is four times lower than the speciation rate, to about 93% when the fossil recovery rate is 25 times the speciation rate (note that in 3 of the 5 sets of simulations, the fossil recovery rate is much higher than the net diversification rate, which is speciation minus extinction rates). This proportion increases with the fossil recovery rate. In our simulations, the approach of Strauss and Sadler (1989) requires a fossil recovery rate several times higher than the speciation and extinction rates in order to be applicable on the majority of extinct taxa. The

total number of extinct taxa starts by increasing with the fossilization rate, then fluctuates around 36000 for all the simulations when the fossilization rate is close to, or greater than the speciation and extinction rates, which may be caused by a saturation phenomena (i.e., there are fossils on almost all terminal branches) and/or by the fact that we keep only the simulations below a certain size.

Fossilization rate	**S.S.**	**Ref.**		**Int.**	
0.005	2.40	4.67	*5.12*	4.93	*5.41*
0.01	3.80	5.05	*5.18*	5.13	*5.74*
0.1	3.92	4.86	*4.95*	5.13	*5.44*
1	4.93	4.74	*4.78*	4.79	*4.84*
5	5.27	5.11	*5.10*	5.20	*5.20*

Table 2: Error percentages obtained from the upper bounds provided by the three methods on the simulated extinct taxa where the **S.S.** computation was feasible (plain text) and on all the extinct taxa (italics; only for methods **Ref.** and **Int.**).

The *error percentage*, that is the percentage of cases where the "real" extinction date is posterior to the upper bound provided, fluctuates around 5%, which is the level of risk required here, both for the methods **Ref.** and **Int.** (Table 2). This was expected for the method **Ref.** since the upper bound is computed according to the actual distribution of the extinction date under the simulation model in this case. The closeness of the error percentage of the method **Int.** to the level of risk required suggests that integrating the extinction date distribution over all the possible FBD rates leads to accurate results. The error percentage obtained from the approach of Strauss and Sadler (1989) depends heavily on the fossil recovery rate and is far from the level of risk required when the fossil recovery rate is small, which certainly reflects the fact that it overestimates the upper bound of the extinction date in this situation (see Table 3 and below).

Fossilization rate	**S.S.**	**Ref.**		**Int.**	
0.005	244.02	26.07	*25.96*	26.71	*25.83*
0.01	181.15	21.74	*21.76*	21.82	*21.42*
0.1	50.46	9.20	*9.20*	9.06	*9.02*
1	6.26	2.23	*2.23*	2.22	*2.22*
5	0.91	0.56	*0.56*	0.56	*0.56*

Table 3: Mean confidence Interval width, i.e. the mean difference between the upper bounds provided by the three methods and the most recent fossil, on the simulated extinct taxa where the **S.S.** computation was feasible (plain text) and on all the extinct taxa (italic; only for methods **Ref.** and **Int.**).

As expected, the average difference between the upper bound provided by each method and the age of the most recent fossil, to which we refer to as the *mean confidence interval width*, tends to be reduced when the fossil discovery rate increases (Table 3). The mean confidence interval widths obtained with the method **Int.** are close to those obtained from the reference method **Ref.**, again supporting the relevance of our way of dealing with the uncertainty on the speciation, extinction and fossilization rates. The mean confidence interval widths provided by the approach of Strauss and Sadler (1989) are several times greater than those obtained with the reference method (we recall that the same order of confidence, i.e., 95%, is required for all the methods), notably when the fossil recovery rate is low. Namely, it is about ten times greater when the fossil discovery rate is 0.05, and is still almost twice as large for a fossilization rate of 5 (Table 3). Note that, for the fossilization rates 1 and 5, the error percentages obtained with the method of Strauss and Sadler (1989) are not significantly lower than those obtained with the methods **Ref.** and **Int.** (Table 2), despite the fact that its mean confidence interval widths are larger than those of these two methods.

The MCMC framework developed here gave us the opportunities to assess the accuracy of our approach to estimate the speciation, extinction and fossilization rates from a phylogenetic tree with extant and extinct taxa in which the only temporal information is given by the fossil ages (i.e., without the speciation dates). The results obtained are presented in Appendix C.

5 Results for the empirical example

The tree showing the probability density distributions of extinction times of the tips shows that many lineages of all three clades were probably extinct well before the Kungurian/Roadian boundary (Fig. 3). These individual extinction times are shown in greater detail in Figure 4. This shows, unsurprisingly, that for nearly all taxa, the peak extinction time probability is well before the Kungurian/Roadian boundary, and that the 95% confidence interval does not reach that boundary, in most cases. One obvious exception is *Dimetrodon angelensis*, the most recent taxon included in this study (from the San Angelo Formation of the Pease River Group). Its peak density is near the Kungurian/Roadian boundary, and the tail of the distribution suggests that it could have become extinct well into the Guadalupian. Despite this exception, our first hypothesis is confirmed; most lineages of the three clades appear to have become extinct before the end of the Kungurian. There results provide strong support for the first of our three hypotheses.

Our results show that the taxa Ophiacodontidae and Edaphosauridae were probably extinct by the end of the Kungurian or early in the Roadian because the 95% confidence interval on their extinction time only extends into the mid-Roadian (Fig. 5). Sphenacodontidae may well have become extinct later because the 95% confidence interval on its extinction time extends into the earliest Capitanian (Fig. 5); however, the peak probability of its extinction time is near the Kungurian/Roadian boundary, as for Ophiacodontidae and Edaphosauridae. Thus, our results provide weak support for our second hypothesis; while the probability that Ophiacodontidae and Edaphosauridae were extinct by the end of the Kungurian is high, the probability that Sphenacodontidae persisted into the Roadian appears fairly high.

Contrary to previous suggestions (Lucas, 2018, p. 430), Ophiacodontidae does not appear to have become extinct before Edaphosauridae; in fact our computations suggest the reverse, but the difference in timing is not statistically significant (the probability that Ophiacodon became extinct after Edaphosauridae is 0.558425), so these extinctions should provisionally be considered more or less simultaneous. However, the difference between extinction time of Sphenadocondidae and that of the other two clades is marginally significant; the probability that Sphenacodontidae became extinct after Ophiacodontidae is 0.945542, and for Edaphosaurida, this is 0.955989. Thus, we cannot confirm the third hypothesis; in fact, our results suggest that Ophiacodontidae may have become extinct slightly later than Edaphosauridae. However, one element of this hypothesis is confirmed: Sphenacodontidae does appear to have become extinct last.

6 Discussion

The simulation study shows that taking into account the diversification process and not only the fossilization events leads to upper bounds of extinction dates which are both tighter and more accurate than those obtained from the method of Strauss and Sadler (1989). Moreover, our approach allows to determine confidence upper bounds of the extinction time of taxa that have left very few or even a single fossil, a situation that is problematic for the method of Strauss and Sadler (1989).

Comparisons between extinction times of individual ophiacodontid, edaphosaurid and sphenacodontid species (Fig. 4) suggest that lineages of these three clades became extinct at various times, which is more consistent with a long crisis than a brief, catastrophic event. These lineage-specific extinction times do not suggest a discrete extinction event associated with the Artinskian/Kungurian boundary, but they are compatible with (without proving) a mild, diffuse crisis spanning much of the Artinskian and Kungurian, as suggested by Benton (1985, 1989) and by Brocklehurst *et al.* (2013). The extinction time of the most recent lineages of each clade and the extinction of the three large clades to which they belong (Fig. 5) reveals only very small differences. This suggests that in this case, the unobserved lineages (without a fossil record) of these clades did not add much to their stratigraphic extension toward the present. This was not entirely expected because Didier *et al.* (2017, p. 981) estimated that "only about 14% of the Permo-Carboniferous eupelycosaur lineages (defined as an internode on the tree) have left a fossil record." These findings rather support the first of the three hypotheses that we test here.

The finding that one of three clades studied here (Sphenacodontidae) has a fairly high probability of having become extinct in the Guadalupian may seem surprising at first sight, given the lack of records after the Kungurian. Even for Edaphosauridae and Ophiacodontidae, an extinction in the early Roadian

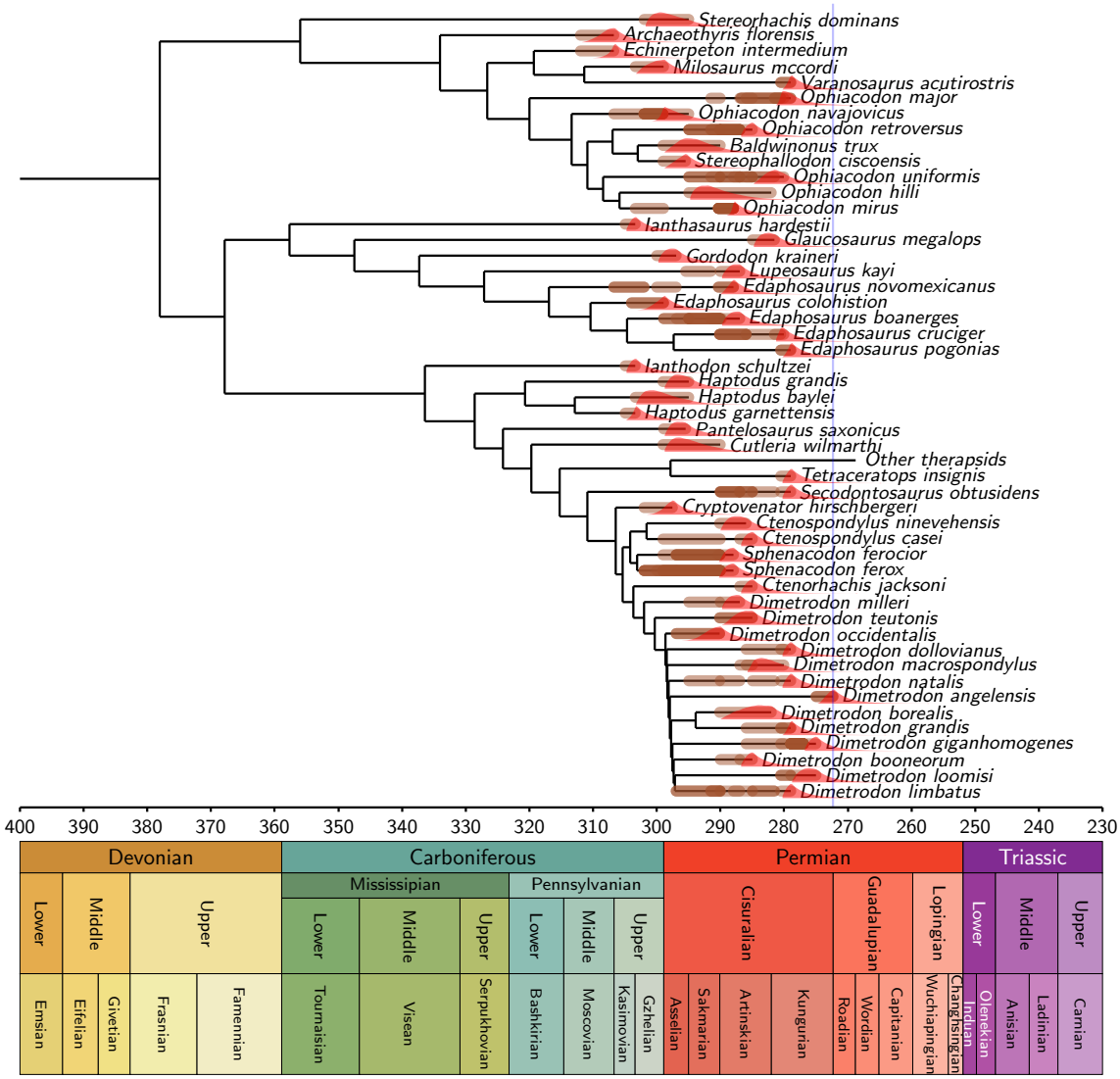

Figure 3: One of the 100 equally parsimonious trees of our dataset and the extinction time probability density distributions of its extinct taxa. The thin blue line represents the Kungurian/Roadian (Cisuralian/Guadalupian) boundary. Only the branch tips are time-calibrated; the position of nodes is arbitrary (here, most are too old). For a version of the tree with time-calibrated nodes, see Figure 7.

Figure 4: Extinction time probability density distributions of the extinct terminal taxa of our dataset. Extinction time probability density distributions of Ophiacodontidae, Edaphosauridae and Sphenacodontidae are drawn in purple, green and blue respectively. Other extinction time probability density distributions are drawn in orange. The colored part under each distribution starts at its 95% confidence upper bound. The thin vertical lines represent the Kungurian/Roadian (Cisuralian/Guadalupian) boundary.

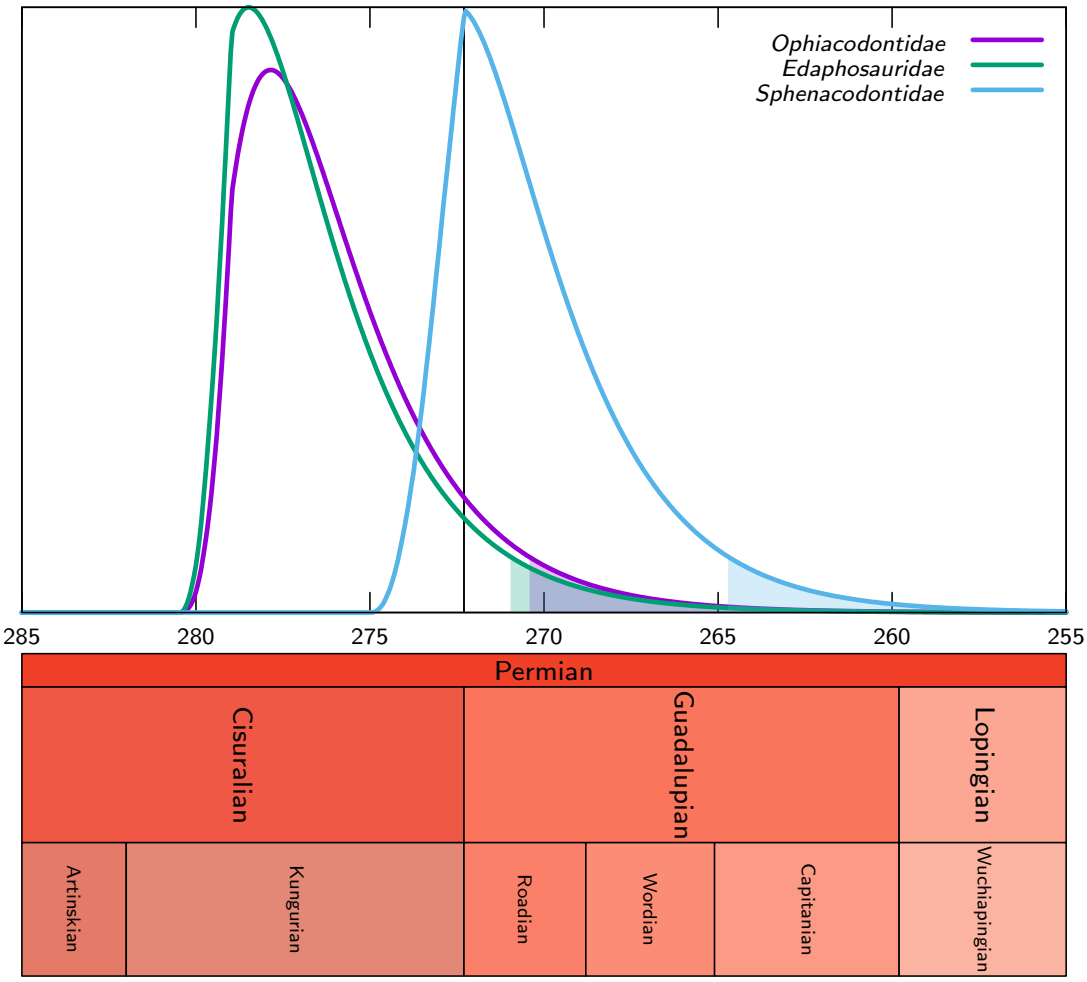

Figure 5: Probability density distributions of the extinction times of the clades Ophiacodontidae, Edaphosauridae and Sphenacodontidae of our dataset. The colored part under each distribution starts at its 95% confidence upper bound. The thin vertical line represents the Kungurian/Roadian (Cisuralian/Guadalupian) boundary.

cannot be ruled out because the 95% confidence interval of their stratigraphic range extends into the mid-Roadian. However, given the notorious incompleteness of the fossil record, it does seem plausible that these taxa could have survived in an area or an environment that did not yield fossiliferous strata. After all, caseids extend into the Roadian and varanopids survived until the Capitanian (Modesto *et al.*, 2011), but both are documented by a very sparse fossil record after the Cisuralian. The recent discovery of a late Permian diadectomorph from China (Liu and Bever, 2015) serves as a reminder that the fossil record can still yield surprising discoveries that refute a long-established consensus about the stratigraphic range of taxa; this taxon was previously thought to have become extinct toward the end of the Early Permian (Laurin, 2015). The recent discovery of two or three dinocephalian skulls that extend the *Tapinocephalus* AZ into the lowermost Poortjie Member of the Teekloof Formation also shows that even in a densely-studied, highly fossiliferous basin such as the Karoo, the delimitation of biozones defined by the extinction of a higher taxon (Dinocephalia is typically ranked as a suborder and considered to include three families) is not immune to revision (Day *et al.*, 2015b). A key element in the definition of the *Tapinocephalus* AZ is the absence (because of their extinction just before its base) of all dinocephalians. Our method could be used to assess the probability and magnitude of potential stratigraphic range extensions of taxa of various sizes, from single lineages to large clades, in addition to providing an additional statistical tool to better assess the evolution of biodiversity over time.

Our findings improve our understanding of the replacement of Permo-Carboniferous synapsids by therapsids in the Guadalupian. Therapsids must have originated in the late Carboniferous, as implied by their sister-group relationships with sphenacodontids (Reisz, 1986; Gauthier *et al.*, 1988; Sidor, 2001; Benson, 2012; Didier and Laurin, 2020) and by our new dating of the eupelycosaur evolutionary radiation (Fig. 7), and more specifically of the synapsid/therapsid divergence (Fig. 8). Yet, therapsids are unknown so far in the Carboniferous, and they may be represented by a single specimen of *Tetraceratops* in the Kungurian, even though its affinities are still debated (Amson and Laurin, 2011; Spindler, 2020), and we have not had time to reply to the latest comments on this point. The first undisputed therapsids date from the Roadian, but they become abundant only toward the end of the Roadian or in the early Wordian. Lozovsky (2005, p. 182) reported that therapsids barely make up about 5% of the Mezen (Roadian) fauna and that the obvious domination of therapsids only occurred in the Tatarian (which started in the Wordian), as preserved in the Ocher and Isheevo localities. According to Golubev (2015, fig. 2), the Ocher subassemblage is early Wordian and Isheevo extends from the late Wordian through the mid-Capitanian. Also, some fragmentary Roadian caseid remains had been misinterpreted as therapsids (Brocklehurst and Fröbisch, 2017). Thus, in the early Roadian, the replacement of Permo-Carboniferous clades of synapsids by therapsids had apparently barely started. The dynamics of biodiversity changes in synapsids similarly shows that therapsids surpassed geologically older synapsid clades in biodiversity sometime in the Roadian (Brocklehurst *et al.*, 2013, fig. 1). All this suggests a very slow initial therapsid diversification, but was the replacement of Permo-Carboniferous synapsids by therapsids competitive or not? Our findings shed new light on this question.

The extinction of Ophiacodontidae and Edaphosauridae near the Kungurian/Roadian boundary supports the hypothesis, recently proposed by Olroyd and Sidor (2017), that the replacement of Permo-Carboniferous synapsids by therapsids was non-competitive because the absence of definite therapsids in the Kungurian fossil record suggests that they remained rare by then. It is thus difficult to envision that they played a major role in the extinction of Ophiacodontidae and Edaphosauridae. The slightly later extinction date of Sphenacodontidae gives a more ambiguous signal on this point. They may also have died out before therapsids had become major competitors, as a literal reading of the Roadian fossil record suggests, but this is less certain. It is conceivable that the replacement of Permo-Carboniferous synapsids by therapsids was partly competitive (for sphenacodontids, and more likely, for caseids and varanopids, which are known to extend at least into the Roadian and Capitanian, respectively), and partly opportunistic, by filling the ecological vacuum left by the extinction of ophiacodontids and edaphosaurids. Nevertheless, our findings suggest that the exinction peak in Permo-Carboniferous clades (Olson's extinction) was near the Kungurian/Roadian boundary, rather than in the Roadian and Wordian, as suggested by Sahney and Benton (2008, p. 760).

We note that our denser sample of the fossil record yields younger divergence times for eupelycosaur clades (Fig. 7) than those of our previous study (Didier and Laurin, 2020). This was to be expected in particular because confidence intervals typically become narrower as sample size increases, and this phenomenon also applies to divergence times; as the fossil record becomes denser, our model adds less unobserved lineages below the first occurrence of a fossil on each lineage.

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A A Metropolis-Hastings importance sampling procedure for the distribution of the extinction times of an arbitrary subset of taxa

We aim to compute the joint probability of a tree $\mathcal{T}$ with fossils (without its divergence times), a fossil age vector $\mathbf{f}$ and its origin time, and that a particular subset S of (extinct at the present time) taxa of $\mathcal{T}$ goes extinct before a time t. Let us put η_S for the extinction time of the taxa in S and for all taxon n of S, $\ell_{\mathbf{f},n}$ for the age of its most recent fossil w.r.t. to the fossil age vector $\mathbf{f}$. The probability density of interest, $\mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_n \leq t)$, reads

$$\mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t) = \mathbf{P}(\mathcal{T}, \mathbf{f}) \prod_{n \in S} \frac{\mathbf{P}(0, t - \ell_{\mathbf{f},n})}{\mathbf{P}(0, T - \ell_{\mathbf{f},n})}.$$

The ratio $\frac{\mathbf{P}(0,t-\ell_{\mathbf{f},n})}{\mathbf{P}(0,T-\ell_{\mathbf{f},n})}$ means that we replace the factor contribution of the unobservable tree ending the evolution of taxon n in $\mathbf{P}(\mathcal{T}, \mathbf{f})$, which is the probability that it goes extinct before the present time, i.e., $\mathbf{P}(0, T - \ell_{\mathbf{f},n})$, by $\mathbf{P}(0, t - \ell_{\mathbf{f},n})$, which is the probability that it goes extinct before t.

The computation of the probability density above holds in the case where both the topology and the fossil ages are exactly known. In practice, there is a lot of uncertainty over these two features. In particular, our dataset contains a set Ω of equiparsimonious topologies and the only information about the age of each fossil f is provided as a geological age interval I_f. Given that with a tree $\mathcal{T} \in \Omega$ and a vector of fossil ages $\mathbf{f} \in \mathbf{I}$, we are able to compute the probability densities $\mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t)$ for all times t, determining distributions from our dataset may be performed by summing over all the topologies and integrating over all the time intervals.

We assume prior distributions in which (i) all the topologies in Ω are equiprobable and (ii) the fossil ages are uniformly distributed over their time intervals. We put $\mathbf{I}$ for the product-set of the time intervals $\mathbf{I} = \bigotimes_f \mathrm{I}_f$. The joint probability density above conditioned on the whole dataset is

$$\frac{\sum_{\mathcal{T} \in \Omega} \int_{\mathbf{I}} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t) \mathrm{d}\mathbf{f}}{\sum_{\mathcal{T} \in \Omega} \int_{\mathbf{I}} \mathbf{P}(\mathcal{T}, \mathbf{f}) \mathrm{d}\mathbf{f}} = \frac{\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t) \mathrm{d}\mathbf{f}}{\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}) \mathrm{d}\mathbf{f}}. \tag{2}$$

Since we have not closed formula for the quantities involved in the ratio above, it has to be numerically computed, for instance by uniformly sampling the fossil ages in $\mathbf{I}$. Being given N uniform samples of fossil age vectors $\mathbf{f}_1, \ldots, \mathbf{f}_N$, the estimated ratio is

$$\frac{\sum_{i=1}^{N} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t)}{\sum_{i=1}^{N} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}_i)}.$$

Unfortunately, because of its variance, the estimator above requires millions of samples to converge in our dataset. We tackle this issue in the same way as in Didier and Laurin (2020), that is by performing importance sampling (see, e.g., Robert and Casella, 2013). Briefly, an importance sampling procedure estimates the integral $\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_n = t) \mathrm{d}\mathbf{f}$ by sampling the fossil ages not uniformly but following a density $\mathrm{q}^\star$ biased toward the ages corresponding to high values of $\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_n = t)$. We have basically that

$$\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t) \mathrm{d}\mathbf{f} = \int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \frac{\mathbf{P}(\mathcal{T}, \mathbf{f}, \eta_S \leq t)}{\mathrm{q}^\star(\mathbf{f})} \mathrm{q}^\star(\mathbf{f}) \mathrm{d}\mathbf{f}.$$

It follows that if $\mathbf{f}'_1, \ldots, \mathbf{f}'_N$ are independently sampled from density $\mathrm{q}^\star$, this integral can be estimated by

$$\frac{1}{N} \sum_{i=1}^{N} \frac{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i, \eta_S \leq t)}{\mathrm{q}^\star(\mathbf{f}'_i)}.$$

As in Didier and Laurin (2020), by noting that $\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}', \eta_S \leq t)$ is bounded by (and strongly related to) $\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}')$, we consider a density $\mathrm{q}^\star(\mathbf{f})$ proportional to $\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f})$ for our importance sampling procedure. Namely, we set

$$\mathrm{q}^\star(\mathbf{f}') = \frac{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}')}{\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}) \mathrm{d}\mathbf{f}}.$$

Given N iid samples $\mathbf{f}'_1, \ldots, \mathbf{f}'_N$ obtained with the density $\mathrm{q}^\star$ just above, the ratio of Equation 2 is estimated by

$$\begin{aligned}
\frac{\frac{1}{N} \sum_{i=1}^{N} \frac{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i, \eta_S \leq t)}{\mathrm{q}^\star(\mathbf{f}'_i)}}{\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}) \mathrm{d}\mathbf{f}} &= \frac{1}{N} \sum_{i=1}^{N} \frac{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i, \eta_S \leq t)}{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i)} \\
&= \frac{1}{N} \sum_{i=1}^{N} \frac{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i) \prod_{n \in S} \frac{\mathbf{P}(0, t - \ell_{\mathbf{f}'_i, n})}{\mathbf{P}(0, T - \ell_{\mathbf{f}'_i, n})}}{\sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}'_i)} \\
&= \frac{1}{N} \sum_{i=1}^{N} \prod_{n \in S} \frac{\mathbf{P}(0, t - \ell_{\mathbf{f}'_i, n})}{\mathbf{P}(0, T - \ell_{\mathbf{f}'_i, n})}.
\end{aligned}$$

Since it is not possible to directly sample following the density $\mathrm{q}^\star$, which is known only up to the intractable normalization constant $\int_{\mathbf{I}} \sum_{\mathcal{T} \in \Omega} \mathbf{P}(\mathcal{T}, \mathbf{f}) \mathrm{d}\mathbf{f}$, we proceed in the same way as Didier and Laurin

(2020) by using the Metropolis-Hastings algorithm (e.g., Robert and Casella, 2013) to build a Markov chain with target density $\mathrm{q}^\star$. Let us recall the details of this procedure. Given the ith vector of fossil ages $\mathbf{f}'_i$ of this chain, we generate a candidate vector $\tilde{\mathbf{f}}$ first by uniformly selecting a fossil f among all the fossils of the dataset and by replacing the corresponding entry of $\mathbf{f}'_i$ by a uniform sample in the interval centered on this entry of width equal to α time the with of the interval I_f that represents the uncertainty on the age of fossil f (i.e., we use a usual sliding window proposal with reflection; α is a user-defined parameter). This proposal transition kernel is basically symmetrical, i.e., getting the candidate vector $\tilde{\mathbf{f}}$ from $\mathbf{f}'_i$ has the same probability as getting the candidate vector $\mathbf{f}'_i$ from $\tilde{\mathbf{f}}$. The next fossil age vector $\mathbf{f}'_{i+1}$ in the Markov chain is

$$\mathbf{f}'_{i+1} = \begin{cases} \tilde{\mathbf{f}} & \text{with probability } \min\left\{\dfrac{\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\tilde{\mathbf{f}})}{\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\mathbf{f}'_i)},1\right\} \text{ and} \\ \mathbf{f}'_i & \text{with probability } 1-\min\left\{\dfrac{\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\tilde{\mathbf{f}})}{\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\mathbf{f}'_i)},1\right\}. \end{cases}$$

In the case where the speciation, extinction and fossilization rates of the model are not given *a priori* (e.g., estimated by maximum likelihood), we sum over all their possible values by assuming that they all follow the improper uniform distribution over $[0,+\infty]$ and by following a similar importance sampling procedure. In plain English, the importance sampling is now performed over both the fossil age vector $\mathbf{f}$ and the model rates $\Theta=(\lambda,\mu,\psi)$ by using the biased density $\mathrm{q}^\star(\mathbf{f},\Theta)$ proportional to $\sum_{\mathcal{T}\in\Omega}\mathbf{P}_\Theta(\mathcal{T},\mathbf{f}')$, where $\mathbf{P}_\Theta(\mathcal{T},\mathbf{f}')$ is the probability of the phylogeny with fossils $\mathcal{T},\mathbf{f}'$ under the FBD model with rates $\Theta=(\lambda,\mu,\psi)$.

The proposal mechanism of the Markov chain used to sample according to this density first draws a Bernoulli random variable with a probability β (provided by the user) according to which either a change in a fossil age or a change in the speciation, extinction or fossilization rate is proposed. The change in a fossil age is proposed in the exact same way as just above. The change in a rate is proposed first by selected randomly the speciation, extinction or fossilization rate according to user-defined probabilities then by using a sliding window of fixed length centered on the current selected rate.

The densities presented in the results section were obtained from the MCMC procedure presented just above by discarding the first 10000 iterations, and by keeping only 1 iteration over 200 for the subsequent iterations. We consider a window of width equal to 80% of the length of the age interval I_f to propose a change in the age of fossil f and windows of size 0.5 to propose changes in the speciation, extinction and fossilization rates respectively. We propose a change in a fossil age with probability 0.75 and a change in the speciation, extinction or fossilization rate otherwise (the rate to be changed among the the speciation, extinction and fossilization rate is then drawn uniformly). We run the MCMC procedure until get 10000 iterations. The iterations thus obtained pass all the convergence tests of the `coda` R package with an effective size greater than 1000 for all the parameters (fossil ages and rates, Plummer *et al.*, 2006). All the parameters of the MCMC were manually tuned in order to get a satisfying behavior. They can be modified by calling the corresponding R function in the package.

B Probability that a subset of extinct taxa goes extinct before another

Let $\mathcal{T}$ be a tree with fossils (without its divergence times), $\mathbf{f}$ be a fossil age vector and A and B be two disjoint subsets of extinct taxa of $\mathcal{T}$ (e.g., two mutually exclusive extinct clades of $\mathcal{T}$). We aim here to compute the probability density $\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A\leq\eta_B)$, which is the joint probability density of the data $(\mathcal{T},\mathbf{f})$ and that the taxa of A go extinct before those of B.

We shall consider the same situation as in Appendix A and assume that data are provided as a set Ω of equiparsimonious trees and that the fossil ages are just bounded by geological intervals summarized in the product-set $\mathbf{I}$. The joint probability density above conditioned on the whole dataset is

$$\frac{\sum_{\mathcal{T}\in\Omega}\int_{\mathbf{I}}\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A\leq\eta_B)\mathrm{d}\mathbf{f}}{\sum_{\mathcal{T}\in\Omega}\int_{\mathbf{I}}\mathbf{P}(\mathcal{T},\mathbf{f})\mathrm{d}\mathbf{f}} = \frac{\int_{\mathbf{I}}\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A\leq\eta_B)\mathrm{d}\mathbf{f}}{\int_{\mathbf{I}}\sum_{\mathcal{T}\in\Omega}\mathbf{P}(\mathcal{T},\mathbf{f})\mathrm{d}\mathbf{f}}. \tag{3}$$

Let us first show how to compute $\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A\leq\eta_B)$. We recall that for all extinct taxa n, $\ell_{\mathbf{f},n}$ stands for the most recent fossil age of n and we put $\ell_{\mathbf{f},A\cup B}$ for the most recent age of fossils of $A\cup B$, i.e.,

$\ell_{\mathbf{f},A\cup B} = \max_{n\in A\cup B} \ell_{\mathbf{f},n}$. The probability density $\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq \eta_B)$ can be obtained by integrating over all the possible ages t of extinction of B, the joint probability density that B goes extinct exactly at t and A goes extinct before t. Note that the possible ages t such that B goes extinct exactly at t and A goes extinct before t run from $\ell_{\mathbf{f},A\cup B}$ to the present time T. Moreover, the probability density that B goes extinct exactly at t is the sum over all the taxa m of B of the probability densities that m goes extinct exactly at t and all the other taxa of B go extinct before t. It follows that the probability density $\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq \eta_B)$ can be written

$$\begin{aligned}
\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq \eta_B) &= \int_{\ell_{\mathbf{f},A\cup B}}^{T} \mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq t, \eta_B = t)\mathrm{d}t \\
&= \int_{\ell_{\mathbf{f},A\cup B}}^{T} \sum_{m\in B} \mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq t, \eta_{B\setminus\{j\}} \leq t, \eta_m = t)\mathrm{d}t \\
&= \frac{\mathbf{P}(\mathcal{T},\mathbf{f}) \sum_{m\in B} \int_{\ell_{\mathbf{f},A\cup B}}^{T} \left(\prod_{n\in A\cup B\setminus\{m\}} \mathbf{P}(0, t-\ell_{\mathbf{f},n})\right) \mathbf{D}(t-\ell_{\mathbf{f},m})\mathrm{d}t}{\prod_{n\in A\cup B} \mathbf{P}(0, T-\ell_{\mathbf{f},n})} \\
&= \frac{\mathbf{P}(\mathcal{T},\mathbf{f})\mathcal{I}_{\mathbf{f},A,B}}{\prod_{n\in A\cup B} \mathbf{P}(0, T-\ell_{\mathbf{f},n})},
\end{aligned}$$

where $\mathcal{I}_{\mathbf{f},A,B} = \sum_{m\in B} \int_{\ell_{\mathbf{f},A\cup B}}^{T} \left(\prod_{n\in A\cup B\setminus\{m\}} \mathbf{P}(0, t-\ell_{\mathbf{f},n})\right) \mathbf{D}(t-\ell_{\mathbf{f},m})\mathrm{d}t$.

Since we assume here that the extant sampling parameter $\rho = 1$, Equations 1 give us that

$$\mathcal{I}_{\mathbf{f},A,B} = \sum_{m\in B} \int_{\ell_{\mathbf{f},A\cup B}}^{T} \left(\prod_{n\in A\cup B\setminus\{m\}} \frac{\alpha\beta(1-\mathrm{e}^{\omega(t-\ell_{\mathbf{f},n})})}{\beta-\alpha\mathrm{e}^{\omega(t-\ell_{\mathbf{f},n})}}\right) \frac{\mu(\beta-\alpha)^2\mathrm{e}^{\omega(t-t_m)}}{(\beta-\alpha\mathrm{e}^{\omega(t-t_m)})^2}\mathrm{d}t.$$

A tedious calculation leads to

$$\begin{aligned}
\mathcal{I}_{\mathbf{f},A,B} = \beta(\beta-\alpha) \sum_{m\in B} &\left(\sum_{n\in A\cup B\setminus\{m\}} \frac{(\beta-\alpha)\Upsilon_{\mathbf{f},m,n}}{1-\mathrm{e}^{\omega(\ell_{\mathbf{f},m}-\ell_{\mathbf{f},n})}} - \beta^{|A\cup B|-1}\right) \left[\frac{1}{\beta-\alpha\mathrm{e}^{\omega(t-\ell_{\mathbf{f},m})}}\right]_{\ell_{\mathbf{f},A\cup B}}^{T} \\
- (\beta-\alpha)^2 \sum_{m\in B} \sum_{n\in A\cup B\setminus\{m\}} &\frac{\Upsilon_{\mathbf{f},m,n}\mathrm{e}^{\omega(\ell_{\mathbf{f},m}-\ell_{\mathbf{f},n})}}{(1-\mathrm{e}^{\omega(\ell_{\mathbf{f},m}-\ell_{\mathbf{f},n})})^2} \left[\log\left(1+\frac{\alpha(1-\mathrm{e}^{\omega(\ell_{\mathbf{f},m}-\ell_{\mathbf{f},n})})}{\beta\mathrm{e}^{\omega(\ell_{\mathbf{f},m}-t)}-\alpha}\right)\right]_{\ell_{\mathbf{f},A\cup B}}^{T},
\end{aligned}$$

where

$$\Upsilon_{\mathbf{f},m,n} = \prod_{k\in(A\cup B)\setminus\{m,n\}} \frac{\beta-\alpha\mathrm{e}^{\omega(\ell_{\mathbf{f},k}-\ell_{\mathbf{f},n})}}{1-\mathrm{e}^{\omega(\ell_{\mathbf{f},k}-\ell_{\mathbf{f},n})}}.$$

We thus have an explicit formula to compute $\mathbf{P}(\mathcal{T},\mathbf{f},\eta_A \leq \eta_B)$ which can be used in the importance sampling procedure presented in Appendix A to estimate the probability that the subset A goes extinct before B. Namely, if $\mathbf{f}'_1, \ldots, \mathbf{f}'_N$ are N iid samples of density $\mathrm{q}^\star$, the ratio of Equation 3 is estimated by

$$\begin{aligned}
\frac{\frac{1}{N}\sum_{i=1}^{N} \frac{\sum_{\mathcal{T}\in\Omega} \mathbf{P}(\mathcal{T},\mathbf{f}'_i,\eta_A\leq\eta_B)}{\mathrm{q}^\star(\mathbf{f}'_i)}}{\int_{\mathbf{I}} \sum_{\mathcal{T}\in\Omega} \mathbf{P}(\mathcal{T},\mathbf{f})\mathrm{d}\mathbf{f}} &= \frac{1}{N}\sum_{i=1}^{N} \frac{\sum_{\mathcal{T}\in\Omega} \mathbf{P}(\mathcal{T},\mathbf{f}'_i,\eta_A\leq\eta_B)}{\sum_{\mathcal{T}\in\Omega} \mathbf{P}(\mathcal{T},\mathbf{f}'_i)} \\
&= \frac{1}{N}\sum_{i=1}^{N} \frac{\mathcal{I}_{\mathbf{f}'_i,A,B}}{\prod_{n\in A\cup B} \mathbf{P}(0, T-\ell_{\mathbf{f}'_i,n})}.
\end{aligned}$$

C Posterior probability density distributions of speciation, extinction and fossilization rates from the simulation study

Figure 6 displays the aggregated posterior densities of the speciation, extinction and fossilization rates corresponding to the five runs of simulations presented in Section 4. Let us recall that we performed five runs of 1000 simulations, all with speciation and extinction rates 0.2 and 0.19 and with fossilization

rates 0.005, 0.01, 0.1, 1 and 5 respectively. For each of the five fossilization rates, we plotted the average posterior density of the speciation, extinction and fossilization rates over the 1000 simulated trees.

We observe that each density is roughly centered on the corresponding rate value used to simulate the data and that the distributions of the speciation and extinction rates become tighter as the fossilization rate increases.

D Divergence time and posterior probability density distributions from the empirical dataset

D.1 Probability density distributions of divergence times

We applied the approach presented in Didier and Laurin (2020) to the empirical dataset used here to compute the divergence time densities of the tree displayed in Figure 4. Figure 7 displays this tree with the divergence time densities associated to all its internal nodes. The denser fossil record and our revisions of the ages of fossils based on recent literature yields slightly more recent divergence times (Fig. 7) than our previous study (Didier and Laurin, 2020, fig. 6).

Figure 8 presents the probability density of the divergence time between therapsids and sphenacontids. Didier and Laurin (2020) estimated that the divergence between sphenacodontids and therapsids dated from about 313 Ma (early Moscovian), but our current analysis places this divergence closer to 301 Ma, in the mid-Gzhelian (Fig. 8).

D.2 Posterior probability density distributions of rates and fossil ages

Figure 9 displays some posterior probability density distributions obtained from the MCMC sampling used to compute Figure 8. Since the fossil ages are given as time intervals in the empirical dataset, they have to be sampled as presented in Appendix A. On top of the posterior distributions of the speciation, extinction and fossilization rates, we plotted those of a selection of fossil ages. Among these, we first observe that, though two fossils of *Dimetrodon limbatus* are associated to the time interval $(297, 290)$, the posterior densities of their age are negligible for ages greater than 293 Ma. Since the posterior density associated to an age value is proportional to the density of the phylogenetic tree when the corresponding fossil age is set to this value, this explains why the density of the speciation time of this taxon is negligible before 293 Ma, as shown in Figure 7. The posterior probability density distributions of fossils ages show various shapes. In particular, unlike that of *Dimetrodon limbatus*, some of them are almost uniform (e.g., that of *Tetraceratops insignis*).

Figure 9 shows that the posterior density of the fossilization rate supports rates about ten times higher than those observed with our dataset of Didier and Laurin (2020). This presumably reflects the incorporation of a fairly large amount of fossil occurrence data from the Paleobiology Database, which resulted in the incorporation of many additional occurrences of several taxa (but no additional taxa), as well as the more recent divergence times, which result in shorter branches. The slightly lower speciation and extinction rates observed in Figure 9 may simply reflect the fact that the taxonomic sample is not the same (the current study focuses on a subset of the clades included in our previous studies).

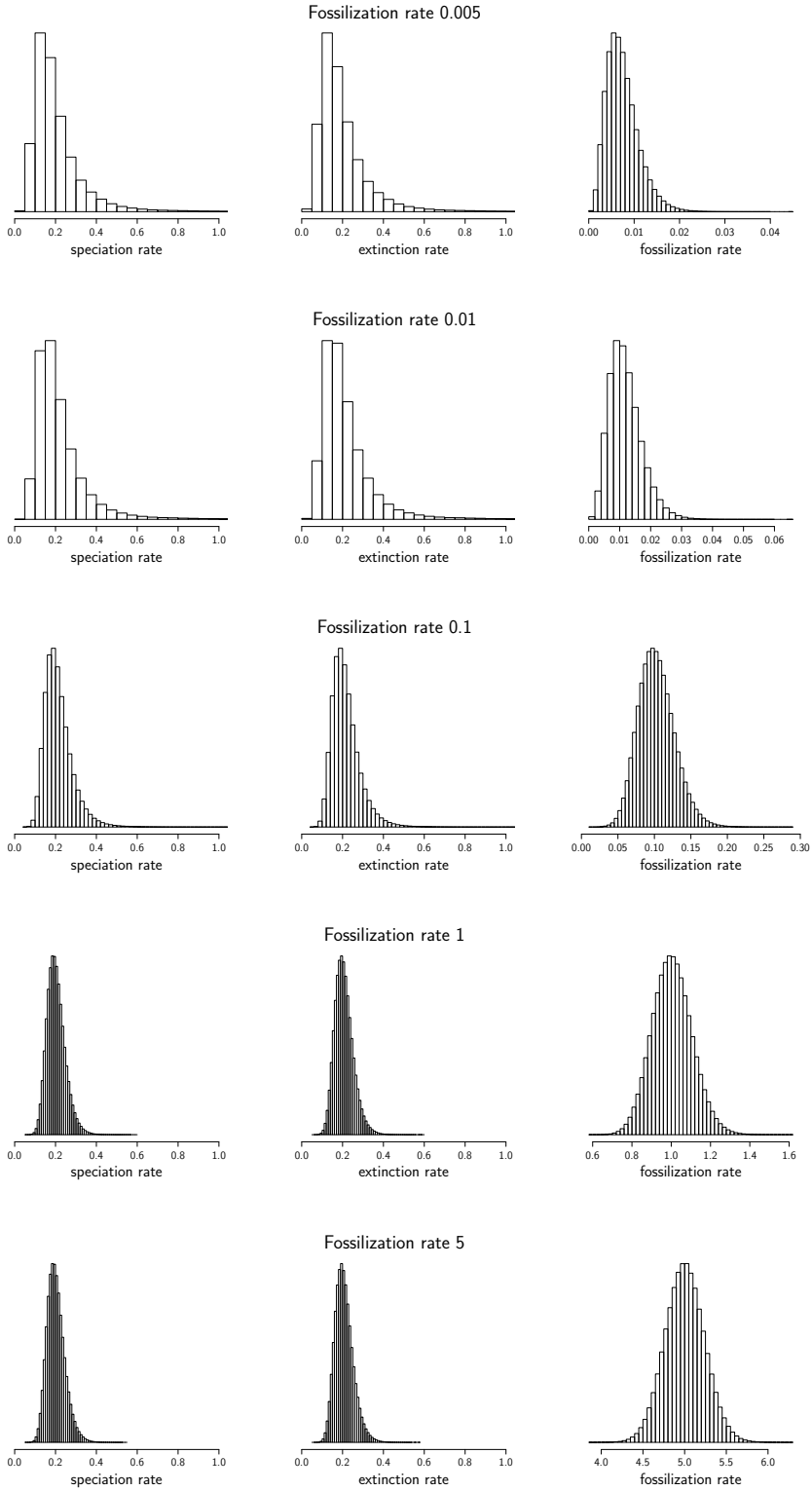

Figure 6: Posterior probability density distributions of the speciation, extinction and fossilization rates obtained from the MCMC procedure used to compute the upper bounds of extinction dates with the method **Int.** (i.e., when the FBD rates are unknown) in our simulation study.

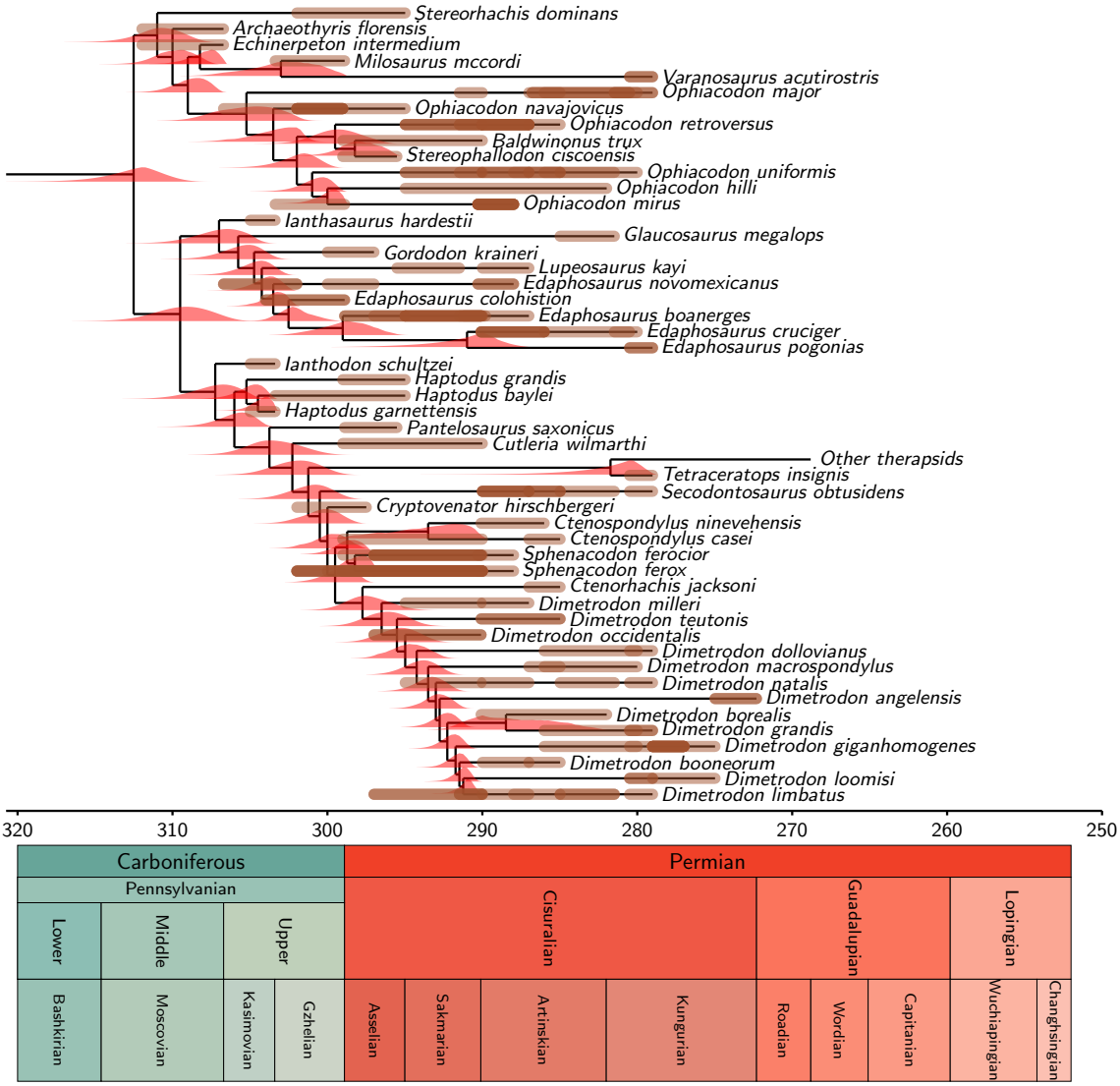

Figure 7: One of the 100 equally parsimonious trees of our dataset with the probability density distributions of its speciation times. The confidence interval on some fossil records extends below their basal node, most noticeably for *Dimetrodon limbatus*. With this tree topology, the oldest part of the range of possible ages of fossils of some taxa leads to very low probability densities of the whole tree with fossil; thus, it does not contribute significantly to the speciation time density distributions (Fig. 9). All nodes are older than the minimal age of all fossils, as they should be.

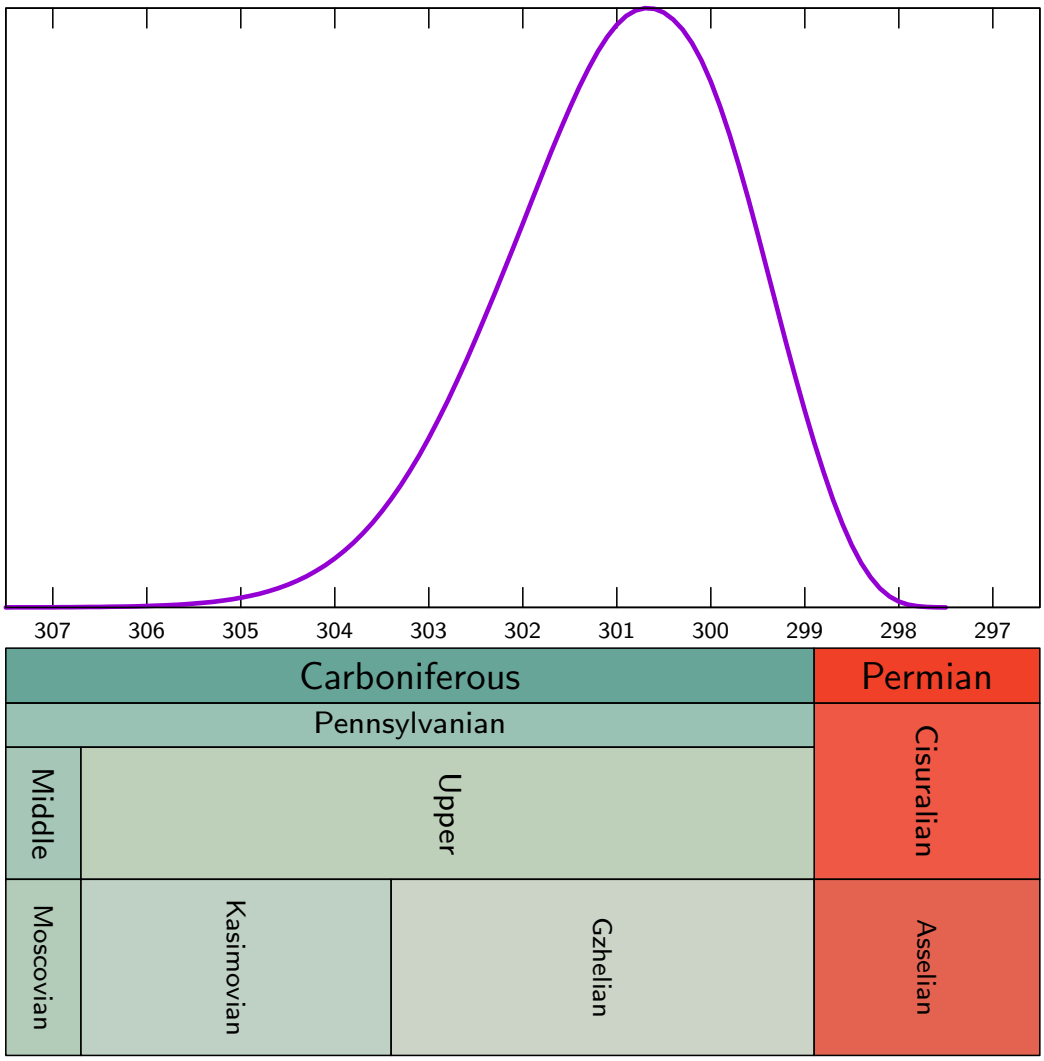

Figure 8: Probability density distribution of the age of the divergence between therapsids and sphenacontids.

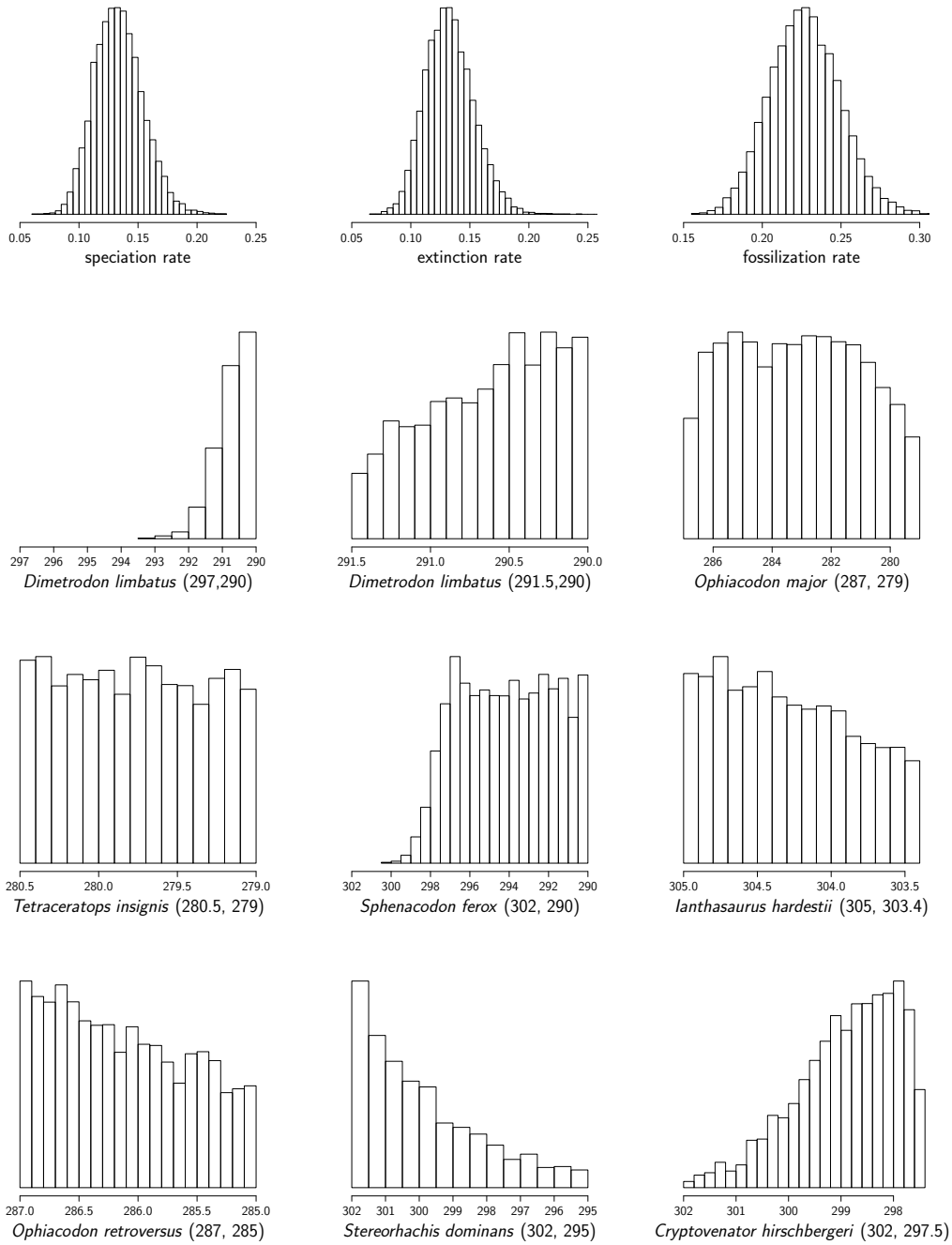

Figure 9: Posterior probability density distributions of the speciation, extinction and fossilization rates and of a selection of fossil ages obtained from the MCMC sampling used to compute the speciation distribution of Fig. 8.