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Assessing the effect of sampling proxies on plesiosaur taxic diversity with comments on implications for Mesozoic sampling design

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Abstract

The fossil record of plesiosaurs, while extensive, is strongly affected by geological and anthropogenic biases that may obscure true diversity patterns. This study evaluates the influence of rock availability and sampling effort on taxic diversity estimates (TDE) of plesiosaurians throughout the Mesozoic period and proposes a method for determining priority stages for future fossil sampling. Two primary proxies—the number of fossiliferous marine formations (FMF) and fossil marine collections (FMC)—are considered. Our findings indicate that neither FMF nor FMC alone accounts for observed diversity peaks and troughs in plesiosaurian TDE. To address this, we integrate phylogenetic diversity estimates (PDE) into our framework, using the difference between PDE and TDE (i.e., phylogenetic residuals) to identify stratigraphic stages where recorded diversity likely underrepresents true lineage richness. This combined approach reveals that some previously recognized declines in TDE—such as during the Berriasian—are consistent with low sampling proxy values and may reflect genuine sampling bias. In contrast, other intervals, particularly the Aalenian–Bathonian, Valanginian and Coniacian ages, exhibit low TDE despite limited rock and collection data but high phylogenetic residuals, highlighting them as high-priority targets for future paleontological fieldwork. These stages represent critical intervals for testing the consistency between diversity models based on sampling proxies and phylogenetically inferred diversity trends.

Key Words

Marine formations, phylogenetic diversity, phylogenetic residuals, plesiosauria, sampling bias, sampling proxies, taxic diversity

Introduction

Plesiosaurians are a clade of diapsid marine reptiles with an extensive fossil record, spanning from the latest Triassic to the final extinction at the end of the Cretaceous (Rieppel 2000; Ketchum and Benson 2010; Wintrich et al. 2017). They represent one of the most successful radiations into the marine realm among reptiles (Motani and Vermeij 2021; Gutarra et al. 2023), occupying a wide range of ecological niches (Stubbs and Benton 2016; O'Keefe et al. 2017; Madzia and Cau 2020; Reeves et al. 2021). Throughout their evolutionary history, the group experienced substantial shifts in diversity identified in several studies (Bakker 1993; Benson et al. 2010, 2012; Bardet et al. 2014; Benson and Druckenmiller 2014; Foffa et al. 2018). However, the estimation of plesiosaurian diversity based solely on the direct evaluation of the fossil record could generate misleading conclusions, as they do not account for biases associated with sampling proxies (e.g., rock availability, collection effort). Although previous studies have attempted to evaluate the influence of these sampling biases on Mesozoic marine reptiles, they have typically focused on broader clades such as Sauropterygia or marine reptiles as a whole (Benson et al. 2010; Benson and Butler 2011). Subsequent research on plesiosaurians has instead examined specimen completeness across their evolutionary history (Tutin and Butler 2017) or investigated the evolution of skeletal paedomorphosis within the clade (Araújo and Smith 2023), but no specific analyses have tested how much the rock availability or collection effort can explain the variations in taxic diversity estimates (TDE) through plesiosaurians' history.

Any attempt to deal with the previous questions has to take into account that the fossil record is inherently incomplete and unevenly sampled (Raup 1976; Alroy 2010; Dunhill et al. 2012). These biases include both geological constraints (e.g., availability of sedimentary rock outcrops, facies type and Lagerstätten effects), and collecting factors (e.g., variation in human collecting effort) all of which can distort or obscure macroevolutionary patterns (Sepkoski 1976; Sheehan 1977; Crampton et al. 2003; Peters 2005; Wall et al. 2009; Mannion et al. 2014; Walker et al. 2017). In response to these issues, several methods have been developed to assess the patchiness of the fossil record when analyzing patterns of diversity through time (Alroy et al. 2001; Smith and McGowan 2007; Loyd 2012).

One widely applied method is the residual-based correction of Smith and McGowan (2007), which models expected diversity based on a sampling proxy and interprets the residuals as reflecting genuine biological variation. This method has been widely applied across different taxonomic groups (Barrett et al. 2009; Butler et al. 2009; Benson et al. 2010; Mannion et al. 2011, 2012; Smith et al. 2012; Brocklehurst et al. 2013; Fröbisch 2013; Walther and Fröbisch 2013; Newham et al. 2014; Minter et al. 2017; Capel et al. 2022). However, this method has been subject to significant criticism. Simulation-based analyses by Brocklehurst (2015) demonstrated that residuals' diversity estimates (RDE) often fail to reliably recover true diversity patterns, particularly when polynomial models or narrow proxies are used. Moreover, Sakamoto et al. (2016) emphasized that artificially pairing unassociated x and y values is statistically problematic, as it decouples an inherently bivariate dataset. Such forced pairings lack a natural interpretation, and as a result, fitting models to these decoupled data can produce spurious predictions and misleading residuals.

In accordance with the previous comments, here we estimate the expected diversity based on sampling proxies using alternative statistical models. Following the recommendations of Sakamoto et al. (2016), we avoid forced pairings and instead implement a generalized linear modeling framework that preserves the inherent bivariate relationships. This comparative framework allows us to identify diversity peaks and troughs that cannot be fully accounted for rock availability (FMF, fossiliferous marine formations) or sampling effort (FMC, fossil marine collections), highlighting intervals that may reflect genuine palaeobiological signals. Additionally, as a parallel approach we use the difference between phylogenetic diversity estimates (PDE) and taxic diversity estimates (TDE) called phylogenetic residuals to explore the supposed diversity not recorded until now but inferred based on the phylogeny. This general approach avoids the methodological pitfalls outlined by Sakamoto et al. (2016), while still allowing the identification of potentially under-sampled intervals worthy of further investigation.

In summary, this study aims to evaluate to what extent the rock availability and sampling effort have shaped the plesiosaurian TDE trends throughout the Mesozoic and to determine whether fluctuations in plesiosaurian TDE could be explained solely by geological and anthropogenic biases. Moreover, by integrating phylogenetic residuals with these sampling proxies, we aim to identify stratigraphic "hot spots" of undiscovered diversity and propose a framework to prioritize future fieldworks in time intervals and regions that may yield significant plesiosaurians' discoveries.

Abbreviations. — **FMC**, fossil marine collections; **FMF**, fossiliferous marine formations; **MDE**, modelled diversity estimate; **PDE**, phylogenetic diversity estimate; **RDE**, residual diversity estimate; **TDE**, taxic diversity estimate.

Materials and methods

To ensure consistency in the estimation of taxic and phylogenetic diversity estimates (TDE and PDE, respectively), we used the plesiosaurian dataset provided by O'Keefe et al. (2025), data available in Suppl. material 1.

Sampling biases on taxic diversity

To assess the influence of sampling biases on this observed diversity, we applied three statistical models in order to estimate the expected diversity based on a regression between plesiosaurians TDE and sampling proxies. First, a simple linear regression of TDE against sampling proxies was performed but, since diversity measures are counts, we also tested Poisson and negative binomial models which are more appropriate for this kind of data (O'Hara and Kotze 2010; Sakamoto et al. 2016). The best-fitting model was selected using the Akaike Information Criterion (AIC) (Johnson and Omland 2004), and modelled diversity estimates (MDE) were generated accordingly. Residual diversity estimate (RDE) was then calculated as the difference between observed and modelled diversity (log RDE = log TDE – log MDE), representing the portion of diversity not attributable to sampling biases and interpreted as a proxy for genuine ancient biodiversity (Butler et al. 2009; Mannion et al. 2012). In this case, positive/negative residuals indicate diversity values that are higher/lower than expected given the sampling proxy, suggesting possible biological signals not accounted for by sampling alone. This method was applied using the software R (v4.4.3) (R Core Team 2025) (see Suppl. material 2).

Two global sampling metrics were used as proxies to account for sampling biases: number of fossiliferous marine formations (FMF) and number of fossil marine collections (FMC). Although the use of formations as a sampling proxy has been subject to several criticisms (Dunhill et al. 2014, 2018), including their arbitrary stratigraphic definitions, potential dependence on fossil occurrence data, sensitivity to time-bin duration, and limited ability to account for collection effort, taphonomic biases, or rock availability (Miller and Foote 1996; Crampton et al. 2003; Peters and Heim 2010; Benton et al. 2011; Benton 2012), formations' counts remain one of the most widely used and accessible proxies for temporal sampling variation (Peters and Foote 2001; Fröbisch 2008; Barrett et al. 2009; Butler et al. 2009; Marx 2009; Benson et al. 2010; Mannion et al. 2011; Benson and Upchurch 2012). We chose to use FMF in our study because it is an objective and simple metric, readily available through the Paleobiology Database (PBDB) and bibliographic sources, and easily updated. Furthermore, FMF counts represent the cumulative efforts of numerous researchers over time, which can help offset individual sampling biases and facilitate comparability across datasets and taxa. As was mentioned, FMC in each time bin were considered as a proxy more focused on human sampling effort (Alroy et al. 2001; Crampton et al. 2003; Upchurch et al. 2011; Butler et al. 2012; Benson et al. 2013b). Data on FMC and FMF was downloaded from the PBDB (http://paleodb.org) on June 26th, 2025 (see Suppl. material 1). It is important to note that FMF and FMC were used as sampling proxies encompassing the broader marine fossil record, providing a more comprehensive estimate of sampling effort and minimizing the risk of redundancy (Benton et al. 2011; Upchurch et al. 2011; Brocklehurst 2015). These proxies also account for non-occurrences, as they include instances where marine rocks have been searched but no plesiosaurian fossils were recovered (Brocklehurst et al. 2013).

In both sampling proxy analyses (FMF and FMC), the best-fitting model selected via Akaike Information Criterion (AIC) was the negative binomial model. This model is particularly suitable for our dataset, as it appropriately accounts for the overdispersion observed (O'Hara and Kotze 2010).

Phylogenetic residuals and sampling design

An alternative way to assess residuals is by calculating them as the difference between phylogenetic diversity estimates (PDE) and taxic diversity estimates (TDE), using the formula phylogenetic residuals = PDE - TDE. These residuals are always positive, as TDE represents a minimum estimate of true biodiversity, being directly tied to an often incomplete and biased fossil record (Pol and Leardi 2015). In contrast, PDE tends to yield higher values because it incorporates ghost lineages (Norell 1992; Norell and Novacek 1992), thus partially compensating for the gaps in the fossil record. The phylogenetic hypotheses used to compute TDE and PDE are based on the comprehensive matrix published by O'Keefe et al. (2025), which is based on Benson and Druckenmiller (2014) and Serratos et al. (2017), with several modifications (Fischer et al. 2018; Morgan and O'Keefe 2019; O'Gorman 2019; O'Gorman et al. 2021, 2023).

The complete data set comprises 130 OTUs and 290 characters compiled using Mesquite v.3.81 (Maddison and Maddison 2011) and is provided in Suppl. material 3. The phylogenetic analysis was carried out in TNT v.1.6 (Goloboff et al. 2008; Goloboff and Morales 2023) with maximum parsimony criteria, using New Technology Search (sectorial search activated: 1,000 random additional sequences with trees collapse, tree fusing activated with the default settings options, ratchet and drift not activated). Tree bisection-reconnection (TBR) algorithm was then applied for most parsimonious trees (MPT´s), and the consensus was scaled using an 'equal' method of branch length reconstruction with the timePaleoPhy function on the paleotree package (Bapst 2012). Stratigraphic calibration was performed using the FAD–LAD dataset provided in Suppl. material 4. Wildcard taxa were retained in order to preserve the integrity of taxic and phylogenetic diversity estimates (TDE and PDE). Nevertheless, polytomies were randomly resolved during the time-calibration process to avoid artificially inflating in PDE (see Suppl. material 2).

Stages levels were then plotted considering its phylogenetic residuals and sampling proxies (FMF and FMC) to assess future sampling designs. The plot was subdivided into four quadrants using the mean values of each proxy as thresholds to distinguish areas of high, median and low priority categories. Stages characterized by high phylogenetic residuals but low rock availability/research effort (FMF/FMC) may represent promising targets for future fieldwork, while stages with low phylogenetic residuals and high number of FMF and FMC likely reflect well-sampled intervals with limited additional diversity to be uncovered. Additionally, the geographical distribution of FMF associated with high, medium, and low priority stages was mapped to illustrate the spatial occurrence and to identify possible geographic biases of outcrops corresponding to each priority level (see Suppl. material 2). This framework enables the identification of stratigraphic "hot spots" of potential hidden diversity and provides a data-driven basis for optimizing future sampling strategies.

Results

Fig. 1 shows the temporal distribution of fossiliferous marine formations (FMF) and fossil marine collections (FMC) for plesiosaurians biochron. Despite some discrepancies, their overall trends are broadly similar with a general correspondence across many stages (Fig. 1), which is consistent with previously documented correlations between these sampling proxies in marine vertebrate studies (Benson et al. 2010; Benson and Butler 2011; Cleary et al. 2015). Both sampling proxies show a peak during the Pliensbachian and Toarcian stages, followed by a marked decline in the Aalenian and a gradual recovery throughout the Middle and Upper Jurassic (Fig. 1). In the Lower Cretaceous, values remain relatively low until a steady increase begins in the Aptian stage. This is followed by a decrease during the Turonian stage and a pronounced trough in the Coniacian stage, likely influenced by the duration of these intervals. Finally, both proxies reach a prominent peak in the Campanian, followed by a gradual decline in the Maastrichtian (Fig. 1). Notably, during the Pliensbachian–Toarcian the FMC peak is relatively more marked than the FMF ones.

Results for sampling biases on taxic diversity

A negative binomial model between each sampling proxy (FMF and FMC) and TDE was best supported following the AIC criterion (see formulae on Suppl. material 2). The primary peaks and troughs in taxic diversity estimates (TDE) for plesiosaurians show some correlation with rock availability (FMF) and collection effort (FMC), but at least some of these TDE peaks cannot be fully explained by these proxies (Fig. 2). In the FMF-based

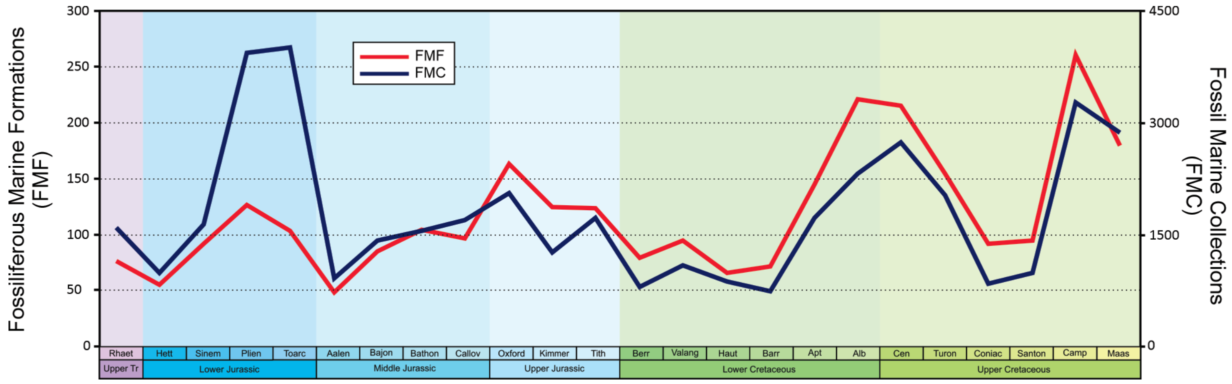

Figure 1. Fossiliferous marine formations (FMF) and fossil marine collections (FMC) plotted against stage level.

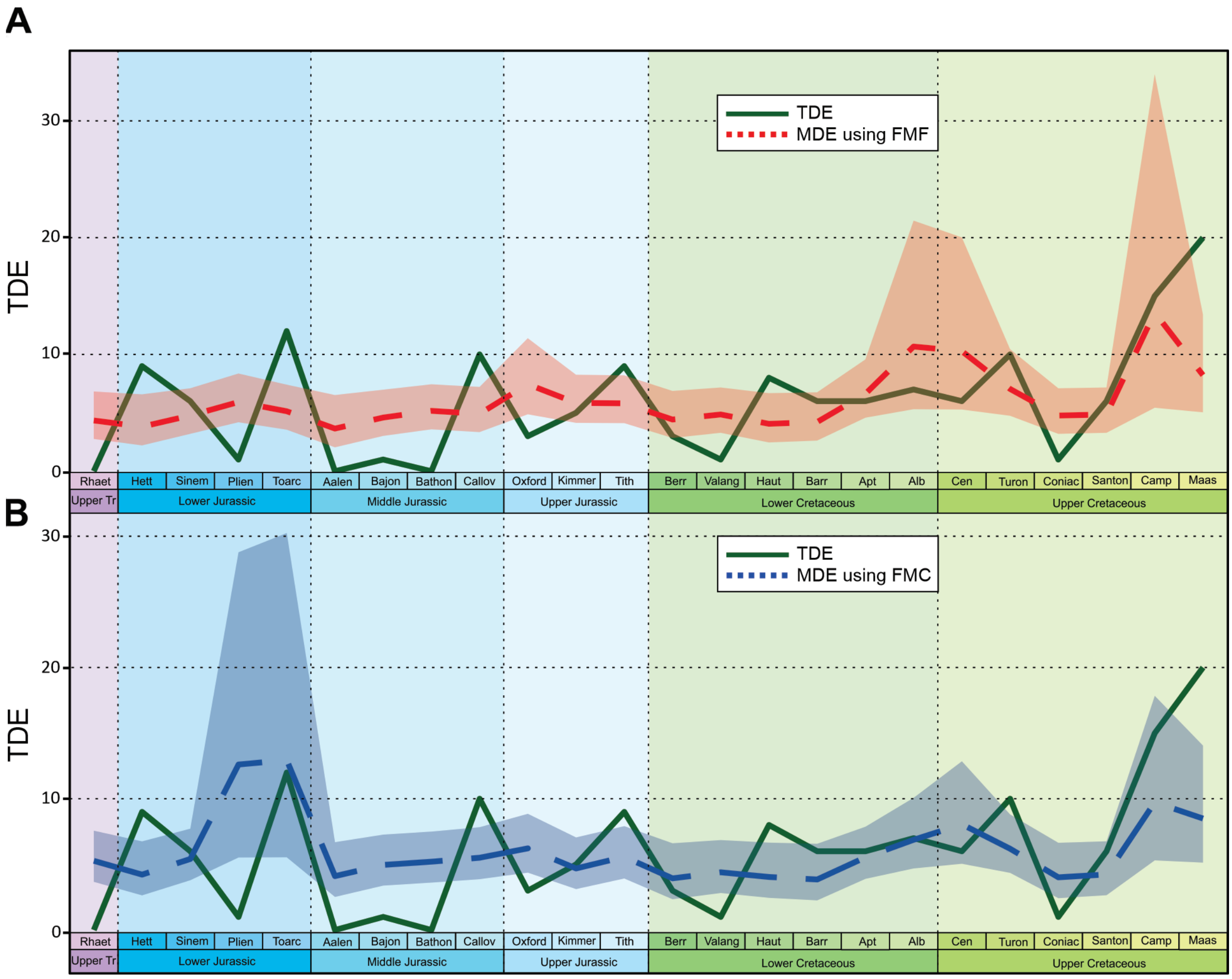

Figure 2. Taxic diversity estimates (TDE) vs. Modelled diversity estimates (MDE) against geological time (stage names abbreviated), using FMF (**A**) and FMC (**B**) as sampling proxies. Green line shows observed TDE, while MDE using FMF and MDE using FMC are in red and blue dashed lines, respectively, with 95% confidence intervals.

model, TDE is notably higher than the MDE during the Hettangian, Toarcian, Callovian, Tithonian, Hauterivian and Maastrichtian stages (Fig. 2A). In contrast, observed diversity (TDE) is significantly lower than expected (MDE) in the Rhaetian, Pliensbachian, Aalenian, Bajocian, Bathonian, Oxfordian, Valanginian, and Coniacian stages. For the remaining stages—Sinemurian, Kimmeridgian, Berriasian, Barremian, Aptian, Albian, Cenomanian, Turonian, Santonian, and Campanian—observed diversity (TDE) closely matches the model predictions (Fig. 2A).

When using FMC, the overall pattern is similar, although there are notable differences in some intervals. Particularly, the Toarcian stages fall within the confidence interval, whereas the Turonian fall above it (Fig. 2B).

Results for phylogenetic residuals and sampling design

The initial phylogenetic analysis of Plesiosauria using Tree New Technology recovered three MPT's with 2,002 steps. The TBR branch swapping on the resulting trees yielded + 20,000 MPT´s with an identical step count. A consensus tree was then made to calculate TDE and PDE (Fig. 3), and phylogenetic residuals are provided in the Suppl. material 1.

To facilitate interpretation, stage-level phylogenetic residuals were plotted against the sampling proxies (FMF and FMC). In the analysis where FMF was used as proxy (Fig. 4A) the high priority stages (proxies higher than the 50% of total) were the Rhaetian, Lower Jurassic epoch,

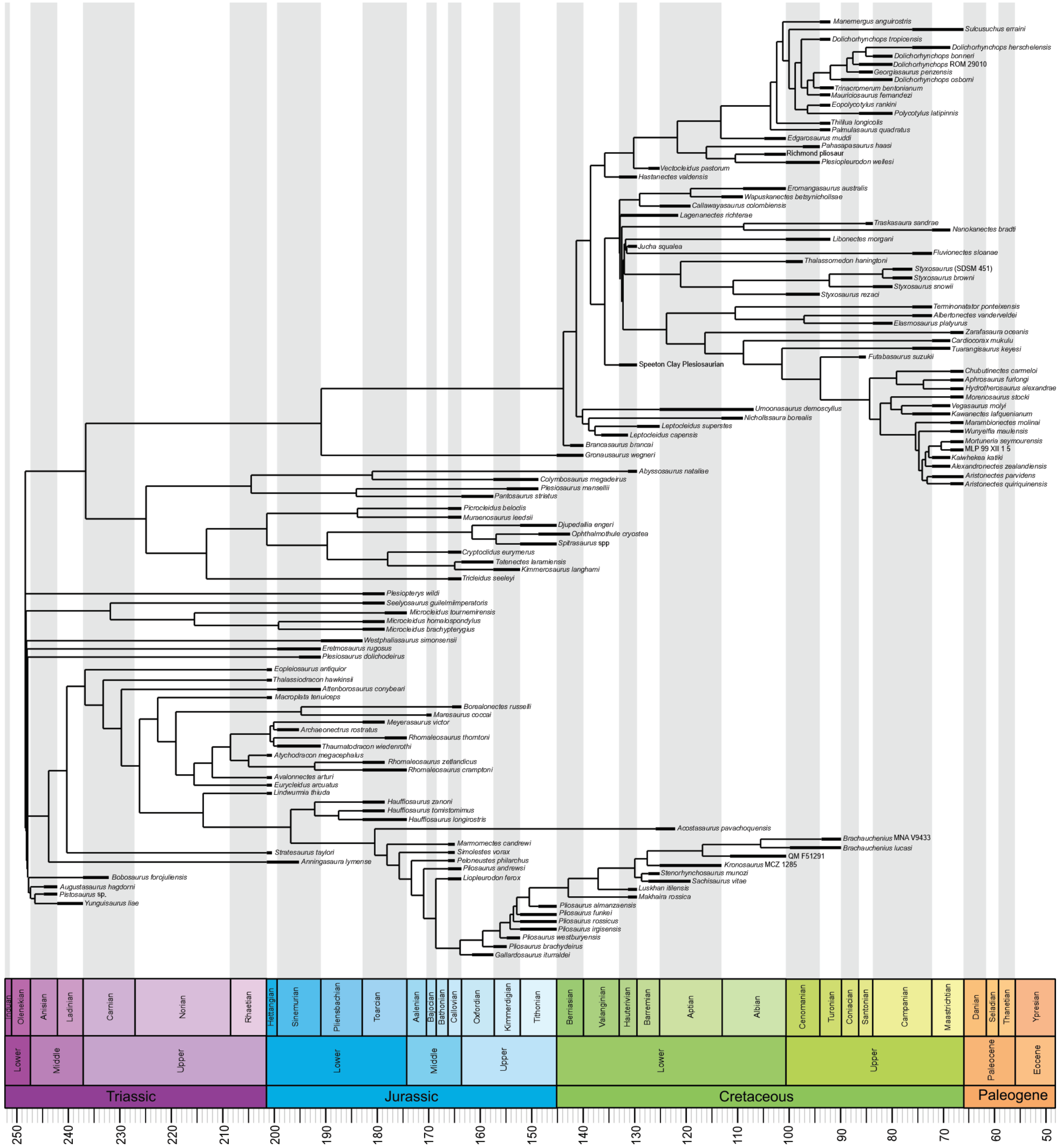

Figure 3. Time-scaled phylogeny of plesiosaurians arising from maximum parsimony analysis, in 'equal' reconstruction branches' lengths.

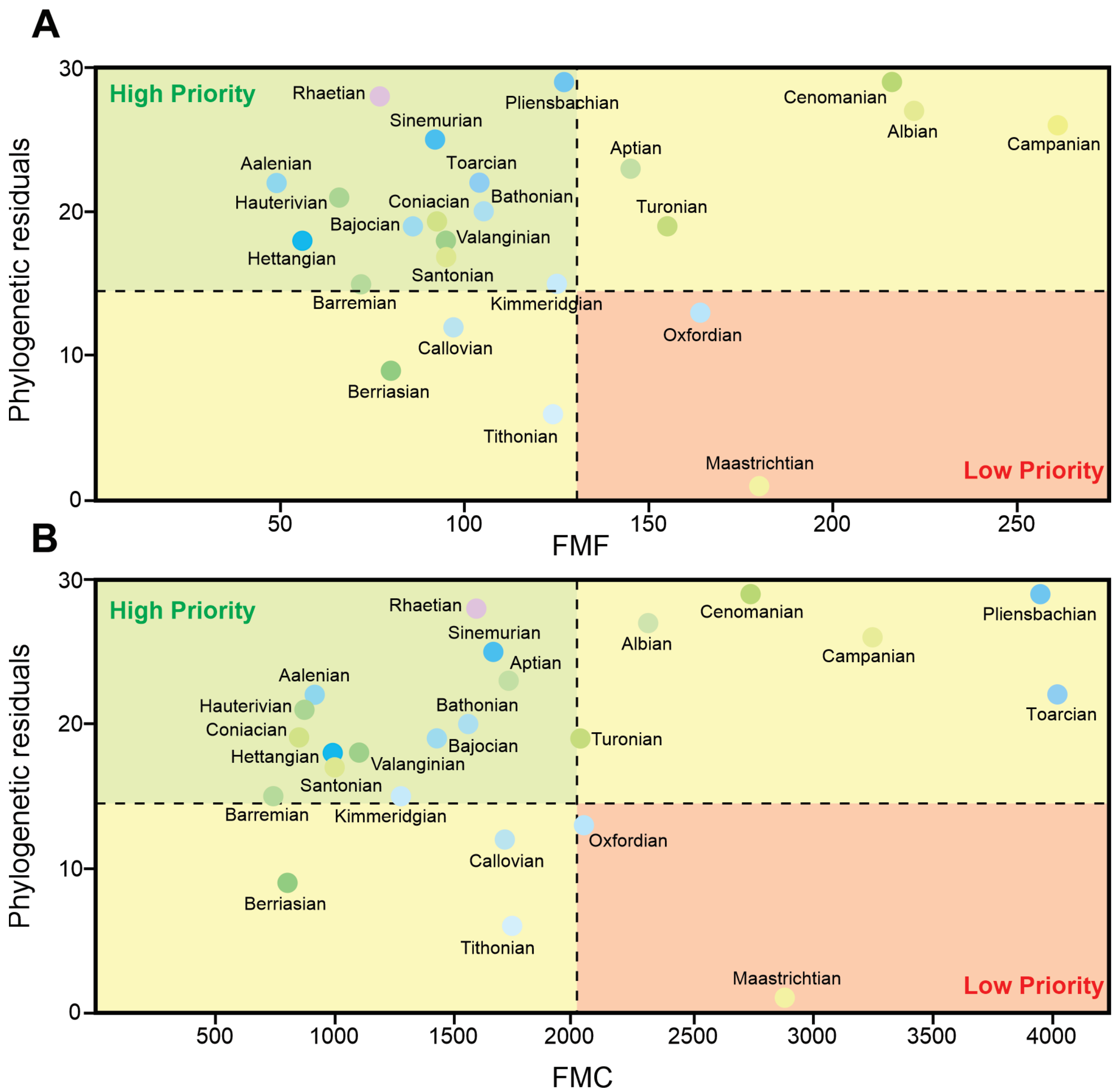

Figure 4. Scatter plot of phylogenetic residuals (PDE - TDE) using FMF (**A**) and FMC (**B**) at the stage level, showing the different quadrants of priority. High priority quadrants are colored in green, medium priority in yellow and low priority in red. Vertical and horizontal dashed lines indicate the midpoints of the FMF/FMC and residual axes, respectively, used to define quadrant boundaries.

Aalenian–Bathonian interval, Kimmeridgian, Barremian, Hauterivian, Valanginian, Coniacian and Santonian stages. The median priority quadrants were characterized by high phylogenetic residuals and high FMF, or low phylogenetic residuals and low rock availability. Stages recovered in these quadrants were the Callovian, Tithonian, Berriasian, Aptian–Turonian interval and Campanian stage. Finally, the low priority quadrant was categorized by a high number of FMF and low phylogenetic residuals, corresponding to the Oxfordian and Maastrichtian stages (Fig. 4A).

A similar analysis was performed using FMC as the sampling proxy (Fig. 4B), yielding broadly consistent results with minor differences. Notably, the Pliensbachian and Toarcian stages shift from high to medium priority due to their relatively high number of collections (see Figs 1, 4A, B). In contrast, the Aptian stage moves from medium to high priority, reflecting its lower FMC values (Fig. 4B).

However, although phylogenetic diversity estimate (PDE) shows a better correlation with true data than the RDE or TDE (Brocklehurst 2015), it shows greater prediction capability during intervals that do not precede mass extinction events. As in such pre-extinction intervals PDE naturally encompass TDE values, the phylogenetic residuals tend to decrease. Using the obtained stage classification in high, medium and low priorities, a plot of geographic distribution of FMF of each stage is given in Fig. 5.

Discussion

Discussion on TDE and sampling proxies

The analysis of whether the peaks and troughs in plesiosaurian taxic diversity estimates (TDE) can be explained

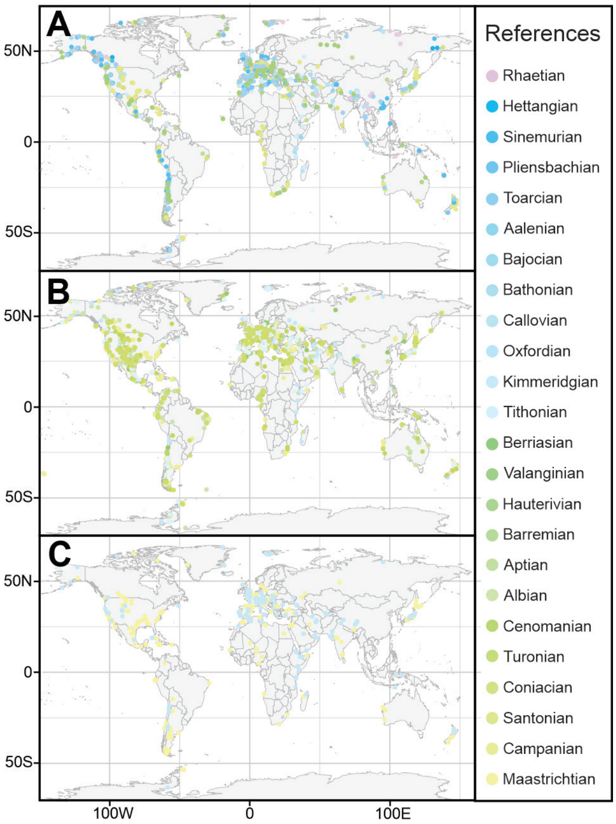

Figure 5. Maps showing the distribution of FMF during the plesiosaurians biochron. **A.** High priority stages; **B.** Medium priority stages; **C.** Low priority stages. Each dot represents a FMF whose GPS point was obtained from the collections from the Paleobiology Database (see Suppl. material 1).

solely by geological and anthropogenic biases reveals significant patterns. Fig. 2A illustrates that the primary peaks and troughs in plesiosaurian TDE show some correlation with rock availability, but at least some of the peaks and valleys cannot be explained by this proxy. Among this, the TDE peak during the Hettangian aligns with the earliest occurrences of rhomaleosaurids and key taxa such as *Avalonnectes arturi*, *Aningasaura lymense*, *Thalassiodracon hawkinsii* and *Lindwurmia thiuda* (Brown and Bardet 1994; Storrs and Taylor 1996; Benson et al. 2012; Vincent and Benson 2012; Vincent and Storrs 2019).

A subsequent peak not explainable by rock availability in the Toarcian stage is primarily driven by diversification within pliosaurids (*Hauffiosaurus* spp.), rhomaleosaurids, and microcleidids, including *Microcleidus* spp. and *Seeleyosaurus guilelmiimperatoris* (Dames 1895; O'Keefe 2001; Smith and Vincent 2010; Marx et al. 2025). The pronounced Callovian peak reflects the abundance of pliosaurids (*Liopleurodon ferox*, *Marmornectes candrewi*, *Simolestes vorax*, *Peloneustes philarchus*), the late-surviving rhomaleosaurid *Borealonectes russelli*, and several cryptoclidids such as *Cryptoclidus eurymerus*, *Muraenosaurus leedsii*, *Picrocleidus beloclis* and *Tricleidus seeleyi* (Sauvage 1873; Seeley 1874; Andrews 1910; Sato and Wu 2008; Ketchum and Benson 2011b; Zverkov et al. 2024).

An increase in diversity during the Tithonian stage is associated with the presence of *Pliosaurus* spp. (Knutsen, 2012; O'Gorman et al. 2018) and the final occurrences of several cryptoclidid genera: *Djupedalia engeri* (Knutsen et al. 2012a), *Spitrasaurus* spp. (Knutsen et al. 2012b), *Ophthalmothule cryostea* (Roberts et al. 2020), *Colymbosaurus megadeirus* (Seeley 1869).

Regarding the Cretaceous (Fig. 2A), the Hauterivian peak marks the appearance of early brachauchenines (*Makhaira rossica*, *Luskhan itilensis*), and the leptocleidids (*Leptocleidus capensis*, *Hastanectes valdensis*), and early elasmosaurids such as *Jucha squalea* and the "Speeton Clay plesiosaur" (Benson et al. 2013a; Fischer et al. 2015, 2017, 2021; Gómez-Pérez and Noè 2017). The final major non-explicable peak of TDE in the Maastrichtian corresponds to a radiation of weddellonectian elasmosaurids (Fig. 2A), particularly among aristonectines (Cruickshank and Fordyce 2002; Vincent et al. 2011; Otero et al. 2014, 2016; O'Gorman 2016, 2019; Otero and Soto Acuña 2021; O'Gorman et al. 2023).

In contrast, certain low-diversity intervals cannot be fully attributed to reduced rock availability. These include the Pliensbachian (represented only by *Westphaliasaurus simonsensii*), the Aalenian–Bathonian (*Maresaurus coccai*), the Oxfordian (*Gallardosaurus iturraldei*, *Tatenectes laramiensis*), the Valanginian (*Leptocleidus capensis*), and the Coniacian (*Dolichorhynchops osborni*) (Williston 1902; Andrews 1911; Cruickshank and Long 1997; Gasparini 1997, 2009; O'Keefe and Street 2009; Schwermann and Sander 2011). These gaps may reflect true biological declines or sampling artefacts, both of which warrant further investigation.

When FMC is considered, the results remain consistent with few exceptions. Particularly, the Toarcian stage now falls within the confidence interval, likely reflecting the influence of intensive fieldwork and the resulting large collections from English formations (9.3%; Suppl. material 1). In contrast, the Turonian stage lies above the confidence interval (Fig. 2B), indicating that collection effort alone cannot account for the observed plesiosaurian TDE.

Of particular interest are some moments of low TDE that have been discussed in terms of how much this decreases depending on sampling biases. Specifically, the Jurassic plesiosaurian fossil record, while taxonomically rich, is heavily biased by its reliance on a limited in number but highly fossiliferous European formations. These include the Lower Jurassic Blue Lias Formation (Rhaetian–Sinemurian, Weedon et al. 2018), Whitby Mudstone Formation (mainly Toarcian, Cox et al. 1999), the Middle–Late Jurassic Oxford Clay Formation (Callovian–early Oxfordian,), and the Late Jurassic Kimmeridge Clay Formation (Kimmeridgian–Tithonian, see Brown 1981; Benson et al. 2010; Ketchum and Benson 2011a; Benson and

Bowdler 2014). Gaps between these formations and post Tithonian corresponds to observed TDE declines in the Pliensbachian, Aalenian–Bathonian, late lower Oxfordian–upper Oxfordian (the "Corallian Gap" of Foffa et al. 2018), and several early Cretaceous stages.

The present results seem to indicate that the Pliensbachian and Aalenian–Bathonian declines in TDE (Fig. 2), widely noted in previous studies (Fischer et al. 2021; Sachs et al. 2024) are observed on a worldwide scale and cannot be explained by rock availability (FMF) or research effort (FMC). The same happened with the "Corallian" gap (Oxfordian, Foffa et al. 2018) decline, linked to the reduction of small to midsize pliosaurids in European faunas, that falls below the confidence interval of predicted TDE in FMF and FMC based models. On the other side, the apparent post Jurassic–Cretaceous boundary (Berriasian) decline in TDE commented by previous authors (Benson and Druckenmiller 2014) is consistent with expected TDE values given by rock availability and fossil collections models. However, the continued decrease of TDE in the Valanginian falls outside the 95% confidence interval based on FMF and FMC models, suggesting a true drop in plesiosaurian diversity (Fig. 2). The final interval of low diversity, the Coniacian, has been previously documented (Tutin and Butler 2017), who even excluded this stage from their specimen's completeness analysis to avoid statistical artifacts.

Discussion on phylogenetic residuals and priority stages

To evaluate how recent species descriptions align with the previously proposed sampling priorities, we examined newly described plesiosaurians from the past five years that are not included in the phylogenetic dataset to avoid redundancy (Table 1). Approximately one-third of these taxa were recovered from high-priority stages. The remaining species are distributed across medium- and low-priority intervals, suggesting that while under-sampled stages with high phylogenetic residuals (indicative of undiscovered diversity) represent promising targets for future exploration, notable discoveries can still be made within intervals previously considered well-sampled (see Table 1). Additionally, when we plot the distribution of FMF in a map of each priority level, it can be seen that they are similarly distributed around the world without strong geographical biases (Fig. 5).

Finally, if the results from both analysis (TDE vs. MDE) and the priority classification are compared, it can be concluded that among the highest priority stages there are three moments in the history of plesiosaurians that are crucial to test the conclusion of this contribution: Aalenian–Bathonian interval, and Valanginian and Coniacian stages. These stages are characterized by a markedly low TDE not explained by sampling proxies (Fig. 2), but also are thought to have an undiscovered diversity amounting to a significant number as inferred from phylogenetic residuals (Fig. 4). These contradictory results are key points to be tested by fieldwork in future investigations.

Conclusions

Taxic diversity of plesiosaurians is influenced by both rock availability and collection effort, but neither FMF nor FMC fully account for all observed peaks and troughs in diversity. Several diversity TDE highs (e.g., Hettangian, Callovian, Tithonian, Hauterivian, Maastrichtian) and lows (e.g., Rhaetian, Pliensbachian, Aalenian–Bathonian, Valanginian, Coniacian) remain unexplained by these sampling proxies, suggesting genuine biological signals.

Phylogenetic residuals highlight intervals with high potential for undiscovered diversity. Of particular interest are these high phylogenetic signal stages with low rock availability/research effort (e.g., Rhaetian, Hettangian, Sinemurian, Aalenian–Bathonian, Kimmeridgian, Valanginian–Barremian, Coniacian and Santonian). These intervals represent high-priority targets for future sampling and fieldwork (Fig. 4).

Some previous stages with noted declines in TDE in European formations, such as Berriasian, appear explainable by sampling proxies, whereas others (e.g., Pliensbachian, Oxfordian, Aalenian–Bathonian and Valanginian) remain unexplained, marking them as critical periods for targeted exploration.

Three key intervals—Aalenian–Bathonian interval and Valanginian and Coniacian ages—emerge as crucial for future testing of the consistency of fossil TDE biases and phylogenetic diversity as these stages combine low TDE, not explainable by sampling proxies, limited rock/collection data but high phylogenetic residuals, making them strong candidates for testing the two approaches followed here.

Table 1. Plesiosaurians species described from 2020–2025 that are not included in the phylogenetic analysis.

Taxa	Age	Priority	Reference
Plesiopharos moelensis	lower Sinemurian	High	Puértolas-Pascual et al. 2021
Lorrainosaurus keileni	upper Bajocian	High	Sachs et al. 2023
Franconiasaurus brevispinus	upper Toarcian	High-Median	Sachs et al. 2024
Eardasaurus powelli	Callovian	Median	Ketchum and Benson 2022
Plesioelasmosaurus walkeri	Cenomanian-Turonian	Median	Schumacher and Everhart 2022
Unktaheela specta	Campanian	Median	Clark et al. 2024
Serpentisuchops pfisterae	lower Maastrichtian	Low	Persons et al. 2022

Declaration of competing interests

The authors declare no competing interests.

Data availability

The data underpinning the analysis reported in this paper is listed as supplementary materials. Link to download fossil marine collections (FMC): http://paleobiodb.org/data1.2/colls/list.csv?datainfo&rowcount&base_name=Life&pres=regular&interval=Rhaetian,Maastrichtian&envtype=marine&colls_created_before=2025-06-26&pgm=gplates&show=full,timebins,timecompare&all_records.

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Supplementary material 1

Data set of plesiosaurians taxic and phylogenetic diversity estimates

Authors: Franco Roger Aspromonte, José Patricio O'Gormán

Data type: xlsx

Explanation note: Data set of plesiosaurians taxic and phylogenetic diversity estimates (TDE and PDE), phylogenetic residuals and the list of fossiliferous marine formations (FMF) and fossil marine collections (FMC).

Link: https://doi.org/10.3897/fr.28.173497.suppl1

Supplementary material 2

R scripts

Authors: Franco Roger Aspromonte, José Patricio O'Gormán

Data type: docx

Explanation note: R scripts used in this study.

Link: https://doi.org/10.3897/fr.28.173497.suppl2

Supplementary material 3

Phylogenetic matrix

Authors: Franco Roger Aspromonte, José Patricio O'Gormán
Data type: nex
Explanation note: Phylogenetic matrix of plesiosaurians derived from O'Keefe et al. 2025.

Link: https://doi.org/10.3897/fr.28.173497.suppl3

Supplementary material 4

FAD-LAD data

Authors: Franco Roger Aspromonte, José Patricio O'Gormán
Data type: txt
Explanation note: FAD-LAD for plesiosaurians species.

Link: https://doi.org/10.3897/fr.28.173497.suppl4