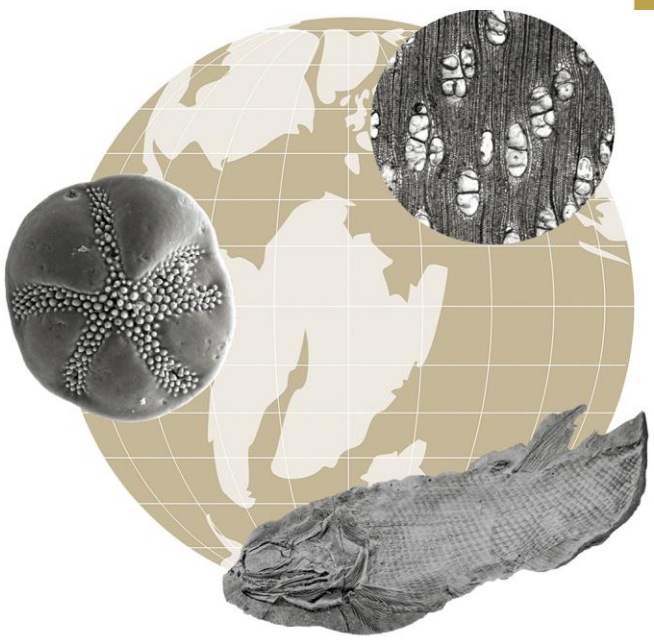
AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL



This file is an uncorrected accepted manuscript (i.e., postprint). Please be aware that this version will change during the production process. This postprint will be removed once the paper is officially published. All legal disclaimers that apply to the journal pertain.

Submitted: 7 July 2026 - **Accepted**: 12 November 2026 - **Posted online**: 13 November 2026

To link and cite this article:

doi: 10.5710/AMGH.12.11.2026.3707

PLEASE SCROLL DOWN FOR ARTICLE

DECOUPLING SAMPLING AND DIVERSITY DYNAMICS IN ABELISAURIDAE (THEROPODA, DINOSAURIA)

FRANCO R. ASPROMONTE[1,2], MAURICIO A. CERRONI[1,3,4], and DIEGO POL[1,5]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

[2]División Paleontología de Vertebrados, Museo de La Plata, Unidades de Investigación Anexo Museo (MLP), Universidad Nacional de La Plata (FCNyM-UNLP), 60 y 122, 1900 La Plata, Buenos Aires, Argentina. f.aspromonte@fcnym.unlp.edu.ar

[3]Área Laboratorio e Investigación, Museo Municipal "Ernesto Bachmann" (MEB), Dr. Natali S/N 8311, Villa El Chocón, Neuquén, Argentina. mauricio.cerroni@gmail.com

[4]Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina.

[5]Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Av. Ángel Gallardo 470, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina. cacopol@gmail.com

***Total number of pages**: 50 pages.

***Running Header**: Aspromonte *et al*.: Decoupling sampling and diversity dynamics

***Short Description**: Abelisaurid diversity through time reveals genuine macroevolutionary signals beyond sampling biases.

***Corresponding author**: División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA, La Plata,

Buenos Aires, Argentina. E-mail address: f.aspromonte@fcnym.unlp.edu.ar (F. R. Aspromonte).

Abstract. Abelisauridae represents one of the most diverse theropod clades in Gondwana, and has been the focus of increasing research in recent years. Despite this, the diversity dynamics of the group have not yet been examined considering the effect of uneven sampling in their fossil record. Here, we analyze abelisaurid taxic diversity dynamics through time using two different sampling proxies (theropod-bearing formations and collections), to test whether fluctuations in their taxic diversity can be explained solely by geological and anthropogenic biases, and identify stages in which deviations from sampling proxies may reflect genuine evolutionary signals. Our results show that several diversity peaks and low diversity values are partially correlated with sampling intensity. However, key deviations from model expectations reveal evolutionary meaningful patterns. In particular, the prolonged low diversity from the Aalenian to the Barremian is not explained by sampling proxies, suggesting an early phase of limited (or null) diversification of the group. Conversely, the diversity peak during the 'mid' Cretaceous indicates a potential diversification signal not fully accounted for by rock availability or collection effort, which coincides with the decline of other large-bodied theropods and likely reflects a broader ecological restructuring of predator guilds rather than a sampling artefact. In contrast, diversity patterns during the Campanian–Maastrichtian closely track sampling proxies, suggesting that the observed increase in diversity during this interval is strongly influenced by intensified sampling. Overall, these results demonstrate that while sampling biases influenced abelisaurid diversity curves, significant departures from sampling expectations reflect important macroevolutionary signals.

Keywords. Abelisaurid. Taxic diversity. PBDB. Occurrences. Sampling proxy. Dinosauria, Gondwana.

DESACOPLANDO LAS DINÁMICAS DE MUESTREO Y DIVERSIDAD EN ABELISAURIDAE (THEROPODA, DINOSAURIA)

Resumen. Abelisauridae representa uno de los clados de terópodos más diversos de Gondwana y han sido objeto de un creciente interés científico. Sin embargo, la dinámica de diversidad del grupo no ha sido examinada considerando el efecto del muestreo desigual a lo largo de su registro fósil. En este trabajo analizamos la dinámica de la diversidad taxonómica de los abelisáuridos utilizando dos proxies de muestreo (formaciones portadoras de terópodos y colecciones), con el objetivo de evaluar si las fluctuaciones en su diversidad pueden explicarse por sesgos geológicos y antropogénicos, e identificar aquellos intervalos en los que las desviaciones podrían reflejar señales evolutivas genuinas. Nuestros resultados muestran que varios picos de diversidad y valores bajos están parcialmente correlacionados con la intensidad de muestreo. Sin embargo, desviaciones respecto del modelo revelan patrones evolutivamente significativos. La prolongada baja diversidad desde el Aaleniano hasta el Barremiano no se explica por los proxies de muestreo, lo que sugiere una fase temprana de diversificación limitada. En cambio, el pico de diversidad durante el "Cretácico medio" no puede explicarse completamente por la disponibilidad de roca o el esfuerzo de muestreo, lo que sugiere una posible señal de diversificación coincidente con el declive de otros terópodos. En contraste, los patrones de diversidad durante el Campaniano–Maastrichtiano siguen de cerca los proxies, sugiriendo que el aumento durante este intervalo está influenciado por un muestreo intensificado. Estos resultados demuestran que, si bien los sesgos de muestreo modelan las curvas de diversidad de los abelisáuridos, las desviaciones significativas respecto de estas tendencias capturan señales macroevolutivas importantes.

Palabras clave. Abelisáuridos. Diversidad táxica. PBDB. Ocurrencias. Muestreo. Dinosauria, Gondwana.

Introduction

Abelisauridae constitutes one of the most diverse and widespread clades of theropod dinosaurs from the Southern Hemisphere (Novas et al., 2013; Pol et al., 2024), with a stratigraphic range starting with certainty in the Early Cretaceous (Sereno & Brusatte, 2008; Zaher et al., 2020) and the origin of the lineage, and possibly its earliest representatives, extending back to the late Early Jurassic (Pol & Rauhut, 2012; Pol et al., 2020). Their diversity increased throughout the Late Cretaceous persisting until the end of the Maastrichtian (Longrich et al., 2017; Pol et al., 2024). Abelisaurid fossils have been found across all regions that were once part of Gondwana, except from Antarctica and Australia where they remain unknown (Bonaparte & Novas, 1985; Sampson et al., 1998; Rauhut, 2011; Zaher et al., 2020; Salem et al., 2022; de Souza-Júnior et al., 2023), with additional few records also in Europe (Accarie et al., 1995; Tortosa et al., 2014; Isasmendi et al., 2021; Buffetaut et al., 2024; Isasmendi & Malafaia, 2025) (Fig. 1A).

Members of this clade are characterized by typically short, deep, and heavily sculptured skulls bearing distinctive cranial ornamentation, including pits, bulges, grooves, horns or knobs on the skull roof and circumorbital bones (Bonaparte et al., 1990; Sampson et al., 1998; Sampson & Witmer, 2007; Canale et al., 2009; Ratsimbaholison et al., 2016; Delcourt, 2018; Cerroni et al., 2020). Their skulls were probably specialized for predatory strategies involving the active use of the head in hunting (Therrien et al., 2005, Sampson & Witmer, 2007; Pereyra et al., 2025a). Additionally, a highly kinetic intramandibular articulation has been proposed for abelisaurids (Mazzetta et al., 1998), although this idea was recently questioned by Rowe et al. (2026). Other features that characterize abelisaurids are their extremely short and reduced forearms, stout hindlimbs, enlarged epipophyses on cervical vertebrae, and the

expanded transverse processes of caudal vertebrae (Bonaparte, 1991; Carrano & Sampson, 2008; Novas, 2009; Baiano et al., 2022).

Since the establishment of the family Abelisauridae, approximately four decades ago (Bonaparte & Novas, 1985), research on this clade has expanded substantially. The number of publications and taxonomic opinions (published interpretations of taxonomic identity and classification) has increased through time following an overall logistic growth pattern (Fig. 1B), characterized by a slow start in the period 1985–1995, an accelerated increase in the period 1995–2015, and a mild deceleration during the last decade (2015–2025) that is more pronounced in the opinions than in the number of publications. This recent pattern may reflect the growing number of studies focused on paleohistology, macroevolutionary analyses, and biomechanics, whereas the taxonomy of the family has become comparatively more stable and widely accepted (Fig. 1B). This growing trend was also accompanied by an increasing number of phylogenetic studies (Krause et al., 2007; Carrano & Sampson, 2008; Canale et al., 2009; Pol & Rauhut, 2012; Novas et al., 2013; Tortosa et al., 2014; Filippi et al., 2016; Hendrickx et al., 2020; Baiano et al., 2022; Cerroni et al., 2022; Pol et al., 2024; Jiménez Velandia et al., 2025) that have reached some degree of consensus in the major branches of the abelisaurid evolutionary history. To date, a total of 34 species of Abelisauridae are recognized (see Table 1), most of which have been described between 1985 and 2025 (Fig. 1B), while only *Majungasaurus crenatissimus* (Depéret, 1896) and *Indosaurus matleyi* (Chatterjee, 1978) were described earlier and later assigned to Abelisauridae. In recent years, macroevolutionary research has become a growing type of study in theropods and other vertebrates, some of which revealed high levels of morphological disparity within abelisaurids (Pol et al., 2024; Pereyra, 2025). Despite these advances, no comprehensive study has yet examined the diversity dynamics of the group through

time, nor evaluated the extent to which observed diversity patterns may be influenced by sampling bias effects. This issue is critical for interpreting the evolutionary history of the clade, because patterns of diversity inferred from the fossil record are inherently shaped by geological, taphonomic, and anthropogenic sampling biases (Raup, 1976; Peters, 2005; Alroy, 2010; Butler et al., 2011; Benson et al., 2021; Raja et al., 2022). Consequently, considerable effort has been devoted to developing methods that quantify or account for these biases, enabling more reliable reconstructions of diversity dynamics through time (Alroy et al., 2001; Smith & McGowan, 2007; Barrett et al., 2009; Lloyd, 2012; Starrfelt & Liow, 2016; Close et al., 2017; Kocsis et al., 2019; Alroy, 2020). Within Theropoda, Barrett et al. (2009) demonstrated that large-scale theropod diversity patterns are strongly correlated with fluctuations in the rock record, suggesting that apparent diversity trends may largely reflect geological megabiases rather than true evolutionary signals. Whether the diversity history of Abelisauridae is similarly shaped by sampling biases, however, remains unknown.

In this contribution, we analyze the fossil record and diversity patterns of Abelisauridae, assessing their temporal dynamics and the potential impact of sampling proxies on their inferred evolutionary history. By taking into account sampling proxies, we test whether fluctuations in abelisaurid taxic diversity estimates (TDE) can be explained solely by geological and anthropogenic biases, and identify stages in which deviations from sampling proxies may reflect genuine biological signals.

MATERIAL AND METHODS

Fossil occurrences

We retrieved and downloaded the fossil records from the Paleobiology Database (PBDB, Uhen et al., 2026) on May 15th, 2026, with the search term “Abelisauridae”,

resulting in 214 occurrences (= occurrence of a taxon in a collection) from 163 collections (= fossil locality, unique in time and space), from 65 strata and formations and 1241 taxonomic opinions (Fig. 1). The dataset was based on a compilation of 167 references (including papers in peer-reviewed journals, books and several abstracts), obtained through both the PBDB reference list and complementary searches in Google Scholar (see Supplementary Online Information 1). During data compilation, several publications on abelisaurid dinosaurs were newly entered into the PBDB or updated to improve taxonomic and occurrence coverage. This database is publicly available and can be accessed at www.paleobiodb.org. Occurrences were binned into geological stages following the International Chronostratigraphic Chart (v2026/06; http://stratigraphy.org/). Two occurrences broadly assigned to the Late Cretaceous, spanning multiple stages, were excluded due to their stratigraphic uncertainty (see Supplementary Online Information 1). Palaeogeographic reconstructions were based on the Seton model and palaeogeographic maps available through the PBDB.

Data used to quantify research trends on Abelisauridae (Fig. 1A, B) were obtained from the PBDB and complemented by literature searches in Google Scholar. Publications were compiled by year of publication, whereas taxonomic opinions were retrieved from the PBDB and assigned to the publication year of their corresponding reference. These data were then summarized by year to evaluate temporal changes in research activity and taxonomic work on Abelisauridae (Fig. 1B).

Taxon sampling

Taxic diversity estimates (TDE) were calculated directly from the set of recognized Abelisauridae species, assigning each taxon to the corresponding stratigraphic stages based on its first and last appearance data (see Table 1). This

estimate is computationally simple and allows the inclusion of all taxa (Mannion et al., 2011), however, it relies on an incomplete and biased fossil record and therefore represents a minimum estimate of true biodiversity (Pol & Leardi, 2015). Other studies also incorporate phylogenetic diversity estimates (PDE) into their analyses, because by including ghost lineages, this approach typically yields higher and more stable diversity values, partially compensating for gaps in the fossil record (Norell, 1992; Norell & Novacek, 1992; Miller et al., 2018). Nevertheless, PDE was not implemented here because currently available phylogenetic matrices for Abelisauridae differ substantially in both taxon sampling and character composition (see Pereyra et al., 2025b). Consequently, the use of any single matrix would necessarily exclude a number of recognized taxa, resulting in an incomplete representation of the group's diversity.

Abelisaurid taxa included in this study were compiled from the most recent phylogenetic hypotheses (Longrich et al., 2017; Cerroni et al., 2020; Agnolín et al., 2021; Baiano et al., 2022; Pol et al., 2024; Jiménez Velandia et al., 2025) (Table 1). *Huinculsaurus montesi* despite being first recovered as an elaphrosaurinae noasaurid (Baiano et al., 2020), in a recent phylogenetic analysis was retrieved as an abelisaurid (see Pol et al., 2024). In the case of *Caletodraco cottardi*, although no formal phylogenetic analysis is currently available, it is provisionally referred to Abelisauridae based on the presence of unequivocal abelisaurid features (see Buffetaut et al., 2024).

The taxonomic status of Indian abelisaurids from Lameta Formation remains uncertain, primarily because many of the specimens originally described by Matley (1923) and von Huene and Matley (1933) were collected from the same quarry area being represented by intermixed fragmentary remains; also, many of them lack overlapping material and even some are damaged or currently lost (see Novas et al., 2004). This affects taxa such as *Lametasaurus indicus*, *Indosuchus raptorius*, and

Indosaurus matleyi, whose diagnostic features cannot be reassessed (Wilson et al., 2003). As a result, these taxa have been regarded as nomina dubia (Novas et al., 2010) or potential synonyms in which *Lametasaurus* would have priority (see Carrano & Sampson, 2008). In this context, *Indosaurus* is retained here in the TDE analysis as it continues to be included as an operational taxonomic unit (OTU) in phylogenetic analyses.

Sampling biases on taxic diversity

To evaluate the extent to which sampling biases may affect the observed taxic diversity patterns in Abelisauridae, we implemented a set of statistical approaches to estimate expected diversity from the relationship between abelisaurid TDE and sampling proxies. This approach differs from sampling-standardization methods such as subsampling or coverage-based rarefaction (Alroy, 2010; Chao & Jost, 2012; Close et al., 2018), which attempt to estimate diversity at a standardized level of sampling completeness. Instead, our approach evaluates whether temporal variation in observed taxonomic richness is consistent with that expected from variation in the selected sampling proxies. Initially we performed a simple linear regression, but since TDE are counts, Poisson and negative binomial models were also tested because those are more appropriate for this kind of data (O'Hara & Kotze, 2010; Sakamoto et al., 2016). The best-fitting model was selected using the Akaike Information Criterion (AIC), 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; Aspromonte & O'Gorman,

2025). In this case, positive/negative residuals indicate diversity values that are higher/lower than expected given the sampling proxy, suggesting possible diversity signals not accounted for by sampling alone (Fig. 2). This method was applied using the MASS package (Venables & Ripley, 2002) in the software R (v4.4.3) (R Core Team, 2025) (see Supplementary Online Information 2 for the R script).

Residual-based approaches have been widely used to explore the relationship between observed diversity and sampling proxies (Smith & McGowan, 2007), but they have also received important criticism. In particular, residual diversity estimates may fail to recover underlying diversity patterns, particularly when polynomial models or narrow proxies are used (Brocklehurst, 2015), while Sakamoto et al. (2016) highlighted the statistical problems associated with artificially pairing unassociated x and y values, which lack a natural interpretation and may generate spurious model predictions. Our approach avoids this specific issue by preserving the temporal correspondence between abelisaurid TDE and each sampling proxy, and modelling these relationships directly using statistical models appropriate for count data. Although this relatively simple framework does not reconstruct sampling-independent or "true" diversity, it provides a transparent way to assess whether temporal variation in TDE is consistent with that expected from the sampling proxies. Residuals are therefore interpreted as deviations from model expectations, highlighting intervals in which observed richness is higher or lower than predicted and identifying patterns that are not fully accounted for by the sampling proxies considered in this study.

To account for these sampling biases, two sampling proxies were retrieved from the PBDB: the number of theropod-bearing formations and the number of theropod-bearing collections (Fig. 2). These proxies were selected because they provide a more comprehensive estimate of sampling effort while minimizing the risk of redundancy

(Benton et al., 2011; Upchurch et al., 2011; Brocklehurst, 2015). Using only formations or collections yielding abelisaurid remains would introduce circularity in the analysis, whereas including all dinosaur-bearing units would likely overestimate sampling effort. Although the use of formation counts as a sampling proxy has been criticized (Dunhill et al., 2014, 2018), it remains one of the most widely used and accessible proxies for capturing temporal variation in the rock record (Peters & Foote, 2001; Barrett et al., 2009; Butler et al., 2009; Marx, 2009; Benson et al., 2010; Mannion et al., 2011; Benson & Upchurch, 2012; Fröbisch, 2013; Aspromonte & O'Gorman, 2025). This proxy also represents the cumulative efforts of numerous researchers over time, which can help offset individual sampling biases and facilitate comparability across datasets and taxa. However, because formations can vary considerably in sampling intensity, we also included the number of theropod collections as a complementary proxy. Collections provide a measure more directly linked to human sampling effort and can help mitigate biases associated with uneven sampling among formations (Alroy et al., 2001; Crampton et al., 2003; Upchurch et al., 2011; Butler et al., 2012; Benson et al., 2013).

Additionally, to account for the spatial component of sampling, the number of occupied equal-area grid cells for each time bin was calculated (Fig. 2). Present-day coordinates of theropod-bearing collections were assigned to equal-area grid cells with 50km spacing using the R package dggridR (Barnes et al., 2018), following similar approaches used to quantify spatial sampling in the terrestrial fossil record (Close et al., 2017, 2020; Dunne et al., 2021). To evaluate the sensitivity of this proxy to spatial resolution, the analysis was repeated using grid spacings of 100 and 200 km also. For each stage, spatial sampling was quantified as the number of unique grid cells containing at least one theropod-bearing collection. The number of occupied grid cells

was then used as an additional sampling proxy alongside the number of theropod-bearing formations and collections (see Supplementary Online Information 2 for the R script).

Data on theropod-bearing formations and collections were downloaded from the PBDB on May 15th, 2026 (see Supplementary Online Information 3). A total of 690 formations and 4,525 collections yielding theropod remains from the Toarcian to the Maastrichtian were retrieved from the PBDB, as the Toarcian represents the earliest putative record of the family Abelisauridae given by the taxon *Eoabelisaurus* (Pol & Rauhut, 2012; Pol et al., 2020). These records were assigned to stratigraphic stages following the International Chronostratigraphic Chart (v2026/06), except for 349 collections that could not be allocated due to limited stratigraphic resolution. Because formations commonly span multiple stages, each unit was assigned to all stages to which it has been referred (Supplementary Information 3).

RESULTS

In the three sampling proxy analyses, the best-fitting model selected via Akaike Information Criterion (AIC) was the negative binomial model, which accounts for the observed overdispersion (O'Hara & Kotze 2010). The primary peaks and troughs in taxic diversity estimates (TDE) for abelisaurids show some correlation with geological formations, collections and occupied grid cells, but at least some of these TDE peaks cannot be fully explained by these proxies (Fig. 3). Observed TDE is higher than the MDE during the Cenomanian, Turonian, and Santonian stages in all three models (Fig. 3), whereas TDE during the Albian stage is also higher than model predictions, but falls within the confidence interval in the occupied grid cells model (Fig. 3C). In contrast, TDE is significantly lower than expected from the Aalenian to the Barremian (Fig. 3).

306 For the remaining stages—Toarcian, Aptian, Coniacian, Campanian and
307 Maastrichtian—observed diversity closely matches the model predictions (Fig. 3).
308 During the Jurassic, the earliest putative record of Abelisauridae corresponds to
309 *Eoabelisaurus mefi* from the Cañadón Asfalto Formation (Toarcian; Pol et al., 2020).
310 According to both formation and collection-based models, taxic diversity estimates
311 (TDE) for this stage are consistent with expectations based on rock availability and
312 sampling effort (Fig. 3). However, from the Aalenian to the Barremian (approximately
313 53.3 Ma), the absence or troughs in abelisaurid TDE are not explained by these
314 sampling proxies (Fig. 3), suggesting that they may reflect a genuine biological signal.
315 During this interval, abelisaurid occurrences are scarce and widely distributed across
316 different paleolatitudes (Fig. 4A-C). In the Jurassic, only a few records are documented
317 in the PBDB, mostly from Gondwana, including a cervical vertebra and associated
318 fragmentary remains from the Cañadón Calcáreo Formation in Patagonia (Rauhut &
319 Pol, 2021); an incomplete lateral tooth from the Tacuarembó Formation in Uruguay
320 (Soto et al., 2023); several teeth from the Sakaraha Formation in Madagascar
321 (Hendrickx et al., 2025), and isolated limb elements from the Tendaguru Formation in
322 Tanzania, including a left tibia from the Middle Dinosaur Member and a right femur
323 and tibia from the Upper Dinosaur Member (Rauhut, 2011). However, an occurrence
324 from northern paleolatitudes is also documented, represented by teeth from the
325 Lourinhã Formation in Portugal (Hendrickx & Mateus, 2014) (Fig. 4A, C).
326 During the Early Cretaceous, the low TDE observed during the Berriasian–
327 Barremian interval cannot be fully explained by the sampling proxies considered here
328 (Fig. 3). The few known records of Abelisauridae during this period are restricted to
329 Gondwana, and include an isolated tibia from the Bajada Colorada Formation in
330 Patagonia (Canale et al., 2017); a tooth from the Chicla Formation in Libya (Smith &

Dalla Vecchia, 2006); and an isolated tooth from the Missão Velha Formation in Brazil (Ribeiro et al., 2024). Nevertheless, during the Aptian–Albian interval, abelisaurid TDE increase and matches model predictions (Fig. 3), except for the Albian stage where TDE remains higher than the formation- and collection-based models (Fig. 3A, B). Recognized species from this stages are *Genusaurus sisteronis* (Accarie et al., 1995), *Spectrovenator ragei* (Zaher et al., 2020), and the maxilla material of *Kryptops palaios* (Sereno & Brusatte, 2008), with additional teeth material from the Quiricó Formation in Brazil (de Carvalho & Santucci, 2018). Although the Candeleros and Huincul formations of Patagonia have traditionally been assigned to the Cenomanian–Turonian interval, recent zircon U–Pb geochronological data have suggested that these units may be older, potentially dating back to the Albian (Maniel et al., 2026). Under this revised chronology, several abelisaurid species are reassigned to the Albian, including *Ekrixinatosaurus novasi*, *Huinculsaurus montesi*, *Ilokelesia aguadagrandensis*, *Skorpiovenator bustingorryi* and *Tralkasaurus cuyi* (Canale et al., 2009; Calvo et al., 2004; Coria and Salgado, 2000; Baiano et al. 2020; Cerroni et al., 2020), contributing to the TDE peak observed (Fig. 3). During this time, Abelisauridae occurrences also increase and remain restricted to relatively medium paleolatitudes, ranging from 30° North to 40° South (Fig. 4A, B).

A marked mid-paleolatitudes expansion of abelisaurid occurrences is observed during the 'mid' Cretaceous, particularly during the Cenomanian, when this group became one of the most abundant predators of their ecosystems in different basins (Ribeiro et al., 2025) (Fig. 3 A, B). During this interval, TDE remains higher than expectations based on the sampling proxies (Fig. 3), with records from Europe (*Caletodraco cottardi*, Buffetaut et al., 2024), Africa (*Rugops primus*, Sereno et al., 2004) and Patagonia (*Xenotarsosaurus bonapartei*, Martinez et al., 1987). In the

Turonian, TDE remains higher than expected based on the three sampling-based models, although occurrences decrease relative to the 'mid' Cretaceous (Fig. 3-4). During the Turonian, abelisaurid occurrences appear to be restricted to the Southern Hemisphere (Fig. 4), including taxa like *Elemgasem nubilus* from Patagonia (Baiano et al., 2022), and *Dahalokely tokana* from Madagascar (Farke & Sertich, 2013).

During the Coniacian, abelisaurid TDE decreases in parallel with a reduction in occurrence counts (Figs. 3, 4B), and the known fossil record appears to have been largely restricted to southern paleolatitudes between 30° and 40°S (Fig. 4A). Although the PBDB includes a Coniacian abelisaurid occurrence from Kazakhstan, this record was excluded from the interpretation because it lacks sufficient supporting information (Riabinin, 1938). During the Santonian, both abelisaurid TDE and occurrence counts increased again, with TDE higher than the three sampling-based models (Fig. 3, 4B). The clade also reappeared in the Northern Hemisphere, as evidenced by a pedal ungual and a femur recovered from the Csehbánya Formation (Ősi et al., 2010; Ősi & Buffetaut, 2011). In the Southern Hemisphere, the Santonian abelisaurid record includes named taxa such as *Llukalkan aliocranianus* (Gianechini et al., 2021), *Thanos simonattoi* (Delcourt & Iori, 2020) and *Viavenator exxoni* (Filippi et al., 2016), in addition to more fragmentary remains (Meso et al., 2021; Gianechini et al., 2022; Méndez et al., 2022).

Finally, during the Campanian–Maastrichtian, abelisaurid occurrences are recorded across a broad paleolatitudinal range, from 40° North to 45° South, similar to the pattern observed in the Cenomanian (Fig. 4A). During this interval, observed TDE closely matches model predictions, although the group reaches its highest values in both occurrences and taxic diversity (Figs. 3, 4). This diversification is reflected in a widespread geographic distribution, with Campanian records including *Arcovenator*

escotae from France (Tortosa et al., 2014), as well as *Guemesia ochoai* (Agnolín et al., 2021) and *Vitosaura colozacani* (Jiménez Velandia et al., 2025) from northwestern Argentina, and *Aucasaurus garridoi* from Patagonia (Coria et al., 2002). Maastrichtian records further highlight this pattern, particularly in Patagonia, where the Allen Formation has yielded *Abelisaurus comahuensis* (Bonaparte & Novas, 1985), *Niebla antiqua* (Aranciaga Rolando et al., 2021), and *Quilmesaurus curriei* (Coria, 2001), while the La Colonia Formation includes *Carnotaurus sastrei* (Bonaparte, 1985) and *Koleken inakayali* (Pol et al., 2024). Notably, abelisaurids remain absent from higher-latitude deposits, such as those represented by the Chorrillo Formation (Novas et al., 2019). Additional South American records include *Pycnonemosaurus nevesi* and *Kurupi itaata* from Brazil (Kellner & Campos, 2002; Iori et al., 2021). Outside South America, abelisaurids species are also recorded in the Lameta Formation of India, including *Indosaurus matleyi* (Chatterjee, 1978), *Rahiolisaurus gujaratensis* (Novas et al., 2010), and *Rajasaurus narmadensis* (Wilson et al., 2003), as well as *Chenanisaurus barbaricus* from Morocco (Longrich et al., 2017), and *Majungasaurus crenatissimus* from Madagascar (Depéret, 1896; Krause et al., 2007).

DISCUSSION

The interpretation of diversity patterns in the fossil record is strongly influenced by geological and anthropogenic biases, which can generate apparent fluctuations unrelated to true biological signals (Peters, 2005; Smith & McGowan, 2007; Chiarenza et al., 2019; Close et al., 2020; Raja et al., 2022; Dunne et al., 2023; Heath et al., 2025). Variations in the amount of fossil-bearing rock, as well as differences in sampling intensity, may produce artificial peaks and troughs in diversity curves, thus complicating macroevolutionary inferences and biodiversity assessments (Barrett et al.,

406 2009; Chiarenza et al., 2019; Aspromonte & O'Gorman, 2025). Nevertheless, once
407 these biases are taken into account, several genuine diversity patterns could become
408 apparent. Our results indicate that the primary peaks and troughs in abelisaurid taxic
409 diversity estimates (TDE) are partially correlated with rock availability and collection
410 effort, although some cannot be explained by these proxies (Fig. 2-3). Among these, the
411 absence or low TDE of abelisaurids from the Aalenian to the Barremian is not
412 accounted for by sampling proxies, indicating that this pattern likely reflects a genuine
413 biological signal rather than a sampling artefact. During this interval, the fossil record of
414 the group is sparse and geographically scattered (Fig. 4C), suggesting that early
415 abelisaurids were rare components of terrestrial ecosystems (Soto et al., 2023).
416 However, this pattern should be interpreted with caution, as the phylogenetic
417 placement of Jurassic and earliest Cretaceous taxa remains uncertain, and some forms
418 traditionally regarded as early abelisaurids (e.g., *Eoabelisaurus* and *Genusaurus*) have
419 also been recovered as more basal ceratosaurs or abelisauroids (Carrano & Sampson,
420 2008; Tortosa et al., 2014; Wang et al., 2017). In this context, if we consider only
421 unambiguous members of the Abelisauridae clade, the Jurassic and pre-Aptian record
422 may be effectively absent, so the observed low diversity would not necessarily reflect
423 ecological rarity, but rather the absence of the group during this interval. Accordingly,
424 the Aptian–Albian record includes taxa such as *Spectrovenator ragei* and *Kryptops*
425 *palaios*, which exhibit derived cranial apomorphies widely regarded as diagnostic of
426 Abelisauridae, providing more secure evidence for the early diversification of the clade.
427 In contrast, the diversity peak observed during the 'mid' Cretaceous (Albian–
428 Cenomanian) cannot be explained by sampling proxies (Figs. 3-4), supporting its
429 interpretation as a genuine biological signal. During this period, abelisaurids coexisted
430 with other large-bodied theropods, including carcharodontosaurids and spinosaurids,

which are frequently recorded in the same assemblages (Sereno & Brusatte, 2008), at least for most Gondwanan landmasses, except for Patagonia where spinosaurids are not recorded. Although these clades were carnivorous, increasing evidence indicates clear niche partitioning, with spinosaurids foraging aquatic environments and abelisaurids and carcharodontosaurids primarily occupying terrestrial predatory roles (Hassler et al., 2018; Fabbri et al., 2022). The increase in abelisaurid TDE (Fig. 3) coincides with their occurrences peak (Fig. 4B), with records distributed across a broad paleolatitudinal range extending from 40°N to 40°S (Fig. 4A). This broad latitudinal distribution during the 'mid' Cretaceous is supported by the records reported from Europe (Buffetaut et al., 2024), numerous remains from Africa (Sereno et al., 2004; Richter et al., 2013), and several specimens and named taxa from South America (Cerroni et al., 2020; Ribeiro et al., 2024) (Fig. 4C).

Across the Cenomanian–Turonian boundary, abelisaurid TDE appears to remain relatively stable (Fig. 3), whereas occurrence counts decline markedly (Fig. 4B). This decline may be related to the broader faunal turnover recognized during this interval (Coria & Salgado, 2005; Novas et al., 2005), which has frequently been associated with global environmental and climatic changes linked to the Cretaceous Thermal Maximum (Huber et al., 2018; Burgener et al., 2023; Boisvert et al., 2026). This turnover involved the extinction of several major theropod lineages, particularly spinosaurids and carcharodontosaurids, and likely prompted a restructuring of terrestrial predator guilds (Novas et al., 2013; Delcourt, 2018). Additionally, across this boundary abelisaurid occurrences also become largely restricted to middle-high paleolatitudes of Gondwana, approximately 30-40°S (Fig. 4A). Given the increasing evidence that climate played an important role in shaping dinosaur biogeographic patterns during the Mesozoic (Chiarenza et al., 2022; 2024), this palaeolatitudinal contraction raises the possibility

that the extreme warming associated with the Cretaceous Thermal Maximum affected the geographic distribution of abelisaurids, reducing the suitability of low-latitude environments and potentially contributing to their apparent contraction toward cooler, middle–high southern palaeolatitudes (Fig. 4A). This pattern may also be consistent with the proposed role of northern Gondwana as a critical region in the extinction of several theropod clades (Jacobs et al., 1993; Candeiro et al., 2018), potentially explaining the reduction of abelisaurid occurrences in lower paleolatitudes.

The persistence of positive residual diversity values during the Turonian (Fig. 3) indicates that, although occurrences and diversity decrease relative to the 'mid' Cretaceous, observed diversity remains higher than expected based on the sampling proxies considered here, suggesting that the pattern cannot be fully explained by sampling alone (Fig. 3). This pattern is consistent with a scenario of ecological restructuring, in which abelisaurids remained a key part of the predator guild of their ecosystems, along with groups that increased their diversity, body size, and abundance in Gondwana, such as megaraptorids (Aranciaga Rolando et al., 2022; Baiano et al., 2022) and later the large sized unenlagiids (Novas et al., 2013).

A notable decline in both TDE and occurrences is observed during the Coniacian stage (Fig. 4B), coinciding with previous theropod diversity curves (Upchurch et al., 2011; Tennant et al., 2018). This could be explained by the number of theropod formations confidently assigned to the Coniacian appears comparatively limited, raising the possibility that the observed decline may at least partly reflect resolution or sampling issues (Fig. 4B). In the Santonian stage, TDE increase and remains not fully explainable by the three sampling-based models (Fig. 3), suggesting a diversification of the group until the latest Cretaceous.

In contrast to earlier intervals, diversity patterns during the Campanian–Maastrichtian appear to be largely explained by sampling proxies (Fig. 3). The increase in both occurrences and TDE across a wide range of paleolatitudes (Fig. 4) suggests that intensified sampling effort seems to play a major role in shaping the observed diversity signal. Although several authors claimed that during this interval, largest body sizes were obtained within the clade (Carrano et al., 2012; Grillo & Delcourt, 2017; Zaher et al., 2020; Aranciaga Rolando et al., 2022), recent work illustrated that body size in abelisaurids remained stable after Cenomanian–Turonian times probably due to constraints on its locomotion and/or feeding strategy (Pereyra et al., 2025c; Boisvert et al., 2026). Nonetheless, abelisaurids are still distinguished by their presence in multiple continental regions, suggesting that this clade occupied prominent ecological roles, potentially as apex predators in several Gondwanan ecosystems (Canale et al., 2017; Cerroni et al., 2020).

Although our analyses identify intervals in which observed abelisaurid taxonomic richness departs from expectations based on sampling proxies, alternative approaches could modify the magnitude of these patterns. Regional analyses would help establish whether the ‘mid’ Cretaceous peak persist within individual basins or partly reflect changes in the geographic composition of the sampled record, whereas phylogenetic approaches could reveal lineage diversification and evolutionary history not captured by taxonomic richness alone, although their results would depend on tree topology, temporal calibration, and taxonomic coverage. Geographic heterogeneity is particularly evident in the Neuquén Basin, which accounts for 14 recognized species (approximately 41% of the total) and 47 occurrences (22% of the dataset). This concentration indicates a strong regional contribution to the global signal, although it does not by itself distinguish greater original diversity from more favorable preservation

505 or more intensive sampling. Temporal comparisons may likewise be affected by the
506 contrast between the sparse Jurassic–Early Cretaceous record and the better-represented
507 and explored Upper Cretaceous record (Fig. 4B). These inequalities potentially reflect
508 interacting effects of fossiliferous outcrop availability, depositional environment,
509 accessibility, historical collecting effort, and financial and logistical resources, whose
510 relative contributions remain to be quantified.
511 Cashmore and Butler (2019) documented temporal and spatial heterogeneity in
512 theropod skeletal completeness, showing in the Berriasian and Hauterivian stages a low
513 percentage of theropod completeness which coincides with the lack of abelisaurid
514 recognized species. However, they also recovered a peak in the Oxfordian–
515 Kimmeridgian and Barremian–Aptian intervals, when abelisaurid low TDE is not fully
516 explained by sampling proxies, suggesting that differences in the availability of
517 diagnostic material could influence species recognition and observed richness,
518 particularly where abelisaurid occurrences comprise isolated or fragmentary remains.
519 Targeted fieldwork and taxonomic reassessment would therefore be especially valuable
520 in Jurassic units yielding putative abelisaurid remains without recognized species,
521 including Cañadón Calcáreo, Tacuarembó, Tendaguru, and Isalo IIIb (Rauhut, 2011;
522 Rauhut & Pol, 2021; Soto et al., 2023; Hendrickx et al., 2025), as well as in poorly
523 represented portions of the early record sampled by the Bajada Colorada, Chicla, and
524 Missão Velha formations (Smith & Dalla Vecchia, 2006; Canale et al., 2017; Ribeiro et
525 al., 2024). Additionally, taxonomic identification is not a major source of bias for
526 theropod dinosaurs (Cashmore et al., 2021), suggesting that actually higher diversity of
527 a particular clade could represent a real pattern, as we identified for abelisaurid
528 diversity. Integrating these efforts with regional comparisons, specimen completeness
529 assessments, and phylogenetic analyses would help determine whether low observed

richness and subsequent diversity peaks primarily reflect biological changes or the heterogeneous geological and research processes shaping the fossil record.

CONCLUSIONS

Recent studies have shown that patterns of theropod diversity and relative abundance are not primarily driven by taxonomic identification bias, and may instead reflect underlying ecological signals. This supports the interpretation that the residual diversity patterns recovered here are not solely artefacts of sampling biases but likely capture real macroevolutionary dynamics. Following this, Abelisauridae evolutionary history is characterized by an early phase of low diversity, followed by a 'mid' Cretaceous marked diversification that largely predates the extinction of competing theropod clades (e.g., carcharodontosaurids), and a final latest Cretaceous diversity increase across a broad range of latitudes, although the latter is possibly due to sampling biases (rock availability and sampling effort).

This pattern highlights the importance of disentangling geological and anthropogenic effects from biological signals when interpreting diversity dynamics in the fossil record. This type of analysis has been feasible for this clade of theropods due to its relatively extensive fossil record, high taxonomic richness, and broad geographic distribution across Gondwanan landmasses, with additional occurrences in Europe. Applying similar approaches to other Gondwanan theropod clades would be a valuable framework for comparing their taxic diversity dynamics with those of abelisaurids. Such comparisons could reveal distinctive evolutionary trajectories or, more interestingly, shared patterns that may reflect a common underlying driver, including response to environmental/ecological processes or systematic biases in current fossil data.

555

556 **ACKNOWLEDGEMENTS**

557 The authors thank all PBDB members who have submitted data on abelisaurid
558 dinosaurs. This research received financial support from CONICET (Consejo Nacional
559 de Investigaciones Científicas y Técnicas) and is part of the National Geographic
560 Society Project “The End of the Dinosaur Era in Patagonia” (NGS- 92822R- 22).
561 Special thanks to Juan Canale (Museo Ernesto Bachmann) and Mauro Aranciaga
562 Rolando (LACEV-MACN) for their guidance and comments on an early draft of the
563 manuscript. We thank Emma Dunne and Emanuel Seculi Pereyra for their valuable
564 comments, which greatly improved this contribution. We also thank editor M. Ezcurra
565 for his helpful guidance and comments during the review process.

566

567 **REFERENCES**

568 Accarie, H., Beaudoin, B., Dejax, J., Fries, G., Michard, J. G., & Taquet, P. (1995).
569 Découverte d'un Dinosaure Théropode nouveau (*Genusaurus sisteronis* ng, n. sp.)
570 dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au
571 Crétacé inférieur de la lignée cératosaurienne. *Comptes rendus de l'Académie des*
572 *sciences. Série 2. Sciences de la terre et des planètes*, 320(4), 327–334.
573 Agnolín, F. L., Cerroni, M. A., Scanferla, A., Goswami, A., Paulina-Carabajal, A.,
574 Halliday, T., Cuff, A. R., & Reuil, S. (2021). First definitive abelisaurid theropod
575 from the Late Cretaceous of Northwestern Argentina. *Journal of Vertebrate*
576 *Paleontology*, 41(4), e2002348. https://doi.org/10.1080/02724634.2021.2002348
577 Alroy, J. (2010). Fair sampling of taxonomic richness and unbiased estimation of
578 origination and extinction rates. *The Paleontological Society Papers*, 16, 55–80.
579 https://doi.org/10.1017/S1089332600001819

Alroy, J. (2020). On four measures of taxonomic richness. *Paleobiology*, 46(2), 158–175. https://doi.org/10.1017/pab.2019.40

Alroy, J., Marshall, C. R., Bambach, R. K., Bezusko, K., Foote, M., Fürsich, F. T., Hansen, T. A., Holland, S. M., Ivany, L., Jablonski, D., Jacobs, D. K., Jones, D. C., Kosnik, M. A., Lidgard, S., Low, S., Miller, A. I., Novack-Gottshall, P. M., Olszewski, T. D., Patzkowsky, M. E., Raup, D. M., Roy, K., Sepkoski Jr, J. J., Sommers, M. G., Wagner, P. J., & Webber, A. (2001). Estimates of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences*, 98(11), 6261–6266. https://doi.org/10.1073/pnas.111144698

Antell, G. T., Benson, R. B., & Saupe, E. E. (2024). Spatial standardization of taxon occurrence data—a call to action. *Paleobiology*, 50(2), 177–193. https://doi.org/10.1017/pab.2023.36

Aranciaga Rolando, M., Cerroni, M. A., Marsà, J. A. G., Motta, M. J., Rozadilla, S., Eglí, F. B., & Novas, F. E. (2021). A new medium-sized abelisaurid (Theropoda, Dinosauria) from the late Cretaceous (Maastrichtian) Allen Formation of Northern Patagonia, Argentina. *Journal of South American Earth Sciences*, 105, 102915. https://doi.org/10.1016/j.jsames.2020.102915

Aranciaga Rolando, A. M., Motta, M. J., Agnolín, F. L., Manabe, M., Tsuihiji, T., & Novas, F. E. (2022). A large Megaraptoridae (Theropoda: Coelurosauria) from Upper Cretaceous (Maastrichtian) of Patagonia, Argentina. *Scientific Reports*, 12(1), 6318. https://doi.org/10.1038/s41598-022-09272-z

Aspromonte, F. R., & O'Gorman, J. P. (2025). Assessing the effect of sampling proxies on plesiosaur taxic diversity with comments on implications for Mesozoic sampling design. *Fossil Record*, 28(2), 397–410. https://doi.org/10.3897/fr.28.e173497

605 Baiano, M. A., Coria, R. A., & Cau, A. (2020). A new abelisauroid (Dinosauria:
606 Theropoda) from the Huincul Formation (Lower upper Cretaceous, Neuquén Basin)
607 of Patagonia, Argentina. *Cretaceous Research*, 110, 104408.
608 https://doi.org/10.1016/j.cretres.2020.104408
609 Baiano, M. A., Pol, D., Bellardini, F., Windholz, G. J., Cerda, I. A., Garrido, A. C., &
610 Coria, R. A. (2022). *Elemgasem nubilus*: a new brachyrostran abelisaurid
611 (Theropoda, Ceratosauria) from the Portezuelo Formation (Upper Cretaceous) of
612 Patagonia, Argentina. *Papers in Palaeontology*, 8(5), e1462.
613 https://doi.org/10.1002/spp2.1462
614 Barnes, R., Sahr, K., Evenden, G., Johnson, A. and Warmerdam, F. 2018. dggridR:
615 discrete Global Grids for R. v. 2.0.3. http://github.com/r-barnes/dggridR
616 Barrett, P. M., McGowan, A. J., & Page, V. (2009). Dinosaur diversity and the rock
617 record. *Proceedings of the Royal Society B: Biological Sciences*, 276(1667), 2667–
618 2674. https://doi.org/10.1098/rspb.2009.0352
619 Benson, R. B., Butler, R., Close, R. A., Saupe, E., & Rabosky, D. L. (2021).
620 Biodiversity across space and time in the fossil record. *Current Biology*, 31(19),
621 R1225–R1236. https://doi.org/10.1016/j.cub.2021.07.071
622 Benson, R. B., Butler, R. J., Lindgren, J., & Smith, A. S. (2010). Mesozoic marine
623 tetrapod diversity: mass extinctions and temporal heterogeneity in geological
624 megabiases affecting vertebrates. *Proceedings of the Royal Society B: Biological*
625 *Sciences*, 277(1683), 829–834. https://doi.org/10.1098/rspb.2009.1845
626 Benson, R. B., Mannion, P. D., Butler, R. J., Upchurch, P., Goswami, A., & Evans, S.
627 E. (2013). Cretaceous tetrapod fossil record sampling and faunal turnover:
628 implications for biogeography and the rise of modern clades. *Palaeogeography,*

Palaeoclimatology, Palaeoecology, 372, 88–107. https://doi.org/10.1016/j.palaeo.2012.10.028

Benson, R. B., & Upchurch, P. (2012). Diversity trends in the establishment of terrestrial vertebrate ecosystems: interactions between spatial and temporal sampling biases. *Geology*, 41(1), 43–46. https://doi.org/10.1130/G33543.1

Benton, M. J., Dunhill, A. M., Lloyd, G. T., & Marx, F. G. (2011). Assessing the quality of the fossil record: insights from vertebrates. *Geological Society, London, Special Publications*, 358, 63–94. https://doi.org/10.1144/SP358.6

Boisvert, C., Perkins, J., Morrison, C., Gascoigne, S. J., Holtz, T. R., & Curtice, B. (2026). Obligate faunivorous megatheropod size class patterns across the Jurassic–Cretaceous Periods. *PeerJ, 14*, e21007. https://doi.org/10.7717/peerj.21007

Bonaparte, J. F. (1985). A horned Cretaceous carnosaur from Patagonia. *National Geographic Research*, 1, 140–151.

Bonaparte, J. F. (1991). The gondwanian theropod families Abelisauridae and Noasauridae. *Historical Biology*, 5(1), 1–25. https://doi.org/10.1080/10292389109380385

Bonaparte, J. F., & Novas, F. E. (1985). *Abelisaurus comahuensis*, n. g., n. sp., Carnosauria from the Late Cretaceous of Patagonia. *Ameghiniana*, 21(2-4), 259–265.

Bonaparte, J. F., Novas, F. E., & Coria, R. A. (1990). *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science*, 416, 1–42.

Brocklehurst, N. (2015). A simulation-based examination of residual diversity estimates as a method of correcting for sampling bias. *Palaeontologia Electronica*, 18.3.7T: 1–15. https://doi.org/10.26879/584

Buffetaut, E., Tong, H., Girard, J., Hoyez, B., & Párraga, J. (2024). *Caletodraco cottardi*: A new furileusaurian abelisaurid (Dinosauria: Theropoda) from the Cenomanian Chalk of Normandy (north-western France). *Fossil Studies*, 2(3), 177–195. https://doi.org/10.3390/fossils2030009

Burgener, L., Hyland, E., Reich, B. J., & Scotese, C. (2023). Cretaceous climates: Mapping paleo-Köppen climatic zones using a Bayesian statistical analysis of lithologic, paleontologic, and geochemical proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 613, 111373. https://doi.org/10.1016/j.palaeo.2022.111373

Butler, R. J., Barrett, P. M., Nowbath, S., & Upchurch, P. (2009). Estimating the effects of sampling biases on pterosaur diversity patterns: implications for hypotheses of bird/pterosaur competitive replacement. *Paleobiology*, 35(3), 432–446. https://doi.org/10.1666/0094-8373-35.3.432

Butler, R. J., Benson, R. B., Carrano, M. T., Mannion, P. D., & Upchurch, P. (2011). Sea level, dinosaur diversity and sampling biases: investigating the 'common cause'hypothesis in the terrestrial realm. *Proceedings of the Royal Society B: Biological Sciences*, 278(1709), 1165–1170. https://doi.org/10.1098/rspb.2010.1754

Butler, R. J., Brusatte, S. L., Andres, B., Benson, R. B. (2012). How do geological sampling biases affect studies of morphological evolution in deep time? A case study of pterosaur (Reptilia: Archosauria) disparity. *Evolution*, 66(1), 147–162. https://doi.org/10.1111/j.1558-5646.2011.01415.x

Calvo, J. O., Rubilar-Rogers, D., & Moreno, K. (2004). A new Abelisauridae (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana*, 41(4), 555–563.

Canale, J. I., Apesteguía, S., Gallina, P. A., Gianechini, F. A., & Haluza, A. (2017). The oldest theropods from the Neuquén Basin: Predatory dinosaur diversity from the

678 Bajada Colorada Formation (Lower Cretaceous: Berriasian–Valanginian), Neuquén,
679 Argentina. *Cretaceous Research*, 71, 63–78.
680 https://doi.org/10.1016/j.cretres.2016.11.010
681 Canale, J. I., Scanferla, C. A., Agnolin, F. L., & Novas, F. E. (2009). New carnivorous
682 dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid
683 theropods. *Naturwissenschaften*, 96(3), 409–414. https://doi.org/10.1007/s00114-
684 008-0487-4
685 Candeiro, R. A., Brusatte, S. L., & de Souza, A. L. (2018). Spinosaurid dinosaurs from
686 the Early Cretaceous of North Africa and Europe: Fossil record, biogeography and
687 extinction. Anuário do Instituto de Geociências, 40, 294–302.
688 https://doi.org/10.11137/2017_3_294_302
689 Cashmore, D. D., & Butler, R. J. (2019). Skeletal completeness of the non-avian
690 theropod dinosaur fossil record. *Palaeontology*, 62(6), 951–981.
691 https://doi.org/10.1111/pala.12436
692 Cashmore, D. D., Butler, R. J., & Maidment, S. C. (2021). Taxonomic identification
693 bias does not drive patterns of abundance and diversity in theropod dinosaurs.
694 *Biology Letters*, 17(7), 20210168. https://doi.org/10.1098/rsbl.2021.0168
695 Carrano, M. T., Benson, R. B., & Sampson, S. D. (2012). The phylogeny of tetanurae
696 (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 10(2), 211–300.
697 Carrano, M. T., & Sampson, S. D. (2008). The phylogeny of Ceratosauria (Dinosauria:
698 Theropoda). *Journal of Systematic Palaeontology*, 6(2), 183–236.
699 https://doi.org/10.1017/S1477201907002246
700 Cerroni, M. A., Canale, J. I., Novas, F. E., & Paulina-Carabajal, A. (2022). An
701 exceptional neurovascular system in abelisaurid theropod skull: new evidence from

Skorpiovenator bustingorryi. *Journal of Anatomy*, 240(4), 612–626. https://doi.org/10.1111/joa.13258

Cerroni, M. A., Motta, M. J., Agnolín, F. L., Rolando, A. A., Egli, F. B., & Novas, F. E. (2020). A new abelisaurid from the Huincul Formation (Cenomanian-Turonian; Upper Cretaceous) of Río Negro province, Argentina. *Journal of South American Earth Sciences*, 98, 102445. https://doi.org/10.1016/j.jsames.2019.102445

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Chatterjee, S. (1978). *Indosuchus* and *Indosaurus*, Cretaceous carnosaurs from India. *Journal of Paleontology*, 52(3), 570–580.

Chiarenza, A. A., Cantalapiedra, J. L., Jones, L. A., Gamboa, S., Galván, S., Farnsworth, A. J., Valdes, P. J., Sotelo, G., & Varela, S. (2024). Early Jurassic origin of avian endothermy and thermophysiological diversity in dinosaurs. *Current Biology*, 34(11), 2517–2527. https://doi.org/10.1016/j.cub.2024.04.051

Chiarenza, A. A., Mannion, P. D., Farnsworth, A., Carrano, M. T., & Varela, S. (2022). Climatic constraints on the biogeographic history of Mesozoic dinosaurs. *Current Biology*, 32(3), 570–585. https://doi.org/10.1016/j.cub.2021.11.061

Chiarenza, A. A., Mannion, P. D., Lunt, D. J., Farnsworth, A., Jones, L. A., Kelland, S. J., & Allison, P. A. (2019). Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature communications*, 10(1), 1091. https://doi.org/10.1038/s41467-019-08997-2

Close, R. A., Benson, R. B., Alroy, J., Carrano, M. T., Cleary, T. J., Dunne, E. M., Mannion, P. D., Uhen, M. D., & Butler, R. J. (2020). The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling biases.

727 *Proceedings of the Royal Society B: Biological Sciences*, 287(1924), 20200372.
728 https://doi.org/10.1098/rspb.2020.0372
729 Close, R. A., Benson, R. B., Upchurch, P., & Butler, R. J. (2017). Controlling for the
730 species-area effect supports constrained long-term Mesozoic terrestrial vertebrate
731 diversification. *Nature Communications*, 8(1), 15381.
732 https://doi.org/10.1038/ncomms15381
733 Close, R. A., Evers, S. W., Alroy, J., & Butler, R. J. (2018). How should we estimate
734 diversity in the fossil record? Testing richness estimators using sampling-
735 standardised discovery curves. *Methods in Ecology and Evolution*, 9(6), 1386–1400.
736 https://doi.org/10.1111/2041-210X.12987
737 Coria, R. A. (2001). A new theropod from the Late Cretaceous of Patagonia. In Tanke,
738 Darren H.; Carpenter, Kenneth (eds.). *Mesozoic Vertebrate Life. Life of the Past* (pp.
739 3–9). Indiana University Press.
740 Coria, R. A., Chiappe, L. M., & Dingus, L. (2002). A new close relative of *Carnotaurus*
741 *sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of
742 Patagonia. *Journal of Vertebrate Paleontology*, 22(2), 460–465.
743 https://doi.org/10.1671/0272-4634(2002)022[0460:ANCROC]2.0.CO;2
744 Coria, R. A., & Salgado, L. (2000). A basal Abelisauria Novas, 1992 (Theropoda-
745 Ceratosauria) from the Cretaceous of Patagonia, Argentina. *Gaia*, 15, 89–102.
746 Coria, R. A., & Salgado, L. (2005). Mid-Cretaceous turnover of saurischian dinosaur
747 communities: evidence from the Neuquén Basin. *Geological Society, London,*
748 *Special Publications*, 252: 317–327. https://doi.org/10.1144/GSL.SP.2005.252.01.16
749 Crampton, J. S., Beu, A. G., Cooper, R. A., Jones, C. M., Marshall, B., & Maxwell,
750 P.A. (2003). Estimating the rock volume bias in paleobiodiversity studies. *Science*,
751 301(5631), 358–360. https://doi.org/10.1126/science.1085075

De Carvalho, J. C., & Santucci, R. M. (2018). New dinosaur remains from the Quiricó Formation, Sanfranciscana Basin (Lower Cretaceous), Southwestern Brazil. *Cretaceous Research*, 85, 20–27. https://doi.org/10.1016/j.cretres.2017.12.017

De Souza-Júnior, A. L., Candeiro, C. R. D. A., Vidal, L. D. S., Brusatte, S. L., & Mortimer, M. (2023). Abelisauroidea (Theropoda, Dinosauria) from Africa: a review of the fossil record. *Papéis Avulsos de Zoologia*, 63, e202363019. https://doi.org/10.11606/1807-0205/2023.63.019

Delcourt, R. (2018). Ceratosaur palaeobiology: new insights on evolution and ecology of the southern rulers. *Scientific Reports*, 8(1), 9730. https://doi.org/10.1038/s41598-018-28154-x

Delcourt, R., & Iori, F. V. (2020). A new Abelisauridae (Dinosauria: Theropoda) from São José do Rio Preto Formation, Upper Cretaceous of Brazil and comments on the Bauru Group fauna. *Historical Biology*, 32(7), 917–924. https://doi.org/10.1080/08912963.2018.1546700

Depéret, C. (1896). Note sur les Dinosauriens Sauropodes et Théropodes du Crétacé supérieur de Madagascar. *Bulletin de la Société Géologique de France*, 21, 176–194.

Dunhill, A. M., Hannisdal, B., & Benton, M. J. (2014). Disentangling rock record bias and common-cause from redundancy in the British fossil record. *Nature communications*, 5(1), 4818. https://doi.org/10.1038/ncomms5818

Dunhill, A. M., Hannisdal, B., Brocklehurst, N., & Benton, M. J. (2018). On formation-based sampling proxies and why they should not be used to correct the fossil record. *Palaeontology*, 61(1), 119–132. https://doi.org/10.1111/pala.12331

Dunne, E. M., Farnsworth, A., Greene, S. E., Lunt, D. J., & Butler, R. J. (2021). Climatic drivers of latitudinal variation in Late Triassic tetrapod diversity. *Palaeontology*, 64(1), 101–117. https://doi.org/10.1111/pala.12514

Dunne, E. M., Thompson, S. E., Butler, R. J., Rosindell, J., & Close, R. A. (2023). Mechanistic neutral models show that sampling biases drive the apparent explosion of early tetrapod diversity. *Nature ecology & evolution*, 7(9), 1480–1489. https://doi.org/10.1038/s41559-023-02128-3

Fabbri, M., Navalón, G., Benson, R. B., Pol, D., O'Connor, J., Bhullar, B. A. S., Erickson, G. M., Norell, M. A., Orkney, A., Lamanna, M. C., Zouhri, S., Becker, J., Emke, A., Dal Sasso, C., Bindellini, G., Maganuco, S., Auditore, M., & Ibrahim, N. (2022). Subaqueous foraging among carnivorous dinosaurs. *Nature*, 603(7903), 852–857. https://doi.org/10.1038/s41586-022-04528-0

Farke, A. A., & Sertich, J. J. (2013). An abelisauroid theropod dinosaur from the Turonian of Madagascar. *PLoS One*, 8(4), e62047. https://doi.org/10.1371/journal.pone.0062047

Filippi, L. S., Méndez, A. H., Valieri, R. D. J., & Garrido, A. C. (2016). A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisaurids. *Cretaceous Research*, 61, 209–219. https://doi.org/10.1016/j.cretres.2015.12.018

Fröbisch, J. (2013). Vertebrate diversity across the end-Permian mass extinction - separating biological and geological signals. P*alaeogeography, Palaeoclimatology, Palaeoecology*, 372, 50–61. https://doi.org/10.1016/j.palaeo.2012.10.036

Gianechini, F. A., Filippi, L. S., Méndez, A. H., & Garrido, A. C. (2022). A non-furileusaurian caudal vertebra from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian) and morphological variation in the tail of Abelisauridae. *Publicación Electrónica de la Asociación Paleontológica Argentina*, 22(2), 58–70. http://dx.doi.org/10.5710/PEAPA.15.10.2022.438

Gianechini, F. A., Méndez, A. H., Filippi, L. S., Paulina-Carabajal, A., Juárez-Valieri, R. D., & Garrido, A. C. (2021). A new furileusaurian abelisaurid from La Invernada (Upper Cretaceous, Santonian, Bajo de la Carpa Formation), northern Patagonia, Argentina. *Journal of Vertebrate Paleontology*, 40(6), e1877151. https://doi.org/10.1080/02724634.2020.1877151

Grillo, O. N., & Delcourt, R. (2017). Allometry and body length of abelisauroid theropods: *Pycnonemosaurus nevesi* is the new king. *Cretaceous Research*, 69, 71–89. https://doi.org/10.1016/j.cretres.2016.09.001

Hassler, A., Martin, J. E., Amiot, R., Tacail, T., Godet, F. A., Allain, R., & Balter, V. (2018). Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, 285(1876): 20180197. https://doi.org/10.1098/rspb.2018.0197

Heath, J. A., Cooper, N., Upchurch, P., & Mannion, P. D. (2025). Accounting for sampling heterogeneity suggests a low paleolatitude origin for dinosaurs. *Current Biology*, 35(5), 941–953. https://doi.org/10.1016/j.cub.2024.12.053

Hendrickx, C., & Mateus, O. (2014). Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa*, 3759(1), 1–74. http://dx.doi.org/10.11646/zootaxa.3759.1.1

Hendrickx, C., Núñez, M. S., Araújo, R., Meso, J. G., Maganuco, S., & Ben-Salahuddin, A. (2025). Isolated abelisaurid teeth from Gondwana and dental evolution in Abelisauridae. *Ameghiniana*, 62(6), 407–451. http://dx.doi.org/10.5710/AMGH.17.09.2025.3654

Hendrickx, C., Tschopp, E., & d Ezcurra, M. (2020). Taxonomic identification of isolated theropod teeth: the case of the shed tooth crown associated with *Aerosteon*

826 (Theropoda: Megaraptora) and the dentition of Abelisauridae. *Cretaceous Research*,
827 108, 104312. https://doi.org/10.1016/j.cretres.2019.104312
828 Huber, B. T., MacLeod, K. G., Watkins, D. K., & Coffin, M. F. (2018). The rise and fall
829 of the Cretaceous Hot Greenhouse climate. *Global and Planetary Change*, 167, 1–
830 23. https://doi.org/10.1016/j.gloplacha.2018.04.004
831 Iori, F. V., de Araujo-Junior, H. I., Tavares, S. A. S., da Silva Marinho, T., &
832 Martinelli, A. G. (2021). New theropod dinosaur from the Late Cretaceous of Brazil
833 improves abelisaurid diversity. *Journal of South American Earth Sciences*, 112(1),
834 103551. https://doi.org/10.1016/j.jsames.2021.103551
835 Isasmendi, E., & Malafaia, E. (2025). New Contributions to the Knowledge of
836 Abelisauridae (Dinosauria, Theropoda) from the Upper Cretaceous Ibero-Armorican
837 Landmass. *Ameghiniana*, 62(6), 452–479.
838 https://doi.org/10.5710/AMGH.17.10.2025.3660
839 Isasmendi, E., Torices, A., Canudo, J. I., & Pereda-Suberbiola, X. (2021). Abelisaurid
840 dinosaurs from the Upper Cretaceous Laño site (Iberian Peninsula). *Ciências da*
841 *Terra Procedia*, 1, 38–41. https://doi.org/10.21695/cterraproc.v1i0.401
842 Jacobs, L. L., Winkler, D. A., Downs, W. R., & Gomani, E. M. (1993). New material of
843 an Early Cretaceous sauropod dinosaur from Africa. *Palaeontology*, 36: 523–534.
844 Jimenez Velandia, H., Ezcurra, M. D., Hechenleitner, E. M., Basilici, G., Martinelli, A.
845 G., & Fiorelli, L. E. (2025). A New Late Cretaceous Abelisaurid Species from La
846 Rioja Province, Northwestern Argentina. *Ameghiniana*, 62(6), 505–527.
847 https://doi.org/10.5710/AMGH.24.09.2025.3653
848 Kellner, A.W.A., & Campos, D. A. (2002). On a theropod dinosaur (Abelisauria) from
849 the continental Cretaceous of Brazil. *Arquivos do Museu Nacional Rio de Janeiro*,
850 60(3), 163–170.

Kocsis, Á. T., Reddin, C. J., Alroy, J., & Kiessling, W. (2019). The R package divDyn for quantifying diversity dynamics using fossil sampling data. *Methods in Ecology and Evolution*, 10(5), 735–743. https://doi.org/10.1111/2041-210X.13161

Krause, D. W., Sampson, S. D., Carrano, M. T., & O'Connor, P. M. (2007). Overview of the history of discovery, taxonomy, phylogeny, and biogeography of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 27(S2), 1–20. https://doi.org/10.1671/0272-4634(2007)27[1:OOTHOD]2.0.CO;2

Longrich, N. R., Pereda-Suberbiola, X., Jalil, N. E., Khaldoune, F., & Jourani, E. (2017). An abelisaurid from the latest Cretaceous (late Maastrichtian) of Morocco, North Africa. *Cretaceous Research*, 76, 40–52. https://doi.org/10.1016/j.cretres.2017.03.021

Lloyd, G. T., Young, J. R., & Smith, A. B. (2012). Taxonomic structure of the fossil record is shaped by sampling bias. *Systematic Biology*, 61(1), 80.https://doi.org/10.1093/sysbio/syr076

Maniel, I. J., Almeida, R., Kimbrough, D. L., de la Puente, G. S., Garrido, A. C., Bellardini, F., & Mahoney, J. B. (2026). Albian zircon U-Pb crystallization ages from tuff beds in the Candeleros and Huincul formations, Neuquén Basin, Argentina. *Gondwana Research*, 159, 193–204. https://doi.org/10.1016/j.gr.2026.06.020

Mannion, P. D., Benson, R. B., Upchurch, P., Butler, R. J., Carrano, M. T., & Barret, P. M. (2012). A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecology and Biogeography*, 21(9), 898–908. https://doi.org/10.1111/j.1466-8238.2011.00735.x

Mannion, P. D., Upchurch, P., Carrano, M. T., & Barrett, P. M. (2011). Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the

876 generic richness of sauropodomorph dinosaurs through time. *Biological Reviews*, 86,
877 157–181. https://doi.org/10.1111/j.1469-185X.2010.00139.x
878 Martínez, R. N., Giménez, O., Rodríguez, J., & Bochatey, G. (1987). *Xenotarsosaurus*
879 *bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la
880 Formación Bajo Barreal, Chubut, Argentina". *IV Congreso Argentino de*
881 *Paleontología y Bioestratigrafía*, 1, 23–31.
882 Martínez, R., Novas, F., & Ambrosio, A. (2004). Abelisaurid remains (Theropoda,
883 Ceratosauria) from southern Patagonia. *Ameghiniana*, 41(4), 577–585.
884 Marx, F. G. (2009). Marine mammals through time: when less is more in studying
885 palaeodiversity. *Proceedings of the Royal Society of London Series B*, 276(1658),
886 887–892. https://doi.org/10.1098/rspb.2008.1473
887 Matley, C. A. (1923). Note on an armoured dinosaur from the Lameta beds of
888 Jubbulpore. *Records of the Geological Survey of India*, 55(2), 105–109.
889 Mazzetta, G. V., Fariña, R. A., & Vizcaíno, S. F. (1998). On the palaeobiology of the
890 South American horned theropod *Carnotaurus sastrei* Bonaparte. *Gaia*, 15(185),
891 185–192.
892 Méndez, A. H., Gianechini, F. A., Paulina-Carabajal, A., Filippi, L. S., Juárez-Valieri,
893 R. D., Cerda, I. A., & Garrido, A. C. (2022). New furileusaurian remains from La
894 Invernada (northern Patagonia, Argentina): A site of unusual abelisaurids abundance.
895 *Cretaceous Research*, 129, 104989. https://doi.org/10.1016/j.cretres.2021.104989
896 Meso, J. G., Valieri, R. J., Porfiri, J. D., Correa, S. A. S., Martinelli, A. G., Casal, G. A.,
897 Canudo, J. I., Poblete, F., & Dos Santos, D. (2021). Testing the persistence of
898 Carcharodontosauridae (Theropoda) in the Upper Cretaceous of Patagonia based on
899 dental evidence. *Cretaceous Research*, 125, 104875.
900 https://doi.org/10.1016/j.cretres.2021.104875

Miller, J. T., Jolley-Rogers, G., Mishler, B. D., & Thornhill, A. H. (2018). Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution*, 56(6), 663–667. https://doi.org/10.1111/jse.12436

Norell, A. M. (1992). Taxic origin and temporal diversity: the effect of phylogeny. In: Novacek, M.J., Wheeler, Q.D. (Eds.), *Extinction & Phylogeny*. Columbia University Press, New York, pp. 89–118.

Norell, M. A., & Novacek, M. J. (1992). Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil evidence. *Cladistics*, 8, 319–337. https://doi.org/10.1111/j.1096-0031.1992.tb00074.x

Novas. F. E. (2009). The age of dinosaurs in South America. Bloomington (IN): Indiana University Press, 452 pp.

Novas, F. E., Agnolín, F. L., & Bandyopadhyay, S. (2004). Cretaceous theropods from India: a review of specimens described by Huene and Matley (1933). *Revista del Museo Argentino de Ciencias Naturales*, 6(1), 67-103.

Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. Cretaceous Research, 45, 174–215. https://doi.org/10.1016/j.cretres.2013.04.001

Novas, F., Agnolin, F., Rozadilla, S., Aranciaga Rolando, A. M., Brisson-Egli, F., Motta, M. J., Cerroni, M., Ezcurra, M. D., Martinelli, A. G., D'Angelo, J. S., Alvarez-Herrera, G., Gentili, A. R., Bogan, S., Chimento, N. R., García-Marsá, J. A., Lo Coco, G., Miquel, S. E., Brito, F. F., Vera, E. I., Perez Loinaze, V. S., Fernández, M. S., & Salgado, L. (2019). Paleontological discoveries in the Chorrillo Formation (upper Campanian–lower Maastrichtian, Upper Cretaceous), Santa Cruz Province,

Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales*, 21(2), 217–293. https://doi.org/10.22179/REVMACN.21.655

Novas, F. E., Chatterjee, S., Rudra, D. K., & Datta, P. M. (2010). *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India. In *New aspects of Mesozoic biodiversity* (pp. 45–62). Berlin, Heidelberg: Springer Berlin Heidelberg.

Novas, F. E., de Valais, S., Vickers-Rich, P., & Rich, T. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, 92(5), 226–230. https://doi.org/10.1007/s00114-005-0623-3

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, 1, 118–122. https://doi.org/10.1111/j.2041-210X.2010.00021.x

Ősi, A., Apesteguía, S., & Kowalewski, M. (2010). Non-avian theropod dinosaurs from the early Late Cretaceous of Central Europe. *Cretaceous Research*, 31(3), 304–320. https://doi.org/10.1016/j.cretres.2010.01.001

Ősi, A., & Buffetaut, E. (2011). Additional non-avian theropod and bird remains from the early Late Cretaceous (Santonian) of Hungary and a review of the European abelisauroid record. *Annales de Paléontologie*, 97 (1-2), 35–49. https://doi.org/10.1016/j.annpal.2011.07.001

Pereyra, E. E. S. (2025). Orbit Shape Evolution in Abelisauridae: Macroevolutionary Trends and Functional Implications. *Cretaceous Research*, 106272. https://doi.org/10.1016/j.cretres.2025.106272

Pereyra, E. E., Ezcurra, M. D., Paschetta, C., & Méndez, A. H. (2025a). Building a predator: macroevolutionary patterns in the skull of abelisaurid dinosaurs.

Proceedings of the Royal Society B: Biological Sciences, 292(2058), 20250943. https://doi.org/10.1098/rspb.2025.0943

Pereyra, E. E. S., Pérez, D. E., Gonzales-Dionis, J., & Ezcurra, M. D. (2025b). The Phylogenetic Data Matrices of Abelisauridae through Time and Methods (With Recommendations). *Ameghiniana*, 62(6), 380–395. https://doi.org/10.5710/AMGH.27.12.2025.3650

Pereyra, E. E. S., Pérez, D. E., & Méndez, A. H. (2025c). Macroevolutionary trends in Ceratosauria body size: insights of phylogenetic comparative methods. *BMC Ecology and Evolution*, 25(1), 32. https://doi.org/10.1186/s12862-025-02374-y

Peters, S. E. (2005). Geologic constraints on the macroevolutionary history of marine animals. *Proceedings of the National Academy of Sciences*, 102(35), 12326–12331. https://doi.org/10.1073/pnas.0502616102

Peters, S. E., & Foote, M. (2001). Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology*, 27(4), 583–601. https://doi.org/10.1666/0094-8373(2001)027<0583:BITPAR>2.0.CO;2

Pol, D., Baiano, M. A., Černý, D., Novas, F. E., Cerda, I. A., & Pittman, M. (2024). A new abelisaurid dinosaur from the end Cretaceous of Patagonia and evolutionary rates among the Ceratosauria. *Cladistics*, 40(3), 307–356. https://doi.org/10.1111/cla.12583

Pol, D., & Leardi, J. M. (2015). Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. In: Fernández M, Herrera Y (Eds) Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini. *Publicación Electrónica de la Asociación Paleontológica Argentina*, 15, 172–186. https://doi.org/10.5710/PEAPA.10.06.2015.108

973 Pol, D., Ramezani, J., Gomez, K., Carballido, J. L., Carabajal, A. P., Rauhut, O. W. M.,
974 Escapa, I. H., & Cúneo, N. R. (2020). Extinction of herbivorous dinosaurs linked to
975 Early Jurassic global warming event. *Proceedings of the Royal Society B: Biological*
976 *Sciences*, 287(1939). https://doi.org/10.1098/rspb.2020.2310
977 Pol, D., & Rauhut, O. W. (2012). A Middle Jurassic abelisaurid from Patagonia and the
978 early diversification of theropod dinosaurs. *Proceedings of the Royal Society B:*
979 *Biological Sciences*, 279(1741), 3170–3175. https://doi.org/10.1098/rspb.2012.0660
980 R Core Team (2025). R: a language and environment for statistical computing. *R*
981 *Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org
982 Raja, N. B., Dunne, E. M., Matiwane, A., Khan, T. M., Nätscher, P. S., Ghilardi, A. M.,
983 & Chattopadhyay, D. (2022). Colonial history and global economics distort our
984 understanding of deep-time biodiversity. *Nature ecology & evolution*, 6(2), 145–154.
985 https://doi.org/10.1038/s41559-021-01608-8
986 Ratsimbaholison, N. O., Felice, R. N., & O'Connor, P. M. (2016). Ontogenetic changes
987 in the craniomandibular skeleton of the abelisaurid dinosaur *Majungasaurus*
988 *crenatissimus* from the Late Cretaceous of Madagascar. *Acta Palaeontologica*
989 *Polonica*, 61(2), 281–292. https://doi.org/10.4202/app.00132.2014
990 Rauhut, O. W. (2011). Theropod dinosaurs from the late Jurassic of Tendaguru
991 (Tanzania). Special Papers in *Palaeontology*, 86(1), 195–239.
992 https://doi.org/10.1111/j.1475-4983.2011.01084.x
993 Rauhut, O. W., & Pol, D. (2021). New theropod remains from the late Jurassic Cañadón
994 Calcáreo formation of Chubut, Argentina. *Journal of South American Earth*
995 *Sciences*, 111, 103434. https://doi.org/10.1016/j.jsames.2021.103434
996 Raup, D. M. (1976). Species diversity in the Phanerozoic: an interpretation.
997 *Paleobiology*, 2(4): 289–297. https://doi.org/10.1017/S0094837300004929

998 Riabinin, A. N. (1938). Some results of the studies of the Upper Cretaceous dinosaurian
999 fauna from the vicinity of the station Sary-Agach, South Kazakhstan. *Problems of*
1000 *Paleontology*, 4, 125–135.
1001 Ribeiro, T. B., Cupello, C., de Mayrink, D., da Costa Pereira, P. V. L. G., & Brito, P.
1002 M. (2024). A theropod tooth from the Missão Velha formation (Late Jurassic–Early
1003 Cretaceous) of the Araripe basin: oldest Brazilian abelisaurid record. *Historical*
1004 *Biology*, 37(4), 827–837. https://doi.org/10.1080/08912963.2024.2336982
1005 Ribeiro, T. B., Vecchietti, L. F., Candeiro, C. R., Canale, J. I., Bergqvist, L. P., Brito, P.
1006 M., & Pereira, P. V. (2025). Overabundance of abelisaurid teeth in the Açu
1007 Formation (Albian-Cenomanian), Potiguar Basin, Northeastern Brazil:
1008 morphometric, cladistic and machine learning approaches. *Journal of Vertebrate*
1009 *Paleontology*, 44(6), e2487366. https://doi.org/10.1080/02724634.2025.2487366
1010 Richter, U., Mudroch, A., & Buckley, L. G. (2013). Isolated theropod teeth from the
1011 Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. *Palaeontologische*
1012 *Zeitschrift*, 87(2), 291–309. https://doi.org/10.1007/s12542-012-0153-1
1013 Rowe, A. J., Cerroni, M. A., & Rayfield, E. J. (2026). Southern hemisphere ceratosaurs
1014 evolved feeding mechanics paralleling those of Northern hemisphere tyrannosaurids.
1015 *Scientific Reports*, 16(1), 2804. https://doi.org/10.1038/s41598-025-32686-4
1016 Sakamoto, M., Venditti, C., & Benton, M. J. (2016). 'Residual diversity estimates' do
1017 not correct for sampling bias in palaeodiversity data. *Methods in Ecology and*
1018 *Evolution*, 8(4), 453–459. https://doi.org/10.1111/2041-210X.12666
1019 Salem, B. S., Lamanna, M. C., O'Connor, P. M., El-Qot, G. M., Shaker, F., Thabet, W.
1020 A., El-Sayed, S., & Sallam, H. M. (2022). First definitive record of Abelisauridae
1021 (Theropoda: Ceratosauria) from the Cretaceous Bahariya Formation, Bahariya Oasis,

Western Desert of Egypt. *Royal Society Open Science*, 9(6), 220106. https://doi.org/10.1098/rsos.220106

Sampson, S. D., & Witmer, L. M. (2007). Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 27(S2), 32–104. https://doi.org/10.1671/0272-4634(2007)27[32:CAOMCT]2.0.CO;2

Sampson, S. D., Witmer, L. M., Forster, C. A., Krause, D. W., O'Connor, P. M., Dodson, P., & Ravoavy, F. (1998). Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science*, 280(5366), 1048–1051. https://doi.org/10.1126/science.280.5366.1048

Sereno, P. C., & Brusatte, S. L. (2008). Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica*, 53(1), 15–46. https://doi.org/10.4202/app.2008.0102

Sereno, P. C., Wilson, J. A., & Conrad, J. L. (2004). New dinosaurs link southern landmasses in the Mid–Cretaceous. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1546), 1325–1330. https://doi.org/10.1098/rspb.2004.2692

Smith, A. B., & McGowan, A. J. (2007). The shape of the Phanerozoic palaeodiversity curve: how much can be predicted from the sedimentary rock record of Western Europe. *Palaeontology*, 50(4), 765–774. https://doi.org/10.1111/j.1475-4983.2007.00693.x

Smith, J. B., & Dalla Vecchia, F. M. (2006). An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla Formation of Libya. Journal of African Earth *Sciences*, 46(3), 240–244. https://doi.org/10.1016/j.jafrearsci.2006.05.007

Soto, M., Delcourt, R., Langer, M. C., & Perea, D. (2023). The first record of Abelisauridae (Theropoda: Ceratosauria) from Uruguay (Late Jurassic, Tacuarembó Formation). *Historical Biology*, 35(12), 2362–2371. https://doi.org/10.1080/08912963.2022.2140425

Starrfelt, J., & Liow, L. H. (2016). How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1691), 20150219.

Tennant, J. P., Chiarenza, A. A., & Baron, M. (2018). How has our knowledge of dinosaur diversity through geologic time changed through research history?. *PeerJ*, 6:e4417 https://doi.org/10.7717/peerj.4417

Therrien, F. D., Henderson, M., & Ruff, C. B. (2005). Bite me: biomechanical models of theropod mandibles and implications for feeding behavior. In K. Carpenter (Eds.), *The Carnivorous Dinosaurs* (pp. 179–237). Indiana University Press.

Tortosa, T., Buffetaut, E., Vialle, N., Dutour, Y., Turini, E., & Cheylan, G. (2014). A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. *Annales de Paléontologie*, 100(1), 63–86. https://doi.org/10.1016/j.annpal.2013.10.003

Uhen, M. D., Allen, B. J., Clapham, M., Cohen, P., Dunne, E. M., Hendy, A., Holroyd, P. A., Hopkins, M., Jardine, P. E., Kocsis, Á. T., Mannion, P., Novack-Gottshall, P., Pimiento, C., & Wagner, P. (2026). Paleobiology Database User Guide Version 2.0. *PaleoBios*, 43(1), 1–54. https://doi.org/10.5070/P9.62178

Upchurch, P., Mannion, P. D., Benson, R. B. J., Butler, R. J., & Carrano, M. T. (2011). Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. *Geological Society of London Special Publication*, 358, 209–240. https://doi.org/10.1144/SP358.14

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth edition. Springer Science & Business Media.

Von Huene, F., & Matley, C. A. (1933). The Cretaceous Saurischia and Ornithischia of the central provinces of India. Memoirs of the Geological Survey of India, 21, 1–74.

Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G. H., Clark, J. M., & Xu, X. (2017). Extreme ontogenetic changes in a ceratosaurian theropod. *Current Biology*, 27(1), 144–148. https://doi.org/10.1016/j.cub.2016.10.043

Wilson, J. A., Sereno, P. C., Srivastava, S., Bhatt, D. K., Khosla, A., & Sahni, A. (2003). A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contributions from the Museum of Paleontology, University of Michigan*, 31(1), 1–42.

Zaher, H., Pol, D., Navarro, B. A., Delcourt, R., & Carvalho, A. B. (2020). An Early Cretaceous theropod dinosaur from Brazil sheds light on the cranial evolution of the Abelisauridae. *Comptes Rendus Palevol*, 19(6), 101–115. http://dx.doi.org/10.5852/cr-palevol2020v19a6

FIGURE CAPTIONS

Figure 1. Abelisauridae records retrieved from the PBDB. **A**, Number of occurrences from each country and continent. Abbreviations: AR, Argentina; BR, Brazil; UY, Uruguay; CL, Chile; CO, Colombia; BO, Bolivia; MG, Madagascar; MA, Morocco; EG, Egypt; NE, Niger; TZ, Tanzania; LY, Libya; IN, India; KZ, Kazakhstan; SA, Saudi Arabia; FR, France; ES, Spain; PT, Portugal; HU, Hungary. **B**, Curve of cumulative publications (light yellow columns) and taxonomic opinions (green line) of Abelisauridae entered in the PBDB, per year. The figure also shows the number of newly described species since the establishment of the family Abelisauridae. Silhouette

from PhyloPic, drawn by Jack Mayer Wood (https://creativecommons.org/licenses/by-sa/3.0/).

Figure 2. Schematic figure showing a guide to the data used and the methodological framework followed.

Figure 3. Taxic diversity estimates (TDE) vs. Modelled diversity estimates (MDE) against geological time (stage names abbreviated), using sampling proxies, formations (**A**), collections (**B**), and equal grid cells (**C**). Green line shows observed Abelisauridae TDE, while MDE using formations, collections and grid cells are shown in red, blue and violet dashed lines, respectively, with 95% confidence intervals.

Figure 4. Abelisauridae occurrences retrieved from the PBDB. **A**, Paleolatitudinal distribution using Seton model; **B**, Number of occurrences of Abelisauridae for each stage and with theropod-bearing formations; **C**, Paleogeographic maps showing principal localities with abelisaurids remains for each period.

Table 1. Detailed information about recognized Abelisauridae species.

Taxa	FAD	LAD	Stage	Formation	References
Abelisaurus comahuensis	72.1	66	Maastrichtian	Allen Fm, Argentina	Bonaparte and Novas, 1985
Arcovenator escotae	75.9	72.1	Late Campanian	Argiles rutilantes Fm, France	Tortosa et al., 2014
Aucasaurus garridoi	83.6	72.1	Campanian	Anacleto Fm, Argentina	Coria et al., 2002
Caletodraco cottardi	100.5	97.2	Early Cenomanian	Glauconitic Chalk of the Pays de Caux, France	Buffetaut et al., 2024
Carnotaurus sastrei	69.05	66	Late Maastrichtian	La Colonia Fm, Argentina	Bonaparte, 1985
Chenanisaurus barbaricus	69.05	66	Late Maastrichtian	Phosphates of Ouled	Longrich et al., 2017

				Abdoun Basin, Morocco	
Dahalokely tokana	93.9	89.8	Turonian	Ambolafotsy Fm, Madagascar	Farke and Sertich, 2013
Ekrixinatosaurus novasi	113.2	100.5	Albian	Candeleros Fm, Argentina	Calvo et al., 2004
Elemgasem nubilus	93.9	85.7	Turonian–Coniacian	Portezuelo Fm, Argentina	Baiano et al., 2022
Eoabelisaurus mefi	184.2	174.7	Toarcian	Cañadón Asfalto Fm, Argentina	Pol and Rauhut, 2012
Genusaurus sisteronis	113.2	100.5	Albian	?, France	Accarie et al., 1995
Guemesia ochoai	83.6	66	Campanian–Maastrichtian	Los Blanquitos Fm, Argentina	Agnolín et al., 2021
Huinculsaurus montesi	113.2	100.5	Albian	Huincul Fm, Argentina	Baiano et al., 2020
Ilokelesia aguadagrandensis	113.2	100.5	Albian	Huincul Fm, Argentina	Coria and Salgado, 2000
Indosaurus matleyi	72.1	66	Maastrichtian	Lameta Fm, India	Chatterjee, 1978
Koleken inakayali	69.05	66	Late Maastrichtian	La Colonia Fm, Argentina	Pol et al., 2024
Kryptops palaios (maxilla)	121.4	100.5	Aptian–Albian	Elrhaz Fm, Niger	Sereno and Brusatte, 2008
Kurupi itaata	72.1	66	Maastrichtian	Marília Fm, Brazil	Iori et al., 2021
Llukalkan aliocranianus	85.7	83.6	Santonian	Bajo de la Carpa Fm, Argentina	Gianechini et al., 2021
Majungasaurus crenatissimus	72.1	66	Maastrichtian	Maevarano Fm, Madagascar	Depéret, 1896
MPM 99	100.5	89.8	Cenomanian–Turonian	Bajo Barreal Fm, Argentina	Martínez et al., 2004
Niebla antiqua	72.1	66	Maastrichtian	Allen Fm, Argentina	Aranciaga Rolando et al., 2021

Pycnonemosaurus nevesi	75.9	66	Late Campanian–Maastrichtian	Bauru Group, Brazil	Kellner and Campos, 2002
Quilmesaurus curriei	72.1	66	Maastrichtian	Allen Fm, Argentina	Coria, 2001
Rahiolisaurus gujaratensis	72.1	66	Maastrichtian	Lameta Fm, India	Novas et al., 2010
Rajasaurus narmadensis	72.1	66	Maastrichtian	Lameta Fm, India	Wilson et al., 2003
Rugops primus	100.5	93.9	Cenomanian	Echkar Fm, Niger	Sereno et al., 2004
Skorpiovenator bustingorryi	113.2	100.5	Albian	Huincul Fm, Argentina	Canale et al., 2009
Spectrovenator ragei	121.4	113.2	Aptian	Quiricó Fm, Brazil	Zaher et al., 2020
Thanos simonattoi	85.8	83.6	Santonian	São José do Rio Preto Fm, Brazil	Delcourt and Iori, 2020
Tralkasaurus cuyi	113.2	100.5	Albian	Huincul Fm, Argentina	Cerroni et al., 2020
Vitosaura colozacani	83.6	72.1	Campanian	Los Llanos Fm, Argentina	Jiménez Velandia et al., 2025
Viavenator exxoni	85.7	83.6	Santonian	Bajo de la Carpa Fm, Argentina	Filippi et al., 2016
Xenotarsosaurus bonapartei	100.5	89.8	Cenomanian-Turonian	Bajo Barreal Fm, Argentina	Martínez et al., 1987

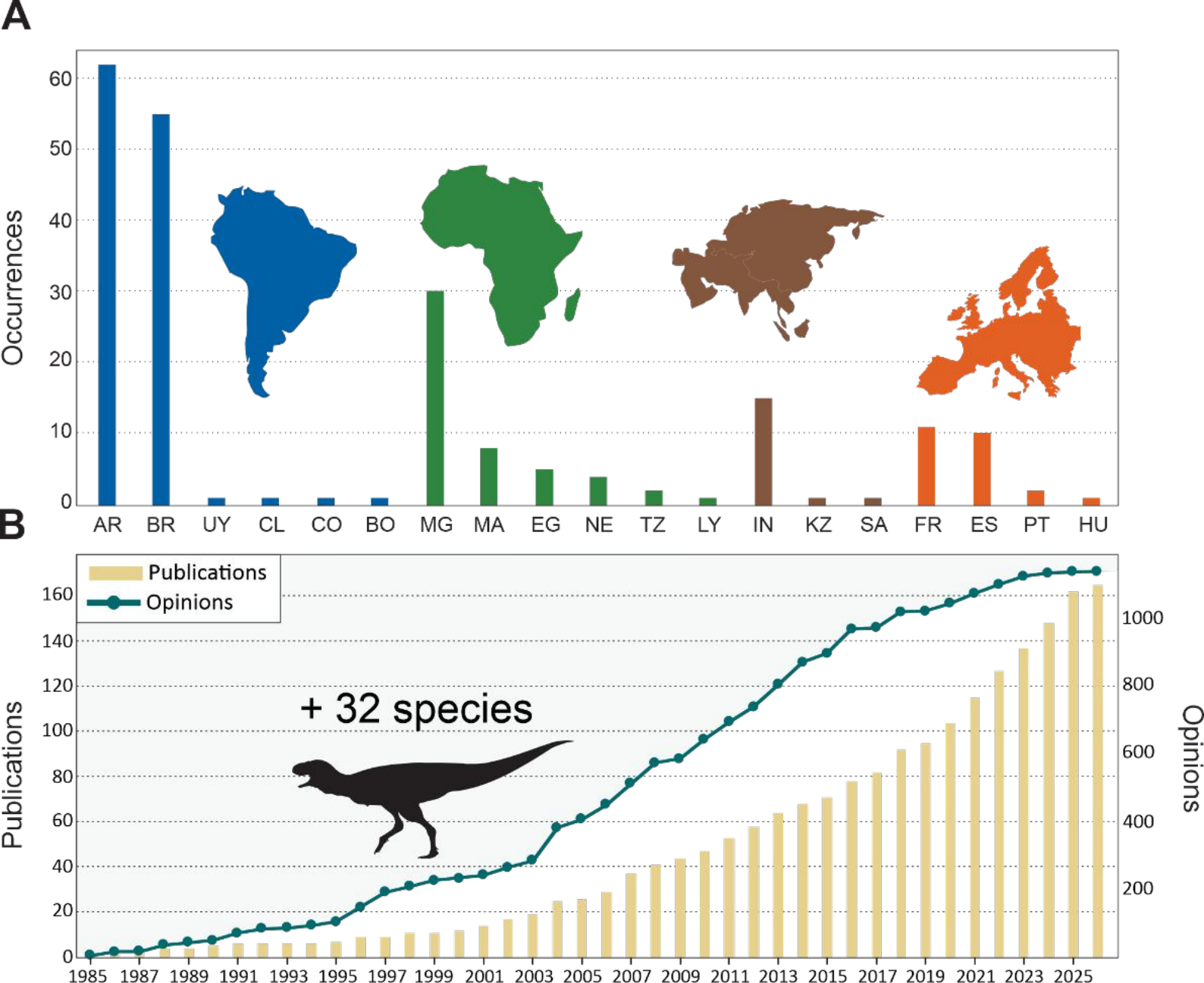
SUPPLEMENTARY ONLINE INFORMATION

Supplementary Online Information 1: Excel file with PBDB data, including occurrences, collections, publications and taxonomic opinions.

Supplementary Online Information 2: R scripts for analyses.

Supplementary Online Information 3: Excel file with data on formations and collections with theropods remains downloaded from the PBDB.

1119


A
Occurrences
0
10
20
30
40
50
60
AR
BR
UY
CL
CO
BO
MG
MA
EG
NE
TZ
LY
IN
KZ
SA
FR
ES
PT
HU
B
Publications
Opinions
+ 32 species
Publications
Opinions
0
20
40
60
80
100
120
140
160
200
400
600
800
1000
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013
2015
2017
2019
2021
2023
2025

Literature

- Publications
- Taxonomic opinions
- Species identification

Paleobiology Database (PBDB)

- Occurrences
- Formations
- Collections
- Paleocoordinates

Abelisauridae fossil record

- Cleaned dataset
- Spatial and temporal distribution

Taxic Diversity Estimate (TDE)

- Number of recognized species for each time bin

Sampling proxies

Formations

Collections

Occupied grid cells

- Number of theropod-bearing formations and collections

Sampling diversity analysis

TDE vs. sampling proxies

Modelled diversity estimate (MDE)

Expected diversity given sampling proxies

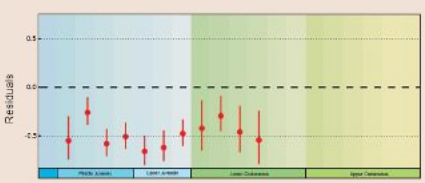
Residual diversity estimate (RDE)

log RDE= log TDE - log MDE

Does observed diversity (TDE) differ from that expected (MDE) from sampling proxies?

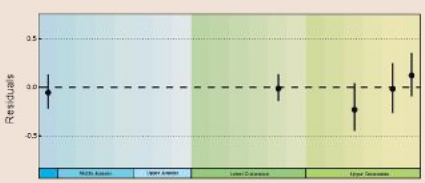
TDE < MDE

Low diversity is not fully accounted by sampling proxies



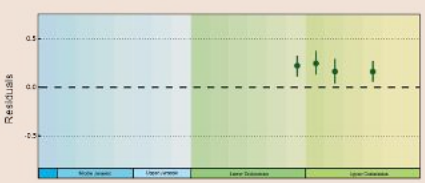
TDE ≈ MDE

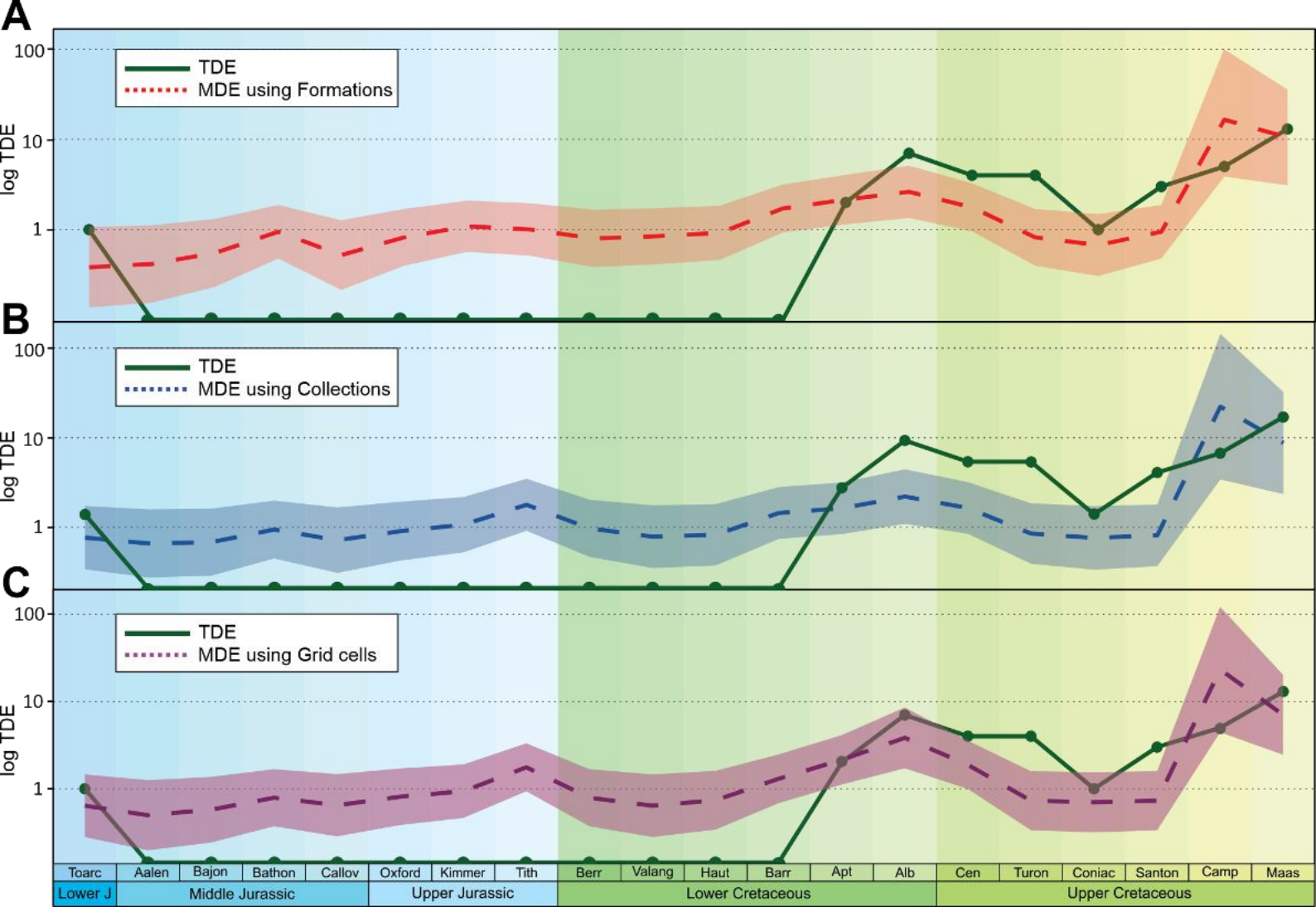
Diversity consistent with sampling proxies



TDE > MDE

High diversity is not fully accounted by sampling proxies




A
B
C
log TDE
100
10
1
TDE
MDE using Formations
MDE using Collections
MDE using Grid cells
Toarc
Aalen
Bajon
Bathon
Callov
Oxford
Kimmer
Tith
Berr
Valang
Haut
Barr
Apt
Alb
Cen
Turon
Coniac
Santon
Camp
Maas
Lower J
Middle Jurassic
Upper Jurassic
Lower Cretaceous
Upper Cretaceous

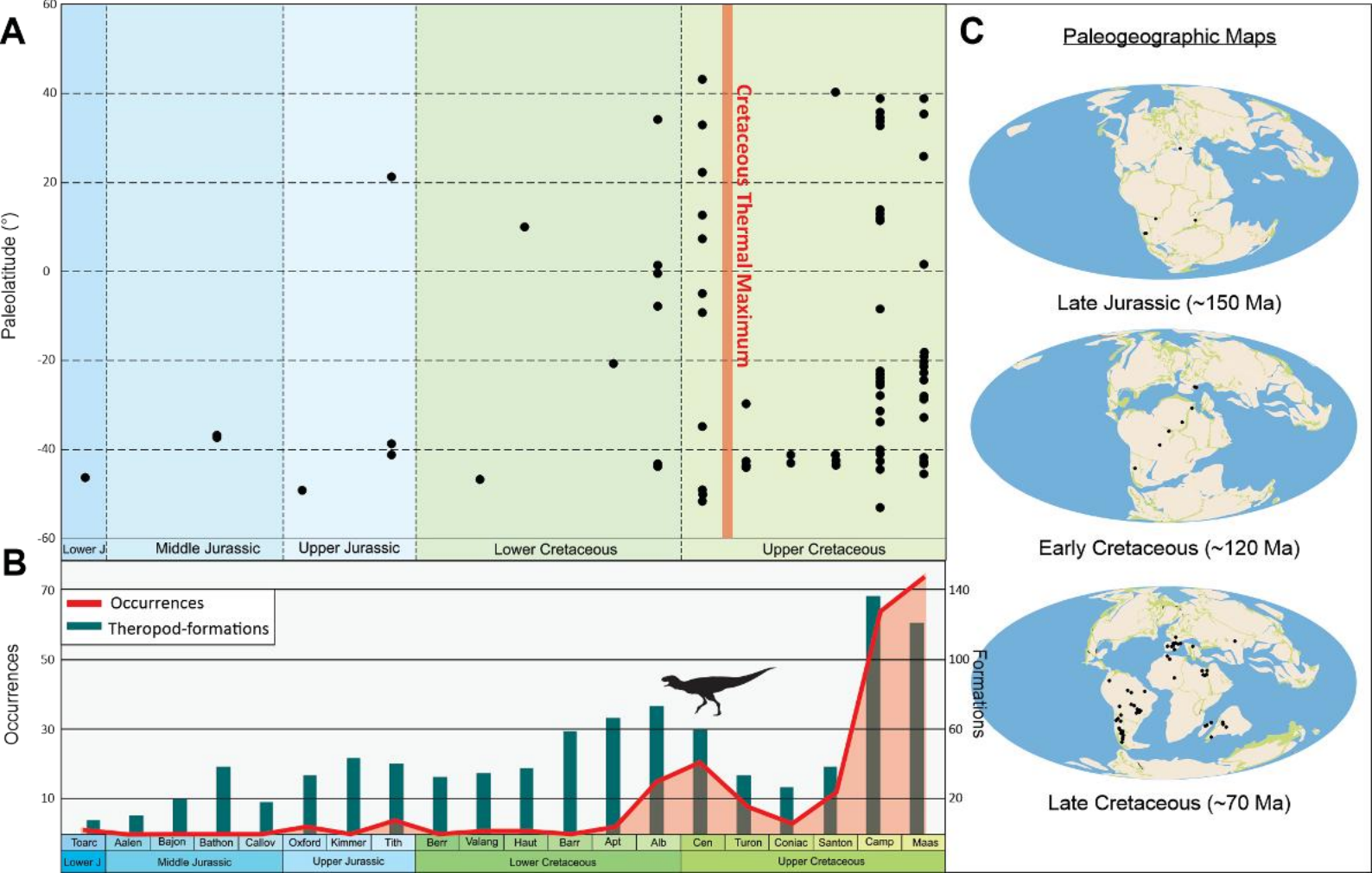

A
Paleolatitude (°)
60
40
20
0
-20
-40
-60
Cretaceous Thermal Maximum
Lower J
Middle Jurassic
Upper Jurassic
Lower Cretaceous
Upper Cretaceous
B
Occurrences
Theropod-formations
Occurrences
Formations
70
50
30
10
140
100
60
20
Toarc
Aalen
Bajon
Bathon
Callov
Oxford
Kimmer
Tith
Berr
Valang
Haut
Barr
Apt
Alb
Cen
Turon
Coniac
Santon
Camp
Maas
Lower J
Middle Jurassic
Upper Jurassic
Lower Cretaceous
Upper Cretaceous
C
Paleogeographic Maps
Late Jurassic (~150 Ma)
Early Cretaceous (~120 Ma)
Late Cretaceous (~70 Ma)

Table 1. Detailed information about recognized Abelisauridae species.

Taxa	FAD	LAD	Stage	Formation	References
Abelisaurus comahuensis	72.1	66	Maastrichtian	Allen Fm, Argentina	Bonaparte and Novas, 1985
Arcovenator escotae	75.9	72.1	Late Campanian	Argiles rutilantes Fm, France	Tortosa et al., 2014
Aucasaurus garridoi	83.6	72.1	Campanian	Anacleto Fm, Argentina	Coria et al., 2002
Caletodraco cottardi	100.5	97.2	Early Cenomanian	Glauconitic Chalk of the Pays de Caux, France	Buffetaut et al., 2024
Carnotaurus sastrei	69.05	66	Late Maastrichtian	La Colonia Fm, Argentina	Bonaparte, 1985
Chenanisaurus barbaricus	69.05	66	Late Maastrichtian	Phosphates of Ouled Abdoun Basin, Morocco	Longrich et al., 2017
Dahalokely tokana	93.9	89.8	Turonian	Ambolafotsy Fm, Madagascar	Farke and Sertich, 2013
Ekrixinatosaurus novasi	113.2	100.5	Albian	Candeleros Fm, Argentina	Calvo et al., 2004
Elemgasem nubilus	93.9	85.7	Turonian–Coniacian	Portezuelo Fm, Argentina	Baiano et al., 2022
Eoabelisaurus mefi	184.2	174.7	Toarcian	Cañadón Asfalto Fm, Argentina	Pol and Rauhut, 2012
Genusaurus sisteronis	113.2	100.5	Albian	?, France	Accarie et al., 1995
Guemesia ochoai	83.6	66	Campanian–Maastrichtian	Los Blanquitos Fm, Argentina	Agnolín et al., 2021
Huinculsaurus montesi	113.2	100.5	Albian	Huincul Fm, Argentina	Baiano et al., 2020
Ilokelesia aguadagrandensis	113.2	100.5	Albian	Huincul Fm, Argentina	Coria and Salgado, 2000

Indosaurus matleyi	72.1	66	Maastrichtian	Lameta Fm, India	Chatterjee, 1978
Koleken inakayali	69.05	66	Late Maastrichtian	La Colonia Fm, Argentina	Pol et al., 2024
Kryptops palaios (maxilla)	121.4	100.5	Aptian–Albian	Elrhaz Fm, Niger	Sereno and Brusatte, 2008
Kurupi itaata	72.1	66	Maastrichtian	Marília Fm, Brazil	Iori et al., 2021
Llukalkan aliocranianus	85.7	83.6	Santonian	Bajo de la Carpa Fm, Argentina	Gianechini et al., 2021
Majungasaurus crenatissimus	72.1	66	Maastrichtian	Maevarano Fm, Madagascar	Depéret, 1896
MPM 99	100.5	89.8	Cenomanian–Turonian	Bajo Barreal Fm, Argentina	Martínez et al., 2004
Niebla antiqua	72.1	66	Maastrichtian	Allen Fm, Argentina	Aranciaga Rolando et al., 2021
Pycnonemosaurus nevesi	75.9	66	Late Campanian–Maastrichtian	Bauru Group, Brazil	Kellner and Campos, 2002
Quilmesaurus curriei	72.1	66	Maastrichtian	Allen Fm, Argentina	Coria, 2001
Rahiolisaurus gujaratensis	72.1	66	Maastrichtian	Lameta Fm, India	Novas et al., 2010
Rajasaurus narmadensis	72.1	66	Maastrichtian	Lameta Fm, India	Wilson et al., 2003
Rugops primus	100.5	93.9	Cenomanian	Echkar Fm, Niger	Sereno et al., 2004
Skorpiovenator bustingorryi	113.2	100.5	Albian	Huincul Fm, Argentina	Canale et al., 2009
Spectrovenator ragei	121.4	113.2	Aptian	Quiricó Fm, Brazil	Zaher et al., 2020
Thanos simonattoi	85.8	83.6	Santonian	São José do Rio Preto Fm, Brazil	Delcourt and Iori, 2020

Tralkasaurus cuyi	113.2	100.5	Albian	Huincul Fm, Argentina	Cerroni et al., 2020
Vitosaura colozacani	83.6	72.1	Campanian	Los Llanos Fm, Argentina	Jiménez Velandia et al., 2025
Viavenator exxoni	85.7	83.6	Santonian	Bajo de la Carpa Fm, Argentina	Filippi et al., 2016
Xenotarsosaurus bonapartei	100.5	89.8	Cenomanian-Turonian	Bajo Barreal Fm, Argentina	Martínez et al., 1987