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Macroevolutionary trends in Ceratosauria body size: insights of phylogenetic comparative methods

Enzo E. Seculi Pereyra[1*], Damian E. Pérez[1] and Ariel H. Méndez[1]

Abstract

Patterns of body size evolution in dinosaurs are relevant for understanding the evolutionary trends that have shaped the disparity of phenotypes observed in the fossil record. In this sense, previous studies have suggested that Abelisauridae followed Cope´s rule and Noasauridae exhibited a phylogenetic trend towards decreasing body size. However, the absence of a comprehensive analysis including ecological, phylogenetic and socio-sexual factors make it necessary to reevaluate body size evolution in Ceretatosauria under a modern phylogenetic comparative approach. Therefore, we aimed to test whether body size evolved in Ceratosauria in accordance with Cope´s rule, evaluate what factors best explain differences in body size within Ceratosauria and examine what patterns of evolution rates, selection strength and constrain explain the diversification body size in Ceratosauria. Differences in body size were found between specialized taxa (= Late Cretaceous abelisaurids) and "generalized taxa" (= Outgroups + Noasauridae). This results suggested that the presence of a specialized feeding strategy in Late Cretaceous abelisaurids was associated with differences in body size, regardless of the phylogenetic topology and evolutionary model used. Additionally, the low levels of morphological disparity, low evolutionary rates for taxa with a specialist feeding behavior in Brownian motion model and the fossil record suggest that the evolution of body size in Late Cretaceous abelisaurids was constrained. The cursorial abilities suggested for abelisaurids joined with the specialized predation strategy could have constrained the increase in body size in Late Cretaceous abelisaurids after the extinction of carcharodontosaurids. On the other hand, Noasauridae exhibited a phylogenetic trend towards decreased body size, likely to avoid niche overlap with medium size theropods and minimize structural and maintenance cost while living in stressful environments and having a generalist diet. Understanding how the dynamics of dinosaur communities, such as competition and predator–prey interactions, operated in South America during the Late Cretaceous is crucial for reconstructing the evolutionary and ecological processes that shaped its unique faunal assemblage. Futures works should be focus on process-based community-evolution model and species distribution modeling to further understand the macroevolution dynamics of South America dinosaur community.

Keywords Abelisauridae, Noasauridae, Macroevolutionary trend, Late Cretaceous, Specialist feeding behavior, Cope´s rule, Body size

Introduction

Body size is usually related to biological factors such as physiology, ecology, sexual characters and life history energetics [1–6]. Therefore, considerable variation in body size signifies variation in biological and evolutionary process [7]. Taking this into account, Cope's rule

*Correspondence:
Enzo E. Seculi Pereyra
emaseculi@gmail.com
[1] CONICET. Instituto Patagónico de Geología y Paleontología (CCT CONICET CENPAT), Bv. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

postulates that lineages evolved towards an increase in body size over time [2, 3]. However, the application of this rule requires certain environmental pressure conditions. It was suggested that Cope's rule applied in two situations [1]: 1) when species interaction depend on relative body size difference and extinction rate of lineage is low and 2) the extinction of top predators induces cyclic evolution toward larger body sizes (the recurrent Cope's rule). On the other hand when species interactions are determined by ecological niches and not only body size, Cope's rule might invert, leading to cyclic evolution toward smaller body size [1]. Moreover, bony cranial ornamentation was linked to rapid evolution of giant theropod dinosaurs [4]. Furthermore, the dynamic community evolution and socio-sexual display mechanisms might influence the evolution of body size in present and past ecosystems.

Patterns of body size evolution in dinosaurs are relevant for understanding the evolutionary trends that have shaped the disparity of phenotypes observed in the fossil record [7]. Ceratosaurs are theropod dinosaurs that include two highly diverse clades, Noasauridae and Abelisauridae, which evolved and persisted until the mass extinction of non-avian dinosaurs [8–10]. These groups are diverse in their morphology [11–14], ecology [13, 15, 16], ornamentation [17] and body size [18]. Whereas, previous studies [18, 19], have suggested that Abelisauridae followed Cope´s rule and Noasauridae decreased in body size towards the phylogeny, recent discoveries of new abelisaurids [11, 20–22] and the absence of a comprehensive analysis that include ecological, phylogenetic and socio-sexual factors make it necessary to reevaluate body size evolution in Ceratosauria under a modern phylogenetic comparative approach. Furthermore, here we aim to use body length (as an approximation of body size) and phylogenetic comparative methods to test whether body size evolution in Ceratosauria followed Cope's rule. We will do this by addressing two principal questions: What factor best explains the difference in body size within Ceratosauria and what patterns of evolutionary rates, selection strength and constraints explain the diversification of Ceratosauria body size.

Material and methods

Tree topology, calibration and sample data

Tree topology

To include the maximum number of informative ceratosaurian taxa and assess how results vary between alternative topologies derived from different methods, we used the Ceratosauria phylogeny obtained through Maximum Parsimony (MP) analysis and Bayesian tip-dating (BY) framework, as presented by Pol and colleagues (2024) [21]. Specifically, we used the reduced strict consensus after removing unstable taxa, and the maximum clade credibility tree obtained under BY, by Pol and colleagues (2024) [21]. The aim for using both topologies lies in their complementary strengths: the MP topology, derived after removing unstable taxa, includes fewer but more informative ceratosaur taxa, whereas the BY topology incorporates a greater number of ceratosaurs but with fragmentary taxa. Consequently, analyzing both topologies enhance our macroevolutionary inferences regarding Ceratosauria body size dynamics. Additionally, this topology differ in how the species were related, firstly the split leading to Noasauridae and Abelisauridae (Supplementary material 1, 2 and 3). To a better understanding of macroevolutionary dynamics, resolved tree topologies are needed. So that, we resolved Noasauridae and Majungasaurinae polytomies present in the MP topology using the relationships obtained in the above mentioned BY topology. On the other hand we added to BY topology *Herrerasaurus*, *Syntarsus*, *Dilophosaurus* and *Allosaurus* with the aim to had not only more taxa in the phylogeny but also body length variation outside of Ceratosauria following the taxa position in MP topology. Notice that all tree calibration methods and phylogenetic comparative methods described below were done in both ceratosaur topologies and then results were qualitatively compared. In consequence, tree topologies considered do not contradict results of Pol et al. (2024) [21].

Time tree calibration

Different stochastic tree calibration methods might produce different results [23], likewise misunderstand macroevolutionary processes. To minimize the difference between calibration methods we used *timePaleoPhy* function in *paleotree* package (v 3.4.5) [24] with two calibration methods, *mbl* with 1 Ma of variation time and *equal* with "*randObs*" data treatment (see Laurin 2004 [25], Brusatte et al. 2008 [26] and Lloyd et al. 2012 [27] for more details). This method randomly samples observation times between the first and last appearance dates, ensuring that the uncertainty in fossil records is appropriately addressed [23]. We generate 1000 calibrated trees for each topology using both methods. Subsequently, we computed a consensus tree for each topology using the *consensus.edge* function from the *phytools* package (v 2.1–1) [28], based on 2000 calibrated trees per topology (Fig. 1 Supplementary data and Supplementary material 4). Finally, we obtained one consensus tree for each topology (MP and BY). The time span interval of each species was taken of paleobiology data base (https://paleobiodb.org; accessed June 2024) (Supplementary data 5).

Body length data and calculation

We used the Ceratosauria body length (BL) measures of the total data set obtained by Grillo and Delcourt (2018) [18] as an approximation to Ceratosauria body size. But since Grillo and Delcourt´s (2018) work, new abelisaurid dinosaurs have been described. First, we looked for BL estimates from the published literature. When two or more body length values were present, we calculate the mean between those values (Table 2, Supplementary data 1). If BL measure does not exist, we employ the formula of Grillo and Delcourt (2018) to calculate the BL (see Table 1 & 2 and Supplementary data 1 for more detail). A total of 42 log transformed BL measures were obtained for BY topology and 28 log transformed BL measures were obtained for MP topology. We did not obtain measures to calculate the BL in *Indosaurus,* CCG20011 and MPM- 99 due to the lack of osteological elements measures in the literature, and neither in *Genyodectes* due this taxa is based only in a partial rostrum and dentary. The Late Cretaceous *Xenotarsosaurus* was resolved as sister taxa of *Eoabelisaurus* by different authors (i.e. [21]. Furthermore *Xenotarsosaurus* was dismissed of the analysis due the plesiomorphic features it presents making difficult to coding it.

Body mass is the most common metric used for studying the evolution of body size in different linage of Dinosauria (e.g., Benson et al. 2018 [7]), typically estimated from femoral circumference [29]. However, are not frequently preserved in ceratosaur fossils, and femoral circumference data are rarely reported in the literature. To address this limitation, we used body length data available in literature, which is more commonly reported. When body length data were unavailable, we applied the formula proposed by Grillo and Delcourt 2017 that allows body length estimation based on various osteological elements. Thus, with the aim to maximize the inclusion of certaosaurid taxa in both topologies, we used the body length as approximation of body size in Ceratosauria.

Moreover, we acknowledge that body mass is a less shape-dependent measure of size than body length. However, in Ceratosauria, the overall proportions (relative skull, trunk, tail lengths, limb robustness, etc.) appear to be relatively consistent among clades in Ceratousaria (Abelisauridae and Noasauridae) [18]. This consistency supports the use of body length as a reliable proxy for overall size.

Phylogenetic comparative methods

Disparity through time analysis

A disparity through time plot (*DTT*) was performed using BL data with the aim to visualize patterns of body length changes within and among clades in Ceratosauria using *dtt* function in *geiger* package (v 2.0.11) [30]. In this method, disparity is estimated for all taxa of the phylogeny and subsequently for each subclade. Relative disparity is obtained by dividing each subclade disparity value by the total disparity of the clade. Finally, the average relative disparity is estimated for each subclade present at the time of each divergence time. The average squared Euclidean distance was used to calculate the disparity index, with 10,000 simulation conducted to ensure robustness.

Factor levels coding (Phylogenetic regimen, Ornamentation and Ecology) and Phylogenetic ANOVA

We coded the Phylogenetic regimen (= taxonomic grouping) factor with four levels based in the Phylogenetic regimen recovered by Pol et al. (2024) [21] and previous authors [11, 12, 14] and added a non-monophyletic group to separate early diverging abelisaurids ("Ancestral abelisaurids") that are outside of the phylogenetic categories implemented: Phylogenetic outgroups (OU), "Ancestral Abelisauridae" (see Supplementary material 1 for more information about this category and taxa that composed it) (AA), Noasauridae (NO), Majungasaurinae abelisaurids (MJ), Furilesauria abelisaurids (FU) and Brachyrostra abelisaurids (BR). These levels were used with the aim to test whether different Phylogenetic regimen differed in BL.

In order of code the Ornamentation factor we use three levels: unornamented skulls (US), Ornamented skull (OS) (sagittal and parasagittal crests, horns and knobs) and Rugose skull (RS). We based the first two levels in Gates et al. (2016) [4] coding and we added the rugose skull level to distinguish abelisaurids. Abelisaurids that have horns, crests and rugosities were consider in the RS level in order to test whether the presence of ornamentations in Abelisauridae were linked with body length evolution. Carrano and Sampson (2007) [31] identified

(See figure on next page.)

Fig. 1 Violins (B, D & F) and phenograms (A, C, E,& G) plots in Bayesian topology showing: **A** The Ceratosauria BL evolution over the time, **B** difference in Log BL between Phylogenetic regimen s, **C** Polygons show the space of BL evolution occupy by Phylogenetic regimen s over the time **D**) difference in Log BL between types of ornament, **E** Polygons show the space of BL evolution occupy by types of ornament over the time, **F** difference in Log BL between types of feeding strategy **G**) Polygons show the space of BL evolution occupy by the types of feeding strategy over the time. Ceratosauria silhouettes from PhyloPic (http://phylopic.org)

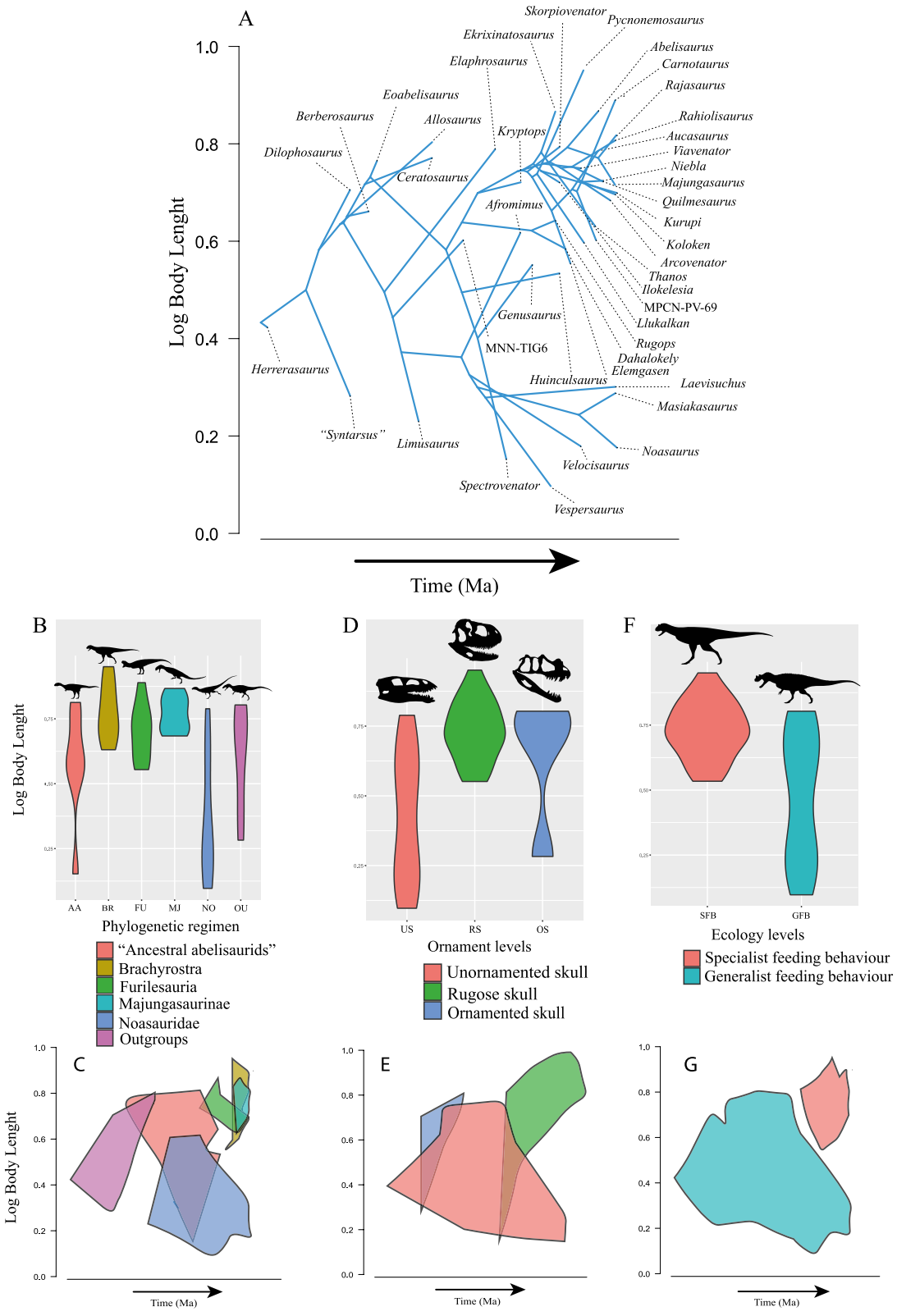

Fig. 1 (See legend on previous page.)

the facial sculpturing abelisaurids as likely a homologous, unambiguous synapomorphy of Abelisauridae. In the case where no skull elements were present, we coded the taxa depending on the phylogenetic position, following the criterion of Gates et al. 2016 [4]. Ontogenetic stage did not affected our ornament coding due theropod dinosaurs reached reproductive maturity before skeletal maturity [32].

"Ecology category" consists of two factors: Specialist feeding behavior (SFB) and Generalist feeding behavior (GFB). These level were based on previously published hypothesis that proposed that Late Cretaceous abelisaurids had a specialist predation strategy based on morphological features in skull and vertebrae [13, 22, 33] and biomechanical studies [15, 16]. This specialized feeding strategy involved primarily the use of primarily the head for hunting, with a short distance sprint, and holding the prey during the kill [13, 34]. Despite different feeding strategy were hypothesized for different abelisaurids (*i.e. Majungasaurus* and *Carnotaurus*) [15, 16], all Late Cretaceous abelisaurids were classified as SFB due to their phylogenetic affinities and shared anatomical and functional traits. On the other hand, taxa lacking these specific features were grouped into the "generalist" level (GFS). However, this does not imply that they were ecological generalists but rather that they lacked the particular suite of traits associated with the specialized feeding strategy of Late Cretaceous abelisaurids. In fact, some of these taxa (e.g., *Dilophosaurus, Limusaurus, Ceratosaurus, Allosaurus*) have been previously suggested to have specialized diets or feeding modes[15, 35–38]. Therefore, this category does not aim to assess the impact of trophic ecology on body size evolution in Ceratosauria broadly. Instead, our goal is to test whether Late Cretaceous abelisaurids exhibited a different macroevolutionary mode of body length evolution compared with other ceratosaurs than other factors such as phylogenetic history or sociosexual mechanism.

Additionally, because the Phylogenetic regimen and Ornamentation categories were unbalanced compared to the Ecology category, we reclassified the Phylogenetic regimen into three levels (Outgroups, Noasauridae and Abelisauridae) and the ornamentation category into two levels (unornamented and ornamented). These reclassification enabled us to evaluate more thoroughly whether our results change or remained consistence with the original categorization. These re-coded categories were employed in the Phylogenetic ANOVA and Phylogenetic linear regression aalysis (see below).

A phylogenetic ANOVA (p-ANOVA) was performed (*phylANOVA* function in phytools package, v 2.3 [28]) with the aim to detect differences of means among the above commented factors levels. This function performs the simulated-based phylogenetic ANOVA and conduct posthoc comparison between groups. In this function we employed 10,000 simulation and the p-values were corrected by Bonferroni correction, in which p-values are multiplied by the number of comparison accounting sample differences between categories levels.

Phylogenetic linear regression models

To elucidate what factor or what combination of factors might best explain the differences between ceratosaurs body size, we employed phylogenetic linear regression models (PLRM) with three explanatory variables: Phylogenetic regimen, Ornamentation and Ecology.

We used six nested PLRM in both topologies with three types of character evolution model (*lambda*, *kappa* and *Brownian motion*) with 1000 independent bootstrap replicates. The decision to choose these three models relies on their ability to capture different evolutionary dynamics of the trait. The lambda model estimates the strength of phylogenetic signal, indicating the extent to which the trait evolution follows Brownian motion versus being more independent among species. The kappa model scales branch lengths to assess whether trait evolution is more gradual or punctuated, while the Brownian motion model represents a neutral, stochastic process of evolution. By incorporating these models, we aimed to encompass a broad range of possible evolutionary scenarios for the body size.

To assess what PLRM explained the difference in Ceratosauria BL better we used Akaike information criterion weight (*AICw*).The models fitted were:

- Log (BL) ~ Phylogenetic regimen
- Log (BL) ~ Ornamentation
- Log (BL) ~ Ecology
- Log (BL) ~ Phylogenetic regimen + Ornamentation
- Log (BL) ~ Phylogenetic regimen + Ecology,
- Log (BL) ~ Ornamentation + Ecology
- Log (BL) ~ Phylogenetic regimen + Ornamentation + Ecology

We employed *phylolm* function in *phylolm* package (v,. 2.6.2) [39] to fit the PLRM and *aicw* function in *phytools* package (v., 2.3) [28] to obtain the *AICw*. Taxa coding for each topology can be found in Supplementary material 6.

Evolutionary models

Different macroevolutionary scenarios can be represented by mathematical models of evolution, elucidating how different phenotypes evolve through the time [40]. To explore and determinate what model explains better the evolution of body size, we fitted five evolutionary models with the *OUwie* function in *OUwie* package (v.,

2.10) [41], mapping the levels of the factor that explained better the difference in Ceratosauria BL in PLRM analysis. The models fitted were: 1) single evolution rate (single Brownian motion (BM)), 2) two evolutionary rates (multiple Brownian motion (BMM)), with only one phenotypic optimum (OU1), with two phenotypic optima and constant evolutionary rate (OUM), and with two phenotypic optimum with different evolution rates (OUMV). The factor levels were mapped using *make.simmap* function in *phytools* package (v., 2.3) [28] with equal rates and the best model was selected using *AICw*. Additionally, to evaluate the adequacy of the best model, we performed 1000 parametric bootstrap replications in the parameters estimated under the best model and built 95% confidence intervals. Parametric bootstrap extract multiple samples with replacement drawn from a simulated data from a distribution (i.e. normal distribution) with parameters estimated by the best model. Then best model is fit to each of the resampled datasets and the evolutionary rates is calculated for each resampled. Finally, the distribution of the parameters over all samples is used to estimate 95% confidence intervals. A model was considered adequate if the observed parameters estimated by the best model fell within its respective confidence interval.

R scripts with the phylogenetic comparative methods analysis can be found in Supplementary data 7 & 8.

Results

Trends in Ceratosauria body length evolution

To visualize patterns and difference between factor levels of ceratosaur BL, we produced phenograms and violin plots for both topologies (Fig. 1 and Supplementary data 1-Fig. 2) and test the mean-differences among factor levels using Phylogenetic ANOVA. MP and BY topologies showed the same patterns of ceratosaurs BL dispersion and evolution through the time, with Late Cretaceous abelisaurids incrementing and maintaining the BL, only varying a few units (Fig. 1-A and Supplementary Data Fig. 2-A). However, BL differences were not clear between Majungasaurinae, Furilesauria and Brachyrostra (Fig. 1-B & C and Supplementary Data 1 Fig. 2-B & C). On the other hand, Noasauridae, "Ancestral abelisaurids" and outgroups showed a large amount of BL variation (Fig. 1-B and C and Supplementary Data 1 Fig. 2- B & C). Moreover, noasaurids decrease in BL through the time, reaching forms like *Masiakasaurus* and *Noasaurus,* showing the opposite evolutionary trend of abelisaurids (Fig. 1- B and C and Supplementary Data 1 Figure B & C). The Ornamentation level showed no clear differences in BL between RS taxa and OS taxa (Fig. 1-D & E and Supplementary Data 1 Fig. 2-D & E). However, differences between those two levels and US taxa were observed (Fig. 1-D & E and Supplementary Data 1 Fig. 2-D & E.

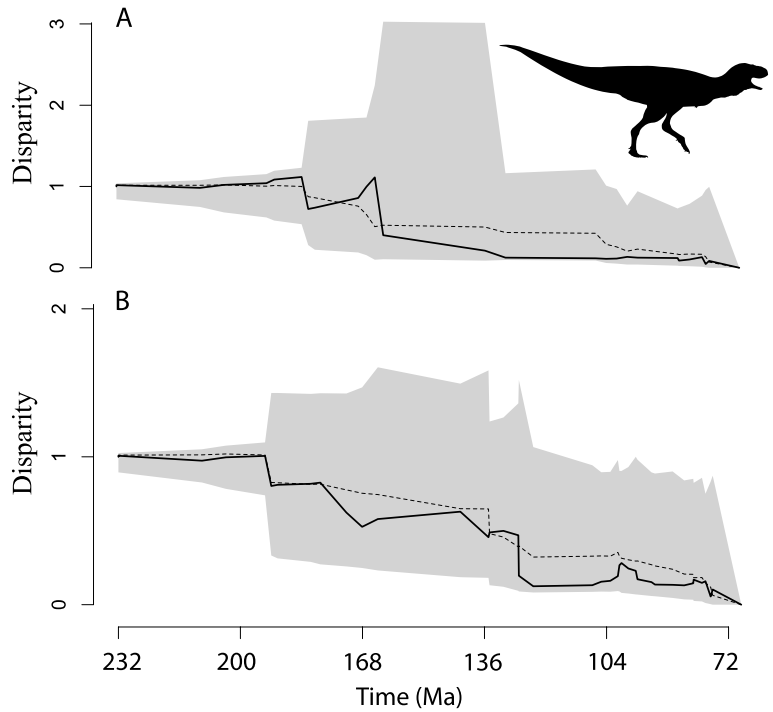

Fig. 2 Disparity through time estimated from BL data in **A**) Parsimony topology and **B**) Bayesian topology. The solid line represents the observed data, the dashed line represents the mean of simulations under the BM model, and the gray area is the 95% confidence interval of the simulated data set. *Aucasaurus* silhouettes from PhyloPic (http://phylopic.org)

The ecology factor showed the most difference between BL (Fig. 1-F & G and Supplementary Data 1 Fig. 1-F & G). SFB taxa showed large BL with a small variance reaching medium and large BL over the time (Fig. 1-F & G and Supplementary Data 1 Figure F & G). Besides, GFB taxa exhibit a large amount of BL variance reaching medium and small BL and decrees in BL over the time (Fig. 1- F & G and Supplementary Data 1 Figure F & G).

Despite the differences observed in the violin plots, the Phylogenetic ANOVA did not showed significant differences among groups for each factor used (Table 3–5, Supplementary data 1). When the categories were re-coded the Phylogenetic ANOVA showed the same pattern and differences among groups were not observed (Tables 6 and 7- Supplementary data 1).

Ceratosauria body length disparity through time

Dtt was performed to assess the Ceratosauria BL disparity. The *dtt* plot in MP topology (Fig. 2-A) showed a decrees in BL disparity between subclades at the beginning of the lower Jurassic followed by an increase in disparity in the late Jurassic. After this period, the disparity dropped sharply showing no differences in BL between subclades during the Cretaceous. On the other hand the *dtt* in BT (Fig. 2-B) showed the same pattern of BL disparity but with a more progressive dropped during the Jurassic and with a sharply dropped during the lower Cretaceous with a slowly decreasing towards the end of the Cretaceous. The *dtt* for both topologies were inside of the 95% confidence interval indicating that the BL evolution in Ceratosauria followed a Brownian motion process. Summarizing, both topologies showed no differences between Ceratosauria BL during the Cretaceous, especially in the Late Cretaceous.

Phylogenetic linear regression models

To test what factor might be related and explained better the difference in ceratosaur BL, we used PLRM with explanatory variables related to the ecology, characters likely linked to sexual selection/species recognition and Phylogenetic regimen s based on phylogenetic history. The Ecology factor explained better the difference in Ceratosauria BL evolution no matter what topology and what evolution model in PLRM was used (Table 1 and Table 8 & 9—Supplementaray data 1) with the mainly categorization. This model had the highest *AICw* values (Table 1 and Table 8 & 9—Supplementaray data 1). On the other hand, when the categories were reclassified, the results for the BY topology remained consistence, with the Ecology factor explained better the difference in Ceratosauria body size evolution (Table 10, Supplementary data 1). However, in the MP topology, the results changed, and the model incorporating both the Phylogenetic regimen and Ecology factors showed the highest *AICw* values (Table 10, Supplementary data 1). Examination of the parameters estimated by this model in the MP topology reveled only a significant effect of Noasauridae, Abelsiauridae and the specialist feeding behavior level (Table 11, Supplementary data 1). This indicates that differences in body size between Abelisauridae and Outgroups, as well as the generalist feeding behavior level, did not have a significant effect on body size (Table 1).

Evolutionary models

We mapped the levels of Ecology, the factor that best explains the difference in Ceratosauria BL in PLRM and fitted different evolutionary models to elucidate the mode of Ceratosauria BL evolution. Brownian motion with two evolution rates was the best model in MP and BY with the highest *AICw* value (Table 2). Regarding the estimated evolution rates for both topologies were lower in SFB taxa than GFB, maintained the BL through

Table 1 *AICw* values for Parsimony and Bayesian topology, using Lambda (λ), Kappa (K) and Brownian motion (BM) models in PLRM. PG: Phylogenetic regimen, Orn: Ornamentation and Eco: Ecology. In bold the model with the highest AICw value

	Topology					
	Parsimony			Bayesian		
Model	λ	K	BM	λ	K	BM
PG	0.254	0.253	0.255	0.036	0.024	0.038
Orn	0.088	0.092	0.088	0.275	0.365	0.271
Eco	**0.445**	**0.443**	**0.445**	**0.656**	**0.590**	**0.657**
PG + Eco	0.213	0.212	0.213	0.032	0.021	0.034
PG + Orn	0.000	0.000	0.000	0.000	0.000	0.000
Orn + Eco	0.000	0.000	0.000	0.000	0.000	0.000
PG + Eco + Orn	0.000	0.000	0.000	0.000	0.000	0.000

Table 2 Evolution model fitted to BL data in Parsimony and Bayesian topology with LogLikelihood (*LogLike*), AKAIKE criterion information (*AIC*), corrected AKAIKE criterion information (*AICc*) and AKAIKE weight (*AICw*). In bold best model of the candidate models

Tree topology	Model	*LogLike*	*AIC*	*AICc*	*AICw*
Parsimony	OU	5.57	− 5.15	− 4.15	0.07
	BM	5.57	− 7.15	− 6.67	0.18
	BMM	**7.82**	**− 9.63**	**− 8.63**	**0.61**
	OUM	6.00	− 4.01	− 2.27	0.04
	OUMV	8.06	− 6.12	− 3.39	0.11
Bayesian	OU	11.90	− 17.79	− 17.16	0.09
	BM	11.90	− 19.79	− 19.49	0.24
	BMM	**13.71**	**− 21.42**	**− 20.79**	**0.55**
	OUM	12.13	− 16.26	− 15.17	0.04
	OUMV	13.82	− 17.65	− 15.98	0.08

the time (Fig. 3) and fall into the 95% confidence interval (normal distribution was used to simulate data with BMM parameters) indicating the adequacy of the estimated parameters in the BMM model for both topologies (Table 12, Supplementary data). On the other hand, since the result on the MP topology changed when categories levels were reclassified and the Phylogenetic regimen category showed a significant effect on the Ceratosauria body size, the levels Outgroups, Noasauridae and Abelisauridae were mapped, and evolutionary models were fitted. Among the tested models, a Brownian motion with a single evolution rate was the best model with the highest *AICw* value (Table 13, Supplementary data 1).

Discussion

Body size could be related to the ecology, phylogenetic history or characters under sexual selection/species recognition [1–3, 7, 25]. Grillo and Delcourt 2017 [18] have claimed that Abelisauridae exhibited a phylogenetic trend towards increasing body size. However, the PLRM indicates that the presence of a specialist feeding behavior in Late Cretaceous abelisaurids explained better the differences in Ceratosauria BL, regardless of the phylogenetic topology or evolutionary model used in the phylogenetic regression. While this supports the idea that feeding behavior may have played a role, it does not exclude other potential factors influencing body length evolution in this group. Moreover, the phylogenetic ANOVA did not detect significant differences in mean body size among groups. This may be due to the large overlap in size between Late Cretaceous abelisaurids and outgroups, as well as the limited number of ceratosaurian taxa in both topologies. When Phylogenetic regimen and

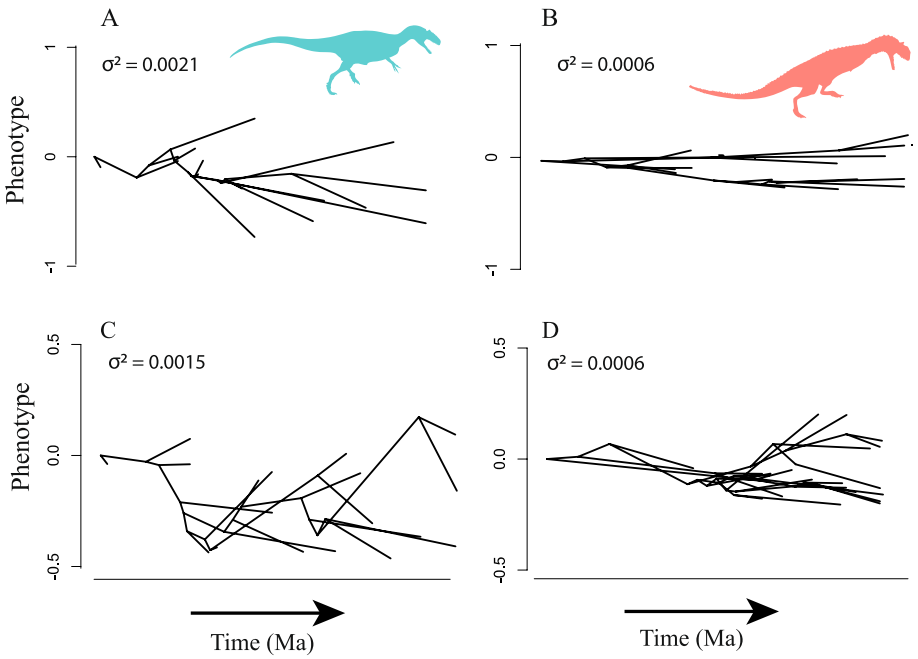

Fig. 3 Simulated phenotype evolution (with *fastBM* function in *phytools* under the evolution rates estimated by BMM model, considering the time span interval of generalist and specialist hunters in each topology. **A** Generalist feeding behavior taxa under Parsimony topology (n taxa = 17), B) Specialist feeding behavior taxa under Parsimony topology (n taxa = 15), **C** Generalist feeding behavior taxa under Bayesian topology (n taxa = 22) and **C** Specialist feeding behavior taxa under Bayesian topology (n taxa = 26). *Majungasaurus* and *Allosaurus* silhouettes from PhyloPic (http://phylopic.org)

Ornamentation categories were reclassified in the MP topology, the Phylogenetic regimen and the "Ecology factor" showed a significant effect on Ceratosauria body size evolution. However, estimated parameters showed not significant difference in body size between Abelisauridae and Outgroups. Additionally, when the Phylogenetic regimen levels were mapped in the MP topology, a Brownian motion model with a single evolutionary rate across the entire clade provide the best fit. This result suggested that the Phylogenetic regimen did not explain better the difference in Ceratosauria better than the presence of a specialist feeding behavior. Difference in body size were observed between Late Cretaceous abelisaurids, and generalist taxa (Outgroups +Noasauridae). Ornamented skull taxa tend to exhibit large body size compared with unornamented skull taxa, and it might be linked to an increase in body size as was observed in Non-avian theropods [4]. However, not significant differences were found between ornamented skull taxa and rugose skull taxa. While ornamental structures may have evolved through species recognition or sexual selection [4, 42], so it is expected to stay under phenotypic selection. However, our result suggests that the acquisition of rugosities did not account for the differences in Ceratosauria body size evolution. Moreover, when the ornamentation coding was reclassified, the model that best explained the difference in Ceratosauria body size evolution always was or contained the Ecology factor. This supports the conclusion that sexual and species recognition mechanisms were not the main drivers in the evolution of body size evolution in Ceratosauria.

The dtt analysis reveled low levels of disparity in Ceratosauria between the Middle Jurassic and the Lower Cretaceous. This result could be related to the scarce record of abelisaurids and noasaurids in this time range and an improved sampling is necessary to test if it is a bias or an actual biological pattern. However, during the Late Cretaceous, ceratosaurids exhibited low levels of body size disparity. Linages with high disparity are tipically functionally and ecologically diverse [43]. Therefore, the low levels of body size disparity and the restricted morphospace occupied by Late Cretaceous abelisaurids in the phenogram may indicate similar ecological function, particularly within Abelisauridae. This findings supports the hypothesis of specialized predation strategy hypothesized for Abelisauridae, as proposed by previous study [13, 15, 16, 22, 33]. However, further disparity and trait evolution analysis are needed to a better support this hypothesis.

During the Aptian-Turonian time span interval, abelisaurids, noasaurids, carcharodontosaurids and spinosaurids shared the environments [9]. The ecological niche of Spinosaurid could be different to abelisaurids and carcharodontosaurids [44], suggesting that niche overlap between those theropod groups was unlikely. In contrast abelisaurids and carcharodontosaurids exhibited similar mechanical advantages scores related to the leverage of the jaw systems [45] and convergent dental morphology [33]. However, Canale et al. 2024 [46] hypothesize that carcharodontosaurids fed on larger prey items avoiding bulky bones more easily from evince of the fossil record. Before the proposed Cenomanian–Turonian turnover, larger representative of abelisaurids and carcharodontosauirds were found in the same time span interval, for example *Ekrixinatosaurus* and *Giganotosaurus* in Albian/Cenomanian, *Ilokelesia*, *Skorpiovenator* and *Mapusaurus* in Cenomanian/Turonian. After the extinction of carcharodontosaurids, Late Cretaceous abelisaurids exhibited relatively low diversity in body size, clustering around medium sizes of ~5.4 ± 1.29 m, and reaching a maximum of 9 m in *Pycnonemosaurus* [18]. This conclusion is supported by the low disparity in *DTT* analysis, the low estimated evolutionary rates for specialist feeding behavior taxa (= Late Cretaceous abelisaurids) in Brownian motion model, and the fossil record. Thus, Late Cretaceous abelisaurids did not increase in body size after the extinction of carcharodontosaurids and may have occupied different ecological niches. Therefore, the recurrent Cope´s rule hypothesized by Roy et al. 2024 [1] does not apply to Late Cretaceous abelisaurids and the evolution of body size in abelisaurids was constrained. The cursorial abilities suggested for abelisaurids [13, 47] joined with the specialized predation behaviour [13, 15, 16, 22] could have constrained the increase in body size of larger body size in Late Cretaceous abelisaurids. This novel predation strategy could have allowed Late Cretaceus abelisaurids to be successful during the Late Cretaceous.

Megaraptorids shared the environments with abelisaurids during Late Cretaceous and reached similar body lengths [48–50]. Megaraptorids are characterized for their large hand claws and powerfully-built forelimbs with highly complex movements as well as enhanced humeral protraction [51]. These features are thought to have played a key role in prey capture and manipulation [51]. In contrast, Late Cretaceous abelisaurids are hypothesized to have had a specialist predation strategy based on morphological features in skull and vertebra [13, 22, 33], and biomechanical studies [15, 16]. This specialized strategy involved using primarily the head for hunt with a short distance sprint and hold the prey throughout the kill [34]. Sampson and Witmer (2008) [13] claimed that *Majungasaurus crenatissimus* was "*adapted for a mode of predation that entailed relatively few, penetrating bites accompanied by powerful neck retraction, as well as bite-and-hold behavior*".

Furthermore, megaraptorids and abelisaurids probably occupied different ecological niche by differences in their predation strategy system, and probably preying over different prey items.

Noasauridae exhibited a phylogenetic trend towards decresed body size, with taxa exceeding 4 m [52]. Noasauridae and Abelisauridae shared not only some time span intervals (i.e. *Majungasaurus* and *Masiakasaurus*) but also some features in skull and vertebrae [19]. In this sense, noasaurids likely led to evolution toward smaller body size by niche overlapping. The inverted Cope's rule hypothesized by Roy et al. 2024 [1] apply in Noasauridae. This hypothesis is supported by the slowed growth found in *Masiakasaurus* [32] and the generalist feeding behavior reported for *Vespersaurus* [53]. Thus, Nosauridae followed an evolutionary trend to avoid niche overlap with medium size theropds and minimize structural and maintenance cost while living in stressful environments and having a generalist diet [32, 53]. Moreover the body plan of Noasauridae remains very different from early diverging ceratosaurs and theropods so that they probably differed in feeding strategy and mechanisms [8, 19], as was hypothesized for *Masiakasaurus* [52]. However, paleobiology studies in noasaurids are scarce and should be studied further in the future.

Regarding the methods used in this study, some body length data were derived from a single osteological element, due to the fragmentary nature of certain taxa. Different osteological elements can yield varying body length estimates due to differences in their allometric scaling relationships to total body length. This can lead to potential errors or biases in the estimated body lengths, particularly when using a single element to infer overall size. On the other hand, the ecological and ornamentation coding could be poor and biased in some taxa. The classification of the remaining ceratosaur taxa as exhibiting a common generalist feeding behavior underscores the limited resolution of current paleobiological knowledge. This categorization, therefore, did not enable us to assess the broader impact of trophic ecology on body size evolution across Ceratosauria. Additionally, Late Cretaceous abelisaurids likely exhibited different predation strategy, and coding them under a single category further underscore the gaps in our understanding of the paleobiology of the entire group. On the other hand, most of the unornamented skull taxa lack cranial element, and were classified based on their phylogenetic affinities with other taxa. New fossil records might improve this coding. Additionally, Paulina Carbajal (2023) [17] suggested that abelisaurids differ in rugosities features. Future macroevolutionary studies should consider the ornaments and ecology variety in Abelisauridae to test different macroevolutionary hypotheses.

Both topologies used in the analysis were consistent with the result obtained when the primary coding was implemented, with differences only observed in the MP topology when the categories were reclassified with fewer levels. This consensus in result could be due to the fact that most taxa did not change position extremely across topologies used, the tree calibration procedure remained similar and the ingroups remains consistent. Both methodologies to infer phylogenies present advantages and disadvantages [54, 55] so it's important to consider and compare the result of both methodologies when phylogenetic analyses are carried out. In particular, Parsimony analysis was demonstrated extensively that implied weighting outperforms equal weighting in simulated [56, 57] and empirical data sets [58] but weighting against homoplasy lacks extensive usage in palaeontology. This approach cpuld enhance our understanding of phylogenetic analyses and subsequent macroevolutionary studies.

Conclusion

Late Cretaceous abelisaurids did not increase in body length in response to top predator extinction and it may have constrained by the type of predation strategy. In contrast, Noasauridae exhibited a phylogenetic trend towards decreasing body size likely avoiding niche overlapping with abelisaurids and other theropods. The ecosystems during the Late Cretaceous of Patagonia appear to have been highly diverse and productive, as indicate by the high diversity in morphology and, primarily, in ecology among non-avian and avian theropods. It is intriguing to consider how the dynamics of dinosaur communities, such as competition and predator–prey interactions, operated in South America during the Late Cretaceous. Futures studies ought to be focus on process-based community-evolution model and species distribution modeling to further explore the diversity, disparity and macroevolution dynamics of dinosaur community during this period.

Supplementary Information

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Supplementary Material 1.
Supplementary Material 2.
Supplementary Material 3.
Supplementary Material 4.
Supplementary Material 5.
Supplementary Material 6.
Supplementary Material 7.
Supplementary Material 8.

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Authors' contributions
ESP wrote the main manuscript, designed the methodology and performed the phylogenetic analysis. DEP participate in taxa coding and reviewed the manuscript. AHM reviewed the manuscript.

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Data availability
Data is provided within the manuscript or supplementary information files.

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