AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL



A NEW AEOLOSAURINI (SAUROPODA, TITANOSAURIA) FROM THE UPPER CRETACEOUS OF URUGUAY

MATÍAS SOTO NÚÑEZ[1]
FELIPE MONTENEGRO[1,2]
DANIEL PEREA[1]

[1]Instituto de Ciencias Geológicas, Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay.
[2]Museo Nacional de Historia Natural, 25 de Mayo 582, 11000 Montevideo, Uruguay.

Submitted: 14 February 2026 - **Accepted:** 19 June 2026 - **Published:** 08 July 2026

To cite this article: Matías Soto Núñez, Felipe Montenegro, & Daniel Perea (2026). A new Aeolosaurini (Sauropoda, Titanosauria) from the Upper Cretaceous of Uruguay. *Ameghiniana*, *63*(4), 279–302.

To link to this article: http://dx.doi.org/10.5710/AMGH.19.06.2026.3689

PLEASE SCROLL DOWN FOR ARTICLE

PALEOENVIRONMENTS OF PAMPA-PATAGONIA TRANSITION

Late Holocene fossil pollen record from Zoko Andi 1 site reconstructs vegetation dynamics and palaeoenvironmental change at multiple spatial scales

BONE HISTOLOGY OF ARGENTINEAN PROTEROCHAMPSIDS

Proterochampsid histology indicates diverse growth modes and ecological specializations preceding early archosaur evolution

A NEW TITANOSAUR FROM URUGUAY

A new sauropod from Uruguay is described, allowing to establish correlations with Upper Cretaceous units from Argentina and Brazil

ISSN 0002-7014

AMEGHINIANA - 2026 - Volume 63(4): 279–302 ARTICLES

A NEW AEOLOSAURINI (SAUROPODA, TITANOSAURIA) FROM THE UPPER CRETACEOUS OF URUGUAY

MATÍAS SOTO NÚÑEZ[1]*, FELIPE MONTENEGRO[1,2], AND DANIEL PEREA[1]

[1]Instituto de Ciencias Geológicas, Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay. *msoto@fcien.edu.uy*

[2]Museo Nacional de Historia Natural, 25 de Mayo 582, 11000 Montevideo, Uruguay.

Abstract. The Upper Cretaceous Guichón Formation (northwestern Uruguay) has yielded remains of notosuchian crocodyliforms, iguanodontian ornithopods, and saltasauroid titanosaurs. Two well-preserved sauropod caudal vertebrae from this unit are described herein from a new locality, Meseta de Artigas. The combination of synapomorphies allows the erection of a new taxon, *Mesetasaurus protector* gen. et sp. nov. It shares characters with members of the clade Aeolosaurini, such as a strongly anteriorly inclined anterior face, a neural arch placed at the level of the anterior border, an anteriorly inclined neural spine, and long prezygapophyses. A phylogenetic analysis retrieves the new taxon deeply nested within Aeolosaurini. Given that Aeolosaurini is a Coniacian–Maastrichtian clade, this new sauropod provides additional evidence that suggests this age for the Guichón Formation. This is the second record of Aeolosaurini in Uruguay, and the second lineage of titanosaurian sauropods from the unit.

Key words. Titanosauria. Aeolosaurini. Upper Cretaceous. Guichón Formation. Uruguay.

Resumen. La Formación Guichón (Cretácico Superior de Uruguay) ha proporcionado restos de crocodiliformes notosuquios, ornitópodos iguanodontes y titanosaurios saltasauroideos. Se describen dos vértebras caudales bien preservadas de una nueva localidad fosilífera, Meseta de Artigas. La combinación de caracteres permite erigir un nuevo taxón, *Mesetasaurus protector* gen. et sp. nov. Comparte con miembros del clado Aeolosaurini una cara anterior fuertemente inclinada hacia adelante, un arco neural ubicado al nivel del borde anterior, una espina neural inclinada anteriormente y largas prezigapófisis. Un análisis filogenético recupera al nuevo taxón como profundamente incluido dentro de Aeolosaurini. Dado que Aeolosaurini es un clado del Coniaciano–Maastrichtiano, este nuevo saurópodo es otra evidencia de la edad Cretácica Tardía de la Formación Guichón. Este es el segundo registro de Aeolosaurini para Uruguay y el segundo linaje de titanosaurios de la unidad.

Palabras clave. Titanosauria. Aeolosaurini. Cretácico Superior. Formación Guichón. Uruguay.

INTRODUCTION

Titanosaurians constituted the most abundant and diverse sauropod clade during the Late Cretaceous, with several dozen genera recognized, particularly in South America (*e.g.*, Wilson, 2006; Carballido *et al.*, 2022). They were already present by the Valanginian (*e.g.*, Gallina *et al.*, 2021), reaching enormous body sizes during the Albian–Cenomanian (Bonaparte & Coria, 1993; Carballido *et al.*, 2017), and were the only sauropods to persist until the end of the Cretaceous (*i.e.*, Maastrichtian; *e.g.*, Santucci & Filippi, 2022 and references therein). Different lines of research are related to titanosaurian sauropods, such as reproductive biology (*e.g.*, Chiappe *et al.*, 1998; Fernández *et al.*, 2022), locomotion (*e.g.*, Wilson & Carrano, 1999; Otero & Hutchinson, 2022), and histology (*e.g.*, Cerda *et al.*, 2021; Cerda, 2022).

The uneven sampling of titanosaur taxa across different regions of the world makes systematics of the group challenging (*e.g.*, Wilson, 2006; Carballido *et al.*, 2022). Indeed, titanosaurs were scarce during the Late Cretaceous of Europe (Le Loeuff, 1993) and absent from the middle Cenomanian to late Campanian in North America during the so-called 'sauropod hiatus' (Lucas & Hunt, 1989; D'Emic & Foster, 2014). Within South America, the knowledge of the group is heavily biased towards Late Cretaceous Patagonian forms, with only a handful of taxa known from northern Argentina, Brazil, Ecuador, Peru, and Uruguay.

Another issue was the scarcity of complete cranial remains. Before the discovery of the cranial material of *Rapetosaurus krausei* Curry Rogers & Forster, 2001, the only known skulls were those of the Asian forms *Nemegtosaurus mongoliensis* Nowinski, 1971 and *Quaesitosaurus orientalis* Kurzanov & Bannikov, 1983, originally believed to be diplodocoids (*e.g.*, Nowinski, 1971; Kurzanov & Bannikov, 1983; Upchurch, 1995). Hence, titanosaurian systematics relied in large part on postcranial characters. The later discovery of the complete skulls of *Tapuiasaurus macedoi* Zaher *et al.*, 2011 and *Sarmientosaurus musacchioi* Martínez *et al.*, 2016 shed more light on the cranial morphology of the group.

Several lineages thrived in South America, such as Andesauroidea, Diamantinasauria, Saltasauridae, Lognkosauria, and Rinconsauria, including Aeolosaurini (Carballido *et al.*, 2022). Among them, the latter clade is an endemic component of South American latest Cretaceous faunas. The particular morphology of their caudal vertebrae makes them easily recognizable and could lead them to be used as a biostratigraphic proxy. The clade Aeolosaurini was originally named by Franco-Rosas *et al.* (2004) to encompass taxa such as *Aeolosaurus rionegrinus* Powell, 1987, *Gondwanatitan faustoi* Kellner & De Azevedo, 1999, and *Rinconsaurus caudamirus* Calvo & González-Riga, 2003. Despite the existence of different proposals of the phylogenetic position of the Aeolosaurini among titanosaurs, the taxonomic content of Aeolosaurini has varied over time, with a recent review made by Carballido *et al.* (2022) placing it within the clade Rinconsauria of Calvo *et al.* (2007a). The current phylogenetic definition of Aeolosaurini establishes this clade as the most recent common ancestor of *Ae. rionegrinus* and *G. faustoi*, and all its descendants (Carballido *et al.*, 2017).

In Uruguay, titanosaur remains were first described by Huene (1929b), leading that author to propose the presence of Upper Cretaceous sedimentary rocks in the western part of the country. Huene (1929b) referred the materials to four species: *Antarctosaurus wichmannianus* Huene, 1929a, *Argyrosaurus superbus* Lydekker, 1893, *Laplatasaurus araukanicus* Huene, 1929a, and *Titanosaurus australis* Lydekker, 1893 (*Neuquensaurus australis* since Powell, 1992). However, due to the fragmentary nature of the remains, they are regarded as indeterminate titanosaurians (Powell, 2003; Mannion & Otero, 2012; Soto *et al.*, 2012, 2022). In later years, a caudal vertebra closely resembling *Aeolosaurus* was described by Soto *et al.* (2022). Moreover, abundant remains of a new saltasauroid, *Udelartitan celeste* Soto *et al.*, 2024, were recently described (Soto *et al.*, 2024).

The purpose of this work is to describe two well-preserved caudal vertebrae from Uruguay that share several morphological traits with Aeolosaurini.

GEOLOGICAL SETTING

The Guichón Formation, defined by Bossi (1966), crops out in northwestern Uruguay, mainly in the Paysandú department (Fig. 1). Along with the overlying Mercedes and Asencio formations, it makes part of the Paysandú Group (Bossi & Navarro, 1988). The Guichón Formation has been hypothesized by several authors (*e.g.*, Gentili & Rimoldi, 1979; Bertolini, 1996; Aceñolaza, 2007; Veroslavsky *et al.*, 2019) to be correlated with the Argentinean Puerto Yeruá Formation erected by De Alba & Serra (1959), which crops out on the opposite shore of the Uruguay River. Concerning Upper Cretaceous deposits in Brazil, the Guichón Formation was recently correlated by Navarro *et al.* (2025) with the basal part of the Baurú Sequence (*sensu* de Paula e Silva *et al.*, 2009), particularly the Santo Anastácio Formation as defined by Soares *et al.* (1980).

The Guichón Formation comprises reddish, fine-grained sandstones of quartz-feldspar composition, with 30–35% clayey matrix (Goso & Perea, 2003). Secondary lithologies include polymictic conglomerates and mudstones. These lithologies have been interpreted as deposited by SW-flowing fluvial channels, although locally there was also some aeolian reworking.

The unit overlies the Hauterivian basaltic flows of the Arapey Formation and, in turn, is overlain by the coarse sandstones and conglomerates of the Campanian–Maastrichtian Mercedes Formation.

The first fossils from the Guichón Formation were reported nearly a century ago. They include several individuals of the uruguaysuchid notosuchian *Uruguaysuchus aznarezi* Rusconi, 1933, redescribed by Soto *et al.* (2011), and three teeth referred by Huene (1934) to ornithomimid theropods and ornithischians, reassigned by Soto *et al.* (2012) to indeterminate theropods and basal iguanodontians, respectively.

Later, abundant remains of a titanosaurian sauropod associated with eggshell fragments were reported by Soto *et al.* (2008, 2012). A recent revision of the skeletal material allowed the erection of a new genus and species, *Udelartitan celeste* Soto *et al.*, 2024, classified either as a non-saltasaurid saltasauroid or a saltasaurine (Soto *et al.*, 2024). The eggshells were referred to the oogenus *Sphaerovum erbeni* Mones, 1980.

Fossil content from the correlated Argentinean unit Puerto Yeruá Formation is sparse. A titanosaurian humerus originally referred to *Argyrosaurus* by Huene (1929a) was considered an indeterminate titanosaur by Mannion and Otero (2012). Fragmentary material not found *in situ* has

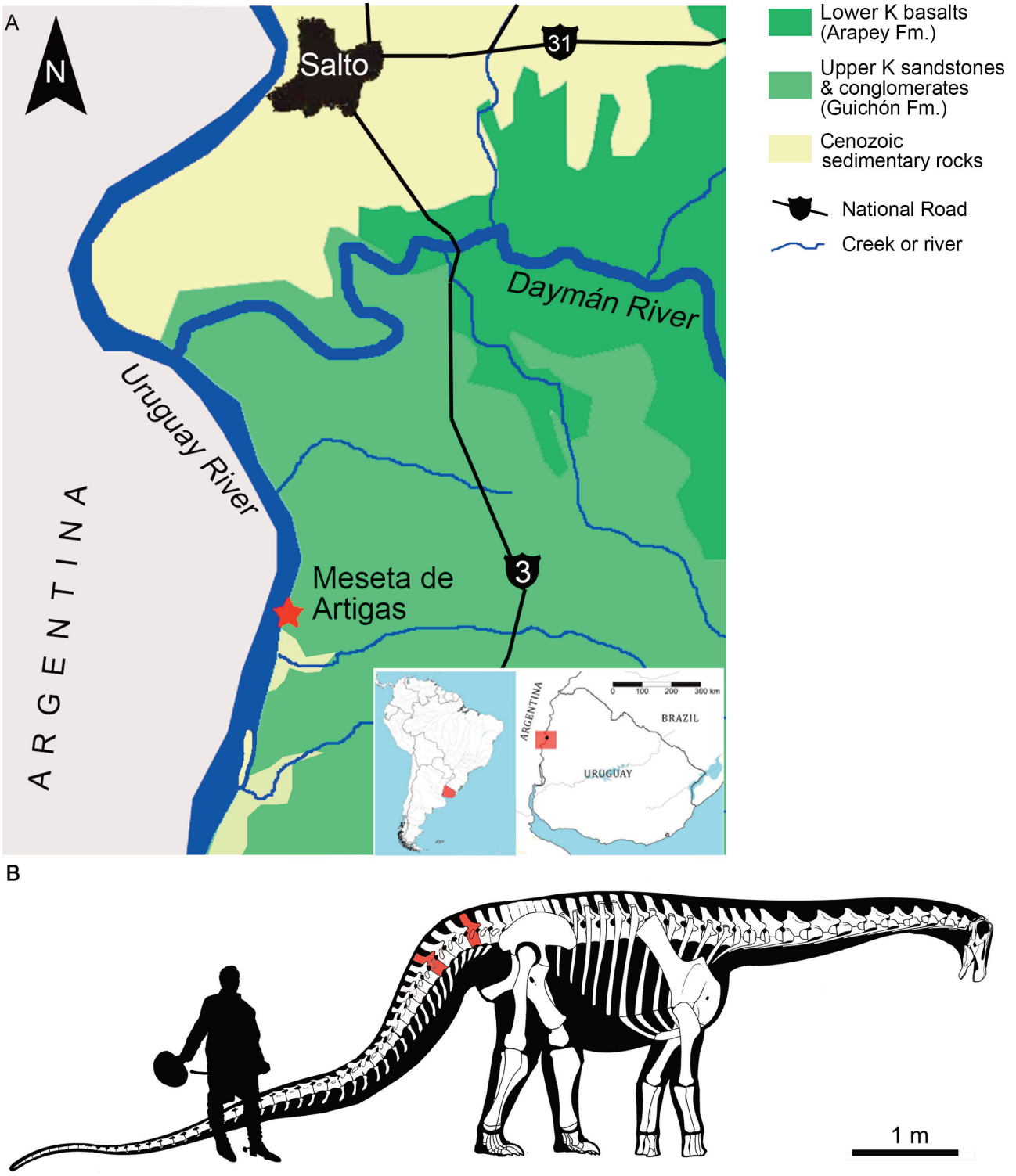


Figure 1. A, Simplified geological map (based on Bossi & Ferrando, 2001). The fossil site is indicated with a red star. The insets at the bottom left and right depict the location of Uruguay within South America and the location of the study area within Uruguay, respectively; **B,** hypothetical reconstruction of ***Mesetasaurus protector*** gen. et sp. nov. with the approximate location of the two known vertebrae in color. For scale, silhouette of José Artigas by Juan Luis Blanes. Sauropod silhouette modified from drawing by Marco Auditore. The protonic tail (*i.e.*, ventrally curved proximal portion of the tail) is inferred due to comparisons with its relative ***Arrudatitan maximus*** Santucci & Arruda-Campos, 2011 (Vidal *et al.*, 2021), with which ***M. protector*** gen. et sp. nov. shares key features. The skull is based on that of the probable aeolosaurine ***Inawentu oslatus*** Filippi *et al.*, 2024.

also been reported by de Valais *et al.* (2003), and includes an ankylosaurian scute, a theropod tooth fragment, and an eggshell fragment (plus an unfigured complete egg) referred to *Sphaerovum* Mones, 1980.

Originally dated as 'Cenomanian or older' (Rusconi, 1933) or even Aptian (Goso & Perea, 2003), recent findings of the derived titanosaurian *Udelartitan celeste* plus *Sphaerovum* eggshells (Soto *et al.*, 2008, 2012, 2024) suggest the Guichón Formation could be considerably younger (see details in Discussion).

The fossil site is located in northern Paysandú department, 20 km south of the city of Salto (Fig. 1). It is called Meseta de Artigas due to its particular plateau-like geomorphology (Fig. 2A). The fossils are two caudal vertebrae, found closely associated on a surface of less than 1 m^2. They were found in the 1980s, included in poorly consolidated, argillaceous, reddish sandstones (patches of which were still adhered to one of the vertebrae prior to preparation) in a small cliff near the west bank of the Uruguay River. Nowadays the cliff is covered by vegetation (Fig. 2B), and thus a sedimentological log cannot be described. However, a complete exposure of dozens of meters to the north was reported by Goso and Perea (2003), corresponding to the sedimentological log given herein (Fig. 2C). Fossils were found towards the base of the profile. Patches of reddish, clayey sandstone were still preserved attached to the material prior to the preparation, particularly in the cotyle and the blind fossae of one of them. They are rather well-preserved. However, we infer there was some degree of fluvial transport to account for the loss of the neural spine, part of the prezygapophyses and of the transverse processes, and slight abrasion of the right ventrolateral part of the cotyle in one of the specimens, and the right dorsolateral part of the condyle in the other specimen.

MATERIAL AND METHODS

The vertebrae were photographed with a Nikon D5100 camera, measured with a Mitutoyo caliper (Table 1), and carefully compared to other titanosaur taxa mostly from Gondwana, examined firsthand or taken from the literature (Table 2).

Centrum length (with and without condyle), condyle height and width, cotyle height and width, and ventral face length and width were measured (Table 1). Several indices were calculated. Two of them express the degree of dorsoventral compression of the centrum and are calculated at the cotyle and condyle, respectively: the Cotyle Dorsoventral Compression Ratio (CtR, Soto *et al.*, 2012) is the cotyle height divided by cotyle width; the Condyle Dorsoventral Compression Ratio (CdR, Soto *et al.*, 2012) is condyle height divided by condyle width. The remaining four ratios express the degree of centrum elongation in different ways: dividing the anteroposterior length per the condyle width (Upchurch, 1998); the anteroposterior length per the centrum width (Wilson & Sereno, 1998); the anteroposterior length (excluding the articular 'ball') divided by the average of condyle height and width (aEI – average Elongation Index of Chure *et al.*, 2010); or as defined herein the anteroposterior length per the cotyle height (CeR – Centrum Elongation Ratio; the cotyle is more reliable because in some sauropods as one advances throughout the caudal series a more pronounced compression of the condyle compared with the cotyle is seen).

To infer the phylogenetic relationships of the new taxon, the most updated taxon/character matrix of Pérez Moreno *et al.* (2026) was analyzed. This matrix includes a large number of titanosaurs traditionally regarded as members of the clade Aeolosaurini. Characters 14, 61, 100, 102, 109, 115, 127, 132, 135, 136, 166, 179, 195, 256, 259, 276, 277, 278, 279, 299, 303, 346, 352, and 354 were considered as additive (= ordered).

A few character states were rescored for *Ae. rionegrinus* (now scored as having ventrolateral ridges; char. 234.1), *Baurutitan britoi* Kellner *et al.*, 2005 (now scored as polymorphic for anteriorly inclined cotyles in anterior caudal vertebra; char. 254.1), and *Caieiria allocaudata* Silva Junior *et al.*, 2022 (now scored as having anteriorly inclined cotyles in middle caudal vertebrae; char. 255.1).

The matrix was analyzed under equal weights with the software TNT version 1.6 (Goloboff *et al.*, 2008). We followed Pérez Moreno *et al.* (2026) in using New Search Technologies, with five rounds of Con*sensus* Stabilization and *a posteriori* second round of tree bisection and reconnection (TBR). Bootstrap and Jackknife support were calculated with 10,000 replicates. Bremer Support was calculated with the bremsup script.

Given uncertainties concerning the age of the Guichón Formation, literature describing Cretaceous archosaur fau-

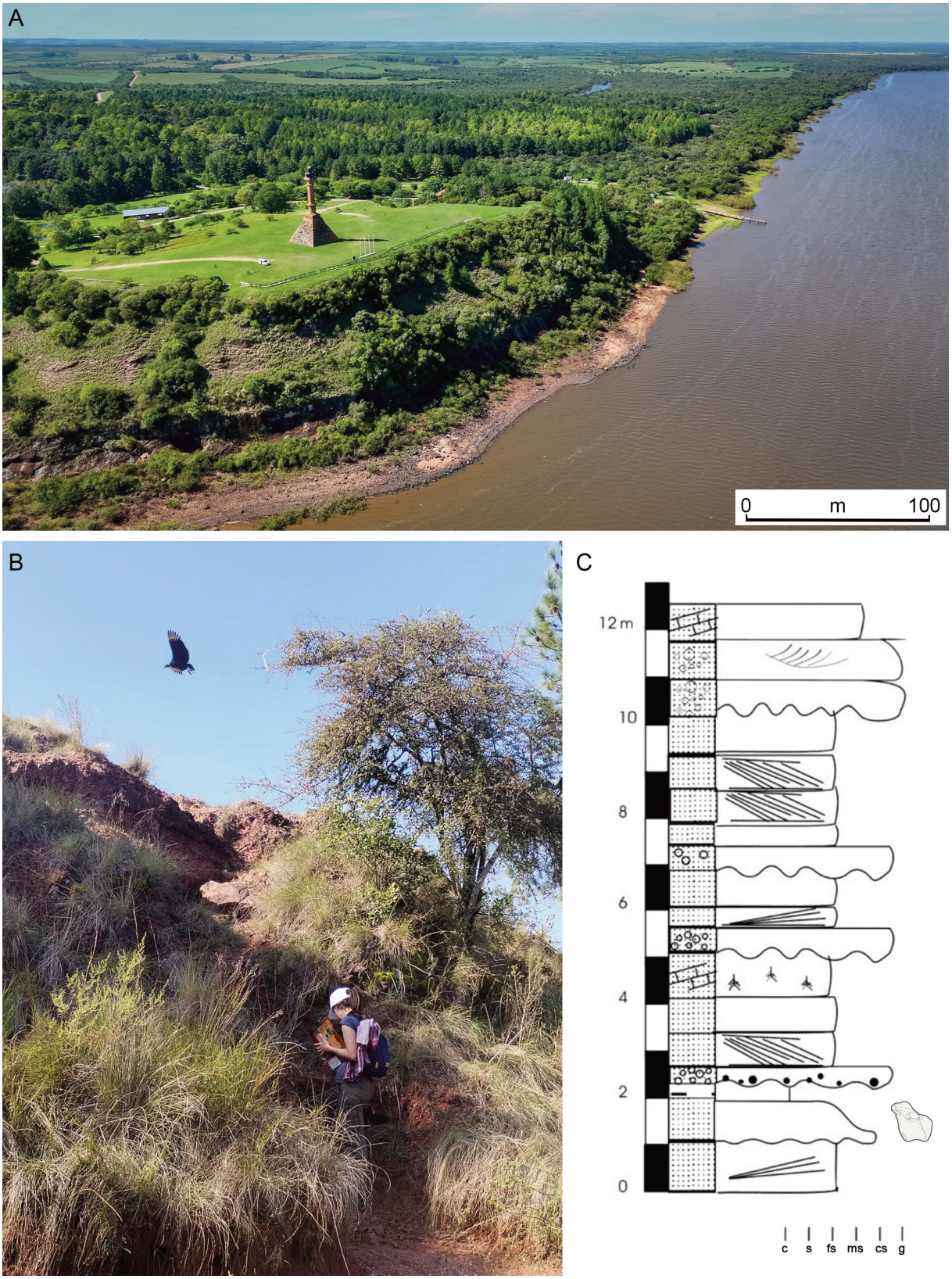


Figure 2. A, General view of the Meseta de Artigas (courtesy of Viviendo el Camino); **B,** fossil site, with human and vulture for scale; **C,** sedimentological profile of the Meseta de Artigas locality. The section was made just north of the site (-31.6153° S, -57.9851° W) by Goso & Perea (2003: fig. 7). The fossils come from the base of the profile, as indicated by the bone icon. Abbreviations: **c,** clay; **cs,** coarse sand; fs, fine sand; **g,** gravel; **ms,** medium sand; **s,** silt.

Table 1. Measurements in cm of *Mesetasaurus protector* gen. et sp. nov.

	FC-DPV 3740A	FC-DPV 3740B
Length (including condyle)	14.5	13.2
Length (excluding condyle)	10.4	9.2
Cotyle height	13.6	10.9
Cotyle width	14.5	12.5
Cotyle dorsoventral compression ratio (CtR)	0.94	0.87
Condyle height	11.6	9.4
Condyle width	12.2	10.9
Condyle dorsoventral compression ratio (CtR)	0.95	0.86
Total height (preserved)	19.2	17.2
Ventral face length	9.3	9.5
Ventral face width (minimum)	9.0	5.3
Centrum elongation ratio (CeR)	1.07	1.21
Elongation index *sensu* Upchurch (1998)	1.19	1.21
Elongation index *sensu* Wilson & Sereno (1998)	1.61	2.49
Average elongation index (aEI *sensu* Chure *et al.*, 2010)	0.87	0.91

nas across South America was thoroughly examined to analyze the similarities among them and potentially identifying some chronological signals. We included only those units which yielded body fossils of at least three confidently determined taxa (see Table 3). Although only containing dinosaur ichnites (Navarro *et al.*, 2025), the Brazilian Santo Anastácio Formation was included to test its supposed similarities with the Guichón/Puerto Yeruá Formation proposed by those authors. A presence/absence matrix of 46 suprageneric taxa (6 pterosaur, 10 crocodyliform, and 30 non-avian dinosaur clades) across 36 units (1 from Madagascar, 1 from Chile, 2 from Uruguay, 5 from Africa, 8 from Brazil, and 19 from Argentina) was con-structed. We chose to use families, subfamilies, or tribes to maximize clustering information. Employing genera or species (such as, in the case of Uruguay, the titanosaurs *Udelartitan* and *Mesetasaurus* and the notosuchian *Uruguaysuchus*) would lend endemic taxa uninformative. Non-monophyletic groups (*e.g.*, basal representatives of some groups) were also included in some cases. A few oofamilies were also considered.

Among crocodyliforms, notosuchians are the most common group (23 out of 36 units, although it was split in several families to maximize the information), followed by peirosaurids (15 units). Concerning ornithischians, elasmarian ornithopods are present in 13 units. The most common theropods are the abelisaurids (26 units), followed by noasaurids, carcharodontosaurids, and megaraptorids (10 units each). Sauropods are overwhelmingly represented by titanosaurs (27 units). As in the case of Notosuchia, to maximize the information, the speciose clade Titanosauria was subdivided into several groups (*i.e.*, basal Titanosauria, Lognkosauria, Aeolosaurini, Saltasaurinae, Saltasauroidea with biconvex first caudal centra) so rebbachisaurids take the lead with 12 units, followed by the Aeolosaurini with 9 units.

The most diverse formations (considering the suprageneric taxa we chose) are the Kem Kem and Allen formations (15 or more taxa each), followed by the Elrhaz and Romualdo formations (10 taxa each), Bajo de la Carpa and Candeleros formations (9 taxa each), and the Bahariya,

Table 2. Selected titanosaurs for anatomical comparison with the material described herein. Asterisk (*) indicates caudal assemblages 2 and 4 of Pérez Moreno et al. (2026), formerly part of *Muyelensaurus pecheni.*

Country	Taxon	Source
Argentina	*Aeolosaurus rionegrinus*	Powell, 2003
	Aeolosaurus ?rionegrinus	Powell, 2003
	Aeolosaurus sp. 1	Salgado & Coria, 1993
	Aeolosaurus sp. 2	Salgado *et al.*, 1997a; García & Salgado, 2013; M.S., pers. obs.
	Aeolosaurus colhuehuapensis	Casal *et al.*, 2007
	Panamericansaurus schoederi	Calvo & Porfiri, 2010
	Punatitan coughlini	Hechenleitner *et al.*, 2020
	Bravasaurus arrierosorum	Hechenleitner *et al.*, 2020
	Titanosauria gen. et sp. indet. 4	García & Salgado, 2013; M.S., pers. obs.
	Mendozasaurus neguyelap	González-Riga, 2003; González-Riga *et al.*, 2018
	Rinconsaurus caudamirus	Calvo & González-Riga, 2003
	Nullotitan glaciaris	Novas *et al.*, 2019
	Rocasaurus muniozi	Salgado & Azpilicueta, 2000; García & Salgado, 2013; M.S., pers.obs.
	Saltasaurus loricatus	Powell, 1992
	Neuquensaurus australis	Lydekker, 1893; Salgado *et al.*, 2005; M.S., pers.obs.
	Pellegrinisaurus powelli	Salgado, 1996; Cerda *et al.*, 2021
	Aeolosaurini gen. et sp. indet.*	Pérez Moreno *et al.*, 2026
Brazil	*Baurutitan britoi*	Kellner et al. 2005
	Uberabatitan ribeiroi	Salgado & Carvalho, 2008
	Caieiria allocaudata	Silva Junior et al., 2022
	Gondwanatitan faustoi	Kellner & Azevedo, 1999
	Arrudatitan maximus	Santucci & De Arruda-Campos, 2011; Silva Junior *et al.*, 2021
USA	*Alamosaurus sanjuanensis*	Gilmore, 1946
Madagascar	*Rapetosaurus krausei*	Curry Rogers, 2009
Uruguay	*Aeolosaurus* sp. 3	Soto *et al.*, 2022; M.S., pers. obs.
	Udelartitan celeste	Soto *et al.*, 2024; M.S., pers. obs.
	Lithostrotia gen. et sp. indet.	Soto *et al.*, 2022; M.S., pers. obs.

Portezuelo, and Adamantina formations (8 taxa each).

In a few cases (Guichón/Puerto Yeruá, Mercedes/Asencio, and Serra da Galga/Marília), information on the units was combined, in the first case because they are undoubtedly correlated and in the other two cases to maximize the information and to avoid doubts regarding fossil provenance. A classical cluster analysis employing the UPGMA algorithm (*e.g.*, Holtz *et al.*, 2004) and the Dice similarity index was performed using the software PAST v. 4.17c (Hammer *et al.*, 2001).

Nomenclatural act. The new genus and species names were registered in Zoobank. The Life Science Identifier (LSID) for this contribution is urn:lsid:zoobank.org:pub: 070DE7BE-8486-43F7-930B-8B6B90439258.

Table 3. Locality/taxon matrix of selected Cretaceous formations, focusing in South America, used in the cluster analysis.

Unit	Pholidosauridae	Uruguaysuchidae	Peirosauridae	Mahajansuchidae	Stomatosuchidae	Dyrosauridae	Itasuchidae	Sphagesauria	Basal Ziphosuchia	Baurusuchidae	Tyreophora basal	Stegosauria	Nodosauridae	Parankylosauria	non-hadrosauriform Ornithopoda	Non-elasmarian,	Basal hadrosauriforms	Elasmaria	Hadrosauroidea	Ceratosauridae	Noasauridae	Abelisauridae	Spinosauridae	Carcharodontosauridae	Megaraptoridae	Basal Maniraptoromorpha	Alvarezsauroidea	Unenlagiidae	Diplodocidae	Dicraeosauridae	Rebbachisauridae	Somphospodyli basal	Titanosauria basal	Saltasauroidea with biconvex first caudal centrum	Aeolosaurini	Futalognkosauria	Saltasaurinae	Anhangueridae	Thalassodromidae	Tapejaridae	Ctenochasmatidae	Ornithocheiriformes	Azdarchoidea	Faveoloolithidae	Megaloolithidae	Fusioolithidae	Elongatoolithidae	Arriagadoolithidae
Elrhaz	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Echkar	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kem Kem	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Wadi Milk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bahariya	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Guichón/Puerto Yeruá	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
Mercedes/Asencio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
Dorotea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mulichinco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
La Amarga	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bajada Colorada	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Candeleros	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Huincul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Portezuelo	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Plottier	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Cerro Lisandro	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Bajo de la Carpa	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Anacleto	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Allen	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1
Bajo Barreal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Colhué Huapí	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Los Alamitos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Cerro Barcino	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Chorrillo	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cerro Fortaleza	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Lecho	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
La Colonia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Romualdo	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Itapecurú	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quiricó	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Marfim	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Rio Paraná	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Santo Anastácio	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adamantina	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Serra da Galga	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Maevarano	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Institutional abbreviations. FC-DPV, Vertebrate Fossil Collection, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA von Huene, 1932
SAUROPODA Marsh, 1878
TITANOSAURIFORMES Salgado, Coria & Calvo, 1997b
TITANOSAURIA Bonaparte & Coria, 1993
RINCONSAURIA Calvo *et al.*, 2007a
AEOLOSAURINI Franco-Rosas *et al.*, 2004
sensu Carballido *et al.*, 2017

Mesetasaurus gen. nov.

LSID urn:lsid:zoobank.org:act:2AA8934F-021E-46F1-9F98-893629A66E6F

Holotype. FC-DPV 3740, two anterior caudal vertebrae. For descriptive purposes, we will refer to 3740A (the more anterior one) and 3740B (the more posterior one).

Etymology. 'Meseta', after the name of the locality, plus '*saurus*', Greek for reptile.

Provenance. Meseta de Artigas, northern Paysandú department, Uruguay. Guichón Formation (Upper Cretaceous).

Diagnosis. Titanosaur diagnosed by the following combination of characters (potential autapomorphy marked with an asterisk): anterior caudal centra strongly procoelous; ventral margins of the caudal centra ranging from a flat to slightly transversely concave surface; neural arch anteriorly displaced. Anterior caudal centra with slightly anteriorly inclined anterior face (about 10°); an ovoid blind fossa situated below the anteroposterior axis of the centrum and very close to the condyle*; wide ventral surface pierced by paired neurovascular foramina; strongly convex (0.58 following the metric proposed by Mannion *et al.*, 2013), slightly eccentric condyle, and long, anterodorsally (30°) projected prezygapophysis. Posterior anterior caudal centra with strongly anteriorly inclined anterior face (about 25°); centrum slightly dorsoventrally compressed (0.86–0.87 dorsoventral compression ratios following Soto *et al.*, 2012; see Table 1); narrow ventral face bounded by ventrolateral ridges; very strongly convex (0.68 following Mannion *et al.*, 2013), strongly eccentric condyle; sub-horizontal (10°) prezygapophyses.

Mesetasaurus protector sp. nov.

Figs. 3–4

LSID urn:lsid:zoobank.org:act:061C5A20-06A7-4B1A-ADCA-CC472978910C

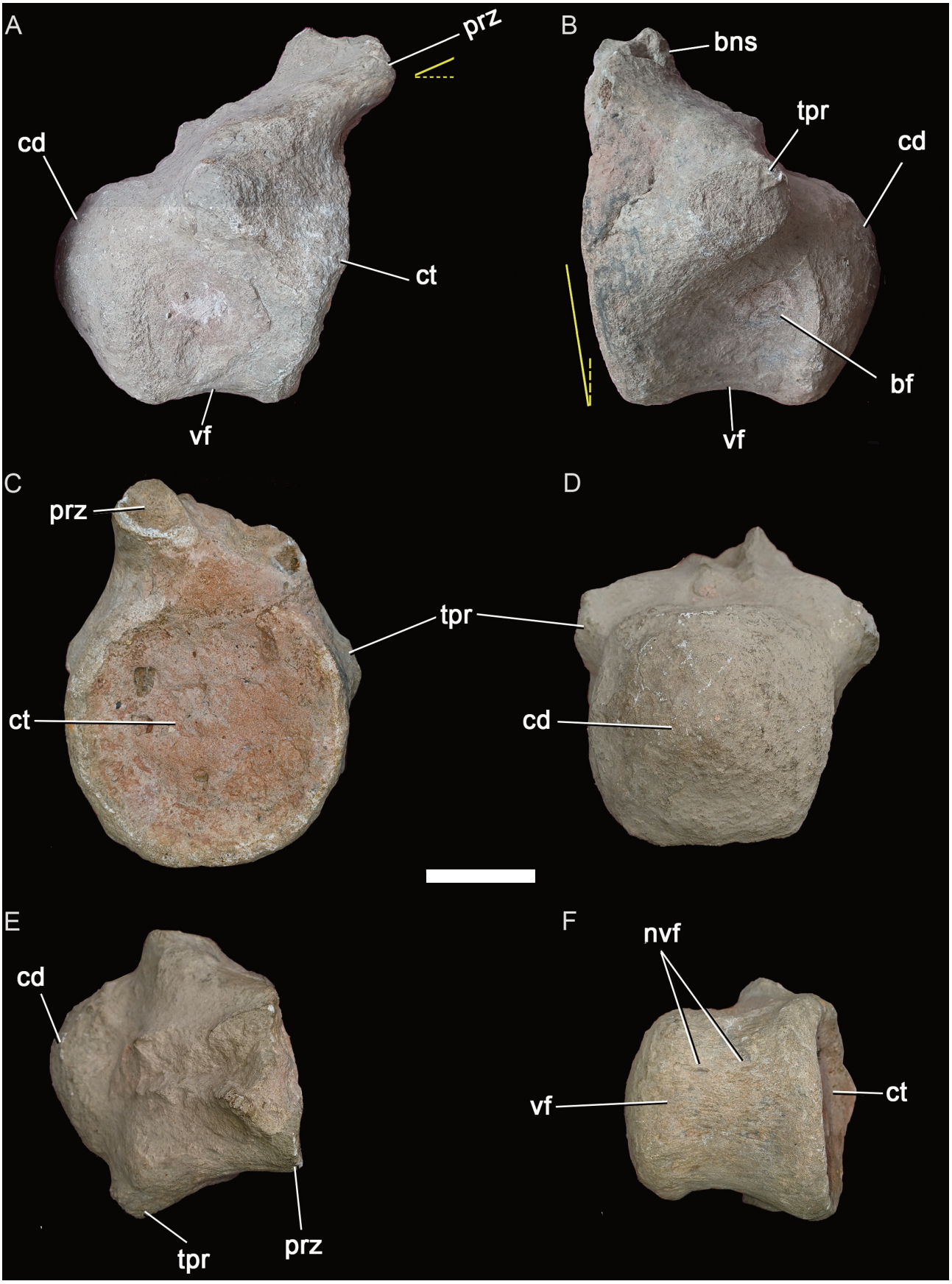
Diagnosis. Same as for genus, by monotypy.

Etymology. Latin for 'the one who protects', in commemoration of José Artigas (1764–1850), an Uruguayan national hero who defeated the Spanish army in 1811 at the battle of Las Piedras, led the 'orientales' during their exodus after rejecting an armistice between Buenos Aires and Spain, and was known for his sensitivity towards the most vulnerable members of the society. He was named 'Protector de los Pueblos Libres' (Protector of the Free Peoples), the title given to the leader of the leader of the Liga Federal (Federal League), also known as the Liga de los Pueblos Libres (League of the Free Peoples), a confederation of provinces which includes what is now Uruguay and part of Argentina. The capital of this League was situated a few kilometers north of the fossil site. Close to the fossil site, on top of the Meseta, there is a large bust of Artigas (Fig. 2A).

Description. FC-DPV 3740A and FC-DPV 3740B are among the best-preserved sauropod vertebrae known in Uruguay. After comparison with materials described by Salgado *et al.* (1997a), Powell (2003), Kellner *et al.* (2005), García and Salgado (2013), and Vidal *et al.* (2021), FC-DPV 3740A and FC-DPV 3740B probably correspond to the 3rd and 6th caudal positions, respectively (Fig. 1B).

The preserved portion of FC-DPV 3740A is larger and dorsoventrally higher than FC-DPV 3740B due to its more anterior position (compare Fig. 3A–B and Fig. 4A–B; see also Table 1). The centrum elongation is aEI= 0.87 for FC-DPV 3740A and aEI = 0.91 for FC-DPV 3740B (for other elongation metrics, see Table 1).

Both caudal centra are strongly procoelous, with a deeply excavated anterior cotyle (Figs. 3C, 4C) and a prominent posterior condyle (Figs. 3B, 3D, 4B, 4D). Both the cotyle and the condyle are slightly wider than tall in both vertebrae, although the proportion differs: the dorsoventral compression ratio is CtR = 0.94 for the cotyle (which is close to a perfect circle; Fig. 3C) and CdR = 0.95 for the condyle in FC-DPV 3740A, whereas CtR = 0.86 and CdR = 0.87 in FC-DPV 3740B. These ratios indicate that FC-DPV 3740B is more dorsoventrally compressed than FC-DPV 3740A (compare Fig. 3C–D and 4C–D), and that in each vertebra,


A
prz
cd
ct
vf
B
bns
tpr
cd
bf
vf
C
prz
tpr
ct
D
cd
E
cd
tpr
prz
F
nvf
vf
ct

the degree of compression does not vary significantly between the condyle and the cotyle.

The apex of the condyle is slightly dorsally shifted in FC-DPV 3740A (Fig. 3A), whereas it is more strongly dorsally shifted in FC-DPV 3740B (Fig. 4B). Applying the metrics of Mannion *et al.* (2013), the degree of convexity is strong in FC-DPV 3740A (0.58) and very strong in FC-DPV 3740B (0.68).

The anterior face of the centrum in FD-DPV 3740A is slightly anteriorly inclined (about 10° relative to the vertical plane), best seen in left lateral view (Fig. 3B). However, in FC-DPV 3740B the anterodorsal border of the centrum is situated far more anteriorly than the anteroventral one. Hence, the anterior face is strongly anteriorly inclined in lateral view, about 25° (Fig. 4B).

The lateral faces are moderately excavated. FC-DPV 3740A bears a 3.5 cm-long, anteroposteriorly elongated ovoid depression (blind fossa) on both lateral faces (Fig. 3B). These fossae are strikingly posteriorly placed, very close to the condyle.

The ventral face of the centrum is slightly transversely concave in lateral view in both vertebrae (Figs. 3A–B, 4A–B). In ventral view, the ventral face is rather flat in FC-DPV 3740A but concave in FC-DPV 3740B (Figs. 3F, 4F). There are four paired neurovascular foramina in FC-DPV 3740A (Fig. 3F). The ventral face is wide in FC-DPV 3740A but narrow in FC-DPV 3740B, despite their lengths being similar (see Table 1). This is due to the presence in the latter of ventrolateral ridges and the lateral constriction of the centrum (Fig. 4F). Thus, the ventral face of FC-DPV 3740A has a squarish profile whereas that of FC-DPV 3740B has a more rectangular outline. The chevron articulations are well developed only in FC-DPV 3740B (Figs. 3D, 4D).

Because only the bases of the transverse processes are preserved, their full morphology cannot be assessed. They appear to be dorsolaterally oriented. Dorsally, they preserve faint eminences that produce a 'shoulder-like' appearance in posterior view (Figs. 3D, 4D). In both vertebrae, they reach at least the beginning of the condyle (Figs. 3E, 4E).

The partially preserved neural canal is filled with sandstone in both vertebrae. The neural arch is anteriorly shifted (Figs. 3A–B, 4A–B), a typical titanosauriform condition (Salgado *et al.*, 1997b).

Only the bases of the neural spines are preserved (Figs. 3A, 4B). We infer that the neural spine in FC-DPV 3740A was nearly vertical, judging from the remnant of the spinoprezygapophyseal lamina. The neural spine was slightly inclined anteriorly in FC-DPV 3740B.

We infer the prezygapophyses would have been elongate when complete, far surpassing the anterior border of the centrum to reach the postzygapophyses of the preceding vertebra. The prezygapophyses were anterodorsally projected (30°) when complete in FC-DPV 3740A, but they were sub-horizontal (10°) in FD-DPV 3740B (compare Figs. 3A, 4A). This difference between vertebrae indicates a change in orientation that depends on position within the caudal series.

The postzygapophyses were not preserved.

Comparisons. As in almost all titanosaurians, caudal centra FC-DPV 3740A and 3740B are strongly procoelous. FC-DPV 3740A is anteroposteriorly short, differing from the anterior caudal centra of *Ae. rionegrinus*, *Aeolosaurus* sp. 2, and *G. faustoi* (Salgado *et al.*, 1997a, Kellner & de Azevedo, 1999, Powell, 2003). Unlike those of Saltasaurinae (Powell, 1992, 2003; Salgado & Azpilicueta, 2000; Salgado *et al.*, 2005), the centrum is not dorsoventrally compressed. FC-DPV 3740B is slightly dorsoventrally compressed but not laterally compressed, unlike *Ae. rionegrinus*, *Aeolosaurus* sp. 1, and *Panamericansaurus schroederi* Calvo & Porfiri, 2010 (Salgado & Coria, 1993; Powell, 2003; Calvo & Porfiri, 2010).

The anterior face of FC-DPV 3740A is only slightly anteriorly inclined (Fig. 3B). It is straight in the most anterior preserved caudal centra of *Ae. rionegrinus*, *Aeolosaurus* sp. 1, and *Aeolosaurus* sp. 2 (Salgado & Coria, 1993; Salgado *et al.*, 1997a; (Powell, 2003; García & Salgado, 2013). In turn, the strong anterior tilt of the anterior face in FC-DPV 3740B

Figure 3. FC-DPV 3740A, anterior caudal vertebra of ***Mesetasaurus protector*** gen. et sp. nov. in **A,** right lateral; **B,** left lateral; **C,** anterior; **D,** posterior; **E,** dorsal; and **F,** ventral views. Anterior is towards the right in E and F. The orientation of the prezygapophysis and the anterior face of the centrum is shown relative to horizontal and vertical, respectively. Abbreviations: **bf,** blind fossa; **bns,** base of neural spine; **cd,** condyle; **ct,** cotyle; **nvf,** neurovascular foramina; **prz,** prezygapophysis; **tpr,** transverse process; **vf,** ventral face. Scale bar equals 5 cm.

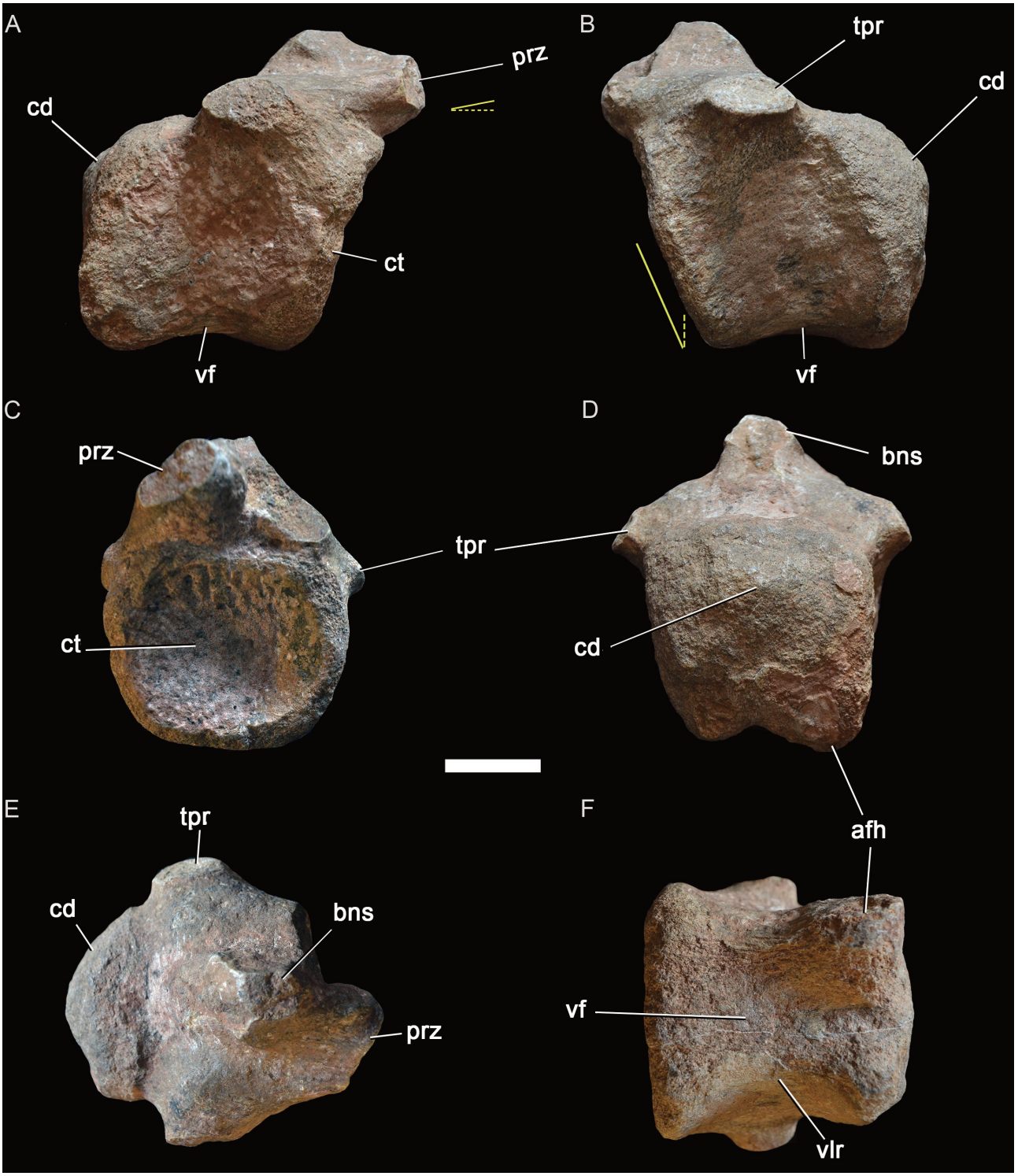


Figure 4. FC-DPV 3740B, anterior caudal vertebra of ***Mesetasaurus protector*** gen. et sp. nov. in **A,** right lateral; **B,** left lateral; **C,** anterior; **D,** posterior; **E,** dorsal; and **F,** ventral views. Anterior is towards the right in E and F. The orientation of the prezygapophysis and the anterior face of the centrum is shown relative to horizontal and vertical, respectively. Abbreviations: **afh,** articular facets for the haemapophyses; **bns,** base of neural spine; **cd,** condyle; **ct,** cotyle; **prz,** prezygapophysis; **tpr,** transverse process; **vf,** ventral face; **vlr,** ventrolateral ridge. Scale bar equals 5 cm.

immediately recalls the remaining anterior caudal centra of *Ae. rionegrinus*, *Aeolosaurus* sp. 1, *Aeolosaurus* sp. 2, *G. faustoi*, *Pa. schroederi*, *C. allocaudata*, and the 5th and 6th caudal vertebrae of *B. britoi* (Salgado & Coria, 1993; Salgado *et al.*, 1997a; Kellner & de Azevedo, 1999; Powell, 2003; Kellner *et al.*, 2005; Calvo & Porfiri, 2010; García & Salgado, 2013; Silva Junior *et al.*, 2022).

The well-defined blind fossa on the lateral face of FC-DPV 3740A is present in the third caudal vertebrae of *Ae. rionegrinus* and *Ae. colhuehuapensis* Casal *et al.*, 2007 (Powell, 2003; Casal *et al.*, 2007). A similar feature is present in the most anterior caudal centra of other titanosaurians, such as *Pellegrinisaurus powelli* Salgado, 1996 and *Nullotitan glaciaris* Novas *et al.*, 2019 (Novas *et al.*, 2019; Cerda *et al.*, 2021). However, the position of the blind fossa is unique in *M. protector* gen. et sp. nov., being situated below the antero-posterior axis and very close to the condyle, which is regarded as an autapomorphic trait of this species. In other titanosaurs, this fossa occupies either an anterior position, or a position immediately below the transverse process (or even posterodorsal to it), but never a posteroventral position (*e.g.*, Casal *et al.*, 2007: fig. 3A; Novas *et al.*, 2019: fig. 17B; Cerda *et al.*, 2021: fig. 5B).

The ventral concavity in lateral view is not as developed as in *Ae. rionegrinus*, *Aeolosaurus* sp. 1, *Aeolosaurus* sp. 3, *Pa. schroederi*, and *G. faustoi*, resembling more *Aeolosaurus* sp. 2 (Salgado & Coria, 1993; Salgado *et al.*, 1997a; Kellner & De Azevedo, 1999; Powell, 2003; Calvo & Porfiri, 2010; García & Salgado, 2013; Soto *et al.*, 2022). In ventral view, the ventral face differs from the grooved condition present in *Ae. rionegrinus*, *Aeolosaurus* sp. 2, *Overosaurus paradasorum* Coria *et al.*, 2013, *Arrudatitan maximus* Santucci & Arruda-Campos, 2011, and *G. faustoi* (Salgado *et al.*, 1997a; Kellner & De Azevedo, 1999; Powell, 2003; Santucci & Arruda-Campos, 2011; Coria *et al.*, 2013; Vidal *et al.*, 2021). It also differs from saltasaurine vertebrae, which may present a wide hollow, as in *Neuquensaurus australis* Lydekker, 1893, or a hollow divided by a septum, as in the saltasaurines *Saltasaurus loricatus* Bonaparte & Powell, 1980 and *Rocasaurus muniozi* Salgado & Azpilicueta, 2000.

The ventral face is very wide in FC-DPV 3740A, as in the most anterior caudal centra of *Aeolosaurus* sp. 2 and *O. paradasorum* (Salgado *et al.*, 1997a; Coria *et al.*, 2013). In FC-DPV 3740B, it is narrow, more so in the middle portion due to a pair of lateral indentations, as in *Ae. rionegrinus*, *Aeolosaurus* sp. 2, *O. paradasorum*, and *Ar. maximus* (Salgado *et al.*, 1997a; Powell, 2003; Coria *et al.*, 2013; Vidal *et al.*, 2021), although in *Ae. rionegrinus* this condition is taken to the extreme, acquiring an hourglass shape (Powell, 2003: pl. 11, fig. 1b, 2b). Ventrolateral ridges are present as in *Ar. maximus* (Vidal *et al.*, 2021), *O. paradasorum* (Coria *et al.*, 2013), and *Punatitan coughlini* Hechenleitner *et al.*, 2020.

The degree of convexity of the condyle is similar to that observed in other titanosaurians. The strong eccentricity of the condyle in FC-DPV 3740B resembles that of *Ae. rionegrinus*, *Aeolosaurus* sp. 1, *Aeolosaurus* sp. 2, *Aeolosaurus* sp. 3, and *Uberabatitan ribeiroi* Salgado & Carvalho, 2008 (Salgado & Coria, 1993; Salgado *et al.*, 1997a; Powell, 2003; García & Salgado, 2013; Silva Junior *et al.* (2019 Soto *et al.*, 2022) but differs from the concentric condyles of *Ae. colhuehuapensis*, *G. faustoi*, and most vertebrae of *Ar. maximus* (Kellner & De Azevedo, 1999; Casal *et al.*, 2007; Vidal *et al.*, 2021), as well as from the extreme eccentric condition of an indeterminate titanosaurian described by García and Salgado (2013), in which the apex of the condyle reaches the dorsal edge of the centrum. In mamenchisaurids and turiasaurians, the apex of the condyle can be ventrally displaced (Bandeira *et al.*, 2025).

The base of the neural spine in FC-DPV 3740B suggests it pointed anteriorly, as in *Ae. rionegrinus*, *Aeolosaurus* sp. 1, and *Pu. coughlini* (Salgado & Coria, 1993; Powell, 2003; García & Salgado, 2013; Hechenleitner *et al.*, 2020).

The anterodorsal orientation of the prezygapophyses in FC-DPV 3740A recalls the most anterior caudal centra of *Ae. rionegrinus*, *Aeolosaurus* sp.1, *Aeolosaurus* sp. 2, *Ae. colhuehuapensis*, and *Pa. schroederi* (Salgado & Coria, 1993; Salgado *et al.*, 1997a; Powell, 2003; Casal *et al.*, 2007; Calvo & Porfiri, 2010; García & Salgado, 2013), although the angle is slightly less, about 30°. The sub-horizontal orientation of the prezygapophyses in FC-DPV 3740B, in turn, recalls *Pa. schroederi* and the 7th–8th caudal of *Ae. rionegrinus* (Powell, 2003; Calvo & Porfiri, 2010). However, at this level *Aeolosaurus* sp. 1., *Ae. colhuehuapensis*, *Ar. maximus*, and *Pu. coughlini* show more anterodorsally oriented prezygapophyses. Although only their bases are preserved, the prezygapophyses are inferred to be long, far surpassing the anterior face of the centrum to reach the postzygapophyses of the preceding vertebra.

Although postzygapophyses are not preserved, the zone corresponding to them lies approximately at the same anteroposterior level as the transverse processes, as in most lithostrotians. In both *Ae. rionegrinus* and *Ae. colhuehuapensis*, the neural arch region and neural spine are even more anterodorsally elongated than in *M. protector* gen. et sp. nov. (Fig. 5), with the postzygapophyses lying approximately at the same level as the cotyle, a synapomorphy of the genus (Casal *et al.*, 2007).

PHYLOGENETIC ANALYSIS

We tested the phylogenetic relationships of *M. protector* gen. et sp. nov. using the modified version of the Pérez Moreno *et al.* (2026) matrix (see Appendix). Under equal weighting, the phylogenetic analysis retrieved more than 10,000 trees of 1,847 steps (Consistency Index = 0.295, Retention Index = 0.694). *Mesetasaurus protector* is deeply nested within Aeolosaurini.

A polytomy among *G. faustoi*, *Inawentu oslatus* Filippi *et al.*, 2024, and a clade composed of the remaining Aeolosaurini is retrieved in the con*sensu*s tree (length: 1978 steps), similar to the result recovered by Pérez Moreno *et al.* (2026). Aeolosaurini (applying the phylogenetic definition of Carballido *et al.*, 2017) is supported by six synapomorphies: anterior process of the cervical prezygapophyses not placed ventrolaterally to the articular surface (char. 130.0), cervical vertebrae posterior articular surface height-to-width ratio between 0.9 and 0.7 (char. 132.2), anterior caudal vertebrae with a transversely concave ventral surface (char. 233.1), anterior and middle caudal postzygapophyses located on the anterior half of the centrum (char. 422.1), middle caudal prezygapophyseal length exceeding 50% of the centrum length (char. 423.2), and middle caudal vertebrae with poorly developed SPOL (chart. 428.1).

Aeolosaurines other than *G. faustoi* and *I. oslatus* (note that *I. oslatus* could be the sister taxon of Aeolosaurini rather than a member of the clade depending on the topology) share six synapomorphies: cervical posterior articular surface height-to-width ratio less than 0.7 (char. 132.3), anterior and middle dorsal vertebrae with strongly posteroventrally oriented zygapophyseal articulation angle (char. 171.2), anterior dorsal neural spines posterodorsally oriented (char. 172.1), middle and posterior dorsal vertebrae with single lamina supporting the hyposphene/postzygapophyses from below (chart. 182.1), anterior caudal neural spines square in transverse section (char. 237.1), and caudal vertebrae without a hyposphene ridge (241.0).

Within this clade, two subclades are recognized, herein

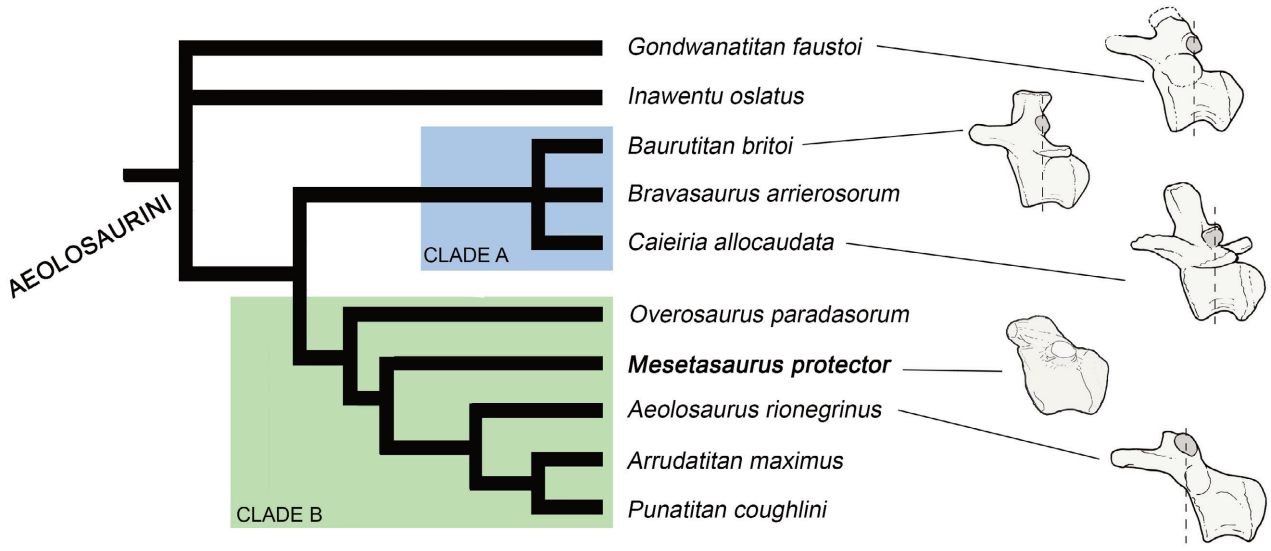


Figure 5. Relationships among Aeolosaurini in the strict con*sensu*s tree resulting from the phylogenetic analysis of the Pérez Moreno *et al.* (2026) matrix. Anterior caudal vertebrae taken from Martinelli *et al.* (2011: fig. 2). Postzygapophyses are shaded in dark gray (not preserved in ***Mesetasaurus***). Dashed lines show the position of the postzygapophysis with respect to the centrum. The ***Mesetasaurus*** drawing is based on FC-DPV 3740B, combining the well-preserved condyle in left lateral view and the better preserved prezygapophysis in right lateral view. Not to scale.

termed 'Clade A' and 'Clade B'. Clade A, which includes *Bravasaurus arrierosorum* Hechenleitner *et al.*, 2020, *C. allocaudata*, and *Baurutitan britoi*, is diagnosed by three synapomorphies: middle to posterior dorsal vertebrae with dorsal margin of the pleurocoel placed at the level of the dorsal margin of the centrum or higher (char. 189.1), first caudal centrum with a convex cotyle (224.2), and lateral margin of humerus almost straight until the proximal third of the bone (307.2).

Clade B, which includes *M. protector*, *O. paradasorum*, *Ae. rionegrinus*, *Ar. maximus*, and *Pu. coughlini* is diagnosed by two synapomorphies: dorsoventrally flattened posterior caudal centra (char. 262.1) and anterior and middle caudal vertebrae with strongly eccentric condyle (419.1). *Mesetasaurus protector* gen. et sp. nov. plus the remaining Aeolosaurini share the presence of ventrolateral ridges in anterior and middle caudal vertebrae (char. 234.1). *Aeolosaurus rionegrinus*, *Pu. coughlini*, and *Ar. maximus* share chevrons with double articular facets (char. 424.1). Finally, *Ar. maximus* and *Pu. coughlini* share the presence of a well-developed posterior protuberance below the articular area of the chevrons (char. 426.1).

Support is unfortunately very low both for Aeolosaurini and clades A and B (Bremer Support of 1 in all cases). Bootstrap and Jackknife resamplings led to a collapse of Eusauropoda into a large polytomy, with a few exceptions (notably the Diplodocoidea, which was retrieved as a clade).

DISCUSSION

Mesetasaurus protector gen. et sp. nov. is recovered as a member of the Aeolosaurini based on characters such as strongly anteriorly inclined cotyles, transversely concave ventral faces, and strongly eccentric condyles (the latter is absent in *Ae. Colhuehuapensis*; see Casal *et al.*, 2007). However, among the characters diagnostic of *Aeolosaurus* and its closest relatives, several are absent in *M. protector* gen. et sp. nov. These include a strongly concave ventral margin in lateral view, a ventral median groove in the centrum, chevron articular facets more ventrally oriented, and ventral marks on the cotyle indicating chevrons with double articular facets. Still other characters are unknown in the available material (*i.e.*, expanded prezygapophyseal articular facets, well-developed hyposphene extending posteriorly).

Although only two vertebrae are available, some tendencies along the anterior portion of the tail are evident: i) strong procoely is maintained, as in almost all highly nested titanosaurs; ii) the degree of dorsoventral compression increases posteriorly; iii) the slight degree of concavity of the ventral face is maintained, differing from *Ae. rionegrinus* and *Aeolosaurus* sp. 1 and 2, in which the posteriormost anterior caudal vertebrae show a strongly concave ventral face; iv) the width of the ventral face decreases posteriorly in the caudal series; v) the eccentricity of the condyle increases posteriorly in the caudal series; vi) the degree of anterior inclination of the cotyle increases along the caudal series; vii) the orientation of the prezygapophyses changes from anterodorsal to sub-horizontal in the caudal series; and viii) the degree of development of the articular facets for the chevrons increases along the caudal series.

On the age of the Guichón Formation

In this section, the biochrons of taxa found in the Guichón/Puerto Yeruá formations will be discussed.

Ankylosaurians have not been recovered from uppermost Cretaceous units from Brazil, but this is not the case in other parts of South America. Genera include the Chilean *Stegouros*, which alongside other Gondwanan taxa form a recently recognized clade: the Parankylosauria (Soto-Acuña *et al.*, 2021), and the nodosaurid *Patagopelta* Riguetti *et al.*, 2022 (we follow here the original interpretation of Riguetti *et al.*, 2022). We suggest the scute of the Puerto Yeruá Formation studied by de Valais *et al.* (2003) should be restudied in a broader context of ankylosaur systematics.

Although iguanodontians are not known from most Upper Cretaceous units from Brazil, they are well known in Patagonia, including elasmarians (*e.g.*, Coria & Salgado, 1996; Martínez, 1998; Calvo *et al.*, 2007b; Novas *et al.*, 2004) and hadrosaurids (*e.g.*, Coria *et al.*, 2012; Cruzado-Caballero & Powell, 2017; Rozadilla *et al.*, 2022). The teeth from Guichón Formation are certainly not from hadrosaurids due to the presence of secondary ridges, but their phylogenetic placement among iguanodontians is uncertain; they may be either non-dryomorph iguanodontians or members of Dryomorpha (Soto *et al.*, 2012).

An often-overlooked component of the fauna is the ziphodont crocodyliform tooth mentioned by Mones (1997), which is interpreted as belonging to a sebecosuchian.

Baurusuchids (*e.g.*, Price, 1959; Carvalho *et al.*, 2005; Montefeltro *et al.*, 2011) are first recorded in the Coniacian of Brazil (age of the Adamantina Formation; Castro *et al.*, 2018) and later appear in the Santonian of Argentina (*e.g.*, Martinelli & Pais, 2008). They have not yet been recovered from the Maastrichtian in South America, although they have been recorded from the Maastrichtian of Pakistan (*Pabwehshi pakistanensis* Wilson *et al.*, 2001).

Concerning sauropods, saltasauroids with a biconvex first caudal centrum are restricted to the late Santonian–Maastrichtian (Soto *et al.*, 2024 and references therein; Fig. 6). Although two biconvex first caudal centra were reported from the Cenomanian Wadi Milk Formation of Sudan (Rauhut, 1999), a Campanian maximum depositional age was recently reported for this unit based on detrital zircon dating (Owusu Agyemang *et al.*, 2019).

Among Aeolosaurini, except for the caudal series originally referred to *Muyelensaurus pecheni* Calvo *et al.*, 2007a from deposits now considered to be late Coniacian (Pérez Moreno *et al.*, 2026) and a few vertebrae described by Filippi *et al.* (2013) from the late Coniacian–early Santonian, most members of the clade lived during the last two stages of the Cretaceous Period (Fig. 6). *Mesetasaurus protector* gen. et sp. nov. is nested among the latter in our phylogenetic analysis.

A third sauropod element present in the Guichón Formation is the group of *Sphaerovum* sp. shells. *Sphaerovum erbeni* Mones, 1980 is an oospecies considered to indicate the Campanian–Maastrichtian interval (Casadío *et al.*, 2002; Fig. 6).

Finally, we note that after nearly a century of collecting, not a single specimen referable to Diplodocoidea has been reported from the Guichón Formation, nor have they been recovered from the overlying Mercedes and Asencio formations. The last surviving diplodocoids in the world were the rebbachisaurids, which were especially diverse in South America and reached the Turonian (Salgado *et al.*, 2022; Fig. 6). We interpret the absence of diplodocoids in the Guichón Formation to indicate a post-Turonian age.

Regarding crocodyliform taxa, according to the more recent phylogenies (*e.g.*, Fernández Dumont *et al.*, 2024), Uruguaysuchidae includes only three genera: *Uruguaysuchus* Rusconi, 1933 from the Guichón Formation, *Anatosuchus* Sereno *et al.*, 2003 from Niger, and the widespread *Araripesuchus* Price, 1959. The latter genus encompasses several species, although it is evidently non-monophyletic and in need of revision. Most uruguaysuchids lived during the Aptian–Turonian interval. These include *Ar. patagonicus* Ortega *et al.*, 2000, *Ar. buitreraensis* Pol & Apesteguía, 2005,

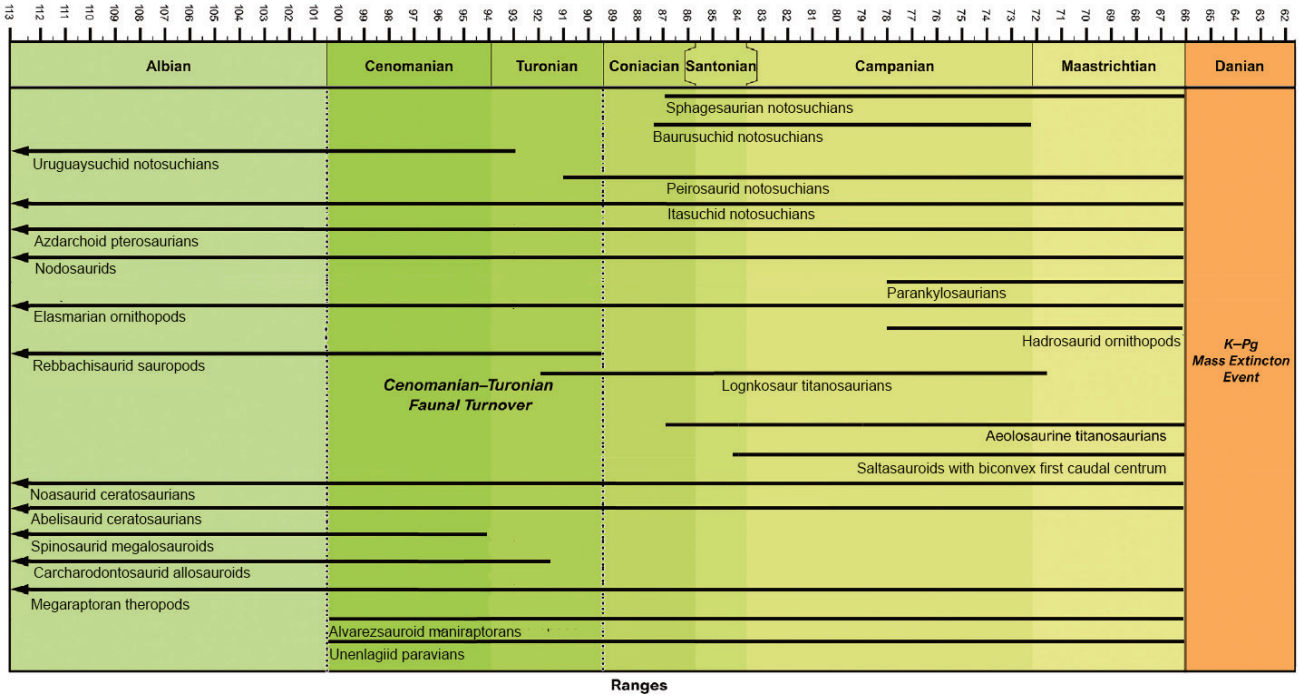


Figure 6. Biochrons of selected archosaurian clades in South America. Modified from Navarro *et al.* (2025: fig. 20).

Ar. manzanensis Fernández Dumont *et al.*, 2024, and the type species, *Ar. gomesii* Price, 1959. If *Uruguaysuchus* is also considered an Aptian–Turonian taxon, this would contradict the latest Cretaceous hypothesis proposed above for the Guichón Formation. However, *Araripesuchus* did reach the Maastrichtian in Madagascar with *Ar. tsangatsangana* Turner, 2006.

Abundant dinosaur footprints from the Brazilian Santo Anastácio Formation (Bauru Group, Paraná Basin) have been recently described (Navarro *et al.*, 2025). The authors identified a diverse assemblage of trackmakers including theropods, ankylosaurians, ornithopods, and sauropods. The notable absence of ornithischian records in the Coniacian–Maastrichtian of the Bauru Group led the authors to recognize an 'ornithischian hiatus'.

Here we question the correlation between the Guichón and Santo Anastácio formations. However, biocorrelation should be made not only with the Bauru Group, but also with other well-known (and at least in part geographically closer) fossiliferous regions, such as northern Argentina or Patagonia (Fig. 7). Indeed, the Guichón/Puerto Yeruá formations share with both Argentinean regions the presence of several higher-level taxa: uruguaysuchids (absent in the Bauru Basin but diversified in Patagonia), basal iguanodontians, ankylosaurians, non-saltasaurine saltasauroids with biconvex first caudal centrum (as demonstrated by Soto *et al.*, 2024), aeolosaurines (this contribution), plus the oogenus *Sphaerovum*.

Contrary to Navarro *et al.* (2025: fig. 19), no abelisaurids nor dromaeosaurids are known from the Guichón/Puerto Yeruá formations so far. The authors probably followed preliminary comparisons mentioned by Soto *et al.* (2012).

Overall, most lines of evidence seem to point to a Late Cretaceous age for the Guichón/Puerto Yeruá Formation, perhaps late Santonian–early Campanian, given that the overlying Mercedes Formation has been considered Campanian–Maastrichtian (Goso & Perea, 2003). Moreover, Daners and Guerstein's (2004) study on dinoflagellates in an offshore well showed that the marine equivalents at the top of the Mercedes Formation are of Maastrichtian age. Furthermore, the limestones of the Queguay Formation (developed due to calcretization of Mercedes-type sandstones) were dated at 71.7+9 Ma (U/Pb in calcite cement – calcretization age; Veroslavsky *et al.*, 2019). Note that

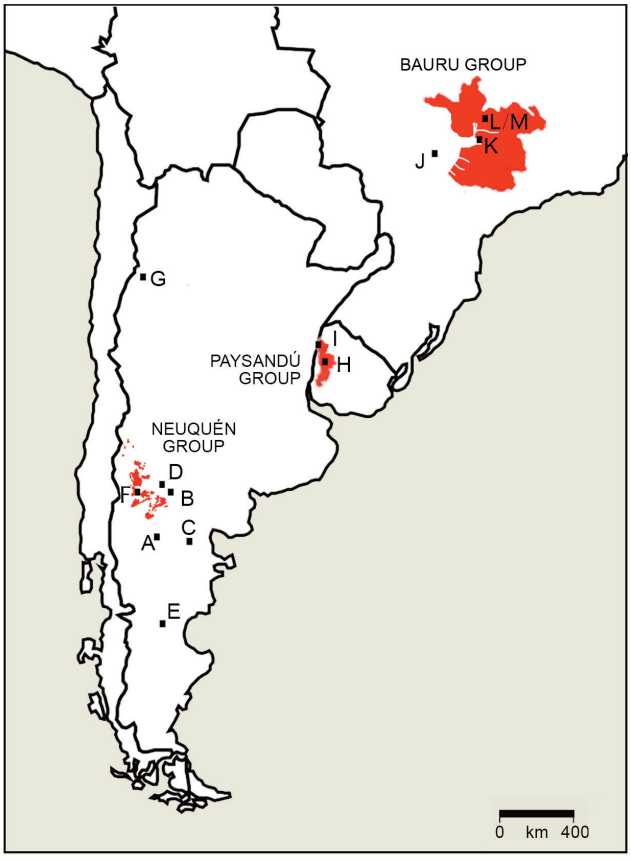


Figure 7. Geographic and stratigraphic provenance of named Aeolosaurini species, plus indeterminate species of ***Aeolosaurus***. **A,** ***Aeolosaurus rionegrinus***, Estancia Maquinchao, Río Negro Province, Argentina (Angostura Colorada Fm.); **B,** ***Aeolosaurus*** sp., Salitral Moreno, Río Negro Province, Argentina (Allen Fm.); **C,** ***Aeolosaurus*** sp., Estancia Los Alamitos and Cona Niyeu, Río Negro Province, Argentina (Los Alamitos Fm.); **D,** ***Panamericansaurus schroederi***, San Patricio del Chañar, Neuquén Province, Argentina (Allen Fm.); **E,** ***Aeolosaurus colhuehuapensis***, Lago Colhué Huapí, Chubut Province, Argentina (Colhué Huapí Fm.); **F,** ***Overosaurus paradasorum***, Cerro Overo, Neuquén Province, Argentina (Anacleto Fm.); **G,** ***Bravasaurus arrierosorum*** and ***Punatitan coughlini***, Quebrada de Santo Domingo, La Rioja Province, Argentina (Ciénaga del Río Huaco Fm.); **H,** ***Aeolosaurus*** sp., Gutiérrez Chico creek, Río Negro Department, Uruguay (Asencio Fm.); **I,** ***Mesetasaurus protector*** gen. et sp. nov., Meseta de Artigas, Paysandú Departament, Uruguay (Guichón Fm.); **J,** ***Gondwanatitan faustoi***, Alvares Machado, São Paulo State, Brazil (Adamantina Fm.); **K,** ***Arrudatitan maximus***, Cândido Rodrigues, São Paulo State, Brazil (Adamantina Fm.); **L–M,** ***Baurutitan britoi*** and ***Caieiria allocaudata***, Peirópolis, Minas Gerais State, Brazil (Serra da Galga Fm.). Updated from Soto *et al.* (2022) and references therein.

Navarro *et al.* (2025) incorrectly assigned an older age to the Mercedes Formation (Turonian–Campanian).

The Guichón/Puerto Yeruá Formation and Mercedes/Asencio Formation faunas recall the Coloradoan and Allenian assemblages of Leanza *et al.* (2004). Theropod and ornithopod material currently under study could shed more light on this topic. The absence of diplodocoids, gigantic

titanosaurs, and amphiplatyan-tailed titanosaurs (see Leanza *et al.*, 2004) is a clear difference compared with older assemblages.

Faunal relationships of South American Cretaceous units

As mentioned above, a cluster analysis of several Cretaceous localities was performed to test the Late Cretaceous hypothesis for the age of the Guichón Formation. The analysis of the locality/taxon matrix is discussed below. The corresponding dendrogram is shown in Figure 8.

Eight clusters were obtained (Fig. 8). The large cluster A includes units from the Aptian–Cenomanian of South America and Africa, which share the presence of abelisaurids, , carcharodontosaurids, and rebbachisaurids. Additionally, some of these units share the presence of peirosaurids, noasaurids, spinosaurids, and (only in African units) stomatosuchids.

The large cluster B includes lower and middle Upper Cretaceous South American units. It is subdivided into a Cenomanian–Turonian cluster, which shares the presence of elasmarians, megaraptorids, and rebbachisaurids (and in some units also lognkosaurs), and a Turonian–Santonian cluster, which shares the presence of peirosaurids, elasmarians, and abelisaurids (and in some units also alvarezsauroids and azhdarchoids). The Cenomanian–Turonian clade includes the Brazilian Santo Anastácio Formation, supporting the interpretation of Navarro *et al.* (2025) for this unit.

Clusters C, D, E, F, and G comprise mostly South American upper Upper Cretaceous units, except for the upper Lower Cretaceous Rio Paraná Formation, and the Guichón/Puerto Yeruá Formation of unknown age.

Cluster C includes two units from Brazil and one from Patagonia which share the presence of peirosaurids, abelisaurids, sphagesaurians, unenlagiids (and in some units also baurusuchids).

Cluster D includes two Patagonian units plus the African Wadi Milk Formation, which share the presence of saltasauroids with biconvex first caudal centra, non-elasmarian iguanodontians, and abelisaurids (and in some units also peirosaurids and megaraptorids). This is consistent with the most recent age determination of the latter unit (Owusu Agyemang *et al.*, 2019), although if confirmed the carcharodontosaurids would be the youngest in the world.

Cluster E includes units from Brazil, northern Argentina and Madagascar, which share the presence of noasaurids, although the remainder of the Rio Paraná Formation paleofauna is compositionally very different due to its older age (*e.g.*, presence of tapejarids, absence of saltasaurines).

Cluster F comprises units of Chile and southern Argentina, which share the presence of hadrosauroids, and megaraptorids (and in some units also parankylosaurs and unenlagiids).

Of special interest to us is cluster G (Fig. 8), which includes the Guichón/Puerto Yeruá, Allen, Mercedes/Asencio, and Los Alamitos formations from Uruguay and Patagonia. They share the presence of Aeolosaurini andfaveoolithid eggs (and in some units also nodosaurids and saltasauroids with biconvex first caudal centra).

Cluster H comprises two Brazilian upper Lower Cretaceous units, which share the presence of spinosaurids and anhanguerids.

Cluster I includes three Argentinean lower Lower Cretaceous units, which share the presence of dicraeosaurids (and in some units also stegosaurs and diplodocids).

CONCLUSIONS

We demonstrated the presence of a member of the Aeolosaurini in the Guichón Formation. The combination of characters allows us to propose the new genus and species, *Mesetasaurus protector* gen. et sp. nov. It appears to be deeply nested within Aeolosaurini. The large amounts of missing data introduce uncertainty in the phylogenetic analysis. More information about the morphology of the prezygapophyseal facets, the positions of postzygapophyses, and the presence of vertebral laminae would help remedy this.

Mesetasaurus protector gen. et sp. nov. is the second sauropod species from Uruguay, belonging to a different titanosaur lineage than the saltasauroid *U. celeste* (Soto *et al.*, 2024).

This is the second record of the Aeolosaurini in Uruguay, besides a caudal vertebra from the latest Cretaceous Asencio Formation referred to *Aeolosaurus* by Soto *et al.* (2022). The strongly transversely concave ventral face and

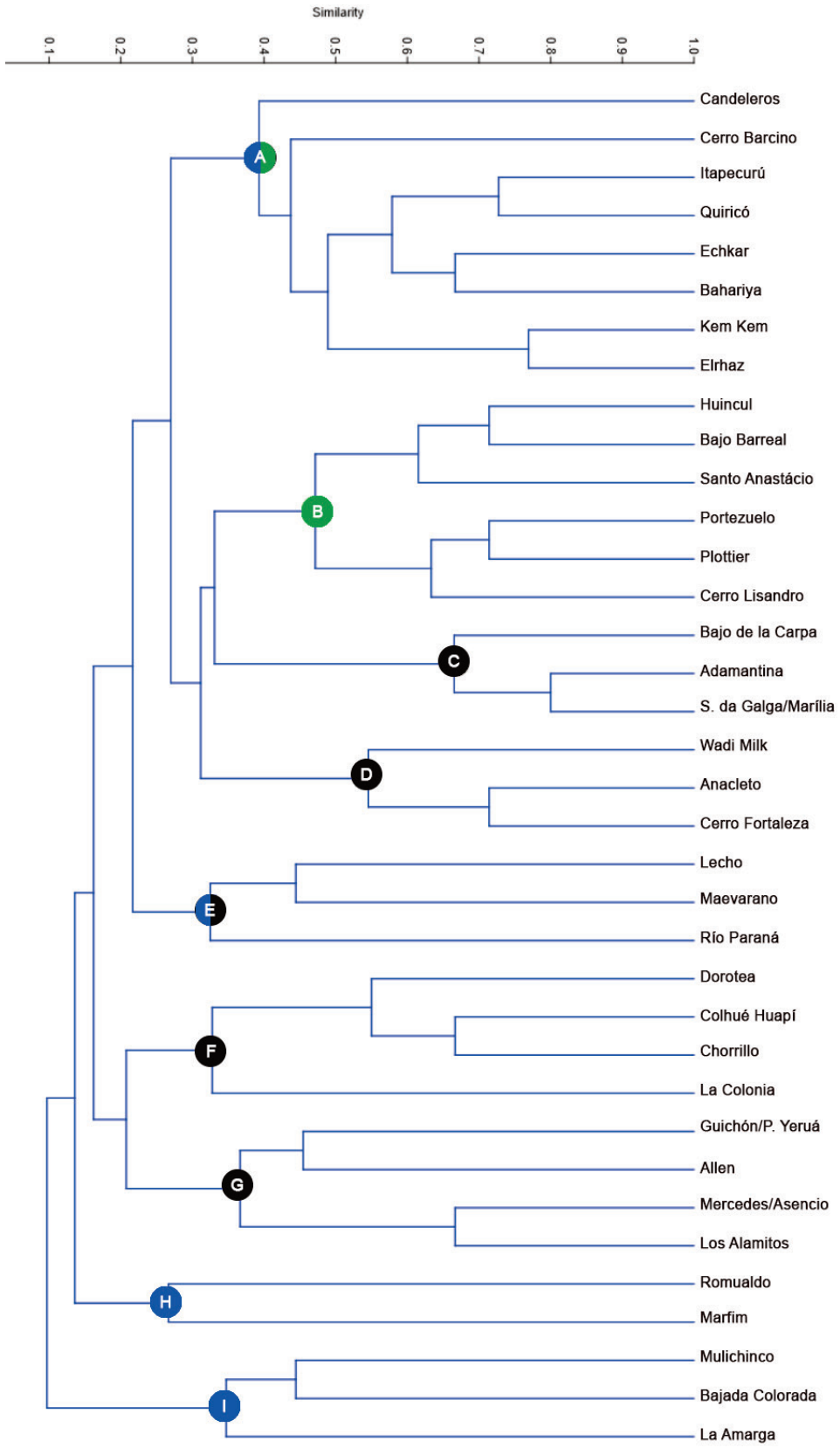


Figure 8. Dendrogram resulting from the cluster analysis of Cretaceous units from Gondwana. Clusters are named A to I. Blue = Lower Cretaceous units. Green = lower Upper Cretaceous units. Black = upper Upper Cretaceous units.

postzygapophyses positioned anterior to the cotyle in the latter specimen warrant the generic distinction from *Mesetasaurus*.

Evidence favors a younger age for the unit (*i.e.*, Santonian or early Campanian) compared to earlier proposals (*i.e.*, Aptian–Cenomanian; Rusconi, 1933; Goso & Perea, 2003). This would imply the survival into the latest Cretaceous of *Uruguaysuchus*, a basally diverging notosuchian crocodyliform (Rusconi, 1933; Soto *et al.*, 2011), a situation comparable to the case of the Malagasy taxon, *Ar. tsangatsangana*.

ACKNOWLEDGEMENTS

We thank Guillermo Sena and Daniel Montano, who found the vertebrae. Gonzalo Curuchaga and Marta Presno (Barros Blancos College) and Daniel Montano kindly allowed the study of the specimens. We acknowledge Ana Clara Badín and especially Valeria Mesa (an expert on the Guichón Formation) for fieldwork support. We are indebted to José Carballido, Agustín Pérez Moreno, Bruno Navarro, Álvaro Mones, Rubén Juárez Valieri, and Guzmán Eastman for bibliographic references. José Carballido and Agustín Pérez Moreno are acknowledged for fruitful discussions. We thank Alejandra Rojas for access to specimens under their care. Comments by an anonymous reviewer, Bruno Navarro, and Pablo Gallina allowed us to greatly improve the original draft of this manuscript. Funding: CSIC/UdelaR Grupo I+D Paleontología de Vertebrados (C302/347, Daniel Perea and Martín Ubilla).

REFERENCES

Aceñolaza, F. (2007). *Geología y Recursos Geológicos de la Mesopotamia Argentina. Serie Correlación Geológica 22*. INSUGEO.

Bandeira, K. L., Navarro, B. A., Pêgas, R. V., Brilhante, N. S., Brum, A. S., de Souza, L. G., & Gallo, V. (2025). A reassessment of the historical fossil findings from Bahia State (Northeast Brazil) reveals a diversified dinosaur fauna in the Lower Cretaceous of South America. *Historical Biology*, *37*(3), 548–589.

Bertolini, J. C. (1996). *Mapa geológico de la provincia de Entre Ríos, República Argentina. Escala 1:500.000*. SEGEMAR.

Bonaparte, J. F., & Coria, R. (1993). Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana*, *30*(3), 271–282.

Bonaparte, J. F., & Powell, J. E. (1980). A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mémoires de la Société Géologique de France, Nouvelle Série*, *139*, 19–28.

Bossi, J. (1966). *Geología del Uruguay*. Departamento de Publicaciones de la Universidad de la República.

Bossi, J., & Ferrando, L. (2001). *Carta Geológica del Uruguay: Escala 1/500.000.* (CD-ROM Version 2.0.). Facultad de Agronomía, Montevideo.

Bossi, J., & Navarro, R. (1988). *Geología del Uruguay*. Departamento de Publicaciones de la Universidad de la República.

Calvo, J. O., & González-Riga, B. J. (2003). *Rinconsaurus caudamirus* gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geológica de Chile*, *30*(2), 333–353.

Calvo, J. O., González-Riga, B. J., & Porfiri, J. D. (2007a). A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro*, *65*(4), 485–504.

Calvo, J. O., & Porfiri, J. D. (2010). *Panamericansaurus schroederi* gen. nov. sp. nov. Un nuevo Sauropoda (Titanosauridae-Aeolosaurini) de la Provincia del Neuquén, Cretácico Superior de Patagonia, Argentina. *Brazilian Geographical Journal: Geosciences and Humanities Research Medium*, *1*, 100–115.

Calvo, J. O., Porfiri, J. D., & Novas, F. E. (2007b). Discovery of a new ornithopod dinosaur from the Portezuelo Formation (Upper Cretaceous), Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro*, *65*(4), 471–483.

Carballido, J. L., Otero, A., Mannion, P. D., Salgado, L., & Pérez Moreno, A. (2022). Titanosauria: a critical reappraisal of its systematics and the relevance of the South American record. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 269–298). Springer International Publishing.

Carballido, J. L., Pol, D., Otero, A., Cerda, I., Salgado, L., Garrido, A., Ramezzani, J., Cúneo, N., & Krause, M. (2017). A new giant titanosaur sheds light on body mass evolution amongst sauropod dinosaurs. *Proceedings of the Royal Society B*, *284*(1860), 20171219. https://doi.org/10.1098/rspb.2017.1219

Carvalho, I. S., Campos, A. C. A., & Nobre, P. H. (2005). *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research*, *8*(1), 11–30.

Casadío, S., Manera, T., Parras, A., & Montalvo, C. I. (2002). Huevos de dinosaurio (Faveloolithidae) del Cretácico Superior de la cuenca del Colorado, provincia de La Pampa, Argentina. *Ameghiniana*, *39*(3), 285–293.

Casal, G., Martinez, R. D., Luna, M., Sciutto, J. C., & Lamanna, M. C. (2007). *Aeolosaurus colhuehuapensis* sp. nov. (Sauropoda, Titanosauria) de la Formación Bajo Barreal, Cretácico superior de Argentina. *Revista Brasileira de Paleontologia*, *10*(1), 53–62.

Castro, M. C., Goin, F. J., Ortiz-Jaureguizar, E., Vieytes, E. C., Tsukui, K., Ramezani, J., Batezelli, A., Marsola, J. C. A., & Langer, M. C. (2018). A Late Cretaceous mammal from Brazil and the first radioisotopic age for the Bauru Group. *Royal Society Open Science*, *5*(5), 180482. https://doi.org/10.1098/rsos.180482

Cerda, I. (2022). South American sauropodomorphs: what their bone histology has revealed to us. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 473–501). Springer International Publishing.

Cerda, I., Zurriaguz, V. L., Carballido, J. L., González, R., & Salgado, L. (2021). Osteology, paleohistology and phylogenetic relationships of *Pellegrinisaurus powelli* (Dinosauria: Sauropoda) from the Upper Cretaceous of Argentinean Patagonia. *Cretaceous Research*, *128*, 104957. https://doi.org/10.1016/j.cretres.2021.104957

Chiappe, L. M., Coria, R. A., Dingus, L., Jackson, F., Chinsamy, A., & Fox, M. (1998). Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature*, *396*, 258–261.

Chure, D., Britt, B. B., Whitlock, J. A., & Wilson, J. A. (2010). First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. *Naturwissenschaften*, *97*, 379–391.

Coria, R. A., Filippi, L. S., Chiappe, L. M., García, R., & Arcucci, A. B. (2013). *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Zootaxa*, *3683*(4), 357–376.

Coria, R. A., González-Riga, B., & Casadío, S. (2012). Un nuevo hadrosáurido (Dinosauria, Ornithopoda) de la Formacion Allen, provincia de La Pampa, Argentina. *Ameghiniana*, *49*(4), 552–572.

Coria, R. A., & Salgado, L. (1996). A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. *Journal of Vertebrate Paleontology*, *16*, 445–457.

Cruzado-Caballero, P., & Powell, J. (2017). *Bonapartesaurus rionegrensis*, a new hadrosaurine dinosaur from South America: implications for phylogenetic and biogeographic relations with North America. *Journal of Vertebrate Paleontology*, *37*(2), e1289381. https://doi.org/10.1080/02724634.2017.1289381

Curry Rogers, K., & Forster, C. A. (2001). The last of the dinosaur titans: a new sauropod from Madagascar. *Nature*, *412*, 530–534.

Curry Rogers, K. (2009). The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, *29*, 1046–1086.

Daners, G., & Guerstein, G. R. (2004). Dinoflagelados del Maastrichtiense–Paleógeno en la Formación Gaviotín, cuenca Punta del Este. In G. Veroslavsky, M. Ubilla, & S. Martínez (Eds.), *Cuencas sedimentarias de Uruguay: Geología, Paleontología y Recursos Naturales. Cenozoico* (pp. 37–62). DIRAC.

De Alba, E., & Serra, N. (1959). Aprovechamiento del Río Uruguay en la zona de Salto Grande. Informe sobre las condiciones y características geológicas. *Anales de la Dirección Nacional de Geología*, *11*, 1–35.

D'Emic, M. D., & Foster, J. R. (2014). The oldest Cretaceous North American sauropod dinosaur. *Historical Biology*, *28*(4), 470–478.

de Valais, S., Apesteguía, S., & Udrizar Sauthier, D. (2003). Nuevas evidencias de dinosaurios de la Formación Puerto Yeruá (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana*, *40*, 507–511.

Fernández, M. S., Vila, B., & Moreno-Azansa, M. (2022). Eggs, nests, and reproductive biology of sauropodomorph dinosaurs from South America. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 393–441). Springer International Publishing.

Fernández Dumont, M. L., Pol, D., Bona, P., & Apesteguía, S. (2024). A new species of *Araripesuchus* with durophagous dentition increases the ecological disparity among uruguaysuchid crocodyliforms. *Journal of Systematic Palaeontology*, *22*(1), 1–27.

Filippi, L. S., Martinelli, A. G., & Garrido, A. G. (2013). Registro de un dinosaurio Aeolosaurini (Sauropoda, Titanosauria) en el Cretácico Superior (Formación Plottier) del Norte de la provincia de Neuquén, Argentina, y comentarios sobre los Aeolosaurini sudamericanos. *Revista Brasileira de Paleontologia*, *16*(1), 147–156.

Filippi, L. S., Valieri, R. D. J., Gallina, P. A., Mendez, A. H., Gianechini, F. A., & Garrido, A. C. (2024). A rebbachisaurid-mimicking titanosaur and evidence of a Late Cretaceous faunal disturbance event in South-west Gondwana. *Cretaceous Research*, *154*, 128021. https://doi.org/10.1016/j.cretres.2023.105754

Franco-Rosas, A. C., Salgado, L., Rosas, C. F., & Carvalho, I. de S. (2004). Nuevos materiales de titanosaurios (Sauropoda) en el Cretácico Superior de Mato Grosso, Brasil. *Revista Brasileira de Paleontologia*, *7*(3), 329–336.

Gallina, P. A., Canale, J. I., & Carballido, J. L. (2021). The earliest known titanosaur sauropod dinosaur. *Ameghiniana*, *58*(1), 35–51.

García, R. A., & Salgado, L. (2013). The titanosaur sauropods from the late Campanian-early Maastrichtian Allen Formation of Salitral Moreno, Río Negro, Argentina. *Acta Palaeontologica Polonica*, *58*(2), 269–284.

Gentili, C. A., & Rimoldi, H. V. (1979). Mesopotamia. *Actas del 2° Simposio de Geología Regional Argentina* (pp. 185–224). Córdoba.

Gilmore, C. W. (1946). Reptilian fauna of the North Horn Formation of central Utah. *U.S. Geological Survey Professional Paper*, *210-C*, 29–51.

Goloboff, P., Farris, J. S., & Nixon, K. C. (2008). TNT, a program for phylogenetic analysis. *Cladistics*, *24*, 774–786.

González Riga, B. J. (2003). A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Ameghiniana*, *40*, 155–172.

González Riga, B. J., Mannion, P. D., Poropat, S. F., Ortiz David, L. D., & Coria, J. P. (2018). Osteology of the Late Cretaceous Argentinean sauropod dinosaur *Mendozasaurus neguyelap*: implications for basal titanosaur relationships. *Zoological Journal of the Linnean Society*, *184*(1), 136–181.

Goso, C. A., & Perea, D. (2003). El Cretácico post-basáltico de la Cuenca Litoral del Río Uruguay: geología y paleontología. In G. Veroslavsky, M. Ubilla, & S. Martínez (Eds.), *Cuencas sedimentarias de Uruguay: Geología, Paleontología y Recursos Naturales. Cenozoico* (pp. 141–169). DIRAC.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, *4*(1), 9 pp.

Hechenleitner, M., Leuzinger, L., Martinelli, A. G., Rocher, S., Fiorelli, L. E., Taborda, J. R. A., & Salgado, L. (2020). Two Late Cretaceous sauropods reveal titanosaurian dispersal across South America. *Communications Biology*, *3*(622), 1–13.

Holtz, T. R. Jr., Chapman, R. E., & Lamanna, M. C. (2004). Mesozoic biogeography of Dinosauria. In D. Weishampel, P. Dodson, P., & H. Osmólska (Eds.), *The Dinosauria*, 2nd Edition (pp. 259–322). University of California Press.

Huene, F. von (1929a). Los sauriquios y ornitisquios del Cretáceo argentino. *Anales del Museo de La Plata,* serie 2, *3*, 1–196

Huene, F. von (1929b). Terrestrische Oberkreide in Uruguay. *Zentralblatt für Geologie, Mineralogie und Pal€aontologie*, v. Ab. B *4*, 107–112.

Huene, F. von. (1932). Die fossile Reptile-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geolgie und Palaeontologie*, *4*, 1–361.

Huene, F. von. (1934). Nuevos dientes de saurios del Cretácico del Uruguay. *Boletín del Instituto Geológico del Uruguay*, *21*, 13–20.

Kellner, A. Z. A., & de Azevedo, S. A. K. (1999). A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil. In Y. Tomida, T. H. Rich, & P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 111–142). Tokyo.

Kellner, A. W. A., Campos, D. de A., & Trotta, M. N. F. (2005). Description of a titanosaurid caudal series from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro*, *63*, 529–564.

Kurzanov, S., & Bannikov, A. (1983). A new sauropod from the Upper Cretaceous of Mongolia. *Paleontologicheskii Zhurnal*, *2*, 90–96.

Leanza, H. A., Apesteguía, S., Novas, F. E., & De la Fuente, M. S. (2004). Cretaceous terrestrial beds from the Neuquén basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, *25*, 1–96.

Le Loeuff, J. (1993). European titanosaurids. *Revue de Paléobiologie*, *7*(7), 105–117.

Lucas, S. G., & Hunt, A. P. (1989). *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. *Paleobiology of the Dinosaurs. Geological Society of America Special Papers*, *238*, 75–86.

Lydekker, R. (1893). Contributions to the study of the fossil vertebrates of Argentina. I, the dinosaurs of Patagonia. *Anales del Museo de La Plata, Paleontología*, *2*, 1–14.

Mannion, P. D., & Otero, A. (2012). A reappraisal of the Late Cretaceous Argentinean sauropod dinosaur *Argyrosaurus superbus*, with a description of a new titanosaur genus. *Journal of Vertebrate Paleontology*, *32*, 614–638.

Mannion, P. D., Upchurch, P., Barnes, R. N., & Mateus, O. (2013). Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. *Zoological Journal of the Linnean Society*, *168*, 98–206.

Marsh, O. C. (1878). Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science and Arts*, *16*(95), 411–416.

Martinelli, A. G., & Pais, D. F. (2008). A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina). *Comptes Rendus Palevol*, *7*(6), 371–381.

Martinelli, A. G., Riff, D., & Lopes, R. P. (2011). Discussion about the occurrence of the genus of the genus *Aeolosaurus* Powell 1987 (Dinosauria, Titanosauria) in the Upper Cretaceous of Brazil. *Gaea*, *7*(1), 34–40.

Martínez, R. D. (1998). *Notohypsilophodon comodorensis*, gen. et sp. nov., un Hypsilophodontidae (Ornithischia: Ornithopoda) del Cretácico Superior de Chubut, Patagonia central, Argentina. *Acta Geologica Leopoldensia*, *21*(46/47), 119–135.

Martínez, R. D. F., Lamanna, M. C., Novas, F. E., Ridgely, R. C., Casal, G. A., Martínez, J. E., Vita, J. R., & Witmer, L. M. (2016). A basal lithostrotian titanosaur (Dinosauria: Sauropoda) with a complete skull: implications for the evolution and paleobiology of Titanosauria. *PLoS ONE*, *11*(4), e0151661. https://doi.org/10.1371/journal.pone.0151661

Mones, Á. (1980). Nuevos elementos de la paleoherpetofauna del Uruguay (Crocodilia y Dinosauria). *Actas del II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología* (pp. 265–277). Buenos Aires.

Mones, Á. (1997). Los vertebrados mesozoicos del Uruguay y sus relaciones con los de áreas vecinas. In J. Arroyo Cabrales & O. J. Polaco (Eds.), *Homenaje al Profesor Ticul Álvarez* (pp. 205–222). Instituto Nacional de Antropología e Historia, México.

Montefeltro, F. C., Larsson, H. C. E., & Langer, M. C. (2011). A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS ONE*, *6*(7), e21916. https://doi.org/10.1371/ journal.pone.0021916

Navarro, B. A., Giaretta, A. A., Fernandes, M. A., Carvalho, A. B., & Zaher, H. (2025). First dinosaur ichnofauna from the Bauru Group Cenomanian-Turonian events led to an 'Ornithischian Hiatus' in the Upper Cretaceous of Southeast Brazil. *Cretaceous Research*, *168*, 106075. https://doi.org/10.1016/j.cretres.2024.106075

Novas, F., Agnolín, F., Rozadilla, S., Aranciaga-Rolando, A., Brissón-Eli, F., Motta, M., Cerroni, M., Ezcurra, M., Martinelli, A., D'Angelo, J., Álvarez-Herrera, J., Gentil, A., Bogan, S., Chimento, N., García-Marsà, J., Lo Coco, G., Miquel, S., Brito, F., Vera, E., … 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.

Novas, F. E., Cambiaso, A. V., & Ambrosio, A. (2004). A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia. *Ameghiniana*, *41*, 75–82.

Nowinski, A. (1971). *Nemegtosaurus mongoliensis* n. gen., n. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeontologia Polonica*, *25*, 57–81.

Ortega, F. J., Gasparini, Z. B., Buscalioni, A. D., & Calvo, J. O. (2000). A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology*, *20*(1), 57–76.

Otero, A., & Hutchinson, R. (2022). Body size evolution and locomotion in Sauropodomorpha: what the South American record tells us. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 443–472). Springer International Publishing.

Owusu Agyemang, P. C., Roberts, E. M., Bussert, R., & Müller, J. (2019). U-Pb detrital zircon constraints on the depositional age and provenance of the dinosaur-bearing Upper Cretaceous Wadi Milk formation of Sudan. *Cretaceous Research*, *97*, 52–72.

Paula e Silva, F. de, Chang, H. K., & Caetano-Chang, M. R. (2009). Sedimentation of the

Cretaceous Bauru Group in São Paulo, Paraná Basin, Brazil. *Journal of South American Earth Sciences*, *28*(1), 25–39.

Pérez Moreno, A., Carballido, J. L., Otero, A., & Salgado, L. (2026). Osteological reassessment of *Muyelensaurus pecheni* (Dinosauria: Sauropoda): systematics and its phylogenetic implications for the clade Rinconsauria. *Historical Biology*, *37*, 792–811.

Pol, D., & Apesteguía, S. (2005). New *Araripesuchus* remains from the early Late Cretaceous (Cenomanian–Turonian) of Patagonia. *American Museum Novitates*, *3490*(1), 1–38.

Powell, J. E. (1987). The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part VI. The titanosaurids. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia*, *3*, 147–153.

Powell, J. E. (1992). Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del Noroeste argentino. In J. L. Sanz & A. D. Buscalioni (Eds.), *Los Dinosaurios y su entorno biótico* (pp. 166–230). Ayuntamiento de Cuenca.

Powell, J. E. (2003). Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, *111*, 1–173.

Price, L. I. (1959). Sobre um crocodilideo notossuquio do Cretacico Brasileiro. *Boletim Divisão de Geologia e Mineralogia de Rio de Janeiro*, *118*, 1–55.

Rauhut, O. W. M. (1999). A dinosaur fauna from the Late Cretaceous (Cenomanian) of northern Sudan. *Palaeontologia Africana*, *35*, 61–84.

Riguetti, F., Pereda-Suberbiola, X., Ponce, D., Salgado, L., Apesteguía, S., Rozadilla, S., & Arbour, V. (2022). A new small-bodied ankylosaurian dinosaur from the Upper Cretaceous of North Patagonia (Río Negro Province, Argentina). *Journal of Systematic Palaeontology*, *20*(1), 2137441.

Rozadilla, S., Brissón-Egli, F., Agnolín, F. L., Aranciaga-Rolando, A. M., & Novas F. E. (2022). A new hadrosaurid (Dinosauria: Ornithischia) from the Late Cretaceous of northern Patagonia and the radiation of South American hadrosaurids. *Journal of Systematic Palaeontology*, *19*(17), 1207–1235.

Rusconi, C. (1933). Sobre reptiles cretáceos del Uruguay (*Uruguaysuchus aznarezi* n. g. n. sp.) y sus relaciones con los notosúquidos de Patagonia. *Boletín del Instituto Geológico del Uruguay*, *19*, 1–64.

Salgado, L. (1996). *Pellegrinisaurus powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, Northwestern Patagonia, Argentina. *Ameghiniana*, *33*(4), 355–365.

Salgado, L., Apesteguía, S., & Heredia, S. E. (2005). A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *Journal of Vertebrate Paleontology*, *25*(3), 623–634.

Salgado, L., & Azpilicueta, C. (2000). Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana*, *37*(3), 259–264.

Salgado, L., & Coria, R. A. (1993). El género *Aeolosaurus* (Sauropoda,

Titanosauridae) en la formación Allen (Campaniano–Maastrichtiano) de la Provincia de Río Negro, Argentina. *Ameghiniana*, *30*(2), 119–128.

Salgado, L., Coria, R. A., & Calvo, J. O. (1997a). Presence of the genus *Aeolosaurus* (Sauropoda, Titanosauridae) in the Los Alamitos Formation (Late Cretaceous) of the Río Negro Province. *Revista Guarulhos–Geociencias*, *2*(6), 44–49.

Salgado, L., Coria, R. A., & Calvo, J. O. (1997b). Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcraneal evidence. *Ameghiniana*, *34*, 3–32.

Salgado, L., & Carvalho, I. de S. (2008). *Uberabatitan ribeiroi*, a new titanosaur from the Marília Formation (Bauru Group, Upper Cretaceous), Minas Gerais, Brazil. *Palaeontology*, *51*(4), 881–901.

Salgado, L., Gallina, P. A., Lezo, L. N., & Canudo, J. I. (2022). Highly specialized diplodocoids: The Rebbachisauridae. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 165–208). Springer International Publishing.

Santucci, R. M., & De Arruda-Campos, A. C. (2011). A new sauropod (Macronaria, Titanosauria) from the Adamantina Formation, Bauru Group, Upper Cretaceous of Brazil and the phylogenetic relationships of Aeolosaurini. *Zootaxa*, *3085*(1), 1–33.

Santucci, R. N., & Filippi, L. S. (2022). Last Titans: Titanosaurs from the Campanian–Maastrichitan age. In A. Otero, J. L. Carballido, & D. Pol (Eds.), *South American Sauropodomorph Dinosaurs* (pp. 341–391). Springer International Publishing.

Seeley, H. G. (1887). On the classification of the fossil animals commonly called Dinosauria. *Royal Society of London*, *43*, 165–171.

Sereno, P. C., Sidor, C. A., Larsson, H. C., & Gado, B. (2003). A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology*, *23*(2), 477–482.

Silva Junior, J. C., Marinho, T. S., Martinelli, A. G., & Langer, M. C. (2019). Osteology and systematics of *Uberabatitan ribeiroi* (Dinosauria, Sauropoda): a Late Cretaceous titanosaur from Minas Gerais, Brazil. *Zootaxa*, *4577*(3), 401–438.

Silva Junior, J. C., Martinelli, A. G., Iori, F. V., Marinho, T. S., Hechenleitner, E. M., & Langer, M. C. (2021). Reassessment of *Aeolosaurus maximus*, a titanosaur dinosaur from the Late Cretaceous of Southeastern Brazil. *Historical Biology*, *34*(3), 403–411.

Silva Junior, J. C., Martinelli, A. G., Marinho, T. S., da Silva, J. I., & Langer, M. C. (2022). New specimens of *Baurutitan britoi* and a taxonomic reassessment of the titanosaur dinosaur fauna (Sauropoda) from the Serra da Galga Formation (Late Cretaceous) of Brazil. *PeerJ*, *10*, e14333. https://doi.org/10.7717/peerj.14333

Soares, P., Landim, P. M. B., Fúlfaro, V. J., & Neto, A. F. (1980). Ensaio de caracterização estratigráfica do Cretâceo no Estado de São Paulo: Grupo Bauru. *Revista Brasileira de Geociencias*, *10*, 177–185.

Soto, M., Carballido, J. L., Langer, M. C., Silva Junior, J. C. G., Montenegro, F., & Perea, D. (2024). Phylogenetic relationships of a new titanosaur from the Upper Cretaceous of Uruguay. *Cretaceous Research*, *160*, 105894. https://doi.org/10.1016/j.cretres.2024.105894

Soto, M., Montenegro, F., Mesa, F., & Perea, D. (2022). Sauropod (Dinosauria: Saurischia) remains from the Mercedes and Asencio formations (*sensu* Bossi, 1966), Upper Cretaceous of Uruguay. *Cretaceous Research*, *131131*, 105072. https://doi.org/10.1016/j.cretres.2021.105072

Soto, M., Perea, D., & Cambiaso, A. (2012). First sauropod (Dinosauria: Saurischia) remains from the Guichón Formation, Late Cretaceous of Uruguay. *Journal of South American Earth Sciences*, *33*(1), 68–79.

Soto, M., Perea, D., Veroslavsky, G., Rinderknecht, A., Ubilla, M., & Lecuona, G. (2008). Nuevos hallazgos de restos de dinosaurios y consideraciones sobre la edad de la Formación Guichón. *Revista de la Sociedad Uruguaya de Geología*, *15*, 11–23.

Soto, M., Pol, D., & Perea, D. (2011). A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the Cretaceous of Uruguay and its phylogenetic relationships. *Zoological Journal of the Linnean Society*, *Special Issue 1st Symposium on the Evolution of Crocodyliforms*, *163*, S173–S198.

Soto-Acuña, S., Vargas, A. O., Kaluza, J., Leppe, M. A., Botelho, J. F., Palma-Liberona, J., Simon-Gutstein, C., Fernández, R. A., Ortiz, H., & Milla, V. (2021). Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile. *Nature*, *600*(7888), 259–263.

Turner, A. H. (2006). Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. *Historical Biology*, *18*(3), 255–369.

Upchurch, P. (1995). The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London B*, *349*, 365–390.

Upchurch, P. (1998). The phylogenetic relationships of sauropods dinosaurs. *Zoological Journal of the Linnean Society*, *124*(1), 43–103.

Veroslavsky, G., Aubet, N., Martínez, S., Heaman, L. M., Cabrera, F., & Mesa, V. (2019). Late Cretaceous stratigraphy of the southeastern Chaco-Paraná basin ("Norte Basin" - Uruguay). The Maastrichtian age of the calcretization process. *Geociencias*, *38*(2), 427–449.

Vidal, L. S., Pereira, P. V. L. G. C., Tavares, T., Brusatte, S. L., Bergqvist, L. P., & Candeiro, C. R. A. (2021). Investigating the enigmatic Aeolosaurini clade: the caudal biomechanics of *Aeolosaurus maximus* (Aeolosaurini/Sauropoda) using the neutral pose method and the first case of protonic tail condition in Sauropoda. *Historical Biology*, *33*, 1–21.

Wilson, J. A. (2006). An overview of titanosaur evolution and phylogeny. *Actas de las III Jornadas sobre Dinosaurios y su Entorno* (pp. 169–190). Salas de los Infantes.

Wilson, J. A., & Carrano, M. T. (1999). Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, *25*, 252–267.

Wilson, J. A., Malkani, M. S., & Gingerich, P. D. (2001). New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitraki, Balochistan (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, *30*(12), 321–336.

Wilson, J. A., & Sereno, P. C. (1998). Higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology*, *18*(Sup002), 1–68.

Zaher, H., Pol, D., Carvalho, A. B., Nascimento, P. M., Riccomini, C., Larson, P., Juarez-Valieri, R., Ricardo Pires-Domingues, N., da Silva Jr., J., & Campos, D. de A. (2011). A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurians. *PLoS ONE*, *6*(2), e16663. https://doi.org/10.1371/journal.pone.0016663

doi: 10.5710/AMGH.19.06.2026.3689

Submitted: 14 February 2026
Accepted: 19 June 2026
Published: 08 July 2026

APPENDIX

Scorings for *Mesetasasaurus protector*

?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? 0??????011 3011???1?? ??????????
0?11?????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ????????1? ???0????1? ?????????

Revised scorings for *Aeolosaurus rionegrinus*

?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? 0??????010 3011?0?100 ??20?1000? 03111????? ????????11 ?????13?0? 110??1???? ???????01?
1110011111 00111????? ?????????? ???????00? 1001100l?? ?????????? ??11011111 0011100l?? ?????????? ??????????
?????????? ??1????011 1121001?0? ?01101111

Revised scorings for *Caieiria allocaudata*

?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
??-??????? ?????????? ?0?2??0010 301000110-0020010003 0311101?00 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
????????00 001?????01 012???1100 ?????????

Revised scorings for *Baurutitan britoi*

?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?11013?0?0 0301020?00 2100001l1? 100??110333 10121?112 2100122?12 0110201010 ?111?01101
11-0??221? 1??31?010? ?022200010 30?001110-0020010000 031[01]0021011 00???0-11 1??1113000 010011???? ?11101?01?
10100120?? ?????????? ?????????? ???????000 1??11000?? ?????????? ?????????? ?????????? ?????????? ??????????
????????00 001????101 0?0000?100 ???????11