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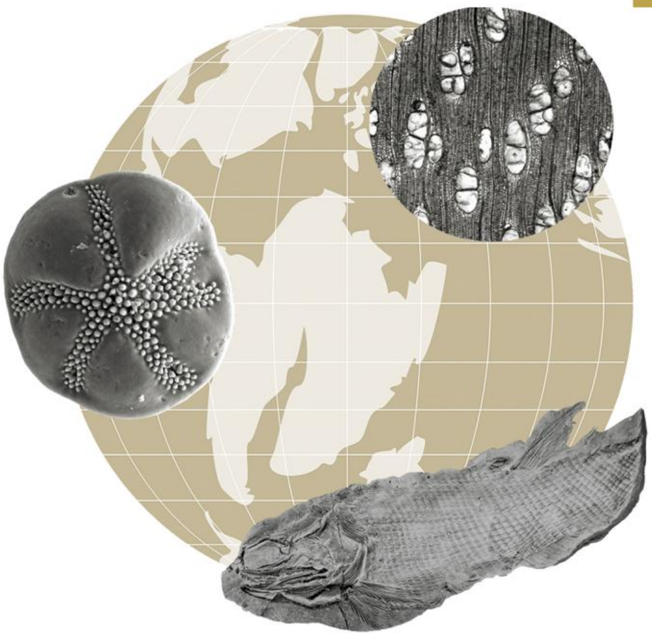

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A NEW AEOLOSAURINI (SAUROPODA, TITANOSAURIA) FROM THE UPPER CRETACEOUS OF URUGUAY

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Short Description: A new sauropod from Uruguay is described. It allows to stablish correlations with Upper Cretaceous units from Argentina and Brazil.

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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 strongly anteriorly inclined anterior face, neural arch placed at the level of the anterior border, 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. Son descritas 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 recobra al nuevo taxon como un Aeolosaurini. Dado que 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.

Key words. Titanosauria, Aeolosaurini, Cretácico Superior, Formación Guichón, Uruguay

1. 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., 2021). 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., 2021). 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, Perú, 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 in 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., 2021). 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, 2003, *Gondwanatitan faustoi* Kellner & De Azevedo (1999), and *Rinconsaurus caudamirus* Calvo & González-Riga (2003). Despite the existence of different proposals of phylogenetic position of the Aeolosaurini among titanosaurs, the taxonomical 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. (2007). 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 (1929a), leading that author to propose the presence of Upper Cretaceous sedimentary rocks in the western part of the country. Huene (1929a) referred the materials to four species: *Antarctosaurus wichmannianus*, *Argyrosaurus superbus*, *Laplatasaurus araukanicus*, and *Titanosaurus australis* (*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*, 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.

2. 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 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 is in turn 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 restudy 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* Mones (1980).

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

Originally dated as ‘Cenomanian or older’ (Rusconi, 1933) or even Aptian (Goso & Perea, 2003), recent findings of the derived titanosaurian *Udelartitan celeste* Soto et al. (2024) plus *Sphaerovum* Mones (1980) 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 in 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 priori to preparation) in a small cliff nearby 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 dozens of meters to the north was reported by Goso & 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 the specimens, and the right dorsolateral part of the condyle in the other specimen.

3. MATERIAL AND METHODS

The vertebrae were photographed with a Nikon d5100 camera, measured with a Mitutoyo caliper 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, either dividing the anteroposterior length per the condyle width (Upchurch, 1998), or the anteroposterior length per the centrum width (Wilson & Sereno, 1998), or 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), *Baurutitan britoi* Campos et al. (2005) (now scored as polymorphic for anteriorly inclined cotyles in anterior caudal vertebra) and *Caieiria allocaudata* Silva Junior et al. (2022) (now scored as having anteriorly inclined cotyles in middle caudal vertebrae).

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 Consensus 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 faunas across South America was thoroughly examined with the objective of analyzing 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 in order 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 constructed. We choose to use families, subfamilies or tribes in order 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, peirosaurids are the most common family (15 out of 35 units), followed by uruguaysuchids (6 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). In order to maximize the information the speciose clade Titanosauria was subdivided in 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, Portezuelo, and Adamantina formations (8 taxa each).

In a few cases (Guichón/Puerto Yeruá, Mercedes/Asencio and Serra da Galga/Marília) information of the units were combined, in the first case because they are undoubtedly correlated and in the other two cases in order to maximize the information and to avoid doubts regarding fossil provenance. A classical cluster analysis employing the UPGMA algorithm (e.g. Weishampel 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: C97C14E5-0AC5-4E1C-B03E-A65368C5A609.

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

4. 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. 2007

Aeolosaurini Franco-Rosas et al., 2004 *sensu* Carballido et al. 2017

Mesetasaurus gen. nov.

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 depressed (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

Diagnosis. Same as for genus, by monotypy.

Etymology. Latin for ‘the one who protects.’ José Artigas (1764–1850) was an Uruguayan national hero known for defeating the Spanish army in 1811 (battle of Las Piedras), for being followed by the ‘orientales’ in an immigration after rejecting an armistice between Buenos Aires and Spain, and for his sensitivity towards the weaker people. He was named ‘Protector de los Pueblos Libres’, i.e. 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 include which is now Uruguay and part of Argentina. The capital of this League was situated a few kilometers northward 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), Salgado & García (2013), and Vidal et al. (2021), FC-PDV 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 vertebrae, 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. 5B).

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 reached 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. There is a change in orientation due to the different position of the vertebrae in the caudal series: in FC-DPV 3740A the prezygapophyses were anterodorsally projected (30°) when complete, but they were sub-horizontal (10°) in FD-DPV 3740B (compare Figs. 3A, 4A).

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* (Powell, 2003), *Ae*. sp. 2 (Salgado et al., 1997a), and *G. faustoi* (Kellner & de Azevedo, 1999). Unlike those of Saltasaurinae (Powell, 1992; Salgado & Azpilicueta, 2000; Powell, 2003; Salgado et al., 2005), the centrum is not dorsoventrally depressed. FC-DPV 3740B is slightly dorsoventrally depressed, but unlike *Ae. rionegrinus* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993), and *Panamericansaurus schroederi* (Calvo & Porfiri, 2010) it is not laterally compressed.

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* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993; Salgado & García, 2013), and *Ae.* sp. 2 (Salgado et al., 1997a). In turn, the strong anterior tilt of the anterior face in FC-DPV 3740B immediately recalls the remaining anterior caudal centra of *Ae. rionegrinus* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993; Salgado & García, 2013), *Ae.* sp. 2 (Salgado et al., 1997a), *G. faustoi* (Kellner & de Azevedo, 1999), *Pa. schroederi* (Calvo & Porfiri, 2010), *C. allocaudata* (Silva Junior et al., 2022), and the 5th and 6th caudal vertebrae of *B. britoi* (Campos et al., 2005).

The well-defined blind fossa on the lateral face of FC-DPV 3740A is present in the third caudal vertebrae of *Ae. rionegrinus* (Powell, 2003) and *Ae. colhuehuapensis* Casal et al. (2007). A similar feature is present in the most anterior caudal centra of other titanosaurians, such as *Pellegrinisaurus powelli* (Cerda et al., 2021) and *Nullotitan glaciaris* Novas et al. (2019). However, the position of the blind fossa is unique in *M. protector*, being situated below the anteroposterior axis and very close to the condyle, which is regarded as an autapomorphic trait of this species. In other titanosaurs this fossa either occupies an anterior position or a position immediately below the or even posterodorsal to the transverse process, but never posteroventral (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* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993; Salgado & García, 2013), *Ae.* sp. 3 (Soto et al., 2022), *Pa. schroederi* (Calvo & Porfiri, 2010), and *G. faustoi* (Kellner & De Azevedo, 1999), resembling more *Ae.* sp. 2 (Salgado et al., 1997a). In ventral view, the ventral face differs from the grooved condition present in *Ae. rionegrinus* (Powell, 2003), *Ae.* sp. 2 (Salgado et al., 1997a), *Overosaurus paradasorum* Coria et al. (2013), *Arrudatitan maximus* Vidal et al. (2021), and *G. faustoi* (Kellner & De Azevedo, 1999). 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 *Ae.* sp. 2 (Salgado et al., 1997a) and *O. paradasorum* (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* (Powell, 2003), *O. paradasorum* (Coria et al., 2013), and *Ar. maximus* (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., 2020), *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* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993; Salgado & García, 2013), *Ae.* sp. 2 (Salgado et al., 1997a), *Ae.* sp. 3 (Soto et al., 2022), and *Uberabatitan ribeiroi* Silva Junior et al. (2019) but differs from the concentric condyles of *Ae. colhuehuapensis* (Casal et al., 2007), *G. faustoi* (Kellner & De Azevedo, 1999), and most vertebrae of *Ar. maximus* (Vidal et al., 2021), as well as from the extreme eccentric condition of an indeterminate titanosaurian described by Salgado & García (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* (Powell, 2003), *Ae.* sp. 1 (Salgado & Coria, 1993; Salgado & García, 2013), and *Pu. coughlini* (Hechenleitner et al., 2020).

The anterodorsal orientation of the prezygapophyses in FC-DPV 3740A recalls the most anterior caudal centra of *Ae. rionegrinus* (Powell, 2003), *Ae*. sp.1 (Salgado & Coria, 1993; Salgado & García, 2003), *Ae*. sp. 2 (Salgado et al., 1997a), *Ae*. *colhuehuapensis* (Casal et al., 2007), and *Pa. schroederi* (Calvo & Porfiri, 2010), although the angle is slightly less, about 30°. The sub-horizontal orientation of the prezygapophyses in FC-DPV 3740B, in turn, recalls *Pa. schroederi* (Calvo & Porfiri, 2010) and the 7th–8th caudal of *Ae. rionegrinus* (Powell, 2003). However, at this level *Ae*. 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* (Fig. 5), with the postzygapophyses lying approximately at the same level at the cotyle, a synapomorphy of the genus (Casal et al., 2007).

5. PHYLOGENETIC ANALYSIS

We tested the phylogenetic relationships of *Me. protector* 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). *M. 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 consensus 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 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). *M. protector* plus the remaining Aeolosaurini share the presence of ventrolateral ridges in anterior and middle caudal vertebrae (char. 234.1). *Ae. 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).

6. DISCUSSION

M. protector 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* Casal, 2007). However, among the characters diagnostic of *Aeolosaurus* and its closest relatives, several are absent in *M. protector*. 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 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.

6.1. On the age of the Guichón Formation

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

Ankylosaurians have not been recovered from uppermost Cretaceous units from Brazil, but this is not the case of 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* (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; Novas et al., 2014; Calvo et al., 2007) 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), 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, with the exception of the caudal series originally referred to *Muyelensaurus pecheni* 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). *M. protector* 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 near a century of collecting, not a single specimen referrable to Diplodocoidea has been reported from the Guichón Formation, nor they have 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., 2021; 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), *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. 8). 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 latest 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 & Guerstein (2004)’s study on dinoflagellates in an offshore well showed that the marine equivalents of the top of the Mercedes Formation are of Maastrichtian age. Furthermore, the limestones of the Queguay Formation (developed due to calcretizacion of Mercedes-type sanstones) were dated at 71.7±9 Ma

(U/Pb in calcite cement – calcretization age; Veroslavsky et al., 2019). Note that 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 in this topic. The absence of diplodocoids, gigantic titanosaurs, and amphiplatyan tailed titanosaurs (see Leanza et al., 2004) is clear difference compared with older assemblages.

6.2. Faunal relationships of South American Cretaceous units

As mentioned above, a cluster analysis of several Cretaceous localities was performed in order 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 7.

Eight clusters were obtained (Fig. 7). The large cluster A includes units from the Aptian–Cenomanian of South America and Africa, which share the presence of abelisaurids, spinosaurids, carcharodontosaurids, rebbachisaurids. Additionally, some of these units share the presence of uruguaysuchids, noasaurids, and stomatosuchids (hereafter, taxa not recorded in all units of a cluster are indicated in brackets).

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, rebbachisaurids, (lognkosaurs), and a Turonian–Santonian cluster, which shares the presence of peirosaurids, elasmarians, abelisaurids, (alvarezsauroids, 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 the widespread peirosaurids and abelisaurids, and sphagesaurians, unenlagiids, (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, abelisaurids, (peirosaurids, 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, megaraptorids, (parankylosaurs, 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, faveoolithid eggs and subordinately 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 stegosaurs, diplodocids and/or dicraeosaurids.

7. 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*. *M. protector* 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.

M. protector 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 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*.

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APPENDIX

Scorings for *Mesetasasaurus protector*

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Revised scorings for *Aeolosaurus rionegrinus*

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Revised scorings for *Caieiria allocaudata*

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Revised scorings for *Baurutitan britoi*

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FIGURE CAPTIONS

Figure 1. A, simplified geological map (based on Bossi & Ferrando, 2001). The fossil site is indicated with a red star. The insets at 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 fom 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* (Vidal et al., 2021), with which *M. protector* shares key features. The skull is based on that of the probable aeolosaurine *Inawentu oslatus* (Filippi *et al*., 2023).

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.

Figure 3. FC-DPV 3740A, anterior caudal vertebra of *Mesetasaurus protector* gen. et sp. nov. in right lateral (A), left lateral (B), anterior (C), posterior (D), dorsal (E) and ventral (F) 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. Scale bar equals 5 cm. Abbreviations: bf, blind fossa; bns, base of neural spine; cd, condyle; ct, cotyle; nvf, neurovascular foramina; prz, prezygapophysis; tpr, transverse process; vf, ventral face.

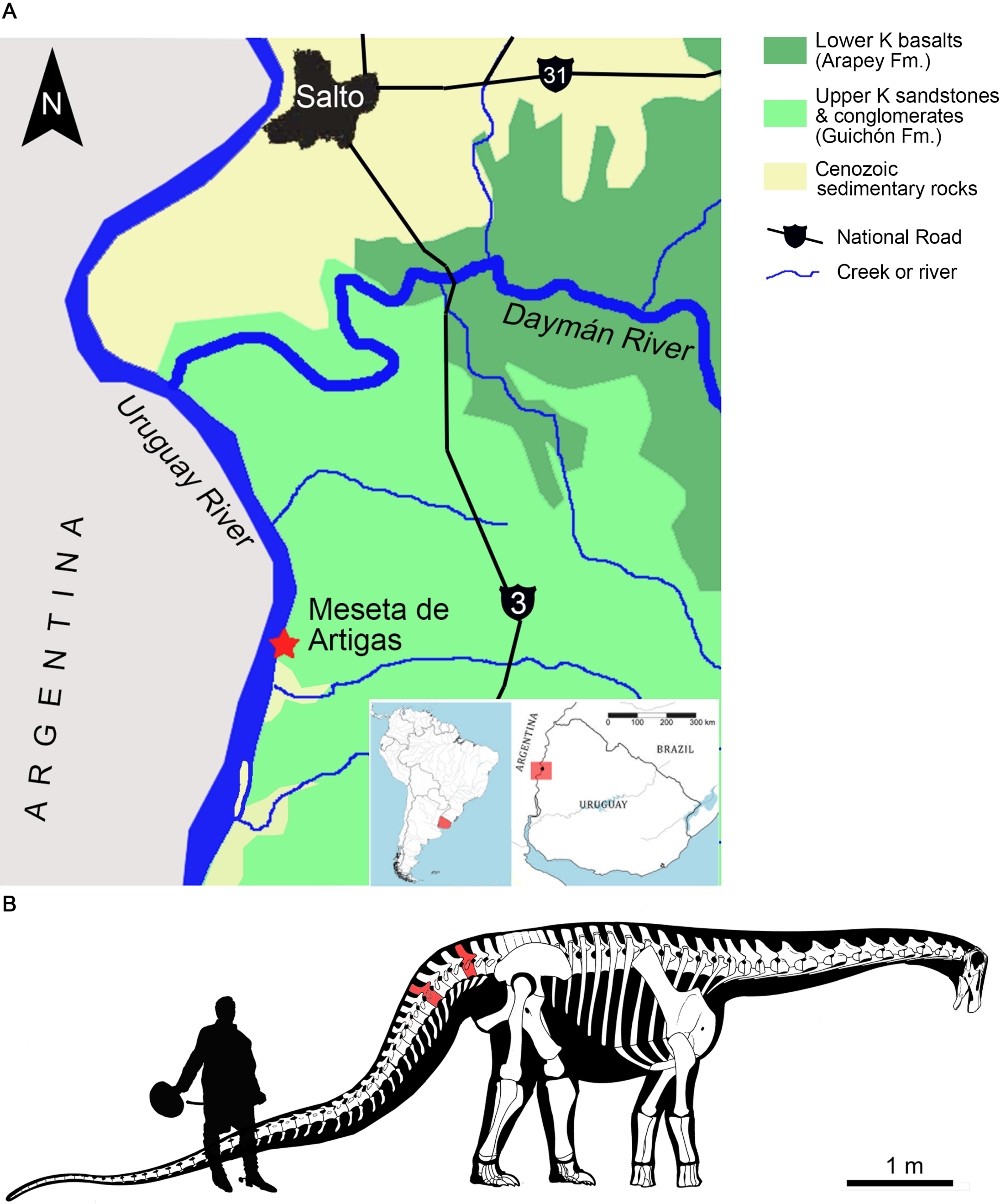
Figure 4. FC-DPV 3740B, anterior caudal vertebra of *Mesetasaurus protector* gen. et sp. nov. in right lateral (A), left lateral (B), anterior (C), posterior (D), dorsal (E) and ventral (F) views. Anterior is towards the right in E and F. The orientation of the prezygapophysis and the anterior face of the centrum is shown relative to horizontal and vertical, respectively. Scale bar equals 5 cm. 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.

Figure 5. Relationships among Aeolosaurini in the strict consensus 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). Not to scale. 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.

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

Figure 7. 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.

Figure 8. 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*, 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.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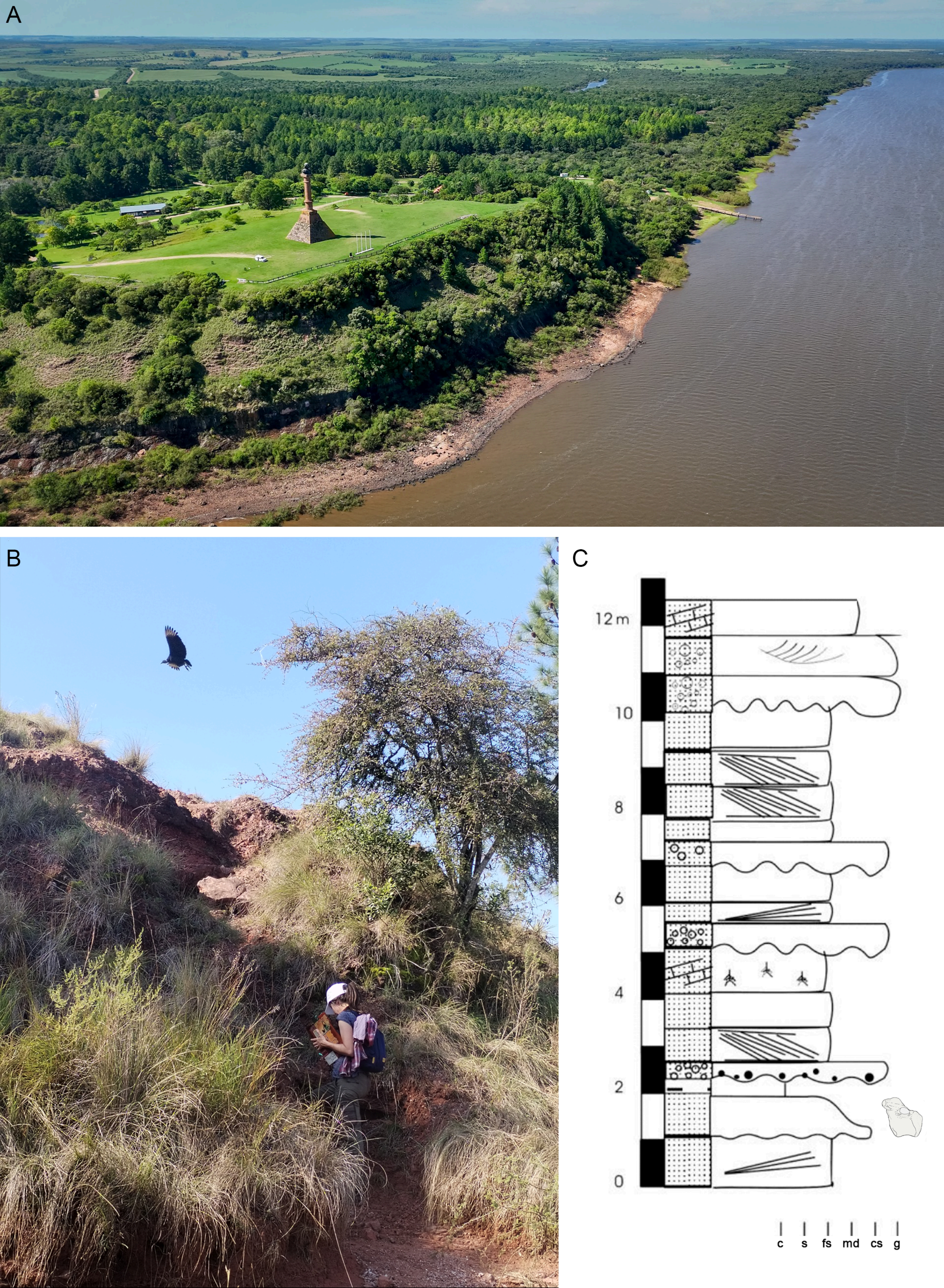
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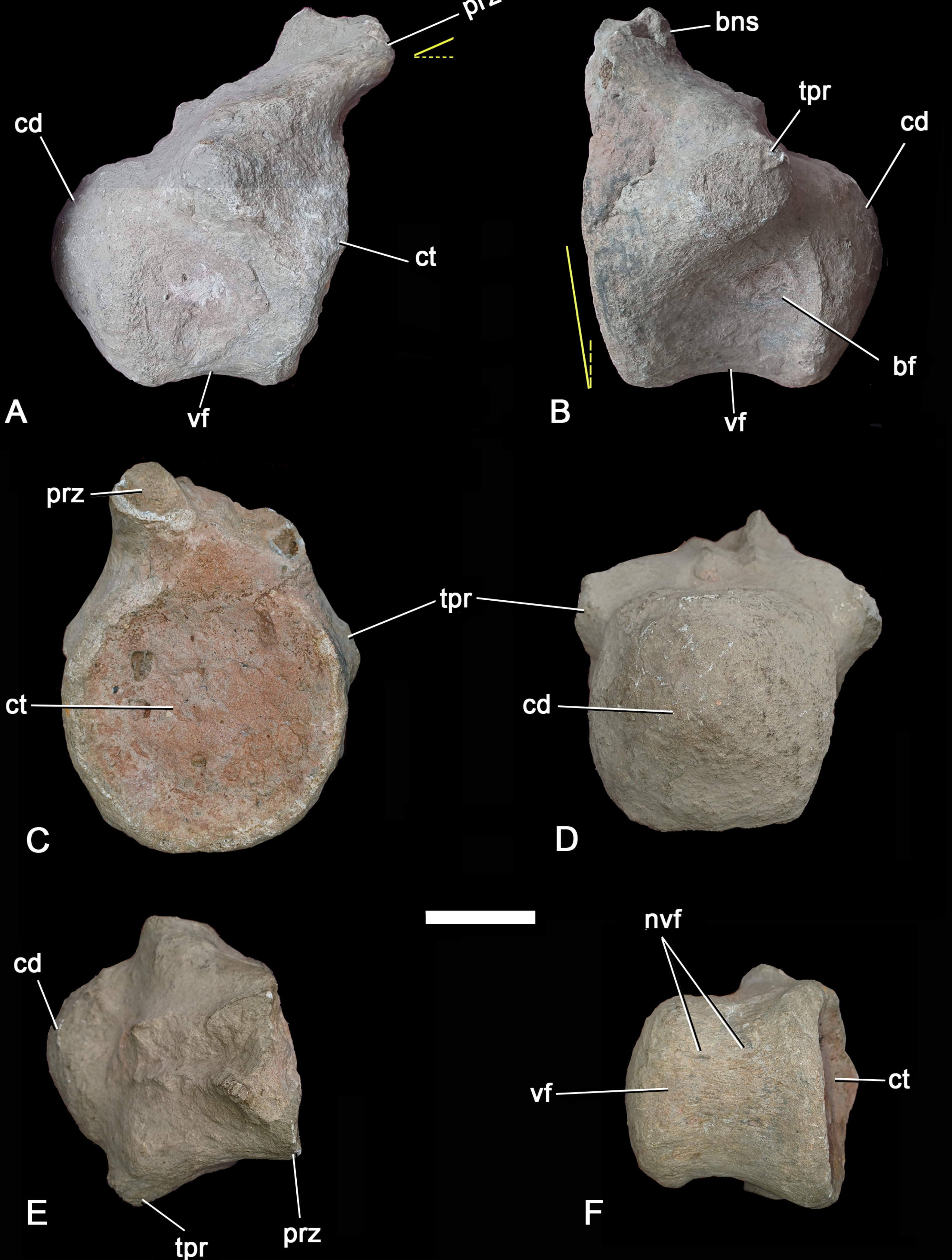
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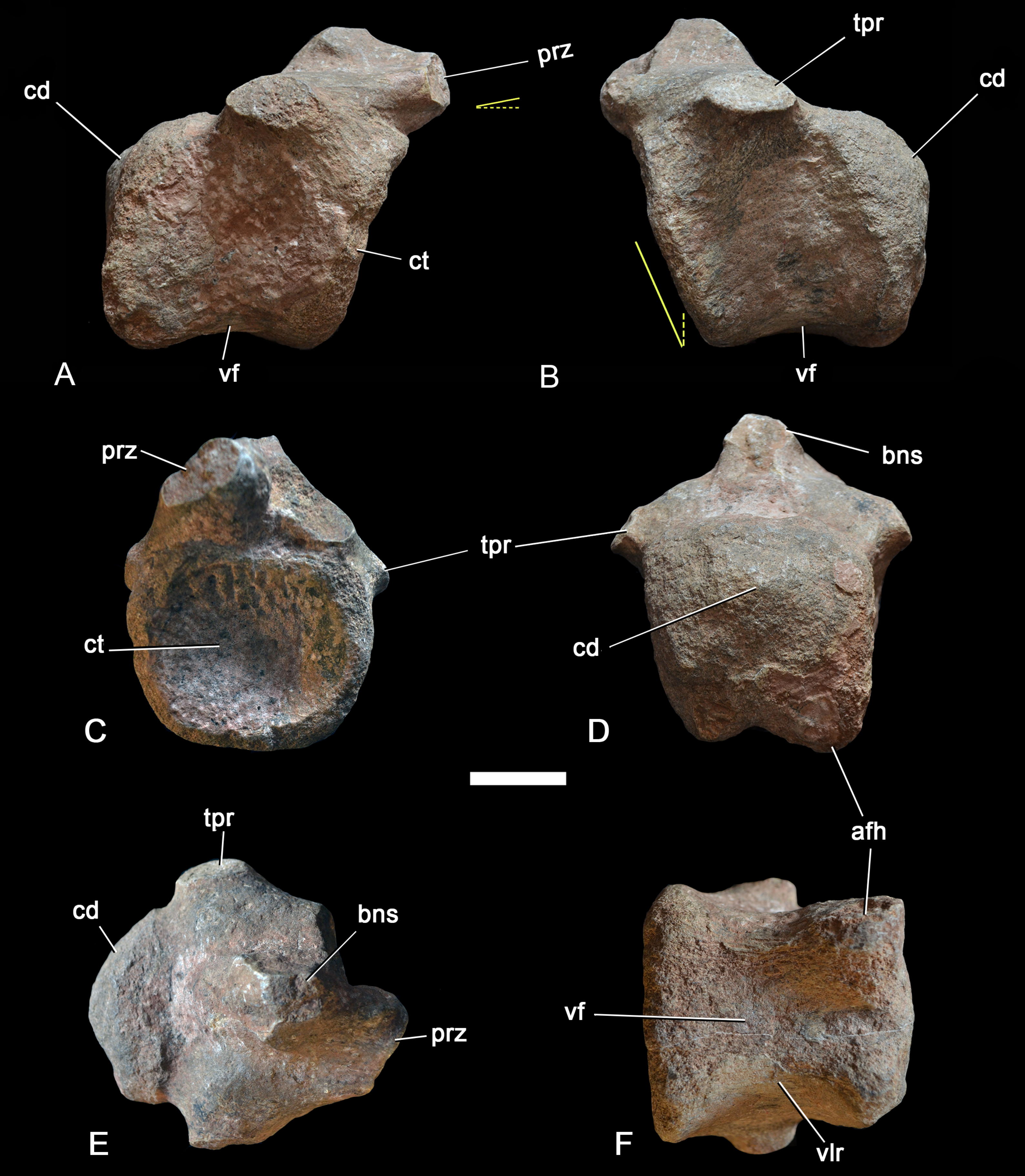
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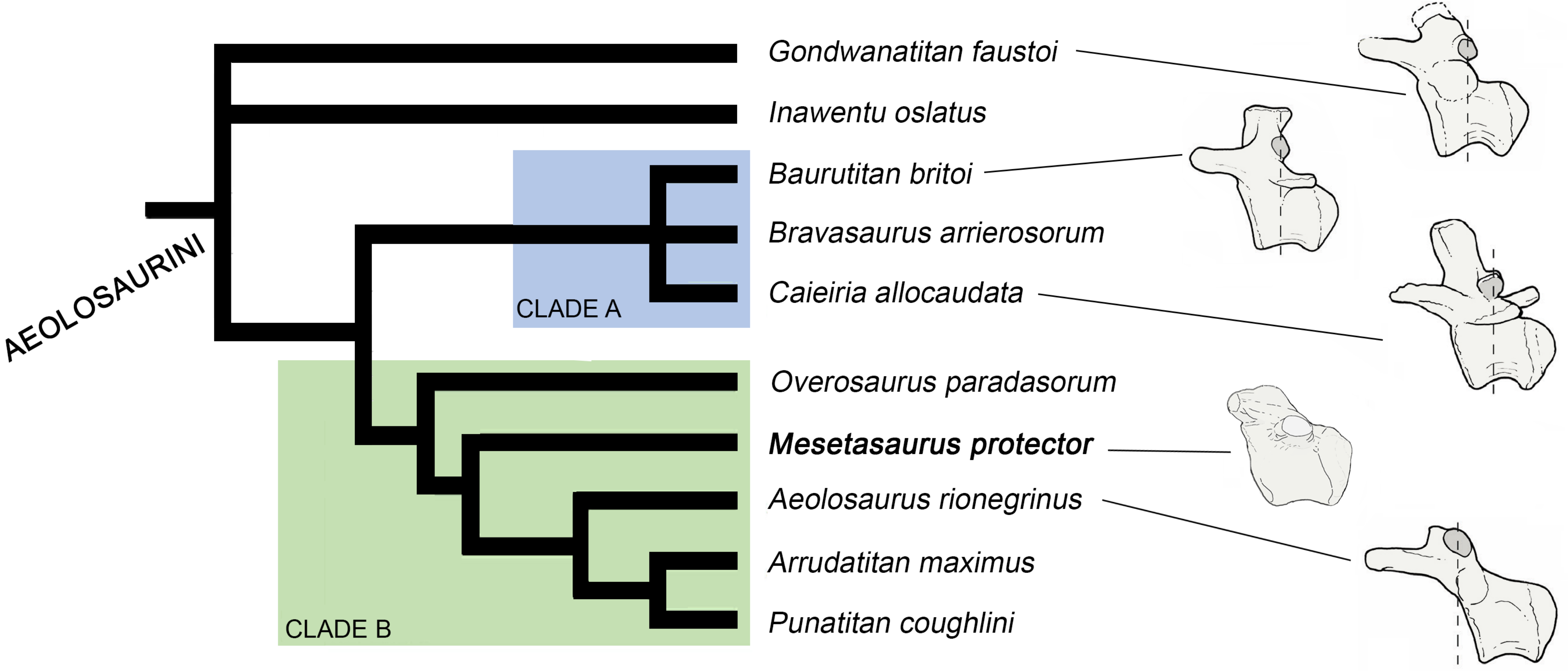
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Inawentu oslatus
Baurutitan britoi
Bravasaurus arrierosorum
Caieiria allocaudata
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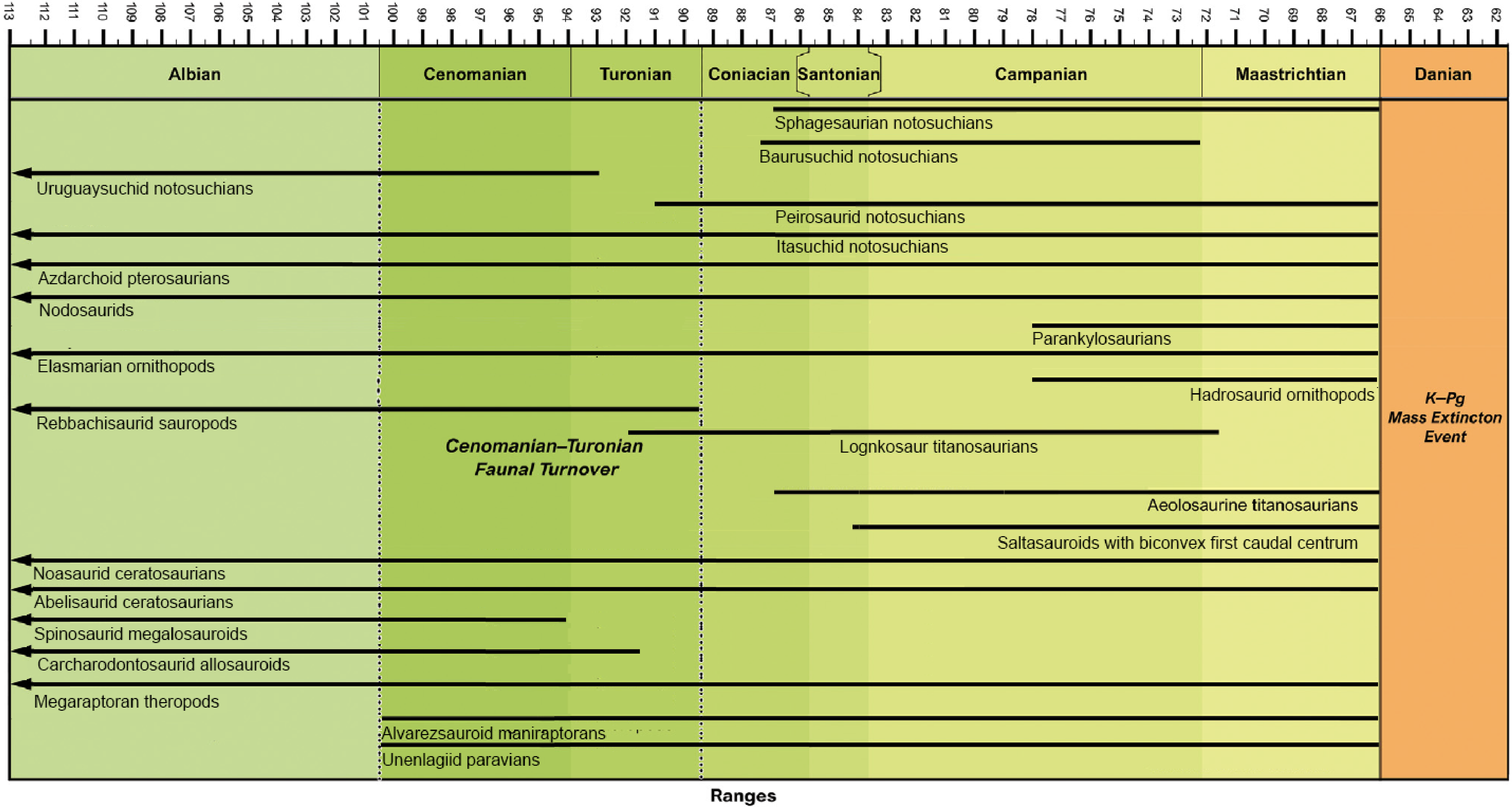
Overosaurus paradasorum
Mesetasaurus protector
Aeolosaurus rionegrinus
Arrudatitan maximus
Punatitan coughlini
CLADE B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Coniacian
Santonian
Campanian
Maastrichtian
Danian
Sphagesaurian notosuchians
Baurusuchid notosuchians
Uruguaysuchid notosuchians
Peirosaurid notosuchians
Itasuchid notosuchians
Azdarchoid pterosaurians
Nodosaurids
Parankylosaurians
Elasmarian ornithopods
Hadrosaurid ornithopods
Rebbachisaurid sauropods
Cenomanian–Turonian Faunal Turnover
Lognkosaur titanosaurians
K–Pg Mass Extincton Event
Aeolosaurine titanosaurians
Saltasauroids with biconvex first caudal centrum
Noasaurid ceratosaurians
Abelisaurid ceratosaurians
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Carcharodontosaurid allosauroids
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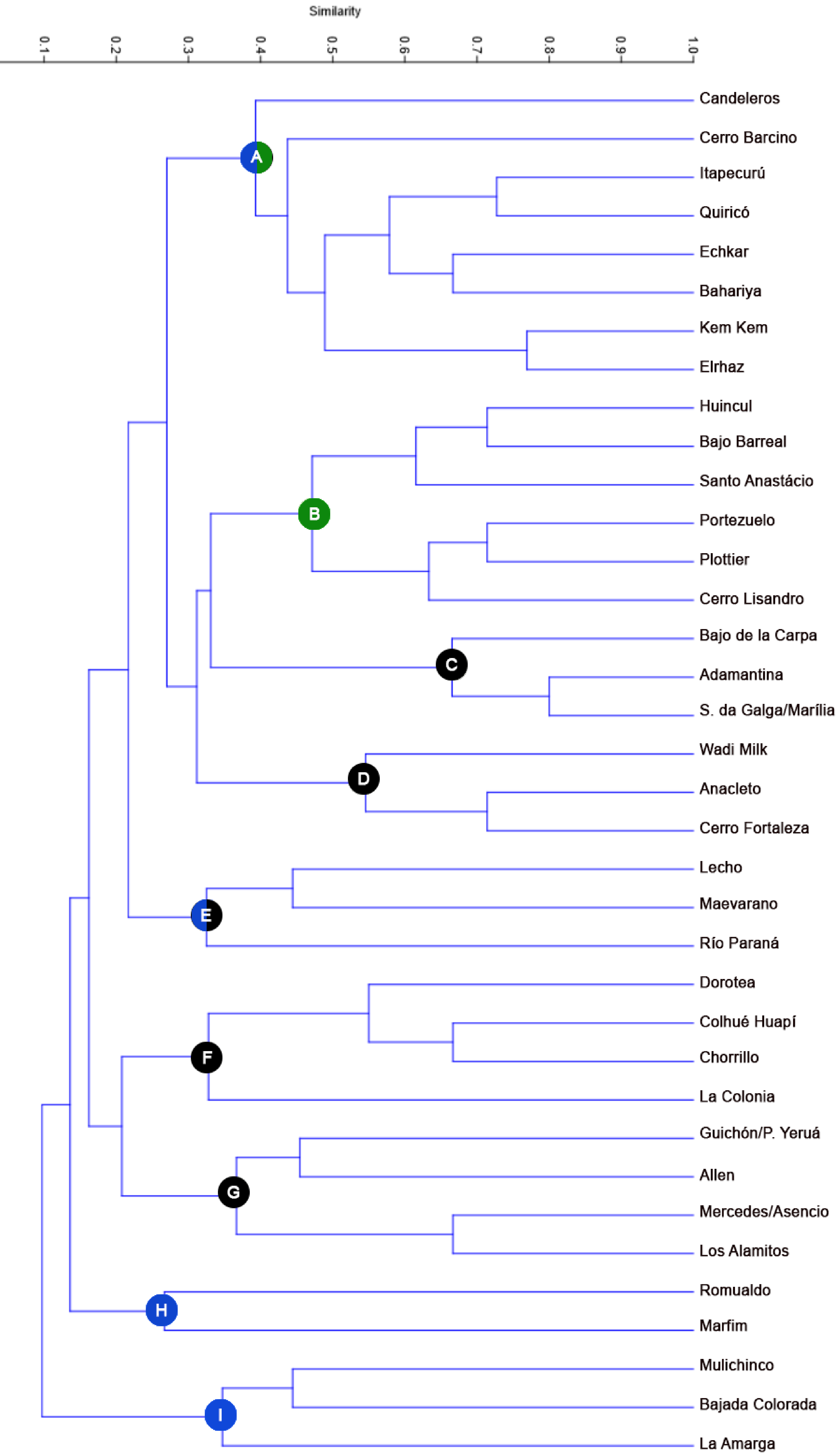
Alvarezsauroid maniraptorans
Unenlagiid paravians
Ranges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Quiricó
Echkar
Bahariya
Kem Kem
Elrhaz
Huincul
Bajo Barreal
Santo Anastácio
Portezuelo
Plottier
Cerro Lisandro
Bajo de la Carpa
Adamantina
S. da Galga/Marília
Wadi Milk
Anacleto
Cerro Fortaleza
Lecho
Maevarano
Río Paraná
Dorotea
Colhué Huapí
Chorrillo
La Colonia
Guichón/P. Yeruá
Allen
Mercedes/Asencio
Los Alamitos
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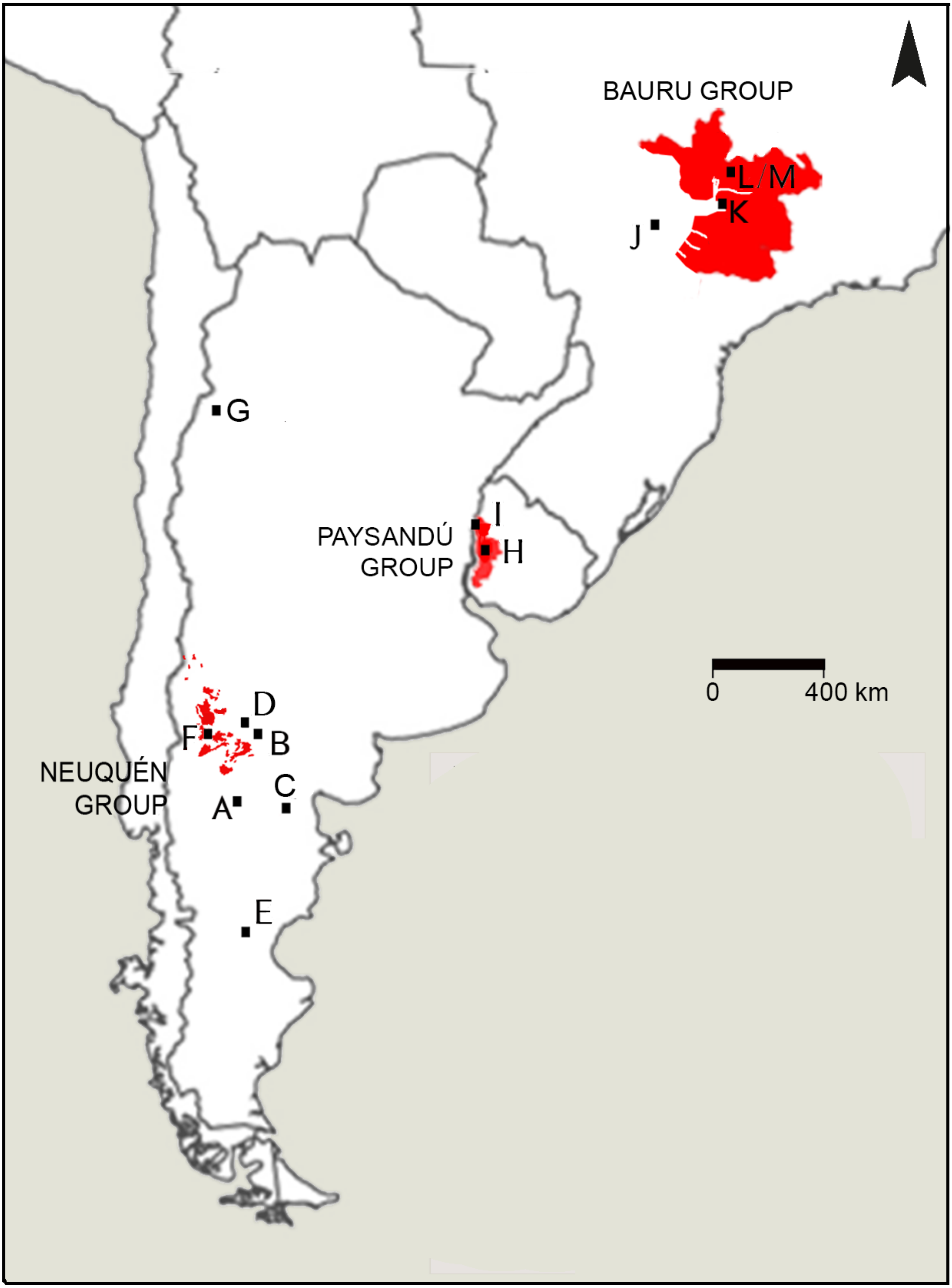
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Table 1. Measurements in cm of *Mesetasaurus protector* gen. et sp. nov.

	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

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, 1986, 2003
	Aeolosaurus ?rionegrinus	Powell, 1986, 2003
	Aeolosaurus sp. 1	Salgado & Coria, 1993
	Aeolosaurus sp. 2	Salgado et al., 1997; García & Salgado, 2013; M.S., pers. obs.
	Aeolosaurus colhuehuapensis	Casal et al., 2007
	Panamericansaurus schoederi	Calvo & Porfiri, 2010
	Punatitan coughlini	Hechenleitner el al., 2020
	Bravasaurus arrierosorum	Hechenleitner el 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 et al., 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.

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-elasmarian, non-hadrosauriform Ornithopoda**	**Basal hadrosauriforms**	**Elasmaria**	**Hadrosauroidea**
Elrhaz	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Echkar	0	0	0	1	1	1	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	1	1	0	0
Wadi Milk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Bahariya	0	0	1	0	1	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
Mercedes/Asencio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorotea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mulichinco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
La Amarga	0	0	0	0	0	0	1	0	0	0	0	1	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
Candeleros	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Huincul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Portezuelo	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Plottier	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cerro Lisandro	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bajo de la Carpa	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Anacleto	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Allen	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
Bajo Barreal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Colhué Huapí	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Los Alamitos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cerro Barcino	0	0	1	0	0	0	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
Cerro Fortaleza	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Lecho	0	0	0	0	0	0	0	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	1
Romualdo	0	1	1	0	0	0	1	0	0	0	0	0	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
Quiricó	0	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
Rio Paraná	0	0	0	0	0	0	0	0	0	0	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
Adamantina	0	0	1	0	0	0	1	1	1	1	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
Maevarano	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0

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**
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0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Azdarchoidea	**Faveoloolithidae**	**Megaloolithidae**	**Fusioolithidae**	**Elongatoolithidae**	**Arriagadoolithidae**
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	1	0	0	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
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	0	0	0	0	0
0	0	1	0	0	0
0	0	0	1	0	0
1	1	1	1	1	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	0	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
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	0	0
0	0	0	0	0	0
0	0	0	0	0	0