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Phylogenetic relationships of a new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Uruguay

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ABSTRACT

The up to 200 m thick Upper Cretaceous deposits of Uruguay includes from base to top the Guichón, Mercedes, and Asencio formations, plus the lateral correlate of the latter, the Queguay Formation. In 2006, the most complete sauropod from the country was excavated from the Guichón Formation near Araújo, Paysandú Department. Augmented by new specimens reported here, the material includes sixty caudal vertebrae (all strongly procoelous, except for the biconvex first one), a partial coracoid, long bone fragments (proximal and distal portions of tibia, proximal portion of fibula), two astragali, and six

metatarsals, as well as associated eggshell fragments. The Uruguayan titanosaur shows a unique combination of characters (biconvex first caudal centrum, pneumatic foramina in the anteriormost caudal centra, dorsal tuberosities on the transverse processes of the anterior caudal vertebrae, well developed fibular knob, pyramidal astragalus), as well as a potential autapomorphy – middle caudal centra condyles with hexagonal contour – allowing the proposition of new genus and species, *Udelartitan celeste*. Phylogenetic analyses were for the first time performed to assess the relations of that taxon, which was recovered either as a saltasaurine saltasaurid or a non-saltasaurid saltasauroid. Further, one of the analyses show *Udelartitan celeste* nested within a clade including Late Cretaceous titanosaurs with a biconvex first caudal vertebra, such as *Alamosaurus sanjuanensis*, *Baurutitan britoi*, and *Pellegrinisaurus powelli*. This contribution demonstrates that at least two titanosaur lineages were present in the Late Cretaceous of Uruguay: Saltasauroidea and Aeolosaurini, the latter recently recognized in the stratigraphically younger Asencio Formation.

Keywords: Late Cretaceous, Uruguay, Titanosauria, Guichón Formation

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INTRODUCTION

With over 80 species, mainly described in this century, titanosaurs represent the most successful and diverse sauropodomorph group (Carballido et al., 2022). They were the most abundant large-bodied herbivorous in the Late Cretaceous of Gondwana, in strong contrast with the ornithischian-dominated coeval faunas of Laurasia. The clade apparently arose in South America (Gorscak and O'Connor, 2016), where it shows its greatest diversity, with records ranging from the Berriasian–Valanginian to the Maastrichtian (e.g., Silva Junior et al., 2019; Gallina et al., 2022).

In Uruguay, titanosaur remains are known since the beginning of the XX century, when four species were recognized based on fragmentary remains (Huene, 1929). Although such referrals have been questioned (Powell, 2003; Mannion and Otero, 2012; Soto et al., 2012, 2022), their titanosaur identity is out of doubt given the strong procoely of the caudal centra. These findings were relevant because they allowed to confirm the presence of Upper Cretaceous rocks in Uruguay (Huene, 1929), although in light of recent South American findings, e.g., *Ninjatitan zapatai* (Gallina et al., 2021), *Tapuiasaurus macedoi* (Zaher et al., 2011), an older age within the Cretaceous cannot be ruled-out in absence of additional data.

Most sauropod findings in Uruguay come from the Mercedes and Asencio formations. Their exact stratigraphic provenance is, however, not always easy to define, given the different lithostratigraphic arrangements proposed for the Uruguayan Cretaceous (Soto et al., 2022) and because the fossils are usually not found in situ. Most historical findings seem to come from the Asencio Formation (sensu Bossi, 1966), including a caudal centrum referred to *Aeolosaurus* sp. (Soto et al., 2022), but some fossils found in situ have been recently reported for the Mercedes Formation. For the underlying Guichón Formation, the first titanosaur remains were found in this century,

64 when dozens of vertebrae and bone fragments were unearthed from a large gully (Figs.
65 1-2; Soto et al., 2008). Soto et al. (2012) described these fossils in more detail and
66 considered them to be closely related to *Alamosaurus sanjuanensis* and *Baurutitan britoi*.
67 However, a phylogenetic analysis including the entire set of remains testing this
68 hypothesis was never published, which is the prime aim of this contribution.
69

70 **GEOLOGICAL AND PALEOFAUNAL SETTING**

71 Bossi (1966) recognized three Cretaceous units in the Norte Basin, Uruguay (from base
72 to top): Guichón, Mercedes, and Asencio formations (Fig. 1). A fourth unit, Queguay
73 Formation (Goso & Bossi, 1966), has been recently included as a lateral correlate of the
74 Asencio Formation, given its recent Campanian–Maastrichtian absolute dating
75 (Veroslavsky et al., 2019). The Guichón Formation crops out in northwestern Uruguay,
76 Paysandú Department (Fig. 2). It comprises reddish, fine-grained wackes of arkosic
77 composition (Fig. 3C). Subordinated lithologies include conglomerates (Fig. 3B) with
78 calcedonia, basalt, and brown pelite clasts. These deposits are silicified in places and
79 bioturbation is locally abundant, indicating paleosol developement. The sandstones and
80 conglomerates have been interpreted as deposited by fluvial channels flowing towards
81 the SW (Goso & Perea, 2004). Finer lithologies were deposited in floodplains and aeolian
82 reworking of fluvial bars is seen locally (e.g., Paso Hervidero).

83 The locality bearing the fossils described here is close to Araújo, Paysandú
84 Department. It corresponds to a large gully produced by erosion, which has been recently
85 stabilized by the growing of trees (Fig. 3A). As the orange sandstones of the Guichón
86 Formation are eroded, bone, eggshell, and wood fragments are found scattered on the
87 sand. A silicified conglomerate forms the bottom of the gullies and towards their margins
88 there are column-like structures, where the sandstones incorporated carbonate due to

89 palaeoedafic processes. These columns were mostly eroded around the gully and only
90 mound-like relics (formed by accumulation of sandstone blocks) survived. The recovered
91 fossils comprise abundant titanosaur skeletal remains (Fig. 4), mostly caudal centra,
92 locally associated with eggshell fragments.
93 Previously, the Guichón Formation has yielded only few other fossils, including several
94 skeletons of the notosuchian *Uruguaysuchus aznarezi* (Rusconi, 1933; Soto et al., 2011),
95 a few isolated iguanodontian teeth, and an indeterminate theropod tooth mistakenly
96 referred to Ornithomimidae (Huene, 1934; Soto et al., 2012).
97 The age of the Guichón Formation has been a matter of debate. Facies similarities with
98 the Migues Formation, Aptian–Albian of the Santa Lucía Basin, led Goso & Perea (2003)
99 to propose a late Early Cretaceous age, which is not contradicted by the affinities of
100 *Uruguaysuchus aznarezi* to *Araripesuchus*, a taxon with a broad (Aptian–Maastrichtian)
101 chronological range within the Cretaceous. If that is the case, the hiatus with the overlying
102 Campanian–Maastrichtian Mercedes Formation (Goso & Perea, 2003; Veroslavsky et al.,
103 2019) would have been significant. However, the presence of a titanosaur with a biconvex
104 first caudal vertebrae and of *Sphaerovum*-like eggshells led Soto et al. (2008, 2012) to
105 propose a younger age, i.e.: Late Cretaceous, for Guichón Formation.
106

107 **MATERIALS AND METHODS**

108 All titanosaur specimens previously described in Soto et al. (2012), plus new unpublished
109 remains from the same locality, were measured and photographed. An effort was made to
110 identify additional characters of taxonomic relevance, apart from those originally
111 reported one decade ago. The elements were identified as mainly pertaining to a single
112 individual (FC-DPV 1900), plus at least two additional bones that indicate the presence

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of a second, younger one. However, we followed more conservative approach and considered only three near-articulated vertebrae as the holotype (FC-DPV 3595; Fig. 4).

In order to estimate the body length of the holotype specimen (the only found in near articulation), we correlated two continuous variables using a linear regression on R environment (Development Core Team 2013): (1) the estimated total body lengths of four exceptionally well-preserved titanosaurs, *Rapetosaurus krausei* (Rogers and Forster, 2001), *Overosaurus paradasorum* (Coria et al., 2013), *Dreadnoughtus schrani* (Lacovara et al., 2014), and *Alamosaurus sanjuanensis* (Tykoski and Fiorillo, 2017); (2) the anteroposterior length of the first three caudal centra of the Uruguayan taxon.

In order to infer the phylogenetic relations of the new taxon, two data sets were analyzed, with the new taxon added to the taxon/character matrices of Cerda et al. (2022) and Navarro et al. (2022), based on the scores of FC-DPV 1900 and 3595. Also, following Silva Junior *et al*. (2022), *Trigonosaurus pricei* was pruned from the two data-sets, with *Baurutiran britoi* re-scored based on the new set of specimens defined by those authors. Both matrices (which can be accessed at doi:10.17632/nz79w2kwsb.1) were then analysed with the software TNT version 1.6 (Goloboff et al., 2008), firstly under equally weighted parsimony (EWA), but also employing extended implied weighting (IWA). Following Goloboff et al. (2018), the IWA analysis was conducted using a k-value (concavity constant; see Goloboff, 1993) of 9 and applied to the data-sets of Cerda et al. (2022) and Navarro et al. (2022). All analyses were performed using New Technologies tree search up to find 30 MPTS and with a tree memory space of 100.000. To produce the "reduced consensus" trees, unstable taxa were identified using the "Pruned Tree" option in TNT.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Code of Zoological

Nomenclature. The ZooBank LSIDs (Life Science Identifiers) is https://zoobank.org/NomenclaturalActs/CB981DBD-84DB-4DD5-AE20-29D96092D1C.

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

SYSTEMATIC PALEONTOLOGY

Sauropoda Marsh, 1878

Macronaria Wilson & Sereno, 1998

Titanosauriformes Salgado et al., 1997

Titanosauria Bonaparte and Coria, 1993

Lithostrotia Upchurch, Barrett & Dodson 2004

Saltasauroidea França, Marsola, Riff, Hsiou & Langer, 2016 sensu Carballido et al. 2022

Udelartitan celeste gen. et sp. nov.

Etimology: The genus name derives from UdelaR, acronym of the Universidad de la República, plus *titan*, after the Greek mythology giants, a common suffix of titanosaur names. The specific epithet name *celeste* (Spanish for sky-blue) is the nickname of Uruguayan teams in international sport competitions.

Diagnosis: *Udelartitan celeste* differs from all other known titanosaurs based on an unique combination of features (autapomorphies marked with *), i.e.: biconvex first caudal centrum, anterior caudal vertebrae with well-developed neural spines with a quadrangular cross-section and well-developed postspinal lamina, pneumatic foramina in the anteriormost caudal centra, anterior caudal vertebrae with dorsal tuberosities on the transverse processes, middle caudal centra cotyles and /or condyles with an hexagonal

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163 contour*, well developed fibular knob, pyramidal astragalus, and marked oblique ridges
164 in the anterior face of metatarsals I and II*.
165 ***Holotype:*** FC-DPV 3595 (Figs. 5-6). This set, identified as caudal vertebrae 1 to 3,
166 corresponds to the only near-articulated specimens.
167 ***Referred material:*** FC-DPV 1900 (lot; Figs. 7-12), sixty caudal vertebrae (all strongly
168 procoelous), a partial coracoid, long bone fragments (distal and proximal tibial portions,
169 proximal fibular portion), six metatarsals, and two astragali.
170 ***Type locality and horizon***: Araújo, near Quebracho, Paysandú Department, Uruguay.
171 Guichón Formation, Upper Cretaceous of Uruguay (Veroslavsky et al., 2019).
172
173 DESCRIPTION
174 Some of the FC-DPV 1900 and 3595 elements were briefly described by Soto et al.
175 (2012), where complete measurements of all vertebrae are provided. Here we will
176 complement that study with newly recovered specimens and summarize characters of
177 phylogenetic significance from the complete set of remains.
178
179 Axial Skeleton

180 *Caudal vertebrae.* The tail elements are represented by the associated first three caudal
181 centra, plus anterior centra and neural arches, and middle to posterior caudal centra (with
182 some of the posteriormost recovered elements preserving the neural arch).

183 The first caudal centrum (Fig. 5) is deformed, so that the right lateral outline
184 appears anteroposteriorly shortened compared to the left one. This centrum is strongly
185 biconvex, with the anterior articular surface larger than the posterior (Fig. 5A). Biconvex
186 first caudal centra have been reported for several titanosaurs (e.g., *Alamosaurus*
187 *sanjuanensis*, *Baurutitan britoi*, *Dreadnoughtus schrani*, *Pellegrinisaurus powelli*;

188 Gilmore, 1946; Salgado, 1996; Salgado et al., 2005; Lacovara et al., 2014) most of which
189 currently considered saltasauroids. This includes *Neuquensaurus australis*, the last sacral
190 element of which could be considered homologous to the first caudal vertebra of
191 titanosaurs with fewer (six) sacral elements. In the Uruguayan material, the neural arch
192 of the first caudal vertebra is mostly lost, but the preserved proximal portion of the
193 transverse processes show that they were laterodorsally and slightly posteriorly directed.
194 The lateral, ventral, and dorsal surfaces of the centrum have several small foramen-like
195 hollows (Fig. 5A) that are related to the internal pneumaticity, as observed in Saltasaurini
196 (e.g., *Neuquensaurus australis*, *Rocasaurus muniozi*, *Saltasaurus loricatus*; Cerda et al.,
197 2012; Zurriaguz and Cerda, 2017).

198 Anterior, middle, and posterior caudal centra are strongly procoelous, as in most
199 Titanosauria, with few exceptions such as *Andesaurus delgadoi* or *Opisthocoelicaudia*
200 *skarzynskii* (e.g. Salgado et al., 1997). The condylar convexity indexes (Mannion et al.,
201 2019) range from 0.5 to 0.99 (see Table 1). Posteriormost caudal centra were not
202 recovered. Anterior caudal vertebrae are represented by several isolated centra that lack
203 the neural arches and two isolated neural spines. As in the first caudal element, some of
204 the anteriormost caudal centra present small foramina on their lateral surfaces. These are
205 subcircular, with diameters of around 0.5 cm. Similar foramina are present in some
206 Saltasauridae titanosaurs, such as *Alamosaurus sanjuanensis*, *Rocasaurus muniozi*, and
207 *Saltasaurus loricatus*. Additionally, as in these taxa, some of the anteriormost caudal
208 vertebrae (including the first one) present one or more foramina on their ventral surfaces.
209 One of the centra bears two anteroposteriorlly elongated foramina, positioned close to the
210 midline of the element and on the anterior half of the ventral surface (Fig. 6B), with
211 smaller foramina at the posterior region of the ventral surface; which shape and position
212 are more reminiscent to the pneumatic foramina of some saltasauroids (e.g., *Alamosaurus*

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213 *sanjuanensis*, *Saltasaurus loricatus*, *Pellegrinisaurus powelli*) than to the vascular
214 foramina present in several non-saltasauroid sauropods.

215 Few other anterior caudal elements present solely small foramina on their ventral surface.
216 As in other titanosaurs, we interpret the foramina present in *Uderlatitan celeste* as
217 pneumatic openings excavated by air sac diverticuli of the tail (Cerda et al., 2022; Taylor
218 and Wedel, 2021). Yet, except for the first element, it was not possible to recognize the
219 presence of internal pneumaticity in the caudal vertebrae (see above). Therefore, we
220 interpreted that the caudal pneumaticity do not reach the middle section of the tail,
221 contrasting with the condition in some Saltasaurini, which bear pneumatic foramina up
222 to the posterior caudal elements. In fact, internal pneumatic cavities are widespread within
223 that clade, even when no external openings are present (Zurriaguz and Cerda, 2017). The
224 ventral surfaces of the FC-DPV 1900 tail vertebrae are anteroposteriorly and transversally
225 concave and mediolaterally narrow. The preserved transverse processes of the anterior
226 caudal vertebrae are triangular, wider at their base and narrower towards the distal end,
227 as common among non-diplodocoid sauropods, with the exception of some Lognkosauria
228 (e.g., *Patagotitan mayorum*, *Futalognkosaurus dukei*). The few preserved transverse
229 processes are posteriorly inclined as in titanosauriforms and related forms. A marked
230 dorsal tuberosity in the transverse process is present in two of the best preserved anterior
231 caudal vertebrae (Figs. 6E, F), a rather widespread character.

232 A horizontal ridge in the middle caudal centra (Fig. 7A, F) is interpreted as
233 homologous to this dorsal tuberosity. Middle caudal centra show cotyles and/or condyles
234 with a hexagonal contour (Fig. 7D-E, I-J). The posterior caudal centra are
235 anteroposteriorly elongated, with convex lateral and ventral surfaces. Their cotyles are
236 less excavated and condyles more gracile than those of the previous vertebrae. One of the
237 posterior caudal centra also shows a cotyle with hexagonal contour (Fig. 8F).

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Two isolated neural spines briefly described, but not figured by Soto et al. (2012) are herein identified as anterior caudal neural spines (Fig. 9), based upon comparisons with more complete titanosaur tails (e.g., *Baurutitan britoi*). Their bases are quadrangular in cross-section, with similar anteroposterior and lateromedial breadths. Distally, the neural spine is somewhat broader lateromedially, although the postspinal lamina is broken. Hence, it can be better described as quadrangular rather than lateromedially expanded, like that of most non-colossosaur titanosaurs (Carballido et al., 2017). The postzygapophyseal facets are roughly elliptic in shape, similar to those of the anterior caudal elements of *Caieiria allocaudata* (Silva Junior et al., 2022:fig. 21), but lacking a hyposphenal ridge. The prezygapophyses are not preserved and the spinoprezygapophyseal lamina seems to be reduced; i.e., medially bound by the prespinal lamina, resembling the lamination pattern of *Caieiria allocaudata*. The lateral edge of the neural spine is formed by the robust and well-marked spinopostzygapophyseal lamina (Fig. 9) and its anterior and posterior surfaces bear pre- and postspinal laminae. The later, flanked by the spinopostzygapophyseal laminae, is broken, but was clearly robust. The prespinal lamina is equally robust and not distally expanded, unlike the condition in lognkosaurs (Carballido et al., 2017). Although the neural spine is distally broken, the lateral edges, formed by the spinopostzygapophyseal lamina, show the beginning of a lateromedial expansion.

Appendicular Skeleton

Pectoral girdle. A partially preserved left coracoid was mentioned, but not figured by Soto et al. (2012). For descriptive purposed the coracoid is described as if the scapula-coracoid was horizontally oriented. Although incomplete, the bone is subquadrangular in lateral/medial views (Fig. 11A). The scapular articulation is not preserved, but the

bone seems to be relatively short anteroposteriorly, unlike the longer coracoid of several titanosaurs, which an anteroposterior length around twice the breadth of the scapular articular surface. The anteroventral margin of the bone is rectangular, as common in saltasaurids and few other titanosaurs (e.g., *Quetecsaurus rusconii*, *Patagotitan mayorum*; González Riga et al., 2019; Otero et al., 2020). The glenoid is well preserved and a marked groove is seen right anterior to it, also seen in most camarasauromorphs (e.g., *Tehuelchesaurus benitezii*, *Xianshanosaurus shijiagouensis*, *Patagotitan mayorum*, *Neuquensaurus australis*). Yet, the infraglenoid groove ends without forming a marked infraglenoid lip, as also observed in some titanosaurs, including non-Saltasauridae Saltasauroidea (e.g., *Isisaurus colberti*). The coracoid foramen (Fig. 11A) is positioned at the posterodorsal margin of the bone.

Hindlimb. Proximal and distal left tibial ends are preserved; the former damaged and not mentioned by Soto et al. (2012). The proximal end of the tibia is transversally expanded, as in most sauropods, and bears a cnemial crest that is, at its base, anterolaterally oriented (Fig 11B). The crest is proximally broken, better preserved more distally, forming a marked concavity where the fibula articulates. The distal end of the tibia is markedly expanded (Fig. 11) compared to the partial mid-shaft, an apomorphic condition among titanosaurs. The medial malleolus (*sensu* Poropat et al. 2015) is short and robust, whereas the lateral malleolus (*sensu* Poropat et al. 2015), which articulates to the ascending process of the astragalus, is around twice longer, but more gracile. This resembles the morphology of saltasaurinae titanosaurs (e.g., *Saltasaurus loricatus*, *Neuquensaurus australis*; Otero, 2010), contrasting with the equally developed malleoli of most other sauropods, including several titanosaurs (e.g., *Bonitasaura salgadoi*, *Dreadnoughtus schrani*).

Only the proximal portion of a right fibula is preserved. The element is robust and mediolaterally expanded. The proximal articulation is slightly convex and with a rugose surface. It shows a gracile anteromedial ridge, that projects anterolaterally. This ridge was defined as the anterior crest of the fibula, which extends medially and becomes sandwiched between the cnemial crest and the body of the tibia (Wilson and Upchurch, 2009) which is a widespread character amongst titanosauriforms, with some exceptions among saltasaurids (*Saltasaurus loricatus*, *Neuquensaurus australis*; D'Emic, 2012). A marked fibular knob, extending anterodistally from the posteroproximal border, is present on the medial surface of the fibula. The knob has a squared anterior outline and expands distally as a thin lamina. The presence of this knob resulted in a posteriorly expanded proximal margin of the fibula, so that its presence can be recognized in medial and proximal views (Fig. 11). A similarly developed fibular knob was described for *Uberabatitan ribeiroi* (Silva Junior et al. 2019) and seems to be also present in *Bonitasaura salgadoi* (Gallina and Apesteguía, 2015), *Rapetosaurus krausei* (Curry Rogers, 2009), *Sauroposeidon proteles* (Rose, 2007). It borders both a lateral and medial fossae, with the latter deeper than the former.

Two right astragali were recovered (Fig. 12). Both have a triangular distal outline, with bevelled posterolateral and posteromedial margins. Both tibial and fibular articulations are marked by well-developed concavities, with the latter larger than the former. The distal surfaces of the astragali are rugose and anteriorly curved. Both astragali are almost as wide as long (Table 1), with the ascending process positioned at the anterior margin, two characters widespread among latter eusauropods. As in most macronarians, the distolateral lip of the astragalus is absent (Mannion et al., 2013). A relatively small dorsal fossa is present on the posteromedial surface of the astragalus (Fig. 12C). As in non-diplodocoid sauropods, the fibular facet of the astragalus faces

laterally, instead of posterolaterally (Whitlock, 2011). The posterior fossa is undivided, resembling the condition of other titanosaurs (e.g., *Opisthocoelicaudia skarzynskii*, *Neuquensaurus australis*, *Diamantinasaurus matildae*, *Pellegrinisaurus powelli*)

The metatarsals were identified, based on comparisons with complete pedes, such as those of the "La Invernada" titanosaur (González Riga et al., 2008) and *Rapetosaurus krausei* (Curry-Rogers, 2009), as left I, III, IV, and V, and right I and II. Their proximal ends are lateromedially expanded with the articular surfaces slightly concave. Those are angled ventromedially on both metatarsals I and perpendicular to the shaft on the remaining ones. Proximally, small concavities mark the articulation facets with the neighbouring metatarsals. Metatarsals I and II show a conspicuous oblique ridge projecting medially. The distal ends are dorsoventrally expanded and have rounded and rugose articular surfaceswhich are slightly angled dorsomedially on all elements.. Metatarsal I is somewhat damaged, but is clearly a robust element (Table 1). Its proximal and distal articulations are wide, with the distal one almost as lateromedially wide as anteroposteriorly long. Metatarsals II are also robust (see Table 1), but with proximal and distal articulations more compressed that those of metatarsal I.

Elements interpreted as osteoderms by Soto et al. (2012) are flat, discoidal structures of the same size and shape. Yet, a thin section of one of the best-preserved of those elements rejected their organic nature (I. Cerda, pers. comm, 2022)., revealing that they are most probably concretions

DISCUSSION

The regressions detailed in the "Material and Methods" indicate that *Udelartitan celeste* was a small-sized titanosaur, measuring from 15 to 16 meters. Its titanosaur affinity is suggested by several anatomical traits, such as strongly procoelous vertebrae spanning

337 throughout the tail, a condition known only in (most) titanosaurs and (several)
338 mamenchisaurids. Also, the placement of the neural arches in the anterior half of the
339 centra, the transverse expansion of the distal end of the tibia, and the pyramidal astragalus
340 are common features of titanosaurs (Salgado et al., 1997; Wilson, 2002). More
341 specifically, a biconvex first caudal centrum is only present in few taxa, including
342 *Alamosaurus sanjuanensis*, *Baurutitan britoi*, *Dreadnoughtus schrani*, and
343 *Pellegrinisaurus powelli* (Gilmore, 1946; Salgado, 1996; Campos et al., 2005; Lacovara
344 et al., 2014), whereas in *Neuquensaurus australis* this was incorporated as the seventh
345 sacral vertebra (Salgado et al., 2005). The conspicuous ridge in metatarsal I is similar to
346 that of *Neuquensaurus australis* (Otero, 2010). Finally, the caudal centra lack the
347 eccentric condyles and the anteriorly tilted anterior faces that characterize vertebrae
348 similar to those of *Aeolosaurus* spp, like that described by Soto et al. (2022) for the
349 Asencio Formation. The apparent anterior tilt in an anterior caudal vertebra of *Udelartitan*
350 *celeste* (Fig. 6) is likely due to breakage of its anteroventral portion.

351 Both Saltasaurinae and Saltasauroidea appear to be a Gondwanan radiation of
352 titanosaurian sauropods, with the single exception of the North American *Alamosaurus*
353 *sanjuanensis*. The new taxon described here reinforces the idea that a great diversification
354 of saltasauroids (or even saltasaurines, depending on the analysis) took place in
355 Gondwana, especially in South America. This supports the hypothesis that saltasauroids
356 dispersed from South to North America at the end of the Cretaceous (dispersion events
357 also were responsible for the arrival of hadrosaurid ornithopods in South America; Estes
358 & Baéz, 1985). It is interesting to highlight the small size of the saltasauroids (including
359 *Udelartitan celeste*) nested together with the larger *Alamosaurus sanjuanensis*, in the
360 phylogenetic analyses conducted here. It is tempting to suggest that such larger size could
361 have resulted from titanosaurs arriving to an ecosystem with vacant niches or with an

362 improved capacity of exploring niches previously occupied by the dominant herbivores
363 from the Northern hemisphere (i.e., ornitischians).

364 The discovery of a saltauroid/saltasaurine in Uruguay with a biconvex first caudal
365 vertebra allows stablishing correlations with other stratigraphic units in southern South
366 America: the Argentinean Neuquén Group and the Brazilian Baurú Group (Fig. 15).
367 Taking into account that araripesuchids and early-branching iguanodontians are also
368 found in the Guichón Formation, the lack of data regarding theropods and turtles hampers
369 correlation with the Cretaceous tetrapod assemblages of the Neuquén Group (Fig. 15;
370 Leanza et al., 2004). On one hand, the presence of araripesuchids and iguanodontians
371 recall the Limayan assemblage (Cenomanian-Early Turonian), although no remains of
372 rebbachisaurids, carcharodontosaurids or abelisaurids have so far been found in the
373 Guichón Formation. On the other hand, the presence of a saltasauroid/saltasaurine recall
374 the Coloradoan assemblage (Santonian-Early Campanian). In turn, the younger Asencio
375 Formation correlates with the Allenian assemblage (Late Campanian-Early
376 Maastrichtian) due to the presence of *Aeolosaurus*. As for the Baurú Group, forms related
377 to *Udelartitan celeste* include *Ibirania parva* and *Baurutitan britoi*. The former was found
378 in the São José do Rio Preto Formation (Santonian-Campanian), along with abelisaurid
379 and putative megaraptoran theropods, and notosuchian crocodyliforms. *Baurutitan britoi*,
380 in turn, comes from the Serra da Galga Formation (Maastrichtian) where it coexisted with
381 other titanosaurs (e.g., *Uberabatitan ribeiroi*, *Caieria allocaudata*), abelisaurid and
382 dromaeosaurid theropods, and peirosaurid and notosuchian crocodyliforms. The scarcity
383 of fossils from the Guichón Formation precluded more detailed comparisons.

384

385 **Phylogenetic analysis**

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386 The description of *Udelartitan celeste* led to the identification of two new characters
387 based on the epipodial anatomy. The first relates to the anteroposterior length of distal
388 malleoli of the tibia, which can be about the same size (0) or the lateral malleolus can be
389 longer than the medial (1). The second character corresponds to the absence (0) or
390 presence (1) of a fibular knob in the posteromedial edge of the proximal end of the fibula.
391 These were added to both data-sets used here, as characters 432 and 433 for Cerda et al.
392 (2021) and 436 and 437 for Navarro et al. (2022).

393 The EWA analysis of the dataset modified from Cerda et al. (2021) retrieved
394 100,000 MPTs (collapsing tree memory) of 1,570 steps. The strict consensus of those
395 trees (see Supplementary Material) shows a large polytomic clade, forming a trichotomy
396 with *Epachthosaurus sciuttoi* and *Choconsaurus baileywillisi*. That polytomy mainly
397 results from the unstable position of several titanosaurs, as identified by the "Pruned
398 Tree" option in TNT, i.e., *Bonitasaura salgadoi, Caieiria allocaudata, Isisaurus colberti,*
399 *Nemegtosaurus mongoliensis, Ninjatitan zapatai, Notocolossus gonzalezparejasi,*
400 *Nullotitan glaciaris*, *Opisthocoelicaudia skarzynskii*, *Puertasaurus reuili*, and
401 *Tapuiasaurus macedoi*. Once these taxa are pruned from the MPTs, the reduced strict
402 consensus tree (Fig. 14a) is better resolved, although some taxa, i.e., *Diamantinasaurus*
403 *matildae, Dreadnoughtus schrani*, and *Malawisaurus dixeyi,* are still recovered in a
404 polytomy with the Saltasauroidea and Colossosauria branches. In fact, that polytomy
405 precludes applying the phylogenetic definitions of those clades by Carballido et al.
406 (2022). *Uderlatitan celeste* is placed in another polytomy in the saltasauroid branch,
407 together with *Alamosaurus sanjuanensis*, *Pellegrinisaurus powelli*, *Rapetosaurus*
408 *krausei*, and two minimal clades composed of *Uberabatitan ribeiroi* plus *Baurutitan*
409 *britoi*, and *Neuquensaurus australis* plus *Saltasaurus loricatus*.

In the second analysis (IWA) we recovered 100,0000 MPTs (collapsing tree memory) of 36.01846 steps. The strict consensus of these trees (see Supplementary Material) recovered an early branching lineage of non-eutitanosaur titanosaurs (e.g., *Diamantinasaurus matildae*, *Isisaurus colberti*, *Malawisaurus dixeyi*, *Ninjatitan zapatai*, *Notocolossus gonzalezparejasi*, and *Nullotitan glaciaris*), most of which were recovered in the Saltasauroidea branch in previous analyses of this dataset and also as unstable taxa in the EWA analysis conducted here (see above). A large polytomy is sister to that lineage, including thirteen species plus the Rinconsauria and Lognkosauria+*Bonitasaura salgadoi* lineages. The reduced strict consensus tree (after pruning *Nemegtosaurus mongoliensis* and *Caieiria allocaudata*) is well resolved (Fig. 14b), recovering Saltasauroidea and Colossosauria *sensu* Carballido et al. (2022), the latter formed by Rinconsauria and Lognkosauria+*Bonitasaura salgadoi*. Irrespective of the topological differences between the EWA and IWA trees, *Uderlatitan celeste* is positioned as a saltasauroid and, in the latter, within a clade including titanosaurs mostly bearing a biconvex first caudal centrum.

The analysis of the Navarro et al. (2022) data-set, with the inclusion of *Udelartitan celeste*, resulted in 100,000 MPTs (collapsing tree memory) of 1,858 steps under EWA and 5 MPTs of 4,217,529 steps under IWA. The strict consensus tree under EWA shows a huge polytomy of titanosaurs (see Supplementary Material), which can be improved if eight OTUs (*Argentinosaurus huinculensis, Bonitasaura salgadoi, Epachthosaurus sciuttoi, Kaijutitan maui, Paludititan nalatzensis, Patagotitan mayorum*, *Tapuiasaurus macedoi,* and BIBE 45854), are pruned from the MPTs. In that three (Fig. 14c), *Malawisaurus dixeyi* is the sister-taxon to a clade composed of two major titanosaur branches, with *Udelartitan celeste* deeply nested within that including *Saltasaurus loricatus*; although the pruning of *Patagotitan mayorum* prevents employing

435 Saltasauroidea *sensu* Carballido et al. (2022). Note that in that topology, Saltasaurinae
436 includes *Alamosaurus sanjuanensis*, *Bonatitan reigi*, *Ibirania parva*, *Neuquensaurus*
437 *australis*, *Rocasaurus muniozi*, *Saltasaurus loricatus*, and BIBE 45854, many of which
438 are not traditionally nested within that group. The strict consensus of the 5 MPTs of the
439 EWA analysis (Fig. 14d) shows an uncommon arrangement, with *Patagotitan mayorum*
440 outside a clade including most eutitanosaurs. Hence, Saltasauroidea *sensu* Carballido et
441 al. (2022) forms the bulk of titanosaurs, with Saltasaurinae including *Udelartitan celeste*
442 in an arrangement similar to that of the IWA reduced consensus.

443 The position here recovered for *Udelartitan celeste* results from the recognition
444 of several apomorphic characters present in the new titanosaur; the numbers of which
445 follow the matrix of Cerda et al. (2022). It shares with most titanosaurs a posteriorly
446 convex articular surface of the first caudal vertebra (ch. 225); with reversions such as in
447 *Opisthocoelicaudia skarzynskii*, the articular surface of which is concave. Also, as in most
448 titanosaurs, except for early diverging taxa such as *Andesaurus delgadoi* or *Malawisaurus*
449 *dixeyi*, the anterior caudal vertebrae of *Udelartitan celeste* are strongly procoelous (ch.
450 231). Two apomorphic characters of Eutitanosauria (Fig. 14b) are also present in
451 *Udelartitan celeste*, i.e.: strongly procoelous posterior caudal vertebrae (ch. 261) and a
452 marked knob at the posteromedial edge of the proximal end of the fibula (ch. 437). As in
453 other saltasauroids, the ventral surface of the anterior caudal centra of *Udelartitan celeste*
454 are transversely concave (ch. 233). In the analyses were *Udelartitan celeste* is nested
455 within Saltasauridae, this position is supported by an astragalus as long as wide (chs. 372,
456 378) and a biconvex first caudal vertebra (ch. 224, 225). Equally, its nesting within
457 Saltasaurinae is supported by middle caudal vertebrae more than twice longer than the
458 height of the centrum (ch. 259), as also seen in *Alamosaurus sanjuanensis*, *Saltasaurus*
459 *loricatus*, and *Neuquensaurus australis,* and a distal lateral malleolus of the tibia longer

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than the medial malleolus (ch. 436). Conversely, *Udelartitan celeste* differs from some saltasaurines such as *Alamosaurus sanjuanensis*, *Saltasaurus loricatus,* and *Rocasaurus muniozi*, because its posterior caudal centra are subcircular in cross section (ch. 262), and not strongly dorsoventrally compressed as in those taxa.

CONCLUSIONS

Udelartitan celeste gen. et sp. nov. represents a second sauropod taxon recognized in Uruguay, after the recently reported *Aeolosaurus* vertebra from the Asencio Formation (Soto et al., 2022). Its phylogenetic relations as either a saltasaurine saltasaurid or a non-saltasaurid saltasauroid documents the presence of saltasauroids in the Guichón Formation. The close relation with taxa such as *Pellegrinisaurus powelli*, *Baurutitan britoi*, and *Alamosaurus sanjuanensis* hypotethized by Soto et al (2012) was partially recovered in some of the trees. Irrespective of the topologies, *Udelartitan celeste* is retrieved within clades formed solely by late Late Cretaceous taxa. This does not necessarily imply this age for the Guichón Formation, but hints into such an inference.

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636 **FIGURE CAPTIONS**

637

638 Figure 1. Relations of the Cretaceous stratigraphic units from Norte Basin, Uruguay.
639 Modified from Veroslavsky et al. (2019).

640

641 Figure 2. Simplified geology of the area based in Bossi & Ferrando (2001). Black star
642 shows the location of the type-locality of *Udelartitan celeste*. Coordinates: 31° 58' 34''S,
643 55°57'43''W. Geological map taken from Bossi & Ferrando (2001). Inset shows
644 Paysandú department in Uruguay.

645

646 Figure 3. A, general view of the gully. B, silicified conglomerates. C, sandstones.

647

648 Figure 4. Titanosaur skeleton with coloured recovered elements of *Udelartitan celeste*
649 gen. et sp. nov. Holotype indicated in green. Typical Uruguayan Carnival drummer and
650 dancer for scale.

651

652 Figure 5. FC-DPV 3595 (holotype of *Udelartitan celeste* gen. et sp. nov.). First caudal
653 centrum in left lateral (A), dorsal (B) and posterior (C) views. Scale bar equals 5 cm.
654 Abbreviations: cd, condyle. ct, cotyle. lf, lateral foramina. tp, transverse process.

655

656 Figure 6. FC-DPV 3595 (holotype of *Udelartitan celeste* gen. et sp. nov.) . Second and
657 third anterior caudal centra in right lateral (A, F), ventral (B, G), dorsal (C, H), anterior

(D, I) and ventral (E, J) views. Scale bar equals 5 cm. Abbreviations: cd, condyle. tp, transverse process. vf, ventral foramina.

Figure 7. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. Middle caudal centra in left lateral (A, F), ventral (B, G), dorsal (C, H), anterior (D, I) and ventral (E, J) views. Scale bar equals 5 cm. Abbreviations: cd, condyle. dt, dorsal tuberosity. na, neural arch.

Figure 8. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. Posterior caudal centra in right lateral (A, E), anterior (B, F), ventral (C, G) and posterior (D, H) views. Scale bar equals 5 cm. Abbreviations: cd, condyle. na, neural arch.

Figure 9. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. Anterior caudal neural spine in right lateral (A), posterior (B), anterior (C) and dorsal (D) views. Scale bar equals 5 cm. Abbreviations: posl, postpinal lamina. posz, postzygapophysis. prsl, prespinal lamina. spol, spinopostzygapophyseal lamina,

Figure 10. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900 Juvenile anterior caudal centra in right lateral (A), anterior (B), ventral (C), dorsal (D) and posterior (E) views. Scale bar equals 5 cm.

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679 Figure 11. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. A, left
680 coracoid in medial view. B-C, proximal tibia in lateral (B) and proximal (C) views. D-E,
681 distal tibia in distal (D) and posterior (E) views. F-G, proximal fibula in anterior (F) and
682 proximal (G) views. Scale bars equal . Abbreviations: asap, articular surface for the
683 ascending process. cc, cnemial crest. cf, coracoidal foramen. cmr, cranomedial ridge. gl,
684 glenoid. lm, lateral malleoulus. mm, medial maleollus. tp, tibial prominence.

685

686 Figure 12. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. Large
687 and small astragali in distal (A, B), posterior (C, D), proximal (E, F), anterior (G, H) and
688 lateral (I, J). Scale bar equals 5 cm. Abbreviations: ap, ascending process. faf, facet for
689 articulation of fíbula.

690

691 Figure 13. *Udelartitan celeste* gen. et sp. nov. referred material. FC-DPV 1900. Right
692 metatarsal II in anterior (A), posterior (B), proximal (C) and distal (D) views. Left
693 metatarsal II in anterior (E), posterior (F), proximal (G) and distal (H) views. Left
694 metatarsal I in anterior (I), posterior (J), proximal (K) and distal (L) views. Left metatarsal
695 IV in anterior (M), posterior (N), proximal (O) and distal (P) views. Right metatarsal I in
696 anterior (Q), posterior (R), proximal (S) and distal (T) views. Left metatarsal V in anterior
697 (U), posterior (V), proximal (W) and distal (X) views. Scale = 5 cm. Abbreviations: r,
698 ridge.

699

700 Figure 14. Excerpts of phylogenetic trees (see complete topologies in the Supplementary
701 Material) depicting the position of *Udelartitan celeste* gen. et sp. nov. A-B, Reduced strict
702 consensus trees based on the data-matrix modified from Cerda et al. (2022), analysed

703 under EWA (A) and IWA (B). C-D, Consensus trees based on the data-matrix modified
704 from Navarro et al. (2022); C, reduced strict consensus of MPTs analysed under EWA.
705 D, strict consensus of MPTs analysed under IWA. Yellow and green highlight
706 respectively indicate Saltasauroidea (or "Saltasauroidea branch") and Saltasauridae.

707

708 Figure 15. Map of southern South America showing distribution of saltasauroids with
709 first biconvex caudal vertebra (7th sacral in the case of *Neuquensaurus*). Upper Cretaceous
710 deposits discussed in text (Paysandú, Neuquén and Baurú Groups) are depicted in red.

711 ~~Figure 15. Hypothetical restoration of *Udelartitan celeste*.~~

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Table 1. Measurements (in mm) of *Udelartitan celeste*.

Condylar convexity measurements (selected vertebrae; for other measurements see Soto et al. 2012)

Anterior vertebrae [Fig. 5 y 6]

0.54, 0.76, 0.99

Middle vertebrae [Fig. 7]

0.47, 0.5

Posterior vertebrae[Fig. 8]

0.86, 0.69

	Maximum preserved lenght	Anteroposterior	Mediolateral
Proximal fibula	147.64	87.07	116.33
Distal tibia	136.00	110.72	155.00

	Anteroposterior (length)	Mediolateral (width)	Proximodistal (height)
Small astragalus	82.53	128.74	71.69
Large astragalus	107.51	150.41	88.71

	Length	Minimum width (mid-shaft)	Maximum width (proximal)	Maximum width (distal)
Right metatarsal I	129.87	66.41	117.59	79.05
Left metatarsal II	117.83	76.30	113.50	82.51
Left metatarsal I	133.47	70.28	84.54	110.43
Right metatarsal II	118.46	63.12	70.80	80.17
Left metatarsal IV	96.89	64.14	89.73	78.15
Left metatarsal V	95.42	55.23	85.43	57.22

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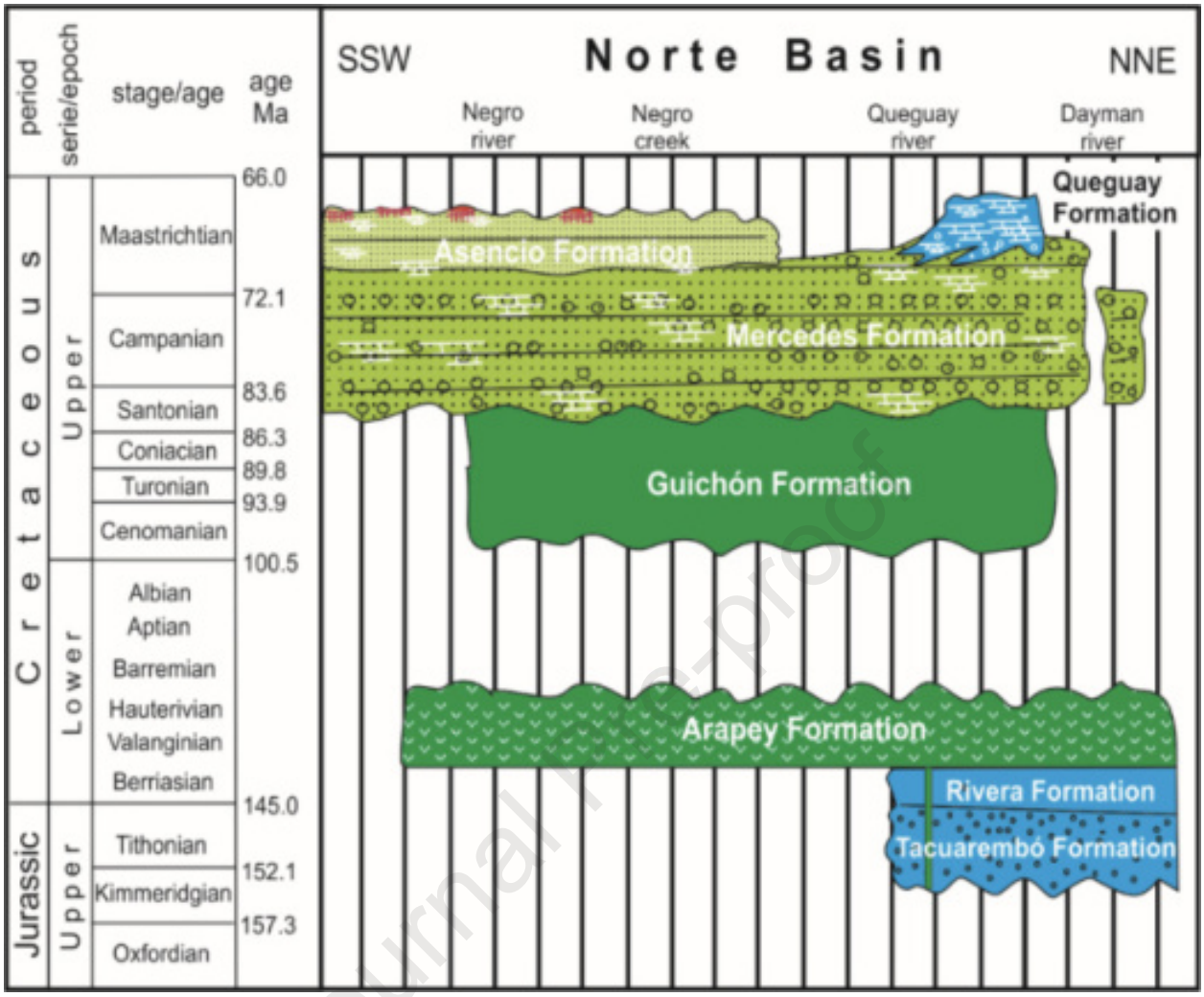

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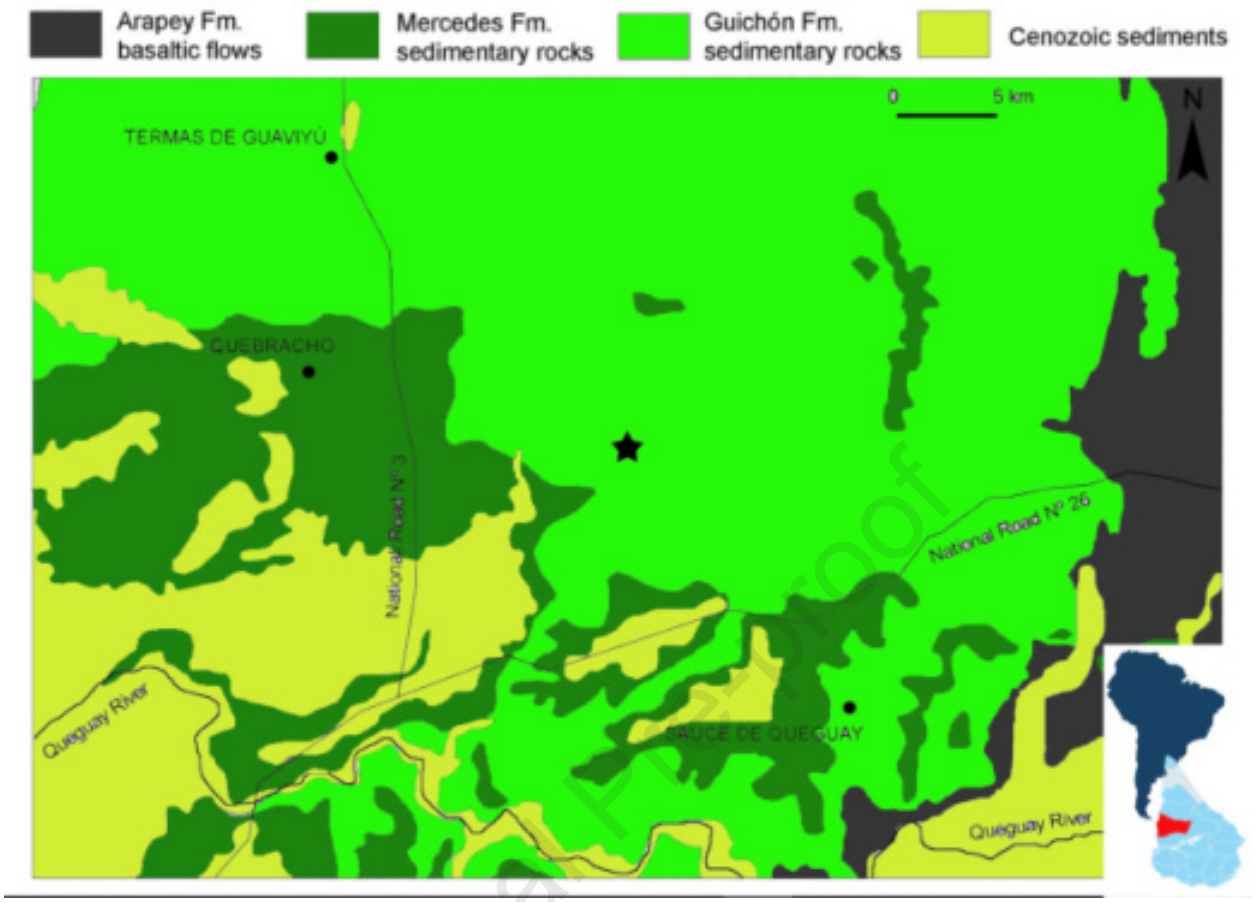

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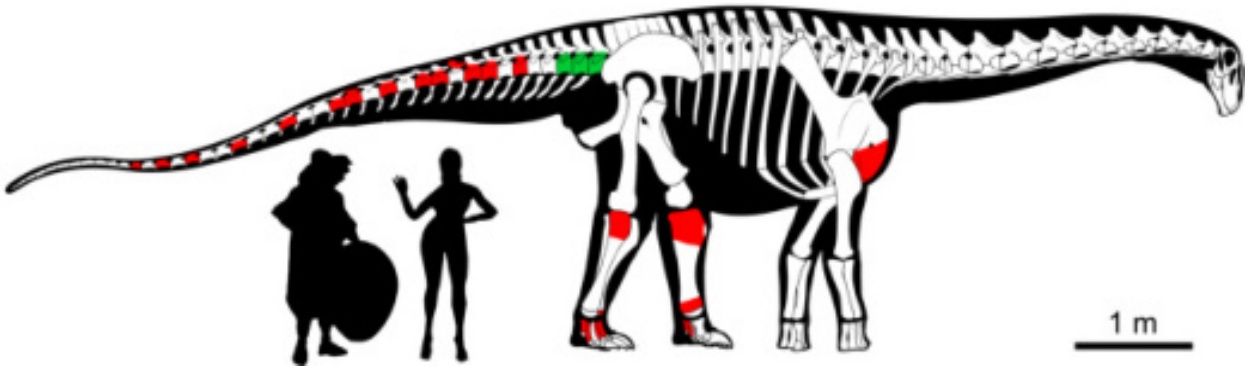

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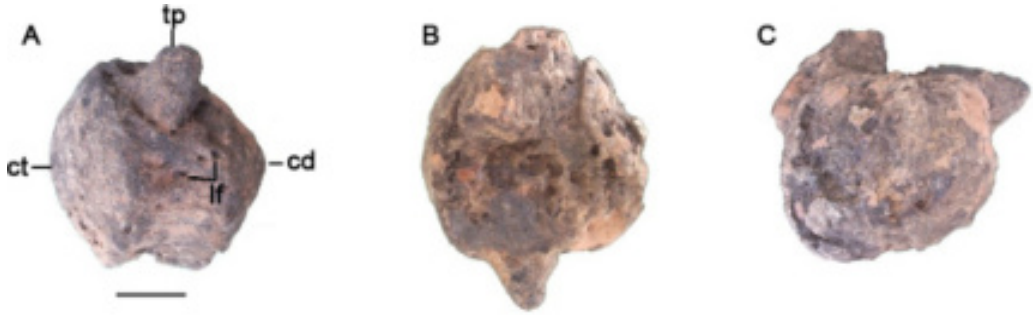

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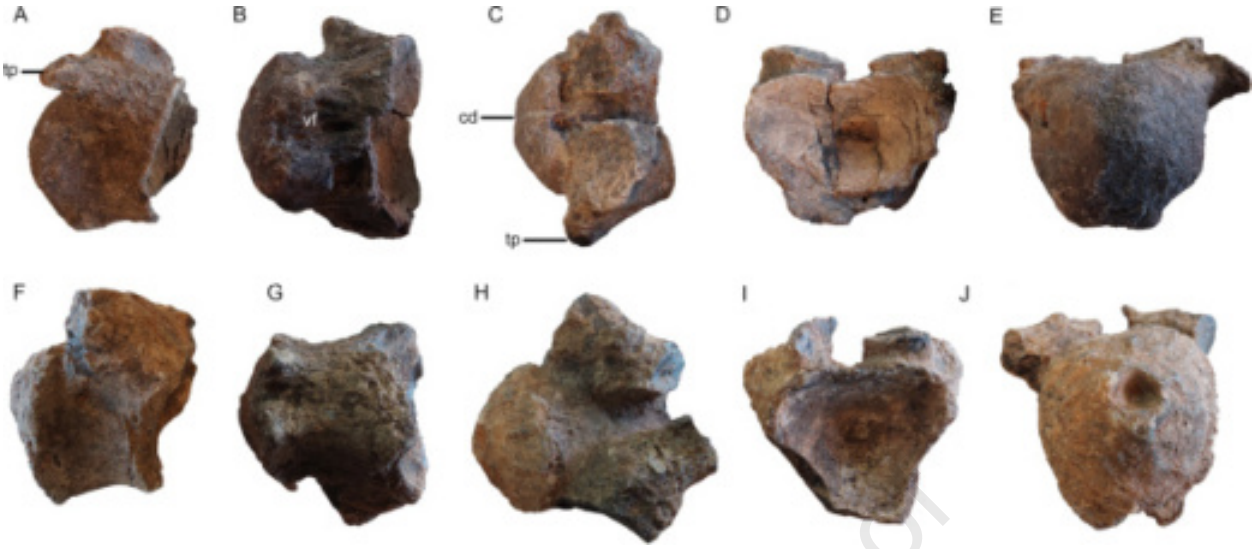

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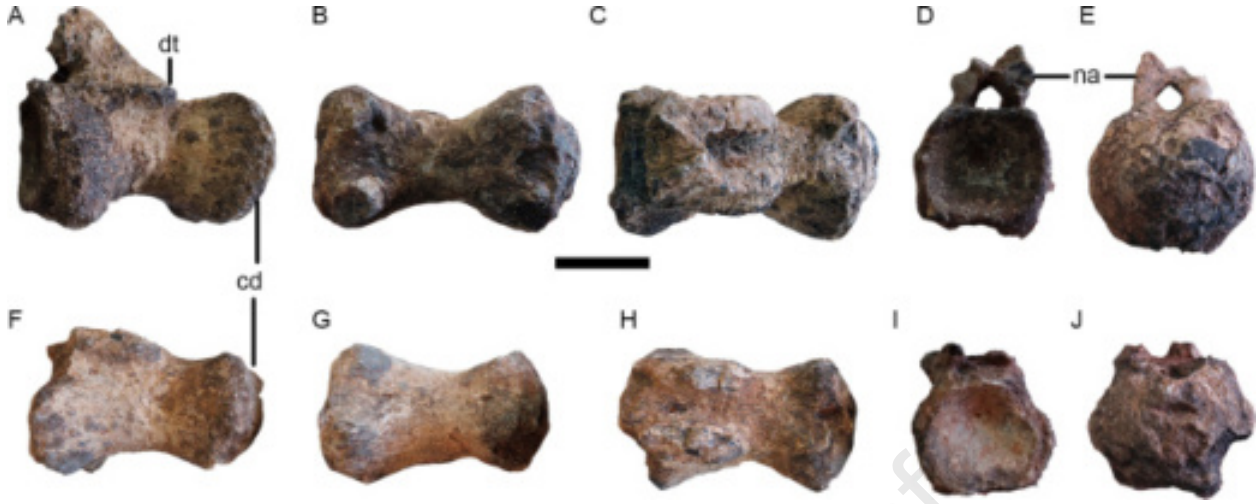

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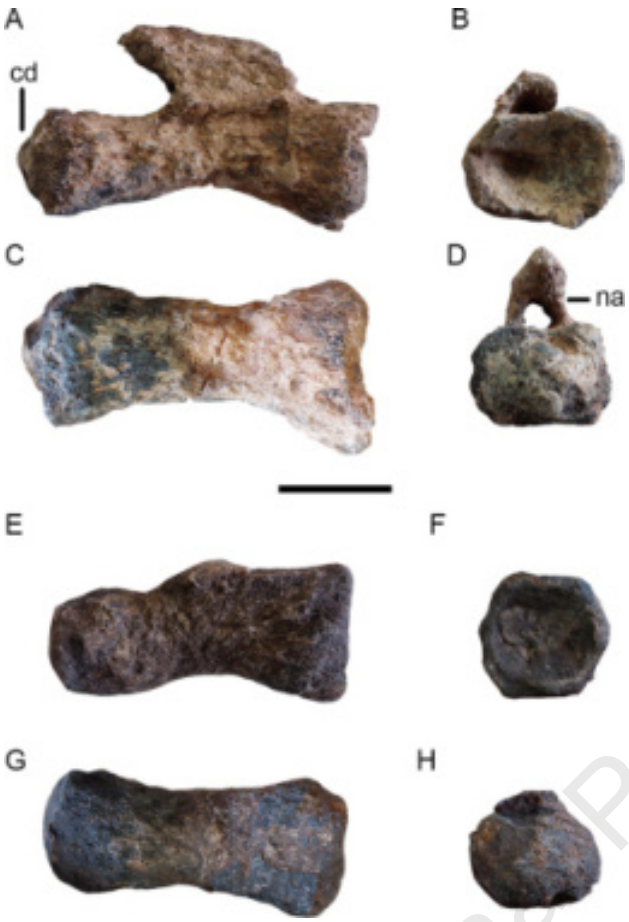

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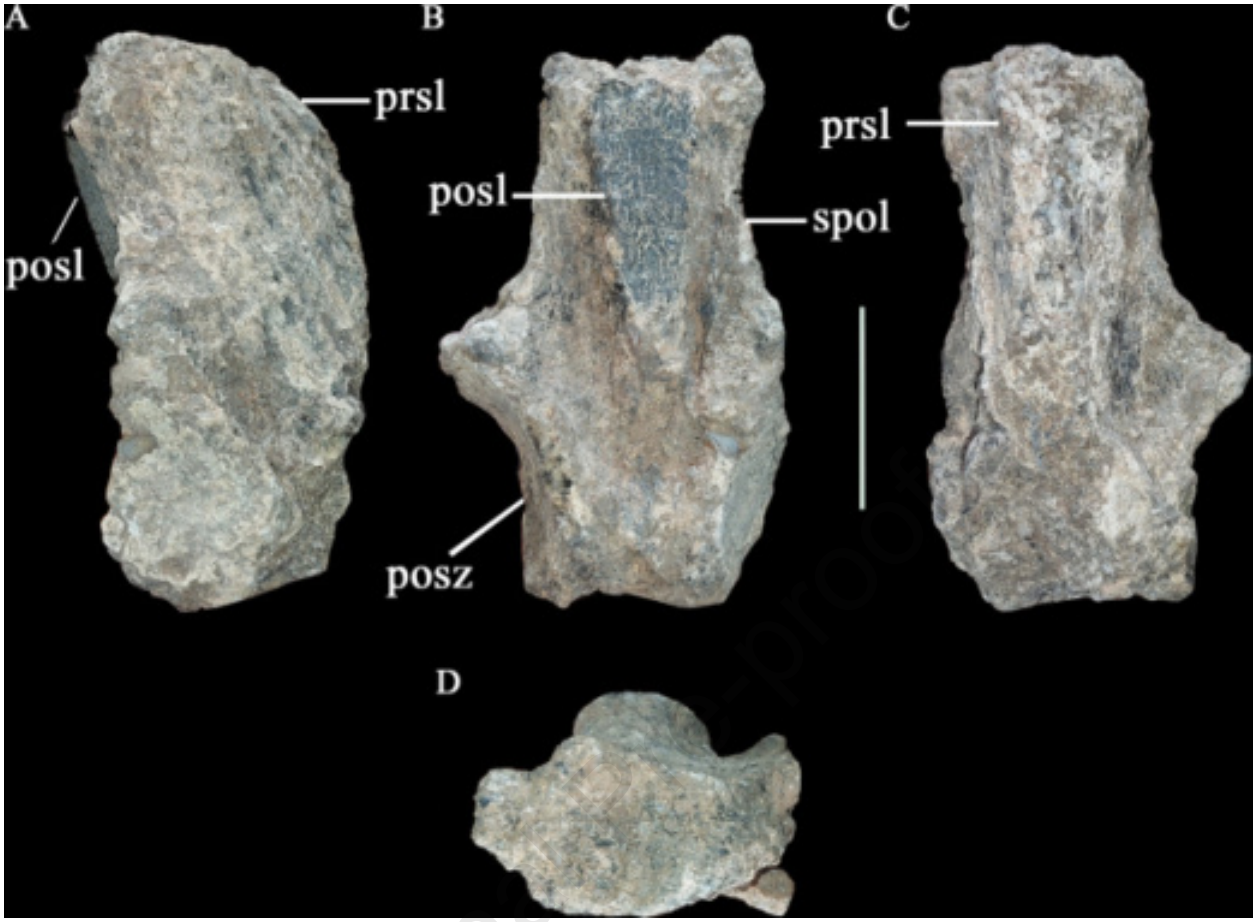

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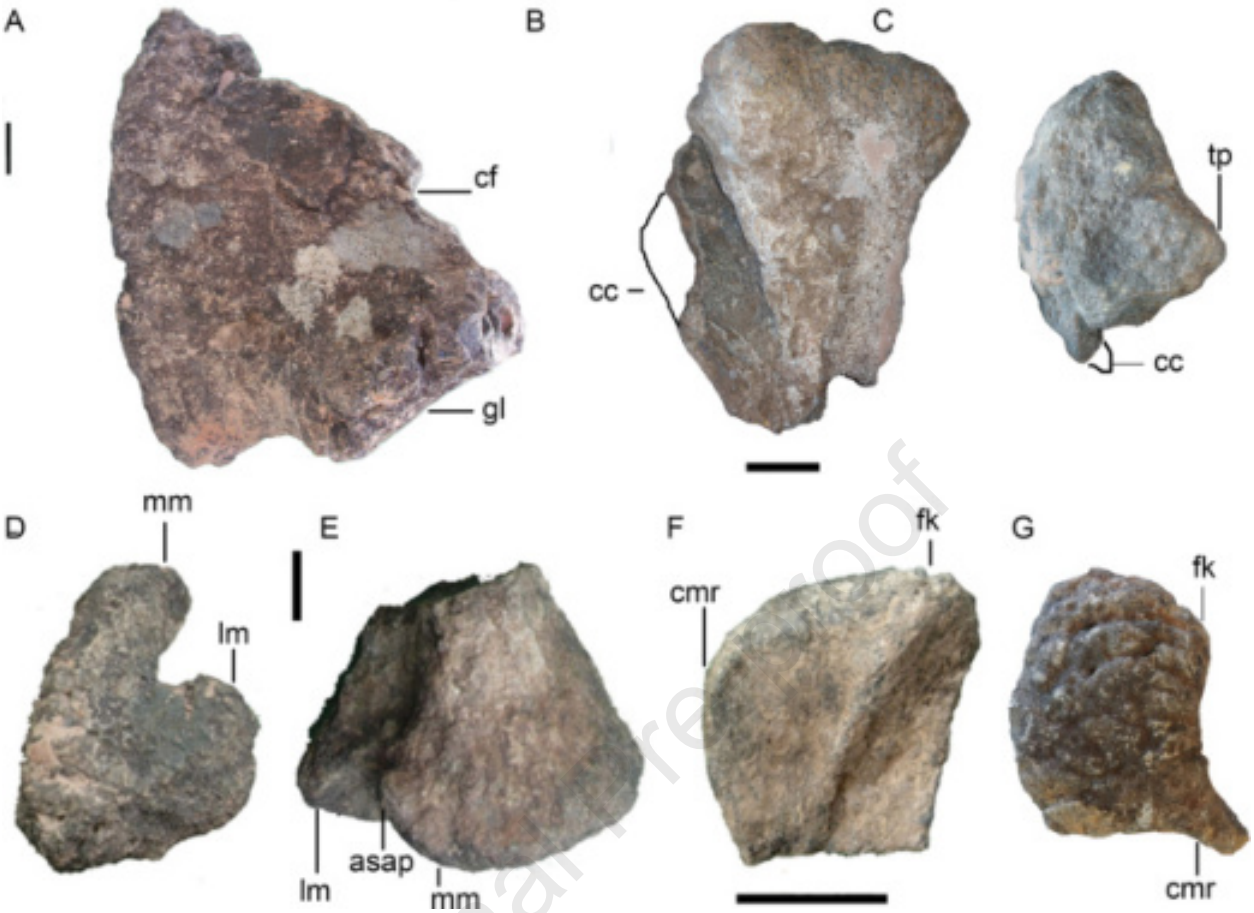

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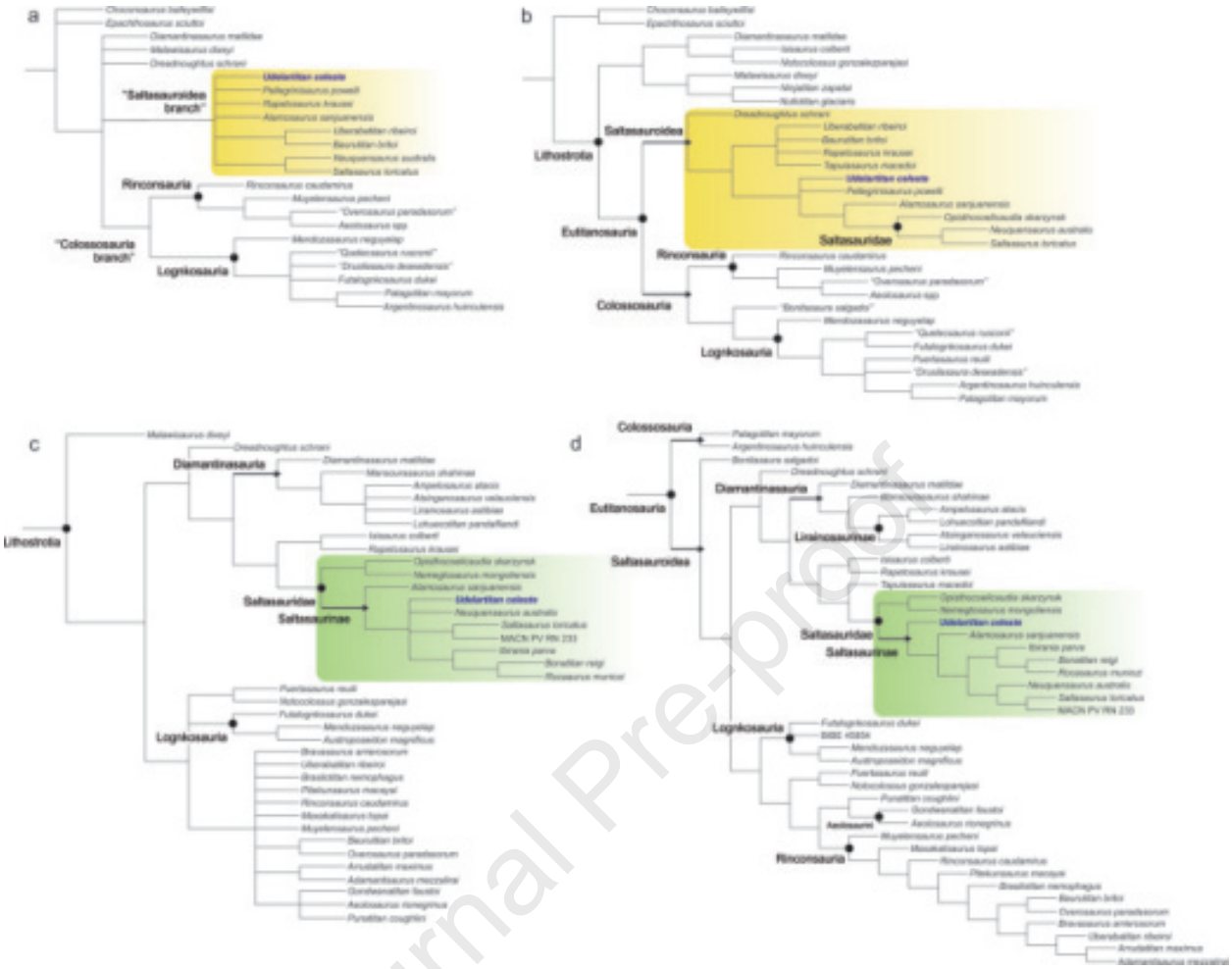

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