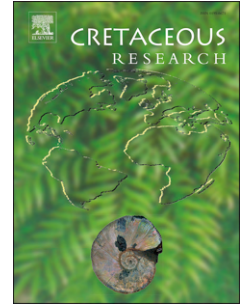


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A rebbachisaurid-mimicking titanosaur and evidence of a Late Cretaceous faunal disturbance event in South-West Gondwana

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AUTHOR STATEMENT

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All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the *Cretaceous Research*.

Authorship contributions

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1 **A rebbachisaurid-mimicking titanosaur and evidence of a Late**
2 **Cretaceous faunal disturbance event in South-West Gondwana**

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25 **Abstract**

26 The evolution of ecosystems during the late Mesozoic on the southern landmasses is
27 complex and still poorly known. Starting from a single vicariant Laurasian-Gondwanan
28 scenario, the paleobiogeographic and biostratigraphic models have become more complex,
29 including vicariant, dispersal, and local extinctions as major drivers of changes in the
30 Cretaceous ecosystems during the isolation and posterior fragmentation of Gondwana.
31 However, the direct effects of replacement and the adaptive evolution of terrestrial
32 vertebrates to fill vacant ecological niches after disruptive ecological events have been
33 poorly discussed. Here, we provide a preliminary description of a nearly complete new
34 titanosaurian sauropod from the Upper Cretaceous of Patagonia, *Inawentu oslatus* gen. et.
35 sp. nov., that shows remarkable convergent anatomical traits with rebbachisaurid
36 sauropods. A phylogenetic analysis recovers it within a not previously recovered
37 titanosaurian subclade, named Clade A, which would be endemic to the Upper Cretaceous
38 of South America. The convergent evolution between rebbachisaurids and Clade A
39 members is interpreted as the result of the same ecological niche exploitation. The
40 biostratigraphic scenario during the Late Cretaceous of South America leads to interpret
41 rapid speciation of the titanosaurs because of filling the empty ecological niche left by the
42 extinction of the rebbachisaurids, an idea concordant with a regional disturbance event of
43 the ecosystems in this continent between 90 and 85 Ma..

44 **Keywords:** Titanosauria, adaptative convergence, Upper Cretaceous, Gondwana.

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50 1. Introduction

51 During the late Mesozoic, sauropod dinosaurs constituted the predominant herbivorous
52 animals in all the non-polar Gondwanan terrestrial ecosystems. With a general bauplan
53 consisting of a quadrupedal and graviportal stance, a proportionally small cranial-to-body
54 ratio, and elongated cervical and caudal series, the sauropods evolved a notable variety of
55 adaptations related to gigantism, locomotion, defense, physiology, and feeding behaviors
56 (Carrano, 2005; Perry et al., 2009; Clauss et al., 2013; Sander, 2013; Bates et al., 2016).
57 They represented the main mid to large-sized herbivorous component of the fauna in most
58 of these southern landmasses, both in diversity and abundance. In this way, it could be
59 expected that the different sauropod clades radiated to cover most of the niche partitioning
60 opportunities, with different strategies from selective to generalists, and from high to low-
61 level browsers. This ecological radiation has been previously proposed for some sauropod
62 clades (Stevens and Parrish, 2005; Whitlock, 2011), and some aspects of this have been
63 discussed previously for Titanosauria (Martínez et al., 2016; Poropat et al., 2021). Among
64 sauropod dinosaurs proposed as low browsers, three distinctive anatomical traits appear to
65 be present: a short and sub-horizontal neck perpendicularly positioned concerning the
66 ground; a broad symphyseal surface of the snout with teeth restricted to the anterior
67 margin; and slender teeth. Diplodocoid sauropods can be considered as the classic low-
68 level browsers, with diplodocids and dicraeosaurids as an abundant component of large
69 herbivorous fauna during the Late Jurassic across North America, Europe, and Gondwana,
70 and also during the earliest Early Cretaceous in western Gondwana (Gallina et al., 2014;
71 McPhee et al., 2016; Gallina et al., 2019). Nevertheless, the archetype of a ground-level
72 browser sauropod is represented by the rebbachisaurids, which survived (and partially
73 replaced) the other families of diplodocoids, becoming an important component of the
74 Cretaceous sauropod faunas in South America, Africa, and Europe until Cenomanian–

75 Turonian times (Lavocat, 1954; Calvo & Salgado, 1995; Bonaparte, 1996; Sereno et al.,
76 1999; Carvalho et al., 2003; Torcida Fernández-Baldor, F. et al., 2011; Mannion et al.,
77 2011; Fanti et al., 2013). The highly derived design present in rebbachisaurids that tended
78 towards low or ground-level browsing adaptations is indicative of feeding specialization,
79 and probably, based on snout shape of *Nigersaurus*, generalist sauropods (Sereno et al.,
80 2007). The diplodocoid extinction, represented by the Rebbachisauridae, may have
81 facilitated the expansion and diversification of derived titanosaurians (Salgado, 2003).
82 After the extinction of rebbachisaurids (Turonian) the diversity of titanosaurs shows a
83 marked increase in its diversity (Mannion et al., 2013). Here we provide a preliminary
84 description of a largely complete new titanosaurian sauropod specimen from the La
85 Invernada area (Rincón de los Sauces, Neuquén, Patagonia Argentina) (Fig. 1), which
86 shows remarkable convergent traits of its skull anatomy with rebbachisaurid sauropods.
87 Exploring the phylogenetic relationships of this titanosaur using cladistic analyses, the new
88 taxon is recovered within a clade of derived titanosaurians, which include already known
89 taxa (e.g., rinconsaurians), some of them sharing these low-browse adaptations.

90 **2. Materials and methods**

91 *2.1 Anatomical abbreviations:* **an**, angular; **aof**, antorbital fenestra; **art**, articular;
92 **bptp**, basipterygoid process; **bt**, basal tuber; **d**, dentary; **en**, external naris; **f**, frontal; **fm**,
93 foramen magnum; **j**, jugal; **la**, lacrimal; **lf**, lacrimal fossa; **ltf**, laterotemporal fenestra; **m**,
94 maxilla; **na**, nasal; **orb**, orbit; **p**, parietal; **pmx**, premaxilla; **po**, postorbital; **pop**,
95 paraoccipital process; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**,
96 surangular; **sq**; squamosal; **so**, supraoccipital; **spl**, splenial; **stf**, supratemporal fenestra.

97 *2.2 Institutional abbreviations:* **CM**– Carnegie Museum of Natural History,
98 Pittsburgh, Pennsylvania, USA; **MAU-Pv** – Museo Municipal Argentino Urquiza, Rincón

99 de los Sauces, Neuquén, Argentina; **MCT** – Museu de Ciências da Terra, Departamento
100 Nacional de Produção Mineral, Rio de Janeiro, Brazil.

101 **3. Geological Setting**

102 The specimen described here (MAU-Pv-LI-595) has been recovered in floodplain from
103 fluvial system deposits belonging to the Bajo de la Carpa Formation (Santonian) (Fig. 1),
104 an integrant unit of the Río Colorado Subgroup, Neuquén Group; from the Upper
105 Cretaceous of the Neuquén Basin (Cazau & Uliana, 1973; Legarreta & Gulisano, 1989;
106 Garrido, 2010). The fossiliferous bearing level is located 11.1 meters below the contact
107 with the overlying Anacleto Formation, over a total thickness measured for the Bajo de la
108 Carpa Formation at the study site of 129.6 meters.

109 Throughout the basin, the Bajo de la Carpa Formation exhibits a multiplicity of
110 paleoenvironments developed under a domain of aeolian and fluvial depositional systems
111 (Garrido, 2010). In the La Invernada-Cerro Overo area, the development of an
112 anastomosed fluvial system characterized by the presence of muddy floodplain and
113 dominant sandy load paleochannels deposits has been established for this unit (Cruzado-
114 Caballero et al., 2018).

115 The recovered skeletal remains were found articulated in a horizon of massive,
116 reddish-colored, edaphized mudstones which are covered by a thin sandy layer
117 (30 centimeters thick) linked to river overbank flooding deposits. The degree of
118 articulation observed in these skeletal remains suggests that the carcass lies closer to the
119 place of death of the animal. The moderate to poor degree of preservation of the bones is
120 attributed to the action of the edaphic processes that affected these deposits during the
121 development of the floodplain, while the missing skeletal pieces have disappeared due to
122 the erosion that affected the outcrops during the last times of the Quaternary.

123 **3. Systematic Paleontology**

124 Sauropoda Marsh, 1878

125 Titanosauria Bonaparte and Coria, 1993

126 Eutitanosauria *sensu* Carballido, Otero, Mannion, Salgado and Pérez-Moreno, 2022

127 *Inawentu oslatus* gen. et. sp. nov.

128 *Etymology.* *Inawentu*, from the Mapundung language ‘*inawentu*’, meaning imitator or
129 mimic; *oslatus*, from the Latin ‘*os*’, mouth, and ‘*latus*’, broad.

130 *Holotype.* MAU-Pv-LI-595 (Fig 2-4). Partially complete and articulated specimen,
131 composed of an almost complete skull, axial sequence from the atlas to the last sacral
132 element, and both ilia.

133 *Diagnosis.* *Inawentu oslatus* gen. et. sp. nov. is a titanosaurian sauropod characterized by a
134 series of autapomorphic characters (marked with *) and a unique combination of
135 characters: **(1)*** posterior region of skull rotated posteroventrally so that it is on the same
136 level as the snout; **(2)*** foramen magnum located subparallel to the tooth row; **(3)** spatulate
137 snout, generated by lateral expansion of the maxillae and dentaries; **(4)*** ridge at the
138 contact between the ascending process and the body of the premaxilla, which generates a
139 prominence in lateral view; **(5)** jugal with a highly elongated maxillary process and a wide
140 and ventrally extended quadratojugal process, **(6)*** a double lateral temporal fenestra
141 formed by an anterior subcircular and a posterior enlarged and laterally compressed
142 opening; **(7)** quadrangular jaw with highly developed lateral expansion; **(8)** dentition
143 restricted to the most anterior border of the maxillae and dentaries; **(9)** anteroposteriorly
144 short jaw that represents half of the total skull length; **(10)*** jaw highest point, twice the
145 height of the dentary, located in the articular sector between the coronoid process and
146 surangular; **(11)** short and slender neck, integrated by 12 cervical vertebrae; and **(12)**
147 anteroposteriorly long and dorsoventrally low ilium.

148 *Locality and Horizon.* The area of La Invernada is located southwest of Rincón de los
149 Saucés city, Neuquén province, Patagonia, Argentina. Bajo de la Carpa Formation
150 (Santonian, Upper Cretaceous), Río Colorado Subgroup, Neuquén Group of the Neuquén
151 Basin (Fig. 1).

152 **4. Description**

153 The skull of *Inawentu* (Fig. 3) resembles the elongated cranial morphology present in
154 some titanosaurs such as *Rapetosaurus* (Curry Rogers & Forster, 2004), *Tapuiasaurus*
155 (Zaher et al., 2011; Wilson et al., 2016), and diplodocoids such as *Nigersaurus* (Serenó et
156 al., 2007), *Diplodocus* (skull CM 11161, McIntosh & Berman, 1975; Tschopp et al., 2015),
157 and *Bajadasaurus* (Gallina et al., 2019), although differing from those “boot-shaped” types
158 that are characteristic of brachiosaurids, such as *Giraffatitan* (Janensch, 1936) and
159 *Abydosaurus* (Chure et al., 2010), some early branching titanosaurs, such as
160 *Sarmientosaurus* (Martínez et al., 2016) and other titanosaurs, such as *Nemegtosaurus*
161 (Wilson, 2005). Additionally, the skull has highly derived characters, including a
162 posteriorly located skull roof, perpendicular to the tooth row (Fig. 3A), which is a feature
163 more pronounced than in *Rapetosaurus*, *Tapuiasaurus*, *Nemegtosaurus*, and
164 *Sarmientosaurus*. Also, the squamosal and quadratojugal are located in a position almost
165 parallel to the longitudinal axis of the skull, accompanied by a strong reduction of the
166 laterotemporal fenestra and an anteroposterior shortening of the jaw, due to the reduction
167 of the angular and surangular (Fig. 3A).

168 The jaw is quadrangular, a shared feature with other titanosaurs, such as *Antarctosaurus*
169 (Huene, 1929), *Bonitasaura* (Apesteguía, 2004; Gallina & Apesteguía, 2011), *Brasilotitan*
170 (Machado et al., 2013), and *Baalsaurus* (Calvo & González Riga, 2019) (Fig. 4). However,
171 the latter taxa are represented by fragmentary specimens that prevent knowing the degree
172 of their skull modifications (except for *Antarctosaurus* which has some parts of the skull).

173 The laterally expanded maxilla of *Inawentu* (Fig. 3B) is similar to that of *Narambuenatitan*
174 (Filippi et al., 2011), which allows us to infer that the latter taxon would have had a similar
175 quadrangular jaw. The new taxon shares with *Rapetosaurus* an anteroposteriorly elongated
176 antorbital fenestra, although in *Inawentu* it is more posterodorsally located and close to the
177 maxilla-lacrima contact (Fig.3A-B). Although the occipital condyle is not preserved, the
178 position of the foramen magnum with respect to the skull roof indicates a highly derived
179 ventral deflection of the snout, as present in the rebbachisaurid *Nigersaurus* (Serenó et al.,
180 2007). The isolated braincases of *Antarctosaurus*, *Saltasaurus* (Powell, 1992, 2003), and
181 *Bonatitan* (Martinelli & Forasiepi, 2004; Salgado et al., 2014) could indicate a similar
182 skull configuration. The quadratojugal shows two ventral hypertrophied structures in its
183 mandibular ramus, homologous to those present in *Tapuiasaurus* and *Nemegtosaurus*, but
184 notably more developed. Besides, the anterior portion of the quadratojugal is
185 dorsoventrally deep, extending dorsally to the contact with the jugal (Fig.3A). The jugal is
186 tetroradiated as in most titanosaurs, although the maxillary process is highly elongated and
187 the quadratojugal process is wide and ventrally extended, a condition not present in other
188 related taxa (e.g., *Nemegtosaurus*, *Rapetosaurus*). A divided laterotemporal fenestra (LTF)
189 is present as in *Tapuiasaurus*, although *Inawentu* shows an anterior subcircular opening
190 and a posterior, laterally compressed, and larger fenestra. In *Tapuiasaurus*, the LTF is 8-
191 shaped, divided by a second postorbital squamosal contact, into a smaller posterodorsal
192 opening and a larger, elongated anteroventral opening (Wilson et al., 2016). *Inawentu*
193 present a LTF divided by a “bone bridge” formed by the contact of the jugal-quadratojugal
194 and jugal-squamosal (Fig.3A).

195 The dentition, is restricted to the most anterior sector of the snout, even more than in the
196 titanosaurids *Nemegtosaurus* and *Tapuiasaurus*, but not as anterior as in the
197 rebbachisaurid *Lavocatisaurus* (Canudo et al., 2018). The snout is markedly transversely

198 wide, developing a spatulate distal morphology (Fig.3A-B). It is wider than the transverse
199 width of the skull at the orbit level, as in *Antarctosaurus* and rebbachisaurid sauropods.
200 The dentaries have a quadrangular L-shaped morphology (Fig.3C and 4A-B), as in some
201 titanosaurs, such as *Antarctosaurus*, *Bonitasaura*, *Brasilotitan*, and *Baalsaurus* (Fig. 4C-
202 F), and in the rebbachisaurids *Lavocatisaurus* and *Nigersaurus*. Both *Inawentu* and
203 *Antarctosaurus* and to a lesser degree, *Brasilotitan* developed a markedly distinctive
204 laterodistal deflection of the tooth row just in the joining zone of the symphyseal portion
205 and the posterior rami of the dentary. This morphology is homologous to that present in
206 the rebbachisaurid *Nigersaurus*. *Inawentu* presents a square jaw with highly developed
207 lateral expansion (Fig.4A-B) which clearly differentiates it from the slight expansion
208 observed in *Antarctosaurus* (Fig.4D). In *Inawentu* the symphyseal sector is relatively
209 robust and wide, similar to *Baalsaurus* and different from *Antarctosaurus* and *Brasilotitan*,
210 which have an anteroposteriorly thinner symphysis. On the other hand, *Inawentu* shares
211 vertical walls with *Antarctosaurus*, *Brasilotitan* and *Baalsaurus*, a condition that
212 differentiates it from *Bonitasaura*, which presents a curved symphyseal sector.
213 The complete neck of *Inawentu* is composed of 12 vertebrae, thus being the titanosaur with
214 the least number of cervical vertebrae known so far. This contrasts with the 17 and 14
215 cervical vertebrae observed in *Rapetosaurus* and *Futalognkosaurus* (Curry Rogers, 2009;
216 Calvo et al., 2007a), respectively. The remaining titanosaurian specimen known with a
217 complete cervical sequence is an unnamed taxon from Brazil (MCT 1487-R) and contains
218 13 cervical vertebrae. The low number of cervical vertebrae and the elongation index (EI=
219 4.3 in C6) in *Inawentu*, results in a proportionally shorter neck than that of other
220 titanosaurs such as *Futalognkosaurus* and *Rapetosaurus*. The cervical ribs were preserved
221 in almost complete articulation. These are relatively short, and their posterior ends reach
222 the posterior edge of the centrum of the subsequent vertebra (Fig. 5B), a condition that is

223 observed in the anterior cervical vertebrae. Thus, the length of the cervical ribs is lesser
224 than that observed in titanosauriforms, in which these elements extend up to three
225 vertebrae posteriorly (Cerda, 2009). This feature is reminiscent of the anteroposteriorly
226 short cervical ribs of most diplodocimorphs. The cervicodorsal vertebrae have highly
227 modified centra and neural arches and are interpreted as a pivotal point enabling
228 multidirectional movement for the entire neck.

229 Except for the atlas-axis (Fig.5A), C11 and C12 (Fig. 5C), the other cervical vertebrae are
230 morphologically similar (Fig.5 B), showing opisthocoelous centra, a slightly
231 anteroposteriorly concave ventral surface, with slightly excavated lateral surface. The
232 cervical vertebrae lack the two different PODL segments present in *Bonitasaura* (Gallina
233 & Apesteguía, 2015; Fig. 3C). The C11 and C12 are different morphologically from the
234 remaining cervical vertebrae and they also differ from each other (Fig. 5C). The C11 has
235 an anteroposteriorly elongated centrum with an anteroposteriorly concave ventral surface
236 like the preceding cervical vertebrae, although it is transversely wider. The neural spine of
237 C11 is very prominent, located at the level of the middle of the vertebral centrum, tilted
238 slightly posteriorly, and the neural spine has lateral expansions that resemble those present
239 in *Futalognkosaurus*, *Mendozasaurus* (González Riga, 2005), and *Bonitasaura*. Overall,
240 the C12 is similar to the C11, except that in C12 the centrum is shorter anteroposteriorly,
241 the neural arch is higher, with pre and postzygapophyses at the same level, and the neural
242 spine is slenderer and anteroposteriorly more compressed. The C12 lacks a ventral keel or
243 a ventral pneumatic fossa, such as that present in the last cervical vertebra of *Overosaurus*
244 (Coria et al., 2013).

245 As in other titanosaurs, the dorsal series of *Inawentu* is composed of ten opisthocoelous
246 vertebrae with acuminate lateral pleurocoels. The first dorsal vertebra has the most
247 anteroposteriorly elongated centrum, with elongated and laterally projected transverse

248 processes. As in *Bonitasaura*, the neural spine of the first dorsal vertebra is dorsoventrally
249 tall, unlike the vertically shortened neural spine of *Overosaurus*. The inclination of the
250 neural spine serially varies in *Inawentu*, it is sub-vertically oriented in the anteriormost
251 dorsal vertebrae, then progressively projects backward in the middle dorsals, and it returns
252 to a vertical orientation in the posteriormost elements. Although this variation in neural
253 spine angle is observed in some titanosaurs, it is more similar to that of *Bonitasaura*
254 (Gallina, 2011), *Trigonosaurus* (Campos et al., 2005), and *Overosaurus*, than in
255 *Rapetosaurus*, *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), and the saltosaurines.
256 The sacrum consists of six vertebrae and has a similar morphology to that of other
257 titanosaur sauropods, with the exception of *Neuquensaurus* (Salgado et al., 2005) which
258 has seven sacral vertebrae. The last sacral centrum has a convex posterior surface, and
259 consequently, the first caudal centrum (not preserved) must have been procoelous. The
260 first sacral vertebra has a delicate rib, similar to the last dorsal ribs, which rests on the
261 anterior edge of the ilium as in *Overosaurus*, *Trigonosaurus*, and *Futalognkosaurus*.
262 Although they are incomplete, the sacral ribs of S6 possibly did not come into direct
263 contact with the ilia. Instead, the S6 sacral ribs appear to be articulated both with the fifth
264 sacral ribs and to the ilium, as in *Overosaurus*, *Trigonosaurus*, and *Malawisaurus*
265 (Gomani, 2005). The pubic and ischial pedicel of the ilium are not preserved. The iliac
266 blade is well expanded anteroposteriorly as in other titanosaurs, but the lateral projection
267 of the preacetabular process is less prominent than in *Saltasaurus* and *Neuquensaurus*,
268 which have laterally wider hips.

269 **5. Phylogenetic Analysis**

270 To elucidate the phylogenetic placement of *Inawentu*, and other related forms among the
271 titanosaurian sauropods, we generated a new dataset primarily derived from that of Gallina
272 et al. (2021). This dataset (see Supp. Data) was modified increasing in several cranial

273 characters and taxa-preserving cranial elements to highlight morphological differences
274 among titanosauriforms and titanosaurians in particular. The resultant dataset is composed
275 of 421 characters and 98 operational taxonomic units. The analysis was carried out using
276 the software T.N.T. 1.5 (Goloboff and Catalano, 2016). Characters were ordered as in the
277 original analysis. The chosen parameters included the tree bisection and reconnection
278 algorithm (TBR), with 1000 replications of Wagner trees and 10 trees saved per
279 replication. This procedure retrieved 890 most parsimonious trees (MPTs) of 1521 steps
280 (CI: 0.34; RI: 0.71), found in 89 of the replicates. The strict consensus shows *Inawentu* as
281 a sister taxon to *Antarctosaurus* within an unresolved group, which includes titanosaurs
282 forms from the Turonian-Maastrichtian time lapse (Supplementary Information Fig. S2).
283 In a second analysis using the TNT command “*Pruned trees*”, seven unstable taxa are
284 eliminated allow improving relationships within unresolved group, positioning to
285 *Uberabatitan* as a sister taxon to *Brasilotitan* (Supplementary Information Fig. S3).
286 Finally, a majority rule consensus was made (+50) (Supplementary Information (Fig. S4),
287 where *Inawentu* is recovered as a deeply nested titanosaur in close association with several
288 Late Cretaceous taxa from South America that share a derived squared mandibular shape,
289 such as *Antarctosaurus* and *Bonitasaura* (Fig. 4). These three taxa form the sister group of
290 a clade that includes other squared-snout titanosaurs. i.e., *Narambuenatitan* and
291 *Brasilotitan*, and Rinconsauria plus Aeolosaurini (Fig. 6). The latter two clades, however,
292 do not preserve cranial elements (except *Muyelensaurus*) and are characterized by mid-to-
293 small-sized and slender bodies. The new topology recovered a clade of square-jawed
294 titanosaurian taxa, here named Clade A, supported by three synapomorphies (Ch. 99-2,
295 tooth rows, shape of anterior portions: rectangular, tooth-bearing portion of jaw
296 perpendicular to jaw rami; Ch. 100-3, tooth rows, length: restricted anterior to subnarial
297 foramen; and Ch. 415-0, ilium, postacetabular posteroventral edge: open concave).

298 Consequently, these results show a novel distant relationship between Lognkosauria and
299 Rinconsauria in a database that is mainly focused on South American taxa (contrasting
300 with the results of Carballido et al., 2017; and Gonzalez Riga et al., 2019). A similar
301 topology is only recovered in Gorscak & O'Connor (2016) and subsequent phylogenetic
302 results obtained from that dataset, which also includes several African and European taxa.
303 On the other hand, in Mannion et al. (2019b), *Antarctosaurus* is recovered in a clade with
304 the Rinconsauria. Although defined in different ways (node based vs. stem-based),
305 Lognkosauria clusters the same taxa as Colossosauria in this phylogeny, similarly to the
306 results obtained by Pérez-Moreno et al., 2022. Besides, the new topology recovered
307 Colossosauria (Lognkosauria + Rinconsauria) outside of Lithostrotia such as the analyses
308 by Pérez-Moreno et al. (2022), which differs from previous analyses (González Riga et al.,
309 2019; Hechenleitner et al., 2020; Gallina et al., 2021). In our analysis, the Clade A is
310 composed of a subclade integrated by two branches, one containing *Bonitasaura* as the
311 sister taxon of *Inawentu* plus *Antarctosaurus*. The second includes *Narambuenatitan* and a
312 series of derived taxa, as the other squared-jaw *Brasilotitan* and several forms which have
313 an unknown snout shape, such as *Uberabatitan* (Salgado & De Souza Carvalho, 2008),
314 *Muyelensaurus* (Calvo et al., 2007b), *Rinconsaurus* (Calvo & González Riga, 2003),
315 *Overosaurus*, *Trigonosaurus*, and *Arrudatitan* (Silva Junior et al., 2021) (Fig. 6). *Inawentu*
316 includes some anatomical traits shared with both *Antarctosaurus* and *Bonitasaura*.
317 *Antarctosaurus* and *Inawentu* overlap part of the skull, and *Bonitasaura* and *Inawentu*
318 overlap in the skull, cervical and dorsal vertebrae. Nevertheless, based on the few
319 comparable materials between these three taxa, such as the dentary, a more similar
320 morphology is observed between *Inawentu* and *Antarctosaurus* than *Bonitasaura*. An
321 example of this is the development of the anterolateral corner of the dentary (character
322 421). Another taxon known by very fragmentary cranial material, *Baalsaurus*, was also

323 included in a posteriori analysis since it presents a derived squared dentary and represents
324 the oldest known evidence of this morphology in the fossil record, as it is found in
325 Coniacian strata (Calvo & González Riga, 2019). *Baalsaurus* is recovered within Clade A
326 in the strict consensus analysis, although the precise placement of this taxon within the
327 clade remains uncertain. Its inclusion generates a clade that is only supported by a single
328 character (character 99).

329 **6. Discussion**

330 The Clade A consisting in a group of deeply nested titanosaurs that were restricted to the
331 last stages of the Late Cretaceous in South America. The discovery of new materials and
332 different data sets that provide new morphological information will allow us to provide
333 better support in future phylogenies that confirm the presence of this clade of square-jawed
334 titanosaurs.

335 *Inawentu* and probably other members of this clade, possess apparent trophic adaptations
336 seen in the preceding rebbachisaurid sauropods, such as a broad snout and a relatively
337 short neck. In this context, the shortened cervical series of *Inawentu* could be in
338 concordance with low-browsing feeding behavior. This would have paleoecological
339 implications, such as a faunistic turnover in post-Turonian times in the Gondwanan
340 continental ecosystems and low-browsing dietary habits in two different lineages of
341 sauropod dinosaurs.

342 Among deeply nested sauropods, i.e., the Neosauropoda, two principal lineages diverged
343 near the Lower to Middle Jurassic: the macronarians and the diplodocoids (Xu et al.,
344 2018). These are abundant components in the Late Jurassic faunas in North America,
345 Europe, Africa, and South America (Marsh, 1884; Rauhut et al., 2015; Mannion et al.,
346 2017, 2019a). These Late Jurassic sauropod faunas are indicative of the existence of niche
347 partition preferences between the low-browser feeder diplodocoids and the higher-browser

348 basal macronarians and basal titanosauriforms (Whitlock, 2011). The cranial morphology
349 of the basal macronarians and basal titanosauriforms (Janensch, 1936; Madsen et al., 1995;
350 Marpmann et al., 2015; Chure et al., 2010; Moore et al., 2018; D’Emic & Carrano, 2020)
351 is plesiomorphic and more reminiscent to that of other clades of non-neosauropod
352 eusauropods (Ouyang & Ye, 2002; Royo-Torres & Upchurch, 2012; Poropat & Kear,
353 2013). In contrast, diplodocids were highly modified in their cranial morphology, as
354 evidenced in the relative position of the occipital condyle with respect to the tooth row, the
355 position of the nares, the slender tooth morphology, and the teeth placement in the front of
356 the snout (Holland, 1906; Berman & McIntosh, 1978; Whitlock et al., 2010; Tschopp &
357 Mateus, 2017; Woodruff et al., 2018).

358 During the Early Cretaceous, the diplodocoids appear to have been globally restricted to
359 Europe and Gondwana (Africa and South America). At this time, the three diplodocoid
360 families of the group, i.e., the diplodocids, the dicraeosaurids, and the rebbachisaurids
361 were present in at least the first stages of the Early Cretaceous (Calvo & Salgado, 1995;
362 Haluza et al., 2012, Ibiricu, et al., 2012, 2013; McPhee et al., 2016; Bellardini et al.,
363 2022). After the Barremian, the rebbachisaurids are the only surviving family of
364 low-browsing diplodocoid sauropods, reaching Turonian times (Gallina & Apesteguía,
365 2005; Haluza et al., 2012; Ibiricu et al., 2013; Bellardini et al., 2022). On the other hand,
366 the titanosauriforms are broadly present in the known faunal contents of large landmasses.

367 During the early Late Cretaceous (Cenomanian–Turonian) the rebbachisaurids appear to
368 be restricted to Africa and South America, which possibly corresponds to a relictual
369 presence of the family in both landmasses since they drifted and reached a complete
370 separation at the Cenomanian times. This could have favored the appearance of
371 independent and vicariant lineages, although both, Africa and South America, suffered
372 sporadic exchanges with other continental masses during the rest of the Cretaceous

373 (McLoughlin, 2001; Ezcurra & Agnolín, 2012; Sallam et al., 2018). The last records of
374 Rebbachisauridae in South America are dated from the early Turonian, following a
375 regional extinction (Calvo et al., 2006; Ibiricu et al., 2020). This extinction event appears
376 to have affected multiple components of the tetrapod fauna of South America, including
377 not only rebbachisaurids but also basal lineages of titanosauriform sauropods (e.g.,
378 *Andesaurus*, *Epachthosaurus*), multiple lineages of theropods, such as spinosaurids,
379 carcharodontosaurids, bahariasaurids, elaphrosaurines, and non-furileusaurian abelisaurids;
380 and the uruguaysuchid and candidodontid crocodylomorphs (Apesteguía, 2002; Coria &
381 Salgado, 2005; Novas, 2009; Novas et al., 2005, 2013; Delcourt et al., 2020; Meso et al.,
382 2021). The change between the “mid-Cretaceous” (Albian-Cenomanian) and post-Turonian
383 vertebrate assemblage, is identified as a major faunal turnover (Kause et al., 2020). In turn,
384 multiple adaptive radiations are recorded in the derived titanosaurs, such as the major
385 diversification of large-body sized lognkosaurians, the small-body sized saltasaurines, and
386 the square-jawed titanosaurs such as *Baalsaurus* and *Inawentu* (Fig. 6). Adaptive
387 radiations also are observed between the megaraptorids and furileusaurian theropods, and
388 the deeply nested notosuchians, peirosaurids, and sebecosuchian crocodylomorphs (Calvo
389 et al., 2019; Baiano et al., 2022). As previously proposed, the extinction of the large
390 herbivorous and carnivorous dinosaurs from South America and Africa appears to be
391 synchronic, but it can be likely an artifact since in Africa there is a very scarce post-
392 Cenomanian fossil record. Before *Inawentu* (Fig. 7) discovery, the extreme adaptations in
393 the snout and neck it was just reported for non-titanosaur rebbachisaurid. So, perhaps the
394 empty niche that rebbachisaurids left (ground-level browsers with quadrangular snout) was
395 rapidly occupied by some lineages of titanosaurs, here named clade A. Although is evident
396 a faunistic replacement event followed by radiation adaptive events, it remains obscure
397 the causes of the fauna changes.

398

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412 **Description of cranial material *Diamantinasaurus matildae* published after the**
413 **conclusion of this study**

414 Posterior to the finalization of this manuscript has been published the description of cranial
415 material of the basal titanosaur *Diamantinasaurus matildae* (Poropat et al., 2023). It
416 displays a suit of anatomical characters that are congruent with those of basal titanosaurs
417 as *Sarmientosaurus* and *Choconsaurus*, but contrast with the derived morphology present
418 in *Inawentu* and their close relatives as *Antarctosaurus*, *Muyelensaurus* or *Bonitasaura*.
419 Although *Diamantinasaurus* is not included in the present phylogenetic analysis, the
420 proper analysis of these authors is not in conflict with our results, displaying
421 *Diamantinasaurus* as a basal member of the group closely related with another ‘Middle’
422 Cretaceous taxa from Australia and southern South America and recovering an unnamed

423 clade including Rinconsauria and Aelosaurini, including *Antarctosaurus* within this last
424 group. We believe that future works, some of these currently under development by some
425 of the current authors, should include more taxa and characters in order to test our results
426 and those of another authors.

427 **Data Availability**

428 The holotype of *Inawentu oslatus* gen. et. sp. nov. is deposited in the collections of the
429 Museo Municipal Argentino Urquiza in the city of Rincón de Los Sauces, Argentina. This
430 published work and the nomenclatural acts it contains have been registered in ZooBank:
431 [http://zoobank.org/urn:lsid:zoobank.org:pub:88A2ED2E-3EDF-4AE2-85F3-](http://zoobank.org/urn:lsid:zoobank.org:pub:88A2ED2E-3EDF-4AE2-85F3-02281760CF28)
432 [02281760CF28](http://zoobank.org/urn:lsid:zoobank.org:pub:88A2ED2E-3EDF-4AE2-85F3-02281760CF28). Additional data, such as additional phylogenetic data matrix, are in the
433 Supplementary Information.

434 **Authors' Contributions**

435 L. S. Filippi: Conceptualization; funding acquisition; investigation, methodology; writing,
436 review, and editing; R. D. Juárez Valieri: Conceptualization; phylogenetic analysis;
437 investigation; writing, review, and editing; P. A. Gallina: Investigation; writing, review,
438 and editing; A. H. Méndez: Image processing, writing, review, and editing; F.A.
439 Gianechini: Image processing, writing, review, and editing; A. C. Garrido: Geological
440 analysis, writing, review, and editing.

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743 **Figure captions**

744 **Figure 1.** Map showing the location of the La Invernada fossil site. The red star indicates
745 the provenance of the holotype of *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595).
746 Location map based on satellite image acquired from Google Earth (9 Jun 2021; Data SIO,
747 NOAA, US Navy, NGA, GEBCO; Image Landsat/Copernicus).

748 **Figure 2.** Articulated holotype of *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595) in
749 left lateral view. (A), skull; (B), atlas and axis; (C), cervical vertebrae from C3 to C10; (D),
750 posterior cervical vertebrae C11-C12; (E), dorsal vertebrae from D1 to part of D9; (F),
751 posterior dorsal vertebrae from part of D9 and D10, complete sacrum (S1-S6), and left ilium.
752 Scale bars for A–F: 10 cm. Scale bar for the silhouette: 1 m.

753 **Figure 3.** Skull of *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595) in left lateral (A),
754 dorsal (B), and ventral (C) view. Diagonal lines represent zones covered with sediment and
755 grey zones are reconstructed parts. Scale bar: 10 cm.

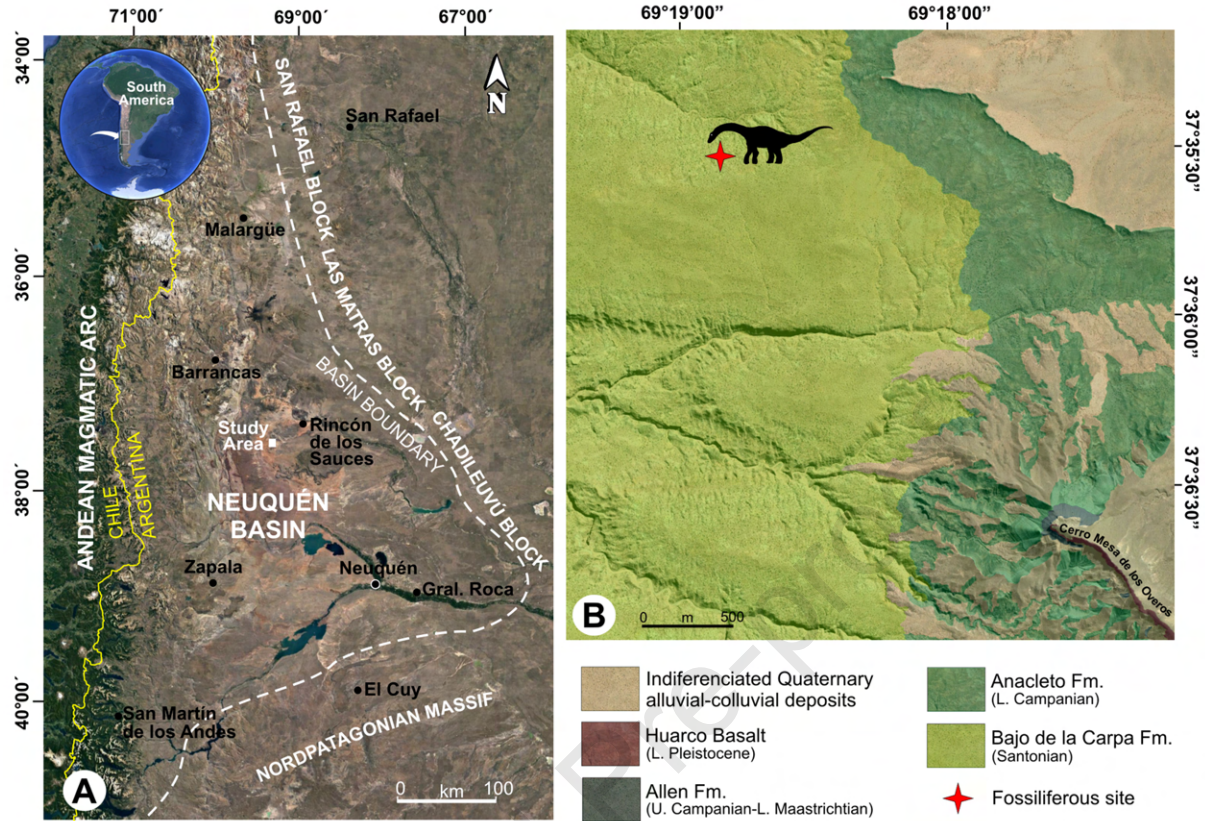
756 **Figure 4.** Compared jaws of basally branching titanosaurs of Clade A, in dorsal view.
757 *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595) (A and B); *Brasilotitan* (C);
758 *Antarctosaurus* (D); *Bonitasaura* (E); and *Baalsaurus* (F). The black arrow indicates the
759 portion of the dentary displaced from its original position. The images are not in scale.

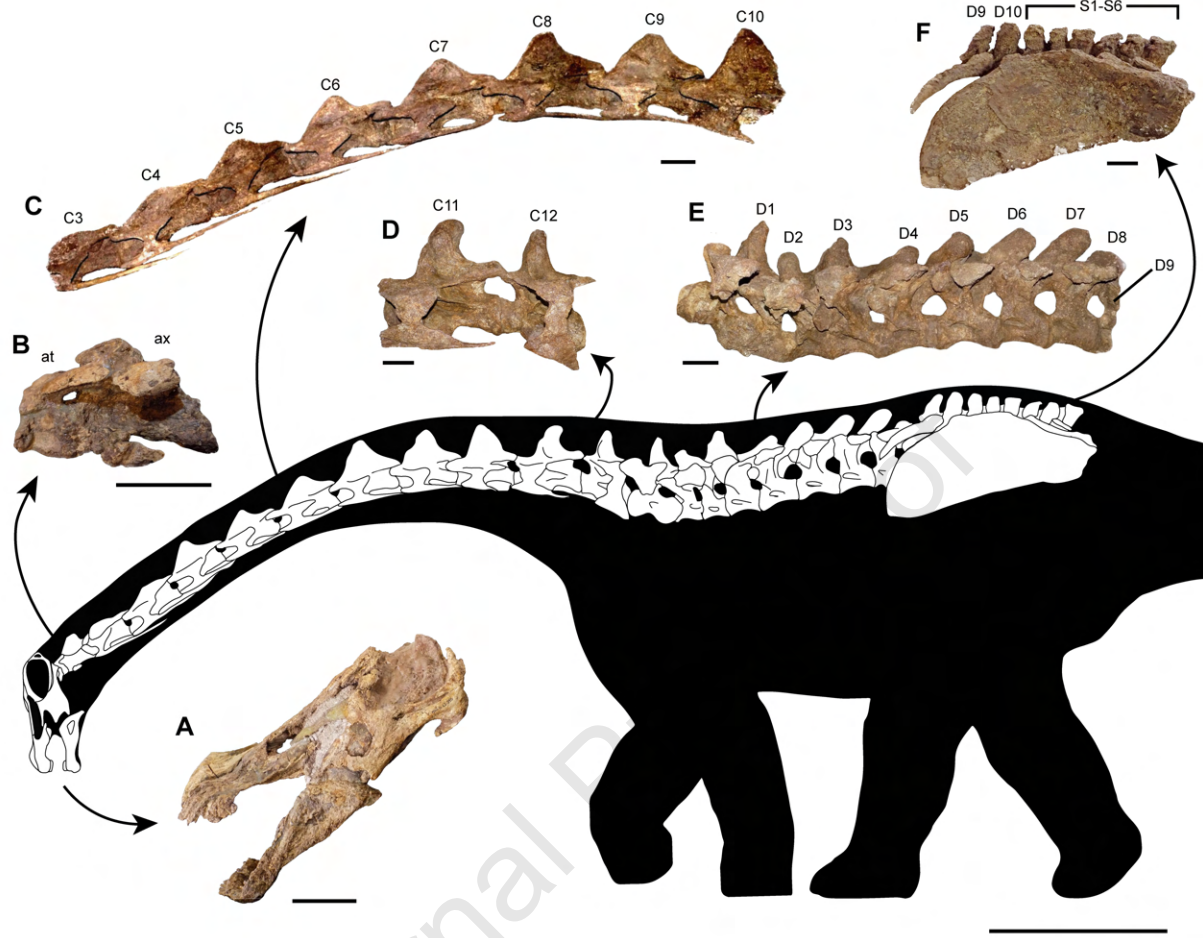
760 **Figure 5.** Cervical vertebrae of *Inawentu oslatus* gen. et sp. nov. (A), Atlas (C1) and Axis
761 (C2); (B), Cervical C4 and C5; (C), Cervical C11 and C12. Anatomical abbreviations: **At**,

762 Atlas; **Ax**, Axis; **ce**, centrum, **cr**, cervical rib; **ic**, intercentrum; **ns**, neural spine; **pa**,
763 parapophysis; **podl**; postzygodiapophyseal lamina; **pos**, postzygapophysis; **pre**,
764 prezigapophysis; **tp**, transverse process. Scale bar: 10 cm

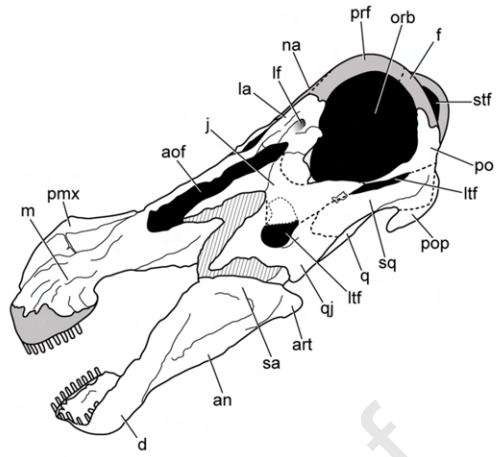
765 **Figure 6.** Phylogenetic relationships of *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595).
766 Time-calibrated simplified majority rule (+50%) consensus tree. **L**, Lower; **U**, Upper; **Alb**,
767 Albian; **Apt**, Aptian; **Bar**, Barremian; **Ber**, Berriasian; **Cam**, Campanian; **Cen**,
768 Cenomanian; **Con**, Coniacian; **Hau**, Hauterivian; **Maa**, Maastrichtian; **San**, Santonian; **Tur**,
769 Turonian; **Vlg**, Valanginian. The titanosaur's jaw images (*Rapetosaurus* is reversed) are not
770 in scale.

771 **Figure 7.** Life reconstruction of *Inawentu oslatus* gen. et sp. nov. (MAU-Pv-LI-595).
772 Illustration by Gabriel Lío.

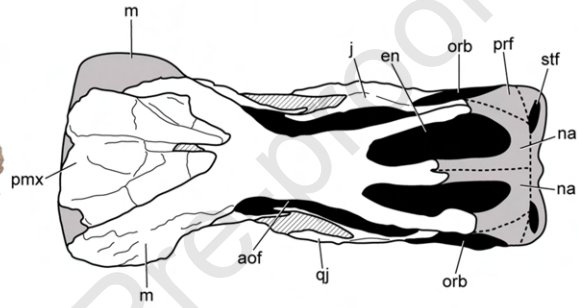




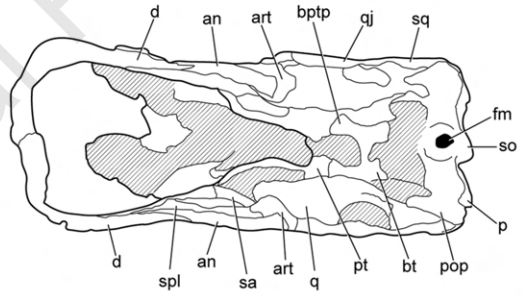
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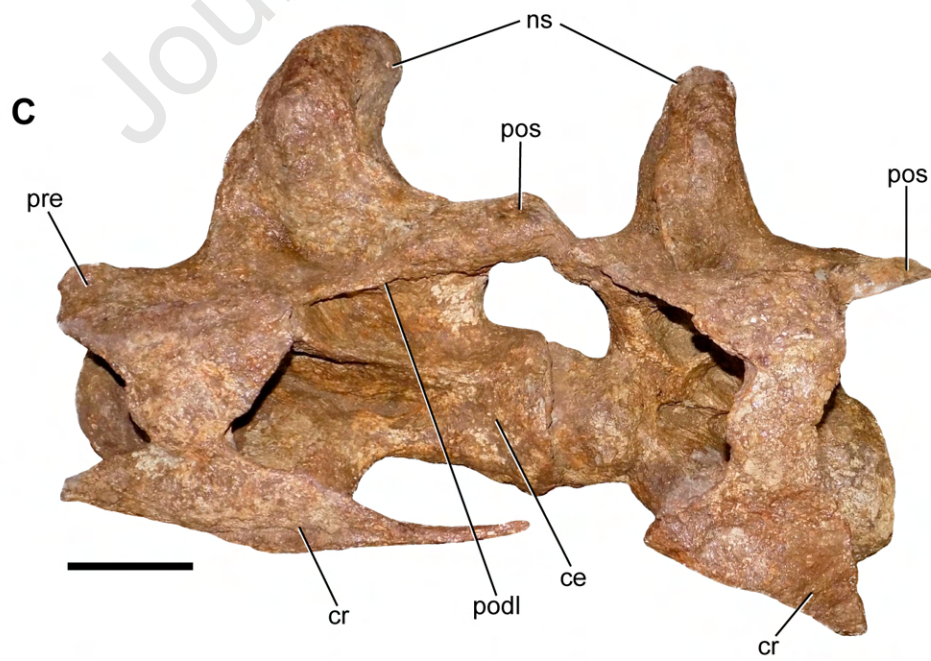
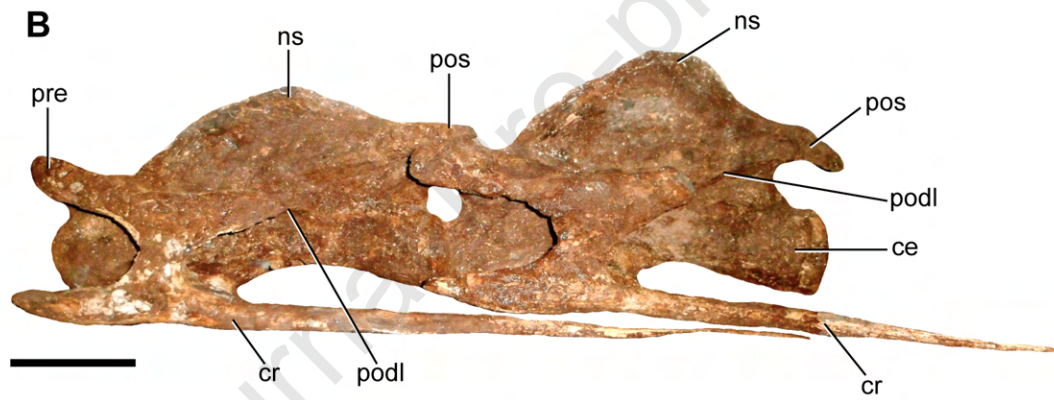
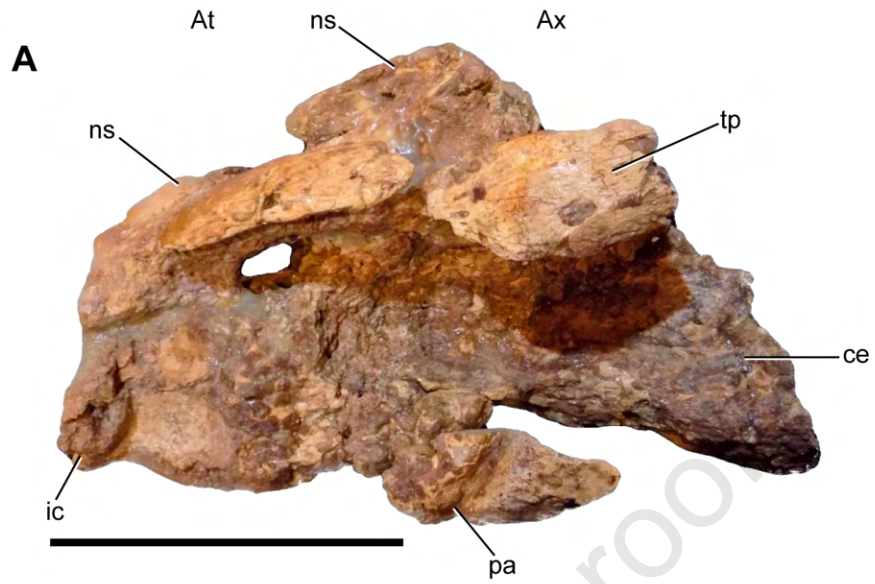


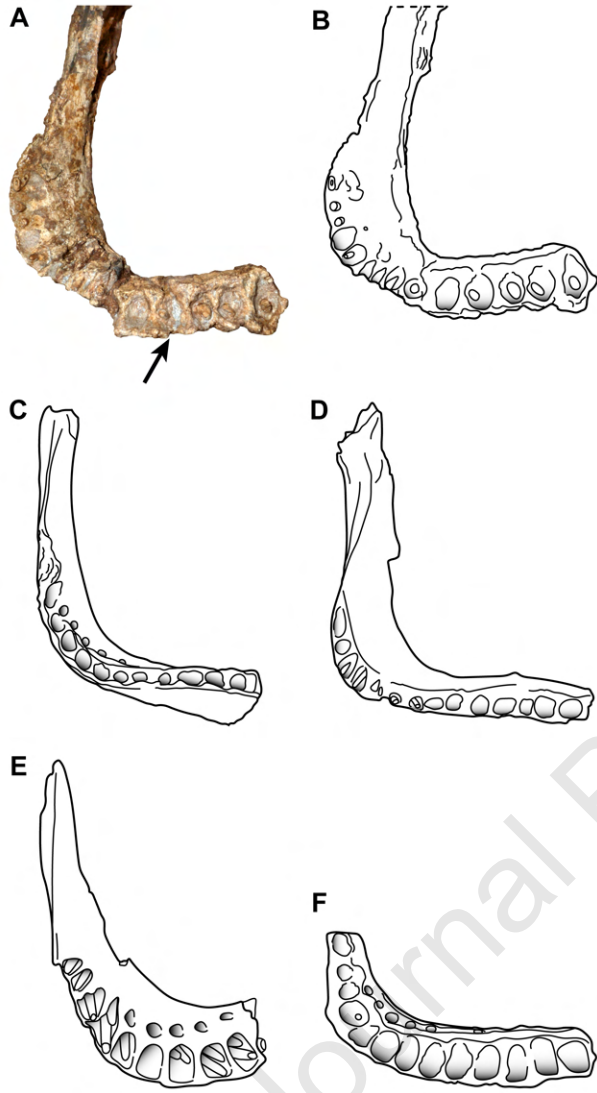
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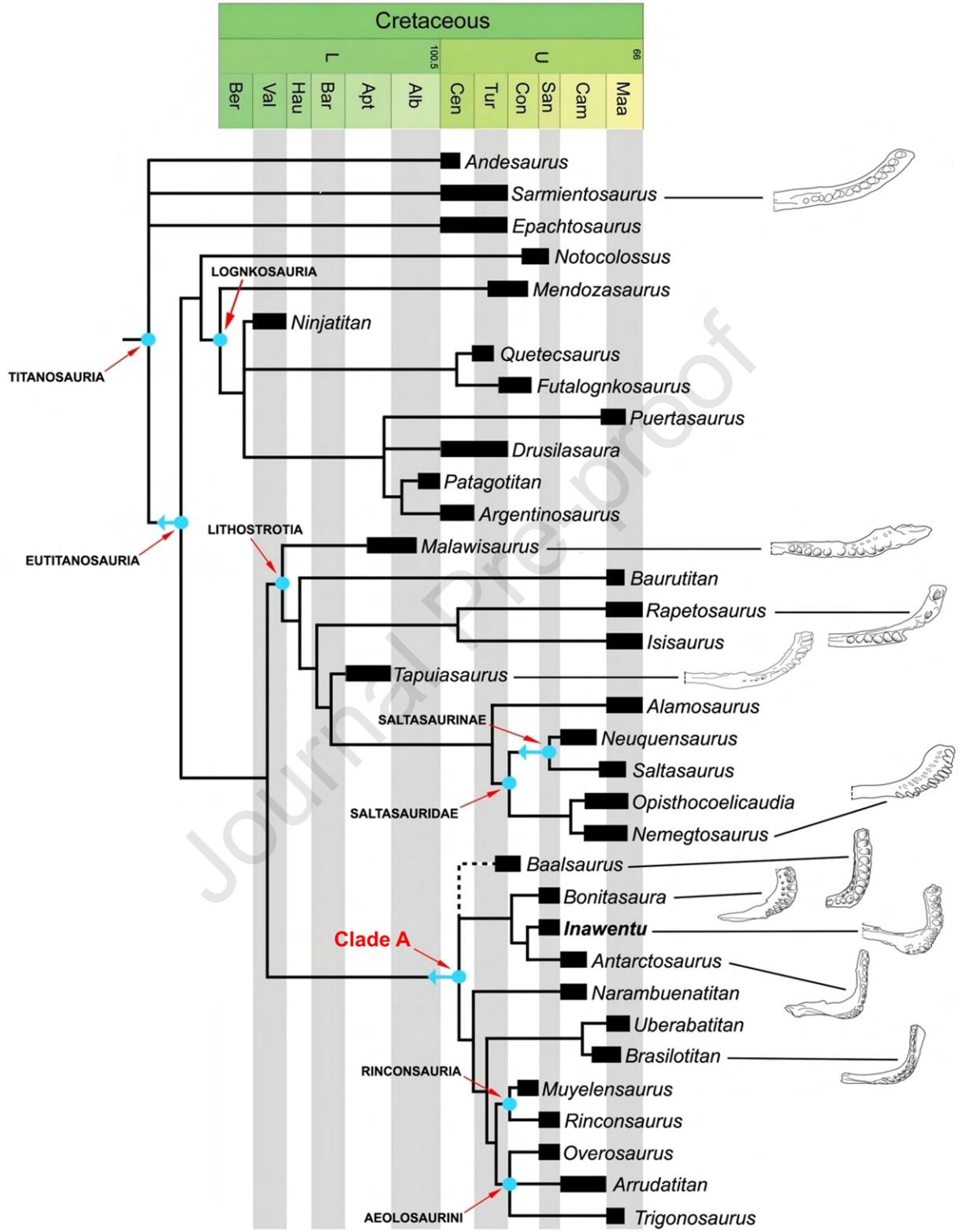


C











Journal Pre-proof

Highlights

- Preliminary description of nearly complete new titanosaurian sauropod from the Late Cretaceous of Patagonia.
- Presence in *Inawentu* of convergent anatomical traits with rebbachisaurid sauropods.
- Phylogenetic analysis recovers a new topology of a probable natural square-jawed titanosaur clade, called Clade A.
- The convergent evolution between rebbachisaurids and basal Clade A members, is interpreted as the result of the same ecological niche exploitation.

DECLARATION OF INTEREST STATEMENT

Manuscript title:

A rebbachisaurid-mimicking titanosaur and evidence of a Late Cretaceous faunal disturbance event in South-West Gondwana

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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