

Sauropod diversity (Dinosauria: Sauropoda) of Cerro Overo – La Invernada (Bajo de la Carpa Formation, Santonian), northeastern Neuquén Basin, and paleoecological implications for Upper Cretaceous sauropod faunas

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SAUROPOD DIVERSITY (DINOSAURIA: SAUROPODA) OF CERRO OVERO – LA INVERNADA (BAJO DE LA CARPA FORMATION, SANTONIAN), NORTHEASTERN NEUQUÉN BASIN, AND PALEOECOLOGICAL IMPLICATIONS FOR UPPER CRETACEOUS SAUROPOD FAUNAS

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Abstract. The Upper Cretaceous fossil vertebrate fauna of the Bajo de la Carpa Formation (Santonian), derived from several different locations in the Neuquén Basin, is relatively abundant and diverse, comprising mainly small to medium-sized reptiles, birds and fishes. The Cerro Overo – La Invernada locality (CO – LI), in the north of the basin, records a similar faunal component for that age, but stands out for its relatively greater abundance and diversity of titanosaur sauropods. The study of the materials presented here allows us to establish the presence of specimens of sauropods other than *Overosaurus*, the only titanosaur recorded so far in the area, the coexistence of small–medium sized forms with larger forms, which in turn represent some forms with more basal characteristics and others with more derived features. The abundance of the record of sauropods in CO – LI shows both morphological and evolutionary variations, so the discovery of more complete specimens will allow paleofaunistic, paleobiological, and paleoecological studies to be carried out. This will provide a better understanding of the role of titanosaurian sauropods in Late Cretaceous ecosystems.

Key words. Sauropoda. Titanosauria. Diversity. Upper Cretaceous. Neuquén Basin.

Resumen. DIVERSIDAD DE SAURÓPODOS (DINOSAURIA: SAUROPODA) DE CERRO OVERO – LA INVERNADA (FORMACIÓN BAJO DE LA CARPA, SANTONIANO), NOROESTE DE LA CUENCA NEUQUINA E IMPLICACIONES PALEOBIOLOGICAS DE LA FAUNA DE SAURÓPODOS DEL CRETÁCICO SUPERIOR. La fauna de vertebrados fósiles del Cretácico Superior proveniente de la Formación Bajo de la Carpa (Santoniano) de diferentes localidades de la Cuenca Neuquina, es relativamente abundante y diversa; está compuesta principalmente por formas de reptiles, aves y peces de pequeño y mediano tamaño. La localidad de Cerro Overo – La Invernada (CO – LI), en el norte de la cuenca, registra para dicha edad, un componente faunístico similar, pero destacándose por una abundancia y diversidad relativamente mayor de saurópodos titanosaurios. El estudio de los materiales presentados aquí permite establecer la presencia de especímenes de saurópodos diferentes a *Overosaurus*, el único titanosaurio registrado hasta el momento en el área, y la coexistencia de formas de pequeño-mediano tamaño con formas más grandes, que representan a su vez algunas formas con características más basales y otras con rasgos más derivados. La abundancia del registro de saurópodos en CO – LI muestra variaciones tanto morfológicas como evolutivas, por lo que el hallazgo de ejemplares más completos permitirá llevar adelante estudios paleofaunísticos, paleobiológicos y paleoecológicos. Esto brindará una mejor comprensión del papel de los saurópodos titanosaurios en los ecosistemas del Cretácico Superior.

Palabras clave. Sauropoda. Titanosauria. Diversidad. Cretácico Superior. Cuenca Neuquina.

CERRO OVERO – LA INVERNADA is a large area near Rincón de los Sauces city (Neuquén Province, Argentina) (Fig. 1), where the continental sediments of the Bajo de la Carpa Formation with a Santonian age (Upper Cretaceous) are exposed. The outcrops of this formation are exposed in different areas of northern Argentinean Patagonia and have shown to have one of the greatest diversity of Cretaceous vertebrates registered in Argentina (Bonaparte, 1991; Calvo & González Riga, 2003; Apesteguía, 2004; Turner & Calvo, 2005; Fiorelli & Calvo, 2007; Ezcurra & Méndez, 2009; Gianechini *et al.*, 2011; Juárez Valieri & Calvo, 2011; Martinelli *et al.*, 2012; Filippi *et al.*, 2015; Porfiri *et al.*, 2018; Lío *et al.*, 2018; Coria *et al.*, 2019). The faunal component of the different localities of the Neuquén Basin where the Bajo de la Carpa Formation crops out and fossil vertebrates have been recorded, corresponds to small-bodied forms such as the theropod dinosaurs *Alvarezsaurus calvoi* (Bonaparte, 1991) and *Velocisaurus unicus* (Bonaparte, 1991), *Achillesaurus*

manazzonei (Martinelli & Vera, 2007), enantiornithine birds such as *Neuquenornis volans* (Bonaparte, 1991) and *Patagopteryx deferrariisi* (Alvarenga & Bonaparte, 1992), crocodyliforms such as *Notosuchus terrestris* (Smith-Woodward, 1896), *Cynodontosuchus rothi* (Smith-Woodward, 1896), *Comahuesuchus brachybuccalis* (Bonaparte, 1991), *Peirosaurus tormini* (Gasparini *et al.*, 1991), *Neuquensuchus universitas* (Fiorelli & Calvo, 2007), *Wargosuchus australis* (Martinelli & Pais, 2008), and *Barrosasuchus neuquenianus* (Coria *et al.*, 2019), snakes such as *Dinilysia patagonica* (Smith-Woodward, 1901), chelid turtles such as *Lomalatachelys neuquina* (Lapparent de Broin & de la Fuente, 2001) and dipnoan fish such as *Ceratodus kaopen* (Apesteguía *et al.*, 2007), and to a lesser extent by medium-sized forms such as the sauropod dinosaurs *Bonitasaura salgadoi* (Apesteguía, 2004) and *Rinconosaurus caudamirus* (Calvo & González Riga, 2003), theropod such as *Tratayenia rosalesi* (Porfiri *et al.*, 2018), and crocodyliforms such as *Pehuenchesuchus enderi*

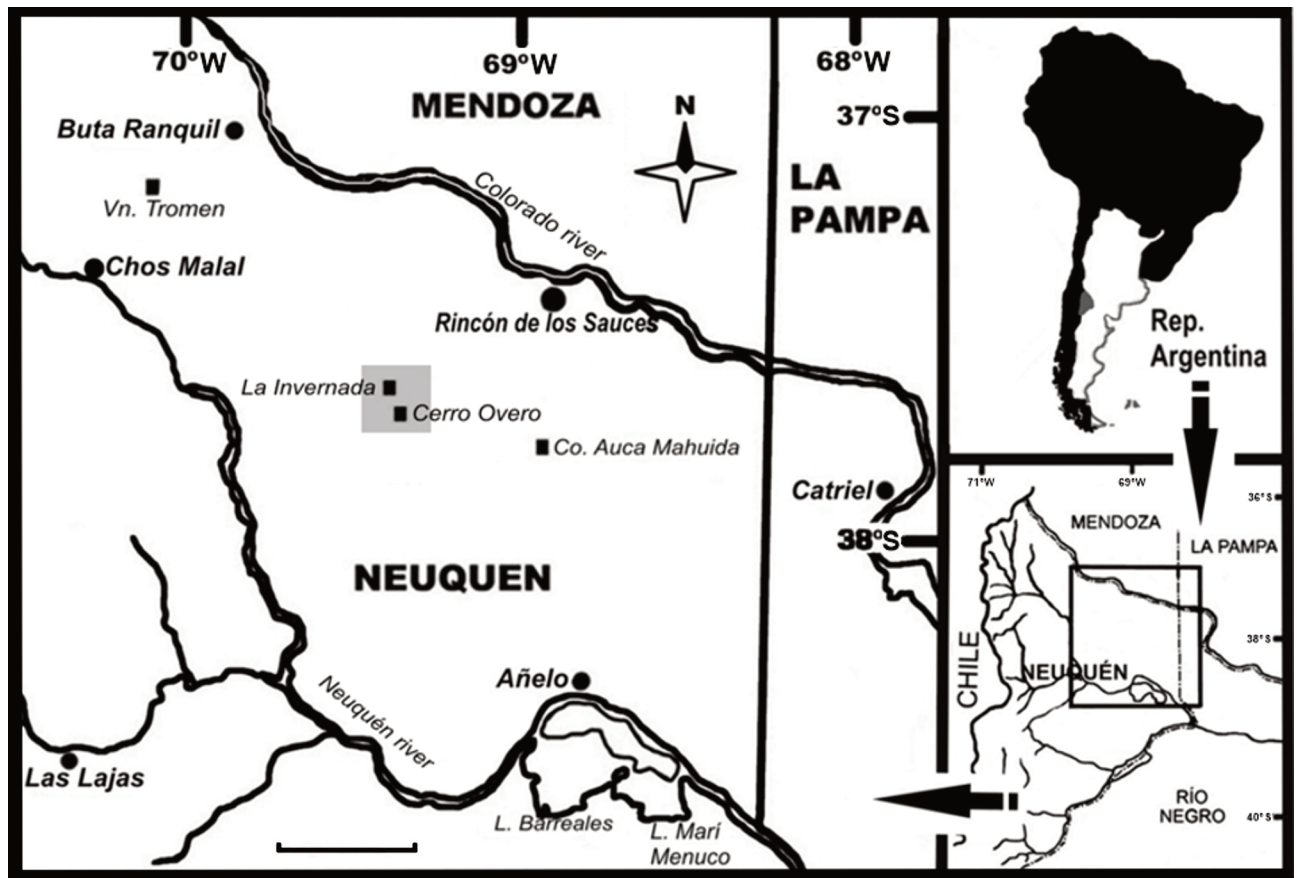


Figure 1. Map showing the location of Cerro Overo – La Invernada (CO – LI) fossil area. Scale bar= 100 km.

(Turner & Calvo, 2005). The CO – LI locality yielded a great diversity of vertebrates including medium-sized theropods (*Viavenator exxoni* Filippi *et al.*, 2016; *Llukalkan aliocranianus* Gianechini *et al.*, 2021), ornithopod (*Mahuidacursor lipanglef* Cruzado-Caballero *et al.*, 2019), and sauropod (*Overosaurus paradasorum* Coria *et al.*, 2013), crocodiles (*Kinesuchus overoi* Filippi *et al.*, 2018), small-sized forms such as dipnoan fishes (*Rinconodus salvadori* Panzeri *et al.*, 2022) and chelidae turtles (under study). Presently, all known sauropod dinosaurs from the Bajo de la Carpa Formation are members of Colossosauria, a clade recently redefined by Carballido *et al.* (2022) as a stem lineage formed by titanosaurs closely related to *Patagotitan mayorum* (Carballido *et al.*, 2017) than to *Saltasaurus loricatus* (Bonaparte & Powell, 1980), most probably representing two lineages of this clade. *Bonitasaura* (Apesteguía, 2004) and *Traukutitan* (Juárez-Valieri & Calvo, 2011) are considered members of Lognkosauria (although the latter has never been included in a phylogenetic analysis), whereas *Overosaurus* (Coria *et al.*, 2013) is considered as an aeolosaurian, a derived lineage of Rinconsauria (Coria *et al.*, 2013; Filippi *et al.*, 2019; Silva Junior *et al.*, 2019; Hechenleitner *et al.*, 2020; Gallina *et al.*, 2021). Despite the diverse vertebrate record from the CO – LI locality, and despite the fact that in most continental Cretaceous outcrops from Patagonia are dominated by sauropods, to this point only the aeolosaurine *Overosaurus* has been reported from this unit. Explorations and fieldwork carried out over the space of more than a decade, enabled the recovery of numerous titanosaur sauropod remains from this locality.

The materials described here, although isolated, show the great diversity of titanosaur forms that probably co-existed in the area during the Santonian Stage. Thus, the described materials contribute to improving the knowledge of the evolution of the Cretaceous ecosystems, at least in this area of Patagonia.

GEOLOGICAL SETTING

The materials described come from the CO – LI area, located 50 km southwest of Rincón de los Sauces (Fig. 1), Neuquén Province, Patagonia, Argentina. The outcrops are assigned to the Bajo de la Carpa Formation, Río Neuquén Subgroup, Upper Cretaceous (Santonian). At its base, this

formation conformably overlies the Plottier Formation of the older Río Neuquén Subgroup, and it is in turn overlain by the Anacleto Formation, the youngest and uppermost formation of the Neuquén Group. The aforementioned formation is composed by thick beds of medium to fine grained size sandstones and interbedded red massive mudstones, interpreted as anastomosed fluvial system deposits (Méndez *et al.*, 2015; Cruzado-Caballero *et al.*, 2018).

MATERIALS AND METHODS

Materials studied. The materials used in this research are as follows: Three isolated teeth (MAU-Pv-LI-645, MAU-Pv-LI-646 and MAU-Pv-CO-650), a partial ?anterior cervical vertebra (MAU-Pv-LI-602), a partial middle-to-posterior dorsal vertebra (MAU-Pv-CO-671), a complete first caudal vertebra (MAU-Pv-LI-670), a partial anterior caudal vertebra (MAU-Pv-CO-407), a partial anterior caudal vertebra with proximal hemal fragments (MAU-Pv-LI-601), a partial distal-most anterior caudal centrum (MAU-Pv-LI-669), a sequence of six articulated middle caudal vertebrae and three hemal arches (MAU-Pv-LI-600) and a partial posterior caudal centrum (MAU-Pv-CO-668).

Anatomical terminology. Anatomical terminology used here follows traditional or 'Romerian' directional terms (*e.g.*, posterior, anterior) for skeletal structures (Wilson, 2006). The nomenclature for vertebral laminae follows Wilson (1999) and the nomenclature for vertebral fossae follows Wilson *et al.* (2011).

Numerical indices. Three numerical indices have been used; the aEI, the CI, and the SI. The average elongation index (**aEI**; *sensu* Chure *et al.*, 2010), calculated as the centrum anteroposterior length (excluding articular ball) divided by the mean average value of the posterior articular surface mediolateral width and dorsoventral height, is considered here instead the elongation index, since this can be influenced by the compaction of the remains. Compression Index (**CI**, *sensu* Díez Díaz *et al.*, 2013b), is calculated as the maximum labiolingual width divided by the maximum mesiodistal width of the crown. Slenderness Index (**SI**, *sensu* Díez Díaz *et al.*, 2013b), calculated as the length of the tooth crown divided by its maximum mesiodistal width, as defined by Upchurch (1998).

Institutional abbreviations. MAU-Pv-CO, Colección Paleon-

tología de Vertebrados Cerro Overo, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina; **MAU-Pv-CRS**, Colección Paleontología de Vertebrados Cañadón Río Seco, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina; **MAU-Pv-LI**, Colección Paleontología de Vertebrados Loma del Lindero, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina; **MLP**, Museo de La Plata, La Plata, Buenos Aires, Argentina; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina.

Anatomical abbreviations. **ACDL**, anterior centrodiapophyseal lamina; **ACPL**, anterior centroparapophyseal lamina; **CPAF**, centroparapophyseal fossa; **CPOF**, centropostzygapophyseal fossa; **CPOL**, centropostzygapophyseal lamina; **cr**, cervical rib; **CPRF**, centroprezygapophyseal fossa; **LCPOL**, lateral centropostzygapophyseal lamina; **PACDF**, parapophyseal centrodiapophyseal fossa; **PCDL**, posterior centrodiapophyseal lamina; **PCPL**, posterior centroparapophyseal lamina; **POCDF**, postzygocentrodiapophyseal fossa; **PODL**, postzygodiapophyseal lamina; **POSL**, post-spinal lamina; **PRDL**, prezygodiapophyseal lamina; **PRSL**, prespinal lamina; **SDF**, spinodiapophyseal fossa; **SPDL**, spinodiapophyseal lamina; **SPOF**, spinopostzygapophyseal fossa; **SPOL**, spinopostzygapophyseal lamina; **SPRF**, spinoprezygapophyseal fossa; **SPRL**, spinoprezygapophyseal lamina; **STPOL**, single intrapostzygapophyseal lamina; **TPOL**, intrapostzygapophyseal lamina; **TPRL**, intraprezygapophyseal lamina.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

SAUROPODA Marsh, 1878

TITANOSAURIFORMES Salgado *et al.*, 1997

SOMPHOSPONDYLI Wilson & Sereno, 1998

Somphospondyli indet.

Figure 2.1–2.4

Material. Isolated tooth MAU-Pv-LI-645 (Fig. 2.1–4).

Description. The material is represented by the tooth MAU-Pv-LI-645 (Morphotype 1) which is robust, with a

lingually beveled crown in its distal third, showing a sub-cylindrical shape in cross-section. In the crown, the lingual surface is slightly flat, whereas the labial surface is convex. This tooth is similar in shape to the teeth of some basal somphospondylians (*e.g.*, *Ligabuesaurus leanzai* Bonaparte *et al.*, 2006) and basal titanosaurs, especially members of Colossosauria (*e.g.*, *Patagotitan* Carballido *et al.*, 2017, *Bonitasaura* Apesteguía, 2004), and differing from the fully circular teeth of the Morphotype 2 (MAU-Pv-LI-646 and MAU-Pv-CO-650) and most members of Saltasaurioidea (*e.g.*, *Tapuiasaurus macedoi*, *Nemegtosaurus mongoliensis*, *Rapetosaurus krausei*, *Lirainosaurus astibiae*; Nowinski, 1971; Sanz *et al.*, 1999; Curry Rogers & Forster, 2001; Zaher *et al.*, 2011). The tooth has longitudinal mesiodistal carinae that delimit the labial face from the lingual one that extend to the apex of the tooth, as in *Antarctosaurus* sp. (Huene, 1929), *Rinconsaurus* (Calvo & González Riga, 2003), *Bonitasaura*, and *Alamosaurus sanjuanensis* (Gilmore, 1922). *Pitekunsaurus macayai* (Filippi & Garrido, 2008) has longitudinal carinae similar to MAU-Pv-LI-645, but they are less marked. In mesiodistal view, the carinae are centered on the tooth in MAU-Pv-LI-645, as in *Bonitasaura*, differing from the lingually displaced carinae observed in *Rinconsaurus* and *Pitekunsaurus* (Filippi & Garrido, 2008). The enamel is well preserved, showing several longitudinal ridges that form rough ornamentation on both labial and lingual surfaces. A single lingual wear facet is present in the tooth MAU-Pv-LI-645, which is clearly recognized given the curvature of its crown.

TITANOSAURIA Bonaparte & Coria, 1993

EUTITANOSAURIA Sanz *et al.*, 1999

Eutitanosauria indet.

Figure 2.5–2.12

Material. Isolated teeth MAU-Pv-LI-646 and MAU-Pv-CO-650 (Fig. 2.5–12).

Description. The material is represented by the teeth MAU-Pv-LI-646 and MAU-Pv-CO-650 (Morphotype 2), which are slightly smaller than MAU-Pv-LI-645, with straight, slender crowns, circular in cross-section, and without carinae on their mesial and distal edges. Although the enamel is not

well preserved, it has smooth surfaces without ornamentation. The absence of wrinkled patterns could reflect a high degree of wear in these teeth. The SI of morphotype 2 teeth is slightly higher than 4, but was probably higher given the degree of wear, while the CI is 1. Following García & Cerda (2010) single and planar wear facets are present in both teeth. MAU-Pv-CO-650 presents two wear facets, the smaller one is here tentatively considered as being on the lingual surface, whereas the larger one is labially located. By contrast MAU-Pv-LI-646 has a single wear facet located on the lingual side.

Comments. According to the general morphology, two morphotypes are recognized amongst the preserved teeth (Morphotype 1, represented by MAU-Pv-LI-645, and Morphotype 2, represented by MAU-Pv-LI-646 and MAU-Pv-CO-650), being the three teeth interpreted as functional teeth due to the presence of apical wear facets on them. We consider MAU-Pv-LI-645, MAU-Pv-LI-646, and MAU-

Pv-CO-650 as narrow crowned (Barrett & Upchurch, 2005) and pencil chisel-like teeth (*sensu* Calvo, 1994), a common shape among diplodocoids (e.g., *Diplodocus* Marsh, 1878; *Dicraeosaurus* sp. Janensch, 1914, *Nigersaurus taqueti* Sereno et al., 1999, *Lavocatisaurus agrioensis* Canudo et al., 2018) and derived titanosaur sauropods (e.g., *Bonitasaura*, *Rinconosaurus*, *Pitekunsaurus*, *Nemegtosaurus*, *Rapetosaurus*, *Antarctosaurus* sp.). Amongst titanosaurs, basal forms such as *Sarmientosaurus musacchioi* (Martínez et al., 2016) and *Diamantinasaurus matildae* (Hocknull et al., 2009; Poropat et al., 2022, 2023), present broad-crowned and compressed cone-chisel-like teeth (*sensu* Calvo, 1994), with sub-cylindrical teeth with relatively low SI (around 3). Our morphotype 1 has a sub-cylindrical shape with a SI higher than 4 and a CI of 0.44, which are more derived characters among titanosaurs. Similar shaped and slender teeth are common amongst relatively basal titanosaurs and members of Colossosauria (e.g., *Patagotitan* [SI= 3.4; CI= 0.8], *Quetecsaurus rusconii* González

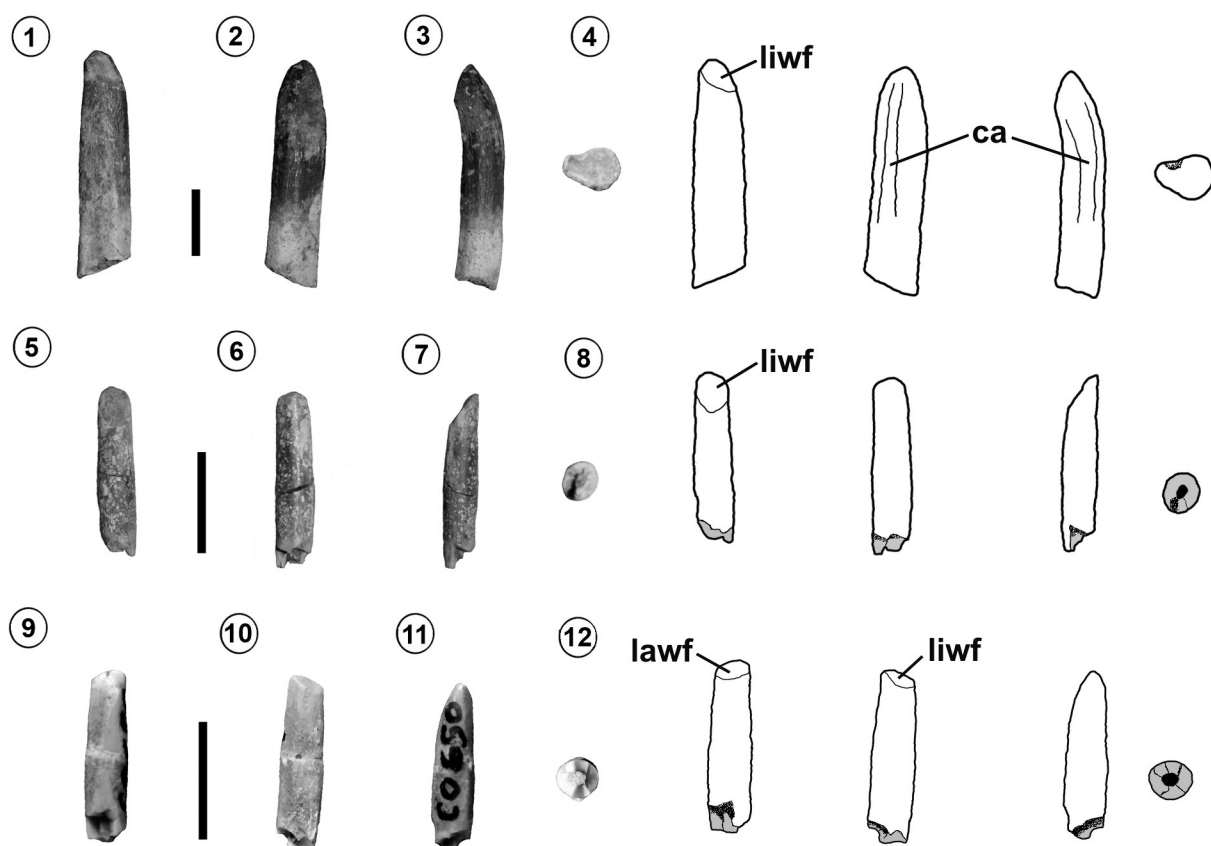


Figure 2. Sauropod teeth MAU-Pv-LI-645, MAU-Pv-LI-646 and MAU-Pv-CO-650 in 1, 5, 9, lingual; 2, 6, 10, labial; 3, 7, 11, lateral; and 4, 8, 12, transversal views. Scale bar= 1 cm. Anatomical abbreviations: ca, carena; lawf, labial wear facet; liwf, lingual wear facet.

Riga & Ortiz, 2014 [SI= 4.3; CI= 0.9]). Additionally, MAU-Pv-LI-645 shares the presence of mesiodistal carinae with some titanosaurs such as *Antarctosaurus* sp. and *Rinconosaurus* but differs from the more derived saltasauroid titanosaurs (Apesteguía, 2004). On the contrary, morphotype 2, with its cylindrical crowns and absence of carena, shares these characters with derived members of Saltasauroida and differs from more basal titanosaurs (e.g., *Rapetosaurus* [SI= 7.8, CI= 1], *Lirainosaurus* [SI= 3.78, CI= 0.91]). Therefore, although both teeth are assigned to Titanosauria indet, morphotype 2 presents some characteristics that allow a more precise assignment to more derived members of Saltasauroida.

TITANOSAURIFORMES Salgado *et al.*, 1997

SOMPONDYLI Wilson & Sereno, 1998

Somphospondyli indet.

Figure 3

Material. Partial ?anterior cervical vertebra MAU-Pv-LI- 602 (Fig. 3).

Description. This cervical vertebra is almost complete, lacking part of the anterior articular surface, right postzygapophysis, and both prezygapophysis. The vertebra is slightly longer than tall, interpreting it as an anterior cervical vertebra on the basis of the ventral position of the parapophysis, the height of the neural spine, the aEI larger than 4, and the marked CPOF. Such elongated centrum is widespread amongst titanosaurs, with few exceptions having proportionally shorter centra (e.g., *Neuquensaurus australis*, *Isisaurus colberti*; Lydekker, 1893; Jain & Bandyopadhyay, 1997). The vertebral centrum is rectangular in lateral and ventral views, with opisthocoelous articulation. In anterior and posterior views, the articular surfaces are subcircular, being almost as tall as they are wide, slightly dorsoventrally compressed (see Tab. S2, Supplementary Information). Amongst titanosaurs, circular articular surfaces are widespread amongst Colossosauria, but probably more common within the Aeolosaurini (e.g., *Overosaurus*). The lateral surfaces are nearly flat, with shallow depressions on the anterior half, without true pneumatic foramina, such as in other titanosaurs. The ventral surface is transversely concave

between the parapophyses and slightly convex posteriorly. In lateral view, the posterior articular surface of the centrum is inclined dorsoanteriorly, with the dorsal edge more advanced than the ventral edge as in *Brasilotitan nemophagus* (Machado *et al.*, 2013). Posteriorly to the diapophysis, there is a longitudinal PCDL, which extends almost until the dorso-lateral margin of the posterior articular surface. The parapophyses are projected lateroventrally at an angle of about 20° with respect to the horizontal plane, causing the cervical ribs to lie below the level of the ventral border of the vertebral centrum, a character found in several titanosaurs (e.g., *Rapetosaurus*, *Overosaurus*, *Kajjutitan maui*; Filippi *et al.*, 2019) and differing with other with an even more ventrally projected parapophysis (e.g., *Patagotitan*). Although the prezygapophysis has not been preserved, the PRDL is present and has a conspicuous longitudinal edge similar to that observed in *Overosaurus*, with a small epipophysis-like prominence distally (Fig. 3.2). Of the zygapophyses, only the left postzygapophysis has been preserved, showing a subcircular articular surface inclined 30° with respect to the ventral surface of the centrum. The postzygapophyses do not extend beyond the posterior articular surface, as in *Saltasaurus*. Dorsally to the postzygapophyses, a latero-posterior prominence is observed that would correspond to the presence of an epipophysis as in the anterior cervical vertebra of *Kajjutitan*. Moreover, a robust SPOL is present. Laterally, the neural arch presents a small POCDF delimited ventrally by the PCDL and anterodorsally by the PODL. The PODL is a single lamina, different from the two PODL segments (diapophyseal and zygapophyseal) present in *Bonitasaura* and *Uberabatitan ribeiroi* (Salgado & de Souza Carvalho, 2008). Dorsally to this fossa, a well-developed SDF is present, delimited posteroventrally by the PODL and anterodorsally by the SPRL. The SPRL is wide and joins the prezygapophysis with the anterolateral border of the neural spine. In anterior view, delimited ventrally by the TPRL and laterally by the SPRL, a SPRF with a subelliptic contour is observed. Posterior to the location of the prezygapophyses, the SPRL presents marked dorsoventrally extended depressions. The neural spine is dorsally incomplete, relatively low in lateral view, and bulbous in anterior view, differing from the triangular and laterally compressed spine in *Malawisaurus dixeyi* (Gomani, 2005), *Futalognkosaurus dukei*

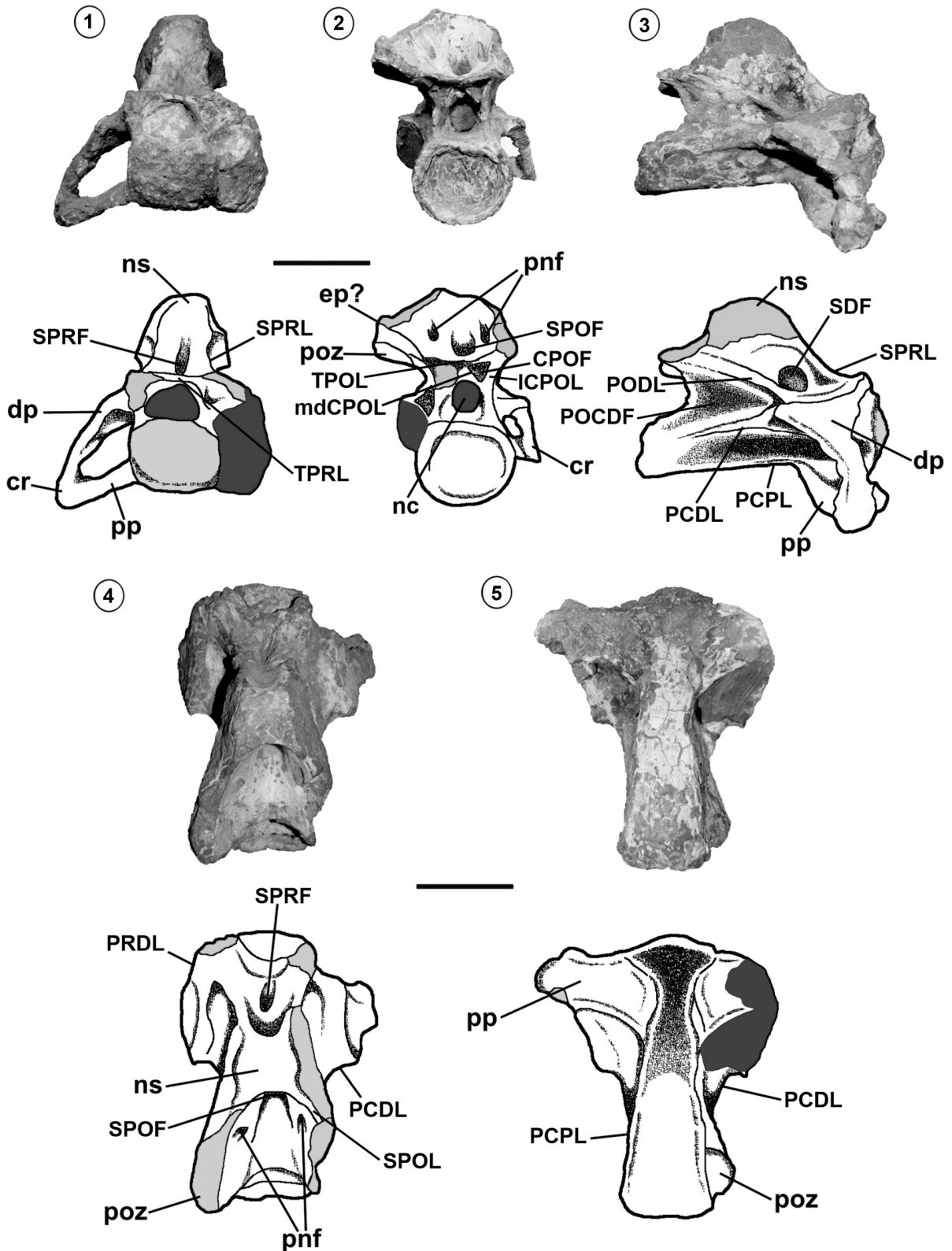


Figure 3. Incomplete anterior cervical vertebra MAU-Pv-LI-602. 1, anterior; 2, posterior; 3, lateral; 4, dorsal; and 5, ventral views. Scale bar=5 cm. Additional anatomical abbreviations: cr, cervical rib; dp, diapophysis; ep, epipophysis; ICPOL, lateral centropostzygapophyseal lamina; mdCPOL, median division of the centropostzygapophyseal lamina; nc, neural canal; ns, neural spine; pnf, pneumatic foramen; poz, postzygapophysis; pp, parapophysis.

(Calvo *et al.*, 2007b, 2007c), and *Uberabatitan*. *Overosaurus* presents in posterior cervicals a similar bulbous neural spine, although more anterior cervical vertebrae of this taxon were not preserved. In the posterior view, positioned posterior to the neural spine and delimited laterally by SPOL, a deep SPOF is observed. Laterally to the SPOF, on both sides, there are two asymmetric, dorsoventrally elongated fossae with a subelliptic contour. In posterior view, over the neural canal, a small CPOF can be observed, delimited laterally by the LCPOF, medially by the medial division of the CPOL, and dorsally by the TPOL. The posterior cervical vertebrae of *Overosaurus* (Coria *et al.*, 2013, fig. 2D), *Rinconsaurus* (Pérez Moreno *et al.*, 2022, fig. 3.4) and *Bonitasaura* (Gallina & Apesteguía, 2015, fig. 4B) have a similar CPOF, but with a different configuration of the laminae that delimit it, probably due to the posterior position of these vertebrae.

Comments. The record of the anterior cervical vertebrae of titanosaurs is scarce, therefore, the possibilities of making good comparisons are limited. Unfortunately, the only titanosaur sauropod known from the study area, *Overosaurus*, has not preserved middle cervical vertebrae. However, some general features present in MAU-Pv-LI-602 (*e.g.*, cervical ribs located below the level of the ventral border of the centrum, presence of a longitudinal border over the PRDL, bulbous neural spine) are shared with the posterior cervical vertebrae of *Overosaurus*. However, the articular surfaces of cervical vertebrae are wider than high in *Overosaurus*, differing from that subcircular one of MAU-Pv-LI-602. Nevertheless, similarly subcircular articular surfaces are widespread amongst titanosaurs related to Aeolosaurini (*e.g.*, *Rinconsaurus*, *Muyelensaurus*, *Patagotitan*). On the other hand, the presence of two pneumatic fossae on both lateral sides of the SPOF, is a character not observed in the anterior cervical vertebrae of other titanosaurs. Therefore, the cervical element, although seems to be related to Colossosauria and probably Aeolosaurini, presents a number of differences with *Overosaurus* that can be interpreted as, at least, species-level differences.

TITANOSAURIA Bonaparte & Coria, 1993.

EUTITANOSAURIA Sanz *et al.*, 1999

Eutitanosauria indet.

Figure 4

Material. Partial middle-to-posterior dorsal vertebra MAU-Pv-CO-671 (Fig. 4).

Description. This element, probably the fourth or fifth dorsal vertebra, is incomplete, lacking part of the dorsal portion of the anterior articular surface, dorsodistal part of transverse processes, the zygapophyses, except part of the right prezygapophysis, and the distal portion of the neural spine. The vertebral centrum is strongly opisthocoelous as in most Sauropoda, slightly wider than tall in posterior view. The lateral surfaces of the centrum are anteroposteriorly concave and have deep and eye-shaped pleurocoels close to the dorsal margin of the centrum, as in several titanosaurs. The ventral surface is slightly anteroposteriorly concave and transversely convex. In anterior view, the parapophysis is dorsolaterally directed and located above the dorsal edge of the neural canal, almost at the level of the prezygapophysis. Although the articular facets of the parapophyses are eroded, a subelliptic morphology is inferred by the long axis dorsoventrally extended and posterodorsally directed. The parapophyses are connected ventrally to the centrum by a robust ACPL and an inclined PCPL. This lamina, together with the ACPL, delimited an elliptical CPAF. Posterodorsally to that, opens a wider, deep, and triangular PACDF, which is delimited posteriorly by the PCDL, dorsally by the diapophysis, and ventrally by the PCPL (Fig. 4.3). The articular surface of the part of the preserved prezygapophysis is elliptic, with its major axis lateromedially directed, and inclined approximately 30° with respect to the horizontal in anterior view. The PRSL is weathered but seems to have been more prominent towards the base of the spine, as in *Baurutitan britoi* (Kellner *et al.*, 2005), *Mendozasaurus neguyelap* (González-Riga, 2003), and *Overosaurus*, than apically, where it is narrow and thin, as in other titanosaurs. The SPRL is absent, a condition that MAU-Pv-CO-671 shares with *Isisaurus*, *Overosaurus*, *Rinconsaurus*, and Saltosauridae (*e.g.*, *Saltasaurus*, *Opisthocoelicaudia skarzynskii*; Borsuk-Bialynicka, 1977). The postzygapophyses show an elliptic morphology with the major axis located dorsoventrally similar to the prezygapophyses, but with a slightly greater angle of inclination. The postzygapophyses

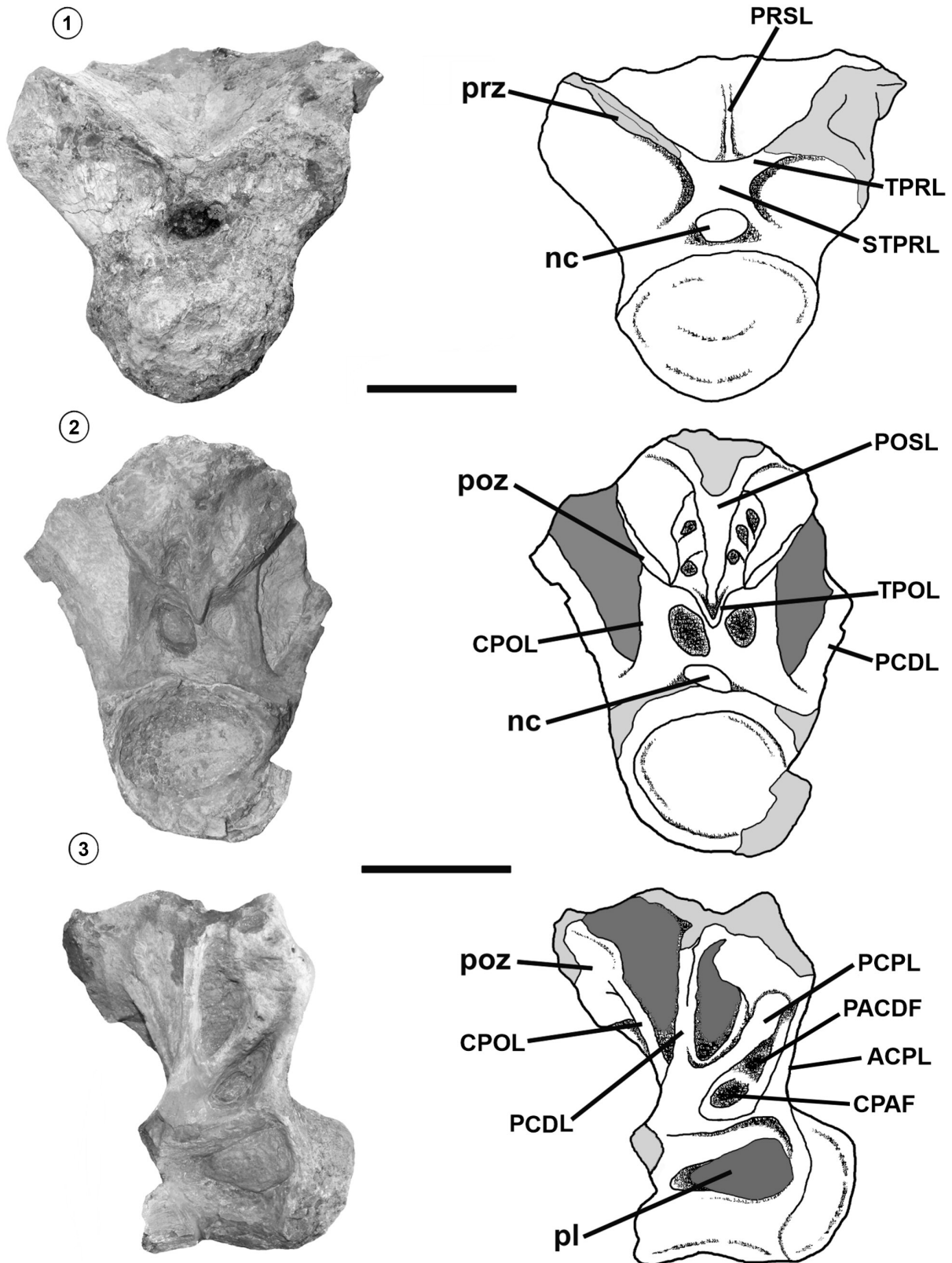


Figure 4. Incomplete middle-to-posterior dorsal vertebra MAU-Pv-CO-671 in 1, anterior; 2, posterior; and 3, lateral views. Scale bar= 10 cm. Additional anatomical abbreviations: ACPL, anterior centroparapophyseal lamina; nc, neural canal; pl, pleurocoel; poz, postzygapophysis; prz, prezygapophysis; STPRL, single intraprezygapophyseal lamina.

are connected to the centrum by robust and prominent CPOL that projects from the middle of the ventral margin of the articular surface, as in *Pitekunsaurus*, running distally to the lateroposterior margin of the PCDL. This condition differs from other titanosaurs (e.g., *Neuquensaurus*, *Overosaurus*, *Bonitasaura*, *Baurutitan*) where the CPOL is projected from the medioventral border of the articular surface of postzygapophysis. Between the postzygapophysis, the TPOL is prominent and V-shaped in posterior view, extending ventrally to form a TPOL as seen in *Bonitasaura* (Gallina & Apesteguía, 2015, fig. 5H). In *Pitekunsaurus*, the V-shaped TPOL is similar but less prominent (Filippi & Garrido, 2008, fig. 6.5). The POSL is prominent proximally and weathered apically, where it seems to be slightly wider. On both sides of this POSL, the SPOF is subdivided by small accessory laminae that unite the postzygapophyses with the POSL, forming small subfossae of irregular contour not seen in other titanosaurs. The neural spine has not been preserved but is tilted posteriorly about 40° from the horizontal in lateral view.

Comments. The new dorsal element MAU-Pv-CO-671 from CO – LI shows a centrum with an opisthocoelous articulation and wide, deep and eye-shaped lateral pneumatic foramen, like in the 7th and 8th dorsal vertebrae of *Overosaurus*. Moreover, they have an anteroposteriorly concave ventral surface in lateral view, and however MAU-Pv-CO-671 lacks the prominent ventral keel seen in *Overosaurus*. In MAU-Pv-CO-671 the parapophysis is oval and connected to the centrum via ACPL and PCPL, which frame a triangular CPAF, as in *Overosaurus*. Moreover, both MAU-Pv-CO-671 and *Overosaurus* lacks SPRL, as in some titanosaurs. On the other hand, they differ in the position of CPOL, which in *Overosaurus* it connects with the centrum from the lateroventral margin of postzygapophysis, whereas in MAU-Pv-CO-671 it starts more medioventrally. Finally, the new material shows POSL, whereas it is absent in *Overosaurus*. The absence of the POSL in the dorsal vertebrae of *Overosaurus* is considered as an autapomorphic feature by Coria *et al.* (2013); however, Vila *et al.* (2022) suggest a more spread dispersion of this character within Sauropoda, being shared by *Muyelensaurus*, *Isisaurus*, and *Abditosaurus* (Vila *et al.*, 2022).

TITANOSAURIFORMES Salgado *et al.*, 1997

SOMPHOSPONDYLI Wilson & Sereno, 1998

Somphospondyli indet.

Figure 5

Material. First caudal vertebra MAU-Pv-LI-670 (Fig. 5).

Description. An incomplete vertebra is here interpreted as the first caudal vertebra, based on the asymmetric articular surfaces of the centrum, being the condyle well-prominent and the cotyle shallowly depressed, and the dorsoventrally tall and anteroposteriorly compressed transverse process. Despite that one more anterior position in the axial series cannot be completely ruled out (as the last sacral), the absence of a marked ventral constriction of the centrum and the lateroventral direction of the transverse process preserved (instead of transversally directed) is more concordant with the caudal morphology than the sacral one. The cotyle is smaller than the condyle, suggesting a morphological transition between the last sacral and the following caudal vertebrae. A marked difference is also observed in the first caudal element of *Overosaurus*. As in other titanosaurs, the centrum is procoelic, with a subcircular anterior articular surface and a posterior articular surface wider than high. Amongst titanosaurs, the procoelous first caudal centrum of this specimen differs from the biconvex first caudal vertebra Saltasauroidae, such as *Baurutitan*, *Alamosaurus*, and *Neuquensaurus* (MLP Ly 1 and 7; D'Emic & Wilson, 2011). On the midline of the dorsal margin of the condyle, there is an elliptic and deep notch. The centrum has lateral and ventral surfaces slightly concave anteroposteriorly. The ventral surface is transversely convex and lacks a ventral keel and lateral ridges, it is relatively wider, differentiating from the transversely compressed ventral surface of sacral vertebrae (e.g., *Overosaurus* or *Neuquensaurus*) and being more similar to the ventral surface of the anterior-most caudal vertebra without articulation for the haemal arches. In the left lateral portion of the centrum, below the transverse process, there is a shallow depression where two small foramina are observed (Fig. 5.3), as in *Alamosaurus*, *Neuquensaurus*, *Rinconsaurus*, and *Overosaurus*; however, in the latter, they are shallower, asymmetric, and located on both lateral faces of the centrum. Although the transverse processes are incomplete, they seem to be projected lateroventrally, with a slight posterior inclination in lateral view. The transverse process is proximally robust and

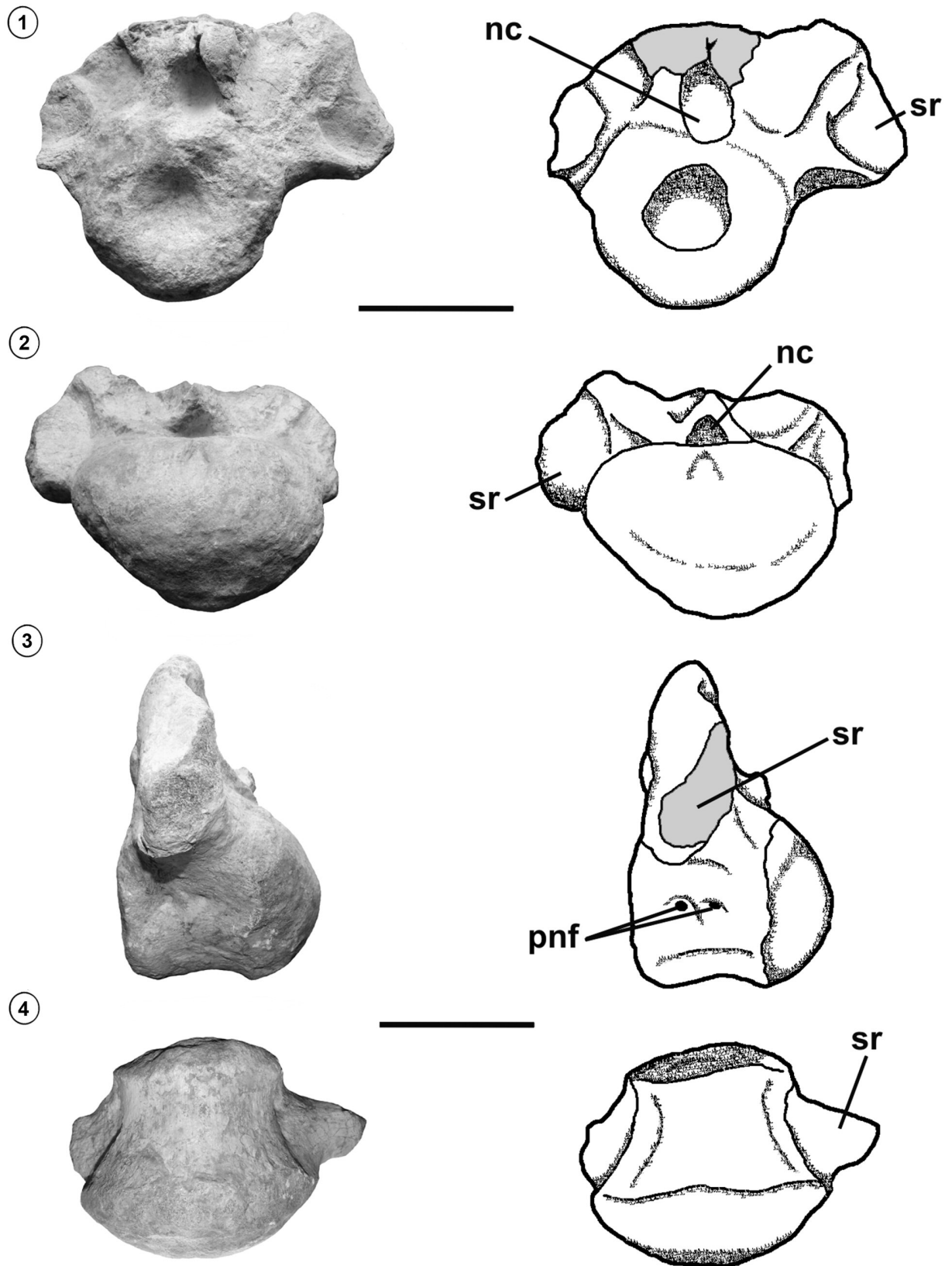


Figure 5. First caudal vertebra MAU-Pv-LI-670 in 1, anterior; 2, posterior; 3, lateral; and 4, ventral views. Scale bar= 10 cm. Anatomical abbreviations: nc, neural canal; pnf, pneumatic foramen; sr, sacral rib.

occupies, except for the condyle, the entire anteroposterior length of the center. The transverse process would be connected to the neural spine by a robust SPDL directed anterolaterally in the dorsal view. The neural arch is located on the anterior border of the vertebral centrum. None of the zygapophyses and neural spine have been preserved.

Comments. MAU-Pv-LI-670, interpreted as the first caudal vertebra, differs from *Overosaurus* for the transversely convex ventral surface of the center, which is broad and slightly transversely concave in *Overosaurus*. Moreover, the first caudal vertebra of *Overosaurus* is quadrangular in posterior view, whereas MAU-Pv-LI-670 is almost subtriangular.

SOMPONDYLI Wilson & Sereno, 1998
TITANOSAURIA Bonaparte & Coria, 1993

Titanosauria indet.

Figure 6

Material. Partial anterior caudal vertebra MAU-Pv-CO-407 (Fig. 6).

Description. This specimen is incomplete, preserving most of the centrum and part of the neural arch, without the right transverse process, both prezygapophyses, and the neural spine (which solely preserves its ventral section). As in most titanosaurs, the caudal vertebra has a strongly procoelic

center, with a centered and prominent condyle. The anterior articular surface is subcircular with slight transversally compression, whereas the posterior articular surface is heart-shaped, with the dorsal surface of the centrum wider than the ventral one. The lateral surfaces of the centrum are deeply excavated and concave anteroposteriorly, whereas the ventral surface is anteroposteriorly concave in lateral view and transversely flat, with two low lateroventral crests connecting articular surfaces for the hemal arches, which are more prominent on the posterior margin of the ventral surface. On the lateral and ventral surfaces, there are small and oval vascular foramina, as in several diplodocoids and titanosaurs (Bellardini *et al.*, 2021). The neural arch is located on the anterior border of the vertebral centrum, as in most titanosauriformes, and has laterally projected and dorsoventrally compressed transverse processes, as in Aeolosaurini and Lognkosauria (Moreno *et al.*, 2021). The transverse process is lateroposteriorly directed in dorsal view, proximally broad, and distally compressed; moreover, it presents a sharp anteroventral border. The postzygapophyses are dorsoventrally concave (Fig. 6.2), similar to *Adamantinasaurus mezzalirai* (Santucci & Bertini, 2006b) and *Arrudatitan maximus* (Santucci & Arruda-Campos, 2011; Silva Junior *et al.*, 2021), acquiring an ear-shaped morphology in the posterior view. Between the postzygapophyses, a small but deep SPOF is observed. Despite

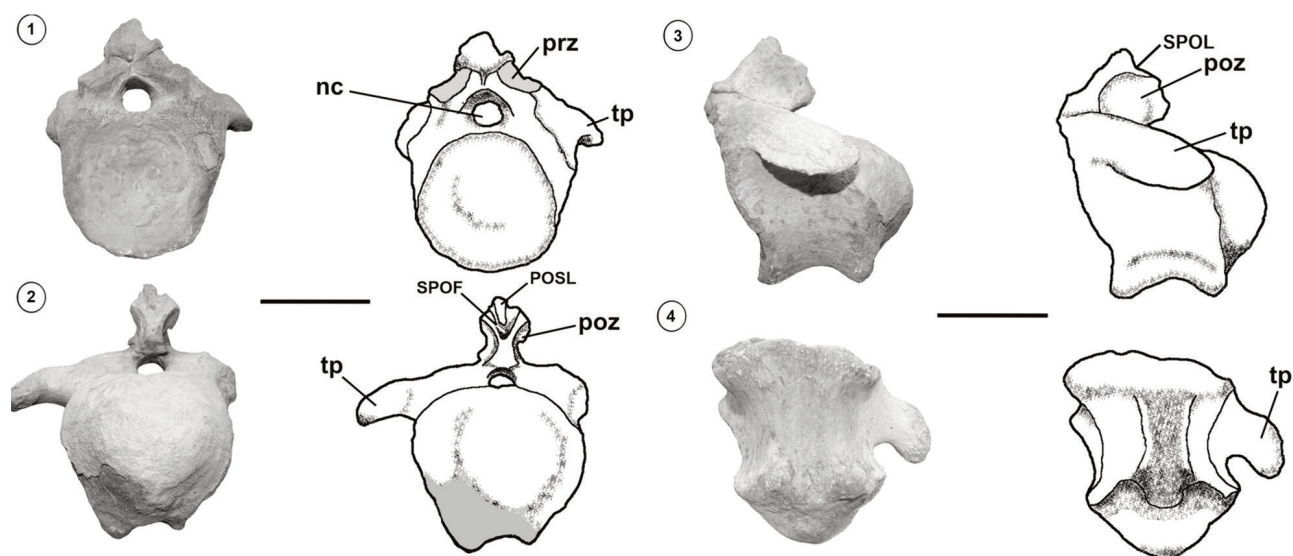


Figure 6. Incomplete anterior caudal vertebra MAU-Pv-CO-407 in 1, anterior; 2, posterior; 3, lateral; and 4, ventral views. Scale bar= 10 cm. Additional anatomical abbreviations: nc, neural canal; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.

Titanosauria indet.

Figure 7

lacking the neural spine, there are short and prominent SPOL. Dorsally to the SPOF, a proximal portion of the POSL is present, with lateral edges distally divergent. Anteriorly to the postzygapophyses, a small POCDF is observed, as in *Bonitasaura*, *Malawisaurus*, *Alamosaurus* (Gilmore, 1946), *Bonatitan reigi* (Martinelli & Forasiepi, 2004), *Mendozasaurus*, *Petrobrasaurus puestohernandezi* (Filippi *et al.*, 2011a) and *Narambuenatita palomoi* (Filippi *et al.*, 2011b). Although the prezygapophyses have not been preserved, remnants of these appearances indicate that they would project anterodorsally in lateral view.

Comments. Concave postzygapophyses articular facets on anterior caudal vertebrae are considered by Santucci & Bertini (2006) as an autapomorphy of *Adamantinasaurus*; however, this condition is shared with MAU-Pv-CO-407, where the concavity is more marked in posterior view. MAU-Pv-CO-407 is an anterior caudal vertebra belonging to a large-sized sauropod specimen (Tab. S2, Supplementary Information); however, the suture on the proximal transverse process suggests an unossified structure, a condition referred to as an immature ontogenetic stage (Brochu, 1996). In this sense, MAU-Pv-CO-407 results in a sauropod specimen larger than *Overosaurus* (Coria *et al.*, 2013), which could be considered an adult specimen due to several osteological conditions of type materials (*e.g.*, fused sacral vertebrae, absence of neural sutures).

Material. Partial anterior caudal vertebra with proximal hemal fragments MAU-Pv-LI-601 (Fig. 7).

Description. This vertebra preserves an almost complete centrum and part of the neural arch, lacking the distal portion of the right transverse process, the right prezygapophysis and the distal part of the left one, both postzygapophyses, and the neural spine. The vertebral centrum is strongly procoelic, with the condyle positioned dorsally in lateral view, as in *Narambuenatitan*, *Mendozasaurus* (González Riga, 2005), *Baurutitan*, *Adamantinasaurus*, and *Aelosaurus* sp. (MPCA 27100). The cotyle is wider and taller than the condyle, as in *Rinconsaurus*, differing from the uniform anterior caudal centrum of *Overosaurus*. Indeed, in MAU-Pv-LI-601 the anterior articular surface is subcircular, slightly dorsoventrally compressed, whereas the posterior articular surface is wider than tall. The posterior half of the centrum shows anteroposteriorly concave lateral surfaces. The ventral face is not clearly observable due to the fusion of the hemapophyses of the haemal arch of the preceding vertebra (Fig. 7.1–3), although it would be narrower than the dorsal surface. The transverse processes are short

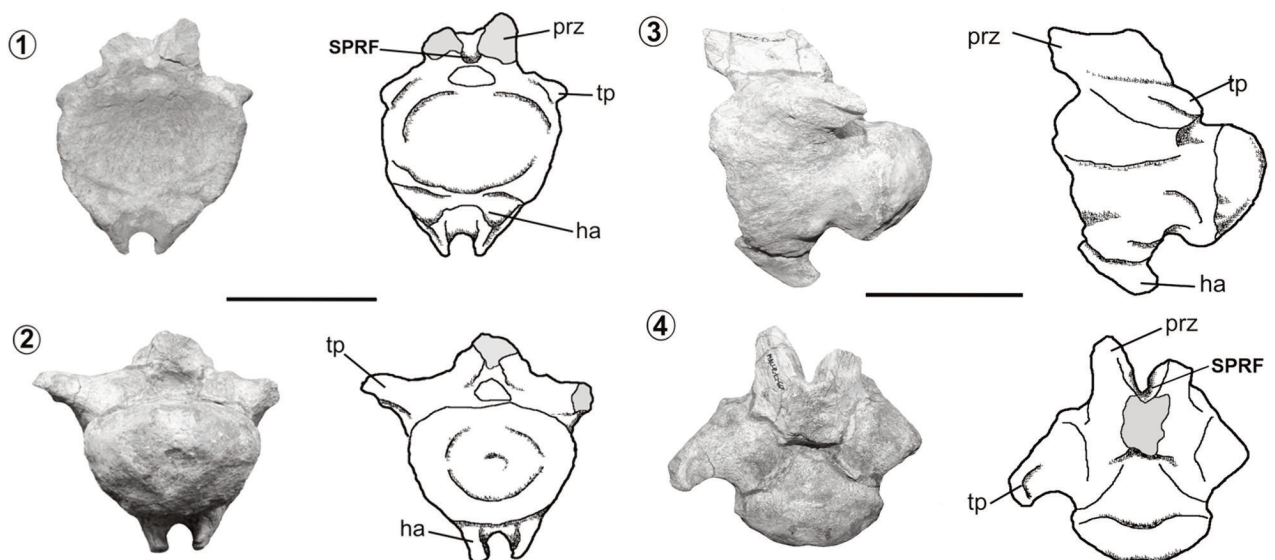


Figure 7. Incomplete anterior caudal vertebrae MAU-Pv-LI-601 in 1, anterior; 2, posterior; 3, lateral; and 4, dorsal views. Scale bar = 10 cm. Additional anatomical abbreviations: ha, haemal arch; prz, prezygapophysis; tp, transverse process.

and tapering, dorsoventrally compressed, lateroposteriorly projected in dorsal view, and laterodorsally curved in anterior view, similar to *Overosaurus*. The neural arch is low and is located in the anterior part of the vertebral centrum. A preserved portion of the left prezygapophysis suggests that it was projected anterodorsal. Between the preserved portions of both prezygapophyses, a deep SPRF is observed, as in different titanosaurs (e.g., *Bonitasaura*, *Pitekunsaurus*, and *Gondwanatitan faustoi*; Kellner & Azevedo, 1999).

Comments. The anterior caudal vertebra MAU-Pv-LI-601 presents a centrum that is wider dorsally than ventrally, different from the transversely wide and ventrally flat anterior caudal centrum of *Overosaurus*. In *Overosaurus*, the lateral surfaces of the centra are slightly anteroposteriorly concave, whereas in *Rinconosaurus* and MAU-Pv-CO-407 they are deeper. In MAU-Pv-LI-601 an unusual condition is observed, the anterior half of the lateral face of the centrum is slightly convex, and the posterior half is concave. Furthermore, MAU-Pv-LI-601 shows evidence of sutures in the neural arch, around the transverse processes, which could be indicating a subadult ontogenetic stage of the specimen. On the other hand, the fusion of the proximal fragments of the haemal arch could correspond to a probable pathological specimen, which is under study.

TITANOSAURIFORMES Salgado *et al.*, 1997

SOMPHOSPONDYLI Wilson & Sereno, 1998

Somphospondyli indet.

Figure 8

Material. Partial distal-most anterior caudal centrum MAU-Pv-LI-669 (Fig. 8)

Description. This specimen is incomplete, preserving most of the centrum and the basal portion of the left transverse process. The centrum is as wide as tall, with amphicoelous articulation; however, the anterior and posterior articular surfaces are unusual, differing from traditional articulation recorded within Sauropoda (e.g., procoelous, opisthocoelous, amphiplatyan, etc.). Indeed, the anterior articular surface is dorsally concave and ventrally almost straight, with a gentle ventromedial prominence; in turn, the posterior articular

surface is ventrally slightly concave, whereas dorsally there are two lateral bulbous prominences. Despite the unusual condition of MAU-Pv-LI-669, we consider that the alternative vertebral articulation proposed by Tidwell *et al.* (2001) as procoelic-dystoplatyan better reflects the type of its joint. Similar articular conditions are observed in other titanosaurs, such as in the distal-most anterior caudal vertebrae of *Traukutitan*, and the middle caudal vertebrae of *Rukwatitan biseptus* (Gorsak *et al.*, 2014), *Malawisaurus*, and *Mendozasaurus*. However, in *Malawisaurus* and *Mendozasaurus* the anterior articular surface is slightly concave and the posterior one shows a single dorsal prominence, which is more reduced in *Mendozasaurus* than *Malawisaurus*. On the other hand, in *Traukutitan* the distal-most anterior caudal vertebrae, originally described as middle caudal vertebrae (Juárez Valieri & Calvo, 2011), still preserve part of the transverse process and are here interpreted as distal-most anterior caudal vertebrae, which shows a procoelic-dystoplatyan articulation. In MAU-Pv-LI-669, the anterior articular surface in the center presents a subcircular contour, while the posterior surface presents a hexagonal contour in the posterior view. The lateral and ventral surfaces of the centrum are anteroposteriorly concave, whereas the ventral surface is transversely straight and compressed, presenting prominent articular surfaces for the hemaphophyses, especially posteriorly. Moreover, there are several small vascular foramina on the ventrolateral and ventral surfaces, as in several neosauropods. In lateral view, the anterodorsal and posterodorsal borders of the articular surfaces are anteriorly inclined, a similar condition is seen in *Traukutitan*. The neural arch is located in the anterior portion of the center. The posterodorsal surface of the vertebral centrum is slightly anteroposteriorly concave, with a slight expansion close to the dorsal margin of the posterior articular border as in *Traukutitan* and *Malawisaurus*. The preserved transverse process is laterally prominent, which allows us to infer that it is a distal-most anterior caudal vertebra.

Comments. The distal-most anterior caudal MAU-Pv-LI-669 differs from the procoelic anterior caudal vertebrae of most titanosaurs; moreover, the anterodorsal and posterodorsal margin of the center are straight in both taxa and not anteriorly inclined as in MAU-Pv-LI-669. On the

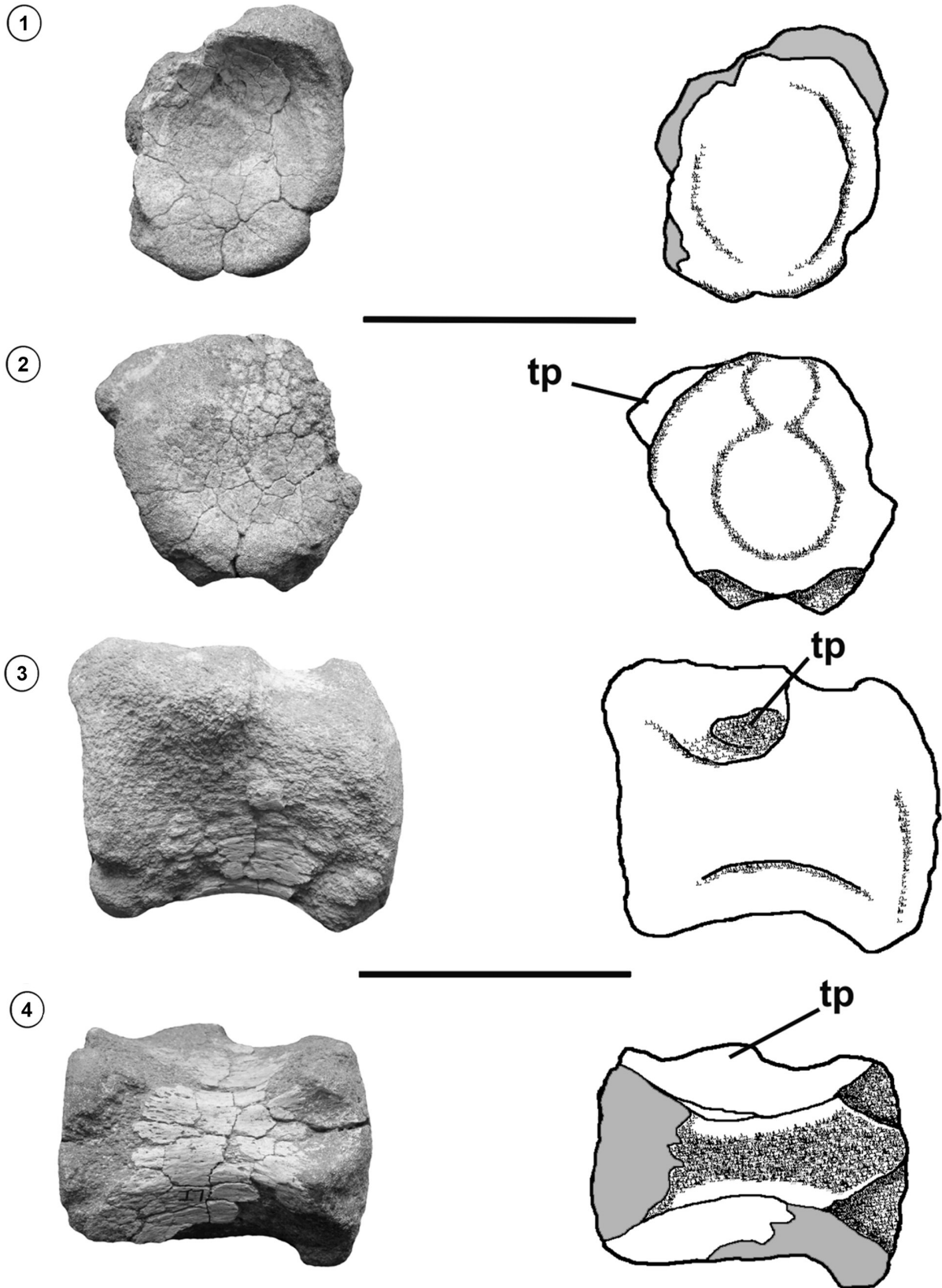


Figure 8. Incomplete distal-most anterior caudal centrum MAU-Pv-LI-669 in 1, anterior; 2, posterior; 3, lateral; and 4, ventral views. Scale bar= 10 cm. Anatomical abbreviations: **tp**, transverse process.

other hand, *Traukutitan* shows an anteriorly inclined anterior articular surface in lateral view, differing from the straight anterior surface of MAU-Pv-LI-669, and a straight posterior articular surface in anterior view, without the posterodorsal bevelling seen in MAU-Pv-LI-669. Moreover, the center of *Traukutitan* is anteriorly and ventrally wider than MAU-Pv-LI-669, showing a general morphology more similar to *Overosaurus* (e.g., ninth and tenth anterior caudal vertebrae) than MAU-Pv-LI-669. However, the posterodorsal margin of the distal-most anterior caudal vertebrae of *Traukutitan* is dorsally prominent, as in MAU-Pv-LI-669.

TITANOSAURIFORMES Salgado *et al.*, 1997

SOMPHOSPONDYLI Wilson & Sereno, 1998

Somphospondyli indet.

Figure 9

Material. Sequence of six articulated middle caudal vertebrae and three hemal arches MAU-Pv-LI-600 (Fig. 9).

Description. The articulated sequence is composed of five almost complete middle caudal vertebrae and the anterior articular surface and prezygapophyses remains of a sixth one, two almost complete haemal arches, and a small fragment of a third. The caudal vertebrae are procoelous, quadrangular in appearance, higher than wide, with slightly anteroposteriorly concave lateral and ventral surfaces. The ventral aspect of the centrum is slightly narrower than the dorsal aspect. On the lateral surface, at the base of the neural arch, lateral prominences corresponding to vestiges of the transverse processes are observed. The neural arch is located in the anterior half of the vertebral centrum, with the prezygapophysis surpassing the centrum, being a length around half the length of the vertebral centrum. They are mainly anterodorsally projected. In the first two elements of MAU-Pv-LI-600, the posterior neural arch pedicels are anteriorly inclined, as in *Aeolosaurus rionegrinus* (Powell, 1987) and *Rapetosaurus*, and particularly tall in lateral view, being almost as tall as the centrum height. The articular facets of the prezygapophyses project mediodorsally, acquiring a pipe-like morphology in lateral view, especially in the first three elements. The neural spine is transversely

compressed and widens posteriorly in dorsal view. The vertebrae present an incipient SPRL, which delimits between the prezygapophyses and the base of the neural spine, a deep SPRF. The neural spine presents an acute, practically straight anterior edge, which differs from the SPRL (clearly observed in the 4th caudal of the sequence), which could be interpreted as a PRSL. The dorsal edge of the spine is convex and distally expanded in lateral view, whereas the posterior edge is straight and more robust than the anterior, which slopes posteriorly, conferring a posterior inclination to the neural spine in lateral view. The postzygapophyses are attached to the posterior part of the spine by a short and robust SPOL. This short and robust SPOL was named “bony process” by Calvo *et al.* (2003) and is one of the main synapomorphies of the Rinconsauria clade, as is a character shared between *Rinconsaurus* and *Muyelensaurus* (amongst other members of the clade). There is a SPOF framed between the SPOL.

The caudal sequence MAU-Pv-LI-600 preserves also three haemal arches, which are open Y-shaped type (Otero *et al.*, 2011) and articulated to the fourth and fifth caudal vertebrae, the latter the best preserved and most complete of the series. The distal process is half the length of the dorsal rami, being laterally compressed and posteriorly curved in lateral view.

Comments. The postzygapophyseal process, considered by Calvo & González Riga (2003) as an autapomorphic feature of *Rinconsaurus*, is a condition with a wider distribution within Sauropoda (e.g., *Overosaurus*, *Pitekunsaurus*) and, although it was recently retained as part of the unique combination of characters in the emended diagnosis of *Rinconsaurus* by Pérez-Moreno *et al.* (2022), it shows to have a more widespread distribution amongst Rinconsauria. In MAU-Pv-LI-600 the postzygapophyseal process is present, but with less development than *Rinconsaurus*, as seen in *Overosaurus* and *Pitekunsaurus*. Furthermore, in MAU-Pv-LI-600 the ventral surface is transversely compressed, narrower than in *Overosaurus*, and the prezygapophyses are pipe-like and not rounded in lateral view as in *Overosaurus*. MAU-Pv-LI-600 differs from *Overosaurus* also in presenting tall, straight, and anteriorly inclined posterior neural pedicles, which are slightly lower and convex in lateral view.

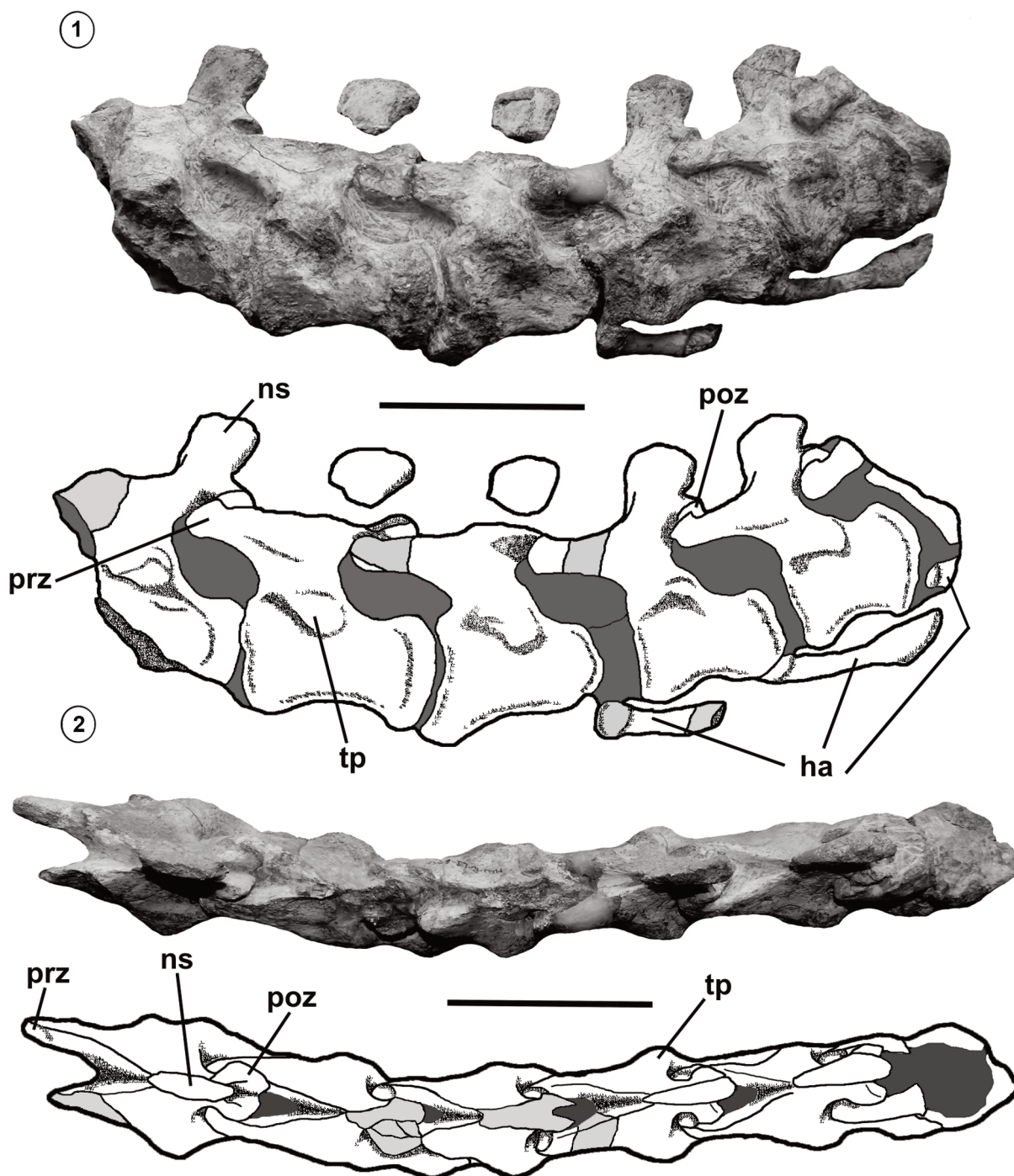


Figure 9. Sequence of six articulated middle caudal vertebrae and three haemal arches MAU-Pv-LI-600 in 1, lateral; and 2, dorsal views. Scale bar= 10 cm. Anatomical abbreviations: **ha**, haemal arch; **ns**, neural spine; **poz**, postzigapophysis; **prz**, prezigapophysis; **tp**, transverse process.

TITANOSAURIA Bonaparte & Coria, 1993

Titanosauria indet.

Figure 10

Material. Partial posterior caudal centrum MAU-Pv-CO-668 (Fig. 10).

Description. This element is composed of the posterior portion of the centrum and the base of the neural arch. The

centrum has a posterior convex condyle, while the anterior cotyle has not been preserved, which makes it impossible to establish if the centrum is procoelous, as in *Overosaurus*, or if the centrum is biconvex as in the posterior caudal of *Rinconsaurus* and *Pitekunsaurus*. The vertebral centrum is characterized by being dorsoventrally compressed in posterior view, causing it to be wider than high. The dorsal and ventral surface of the centrum is practically flat, the ventral being slightly concave anteroposteriorly in lateral view. The lateral surfaces of the centrum are dorsoventrally convex and anteroposteriorly concave. According to the preserved portion of the base of the neural arch, it would be located in the anterior half of the vertebral centrum, as seen in most titanosauriformes (e.g., *Rinconsaurus*, *Muyelensaurus*, *Overosaurus*, *Aelosaurus*, *Arrudatitan*, *Punatitan coughlini*; Hechenleitner *et al.*, 2020).

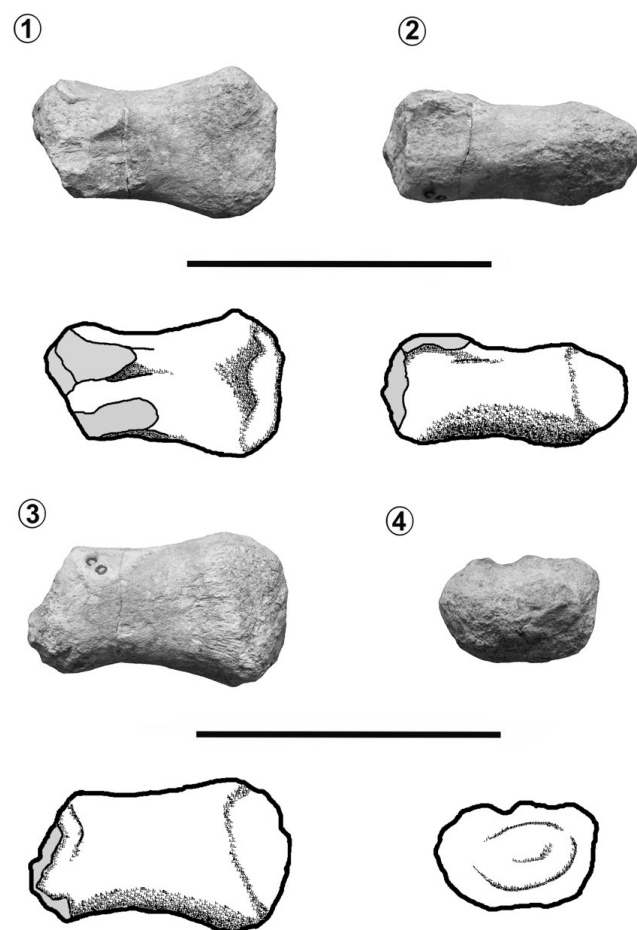


Figure 10. Incomplete posterior caudal center MAU-Pv-CO-668 in 1, dorsal; 2, lateral; 3, ventral; and 4, posterior views. Scale bar= 10 cm.

Comments. The caudal centrum MAU-Pv-CO-668 is dorsoventrally compressed, a characteristic present in posterior caudal vertebrae of *Rinconsaurus* (MAU-Pv-CRS-29, 30) and Saltosaurinae (e.g., *Neuquensaurus*), different from the proportional (wide as tall) posterior caudal vertebrae of other titanosaurians (e.g., *Malawisaurus*, *Uberabatitan*, *Overosaurus*, *Pitekunsaurus*, and *Bonitasaura*). One of the characteristics that define Rinconsauria (Calvo *et al.*, 2007a), a clade that included *Rinconsaurus* and *Muyelensaurus*, is the presence of posterior caudal vertebrae with posteriorly compressed centra. Nevertheless, this character cannot be evaluated, because the anterior portion of the centrum MAU-Pv-CO-668 is incomplete, although it is inferred that the centrum would have been compressed dorsoventrally.

Comparisons with other sauropods from Bajo de la Carpa Formation. With the aim to test the hypothesis of a more diversified sauropod fauna in the northeastern Neuquén Basin during the Santonian, we compared the new fossil evidence from CO – LI locality with the sauropod taxa from the Bajo de la Carpa Formation. The sauropod fossil record from Bajo de la Carpa Formation is composed of *Overosaurus* and *Rinconsaurus*, from the northeastern Neuquén Basin, and *Bonitasaura*, from the southeastern. Below, we synthesize the main morphological differences between the compared specimens, being more detailed in the similarities in the description section.

Overosaurus was formalized on the basis of an articulated specimen from CO – LI locality (Coria *et al.*, 2013), and originally described as coming from the Anacleto Formation but reconsidered as belonging to Bajo de la Carpa Formation by Filippi *et al.* (2015). The type material of *Overosaurus* (MAU-Pv-CO-439) is composed of 40 articulated vertebrae, including the last four cervical vertebrae, ten dorsal vertebrae, six sacral vertebrae, and 20 caudal vertebrae, cervical and dorsal ribs, complete right ilium and part of the left one. Thus, considering the overlapping material, we carry out the morphological comparisons with *Overosaurus* of the following new elements: middle-posterior dorsal vertebra MAU-Pv-CO-671; anterior caudal vertebrae MAU-Pv-LI-601, 669, 670, and MAU-Pv-CO-407; and middle caudal vertebrae MAU-Pv-LI-600. As mentioned before, the new dorsal element MAU-Pv-CO-671 differs from *Overosaurus* in lacking the ventral keel of the vertebral centrum, showing

the POSL, presence of a single PCDL without a fossae between the PCDL and ACDL, and for the medioventral position of the CPOL (Fig. 11.1–6). Taking into account the new anterior caudal vertebrae, MAU-Pv-LI-670 differs from *Overosaurus* in the convex ventral surface and the subtriangular posterior surface of the centrum. MAU-Pv-LI-601 shows the dorsal half of the centrum wider than the ventral one and sinusoidal lateral surfaces of the centrum, unlike in *Overosaurus*, where the centrum is quadrangular and the lateral surface is slightly anteroposteriorly concave. MAU-Pv-LI-669 has a procoelous-opisthoplatyan centrum and the dorsal margins of the anterior and posterior articular surfaces are inclined similar to *Traukutitan* (Fig. 11.7–8), whereas *Overosaurus* caudal vertebra is procoelous and shows straight anterodorsal and posterodorsal margins of the centrum. Finally, MAU-Pv-CO-407 differs from *Overosaurus* for the concave articular surfaces of the postzygapophysis.

Other sauropod taxon from the Bajo de la Carpa Formation is represented by *Rinconsaurus*, which was originally described by Calvo & González Riga (2003) as coming from the Río Neuquén Subgroup (Turonian–Coniacian), but recently lithostratigraphically reassessed by Filippi *et al.* (2015). The *Rinconsaurus* type material is composed of several cranial and postcranial elements coming from the proximities of Rincón de los Sauces city and was partially redescribed by Moreno *et al.* (2021, 2022). The morphological comparisons with *Rinconsaurus* focused on the following new elements: teeth (MAU-Pv-LI-645, 646, and MAU-Pv-CO-650); middle-to-posterior dorsal vertebra MAU-Pv-CO-671; and the caudal vertebrae MAU-Pv-LI-600, 601, 669, 670, and MAU-Pv-CO-407, 668, 671. The tooth MAU-Pv-LI-645 differs from *Rinconsaurus* teeth for the straight carinae, whereas MAU-Pv-LI-646 and MAU-Pv-CO-650 lack carinae. The middle-to-posterior dorsal vertebra MAU-Pv-CO-671 differs from *Rinconsaurus* due to its distinct configuration of the lateral laminae and fossae of the centrum and the presence of prominent TPOL and a ventrally directed single STPOL. The most anterior new caudal vertebra MAU-Pv-LI-670 differs from *Rinconsaurus* in the laterally directed transverse process and for lacking the wide pneumatic lateral fossa and the slightly convex ventral surface of the centrum. The anterior caudal vertebra MAU-Pv-CO-407 differs from

Rinconsaurus for the vascular foramina on the lateroventral surface of the centrum, the presence of the POCDF, for lacking the hour-glasses morphology of the centrum in ventral view, and the TPOL ventrally to the postzygapophyses. The caudal vertebra MAU-Pv-LI-601 differs from *Rinconsaurus* for lacking the TPRL, as well the hour-glass morphology of the centrum in ventral view. The new anterior caudal vertebra MAU-Pv-LI-669 differs from *Rinconsaurus* for the procoelous-opisthoplatyan articulation of the centrum, the presence of vascular foramina on the lateroventral surfaces of the centrum, the inclined dorsal margin of the anterior and posterior articular surfaces of the centrum, and for lacking the hour-glass morphology of the centrum in ventral view. Despite some differences (absence of TPRL, TPOL, and convex dorsal surface of neural spine), the main morphology of the new middle caudal vertebrae MAU-Pv-LI-600 resembles the middle caudals of *Rinconsaurus* and similar to *Overosaurus* (Fig. 11.10–12). Indeed, MAU-Pv-LI-600 have quadrangular centra with strongly procoelous articulation and anteroposteriorly concave lateral surfaces without pneumatic fossae or foramina; moreover, in the neural arch, there are narrow SPRF and SPOF, framed for SPRL and SPOL in both specimens. Convergently, the articulated new caudal elements MAU-Pv-LI-600 show postzygapophyseal processes, as in other rinconsaurian (*e.g.*, *Rinconsaurus*, *Pitekunsaurus*). Finally, the posterior new caudal elements MAU-Pv-LI-668 are broadly fragmented and the comparisons with *Rinconsaurus* are limited to the general morphology of the centrum, which seems to be dorsoventrally compressed in both specimens (Fig. 11.13–14).

The Santonian outcrops of the southeastern Neuquén Basin (Río Negro Province) yielded the third sauropod taxon from the Bajo de la Carpa Formation *Bonitasaura*. It was described on the basis of cranial and postcranial elements belonging to a subadult individual, including different bones of the skull, isolated tooth, axis, three cervical, five dorsal, and 25 caudal vertebrae, several cervical and dorsal ribs, five chevrons, a fragment of sternal plate, incomplete humerus, two metacarpals, pubis, ischium, femur, tibia, fragmentary fibula, both astragali, and several metatarsals and phalanges. Considering the overlapping elements, we compare *Bonitasaura* type materials with all new specimens.

The new isolated tooth MAU-Pv-LI-645 differs from

Bonitasaura in being narrower and cone chisel-like, whereas the teeth MAU-Pv-LI-646 and MAU-Pv-CO-650 lack of carinae and hexagonal cross-section of the crown, two morphological conditions seen in *Bonitasaura*. The new anterior cervical vertebra MAU-Pv-LI-602 differs from *Bonitasaura* for showing a CPOF, a divided CPOL, and for lacking the constriction of the neural canal. The new middle-to-posterior dorsal vertebra MAU-Pv-CO-671 differs from *Bonitasaura* for the ventrolateral position of the CPOL, the presence of a single SPOL, and for lacking a wide CPRF and the TPRL. The most anterior new caudal vertebra MAU-Pv-LI-670 differs from *Bonitasaura* for showing pneumatic foramina in the dorsolateral surface of the centrum and for lacking the

trapezoidal anterior articular surface of the centrum. The anterior caudal MAU-Pv-CO-407 differs from *Bonitasaura* for showing vascular foramina in the lateroventral surfaces of the centrum, dorsoventrally compressed transverse process, slightly concave postzygapophysis articular surface, and deep SPOF. The new anterior caudal MAU-Pv-LI-601 differs from *Bonitasaura* for the morphology of the centrum, where the dorsal portion is wider than the ventral one, and the anterolateral surface is convex. The new anterior caudal MAU-Pv-LI-669 differs from *Bonitasaura* for the procoelous-opisthoplatyan articulation of the centrum, showing vascular foramina on the lateroventral surfaces of the centrum, and for the inclined dorsal margin of the ante-

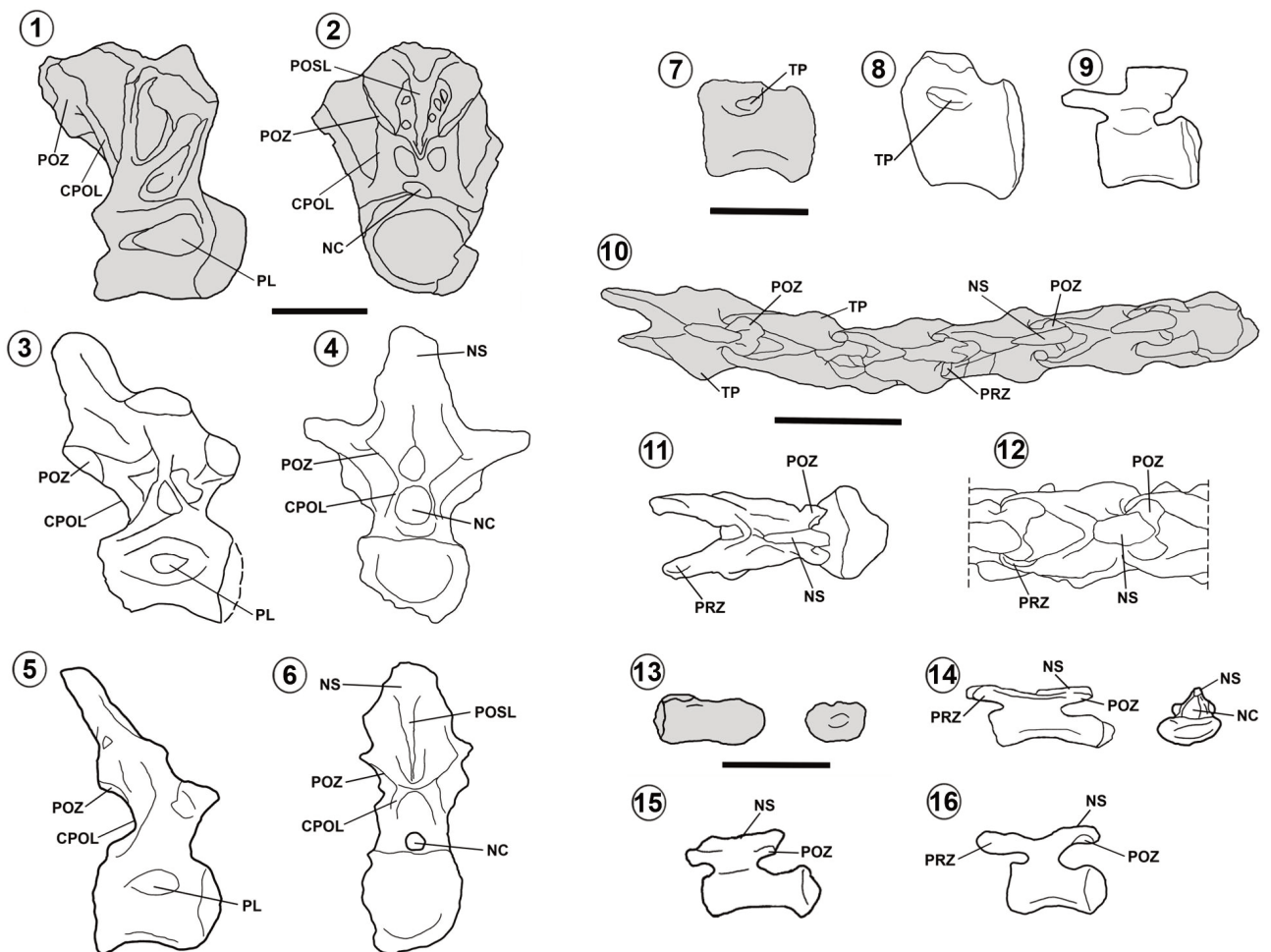


Figure 11. Comparative images of axial elements from CO – LI. 1–2, Middle-posterior dorsal vertebra MAU-Pv-CO-671 in 1, lateral; and 2, posterior views. Middle-posterior dorsal vertebra from *Overosaurus* in 3, lateral; and 4, posterior views. Posterior dorsal vertebra from *Bonitasaura* in 5, lateral; and 6, posterior views. 7–9, Distalmost anterior caudal vertebrae in left lateral view 7, MAU-Pv-LI-669; 8, *Traukutitan*; and 9, *Mendozasaurus*. 10–12, Middle caudal vertebrae in dorsal view, 10, MAU-Pv-LI-600; 11, *Rinconosaurus*; and 12, *Overosaurus*. 13–16, Posterior caudal vertebra, 13, MAU-Pv-CO-668, in left lateral and posterior views; 14, *Rinconosaurus*, in left lateral and posterior views; 15, *Bonitasaura* in left lateral view; and 16, *Overosaurus*, in lateral view. For anatomical abbreviations, see previous figures. Scale bar= 10 cm.

rior and posterior articular surfaces of the centrum. MAU-Pv-LI-600 differs from *Bonitasaura* for showing an incipient PRSL and the postzygapophyseal process. Finally, the new posterior caudal vertebrae MAU-Pv-LI-668 differs from *Bonitasaura* for the dorsoventrally compressed posterior half of the centrum (Fig. 11.15).

The resulting comparisons revealed morphological differences between the new findings and the known sauropod taxa from Bajo de la Carpa Formation which would exclude new occurrences of *Overosaurus*, *Rinconsaurus*, and *Bonitasaurua* from the CO–LI locality. Moreover, none of the new elements share diagnostic features with the aforementioned sauropods, which would allow referring them to any other kind of formalized sauropod taxa. Indeed, only the new middle caudal vertebrae MAU-Pv-LI-600 strongly resembles *Rinconsaurus*, sharing different morphological features of both centrum and neural arch; however, among these, the most peculiar is the presence of the postzygapophyseal process that is considered as a synapomorphic condition of Rinconsauria and not diagnostic of *Rinconsaurus*. Pending a new, more complete, and better-preserved specimen, we consider the morphological differences here recorded as evidence of a more diversified sauropod fauna in the northeastern Neuquén Basin, at least during the Santonian.

DISCUSSION

The sauropod dinosaur fauna of the Bajo de la Carpa Formation has been relatively scarce in the different localities where it has been founded (Neuquén City, “Cañadón Río Seco”, Rincón de los Sauces, Sierra Barrosa, and the northern coast of Los Barreales Lake in Neuquén Province; “La Bonita” and Cerro Policía in Río Negro Province; Garrido, 2010). However, the CO – LI area records a remarkable abundance and diversity of somphospondylans sauropod remains (in addition to *Overosaurus*), which include not only different body sizes but also morphological differences that indicate the presence of different taxa. Although it is not possible to establish the ontogenetic stage of the specimens to which the materials presented here correspond, they show the presence of small to medium-sized forms (e.g., teeth MAU-Pv-LI-646 and MAU-Pv-CO-650; anterior cervical vertebrae MAU-Pv-LI-602) as well as large forms (e.g., tooth MAU-Pv-

LI-645; anterior caudal vertebra MAU-Pv-CO-407). Furthermore, this evidence would allow us to infer that, at least in this region of Gondwana, a lineage of basal titanosaurs could have survived even until the end of the Cretaceous, in contrast to the interpretations made by Leanza *et al.* (2004) and Salgado & Bonaparte (2007), where they established the extinction of the basal titanosaurs before the Santonian.

Taxonomic status of materials from CO – LI

MAU-Pv-LI-645, MAU-Pv-LI-646, and MAU-Pv-CO-650. These teeth display distinct features indicative of a titanosaurian phylogenetic signal. Notably, these teeth exhibit dental crowns with a cross-sectional shape resembling half-cylindrical crowns, indicating a rounded or semi-circular profile. The SI values for these dental crowns fall within the range of 3–5, further confirming their alignment with titanosaurian dental characteristics. Moreover, the presence of slightly developed marginal wear facets on these teeth supports their affinity with titanosaurians. Collectively, these features strongly suggest the presence of titanosaurian traits in these teeth, emphasizing their significance within the broader context of titanosaurian dinosaur paleontology.

MAU-Pv-LI-602. These cervical vertebrae showcase distinctive characteristics that signify a phylogenetic signal associated with the Eutitanosauria clade. These traits comprise moderately developed parapophyses, which are ventrally oriented and result in the displacement of cervical ribs. Furthermore, there is an absence of pleurocoels in the cervical centra, except in the posteriormost vertebrae. Notably, a deep lateral fossa with pneumatopores communicating with internal pneumatic cavities is present. Additionally, the neural arch lamination is rudimentary, with either absent or slightly marked diapophyseal laminae. These features collectively point to the classification of MAU-Pv-LI-602 within the Eutitanosauria clade.

MAU-Pv-CO-671. This dorsal vertebra displays distinct characteristics that place it within the Eutitanosauria clade. Notably, key features include the absence of the SPRL in both anterior and middle dorsal neural spines, as well as the projection of the anterior edge of the neural spine posteriorly to the diapophysis in middle dorsal neural arches. Additionally, there is a slight inclination of both middle and posterior dorsal neural spines at an angle of approximately 70°. These

traits collectively provide a robust phylogenetic signal, firmly associating MAU-Pv-CO-671 with the Eutitanosauria clade.

MAU-Pv-LI-670. This caudal centrum is characterized by a markedly convex posterior articular surface and the absence of ventral protrusions on the transverse process. Another distinguishing feature of MAU-Pv-LI-670 is the presence of a lateral pneumatic foramen on the anterior caudal vertebra. In addition, the shape of the articular face of the caudal centrum is procoelous. These unique features contribute to a global understanding of the taxonomic placement of MAU-Pv-LI-670 within the Somphospondyli clade.

MAU-Pv-CO-407. This anterior caudal centrum exhibits a procoelous articular face shape. Furthermore, the shape of the anterior caudal transverse processes is distinctive, characterized by a dorsomedially oriented high lateral margin instead of a vertical tapering distal end. In this anterior caudal vertebra, there is a noticeable inclination of the anterior face strongly forward. The neural arch in this vertebra displays poorly developed SPOL, resulting in the articular facet of the postzygapophysis projecting slightly from the midline. These distinctive traits contribute to the classification of MAU-Pv-CO-407 within the Aeolosaurini group and provide valuable insights into its phylogenetic signal.

MAU-Pv-LI-601. This procoelous anterior caudal centrum has a well-developed SPRL that extends into the anterolateral edge of the neural spine. Furthermore, the shape of the anterior caudal transverse processes is notable, with a dorsomedially oriented high lateral margin instead of a distally tapering and vertically oriented one. These distinctive anatomical traits are indicative of MAU-Pv-LI-601's affiliation with Eutitanosauria.

MAU-Pv-LI-669. This anterior caudal centrum exhibits a procoelous-distoplatyan articulation. Additionally, its ventral surface displays a concave transverse configuration. These features align with the distinctive traits associated with Somphospondyli.

MAU-Pv-LI-600. These caudal vertebrae stand out due to its unique anatomical characteristics, including a cylindrical mid-caudal centrum and distinctive articular facets of the prezygapophyses characterized by broad expansions, both dorsal and ventral. Another noteworthy feature distinguishing MAU-Pv-LI-600 is the presence of postzy-

gapophyses located in the anterior half of the centrum in both anterior and middle caudal vertebrae. Particularly in the middle caudal vertebrae, the SPOL development in the neural arch is slightly underdeveloped, causing the articular facet of the postzygapophyses to protrude from the midline. These specific anatomical traits play a crucial role in classifying MAU-Pv-LI-600 within the Aeolosaurini.

MAU-Pv-LI-668. This posterior caudal vertebra exhibits distinctive features, including neural arches situated on the anterior half of the centrum and a dorsoventrally flattened centrum with a width at least double its height. Moreover, the apex of the convexity in the posterior joint is concentric, a defining characteristic that places MAU-Pv-LI-668 within the Rinconsauria.

CONCLUSIONS

The CO – LI area records the presence of a remarkable diversity of titanosauriform sauropod that probably lived together in the same environment, which can be correlated with the diversity of the record of abelisaurid theropods (Filippi *et al.*, 2016; Méndez *et al.*, 2018, 2021; Gianechini *et al.*, 2021) and chelid turtles (Maniel & De la Fuente, 2017) that have been found in the same area. This great faunal diversity is related to a particular paleoenvironmental development, for which studies about this (*e.g.*, palynology, sedimentary) will be necessary in the future, in order to evaluate the conditions that generated this scenario.

The materials presented here show morphological and evolutionary variations, which highlight the potentiality of the area. The discovery of new and more complete specimens to carry paleofaunistic, paleobiological, and paleoecological studies, will allow a better understanding of the role of somphospondyli sauropods in the Upper Cretaceous ecosystems.

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