

# A well-preserved vertebra provides new insights into rebbachisaurid sauropod caudal anatomical and pneumatic features

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Rebbachisauridae is a clade of sauropod dinosaurs whose maximum diversification and abundance are known from the Cretaceous of South America. We describe an anterior caudal vertebra, MDPa-Pv 007, from the Upper Cretaceous of Argentine Patagonia, whose characters allow it to be referred to this clade. Also, two phylogenetic analyses reinforce the referral of the new material more exclusively to Rebbachisaurinae. We analyze pneumatic structures using the first CT scans of a caudal element of a rebbachisaurid. The excellent preservation of MDPa-Pv 007, combined with CT images, allows us to document external fossae and foramina that connect to larger internal chambers, constituting unambiguous evidence of pneumaticity. The centrum of MDPa-Pv 007 is camerate, with large interconnected internal chambers; this is accompanied by a neural arch with wide and deep fossae. Caudal pneumaticity has a complex phylogenetic distribution among neosauropods. This feature may have evolved independently in diplodocoids and titanosauriforms, or it could be ancestral for Neosauropoda but secondarily lost in a few lineages. Future investigations, taking advantage of new technologies, will provide insights into the phylogenetic distribution and paleobiological implications of pneumaticity in sauropod dinosaurs and other fossil archosaurs.

Key words: Dinosauria, Sauropoda, Diplodocoidea, Rebbachisauridae, pneumaticity, Cretaceous, Neuquén Basin, Argentina.

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## Introduction

Rebbachisauridae is a clade of sauropod dinosaurs that probably originated in the Jurassic but which flourished during the Cretaceous (Salgado et al. 2022). Fossils of rebbachisaurids are primarily known from Africa, Europe and South

America. A record of a rebbachisaurid from Asia has recently been reported (Averianov and Sues 2021), but its taxonomic assignment has been questioned (Lerzo et al. 2021), and the enigmatic North American taxon *Maraapunisaurus* (formerly *Amphicoelias*) *fragillimus* has been referred to Rebbachisauridae, albeit on the basis of missing material (Carpenter 2018). Despite the broad paleogeographic distri-

bution of the group, the greatest diversity and abundance of rebbachisaurid sauropods are known from the Cretaceous of South America, especially in Neuquén Basin from Argentina (Calvo and Salgado 1995; Bonaparte 1996, 1997; Dalla Vecchia 1998; Sereno et al. 1999; Carvalho et al. 2003; Gallina and Apesteguía 2005; Salgado et al. 2006; Apesteguía 2007; Taylor and Naish 2007; Carballido et al. 2010; Torcida et al. 2011; Salgado et al. 2012; Fanti 2013, 2015; Ibiricu et al. 2013, 2015; Canudo et al. 2018; Lindoso et al. 2019; Bellardini et al. 2022).

The Candeleros Formation (Cenomanian, Upper Cretaceous) presents extensive outcrops in Argentine Patagonia (Garrido 2010). This stratigraphic unit has provided a diverse fauna of fossil reptiles and other continental vertebrates from the Neuquén Basin, among which the sauropod dinosaurs stand out. Candeleros Formation sauropods include the titanosaur *Andesaurus delgadoi* (Calvo and Bonaparte 1991) and the rebbachisaurids *Limaysaurus tessonei* (Calvo and Salgado 1995), *Nopcsaspondylus alarconensis* (Apesteguía 2007), and *Rayososaurus agrioensis* (Bonaparte 1996; Carballido et al. 2010). The anterior caudal vertebrae described herein, MDPa-Pv 007, is from the Candeleros Formation and is referred to the family Rebbachisauridae.

Birds are the only clade of extant amniotes with postcranial skeletal pneumaticity (PSP). This means that the interior of the bones is invaded by diverticulae from the lungs and air sacs of the respiratory system; these pneumatic diverticulae induce bone resorption to produce internal cavities or chambers filled with air. Among fossil vertebrates, unambiguous PSP is known only in pterosaurs and saurischian dinosaurs, including sauropods (Britt 1997; Wedel 2003, 2005; O'Connor 2006; Claessens et al. 2009). Among sauropods, rebbachisaurids have been characterized as having highly pneumatic vertebrae, based on external fossae and foramina (Fanti et al. 2015) revealed by natural fractures (Windholz et al. 2022a) as well as computed tomography (CT) scans of dorsal vertebrae of *Nigersaurus taqueti* (Sereno et al. 2007) and *Katapultosaurus goicoecheai* (Ibiricu et al. 2013). Here we present the first CT scans of a caudal element of a rebbachisaurid. The vertebra described herein records exquisite laminar architecture, which alongside the CT scan images, provides new anatomical and paleobiological information on rebbachisaurid sauropods.

**Institutional abbreviations.**—MAU, “Museo Municipal Argentino Urquiza”, Rincón de los Sauces, Argentina; MDPa, Museo del Desierto Patagónico de Añelo, Argentina; MIWG, Museum of Isle of Wight Geology (now Dinosaur Isle Visitor Centre), Sandown, Isle of Wight, UK; NHMUK, Natural History Museum, London, UK; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina.

**Other abbreviations.**—acdl, anterior centrodiapophyseal lamina; amedl, anterior medial lamina; cdf, centrodiapophyseal fossa; cpol, centropostzygapophyseal lamina; cpri, centroprezygapophyseal laminae; nc, neural canal; pcdl,

posterior centrodiapophyseal lamina; pmedl, posterior medial lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; pocdf-l, postzygapophyseal centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; prcdf, prezygapophyseal centrodiapophyseal fossa; prcdf-l, prezygapophyseal centrodiapophyseal lamina; prdl, prezygodiapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; PSP, postcranial skeletal pneumaticity; pz, postzygapophyses; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal laminae.

## Material and methods

The element described herein, MDPa-Pv 007, is a previously unpublished rebbachisaurid caudal vertebra from the Sierra Chata locality (Neuquén Province) (Fig. 1), Candeleros Formation, Cenomanian (Upper Cretaceous) (Garrido 2010). It is housed in the “Museo del Desierto Patagónico de Añelo”, located in Añelo city, Neuquén Province, Argentina. The serial position was inferred by comparison with the well-preserved vertebral caudal sequences of *Limaysaurus* (Calvo and Salgado 1995; Salgado et al. 2004). Based on the size and development of the wing-like transverse processes, we interpret this element as one of the most anterior caudal vertebrae.

The nomenclature for sauropod vertebral laminae (Wilson 1999, 2012) and fossae (Wilson et al. 2011) are adopted in osteological description. In addition, the osteological correlates linked to pneumaticity are described, on both the

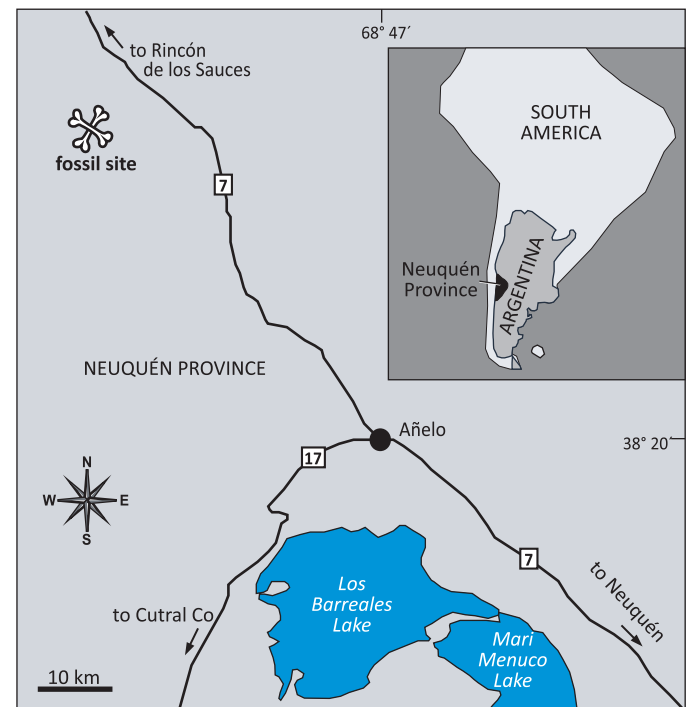


Fig. 1. Maps showing location of Sierra Chata fossil site within Neuquén Province, Argentina.

external and internal surfaces of the bone. The internal anatomy has been characterized from CT images, representing the first published CT scan of a rebbachisaurid caudal vertebra. Here we follow the nomenclature for pneumatic structures proposed by Wedel et al. (2000), Wedel (2003) and O'Connor (2006). The CT scans were carried out in “Clínica de Imágenes SA” located in Neuquén city, Neuquén Province, Argentina. Scans were obtained using a SIEMENS Somatom Definition Edge CT scanner, with a slice thickness of 0.75 mm at 0.8 mm intervals.

## Results

**External anatomy.**—MDPA-Pv 007 is well preserved, possibly the 1st or 2nd caudal vertebra. The centrum is platycocleous, slightly wider than high, with a subcircular outline in anterior and posterior views (Fig. 2A<sub>1</sub>–A<sub>6</sub>). In lateral view, the centrum is anteroposteriorly short and lacks lateral fossae or pleurocoels. However, the centrum has several foramina irregularly distributed on its lateral and lateroventral surfaces (Fig. 2A<sub>7</sub>–A<sub>9</sub>). Such foramina are present on caudal vertebrae of many other neosauropod species (e.g., belonging to *Malawisaurus*, *Rocasaurus*, *Saltasaurus*, and *Tornieria*) including rebbachisaurids belonging to *Tataouinea* and *Comahuesaurus* (Carballido et al. 2012; Cerda et al. 2012; Wedel and Taylor 2013; Fanti et al. 2015; Ibiricu et al. 2015; Zurriaguz and Cerda 2017). The ventral surface is concave, with the posteroventral margin narrower and more ventrally prominent than the anteroventral one in lateral view. The entrance to the neural canal has an elliptical outline, taller dorsoventrally than wide.

The transverse processes are dorsoventrally tall, anteroposteriorly short, and inclined dorsally 25° from the horizontal axis. Transverse processes laterodorsally oriented in anterior caudal vertebrae is a condition also presents in other non-diplodocid diplodocoids as Rebbachisauridae and Dicraeosauridae (e.g., Janensch 1929; Calvo and Salgado 1995; Salgado et al. 2004; Mannion and Barrett 2013; Ibiricu et al. 2013, 2015; Windholz et al. 2022b). In MDPA-Pv-007, the transverse processes are composed of two bone bars: a ventral, robust and laterodorsally oriented bar; and a dorsal, slender and lateroventrally inclined bar (Fig. 2A<sub>1</sub>–A<sub>6</sub>). These bars converge and contact apically, enclosing a system of neural laminae, fossae and fenestrae. The presence of a composite and perforated transverse process is an atypical condition within Sauropoda, being recorded in the first caudal vertebrae of *Limaysaurus tessonei*, and considered as an autapomorphic feature by Calvo and Salgado (1995). Despite sharing this morphological feature, the comparisons between specimens included into *Limaysaurus tessonei* and MDPA-Pv-007 are limited by the poorly preserved anterior caudal vertebrae of the former, which lack the set of neural structures seen in MDPA-Pv-007.

In anterior view, the neural arch presents a wide, elliptic and laterodorsally elongated prezygapophyseal centro-

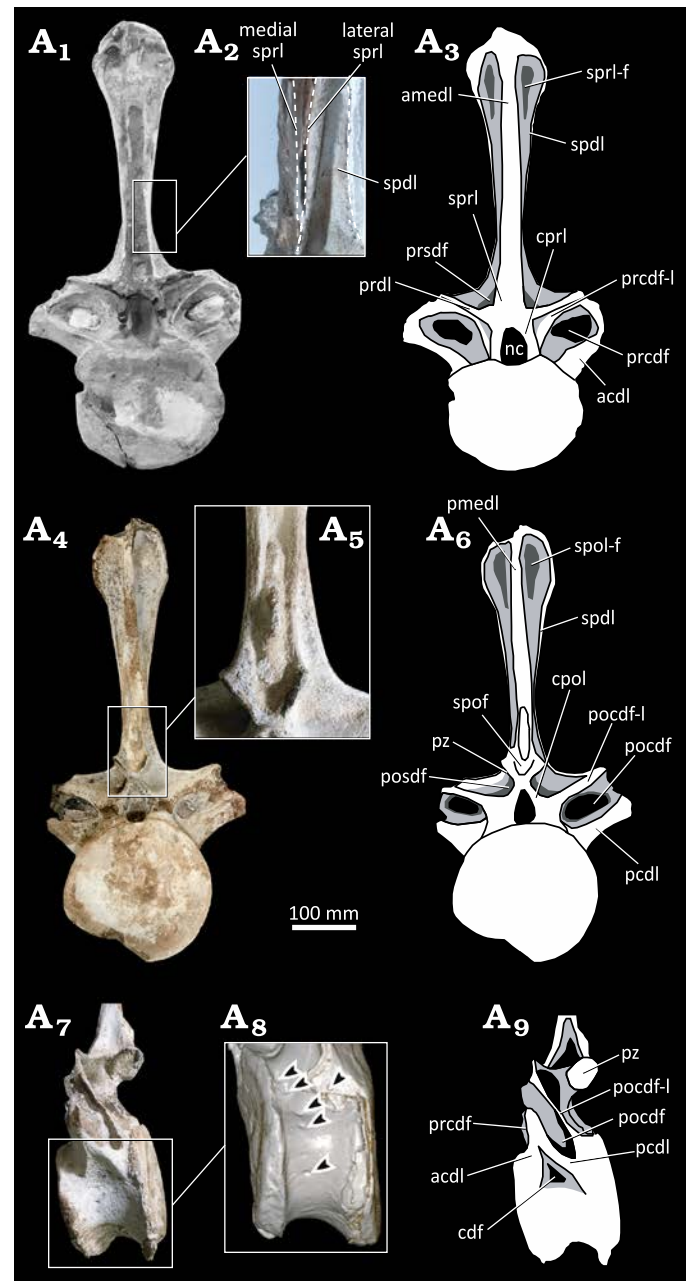


Fig. 2. Rebbachisauridae indet. (MDPA-Pv 007) from the Sierra Chata locality (Candeleros Formation) Cenomanian (Upper Cretaceous). Anterior caudal vertebra in anterior (A<sub>1</sub>, A<sub>3</sub>), posterior (A<sub>4</sub>, A<sub>6</sub>), and left lateral (A<sub>7</sub>, A<sub>9</sub>) views. Close ups showing lateral spinal laminae (A<sub>2</sub>), accessory bony lamina located inside of spof (A<sub>5</sub>), foramina in the lateral surface of the centrum, arrowheads indicate the presence of foramina (A<sub>8</sub>). Abbreviations: acdl, anterior centrodiapophyseal lamina; amedl, anterior medial lamina; cdf, centrodiapophyseal fossa; cpol, centropostzygapophyseal lamina; cprl, centropostzygapophyseal laminae; nc, neural canal; pcdl, posterior centrodiapophyseal lamina; pmedl, posterior medial lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; pocdf-l, postzygapophyseal centrodiapophyseal fossa lamina; posdf, postzygapophyseal spinodiapophyseal fossa; prcdf, prezygapophyseal centrodiapophyseal fossa; prcdf-l, prezygapophyseal centrodiapophyseal fossa lamina; prdl, prezygodiapophyseal lamina; prsd, prezygapophyseal spinodiapophyseal fossa; pz, postzygapophyses; spof, spinopostzygapophyseal fossa; spdl, spinodiapophyseal lamina; spol-f, spinopostzygapophyseal lamina fossa; sprl, spinoprezygapophyseal laminae; sprl-f, spinoprezygapophyseal lamina fossa.

diapophyseal fossa (prcdf), which is dorsally framed by a thin and prominent prezygodiapophyseal lamina (prdl) and ventrally by a robust anterior centrodiapophyseal lamina (acd1). Close to the medial margin of the prcdf, there is a wide prezygapophyseal centrodiapophyseal fossa-lamina (prcdf-l). Obliquely oriented prcdf-l are a feature also present in anterior caudal vertebrae of rebbachisaurids *Itapeuasaurus cajapioensis*, *Katepensaurus goicoecheai*, Rebbachisauridae indet. NHMUK R36636 and Rebbachisauridae indet. MIWG 5384 (Mannion et al. 2011; Mannion and Barrett 2013; Ibiricu et al. 2013, 2015; Lindoso et al. 2019). Articular facets of the prezygapophyses are not preserved. In lateral view, the base of neural arch bears a shallow triangular-shaped centrodiapophyseal fossa (cdf). In posterior view, the neural arch bears well-developed posterior centrodiapophyseal (pcdl) and postzygapophyseal centrodiapophyseal fossa (pocdf-l) laminae. These laminae frame a wide postzygapophyseal centrodiapophyseal fossa (pocdf). Additionally, postzygapophyseal centrodiapophyseal fossa (pocdf-l), centropostzygapophyseal (cpol) and postzygodiapophyseal (podl) laminae, delimit a broad, triangular postzygapophyseal spinodiapophyseal fossa (posdf). The articular facets of postzygapophyses diverge ventrolaterally at an angle of 290°. The vertebra lacks a hypospheneal ridge, as in the anterior caudal vertebrae of some titanosauriforms and most rebbachisaurids (Mannion et al. 2011).

The neural spine is simple, unlike the anterior caudal vertebrae of some diplodocids (whose anterior caudal neural spines are slightly bifurcate distally, e.g., *Barosaurus* and *Diplodocus*, Wedel and Taylor 2013); and tall, at least twice as tall as the vertebral centrum (Table 1), as occurs in most diplodocoids, including rebbachisaurid members. The neural spine is petal-shaped, with a proximal transversal constriction and presents an abrupt distal expansion (triangular lateral process), which is nearly twice as wide transversely as the neural spine base. The transversal constriction of the neural spine is proximal, close to the base of the spine, as in several rebbachisaurids (e.g., *Amazonsaurus maranhensis*, *Itapeuasaurus cajapioensis*, *Limaysaurus tessonei*, *Tataouinea hannibalis*, and Rebbachisauridae indet. MAU-PV-EO-666), and differing from *Demandasaurus darwini*, Rebbachisauridae indet. UNPSJB-PV 580 and Rebbachisauridae indet. MIWG 5384,

Table 1. Measurements (in mm) of new specimen MDPa-Pv 007.

Total height	395
Centrum length	95
Neural spine height	315
Maximum neural spine width	110
Minimum neural spine width	35
Anterior centrum height	150
Anterior centrum width	165
Posterior centrum height	145
Posterior centrum width	155
Minimum ventral width of the centrum	130
Postzygapophyses length	40
Postzygapophyses width	30

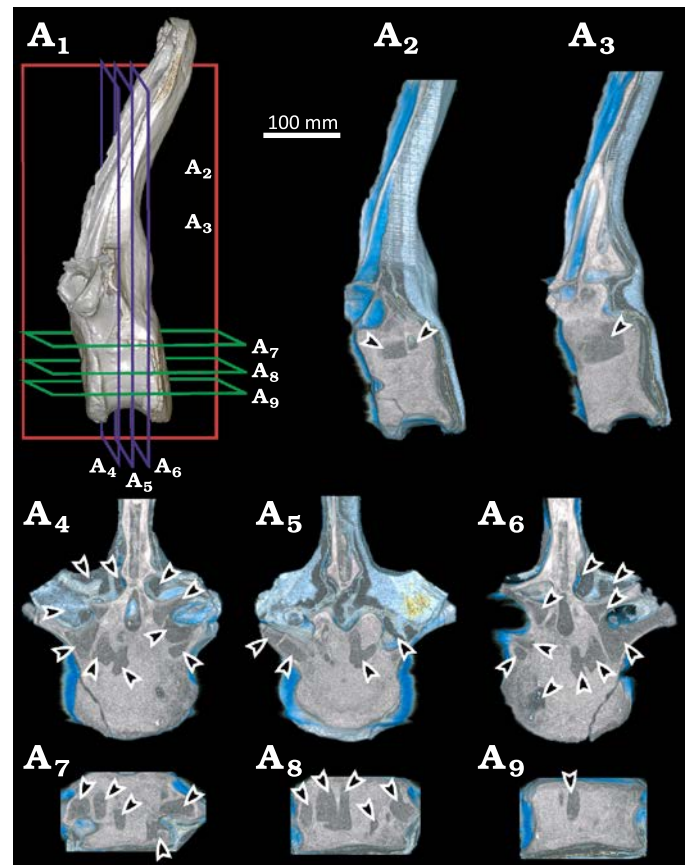


Fig. 3. Three-dimensional reconstruction of Rebbachisauridae indet. (MDPA-Pv 007) from the Sierra Chata locality (Candeleros Formation) Cenomanian (Upper Cretaceous). Vertebra in lateral view (A<sub>1</sub>), parasagittal sections (A<sub>2</sub>, A<sub>3</sub>), transverse sections (A<sub>4</sub>–A<sub>6</sub>), frontal sections (A<sub>7</sub>–A<sub>9</sub>). Arrowheads show the presence of pneumatic internal cameras.

where the minimum width is more distal, over the mid-height of the spine (Fanti et al. 2013, 2015; Bellardini et al. 2022). On the other hand, triangular lateral processes are also present in caudal vertebrae of *Demandasaurus darwini*, *Katepensaurus goicoecheai*, *Nigersaurus taqueti*, *Rebbachisaurus garasbae*, *Zapalasaurus bonapartei*, Rebbachisauridae indet. MIWG 5384, and Rebbachisauridae indet. MAU-PV-EO-666 (Mannion et al. 2011; Whitlock 2011; Ibiricu et al. 2013). In anterior view, the neural spine has a robust anterior medial lamina (amedl) and a pair of bifid spinoprezygapophyseal laminae (medial and lateral sprl) that medially frame wide prezygapophyseal spinodiapophyseal fossa (prsdf). In posterior view the posterior medial lamina (pmedl) is prominent. Unlike caudal vertebrae of other rebbachisaurid sauropods, MDPa-Pv 007 bears an accessory bony lamina located inside the spinopostzygapophyseal fossa (spof). In lateral view, the neural spine is directed backwards as occurs in most anterior caudal vertebrae of rebbachisaurids (Pereda Suberbiola et al. 2003; Gallina and Apesteguía 2005; Torcida et al. 2011; Ibiricu et al. 2013, 2015). Furthermore, the neural spine of MDPa-Pv 007 is straight rather than curved, as in anterior caudal vertebra of specimens belonging to *Amazonsaurus maranhensis* (Carvalho et al. 2003), *Itapeuasaurus cajap-*

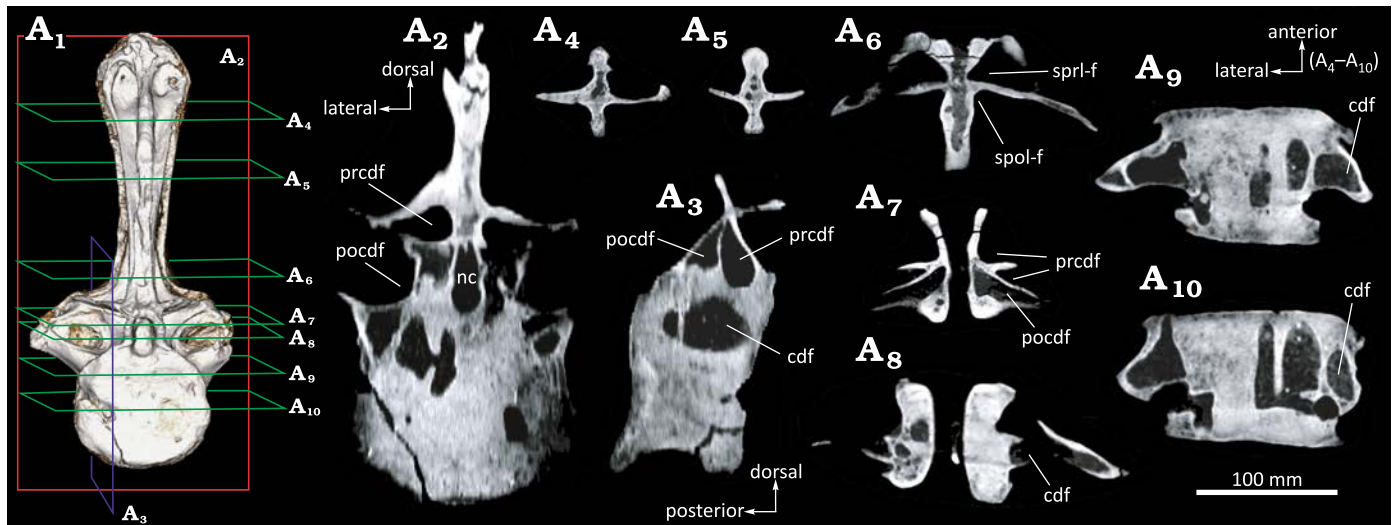


Fig. 4. Selected computed tomographic sections of Rebbachisauridae indet. (MDPA-Pv 007) from the Sierra Chata locality (Candeleros Formation) Cenomanian (Upper Cretaceous). Vertebra in anterior view ( $A_1$ ), transverse section taken at mid-length of the element ( $A_2$ ), parasagittal section ( $A_3$ ), frontal sections ( $A_4$ – $A_{10}$ ). Abbreviations: cdf, centrodiapophyseal fossa; nc, neural canal; pocdf, postzygapophyseal centrodiapophyseal fossa; prcdf, prezygapophyseal centrodiapophyseal fossa; spol-f, spinopostzygapophyseal lamina fossa; sprl-f, spinoprezygapophyseal lamina fossa.

*ioensis* (Lindoso et al. 2019), *Katpensaurus goicoecheai* (Ibárricu et al. 2013), *Limaysaurus tessonei* (Calvo and Salgado 1995; Salgado et al. 2004), and *Tataouinea hannibalis* (Fanti et al. 2013). In anterior view, the apex of the neural spine is convex, as in most of Rebbachisauridae (e.g., *Amazonsaurus maranhensis*, *Demandasaurus darwini*, *Nigersaurus taqueti*, *Rebbachisaurus garasbae*, Rebbachisauridae indet. MIGW 5384; Sereno et al. 1999; Carvalho et al. 2003; Mannion et al. 2011; Torcida et al. 2011; Wilson and Allain 2015), differing from *Zapalasaurus bonapartei* and Rebbachisauridae indet. MAU-PV-EO-666 whose the dorsal surface of the spine is slightly transversely concave.

**Internal anatomy.**—The ventral region of the centrum is thick and solid (Fig. 3). However, the dorsal half of the vertebral centrum is invaded by large, interconnected, enclosed camerae (Figs. 3, 4A<sub>1</sub>–A<sub>4</sub>). The presence of interconnecting large internal chambers (camerae) and relatively thick-walled centra was termed camerate (Britt 1997; Wedel 2003). This form of vertebral pneumatization differs substantially from the typical “camellate” internal structures (Britt 1997) displayed by caudal vertebrae of some saltasaurines as *Rocasaurus* and *Saltasaurus* (Cerda et al. 2012; Zurriaguz and Cerda 2017), “procamerate” condition of diplodocid *Tornieria* (as seen in Wedel and Taylor 2013: fig. 1); and the apneumatic centra of the basal lithostrotian *Malawisaurus* (Wedel 2009: fig. 2) and derived dicraeosaurids as *Pilmatueia* (Windholz et al. 2019). The internal camerae in the centrum of MDPV-007 communicate with foramina on the external surface (Figs. 2A<sub>7</sub>–A<sub>9</sub>, 3A<sub>4</sub>).

The above described internal camerae of the centrum connect internally with the neural arch (Fig. 4A<sub>6</sub>); however, no pneumatic foramina connect to the neural canal, as has been documented in the brachiosaurid *Giraffatitan* (Schwarz and Fritsch 2006) and the saltasaurine *Ibirania* (Aureliano et

al. 2021). The region lateral to the neural canal bears internal camerae that are connected to each other, and simultaneously, with the external surface of the bone (Fig. 4A<sub>1</sub>–A<sub>3</sub>). Neural fossae are broad and deep, reaching almost to the axial plane of the element (Fig. 4A<sub>7</sub>, A<sub>8</sub>). The neural spine presents deep fossae, resulting in a tetradiate outline in cross section. Internally, it presents a variation in bone tissue density that corresponds to small chambers that connect with the rest of the neural arch (Fig. 4A<sub>9</sub>, A<sub>10</sub>).

**Phylogenetic context in Bellardini et al. (2022; Appendix 1).**—We coded 23 characters observed on MDPV-007 into the character matrix of Bellardini et al. (2022) to determine its phylogenetic affinities. The data matrix has 418 characters distributed in 95 OTUs (Operational Taxonomic Units) counting MDPV-007. A heuristic tree search was carried out using TNT v.1.6 software (Goloboff and Catalano 2016). The cladistic analysis retrieved 390 most parsimonious trees (MPTs) of 1429 steps, consistency index (CI) = 0.341; retention index (RI) = 0.692. The obtained trees underwent an extra round of branch swapping (TBR), resulting in 10000 trees of 1429 steps. MDPV-007 was recovered well nested among the rebbachisaurids (Fig. 5A). In general, Rebbachisauridae is well-resolved in this analysis. However, two small polytomies are recovered, but they do not involve the specimen under study; one occurs among the basal rebbachisaurids (*Comahuesaurus*, *Lavocatisaurus*, *Zapalasaurus*, and *Histriasaurus*) and the other one among more derived genera (*Demandasaurus*, *Nigersaurus*, *Tataouinea*, and *Rebbachisaurus*).

The inclusion of MDPV-007 among the rebbachisaurids is based on the absence of the hypospheneal ridge (character 241, shared state with some macronarians; among rebbachisaurids: apomorphic state in *Demandasaurus* and *Tataouinea*; unknown in *Histriasaurus*, *Rayososaurus*, and

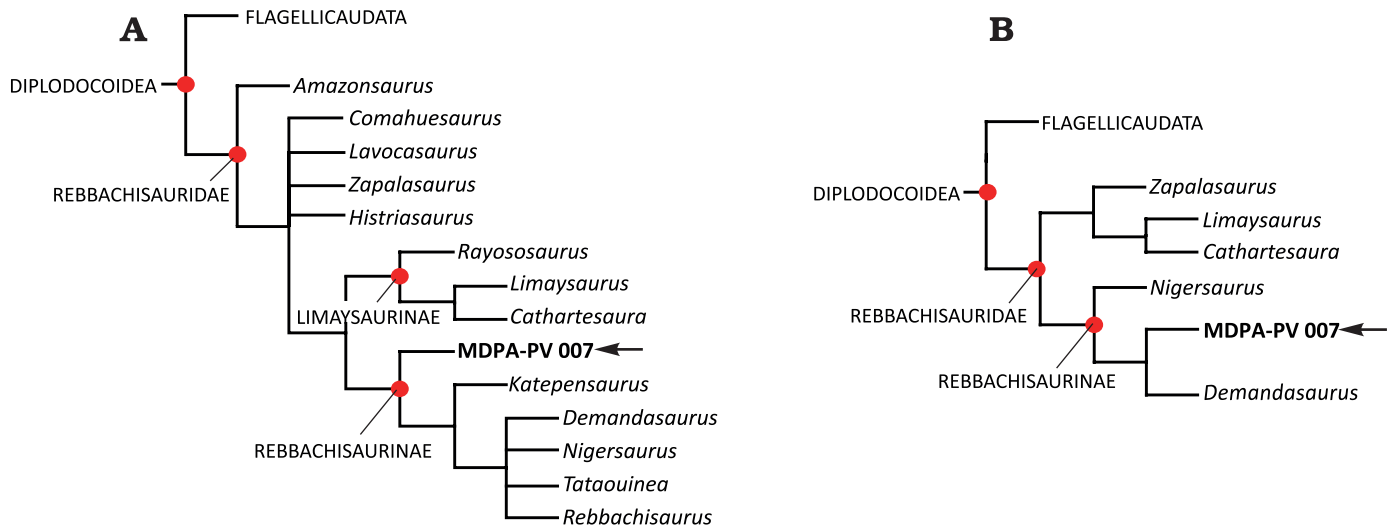


Fig. 5. Simplified strict consensus showing the position of new specimen MDPa-Pv 007 among rebbachisaurids coded in: Bellardini et al. 2022 (A) and Windholz et al. 2022b (B).

*Rebbachisaurus*); and the presence of the spinodiapophyseal lamina (character 244, shared with Lognkosauria; unknown in rebbachisaurids *Comahuesaurus*, *Lavocatisaurus*, *Zapalasauros*, *Histriasaurus*, *Rayososaurus*, and *Limaysaurus*) in anterior caudal vertebrae. At the same time, the analysis shows MDPa-Pv 007 as the most basal member of the subfamily Rebbachisaurinae. Thus, MDPa-Pv 007 is recovered in sister taxon to a clade containing *Katempensaurus* and all more derived rebbachisaurids. This is based on the presence of triangular lateral processes in the neural spines of anterior and middle caudal vertebrae (character 235, also present in *Losillasaurus* and unknown in the *Rebbachisaurus*).

*Phylogenetic context in Windholz et al.* (2022b; Appendix 2).— We coded 34 characters observed on MDPa-Pv 007, resulting in a matrix of 494 characters distributed in 40 OTUs. The cladistic analysis was carried out with the same software and parameters as the previous analysis, retrieved 4 MPTs of 1595 steps (CI = 0.345 and RI = 0.547). Rebbachisauridae is well-resolved in this analysis, with MDPa-Pv 007 well nested among them as a Rebbachisaurinae member (Fig. 5B).

The inclusion of MDPa-Pv 007 among rebbachisaurids is based on the presence of “petal” shaped caudal neural spines (character 304); anterior caudal neural spine, not including arch, more than 1.5 times centrum height (character 312); and transverse processes of anterior caudal vertebrae directed laterodorsally (character 322). Furthermore, MDPa-Pv 007 shares with other Rebbachisaurinae members the presence of triangular lateral processes in caudal neural spines (character 303).

## Discussion

MDPa-Pv 007 presents characters that allow it to be referred to the diplodocoid sauropods, including anterior caudal vertebrae with broad, “wing-like” transverse processes, and the

presence of a tall neural spine, at least twice as tall as the respective vertebral centrum. Furthermore, it shows affinities with the family Rebbachisauridae, such as laterodorsally oriented transverse processes, and lobed-shaped neural spines with a tetradial outline in cross section (Whitlock 2011; Bellardini et al. 2022). The phylogenetic analyses reinforces the referral of the new material to Rebbachisauridae, and more exclusively to Rebbachisaurinae. MDPa-Pv 007 shares synapomorphies with other rebbachisaurids, but differs from all other known rebbachisaurids in having an accessory bony lamina located inside the spinopostzygapophyseal fossa (spof). However, given that MDPa-Pv 007 is a single isolated element, it seems prudent to treat it as Rebbachisaurinae indet., as opposed to erecting a new taxon. Additional specimens may further elucidate the specimen’s phylogenetic and taxonomic status. Nevertheless, MDPa-Pv 007 suggests that the diversity of rebbachisaurids in the Candeleros Formation is greater than currently recognized.

MDPa-Pv 007 adds to the known fossil record of rebbachisaurid genera from the Candeleros Formation, so far represented by *Limaysaurus* (Calvo and Salgado 1995), *Nopcsaspondylus* (Apesteguía 2007), *Rayososaurus* (Bonaparte 1996; Carballido et al. 2010) and some remains of Rebbachisauridae indet. (Paulina Carabajal et al. 2016). These records, plus those from the Alcántara Formation (Lindoso et al. 2019), Bajo Barreal Formation (Ibiricu et al. 2012, 2015), and Huincul Formation (Calvo and Salgado 1995; Gallina and Apesteguía 2005; Apesteguía et al. 2010; Haluza et al. 2012; Bellardini et al. 2022) show that representatives of this family constituted one of the most diverse sauropod clades during the Cenomanian of South America. This caudal vertebra is the first record of a rebbachisaurid sauropod in the Sierra Chata locality. We noted that, despite the extensive record of rebbachisaurids, MDPa-Pv 007 is possibly the best preserved anterior caudal vertebra of the family. The excellent preservation of MDPa-Pv 007, combined with CT images, allows us to document external fos-

sae and foramina that connect to larger internal chambers. Together, these features constitute unambiguous evidence of pneumaticity (O'Connor 2006), and the best documentation to date of caudal pneumaticity in rebbachisaurids (see Wedel and Taylor 2013 and references therein).

The centrum of MDPA-Pv 007 is camerate, with large interconnected internal chambers and extensive fossae on the neural arch. The dorsal half of the centrum and the lower portion of the neural arch are extensively pneumatized, but internal pneumatization of both the centrum and the neural arch and spine is less extensive than in the caudal vertebrae of saltasaurine sauropods such as *Rocasaurus* and *Saltasaurus* (Cerda et al. 2012; Zurriaguz and Cerda 2017). Both the external foramina and the internal pneumatic chambers in MDPA-Pv 007 are bilaterally asymmetric, as often occurs in other sauropods with caudal pneumaticity (Wedel and Taylor 2013). This asymmetry is consistent with the hypothesis that the pneumatization process was essentially opportunistic (Witmer 1997), possibly as a result of developing pneumatic diverticulae following inherently variable blood vessels (Taylor and Wedel 2021). Although most rebbachisaurids are small- to medium-sized sauropods, they were still large terrestrial animals; e.g., estimates for *Rebbachisaurus garasbae* suggest a body mass of 7915–12 015 kg (Wilson and Allain 2015), while the estimated length for *Tataouinea hannibalis* was 12 meters (Fanti et al. 2015); *Maraapunisaurus fragillimus* would have been one of the largest known sauropods if it was as large as claimed (Carpenter 2018). Extensive skeletal pneumaticity, as shown by the new specimen and by other rebbachisaurids, is consistent with the hypothesis that by reducing bone mass, the muscular energy necessary to propel the body would consequently be reduced (O'Connor 2009; Ibiricu et al. 2015).

Caudal pneumaticity has a complex phylogenetic distribution among neosauropods (Wedel and Taylor 2013). Pneumatic tail vertebrae have been documented in numerous brachiosaurids (*Giraffatitan*, *Cedarosaurus*, *Venenosaurus*) and titanosaurians, especially saltasaurids (*Neuquensaurus*, *Rocasaurus*, and *Saltasaurus*), and in virtually all diplodocoids, including *Haplocanthosaurus*, diplodocids, and rebbachisaurids, but excluding dicraeosaurids (Cerda et al. 2012; Fanti et al. 2013; Wedel and Taylor 2013). Caudal pneumaticity may have evolved independently in diplodocoids and titanosauriforms, or it could be ancestral for Neosauropoda but secondarily lost in a few lineages (e.g., Dicraeosauridae, *Camarasaurus*). We note that even in clades in which caudal pneumaticity is the norm, certain taxa lack it, presumably through phylogenetic reversals; examples include *Nigersaurus* among Rebbachisauridae and *Opisthocoelicaudia* among derived titanosaurs. It should be noted, however, that there are few broad studies of caudal pneumaticity in sauropods. Future investigations, taking advantage of new technologies, will hopefully allow us to further unravel the phylogenetic distribution and paleobiological implications of pneumaticity in sauropod dinosaurs and other fossil archosaurs.

## Conclusions

We present a new caudal vertebra MDPA-Pv 007 from Candeleros Formation (Cenomanian, Upper Cretaceous) Patagonia, Argentina. External anatomy indicates unequivocal affinities to Rebbachisauridae, and two phylogenetic analyses recover the specimen as a member of the more exclusive clade Rebbachisaurinae. The new specimen differs from all other known rebbachisaurids in having an accessory bony lamina located inside the spinopostzygapophyseal fossa (spof). However, given that MDPA-Pv 007 is a single isolated element, we prefer to treat it as Rebbachisaurinae indet. Also, paleobiological aspects of caudal pneumaticity of a new rebbachisaurid specimen were studied. This specimen preserves unambiguous evidence of pneumaticity and is the best documentation to date of pneumaticity in rebbachisaurid caudal vertebrae. This research complements the few studies of caudal pneumaticity in neosauropods, and helps to elucidate its complex phylogenetic distribution. Finally, in light of new findings and taking advantage of new technologies, we encourage continuing investigating the phylogenetic distribution and paleobiological implications of pneumaticity in sauropod dinosaurs and other fossil archosaurs.

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