

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/315502961>

A saltasaurine titanosaur (Sauropoda: Titanosauriformes) from the Angostura Colorada Formation (upper...

Article in *Cretaceous Research* · March 2017

DOI: 10.1016/j.cretres.2017.03.016

CITATIONS

0

READS

51

4 authors, including:



[Virginia Zurriaguz](#)

Universidad Nacional de Río Negro

10 PUBLICATIONS 15 CITATIONS

[SEE PROFILE](#)



[Agustin G. Martinelli](#)

Universidade Federal do Rio Grande do Sul

132 PUBLICATIONS 1,178 CITATIONS

[SEE PROFILE](#)



[Martin Ezcurra](#)

Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"

95 PUBLICATIONS 1,214 CITATIONS

[SEE PROFILE](#)

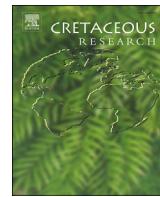
Some of the authors of this publication are also working on these related projects:



Testing the effect of different terminal sampling strategies in phylogenetic analyses using morphological data matrixes [View project](#)



Recovery of continental tetrapod communities in Southwestern Pangaea following the Permo-Triassic mass extinction [View project](#)



A saltasaurine titanosaur (Sauropoda: Titanosauriformes) from the Angostura Colorado Formation (upper Campanian, Cretaceous) of northwestern Patagonia, Argentina

Virginia Zurriaguz ^{a, b,*}, Agustín Martinelli ^c, Guillermo W. Rougier ^d, Martín D. Ezcurra ^{b, e}

^a Instituto de Investigaciones en Paleobiología y Geología, Universidad Nacional de Río Negro, Avenida Roca 1242, General Roca, 8332, Río Negro, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Avenida Rivadavia 1917, C1033AAJ, Ciudad Autónoma de Buenos Aires, Argentina

^c Laboratório de Paleontologia de Vertebrados, Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul (UFRGS), Ave. Bento Gonçalves 9500, Agronomia, 91540–000, Porto Alegre, RS, Brazil

^d Department of Anatomical Sciences and Neurobiology, University of Louisville, 511 Floyd Street (40202), Louisville, USA

^e Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avenida Ángel Gallardo 490, C1405DJR, Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 24 December 2016

Accepted in revised form 18 March 2017

Available online 21 March 2017

Keywords:

Saltasaurini

Caudal vertebra

Osteoderm

Pneumaticity

South America

ABSTRACT

Saltasaurine titanosaurs are characterized by their relatively small size compared to other sauropods, extreme postcranial pneumaticity, and dermal armour covering the body. This group has been reported in the Upper Cretaceous of the Lecho, Allen, and Anacleto formations of Argentina. We describe here a new saltasaurine specimen (MACN-Pv RN 233) from the Campanian of the Angostura Colorado Formation (Río Negro Province) that is represented by eight caudal vertebrae and six osteoderms. This specimen is described in detail and its phylogenetic relationships with the other three known saltasaurines, as well as its implications to the knowledge of caudal vertebra and osteoderm anatomy, are discussed. Our results place MACN-Pv RN 233 more closely related to *Saltasaurus loricatus* and *Rocasaurus muniozi* than to *Neuquensaurus australis*. MACN-Pv RN 233 possesses a combination of features that differ from other saltasaurines, but because of the fragmentary nature of the specimen we decided for the sake of taxonomic stability to not erect a new taxon. This specimen shows the first unambiguous evidence of chevron pneumatisation for a sauropodomorph, implying a broader osteological invasion of the diverticula from the abdominal air sac than previously thought for this group of dinosaurs. MACN-Pv RN 233 preserves two osteoderm morphotypes, one similar to those reported for *Neuquensaurus australis* and *Saltasaurus loricatus*. This new specimen expands the distribution of the group to a new geological unit and increases the dinosaur diversity known for the Angostura Colorado Formation.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

Titanosaurs were the dominant medium to large-sized herbivores in Gondwanan continental ecosystems during the Cretaceous ([García et al., 2015](#)). The deepest nested clade within Titanosauria is Saltasaurinae, which is composed of relatively small-sized animals (adult total length around 8 m) currently endemic to the Late

Cretaceous of Argentina ([Salgado and Bonaparte, 2007](#)). Only three saltasaurine species have been formally described so far: *Neuquensaurus australis* ([Lydekker, 1893](#)), *Rocasaurus muniozi* [Salgado and Azpilicueta 2000](#), and *Saltasaurus loricatus* [Bonaparte and Powell 1980](#). The first two species come from the Anacleto and Allen formations, respectively, of the Río Negro Province (northwestern Patagonia), and the latter from the Lecho Formation of the Salta Province (northern Argentina). Saltasaurines have extreme axial and appendicular pneumaticity ([Cerda et al., 2012](#)), represented by a camellate internal bone structure that is invaded by pneumatic diverticula through large cortical foramina ([O'Connor and Classens, 2005; O'Connor, 2006; Cerda et al., 2012](#)). This group exhibits a dorsal armour distributed along the longitudinal axis of the body that is composed of osteoderms that do not

* Corresponding author. Instituto de Investigaciones en Paleobiología y Geología, Universidad Nacional de Río Negro, Avenida Roca 1242, General Roca, 8332, Río Negro, Argentina.

E-mail addresses: vzurriaguz@gmail.com (V. Zurriaguz), agustin_martinelli@yahoo.com.ar (A. Martinelli), guillermo.rougier@louisville.edu (G.W. Rougier), martinezcurra@yahoo.com.ar (M.D. Ezcurra).

articulate with each other, in addition to small ossicles (Powell, 1980; Salgado, 2003; Cerda and Powell, 2010; Cerda et al., 2015).

Saltasaurines are an interesting group of dinosaurs because of their restricted geographic and temporal occurrence to the latest Cretaceous of Argentina and their phylogenetic position as some of the most derived titanosaurs (e.g. Calvo et al., 2007; Coria et al., 2013; Li et al., 2014; Salgado et al., 2014). Here, we enrich the saltasaurine record with the description of a new specimen collected from the uppermost Cretaceous Angostura Colorado Formation, northwestern Patagonia, Argentina. This specimen is described and compared in detail and its phylogenetic relationships are discussed.

2. Geological and palaeontological settings of MACN-Pv RN 233

MACN-Pv RN 233 comes from the Angostura Colorado Formation (Volkheimer, 1973). This unit crops out at several spots on the southwest of the Río Negro Province, but, only two dinosaur-bearing localities have been reported so far. The first locality, known as Casa de Piedra (Estancia Maquinchao), yielded the partial postcranium of the holotype of *Aeolosaurus rionegrinus* and isolated teeth and eggshells of indeterminate titanosaurid sauropods (Powell, 1987). More recently, Cruzado-Caballero (2015) reported hadrosaurid ornithischian remains from a second locality, Bajo Colorado. The Angostura Colorado Formation has been poorly studied and available geological information is scarce. The unit was originally described by Volkheimer (1973), who considered it as an outcrop of the western sector of the North Patagonian Massif. The Angostura Colorado Formation was deposited within a rift sequence and is divided into three members, which show vertical and lateral variations (Manassero, 1997) (Fig. 1). The lower member is composed of alluvial fan gravels, the middle by sandstones deposited in a braided system, and the upper member by shales deposited in a flood plain (Manassero, 1997). The Angostura Colorado Formation lacks well constrained biostratigraphical information, but Manassero (1997) considered it as upper Campanian because there is an unconformity with the base of the Paso del Sapo Formation that is interpreted

to correspond to the late Campanian tectonic event at the end of the Neuquenian cycle (Uliana and Dellape, 1981).

Institutional Abbreviations

MACN-Pv RN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Paleovertebrados, Colección Río Negro, Buenos Aires, Argentina.

MCS-Pv: Museo de Cinco Saltos, Cinco Saltos, Río Negro, Argentina.

MLP-Pv CS/Ly: Museo de La Plata, Sección Paleontología de Vertebrados, La Plata, Buenos Aires, Argentina.

MMCH: Área Laboratorio e Investigación del Museo “Ernesto Bachmann”, Villa El Chocón, Neuquén, Argentina.

MPCA-Pv: Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina.

3. Materials and methods

3.1. Anatomical description, computed tomography scans, and comparisons

This study is based on the first hand description of MACN-Pv RN 233. This specimen is composed of eight caudal vertebrae (MACN-Pv RN 233 1–8) and six osteoderms (MACN-Pv RN 233 a–f). The caudal vertebrae were prepared mechanically with air scribers and the osteoderms chemically, with acetic acid 5% that was subsequently neutralized with water during a period ten times longer than the exposition of the bone to the acid. Computed tomography (CT) scans of an osteoderm (MACN-Pv RN 233a) and a vertebra (MACN-Pv RN 233 5) were conducted in the Clínica La Sagrada Familia (Buenos Aires) on a 64-channel axial CT scanner. The CT scans were analysed and processed with the program InVesalius 3.0 (Amorim et al., 2015). MACN-Pv RN 233 was compared mainly with the other three known saltasaurines: *Rocasaurus muniozi*, *Neuquensaurus australis*, and *Saltasaurus loricatus*. These comparisons were made after first hand observations of the specimens and published bibliography. All the material assigned to *Rocasaurus muniozi* came from the Allen Formation (middle Campanian-lower Maastrichtian), at the Salitrillo Moreno locality (Río Negro Province, Argentina) (Salgado and Azpilicueta, 2000; García and Salgado, 2013). The examined specimens of *Neuquensaurus australis* were recovered from the localities of Cinco Saltos and Lago Pellegrini (Río Negro Province, Argentina) in deposits of the Anacleto Formation (lower Campanian) (Powell, 2003; Salgado et al., 2005; Otero, 2010). Finally, *Saltasaurus loricatus* was collected in deposits of the Lecho Formation (?upper Campanian-Maastrichtian) at El Brete locality (Salta Province, Argentina) (Bonaparte and Powell, 1980; Powell, 1987; Powell, 1992; Powell, 2003).

The nomenclature of the vertebral laminae follows Wilson (1999) and of the vertebral fossae follows Wilson et al. (2011). We use Romerian terminology (Wilson, 2006), which divides the body into anterior, posterior, ventral, and dorsal portions (Romer, 1956). Nomenclature for internal pneumatic structures follows Britt (1997) and Wedel et al. (2000). Nomenclature of the haemal arches follows Otero et al. (2011) and nomenclature of the osteoderms follows D'Emic et al. (2009). The caudal vertebrae were numbered from 1 to 8 following a logic sequence in the tail but not necessarily a continuous anteroposterior sequence (Table 1). Osteoderms were ordered from “a” to “f”, following a decreasing size sequence (Table 1A and B).

3.2. Phylogenetic analysis

In order to test the phylogenetic affinities of MACN-Pv RN 233, this specimen was included in the data matrix published by Salgado

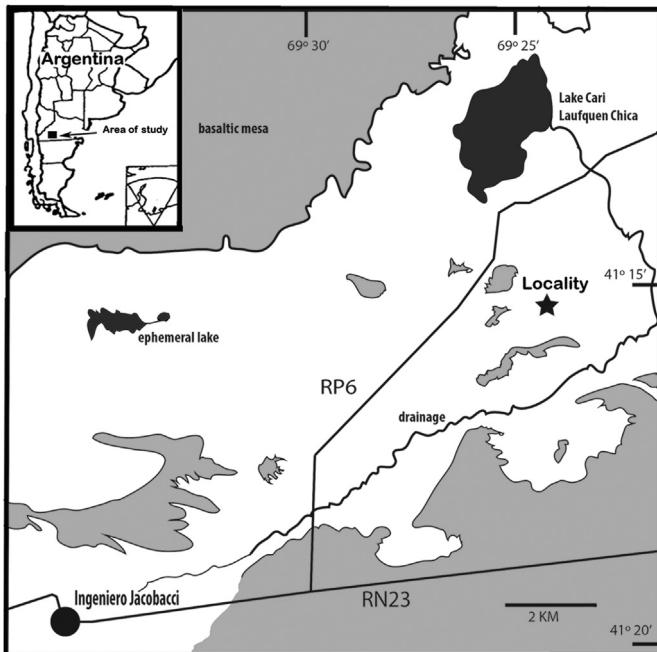


Fig. 1. Location of the Angostura Colorado Formation in southwestern Río Negro Province, Patagonia, Argentina. Modified from Manassero (1997).

Table 1A

Saltasaurinae indet. (MACN-Pv RN 233) from the Angostura Colorada Formation: list of caudal vertebrae (A).

	MACN-Pv RN 233-1	MACN-Pv RN 233-2	MACN-Pv RN 233-3	MACN-Pv RN 233-4	MACN-Pv RN 233-5	MACN-Pv RN 233-6	MACN-Pv RN 233-7	MACN-Pv RN 233-8
Centrum length	18.32	18.33	20	18.8	16.6	18	16.34	17.71
Total height	20.5	14.05	16.66	14.57	12.76	14.16	13.12	—
Anterior height	8.44	9.40	11.64	9.48	8.1	8.75	8.33	10.04
Posterior height	—	8.60	—	7.49	7.82	7.74	6.1	[5.2]
Anterior width	8.85*	11.61	11.82	10.35	10	10.25	9.37	[9.27]
Posterior width	—	10.84	—	9.58	10.62	11.87	11.55	8.12
Distance between zygapophyses	23.85	18.95	20.01	18.43	18.70	20.10	19.34	—

Note: All values are expressed in centimeters (cm). “*” indicates estimated values, “—” indicates lack of data, and “[]” indicates incomplete measurement.

Table 1B

Saltasaurinae indet. (MACN-Pv RN 233) from the Angostura Colorada Formation: osteoderms (B).

	MACN-Pv RN 233a	MACN-Pv RN 233b	MACN-Pv RN 233c	MACN-Pv RN 233d	MACN-Pv RN 233e	MACN-Pv RN 233f
Maximum longitudinal length	23.63	13.42	14.76	13.19	10.11	6.21
Maximum transverse width	14.98	9.50	7.76	—	7.44	4.85
Maximum height	8.21	5.47	4.01	4.37	24.6	2.16

Note: All values are expressed in centimeters (cm). “—” indicates lack of data.

et al. (2014), which is focused on the phylogenetic relationships of derived titanosaurian sauropods. The presence of a lateral pneumatic foramen on the centrum of anterior and middle caudal vertebrae was added as an additional character and some scorings were modified for *Saltasaurus loricatus* and *Rocasaurus muniozi* (see Supplementary Information). The modified version of the data matrix was analysed under equally-weighted parsimony using TNT 1.5 (Goloboff et al., 2008). A heuristic search of 50 replications of Wagner trees followed by TBR branch-swapping algorithm (holding 10 trees per replication) was performed. It was not necessary to conduct a second round of TBR branch swapping. Branches with a maximum possible length of zero among any of the recovered most parsimonious trees (MPTs) were collapsed (rule 3 of Swofford and Begle, 1993; Coddington and Scharff, 1994). All characters were treated as unordered (= non-additive), following the original setting of Salgado et al. (2014). As a measure of branch support, decay indices (= Bremer support) were calculated (Bremer, 1988, 1994), and as a measure of branch stability, a bootstrap resampling analysis (Felsenstein, 1985) was conducted, performing 10,000 pseudoreplications. Both absolute and GC (i.e., difference between the frequency whereby the original group and the most frequent contradictory group are recovered in the pseudoreplications; Goloboff et al., 2003) bootstrap frequencies are reported. Finally, analyses forcing topological constraints were conducted to find the minimum number of steps necessary to force the position of MACN-Pv RN 233 in alternative suboptimal positions.

4. Systematic palaeontology

Dinosauria Owen 1842
 Sauropoda Marsh 1878
 Titanosauria Bonaparte and Coria 1993
 Saltasaurinae Powell 1992
 Gen. et sp. indet.

Material. MACN-Pv RN 233: partial tail, including four anterior-middle caudal vertebrae, two of them fused to their respective chevrons (MACN-Pv RN 233-1–4), four posterior caudal vertebrae (MACN-Pv RN 233-5–8), and six associated osteoderms (MACN-Pv RN 233-a–f).

Geographic and Stratigraphic occurrence. MACN-Pv RN 233 was found in January of 1987 during the XII Palaeontological Expedition to Patagonia led by Dr. José F. Bonaparte (Bonaparte and

Migale, 2010), in which one of the authors was present (GWR). The quarry that yielded this specimen is located within 100 m of the coordinates 41°15'22.83"S 69°24'31.99"W, between the Centinela Hill and Carri Laufquen Lake, east to the road to Ingeniero Jacobacci city (southwestern Río Negro Province, Argentina) (Fig. 1); Angostura Colorada Formation (upper Campanian).

5. Results

5.1. Description

MACN-Pv RN 233 includes eight caudal vertebrae that belong to the anterior-middle and posterior regions of the tail (Table 1A), and six osteoderms (Table 1B). The bones are preserved in a reddish fine-grained sandstone and possess several cracks and broken surfaces, exposing the internal structure of the bone. These elements are slightly taphonomically distorted and the bone surface is generally well preserved and light brownish to yellowish. The available caudal vertebrae possess an anatomical variation between each other that is congruent with the anterior to posterior morphological changes documented in the tail of titanosaur sauropods, including elongation of the centra and decrease in the development of the transverse processes and neural spines, and depth and extension of the spinoprezygapophyseal fossae (e.g. Salgado and García, 2002). Beyond this variation, the vertebrae possess a series of features that remain constant through the sampled sequence. The centra are strongly procoelic, being considerably anteroposteriorly longer than tall. Most of the ventral surface of the centra is invaded by an anteroposteriorly long and considerably deep median fossa, which is completely subdivided by a longitudinal septum. The exposed internal structure of the centra and neural arches is camellate in all the elements, as occurs in the anterior two-thirds of the caudal series of other saltasaurine titanosaurs (Cerdá et al., 2012). CT data of one of the posterior caudals (MACN-Pv RN 233-5) shows that the camellate internal structure extends through the entire centrum and neural arch. The neurocentral suture is closed in all the vertebrae, probably indicating that the animal was not a juvenile at the time of its death (Brochu, 1996). In addition, the proximal pedicles of the chevrons are completely fused to their respective centrum in two of the preserved anterior-middle caudal vertebrae (MACN-Pv RN 233-2, 4) and only one pedicle in one of the posterior caudal vertebrae (MACN-Pv RN 233-

5). The internal structure of the chevrons is also camellate in the broken areas (e.g. MACN-Pv RN 233-2).

5.1.1. Anterior-middle caudal vertebrae

There are four preserved anterior-middle caudal vertebrae (MACN-Pv RN 233-1–4) (Fig. 2 A–K). Three of these vertebrae are fairly complete (MACN-Pv RN 233-2 lacks the left prezygapophysis and MACN-Pv RN 233-3 lacks the right posterolateral corner of the centrum). The right side of MACN-Pv RN 233-1 is heavily weathered. The anterior-middle caudal centra are 1.72–2.17 times longer

than its anterior height. The anterior and posterior articular surfaces of the centrum are placed at approximately the same dorsoventral level. The anterior surface is sub-quadrangular to sub-rectangular, being 1.01–1.23 times broader than dorsoventrally tall, and homogenously concave. The posterior surface is sub-oval, being 1.26–1.28 transversely broader than tall. This articular surface is semi-spherical in lateral view (Fig. 2A, C, F, I), in which its dorsal and ventral margins are placed at the same anteroposterior level, resembling the condition in the anterior caudal vertebrae of most non-aelosaurine titanosaurs (e.g. *Bonatitan reigi*: [Martinelli and Forasiepi, 2004](#); *Saltasaurus loricatus*: [Powell, 1992, 2003](#); *Neuquensaurus australis*: [Salgado et al., 2005](#)). The ventral margin of the centrum of the anterior-middle caudal vertebrae is straight to slightly concave in posterior view (Fig. 2E, H, K). The centrum is slightly constricted transversely at mid-length, with concave lateral margins. The ventral margin of the centrum is dorsally arched in lateral view and separated from the lateral surface by a longitudinal, distinct change in slope. The ventral surface possesses an oval fossa (76.3 mm of maximum length versus 51.5 mm of maximum width in MACN-Pv RN 233-4) (Fig. 3) that occupies most of the area between the anterior and posterior articular facets, and it is anteriorly displaced from the mid-length of the centrum, resembling

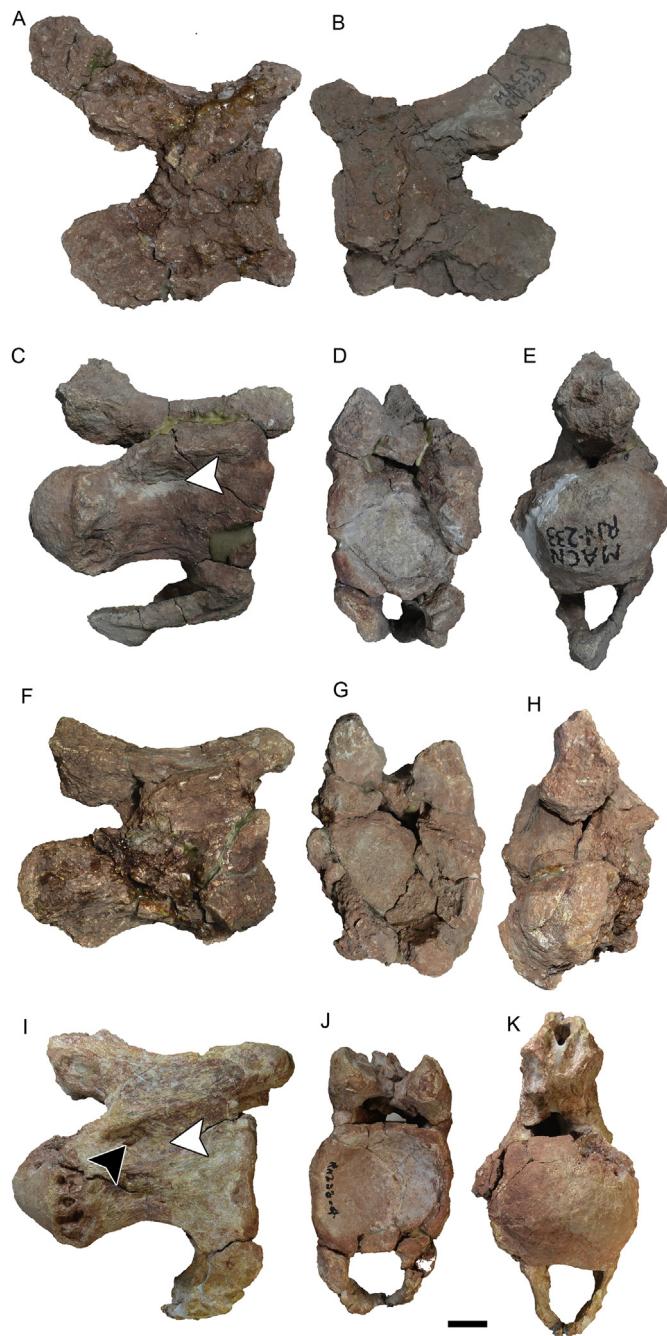


Fig. 2. Saltasaurinae indet. from the Angostura Colorado Formation. Anterior caudal vertebrae of MACN-Pv RN 233 in lateral, anterior and posterior views showing their main anatomic features. MACN-Pv RN 233-1 (A,B), MACN-Pv RN 233-2 (C,D,E), MACN-Pv RN 233-3 (F,G,H) and MACN-Pv RN 233-4 (I,J,K). The black arrow indicates the lateral pneumatic foramen of MACN-Pv RN 233-4. The white arrow indicates the shallow depression below the neural arch. Scale bar: 3 cm.



Fig. 3. Saltasaurinae indet. from the Angostura Colorado Formation: MACN-Pv RN 233-4 in ventral view showing the ventral fossa divided by a bifurcated longitudinal septum indicated by a black arrow. Scale bar: 1 cm.

the condition in the anterior caudals of *Saltasaurus loricatus* (Powell, 1992, 2003) and *Rocasaurus muniozi* (García and Salgado, 2013). *Neuquensaurus australis* lacks a ventral fossa on the anterior-middle caudal vertebrae (Salgado et al., 2005). The ventral fossa of the anterior-middle caudals of MACN-Pv RN 233 is relatively deep, invading slightly less than 1/3 of the height of the centrum, as occurs in *Saltasaurus loricatus* (Powell, 1992, 2003). By contrast, the ventral fossa is considerably deeper in a referred caudal of *Rocasaurus muniozi* (García and Salgado, 2013: fig. 7f). The longitudinal septum that subdivides the ventral fossa bifurcates anteriorly and posteriorly in the two best preserved anterior-middle caudals of the specimen (MACN-Pv RN 233-3, 4) (Fig. 3). The posterior bifurcation is broader than the anterior one and delimits a subtriangular blind depression. A bifurcated longitudinal ventral septum is absent in the anterior-middle caudal vertebrae of *Saltasaurus loricatus* (Powell, 1992, 2003) and *Rocasaurus muniozi* (e.g. MPCA-PV 58; Salgado and Azpilicueta, 2000; García and Salgado, 2013). The ventral fossa of at least one of the anterior-middle caudals possesses an accessory fossa that is subdivided by a longitudinal ridge (MACN-Pv RN 233-4) (Fig. 3). The facets for articulation with the chevrons are restricted to the anterior region of the ventral surface of the centrum and the articular facet is slightly convex in the elements that are not fused to their respective chevron (MACN-Pv RN 233-1, 3).

The lateral surface of the centrum is slightly dorsoventrally convex and possesses a single pair of oval and medium-sized pneumatic foramina (Fig. 2C, F, I), as occurs in the anterior-middle caudal vertebrae of *Saltasaurus loricatus* (Powell, 1992, 2003) and *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000). By contrast, *Neuquensaurus australis* lacks lateral foramina in the caudal series (MCS-5 and MLP CS/MLP Ly). The lateral foramen of MACN-Pv RN 233 has a sub-horizontal to slightly oblique main axis, and it is internally subdivided by a diagonal septum, which is anterodorsally to posteroventrally oriented in one of the anterior-middle caudals (MACN-Pv RN 233-4) (Fig. 2C, F, I). This foramen is slightly posteriorly displaced from the mid-length of the centrum and placed immediately below the base of the neural arch. The size, morphology, and depth of these pneumatic foramina and fossa varies between the sides of the same element, as occurs in the postcranial axial series of other titanosaurs (e.g. Santucci and Bertini, 2006; Zurriaguz and Álvarez, 2013).

At the boundary between the centrum and neural arch, the anterior-middle caudals possess a low, anteroposteriorly elongated, and dorsoventrally thick transverse process that decreases in height posteriorly in the sequence. The main axis of the transverse process is slightly anterodorsally to posteroventrally oriented and becomes more horizontal backwards in the caudal sequence. A very shallow depression is presents dorsal to the base of the transverse process, on the lateral surface of the neural arch. The prezygapophysis slants slightly dorsally in lateral view and the postzygapophysis is sub-horizontal. The prezygapophysis extends anteriorly beyond the level of the anterior border of the centrum, but the postzygapophysis does not extend posteriorly beyond level of the posterior facet of the centrum, as occurs in the anterior-middle vertebrae of most titanosauriforms (e.g. *Chubutisaurus insignis*: Carballido et al., 2011; *Oversaurus paradisosorum*: Coria et al., 2013; *Saltasaurus loricatus*: Powell, 1992). The lateral walls of the neural canal are dorsoventrally low and, as a result, its anterior and posterior opening is transversely broader than tall. The dorsoventral compression of the neural canal is stronger anteriorly. The articular facet of the prezygapophysis is dorsomedially facing at an angle of around 45°. Similarly, the articular facet of the postzygapophysis is ventromedially oriented. The neural spine is approximately as tall as the centrum in the possibly most anteriorly preserved caudal (MACN-Pv RN 233-1) (Fig. 2A, B). The neural spine

is restricted to the posterior region of the neural arch and does not extend anteriorly beyond the level of the anterior margin of the postzygapophyseal facet (Fig. 2A, B). The base of the neural spine extends posteriorly beyond the rest of the neural arch. The base of the neural spine is sub-quadrangular in cross-section, as in other saltasaurines (Salgado et al., 2014: character 52). The pair of spinoprezygapophyseal laminae is sharp and delimits a deep and broad spinoprezygapophyseal fossa, as occurs in several other titanosaurs (e.g. *Saltasaurus loricatus*: Bonaparte and Powell, 1980; *Narambutenitan palomoi*: Filippi et al., 2011a,b; *Bonatitan reigi*: Martinelli and Forasiepi, 2004; *Petrobrasaurus puestohernandezi*: Filippi et al., 2011a,b; *Baurutitan britoi*: Kellner et al., 2005; *Tambatitanis amicitiae*: Saegusa and Ikeda, 2014).

5.1.2. Posterior caudal vertebrae

There are four preserved posterior caudal vertebrae (MACN-Pv RN 233-5–8) (Fig. 4A–L). The morphology of these vertebrae is generally consistent with that of the anterior-middle caudals and here we describe only the features that differ between both regions. Three of the posterior caudals are fairly complete (MACN-Pv RN 233-5–7), but a fourth vertebra preserves only its centrum (MACN-Pv RN 233-8). The posterior centra are 1.76–2.06 times longer than

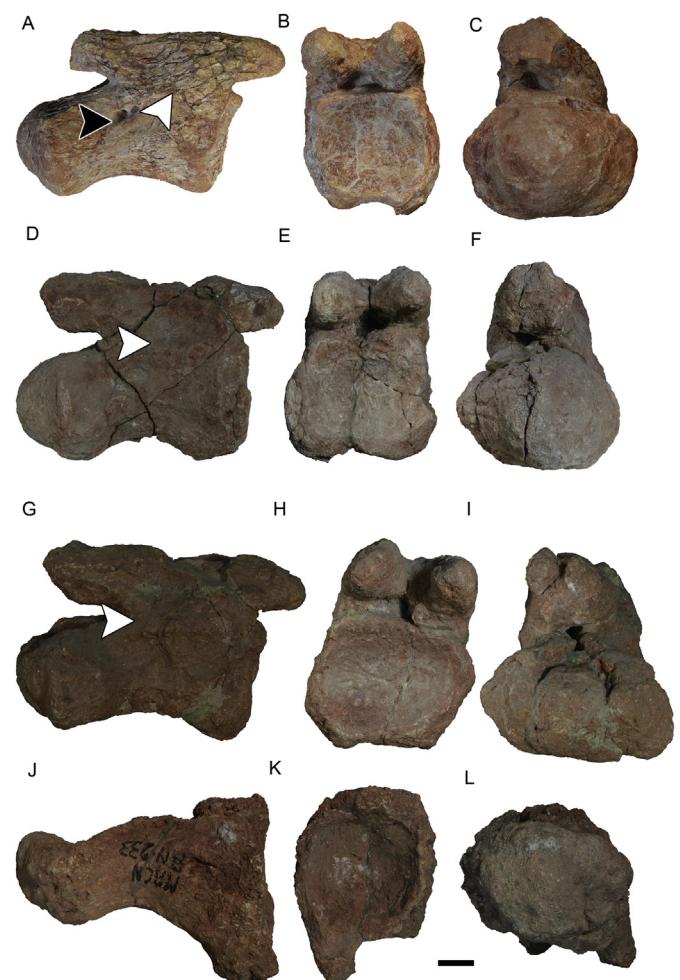


Fig. 4. Saltasaurinae indet. from the Angostura Colorado Formation: Posterior caudal vertebrae of MACN-Pv RN 233 in lateral, anterior and posterior views showing their main anatomic features. MACN-Pv RN 233-5 (A, C), MACN-Pv RN 233-6 (D, E, F), MACN-Pv RN 233-7 (G, H, I), and MACN-Pv RN 233-8 (J, K, L). The black arrow indicates the lateral pneumatic foramen of MACN-Pv RN 233-5. The white arrows indicate the shallow depression below the neural arch. Scale bar: 3 cm.

its anterior height, thus resembling the elongation of the anterior-middle caudal centra (Fig. 4A–L). The anterior surface is sub-rectangular, being 1.12–1.23 times transversely broader than tall, and homogenously concave (Fig. 4B, E, H, K). The posterior surface is sub-oval, being 1.36–1.89 transversely broader than tall and proportionally broader than in the anterior-middle caudal vertebrae. This articular surface is semi-spherical in lateral view, in which its dorsal and ventral margins are placed at the same anteroposterior level (Fig. 4C, F, I, L), resembling the condition in *Saltasaurus loricatus* (Powell, 1992, 2003) and *Neuquensaurus australis* (Salgado et al., 2005). By contrast, the posterior articular surface of the centrum of *Rocasaurus muniozi* is asymmetric in lateral view, with the ventral margin being more anteriorly extended than the dorsal one (Salgado and Azpilicueta, 2000). The ventral margin of the centrum of the posterior caudal vertebrae of MACN-Pv RN 233, *Saltasaurus loricatus* (Powell, 1992, 2003), and *Neuquensaurus australis* (Salgado et al., 2005) is straight in posterior view (Fig. 4C, F, I, L), contrasting with the distinctly concave ventral margin present in *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000). The ventral surface also possesses a transversely broad fossa (87.3 mm of maximum length versus 55.18 mm of maximum width in MACN-Pv RN 233 -5) (Fig. 5), closely resembling in proportions and position that of the anterior-middle caudal vertebrae. *Saltasaurus loricatus* (Powell, 1992, 2003) and *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000) also possess a large ventral fossa in the posterior caudal vertebrae, but *Neuquensaurus australis* lacks such ventral fossa (Salgado et al., 2005). Contrasting with MACN-Pv RN 233, the ventral fossa of *Rocasaurus muniozi* is considerably deeper, extending dorsally through most of the height of the centrum (MPCA-Pv 46, 58). The ventral fossa of MACN-Pv RN 233 possesses a pair of accessory fossae that are displaced slightly posterior to the mid-length of the main fossa and occur at both sides of a median longitudinal septum. A few pneumatic foramina pierce the surface of the main ventral fossa. The lateral surface of the centrum possesses a single pair of oval and medium-sized pneumatic foramina (Fig. 4A, D, G, J), as occurs in the anterior-middle caudals of MACN-Pv RN 233 and the posterior caudal vertebrae of *Saltasaurus loricatus* (Powell, 1992, 2003) and *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000). *Neuquensaurus australis* lacks pneumatic foramina in the posterior caudal vertebrae (MCS-5 and MLP CS/Ly). This lateral foramen is oval, with an anterodorsal to posteroventral main axis, and internally subdivided by an oblique, anteroventrally to posterodorsally oriented septum (Fig. 4A, D, G, J). The position of this foramen is similar to that of the more anterior caudal vertebrae. In MACN-Pv RN 233-5, the lateral pneumatic foramina are asymmetric, in which the opening is fully developed on the right side

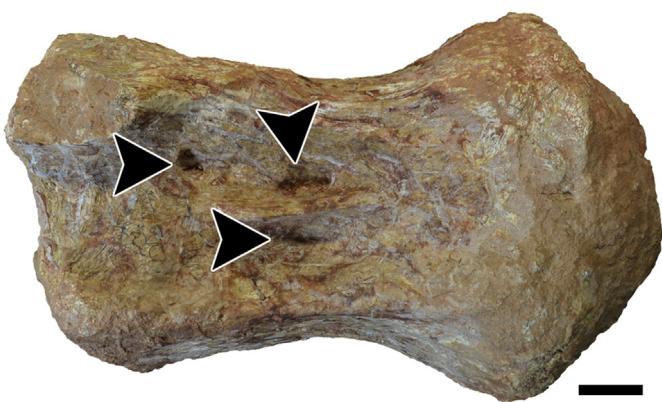


Fig. 5. Saltasaurinae indet. from the Angostura Colorado Formation: MACN-Pv RN 233-5 in ventral view showing the ventral fossa pierced by a pneumatic foramina as indicated by black arrows. Scale bar: 2 cm.

(Fig. 6A) and expressed as a shallow, blind fossa on the left side (Fig. 6B). In this element, there is a shallow subtriangular fossa present anteroventrally to the pneumatic foramen. These two structures are separated from each other by a thick, anterodorsally to posteroventrally oriented ridge.

At the boundary between the centrum and neural arch pedicel, the posterior caudals possess a low and thick relict of the transverse process, which extends anteroposteriorly through most of the base of the neural arch. This process slants slightly dorsally in lateral view. A shallow, large depression is presents dorsal to the base of the relictual transverse process, on the lateral surface of the neural arch. The position of this fossa seems to be topologically equivalent to the spinodiapophyseal fossa of the presacral vertebrae of most titanosauriforms (Wilson et al., 2011). The zygapophyses are mainly horizontal in lateral view. The prezygapophysis extends anteriorly beyond the level of the anterior border of the centrum, but the postzygapophysis finishes posteriorly before reaching the posterior level of the centrum, as occurs in the posterior caudal vertebrae of most titanosauriforms (e.g. *Chubutisaurus insignis*: Carballido et al., 2011; *Overosaurus paradasorum*: Coria et al., 2013; *Saltasaurus loricatus*: Powell, 1992). The neural spine is extremely low and from its base extends a thick and long spinoprezygapophyseal lamina and a very short spinopostzygapophyseal lamina (Fig. 4A, D, G, J). The spinoprezygapophyseal fossa is broad, but very shallow and there are some pneumatic, anterodorsally opened pockets and foramina on its surface (Fig. 7). The spinopostzygapophyseal fossa is dorsoventrally low and separates both postzygapophyses in dorsal view (Fig. 7). The base of the neural spine extends posteriorly beyond the level of the articular facet of the postzygapophysis. There is a shallow, anteroposteriorly long, and dorsally facing fossa adjacent to the anterior half of the base of the neural spine.

5.1.3. Chevrons

Two anterior to middle chevrons are preserved and they are articulated to their respective vertebrae (MACN-Pv RN 233-2, 4) (Fig. 2C, D, E–I, J, K). Among the posterior caudal series, only the left proximal tip of the chevron of MACN-Pv RN 233-5 is preserved. Both anterior-middle chevrons are “asymmetric” (A) and possess the “open V-shaped” (VS) morphology described by Otero et al. (2011) (Fig. 8A–D), resembling the condition in basal titanosaurs (e.g. the unnamed titanosaur MMCH-Pv 47). By contrast, the middle to posterior chevrons of *Saltasaurus loricatus* are “curved V-shaped” (CVS) (Otero et al., 2011). The two preserved anterior-middle chevrons and the proximal tip of a posterior chevron are fused to their respective centrum (Fig. 8B, D), but in the other centra the chevrons were not fused and they are not preserved. Fused chevrons to their respective centrum have been also described for other titanosaurs (e.g. Borsuk-Bialynicka, 1977; Martin et al., 1994). The chevrons contact the anterolateral corner of the ventral surface of their respective centrum and project posteroventrally in lateral

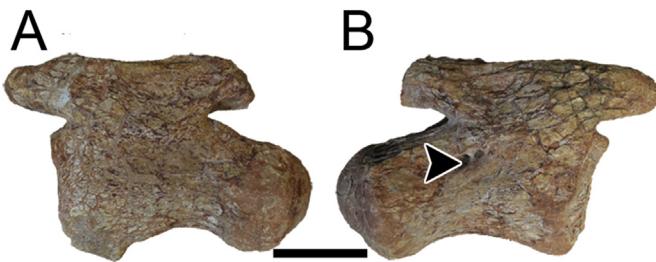


Fig. 6. Saltasaurinae indet. from the Angostura Colorado Formation: MACN-Pv RN 233-5 in right lateral (A) and left lateral (B) views, showing its asymmetric lateral pneumatic foramina. Scale bar: 8 cm.



Fig. 7. Saltasaurinae indet. from the Angostura Colorado Formation: MACN-Pv RN 233-5 in dorsal view showing its pneumatic foramina into the spinoprezygapophyseal fossa (black arrows), with detail of the pneumatic foramina. Scale bar: 3 cm.

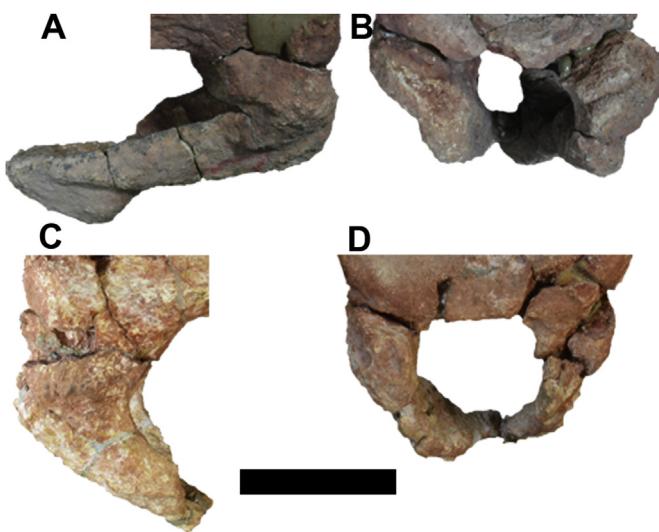


Fig. 8. Saltasaurinae indet. from the Angostura Colorado Formation: Chevrons of MACN-Pv RN 233-2 (A, B) in anterior and lateral views and chevrons of MACN-Pv 233-4 (C, D) in anterior and lateral views showing their "asymmetric" (A,C) and "V-shaped" (B,D) outline. Scale bar: 5 cm.

view (Fig. 8A, C). The chevron of MACN-Pv RN 233-2 extends posteriorly up to the base of the semi-spherical posterior articular surface of its respective centrum. The proximal end of this chevron is transversely thick and its shaft narrows to a plate-like structure, which is flat medially and slightly dorsoventrally convex laterally (Fig. 8A, B). The shaft is straight in lateral and anterior views. The

distal end of the chevron possesses a ventral expansion, which forms a distinct keel that extends along the entire ventral surface of the distal end of the element. As a result, the distal end of the chevron shows a distinct subtriangular cross-section, with a flat dorsal surface.

The chevron of MACN-Pv RN 233-4 lacks its distal tip, but the broken portion is very narrow and indicates that the element should not have extended much further posteriorly. As a result, this chevron should have been considerably shorter than that of MACN-Pv RN 233-2, being projected approximately up to the mid-length of its respective centrum. The chevron of MACN-Pv RN 233-4 has a transversely thick proximal end that narrows towards its shaft. The shaft of this element is gently bowed posteriorly in lateral view and medially in anterior view. The distal end of the chevron is broken off, but apparently the distal expansion present in MACN-Pv RN 233-2 was absent. The hemal canal of MACN-Pv RN 233-4 is transversely broader than in MACN-Pv RN 233-2 because the walls of the chevron are proportionally thinner transversely (Fig. 8B, D).

The chevron of MACN-Pv RN 233-4 is pierced by a circular, small foramen on its medial surface (Fig. 9) (the condition in MACN-Pv RN 233-2 cannot be determined because it is covered with matrix). This foramen is placed close to mid-length of the element. Due to the presence of a camellate internal structure in both preserved chevrons we hypothesize that this foramen may have allowed the entrance of a pneumatic diverticulum into the bone (Fig. 9). The presence of a pneumatic foramen on the chevron has not been reported in other sauropodomorph that we are aware.

5.1.4. Osteoderms

MACN-Pv RN 233 includes six osteoderms, five of them are complete (MACN-Pv RN 233 a–c, e–f) and one lacks most of a lateral side (MACN-Pv RN 233d) (Fig. 10A–F). For descriptive proposes, we assume that in dorsal view the longest axis is longitudinal and the shortest transverse. The most obtuse margin along the longitudinal



Fig. 9. Saltasaurinae indet. from the Angostura Colorado Formation: Pneumatic foramen in the inner face of MACN-Pv RN 233-4 (black arrow). Scale bar: 0.5 cm.

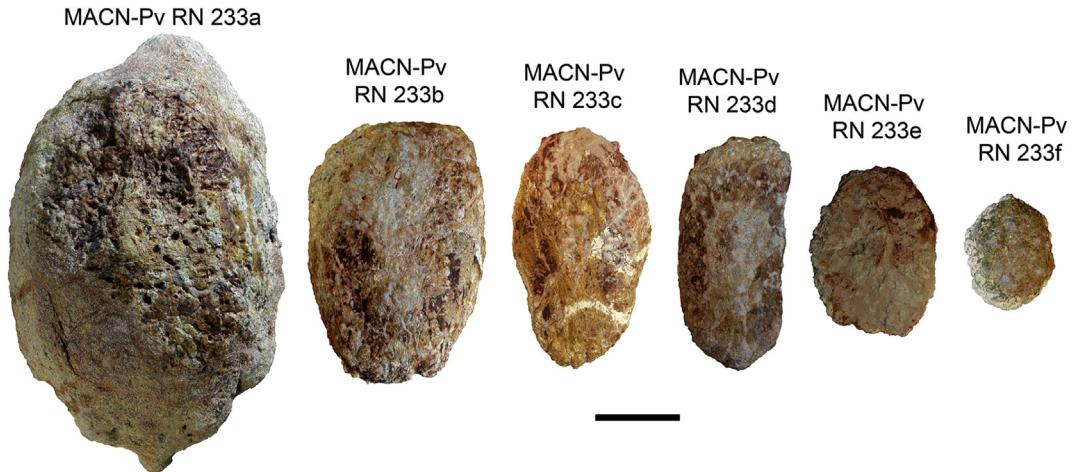


Fig. 10. Osteoderms of MACN-Pv RN 233 (Saltasaurinae gen. et sp. indet.) from the Angostura Colorada Formation, Patagonia, Argentina, arranged from large to small size with their respective catalogue number. Scale bar: 0.5 cm.

axis is considered anterior. The transverse axis defines medial and lateral edges, and the wider surface adjacent to the ventral keel (when they are asymmetric) is considered lateral. Such orientation is based on comparisons with osteoderms of other archosaurs, such as crocodilians (e.g. [Ross and Mayer, 1983](#)), and previous studies on titanosaurian osteoderms (e.g. [Cerda et al., 2015](#)).

The size (length) of the osteoderms varies considerably, ranging from 23.6 cm to 6.21 cm (see Table 1B). In particular, the osteoderm MACN-Pv RN 233a is considerably larger than the others, being about two times longer than the subsequent larger osteoderm (MACN-Pv RN 233b) ([Fig. 10A, B](#)). The external surfaces of osteoderms have a texture and ornamentation that suggests that they were vascularized structures ([Curry-Rogers et al., 2011](#); [Cerda et al., 2015](#)). All osteoderms are oval in external outline, with two morphotypes, which are classified following [D'Emic et al. \(2009\)](#). Morphotype 1 includes osteoderms with a convex external surface and a prominent longitudinal keel on the internal surface, dividing concave medial and lateral areas, respectively. Osteoderms MACN-Pv RN 233a–d are included in morphotype 1 ([Fig. 10A–D](#)). By contrast, morphotype 2 is characterized by straight to subtle convex external and internal surfaces, without a longitudinal keel on the latter surface. Osteoderms MACN-Pv RN 233e–f are included in morphotype 2. The texture of the surfaces of all these osteoderms is mainly composed of anastomosed and parallel fibre-like tissues, with a random distribution of abundant vascular foramina and grooves ([Fig. 10E, F](#)).

MACN-Pv RN 233a ([Fig. 11A–E](#)) is a dome-shaped osteoderm and the largest preserved. The external surface is strongly convex, with two distinctive structures: a central figure, highly vascularized, and a broad cingulum with compact tissue. The central figure consists of a median, rounded elevation bordered by a subtle concave depression. This depression delimits a lateral concentric fringe with some elevated points. All over the central figure there are several circular to oval foramina and in the lateral edges there are concentric, irregular furrows that end at the base of the cingulum. The cingulum occupies a broad portion of the dorsal surface of the osteoderm and it slopes abruptly at the outer edges. The boundary between the central figure and cingulum is clearly differentiated by different textures. The cingulum has very few vascular foramina and there is highly compact tissue bearing parallel fibres. In dorsal view, the cingulum has anterior and posterior protruding processes, being the posterior one sharper. In ventral view, there is a ventral, blunt longitudinal keel that separates two concave surfaces. The keel is slightly, possibly laterally, displaced

from the median line of the osteoderm, producing asymmetric surfaces. It becomes taller and wider posteriorly. The lateral surface is wider and more concave than the medial one, and forms a sharp edge. By contrast, the medial concave surface has a rounded and robust medial edge.

Following [D'Emic et al. \(2009\)](#), these four osteoderms (MACN-Pv RN 233 a–d) are keeled.

MACN-Pv RN 233a was also analysed using a CT scan ([Fig. 11E](#)). In the anterior half of the osteoderm, the internal density seems to be homogeneous, indicating the presence of dense bone, whereas in the lateral portion of the posterior half there is an irregular cavity that seems to be filled with material of a different density.

MACN-Pv RN 233b ([Fig. 11F–J](#)) has a similar morphology to that of MACN-Pv RN 233a. However, it is much smaller, the central figure is less evident, and the external outline more trapezoidal, because the anterior edge is straight to slightly convex and about two times broader than the posterior one. The texture of the dorsal surface is slightly worn out, with an elongated central figure bordered by a sloping cingulum. Vascular foramina and irregular grooves predominate on the external surface, being also present, but in a lower degree, on the cingulum. Patches of parallel fibres are observed on the lateral and medial edges. The posterior edge of the osteoderm is rounded. On the posterior portion of the lateral edge and in the medial half of the posterior end there are two longitudinal grooves that curve into the internal surface of the osteoderm. In ventral view, the ventral keel is prominent but differs from MACN-Pv RN 233a in that it occupies only the posterior two-thirds of the osteoderm. The keel becomes lower posteriorly. Between the anterior edge of the osteoderm and the anterior end of the keel there is a broad surface that is straight to slightly convex. This surface slopes towards the external surface in lateral view and resembles an articular surface for reception of a preceding osteoderm ([Fig. 11G](#)). This kind of surface is not observed in the osteoderm of any other titanosaur that we are aware and, as a result, we are not confident that it really represents an articular facet, as occurs in the osteoderms of several archosaur clades (e.g., doswelliids, aetosaurs, crocodyliforms; [Sues et al., 2013](#); [Desojo et al., 2013](#); [Irmis et al., 2013](#)). In internal view, the medial surface is slightly concave whereas the lateral one is almost flat. Some randomly distributed vascular foramina occur at both sides of the keel on the internal surface of the osteoderm.

MACN-Pv RN 233c ([Fig. 12A–D](#)) is an oval osteoderm in external view, approximately two times longer than broad. In the centre of the external surface, there is a low elevation ornamented by large

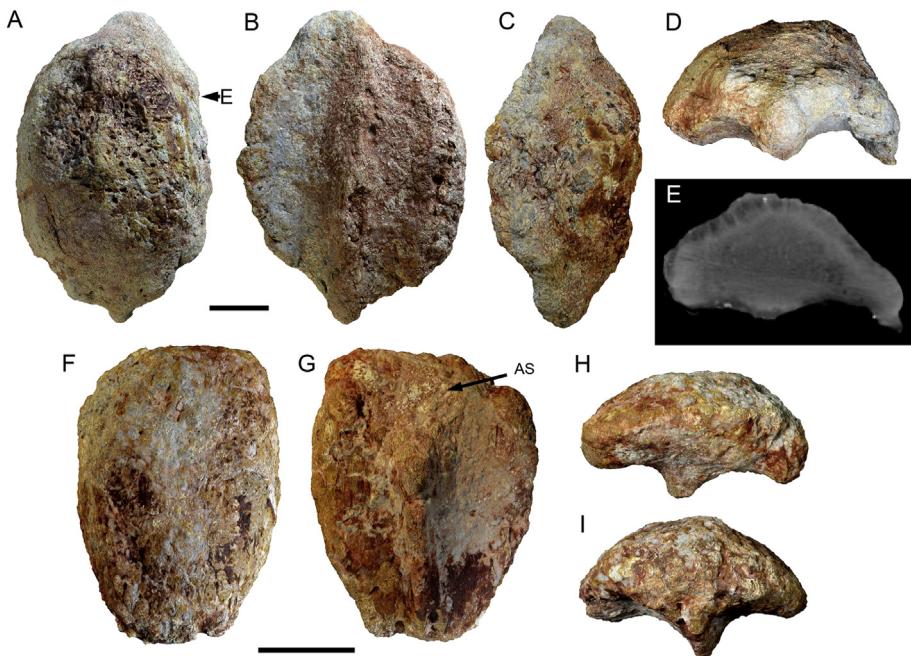


Fig. 11. Osteoderms of MACN-Pv RN 233 (*Saltasaurinae* gen. et sp. indet.) from the Angostura Colorada Formation, Patagonia, Argentina. Specimen MACN-Pv RN 233a in dorsal (A), ventral (B), lateral (C), and anterior (D) views with detail of its inner structure based on CT Scan (E). Specimen MACN-Pv RN 233b in dorsal (F), ventral (G), anterior (H), and posterior (I) views. The black arrow in (G) indicates articular surface. Scale bar: 0.5 cm.

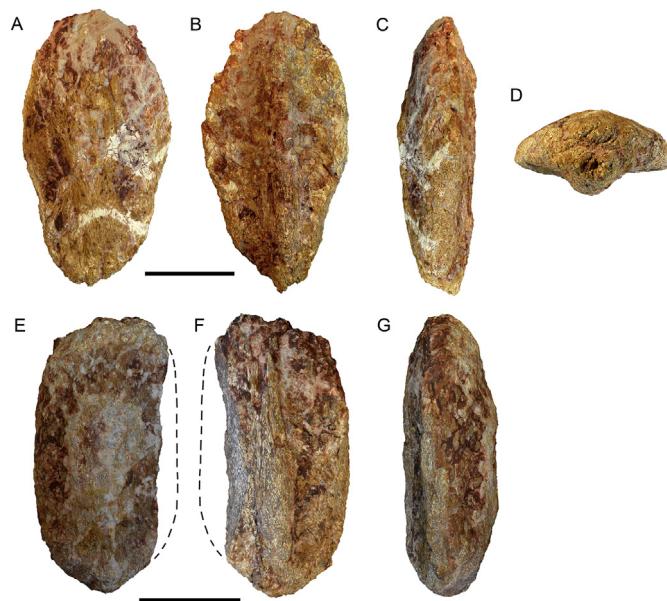


Fig. 12. Osteoderms of MACN-Pv RN 233 (*Saltasaurinae* gen. et sp. indet.) from the Angostura Colorada Formation, Patagonia, Argentina. Specimen MACN-Pv RN 233c in dorsal (A), ventral (B), lateral (C), and posterior (D) views. Specimen MACN-Pv RN 233d in dorsal (E), ventral (F), and lateral (G) views. Scale bar: 0.5 cm.

foramina and broad grooves. This elevation decreases slightly posteriorly. Contrasting with the other osteoderms, there is no clear distinction between a central figure and a cingulum, and the texture of the external surface is quite homogeneous, including short grooves and vascular foramina within parallel and criss-crossed fibre tissue. In internal view, the keel is placed just slightly lateral to the median line. The keel starts slightly posterior to the anterior edge of the osteoderm and extends beyond the posterior edge of the external surface of the bone. The surfaces adjacent to

the keel are slightly concave and the medial one has two large foramina with associated short grooves (Fig. 12B–D).

MACN-Pv RN 233d is similar to MACN-Pv RN 233c (Fig. 12E–G), although it is poorly preserved, lacking almost half of its medial side and the posterior portion seems to be eroded away. The external surface preserves clearly the central figure, which is a tear-drop-shaped concavity, with rugosities in the centre, and bordered by a ring of bone that slopes towards the internal surface gradually.

MACN-Pv RN 233e and MACN-Pv RN 233f (Fig. 13A–G) belong to the morphotype 2. They are the smallest osteoderms, being MACN-Pv RN 233e two times smaller than MACN-Pv RN 233a. They are

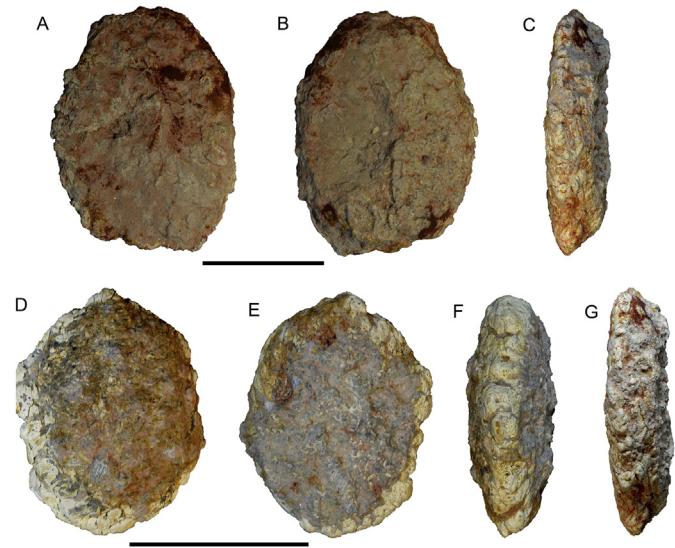


Fig. 13. Osteoderms of MACN-Pv RN 233 (*Saltasaurinae* gen. et sp. indet.) from the Angostura Colorada Formation, Patagonia, Argentina. Specimen MACN-Pv RN 233e in dorsal (A), ventral (B), and lateral (C) views. Specimen MACN-Pv RN 233f in dorsal (D), ventral (E), and both lateral (F–G) views. Scale bar: 0.5 cm.

sub-hexagonal and lack a keel. We interpreted the dorsal surface as that one with several grooves, pits, and rugosities, whereas the internal surface has no such structures and is flat to slightly convex. The edges of these osteoderms are rounded and have some grooves and very small pits (Fig. 13C, F, G). Following D'Emic et al. (2009), these two osteoderms are cylindrical.

5.2. Results of the phylogenetic analysis

The analysis of the modified version of the data matrix of Salgado et al. (2014) found three most parsimonious trees (MPTs) of 141 steps, with a consistency index (CI) of 0.6738 and a retention index (RI) of 0.7310, and the best score reached 48 times of the 50 replications. The topology of the strict consensus tree (SCT) generated from these MPTs is completely consistent with that recovered by Salgado et al. (2014). The a posteriori exclusion of *Nemegtosaurus mongoliensis* from the SCT resolved the massive polytomy found among derived titanosaurs, as occurred in the original analysis of Salgado et al. (2014). MACN-Pv RN 233 is found as a saltasaurine titanosaur, being more closely related to *Saltasaurus loricatus* and *Rocasaurus muniozi* than to *Neuquensaurus australis*. The relationships of MACN-Pv RN 233, *Saltasaurus loricatus*, and *Rocasaurus muniozi* are unresolved because the new specimen can be alternatively placed as the sister-taxon of any of the latter two taxa, respectively, or of the clade formed by them (Fig. 14). The position of MACN-Pv RN 233 within Saltasaurinae is supported by the following two synapomorphies: anterior and middle caudal centra wider than high (character 45: 0 → 1) and middle caudal vertebrae with the anterodorsal border of neural spine located posteriorly with respect to the anterior border of the postzygapophyses (character 50: 0 → 1). The clade formed by the new specimen, *Saltasaurus loricatus*, and *Rocasaurus muniozi* is supported by the following two synapomorphies: anterior and middle caudal vertebrae with a ventral depression divided by a longitudinal septum (character 55: 0 → 1) and a lateral pneumatic foramen on the centrum (character 78: 0 → 1). Saltasaurinae and

its lesser inclusive clade possess minimal Bremer values (= 1), but the bootstrap frequencies are relatively high (68–72%) and show low contradictory evidence (i.e. similar absolute and GC frequencies for each branch, difference = 0–2%). Under a topologically constrained search, two additional steps are necessary to force the position of MACN-Pv RN 233 as the sister-taxon of *Neuquensaurus australis* or of all the other saltasaurines. Four additional steps result in the position of the new specimen as the most basal saltasaurine or as a non-saltasaurine titanosaur (e.g. sister-taxon of *Bonatitan reigi* or *Nemegtosaurus mongoliensis*).

6. Discussion

6.1. The taxonomy of MACN-Pv RN 233

The result of the phylogenetic analysis, which places MACN-Pv RN 233 as a saltasaurine titanosaur more derived than *Neuquensaurus australis*, indicates that the new specimen differs from the latter species (Fig. 14). These differences include for example the absence of a ventral fossa and a lateral pneumatic foramen on the caudal centra of *Neuquensaurus australis*. Among the most deeply nested saltasaurines, MACN-Pv RN 233 differs from *Saltasaurus loricatus* and *Rocasaurus muniozi* in the presence of a posteriorly bifurcated median longitudinal septum on the ventral fossa. In particular, MACN-Pv RN 233 can be distinguished from *Rocasaurus muniozi* in the presence of caudal centra with a symmetric posterior articular facet in lateral view and a straight ventral margin in posterior view; and from *Saltasaurus loricatus* in the presence of “open V-shaped” chevrons in the anterior region of the tail and osteoderms with a ventral keel slightly displaced from the median line. This combination of features may allow a distinction between MACN-Pv RN 233 and the other known saltasaurines and hence the recognition of a new species. However, because of the fragmentary nature of the specimen reported here, we decided for the sake of taxonomic stability to not erect a new taxon. The erection of a new species based on the specimen described here may result in problems at the time of discussing the taxonomy of other saltasaurine individuals without a preserved tail from the Angostura Colorado Formation, even if they are represented by rather complete specimens.

6.2. Pneumaticity

The presence of postcranial pneumaticity in sauropods is known since the mid-twentieth century, though it is still only partially studied. One of the first authors to study this topic in detail was Janensch (1947), who described in detail foramina and their relation to vertebral pneumaticity. Several years later, these kind of studies become more common and comprehensive, including more groups of sauropods (e.g. Wedel et al., 2000, Wedel 2003a,b, Wedel, 2009, Wedel and Taylor, 2013; Cerda et al., 2012; Fanti et al., 2013, 2015) and even theropods (e.g. Britt, 1993; Benson et al., 2012). Unequivocal osteological correlates of postcranial pneumaticity are the presence of camellated tissue inside the vertebrae (Britt, 1993, 1997) and cortical foramina connected with the interior of the bone (O'Connor, 2006). The three known saltasaurines have these unequivocal correlates of postcranial pneumaticity.

As occurs in the saltasaurines *Saltasaurus loricatus* and *Rocasaurus muniozi* and even non-saltasaurine titanosaurs (e.g. *Bonatitan reigi*), MACN-Pv RN 233 possesses camellated tissue at both the centrum and neural arch of the preserved caudal vertebrae (Fig. 15). The neural arches have visible pneumatic foramina in the spinoprezygapophyseal fossa, and the centra have lateral pneumatic foramina and the ventral fossa is also apparently pneumatic in origin (Figs. 3 and 5), resembling the condition in *Rocasaurus*

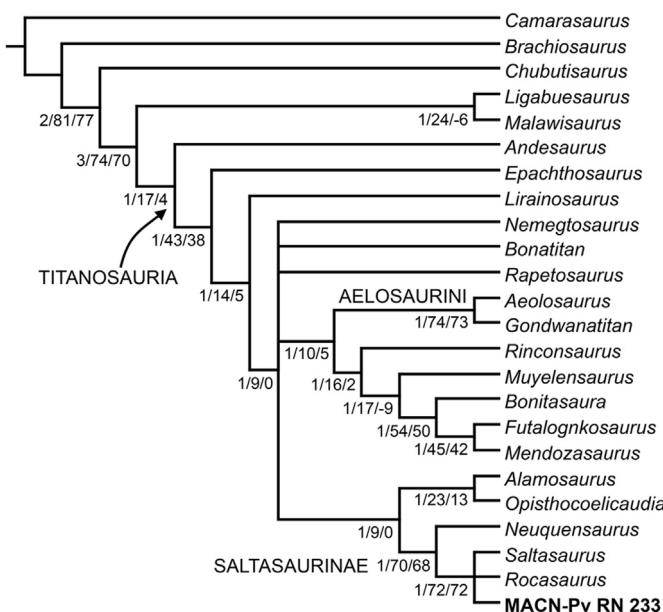


Fig. 14. Strict consensus tree depicting the phylogenetic relationships of the Saltasaurinae indet. from the Angostura Colorado Formation (MACN-Pv RN 233) and other saltasaurine titanosaurs. Consistency index (CI): 0.6738, Retention index (RI): 0.7310. Numbers below each node indicate Bremer supports and absolute and GC bootstrap frequencies, respectively.

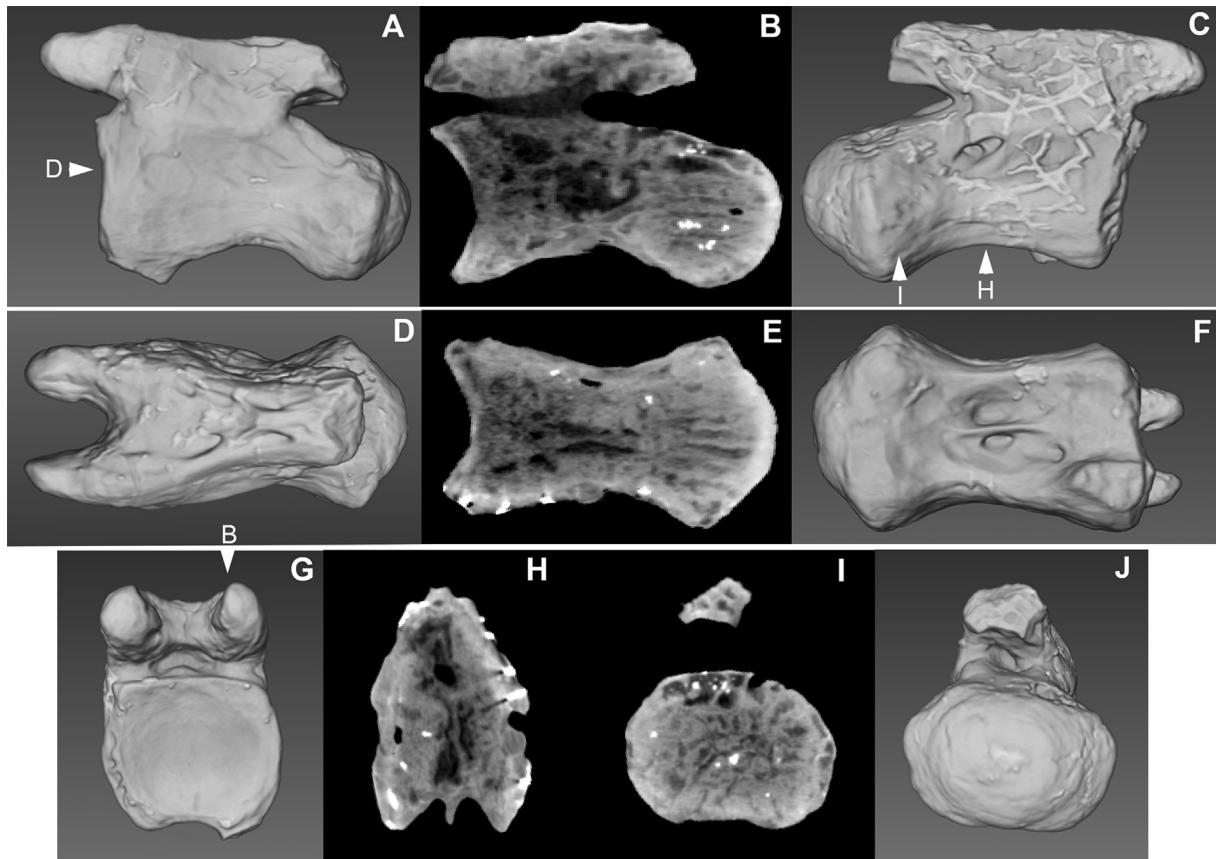


Fig. 15. Saltasaurine indet. from Angostura Colorada Formation: 3 D images (A, C, D, F, G, J) and CT SCAN of MACN Pv 233-5 in right longitudinal (B), ventral (E), and transverse (H, I) views show camellate tissue (B, H, I) and ventral fossa (E). In longitudinal view can be seen the lateral pneumatic foramen (C).

muniozi and *Saltasaurus loricatus*. By contrast, the pneumatization of the caudal vertebrae occurs only in the neural arches in *Neuquensaurus australis* ([Salgado et al., 2005](#)). The CT scans of MACN-Pv RN 233 revealed that there are numerous internal cavities in the caudal vertebrae, as occurs in *Rocasaurus muniozi*, thus the degree of pneumatization is comparable to this saltasaurine.

The pneumaticity of MACN-Pv RN 233 is well developed and has some peculiarities. There is an asymmetric presence/absence of lateral pneumatic foramina in some vertebrae (i.e. a foramen is present on one side of the centrum but not in the other). This asymmetry also occurs in the saltasaurine *Rocasaurus muniozi* and some other sauropods. In the case of *Apatosaurus* and *Giraffatitan brancai* the assymmetric condition was attributed to "gaps in vertebral pneumatization" ([Wedel and Taylor, 2013](#)), but in contrast to saltasaurines, these sauropods have a medial septum that divides the vertebral centra in two halves. MACN-Pv RN 233 and the others saltasaurines fit with the model proposed by [Benson et al. \(2012\)](#), in which there are no gaps in vertebral pneumatization. This model applies to theropods ([Benson et al., 2012](#)) and other sauropods, e.g. rebbachisaurids ([Fanti et al., 2013, 2015](#)). In the case of saltasaurines, we do not observe gaps perhaps because of the absence of complete caudal sequences. However, due to the extreme pneumaticity of this group, which reaches the posterior region of the tail in *Rocasaurus muniozi*, we infer that the pneumatization was not interrupted despite the existence of asymmetry in the presence and absence of lateral pneumatic foramina. The lack of a sagittal septum in saltasaurines is interpreted as a trait that facilitated the achievement of an extensively pneumatic centrum despite of the asymmetric presence/absence of lateral pneumatic foramina. MACN-PV RN 233

shares with *Saltasaurus* and *Rocasaurus* the presence a ventral fossa on the centrum, which is pierced by numerous pneumatic foramina. Due to the presence of such pneumatic foramina, this fossa could be interpreted as pneumatic in origin.

The pneumaticity in the caudal vertebrae and chevrons of MACN-Pv RN 233 indicates that the diverticula from the abdominal air sac reached the caudal region to pneumaticize both the centrum and neural arch. In MACN-Pv RN 233, the fused chevrons suggest that this specimen was probably an adult specimen and its pneumaticity was extended to both posterior caudal vertebrae and chevrons. Pneumaticity in posterior caudal vertebrae is very unusual among dinosaurs, being present in only some sauropods (e.g. *Rocasaurus muniozi*: [Cerda et al., 2012](#); *Giraffatitan brancai*: [Wedel and Taylor, 2013](#)) and theropods (e.g. oviraptorosaurs, megaraptorids; [Sereno et al., 2008](#); [Benson et al., 2012](#)).

The most remarkable features of MACN-Pv RN 233 are the morphology of the chevrons. This specimen has asymmetric chevrons, similar to those of more basal sauropods ([Otero et al., 2011](#)), such as the unnamed titanosaur MMCH-Pv 47 and *Andesaurus delgadoi*. Thus, the condition in MACN-Pv RN 233 could be interpreted as a reversion. As occurs in *Saltasaurus* and *Rocasaurus*, MACN-Pv RN 233 possesses foramina and camellated tissue in the centra and neural arches of even the posterior caudal vertebrae, but it is the first time that pneumaticity is recorded in the chevrons of a sauropodomorph, being previously documented only in the megaraptoran theropod *Aoniraptor libertatem* among dinosaurs ([Motta et al., 2016](#)). The pneumatization of the chevrons should have occurred through diverticula projected from a probably very well-developed abdominal air sac.

6.3. Osteoderms

The association of the osteoderms to the caudal series is based on the fact that all the elements were found together in the same site and no other tetrapod bones were found in association or close to the quarry. The bones share the same type of preservation and we do not find positive evidence to split out the osteoderms from the rest of the specimen. The differences in size and the presence of at least two morphotypes (keeled and cylindrical) of osteoderms in MACN-Pv RN 233 suggest that they could not have been restricted to the tail and may correspond to different parts of the body. High disparity of osteoderm sizes and morphologies is hitherto unknown for a single titanosaurian individual, but explanations for the high diversity of osteoderms from single Cretaceous localities of northern Patagonia include individual and intraspecific variations, developmental state of the osteoderm, osteoderm function to taxonomic variation (e.g. Curry Rogers et al., 2011; Cerda et al., 2015). Among the diversity of Argentinean titanosaurs, osteoderms are only unambiguously associated to *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1980, 2003), *Neuquensaurus australis* (Salgado et al., 2005), and *Aeolosaurus* (Salgado and Coria, 1993).

The morphotype 1 of osteoderms of MACN-Pv RN 233a–d resembles the overall morphology of those referred to *Neuquensaurus australis* (Salgado et al., 2005; Cerda et al., 2015), *Saltasaurus loricatus* (Powell, 1980, 2003), and isolated osteoderms from the Upper Cretaceous of Patagonia (e.g. Cerda et al., 2015: figs 2, E–L). Nonetheless, the osteoderms MACN-Pv RN 233a–d have the ventral keel slightly displaced from the median line, producing asymmetrical concave surfaces not observed in other titanosaur osteoderms of Patagonia. In fact, this asymmetry suggests that the osteoderm morphology changes markedly according to its position on the body. Particularly, one osteoderm, MACN-Pv RN 233b, has a flat to slightly convex surface on its internal side, which is sub-square in outline and located on the anterior 1/3 of the length of the bone. This surface is reminiscent to an articular facet for a preceding osteoderm. Our evidence on this hypothesis is not conclusive at all and only new specimens would shed light on this inference.

7. Conclusions

We describe here a new sauropod specimen from the uppermost Cretaceous Angostura Colorado Formation, MACN-Pv RN 233. This specimen is composed of eight caudal vertebrae with a pair of chevrons and six osteoderms. MACN-Pv RN 233 was recovered as a saltasaurine titanosaur in a cladistics analysis, being more closely related to *Rocasaurus munizoi* and *Saltasaurus loricatus* than to *Neuquensaurus australis*. Some features distinguish MACN-Pv RN 233 from other saltasaurines, including a bifurcated ventral septum on the caudal centra and the shape of the chevrons and osteoderms. However, we decided to not erect a new taxon for the sake of taxonomic stability because of the fragmentary nature of the specimen and the lack of autapomorphic features. MACN-Pv RN 233 provides the first evidence of pneumatic chevrons in sauropodomorphs and increases the morphological diversity of sauropod osteoderms. This discovery expands the distribution of saltasaurines to a new geological unit, in which the sauropod record of the Laguna Colorada Formation was previously restricted to aeolosaurine specimens and titanosaurian eggshells (Powell, 1987).

Acknowledgements

We thank Guillermo Aguirre-Zabala for the mechanical preparation of some of the vertebrae. VLZ thanks the Jurassic Foundation

and Foncyt (PICT 2015-1021) for the partial funding of this project. AGM thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Laboratório de Paleontologia de Vertebrados of the Universidade Federal do Rio Grande do Sul (UFRGS) for continuous support. We thank Eduardo Koutsoukos, Editor in Chief of Cretaceous Research, for his editorial work and corrections and the reviewers, Stephen Poropat and Verónica Díez-Díaz for their valuable work and useful recommendations. We also thank Clínica La Sagrada Familia (Buenos Aires, <http://www.sagradafamilia.com.ar/>) for carrying out the CT scans of the specimen described here. The comments of Alejandro Otero, Ignacio Cerda, and Alberto Garrido improved different aspects of the manuscript. We thank Alejandro Kramarz for access to specimens under his care.

References

- Amorim, P., Moraes, T., Silva, J., Pedrini, H., 2015. InVesalius: an interactive rendering framework for health care support. In: Bebis, G., et al. (Eds.), Advances in Visual Computing. Lecture Notes in Computer Science. 9474. Springer.
- Benson, R.B., Butler, R.J., Carrano, M.T., O'Connor, P.M., 2012. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'–bird transition. Biological Reviews 87 (1), 168–193.
- Bonaparte, J.F., Coria, R.A., 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiense-Cenomaniense) de la Provincia del Neuquén, Argentina. Ameghiniana 30, 271–282.
- Bonaparte, J.F., Migale, L.A., 2010. Protomamíferos y mamíferos Mesozoicos de América del Sur. Museo de Ciencias Naturales Carlos Ameghino. Mercedes, Buenos Aires, p. 441.
- Bonaparte, J.F., Powell, J.E., 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Cetiosauria-Carnosauria-Aves). Mémoires de la Société géologique de France 139, 19–28.
- Borsuk-Bialynicka, M., 1977. A new camarasauroid sauropod *Opisthocoelicaudia skarzynskii*, gen. n. sp. n. from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 37, 5–64.
- Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42, 795–803.
- Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.
- Britt, B.B., 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. PhD thesis. University of Calgary, pp. 1–400.
- Britt, B.B., 1997. Postcranial pneumaticity. In: Currie, P.J., Padian, K. (Eds.), The Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 590–593.
- Brochu, C., 1996. Closure of neurocentral sutures during crocodilian ontogeny: Implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16 (1), 49–62.
- Calvo, J.O., Porfiri, J.D., González-Riga, B.J., Kellner, A., 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. Anais da Academia Brasileira de Ciências 79 (3), 529–541.
- Carballido, J.L., Pol, D., Cerda, I., Salgado, L., 2011. The osteology of *Chubutisaurus insignis* del Corro, 1975 (Dinosauria: Neosauropoda) from the 'middle' Cretaceous of central Patagonia, Argentina. Journal of Vertebrate Paleontology 31 (1), 93–110.
- Cerda, I.A., Powell, J.E., 2010. Dermal armor histology of *Saltasaurus loricatus*, an Upper Cretaceous sauropod dinosaur from Northwest Argentina. Acta Palaeontologica Polonica 55 (3), 389–398.
- Cerda, I.A., Salgado, L., Powell, J.E., 2012. Extreme postcranial pneumaticity in sauropod dinosaurs from South America. Paläontologische Zeitschrift 86 (4), 441–449.
- Cerda, I.A., García, R.A., Powell, J.E., Lopez, O., 2015. Morphology, microanatomy, and histology of titanosaur (Dinosauria, Sauropoda) osteoderms from the Upper Cretaceous of Patagonia. Journal of Vertebrate Paleontology 35 (1), e905791. <http://dx.doi.org/10.1080/02724634.2014.905791>.
- Coddington, J., Scharff, N., 1994. Problems with Zero-Length Branches. Cladistics 10, 415–423.
- Coria, R.A., Filippi, L.S., Chiappe, L.M., García, R., Arcucci, A.B., 2013. *Oversaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. Zootaxa 3683 (4), 357–376.
- Cruzado Caballero, P., 2015. Nuevos restos de dinosaurios hadrosáuridos del Valle de Huahuel Niyeo (Río Negro, Argentina). Ameghiniana 52 (1), 6–7.
- Curry-Rogers, K., D'Emic, M.D., Vickaryous, M., Cagan, A., 2011. Sauropod dinosaur osteoderms from the Late Cretaceous of Madagascar. Nature Communications 2, 564. <http://dx.doi.org/10.1038/ncomms1578>.
- D'Emic, M.D., Wilson, J.A., Chatterjee, S., 2009. The titanosaur (Dinosauria: Sauropoda) osteoderm record: review and first definitive specimen from India. Journal of Vertebrate Paleontology 29, 165–177.
- Desojo, J.B., Heckert, A.B., Martz, J.W., Parker, W.G., Schoch, R.R., Small, B.J., et al., 2013. Aetosauria: clade of armoured pseudosuchians from the Late Triassic continental beds. In: Nesbitt, S.J., Desojo, J.B., Irmis, R.B. (Eds.), Anatomy,

- Phylogeny and Palaeobiology of Early Archosaurs and their Kin.** Geological Society, Special Publications, London, pp. 203–239, 379 pp.
- Fanti, F., Cau, A., Hassine, M., Contessi, M., 2013. A new sauropod dinosaur from the Early Cretaceous of Tunisia with extreme avian-like pneumatisation. *Nature Communications* 4 (2080), 1–7. <http://dx.doi.org/10.1038/ncomms3080>.
- Fanti, F., Cau, A., Cantelli, L., Hassine, M., Auditore, M., 2015. New information on *Tataouinea hannibalis* from the early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. *PLoS ONE* 10 (4), e0123475. <http://dx.doi.org/10.1371/journal.pone.0123475>.
- Felsenstein, J., 1985. Phylogenies and the comparative methods. *The American Naturalist* 125 (1), 1–15.
- Filippi, L.S., Canudo, J.I., Salgado, L., Garrido, A.C., García, R.A., Cerda, I.A., Otero, A., 2011a. A new sauropod titanosaur from the Plottier Formation (Upper Cretaceous) of Patagonia (Argentina). *Geológica Acta* 9 (1), 1–12.
- Filippi, L.S., García, R.A., Garrido, A.C., 2011b. A new titanosaur sauropod dinosaur from the Upper Cretaceous of North Patagonia, Argentina. *Acta Palaeontologica Polonica* 56 (3), 505–520.
- García, R.A., Salgado, L., 2013. The titanosaur sauropods from the late Campanian–early Maastrichtian Allen Formation of Salitrillo Moreno, Río Negro, Argentina. *Acta Palaeontologica Polonica* 58 (2), 269–284.
- García, R.A., Salgado, L., Fernández, M.S., Cerda, I.A., Paulina-Carabajal, A., Otero, A., Coria, R.A., Fiorelli, L., 2015. Paleobiology of titanosaurs: reproduction, development, histology, pneumaticity, locomotion and neuroanatomy from the South American fossil record. *Ameghiniana* 52 (1), 29–68.
- Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J., Szumik, C.A., 2003. Improvements to resampling measures of group support. *Cladistics* 19, 324–332.
- Goloboff, P.A., Farris, J.S., Nixon, K., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Irmis, R.B., Nesbitt, S.J., Sues, H.-D., 2013. Early Crocodylomorpha. 275–302. In: Nesbitt, S.J., Desojo, J.B., Irmis, R.B. (Eds.), Anatomy, phylogeny and palaeobiology of early archosaurs and their kin, Geological Society, London, Special Publications, 379, p. 608.
- Janensch, W., 1947. Pneumatizität bei Wirbeln von Sauropoden und anderen Sauropsiern. *Palaeontographica* 7 (I.3), 1–25.
- Kellner, A., Campos, D., Trotta, M., 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil, 63(3). *Arquivos do Museu Nacional, Rio de Janeiro*, pp. 529–564.
- Li, L.-G., Li, D.-Q., You, H.-L., Dodson, P., 2014. A New Titanosaurian Sauropod from the Hekou Group (Lower Cretaceous) of the Lanzhou-Minhe Basin, Gansu Province, China. *PLoS One* 9 (1), e85979. <http://dx.doi.org/10.1371/journal.pone.0085979>.
- Lydekker, R., 1893. The dinosaurs of Patagonia. *Anales del Museo de La Plata* 2, 1–14.
- Manassero, M., 1997. Sedimentology of the upper cretaceous red beds of Angostura Colorada Formation in the western sector of the Northpatagonian Massif, Argentina. *Journal of South American Earth Sciences* 10 (1), 81–90.
- Martin, V., Buffetaut, E., Suteehorn, V., 1994. A new genus of sauropod dinosaur from the Sao Khua formation (Late Jurassic or early Cretaceous) of northeastern Thailand. *Comptes Rendus de l' Academie des Science de Paris* 319 (2), 1085–1092.
- Martinetto, A.G., Forasiepi, A.M., 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Rio Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista Museo Argentino de Ciencias Naturales* 6 (2), 257–305.
- Motta, M., Aranciaga-Roldano, A., Rozadilla, S., Agnolín, F.E., Chimento, N.E., Brissón-Egli, F., Novas, F.E., 2016. New theropod fauna from the Upper Cretaceous (Huincul Formation) of Northwestern Patagonia, Argentina. Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin 71, 231–253.
- O'Connor, P.M., 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology* 267, 1199–1226.
- O'Connor, P.M., Claessens, L., 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436, 253–256.
- Otero, A., 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica* 55 (3), 399–426.
- Otero, A., Gallina, P.A., Canale, J.I., Haluza, A., 2011. Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. *Historical Biology* 24, 243–256.
- Powell, J.E., 1980. Sobre la presencia de armadura dérmica en algunos dinosaurios titanosáuridos. *Acta Geológica Lilloana* 15, 41–47.
- Powell, J.E., 1987. The Late Cretaceous Fauna of Los Alamos, Patagonia, Argentina. Part VI—The titanosaurs. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 3, 147–153.
- Powell, J.E., 1992. Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del noroeste Argentino. 1992. In: Sanz, J., Buscalioni, A. (Eds.), Los dinosaurios y su entorno biótico: Actas del Segundo Curso de Paleontología en Cuenca, pp. 165–230.
- Powell, J.E., 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical, and phylogenetic aspects. *Records of the Queen Victoria Museum* 111, 1–173.
- Romer, A.S., 1956. Osteology of the reptiles. University of Chicago Press, Chicago, Illinois.
- Ross, F.D., Mayer, G.C., 1983. On the dorsal armor of the Crocodilia. In: Rhodin, A.G. (Ed.), Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Cambridge, MA, pp. 305–331.
- Saegusa, H., Ikeda, T., 2014. A new titanosauriform sauropod (Dinosauria: Sauropoda) from the Lower Cretaceous of Hyogo, Japan. *Zootaxa* 3848 (1), 1–66.
- Salgado, L., 2003. Considerations on the bony plates assigned to titanosaurs (Dinosauria, Sauropoda). *Ameghiniana* 40, 441–456.
- Salgado, L., Azpilicueta, C., 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la Provincia de Río Negro (Formación Allen, Cretácico Superior) Patagonia Argentina. *Ameghiniana* 37 (3), 259–264.
- Salgado, L., Bonaparte, J.F., 2007. Sauropodomorphs. In: Gasparini, Z., Salgado, L., Coria, R.A. (Eds.), Patagonian mesozoic reptiles. Indiana University Press, Bloomington, IN, pp. 188–228.
- Salgado, L., Coria, R.A., 1993. El género *Aeolosaurus* (Sauropoda, Titanosauridae) en la Formación Allen (Campaniano–Maastrichtiano) de la Provincia de Río Negro, Argentina. *Ameghiniana* 30 (2), 119–128.
- Salgado, L., García, R., 2002. Variación morfológica en la secuencia de vértebras caudales de algunos saurópodos titanosauros. *Revista Española de Paleontología* 17 (2), 211–216.
- Salgado, L., Apóstegui, S., Heredia, S., 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from North Patagonia. *Journal of Vertebrate Paleontology* 25 (3), 623–634.
- Salgado, L., Gallina, P.A., Paulina Carabajal, A., 2014. Redescription of *Bonatitan reigi* (Sauropoda: Titanosauria), from the Campanian–Maastrichtian of the Río Negro Province (Argentina). <http://dx.doi.org/10.1080/08912963.2014.894038>.
- Santucci, R.M., Bertini, R.J., 2006. A large sauropod titanosaur from Peirópolis, Bauru Group, Brazil. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 6, 344–360.
- Sereno, P.C., Martínez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A., Larsson, H.C., 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE* 3 (9), e3303:1–20.
- Sues, H.-D., Desojo, J.B., Ezcurra, M.D., 2013. Doswelliidae: a clade of unusual armoured archosauriforms from the Middle and Late Triassic. In: Nesbitt, S.J., Desojo, J.B., Irmis, R.B. (Eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin, London: Geological Society, Special Publication 379, pp. 49–58.
- Swofford, D.L., Begle, D.P., 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Illinois Natural History Survey, Champaign, Illinois.
- Uliana, M., Dellape, D., 1981. Estratigrafía y evolución paleoambiental de la sucesión Maastrichtiana Eoteraria del Engolfamiento Neuquino, Patagonia Septentrional, VII Congreso Geológico Argentino. San Luis 8 (3), 673–711.
- Volkheimer, W., 1973. Observaciones geológicas en el área de Ing. Jacobacci y adyacencias, Provincia de Río Negro. *Revista de la Asociación Geológica Argentina* 28, 1–13.
- Wedel, M.J., 2003a. The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology* 23 (2), 344–357.
- Wedel, M.J., 2003b. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* 29 (2), 243–255.
- Wedel, M.J., 2009. Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of Experimental Zoology* 311A. <http://dx.doi.org/10.1002/jez.513>.
- Wedel, M.J., Taylor, M.P., 2013. Caudal pneumaticity and pneumatic hiatuses in the sauropod dinosaurs giraffatitan and apatosaurus. *PLoS One* 8 (10), e78213. <http://dx.doi.org/10.1371/journal.pone.0078213>.
- Wedel, M.J., Cifelli, R.L., Sanders, R.K., 2000. *Sauroposeidon proteles*, a new sauropod from the Early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* 20 (1), 109–114.
- Wilson, J.A., 1999. A nomenclature for vertebral laminae in sauropods and other saurischians dinosaurs. *Journal of Vertebrate Paleontology* 19 (4), 639–653.
- Wilson, J.A., 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or 'lingua franca'? *Journal of Vertebrate Paleontology* 26 (3), 511–518.
- Wilson, J.A., D'Emic, M.D., Ikejiri, T., Moacan, E.M., Whitlock, J.A., 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS One* 6 (2), e17114. <http://dx.doi.org/10.1371/journal.pone.0017114>.
- Zurriaguz, V., Álvarez, A., 2013. Shape variation in presacral vertebrae of saltasaurine titanosaurs (Dinosauria, Sauropoda). *Historical Biology* 26 (6), 801–809.

Appendix

Anatomical Abbreviations

CH	Chevrons
CPOL	Centropostzygapophyseal lamina
LPF	Lateral pneumatic foramina
PO	Postzygapophyses
PR	Prezygapophyses
PRSL	Prespinal lamina
SPOL	Spinopostzygapophyseal lamina
SPRF	Spinoprezygapophyseal fossa
SPRL	Spinoprezygapophyseal lamina
TPOL	Intrapostzygapophyseal lamina

Scorings modified from [Salgado et al. \(2014\)](#):

Character 43: the scoring was changed from (0) to (1) in *Saltasaurus loricatus* and from (?) to (1) in *Rocasaurus muniozi* because both species possess a deep and broad interzygapophyseal fossa (= spinoprezygapophyseal fossa) ([Salgado and Azpilicueta, 2000](#): fig. 8c; [Cerda et al., 2012](#): fig. 1j).

Characters added to the data matrix of [Salgado et al. \(2014\)](#):

Character 78. Caudal vertebrae, anterior-middle centra: without a pneumatic lateral foramen (0); with a pneumatic lateral foramen (1).