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New contributions to the presacral osteology of *Saltasaurus loricatus* (Sauropoda, Titanosauria) from the Upper Cretaceous of northern Argentina

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ABSTRACT

Saltasaurus loricatus is a derived form of sauropod dinosaur from the Upper Cretaceous of northern Argentina. In this work, we expand the information of the presacral vertebral column of *Saltasaurus loricatus*, including a detailed description of neural laminae, fossae and pneumatic foramina of the neural arch, and establish a comparative analysis with closely related taxa (*Neuquensaurus australis* and *Rocasaurus muniozi*). Our data does not support previous phylogenetic hypothesis in which *S. loricatus* is more closely related to *R. muniozi* than *N. australis*. A conservative pattern of distribution of pneumatic foramina in the neural arch of cervical vertebrae cannot be recognized. Although variation in the pneumatic foramina distribution is also present in dorsal vertebrae, these structures are more commonly observed in certain regions (within the postzygapophyseal spinodiapophyseal fossa and spinoprezygapophyseal fossa + prezygapophyseal spinodiapophyseal fossa and in the dorsal border of the spinodiapophyseal lamina). Our data reveal that, despite its value in paleobiological and systematic studies, the presence and distribution pattern of pneumatic foramina in neural arches of presacral vertebrae appears to be underestimated in previous anatomical studies.

1. Introduction

Saltasaurus loricatus represents one of the more derived forms of sauropod dinosaurs. A large number of specimens, including materials of adult and sub-adult individuals, have been collected from an Upper Cretaceous site of northern Argentina (Bonaparte and Powell, 1980; Powell, 2003). As in other Saltasaurini titanosaurs (e.g. *Neuquensaurus australis*), *Saltasaurus* is an armored form characterized by a relatively small body size and a high degree of postcranial skeletal pneumaticity (Salgado and Bonaparte, 2007; Cerda et al., 2012; García and Salgado, 2013).

Both cranial and postcranial anatomy of *Saltasaurus* has been described by Powell (1992, 2003). Although the osteological description in these previous studies is extensive, detailed analysis of neural arch laminae and pneumatic fossae and foramina of the vertebral column were not performed. Interestingly, several approaches carried out in the last years have demonstrated the importance of these anatomical structures, not only as tools for systematics, but also for soft tissue reconstruction in sauropod dinosaurs, especially those related with the respiratory system (e.g. Britt, 1997; Salgado et al., 2006; Salgado and Powell, 2010; Schwartz et al., 2007; Wedel, 2003a,b, 2009; Wilson, 1999; Yates et al., 2012). For this reason, a detailed knowledge about the anatomy of the vertebral column (particularly the presacral elements) is necessary to interpret its main morpho-functional significance.

The main goals of this work are: 1) to expand our knowledge of the vertebral anatomy of *S. loricatus*, including a detailed description of the vertebral laminae, fossae and pneumatic foramina of the presacral elements; 2) compare our findings with closely related species (*Rocasaurus muniozi* and *Neuquensaurus australis*) in order to establish the main differences among these taxa; 3) determine the pattern of distribution of pneumatic foramina in *S. loricatus* and other Saltasaurini and evaluate their systematic value.

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Institutional abbreviations
MCS Pv: Paleontology collection of the Museo de Cinco Saltos, Río Negro Province, Argentina.
MPCA Pv: Vertebrate Paleontology collection of the Museo Provincial de Cipolletti "Carlos Ameghino", Río Negro Province, Argentina.
PVL: Vertebrate Paleontology collection of the Instituto "Miguel Lillo", Tucuman Province, Argentina.

2. Materials and methods

This study is based on first hand observations of diverse materials assigned to *S. loricatus*, including 11 cervical and 12 dorsal vertebrae (Tables 1–3). The examined material was collected from the Upper Cretaceous (?upper Campanian–Maastrichtian) deposits of the Lecho Formation at the locality of El Brete (South of Salta Province, Argentina) (Fig. 1A) (Bonaparte and Powell, 1980; Powell, 2003). The comparison of the axial skeleton of *S. loricatus* is focused on the other two definite Saltasaurini taxa: *Rocasaurus muniozi* and *Neuquensaurus australis*. All the material assigned to *R. muniozi* (Table 1) came from sedimentary rocks of the Allen Formation (middle Campanian–lower Maastrichtian) (Fig. 1B) of the locality of Salitral Moreno (Río Negro Province, Argentina) (Fig. 1C) (Salgado and Azpilicueta, 2000; García and Salgado, 2013). In the case of *N. australis*, the examined specimens were recovered from the localities of Cinco Saltos and Lago Pellegrini (Río Negro Province, Argentina), from deposits of the Anacleto Formation (lower Campanian) (Powell, 2003; Salgado et al., 2005; Otero, 2010). Although several presacral vertebrae housed in the Museo de La Plata (Buenos Aires) have been assigned to *Neuquensaurus* in the past (Lydekker, 1893; Von Huene, 1929), such assignment is not confident for all of them (D'Emic and Wilson, 2011; Zurriaguz and Otero, 2013). Among these specimens, many of them are actually incomplete, lacking neural laminae and even neural arches. For these reasons, since the referred specimen of *N. australis* MCS Pv 5 (Table 1) is the one individual that overlaps and shares diagnostic features with the holotypic remains, we only considered this specimen for comparison with *S. loricatus*.

Anatomical nomenclature follows Wilson (1999) for the vertebral laminae and Wilson et al. (2011) for neural fossae, except for the udl (unnamed diapophyseal lamina) and upl (unnamed parapophyseal lamina) where we have followed the names suggested by Salgado et al. (2005) for these laminae. We also use Romerian terminology (Wilson, 2006), which divides the body into anterior, posterior, ventral and dorsal portions (Romer, 1956), instead of avian nomenclature used by Harris (2004). Nomenclature for internal pneumatic structure follows Britt (1997) and Wedel et al. (2000). There is no complete presacral sequence of *Saltasaurus loricatus*, therefore, the possible position of each vertebra is

Table 1
List of all presacral vertebrae examined in this study.

Taxon	Material	Collection number
S. loricatus	Axis	PVL 4017-1
	Most Anterior Cervical	PVL 4017-2
	Most Anterior Cervical	PVL 4017-3
	Middle Anterior Cervical	PVL 4017-4
	Middle Anterior Cervical	PVL 4017-139
	Last Anterior Cervical	PVL 4017-5
	Last Anterior Cervical	PVL 4017-6
	First Posterior Cervical	PVL 4017-7
	Last Posterior Cervical	PVL 4017-8
	Last Posterior Cervical	PVL 4017-9
	First Posterior Cervical	PVL 4017-212
	First Posterior Cervical	PVL 4017-40
	First Dorsal	PVL 4017-10
	Anterior Dorsal	PVL 4017-11
	Anterior Dorsal	PVL 4017-12
	Anterior Middle Dorsal	PVL 4017-13
	Anterior Middle Dorsal	PVL 4017-14
	Anterior Middle Dorsal	PVL 4017-15
	Last Posterior Dorsal	PVL 4017-16
	First Posterior Dorsal	PVL 4017-17
	Last Posterior Dorsal	PVL 4017-135
	Last Posterior Dorsal	PVL 4017-136
	First Posterior Dorsal	PVL 4017-137
	Posterior Middle Dorsal	PVL 4017-138
N. australis	Posterior Cervical	MCS Pv 5-17
	Middle Dorsal	MCS Pv 5-18
	Middle Dorsal	MCS Pv 5-19
	Posterior Dorsal	MCS Pv 5-20
	Posterior Dorsal	MCS Pv 5-21
	posterior Dorsal	MCS Pv 5-22
	posterior Dorsal	MCS Pv 5-23
R. muniozi	Anterior? Cervical	MPCA Pv 46/1
	Anterior? Cervical	MPCA Pv 46/2
	Middle Cervical	MPCA Pv 858
	Middle Cervical	MPCA Pv 859
	Middle Cervical	MPCA Pv 860
	Middle Dorsal	MPCA Pv 46/3
	Middle Dorsal	MPCA Pv 46/4
	Middle Dorsal	MPCA Pv 46/5
	Middle Dorsal	MPCA Pv 46/6
	Middle Dorsal	MPCA Pv 46/7
	Middle Dorsal	MPCA Pv 46/8

Table 2
Measurements of the cervical vertebrae of *S. loricatus*. The * indicates that the measurements are approximated.

Cervical vertebrae	Length with odontoid process	Length without odontoid process	Total length	Height of the posterior articulation	Total height	Width of the posterior articulation
4017-1 (Axis)	6.5 cm	5.5 cm	6.5 cm	3.7 cm	11.4 cm	3.6 cm
4017-2	–	–	14.3 cm	4.6 cm	10.8 cm	6.6 cm
4017-3	–	–	14 cm	5 cm	11 cm	7.4 cm
4017-4	–	–	15.6 cm	6 cm	14.3 cm	7.5 cm
4017-139	–	–	14.5 cm	5.3 cm	11.3 cm	7.6 cm
4017-5	–	–	14 cm	8.8 cm	16.1 cm	7.7 cm
4017-6	–	–	15.8 cm*	–	15.6 cm*	–
4017-212	–	–	14.5 cm*	–	–	–
4017-40	–	–	–	–	–	–
4017-7	–	–	13.7 cm	6.5 cm	16.9 cm	7.1 cm
4017-8	–	–	–	–	–	–
4017-9	–	–	12.2 cm	7.9 cm	17.7 cm	8.1 cm

Table 3
Measurements of dorsal vertebrae of *S. loricatus*. The * indicates that the measurements are approximated.

Dorsal vertebrae	Total length	Height of the posterior articulation	Total height	Width of the posterior articulation
4017-10	–	–	–	–
4017-11	16.2 cm*	–	26.8 cm*	–
4017-12	–	–	–	–
4017-13	13.8 cm	10.1 cm	29.3 cm	14.1 cm
4017-14	12.2 cm*	8.4 cm	26.7 cm	9.8 cm
4017-15	12.3 cm	10.6 cm	29.8 cm	11.1 cm
4017-138	–	–	–	–
4017-16	13 cm	9.4 cm	30 cm	10.9 cm
4017-137	12.4 cm	8.7 cm	31.2 cm	11.7 cm
4017-17	12.8 cm	8.2 cm	–	8.5 cm
4017-136	16.1 cm	10.2 cm	30.1 cm	11.2 cm
4017-135	15.6 cm	9.6 cm	32.8 cm	12.8 cm

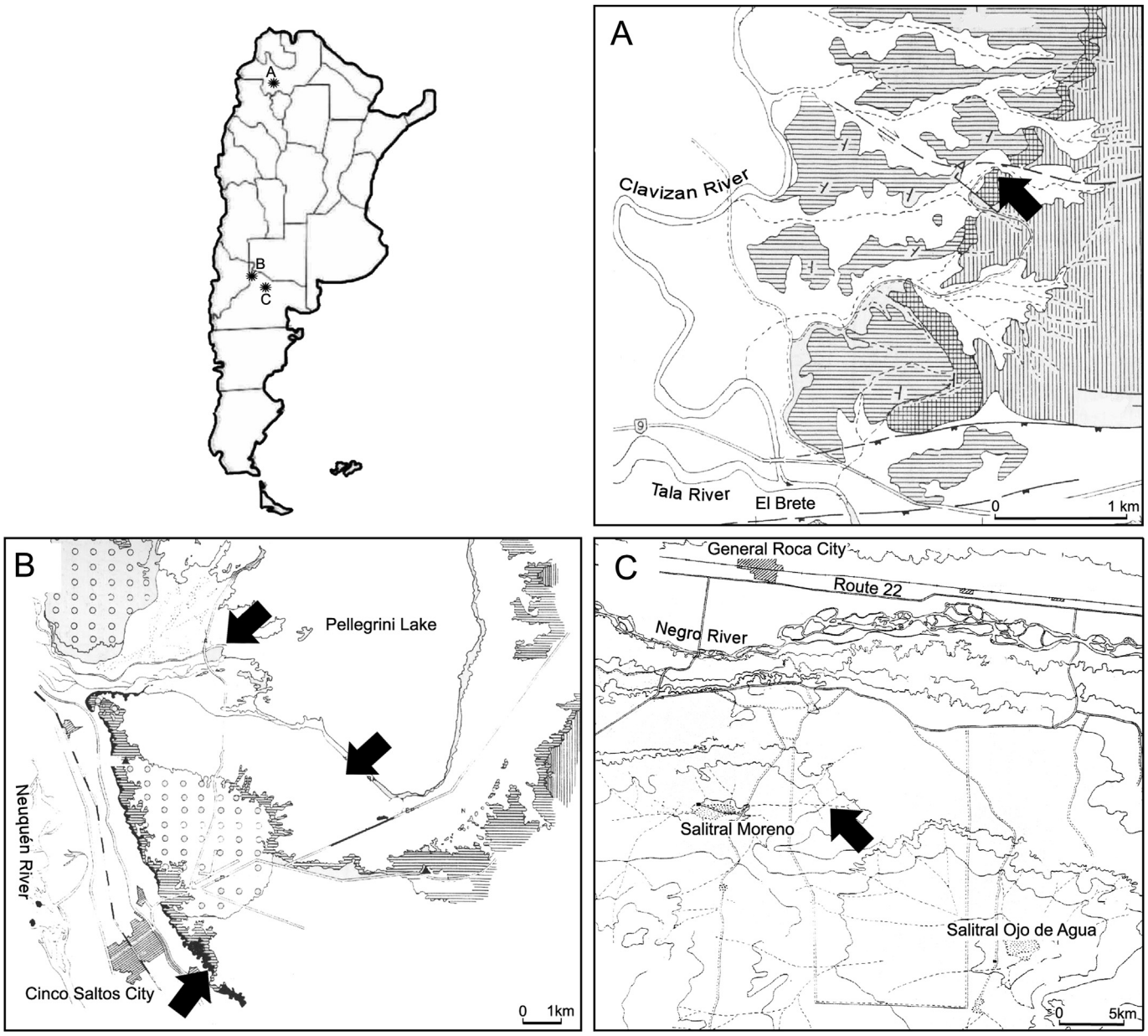

Fig. 1. Location map of the localities of El Brete (A), Cinco Saltos-Lago Pellegrini (B) and Salitral Moreno (C). Black arrows indicate the site where the studied material were collected. Scale bar: 1 km. Modified from Powell (2003).

determined by comparison with the observed sequence in *Trigonosaurus pricei* (Campos et al., 2005) and *Overosaurus paradasorum* (Coria et al., 2013).

Anatomical abbreviations: acpl, anterior centroparapophyseal lamina; cpaf, centroparapophyseal fossa; cpol, centropostzygapophyseal lamina; cpof, centropostzygapophyseal fossa; cprl, centroprezygapophyseal lamina; cprf, centroprezygapophyseal fossa; eprl, epipophyseal–prezygapophyseal lamina; pacdf, parapophyseal centrodiapophyseal fossa; pacprf, parapocentrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; posl, postspinal lamina; ppdl, paradiapophyseal lamina; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl, prezygodiapophyseal lamina; prpl, prezygoparapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; prsl, prespinal lamina; sdf, spinodiapophyseal fossa; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; spof, spinopostzygapophyseal fossa; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tpol, intrapostzygapophyseal lamina; tprl, intraprezygapophyseal lamina; udl, unnamed diapophyseal lamina; upl, unnamed parapophyseal lamina, lpf, lateral pneumatic foramen.

Systematic paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Titanosauria Bonaparte and Coria, 1993

Saltasaurinae Powell 1992 (Saltasaurini Salgado and Bonaparte, 2007)
Saltasaurus loricatus Bonaparte and Powell, 1980

Holotype: PVL 4017-92. A complete sacrum fused to two ilia.

3. Description

3.1. Cervical vertebrae

3.1.1. General features

A total of 12 cervical vertebrae have been assigned to *S. loricatus*. The vertebral centra are opisthocoelous, short and wide and they possess small "eye shaped" lateral pneumatic foramina ("pleurocoels", lpf). The anterior cervical vertebrae are elongated and the neural arches are low and long. The postzygapophyses are long and project beyond the posterior articular face of the centrum. The prezygapophyseal facets are subcircular. The posterior cervical vertebrae are proportionally shorter and wider than the anterior elements. Occasionally, the lpf have a dividing lamina. The prezygapophyses are laterally oriented to both sides of the neural spine. The articular surface of the prezygapophyses is subcircular. The postzygapophyses constitute processes that are stouter and shorter than those of the anterior cervicals. Internally, both centra and neural arches are composed of camellate tissue (Britt, 1997; Wedel 2003a). The cprl, podl, the sprl, the spinopostzygapophyseal lamina (spol) and the pcdl are well developed and

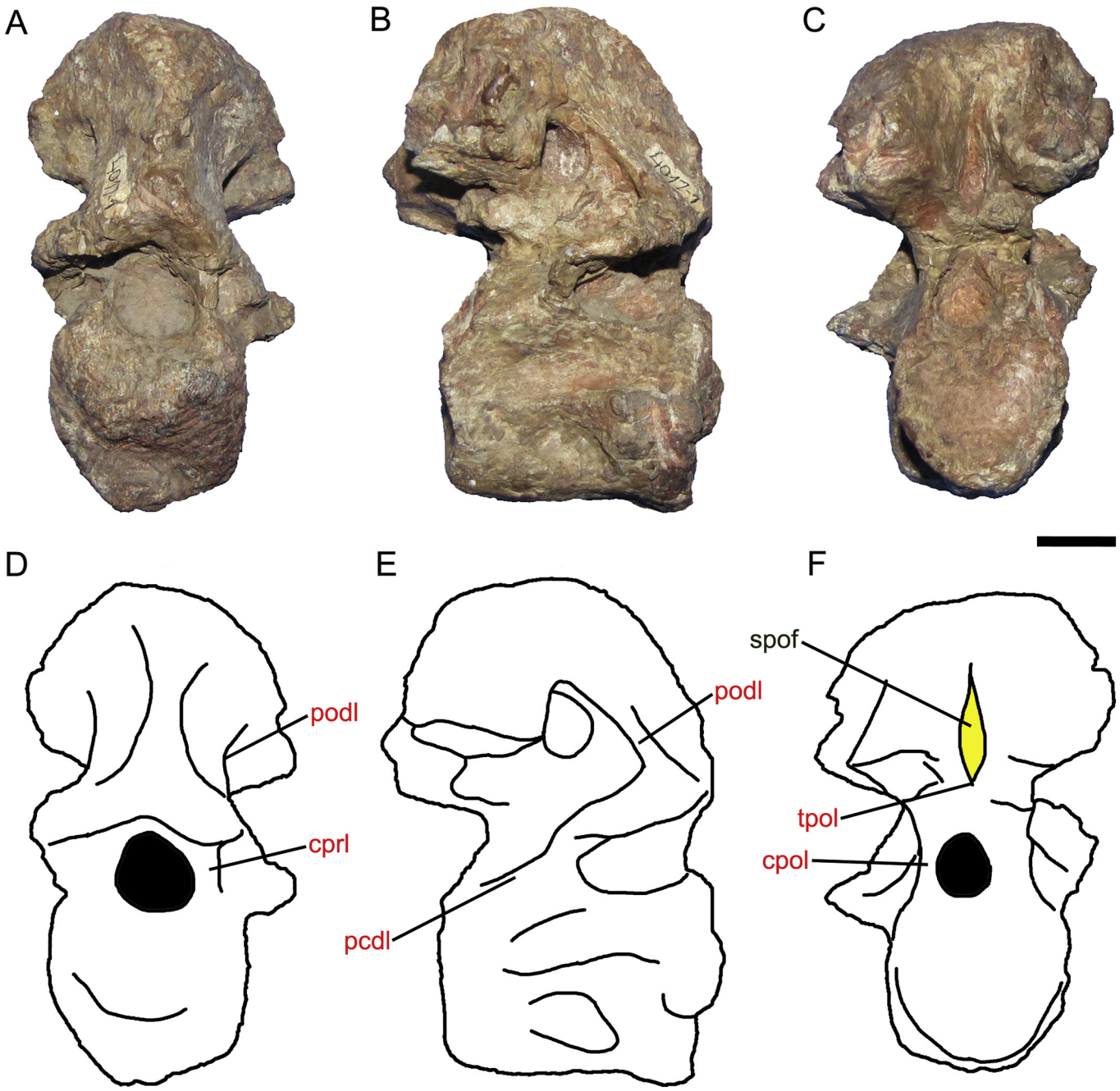

Fig. 2. Axis (PVL 4017-1) of *Saltasaurus loricatus* in anterior (A), lateral (B) and posterior (C) views. D, E and F, interpretative line drawings of A, B and C. Abbreviations as in the text. Scale bar: 2 cm.

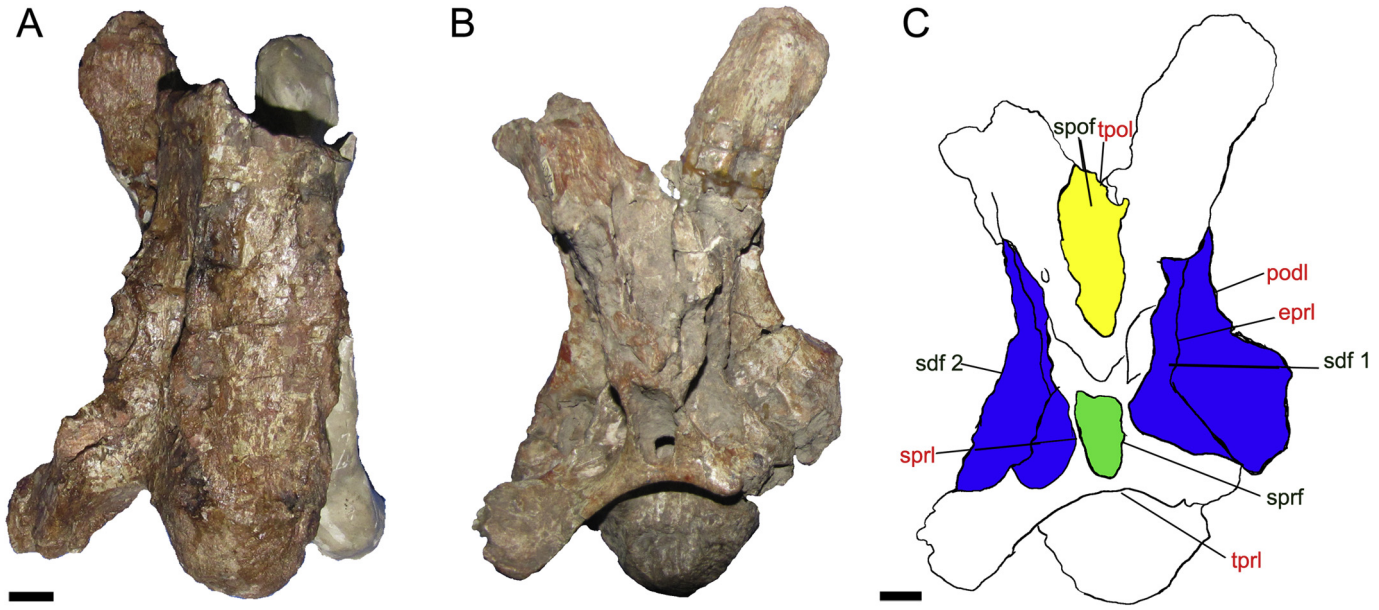

Fig. 3. Anterior cervical vertebrae (PVL 4017-2, PVL 4017-3) of *Saltasaurus loricatus*. A. (PVL 4017-2). B. Dorsal view (PVL 4017-3). C. Interpretative line drawing. Scale bar: 2 cm. Fossae are in different color tones depending on their landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

conservative, showing no significant morphological variations along the series. Regarding the spol and pcdl, they become more vertical towards the end of the sequence. The tprl has predominantly an inverted U shape. The tpol is developed and exhibits a variable morphology (V or U-shaped). The spinodiapophyseal fossa (sdf) is divided by the eprl in sdf 1 and sdf 2 (Wilson et al., 2011; Wilson, 2012). These fossae and the eprl are prominent in the axis, but the lamina is reduced and the fossa disappears towards the end of the sequence. Therefore, the position occupied for both sdf in the anterior elements becomes occupied by the prsdf, in which only a remnant of the eprl is visible.

3.1.2. *Axis (PVL 4017-1)*

It is a small vertebra (Figs. 2A, D) with a ventral surface that has a gentle marked crest in its middle portion. The axis has a small, shallow and oval shaped lpf, which are divided by a horizontal and thin lamina (Figs. 2B, E). The odontoid process occupies 1/5 of the centrum. The parapophyses are partially preserved; these

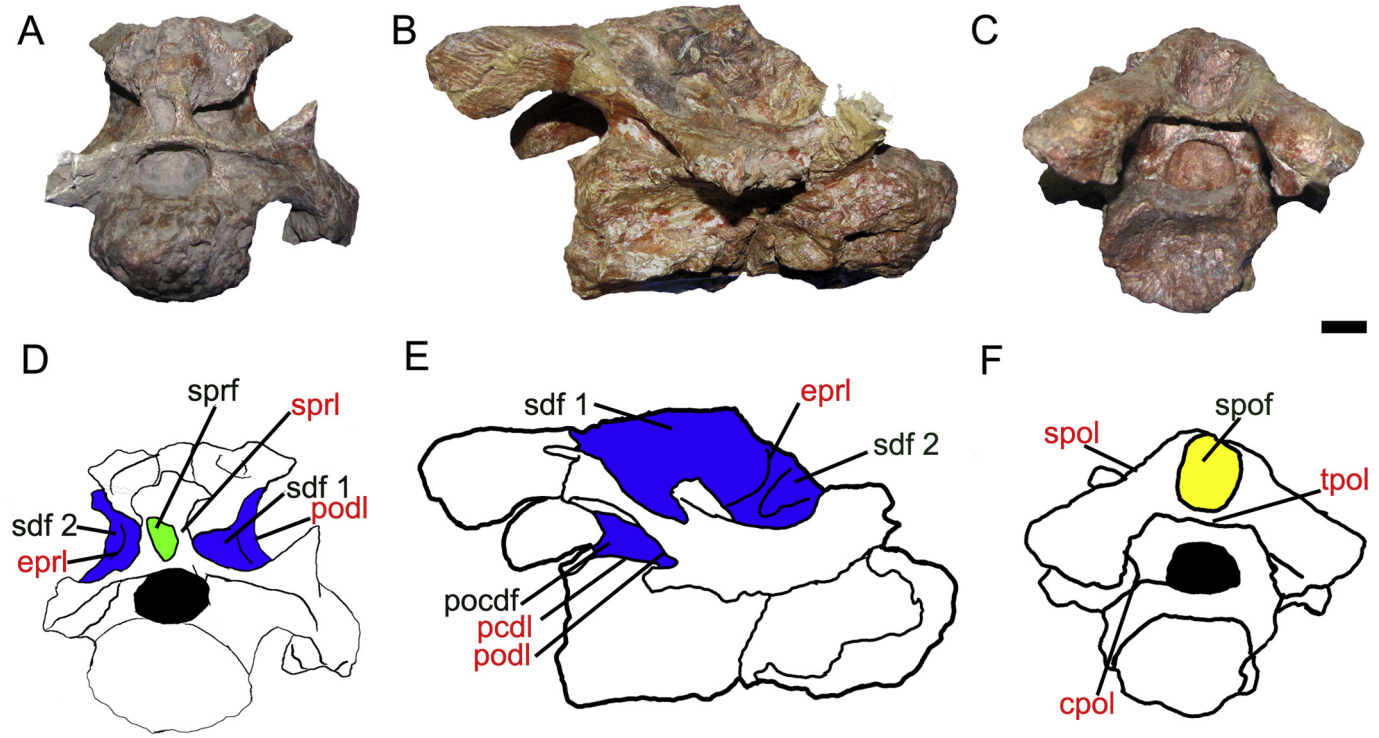

Fig. 4. Middle anterior cervical (PVL 4017-139) of *Saltasaurus loricatus* in anterior (A), lateral (B) and posterior (C) views. D, E and F, interpretative line drawings of A, B and C. Scale bar: 2 cm.

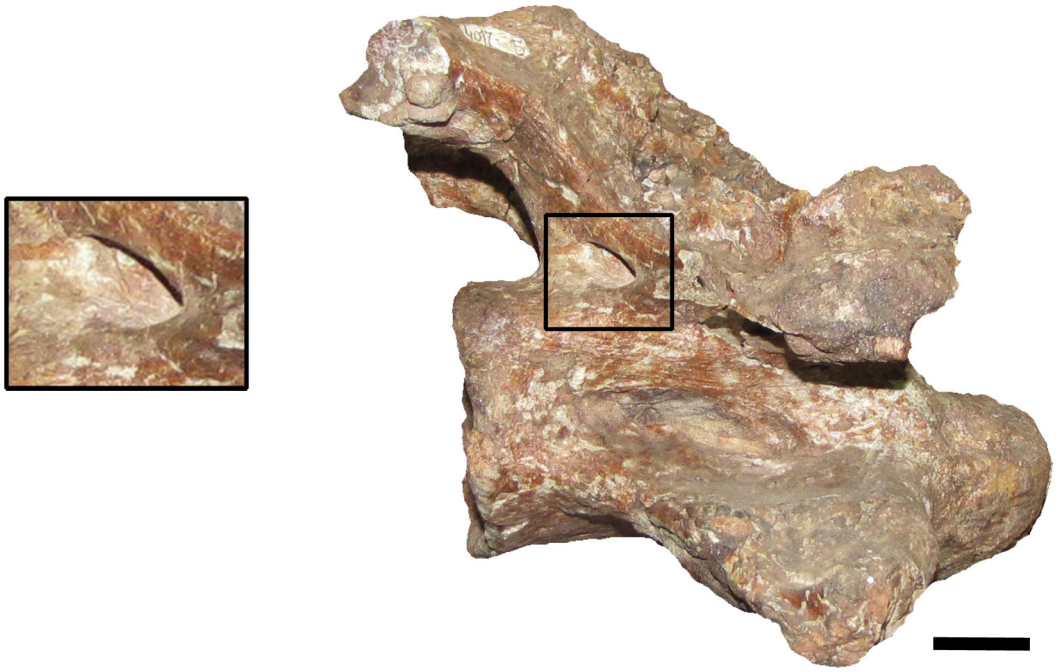

Fig. 5. Last anterior cervical vertebra (PVL 4017-5) of *Saltasaurus loricatus* in right lateral view. The inset square shows a "half-moon" shaped pneumatic foramen between the dorsal margin of the pcdl and ventral margin of the podl. Scale bar: 2 cm.

structures are rounded and are located in the lower portion of lateral surface of the centrum, ahead of the lpf. The prezygapophyses are not preserved and the postzygapophyses, which are well preserved, are angled 45° to the horizontal plane.

The neural spine is high and massive, with a hemispherical surface. In the anterior surface, the neural spine shows a prominent crest (Figs. 2A, D). Between the neural spine and the postzygapophyses (below the podl), in the left and right surfaces of the vertebra, there is a pneumatic foramen within a fossa, which is divided by an accessory lamina (Figs. 2B, E).

The centroprezygapophyseal lamina (cprl) and centropostzygapophyseal lamina (cpol) are straight, and they expand transversely where they contact with the prezygapophyses and postzygapophyses respectively (Figs. 2A, D, C, F). The cprl further defines one of the limits of the prezygapophyseal centrodiapophyseal fossa (prcdf). This fossa is triangular and shallow. The posterior centrodiapophyseal lamina (pcdl) is short, slightly oblique and expanded in contact with the diapophysis and the posterior centrum margin. The postzygodiapophyseal lamina (podl) is well developed. Its contact with the postzygapophysis is unclear. Together with the pcdl and cpol, the podl delimits the postzygapophyseal centrodiapophyseal fossa (pocdf), which on the left side is divided into three sub-fossae by two little accessory lamina (Figs. 2B, E). In the left fossa, there is another lamina that extends from the postzygapophysis and fades out inside the fossa. On the right side, the pocdf is divided by an accessory lamina that connects the postzygapophysis with the podl. The intrapostzygapophyseal lamina (tpol) is well developed and "V-shaped". The thickness of this lamina increases toward the postzygapophysis. The tpol also defines a strongly deep spinopostzygapophyseal fossa (spof), which is oval in shape (Figs. 2C, F).

3.1.3. *Most anterior cervical vertebrae (PVL 4017-2 and PVL 4017-3)*

These vertebrae appear to correspond with the 3rd and 4th cervical vertebrae (Powell, 2003). The ventral surfaces are smooth and slightly concave (Fig. 3A). These vertebrae have small, oval-shaped lpf in the centra, which are slightly displaced to the

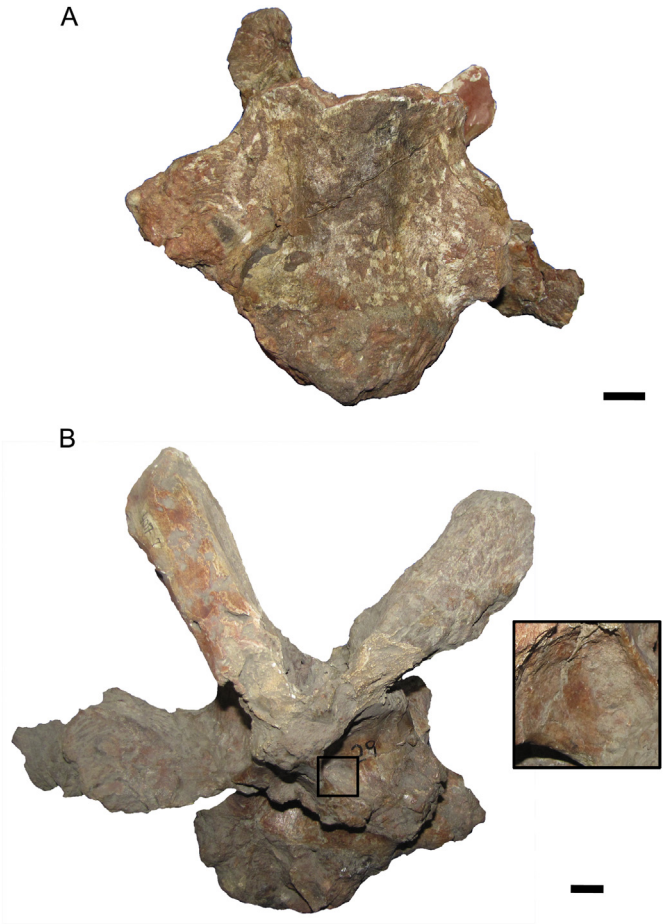

Fig. 6. First posterior cervical vertebra (PVL 4017-7) in ventral (A) and dorsal (B) view. The inset square shows the absence of the eprl. The sdf retains its orientation, but it is not divided in sdf 1 and sdf 2. Scale bar: 2 cm.

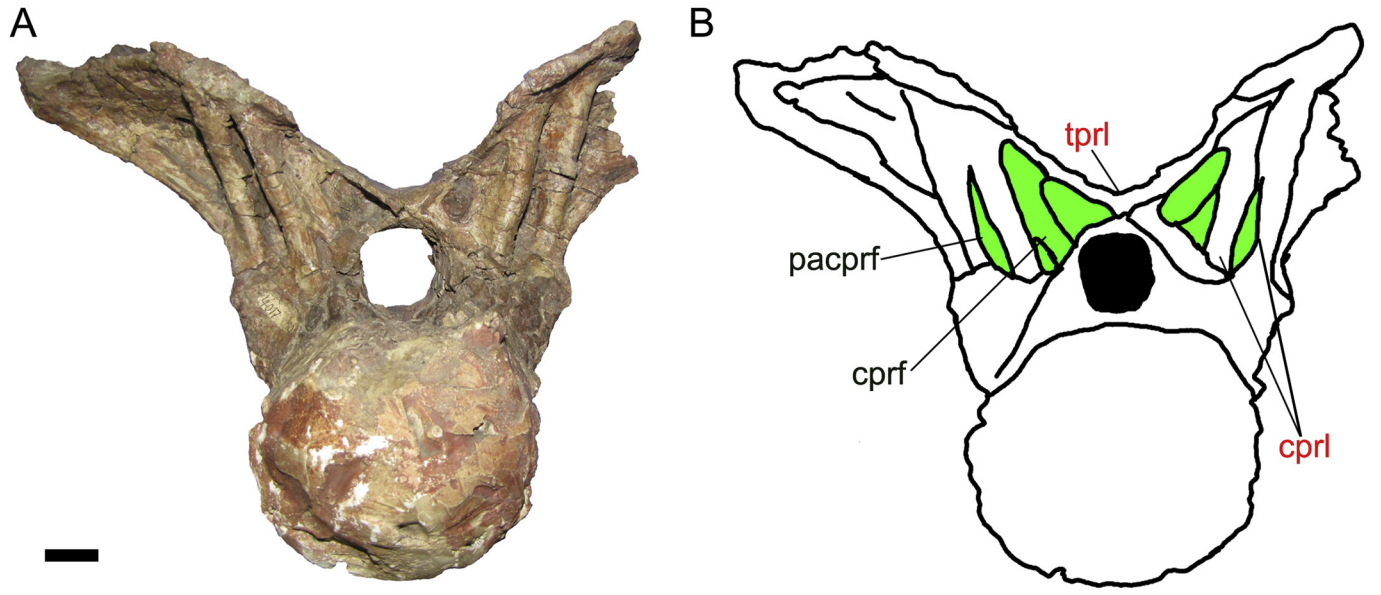

Fig. 7. First dorsal vertebra (PVL 4017-10) of *Saltasaurus loricatus*. A. Anterior view; B. interpretative line drawing. Note the double and massive cprl and fossae that they delimited (pacprf). Scale bar: 2 cm.

anterior region of the vertebra. These foramina are deep and seem to be in contact with the middle portion of the centrum. The left pneumatic lateral foramen is divided by a septum. The parapophyses are not well preserved, show mainly their bases. The parapophyses are behind the condyle and ahead of lpf. Only one parapophyses is preserved (right parapophyses of PVL 4017-3), it possesses a slightly conical shape, with a wide basis. This structure forms an angle of 45° with the horizontal plane. The prezygapophyses and postzygapophyses are large and well developed. The prezygapophyses are laterally expanded. The diapophyses are prominent and inclined to the lateral margins of the vertebra. The neural spines are low, massive and are surrounded by the bases of the prezygapophyses and postzygapophyses (Figs. 3B, C). The cprl and cpol are columnar, except in PVL 4017-3, where the cpol is narrow. The intraprezygapophyseal lamina (tprl) has an inverted U-shaped and the spinoprezygapophyseal lamina (sprl) is parallel and widened in contact with the prezygapophyses. These three laminae delimit the srpf, which is oval-shaped and deep (Figs. 3B, C).

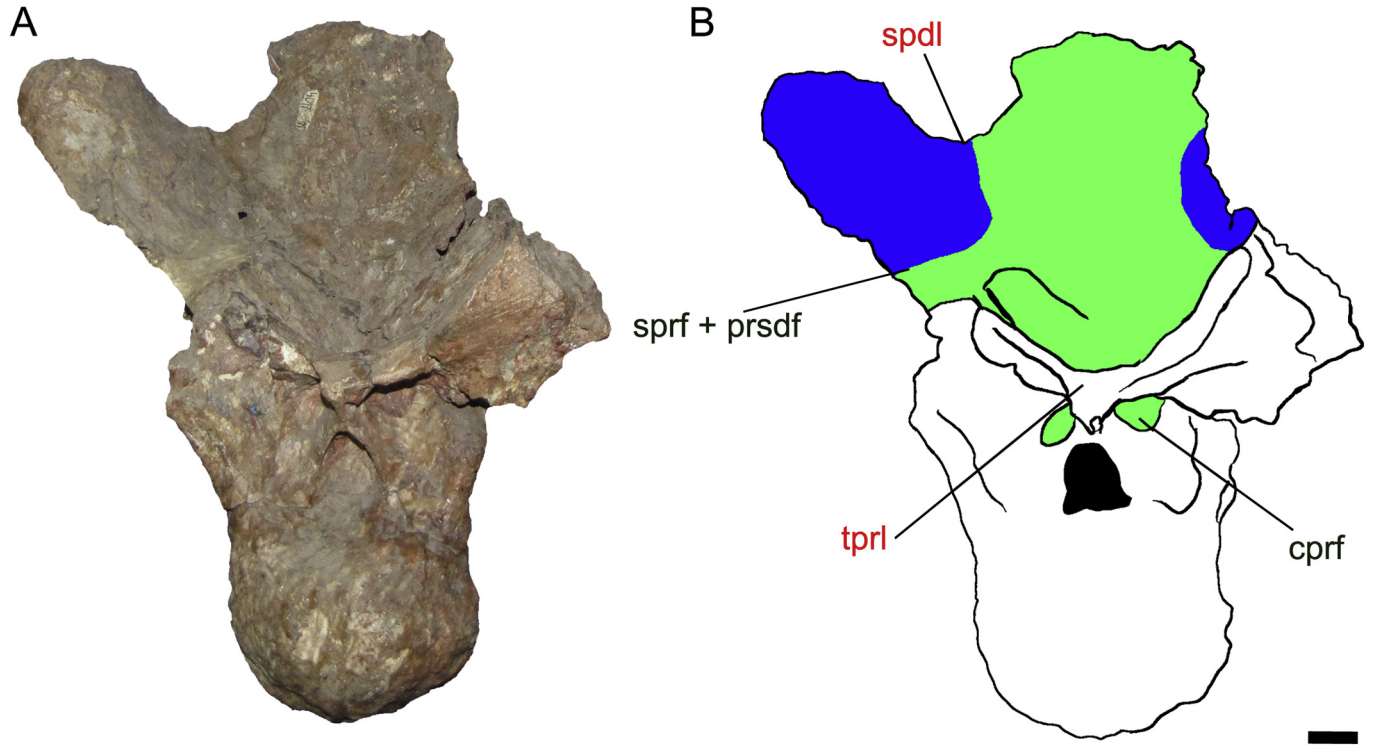

Fig. 8. Anterior dorsal vertebra PVL 4017-11. A. Anterior view; B. interpretative line drawing. Note the wide sprf + prsdf without prsl and two triangular and shallow cprf and the spdl and tprl. Scale bar: 2 cm.

Fig. 9. Anterior middle dorsal vertebra (PVL 4017-15) of *Saltasaurus loricatus* in ventral view. Note the presence of a longitudinal ventral keel (white arrowhead) and a foramen (black arrow). Scale bar: 2 cm.

There is a lamina that arises of the prezygapophyses and bounds the spinodiapophyseal fossa 1 (sdf 1) and spinodiapophyseal fossa (sdf 2). This lamina would correspond to the epipophyseal–prezygapophyseal lamina (eprl). This probable eprl is well developed in these vertebral elements (Figs. 3B, C). In PVL 4017-2, between the left sdf and left postzygapophysis, there is an oval-shaped foramen and in PVL 4017-3 there is a large foramen within the right sdf. The pcdl is parallel to the horizontal plane and slightly curved in the contact with the diapophysis. The podl is well developed and parallel to the pcdl in the mid portion. The pcdl and the podl delimit the pocdf, which is a triangular, small and shallow fossa. The tpol is short, thin and straight, and delimits a small and very shallow centropostzygapophyseal fossa (cpof) and a deep and large spof. The spof is parallel to the longitudinal plane to the centrum and can be seen in dorsal view (Figs. 3B, C).

3.1.4. Middle anterior cervical vertebrae (PVL 4017-4 and PVL 4017-139)

The ventral surfaces of PVL 4017-4 and PVL 4017-139 centra are smooth and mainly concave. These vertebrae have a medium-size and shallow lpf in the centra. The right lpf is shallow and divided by a short and thick oblique septum. In the case of PVL 4017-4, the lpf deeper and its dividing lamina is oblique and the left lpf is smaller than the right. In both cases, the foramina are in the middle region of the centrum. The parapophyses are well developed. They are behind the condyle and below the lpf and their orientation is ventral. In these vertebrae, the parapophyses are more massive than the anterior element and their bases are more separated of the centrum (Figs. 4A, D). The prezygapophyses are smaller than the prezygapophyses of the most anterior cervical vertebrae, while the postzygapophyses maintain the same size. The left diapophysis of the PVL 4017-4 possesses a triangular pneumatic foramen. The neural spine is more elevated and slender with respect to the most anterior cervical vertebrae (Figs. 4B, E). The crpl and cpol are columnar in PVL 4017-139 (Figs. 4A, C, D, F) and laminar in PVL 4017-4. The tprl exhibits a straight (PVL 4017-4) or inverted U shape (PVL 4017-139). This lamina, together with the sprl, delimits the spinoprezygapophyseal fossa (sprf), which has an inverted triangle shape and a medium depth (Figs. 4A, D). The probable eprl is gradually reduced until the sdf, where it disappears entirely. This lamina is shorter than the eprl of the most anterior cervical vertebrae (Figs. 4A, D). The pcdl is parallel to the long axis of centrum and marks its dorsal limit (Figs. 4B, E). The podl is well developed and together with the pcdl and cpol, delimits the pocdf, which is oval-shaped in PVL 4017-139 and triangular in PVL 4017-4. A small and elliptical pneumatic foramen is located in the podl of the left side of PVL 4017-139, near the postzygapophysis. Whereas in PVL 4017-139 the tpol is straight and short, this lamina possesses an inverted U shape in PVL 4017-4. This lamina is the ventral limit of the deep spof, which is parallel to the longitudinal plane of the centrum. In turn, the tpol is the dorsal limit of the cpof, a small, triangular and shallow fossa (except in PVL 4017-4, in which it is more deeply excavated). Two pneumatic foramina are opened below to the spol in the spof of PVL 4017-4.

3.1.5. Posterior anterior cervical vertebrae (PVL 4017-5 and PVL 4017-6)

The ventral surfaces are slightly concave and show a poorly pronounced longitudinal keel. These elements possess shallow, oval-shaped lpf in the centra, which are lightly displaced to the posterior region of the vertebral centrum. The left foramen is smaller than the right in both vertebrae. The parapophyses are wide, orientated parallel to the diapophyses and their bases occupy almost 2/3 of the centrum. These structures have a truncated cone shape. The prezygapophyses and the postzygapophyses have the same size as in the middle anterior cervical vertebrae. The neural spine is high, thin and almost perpendicular to the centrum (Fig. 5).

With respect to the laminae and fossae, the cprl and cpol are columnar in both vertebrae. The same occurs for the trpl, which has an inverted U-shaped in the two vertebral elements. The sprl is more lateralized, widening the sprf and shortening the sdf 1 and sdf 2. Into these fossae, the probable eprl, is shorter and less conspicuous. The pcdl and the podl remain as in the anterior portion of the vertebral sequence, and delimit a shallow and small pocdf. Moreover, the podl is pierced by a large pneumatic foramen in PVL 4017-5 (Fig. 5). The tpol is V-shaped in PVL 4017-5 and straight in PVL 4017-6. This lamina is the ventral boundary of the spof, which is deep and well developed. In this portion of vertebral sequence, the spof begins to lose its parallelism with the longitudinal plane of the centrum and becomes more vertical. The tpol is also the dorsal limit of a small and triangular cpof.

3.1.6. First posterior cervical vertebrae (PVL 4017-212, PVL 4017-40 and PVL 4017-7)

The ventral surfaces are smooth and concave (Fig. 6A). PVL 4017-40 seems to show a slightly developed keel. Pneumatic foramina are present in the ventral surface of the centrum of PVL 4017-7 and PVL 4017-212. In PVL 4017-7, the pneumatic foramen is in the left side, behind the condyle and near to parapophysis and, in PVL 4017-212, the pneumatic foramen is in the middle of the concavity of the ventral surface. The vertebral centra possess shallow, oval shaped and centrally located lpf. The parapophyses are wide and located behind the condyle and below to lpf. They are orientated parallel to the diapophysis and their form is a truncated cone. Whereas the prezygapophyses are smaller than the

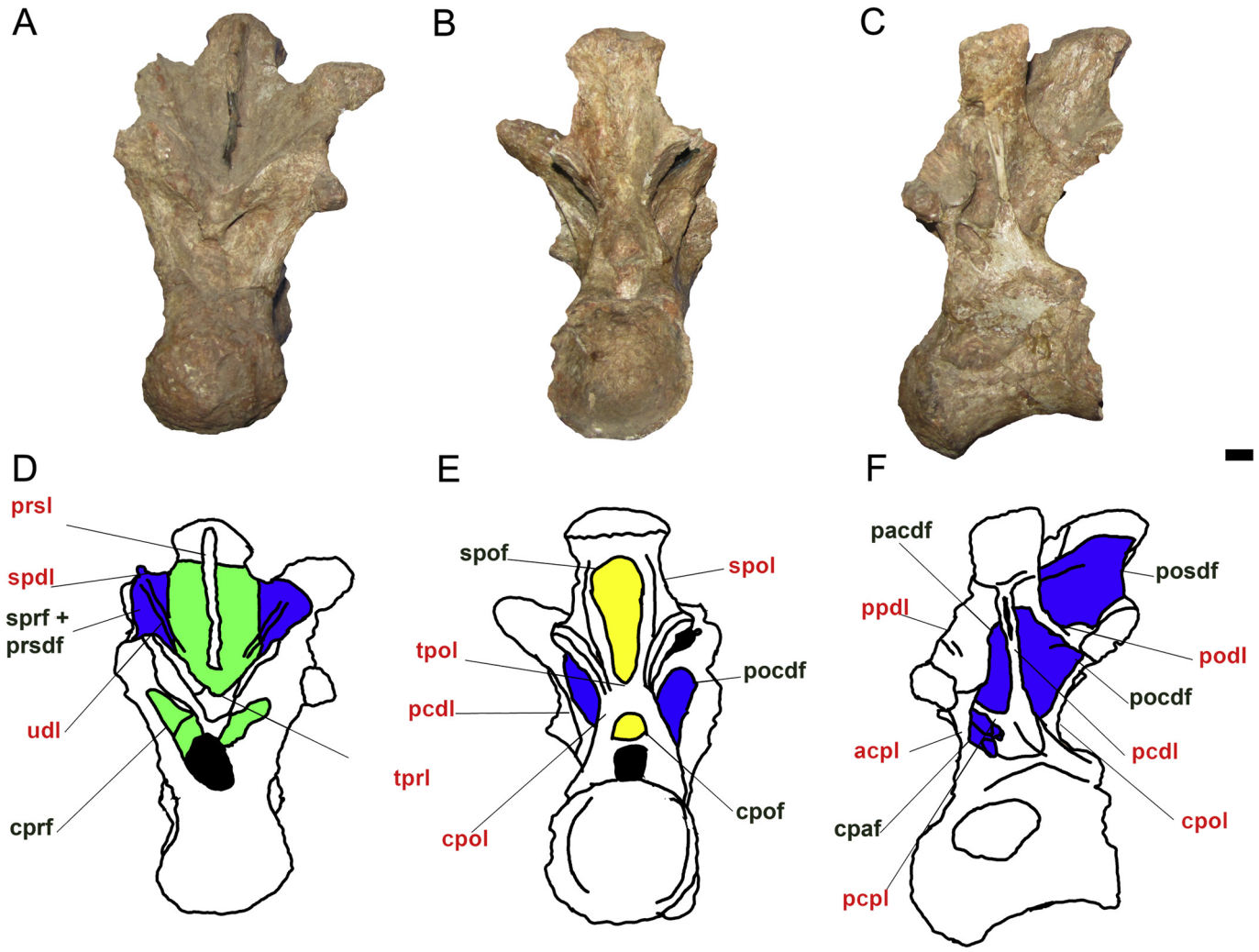

Fig. 10. Anterior middle dorsal vertebra (PVL 4017-15) of *Saltasaurus loricatus* in anterior (A), posterior (B) and lateral (C) views. D, E and F interpretative line drawing of A, B and C. Scale bar: 2 cm.

prezygapophyses of the anterior cervical vertebrae, the postzygapophyses maintain the same size and degree of development. The neural spine is straight and perpendicular to the centrum.

Regarding the laminae and fossae, the cprl (except in PVL 4017-7) is columnar. Because of this, PVL 4017-7 has a very small centroprezygapophyseal fossa (cprf), roughly oval in shape. The cpol is columnar in all the elements. The tprl is thin and straight. This lamina, together with the sprl, delimits the sprf, a shallow and oval fossa. The sprf has an incipient prespinal lamina (prsl) in PVL 4017-7. The sdf is a wide and shallow fossa and does not present the probable eprl (Fig. 6). The pcdl and the podl are well developed and conspicuous. Both delimit the pocdf, which possesses a triangular shape. The tpol is V-shaped and ventrally delimits the spof, which is deeply excavated and possess an isosceles triangle shape, in which the base is, precisely, the tpol. This lamina limits dorsally the cpof, a paired fossa with a triangular shape.

3.1.7. *Last posterior cervical vertebrae (PVL 4017-8 and PVL 4017-9)*

The ventral surfaces are not well preserved, which prevents seeing detail of the morphology of the centrum. The lpf in the centra are small, oval shaped and shallow. The bases of parapophyses are higher than in the rest of cervical vertebrae and they are located behind the condyle anteriorly of the anterior margin of lpf. The complete parapophyses are not preserved. The prezygapophyses are smaller than the prezygapophyses of the anterior cervical vertebrae, whereas the postzygapophyses are equally developed throughout the cervical sequence. The neural spine is straight, massive and high.

The cprl and the cpol possess columnar and laminar shapes respectively. The tprl has a U-shaped, describing a gentle curvature towards the prezygapophyses. The left sprl of PVL 4017-8 has an oval pneumatic foramen. This lamina, together with the tprl and sprl, delimit the sprf, which is triangular-shaped and shallow. The sdf is wide and totally lateralized. Contrary to that observed in first the posterior cervical, the probable eprl is not observed on this fossa. The pcdl and podl are well developed and delimit a small, triangular and shallow pocdf. The tpol, which exhibits a V shape, ventrally delimits the spof, a deep fossa and dorsally the cpof, a triangular and shallow fossa.

3.2. *Dorsal vertebrae*

3.2.1. *General features*

A total set of twenty dorsal vertebrae has been assigned to *S. loricatus*. The dorsal vertebrae are short and rather tall. The centrum has reduced lpf, which communicates with the internal

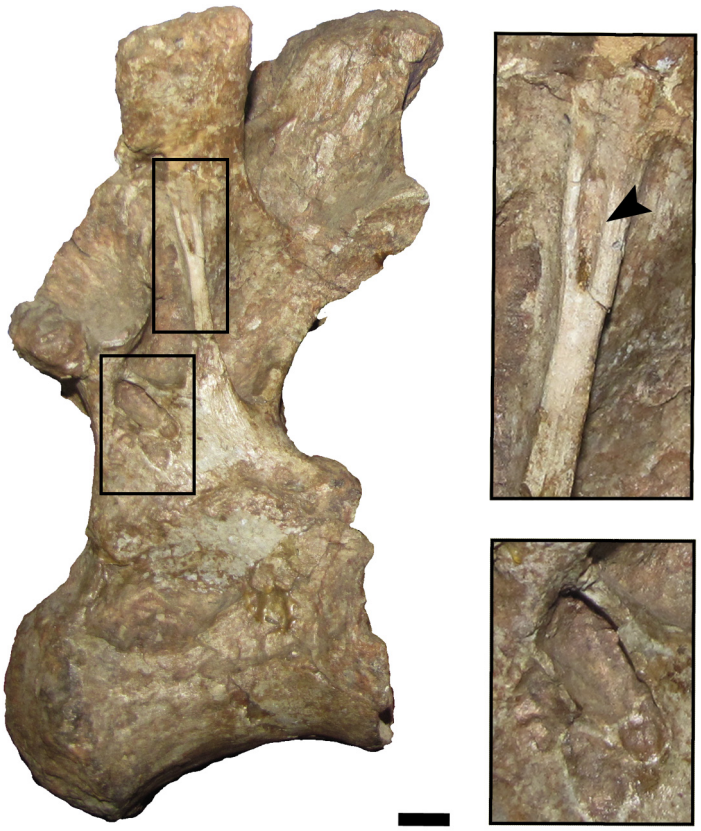

Fig. 11. Left lateral view of PVL 4017-15 shows an accessory septum that dividing the pacdf (lower box inset) and a pneumatic foramen (arrowhead) in the border of the pcdl (upper box inset). Scale bar: 2 cm.

camellate tissue. Some centra possess a poorly developed ventral keel. The prezygapophyses are small and generally oval-shaped, especially in the last dorsal vertebrae. The postzygapophyses are small in all of the sequence. The diapophyses and parapophyses are large and well developed. The neural arches present pneumatic foramina, some distributed near to the neural spine and spinodiapophyseal lamina (spdl). The acpl (fused to the cprl), the pcdl, ppdl, the posterior centroparapophyseal lamina (pcpl), spol, podl and prsl are well developed and conservative in the sequence. The udl is present in almost all dorsals. The spdl is well developed and shows pneumatic foramina mainly in the posterior dorsal vertebrae. The sprf + prsdf, is shallow and wide, becoming narrow towards the end of the sequence. The cprf, the centroparapophyseal fossa (cpaf), the spof, the pacdf and the pocdf are conservative; these four fossae are triangular and deep.

3.2.2. Anterior dorsal vertebrae (PVL 4017-10, PVL 4017-11 and PVL 4017-12)

The ventral surface of PVL 4017-11 is concave and mostly smooth. Specimens, PVL 4017-11 and PVL 4017-12 lack ventral

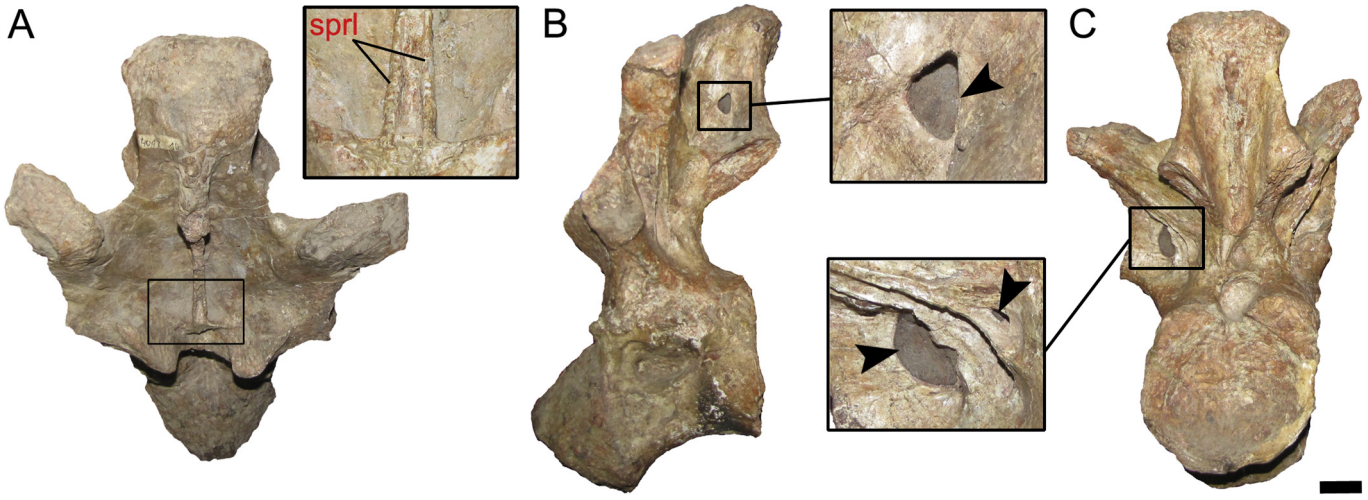

Fig. 12. PVL 4017-16 in dorsal (A), lateral (B) and posterior (C) views. The square inset in A shows a detailed of the two sprl that join to form the prsl. Squares inset in B and C shows detailed views of pneumatic foramina (arrowheads) in the left posdf (B) and pneumatic foramina below and above of pcdl (C). Scale bar: 2 cm.

surface. The lpf in PVL 4017-11 is oval-shaped and is in the middle of centrum. Incomplete parapophyses are only preserved in PVL 4017-10 in which they appear to be located over the dorsal margin of the centrum. The postzygapophyses are smaller compared with the prezygapophyses. The neural spine of PVL 4017-11 is angled 45° with respect to the horizontal plane.

The cprl is columnar shaped and, together with the lateral walls of the neural channel, defines the cprf. This fossa has a middle depth and is triangular shaped. In PVL 4017-10, the cprl is double, therefore, there are four parallel cprl of the same thickness (Figs. 7A, B). This lamina retains only the portion that connects to the prezygapophysis, but not the connection with the centrum. The tprl is thin and U-shaped. This lamina forms, with the diapophyses and neural spine, the spinoprezygapophyseal fossa + prezygapophyseal spinodiapophyseal fossa (sprf + prsdf) complex, a wide and shallow fossa that possesses an incipient prsl (Figs. 8A, B). Another of the boundaries of the sprf + prsdf is the spdl, which is thick and well developed. In PVL 4017-12, the left spdl has an oval shape and a large pneumatic foramen. The pcdl is approximately perpendicular to the horizontal plane and, together with the ppdl and pcpl, delimits the pacdf, which is triangular and shallow. The pcpl is well developed and delimits a small cpaf. The postzygapophyseal spinodiapophyseal fossa (posdf) is a "half-moon" shaped fossa that is present only in PVL 4017-12. This shallow fossa exhibits a pneumatic foramen near to the left diapophysis. The cpol is laminar and elongated and delimits, together with the pcdl and podl, the pocdf. The spof is present. It is a rhomboidal and deep fossa, which is divided by a prominent postspinal lamina (posl).

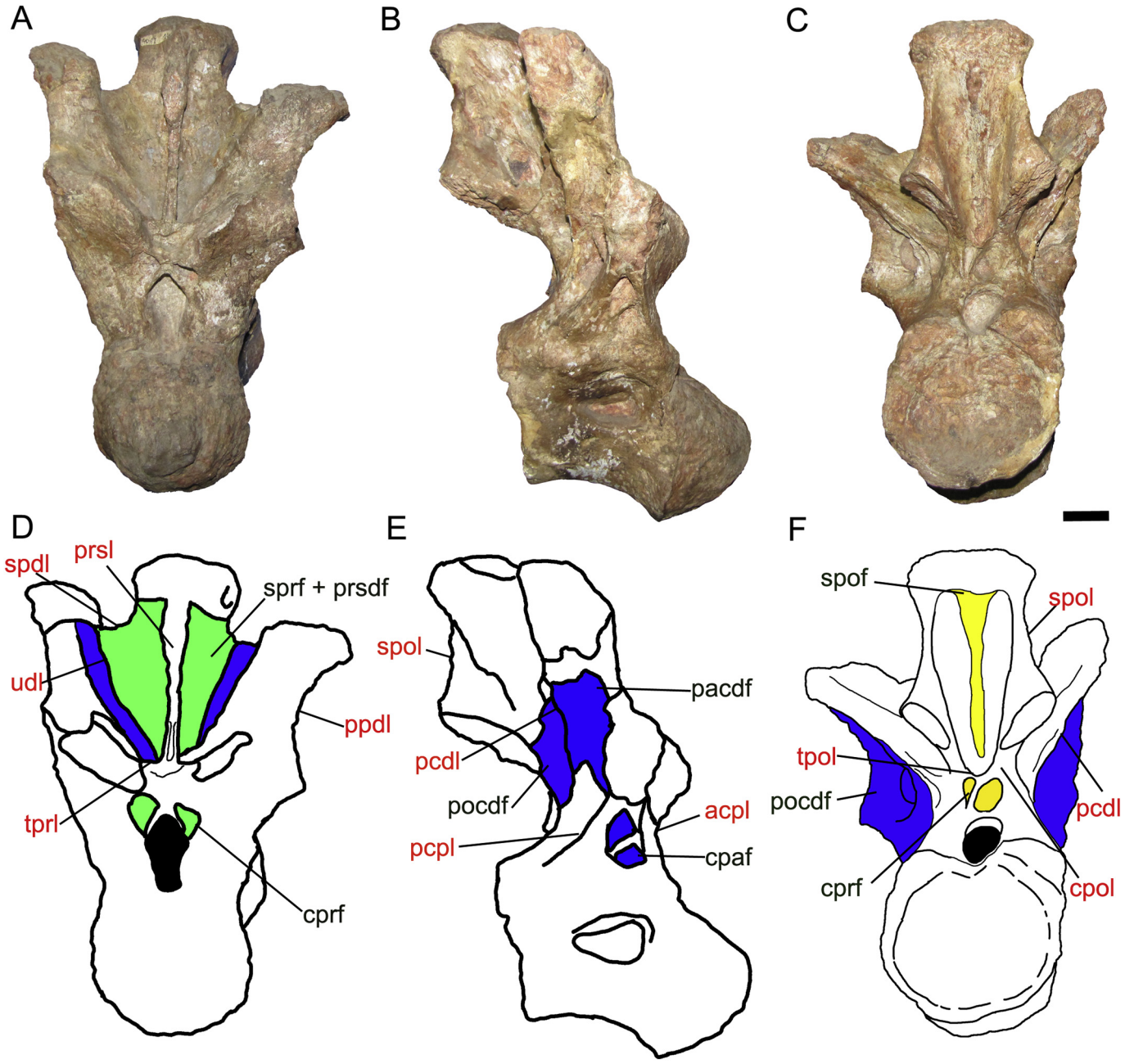

Fig. 13. First posterior dorsal vertebra (PVL 4017-16) of *Saltasaurus loricatus* in anterior (A), lateral (B) and posterior (C) views. D, E and F: interpretative line drawing of A, B and C. Scale bar: 2 cm.

3.2.3. Anterior middle dorsal vertebrae (PVL 4017-13, PVL 4017-14 and PVL 4017-15)

The centra of these vertebrae are short and concave; their ventral surface is mostly smooth, except in PVL 4017-15, which has a gentle marked keel (Fig. 9). Several foramina pierce the ventral surface of the centrum of PVL 4017-13. These vertebrae have oval shaped lpf located in the central area or slightly posteriorly displaced. These foramina are relatively small and shallow compared with the anterior most dorsal vertebrae. The parapophyses are in the same level as the prezygapophyses and below to the diapophyses. These structures are dorsoventrally orientated in PVL 4017-13 and lateromedially orientated in PVL 4017-15 (Figs. 10A, D). The prezygapophyses are small, oval shaped and are lateromedially orientated. The postzygapophyses are small and oval shaped or subcircular. The neural spine is high and almost perpendicular to the centrum in PVL 4017-13 and 4017-14. In PVL 4017-15, the neural spine is angled less than 90° to the horizontal plane (Figs. 10B, E). The cprl is columnar and the tprl is U-shaped. Both laminae delimit the cprf, which is small but deep and possesses a triangular outline. The tprl also delimits the lower portion of the sprf + prsdf. The sprf + prsdf is a wide and shallow fossa, divided in half by a thick prsl. Each of these "half-fossae" contains an extensive and thick udl (Figs. 10C, F). Two pneumatic foramina are located in the right side of srpf + prsdf in specimen PVL 4017-13, one in contact with the paradiapophyseal lamina (ppdl) and other in contact with the spdl. In PVL 4017-14, a single foramen is present in the right srpf + prsdf, closer to prsl.

The anterior centroparapophyseal lamina (acpl) is straight and vertical and its base seems fused to the cprl. This lamina forms an angle of 45° with the pcpl. Both laminae dorsally delimit the cpaf, which is a triangular, small and shallow fossa. The pcpl, the podl and the pcdl also delimit the pacdf. The pcdl is almost perpendicular to the centrum. In the specimen PVL 4017-15 (Figs. 10C, F, Fig. 11), this lamina is penetrated by a pneumatic foramen near its contact with the diapophyses. Regarding the pacdf, this is a triangular and deep fossa. In PVL 4017-15, the left pacdf has a small dividing lamina or septum. The cpol is narrow and well developed. Together the pcdl and podl delimits the pocdf, which is triangular and shallow. The podl also delimits the posdf, which possesses a triangular shape

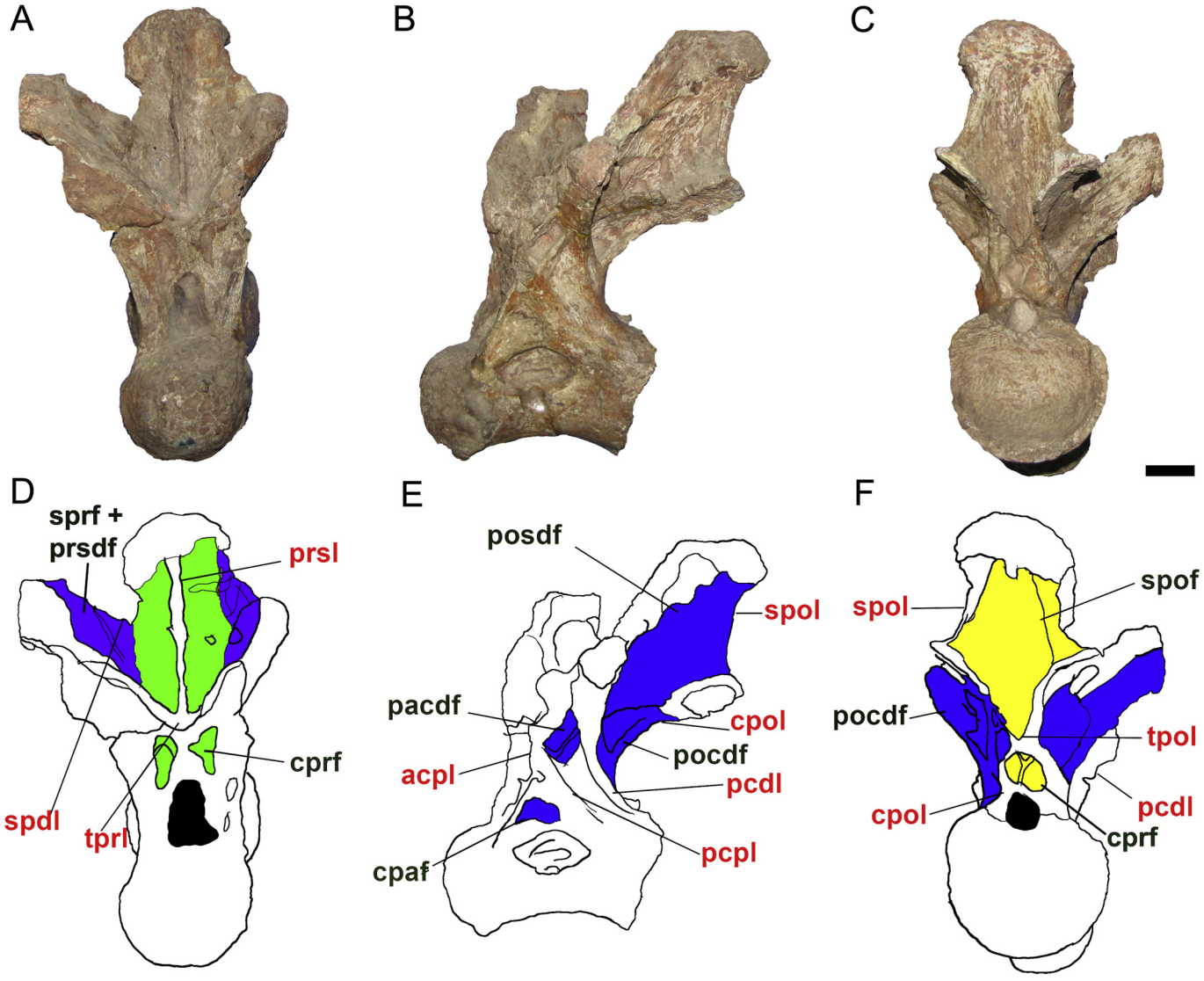

Fig. 14. First posterior dorsal (PVL 4017-137) of *Saltasaurus loricatus* in anterior (A), lateral (B) and posterior (C) views. D, E and F: interpretative line drawing of A, B and C. Scale bar: 2 cm.

and a variable depth. In PVL 4017-13, this fossa exhibits three foramina in the right side of the neural arch, near to the spinopostzygapophyseal lamina (spol). The spol is conspicuous and, together with a V-shaped tpol, marks the bounds of a deep spof. A large posl is developed inside this fossa.

3.2.4. Posterior middle dorsal vertebrae (PVL 4017-138)

Since that the centrum is deteriorated and it is not possible to distinguish anatomical details of the ventral surface and the lpf. The parapophyses are at the same level as the prezygapophyses. The prezygapophyses are relatively small and the postzygapophyses are oval shaped. The neural spine is angled 45° to the horizontal plane.

The cprl is massive and the cpol is extense and narrow. The tprl is U-shaped, and together with the cprl delimits the sprf + prsdf, which is wide and shallow. Within the sprf + prsdf there are the udl and the prsl. The latter has a circular foramen on its right side. Together with the pcpl, the acpl, which fuses with the cprl, delimits the cpaf, a triangular and shallow fossa. Also, the pcpl and pcdl, which are perpendicular to the centrum, delimit the pacdf, which in turn is divided by the apcdl. The pcdl, cpol and podl delimit the pocdf, which is triangular, wide and deeply excavated. The cpof is triangular and shallow and the spof is oval shaped, vertical and deep. This fossa is divided by a thin posl.

3.2.5. First posterior dorsal vertebrae (PVL 4017-16 and PVL 4017-137)

The centra of these vertebrae are short, with a longitudinal keel in PVL 4017-16. PVL 4017-137 is pierced by a few pneumatic foramina on its ventral surface, near to the posterior margin of the condyle. In these centra, the lpf are located in the mid of the centrum (discounting the condyle), slightly dorsally displaced. In PVL 4017-137, this foramen has a dividing lamina. In both cases, the foramina are deep and oval shaped. The parapophyses are at the same level as the prezygapophyses and not exceed the lateral margin of the centrum. Their articular facets are perpendicular to the horizontal plane. The prezygapophyses are small (Fig. 12A) and the postzygapophyses are larger than in the first dorsal vertebrae (Fig 12B). The neural spines are almost perpendicular to the horizontal plane. The top of the neural spines shows a well developed aliform process (Fig. 12B, Figs. 13A, B, D, E, Figs. 14A, D).

Regarding the laminae and fossae, the cprl are massive and the tprl are U-shaped. The cprf is triangular, small and shallow. The tprl delimits the sprf + prsdf, which is deep and narrow. The prsl is well developed and, in PVL 4017-16, is formed by two short and thin sprl (Fig. 12A). In specimen PVL 4017-137, a single pneumatic foramen is located, in the right side of sprf + prsdf, next to the prsl. Also, PVL 4017-137 has two foramina near to the left prezygapophyses and parapophyses.

The acpl is straight and perpendicular to the centrum. This lamina fuses with the pcpl in the parapophyses. Anteriorly both form an angle of 45° and delimit the cpaf, a triangular fossa. In PVL 4017-16, the cpaf has an accessory lamina (Fig. 13E) parallel to the apcdl. The apcdl goes across the pacdf, which is triangular and deep. In PVL 4017-16, the right pacdf has an accessory lamina. The pcdl is perpendicular to the centrum and the cpol. Together with this lamina and the podl, they bound the pocdf, which is triangular and shallow. The podl, the spdl and the neural spine delimit the posdf, a triangular and deep fossa. In both cases, this fossa has several pneumatic foramina (Fig. 12B) and PVL 4017-137 has one in the margin of the left spdl. The tpol is V-shaped and thin. In PVL 4017-16, this lamina, in contact with the cpol, exhibits a foramen. Together, both lamina delimit, in PVL 4017-137, the cpof, deep and triangular, has a foramen in its right side. This fossa is divided by an accessory Y-shaped lamina (Figs. 13C, F, Figs. 14C, F). The spof is narrow and rhomboidal with a prominent posl.

3.2.6. Last posterior dorsal vertebrae (PVL 4017-17, PVL 4017-136 and PVL 4017-135)

These vertebrae have short and concave centra. Few foramina pierce the ventral surface of PVL 4017-135 centrum (Fig. 15), near to the right and left ventral margins. In the centra of these elements, the lpf are deep and dorsally displaced. The parapophyses are above and behind to the prezygapophysis. The articular facets of parapophyses are perpendicular to the horizontal plane of the centrum. The prezygapophyses are smaller than the postzygapophyses. The neural spines are perpendicular to the centrum and have an aliform process (Figs. 16A, B).

The cprl is columnar and massive and the tprl is U-shaped and wide. All these laminae delimit a triangular and shallow cprf. The tprl also delimits, together with a well developed prsl, a narrow and elongated fossa (sprf + prsdf). In PVL 4017-135, the prsl is linked to the tprl by two small laminae. Pneumatic foramina are formed in the prsl of the same vertebral element. The foramen located in the left prsl is divided by a short lamina (Fig. 16B). In PVL 4017-17, the sprf + prsdf possess several foramina. The acpl is straight and thick and in 4017-17 has a pneumatic foramen (Fig. 17). This lamina is perpendicular to the centrum and forms an angle of 45° with the pcpl. Both laminae delimit the cpaf, a triangular and shallow fossa.

In these vertebrae, the pcpl is not well developed. This lamina, together with the ppdl and podl, delimits the pacdf, which is triangular and shallow. This fossa is divided by the apcdl.

The pcdl is vertical and delimits anteriorly a triangular and shallow pocdf. An oblique accessory lamina is present within the left pocdf of the specimen PVL 4017-136. Two pneumatic foramina are formed in the right and left sides of this fossa in PVL 4017-135 (Fig. 16C) and PVL 4017-17 respectively. The podl, spdl, spol and the neural spine mark the limits of the posdf, a triangular and deep fossa. In PVL 4017-135, the spdl are pierced by pneumatic foramina (Fig. 16A), whereas in PVL 4017-136 there is only a single foramen on the right side. The tpol is V-shaped and thin. This lamina dorsally

Fig. 15. Posterior dorsal (PVL 4017-135) of *Saltasaurus loricatus* in ventral view. Scale bar: 2 cm.

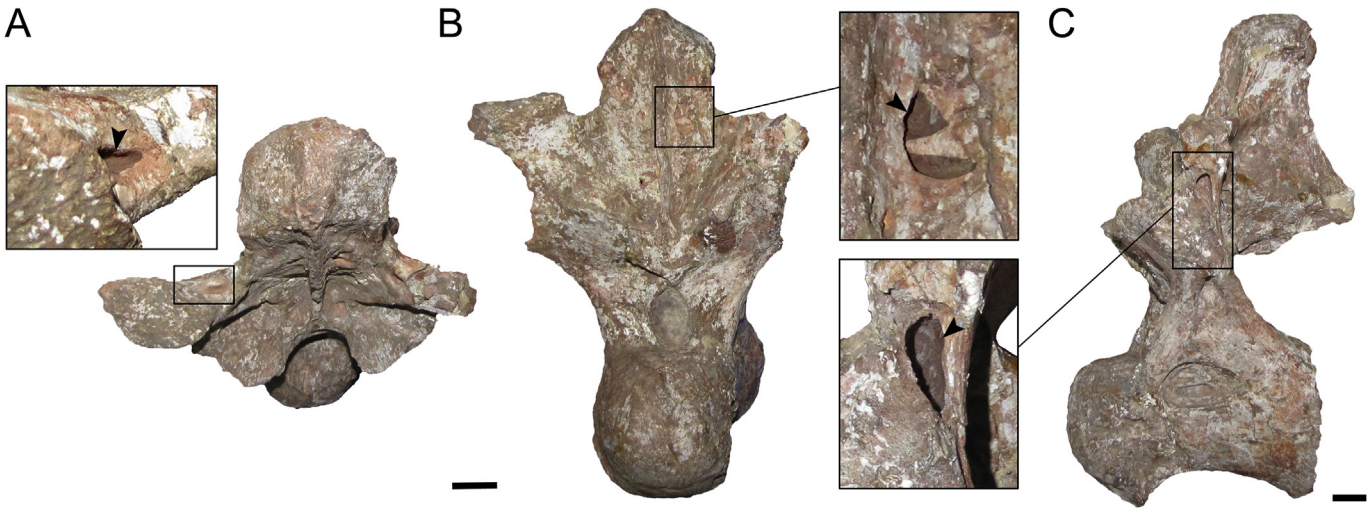

Fig. 16. Last posterior dorsal (PVL 4017-135) in dorsal (A), anterior (B) and lateral (C) views. The inset squares show pneumatic foramina (arrowheads) in the left spdl (A), near to prsl (B) and in the left pcdl (C). Note that the foramen in B (located in the surface of the sprf + prsdf) is divided by septum. Scale bar: 2 cm.

bounds the cpof, a triangular, small and shallow fossa. The tpol, together with the spol and neural spine, also bounds the spof, a deep fossa which is divided by a conspicuous posl.

4. Discussion

4.1. Comparison in vertebral laminae and fossae between S. loricatus, R. muniozi *and* N. australis

The obtained data allow the establishment of the main anatomical variations between *S. loricatus* and the other saltasaurini (*Neuquensaurus australis* and *Rocasaurus muniozi*). Given that the anatomical comparison can be only performed between equivalent elements, the relative scarcity of presacral vertebrae in *N. australis* and *R. muniozi* (Table 1) precludes a complete comparison between the taxa. This difficulty is exacerbated in the cervical vertebra, since the comparison material comprises a single posterior element of *N. australis* and five incomplete middle vertebrae of *R. muniozi*, two possibly anterior and three middle.

In the cervical vertebrae of *S. loricatus* the tprl has predominantly an inverted U shape. Conversely, this lamina is straight in *N. australis* and *R. muniozi* (Figs. 18A, B). Also, the tprl in *N. australis*

Fig. 17. Last posterior dorsal vertebra (PVL 4017-17) of *Saltasaurus loricatus* in anterior view. The inset box shows a detailed view of the depth and irregular shaped pneumatic foramen upon the dorsal margin of acpl. Scale bar: 2 cm.

is eave-shaped (Figs. 18C, D). The second difference is related with the development of the cprf, which is developed in the most posterior cervical vertebra of *S. loricatus*, but absent in *N. australis*.

Regarding the dorsal vertebrae, the presence of several equivalent elements in the three taxa allows a more deep comparison. In this sense, the dorsal series of *S. loricatus* can be compared with six complete vertebrae of *N. australis* (interpreted by Salgado et al., 2005 as the fourth, fifth, seventh, eighth, ninth and tenth elements) and three incomplete neural arches of *R. muniozi* (inferred by García and Salgado 2013 as the fifth, eighth and tenth neural arches). The first difference observed correspond with the shape of the apcdl, which is not well developed in *S. loricatus*, but is thick and prominent in the other two taxa. The udl is only present in posterior dorsals of *N. australis* and in almost all dorsals of *S. loricatus*, but is absent in *R. muniozi*. The cpof is variable in *S. loricatus*, but conservative in the other two taxa. The cpaf are triangular and deep, although is poorly developed in *N. australis*. The pacdf is generally undivided in *S. loricatus* and in other taxa is divided by a very developed apcdl (Fig. 19). An upl (unnamed parapophyseal lamina of Salgado et al., 2005) is formed in the pacdf of *N. australis* and *R. muniozi*, but absent in *S. loricatus*. In several specimens of *N. australis* (e.g. MCS Pv 5-22) the pacdf is also divided by accessory laminae. The parapocentrodiapophyseal fossa (pacprf) is present in some of most posterior dorsal vertebrae in *N. australis* (e.g. MCS Pv 5-23), but is absent in *S. loricatus* (at least in the same position). This fossa does not seem to be in *R. muniozi*, but therefore cannot be said that such lamina and fossa have been present. The podl is well developed in *S. loricatus*, but is absent in *R. muniozi* and poorly developed in *N. australis*. In the last taxon, the podl arises near to the postzygapophyses and loses inside the posdf, in fact, the posdf and the pocdf are not well differentiated in *N. australis* and *R. muniozi*.

The main differences observed in the morphology of the presacral vertebral skeleton of Saltasaurini titanosaurs, could be discussed in phylogenetic context. Different phylogenetic analysis recover *N. australis* as the sister group of the clade *S. loricatus* + *R. muniozi* (Calvo et al., 2007; Salgado et al., 2014). Despite to their phylogenetic relationships, our study reveals that, at least for the presacral vertebrae, *R. muniozi* share more characters with *N. australis* than with *S. loricatus*. On this regard, at least five characters are present in *N. australis* and *R. muniozi* (straight tprl in cervical vertebrae; thick and prominent acpdl in dorsal vertebrae; pacdf divided by an apcdl in dorsal vertebrae; presence of upl in dorsal vertebrae; and poorly developed podl in dorsal vertebrae) but absent/modified in *S. loricatus*. Based on the phylogenetic framework, the modified condition of these characters in

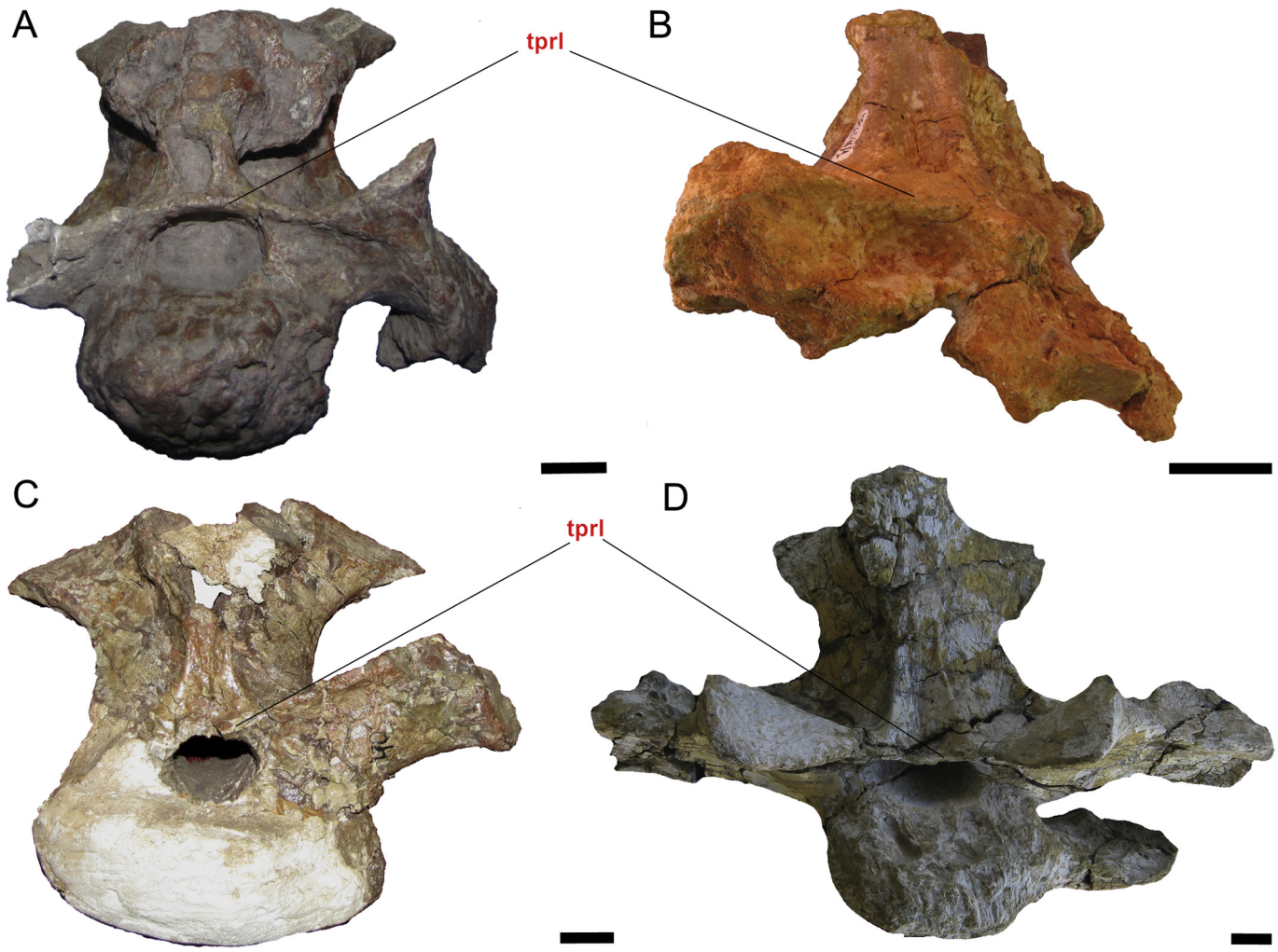

Fig. 18. Comparison between cervical vertebrae of Saltasaurini titanosaurs. A. Middle cervical vertebra (PVL 4017-139) of *Saltasaurus loricatus*. B. Middle cervical vertebra (MPCA Pv 46-2) of *Rocasaurus muniozi*. C. Posterior cervical vertebra (PVL 4017-8) of *Saltasaurus loricatus*. D. Posterior cervical vertebra (MCS Pv 5-17) of *Neuquensaurus australis*. All pictures in anterior view.

S. loricatus could be interpreted as derived (autapomorphic) feature for this taxon. It is necessary to perform a more detailed study of these characters in other non Saltasaurini titanosaurs to corroborate this hypothesis. Other interesting character is presence of the udl in the dorsal vertebrae, which is only observed in *S. loricatus* and *N. australis*. Its presence could be interpreted as a plesiomorphic condition in Saltasaurini. Another possible explanation is related with the morphological variations that occur during the ontogeny. On this regard, Carballido and Sander (2013) defined five Morphological Ontogenetic Stages (MOS) in a recent anatomical study of the basal macronarian *Europasaurs holgeri*. These MOS are defined on the anatomical changes that occur during the development (for example, the prsl is formed in the MOS 3). Given that the studied specimen of *R. muniozi* is actually a juvenile/subadult individual (cervical and dorsal vertebra possesses opened neurocentral sutures), the udl is perhaps formed in this taxon, but in latter ontogenetic stages.

4.2. Pneumatic diverticula and musculature associated to changes in morphology of neural laminae and fossae

The neural lamina possesses a structural function, providing support to the associated musculature and pneumatic diverticula (Britt, 1997). Hence, changes in the neural laminae structures are conditioned by presence and degree of development of musculature and pneumatic structures. For example the changes in the spof observed in *S. loricatus* can be caused by an elastic ligament that attached in the neural spine (Tsuhiji, 2004) between mid and last cervical vertebra. This ligament attaches at the top of neural spine and is surrounded by muscles, which attached in the spof. The same ligament also may have been associated to the sprf, because this fossa presents a wrinkled surface, like the neural spine and the spof, and its depth is variable. The last cervical vertebrae show a shallow prsdf, which could have housed a portion of cervical air sac. This inference is based on the distribution of the cervical air sac in extant birds, which is located at the level of the last cervical vertebrae (O'Connor, 2006; Wedel, 2009) and in the superficial texture of the fossa, which is smooth (Britt, 1993).

In the prsdf + prsdf, more exactly, near to the prsl there are some foramina; the same occurs in posdf, which there are foramina near or in the spdl, sometimes in one side or both sides of the spdl. This pattern can be inferred the presence of the pneumatic diverticula from the cervical air sac, abdominal air sac or lungs, depending on whether first, middle or last dorsal vertebrae (Wedel, 2009).

4.3. Distribution of pneumatic foramina

The recorded data regarding the presence and anatomical position of pneumatic foramina in the neural arch of *S. loricatus* and other Saltasurini allows discuss the pattern of distribution of these structures, their origin and evaluate their value as tool in systematic studies. In cervical vertebra neural arches, pneumatic foramina do not appears to follow any particular pattern with regard to their distribution. When present, these structures possess an asymmetric distribution. Conversely, in the dorsal vertebrae, although there is an irregular distribution of pneumatic foramina, there are points where it is more common to find pneumatic foramina; for example the sprf + prsdf. Pneumatic foramina are commonly observed in this fossa, especially near to the prsl, in the three analyzed species. The same occurs with the spdl, in which there are foramina in one or both sides of the neural arch. This pattern is present in *S. loricatus*, *N. australis* and *R. muniozi* (Fig. 20). We must note that this is the first record of pneumatic foramina penetrating the border of a single lamina. This is an interesting finding, since it demonstrates that the pneumatic foramina could not only be formed on the surface of fossae, but also in the sharp borders of thin laminae.

With the exception of the lpf, there does not exist a pattern for the position of pneumatic foramina in other derived titanosaurs, and they appear to be irregularly distributed in the centra and the neural arches. For example, the “axis of Nand” (Wilson and Mohabey, 2006) has a neural arch less pneumatized than the centrum and its pneumatization has an irregular and asymmetrical distribution throughout the centrum. In *Narambuenatitan palomoi* (Filippi et al., 2011) there are pneumatic cavities in the pcpl and pcdl in dorsal vertebrae. In *Rapetosaurus krausei* (Curry Rogers, 2009) there are possible foramina in the srpf, the spof, the pocdf and the prcdf in cervical vertebrae. Although Campos et al. (2005) do not describe the presence of pneumatic foramina in

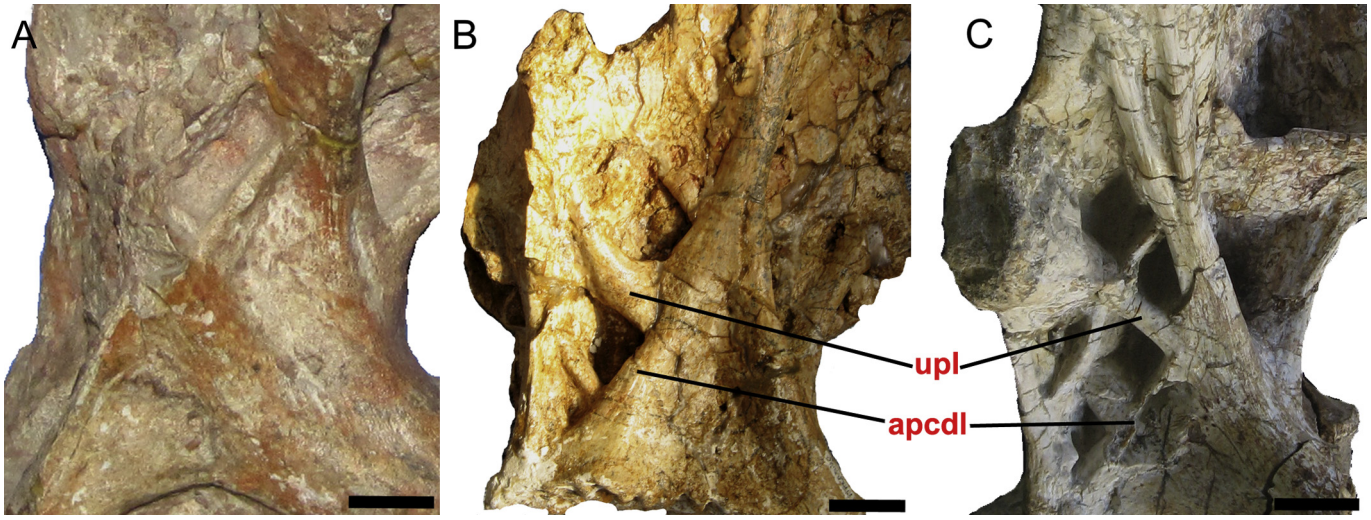

Fig. 19. Comparison between dorsal vertebrae of Saltasaurini titanosaurs. A. Middle dorsal vertebra (PVL 4017-137) of *Saltasaurus loricatus*. B. Middle dorsal vertebra (MPCA Pv 46-4) of *Rocasaurus muniozi*. C. Posterior dorsal vertebra (MCS Pv 5-22) of *Neuquensaurus australis*. Note the absence of the udl and the apcdl in *Saltasaurus loricatus*. All pictures in lateral left view.

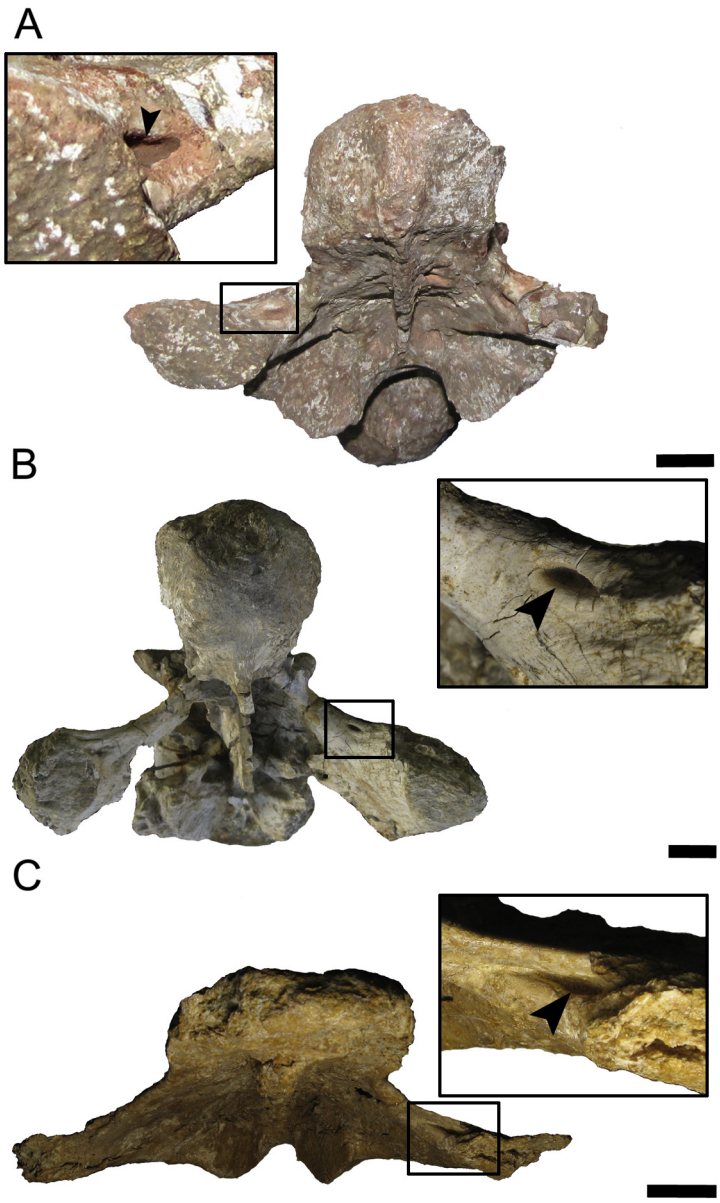

Fig. 20. Pneumatic foramina (arrowheads) in the border of the spdl in dorsal vertebrae of *Saltasaurus loricatus* PVL 4017-135 (A), *Neuquensaurus australis* MCS Pv 5-21 (B) and *Rocasaurus muniozi* MPCA Pv 46-5 (C). All the elements are in dorsal view. Scale bar: 2 cm.

Trigonosaurus pricei, based on the published figures, one of these structures appears to be present in the spof of the fifth dorsal vertebrae. In basal titanosauriforms such as *Chubutisaurus insignis* (Carballido et al., 2011a) and *Tehuelchesaurus benitezii* (Carballido et al., 2011b), pneumatic characters are mainly present in the centrum in both species. *Chubutisaurus insignis* also possesses pneumatic foramina in the neural arch, but their pattern of distribution is not regular.

In other works (e.g. Wilson and Sereno, 1998; D'Emic, 2012; Carballido and Sander, 2013; Mannion et al., 2013) the study of pneumaticity as a phylogenetic character is focused mainly on the internal bone structure of the vertebrae, ribs and ilia; presence, shape and degree of development of the lpf the vertebral centra; and presence of pneumatic foramina in the dorsal ribs. The lack of data on pneumatic foramina in the neural arch of presacral vertebrae, not only in titanosauriforms, but also sauropods in general, may be due to a true absence of them or, conversely, that these structures have not been considered in most of the anatomical descriptions. The last hypothesis seems the most possible because, as occurs in this work, new descriptions of previously studied taxa indicates that pneumatic foramina in the neural arch of presacral vertebrae have actually been missed in the past. A careful review of key sauropod taxa will us to allow establish if the pattern observed in saltasaurini is only present in this clade or, conversely, if it is a feature shared by a more inclusive group.

5. Concluding remarks

- Despite to its phylogenetic relationship, the presacral vertebrae of *R. muniozi* share more characters with *N. australis* than with *S. loricatus*.
- A conservative pattern of distribution of pneumatic foramina in the cervical vertebrae cannot be recognized among Saltasaurini titanosaurs. Conversely, the neural arches of dorsal vertebrae exhibit several regions in which these kinds of foramina are more commonly formed.

- Contrary to the expected, pneumatic foramina are not only formed within pneumatic fossae, but also in the border of neural laminae.
- The redescription of *Saltasaurus loricatus* and other Saltasaurini reveals that the presence and distribution of pneumatic foramina in the neural arch of the presacral vertebra the several titanosaurian taxa (and possibly other sauropod dinosaurs) has been largely missed in the past.

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References

Bonaparte, J.F., Powell, J.E., 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). Mémoires de la Societé geologique de France 139, 19–28.

Britt, B.B., 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. PhD thesis. University of Calgary.

Britt, B.B., 1997. Postcranial pneumaticity. In: Currie, P.J., Padian, K. (Eds.), The Encyclopedia of Dinosaurs. Academic Press., San Diego, pp. 590–593.

Calvo, J.O., Porfiri, J.D., González Riga, B.J., Kellner, A.W.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.

Campos, D.A., Kellner, A.W.A., Bertini, R.J., Santucci, R.M., 2005. On a Titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. Arquivos do Museu Nacional, Rio de Janeiro 63 (3), 565–593.

Carballido, J.L., Sander, P.M., 2013. Postcranial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. http://dx.doi.org/10.1080/14772019.2013.764935.

Carballido, J.L., Rauhut, O.W.M., Pol, D., Salgado, L., 2011a. Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. Zoological Journal of the Linnean Society 163, 605–662.

Carballido, J.L., Pol, D., Cerda, I., Salgado, L., 2011b. 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., Salgado, L., Powell, J.E., 2012. Extreme postcranial pneumaticity in sauropod dinosaurs from South America. Paläontologische Zeitschrift 86 (4), 441–449.

Coria, R.A., Filippi, L.S., Chiappe, L.M., García, R., Arcucci, A.B., 2013. *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. Zootaxa 3683 (4), 357–376.

Curry Rogers, K., 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 29 (4), 1046–1086.

D'Emic, M.D., Wilson, J.A., 2011. New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. Acta Palaeontologica Polonica 56 (1), 61–73.

D'Emic, M.D., 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society 166, 624–671.

Filippi, L.S., García, R.A., Garrido, A.C., 2011. 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 Salitral Moreno, Río Negro, Argentina. Acta Palaeontologica Polonica 58 (2), 269–284.

Harris, J.D., 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. The Anatomical Record 281 a, 1240–1246.

Huene, F. von, 1929. Los Saurisquios y Ornitisquios del Cretáceo Argentino. Anales del Museo de La Plata 2, 1–196.

Lydekker, R., 1893. The dinosaurs of Patagonia. Anales del Museo de La Plata 2, 1–14.

Mannion, P.D., Upchurch, P., Barnes, R., Mateus, O., 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur Lusotitan atalaiensis (Macronaria) and the evolutionary history of basal titanosauriforms. Zoological Journal of the Linnean Society 168, 98–206.

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.

Otero, A., 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. Acta Palaeontologica Polonica 55 (3), 399–426.

Powell, J.E., 1992. Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del noroeste Argentino. In: Sanz, J., Buscalioni, A. (Eds.), Los dinosaurios y su entorno biótico: Actas del Segundo Curso de Paleontología in 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.

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. Sauropodomorpha. In: Gasparini, Z., Salgado, L., Coria, R.A. (Eds.), Patagonian mesozoic reptiles. Indiana University Press, Bloomington, IN, pp. 188–228.

Salgado, L., Powell, J.E., 2010. Reassessment of the vertebral laminae in some south American titanosaurian sauropods. Journal of Vertebrate Paleontology 30 (6), 1760–1772.

Salgado, L., Apesteguía, 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., García, R.A., Daza, J.D., 2006. Consideraciones sobre las láminas neurales de los dinosaurios saurópodos y su significado morfofuncional. Revista del Museo Argentino de Ciencias Naturales 8 (1), 69–79.

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.

Schwartz, D., Frey, E., Meyer, C.A., 2007. Pneumaticity and soft-tissue reconstructions in the neck of diplodocid and dicraeosaurid sauropods. Acta Palaeontologica Polonica 52 (1), 167–188.

Tsuhiji, T., 2004. The ligament system in the neck of *Rhea americana* and its implication for the bifurcated neural spines of sauropod dinosaurs. Journal of Vertebrate Paleontology 24 (1), 165–172.

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 311 a, 611–628.

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., 2012. New vertebral laminae and patterns of serial variation in vertebral laminae of sauropod dinosaurs. Contributions from the Museum of Paleontology, University of Michigan 32 (7), 91–110.

Wilson, J.A., D'Emic, M.D., Ikejiri, T., Moacdieh, 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.

Wilson, J.A., Mohabey, D.M., 2006. A titanosauriform (Dinosauria: Sauropoda) axis from the Lameta Formation (Upper Cretaceous: Maastrichtian) of Nand, India. Journal of Vertebrate Paleontology 26 (2), 471–479.

Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memories 5, 1–68 (supplement to Journal of Vertebrate Paleontology 18).

Yates, A.M., Wedel, M.J., Bonnan, M.F., 2012. The early evolution of postcranial skeletal pneumaticity in sauropodomorph dinosaurs. Acta Palaeontologica Polonica 57 (1), 85–100.

Zurriaguz, V.L., Otero, A., 2013. Reevaluation of the axial skeleton referred to *Neuquensaurus robustus* (Huene, 1929) and its taxonomic separation from *Neuquensaurus australis* (Lydekker, 1893). Ameghiniana 50 (4), 32–33.