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# New record of titanosaurian (Dinosauria: Sauropodomorpha) osteoderms from the Upper Cretaceous of North Patagonia

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The idea that titanosaurs had osteoderms was proposed in the late nineteenth century by Depéret. However, this idea was given little credence by other researchers until 1980 when unequivocal evidence of armoured titanosaurs was reported. Since then, many discoveries of titanosaurian osteoderms have been made worldwide. In this work, seven osteoderms are described from the Allen Formation (upper Campanian–lower Maastrichtian), Salitral Moreno locality, Río Negro Province, Argentina. Among the described osteoderms it was possible to recognize three morphologies (keeled, ellipsoidal and cylindrical), with the first of these being most prevalent. Although the osteoderms from Salitral Moreno resemble osteoderms found in other parts of the world, no osteoderms of a similar morphotype are known from this locality, or from Lago Pellegrini or Cinco Saltos.


## 1. Introduction

The presence of osteoderms (i.e. dermal bones) in sauropod dinosaurs was first reported by Depéret (1896), who described a thick bone tentatively assigned to a titanosaur from Madagascar. However, this idea was rejected by other researchers, who asserted that thyreophorans were the only osteoderm-bearing dinosaurs (Piveteau 1926; Huene 1929). Definitive evidence of osteoderms in sauropod dinosaurs was presented by Bonaparte and Powell (1980) for *Saltasaurus loricatus*, a small-bodied titanosaur from Argentina (Bonaparte and Powell 1980; Powell 1980, 2003). Several subsequent discoveries have supported Depéret's hypothesis (e.g. Sanz and Buscalioni 1987; Le Loeuff et al. 1994; Dodson et al. 1998; Csiki 1999; González Riga 2003; Salgado 2003; O'Leary et al. 2004; Marinho and Candeiro 2005; D'Emic et al. 2009; Díez Díaz et al. 2013; Vidal et al., 2014, 2016; Cerda et al. 2015). Among Sauropoda, however, osteoderms are restricted to derived titanosaurs, being a synapomorphy of Lithostrotia (D'Emic 2012).

Although titanosaurian osteoderms have been reported from almost all landmasses, they have been found in greatest abundance in South America, especially Argentina (e.g. Huene 1929; Powell 1980; Cerda et al. 2015). One locality which has provided a very important osteoderm sample is Salitral Moreno, which is located approximately 25 km from General Roca City, Río Negro Province, Argentina (Fig. 1). Two titanosaurian species have been recognized from this locality (*Rocasaurus muniozi* (Salgado and Azpilicueta 2000) and *Aeolosaurus* sp. (García and Salgado 2013)), with other remains referred to Titanosauria indet (García and Salgado 2013). The first titanosaurian osteoderms from this locality were described by Salgado and Coria (1993) and assigned to the genus *Aeolosaurus*, and subsequent discoveries have been reported by Salgado (2003) and Cerda et al. (2015). Here I report new findings of titanosaurian osteoderms from Salitral Moreno, providing new data on the morphological variation of these elements in this locality. I also compare the new sample with previously reported osteoderms from other localities (e.g. Cinco Saltos). Finally, I discuss the possible function(s) of these elements in titanosaurs.
Institutional Abbreviations.

FMNH: Field Museum of Natural History, Chicago, United States.
MCS Pv: Vertebrate Paleontology collections of the Museo de Cinco Saltos, Cinco Saltos, Río Negro, Argentina.
MOZ Pv: Vertebrate Paleontology collections of the Museo Provincial de Ciencias Naturales "Profesor Juan. A. Olsacher", Zapala, Neuquén, Argentina.
MPCA Pv: Vertebrate Paleontology collections of the Museo Provincial de Cipolletti "Carlos Ameghino", Río Negro Province, Argentina.

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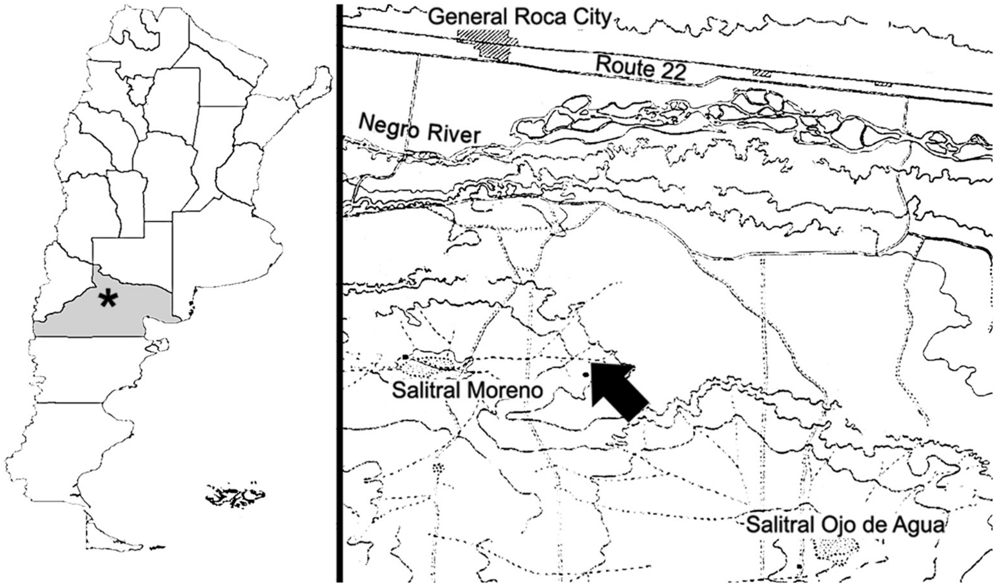


**Fig. 1.** Map of the Salitral Moreno locality. The asterisk (*) indicates the site where the studied material was collected.

PVL-Pv: Instituto "Miguel Lillo", Colección de Paleontología de Vertebrados, San Miguel de Tucumán, Tucumán, Argentina.

## 2. Materials and methods

A total of seven osteoderms were analyzed in this study. Six of these elements (MPCA Pv 607–612) were collected in the Salitral Moreno locality (Allen Formation, Río Negro, Argentina) by Jaime Powell in the late 1980s. These elements were collected from sediments of the Allen Formation (upper Campanian–lower Maastrichtian). A single specimen housed in the Olsacher Museum of Zapala (MOZ Pv 2556) is also included in this paper. Despite the inexact provenance of this osteoderm (the catalogue file only refers to "General Roca"), I infer that this specimen actually comes from Salitral Moreno based on the characteristics of the associated sediment and the colour of the bone, which varies among specimens from this site from yellowish to brownish. The measurement of the three main axes of each element was obtained using digital calipers (Table 1). Anatomical nomenclature used herein follows Cerda et al. (2015); thus, the relative positions of the elements are referred to as 'superficial/deep', which correspond with dorsal/ventral, external/basal, external/internal and distal/proximal of other authors (Salgado 2003; Scheyer and Sander 2004; Main et al. 2005; Hill 2006; D'Emic et al. 2009). I use the term 'marginal region' to refer to the area of contact between the superficial and deep faces. Following previous studies, I consider that the main axis of the osteoderms is parallel to the craniocaudal axis of the body. However, given that I cannot establish which end of a given osteoderm is cranial or caudal, I use the term 'cranial/caudal' (cr/ca) to refer to these ends of the osteoderm. I use the term 'cingulum' to refer to a marginal ring of tuberosities in the osteoderms (Huene 1929; Salgado 2003). For the morphological descriptions, I follow the nomenclature proposed by D'Emic et al. (2009).

**Table 1**
Table of measurements of osteoderms from Salitral Moreno. Values are in centimeters (cm).

| Specimen number | Maximum longitudinal length | Maximum transversal width | Height |
|---|---|---|---|
| MPCA Pv 612 | 11.2 | 8.1 | 4.2 |
| MPCA Pv 609 | 7.9 | 5.3 | 4.1 |
| MPCA Pv 608 | 10.6 | 8.1 | 6.5 |
| MPCA Pv 610 | 16 | 14.1 | 7.8 |
| MPCA Pv 613 | 24.5 | 17.2 | 13.9 |
| MPCA Pv 611 | 26.3[a] | 20.2 | 13.5 |
| MPCA Pv 607 | 7.8 | 4.4 | 4 |
| MOZ Pv 2556 | 14.2 | 11.2 | 7.7 |

[a] Estimated values.

## 3. Description

Seven osteoderms are described herein. Their lengths vary from 7.8 cm to 25 cm approximately, whereas their widths range from 4.4 cm to 20.2 cm (Table 1). The morphology of the osteoderms is also quite variable, with external faces mostly ornamented with pits and foramina, and inner faces mostly irregular, slightly convex and eroded. All of them present a yellowish to brownish color.

### 3.1. MPCA Pv 608

This keeled osteoderm is oval in shape in superficial view, being slightly longer than wide. The superficial surface exhibits pits, grooves and foramina (Fig. 2A). The internal texture cannot be seen. The face of the osteoderm has a well-developed crest, which culminates in a broken peak slightly displaced from the centre. The superficial face presents a "ring", with a depression in the center (Fig. 2B). This depression exhibits several small ridges, a high density of excavations, and is adjacent to the cingulum. The cingulum is eroded and has almost no ornamentation (Fig. 2C). A longitudinal keel is well developed in the deep surface, which is more pronounced towards one of the cr/ca edges (Fig. 2D).

### 3.2. MPCA Pv 612

Following the classification of D'Emic et al. (2009), this element is a keeled osteoderm, oval in shape in superficial view and elongated craniocaudally. The superficial face presents a thick keel displaced longitudinally towards the cr/ca edges. This face has pits of variable size and shaped (e.g. 4.6 × 5.3 mm) and little wrinkles,

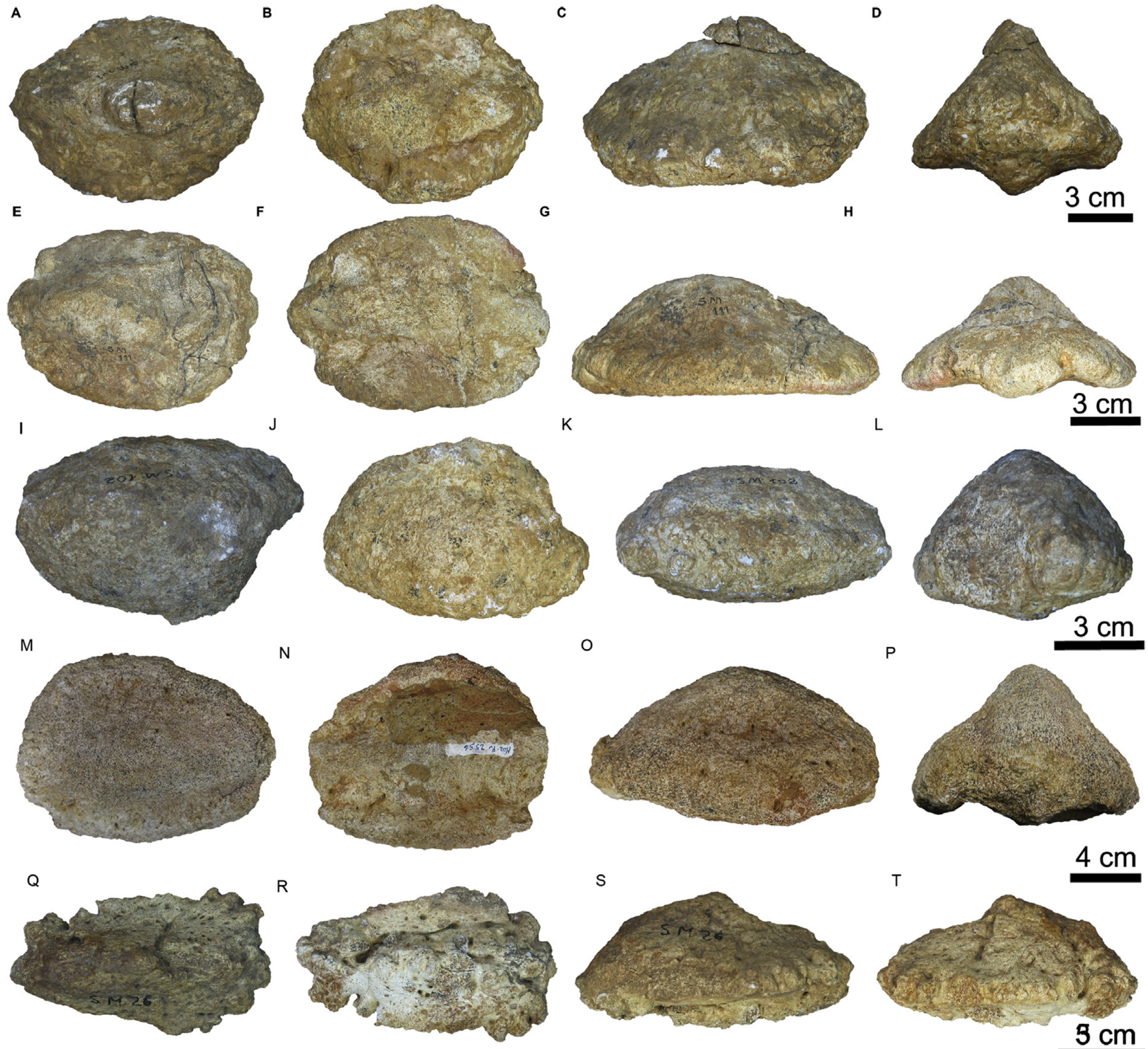


**Fig. 2.** Keeled osteoderms: MPCA Pv 608 in superficial (A), deep (B), lateral (C) and anteroposterior (D) views; MPCA Pv 612 in superficial (E), deep (F), lateral (G) and anteroposterior (H) views; MPCA Pv 609 in superficial (I), deep (J), lateral (K) and anteroposterior (L) views; MOZ 2556 in superficial (M), deep (N), lateral (O) and anteroposterior (P) views; and MPCA Pv 607 in superficial (Q), deep (R), lateral (S) and anteroposterior (T) views. Scale bars for MPCA Pv 609, MPCA Pv 612, MPCA Pv 609 and MPCA Pv 607 = 3 cm; scale bar for MOZ 2556 = 4 cm.

mostly concentrated at the apex of the keel (Fig. 2E). The deep face has a prominent and thick keel. This keel is penetrated by numerous pits, is oval to subquadrangular in shape, and is slightly eroded. With the sole exception of a few wrinkles near the cingulum (Fig. 2F), a distinct ornamentation is absent on the deep face of the osteoderm. The cingulum is well developed, exhibiting an ornamentation of tuberosities, but becomes narrower towards one of the cr/ca edges (Fig. 2G, H).

### 3.3. MPCA Pv 609

This keeled osteoderm exhibits little ornamentation on the superficial face (Fig. 2I). A thick keel occupies the entire superficial surface. The deep surface is convex, showing a poorly defined keel. This surface presents small foramina and wrinkles, mostly localized towards the center of osteoderm (Fig. 2J). The lateral margins of the ventral surface appear to be strongly eroded. The cingulum is poorly developed, with some protuberances (Fig. 2K,L).

### 3.4. MOZ-Pv 2556

This element is keeled. The external surface is conical and possesses numerous small striations and some circular foramina, mostly located towards the margins (Fig. 2M). The tip of the superficial surface is rounded. The cingulum is developed and shows grooves. Several vascular foramina are opened in the superficial surface near the cingulum. The deep surface is partially eroded, and exhibits striations and small wrinkles. A well-developed deep keel runs longitudinally (Fig. 2N,O,P).

### 3.5. MPCA Pv 607

This keeled osteoderm is quite different to those previously described. The superficial face is dominated by a sharp crest with straight lateral sides which is very gently concave towards the cr/ca ends (Fig. 2Q). The surface of this crest is pierced by abundant foramina and some grooves. The texture is smooth, with thin fibers irregularly organized. The cingulum is well-developed, and ornamented with protuberances, grooves and foramina. The deep face has a ridge with protuberances, though the typical longitudinal fibers of keeled osteoderms are not observed. This surface is irregular and exhibits numerous grooves of different sizes, which branch and coalesce into irregular foramina. Vascular foramina are less abundant and more extensive on the deep surface than on the superficial surface. These foramina exhibit a variety of sizes and shapes, and one of them is divided by a small septum (Fig. 2R,S,T).

### 3.6. MPCA Pv 610

This osteoderm is cylindrical and very slightly narrowed towards one of the cr/ca ends. The outer side is truncated and possesses abundant small (oval or circular) foramina, some of which communicate with irregular grooves (Fig. 3A). The foramina are mostly located near the cingulum. The marginal region is high and straight in some sectors. It presents numerous radial grooves, some of them partially closed, and near one of the cr/ca extremes an excavation of 3 cm × 4.8 cm is seen. The fine texture constitutes radially oriented thin fibers. Although the margins of the osteoderms are irregular, the cingulum is very poorly developed. The deep face is only partially preserved and does not seem to have had a ventral crest. This face is convex and its texture and fiber pattern are more irregular. A fractured section of this specimen reveals that the osteoderm is spongy internally, with abundant straight and large channels oriented in different directions (Fig. 3B,C,D).

### 3.7. MPCA Pv 611

This ellipsoid osteoderm is shaped like a “root and bulb”, with a fragmented root and a prominent and sub-circular bulb. In superficial view, some asymmetry is observed in this osteoderm: the major axis of the bulb and the root are not parallel. The superficial surface of the bulb is flat, slightly concave, and ornamented with numerous pits (Fig. 4A). The marginal region, as in other cases, has several grooves and radial fibers. This element is fragmented near one of its margins. The deep margin of the bulb is well marked and extremely irregular, with abundant protuberances of different shape and size. The inner side is partially eroded and presents a great rupture close to one of its margins on its deep face (Fig. 4B,C,D).

### 3.8. MPCA Pv 613

This ellipsoid osteoderm is also shaped like a “root and bulb”, with only an incipient “root”. As observed in MPCA Pv 611, some degree of asymmetry is detected in superficial view. The superficial surface is eroded, but seems as if it was smooth in life, with several foramina, grooves and radially oriented fibers. The bulb terminates ventrally in a well-defined margin, which continues with a very irregular edge, ornamented with some circular foramina and abundant protuberances. These protuberances are better preserved towards the root, which is poorly developed and protrudes approximately 50 mm below the bulb, with an irregular texture composed of striations (Fig. 4E). The deep face is irregular and slightly convex with an incipient crest. Its surface is wrinkles and also bears some foramina (Fig. 4F).

## 4. Discussion

### 4.1. Comparative morphology

The osteoderms described here generally present a keeled morphology (Fig. 2). The other two morphologies, cylindrical and ellipsoidal, are less common (Figs. 3 and 4). All these elements are similar to those previously described in other titanosaurs.

The keeled elements (Fig. 2) bear similarities to titanosaur osteoderms reported in other works. As an example, MPCA Pv 612 is similar to MPCA Pv 44 and MPCA Pv 62 (Cerda et al. 2015), which also come from the Salitral Moreno locality and might pertain to *Rocasaurus muniozi*. Another osteoderm from this locality, MPCA Pv 27176 (Salgado 2003) was assigned to *Aeolosaurus* sp. and is morphologically incongruent with the specimens described herein. Consequently, the seven osteoderms described in this paper are thought not to pertain to *Aeolosaurus*. On the other hand, MOZ 2556 is similar to MPCA Pv 45 (Cerda et al. 2015), another osteoderm from Salitral Moreno, which was assigned to Titanosauria indet. MPCA Pv 607 is similar to MPCA Pv 64 (Cerda et al. 2015), mainly in the aspect to superficial surface.

Other “keeled” osteoderms have been reported from the Anacleto Formation and have been assigned to *Neuquensaurus* (Cerda et al. 2015)., However, unlike those from Salitral Moreno, these osteoderms possess a “crater-like” end morphology, not seen in the osteoderms presented in this work, indicating that there is no overlap between morphotypes. Other “keeled” osteoderms have been found in the Maevarano Formation, Madagascar (Dodson et al. 1998: FMNH PR 2021 and UA 8675), but, unlike those from Salitral Moreno, the osteoderms from this locality possess two keels instead of one.

The cylindrical element (MPCA Pv 610) (Fig. 3) bears some similarity to previously described osteoderms, including the “Lameta osteoderm” (D'Emic et al. 2009) which apparently pertains to *Jainosaurus*, as well as to MPCA Pv 367/2 (also from Salitral Moreno) which was described as having similar features by Cerda et al. (2015) and assigned to Titanosauria indet. Curiously, MPCA Pv 610 is also similar to MPCA Pv 611 and MPCA Pv 613, described in this work, which belong to the ellipsoidal morphotype. As there is no sign of breakage in this specimen, this similarity may be a consequence of ontogenetic stage (i.e. the ellipsoidal form develops as the animal grows, implying that this osteoderm came from a juvenile), intraspecific (Vidal et al., 2014, 2016; Cerda et al. 2015),

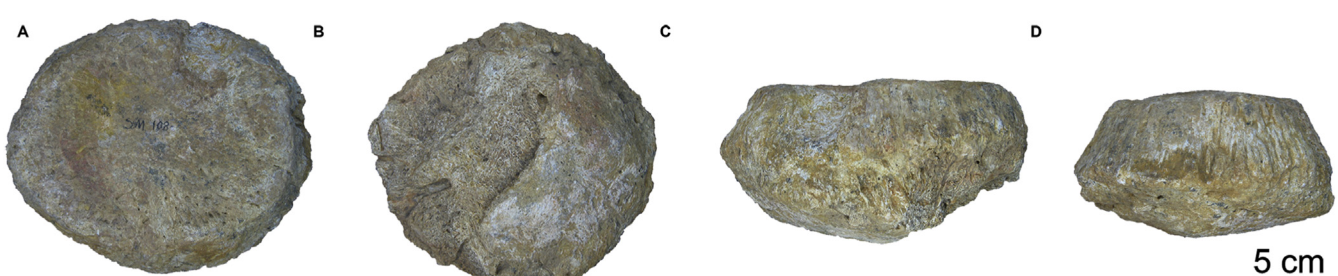


**Fig. 3.** Cylindrical osteoderms: MPCA Pv 610 in superficial (A), deep (B), lateral (C) and anteroposterior (D) views. Scale bar: 5 cm.

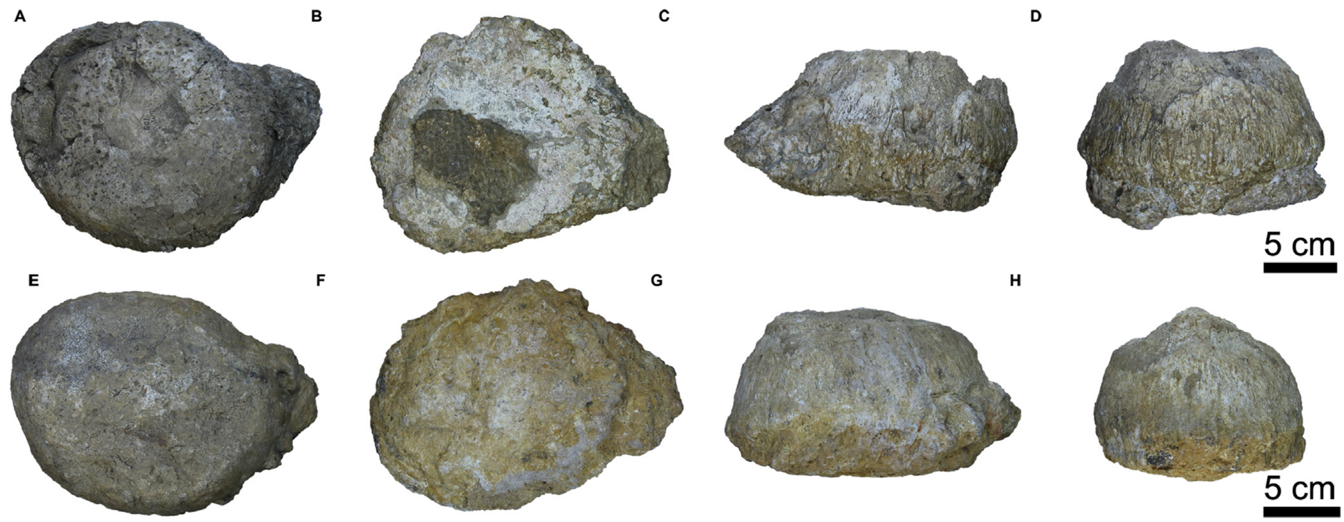


**Fig. 4.** Ellipsoidal osteoderms: MPCA Pv 611 in superficial (A), deep (B), lateral (C) and anterior/posterior (D) views; and MPCA Pv 613 in superficial (E), deep (F), lateral (G) and anterior/posterior (H) views. Scale bar: 5 cm.

interspecific (Cerda et al. 2015) or intraeskeletal variation (Powell 1980; Salgado 2003).

The ellipsoidal morphology (MPCA Pv 611 and MPCA Pv 611) (Fig. 4) is similar to the "bulb and root" morphology. In this sample, only two ellipsoidal osteoderms were recovered. This morphology is, perhaps, the most common, being described in several taxa. e.g. *Rapetosaurus krausei, Lirainosaurus astibiae, Magyarosaurus dacus* and *Malawisaurus dixeyi.* Curry Rogers et al. 2011; Díez Díaz et al. 2013; Cziki 1999; Gomani 2005. They have also been reported from deposits with no association to any particular species (Le Loeuff 1994; O'Leary et al. 2004; Vidal et al., 2014, 2016). Even within Saltasauridae, ellipsoidal-like "root and bulb" osteoderms have been found in association with *Alamosaurus sanjuanensis* (Carrano and D'Emic 2015). It is possible that the presence of ellipsoid-like "root and bulb" osteoderms might be plesiomorphic for Lithostrotia, and that this feature was lost in highly derived taxa (e.g. *Saltasaurus loricatus, Neuquensaurus australis*). However, it should be noted that Zurriaguz et al. (2016) described ellipsoidal osteoderms—which are not "root and bulb"-like—associated with an Indeterminate saltasaurine from Angostura Colorada Formation.

The only osteoderm morphotype not registered amongst the Salitral Moreno specimens described herein is the "mosaic" type (D'Emic 2009). This morphotype, termed "ossicles" by Powell (1980), was described as being present in *Saltasaurus loricatus* (Powell 1980) and in indeterminate titanosaurs from Madagascar (Dodson et al. 1998) and India (D'Emic 2009). The absence of this osteoderm morphotype might reflect the true absence of these osteoderms in the Salitral Moreno titanosaurs; however, it might also represent a taphonomic artifact: small (i.e. millimeter sized) elements are more difficult to find and recognize in the field.

In conclusion, the osteoderms described in this paper mostly resemble those previously reported from Salitral Moreno. The keeled morphotype shows some similarity to osteoderms found at the Cinco Saltos and Lago Pellegrini localities (Salgado 2003; Cerda et al. 2015), both of which pertain to the Anacleto Formation. The taxonomic associations of this osteoderm morphotype is quite complicated, in part because osteoderms have generally not been found in association with specific titanosaurian materials; when they have been, the non-osteoderm remains have been indeterminate (e.g. Titanosauria indet. from Salitral Moreno in García and Salgado 2013). On the other hand, it has proven difficult to establish the number of osteoderm morphotypes possessed by any given taxon since, for example, both *Saltasaurus loricatus* and *Neuquensaurus australis* possess at least two distinct kinds of osteoderms (Cerda et al. 2015).

Of the osteoderms from Salitral Moreno described in this paper, none coincides with the osteoderm morphotype previously described for *Aeolosaurus* from the same locality; however, they might pertain to *Rocasaurus muniozi* or to Titanosauria indet.

### 4.2. Function of osteoderms

The function of titanosaur osteoderms has been much debated, and several hypotheses have arisen. Some have suggested that osteoderms might have been related to mineral storage (e.g. calcium) in titanosaurs (Sturkie 1967; Curry Rogers et al. 2011; Cerda et al. 2015), due the structure of osteoderms, which have large vascular spaces, which allowed the rapid mobilization of minerals to the body (Curry Rogers et al. 2011) or during the oogenesis (Vidal et al. 2016). Other possible functions that have been ascribed to osteoderms are ornamentation, temperature control and prevention of skin damage (Czercas 1994), based on osteoderms of diplodocids. Finally, the last hypothesized function, is that osteoderms played a defensive role, especially in small species such as saltasaurines, which possibly needed extra defense against predators because of their small size or in early stages of ontogeny in large taxa (Marinho and Iori 2011).

## 5. Concluding remarks

New titanosaurian osteoderms from the Allen Formation of Rio Negro Province are described. The predominant morphology is "keeled", followed by the ellipsoidal and, finally, the cylindrical morphologies. The "mosaic" morphology was not found. These osteoderms resemble, mostly, those previously found in Salitral Moreno, except for those described for *Aeolosaurus.*

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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.

Carrano, M., D'Emic, M.D., 2015. Osteoderms of the titanosaur sauropod dinosaur Alamosaurus sanjuanensis Gilmore, 1922. Journal of Vertebrate Paleontology 35 (1). http://dx.doi.org/10.1080/02724634.2014.901334.

Cerda, A.I., 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.

Csiki, Z., 1999. New evidence of armoured titanosaurids in the Late Cretaceous *Magyarosaurus dacus* from the Hateg Basin (Romania). Oryctos 2, 93–99.

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.

Czercas, S.A., 1994. The history and interpretation of sauropod skin impressions. Gaia 10, 173–182.

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

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.

Deperet, C., 1896. Note sur le dinosauriens sauropodes et theropodes du Cretace Superieur de Madagascar. Bulletin de la Societe Geologique de France 24, 176–194.

Díez-Díaz, V., Pereda Suberbiola, X., Sanz, J.L., 2013. Appendicular skeleton and dermal armour of the Late Cretaceous titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from Spain. Palaeontologia Electronica 16 (2), 1–18.

Dodson, P., Krause, D.W., Forster, C.A., Sampson, S.D., Ravoavy, F., 1998. Titanosaurid (Sauropoda) osteoderms from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 18, 563–568.

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.

Gomani, E.M., 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa. Palaeontologia Electronica 8, 27A.

Gonzalez Riga, B.J., 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. Ameghiniana 40, 155–172.

Hill, R.V., 2006. Comparative anatomy and histology of xenarthran osteoderms. Journal of Morphology 267 (12), 1441–1460.

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

Le Loeuff, Buffetaut, J.E., Cavin, L., Martin, M., Martin, V., Tong, H., 1994. An armoured titanosaurid sauropod from the Late Cretaceous of Southern France and the occurrence of osteoderms in the Titanosauridae. Gaia 10, 155–159.

Main, R.P., de Ricqles, A., Horner, J.R., Padian, K., 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. Paleobiology 31, 291–314.

Marinho, T.S., Candeiro, C.R.A., 2005. Titanosaur (Dinosauria: Sauropoda) osteoderms from the Maastrichtian of Uberaba, Minas Gerais State, Brazil. Gondwana Research 8, 473–477.

Marinho, T.S., Iori, F., 2011. A large titanosaur (Dinosauria, Sauropoda) osteoderm with possible bite marks from Ibirá, São Paulo state, Brazil. In: de Souza Carvalho, Ismar, Srivastava, Narendra Kumar, Strochschoen Jr., Oscar, Lana, Cecília Cunha (Eds.), Paleontologia: Cenários de Vida, Volume 4, pp. 339–349.

O'Leary, M.A., Roberts, E.M., Head, J.J., Sissoko, F., Bouare, M.L., 2004. Titanosaurian (Dinosauria: Sauropoda) remains from the 'Continental Intercalaire' of Mali. Journal of Vertebrate Paleontology 24, 923–930.

Piveteau, J., 1926. Contribution a' l'étude des formations lagunaires du Nord-Ouest de Madagascar. Bulletin de la Société Géologique de France 4, 33–38.

Powell, J.E., 1980. Sobre la presencia de armadura dermica en algunos dinosaurios titanosauridos. Acta Geologica Lilloana 15, 41–47.

Powell, J.E., 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. Records of the Queen Victoria Museum 111, 1–173.

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 RíoNegro (Formación Allen, Cretácico Superior), Patagonia, Argentina. Ameghiniana 37, 259–264.

Salgado, L., Coria, R.A., 1993. El género *Aeolosaurus* (Saurópoda, Titanosauridae) en la Formación Allen (Campaniano–Maastrichtiano) de la provincia de Río Negro, Argentina. Ameghiniana 30, 119–128.

Sanz, J.L., Buscalioni, A.D., 1987. New evidence of armored dinosaurs in the Upper Cretaceous of Spain, pp. 199–204. In: Currie, P.M., Koster, E.H. (Eds.), 4th Symposium of Mesozoic Terrestrial Ecosystems, Drumheller, Alberta, 10–14 August 1987. Short Papers. Royal Tyrrell Museum, Paleontology, Drumheller, Alberta.

Scheyer, T.M., Sander, P.M., 2004. Histology of ankylosaur osteoderms: Implication for systematics and function. Journal of Vertebrate Paleontology 24 (4), 874–893.

Sturkie, P.D., 1967. Fisiología Aviar. Editorial Acribia, Zaragoza, 607 pp.

Vidal, D., Ortega, F., Gascó, F., Serrano-Martínez, A., Sanz, J.L., 2014. The internal anatomy of titanosaur osteoderms from the Upper Cretaceous of Spain is compatible with a role in oogenesis. Scientific Reports 7 (42035). http://dx.doi.org/10.1038/srep42035.

Vidal, D., Ortega, F., Sanz, J.L., 2016. Titanosaur Osteoderms from the Upper Cretaceous of Lo Hueco (Spain) and Their Implications on the Armor of Laurasian Titanosaurs. PLoS One 9 (8), e102488. http://dx.doi.org/10.1371/journal.pone.0102488.

Zurriaguz, V., Martinelli, A., Ezcurra, M., 2016. Un dinosaurio saltasaurino (Sauropoda: Titanosauria) de la Formación Angostura Colorada (Campaniano tardío), cercanías de Ingeniero Jacobacci, Provincia de Río Negro. Libro de Resúmenes del Congreso de la Asociación Paleontológica Argentina 103–104.