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Considerations on the bony plates assigned to titanosaurs (Dinosauria, Sauropoda)

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Abstract. Several bony plates referred to titanosaurs are reviewed. Two groups of plates, exhumated from two different localities, LagoPellegrini-Cinco Saltos and Salitral Moreno, in the province of Río Negro, are described. Several characters diferenciate the two groups, as the presence in one group of a shallow dorsal depression (Type I *sensu* Huene), a dorsal awn, a ventral ridge, and a *cingulum*. Generally, most of the plates are symmetrical, although a few present a marked asymmetry. The former apparently were located in the midline of the body over the neural spines, and the others laterally on both sides of the animal body. Histologically, the plates are composed ventrally by cancellous bone and externally by Haversian bone, and the Sharpey's fibers are present, mainly, in the periphery on the dorsal surface of the plates.

Resumen. CONSIDERACIONES SOBRE PLACAS ÓSEAS ASIGNADAS A TITANOSAURIOS (DINOSAURIA, SAUROPODA). En este trabajo se revisan varias placas óseas asignadas a titanosaurios. Así, se describen dos nuevos conjuntos de placas, uno proveniente de Lago Pellegrini-Cinco Saltos, el otro de Salitral Moreno, en la provincia argentina de Río Negro. Ambos grupos presentan varias diferencias como la existencia, en el primero de ellos, de una poco profunda depresión dorsal (Tipo I de Huene), variación en cuanto a la presencia de una angulosidad dorsal, el desarrollo de una cresta ventral, y de un *cingulum.* Si bien la gran mayoría de las placas son bilateralmente simétricas, unas pocas son asimétricas. Las placas simétricas se habrían dispuesto sobre la línea media del cuerpo, por encima de las espinas neurales de las vértebras. Las asimétricas, en cambio, lo habrían hecho sobre los laterales. Examinadas histológicamente, las placas muestran tejido esponjoso en su parte ventral y tejido Haversiano en su parte dorsal, mientras que las fibras de Sharpey se disponen principalmente en la región periférica.

Key words. Sauropoda. Titanosauria. Bony plates.

Palabras clave. Sauropoda. Titanosauria. Placas óseas.

Introduction

One of the most striking features of titanosaurs is the presence of bony plates (Bonaparte and Powell, 1980; Powell, 1980; Powell, 1986; Dodson *et al.*, 1998). These ossifications, identified for the first time by Deperet (1896), were originally assigned to *Titanosaurus madagascariensis* Deperet. In a posterior review, Piveteau (1926) considered that the plates did not pertain to a sauropod but to a new ornithischian (*Stegosaurus madagascariensis*) because, supposedly, sauropods were not armored dinosaurs. This interpretation was embraced by Huene (1929), who assigned a group of plates from the locality of Cinco Saltos-Lago Pellegrini (Río Negro Province, Argentina, Río Colorado Formation, Campanian-Maastrichtian, Heredia and Salgado, 1999) to *Loricosaurus scutatus*, a tyreophoran (denomination given by F. Nopcsa for ceratopsians, ankylosaurs and stegosaurs, and actually restricted to include ankylosaurs, stegosaurs and their basal related taxa, Weishampel, 1990), more precisely, a polacanthid. In addition, Huene (1929) described and assigned to the same group of ornithischians, one metatarsal, one metacarpal, a fragment of sacrum and a series of bones from several localities of Patagonia. The plates upon which *Loricosaurus scutatus* Huene was based, were not typical tyreophoran scutes, as Huene suggestively recognized. Most of the plates were unique in having two well differentiated faces: one of these (which Huene interpreted as dorsal) was concave, with a well-developed longitudinal ridge, whereas the other one (considered by Huene as ventral) was convex, and bore an occasional shallow central depression.

Subsequent discoveries of titanosaur bones associated to bony plates in northern Argentina, led to Bonaparte and Powell (1980) and Powell (1980) to restore Deperet´s former interpretation, confirming, beyond all doubt, that the plates belonged to sauropods. Since then, elements of this kind have been collected from various localities of Europe (Sanz and Buscalioni, 1987; Le Loeuff *et al.* 1994), Madagascar (Dodson *et al.*, 1997, 1998) and Brazil (Azevedo and Kellner, 1998). These discoveries, by the other hand, revealed a relatively thick diversity in morphology and size.

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The aim of this paper is to review the available evidence on the plates assigned to titanosaurs, to describe their morphology and histology, and to evaluate their probable biological significance, both from a functional and evolutionary point of view.

Abbreviations. CS: Collection of Cinco Saltos of the Museum of La Plata; FMNH: Field Museum of Natural History, Chicago; MCS: Museum of Cinco Saltos, Río Negro, Argentina; MPCA: Collection of the Museum of Cipolletti, "Carlos Ameghino", Río Negro, Argentina; MPCA-Pv: Collection of paleovertebrates of the Museum of Cipolletti "Carlos Ameghino". Río Negro, Argentina; UA: University of Antananarivo, Antananarivo, Madagascar.

Identity of the plate-bearer titanosaurs

Introduction

In spite of their plentiful record, it is not certain which species of titanosaurs bore plates of bone, in part because these are usually found either isolated or loosely associated to other postcranial bones.

Besides of *Titanosaurus madagascariensis*, bony plates were claimed to be present in other titanosaur species: *Saltasaurus loricatus* (Bonaparte and Powell, 1980), *Aeolosaurus* sp. Powel, *Titanosaurus araukanicus* Huene, *Ampelosaurus atacis* (Le Loeuff *et al.*, 1994), *Neuquensaurus australis* Lydekker, *Lirainosaurus astibiae* (Sanz *et al.*, 1999) and, with doubts, *Malawisaurus dixeyi* (Jacobs *et al.*, 1993).

Lecho Formation. In the case of the plates from El Brete (Lecho Formation, Campanian?-Maastrichtian, Salta Province, North Argentina) (Powell, 1980; Powell, 1992) the association is well founded, since *Saltasaurus loricatus* is the only sauropod recorded in that locality.

Río Colorado Formation. In Patagonia, the association of plates to other bones is not clear. For instance, in Cinco Saltos-Lago Pellegrini, where a significant number of plates was collected from the Río Colorado Formation, there are, at least, three titanosaurs: *Titanosaurus araukanicus* Huene, *Neuquensaurus australis* Lydekker and *Pellegrinisaurus powelli* Salgado. The association of plates with *Titanosaurus araukanicus*, was based on the supposed impossibility that the plates of Type I established by Huene, at least those that bore a dorsal shallow depression (Huene, 1929; pl. 43, 2), belonged to a small saltasaurine, like *Neuquensaurus* (Powell, 1980: 45). But the recent discovery of the plates MCS-33 and MCS-34, associated to a partial skeleton of *Neuquensaurus australis* in Cinco Saltos (Salgado *et al.*, in press), invalidates Powell´s claiming.

Allen Formation. In the locality of Salitral Moreno (Allen Formation, Campanian-Maastrichtian, Río Negro Province, Argentina, Uliana and Dellapé, 1981), three sauropod species are known: *Aeolosaurus* sp., *Rocasaurus muniozi* Salgado and Azpilicueta and *Titanosaurus* sp. (Salgado and Coria, 1993, Salgado and Azpilicueta, 2000, unpublished data). The plates attributed to *Aeolosaurus* sp. were found close to material assigned to this sauropod (Salgado and Coria, 1993), but mixed with hadrosaurid bones, which means that the association is not certain.

Phylogenetic implications

There is no agreement with respect to the phylogenetic significance of the plates. Powell (1986: 77) interpreted the presence of osteoderms and intradermal ossicles as diagnostic of *Saltasaurus* (the specific name *S. loricatus* refers to the existence of an armor of scutes). In turn, Upchurch (1995) understood that the presence of dermal scutes is a derived condition that unites the Titanosauridae. Salgado *et al.* (1997), viewed the same character as having a dubious distribution among titanosaurids. Sanz *et al.* (1999) postulated that the occurrence of armor plates was a synapomorphy of the clade named by them Eutitanosauria, assuming the existence of plates in five cases: *Ampelosaurus*, *Lirainosaurus*, *Saltasaurus*, *Titanosaurus* and *Neuquensaurus* (although the presence of bony plates was not included by Powell (1986: 161-162) in his own diagnosis of *Neuquensaurus*). Finally, Le Loeuff (1995) interpreted the same character as diagnostic of *Ampelosaurus atacis* Le Loeuff. As we see, most workers regard the occurrence of bony plates as diagnostic at specific or, at most, generic level. The opinion of Sanz *et al.* (1999) and Upchurch (1995) are, in this sense, different from the others.

In view of the dubious specific association of most of the plates (particularly, these from Patagonia), it is difficult to assert whether these have emerged once or more than once in the evolution of titanosaurs. Quite probably, not only saltasaurines (*Saltasaurus*, *Neuquensaurus* and all descendants of their most recent common ancestor) but other titanosaurus bore plates as well. This is known because plates assignable to titanosaurs are found outside South America, for example in Madagascar and Europe, where saltasaurines are unknown (Salgado and Azpilicueta, 2000). Another important fact is that bony plates are not recorded in stratigraphic levels older than Campanian: all the plates, if the ossicles of *Malawisaurus* are excepted, are recorded in Campanian-Maastrichtian beds of South America, Madagascar and Europe.

General morphology of the plates

Introduction

As already said, the bony plates assignable to ti-

Figure 1. Bony plates from several localities of the world / *Placas óseas provenientes de distintas localidades del mundo.* Bony plates referred to / *Placas óseas referidas a Titanosaurus madagascariensis* in lateral / *en vista lateral* **(A)** and dorsal / *y dorsal* **(B)** views; bony plates referred to / *placas óseas referidas a Saltasaurus loricatus* in ventral / *en vista ventral* **(C)** and dorsal / *y dorsal* **(D)** views; bony plate from Brazil in dorsal / *placas óseas provenientes de Brasil en vista dorsal* **(E)** and lateral / *y lateral* **(F)** views; bony plate from Spain in lateral / *placas óseas provenientes de España en vista lateral* **(G)** and dorsal / *y dorsal* **(H)** views. Redrawn from / *Redibujadas de* Depéret 1896 **(A, B)**, Powell, 1992 **(C, D)**, Azevedo and Kellner 1998 **(E, F)**, Sanz and Buscalioni, 1987 **(G, H)**.

tanosaurs vary both in size and morphology (figure 1). The plates of *Saltasaurus* have been described by Powell (1986: 155, figure 1.D-C). These are oval, with the greater axis longitudinally oriented; the dorsal face is conical and the flat to slightly concave ventral face has a longitudinal ridge; there is a marginal ring of small tuberosities, the so-called cingulum. In *Saltasaurus*, besides the osteoderms, small, intradermic, subspherical ossicles with a diameter not less than 7 mm were described, which, according to Powell (1986), would have been immersed in the dermis of the animal.

At Cinco Saltos-Lago Pellegrini, a considerable number of osseous plates was collected, twenty-six of which have been described in detail by Huene (1929: 150-151) and, as said above, initially attributed to a tyreoforan polacantid (*Loricosaurus scutatus*). In the Museum of Cipolletti “Carlos Ameghino” (Río Negro Province, Argentina), there is an additional lot of plates collected from the same quarry (MPCA-3026; MPCA 6698; MPCA 12342; MPCA-6697; MPCA 11093) (figures 2 and 3). In the Museum of Cinco Saltos (Río Negro Province, Argentina), there are the series MCS-9 to MCS-14, and MCS-33-MCS-34. The last one, as already said, was associated to a skeleton of *Neuquensaurus australis*.

Huene (1929) distinguished informally three different morphotypes of plates from this locality:

Type 1, of large size *“están provistas de una cresta longitudinal y, en parte, también de un borde perlado. La cresta longitudinal de esas placas más o menos ovaladas tiene arriba un espesor de 1 a 1,5 centímetros. En ninguna de las placas, que tenemos a la vista, tiene una altura mayor de 2 centímetros. El declive es pendiente al principio y suave después. (...) Esta placa de caparazón tiene una doble corona de perlas en el borde, groseras e irregulares, sobrepasando la corona interior a la exterior; desde la corona interna, la superficie decae en forma cóncava hasta la corona exterior. La superficie dorsal, en todas ellas, no es del todo lisa, sino que se halla provista de pequeños surcos y pozos, así como también de pequeñas tuberosidades, rara vez algo más grandes (...) El lado inferior de las placas decae relativamente plana y oblicuamente hacia adentro, hasta haber llegado a su máximo espesor (...) Abajo, en el medio, las placas son, no tan sólo planas, sino que presentan una entrante cóncava y ovalada.”*

Type 2. *“Las placas de mediano tamaño, ovaladas hasta circulares, no tienen crestas del lado dorsal, pero si una corona perlada, generalmente fina, aunque visible (C.S. 1232), muchas veces gruesa (p.ej.C.S. 1231), a veces apenas perceptible (C.S. 1226), que circunda el borde. La superficie dorsal es llana, hasta cóncava (C.S. 1232), o también convexa, pero siempre la superficie inferior es la más abovedada”.*

Type 3. *“Las osificaciones pequeñas, o muy pequeñas presentan cada vez formas más irregulares. Varias de ellas tienen aún rastros de nudos redondos, algunas también tienen tuberosidades irregulares. La mayoría de las veces se puede distinguir el lado superior del inferior. Algunas son muy gruesas, otras chatas; entre las muy pequeñas se encuentran algunas en forma de botón, pero también formas completamente irregulares alargadas (Huene, 1929: 150-151).”*

Discussion

Unlike *Saltasaurus*, many of the plates of the Type I studied by Huene show an oval, shallow depression on the center of the dorsal face, which, in turn, is divided by a tenuous longitudinal ridge (figures 2.A-C). This depression, as Powell (1980) believes, would have supported a horny element, possibly formed from the epidermis. In many plates (MPCA-6696, figures 2.D-F, and MPCA-12342), this depression cannot be clearly distinguished.

MPCA-11093 (figures 3.A-C) is a rather small bone (see Table 1), which does not show neither a ventral ridge nor a dorsal awn. The cingulum, that occupies the periphery as in the other cases, shows the typical pattern of intersecting bundles of bone, that is characteristic of most of plates. According to Huene (1929), this plate could be included into Type 2. The plate MCS-33 is basically similar to MPCA-3026, with a dorsal, shallow depression and a ventral ridge.

The series of plates from Cinco Saltos-Lago Pellegrini MCS-9 to MCS-14 ranges from Type 2 to Type 3. These are small and irregular in shape, with no evidence of a ventral keel.

In summary, the new evidence of plates from the locality of Cinco Saltos-Lago Pellegrini is consistent with Huene´s study. The bony plates can be grouped in three basic types, considering their size and morphology.

There is greater morphological diversity in the collection from Salitral Moreno than in that from Cinco Saltos-Lago Pellegrini (MPCA-Pv 39; MPCA-Pv 40; MPCA-Pv 44; MPCA-Pv 45; MPCA-Pv 61; MPCA-Pv 62; MPCA-Pv 63; MPCA-Pv 64, MPCA-Pv 65 and MPCA-Pv 67) (figures 4 and 5). All the plates are typically suboval, with the longer axis longitudinally oriented. Plates of Type I are absent; at least, none of the plates from this locality has the typical dorsal shallow depression. Many plates from Salitral Moreno are proportionally thicker than those from Cinco Saltos-Lago Pellegrini and Salta. Like the plates from El Brete (Powell, 1980, figure 1), many of the plates from Salitral Moreno (MPCA-Pv 40; MPCA-Pv 62) present a dorsal awn, which, at least in one case (MPCA-Pv 39), ends in two cusps, one anterior and the other posterior, giving it a saddle-like appearance (figures 4.A-C). In other plates, the dorsal

Figure 2. Bony plates (Type I) from Cinco Saltos-Lago Pellegrini / *Placas óseas (Tipo I) provenientes de Cinco Saltos-Lago Pellegrini.* **A-C:** MPCA 3026; **D-E:** MPCA 6696.

awn is absent, being replaced by a rather flat surface (MPCA-Pv 44, figures 4.D-F). In many of the ossifications, there is an appreciable anteroposterior asymmetry, although it is impossible to discern which ex-

Figure 3. Bony Plates from Cinco Saltos-Lago Pellegrini (Type II) / *Placas óseas provenientes de Cinco Saltos-Lago Pellegrini (Tipo II)* (**A-C,** MPCA 11093) and Salinas de Trapalcó / *y Salinas de Trapalcó* (**D-F,** MPCA 4066).

tremity is anterior and which is posterior (figure 5). The cingulum of irregular nodules seems to be less developed than in the plates from Salta assigned to *Saltasaurus*. In many cases (MPCA-Pv 61; MPCA-Pv 63 and MPCA-Pv 66) (figure 5.A) the ventral ridge becomes more pronounced towards one of the extremities. Plates of the Type 3 are absent.

The plates MPCA 27176 and MPCA 27177, which have been assigned by Salgado and Coria (1993) to *Aeolosaurus* sp., come from the locality of Salitral Moreno. The plates have a vaulted, smooth dorsal face. The ventral face, in turn, is more irregular. Ventrally, the margins of the plate are rugose. There is no indication of a ventral ridge.

Figure 4. Bony plates from Salitral Moreno / *Placas óseas provenientes de Salitral Moreno.* **A-C**: MPCA-Pv 39, **D-F**: MPCA-Pv 44.

As already said, it is not possible to know whether the collection of plates from Salitral Moreno belongs to one or more taxa.

The plate MPCA-4066 comes from the locality of Trapalcó (Río Negro Province, Allen Formation, Upper Cretaceous, figures 3.D-F). It is characterized by having a flat surface on the posterior (or anterior?) extremity, which gives the whole plate a pyramidal morphology. Possibly, the peculiar morphology of this plate is due to its partial imbrication with the contiguous plate (figure 3.D).

Azevedo and Kellner (1998) described the first "osteoderm" from Brazil (Upper Cretaceous, Minas Gerais State). The plate is small (48 mm long), oval and flat. On the dorsal face there is a smooth ridge that runs longitudinally (figures 1.E-F). It is possible that many of the characters mentioned by these authors (i.e. absence of a pronounced keel, flattening of the plate) may be due to the small size of the element, although it is impossible to assert whether small plates correspond to a small species, to a young individual or to an early histogenetic stage. Morphologically, the plate from Brazil may be readily included into the Type 2 described by Huene (1929).

Sanz and Buscalioni (1987) described two plates from the Campanian-Maastrichtian of Segovia, Spain (figures 1.G-H). Morphologically, the ossifications roughly coincide with those of *Saltasaurus*, without the dorsal shallow depression, typical of many of the plates from Cinco Saltos-Lago Pellegrini. However, the plates from Segovia are conical, whereas the plates of *Saltasaurus*, like others collected in Patagonia, present a dorsal awn. A conical morphology is also found in the spines of *Ampelosaurus atacis* (Le Loeuff *et al.*, 1994, figure 1) and in a giant similar plate from Salitral Moreno (Powell, 1986, pl. 77, 1), as described immediately below.

Le Loeuff *et al.* (1994), have described material from the locality of Campagne-sur-Aude, in South France (Lower Maastrichtian). The plates were later assigned to the titanosaur *Ampelosaurus atacis* by Le Loeuff (1995). The large size of the plates (all longer than 28 cm) is notable, taking into account that *Ampelosaurus atacis* is not a particularly large sauropod (Le Loeuff *et al.*, 1994). Le Loeuff *et al.* (1994) rec-

Figure 5. Bony plates from Salitral Moreno / *Placas óseas provenientes de Salitral Moreno.* **A,B:** MPCA-Pv 45; **C-D:** MPCA-Pv 61.

ognized three different types of osteoderms (spines, bulbs and scutes), assuming that each of these types would correspond to different positions on the body. The spine is 25 cm long and 14 cm wide (Le Loeuff *et al.*, 1994, figure 1). The internal face is oval, smooth, with a peculiar pattern of intersecting bone fibers which is seen also in the other osteoderms. It has a longitudinal, bilobate ridge which is less marked opposite to the spine. According to those authors, the osteoderm has two parts clearly different in lateral view: one half is low and thickens progressively to constitute a kind of cingulum at the base of the other half. The two halves of the osteoderm have different textures: the low part shows an irregular pattern of nodules and holes, whereas the spine itself shows a pattern more regular of radiating fibers.

The bulbous osteoderm lacks a spine. This plate is dorsally flattened and is 27 cm long (Le Loeuff *et al.*, 1994, figure 2). The lower half of the plate exhibits the typical irregular pattern of nodules and ducts. Finally, the scute is 28 cm long and 18 cm wide; the internal face shows bundles of intersecting fibers, the internal face is concave- convex with a smooth bilobate ridge, the ducts open in this ridge. The external half of the plate is divided by a cingulum; at this level, the plates reach a thickness of 5.5 cm (Le Loeuff *et al.*, 1994, figure 3).

The spines of *Ampelosaurus atacis* are very similar to a giant bony plate from Salitral Moreno (Río Negro Province, Argentina), described and figured by Powell (1986, pl. 77-1). From Salitral Moreno also comes a fragment of another apparently conical plate MPCA-Pv 67, although in this case only approximately a quarter of the plate has been preserved. The lower surface of this plate presents intersecting fibers, while, in the cingulum area, there are radiating bundles of bone, which become more pronounced towards the base. Unlike the spine assigned to *Ampelosaurus*, there is not a well-developed cingulum (Le Loeuff *et al.*, 1994). Like the other plates assigned to titanosaurs, the plate from Salitral Moreno is rather massive, more spongy in the basal portion. Due to the fact that these plates are asymmetric, Le Loeuff *et al.* (1994) hypothesized that these would not have been arranged on the midline of the body, but probably in parallel longitudinal series.

The plates of *Titanosaurus madagascariensis* (Deperet, 1896, pl. 6, 3) (figures 1.A-B) are flattened and subcircular. There is a well defined cingulum with radially directed fibers. The new material of the Maevarano Formation (Campanian?), described by Dodson *et al.* (1997, 1998) has provided more information on the bony plates from Madagascar. According to Dodson *et al.* (1997, 1998), one of the recovered plates (FMNH-PR 20021) is biconvex, robust and subcircular, with two parasagital ridges. Its measurements are: 17 cm long, 15.5 cm wide and 6.5 cm thick. Another osteoderm (UA 8675) lacks those ridges and measures 12 cm long, 9 cm wide and 6.5 cm thick. A small pyramidal plate measures 5 cm long. Besides these plates, there is a group of eight irregular plates that have a fibrous and porous texture.

Sometimes, small ossicles have been related, based on their probable position and origin, to the bony plates we are referring. In *Saltasaurus*, for instance, Powell (1986: 155) mentioned the presence of a pavement of small, irregularly arranged, intradermic subspherical ossicles. The small ossicles associated to the partial skeleton of *Malawisaurus* are different to the ossicles reported in *Saltasaurus*. For this reason, Jacobs *et al.* (1993) doubted if these were in fact titanosaurid osteoderms, although accepting their organic nature.

Chiappe *et al.* (1998) announced the discovery, in the locality of Auca Mahuevo (Neuquén Province, Argentina), of thousands of sauropod eggs and embryos, many of which had preserved fragments of skin. These pieces consist of scales arranged according different patterns. Sometimes, there is a large central scale which is surrounded by ten smaller scales. Although there is no evidence for the existence of bony plates in the embryonic skin, Chiappe *et al.* (1998) noted the similarity between these embryonic scales and the ossicles of *Saltasaurus* (Bonaparte and Powell, 1980; Powell, 1986). The embryos of living reptiles that bear osteoderms in adulthood, as the lizard *Cordylus cataphractus* Laurentis and the crocodile *Crocodylus niloticus* Laurentis, do not have osteoderms, which means that the ossification of the osteoderms, at least in these species, occurs after hatching (Chiappe *et al.*, 1998). Chiappe *et al.* (1998) arrive to the conclusion that the ossification pattern of the osteoderms in the sauropod of Auca Mahuida is, in this regard, of a reptilian type. These authors understood that absence of osteoderms in the embryo does not imply necessarily absence of plates in the adult.

Possible arrangement

Regarding the placement of the plates in the body of the animal, most authors agree that, unlike ankylosaurs and other groups of reptiles, the bony plates of titanosaurs are not pieces of a complete armor (Dodson *et al.*, 1998). Powell (1980: 43) mentioned that in *Saltasaurus* (the plates) *"podrían estar situadas sobre la columna vertebral (...) (o) en número reducido sobre la cola..." In a later paper, Powell (1986: 155) suggested that "es posible que éstas se hayan dispuesto en una o dos hileras sobre el tronco y la parte anterior de la cola (....) si bien no pueden descartarse otras posiciones posibles"*. Sanz and Buscalioni (1987), in turn, postulated that the plates would have been placed dorsolaterally, in the sacro-pelvic region, having based this interpretation on supposed similarities with the sacro-pelvic anatomy of ankylosaurs, such as the addition of a vertebra to a strongly coosified sacrum and the elongate preacetabular process of the ilium. However, Sanz *et al.* (1999) later recognized that the many modifications in the pelvis and the presence of a dermal armor were decoupled characters, since some undoubtedly unarmed sauropods (i.e. *Opisthocoelicaudia*) have the same pelvic morphology as other dinosaurs with armor.

Taking into account the bilateral symmetry of most of the plates, we can state that these would have been arranged in a longitudinal row, in the midline of the body. Seidel (1979) studied the organization and function of the osteoderms of *Alligator*. He saw that, in those osteoderms that are not in the midline of the body, the dorsal ridge is displaced from the center. If this criterion is applied to titanosaurs, it is possible to infer that the plates were arranged in one row in the midline, because the ridge (in this case, ventral) and the awns (dorsal) are, in the majority of the plates, centrally placed. As said above, some of these plates were probably imbricated, so that at least in some areas of the body, the plates would have constituted a continuous series (figures 3.D-F).

If the proposition of Sanz and Buscalioni (1987) that the plates were placed on the hip area is accepted, an individual should have no more than 6-7 bony plates, bearing in mind that titanosaurids have 6 sacral vertebrae. However, it should be said that the previous considerations are valid neither for the spines of *Ampelosaurus*, because of its lateral asymmetry, nor for the plate FMNH-PR-2021 and the group of eight irregular plates from the Upper Cretaceous of Madagascar, described by Dodson *et al.* (1998).

In the case of *Ampelosaurus atacis*, Le Loeuff *et al.* (1994) hypothesized that the plates could have been arranged on the scapular area and in the posterior region of the body. Herein, the considerations made for the plates from Patagonia are valid: the plates that are symmetric would have been placed on the midline, whereas the asymmetric ones would spread on the trunk of the animal.

A single row of bony plates in the midline has been demonstrated in other sauropods. For instance, Czerkas (1992, 1994) has described a series of spines of up to 18 cm thick, which would have been along the midline of the tail and, perhaps, throughout the entire animal. Recently, Bonaparte (1999) described *Agustinia ligabuei*, a new sauropod of uncertain phylogenetic relationships from the Neuquén Province, Argentina (Lohan Cura Formation, Aptian, Leanza, 1999). In this species, there are four different types of osteoderms (see Bonaparte, 1999, p. 6), which would have been above the neural spines.

Bearing in mind the opinion of Buffrénil *et al.* (1986) about the condition in *Stegosaurus*, it is probable that the plates of titanosaurs were not naked in life, but covered by a metabolically active tissue. The presence of many small ducts, both on the dorsal and the ventral face, shows the existence of a profuse net of vascular canals in the surrounding tissue of the plates.

Final comment

Titanosaur plates have two different zones that, in some cases, can be clearly distinguished (Sanz and Buscalioni, 1987). A central area (sometimes conical, sometimes a dome, sometimes an awn) and a surrounding cingulum of variable development. The central area is usually composed of radiating parallel fibers, whereas the surface of the cingulum presents, invariably, a greater heterogeneity, with nodules and intersecting fibers. On the surface of the plates (both ventral and dorsally) there are perforations that communicate with inner ducts which, as Sanz and Buscalioni (1987) pointed out, distinguishes these plates from the those of ankylosaurs. In many cases, the larger perforations are mainly in the cingulum zone, in others, one or two large ducts open close to the longitudinal ridge, on the ventral face.

The participation of these two zones in the conformation of the plates is variable. In the case of the plates from Cinco Saltos-Lago Pellegrini belonging to the Type I, the cingulum has a noticeable development and the central cone is usually truncated. In Salitral Moreno, in turn, the central area seems to be thicker, showing a more variable morphology.

Another character that distinguishes the plates of titanosaurs is the presence on them of a longitudinal ventral ridge. This is unusual for osteoderms. More typical is the condition in the nodosaurids *Hylaeosaurus* and *Polacanthus* (Pereda-Suberbiola, 1993), where the ridges are dorsal. This is probably the reason Huene (1929) oriented the plates upside down.

Usually, the ventral ridge is more accentuated in the center of the plate, being less pronounced towards the extremities. In some cases, however, the ridge becomes deeper towards one of the extremities (figures 4.C, 5.A).

Another important subject refers to the nature of the small ossicles of *Saltasaurus*. Do these correspond to the plates of the Type 3 described by Huene? If not, may these be homologated or histologically related to the skin scales described by Chiappe *et al.* (1998)? These are questions for which we still do not have a convincing answer.

Histological observations

In order to study the osseous microestructure of the plates, thin sections were cut through a plate of 9 cm long, 7.2 cm wide and 6 cm thick, from Salitral Moreno (Río Negro, Argentina). The plate sectioned is globose, similar to one referred to *Aeolosaurus* sp. (Salgado and Coria, 1993, pl. 1-G). It has a convex dorsal surface and a ventral ridge slightly developed. Two cuts were made: MUCPh-5´ is a transverse section, perpendicular to the axial plane, approximately at the mid length of the plate, and MUCPh-5´´, a longitudinal section, perpendicular to the axial plane, just above the cingulum (figure 6). The plate is characterized in being thickly vascularized and internally remodeled, which is reflected by the profuse development of Haversian and spongy bone, as well as by the presence of fibers, particularly on the periphery of the plate. Vascular canals are oriented both longitudinal and transversely.

MUCPh-5´ (figure 7.A-C). Ventrally, the plate is composed mainly by reconstructed cancellous bone (Reid, 1996) whereas, dorsally, Haversian bone predominates. The trabeculae of the cancellous bone, which are composed by preexisting Haversian bone, enclose large spaces, which become larger towards the center of the plate. On the latero-ventral surfaces of the plate, that is, between the longitudinal ventral ridge and the cingulum, there is a thin layer of avascular tissue with fibers of, possibly, metaplastic origin (figure 7.A-B). Metaplastic is a term applied to bone formed without the participation of osteoblasts. Thus, *metaplasia* is the transformation (not the replacement) of a completely formed tissue (e.g. cartilage, tendons) in other (Reid, 1996). Small quantities of metaplastic tissue is a normal constituent of many bones.

Buffrénil *et al.* (1986) stated that the existence of fibers in the lower third of the plates of *Stegosaurus*

Figure 6. General aspect of the cross sections in the bony plate. The rectangles localize the photographs displayed on figure 7. / *Aspecto general de los cortes efectuados en las placas óseas. El rectángulo localiza las fotografías de la figura 7.*

indicates that the plate has incorporated preexisting fibrous tissue, from which is deduced that the base of the plate would have been embedded in the skin of the animal. Undoubtedly, the same can be applied to the titanosaur plates.

In transverse section, the ventral surface of the plate determinates a succession of "peaks" and "valleys" (figures 7.A-B). The fibers are parallel to the surface in the "hillsides" and perpendicular to the surface both in the "peaks" and the "valleys". Between the fibers, there is a large amount of lacunae or small spaces wherein the osseous cells were once housed (figures 7.A-B). In magnified view, these spaces do not present the typical net of interconnecting canaliculi. Reid (1996) estimated that the absence of canaliculi is common in metaplastic bones, since the cells (originally condrocites or fibrocites), lack the delicate connections that osteoblasts establish before becoming enclosed as typical osteocytes. However, Reid (1996) pointed out that, in fossils, the canaliculi are usually obliterated or damaged. According to him, the rule should be the following: the presence of well-developed canaliculi is positive evidence against metaplasy. Its absence, however, is not an evidence in favor of it.

As already said, in the dorsal half of the plate, there is dense Haversian bone, with the interstitial bone formed by secondary bone (figure 7.C). In some places, there are elongated canals radially oriented, within which endosteal bone has been centripetally deposited. On the dorsal surface of the plates there are also Sharpey´s fibers, though less than on the latero-ventral areas. Apparently, the fibers show an orientation predominantly perpendicular to the surface of the plate.

MUCPh 5´´ (figures 7.D-F). The cortical bone is formed by Haversian bone, with elongated, radially oriented canals (figures 7.D-F). Some of these open superficially, extending towards the innermost part of the plate. The walls of the canals are covered by a thin layer of endosteal tissue. Fibers seem to be more frequent in the periphery of the bone, with bundles that have a prevailing radial orientation. Towards the center of the piece, the Haversian bone gives way to the secondary cancellous bone. The elongated canals or ducts represent vessels that pierce the plate with an angle slightly different than the horizontal plane, whereas the subcircular osteons are vessels perpendicular to the horizontal plane.

Discussion

The bony plates described here differ histologically from those of *Stegosaurus* (Buffrénil *et al.*, 1986). In this genus, there is lamelar-zonal tissue on the apex of the plate, whereas in the mid part, dense Haversian bone predominates. Towards the base of

Figure 7. Histological characteristics of the bony plates of titanosaurs / *Características histológicas de las placas óseas de los titanosaurios.* **A-B,** periphereal region of the cortex is made of a thin layer of avascular bone, with fibers / *la región periférica de la corteza está formada de hueso avascular, con fibras.* **C,** dense Haversian bone, / *hueso Harvesiano denso,* **D-F,** Haversian bone with oblique vascular ducts which open in the cingulum zone / *hueso Harvesiano con conductos vasculares oblicuos que abren en la zona del cingulum.* The scale is 0.5 mm in **B** and 1mm in the other images / *La escala es 0.5 mm en b, y 1 mm en las otras imágenes.*

the plate, there is a cortex of primary bone and, more deeply, large cavities of reabsortion limited by trabeculae of endosteal bone. The Sharpey´s fibers are abundant only in the basal third of the plate, mostly in the cortex. On the contrary, in the titanosaur bony plate, zonal bone is absent (there is no indication of cyclical deposition of bone). Fibers are rather scarce, being restricted to the periphery, particularly on the lateroventral areas, although it is possible that the scantiness of fibers in other parts of the plates may be due to the elimination of most of the primary tissue. The plates of *Stegosaurus* are light, whereas the ones assigned to titanosaurs, though porous, are more dense or massive. Both are similar in that the erosive spaces are placed preferentially on the ventral half of the plate.

At the time of the death of the titanosaur, the dissolution of bone was probably more intense in the ventral half of the plate. Evidently, the dorsal half of the plate also experienced remodeling (erosion and redepositation), because of the occurrence of deep Haversian bone. Possibly, the bony tissue was relocated from the ventral half to the dorsal one. In this regard, the remodeling pattern of the plate would be similar to that found in *Stegosaurus* (Buffrénil *et al.*, 1986).

Are the bony plates osteoderms?

Almost all authors agree that the plates are osteoderms, assuming their intramembranous origin (Bonaparte and Powell, 1980; Powell, 1986; Salgado and Coria, 1993; Dodson *et al.*, 1998). In fact, dermal bones or osteoderms are common in a wide variety of living and extinct tetrapods (Romer, 1956). Among dinosaurs, the existence of osteoderms in ankylosaurs, ornithopods, stegosaurs and sauropods was mentioned (Bonaparte and Powell, 1980; Bonaparte, 1999). Histologically, typical osteoderms may be formed either from osteoblastic or metaplastic bone, or a mixture of both (Reid, 1996); these tissues are distinguishable microscopically. However, whether the plates were formed from an ossification center immersed in the dermis (that is, if the plates are, in fact, osteoderms), or from a previous cartilaginous center, is much more difficult to determine. For this reason, it must be remembered that there are not obvious differences in the microstructure of periosteal-osteoblastic bone, formed from connective tissue, and other formed from cartilage. The terms membranous-cartilaginous or dermal-endochondral, in fact, refer to the way by which the bone begins its formation; they do not necessarily reflect differences in the histological structure of the mature bone. In some cases, endochondral bone can be distinguished by islands or columns of calcified cartilage (Reid, 1996). The absence of these structures, however, does not imply a membranous origin (either periosteal, endosteal or dermal). In most cases, endochondral bone is finally replaced by periosteal or endosteal bone.

In spite of the difficulty in distinguishing dermal bone histologically, one can characterize macroscopically the true dermal ossifications of living reptiles (Romer, 1956). In turtles and crocodiles, for instance, the osteoderms have, typically, a flat to slightly concave ventral face and a dorsal one, which sometimes is ornamented. Hence, it is possible to argue that the fossil structures that show the same characteristics are also true osteoderms. In these cases in which the plates are spread irregularly in the body of the animal, or forming an armor as in the ankylosaurs, the dermal origin of the plates seems to be incontestable. However, as we saw, most of the titanosaur plates are rather globose and massive, with an important ventral ridge and an irregular cingulum of nodules. From this point of view, the bony plates of titanosaurs are unlike the osteoderms seen in most living reptiles.

Regarding their microestructure, it is probable, from the presence of an appreciable number of Sharpey's fibers, that the plates of titanosaurs have incorporated connective tissue. But the mere presence of Sharpey´s fibers does not imply necessarily a dermal origin of the whole piece, since the fibers could be incorporated from tendons or from the connective layer of the periostium.

An alternate interpretation is that at least some plates are not true dermal plates but epiphyseal bones developed on the tip of the neural spines (Haines, 1969). In mammals, once adulthood is reached, growth usually stops, the epiphyseal plate ossifies and the epiphysis fuses to the diaphysis. In reptiles, commonly, the epiphyses remain as isolated cartilaginous elements. This is where additional ossifications may occur. For instance, Haines (1969) reported the existence of ossified epiphyses on the tip of the neural spines of *Sphenodon*, *Agama* and *Hemidactylus.* In the last two genera a center of massive calcification in the cartilaginous epiphyses was observed and, above that, metaplastic bone formed from the surrounding tissue. An analogous process can apply to some of the bony plates of titanosaurs. Nevertheless, it is impossible to determinate, at present, whether the plates of titanosaurs are true osteoderms or epiphyseal bones.

Regardless of the origin of the plates, it is possible that a supraspinal tendon inserted on the ventral ridge. This is based on the pattern of numerous bundles of bone placed longitudinally of the external surface of the ventral ridge, which is basically the same as that seen on the distal surface of the neural spines of sacrals and caudals of some titanosaurs, indicating the possibility of a tendinous or cartilaginous connection between plates and vertebrae.

Probable functions

Powell (1992), Sanz and Buscalioni (1987) and a number of authors, have postulated adaptionist explanations for the bony plates attributed to titanosaurs. Mostly, the inferred function was that of passive defense. The term "scute", commonly used as synonymous with "plate", refers to this possible function. Sanz and Buscalioni (1987) associated the existence of armor to the capability of using the tail as a whip. Powell (1992), in turn, linked the acquisition of a defensive armor to the fact that adult

Table 1. Measurements (cm) of the bony plates of titanosaurs housed in the collections of Cipolletti and Cinco Saltos Museums.

Plate	Length	Width	Height
MPCA-Pv 39	12	8.7	8.4
MPCA-Pv 40	9.7	6.1	6.4
MPCA-Pv 44	12.2	9.5	6.6
MPCA-Pv 45	20	11	9
MPCA-Pv 61	13	10.2	7.8
MPCA-Pv 62	8.8	6	3.6
MPCA-Pv 63	11	7.2	3.8
MPCA-Pv 64	13.2	9	6.7
MPCA-Pv 65	12.5	7.5	4.5
MPCA-Pv 66	11.5	8.5	6.1
MPCA-3026	18	14	6.5
MPCA-4066	12.5	10.5	5.9
MPCA-6696	10.3	8.4	3.9
MPCA-6697	17	13.6	6.9
MPCA-11093	8.8	7.7	3.5
MPCA-12342	12.6	10.8	4.9
MPCA-27176	15	13	6
MCS-9	4.6	3.1	1.7
MCS-10	6.3	5	2.7
MCS-11	5.9	5.2	2.5
MCS-12	7.4	5.8	2.8
MCS-13	7	6.8	2.8
MCS-14	10.3	5.9	3.5
MCS-33	17.5	13	6.8
MCS-34	10.9	9	3.6

saltasaurines did not reach a large body size, enough to dissuade predators. According to this author, the juveniles would be defended merely by the grouping of the adults. This hypothesis, however, could not be applied to larger titanosaurs, such as *Titanosaurus araukanicus* and *Aeolosaurus* sp., which also would have had bony plates.

In the case of *Stegosaurus*, Buffrénil *et al.* (1986) discounted the defensive function of the plates in view of their fragility. Rather, they hypothesize that the plates would have functioned as structures of heat exchange with the environment: absorbing heat, if *Stegosaurus* was an ectoterm, or dissipating it if that genus was an endotherm. Likewise, for *Alligator mississippiensis* Cuvier, Seidel (1979) proposed the function of heat transfer; once absorbed, heat would be immediately transferred throughout the mineral phase of the plate and dissipate to the rest of the body. According to Seidel (1979), the osteoderms of *Alligator* could be used for either heat absortion or dissipation.

Can the thermoregulatory hypothesis be applied to the bony plates of titanosaurs? First, we should reiterate that there are significant morphological differences between the plates of titanosaurs and stegosaurs. In these ornithischians, like in *Alligator*, the plates are broad, flat and hollow to house an internal vascular network (Farlow *et al.*, 1976). In contrast, some of the plates attributed to titanosaurs are massive, with a low surface-volume ratio. This fact weakens the thermoregulatory hypothesis.

Another possible function of the bony plates is calcium storage. This is the other of the possibility considered by Seidel (1979) for the plates of *Alligator mississippiensis*. While it is possible that the titanosaur plates supplied calcium in some phase of the animal life-cycle, for instance, during the reproduction, especially when the availability of food rich in calcium was reduced, it is improbable that the storage function is the cause for the emergence of the plates, because, as Sturkie (1967) pointed out for birds, the calcium needed during the reproductive period can be taken directly from the bones.

The fact that the plates of titanosaurs are rather massive, with no large internal spaces, does not support the calcium storage hypothesis, although there is still the possibility that the dissolution of osseous matter would have taken place on the external surface of the bone, as Sturkie (1967) has stated occurs in some birds.

Czerkas (1994) inferred different functions for the osseous plates of the diplodocids. This author suggests three functional possibilities: the plates as protective elements that would avoid the damage of the skin, the plates as ornamentations and as thermoregulatory structures.

While the prevailing view is that the bony plates of titanosaurs had a specific function (as a protective, defensive, thermoregulatory or store structure), no researcher ever claimed explicitly that the plates emerged as an adaptive response, by natural selection. In other words, not one hypothesized what the primary function of the plates was.

The adaptive scenario involves two different aspects. The first one, to establish if the plates could ever execute some function; the other one, to determine if the adduced function can account for the evolutionary rise of the plates. Without doubts, the second issue is the most arduous, in view of the impossibility of experimental demonstration.

An alternative to the functional scenario would be that the plates were formed during the reproductive season, when the intestine absorbed more calcium than the required for the calcification of the eggshells. This is one of the many alternatives postulated by Sturkie (1967) for the plates of *Alligator* and differs from the other explanations in that the plates are here regarded as a consequence of some other process (not a necessary adaptation), in this case, a process related to the calcium metabolism. On the other hand, the rise of plates and ossicles in titanosaurs may reflect the implementation of an evolutionary process involving changes in the distribution of the osseous matter during growth, or the consequence of a difference between the deposition rate of bony tissue and the growth rate of the animal.

These speculations do not invalidate the possible functions postulated by several authors. For instance, the animal could well develop *a posteriori* a defensive behavior, using the plates as defensive structures. Perhaps the smallest species, such as those of *Saltasaurus* and *Neuquensaurus,* were favored more than the largest ones, although it is hard to imagine how a single row of bony "scutes" could diminish the effects of predation. On the other hand, the animal could take calcium from the plates, under extreme conditions. The osteohistology of the plates does not shed light on this important aspect of titanosaur biology. Following the terminology proposed by Gould and Vrba (1982), I am inclined to see the bony plates of titanosaurs as possible exaptations, that is, structures originally neutral that were possibly selected for defensive, termoregulatory, and / or storage functions (see Amundson, 1996).

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