OSTEOLOGY **OF *SALTASAURUS LORICATUS***

(Sauropoda-Titanosauridae) of the Upper Cretaceous of Northwest Argentina*

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ABSTRACT

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* Original citation: Powell, J. E. 1992. Osteologia de *Saltasaurus loricatus* (Sauropoda - Titanosauridae) del Cretácico Superior del noroeste Argentino. *In* J. L. Sanz and A. D. Buscalioni (eds.), *Los Dinosaurios y Su Entorno Biotico: Actas del Segundo Curso de Paleontologia in Cuenca*. Institutio "Juan de Valdes", Cuenca, Argentina:165-230.

The anatomy of the titanosaurid dinosaur *Saltasaurus loricatus* Bonaparte and Powell is described, based upon a great number of bones found in the Lecho Formation, Southern Salta Province, Northwestern Argentina. This dinosaur was a medium-sized sauropod with short and robust limbs, characterized by a dermal armor integrated by scutes and small rounded intradermal ossicles. The skull has a long and recurved paroccipital process considered as a synapomorphy for the Titanosauridae. As in all titanosaurids, *Saltasaurus loricatus* has cancellous bone in sacral and presacral centra, but this condition is also present in the anterior caudals. A new subfamily is proposed: Saltasaurinae.

INTRODUCTION

The family Titanosauridae includes sauropod dinosaurs from medium size to gigantic, constituting the most conspicuous group of large herbivores in the Upper Cretaceous in South America. Its presence on the subcontinent was recognized by Lydekker (1893) on the basis of remains originating in Patagonia, Argentina (provinces of Neuquen and Chubut). Huene (1929) later completed an important study about the dinosaurs of the Upper Cretaceous in South America, devoting himself especially to the analysis of titanosaurs. His studies were based on important collections coming mainly from Patagonia, deposited in the museums of La Plata and Buenos Aires.

If this family is well represented in such diverse parts of the world as North America, Europe, Africa, Madagascar and Peninsular India, its record in South America is much richer in diversity and abundance.

The objective of the present work is to make known the osteological aspects of *Saltasaurus loricatus* (Bonaparte and Powell, 1981). This species is known from a considerable quantity of elements discovered in a single quarry, which permits the study of important aspects of titanosaur anatomy.

THE 'EL BRETE' FORMATION

The area of El Brete caught the attention of investigators soon after the discovery of radioactive bone fragments, reported by Danieli *et al.* (1960). The poor condition and fragmentary nature of the materials impeded the identification of the taxonomic group to which they would have belonged.

In 1975 a commission of paleontological exploration, composed of personnel from the Miguel Lillo Foundation, and directed by Dr. J. F. Bonaparte found an assemblage of bones on top of a tree-covered hill situated near a lime quarry close to Gonzalez Creek on the "El Brete" ranch.

The dig continued at this site for several more months that year and the two following years with help from several institutions such as: CONICET, Chapman Foundation, Program No. 18 of the Council of Investigations of the National University of Tucumán. The discovery was reported by Bonaparte *et al.* (1977), who also described the geological characteristics of the region and the sedimentary features of the outcrop. Bonaparte and Powell announced, in preliminary form, that the fauna present in the bed include sauropods, carnosaurs, coelurosaurs and birds.

Walker (1981) has made a preliminary study of a large part of the remains of birds found in association with the titanosaurs, emphasizing a number of peculiarities that, in his judgment, justify their inclusion in a distinct subclass : Enanthiornithes.

Geographic Location

Some 500 m. to the east of a limestone quarry located in the vicinity of Gonzalez Creek on the "El Brete" Ranch. This establishment is located 11 km. west of El Tala on National Route No. 9 in the Candelaria Department, south of the Salta Province, very close to the Tucumán border. The geological characteristics of the region have been analyzed by Bonaparte *et al.* (1977).

Stratigraphic Position

Lecho Formation, Subgroup Balbuena, Group Salta. The fossil level is located 22 m. from the base of this formation.

Age

Upper Cretaceous; Senonian: Upper Campanian (possibly), Lower Maastrichtian.

The only paleontological evidence of chronological value for this formation is the remains of the titanosaurs found in El Brete. Using these remains as their basis, Bonaparte *et al.* (1977) assigned to the fossil bearing unit the age of late Senonian, probably Maastrichtian.
The close similarities of the titanosaur *Saltasaurus loricatus* (Bonaparte and Powell) with *Neuquensaurus australis* (see Powell, 1986), documented from the Colorado River (Campanian) Formation and the Allen (Lower Maastrichtian) Formation from the Neuquina River Basin infers a Campanian-Maastrichtian age for the Lecho Formation.

The Lecho Formation in El Brete underlies the Yacoraite Formation, whose equivalent in Bolivia, the El Molino Formation has yielded remains of fish of Maastrichtian age (De Muizón, *et al.*, 1983). Therefore, the Lecho Formation ought to be limited to the lower part of the Maastrichtian or, possibly, to the Upper Campanian, taking into account the fact that the Campanian age of the Las Curtiembres Formation was determined from radiometric data (Reyes *et al.*, 1976, and Valencio, *et al.*, 1976) and is the suggested age in this work for the Los Blanquitos Formation.

This interpretation supports the correlation of the Yacoraite Formation with the Allen and Jaqüel Formations, as suggested by Powell (1981), the deposits of which could have been related to the same transgressive episodes.

Characteristics of the Fossil-Bearing Sediments

Fine greenish-grey sandstone, characterized by a thick, irregular stratification. In some layers cross-bedding and bioturbation can be seen.

Bossi. *in* Bonaparte *et al.* (1979), has interpreted this sequence as a fluvial-lacustrine coastal plain with frequent swamps and abundant vegetation, where the character of the reducing environment caused the coloration of the sediments.

Fauna Documented in the Locality

Sauropoda
  Titanosauridae

Saltasaurus loricatus Bonaparte and Powell, 1980.

Coelurosauria
Noasauridae

Systematics

Order: SAURISCHIA Seeley, 1988.
SAUROPODOMORPHA Huene, 1932.
TITANOSAURIDAE Lydekker, 1893.
SALTASAURINAE nov.

Definition of the subfamily

Titanosaurs of medium size, smaller than those in the remaining subfamilies. The skull with basal tubera fused medially. The supratemporal fenestra is closed. There are complex triangular basipterygoids with a prominent sagittal crest. The *fenestra ovalis* is open for the passage of nerves IX - XI. The foramen for the internal carotids are situated medially and anterior to the basipterygoids. The pleurocoels on the centra of the cervical and dorsal vertebrae are reduced. The cervical vertebrae are shorter and more robust than those of the Titanosaurinae. The neural spine of the dorsals is extremely thick and rounded. The centra of the caudal vertebrae are broader than tall, with variable development of spongy bone. The spines of the caudal vertebrae are posteriorly inclined, spines of the anterior vertebrae are low. Medial prominence is close to the upper edge of the scapula. There is a broad pelvis with ilia whose preacetabular process is extended laterally.

Genus:

SALTASAURUS Bonaparte and Powell, 1980.

Saltasaurus Bonaparte and Powell, 1980, p. 20.

Type Species: *Saltasaurus loricatus* Bonaparte and Powell, 1980.

Distribution: Upper Cretaceous (Upper Campanian? - Lower Maastrichtian) Salta, Argentina.

SALTASAURUS LORICATUS Bonaparte and Powell. 1980.
Saltasaurus loricatus Bonaparte and Powell, 1980. pp. 20-23, also 3-6; Powell, 1980, pp. 41-43, fig. 1.
Holotype : PVL 4017-92. Complete sacrum fused to the two ilia.
Locality: El Brete, Department Candelaria, south of the province of Salta, Argentina.
Stratigraphy: Lecho Formation, Subgroup Balbuena Group Salta.
Age: Upper Cretaceous. Senonian. Campanian?- Maastrichtian.
Hypodigm: All the materials that are identified as PVL 4017, and in addition, pieces CNS V 10.023 and 10.024, corresponding to no fewer than five adults and subadults. Included are three fragments of distinct skulls, an axis, fourteen cervical vertebrae, twenty dorsals, three sacra, twenty-six caudal vertebrae, four scapulae, three coracoids, four sternal plates, ten humeri,

five ulnas, four radii, five metacarpals, five ilia, four pubes, two ischia, five femora, five tibias, four fibulas, seven metatarsals, six dermal plates, and four related groups of dermal ossicles. The numbering and characteristics of the material will be detailed in the description of each piece.

Modified Diagnosis

Skull with supratemporal fenestra more reduced than in *Antarctosaurus*, closed dorsally by fusion of the parietal and frontal: basisphenoid complex of triangular shape in ventral view, with a transversely narrow base and a pronounced sagittal crest; fenestra ovalis open to the passage of nerves IX-XI, basipterygoids joined proximally; basal tubera of the basioccipital are fused.

The cervical vertebrae are relatively shorter and broader than those of the known titanosaurs. Dorsal vertebrae centra lack ventral keels. The neural spines are very thick and round. Dorsal surface of the diapophysis is flat distally.

The sacrum has six fused vertebrae with the articular surfaces convex anteriorly and posteriorly. The first caudal is procoelous. The broad neural spine is compressed anteroposteriorly, and also is somewhat inclined toward the back in the anterior caudals.

The scapula shows a medial prominence close to the anterodorsal edge. The long bones are relatively short and sturdy. The metacarpals are shorter than in *Antarctosaurus*, *Argyrosaurus* and the titanosaurs.

DESCRIPTION

Cranium

Material: PVL 4017/16 I (Figs I & 2) Left half of the posterior portion of the cranium: left orbitosphenoids and a fragment that corresponds to the ventral part of the right: left laterosphenoids: left prootic, opisthotic and occipital: left basipterygoids and part of the right: incomplete supraoccipital; basisphenoids, and incomplete presphenoids

PVL 4O17/162 (Fig 3) Posterodorsal part of the cranium with right and left frontals, left parietal; almost complete supraoccipital; both latero- and orbitosphenoids almost complete, and part of the left exoccipital.

PVL 4017/211. Right frontal of a juvenile

In agreement with the materials that have been available until now, the cranium of Saltasaurus loricatus resembles generally that of *Antarctosaurus wichmannianus*, according to the description by Huene (1929a).

The two groups of articulated cranial bones that are described here undoubtedly belong to adults. A strong coossification in the sutures prevents, for the most part, the delineation of the distinct bony elements that make up the cranium.

The long paroccipitals, recurved forward and down, constitute the “showiest”- character of the occipital view and bring to mind, in certain form, similar elements in the hadrosaurs. This morphology; not common among saurischians is seen also in *Antarctosaurus wichmannianus*, although these processes have not been preserved completely in the material assigned to this species.

The occipital condyle is almost perpendicular to the axis of the basicranium and its articular facet is ventrally oriented.

The medial tuberosity of the supraoccipital projects dorsally above the skull roof. The foramen of the hypoglossal nerve (XII) opens toward the back, close to the lower edge of the exoccipital, between the base of the paroccipital and the neck of the occipital condyle.

The basioccipital forms almost the entire occipital condyle. The exoccipital seems to form the dorsolateral corner and walls of the condyle. At the same time the exoccipital probably forms a large part of the floor of the neural canal.

The basal tubera of the basioccipital are almost flat and there is no distinct separation between halves, contrary to what is seen in *Antarctosaurus wichmannianus* and *Diplodocus* (sensu Berman and McIntosh. 1978).

The basipterygoids, together with the basal tubera. form a wide surface that faces ventrally; merging in the middle along the greater part of the preserved area (figs 1 & 3).

The orbito- and laterosphenoids are totally fused together. The suture between them can be seen only in the dorsal margins of these bones, where both articulate with the frontal. These elements are laminar bones about 7mm. thick and they form a “V” with their pairs on the opposite side. At the sutures, in front of the foramen of the optic nerve (II), both orbitosphenoids are broadest.

The foramen of the optic nerve (II) opens in the orbitosphenoids, a short distance from the anterior edge of this bone. It is oval shaped and is of 6 mm. - 8 mm. diameter. This foramen is separated from its equivalent on the opposite side by a bone of 1cm. thickness.

Farther back and a little above the foramen of the optic nerve, a small foramen of 2 mm. diameter is seen that corresponds to the trochlear nerve (IV). Below this is found the foramen of the oculomotor (III) which is approximately circular and of 4 cm. diameter. The position of the openings of these nerves coincides with the suture line of the orbito- and laterosphenoids, as has been deduced from the study of other sauropods like *Diplodocus* (Berman and McIntosh, 1978).

The laterosphenoid, has a crest on its posterior edge that extends above the trigeminal nerve (V) outlet, which is known as the *crista antotica* (Berman and McIntosh, 1978). This wing of the laterosphenoid, contributes to the formation of the posterior wall of the orbit, separating it from the supratemporal fenestra.

The foramen of the trigeminal nerve (V) appears between the laterosphenoids, and the prootic that limit it anteriorly and posteriorly; its diameter is 6 mm. to 8 mm.

From behind the facial nerve (VII) that emerges through a very small foramen, the prootic shows a posterior edge outwardly concave, which is known as the *crista prootica* (Berman and McIntosh, 1978).

The opisthotic is hidden to a great extent by the prootic , being exposed in lateral view above the paroccipital and also above the large foramen of the glossopharyngeal, vagus and accessory nerves (IX, X, and XI). The external diameter of this large foramen is from 7 mm. to 15 mm.

The *fenestra ovalis* opens to the same conduit that serves as outlet to these nerves, I cm. inside the external edge that surrounds the foramen and above the front wall of the conduit.

The posterior dorsal area of the cranium has been partially preserved in two pieces: PVL 4017-162 (Fig. 3) and PVL 4017-211, which correspond to the frontal of a juvenile.

The frontals are found divided into two well-defined areas: one latero-orbital, and the other medial.

The orbital portion is ventrally concave and forms the posterior dorsal part of the orbit. According to the radius of curvature, the orbit would have a diameter of about 8cm., supposing that it were approximately circular.

The orbital portion of the frontal is separated ventrally from the medial portion by the area of articulation of this bone with the orbito-laterosphenoid complex.

The medial portion covers part of the brain and the olfactory peduncles.

Over the dorsal surface of the frontal the two portions of the bone can also be distinguished: the orbit is convex and has a lateral edge marked by small but well-defined tuberosities. Separated by a wide "valley," the medial portions of both frontals fashion an area that shows three round projections aligned transversely the largest of which is crossed by the sagittal plane.

The ventral side of the brain case is formed posteriorly to anteriorly by the exoccipitals, and the basisphenoids; sutures between the referred elements cannot be seen.

Slightly posterior to the trigeminal foramen is a small opening through which emerges the abducens nerve (VI).

The pituitary fossa is very deep, on its floor open the foramina of the internal carotid artery which expand ventrally on the angled basipterygoid lamina.

Approximately half way down the basipterygoids a foramen that could also be related to the internal carotid artery passage crosses the lateral lamina.

AXIAL SKELETON

Axis (Fig. 4)

Only one axis (PVL 4017-1) has been recovered. A relatively small element, it is short, high and provided with a strong neural spine.

The centrum has a somewhat prominent odontoid process in the form of a half moon. Lateroventrally a depression corresponds to the position of the intercentrum that has not been preserved. In addition, it has two lateral pleurocoels, one dorsal and the other ventral to the parapophysis; these are partially preserved.

The neural arch is high. The prezygapophyses have not been preserved. The neural spine has a triangular cross section with the acute angle oriented forward. Posteroventrally the spine is divided into two robust processes that form the postzygapophyses. The articular facets of these are slightly inclined lateroventrally.

The neural spine shows lateral foremen that are located in a fossa that is dorsomedial to the diapophysis.

Anterior Cervical Vertebrae (Figs 5-7)

Three almost complete anterior cervical vertebrae (PVL 4017-3/50/139) have been recovered that belong to adult individuals, and one small centrum of a juvenile.

The vertebrae are long and low, with centra, prezygapophyses, postzygapophyses and diapophyses composed of large cells.

The centrum is opisthocoelous with articular surfaces wider than tall. The posterior surface has an depression on its dorsal edge that becomes the floor of the neural canal. The pleurocoels on the centrum are short but deep.

The neural arch is low and long.

The prezygapophyses are situated dorsally to the diapophyses and are found reinforced by a strong spinal-prezygapophyseal lamina. Another slim lamina connects with the neural arch.

The facets of the prezygapophyses are subcircular and are inclined medially about 30 degrees. The articular surfaces are widely spaced and are firmly joined to stalks arising from the neural arch above the anterior portion of the diapophyses.

The postzygapophyses are long and project beyond the posterior articular face. Proximally, they are joined by an infrapostzygapophyseal lamina that floors the wide, post-spinal depression. The postzygapophysis is joined to the diapophysis by an oblique lamina.

Behind the prezygapophyses and on both sides of the neural spine, there is a fossa divided by a thin plate that is divided into dorsal and ventral areas. The parapophyses and diapophyses are wide processes directed lateroventrally forming a wide canal that parallels the pleurocoel of the centrum.

Posterior Cervical Vertebrae (Fig 8)

Seven vertebrae, more or less complete, and five fragments (PVL 4017/5-9/190/213/214) have been preserved, among which is a small centrum belonging to a juvenile. These vertebrae are proportionately shorter and wider than the anterior cervicals.

The centrum has marked lateral fossa that contain reduced, deep pleurocoels, sometimes divided by an oblique septum. The posterior articular surface is profoundly concave and has an oval outline which is wider than tall. A groove again marks the passage of the neural canal. The ventral side of the centrum is concave.

The prezygapophyses project laterally at both sides of the neural spine and are situated farther back than those of the anterior cervical vertebrae. The articular surface of the prezygapophysis is subcircular and inclined posteromedially. Behind these prezygapophyses are deep fossae that allow free movement of the postzygapophyses of the adjacent vertebra.

The postzygapophyses are shorter, more robust and more divergent than those of the anterior cervicals.

As in the anterior cervicals, the postzygapophyses are joined close to their base by an intrapostzygapophyseal lamina.

The neural spine is low and undivided. It is linked with the postzygapophyses by a wide spinal-postzygapophyseal lamina. Laterally it is rugose.

The parapophyses and diapophyses are robust, lateral projections, oriented somewhat ventrally; longer and narrower than those of the anterior vertebrae, which are sometimes fused to the cervical rib. Both structures have wide laminae that extend the length of the centrum. The reinforcing laminae (dia-postzygapophyseal and spinal-prezygapophyseal) are thicker than in the anterior cervical vertebrae.

The posterior edge of the parapophysis bifurcates toward the base in two laminae: one is the dia-postzygapophyseal, and the other is linked to the centrum creating a triangular fossa.

Dorsal Vertebrae

The dorsal vertebrae are short and relatively high. The centra possess small pleurocoels, and are composed of a spongy internal structure composed of large cells. This structure constitutes 60 per cent of the volume of the centrum. This same type of structure is present in the neural arch, diapophyses, prezygapophyses, postzygapophyses and neural spine, and contributes to the notably light vertebrae (Fig. 16).

Anterior Dorsal Vertebrae (Figs 9 a 12)

Only three incomplete anterior dorsal vertebrae (PVL 4017-10/11/12) and one neural arch (PVL 4017-44) have been recovered.

The piece PVL 4017-10 (Fig. 9) corresponds to the proximal dorsal. It has a high, wide, but short, neural arch that is fused to the posterior portion of the centrum.

The prezygapophyses are short and are supported by columns that rest on a portion of the infradiapophyseal lamina. The articular facets are subcircular with a diameter of 6 cm. The diapophyses project laterally from behind the prezygapophyses and are arranged perpendicularly to the vertebral body. They are supported by a well-developed infradiapophyseal lamina that bifurcates downward, making a deep triangular depression between the branches.

The parapophysis is situated on this anterior branch, above which are also resting the bases of the infradiapophyseal columns. The parapophyses are situated very low, just above the centrum.

In one piece previously listed, (PVL 1027-10). the neural spine and postzygapophyses have not been preserved; in addition, the greater part of the centrum is missing.

The vertebra PVL 4017-12 (Fig. 10) probably corresponds to the second or third dorsal. Preserved incomplete, it is lacking a great part of the centrum and the postzygapophysis. The neural spine is very wide and low; it joins the diapophysis by means of a strong supradiapophyseal lamina at an oblique angle. At the same time. the anterior horizontal lamina is comparatively well developed compared with the posterior dorsals, making an ample infradiapophyseal depression. In this element there is evidence of a postspinal lamina and, although it has not been preserved, a broken surface indicates the presence of a prespinal lamina.

The articular facet of the prezygapophysis is very broad, as normally occurs in the anterior dorsal vertebrae.

The neural arch, PVL 4017-44, is very well preserved; a wide spine can still be seen. The prezygapophyses are supported by only one infraprezygapophyseal column, but the articular surfaces are more reduced than in the dorsals previously described.

The diapophyses here are short and extremely thick with a flat, broad dorsal surface.

The parapophyses have articular facets with an "eye" outline with the pointed part directed dorsally. They are located on the same level as the prezygapophyses, but a little below and somewhat anterior to the diapophyses.

The neural spine has pre and post-spinal laminae and is not divided.

Rear Dorsal Vertebrae (Figs 13-16)

The greater part of the available dorsal vertebrae correspond to the posterior dorsal area and include the following pieces: PVL 4017-13-16/41*/42/43*/47/48/53*/58*/59/86*/135-138/185/215. (The group consists, in the greater part, of almost complete vertebrae, except in the case of the pieces marked with an asterisk which are fragmentary.)

Two groups of articulated vertebrae, each with three elements, have been recovered. These have permitted some understanding of the morphological variation, in accordance with the position they occupy within this area of the vertebral column.

The piece PVL 4017-137 (Fig. 16) is anteriorly placed (8th dorsal?) in one of the groups mentioned above. The centrum is constricted medially, with a reduced pleurocoel.

The neural arch is high and narrow, although a little wider in front below the parapophysis.

The prezygapophyses have not been preserved. The postzygapophyses are attached to the neural spine by suprapostzygapophyseal laminae, thickened at the posterior edge. They join the diapophysis through the posterior horizontal lamina. The articular facets of the postzygapophyses are oval; they tilt posterolaterally.

The diapophyses are short and project dorsolaterally, almost reaching the height of the neural spine apex. The diapophysis is linked to the prezygapophysis by the anterior horizontal lamina, and with the neural spine by a broad supradiapophyseal lamina.

The neural spine is also tilted posteriorly and is robust at the apex. On the other hand, its base is reenforced by robust laminae that link it to the diapophysis, the postzygapophysis and to the pre and post-spinal laminae.

This vertebra shows three well-delimited lateral fossa: two of them situated below the horizontal lamina and here named anterior and posterior infradiapophyseal fossa, since they are anterior and posterior to the infradiapophyseal lamina. The third depression is situated laterally with respect to the spine; bordered anteriorly by the supradiapophyseal lamina, posteriorly by the suprapostzygapophyseal and ventrally by the posterior horizontal lamina.

The vertebra PVL 4017-135 (Fig. 15) is the third in the articulated group discussed here and ought to correspond to the ninth or tenth dorsal. Its general characteristics coincide with the piece described above; however, it differs by having a short, thick centrum, with the neural spine positioned more vertically, and a posterior displacement of the parapophysis, which is located partly below the diapophysis. This arrangement causes some changes: the near obliteration of the anterior infradiapophyseal fossa and the noticeable development of two thick infraparapophyseal laminae that surround a small, but deep, triangular fossa. The lower part of the infradiapophyseal lamina joins the infraparapophyseal plate.

The dorsal edge of the diapophyses of this vertebra have an almost horizontal flat surface, which is observed in other vertebrae of the series.

Piece PVL 4017-42 belongs to the second group of three articulated dorsals. These are almost complete and probably correspond to the fifth, sixth and seventh dorsals. They belong to an individual of smaller size than those represented by the previously documented vertebrae in the quarry and are probably from a young adult. The centrum is relatively long, comparable with piece PVL 4017-137 of the other articulated series. The neural spine leans some 45 degrees with respect to the axis of the vertebra and is wider proximally in the series, becoming slender posteriorly.

Another piece, PVL 4017-138 belongs to a large adult and is probably a sixth dorsal, judging by the similarity of traits it possesses to the seventh included in the series with PVL 4017-42.

Sacrum

Of the three sacra recovered, the type specimen (PVL-4017. Figs. 17 and 18) and piece PVL 4017-93 are fused to both ilia. The third sacrum (PVL 4017-18) is incomplete.

The type specimen is made up of six fused vertebrae that form a group provided with convex articulations oriented anteriorly in the first vertebral sacrum, and posteriorly in the last.

The first vertebra is a recently incorporated dorsosacral. The centrum expands at both ends, and the neural arch is similar to that of the rear dorsals. It also has a lateral fossa. The base of the parapophysis is raised above the neural arch. The neural spine has not been preserved - neither parapophysis nor diapophysis.

The body of the second sacral has a posterior edge that is difficult to see. The parapophyses and diapophyses form a vertical lamina. The rib fused to these processes is placed as a vertical plate with a subcircular window in its proximal portion.

The centra of the third through the fifth sacral vertebrae are narrow, and edges between them cannot be seen. The prezygapophyses and the postzygapophyses are fused with the adjacent vertebrae. Although the neural spines have not been preserved, it can be seen that the bases of these are joined by a half partition, formed by the coalescence of the pre and post-spinal laminae of adjacent vertebrae. The diapophyses and parapophyses are fused with the ribs that project laterally like a lamina with two enlargements: one dorsal that continues to the transverse process, and the other ventral which corresponds to the parapophysis.

The rib of the third vertebra has a small subcircular window in the proximal portion and another, of greater diameter, adjacent to the ilium, which can be seen on the ribs of the fourth and fifth sacral vertebrae.

All the sacral ribs have a distal extension above and below by which they are fused among themselves and to the ilium. The lower distal extensions of the ribs of the last four sacral. vertebrae coalesce, close to the ilium, in the formation of the articular surface of the acetabulum. This process is similar to what is observed in other titanosaurids and also in *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977) from the Upper Cretaceous in Mongolia.

CAUDAL VERTEBRAE

The caudal vertebrae of *Saltasaurus loricatus* are, throughout the entire sequence low, similar in this respect to those of *Neuquensaurus*. Like the cervicals and dorsals, they possess a structure of large cells in the centrum of the anterior, middle, and at least part of the posterior centra.

Proximal and Second Caudals

The centrum is procoelous, short and relatively low and wide. The anterior articular surface is slightly concave and has an oval outline.

The neural arch leans some 35 degrees toward the back and its anterior surface is divided by a medial septum that, in the case of piece PVL 4017-19 (Figs. 19 and 20), is relatively thick. In rear view, the neural spine has a deep fossa, bordered laterally by the suprapostzygapophyseal laminae. Its articular facets are oval and oriented so that their large diameters converge medially. There they meet the small hyposphene.

The transverse process is noticeably elongate, similar to that of the last sacrum. The distal end twists, with the ventral edge projecting posteriorly to a greater degree than the dorsal edge. Anteriorly, a deep fossa occupies the upper portion of the transverse process. meanwhile, on the posterior side of two of the elements (PVL 4017-19 and 21) can be seen an elongated ridge for muscle or ligament insertion.

Anterior Caudal Vertebrae (3 to 6)

The collection of vertebrae corresponding to this portion of the tail is composed of the complete elements PVL 4017-22/24/25/26.

As in all the caudals of *Saltasaurus*, these are procoelous, relatively low and wide.

The centrum is short and wide with articular surfaces more strongly concave and convex than in the first and second caudal. Its ventral side has a smooth, wide concavity that gets deeper and narrower posteriorly in this section of the sequence.

The prezygapophyses are quite robust and very short in comparison with *Aeolosaurus* and cf. *Titanosaurus* of Brazil, which have large articular facets. In the case of vertebra PVL 4017-23 (Fig. 21) part of the hypantrum has been preserved.

The postzygapophyses, with large articular facets, descend from the neural spine by thick laminae whose external faces are rugose, for muscle or ligament insertion.

The wide neural spine leans somewhat posteriorly, with the anterior face divided by a prespinal lamina. Posteriorly, between the suprapostzygapophyseal laminae is found a deep fossa.

The transverse processes are reduced and are directed lateroventrally.

Middle Caudal Vertebrae (Figs 22 and 23)

The centrum is longer than that of the anterior caudals. The anterior and posterior articular surfaces are compressed dorsoventrally. The ventral side has a longitudinal groove much narrower than that seen in *Neuquensaurus* Powell (1986), the groove in *Saltasaurus* is bisected by a longitudinal ridge.

The long neural arch is situated over the anterior portion of the centrum. The prezygapophyses form short processes extending anteriorly, with articular facets reduced and somewhat inclined medially.

The posterior slant of the neural spine progressively increases toward the distal portion of the tail. The neural spine also displays prominent supraprezygapophyseal laminae.

The transverse processes are reduced and directed latero-ventrally.

Posterior Caudal Vertebrae and Haemal Arches (Figs. 24-27)

Ten elements of this section of the tail are available: PVL 4017-)2/38/39/140/141/191/ 207/217/219/220.

These vertebrae are long and low, expanded at each end. They are low owing to the reduction of the neural spine, which begins to be manifested at the sixteenth caudal, appearing more like a crest by the twentieth caudal.

The neural arch is low, occupying the anterior half of the centrum.

The prezygapophyses are formed by long cylindrical processes directed anteriorly, that do not show defined articular surfaces.

The postzygapophyses are fused and they support the neural spine ventrally.

APPENDICULAR SKELETON AND PECTORAL GIRDLE

Scapula (Figs. 28)

From the El Brete collection, a pair of juvenile scapulas (PVL 4017-104 and 105), left and right respectively, are available and also two right scapulas belonging to adults.

In general the scapula is similar to that of *Neuquensaurus australis* (Huene, 1929). It is, however, wider, with a greater angle between the axis of the scapular blade and the acromion.

The edges of the blade are sharp except for the proximal part of the anterodorsal edge where an extension, produced by a medial prominence, exists. This is the same type of extension that appears on *Neuquensaurus australis* (Huene, 1929).

The anterodorsal edge is less concave than in *Neuquensaurus australis* in the narrowest area of the blade. The posteroventral edge is not as straight as that illustrated by Huene (1929; plate 9:3a), rather, there is a concave contour throughout the blade - a trait determined by the distal narrowing of the scapular plate.

The thickest part of the scapular blade corresponds to the area of its greatest narrowing; in this area the lateral side is strongly convex.

The area of articulation with the coracoids is not clear; not one has been found that was articulated to the scapula. The scapular portion of the glenoid is oriented anteromedially.

Coracoids

Two left coracoids have been preserved: (PVL 4017-100and 101) and one right one (PVL 4017-103).

The coracoid has a roughly quadrangular outline and is provided with a robust articular surface for the humerus.

The anteromedial edge is straight and forms a 90 degree angle with the medial edge. Above the glenoid articulation is a thickening of the bone that continues as a longitudinal ridge that extends parallel to the anteromedial edge.

The coracoid foramen is clearly visible laterally since it is surrounded by a fossa oriented toward the anteromedial edge.

Sternal Plates (Fig. 30)

These are large, laminar bones, very similar to those referred to *Neuquensaurus australis* (Huene, 1929: plate 9).

Two right sternal plates are available (PVL 4017-109/110), in addition to one left sternal plate (PVL 4017-108) and one anterior extremity of the left sternal plate (PVL 4017-111).

For the description of these pieces, the orientation proposed by Huene (1929) has been followed here. This proposition agrees with observations by the author of a work on a juvenile model of *Mussaurus patagonicus*, Bonaparte and Vince (1979). Among these remains have been preserved a pair of partially articulated sternal plates, where the lateral and medial edges can be determined by inferring that the wider anterior extremity articulates with the coracoids, also preserved in this unpublished material.

The lateral edge is thick and rounded, with a markedly concave outline. All of the area close to this edge is relatively thick, whereas, toward the medial edge the density is considerably reduced.

The anterolateral border is thickened by the presence of an obtuse crest that extends 8 cm. along the ventral side from the anterior end of the bone toward the posterior.

The dorsal side is very smooth and does not show any definite details.

Humerus (Fig. 31)

The humerus is the appendicular element most commonly found in the El Brete quarry, represented by a left and right pair (PVL 4017-70/7 1) corresponding to one juvenile; a right and left pair (CNS-V 10023 and PVL 4017-69) of a mid-sized individual; and three right and left pairs, respectively (PVL 4017-62/63, PVL 4017-64/65 and PVL 4017-66/67) pertaining to large adults.

The humerus is a robust bone, relatively short, very wide and flattened in the proximal third. The distal end is found twisted some 35 degrees with respect to the proximal.

Because of the position of the articulations and the robust stature, it is assumed in this work that the position of the humerus of the living *Saltasaurus loricatus* was subvertical, with the proximal end a very little bit forward of the distal. Therefore, here we refer to that position upon saying posterior face (or dorsal) and anterior face (or ventral).

The proximal edge is sigmoidal, with the convexity located above the articular head and the internal tuberosity; the concavity is above the lateral process, where the lateral corner is elevated.

The lateral process is slender, thickening toward the lateral edge where it forms, anteriorly, the deltopectoral crest. This crest is relatively low with rounded edges. It extends obliquely from the supra-lateral corner to just above mid-shaft.. It follows an imaginary line that unites that corner with the medial condyle of the distal extremity. The well developed internal tuberosity is triangular in form.

The anterior concavity of the proximal end is very wide and well-delimited laterally by the deltopectoral crest, and proximally, by the thickening of the proximal edge. This concavity bears a transversely oriented ridge which corresponds to the insertion of the coracobrachialis muscle.

Some rugosities are evident on the posterior (dorsal) surface of the bone that indicate muscular insertions. A very prominent one is located above the lateral edge, in the portion of the bone that corresponds, on the anterior side, to the deltopectoral crest. Another rugosity is located at approximately mid-shaft and close to the external side, which we have not been able to interpret.

On the anterior surface can be clearly distinguished the distal articular surfaces, of which the medial is more developed in the anteroposterior sense, and the lateral transversely. Near mid-shaft, the radial condyle emerges prominently. It continues toward the distal end as an ridge, limited laterally by two longitudinal depressions.

The distal end of the bone is wide; its posterior face has a broad depression between two supracondylar crests, of which the medial is the more pronounced.

The entepicondyle and the ectepicondyle are little developed. Above the medial edge is a projection in the manner of a supra-ectepicondylar crest somewhat developed.

Among the collection of recovered humeri, variations can be noticed that are here interpreted as intraspecific. For example: the pair of humeri, pieces PVL 4017-69 and CNS-V 10023, differ from the rest of the material by having an area of insertion stronger and more rugose, and also for lacking a concave area situated medially with respect to the above-referred area of muscle insertion. The posterior depression is narrower and deeper, separating the crests that culminate in the articular condyles of the distal end.

Ulna (Fig. 32)

The ulna of *Saltasaurus loricatus* is very similar to that of *Neuquensaurus robustus* as described by Huene (1929); five elements have been recovered: PVL 4017-72/73/74 75.

One element is straight and very robust, triangular in its proximal end.

The medial face of the bone is wider. In the proximal half, this face is concave as much transversely as longitudinally. It joins the remaining faces at a sharp angle..

The anterolateral face is concave in the proximal section, losing that trait distally. In the distal half it shows a crest for muscular insertion of the pronator.

The distal articulation forms a rounded surface with a slight depression on the medial face.

Among the ulnas in the El Brete collection, two different sizes can be distinguished that correspond to large and medium adults.

Unfortunately, articulated elements of the fore limb of *Saltasaurus loricatus* have not been found. An examination of the various sizes in the collection available permits us to estimate the possible size relationships between the distinct elements of the fore limb.

In accordance with these estimations, the ulna would be seventy-four per cent the length of the humerus. It must be pointed out that this value, because of its subjectivity, ought not to be used as diagnostic data.

Radius (Figs. 33 and 34)

The radius of *Saltasaurus loricatus* is a long bone, whose anterior and posterior ends bear asymmetrical expansions that give it a sigmoidal outline.

Two right radii of large individuals (PVL 4017-76/15 1). the left radius of a middle-sized individual (PVL 401777). and the left radius of a juvenile (PVL 4017-18) have been preserved.

The anterolateral side is rather flat and superficially excavated on the proximal half. On the other hand, the ulnar side is strongly convex and is grooved by a lengthwise depression fashioned by two smooth ridges that cross the bone obliquely - from the anterolateral border toward the posterior-ventral side. The longer of these ridges, situated anteriorly, ends in a strong distal prominence on the ulnar surface.

The proximal articulation is a smoothly concave surface characterized by an anteromedial prominence.

In the smallest of the radii available, the sigmoidal outline is more accentuated than in the rest of the elements.

As has been pointed out in the description of the ulna, the lack of articulated material impedes the establishment, with precision, of the relative proportions of the radii. A probable estimate is a length equivalent to sixty-six per cent of the humerus - using as a basis the humerus PVL 4017-64 and the radius PVL 4017-76.

Metacarpals

The metacarpals are characterized as being proportionately short and robust when compared with those of *Antarctosaurus wichmannianus* and *Titanosaurus araukanicus* (Huene, 1929) n. comb. This same author described some metacarpal fragments that he assigned (with some doubt) to *Neuquensaurus* (= "*Titanosaurus*") *australis*, recognizing, however. that they could belong to *Titanosaurus* (= "*Laplatasaurus*"). The characteristics of the metacarpals of *Saltasaurus* support this last hypothesis.

The metacarpal interpreted here as III (PVL 4017-125) has a flat proximal articular surface, of triangular outline, while the distal is smoothly convex.

Metacarpal IV? (PVL 4017-128) is less robust than the one described above. Its proximal articular face is roughly rectangular, with a marked lateral projection on one of the anterior corners.

The distal articulation is also convex, but not as broad as in metacarpal III.

Other metacarpals have been recovered although it's not yet determined which of them correspond to the following numbers of the collection: PVL 4017-180/126/127.

The length of the metacarpals represents between 26.7 and 30.5 per cent of the length of the humerus, using as a basis humerus PVL 4017-83 and the available metacarpals.

APPENDICULAR SKELETON AND PELVIC GIRDLE

Ilium (Figs. 17 and 18)

The ilium of *Saltasaurus loricatus* is characterized by being low with a long preacetabular blade directed anteriorly and laterally, as occurs in other South American titanosaurs and, in addition to this family, also in *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977). The postacetabular process is short and has not been well preserved in any of the recovered elements.

The pubic peduncle is broad transversely to the axis of the sacrum, but much more narrow anteroposteriorly. The ischial peduncle is hardly manifested.

The greater part of the articular surface of the acetabulum is composed of the ilium and the lower distal expansions of the third to fifth sacral ribs. The outline of the iliac portion of the acetabulum appears like a parabola, with the point of inflection located near the union of the pubic peduncle with the ventral edge of the iliac blade.

The pieces PVL 4017-93 (left and right ilia fused to the sacrum) and PVL 4017-94 (left ilium fused to the distal end of the last sacral) are characterized by having a small expansion in the anterior end of the iliac blade. This arrangement does not occur in the holotype PVL 4017-92 (left and right ilia fused to the sacrum). In this last case, the preacetabular portion of the blade is a little broader and the anterior edges are rounded.

Pubis (Fig. 35)

The elements recovered correspond to a right pubis (PVL 4017-95); an incomplete right pubis which is lacking the distal half (PVL 4017-96); and two pubes, right and left respectively, incomplete because of the lack of proximal portions (PVL 4017-97/98).

The pubis is a relatively slender laminar bone with the typical concavity above the dorsal face of the proximal end. The proximal end has an articular surface that is very extended mediolaterally. It is broader in the area next to the acetabulum and the pubic foramen, and becomes thinner toward the medial edge - as occurs in the entire bone.

The iliac articular process rises well above the acetabular portion of the pubis and the ischial process.

The pubic foramen is small and closed. It is located close to the angle that joins the articular surface for the ischium, with the pubic portion of the acetabulum.

The pubic blade is broad and flattened, and its lateral edge, which constitutes the thickest portion, is concave. The medial edge is very thin and generally not well-preserved. The pubic blade lacks the distal thickening observed in other sauropods.

The right pubis (PVL 4017-95) has an interesting variation not seen in the rest of the elements. This consists of a robust longitudinal ridge that., as a means of reinforcement, covers the ventral face of the pubis in a manner similar to that described for "*Laplatasaurus*" (sensu Powell, 1979). It is supposed that this characteristic can be an individual variation, or related to the sex of the individual. However, the possibility cannot be discarded that more detailed studies or the gathering of additional material might prove the existence of another form of sauropod in this quarry.

Ischium (Fig. 36)

Knowledge of the ischium of *Saltasaurus loricatus* is acquired from the study of two pieces from the right side (PVL 4017-99/154), and is very similar to the description of *Neuquensaurus australis* (Huene, 1929). It's a relatively short, laminar bone, with a deep dorsal cavity that separates the pubic pedicle from the ilium, and also forms the ischial portion of the acetabulum.

The dorsal face of the ischium is somewhat concave in the area adjacent to the articulation with the pubis.

The proximal portion of this bone lies transversely to the axis of the pelvis, while the distal part becomes parallel to the sagittal plane.

The posterolateral border is rounded and thick, and exhibits an outline strongly concave posteriorly. Above the anterior face, and situated close to and parallel with that edge, is observed a longitudinal ridge for muscular insertion.

A definitive characteristic of this bone is the fact that the proximal portion (iliac pedicle, pubic pedicle and acetabular area) constitutes more than half of its length.

Although the distal extremity of the ischial blade has not been well-preserved, it can be inferred that it was not thick.

In agreement with what has been able to be interpreted (Bonaparte and Powell, 1980), this element would be oriented with its major axis disposed transversely to the axis of the body.

Femur (Fig. 37)

The femur is represented by pieces PVL 4017-79/80/82/83 and CNS-V 10.024.

These are long bones, rather straight and somewhat flattened anteroposteriorly, especially in their proximal half.

At approximately one quarter of the length from the dorsal end, a comparatively thin, lateral projection of the greater trochanter is seen.

Above the posterior face, the greater trochanter extends ventrally in an ridge present only in the upper third of the bone.

Anteriorly, some femora present a long wrinkle over the medial edge of their proximal end.

The femur of *Saltasaurus loricatus* does not have the medial articular surface, which is commonly present in the Jurassic forms and in titanosaurs like *Argyrosaurus* and *Neuquensaurus*.

On the distal extremity, the medial condyle is the most developed. The intercondylar groove is not very pronounced.

Tibia (Figs. 38 and 39)

Among the tibia found in El Brete, two superficially distinct types can be distinguished: one, represented by the element PVL 4017-84, is characterized by possessing markedly robust distal and proximal ends. The remaining ones (PVL 4017-46/65/88) are more slender, including PVL 4017-87, which corresponds to a juvenile.

The head of the tibia has a rather flat, articular surface, somewhat depressed in the center. Anteriorly the cnemial crest stands out as an outwardly curved, thick triangular blade.

In agreement with the size relationship observed between the femur (PVL 4017-83), the tibia (4017-84), and the fibula (PVL 4017-85) that were found together, and surely belong to one individual, the tibia would be about 54.4 percent of the length of the femur.

Fibula (Fig. 40)

The fibula of *Saltasaurus loricatus* is long, of sigmoidal outline in lateral view.

The entire length of the lateral surface of the fibula is convex, a trait that is accentuated in the distal half of the bone. A well-developed tuberosity extends obliquely anteroproximally to posteriodistally. The ridge on this tuberosity would correspond to the area of insertion of the iliofibularis muscle, interpreted by Huene (1929a) as corresponding to the peroneal muscle. This insertion differs noticeably from that of *Titanosaurus araukanicus* (Huene) and *Titanosaurus indicus* Lydekker (Swinton, 1947), resembling the type present in *Neuquensaurus australis*.

The medial side of the proximal end is rather flattened, becoming markedly concave in the distal end.

In agreement with the figures determined above for the group of associated elements, the fibula represents approximately 59.8 percent of the length of the femur.

Metatarsals

The metatarsals are especially short and robust. Metatarsal I (PVL 4017-131/122) is very short; its proximal articular surface is roughly triangular, with the base above and the sharper apex below. Upon the lateral face is seen a facet for the articulation with metatarsal II.

Metatarsal V (PVL 4017-121) is flattened and more robust than the one illustrated for *Neuquensaurus australis*.

Metatarsal II (PVL 4017-124) is very similar to metatarsal I, differing because the proximal articular surface is rather oval-shaped.

Other elements have been identified as PVL 4017-123/133/182, although their exact position in the pes has not been determined.

Bony armor

One of the most definitive characteristics documented in *Saltasaurus loricatus* is the possession of dermal armor, recognized for the first time among sauropods (Bonaparte and Powell, 1980; and Powell, 1980).

This armor is composed of bony plates of approximately 12 cm. maximum diameter that would probably support spikes. Although there is no direct evidence, it is possible that these plates were arranged in one or two rows over the trunk and anterior portion of the tail (fig 44); however, the possibility of other arrangements ought not to be discarded. They would have, in addition, intradermal ossicles like the mylodontine mammals, of somewhat less than 1 cm. diameter, that would protect a great part of the posterior portion of the body.

Plates (Figs. 41-43)

Six of the plates that have been recovered (PVL 4017-112/113/114/115/116/134) have a more or less oval outline, with irregular margins. The dorsal surface is roughly conical and is ornamented with numerous wrinkles made by fossae of variable size.

A "ring" of small tuberosities is located next to the margin of the plate. The ventral surface is more or less flat with irregular furrows disposed close to and approximately perpendicular to the edge. In some plates this surface is crossed by a longitudinal crest oriented along the greatest diameter. On others that crest is not present, and the ventral surface is concave.

On plate PVL 4017-115 (Fig. 42) subspherical ossicles can be seen that are fused to the edge of the plate.

INTRADERMAL OSSICLES

Four groups of associated ossicles in their original position have been retrieved: PVL 4017117/118/119/120 and also numerous others, isolated or in groups.

These small, bony elements are subspherical and do not have a regular morphology. The diameter of these elements varies about 7 mm.

They lie side by side, almost touching each other, forming a cape arranged in a mosaic of irregular design, with a density of about twenty-seven elements for each 10 square cm.

Only in the group of ossicles numbered PVL 4017-119 is seen an element larger than the rest which, in general, are of uniform size.

COMPARISON

Neuquensaurus (= *Titanosaurus sensu* Huene 1929a) is the type that presents the greatest affinity with *Saltasaurus*. Both are represented by medium to small-sized forms (in the context of sauropods), showing a notable similarity in morphology and proportion of the limbs. In addition, they share the particularity of possessing caudal vertebrae having a low profile, with a structure of large cells at least in parts of the sequence, although developed to differing degrees.

A series of differences exists, however, that clearly justifies the recognition of a different genus for the forms in question. The preacetabular processes of the iliac blade are very long and more expanded in *Saltasaurus*. The postacetabular processes and a defined ischial peduncle are lacking, which are observed in the material assigned by Huene (1929) to *Neuquensaurus* (= "*Titanosaurus" robustus*, Huene 1929; plate 19: 1).

In the axial skeleton it is difficult to make comparisons because of the poor preservation of the dorsals and cervicals of *Neuquensaurus*. The caudal series is very similar in both types, except the proximal caudal which is biconvex in *Neuquensaurus* and procoelous in *Saltasaurus*. The ventral depression is very broad in *Neuquensaurus* and normally does not present the medial ridge seen in *Saltasaurus*. The process of "cellulation" of the caudal vertebral centra is more advanced in *Saltasaurus*.

The scapula of *Saltasaurus loricatus* is wider and the blade is joined to the proximal portion, producing a greater angle with respect to the acromion.

Antarctosaurus wichmannianus shows clear differences from *Saltasaurus loricatus*, not only in size and general proportions, but also in the morphology of the cranium and the postcranial skeleton.

The fragments of cranium assigned to *Antarctosaurus wichmannianus* by Huene (1929) show, equally with the *Salt*. species, the long, recurved, definitive paroccipital process. These appear to constitute a derived trait, thus far seen exclusively in the family Titanosauridae, among the sauropods and even known saurischians.

Among the more important differences in both craniums must be pointed out the morphology of the basal tuberosities of the basioccipital, the basipterygoid process, the supratemporal fossae and the basipresphenoid complex .

In the postcranial skeleton, *Antarctosaurus wichmannianus* is distinguished from *Saltasaurus loricatus* by having a relatively narrow scapular blade and a broader proximal region. The metacarpals are longer and the femur shows an articular facet situated medially with respect to the femoral head - not observed in *Saltasaurus*.

Titanosaurus araukanicus differs basically in the gracile nature that characterizes its long bones, the moderate size of its adult forms and the morphology of the lateral tuberosity of the fibula which has an additional prominence oriented distally. The scapula also is different in that it does not show the medial process next to the anterosuperior edge for muscular insertion, a characteristic so common in *Neuquensaurus* and *Saltasaurus*, and also seen in *Aeolosaurus* Powell (1987). The metacarpals are noticeably longer and more gracile than in the form from El

Brete.

Except for the robustness that characterizes the humerus, *Argyrosaurus* differs notably in the size of individual adults and in the proportions of the dorsal and caudal vertebrae. There is also a difference in the design of the laminae that reinforce the edges of the neural arch.

The vertebral structure of the dorsal region shows significant differences from *Epachthosaurus sciuttoi*, especially with respect to the proportions of the vertebra, the relative size of the pleurocoels and the characteristics of the prespinal lamina.

MORPHOLOGICAL AND SYSTEMATIC CONSIDERATIONS

Saltasaurus loricatus is here proposed as the type genus of the subfamily Saltasaurinae, defined on the basis of cranial and postcranial characteristics.

This species shows a group of traits derived as much in the cranium as in the axial skeleton, that would indicate an advanced form of titanosaur, a fact that coincides with the late appearance of the subfamily in the Upper Senonian in South America.

Currently, this species constitutes one of the best-known forms of dinosaurs of the family Titanosauridae. It is represented by a great part of the postcranial skeleton, and it offers a comprehensive view of the anatomy of the integral parts of this grouping that, for lack of evidence, has not been able to be adequately considered previously.

There exists a series of derived characteristics revealed as much in the cranium as in the postcranium, that ought to be emphasized:

1. The long and recurved paroccipitals, a trait shared with *Antarctosaurus wichmannianus*, are absent in sauropods and saurischians. This trait is infrequent in the archosaurs, yet is present in similar form in the ornithischians of the family Hadrosauridae. It is considered derived and a synapomorphy for the titanosaurs.

2. The basal tuberosities of the basioccipital, flat and fused together sagittally, are typical of this genus and are considered autapomorphies of the subfamily Saltasaurinae.

3. The fenestra ovalis, open toward the conduit through which emerge nerves IX-11, has not been observed in sauropods and is interpreted as being an autapomorphy of the saltasaurids.

4. The presence of large cells in the centra of sacral and presacral vertebrae constitutes a trait characteristic of the titanosaurs (Powell, 1986). In the majority of the known sauropods, the centra are lightened by the presence of large pleurocoels in the presacral vertebrae, and a spongy tissue is normal or generalized throughout the vertebral sequence. The large cells have been referred to only in *Ornithopsis* and *Tornieria* (Huene, 1929).

   The extension of this attribute to the caudal vertebrae is seen particularly in *Neuquensaurus australis* (Powell, 1986), reaching a more advanced degree in *Saltasaurus loricatus*, in which even the distal caudal centra are implicated. The presence of cells, instead of bony tissue generalized in the caudal vertebrae, is considered a synapomorphy of the family.

5. The general robustness observed in the appendicular bones is manifested in the axial skeleton, with the shortening of the neck by a reduction in the length and increase in the

width of the cervical vertebrae. In the tail the strength is seen in the widening and depression of the vertebral centra, accentuated in the first elements of the caudal series by the length of the transverse processes.

The differences observed in some of the pieces from El Brete are interpreted provisionally as individual variations or related to the sex of the animal, however, it is probable that new discoveries will modify this position.

MORPHOFUNCTIONAL CONSIDERATIONS

Saltasaurus loricatus is a short sauropod, of robust limbs and a barrel shaped trunk, accentuated by the width of the pelvis. This description suggests a hippopotamoid form, of relatively long neck, that probably frequented bodies of water such as lakes and rivers. It ought to be pointed out that this type of similar adaptation is unusual in the Subfamily Titanosaurinae, characterized by possessing long, slender appendicular bones. *Aeolosaurus rionegrinus* (Powell, 1989) is a titanosaur of robust limbs.

The dermal armor is one of the more definitive aspects of this species. The rounded intradermal ossicles, arranged in a close fitting pattern, would cover a large part of the body. Bony plates supporting tough spines would be included. The armor of intradermal ossicles would conform to a passive defense system similar to that which the mylodonts (hairy anteaters) flaunted.

The evidence recognized until now indicates that the saltasaurids were relatively small forms among the sauropods. In addition, the proportions and characteristics of the appendicular bones suggest slow moving animals.

Taking into account those qualities, the possession of dermal armor would have protected them in part from depredation during the reproductive adult age. The juveniles would probably have been protected by a "group" behavior, as seen in forms of herbivorous mammals; a fact that would be endorsed for sauropods in general, according to ichnological evidence.

STRATIGRAPHIC CONSIDERATIONS

Saltasaurus loricatus is documented in the Lecho Formation south of the province of Salta. The close similarities between this species and *Neuquensaurus australis* (Powell, 1986), that is present in the Colorado River Formation (Campanian?) and the Lower Member of the Allen Formation (Lower Maastrichtian) of the Neuquen Basin, permits the inference of a Campanian- Maastrichtian age for the Lecho Formation. Currently, no data are known that indicate the presence of the subfamily in levels more ancient in South America.

The Lecho Formation lies in El Brete below the Yacoraite Formation, whose equivalent in Bolivia is the El Molino Formation which has yielded the remains of fish of Maastrichtian age (De Muizón *et al.*, 1983). Therefore, the Lecho Formation ought to be restricted to the lower part of the Maastrichtian or, with less probability, the Late Campanian, taking into account the Campanian age the of Las Curtiembres determined with radiometric methods (Reyes *et al.*, 1976, and Valencio *et al.*, 1976) - and the age suggested by Bonaparte and Bossi (1967) and Powell (1980).

This interpretation is consistent with the correlation of the Yacoraite Formation with the Allen and Jaquel Formation suggested by Powell (1986), whose deposition can have been related to the same transgressive episodes.

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