A NEW AND HUGE TITANOSAUR SAUROPOD FROM THE RÍO LIMAY FORMATION (ALBIAN-CENOMANIAN) OF NEUQUÉN PROVINCE, ARGENTINA*

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Translated by Matthew C. Lamanna
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January-April 2001

ORIGINAL ENGLISH ABSTRACT: *A NEW AND HUGE TITANOSAUR SAUROPOD FROM RIO LIMAY FORMATION (ALBIAN-CENOMANIAN) OF NEUQUEN PROVINCE, ARGENTINA. Argentinosaurus huinculensis* gen. et sp. nov. is a giant titanosaur sauropod characterized by dorsal vertebrae with large hyposphene-hypantrum bearing extra articulations; bodies of sacral vertebrae 2-5 very reduced; hollow, cylindrical ribs; slender tibia 155 cm long. The family Andesauridae is proposed as a new rank to include *Andesaurus*, *Argentinosaurus*, and *Epachthosaurus* considering that the presence of hyposphene-hypantrum is a character not recorded in the Titanosauridae sensu Powell (1986). The systematics of the titanosaurs is briefly discussed and the new taxon Titanosauria is proposed to include the families Andesauridae and Titanosauridae.

INTRODUCTION

From the end of the last century when Lydekker (1893) reported the forelimb of *Argyrosaurus superbus* the existence of gigantic sauropods in Patagonia was recognized. Later, Huene (1929), communicated another sauropod of great size, *Antarctosaurus giganteus* coming from the Province of Neuquén, considered as the Cretaceous sauropod of largest size (Van Valen, 1969).

The discovery that is communicated in this work comes from the Huincul Member of the Río Limay Formation (Province of Neuquén), characterized by fluvial deposits of medium energy, with abundant fossilized trunks in distinct localities of its outcrops. These levels seem to represent the ecological optimum in the region of the Neuquén Basin for the development of giant dinosaurs.

The new materials that are presented confirm the existence of giant sauropods in the Cretaceous of Patagonia, but in this opportunity with osseous remains that allow us to come a little closer to their systematic interpretation and to evaluate some bony adaptations resultant from this gigantism. The study of these giant sauropods reveals that, apart from the derived osseous characters for the sustaining biomechanic function, other very specialized biological aspects should exist, as for example in the sanguine circulation, in the nervous and digestive systems, and especially in the behavioral aspects of individuals that for their long life, inferred by the great size that they reached, they should overcome very diverse situations.

The largest sauropods in North America and Africa were characteristic of the latest times of the Jurassic (Janensch, 1914; Jensen, 1985; Paul, 1988), meanwhile in our

continent the gigantism of the sauropods would have been developed between the Aptian (Rayoso Formation) and the Upper Cretaceous, Coniacian (Río Neuquén Formation). These manifestations of extreme gigantism happened, according to the fossil record, at different geologic times and in different sauropod clades, for reasons that we do not yet know.

The material that is described and discussed briefly in this work is useful for investigating, in the future, some biomechanic, physiologic, and behavioral problems of these gigantic sauropods. For the time being we limit ourselves to consider some aspects of the systematics of the titanosaurs, starting from the material that we communicate, and of diverse discoveries and recent studies (Powell, 1986, 1987a, 1987b, 1990; Calvo and Bonaparte, 1991) that have enriched the available information on them.

The sauropod that is described was found thanks to the denunciation of Mr. Guillermo Heredia, of the farm "Las Overas" of Plaza Huincul. In that moment, personnel of the Museo "Carmen Funes" extracted a tibia that was deposited in the exhibition room of the mentioned Museum. Some time later, in the summer of 1989, a commission of the Museo Argentino de Ciencias Naturales of Buenos Aires, directed by one of the authors (J. F. B.) carried out the extraction of the fossil material, as part of the field work of an investigation project financed by the National Geographic Society. These materials were communicated in the VI Jornadas Argentinas de Paleontología de Vertebrados (Bonaparte, 1989), and they are deposited in the Colleccíon de Paleontología de Vertebrados in the Museo Municipal "Carmen Funes" of Plaza Huincul, Province of Neuquén, with the acronym PVPH-1.

SYSTEMATICS

SAURISCHIA Seeley 1888
SAUROPODOMORPHA Huene 1932
SAUROPODA Marsh 1878
TITANOSAURIA nov.

DIAGNOSIS: Sauropods with small pleurocoels located in the anterior sector of an ovoid depression, anteroposteriorly lengthened, located in the upper half and middle-anterior of the vertebral body; lateral face of the inferior half of the neural arch with two or more well defined, deep and angular depressions.

Family ANDESAURIDAE (Calvo and Bonaparte, 1991)
New rank

DIAGNOSIS: Titanosaurs that possess the following associated characters: small pleurocoels located in the anterior region of an ovoid pleurocoelic depression; two or three deep triangular depressions in the lateral face of the neural arch; neural arch and neural spine of the dorsal vertebrae more high than in Titanosauridae; very developed hyposphene-hypantrum, in some genera with extra articular sides; middle and distal caudal vertebrae amphiplatyan with short prezygapophysial processes.

Argentinosaurus gen. nov.

ORIGIN OF NAME: *Argentino*, coming from Argentina; *saurus*, lizard.

TYPE SPECIES: *Argentinosaurus huinculensis* sp. nov.

KNOWN DISTRIBUTION: Huincul Member, Río Limay Formation, Albian-Cenomanian of the Province of Neuquén, Argentina.

DIAGNOSIS: Titanosaurs of great size with the following associated characters: opisthocoelous dorsal vertebrae provided with very developed hyposphene-hypantra, with extra articulations between them. Anterior dorsals with transversely wide and anteroposteriorly planar neural spines, endowed with robust prespinal laminae. Middle and posterior dorsals with low and wide vertebral bodies, with the ventral face almost planar, and with pleurocoels located in the anterior half of the body. Sacral vertebral bodies 2 to 5 very reduced. Dorsal ribs of tubular, cylindrical, and hollow structure. Bony macrocells in the sacrum and presacral vertebrae. Slender tibia with short cnemial crest.

Argentinosaurus huinculensis sp. nov.
Figs. 2 to 8

ORIGIN OF NAME: *huinculensis*, referring to Plaza Huincul, town where the holotype was found.

HOLOTYPE: PVPH-1, composed of three anterior dorsal vertebrae and three posterior dorsals, the most anterior dorsals without the vertebral body and the remaining ones incomplete; ventral sector of the sacrum including the vertebral bodies 1 to 5, without the last sacral vertebra, with most of the sacral ribs of the right side; great part of a fragmented dorsal rib, and the right tibia with the external face weathered.

STRATIGRAPHIC AND GEOGRAPHIC PROVENANCE: Río Limay Formation, Huincul Member, Albian-Cenomanian; about 8 km to the east of the city of Plaza Huincul, Province of Neuquén, Argentina (figure 1).

DIAGNOSIS: The same as for the genus.

ABBREVIATIONS: MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; PVPH, Paleontologia de Vertebrados, Museo "Carmen Funes", Plaza Huincul, Province of Neuquén, Argentina.

DESCRIPTION: **First? dorsal vertebra**, (Fig. 2). This vertebra possibly corresponds to the first dorsal. The entirety of the neural arch united to the superior part of the vertebral body has been conserved. The rest of the centrum has been eroded. The neural arch is very short anteroposteriorly, measuring 41 cm between the most anterior border of the prezygapophyses and the most posterior of the postzygapophyses.

In anterior view (Fig. 2A) the neural arch possesses the diapophysis projected horizontally, forming an angle of 90^0 with respect to the neural spine, reaching a maximum width of 129 cm.

The neural spine is proportionally short, united to the diapophysis by the supradiapophyseal lamina. In the axial plane of the spine a prespinal edge is observed, thick from the dorsal extreme until approximately the half of the spine where it forks in a

ventrolateral direction toward each of the prezygapophyses. Under this bifurcation a thinner prespinal lamina is observed approximately at level of the diapophyses.

The parapophyses are well separated from the diapophyses and located under them. The distance between the external borders of the parapophyses is 77 cm.

Below the prezygapophyses the hypantrum is projected ventrally, forming a plane inclined below and outward that is supported on the wide structure, very derived, present in the hyposphene.

The posterior view of this vertebra (Fig. 2B) is incomplete, although the more well complete postzygapophyses and the very divergent continuation of the lateral borders of the hyposphene are observed. Between the conserved portion of the hyposphene and the lateral projection that culminates in the diapophyses, a wide concave region exists.

In lateral view (Fig. 2C) it is appreciated that the neural spine is relatively laminar, except for the prespinal edge that is more marked in the dorsal sector. To the height of the prezygapophyses, a wide fossa lengthened dorsoventrally and of little anteroposterior expression is exposed laterally. The diapophyses present a posterior dorsal crest, as long as they are thick ventrally, of concave form, with an anterior and another posterior lamina.

The total height of this vertebra between the dorsal extreme of the spine and the ventral border (reconstructed) of the vertebral body, is 159 cm considering that it had a similar vertebral centrum to that of the other preserved dorsal vertebrae.

Second? dorsal vertebra, (Fig. 3). This dorsal vertebra has conserved a great part of the neural arch and of the vertebral body. The whole anterior sector of the vertebra is affected by weathering lacking the prezygapohyses, parapophyses, part of the diapophyses and the anterior border of the vertebral body.

The left transverse process is lacking, while most of the right diapophysis has been conserved. Approximately the basal third of the neural spine has been conserved. The vertebra as is conserved measures 115 cm in height. It is probable that this vertebra corresponds to the second dorsal, since the morphology and disposition of the diapophyses are similar to the vertebra described. In both the diapophyses unite perpendicularly to the neural arch, they are wide dorsoventrally and narrow in anteroposterior sense.

The neural spine is transversely wide and anteroposteriorly compressed, constituting a bony sheet of scant centimeters of thickness reinforced by a thick prespinal lamina, poorly conserved. The conserved prezygapophysis, of the left side, presents similar inclination and width to those observed in the rest of the available vertebrae.

In posterior view (Fig. 3A) the robust postzygapophyses are observed with wide articular facets oriented ventrolaterally. The hyposphene is projected down and out, with its ventral continuations bordering the space of the neural canal. These continuations are stronger in their inferior half where they form a surface for the extra articulation with the hypantrum. Lateral and anteriorly to the hyposphene a fenestra is observed that communicates with the interior of the vertebra. In the sector located over and ahead of the postzygapophyses another similar pneumatic cavity is observed.

In lateral view (Fig. 3B) it is observed that the thick infradiapophyseal lamina forks slightly before its union with the vertebral body.

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The posterior face of the vertebral body shows a marked opisthocoelia, and it measures 47 cm by 60 cm wide. In lateral view the pleurocoel is appreciated defined by a dorsal bony border and another ventral, and is located in the anterior sector of the vertebral body.

Middle or anterior dorsal vertebra (Fig. 4†). The complete body and part of the neural arch of this vertebra are conserved, except the dorsal portion of the spine. It is differentiated from the first? dorsal in that the basal region of the spine presents a wide concave depression anteriorly, deep, that surpassses in 13 cm the posterior border of the prezygapophyses, and in that the neural spine would be projected more vertically. Vestiges of the prespinal lamina are not observed in the preserved sector of the spine.

In anterior view (Fig. 4A) the prezygapophyses present certain topographical continuity with the transverse processes; the hypantrum, very exposed in this vertebra, is it sensibly more large that in the first? dorsal. In their ventrolateral extreme the extra articulation is observed for the hyposphene. The parapophysis is more projected forward.

The vertebral body is opisthocoelous, 49 cm in length, with the anterior horizontal diameter of 48 cm and the vertical of 40 cm, indicating that the same is more low and less wide that in the vertebra described previously, a character that is accentuated in the posterior dorsals. The posterior face of the body shows a wide, but relatively thin lateral edge. The depression of the pleurocoel is wide and deep, and is located in the anterior half of the body.

Posterior dorsal vertebrae (Fig. 5). The posterior dorsal vertebra (Fig. 5A) possesses the complete vertebral body, and most of the neural arch, although only the base of the neural spine. The body measures 50 cm long, 39 cm high, 46 cm wide in the anterior part, and approximately 60 cm wide in the posterior face, being characterized to be more wide than high. The pleurocoel is deep, located more dorsally than in the preceding vertebra described. The right lateral view of the neural arch shows morphological details of interest. Parapophyses and diapophyses exhibit a strong structure, united dorsally by the diapoparapophyseal lamina. The diapophysis possesses a strong infradiapophyseal lamina, as well as the parapophysis possesses two ventral laminae that form an infradiapophyseal cavity. Between the parapophysis and the diapophysis exists a wide depression, deep, that is exposed laterally. From behind of the base of the infradiapophyseal lamina, is observed part of the ventrolateral projection of the hyposphene that in this species is very developed, representing one of the most notable derived characters that distinguishes it.

In anterior view, the prezygapophysis of the right side is very well preserved. Its articular side measures 27 cm in transverse sense and 14 cm in axial sense, and is inclined down in an axial direction. The wide articulation of the hypantrum extends ventral and laterally, well defined anteroposteriorly.

The two dorsal vertebrae united to each other (Fig. 5B) we interpret as posterior dorsals, partly for the smaller size of the parapophysis and also to have been maintained united, supposedly by a process of fusion among the vertebral bodies that would link them to the sacrum.

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†In the original Spanish version, the reader is referred to Fig. 5.

Both vertebrae are eroded in the left lateral half of the neural arch, and the neural spines have not been preserved. The vertebral bodies are almost complete, and there are good details of the anterior and right lateral view of the neural arches. The two united centra measure 90 cm in axial longitude, and 57 cm in transverse maximum width in the place of union between both. The height of these bodies is 41 cm in the anterior face and 51 cm in the posterior face. The pleurocoels are very similar to those already described.

The proportions of these bodies show that they are very wide and low, with a relatively flat ventral surface. It is probable that these features represent another derived character of this species, possibly related with the great size that it developed.

In the neural arch the diapophyses and parapophyses are projected more dorsally than in the anterior dorsal vertebrae. In lateral view the neural arch shows some typical features of the Titanosauria, such as the deep depression of angular base that defines the infradiapophyseal and infraparapophyseal laminae when uniting, as well as the minor triangular depressions located below the mentioned laminae. In this view the union of the articular processes, of lateral position, of the hyposphene and of the hypantrum is clearly observed, this last superimposed to the anterior.

Hyposphene and hypantrum (Fig. 6B). The most excellent characters of the dorsal vertebrae of *Argentinosaurus huinculensis* are in the morphology and development of these structures, that are shown schematically in figure 6B and partially in figures 3A and 4A.

The hyposphene is a very robust structure that would have been developed starting from a strong lateral and ventral expansion of the typical hyposphene present in diverse sauropods, for example *Patagosaurus* (Bonaparte, 1986), represented schematically in figure 6A, and that is not present in *Titanosaurus* and other Titanosauridae sensu Powell (1986) that are shown in figure 6C. Apart from the adaptive novelty of their great expansion, is developed an accessory articulation in the lateroventral region of the hyposphene (projected dorsally) and of the hypantrum (projected ventrally).

The hypantrum is expanded lateral and ventrally from the interzygapophyseal region where it measures 5 cm of width, until reaching 25 cm of width in the 3rd ? dorsal, with an anteroposterior expression of 12 cm. The extra articular facet of the hypantrum is projected ventrally. It seems undoubtedly the hypertrophy of the combined hyposphene-hypantrum is related with the development of giant sizes, achieving in this way a connection more solid, although not rigid, among the vertebrae.

Sacrum (Fig. 7). A great part of the ventral face of the sacrum has been conserved with some fused sacral ribs. The first sacral vertebra is incomplete and it is naturally larger than the remaining four vertebrae to which it is fused. The sacral vertebrae, 2, 3, and 4 that are fused between them are, each one of them, approximately half of the size of the 1st sacral. The ventral face of the vertebral bodies is slightly convex in transverse sense, especially in the second sacral vertebra.

The second sacral rib is the most large of the four preserved, (the first is incomplete). They are slightly curved down, with the distal articulation projected about 45^{0} down. This region of fixation with the ilium forms a concave surface, transversely narrower behind than forward, and with a sector more depressed to the height of the 4th

rib that could correspond to the internal sector of the acetabular region, in the place where the sacrum participated.

The preservation of the sacrum suggests that it lacks the last vertebra, and that the number of sacrals was six. The total length of the five preserved sacral vertebrae is 120 cm; the maximum width between the extremes of the sacral ribs is 123 cm; and the minimum width in the acetabular region is 106 cm. The bony tissue of the sacrum presents macrocells of great size (5 cm diameter), relatively larger than those observed in other sauropods, and separated by very thin bony laminae.

Ribs. An incomplete rib has been conserved possibly of the left side. The proximal end possesses the tuberculum and the capitulum united by a thin bony lamina, that determines the presence of a wide depression in the anterior face of the piece. The distal end of the proximal portion is of subcylindrical section. The fracture exposed there allows one to observe that the internal morphology is extremely pneumatic, with a relatively thin external wall. The total length of the fragment from the proximal end is of 87 cm; the maximum width in the proximal end is of 31 cm and in the distal end 9 cm. The rib fragment presents a light curvature inward and forward, with the capitulum strongly projected dorsally and medially. The distal fragments of available ribs indicate a reduction of the transverse diameter in the distal ends, for what we interpret that the proximal half of the ribs should be subcylindrical and the distal half mostly planar. The hollow condition of the ribs is even observed in the distal sectors.

Tibia (Fig. 8). The only available bone of the extremities is a right tibia, with most of the lateral face eroded. The medial face is relatively straight, flat, with a light anterior distal expansion and a moderate expansion in the superior third for the development of the cnemial crest, and for a posterior projection of the articular region with the femur. The cnemial crest is proportionally modest. Between it and the proximal internal region a shallow furrow exists. The proximal and distal articular regions of this piece do not offer better morphological details. Its total length, of 155 cm has not been registered in other titanosaurs. Based on the proportions between tibia and existing femur in the few well-known titanosaurs with those bones associated, for example *Saltasaurus*, *Argyrosaurus*, and *Aeolosaurus*, and having present the proportions of *Patagosaurus*, we interpret that the femur of *Argentinosaurus huinculensis* should not measure less than 240 cm.

COMPARISONS

In this work we interpret that the diversity of titanosaur sauropods contained in the families Andesauridae nov. and Titanosauridae Lydekker 1893, should join in a more inclusive taxonomic entity, for which we propose the Titanosauria, that is diagnosed above starting from and finishing with associated characters.

Argentinosaurus huinculensis is identified basically with Titanosauria, by the presence of diverse characters whose association is characteristic of this clade, and that have in part been already been pointed out and illustrated by Powell (1986): a) opisthocoelous dorsal vertebrae with relatively small, elliptic pleurocoels, located in the middle and anterior sector of the vertebral body, in a wide pleurocoelic depression of

oval form, more wide in the anterior sector than in the posterior; b) presence of very clear, angular fossae, in the lateral face of the neural arch of the dorsal vertebrae; c) neural spines of the anterior dorsals rather flat, wide transversely, and without vestiges of bifurcation; d) presence of large bony cells in the entirety of the spongy tissue of the dorsal and sacral vertebrae.

The presence of the very developed hyposphene and hypantrum in *Argentinosaurus huinculensis* differentiate it from the diverse genera of Titanosauridae in which complete dorsal vertebrae are known, such as *Saltasaurus* (Bonaparte and Powell, 1980), *Titanosaurus* sp. of the Baurú Group, Brazil (Powell, 1987), *Neuquensaurus* (Powell, 1986), and *Argyrosaurus* (Powell, 1986).

COMPARISON WITH *EPACHTHOSAURUS SCIUTTOI* POWELL, 1990

Powell (1990) made known the species *Epachthosaurus sciuttoi* based on an incomplete posterior dorsal vertebra, and determined as paraplastotype of this species a cast of the left lateral view of a sequence of six posterior dorsal vertebrae united to the sacrum and a portion of the ilium, obtained from another example of larger size from the same locality. In the vertebra of the holotype, illustrated in three views (Powell, 1990) features are not appreciated that can be compared with the hyposphene-hypantrum structures present in *Argentinosaurus huinculensis*. But in the paraplastotype of *Epachthosaurus sciuttoi* there are characters comparable with the species that we describe, which raises doubts if the mentioned paraplastotype corresponds with the holotype of *E. sciuttoi*.

We have observed in the mentioned paraplastotype hyposphene-hypantrum comparable to those of *Argentinosaurus huinculensis*, which indicates to us a grade of more affinity than with any other titanosaur, and that allows us to join to both taxa in the same family. At the same time we observe the following significant differences to recognize that they are two different genera: a) vertebral bodies of the posterior dorsals very low and wide in the paraplastotype of *E. sciuttoi*; b) pleurocoels of very ventral position in the lateral face and anteroposteriorly extensive in the paraplastotype of *E. sciuttoi*; sacral vertebral bodies 2 to 5 less reduced than in *Argentinosaurus huinculensis*, and with an axial depression in the ventral face of those bodies that is not possessed by the species that we describe.

COMPARISON WITH *ANDESAURUS DELGADOI* CALVO AND BONAPARTE, 1991

The genera *Andesaurus* and *Argentinosaurus* are united in the same family, Andesauridae nov. for their possession of well developed hyposphene-hypantrum, associated with other characters of the pleurocoels and of the lateral face of the neural arch, those that in turn identify them in a higher systematic level.

Contrary to *Argentinosaurus huinculensis*, *Andesaurus delgadoi* does not possess the pronounced lateral expansions of the hyposphene-hypantrum, nor the extra articulation among them, which we interpret as good differences of genus level.

COMPARISON WITH OTHER SAUROPODS

The comparison of the vertebrae of *Argentinosaurus huinculensis* with forms of other continents, limits us to those sauropods that do not present bifurcated spines in the anterior dorsals, such as the Cetiosauridae, Brachiosauridae, *Haplocanthosaurus* (Hatcher, 1903), and *Rebbachisaurus* (Lavocat, 1954). The derived character of bifurcated neural spines present in Diplodocidae, Dicraeosauridae, and Camarasauridae has not been registered among the Titanosauria.

In the Cetiosauridae (*Barapasaurus*, *Cetiosaurus*, *Patagosaurus*, *Volkheimeria* etc.) the neural spines of the middle and posterior dorsal vertebrae are comprised of four divergent laminae, and a massive sector in the dorsal end of the spine, characters that are very different from the more well laminar neural spine provided with a prespinal lamina of *Argentinosaurus huinculensis*. Also, the presence of hypertrophied hyposphene-hypantrum as in the species that we describe is not known among the Cetiosauridae.

In *Brachiosaurus*, being the example from Tendaguru that is exhibited in Berlin, *B. brancai*, as in those of *B. altithorax* of the Morrison Formation, indications of the lateral expansion of the complex hyposphene-hypantrum are not observed, although they possess it with normal development. The neural spine of the anterior dorsals of *Brachiosaurus* is anteroposteriorly thick and narrow in transverse sense, characters that differentiate it from the more well planar and wide neural spine of *Argentinosaurus huinculensis*. Another differential character that seems to be constant in the dorsal vertebrae of *Brachiosaurus* is the large pleurocoel that it possesses, and the absence of a well defined pleurocoelic depression as is the case in the titanosaurs, including the species that we describe.

The comparison with *Haplocanthosaurus*, shows us that its dorsal vertebrae are characterized to have relatively short spines; the distance between the zygapophyses and the dorsal border of the vertebral body is very extensive; there are no indications of lateral expansion of the hyposphene-hypantrum; the pleurocoels are very large, subcircular, and they are not surrounded by a pleurocoelic depression defined by a clear edge, that which forms a group of very significant differences with the vertebrae of *Argentinosaurus huinculensis*.

The comparison with *Rebbachisaurus garasbae* of the Albian of Morocco, Africa, (Lavocat, 1954) of which a middle dorsal vertebra is known, possesses a high and narrow neural spine, with very derived characters. Indeed, the neural spine is formed by 4 laminae arranged at right angles, very thin, of similar development among them, and with a bony enlargement along the border of these laminae. It does not possess hypertrophied hyposphene-hypantrum as in the species that we describe. In such a way the comparison with non-titanosaur groups of sauropods, reveals important differences as to dismiss its possible identity with some of them.

DISCUSSION

From the analysis above it arises that *Argentinosaurus huinculensis* is a titanosaurian sauropod characterized with significant morphological features that we try to interpret in a systematic context. Its comparison shows us characteristic features to recognize that it is a genus different from the remaining titanosaurs. The systematic interpretation that unites the genera *Andesaurus*, *Epachthosaurus*, and *Argentinosaurus*

in the family Andesauridae nov. is supported by the presence of the hyposphene-hypantrum and other characters cited in the diagnosis of this family. In that way the Andesauridae differs from the Titanosauridae (*sensu* Powell, 1986) that show the derived character of the absence of the hyposphene.

The recognition of a new family of Titanosauria has raised the question of if it is opportune to recognize to a larger entity that unites Andesauridae with hyposphene-hypantrum and amphiplatyan caudals next to Titanosauridae without hyposphene and with procoelous caudals.

The recognition of Titanosauria, of suprafamiliar rank, is a response to the growing diversity in recent years of taxa of discovered titanosaurs that cannot be placed in the family Titanosauridae.

It is evident that the two families of Titanosauria are composed with varied forms that show different levels of organization in certain parts of the skeleton, and that seem to correspond, in general, to different ages within the Upper Cretaceous.

Andesauridae is composed of the titanosaurs with normal hyposphene-hypantrum such as *Andesaurus*, or hypertrophied as in *Argentinosaurus* and *Epachthosaurus*, with amphiplatyan caudals registered in *Andesaurus* (Calvo and Bonaparte, 1991), coming from pre-Senonian levels.

Titanosauridae includes the typical titanosaurs of the Senonian lacking the hyposphene and provided with procoelous caudals, including the subfamilies recognized by Powell (1986): Saltasaurinae, Argyrosaurinae, Antarctosaurinae, and Titanosaurinae.

Nevertheless, this systematic stance faces queries that arise from partial knowledge of the taxa that cannot be widely interpreted at the present time, those that form reservations for the good foundation of the proposal.

We can point out in this way the following questions:

a) Did the amphiplatyan caudals of the Andesauridae extend the entire length of the caudal vertebrae or were they limited to the central and distal regions only?

b) Was the presence of the hyposphene-hypantrum only associated with amphiplatyan caudals or was it also with procoelous caudals?

c) Does the character of the very derived hyposphene-hypantrum of *Argentinosaurus* have phylogenetic implications of relevance or is it simply a functional solution to the extreme size of *Argentinosaurus huinculensis*?

d) The proven presence in some genera of Titanosauridae, *sensu* Powell (1986), such as *Aeolosaurus*, *Titanosaurus*, of amphiplatyan caudal vertebrae inserted among the strongly procoelous can be the result of ontogenetic anomalies that we do not know and that probably have a complex evolutionary history. For this a systematic definition based on the presence or absence of amphiplatyan or procoelous caudals should be interpreted with reservations, until much better information is prepared.

The stratigraphic record of the diverse titanosaurs of Argentina serves to confirm the existence of taxa with hyposphene-hypantrum and sequences of amphiplatyan caudals in levels more ancient than those where the subfamilies of Titanosauridae come from, that, as we have pointed out do not possess hyposphene and have procoelous caudal

vertebrae. We have *Andesaurus delgadoi*, with hyposphene-hypantrum of normal development and a sequence of amphiplatyan middle and distal caudals, that has been registered in the same levels of the Candeleros Member of the Río Limay Formation that have offered us a remarkable footprint association referred by Calvo (1991) to the Albian-Cenomanian interval.

The chronological interpretation of Calvo is based on the frequent presence of iguanodont footprints in that association, a group of ornithischians that in other regions of the world did not survive the Aptian-Albian (Norman and Weishampel, 1990).

We believe that such an interpretation is correct and that the antiquity of the ichnites and of *Andesaurus* is more probably Albian-Cenomanian according to that suggested by the iguanodont record. Legarreta and Gulisano (1987), after an analysis of sequential stratigraphy of the Cretaceous of the Neuquén Basin assigned a Cenomanian-Turonian age to the Río Limay Formation, an interpretation that anyway indicates pre-Senonian antiquity for *Andesaurus* and *Argentinosaurus*, the latter of the Huincul Member of the Río Limay Formation.

On the other hand the titanosaurs with dorsal vertebrae without hyposphene and with sequences of procoelous caudals come from the Río Colorado, Allen, and equivalent formations, the first interpreted by Bonaparte (1991) as of Coniacian age, and the latter largely Campanian (Bonaparte et al., 1987).

We thus have that the Andesauridae titanosaurs compose faunistic associations with iguanodont dinosaurs, and that the family Titanosauridae composes different, more recent associations, without iguanodonts. Probably the higher taxonomic diversity in the Senonian titanosaurs represented by the family Titanosauridae is a consequence of the regional extinction of the iguanodonts and the andesaurids.

In figure 6 the interpretation on the possible phylogenetic relationships between the Titanosauria is schematized beginning from the characters of the articulations among the neural arches of the dorsal vertebrae. We thus have the primitive characters of this region of the vertebrae of *Andesaurus* (Calvo and Bonaparte, 1991, Fig. 3A) representing the widespread condition observed in primitive sauropods such as *Patagosaurus*, *Volkheimeria* (Bonaparte, 1986) and other Cetiosauridae. Starting from the condition of *Andesaurus* (Fig. 6A) there would have originated two distinct types of intervertebral articulation. One that is present in *Argentinosaurus* and the paraplastotype of *Epachthosaurus* (Fig. 6B) with increase of the contact surfaces between the hyposphene and hypantrum and the development of extra articulations among them. And the remaining type that is present in the Titanosauridae *sensu* Powell (1986), that shows the virtual disappearance of the hyposphene, (Fig. 6C) possibly for the development of intervertebral ligaments that made their presence unnecessary.

Bonaparte and Kielan-Jaworowska (1987) briefly pointed out the adaptive diversity of the Titanosauridae starting from the studies of Powell (1986), partly paralleling the ornithischians of the Northern Hemisphere. The vertebral anatomy of *Argentinosaurus* serves to confirm that appreciation since evidently it represents an adaptive type different from that of the remaining and varied titanosaurs.

The evolution of the Cretaceous ornithischians of Laurasia shows adaptive types more disparate than in the case of the titanosaurs: hadrosaurs and pachycephalosaurs as semi-bipedal forms, ceratopsians and ankylosaurs as quadrupedal forms, with ecological niches that were probably very different judging by the so disparate adaptive types. On

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the other hand, the evolution of the titanosaurs of South America, documented starting from the Albian-Cenomanian with *Andesaurus*, shows us that the adaptive diversity was limited to quadrupedal forms of medium to large sizes such as *Saltasaurus*, provided invariably with long necks and anterior extremities somewhat shorter than the posterior.

Probably between them the titanosaurs covered very diverse ecological niches. Proof of that exists in the relative diversity that is shown by some appendicular bones and the vertebrae of the different families, such as the presence of some armored forms such as *Saltasaurus*. The osteologic differences of the titanosaurs are less apparent compared with those of the ornithischians; that could be interpreted that the ecological niches were better defined among the ornithischians of the Northern Hemisphere than among the titanosaurs of South America. Nevertheless, the Sauropodomorpha was characterized by a more conservative tendency in that they have a basic adaptive type, of quadrupedal herbivores provided with long necks, with a rhythm of skeletal differentiation, especially of the skull, less manifested than in the ornithischians.

The ecological differences among the sauropods in general and in the titanosaurs in particular, would have corresponded to adaptations in characters that are difficult to detect in the fossil record, such as anatomy of the soft parts, or physiologic or behavioral differences. As Bonaparte and Kielan-Jaworowska pointed out (1987) the evolution of the large herbivores of the Cretaceous of Gondwana is shown in a taxonomic group different from that of Laurasia, with a distinct phylogenetic history, and with different adaptive characters and strategies.

ACKNOWLEDGEMENTS

BIBLIOGRAPHY see original publication

FIGURE CAPTIONS

Figure 1. Location map of the place of the discovery of the fossil remains that are described in this work.

Figure 2. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. Anterior dorsal vertebra (first? dorsal), in views: A, anterior; B, posterior; and C, lateral. Abbreviations: AAH, accessory articulation of the hypantrum; CN, neural canal; DP, diapophysis; H, hypantrum; HY, hyposphene; LPR, prespinal lamina; PP, parapophysis; PRZ, prezygapophysis; PZ, postzygapophysis; RPR, prespinal lamina. Scale bar: 50 cm.

Figure 3. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. Anterior dorsal vertebra, (second? dorsal) in views: A, posterior and B, lateral. Abbreviations as in figure 2 and also AAHY, accessory articulation of the hyposphene; EN, neural spine. Scale bar: 50 cm.

Figure 4. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. Anterior dorsal vertebra, (third? dorsal) in views: A, anterior and B, lateral. Abbreviations: as in the previous figures. Scale bar: 50 cm.

Figure 5. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. A, isolated posterior dorsal vertebra; B, united posterior dorsal vertebrae. Abbreviations; as in the previous figures and also: X, contact of the accessory articulations of the hyposphene-hypantrum. Scale bar: 50 cm.

Figure 6. Outlines indicating the morphology of the zygapophyses and of the hyposphene-hypantrum according to a transversal plane at the level of the intervertebral articulations. A, *Andesaurus*; B, *Argentinosaurus*; C, *Saltasaurus*. The phylogenetic relationships are indicated that suggest diverse types of intervertebral union.

Figure 7. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. Sacrum in ventral view. Abbreviations: SAC, sector corresponding to the acetabulum; S1 to S5, 1st to 5th sacral vertebrae. Scale bar: 50 cm.

Figure 8. *Argentinosaurus huinculensis* gen. et sp. nov. Holotype PVPH-1. Right tibia in medial view. Abbreviation: CC, cnemial crest. Scale bar: 50 cm.