ANDESAURUS DELGADOI GEN. ET SP. NOV. (SAURISCHIA–SAUROPODA), TITANOSAURID DINOSAUR FROM THE RÍO LIMAY FORMATION (ALBIAN–CENOMANIAN), NEUQUÉN, ARGENTINA†

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ORIGINAL ENGLISH ABSTRACT: *Andesaurus delgadoi* gen. et sp. nov. (Saurischia–Sauropoda), titanosaurid dinosaur from the Río Limay Formation (Albian–Cenomanian), Neuquén, Argentina. A good part of the postcranial skeleton of an Albian-Cenomanian primitive titanosaurid from Patagonia is described and discussed. The posterior dorsal vertebrae are high, with a slightly opisthocoelous centrum, a tall neural spine, and hyposphene-hypantrum articulations. The medial and distal caudal vertebrae are amphiplatyan, bearing flat, quadrangular neural spines. Ischium and pubis show clear titanosaurid features. Some characters of the dorsal vertebrae and pubis resemble those of ?*Argyrosaurus superbus*, but it is not possible to recognize any direct relationship. The relative primitive condition of this new titanosaurid permitted the proposal of a new subfamily for it, Andesaurinae nov., representing a stage of evolution less derived than that of typical Senonian titanosaurids. It is argued that the latter were endemic and diversified, representing the major herbivorous group of the Late Cretaceous fauna of Gondwana.

KEY WORDS: Saurischia, Titanosauridae, Río Limay Formation, Upper Cretaceous.

INTRODUCTION

In May of 1987, during a paleontological campaign organized by the Museo Argentino de Ciencias Naturales (MACN) and the Universidad Nacional del Comahue (UNC), with the technical cooperation of the MACN, a large part of a postcranial skeleton of a primitive titanosaur was extracted from the lower section of the Río Limay Formation in the vicinity of El Chocón, Neuquén Province.

These are the first remains of a titanosaurid sauropod to come from the lower levels of the Río Limay Formation (Neuquén Group). The majority of titanosaurids collected in this region since the last century have come from more recent levels, especially the Río Colorado and Allen Formations.

The gross of reports on titanosaurid sauropods are based primarily on specimens that come from the Upper Cretaceous of South America (Senonian), and are complemented by evidence from India (Lydekker, 1877; Huene and Matley, 1933), Africa (Stromer, 1932; Taquet, 1976), Madagascar (Deperet, 1876), North America (Gilmore, 1922, 1946), and Europe (Seeley, 1869; 1876; Huene, 1929, 1932; Matheron, 1869).

Recently, Powell (1986) restudied the collection of South American titanosaurs, reinterpreting the systematic and taxonomic relationships of this family. Powell proposed recognition of four subfamilies within the Family Titanosauridae, emphasizing

the notable taxonomic variety of this group of large herbivorous sauropods. South America has offered the most numerous and varied discoveries of this family (see Powell, 1986), and to a lesser degree, India, Africa, Madagascar, Europe, and North America.

Bonaparte (1986) interpreted the dominant distribution of titanosaurids in Africa, India, and South America as demonstrating the endemic condition for this family on the "Gondwanan" continents. The biogeographic isolation during the length of the Cretaceous (except the Campanian and Maastrichtian) between the supercontinents of Laurasia and Gondwana had conditioned the dominance of the titanosaurs on Gondwana and ornithischians on Laurasia during the Late Cretaceous. Bonaparte interpreted the discoveries of titanosaurids in Laurasia (restricted to the Maastrichtian) and of hadrosaurs and pachycephalosaurs in Gondwana (restricted to the Campanian-Maastrichtian) as the result of bilateral migrations at the end of the Cretaceous between North America and South America and between Europe and Africa.

Curiously, since some years the Neuquén Group has been referred to as "the strata with dinosaurs" in spite of the fact that discoveries in the intermediate unit (Río Neuquén Formation) and lower unit (Río Limay Formation) have been scarce or non-existent until this time. The discovery that we will describe here comes from the Candeleros Member of the Río Limay Formation, where an association of trackways from theropods, sauropods, and ornithischians has been described (Calvo, 1991). The age suggested by the study and comparison of these fossil footprints indicates that the Candeleros Member is not younger than late Albian-Cenomanian, because of the frequency of iguanodont ichnites, which are characteristic of the Aptian and to a lesser extent the Albian of other regions of South America and other continents. The primitive characters of the material described here supports the chronological estimation forwarded by Calvo (1991), in view of the substantial differences with Senonian sauropods.

SYSTEMATICS AND DESCRIPTION

Order SAURISCHIA Seeley, 1887
Suborder SAUROPODOMORPHA Huene, 1932
Infraorder SAUROPODA Marsh, 1878
Family TITANOSAURIDAE Lydekker, 1893
Subfamily ANDESAURINAE nov.

Andesaurus gen. nov.

ETYMOLOGY: In reference to the Andes Mountains, for their proximity to the place of discovery.

DIAGNOSIS: Titanosaurid of large size, with tall posterior dorsal vertebrae formed by a vertebral centrum relatively lower and longer than that of *Argyrosaurus* and a neural arch proportionately taller than that of other titanosaurs, with hyposphene-hypantrum extravertebral articulations, prespinal lamina developed but bifurcate inferiorly. Amphiplatyan or platycoelous caudal vertebrae without indication of procoely, with laminate, broad neural spines, and a neural arch placed somewhat more anteriorly than in other titanosaurs. Humerus long, proportionately more gracile than in *Argyrosaurus*. Pubis with wide proximolateral process and pubic foramen located far from the lateral border. Ischium with small iliac peduncle.

HOLOTYPE: An associated specimen composed of four articulated posterior dorsal vertebrae, 27 articulated caudal vertebrae in two sections corresponding to the anterior and middle portions of the tail, an almost complete left and an incomplete right ischium, an almost complete left pubis, an incomplete right humerus and femur, and various incomplete ribs. The material is in the collections of the Museo de Ciencias Naturales at the Universidad Nacional del Comahue, number MUCPv 132.

Andesaurus delgadoi sp. nov.

ETYMOLOGY: In honor of Sr. Alejandro Delgado, discoverer of the material described here.

DIAGNOSIS: As for the genus by virtue of its monotypy.

HORIZON AND LOCALITY: Medium sands of the lower section of the Candeleros Member of the Río Limay Formation, Neuquén Group, 5 km southeast of the El Chocón locality, Confluencia Department, Neuquén Province, Patagonia, Argentina. Age: Albian-Cenomanian (Figs. 1, 2).

DESCRIPTION: **Dorsal vertebrae**. Four articulated posterior dorsal vertebrae are preserved, one of them is practically complete (Fig. 3). They are characterized by being very tall, provided with a centrum that is lower and longer than is common in the Titanosaurinae and Saltasaurinae (Powell, 1986), but with a neural arch proportionately taller than in other titanosaurids. The neural arch represents three-quarters the height of the vertebrae, with a long neural spine that does not extend beyond the anterior or posterior borders of the centrum. The prespinal lamina is wide, a trait characteristic of the Titanosauridae, and bifurcate in the inferior portion. The spinoprezygapophyseal laminae, a reduced postspinal lamina, and a supradiapophyseal lamina are present.

Essentially the spine is comprised of four laminae, of which the anterior is the most developed.

The parapophysis and diapophysis are not close to each other and occupy a mediodorsal position. Between their bases is a fossa, and there is also a depression between the base of the prezygapophysis and the parapophysis. The zygapophyses have a subhorizontal and vertical portion, forming the hyposphene-hypantrum. This is visible in lateral view (Fig. 3).

The centra are low, elongate, and moderately opisthocoelous. The pleurocoel is elongate anteroposteriorly and low dorsoventrally, rounded, and tapering posteriorly as is typical of titanosaurs. These vertebrae coincide with the morphology of titanosaurids in the form and location of the pleurocoel, form of the centrum, presence of a large prespinal lamina on the neural spine, and the morphology of the region of the diapophysis. They also possess, as in other titanosaurs, spongy textured bone composed of large cells. Nevertheless, the notable height of the neural arch that represents three-quarters the height of the vertebrae, especially the height of the neural spine, as well as the presence of the hyposphene-hypantrum, distinguish these vertebrae from the rest of titanosaurs. The reduced opisthocoely, as well as other interesting traits of the neural spine are shared by *Andesaurus delgadoi* and ?*Argyrosaurus superbus* (Powell, 1986:pl. 86, fig. 2).

We consider the type of dorsal vertebrae present in *Andesaurus delgadoi* as representing an evolutionary stage more primitive than in other titanosaurids. This implies that the presence of hyposphene-hypantrum articulations in *Andesaurus delgadoi* would be a plesiomorphic feature with respect to the rest of titanosaurs, which do not have them (Powell, 1986). Or it may be that their absence in titanosaurs is because of loss of this character, and for this it should be interpreted as an apomorphy.

Caudal Vertebrae. (Fig. 4). Two sections of articulated caudal vertebrae are preserved. The more proximal section, comprised of anterior caudals, includes 9 vertebrae and their corresponding chevrons. The other section is of middle and posterior caudals, with 18 complete vertebrae and their chevrons.

The centra are amphiplatyan (platycoelous), relatively abbreviate and tall, and slightly concave at their extremes. Amphiplatyan centra are also present in the middle and posterior caudal vertebrae of *Tornieria* (Sternfeld, 1911) of the Jurassic of Tanzania, and also in middle and some posterior caudals of *Macrurosaurus semnus* (Seeley, 1869, 1876) of the Albian-Cenomanian of England, however in *Andesaurus delgadoi* amphiplaty is present in all the available caudal vertebrae. On the other hand, *A. delgadoi* has a longitudinal groove on its inferior surface that is not present in the two taxa cited above. The transverse process is located near the superior border of the lateral face of the

centrum, at midlength. In the anterior caudals, the transverse processes are well developed and curve posteriorly. The neural arch is placed on the anterior half of the vertebral centrum, but does not reach the anterior position shown in the different species of titanosaurs cited in Powell (1986). The most outstanding, distinctive feature of these caudal vertebrae is that they are amphiplatyan, with a slight concavity in both extremes, and this is present in all available vertebrae. The primitive character of the neural spine, laminar and with an axially extensive base, supports the nature of the plesiomorphic characters present in *A. delgadoi*, which substantially differentiate it from Senonian titanosaurs. These characters are of systematic importance, and together with the characteristics of the dorsals, permits improve the knowledge of titanosaur morphology. The species that we describe presents the most primitive character in the organization of centra and neural arches in the Titanosauridae.

Chevrons. (Fig. 4F). Of the chevrons preserved, that corresponding to a middle caudal (caudal 17) is completely preserved. It is characterized by the profound separation of its proximal rami, a relatively short axial portion, and by being somewhat expanded lateral view and curved posteriorly. In the anterior chevrons, these proportions are inverted, with a bifurcate proximal section notably shorter than the distal or axial sections. The proximal rami are not expanded and the articular faces are little differentiated. This type of chevron is comparable to those of the titanosaurids *Aeolosaurus* and *Saltasaurus* (Powell, 1986).

Ischium. (Fig. 5). A nearly complete left ischium and half of the right ischium are preserved. This piece is more similar to those of titanosaurids, especially those of *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1986) Nonetheless, it is differentiable from S. loricatus by possessing a smaller iliac peduncle, the more extensive and distally expansive posterior portion, the possession of a larger ischial symphysis, and its more narrow processes.

Pubis. (Fig. 6). A nearly complete left pubis is preserved, with some dorsoventral deformation. In general, it resembles those of titanosaurids, both in terms of its proportions and its proximolateral projection and slight distal extension of the pubic lamina. It has its own distinct features, however, especially the marked proximolateral expansion and the location of the pubic foramen. The principal differences with *Saltasaurus loricatus* pertain to the orientation of the extensive pubic contact, which forms a larger angle with the pubic symphysis in this species, resembling the condition in ?*Argyrosaurus superbus* (Powell, 1986: pl. 68, fig. 1).

The only available pieces of the pelvis of *Andesaurus delgadoi* clearly indicate affinities with the Titanosauridae, with differences that we interpret as indicating a genus distinct from those Powell recognized in his revision of the Titanosauridae.

Femur. (Fig. 7). Of the left femur, only a sector of the central region of the diaphysis and a natural mold of the missing pieces are preserved. From these elements its total length has been reconstructed. It has not been possible to observe certain characters, such as the position of the internal trochanter, the morphology of the distal section, etc. The length of the piece is 1.55m and its proportions resemble those of the type of ?*Argyrosaurus superbus* and *Antarctosaurus wichnmannianus* more than the type of *S. loricatus*.

Humerus. (Fig. 8). A partial right humerus is preserved, represented by the distal half in bone and the proximal in natural mold in the rock, of which we have obtained a cast. A well defined deltopectoral crest is present on the ventral and anterior face, and there is a moderate distal expansion. In this region, the posterior surface has a wide, well-marked supracondylar depression.

The proportions of this element are slender, more gracile than ?*A. superbus* (Powell, 1986:pl. 66. fig. 1) and very distinct from those of *S. loricatus* (Fig. 8). The length of the humerus of *Andesaurus delgadoi* is 1.35m. It resembles that of *Titanosaurus* sp. in the slenderness but not in tits shape, as the distal portion is much wider and rounded than in *A. delgadoi*.

The morphology of most available elements indicates the inclusion of *Andesaurus delgadoi* within Titanosauridae, on the general basis of the dorsal vertebrae, which have large centra with elongate pleurocoels located anteriorly, and for the neural arch , which presents clear affinities with titanosaurids, especially in the conformation of the neural spine, the strong triangular depression between the base of the prezygapophysis and the parapophysis, and the presence of spongy bone texture composed of large cells. Together, these dorsal vertebrae show most affinities with those taxa referred by Powell (1986z) to the subfamily Argyrosaurinae.

The caudal vertebrae resemble those of titanosaurids in the general position of the prezygapophyses and the transverse processes, but not in the amphiplatyan character of the centra. The pubis and ischium resemble those observed in the subfamily Saltasauridae in some traits, and in others they resemble Argyrosaurinae. The femur and humerus, as preserved, do not contradict assignment to Titanosauridae.

These characters permit the recognition of the genus we describe as a member to the Family Titanosauridae, although diverse, differential primitive characters distinguish it from other genera in the family. Our attitude in considering it a titanosaurid is, naturally,

subjective and could well be interpreted another way. Nevertheless, we think it most practical to include it in this family, distinguishing it as a subfamily more primitive than those recognized by Powell (1986). It is possible that future studies will demonstrate that titanosaurs should be grouped as a larger clade, perhaps a superfamiliar taxon in which *Andesaurus* will eventually represent a family more primitive than Titanosauridae. We think that the incompleteness of the material of *Andesaurus* puts strong restrictions on the proposal of a new titanosaur family.

The characters that distinguish *Andesaurus delgadoi* from the rest of Titanosauridae are the following: amphiplatyan caudal vertebrae with the neural arch implanted on the centroanterior part of the centrum, with a laminar spine and short prezygapophyses, dorsal vertebrae with hyposphene-hypantrum articulations and tall neural arches. These characters are interpreted as good morphological indicators that have revealed a new titanosaurid entity of subfamily level, following our systematic interpretation: Andesaurinae nov.

DEFINITION OF ANDESAURINAE

Primitive titanosaurs of considerable size, with posterior dorsal vertebrae provided with tall neural arches, a neural spine formed by an extensive prespinal lamina, a lateral lamina that rises from the diapophysis and from the postzygapophyses, and a weak postspinal lamina. Presence of hyposphene-hypantrum in the dorsals. Low dorsal centra, approximately one-quarter the height of the vertebrae, and with slight opisthocoely. Amphiplatyan middle caudal vertebrae, provided with an axially extensive, laminar neural spine and short, horizontally-oriented prezygapophyses. Pubis and ischium of the type present in Saltasaurinae and somewhat like those of Argyrosaurinae.

These characters reveal a condition that is more primitive than previously noted in Senonian titanosaurs of South America. At the same time it introduces the unexpected and uncommon character into the Titanosauridae of amphiplatyan middle caudal vertebrae with laminar spines.

Although Powell (1986) noted amphicoely in some caudal vertebrae of Senonian titanosaurs, in *Andesaurus delgadoi* the articulated series of amphiplatyan caudal vertebrae are provided with a type of neural spine not previously noted in Titanosauridae. It is possible that the character of procoelous caudals in Titanosauridae was an adaptive character that developed from the anterior caudals posteriorly, as procoely in anterior caudal vertebrae has been demonstrated in several Jurassic sauropods,

among them *Patagosaurus* Bonaparte (1986), *Tornieria* Sternfeld (1911), and *Dicraeosaurus* Janensch (1914).

We think that in the first taxonomic instance, the differential characters of Andesaurinae broaden the morphological concept of the familial entity Titanosauridae. The alternative taxonomic interpretation of maintaining the definition of Titanosauridae after Powell (1986), lamentably unpublished, and interpreting *Andesaurus* as the type genus of a new family is not well founded anatomically. However, *Andesaurus* presents several important differential characters in its axial skeleton, as well as a group of characters in common with Senonian titanosaurs.

Lamentably, until now the only relatively well known titanosaurids have been Senonian species. The materials cited and sometimes illustrated from the Aptian of Niger (Taquet, 1976), the Cloverly Formation (Ostrom, 1970), the Cenomanian of Egypt (Stromer, 1932), the Jurassic of Tanzania (Fraas, 1908), and the Albian-Cenomanian of England (Seeley, 1876) offer very little knowledge of the pre-Senonian titanosaurs. Because of this, the discovery of *Andesaurus delgadoi* is practically the only evidence of the evolutionary history preceding the Senonian titanosaurs.

As is suggested by *A. delgadoi*, the loss of hyposphene-hypantrum articulations is a derived character of Senonian titanosaurs. Similarly, the characters of procoely and reduced neural spines in middle caudal vertebrae were probably developed in Senonian titanosaurs from species comparable to *Andesaurus delgadoi* of the late Albian-Cenomanian.

DISCUSSION OF TITANOSAURIDAE

The revision of the titanosaurids by Powell (1986), unpublished as mentioned already, offered us a picture of this most interesting group of large sauropods that gained a substantial ecological and distributional success during the Senonian. In South America, where they are best documented, Powell recognized the presence of four subfamilies and ten genera that developed a variety of adaptive types and covered a large diversity of ecological niches, both in the "highlands" and in the "lowlands". A similar phenomenon probably occurred in Africa (Stromer, 1932), Madagascar (Deperet, 1896), and India (Lydekker, 1877; Huene and Matley, 1933). Currently the Senonian titanosaurs represent a grouping of large tetrapods that held a monopoly on the primary consumption on the continents of Africa, South America, and India during the Senonian. In the Laurasian continents, the primary consumers were ornithischian dinosaurs (Bonaparte,

1986; Bonaparte and Kielan-Jaworowska, 1987), reflecting the strong biogeographical difference between these supercontinents.

If, as suggested by Bonaparte (1986), these strong compositional differences of the primary consumers has a paleogeographic origin before the Late Jurassic, it is expected that the endemic evolution occurring in Gondwanan sauropods produced a great diversity, eventually of suprafamilliar level (and not subfamiliar, as suggested by Powell [1986]).

The evolutionary history of titanosaurids is little known and confusing, owing to the limited quality and variety of available materials. The oldest sauropod assigned to Titanosauridae is *Tornieria* from the Late Jurassic of Tanzania, which has vertebrae that suggest proximity to this group, although it may eventually be shown to be in a different, perhaps ancestral, family.

After the Late Jurassic, pre-Senonian "titanosaurs" were documented in the Berriasian-Barremian of England (*Titanosaurus valdensis* Huene, 1929), Albian-Cenomanian of England (*Macrurosaurus semnus* Seeley, 1876), Cenomanian of Egypt (*Aegyptosaurus bahariensis* Stromer, 1932), etc., but lamentably in each case the remains are fragmentary.

Recently, in the Albian-Cenomanian of Neuquén, Argentina, we have discovered a specimen sufficiently diagnostic to permit its classification within titanosaurs, but more primitive than the Senonian types from South America, Africa, India, Europe, and U.S.A. Curiously, the evolutionary grade of the caudal vertebrae of *Andesaurus* is apparently less than those documented in *Tornieria* (Sternfeld, 1911) and *Macrurosaurus* (Seeley, 1876). This incoherence suggests that the cited genera have developed these characteristics precociously, raising the possibility that the adaptations of distinct grade occurred in the Late Jurassic. *Andesaurus*, with primitive caudals and the presence of hyposphene-hypantrum articulations, could well be ancestral to some of the numerous Senonian titanosaurs, especially Argyrosaurinae, which raises the possibility that these subfamilies of Titanosauridae had a particular evolutionary history previous to the Senonian.

Following footprint evidence from the Río Limay Formation from Calvo (1991) and osteological evidence, the community of dinosaurs in this epoch (and in Patagonia) were integrated with an appreciable proportion of iguanodonts, sauropods, theropods, crocodiles, frogs, and turtles. This reveals that the Titanosauridae of the Río Limay Formation shared herbivory with ornithischians and at least one of the non-titanosaur sauropod families (Calvo and Bonaparte, 1988).

The community present in the Albian-Cenomanian of Patagonia (registered in the Candeleros Member of the Río Limay Formation) was replaced, after the extinction of iguanodonts and other sauropods, by a community comprised almost exclusively of titanosaurs, documented especially in the Río Neuquén and Allen Formations.

CONCLUSIONS

From everything expressed, we consider *Andesaurus delgadoi* a titanosaurid sauropod. It represents a primitive clade of this family, one that possesses very peculiar characters such as the presence of amphicoelous caudals and dorsal vertebrae with hyposphene-hypantrum articulations. These elements are good evidence for including the genus within a new titanosaur subfamily, Andesaurinae nov. The authors admit that future studies of these sauropods may indicate that *Andesaurus* may correspond to a family that is differentiable from Titanosauridae.

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FIGURE CAPTIONS

Figure 1. Rough sketch of the site of the fossil locality where the remains of *Andesaurus delgadoi* gen. et sp. nov. were excavated.

Figure 2. Schematic geological profile of a section of the Candeleros Member of the Río Limay Formation, with indication of the level from which the remains of *Andesaurus delgadoi*, gen. et sp. nov. were excavated.

Figure 3. Posterior dorsal vertebrae in lateral view of **A**, **Andesaurus delgadoi**, gen. et sp. nov.; **B**. **Saltasaurus loricatus**; and **C**. **?Argyrosaurus superbus** fide Powell (1986). **B**

and **C** based on Powell (1986). Abbreviations: hy, hyposphene; l. pres., prespinal lamina; l. post., postspinal lamina; l. sd., supradiapophyseal lamina; poz, postzygapophysis; prz, prezygapophysis.

Figure 4. **Andesaurus delgadoi**, gen. et sp. nov. **A**, lateral view of a middle caudal vertebra; **B** and **C**, lateral and anterior views of a posterior-middle caudal vertebra, compared with caudal vertebrae of Senonian titanosaurs: **D**, lateral view of a middle caudal of **"Titanosaurus" australis**; and **E**, lateral view of a middle caudal of **Saltasaurus loricatus**. **F**, chevron of vertebra 17 in posterior and lateral views. **D** and **E** based on Powell (1986)

Figure 5. **A**, left ischium in ventral view of **Andesaurus delgadoi**, gen. et sp. nov. **B**, right ischiumof **Saltasaurus loricatus** in dorsomedial view. **B** based on Powell (1986).

Figure 6. **A**, right pubis of **Andesaurus delgadoi**, gen. et sp. nov. in dorsoanterior view; **B**, right pubis of **Saltasaurus loricatus** in the same view; and **C**, right pubis of **?Argyrosaurus superbus** in the same view.

Figure 7. **Andesaurus delgadoi**, gen. et sp. nov., incomplete femur in anterior view, restored from natural molds in the rock.

Figure 8. **A**, incomplete right humerus of **Andesaurus delgadoi**, gen. et sp. nov. in posterior view, restored from natural molds in the rock; **B**, right humerus of **?Argyrosaurus superbus** in anterior view; and left humerus of **Saltasaurus loricatus** in anterior view. **B** and **C** based on Powell (1986).

† Original reference: Calvo, J. O. and Bonaparte, J. F. 1991. *Andesaurus delgadoi*, gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio titanosauridae de la Formacíon Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. Ameghiniana 28:303-310.