



A NEW TITANOSAUR SAUROPOD
FROM THE LATE CRETACEOUS OF NEUQUÉN, PATAGONIA, ARGENTINA ¹
(With 14 figures)

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ABSTRACT: The discovery of *Muyelensaurus pecheni* gen. et sp.nov., a new slender titanosaurid, is relevant from anatomical and systematic viewpoints. The specimens come from the Upper Cretaceous strata of the Portezuelo Formation (Turonian-Early Coniacian) at Loma del Lindero, Rincón de los Sauces area, Neuquén Province, Argentina. The remains include a braincase, cervical, dorsal, sacral and caudal vertebrae, and numerous appendicular bones. It is characterized by the following association of autapomorphies: basal tubera diverge 70 degrees from each other; thin and concave lamina that unit basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae, distal end of pubic blade rectangular and medially thick. A cladistic phylogenetic analysis placed *Muyelensaurus pecheni* gen. et sp.nov. and *Rinconsaurus caudamirus* in a new eutitanosaur clade named herein Rinconsauria. This new clade include middle-sized sauropods different from Aeolosaurini, Opisthocoelicaudiinae or Saltasaurinae taxa.

Key words: Sauropoda. Titanosauria. Rinconsauria. *Muyelensaurus pecheni* gen. et. sp.nov. Late Cretaceous.

RESUMEN: Un nuevo saurópodo Titanosaurio del Cretácico superior de Neuquén, Patagonia, Argentina. El descubrimiento de *Muyelensaurus pecheni* gen. et. sp. nov., un nuevo y esbelto titanosaurio, es relevante tanto desde el punto de vista anatómico como sistemático. Los especímenes proceden de los estratos del Cretácico superior de la Formación Portezuelo (Turoniano-Coniaciano temprano) de Loma del Lindero, en la zona de Rincón de los Sauces, Provincia del Neuquén, Argentina. Los restos incluyen un basicráneo, vértebras cervicales, dorsales, sacras y caudales y numerosos huesos apendiculares. Esta caracterizado por la siguiente asociación de autopomorfias: tubera basal diverge 70 grados una de otra; tubera basal unida ventralmente por una lámina delgada y cóncava; cóndilo basioccipital mas ancho que la porción proximal de la tubera basal; espinas neurales en la vértebras dorsales posteriores con una lámina preespinal larga y reforzada por dos pequeñas láminas accesorias; extremo distal de la lámina púbica de forma rectangular y gruesa medialmente. El análisis filogenético cladístico ubica a *Muyelensaurus pecheni* gen. et sp. nov. y a *Rinconsaurus caudamirus* en un nuevo clado de Eutitanosaurio que denominamos aquí como Rinconsauria. Este clado incluye a saurópodos de mediano tamaño diferentes de otros taxa de Aeolosaurini, Opisthocoelicaudiinae o Saltasaurinae.

Palabras clave: Sauropoda. Titanosauria. Rinconsauria. *Muyelensaurus pecheni* gen. et. sp.nov. Cretácico Superior.

INTRODUCTION

Titanosauria is the most diverse and geographically widespread Cretaceous sauropod clade. In spite of that, most of titanosaurs are represented by incomplete skeletal elements lacking well-preserved cranial remains. In this context, the discovery of a new genus and species represented by a braincase associated with numerous axial

and appendicular bones is relevant from anatomical and systematic viewpoints.

In Argentina, only the titanosaurids *Antarctosaurus wichmannianus* (HUENE, 1929), *Saltasaurus loricatus* (BONAPARTE & POWELL, 1980), *Bonitasaura salgadoi* (APESTEGUÍA, 2004), *Bonatitan reigi* (MARTINELLI & FORASIEPI, 2004), and an unnamed specimen from Bajo de Añelo, Neuquén Province (CALVO & KELLNER, 2006) include descriptions of braincase. In contrast, well-preserved

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titanosaurids recently recovered in Patagonia that include cranial remains (CALVO *et al.*, 1997; CORIA & SALGADO, 1998) have not been described yet.

In Northwestern Patagonia, the Neuquén Group is the richest dinosaur bearing unit. It comprises a thick continental succession (maximum thickness 1,300m) deposited between Early Cenomanian to Early Campanian (LEANZA & HUGO, 2001). The Neuquén Group has given since 1882 numerous titanosaur species (HUENE, 1929; POWELL, 1986; CALVO & BONAPARTE, 1991; BONAPARTE & CORIA, 1993; GONZÁLEZ RIGA, 2003; 2005).

In the last years, extraordinary titanosaur fossils were found in Rincón de los Sauces area, Northern Neuquén Province, Patagonia. *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003) is the first species described from this locality. Moreover, other discoveries carried out in Rincón de los Sauces include articulated specimens that have not been described yet (CALVO *et al.*, 1997; CORIA & SALGADO, 1998).

The objective of this work is to describe a new and slender titanosaur from the Late Cretaceous, and to analyze their phylogenetic relationships. The study of this taxon, the second species described in Rincón de los Sauces, is a new evidence of the morphologic diversity of the South American titanosaurs.

MATERIAL AND METHODS

The fossils had been found at Loma del Lindero site, 10km west to Rincón de los Sauces Town (Fig.1). This site was excavated during four years (1998-2001) under the direction of the first author (J.O.C.). The first fossil remains from Loma del Lindero site were found by Marcelino Palomo and communicated to authors by Salvador Palomo in 1997. At Loma del Lindero locality, numerous titanosaur remains (~ 300 bones) associated with a turtle specimen and theropods have been found (CALVO & GONZÁLEZ RIGA, 1999; de la Fuente *et al.*, 2007). Fossil remains are housed at the Laboratory of Rincón de los Sauces Museum.

GEOLOGICAL SETTING

In the last years, well-preserved titanosaur sauropods were found in Rincón de los Sauces area, Northern Neuquén Province, Patagonia. In the Río Seco site, located 2km South to Rincón de los Sauces Town, a slender eutitanosaur named *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003) and a basal sebecosuchian crocodyliform

named *Pehuenchesuchus enderi* (TURNER & CALVO, 2005) were found in strata tentatively assigned to Río Neuquén Subgroup (Late Turonian-Coniacian).

In Loma del Lindero site, 10km West to Rincón de los Sauces Town, numerous sauropod bones were collected in fluvial facies assigned to the Portezuelo Formation, base of the Río Neuquén Subgroup (Late Turonian-Early Coniacian after LEANZA & HUGO, 2001). The fossils come from reddish pelites and yellowish sandstones of overbank facies. A partially similar sedimentary context is also present in Cerro Guillermo area (Mendoza Province) (GONZÁLEZ RIGA & ASTINI, 2007), where the titanosaur *Mendozasaurus nequyelap* was found (GONZÁLEZ RIGA, 2003; 2005).

Institutional abbreviation – FMNH PR, Field Museum of Natural History, Chicago, USA; MRS-Pv, Museo de Rincón de los Sauces, Neuquén, Argentina; MUCPv. Museo de Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina.



Fig.1- Map of Neuquén basin (Patagonia, Argentina) showing the locality where the holotype of *Muyelensaurus pecheri* gen. et sp.nov. was found.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
 SAUROPODA Marsh, 1878
 TITANOSAURIA Bonaparte & Coria, 1993
 TITANOSAURIDAE Lydekker, 1893
 RINCONSAURIA new taxon

Etymology – In reference to Rincón de los Sauces area, Neuquén Province, Patagonia, Argentina.

Definition – *Muyelensaurus*, *Rinconsaurus*, their most recent common ancestor and all of its descendants.

Diagnosis – Titanosaurids with the following association of characters: suboval teeth with labial and lingual faces well differentiated by crests, bony processes that support the postzygapophyseal facets in middle caudal vertebrae, and posterior caudal centra depressed posteriorly.

Included species – *Rinconsaurus caudamirus* Calvo & González Riga, 2003, and *Muyelensaurus pecheni* gen. et sp.nov.

Muyelensaurus gen.nov.

Etymology – From *Muyelen*, one of the names of the Colorado river after the Mapuche indigenous language (ERIZE, 1988); *saurus* (Greek), lizard.

Type-species – *Muyelensaurus pecheni* sp.nov.

Diagnosis – Slender Rinconsauria characterized by the following association of autapomorphies: basal tubera diverge 70 degree from each other; extensive, thin and concave medial lamina that unit basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae, distal end of pubic blade rectangular and medially thick. In contrast to *Rinconsaurus*, *Muyelensaurus* gen.nov has anterior dorsals with neural spines posteriorly directed less than 45 degree with respect to the vertical, posterior dorsals with large and deep infradiapophyseal fossa and ventral face of posterior cervical centra narrow and strongly concave at level of the parapophysis. Moreover, different from *Rinconsaurus*, *Muyelensaurus* gen.nov. lacks an accessory centroparapophyseal lamina in posterior dorsals, anterior caudals with postzygapophyseal process, and amphicoelous-biconvex or amphicoelous-opisthocelous-biconvex caudal centra.

Muyelensaurus pecheni sp.nov.

Etymology – In honor of Dra. Ana María Pechen, Main head of the National University of Comahue (2002-2006), who supported the study of dinosaur fossils in Neuquén Province, Patagonia.

Holotype – MRS-PV 207, a braincase including partial frontal and parietal, basioccipital, incomplete basipterigoid process, supraoccipital, exoccipital, basisphenoidals tubers, orbitosphenoids, and incomplete parasphenoids.

Paratype – The following bones associated with the holotype are included: represented by a premaxilar (MRS-Pv 59, 60, 337), cervical vertebrae (MRS-Pv 65, 66, 121, 122, 204, 230, 232, 229, 279, 391, 392, 420, 422, 428), dorsal vertebrae (MRS-Pv 67, 68, 224, 404, 412, 421), sacrum (MRS-Pv 355), caudal vertebrae (MRS-Pv 135, 137, 164, 170, 171, 173, 174, 189, 190, 193, 200, 209, 214, 252, 377, 408), scapula (MRS-Pv 396, 397, 259), sternal plate (MRS-Pv 125), humerus (MRS-Pv 70, 132, 212, 352, 357, 387), ulnae (MRS-Pv 72, 243, 353, 182), radio (MRS-Pv 71, 139) metacarpals (MRS-Pv 127, 152, 157, 181, 198, 231, 235, 236), ischia (MRS-Pv 87, 199, 247, 251), ilia (MRS-Pv 131, 134, 202, 399), pubes (MRS-Pv 88, 154, 204, 371), femora (MRS-Pv 89, 91, 352, 356, 358, 389, 429), tibiae (MRS-Pv 161, 162, 257, 266), fibulae (MRS-Pv 90, 245, 246, 258, 271, 369, 375), astragalus (MRS-Pv 187), metatarsals (MRS-Pv 50-54, 128, 141, 142, 166, 168, 242, 273, 274, 378, 379), and phalanges (MRS-Pv 55, 56, 57, 58, 143, 144-147, 165, 237).

Referred material – posterior dorsal vertebrae (MRS-Pv 123, 203, 419 and 431).

Specimens – The holotype and paratypes of *Muyelensaurus pecheni* sp.nov. correspond to four adult and one juvenile individuals. All fossil remains were found disarticulated but associated in the same site and include cranial remains, cervical, dorsal, sacral, and caudal vertebrae, and appendicular bones (Fig.2). Duplicate bones represented by appendicular bones exhibit the same morphological characters. This evidences the presence of a monospecific assemblage.

Horizon, age and locality: Portezuelo Formation, Rio Neuquén Subgroup, Neuquén Group, Late Cretaceous, Late Turonian-Early Coniacian (after LEANZA & HUGO, 2001). The fossils come from Loma del Lindero site, 10km West to Rincón de los Sauces City, Neuquén Province, Patagonia, Argentina.



Fig.2- *Muyelensaurus pecheni* gen. et sp.nov., preserved bones (in black) shown in a titanosaur skeletal reconstruction of LEHMAN & COULSON (2002).

DESCRIPTION

Skull – Premaxilar fragments with teeth (Fig.3), and an incomplete braincase (Fig.4) were recovered. Suboval teeth are characterized by the presence of labial and lingual faces well differentiated by crests, like in *Rinconosaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003). The braincase is slightly crushed. It preserves a fragment of the left parietal and frontal, a fragment parietal, complete supraoccipital, the right paraoccipital process, basioccipital condyle, basal tubera, a fragment of the right basipterygoid process, and partially preserved orbitosphenoid, crista prootica, and parasphenoid.

The frontal, represented by a small fragment, forms the posterior rim of the orbit. In anterior view, it is fused to the orbitosphenoid. The parietal is robust and axially elongated. The supratemporal fenestrae are relatively reduced, transversely orientated and laterally directed, as in the titanosaur *Saltasaurus* and some other sauropods (WILSON & SERENO, 1998; CURRY ROGERS & FORSTER, 2001). The preserved medial border of the supratemporal fenestra is formed by the parietal. On the anterior rim of the supratemporal fenestra participates the frontal, like in *Rapetosaurus* (CURRY ROGERS & FORSTER, 2004), *Nemegtosaurus* and *Saltasaurus* (contra WILSON, 2002), and *Bonatitan* (MARTINELLI & FORASIEPI, 2004).

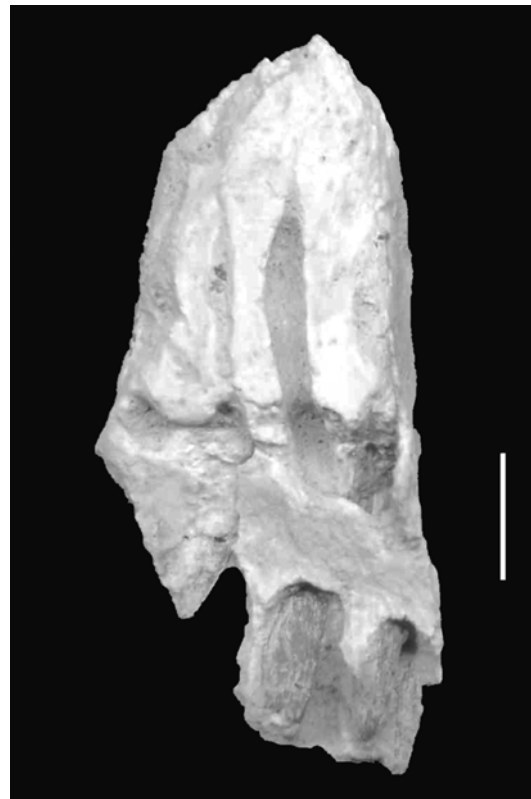


Fig.3- *Muyelensaurus pecheni* gen. et sp.nov., a fragment of premaxilar with teeth (MRS-Pv 59) in lateral view. Scale bar = 1cm.

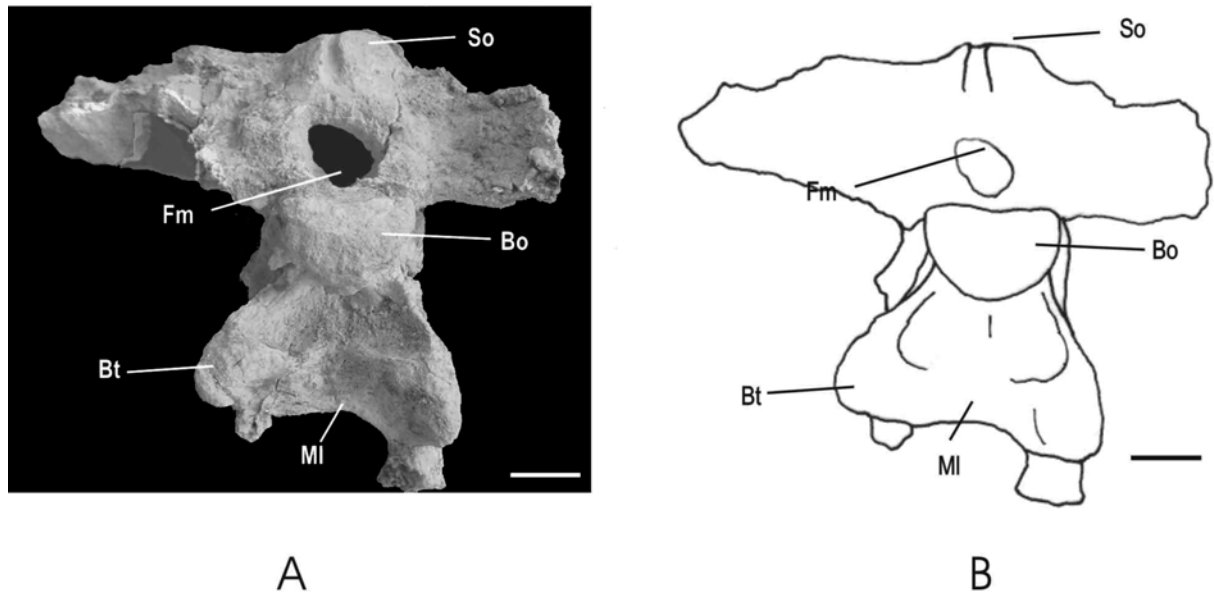


Fig.4- *Muyelensaurus pecheni* gen. et sp.nov., braincase (MRS-Pv 207) in occipital view (A, picture; B, drawing). (Bo) basioccipital, (Bt), basitubera, (Fm), foramen magnum, (MI), medial lamina, (So) supraoccipital. Scale bar = 2cm.

The proximal portion of the supraoccipital has a subquadrangular shape. In spite of that the distal end is not preserved. There is a small process that shows that it was directed ventrally as in *Saltasaurus*.

The basioccipital is slightly deformed by compression. In posteroventral view, it is subtriangular with its dorsal border slightly concave and their lateroventral sides convex. The neck is constricted transversely and concave anteroposteriorly; therefore, the condyle has a mushroom shape, an unusual morphology among sauropods.

The basisphenoid is formed by the tubera and the basipterygoid processes. The first ones are complete but the second ones are missing except by the proximal portion of the right process. Basal tubera are well separated by an extended and thin medial lamina (see MI in Fig.4) that has a concave ventral contour in a posterior view. Basal tubera diverge 70 degree from each other (Fig.4). A lateral ridge connects each basal tubera with the condylar neck on its external side; and a small ridge unites each tubera with the midline. In between these ridges, a wide depression is developed opened only on the ventral side. The proximal portion of the right basipterygoid process is preserved. According to the evidence they are well separated and were directed almost parallel.

Cervical vertebrae – An almost complete middle cervical vertebra and numerous incomplete remains were collected (Fig.5; MRS-Pv 65). This cervical has an opisthocoelel centrum as wide as high in posterior view and relatively long (ratio: total length / height of cotyle more than 4.0). In contrast to *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003), the lateral faces have a deep concavity, but lack a true pleurocoels. The posterior centrodiapophyseal and postzygodiapophyseal laminae are well defined, as in other titanosaurs like *Rapetosaurus krausei* (CURRY ROGERS & FORSTER, 2001). The neural spine is formed by the fusion of spinoprezygapophyseal and spinopostzygapophyseal laminae. It has a triangular contour in lateral view and is thinner distally than those of titanosaur specimen “Series A” from Peirópolis, Brazil (POWELL, 1987). Prezygapophysis process surpasses the anterior border of the centrum, but in contrast to *Rinconsaurus*, the postzygapophyses do not extend beyond the posterior border. The prezygapophyseal facets are slightly oriented dorsomedially. The diapophysis is reinforced by the posterior centrodiapophyseal, prezygodiapophyseal and postzygodiapophyseal laminae. Likewise some titanosaurs (*Saltasaurus*, *Rapetosaurus*), these laminae form a supradiapophyseal concavity lacking well-defined borders (GONZÁLEZ RIGA, 2005).

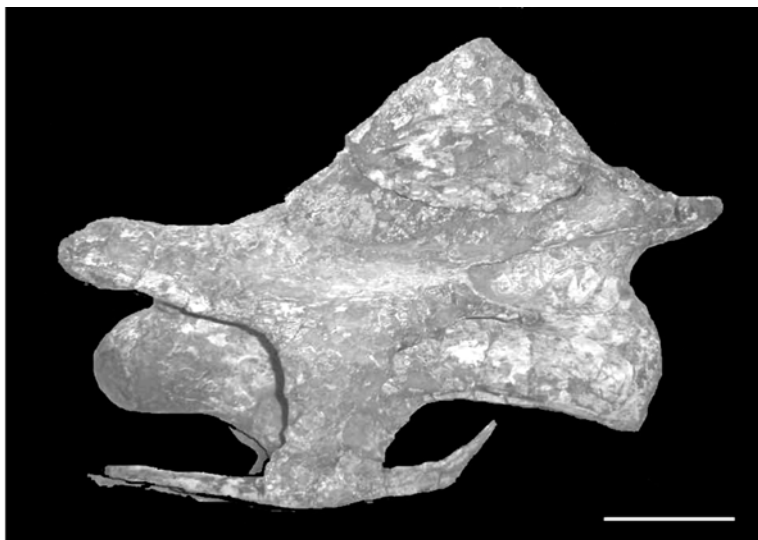


Fig.5- *Muyelensaurus pecheni* gen. et sp.nov., middle cervical vertebra (MRS-Pv 65) in lateral view. Scale bar = 5cm.

The parapophyses, located in the anterior half of the vertebral body, are laminar and subtriangular in shape. In contrast to *Rinconosaurus*, the ventral face is narrow and strongly concave at level of the parapophysis. Other cervicals (MRS-Pv 121, 391, 392, 420, 422, 229, 428, and 279) are crusted and damaged, but have a similar size to the cervical vertebra described. In contrast, one cervical (MRS-Pv 122) is assigned to a larger specimen (centrum length: 43cm). It shows a tall neural spine that have a subtriangular contour in lateral view. Other cervicals of large size, but fragmentary preserved,

have been recovered (MRS-Pv 204, 230, 232, and 66).

Anterior dorsal vertebra – One complete anterior dorsal vertebra have been recovered (Fig.6; MRS-Pv 404). The neural arch is three times higher than the centrum and is placed anteriorly. The centrum has a deep pleurocoel that occupies the half of the length. The parapophysis is placed on the top of the centrum. The prezygapophysis are wide and have an oval shape. They are well separated from the midline. The centroprezygapophyseal and diapoprezygapophyseal lamina are robust. The diapophysis is connected to the neural spine by a robust spinodiapophyseal lamina. Ventrally, the diapophysis is reinforced by a paradiapophyseal lamina and a centrodiaopophyseal lamina. In contrast to this taxon, the centroprezygapophyseal laminae are absent in *Rinconosaurus*.

Small accessory centrodiaopophyseal laminae are born on the base of the diapoparapophyseal laminae and are connected to the centrodiaopophyseal laminae. Therefore two deep depressions are developed below the diapophysis. In posterior view a centro postzygapophyseal lamina is present. The single neural spine is directed posteriorly around 45 degree with respect to the vertical, in contrast to *Rinconosaurus* that reaches 60 degree. The prespinal lamina is present and transverse processes are directed dorsolaterally.

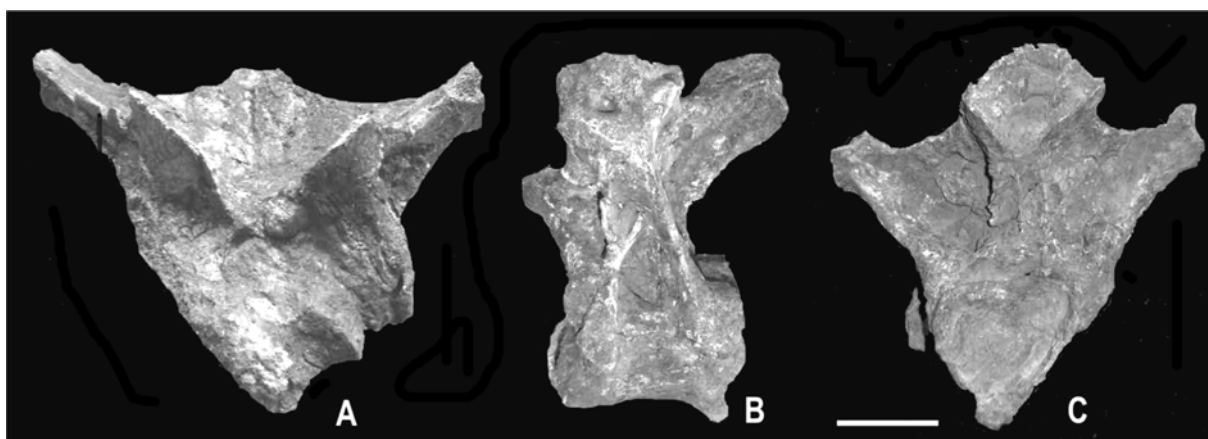


Fig.6- *Muyelensaurus pecheni* gen. et sp.nov., anterior dorsal vertebra (MRS-Pv 404) in anterior (A), lateral (B), and posterior (C) views. Scale bar = 5cm.

Posterior dorsal vertebrae – Several disarticulated posterior dorsal vertebrae (MRS-Pv 67, 68, 412, and 224) and incomplete posterior dorsal arch (MRS-Pv 421) were preserved. The posterior dorsals have opisthocoelous and subcircular centra, as wide as high (Fig.7). The lateral and ventral faces are anteroposteriorly concave. The

lateral faces of the centrum (Fig.8A) show deep eye-shaped pleurocoels with acuminate posterior contour, a synapomorphy of Titanosauria (*sensu* SALGADO *et al.*, 1997a). They lack hyposphene-hypantrum articulations. Post zygapophyseal facets are elongated, narrow, relatively small and directed ventromedially (Fig.8B).

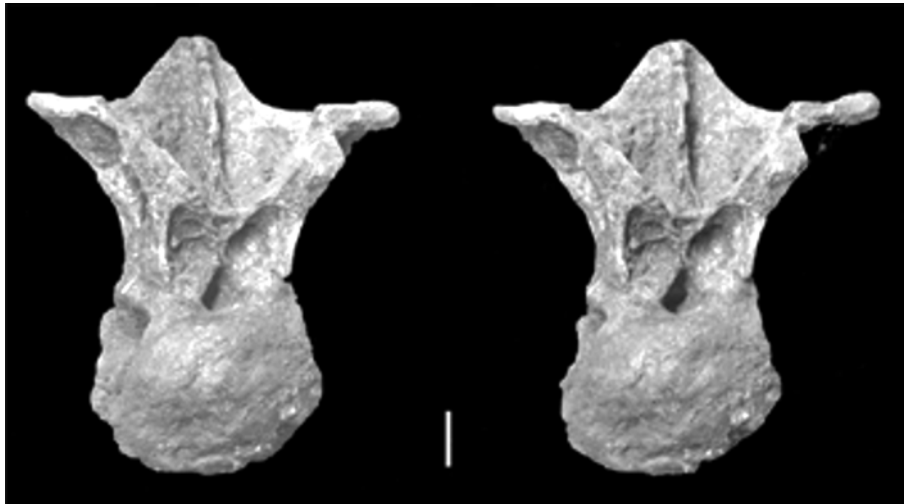


Fig.7- *Muyelensaurus pecheni* gen. et sp.nov., stereophotographs of the posterior dorsal vertebra (MRS-Pv 412) in anterior view. Scale bar = 5cm.

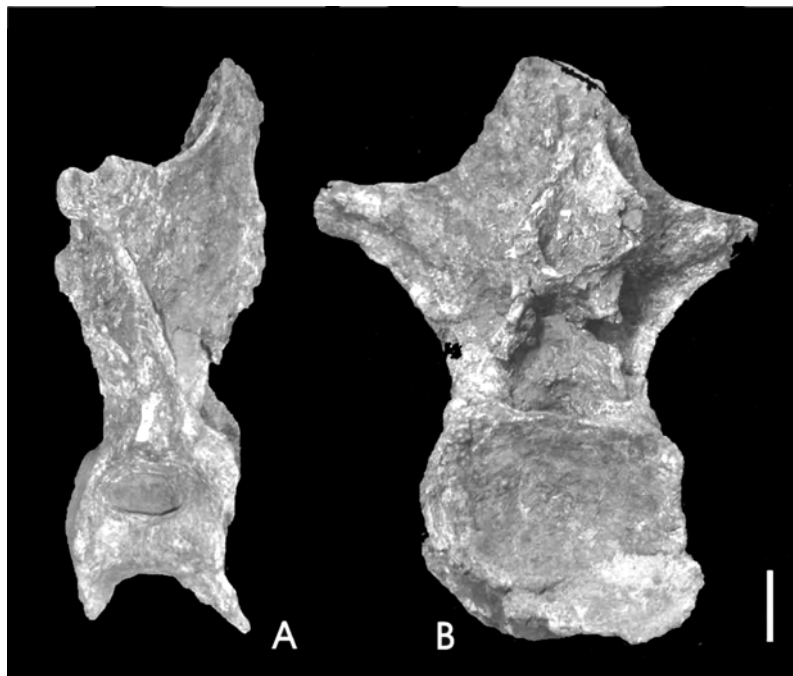


Fig.8- *Muyelensaurus pecheni* gen. et sp.nov., posterior dorsal vertebra (MRS-Pv 412) in lateral (A) and posterior (B) views. Scale bar = 5cm.

They are connected to the centropostzygapophyseal laminae. In contrast to *Rinconsaurus caudamirus* (MRS-Pv 17, 18), the most posterior dorsals lack postzygodiapophyseal lamina. The diapophyses are supported by posterior and anterior centrodiapophyseal laminae. These laminae delimit a subtriangular infradiapophyseal depression in some dorsals (MRS-Pv 67 and 68) and a true infradiapophyseal fossa in the dorsal MRS-Pv 412. A less developed infradiapophyseal depression is present in posterior dorsal of *Rinconsaurus caudamirus* (MRS-Pv 13). The prespinal lamina is large anteroposteriorly and reaches the base of the neural arch. There are two small accessory prespinal laminae bifurcated close to the base of the neural arch (Fig.7). This character has not been described in any other posterior dorsal vertebrae of titanosaurs and is considered herein as a probable autapomorphy of *Muyelensaurus*. In *Mendozasaurus*, anterior dorsals have a similar structure but they are small spinoprezygapophyseal laminae that are directed to the prezygapophysis (GONZÁLEZ RIGA, 2003). Other peculiar character of the dorsals is the presence of accessory spinodiapophyseal lamina. This lamina exhibits a variable morphology: it is extensive in some dorsals (MRS-Pv 67 and 68) whereas it is reduced or absent in other dorsals. Accessory spinodiapophyseal laminae, but with less development, are also present in *Argentinosaurus huinculensis* (BONAPARTE & CORIA, 1993). The neural canal is reduced and shows a subtriangular contour. Over the neural canal, there is a deep fossa divided by a medial septum. The neural spines are less posteriorly directed toward the posterior section of the series. The neural spines have lanceolate anterior and posterior contours due to the development of lateral process of the spinodiapophyseal lamina. Other middle and posterior dorsal vertebrae recovered are distorted and considered as refereed material (MRS-Pv 123, 203, 419, and 431). They exhibit a large and very deep infradiapophyseal fossa limited by the anterior and posterior centrodiapophyseal laminae. Finally, in contrast to *Muyelensaurus*, the posterior dorsal vertebrae of *Rinconsaurus* have an accessory centroparapophyseal lamina, which is extended from the base of the parapophysis to the base of centrodiapophyseal lamina (MRS-Pv 17 and 18). This structure is absent in other titanosaurs and can be interpreted as an autapomorphy of *Rinconsaurus*.

Sacrum – Five sacral vertebrae partially preserved

have been collected (MRS-Pv 355). They are fused and have neural spines united each other by an interspinal medial lamina. The sacral ribs are laminar and dorsally expanded reaching the level of the neural spines.

Caudal vertebrae – Numerous caudal vertebrae corresponding to several individuals of different sizes were recovered. All caudals have strongly procoelous centra, in contrast to *Rinconsaurus* that is characterized by the intercalation of amphicoelous-biconvex or amphicoelous-opisthocelous-biconvex centra.

The most anterior caudal recovered (Fig.9; MRS-Pv 200) is large and have a centrum slightly inclined anteriorly less than *Gondwanatitan* (KELLNER & AZEVEDO, 1999) and *Aeolosaurus* POWELL, 1986. The anterior face of the centrum is as wide as high. The neural arch is located over the anterior border of the centrum, like *Aeolosaurini* species. The neural spine is thicker distally, and has a quadrangular contour in dorsal view. It is supported by the prespinal and postspinal laminae.

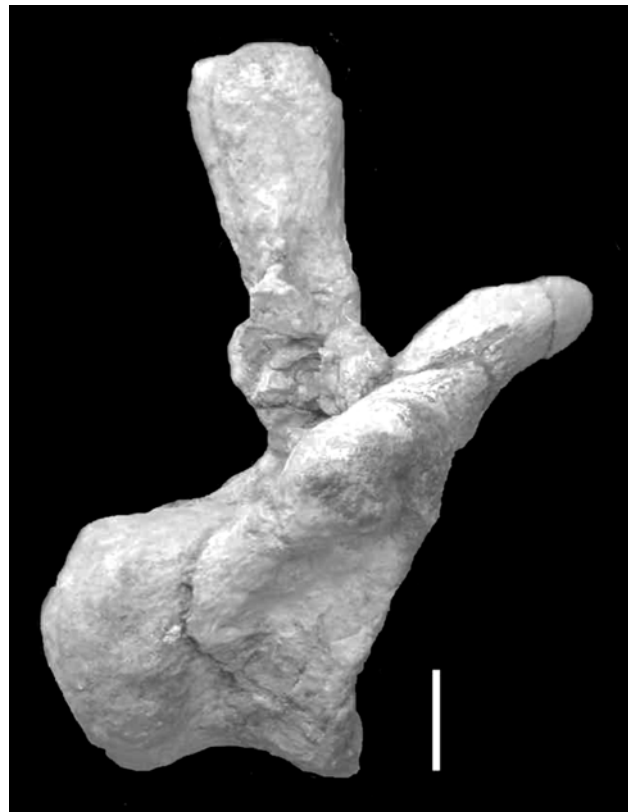


Fig.9- *Muyelensaurus pecheni* gen. et sp.nov., anterior caudal vertebra (MRS-Pv 200) in lateral view. Scale bar = 5cm.

In *Rinconsaurus* the neural spines of the anterior caudals are less thick than they are distally. The partially preserved transverse processes are wide and posteriorly directed. The characteristic process of the postzygapophyseal facets, present in *Rinconsaurus caudamirus* (MRS-Pv 23), is absent in *Muyelensaurus*.

Other anterior and middle caudal vertebrae correspond to a middle-sized specimen (MRS-Pv 377, 137, 174, 408, 214, 252, and 173) or to a juvenile specimen (MRS-Pv 164 and 193). In anterior caudals (MRS-Pv 137) the centra are slightly inclined anteriorly, but this character disappears toward the middle section of the tail.

All anterior caudals lack the postzygapophyseal

process that is present in *Rinconsaurus*. In contrast, middle and middle-posterior caudals (MRS-Pv 193, 164, and 135) share with *Rinconsaurus* the presence of a postzygapophyseal process (Figs.10-11). The neural spines are incomplete, but the preserved portion indicates an elongate morphology axially extended, and posterior caudal centra are depressed posteriorly. The distal caudals (MRS-Pv 170, 171, 190, 189, and 209) are similar to those of *Rinconsaurus*. They have very reduced neural spines slightly inclined anteriorly that become horizontal toward the distal end of the tail. In contrast to *Rinconsaurus*, the neural arch of the distal caudal are reduced anteroposteriorly since they never reach the half of the centrum length.

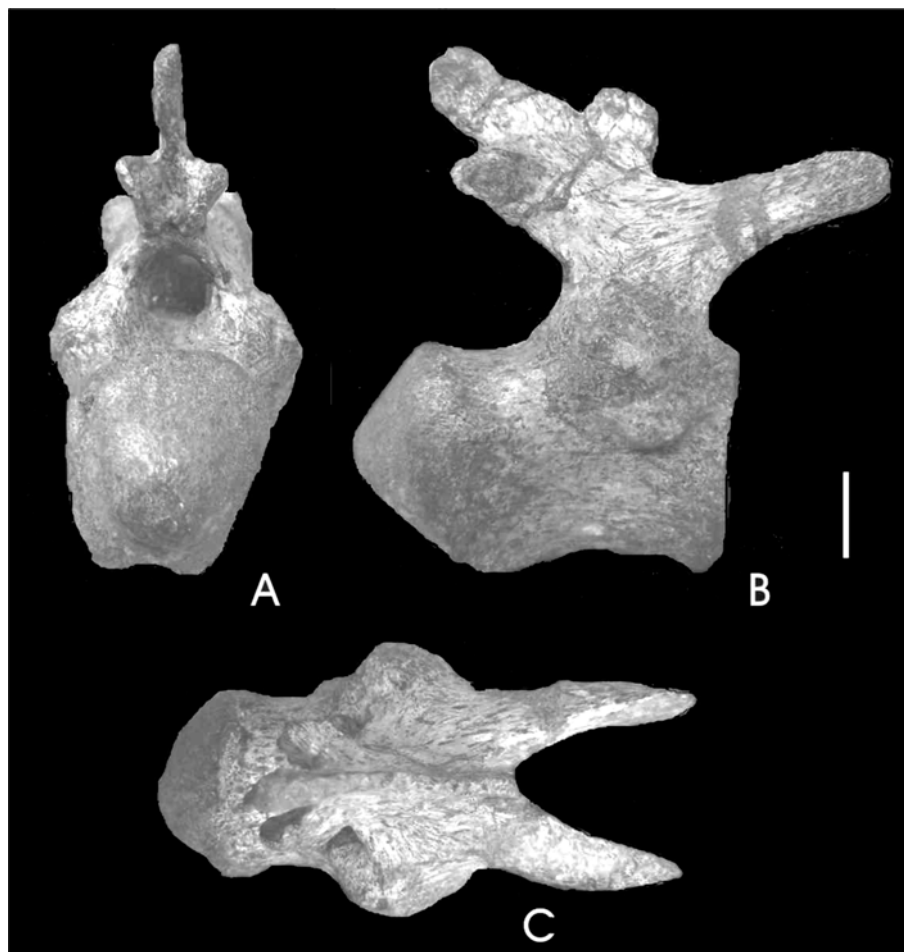


Fig.10- *Muyelensaurus pecheni* gen. et sp.nov., middle caudal vertebra (MRS-Pv 164) in anterior (A), lateral (B) and dorsal (C) views. Scale bar = 2cm.

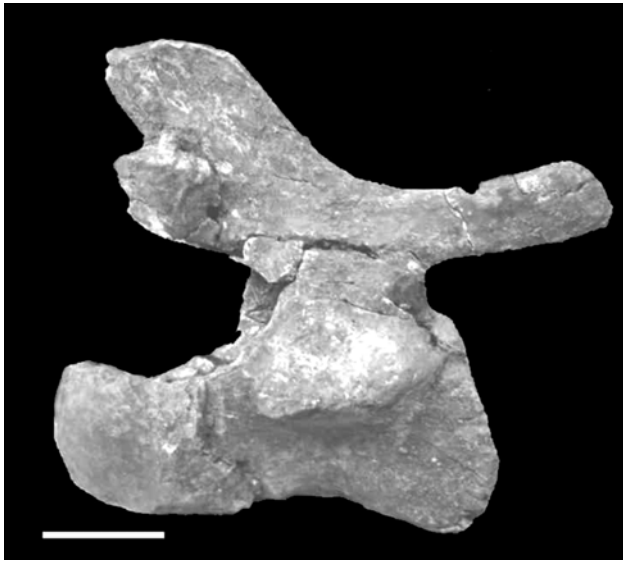


Fig.11- *Muyelensaurus pecheni* gen. et sp.nov., posterior caudal vertebra (MRS-Pv 135) in lateral view. Scale bar = 2cm.

Appendicular bones – The abundant bones recovered are similar to those of *Rinconsaurus* and other titanosaurs, but show some differences. They will be described in detail elsewhere. The sternal plate (MRS-Pv 125) exhibits a typical semilunar contour, and its posterior border is not straight as that present in some titanosaurs, like *Mendozasaurus* and *Malawisaurus* (GONZÁLEZ RIGA, 2003).

A complete right scapula (Fig. 12.A; MRS-Pv 259) and two partial scapular blades (MRS-Pv 396 and 397) were recovered. The scapula, a long and laminar bone, has a thin and slender scapular blade. The distal end is expanded, the diagonal acromion is thin and the supracoracoideus fossa is very prominent. The ventral border is slightly concave up to its union with the proximal end, where begins a new concave border. Six humeri were collected (MRS-Pv 70, 132, 212, 352, 357, and 387). One left humerus (Fig.12B; MRS-Pv 70) is the best preserved. It is relatively slender, since the proximal width reaches the 25 percent of the total length.



Fig.12- *Muyelensaurus pecheni* gen. et sp.nov., right scapula (MRS-Pv 259) in lateral view (A), left humerus (MRS-Pv-70) in anterior view (B). Scale bar = 10cm.

The proximal end is straight and the humeral head is small, prominent and acute; morphology has not been described in other titanosaurs. In the anterior face, the deltopectoral crest is thin, well developed and extend more than a half of the proximal portion. In posterior view, the distal end shows the radial condyle greater than the ulnar condyle.

The ulna, radius and metacarpals are similar to those of *Rinconsaurus*. In particular, the metacarpals exhibit expanded ends, reduced diaphyses and have not convex phalangeal articular facets, like in all Titanosauria (SALGADO *et al.*, 1997a; CALVO & GONZÁLEZ RIGA, 2003).

The ilium, ischium and pubis are similar (Fig.13), in general lines, to those of *Rinconsaurus*. However, the pubis has an open foramen and a quadrangular and thicker medially distal end, in contrast to *Rinconsaurus* that shows a more rounded and thin end.

The femora and tibiae remains suggest the presence of five specimens. The femur is long and straight. It has a lateral bulge poor developed comparing to others titanosaurs and in anterior view it has a convex border less acute than *Rinconsaurus*. The femoral head is small and it extends dorsally surpassing the

greater trochanter. The fourth trochanter is placed at over the midhalf of the total length. The tibial condyle is slightly smaller than the fibular one.

The tibia is a slender bone wider on proximal end than on the distal end. The cnemial crest is curved and anterolaterally directed. The fibulae are long and of sigmoidal shape. In lateral view, the proximal end has the dorsal border convex and it is more expanded than the distal one. The distal border is straight. The anterior border is concave except on the distal end where it is inclined posteriorly. The left astragalus has been preserved (MRS-Pv 187). It is subtriangular and robust. The ascending process is a small ridge. There is a smooth longitudinal depression below the ascending process for articulation of the fibula. In posterior view, the posterior astragalar fossa is small and it is restricted to the upper portion. The entire astragalar surface displays rugosities of cartilaginous insertion. Several metatarsals corresponding to two specimens, a smaller (MRS-Pv 142, 54, and 50) and one larger (MRS-Pv 168, 166, 52, 51, 128, and 141) have been recovered. The phalanges are similar, in general lines, to those of *Mendozasaurus* (GONZÁLEZ RIGA, 2003) and *Epachthosaurus* (MARTÍNEZ *et al.* 2004).

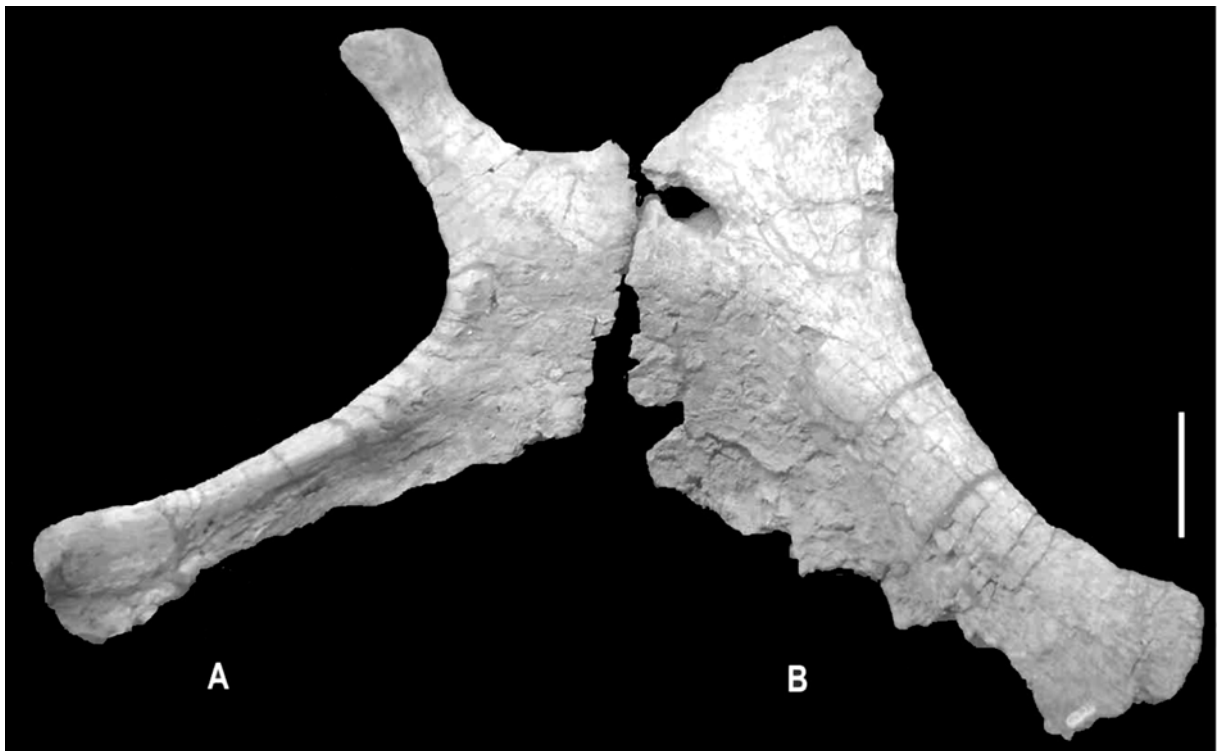


Fig.13- *Muyelensaurus pecheni* gen. et sp.nov., pubis and ischium (MRS-Pv 88) in lateral view. Scale bar = 10cm.

COMPARISON AND DISCUSSION

Cladistic analyses of Titanosauria have been worked by several authors since 1995 (SALGADO *et al.*, 1997a; WILSON & SERENO, 1998; UPCHURCH, 1998; WILSON & UPCHURCH, 2003). In most of these analyses few titanosaur taxa were included because the objective was to support the higher level of the Sauropoda phylogeny. Then, it was used similar titanosaurid taxa choosing different characters; therefore, taxon names have changed as well as node names in the different published trees. In order to improve the phylogenetic position of taxa inside the Titanosauria, in this paper, we have used the data matrix and characters proposed by SALGADO *et al.* (1997a), WILSON & SERENO (1998), UPCHURCH (1998), WILSON (2002), WILSON & UPCHURCH (2003), GONZÁLEZ RIGA (2003), CALVO & GONZÁLEZ RIGA (2003) and we have evaluated all them adding new ones. The phylogenetic relationships of *Muyelensaurus pecheni* plus 17 other taxa were analyzed through a parsimony cladistic analysis based on 65 characters (see Appendix, Tab.1).

Camarasaurus grandis (COPE, 1877) was considered as outgroup, and *Brachiosaurus brancai* (JANENSCH, 1950), *Chubutisaurus insignis* (DEL CORRO, 1975; SALGADO, 1993), *Andesaurus delgadoi* (CALVO & BONAPARTE, 1991), *Malawisaurus dixeyi* (JACOBS *et al.* 1993), *Mendozasaurus neguyelap* (GONZÁLEZ RIGA, 2003; 2005), *Epachthosaurus sciuttoi* (POWELL, 1990; MARTÍNEZ *et al.*, 2004), *Aeolosaurus rionegrinus* (POWELL, 1986; SALGADO & CORIA, 1993; SALGADO *et al.*, 1997b), *Gondwanatitan faustoi* (KELLNER & AZEVEDO, 1999), *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003), *Rapetosaurus krausei* (CURRY ROGERS & FORSTER, 2001, 2004), *Lirainosaurus astibiae* (SANZ *et al.*, 1999), *Alamosaurus sanjuanensis* (GILMORE, 1946), *Neuquensaurus australis* (HUENE, 1929; POWELL, 1986; SALGADO *et al.*, 2005), *Opisthocoelicaudia skarzynskii* (BORSUK-BIALYNICKA, 1977), *Saltasaurus loricatus* (BONAPARTE & POWELL, 1980; POWELL, 1992), *Rocasaurus muniozi* (SALGADO & AZPILICUETA, 2000), and *Muyelensaurus pecheni* gen. et sp.nov. formed the ingroup.

The data matrix was analyzed with Nona, version 2.0 (GOLOBOFF, 1993). The application of the heuristic method produced one most parsimonious tree with a length of 105 steps and high consistency and retention indices (C.I. = 0.76; R.I. = 0.78). The multistate characters were considered unordered. The cladogram obtained (Fig.14) is similar, in general lines, to previous studies (SALGADO *et al.*,

1997a; WILSON, 2002; GONZÁLEZ RIGA, 2003; CALVO & GONZÁLEZ RIGA, 2003) but presents differences due to the inclusion of new taxa and characters.

Titanosauria, proposed originally by BONAPARTE & CORIA (1993), was defined as the most recent common ancestor of *Andesaurus delgadoi* and Titanosauridae, and all of its descendants (SALGADO *et al.*, 1997a). This node-based group, was redefined by different criteria or replaced by other names, but in a recent analysis, WILSON & UPCHURCH (2003) follow the original definition of SALGADO *et al.* (1997a). In our analysis, Titanosauria (Fig.14, node 3) is supported by seven synapomorphies obtained by delayed optimization: centroparapophyseal lamina in posterior dorsal vertebrae (26.1), ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae (27.1), posteriorly acuminate pleurocoels in dorsal vertebrae (29.1), laminated and anteroposteriorly elongated neural spine in middle caudal vertebrae (43.1), absence of distal phalangeal articular facets in metacarpals (55.1), pubis longer than ischium (56.1), and posterior process of the ischium less than the twice of the length of pubis articulation (57.1).

Titanosauridae was defined originally by SALGADO *et al.* (1997a) as the clade including the most recent common ancestor of *Malawisaurus*, *Epachthosaurus*, *Argentinosaurus*, *Opisthocoelicaudia*, *Aeolosaurus*, *Alamosaurus*, Saltosaurinae, and all of its descendants. In posterior analyses, SERENO (1998) and WILSON & UPCHURCH (2003) claimed that Titanosauridae must be abandoned due to the type species of *Titanosaurus indicus* that is invalid. However, SALGADO (2003) indicated that the name Titanosauridae, according the Phylocode, should not necessarily be abandoned, and redefined this clade again. During this controversial positions, diverse authors avoided the use of Titanosauridae and it was replaced by others (*e.g.* Titanosauria, Titanosauroidae, Saltosauridae) (see SALGADO, 2003). In this confusing context, it is important to remark that:

- 1) Several authors propose to replace Titanosauridae for Saltosauridae, but this last clade is less inclusive (SERENO, 1998; WILSON & UPCHURCH, 2003); in other words, Saltosauridae and Titanosauridae are not equivalent groups such as claimed by SALGADO (2003). Saltosauridae *sensu* SERENO (1998) exclude *Malawisaurus*, *Mendozasaurus*, and other taxa that lack strongly procoelous middle caudals. Summing-up, all these hypothesis include few titanosaurid taxa, excluding important species like *Aeolosaurus*.

- 2) Titanosauridae *sensu* SALGADO *et al.* (1997a) has nomenclatural priority in relation to the clade Lithostrotia proposed by WILSON & UPCHURCH (2003) because it was defined in the same way.
- 3) The new definition of Titanosauridae of SALGADO (2003) excludes *Malawisaurus* because this taxon lacks strongly procoelous middle caudals. However, *Opisthocoelicaudia* has not this character and is included within Titanosauridae. In this context, we think that the definition of a clade must be founded in a group of characters supported by cladistic analyses. Moreover, the procoely of the caudal series is a variable character in titanosaurs. For example, *Rinconosaurus* shows a typical

strongly procoelous caudal sequence discontinued by amphicoelous, opisthocoelous, and biconvex centra (CALVO & GONZÁLEZ RIGA, 2003). On the other hand, *Mendozasaurus* has slightly procoelous middle caudal centra with reduced posterior condyles, associated with typical strongly procoelous anterior caudal vertebrae (GONZÁLEZ RIGA, 2003). A particular case is observed in *Malawisaurus*, from the Lower Cretaceous of Africa. It has strongly procoelous anterior caudal centra apparently associated with gently amphicoelous or platycoelous middle and posterior caudals (JACOBS *et al.*, 1993; GOMANI, 1999).

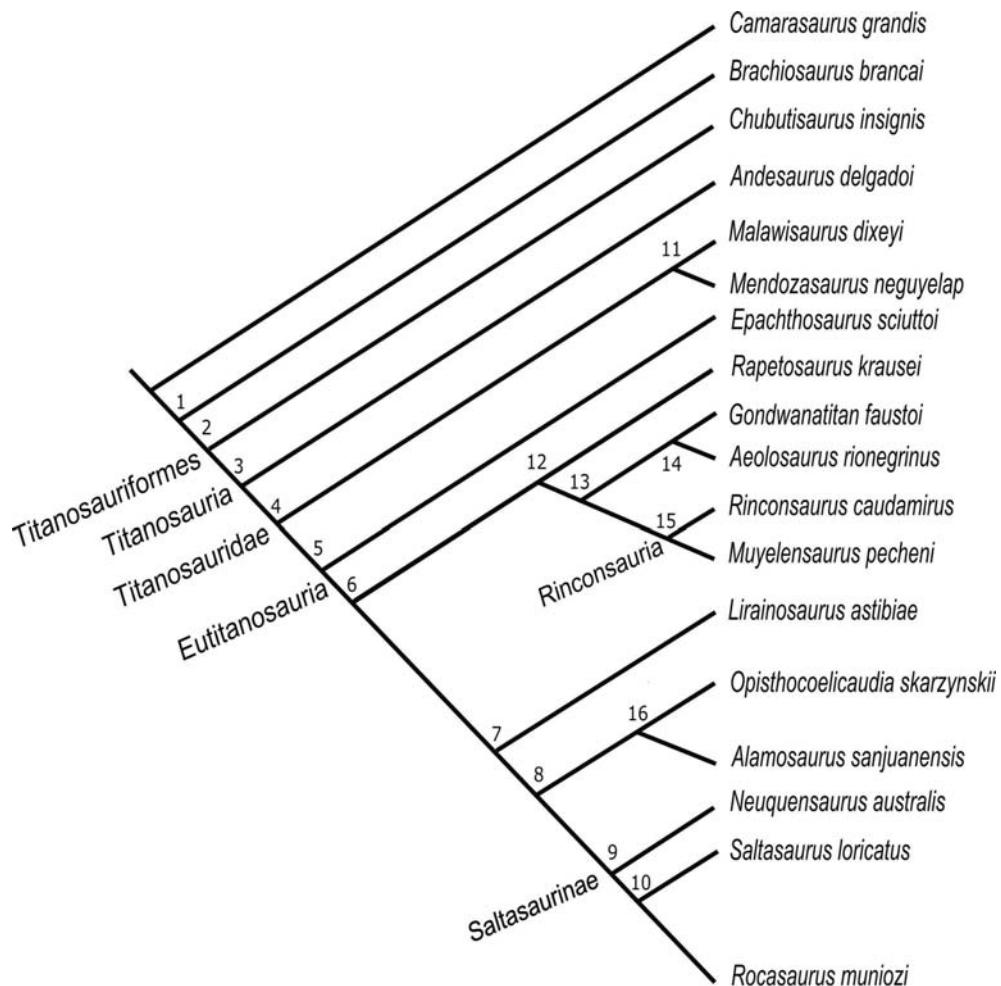


Fig. 14- A most parsimonious tree determined by cladistic analysis (105 steps; CI 0.76; RI 0.78; see matrix in Appendix) showing the phylogenetic relationships of *Muyelensaurus pecheni* gen. et sp.nov. References: Aeolosaurini (node 14), Rinconsauria (node 15), Opisthocoelicaudinae (node 16) and Saltasaurinae (node 9).

In this context, we prefer to use the original phylogenetic definition of Titanosauridae *sensu* SALGADO *et al.* (1997a), since this name has a long usage, it is compatible with the PhyloCode (CANTINO & QUEIROZ, 2000) and it is supported by a cladistic analysis of many Titanosauridae taxa.

In our phylogenetic analysis, we use 14 Titanosauridae taxa. Herein, Titanosauridae (Fig. 14, node 4) is supported by 10 synapomorphies defined by delayed optimization: pencil chisel-like (8.1), absence of cervical pleurocoels divided by septa (13.1), procoelous first caudal vertebra (31.1), strongly procoelous anterior caudal centra, with prominent condyles (37.2), prezygapophyses length between 40 to 50 percent with respect to the centrum length in middle caudal vertebrae (44.1), scapular glenoid strongly beveled medially (48.1), humerus with straight or slightly curved proximal border (50.1), prominent ulnar olecranon process (51.1), semilunar sternal plates (52.1), and presence of osteoderms (65.1).

This phylogenetic analysis confirms the hypothesis proposed by GONZÁLEZ RIGA (2003) that *Malawisaurus* is the sister group of *Mendozasaurus* and these two taxa are considered basal titanosaurids.

Muyelensaurus, a more derived titanosaurid, can be clearly diagnosed as an Eutitanosauria SANZ *et al.*, 1999, but following the new phylogenetic definition of SALGADO (2003): "all titanosaurs closer to *Saltasaurus* than to *Epachthosaurus*". Within Eutitanosauria, we recognize two different clades: Aeolosaurini (FRANCO-ROSAS *et al.*, 2004) and Rinconsauria *nov.* (Fig. 14, node 15).

Aeolosaurini FRANCO-ROSAS *et al.* (2004) was diagnosed by having: 1) anterior and middle caudal centra with the anterior faces inclined forward, 2) neural arches located over the anterior border in middle caudal centra, 3) middle caudal neural spines forward directed, 4) elongated prezygapophysis in middle caudals with respect to the displacement of the neural arch forward, 5) prezygapophyseal and postzygapophyseal facets elongated anteroposteriorly, at least in anterior and middle caudals. They include *Aeolosaurus*, *Gondwanatitan*, and *Rinconsaurus*, but they did not support it by a cladistic analysis. However, *Rinconsaurus* lacks characters 1, 2 and 3, and the 4 and 5 are difficult to evaluate; for this reason *Rinconsaurus* should be excluded.

The most important aspect of our analysis is the definition of a new clade named herein Rinconsauria (node 15) that includes *Rinconsaurus*

and *Muyelensaurus*. Both taxa are relatively slender and middle-sized Eutitanosauria that have suboval teeth with labial and lingual faces well differentiated by crests, bony processes that support the postzygapophyseal facets in middle caudal vertebrae, and posterior caudal centra depressed posteriorly. The robustness of the Rinconsauria node was valued by bootstrap and jackknife indices that reach values of 90 and 74, respectively.

The finding of *Muyelensaurus* allows us to improve the diagnosis of *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003) as the following association of features: neural spines in mid-anterior dorsal vertebrae inclined posteriorly more than 60 degree with respect to the vertical; anterior caudal vertebrae with bony processes that support the postzygapophyseal facets; accessory centroparapophyseal lamina extended from the base of the parapophysis to the base of centrodiapophyseal lamina in posterior dorsal vertebrae; procoelous posterior caudal centra with intercalation of a series of amphicoelous-biconvex centra.

Muyelensaurus pecheni gen. et sp.nov. is characterized by the following autapomorphies: basal tubera diverge 70 degree from each other; extensive, thin and concave lamina that unites basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae. With respect to the basal tubera, we recognized a diverse morphology. For example, the basal tubera of *Rapaetosaurus* (FMNH PR 2197; CURRY ROGERS & FORSTER, 2004) diverge 55 degree and lacks a concave ventral lamina. *Nemegtosaurus* (NOWINSKI, 1971) shows basal tubera that diverge less than 30 degree and they have not an extensive ventral lamina. In similar way, *Quaesitosaurus orientalis* (KURZANOV & BANNIKOV, 1983) shows basal tubera that diverges 45 degree and have a fossa under the basioccipital. Moreover, the basal tubera are not well differentiated to robust basipterygoid processes. In an unnamed titanosaurid from Patagonia (MUCPv 334; CALVO & KELLNER, 2006), the basal tubera diverge 50 degree, and are united ventrally by a thick bony bridge. In *Antarctosaurus septentrionalis* (CHATTERJEE & RUDRA, 1996), the basal tubera are very separated from each other, but not diverge from the basioccipital. Moreover, the basal tubera are not united by a slightly concave ventral lamina, and show facets divided ventrally in two small processes. In unnamed titanosauriform from Texas (TIDWELL & CARPENTER, 2003), the basal tubera diverge only 15

degree and are relatively short and robust, and lack the bony lamina. In *Bonatitan reigi* (MCN-PV RN 821; MARTINELLI & FORASIEPI, 2004), the basal tubera diverge less than 60 degree and lack the ventral lamina. Finally, complete different are basal tubera present in *Titanosaurus indicus* (CHATTERJEE & RUDRA, 1996) because they are subdued and completely fused with the basiptyergoid process.

The discovery of *Muyelensaurus* shows that the eutitanosaurs from Patagonia form a new clade named herein Rinconsauria, that include small and middle-sized sauropods different from the Aeolosaurini taxa (*Aeolosaurus* and *Gondwanatitan*) as well as from more derived species belonging to the clade Opisthocoelicaudiinae (McINTOSH, 1990) and Saltasaurinae (SALGADO *et al.*, 1997a).

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APPENDIX:

TABLE 1

In the Character-Taxon Matrix is shown the distribution of 65 characters corresponding to 17 taxa of sauropods. Characters have been defined or modified by the authors cited in the list.

CHARACTER	TAXON MATRIX							
<i>Camarasaurus grandis</i>	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000000
<i>Brachiosaurus brancai</i>	0001000110	1000001001	0100100000	0000000010	0000000000	0000000010	0000000010	11100
<i>Chubutisaurus insignis</i>	??????????	??????????	???2?0001	?0?00001?	???0???00	???0?????	????1110??	?01??
<i>Andesaurus delgadoi</i>	??????????	??????????	?1?0111011	?0?0001010	0010000?0?	???1110??	????1110??	?01??
<i>Malawisaurus dixeyi</i>	???????210	?11000?00?	?1?0211111	??10002010	0?11000???	1110?10??	????1110??	???11
<i>Mendozasaurus neguyelap</i>	??????????	??1010?122	?10?2??111	?110002110	0111000101	111?1?????	????1110??	?0111
<i>Epachthosaurus sciuttoi</i>	??????????	??????????	?111211011	1?0002210	0011000101	11?11?111	????1110??	1011?
<i>Rapetosaurus krausei</i>	1110111212	201000100?	1111211111	1?00002210	010?000101	110?111011	????1110??	101?1
<i>Lirainosaurus astibiae</i>	???????21?	??????????	?1?1211111	?11?002210	0000000?01	?101??????	????1110??	?01?1
<i>Rinconsaurus caudamirus</i>	???????211	?010001011	?111211111	1??002210	0101011101	1101111111	????1110??	101??
<i>Muyelensaurus pecheni</i>	1110111211	?11000?011	?111211111	1?0?002210	0201011101	110?111111	????1110??	1011?
<i>Gondwanatitan faustoi</i>	??????????	??????????	?111211111	11??12220	1002001?0?	?????0111	????1110??	??1??
<i>Aeolosaurus rionegrinus</i>	???????212	??????????	?1??2?????	?30?012220	1102001?01	?10?1101??	????1110??	??11?
<i>Opisthocoelicaudia skarzynskii</i>	??????????	??????????	1011210111	1211000010	0200000111	1101111111	????1110??	1011?
<i>Alamosaurus sanjuanensis</i>	???????2?2	?010001001	?1?1200111	1311002210	0200000101	1111111211	????1110??	1011?
<i>Neuquensaurus australis</i>	??????????	?011001012	?111211111	131?102211	0200000101	11011?1211	????1110??	1?111
<i>Saltasaurus loricatus</i>	1?10010212	?001011012	?111211111	110?102211	0200100112	1101111211	????1110??	10111
<i>Rocasaurus muniozi</i>	??????????	???????01?	?111211111	???102211	0?00100???	????111211	????1110??	1?1??

LIST OF CHARACTERS

1. Frontal contribution to supratemporal fossa: absent (0); present (1) (WILSON & SERENO, 1998).
2. Parietal occipital process, dorsoventral height: deep, nearly twice the diameter of the foramen magnum (0); short, less than the diameter of the foramen magnum (1) (WILSON, 2002).
3. Parietal, contribution to post-temporal fenestra: absent (0); present (1) (WILSON, 2002).
4. Parietal, distance separating supratemporal fenestrae: less than (0); or twice (1); the long axis of supratemporal fenestra (WILSON, 2002).
5. Supraoccipital, height: twice (0); subequal (1); or less (2) than height of foramen magnum (WILSON, 2002).
6. Paroccipital process, ventral non-articular process: absent (0); present (1) (WILSON, 2002).
7. Longitudinal groove on the supraoccipital: absent (0); present (1) (CURRY ROGERS, 2005).
8. Tooth shape: spoon-like (0); compressed cone chisel-like (1); pencil chisel-like (2) (modified from CALVO, 1994 by CALVO & GONZÁLEZ RIGA, 2003).
9. Wear facets of teeth sharply inclined: absent (0); present (1) (SALGADO & CALVO, 1997).
10. Tooth crowns, cross-sectional shape at mid-crown: D-shaped (0); subcylindrical with smooth crest (1); cylindrical (2) (modified from WILSON & SERENO, 1998).
11. Cervical vertebrae, number: 12 (0); 13 (1); 14 or more (2) (UPCHURCH, 1998).
12. Pleurocoels in anterior and middle cervical vertebrae: present (0); absent (1) (modified from CALVO & SALGADO, 1995).
13. Cervical pleurocoel divided by lamina or septa: present (0); absent (1) (UPCHURCH, 1998).
14. Cervical prezygapophyses, relative length: articular facets that surpass (0); or not surpass (1) the centra (SALGADO *et al.*, 1997a).
15. Posterior cervical neural spines laterally expanded and wider than the centra: absent (0); present (1) (GONZÁLEZ RIGA, 2005).
16. Neural spines in cervical vertebrae: tall (0); small (1) (modified from CALVO & SALGADO, 1995).
17. Anterior cervical neural spines: bifid (0); single (1) (UPCHURCH, 1998).
18. Posterior cervical vertebrae, proportions - ratio total height / centrum length: less (0); or more (1) than 1.5 (modified from CALVO & SALGADO, 1995 by GONZÁLEZ RIGA, 2005).

19. Supradiapophyseal fossa in posterior cervical vertebrae: absent (0); shallow or reduced (1); deep and extended (2) (GONZÁLEZ RIGA, 2005).
20. Posterior cervical centra, proportions: ratio anteroposterior length / height of posterior face: >3 (0); between 2,5 and 1,5 (1); less than 1,5 (2) (modified from WILSON, 2002).
21. Dorsal vertebrae, number: 12 (0); 11 (1) (McINTOSH, 1990).
22. Anterior dorsal neural spines, shape: bifid (0); single (1) (McINTOSH, 1990).
23. Anterior dorsal neural spines inclined posteriorly more than 20 degree from vertical: absent (0); present (1) (modified from WILSON & SERENO, 1998).
24. Posterior dorsal neural spines, dorsal development: more (0); or less (1) than 20 percent of the total height of the vertebra (modified from SANZ *et al.*, 1999 from GONZÁLEZ RIGA, 2003).
25. Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of neural spine (1); present all along the neural spine (2) (SALGADO *et al.*, 1997a).
26. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (BONAPARTE & CORIA, 1993).
27. Ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (SALGADO *et al.*, 1997a).
28. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (SALGADO *et al.*, 1997a).
29. Pleurocoels in dorsal vertebrae, shape: circular or elliptical (0); posteriorly acuminate (1) (SALGADO *et al.*, 1997a).
30. Camellate or somphospondylous types of internal structures of presacral vertebrae: absent (0); present (1) (modified from WILSON & SERENO, 1998 by GONZÁLEZ RIGA, 2003).
31. Sacral vertebrae, number: five (0); six or more (1) (McINTOSH, 1990).
32. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3) (SALGADO *et al.*, 1997a).
33. Wide and deep interzygapophyseal cavity in caudal vertebrae: absent (0); present (1).
34. Caudal transverse processes: disappear by caudal 15 (0); disappear by caudal 10 (1) (WILSON, 2002).
35. Anterior and middle caudal centra, proportions: as high as wide (0); depressed, wider than high (1) (SALGADO *et al.*, 1997a).
36. Mid caudal centra with the anterior face strongly inclined anteriorly: absent (0); present (1) (FRANCO-ROSAS *et al.*, 2004).
37. Articular face shape on anterior caudal centra: non-procoelous (0); slightly procoelous (1); strongly procoelous with prominent condyles (2) (modified from SALGADO *et al.*, 1997a by GONZÁLEZ RIGA, 2003).
38. Articular face shape on middle caudal centra: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2) (modified from SALGADO *et al.*, 1997a by GONZÁLEZ RIGA, 2003).
39. Neural arch in anterior caudal vertebrae: placed in the middle of the centrum (0); anteriorly (1); on the anterior border (2) (SALGADO *et al.*, 1997a).
40. Anterodorsal border of neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0); present (1) (SALGADO *et al.*, 1997a).
41. Anteriorly directed anterior caudal neural spine: absent (0); present (1).
42. Shape of the section of neural spines in most anterior caudal vertebrae in dorsal view: axially elongated (0); transversely elongated (1); quadrangular (2).
43. Neural spine in middle caudal vertebrae, shape: short anteroposteriorly (0); laminated and anteroposteriorly elongated (1) (modified from GONZÁLEZ RIGA, 2003 by BONAPARTE *et al.*, 2006).
44. Length proportions of prezygapophyses with respect to the centrum length in middle caudal vertebrae: shorter than 50 % (0); between 40 to 50% (1); longer than 50 % (2) (modified from GONZÁLEZ RIGA, 2003).
45. Ventral depression divided by a longitudinal septum in anterior and middle caudal vertebrae: absent (0); present (1) (SALGADO & AZPILICUETA, 2000).
46. Postzygapophyseal process in middle caudal vertebra: absent (0); present (1).
47. Well developed interprezygapophyseal lamina in middle caudal vertebrae: absent (0); present (1).
48. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (WILSON and SERENO, 1998).
49. Humerus, breadth of proximal end with respect to the total length: less (0); or more (1) than the 50 percent (GONZÁLEZ RIGA, 2003).
50. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2) (modified from UPCHURCH, 1998 by GONZÁLEZ RIGA, 2002).
51. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1) (WILSON and SERENO, 1998).
52. Sternal plates, shape: suboval (0); semilunar (1) (SALGADO *et al.*, 1997a).
53. Semilunar sternal plate with straight posterior border: absent (0); present (1) (GONZÁLEZ RIGA, 2003).
54. Coracoid, shape: suboval (0); quadrangular (1) (SALGADO *et al.*, 1997a).
55. Metacarpals, distal phalangeal articular facets: present (0); absent (1) (SALGADO *et al.*, 1997a).
56. Pubis, length with respect to ischium length: shorter or equal (0); longer (1) (SALGADO *et al.*, 1997a).
57. Ischium, posterior process twice or more the length of pubis articulation: present (0); absent (1) (modified from SALGADO *et al.*, 1997a by CALVO & GONZÁLEZ RIGA, 2003).

58. Ischium, iliac pedicel: short and poorly developed (0); slender and well developed (1); wide and well developed (2) (CALVO & GONZÁLEZ RIGA, 2003).
59. Shape of preacetabular lobe of ilium: moderately expanded (0); broadly expanded and directed upward (1) (SALGADO *et al.*, 1997a). 60. Orientation of preacetabular lobe of ilium: nearly vertical (0); nearly horizontal and laterally projected (1) (SALGADO *et al.*, 1997a).
61. Relative orientation of the pubic peduncle of ilium: angled (0); perpendicular with respect to the sacral axis (1) (SALGADO *et al.*, 1997a).
62. Humerus / femoral ratio of 0.90 or more: absent (0); present (1) (McINTOSH, 1990).
63. Lateral bulge of femur, below the greater trochanter: absent (0); present (1) (McINTOSH, 1990).
64. Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1) (SALGADO *et al.*, 1997a).
65. Osteoderms: absent (0); present (1) (SANZ *et al.*, 1999).