Rinconsaurus caudamirus gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina

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ABSTRACT

Rinconsaurus caudamirus gen. et sp. nov. (Dinosauria, Sauropoda) is a new and slender Titanosauridae. The specimens come from the Upper Cretaceous strata of the Río Neuquén Formation at Rincón de los Sauces, Neuquén Province, Patagonia, Argentina. The remains include 13 articulated caudal vertebrae and disarticulated cranial, cervical, dorsal and appendicular materials. These fossils belong to three individuals, two adults and one juvenile. This new species is characterized by the following association of autapomorphies: (1) neural spines in mid-anterior dorsal vertebrae inclined posteriorly more than 60 degrees with respect to the vertical, (2) middle caudal vertebrae with bony processes that support the articular surfaces of postzygapophyses, and (3) procoelous posterior caudal centra with intercalation of a series of amphicoelous-biconvex or amphicoelous-opisthocoelous-biconvex centra. A cladistic phylogenetic analysis placed *Rinconsaurus* in the family Titanosauridae. Within Titanosauridae (*Rinconsaurus* + *Aeolosaurus*) is considered a sister group of the clade (*Opisthocoelicaudia* + (*Alamosaurus* + (*Neuquensaurus* + *Saltasaurus*))). *Rinconsaurus caudamirus* has preserved short articulated posterior caudal series with amphicoelous, opisthocoelous and biconvex centra. This unusual morphology represents the first such occurrence in sauropod dinosaurs. From the systematic point of view, this discovery is important because Titanosauridae were traditionally defined, among other characters, by strongly developed procoelia in their caudal vertebrae.

Key words: Dinosauria, Sauropoda, Titanosauridae, Late Cretaceous, Neuquén, Argentina.

RESUMEN

***Rinconsaurus caudamirus* gen. et sp. nov., un nuevo titanosáurido (Dinosauria, Sauropoda) del Cretácico Tardío de Patagonia, Argentina.** *Rinconsaurus caudamirus* gen et sp. nov. (Dinosauria, Saurpoda) es un nuevo y esbelto Titanosauridae proveniente de la Formación Río Neuquén, Cretácico Superior de Rincón de los Sauces, Provincia de Neuquén, Patagonia, Argentina. Sus restos están integrados por 13 vértebras caudales articuladas y materiales craneales, cervicales, dorsales y apendiculares desarticulados, que pertenecen a tres individuos, dos adultos y un juvenil. Este nuevo taxón se caracteriza por la siguiente asociación de autapomorfías: (1) vértebras dorsales medioanteriores con espinas neurales inclinadas posteriormente más de 60 grados con respecto a la vertical, (2)

vértebras caudales medias con procesos óseos que sostienen las carillas articulares de las poszigapófisis y (3) vértebras caudales procélicas con intercalaciones de series con centros anficélicos y bioconvexos, o con centros anficélicos, opistocélicos y biconvexos. Un análisis filogenético cladista permite incluir a *Rinconsaurus* en la familia Titanosauridae. Dentro de Titanosauridae (*Rinconsaurus* + *Aeolosaurus*) es considerado un grupo hermano del clado (*Opisthocoelicaudia* + (*Alamosaurus* + (*Neuquensaurus* + *Saltasaurus*))). *Rinconsaurus caudamirus* presenta dos cortas secuencias caudales posteriores articuladas con centros anficélicos, opistocélicos y biconvexos. Esta inusual morfología se registra por primera vez en dinosaurios saurópodos. Es importante desde el punto de vista sistemático, ya que Titanosauridae ha sido tradicionalmente definido, entre otros caracteres, por la presencia de fuerte procelia en sus vértebras caudales.

Palabras claves: Dinosauria, Sauropoda, Titanosauridae, Cretácico Tardío, Neuquén, Argentina.

INTRODUCTION

Titanosauridae constitutes a group of sauropod dinosaurs with a wide geographical distribution and diverse adaptive types (Salgado *et al.*, 1997a). In South America the record of Titanosauridae is particularly abundant. They are known since the XIX century (Lyddeker, 1893). During the Late Cretaceous, titanosaurids were important primary consumers in the ecosystems of Patagonia, as the ornithischians were in the North America. This difference has been explained by the gradual isolation of South America during most of the Late Cretaceous (Huene, 1929; Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987). Recent studies show that the biogeographic history of the titanosaurs is a complex subject to analyze (Wilson and Sereno, 1998; Curry Rogers and Foster, 2001).

Text-FIG. 1. Map of Neuquén Basin (Patagonia, Argentina) showing the locality where the holotype of *Rinconsaurus caudamirus* gen. sp. nov. was found.

The Neuquén Province, situated in northern Patagonia, has yielded many well preserved titanosaurid fossils from the Neuquén and Malargüe Groups (Calvo and Bonaparte, 1991; Bonaparte and Coria, 1993; Salgado and Calvo, 1993; Calvo and Salgado, 1995).

In the last five years, extraordinary titanosaurid fossils were found in the region of Rincón de los Sauces, northern Neuquén Province. Some of these discoveries include articulated specimens (Calvo *et al.*, 1997; Coria and Salgado, 1998; Calvo and González Riga, 1999; González Riga and Calvo, 1999; 2001). The excavations of these discoveries were coordinated by investigators of the National University of Comahue and they have been partially supported by the local Town Hall.

The aim of this work is to describe a new titanosaurid from the Río Neuquén Formation, *Rinconsaurus caudamirus* gen. et sp. nov.

The specimens described here were found in 1997 by Gabriel Benítez at Cañadón Río Seco, 2 km north of Rincón de los Sauces (text Fig. 1). They were extracted by the paleontologist J. Calvo and his team of the Paleontology Museum of the National University of Comahue. Fossil remains are housed at the Laboratory of Rincón de los Sauces Museum under the abbreviation MRS-Pv.

SYSTEMATIC PALEONTOLOGY

Order Saurischia Seeley, 1887
Suborden Sauropodomorpha Von Huene, 1932
Infraorden Sauropoda Marsh, 1878
Superfamily Titanosauria Bonaparte and Coria, 1993
Family Titanosauridae Lyddeker, 1893
***Rinconsaurus* gen. nov.**

Type species: *Rinconsaurus caudamirus* sp. nov., is described below.

Diagnosis: slender titanosaurid characterized by the following association of autapomorphies: (1) neural spines in mid-anterior dorsal vertebrae inclined posteriorly more than 60 degrees with respect to the vertical; (2) middle caudal vertebrae with bony processes that support the articular facets of postzygapophyses; (3) procoelous posterior caudal centra with the eventual intercalation of a series of amphicoelous-biconvex or amphicoelous-opisthocoelous-biconvex centra. These autapomorphies are associated with the following combination of 'synapomorphic' characters: pencil-chisel-like teeth with wear facets sharply inclined; suboval teeth with labial and lingual faces well differentiated by crests; acuminate (eye-shaped) pleurocoels in dorsal vertebrae; absence of hyposphene-hypantrum articulation in dorsal vertebrae; prespinal lamina in dorsal vertebrae well developed until the base of the neural spine; centroparapophyseal lamina in posterior dorsal vertebrae; forked centrodiapophyseal lamina in posterior dorsal vertebrae; anterior and middle caudal centra strongly procoelous; neural arches in middle and posterior caudals placed anteriorly; coracoid of quadrangular shape; semilunar sternal plates; absence of phalangeal articular facets on the metacarpals; relatively short posterior process of ischium; slender and well developed iliac pedicel of ischium; expanded and laterodorsally directed preacetabular lamina of ilium; diapophyses in dorsal vertebrae with horizontal surfaces in their distal end; haemal arch articulations open proximally; femur with a lateral bulge below the greater trochanter.

Etymology: in reference to Rincón de los Sauces (Neuquén Province, Argentina) where the dinosaur was found; *saurus* (Greek), lizard.

Rinconsaurus caudamirus sp. nov.

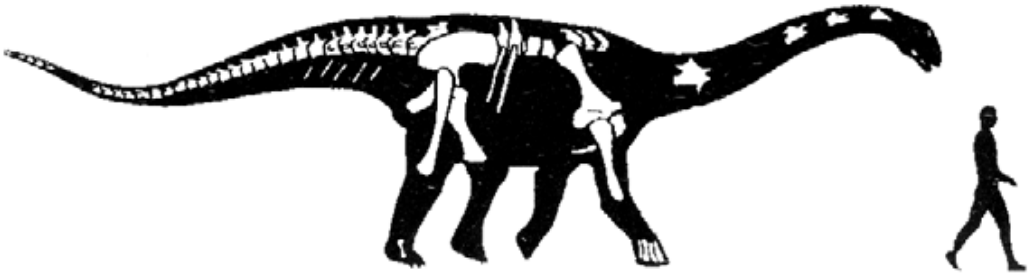
(Pl. 1, A-H; Pl. 2, A-C; Pl. 3, A-B; text-Figs. 2, 3)

Diagnosis: same as for genus.

Etymology: *cauda* (Latin), tail, *mirus* (Latin), astonishing, amazing, in reference to the unusual morphology of posterior caudal vertebrae; freely 'the dinosaur from Rincón with amazing tail'.

Holotype: MRS-Pv 26, 13 articulated anterior-middle and middle-posterior caudal vertebrae and two ilia.

Paratypes: the following bones associated with the holotype are included: teeth (MRS-Pv 117, 263), prefrontal (MRS-Pv 102), angular and surangular



Text- FIG. 2. Skeletal reconstruction of *Rinconsaurus caudamirus* gen. et sp. nov., showing preserved bones (estimated total length: 11 m).

(MRS-Pv 112), cervical vertebrae (MRS-Pv 2, 3, 8, 4 and 21), dorsal vertebrae (MRS-Pv 5, 6, 9, 11, 13, 16, 17, 18 and 19), anterior caudal vertebrae (MRS-Pv 22, 23, 24, 25 and 27), middle caudal vertebrae (MRS-Pv 27, 28 and 31), posterior caudal vertebrae (MRS-Pv 29, 30, 32-40), haemal arches (MRS-Pv 20, 42, 93; 99, 109, 113), scapula and coracoid (MRS-Pv 43), sternal plates (MRS-Pv 46, 103, 104), humerus (MRS-Pv 47), metacarpals (MRS-Pv 98), ischia (MRS-Pv 94, 101), ilia (MRS-Pv 96), pubes (MRS-Pv 97, 100), femora (MRS-Pv 49, 92) and metatarsal (MRS-Pv 111).

Specimens: the holotype and paratypes of *Rinconsaurus caudamirus* correspond to three individuals, two adults and one juvenile. All fossil remains (dorsal vertebrae, articulated caudal vertebrae and appendicular bones of different sizes) were found associated, exhibit similar morphologies and constitute a monospecific assemblage. The best preserved bones, the articulated caudal series MRS-Pv 26, were associated 'in life position' with two ilia. Moreover, associated with them, several articulated dorsal vertebrae (MRS-Pv 05) were preserved that probably correspond to the same specimen, as well as several limb bones. In the same fossil assemblage were found several articulated vertebrae and limb bones that correspond to other two specimens. Duplicate bones represented by caudal vertebrae, ilia, sternal plates, ischium and femur exhibit the same morphological characters. These paleontological evidences confirm the presence of a monospecific assemblage. For this reason, all bones recovered were included in the same type series (holotype and paratypes) such as the Comisión Internacional de Nomenclatura Zoológica (2000) indicates.

Horizon, age and locality: Río Neuquén Formation (Neuquén Group), Late Cretaceous, late Turonian-Coniacian according to Leanza and Hugo (2001). The fossils come from Cañadón Río Seco site, 2 km north of Rincón de los Sauces, Neuquén Province, Patagonia, Argentina (text Fig. 1).

Description: skull and jaw (Pl. 1, A-D). A cranial fragment, one mandible and teeth have been recovered. The right prefrontal (MRS-Pv 102) is small and anteroposteriorly elongated. Its posterior end is transversally wide and it is arched posteroventrally. The anterior end is acute in its exposed portion. The articular surface for the nasal is extensive. Its posterior border is concave and of triangular shape. The lateral border of the prefrontal contributes to the skull roof and the posterodorsal border of the orbit. Its rugose surface contains small grooves.

The posterior portion of the mandible includes a portion of the angular and surangular (MRS-Pv 112), both form a kind of a bar (Pl. 1, B). The surangular is a delicate and elongated bone lamina. Posteriorly, the ventral border is slightly convex in lateral view and it becomes concave anteriorly. In medial view, the angular forms a weakly concave surface.

Two long and thin teeth have been preserved (Pl. 1, C, D). One of them (MRS-Pv 117) has a suboval section, and has two crests that allow us to differentiate slightly convex lingual and more convex labial surfaces. Its apex is incomplete. The other tooth (MRS-Pv 263), more complete and bowed lingually, presents the same features as the anterior one but in more marked form. The worn surface is parallel to the tooth axis. It is remarkable with respect to the development of sharp crests forming the anterior and posterior borders. In general, titanosaurid teeth are pencil-chisel like (Calvo, 1994) with a sharp worn surface placed almost parallel to the tooth axis. Some have oval section with rounded borders depending the position in the jaws. The suboval teeth with labial and lingual faces well differentiated by crests present in *Rinconsaurus caudamirus* (Pl. 1, C) is an unusual character for derived titanosaurids. However, a similar morphology, with some differences in the cross-sectional shape, is also present in the basal titanosaurid *Malawisaurus dixeyi* (Jacobs *et al.*, 1993).

Cervical vertebrae (Pl. 1, E, F). Two anterior cervical vertebrae were recovered (MRS-Pv 08, 21). They possess relatively short, opisthocoelous centra, wider than high. In their lateral side is a deep, acute depression that defines the pleurocoels. The parapophyses are located at the base of the centra. Laterally, the centroprezygapophyseal and centrodiapophyseal laminae are inclined strongly forward. This inclination differs considerably from that of the Saltasaurinae (Bonaparte and Powell, 1980; Powell, 1992), but it is very similar to the inclination observed in the Titanosauridae indet. 'Series B' from Brazil (Powell, 1987).

Posteriorly, the opisthocoelous centra increase in length. This character is observed in the middle cervical vertebra MRS-Pv 02 and in the posterior cervical vertebrae MRS-Pv 03 and MRS-Pv 04, the

TABLE 1. MEASUREMENTS (MM) OF VERTEBRAE OF *RINCONSAURUS CAUDAMIRUS*.

Registration Nos.	Cervical MRS-Pv 03	Dorsal MRS-Pv 17	Middle caudal MRS-Pv 26/3	Posterior caudal MRS-Pv 27/1
Height of the centrum	134	137	81	58
Width of the centrum	137	145	46 *	62
Length of the centrum	495	130	128	114
Overall height	320 *	385	165	121

* Incomplete or distorted.

last one not complete (Pl. 1, E, F). They are relatively slender and wider than high (Table 1). The ventral face is wide and smoothly concave anteroposteriorly. In the lateral face of the centum there is a long anteroposterior depression with small pleurocoels. This depression is divided by a posteroventrally directed lamina. The parapophyses are laminar and subtriangular. They are located in the anterior half of the vertebral body and extend lateromedially. In anterior view, the spinodiapophyseal and spinoprezygapophyseal laminae reach each other at the level of the postzygapophysis, defining a subtriangular depression. The diapophysis is located on the anterior half of the body, at the level of the prezygapophysis. It is reinforced by the anterior and posterior centrodiapophyseal laminae, the prezygadiapophyseal lamina and the postzygadiapophyseal lamina. In this way, these laminae form four deep depressions around the diapophysis. The prezygapophyses are relatively long, extending beyond the anterior end of the vertebral body; the postzygapophyses do not extend beyond the center. The opposite is observed in *Saltasaurus* (Powell, 1992; Salgado *et al.*, 1997a). The articular surfaces of the prezygapophyses are elongated anteroposteriorly and inclined toward the medial plane. The prezygapophyses are reinforced by two centroprezygapophyseal laminae that in anterior view define a deep depression. The neural spine is low and distally expanded.

Dorsal vertebrae (Pl. 1, G, H). The authors have collected three articulated anteromedial dorsal neural arches (MRS-Pv 05). The neural arches are wider than long and have suffered dorsoventral compression. The prezygapophyseal facets are reduced and have an oval outline. The centroprezygapophyseal lamina is absent. In contrast, *Saltasaurus* possesses two centroprezygapophyseal laminae (Powell, 1992) and *Lirainosaurus* one (Sanz *et al.*, 1999). In the most anterior dorsal, an accessory centrodiapophyseal lamina extends parallel to the centrodiapophyseal lamina. At this level, the anterior and posterior centrodiapophyseal laminae are not forked as they occur in the middle-posterior dorsal arches (MRS-Pv 06). The prezygadiapophyseal lamina presents a straight border in dorsal view. The almost horizontal postygadiapophyseal lamina has a concave border in dorsal view.

The neural spine is reduced and transversely expanded distally. It is reinforced ventrally by a spinopostzygapophyseal lamina. The neural spines is strongly inclined posteriorly. In spite of that, in most of titanosaurs an inclination of the neural spine in anterior dorsal vertebrae is present (Wilson and Sereno, 1998) no specimen described up to now has an inclination of more than 60 degrees with respect to the vertical (Pl. 1, G). For this reason, this character can be considered an autopomorphy of *Rinconsaurus caudamirus*.

The prespinal lamina extends to the base of the neural arch. The accessory spinodiapophyseal laminae are not present. In contrast, these laminae are present in *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Lirainosaurus astibiae* (Sanz *et al.*, 1999) and the Titanosauridae indet. DGM 'Series B' from Brazil (Powell, 1987).

The authors have also recovered an isolated middle-posterior dorsal neural arch (MRS-Pv 06). In lateral view, there is a bifurcation of the centrodiapophyseal lamina. The neural spine is reinforced by a prespinal and postspinal laminae. In dorsal view, the spinodiapophyseal and spinoprezygapophyseal laminae form a wide and deep cavity.

The posterior dorsal vertebrae (MRS-Pv 17, 18) exhibit relatively short opisthocoelous centra, wider than high (Table 1). In their lateral faces, they have well developed, eye-shaped pleurocoels. The pleuro-

coels are elongated and deep, and they occupy 60 percent of the centrum length. The hyposphene-hypantrum articulation is absent. In only few posterior dorsal vertebrae the neural arch is partially preserved. The neural arch has a wide lateral base, which occupies more than 60 percent of the centrum. The transverse process is relatively thin. The diapophyses are directed laterally and upward. They are reinforced ventrally by centrodiapophyseal, postygadiapophyseal and paradiapophyseal laminae, and are supported dorsally by the spinodiapophyseal lamina. The distal end of the diapophysis present a horizontal and plane surface, similar to that in *Saltasaurus* (Powell, 1992) and *Lirainosaurus* (Sanz *et al.*, 1999). The parapophyses are not well preserved but they are reinforced ventrally by robust anterior and slender posterior centroparapophyseal laminae. The last one unites to the inferior portion of the centrodiapophyseal lamina, similar to that of *Saltasaurus*. The articular surface of the postzygapophysis prolongs as the postzygadiapophyseal laminae. The postzygapophyses are well separated. The neural spine is undivided. It is composed by the spinodiapophyseal, spinopostzygapophyseal, prespinal and postspinal laminae; all unite in the transversal broadening of the distal end. The prespinal lamina is well developed, extending to the base of the neural spine. Besides the described materials we have collected 6 dorsal centra, some with incomplete neural arches (MRS-Pv 9, 11, 13, 16, 19).

Sacrum. Two fused centra have been preserved (MRS-Pv 41) without any diagnostic character.

Caudal vertebrae. The authors have collected several caudal vertebrae; some are isolated, but others are articulated. Below, the authors describe their shape and morphology in different parts of the tail. All the caudals collected belong to two individuals of *Rinconsaurus caudamirus*.

Anterior caudal vertebrae . The first part of the tail is represented by two poorly preserved centra and neural arches. The ?first caudal (MRS-Pv 22) has thin, laminar and laterally directed transverse processes. At the base of the postzygapophyses, the transverse processes possess two foramina. The second caudal (MRS-Pv 23) is strongly procoelous and has smaller lateral expansion than the first one. In lateral view, the centrum presents a depression with the shape of a pleurocoel.

The series of anterior caudals is not complete. Three articulated series have been collected. MRS-Pv 23 is represented by five vertebrae, MRS-Pv 24 by six vertebrae and MRS-Pv 25 by three vertebrae. The holotype (Pl. 2, A) includes an articulated series of caudals (MRS-Pv 26) represented by four anterior caudals, eight middle caudals and five posterior ones.

The centra of anterior caudals are higher than wide, and are strongly procoelous. The lateral faces are slightly concave anteroposteriorly. The ventral face is flat and becoming narrower toward the middle caudals. The articulations for the chevrons are well developed and they are placed at the posterior end of the centra. The posterior borders of the neural arches are located approximately in the middle of the centra. The transverse processes, directed laterally, are projected posteriorly. The anterior border of the neural arch is placed almost on the anterior border of the centra. The neural arch is higher than the vertebral body. The base of the prezygapophyses are born almost on the anterior border of the centrum and they are directed slightly upward. The articular facets of the postzygapophyses are directed lateromedially and they are relatively reduced. The postzygapophyses are located before the posterior end of the vertebral body. The neural spine, narrow anteroposteriorly, is directed vertically and it presents a slightly expanded distal end. The articular faces of the postzygapophyses are separated from the neural spine by a bony process, absent in other titanosaurids.

Middle caudal vertebrae (Pl. 2, A-C). The holotype (MRS-Pv 26) preserves eight middle caudal vertebrae and five posterior ones. There is also an articulate series of three middle caudals (MRS-Pv 27), two incomplete disarticulated middle caudals (MRS-Pv 28) and an isolated one (MRS-Pv 31).

Middle caudals are similar to the anterior caudals except for the neural spine, that is directed posteriorly, and for the absence of transverse processes. Middle caudal centra are strongly procoelous, as high as wide. The lateral faces are flat, slightly concave anteroposteriorly. The ventral face of the centra is narrow and flat, with a strong compression in its middle part. The prezygapophyses are directed horizontally or slightly upward. Both prezygapophyses fuse proximally, developing a small platform.

The articular faces of the postzygapophyses are inclined lateroventrally. They are placed at the level of the posterior border of the centra. As in anterior caudals, the articular faces of the postzygapophyses

are separated from the neural spine by a bony process which can be seen clearly in dorsal view (Pl. 2, C). This character, absent in other titanosaurs, is considered here an autapomorphy of *Rinconsaurus* (Pl. 2, C). The postzygapophyses and the prezygapophyses are well separated from the axial plane due to the development of the postzygapophyseal processes.

Posterior caudal vertebrae (Pl. 3, A, B) . There is an articulated section of five posterior vertebrae that are part of the holotype (MRS-Pv 26). There are also two series of three articulated caudals each one (MRS-Pv 29, 30) and several isolated posterior caudals (MRS-Pv 32, 33, 34, 35, 36, 37, 38, 39, 40). All these posterior caudals are similar to the middle caudals in having the typical procoelous centrum. The bony process of the postzygapophysis is not present.

In contrast to the caudals described above, the authors have recovered two articulated series with an unusual centrum. One of the series (MRS-Pv 29) is composed of a procoelous vertebra, an amphicoelous vertebra and a biconvex vertebra (Pl. 3, A). The centrum, dorsoventrally compressed, is wider than high. The lateral faces are convex laterodorsally. The ventral border is slightly convex. The posterior border of the neural arch is placed in the posterior half of the centrum. The postzygapophyses are placed at the level of the posterior border of the centra. The distal ends of the neural spine reach the posterior border of the centra. The anterior border of the neural spine is at a lower level than the posterior one. The processes for the chevrons are not present. The prezygapophyses fuse in their proximal end, developing a small platform as in anterior and middle caudal vertebrae. Measurements of the caudal MRS-Pv 29/2: length, width and height of the centrum: 104, 82 and 38 mm, respectively.

The other series (MRS-Pv 30) is composed of three articulated caudals: an opisthocoelous vertebra, a biconvex vertebra and a procoelous vertebra (Pl. 3, B). They present characteristics similar to the anterior series, although their neural spines are more reduced due to their more posterior position in the sequence.

Although isolated amphicoelous middle caudals have been found in other titanosaurids (Huene, 1929; Huene and Matley, 1933), *Rinconsaurus caudamirus* has a short articulated posterior series with amphicoelous, opisthocoelous and biconvex centra (Pl. 3, A, B). This unusual morphology can be interpreted as an autapomorphy of this new taxon. As indicated González Riga and Calvo (1999), the finding of non-procoelous isolated caudal vertebrae in the Late Cretaceous must be interpreted carefully because they can belong to a titanosaurid.

Measurements of the caudal MRS-Pv 30/1: length, width and height of the centrum: 114, 57 and 33 mm, respectively.

Haemal arches. There are several haemal arches; some are deformed and others are incomplete (MRS-Pv 20, 42, 93; 99, 109, 113). In general, they are relatively long and thin, open proximally, and lack strong articular faces.

Scapula and coracoid. The authors have collected a complete right scapula (MRS-Pv 43). It is a relatively long and laminar bone with its external face convex. The scapular blade is thin and slender. The contact between the scapular blade and the proximal end is narrow and there is a crest that separates both of them. The ventral border is straight up to its union with the proximal end, forming an angle of approximately 140 degrees. The supraglenoid process is prominent. The supracoracoid depression is wide because the diagonal acromion coincides with the border of the acromial process. The proximal end of the scapula contacts the coracoid. The distal end, although incomplete, has a convex border. The coracoid has a square shape. Its posteromedial border forms a 90 degree angle with the anteromedial border of the scapula. The coracoid foramen, in the external face, is surrounded by a depression directed toward the anteromedial border. Measurements: length: 820 mm; proximal width: 440 mm; distal width: 215 mm; minimum width of the blade: 130 mm.

Sternal plate (Pl. 3, D). Three sternal plates have been preserved (MRS-Pv 46, 103 and 104). The right sternal plate MRS-Pv 46 is relatively complete. It is laminar and it has a semilunar shape. The concave external border is very thin, while the internal one is convex. Measurements: length: 560 mm; width: 260 mm. The other sternal plates are not well preserved.

Humerus (Pl. 3, C). The incomplete left humerus is relatively slender (MRS-Pv 47). Its anterior face presents a prominent deltopectoral crest anteriorly projected. In its distal end, the radial condyle is well developed. Measurements: estimated length: 790 mm; preserved length: 740 mm; proximal width: 260 mm; distal width: 210 mm; perimeter and diameter of the diaphysis: 300 and 120 mm, respectively.

Metacarpals. The authors have recovered five isolated metacarpals with their ends eroded. Their lengths range between 260 and 240 mm.

Metacarpal I? (MRS-Pv 98/5) exhibits a robust proximal end of subtriangular shape. One of its lateral sides is slightly rounded. Its distal end is relatively reduced and it has been crushed.

Metacarpal II? (MRS-Pv 98/4) presents a subtriangular shape at the distal end. Both extremities are well developed.

Metacarpal III? (MRS-Pv 98/1) presents an incomplete proximal end of subtriangular shape. It is characterized by slender shape. The diaphysis has two flat faces, with the sharp angle directed toward the posterior side.

Metacarpal IV? (MRS-Pv 98/2) exhibits a very robust distal end of subtriangular shape. The proximal end is incomplete.

Metacarpal V? (MRS-Pv 98/3), strongly crushed, is characterized by having the distal end more developed than the proximal one.

Ilium (text Fig. 3B).The authors have recovered four incomplete ilia corresponding to two individuals. One pair (MRS-Pv 26) is associated with a series of caudal vertebrae. The other pair is incomplete (MRS-Pv 96).

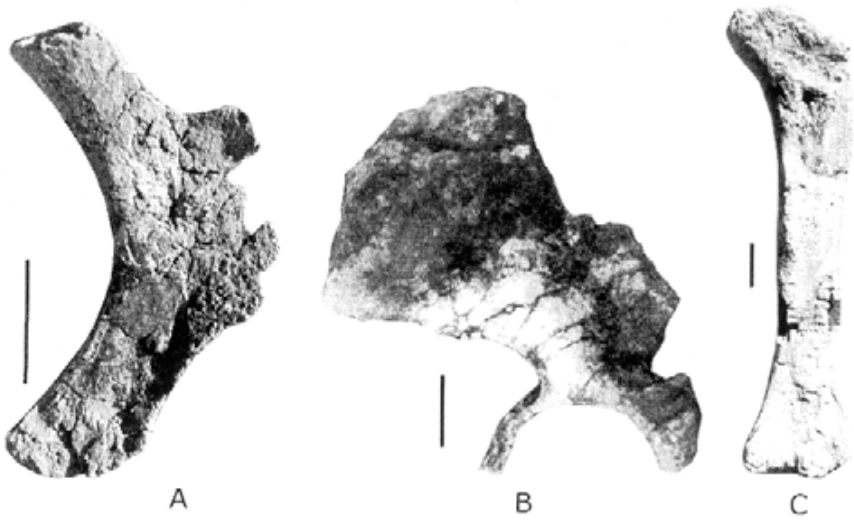
Specimen MRS-Pv 96 possesses a left ilium that preserves the acetabulum and great part of the preacetabular lamina. This lamina is wide, and it is directed upward and outward. The incomplete right ilium also preserves the acetabulum, and the lower part of the preacetabular and postacetabular laminae.

Specimen MRS-Pv 26 possesses a right ilium that preserves the preacetabular lamina, most of the postacetabular one, and also the complete acetabula and their peduncles. The preacetabular lamina exhibits a straight ventral border and a curved anterodorsal border. The left ilium lacks part of the iliac lamina, but it is complete in the lower part of the postacetabular and preacetabular laminae, the acetabulum and their peduncles. The length of the left ischium is 480 mm and the diameter of the acetabulum is 110 mm. The postacetabular lamina presents a rounded posterior border. The pubic peduncle is wide transversally.

Pubis (Pl. 3, E). The authors have collected three pubes. One specimen has both pubes preserved (MRS-Pv 97), and the other specimen has just the right pubis (MRS-Pv 100).

The right pubis of MRS-Pv 97 is a relatively thin and laminar bone. The oval pubic foramen is closed. The pubic blade is wide and flattened, with its thick lateral border concave. The medial border is thin, and not well preserved. The distal end becomes wider anteroposteriorly. The acetabulum is reduced. Measurements: length: 770 mm; pubic foramen: 70 x 35 mm; distal with: 255 mm.

The incomplete pubis MRS-Pv 100 lacks its



Text-FIG. 3. *Rinconsaurus caudamirus* gen. et sp. nov. A, right ischium in lateral view, MRS-Pv 101. B, left ilium in lateral view, MRS-Pv 96, C, right femur in posterior view, MRS-Pv 49. Scale bars equal 10 cm.

distal end, part of the proximal one in the area of the pubic foramen and part of the pubic lamina; it corresponds to a smaller specimen than the one describe above.

Ischium (text Fig. 3A). Two ischia have been collected (MRS-Pv 94 and 101) corresponding to two individuals. Specimen MRS-Pv 101 is an almost complete right ischium of small size. It lacks only a small central portion of the contact region with the pubis. This contact occupies 50 percent of the total length of the ischium. The acetabulum is complete and the thin iliac pedicel is well developed; it is as large as that of *Aeolosaurus* (Salgado and Coria, 1993; Salgado *et al.*, 1997b) and different from that of *Alamosaurus* (Gilmore, 1946) and *Saltasaurus* (Powell, 1992). The distal lamina of the ischium is relatively wide with regard to the width of the ischiac articulation. Measurements: length: 360 mm, width 130 mm.

Specimen MRS-Pv 94, from larger animal, is not well preserved.

Femur (text Fig. 3C). Two femora have been collected; the right one is complete and the left one is incomplete (MRS-Pv 49 and 92). The most complete is relatively slender. The anteroposterior diameter of the traverse section at the level of the diaphysis is shorter than the posteromedial one. The fourth trochanter is well developed and it is 490 mm below the femoral head. The femoral head is placed at a right angle with respect to the axis. On the lateral margin, the lateral bulge is present as in *Brachiosaurus*, *Chubutisaurus* and Titanosauria (Janensch, 1950; Salgado, 1993; Salgado *et al.*, 1997a). Measurements: length: 990 mm; greatest diameter and perimeter of the diaphysis: 140 and 340 mm, respectively.

Metatarsal. Just one metatarsal has been recovered. It is probably metatarsal III? (MRS-Pv 111). It is relatively slender and twisted. The proximal end, more developed than the distal one, has a subtriangular shape. The distal end presents a convex articular surface. Measurements: length: 160 mm; diameter of the diaphysis: 30 mm.

PHYLOGENETIC RELATIONSHIPS AND CONCLUSIONS

Most of sauropod titanosaurs are represented by incomplete and fragmentary skeletal elements. In this context, the discovery of *Rinconsaurus caudamirus* gen. et sp. nov., integrated by cranial, vertebral and appedicular remains, is relevant from a systematic viewpoint.

This section has the objective to fit the new species, *Rinconsaurus caudamirus*, in cladistic analyses already proposed by other authors. The authors have improved characters proposed by Salgado *et al.* (1997a) and Wilson and Sereno (1998), and have added new characters according to the evidence presented by this new taxon. This paper does not comprise a phylogenetic reevaluation of the Titanosauridae family, because more taxa and characters should be included. The phylogenetic relationships of *Rinconsaurus caudamirus* with other titanosaurs were analyzed through a parsimony cladistic analysis based on 46 characters corresponding to 12 taxa (see Appendix).

Camarasaurus grandis (Cope, 1877) was considered as outgroup, and *Brachiosaurus brancai* (Janensch, 1950), *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), *Malawisaurus dixeyi* (Jacobs *et al.*, 1993), *Aeolosaurus rionegrinus* (Powell, 1986; Salgado and Coria, 1993; Salgado *et al.*, 1997b), *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Alamosaurus sanjuanensis* (Gilmore, 1946), *Neuquensaurus australis* (Huene, 1929; Powell, 1986), *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1992) and *Rinconsaurus caudamirus* gen. et sp. nov. (this paper) formed the ingroup.

The data matrix was analyzed with PAUP, version 3.0 (Swofford, 1989) and Nona, version 2.0 (Goloboff, 1993). The application of the heuristic method produced one most parsimonious tree (text Fig. 4) with a length of 68 steps and high consistency and retention indices (C.I. = 0.79; R.I. = 0.78). The multi-state characters were considered unordered.

Even though the cladogram obtained is similar, in general lines, to that of Salgado *et al.* (1997a), it presents differences due to the inclusion of new taxa and characters. They allow the authors to improve the knowledge of the relationships among

different titanosaurid species (see text Fig. 4).

Node 2. The authors' analysis supports monophyly of Titanosauriformes, defined by Salgado *et al.* (1997a) as 'the most recent common ancestor of *Brachiosaurus brancai*, *Chubutisaurus insignis* and Titanosauria and all of its descendants'. The clade is supported by nine synapomorphies defined by delayed optimization: teeth with sharply inclined wear facets (2.1), single (non-bifurcated) neural spine in cervical vertebrae (6.1), elongate cervical centra (7.1), single (non-bifurcated) neural spine in anterior dorsal vertebrae (10.1), prespinal lamina present in the distal end of neural spines in dorsal vertebrae (12.1), neural arches placed anteriorly in middle and posterior caudal centra (26.1), pubic peduncle of the ilium perpendicular to the sacral axis (40.1), preacetabular lobe of ilium expanded and dorsally directed (41.1) and lateral bulge of femur below the greater trochanter (46.1).

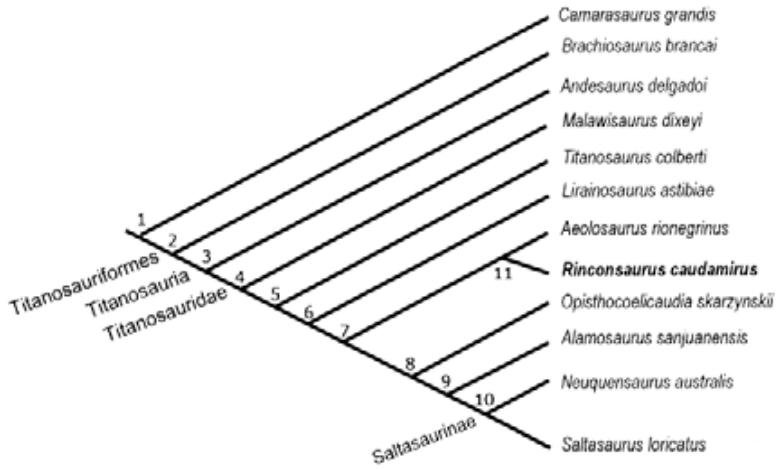
Node 3. Titanosauria, proposed originally by Bonaparte and Coria (1993), was defined as the most recent common ancestor of *Andesaurus delgadoi* and Titanosauridae, and all of its descendants (Salgado *et al.*, 1997a). In the authors' analysis it is united by five unambiguous synapomorphies: centroparapophyseal lamina in posterior dorsal vertebrae (13.1), slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae (14.1), acuminate (eye shaped) pleurocoels in dorsal vertebrae (16.1), bone internal structure of sompho-spondylous-camellate type (18.1), and pubis longer than ischium (39.1).

Node 4. Titanosauridae was defined by Salgado *et al.* (1997a) as the clade including the most recent common ancestor of *Malawisaurus, Epachthosaurus, Argentinosaurus, Opisthocoelicaudia, Aeolosaurus, Alamosaurus,* Saltasaurinae and all of its descendants. In this analysis, it is supported by five synapomorphies defined by delayed optimization: presence of pencil-chisel like teeth (1.2), absence of cervical pleurocoels divided by septa (5.1), absence of hyposphene-hypantrum articulation in posterior dorsal vertebrae (15.1), anterior caudal centra strongly procoelous with prominent posterior condyles (24.2), and semilunar sternal plates (34.1).

Two characters originally proposed as synapomorphies of Titanosauridae (Salgado *et al.*, 1997a) have ambiguous distributions in the authors' analysis and might be excluded from the diagnosis of this clade. They are: middle and posterior caudal centra strongly procoelous with prominent condyles (25.1), absent in *Malawisaurus*, and six sacral vertebrae (19.1), which is unknown in most of the analyzed taxa.

Traditionally, Titanosauridae were diagnosed by possessing strongly procoelous caudal vertebrae throughout the tail (Huene, 1929; McIntosh, 1990), although the occasional intercalation of amphiplatyan centrum was described (Powell, 1986).

However, the discovery of *Rinconsaurus* and



Text-FIG. 4. Cladogram determined by cladistic analysis (68 steps; CI 0.79; RI 0. 78) showing the phylogenetic relationships of *Rinconsaurus caudamirus* gen. et sp. nov. Synapomorphies supporting each node are listed and discussed in the text.

other titanosaurid specimens (Powell, 1986), show that the caudal procoelia was not a permanent and uniform character. In these sauropods, the mid and posterior section of the tail exhibit complex morphological variation that must be analyzed carefully. For example, *Rinconsaurus* shows a typical strongly procoelous caudal sequence discontinued by amphicoelous, opisthocoelous, and biconvex centra. On the other hand, a new titanosaurid from Mendoza Province has slightly procoelous middle caudal centra with reduced posterior condyles, associated with typical strongly procoelous anterior caudal vertebrae (González Riga and Calvo, 1999; González Riga, 2002).

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). *Malawisaurus* shares with *Andesaurus* and other basal member of Titanosauria the complete absence of procoelia in mid and posterior caudal centra and other plesiomorphic characters (Calvo, 1999). As Bonaparte *et al.* (2000) stated, the morphology of cervical vertebrae in *Malawisaurus* is very different from those of typical Titanosauridae. Detailed studies of *Malawisaurus* will be important to evaluate the relationships between basal and derived titanosaurids.

Node 5. It is united by three unambiguous characters: presence of prespinal lamina in posterior dorsal vertebrae up to the base of the neural spine (12.2), middle caudal centra strongly procoelous with prominent condyles (25.1), and slender and well-developed iliac pedicel of ischium (43.1). The first two characters were cited by Salgado *et al.* (1997a). The third is proposed in this paper. This character has allowed recognition of morphological variation in the ischium of Titanosauridae.

Node 6. It Is supported by two unambiguous characters: humerus with slightly curved proximal border (33.1) and coracoid of quadrangular shape (36.1).

Node 7. It is supported by three characters defined by delayed optimization: teeth with cylindrical cross-section (3.1), reduced neural spines on posterior dorsal vertebrae (17.1), and absence of phalangeal articular facets on the metacarpals (38.1). Node 7 includes node 11 (*Rinconsaurus* + *Aeolosaurus*) and the node 8 (*Opisthocoelicaudia* + (*Alamosaurus* + (*Neuquensaurus* + *Saltasaurus*))).

Node 8. It is supported by three characters defined by delayed optimization: posteriorly inclined neural spines (20 to 50 degree from vertical) on anterior and middle dorsal vertebrae (11.1), 35 or fewer caudal vertebrae (21.1), and metacarpal I longer than metacarpal IV (37.1).

Node 9. It includes *Alamosaurus* + Saltasaurinae. This clade is supported by three unambiguous characters: the presence of depressed middle and posterior caudal centra (23.1), prominent lateral crest in the base of the neural arch in middle caudals (27.1) and wide and well developed iliac pedicel of ischium (43.2).

Node 10. Saltasaurinae is defined as the clade including the most recent common ancestor of *Neuquensaurus australis* and *Saltasaurus loricatus*, and all of its descendants (Salgado *et al.* (1997a). It is diagnosed by two unambiguous synapomorphies: depressed anterior caudal centra (22.1) and the posterior orientation of the anterodorsal border of the neural spine in middle caudals (28.1).

Node 11. It links *Rinconsaurus caudamirus* with *Aeolosaurus rionegrinus* (Salgado and Coria, 1993; Salgado *et al.*, 1997b). It is supported by one character: the presence of relatively long prezygapophyses (29.1). This character is not exclusive of these taxa, since it is also present in *Titanosaurus* sp. (DGM 'Series C' from Brazil, see Powell, 1987) and *Malawisaurus* (Jacobs *et al.*, 1993).

The discovery of *Rinconsaurus* shows that the caudal morphology of titanosaurs is a complex subject to analyze. The inclusion of *Rinconsaurus* among Titanosauridae is well recorded according to the morphological evidence. However, unique among sauropods, *Rinconsaurus* has procoelous posterior caudal centra with intercalation of a series of amphicoelous-biconvex or amphicoelous-opisthocoelous-biconvex centra. This unusual morphology is important because Titanosauridae were usually defined, among other characters, by having procoelous caudal vertebrae.

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PLATE 1

***Rinconsaurus caudamirus* gen. et sp. nov.**

Figures

A Right prefrontal, MRS-Pv 102.

B. Angular and surangular, MRS-Pv 112.

C-D Tooth in transverse section (C) and lateral view (D), MRS-Pv 117.

E Middle cervical vertebra in lateral view, MRS-Pv 02.

F Posterior cervical vertebra in lateral view, MRS-Pv 03.

G-H Anteromedial dorsal neural arch in lateral (G) and anterior (H) views, MRS-Pv 05/3.

References: Dp: diapophysis, Ne: neural spine, Poz: postzygapophysis. Scale bar equals 1 cm in figure D and 5 cm in the other figures.

PLATE 1

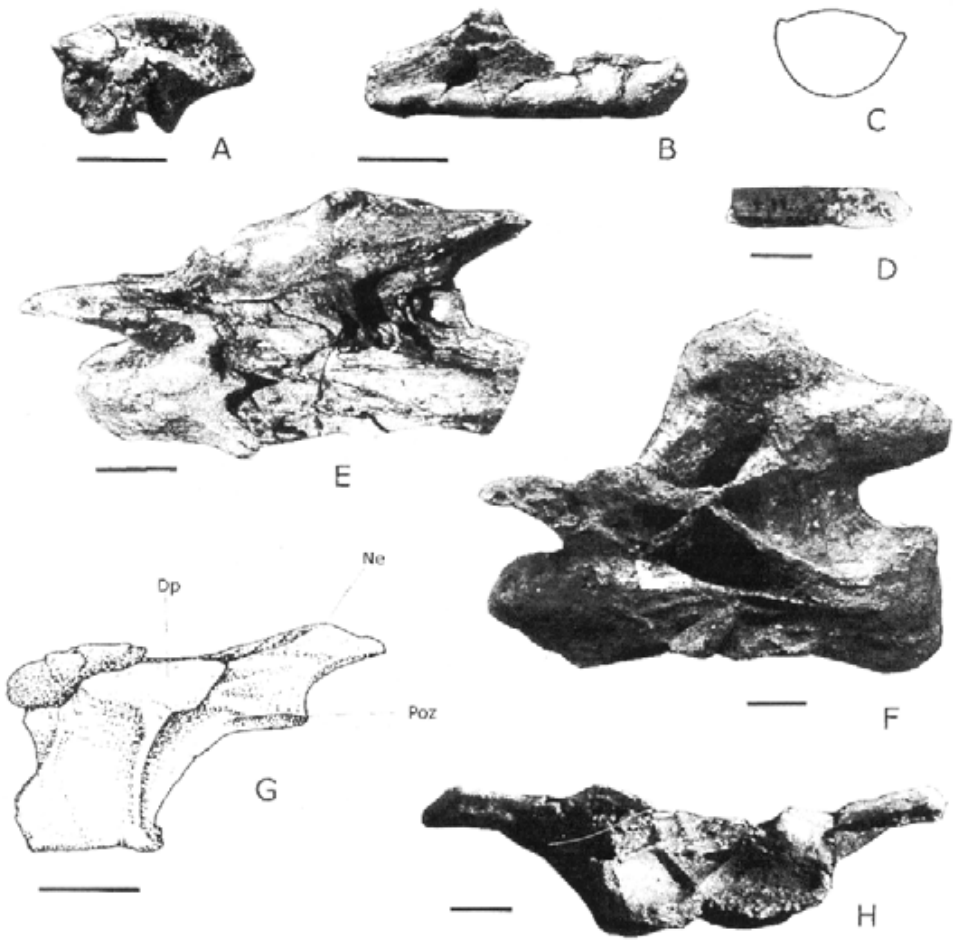


PLATE 2

***Rinconsaurus caudamirus* gen. et sp. nov.**

Figures

A Articulated series of anterior-middle caudal vertebrae in lateral view, MRS-Pv 26.

B Articulated series of middle caudal vertebrae in lateral view, MRS-Pv 27.

C Two middle articulated caudal vertebrae in dorsal view, MRS-Pv 27.

References: Cc: caudal centrum, Ne: neural spine, Poz: postzygapohysis, PozP: process of the postzygapophysis. Scale bars equal 5 cm.

PLATE 2

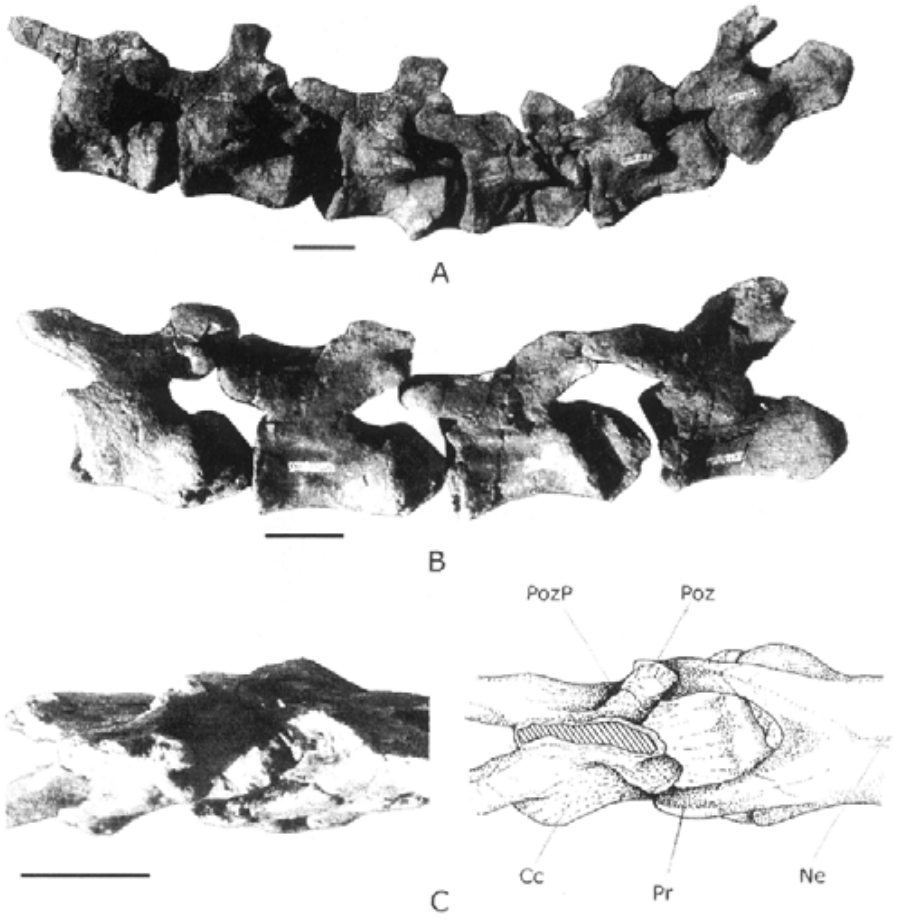


PLATE 3

***Rinconsaurus caudamirus* gen. et sp. nov.**

Figures

A Articulated posterior caudal vertebrae with procoelous, amphicoelous and biconvex centra, MRS-Pv 29.

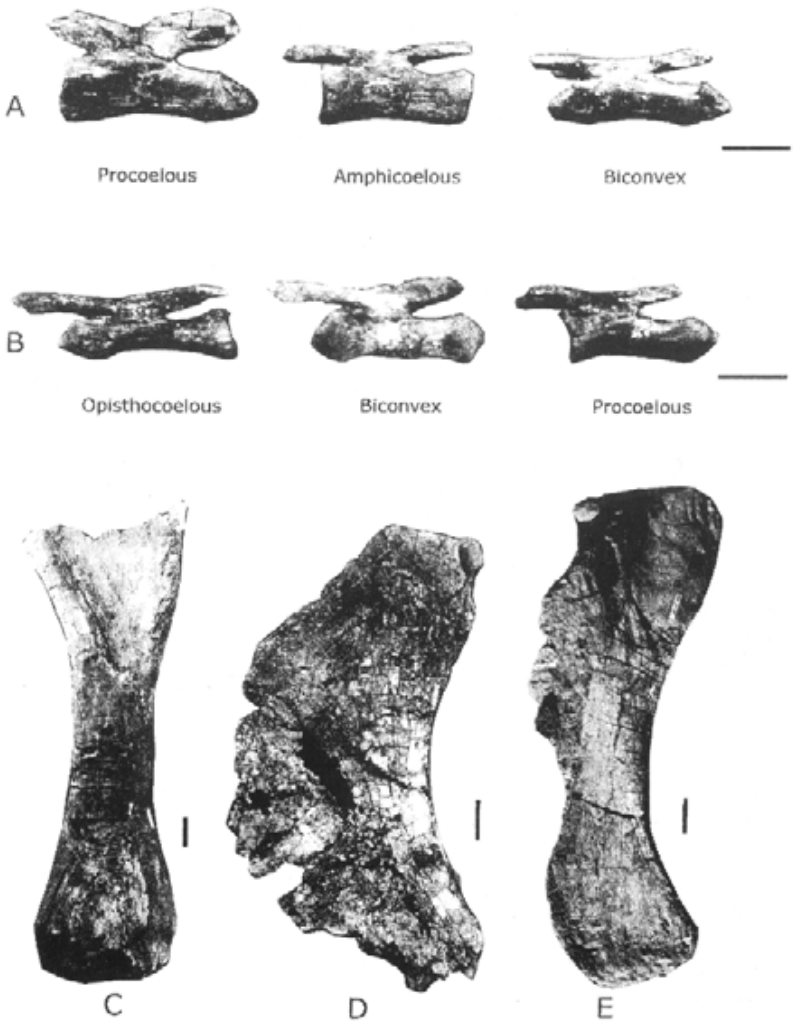
B Articulated posterior caudal vertebrae with opisthocoelous, biconvex and procoelous centra, MRS-Pv 30.

C Incomplete left humerus in anterior view, MRS-Pv 47.

D Sternal plate, MRS-Pv 46.

E Left pubis in dorsal view, MRS-Pv 97. Scale bars equal 5 cm.

PLATE 3


A
Procoelous
Amphicoelous
Biconvex
B
Opisthocoelous
Biconvex
Procoelous
C
D
E

APPENDIX

MATRIX OF THE PHYLOGENETIC ANALYSIS

In the Character-Taxon Matrix (Table 1) the distribution of 46 characters corresponding to 12 taxa of sauropods is shown. In this work, characters 32 and 43 are proposed, and characters 1, 7, 11, 18, 24, 25 and 44 are redefined. The other characters have been proposed by the authors indicated on the list. The data matrix was analyzed with the computer programs Paup (Swofford, 1989) and Nona (Goloboff, 1993). The application of heuristic method produced one most parsimonious tree with a length of 68 steps, C.I. = 0.79 and R.I. = 0.78. The multi-state characters were considered unordered.

TABLE 1. CHARACTER-TAXON MATRIX.

Taxon	Character 1-10	11-20	21-30	31-40	41-46
Camarasaurus grandis	0000000000	0000000000	0000000101	0000000000	000000
Brachiosaurus brancai	1100011001	0100000000	?000010101	0000000001	100011
Andesaurus delgadoi	??????????1	0111010?0	?001010101	?0???????1?	??0001
Malawisaurus dixeyi	2100111??1	111111?1??	?002010111	???110????	??00??
Titanosaurus colberti	???0112071	0201110111	?002110101	100??0??11	111171
Lirainosaurus astibiae	21????????1	?211110171	?002110?0?	?01101????	?????1
Aeolosaurus rionegrinus	??????????1	?2????1???3	?002110111	???110??11?	??10?1
Rinconsaurus caudamirus	2110111071	2211111??	?002110111	10?101?111	111101
Opisthocoelicaudia skarzynskii	????????010	121?111112	1000010101	1111011111	??1101
Alamosaurus sanjuanensis	2?1?111??1	1?00111113	1012111101	1011111111	1121?1
Neuquensaurus australis	????110??1	1211111113	?112111001	101101???1	1121?1
Saltasaurus loricatus	2111010171	1211111111	?112111001	112101?111	112101

List of characters

1. Tooth shape: spoon-like (0); compressed cone-chisel-like (1); pencil-chisel-like (2) (modified from Calvo, 1994).
2. Teeth with wear facets sharply inclined with respect to the labio-lingual axis: absent (0); present (1) (Salgado and Calvo, 1997).
3. Tooth, cross-sectional shape at mid-crown: D-shaped (0); cylindrical (1) (Wilson and Sereno, 1998).
4. Cervical prezygapophyses, relative length: long, with articular facets that surpass the centra (0); short, with articular facets that do not surpass the centra (1) (Salgado *et al.*, 1997a).
5. Cervical pleurocoels divided by septa: present (0); absent (1) (Upchurch, 1998; Bonaparte, 1999).
6. Cervical neural spines, shape: single (0); bifid (1) (Upchurch, 1998).
7. Middle cervical centra, anteroposterior length / height of the posterior face: between 2.5-3 (0); more than 3 (1); less than 2.5 (modified from Wilson and Sereno, 1998).
8. Centroprezygapophyseal lamina in middle and posterior cervical vertebrae: single (1); divided (2) (Upchurch, 1998).
9. Dorsal vertebrae, number: 12 (0); 11 (1); 10 or fewer (2) (McIntosh,.1990).
10. Neural spine in anterior dorsal vertebrae: bifid (0); single (1) (McIntosh, 1990; Wilson and Sereno, 1998).
11. Anterior and mid-dorsal neural spine, inclination: vertically, 0 to 20 degree from vertical (0); posteriorly inclined, 20 to 50 degree (1); posteriorly inclined, more than 50 degree (2) (modified from Wilson and Sereno, 1998).
12. Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of the neural spine (1); well developed up to the base of the neural spine (2) (Salgado *et al.*, 1997a).
13. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (Bonaparte and Coria, 1993; Salgado *et al.*, 1997a).
14. Ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado *et al.*, 1997a).

15. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (Salgado *et al.*, 1997a).
16. Acuminate (eye-shaped) pleurocoels in dorsal vertebrae: absent (0); present (1) (Bonaparte and Powell, 1980; Calvo and Bonaparte, 1991; Salgado *et al.*, 1997a).
17. Reduced posterior dorsal neural spines: *i.e.*, the height of the neural spine taken from dorsal border of the diapophysis is less than 20 percent of the total height of the vertebra: absent (0); present (1) (modified from Sanz *et al.*, 1999 by González Riga, 2002).
18. Bone internal structure of somphospondylous-camellate type on presacral vertebrae: absent (0); present (1) (modified from Wilson and Sereno, 1998 using terminology of Wedel *et al.*, 2000).
19. Number of sacral vertebrae: five (0); six (1) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998).
20. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3) (Salgado *et al.*, 1997a).
21. Caudal vertebrae, number: more than 45 (0); 35 or fewer (1) (McIntosh, 1990).
22. Anterior caudal centra, relative proportions: as high as wide (0); depressed, wider than high (1) (Powell, 1986, 1992; Salgado *et al.*, 1997a).
23. Middle and posterior caudal centra, relative proportions: as high as wide (0); depressed, wider than high (1) (Powell, 1986; Salgado *et al.*, 1997a).
24. Anterior caudal centra: non-procoelous (0); slightly procoelous without developed posterior condyles (1); strongly procoelous with prominent posterior condyles (2) (Modified from Salgado *et al.*, 1997a).
25. Strongly procoelous middle and posterior caudal centra, with prominent posterior condyles: absent (0); present (1) (modified from Salgado *et al.*, 1997a).
26. Neural arches in middle and posterior caudal vertebrae placed: in the middle (0) or anteriorly on the centra (1) (Huene, 1929; Powell, 1986; Salgado *et al.*, 1997a).
27. Prominent lateral crest in the base of the neural arch in middle caudal vertebrae: absent (0); present (1) (Salgado *et al.*, 1997a).
28. Anterodorsal border of the neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0) present (1) (Salgado *et al.*, 1997a).
29. Prezygapophyses in middle caudal vertebrae, relative length: shorter (0) or longer (1) than the 40 percent of the length of the centrum without the posterior articular condyle (González Riga, 2002).
30. Haemal canal in anterior caudal vertebrae: closed (0); opened (1) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998).
31. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (Wilson and Sereno, 1998).
32. Humerus, breadth of proximal end: less than 50 percent of total length (0); more than 50 percent of total length (1).
33. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2) (modified from Upchurch, 1998 by González Riga, 2002).
34. Sternal plate, shape: suboval (0); semilunar (1) (Salgado *et al.*, 1997a).
35. Semilunar sternal plate with straight posterior border: absent (0); present (1) (González Riga, 2002).
36. Coracoid, shape: suboval (0); quadrangular (1) (Salgado *et al.*, 1997a).
37. Metacarpal I, length: shorter (0) or longer (1) than metacarpal IV (Wilson and Sereno, 1998).
38. Distal phalangeal articular facets on metacarpals: present (0) absent (1) (Giménez, 1992; Salgado *et al.*, 1997a).
39. Pubis length respect to ischium length: shorter or equal (0); longer (1) (Salgado *et al.*, 1997a).
40. Ilium, relative orientation of pubic peduncle: angled (0) or perpendicular (1) with respect to the sacral axis (Salgado *et al.*, 1997a).
41. Ilium, shape of preacetabular lobe: moderately expanded (0); broadly expanded and directed upward (1) (Salgado *et al.*, 1997a).
42. Ilium, orientation of preacetabular lobe: nearly vertical (0); nearly horizontal, laterally projected (1) (Salgado *et al.*, 1997a).
43. Iliac pedicel of ischium: short and poor developed (0); slender and well developed (1); wide and well developed (2).
44. Posterior process of the ischium twice or more the length of pubis articulation: present (0) absent (1) (modified from Salgado *et al.*, 1997a).
45. Humerus/femoral ratio of 0,90 or more: absent (0); present (1). (McIntosh, 1990).
46. Lateral bulge of femur below the greater trochanter: absent (0); present (1) (McIntosh, 1990; Salgado, 1993; Calvo and Salgado, 1995; Salgado *et al.*, 1997a; Wilson and Sereno, 1998).