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

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ABSTRACT

Rincónsaurus 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 Rincónsaurus in the family Titanosauridae. Within Titanosauridae (Rincónsaurus + Aeolosaurus) is considered a sister group of the clade (Opisthocoelicauda + Alamosaurus + (Neuquensaurus + Saltasaurus)). Rincónsaurus 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

Rincónsaurus caudamirus gen. et sp. nov., un nuevo titanosaurido (Dinosauria, Sauropoda) del Cretácico Tardío de Patagonia, Argentina. Rincónsaurus caudamirus gen. et sp. nov. (Dinosauria, Sauropoda) 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 apófisis articulares desarticulados, que pertenecen a tres individuos, dos adultos y un juvenil. Este nuevo taxón se caracteriza por la siguiente asociación de autapomorfías: (1) vértebras caudales anteriores inclinadas posteriormente más de 60 grados con respecto a la vertical, (2)
vértebras caudales medias con procesos ósos que sostienen las carillas articulares de las poszigápforias y (3) vértebras caudales procélicas con intercalaciones de series con centros amelocéllicos y bioconvexas, o con centros amelocéllicos, opistocéllicos y biconvexas. Un análisis filogenético cadista permite incluir a Rinconsaurus en la familia Titanosauridae. Dentro de Titanosauridae (Rinconsaurus + Aelosaurus) es considerado un grupo hermano del clado (Opisthocoelicaudia + (Aelosaurus + (Neuquensaurus + Saltasaurus))). Rinconsaurus caudamirus presenta dos cortas secuencias caudales posteriores articuladas con centros amelocéllicos, opistocéllicos y bioconvexas. 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 procélia en sus vértebras caudales.

Palabras clave: 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 (Lydekker, 1893). During the Late Cretaceous, titanosaurids were important primary consumers in the ecosystems of Patagonia, as the omphithischians 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 titanosaurids is a complex subject to analyze (Wilson and Sereno, 1998; Currie Rogers and Foster, 2001).

The Neuquén Province, situated in northern Patagonia, has yielded many well preserved titanosaur fossils from the Neuquen and Malargue 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, 2km 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
Suborder Sauropodomorpha Von Huene, 1932
Infraorder Sauropoda Marsh, 1876
Superfamily Titanosauria Bonaparte and Coria, 1993
Family Titanosauridae Lycieker, 1893
Rinconsaurus gen. nov.

**Type species:** Rinconsaurus caudamirus sp. nov., 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 hyposphen-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 centrodiaaphyseal 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 plate; absence of phalangeal articular facets on the metacarpals; relatively short posterior process of ischium; slender and well developed iliac pedicle of ischium; expanded and laterodorsally directed preacetabular lamina of ilium; diaphyses 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; sauroid (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:** caud (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).
Rinconsaurus caudamirus gen. et sp. nov. a new titanosaurid (Dinosauria Sauropoda) from...

(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, 22, 28, 39), scapula and coracoid (MRS-Pv 43), sternal plates (MRS-Pv 46, 103, 104), humerus (MRS-Pv 47), metacarpals (MRS-Pv 98), scapula (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 28, 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, ischiun and femur exhibit the same morphological characters. These palaeontological 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 Canadén Río Seco site, 2 km north of Rincon 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 antroposteriorly elongated. Its posterior end is transversely wide and it is arched posterodorsally. 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 posteroventral 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 ventral surfaces. Its apex is incomplete. The other tooth (MRS-Pv 283), 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 (Culver, 1994) with a sharp worn surface placed almost parallel to the tooth axis. Some have oval sections with rounded borders depending the position in the jaws. The suboval teeth with lingual and lingual faces well differentiated by crests present in Rinconsaurus caudamirus (Pl. 1, C) is an unusual character for derived titanosaurs. However, a similar morphology, with some differences in the cross-sectional shape, is also present in the basal titanosaur 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. Lateral to the centroprezygapophysal and centrodiapophysal 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
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 centrum there is a long anteroposterior depression with small pleurocoels. This depression is divided by a posteroventrally directed lamina. The parapophyses are laminar and subangular. They are located in the anterior half of the vertebral body and extend lateromedially. In anterior view, the spinodiaphyseal and spinoprezygapophyseal laminae reach each other at the level of the postzygapophysis, defining a subtriangular depression. The diaphysis is located on the anterior half of the body, at the level of the prezygapophysis. It is reinforced by the anterior and posterior centrodiaophyseal laminae, the prezygapophyseal lamina and the postzygapophyseal lamina. In this way, these laminae form four deep depressions around the diaphysis. 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 (Sanz et al., 1999). In the most anterior dorsal, an accessory centrodiaophyseal lamina extends parallel to the centrodiaophyseal lamina. At this level, the anterior and posterior centrodiaophyseal laminae are not forked as they occur in the middle-posterior dorsal arches (MRS-Pv 08). The prezygapophyseal lamina presents a straight border in dorsal view. The almost horizontal postzygapophyseal lamina has a concave border in dorsal view.

The neural spine is reduced and transversely expanded distally. It is reinforced ventrally by a spinoprezygapophyseal lamina. The neural spines are strongly inclined posteriorly. In spite of that, in most of titanosaurans 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 autopomorph of *Rincosaurus caudamirus*.

The prespinal lamina extends to the base of the neural arch. The accessory spinodiaphyseal laminae are not present. In contrast, these laminae are present in *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993). *Opisthocoelicauda* skarzynski* (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 centrodiaophyseal lamina. The neural spine is reinforced by a prespinal and postspinal laminae. In dorsal view, the spinodiaphyseal 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 hypopheno-
hyptencrum 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 centrodiaaphyses, postyagadiaphyseseal and paradiaphyseseal
laminae, and are supported dorsally by the spinodia-
aphyseseal lamina. The distal end of the diapophysis
present a horizontal and plane surface, similar to
that in Saltasaurus (Powell, 1992) and Liranosaurus
(Sanz et al., 1999). The parapophyses are not well
preserved but they are reinforced ventrally by robust
anterior and longer posterior centroparaphyseseal
laminae. The last one unites to the interior portion
of the centrodiaaphyseseal lamina, similar to that of
Saltasaurus. The articular surface of the postzy-
gapophysis prolongs as the postyagadiaphyseseal
laminae. The postzygapophyses are well separated.
The neural spine is undivided. It is composed by the
spinodiaaphyseseal, spinopretzygapophyseseal,
prospinal and postspinal laminae; all unite in the
transversal broadening of the distal end. The
prospinal 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 caudinus.
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
postzygapophyses are born almost on the anterior
border of the centra and they are directed slightly
upward. The articular facets of the postzygapo-

physes 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 facets of the postzygapo-

physes are separated from the neural spine by a
bony process, absent in other litanosaurids.

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 centrum 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 facets 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 facets 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 host type (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 centrum. The distal ends of the neural spine reach the posterior border of the centrum. 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, 62 and 36 mm, respectively.

The other series (MRS-Pv 30) is composed of three articulated caudals: an amphicoelous 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 titanosaurs (Huene, 1929; Huene and Matley, 1933), Rinconsaurus caudamis has a short articulated posterior series with amphicoelous, amphicoelous 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 titanosaur.

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 postero medial 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-Py 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 and 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 transversely.

**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 pubic 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 width: 255 mm.

The incomplete pubis MRS-Pv 100 lacks its
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 described above.

**Ishium** (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 pedicle is well developed; it is as large as that of *Aeolosaurus* (Salgado and Coria, 1993; Salgado et al., 1997b) and different from that of *Atamosaurus* (Gilmore, 1946) and *Saltasaurus* (Powell, 1952). The distal lamina of the ischium is relatively wide with regard to the width of the ischial 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*, *Cetiosaurus* and *Titanosaurus* (Janensch, 1950; Salgado, 1983; 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 titanosauras are represented by incomplete and fragmentary skeletal elements. In this context, the discovery of *Rincosaurus caudimurus* gen. et sp. nov., integrated by cranial, vertebral and appendicular remains, is relevant from a systematic viewpoint.

This section has the objective to fit the new species, *Rincosaurus caudimurus*, 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 *Rincosaurus caudimurus* with other titanosauras were analyzed through a parsimony cladistic analysis based on 46 characters corresponding to 12 taxa (see Appendix).

*Camarasaurus granis* (Cope, 1877) was considered as outgroup, and *Brachiosaurus brancaii* (Janensch, 1950), *Antasaurus delgadoi* (Caívo and Bonaparte, 1991), *Malawisaurus dixyi* (Jacobs et al., 1993), *Aeolosaurus noae* (Powell, 1988; Salgado and Coria, 1993; Salgado et al., 1997b), *Lirainosaurus astibi* (Sanz et al., 1999), *Atamosaurus sanjuanensis* (Gilmore, 1946), *Neuquensaurus australis* (Huene, 1929; Powell, 1986), *Titanosaurus colberti* (Jain and Dandypadyey, 1997), *Opisthocoelicaudia skarzynski* (Borsuk-Bialynicka, 1977), *Saltasaurus lonquensis* (Bonaparte and Powell, 1980; Powell, 1992) and *Rincosaurus caudimurus* 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 Titanosauromorpha, defined by Salgado et al. (1997a) as 'the most recent common ancestor of Brachiosaurus brancai, Chubutisaurus insignis and Titanosaurus 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), prespiral lamina present in the distal end of neural spines in dorsal vertebrae (12.1), neural arches placed anterolaterally in middle and posterior caudal centra (25.1), 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 (45.1).

**Node 3.** Titanosaurus, proposed originally by Bonaparte and Coria (1993), was defined as the most recent common ancestor of Andosaurus delgadoi and Titanosauridae, and all of its descendants (Salgado et al., 1997a). In the authors' analysis it is united by five unambiguous synapomorphies: centra preapophyseal lamina in posterior dorsal vertebrae (13.1), slightly forked centrodiaaphyseal laminae in posterior dorsal vertebrae (14.1), acuminate (eye shaped) pleurocoels in dorsal vertebrae (16.1), bone internal structure of synphopospondylous-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, Opisthocoelicauda, Aequori- saurus, Ailamosaurus. Saltasauroidea 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 hypophyseal-epiphyseal articulation in posterior dorsal vertebrae (15.1), anterior caudal centra strongly procumbent 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 procumbent 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 procumbent 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

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**Text-FIG. 4.** Cladogram determined by cladistic analysis (88 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 procoelous 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 disrupted 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 conules, 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 posterior caudal centra apparently associated with gently amphicoelous or platycoelous middle and posterior caudals (Jacobs et al., 1993; Gomani, 1999). Malawisaurus shares with Andeosaurus and other basal members 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 titanosaurs.

Node 5. It is defined 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 conules (25.1), and slender and well-developed iliac pedicle 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 defined by two unambiguous characters: humerus with slightly curved proximal border (33.1) and coracoid of quadrangular shape (36.1).

Node 7. It is defined 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 degrees 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 + Saltasaurus. 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 pedicle of ischium (43.2).

Node 10. Saltasaurinae is defined as the clade including the most recent common ancestor of Neuquensaurus australis and Saltasaurus lonquex, 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 (26.1).

Node 11. It links Rinconsaurus caudemirus 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. (OGM, Seems G 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.
ACKNOWLEDGEMENTS

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

References: Dp: diapophysis, Ne: neural spine, Poz: posizygaphyosia. Scale bar equals 1 cm in figure D and 5 cm in the other figures.
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: postzygapophysis, Pozp: process of the postzygapophysis. Scale bars equal 5 cm.
PLATE 3

Rinconsaurus caudamirus gen. et sp. nov.

Figures

A  Articulated posterior caudal vertebrae with prococoeus, amnicoideous and biconvex centra, MRS-Pv 29.

B  Articulated posterior caudal vertebrae with opisthocoenous, biconvex and prococoeus 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.
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, 13, 24, 26, and 44 are redefined. The other characters were proposed by the authors indicated on the list. The data matrix was analyzed with the computer programs Peep (Swoford, 1969) and Nona (Goloboff, 1993). The application of neural method produced one most parsimonious tree with a length of 88 steps, C.I. = 0.79 and R.I. = 0.78. The multi-state characters were considered unordered.

TABLE 1. CHARACTER-TAXON MATRIX.

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</tr>
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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 prezygapophyseal process length, 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); bident (1) (Upchurch, 1998).
7. Middle cervical centra, antero-posterior length/height of the posterior face: between 2.5-3 (0); more than 3 (1); less than 2.5 (modified from Wilson and Serreno, 1999).
8. Centroprezygapophyseal lamina in middle and posterior cervical vertebra: 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: bident (0); single (1) (McIntosh, 1990; Wilson and Sereno, 1998).
11. Anterior and mid-dorsal neural spine, inclination: vertically, 0 to 20 degrees from vertical (0); posteriorly inclined, 20 to 50 degree (1); posteriorly inclined, more than 50 degrees (2) (modified from Wilson and Sereno, 1998).
12. Preapinal 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. Centroapapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (Bonaparte and Coria, 1993; Salgado et al., 1997a).
14. Vertically widened or slightly forked centroapopphyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado et al., 1997a).
15. Hypophene-hyptentre articulation in dorsal vertebrae: present (0); absent (1) (Salgado et al., 1997a).
16. Acuminated (eye-shaped) pleurocoels in dorsal vertebrae: absent (0); present (1) (Bonaparte and Powell, 1980; Calvo and Bonaparte, 1981; 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 somphosphondylosis-radius type on presacral vertebrae: absent (0); present (1) (modified from Wilson and Sereno, 1996 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: pleurocoelous (0); procoelous (1); opporhocoelous (2); bicourve (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, 1985, 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. Ventral 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. Postzygapophyses 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 canals in anterior caudal vertebrae: closed (0); opened (1) (Salgado et al., 1997a; Wilson and Sereno, 1996).
31. Scapular glenoid orientation: relatively flat (0); strongly beved mediolaterally (1) (Wilson and Sereno, 1996).
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, 1988 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. Deltoid postglenoid 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 presacetabular 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 poorly developed (0); slender and well developed (1); wide and well developed (2).
44. Posterior process of the ischiium twice or more the length of pubic articulation: present (0); absent (1) (modified from Salgado et al., 1997a).
45. Humeral/bifemoral ratio of 0.90 or more: absent (0); present (1) (McIntosh, 1980).
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).