A NEW TITANOSAUR (DINOSAURIA, SAUROPODA) FROM THE UPPER CRETACEOUS (CERRO LISANDRO FORMATION) OF MENDOZA PROVINCE, ARGENTINA

BERNARDO J. GONZÁLEZ RIGA1,2 AND LEONARDO ORTIZ DAVID1

1Laboratorio de Dinosaurios, Instituto de Ciencias Básicas, Universidad Nacional de Cuyo, Avenida Padre Contreras 1300, Parque General San Martín, 5500 Mendoza, Argentina.
2Departamento de Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Consejo Nacional de Investigaciones Científicas y Técnicas, Centro Científico Tecnológico, Avenida Ruíz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina.

Abstract. Quetecsaurus rusconii gen. et sp. nov. is a new titanosaur (Dinosauria, Sauropoda) from the Neuquén Basin of Mendoza Province, Argentina. The specimen comes from red mudstones of the Cerro Lisandro Formation (middle-late Turonian, Upper Cretaceous), and is the first sauropod with well-preserved remains to be discovered in this formation. The holotype includes a postorbital, teeth, the atlas, a posterior cervical vertebra, an incomplete dorsal vertebra, a posterior caudal centrum, dorsal ribs, a coracoid, fragments of a humerus, radius and ulna, and five metacarpals. It is characterized by the following combination of autapomorphies: (1) intercentrum of atlas with a prominent anteroventral border and expanded posteroventral processes; (2) posterior cervical neural spines with incipient lateral expansions; and (3) humerus with strongly sigmoid proximal border, rounded proximomedial border, and angular proximolateral corner. A preliminary cladistic analysis placed Quetecsaurus as a sister taxon of Lognkosauria (Mendozasaurus + Futalognkosaurus). Quetecsaurus shares with the lognkosaurs the presence of cervical neural spines with ‘lateral laminae’, but relatively reduced in comparison with those taxa. This discovery provides new information on the diagnosis of Lognkosauria within South American titanosaurs.


Resumen. Quetecsaurus rusconii gen. et sp. nov. es un nuevo titanosaurio (Dinosauria, Sauropoda) hallado en la Cuenca Neuquina, Provincia de Mendoza, Argentina. El espécimen proviene de fangolitas rojas de la Formación Cerro Lisandro (Turoniano medio-tardío, Cretácico Superior) y es el primer saurópodo con huesos bien preservados descubierto en esta formación. El holotipo comprende un postoral, dientes, el atlas, una vértebra cervical posterior, una vértebra dorsal incompleta, un centro caudal anterior, costillas dorsales, un coracoides, fragmentos de húmero, radio y ulna, y cinco metacarpales. Se caracteriza por la siguiente asociación de autapomorfías: (1) intercentro del atlas con un borde anteromedial fuertemente sigmoidal, borde proximomedial redondeado y esquina proximolateral angular. Un análisis cladístico preliminar ubica a Quetecsaurus como un taxón hermano de Lognkosauria (Mendozasaurus + Futalognkosaurus). Quetecsaurus comparte con los lognkosaurios la presencia de espinas neurales cervicales con láminas laterales, pero relativamente reducidas en comparación con esos taxa. Este descubrimiento brinda nueva información sobre la diagnosis de Lognkosauria, dentro de los titanosaurios de América del Sur.

possibly the heaviest terrestrial vertebrates that ever existed (~73 metric tons for *Argentinosaurus* according to Mazzetta *et al.*, 2004).

In South America, the most abundant titanosaur record comes from the Neuquén Basin in northwestern Patagonia. Most of these titanosaurids have been found in Upper Cretaceous strata from the Neuquén Basin in northwestern Patagonia. Most of these titanosaurids have been found in Upper Cretaceous strata of the Neuquén Group and the Allen Formation (Leanza *et al.*, 2004; de la Fuente *et al.*, 2007; González Riga, 2010; Calvo *et al.*, 2011). Although their record is diverse, titanosaur remains are still unknown from some stratigraphic intervals in the Neuquén Basin. For example, until this paper, there was no record of well-preserved titanosaur fossils from the Cerro Lisandro Formation (middle-late Turonian; Garrido, 2010), and only fragmentary titanosaur bones and teeth were known from this unit (Salgado *et al.*, 2009).

The aim of this paper is to describe a new genus and species of titanosaur, *Quetecsaurus rusconii*, from the middle-late Turonian in Cerro Lisandro Formation of Mendoza Province near the northwestern border of Patagonia. This discovery provides new morphological information relevant to the understanding of titanosaur evolution during the Cretaceous.

*Quetecsaurus* is the third sauropod discovered in Mendoza; the others are *Mendozasaurus neguyelap* González Riga, 2003 and *Malarguesaurus florenciae* González Riga, Previtera and Pirrone, 2009. These dinosaurs come from middle levels of the Neuquén Group. *Malarguesaurus* was found in strata assigned to Los Bastos Formation (early-middle Coniacian) whereas *Mendozasaurus* was discovered in the upper levels of the Sierra Barrosa Formation (middle-late Coniacian). Other titanosaur remains found in Mendoza Province include a distal caudal series from “Cañadón Amarillo” (Wilson *et al.*, 1999). Finally, exceptionally preserved articulated specimens were recently discovered in upper levels of the Plottier Formation (late Coniacian-early Santonian) (González Riga *et al.*, 2012, 2013).

The specimen described herein was collected during the development of the mining project ‘Proyecto Potasio Río Colorado’ (Vale S.A.). The fieldwork, led by the first author (B.G.R.), was carried out by a team of paleontologists and technicians in strict compliance with laws pertaining to the preservation of the paleontological heritage of Argentina. This paper is partly based on the first description of the specimen, which was part of the degree thesis of the second author (L.O.D.).

### GEOLOGICAL SETTING

In Neuquén Province, northern Patagonia, the Cerro Lisandro Formation has provided a rich fossil record that includes freshwater bivalves represented by the genus *Diplodon* (Manceño and Damborenea, 1984; Garrido, 2000; Leanza *et al.*, 2004; Salgado *et al.*, 2009), lungfish remains (*Ceratodus* sp.), osteichthyan vertebrae assigned to *Lepisosteidae* (Coria *et al.*, 1996; Leanza *et al.*, 2004; Apesteguía *et al.*, 2007; Salgado *et al.*, 2009), and teeth and bones of crocodiles and turtles (Garrido, 2000; Salgado *et al.*, 2009). Dinosaur remains include those of ornithischians (*Anabisetia saldiviai* Coria and Calvo, 2002; Iguanodontia indet. Coria *et al.*, 1996) and theropods (Coria *et al.*, 1996, Coria and Currie, 2006). Sauropod fossils are scarce and limited to isolated teeth and fragmentary bones (Salgado *et al.*, 2009).

The Cerro Lisandro Formation is widely exposed in Neuquén Province and is composed of fine clastic deposits, mainly monotonous banks of red mudstones interbedded with thin levels of fine, yellow and gray-green sandstones (Garrido, 2010). This facies association is interpreted to represent distal mud flats of fluvial systems (Leanza and Hugo, 2001). The mudstones indicate a dominance of illite and interstratified illite-smectite, with secondary involvement of kaolinite and chloride (Giusiano and Pettinari, 1999; Pettinari *et al.*, 1999).

*Quetecsaurus* comes from Cañada del Pichanal, in the southern end of Mendoza Province, near the Río Colorado and very close to Neuquén Province (Fig. 1). In this region, the Cerro Lisandro Formation is the oldest unit of the Neuquén Group, and it crops out in low anticlinal and synclinal structures that are generally North-South oriented (González Riga, 2002).

At the *Quetecsaurus* site, the dominant facies are massive and laminated red-purple mudstones. The presence of clay minerals is easily recognizable by flooded soils and sparse vegetation. The facies association includes massive mudstones and thin, lenticular gray shales and sandstones. Fibrous gypsum beds are also common. The sequence represents a muddy floodplain where clay sediments accumulated in ephemeral bodies of water. In some areas there are reactivation surfaces (lag deposits) that represent episodes of flooding, drying, and reworking. The contact with the Portezuelo Formation is located 2 km east of the fossil site, and is easily identified by the presence of yellow, coarse sandy channel beds.

Within the Cerro Lisandro Formation, isolated sand bod-
ies up to 50 m in width are present, and represent fluvial channels with low to moderate lateral migration. These sand bodies are well exposed near the Pata Mora bridge, on the southern margin of the Río Colorado, 20 km east of Cañada del Pichanal.

The *Quetecsaurus* specimen consists of cranial remains, the atlas, a cervical vertebra, a dorsal vertebra, some dorsal ribs, a caudal centrum, and appendicular bones. From a taphonomic viewpoint, the skeletal elements were disarticulated, with the exception of the metacarpals, which lay in a semi-articulated position. The bones showed no preferential orientation due to hydraulic processes, which is consistent with the presence of mudstone facies that were deposited in the floodplain. The preservation of small, fragile elements such as teeth and skull bones confirms that the dispersal and transport of the bones was minimal. After burial, the metacarpals underwent fracturing and plastic deformation due to lithostatic pressure. In contrast, the cervical and dorsal vertebrae were less affected, and preserve their original anatomical shape. From a systematic viewpoint, it is important to mention that all the skeletal elements were associated and belong to the same specimen. No duplicate bones were found (Fig. 2).

![Figure 1. Locality map of the Neuquén Basin showing La Cañada del Pichanal, the site where fossils of *Quetecsaurus rusconii* were recovered.](image1)

![Figure 2. Preserved skeletal elements of *Quetecsaurus rusconii*, UNCUYO-LD-300.](image2)

Anatomical nomenclature. For the axial skeleton, we use the terminology proposed by Wilson (1999) and Wilson *et al.* (2011). We also incorporate selected terms proposed by Salgado and Powell (2010). Appendicular nomenclature follows several recent papers (*e.g.*, Salgado *et al.*, 1997; González Riga, 2005; Curry Rogers, 2009; Otero, 2010).

**SYSTEMATIC PALEONTOLOGY**

**DINOSAURIA** Owen, 1842  
**SAURISCHIA** Seeley, 1887  
**SAUROPODA** Marsh, 1878  
**NEOSAUROPODA** Bonaparte, 1986  
**MACRONARIA** Wilson and Sereno, 1998  
**TITANOSAURIFORMES** Salgado, Coria, and Calvo, 1997  
**SOMPHOSPONDIYLA** Wilson and Sereno, 1998  
**TITANOSAURIA** Bonaparte and Coria, 1993  
**LITHOSTROTIA** Wilson and Upchurch, 2003

**Genus** Quetecsaurus gen. nov.

**Type species.** *Quetecsaurus rusconii* sp. nov.

**Derivation of name.** From Quetec, fire (Milcayac, the language used by the people who inhabited the region of Mendoza); *saurus* (Greek), lizard.

**Diagnosis.** Titanosaurian sauropod characterized by the following combination of autapomorphies: (1) intercentrum of atlas with prominent anteroventral border and expanded posteroventral processes; (2) posterior cervical neural spines with incipient lateral laminae; and (3) humerus with strongly sigmoid proximal border, rounded proximomedial corner, and angular proximolateral corner. *Quetecsaurus* is also diagnosed by the following unique combination of characters: (1) opisthocoelous cervical centra; (2) deep spinoprezygapophyseal and spinopostzygapophyseal fossae on posterior cervical vertebrae; (3) accessory posterior centrodiapophyseal lamina on posterior cervical vertebrae; (4) posterior cervical centra relatively elongate (total length/posterior cotyle height greater than 2.5); (5) cervical vertebra height/centrum length less than 1.5; (6) prespinal lamina extends to the base of the neural spine on anterior dorsal vertebrae; (7) opisthocoelous anterior dorsal centra; (8) procoelous anterior caudal centra; (9) neural arch located anteriorly on anterior caudal centra; (10) infraglenoid lip very developed on the coracoid; (11) quadrangular coracoid with an anterodorsal angle around 90°; (12) hemal arches with open proximal articular facets; and (13) metacarpals without distal articular facets.

**Quetecsaurus rusconii** sp. nov.

Figures 2–15

**Derivation of name.** Rusconii, in honor of Carlos Rusconi (1898-1969), a naturalist who worked extensively in Mendoza Province and was Director of the Museum of Natural Sciences “Juan Cornelio Moyano”.

**Holotype.** UNCUYO-LD-300, represented by the following associated bones belonging to a single individual: postorbital, two teeth, atlas, one posterior cervical vertebra, one incomplete anterior dorsal vertebra, one anterior caudal vertebra, eight dorsal ribs, a coracoid, an incomplete humerus, distal fragments of a radius and an ulna, and five metacarpals.

**Horizon and locality.** Uppermost levels of the Cerro Lisandro Formation (late Cenomanian-early Turonian after Hugo and Leanza [2001], middle Turonian after Legarreta and Gulisano [1989]; middle-late Turonian after Garrido [2010]), Neuquén Group, Cañada del Pichanal section, Malargüe Department, Mendoza Province, Argentina.

**Description and comparisons**

**Postorbital.** The only preserved skull bone is a right postorbital (UNCUYO-LD-300.1; Fig. 3). The bone is not well preserved and has a narrow anterior process and a wide and quadrangular posterior section. Between them, the anterior and posterior portions form an angle of ~90°. As in most neosauropods this bone has a posterior process and a jugal process that is dorsoventrally flattened. The morphology of the postorbital is similar, in general terms, to that of *Nemegtosaurus mongoliensis* Nowinski, 1971, from Maastrichtian strata of Mongolia, and to that of *Tapuiasaurus macedoi* Zaher, Pol, Carvalho, Nascimento, Riccomini, Larson, Juarez-Valieri, Pires-Domingues, da Silva, and Campos, 2011, from the Early Cretaceous of Brazil. However, in contrast to these two taxa, the posterior process is more rounded (Fig. 3).

**Teeth.** Two teeth have been preserved, one of them is almost complete (UNCUYO-LD-300.2; Fig 4). The best-preserved tooth has an elliptical section, as in most derived titanosaurids in which the teeth have been described as “pencil-chisel like” (*e.g.*, Calvo, 1994; Canudo, 2002; Apesteguía, 2004; Garcia and Cerda, 2010). In the apex, the crown is labiolingually...
compressed, but this morphology is subcircular toward the roof (Fig. 4). It has longitudinal, denticulate carinae that are visible to the naked eye. The carinae extend from the apex to the middle portion of the tooth on their mesial and distal edges, separating the labial and lingual sides, as in *Tapuiasaurus* (Zaher et al., 2011). The enamel has an ornamentation similar to that seen in *Petrobrasaurus* Filippi, Canudo, Salgado, Garrido, Garcia, Cerda and Otero, 2011; *Tapuiasaurus*; and *Rapetosaurus* Curry Rogers and Foster, 2001. It lacks the “bisel” surface, interpreted as a feature of a replacement tooth.

**Atlas.** The atlas is incomplete but shows important characters (UNCUYO-LD-300.3; Fig. 5). The intercentrum is robust and has a wide ventral face with a prominent anteroventral border. In contrast, the atlas of *Rapetosaurus* has a short and poorly developed anteroventral border. In *Futalognkosaurus duxei* Calvo, Porfiri, González Riga and Kellner, 2007, the intercentrum is thin with a short anteroventral border. The atlas of *Quetecsaurus* is also different from that of *Erketu ellisoni* Ksepka and Norell, 2006, from the Early Cretaceous of Mongolia, and from that of *Kotasaurus yamanpalliensis* Yadagiri, 1988 (Yadagiri, 2001) from the Early Jurassic of India. In these sauropods, the intercentrum is relatively wide and the anteroventral border is not prominent. In *Quetecsaurus*, the articulation with the occipital condyle is wider than high. The anterior face of the centrum is concave, and the canal with the articulation with the odontoid process is open and has a subcircular contour. The posterior face of the intercentrum is flat and has a quadrangular contour, somewhat similar to that of *Erketu*. Moreover, there are two well-developed posteroventral processes that are absent in *Rapetosaurus* and *Futalognkosaurus* and very reduced in *Erketu*. The ventral face of the intercentrum is relatively wide and anteroposteriorly concave, and it is well demarcated from the lateral faces by ridges connected to the posteroventral processes. The anteroventral border is ventrally oriented and extends anteriorly 1 cm. The total distance between the posterior processes is 4.7 cm. Other measurements are given in Tab. 1.

**Cervical vertebra.** A partially complete posterior cervical vertebra is preserved (UNCUYO-LD-300.4; Fig. 6). The centrum is dorsoventrally compressed and opisthocoelous, as in other titanosaurs (*e.g.*, *Futalognkosaurus*, *Ligabuesaurus lean扎i* Boneparte, González Riga and Apesteguía, 2006, *Mendozasaurus*, and *Pitekunsaurus macayai* Filippi and Garrido, 2008). The ventral face of the centrum is anteroposteriorly concave. The postzygapophyseal processes are relatively short and have wide, ventrolaterally directed articular facets. The prezygapophyseal processes are relatively long and surpass the anterior face of the centrum. The postzygapophyseal facets are connected by the intrapostzygapophyseal lamina. As seen in posterior view, there is a deep spinopostzygapophyseal fossa that is delimited by the spinopostzygapophyseal laminae and the intrapostzygapophyseal lamina. The prezygapophyses exhibit robust, semicircular articular facets. In anterior view, a relatively wide intraprezygapophyseal lamina connects the prezygapophyses, forming a roof over the neural canal, as also occurs in *Ligabuesaurus* and titanosaurs. Together with the spinoprezygapophyseal laminae, the intraprezygapophyseal lamina circumscribes the deep spinoprezygapophyseal fossa. The spinoprezygapophyseal lamina is strongly curved anteriorly and reaches the tip of the neural spine. This lamina is similar to that of *Futalognkosaurus*. In contrast, in *Mendozasaurus* and *Puertasaurus* the spinoprezygapophyseal laminae are well separated and only reach the middle part of the neu-
ral spine. In other titanosaurs such as Saltasaurinae (Powell, 1986) and Rinconsaurini (sensu Calvo et al., 2007c) this character is present but is not associated with a very deep spino-prezygapophyseal fossa. The neural spine is posteriorly oriented and placed on the posterior portion of the neural arch, as in Futalognkosaurus. Its morphology differs from that of

Figure 5. Quetecsaurus rusconii gen. et sp. nov., UNCUYO-LD-300.3, atlas. 1–1’, anterior view; 2–2’, left lateral view; 3–3’, dorsal view; 4–4’, posterior view; 5–5’, right lateral view; 6–6’, ventral view. Abbreviations: na: neurapophysis; awb: wide anteroventral border; pvp: posteroventral process. Scale bar= 1 cm.
Figure 6. Quetecsaurus rusconii gen. et sp. nov., UNCUYO-LD-300.4, middle-posterior cervical vertebra. 1–1’, right lateral view; 2–2’, posterior view. Abbreviations: nc: neural canal; dp: diapophysis; sdf: spinodiapophyseal fossa; spof: spinopostzygapophyseal fosa; pcdl: posterior centrodiapophyseal lamina; tpol: intrapostzygapophyseal lamina; spol: spinopostzygapophyseal lamina; sprl: spinoprezygapophyseal lamina; ll: lateral laminae; podl: postzygodiapophyseal lamina; pp: parapophysis; poz: postzygapophysis; prz: prezygapophysis. Scale bar= 10 cm.
Isisaurus Colberti Jain and Bandyopadhyay, 1997 (Wilson and Upchurch, 2003) from the Maasrichtian of India, Puer-
taxaurus, and Mendoza
taurus, where the neural spines are lat-
erally expanded, reaching or surpassing the width of the vertebral centrum. The neural spine expands distally through
the development of lateral laminae (i.e., ‘lateral expansions’), a feature also present in Mendoza
taurus (Gonzalez Riga, 2005)
and Futalogknosaurus (Calvo et al., 2007b), although this con-
dition appears to be less developed than in these taxa. Based on
comparisons with the articulated cervical vertebrae of Futa-
logknosaurus, the cervical vertebra of Quetecsaurus is prelimi-
nary assigned to an 11th place on the series. In the posterior
cervical of Quetecsaurus, the neural spine is ~13 cm wide,
which is much less than the width of the centrum (Tab. 1). In
Mendoza
taurus, by contrast, the lateral laminae are so promi-
nent that the neural spine is wider than the centrum; this char-
acter is less pronounced in Futalogknosaurus, where the spine
is equal in width or narrower than the centrum. Moreover, in
Ligabuesaurus, the neural spines are expanded, but these ex-
|pansions are constructed from lateral spinoprezygapophyal
|la
tinae, not from lateral laminae that originate in the spin-
|odiaphyeal fossa (Gonzalez Riga, 2005). In Quetecsaurus, the spinodiaphyeal fossa is well de-
|fined, but it is shallower than in Mendoza
taurus. It is bounded by
|spinopostzygapophyal and spinoprezygapophyal lami-
|nae. Pleurocoels are absent, but the centrum has a large lon-
gitudinal cavity ventral to the posterior centrodia
|phyeal lamina. Dorsal to this lamina there are two small cavities
|that are delimited by an accessory posterior centrodia
|phyeal lamina and the postzygodiaphyeal lamina. The para-
pophyses are robust and anteroventrally directed, and the dia-
pophyses are short and posteroventrally oriente
d. A fragmentary anterior dorsal vertebra is
|preserved (UNCUYO-LD-300.5; Fig. 7). It retains a portion
|of the neural arch and spine, and part of the posterior cotyle
|and anterior condyle, but lacks most of the centrum, prezy-
|gapophyses, and diapophyses. It has an opisthocoelous cen-
|trum with a circular anterior and posterior contour. The
|neural spine is single, short, and vertically directed, as in
|Pitekunsaurus, Mendoza
taurus, and Drusilasaura deseadensis
|Navarrete, Casal and Martinez, 2011. It exhibits a prespinal
|lamina that reaches the spinodiaphyeal laminae. The right
diapophysis is partially preserved, and its morphology demon-
|strates that the vertebra is wider than high (Tab. 1). The spin-
|odia

Figure 7. Quetecsaurus rusconii gen. et sp. nov., UNCUYO-LD-300.5, an-
terior dorsal vertebrae. 1–1’, anterior view; 2–2’, posterior view. Abbre-
viations: nc: neural canal; vc: vertebral centrum; dp: diapophysis; ns:
neural spine; spd: spinodiaphyeal lamina; prsl: prespinal lamina; spol:
spinopostzygapophyal lamina; poz: postzygapophysis. Scale bar= 10 cm.
Dorsal ribs. Eight dorsal ribs are preserved, some of them complete (UNCUYO-LD-300.7-14; Fig. 9). In the better preserved ribs, there are pneumatic cavities between the tuberculum and capitulum, as has been described for Titanosauri-
formes (Wilson and Sereno, 1998). The tuberculum is longer and more robust than the capitulum. All ribs have elliptical sections.

**Coracoid.** A nearly complete right coracoid is preserved (UNCUYO-LD-300.15; Figs. 10–11). The lateral surface is convex and the medial surface is concave. On the lateral surface there is a slight ridge that extends posterventrally, ventral to the coracoid foramen. The bone is very robust in its posteroverentral portion; that is, in the area of contact with the scapula, the glenoid fossa, and the infraglenoid lip. In contrast, the anterodorsal portion is thinner (Tab. 2). The coracoid shows a very well developed infraglenoid lip that forms an angle of approximately 90° with the anterior border. The anterior border is straight and intersects the dorsal border with an angle of ~90°. Because of this, the coracoid exhibits a quadrangular contour, as in *Neuquensaurus* (Otero, 2010), *Saltasaurus* (Powell, 1992, 2003), and *Rinconsaurus caudamirus* Calvo and González Riga, 2003. In contrast, other titanosaurs, such as *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977, *Rapetosaurus* and *Iisisaurus*, have a more rounded or subrectangular outline. The contact with the scapula is almost straight and it is relatively extended in relation with the anteroposterior length of the bone. The coracoid foramen is closed and placed posteromedially, very close to the posterior border.

**Humerus.** The proximal end of the left humerus has been recovered (UNCUYO-LD-300.16; Fig. 12). The humeral head is robust and the dorsal border of the bone has a strongly sigmoidal outline. This morphology is different from that of other titanosaurs, and is herein considered an autapomorphy of *Quetecsaurus* (Fig. 12). The titanosaurs *Saltasaurus* and *Paralititan* Smith, Lamanna, Lacovara, Dodson, Smith, Poole, Giegengack, and Attia 2001, from the Late Cretaceous of

<table>
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<th>Skeletal element</th>
<th>Total height</th>
<th>Length of center</th>
<th>Center height</th>
<th>Center Width</th>
<th>Relationship overall height / length of the center</th>
<th>Ratio total height / height of the center</th>
<th>Ratio length / height of the center</th>
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<td>1,642</td>
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<tr>
<td>Anterior dorsal vertebra</td>
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<td>—</td>
<td>20</td>
<td>24*</td>
<td>—</td>
<td>1.95</td>
<td>—</td>
</tr>
<tr>
<td>Anterior caudal vertebra</td>
<td>—</td>
<td>16</td>
<td>14</td>
<td>13</td>
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<td>1.143</td>
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*Measurements in cm*
Egypt have sigmoidal proximal humeri, but this condition is relatively less pronounced than that of *Quetecsaurus*. Moreover, the humerus of *Quetecsaurus* has a broad and rounded proximomedial border and an angular proximolateral corner, the proximal and lateral margins of which form an obtuse angle (Fig. 12). Wilson (2002) described the proximal end of the sauropod humerus based on the shape of its proximolateral corner, differentiating between rounded and square morphologies (Wilson, 2002; character 159). Later, in a character matrix, González Riga (2003; character 27) described the morphology of the proximal ends of sauropod humeri as strongly rounded, straight or slightly rounded, or sigmoidal (Fig. 16). In fact, in basal titanosauriforms such as *Ligabuesaurus*, the proximal border is slightly rounded. Conversely, in most derived titanosaurs, the proximal end is straight (*e.g.*, *Rapetosaurus*, *Mendozaeasaurus*). In *Quetecsaurus*, a broad and deep cavity extends in the anterior margin, below the humeral head; this is different from the conditions in *Neuquensaurus* and *Rapetosaurus*. The deltopectoral crest is relatively reduced and positioned medially. The robustness of the humeral head is correlated with the broad glenoid fossa of the coracoid.

**Radius and ulna.** Only the distal ends of a radius and an ulna have been preserved (UNCUYO-LD-300.17-18; Fig. 13). The radius has an anteroposteriorly expanded distal end and displays a slight depression corresponding to the ulnar articular surface. The distal end of the ulna has a triangular outline, with a typical radial articular surface. The distal articular surface has noticeable rugosities and tuberosities which are interpreted as sites of ligament insertion.

**Metacarpals.** The five left metacarpals have been preserved (UNCUYO-LD-300.19-23; Figs. 14–15; Tab. 3). Metacarpals

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**Figure 11. Quetecsaurus rusconii** gen. et sp. nov., UNCUYO-LD-300.15, right coracoid, glenoid view. Abbreviations: igl: infraglenoid lip; gf: glenoid fossa; scs: scapulocoracoid suture; cf: coracoid foramen. Scale bar= 10 cm.

**Figure 12. Quetecsaurus rusconii** gen. et sp. nov., UNCUYO-LD-300.16, left humerus in anterior view. Abbreviations: hh: humeral head; dpc: deltopectoral crest; erpb: expanded and rounded proximomedial corner; apc: angular proximolateral corner. Scale bar= 10 cm.
II, III, and IV were articulated whereas metacarpals I and V were displaced a few centimeters from their original anatomical positions. The complete metacarpal structure is known in some titanosaurids such as *Rapetosaurus*, *Opisthocoelicaudia*, and *Epachthosaurus sciuttoi* Powell, 1990.

The proximal and distal ends are well preserved, whereas the shafts are broken at their mid sections and exhibit numerous diagenetic fractures. When articulated, the metacarpals are oriented almost vertically and form a semilunate arch with a flat proximal surface (Fig. 15). Due to breakage of the shafts, it is not possible to precisely measure the length of most metacarpals, but the length of metacarpal III can be estimated at about 36 cm.

Metacarpal I has a dorsomedially elongate proximal end. The diaphysis is flattened on its medial and lateral faces; a different condition is observed in *Epachthosaurus*, where metacarpal I is the most robust of the series. The lateral surface of the proximal shaft has a broad concavity for articulation with metacarpal II. The distal end has a subtriangular outline, being rounded at its medial border. Metacarpal II has the most robust proximal end of the series, and has a subcircular outline as in *Petrobrasaurus*. The proximal end is more robust than the distal end. The shaft has a triangular cross section and its medial side has a slightly concave surface for articulation with metacarpal III. The distal end has a subquadrangular outline and is slightly concave. Metacarpal III has the most slender shaft of the series; it has a circular cross section. The proximal end has a triangular outline; the distal end is dorsoventrally compressed and shows a subquadrangular outline. The surface of the distal end is not perpendicular to the shaft but instead

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**Figure 13. Quetecsaurus rusconii** gen. et sp. nov., UNCUYO-LD-300.17, UNCUYO-LD-300.18, left radius and ulna. 1–1', distal shaft of radius in posterior view; 2–2', distal shaft of ulna in anterior view; 3, distal shaft of radius in ventral view; 4, distal shaft of ulna in ventral view. Abbreviations: uas: ulnar articular surface; ras: radial articular surface. Scale bar= 5 cm.

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**Table 2 - Measures of various skeletal elements of Quetecsaurus rusconii** gen. et sp. nov. (LD-Pv 1)

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Height</th>
<th>Width in previous portion</th>
<th>Width at posterior portion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Postorbital</td>
<td>11,8</td>
<td>4,3</td>
<td>1,5</td>
<td>3,3</td>
</tr>
<tr>
<td>Width of the middle section</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tooth</td>
<td>4</td>
<td>0,5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal rib</td>
<td>132</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Postero-dorsal border length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anteroventral border length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coracoid</td>
<td>32</td>
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<td>34</td>
<td>16</td>
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<td></td>
<td></td>
<td></td>
<td>Infraglenoid lip length</td>
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<td>Proximal border width</td>
<td>37</td>
<td>15,5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width of the diaphysis at proximal portion</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Measurements in cm
is oriented toward the ventral side. Metacarpal IV is proximally incomplete. The distal end is subquadrangular and slightly concave lateromedially. On the ventral side, the distal end has a prominent process. The diaphysis is expanded dorsomedially and has a concave articular surface for metacarpal III. Metacarpal V has a dorsoventrally elongate proximal end. The distal end is subquadrangular and slightly concave. This element has been distorted by taphonomic processes.

Although their preservation is poor, the distal ends of the metacarpals show important characters. The articular surfaces for the phalanges are not well defined, as in most titanosaurs. However, in metacarpal I and IV there is a prominent, ventrally-directed process. Moreover, metacarpals II and V have a lateromedially concave surface. The described structure is similar to those of other titanosaurs, following the detailed study of Apesteguia (2005).

**PHYLOGENETIC ANALYSIS AND DISCUSSION**

*Quetecsaurus rusconii* displays a unique combination of characters within Titanosauroidea, which justifies its diagnosis as a new taxon. Three characters are here considered autapomorphies: (1) intercentrum of atlas with a prominent anterioventral border and expanded posterioventral processes; (2) posterior cervical neural spines with an incipient lateral lamina; and (3) humerus with a strongly sigmoidal proximal border, a rounded proximomedial border, and an angular proximolateral corner.

A morphological comparison of the proximal ends of titanosaur humeri revealed interesting information (Fig. 16). For example, *Rapetosaurus* and *Mendozasaurus* have a straight proximal end, with a proximolateral corner that forms an angle of ~90°. In contrast, *Quetecsaurus* is the only titanosaur that has a strongly sigmoidal proximal end, with an expanded and rounded proximomedial border and an angular proximolateral corner that describes an obtuse angle (Fig. 16). Only *Saltasaurus* and *Paralititan* show a partly similar morphology, but with a less sigmoidal outline; moreover, the humeri of

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Figure 14. *Quetecsaurus rusconii* gen. et sp. nov., UNCUYO-LD-300.19, UNCUYO-LD-300.20, UNCUYO-LD-300.21 UNCUYO-LD-300.22, UNCUYO-LD-300.23, left metacarpals. 1–4, metacarpal I; 1, medial view; 2, lateral view; 3, proximal view; 4, distal view. 5–8, metacarpal II; 5, dorsal view; 6, ventral view; 7, proximal view; 8, distal view. 9–12, metacarpal III; 9, dorsal view; 10, ventral view; 11, proximal view; 12, distal view. 13–16, metacarpal IV; 13, medial view; 14, lateral view; 15, proximal view; 16, distal view. 17–20, metacarpal V; 17, medial view; 18, lateral view; 19, proximal view; 20, distal view. Scale bar= 5 cm.
these two taxa do not have a rounded and expanded proxi-
molateral border (Fig. 16).
The phylogenetic relationships of Quetecsaurus were tested
through a cladistic analysis based on 82 characters scored
for 22 taxa (see Tab. 4 and Appendix). Camarasaurus gran-
dis (Cope, 1877) was considered as the outgroup of 21 ti-

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**Figure 15.** Quetecsaurus rusconii gen. et sp. nov., UNCUYO-LD-300.19, UNCUYO-LD-300.20, UNCUYO-LD-300.21, UNCUYO-LD-300.22, UNCUYO-LD-300.23, left metacarpus. 1–1’, proximal view; 2–2’, distal view. Abbreviations: mcI: metacarpal I; mcII: metacarpal II; mcIII: metacarpal III; mcIV: metacarpal IV; mcV: metacarpal V. Scale bar= 5 cm.

**Table 3 - Measures of the metacarpals of Quetecsaurus rusconii gen. et sp. nov. (LD-Pv 1)**

<table>
<thead>
<tr>
<th>Metacarpal</th>
<th>Estimated total length</th>
<th>Width of the middle section</th>
<th>Proximal epiphysis</th>
<th>Distal epiphysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Length</td>
<td>Width</td>
</tr>
<tr>
<td>Metacarpal I</td>
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<td>12.8</td>
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<td>Metacarpal II</td>
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<td>7</td>
<td>9.8</td>
<td>9.3</td>
</tr>
<tr>
<td>Metacarpal III</td>
<td>29.2</td>
<td>4.5</td>
<td>9.2</td>
<td>8.7</td>
</tr>
<tr>
<td>Metacarpal IV</td>
<td>30.3</td>
<td>7.5</td>
<td>8.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Metacarpal V</td>
<td>25.1</td>
<td>6.5</td>
<td>10.4</td>
<td>5.3</td>
</tr>
</tbody>
</table>

Measurements in cm
tanosauriform taxa, which include two basal forms (Brachiosaurus brancai Janensch, 1950, and Chubutisaurus insignis Del Corro, 1975) and a diverse sample of 19 titanosaurids (see Tab. 4). We used a list of characters derived from previous analyses (e.g. Wilson, 2002; Gonzalez Riga, 2003; Curry Rogers, 2005; Calvo et al., 2007a; Gonzalez Riga et al., 2009; Gallina and Apesteguía, 2011; Zaher et al., 2011) after a revision of each of them, we redefined two characters (58 and 82), and added three new characters referred to the cervical vertebrae (24, 26 and 27) (see Tab. 4 and Appendix).

The data matrix was analyzed using the program NONA, version 2.0 (Goloboff, 1993), with multistate characters considered unordered, and the character polarity was determined by comparison with the outgroup. Two most parsimonious trees (157 steps, C.I.: 0.64; R.I.: 0.71) were obtained after the tree search. The strict consensus cladogram (Fig. 18) shows some differences with recent studies (e.g. Gonzalez Riga et al., 2009; Gallina and Apesteguía, 2011), particularly in the polytomy formed by Drusilasaura Navarrete, Casal and Martinez, 2011 and the clade (Bonitasaurus + (Quetecasaurus + (Mendoza- saurus + Futalognkosaurus)))) (Fig. 18). Most titanosaurids are represented by very incomplete skeletons: some have caudal vertebrae, others dorsal vertebrae, or cranial remains without postcranial bones. This results in the weak support of some terminal taxa and nodes (see Gonzalez Riga, 2010). In this case Drusilasaura is represented by an incomplete skeleton: dorsal and caudal vertebrae, one sacral vertebra, a scapula, and rib fragments (Navarrete et al., 2011).

Titanosauria, defined as ‘Andesaurus delgadoi’ (Calvo and Bonaparte, 1991), Saltasaurus horricattus (Bonaparte and Pow-

---

**Table 4 - Matrix of characters used for the phylogenetic analysis**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>1-10</th>
<th>11-20</th>
<th>21-30</th>
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<th>61-70</th>
<th>71-80</th>
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</table>
ell, 1980), their most recent common ancestor and all descendents’ (Salgado et al., 1997, modified by Wilson and Upchurch, 2003) is supported by two unambiguous synapomorphies: absence of well-developed distal phalangeal articular facets on metacarpals (character 71, state 1), and humerus/femoral ratio less than 0.9 (character 77, state 1). Within Titanosauria, the node-based Lithostrotia (defined as ‘the most recent common ancestor of Malawisaurus and Saltasaurus, and all the descendants of that ancestor’ sensu Upchurch et al., 2004), is supported by three unambiguous synapomorphies: articular face shape on anterior caudal centra strongly procoelous with prominent condyles (character 51, state 3), articular face shape on middle caudal centra strongly procoelous with prominent condyles (character 52, state 2), and length proportions of prezygapophyses between 40 to 50% with respect to the centrum length in middle caudal vertebrae (character 59, state 1).

Within Lithostrotia we recognize five different clades: Longkosauria, Rinconsauria, Opisthocoelicaudinae, Aeolosaurini and Saltasaurinae (Fig. 18), all supported by unambiguous synapomorphies. Bootstrap and Jackknife values up to 50% are indicated in selected nodes of the strict consensus tree. Obviously, a more detailed analysis including all new taxa recently described from Brazil and other countries is necessary for clarifying the phylogenetic relationships of these clades, a goal beyond the scope of this contribution.

Our analysis recovers Quetecsaurus rusconii as the sister taxon of Lognkosauria (Mendozasaurus + Futalognkosaurus). Lognkosauria was defined by Calvo et al. (2007a) as ‘the most recent common ancestor of Mendozasaurus neguyelap (González Riga, 2003) and Futalognkosaurus dukei (Calvo et al., 2007a), and all of its descendents’. In the original paper, five synapomorphies supported this clade: (1) presence of laterally expanded posterior cervical neural spines that are wider than their respective centra; (2) posterior cervical vertebrae 1.5 times taller than long; (3) deep and extended spinodiapophyseal fossa in posterior cervical vertebrae; (4) ratio of anteroposterior length/height of posterior face in posterior cervical centra less than 1.5; and (5) anteriormost caudal vertebrae with transversely expanded neural spines.

In our analysis, Lognkosauria is supported by three unambiguous synapomorphies: (1) laterodorsally expanded cervical neural spines originated by lateral laminae that reach or surpass the wide of the centra (character 27, state 1); (2) pos-
terior cervical vertebrae 1.5 times taller than long (character 31, state 1); and (3) deep and extended spinodiapophyseal fossa in posterior cervical vertebrae (character 32, state 2).

The synapomorphy defined by Calvo et al. (2007a) as ‘anteriormost caudal vertebrae with transversely expanded neural spines’ (character 56, state 1, in this paper) is not recognized here as diagnostic of Longkosauria diagnosis since it has a broader distribution (e.g., Rapetosaurus, Muyelensaurus, Rinconsaurus, Bonitasaura, Aeolosaurus, Drusilasaura). In particular, Drusilasaura (Navarrete et al., 2011: fig. 9.A) shares with Futalognkosaurus (Calvo et al., 2007b: figs. 16–17) a robust neural spine in the most anterior caudals with well-developed lateral expansion. This condition is absent in Mendozasaurus, which has a transversely expanded neural spine (González Riga, 2005, figs. 2–3; Calvo et al., 2007b, fig. 11). Thus, synapomorphy 1 of Lognkosauria has been here redefined as ‘laterodorsally expanded cervical neural spines originated by lateral laminae that reach or surpass the wide of the centra’. It is relevant to note that these same lateral laminae are also present in Quetecsaures, but are less strongly developed. In the second type, the huge neural spines of Ligabuesaurus are formed by splayed lateral spinoprezygapophyseal laminae (Bonaparte et al., 2006;
González Riga, 2010). Bonitasaura Apesteguía, 2004, is another titanosaur that also has a huge cervical neural spine, which was described by Gallina (2011) as a ‘rhomboid-shaped neural spine forming a simple expansion of the distal spine without a clear contribution of anterior or posterior laminae’. Therefore, the broad neural spine of Bonitasaura lacks the lateral laminae that form the lateral border of the neural spines in lognkosaurs.

Other lognkosaurian characters are not present in Quetecatasaurus. For example, with regard to synapomorphy 2, the ratio of the height of the cervical vertebra to the length of its centrum is less than 1.5 (see Tab. 1). The synapomorphy 3, the deep spinodiaphyseal fossa that is characteristic of Mendozasaurus (González Riga, 2005: fig. 2) and Futalognkosaurus (Calvo et al., 2007b: fig. 11), does not have the same development in Quetecatasaurus, where this fossa is smaller and shallower. In this context, Quetecatasaurus does not appear to be a member of Lognkosauria, but is instead recovered as a close phylogenetic relative of the lognkosaurs.

ACKNOWLEDGMENTS

We thank M. Tovar, Director of the Instituto de Ciencias Básicas, and A. So- moza, Rector of the Universidad Nacional de Cuyo, for their permanent support in our research in the Laboratorio de Dinosaurios. We are grateful to the Dirección de Patrimonio del Gobierno de Mendoza for its management in the preservation of the dinosaur fossils (Directora Prof. R. Aguero, Vice-Director Arq. E. Prieto, Lic. E. Albahán). We thanks the Editor, D. Pol, for its accurate and valuable revision, and two anonymous reviewers that greatly improved the early version of the paper. We also wish to thank to M. Lamanna who improved the English of the manuscript and provided important scientific comments. We are grateful to participants in paleontological team that worked in the field (J. Porfiri, G. Retamal, D. Eseisa, D. Rosales, C. Fuentes, G. Garat, M. Milani, and J. Giacoboni) and F. Ortiz for the preparation of the fossils in laboratory. We thank the company Vale S.A. of the “Proyecto Potasio Río Colorado” and their environmental consultant, Knight Piésold Argentina, for their willingness to comply with the procedures established by law for the collection and preservation of the fossils discovered during construction of the mine (Ch. Monárdez, J. Leis, C. Delgado, A. Demonte, and their team). The collaboration of the following students in the laboratory work was also important: G. Sanchez Tiviroli, P. Gutiérrez, R. Sánchez Domínguez, L. Pinto, L. Resa, J. Menéndez, F. Jofré, L. Martínez, V. Penas, M. Pascual, R. López, D. Solís, M. Fredes, and F. Santos. This research was supported by R. Villalba and S. Londero from the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, and funded by grants from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET 713/09), the Agencia Nacional de Promoción Científica y Tecnológica (FONCYT PICT-2011-2591), and the Universidad Nacional de Cuyo (06/M044) to B. González Riga.

REFERENCES


**APPENDIX 1**

**List of characters used for the phylogenetic analysis**

1. Short, deep snout: present (0); absent (1) (modified from Upchurch 1998 by Curry Rogers, 2005).
2. Frontal contribution to supratemporal fossa: present (0); absent (1) (Wilson and Sereno, 1998).
3. Frontal, dorsal texture: smooth (0); rugose (1) (Gallina and Apesteguía, 2011).
4. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1) (Zaher et al., 2011).
5. Postorbital, posterior process shape: transversely narrow (0); broader transversely than anteroposteriorly (1) (Wilson et al., 2011).
6. Postorbital, posterior process shape: transversely narrow (0); broader transversely than anteroposteriorly (1) (Zaher et al., 2011).
7. Parital occipital process, dorsoventral height: deep, nearly twice the diameter of the foramen magnum (0); short, less than the diameter of the foramen magnum (1) (Wilson, 2002).
8. Parial, elongate lateral process: absent (0); present (1) (Curry Rogers, 2005).
9. Parial, cranial inclination with wide postero dorsal exposure of crest: absent (0); present (1) (Salgado and Calvo, 1997).
10. Parial, contribution to post-temporal fenestra: present (0); absent (1) (Wilson, 2002).
11. Parial, distance separating supratemporal fenestrae: less than (0); or twice the transverse diameter of the supratemporal fenestra (Wilson, 2002).
12. Ascending process of premaxilla: directed dorsally (0); directed posterodorsally (1) (Gauthier 1986).
13. External nares, configuration of lateral margin: lacrimal excluded, maxilla-nasal contact (0); lacrimal participates, separates maxilla and nasal (1) (Gallina and Apesteguía, 2011).
14. Preantorbital fenestra: absent (0); present (1) (Wilson and Sereno, 1998).
15. Supraoccipital, height: twice (0); or subequal (1) than the height of the foramen magnum (Wilson, 2002).
16. Paroccipital process, ventral non-articular process: absent (0); present (1) (Wilson, 2002).
17. Longitudinal groove on the supraoccipital: absent (0); present (1) (Curry Rogers, 2005).
18. Basipterygoid processes, angle of divergence: approximately 45° (0); less than 30° (1) (Wilson, 1998).
19. Basal tubera, anteroposterior depth: approximately half the dorsosventral height (0); sheeplike, 20% the dorsosventral height (1) (Wilson, 1998).
20. Mandible shape: U shape (0); L shape (1) (Gallina and Apesteguía, 2011).
21. Tooth shape: spoon-like (0); compressed conch chisel-like (1); pencil chisel-like (2) (modified from Calvo, 1994; modified from Calvo and Gómez Riga, 2003).
22. Tooth crowns, cross-sectional shape at mid-crown: D-shaped (0); subcylindrical with crest (1); cylindrical (2) (modified from Wilson and Sereno, 1998 by Calvo et al., 2007b).
23. Wear facets of teeth sharply inclined: absent (0); present (1) (Salgado and Calvo, 1997).
24. Atlas, anteroventral border of the intercentrum: reduced (0); extended (1) (this paper).
25. Cervical vertebrae, number: 12 (0); 13 (1); 14 or more (2) (Upchurch, 1998).
26. Lateral laminae on posterior cervical neural spines: absent (0); present (1) (this paper).
27. Laterodorsally expanded cervical neural spines originated by lateral laminae, that reach or surpass the wide of the centrum: absent (0); present (1) (this paper).
28. Cervical prezygapophyses, relative length: articular facets that surpass (0); or not surpass (1) the centrum (Salgado et al., 1997).
29. Neural spines in cervical vertebrae: tall (0); small (1) (Calvo et al., 2007b).
30. Anterior cervical neural spines: bifid (0); single (1) (Upchurch, 1998).
31. Posterior cervical vertebrae, proportions: ratio total height-centrum length; less (0); or more (1) than 1.5 (modified from Calvo and Salgado, 1995 by González Riga, 2005).
32. Spinodiapophyseal fossa in posterior cervical vertebrae: absent (0); shallow or reduced (1); deep and extended (2) (González Riga, 2005).
33. Posterior cervical vertebrae, proportions: ratio anteroposterior length/height of posterior face: >3 (0); 2.5 to 1.5 (1); less than 1.5 (2) (modified from Wilson, 2002 by Calvo et al., 2007b).
34. Dorsal vertebrae, number: 12 or more (0); 11 (1), 10 or fewer (2) (Wilson and Sereno, 1998).
35. Anterior dorsal neural spines, shape: bifid (0); single (1) (McIntosh, 1990).
36. Anterior dorsal vertebrae, infrapostzygapophyseal fossa: absent (0); present not divided (1); present divided in two subtriangular fossa (2) (Galina and Apesteguía, 2011).
37. Anterior cervical neural spines inclined posteriorly more than 20º from vertical: absent (0); present (1) (modified from Wilson and Sereno, 1998) by González Riga, 2003.
38. Anterior dorsal neural spines, dorsal development: more (0); or less (1) than 20% the total height of the vertebra (modified from Sanz et al., 1999 by González Riga, 2003).
39. Preapinal lamina in dorsal vertebrae: absent (0); present in the distal end of neural spine (1); well developed up to the base of the neural spine (2) (modified from Salgado et al., 1997 by Bonaparte et al., 2006).
40. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (Bonaparte and Coria, 1993).
41. Ventrally widened or slightly forked centrodiaiaphyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado et al., 1997).
42. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (Salgado et al., 1997).
43. Pleurocoels in dorsal vertebrae, shape: circular or elliptical (0); caudally acuminate (1) (Salgado et al., 1997).
44. Camellate or somphospondylyous types of internal structures of presacral vertebrae: absent (0); present (1) (Wilson and Sereno, 1998).
45. Sacral vertebrae, number: five (0); six of more (1) (McIntosh, 1990).
46. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3) (Salgado et al., 1997).
47. Wide and deep interzigeapophyseal cavity in proximal caudal vertebrae: absent (0); present (1) (Calvo et al., 2007b).
48. Caudal transverse processes: disappear by caudal 15 (0); disappear by caudal 10 (1) (Wilson, 2002).
49. Anterior and middle caudal centra, proportions: as high as wide (0); depressed, wider than high (1) (Salgado et al., 1997).
50. Mid caudal centra with the anterior face strongly inclined anteriorly: absent (0); present (1) (Franco-Rosas et al., 2004).
51. Articular face shape on anterior caudal centra: non-procoelous (0); procoelous-distoplatyan (1); slightly procoelous (2); strongly procoelous with prominent condyles (3) (modified from González Riga, 2003 by González Riga et al., 2009).
52. Articular face shape on middle caudal centra: non-procoelous (0); procoelous-distoplatyan (1); slightly procoelous (2); strongly procoelous with prominent condyles (3) (modified from González Riga, 2003 by González Riga et al., 2009).
53. Articular face shape on posterior caudal centra: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2) (González Riga et al., 2009).
54. Anterodorsal border of neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0); present (1) (Salgado et al., 1997).
55. Anteriorly directed anterior caudal neural spine: absent (0); present (1) (Calvo et al., 2007c).
56. Shape of the section of neural spines in most anterior caudal vertebrae in dorsal view: axially elongated (0); transversely elongated (1); quadrangular (2) (Calvo et al., 2007c).
57. Neural arch in anterior caudal vertebrae: placed in the middle of the centrum (0); anteriorly (1); on the anterior border (2) (modified from Salgado et al., 1997 by Calvo et al., 2007b).
58. Neural spine in middle caudal vertebrae, shape: tall and short anteroposteriorly (0); low, anteroposteriorly elongated, laminated, with a subquadrangular contour (1) (modified from González Riga, 2003 by this paper).
59. Length proportions of prezygapophyses with respect to the centrum length in middle caudal vertebrae: shorter than 50% (0); between 40 to 50% (1); longer than 50% (2) (modified from González Riga 2003 by Calvo et al., 2007b).
60. Ventral depression divided by a longitudinal septum in anterior and middle caudal vertebrae: absent (0); present (1) (Salgado and Arpilicueta, 2000).
61. Postzygapophysial process in middle caudal vertebrae: absent (0); present (1) (Calvo et al., 2007b).
62. Well-developed interprezgapophysial lamina in middle caudal vertebrae: absent (0); present (1) (Calvo et al., 2007b).
63. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (Wilson and Sereno, 1998).
64. Humerus, breadth of proximal end: less (0); equals or more than 50% (1) the humeral length (González Riga, 2003).
65. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2) (modified from Upchurch, 1998 by González Riga, 2003).
66. Ulnar olecranon process, development: rudimentary, levels with proximal articulation (0); prominent, projecting above proximal articulation (1) (Wilson and Sereno, 1998).
67. Sterna1 plates, shape: suboval (0); semilunar (1) (Salgado et al., 1997).
68. Semilunar sterneal plate with straight caudal border: absent (0); present (1) (González Riga, 2003).
69. Coracoid, shape: suboval (0); quadrangular (1) (Salgado et al., 1997).
70. Pubis, length with respect to ischium length: shorter or equal (0); longer (1) (Salgado et al., 1997).
71. Metacarpals, distal phalangeal articular facets well developed: present (0); absent (1) (Salgado et al., 2006).
72. Ulnar olecranon process, development: rudimentary, levels with proximal articulation (0); prominent, projecting above proximal articulation (1) (Wilson and Sereno, 1998).
73. Ischium, iliac pedicel: short and poorly developed (0); slender and well developed (1); wide and well developed (2) (Calvo and González Riga, 2003).
74. Shape of preacetabular lobe of ilium: moderately expanded (0); broadly expanded and dorsally directed (1) (Salgado et al., 1997).
75. Orientation of preacetabular lobe of ilium: nearly vertical (0); nearly horizontal and laterally projected (1) (Salgado et al., 1997).
76. Relative orientation of the pubic peduncle of ilium: angled (0); perpendicular with respect to the sacral axis (1) (Salgado et al., 1997a).
77. Humerus/femoral ratio of 0.90 or more: absent (0); present (1) (McIntosh, 1990).
78. Lateral bulge of femur, below the major trochanter: absent (0); present (1) (McIntosh, 1990).
79. Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1) (Salgado et al., 1997).
80. Metatarsal I, length: shortest metatarsal (0); metatarsal V shorter than metatarsal I (1) (Curry Rogers, 2005).
81. Calcaneum: present (0); ossified calcaneum absent (1) (McIntosh, 1990).
82. Osteoderm: absent (0); present, ellipsoid (1); present, keeled (2) (modified from Curry Rogers, 2005 by this paper).

Recibido: 23 de octubre de 2013
Aceptado: 26 de diciembre de 2013