New fossil remains of *Mendozasaurus neguyelap* (Sauropoda, Titanosauria) of the Late Cretaceous of Mendoza, Argentina[1]

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Abstract

In South America, most titanosaur species are represented by incomplete skeletal elements lacking well-preserved cervical vertebrae. In this context, the discovery of cervical remains assigned to *Mendozasaurus neguyelap* González Riga is relevant from a systematic viewpoint. The fossils were found in the paleontological site and assemblage of the holotype, Río Neuquén Subgroup, late Turonian – late Coniacian from Mendoza Province, Argentina. The cervical vertebrae of *Mendozasaurus* exhibit differences with those of most titanosaurs; however, they share with *Isisaurus colberti* (Jain and Bandyopadhyay 1997) from Maastrichthian of India the presence of: a) short vertebral centra (ratio: total length/height of cotyle less than 2.5), b) large and deep supradiapophyseal fossa, and c) relatively tall neural spines (ratio: vertebral height / centrum length more than 1.5). The fossils recovered show an autapomorphic character that enlarges the diagnosis of *Mendozasaurus* : tall, laminar and transversally expanded mid-posterior cervical neural spines that are wider than vertebral centra and 'fan-like' or 'subrhomboid' in shape due to lateral expansions and a subrounded dorsal border. The fossil record of titanosaurs shows a notable morphologic diversity in the cervical series. In particular, *Mendozasauru[1]s neguyelap* and *Isisaurus colberti* possess tall neural spines associated with the proportionally shortest cervical centra of any titanosaur. This unusual morphology suggests the development of relatively wide, robust and short necks in Late Cretaceous sauropods from Argentina and India.

Key Words: Dinosauria, Titanosauria, Cervical vertebrae, Late Cretaceous, Mendoza, Argentina.

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Introduction:

In South America the record of titanosaur sauropod dinosaurs is abundant and diverse. While more than ten species have been described, most of those are represented by incomplete skeletons mostly composed of caudal vertebrae and disarticulated appendicular bones. In this regard, cervical remains are scarce. For example, in the titanosaurs *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), *Aeolosaurus rionegrinus* (Powell, 1986, 2003; Salgado and Coria, 1993; Salgado *et al* ., 1997b), *Pellegrinisaurus powelli* (Salgado, 1996), *Argyrosaurus superbus*

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(Lydekker, 1893; Powell, 1986) and *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993) cervical remains are unknown. Similarly, available cervical remains of *Rocasaurus muniozi* (Salgado y Azpilicueta, 2000), *Laplatosaurus araukanicus* (Huene, 1929; Powell, 1986; Salgado, 2003), *Gondwanatitan faustoi* (Kellner and Acevedo, 1999) y *Titanosaurus ?nanus* (Lydekker, 1893; Powell, 1986) are incomplete and relatively fragmentary. In contrast, only *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 2003), *Neuquensaurus australis* (Salgado *et al* ., in press), Titanosauria indet. DGM "Serie A" and "Serie B" of Brazil (Powell, 1987; 2003), *Rinconsaurus caudamirus* (González Riga and Calvo, 2001; Calvo and González Riga, 2003) and new recently found examples (Calvo *et al* ., 1997) show well-preserved cervicals. The incomplete record of the cervical series limits the study of the clade. Because of this, finds of new cervical remains are relevant from a systematic point of view and warrant analyses in phylogeny and functional morphology.

In this paper cervical vertebrae assigned to *Mendozasaurus neguyelap* are systematically described and analyzed. The type series of this species included dorsal and caudal vertebrae and the major part of the anterior and posterior limbs (González Riga, 2002; 2003a). The fossils here described were found and prepared by the author and assistants from 2001-2003. They come from Arroyo Seco, a locality south of the Cerro Guillermo, in the province of Mendoza, at the same paleontological site and fossil assemblage as the holotype of *Mendozasaurus*. At this site titanosaur bones of diverse sizes and ontogenetic stages have been found along with fragmentary remains of theropod dinosaurs. The fossils came from crevasse-splay deposits related to fluvial systems of moderate to high sinuosity (meandering) developed upon extensive floodplains (Figure 1). The site corresponds to a taphonomic mode (sensu Behrensmeyer and Hook, 1992) designated "bone-rich crevasse-splay accumulations," characterized by autochthonous and parautochthonous accumulations of articulated and disarticulated bones deposited in fluvial crevasse-splay facies (González Riga *et al*., 2003; 2004). The taphonomic history indicates a primary phase of biostratification in which the processes of disarticulation and orientation of bones is controlled by torrents from overbank flows. The remains, covered by sediments before the complete decomposition of soft tissues, come from micaceous feldspar wackes that indicate intense rain and bioturbation. The second taphonomic phase (diagenesis) includes the processes of permineralization and lithostatic compression (Gonázlez Riga, 2002). From a paleoenvironmental and paleoecological perspective, the abundance of large herbivorous vertebrates, conifer trunks, traces, and bioturbation indicate that this region of the Neuquina basin in the Late Turonian to Late Coniacian was a time of intense biological activity and development of vegetation on relatively well-drained fluvial plains subject to periodic flooding (González Riga, 2003b).

Institutional Abbreviations: DGM, Museo de la Divisao Geologia y Mineralogia, Rio de Janeiro, Brasil; IANIGLA-PV, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Colección Paleovertebrados, Mendoza, Argentina; MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Neuquén, Argentina; PVL, Colección de Paleontología de Vertebrados de la Fundación Instituto Miguel Lillo, Tucumán, Argentina.

Systematic Paleontology

Saurischia Seeley, 1888
Sauropoda Marsh, 1878
Titanosauria Bonaparte and Coria, 1993
Mendozasaurus neguyelap González Riga, 2003a
Figures 2-8

Modified Diagnosis:

Large titanosaur (18-25 m in length) characterized by the following association of unique characters: 1, mid-posterior cervical vertebrae with high neural spines, sheet-like and transversely expanded (much wider than the centra) with "fan-shaped" or sub-rhomboidal anterior contour with the development of lateral expansion and a sub-circular dorsal margin; 2, interzygapophyseal cavity of anterior caudal vertebrae extended dorsoventrally and delimited dorsally by postzygapophyseal and prezygapophyseal spines; 3, mid-caudal centra mildly procoelous with posterior condyles very reduced and displaced dorsally; 4, neural spines of middle and posterior caudal vertebrae sheet-like, dorsal border horizontal and angled anterodorsally; 5, large subconical/subspherical osteoderms without a cingulum. The presence of the following synapomorphies characterize the new taxon: mid-cervical centra relatively short (total length/height of cotyle < 2.5), cervical vertebrae with greatly enlarged supradiapophyseal fossa; height of cervical vertebra/length of centrum > 1.5; cervical transverse processes wing-like in anterior and ventral views owing to the presence of enlarged prezygapophyseal laminae on the anterior convex border; prespinal laminae extend to the base of the neural spine in anterior dorsal vertebrae; sharply bounded pleurocoels in anterior dorsal vertebrae; absence of hyposphene-hypantrum articulation in anterior dorsal vertebrae; neural arches of middle and posterior caudals located on the middle of the centra; anterodorsal angle of mid-caudal neural spines situated anteriorly with respect to the anterior margin of the postzygapophysis; neural spines axially elongated and sheet-like in mid-caudal vertebrae; prezygapophyses relatively large in mid-caudal vertebra; proximal articulation of hemapophyses open; sternal plate semilunar in shape with a relatively straight posterior border; anterior border of the scapular blade concave proximally and straight distally; proximal border of humerus relatively straight, curved in medial extreme; metacarpals without distal articular facets; femur with lateral protuberance under the greater trochanter.

Observations:

With respect to the original diagnosis (González Riga, 2003a) one cervical character is added here (Character 1) and two anterior dorsal characters are excluded which were previously proposed but are probably autapomorphies: the presence of two subtriangular infrapostzygapophyseal fossae and the development of postzygapophyseal laminae parallel to the planes of the postzygapophyseal facets. These characters were found to be present, with some morphological variation, in some recently discovered titanosaurs in northern Patagonia, in particular a new taxon coming from Rincón de los Sauces (Calvo and González Riga, in prep.) and in *Bonitasaura salgadoi* (Apesteguía, 2004, pers. comm.).

On the other hand, the recent publication of a well-preserved specimen of *Epachthosaurus sciutoi* (Martinez *et al*., 2004) of the Late Cenomanian-Early Turonian of Patagonia permits comparison with *Mendozasaurus neguyelap*. In the first place, Epachthosaurus shows a progressive reduction of the posterior articular condyles in the middle and posterior caudals (Martínez *et al*., 2004). Nevertheless, it does not show the morphology present in *Mendozasaurus* (character 3), wherein the posterior articular face of the vertebral centra is planar in its inferior half and shows a highly reduced/nearly absent condyle in its superior half. In the second place, while the neural spines of the middle and posterior caudal vertebrae are similar in both taxa, differences are observed. In contrast with *Mendozasaurus* (see character 4), *Epachthosaurus* possesses neural spines angled obtusely antero-dorsally and a dorsal border that smoothly descends toward the posterior. Finally, the neural spines of the mid-posterior caudal vertebrae of *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), while also having some similarities with the titanosaurs mentioned, differ from *Mendozasaurus* in their possession of a slightly curved dorsal border that is elevated posteriorly and a much more rounded anterodorsal angle.

Assigned Material:

IANIGLA-PV 076/1-4: four associated cervical vertebrae, one of which is almost complete, pertaining to an adult specimen. IANIGLA-PV 084: one posterior cervical attributed to an adult specimen of great size.

Stratigraphic Origin and Geography:

Levels assigned to the Subgroup Río Neuquén (Late Turonian-Late Coniacian following Leanza and Hugo, 2001), Arroyo Seco, region south of Cerro Guillermo, department of Malargue, province of Mendoza, Neuquina Basin.

Description:

Methodologically, the nomenclature proposed by Janensch (1929, 1950) and Wilson (1999) is adopted.

Middle Posterior Cervical Vertebrae (figures 2-3):

One almost complete cervical vertebra has been recovered lying *in situ* on its anterior face. This vertebra was articulated with another cervical, which only had part of its neural spine and postzygapophysis preserved. The most complete vertebra (Figure 2, IANIGLA-PV 076/1) exhibits an opisthocoelous centrum that is dorsoventrally depressed. It is relatively short, with an index of elongation (IE = length of centrum/height of cotyle *sensu* Wedel *et al*., 2000) less than 2.5 (Table 1). Evidence of crushing in the neural arch was not observed, which indicated that the unusual length of the centrum constituted a morphologic character, while the convexity of the condyle could have been lightly modified by lithostatic pressure. The condyle shows an ellipsoidal contour that is much reduced compared with the cotyle. The parapophyses are extended and oriented lateroventrally. They are located in the middle anterior of the centrum and unite medially in an enlarged centroparapophyseal lamina (sensu Wedel et al., 2000), which extends to the posterior border of the vertebral body.

The ventral face of the centrum (Figure 2.C) is strongly concave in a lateromedial sense and shows a smooth keel or medial crest in the anterior portion. In contrast, the posterior portion is convex in an anteroposterior and lateromedial sense.

The lateral face of the centrum (Figure 2.B) exhibits an extensive and deep cavity delimited ventrally by the posterior centroparapophyseal lamina and dorsally by a horizontal accessory lamina. Above this two subtriangular infradiapophysyal cavities are developed, separated by the anterior centrodiapophyseal lamina. This lamina, partially preserved, is a very thin structure (~1-2 mm). The anterior and posterior centrodiapophyseal laminae unite near the articular facet of the diapophysis.

The diapophysis is found above the parapophysis but in a relatively low position, at the level of the middle of the vertebral centrum. The transverse processes extend far laterally. They are supported by extensive prezygapophyseal and posterior centrodiapophyseal laminae, which form an extensive posteroventrally inclined surface. The anterior convex border of the prezygapophyseal laminae connects to the transverse processes in the form of a "wing" in ventral and anterior view (Figures 2.A, 2.C). This morphology constitutes a novel character among the titanosaurs. While some other sauropods appear to have relatively extended prezygapophyseal laminae, they don't show transverse processes with the form of a "wing." For example, in *Jobaria tiguidensis* a lower Cretaceous member of Eusauropoda from Niger, Sereno *et al.* (1999) describe an anterior accessory process near the prezygapophysis. On the other hand, in the last cervical and first dorsal of *Haplocathosaurus priscus*, Hatcher (1903) describes expansions of the transverse processes which probably were related to the insertion of the muscles of the scapula.

The neural arch and spine are displaced anteriorly (Figure 2.B), of such form that the prezygapophysis surpasses the anterior border of the condyle. Laterally, the neural arch exhibits an extensive and deep supradiapophyseal cavity that reaches almost to the medial plane of the vertebra. This cavity is bound dorsally by the spinopostzygapophyseal and spinoprezygapophyseal laminae. The prezygapophysis and postzygapophysis are projected so far laterally (Figure 2.A) that they reach a position more lateral than the parapophyses. This character is also present in other titanosaurs such as *Saltasaurus* and in Titanosauria indet. DGM "Serie A" of Brazil (Powell, 1987; Bonaparte, 1999). The prezygapophysis shows extensive subtriangular articular facets. These unite between by means of a robust intraprezygapophyseal lamina, which outlines a concave contour dorsally. The spinoprezygapophyseal laminae constitute pillars that converge at the middle of the height of the neural spine.

In posterior view, (Figure 3) the neural arch shows two thick spinopostzygapophyseal laminae that extend dorsally but do not converge. Between these an extensive cavity is developed, and the postspinal lamina is absent.

The neural spine is undivided, tall, laminated, and greatly expanded laterally. In anterior and posterior views it exhibits a peculiar "fan-shaped" or sub-rhomboidal contour, with a rounded dorsal border and two lateral expansions that form an obtuse angle. The relative size of the spine in relation to the vertebral centrum, and also as its morphology characterized by two lateral expansions, constitute a probable autapomorphy of *Mendozasaurus*. The dorsal border of the neural spine is relatively thick (~30-35 mm) and slightly concave in its posterior face. A prespinal lamina was not observed, although a bony edge was partially preserved suggesting the presence of an incipient and short prespinal lamina, situated at the base of the neural spine.

There is fossil material in preparation (IANIGLA-PV 84) that comes from the same site that corresponds with an adult specimen of gigantic size. Among the fossils recovered it is emphasized that one cervical vertebra is about 100 cm wide and 90 cm tall. Preliminary observations show that this cervical is morphologically similar to the one described, with some variation in the shape of the neural spine, which is relatively taller and anteriorly shaped more quadrangularly. Notwithstanding, the lack of complete and articulated material impedes, for the moment, the precise description of morphological changes in the neural spine in the longer cervical and dorsal sequence.

Posterior Cervical Vertebrae (Figure 4):

An incomplete posterior cervical vertebra was found (IANIGLA-PV 076/3) with a preserved centrum, right prezygapophysis, and right diapophysis. It has been dorsoventrally crushed by lithostatic pressure and its neural arch has been displaced toward the right side (Figure 4.C). The centrum is opisthocoelous and longer than the mid-posterior cervical centrum. The distortion of the centrum precludes the measurement of the height of the cotyle. Nevertheless, the estimated measurement of the cotyle height is 180 mm, so the index of elongation of the vertebral centrum will be less than 2.5 (Table 1). Differing from the mid-posterior cervical, the ventral face of the centrum (Figure 4.B) is anteroposteriorly convex in its anterior extreme and concave in its posterior portion. It lacks a medial crest and exhibits parapophysis with extensive articular facets, located in the middle of the centrum.

The lateral face of the centrum is similar to that of the mid-posterior centrum. A deep and elongate lateral cavity is observed, without septae (Figure 4A). Dorsally, an accessory horizontal lamina separates this cavity from a subtriangular lateral fossa, bound by the anterior and posterior centrodiapophyseal laminae. The posteroventral border of the centrum extends posteriorly with respect to the posterodorsal border. This character, present in other titanosaurs, is related to the natural curvature of the neck in life position (Lehman and Coulson, 2002). It shares the large lateral development of the transverse processes with the mid-posterior cervical vertebra (IANIGLA-PV 076/1), with extensive prezygapophyseal and posterior centrodiapophyseal laminae (there is 400 mm between the center of the neural canal and the diapophysis). In contrast with the mid-posterior cervicals, the diapophysis shows a more robust and subtriangularly shaped articular facet (Figure 3.A). The diapophysis is supported by the anterior and posterior centrodiapophyseal, prezygapophyseal, and spinodiapophyseal laminae. The latter lamina, characteristic of the dorsal vertebrae of sauropods (Wilson 1999), is incipient in *Mendozasaurus* in the posterior cervical series.

The anterior and posterior centrodiapophyseal laminae are very thin and unite before they reach the diapophysis, a difference from what occurs in the mid-posterior cervicals. The posterior centrodiapophyseal lamina, near the articular facet of the diapophysis, circumscribes a small posterior depression (Figure 4.B). The dorsal face of this neural arch is not well preserved and the prezygapophysis that is preserved has undergone strong crushing. Nevertheless, the presences of spinoprezygapophyseal and spinodiapophyseal laminae that dorsally support the transverse process are recognized.

Cervico-dorsal Vertebrae (Figures 5.A-B):

An incomplete neural arch belonging to a cervico-dorsal or first dorsal was preserved (IANIGLA-PV 076/4). Weighing this fragmentary character, it is significant because it serves as a link between the aforementioned cervicals and the anterior dorsals (IANIGLA-PV066; González Riga, 2003a), which probably correspond to a third dorsal (Figure 5.C).

On the one hand, this cervico-dorsal arch (Figures 5.A-B) has the same transverse process shape as the cervical vertebrae, with extensive prezygapophyseal and posterior centrodiapophysial laminae, and a relatively low position of the diapophysis, located at the level of the base of the neural arch. Besides this, the spinoprezygapophyseal lamina is robust, not as dorsally extended as in the cervicals, but much longer and more developed than in the third anterior dorsal (Figure 5.C). On the other hand, this neural arch shares with the dorsal vertebrae the presence of a spinodiapophyseal lamina, characteristic of dorsal vertebrae of sauropods (Wilson, 1999). Notwithstanding, in this cervico-dorsal arch the spinodiapophsyeal lamina is much thinner than the spinoprezygapophyseal lamina, contrasting what is found in the third dorsal vertebra (Figure 5C). In this last vertebra, the spinodiapophyseal lamina makes up a large structure that forms the dorsal border of the transverse process. Also, the cervico-dorsal arch, similarly to those in the dorsal vertebrae, exhibits a well-defined prespinal lamina.

Finally, a character that cannot be precisely described in these remains is the form in which the wide neural spines of the cervical vertebrae are gradually reduced in transverse development toward the dorsal series. Notwithstanding, the available evidence permits the inference that the widths of the neural spines of the cervical vertebrae of *Mendozasaurus* reach their maximum development in the mid-posterior section of the series (Figure 2), from where their transverse diameters are reduced gradually toward the cervico-dorsal section (Figures 5.A-B). Finally, the third dorsal (Figure 5.C) has a relatively narrow neural spine, even taking into account the deficient state of preservation of its lateral borders, which suggest more transverse development than what is preserved. It is important to note that in sauropods, a distinct morphological change is frequently observed in the cervico-dorsal transition that involves the shape of the neural spine, ribs, arch, and centra (McIntosh, 1990; Bonaparte, 1999; Wedel *et al.,* 2000).

Comparisons:

The cervical remains of the titanosaurs *Malawisaurus dixeyi* (Jacobs *et al.*, 1993) of the lower Cretaceous of Africa, *Isisaurus colberti* (Jain and Bandyopadhyay, 1997; Wilson and Upchurch, 2003) of the Maastrichtian India, *Rapetosaurus krausei* (Curry Rogers and Forster, 2001; 2004) of the Maastrichtian of Madagascar, *Alamosaurus sanjuanensis* (Lehman and Coulson, 2002) of the Maastrichtian of North America, Titanosauridae indet. DGM "Serie A" of the late Cretaceous of Brazil (Powell, 1987; 2003), *Neuquensaurus australis* (Salgado *et al.*, in press) of the early Campanian of Argentina, *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell 1992) of the Campanian-Maastrichtian of Argentina, and *Rinconsaurus caudamirus* (Calvo and González Riga, 2003) and *Mendozasaurus neguyelap* (González Riga, 2003a), both of the late Turonian-late Coniacian of Argentina, show notable morphological diversity.

A primary comparative analysis (Figure 6; Table 2) permits the recognition of large differences in size between the cervical vertebrae of titanosaurs, with those of *Isisaurus colberti* and *Mendozasaurus neguyelap* being the largest. Also observed are a notable variation in the form and height of the neural spines, the position and form of the zygapophyses, the development of the laminae and suprazygapophyseal cavities, and the proportions of the vertebral centra.

The cervical vertebrae of *Mendozasaurus* are notably different from the basal titanosaur *Malawisaurus dixeyi* (Jacobs *et al.*, 1993). This African species exhibits relatively long centra, with indices of elongation (EI)>3, and the absence of pleurocoels or lateral cavities (Figure 6.A). The neural spine, proportionally shorter than in *Mendozasaurus*, exhibits a dorsal border that is axially elongate. In addition, the neural arch shows scarce development of the diapophyseal laminae (Wilson and Sereno, 1998), and lacks a prezygodiapophyseal lamina and supradiapophyseal cavity. Evidently, *Malawisaurus* exhibits a distinct morphology from that of *Mendozasaurus* and other more derived titanosaurs (Calvo, 1999, Bonaparte et al., 2000; González Riga, 2002).

On the other hand, the cervicals of *Mendozasaurus* are clearly distinct from those of *Rapetosaurus krausei* (Curry Rogers and Forster, 2001), Titanosauria indet. "Serie A" of Brazil (Powell, 1987), and *Alamosaurus sanjuanensis* (Lehman and Coulson, 2002) (Figure 6 B-C) In contrast to *Mendozasaurus*, these titanosaurs exhibit elongate cervical centra (EI>3), relatively short neural arches, the absence of deep supradiapophyseal cavities, and dorsally reduced neural spines. *Rinconsaurus caudamirus* (Calvo and González Riga, 2003) also shows cervicals that are very different from those of *Mendozasaurus*, with relatively long centra (EI>3), short neural spines and deep but reduced supradiapophyseal fossae (Figure 6D). In particular *Rinconsaurus* is distinguished by the presence of a divided centroprezygapophyseal lamina that bounds an elongate depression under the prezygapophysis. A partially similar character has been described in anterior dorsals of *Saltasaurus loricatus* (Powell, 1992; 2003) and in Diplodocidae (Wilson, 2002).

The cervicals of *Saltasaurus loricatus* (Figure 6E) (Bonaparte and Powell, 1980; Powell, 1992) are also notably distinct from those of *Mendozasaurus*. On the one hand, the vertebral centra, while not as elongate as those of other titanosaurs (EI=2.5-3), they are proportionally longer than those of *Mendozasaurus*. Besides, the centra of *Saltasaurus* are small pleurocoels divided by laminae, which is considered an autapomorphic reversion by Wilson (2002). On the other hand, the neural spines of *Saltasaurus* are so dorsally reduced that they barely surpass the height of the postzygapophysis (Powell, 1992; Bonaparte, 1999). Besides, they are transversely short and have an asymmetric lateral profile, with an anterior border that is strongly inclined toward the prezygapophyses. In addition, the neural spine connects with robust spinoposyzygapophyseal laminae that are gently inclined towards the posterior (González Riga, 2002). In contrast to *Saltasaurus*, the Saltasaurine *Neuquensaurus australis* (Huene, 1929); Powell, 1986) shows relatively taller neural spines. While the cervical remains of *Neuquensaurus* are fragmentary, new material from the Cinco Saltos (Anacleto Formation, Río Negro province) (Salgado *et al*., in press), amplify the systematic knowledge of this genus. Just as was proposed by Salgado *et al*. (1997a), *Neuquensaurus* and *Saltasaurus* share the presence of relatively short prezygapophyses that do not surpass the anterior border of the centra (and concordantly, postzygapophyses projecting posteriorly), synapomorphic characters of the Saltasaurinae. The posterior cervicals of *Neuquensaurus* exhibit a neural spine which is more elevated than in *Saltasaurus* and that ends dorsally in a hemispheric protuberance, a character also present in the titanosaur of Perióopis DGM "Serie A" of Brazil (Salgado *et al*., in press).

In contrast with the titanosaurs analyzed, *Mendozasaurus neguyelap* shares the following characters with *Isisaurus colberti* (Jain and Bandyopadhyay, 1997):

1) Cervical vertebra with relatively short centra, with EI <2.5. The length of cervical vertebrae vary in distinct genera and species, and also the same species during ontogeny (Carpenter and McIntosh, 1994). The index of elongation allows the knowledge of titanosaurs with: a) very short centra (EI<2.5) like in *Mendozasaurus neguyelap* and *Isisaurus colberti*, b) short centra (EI=2.5-3) like in *Saltasaurus*, and c) long centra (EI>3) like in *Alamosaurus*, and d) very long centra (EI>4) like in *Rapetosaurus*.

In sauropods the length of the cervical centra is related with the length of the neck and its life position (Wedel *et al.,* 2000). For example, in adult specimens the mid- and posterior cervical centra (Powell, 2003, plates 48 and 49; PVL 4017-30 and 4017-139) are relatively long (EI>2.5); while juvenile examples (PVL4017-4) exhibit proportionally short centra (EI<2). It is opportune to mention that some remains of *Neuquensaurus australis*, described by Salgado *et al*. (in press) have posterior cervical centra that are relatively short (EI<2.5). Evidently, the shortness of the cervical centra is seen more in titanosaurs of great size with high neural spines and deep supradiapophyseal fossae (*Mendozasaurus*, *Isisaurus*) than in derived titanosaurs of medium size (*Saltasaurus*, *Neuquensaurus*) grouped in the clade Saltasaurinae.

In the majority of titanosaurs the number of cervical vertebrae that make up the cervical series is unknown. Notwithstanding, if one assumes that *Mendozasaurus* has 16 cervical vertebrae, as did *Rapetosaurus krausei* (Curry Rogers and Forster, 2001), it is supposed that it had a relatively short neck no longer than 6 meters in length (Figure 7). In contrast the neck of *Mendozasaurus* would have been relatively thick, with a dorsoventral diameter in midsection of 120 cm, judging by the size of cervical vertebrae that are 71 cm in height and 80 cm in width.

2) Supradiapophyseal fossa dorsoventrally extended, bounded by the spinoprezygapophyseal, spinopostzygapophyseal, prezygadiapophyseal and postzygadiapophyseal laminae. In *Euhelopus zdanskyi* (Wiman, 1929) and the majority of titanosaurs is observed an important reduction in the laminae of the cervical arch (Wilson and Sereno, 1998; Wilson, 2002). This simplification of laminar structure can be described with more precision if one keeps in mind the presence of absence of some characters of the cervical arch, such as the supradiapophyseal fossa (Table 2), present in *Apatosaurus louisae* and other Sauropods (Gilmore, 1936, Wilson, 1999). In the majority of titanosaurs this fossa is absent (*Malawisaurus*, *Alamosaurus*), is reduced (*Rinconsaurus*), or appears as a lateral cavity without defined borders (*Saltasaurus*). In contrast, *Mendozasaurus* and Isisaurus show a supradiapophyseal fossa with deep dorsoventral development, bounded by spinoprezygapophyseal, spinopostzygapophyseal, prezygadiapophyseal and postzygadiapophyseal laminae. In particular, *Mendozasaurus* shows a supradiapophyseal cavity so deep that it almost reaches the axial plane. As opposed to what occurs in *Isisaurus colberti*, this fossa is partially bound dorsally by the lateral expansion of the neural spine (Figure 6G).

3) Cervical vertebrae with high neural spines. In the majority of Titanosauriformes Salgado et al., 1997) the cervical vertebra exhibit neural spines that are relatively short and centra that are axially elongate. In contrast, *Mendozasaurus neguyelap* and *Isisaurus colberti* show neural spines that are relatively tall, where the relationship: total height of the vertebra/length of the centrum is more than 1.5.

Discussion and Conclusions:

While the cervical vertebrae of *Mendozasaurus neguyelap* exhibit similarities with *Isisaurus colberti*, they show some significant differences relating to the form of the transverse processes and neural spine. In particular in *Mendozasaurus* is emphasized a novel character in the mid-posterior cervicals that constitutes a probable autapomorphy: the presence of laminated neural spines that are expanded transversely, much shorter than the centra and with a "fan-shaped" or sub-rhomboidal anterior contour by the lateral expansion and a sub-rectangular dorsal extreme. These expansions of the neural spine project laterally with respect to the spinopostzygapophyseal lamina and bifurcate ventrally in two laminae, one that terminates inside the supradiapophyseal cavity and another than delimits the posterior border of the supradiapophyseal cavity (Figure 2B). In contrast, *Isisaurus* exhibits neural spines of subtriangular or subtrapezoidal posterior contour (Jain and Bandyopadhyay, 1997, figs. 3-5). Besides, as it lacks lateral expansions, the lateral border of the neural spine is defined by the spinopostzygapophyseal laminae (Figure 6F).

The cervical spines of *Mendozasaurus* also are different from those of a new basal titanosaur (MCF-PVPH-233) from the Lohan Cura Formation, Aptian-Albian of the Neuquén Province (Bonaparte, González Riga and Apesteguia, in study). In this taxon the posterior cervical vertebrae have neural spines slightly wider than the centra and of rhomboidal contour. Notwithstanding, in this titanosaur from Neuquén the neural spine is relatively shorter and exhibits a dorsal border with a more defined angle. Besides, other differences are observed: in *Mendozasaurus* the sub-rhomboidal contour is made up by lateral projections of the neural spine. On the other hand in this new taxon, the lateral border of the neural spine is formed by projections of the lateral spinoprezygapophyseal laminae, laminae that are absent in *Mendozasaurus*.

The fossil record of cervical vertebrae of titanosaurs, as much in South America as in other parts of the world, show a notable morphological diversity that involves the form and height of the neural spines, the position of the zygapophyses, the development of diapophyseal laminae and cavities, and the proportions of the vertebral centra. In particular, *Mendozasaurus neguyelap* is found within the titanosaurs that posses cervical centra that are proportionally shorter associated with high neural spines, evidenced by the presence of sauropods with relatively wide, robust, and short in the Late Cretaceous of Argentina. It is probable that the cervical morphological diversity of titanosaurs is related to distinct ecological adaptations. Notwithstanding, this requires detailed paleobiomechanical and paleoecological study to establish the relations that existed between the bone structure of these giant vertebrates and their particular morphofunctional adaptations.