AMEGHINIANA (Rev. Asoc. Paleontol. Argent.) - 40 (2): 155-172. Buenos Aires, 30-06-2003 ISSN 0002-7014

A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina

Bernardo J. GONZÁLEZ RIGA[1]

Abstract. *Mendozasaurus neguyelap* gen. et sp. nov. is a new titanosaur from the Upper Cretaceous of Neuquén Basin and the first known dinosaur species from Mendoza Province, Argentina. The remains were found in levels provisionally referred to the Río Neuquén Formation (late Turonian-late Coniacian) of the Neuquén Group. They consist of 22 mostly articulated caudal vertebrae, a dorsal vertebra, numerous disarticulated appendicular bones and osteoderms. Autapomorphies of *Mendozasaurus* are: (1) subtriangular infrapostzygapophyseal fossae in anterior dorsal vertebrae; (2) postzygapostspinal laminae parallel to the plane of the postzygapophyseal facets in anterior dorsal vertebrae; (3) interzygapophyseal cavity dorsoventrally extended and limited by the spinopostzygapophyseal and spinoprezygapophyseal laminae in anterior caudal vertebrae; (4) middle caudal vertebrae slightly procoelous with reduced posterior condyles displaced dorsally; (5) laminar mid-posterior caudal neural spines with horizontal and straight dorsal border, and anterodorsal corner forming a right angle; (6) large subconic-spherical osteoderms lacking cingulum. A cladistic analysis permits the inclusion of *Mendozasaurus* within Titanosauridae, according to the phylogenetic definition of this clade. Although this new species exhibits almost all the titanosaurid synapomorphies proposed by some authors, it lacks prominent posterior condyles in middle caudal centra. This and other plesiomorphic traits suggest that *Mendozasaurus* is a basal titanosaurid, more derived than *Malawisaurus* in the caudal procoely.

Resumen. Un nuevo titanosaurio (Dinosauria, Sauropoda) del Cretácico Superior de la provincia de Mendoza, Argentina. *Mendozasaurus neguyelap* nov. gen. et sp. es un nuevo titanosaurio del Cretácico Superior de la Cuenca Neuquina y la primera especie de dinosaurio proveniente de la provincia de Mendoza, Argentina. Procede de niveles asignados preliminarmente a la Formación Río Neuquén (Turoniano tardío-Coniaciano tardío) del Grupo Neuquén. Está representado por 22 vértebras caudales en su mayoría articuladas y numerosos restos desarticulados: una vértebra dorsal, arcos hemales, huesos apendiculares y grandes osteodermos. Son autapomorfías de *Mendozasaurus:* (1) fosas infrapostzigapofisiales subtriangulares en vértebras dorsales anteriores; (2) láminas postzigapostespinales paralelas a los planos de las facetas articulares de las postzigapófisis en vértebras dorsales anteriores; (3) cavidad interzigapofisial dorsoventralmente extendida y limitada por las láminas espinopostzigapofisial y espinoprezigapofisial en vértebras caudales anteriores; (4) centros caudales medios suavemente procélicos con cóndilos posteriores reducidos y desplazados dorsalmente; (5) espinas neurales de vértebras caudales medias-posteriores laminares y anteroposteriormente elongadas, con un borde dorsal horizontal y un ángulo ánterodorsal recto y (6) grandes osteodermos subcónicos-subesféricos sin cingulum. Un análisis cladístico permite incluir a *Mendozasaurus* dentro de Titanosauridae, según definiciones filogenéticas de este clado. Si bien exhibe casi todas las sinapomorfías propuestas por algunos autores para caracterizar a Titanosauridae, carece de cóndilos posteriores prominentes en sus vértebras caudales medias. Éste y otros caracteres plesiomórficos sugieren que *Mendozasaurus* es un titanosáurido basal, más derivado que *Malawisaurus* en su procelia caudal.

Key words. Saurischia. Sauropoda. Titanosauria. Late Cretaceous. Mendoza. Argentina.

Palabras clave. Saurischia. Sauropoda. Titanosauria. Cretácico Tardío. Mendoza. Argentina.

Introduction

The Titanosauria comprises diverse Cretaceous sauropods of wide geographical distribution. The evolution and phylogenetic relationships of titanosaurs are still not well known, although important studies on these topics were accomplished (Salgado *et al.*, 1997a; Sanz *et al.*, 1999; Curry Rogers and Foster, 2001). During most of Late Cretaceous, titanosaurs had an important role as large primary consumers in the faunas of Patagonia, while in North America the dominant herbivorous vertebrates were the ornithischian dinosaurs (Bonaparte, 1986a).

In Patagonia, titanosaur fossils became particularly abundant since the first discovery carried out in the 19th century (Lydekker, 1893). Most titanosaur remains were recovered from the Neuquén and Malargüe Groups (Bonaparte and Coria, 1993; Calvo and Bonaparte, 1991; Salgado, 1996; Calvo *et al.*, 1997;

[1]Laboratorio de Paleovertebrados, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Centro Regional de Investigaciones Científicas y Tecnológicas, C. Correo 330, 5500 Mendoza, Argentina.
bgonriga@lab.cricyt.edu.ar

 AMGHB2-0002-7014/03$00.00+.50

González Riga and Calvo, 2001 among others). These Patagonian sedimentary sequences crop out in Mendoza Province. However, until a few years ago, well preserved dinosaur fossils from this province were not known.

Dinosaur bones from Mendoza were first mentioned by Wichmann (1927), who described rocks of late Campanian-early Maastrichtian age. At present, these continental and marginal-marine deposits are assigned to the Loncoche Formation from the Malargüe Group (Groeber, 1946; González Riga and Parras, 1998; Parras *et al.*, 1998). During the last decade, J.F. Bonaparte and subsequently the author, collected fossil vertebrates (fishes, turtles, snakes, plesiosaurs and dinosaurs) from this formation, and began their systematic study (González Riga, 1995, 1999b). Later on, various paleontological expeditions have found numerous titanosaur bones in the widely exposed strata of the Neuquén Group (Cenomanian-early Campanian according to Leanza and Hugo, 2001) outcropping in the southern extreme of Mendoza Province (Alcober *et al.*, 1995; Wilson *et al.*, 1999; González Riga, 1999a; González Riga and Calvo, 1999).

In this paper, *Mendozasaurus neguyelap* gen. et sp. nov., the first known dinosaur species of Mendoza Province is described. This species gives new evidence to interpret the diversity of titanosaurs in South America. The fossils herein described were found in the southern region of Cerro Guillermo, Malargüe Department, Mendoza Province (figure 1).

In this locality, sauropod bones (Titanosauridae indet.) had been found by the oil workmen R. Sprenjer and A. Chávez.

Between 1998-2001, five paleontological expeditions were carried out by the author and collaborators in this area. Several fossiliferous sites were localized and the holotype of *Mendozasaurus*, various titanosaur specimens, and remains of theropods and turtles were collected.

The material described is housed at the

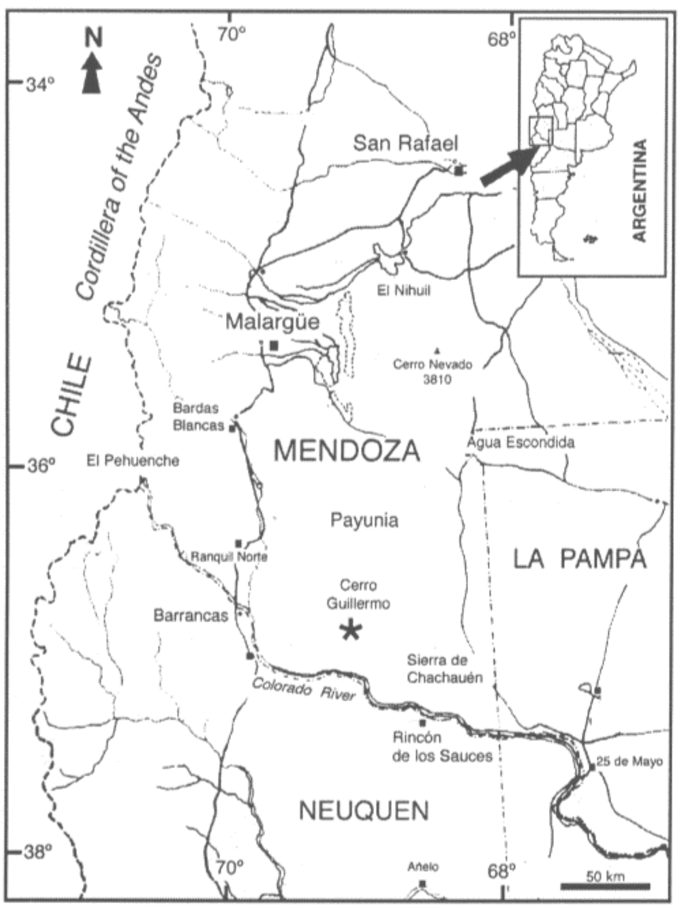


Figure 1. Map showing the locality where the holotype of *Mendozasaurus neguyelap* nov. gen. et sp. was found. / *Mapa que indica la localidad donde fue hallado el holotipo de* Mendozasaurus neguyelap *nov. gen. et sp.*

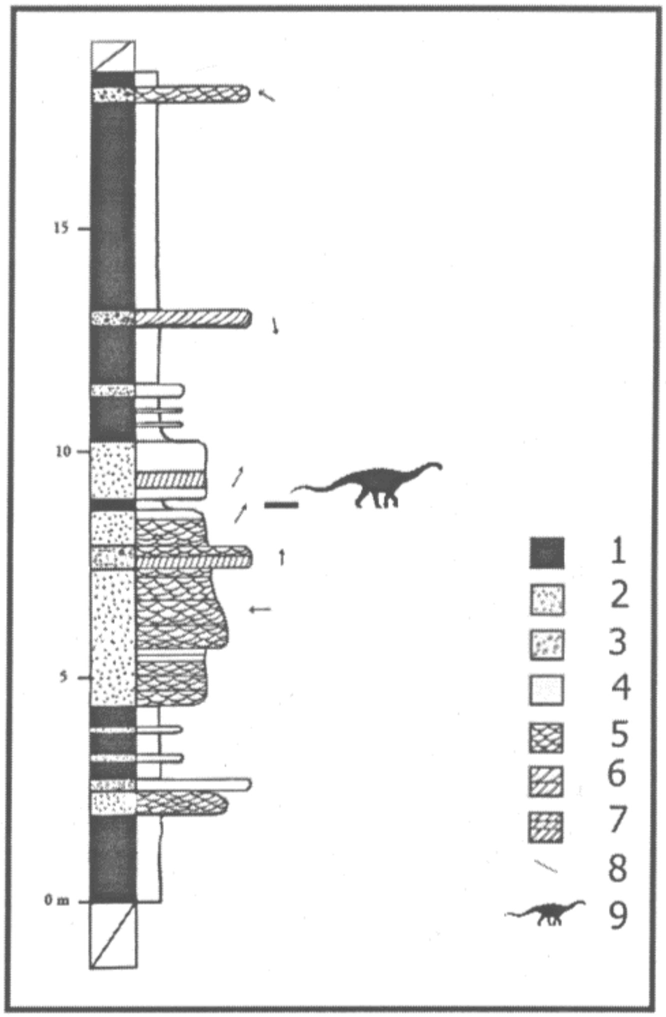


Figure 2. Stratigraphic column of the Río Neuquén Formation at the fossiliferous site of Cerro Guillermo (Mendoza Province, Argentina) showing stratigraphic level of the quarry / *Columna estratigráfica de la Formación Río Neuquén en el sitio fosilífero de Cerro Guillermo (provincia de Mendoza, Argentina), mostrando el nivel estratigráfico de la excavación.* References / *Referencias:* 1, pelite / *pelita*; 2, sandstone / *arenisca*; 3, conglomerate / *conglomerado*; 4, massive structure / *estructura maciza*, 5, trough-cross bedding / *estratificación entrecruzada en artesa*, 6, tangential cross bedding / *estratificación entrecruzada tangencial*, 7, planar cross bedding / *estratificación entrecruzada planar*, 8, paleocurrent data / *dato de paleocorrientes*; 9, Fossils of *Mendozasaurus neguyelap* and Theropoda indet. / *fósiles de* Mendozasaurus neguyelap *y Theropoda indet.*

Laboratory of Paleovertebrates of the Paleontology Unit of IANIGLA (Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales) under the abbreviation IANIGLA-PV.

Systematic paleontology

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
SAUROPODA Marsh, 1878
TITANOSAURIA Bonaparte and Coria, 1993
TITANOSAURIDAE Lydekker, 1893
Mendozasaurus gen. nov.

Etymology. In reference to Mendoza Province (Argentina) where the dinosaur was found; *saurus* (Greek), lizard.
Type species. *Mendozasaurus neguyelap* sp. nov.
Diagnosis. Large titanosaur (18-25 meters long) characterized by the following association of autapomorphies: (1) two subtriangular infrapostzygapophyseal fossae in anterior dorsal vertebrae; (2) postzygapostspinal laminae parallel to the plane of postzygapophyseal facets in anterior dorsal vertebrae; (3) interzygapophyseal cavity dorsoventrally extended and limited by the spinopostzygapophyseal and spinoprezygapophyseal laminae in anterior caudal vertebrae; (4) middle caudals slightly procoelous with reduced posterior condyles displaced dorsally; (5) laminar mid-posterior caudal neural spines with horizontal and straight dorsal border, and anterodorsal corner forming right angle; (6) large subconic-spherical osteoderms lacking cingulum. These autapomorphies are associated with the following synapomorphies: prespinal lamina extended until the base of the neural spine in anterior dorsal vertebrae; acuminate pleurocoels (eye-shaped) in dorsal vertebrae; absence of hyposphene-hypantrum articulation in anterior dorsal vertebrae; strongly procoelous anterior caudal vertebrae with prominent condyles; neural arches positioned anteriorly in mid and posterior caudal centra; anterodorsal edge of neural spine placed posteriorly with respect to the anterior margin of mid-caudal postzygapophyses; laminar and anteroposteriorly elongated neural spines in middle caudal vertebrae; prezygapophyses relatively long in middle caudal vertebrae, haemal arches articulations open proximally; semilunar sternal plates with relatively straight posterior border; anterior border of the scapular blade concave in their proximal section and straight in their distal section; humerus with proximal border relatively straight and curved medially; metacarpals without distal articular facets and femur with a lateral bulge below the greater trochanter.

Mendozasaurus neguyelap sp. nov.
Figures 3-8

Etymology. From *neguy*, first, and *yelap*, beast, Huarpes indigenous terms (Millcayac language, Márquez Miranda, 1943) referring to the first species of dinosaur discovered in Mendoza Province. The ending of the term *yelap* has not been modified, since is not a latin or latinized word (Art. 31.2.3. Comisión Internacional de Nomenclatura Zoológica, 2000).
Holotype. IANIGLA-PV 065/1-24: 22 mostly articulated caudal vertebrae and two anterior chevrons.
Paratypes. The following disarticulated bones associated with the holotype: anterior dorsal vertebra (IANIGLA-PV 066), sternal plate (IANIGLA-PV 067), scapula (IANIGLA-PV 068), humerus (IANIGLA-PV 069), radius and ulna (IANIGLA-PV 070/1-2), four metacarpals (IANIGLA-PV 071/1-4), a fragment of pubis (IANIGLA-PV 072), femur and tibia (IANIGLA-PV 073/1-2), two tibiae and fibula (IANIGLA-PV 074/1-3), five metatarsals (IANIGLA-PV 077/1-5), two ungeal phalanges (IANIGLA-PV 078, 079) and four osteoderms (IANIGLA-PV 080/1-2, 081/1-2).
Specimens. It is probable that the caudal sequence of the holotype together with the dorsal vertebra (IANIGLA-PV 066), scapula (IANIGLA-PV 068), humerus (IANIGLA-PV 069), metacarpals (IANIGLA-PV 071) and femur and tibia (IANIGLA-PV 073) belong to an adult specimen of relatively slender proportions (fig-

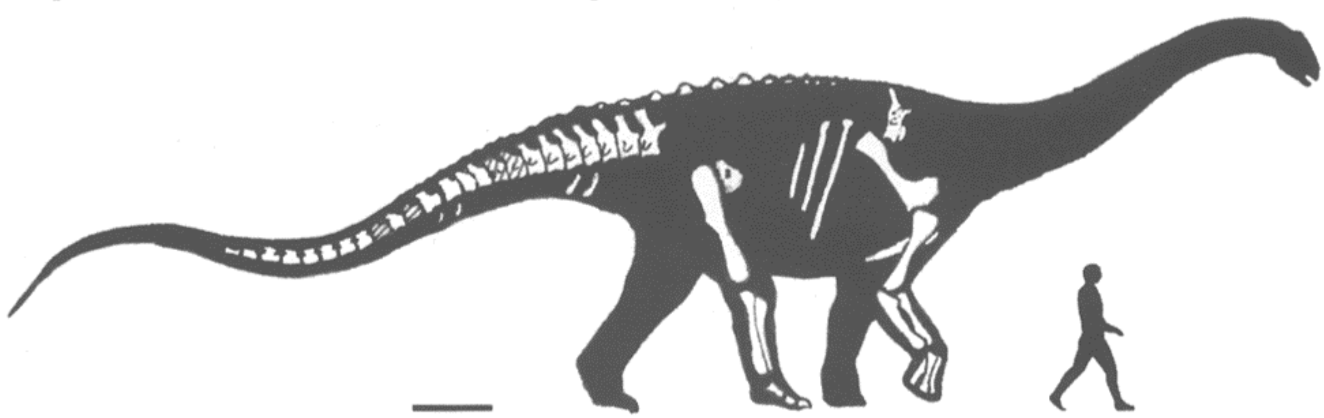


Figure 3. Skeletal reconstruction of *Mendozasaurus neguyelap* gen. et sp. nov. showing preserved bones (total length: 18 m, scale bar, 1 m) / *Reconstrucción esqueletal de* Mendozasaurus neguyelap *gen et sp nov. con indicación de los huesos preservados (largo total: 18 m, escala gráfica: 1 m).*

ure 3). On the other hand, the sternal plate (IANIGLA-PV 067), and the fibula and two tibiae (IANIGLA-PV 074/1-3) correspond to an adult specimen approximately a 15% larger than the previous.

Furthermore, near these remains were found fossils of an adult specimen of large size (IANIGLA-PV 084).

Horizon, age and locality. Levels provisionally assigned to the upper section of the Río Neuquén Formation (or Río Neuquén Subgroup according to Leanza and Hugo, 2001), Late Cretaceous, late Turonian-late Coniaciian age, south of Cerro Guillermo, Malargüe Department, Mendoza Province, Argentina (figure 1). The dinosaur bones come from overbank deposits related with sandy fluvial channels developed on a huge muddy flood plain (figure 2).

Diagnosis. Same as for the genus.

Institutional abbreviations. IANIGLA-PV, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Colección Paleovertebrados, Mendoza, Argentina; DGM / NDPM, Museo de la Divisão Geologia y Mineralogia, Rio de Janeiro, Brasil; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPCA, Museo Provincial "Carlos Ameghino", Cipolletti, Argentina; MUCPv, Museo de Paleontología de la Universidad Nacional del Comahue, Colección Paleovertebrados, Neuquén, Argentina.

Description. *Dorsal vertebra* (IANIGLA-PV 066; figures 4.A-C). It presents a relatively short, small and depressed opisthocoelous centrum. The posterior articular face is larger than the anterior one. The lateral and ventral faces are anteroposteriorly concave. The lateral faces of the centrum show small eye-shaped pleurocoels with an acuminate posterior contour, a synapomorphy of Titanosauria (Bonaparte and Coria, 1993; Salgado *et al.*, 1997a). The long and robust diapohyses are laterally projected. They are supported by the spinodiapophyseal, prezygadiapophyseal, paradiapophyseal and posterior centrodiapophyseal laminae. The postzygadiapophyseal lamina is very short. The posterior centrodiapophyseal and the paradiapophyseal laminae delimit an infradiapophyseal fossa of subtriangular contour. In lateral view, the spinopostzygapophyseal, spinodiapophyseal and postzygadiapophyseal laminae delimit a supradiapophyseal fossa. The dorsoventrally extended parapophyses are located at the base of the neural arch. For this reason, the anterior centroparapophyseal lamina is short. The prezygapophyses are robust and have oval articular surfaces dorsomedially orientated. They are connected by an intraprezygapophyseal lamina. Between this lamina and the roof of the neural canal, a thick medial pillar is developed. The hyposphene-hypantrum articulation is absent. Under the prezygapophyses, the prezygaparapophyseal, prezygadiapophyseal and paradiapophyseal laminae delimit a deep and wide lateral infraprezygapohyseal cavity, which exhibits a semicircular contour in anterior view. In posterior view, the postygapophyses present wide articular surfaces ventrolaterally orientated. In lateral view, the spinopostzygapophyseal lamina is more robust than the spinodiapophyseal lamina. There are two oblique laminae that connect the articular surfaces of the postzygapophyses with the base of the postspinal lamina. These structures, designated as postzygapostspinal laminae herein, are parallel to the postzygapophyseal facets. The shape and orientation of these laminae are considered a probable autapomorphy of *Mendozasaurus* (figure 4.C).

There are two subtriangular infrapostzygapophyseal fossae between the postzygapophyses and the roof of the neural arch (figure 4.C). In some titanosaurs, such as *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), these infrapostzygapophyseal fossae are absent. In other titanosaurs, such as *Malawisaurus* (Gomani *et al.*, 1999), the infrapostzygapophyseal fossa is not divided. Therefore, the presence of this character may be interpreted as an autapomorphy of *Mendozasaurus*.

The neural spine is not bifurcated. It is narrow and slightly inclined posteriorly. The prespinal and postspinal laminae are well defined up to the base of the neural spine. The prespinal lamina is not bifurcated proximally and continues up to the intraprezygapophyseal lamina, like in other titanosaurids. However, this vertebra retains small spinoprezygapophyseal laminae that connect the prezygapophyses with the base of prespinal lamina (figure 4.A). In this case, the prespinal lamina is a complex structure formed by the spinoprezygapophyseal laminae and an anterior medial lamina, such as was described by Wilson (1999). The spinoprezygapophyseal laminae are different to the accessory spinodiapophyseal laminae present in *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977, *Lirainosaurus astibiae* (Sanz *et al.*, 1999) and the Titanosaurinae indet. DGM "Serie B" of Brazil (Powell, 1987), since these laminae extend from the diapophyses.

Caudal vertebrae (figures 4.D-E; 5.A-F). Twenty-two caudal vertebrae are preserved. The four most anterior caudals were disarticulated (IANIGLA-PV 065/1-4), followed by nine semi-articulated anterior and middle caudals (IANIGLA-PV 065/5-13). There are, furthermore, six middle caudals articulated (IANIGLA-PV 065/14-19). Finally, there are three disarticulated posterior caudal centra (IANIGLA-PV

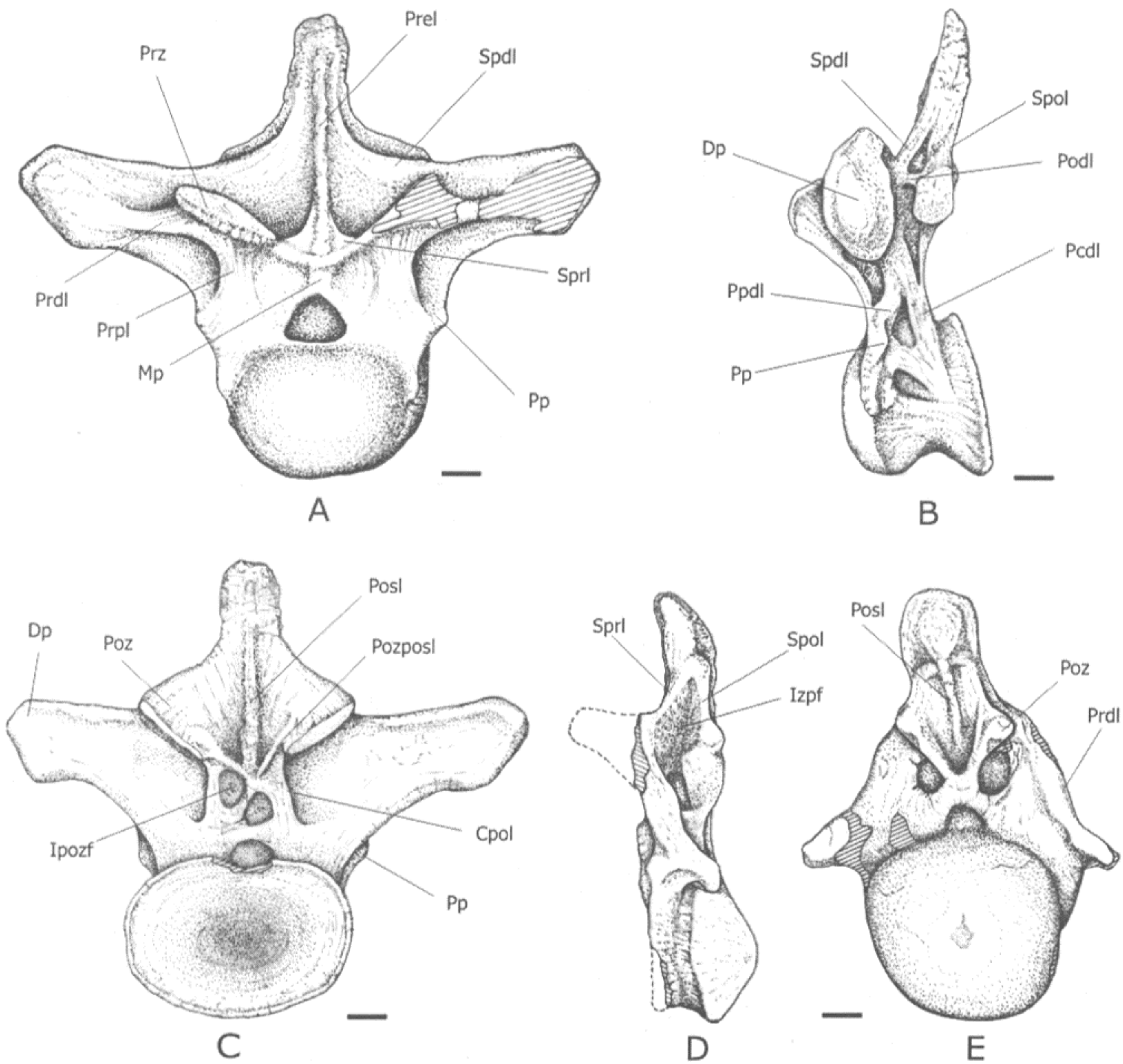


Figure 4. ***Mendozasaurus neguyelap*** gen. et sp. nov. **A-C,** anterior dorsal vertebra in anterior (A) lateral (B) and posterior (C) views / *vértebra dorsal anterior en vista anterior (A), lateral (B) y posterior (C)*, paratype /*paratipo*, IANIGLA-PV 066; **D-E,** anterior caudal vertebra in lateral (D) and posterior (E) views / *vértebra caudal anterior en vista lateral (D) y posterior (E)*, holotype / *holotipo*, IANIGLA-PV 065/1. References / *Referencias*: Cpol: centropostzygapophyseal lamina / *lámina centropostzigapofisial*; Dp: diapophysis / *diapófisis*; Ipozf: infrapostzygapophyseal fossa / *fosa infrapostzigapofisial*; Izpf: interzygapophyseal fossa / *fosa interzigapofisial*; Mp: medial pillar / *pilar medial*; Pcdl: posterior centrodiapophyseal lamina / *lámina centrodiapofisial posterior*; Podl: postzygadiapophyseal lamina / *lámina postzigadiapofisial*; Posl: postspinal lamina / *lámina postespinal*; Poz: postzygapophysis / *postzigapófisis*; Pozposl: postzygapostspinal lamina / *lámina postzigapostespinal*; Pp: parapophysis / *parapófisis*; Ppdl: paradiapophyseal lamina / *lámina paradiapofisial*; Prdl: prezygadiapophyseal lamina / *lámina prezigadiapofisial*; Prel: prespinal lamina / *lámina prespinal*; Prpl: prezygaparapophyseal lamina / *lámina prezigaparapofisial*; Prz: prezygapophysis / *prezigapófisis*; Spdl: spinodiapophyseal lamina / *lámina espinodiapofisial*; Spol: spinopostzygapophyseal lamina / *lámina espinopostzigapofisial*; Sprl: spinoprezygapophyseal lamina / *lámina espinoprezigapofisial*. Scale bar: 5 cm / *escala gráfica*: 5 cm.

20-22). Approximate numbering was made according to the caudal sequence of cf. *Titanosaurus* sp. DGM "Serie C" of Brazil (Powell, 1987).

The vertebra IANIGLA-PV 065/1 (figures 4.D-E; 7.B) probably consists of the first or second caudal. It has suffered anteroposterior compression and has a short procoelous centrum. The posterior articular face of the centrum is prominent and exhibits a small depression, less developed than the condylar groove of the distal caudals of *Lirainosaurus* (Sanz *et al.*, 1999). The lateral and ventral faces of the centrum are anteroposteriorly concave. The transverse processes are projected backward and are joined to the prezygapophyses by large prezygadiapophyseal laminae.

The arch and neural spine are relatively high, surpassing the height of one and half times the centrum (table 1). The neural spine is transversely broad and it is reinforced by the prespinal and postspinal laminae. In lateral view, the spinopostzygapophyseal and spinoprezygapophyseal laminae are joined to form a lateral lamina, delimiting a large interzygapophyseal cavity of dorsal subtriangular contour. This cavity reaches a high point in the neural spine. It extends dorsally over the dorsal border of the postzygapophysis a distance larger than the length of the postzygapophyseal facet. The development of this cavity is a probable autapomorphy of *Mendozasaurus* (figure 4.D). Ventrally, near the base of the postygapophysis, this cavity developed a deep and oval infrapostzygapophyseal fossa. The postzygapophyses present an elongate articular facets, lateroventrally orientated and joined in a robust bridge over the neural canal.

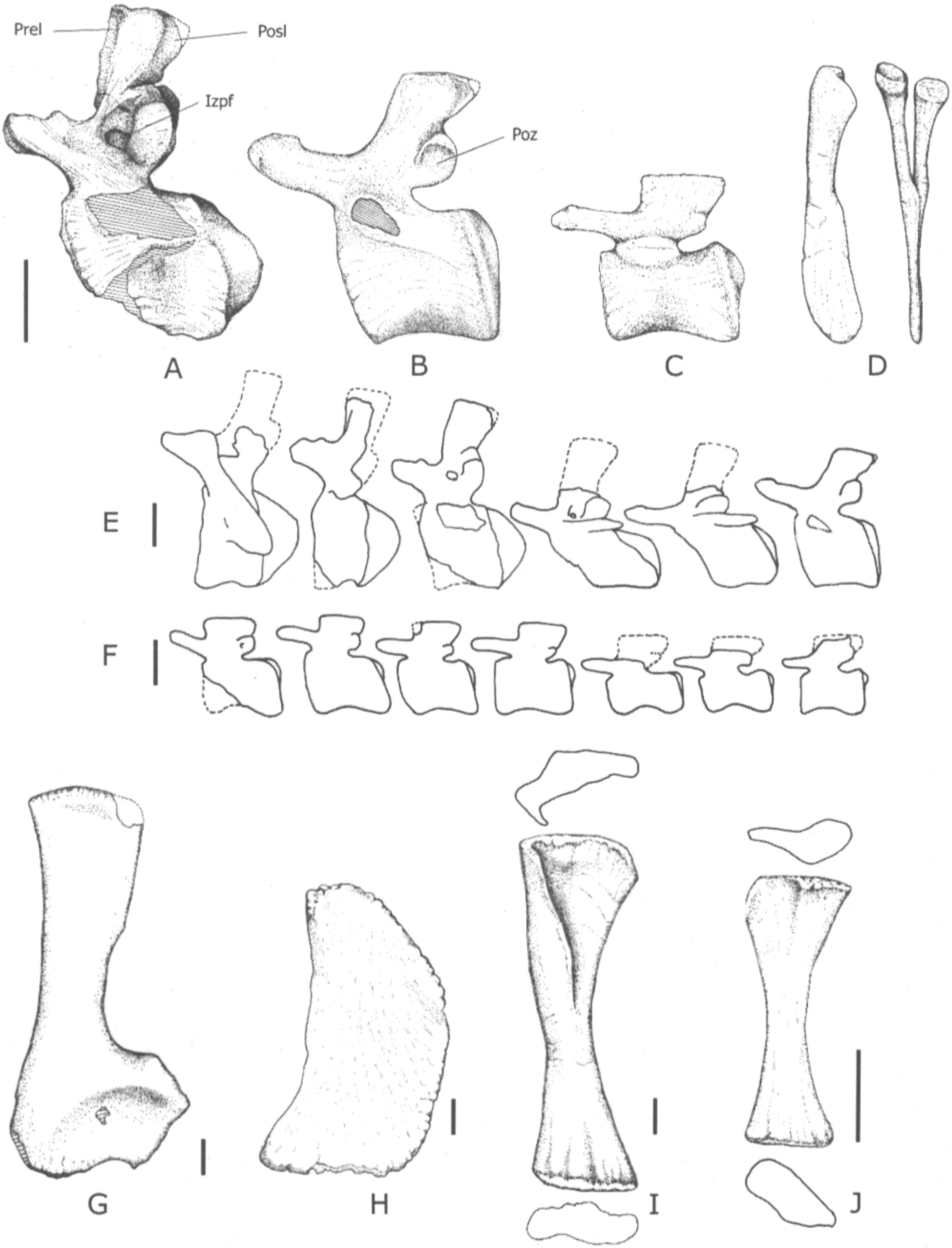
The following anterior caudals (figures 5.A-B, 5.E) exhibit lateral, anteroposterior or dorsoventral deformations. The centra have subcircular articular faces and they are strongly procoelous, with prominent posterior condyles up to the 5th caudal (figure 5.E; IANIGLA-PV 065/5). More distally, the procoely of caudal centra decreases. The transverse processes, wide anteroposteriorly, are oriented posterolaterally. The neural arches are typically located in the anterior halves of the centra, as in all titanosaurs. In most anterior caudals the prezygapophyses have robust processes, with wide articular facets of quadrangular contour dorsomedially projected. Over the dorsal edge of these processes, there are peculiar bony prominences (figure 5.A). The taxonomic value of this trait has still not been evaluated, but a similar condition is present in *Alamosaurus sanjuanensis* (Gilmore, 1946) and in the holotype of *Aeolosaurus rionegrinus*, but is absent in the specimen MPCA 27174 assigned to the same genus (Salgado and Coria, 1993; Salgado *et al.*, 1997b). The articular facets of the anterior caudal postzygapophyses are wide, oval-shaped and slightly concave. They are lateroventrally oriented. From the 6th caudal (IANIGLA -PV 065/6) the postzygapophyseal facets are reduced and acquire a subcircular contour. The interzygapophyseal fossa located on the anterior border of the postzygapophysis persists until the 5th caudal (figure 5, A). The neural spines are laterally compressed in the base, but they are broaden distally. The prespinal and postspinal laminae are well developed. The neural spines are slightly oriented posteriorly, with their posterodorsal edge placed posteriorly with respect to the posterior margin of the postzygapophyses.

The middle caudal vertebrae (figures 5.C, 5.F) exhibit less deformation than the anterior ones. They were found partly (10 -15th) or completely articulated (17 - 22th). The centra exhibit circular anterior faces and quadrangular posterior ones, due to the development of processes for the chevrons. The centrum height is approximately equal to the centrum width. The centra are slightly procoelous, with concave anterior faces. Their posterior faces are relatively flat, except for the presence of reduced condyles that are displaced dorsally. This character, absent in other titanosaurs, is considered an autapomorphy of *Mendozasaurus* (figure 5.C). The middle caudal centra present lateral and ventral faces anteroposteriorly concave. The neural spines are relatively depressed and elongated anteroposteriorly. In the 12th and 13th caudals, the anterodorsal corner of the neural spine is higher and thicker than the posterodorsal one. However, from the 17th caudal this condition disappears, since their dorsal border straightens and becomes horizontal. In that mid-posterior section of the tail, the neural spine is laminar and anteroposteriorly elongated, like in *Malawisaurus* (Jacobs *et al.*, 1993) and *Andesaurus* (Calvo y Bonaparte, 1991). Nevertheless, the spines of *Mendozasaurus* have a straight and horizontal border, with an anterodorsal corner forming a right angle (figure 5.C). This morphology is considered an autapomorphy. In middle caudal vertebrae the prezygapophyses are relatively long, decreasing towards the distal end of the tail.

Three disarticulated posterior caudal centra were collected (IANIGLA-PV 065/20-22). They are slightly procoelous, with reduced condyles displaced dorsally. The height and width of the caudal centra decrease distally throughout the tail in a greater proportion than their length, producing relatively long centra.

Chevrons (figure 5.D). Two anterior chevrons were collected (IANIGLA-PV 065/23 -24). The axial por-

Figure 5. ***Mendozasaurus neguyelap*** gen. et sp. nov. **A-F,** holotype / *holotipo;* **G-K,** paratype / *paratipo.* **A,** anterior caudal vertebra in lateral view / *vértebra caudal anterior en vista lateral,* IANIGLA-PV 065/4; **B,** anterior caudal vertebra in lateral view / *vértebra caudal anterior en vista lateral,* IANIGLA-PV 065/7; **C,** middle-posterior caudal vertebra in lateral view / *vértebra caudal media-posterior en vista lateral,* IANIGLA-PV 065/16; **D,** anterior chevron in lateral and posterior views / *arco hemal anterior en vista lateral y posterior,* IANIGLA-PV 065/23; **E,** anterior caudal sequence in lateral view / *secuencia caudal anterior en vista lateral;* **F,** mid-posterior caudal sequence in lateral view / *secuencia caudal media-posterior en vista lateral;* **G,** right scapula in lateral view / *escápula derecha en vista lateral,* IANIGLA-PV 068; **H,** left sternal plate / *placa esternal izquierda,* IANIGLA-PV 067; **I,** right humerus in proximal, anterior and distal views / *húmero derecho en vista proximal, anterior y distal,* IANIGLA-PV 069; **J,** rigth metacarpal IV? in proximal, posterior and distal views / *metacarpo derecho IV? en vista proximal, posterior y distal,* IANIGLA-PV 071/1. References / *Referencias:* Izpf: interzygapophyseal fossa / *fosa interzigapofisial;* Posl: postspinal lamina / *lámina postespinal;* Poz: postzygapophysis / *postzigapófisis;* Prel: prespinal lamina / *lámina prespinal.* Scale bar: 10 cm / *escala gráfica:* 10 cm.


Prel
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tion is curved and expanded posteriorly. The proximal sections are open such as other taxa of Camarasauromorpha (Salgado *et al.*, 1997a). *Mendozasaurus* shares with *Aeolosaurus* the presence of chevrons with double articular facets in the proximal ends (see Salgado and Coria, 1993, pág. 21; Bonaparte, 1996, pág. 104).

Sternal plate (figure 5.H). A complete left sternal plate was recovered (IANIGLA-PV 067). Like in other titanosaurids (Salgado *et al.*, 1997a), it exhibits a semilunar shape, with a concave lateral border and a strongly convex medial border. The anterior end, portion of articulation with the coracoids, exhibits rounded indentation of modest development. There, it reaches the maximum thickness (45 mm), although is relatively thin in comparison with sternal plates of *Neuquensaurus* (Huene, 1929; Powell, 1986), *Alamosaurus* (Gilmore, 1946) and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). The plate becomes thinner medially (8 mm). Posterolaterally, there are indentations that reach 19 mm of height related with the articulation of the sternal cartilaginous ribs (*sensu* Borsuk-Bialynicka (1977).

The posterior border of the plate is relatively straight, like in *Malawisaurus* (Jacobs *et al.*, 1993) and *Alamosaurus* (Gilmore, 1946). In contrast, *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), *Saltasaurus* (Powell, 1992) and *Aeolosaurus* (Salgado *et al.*, 1997b) have a curved posterior border. Measurements: length: 855 mm; width: 380 mm.

Scapula (figure 5.G). A right scapula is preserved (IANIGLA-PV 068). The distal end is relatively expanded for a titanosaur, reaching 177 percent of the minimum diameter of the scapular blade. The distal end has a rectangular general morphology, with a distal border slightly curved. The posterodistal corner forms a right angle. The anterodistal corner is not preserved. The rugosity of the distal end indicates a contact with the suprascapular cartilage, as is interpreted in *Alamosaurus* (Gilmore, 1946) and *Opisthocoelicaudia* (Borsuk -Bialynicka, 1977).

The scapular blade has a concave anterior border in its proximal section and straight in its distal section. A similar character is present in an indeterminate titanosaur from Periopolis, Brazil (materials of DNPM, Calvo, pers. comm.) and *Neuquensaurus australis* (Huene, 1929; Powell, 1986), but is absent in *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), *Antarctosaurus wichmanianus* (Huene, 1929), *Alamosaurus sanjuanensis* (Gilmore, 1946), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Saltasaurus loricatus* (Powell, 1992) and *Rapetosaurus krausei* (Curry Rogers and Foster, 2001). The posterior border is slightly concave and thicker than the anterior one. In the posterior border a longitudinal process is developed to 190 mm of the glenoid cavity (figure 5.G). The posterior or supraglenoid process frames the glenoid cavity. This cavity is lateromedially wide, reaching a width of 155 mm. The diagonal acromion separates a large lower acromial depression from the small upper acromial depression. Measurements: length: 1150 mm, distal width: 320 mm; minimal width of the scapular blade: 180 mm; proximal width: 495 mm.

Humerus (figure 5.I). A slender right humerus was recovered (IANIGLA-PV 069). The proximal end is relatively narrow, reaching only a 33 percent of the total length of the bone. In contrast, *Saltasaurus*, *Neuquensaurus*, *Opisthocoelocaudia* and *Argyrosaurus* (Powell, 1986; Borsuk-Bialynicka, 1977) have relatively wide and robust humeri, with a proximal width index (proximal width / total length x100) greater than 40. The proximal border of the humerus is relatively straight, but exhibits a medial curvature. This type of proximal border is different from the sigmoid border present in *Saltasaurus* (Powell, 1992) and the strongly convex border of *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997) and *Chubutisaurus* (Salgado, 1993). In the anterior face, the deltopectoral crest is prominent. In the posterior face, the distal portion exhibits a pronounced olecranon groove. Measurements: total length: 1060 mm; proximal width: 350 mm; distal width: 325 mm; minimum diameter of the diaphysis: 145 mm.

Ulna and radius. The ulna is poorly preserved (IANIGLA-PV 070/1). It is a straight bone, slightly curved anteriorly. The proximal end is expanded and triradiate, a synapomorphy of Sauropoda (Wilson and Sereno, 1998). The proximal portion of the radial face exhibits a pronounced concavity for the head of the radius. Length (preserved): 720 mm; proximal width: 240 mm; distal width: 185 mm.

The radius (IANIGLA-PV 070/2) is incomplete and distorted. It is a slender bone with an oval-shaped diaphysis and expanded ends. Length: 720 mm; proximal width: 190 mm; distal width: 170 mm.

Metacarpals. Four relatively slender metacarpals have been recovered. They have expanded ends and reduced diaphyses. Their distal ends are flat, so that they have not convex phalangeal articular facets.

The right metacarpal II? (IANIGLA-PV 071/4) has a weathered proximal end. The distal end is flat and shows a sub-rhomboidal outline. Length: 330 mm. The right metacarpal IV? (IANIGLA-PV 071/1) presents torsion between the proximal and distal ends and has a reduced diaphysis. It exhibits a cuneiform proximal end that is wedged on the palmar face. The distal end has a subtriangular outline (figure 5.J). Length: 335 mm. The left metacarpal IV? (IANIGLA Pv 071/2) is similar to the right

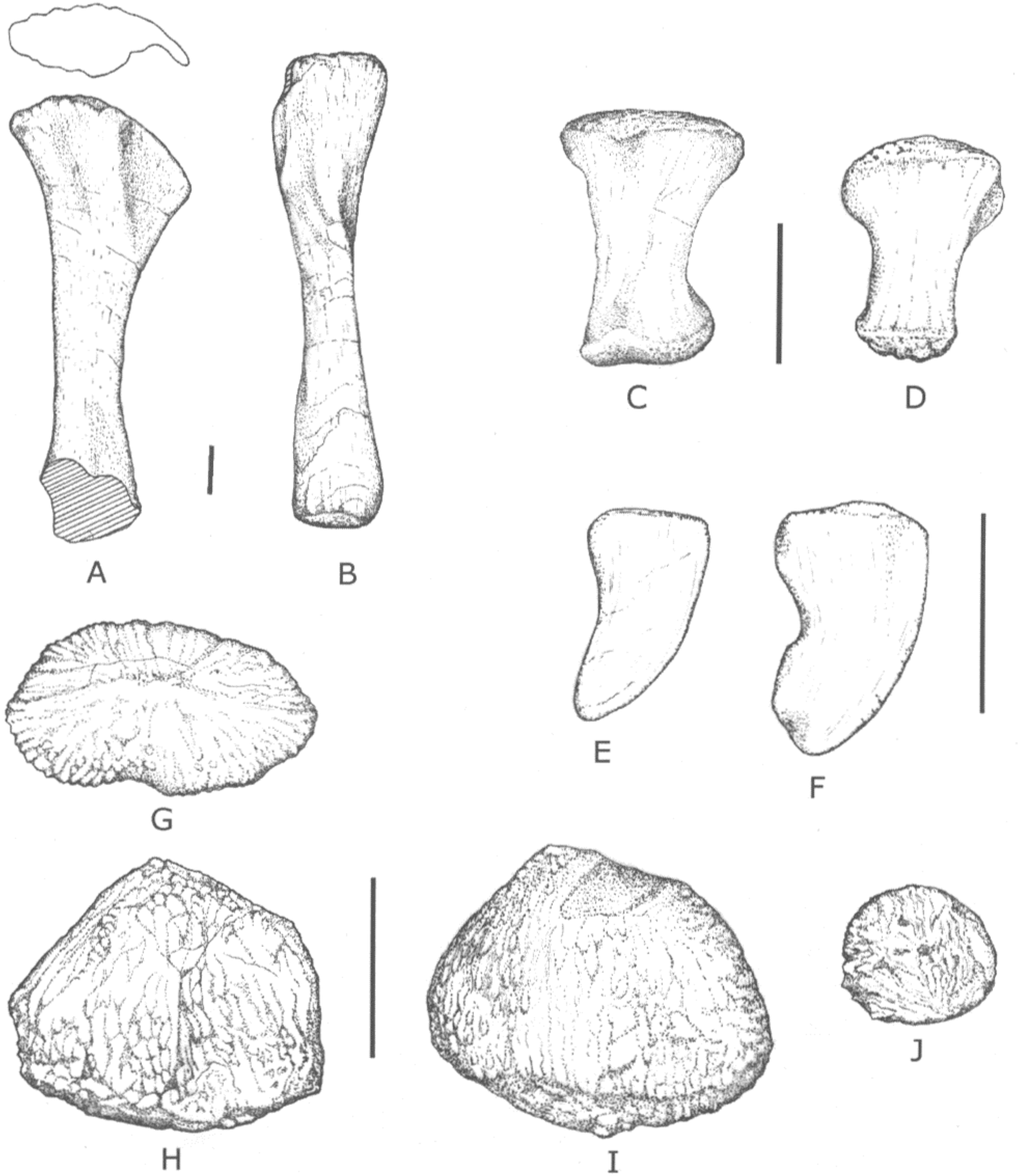

Figure 6. ***Mendozasaurus neguyelap*** gen. et sp. nov., paratype / *paratipo*. **A,** rigth tibia in proximal and lateral views / *tibia derecha en vistas proximal y lateral*, IANIGLA-PV 074/1; **B,** left fibula in lateral view / *fíbula izquierda en vista lateral*, IANIGLA-PV 074/3; **C,** rigth metatarsal III? in anterolateral view / *metatarso III? derecho en vista ánterolateral*, IANIGLA-PV 077/3; **D,** left metatarsal V? in anterolateral view / *metatarso V? izquierdo en vista ánterolateral*, IANIGLA-PV 077/5; **E,** pedial ungual in lateral view / *ungeal pedial en vista lateral*, IANIGLA-PV 079; **F,** pedial ungual in lateral view / *ungeal pedial en vista lateral*, IANIGLA-PV 078; **G-H,** osteoderm in dorsal (G) and lateral (H) views / *osteodermo en vista dorsal (G) y lateral* (H), IANIGLA-PV 080/2; **I,** osteoderm in lateral view / *osteodermo en vista lateral*, IANIGLA-PV 080/1; **J,** osteoderm in dorsal view / *osteodermo en vista dorsal*, IANIGLA-PV 081/1. Scale bar: 10 cm / *escala gráfica*: 10 cm.

metacarpal IV?, but is incomplete. The right metacarpus V? (IANIGLA-PV 071/3) is distorted and shows an incomplete proximal end. It is characterized by an expanded subtriangular distal end, similar to that of *Alamosaurus* (Gilmore, 1946). Length: 332 mm.

The morphology of the metacarpals indicates that they were vertically oriented forming a semicircle, such as is described in titanosaurs (Huene, 1929). The absence of convex articular facets in the distal end of the metacarpals is considered a synapomorphy of

Titanosauridae by Giménez (1992) and Salgado *et al.* (1997a).

Pubis. A proximal fragment of right pubis was collected (IANIGLA-PV 072). The oval-shaped pubic foramen is closed. The iliac peduncle is robust and prominent. The acetabulum is reduced and shows a semi-circular contour. The ischiadic peduncle is partly preserved.

Femur. The proximal part of a right femur was recovered (IANIGLA-PV073/1). It shows a lateral bulge on the lateral and proximal portion of the shaft, like in *Brachiosaurus*, *Chubutisaurus* and Titanosauria (McIntosh, 1990; Salgado, 1993; Salgado *et al.*, 1997a; Wilson and Sereno, 1998).

Tibia. (figures 6.A; 7.E). Two tibiae, right and left (IANIGLA-PV 074/1-2), and a right smaller tibia (IANIGLA-PV 073/2) were recovered. They are characterized by relatively slender proportions and anteroposteriorly expanded proximal ends. The cnemial crest is directed anterolaterally, as in all Eusauropoda (Wilson and Sereno, 1998). Measurements: IANIGLA-PV 073/2: length: 840 mm; proximal width including the cnemial crest: 320 mm; diaphysis: 135 mm; IANIGLA-PV 074/1: length: 990 mm; proximal width including the cnemial crest: 375 mm; diaphysis: 145 mm.

Fibula. (figure 6.B). A left slender fibula was recovered (IANIGLA-PV 074/3). The proximal end is anteroposteriorly expanded and the distal end has a subtriangular contour. The anterior margin is sigmoid in the proximal two-thirds, and the posterior margin is slightly concave. On the lateral face, the lateral trochanter (incompleely preserved) is not as prominent as the ones in *Titanosaurus araukanicus* and *Saltasaurus loricatus* (Powell, 1986). An anterolateral trochanter is present, though it is not as well defined as in *Titanosaurus araukanicus* (Huene, 1929; Powell, 1986). Furthermore, unlike *T. araukanicus*, it shows two reduced crests, which extend from the lateral trochanter towards the anteroproximal face. *Measurements: length*: 920 mm; proximal width: 205 mm; distal width: 165 mm; diaphysis: 90 mm.

Metatarsals and phalanges (figures 6.C-F). Several disarticulated metatarsals and phalanges corresponding to specimens of different sizes were recovered. Among them, five metatarsals probably correspond to an adult specimen of middle size.

The left metatarsal I? (IANILGA-PV 077/1) is short and robust. The proximal end is expanded and shows an articular face inclined with respect to the axis of the bone. The distal end exhibits a large and slightly convex articular face of subcircular contour. The right metatarsal II? (IANIGLA-PV 077/2) is less robust than the left metatarsal I?. The proximal end is strongly inclined and the distal end presents a convex subtriangular surface. The right metatarsal III? (IANIGLA-PV 077/3) is longer than metatarsals I and II. The proximal end is larger than the distal one. It exhibits a rugose and irregular surface. The distal end is characterized by a strongly convex articular surface of semicircular contour in distal view. The left metatarsal IV? (IANIGLA-PV 077/4) is the longest of all and presents an expanded proximal end. The left metatarsal V? (IANIGLA-PV 77/5) shows an anteromedial face slightly convex and a posterolateral face slightly concave proximally. The proximal end is expanded, with a rugose surface. In contrast, the distal end is reduced, offering a small articular surface. Measurements: length of the metacarpals I, II, III, IV and V: 140 mm, 156 mm, 178 mm, 205 mm and 165 mm, respectively.

Two pedal ungual phalanges were collected (IANIGLA-PV 078, 079). They are laterally compressed with convex dorsal border and concave ventral border (typical "sickle" shape). In ventral view, they are not symmetrical since one of their lateral faces is convex and the other is slightly concave anteroposteriorly. The distal end is relatively blunt (figure 6.F) or bears a ventral projection (figure 6.G).

The *Mendozasaurus* foot is comparable to the metatarsals and ungual phalanges of *Antarctosaurus* (MACN 6809, Huene, 1929) and *Aeolosaurus* (MPCA 27100, Salgado *et al.*, 1997b). Nevertheless, detailed comparative studies of titanosaur foot could be made when some important articulated specimens from Patagonia (Martínez *et al.*, 1989; Giménez, 1992; Calvo *et al.*, 1997) are published.

Osteoderms (figures 6.H-J). Two types of osteoderms in association with the caudal vertebrae of the holotype were found. The small-sized osteoderms (IANIGLA-PV 081/1-2) present a "bulb morphology" (see Le Loeuff *et al.*, 1994), with bulbous aspect (81 mm length and 44 mm high). They have an ellipsoidal form in lateral and dorsal views, with convex ventral and dorsal faces (figure 6.J). In contrast to the bone plates of *Saltasaurus loricatus* (Powell, 1980, 1986), they lack spines. The dorsal surface shows an irregular pattern, with bony fibers that form grooves and nodules. They are similar to the plates of *Aeolosaurus* (Salgado and Coria, 1993) although they are smaller and exhibit a more irregular and rugose surface. They are also smaller and less elongated than the osteoderms of *Ampelosaurus atacis* (Le Loeuff *et al.*, 1994; Le Loeuff, 1995).

Two large-sized osteoderms were found. The osteoderm IANIGLA-PV 080/2 (figures 6.G-H; 7.F-G) has a subconical shape, with the dorsal surface dominated by an apex (153 mm high) where fibers and grooves converge. In one of the lateral faces, abundant acute nodules located on the radial crests are developed. The ventral surface is slightly convex and irregular, with an elliptical contour (175 mm and 99 mm).

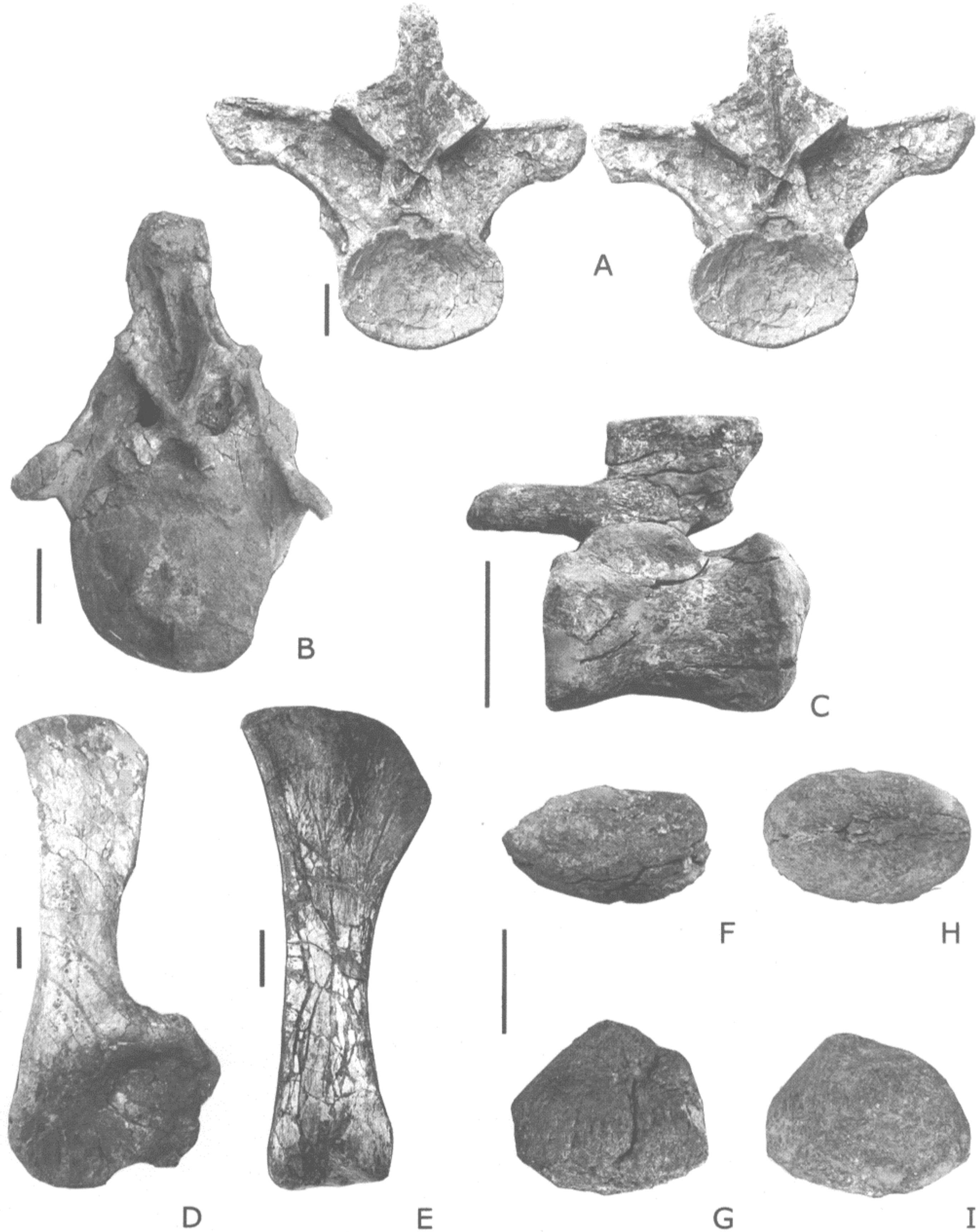

Figure 7. ***Mendozasaurus neguyelap*** gen. et sp. nov. **A,** Stereophotographs of the anterior dorsal vertebra in posterior view, paratype / *estereofotografías de la vértebra dorsal anterior en vista posterior, paratipo*, IANIGLA-PV 066. **B,** anterior caudal vertebra in posterior view / *vértebra caudal anterior en vista posterior*, holotype / *holotipo*, IANIGLA-PV 065/1. **C,** middle-posterior caudal vertebra in lateral view / *vértebra caudal media-posterior en vista lateral*, holotype / *holotipo*, IANIGLA-PV 065/16. **D,** right scapula in lateral view / *escápula derecha en vista lateral*, IANIGLA-PV 068; **E,** rigth tibia in lateral view / *tibia derecha en vista lateral*, IANIGLA-PV 073/2; **F-G,** osteoderm in dorsal (F) and lateral (G) views / *osteodermo en vista dorsal (F) y lateral (G)*, IANIGLA-PV 080/2; **H-I,** osteoderm in dorsal (H) and lateral (I) views / *osteodermo en vista dorsal (H) y lateral (I)*, IANIGLA-PV 080/1. Scale bar: 10 cm / *escala gráfica*: 10 cm.

Table 1. Measurements (in millimeters) of vertebrae of *Mendozasaurus neguyelap.*

Registration nos.	Greatest overall height	Height of centers	Width of centers	Length of centers
Anterior dorsal IANIGLA-PV 066	560	195	260	165
Anteriomost caudal IANIGLA-PV 065/1	545	215	225	120*
Anterior caudal (?3th) IANIGLA-PV 065/3	380(-)	190	230	150*
Anterior caudal (?4th) IANIGLA-PV 065/4	400	170	—	235*
Anterior caudal (?7th) IANIGLA-PV 065/7	350	150	—	157
Midcaudal (?15th) IANIGLA-PV 065/13	185	111	117	170
Mid-posterior caudal (?19th) IANIGLA-PV 065/16	190	107	121	163
Mid-posterior caudal (?22th) IANIGLA-PV 065/19	180	105	106	141

*Compressed and/or distorted
(-) Incomplete

The specimen IANIGLA-PV 080/1 (figures 6.I; 7.H-I) is similar to the previous one, although it presents a more spherical form, with a less pronounced dorsal apex. The large osteoderms of *Mendozasaurus* are very different from the bone plates described for South American titanosaurs as *Saltasaurus* (Powell, 1992) and *Aeolosaurus* (Salgado and Coria, 1993). On the other hand, even though they are similar to the plates of *Ampelosaurus* (Le Loeuff *et al.*, 1994; Le Loeuff, 1995), they lack the cingulum present in this species.

Autapomorphic characters of *Mendozasaurus*

Mendozasaurus neguyelap gen. et sp. nov. is characterized by the following autapomorphies:

1) Two subtriangular infrapostzygapophyseal fossae in anterior dorsal vertebrae located over the neural canal. In other titanosaurs, these fossae are absent, like in *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), or are undivided, like in *Malawisaurus* (Gomani *et al.*, 1999). Furthermore, even though some non-titanosaur sauropods as *Apatosaurus louisae* (Wilson, 1999) present fossae in the same position in the first dorsal, these cavities are dorsoventrally extended, reaching the base of the neural canal, and they are not subtriangular in shape.

2) Postzygapostspinal laminae in anterior dorsal vertebrae parallel to the plane of postzygapophyseal facets. These laminae connect the articular surfaces of the postzygapophyses with the base of the postspinal lamina. The postzygapostspinal laminae are different from the intrapostzygapophyseal laminae present in cervical and anterior dorsal vertebrae of diplodocids (Wilson, 1999) because the latter are not connected to the postspinal lamina.

Although the presence of subtriangular infrapostzygapophyseal fossae and the postzygapostspinal laminae are considered probable autapomorphies of *Mendozasaurus*, it is important to keep in mind that the absence of these characters can not be confirmed in titanosaurs lacking well preserved anterior dorsal vertebrae, like *Aeolosaurus* (Powell, 1986; Salgado and Coria, 1993), *Pellegrinisaurus* (Salgado, 1996), *Rocasaurus* (Salgado and Azpilicueta, 2000), *Gondwanatitan* (Kellner and Azevedo, 2000), *Malawisaurus* (Jacobs *et al.*, 1993; Gomani *et al.* 1999) and *Alamosaurus* (Gilmore, 1946; Lucas and Hunt, 1989).

3) Dorsoventrally extended interzygapophyseal cavity in anterior caudal vertebrae, limited by the spinopostzygapophyseal and spinoprezygapophyseal laminae. The development of this cavity, that reaches a high point in the neural spine, is absent in other titanosaurs. This cavity surpasses the dorsal border of the postzygapophysis a distance greater than the length of the postzygapophyseal facet. In *Malawisaurus* the interzygapophyseal cavity is not as developed dorsally, according to the fossils described by Gomani (1999, fig. 1.A). On the other hand, *Lirainosaurus astibiae* shows an interzygapophyseal fossa divided by a lamina parallel to the spinoprezygapophyseal lamina (Sanz *et al.*, 1999).

4) Middle caudals slightly procoelous, with reduced posterior condyles displaced dorsally. Some sauropods have strongly procoelous anterior caudal centra associated with non-procoelous middle and posterior caudals. However, *Mendozasaurus* is unique in having posterior articular surfaces with reduced prominences (condyles) displaced dorsally in middle caudal centra. In contrast, *Andesaurus* has anterior caudals slightly procoelous (Salgado *et al.*, 1997a) and amphiplatyan (Calvo and Bonaparte, 1991) or platy-

coelous (*sensu* Romer, 1956) middle caudals, with slightly hollow anterior and posterior faces. *Malawisaurus*, from the Lower Cretaceous of Africa, has anterior caudals strongly procoelous and middle and posterior caudals gently amphicoelous (Jacobs *et al.*, 1993) or platycoelous (Gomani, 1999). *Janenschia*, from the Late Jurassic of Tanzania (Wild, 1991; Jacobs *et al.*, 1993), exhibits procoelous anterior caudals associated with amphiplatyan and amphicoelous middle and posterior caudals. A recent review of Bonaparte *et al.* (2000) indicates that this caudal section cannot be properly referred to *Janenschia* due to the incompleteness of the type material of *Janenschia robusta*.

The specimen MUCPv 204 "Titanosauria indet." from the Río Colorado Formation (Neuquén, Argentina) is an incomplete caudal sequence lacking arches and neural spines. It exhibits strongly procoelous anterior caudals associated with amphiplatyan middle caudals (Salgado and Calvo, 1993). Some of these middle caudals have gently convex posterior faces, but they have not reduced posterior condyles such as those in *Mendozasaurus*.

Finally, the middle caudals of *Mendozasaurus* are different from the middle and posterior caudals of *Lirainosaurus astibiae* (Sanz *et al.*, 1999). In contrast to *Mendozasaurus*, *Lirainosaurus* shows strongly procoelous middle caudals. Furthermore, although the distal caudals of *Lirainosaurus* have posterior condyles reduced, they are more developed than the posterior condyles of *Mendozasaurus*, and they are not displaced dorsally.

5) Laminar mid-posterior caudal neural spines with horizontal and straight dorsal border, and anterodorsal corner forming a right angle. *Mendozasaurus* shares with *Malawisaurus* (Jacobs *et al.*, 1993) and *Andesaurus* (Calvo and Bonaparte, 1991) the presence of laminated and anteroposteriorly elongated mid-caudal neural spines. However, the spines of *Mendozasaurus* have a horizontal and straight dorsal border, with anterodorsal right angle. They are also different to the caudal sequence referred with doubts to *Janenschia robusta* by Bonaparte *et al.* (2000). In that material, the posterior caudal neural spines have irregular and convex dorsal borders. Furthermore, they are projected posteriorly, surpassing the posterior border of the centra (Bonaparte *et al.*, 2000, plate 12).

6) Presence of large, subconic-spherical osteoderms lacking cingulum. These large osteoderms are different from those of *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1992) since they lack a peripheral ring with tubercles and a longitudinal ventral crest. On the other hand, they are similar to the titanosaur osteoderms described by Sanz and Buscalioni (1987) and the large osteoderms of *Ampelosaurus atacis* (Le Loeuff *et al.*, 1994; Le Loeuff, 1995), but they lack the large cingulum present in these European titanosaurs.

Phylogenetic relationships and conclusions

Unique among titanosaurs, *Mendozasaurus neguyelap* gen. et sp. nov. has slightly procoelous middle caudal vertebrae with reduced posterior condyles displaced dorsally, associated with typical strongly procoelous anterior caudal vertebrae. Furthermore, among other autapomorphies, the presence of large subconic-spherical osteoderms is emphasized.

The phylogenetic relationships of *Mendozasaurus* were analyzed by a cladistic analysis based on 39 postcranial characters corresponding to 15 taxa (see Appendix). *Patagosaurus fariasi* (Bonaparte, 1986b), Diplodocidae (McIntosh, 1990; Calvo and Salgado, 1995) and *Camarasaurus grandis* (Cope, 1877) were considered as external groups, and *Brachiosaurus brancai* (Janensch, 1950), *Chubutisaurus insignis* (Del Corro, 1975), *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), *Malawisaurus dixeyi* (Jacobs *et al.*, 1993), *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Alamosaurus sanjuanensis* (Gilmore, 1946), *Neuquensaurus australis* (Huene, 1929; Powell, 1986), *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell 1992), *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000) and *Mendozasaurus neguyelap* gen. et sp. nov. (this paper) formed the ingroup.

The data matrix was run using the program NONA, version 2.0 (Goloboff, 1993). The multistate characters were considered unordered. The application of heuristic method resulted in one most parsimonious tree with a length of 56 steps, CI = 78 and RI = 88. The synapomorphies listed in the Titanosauria and Titanosauridae nodes, by delayed (slow) optimization were defined. The cladogram obtained (figure 8) displays new information with regard to analyses of Salgado *et al.* (1997a) and Wilson and Sereno (1998), due to the incorporation of new taxa and characters.

Titanosauriformes (node 3) was defined as the most recent common ancestor of *Brachiosaurus brancai*, *Chubutisaurus insignis*, Titanosauria and all of its descendants (Salgado *et al.*, 1997a). In this analysis Titanosauriformes is diagnosed by the following unambiguous characters: neural arches located anteriorly in middle and posterior caudal vertebrae (18.1), perpendicular orientation of pubic peduncle with respect to the sacral axis (34.1), preacetabular lobe of ilium broadly expanded and upwardly directed (37.1) and lateral bulge below the greater trochanter in the femur (39.1).

Figure 8. Cladogram (56 steps; CI: 78; RI: 88) showing the phylogenetic relationships of *Mendozasaurus neguyelap*. Synapomorphies are listed and discussed in the text. / *Cladograma (56 pasos; CI: 78; RI: 88) mostrando las relaciones filogenéticas de* Mendozasaurus neguyelap. *Las sinapomorfías son enumeradas y discutidas en el texto.*

Titanosauria (node 5), proposed originally by Bonaparte and Coria (1993), was defined as the most recent common ancestor of *Andesaurus delgadoi* and Titanosauridae, and all of its descendants (Salgado *et al.*, 1997a). Titanosauria is supported by the following synapomorphies: ventrally widened or slightly forked infradiapophyseal laminae in posterior dorsal vertebrae (7.1), acuminate (eye shaped) pleurocoels in dorsal centra (10.1), slightly procoelous anterior caudal centra (16.1), pubis longer than ischium (33.1) and centroparapophyseal lamina in posterior dorsal vertebrae (6.1) such as was proposed by Salgado *et al.* (1997a). The centroparapophyseal laminae are also present in *Diplodocus* (Hatcher, 1901; Salgado *et al.*, 1997a), *Apatosaurus louisae* and *Apatosaurus excelsus* (Gilmore, 1936; Gomani, 1999; Wilson, 1999), a condition interpreted as probable convergence.

Titanosauridae (node 6) was defined as the clade including the most recent common ancestor of *Malawisaurus*, *Epachthosaurus*, *Argentinosaurus*, *Opisthocoelicaudia*, *Aeolosaurus*, *Alamosaurus*, Saltasaurinae and all of its descendants (Salgado *et al.*, 1997a). In this analysis Titanosauridae is characterized by the following synapomorphies: absence of hyposphene-hypantrum articulation in dorsal vertebrae (8.1), anterior caudal centra strongly procoelous with prominent condyles (16.2), semilunar sternal plates (28.1) and absence of phalangeal articular facets on metacarpals (32.1). Salgado *et al.* (1997a) supported Titanosauridae with three other characters, two of which are the presence of six sacral vertebrae (13.1) and the preacetabular lobe of ilium laterally projected (38.1). In the present analysis both characters have an ambiguous distribution because they are unknown in *Malawisaurus* and *Mendozasaurus*. The third character proposed by the mentioned authors was the development of strongly procoely in mid and posterior caudal vertebrae (character 23.3 of Salgado *et al.*, 1997a, p. 21).

According to the phylogenetic definition of Titanosauridae proposed by Salgado *et al.* (1997a) *Mendozasaurus* can also be included in this clade. However, the diagnosis of Titanosauridae must be modified. The synapomorphy "strongly procoely in middle caudal vertebrae" (17.2) is present in titanosaurids more derived than *Mendozasaurus* and appears as an unambiguous character in the node 7 (figure 8). For this reason, this synapomorphy should be excluded from the diagnosis of Titanosauridae.

The node 13, supported by three traits (21.2, 22.1 and 29.1) links *Malawisaurus* with *Mendozasaurus*. One of these characters is the presence of laminated and anteroposteriorly elongated neural spine in middle caudal vertebrae, located on the middle of the centrum (21.2). Even though some species have similar neural spines, they are posteriorly projected, reaching or surpassing the posterior border of the centra, like in *Andesaurus* or in material questionably referred to *Janenschia* (Calvo and Bonaparte, 1991; Bonaparte *et al.*, 2000). *Mendozasaurus* also shares with *Malawisaurus* the development of prezygapophyses relatively long (22.1) and semilunar sternal plate with straight posterior border (29.1). The first character (22.1) is also present in *Titanosaurus* sp. (DGM "Serie C" Brazil) and *Aeolosaurus rionegrinus* (Salgado and Coria, 1993; Salgado *et al.*, 1997b), while the second character (29.1) is also present in *Alamosaurus* (Gilmore, 1946; Lucas and Hunt, 1989).

The discoveries of *Mendozasaurus* and other titanosaurs like *Andesaurus* and *Malawisaurus* show that the caudal procoely of this clade is a complex subject to analyze. Regarding this matter, it is important to keep in mind the following observations: 1) In the cladistic analyses (Salgado *et al.*, 1997a; this paper) all titanosaurs lacking strongly procoelous middle caudal centra (*Andesaurus*, *Malawisaurus*, *Mendozasaurus*) can be considered as basal taxa with respect to derived titanosaurids (e.g. Saltasaurinae); 2) A titanosaur species with strongly procoelous middle or posterior caudal centra associated with non-procoelous anterior caudals has never been found; 3) In the cladistic analysis the processing of multistate characters referring to the progressive development of the procoely resulted in a cladogram with equal topology, considering these traits both as unordered and as ordered. These observations suggest that in titanosaurs the procoely could have advanced from anterior to distal segments of the tail, such as interpreted Bonaparte (1996). Nevertheless, to verify this preliminar interpretation more complete comparative studies are necessary.

Acknowledgments

I thank W. Volkheimer and J. Bonaparte the direction of my Doctoral Thesis. I am grateful to J. Calvo for his valuable advice and support. I thank M. Bourget, F. Piccolella, S. Londero, S. González Riga, F. Fernández Favarón, A. Santini, E. Previtera and C. Sancho for their generous collaboration in the paleontological excavations and laboratory works during four years. I am grateful to R. Coria and L. Salgado for their comments and critical review. I thank O. Sprenjer and A. Chávez for communicating their finding of dinosaur fossils. I am grateful to students G. Del Favero, A. Stoisa, M. Calderón, C. Pirrone, D. Lazzarini, R. Giménez, L. Bauzá, G. Depetris and G. Méndez for their collaboration in the technical preparation of fossils and other works. I am grateful to M. Tellechea (Tellechea Mineralogical Museum, CRICYT) and O. Funes (CENTRILIF) for their collaboration and support in the field work of January 1998. I thank the Municipality of Malargüe, E. Castilla (AKAPOL S.A.), G. Villegas, C. Sota (Grúas López S.A.) for their field assistance. This research was supported by the Paleontology Unit of IANIGLA (CRICYT, CONICET) and mostly financed by projects of the National Agency of Scientific and Technological Promotion, Argentina (PICT 07-01513, director: J. Calvo) and National University of Comahue (T-013, director: J. Calvo).

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Recibido: 15 de noviembre de 2001.
Aceptado: 17 de octubre de 2002.

Appendix

The distribution and coding of 39 postcranial characters corresponding to 15 taxa of sauropods is shown below (table 2). The traits have been defined by the authors cited in the list, except the characters 21, 22, 26, 27 and 29 that are proposed herein.

Table 2. Character-Taxon Matrix

Taxon	Characters							
	1-5	6-10	1-15	16-20	21-25	26-30	31-35	36-39
Patagosaurus fariasi	00000	00000	00000	00000	00000	00000	00000	0000
Diplodocidae	00102	10010	00000	00000	00000	00000	00000	0000
Camarasaurus grandis	01100	00010	00000	00001	00010	00000	10001	0000
Brachiosaurus brancai	01001	00010	00000	00101	00010	00000	10011	0101
Chubutisaurus insignis	?1??2	?0010	?1?00	0010?	??0?1	00???	10???	???1
Andesaurus delgadoi	?10?1	11011	01?00	10101	1001?	0????	1?1?1	0???
Malawisaurus dixeyi	01012	11111	?1?00	20101	2101?	??110	????1	0???
Mendozasaurus neguyelap	??002	??111	?1?00	21101	21011	0111?	11???	???1
Titanosaurus colberti	01002	11111	01100	22101	00011	00??0	??111	111?
Lirainosaurus astibiae	?10?2	11111	01?00	2210?	?00??	01101	?????	???1
Opisthocoelicaudia skarzynskii	01112	1?111	11100	00101	00011	11101	11111	1??1
Alamosaurus sanjuanensis	??0??	?????	???01	22111	00011	01111	11?11	111?
Neuquensaurus australis	11012	11111	11111	22110	00011	011?1	???11	1111
Rocasaurus muniozi	?1012	11111	11?11	22110	001??	?????	??111	11?1
Saltasaurus loricatus	11012	11111	11111	22110	00111	12101	11111	1111

Postcranial axial skeleton

1- Cervical prezygapophyses, relative length: long, with articular facets that surpass the centra (0); short, with articular facets that do not surpass the centra (1) (Salgado *et al.*, 1997a).

2- Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998; Bonaparte, 1999; Sanz *et al.*, 1999).

3- Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (McIntosh, 1992; Wilson ad Sereno, 1998).

4- Anterior dorsal neural spines, inclination: vertically or slightly inclined posterodorsally (0); inclined posterodorsally more than 20 degree from vertical (1) (modified from Wilson and Sereno, 1998).

5- Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of the neural spine (1); formed down to the base of the neural spine (2) (Salgado *et al.*, 1997a).

6- Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (Bonaparte and Coria, 1993; Salgado *et al.*, 1997a).

7- Ventrally widened or slightly forked infradiapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado *et al.*, 1997a).

8- Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (Salgado *et al.*, 1997a).

9- Pleurocoels in cervical and dorsal vertebrae: absent (0); present (1) (Calvo and Salgado, 1995; Bonaparte, 1999).

10- Acuminate (eye-shaped) pleurocoels in dorsal vertebrae: absent (0); present (1) (Bonaparte and Powell, 1980; Calvo and Bonaparte, 1991; Salgado *et al.*, 1997a).

11- Relative height of neural spine in posterior dorsal vertebrae: i.e. the height taken from dorsal border of the diapophysis is more (0) or less (1) than 25 percent of the total height of the vertebra (modified of Sanz *et al.*, 1999).

12- Bone internal structure of somphospondylous-camellate type on presacral vertebrae: absent (0); present (1) (modified of Wilson and Sereno, 1998 using terminology of Wedel *et al.*, 2000).

13- Number of sacral vertebrae: five (0), six (1) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998).

14- Anterior caudal centra, relative proportions: centrum height equal or greater than centrum width (0); centrum width greater than centrum height (1) (Powell, 1986; Salgado *et al.*, 1997a).

15- Middle and posterior caudal centra, relative proportions: centrum height equal or greater than centrum width (0); centrum width greater than centrum height (1) (Powell, 1986; Salgado *et al.*, 1997a).

16- Anterior caudal centra, articular face shape: non-procoelous (0); slightly procoelous (1); strongly procoelous with prominent condyles (2) (modified of Salgado *et al.*, 1997a).

17- Middle caudal centra, articular face shape: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2) (modified of Salgado *et al.*, 1997a).

18- Mid point of the lateral face of the neural arch in middle and posterior caudal vertebrae placed: in the middle of the centrum (0), anteriorly (1), (Huene, 1927; Powell, 1986; Salgado *et al.*, 1997a).

19- Prominent lateral crest on the base of the neural arch in middle caudal vertebrae: absent (0); present (1) (Salgado *et al.*, 1997a).

20- Relative position of anterodorsal border of neural spine in middle caudal vertebrae: anterior (0) or posterior (1) with respect to anterior border of the postzygapophyses (1) (Salgado *et al.*, 1997a).

21- Neural spine in the middle caudal vertebrae, shape: short anteroposteriorly (0); laminated, anteroposteriorly elongated and posteriorly projected reaching the posterior border of the centrum (1); laminated, anteroposteriorly elongated and located over the middle of the centrum (2).

22- Prezygapophyses in middle caudal vertebrae, relative length: shorter (0) or longer (1) than the 40 percent of the length of the centrum without the posterior articular condyle.

23- Ventral depression divided by a longitudinal lamina (septum) on anterior and middle caudal vertebrae: absent (0); present (1) (Salgado and Azpilicueta, 2000).

24- Haemal canal in anterior caudal vertebrae: closed (0); opened (1) (Upchurch, 1995; Salgado *et al.*, 1997a; Wilson and Sereno, 1998).

Appendicular skeleton

25- Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (Wilson and Sereno, 1998).

26- Humerus, breadth of proximal end: less than 50 percent of total length (0); more than 50 percent of total length (1).

27- Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2).

28- Sternal plate, shape: suboval (0); semilunar (1) (Salgado *et al.*, 1997a).

29- Semilunar sternal plate with straight posterior border: absent (0); present (1).

30- Coracoid, shape: suboval (0); quadrangular (1) (Salgado *et al.*, 1997a).

31- Relative metacarpal length: less than 40 percent of radius length; more than 40 percent radius length (1) (McIntosh, 1990b; Salgado *et al.*, 1997a).

32- Metacarpals, distal phalangeal articular facets: present (0) absent (1) (Giménez, 1992; Salgado *et al.*, 1997a).

33- Pubis length respect to ischium length: shorter or equal (0); larger (1) (Salgado *et al.*, 1997a).

34- Ilium, relative orientation of pubic peduncle: angled (0) or perpendicular (1) with respect to the sacral axis (Salgado *et al.*, 1997a).

35- Ischium, pubic articulation: short (0); long, extended dorsoventrally (1) (Salgado *et al.*, 1997a).

36- Ischium, length of posterior process: twice longer or more than the pubis articulation (0); less than twice length of pubis articulation (1) (modified of Salgado *et al.*, 1997a).

37- Ilium, shape of preacetabular lobe: moderately expanded (0); broadly expanded and upwardly directed (1) (Salgado *et al.*, 1997a).

38- Ilium, orientation of preacetabular lobe: nearly vertical (0); nearly horizontal, laterally projected (1) (Salgado *et al.*, 1997a).

39- Femur, lateral bulge below the greater trochanter: absent (0); present (1) (McIntosh, 1990; Salgado, 1993; Calvo and Salgado, 1995; Salgado *et al.*, 1997a, Wilson and Sereno, 1998).