

A New Titanosaur Sauropod Dinosaur from the Upper Cretaceous of North Patagonia, Argentina

Authors: Filippi, Leonardo S., García, Rodolfo A., and Garrido, Alberto C.

Source: Acta Palaeontologica Polonica, 56(3) : 505-520

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2010.0019>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A new titanosaur sauropod dinosaur from the Upper Cretaceous of North Patagonia, Argentina

LEONARDO S. FILIPPI, RODOLFO A. GARCÍA, and ALBERTO C. GARRIDO



Filippi, L.S., García, R.A., and Garrido, A.C. 2011. A new titanosaur sauropod dinosaur from the Upper Cretaceous of North Patagonia, Argentina. *Acta Palaeontologica Polonica* 56 (3): 505–520.

A new sauropod titanosaur from the Upper Cretaceous Anacleto Formation is described. *Narambuenatitan palomoi* gen. et sp. nov., is diagnosed by cranial and axial autapomorphies. The holotype, which represent a subadult individual, consists of the left premaxilla and maxilla, braincase, both quadrates, one cervical vertebrae, one dorsal vertebra, fragments of cervical and dorsal ribs, seventeen caudal vertebrae, caudal transverse processes, fragments of haemal arches, left sternal plate, right coracoid, left humerus, left ulnae, both pubes, iliac pedicel, proximal fragment of right ischia, and an incomplete left femur. The phylogenetic analysis indicates that *Narambuenatitan* is a non-eutitanosaurian lithostrotian, and that it shares with *Epachthosaurus* a neural spine in middle caudal vertebrae which are laminar and posteriorly elongated.

Key words: Sauropoda, Titanosauria, phylogeny, Campanian, Cretaceous, Anacleto Formation, Neuquén Basin, Argentina.

Leonardo S. Filippi [lsfilippi@yahoo.com.ar], Museo “Carmen Funes”, Av. Córdoba 55, (8318) Plaza Huincul, Neuquén, Argentina;

Rodolfo A. García [rgarcia@uncoma.edu.ar], Inibioma – Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400, (8300) Neuquén, Argentina;

Alberto C. Garrido [algene@copelnet.com.ar], Museo Provincial “Prof. Dr. Juan Olsacher”, Dirección General de Minería, Elena de Vega 472, (8340) Zapala, Neuquén, Argentina.

Received 7 February 2010, accepted 23 December 2010, available online 29 December 2010.

Introduction

Although titanosaurian sauropods are the most abundant herbivorous dinosaurs in the Cretaceous of Patagonia, showing a great diversity of forms, most of the representatives of the clade are based on fragmentary and incomplete materials. Specimens that have abundant associated elements including well preserved cranial and postcranial are relatively scarce: *Antarctosaurus wichmanianus* (Huene 1929), *Saltasaurus loricatus* (Bonaparte and Powell 1980; Powell 1992; 2003), *Rapetosaurus krausei* (Curry Rogers and Forster 2001), *Bonatitan reigi* (Martinelli and Forasiepi 2004) *Bonitasaura salgadoi* (Apesteguía 2004), *Malawisaurus dixeyi* (Gomani 2005), *Muyelensaurus pecheni* (Calvo et al. 1997; 2007a), and *Pitekunsaurus macayai* (Filippi and Garrido 2008). In this work, a new titanosaurian sauropod is described, based on well preserved cranial and postcranial elements. The specimen was collected during several field-trips carried out between 2005 and 2006 by the authors. The outcrops correspond to the Anacleto Formation (lower–middle Campanian), and the locality is named Puesto Narambuena (Fig. 1), situated 20 km west of Rincón de los Sauces City, Neuquén, Argentina. The main objective of this paper is to describe this specimen and discuss its phylogenetic position.

Institutional abbreviations.—MAU, Museo Argentino Urqu-

iza, Rincón de los Sauces, Neuquén, Argentina; MGPIFD-GR, Museo de Geología y Paleontología del Instituto de Formación Docente Continúa de General Roca, General Roca, Río Negro, Argentina; MML, Museo Municipal de Lamarque, Río Negro, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; UFRJ-MN, Universidad Federal de Río de Janeiro, Museo Nacional, Río de Janeiro, Brazil.

Geological setting

The specimen was recovered from the lower third of the Anacleto Formation, approximately at 21 m from the base (Fig. 2). This unit corresponds to the upper part of the Neuquén Group (Cenomanian–middle Campanian) and has been attributed by paleomagnetic dates as early as middle Campanian age (Dingus et al. 2000). The sediments are predominantly of fluvial origin, and consist of alternating sandstone and mudstone levels (Cazau and Uliana 1973).

The Anacleto Formation at the Puesto Narambuena site consists of pale yellow, fine-grained sandstone, moderate orange pink siltstone and pale reddish brown mudstone. According to Miall’s lithofacies nomenclature (Miall 1996), the sandy canalized bodies are conformed mainly by Sp, sandstone with planar cross-stratification; associated with Ss, medium to coarse-grained sandstone with pebbles and intra-

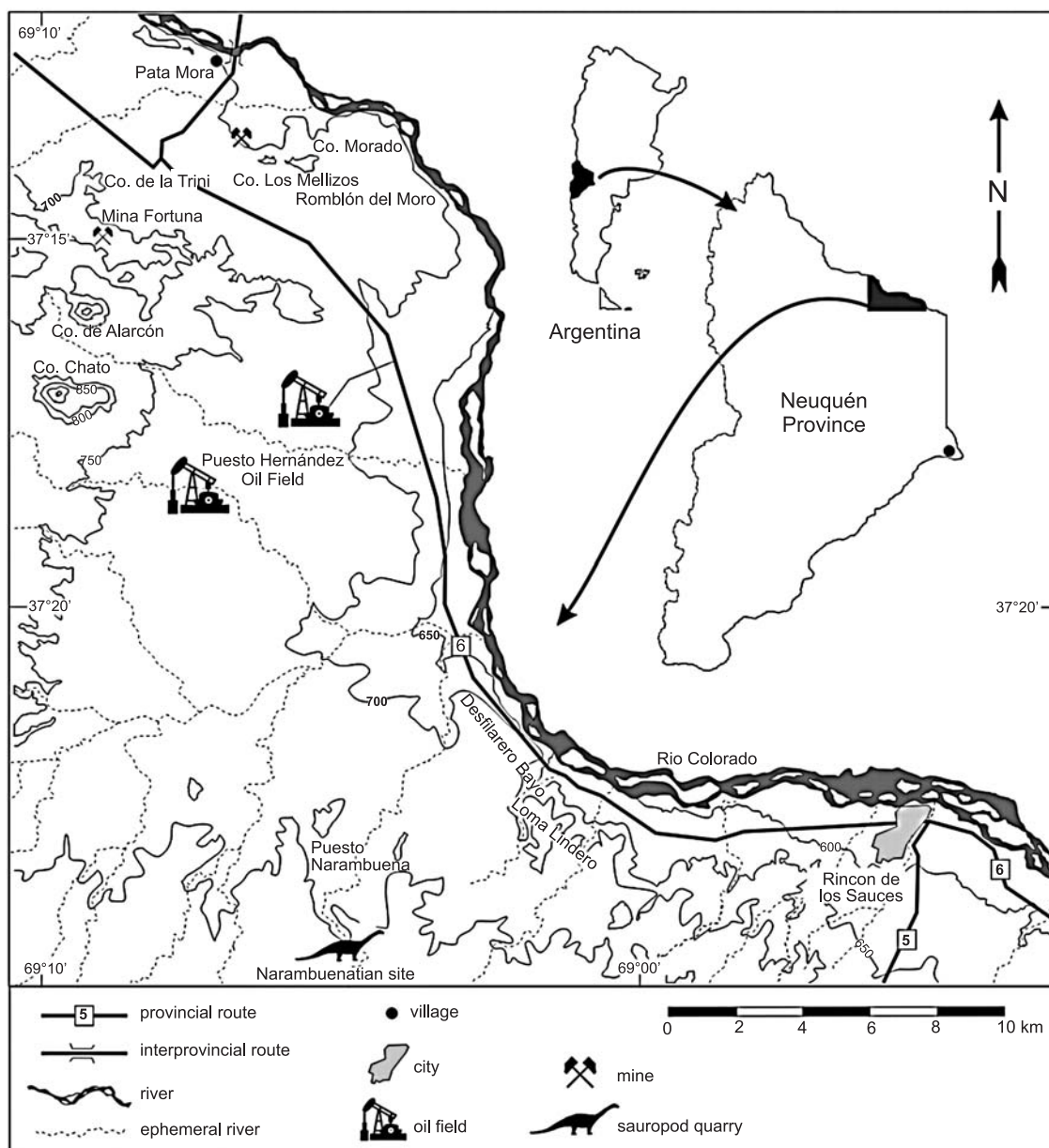


Fig. 1. Location map where the holotype of *Nambuenatitan palomoi* was found.

clasts; Sh, sandstone with horizontal stratification; Sl, sandstone with low-angle cross-stratification; and Sr, sandstone with ripple-lamination facies. Associated sandy and silty tabular bodies are massive or composed of Sr, heterolithic climbing-rippled lamination and Scl, convolute lamination facies. Finally, muddy levels are represented by Fm, massive, tabular bodies with P, scattered development of caliche; and Fl, muddy, laminated, channelized bodies.

A similar lithostratigraphic succession was described by Filippi and Garrido (2008) for the Anacleto Formation at the *Pitekunsaurus macayai* site, located approximately 14 km southeast of Puesto Nambuenatitan. Likewise, this succession is interpreted as low-sinuosity, sandy-load channel deposits and associated overbank (levee, abandoned channels and muddy floodplain) deposits.

The fossiliferous level (Fig. 2) is comprised of mixed and amalgamated deposits of massive, fine-grained sandstones, and grayish green, laminated mudstones. In these sediments the bones were associated with logs braches, coalified plant debris and small and poorly preserved gastropods. These characteristics are indicative of a pond or swamp developed over the inter-channel areas (Collinson 1986). In general, the recovered bones were associated in an area less than 15 m².

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Sauropoda Marsh, 1878

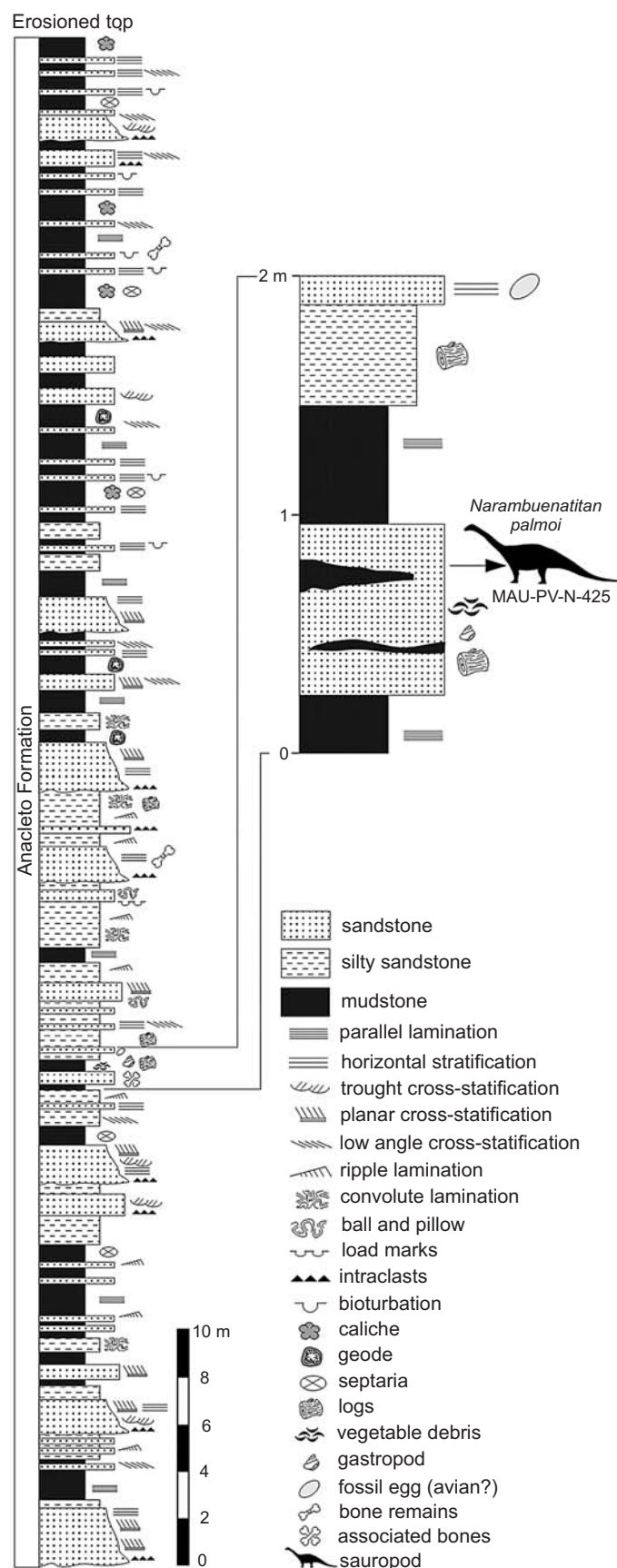


Fig. 2. Stratigraphic column of the Campanian (Upper Cretaceous) Anacleto Formation in the Nambuenena area, showing fossiliferous levels.

Titanosauriformes Salgado, Coria, and Calvo, 1997

Titanosauria Bonaparte and Coria, 1993

Lithostrotia Upchurch, Barrett, and Dodson, 2004

Genus *Nambuenatitan* nov.

Type species: *Nambuenatitan palmoi* gen. et sp. nov.; see below.

Etymology: In reference to Puesto Nambuenena, the area where the holotype of the type species was found, and Greek *titan*, to correspond to a titanosaur specimen.

Diagnosis.—The same of the type species.

Nambuenatitan palmoi sp. nov.

Figs. 3–11.

Etymology: In reference to Salvador Palomo, technician of the Museo Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén, who found the specimen, and in acknowledgment of his permanent contribution to the local paleontology.

Holotype: MAU-Pv-N-425, partial skeleton consisting of the following associated elements: left premaxilla and maxilla; braincase; left and right quadrates; anterior cervical vertebra; cervical rib fragments; posterior dorsal vertebra; three dorsal ribs; eleven anterior caudal vertebrae; six middle caudal vertebrae; two caudal transverse processes; two fragments of haemal arches; left sternal plate; right coracoid; left humerus; left ulna; left and right pubes; pubic peduncle of the left ilium; proximal fragment of the right ischium; and incomplete left femur.

Type horizon: Neuquén Group (Upper Cretaceous), Río Colorado Subgroup, Anacleto Formation (lower to middle Campanian, Dingus et al. 2000).

Type locality: “Puesto Nambuenena”, situated about 20 km west from Rincón de los Sauces, Neuquén Province, Argentina.

Diagnosis.—Titanosaur characterized by the following autapomorphies: (1) great participation of the frontal to the rostral border of the supratemporal fossa, (2) absence of ornamentation on the supraorbital or lateral borders of the frontal, (3) presence of a lamina joining each parietal crest with the rostral surface of the supratemporal, (4) pleurocoel dorsal border defined by a prominent convex bony edge in posterior dorsal vertebrae, (5) distal enlargement of the prespinal lamina in posterior dorsal vertebrae, matching with a lateral enlarged of the neural spine, (6) kidney-shaped prezygapophysis in posterior dorsal vertebrae, (7) presence of numerous pneumatic cavities located posterior to the centroparapophyseal lamina and centrodiaepophyseal lamina in posterior dorsal vertebrae, (8) middle-anterior caudal vertebrae with the anterodorsal border of the neural spine anteriorly inclined, (9) middle caudal vertebra with a slender prezygapophysis and neural arch.

Description

Skull

The cranial material of the holotype of *Nambuenatitan palmoi* is well preserved. However, the ventral portion of the braincase, from the base of the occipital condyle toward the basiptyergoid processes, is lightly deformed toward the right lateral side. The sedimentary matrix obscures the interior of the neurocranium, though it is possible to identify some of the foramina for exit of the cranial nerves.

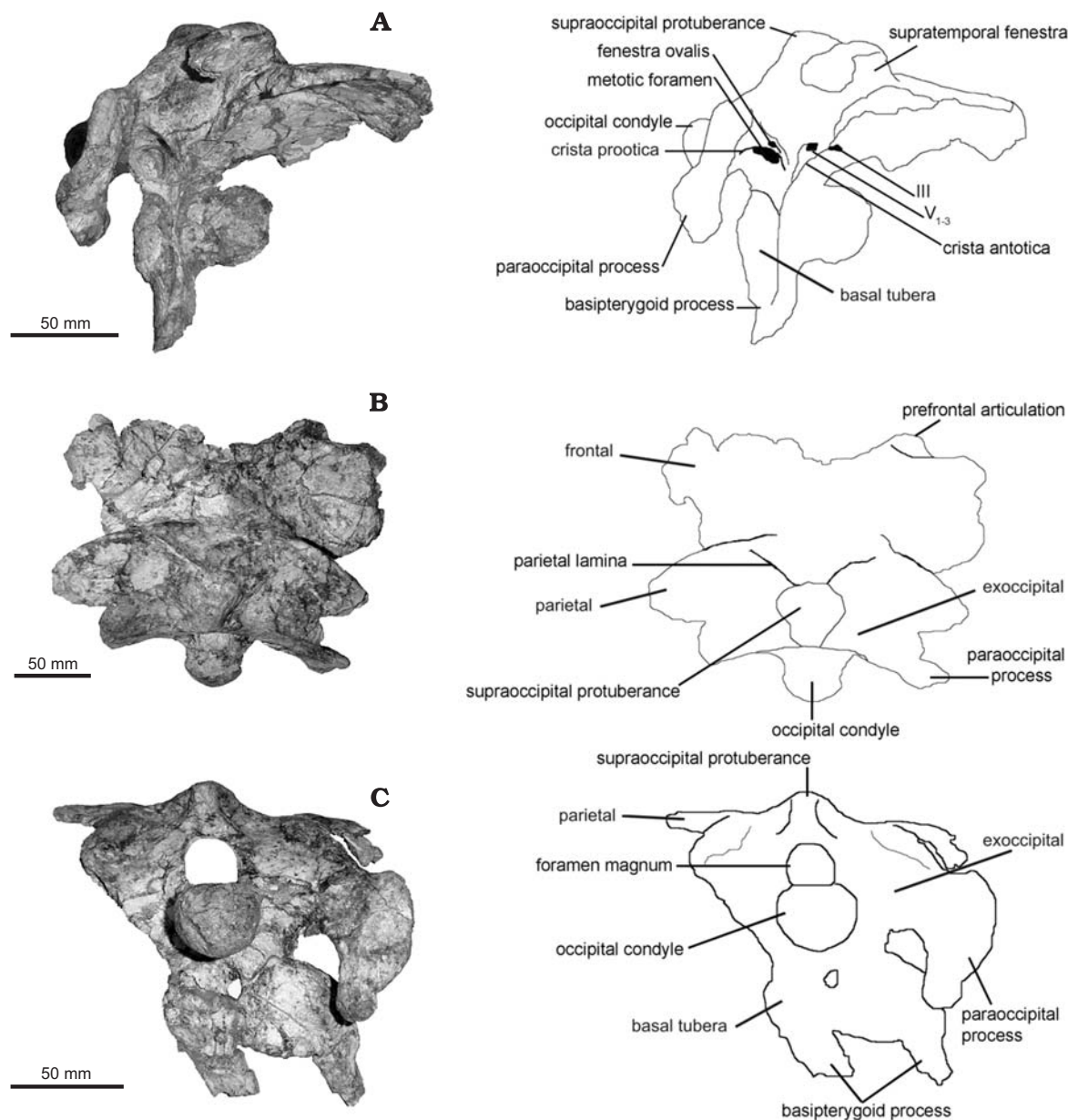


Fig. 3. Braincase of the titanosaur sauropod *Narambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype), in lateral (A), dorsal (B), and caudal (C) views.

Most of the sutures of the skull cannot be recognized. In spite of this, the following elements can be identified: braincase, frontals, parietal, supraoccipital, right exoccipital–opisthotic, left exoccipital–incomplete opisthotic, prootic, basioccipital, basisphenoid, incomplete laterosphenoid–orbitosphenoid in their ventral portion, and caudal portion of the presphenoid (Fig. 3).

The left premaxilla and maxilla are articulated and preserve some of their processes (Fig. 4). The right quadrate is complete (Fig. 5) and the left one is incomplete and slightly deformed.

Premaxilla.—The left premaxilla is almost complete; only the distalmost part of the nasal process is missing. This element is articulated joined to the maxilla. The main pre-

maxillary body has a robust aspect, is taller (without taking into account the nasal process) than wide and is convex rostrally. The premaxilla body extends caudodorsally with the nasal process, a delicate and narrow bony bar of 24 cm of length (Fig. 4). The medial face is a plane surface that corresponds to the symphysis among both premaxillae. The nasal process with the anteriorly ascending process of the maxilla (distally incomplete) defines the rostradorsal limit of the nasal openings. The ventral limit of the nasal openings, which extend rostrolaterally through the posterior ascending process (incomplete), forming a semilunar contour (Fig. 4A₁).

In medial view, the premaxilla reaches its maximum thickness a few centimeters above the alveolar border (Fig. 4A₁), where the replacement teeth were presumably kept,

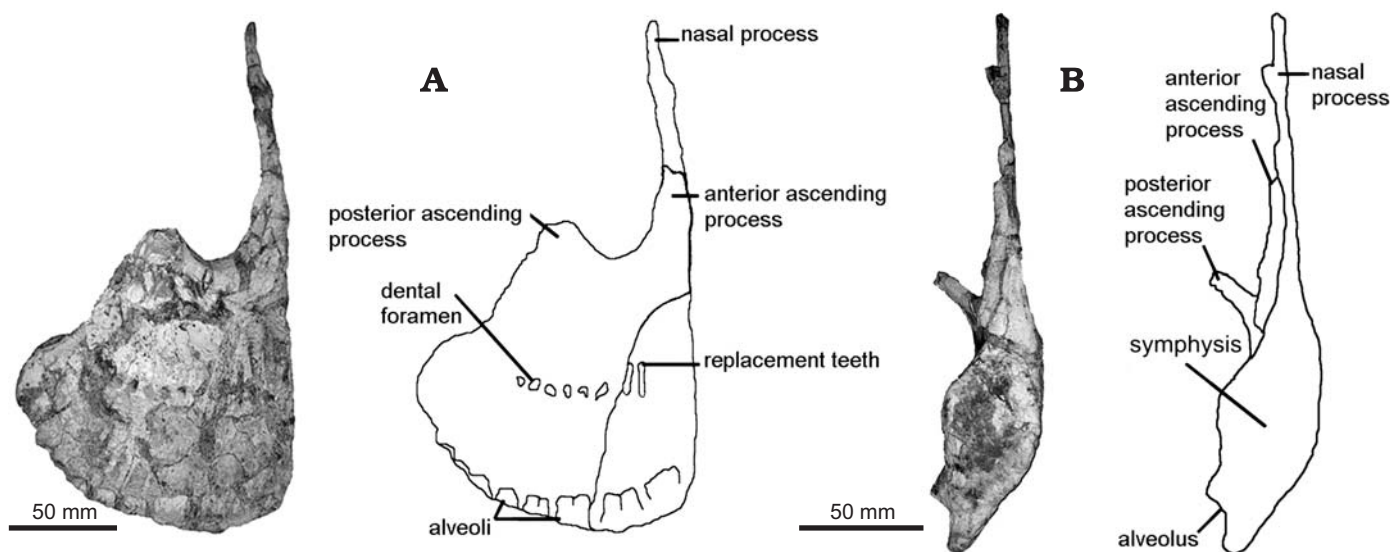


Fig. 4. Premaxilla-maxilla of the titanosaur sauropod *Nambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype), in ventral (A) and medial (B) views.

and becomes thinner distal to the nasal process. The premaxilla has four alveoli, as typically in titanosaurs (Powell 1979; Bonaparte 1986; Britt and Naylor 1994; Chatterjee and Zheng 2002, 2005; Upchurch et al. 2004; Wilson 2005). In this case functional teeth have not been preserved, however the replacement teeth (non erupting) of each alveolus, can be seen in a more internal position of the alveolus, due to incomplete preservation of the lingual wall (Fig. 4A₁). These teeth appear to have a diameter of about 0.5 cm.

Maxilla.—The left maxilla is preserved almost complete and in articulation with the premaxilla. The alveolar margin of the maxilla has eight alveoli; the size of the alveoli decreases caudally (Fig. 4A₁). In any of the alveolus were found functional teeth pieces. However, as with the premaxilla, the lingual wall is incompletely preserved. About about 4 cm dorsal to the alveolar border a row of six replacement teeth can be observed.

The anteriorly ascending process is dorsocaudally overlapped by the premaxilla nasal process along at least 5 cm. Because of the partial preservation of this process, it is not possible to determine if it was extended near the premaxilla process. Both processes define the nasal opening rostrodorsally. The posterior ascending process, which only preserves its basal portion, is thin and could have a caudodorsal inclination. However, it cannot be determined how long it would have been. Caudal to the posterior ascending process and to the posteriormost alveoli, the maxilla is incomplete; the contact with the jugal is not preserved. As a consequence of the incomplete preservation of its caudal portion, the shape and the size of the antorbital fenestra cannot be determined with precision. The main body of the maxilla loses thickness from its symphysis portion with the premaxilla toward its more caudal portion, where it is only 0.3 cm thick, by which we surmise that the jugal process would have been thin (Fig. 4A₂). Although, the region of the antorbital fenestra is not preserved, it is possible to infer that the row of

maxillary teeth would have been located in the rostral portion of the snout.

Frontal.—Both frontals are preserved (Fig. 3A₁, A₂), the left being incomplete along its rostrolateral border. The right frontal, has its lateromedial axis equivalent to 75% of the rostrocaudal axis, approaching a quadrangular form, almost as wide as long. This condition is different in other neosauropods, where the difference between its axes brings closer to a more mediolaterally rectangular form (Martinelli and Forasiepi 2004; Paulina-Carabajal and Salgado 2007). Each frontal is 8.7 cm wide, from the lateral border to the midline, which would comprise 17.4 cm. of total width of the skull. The reconstructed size of this new specimen's skull is similar to that of specimens described by Powell (2003); Martinelli and Forasiepi (2004); Paulina-Carabajal and Salgado (2007) and García et al. (2008). It is not possible to distinguish the interfrontal and the fronto-parietal sutures, due to the advanced state of fusion. Nevertheless, the interfrontal suture is high along the contact defining its position. The frontal presents on its rostrolateral border a small prominence, preceded by a concavity of subcircular contour that would correspond to the articulation with the prefrontal (Fig. 3A₂). This border is also present in *Pitekunsaurus macayai* and *Rapetosaurus krausei* (Filippi and Garrido 2008; Curry Rogers and Forster 2004). Between the articular prominences for the prefrontals (only the right is preserved) a slight depression is observed, which surely corresponds to the contact with the nasals. The frontal participates as much in the fossa as in the supratemporal fenestra, defining it rostrally in the same way as is observed in *Antarctosaurus wichmannianus* (Huene 1929: fig. 28.2), *Bonatitan reigi* (Martinelli and Forasiepi 2004: figs. 7A, 8) and *Muyelensaurus pecheni* (Calvo and González Riga 2004, Calvo et al. 2007a) (contra Wilson and Sereno 1998: character 65; Upchurch et al. 2004: 276). This fenestra projects a wide supratemporal fossa di-

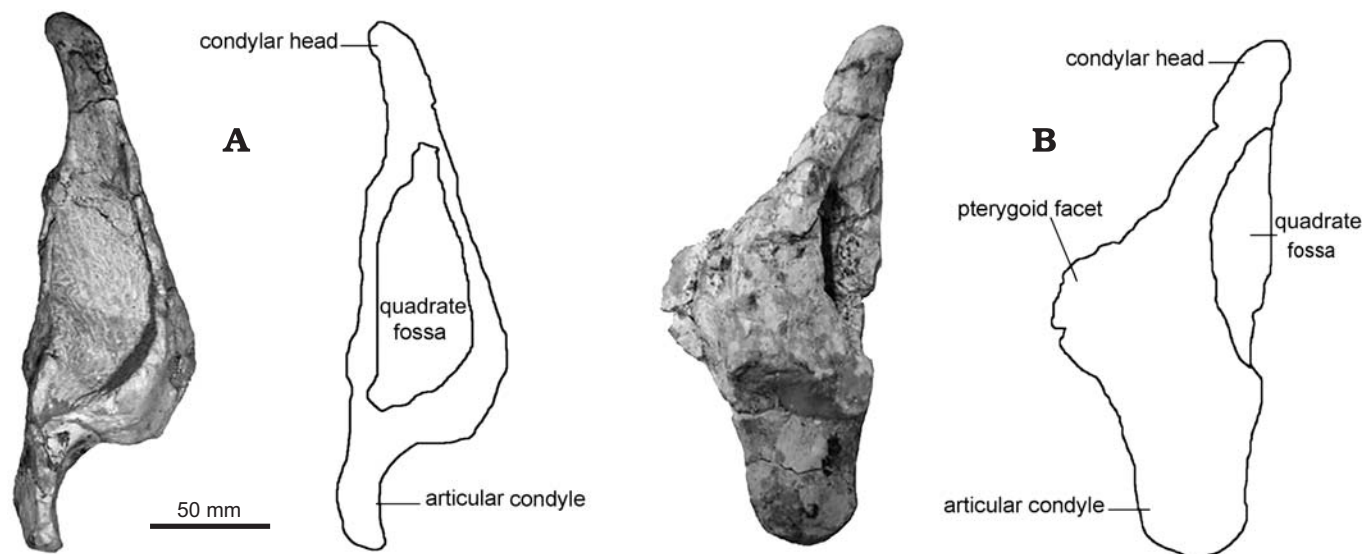


Fig. 5. Quadrato of the titanosaur sauropod *Narambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype), in posterior (A) and medial (B) views.

rected medially, reducing in this way the distance between both fenestrae. The frontal has a great participation of the rostral border of the supratemporal fossa, unlike the condition in other neosauropods (Wilson and Sereno 1998). The articular surface for the postorbital is reduced and it is caudolaterally directed. Although the frontal is incompletely preserved, it lacks ornamentation, like other sauropods, particularly on the lateral or supraorbital borders.

Parietal.—Both parietals are preserved complete, except a small portion of the distal border of the left element (Fig. 3A₂, A₃). These bones are mediolaterally expanded, with their minor axis rostrocaudally oriented like in all titanosaurs. The fronto-parietal contact is restricted to half of the skull width, owing to the fact that the contact surface is reduced by the supratemporal fenestrae. Posterolateral to the supratemporal fenestra, the parietal surface presents a marked, semilunar crest (parietal crest) which extends mediolaterally for the entire length of the element. This parietal edge defines the supratemporal fenestra caudally as in other Patagonian titanosaurs (e.g., *Antarctosaurus* [Huene 1929], *Bonatitan* [Martinelli and Forasiepi 2004], MGPIFD-GR 118, and a Titanosauria indet. [Paulina-Carabajal and Salgado 2007]). A unique character of *Narambuenatitan* is the presence of a lamina or small crest that joins the parietal crests with the rostral portion of the supratemporal protuberance (Fig. 3A₂). The suture between the parietals cannot be distinguished.

Supraoccipital.—The supraoccipital and the exoccipitals form the caudodorsal margin of the skull and the dorsal margin of the foramen magnum. This foramen has a subcircular contour or an arch form, with its base formed by the dorsal portion of the occipital condyle (Fig. 3).

The highest point of the braincase is a robust protuberance of the supraoccipital that is defined by lateral depressions. This supraoccipital protuberance is also present in

other titanosaurs: MGPIFD-GR-118, from Salitral Ojo de Agua, Río Negro, Argentina (Paulina Carabajal and Salgado 2007), UFRJ-MN 6913-V, a cast of the specimen MUCPv-334, described by Calvo and Kellner (2006), *Pitekunsaurus macayai* (Filippi and Garrido 2008), from Rincón de los Sauces, and in *Antarctosaurus wichmannianus* (Powell 2003). A medial groove is lacking (Fig. 3B, C). The supraoccipital protuberance with a medial groove is present in *Saltasaurus* (Powell 2003), *Rapetosaurus* (Curry Rogers and Forster 2004), *Bonatitan* (Martinelli and Forasiepi 2004) and the specimen MML-194 of Loma Salamanca, Río Negro province, Argentina, studied by García et al. (2008). On each lateral surface of the supraoccipital protuberance, it is possible to observe a depression that involves the exoccipitals in their dorsal region. These depressions are also present in other titanosaurs (Huene 1929; Paulina-Carabajal and Salgado 2007; García et al. 2008), and they probably mark the insertion points of some of the neck musculature.

Exoccipital–opisthotic–prootic complex.—The three elements that form this complex fuse in ontogeny (Berman and McIntosh 1978); in this specimen, the sutures between them are not observable (Fig. 3).

As in other sauropods, the exoccipital makes up the lateral margin of the foramen magnum and the lateral and dorsal portions of the occipital condyle. The occipital condyle, of subcircular contour, is notably bigger than the foramen magnum, as in *Nemegtosaurus mongoliensis* (Nowiński 1971: fig. 5; Wilson 2005: fig. 18), *Quaesitosaurus orientalis* (Kurzban and Bannikov 1983: fig. 2) and basal sauropods such as *Shunosaurus lii* (Chatterjee and Zheng 2002).

The articulation of the exoccipital with the opisthotic constitutes the paroccipital process, only the right of which is preserved. This process is robust mainly in its medial portion, bending ventrolaterally, as in all titanosaurs (Huene 1929; Salgado and Calvo 1997; Martinelli and Forasiepi

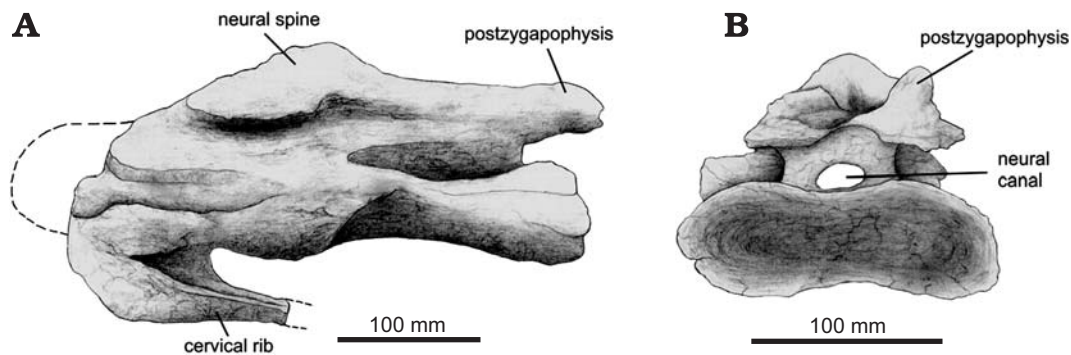


Fig. 6. Anterior cervical vertebra of the titanosaur sauropod *Narambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype), in lateral (A) and posterior (B) views.

2004; García et al. 2008). However, in this taxon the distal end of the paroccipital process ventrally surpasses to the occipital condyle, reaching the level of the basal tuberosities, a condition otherwise known only in *Saltasaurus*.

The opisthotic is completely fused to the prootic caudally; the two comprise a bony complex that contains the inner ear. In lateral view, along the crest that defines the ventral border of the paroccipital process and the prootic crista opens a great depression corresponding to the middle ear, there is a wide metotic foramen for the cranial nerves that would have exited here (IX, Glossopharyngeal; X, Vagus; XI, Accessory), together with the jugular vein (Chatterjee and Zheng 2002; 2005; García et al. 2008). In an immediately dorsal position to the metotic foramen opens the fenestra ovalis (Fig. 3A₁). The fenestra ovalis position, dorsal to the metotic foramen, is a distinctive difference from the condition in other titanosaurs, where it can be observed rostral to the metotic foramen. The foramen for the exit of nerve VII, which in other titanosaurs shows up between the fenestra ovalis and the exit for nerve V, cannot be observed in this specimen. The exit foramen of nerve V (Trigeminal, with three branches: ophthalmic, maxillary, mandibular), opens between the middle ear (caudal), and the opening for the exit of nerve III (Oculomotor)(rostral). The border rostral to the foramen for V1–3 is limited for a remarkable antotic crista that defines the caudal limit of the laterosphenoid. The ventral border of this foramen continuous ventrally, forming a gutter that goes along the basipterygoid process, where the maxillary branch of the Trigeminal nerve (V2) went through (White 1958; Martinelli and Forasiepi 2004). From the corner dorsorostral to the foramen for nerve V, it extends to the roof of the skull, a crest that corresponds to the contact between the orbito-laterosphenoid complex and the exoccipital–opisthotic–prootic complex.

Laterosphenoid–orbitosphenoid complex.—The elements that comprise this complex are strongly fused and the suture between the elements is indistinguishable (Fig. 3A₁). In this specimen only the dorsal portion of the complex was preserved, so that the region that has the foramina for the exit of nerves IV, VI and VII is not present. This complex is caudally articulated with the previously described complex (exoccipital–opisthotic–prootic) and with the frontal in its

dorsal part, without a visible suture between the complexes. The foramen of nerve III (Oculomotor) has a circular form; it opens rostral to the foramen for nerve V, immediately anterior to the antotic crista.

Basioccipital–basisphenoid complex.—The elements of this complex are completely fused to each other and to the presphenoid. The bony complex corresponds to the floor of the braincase, taking part in the basal tuberosities, basipterygoid processes, occipital condyle and the (not preserved) cultriform process (Fig. 3A₁, A₃). This complex is distorted, showing a marked inclination toward the right flank. The basioccipital forms most of the occipital condyle. The occipital condyle is subspheroidal and is slightly flattened dorsally, adjacent to the foramen magnum. The foramen magnum is subcircular, with a greater dorsoventral than mediolateral diameter. The highest point of the braincase in the supraoccipital protuberance and the foramen magnum is located in a vertical plane, showing the occipital condyle caudoventrally inclined of 135° with regard to this plane.

The only element that forms the basal tuberosities is the basioccipital. The basal tuberosities are well developed and show a subcircular contour in lateral view. Between the basal tuberosities lies a shallow depression that is immediately ventral to the occipital condyle and has a hole, which is probably not a natural opening.

The basipterygoid processes are completely formed by the basisphenoid. Due to deformation, it is not possible to appreciate the divergence degree between the two processes. These processes have a subcircular contour; in section the foramina for exit of the carotids are observed. Ventrally, between the basipterygoid processes, there is a deep fossa defined by a crest that joins the processes. This fossa defines the floor of the pituitary cavity.

Quadrate.—The right quadrate is complete; only part of the left is preserved (Fig. 5A₁, A₂). The quadrate measures 19 cm high from the condylar head to the distal articular surface. The dorsal process bears the condylar head, which articulates with the paroccipital process and the squamosal. The quadrate is short and straight, except in its distal end, where a light caudomedially inclination can be seen (Fig. 5). In caudal view, the main body of the quadrate possesses a very deep fossa, of

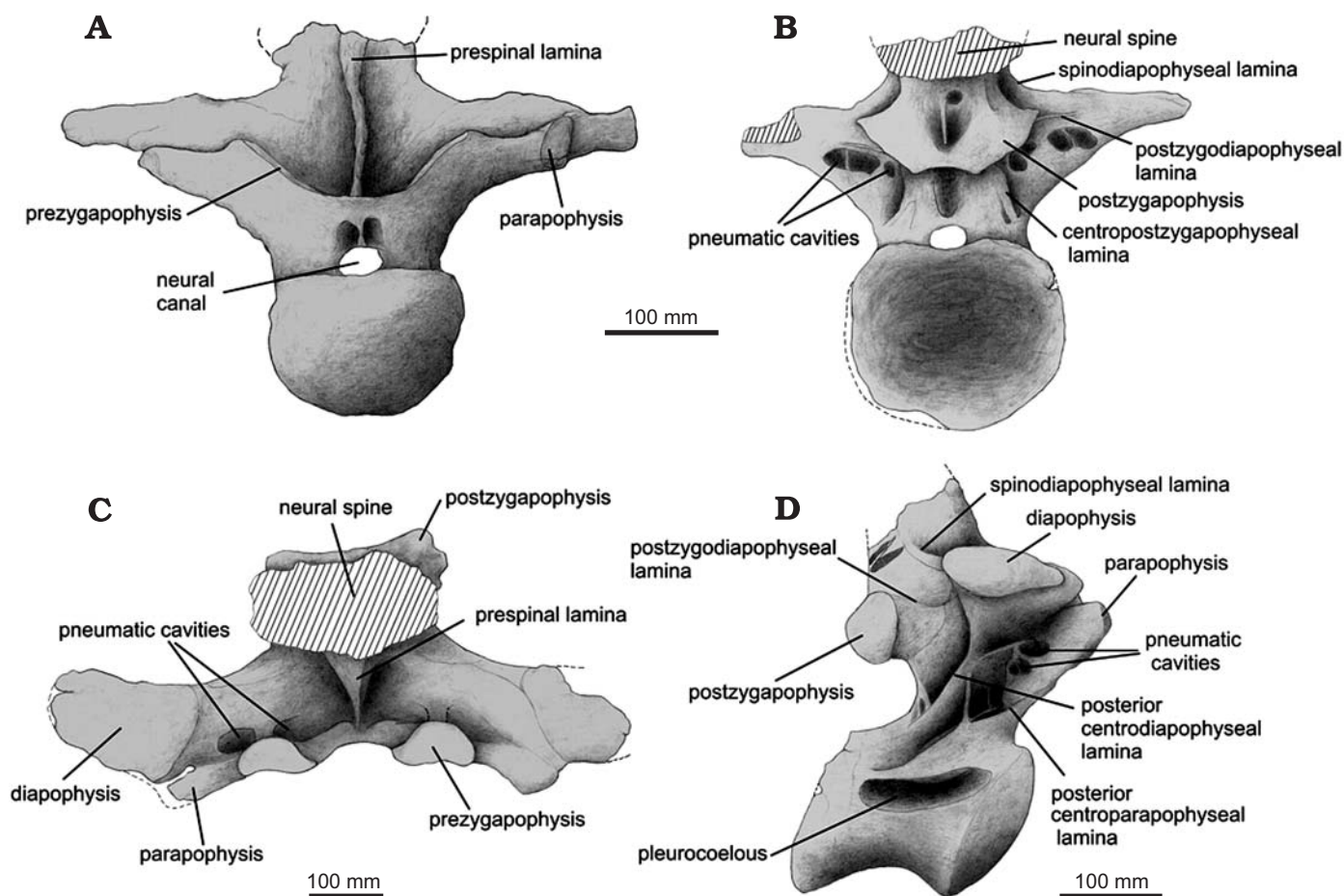


Fig. 7. Posterior dorsal vertebra of the titanosaur sauropod *Nambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype), in anterior (A), posterior (B), dorsal (C), and lateral (D) views.

kidney shape contour, 3 cm wide (mediolaterally) by 7.5 cm high (dorsocaudally). The lateral and medial walls of the fossa are 0.4 cm thick.

The main body of the quadrate in lateral view expands rostrally, and its maximum total length is 8.9 cm. This portion corresponds to the process for the pterygoid articulation, and this process has a triangular form and its mediolateral thickness is very thin. Ventrally to the fossa, this element is projected 4 cm, forming the articular condyle, which is mediolaterally compressed, with a concave lateral surface and a convex medial surface.

Vertebrae

Anterior cervical vertebra.—Only an anterior cervical vertebra, not well preserved and dorsoventrally crushed, is known (Fig. 6). The centrum is long and cylindrical, with an incomplete anterior articulation region. The neural spine is low. The postzygapophyses possess an articular surface that is almost horizontal and that surpasses the posterior border of the centrum, as in *Saltasaurus* (Powell 1992; 2003), and unlike several titanosaurs such as *Rinconosaurus* (Calvo and González Riga 2003), *Mendozasaurus* (González Riga 2005), *Alamosaurus* (Lehman and Coulson 2002) and *Trigonosaurus pricei*

(Campos et al. 2005), which have short postzygapophyses that do not surpass the vertebral centrum. The postzygapophyses are joined by an interpostzygapophyseal lamina, forming a deep postspinal fossa. Remains of the capitulum and tuberculum of both cervical ribs are preserved, fused to the diapophyses and parapophyses of the centrum.

Posterior dorsal vertebra.—Among the materials corresponding to the dorsal region of the axial skeleton, only a posterior dorsal vertebra was recovered (Fig. 7). The neural spine is incomplete in its distal extreme. According to comparisons with specimens that have complete and well-preserved dorsal series such as *Trigonosaurus* (Campos et al. 2005) and an unpublished titanosaur specimen MAU-Pv-CO-439, regarded as a posterior dorsal (probably the seventh). The centrum is opisthocoelous, wider than high, with the anterior and posterior articular surfaces inclined anterodorsally (Fig. 7A₄). As in most of the well-known titanosaurs, it lacks a hyposphene–hypantrum complex, unlike *Andesaurus delgadoi* (Calvo and Bonaparte 1991), *Argentinosaurus huinculensis* (Bonaparte and Coria 1993) and *Epachthosaurus sciuttoi* (Martínez et al. 2004). The pleurocoel is dorsally placed, and it is distinguished for being very deep, and occupying nearly half of the vertebral centrum. The pleurocoel is dorsally defined by a

very marked convex bony edge, a character considered as autapomorphic for this species (Fig. 7A₄). The spinal sector where the spinodiapophyseal lamina starts to project has a lateral enlargement. The prespinal lamina is very well developed anteriorly, extending to the base of the neural spine. Although the distal portion of the spine has not been preserved, it can be observed that dorsodistally, the prespinal lamina presents a lateral enlargement that coincides with the lateral enlargement of the neural spine (Fig. 7A₁, A₃). Probably, the neural spine had a rhomboidal aspect in anterior view. This character is similar in *Barrosasaurus casamiquelai* (Salgado and Coria 2009), which present small lateral expansions of the neural spine, considered to be probably homologous to the aliform processes of *Epachthosaurus* (Salgado and Coria 2009). The distal enlargement of the prespinal lamina is absent in other well-known titanosaurs, and it is here considered as an autapomorphic character for this species. The prezygapophyses are strongly inclined dorsomedially; their articular surface has a kidney shape, very wide and with a sharp and prominent anteromedial border (Fig. 7A₃). The articular surface of the prezygapophyses in well-known titanosaurs have a subcircular or subelliptical contour, therefore the presence of prezygapophyses with a kidney-shaped contour in posterior dorsal vertebrae is considered to be an autapomorphic character for this species. The dorsal surface of the diapophysis is flat, as occurs in posterior dorsal vertebrae of titanosaurs, such as *Saltasaurus* (Powell 1992; 2003), *Lirainosaurus astibiae* (Sanz et al. 1999), *Rinconosaurus* (Calvo and González Riga 2003) and *Muyelensaurus* (Calvo et al. 2007a). Ventrally, the diapophysis is reinforced by the posterior centrodiapophyseal (pcdl) and accessory posterior centrodiapophyseal laminae (apcdl), which are connected. The accessory lamina of the posterior centrodiapophyseal lamina joins ventrally with the anterior centroparapophyseal lamina (acpl), forming a deep cavity. The parapophyses are placed before the diapophyses and almost at the same level so that the paradiapophyseal lamina is not clearly distinguished. Posterior to the anterior centroparapophyseal (acpl) and posterior centrodiapophyseal laminae (pcdl) a series of pneumatic cavities of different size and with subcircular to subelliptical contour can be observed (Fig. 7A₂, A₄). These cavities are not known in any other well-known titanosaurs, and their presence is considered as an autapomorphic feature. The postzygapophyses possess an articular surface with a subelliptic contour and they are strongly inclined medially. Laterally, the postzygapophyses join the diapophyses to form a postzygodiapophyseal lamina (podl); this lamina does not join to the spinodiapophyseal lamina (spdl), but rather, it is over and near the pneumatic cavities previously described (Fig. 7A₂, A₄). The postzygodiapophyseal lamina (podl) is present in other titanosaurs such as *Neuquensaurus* (Salgado et al. 2005), *Muyelensaurus* (Calvo et al. 2007a), *Epachthosaurus* (Martínez et al. 2004), and an unpublished titanosaur specimen (MAU-PV-CO-439) collected 50 km south of Rincon de los Sauces, Neuquen, Argentina (R.A. Coria, personal communication 2009). This lamina is scarcely developed in *Trigonosaurus* (Campos et al. 2005)

and absent in *Opisthocoelicaudia skarzynskii* (Borsuk-Białynicka 1977). Ventrally, the postzygapophyses are reinforced by a centropostzygapophyseal lamina (cpol) which join to the posterior centrodiapophyseal lamina (pcdl) in the posterior border of the neural arch. The postzygapophysis is dorsally connected to the spine by a ramification of the spinopostzygapophyseal lamina (spol) (Wilson 1999), generating a fossa between the two laminae. One of the branches, the medial one, is more robust and connects the postzygapophysis with the neural spine, while the other one does it laterally with the spinodiapophyseal lamina (spdl). Posteriorly, the cavity between the postzygapophyses is divided by a short and a scarcely developed postspinal lamina.

Caudal vertebrae

Eleven anterior caudal vertebrae were recovered, including a series of three articulate elements (Fig. 8), and six middle caudal vertebrae, which include two pairs of articulated vertebrae, have been found (Fig. 9).

In most of the anterior caudal vertebrae are observed very evident sutures corresponding to the fusion between the centra, the neural arches and the transverse processes. Additionally, some disarticulated transverse processes and caudal vertebrae without the neural arch are known. In the middle caudals, the sutures between the vertebral centra and the neural arches are also present, but they are less evident. The sequence of the neurocentral suture closure is one criterion for the determination of the ontogenetic stage in extant crocodylians (Brochu 1996). For this reason, the material of *Nambuenatitan* is regarded as that of a subadult specimen.

Anterior caudal vertebrae.—The first caudal vertebra (Fig. 8A₁–A₃), which is laterally deformed, has a strongly procoelous centrum as in the remainder of the recovered caudal vertebrae. The centrum is compressed anteroposteriorly, with its ventral and lateral faces anteroposteriorly concave. This is in contrast with the condition in titanosaurs such as *Baurutitan britoi* (Kellner et al. 2005), *Alamosaurus* (Lehman and Coulson 2002), *Pellegrinisaurus powelli* (Salgado 1996) and *Neuquensaurus* (Powell 2003; Salgado et al. 2005), where the first caudal vertebra is biconvex. The neural arch of *Nambuenatitan* is high and shows basally a suture between it and the centrum. (Fig. 8A₁, A₃). The prezygapophyses are incomplete; nevertheless, the preserved portion of the left prezygapophysis suggests that they were dorsoventrally compressed. The transverse processes are slightly projected posteriorly and join the prezygapophyses to form a prezygadiapophyseal lamina with a sharp border. The neural spine is straight, robust and transversely wide, generally similar to that observed in *Adamantisaurus mezzalirai* (Santucci and Bertini 2006), but differing in having two bulbous lateral prominences in its distal extreme (Fig. 8A₁, A₃). The spine is reinforced by the robust prespinal and postspinal laminae that extend to the base of the arch, similar to *Adamantisaurus* (Santucci and Bertini 2006). The spine is connected to the prezygapophyses to form a spinoprezygapophyseal lamina, and to the postzygapophyses to form a spinopostzygapophyseal lamina. These lami-

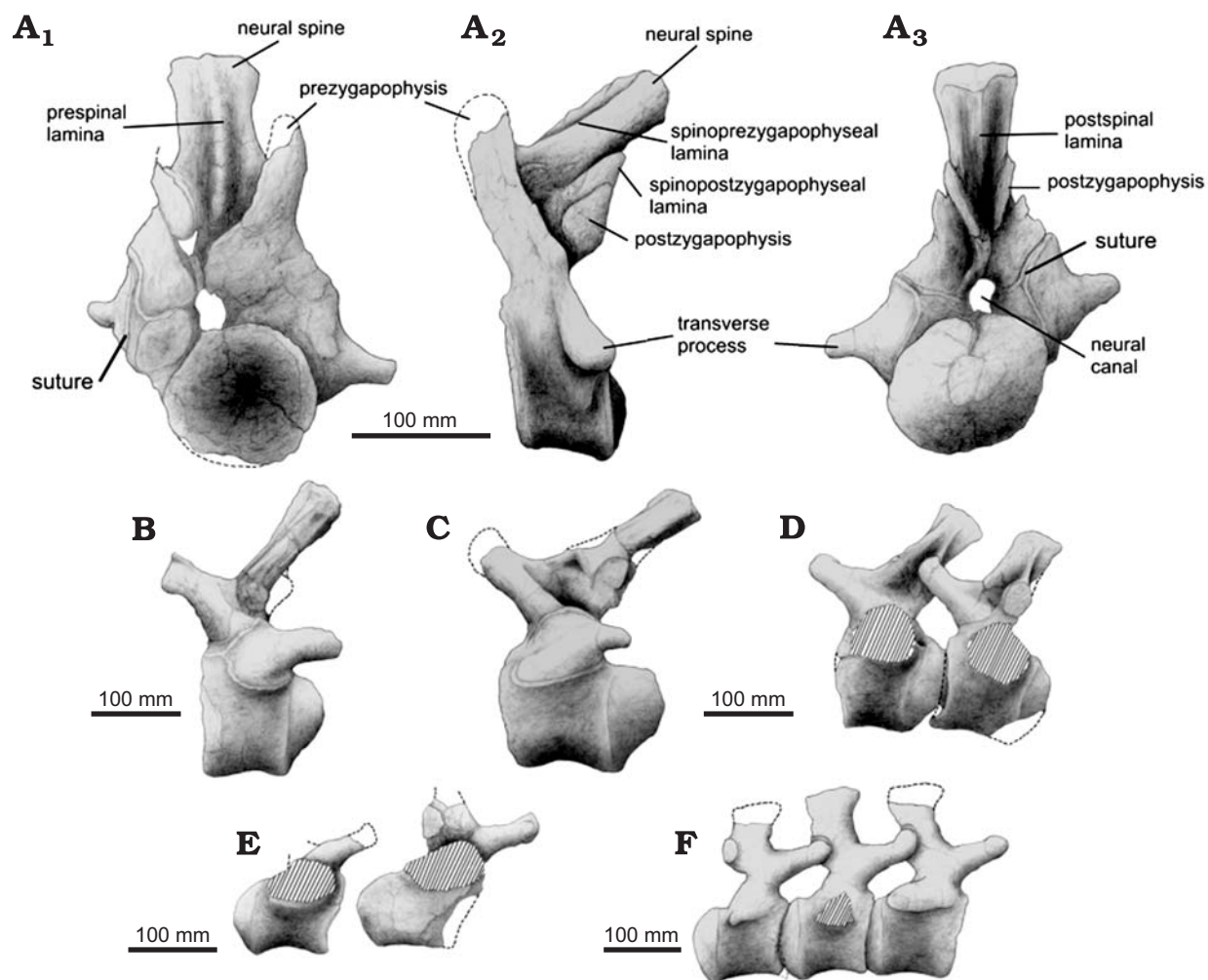


Fig. 8. Anterior caudal vertebrae of the titanosaur sauropod *Narambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype). **A**. First caudal vertebra in anterior (**A₁**), lateral (**A₂**), and posterior (**A₃**) views. **B–F**. Anterior caudal vertebrae in left lateral (**B**, **C**, **D**) and in right lateral (**E**, **F**) views.

nae are positioned laterally in the neural spine, and they differ strongly from *Mendozasaurus* (González Riga 2003), in that they extend practically up to the distal extreme of the spine. The articular surfaces of the postzygapophyses are wide and of subtriangular contour, with the biggest angle ventrally orientated (Fig. 8A₂). The postzygapophyses are joined ventrally, forming a robust bridge on the neural canal, with a deep postspinal fossa between the two.

The centra of the remainder anterior caudal vertebrae (Fig. 8B–F) are proportionally wider than high. The lateral and ventral faces are anteroposteriorly concave. The anterior caudal vertebrae lack a ventral keel, unlike the condition in *Bonatitan reigi* (Martinelli and Forasiepi 2004). The neural arch is robust and low, positioned in the anterior portion of the centra, and anteriorly inclined. The transverse processes are prominent and posterolaterally projected. The prezygapophyses are robust and relatively short, anterodorsally projected to a very marked angle. Between them, there is a deep prespinal fossa delimited by short spinoprezygapophyseal laminae. The articular surfaces of the prezygapophyses are very wide, with an elliptical shape, and medially orientated.

The postzygapophyses are wide and have a subtriangular contour; they are medially oriented and are joined to the base of the spine for a short process. The neural spine in the first anterior caudal is more inclined than in *Adamantisaurus* (Santucci and Bertini 2006). In the articulated series of three caudals (Fig. 8 F), the neural spine is laterally compressed, with a big anteroposteriorly development. The most anterior caudal has a neural spine reinforced by a well developed spinoprezygapophyseal lamina that extends up to the distal portion of the spine, and posterior for a short spinopostzygapophyseal lamina. With the exception of the first caudal, where the prespinal lamina is well developed up to the base of the spine, following anterior caudals have a prespinal lamina that is smoothly developed and disappears toward the middle part of the spine. On the contrary, the postspinal lamina is robust, distally enlarged as in *Adamantisaurus* (Santucci and Bertini 2006).

Middle caudal vertebrae.—The middle caudal vertebrae are procoelous, characterized by centers of quadrangular aspect both in anterior and lateral views, with slender prezygapo-

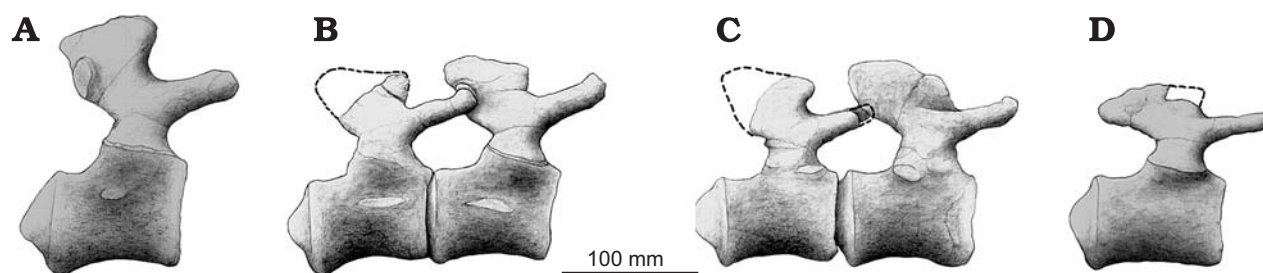


Fig. 9. Middle caudal vertebrae of the titanosaur sauropod *Nambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype). A–D. Middle caudals in right lateral views.

physes and neural arches (Fig. 9). This condition is interpreted as an autapomorphic feature of this taxon. The posterior condyle is prominent, with a centrally-placed apex. In *Mendozasaurus* (González Riga 2003), the posterior articular facet of the caudal centra presents surfaces practically planar, with reduced articular condyles that are dorsally displaced. The neural arch is located in the anterior portion of the vertebral centra and slightly inclined anteriorly. The prezygapophyses are thin, laterally compressed and antero-dorsally projected. The articular surfaces of the prezygapophyses are subcircular and are located practically parallel to the axial plane. In anterior view and between the prezygapophyses, a small prespinal fossa is observed. The neural spine is laterally compressed and posteriorly elongated, similar to what is observed in *Epachthosaurus* (Martínez et al. 2004). Nevertheless, in *Nambuenatitan* it is more dorsoventrally and posteriorly developed (Fig. 9C, D). The middle caudal vertebrae are procoelous, characterized by a square aspect in both anterior and lateral views, with slender prezygapophyses and neural arches (Fig. 9B–D), a condition interpreted as an autapomorphic feature of this species.

Appendicular skeleton

Sternal plate.—A left sternal has the typical semilunar form present in titanosaurs (Fig. 10D) (Salgado et al. 1997). Moreover, it shows the medial inside border in its half portion, and the notorious concave (external) lateral border. It is robust in its lateral border and very thin toward the medial border. The posterior border is rounded, differing from the relatively straight border presents in *Mendozasaurus* (González Riga 2003), *Malawisaurus* (Jacobs et al. 1993; Gomani 2005) and *Alamosaurus* (Gilmore 1946). The proximal end is prominent and robust, rugose in the anteroventral crest, as in MAU-Pv-PH-449 (Filippi et al. in press).

Coracoid.—Although the right coracoid is incomplete, it can be inferred that it had a quadrangular shape, as typically in titanosaurs. (Fig. 10C). The lateral surface is convex and the medial one is concave as in *Isisaurus colberti* (Jain and Bandyopadhyay 1997) and *Malawisaurus* (Gomani 2005). The articulation for the scapula has a slightly concave surface, while the surface corresponding to the glenoid cavity is robust and rough. The coracoid foramen is elliptic and it is restricted to the dorsal border as in *Malawisaurus*.

Table 1. Measurements of vertebrae and appendicular skeleton of *Nambuenatitan palomoi*. All measurements in cm.

Vertebra	Repository number	Vertebra height	Centrum height	Centrum wide	Centrum length
Anterior cervical	MAU-Pv-425/17	17*	5.5*	17.3*	37.4*
Posterior dorsal	MAU-Pv-425/28	39*	16.5	17	19.4
First caudal vertebra	MAU-Pv-425/01	38.5	14*	16*	9*
Anterior caudal	MAU-Pv-425/04	33	13.3	17	15.5
Anterior caudal	MAU-Pv-425/03	30.5	12	18.3	14
Anterior caudal	MAU-Pv-425/02	29.5	10.4*	16.5*	13.5*
Anterior caudal	MAU-Pv-425/10	23.5	9.5	9	12
Middle caudal	MAU-Pv-425/08	19	8	7.5	11.8
Middle caudal	MAU-Pv-425/09	13.5	6.3	6	10.8

Appendicular skeleton	Length	Minimum diaphysis width
Sternal plate	53.7	25.7
Ulna	60.5	8
Humerus	92	12
Femur	81*	16*
Pubis (left)	77	17
Ischium	35*	?

* distorted or incomplete material

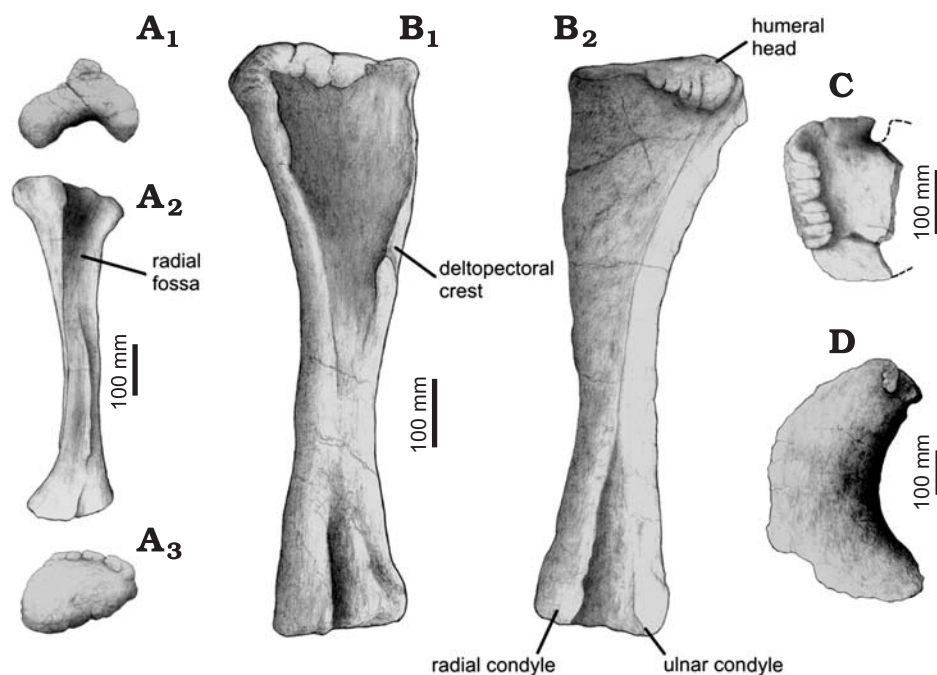


Fig. 10. Anterior appendicular skeleton of the titanosaur sauropod *Narambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype). **A.** Left ulna in lateral (A₁), proximal (A₂), and distal (A₃) views. **B.** Left humerus in anterior (B₁) and posterior (B₂) views. **C.** Right coracoid in lateral view. **D.** Left sternal plate in anterior view.

Humerus.—The left humerus is in a very good state of preservation, corresponding to a graceful bone with not very expanded ends, although its proximal end is more developed than the distal one (Fig. 10B₁, B₂). The head of the humerus is medially less projected than in *Alamosaurus* (Lehman and Coulson 2002). In posterior view, the humerus head is prominent and subspherical (Fig. 10B₂); this character is also present in *Brachiosaurus brancai* (Janensch, 1950) and it is strongly developed in *Ligabuesaurus leanzai* (Bonaparte et al. 2006). The dorsal margin of the proximal end is lightly sigmoid, similar to what has been described for *Saltasaurus* (Powell 1992; 2003). Nevertheless, in *Saltasaurus* the curve is very marked and the proximal end of the humerus is much expanded mediolaterally. The deltopectoral crest extends up to the half portion of the diaphysis, and it is medially inclined (Fig. 10B₁), differing from the strong medial projection present in *Gondwanatitan faustoi* (Kellner and Azevedo 1999). Anteriorly, delimited by the deltopectoral crest and the lateromedial border, a deep fossa is observed that extends up to the half part of the diaphysis. The radial and ulnar condyles are slightly twisted with regard to the proximal end of the humerus. In the distal end, two intercondylar grooves are observed, one anterior and one posterior that is deeper.

Ulna.—The left ulna is relatively robust and proximally more expanded (Fig. 10A). The proximal end is triradiate, with an olecranon process less prominent than in *Epachthosaurus* (Martínez et al. 2004) and *Saltasaurus* (Powell 1992; 2003). The distal end has a semicircular contour with rounded borders. The medial face is concave and proximally wider, it possesses a deep depression. The radial side distally has a crest or strongly developed longitudinal tuberosities.

Pubis.—Both pubes are in a very good state of preservation, the right one incomplete. They are robust in the lateral border, but medially become more laminar. The articular surface

for the iliac pedicel is transversely wide, robust and with a subelliptic contour. The acetabulum is reduced as in *Rinconosaurus* (Calvo and González Riga 2003). The pubic foramen is closed, big and with a subcircular contour (Fig. 11B). As in *Saltasaurus* (Powell 1992; 2003), that foramen is located near the angle that forms the articular surface for the ischium and the acetabular region of the pubis. The articular surface for the ischiatic pedicel is very extensive and have a concave border. The pubic symphysis is straight and short. The distal end of the pubis is transversely wide, robust and with a subquadrangular contour in anterior view (Fig. 11B). The lateral border of the pubis is concave with the distal end straight and laterally oriented. The medial border of the pubis is also straight.

Ischium.—The proximal portion of the left ischium (Fig. 11C) has been recovered. Only the iliac pedicel has been completely preserved. It is slender and laterally inclined, with a rounded articular surface. The contact surface with the pubis is not complete, but it is inferred that it was not extensive. The diaphysis of the ischium is very narrow.

Femur.—From the left femur, only the distal end and the half of the diaphysis that preserves the fourth trochanter have been found (Fig. 11A). The transverse section of the diaphysis is anteroposteriorly compressed, while the distal end is slightly laterally expanded. The fourth trochanter is well developed; medially, it has a flat surface and has a subelliptical contour. In anterior view, an incipient crest is observed distally on the tibial condyle, defining medially the intercondylar anterior groove. In posterior view, the tibial condyle is very well developed and laterally compressed. The condyle is transversely wider and more robust than the epicondyle. Between the tibial and the fibular condyles, a wide and deep posterior intercondylar groove is observed. In ventral view, the condyles are medially inclined.

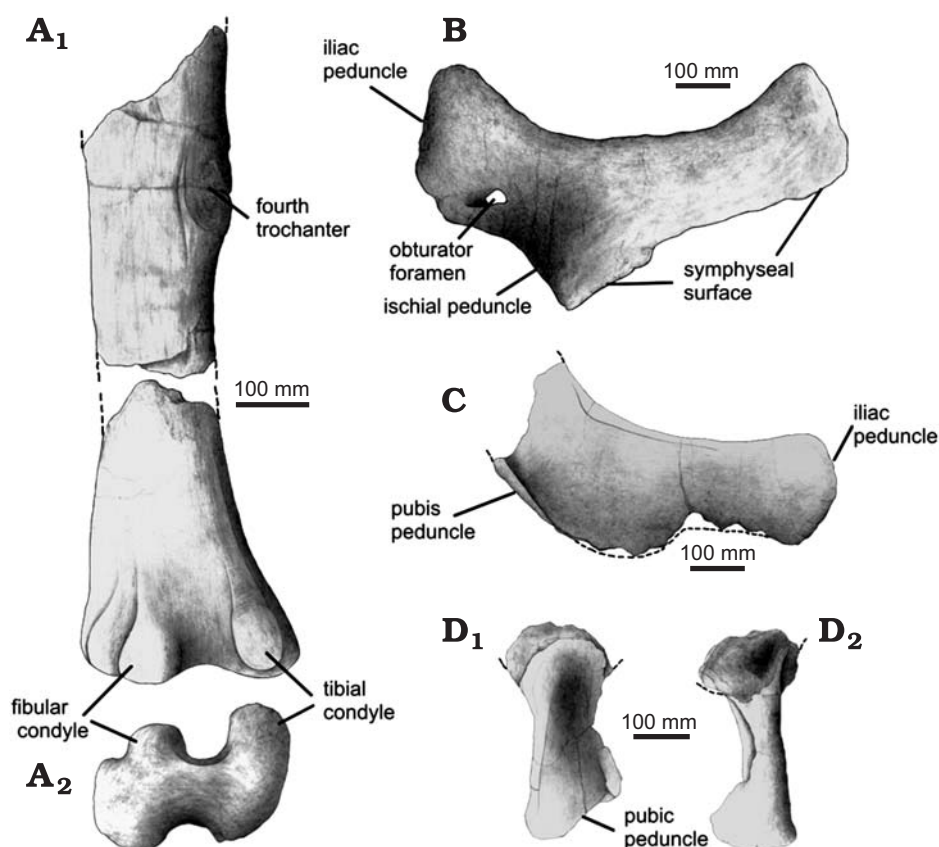


Fig. 11. Posterior appendicular skeleton of the titanosaur sauropod *Nambuenatitan palomoi* gen. et sp. nov. from the Campanian (Late Cretaceous) Anacleto Formation of Neuquén Province, Argentina; MAU-Pv-N-425 (holotype). **A**. Left femur in posterior (A_1) and distal (A_2) views. **B**. Left pubis in ventral view. **C**. Left ischium in ventral view. **D**. Peduncle of the left ilium in posterolateral (D_1) and medial (D_2) views.

Phylogenetic relationships and discussion

The phylogenetic relationships of *Nambuenatitan palomoi* gen. et sp. nov. have been analyzed with respect to 21 other taxa through a parsimonious cladistic analysis based on 65 characters (see Appendix 1). The data matrix employed was that of Calvo et al. (2007a), which in turn was based on characters proposed by other researchers in previous works (McIntosh 1990; Salgado et al. 1997; Upchurch 1998, 1999; Wilson and Sereno 1998; Curry Rogers and Forster 2001; Wilson 2002; González Riga 2003; Calvo and González Riga 2003; Franco-Rosas et al. 2004; Bonaparte et al. 2006), with the inclusion of new taxa such as *Argentinosaurus huinculensis* (Bonaparte and Coria 1993) and *Bonatitan reigi* (Martinelli and Forasiepi 2004).

In this analysis, *Camarasaurus grandis* (Cope, 1877) is considered as outgroup, while *Brachiosaurus brancai* (Janensch 1950), *Chubutisaurus insignis* (Del Corro 1975; Salgado 1993), *Andesaurus delgadoi* (Calvo and Bonaparte 1991), *Argentinosaurus huinculensis* (Bonaparte and Coria 1993), *Malawisaurus dixeyi* (Jacobs et al. 1993; Goman 2005), *Rinconosaurus caudamirus* (Calvo and González Riga 2003), *Muyenlensaurus pecheni* (Calvo et al. 2007a), *Mendosaurus neguyelap* (González Riga 2003), *Futalognkosaurus dukei* (Calvo et al. 2007b, c), *Epachthosaurus sciuttoi* (Martínez et al. 2004), *Lirainosaurus astibiae* (Sanz et al.

1999), *Opisthocoelicaudia skarzynskii* (Borsuk-Białynicka 1977), *Alamosaurus sanjuanensis* (Gilmore 1946; Lehman and Coulson 2002), *Aeolosaurus rionegrinus* (Salgado and Coria 1993; Salgado et al. 1997; Powell 2003), *Gondwanatitan faustosi* (Kellner and Azevedo 1999), *Rapetosaurus krausei* (Curry Rogers and Forster 2001, 2004), *Neuquensaurus australis* (Huene 1929; Powell 2003; Salgado et al. 2005), *Bonatitan reigi* (Martinelli and Forasiepi 2004), *Rocasaurus muniozi* (Salgado and Azpilicueta 2000), *Saltasaurus loricatus* (Bonaparte and Powell 1980; Powell 1992, 2003) and *Nambuenatitan palomoi* gen. et sp. nov. form the ingroup.

The data matrix was analyzed with TNT, version 1.1 (Goloboff et al. 2003); multistate characters were considered unordered. The analysis generated only one most parsimonious tree with 114 steps and relatively high consistency and retention indexes (C.I. = 0.71; R.I. = 0.75) (Fig. 12).

According to this analysis, *Nambuenatitan palomoi* gen. et sp. nov. is a member of the following nested series of taxa based on apomorphies as indicated: Titanosauriformes (Salgado et al. 1997): anterior neural cervical spines non-bifurcated (17.1). Titanosauria (Bonaparte and Coria 1993): presence of centroparapophyseal lamina in the posterior dorsal vertebrae (26.1) and of an accessory posterior, centrodiaepophyseal lamina in dorsal vertebrae (27.1), the absence of hyposphene-hypantrum articulations in dorsal vertebrae (28.1), and the eye-shaped pleurocoels in dorsal vertebrae (29.1). Lithostrotia (Upchurch et al. 2004): anterior caudals

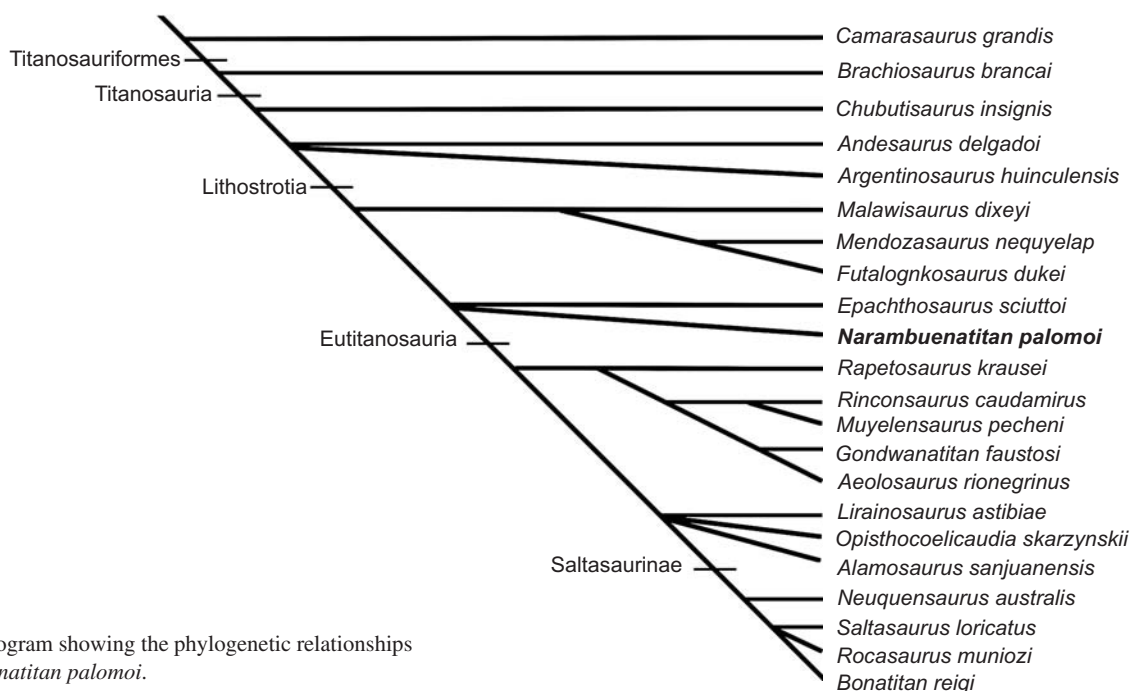


Fig. 12. Cladogram showing the phylogenetic relationships of *Narambuenatitan palomoi*.

have strongly procoelous centra with prominent condyles (37.1) and the semilunar sternal plate (52.1). Non-Eutitanosauria (Sanz et al. 1999): lack of osteoderms (65.0). In the cladogram, *Narambuenatitan* forms an unresolved trichotomy with *Epachthosaurus* and Eutitanosauria. This node is supported by the presence of a laminar and posterior elongated neural spine in middle caudal vertebrae (43.1), a character also present in *Andesaurus*, *Malawisaurus*, and *Mendozasaurus*. Nevertheless, *Narambuenatitan* differs from *Epachthosaurus* in the absence of hypospheno-hypantrum in anterior caudals, a character considered as autapomorphic for the last genus (Martínez et al. 2004).

This analysis confirms the membership of *Bonatitan reigi* in the Saltasaurinae group, as Martinelli and Forasiepi (2004) suggested, based on the following characters: anterodorsal border of the neural spine in middle caudal vertebrae, posterior located on regarding the anterior border of the postzygapophyses (37.1), and distal condyle of the femur anteriorly expanded (64.1).

Acknowledgements

Our acknowledgements to Leonardo Salgado (MUCPV), Jeffrey A. Wilson (Museum of Paleontology and Department of Geological Sciences, University of Michigan, Michigan, USA), José Ignacio Canudo (Grupo Aragosaurus – IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Spain), Andrea B. Arcucci (Universidad Nacional de San Luis, San Luis, Argentina), and Xavier Pereda-Suberbiola (Universidad del País Vasco/EHU, Facultad de Ciencia y Tecnología, Departamento Estratigrafía y Paleontología, Bilbao, Spain) for the critical reading and constructive comments, to Paulina Carabajal (CONICET – Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina) for her attendance and discussion on punctual aspects of the software used in the presented phylogenetic analysis, to the technicians

Carlos Fuentes, Ademar Paillán, and Salvador Palomo (MAU) for their active participation during the field works and the preparation of the materials, to the Municipalidad de Rincón de los Sauces for the logistical support provided during 2005–2006. The illustrations of the postcranial material were realized by Salvador Palomo; and finally, our particularly grateful to Cecilia Sendón and Mariela Alonso (Rincón de los Sauces, Argentina) for the help with the final versions of the manuscript.

References

- Apesteguía, S. 2004. *Bonitasaura salgadoi* gen. et sp. nov.: A break sauropod from the Late Cretaceous of Patagonia. *Naturwissenschaften* 91: 493–497.
- Berman, D.S. and McIntosh, J.S. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History* 8: 1–35.
- Bonaparte, J.F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique Moyen de Cerro Cónor (Chubut, Argentine). *Annales de Paléontologie* 72 (4): 325–386.
- Bonaparte, J.F. and Coria, R.A. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano–Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana* 30: 271–282.
- Bonaparte, J.F., Gonzalez Riga, B., and Apesteguía, S. 2006. *Ligabue-saurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* 27: 364–376.
- Bonaparte, J.F. and Powell, J.E. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, North-western Argentina (Sauropoda–Coelurosauria–Carnosauria–Aves). *Mémoires de la Société Géologique de France, N.S.* 59: 18–28.
- Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia* gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* 37: 5–64.
- Britt, B.B. and Naylor, B.G. 1994. An embryonic *Camarasaurus* (Dinosauria, Sauropoda) from the Upper Jurassic Morrison Formation (Dry Mesa Quarry, Colorado). In: K. Carpenter, K.F. Hirsch, and J.R. Horner

- (eds.), *Dinosaur Eggs and Babies*, 256–264. Cambridge University Press, New York.
- Brochu, C.A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* 16: 49–62.
- Calvo, J.O. and Bonaparte, J.F. 1991. *Andesaurus delgadoi* n.g. n. sp. (Saurischia, Sauropoda) dinosaurio Titanosauridae de la Formación Río Limay (Albiano–Cenomaniano), Neuquén, Argentina. *Ameghiniana* 28: 303–310.
- Calvo, J.O. and González Riga, B.J. 2003. *Rinconsaurus caudamirus* gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geológica de Chile* 30: 333–353.
- Calvo, J.O. and González Riga, B.J. 2004. A new braincase from Neuquén Province, northern Patagonia, Argentina. *Ameghiniana* 41 (Suplemento): 38R.
- Calvo, J.O. and Kellner, A.W. 2006. Description of a sauropod dinosaur braincase (Titanosauridae) from the Late Cretaceous Rio Colorado Subgroup, Patagonia. *Anais da Academia Brasileira de Ciências* 78: 175–182.
- Calvo, J.O., Coria, R.A., and Salgado, L. 1997. Uno de los más completos titanosáuridos (Dinosauria-Sauropoda) registrados en el mundo. *Ameghiniana* 34: 534.
- Calvo, J.O., González Riga, B.J., and Porfiri, J. 2007a. A new titanosaur sauropod from Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* 65: 487–504.
- Calvo, J.O., Porfiri, J.D., González Riga, B.J., and Kellner, A.W.A. 2007b. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências* 79 (3): 1–13.
- Calvo, J.O., Porfiri, J.D., González Riga, B.J., and Kellner, A.W.A. 2007c. Anatomy of *Futalognkosaurus dukei* Calvo, Porfiri, González Riga & Kellner, 2007 (Dinosauria, Titanosauridae) from the Neuquén Group (Late Cretaceous), Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* 65 (4): 511–526.
- Campos, D.A., Kellner, A.W.A., Bertini, R.J., and Santucci, R.M. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro* 63 (3): 565–593.
- Cazau, L.B. and Uliana, M.A. 1973. El Cretácico Superior continental de la Cuenca Neuquina. *5th Congreso Geológico Argentino, Buenos Aires, Actas* 3: 131–163.
- Chatterjee, S. and Zheng, Z. 2002. Cranial anatomy of *Shunosaurus*, a basal sauropod dinosaur from the Jurassic of China. *Zoological Journal of the Linnean Society* 136: 145–169.
- Chatterjee, S. and Zheng, Z. 2005. Neuroanatomy and dentition of *Camarasaurus lentus*. In: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaur*, 199–211. Indiana University Press, Bloomington.
- Collinson, J.D. 1986. Alluvial sediments. In: H.G. Reading (ed.), *Sedimentary Environments and Facies, Second Edition*, 20–62. Blackwell Science Publications, Oxford.
- Cope, E.D. 1877. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontological Bulletin* 25: 5–10.
- Curry Rogers, K. and Forster C.A. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. *Nature* 412: 530–534.
- Curry Rogers, K. and Forster, C.A. 2004. The skull of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 24: 121–144.
- Del Corro, G. 1975. Un nuevo saurópodo del Cretácico Superior. *Chubutisaurus insignis* gen. et sp. nov. (Saurischia-Chubutisauridae nov.) del Cretácico Superior (Chubutiano) Chubut, Argentina. *Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán* 2: 229–240.
- Dingus, L., Clark, J., Scott, G.R., Swisher, C.C. III, and Coria, R. 2000. Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates* 3290: 1–11.
- Filippi, L.S. and Garrido, A.C. 2008. *Pitekunsaurus macayai* gen. et sp. nov., nuevo titanosaurio (Saurischia, Sauropoda) del Cretácico Superior de la Cuenca Neuquina, Argentina. *Ameghiniana* 45: 575–590.
- Filippi, L.S., Canudo, J. I., Salgado, L., Garrido, A., García, R., Cerda, I.A. and Otero, A. 2011. A new sauropod: *Petrobrasaurus puestohernandezii* gen. et sp. nov. from the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces, Neuquén (Argentina). *Geologica Acta* 9 (1): 1–12.
- Franco-Rosas, A.C., Salgado, L., Rosas, C.F., and Carvalho, I.S. 2004. Nuevos materiales de titanosaurios (Sauropoda) en el Cretácico Superior de Mato Grosso, Brasil. *Revista Brasileira de Paleontología* 7: 329–336.
- García, R., Paulina-Carabajal, A., and Salgado, L. 2008. Un nuevo basicráneo de titanosaurio de la Formación Allen (Campaniano–Maastrichtiano), Provincia de Río Negro, Patagonia, Argentina. *Geobios* 41: 625–633.
- Gilmore, C.W. 1946. Reptilian fauna of the North Horn Formation. *United States Geological Survey* 210: 1–15.
- Goloboff, P., Farris, J., and Nixon, K. 2003. *TNT: Tree Analysis Using New Technology. Program and Documentation*. Available from the authors and at www.zmuc.dk/public/phylogeny.
- Gomani, E. 2005. Sauropod dinosaur from the Early Cretaceous of Malawi, Africa. *Palaeontologia Electronica* 8: 1–37.
- González Riga, B.J. 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. *Ameghiniana* 40: 155–172.
- González Riga, B.J. 2005. Nuevos restos fósiles de *Mendozasaurus neguyelap* (Sauropoda, Titanosauria) del Cretácico Tardío de Mendoza, Argentina. *Ameghiniana* 42 (3): 535–548.
- Huene, F. von 1929. Los Saurisquios y Ornithisquios del Cretácico Argentino. *Anales del Museo de La Plata, 2ª Serie* 3: 1–196.
- Jacobs, L.L., Winkler, D.A., Downs W.R., and Gomani, E.M. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology* 36: 523–534.
- Jain, S.L. and Bandyopadhyay, S. 1997. New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. *Journal of Vertebrate Paleontology* 17: 114–136.
- Janensch, W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica* 7 (Supplement): 27–93.
- Kellner, A.W. and Azevedo, S.A. 1999. A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil. *Proceedings of the Second Gondwanan Dinosaur Symposium, National Science Museum Monographs* 15: 111–142.
- Kellner, A.W., Campos, D.A., and Trotta, M.N. 2005. Description of titanosaurid caudal series from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional do Rio de Janeiro* 63 (3): 529–564.
- Kurzanov, S.M. and Bannikov, A.F. 1983. A new sauropod from the Upper Cretaceous of Mongolia [in Russian with English translation]. *Paleontologicheskij zhurnal* 1983 (2): 90–97.
- Lehman, T.M. and Coulson, A.B. 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology* 76: 156–172.
- Martinelli, A.G. and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista Museo Argentino de Ciencias Naturales, Nueva Serie* 6: 257–305.
- Martinez, R.D., Giménez, O., Rodríguez, J., Luna, M., and Lamanna, M.C. 2004. An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciutoi* from the Early Late Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. *Journal of Vertebrate Paleontology* 24: 107–120.
- McIntosh, J.S. 1990. Sauropoda. In: D. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, first edition, 345–401. University of California Press, Berkeley.
- Miall, A.D. 1996. *The Geology of Fluvial Deposits. Sedimentary Facies, Basin Analysis, and Petroleum Geology*. 582 pp. Springer, New York.
- Nowiński, A. 1971. *Nemegtosaurus mongoliensis* nov. gen., nov. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeontologia Polonica* 25: 57–81.
- Paulina Carabajal, A. and Salgado, L. 2007. El basicráneo de un titanosaurio (Dinosauria, Sauropoda) del Cretácico Superior del norte de Patagonia:

descripción y aportes al conocimiento del oído interno de los dinosaurios. *Ameghiniana* 44: 109–120.

Powell, J.E. 1979. Sobre una asociación de dinosaurios y otras evidencias de vertebrados del Cretácico Superior de la región de La Candelaria, Provincia de Salta, Argentina. *Ameghiniana* 16: 191–204.

Powell, J.E. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior del noroeste Argentino. In: J.L. Sanz and A.D. Buscalioni (eds.), *Los Dinosaurios y Su Entorno Biótico*, 165–230. Instituto “Juan de Valdés”, Cuenca.

Powell, J.E. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum, Launceston* 111: 1–173.

Salgado, L. 1993. Comments on *Chubutisaurus insignis* Del Corro (Saurischia, Sauropoda). *Ameghiniana* 30: 265–270.

Salgado, L. 1996. *Pellegrinisaurus powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, north-western Patagonia, Argentina. *Ameghiniana* 33: 355–365.

Salgado, L. and Azpilicueta, C. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la Provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana* 37: 259–264.

Salgado, L. and Calvo, J.O. 1997. Evolution of titanosaurid sauropods. II The cranial evidence. *Ameghiniana* 34: 33–48.

Salgado, L. and Coria, R.A. 1993. El género *Aeolosaurus* (Sauropoda-Titanosauridae) en la Formación Allen (Campaniano–Maastrichtiano) de la Provincia de Río Negro, Argentina. *Ameghiniana* 30: 119–128.

Salgado, L. and Coria, R.A. 2009. *Barrosasaurus casamiquelai* gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Anacleto Formation (Late Cretaceous: early Campanian) of Sierra Barrosa (Neuquén, Argentina). *Zootaxa* 2222: 1–16.

Salgado, L., Apesteguía, S., and Heredia, S.E. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *Journal of Vertebrate Paleontology* 25: 623–634.

Salgado, L., Coria, R.A., and Calvo, J.O. 1997. Evolution of titanosaurid sauropods I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3–32.

Santucci, R.M. and Bertini, R.J. 2006. A new titanosaur from western São Paulo State, Upper Cretaceous Baurú Group, south-east Brazil. *Palaeontology* 49: 59–66.

Sanz, J.L., Powell, J., Le Loeuff, J., Martinez, R., and Pereda Suberbiola, X. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Alava* 14 (Número Especial 1): 235–255.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124: 43–103.

Upchurch, P. 1999. The phylogenetic relationships of the Nemegtosauridae. *Journal of Vertebrate Paleontology* 19: 106–125.

Upchurch, P., Barrett, P.M., and Dodson, P. 2004. Sauropoda. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition, 259–322. University California Press, Berkeley.

White, T.E. 1958. The braincase of *Camarasaurus lentus* (Marsh). *Journal of Paleontology* 32: 477–493.

Wilson, J.A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19: 639–653.

Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 217–276.

Wilson, J.A. 2005. Redescription of the Mongolian sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous sauropod diversity. *Journal of Systematic Palaeontology* 3: 283–318.

Wilson, J.A. and Sereno, P.C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology, Memoir* 5: 1–68.

Appendix 1

Scores of the data set of the phylogenetic analysis of *Narambuenatitan palomoi*.

Taxon	Characters						
	1-10	11-20	21-30	31-40	41-50	51-60	61-65
<i>Camarasaurus grandis</i>	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00000
<i>Brachiosaurus brancai</i>	0001000110	1000001001	0100100000	0000000010	0000000000	0000000010	11100
<i>Chubutisaurus insignis</i>	??????????	??????????	???2?0001	?0?00001?	???0?000	???0?000?	?111?
<i>Andesaurus delgadoi</i>	??????????	??????????	?1?0111011	?0?0001010	0010000?0?	???1110??	?01??
<i>Argentinosaurus huinculensis</i>	??????????	??????????	?????1101?	0?????????	??????????	??????????	???1?
<i>Malawisaurus dixeyi</i>	???????210	?11000?00?	?1?0111111	??10002010	0?11000???	1110??10??	???11
<i>Mendozasaurus neguyelap</i>	??????????	??1010?122	?10?2??111	?110002110	0111000101	111?1?????	?0111
<i>Futalognkosaurus dukei</i>	??????????	2110101122	210?2??111	111?0?2?1?	?1?0?0????	?????11211	1????
<i>Epachthosaurus sciuttoi</i>	??????????	??????????	?111211011	11?0002210	0011000101	11??11?111	1011?
<i>Narambuenatitan palomoi</i>	1100110???	?????11???	????21111?	?10?002210	0211000?01	110?????1??	?01??
<i>Rapetosaurus krausei</i>	1110111212	201000100?	1111211111	1?00002210	010?000101	110??11011	101?1
<i>Lirainosaurus astibiae</i>	???????21?	??????????	?1?1211111	?11?002210	0000000?01	?101??????	??1?1
<i>Rinconsaurus caudamirus</i>	???????211	?010001011	?111211111	1???002210	0101011101	1101111111	101??
<i>Muyelensaurus pecheni</i>	1110111211	?11000?011	?111211111	1?0?002210	0201011101	110?111111	1011?
<i>Gondwanatitan faustosi</i>	??????????	??????????	?111211111	11???12220	1002001?0?	?????0111	???1?
<i>Aeolosaurus rionegrinus</i>	???????212	??????????	?1???2????	?30?012220	1102001?01	?10?1101??	???1?
<i>Opisthocoelicaudia skarzynskii</i>	??????????	??????????	1011210111	1211000010	0200000111	1101111111	1011?
<i>Alamosaurus sanjuanensis</i>	???????2?2	?010001001	?1?1200111	1311002210	0200000101	1111111211	1011?
<i>Neuquensaurus australis</i>	??????????	?011001012	?111211111	131?102211	0200000101	11011?1211	1?111
<i>Saltasaurus loricatus</i>	1?10010212	?001011012	?111211111	110?102211	0200100112	1101111211	10111
<i>Rocasaurus muniozi</i>	??????????	???????01?	?111211111	????102211	0?00100???	?????11211	1?1??
<i>Bonatitan reigi</i>	1100111???	?00???????	????2??111	??0???2?11	020?000?01	1?????????	?011?