

The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina)

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Abstract

A study of the abundant and undescribed isolated and associated bones and teeth from the La Amarga Formation (Barremian of Neuquén, Argentina) permitted the recognition of additional clades of sauropod dinosaurs: basal titanosauriforms, both basal and derived titanosaurs, and rebbachisauroid diplodocoids, which are now added to the already known dicraeosaurids and a recently published basal diplodocoid. These forms substantially increase the knowledge on the Early Cretaceous sauropod diversity in Gondwana.

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Keywords: Paleontology; Sauropods; Early Cretaceous; Argentina

1. Introduction

La Amarga Formation is a terrestrial unit established by Musacchio (1970), constrained between the marine Agrio Formation and the terrestrial Lohan Cura Formation. Coarse sandy levels of the lower section (Puesto Antigüal Member) of the La Amarga Formation are mainly exposed close to La Amarga stream, north of China Muerta Hill, Neuquén Province, Argentina. They are considered Barremian to Early Aptian in age (Volkheimer, 1978; Leanza and Hugo, 1995, 1997). The three members are (from base to top): Puesto Antigüal Member, Bañados de Caichigüe Member, and Piedra Parada Member (Leanza and Hugo, 1995) (Fig. 1).

In the late 1980's a team led by José F. Bonaparte discovered in sediments of the Puesto Antigüal Member an interesting diversity of tetrapod taxa preserved in sediments deposited in an environment dominated by alluvial systems with fluvial channels, swamps and palaeosols (Leanza and Hugo, 1995, 1997). The specimens here described were collected on the 1983 and 1986 fieldtrips. Later, in 1995, remains of a sauropod were collected in the youngest Piedra Parada Member at the Puesto Morales sublocality (Salgado et al., 2006).

The Amargan assemblage (Leanza et al., 2004) includes the abelisaurian theropod *Ligabueino andesi* (Bonaparte, 1996) plus several theropod teeth of uncertain affinities, probably related to basal tetanurans because of the close resemblance to those referred to as *Acrocanthosaurus* (pers. obs.); fragmentary remains of the only known South American stegosaur (Bonaparte, 1996); the mesoeucrocodylian *Amargasuchus minor* (Chiappe, 1988) and several specimens of the cladotherian mammal *Vincelestes neuquenianus* (Bonaparte, 1986a; Rougier, 1993), the only Early Cretaceous mammal known for South America. Completing this assemblage are the 'spiny' dicraeosaurid sauropod *Amargasaurus cazaui* (Salgado and Bonaparte, 1991) represented by the holotype (MACN PV N15) and two additional specimens (Bonaparte, in prep.), as well as a recently described basal diplodocoid from the uppermost member of the unit (Salgado et al., 2006).

Further consideration of the abundant unstudied materials collected by Bonaparte and collaborators led author to recognize remains of additional clades of sauropod dinosaurs: titanosauriforms and rebbachisaurids, based on both isolated and associated bones and teeth.

The most abundant remains are isolated teeth that are here referred to as dicraeosaurid and rebbachisaurid diplodocoids

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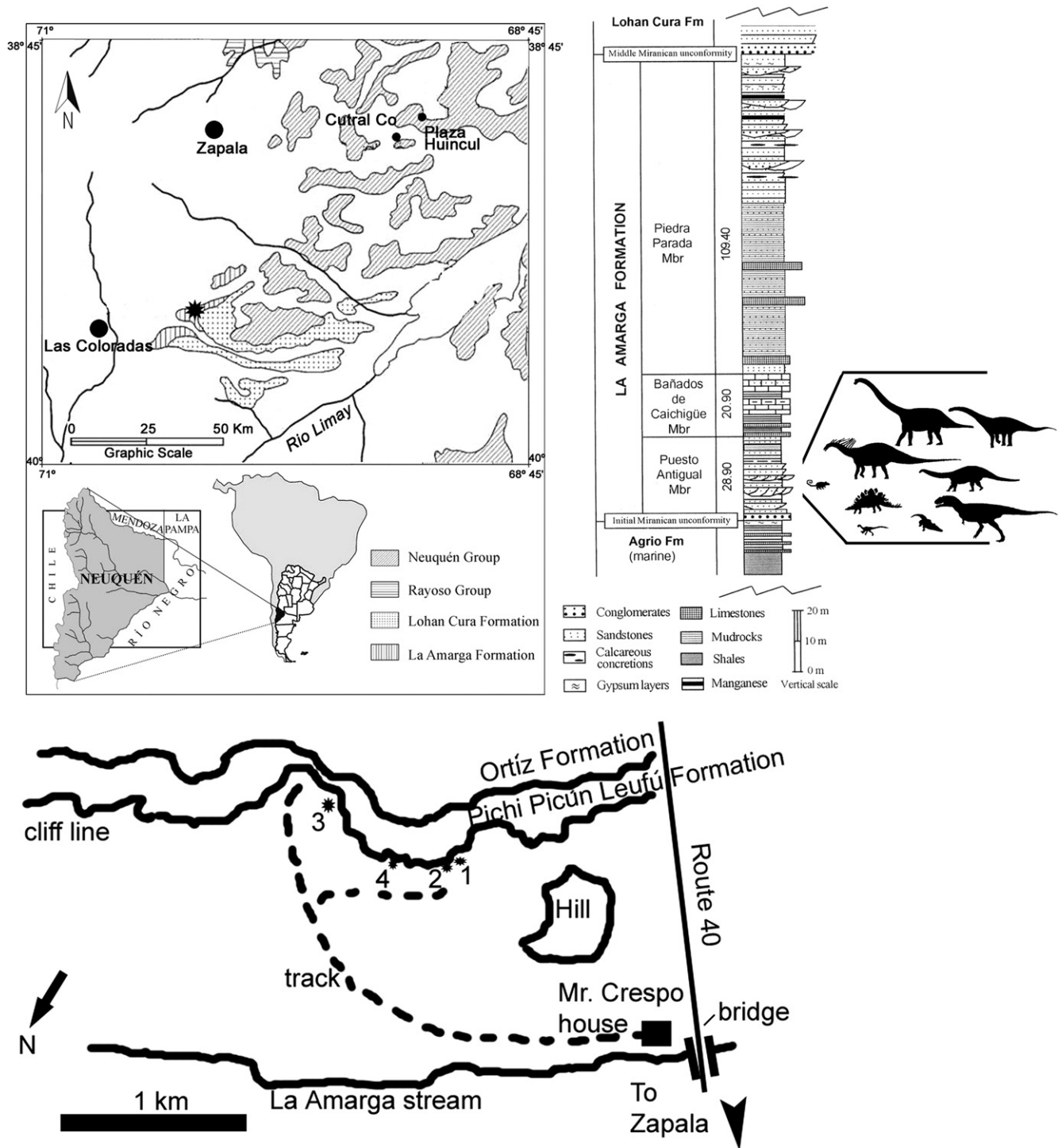


Fig. 1. Map of the La Amarga region, Neuquén Province (left), and stratigraphic column of the La Amarga Formation (right) showing the vertebrate bearing levels. Silhouettes of vertebrates represent basal and advanced titanosaurs (top), dicraeosaurid and rebbachisaurid diplodocoids (center), cladotherian mammals, stegosaurs, small noasaurid abelisauroids, trematochampsid crocodyliforms and carcharodontosaurid-like basal tetanurans (bottom). Map, column and silhouettes were modified from [Leanza et al. \(2004\)](#). At the bottom, sketch of the bonebeds reproduced from the J. Bonaparte's 1983 field book, showing the exact location of the bones, where site 1 is the richest bonebed, which provided two anterior and one mid caudal vertebrae, one scapula, femur, and astragalus as well as a partial tibia, fibula, and ischium, two phalanges and broken metapodials; site 2 provided another caudal vertebra, site 3 (slightly higher stratigraphical level) provided three haemal arches, one rib, and another caudal vertebra with a laminate spine; site 4 provided a small pterosaur femur, an incomplete neural arch and a theropod tooth. Note that the formational names involved are the Pichi Picún Leufú and Ortiz Formations. Later, Bonaparte considered these localities to all be in the La Amarga Formation.

as well as to derived titanosauriforms, most probably basal titanosaurs. The collected postcranial bones indicate two main sauropod lineages: a diplodocoid dorsal neural arch, here con-

sidered from a low-spined early rebbachisauroid, and the partial skeleton of a small and unusual titanosaur, comprising the scapula, femur, astragalus and some caudal vertebrae.

Abbreviations. BYU, Brigham Young University, Vertebrate Paleontology Collection; MACN, Museo Argentino de Ciencias Naturales “B. Rivadavia”; PVL, Instituto Miguel Lillo, Tucumán, Vertebrate Paleontology Collection; QM, Queensland Museum; SM, Salitral Moreno specimen for *Aeolosaurus*; YPM, Yale Peabody Museum, Vertebrate Paleontology Collection; WN-V, Vertebrate Paleontology Collection of the Municipality of Bale, Croatia.

Systematics

Diplodocoidea Marsh, 1884 (*sensu* Wilson and Sereno, 1998).

Diplodocimorpha Calvo and Salgado, 1995 (*sensu* Taylor and Naish, 2005).

Rebbachisauroida nov.

Definition (node-based): The most inclusive clade containing WN-V6 (*Histriasaurus boscarollii*, see Appendix A), *Rebbachisaurus garasbae* Lavocat, 1954, and *Limaysaurus tessonei* (Calvo and Salgado, 1995), and MACN PV N35.

MACN PV N35 (Fig. 2). Represented by a diplodocoid complete mid to posterior dorsal neural arch collected in 1986. It is characterized by extended prezygodiapophyseal laminae oriented in the same structural plane as the prezygapophyses. A similar plane is present on the posterior side, continuous from the hyposphene to the tip of the diapophysis. Parapophyses and diapophyses developed as distinct columns. Low neural spine with an expanded tip. Open connection between the fossa framed by prespinal, spinodiapophyseal and prezygodiapophyseal

laminae, and that framed by centrodiapophyseal, and centroparapophyseal laminae. Postzygapophyses connected to the diapophyses by extended, shelf-like postzygodiapophyseal laminae.

This complete mid to posterior dorsal neural arch includes a complete neural spine that expands slightly from its base to a distal narrowing. Both pre- and postzygapophyses are anteroposteriorly extended and well developed in width, reaching half the extent of the entire diapophysis. They are located very close to each other toward the center of the neural arch. The prezygapophyses are not connected by an intraprezygapophyseal lamina, and there is a well-developed hypantrum above the neural canal.

The prezygapophyses are separated by a short space and there are shallow centroprezygapophyseal laminae. The prezygapophyses are connected to the parapophyses by well-developed prezygoparapophyseal laminae and to the diapophyses by distinct prezygodiapophyseal laminae. Because of the separation of the para- and diapophyses there are no paradiapophyseal laminae.

The prespinal, spinodiapophyseal and prezygodiapophyseal laminae frame a deep fossa, which is pierced by a large foramen. This connection opens into the ventrolateral fossa framed by centrodiapophyseal, and centroparapophyseal laminae, under the diapophysis. The connection from prezygapophyses to neural spine is made by a single prespinal lamina. There are no well developed spinoprezygapophyseal laminae, perhaps because of its very posterior position.

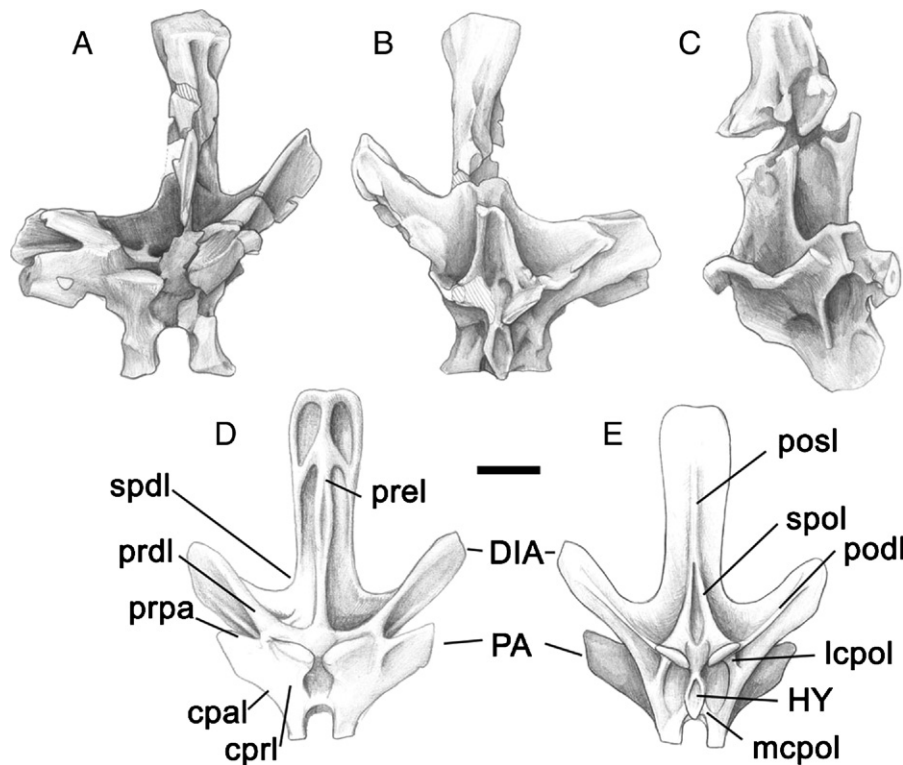


Fig. 2. MACN PV N35. Mid to posterior dorsal neural arch in A, anterior view; B, posterior view; C, right lateral view; D, anterior reconstructed view; and E, posterior reconstructed view. Abbreviations: cpal: centroparapophyseal lamina; cprl: centroprezygapophyseal lamina; DIA: diapophysis; HY: hypantrum; lcpol: lateral centropozygapophyseal lamina; mcpol: medial centropozygapophyseal lamina; PA: parapophysis; podl: postzygodiapophyseal lamina; posl: postspinal lamina; prel: prespinal lamina; prdl: prezygodiapophyseal lamina; prpa: prezygoparapophyseal lamina; spdl: spinodiapophyseal lamina; spol: spinopostzygapophyseal lamina. Scale bar: 50 mm.

The prespinal lamina arises from the base of the neural arch and shows a short split into two sublaminae at mid height, evidencing its dual origin, as also shown along its total length by Pv-6722-MOZ, assigned by Salgado et al. (2004) to *Limaysaurus*, and a possible rebbachisaurid from the Early Cretaceous of Cerro Castaño, Chubut province. After the split, both sublaminae join again before reaching the tip of the spine and, after the addition of two paired and short laminae originating from the spinodiapophyseal laminae, which fuse to the prespinal laminae reaches the tip of the spine as a single lamina. The tip of the spine is not well preserved and shows some degree of deformation. However, it has been reconstructed (Fig. 2) to show its apparently unusual shape.

The postzygapophyses are separated by the hyposphene, which is primitive in being rhomboid but advanced in being posteriorly hollow, as in *Histriasaurus*. The distal region of the hyposphene is connected to the neural arch base by means of two robust ridges which also frame the neural canal: the medial centropostzygapophyseal laminae (see Apesteguía, 2005). Two lateral centropostzygapophyseal laminae reach the postzygapophyses approximately at the middle of their extent and join the centrodiapophyseal laminae before meeting the centrum. The postzygapophyses are also connected to the diapophyses by important, shelf-like postzygodiapophyseal laminae. There are no accessory laminae connecting the spinopostzygapophyseal laminae with the spinoprezygapophyseal or spinodiapophyseal laminae (or both are united in the “lateral” lamina). However, a short lamina rises from the postzygodiapophyseal to reach the spinopostzygapophyseal not far from the postzygapophysis.

The connection between postzygapophyses and neural spine is made by paired spinopostzygapophyseal laminae which converge with each other right above the meeting point of the diapophyses with the neural spine, and continue as a single lamina to the spine tip, as also occurs in *Histriasaurus* and the material studied by Nopcsa (1902). *L. tessonei* and the material from Cerro Leon, assigned by Salgado et al. (2004) also to *Limaysaurus* seem to differ, because their spinopostzygapophyseal laminae do not meet each other, remaining as a central canal on the posterior view of the preserved dorsal vertebra.

As seen from above, the neural spine is formed by several laminae which are, as in most rebbachisaurids, well developed and basically “+”-shaped in section, as also described for the rebbachisaurid from Cerro Leon (Salgado et al., 2004). Determining the position of the vertebra along its corresponding series is problematic because, as an artifact of preservation, one of the diapophyses is elevated whereas the other is rather horizontal. However, considering the relative level of the parapophysis, which is highly positioned with respect to the prezygapophyseal level, the absence of spinoprezygapophyseal laminae, and the proximity of the prezygapophyses, it is likely to be a mid to posterior dorsal vertebra.

MACN PV N35 is considered here a basal diplodocoid because of the shape of its dorsal neural arch, its tetralaminar configuration, and the neural spine shape, which expands from its base to narrow again distally, as occurs (in a more marked way) in other basal diplodocoids (i.e., rebbachisaurids). Additionally, the single character of the neural spine precludes its

assignment within the Flagellicaudata (Harris and Dodson, 2004).

Considering the presence of other basal diplodocoids in a younger member of the La Amarga Formation (i.e., *Zapalasaurus bonapartei*), whose dorsal neural arches are unknown, it is possible that MACN PV N35 could belong to a form related to *Zapalasaurus* or that taxon itself. However, I prefer to maintain the distinction of MACN PV N35 from *Zapalasaurus* considering that a characteristic feature of the latter, although proposed for cervical vertebrae, is that the neural arch has a reduced postzygodiapophyseal lamina on the diapophyseal area, a feature that in MACN PV N35, although belonging to a different anatomical region, is exactly the opposite on its dorsal neural arch.

MACN PV N35 shares with rebbachisaurids tall neural arches, large postzygapophyses, and a neural spine which originates narrow, expands dorsally and becomes narrow again close to the distal region, although in a much more slight way than in rebbachisaurids. It must be noted, however, that the presence of a well-developed hyposphene shows a very basal position in the clade, like that of *Histriasaurus boscarionii* (Dalla Vecchia, 1998). Additionally, MACN PV N35 lacks all the following rebbachisaurid diagnostic dorsal neural arch features, the La Amarga taxon having a plesiomorphical condition for all of them: absence of hyposphene–hypantrum articular complex in dorsal vertebrae; posterior dorsal neural spine reaching four times the length of the centrum; and petal-shaped posterior dorsal and anterior caudal neural spines. All these features point to the need for creating a more inclusive category to include rebbachisaurids and the basal most forms related to them, as a lineage related to rebbachisaurids, but lacking several of their diagnostic node-based features.

Rebbachisauridae Bonaparte, 1997 (*sensu* Sereno et al., 1999).

MACN PV N101 (Fig. 3f–i). This is a rather complete tooth crown. It is very long, gently curved and slender, as described for *Nigersaurus taqueti* (Sereno and Wilson, 2005), with a circular cross section at the base and the top but slightly compressed oval section at mid-shaft of the crown. It is 27 mm in length. At the middle, where it is rather flattened and trapezoidal, as in *Nigersaurus*, its minimal width is 3 mm and its maximum 4.73 mm. At the apex, the crown tip is about 2.55 mm × 2.13 mm. The crown ends in a very thin tip with a poorly preserved wear facet. In the same way, the *Nigersaurus* holotype does not bear any wear facets on its teeth, and the description of the rare two-sided wear facets in the African taxon comes from isolated narrow-crowned, asymmetrically enameled teeth collected from many sites in the Gadoufaoua beds.

Although in *Nigersaurus* (Sereno et al., 1999) tooth crowns were described as having a highly asymmetrical enamel thickness, this is not possible to observe in MACN PV N101. As in *Nigersaurus*, MACN PV N101 shows more than six longitudinal grooves and ribs along the lingual surface.

It is included in Rebbachisauridae because only in this lineage are teeth very long, narrow, striated and less than 5 mm in width, with an elongation index of 4.73/27, as shown by the material from *Limaysaurus* (Calvo and Salgado, 1995) and the

unnamed form from the Bajo Barreal Formation (Chubut Province, Argentina; Powell et al., 1989). Conversely, in *Diplodocus* and *Dicraeosaurus*, the teeth are proportionally shorter and more robust (Hatcher, 1901).

Flagellicaudata Harris and Dodson, 2004.

Dicraeosauridae Von Huene, 1927.

MACN PV N100 (Fig. 3a–e). This tooth is a long cylindrical uniform upper crown, with a diameter of 8 mm, no broader than the root. The crown is bowed, being convex on the labial side and lingually concave. It is 34 mm in length. At the middle, where it is only slightly flattened, its minimal width is 6.5 mm and its maximum 8.4 mm. Although the angle of the wear facet is commonly thought to differentiate titanosauriform from diplodocoid teeth, Upchurch (1999) noted that in the dicraeosaurid *Dicraeosaurus hansemanni* the teeth are slender, labially convex and lingually rather flat, but the wear facets are high-angled. In the same way, MACN PV N100 has a high angle on its chisel-like wear on the lingual side.

The tooth is closely similar to that assigned by Janensch (1935–1936) to *Dicraeosaurus* and illustrated in his Fig. 23a. Later, Upchurch illustrated the same tooth, adding a slightly striated pattern of the enamel on the lingual side. As MACN PV N100 did not preserve any trace of enamel, it is not possible to evaluate that feature.

This dicraeosaurid *A. cazaui* Salgado and Bonaparte, 1991, known to come from the same strata, is characterized by a remarkable enlargement of the bifid neural spines on cervical and dorsal vertebrae. The most closely related species come from the Late Jurassic of Tanzania (Janensch, 1929; Salgado and Bonaparte, 1991) and Chubut Province (Rauhut et al., 2005). No teeth were found with the *Amargasaurus* specimen, but based on the general resemblance to *D. hansemanni* teeth (Janensch, 1935–1936) and by proximity to the holotype, these two isolated teeth are considered here as belonging to a dicraeosaurid, perhaps *Amargasaurus* itself.

MACN PV N99 (Fig. 4p–t). This tooth is also cylindrical and uniform in shape, and also lacks any trace of enamel. However, the tooth is labiolingually compressed and the diameter is about 8 mm on the labial view and 5 on the mesial view. It is 29.6 mm in length. At the middle, where is flattened, its minimal width is 5.7 mm and its lateromedial maximum is 8.5 mm. At the base, the crown is about 9.19 mm × 6.5 mm.

The crown is flat on the labial side except for the last 5 mm in which the crown tip is angled toward the main axis. It is also lingually flat except for the last centimeter in which the crown forms a slight concavity resembling the ‘spoon’ of camarasaurid teeth. This last feature makes it difficult to assign this tooth to dicraeosaurids, but its general aspect and the tooth illustrated by Janensch (1935–1936) as Fig. 16a and b, suggest that there exists some variation with tooth position in the dicraeosaurid dentition. A mesial flat surface at the top that could be a wear facet.

Titanosauriformes Salgado, Coria and Calvo, 1997.

Titanosauria Bonaparte and Coria (1993).

“Broad-crowned forms”

MACN PV N97 (Fig. 4a–e). This tooth has an oval labiolingually compressed root and a crown only slightly broader

than the root. It is 39.87 mm in length. At the middle, where is flattened, its minimal anteroposterior width is 9.9 mm and its maximum lateromedial is 13.3 mm. The crown is convex on the labial side and lingually concave. The wear facet was not well preserved.

The tooth differs from those of Camarasauridae (McIntosh et al., 1996), bearing a strong central axis with a single lateral expansion. As in most Titanosauriformes, a single laterally concave wing in a comma shape that gives the crown a ‘half-spoon’ shape replaces the two lateral expansions of *Camarasaurus*. These kinds of teeth are similar to those from a new

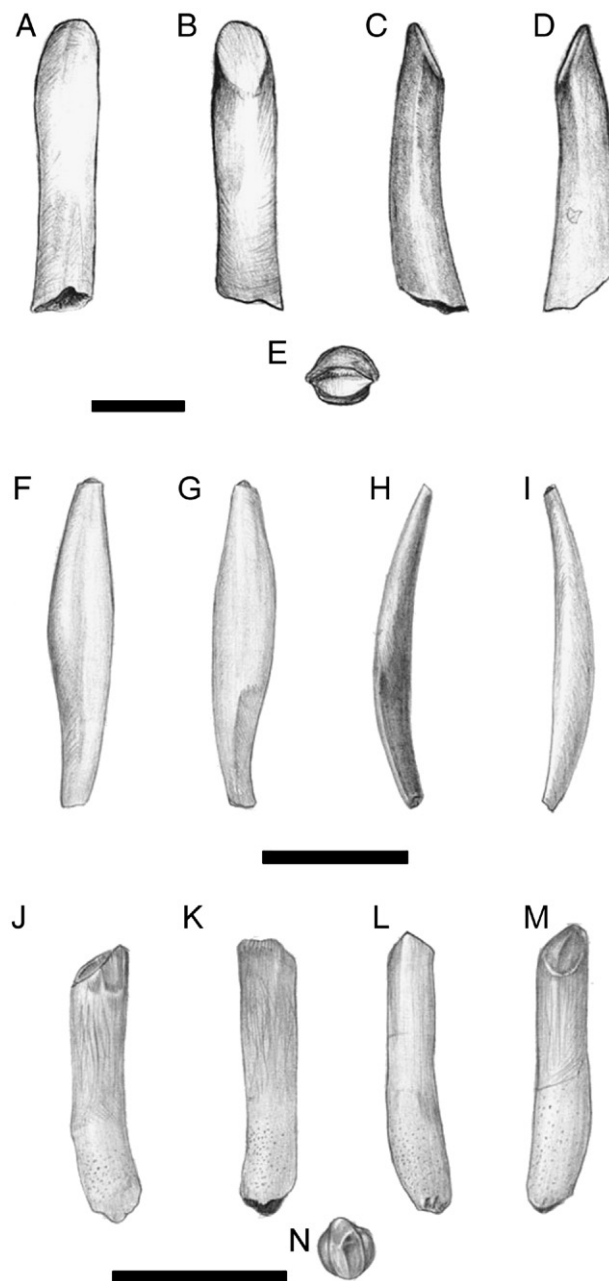


Fig. 3. A–E. MACN PV N100. Dicraeosaurid tooth in labial, lingual, lateral, medial and occlusal views. F–I. MACN PV N101. Rebbachisaurid tooth in labial, lingual, lateral and medial views. J–N. MACN PV N102. Titanosauriform tooth in lateral, and medial, labial, lingual, and occlusal views. Scale bar: 10 mm.

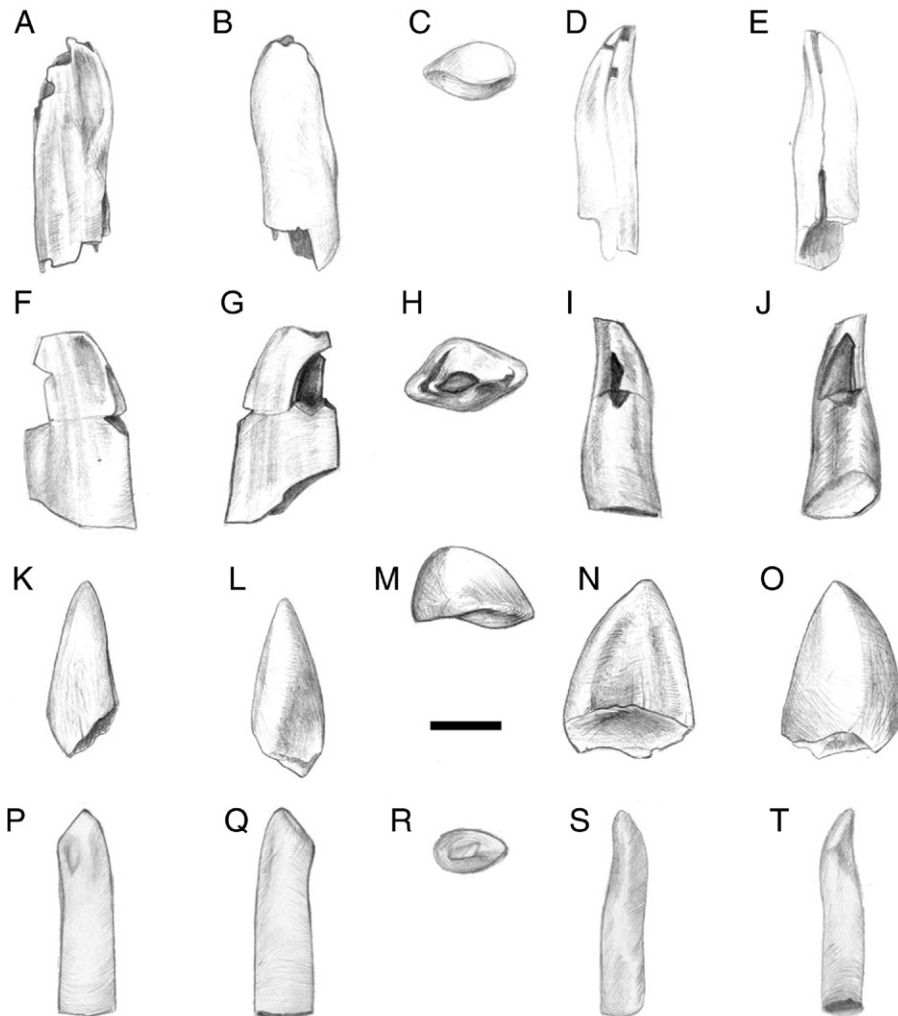


Fig. 4. A–E. MACN PV N97. Titanosauriform tooth in lingual, labial, occlusal, lateral, and medial views. F–J. MACN PV N98. Titanosauriform tooth in lingual, labial, occlusal, lateral, and medial views. K–O. MACN PV N68. Titanosauriform tooth in lingual, labial, occlusal, lateral, and medial views. P–T. Dicraeosaurid tooth in lingual, labial, lateral, medial and occlusal views. MACN PV N99. Scale bar: 10 mm.

titanosaur from the Aptian of Neuquén, and from *Brachiosaurus* (Janensch, 1950; Calvo and Salgado, 1995).

As expected in titanosauriforms, it lacks any trace of marginal denticles (Wilson and Sereno, 1998), but the enamel has not been preserved on most of the tooth. A surprising feature also present in later titanosaurids (i.e., *Clasmodosaurus spatula*) is that the lingual surface shows no less than four polygonal facets (Ameghino, 1898).

MACN PV N98 (Fig. 4f–j). Because of its bulky aspect and low height, this tooth probably corresponds to a more posterior position of the same taxon as that of MACN PV N97. As in that form, the crown is labio-lingually compressed. It is 30.66 mm in length. At the middle, where is flattened, its minimal width is 9.88 mm and its maximum 12.34 mm. Close to the apex; the crown tip is about 6.97 mm. The convex labial side is strongly asymmetrical, with the main bulge located distally. The wear facet is poorly preserved because most of the tip was lost. The concave lingual facet has a central ridge and a single distal lateral expansion with a deep comma-like concavity. A vertical

bulge, made by facets as in MACN PV N97, makes up the rest of the lingual side. The enamel surface is eroded.

MACN PV N68 (Fig. 4k–o). This tooth is thought to be even more posterior than MACN PV N97 and it lacks any trace of wear facet, thus precluding precise identification as maxillary or dentary. The crown is very asymmetrical and compressed labio-lingually. It is 22.16 mm in length. At the middle, where is flattened, its minimal width is 8.9 mm and its maximum 14.3 mm. The labial side is convex, very asymmetrical when compared to the two-winged teeth of non-neosauropod forms (e.g., *Chebsaurus*, Mahammed et al., 2005) and basal macro-narians (e.g., *Camarasaurus*, McIntosh et al., 1996), and with a rather homogeneous but variegated enamel cover on the crown and completely devoid of any trace of denticles. On the other side, the lingual side, as in most titanosauriforms, and especially basal titanosaurs, has a broad base with an eccentric main axis and a deep comma-like concavity.

Fortunately, and differing from most other teeth, the enamel is completely preserved along the entire surface, allowing

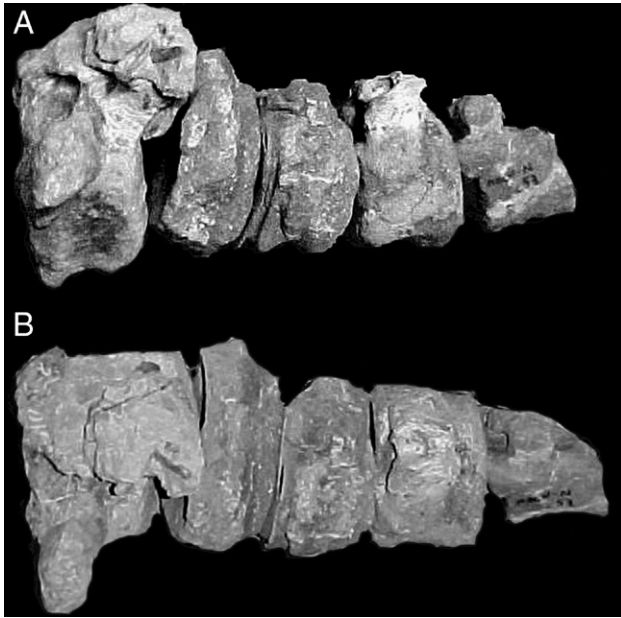


Fig. 5. *Amargatitanis macni* gen. et sp. nov. MACN PV N53 and 51. Anterior to mid caudal vertebrae series in left (A) and dorsal (B) views.

observation of the variation of the sculpture pattern in the same piece. On the lingual side, opposite to the comma-like concavity, the enamel has a very complex rugosity pattern. Close to the main axis, the enamel forms a striated and wrinkled pattern. The center of the shallow concavity shows a bulging globular texture and close to the border the enamel is composed of rosette-like tuberculate enamel formations, not as tall as others but very precisely developed. This variation in the enamel structure should be better studied in other forms to allow comparisons.

“Narrow-crowned forms”

MACN PV N102 (Fig. 3j–n). It consists on a rather complete crown. It is long, gently curved and slender. It is 18.26 mm in length. At the middle, its maximum width is 3.67 mm. At the apex, the crown tip is about 2.76 mm × 3.7 mm. The cross section is circular on the entire crown, flattening just a few in the last 5 mm. The crown bears a partially broken wear facet developed not labially or lingually but laterally. As in most basal titanosaurs, the facet begins with a small circle and continues laterally forming a comma-like facet. Although easily confused with a diplodocoid tooth because of its slender shape, the dendritical enamel pattern clearly shows its titanosaur affinities. Furthermore, its homogeneous slenderness is a feature of advanced titanosaurs.

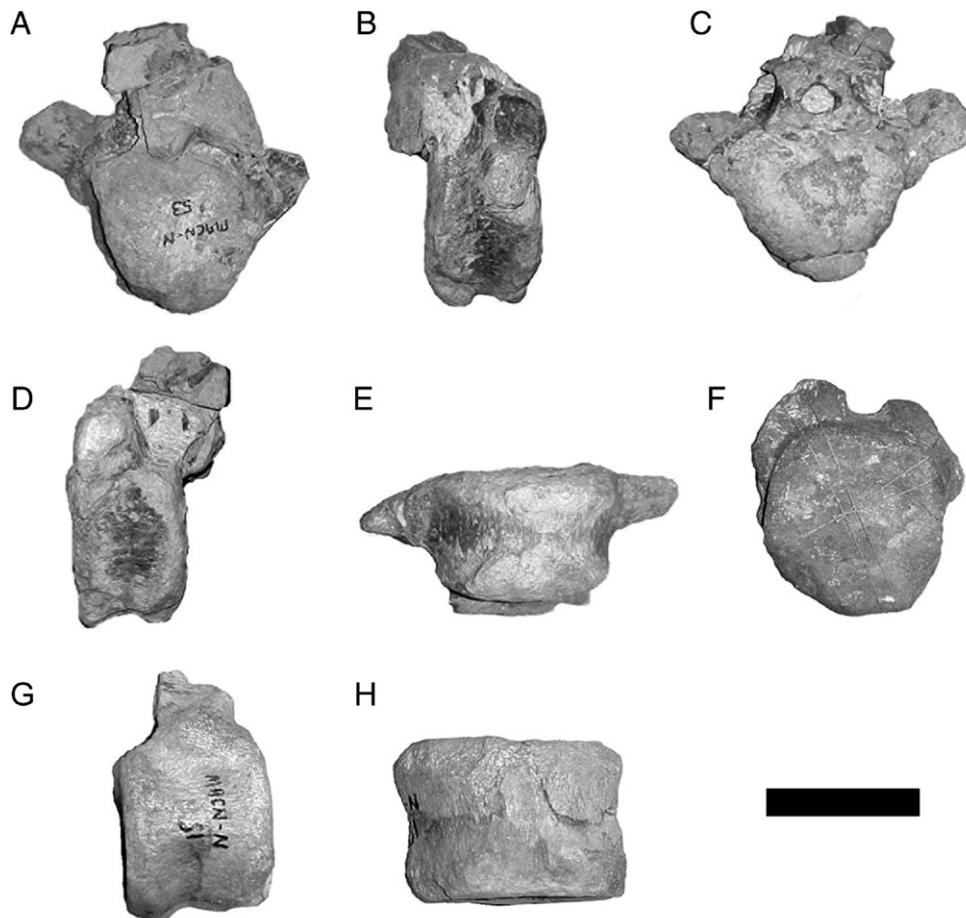


Fig. 6. *Amargatitanis macni* gen. et sp. nov. MACN PV N53. Anterior caudal vertebra in posterior (A), right (B), anterior (C), left (D), and ventral (E) views. MACN PV N51-A. Anterior caudal vertebra in posterior view (F). MACN PV N51-B. Mid caudal vertebra in right (G) and ventral (H) views. Scale bar: 50 mm.

Titanosauria Bonaparte and Coria, 1993

AMARGATITANIS gen. nov.

Type species: *Amargatitanis macni* sp. nov.

Diagnosis: *A. macni* is diagnosed by the following associated characters. Robust, wide and flat scapula developed in a single plane, with straight, parallel anterior and posterior borders of the diaphysis. Acromion developed in straight line with respect to the diaphysis. Very short glenoid region, straight articulation for the coracoid, obtuse angle of coracoid articular surface with respect to the glenoid–scapular line, absence of scapular ventromedial process. Femoral fourth trochanter located at mid femur. Femur with a prominent head with respect to a moderately developed distal region. High astragalus with a deep crescent-shaped fossa that bears two pairs of foramina on the upper part of the tibial side of the posterior astragalar fossa. On the fibular side, two foramina are visible also in a deep concavity.

Etymology: *Amarga*, referring the fossil locality; *titanis* (Greek), titan, giant, because of the affinities of the specimen with the titanosaurs.

A. macni nov. sp.

Figs. 5–8

Diagnosis: same as for genus.

Etymology: In honor of the Museo Argentino de Ciencias Naturales (MACN) for the sustained contribution and human resources formed in Vertebrate Paleontology during the 19th and 20th centuries.

Holotype: MACN PV N51, 53, 34 (Figs. 5–8), represented by the following associated material collected in 1983: six caudal vertebrae, a scapula, a femur and one astragalus.

Horizont and locality: the fossil locality, as shown by the geologist Luis Cazau to Bonaparte, is located at the foot of the hill that rises over the left bank of the La Amarga stream, 2.5 km east from the 40th National Road. As described by Cazau and written by Bonaparte in his notebook, the levels correspond to the Kimmeridgian Pichi Picún Leufú Formation (Fossa Mancini et al., 1938), the basal unit of the Fortín Nogueira Group. If true, these fossils are much older than expected and very important because of their good preservation. However, the preservation is

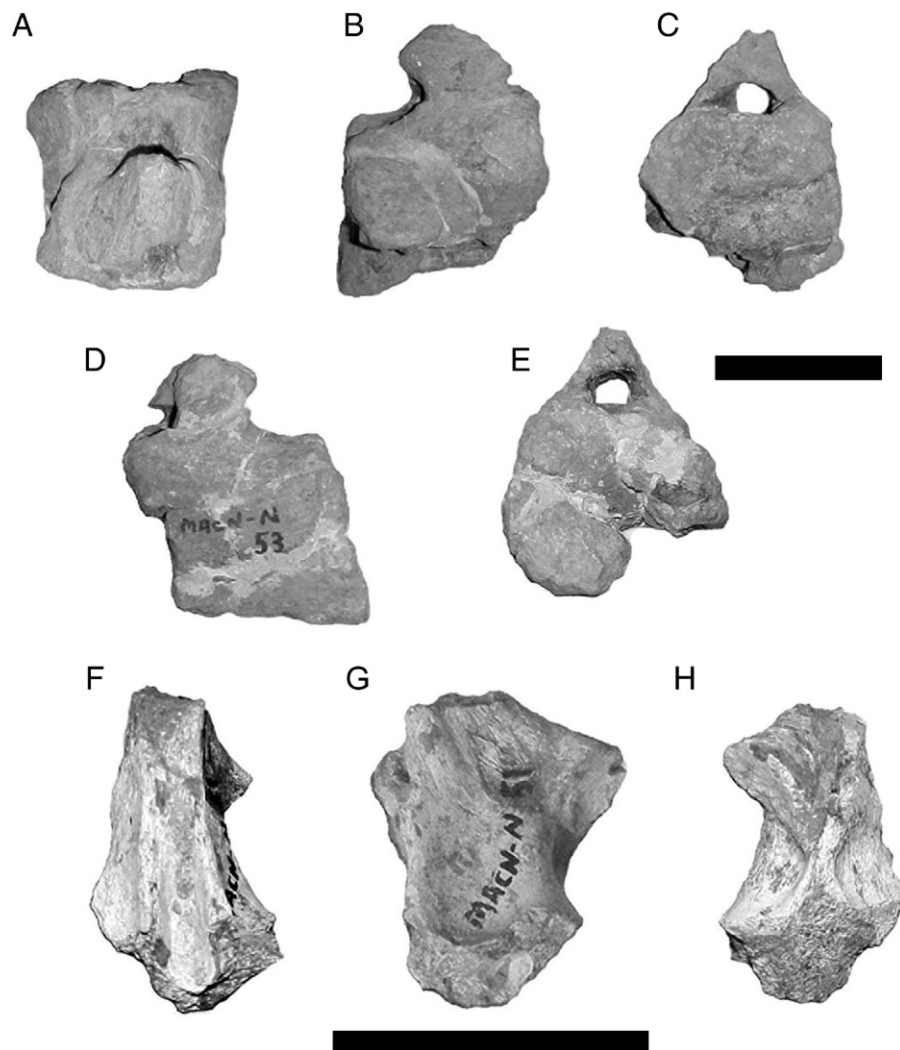


Fig. 7. *Amargatitanis macni* gen. et sp. nov. MACN PV N51-E. Mid to posterior caudal vertebra in dorsal (A), right lateral (B), anterior (C), left lateral (D), and posterior (E) views. Note the anterior position of the neural arch. MACN PV N51-F. Posterior caudal neural arch in anterior (F), left lateral (G) and posterior (H) views. Scale bar: 50 mm.

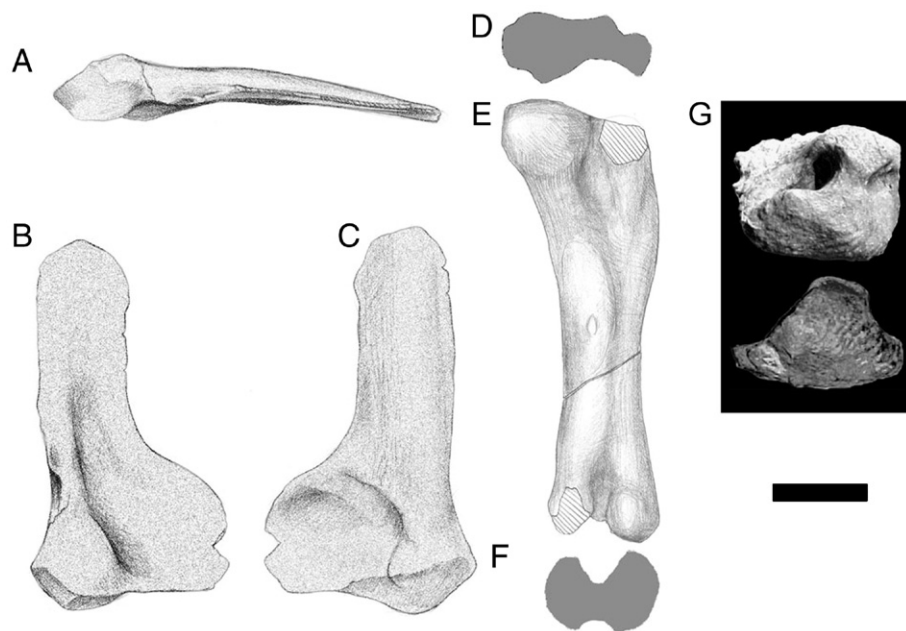


Fig. 8. *Amargatitanis macni* gen. et sp. nov. MACN PV N34. Left scapula in ventral (A), medial (B), and lateral (C) views. MACN PV N53. Right femur in proximal (D), posterior (E) and distal (F) views. G, astragalus in proximal and anterior view. Scale bar: 216 mm (for A–F); 50 mm (for G–H).

identical to that of bones coming from the La Amarga Formation and is here considered in that context.

2. Description

MACN PV N53 and 51 (Figs. 5–7). Caudal vertebrae. There are six preserved caudal vertebrae presumably referable to the same specimen, and will be here referred here as 53 and 51-A, B, C, D, and E, respectively.

53 (Fig. 6a–e) is an anterior caudal vertebrae. The centrum is slightly procoelous, not really circular but heart-shaped, as in several ornithischians. The neural arch is clearly positioned in the anterior part of the vertebra and the transverse process arises dorsolaterally. Spinodiapophysial laminae are well developed and the neural spine, although not preserved, seems to have pointed backwards.

51-A (Fig. 6f) is a poorly preserved anterior caudal vertebrae. The centrum is tall, anteroposteriorly short and slightly procoelous. The neural arch is on the anterior part of the vertebra and the transverse processes are still separated into visible diapophyses and parapophyses on the left side. This vertebra was found separated from the others and perhaps does not belong to the same specimen.

51-B (Fig. 6g–h) and C (not figured) are similar to each other, with short and tall, rounded centra, and completely devoid of the neural arch. The transverse processes were not preserved but their scars remain on the lateral side of the centra. They were laterally directed.

51-D (not figured) is slightly longer. The base of the neural arch is preserved. The marks for diapophyses and parapophyses are distinct and both located on the upper half of the centrum. The neural arch is also located on the anterior half of the vertebra.

51-E (Fig. 7a–e) is a mid-distal caudal. It is slightly longer than all the previous and very low. Although only the left side of the centrum was preserved, it shows that the neural arch was clearly located on the anterior half of the centrum. The base of the neural arch is well preserved, and shows that the neural spine was probably inclined backwards.

51-F (Fig. 7f–h) is an isolated neural arch which preserves the left postzygapophysis, which is rounded and large, and the base of the neural spine. On the anterior side, the spine is formed by two parallel spinoprezygapophyseal laminae, which follow the spine upwards with no sign of merging. On the posterior side, the spinopostzygapophyseal laminae frame a centered spinal cavity. From the postzygapophyses, laminae run ventromedially to meet each other above the neural canal.

MACN PV N34 (Fig. 8a–c). This complete left scapula collected in 1983 is a very peculiar medium sized piece, reaching 0.80 m in length, 0.44 m in maximum width (by the acromium, which reaches 0.35 m anteroposteriorly) and 0.18 m at the minimum section of the postacromial region. The coracoid is lacking.

The scapular diaphysis is very wide, 0.2 m at the narrowest part. The diaphysis is straight as in *Aeolosaurus* (Powell, 2003), *Antarctosaurus wichmannianus* (Von Huene, 1929), *Chubutisaurus insignis* (Apesteguía, pers. obs.), *Isisaurus colberti* (Jain and Bandyopadhyay, 1997), *Laplatasaurus araukanicus* (Lydekker, 1893), and *Lirainosaurus astibiae* (Sanz et al., 1999), clearly differing from saltasaurine titanosaurs.

The distal end is preserved but the exact outline may have been slightly distorted. It is symmetrical and slightly rounded, as in *Alamosaurus* (Gilmore, 1922) and *Ampelosaurus* (Le Loeuff, 1995), differing from the squared outline of *Aeolosaurus* (Salgado and Coria, 1993), *Ligabuesaurus* (Bonaparte et al., 2006),

Epachthosaurus (Powell, 1990), *Opisthocoelicaudia* (Borsuk-Bialynika, 1977) and *Isisaurus*. Although the coracoid is absent, the scapular glenoid surface is medially exposed, as pointed by Wilson and Sereno (1998) for the Somphospondyli, being also this way in *Brachiosaurus brancai* SII (Janensch, 1914), *Camarasaurus grandis* (Marsh, 1878), and titanosaurs.

The most striking feature of this bone is the wide and short profile and the short glenoid region. Additionally MACN PV N34 and the Australian QM F7292 (Coombs and Molnar, 1980) share a straight scapular post-acromial region. Although several titanosaurs are characterized as having a straight dorsal border on the scapula, this is only partially true, giving the scapula a slightly increasing profile, in which the dorsal border of the scapula is half straight and half curved, as occurs in *Aeolosaurus*, *BYU9462*, *Gondwanatitan* (Kellner and de Azevedo, 1999), *Jainosaurus*, *Neuquensaurus* (Powell, 1992) and *Pelorosaurus* (Mantell, 1850); or slightly increasing, as in *Ligabuesaurus* (Bonaparte et al., 2006), *Alamosaurus*, *A. wichmannianus*, *Argyrosaurus* 'superbus' (PVL 4628), *Chubutisaurus*, *Epachthosaurus*, *Euhelopus* (Wiman, 1929), *Opisthocoelicaudia* and *Saltasaurus* (Powell, 1992). A curved dorsal scapular margin is present in *Bellusaurus* (Dong, 1990), *C. grandis*, *Elosaurus* (Peterson and Gilmore, 1902), *L. araukanicus* and *I. colberti*.

MACN PV N34 has a straight articulation for the coracoid, as in *Ligabuesaurus*, *B. brancai* SII, *C. grandis* and *Pelorosaurus*, in which is straight and perpendicular to the long axis of the blade, whereas in several basal titanosaurs (Apesteguía and Giménez, 2001), this contact is sigmoid in shape or having a marked step, as in *Alamosaurus*, *A. wichmannianus*, *Bellusaurus*, *Elosaurus parvus*, *Euhelopus* and *I. colberti*. In *Chubutisaurus*, *Epachthosaurus*, *Jainosaurus*, *Neuquensaurus*, *Saltasaurus* and *L. araukanicus*, on the other hand, the suture is straight and inclined backwards.

From another point of view, the angle of the coracoid articular surface with respect to the scapular glenoid line is oriented obtusely with respect to the diaphyseal axis, with the surface forwards, as in *A. 'superbus'* (PVL 4628), *Bellusaurus*, *Chubutisaurus*, *Epachthosaurus*, *Jainosaurus*, *Neuquensaurus*, *Opisthocoelicaudia*, *Saltasaurus* and *L. araukanicus*. On the other hand, this surface is perpendicular or downwardly directed in *Aeolosaurus*, *Alamosaurus*, *Ligabuesaurus* (Bonaparte et al., 2006), *A. wichmannianus*, *Brachiosaurus* SII, *BYU 9462*, *C. grandis*, *Elosaurus*, *Euhelopus*, *Pelorosaurus* and *I. colberti*. Conversely, it is backwardly oriented in *Aeolosaurus* (Powell, 2003), *Alamosaurus*, *Agustinia*, *A. wichmannianus*, *Brachiosaurus* SII, *BYU 9462*, *C. grandis*, *Elosaurus*, *Euhelopus*, *Pelorosaurus* and *I. colberti*. In *A. 'superbus'* (PVL 4628), *Bellusaurus*, *Chubutisaurus*, a new titanosaur from the Aptian of Chubut, *Epachthosaurus*, *Jainosaurus*, *Neuquensaurus*, *Opisthocoelicaudia*, *Saltasaurus* and *L. araukanicus*, the orientation angle of the coracoid articulation surface with respect to the glenoid–scapular line is upwardly straight.

The acromial region arises from the scapular diaphyseal axis at more than 100° as in *C. grandis* (100°), *Supersaurus* (100°), *Elosaurus* (120°) and *Cetiosaurus* (132°). Powell (2003) indicated an angle more acute than that of the post supraglenoid depression ridge for *Neuquensaurus*. In *Apatosaurus louisae*

(Gilmore, 1936), *Apatosaurus* YPM 1980 and *Pelorosaurus* it arises at 90°, whereas it is even less in *Brachiosaurus altithorax* (70°), *BYU 9462* (78°), *Bellusaurus* (80°) and *B. brancai* SII (80°). The lesser angle is present in diplodocoids, being 70° in *Diplodocus* (Hatcher, 1901).

The ventral border of MACN PV N34 is almost straight as in *Ligabuesaurus* (Bonaparte et al., 2006), *Bellusaurus*, *Chubutisaurus*, *Epachthosaurus*, *Jainosaurus*, *Opisthocoelicaudia*, *L. araukanicus* and *I. colberti*. There is a uniform curvature in *Aeolosaurus*, *Alamosaurus*, *A. wichmannianus*, *Argyrosaurus* PVL 4628, *B. brancai* SII, *BYU 9462*, *C. grandis*, *Elosaurus*, *Euhelopus* and *Pelorosaurus*. Perhaps related to the poor development of the scapular glenoid process, the ventromedial process commonly present in basal titanosauriforms is only slight, but its deflected shape is clear.

MACN PV N53 (Fig. 8d–f). This right sauropod femur is 1.03 m in length, and 0.22 m in minimal width, which expands to 0.28 m in the proximal region and 0.27 in the distal one. The femur is complete, lacking only part of the posterior portion of the tibial condyle. Along the proximolateral border, the lateral bulge that characterizes titanosauriformes (Salgado et al., 1997), as evident in *Brachiosaurus*, *Chubutisaurus*, *Austrosaurus* (Longman, 1933), *Aegyptosaurus* (Stromer, 1932), *Phuwiangosaurus* (Martin et al., 1994) and most titanosaurs, is present (Janensch, 1950; Salgado, 1993; Salgado et al., 1997; Wilson and Sereno, 1998). Distal condylar asymmetry is also present, interpreted by Wilson and Carrano (1999) as related to a redistribution of the corporal mass in basal Titanosauriformes.

The anteroposterior compression common in large titanosauriforms (e.g., *Chubutisaurus* and *Ligabuesaurus*) is already present in MACN 53f. Although compression is also present in large diplodocoids (e.g., *Diplodocus*, *Apatosaurus*), titanosauriform femora are more squared than oval in outline. The distal end, not exceptionally widened, is asymmetrical as in titanosaurs (e.g., *Neuquensaurus australis*), with the lateral condyle better developed than the medial. The femoral head is located above the level of the larger trochanter (although the latter is not complete), as in *B. altithorax* (Riggs, 1904) and *Phuwiangosaurus sirindhorneae* (Martin et al., 1994, 1999). The fourth trochanter is located at mid length on the femur and is clearly located on the posterior side rather than medially.

MACN PV N53 (Fig. 8g). The astragalus is high when compared to that of titanosaurs. Its shape is rather pyramidal and stout as in most sauropods, and it bears a distal convex and rugose surface whereas the proximal is concave and complex. The astragalus of *Amargatitanis* has a pronounced ascending process that gives height to the bone. The process extends through a wide and well-developed 3 cm-wide ridge, splitting the posterior fossa in two concave zones: the stepped fibular articular surface, and the wide tibial articular surface. The latter lacks part of its medial development where it should taper. A posterior astragalar fossa crest is absent, just as occurs in *Opisthocoelicaudia* (Borsuk-Bialynika, 1977) and *Dyslocosaurus* (McIntosh et al., 1992).

In *Amargatitanis*, the tibial side of the posterior astragalar fossa bears a deep crescent-shaped fossa on the upper part, with two pairs of deep foramina. In *Bonitasaura* (Apesteguía, 2004),

conversely, there is only one large foramen present in the caudal part of the tibial side of the fossa, very close to the end of the crest. On the fibular side, the posterior fossa bears a deep concavity in which two foramina are visible. Considering its position, they are likely related to the calcaneum.

3. Discussion

Up to now, sauropod material from the La Amarga Formation was restricted to two specimens of the dicraeosaurid *Amargasaurus* (Bonaparte, 1996) and the fragmentary basal diplodocoid *Z. bonapartei* (Salgado et al., 2006). Following from the presence in Central Patagonian basins of Latest Jurassic and Early Cretaceous associations of basal titanosauriforms (Rauhut et al., 2001; Apesteguía and Giménez, 2001) and dicraeosaurids (Rauhut et al., 2005), the discovery of titanosauriforms in the La Amarga was expected. In this work the sauropod diversity of the unit is increased, with evidence of additional lineages of sauropod dinosaurs, namely titanosauriforms and rebbachisauroids.

Among La Amarga diplodocimorphs, that include both dicraeosaurids and rebbachisauroids, the former clade was already known from the Late Jurassic of Tanzania (Janensch, 1929) and Chubut Province (Rauhut et al., 2005). Primitive forms of Rebbachisauroidea, on the other hand, are known from sediments of the same age (Barremian–Aptian) in Spain (Casanovas et al., 2001; Pereda Suberbiola et al., 2003) and Istria (Dalla Vecchia, 1998), as well as the Aptian to Cenomanian of north Africa (Lavocat, 1954; Sereno et al., 1999) and Brazil (Carvalho et al., 2003). In Argentina, remains of rebbachisaurids come from the Aptian (Salgado et al., 2004) and Coniacian of Neuquén Province (Calvo and Salgado, 1995), the Coniacian of Río Negro Province (Gallina and Apesteguía, 2005), and the Cenomanian of Chubut Province (Powell et al., 1989; Lamanna et al., 2001).

The presence at La Amarga of basal diplodocoids such as *Zapalasaurus* and now MACN PV N35 has important phylogenetic and biogeographical implications. Although diplodocoids were once considered a mainly Laurasian clade, the finding of basal forms (Salgado et al., 2006) – rebbachisaurids (this contribution), and dicraeosaurids (Salgado and Bonaparte, 1991) – supports the existence of an important diplodocoid radiation of forms during the Late Jurassic to Early Cretaceous, that was later restricted to rebbachisaurids during the Cenomanian–Coniacian interval, until their complete disappearance from the fossil record (Apesteguía, 2002).

Rebbachisaurids are classically characterized by extremely tall neural spines and reduced but pneumatized vertebral centra (Gallina and Apesteguía, 2005). However, the specimens collected in South America commonly show a moderate development of the neural spine. Adequate phylogenetic analyses will clarify if this is the original condition in rebbachisaurids or the derived one. Considering the prominent extent of the dicraeosaurid neural spines, it is possible that the relatively low neural spines of the South American basal rebbachisauroids could represent the sign of a radiation of a local lineage. This lineage was first known from the dorsal vertebra from Barda Alarcón, which was described by Baron Ferenc Nopcsa in 1902.

However, although the material from Barda Alarcón and MACN PV N35 indicate low spined rebbachisaurids, the latter specimen also retains a well-developed hyposphene. It is becoming clear that there is a lineage related to rebbachisaurids, but lacking several of their diagnostic node-based features, considered here as basal Rebbachisauroidea, or that they represent different lineages of basal diplodocimorphs that radiated in southern continents independently from dicraeosaurids or true rebbachisaurids.

Titanosauriforms are widely recorded from Late Jurassic (Kimmeridgian) to Maastrichtian times (Apesteguía and Giménez, 2001). As an abundant Late Pangean taxon, their remains were collected worldwide and they are thus expected to be present as part of the Amargan assemblage (Leanza et al., 2004). However, as evidenced by several titanosauriforms (e.g., *Brachiosaurus*, *Atlasaurus*), Late Jurassic to Barremian titanosauriforms commonly bear broad-crowned teeth, since it corresponds to their plesiomorphic condition. The finding of a slender-crowned titanosauriform tooth is thus completely unexpected for Barremian times.

Although the tooth shape of *Amargatitanis* is unknown, the presence of its advanced titanosaurian scapula plus the slender-crowned titanosauriform tooth pushes back the origins of the derived titanosaurs widely known from the latest Cretaceous.

4. Conclusions

Early Cretaceous dinosaurs include a wide group of lineages distributed worldwide since the Late Pangean times (Apesteguía, 2002; Leanza et al., 2004); these include elements of clades distributed over Pangea during early to mid-Jurassic (e.g., basal neosauropods; basal neotetanurans; basal neoceratosaurs; eurypodans and basal iguanodontians). However, although supercontinents were still amalgamated, those taxa already acquired some degree of incipient Laurasian–Gondwanan provincialism (Bonaparte, 1979, 1986b; Rauhut, 2002).

In their characterization of the Amargan assemblage, Leanza et al. (2004) remarked on the co-occurrence of those Late Pangean dinosaurs at La Amarga. The dinosaurian taxa recorded by Bonaparte's expeditions in those outcrops include non-diplodocid diplodocoid sauropods (i.e., dicraeosaurids and, now, other basal forms); basal abelisauroid theropods and stegosaurs related to *Kentrosaurus*. The taxonomic similarities among most of the Amargan fauna and the Late Jurassic African fauna were used in order to support a Gondwanan signature (Bonaparte, 1986b; Salgado and Bonaparte, 1991).

Although *Ligabueino* (Bonaparte, 1996) was described as an abelisauroid theropod, and a large quantity of isolated teeth comparable to those of large basal tetanurans (e.g., *Carcharodontosauridae*) were recovered, La Amarga theropods remain mostly unknown. Ornithischians are only known from the stegosaur (Bonaparte, 1996), but the locality is far from being exhausted. Furthermore, the discovery in Australia (Rich, 1996) of a large diversity of unexpected lineages for the Early Cretaceous of Gondwana, opens the possibility of finding representatives of such groups in the La Amarga outcrops.

The addition to the La Amarga fauna of low-spined rebbachisauroids and both basal and derived, broad and

slender-crowned titanosauriforms, suggests not only that the main dinosaurian lineages that would rule the Late Cretaceous ecosystems (i.e., titanosaurs and abelisaurids) were already present since Barremian times, but also that those advanced lineages arose and diversified much earlier than previously recorded.

As described by Apesteguía (2002) and Leanza et al. (2004), the Late Pangean lineages that ruled Early to “Mid” Cretaceous South American ecosystems survived in most cases to Late Cretaceous. However, some others became extinct. The evident diplodocoid radiation of forms present in southern continents during the Late Jurassic to Early Cretaceous points to a Pangean origin of the diplodocoid clade, with a wide distribution of basal forms, as found mostly in southern landmasses and also in the Wealden (Naish and Martill, 2001; Taylor and Naish, 2005). The clade continued in South America up to the Coniacian (Apesteguía, 2002), well after their conspicuous absence from North American Early Cretaceous terrestrial ecosystems.

After the Cenomanian, North American titanosauriforms completely disappear from the fossil record, until their reappearance by Maastrichtian times (e.g., Lehman and Coulson, 2001), probably after their arrival from South America. After Coniacian times, South American diplodocoids followed the same path and became extinct. This was associated by some authors (Apesteguía, 2002; Leanza et al., 2004; Salgado, 2000) with the change in abundance of broad-crowned to slender-crowned titanosaurs, and the rise of the saltasaurines. In a wider faunal context, it coincides with the carcharodontosaurid extinction and the rise of a dromaeosaurid and later abelisaurid theropod domain (Apesteguía, 2002).

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Appendix A. Systematic definitions

Diplodocimorpha Calvo and Salgado, 1995.

Rebbachisauroida.

Histriasaurus boscarolli

Emended diagnosis: diplodocoid sauropod characterized by the following combination of features: mid to posterior dorsal vertebrae with extended lateral spinopostzygapophyseal laminae forming the lateral aspect of the neural spine, neural spine wider than anteroposteriorly extended (convergent with basal macronarians), additional lamina that reaches the postzygapophyses externalmost border like centropostzygapophyseal laminae, but departing from the middle of the extent of the centrodiapophyseal laminae and not from the centrum, centrodiapophyseal lamina with a branch that arises from its mid extension to reach the parapophysis, spinopostzygapophyseal lamina with a branch that arises at the distal region and is directed toward the

postspinal lamina (as this not preserved, it is not possible to know if it reaches it), paired branches from the postspinal lamina directed laterally, non-hollow rhomboidal hyposphene.

Etymology: *Histria*, referring the Latin name of the fossil locality; *saurus*, Gr. reptile. The species honors Mr. Darío Boscarolli, discoverer of the site.

Holotype: WN-V6 (Fig. 13D–E), represented by a complete mid to posterior dorsal neural arch.

Horizon and locality: lacustrine limestone formed in the Adriatic Dinaric Platform, Late Hauterivian–Barremian (Boscarolli et al., 1993; Tunis et al., 1994); at the Kolone locality, near Bale, southwestern coast of Istria, Croatia.

Description: see Dalla Vecchia, 1998, 1999, Fig. 45–Fifty *Nopcsaspondylus* gen. nov.

Type species: *Nopcsaspondylus alarconensis* sp. nov.

Diagnosis: diplodocoid sauropod characterized by mid to posterior dorsal vertebrae with very reduced centra, forked medial centropostzygapophyseal lamina, lateral lamina of the neural spine formed by the spinodiapophyseal lamina plus a lateral spinopostzygapophyseal (different from that forming the postspinal lamina).

Etymology: *Nopcsa*, referring the researcher that first studied this material; *spondylus*, Gr. vertebra.

Nopcsaspondylus alarconensis nov. sp.

Fig. 2

Diagnosis: same as for genus.

Etymology: referring to Barda Alarcón, the original locality where from it was collected by the end of 19th century.

Holotype (lost), represented by a complete mid to posterior dorsal vertebra, with centrum and neural arch separated. The small centrum and large pleurocoel suggest that they derive from the same vertebra, as this is a common feature in rebbachisauroids.

Horizon and locality: coarse sandy levels of the lower section of the Candeleros Formation (presumably), Coniacian (Leanza and Hugo, 1997); Barda Alarcón, NE from Picún Leufú town, Neuquén Province, Argentina.

Description: see Nopcsa, 1902.

Comments: the small centrum and large pleurocoel present in *Nopcsaspondylus* are common features in rebbachisauroid sauropods that, combined with several other allometries, depict its highly heterochronic characteristics.

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