The titanosaur sauropods from the late Campanian–early Maastrichtian Allen Formation of Salitral Moreno, Río Negro, Argentina

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The dinosaur record of the Salitral Moreno locality (Río Negro Province, Argentina) is characterized by a high diversity of herbivore taxa, among them hadrosaurs, ankylosaurs, and titanosaur sauropods, but carnivores are rare, consisting of only a few fragmentary bones of small forms. Titanosaurs are represented by *Rocasaurus muniozi* and *Aeolosaurus* sp., and at least four other taxa, represented by fragmentary material. The elements preserved include a cervical, dorsal and caudal vertebrae, chevron, humerii, ulnae, radii, metacarpal, femora, tibiae, metatarsal, ischia, pubis, and ilium. The Allen Formation is thought to be correlated with the Marília Formation in Brazil, and their faunas have certain elements in common such as aeolosaurines, but saltasaurines and hadrosaurs, are known exclusively from the Allen Formation. These absences, and particularly that of the saltasaurines, may be because those sauropods originated late in the Cretaceous, probably in southern South America (Northern Patagonia?), and they did not have time to disperse to northern South America.

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Introduction

The fossil record of Patagonian titanosaurs spans from the upper Lower Cretaceous (Aptian–Albian) to the latest Cretaceous (Campanian–Maastrichtian). In northern Patagonia, the Late Cretaceous is characterized by an unusually high titanosaur diversity, which does not seem to diminish up to the end of the period (Salgado and Bonaparte 2007); in fact, the many titanosaurs recorded in the Allen Formation as well as in other correlated units (e.g., Los Alamitos Formation), are among the latest Patagonian non-avian dinosaurs.

Four titanosaurian taxa have been identified in the Allen Formation: *Rocasaurus muniozi* (Salgado and Azpilicueta 2000), *Aeolosaurus* sp. (Salgado and Coria 1993), *Bonatitan reigi* (Martinelli and Forasiepi 2004), and *Antarctosaurus wichmannianus* (Huene 1929); in addition, fragmentary material belonging to two indeterminate titanosaurs from the same levels has been described recently (Paulina Carabajal and Salgado 2007; García et al. 2008). Finally, numerous dinosaur eggs and eggshells were recovered from the Allen Formation (Powell 1987a, 1992a; Magalhaes Ribeiro 1997; Simón 2006;

Salgado et al. 2007, 2009), some belonging to the oofamily Megaloolithidae, currently assigned to titanosaurs (Powell 1987a, 1992a; Simón 2006; Salgado et al. 2007, 2009).

Here we present detailed re-descriptions of *Rocasaurus muniozi* and *Aeolosaurus* sp., the only two sauropod taxa formally recognized from the locality of Salitral Moreno (Northern Río Negro Province), one of the most prolific sites for dinosaur remains in northern Patagonia, and describe for the first time new material from the same locality belonging to at least another four titanosaurs. All the specimens, collected between 1989 and 1994 in successive expeditions carried out by the Museo de Geología y Paleontología de la Universidad Nacional del Comahue (at Neuquén, Argentina) and the Museo de Cipolletti "Carlos Ameghino" (Río Negro, Argentina), are housed in this last institution. These materials give us an idea of the high diversity that titanosaurs achieved at the end of the Cretaceous, at least in some areas of Patagonia.

Institutional abbreviations.—MPCA-Pv, Vertebrate Paleontology collection of the Museo Provincial de Cipolletti "Carlos Ameghino", Río Negro, Argentina.

Location and geological setting

Salitral Moreno is approximately 25 km south of General Roca city, in the centre-north of Río Negro province, Argentina (Fig. 1). Here, sediments of the Allen Formation are partially exposed, and they have been dated as early Maastrichtian (Bertels 1964, 1969; Legarreta and Gulisano 1989), Campanian–Maastrichtian (Ballent 1980; Uliana and Dellapé 1981) and late Campanian–early Maastrichtian (Hugo and Leanza 2001).

The exposures of the Allen Formation at Salitral Moreno, and at the neighbouring locality of Salitral Ojo de Agua, probably correspond to its Mid Member (Salgado et al. 2007), recognized for the first time by Andreis et al. (1974) in the area of Lago Pellegrini-Cinco Saltos (Río Negro Province). All the specimens described in this work, as well as those assigned to hadrosaurs (Coria 2009) and ankylosaurs (Salgado and Coria 1996), and theropods (Coria and Salgado 2005), come from at least four small quarries in an area of 0.12 km², defined by the following coordinates: 39°17'51. 39"S, 67°32'35.74"W; 39°17'48.28"S. 67°32'3.24"W; 39° 17'56.45"S, 67°23'35.90"W, and 39°17'52.98"S, 67°32' 1.88"E. In the stratigraphic profiles of Simón (2006: fig. 2), the specimens come from NF1 and NF4, at the base of the sequences. In particular, *Rocasaurus muniozi* gen. et sp. indet. 1, and the ankylosaur materials probably come from NF1, whereas *Aeolosaurus* gen. et sp. indet. 2–4, probably come from NF4.

Systematic paleontology

Saurischia Seeley, 1888

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Titanosauria Bonaparte and Coria, 1993

Genus *Aeolosaurus* Powell, 1987a

Type species: *Aeolosaurus rionegrinus* Powell, 1986; Ingeniero Jacobacci, Maastrichtian.

Aeolosaurus sp.
Figs. 2–4, 5A.

Material.—A single specimen (MPCA-Pv 27174) represented by three anterior caudal vertebrae, one mid-caudal, one mid-posterior caudal, right ulna, left radius, metacarpal III, left pubis, and right ischium. A second specimen (MPCA-Pv 27175) is represented only by a left ulna. Salgado and Coria (1993) provided a brief description of most of these elements. In this work, we re-describe the already published material and describe for the first time other material very probably belonging to a third specimen, a left ulna, MPCA-Pv 27180. Besides, there is a lot of material of *Aeolosaurus* sp. that could belong to any of these three specimens: a left humerus (MPCA-Pv 27176), a left femur (MPCA-Pv 27177), a meta-
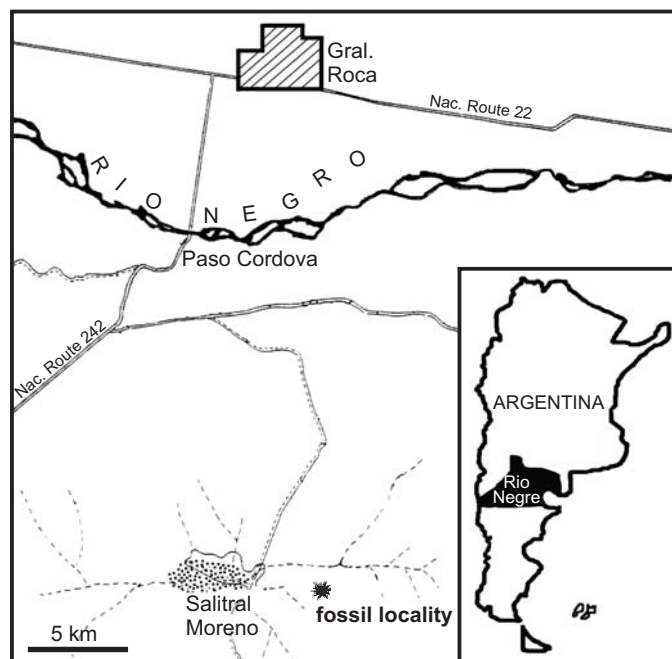

Fig. 1. Site map showing the geographical location of Salitral Moreno, where specimens of titanosaurs were collected.

tarsal I (MPCA-Pv 27178), and a haemal arch (MPCA-Pv 27179). In addition, there is a partial sacrum, assigned to the specimen MPCA-Pv 27174 by Salgado et al. (1997), that clearly comes from a much smaller sauropod. All from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Description

Anterior (1st and 2nd?) caudal vertebra.—Salgado and Coria (1993) mentioned but did not describe two large, anterior caudal vertebrae, which confidently belong to the specimen MPCA-Pv 27174. These elements are incomplete and badly crushed, but some characters are easily distinguishable. The wide centrum is only slightly procoelous; its lateral faces are anteroposteriorly concave and dorsoventrally plane; in lateral view, the robust articulations for the haemapophyses are prominent. The neural arch is robust and the neural canal is wide. The small and slender transverse processes are clearly observed (Fig. 2A). The neural spine is not preserved.

Anterior (3rd?) caudal vertebra.—Unlike the elements previously described, the centrum of this vertebra is strongly procoelous, with broad articular surfaces (Salgado and Coria 1993). Its lateral faces are anteroposteriorly concave and dorsoventraly plane. The ventral face is only slightly anteroposteriorly concave.

The base of the neural arch occupies all the anteroposterior length of the centrum. The transverse processes are placed on the neural arch, just above the centrum-arch boundary. These are robust and directed posterolaterally (Fig. 2B, Supplementary Online Material: SOM 1 available at http://app.pan.pl/SOM/app58-Garcia_Salgado_SOM.pdf)
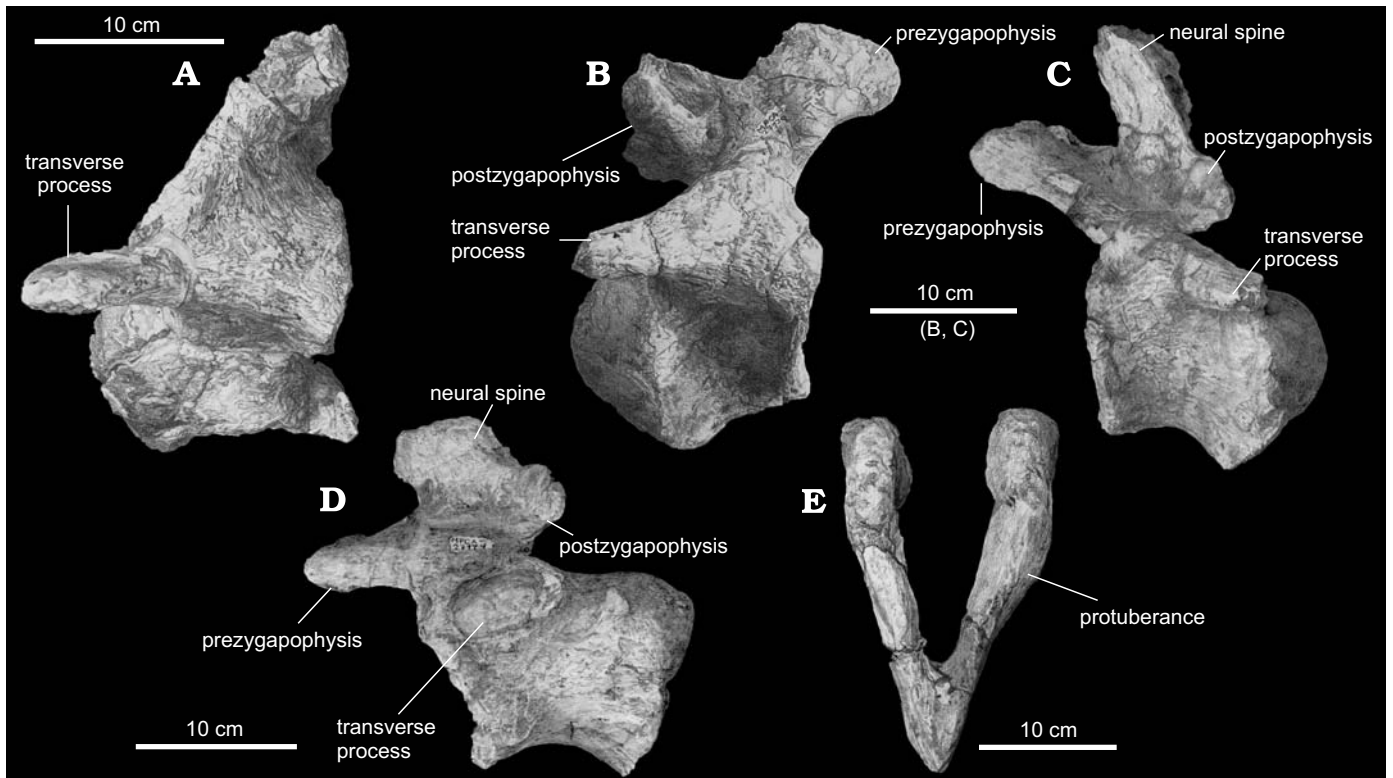
Fig. 2. Titanosaur sauropod *Aeolosaurus* sp. (MPCA-Pv 27174) from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. First ? anterior caudal vertebrae, in right lateral view. **B**. Third? anterior caudal vertebrate, in right lateral view. **C**. Fifth? anterior caudal vertebrae, in left lateral view. **D**. Tenth? anterior caudal vertebrae, in left lateral view. **E**. Haemal arch, in anterior view.

As described by Salgado and Coria (1993), the prezygapophyses are robust, anterodorsally projected at an angle of nearly 60° above the floor of the neural canal. The articular facets of the prezygapophyses are broad, ellipsoid, with their greater axes anteroposteriorly oriented, and their articular surfaces almost vertical. The postzygapophyses are equidistant from the anterior and posterior borders of the centrum; these are short and are, like the prezygapophyses, substantial. The articular surfaces of the postzygapophyses are broad and kidney-shaped, with their greater axes dorsocaudally oriented. The neural spine is not preserved.

Mid (5th?) caudal vertebra.—The centrum has broad, high lateral faces, which are anteroposteriorly concave and dorsoventrally plane. The ventral face is narrow, with the articulations for the haemapophyses well developed, enclosing a deep furrow between them. In lateral view (Fig. 2C), the ventral border of the centrum is very concave.

The transverse processes are robust and posterolateraly projected. They are ventral to the postzygapophyses, rather below the position in the anterior caudals (Fig. 2A–C). The neural arch is on the anterior-mid part of the centrum, more anterior than in the anterior caudals, and it is more anteriorly inclined.

The prezygapophyses are more elongate and more anteroventrally inclined than in the anterior caudals; they form an angle of 40° to the base of the neural canal. The articular facets are subcircular and subvertical. The pre- and postzygapophyses are horizontal and level, a condition that changes to-

wards the posterior caudals; obviously, this is explained by the different curvatures of the successive portions of the tail.

The postzygapophyses are at the base of the neural spine, on the middle of the vertebral centrum, dorsal to the anterior portion of the transverse processes. The articular surface of the postzygapophysis is subtriangular, slightly concave dorsoventrally, and smaller than the articular surface of the prezygapophyses. The spinopostzygapophyseal lamina is well developed.

The neural spine is anterodorsally inclined at 80° to the base of the neural canal, and at 40° to the prezygapophyses; it is lateromedially compressed, mostly in its mid portion. The distal end of the neural spine surpasses the anterior border of the centrum. On the right lateral side of the neural spine, where the bone is damaged, it is not possible to observe pneumatic tissue. The spinoprezygapophyseal lamina and spinopostzygapophyseal lamina are preserved only on the left side of the neural spine: these laminae contact the neural spine with the pre- and postzygapophyses, respectively.

Mid-posterior (10th?) caudal vertebra.—The centrum (Fig. 2D) is similar to that of the mid caudal, except for the articular condyle, which is less pronounced and more dorsally pointing. The lateral sides of the centrum are somewhat less concave than in the mid caudal, and the ventral face is broader. The articulations for the haemapophysis, although incompletely preserved, are well developed, more than in the anterior and mid caudal.

The well-developed prezygapophyses are robust, anteriorly projected, and placed just above the centrum-neural arch boundary. The articular surfaces of these apophyses are slightly convex, and their planes are practically vertical. The postzygapophyses are placed at a higher level than the prezygapophyses, unlike the condition in the anterior and mid caudals. The articular surface of the postzygapophysis is concave, being in the vertical plane, mostly its lower half. The neural spine is low and notably compressed lateromedially, more than in the mid caudal; it is anteriorly directed, but not as much as in the caudal vertebrae already described.

Chevron.—A complete, probably mid-distal haemal arch (MPCA-Pv-27179) is well preserved. This element (Fig. 2E) was not previously described. The haemal spine is very short; the haemal canal is wide, and, in lateral view, the haemal peduncles are angled 40° posteriorly, with respect to the haemal spine. The articular surfaces for the vertebral centrum are well developed. The right process has a protuberance, probably a deformation or a scar.

Humerus.—A left humerus is preserved, and is described here for the first time (Fig. 3A). The humeral head and deltopectoral crest are partially preserved; however, it is possible to infer that the proximal portion of the bone was expanded lateromedially, much like the humerus of *Aeolosaurus* from the Los Alamitos Formation described by Salgado et al. (1997a). In anterior view, the medial margin is markedly concave, much more than the lateral margin, which is straighter (Fig. 3A$_1$, A$_2$), but not as concave as in *Neuquensaurus* (Salgado et al. 2005; Otero 2010). The deltopectoral crest, although partially preserved, is robust and presents a protuberance on its lateral margin. In posterior view (Fig. 3A$_4$), the cuboid fossa or intra-condylar furrow on the distal end of the bone is broader than that of the humerus of the titanosaur described below (MPCA-Pv 88/A) and other titanosaurs. The ratio between the minimum shaft diameter and the length of the bone is 0.17 (14 cm /81.5 cm) (see SOM 1). This value shows that this element is robust when compared with the same bone of the Titanosauria gen. et sp. indet. 2 (MPCA-Pv 88/A) described below.

Ulna.—Three basically similar ulnae (Fig. 3C, D), one right (MPCA-Pv 27174), belonging to the same specimen as the other pieces, and two left, one of a greater size (MPCA-Pv 27175) and the other one, smaller (MPCA-Pv 271780), are relatively well preserved, although the anterolateral process of the MPCA-Pv 27175, and the olecranon process of the MPCA-Pv 271780) are incomplete (see SOM 1). The morphology of the ulnae is similar to that of *Aeolosaurus rionegrinus*. The bone has three main structures, which in proximal view are easily observed. There are two conspicuous processes, the anteromedial and anterolateral, which run longitudinally, becoming less developed to the distal end, and the olecranon process, which is placed posterolaterally at the most proximal end of the bone.

Posteriorly, the ulna has a broad, concave surface that reaches the mid portion of the bone: from there up to the distal condyle, the bone surface is plane. In lateral view (Fig. 3C$_1$), on the radial face, the three specimens show a notable anterolateral process (in the largest ulna this process is only represented by its base), which runs along the length of the bone, dividing two surfaces, one broader than the other, the first one being that that for articulation with the radius.

Near the most proximal anteromedial process, on the broader surface, an osseous protuberance (scar) is observed, probably for muscular attachment. Proximally, as noted by Salgado and Coria (1993), the ulna is triradiate and the olecranon is prominent, as is common in titanosaurs (Fig. 3C$_2$, C$_3$). The distal articulation is semicircular (Fig. 3C$_4$). The greater axis of the distal epiphysis (articular surface) is perpendicular to the greater axis of the proximal epiphysis (articular surface).

Radius.—A left radius is preserved (MPCA-Pv 27174). This bone matches perfectly with the right ulna MPCA-Pv 27174 (Salgado and Coria 1993), and these probably belong to the same individual (see SOM 1). It is a slightly curved bone, lateromedially compressed, with its epiphyses (distal and proximal) expanded, the proximal epiphysis being more expanded than the distal one (Fig. 3E). The lateral margin is slightly concave, while the medial is straight. Distally on its lateral face, a rugose, very developed prominence is present; this is perhaps for the insertion of M. flexor carpi radialis (Borsuk-Białynicka 1977). In posterior or ulnar view, the interosseous ridge runs from the proximomedial portion three-quarters of the way along the bone, but it is not so developed as in other titanosaurs such as *Rapetosaurus* (Curry Rogers 2009) and *Neuquensaurus* (Otero 2010). The width of the proximal expansion practically doubles the narrowest portion of the diaphysis, and its proximal margin is oriented perpendicular to the long axis of the diaphysis, while the distal margin is oblique to the long axis.

Metacarpal.—The only bone of the metacarpus that is preserved is a third metacarpal (Salgado and Coria 1993). It is straight and robust; however, it is less robust than the metacarpal reassigned to *Neuquensaurus robustus* by Otero (2010). At mid-shaft the section of the bone is elliptic, and its ends are only slightly expanded (Fig. 3B, SOM 1). The proximal articular surface is markedly wider than the distal articular end, and has a triangular contour in proximal view. Distally, the articular surface is elliptical. The metacarpal/radius ratio is 0.73, the highest value in a sauropod, which raises doubts about the association of the two elements. Likewise, the metacarpal is 73.3% of the radius, much higher than the values in *Camarasaurus* (47%), and in the titanosaurs *Opisthocoelicaudia* (46%) and *Alamosaurus sanjuanensis* (51%) (Apesteguía 2005).

Pubis.—A left pubis (MPCA-Pv 27174) is preserved. Compared with the pubis of other titanosaurs (e.g., *Neuquensaurus*) it is a robust bone (Fig. 4B). Its distal end is practically complete, except for the distalmost portion, which appears not to have been strongly expanded. It is wide dorsolatero-ventromedially, and its lateroventral face bears a longitudinal crest ("ventral crest" of Powell 2003 and Otero
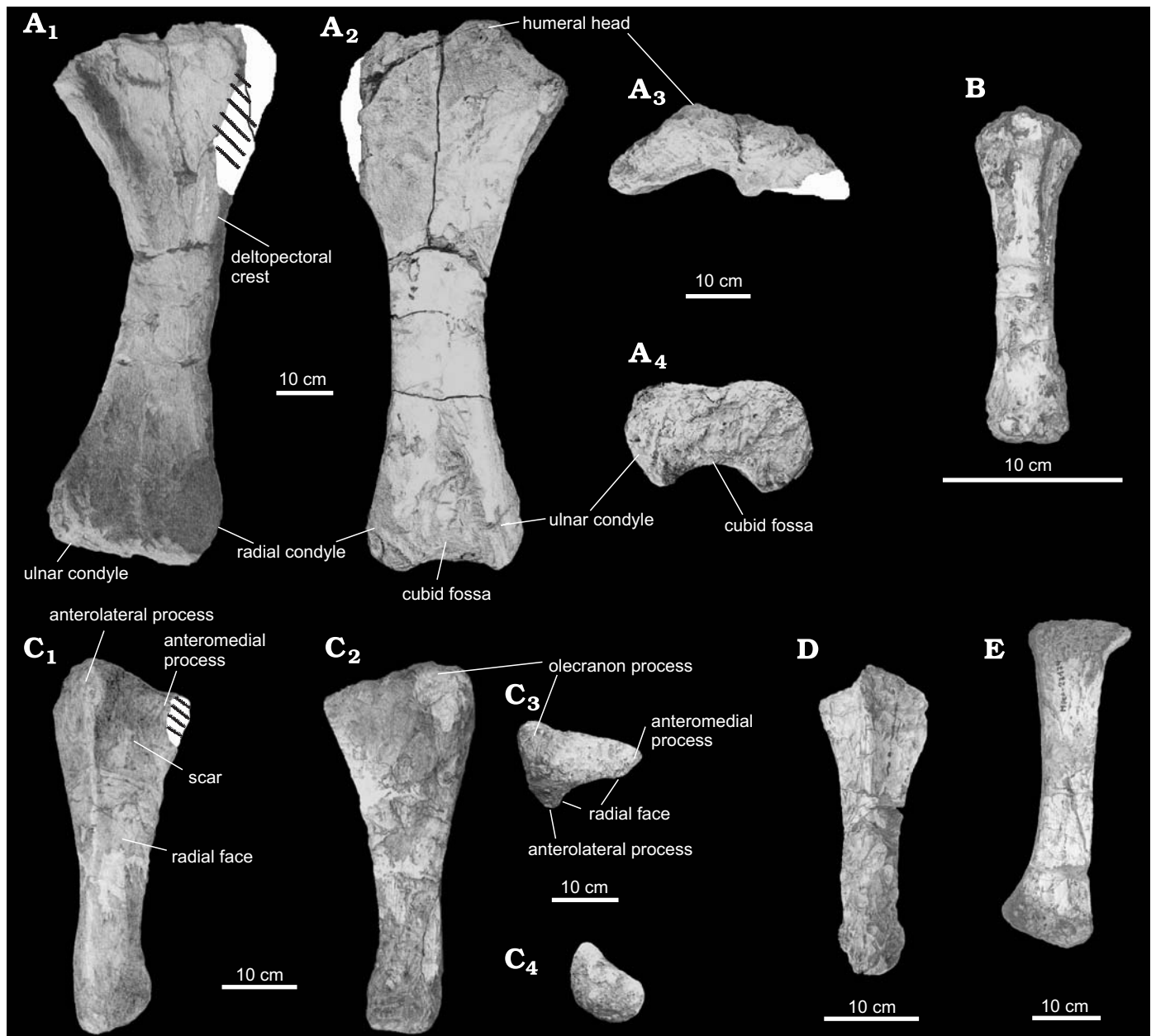
Fig. 3. Titanosaur sauropod *Aeolosaurus* sp., forelimb from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Left humerus (MPCA-Pv 27176), in anterior (A_1), posterior (A_2), proximal (A_3), and distal (A_4) views. **B**. Metacarpal III (MPCA-Pv 27174), in anterior view. **C**. Right ulna (MPCA-Pv 27174), in lateral (C_1), posterior (C_2), proximal (C_3), and distal (C_4) views. **D**. Left ulna (MPCA-Pv 27180), in lateral view. **E**. Left radius (MPCA-Pv 27174), in posterior view.

2010) that divides two surfaces, much like the crest observed in other titanosaurs, such as *Uberabatitan* (Salgado and Carvalho 2008). At its mid part, the pubis has a nearly elliptical cross-section. The laterodorsal margin of the pubis is concave, whereas the medioventral margin is irregular, in part due to its poor preservation. The articular surface for the ischium is the thickest portion of the bone, becoming abruptly laminar and thin towards its ventral portion. The articulation with the ilium is not completely preserved. The obturator foramen is placed near the puboischiatic contact.

Ischium.—The right ischium is practically complete (Fig. 4C). The iliac peduncle is relatively short, and significantly less robust than in the holotype of *Aeolosaurus rionegrinus*. The acetabular border is short, notably less extensive than in the holotype. The distal process is laminar, narrow at its mid portion, and distally expanded: it is not possible to appreciate the ischial tuberosity, as in *Neuquensaurus australis* (Otero 2010). The caudal margin of the ischium is less concave than in *Aeolosaurus rionegrinus*. The pubic peduncle is proximally wide; it is the thickest portion of the bone, as is the articular surface for the ischium of the pubis, which indicates a robust contact. Ventrally, the pubic peduncle becomes thin, becoming only a few millimetres thick (Fig. 4C, SOM 1).

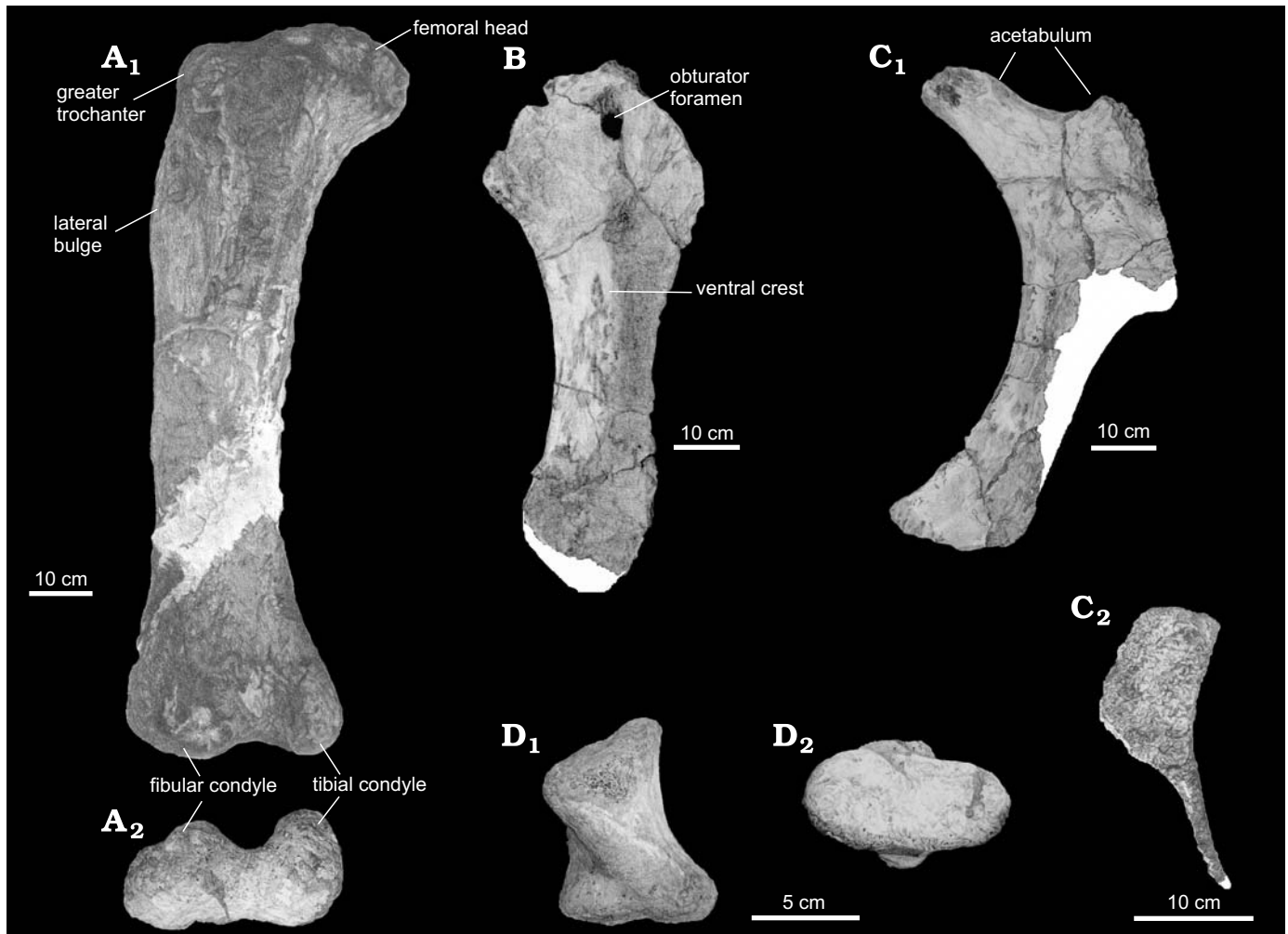*Femur*.—The preserved left femur of this specimen was not

Fig. 4. Titanosaur sauropod *Aeolosaurus* sp. from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Left femur (MPCA-Pv 27177), in posterior (A_1) and distal (A_2) views. **B**. Left pubis (MPCA-Pv 27174), in anterolateral view. **C**. Right ischium (MPCA-Pv 27174), in lateral (C_1) and pubis articular surface (C_2) views. **D**. Metatarsal I (MPCA-Pv 27178), in medial (D_1) and proximal (D_2) views.

described by Salgado and Coria (1993); it is straight, with its lateral and medial margins being virtually parallel (Fig. 4A). It is anteroposterioly compressed, and mediolaterally wide (mediolateral/anteroposterior index is 2.08). The lateral bulge that characterizes the femora of titanosauriformes is somewhat less developed than in other titanosaurs (e.g., *Neuquensaurus* [Otero 2010]; *Rocasaurus* [Salgado and Azpilicueta 2000]; *Titanosauria* indet. here described). The greater trochanter is developed at the intersection of the virtual extension of the dorsal surface of the femoral head with the virtual extension of the line that contains the most lateral point of the lateral bulge. The angle formed by these two straight lines is 114°, which is less than in *Rocasaurus* and Titanosauria gen. et sp. indet. (MPCA-Pv 33/2) (Fig. 5). The ratio between the minimum shaft width and the bone length, the so-called robustness index, is 0.19 (see SOM 1). The distal end of the femur, including the tibial and fibular condyles, seems to be somewhat less expanded than in other taxa (Fig. 5). The posterior intercondylar groove is shallow, and reaches dorsally only 15% of total femur length.

Metatarsal.—The bone (MPCA-Pv 21778), here interpreted as a metatarsal I, was found associated with the other elements above described. It is short, with expanded proximal and distal ends (Fig. 4D). The proximal and distal articulations have elliptical contours, and form an angle of 90°. This rotation is the main difference between this bone and the same bone in *Rapetosaurus* (Curry Rogers 2009).

Saltasaurinae Powell, 1992b

Genus *Rocasaurus* Salgado and Azpilicueta, 2000

Type species: *Rocasaurus muniozi*; Salitral Moreno locality, Campanian–Maastrichtian.

Rocasaurus muniozi Salgado and Azpilicueta, 2000
Figs. 5B, 6, 7, 8.

Holotype: One cervical centrum, MPCA-Pv 46/1; one cervical neural arch, MPCA-Pv 46/2; two dorsal centra, MPCA-Pv 46/7 and MPCA-Pv 46/8; and four neural arches, MPCA-Pv 46/3, MPCA-Pv 46/4, MPCA-Pv 46/5, and MPCA-Pv 46/6; one mid caudal vertebra, MPCA-Pv 46/9; one posterior caudal vertebra, MPCA-Pv 46/10; both ischia, MPCA-Pv

46/11 (left) and MPCA-Pv 46/14 (right); left pubis, MPCA-Pv 46/15; left ilium, MPCA-Pv 46/12 and fragment of the right one, MPCA-Pv 46/13; left femur, MPCA-Pv 46/16. All from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Referred material.—Cervical vertebrae, MPCA-Pv 858, MPCA-Pv 859 and MPCA-Pv 860; cervical neural arch, MPCA-Pv 46; anterior caudal vertebrae, MPCA-Pv 47, MPCA-Pv 48, MPCA-Pv 57, and MPCA-Pv 60; mid caudal vertebrae, MPCA-Pv 49 and MPCA-Pv 58; posterior caudal vertebra, MPCA-Pv 50; distal caudal vertebrae, MPCA-Pv 51, MPCA-Pv 54, MPCA-Pv 56, and MPCA-Pv 56/1. All from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Description

Cervical vertebrae.—The cervical vertebrae are represented by one centrum and a partial neural arch of the holotype (MPCA-Pv 46/1, 46/2). There are also three undescribed posterior cervical vertebrae (MPCA-Pv 858, MPCA-Pv 859, and MPCA-Pv 860), which are here referred to *Rocasaurus muniozi*.

The cervical centrum of the holotype is extremely depressed, but this arises from its bad preservation (Salgado and Azpilicueta 2000). However, it is still possible to observe a dorsally open neural canal, which is laterally limited by the sutural rugosities by which the centrum articulated to the neural arch. The lack of fusion between centrum and neural arch suggests that the specimen is a juvenile.

The centrum of the cervical vertebrae is opisthocoelous. In lateral view, it shows a badly preserved, low pleurocoel, which occupies most of the lateral face of the centrum (41%). Ventrally, the bases of the laterally projected parapophyses are present. The neural arch of the type material presents some deformation, which does not allow a precise identification of its structures.

The vertebrae MPCA-Pv 858 to 860 (Fig. 6) come from approximately 200 m east of the quarry that produced the holotype of *Rocasaurus muniozi*. The centra are low, with the pleurocoels somewhat more developed than in the type specimen (it occupies 47% of the centrum length) (SOM 2).

The pleurocoel is deep, reaching almost to the sagittal plane of the centrum. In MPCA-Pv 860, this depression is divided by an anteroposteriorly directed thin lamina, also present in *Saltasaurus* (Powell 1986, 2003), *Bonatitan* (Martinelli and Forasiepi 2004) and *Rinconsaurus* (Calvo and Gonzalez-Riga 2003). Both centrum and neural arch are composed of highly spongy osseous tissue.

The ventral face of the centrum is plane; it has only a shallow concavity produced by the lateroventral elongation of the parapophyses. The neural canal is relatively broader than in the holotype. The neural arch height, excluding the neural spine, which is not preserved in any specimen, is 56% of the total vertebral height.

The prezygapophyses, only preserved in MPCA-Pv 859, are low and notably developed; the articular surface is ellipsoid with a length of 4.5 cm on its greater axis (Fig. 6A). The
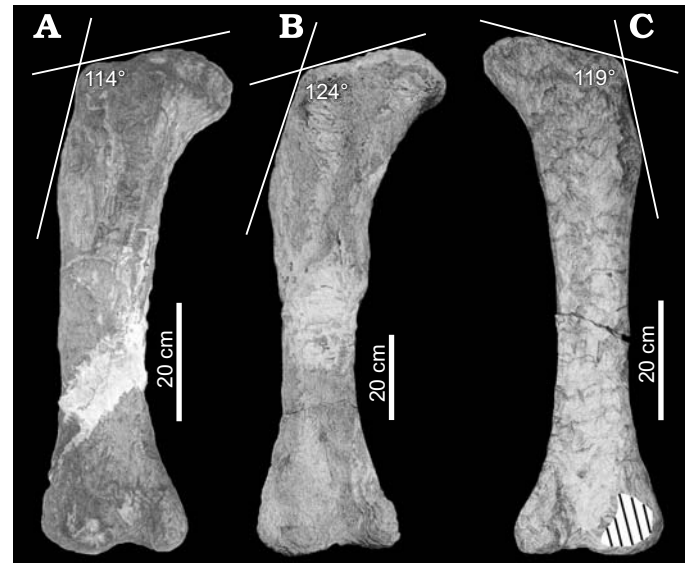

Fig. 5. Femora of titanosaurs from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous, showing the greater trochanter angle. **A**. *Aeolosaurus* sp. (MPCA-Pv 27174). **B**. *Rocasaurus muniozi* Salgado and Azpilicueta, 2000 (MPCA-Pv 46/6). **C**. *Titanosaurus* sp. (MPCA-Pv 33/2).

postzygapophyses are more robust than the prezygapophyses. The articular surface is tear-drop-shaped, and has a length of 5 cm in MPCA-Pv 859 and 5.7 cm in MPCA-Pv 860. The greater axis of the articular surface of the postzygapophyses, dorsoventrally oriented, lies parallel to the sagittal plane of the vertebra.

In MPCA-Pv 858 to 860, a well developed posterior centrodiapophyseal lamina roofs dorsally an anteroposteriorly extended pleurocoel (Fig. 6A, C). The postzygodiapophyseal lamina is well developed; notably, this lamina is distally forked in MPCA-Pv 860. The spinodiapophyseal is also well developed.

Dorsal vertebrae.—There are two vertebral centra (MPCA-Pv 46/7, MPCA-Pv 46/8) and four neural arches (MPCA-Pv 46/3, MPCA-Pv 46/4, MPCA-Pv 46/5, MPCA-Pv 46/6), two of which are only represented by their lateral portions (Fig. 7). The two centra are strongly opisthocoelous, bearing small pleurocoels that are placed high on the centrum, practically at the base of the neural arch (Salgado and Azpilicueta 2000) (SOM 2).

The lateral faces of the centra are flat, both anteroposteriorly and dorsocaudally. Their ventral faces are deeply concave anteroposteriorly. The two centra show, in dorsal view (Fig. 7A$_2$), a wide neural canal laterally bounded by rugose, low neural peduncles.

From the four neural arches preserved, probably three belong to a fifth, eighth, and tenth dorsal, respectively. The absence of fusion between the centra and the arches, as in the cervical vertebrae, suggests this ia an immature animal. The anteriormost neural arch preserved (the fifth) belongs to the holotype (Salgado and Azpilicueta 2000: fig. 3); it is transversely wide, with a posterodorsal inclination of 50° to the hor-
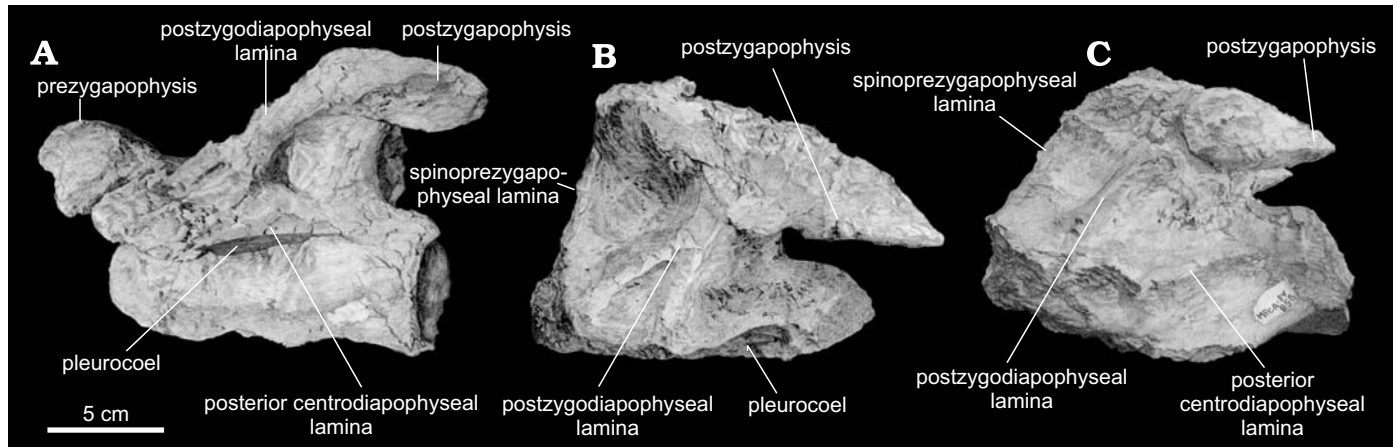
Fig. 6. Titanosaur sauropod *Rocasaurus muniozi* Salgado and Azpilicueta, 2000 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. Cervical vertebrae MPCA-Pv 859 (**A**), MPCA-Pv 860 (**B**), and MPCA-Pv 858 (**C**) in lateral views.

izontal. In anterior view (Fig. 7B), it exposes a broad surface, extending ventrodorsally, along its entire extent, by a prespinal lamina. The neural spine, notably wide, unites to the well-developed diapophyses by means of the spinodiapophyseal laminae. The diapophyses are dorsolaterally projected, being ventrally united to the modestly developed parapophyses by means of the paradiapophyseal laminae, and to the prezygapophyses by means of the prezygodiapophyseal laminae. Both the diapophyses and parapophyses are strongly anteroposteriorly compressed. The prezygapopyses are broad, lanceolate, and their planes form a V, with an angle of nearly 75°.

In posterior view (Fig. 7C), it is possible to observe a stout postspinal, which goes from the contact between the postzygapophyses, one of which is very incomplete, to the neural spine (Salgado and Azpilicueta 2000: fig. 3). The centropostzygapophyseal laminae join to the posterior centrodiapophyseal laminae at the base of the neural arch. The posterior centrodiapophyseal laminae is the most developed lamina. Towards its distal end it is expanded.

None of the preserved neural arches possesses a hyposphene, like other titanosaurs (Salgado et al. 1997b; Powell 2003). Considering the preserved four neural arches, it may be inferred that their width decreased toward the posterior vertebrae.

The dorsal neural arch of the 8th? is incomplete and lateromedially deformed, but it is possible to see some details that are not appreciable in other materials (Fig. 7B). The posterior centrodiapophyseal laminae is notably bifurcated at its base (Salgado and Azpilicueta 2000: fig. 5), which produces a triangular depression between the bifurcation and the base of the neural arch. From the anterior ramus of this bifurcation, the accessory posterior centrodiapophyseal laminae, according to Salgado et al. (2005), originate three small, parallel laminae: the mid lamina (the greater of the three) is the posterior centroparapophyseal laminae; dorsal to it there is the unnamed parapophyseal lamina, and ventral is the accessory laminae. These laminae contact the anterior centroparapophyseal laminae, which are very sharp in this species. The unnamed para-

pophyseal lamina originates from a non-bifurcated portion of the posterior centrodiapophyseal laminae.

The dorsal neural arch of the 10th? vertebra is complete and somewhat anteriorly inclined, perhaps as a consequence of deformation post-mortem (Fig. 7C). In anterior view, the most distinctive feature of this element is a robust prespinal lamina (prsl) that is directed from the distal extreme of the neural spine to its contact with the prezygapophysis. From the contact between the postzygapophyses and the neural spine originates the posl, which is internal and parallel to the spinopostzygapophyseal laminae. Ventral to the postzygapophyses, there are the well developed but short centropostzygapophyseal laminae. This reveals that, in this vertebra, unlike the fifth? dorsal vertebra, the postzygapophyses are closer to the neural canal.

Anterior caudal vertebrae.—The anterior caudals are represented by four elements (referred materials, MPCA-Pv 47, MPCA-Pv 48, MPCA-Pv 57, MPCA-Pv 60, see SOM 2), all procoelous (Fig. 7D, F). The procoely becomes more pronounced towards the most posterior vertebrae.

These vertebrae are short and tall, wider than long and, as noted by Salgado and Azpilicueta (2000), all the caudal vertebrae possess a deep ventral cavity divided by a longitudinal septum, which is a character shared with *Saltasaurus* Powell, 1986. This cavity reaches its greatest depth in the mid caudals (here, it is 50% of the centrum depth) and becomes shallow in the posterior caudals (Fig. 7E$_2$).

Throughout the broken surfaces of MPCA-Pv 48 it is possible to observe the cavernous osseous tissue. The pleurocoel is very small and placed on the ventral half of the lateral face, equidistant from the anterior and posterior margins, just below the base of the caudal rib. On the left lateral face of vertebra MPCA-Pv 57, the border that limits the posterior articular surface of the centrum presents an osseous overgrowth, with a lateral continuation of the centrum, probably pathological.

Mid caudal vertebrae.—All the mid and posterior caudal vertebrae (both in the holotype MPCA-Pv 46/9 and referred
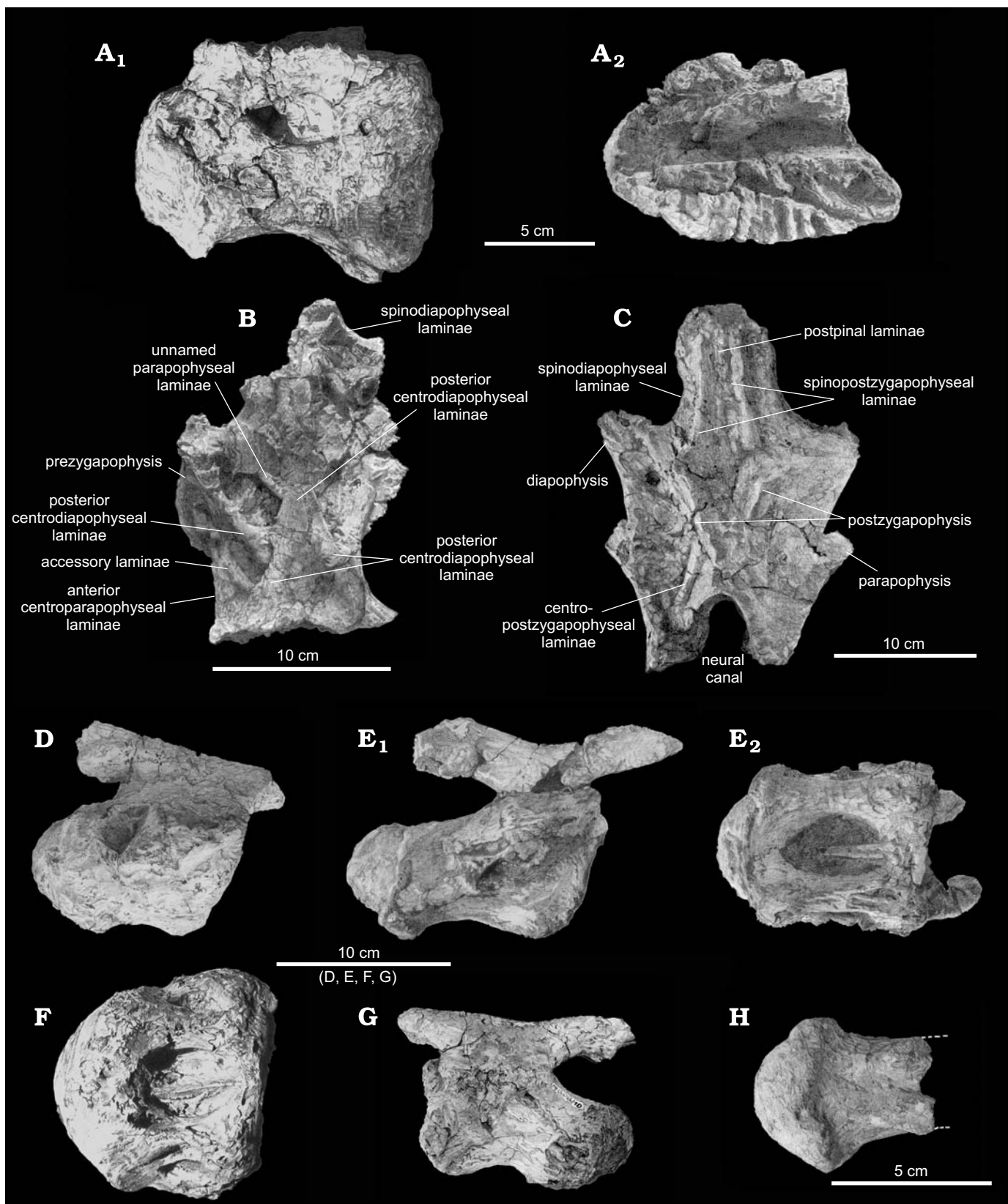
Fig. 7. Titanosaur sauropod *Rocasaurus muniozi* Salgado and Azpilicueta, 2000, vertebrae from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Dorsal vertebra (MPCA-Pv 46/8), in lateral (A₁) and dorsal (A₂) views. **B**. Dorsal neural arch of the 8th? (MPCA-Pv 46/4), in lateral view. **C**. Dorsal neural arch of the 10th? (MPCA-Pv 46/5), in posterior view. **D**. Anterior caudal vertebra (MPCA-Pv 57), in lateral view. **E**. Mid caudal vertebra (MPCA-Pv 58), in lateral (E₁) and ventral (E₂) views. **F**. Anterior caudal vertebra (MPCA-Pv 47), in ventral view. **G**. Posterior caudal vertebra (MPCA-Pv 46/10), in lateral view. **H**. Distal posterior caudal vertebra (MPCA-Pv 56), in dorsal view.

material, MPCA-Pv 49 and MPCA-Pv 58, see SOM 2) are strongly procoelous. In these vertebrae (Fig. 7E), characteristically, the posterior articulation of the centrum is placed slightly dorsally with respect to the mid longitudinal axis of the centrum.

In posterior view, the articulation shows a peripherical rim which completes the contour of the centrum. The rim becomes thicker, more robust, in the articulation for the haemapophyses, which resembles the condition observed in Titanosauria gen. et sp. indet. 4. On the lateral faces of vertebrae MPCA-Pv 49 and MPCA-Pv 58, two small, vertically aligned pleurocoels are observed. The lateral face of the holotype is convex and lack pleurocoels. Internally, the caudal vertebrae, as noted by Salgado and Azpilicueta (2000), present a great development of spongy tissue, composed of numerous and irregular cells.

The prezygapophyses are relatively short, surpassing the anterior border of the vertebral centrum (Fig. 7E$_1$). The articular faces are well developed and elliptical, their planes inclining medially at 45–50° to the horizontal.

In the mid and mid-posterior caudals, the neural arches are placed on the anterior half of the centrum, and are strongly inclined backwards, the neural spine surpassing the posterior border of the vertebral centrum (Fig. 7E$_1$). The neural arches are low, much lower than in other titanosaurs (e.g., *Neuquensaurus*).

The postzygapophyses are posteriorly directed to reach the mid-posterior portion of the centrum. Their articular facets are subcircular and incline lateroventrally 45°. The articulations for the haemapophyses are well developed in all caudal vertebrae. In these vertebrae (in MPCA-Pv 58 and in the holotype), the ventral cavity attains its greatest development, perforating almost the whole vertebral centrum (Fig. 7E$_1$).

Posterior caudal vertebrae.—As in the mid caudals, the posterior caudal vertebrae (MPCA-Pv 46/10 and referred material, MPCA-Pv 50, see SOM 2) are procoelous (Fig. 7G). Their ventral cavity is not as deep as in the mid caudals; however, this cavity occupies the greater part of the ventral face of the centrum. The pleurocoel is small and it is placed on the dorsal portion of the lateral face of the centrum. The neural arch is low; the prezygapophyses have a curvature towards the mid-line, their articular surfaces being placed very close one to each other.

Posterior-distal caudals.—The material that Salgado and Azpilicueta (2000: fig. 8D–F) referred to *Rocasaurus* is composed of four vertebral centra (MPCA-Pv 51, MPCA-Pv 54, MPCA-Pv 56, MPCA-Pv 56/1), some of which are partially preserved. These vertebrae are strongly compressed dorsoventrally. The ventral cavity, typical of this taxon, is here a shallow depression, except in MPCA-Pv 54 where a relatively deep depression is observed. The most notable character of these distal vertebrae is the posterior articulation of the centrum, which is wide and flattened (Fig. 7H). The vertebral centrum, as seen in MPCA-Pv 54, is completely pneumatic, composed by large cavities limited by strong septa.

Femur.—The femur of *Rocasaurus muniozi* is straight. On its lateral margin, immediately below the greater trochanter, there is a strong curvature, the so-called lateral bulge (Fig. 8A$_1$); this has been proposed as a synapomorphy of Titanosauriformes (Salgado et al. 1997b; Upchurch 1998; Wilson and Sereno 1998). The angle between the intersection of the virtual extension of the dorsal surface of the femoral head, and the line that contains the most lateral point of the lateral bulge, is 124°, which is the greatest angle observed in the three femora described in this work (Figs. 5, 8A$_1$).

The robustness index is 0.16 (see SOM 2), intermediate between *Aeolosaurus* sp. and the Titanosauria gen. et sp. indet. described below. This element is anteroposteriorly compressed through the entire diaphysis and proximal epiphysis. Distally, the bone becomes more cylindrical, with a mediolateral/anteroposterior index of 1.83 (see SOM 2).

The tibial condyle is anteroposteriorly well developed, whereas the lateral or fibular condyle is more lateromedially developed (Fig. 8A). The intercondylar groove extends through the first distal third of the bone, continuing towards the upper part by a low crest, which is more developed than in other titanosaurs. This crest decreases proximally to disappear in the proximal third of the bone.

Ilium.—Both elements are preserved; the left one, which is complete (MPCA-Pv 46/12; Fig. 8B), and the acetabular portion of the right one (MPCA-Pv 46/13). The pubic peduncle is perpendicular to the axis of the main body of the bone (pre- and postacetabular lobes). The preacetabular lobe is broad (being 29 cm in dorsoventral depth), semicircular, and unlike other titanosaurs (*Saltasaurus*, Powell 2003; *Neuquensaurus* Salgado et al. 2005) it is not laterally twisted, although this could a result of deformation. The postacetabular lobe is slightly smaller than the preacetabular lobe, and of a rather elliptical contour (Fig. 8B, SOM 2). On the posteroventral portion of the postacetabular lobe, a rugose surface is clearly visible, the articulation for the ischium.

Pubis.—The left pubis (MPCA-Pv 46/15) is a laminar bone with a slight torsion on its longitudinal axis (Fig. 8D). The bone thins abruptly from lateral to medial parts. A well-developed obturator foramen is near the acetabulum and the articulation for the iliac peduncle. This foramen opens on the medial side of the pubis at the bottom of a deep obturator fossa, which practically reaches the border of the iliac peduncle. Distally, the pubis is slightly expanded.

Ischium.—Both ischia are preserved (MPCA-PV 46/11, MPCA-PV 46/14), the first being nearly complete (Fig. 8C). This bone is mostly laminar, but the pubic peduncle is robust; it decreases in thickness distally. The contact with the pubis is greater than in *Saltasaurus* and *Neuquensaurus* (Salgado and Azpilicueta 2000). The acetabular surface is almost twice as thick as the rest of the bone. Immediately below the acetabular surface, both on the medial and lateral faces, asymmetrical protuberances are observed, which are interpreted as muscular attachments.
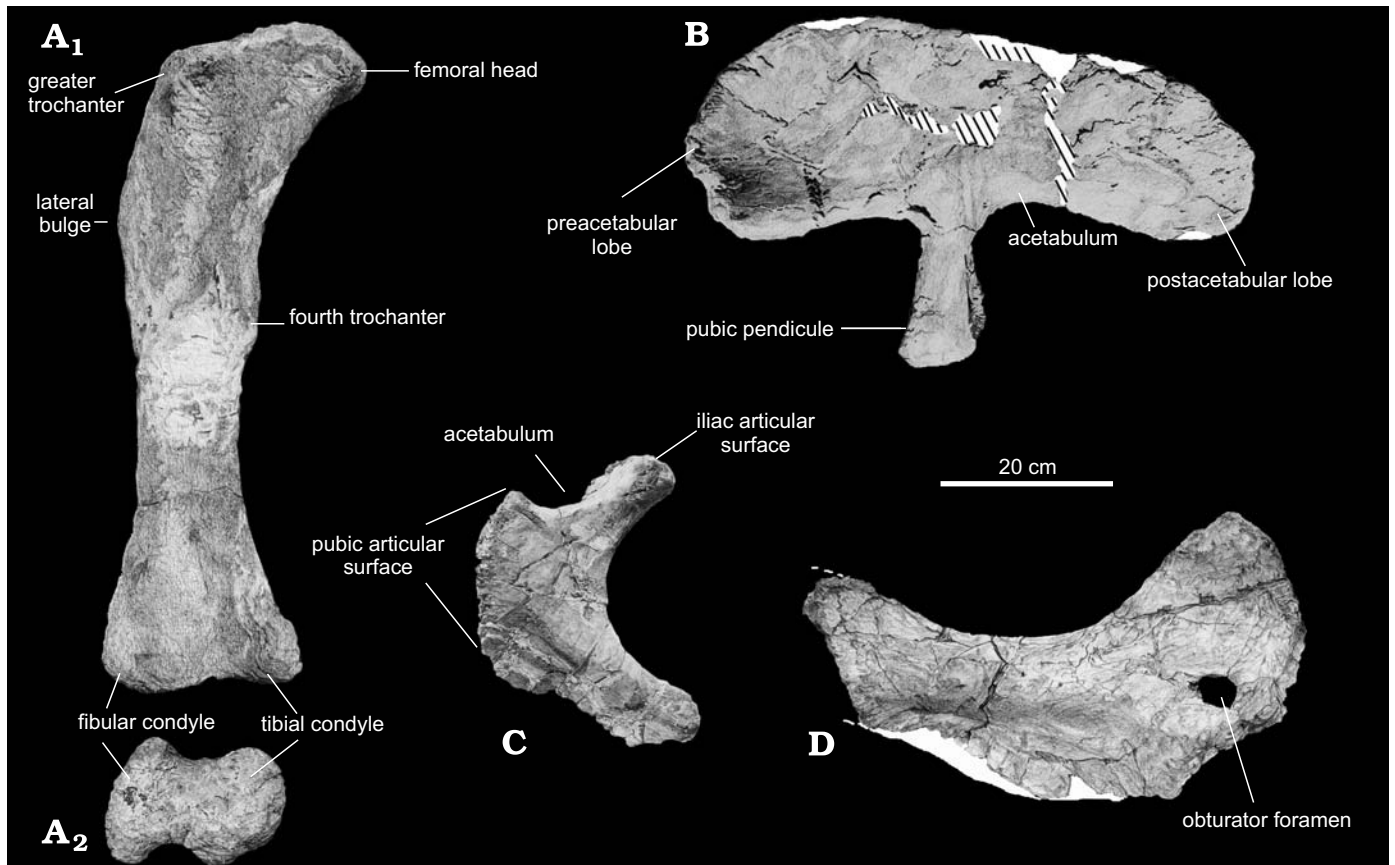
Fig. 8. Titanosaur sauropod *Rocasaurus muniozi* Salgado and Azpilicueta, 2000 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Left femur (MPCA-Pv 46/16), in posterior (A$_1$) and distal (A$_2$) views. **B**. Left ilium (MPCA-Pv 46/12), in lateral view. **C**. Left ischium (MPCA-Pv 46/11), in lateral view. **D**. Left pubis (MPCA-Pv 46/15), in lateral view.

Titanosauria incertae sedis
Gen. et sp. indet. 1
Fig. 9.

Material.—Two mid caudal vertebrae, MPCA-Pv 866 and MPCA-Pv 867; right humerus, MPCA-Pv 33; right tibia, MPCA-Pv 33/1; right femur, MPCA-Pv 33/2. All from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Remarks.—This specimen was associated with the holotype of *Rocasaurus muniozi*. Because of the slenderness of its appendicular bones and the morphology of the caudal vertebrae, it is obvious that it belongs to another, more gracile, non-saltasaurine species; it also clearly differs from *Aeolosaurus* in many features, as mentioned in the description.

Description

Caudal vertebrae.—The caudal vertebrae MPCA-Pv 866 and MPCA-Pv 867 are strongly procoelous, with their lateral faces flat and relatively high. The ventral face of the centrum is slightly convex; the articulations for the haemal arches are poorly developed. The neural arch, preserved only in MPCA-Pv 867, is placed on the anterior half of the centrum, as in other titanosaurs, and the neural spine is low and transversely wide (Fig. 9B, SOM 3). The prezygapophyses are anteriorly extended, surpassing the anterior border of the centrum by 46% of centrum length. The articular surfaces of the prezygapophyses are practically parallel to the axial plane. The postzygapophyses are located at the base of the neural spine, approximately at the middle of the centrum. There is a distinctive furrow between the articular surfaces of the postzygapophyses.

Humerus.—The right humerus (MPCA-Pv 33) is the smallest of the three humerii here described. The humeral head and the deltopectoral crest are partially preserved (Fig. 9C). The deltopectoral crest is small and higher than in *Aeolosaurus* (MPCA-Pv 88/A) and other titanosaurs (e.g., *Neuquensaurus*). The robustness index cannot be calculated because the distal portion of the humerus was not preserved. As in other titanosaurs (Alejandro Otero, personal communication 2010) the bone presents a sharp lateral ridge on its distal half, but in this specimen this structure is particularly well developed.

Femur.—The right femur (MPCA-Pv 33/2) is slender; its robustness index is only 0.15 (SOM 3), the lowest value of the three femora described here. The mediolateral/anteroposterior index (M.A. index = 1.56) is also the lowest recorded in Salitral Moreno, being closer to the values obtained in *Neuquensaurus* (Otero 2010). A feature that distinguishes this ma-
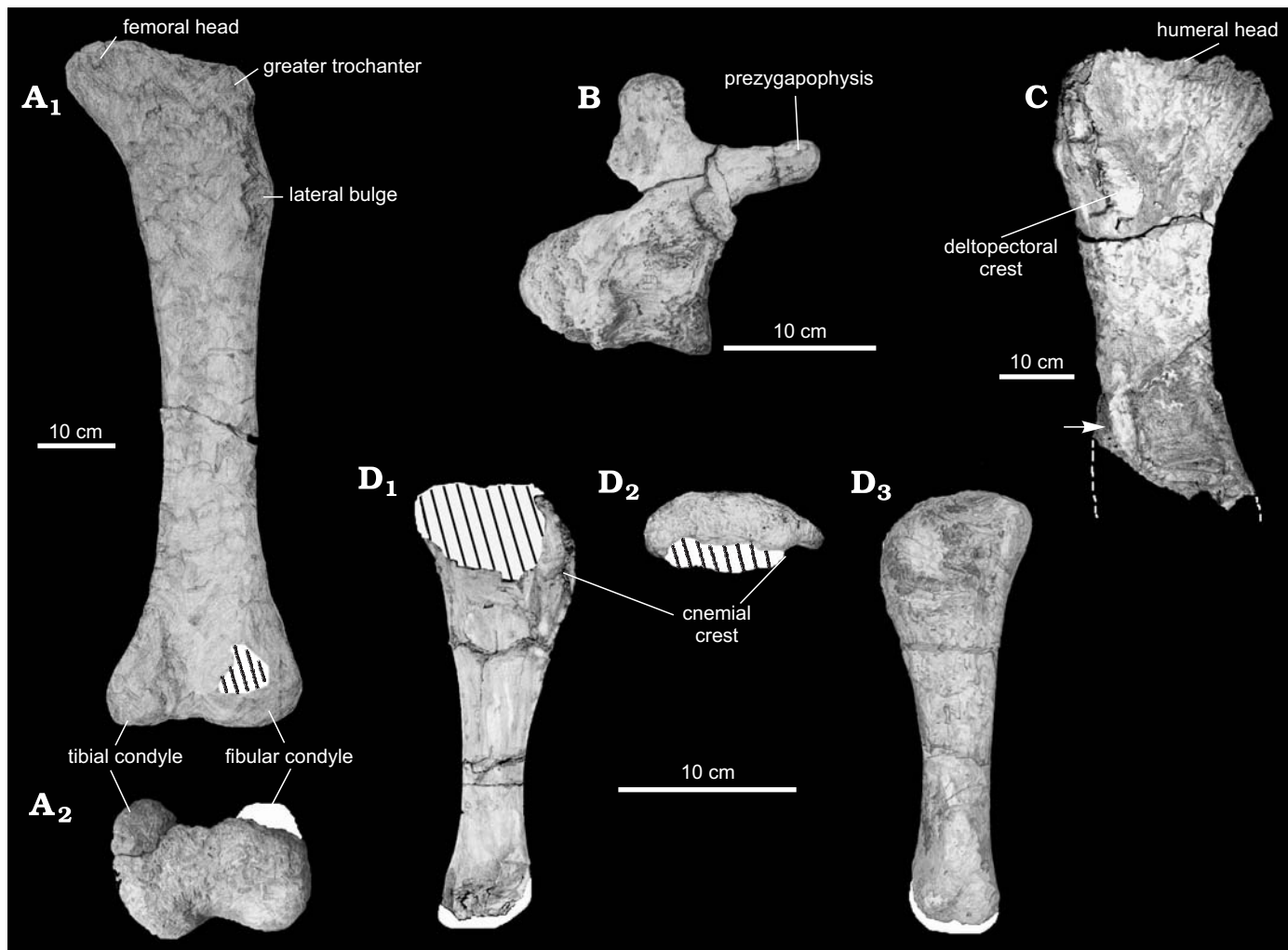
Fig. 9. Titanosauria gen. et sp. indet. 1 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Right femur (MPCA-Pv 33/2), in posterior (A_1) and distal (A_2) views. **B**. Mid caudal vertebrae (MPCA-Pv 867), in lateral view. **C**. Right humerus (MPCA-Pv 33), in anterior view. **D**. Right tibia (MPCA-Pv 33/1), in lateral (D_1), proximal (D_2), and medial (D_3) views. The arrow shows a sharp lateral ridge.

terial from *Rocasaurus* and *Aeolosaurus* is its poorly developed anterior intercondylar groove, which is only pronounced in the distalmost portions of the condyles (Fig. 9A). The lateral bulge is close to the greater trochanter, closer than in *Rocasaurus*. The angle of the intersection of the virtual extension of the dorsal surface of the femoral head and the virtual extension of the line that contains the most lateral point of the lateral bulge (119°), is higher than in *Aeolosaurus* (114°) but lower than in *Rocasaurus* (124°) (Fig. 5).

The posterior face of the femur is plane along its shaft, while the anterior surface is plane only proximally (near the lateral bulge), and the rest of the shaft being convex.

Tibia.—The right tibia (MPCA-Pv 33/1) is almost complete, only lacking the proximal lateral portion and the distal condyles (Fig. 9D). The bone is gracile, 35% shorter than the femur (SOM 3). Proximally, the medial surface of the tibia is slightly convex; this convexity accentuates distally. The incomplete preservation of the distal end means it is not possible to observe the articulation for the astragalus. The lateral surface is mostly plane, and the posterior margin is practically straight, while the anterior margin is slightly concave (Fig. $9D_1$). The cnemial crest, although incomplete, is poorly developed compared with *Neuquensaurus robustus* (Otero 2010).

Titanosauria gen. et sp. indet. 2
Fig. 10.

Material.—Three caudal vertebrae, MPCA-Pv 88/B, MPCA-Pv 88/C, and MPCA-Pv 88/D; right humerus, MPCA-Pv 88/A. The last was found 2.5 m from the three vertebrae, so we interpret all these bones as belonging to a single specimen. All from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Description

Caudal vertebrae.—The two anterior (MPCA-Pv 88/B, MPCA-Pv 88/C) and one mid caudal vertebrae (MPCA-Pv 88/D) are short, slightly procoelous, with with wide articular surfaces (Fig. $10A_1$, SOM 4). The lateral faces are anteroposteriorly concave, and the flat ventral surface is pierced by numerous foramina. The neural arch, although
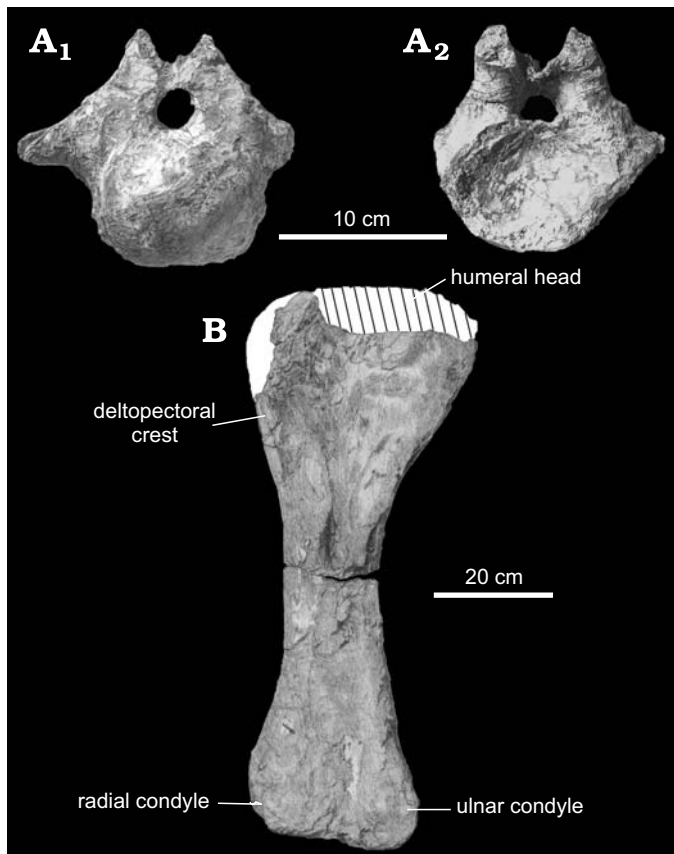
Fig.10. Titanosauria gen. et sp. indet. 2. from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Caudal vertebrae (MPCA-Pv 88/B), in posterior (A_1) and anterior (A_2) views. **B**. Right humerus (MPCA-Pv 88/A), in anterior view.

and posterior articulations, so the lateral faces of the centra are anteroposteriorly concave. The ventral surface of the centrum is plane. The most distinctive feature is the morphology of the posterior articulation, which is transversely wide, dorsoventrally compressed, as is the whole vertebra, and posteriorly extended forming a pointing protuberance. The vertebra is camellate.

These vertebrae were referred by Salgado and Azpilicueta (2000) to *Rocasaurus muniozi*. However, the general mor-

not well preserved, is low and transversely wide, with diapophyses wide and short and that become slender toward their distal ends.

Humerus.—The right humerus (MPCA-Pv 88/A) has a proximal expansion 12% greater than the distal (Fig. 10B). In anterior view, the lateral margin of the bone is slightly concave, while the medial margin is straight. The deltopectoral crest, although incomplete, is not much developed, but it does extend to the mid-length of the bone, as in *Aeolosaurus* and different from *Neuquensaurus australis*. The minimum diameter is at mid-shaft. The radial epicondyle seems to be larger than the ulnar epicondyle, as in all titanosaurs. The robustness index of this humerus is 0.16 (see SOM 4), slightly less than for the humerus of *Aeolosaurus*.

Titanosauria gen. et sp. indet. 3
Fig. 11.

Material.—Three distal caudal vertebrae, MPCA-Pv 52, MPCA-Pv 53, and MPCA-Pv 55 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Description.—These three small, dorsoventrally compressed caudal centra (Fig. 11) have their widest points at the anterior
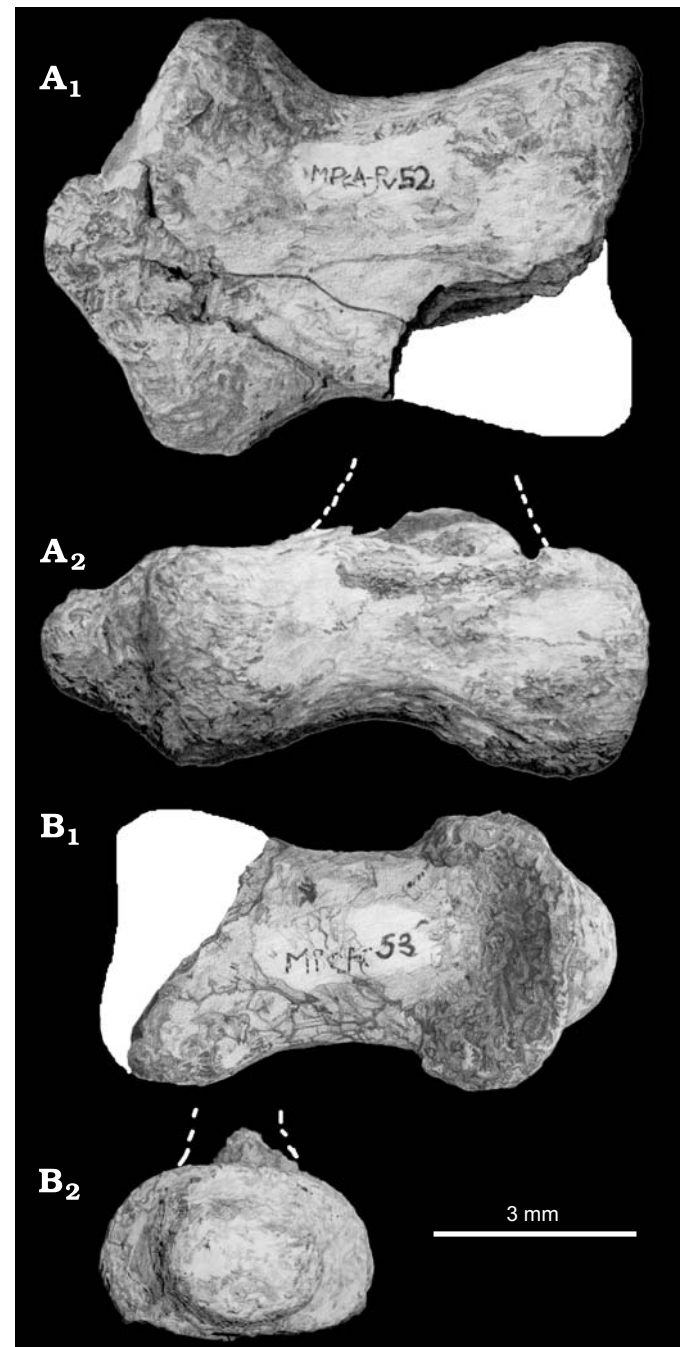

Fig. 11. Titanosauria gen. et sp. indet. 3, distal caudal vertebrae from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. MPCA-Pv 52, in ventral (A_1) and lateral (A_2) views. **B**. MPCA-Pv 53, in ventral (B_1) and posterior (B_2) views.
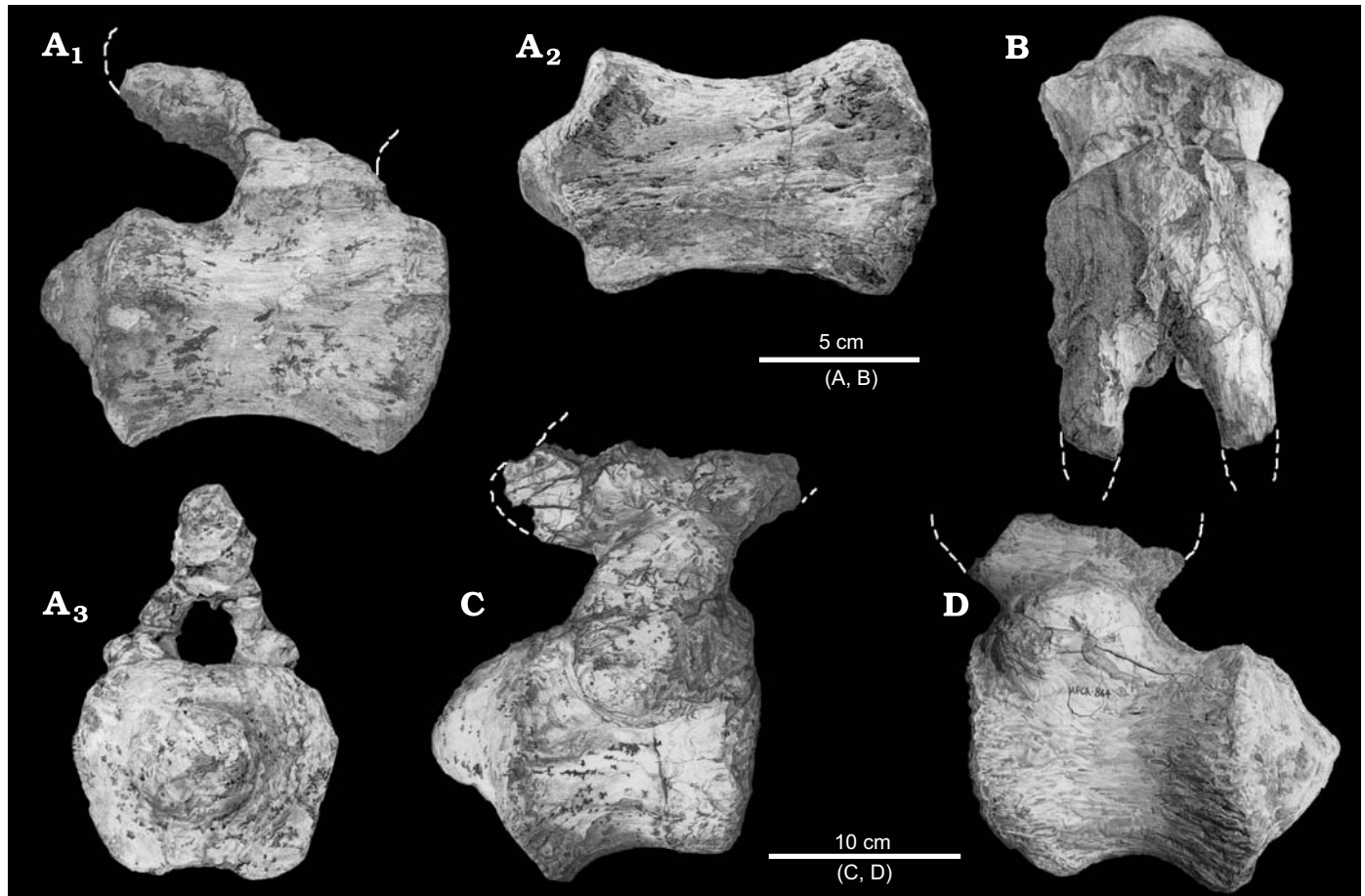
Fig. 12. Titanosauria gen. et sp. indet. 4 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous. **A**. Mid-posterior caudal vertebra (MPCA-Pv 862), in lateral (A_1), ventral (A_2), and posterior (A_3) views. **B**. Mid-posterior caudal vertebra (MPCA-Pv 861), in dorsal view. **C**. Anterior-mid caudal vertebra (MPCA-Pv 863), in lateral view. **D**. Mid caudal vertebra (MPCA-Pv 864), in lateral view.

phology, and, particularly, the morphology of the posterior articular surfaces, is notably different from the distalmost caudal vertebrae of this species.

Titanosauria gen. et sp. indet. 4

Fig. 12.

Material.—Six caudal vertebrae, MPCA-Pv 861 to 866 from Salitral Moreno locality, Rio Negro, Argentina, Campanian–Maastrichtian, Upper Cretaceous.

Description.—These caudal vertebrae include two anterior-mid, one mid, and three mid-posterior elements (Fig. 12, SOM 5). All are markedly procoelous, and their most distinctive character is the pointing posterior condyle, much like the previous morphotype. There is a bony cingulum bordering the condyle, which extends as two lobes to the articulations for the haemapophyses.

In all the vertebrae the neural canal is very wide; the distinctive character of these bones is their flat neural canal divided by a small septum, throughout its entire base.

In lateral view (Fig. 12A_1, C, D), the vertebral centra are quadrangular. At least the centra of MPCA-Pv 861 and MPCA-Pv 864 are compact, massive, without inner spaces

(which can be observed through a broken area); this is a clear difference from the condition in other titanosaurs recorded in the area, such as *Rocasaurus*. Numerous lanceolated foramina pierce all the surface of the centrum, both ventral and the lateral surfaces. The number of foramina increases to the distalmost caudals. The lateral faces are anteroposteriorly concave and their ventral face is plane. The articulations for the haemapophyses are well developed. Although the neural spine of MPCA-Pv 861 and MPCA-Pv 862 is badly preserved, these probably reached the posterior border of the centrum.

Discussion and conclusions

The Allen Formation has produced a wide variety of sauropods from different localities in Neuquén and, principally, Río Negro provinces. In Salitral Moreno, the diversity of sauropods is remarkable, with at least six species in a small, poorly exposed area.

Up to now, only two titanosaurs were known from this locality (*Aeolosaurus* sp. and *Rocasaurus muniozi*), and a col-

Table 1. Vertebrate taxa from Salitral Moreno.

Vertebrate taxa	References
Rocasaurus muniozi	Salgado and Azpilicueta (2000)
Aeolosaurus sp.	Salgado and Coria (1993)
Ankylosaur	Salgado and Coria (1996)
Hadrosaur	Powell (1987b); Coria (2009); Juárez Valieri et al. (2010)
Theropoda	Coria and Salgado (2005)
cf. Neornithes	Agnolin and Novas (2012)

lection of osteoderms of undetermined titanosaurs (Salgado 2003). We have now added a further four titanosaurs, which are different from *Rocasaurus* and *Aeolosaurus*. Our new materials assigned to *Aeolosaurus* sp. very probably belong with the specimens described by Salgado and Coria (1993); in fact, all these bones come from a small quarry of approximately 16 m², and all show morphological similarities with the holotype of *Aeolosaurus rionegrinus*.

The titanosaur taxa from Salitral Moreno show different body sizes and different robustness indices of their appendicular bones; it is evident that the environment in which they lived could support numerous herbivores from different populations, not only of titanosaurs but also hadrosaurs and ankylosaurs (Salgado and Coria 1996; see Table 1).

The hadrosaurs are apparently not so diverse; although they are as abundant as the sauropods, there was only one, or at most two, species (Coria 2009). The poor record of carnivorous dinosaurs at Salitral Moreno is noteworthy: only a few fragmentary bones described by Coria and Salgado (2005), mostly belonging to small forms. This contrasts with other neighbouring localities (Salitral Ojo de Agua, Salitral de Santa Rosa), which have produced good samples of theropods (Novas et al. 2009; Paulina Carabajal et al. 2009).

The Allen Formation is famous for its great palaeontological richness, the so-called Allenian tetrapod assemblage (Leanza et al. 2004), consisting of several typical Gondwanan lineages. Among the dinosaurs are theropods (abelisaurids, dromaeosaurids), ornithischians (hadrosaurids, nodosaurids), and titanosaur sauropods (Powell 1986, 1987b; Salgado and Coria 1993, 1996; Salgado and Azpilicueta 2000; Coria 2001; Martinelli and Forasiepi 2004). The dinosaur record of Salitral Moreno confirms this broad characterization.

The Allen Formation is chronologically equivalent to the Marília Formation (Bauru Group, Brazil), and their faunas have much in common. Up to now, there is a good record of sauropods in the Marilia Formation, including aeolosaurines (Santucci and Bertini 2001) and abelisaurs (Candeiro 2005), but not saltasaurines or hadrosaurs. The absence of saltasaurines may be because these sauropods originated late in the Cretaceous, probably in southern South America (northern Patagonia?), and there was no time for their dispersal (Salgado and Azpilicueta 2000). In the case of the hadrosaurs, it is not clear what may be the reason for their absence in the Bauru Group, although it might relate to progressive increase in aridity of the basin (Salgado and Carvalho 2008).

We agree with the proposal by Mannion et al. (2011) that diversity patterns observed directly from the fossil record are strongly influenced by fluctuations in the quality of our sampling of the rock record. However, the Salitral Moreno locality clearly exhibits a higher dinosaur diversity than other localities in the Allen Formation or correlated units (e.g., Los Alamitos, Uberaba, Lago Pellegrini). There is no ready explanation for this unusual diversity, but is clear that the palaeoecological conditions in the area were optimal for many species of large-sized herbivorous dinosaurs.

Acknowledgements

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