*geologica*acta

A new sauropod titanosaur from the Plottier Formation (Upper Cretaceous) of Patagonia (Argentina)

L.S. FILIPPI [1] **J.I. CANUDO** [2] **J.L. SALGADO** [3] **A. GARRIDO** [4] **R. GARCÍA** [3] **I. CERDA** [3] **A. OTERO** [3]

[1] **Museo Municipal "Argentino Urquiza"**
Jujuy y Chaco s/n, 8319 Rincón de los Sauces, Neuquén, Argentina.   E-mail: lsfilippi@yahoo.com.ar

[2] **Grupo Aragosaurus - IUCA (www.aragosaurus.com), Paleontología, Facultad de Ciencias, Universidad de Zaragoza**
Pedro Cerbuna 12, 50009 Zaragoza, Spain.   E-mail: jicanudo@unizar.es

[3] **CONICET-INIBIOMA, Museo de Geología y Paleontología, Universidad Nacional del Comahue**
Buenos Aires 1400, 8300 Neuquén, Argentina. Salgado E-mail: lsalgado@uncoma.edu.ar García E-mail: rgarcia@uncoma.edu.ar
Cerda E-mail: nachocerda6@yahoo.com.ar   Otero E-mail: alexandros.otero@gmail.com

[4] **Museo Provincial de Ciencias Naturales "Prof. Dr. Juan Olsacher"**
Dirección Provincial de Minería, Etcheluz y Ejército Argentino, 8340 Zapala, Neuquén, Argentina.   E-mail: algene@copelnet.com.ar

⊣ **A B S T R A C T** ⊢

This paper presents a new titanosaur sauropod, collected from levels of reddish clays assigned to the Plottier Formation (Coniacian-Santonian). The holotype of *Petrobrasaurus puestohernandezi* gen. et. sp. nov. is a disarticulated specimen, from which teeth, cervical, dorsal and caudal vertebrae, sternal plates, metacarpals, femora, tibia, a fragment of ilium, pubis, haemal arches, and cervical and dorsal ribs have been preserved. This period is of particular interest because it saw the definitive isolation of the vertebrate faunas of Patagonia, with the separation of South America from the rest of Gondwana, a process that had begun during the Early Cretaceous. Although some of the characters observed in *Petrobrasaurus* gen. nov. suggest a relationship with the South American clade Lognkosauria, this new sauropod is regarded as Titanosauria *incertae sedis* until a more profound analysis of the Titanosauria that in which it is included is undertaken.

KEYWORDS | Titanosauria. Plottier Formation. Coniacian-Santonian. Late Cretaceous. Río Neuquén Subgroup. Argentina.

INTRODUCTION

The separation of South America from the rest of Gondwana at the end of the Early Cretaceous produced a gradual evolutionary differentiation among the groups of tetrapods that lived on either side of the incipient South Atlantic (Gasparini et al., 2007). The question of when the definitive separation of Africa and South America actually took place raises certain doubts, since the traditional model, which posits the separation of the two continents in

the Early Cretaceous (Sampson et al., 1998), encounters problems with the dinosaur record. On the basis of the presence of abelisauroid theropods in Africa, Sereno et al. (2004) propose that the connection was operative at least until 95 million years ago (Cenomanian) and could have persisted intermittently until the Coniacian. Upchurch (2008), on the other hand, developed a new model of Gondwanan fragmentation and re-connection, according to which the isolation of Africa would have started some 100 million years ago. The best way of contributing new arguments to this discussion is by providing new evidence of dinosaurs of the Cenomanian-Turonian and establishing what their phylogenetic relations are. Studies of the Late Turonian/Coniacian dinosaurs of South America are particularly significant in assessing the time and the manner of this differentiation. Leanza et al. (2004) proposed a specific term to distinguish a particular faunal association for the Late Turonian/ Coniacian, the 'Neuquenian Tetrapod' association in the specific case of the Neuquén Basin.

In stratigraphic terms, the Neuquenian is located in the Río Neuquén Subgroup, which is divided into the Portezuelo and Plottier Formations (Ramos, 1981; Leanza et al., 2004). In recent years, the Portezuelo Formation has yielded important vertebrate remains such as *Patagonykus puertai* Novas 1996, *Megaraptor namunhuaiquii* Novas 1998, *Neuquenraptor argentinus* Novas and Pol, 2005. The Neuquenian is characterized by a singular fauna (Gasparini et al., 2007), marked by the apparent extinction of rebbachisaurid sauropods and the presence of large-sized titanosaurs such as *Futalognkosaurus dukei* Calvo et al., 2007a, and of theropods including putative basal tetanurans such as *Megaraptor,* unenlagines (Bonaparte, 1999) and alvaresaurids (Novas, 1997). The outcrops of the Río Neuquén Subgroup, around the city of Rincón de los Sauces, have proved to be especially prolific in the discovery of sauropods like *Rinconsaurus caudamirus* Calvo and González-Riga, 2003, and *Muyelensaurus pecheni* Calvo et al., 2007b. Also, in the nearby province of Mendoza, *Mendozasaurus neguyelap* González-Riga, 2003, and *Malarguesaurus florenciae* González-Riga et al., 2009 has been collected.

By contrast, the dinosaur fossil record of the Plottier Formation (from the late part of the Coniacian to the early part of the Santonian; Legarreta and Gulisano, 1989; Cruz et al., 1989) is very sparse, being limited to remains of a large coelurosaur theropod and fragmentary remains of titanosaur sauropods, assigned to cf. *Antarctosaurus giganteus* (see the references in Leanza et al., 2004, and Gasparini et al., 2007). Here we describe a new species of titanosaur sauropod recovered from the Plottier Formation at Rincón de los Sauces (Fig. 1).

The quarry where the remains were found was produced by land-levelling operations prior to the installation of the PH 1597 oil well by the Petrobras oil company. During the course of the autumn of 2006 and the spring of 2007, excavation work was carried out as part of a cooperative project between the Museum of Rincón de los Sauces, the Universidad El Comahue (Argentina) and the Universidad de Zaragoza (Spain). The objective of this paper is to describe this specimen of sauropod and to discuss its phylogenetic position and its palaeobiogeographical implications.

GEOLOGICAL SETTING. STRATIGRAPHY

The fossils were excavated in the vicinity of the PH 1597 oil well, within the Puesto Hernández production field. The well is located 25km to the north-west of the city of Rincón de los Sauces, in the north of the province of Neuquén, Patagonia, Argentina (Fig. 1).

The quarry is located in the mid-high part of the Plottier Formation (Fig. 2), dated by Musacchio and Vallati (2007) on the basis of their non-marine microfossil assemblage to the Coniacian-Santonian interval. This unit is composed of alternating whitish quartzite sandstones and reddish mudstones. The sandstone levels are made up of normal-grading deposits disposed in amalgamated channelized

FIGURE 1 | **Location Map of Puesto Hernández (Neuquén, Patagonia, Argentina).**

bodies, showing a predominance of downstream accretion and sandy bedform architectural element types (*sensu* Miall, 1996). These sediments are interpreted as fluvial deposits belonging to sandy braided channel systems.

The fossil-bearing levels comprise ruddy brown mudstones approximately three metres thick, characterized by a high sand content microconglomerate-sized heterometric detrital grains of a siliceous and carbonate nature. The fossil remains of the sauropod were found at the base of this level, there being no other fossil vertebrates in the rest of the level (Fig. 2). The detritus is irregularly distributed in the form of carbonate nodules of a possibly pedogenic origin, as well as small transported cylindrical galleries of invertebrates, which are not found 'in situ'. Small logs and plant debris are also frequent components within this level. The sauropod bones were found to be associated and disarticulated, but respecting approximately the original position within the skeleton. The long bones and the vertebrae were complete and without any taphonomic breaks, whereas some of the ribs were fragmented and the teeth of the sauropod were isolated. The bones do not show signs of transport such as abrasion or erosion. This indicates that the transport of the bony remains was minor and restricted to a small area. The sedimentological characteristics of the fossiliferous level suggest a deposition mechanism linked to a dense muddy flow.

The remains were scattered over an area of 60m^2 and with no repeated pieces, suggesting they belong to a single specimen. Five isolated theropod tooth crowns were associated with the sauropod bones. We interpreted these as being the result of scavengers feeding on the carcass of the sauropod, since there are no signs of transport (Canudo et al., 2009b).

Institutional Abbreviations: MAU-Pv-PH: Museo Argentino Urquiza – Paleontología de Vertebrados – Puesto Hernández.

Anatomical Nomenclature: acpl: anterior centroparapophyseal lamina, apcdl: accessory posterior centrodiapophyseal lamina, cap: capitulum; cc: cnemial crest, cpol: centropostzygapophyseal lamina, dp: diapophysis, dpc: deltopectoral crest, f: small fossae, fa: articular facet, fi: interzygapophyseal fossa, fp: pubic foramen, ft: fourth trochanter, hd: articular head, ilped: iliac peduncle, lb: lateral bulge, nc: neural canal, ns: neural spine, pcdl: posterior centrodiapophyseal lamina, pcpl: posterior centroparapophyseal lamina, pl: pleurocoel, pn c: pneumatic cavity, ppdl: paradiapophyseal lamina, posl: postspinal lamina, pp: parapophysis, prdl: prezygodiapophyseal lamina, prsl: prespinal lamina, prz: prezygapophyses, pz: postzygapophyses, rac: radial condyle, pig: posterior intercondylar groove, spdl: spinodiapophyseal lamina, sprl:

spinoprezygapophyseal lamina, tp: transverse process, tu: tuberculum, ulc: ulnar condyle.
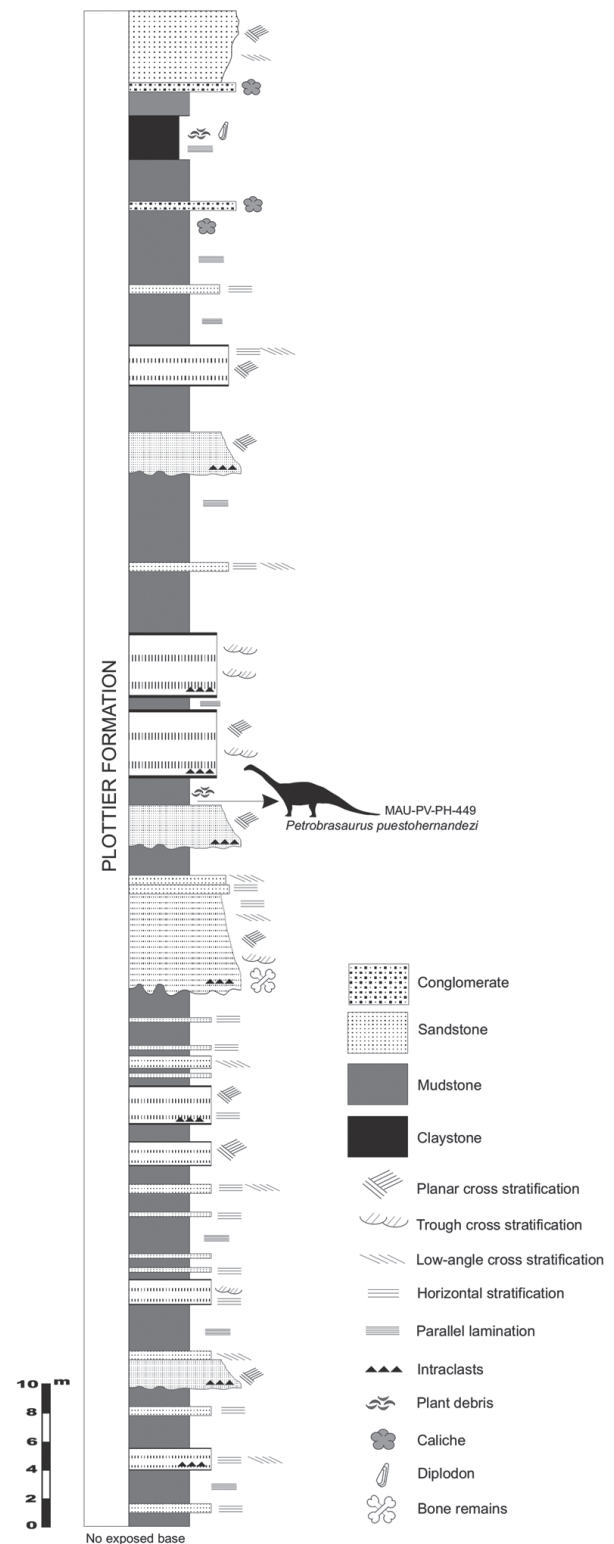
FIGURE 2 | **Lithostratigraphic section of the Plottier Formation. Sauropod quarry site.**

SYSTEMATIC PALEONTOLOGY

Superorder Dinosauria OWEN, 1842
Order Saurischia SEELEY, 1888
Infraorder Sauropoda MARSH, 1878
Titanosauriformes SALGADO, CORIA AND CALVO, 1997
Titanosauria BONAPARTE AND CORIA, 1993

Petrobrasaurus gen. nov.

Etymology. Petrobrasaurus: in recognition of the Petrobras oil company for its constant collaboration in the maintenance and preservation of the palaeontological heritage in the area of Rincón de los Sauces.

Type species. *Petrobrasaurus puestohernandezi* sp. nov.

Diagnosis. Same as for the type species.

Petrobrasaurus puestohernandezi sp. nov.
Figures 3-6. Table 1.

Etymology. *puestohernandezi*: refers to the Puesto Hernández oil field, where the fossil remains were found.

Locality and Age. PH 1597 locality (37°22'42.5" south /69°04'23.1" west), Rincón de los Sauces, Patagonia, Argentina. Claystones of the Plottier Formation. Santonian (Upper Cretaceous) of the Neuquén Basin.

Holotype. Two isolated teeth (MAU-Pv-PH-449/1 and 22), posterior portion of possibly middle cervical vertebra (MAU-Pv-PH-449/37), three incomplete posterior dorsal vertebrae (MAU-Pv-PH-449/18, 19 and 26), incomplete posterior dorsal arch (MAU-Pv-PH-449/20), incomplete dorsal vertebral centrum (MAU-Pv-PH-449/27), incomplete first caudal centrum (MAU-Pv-PH-449/15),

FIGURE 3 | **The skeletal reconstruction showing the preserved bones and teeth of *Petrobrasaurus puestohernandezi* gen. et sp. nov. and the. A) Lateral view (MAU-Pv-PH-449/1). B) Labial view (MAU-Pv-PH-449/1 and 22). Reconstruction scale bar: 1m. Teeth scale bar: 1cm.**

five anterior caudal vertebrae (MAU-Pv-PH-449/2, 3, 4, 5 and 6), right humerus (MAU-Pv-PH-449/36), right and left sternal plates (MAU-Pv-PH-449/10 and 25), four metacarpals (II, IV and V), one of which is incomplete (MAU-Pv-PH-449/11, 12, 13 and 35), right and left femur (MAU-Pv-PH-449/7 and 8), left tibia lacking distal end (MAU-Pv-PH-449/9), distal end of right tibia (MAU-Pv-PH-449/17), distal fragment of iliac peduncle (MAU-Pv-PH-449/14), left pubis (MAU-Pv-PH-449/16), fragments of haemal arches (MAU-Pv-PH-449/29, 30, 31 and 32), dorsal ribs, fragments of cervical ribs and indeterminate remains.

Diagnosis. Large sauropod dinosaur characterized by the following combination of derived features: 1) accessory posterior centrodiapophyseal lamina more developed than the posterior centrodiapophyseal lamina; 2) posterior centroparapophyseal lamina extends from the point of contact with the accessory posterior centrodiapophyseal lamina; 3) presence of a broad concave surface delimited by the bony rim of the posterior centroparapophyseal lamina and a rim located on the dorsal edge of the pleurocoel; 4) presence of a deep fossa, sub-circular in outline, on a slightly concave surface delimited by the accessory posterior centrodiapophyseal lamina, the posterior centrodiapophyseal lamina, and a bony rim corresponding to the extension of the posterior centroparapophyseal lamina; 5) presence of a T-shaped anteroposterior expansion on the laminae of the neural arch (pcdl and apcdl); and the anterior caudal vertebrae characterized by: 6) the presence of a deep fossa between the spinoprezygapophyseal lamina and the postzygapophysis, bearing small fossae; 7) prespinal lamina distally thickened; 8) sub-circular small fossae on both sides of the base of the prespinal lamina; and 9) presence of a T-shaped anteroposterior expansion in the spinoprezygapophyseal lamina.

Description. Teeth (Figs. 3A-B). Two incomplete teeth were recovered that preserved their dental crowns and part of the roots (MAU-Pv-PH-449/1 and 22). These teeth are cylindrical ('pencil-like') and slightly curved lingually. The crowns display a sub-circular section with well-developed longitudinal carenae. The apex is conical and slightly flattened lateromedially. The enamel displays a rugose ornamentation, which is visible to the naked eye. We interpret both of them as replacement teeth since they lack any wearing surface.

Cervical vertebrae. The specimen includes the posterior part of a middle cervical centrum (MAU-Pv-PH-449/37). It is opisthocoelous, anteroposteriorly elongated and low. The ventral face is concave both transversely and longitudinally. The lateral sides are dorsoventrally concave.
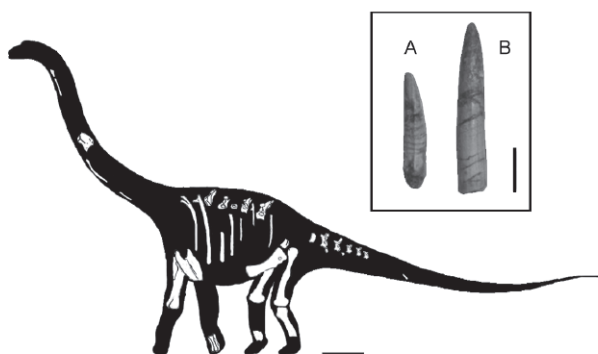
TABLE 1 | **Measurements (in mm) of the humerus (MAU-Pv-PH-449/36), metacarpals (MAU-Pv-PH-449/11-13) and both femur (MAU-Pv-PH-449/7 y 8), of** *Petrobrasaurus puestohernandezi* **gen. et sp. nov.**

Humerus Measurements	mm		
Total length	1200		
Proximal mediolateral width	400		
Length of deltoid crest	450		
Proximal length to minimum shaft mediolateral width	660		
Shaft minimum width anteroposterior	**		
Shaft minimum width mediolateral	155		
Distal mediolateral width	350		
Anteroposterior width of radial condyle	100		
Anteroposterior width of ulnar condyle	145		
Mediolateral width of radial condyle	150		
Mediolateral width of ulnar condyle	230		
Femur Measurements	**Right (mm)**	**Left (mm)**	
Total length	1572	1575	
Proximal mediolateral width	340	320	
Mediolateral width of articular head	250	253	
Anteroposterior width of femur articular head	90*	89*	
Anteroposterior width of femur greater trochanter	62*	65*	
Length of lateral bulge	410	400	
Lateral bulge medilateral width	90	85	
Proximal length to proximal end of 4th trochanter	560	580	
Proximal length to minimum shaft mediolateral width	970	910	
Shaft minimum width anteroposterior	**	**	
Shaft minimum width mediolateral	230	235	
Distal mediolateral width	415	400	
Anteroposterior width of fibular condyle	130*	125*	
Anteroposterior width of tibial condyle	135*	133*	
Mediolateral width of fibular condyle	230	210	
Mediolateral width of tibial condyle	110	120	
Metacarpals Measurements	**II (mm)**	**IV (mm)**	**V (mm)**
Total length	395	350	315
Shaft minimum width mediolateral	65	65	55

** The Humerus and Femora have not been extracted completely of plaster jacket, reason why this measurements cannot be taken.
* Estimated measurements.

The parapophyses are on its anterior margin, from which a slender lamina extends longitudinally almost as far as the posterior edge of the centrum.

Cervical ribs. Several fragments of long cervical ribs have been collected. They are dorsoventrally flattened at their proximal end, becoming more rod-shaped distally. The surface of the ribs has a striate aspect as in elongated cervical ribs in other sauropods.

Dorsal vertebrae (Figs. 4A-D, F and G). There are five incomplete posterior dorsal vertebrae (three incomplete posterior dorsal vertebrae, an incomplete posterior dorsal neural arch, and an incomplete dorsal vertebral centrum, MAU-Pv-PH-449/18, 19, 20, 26 and 27).

The dorsal arch MAU-Pv-PH-449/20 displays the remains of a prespinal lamina, which seems to fork towards its base into two branches that connect with the posterior margins of the prezygapophyses. A similar bifurcation is observed in an anterior dorsal vertebra of *Mendozasaurus neguyelap*, which was interpreted as small spinoprezygapophyseal laminae (González Riga, 2003). Although the neural spine in *Petrobrasaurus* gen. et sp. nov. is not preserved, it is united to the diapophysis by a fine spinodiapophyseal lamina. The prezygapophysis has a sub-elliptic outline, and is laterodorso-medioventrally oriented. In lateral view, both

the accessory posterior centrodiapophyseal lamina and the posterior centrodiapophyseal lamina delimit a small fossa with a triangular outline (Fig. 4B). The accessory posterior centrodiapophyseal lamina is linked to the posterior centroparapophyseal lamina, which is poorly developed, and to a very slender anterior centroparapophyseal lamina, forming a small fossa with a sub-triangular outline. Posteriorly to the parapophysis there is a fossa that is dorsally divided by a short lamina. Between the accessory posterior centrodiapophyseal lamina and the posterior centrodiapophyseal lamina there is a very deep fossa with a triangular outline.

The vertebral centrum (MAU-Pv-PH-449/27) is opisthocoelous, with a convex anterior face. The lateral sides are anteroposteriorly concave and slightly convex dorsoventrally. The ventral face is rather flat anteroposteriorly. The lateral faces display a deep, subcircular pleurocoel, situated in a dorsal position and occupying most of the length of the centrum. The width of the pleurocoel is similar to the height.

The neural spine is inclined posteriorly. The diapophyses are reinforced ventrally by two well-defined laminae: the accessory posterior centrodiapophyseal lamina and the posterior centrodiapophyseal lamina. Laterally, two deep fossae with a triangular outline can be observed, the postparapophyseal fossa and the posterior infradiapophyseal cavity. The anterior fossa is delimited by the posterior centroparapophyseal lamina and the accessory posterior centrodiapophyseal lamina, and the posterior fossa by the posterior centrodiapophyseal lamina and the centropostzygapophyseal lamina. In MAU-Pv-PH-449/19 the anterior fossa is divided by two accessory laminae, the more robust of which is located ventrally within the fossa, oriented anteroposteriorly and practically parallel to the accessory posterior centroparapophyseal lamina, whereas the more slender one is dorsoventrally oriented, almost parallel to the posterior centrodiapophyseal lamina. In the more posterior dorsal vertebrae (MAU-Pv-PH-449/18 and 26), the accessory posterior centrodiapophyseal lamina is more developed than the posterior centrodiapophyseal lamina, a character considered autapomorphic in *Petrobrasaurus puestohernandezi* gen. et. sp. nov. Shows the unique condition of having an accessory posterior centrodiapophyseal lamina more developed than the posterior centrodiapophyseal lamina. By contrast, other titanosaurs such as *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977) and *Saltasaurus loricatus* (Bonaparte and Powell, 1980) lack an accessory centrodiapophyseal lamina in their dorsal vertebrae. *Petrobrasaurus puestohernandezi* gen. et sp. nov. is also unique in having a posterior centroparapophyseal lamina that extends beyond its connection with the accessory posterior centrodiapophyseal lamina, in the form of an
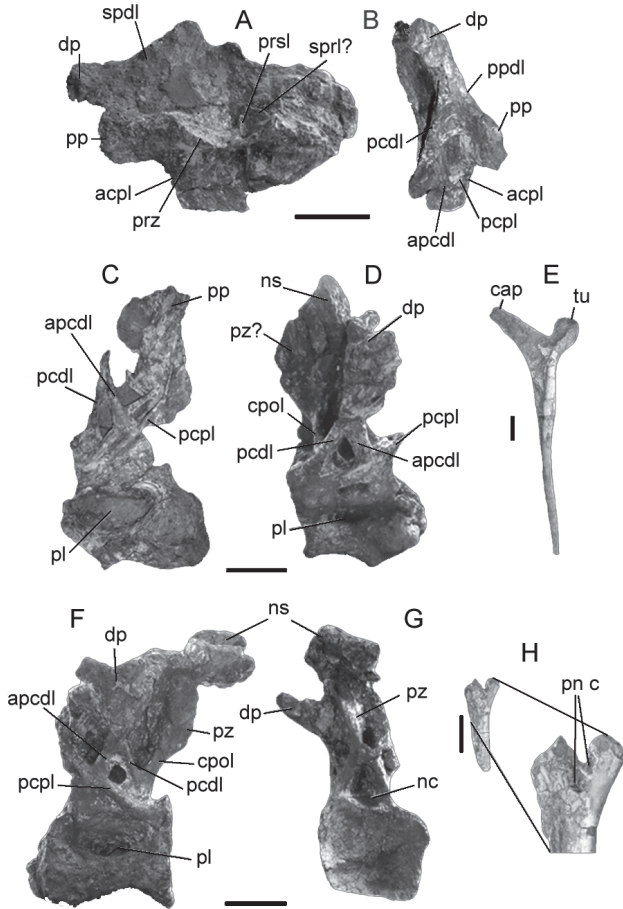
FIGURE 4 | **Posterior dorsal arch in A) anterior view and B) right lateral view (MAU-Pv-PH-449/26); posterior dorsal vertebrae in C) anterior view (MAU-Pv-PH-449/19), D) right lateral view (MAU-Pv-PH-449/26), F) left lateral view and G) posterior view (MAU-Pv-PH-449/18) and dorsal ribs of *Petrobrasaurus puestohernandezi* gen. et sp. nov. in E) anterior view of the left dorsal rib (MAU-Pv-PH-449/38) and H) detail of the proximal end with pneumatic cavity (MAU-Pv-PH-449/40). Abbreviations are in the Anatomical Nomenclature. Scale bar: 10cm.**

oblique bony rim that becomes more robust towards the base of the lateral face of the neural arch. In MAU-Pv-PH-449/18 a slightly concave surface develops between the accessory posterior centrodiapophyseal lamina and the posterior centrodiapophyseal lamina, limited ventrally by a bony rim that is continued with the posterior centroparapophyseal lamina. At the bottom of this concavity there is a deep fossa with a sub-circular outline not observed in other titanosaurs, as a result of which it is considered autapomorphic in *Petrobrasaurus puestohernandezi* gen. et. sp. nov. The anteriormost dorsal vertebrae preserved (MAU-Pv-PH-449/19 and 26) keep this fossa, although the surface where it is found is more concave, which suggests that this cavity is eradicated towards the more posterior dorsals, leaving just a reduced but deep sub-circular fossa. A broad concave surface is delimited by the bony rim of the posterior centroparapophyseal lamina and a rim situated on

the dorsal edge of the pleurocoel, a character considered autapomorphic in *Petrobrasaurus puestohernandezi* gen. et. sp. nov. It lacks a hyposphene. The postzygapophysis has a very broad articular surface, but its outline is not well defined. It is lateroventrally oriented and is connected to the base of the neural arch by a robust centropostzygapophyseal lamina. The postzygodiapophyseal lamina is absent as in other titanosaurs, such as *Opisthocoelicaudia*. The neural arch laminae in the dorsal vertebrae (pcdl and apcdl) have a T-shaped anteroposterior expansion, a character considered to be autapomorphic.

Dorsal ribs (Fig. 4E and H). Several rib fragments have been recovered, including the first left dorsal rib (MAU-Pv-PH-449/38). In this specimen, the capitulum is more developed than the tuberculum, due to the long transverse process. The shaft of MAU-Pv-PH-449/38 exhibits an elliptic cross section proximally and a circular section distally.

The other anterior ribs have a capitulum and tuberculum that are similar in size, and the section of the shaft is compressed lateromedially. The middle and posterior ribs have sub-circular sections. Proximally, the ribs have inner pneumatic cavities (MAU-Pv-PH-449/40), which is considered a synapomorphy of the Titanosauriformes (Wilson and Sereno, 1998).

Caudal vertebrae (Figs. 5A-L). Six anterior caudal vertebrae have been recovered, including the first one (MAU-Pv-PH-449/2-6 and 15).

The vertebral centrum of the first caudal (MAU-Pv-PH-449/15) is procoelous, slightly wider than high, and provided with a very convex posterior articular condyle. The vertebral centrum is anteroposteriorly compressed as in *Mendozasaurus neguyelap*, *Gondwanatitan faustoi* Kellner and de Azevedo, 1999 and *Neuquensaurus australis* Lydekker, 1893. MAU-Pv-PH-449/5 and 6 are interpreted as anterior caudals. The centra are higher than wide, with anteroposteriorly concave lateral and ventral faces (Fig. 5C and E). In ventral view, *Petrobrasaurus* gen. nov. differs from other titanosaurs such as *Bonatitan reigi* Martinelli and Forasiepi, 2004, in which the caudal centrum displays a ventral keel. The neural spine is robust, with a quadrangular cross section, and gently inclined posteriorly. It has a prespinal lamina that is significantly wider in the distal part, a character considered autapomorphic for the new species. The prespinal lamina is well delimited by the spinoprezygapophyseal laminae that extend from the distal part up to the base of the neural spine. On both sides of its base, the prespinal lamina shows small sub-circular small fossae, unlike *Bonatitan reigi* and *Neuquensaurus australis,* which display similar structures (Martinelli and Forasiepi, 2004; Salgado et al., 2005), but whose small

fossae are more numerous and are located almost on the border of the prespinal lamina.

The postspinal lamina is robust and widens distally. Laterally, there is a deep elliptical fossa in the base of the neural spine, delimited by the spinoprezygapophyseal lamina and the anterior edge of the postzygapophyses, and bearing small fossae at the bottom (Figs. 5C, E and L). The presence of this fossa and the small fossae inside are considered autapomorphic for *Petrobrasaurus* gen. nov. *Bonatitan reigi* presents a similar morphology and also an accessory lamina that divides this fossa transversely. This lamina has been described in *Lirainosaurus astibiae* (Sanz et al., 1999). *Mendozasaurus neguyelap* displays a similar fossa (named the interzygapophyseal fossa, González Riga, 2003), but it lacks an accessory lamina as in *Lirainosaurus* and the small fossae situated ventrally as in *Petrobrasaurus puestohernandezi* gen. et sp. nov. The caudal vertebrae of the Brazilian titanosaur *Adamantisaurus mezzalirai*

Santucci and Bertini, 2006 exhibit a smaller and less deep fossa, but it is situated in an anterior position with respect to the postzygapophyses and more dorsally to the base of the neural spine. Another taxon that presents similar fossae is *Aeolosaurus colhuehuapensis* (Casal et al., 2007). These are situated between the transverse process and the base of the neural spine, although they show no small inner small fossae. The anterior caudals of *Petrobrasaurus* gen. nov. display a T-shaped anteroposterior expansion of the spinoprezygapophyseal lamina, as in the dorsal vertebrae, a character considered to be autapomorphic for this dinosaur. The prezygapophyses are robust and project anterodorsally, and they show articular surfaces with a sub-circular outline and dorsoventrally expanded edges. The transverse processes are slightly compressed dorsoventrally and project lateroposteriorly perpendicular to the base of the neural arch. The postzygapophyses have a sub-triangular outline, and they are closer to the base of the neural arch and project more laterally than in *Bonatitan reigi*.
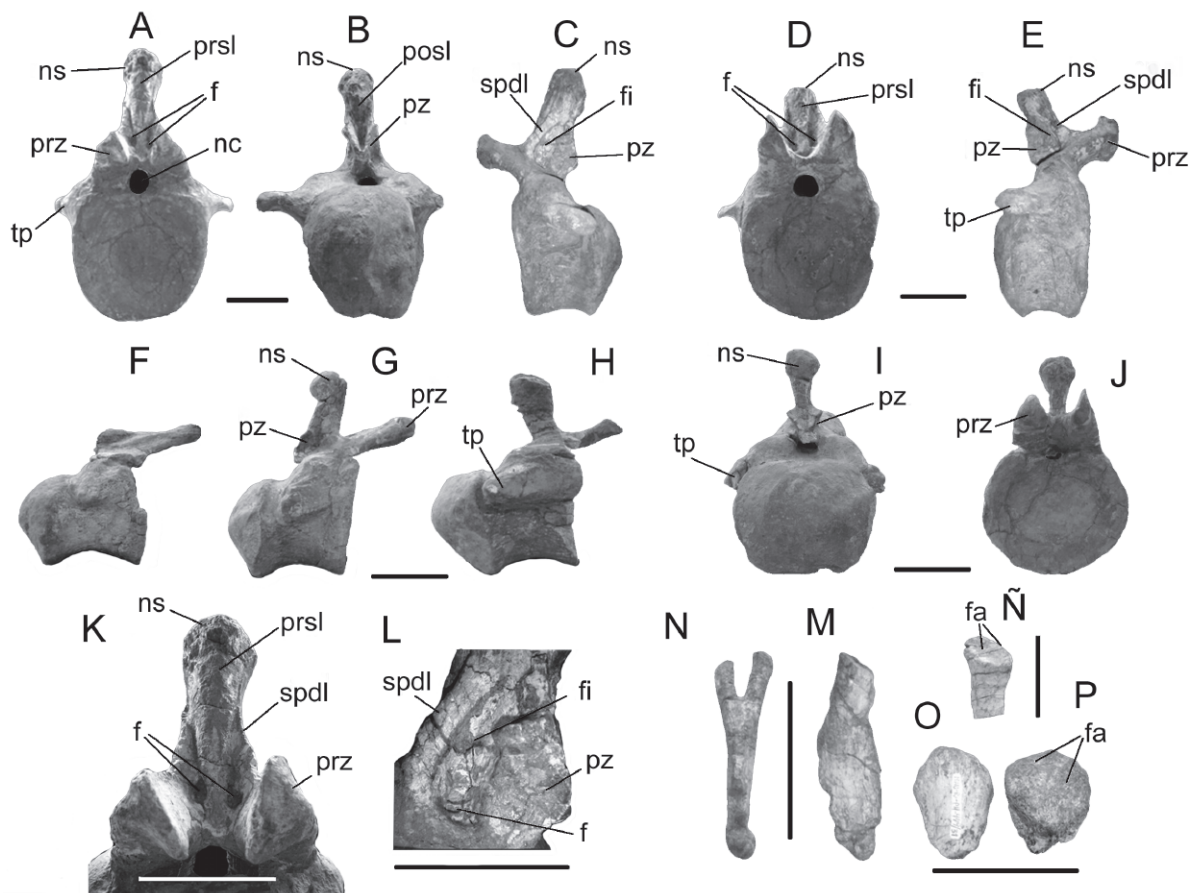
FIGURE 5 | **Caudal anterior vertebrae in A) anterior view, B) posterior view, C) left lateral view (MAU-Pv-PH-449/5), D) anterior view and E) right lateral view (MAU-Pv-PH-449/6); caudal middle-anterior vertebrae in F-H) lateral view (MAU-Pv-PH-449/2-4), I) posterior view and J) anterior view (MAU-Pv-PH-449/3); caudal anterior vertebra in K) detail of anterior view and L) lateral view of the small fossae (MAU-Pv-PH-449/5) and haemal arch of *Petrobrasaurus puestohernandezi* gen. et sp. nov. in N) anterior view (MAU-Pv-PH-449/29), M) lateral view (MAU-Pv-PH-449/29), Ñ) medial view (MAU-Pv-PH-449/30), O) lateral view (MAU-Pv-PH-449/31) and P) medial view (MAU-Pv-PH-449/31). Abbreviations are in the Anatomical Nomenclature. Scale bar: 10cm.**

In the other anterior caudals (MAU-Pv-PH-449/2, 3 and 4), the vertebral centrum is more elongated anteroposteriorly, and is as high as wide (Figs. 5F-H). The lateral and ventral faces are anteroposteriorly concave. The neural spine is less robust than in the preceding caudal vertebrae, with a prominent lateral distal expansion (Figs. 5I and J) as in *Trigonosaurus pricei* (Campos et al., 2005). This lateral expansion is also present as a diagnostic character in *Adamantisaurus mezzalirai* (Santucci and Bertini, 2006), but in the Brazilian species the neural spine is very robust transversely. The articulations of the prezygapophyses are large, their surfaces are sub-circular in outline, and they project anterodorsally. The transverse processes are very reduced, rather compressed dorsoventrally, and they project lateroposteriorly.

Haemal arches (Figs. 5N-P). One incomplete haemal arch has been recovered (MAU-Pv-PH-449/29), as well as various fragments of proximal ends (MAU-Pv-PH-449/30 and 31). MAU-Pv-PH-449/29 show a distal end laterally compressed and slightly curved posteriorly (Figs. 5N and M). The preserved fragments of the proximal ends shows double articular facets and are open proximally, as in other macronarians (Wilson and Sereno, 1998). However, it should be noted that this is not necessarily diagnostic of a macronarian, open chevrons are also known in rebbachisaurs and in the basal form *Shunosaurus* (Upchurch, 1998).

Sternal plate (Figs. 6B and C). Two sternal plates have been recovered (MAU-Pv-N-449/10 and 25). They are large and longer than wide. Both present the typical kidney shape observed in titanosaurs (Salgado et al., 1997), with a convex medial edge and a markedly concave lateral edge. In *Mendozasaurus* the lateral edge is slightly concave (González Riga, 2003), whereas in *Malawisaurus* it is much more concave (Gomani, 2005). In *Petrobrasaurus* gen. nov., the posterior edge is curved as in *Opisthocoelicaudia*, *Saltasaurus* and *Aeolosaurus* (Borsuk-Bialynicka, 1977; Powell, 1992; Salgado et al., 1997), unlike the relatively straight edge present in *Alamosaurus, Malawisaurus* and *Mendozasaurus* (Gilmore, 1946; Gomani, 2005; González Riga, 2003). Both plates are thick at the lateral edge, becoming very thin towards the medial edge. The proximal end is prominent and robust, displaying rugosities on the anteroventral margin.

Humerus (Fig. 6A). An almost complete, well preserved right humerus was recovered (MAU-Pv-N-449/36). This bone is slender, straight in anterior view, with proximal and distal ends slightly expanded transversely. The transverse width of the proximal end is 33% of the humerus length (Table 1), unlike *Opisthocoelicaudia* and *Saltasaurus,* which have more robust humeri, reaching values around 50%. The humerus is short in relation to the femur (Lhu/Lfe=0.764), like in other titanosaurs such as *Opisthocoelicaudia (*Borsuk-Bialynicka, 1977). The dorsal margin of the proximal end is relatively straight as in *Lirainosaurus, Rapetosaurus, Mendozasaurus* and *Epachthosaurus* (Sanz et al., 1999; Curry Rogers and Forster, 2001; González Riga, 2003; Martínez et al., 2004), and clearly different from the sigmoid edge present in more derived titanosaurs such as *Opisthocoelicaudia* and *Saltasaurus* (Borsuk-Bialynicka, 1977; Powell, 1992). The deltoid crest is well developed, as in other titanosaurs (Borsuk-Bialynicka, 1977; Smith et al., 2001) and the macronarians *Camarasaurus* and *Galvesaurus* (Ostrom and McIntosh, 1966; Barco et al., 2006). The humerus of *Petrobrasaurus* gen. nov. shows a deltopectoral crest that projects strongly medially. In contrast, in other titanosaurs such as *Alamosaurus*, *Rinconsaurus*, *Malawisaurus*, *Ligabuesaurus*, and *Saltasaurus*, the deltopectoral crest projects more anteriorly (Lehman and Coulson, 2002; Calvo and González Riga, 2003; Gomani, 2005; Bonaparte
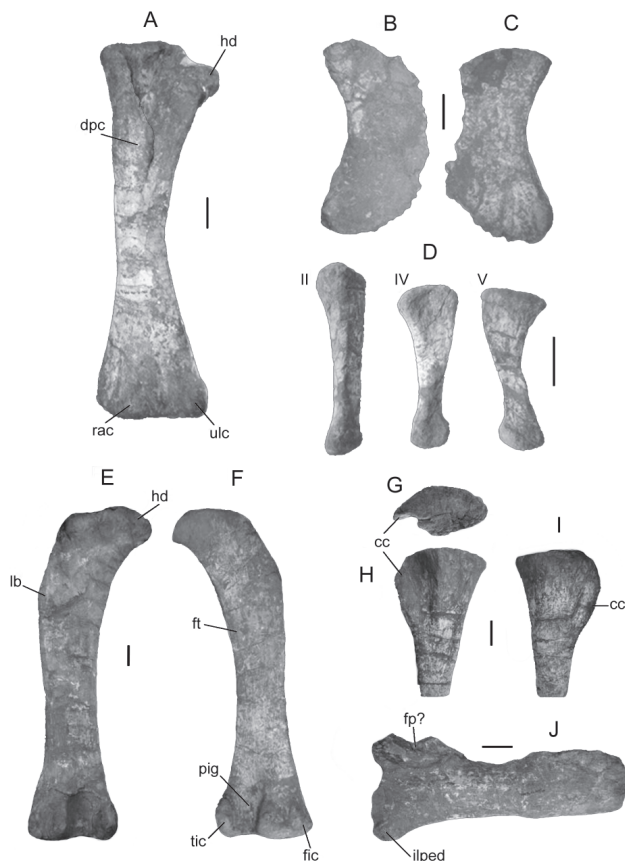

FIGURE 6 | **A) Right humerus in anterior view (MAU-Pv-N-449/36); sternal plates B-C) in anteroventral view (MAU-Pv-N-449/10 and 25); D) left metacarpals in lateromedial view (MAU-Pv-PH-449/11, 12 and 13); F) right femur (MAU-Pv-PH-449/7) in posterior view; G) left femur in posterior view (MAU-Pv-PH-4498), G) left tibia in proximal view, H) lateral view and I) medial view (MAU-Pv-PH-449/9); and J) left pubis in ventral view (MAU-Pv-PH-449/16). Abbreviations are in the Anatomical Nomenclature. Scale bar: 10cm.**

et al., 2006). The marked medial projection of the deltoid crest has been considered a diagnostic character of *Gondwanatitan* (Kellner and de Azevedo, 1999), but it is present in other titanosaurs such as *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). The distal shaft is slightly twisted with respect to the proximal end of the humerus.

Metacarpals (Figs. 6D). Three complete metacarpals (MAU-Pv-PH-449/11, 12, 13) and one incomplete one (MAU-Pv-PH-35) have been recovered. The first three, correspond to the left metacarpals, II, IV and V. Metacarpal II is slightly longer than the others (Table 1). The metacarpal-humerus length ratio is 0.33. The diaphysis of metacarpal II is straight, with the ends little expanded. The proximal articular surface has a sub-circular outline, whereas the distal is more squared. There is a major rim on the palmar face. The anterolateral face of the diaphysis of metacarpal IV is slightly convex, and the palmar face concave. Both ends are expanded, the proximal notably more expanded perpendicularly in relation to the distal. In the proximal view, the articular surface has a kidney-shaped outline, whereas the distal is sub-circular in outline. On its palmar face a crest extends from the middle of the shaft up to the distal articular surface. Metacarpal V has a sigmoid shaft, with a convex anterodorsal face and a palmar face virtually flat. As in metacarpal IV, both ends are equally expanded. The proximal articular surface exhibits an elliptic outline, whereas the distal is sub-quadrangular in outline. As in metacarpal IV, the palmar face exhibits a more developed crest that extends from the middle of the shaft up to the distal articular surface.

Femur (Figs. 6E-F). Both complete femora have been recovered (MAU-Pv-PH-449/7 and 8). They are anteroposteriorly flattened. The femoral head is well developed and shows a significant medial displacement, as occurs in many titanosaurs (Wilson and Carrano, 1999). On the lateral margin there is a lateral bulge, which is well developed distally, extending beneath the position of the fourth trochanter. The minimum diameter of the shaft occurs in the distal third of the femur (Table 1). The fourth trochanter is small and is located approximately a third of the total length from the femoral head in a posterior position close to the medial edge. Distally, the fibular condyle is divided into two subcondyles, one medial and the other lateral or epicondylar, separated by a smooth, narrow notch. The medial condyle is more robust and wider than the lateral. The tibial condyle, which is more delicate and compressed laterally, is separated from the fibular condyle by a deep posterior intercondylar groove. Both the fibular and tibial condyles are medially inclined.

Tibia (Figs. 6G-I). The proximal ends of the left tibia and part of its shaft have been recovered (MAU-Pv-PH-449/9), as well as the distal end of the right tibia (MAU-Pv-PH-449/17). The proximal articulation of the tibia is oval in outline, with the greatest diameter anteroposteriorly oriented. The articular surface for the tibial condyle of the femur is slightly concave and rugose. It differs from the tibia of *Mendozasaurus* in having a proximal end wider lateromedially than transversely, although this difference may be due to the fact that in *Mendozasaurus* the tibia was flattened in diagenesis. The cnemial crest is very well developed, and projects anterolaterally, as in all the Eusauropoda (Wilson and Sereno, 1998). The anterior part of the lateral face is concave anteroposteriorly. Beneath the cnemial crest the lateral face becomes flat. The proximal part and the medial face are convex. MAU-Pv-PH-449/17 preserves both malleoli, and the intercondylar groove is well developed.

Ilium. The distal end of the iliac peduncle of the right ilium has been recovered (MAU-Pv-PH-449/14). It is wider lateromedially than anteroposteriorly, with the surface of the anterior face slightly convex and the posterior concave. The pubic articular surface is gently concave, sub-elliptic in outline, and presents rugosities on its anterior edge.

Pubis (Fig. 6J). A left pubis has been recovered (MAU-Pv-PH-449/16), which is incomplete in its acetabular region. Its distal end is more robust and slightly wider dorsoventrally with respect to the pubic blade. The distal end is rounded in lateral view. The laterodorsal edge is concave anteroposteriorly. It has a longitudinal rim similar to the one present in *Saltasaurus* and *Aeolosaurus* (Powell, 1992; Salgado and Coria, 1993), which proximally delimits two faces, a flatter dorsal one and a more concave ventral one. The pubic foramen, although incomplete, seems to have been oval in outline.

DISCUSSION AND CONCLUSIONS

Petrobrasaurus puestohernandezi gen. et sp. nov. shares with the Titanosauriformes the presence of pneumatic cavities in the dorsal ribs, the medial displacement of the upper third of the diaphysis of the femur, the existence of a lateral bulge beneath the greater trochanter, and the neural arch positioned anteriorly in the anterior caudal vertebrae (Salgado et al., 1997; Wilson and Sereno, 1998). On the other hand, the presence in *Petrobrasaurus puestohernandezi* gen. et sp. nov. of pointed pleurocoels in the dorsal vertebral centra (Bonaparte and Coria, 1993), procoelous anterior caudal vertebral centra with a markedly convex posterior articular face (McIntosh, 1990), and forked haemal arches (Wilson, 2002) are synapomorphies that allow this new taxon to be included within Titanosauria.

In a recent phylogenetic proposal for titanosaurs, Calvo et al. (2007a) defined the clade Lognkosauria as including "the most recent common ancestor of *Mendozasaurus*

neguyelap and *Futalognkosaurus dukei* and all its descendants". What is interesting about their proposal is that the sister group of Lognkosauria is *Malawisaurus*, from the Lower Cretaceous of Malawi (Jacobs et al., 1993). The morphological similarity of *Petrobrasaurus* with *Mendozasaurus* might suggest that the new taxon falls in the Lognkosauria clade. Nevertheless, the inclusion of *Petrobrasaurus* gen. nov. in the data matrix of Calvo et al., 2007a, resulted in a polytomy at the base of Eutitanosauria. Therefore, the relationship of *Petrobrasaurus* gen. nov. with the Lognkosauria is not confirmed; nor is its relationship with any other titanosaur subgroup. Until this polytomy can be resolved, which could be achieved with a new phylogenetic analysis of the Titanosauria, or with new material from *Petrobrasaurus* gen. nov., it is only possible to assign it to Titanosauria *incertae sedis*.

The palaeontological record usually incomplete and strongly biased, and this is particularly true for the record of Patagonian dinosaurs. Even so, the efforts made in recent years are making it possible to fill in these gaps in our knowledge. One of the groups of dinosaurs where the greatest advances have been made is precisely the titanosaur sauropods (Salgado and Bonaparte, 2007). The titanosaur record of the Neuquén Basin is relatively abundant and diverse throughout the Late Cretaceous, but there are intervals in which the titanosaurs are poorly known, as is the case with the Plottier Formation, one of the latest units containing fossils of the Neuquenian Tetrapod Assemblage (NTA) (Leanza et al., 2004). From the Portezuelo Formation, by contrast, a number of titanosaurs in the Neuquén Basin have recently been described: *Mendozasaurus*, *Futalognkosaurus* and *Rinconsaurus*, which clearly differ from the more derived forms (saltasaurids) of the Latest Cretaceous.

The fragmentation of Pangaea and the separation of the landmasses became more marked at the beginning of the Cretaceous with the opening of the central part of the Atlantic and its communication with the Tethys (Blakey, 2004). These palaeogeographic circumstances made the free passage of dinosaurs between Laurasia and Gondwana, and moreover between the different parts of Gondwana (Africa and South America), more difficult or even impossible from the Early Cretaceous onwards. This isolation seems to be the main cause of the differences between the dinosaur fossil associations in the continents into the Late Cretaceous (Upchurch et al., 2002; Holtz et al., 2004). The faunal connection of the dinosaurs between Laurasia and Gondwana continued intermittently during the rest of the Cretaceous by means of the Apulian Route (Gheerbrant and Rage, 2006; Canudo et al., 2009a). However, the situation was different in the continents of the southern hemisphere. At the end of the Early Cretaceous, the separation of Africa and South America took place,

with the definitive opening of the South Atlantic. The presence of rebbachisaurid sauropods and abelisauroid theropods in both continents has been interpreted in terms of a persisting land connection at the end of the Early Cretaceous and in the Late Cretaceous (Sereno et al., 2004). However, Upchurch (2008) criticizes this point of view and argues that there was no geographical connection between Africa and South America. He further suggests that the faunal exchange between South America and other parts of Gondwana (except Africa) would have taken place in the Late Cretaceous using the Antarctic Route.

As pointed out above, the NTA represents a faunal association in the time interval of the definitive fragmentation of the faunas of South America and Africa. The existence in the NTA of taxa related to basal titanosaurs such as *Malawisaurus* would indicate that basal forms of this clade were still present in the Neuquén Basin at this time (Calvo *et al.*, 2007a). Another consequence of the record of *Petrobrasaurus* gen. nov. is that the latest levels of the NTA yield an association of titanosaur sauropods similar to that recorded in the lower part. For the moment, there is no record in the NTA of the more derived forms such as the saltasaurids, which are the forms that will dominate the end of the Cretaceous in the Neuquén Basin.

ACKNOWLEDGMENTS

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