Cretaceous Research 72 (2017) 1–15

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

New materials of lithostrotian titanosaurs (Dinosauria: Sauropoda) from the Upper Cretaceous of central Patagonia

Lucio M. Ibiricu [a, *], Gabriel A. Casal [b], Rubén D. Martínez [b], Marcelo Luna [b], Ezequiel González Svoboda [b], Ignacio A. Cerda [c]

[a] Instituto Patagónico de Geología y Paleontología (IPGP–CONICET), Boulevard Almirante Brown 2915, 9120, Puerto Madryn, Chubut, Argentina
[b] Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia San Juan Bosco, C.C. 360, 9000, Comodoro Rivadavia, Chubut, Argentina
[c] Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo 'Carlos Ameghino', Belgrano 1700, Paraje Pichi Ruca (prédio Marabunta), 8300, Cipolletti, Río Negro, Argentina

ARTICLE INFO

Article history:
Received 24 August 2016
Accepted in revised form 16 December 2016
Available online 30 December 2016

Keywords:
Titanosauria
Lago Colhué
Huapi Formation
Late Cretaceous
Central Patagonia
Titanosaur diversity

ABSTRACT

Continental Cretaceous deposits exposed in central Patagonia, Argentina, preserve a rich and important record of titanosaurian evolution that spans the entire Upper Cretaceous. Recently, a new lithostratigraphic unit, the Lago Colhué Huapi Formation (Coniacian – Maastrichtian), was located in the Golfo San Jorge Basin. Here, we describe new titanosaurian sauropod material from that formation (UNPSJB-Pv 1051). The material consists of a partially articulated left hind limb and disarticulated but associated skeletal elements. They are confidently referred to Titanosauria, and within that clade, to Lithostrotia, probably occupying a derived position. We interpret the bone concentration as an assemblage of hydraulic origin deposited in a fluvial channel. This new material begins the incipient fossil record of the Lago Colhué Huapi Formation, thereby also increasing the titanosaurian diversity of the latest Cretaceous. Additionally, the new titanosaurian enhances evidence in support of strong faunal similarities among the Allen and Marilia formations, chronological equivalents in the Cretaceous of South America. Furthermore, the Lago Colhué Huapi specimen adds to the Late Cretaceous record of Titanosauria and augments our knowledge of central Patagonian terrestrial vertebrate assemblages during this interval.

1. Introduction

The south central region of Patagonia, Argentina (Fig. 1), preserves a rich and important Cretaceous vertebrate fossil record (Martínez, 1998; Lamanna et al., 2003; Martínez et al., 2004; Martínez and Novas, 2006; Casal et al., 2009; Ibiricu et al., 2012a,b, 2013a,b, 2015; Casal et al., 2016; Martínez et al., 2016). Most of the knowledge on these continental Cretaceous assemblages derives from the Bajo Barreal Formation (lower Cenomanian–upper Turonian; Casal et al., 2016). The lower part of the Upper Member of the Bajo Barreal Formation is characterized by gray mudstones, whereas towards the top there is a clear predominance of white sandstones and red mudstones. Based on lithological and paleontological interpretations and stratigraphic relationships, Casal et al. (2015a) recently proposed a new lithostratigraphic unit (those characterized for white sandstones and red mudstones) in the Golfo San Jorge Basin (Chubut Group) in the top portion of the Bajo Barreal Formation Upper Member, which they named the Lago Colhué Huapi Formation (Coniacian–Maastrichtian; Fig. 2). In these levels, which are well exposed in the southeastern region of Lago Colhué Huapi, the fossil record has recently increased (Luna et al., 2003; Casal et al., 2007; Casal et al., 2010; Ibiricu et al., 2010; Casal et al., 2015b). Nevertheless, several of the dinosaurs discovered there are controversial, particularly concerning the lack of a clear stratigraphic provenance and/or the loss of holotypes (see Coria and Cambiaso, 2007; Ibiricu et al., 2010). The first of these controversies has been, in part, clarified by the newly recognized lithostratigraphic unit (Casal et al., 2015a, 2016). Vertebrate fossils reported from this Upper Cretaceous unit include a crocodyliform (Lamanna et al., 2003), theropod teeth (of dromaeosaurids, megaraptorids; Casal et al., 2015b), fragmentary iguanodontian and non-hadrosaurid

* Corresponding author.
E-mail addresses: ibiricu@cenpat-conicet.gob.ar (L.M. Ibiricu), paleogac@yahoo.com.ar (G.A. Casal), rudaframartinez@gmail.com (R.D. Martínez), paleoambiental@yahoo.com (M. Luna), ezequiel.fotografia@gmail.com (E.G. Svoboda), nachocerda6@yahoo.com.ar (I.A. Cerda).

http://dx.doi.org/10.1016/j.cretres.2016.12.015
0195-6671/

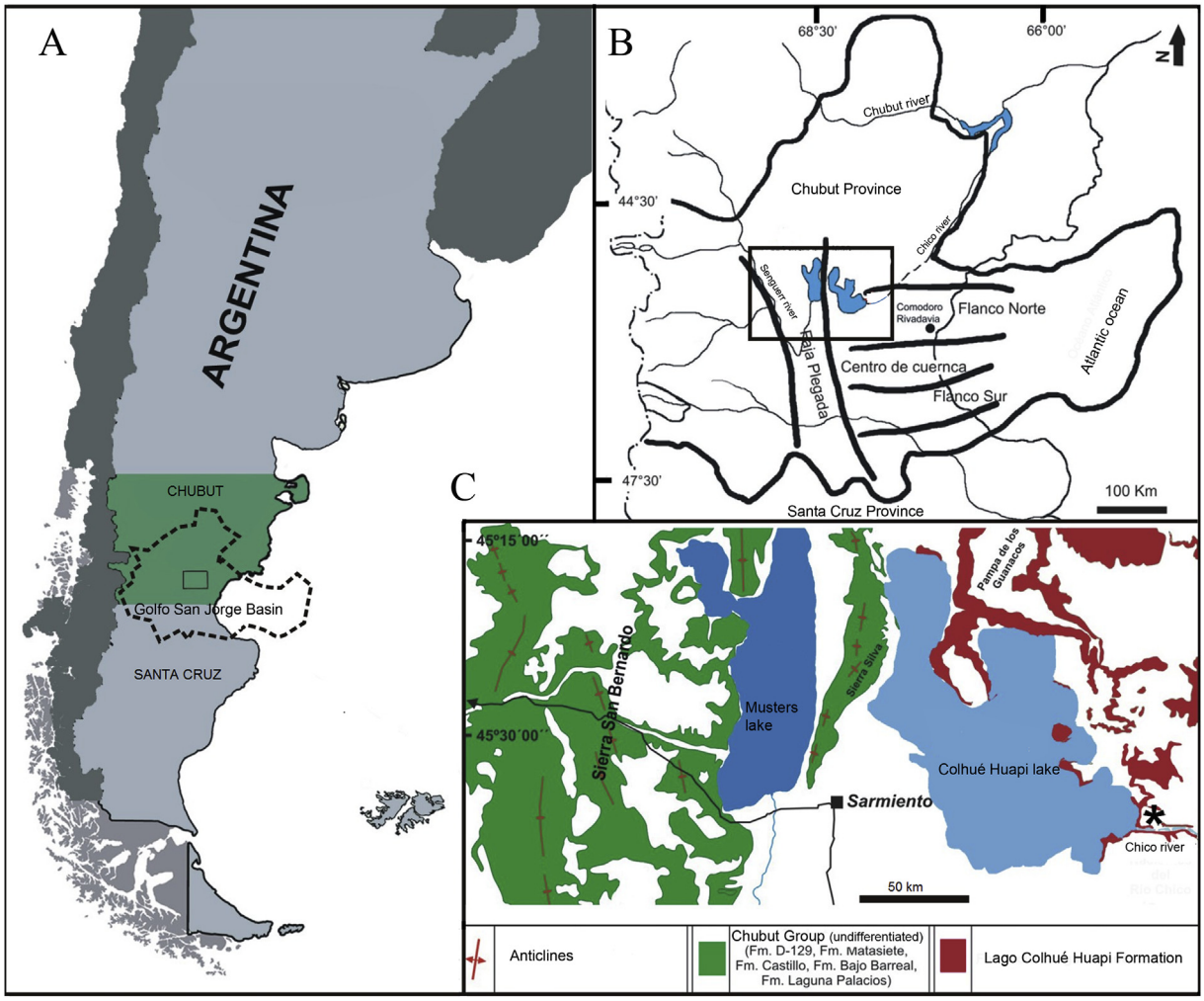

Fig. 1. A, Map of Argentina showing the location of the Golfo San Jorge Basin. B, Structural division of the Golfo San Jorge Basin (modified from Figari et al., 2002). C, Discovery site of UNPSJB-Pv 1051 (denoted by black asterisk).

ornithopod material (Luna et al., 2003; Ibiricu et al., 2010), the controversial *Secernosaurus koerneri* (Brett-Surman, 1979), and *Notoceratops bonarelli* (Tapia, 1919). The vertebrate fauna reported from these beds also includes the titanosaurian sauropods *Aeolosaurus colhuehuapensis* (Casal et al., 2007) and MDT-Pv 4 (a large and partially articulated specimen; Casal et al., 2010). Additionally, the titanosaurian fauna in the Lago Colhué Huapi Formation currently includes the titanosaurs *Argyrosaurus superbus* and *Elaltitan lilloi* (Mannion and Otero, 2012; but also see Casal et al., 2015a, 2016). The stratigraphic precedence of *Elaltitan* is in the lower part of the Lago Colhué Huapi Formation (Coniacian), whereas *Argyrosaurus* and *Aeolosaurus* come from the upper part of the new formation (i.e., Campanian–Maastricthian).

Here, we report new fossil materials from deposits of the Upper Cretaceous (Campanian–Masstrichtian) Lago Colhué Huapi Formation exposed in the southeastern region of Lago Colhué Huapi and the Chico River headwaters. This set of fossils includes a partially articulated hind limb and associated materials pertaining to a subadult titanosaur sauropod. The addition of this sauropod material to the fauna of the Lago Colhué Huapi Formation is significant because it adds to the fossil record of this new unit and therefore augments our understanding of the evolution and diversity of Titanosauria. In addition, we performed a detailed taphonomic and histological study, which provide opportunities to infer the implications of these aspects for of the new titanosaur. Finally, this study provides new evidence on faunal correlations and associations with chronologically equivalent units in northern Patagonia and Brazil. The fossil record of these strata suggests that derived titanosaurs achieved a high diversity and displayed a wide distribution during the latest Cretaceous, at least in some areas of Patagonia and southern Brazil.

Institutional abbreviations. **MACN-Pv RN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", colección de paleontología de vertebrados, Rio Negro, Buenos Aires, Argentina. **MDT-Pv**, Museo "Desiderio Torres", Paleontologia de Vertebrados, Chubut, Argentina. **MPCA-Pv**, Museo Provincial de Cipolletti "Carlos Ameghino", colección de paleontología de vertebrados, Rio Negro, Argentina. **UNPSJB-Pv,** Universidad de la Patagonia "San Juan Bosco", colección de Paleovertebrados, Chubut, Argentina.

2. Materials and methods

An articulated left hind limb (femur [UNPSJB-Pv 1051/1], tibia [UNPSJB-Pv 1051/2], and fibula [UNPSJB-Pv 1051/3]) were recovered. The specimen additionally includes a fragment of the left radius (UNPSJB-Pv 1051/12), a fragment of the right coracoid (UNPSJB-PV 1051/11), left and right metacarpals I (UNPSJB-Pv 1051/7 and UNPSJB-Pv 1051/8), right metacarpal III (UNPSJB-Pv 1051/9),

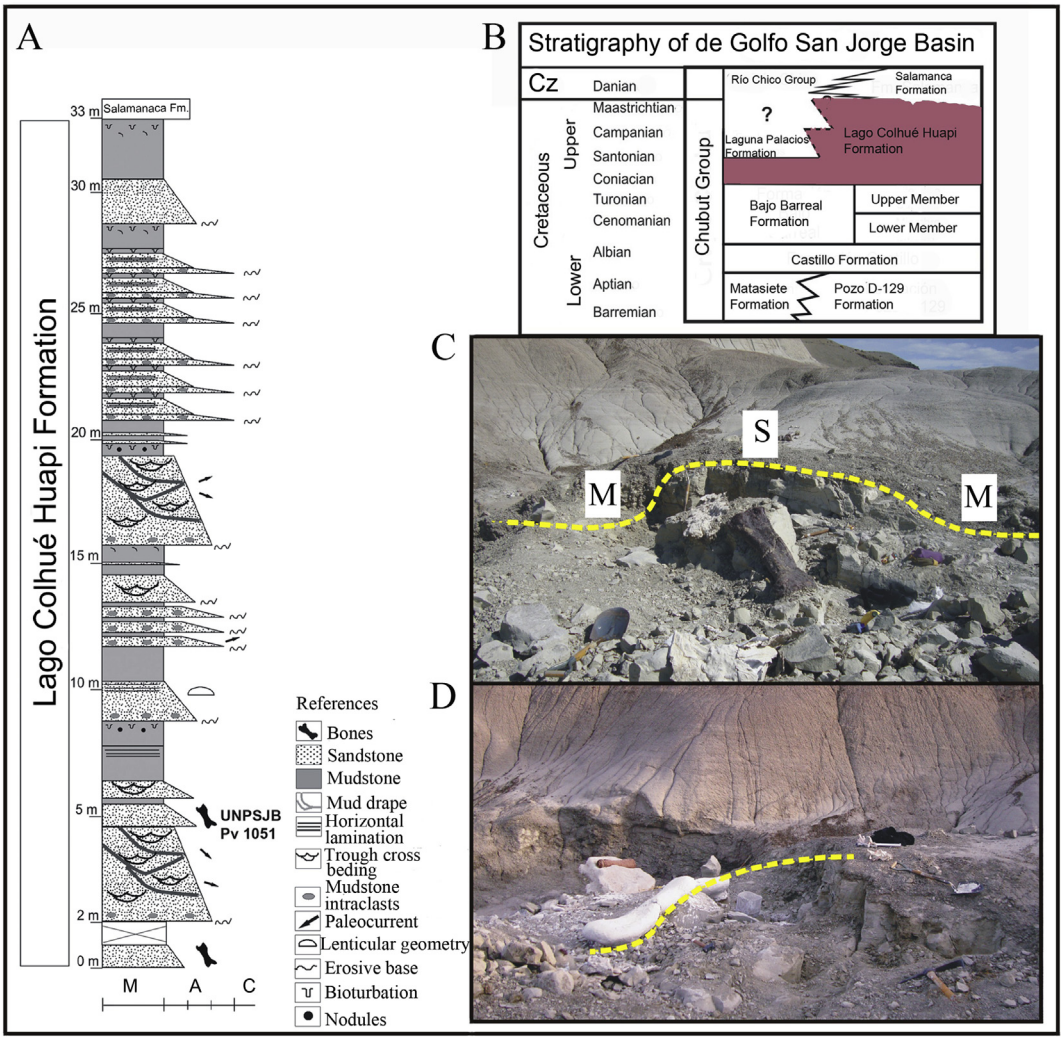

Fig. 2. A, Stratigraphic column of the Lago Colhué Huapi Formation at the headwaters of the Chico River. B, Stratigraphic nomenclature for the Cretaceous beds (Chubut Group) in the study area (from Casal et al., 2015a). C, Transverse section of entombing sand bar deposits (S) and floodplain-derived mudstones (M) beside them. D, Longitudinal section of the central sand bar (axis denoted by the yellow dotted line), including the titanosaurian fossils described herein.

left metacarpal V (UNPSJB-Pv 1051/10), a putative shaft fragment, probable metatarsal III (UNPSJB-Pv 1051/4), a probable proximal end of a metatarsal (UNPSJB-Pv 1051/5), the left astragalus (UNPSJB-PV 1051/13), and a pedal phalanx (UNPSJB-Pv 1051/6). All these materials were found associated in the same stratigraphic horizon.

Stratigraphic sections were measured using a Jacob's staff. The orientation of paleocurrent indicators and bones were determined with a Brunton compass. Rock thin sections were prepared for petrographic characterization via standard techniques. The paleoenvironment of the site was analyzed based on facies and fluvial architecture according to Miall (1996). Taphonomic characteristics currently analyzed include weathering, following the categories of Behrensmeyer (1978), and bone integrity, following Alcalá (1994). Tomassini et al. (2010) considered three types of breaking: longitudinal (angle between 0° and 29°); oblique (angle between 30° and 59°); and transversal (angle between 60° and 90°); these criteria were followed here. Degree of abrasion was determined following Alcalá (1994), and determination of bone orientations and degree of articulation were assessed following the methods of Behrensmeyer (1991). Plastic deformation and bone permineralization were evaluated following Fernández-López (2000). In further assess bone permineralization, we performed chemical analyses including the grinding of a fragment of the fossil material, acidification (HCl 1:1), and KSNC 0.1 (Skoog et al., 2005). Thin sections of ~30 μm were prepared and the samples were described using a petrographic microscope (at 2.5× and 10×). Mineral composition of the fossils was carried out using X-ray diffraction (XRD) following Moore and Reynolds (1989). Preparation of the chemical and diffraction samples was carried out in the Departamento de Geología (Universidad Nacional de la Patagonia San Juan Bosco; Comodoro Rivadavia, Provincia de Chubut, Argentina).

In order to assess the ontogenetic stage of the studied specimen, histological thin sections were made from the tibia and the femur of UNPSJB-Pv 1051. Samples for sectioning were obtained from the mid-shaft of each element. Preparation of the histological sections was carried out in the Departamento de Geología of the Universidad Nacional de San Luis (Argentina). Sections were prepared using the method outlined by Chinsamy and Raath (1992) and studied using a petrographic polarizing microscope (Nikon E200 pol). Histological nomenclature and definitions of structures used in this study are derived from Francillont-Viellot et al. (1990) and Chinsamy Turan (2005).

2.1. Locality and horizon

Southeastern region of Lago Colhué Huapi (45°35′52″S, 68°37′20″W), approximately 80 km east of the town of Sarmiento, southern Chubut Province, central Patagonia, Argentina (Fig. 1). Lago Colhué Huapi Formation (Coniacian–Maastrichtian; Casal et al., 2015a).

2.2. Geologic and paleoenvironmental context

The south-central region of central Patagonia exposes well represented outcrops of continental Cretaceous sequences, forming part of the infill of the Golfo San Jorge Basin. The recently recognized Lago Colhué Huapi Formation overlies the Bajo Barreal Formation (Upper Cretaceous), whereas in the Colhué Huapi Lake and Chico River regions it shows a gradational or erosive contact with the overlying Salamanca Formation (Maastrichtian–Danian/lower Danian; see Casal et al., 2015a and Casal et al., 2016, fig. 2).

In its type locality, the depositional setting of the Lago Colhué Huapi Formation is interpreted as a fluvial system, showing an increase in channel sinuosity up section. Well-drained floodplains characterized by reddish mudstones are also observed. Based on the presence of mud cracks and sepiolite clays, the levels where fossils are commonly found are interpreted to have been deposited in a semiarid climate (Zaaboub et al., 2005; Casal et al., 2015a). Nevertheless, palynological information from the top of the unit indicates paleoclimatic conditions were relatively warm and humid (Vallati et al., 2015, 2016a). The age of the Lago Colhué Huapi Formation ranges from Coniacian to Maastricthian; however, at the top of the unit the age of the levels where UNPSJB-Pv 1051 were recovered is Campanian–Maastrichtian (Casal et al., 2015a). This age is supported by its stratigraphic relationships (Casal et al., 2015a), the presence of hadrosaurids (a group of dinosaurs only known from that interval of time; Casal et al., 2016), and by the presence of diagnostic palynomorphs (Vallati et al., 2016a,b).

The fossils described herein (UNPSJB-Pv 1051) were recovered from medium sandstones that grade upward to fine sandstones at the top of the section (Fig. 2). These sandstones are massive at the base and near the top and exhibit parallel lamination. They also show lenticular geometry, with concave-up bases and planar tops (Fig. 2C). The deposits in which the titanosaurian fossils were found are interpreted as a central bar developed within the main fluvial channel, which originated from a tractive and unidirectional flow. We base this interpretation on its position among coeval channels (Bridge, 2003). A paleocurrent towards the southeast (N141°) was determined based on the transversal geometry of the central bar. This value is in accordance with those obtained from other sedimentary bodies (sand bars) in the same outcrop. However, elsewhere in the Lago Colhué Huapi Formation outcrops these values are difficult to discern due to the abundance of cut and fill structures which preclude the identification of laterally contiguous deposits (Casal et al., 2015a). Nevertheless, the sedimentary deposit containing the fossils preserves a clear geometry of a bar showing a height of 1.10 m, a transverse width of 4.50 m, and a depth for the active channel of 3.30 m. Mudstone deposits, laterally positioned relative to the central bar, are a product of fluctuations in the paleo-discharge. The mudstones settled due to cessation of suspension transport during decreases of discharge or during the temporary abandonment of the channel (Miall, 1996; Lynds and Hajek, 2006). This possibly suggests seasonal variations in the paleo-discharge (Schumm, 2005) that may have characterized the semiarid middle section of the Lago Colhué Huapi Formation (Allard and Casal, 2013; Casal et al., 2015a).

3. Taphonomic context

3.1. Biostratinomy

Waning flow energy resulted in deposition of the fossils at the end of a sand bar (Figs. 2C–D, 3). The fossils show evidence of incipient weathering caused by subaerial exposure, in the form of a few longitudinal striations parallel to the main axis of the bones, and, on occasion, superficial exfoliations. These taphonomic features allow us to assign the fossils to weathering stage 1 of Behrensmeyer (1978).

The left femur (UNPSJB-PV 1051/1) and tibia (UNPSJB-PV 1051/2) are complete, whereas the distal end of the left fibula (UNPSJB-PV 1051/3) has not been preserved. This may be due to loss during transport, which could have resulted in the degradation and loss of thinner portions of bones. On the other hand, the smaller fossils with comparatively constant shaft width (i.e., metacarpals) are complete. The subparallel orientation of the 12 bones recovered is likely a product of hydraulic transport toward the southeast. Transport of such large bones would have most likely occurred as part of the bed load, via rolling and dragging. Such transport affected the distal ends and protruding structures of the bones, particularly by abrasion. The extent of abrasion of the bones can be assigned to Level 2 of the scale developed by Alcalá (1994). The left hind limb was articulated at the time of burial, suggesting the presence of connective soft tissue (Behrensmeyer, 1991). The rest of the bones were disarticulated and associated.

3.2. Fossil diagenesis

Sinuosity of the left femur (Fig. 3B) was caused by pressure exerted by the overlying sediment. Lithostatic compression also

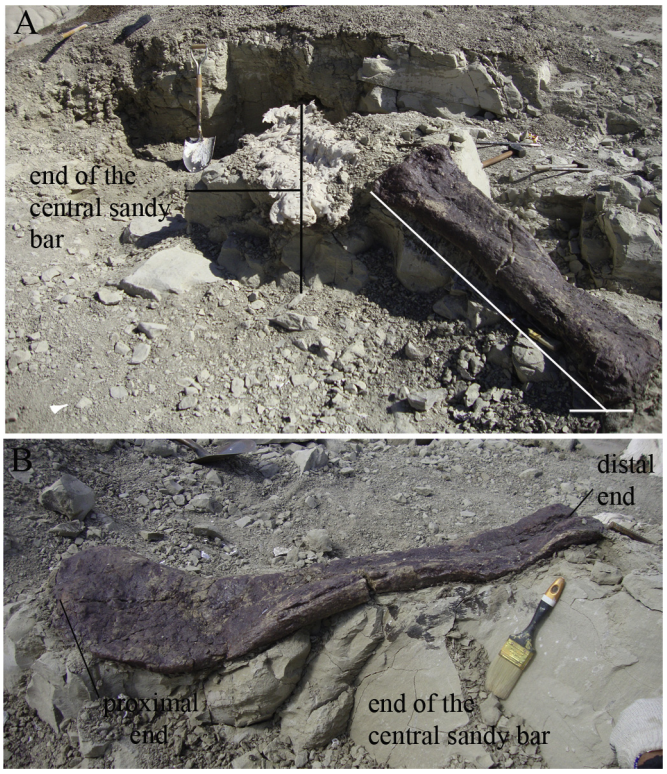

Fig. 3. A, Excavation site showing the end of the central sand bar and the left femur (UNPSJB-Pv 1051/1) in anteromedial view. The white line indicates the inclination angle of the femur (43°). B, Femur UNPSJB-Pv 1051/1 in posterolateral view, showing plastic deformation induced by lithostatic pressure.

resulted in anteroposterior compression of the distal end of the left tibia. In support of this conclusion, thin sections exhibited crushing or deformation of osteons (see below). All of the bones recovered exhibit a reddish-brown color, suggesting permineralization with iron-oxide minerals (diagenetic Category 4 of Tomassini et al., 2014). In agreement with this inference, x-ray diffraction of thin sections indicated the presence of hematite infilling bone fractures and Haversian canals. The fossils primarily exhibit transverse and diagonal fractures.

4. Bone histology

The left tibia and femur exhibit strong diagenetic alteration, which is more pronounced in the tibia fragment, in which it is almost impossible to recognize the original bone tissue. The femur exhibits a thick cortex of compact bone surrounding the medullary cavity of cancellous bone. The medullary region is badly crushed (possibly due to lithostatic compression) and the original cancellous structure, made up of bony trabeculae, is destroyed and compressed together (Fig. 4A). Large resorption cavities are distributed throughout the medullary cavity. These spaces commonly coalesce and form larger cavities of irregular shape (Fig. 4B). The cortical bone is composed almost entirely of dense Haversian tissue (Fig. 4C). Secondary osteons representing multiple generations are abundant and reach the outermost preserved portion of the cortex. Remnants of strongly altered, primary bone tissue also appear to be preserved in a few areas. The outer cortex is either eroded or strongly altered, precluding certain identification of subperiosteal bone tissue.

5. Systematic paleontology

Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Titanosauriformes Salgado et al., 1997
Titanosauria Bonaparte and Coria, 1993
Lithostrotia Upchurch et al., 2004

6. Comparative description

To ascertain the evolutionary affinities of UNPSJB-Pv 1051 within Titanosauria, we compared the fossils to corresponding skeletal elements of the following taxa: *Aeolosaurus rionegrinus* (Salgado and Coria, 1993), *Aeolosaurus* sp. (García and Salgado, 2013), *Alamosaurus sanjuanensis* (Lehman and Coulson, 2002), *Andesaurus delgadoi* (Calvo and Bonaparte, 1991; Mannion and Calvo, 2011), *Antarctosaurus wichmannianus* (Huene, 1929), *Argyrosaurus superbus* (Lydekker, 1893; Mannion and Otero, 2012), *Bonatitan reigi* (Martinelli and Forasiepi, 2004; Salgado et al., 2014), *Dreadnoughtus schrani* (Lacovara et al., 2014), *Diamantinasaurus matildae* (Hocknull et al., 2009; Poropat et al., 2015b), *Elaltitan lilloi* (Mannion and Otero, 2012), *Epachthosaurus sciuttoi* (Martinez et al., 2004), *Laplatasaurus araukanicus* (Huene, 1929; Gallina and Otero, 2015), *Lirainosaurus astibiae* (Sanz et al., 1999; Díez Diaz et al., 2013), *Mendozasaurus neguyelap* (González Riga, 2003), *Neuquensaurus australis* (Lydekker, 1893; Salgado et al., 2005; Otero, 2010), *Opisthocoelicaudia skarzynskii* (Borsuk-Białynicka, 1977), *Petrobrasaurus puestohernandezi* (Filippi et al., 2011), *Quetecsaurus rusconii* (Gonzalez Riga et al., 2014), *Rapetosaurus krausei* (Curry Rogers, 2009), *Rinconsaurus caudamirus* (Calvo and González Riga, 2003), *Rocasaurus muniozi* (Salgado and Azpilicueta, 2000), *Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1992), and *Uberabatitan ribeiroi* (Salgado and Carvalho, 2008).

Coracoid (Fig. 5). The right coracoid (UNPSJB-Pv 1051/11) displays a subquadrangular outline as in *Diamantinasaurus*, *Quetecsaurus*, *Lirainosaurus*, *Uberabatitan*, *Rinconsaurus*, and saltasaurines. In contrast, other titanosaurs, such as *Dreadnoughtus*, *Opisthocoelicaudia*, and *Rapetosaurus*, exhibit more rounded coracoids. The lateral surface of the right coracoid is irregularly convex, whereas the medial face is concave. This condition is shared with several

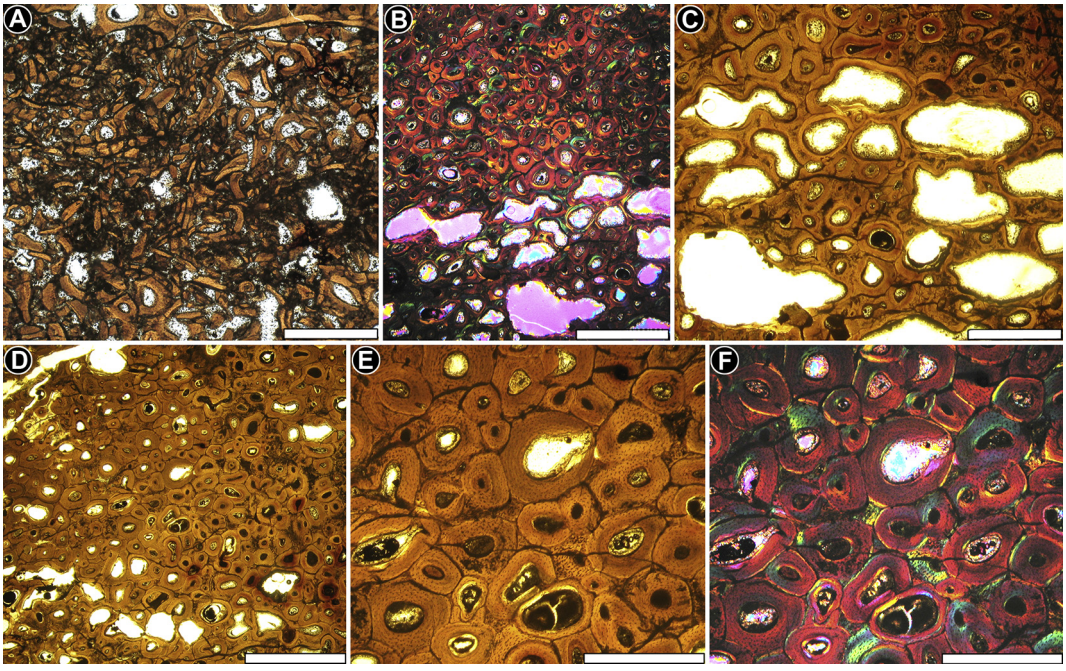

Fig. 4. Histology of the femur of UNPSJB-PV 1051. A, Trabecular bone crushed and compacted in the medullary cavity. B, General view of the perimedullary region showing dense Haversian bone and resorption cavities. C, Detail of the resorption cavities. D, Cortical bone composed almost entirely of dense Haversian tissue. E and F, Details of the Haversian bone showing several generations of secondary osteons. Images in A, C, D, and E were taken under plane-polarized light, whereas images in B and F were taken under cross-polarized light with a lambda compensator. Scale Bars: 1 mm (in A), 2 mm (in B and D), 1.2 mm (in C), and 0.8 mm (in E and F).

titanosaurs (e.g., *Quetecsaurus*, *Lirainosaurus*, *Rapetosaurus*). On the lateral surface there is a relatively well-marked ridge that extends anteroposteriorly, ventral to the coracoid foramen. The ridge may represent an attachment site for the M. biceps branchii. This ridge is similar in its position to that described in *Rapetosaurus*, and it is more developed than that seen in *Quetecsaurus.* The coracoid foramen is open. The right coracoid shows a relatively well developed infraglenoid lip, but it is less developed than those seen in, for example, *Dreadnoughtus*, *Quetecsaurus*, and macronarians in general (Lacovara et al., 2014). The infraglenoid lip forms an angle of 90° with the anterior margin, as in *Quetecsaurus.* The coracoid is thicker in its posteroventral portion, whereas in the anterior portion it is thinner. The glenoid surface is slightly longer anteroposteriorly than mediolaterally. This condition differs from that seen in several titanosaurs (e.g., *Quetecsaurus*, *Rapetosaurus* and *Opisthocoelicaudia*) in which this surface is mediolaterally compressed. In contrast, the condition observed in UNPSJB-PV 1051/11 is instead similar to that present in *Uberabatitan* (see Salgado and Carvalho, 2008, fig. 17b).

Left radius (Fig. 6). This fragment is identified as a left radius (UNPSJB-PV 1051/12). The proximal end and a portion of the shaft are missing. The preserved diaphysis length is 37.5 cm and the distal end width (transverse expansion) is 16 cm, whereas the minimum shaft width is 8 cm. The anterior surface is mediolaterally convex, whereas the posterior surface is flat. The lateral margin is concave. The medial margin is comparatively flat and straight. In posterior view, there is a relatively well-marked ridge on the lateral margin (possibly the interosseous ridge *sensu* Curry Rogers, 2009). This ridge (denoting the margin of articulation between the radius and ulna) could have been the site of insertion of the M. pronator teres (Borsuk-Białynicka, 1977). The distal end is mediolaterally expanded compared to the radial shaft. This transverse expansion is variable among titanosaurians (Poropat et al., 2015b). For example, the expansion in *Epachthosaurus* is greater than that seen in *Diamantinasaurus*, whereas in *Aeolosaurus*, *Argyrosaurus*, *Elaltitan*, and *Rapetosaurus* this transverse expansion is less marked. In UNPSJB-PV 1051/12, the distal transverse expansion is double the shaft width. In this regard, it resembles *Uberabatitan and Opisthocoelicaudia*, although in the latter the relative expansion is greater. The distal end is mediolaterally convex and rugose. The distal articular surface has an ovoid outline (probably slightly taphonomically enhanced). The shape of the distal articular surface of UNPSJB-PV 1051/12 contrasts with the oval (e.g., *Diamantinasaurus*, *Elaltitan*, *Neuquensaurus*, *Saltasaurus*), nearly square (e.g., *Dreadnoughtus*), or sub-triangular (e.g., *Argyrosaurus*, *Quetecsaurus*) distal radii of other titanosaurs (see Upchurch et al., 2015). The strongly mediolaterally expanded and anteroposteriorly compressed distal articular surface is similar to that described in *Rapetosaurus* (although in UNPSJB-PV 1051/12 it is more expanded).

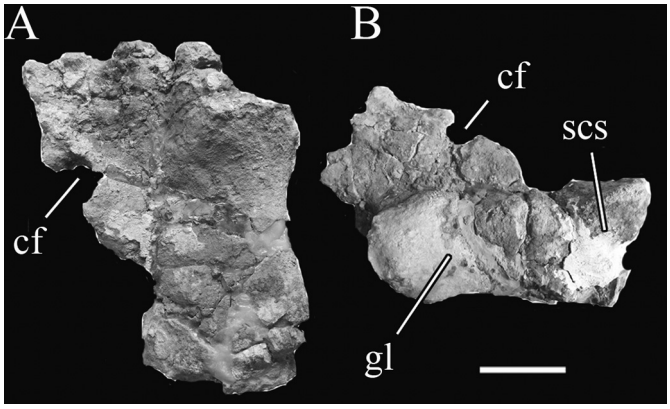

Fig. 5. A, Right coracoid (UNPSJB-Pv 1051/11) in medial view. B, Right coracoid (UNPSJB-Pv 1051/11) in glenoid (articular) view. Abbreviations: cf, coracoid foramen; gl, glenoid; scs, scapulacoracoid suture. Scale bar: 10 cm.

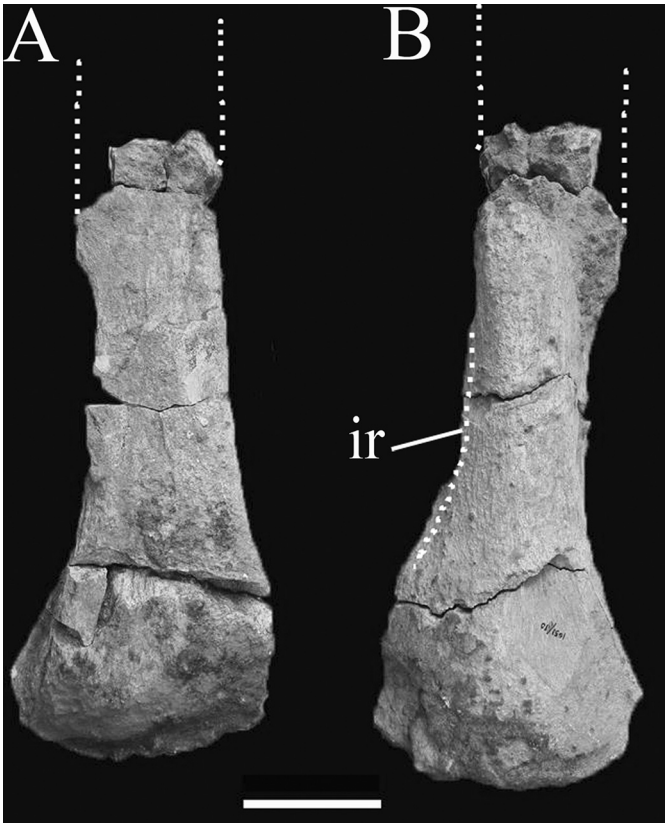

Fig. 6. A, Left radius (UNPSJB-Pv 1051/12) in anterior view. B, Left radius (UNPSJB-Pv 1051/12) in posterior view. Abbreviation: ir, interosseous ridge. Scale bar: 10 cm.

Metacarpals (Fig. 7). Four metacarpals were recovered. Though isolated, they were associated with the partially articulated hind limb (see below). UNPSJB-PV 1051/7 and 8 are identified as left and right metacarpal I (Mc I). These are the best preserved of the manual bones. The other two recovered metacarpals (UNPSJB-PV 1051/9 and 10), probably represent right metacarpal III (Mc III) and left metacarpal V (Mc V), respectively (Fig. 8). Metacarpal I (left and right) is subtriangular in dorsal view (i.e., dorsoventrally compressed and mediolaterally elongated), as in *Andesaurus*, *Argyrosaurus*, *Bonatitan*, *Epachthosaurus*, *Quetecsaurus*, and *Rapetosaurus.* Conversely, in some titanosaurs (e.g., *Alamosaurus*, *Diamantinasaurus*, and *Opisthocoelicaudia*) the proximal end is more ovate or "D-shaped" in outline (Apesteguía, 2005, fig. 15.5; Mannion and Calvo, 2011; Poropat et al., 2015b; but also see Poropat et al., 2015a). In the proximal third, the dorsal surface is slightly concave to receive Mc II. The dorsal surface then becomes mediolaterally convex distally, being at the midshaft mediolaterally convex (this feature is particularly pronounced in UNPSJB-PV 1051/8). The Mc I shaft is straight, as in *Bonatitan*, *Diamantinasaurus*, *Epachthosaurus*, *Quetecsaurus*, and *Rapetosaurus.* This straight morphology differs from the laterally-bowed metacarpal shafts of other titanosaurs, such as *Andesaurus*, *Antarctosaurus*, and *Argyrosaurus* (Apesteguía, 2005). The distal end exhibits a "D-shaped" outline as in several titanosaurs (e.g., *Andesaurus*, *Argyrosaurus*, *Diamantinasaurus*). In the distal portion of Mc I, the lateral condyle is taller than the medial one (i.e., the lateral condyle projects more distally than the medial condyle). This distal beveling is similar to that described in *Diamantinasaurus* (Poropat et al., 2015b, fig. 13g). There are no well-marked ridges on the shaft of metacarpal I.

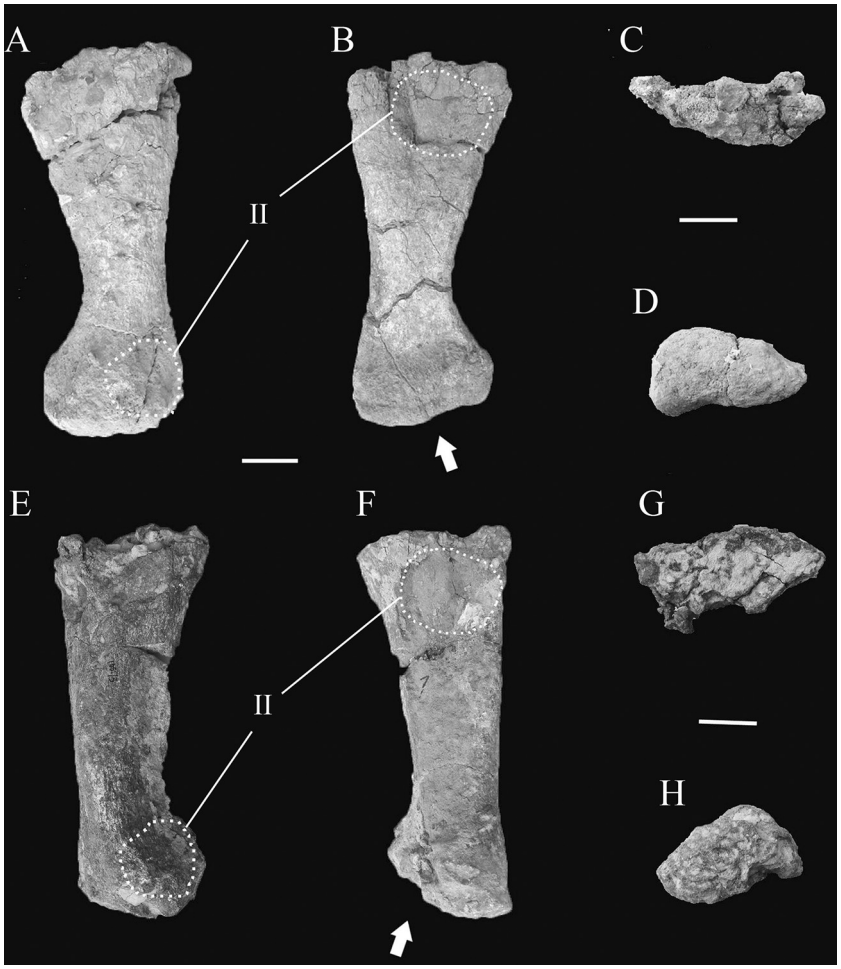

Fig. 7. Right metacarpal I (UNPSJB-PV 1051/8) in lateral (A), ventral (B), proximal (C), and distal (D) views. Left metacarpal I (UNPSJB-PV 1051/7) in lateral (E), ventral (F), proximal (G), and distal (H) views. The white dots indicate the surface area for articulation of metacarpal II, and white arrows denote distal beveling of metacarpal I. Scale bar: 5 cm.

The proximal end of Mc III is taphonomically affected; however, the preserved portion appears to be subtriangular in outline, with a relatively expanded apex. In dorsal view, a feint ridge is present. This ridge extends along almost the entire length of the preserved metacarpal shaft. On the ventral surface, there is a gently marked concavity. The distal end is incomplete; it is mediolaterally wide and dorsoventrally narrows toward the lateral and medial margins. In posteromedial view, there is a well pronounced "V shaped" surface for articulation with Mc II. The distal articulation displays a subcircular outline. Mc III of UNPSJB-Pv 1051/9, in overall morphology, resembles those described in *Argyrosaurus*, *Diamantinasaurus*, *Epachthosaurus*, and *Rapetosaurus*. The "V-shaped" articular facet for Mc III is similar to that observed in *Rapetosaurus*, although UNPSJB-PV 1051/9 is more robust. The dorsal ridge and ventral concavity are features shared with *Argyrosaurus*, but in UNPSJB-PV 1051/9 they are less pronounced. In contrast, the well-marked, dorsoventrally-oriented ridge described in *Argyrosaurus* is absent in UNPSJB-PV 1051/9. Also, this Mc III clearly differs from those seen in derived titanosaurs such as saltasaurines in terms of general robustness.

Although its preservation is poor, a probable left Mc V was also recovered. The dorsal surface is flat, whereas the ventral face is slightly mediolaterally convex. These features are also described in *Argyrosaurus*, *Bonatitan*, and *Rapetosaurus*. The preserved portion of the distal end twists with respect to the proximal end, as in *Andesaurus* and *Bonatitan*.

Femur (Fig. 9). The relatively robust and medium-sized (robustness index: 0.17) left femur (UNPSJB-PV 1051/1) is complete but taphonomically affected (see below). The shaft is straight and strongly anteroposteriorly compressed (eccentricity index: 0.26), exhibiting medial and lateral margins that are nearly parallel. The proximodistal length of the femur is 121 cm whereas its proximal and distal widths are 34.5 cm and 34.0 cm, respectively. The posterior surface of the femoral diaphysis is slightly more concave than its anterior surface, and its minimum shaft width (mediolaterally) is 21 cm. The femoral head is convex and its dorsal end is above the level of the greater trochanter. The proximal third of the femur is deflected medially (i.e., the femoral head is positioned dorsomedial to the greater trochanter). Distal to the greater trochanter, on the lateral margin of the shaft, there is a relatively well-developed lateral bulge. The length from the apex of the lateral bulge to the greater trochanter is 22 cm. The lateral bulge is rugose, possibly reflecting attachment of soft tissues (see below). The posteromedial surface of the femoral shaft exhibits a low and rugose fourth trochanter, situated slightly dorsal to the midshaft. Distally, the femur exhibits two articular condyles (tibial = medial; fibular = lateral). These condyles are slightly expanded and dorsomedially inclined (i.e., beveled). The fibular condyle is slightly more developed (robust) than the tibial condyle. The posterior intercondylar groove is shallow and ascends for approximately 13% of the total length of the femur.

UNPSJB-PV 1051/1 does not present the robust femoral morphology of derived titanosaurs (e.g., *Neuquensaurus*, *Saltasaurus*). Thus, the absence of the intermuscularis cranialis line, and weak development of the lateral bulge, distal condyles, and

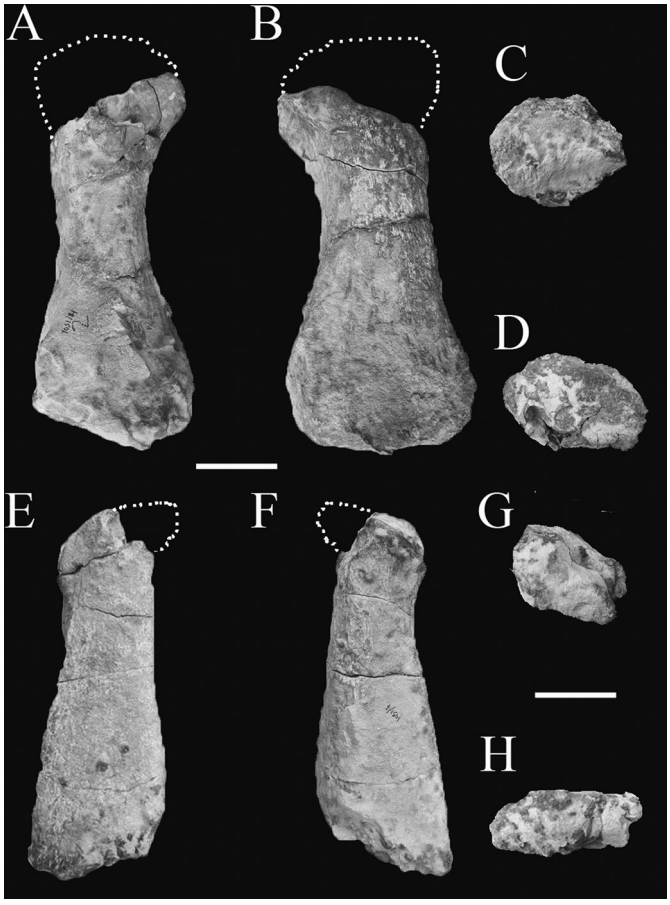

Fig. 8. Right metacarpal III (UNPSJB-Pv 1051/9) in dorsal (A), ventral (B), proximal (C), and distal (D) views. Left metacarpal V (UNPSJB-Pv 1051/10) in medial (E), ventral (F), proximal (G), and distal (H) views. Scale bar: 5 cm.

intercondylar groove distinguish UNPSJB-PV 1051/1 from *Bonatitan*, *Lirainosaurus*, *Neuquensaurus*, and *Saltasaurus*. Although the femoral head in UNPSJB-PV 1051/1 is convex, that seen in derived titanosaurs is more prominent and robust (i.e., globose femoral head). A sigmoidal ridge (trochanteric shelf described throughout archosaurian evolution; see Otero [2010] and Mannion et al., [2013]) is present in derived titanosaurs (e.g., *Neuquensaurus*), *Bonatitan* (MACN-PV RN 821), and *Lirainosaurus*; this structure is absent in UNPSJB-PV 1051/1. The strongly anteroposteriorly compressed diaphysis (enhanced by diagenetic deformation) is a feature that UNPSJB-PV 1051/1 shares with several titanosaurs, such as the basal titanosaurs *Andesaurus* (Mannion and Calvo, 2011), *Diamantinasaurus*, *Lirainosaurus* (Company, 2009; Díez Díaz et al., 2013), *Aeolosaurus* sp. (García and Salgado, 2013), *Petrobrasaurus*, *Rapetosaurus*, and MPCA-Pv 33/2 (García and Salgado, 2013). Dorsomedial deflection of the femoral head is shared with several titanosaurs (e.g., *Diamantinasaurus*, *Epachthosaurus*, *Lirainosaurus*; also see Wilson and Carrano, 1999), but the deflection is less marked than in saltasaurines. Conversely, in *Aeolosaurus* sp. and *Bonatitan* (MACN-PV RN 821; Salgado et al., 2014) the greater trochanter is almost at the same level as the femoral head. The fourth trochanter is reduced compared to *Elaltitan*, *Lirainosaurus*, and *Uberabatitan*.

Tibia (Fig. 10). The left tibia (UNPSJB-PV 1051/2) is affected by diagenetic deformation (see below); however, several features can be observed. The tibia is elongated with expanded ends, particularly the proximal end (RI: 0.20). The tibia exhibits straight anterior and posterior shaft margins in proximal view. The proximal anteroposterior length is 27 cm and the distal anteroposterior length is 20 cm; the minimum mediolateral shaft width is 15 cm. The shaft is longer anteroposteriorly than it is wide mediolaterally, a feature which might have been enhanced by diagenetic compression. The total length of the left tibia is 74 cm, which is greater than 60% of the femur length. In proximal view, the tibia exhibits a sub-ovoid outline, as in most sauropods, and its proximal end is relatively expanded mediolaterally. The cnemial crest is well developed and projects laterally. The recess to receive the anterior part of the proximal end of the fibula is narrow. This recess occupies about 30% of the total length of the tibia. Salgado and Carvalho (2008) described a tibial protuberance placed posterolaterally to the cnemial crest in *Uberabatitan*; a similar feature was also described in *Laplatasaurus*, *Dreadnoughtus*, and *Opisthocoelicaudia.* This tibial protuberance appears to be present in UNPSJB-PV 1051/2, but it is less developed than in *Uberabatitan.*

The anteroposteriorly expanded tibial proximal end and straight shaft borders are shared with several titanosaurs, such as *Epachthosaurus*, *Mendozasaurus*, *Laplatasaurus*, *Rapetosaurus*, and *Uberabatitan*. Derived titanosaurs (e.g., *Neuquensaurus*) exhibit short and robust tibiae (RI: $\geq$0.30; Gallina and Otero, 2015). In contrast, UNPSJB-Pv 1051/2 is slender. Additionally, saltasaurines have more pronounced cnemial crests than that observed in UNPSJB-PV 1051/2. The narrow recess for the proximal fibula is similar in overall morphology to that described in *Uberabatitan*. The shaft is broader anteroposteriorly than mediolaterally, as in most sauropods. The lateral projection of the cnemial crest is a condition present in Eusauropoda (Wilson and Sereno, 1998; Filippi et al., 2011).

Fibula (Fig. 10). The left fibula (UNPSJB-PV 1051/3) is almost complete, missing only a portion of the distal end. The fibula is slender (RI: 0.17), as in *Bonatitan*, *Epachthosaurus*, *Laplatasaurus*, *Lirainosaurus*, and *Mendozasaurus*. The fibular shaft is slightly sigmoid, as in *Rapetosaurus*, however it is less sigmoid than the fibulae of *Neuquensaurus* and *Saltasaurus.* The proximal epiphysis is gently expanded, as in *Bonatitan* and *Laplatasaurus.* Proximally, the articular surface displays a suboval outline and is slightly concave. The fibular diaphysis expands in its distal third, to become narrow distally. Although it is difficult to determine due to diagenetic deformation, the lateral tuberosity appears to be relatively well-marked, as in *Bonatitan*, *Epachthosaurus*, and *Rapetosaurus.* This condition is unlike the feint, ridged lateral tuberosities of *Laplatasaurus* ("a double lateral tuberosity") and *Uberabatitan.* At the proximal end of the fibula, there is a relatively thin, mediolaterally projected, knob-like structure which is similar in appearance to that seen in *Uberabatitan* (Salgado and Carvalho, 2008, fig. 19i-j). In medial view, UNPSJB-PV 1051/3 bears a relatively well-marked concavity at its proximal end, probably enhanced by taphonomic crushing. This concavity is ventrally limited by a ridge. Poropat et al. (2015b) described a triangular scar in the same position in *Diamantinasaurus.* The fibula also exhibits an anterior proximal depression, similar to that described in *Laplatasaurus*, *Mendozasaurus*, and *Uberabatitan* (Gallina and Otero, 2015).

Astragalus (Fig. 11). The left astragalus (UNPSJB-PV 1051/13) was isolated but associated with the articulated tibia and fibula. UNPSJB-PV 1051/13 also includes a fragment which could possibly represent at least a portion of the missing distal end of the fibula; however, plastic deformation makes this difficult to confirm. The left astragalus has a sub-pyramidal shape, as in most other titanosaurs (e.g., *Neuquensaurus*, *Opisthocoelicaudia*, *Uberabatitan*). The surface of the astragalus is rugose, as in all titanosaurs. The ascending process is low and rounded, as in *Bonatitan* and *Uberabatitan.* Although the distal ends of the fibula and tibia are either incompletely preserved or taphonomically affected, the astragalus appears to occupy about 70% of the distal expansion, which is

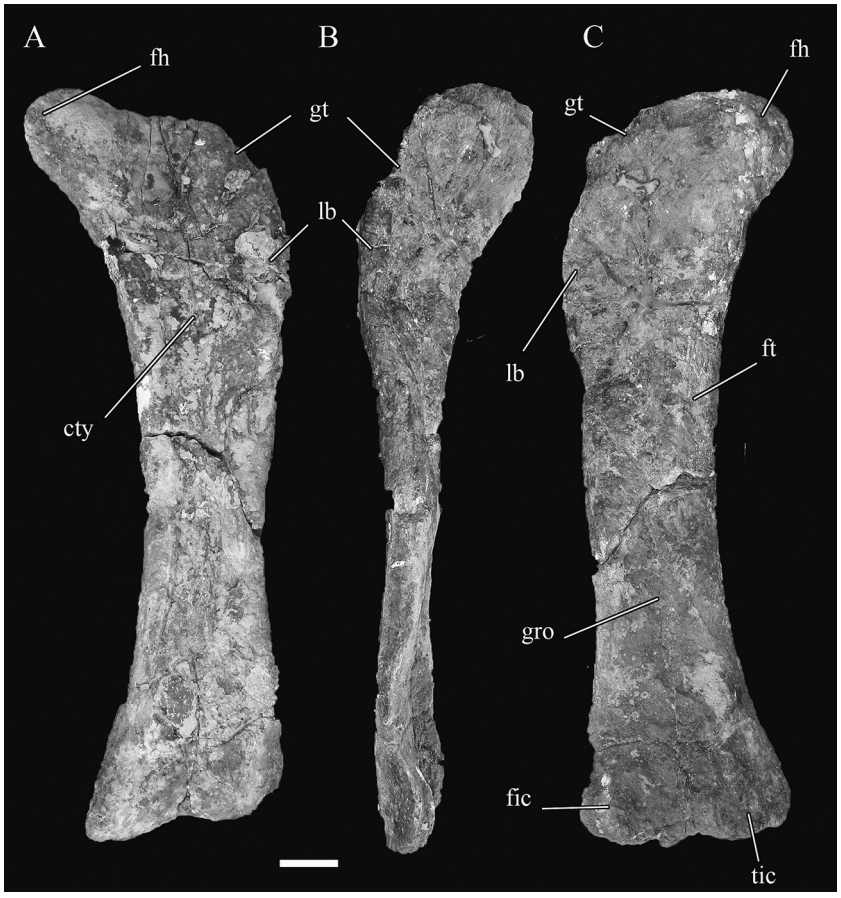

Fig. 9. Left femur (UNPSJB-PV 1051/1) in anterior (A), medial (B), and posterior (C) views. Abbreviations: cty, concavity; fh, femoral head; fic, fibular condyle; ft, fourth trochanter; gro, groove; gt, greater trochanter; lb, lateral bulge; tic, tibial condyle. Scale bar: 10 cm.

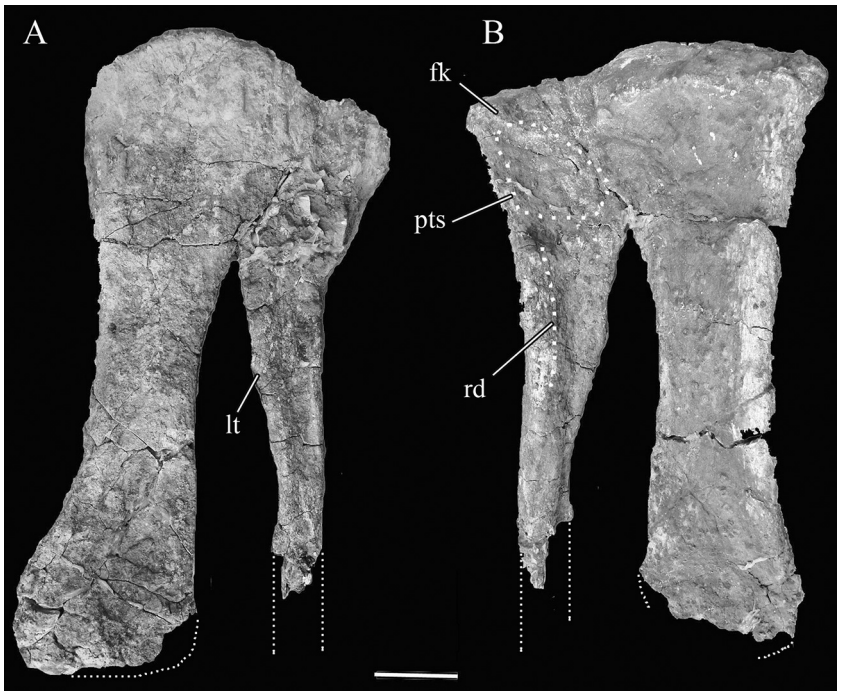

Fig. 10. Left tibia (UNPSJB-Pv 1051/2) and fibula (UNPSJB-Pv 1051/3) in medial (tibia) and posterior (fibula) (A), and lateral (tibia) and medial (fibula) (B) views. Abbreviations: fk, fibular knob; lt, lateral tuberosity; pts, proximal triangular scar; rd, ridge. Scale bar: 10 cm. Note: the articulated tibia and fibula have been twisted during diagenesis (see main text).

greater than in *Neuquensaurus* and *Opisthocoelicaudia* (Salgado and Carvalho, 2008). The tibial articular surface is broader than the fibular articular surface. Both of these articular surfaces are concave, but the former is more concave than the latter. Between the tibial and fibular articulations, there is a relatively planar surface, alike that described in *Uberabatitan* (Salgado and Carvalho, 2008, pg. 898, fig. 20).

Metatarsals and pedal phalanges (Fig. 12). A putative shaft fragment, probably pertaining to a metatarsal III (UNPSJB-PV 1051/4), was recovered isolated but associated with the left hind limb. The preserved fragment is relatively gracile, only 8.5 cm wide at the middle of the shaft. A proximal end of a metatarsal was also recovered (UNPSJB-PV 1051/5). This proximal end exhibits a mediolateral length of 10.5 cm. It is possible that this fragment could represent the proximal end of UNPSJB-PV 1051/4. A pedal phalanx was also recovered (UNPSJB-PV 1051/6). This pedal element is robust and displays a suboval proximal articulation.

7. Discussion

7.1. Taphonomic implications

It is expected that rapid burial and minimal transport may favor the preservation of articulated skeletons. Therefore, when the animal dies and decays near an active channel, it increases the possibility of bone disarticulation, abrasion, and fragmentation. Based on the type of fabric and the extent of abrasion of the bones, they were transported as part of the bed-load for at least a short distance and time. Waning of fluid flow capacity eventually lead to deposition of the bones at the downstream end of a longitudinal sand bar with the bones acquiring plunges reflecting the inclination of the leeward slope of the bar. Turbulent-flows increase the frequency of rolling abrasion, impact-induced breakage, and spatial dispersion of bones upon deposition. As each of these features are minimal for UNPSJB-PV 1051, it appears likely that they were deposited in a single event (and were not reworked) by a unidirectional hydraulic flow. In this context, we suggest that disarticulation of the skeleton occurred during transport, with the exception of the heaviest and densest bones of the hind limb (femur, tibia, and fibula). Depending on their characteristics, some bones are more easily transported by hydraulic flow than others (Voorhies, 1969; Behrensmeyer, 1975). Voorhies (1969) proposed three transportation groups based on bone size, shape, and density; these groups are frequently utilized to detect potential winnowing and sorting in fossil assemblages (e.g., Shipman et al., 1981). Following Voorhies' (1969) classification, the bones of UNPSJB-PV 1051 are mostly from Group 2 (e.g., femur, tibia, fibula, radius, metacarpals). Aslan and Behrensmeyer (1996) suggested that fluvial winnowing initially removes vertebrae, since they are more easily transported by weak flows due to their isometric shape, high surface area, and low densities. Therefore, their absence in our quarry may be attributable to fluvial winnowing.

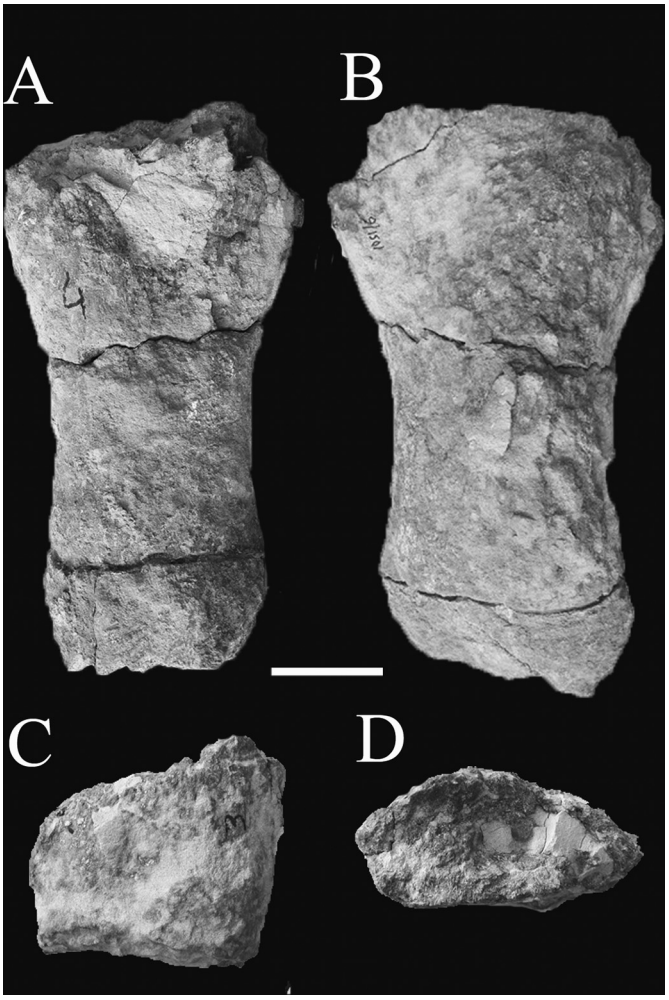

Fig. 12. Probable fragment of a metatarsal III (UNPSJB-PV 1051/4) in medial (A) and lateral (B) views. Proximal end of a metatarsal (UNPSJB-PV 1051/5) (C) and a probable pedal phalanx (D). Scale bar: 5 cm.

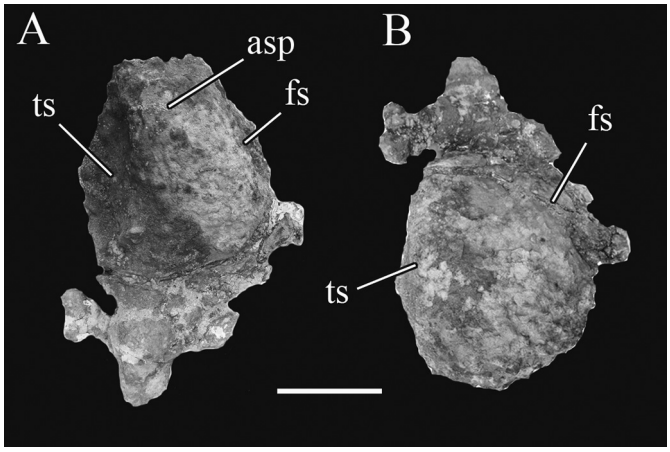

Fig. 11. Left astragalus (UNPSJB-PV 1051/13) in dorsal (A) and anterior (B) views. Abbreviations: asp, ascending process; fs, fibular surface; ts, tibial surface. Scale bar: 10 cm.

The plastic deformation of the femur and tibia was caused by a vertical load of lithostatic origin, prior to mineral replacement. Fresh bone is still ductile and exhibits a degree of plasticity, specifically when an external force acts upon it (Polonio and López-Martínez, 2000). The transverse fractures in the bones may have formed after they were diagenetically altered (Myers et al., 1980). Alternatively, the fractures in the bones might have been modified by modern soil freezing during recent winters (e.g., Gangloff and Fiorillo, 2010).

To summarize, concentration of the bones at this site is due to fluvial action. The bones were subjected to minimal subaerial exposure and were relatively rapidly buried in the channel. The partial disarticulation, dispersion, and orientation of the bones are products of deposition during unidirectional fluvial transport. Finally, waning fluid flow resulted in the final deposition and burial

of the bones at the downstream end of a longitudinal sand bar, with their plunges mirroring the inclination of the sedimentary facies (Fig. 3A–B). After burial and prior to permineralization, the bones were plastically deformed by lithostatic compression.

7.2. Ontogenetic stage of UNPSJB-PV 1051

Ontogenetic stage of fossil vertebrates can be assessed on the basis of both macroscopic and microscopic features. Gross anatomical features usually employed for ontogenetic stage determination in sauropods include the degree of fusion of vertebral neurocentral sutures and between the scapula and coracoid, and the degree to which the coracoid foramen has closed (e.g., Ikejiri et al., 2005). Specifically, fusion between the scapula and coracoid and closure of the coracoid foramen are thought to correspond with somatic maturity in sauropod dinosaurs. The open condition of the coracoid foramen and apparent lack of fusion between scapula and coracoid in UNPSJB-Pv 1051 suggest somatic immaturity of this individual.

Regarding bone histology, the poor preservation of the bone samples makes it difficult to assess the ontogenetic stage of UNPSJB-Pv 1051 using this technique alone. The prevalence of dense Haversian bone tissue in the cortex has previously been employed to infer a very advanced (senescent) ontogenetic stage in neosauropods (e.g., Klein and Sander, 2008). Nevertheless, several histological studies focusing on titanosaurs (e.g., Klein et al., 2009, 2012; Stein et al., 2010; Company, 2011) have showed that these taxa displayed a high degree of secondary remodeling during ontogeny, which resulted in the formation of dense Haversian bone in non-fully grown individuals. To date, the presence of an Outer Circumferential Layer (OCL, or External Fundamental System, EFS) is the only histological feature that facilitates the unambiguous inference of somatic maturity in fossil vertebrates (Chinsamy Turan, 2005). The absence of well-preserved subperiosteal bone in our sample precludes us from determining whether or not the OCL had formed in the cortex and, therefore, if somatic maturity was achieved in this individual. As a result, based on morphological features (absence of fusion between scapula and coracoid, open coracoid foramen), general body size, and microscopic evidence (predominance of dense Haversian bone tissue), we infer at least subadult ontogenetic stage for UNPSJB-PV 1051.

7.3. Systematic assessment

The fossils described herein display derived characters that support their inclusion in Titanosauriformes (Salgado et al., 1997). For example, the femoral head of the left femur (UNPSJB-PV 1051/1) is deflected dorsomedially with respect to the greater trochanter, and the femoral shaft exhibits a relatively well-developed bulge on its lateral surface. The left femur also exhibits a reduced fourth trochanter (a subtle bulge, site of insertion of the *M. caudofemoralis* [Ibiricu et al., 2013]), a feature that has accordingly been proposed as a synapomorphy of Somphospondyli (D'Emic, 2012; also see Díez Díaz et al., [2013] and Mannion et al., [2013]). Within Titanosauria, UNPSJB-PV 1051 shares several morphological features with a wide range of titanosaurs. Nevertheless, UNPSJB-PV 1051 does not present hind limb features seen in derived titanosaurs such as saltasaurines. For example, an eccentric femoral midshaft and the well-developed linea intermuscularis cranialis for insertion of the *M. femorotibialis* (Otero and Vizcaino, 2008; Otero, 2010) are absent in the left femur (UNPSJB-PV 1051/1). Additionally, the tibia (UNPSJB-PV 1051/2) does not display distinct robustness and substantial development of the cnemial crest, features which characterize saltasaurines (e.g., *Neuquensaurus* and *Saltasaurus*).

The fibular lateral tuberosity is a character present in Eusauropoda. This lateral protuberance, probably for insertion of the *M. iliofibularis* (Otero, 2010), is present in UNPSJB-PV 1051/3 as an elliptical bump. Conversely, in saltasaurines the fibular tuberosity is strongly developed and marked. The left hind limb of UNPSJB-PV 1051, in overall morphology, resembles that described in many lithostrotian titanosaurs. Indeed, UNPSJB-Pv 1051 is closely comparable to *Lirainosaurus*, *Bonatitan*, *Laplatasaurus,* and *Uberabatitan*. For example, the left fibula shows a well-marked proximal knob, as in *Uberabatitan*. This ridge represents the positive structure of the tibial protuberance (Salgado and Carvalho, 2008), though this is slightly taphonomically affected in UNPSJB-PV 1051/2. This structure is also present, albeit less developed, in *Laplatasaurus* (Otero and Gallina, 2015).

Metacarpal I (UNPSJB-Pv 1051/7, 8) has a beveled distal end, as in the Australian lithostrotian *Diamantinasaurus*. In contrast, in basal titanosauriforms the distal end is perpendicular in relation to the shaft (Poropat et al., 2015b). Titanosaurian metacarpals exhibit distinct relative lengths; Mc I being the longest metacarpal represents a derived feature within the group. Although the metacarpals described herein are slightly taphonomically altered, Mc I (UNPSJB-PV 1051/7, 8) appears to be longer than both UNPSJB-PV 1051/9 and 10 (Mc II and III, respectively). This condition is shared with the derived titanosaurs *Alamosaurus* and *Opisthocoelicaudia*. A bowed Mc I, as seen in *Andesaurus* and *Argyrosaurus,* has been considered a possible synapomorphy of Titanosauria (Apesteguía, 2005). Mc I in the individual described herein (UNPSJB-PV 1051/7, 8) is straight, as in *Epachthosaurus* and saltasaurines, which could represent a local reversal (cf. Apesteguía, 2005).

In general, the specimens described herein bear many morphological similarities with *Uberabatitan*, *Laplatasaurus*, *Bonitasaura*, *Mendozasaurus*, *Futalognkosaurus*, *Bonatitan*, and *Lirainosaurus*. In a recent cladistic analysis, Otero and Gallina (2015) recovered *Laplatasaurus* together with *Uberabatitan* as a sister clade of *Bonitasaura* + (*Mendozasaurus* + *Futalognkosaurus*). Also, Salgado et al. (2014) recovered *Bonatitan* (originally considered a saltasaurine; Martinelli and Forasiepi, 2004) as a basal member of a broad group of titanosaurs. In these analyses, *Lirainosaurus*, probably one of the most abundant sauropods in the Iberian Peninsula (Company et al., 2009; Díez Díaz, et al., 2013), was considered a derived lithostrotian.

The contemporaneous taxon *Aeolosaurus colhuehuapensis* (Casal et al., 2007) does not preserve appendicular bones; therefore comparison between it and the specimens described herein is not possible. However, a femur assigned to *Aeolosaurus* sp. from the Salitral Moreno locality (García and Salgado, 2013, fig. 4a), shows some general similarities with UNPSJB-PV 1051. However, robustness indices and the angle formed between the greater trochanter and the femoral head differ between *Aeolosaurus* sp. and UNPSJB-PV 1051 (García and Salgado, 2013, fig. 5). Also, the degree of transverse expansion of the distal end of the radius (UNPSJB-PV 1051/12) in relation to the shaft width is clearly greater than that seen in *Aeolosaurus* sp. (Salgado and Coria, 1993; Garcia and Salgado, 2013). These features suggest that UNPSJB-PV 1051 represents different taxon than *Aeolosaurus* sp.

Another contemporaneous taxon was *Argyrosaurus superbus* (Mannion and Otero, 2012). The only overlapping elements of the holotype of *Argyrosaurus superbus* and UNPSJB-PV 1051 are the radius and metacarpals (which are also broken in *A. superbus*; Mannion and Otero, 2012). The degree of transverse distal expansion of the radius is greater in UNPSJB-PV 1051/12 than in *Argyrosaurus*. In addition, the distal articular surface outline differs between UNPSJB-PV 1051 and *Argyrosaurus*. Further, metacarpal I of the new individual (UNPSJB-PV 1051/7, 8) exhibits a straight shaft and beveled distal condyles relative to the shaft (i.e., the

lateral condyle is slightly taller than the medial one), whereas in *Argyrosaurus* the distal end is perpendicular. Thus, these features suggest that UNPSJB-PV 1051 also represents a taxon distinct from *Argyrosaurus*.

Finally, Poropat et al. (2015b) recently provided a redescription of *Diamantinasaurus*. They included this Australian sauropod within Titanosauria, specifically within Lithostrotia (and probably related to derived forms within that group). *Diamantinasaurus* and UNPSJB-Pv 1051 share two local autapomorphic characters described in the former. These features are beveled distal ends of Mc I and a well-marked fibular scar. However, as mentioned above, the fossils studied herein have been taphonomically altered, especially the fibula, meaning that these characters might have been exaggerated in this specimen. Consequently, the new fossils from the Lago Colhué Huapi Formation may be confidently referred to Titanosauria, and within that clade, to Lithostrotia, probably occupying a derived position close to some South American forms such as *Laplatasaurus* and *Uberabatitan*.

7.4. Titanosaurian diversity in the Late Cretaceous of central Patagonia

Aside from the material described here, additional titanosaur fossils recorded from the Lago Colhué Huapi Formation include the derived lithostrotians *Aeolosaurus colhuehuapensis*, *Argyrosaurus superbus*, *Elaltitan lilloi*, and an as yet undescribed specimen (MDT-PV 4; Casal et al., 2015a). Although diversity patterns in the fossil record are strongly influenced by sampling biases (e.g., Mannion et al., 2011), those seen in the Cretaceous sedimentary units of central Patagonian are by far dominated by titanosaurian sauropods (Ibiricu et al., 2012a,b). The titanosaurian record taxonomically appears to be more diverse in the Lago Colhué Huapi Formation than in the Bajo Barreal Formation, which includes *Campylodon ameghinoi*, *Drusilasaura deseadensis*, *Epachthosaurus sciuttoi*, and *Sarmientosaurus musacchioi* (see Casal et al., [2016] for more details). A similar pattern regarding titanosaurian diversity is encountered in other South American Upper Cretaceous units (e.g.,

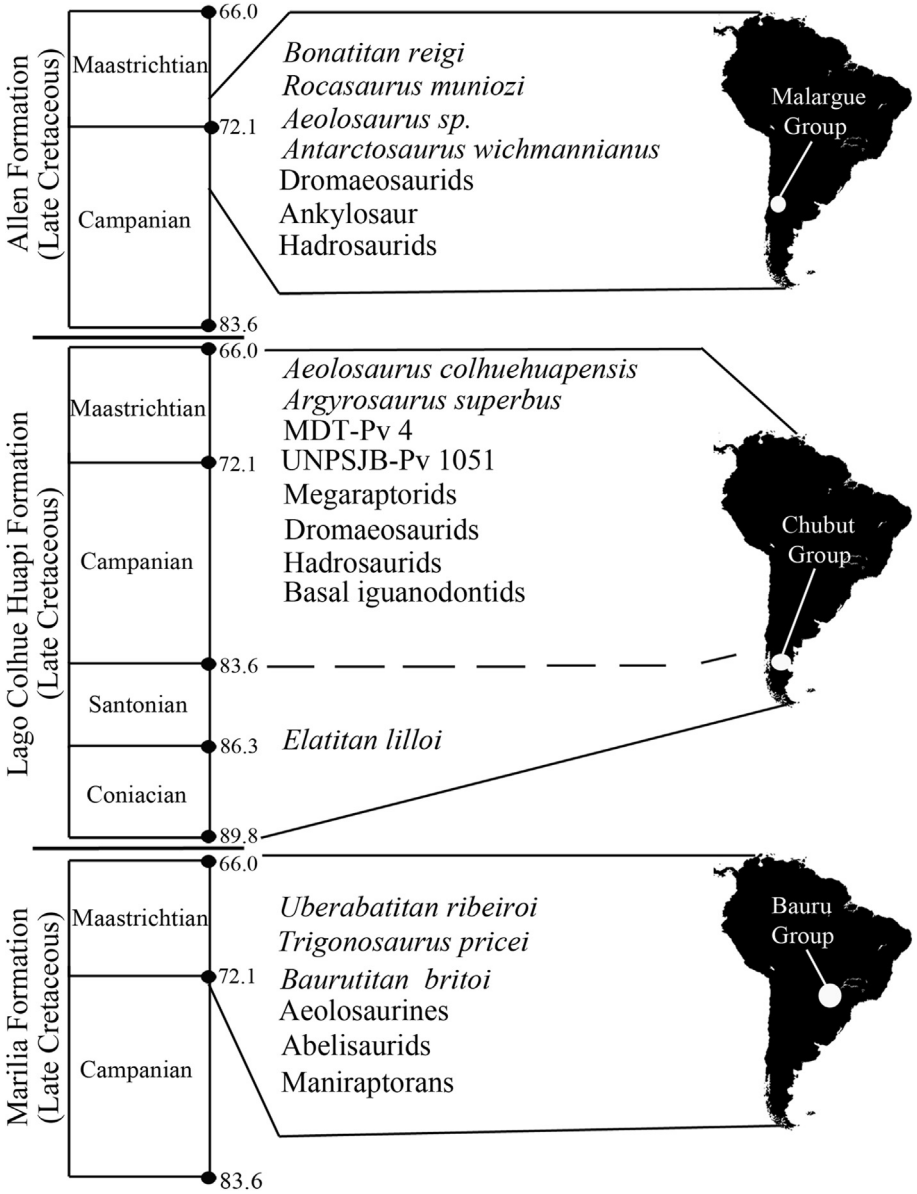

Fig. 13. Occurrence and chronostratigraphy of dinosaur discoveries from the latest Cretaceous South American Allen, Lago Colhué Huapi, and Marília formations. White dots indicate the approximate outcrop areas of these three Cretaceous formations.

Candeleros and Allen formations, Neuquén and Malargüe Groups). Overall, the new titanosaurian individual described here adds to the incipient fossil record of the Lago Colhué Huapi Formation, increasing known titanosaur diversity of the latest Cretaceous of central Patagonia, Argentina.

7.5. Faunal correlation among South American latest Cretaceous formations

Upper Cretaceous (Cenomanian–Maastricthian) continental deposits are well represented in Patagonia, Argentina. Three major stratigraphic units, both in lateral extent and fossil richness, are exposed in north and central Patagonia. These stratigraphic units are the Neuquén, Malargüe, and Chubut groups. Canale et al. (2011) mentioned and statistically supported that dinosaurian faunas of these units show a remarkably strong association. In addition, cluster analysis performed by Canale et al. (2011) supports strong grouping between the Bajo Barreal (Cenomanian–Turonian, Chubut Group) and Candeleros (Cenomanian–Turonian, Neuquén Group) formations and between the Allen (Campanian–Maastrichtian, Malargüe Group) and Lago Colhué Huapi (Coniacian–Maastrichtian, Chubut Group) formations (Fig. 13). García and Salgado (2013) also highlighted similarities between the faunas of the Allen and the Marilia formations (Bauru Group, Maastrichtian, Brazil).

The Allen, Marilia, and Lago Colhué Huapi formations are chronological equivalents. At the moment, the Marilia Formation includes titanosaurs (i.e., aeolosaurines, *Baurutitan britoi* [Kellner et al., 2005], *Trigonosaurus pricei* [Campos et al., 2005], *Uberabatitan*) and abelisaurid theropods (García and Salgado, 2013; Faria et al., 2015), but not saltasaurines or hadrosaurids. The Allen Formation is one of the most fossiliferous Cretaceous units in Patagonia (García and Salgado, 2013), including (among dinosaurs) abelisaurid and dromaeosaurid theropods, hadrosaurid and nodosaurid ornithischians, and a relatively high diversity of titanosaurs (e.g., aeolosaurines, *Antarctosaurus*, *Bonatitan, Panamericansaurus schroederi* [Calvo and Porfiri, 2010], and *Rocasaurus*). The dinosaur fauna of the recently-recognized Lago Colhué Huapi Formation now includes hadrosaurid and non-hadrosaurid ornithopods (Casal et al., 2007; Ibiricu et al., 2010; Casal et al., 2015a,b; Casal et al., 2016), theropods (dromaeosaurids, megaraptorians), aeolosaurine titanosaurians (Casal et al., 2007), *Argyrosaurus superbus* (Mannion and Otero, 2012; Casal et al., 2015a), and an undescribed lithostrotian titanosaur (MDT-PV 4; Casal et al., 2015a). We have now added to this titanosaur fauna a new specimen, UNPSJB-PV 1051, which is not assignable to *Aeolosaurus* or *Argyrosaurus* and most likely does not pertain to the same genus as MDT-PV 4.

In conclusion, based on the fossil record, uppermost Cretaceous units in Patagonia (i.e., the Lago Colhué Huapi, Allen, and Marília formations) show strong faunal similarities, particularly concerning their nonavian dinosaur faunas (Fig. 13). This pattern strongly suggests that the dinosaurian taxa in the region, especially titanosaurian sauropods, inhabited wide geographic ranges during the latest Cretaceous.

8. Conclusions

A new titanosaurian sauropod (UNPSJB-PV 1051) is described from the Upper Cretaceous of Patagonia, Argentina. The material came from the Lago Colhué Huapi Formation (Coniacian–Maastrichtian), a recently-described formation in central Patagonia. The specimen consists of a partially articulated left hind limb and disarticulated but associated appendicular skeletal elements. Burial of the remains can be attributed to fluvial processes. The bones were subjected to little if any subaerial exposure and were relatively rapidly buried in a fluvial channel, wherein waning fluid flow resulted in deposition of the bones at the downstream end of a longitudinal sand bar. UNPSJB-PV 1051 may be confidently referred to Titanosauria and, within that clade, to Lithostrotia, probably occupying a derived position within the latter. Based on morphological and microscopic evidence, we infer at least subadult ontogenetic stage for UNPSJB-PV 1051. This new material adds to the incipient fossil record of the Lago Colhué Huapi Formation, thereby increasing known titanosaur diversity in Patagonia in the latest Cretaceous. Additionally, the new titanosaur enhances evidence in support of strong faunal similarities among chronologically equivalent Cretaceous formations of South America, such as the Allen and Marilia formations. Finally, UNPSJB-PV 1051 adds to the Late Cretaceous record of Titanosauria and augments our knowledge of central Patagonian terrestrial vertebrate assemblages during this interval.

Acknowledgements

We thank E. Ivany of the UNPSJB for his continued assistance in the field during several years. We are grateful to Hector and Chiche Martinez (owners of the Estancia) for the support during the extraction and Luis Insua, owner of the ranch where UNPSJB-Pv 1051 was discovered. For assistance with the fossil recovery (field work), we thank J.M. Iturra, J.I. Vargas and L. Penayo (UNPSJB). We thank to Jose Allard and Nicolas Foix for their comments on the geology of the area and the Departamento de Geología (UNPSJB). We greatly appreciate the English revision of the manuscript to P. Ullmann. The manuscript benefited from constructive comments from the editor E. Koutsoukos. The manuscript was improved by reviews of P. Mannion and S. Poropat. This research was supported by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2012-2884 to LMI; PICT 2015-1021 to IAC).

References

Alcalá, L., 1994. Macromamiferos Neogenos de la fosa de Alfambra-Teruel. Instituto de Estudios Turolenses y Museo Nacional Ciencias Naturales, Madrid, 554 pp.

Allard, J.O., Casal, G.A., 2013. Análogos de afloramientos del Cretácico Superior en las nacientes del río Chico: sedimentología, paleoambiente, características geométricas y heterogeneidades intra-reservorio. In: Jornadas Geológicas de la Cuenca del Golfo San Jorge, 1, pp. 17–18, 2013. Actas, Comodoro Rivadavia.

Apesteguía, S., 2005. Evolution of the titanosaur metacarpus. In: Tidwell, V., Carpenter, K. (Eds.), Thunder Lizards. The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, pp. 321–345.

Aslan, A., Behrensmeyer, A.K., 1996. Taphonomy and time resolution of bone assemblage in a contemporary fluvial system: the east Fork River, Wyoming. Palaios 11, 411–421.

Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages of Lake Rudolf, Kenya. Bulletin of the Museum of Comparative Zoology 146, 473–578.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Behrensmeyer, A.K., 1991. Terrestrial vertebrate accumulations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record. Plenum Press, New York, pp. 291–335.

Bonaparte, J.F., 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. Actas IV Congreso Argentino de Paleontología y Bioestratigrafía (Mendoza), Resúmenes 2, 63–95.

Bonaparte, J.F., Coria, R.A., 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Rio Limay (Albiano-Cenomaniano) de la Provincia de Neuquén, Argentina. Ameghiniana 30, 271–282.

Bonaparte, J.F., Powell, J.E., 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). Mémoires de la Société Géologique de France (Nouvelle Série) 139, 19–28.

Borsuk-Białynicka, M., 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n. sp. n. from the Upper Cretaceous of Mongolia. Paleontologia Polonica 37, 5–64.

Brett Surman, M.K., 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. Nature 277, 560–562.

Bridge, J.S., 2003. Rivers and Floodplains: Forms, Processes and Sedimentary Record. Blackwell, Oxford, 491 p.
Calvo, J.O., Bonaparte, J.F., 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. Ameghiniana 28, 303–310.
Calvo, J.O., González Riga, B., 2003. *Rinconsaurus caudamirus* gen. et. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. Revista Geológica de Chile 30, 333–353.
Calvo, J.O., Porfiri, J.D., 2010. *Panamericansaurus schroederi* gen. nov. sp. nov. Un nuevo Sauropoda (Titanosauridae-Aeolosaurini) de la Provincia del Neuquen, Cretacico Superior de la Patagonia, Argentina. Brazilian Geographical Journal: Geosciences and Humanities Research Médium 1, 100–115.
Campos, D.de Almeida, Kellner, A.W.A., Bertini, R.I., Santucci, R.M., 2005. On the titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. Arquivos do Museu Nacional, Rio de Janeiro 63, 565–593.
Canale, J.I., Ibiricu, L.M., Haluza, A., Casal, G.A., 2011. The continental Cenomanian of Patagonia: a comparison between the fossil vertebrate faunas of the Río Limay Subgroup (Neuquén Group) and the Bajo Barreal Formation (Chubut Group) Fossil vertebrate faunas. Ameghiniana 48, 98R.
Casal, G.A., Martínez, R.D., Luna, M., Sciutto, J.C., Lamanna, M.C., 2007. *Aeolosaurus colhuehuapensis* sp. nov. (Sauropoda, Titanosauria) de la Formación Bajo Barreal, Cretácico Superior de Argentina. Revista Brasileira de Paleontologia 10, 53–62.
Casal, G.A., Candeiro, C.R., Martínez, R.D., Ivany, E., Ibiricu, L.M., 2009. Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. Geobios 39, 553–560.
Casal, G.A., Martínez, R.D., Luna, M., Ivany, E., Ibiricu, L.M., 2010. Un nuevo titanosaurio articulado de la Formación Bajo Barreal, Cretácico Superior tardío del Sur de Chubut. Aspectos ambientales y tafonómicos. Ameghiniana 47, 6R.
Casal, G.A., Allard, J.O., Foix, N., 2015a. Análisis estratigráfico y paleontológico de afloramientos del Cretácico Superior en la cuenca del Golfo San Jorge: propuesta de nueva unidad litoestratigráfica para el Grupo Chubut. Revista de la Asociación Geológica Argentina 72, 81–99.
Casal, G.A., Ibiricu, L.M., Martínez, R.D., Luna, M., González Svoboda, E., Ivany, E., 2015b. El registro fósil de la Formación Lago Colhué Huapi (Coniaciano-Maastrichtiano), Grupo Chubut, Argentina. Ameghiniana 52, 210–211.
Casal, G.A., Martínez, R.D., Luna, M., Ibiricu, L.M., 2016. Ordenamiento y caracterización faunística del Cretácico superior del Grupo Chubut, Cuenca del Golfo San Jorge, Argentina. Revista Brasileira de Paleontologia 19, 53–70.
Chinsamy Turan, A., 2005. The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-scale Techniques. Johns Hopkins University Press, Baltimore, 216 pp.
Chinsamy, A., Raath, M.A., 1992. Preparation of fossil bone for histological examination. Palaeontologia Africana 29, 39–44.
Company, J., 2011. Bone histology of the titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from the Latest Cretaceous of Spain. Naturwissenschaften 98, 67–78.
Company, J., Pereda Suberbiola, X., Ruiz-Omeñaca, J.I., 2009. Nuevos restos fósiles del dinosaurio *Lirainosaurus* (Sauropoda, Titanosauria) en el Cretácico Superior (Campaniano-Maastrichtiano) de la Península Ibérica. Ameghiniana 46, 391–405.
Coria, R.A., Cambiaso, A.V., 2007. Ornithischia. In: Gasparini, Z., Salgado, L., Coria, R.A. (Eds.), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington, pp. 167–187.
Curry Rogers, K., 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 29, 1046–1086.
D'Emic, M.D., 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society 166, 624–671.
Díaz Díez, V., Pereda Suberbiola, X., Sanz, J.L., 2013. Appendicular skeleton and dermal armour of the Late Cretaceous titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from Spain. Palaeontologia Electronica 16, 1–18. palaeo-electronica.org/cont/2013/502-titanosaur-skeleton.
Faria, C.C. de Jesus, González Riga, B., Candeiro, C.R., Marinho, T. da Silva., Ortiz, L., Simbras, F., Castanho, R.B., Muniz, F.P., Pereira, P.V.L.G. da Costa, 2015. Cretaceous sauropod diversity and taxonomic succession in South America. Journal of South American Earth Sciences 61, 154–163.
Fernández-López, S.R., 2000. Temas de tafonomía. Departamento de Paleontologia, Universidad Complutense de Madrid, España, 167 pp.
Figari, E.G., Strelkov, E., Cid de La Paz, M.S., Celaya, J., Laffitte, G., Villar, H., 2002. Cuenca del Golfo San Jorge: síntesis estructural, estratigráfica y geoquímica. In: XV Congreso Geológico Argentino, Relatorio, pp. 571–601.
Filippi, L.S., Canudo, J.I., Salgado, L., Garrido, A., García, R., Cerda, I., Otero, A., 2011. A new sauropod titanosaur from the Plottier Formation (Upper Cretaceous) of Patagonia (Argentina). Geologica Acta 9, 1–12.
Francillon-Vieillot, H., Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L., de Ricqles, A., 1990. Microstructures and mineralization of vertebrate skeletal tissues. In: Carter, J. (Ed.), Skeletal Biomineralization: Patterns, Process and Evolutionary Trends. Van Nostrand Reinhold, New York, pp. 471–530.
Gallina, P.A., Otero, A., 2015. Reassessment of *Laplatasaurus araukanicus* (Sauropoda: Titanosauria) from the Upper Cretaceous of Patagonia, Argentina. Ameghiniana 52, 487–501.
Gangloff, R.A., Fiorillo, A.R., 2010. Taphonomy and paleoecology of a bonebed from the Prince Creek Formation, north slope, Alaska. Palaios 25, 299–317.
García, R., Salgado, L., 2013. The titanosaur sauropods from the late Campanian-early Maastrichtian Allen Formation of Salitral Moreno, Río Negro, Argentina. Acta Paleontologica Polonica 58, 269–284.
González Riga, B.J., 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. Ameghiniana 40, 155–172.
González Riga, B.J., Ortiz, L.D., 2014. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous (Cerro Lisandro Formation) of Mendoza Province, Argentina. Ameghiniana 51, 3–25.
Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New mid-Cretaceous (latest Albian) dinosaur from Winton, Queensland, Australia. PLoS One 4, e6190. http://dx.doi.org/10.1371/jornal.pone.0006190.
Huene, F. von, 1929. Los saurisquios y ornitisquios del Cretácico Argentino. Anales del Museo de La Plata 3, 1–196.
Ibiricu, L.M., Martínez, R.D., Lamanna, M.C., Casal, G.A., Luna, M., Harris, J., Lacovara, K.J., 2010. A medium sized Ornithopod (Dinosauria: Ornithischia) from the Upper Cretaceous Bajo Barreal Formation of Lago Colhué Huapi, Southern Chubut province, Argentina. Annals of the Carnegie Museum 79, 39–50.
Ibiricu, L.M., Casal, G.A., Lamanna, M.C., Martínez, R.D., Harris, J., Lacovara, J.K., 2012a. The southernmost records of Rebbachisauridae (Sauropoda: Diplodocoidea), from the early Late Cretaceous of central Patagonia. Cretaceous Research 34, 220–232. http://dx.doi.org/10.1016/j.cretres.2011.11.003.
Ibiricu, L.M., Martínez, R.D., Casal, G.A., 2012b. The first record of Pterosauria in Bajo Barreal Formation (Upper Cretaceous), central Patagonia, Argentina. Ameghiniana 49, 657–661.
Ibiricu, L.M., Casal, G.A., Martínez, R.D., Lamanna, M.C., Salgado, L., 2013a. *Katepensaurus goicoecheai* gen. et sp. nov., a Late Cretaceous rebbachisaurid (Sauropoda, Diplodocoidea) from central Patagonia, Argentina. Journal of Vertebrate Paleontology 33, 1351–1366.
Ibiricu, L.M., Lamanna, M.C., Lacovara, K.J., 2013b. The influence of caudofemoral musculature on the titanosaurian (Saurischia: Sauropoda) tail skeleton: morphological and phylogenetic implications. Historical Biology: International Journal of Paleobiology. http://dx.doi.org/10.1080/08912963.2013.787069.
Ibiricu, L.M., Casal, G.A., Martínez, R.D., Lamanna, M.C., Luna, M., Salgado, L., 2015. New material of *Katepensaurus goicoecheai* (Sauropoda: Diplodocoidea) and its significance for the morphology and evolution of Rebbachisauridae. Ameghiniana 52, 430–446.
Ikejiri, T., Tidwell, V., Trexler, D.L., 2005. New adult specimens of *Camarasaurus lentus* highlight ontogenetic variation within the species. In: Tidwell, V., Carpenter, K. (Eds.), Thunder-lizards: the Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, pp. 154–179.
Kellner, A.W.A., Campos, D. de Almeida, Trotta, M.N.F., 2005. Description of a titanosaurid caudal series from the Bauru Group, Late Cretaceous of Brazil. Arquivos do Museu Nacional, Rio de Janeiro 63, 529–564.
Klein, N., Sander, P.M., 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. Paleobiology 34, 247–263.
Klein, N., Sander, P.M., Suteethorn, V., 2009. Bone histology and its implications for the life history and growth of the Early Cretaceous titanosaur *Phuwiangosaurus sirindhornae*. Geological Society, London, Special Publications 315, 217–228.
Klein, N., Sander, P.M., Stein, K., Le Loeuff, J., Carballido, J.L., Buffetaut, E., 2012. Modified laminar bone in *Ampelosaurus atacis* and other titanosaurs (Sauropoda): implications for life history and physiology. PLoS One e36907. http://dx.doi.org/10.1371/journal.pone.0036907.
Lacovara, K.J., Lamanna, M.C., Ibiricu, L.M., Poole, J.C., Schroeter, E., Ullmann, P.V., Voegele, K.K., Boles, Z.M., Carter, A.M., Fowler, E.K., Egerton, V.M., Moyer, A.E., Coughenour, C.L., Schein, J.P., Harris, J.D., Martínez, R.D., Novas, F.E., 2014. A gigantic, exceptionally complete titanosaurian sauropod dinosaur from southern Patagonia, Argentina. Scientific Reports 4, 6196. http://dx.doi.org/10.1038/srep06196.
Lamanna, M.C., Luna, M., Casal, G.A., Martínez, R.D., Ibiricu, L.M., Sciutto, J.C., 2003. New crocodyliform and dinosaur discoveries from the Upper Cretaceous (Campanian-Maastrichtian?) Upper Member of the Bajo Barreal Formation, Southern Chubut Province, Argentina. Journal of Vertebrate Paleontology 23, 70A.
Lehman, T.M., Coulson, A.B., 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Upper Cretaceous of Big Bend National Park, Texas. Journal of Vertebrate Paleontology 76, 156–172.
Luna, M., Casal, G.A., Martínez, R.D., Lamanna, M.C., Ibiricu, L.M., Ivany, E., 2003. La presencia de un Ornitopoda en el Miembro Superior de La Formación Bajo Barreal, Cretácico Superior (Campaniano-Maastrichtiano?) del Sur de Chubut. Ameghiniana 40, 61R.
Lynds, R., Hajek, E., 2006. Conceptual model for predicting mudstone dimensions in sandy braided-river reservoirs. AAPG Bulletin 90, 1273–1288.
Mannion, P.D., Calvo, J.O., 2011. Anatomy of the basal titanosaur (Dinosauria, Sauropoda) Andesaurus delgadoi from the mid-Cretaceous (Albian-early Cenomanian) Rio Limay Formation, Neuquen Province, Argentina: implications for titanosaur systematics. Zoological Journal of the Linnean Society 163, 155–181.
Mannion, P.D., Otero, A., 2012. A reappraisal of the Late Cretaceous Argentinean sauropod dinosaur *Argyrosaurus superbus*, with a description of a new titanosaur genus. Journal of Vertebrate Paleontology 32, 614–638.
Mannion, P.D., Upchurch, P., Carrano, M.T., Barrett, P.M., 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. Biological Reviews 86, 157–181.

Mannion, P.D., Upchurch, P., Barnes, R.N., Mateus, O., 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. Zoological Journal of the Linnean Society 168, 98–206.
Marsh, O.C., 1878. Principal characters of American Jurassic dinosaurs. Part I. American Journal of Science, Series 316, 411–416.
Martinelli, A., Forasiepi, A.M., 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with description of a new sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias Naturales 6, 257–305.
Martínez, R.D., 1998. *Notohypsilophodon comodorensis* gen. sp. nov., un Hypsilophodontidae (Ornithischia: Ornithopoda) del Cretácico Superior de Chubut, Patagonia Central, Argentina. Acta Geológica Leopoldensia 21, 119–135.
Martínez, R.D., Novas, F.E., 2006. *Aniksosaurus darwini* gen. et sp. nov., a new coelurosaurian theropod from the Early Late Cretaceous of Central Patagonia, Argentina. Revista del Museo Argentino de Ciencias Naturales 8, 243–259.
Martínez, R.D., Giménez, O., Rodríguez, J., Luna, M., Lamanna, M.C., 2004. An articulated specimen of the basal Titanosaurian (Dinosauria: Saurópoda) *Epachthosaurus sciuttoi* from the Early Late Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. Journal of Vertebrate Paleontology 24, 107–120.
Martínez, R.D., Lamanna, M.C., Novas, F.E., Ridgely, R.C., Casal, G.A., Martínez, J.E., Vita, J.R., Witmer, L.M., 2016. A basal lithostrotian titanosaur (Dinosauria: Sauropoda) with a complete skull: implications for the evolution and paleobiology of Titanosauria. PLoS One 11, e0151661. http://dx.doi.org/10.1371/journal.pone.0151661.
Miall, A.D., 1996. The Geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis and Petroleum Geology. Springer-Verlag, Berlin, 582 p.
Moore, D.M., Reynolds, R.C., 1989. X-ray Diffraction and the Identification and Analysis of Clay Minerals. Oxford University Press, New York, 332 pp.
Myers, T.P., Voorhies, M.R., Corner, R.G., 1980. Spiral fractures and bone pseudotools at palentological sites. American Antiquity 45, 483–490.
Otero, A., 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. Acta Paleontologica Polonica 55, 399–426.
Otero, A., Vizcaíno, S.F., 2008. Hindlimb musculature and function of Neuquensaurus australis (Sauropoda: Titanosauria). Ameghiniana 4, 333–348.
Polonio, I., López-Martínez, N., 2000. Análisis tafonómico de los yacimientos de Somosaguas (Mioceno medio, Madrid). Coloquios de Paleontología 51, 235–265.
Poropat, S.F., Mannion, P.D., Upchurch, P., Hocnull, S.A., Kear, B.P., Elliott, D.A., 2015a. Reassessment of the non-titanosaurian somphospondylan *Wintonotitan wattsi* (Dinosauria: Sauropoda: Titanosauriformes) from the Mid-Cretaceous Winton Formation, Queensland, Australia. Papers in Paleontology 1, 59–106.
Poropat, S.F., Upchurch, P., Mannion, P.D., Hockull, S.A., Kear, B.P., Sloan, T., Sinapius, H.K., Elliott, D.A., 2015b. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid- Cretaceous of Australia: Implications for Gondwanan titanosauriform dispersal. Gondwana Research 27, 995–1033.
Powell, J.E., 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Creta cico Superior del noroeste Argentino. In: Sanz, J.L., Buscalioni, A.D. (Eds.), Los dinosaurios y su entorno biótico. Actas del segundo curso de Paleontología, Cuenca, España, pp. 165–230.
Salgado, L., Coria, R.A., 1993. El género *Aeolosaurus* (Sauropoda. Titanosauridae) en la Formación Allen (Campaniano-Maastrichtiano) de la Provincia de Río Negro, Argentina. Ameghiniana 30, 119–128.
Salgado, L., Azpilicueta, C., 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincial de Rio Negro (Formación Allen, Cretácico Superior), Patagonia Argentina. Ameghiniana 37, 259–264.
Salgado, L., Carvalho, I. de Souza, 2008. *Uberabatitan ribeiroi*, a new titanosaur from the Marília Formation (Bauru Group, Upper Cretaceous), Minas Gerais, Brazil. Paleontology 51, 881–901.
Salgado, L., Coria, R.A., Calvo, J.O., 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. Ameghiniana 34, 3–32.
Salgado, L., Apesteguia, S., Heredia, S.A., 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. Journal of Vertebrate Paleontology 25, 623–634.
Salgado, L., Gallina, P.A., Paulina Carabajal, A., 2014. Redescription of *Bonatitan reigi* (Sauropoda: Titanosauria), from the Campanian-Maastrichtian of the Rio Negro Province (Argentina). Historical Biology: An International Journal of Paleobiology. http://dx.doi.org/10.1080/08912963.2014.894038.
Sanz, J.L., Powell, J.E., Le Loeuff, J., Martinez, R., Pereda Suberbiola, X., 1999. Sauropod remains from the Upper Cretaceous of Laño (North-central Spain). Titanosaur phylogenetic relationships. Estudios del Museo de Ciencias Naturales de álava 14, 235–255.
Schumm, S.A., 2005. River Variability and Complexity. Cambridge University Press, Cambridge, 220 p.
Seeley, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43, 165–171.
Shipman, P., Bosler, W., Davis, K.L., 1981. Butchering of giant Geladas in an Acheulian site. Current Anthropology 22, 257–268.
Skoog, D., West, D., Holler, F., Crouch, S., 2005. Valoraciones: valoración por precipitación. In: Fundamentos de química analítica. International Thompson Editors, Mexico, pp. 341–371.
Stein, K., Csiki, Z., Curry Rogers, K.A., Weishampel, D.B., Redelstorff, R., Carballido, J.L., Sander, P.M., 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Proceeding of the Natural Academy of Sciences of the United States of America 107, 9258–9263.
Tapia, A., 1919. Una mandibula de Dinosaurio procedente de Patagonia. Revista de la Sociedad Argentina de Ciencias Naturales 4, 369–370.
Tomassini, R.L., Montalvo, C.I., Manera, T., Oliva, C., 2010. Estudios tafonómico de los mamíferos pleistocenos del yacimiento de Playa del Barco (Pehuén Co), provincia de Buenos Aires, Argentina. Ameghiniana 47, 137–152.
Tomassini, R.L., Montalvo, C.I., Manera, T., Visconti, G., 2014. Mineralogy, Geochemistry and Paleohistology of Pliocene mammals from the Monte Hermoso Formation (Argentina). *Paedotherium bonaerense* (Notoungulata, Hegetotheriidae) as a case of study. Ameghiniana 51, 385–395.
Upchurch, P., Barnett, P.M., Dodson, P., 2004. Sauropoda. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, 2° Edition. University of California Press, Berkley, pp. 252–322.
Upchurch, P., Mannion, P.D., Taylor, M.P., 2015. The anatomy and phylogenetic relationships of "*Pelorosaurus*" *becklesii* (Neosauropoda, Macronaria) from the Early Cretaceous of England. PLoS One 10, e0125819. http://dx.doi.org/10.1371/journal.pone.0125819.
Vallati, P., Casal, G.A., Foix, N., Allard, J.O., De Sosa Tomas, A., Calo, M., 2015. Una palinoflora del Maastrichtiano de la cuenca del Golfo San Jorge. Reunión de Comunicaciones de la Asociación Paleontológica Argentina (RCAPA 2015). Mar del Plata.
Vallati, P., Casal, G.A., Foix, N., Allard, J.O., De Sosa Tomas, A., Calo, M., 2016a. Palinomorfos del Cretácico tardío en la cuenca del Golfo san Jorge: interés bioestratigráfico, paleobiogeográfico y paleoecológico. In: II Jornadas Geológicas de la Cuenca del Golfo San Jorge, Resúmenes, 98. Comodoro Rivadavia, Argentina.
Valatti, P., Casal, G.A., Foix, N., Allard, J., de Sosa Tomas, A., Calo, M., 2016b. First report of a Maastrichtian palynoflora from the Golfo San Jorge Basin, central Patagonia, Argentina. Ameghiniana. http://dx.doi.org/10.5710/AMGH.28.12.2015.2948.
Voorhies, M.R., 1969. Taphonomy and population dynamics of the early Pliocene vertebrate fauna, Knox Country, Nebraska. Contributions of the Geological Society, Special Papers 1, 1–69.
Wilson, J.A., Carrano, M.T., 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology 1, 252–267.
Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir 5, 1–68.
Zaaboub, N., Abdeljaouad, S., López-Galindo, A., 2005. Origin of fibrous clays in Tunisian Paleogene continental deposits. Journal of African Earth Sciences 43, 491–504.

Further reading

Casal, G.A., Luna, M., Martínez, R.D., Lamanna, M.C., Sciutto, J.C., Ivany, E., 2006. La fauna Campaniana-Maastrichtiana? de la Formación Bajo Barreal en el E-SE del Lago Colhué Huapi, Provincia de Chubut, Argentina. Ameghiniana 40, 61R.
González Riga, B.J., Calvo, J.O., Porfiri, J., 2008. An articulated titanosaur from Patagonia (Argentina): new evidence of neosauropod pedal evolution. Paleoword 17, 33–40.
Ibiricu, L.M., Casal, G.A., Martínez, R.D., Navarrete, C., 2011. Materiales asignables a Titanosauria (Saurischia; Sauropoda) de la Formación Bajo Barreal, Cretácico Superior, Patagonia Central. Brazilian Geographical Journal: Geosciences and Humanities Research Medium 2, 337–353.
Ibiricu, L.M., Martínez, R.D., Casal, G.A., Cerda, I.A., 2013c. The behavioural implications of a multi-individual bonebed of a small theropod dinosaur. PLoS One 8, e64253. http://dx.doi.org/10.1371/journal.pone.0064253.
Lydekker, R., 1983. The dinosaurs of Patagonia. Anales del Museo de La Plata, Sección de Paleontología 2, 1–14.
Martin, V., 1994. Baby sauropods from the Sao Khua Formation (Lower Cretaceous) in northeastern Thailand. GAIA 10, 147–153.
Vila, B., Galobart, A., Canudo, J.I., Le Loeuff, J., Dinares-Turell, J., Riera, V., Oms, O., Tortosa, T., Gaete, R., 2012. The diversity of sauropod dinosaurs and their first taxonomic succession from the latest Cretaceous of southwestern Europe: clues to demise and extinction. Paleogeography, Paleoclimatology, Paleoecology 350, 19–38.