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Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina

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Abstract

Some fragmentary dinosaur remains from the uppermost Hauterivian–Barremian La Paloma Member of the Cerro Barcino Formation of northern Chubut, Argentina are described. Together with the fauna from the La Amarga Formation of Neuquén, Argentina, this material represent the oldest known Cretaceous dinosaur fauna from South America. It includes remains of a probable titanosaurian sauropod and an abelisaurian, probable abelisaurid, theropod. This is the oldest record of titanosaurs from South America and the oldest record of abelisaurids globally. The presence of both small-bodied noasaurids in the La Amarga Formation and medium-sized–large abelisaurids in the Cerro Barcino Formation, in the middle Lower Cretaceous of Argentina, indicates that abelisaurian diversification began well before the final fragmentation of Gondwana. Whereas this explains the wide distribution of abelisaurs in the Late Cretaceous, reasons other than vicariance must be invoked for their apparent absence in the 'middle' Cretaceous of Africa.

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1. Introduction

Argentina has yielded some of the richest and most interesting dinosaur faunas known (see Bonaparte, 1996; Novas, 1997). Diverse faunas are especially well known from the latest Early and most ages of the Late Cretaceous (Novas, 1997). Rare ornithischians and a wide variety of saurischian taxa were present during the early Late Cretaceous, the latter including abelisaurian (Martínez et al., 1986; Bonaparte, 1991; Coria & Salgado, 2000; Lamanna et al., 2002), basal tetanuran (Coria & Salgado, 1995) and coelurosaurian theropods (Bonaparte, 1991; Novas, 1996, 1998; Novas & Puerta, 1997) and rebbachisaurid (Calvo & Salgado, 1995) and

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titanosaurian sauropods (Powell, 1986, 1990; Calvo & Bonaparte, 1991; Bonaparte & Coria, 1993). During the Campanian-Maastrichtian, saurischian faunas appear to have been less diverse at a higher taxonomic level, with only abelisaurian theropods (Bonaparte & Novas, 1985; Coria et al., 2002) and titanosaurian sauropods reported (Huene, 1929; Bonaparte & Powell, 1980; Powell, 1986, Powell, 2003). Unfortunately, however, our understanding of Early Cretaceous dinosaur faunas from South America remains poor (Novas, 1997). Consequently, the origin and evolutionary history of the Late Cretaceous dinosaur faunas of South America remains very poorly known.

Early Cretaceous dinosaurs have been reported from the Hauterivian–Barremian of the La Amarga Formation of Neuquén, from which the dicraeosaurid sauropod *Amargasaurus*, the small, probable abelisaurian theropod *Ligabueno*, and an undetermined stegosaur have been described (Salgado & Bonaparte, 1991;

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Bonaparte, 1996). Several theropods have recently been reported from the Santana Formation (Aptian) of Brazil, including spinosaurids (Kellner & Campos, 1996; Martill et al., 1996) and coelurosaurs (Frey & Martill, 1995; Kellner, 1999; Martill et al., 2000). Some theropod material of Aptian age, including two partial skeletons of an undescribed carcharodontosaurid, have also been reported from the Chubut Group of Argentina (Rich et al., 2000).

In this paper, we describe fragmentary dinosaur remains from the La Paloma Member of the Cerro Barcino Formation (uppermost Hauterivian– Barremian) of the Chubut Group, Chubut Province, Argentina. These remains not only represent the oldest Cretaceous dinosaur record from this province, but, together with the material from the broadly contemperaneous La Amarga Formation, also the oldest Cretaceous dinosaur fauna known from South America.

2. Geological and palaeontological setting

The Chubut Group comprises the lower Los Adobes and the upper Cerro Barcino formations (Codignotto et al., 1978; Figari & Courtade, 1993; Page et al., 1999). It unconformably overlies Middle–Upper Jurassic units usually grouped in the Cañadón Asfalto Formation, and older Jurassic units, and is overlain unconformably by uppermost Cretaceous units, the Campanian-Maastrichtian La Colonia, Paso de Sapo, and Lefipan formations and their lateral equivalents. Both the Los Adobes and Cerro Barcino formations are composed mainly of fluvial and volcaniclastic sediments (Figari & Courtade, 1993; Page et al., 1999; Manassero et al., 2000), although considerable differences in detailed sedimentology exists between the distinct members of the two formations. The Los Adobes Formation is considered to be Late Valanginian-Hauterivian in age (Cortiñas, 1996; Page et al., 1999), whereas the Cerro Barcino Formation might represent the latest Hauterivian-Senonian (?Campanian), although the youngest part may be Cenomanian in most areas (Page et al., 1999).

Both formations can be subdivided into several members. The Los Adobes Formation begins with the Arroyo del Pajarito Member, which is mainly composed of coarse fluvial sediments and pyroclastics. This member is overlain by the Bardas Coloradas Member, a unit consisting mainly of reddish fluvial and fine-grained overbank deposits. The base of the Cerro Barcino Formation is marked by a notable change in sediment composition, indicating a climatic change from the wet conditions of the Bardas Coloradas Member to the more arid environments of the La Paloma Member. The latter is dominated by pyroclastic and fluvial deposits with some intercalated dune sediments. It is overlain by the Cerro Castaño Member, which indicates a return to more humid conditions, with mainly fluvial and overbank deposits. Several higher members, the Las Plumas, Bayo Overo and Puesto Manuel Arce members, have been distinguished to the east and north-east of the area studied. These are probably latest Early–Late Cretaceous in age (?Albian–?Campanian), and might be separated by small unconformities (Cortiñas, 1996).

Although the sediments of the Chubut Group cover vast areas of Chubut Province, the vertebrate fauna from this unit is still poorly known. This might be owing to the comparative rarity of vertebrate fossils in most members of the two formations, but the relatively small amount of palaeontological fieldwork carried out in these areas, as compared to the Cretaceous of Neuquén, for example, is certainly another factor.

No vertebrates have so far been recorded from the Los Adobes Formation. The La Paloma Member has vielded some undescribed turtle remains. The only dinosaur fossil previously reported from this unit is a single theropod tooth fragment from the locality 'Turtle Town', which was originally thought to be within the Cerro Castaño Member (Rich et al., 2000). Several dinosaur remains have been reported from the Cerro Castaño Member, including two partial skeletons of a large, undescribed carcharodontosaurid and several theropod teeth (Vickers-Rich et al., 1999; Rich et al., 2000). Recently discovered vertebrate material in this member also includes remains of a titanosauriform sauropod, a probable coelurosaurian theropod, crocodile remains, and a partial turtle carapace (Rauhut, unpublished data). The Bayo Overo Member has yielded the sauropod Chubutisaurus (Del Corro, 1975), an undescribed sauropod, and several theropod teeth (Rich et al., 2000). Though frequently cited as being derived from the Aptian-Albian (e.g. Weishampel, 1990; Bonaparte, 1996; Novas, 1997) Chubutisaurus is thus most probably of Late Cretaceous age (Page et al., 1999; Rich et al., 2000). Likewise, the abelisaurid *Carnotaurus*, originally thought to be from the Albian of the Cerro Barcino (=Gorro Frigio) Formation (Bonaparte, 1985; Bonaparte et al., 1990), is now known to have come from the La Colonia Formation, which, according to new palynological evidence, is Maastrichtian in age (A. Archangelsky, pers. comm. 2001).

The specimens described herein come from the La Paloma Member of the Cerro Barcino Formation at Cerro Chivo in north-central Chubut (Fig. 1). Extensive outcrops of the Chubut Group are exposed on the eastern, northern and north-western flank of the Cerro Chivo, spanning the Bardas Coloradas Member of the Los Adobes Formation through the La Paloma Member to the Cerro Castaño Member of the Cerro Barcino Formation.

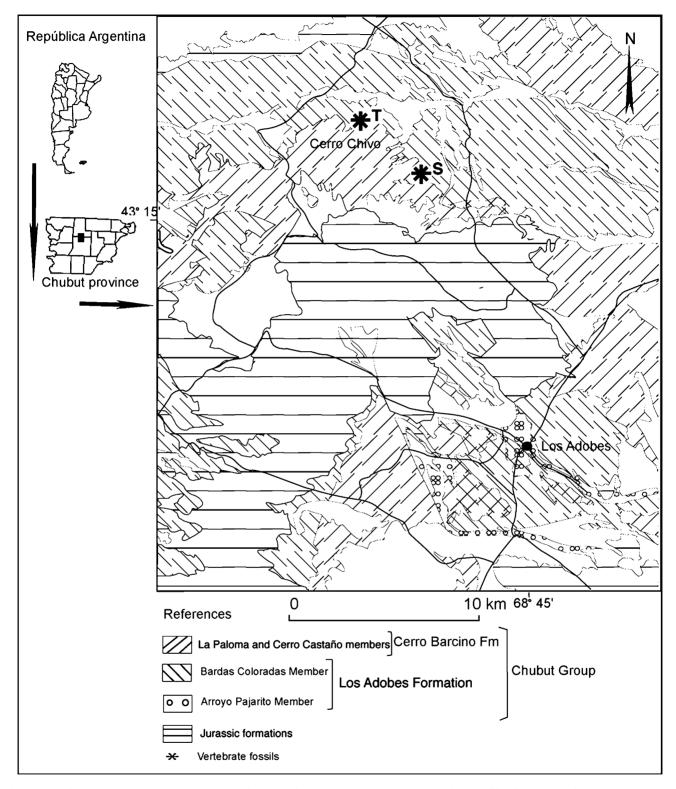


Fig. 1. Map of the Cretaceous outcrops in the area of Cerro Chivo, north-central Chubut, Argentina; modified from Proserpio (1987). S, sauropod locality; T, theropod locality.

The exposed La Paloma Member on the northern flank of the Cerro Chivo is over 20 m thick and composed mainly of fine tuffs and light red or green massive or laminated mudstones (Fig. 2). Occasionally, a few mud cracks are found in these beds. These fine sediments alternate with grey, massive, sandstone beds up to 0.50 m thick, or cross-bedded sandstones up to 2 m thick with sporadic ripple marks. Both mudstones and

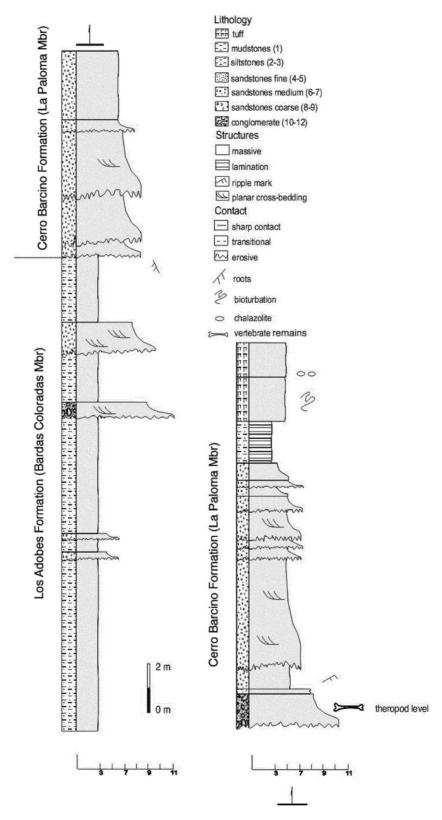


Fig. 2. Section of the upper part of the Los Adobes Formation (Bardas Coloradas Member) and the La Paloma Member of the Cerro Barcino Formation at the 'El Jujeño' locality, northern flank of Cerro Chivo.

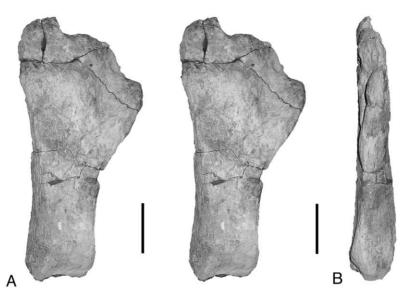


Fig. 3. Partial sauropod tibia from the La Paloma Member of the Cerro Barcino Formation at Cerro Chivo (MPEF V 1698). A, lateral view (stereophotographs). B, anterior view. Scale bar represents 10 cm.

sandstones occur in tabular bodies. The sandstone ratio increases considerably towards the upper part of the section. In this part of the succession, the sandstones exhibit large-scale cross-bedded structures, reaching 5 m thick, with east-south-east trending palaeocurrents. In these levels debris flows are very common.

This suggests that beds of the La Paloma Member at Cerro Chivo were deposited in a playa lake environment (with eolian deposits) that was subjected to influxes of sediment from ephemeral fluvial systems and debris flows from higher elevations.

Dinosaur remains were found in two localities, on the northern and eastern flanks of Cerro Chivo, respectively (Fig. 1). At both localities, the fossils were found as disarticulated elements in channels of reworked, conglomeratic tuffs, some 3–5 m above the junction between the Los Adobes and Cerro Barcino formations. These fossils are thus derived from the basalmost units of the latter formation and are, therefore, of latest Hauterivian–Barremian age.

Institutional abbreviations. FMNH/UA, Field Museum of Natural History, Chicago, USA/University of Antananarivo, Madagascar; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; PVL, Paleontología de Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina.

3. Dinosaur remains from the La Paloma Member

3.1. Sauropoda

Sauropod dinosaurs are represented by two partial presacral vertebral centra, a fragmentary tibia and

another unidentified limb bone (MPEF V 1698), all from the locality 'El Indio' on the eastern side of Cerro Chivo. The material is incomplete and poorly preserved, so little morphology can be discerned. Furthermore, the specimens were found several metres apart and may not represent a single individual. However, at least the vertebrae and tibia are from animals of approximately the same size and were found in close proximity.

Description. The vertebrae are represented by partial centra of (?)dorsal vertebrae with large dorsolaterally positioned pleurocoel that extend for almost the entire length of the centrum. The elements are too strongly damaged to enable anything to be said about the shape of the pleurocoel or the anterior articular surface. Only the shaft and the cnemial crest of a right tibia are preserved (Fig. 3). The shaft is strongly flattened transversely in its proximal part and the large cnemial crest is mainly directed anteriorly and only slightly flexed laterally. A shallow, but large depression is present on the lateral side of the bone posteroventral to the cnemial crest. Distally, the shaft becomes more massive and its outline is subtriangular with a flattened lateral side. The length of the element as preserved is 49 cm, and it is estimated that at least 15-20 cm of the distal end are missing.

Discussion. Salgado et al. (1997) mentioned the presence of elongate, eye-shaped pleurocoels in the dorsal vertebrae as a titanosaurian synapomorphy. Although the exact shape of the pleurocoel in the dorsal vertebrae of MPEF-PV 1698 cannot be determined, it is certainly elongate, extending over almost the entire length of the centrum, indicating that the derived state was probably present. The tibia is most similar to that of the Late Cretaceous titanosaur *Gondwanatitan* from Brazil (Kellner & Azevedo, 1999). Similarities include the more

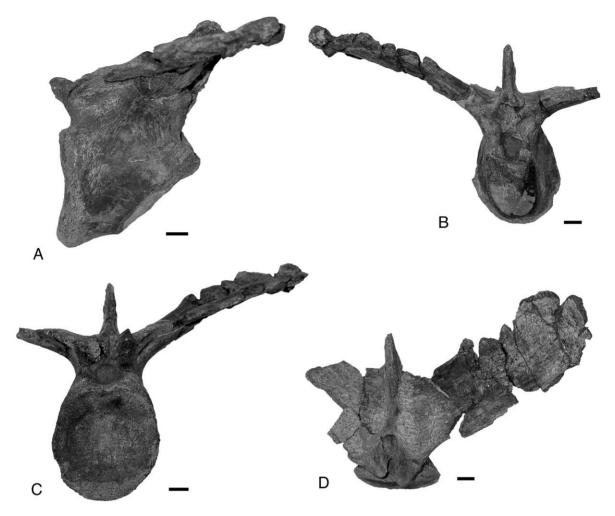


Fig. 4. Anterior caudal vertebra of an abelisaurian theropod from the La Paloma Member of the Cerro Barcino Formation at Cerro Chivo (MPEF V 1699). A, left lateral view. B, posterior view. C, anterior view. D, dorsal view. Scale bars represent 1 cm.

anteriorly than laterally directed cnemial crest, the strongly transversely flattened proximal end, and the presence of a large shallow groove on the lateral side posteroventral to the cnemial crest on the otherwise plain lateral side. The first character was noted as an autapomorphy for Gondwanatitan by Kellner & Azevedo (1999). Together with the strong flattening of the proximal end, which is also unlike any other sauropod (although it should be mentioned that Kellner & Azevedo noted that this flattening might be partly due to deformation in Gondwanatitan), this character might thus indicate that the material from Chubut belongs to the same titanosaur lineage as the much younger Gondwanatitan. However, more material is needed to firmly establish the affinities of the sauropod from the La Paloma Member; at the moment it can only be regarded as Titanosauria(?) indet.

3.2. Theropoda

Theropod dinosaurs are represented by two caudal vertebrae (Figs. 4 and 5) and a tooth fragment (MPEF V

1699) from the locality 'El Jujeño' on the northern flank of Cerro Chivo. Although both vertebrae have been eroded, the preservational quality of the elements is excellent. In contrast, the tooth was extremely fragmentary and crumbled during the attempt to extract it from the rock, so that only impressions of it remain in a hematite coating.

Description. Little can be said about the morphology of the tooth. It is small, with a mesiodistal length of approximately 10 mm. It is recurved, with both anterior and posterior carinae serrated, and was obviously rather broad labiolingually in its mesial portion.

The caudal vertebrae are considerably more informative (Figs. 4 and 5). Based on their very similar morphology and preservation, and closely matching size (Table 1) they probably represent the same individual. The slightly larger vertebra represents an anterior caudal, whereas the other specimen pertains to the anterior mid-caudal section.

The vertebral centra are slender and spool-shaped, with only a moderate constriction between the articular

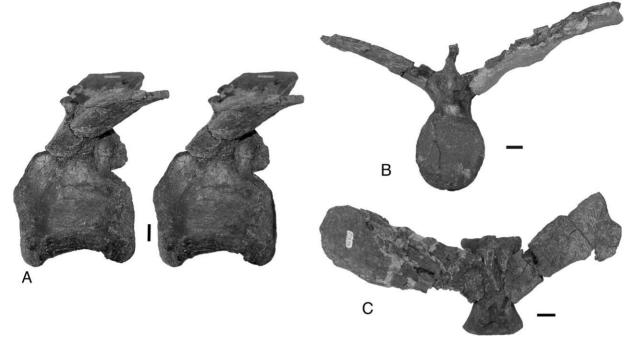


Fig. 5. Anterior mid-caudal vertebra of an abelisaurian theropod from the La Paloma Member of the Cerro Barcino Formation at Cerro Chivo (MPEF V 1699). A, left lateral view (stereophotographs). B, posterior view. C, dorsal view. Scale bars represent 1 cm.

Table 1 Measurements of theropod caudal vertebrae from the La Paloma Member (in mm)

Element	Centrum length	Centrum height	Centrum width
MPEF-PV 1699/1	65*	55	51
MPEF-PV 1699/2	62	46	40

*Centrum slightly damaged posteriorly.

surfaces. The articulation is amphi-platycoelous, with the anterior facet being slightly more concave than the posterior. The articular surfaces have an elongate oval outline. Undivided chevron facets are developed anteriorly and posteriorly. A broad but shallow groove is present on the ventral surface of the centra. The posteriorly broken vertebral body of the more anterior vertebra demonstrates that the ventral half of the centrum was hollow (Fig. 4B).

The neural arches are low and extend along almost the entire length of the centra. The neural canal is relatively small and round. The most striking character of the neural arches is the extremely long and considerably dorsolaterally, and somewhat posteriorly, directed transverse processes. In both vertebrae, the transverse processes of each side were originally approximately 1.6 times the length of the centrum and are situated on the dorsal part of the neural arch. The transverse processes have thin anterior and posterior margins and a slightly more massive and ventrally convex central part. The latter are connected with rudimentary anterior and posterior centrodiapophyseal laminae, which are developed as low, broad, rounded ridges on the lateral surface of the neural arch (Fig. 5A). The distal ends of the transverse processes are damaged, so it cannot be determined with certainty if an anterior expansion was present. However, on the only preserved transverse process of the more anterior vertebra, the anterior border of the process flexes slightly anteriorly just before the damaged anterodistal corner of this process, and the distal end of the transverse process is slightly thickened, indicating that such an expansion was probably present.

The pre- and postzygapophyses (only one prezygapophysis is preserved in the more anterior vertebra and only the postzygapophyses in the more posterior one) are small and strongly inclined, standing at an angle of approximately 90° to each other (Fig. 4C). An additional hyposphene-hypantrum articulation is present in both vertebrae. From the prezygapophyses, two low, converging ridges run posteromedially to the base of the neural spine; between the ridges, a broad, deep depression is present anterior to the base of the spine. However, a longitudinal furrow in the anterior base of the spine, present in basal theropods (e.g. Welles, 1984) and tetanurans (e.g. Madsen, 1976), is absent.

The neural spines are damaged in both specimens. They were both anteroposteriorly and transversely narrow, and restricted to the posterior half of the neural arch. In the more anterior vertebra on particular, the spine was inclined strongly posteriorly.

Discussion. In all preserved characters, the vertebrae are very similar to caudals of abelisaurs (Bonaparte et al., 1990; Coria & Salgado, 2000; Coria et al., 2002). In detail, they show the following characters that probably represent neoceratosaurian and abelisaurian synapomorphies:

1. Hollow centrum. As illustrated by Madsen (1976), fig. 26), the interior of the caudal vertebral centra of basal tetanurans are composed of spongy osseous tissue, whereas the neoceratosaur *Ceratosaurus* has a large cavity in the ventral half of the centrum. A very similar cavity is present in the more anterior caudal vertebra of MPEF V 1699. However, it is unclear whether this character is present in other neoceratosaurs; more studies of abelisaur caudal morphology are, therefore, needed to establish whether or not it is a neoceratosaurian synapomorphy.

2. Presence of rudimentary centrodiapophyseal laminae in anterior and anterior mid-caudals. In Allosaurus, only the first caudal vertebra shows a weak indication of the centrodiapophyseal laminae; no trace of these laminae is present on more posterior vertebrae (Madsen, 1976). The same seems to be true for Ceratosaurus (Gilmore, 1920). In contrast, in the abelisaurs Carnotaurus (Bonaparte et al., 1990) and Aucasaurus (Coria et al., 2002), rudimentary centrodiapophyseal laminae are found on all anterior and anterior mid-caudals, as is also the case in MPEF V 1699. It is uncertain at which level within Abelisauria this character represents a synapomorphy, since no anterior or anterior mid-caudals are known or have been described in the more basal taxa Majungatholus (Sampson et al., 1998), Abelisaurus (Bonaparte & Novas, 1985), and Ilokelesia (Coria & Salgado, 2000). It should also be noted that similar structures are present in at least some basal tetanurans (e.g. Torvosaurus; Britt, 1991).

3. Transverse processes more than 1.4 times the length of the caudal vertebral centrum (as measured from the neural spine to the distal tip of the process). In basal theropods (e.g. Liliensternus: Huene, 1934; Dilophosaurus: Welles, 1984), basal tetanurans (Piatnitzkysaurus: PVL 4073), carnosaurs (Allosaurus: Madsen, 1976; Sinraptor: Currie & Zhao, 1993) and basal coelurosaurs (e.g. ornithomimosaurs; Osmólska et al., 1972; tyrannosaurs; Osborn, 1916), the caudal transverse processes are approximately as long as the caudal vertebral centrum, or slightly longer. The basal neoceratosaur Ceratosaurus has somewhat elongate caudal transverse processes, which are more than 1.2 times the length of the vertebral centrum (Gilmore, 1920). In Aucasaurus (Coria et al., 2002) and Carnotaurus (MACN CH 894), the transverse processes of especially the anterior midcaudals are strongly elongated and each process is more than 1.4 times the length of the vertebral centrum. Again, the lack of anterior caudal vertebrae in more basal abelisaurs makes it difficult to evaluate at which node within Abelisauria this character represents a synapomorphy. However, the probable monophyletic group of small abelisaurs including *Noasaurus* and *Masiakasaurus* (Carrano et al., 2002), and perhaps *Ligabueno* (Coria & Salgado, 2000), does not seem to have the derived character state, since the transverse processes are very short in a posterior mid-caudal of *Ligabueno* (Bonaparte, 1996) and seemingly also in *Masiakasaurus* (Carrano et al., 2002). Thus, the strongly elongate transverse processes appear to be a synapomorphy of the Abelisauridae.

4. Large medial depression anterior to the base of the neural spine and lack of a longitudinal furrow on the anterior basal part of the spine. In basal theropods (e.g. Dilophosaurus; Welles, 1984) and basal tetanurans (e.g. Allosaurus; Madsen, 1976), a narrow groove extends from between the prezygapophyses posteriorly to the base of the neural spine and also invades the lower part of the anterior side of the spine. This is also the case in basal neoceratosaurs, such as Elaphrosaurus (Janensch, 1925). By contrast, in abelisaurs, such as Carnotaurus (MACN CH 894) and Majungatholus (FMNH/UA field Nr. 96313), and in MPEF V 1699, a widened, deep depression is developed behind the prezygapophyses, anterior to the neural spine. This depression is bordered posteriorly by a dorsal roof of bone in between the spinoprezygapophyseal laminae, which are developed as low ridges. Thus, no groove is present on the anterior ventral part of the neural spine. Coria & Salgado (2000) also listed the presence of deep pre- and postspinal depressions as synapomorphies of abelisaurs, although in reference to the presacral vertebrae.

5. Presence of an anterior expansion of the distal end of the transverse process. Although in some dinosaurs the transverse processes are slightly expanded distally, only in abelisaurs, including *Ilokelesia* (Coria & Salgado, 2000), *Carnotaurus* (Bonaparte et al., 1990) and *Aucasaurus* (Coria et al., 2002), is a strongly expanded, narrow anterior process present at the distal tip of these processes. This process is usually associated with a thickening of the distal margin of the transverse process (Coria et al., 2002, fig. 2B). As mentioned above, it cannot be determined with certainty whether an anterior process of the transverse processes was present in MPEF V 1699, but the thickening of the distal end indicates that this was probably the case.

In summary, the characters exhibited by the caudal vertebrae from the La Paloma Member clearly indicate that they represent an abelisaurian, probably abelisaurid, theropod. Coria et al. (2002) noted the presence of hyposphene-hypantrum articulations in the caudal vertebrae as a synapomorphy of the Carnotaurini within the Abelisauria. However, the distribution of this character is problematic. These accessory articulations are present in Aucasaurus and Carnotaurus, but not in Ceratosaurus. They also seem to be present in the anterior caudal vertebrae of Majungatholus (FMNH/UA field Nr. 96313). However, their presence or absence cannot be established in other abelisaurs, since, if present in the caudal series, they are usually restricted to the anterior half of the tail and only distal caudals are known for Ilokelesia (Coria & Salgado, 2000) and Ligabueno (Bonaparte, 1996). Moreover, since caudal hyposphene-hypantrum articulations are known from some basal theropods (e.g. Dilophosaurus; Welles, 1984) and basal tetanurans (e.g. *Monolophosaurus*: Sinraptor: Currie & Zhao, 1993), their presence might represent the plesiomorphic character state for basal theropods. Analysis of the distribution of this character within a more extensive phylogenetic analysis of basal theropods is necessary to solve this problem.

4. Discussion

The fossils described here represent the first identifiable dinosaur remains from the La Paloma Member of the Cerro Barcino Formation. Hitherto, reports of Early Cretaceous neoceratosaurs and titanosaurs in South America have been very rare (e.g. Bonaparte, 1996; Novas, 1997). This is the oldest Early Cretaceous record of a probable titanosaur from South America (Novas, 1997). The only other Early Cretaceous sauropods known from South America are the diplodocoids Amargasaurus (Salgado & Bonaparte, 1991) and Rayososaurus (Bonaparte, 1996), and the probable titanosaur Agustina (Bonaparte, 1999; Wilson, 2002). The only possible abelisaur previously reported from the Lower Cretaceous is the small form Ligabueno (Bonaparte, 1996), which might be part of a radiation of small basal abelisaurs (Coria & Salgado, 2000). Sampson et al. (1998) suggested that the apparent absence of abelisaurs, and especially abelisaurids, in Africa might reflect their radiation after the final separation of Africa and South America, a view recently refuted by Lamanna et al. (2002) on the basis of an abelisaurid record from the Cenomanian-Turonian of Chubut. The presence of a probable abelisaurid in deposits of middle Early Cretaceous age in Chubut, well before the final separation of Africa and South America (Scotese, 1991) significantly strengthens the hypothesis of Lamanna et al. (2002). The occurrence of both the small-bodied Noasauridae (Coria & Salgado, 2000) and the medium-sized to large Abelisauridae in Argentina during the mid Early Cretaceous indicates that abelisaurian diversification was well under way by then. Their apparent absence in Africa, therefore, has to be explained in other ways. Whereas the La Paloma Member represents a rather arid environment, the overlying Cerro Castaño Member indicates a return to more humid conditions. The sparse dinosaur fauna

from the Cerro Castaño Member, with the presence of carcharodontosaurids (Rich et al., 2000), a large coelurosaur, and titanosauriform sauropods (Rauhut, unpublished data) is reminiscent of 'middle' Cretaceous dinosaur faunas reported from Africa (Stromer, 1936; Sereno et al., 1996; Rauhut, 1999), but no evidence of abelisaurs has been found in this most productive member of the Chubut Group. Thus, a possible, though rather speculative, explanation might be that at least early abelisaurs preferred more arid environments and are, therefore, absent, or at least very rare, in the 'middle' Cretaceous of Africa, where a slightly higher percentage of fern spores than in other areas of the African-South American palymofloral province seems to indicate more humid conditions (Schrank, 1990). This hypothesis can only be tested by new finds and increased sampling of Early Cretaceous sediments in Africa and South America.

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