**The oldest theropods from the Neuquén Basin:
predatory dinosaur diversity from the Bajada Colorada Formation (Lower
Cretaceous: Berriasian-Valanginian), Neuquén, Argentina**

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26 **Abstract.**

27 Here, we describe new theropod materials (several isolated teeth, an axis, two caudal
28 centra and a proximal left tibia) from the type locality of the Bajada Colorada Formation
29 (Lower Cretaceous, Berriasian-Valanginian). Although fragmentary, the recovered
30 material shows a diverse association of meat-eating dinosaurs for this poorly understood
31 period of time. Three techniques were used to assess the phylogenetic position of the
32 isolated teeth: multivariate (PCA), discriminant and phylogenetic analyses. The
33 morphotypes 1, 2 and 3 (small non-recurved isolated crowns) were regarded as
34 Theropoda indet., as our analyses failed to support a more precise classification. Two
35 large almost complete ziphodont crowns, considered morphotype 4, were identified as
36 belonging to megalosaurid tetanurans by phylogenetic, discriminant and multivariate
37 analyses, thus likely representing the first record of this ancient family in South
38 America, and the youngest worldwide. We refer the axis to a small abelisauroid
39 ceratosaurian based on the following suite of characters; long and pointed epipophyses, a
40 pneumatic foramen in the centrum, the invaginated spinopostzygapophyseal lamina, and
41 the anteroposteriorly long, dorsally convex, and dorsally/posteriorly unexpanded neural
42 spine. The caudal centra can be referred to a theropod, and tentatively to
43 Abelisauroidae, suggesting that they may belong to the same taxon as that represented
44 by the axis. The tibia lacks the *incisura tibialis*, presents a low, sharp and proximally
45 positioned fibular crest, and has a deep lateral fossa, which is limited dorsally by a
46 coarse, rounded in section and anteriorly directed crest. This combination of features
47 allows us to refer it to a large abelisaurid. The Bajada Colorada dinosaur record includes so
48 far a small abelisauroid, a large abelisaurid, a probably medium to large megalosaurid
49 tetanuran, diplodocid and dicraeosaurid sauropods. It shows some similarities with
50 Middle and Upper Jurassic units in central Patagonia, Africa and Portugal, suggesting

that no significant dinosaur faunal turnover took place through the Jurassic-Cretaceous event in the southern part of South America.

Keywords-Theropoda; Ceratosauria; Megalosauridae; Lower Cretaceous; South America

1.INTRODUCTION

The Upper Cretaceous outcrops of Patagonia yield one of the most abundant and diverse faunal assemblages from the Mesozoic period (Leanza et al., 2004; Novas, 2009). However, they are composed of the survivors from the poorly known faunas that existed in South America during the Early Cretaceous. Compared to the abundant record of Late Cretaceous terrestrial assemblages, Early Cretaceous assemblages are very poorly known (Salgado and Bonaparte, 1991; Del Corro, 1975; Bonaparte, 1999, Apesteguía and Giménez, 2001a, b; Rauhut, et al., 2003; Novas, 2009; Carballido et al., 2012; Gallina et al., 2014a). Only recently have workers begun exploring the Lower Cretaceous outcrops in Patagonia (Gianechini et al., 2011; Coria et al. 2010; Gallina et al., 2014a b; Canale et al., 2015).

Early Cretaceous dinosaurs from South America remained almost unknown for most of the 20th century. During the early 80's, fossils collected by José Bonaparte from the La Amarga Formation in the Neuquén Basin substantially changed our understanding of this assemblage. Bonaparte successfully explored Early Cretaceous outcrops of the Neuquén province and made important discoveries; including dicraeosaurids and small abelisauroids at La Amarga Formation and large titanosaurs at Lohan Cura Formation (Salgado and Bonaparte, 1991; Bonaparte, 1996; Bonaparte et al., 2006). However, all those sedimentary units represent the younger part of the Early Cretaceous.

The expedition led by Jose Bonaparte to the El Marucho Hill Area, Neuquén, in which the Bajada Colorada Formation widely outcrops, resulted in the discovery of a sauropod vertebra and a large theropod femur, which were only briefly described in an abstract (Apesteguía and Bonaparte, 2004). Recently, new sauropod and theropod dinosaurs specimens were recovered through successive field expeditions carried out by the authors to the type locality of the Bajada Colorada Formation (Berriasian-Valanginian). They include the first diplodocid sauropod from South America *Leinkupal laticauda* (Gallina et al., 2014a), an indetermined dicraeosaurid (Gallina et al., 2014b), and few theropod isolated remains, composed by teeth and bones, which are the main focus of the present contribution.

2. GEOLOGICAL SETTING

The materials here described come from the Bajada Colorada Formation (Neuquén Basin) at its type locality, 40 km south of the town of Picún Leufú on the national route 237, in the southeastern part of the Neuquén Province, Patagonia, Argentina (Fig. 1). This unit is composed of red and greenish-brown, fine to coarse-grained conglomerates and sandstones with well-developed bands of light brown siltstones and reddish claystones. The unit is mostly dominated by a fluvial regime, and the paleoenvironment resembles braided river systems where well-preserved channels with cross stratification and paleosols are present (Leanza and Hugo 1997; Leanza 1999).

The age of Bajada Colorada Formation (late Berriasian-Valanginian) was determined by seismological, surface geological and biostratigraphical studies (Leanza and Hugo 1997; Foucault et al., 1987). This unit conformably overlies the marine Picún Leufú Formation (Tithonian–early Berriasian) and is unconformably covered by

themarine Agrio Formation (late Valanginian– late Hauterivian) (Leanza et al., 2004; Leanza and Hugo, 1997).

3. MATERIAL AND METHODS

The isolated teeth and the vertebral elements were found isolated in a bonebed, and mixed with sauropod bones of the diplodocid *Leinkupal laticauda* and a dicraeosaurid sauropod (Gallina et al., 2014a,b). The proximal tibia was recovered from a different level, located 3 meters below and 40 meters away from the level of the bonebed.

The teeth recovered are well to badly preserved, and all lack the root and some part of the crown. Only ten teeth provide enough information to assign them to discrete morphotypes. The terminology used to describe the teeth follows that of Hendrickx et al. (2015a), which is a synthesis of several previous works (i.e., Currie et al., 1990; Farlow et al., 1991; Smith et al., 2005; Fanti and Therrien, 2007; Hendrickx and Mateus, 2014a). The denticle morphology of some teeth was viewed and photographed with the Zeiss EVO MA 15 Scanning Electron Microscope from the Instituto de Investigaciones en Paleobiología y Geología (IIPG), General Roca, Rio Negro, Argentina.

The following dental measurements and ratios (proposed by Smith et al., 2005) were used in the morphometric analysis (measurements taken with a digital caliper): AL, apical length (in mm); CBL, crown base length, measured at the base of the crown from its mesialmost to its distalmost extension (excluding the carinae; in mm); CBR, crown base ratio, numerical value derived from dividing CBW through CBL (= labiolingual compression); CBW, crown base width, labiolingual extension of the crown at its base (in mm); CH, crown height, measured from the basodistal most point of the crown toward its tip (in mm); CHR, crown height ratio, numerical value derived

from dividing CH through CBL; DC, denticle density for distal mid-crown serration, i.e., denticles per 5 mm at the mid-crown part of the distal carina; MC, denticle density for mesial mid-crown serration, i.e., denticles per 5 mm at the mid-crown part of the mesial carina; MCL, mid-crown length, maximum mesiodistal extent of the tooth at mid-height of the crown; MCR, mid-crown ratio, thickness of the mid-crown corresponding to the quotient of MCW by MCL; MCW, mid-crown width, maximum labiolingual extent of the tooth, perpendicular to the MCL, at mid-height of the crown (Table 1).

Three techniques were used to investigate the phylogenetic distribution of each tooth morphotype. First, we compared the gross morphology of the teeth using Principal Component Analysis (PCA) (Fig.2) by adding our specimens to the large database compiled and published by Hendrickx et al. (2015b) (see Appendix A). We excluded the isolated tooth assigned to *Aerosteon* given the caveats made by previous authors about its assignment to the holotype (Novas et al., 2013). Following the suggestions of Carrano et al. (2012), we included *Erectopus* in “basal Allosauroidae”; together with *Allosaurus*. Also, according to the classification of Novas et al. *op cit.*, we consider *Neovenator* as part of the clade Carcharodontosauridae. The values of CBL, CBW, CH, AL, MCL, MCW, MC and DC were log-transformed prior to the analysis, missing data cells were estimated with a mean value from across the sample, and the PCA was run using a correlation matrix. The PCA was run with the program PAST v3.10 (Hammer et al., 2001).

Also, we used the same database of tooth measurements to conduct a Discriminant Analysis in PAST, which uses pre-determined groups (taxonomic in this case) to create a morphospace in which these groups are maximally separated. Isolated teeth can be classified according to which group it is most similar to in this discriminant space.

Finally, we performed a phylogenetic analysis, including our scorings (see Appendix B) in the dataset published by Hendrickx and Mateus (2014a). The phylogenetic analyses were performed with the program TNT (Goloboff et al., 2008), using exactly the same parameters set by Hendrickx and Mateus *op cit.*, including the “New Technology Search”, with the “driven search” option (Tree Drift, Tree Fusing, Ratchet, and Sectorial Searches selected with default parameters), and stabilizing the consensus twice with a factor of 75.

4. INSTITUTIONAL ABBREVIATIONS

MCF: Museo “Carmen Funes”, Plaza Huincul, Neuquén, Argentina. MMCh: Museo Municipal “Ernesto Bachmann”, Villa El Chocón, Neuquén, Argentina. MPCA: Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina. MPEF: Museo Paleontológico “Egidio Feruglio”, Trelew, Chubut, Argentina. UMNH: Utah Museum of Natural History, Salt Lake City, Utah, USA. UNSM: National Museum of Natural History, Smithsonian Institution, Washington, USA.

5. SYSTEMATIC PALEONTOLOGY

5.1 *Teeth*

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

THEROPODA Marsh, 1881

Theropoda indet.

Theropod tooth morphotype 1

176 Figure 3

177 *Material*: MMCh-PV 68-5, MMCh-PV 68-10, two isolated lateral dental crowns.

178 We tentatively assign a third almost complete isolated crown to this morphotype;
179 MMCh-PV 68-8.

180 *Description*: This description is based on the specimens MMCh-PV 68-5 and MMCh-
181 PV 68-10. Both crowns are fairly complete, with the specimen MMCh-PV 68-5 lacking
182 the tip and part of the base, and the specimen MMCh-PV 68-10 showing three
183 transversal fractures and lacking the basal sector of the distal margin. They are
184 ziphodont; small to medium sized (CH slightly less than 10 mm), moderately elongated
185 baso-apically (CHR: 1.78, in MMCh-PV 68-10, although the value should be similar in
186 MMCh-PV 68-5). Both crowns are moderately labiolingually compressed (CBR 0.50 in
187 MMCh-PV 68-5 and 0.52 in MMCh-PV 68-10). In lateral view the crowns have a
188 strongly convex mesial margin and a straight distal margin (Fig. 3A, C). The mesial
189 carina is centrally positioned in its apical sector, and sharply twisted lingually towards
190 the base (Fig. 3F). They show small, extremely worn denticles. The distal carina is
191 labially deflected, especially their basal half (Fig. 3B) and appears to be fully serrated.
192 The cross-section of both crown bases is oval to lanceolate (Fig. 3E). The MC is 20 and
193 DC 16 in MMCh-PV 68-10. The denticles in the central part of the distal carina are well
194 preserved in specimen MMCh-PV 68-10; they are asymmetrically convex in shape in
195 lateral view, with narrow interdenticular spaces and poorly developed interdenticular
196 sulci. The distal denticles in specimen MMCh-PV 68-5 are poorly preserved, so we
197 cannot determine their morphology. The denticles of the central part of the mesial
198 carina are extremely worn, making it difficult to interpret its extension and morphology.
199 The poor preservation of the specimen MMCh-PV 68-5 only allows to determine the
200 DC, which has a value of 16.

201

202 *Remarks:*This tooth morphotype is characterized by moderately elongated and
203 moderately labiolingually compressed crowns. They show straight distal carinae in
204 lateral view, which are labially deflected in posterior view. The mesial carina is sharply
205 twisted lingually towards the base. Another isolated crown, MMCh-PV 68-8, shows
206 very similar dimensions, crown base ratio, crown elongation and DC with respect to the
207 former specimens. However, some key characters, such as the sharply lingually twisted
208 mesial carina, cannot be distinguished due to the poor preservation, so we only
209 tentatively assign MMCh-PV 68-8 to this morphotype.

210 There is no agreement between the analyses performed on the specimens referred to
211 Morphotype 1. Given the low CBR of both teeth we ran two different analyses for each
212 specimen (see Appendix C), coding them as mesial and lateral teeth
213 respectively. MMCh-PV 68-5 was recovered as an abelisaurid when coded as a lateral
214 tooth, and as sister group of *Dilophosaurus* when coded as a mesial tooth. In the PCA,
215 MMCh-PV 68-5 falls within the convex hull of Coelophysoidea, Megaraptora, basal
216 Tyrannosauroidae and Dromaeosauridae (Fig. 2). Finally, the Discriminant Analysis
217 classifies MMCh-PV 68-5 as a Basal Tyrannosauroidae. On the other hand, the
218 specimen MMCh-PV 68-10 is recovered in a large polytomy when coded as mesial
219 teeth and as a basal Theropod when coded as lateral teeth in the Phylogenetic Analysis,
220 falls within the convex hull of Basal Theropoda, Coelophysoidea, Megaraptora,
221 Troodontidae, Dromaeosauridae, and basal Tyrannosauroidae in the PCA (Fig. 2), and
222 is classified as a Basal Tyrannosauroidae by the Discriminant Analysis.

223 Given the fact that the phylogenetic, principal components and discriminant analyses
224 could not classify Morphotype 1 to a certain clade unequivocally, this morphotype is
225 here referred to Theropoda indet.

226

227 Theropoda indet.

228 *Theropod tooth morphotype 2*

229 Figure 4

230 *Material:* MMCh-PV 68-9, an isolated crown

231 *Description:* Both the crown and basal portion of the root are preserved, and the crown
232 only lacks the apical third of the distal carina. The crown is ziphodont, small (CH less
233 than 10 mm), weakly baso-apically elongated (CHR: 1.43) and strongly labiolingually
234 narrow (CBR: 0.39). In lateral view, the crown is posteriorly recurved, with a convex
235 mesial margin and a straight distal margin (Fig. 4A, C). The mesial and distal carinae
236 are serrated and centrally positioned on the crown in both mesial and distal view (Fig.
237 4B, D). The denticle density is almost the same in both carinae, with an MC of 19 and a
238 DC of 17 denticles per 5 mm, respectively. The denticles of the central part of the distal
239 carina are hooked to asymmetrically convex in lateral view; they show narrow
240 interdenticular spaces and well-developed interdenticular sulci (Fig. 4E). The denticles
241 of the central part of the mesial carina are poorly preserved, but they appear to be
242 asymmetrically convex, with narrow interdenticular spaces and poorly developed
243 interdenticular sulci. The cross-section of both crown bases is lenticular (Fig. 4F)

244

245 *Remarks:* Although represented by one isolated crown, this morphotype shows enough
246 features to differentiate it from the other teeth recovered in the quarry. It is
247 characterized by a small, low and extremely narrow crown, with straight distal margin
248 in lateral view, fully serrated mesial and distal carinae with similar denticle
249 density, hooked distal denticles with well-developed interdenticular sulci and lenticular
250 basal cross-section.

Our analyses did not support a concrete classification for this morphotype. The phylogenetic analysis showed the specimen MMCh-PV 68-9 deeply nested inside Abelisauridae (see Appendix C). On the other hand the PCA shows MMCh-PV 68-9 falling within the convex hull of Dromaeosauridae, Troodontidae, Noasauridae and Coelophysoidea (Fig. 2), but it does not show any of the synapomorphies of the former theropod clades. Finally, the Discriminant Analysis classifies MMCh-PV 68-9 as a basal Tyrannosauroidae. One possible explanation of this lack of correspondence between the analyses is the small size of the specimen. It shows a combination of abelisaurid characteristics (like the hooked distal denticles, and straight distal margin) so is recovered as one in the phylogenetic analysis. But with respect to the multivariate analyses; the samples of abelisaurid specimens included (and, in fact, most abelisaurids known) are medium to large size theropods, so is expectable that the specimen MMCh-PV 68-9 falls outside the morphospace of this group. It is remarkable that from the same quarry they were found some postcranial remains of a small abelisauroid. Given the discrepancies between different analyses we prefer to refer this morphotype to Theropoda indet.

Theropoda indet.

Theropod tooth morphotype 3

Figure 5

Material: MMCh-PV 68-2 and MMCh-PV 68-3, two isolated mesial crowns.

Descriptions: Both teeth are almost complete, showing part of the root and lacking the apex. The specimen MMCh-PV 68-3 also lacks the basal-most part of the distal carina. They are small (CH about 10 mm), ziphodont, and moderately to weakly elongated basoapically (CHR 1.66 in MMCh-PV 68-2, and 1.34 in MMCh-PV 68-3). Both crowns are

weakly labiolingually compressed, with a CBR of 0.63 in MMCh-PV 68-2 and 0.5 in MMCh-PV 68-3. In lateral view the crowns are weakly recurved, with a convex mesial margin and a straight distal margin (Fig. 5A, C). The distal carinae are fully serrated, with a DC of 20. In distal view the distal carina is mainly centrally positioned, only slightly labially displaced (Fig. 5B). The denticles of the apical part of the distal carina are subquadrangular in lateral view, with narrow interdenticular spaces and no interdenticular sulci. The denticles of the central part of this carina are proximodistally subrectangular (Fig. 5E). The mesial carina is slightly visible, extends to the cervix and the denticles are so extremely worn down/eroded that their number and morphology cannot be known. The basal cross-section is oval to lanceolate in both specimens (Fig. 5F).

Remarks: This morphotype can be clearly differentiated from the other teeth recovered in the quarry by its small-sized, low, non-recurved and moderately labiolingually compressed crowns, with straight distal carinae in lateral view and with a DC of 20. As with morphotypes 1 and 2, our analyses were not consistent enough to allow us to confidently identify Morphotype 3. The phylogenetic analyses showed both specimens included in extensive polytomies, when coded as mesial or lateral teeth (see Appendix C). The PCA (Fig. 2) showed MMCh-PV 68-2 positioned within the convex hull of Coelophysoidea, Megaraptora, Basal Tyrannosauroidae, Dromaeosauridae and Troodontidae. MMCh-PV 68-3 falls within the convex hull of Coelophysoidea, Basal Tyrannosauroidae, Dromaeosauridae, Troodontidae and Noasauridae. Finally the Discriminant Analysis classifies MMCh-PV 68-2 as a Megaraptora and MMCh-PV 68-3 as a Basal Tyrannosauroidae.

Both multivariate analyses performed on MMCh-PV 68-2 support this specimen as part of Megaraptora, a theropod group which is well documented in the Upper Cretaceous outcrops of Patagonia. However, the specimen MMCh-PV 68-2 shows some important morphological differences from this theropod clade. If we consider MMCh-PV 68-2 as a lateral tooth; it strongly differs with the teeth of megaraptorans in having a straight distal margin and an oval basal cross section, while in *Australovenator* (Hocknull et al., 2009), *Fukuiraptor* (Currie and Azuma, 2006), *Megaraptor* (Porfiri et al., 2014) and *Orkoraptor* (Novas et al., 2008) the distal margin is strongly recurved, and *Megaraptor* and *Orkoraptor* show a figure-8-shaped basal cross section. If we consider MMCh-PV 68-2 as a mesial tooth, the basal cross section in premaxillary teeth in *Megaraptor*, *Fukuiraptor* and *Orkoraptor* is D-shaped with a rotated mesial carina, again distinct from the oval cross section of the Bajada Colorada specimen. Also in both mesial and lateral teeth of *Megaraptor* and *Orkoraptor* the mesial carina is unserrated, and in *Australovenator* the serrations are located only on its apical sector, while in MMCh-PV 68-2 the mesial carina is fully serrated.

Given these inconsistent results we prefer to refer this morphotype as Theropoda indet.

TETANURAE Gauthier, 1986

MEGALOSAUROIDEA Fitzinger, 1843

MEGALOSAURIDAE Fitzinger, 1843

Megalosauridae indet.

Theropod tooth morphotype 4

Figures 6 and 7

Material: MMCh-PV 68-6 and MMCh-PV 68-7, two almost complete isolated lateral dental crowns. Two fragmentary tooth crowns (MMCh-PV 68-1, MMCh-PV 68-4) are also tentatively referred to this morphotype.

Description: Two specimens can be assigned to this morphotype: MMCh-PV 68-6 and MMCh-PV 68-7 based on similar size and morphology, so the description is based in both.

The crowns are almost complete, lacking the roots. The general morphology of the crowns is ziphodont; they are medium to large-sized (average CH: 35 mm), moderately basoapically elongated (CHR 2.20 in MMCh-PV 68-6, and 2.41 in MMCh-PV 68-7). Both are moderately to strongly labiolingually narrow, with a CBR of 0.5 for MMCh-PV 68-6 and 0.43 for MMCh-PV 68-7. In lateral view, the crowns are posteriorly curved, with a concave distal margin (Fig. 6A, C; Fig. 7A, C). Both labial and lingual surfaces are slightly convex. The mesial carina is centrally positioned on the crown in mesial view, and extends over the apical half of the crown. Due to the bad preservation of the specimens, the mesial denticles are almost fully worn and can only be observed in some parts of the crown. Consequently, the morphology and number of denticles per five mm cannot be known. The distal carinae are fully serrated and extend from the apex to the crown base (Fig. 6B, 7B). In distal view the distal carinae are sigmoid (which is more evident in MMCh-PV 68-7) and centrally positioned. The cross-section of both crown bases are oval, nearly lanceolate (Fig. 6E; 7F). The DC is 18 in both crowns. The distal denticles are subquadrangular, with narrow interdenticular spaces and have slightly developed interdenticular sulci (Fig. 7E).

347 *Remarks:* The phylogenetic analysis performed yielded 39 most parsimonious trees
348 (MPTs), in which the strict consensus tree (700 steps; CI: 0.317; RI: 0.521) shows
349 MMCh-PV 68-6 and MMCh-PV 68-7 nested among Megalosauridae (Fig. 8). This is
350 supported by the following character: lenticular-lanceolate basal cross-section of the
351 lateral crowns (Char. 72:1). Inside Megalosauridae, they are clustered in a small clade
352 with *Dubreuillosaurus* and *Eustreptospondylus*, a position supported by the
353 subquadrangular denticles of the middle part of the distal carinae (Char. 92:0). Likewise
354 both Bajada Colorado specimens are within a small clade with *Eustreptospondylus*, as
355 they share a higher number of denticles in the apical part of the distal carina than at the
356 middle part (Char. 100: 0).

357 The PCA resulted in a two-dimensional morphospace where MMCh-PV 68-6
358 and MMCh-PV 68-7 plot within the convex hull of several medium to large-sized
359 theropods (Fig. 2). Both specimens fall into the maximum morphospace occupation area
360 of Spinosauridae, basal Allosauroidea and Megalosauridae, and the specimen MMCh-
361 PV 68- 6 also falls within basal Tyrannosauroidae and Abelisauridae. The Bajada
362 Colorado specimens lack dental characters of most of the clades mentioned other than
363 Megalosauridae, based on the diagnoses presented by Hendrickx and Mateus (2014a).
364 We can discard the possibility that the MMCh-PV 68-6 and 7 pertain to spinosaurids
365 because this family possessed very specialized teeth with several diagnostic characters
366 like the incrassate-subconical crowns ornamented with flutes, veined/anastomosed
367 enamel texture and minute to absent denticles. Also, these teeth do not show the
368 strongly labially deflected distal carina present in Tyrannosauroidae. These teeth also
369 lack of the almost straight distal margin, hooked denticles and mesial carina reaching
370 the crown base present in Abelisauridae. Finally MMCh-PV 68-6 and 7 lack the large

transversal undulations present in some lateral teeth of basal Allosauroidea. The discriminant analysis classifies both MMCh-PV 68-6 and 7 as megalosaurids.

At this point it is worth to mention that the large transverse undulations cited as typical of Allosauroidea are not present in all allosauroid teeth; and in fact it can be difficult to differentiate lateral teeth of megalosaurid from allosauroid tetanurans (Hendrickx et al., 2015b). So, although the results of the analyses applied strongly suggest that MMCh-PV 68-6 and 7 belong to megalosaurids, we cannot completely dismiss the possibility that they actually pertain to a basal allosauroid.

Other megalosaurids recovered in South America, aside from the highly specialized Cretaceous Spinosauridae, includes the Piatnitzkysauridae from the Middle Jurassic of Patagonia (Carrano et al., 2012). Comparisons with the specimens from Bajada Colorada show that the lateral teeth of *Piatnitzkysaurus* have a mesial carina that reached the cervix, and both in *Piatnitzkysaurus* and *Condorraptor* the teeth are labiolingually thicker (Hendrickx et al., 2015b).

In summary, the three analyses all support megalosaurid affinities for the specimens MMCh-PV 68-6 and MMCh-PV 68-7.

5.2. Postcranial remains

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

THEROPODA Marsh, 1881

CERATOSAURIA Marsh, 1884

ABELISAUROIDEA Bonaparte, 1991

Abelisauroidea indet.

396 *Figure 9*

397 *Material:* MMCh-PV 67, an almost complete axis, with part of the right half and
398 theodontoid process missing.

399 *Description:* In lateral view, the centrum shows a relatively small, rounded pneumatic
400 foramen, partially covered by the pendant diapophysis (Fig. 9A, D). Part of the posterior
401 articular facet shows that the centrum was strongly opisthocoelus. The neural spine is
402 transversely thin, anteroposteriorly extended and dorsally arched. It does not show any
403 dorsal or posterior expansion (Fig. 9B, E). The prezygapophyses are relatively
404 small, dorsolaterally faced and with an elliptical contour (Fig. 9A, D, C, F). The
405 diapophyses and postzygapophyses are connected by strong postzygodiapophyseal
406 laminae (Fig. 9A, D). The spinopostzygapophyseal lamina display an anteriorly concave
407 profile in lateral view. Pronounced and pointed epipophyses are located over the
408 postzygapophyses, surpassing them well posteriorly. They are extremely developed,
409 being as long as the postzygapophyseal facets (Fig. 9A, D). The postzygapophyses are
410 wide and have a kidney-shaped contour. In dorsal view, the axis is subtriangular, with
411 the epipophyses surpassing posteriorly the posterior end of the neural spine. In posterior
412 view and covering the posterior aspect of the neural arch, a large postspinal fossa can be
413 observed, which is subdivided by a strong, vertically oriented interspinous ligament
414 ridge (Fig. 9B, E).

415 *Remarks:* The axis possesses a combination of characters only present in abelisauroid
416 ceratosaurs, such as the invaginated spinopostzygapophyseal lamina (cited as a
417 synapomorphy of Abelisauroida by Carrano et al., 2012); the pneumatic foramen in the
418 centrum; the extremely developed, projected and pointed epipophyses; the lack of
419 ventral keel; and the anteroposteriorly long, transversely compressed neural spine, with a

gently convex and unexpanded dorsal margin(Rauhut, 2003; Carrano and Sampson; 2008;Carrano et al., 2012).

Its general morphology closely resembles that of *Carnotaurus* (Mendez, 2014) and *Masiakasaurus* (Carrano et al., 2011), but with a few differences. For instance in MMCh-PV 67 and *Masiakasaurus*, the epipophyses surpass widely the posterior limit of the neural spine, while in *Carnotaurus* they are at the same level. Moreover, the epipophyses in MMCh-PV 67 are much more developed than in *Carnotaurus* and *Masiakasaurus*, being as long as the postzygapophyseal articular facet. Nevertheless, these differences are not sufficient to refer the axis to Noosauridae or Abelisauridae, and because of this we opt to refer it to Abelisauroida.

We performed an estimation of body length for the specimen MMCh-PV 67 using the method proposed by Grillo and Delcourt (2016), which is based on the dimensions of the axis centrum (length: 30 mm, width: 17.5 mm, height: 24.2 mm). The resulting values of body length for MMCh-PV 67 is 2.1 m calculated from the axis centrum length; 2.3 m from the centrum width and 3.5 m from the centrum height.

Abelisauroida? indet.

Figure 10

Material: Two isolated caudal centra; one from the mid-posterior region of the tail(MMCh-PV 76), and the other from the posterior region (MMCh-PV77). Both of them lack the neural arch entirely.

*Description:*Both centra show some deformation. The bases of the neural arches are broken, probably during the biostratinomical post-mortem transportation.

Both centra are anteroposteriorly elongated, almost three times longer than the height of the central sector (Fig. 10A, B), as is usual in mid-posterior caudal vertebrae of Theropoda. MMCh-PV 76 has both ends expanded in lateral and ventral views (Fig. 10A, C), while they are far less expanded in MMCh-PV 77 (Fig. 10B, D). Both vertebrae show long and shallow lateral fossae on the lateral faces of the centra (Fig. 10A, B). The articular surfaces are taller than wide (Fig. 10E, F).

Remarks: The neural canals of both centra are not inflated like in crocodilians (Lio et al., 2012), but are laterally narrow like in theropod dinosaurs. The articular surfaces are also slightly amphicoelus, differing from the biconvex condition seen in distal caudals of most Neosauropoda (Wilson et al., 1999; Cau and Maganuco, 2009).

We are unable to find synapomorphies which allow to provide a more precise taxonomic identification of these specimens than Theropoda, but we observe that articular surfaces that are taller than wide is a condition seen in several ceratosaurs like *Ceratosaurus* (Madsen & Welles, 2000), *Majungasaurus* (O'Connor, 2007) and *Masiakasaurus* (Carrano et al., 2011), while in tetanurans like *Allosaurus* (UMNH VP 8574) and *Tyrannosaurus* (Brochu, 2003) the articular surfaces are rounded or wider than tall. Given this similarity in the articular surface morphology, and given the facts that both centra were found close to the axis (the three elements were collected in a surface area of less than one square meter) and match in size with the axis, we suggest that they probably pertain to the same taxon, if not the same specimen.

ABELISAUROIDAE Bonaparte & Novas, 1985

Abelisauridae indet.

Figure 11

469 *Material:* MMCh-PV 66, a proximal half of a left tibia lacking the distal end of the
470 cnemial crest.

471 *Description:* In proximal view, the tibia has a triangular outline, longer
472 anteroposteriorly than lateromedially wide in the condylar sector, with the lateral
473 condyle continuous with the cnemial crest (Fig. 11A, F). Both condyles are slightly
474 eroded, yet the medial condyle is more posteriorly projected than the lateral one. In
475 lateral view, although the complete morphology and outline of the cnemial crest is
476 unknown, based on the preserved portion (which is as tall as anteroposteriorly long) we
477 can infer that it was well-developed and anterodorsally projected (Fig. 11C, H). The
478 fibular crest is thin and continues proximally to bifurcate in two branches: a very low
479 ridge which continues toward the proximal articular end and a strong and rounded ridge
480 that curves anteriorly and runs along the dorsal border of the cnemial crest (Fig. 11C,
481 H). Anteriorly to the fibular crest and occupying the ventral part of the cnemial crest a
482 deep and well-developed lateral fossa can be seen. It is dorsally limited by the anterior
483 branch of the fibular crest. The medial surface of the proximal end is covered by a wide
484 fossa (Fig. 11D, I), referred to as the “cranial tibial incisure” by Smith et al. (2010). The
485 tibial shaft is subcircular in cross-section.

486
487 *Remarks:* MMCh-PV 66 lacks the *incisura tibialis*, i.e., a rounded lateral embayment
488 observable in proximal view, which separates the cnemial crest and the lateral condyle
489 in tetanurans (Rauhut, 2003). It is referred to Ceratosauria by the hypertrophied cnemial
490 crest, the lateral fossa, and the fibular crest reaching the proximal end (Carrano et al.,
491 2002; Rauhut, 2003; Sereno et al., 2004; Rauhut, 2005a). It can be referred to
492 Abelisauroidae (Abelisauridae + Noasauridae) due to the low and laterally projected
493 fibular crest as in *Masiakasaurus* (Carrano et al., 2002), *Skorpiovenator* (MMCh-PV

48), *Aucasaurus* (MCF-PVPH 236) and *Quilmesaurus* (MPCA-PV 100), while in basal ceratosaurs like *Ceratosaurus* (UNSM 4735), *Elaphrosaurus* (Rauhut and Carrano, 2016) and even *Eoabelisaurus* (MPEF-PV 3990) this crest is more developed, forming an anterolaterally projected “lip”. Among abelisauroids, MMCh-PV 66 can be referred to Abelisauridae by the presence of a fibular crest curving anteriorly and runs along the dorsal margin of the cnemial crest, a feature absent in noasaurids like *Masiakasaurus* (Carrano et al., 2002) and *Velocisaurus* (Brisson Egli et al., 2016). This agrees with the large size of the specimen, which is more commonly observed in abelisaurids than noasaurids.

Using the method proposed by Grillo and Delcourt (2016), we estimated the body length of specimen MMCh-PV 66 using bivariate equations with two measurements of the tibial shaft (anteroposterior diameter: 84 mm, lateromedial width: 70 mm). This approach suggested a body length of 7.6 m based on anteroposterior diameter of the shaft, and 5.6 m based on the shaft width (probably an underestimated value, given some lateral crushing of the tibial shaft). This suggests that MMCh-PV 66 was an abelisaurid of large body size, like *Skorpiovenator* (estimated body length 6 m; Canale et al., 2009) or *Ekrixinatosaurus* (estimated body length 7.4 m, Grillo and Delcourt, 2016).

6. DISCUSSION.

The Early Cretaceous faunas of South America were thought to be characterized by relics of widespread global Jurassic faunas (Apesteguía, 2002), with some degree of austral endemism, and local peculiarities or adaptations. These faunas were later called by Leanza et al (2004) ‘Late Pangean’, implying that their components were members

of clades that had been distributed across Pangea during the Jurassic (e.g., basal neosauropods; basal avetheropods; basal ceratosaurians; eurypodans, and purported basal iguanodontians). In this context, coelurosaurs and abelisauroids were thought of as small-bodied and not abundant members of environments dominated by large basal tetanurans.

The theropod assemblage from Bajada Colorado site described here improves our knowledge of the poorly known faunal assemblages of the earliest Cretaceous in the Southern Hemisphere. It includes a small abelisauroid ceratosaurian of about 2.5 m of body length (represented by an axis and probably two caudal centra), a mid- to large-sized abelisauroid of about 6.5 m of body length (represented by a proximal end of a left tibia), and a mid- to large-sized basal tetanuran classified with a good degree of certainty as a megalosaurid (represented by at least two isolated teeth), plus several teeth referred to three different morphotypes assigned to Theropoda indet.

It seems improbable that the small abelisauroid could represent a juvenile individual of the large one, given that the axis shows a complete fusion between neural arch and centrum, and both caudal centra show the bases of their neural arches were broken not unfused.

Previously, Gondwanan Megalosauridae were known only from the Middle and Late Jurassic of Africa (Sereno et al., 1994; Rauhut and Lopez Arbrellero, 2009; Carrano et al., 2012; Serrano Martínez et al., 2016). This way, if the classification of the Bajada Colorado specimen is correct, then they represent the first record of a megalosaurid for South America, and the youngest record worldwide. This hypothesis is supported by the presence of the diplodocid sauropod *Leinkupal laticauda* (Gallina et al., 2014a), also recovered from the Bajada Colorado Formation, as the two clades constitute the first

record of their families for South America; and they both represent the youngest record at family level worldwide.

The dinosaur faunal diversity known hitherto at the Lower Cretaceous (Berriasian-Valanginian) of the Bajada Colorada Formation shows similarities with that recorded in the Middle and Upper Jurassic units of Africa, Portugal and central Patagonia.

In Africa, several units show faunal similarities with the Bajada Colorada Formation. The Tiouarén Formation in Niger was the focus of an intense debate about its age. It was regarded as Lower Cretaceous by several authors (Aptian-Albian, Moody and Sutcliffe, 1991; Hauterivian-Barremian, Sereno et al., 1994), and Middle Jurassic by others (Rauhut and López-Arbarelo, 2009). The Tiouarén and Bajada Colorada share the presence of megalosaurids, e.g. *Afrovenator* (Sereno et al., 1994), and in a more general, of Ceratosauria, e.g. the basal ceratosaur or abelisauroid *Spinostropheus* (Sereno et al., 2004; Carrano and Sampson, 2008). The Tendaguru Formation of Tanzania (Oxfordian-Tithonian) shows a quite diverse dinosaur faunal assemblage, which shares with the Bajada Colorada Formation the presence of possible abelisaurids, small abelisauroids, and megalosauroid theropods (Rauhut, 2005a, 2011), as well as diplodocid and dicraeosaurid sauropods (Upchurch et al., 2004; Remes, 2007). Two other geological units from Africa, from the Early Cretaceous: the Cabao and Kirkwood formations, shows fewer similarities with the Bajada Colorada Fm. The Cabao Formation in NW Libya (Hauterivian-Barremian or Berriasian-Valanginian) has yielded a faunal diversity which includes an abelisaurid, a spinosaurid megalosauroid and a large sauropod with spatulate teeth (Le Loeuff et al., 2010). The Kirkwood Formation of South Africa (Berriasian-Valanginian, Algoa Group) only shares the presence of possible diplodocids with the Bajada Colorada (de Klerk et al., 1997), while

theropods are represented by the basal ornithomimosaur *Nqwebasaurus* (de Klerk et al., 2000; Choiniere et al., 2012), and an isolated proximal end of a femur belonging to a basal tetanuran (Forster et al., 2009).

In Portugal, the Lourinhã Formation (Upper Jurassic, Kimmeridgian-Tithonian) shows a diverse dinosaur fauna, that shares with the Bajada Colorada Fm. the presence of megalosaurid and abelisaurid theropods, as well as diplodocid sauropods (Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mannion et al., 2012; Hendrickx and Mateus, 2014a, b). Furthermore, this unit also bears stegosaurs, whose dermal plates were already noticed in the Bajada Colorada Formation (Apesteguía et al., 2015).

In Central Patagonia, the Middle Jurassic Cañadón Asfalto Formation (Aalenian-Bajocian) shares with Bajada Colorada the presence of dicreosaurids (*Brachytrachelopan*, Rauhut et al., 2005), diplodocids (*Diplodocidae* indet. Rauhut, 2015), megalosauroids (the piatnitzkysaurids *Piatnitzkysaurus* Bonaparte, 1986 and *Condorraptor* Rauhut, 2005b), and the ceratosaurian *Eoabelisaurus*; considered either as an abelisaurid (Pol and Rauhut, 2012; Rauhut and Carrano, 2016), or a basal ceratosaurian (Novas et al., 2013; Tortosa et al., 2014).

The new fossil specimens from the Bajada Colorada add new evidence supporting the hypothesis of geographically selective extinction in sauropod and theropod dinosaurs through the Jurassic-Cretaceous boundary (Tennant et al., 2016) given that, unlike Euamerican taxa, the southwest Gondwanan saurischian faunas apparently remained unaffected.

The presence of abelisaurids in the earliest Cretaceous of Gondwana was expected, given that recent phylogenies indicate Abelisauridae and Noasauridae diverged no later than Middle Jurassic (Pol and Rauhut, 2012; Rauhut and Carrano, 2016). However, the abelisaurid tibia reveals that members of this ceratosaur clade were

present in the west of Gondwanaterrestrial ecosystemsand already large-bodied by the earliest Cretaceous.Further, the new material shows that these abelisaurids shared their habitat with several large theropod groups, which successively became extinct in their respective ecosystems (i.e.: basal megalosauroids, carcharodontosaurids, spinosaurids, megaraptorans) while abelisaurids endured until the end of the Cretaceous.

7. CONCLUSIONS

We present the first Early Cretaceous (Berriasian-Valanginian) theropod faunal assemblage from South America, collected fromthe Bajada Colorada Formation of Neuquén, Patagonia, Argentina. The assemblage is composed ofa small-sized abelisauroid ceratosaurian, a mid- to large-sized abelisaurid, and a mid- to large-sized megalosaurid tetanuran, plus several teeth referred to three different morphotypes assigned to Theropoda indet. If our classifications arecorrect;then the megalosaurid teeth recoveredfrom Bajada Colorada represents the first record of the group in South America, and the youngest record of the clade Megalosauridae worldwide.The dinosaur faunal assemblage of Bajada Colorada, which also includes records of diplodocid and dicraeosaurid sauropods, shows similarities with Middle and Late Jurassic faunas of Central Patagonia, Iberia and some localities in Africa, mainly the Tendaguru beds of Tanzania. The available evidencesuggests that no significant dinosaur faunal turnover took place at the Jurassic-Cretaceous event, at least in southern South America.

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FIGURE CAPTIONS

Figure 1: Location of the Bajada Colorada fossiliferous quarry (indicated by a white
star).

FIGURE NOT IN COLOR IN PRINTED VERSION

Table 1: Measurements of Bajada Colorada theropod teeth, used in the multivariate analyses (in millimeters).

Figure 2: Dental morphospace for theropod dinosaurs based on the principal component analysis of eleven dental measurements. Bivariate plot showing PC1 and PC2, which account for 65.708 and 17.492 % of total variance, respectively. For interpretation references to colour in this figure, the reader is referred to the web version of this article.

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Figure 3: Theropod tooth morphotype 1: Theropoda indet. MMCh-PV 68-5. A: lingual view. B: distal view. C: labial view. D: mesial view. E: basal view. F: mesiolingual view; detail of the lingually twisted mesial carina (indicated by a white arrow).

FIGURE NOT IN COLOR IN PRINTED VERSION

Figure 4: Theropod tooth morphotype 2: Theropoda indet. MMCh-PV 68-9. A: lingual view. B: distal view. C: labial view. D: mesial view. E: SEM image with detail of the mesiodistal denticles. F: basal view.

FIGURE NOT IN COLOR IN PRINTED VERSION

Figure 5: Theropod tooth morphotype 3: Theropoda indet. MMCh-PV 68-2. A: lingual view. B: distal view. C: labial view. D: mesial view. E: SEM image with detail of the mesiodistal denticles. F: basal view.

913 FIGURE NOT IN COLOR IN PRINTED VERSION

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915 Figure 6: Theropod tooth morphotype 4: Megalosauridae indet. MMCh-PV 68-6. A:

916 labial view. B: distal view. C: lingual view. D: mesial view. E: basal view.

917 FIGURE NOT IN COLOR IN PRINTED VERSION

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919 Figure 7: Theropod tooth morphotype 4: Megalosauridae indet. MMCh-PV 68-7. A:

920 labial view. B: distal view. C: lingual view. D: mesial view. E: SEM image with detail

921 of the mesiodistal denticles. F: basal view.

922 FIGURE NOT IN COLOR IN PRINTED VERSION

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924 Figure 8: Strict consensus of 39 most parsimonious trees showing the position of the

925 specimens MCh-PV 68-6 and MMCh-PV 68-7; nested in the clade Megalosauridae.

926

927 Figure 9: Abelisauroides indet. Axis MMCh-PV 67. A, D: leftlateral view. B, E:

928 posterior view. C, F: anterior view. Abbreviations: dia, diapophysis; ep, epipophysis;

929 lr, ligament ridge; nc, neural canal; ns, neural spine; pf, pneumatic foramen; podl,

930 postzygodiapophyseal lamina; poz, postzygapophysis; prz, prezygapophysis; spol,

931 spinopostzygapophyseal lamina.

932 FIGURE NOT IN COLOR IN PRINTED VERSION

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934 Figure 10: Abelisauroides? indet. MMCh-PV 76 mid-posterior caudal vertebral

935 centrum(A, C, E); MMCh-PV 77 posterior caudal vertebral centrum (B, D, F). A, B:

936 lateral view. C, D: ventral view. E, F: articular view.

937 FIGURE NOT IN COLOR IN PRINTED VERSION

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939 Figure 11: Abelisauridae indet. Tibia MMCh-PV 66. A, F: proximal view. B, G:
940 anterior view. C, H: lateral view. D, I: medial view. E, J: posterior view. Abbreviations:
941 abfc, anterior branch of fibular crest; cc, cnemial crest; f, fossa; fc, fibular crest; lc,
942 lateral condyle; lf, lateral fossa; mc, medial crest.

943 FIGURE NOT IN COLOR IN PRINTED VERSION

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Figure 11

Table 1: Measurements of Bajada Colorada theropod teeth, used in the multivariate analyses (in millimeters).

Collection number	Morphotype	Assignment	CBL	CBW	CH	AL	CBR	CHR	MCL	MCW	MCR	MC	DC
MMCh-PV 68-1	Morphotype 4?	Megalosauridae?	14.4	7.32	-	-	0.5	-	13.1	6.33	0.48	-	18
MMCh-PV 68-2	Morphotype 3	Theropoda	7.25	4.6	12.05	13.26	0.63	1.66	6.17	3.46	0.56	-	20
MMCh-PV 68-3	Morphotype 3	Theropoda	6.75	3.35	9.1	12.4	0.49	1.34	6.06	2.6	0.42	-	20
MMCh-PV 68-4	Morphotype 4?	Megalosauridae?	10.88	5.87	-	-	0.53	-	8.81	5.31	0.6	-	18
MMCh-PV 68-5	Morphotype 1	Theropoda	9.1	4.49	17.55	18.55	0.49	1.92	7.91	3.71	0.46	-	16
MMCh-PV 68-6	Morphotype 4	Megalosauridae	16.27	7.8	35.9	38.62	0.48	2.2	13.3	6.33	0.47	-	18
MMCh-PV 68-7	Morphotype 4	Megalosauridae	15.33	6.93	37.05	39.1	0.45	2.41	12.2	5.89	0.48	-	18
MMCh-PV 68-8	Morphotype 1?	Theropoda	8.5	3.8	15.6	20.8	0.44	1.83	7.2	3.3	0.45	-	19
MMCh-PV 68-9	Morphotype 2	Theropoda	6.9	2.7	9.9	12.5	0.39	1.43	6.2	2.7	0.43	19	17
MMCh-PV 68-10	Morphotype 1	Theropoda	7.4	3.92	13.2	15.5	0.47	1.78	5.7	2.7	0.47	20	16