Cretaceous Research 61 (2016) 209–219

Contents lists available at ScienceDirect

Cretaceous Research

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

A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisaurids

Leonardo S. Filippi [a], [*], Ariel H. Méndez [b], Rubén D. Juárez Valieri [c], Alberto C. Garrido [d]

[a] Museo Municipal Argentino Urquiza, Jujuy y Chaco s/n, 8319, Rincón de los Sauces, Neuquén, Argentina
[b] CONICET, Instituto de Investigación en Paleobiología y Geología (CONICET-UNRN), Av. Roca 1242, 8332, General Roca, Río Negro, Argentina
[c] Secretaría de Cultura de la Provincia de Río Negro, 8332, General Roca, Río Negro, Argentina
[d] Museo Provincial de Ciencias Naturales Prof. Dr. Juan Olsacher, Dirección Provincial de Minería, Etcheluz y Ejército Argentino, 8340, Zapala, Neuquén, Argentina

ARTICLE INFO

Article history:
Received 15 September 2015
Received in revised form
26 December 2015
Accepted in revised form 28 December 2015
Available online xxx

Keywords:
Abelisauridae
Brachyrostra
Furileusaira
Bajo de la Carpa
Upper Cretaceous
Neuquén Basin

ABSTRACT

A well preserved skeleton of a new abelisaurid is reported here. The holotype of *Viavenator exxoni* was found in the outcrops of the Bajo de la Carpa Formation (Santonian, Upper Cretaceous), northwestern Patagonia, Argentina. This new taxon belongs to the South American clade of abelisaurids, the brachyrostrans. The current phylogenetic analysis places it as the basalmost member of a new clade of derived brachyrostrans, named Furileusauria, characterized by distinctive cranial, axial and appendicular anatomical features. The Santonian age of *Viavenator* allows filling the stratigraphic gap exhibited between the basal brachyrostrans of Cenomanian–Turonian age, and the derived forms from the Campanian-Maastrichtian. The evolution of abelisaurids during the Late Cretaceous, faunal replacements, and the adaptive radiation that occurred during that period of time in South America are discussed.

1. Introduction

Abelisaurid theropods comprised a clade of medium to big sized theropods broadly represented in most of the Gondwanan and southern European landmasses during the Cretaceous period (Carrano and Sampson, 2008; Farke and Sertich, 2013; Gianechini et al., 2015; Novas et al., 2013, 2004; Sereno and Brusatte, 2008; Smith et al., 2010; Tortosa et al., 2014). This clade is included among the Abelisauroidea, and together with other ceratosaurians comprises a lineage that splitted of the tetanuran averostrans during the Early Jurassic. Confident abelisaurid record comes from the Aptian-Albian (Rauhut et al., 2003; Sereno and Brusatte, 2008), although the phylogenetic placement of several taxa as *Eoabelisaurus*, *Ligabueino* or *Genusaurs* could suggest an earlier split of this clade (see phylogenetic results).

Among other anatomical peculiarities, this clade is characterized by axial stiffness, evidenced in the highly developed of structures as epipophyseal processes in the cervicals, hyposphene–hypantrum structures in the dorsals, fused sacral complex, and distal tip of caudal transverse processes. In this work we present a new, beautifully preserved abelisaurid skeleton representing a new taxon, *Viavenator exxoni* gen. et sp. nov., from the Santonian of Patagonia, Argentina. This new taxon exhibits axial features with a higher degree of development than in other abelisaurids, plus previously unrecognized structures. *Viavenator* fills an extensive hiatus among the South American abelisaurid lineage, the brachyrostrans, as phylogenetic analysis found it as a transitional form between their primitive members of Cenomanian-early Turonian age and the highly derived forms from the Campanian-Maastrichtian, and clarified the relationships within the group, recognizing a late radiation of post-Cenomanian brachyrostrans.

2. Materials and methods

2.1. Anatomical abbreviations

a, acromion; **ape**, anterior projection of epipophysis; **aptp**, anterior projection of transverse process; **ati**, atlantal intercentrum; **bpt**, basipterygoid process; **bt**, basal tuber; **cdl**, centrodiapophyseal lamina; **cf**, coracoid foramen; **dex**, distal

---

[*] Corresponding author.
E-mail address: lsfilippi@gmail.com (L.S. Filippi).

http://dx.doi.org/10.1016/j.cretres.2015.12.018
0195-6671/© 2016 Elsevier Ltd. All rights reserved.

expansion of chevron; **dp**, diapophysis; **ep**, epipophyses; **F**, frontal; **gc**, glenoid cavity; **hc**, haemal canal; **hp**, hyposphene; **hy**, hypantrum; **iaas**, interspinous accessory articulation system; **ipof**, infrapostzygapophyseal fossa; **lpf**, laminopeduncular foramen; **n**, neurapophyses; **nc**, neural canal; **ns**, neural spine; **oc**, occipital condyle; **oca**, occipital condyle articulation; **oa**, odontoid articulation; **P**, parietal; **pcdl**, posterior centrodiapophyseal lamina; **pe**, parietal eminence; **pf**, pneumatic foramen; **Po**, postorbital; **po**, postzygapophysis; **pop**, paraoccipital process; **posf**, postspinal fossa; **pp**, parapophysis; **pr**, prezygapophysis; **prel**, prezygoepopiphyseal lamina; **pvp**, posteroventral process; **S**, squamosal; **sot**, supraoccipital tuberosity; **stf**, supratemporal fenestra; **vp**, ventral processes.

2.2. Institutional abbreviations

MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MAU**, Museo Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén, Argentina; **MCF**, Museo Municipal “Carmen Funes”, Plaza Huincul, Neuquén, Argentina; **UNPSJB**, Universidad Nacional de la Patagonia “San Juan Bosco”, Comodoro Rivadavia, Chubut, Argentina.

3. Systematic paleontology

Theropoda Marsh, 1881
Ceratosauria Marsh, 1884
Abelisauridae Bonaparte & Novas, 1985
Brachyrostra Canale et al., 2009
Furileusauria clade nov.

Derivation of name. From Mapudungun language ‘*Furileu*’ stiff back, and Greek language ‘*sauria*’ lizard, in reference to the extreme level of stiffness in their axial skeletons.

Definition. The most inclusive clade containing to *Carnotaurus sastrei* but not *Ilokelesia aguadagrandensis, Skorpiovenator bustingoryi or Majungasaurus crenatissimus*.

Diagnosis. Furileusauria differs from all other brachyrostrans and other abelisaurids in the **(1)** presence of a tip in the middle area of the posterior surface of the ventral process of the postorbital, **(2)** presence of a knob followed by a deep notch in the postorbital-squamosal contact, **(3)** absence of fenestra between the frontal, postorbital and lacrimal, **(4)** anterior projection of the distal end of cervical epiphophyses, **(5)** posterior margin of the postzygapophyses at level with the intervertebral articulation in dorsal vertebrae, **(6)** crescent-shaped morphology of the distal tip of the transverse processes in anterior and middle caudal vertebrae, **(7)** transverse processes of anterior caudal vertebrae distally expanded and only anteriorly projected, **(8)** convex external margin of the transverse processes in the anterior caudals, **(9)** and cnemial crest of the tibia with a downturned process.

Included species. *Viavenator exxoni*, *Carnotaurus sastrei*, *Abelisaurus comahuensis*, *Aucasaurus garridoi*, *Quilmesaurus curriei*, *Pycnonemosaurus nevesi*.

Viavenator exxoni gen. et sp. nov.

Derivation of name. From latin ‘*Via*’ road, and ‘*venator*’ hunter, meaning the hunter of the road, ‘*exxoni*’ is in recognition of Exxonmobil's commitment to the preservation of paleontological heritage of the La Invernada area, Rincón de los Sauces, Neuquén, Patagonia Argentina.

Holotype. MAU-Pv-LI-530. (Figs. 1–8) Partially associated skeleton, integrated by neurocranium complete articulated to postorbitals and squamosals, hyoid bone, incomplete tooth and fragment of crown, atlas, 3rd, 4th, 5th, 7th to 10th cervical vertebrae, 2nd, 4th, 5th and 7th to 10th dorsal vertebrae, five anterior caudal vertebrae, five middle caudal vertebrae, one distal caudal vertebrae and a most distal caudal vertebrae, left scapulacoracoid, ischium foot, cervical and dorsal ribs, fragments of gastralia, and one haemal arch.

Diagnosis. The new taxon is characterized for the following autapomorphies (*) and characters combination: **(1)** absence of dorsal single or paired prominences in frontals; **(2)** dorsal edge of postorbital do not expanded with the jugal process anteriorly projected and anteroposteriorly narrow; **(3*)** parietal depression transversally compressed, on both sides of the supraoccipital crest; **(4*)** small paraoccipital processes with ventral edge located above the level of the dorsal edge of the occipital condyle; **(5*)** basioccipital – opisthotic complex, about two and a half times the width of the occipital condyle and almost twice the height of the occipital condyle in posterior view; **(6*)** high and well developed crest below the occipital condyle, diverging laterally toward the basal tubercles, defining the ventral subcondylar recess; **(7*)** basisphenoidal recess highly developed and deeply excavated, whose sub-circular contour opening ventrally oriented has a well-defined borders, with its major axis transversely positioned; **(8*)** basipterygoid processes, positioning horizontally the cranial roof, located on a level slightly upper to basal tubers; **(9)** anterior surface of cervical vertebrae with poorly developed articular condyle; **(10)** anterior projection of epipophysis in cervicals, which are well developed between the 4th and 7th element; **(11*)** mid and posterior cervicals centra with slightly convex lateral and ventral surfaces; **(12*)** hyposphene-hypanthrum articulation present from dorsal 2; **(13*)** interspinous accessory articulation system developed in middle and posterior dorsal vertebrae; **(14*)** presence of a pair of pneumatic foramina within the prespinal fossa in anterior caudal vertebrae; **(15)** anterior and mid caudal vertebrae with distal edge of the transverse process convex, and strong development of an anterior projection; **(16*)** distal end of the scapular blade posteriorly recurved.

Type locality. La Invernada area (Fig. 1), located 50 km southwest from the Rincón de los Sauces city, Neuquén province, Patagonia, Argentina.

Stratigraphic horizon. Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group of the Neuquén basin. Santonian, Upper Cretaceous. The continental deposits of this lithostratigraphic unit have provided scant evidence relative to theropod dinosaurs. Small-sized forms include the noasaurid *Velocisaurus unicus* and the alvarezsaurids *Alvarezsaurus calvoi* and *Achillesaurus manazzonnei* (Bonaparte, 1991a; Martinelli and Vera, 2007). Mid and big sized theropods include a tetanuran possibly related to Carcharodontosauridae or Megaraptora (Porfiri et al., 2008) and indeterminate abelisaurid materials previously referred as Carnotaurines (Ezcurra and Méndez, 2009; Porfiri and Calvo, 2006), some of these found in the La Invernada area (see below).

4. Anatomic description

4.1. Skull

Cranial elements of this specimen include the complete neurocranium (Fig. 2), composed by: frontals, parietals, sphenethmoids, orbitosphenoids, laterosphenoids, prootics, opisthotics, supraoccipital, exoccipitals, basioccipital, parasphenoids and basisphenoids, which are interconnected with other cranial elements: both postorbitals and squamosals. In addition, the specimen has preserved the interorbital septum. Frontals are practically flat in *Viavenator*, similar to the present in *Ekrixinatosaurus* and *Arcovenator* (Juárez-Valieri et al., 2011b; Tortosa et al., 2014), and unlike of

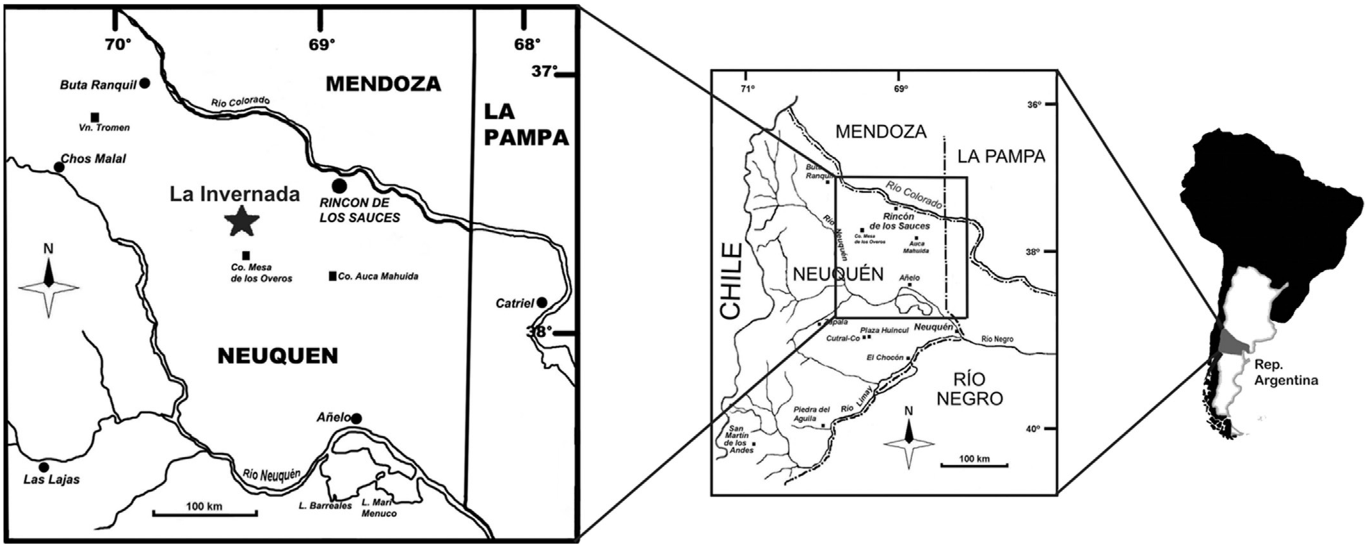

Fig. 1. Map of La Invernada fossil site.

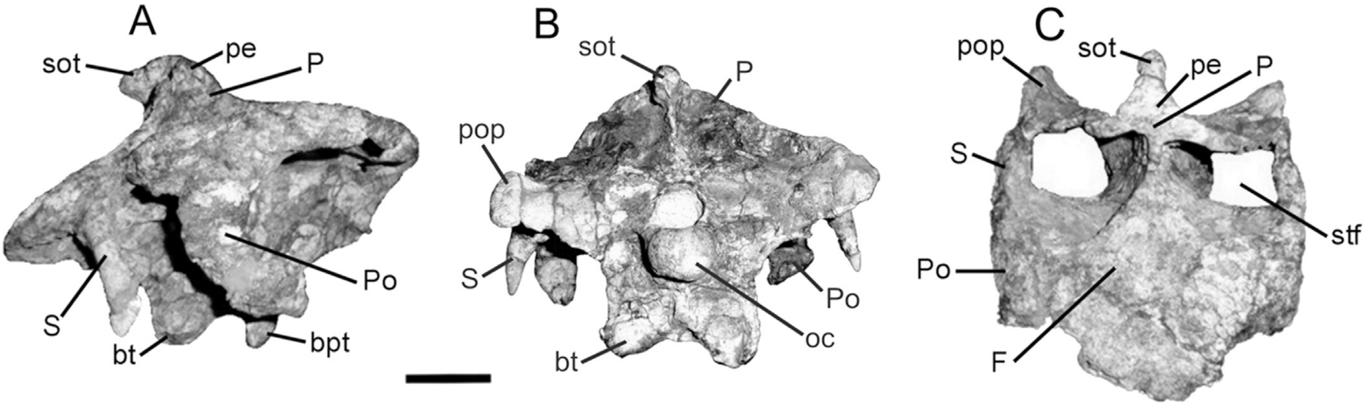

Fig. 2. Skull of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), right lateral, (B) posterior and (C) dorsal views. Scale bar: 10 cm.

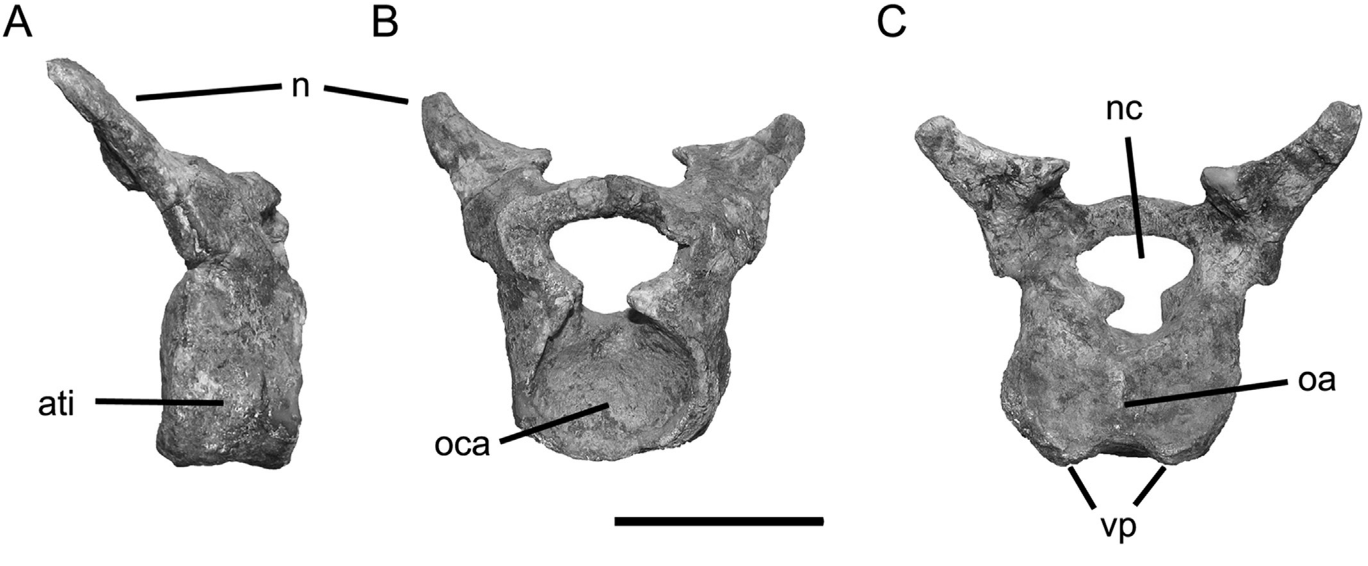

Fig. 3. Atlas of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. in (A), right lateral, (B), anterior, (C), posterior views. Scale bar: 5 cm.

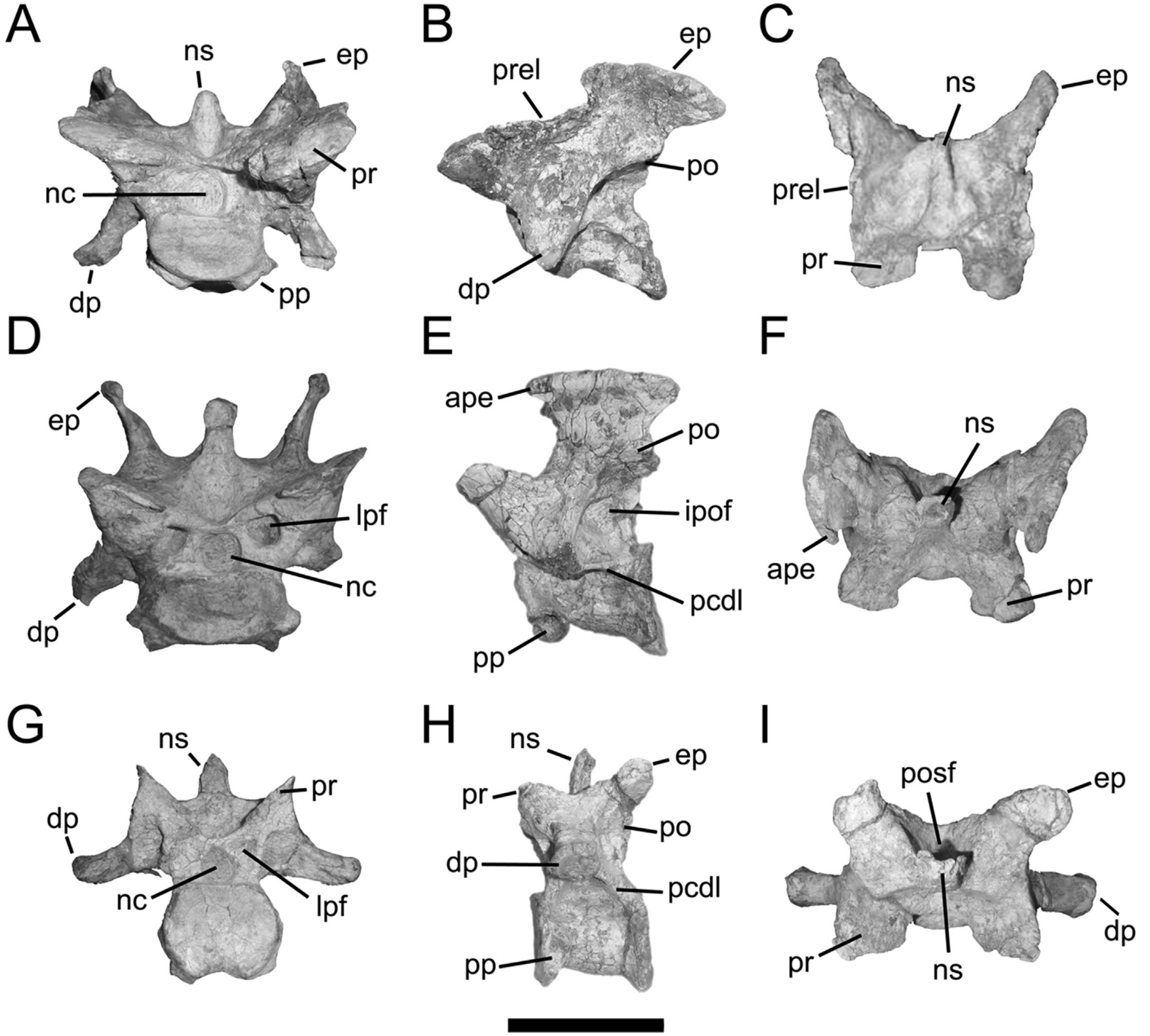

Fig. 4. Cervical vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A, B, C), fourth, (D, E, F), seventh, (G, H, I), tenth, in anterior, left lateral and dorsal views, respectively. Scale bar: 10 cm.

that of *Abelisaurus* and *Aucasaurus* in which frontals are elevated, developing characteristic orbital bulges (Paulina-Carabajal, 2011a), which appear to be homologous structures to the horns present in *Carnotaurus*. *Viavenator* also differs of forms as *Majungasaurus* and *Rajasaurus*, which exhibits a single medial projection (Sampson and Witmer, 2007; Wilson et al., 2003). We are in accord with previous authors (Novas, 1997; Novas, et al., 2004) that these two kinds of ornametal structures are not homologous. *Viavenator* lacks the plesiomorphic fenestra placed between the frontal, postorbital, and lacrimal present in *Rugops*, *Ekrixinatosaurus*, and the majungasaurines (Juárez-Valieri et al., 2011b; Sampson and Witmer, 2007; Sereno et al., 2004; Tortosa et al., 2014), but absent in the most derived furileusaurians *Abelisaurus*, *Aucasaurus* and *Carnotaurus* (Paulina-Carabajal, 2011a,b). The absence of a fenestra may constitute a possible additional synapomorphy of Furileusauria. As in other abelisaurids such as *Carnotaurus, Abelisaurus, Ekrixinatosaurus* and *Majungasaurus*, lateral and ventral walls of the cavities of the olfactory tracts and olfactory bulbs are ossified (Paulina-Carabajal and Currie, 2012; Paulina-Carabajal, 2011a,b; Sampson and Witmer, 2007). The inteorbital septum in *Viavenator* is ossified, as in other ceratosaurs like *Eoabelisaurus, Carnotaurus, Abelisaurus* and *Majungasaurus* (Pol and Rauhut, 2012). It also exhibits a derived L-shaped postorbital, present in other abelisaurids like *Carnotaurus*, *Majungasaurus* and *Skorpiovenator* (Canale et al., 2009; Tortosa et al., 2014). As *Carnotaurus*, the postorbital (Fig. 2) is proportionately long, with an anteroventral process that defines the bottom of the closing orbit closed to the location where the lacrimal is located. The postorbital has a dorsal border ornate as in most abelisaurs, but differing from the strongly raised border present in *Skorpiovenator, Ekrixinatosaurus novasi* Calvo et al. (2004)

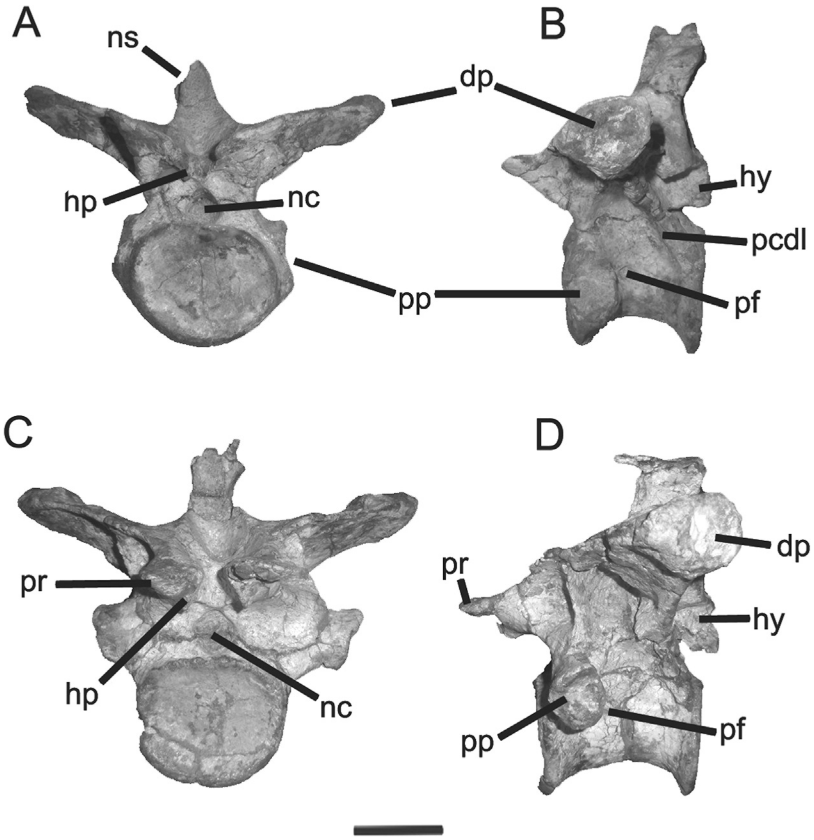

Fig. 5. Dorsal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A, B), second, (C, D), fourth, in anterior and left lateral views, respectively. Scale bar: 10 cm.

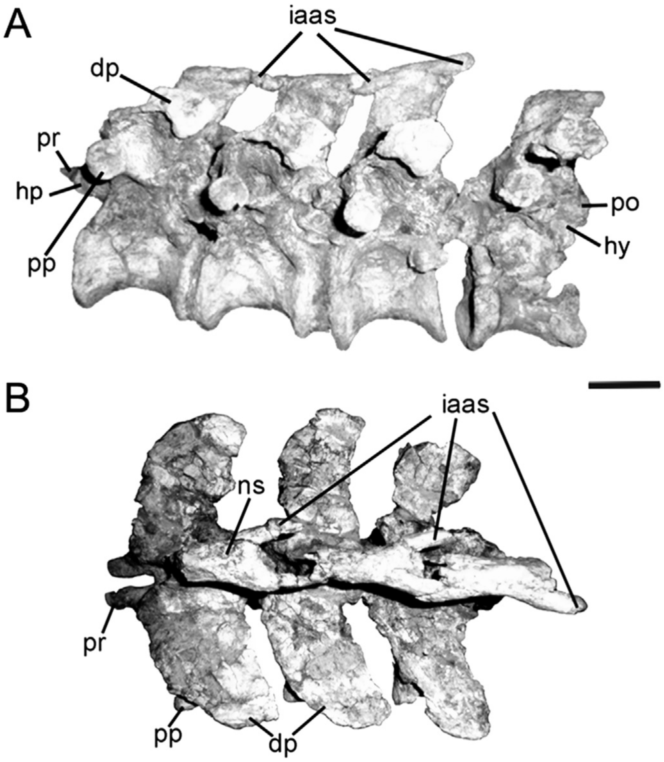

Fig. 6. Dorsal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), seventh to tenth, (B), seventh to ninth, in left lateral and dorsal views, respectively. Scale bar: 10 cm.

and *Arcovenator escotae* Tortosa et al. (2014). Additionally, at the mid-length of the posterior border of the jugal process *Vianenator* exhibits a distinctive kink, as present in *Carnotaurus* and *Abelisaurus*, but absent in the non furileusarian abelisaurids (Juárez Valieri et al., in prep.).

4.2. Axial skeleton

4.2.1. Cervical vertebrae

The atlas of *Viavenator* is complete (Fig. 3), being less robust and shorter than the atlas of *Carnotaurus*. Ventrally, the intercentrum has two small lateral processes separated by a large furrow. The neurapophysis is caudally elongated, similar to the “L” condition presented in other ceratosaurians (Madsen and Welles, 2000; Méndez, 2014a). The anterior cervical vertebrae exhibit low and long vertebral centra, becoming dorsoventrally taller in posterior direction along the sequence (Fig. 4). The inclination of the articular surfaces is remarkable in the anterior half of the series. Cervical epipophyses have an extreme development in both height and surface, which would provide a wider space for the insertion of neck muscles, possibly the *Mm. longus colli dorsalis*, *m. complexus* and *m.cervicalis ascendens*, present in living birds and whose function is linked to dorsiflexion of the neck (Méndez, 2014a) large epipophyses, only comparable with that of *Carnotaurus*. The distal end of the epipophysis exhibits a marked posterior projection, which is reduced toward the base of the neck, and an anterior projection that is present in almost all cervicals, except in the last element (Fig. 2). The neural spines are narrow and reduced in height. The pneumaticity is widespread throughout the cervical series in the form of fossae and pneumatic foramina. The cv5 presents a foramen on the ventral surface of the

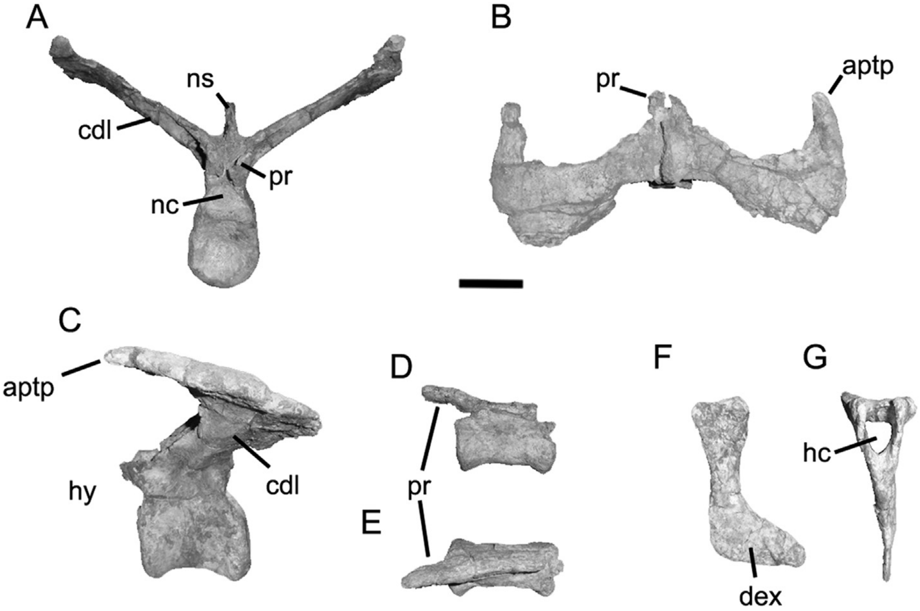

Fig. 7. *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Anterior caudal vertebra in (A) anterior, (B) dorsal, (C) left lateral views. Posterior caudal vertebra in (D) left lateral and (E) dorsal views. Posterior chevron in (F) left lateral and (G) anterior views. Scale bar: 10 cm.

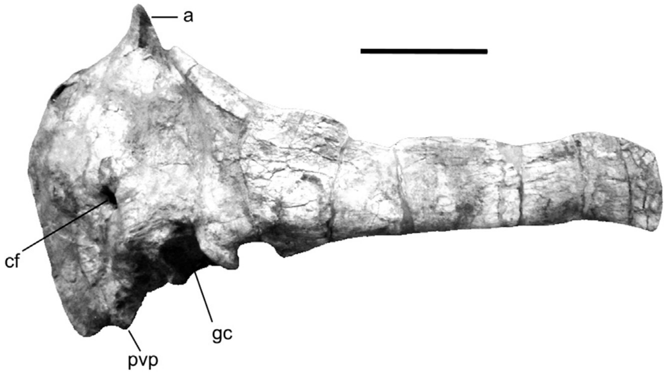

Fig. 8. Scapulocoracoid of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. in lateral view. Scale bar: 10 cm.

vertebral body, a feature that has not been registered in any other theropod.

4.2.2. *Dorsal vertebrae*

These vertebrae exhibit spool-shaped morphology of dorsal centra. Anterior dorsal vertebrae show a shallow groove on the ventral surface (Fig. 5). A pair of pneumatic foramina on the lateral side of centra is present, except in d2 where there is a single foramen. The lamination of the dorsal vertebrae is becoming more complex posteriorly in the series. The accessory hyposphene-hypantrum articulation is very well developed from the second to ten dorsal; the hyposphene present the inverted cone morphology observed in *Carnotaurus* (Méndez, 2010). In d2 and d5, on the dorsal surface of the distal third of diapophysis, remarkable crests are located at the posterior half of the posterior edge of the diapophysis. These structures can be interpreted as muscle attachments marks (e.g., *m. tendinoarticularis* of Crocodylia or *m. ascendens thoracicus* of Aves; Organ 2006) or the attachments of intervertebral ligaments. The neural spine of the dorsal vertebrae has a quadrangular contour and is slightly posteriorly reclined. The neural spine of d2 has wide anterior and posterior surfaces with a bulbous structure. D4 and D5 lack these bulbous structures but at the distal end have forward projections, which are interpreted as part of a system of accessory of interspinous articulations. The dorsal vertebrae 7–10 were found in articulation (Fig. 6), which allows observing a novel feature: an accessory joint system in which the neural spine is linked to the preceding one by a pair of subparallel bony projections that embrace the neural spine of the previous vertebra. Such structures, strongly developed in *Viavenator* are not comparable with those observed in the abelisauroid *Dahalokely* which has short anterior and posterior projections of the distal end of the neural spines in posterior dorsal vertebrae (Farke and Sertich, 2013).

4.2.3. *Caudal vertebrae*

The anterior caudal vertebrae of *Viavenator* (Fig. 7A–C) exhibit slightly amphicoelic, spool-shaped centra, without any traces of pneumaticity, features typical of abelisaurids (Méndez, 2014b). The ventral surface of vertebral bodies has a shallow groove. The neural arch is dominated by hypertrophied transverse processes. Accessory articulation hyposphene-hypantrum is present and well developed. The neural spine is thin and the prespinal fossa exhibits a pair of cavities separated by a septum. The dorsal inclination of the transverse process is of approximately 40 degrees, similar to that observed in other abelisaurids (e.g. *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus*, MACN-RN-1012). The distal tip of the transverse process shows a remarkable expansion with a tapering anteriorly directed process, similar to that observed in *Carnotaurus* and *Aucasaurus* (Fig. 4). A well developed centrodiapophyseal lamina is present on the ventral side of the transverse process. In the distal third of the tranverse processes, in ventral view, a sagittal crest is present as well as in other derived abelisaurids like *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus* and MACN-PVPH-RN 1012 (Ezcurra and Méndez, 2009; Méndez, 2014b). Mid-caudal vertebral centra are amphyplatian, elongated and spool-shaped. They exhibit a shallow groove on the ventral surface. These caudal vertebrae lack the hyposphene-hypantrum. The transverse processes are distally expanded with well developed anterior and posterior projections. Pre- and postzygapophysis are more elongated, and projected beyond the margins of the vertebral body. The two preserved distal caudal vertebrae have elongated centra, and show a polygonal contour, in anterior and posterior views, due to the marked longitudinal ridges separating the lateral surface from the ventral surfaces. The neural arch is low and occupies almost the entire length of the vertebral body. The prezygapophysis is graceful and curved, exceeding the anterior edge of the vertebral body in a third of its length (Fig. 7D and E).

4.3. Scapulocoracoid

The complete left scapulocoracoid (Fig. 8) is the only part of the pectoral girdle of *Viavenator* that was recovered. The scapular blade is relatively shorter and anteroposterior narrower than in *Majungasaurus* (Burch and Carrano, 2012). The distal end of the scapular blade widens slightly in *Ceratosaurus as in Majungasaurus*, while *Carnotaurus* lacks any widening (Burch and Carrano, 2012). By contrast, *Viavenator* presents a marked widening posteroventral, which gives a recurve appearance.

5. Discussions

5.1. Morphofunctional traits

The vertebral column of abelisaurids have a series of anatomical features associated with the restriction of intervertebral movements and the concomitant development of some muscle groups linked with locomotion and cranio-cervical mobility (i.e. hypertrophied cervical epipophyses, hyposphene-hypantrum articulation in posterior dorsals and anterior caudals, sacral fusion, longer and higher transverse processes with expanded distal ends (Méndez, 2014a,b). The members of this new clade, except *Abelisaurus* which is only known by cranial remains (Bonaparte and Novas, 1985), have features much more developed than the more basal abelisaurids (i.e., distal ends of the epipophysis with strong anterior and posterior projections, hyposphene-hypantrum articulation in anterior dorsal vertebrae, distal ends of caudal transverse processes with forward and backward projections).

Viavenator shows further development of posterior projection in epipophyses, presence of hyposphene-hypantrum articulation since the second dorsal vertebra, and a system of accessory joints, not documented before in theropods. These joints, located in posterior dorsal vertebrae, restrict movements between vertebrae linking adjacent elements by bony anterior projections that "embrace" the preceeding neural spine.

This set of axial characters, reflects an increase in the backbone rigidity from the neck to the proximal third of the tail, resulting in that these dinosaurs may act as a sort of seesaw, pivoting on its pelvic girdle.

5.2. Phylogenetic analysis

The present analysis was assembled as an extended and amended version of the dataset performed by Tortosa and colleagues (Tortosa et al., 2014), since such analysis was based on several previous works concerning ceratosaurs (Allain et al., 2007; Canale et al., 2009; Carrano and Sampson, 2008; Ezcurra et al., 2010; Farke and Sertich, 2013; Pol and Rauhut, 2012; Sereno and Brusatte, 2008; Xu et al., 2009), and include previously neglected abelisaurid taxa, as *Arcovenator escotae*, *Tarascosaurus salluvicus*, or MCF-PVPH 237 to the data matrix. We added *Viavenator exxoni* as a new operational taxonomic unit (OTU). *Kryptops palaios* was dissembled into two OTUs, one including the cranial material and the other the postcrania, following previous conclusions about the chimeric nature of the holotype (Carrano et al., 2012; Farke and Sertich, 2013; Novas et al., 2013). The abelisaurids *Xenotarsosaurus bonapartei* and UNPSJB-PV 247 were considered both, as separated and as a single OTU. New characters were included and a number of existing characters were modified. The resulting dataset includes 416 characters, and 41 OTUs (see Supplementary information). Some of the multistate characters were considered as additive. The program used to analyze the data was the software T.N.T. 1.165 (Goloboff et al., 2008). The chosen parameters included the algorithm of Tree bisection reconnection (TBR), with 3000 replications and 100 trees to save per replication. Two runnings were made, the first including all the OTUs, resulting in a best score of 870 steps and 8201 trees retained. The second running was derived from the exclusion of two taxa, *Tarascosaurus salluvicus* and the unnamed Cerro Bayo Mesa taxon (MCF-PVPH 237), and resulted in a best score of 870 steps and 100 trees retained (C.I.: 0.607; RI: 0.740) (The strict consensus of both analysis are illustrated in the Supplementary data).

5.2.1. Results of the phylogenetic analysis

The resulting cladograms of the strict consensus of both analyses are concordant in previous phylogenies that found *Coelophysis* and *Allosaurus* as successive stems of a monophylecic Ceratosauria, and a monophyletic Abelisauroidea comprised by Noasauridae and Abelisauridae, and within the later, Brachyrostra was recovered as a monophyletic clade. *Eoabelisaurus* resulted as the basalmost abelisauroid, which is in accordance to recent analysis (Farke and Sertich, 2013; Tortosa et al., 2014; contra Pol and Rauhut, 2012). *Ligabueino* was found as the sister taxa to the node formed by Noasauridae plus Abelisauridae, a novel but not unexpected placement for the taxon (see Supplementary data for the characters list and codifications). Both the Gadoafaoua taxon, which is the OTU of the postcranium originally referred to *Kryptops* (Sereno and Brusatte, 2008; Carrano et al., 2012) and the Pourcieux taxon (alleged abelisaurid maxilla from France, Buffetaut et al., 1988) are found outside of the clade formed by *Elaphrosaurus*, *Ceratosaurus* and the abelisauroids (i.e., Ceratosauria). This suggests that both specimens belong to Tetanurae, as it has been suggested by previous authors (Carrano and Sampson, 2008; Farke and Sertich, 2013; Novas et al., 2013). A broader dataset sampling multiple ceratosaurians and tetanurans could help to elucidate the precise phylogenetic position of these problematic forms.

With the posterior pruning of two unstable OTUs (i.e., *Tarascosaurus* and the Cerro Bayo Mesa taxon; Le Loeuff and Buffetaut, 1991; Coria et al., 2006) we obtained a cladogram with a higher resolution within the Abelisauridae. We found *Kryptops* and *Rugops* as the basalmost abelisaurids, representing successive sister taxa of a clade including two monophyletic groups, Majungasaurinae and Brachyrostra. Inside the first, two subgroups were obtained, one composed by the Indo-Malagasian taxa *Majungasaurus*, *Rajasaurus* and *Indosaurus*; and the other including the European taxa *Genusaurus*, *Tarascosaurus* and La Boucharde form. This is the first time that a lower level resolution is found in Majungasaurinae. Although sometimes recorded as an Noasauridae (Carrano and Sampson, 2008; Farke and Sertich, 2013), the inclusion of *Genusaurus* within Abelisaridae is new but not unexpected, since it shares derived characters with other European abelisaurids (Tortosa et al., 2014).

The position of *Xenotarsosaurus* as the basalmost brachyrostran is constant both if it is codified based only in the holotype postcranial material or if it also includes referred cranial elements (see above), but is weakly supported by the analysis (see Supplementary data). *Dahalokely* and *Rahiolisaurus* are positioned as the basalmost brachyrostrans. The phylogenetic position of these forms was unstable and previously considered as an uncertain basal noasaurid and an abelisaurid, respectively (i.e. Farke and Sertich, 2013; Tortosa et al., 2014).The remaining brachyrostrans are splitted in two subgroups, one comprised by *Skorpiovenator* and relatives, and the other *Abelisaurus, Carnotaurus* and their kin. The first of these clades includes *Ilokelesia* as the sister taxon of a node comprising *Skorpiovenator* and *Ekrixinatosaurus* in accordance with previous works which found it as monophyletic (Canale et al., 2009; Pol and Rauhut, 2012), contrary to others that found it as successive sister taxa to Furileusauria (Tortosa et al., 2014). The placement of *Abelisaurus* as a close relative of *Carnotaurus* than *Ilokelesia* is in accordance to Tortosa et al. (2014), but it differs of previous results that place it as a basal brachyrostran and sister taxon of *Ilokelesia* (Farke and Sertich, 2013; Gianechini et al., 2015), or even as the sister taxon of the clade linking the majungasaurines and brachyrostrans (Carrano and Sampson, 2008; Canale et al. 2009, Pol and Rauhut, 2012). The Furileusauria is found to be comprised by *Viavenator* as the basalmost taxon, which is the sister taxon of the more derived forms. Finally, *Abelisaurus* and *Aucasaurus* comprise a monophyletic group, and *Carnotaurus* results as the sister taxon of this clade. This arrangement has not been previously reported and implies deep changes in the systematic and biostratigraphic hypotheses (see below).

6. Discussion

6.1. Paleobiogeographic implications

The resulting cladogram has deep palaeobiogeographical implications. The high resolution record of the Abelisauridae allows to sustain more complex scenarios for the history of the group. The exclusion of the Aalenian-Bajocian *Eoabelisaurus* taxon of the Abelisauridae, as reported in other recent studies, eliminates the need for a minimum common origin (MCO) of Abelisauridae and Abelisauroidea in the earliest Middle Jurassic, discarding the presumption of a long ghost-lineage and a Pangeic geographical range of origin. A similar conclusion can be inferred by *Ligabueino*, which sometimes has been included inside Noasauridae (Tortosa et al., 2014), its late Hauterivian-early Barremian age implies a MCO of the Abelisauroidea at this age and a ghost lineage from this period. The placing of *Ligabueino* outside of the node-based clade Abelisauroidea leaves to *Kryptops* as the oldest known Abelisauroid, which is conformably found as the basalmost abelisaurid, and gives an Aptian-Albian MCO for the Abelisauroidea and Abelisauridae. Previous assignments of fragmentary materials to Abelisauroidea from the Upper Jurassic and Lower Cretaceous of Gondwana (Rauhut, 2005, 2011; Rauhut et al., 2003) could be representing forms closely related but outside to Abelisauroidea, as found *Eoabelisaurus* and *Ligabueino*.The early dichotomy of Abelisauridae in Majungasaurinae and Brachyrostra is first indicated by the occurrence of the Albian European *Genusaurus* and the Cenomanian South American *Xenotarsosaurus*, respectively, that in addition to the African *Kryptops* and *Rugops* is concordant with a Pan-Gondwanan (Gondwana + southern European landmasses) origin of the clade followed by a vicariant pattern conditioned by the aperture of the Atlantic ocean in the middle Cretaceous. In respect to the Majungasaurinae, a previously unrecognized split among the European and Indo-Malagasy forms implies a vicariant model for the group, correlated to the activation of a faunal barrier, possibly in the Tethys or the Mozambique channel, but is not concordant with the scenario of an ‘Africa-first’ model (Sampson et al., 1998), since the dispersal of majungasaurines implies the use of this continent as a necessary corridor. Inside brachyrostrans, the Malagasy *Dahalokely* are placed as the sister taxon of of *Rahiolisaurus,* the most derived brachyrostrans from South America. This result is consistent with a mosaic pattern in the vicariant speciation of the derived abelisaurids. The remaining brachyrostrans are found to be endemic of South America. The furileusarian nature of *Pycnonemosaurus* do not support an intracontinental isolation of the northern and southern South America.

6.2. Systematic implications

Historically, the abelisaurids and their kind suffered multiple interpretations of their systematics and their phylogenetic relationships (Bonaparte, 1991b; Canale et al., 2009; Carrano and Sampson, 2008; Novas, 1992; Sereno, 1998; Tortosa et al., 2014; Wilson et al., 2003). Specifically one taxon, *Abelisaurus comahuensis*, seems to have played a pivotal role on the successive phylogenetic analysis. *Abelisaurus* is known solely by a partial skull, which gave name to the Linnaean-ranked family Abelisauridae (Bonaparte and Novas, 1985) and other more inclusive groups as Abelisauroidea (Bonaparte, 1991b) or Abelisauria (Novas, 1992). It was usually interpreted as a basal form distantly related from *Carnotaurus* (i.e. Carrano et al., 2001; Coria et al., 2002; Lamanna et al., 2002) and a proper subfamily, Abelisaurinae, was erected to conform together with Carnotaurinae a node-stem triplet into Abelisauridae (Sereno, 1998). Later, Abelisauridae was considered both a node-based (Sampson et al., 2001) or a stem-based taxon (Wilson et al., 2003) included within Abelisauroidea. The phylogenetic separation of *Abelisaurus* and *Carnotaurus* favored the erection of new clades based on different specifiers, resulting in clades as Carnotaurini (Coria et al., 2002) and Brachyrostra (Canale et al., 2009). The resulting topology of the current analysis is in conflict with previous systematic denominations of some clades, particularly Abelisauridae, Abelisaurinae, Carnotaurinae, and Carnotaurini. In order to preserve stability, reduce the amount of specifiers, following the priority principle, we propose the use of the node-stem triplet Abelisauroidea, Abelisauridae and Noasauridae as proposed by Wilson and colleagues (Wilson et al., 2003), but changing one of their specifiers from *Carnotaurus sastrei* to *Abelisaurus comahuensis*. In this way, the stem-based condition of Abelisauridae shelter the inclusion of most of the taxa classically considered abelisaurids, as *Rugops*, *Xenotarsosaurus*, *Majungasaurus*, *Ekrixinatosaurus*, etc. In respect to Abelisaurinae and Carnotaurinae, we employ both as stem-based taxa with *Abelisaurus comahuensis* and *Carnotaurus sastrei* as specifiers, as originally defined by Sereno (1998), but not conforming a node-stem triplet with a nominated clade for the node-based taxon, pending the elucidation of the phylogenetic position of derived furileusarians *Quilmesaurus* and *Pycnonemosaurus*. In respect to Carnotaurini (Coria et al., 2002), we opted not to employ this term, because present phylogenetic analysis of Carnotaurinae results monotypic. Further, Coria et al. (2002) in the original definition employed the specifiers *Carnotaurus sastrei* plus *Aucasaurus garridoi* to make unviable their use, because the paper was not based on Linnean Taxonomy, and thus the “ranks” were not important. The discovery of *Viavenator exxoni* is crucial to elucidate the phylogeny and systematics of the highly derived abelisaurids. In our analysis (see above), this taxon is considered as the basalmost furileusaurian, wich is nested deeply inside Brachyrostra (Fig. 9), the clade of South American derived abelisaurids, and *Viavenator* as the sister-taxon of *Carnotaurus* + (*Abelisaurus* + *Aucasaurus*) fitting in a transitional position between the Cenomanian-Turonian and the Campanian-Maastrichtian taxa. In this context, the Santonian age of *Viavenator* is in accordance with its intermediate phylogenetic placement. Additionally, *Viavenator* displays at highly-derived postcranial morphology of *Aucasaurus* and *Carnotaurus,* with a relatively plesiomorphic skull in respect to these two taxa.

6.3. Biostratigraphic implications

The record of large vertebrate assemblages from South America is relatively continuous along the Cretaceous period between the Aptian and Maastrichtian (Leanza et al., 2004; Juárez-Valieri et al., 2011a, 2011b). However, many of these associations are poorly

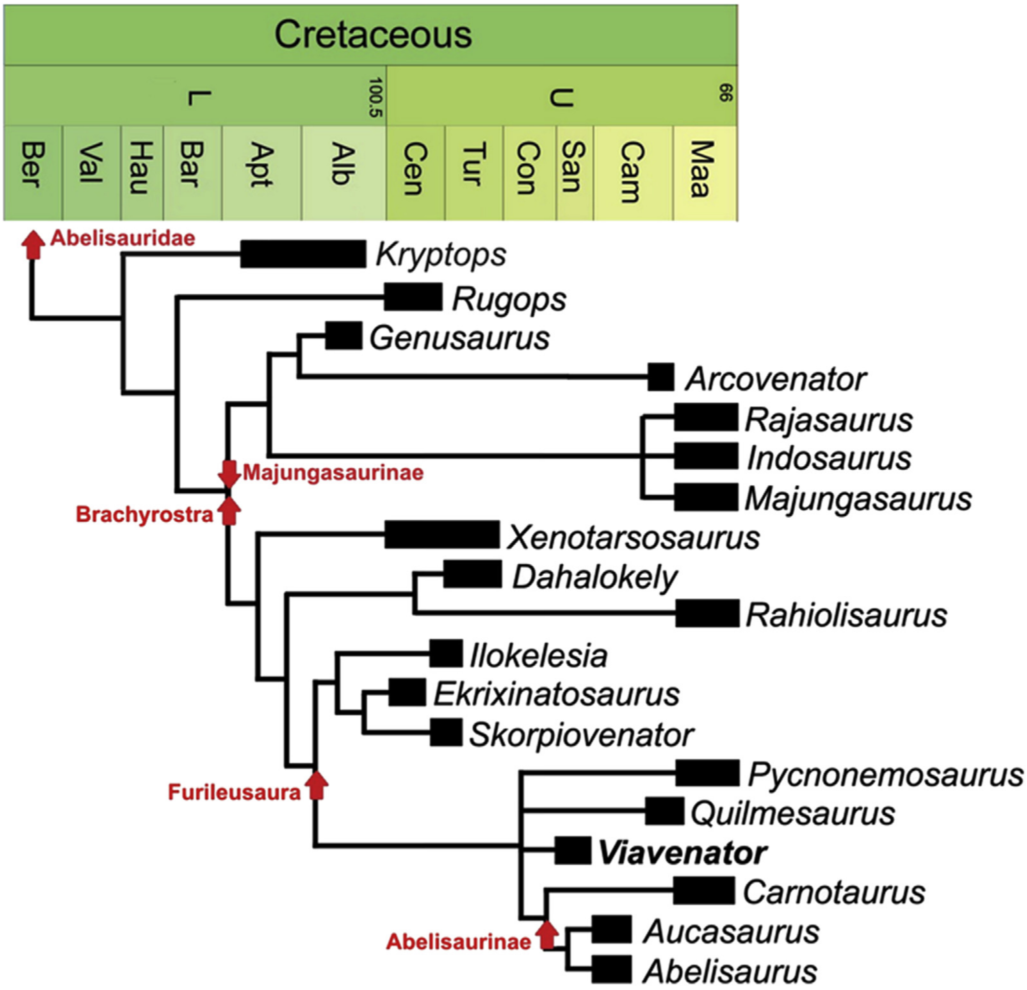

Fig. 9. Phylogenetic relationships of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Time-calibrated simplified strict consensus tree of abelisauroids theropod dinosaurs. The red arrows indicate the placement of the stem-based nodes as used in this work. Abbreviations: **L**, Lower; **U**, Upper; **Alb**, Albian; **Apt,** Aptian; **Bar,** Barremian; **Ber,** Berriasian; **Cam**, Campanian; **Cen**, Cenomanian; **Con,** Coniacian; **Hau,** Hauterivian; **Maa,** Maastrichtian; **San,** Santonian; **Tur**, Turonian; **Vlg**, Valanginian. Numbers indicate millions of years ago.

known, particularly with regard to large predators. In this context, abelisaurids belonging to the endemic South American derived brachyrostrans are represented in the Cenomanian-early Turonian by several basal taxa, such as *Xenotarsosaurus*, *Ekrixinatosaurus*, *Skorpiovenator* and *Ilokelesia* (Canale et al., 2009; Coria and Salgado, 1998; Juárez-Valieri et al., 2011b; Lamanna et al., 2002; Martínez et al., 1986). This time span corresponds to the final separation of South America and Africa, exhibiting closely related forms from several tetrapod clades, although some groups as carcharodontosaurians and abelisaurid theropods and rebbachisaurid sauropods indicate an incipient vicariant process at that time (Apesteguía et al., 2013; Canale et al., 2014; Gorscak et al., 2014; Herne, 2013; Kellner et al., 2011; Sereno and Larsson, 2009; Sereno et al., 2004; Wilson and Allain, 2015). A possible dispersal event of basal brachyrostrans from South America to eastern Gondwana is suggested in our analysis by the placement of *Dahalokely* and *Rahiolisaurus* as more derived than the basalmost brachyrostran *Xenotarsosaurus,* but outside the node embracing *Skorpiovenator* and *Carnotaurus*. Faunas from the late Turonian to the early Campanian are in agreement with the complete isolation of South America from other landmasses, with the exception of Antarctica and possibly Australia (Coria and Salgado, 2005; Herne, 2013; Novas et al., 2013). The abelisaurid record in the continent is scarce for most of this period, with indeterminate fragmentary material from several areas from Patagonia, and only in the early Campanian the taxa *Abelisaurus* and *Aucasaurus* are registered (Bonaparte and Novas, 1985; Coria et al., 2006, 2002; Gianechini et al., 2015). This time span is characterized by the abundance of Megaraptora among the large theropods, and several clades of derived titanosaurs and endemic euornithopods (Calvo et al., 2007; Coria and Salgado, 1996; Coria et al., 2013; Novas et al., 2013; Rozadilla et al., 2016). Finally, the third period of faunal assemblages is comprised between the late Campanian and Maastrichtian. The continent suffers the transgression of the Atlantic ocean in several areas, allowing the establishment of an archipelago in Patagonia (Gasparini et al., 2015; Spalletti and Franzese, 2007). At the same time a biotic interchange with North America derives in the presence of hadrosaurs and possibly ankylosaurs (Coria and Salgado, 2001; Juárez-Valieri et al., 2010). The abelisaurids are comprised by the highly derived taxa *Carnotaurus*, *Quilmesaurus* and *Pycnonemosaurus* (Bonaparte, 1985; Juárez-Valieri et al., 2007; Kellner and Campos, 2002). Previous works indicate a faunal extinction event in South America posterior to the early Turonian, including the disappearence of carcharodontosaurids and rebbachisaurids (Canale et al., 2014; Coria and Salgado, 2005; Juárez-Valieri et al., 2011a; Lamanna et al., 2001). In this context, the Santonian *Viavenator* represents part of a subclade of derived brachyrostrans and more distantly related with the earlier lineages, along with the derived positioning of *Abelisaurus* better supported by the present phylogenetic analysis, suggests that the brachyrostran clade could be pruned in the post-Cenomanian extinction event and generated a new radiation posteriorly.

7. Concluding remarks

In the present paper, we describe a new abelisaurid theropod from the Santonian of Patagonia, Argentina. The new form is here named *Viavenator exxoni* gen. et sp. nov., and possesses, among other characteristics, hypertrophied structures in the presacral axial skeleton.

Based in our phylogenetic analysis, *Viavenator* is found as a transitional brachyrostran, as the oldest member of a late radiation clade of the South American forms, named Furileusauria, and includes all the currently known abelisaurid taxa of this continent found in Santonian to Maastrichtian strata. The assemblages are found in a more complex biogeographic scenario with a division among European and Indo-Malagasy majungasaurines , with possible basal brachyrostrans in India and Madagascar.

Here we interpret that the furileusarians are supporting evidence of a late radiation of brachyrostran abelisaurids that fit with a faunal replacement that happened during the Turonian in South America, and is concordant with other dinosaur clades as the carcharodontosaurians, rebbachisaurids and derived lithostrotians.

Acknowledgments

We thank to ExxonMobil for funding fieldworks that led to the discovery and recovery of study specimen; to the *Argentino Urquiza* Municipal Museum technicians, S. Palomo and C. Fuentes, for finding the specimen and materials preparation, to I. Tapia and C. Choy for their active participation in the second phase of fieldwork, to F. Bellardini, R. Barbieri, J. Calvo and J. Canale for allowing us to see material housed under their care, to T. Tortosa, F. Agnolín and G. Casal for providing information or photographies, to Mrs. M. Oviedo, for the Mapudungun language translation, to Proactiva for the logistic provided in a camp and finally to the Town Hall of Rincon de los Sauces for providing significant support that allowed the development of paleontological project in the *La Invernada* area. We thank to two anonymous reviewers for the useful comments that improved the quality of this contribution. A.H.M. thanks to Agencia Nacional de Promoción Científica y Técnica for financial support (PICT 2011-1989).

References

Allain, R., Tykoski, R.S., Aquesbi, N., Jalil, N.-E., Monbaron, M., Russell, D.A., Taquet, P., 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. 1. Journal of Vertebrate Paleontology 27, 610–624.

Apesteguía, S., Makovicky, P.J., Smith, N., Juárez-Valieri, R.D., 2013. A new theropod with a didactyl manus and African affinities from the Upper Cretaceous of Patagonia. In: 3. Congreso Latinoamericano de Paleontología. Aguas Calientes, pp. 34–35.

Bonaparte, J.F., 1985. A horned cretaceous carnosaur from Patagonia. 1. National Geographic Research & Exploration 1, 149–151.

Bonaparte, J.F., 1991a. Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico superior, Argentina. 1. Revista del Museo Argentino de Ciencias Naturales: Paleontologia 4, 17–123.

Bonaparte, J.F., 1991b. The gondwanan theropod families Abelisauridae and Noasauridae. 1. Historical Biology 5, 1–25.

Bonaparte, J.F., Novas, F.E., 1985. Abelisaurus comahuensis, n.g., n.sp., Carnosauria del Cretácico tardío de Patagonia. 1. Ameghiniana 21, 259–265.

Buffetaut, E., Mechin, P., Mechin-Salessy, A., 1988. Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. Comptes Rendus de l'Académie de Science. Série II A 206, 153–158.

Burch, S.H., Carrano, M.T., 2012. An articulated pectoral girdle and forelimb of the abelisaurid theropod Majungasaurus crenatissimus from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 32, 1–16.

Calvo, J.O., Porfiri, J.D., Novas, F.E., 2007. Discovery of a new ornithopod dinosaur from the Portezuelo Formation (Upper Cretaceous), Neuquén, Patagonia, Argentina. 1. Arquivos do Museu Nacional do Rio de Janeiro 65, 471–483.

Canale, J.I., Scanferla, C.A., Agnolín, F.L., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. 1. Naturwissenschaften 96, 409–414.

Canale, J.I., Novas, F.E., Pol, D., 2014. Osteology and phylogenetic relationships of Tyrannotitan chubutensis Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. 1. Historical Biology 1–32. http://dx.doi.org/10.1080/08912963.2013.861830.

Carrano, M.T., Sampson, S.D., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). 1. Journal of Systematic Palaeontology 6, 183–236.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). 1. Journal of Systematic Palaeontology 10, 211–300.

Coria, R.A., Salgado, L., 1996. A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. 1. Journal of Vertebrate Paleontology 16, 445–457.

Coria, R.A., Salgado, L., 1998. A basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. In: Pérez-Moreno, B.P., Holtz, T.R.J., Sanz, J.L., Moratalla-García, J.J. (Eds.), 2. Aspects of the Theropod Paleobiology – 1. Gaia, pp. 89–102.

Coria, R.A., Salgado, L., 2001. South American ankylosaurs. In: Carpenter, K. (Ed.), 2. The Armored Dinosaurs, pp. 159–168.

Coria, R.A., Salgado, L., 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. 2. Neuquén Basin, Argentina A Case Study Seq. Stratigr. Basin Dyn. – 1. Geological Society London Special Publications 252, 317–327.

Coria, R.A., Chiappe, L.M., Dingus, L., 2002. A new close relative of Carnotaurus sastrei Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. 1. Journal of Vertebrate Paleontology 22, 460–465.

Coria, R.A., Currie, P.J., Paulina-Carabajal, A., 2006. A new abelisauroid theropod from northwestern Patagonia. 1. Canadian Journal of Earth Sciences 43, 1283–1289.

Coria, R.A., Filippi, L.S., Chiappe, L.M., García, R.A., Arcucci, A.B., 2013. Overosaurus paradasorum gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. 1. Zootaxa 3683, 357–376.

Ezcurra, M.D., Méndez, A.H., 2009. First report of a derived abelisaurid theropod from the Bajo de la Carpa Formation (Late Cretaceous), Patagonia, Argentina. 1. Bulletin of Geosciences 84, 547–554. http://dx.doi.org/10.3140/bull.geosci.1106.

Ezcurra, M.D., Agnolín, F.L., Novas, F.E., 2010. An abelisauroid dinosaur with a non-atrophied manus from the Late Cretaceous Pari Aike Formation of southern Patagonia. 1. Zootaxa 2450, 1–25.

Farke, A.A., Sertich, J.J.-W., 2013. An abelisauroid theropod dinosaur from the Turonian of Madagascar. 1. PLoS One 8, e62047. http://dx.doi.org/10.1371/journal.pone.0062047.

Gasparini, Z., Sterli, J., Parras, A., O'Gorman, J.P., Salgado, L., Varela, J., Pol, D., 2015. Late Cretaceous reptilian biota of the La Colonia Formation, central Patagonia, Argentina: Occurrences, preservation and paleoenvironments. 1. Cretaceous Research 54, 154–168. http://dx.doi.org/10.1016/j.cretres.2014.11.010.

Gianechini, F.A., Apesteguía, S., Landini, W., Finotti, F., Juárez-Valieri, R.D., Zandonai, F., 2015. New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. 1. Cretaceous Research 54, 1–16. http://dx.doi.org/10.1016/j.cretres.2014.11.009.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. 1. Cladistics 24, 1–13.

Gorscak, E., O'Connor, P.M., Stevens, N.J., Roberts, E.M., 2014. The basal titanosaurian Rukwatitan bisepultus (Dinosauria, Sauropoda) from the middle Cretaceous Galula Formation, Rukwa Rift Basin, southwestern Tanzania. 1. Journal of Vertebrate Paleontology 34, 1133–1154. http://dx.doi.org/10.1080/02724634.2014.845568.

Herne, M.C., 2013. Anatomy, Systematics and Phylogenetic Relationships of the Early Cretaceous Ornithopod Dinosaurs of the Australian-Antarctic Rift System. 4 (Thesis). The University of Queensland.

Juárez-Valieri, R.D., Fiorelli, L.E., Cruz, L.E., 2007. Quilmesaurus curriei Coria, 2001. Su validez taxonómica y relaciones filogenéticas. 1. Revista del Museo Argentino de Ciencias Naturales, Nueva Serie 9, 59–66.

Juárez-Valieri, R.D., Haro, J.A., Fiorelli, L.E., Calvo, J.O., 2010. A new hadrosauroid (Dinosauria: Ornithopoda) from the Allen Formation (Late Cretaceous) of Patagonia, Argentina. 1. Revista del Museo Argentino de Ciencias Naturales, Nueva Serie 12, 217–231.

Juárez-Valieri, R.D., Calvo, J.O., Ríos Díaz, S.D., 2011a. Sauropods crossing formations: biostratigraphical implications for patagonian faunal assemblages. In: Calvo, J.O., Porfiri, J.D., González Riga, B.J., Dos Santos, D.D. (Eds.), 2. Paleontología Y Dinosaurios Desde América Latina, pp. 153–160.

Juárez-Valieri, R.D., Porfiri, J.D., Calvo, J.O., 2011b. New Information on Ekrixinatosaurus novasi Calvo et al 2004, a giant and massively-constructed Abelisauroid from the "Middle Cretaceous" of Patagonia. In: Calvo, J.O., Porfiri, J.D., González Riga, B.J., Dos Santos, D.D. (Eds.), 2. Paleontología Y Dinosaurios Desde América Latina, pp. 161–169.

Kellner, A.W.A., Campos, D. de A., 2002. On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. 1. Arquivos do Museu Nacional (Rio de Janeiro) 60, 163–170.

Kellner, A.W.A., de Azevedo, S.A.K., Machado, E.B., de Carvalho, L.B., Henriques, D.D.R., 2011. A new dinosaur (Theropoda, Spinosauridae) from the

Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. In: Kellner, A.W.A., Tomida, Y. (Eds.), 2. Proceedings of the Third Gondwanan Dinosaur Symposium – 1. Anais Da Academia Brasileira de Ciências, pp. 99–108.

Lamanna, M.C., Martínez, R.D., Luna, M., Casal, G.A., Dodson, P.D., Smith, J.B., 2001. Sauropod faunal transition through the Cretaceous Chubut Group of central Patagonia. In: 3. Annual Meeting of the Society of Vertebrate Paleontology, USA, p. 70A.

Lamanna, M.C., Martínez, R.D., Smith, J.B., 2002. A definitive abelisaurid theropod dinosaur from the Early Late Cretaceous of Patagonia. 1. Journal of Vertebrate Paleontology 22, 58–69.

Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretaceous Research 25, 61–87.

Le Loeuff, J., Buffetaut, E., 1991. Tarascosaurus salluvicus nov. gen., nov. sp., dinosaure théropode du Crétacé Supérieur du sud de la France. 1. Geobios 25, 585–594.

Madsen, J.H.J., Welles, S.P., 2000. Ceratosaurus (Dinosauria, Theropoda), a revised osteology. In: 1. Utah Geological Survey Miscellaneous Publications, pp. 1–80.

Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science 21, 418–423.

Marsh, O.C., 1884. Principal characters of American Jurassic dinosaurs. Part VIII. The order Theropoda. American Journal of Science 27, 329–340.

Martinelli, A.G., Vera, E.I., 2007. Achillesaurus manazzonei, a new alvarezsaurid theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation, Río Negro Province, Argentina. 1. Zootaxa 1582, 1–17.

Martínez, R.D., Giménez, O., del, V., Rodríguez, J., Bochatey, G., 1986. Xenotarsosaurus bonapartei gen. et. sp. nov. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina. In: 3. Congreso Argentino de Paleontología Y Bioestratigrafía. Actas, pp. 23–31.

Méndez, A.H., 2010. Estudio anatómico, filogenético y funcional de la columna vertebral de los terópodos abelisáuridos (Dinosauria, Theropoda, Ceratosauria). 4 (Thesis). Universidad de Buenos Aires.

Méndez, A.H., 2014a. The cervical vertebrae of the Late Cretaceous abelisaurid dinosaur Carnotaurus sastrei. 1. Acta Palaeontologica Polonica 59, 569–579.

Méndez, A.H., 2014b. The caudal vertebral series in abelisaurid dinosaurs. 1. Acta Palaeontologica Polonica 59, 99–107.

Novas, F.E., 1992. La evolución de los dinosaurios carnívoros. In: 2. Los Dinosaurios Y Su Entorno Biótico: Actas Del Segundo Curso de Paleontologia in Cuenca, pp. 125–163.

Novas, F.E., 1997. Abelisauridae. In: Currie, P., Padian, K. (Eds.), Encyclopaedia of Dinosaurs. Academic Press, pp. 1–2.

Novas, F.E., Agnolín, F.L., Bandyopadhyay, S., 2004. Cretaceous theropods from India: a review of specimens described by Huene and Matley (1933). 1. Revista del Museo Argentino de Ciencias Naturales, Nueva Serie 6, 67–103.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J.D., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. 1. Cretaceous Research 45, 174–215.

Organ, C.L., 2006. Thoracic epaxial muscles in living archosaurs and ornithopod dinosaurs. Anatomical Record A288, 782–793.

Paulina-Carabajal, A., 2011a. Braincases of abelisaurid theropods from the Upper Cretaceous of north Patagonia. 1. Palaeontology 54, 793–806. http://dx.doi.org/10.1111/j.1475-4983.2011.01055.x.

Paulina-Carabajal, A., 2011b. The braincase anatomy of Carnotaurus sastrei (Theropoda: Abelisauridae) from the Upper Cretaceous of Patagonia. 1. Journal of Vertebrate Paleontology 31, 378–386.

Paulina-Carabajal, A., Currie, P.J., 2012. New information on the braincase of Sinraptor dongi Currie and Zhao (Theropoda, Allosauroidea): ethmoidal region, endocranial anatomy and pneumaticity. 1. Vertebrata PalAsiatica 50, 85–101.

Pol, D., Rauhut, O.W.M., 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. 1. Proceedings of the Royal Society of London 279, 3170–3175. http://dx.doi.org/10.1098/rspb.2012.0660.

Porfiri, J.D., Calvo, J.O., 2006. A new record of Carnotaurinae (Theropoda: Abelisauridae) from the Upper Cretaceous of Neuquén, Patagonia. In: 3. Annual Meeting of the Society of Vertebrate Paleontology, USA, pp. 111A–112A.

Porfiri, J.D., Calvo, J.O., Juárez-Valieri, R.D., Dos Santos, D.D., 2008. A new large theropod dinosaur from the Bajo de La Carpa Formation (Late Cretaceous) of Neuquén, Patagonia. In: Calv (Ed.), 3. Congreso Latinoamericano de Paleontología de Vertebrados, p. 202.

Rauhut, O.W.M., 2005. Post-cranial remains of "coelurosaurs" (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. Geological Magazine 142, 97–107.

Rauhut, O.W.M., 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). In: Barrett, P.M., Milner, A.R.C. (Eds.), Studies on Fossil Tetrapods - Special Papers in Palaeontology, pp. 195–239.

Rauhut, O.W.M., Cladera, G., Vickers-Rich, P., Rich, T.H., 2003. Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. 1. Cretaceous Research 24, 487–497.

Rozadilla, S., Agnolín, F.L., Novas, F.E., Aranciaga Rolando, A.M., Motta, M.J., Lirio, J.M., Isasi, M.P., 2016. A new ornithopod (Dinosauria, Ornithischia) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications. Cretaceous Research 57, 311–324. http://dx.doi.org/10.1016/j.cretres.2015.09.009.

Sampson, S.D., Witmer, L.M., 2007. Craniofacial anatomy of Majungasaurus crenatissimus (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. 2. Majungasaurus crenatissimus (Theropoda Abelisauridae) from Late Cretac. Madagascar 8, pp. 32–102.

Sampson, S.D., Witmer, L.M., Forster, C.A., Krause, D.W., O'Connor, P.M., Dodson, P.D., Ravoavy, F., 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. Science 280, 1048–1051.

Sampson, S.D., Carrano, M.T., Forster, C.A., 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. 1. Nature 409, 504–506.

Sereno, P.C., 1998. A rationale for phylogenetic definitions, with application to the higher level taxonomy of Dinosauria. 1. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen 210, 41–83.

Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. 1. Acta Palaeontologica Polonica 53, 15–46.

Sereno, P.C., Larsson, H.C.E., 2009. Cretaceous crocodyliforms from the Sahara. 1. ZooKeys 28, 1–143.

Sereno, P.C., Wilson, J.A., Conrad, J.L., 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. 1. Proceedings of the Royal Society of London, Series B (Biological Sciences) 271, 1325–1330.

Smith, J.B., Lamanna, M.C., Askar, A.S., Bergig, K.A., Tshakreen, S.O., Abugares, M.M., Rasmussen, D.T., 2010. A large abelisauroid theropod dinosaur from e Early Cretaceous of Libya. 1. Journal of Paleontology 84, 927–934.

Spalletti, L.A., Franzese, J.R., 2007. Mesozoic paleogeography and paleoenvironmental evolution of Patagonia (southern South America). In: Gasparini, Z., Salgado, L., Coria, R.A. (Eds.), 2. Patagonian Mesozoic Reptiles, pp. 29–49.

Tortosa, T., Buffetaut, E., Vialle, N., Dutour, Y., Turini, E., Cheylan, G., 2014. A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. 1. Annales de Paléontologie 100, 63–86.

Wilson, J.A., Allain, R., 2015. Osteology of *Rebbachisaurus garasbae* Lavocat, 1954, a diplodocoid (Dinosauria, Sauropoda) from the early Late Cretaceous–aged Kem Kem beds of southeastern Morocco. Journal of Vertebrate Paleontology 35, e1000701. http://dx.doi.org/10.1080/02724634.2014.1000701.

Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A., Sahni, A., 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. Contributions from the Museum of Paleontology, University of Michigan 31, 1–42.

Xu, X., Clark, J.M., Mo, J., Choiniere, J.N., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S.J., Zhao, Q., Hernández-Rivera, R., Jia, C., Han, F., Guo, Y., 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459, 940–944.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.12.018.