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**Osteology of *Viavenator exxoni* (Abelisauridae; Furileusauria) from the Bajo de la Carpa Formation, NW Patagonia, Argentina.**

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**Abstract**

The complete osteology of the abelisaurid *Viavenator exxoni*, from the Bajo de la Carpa Formation (Santonian, Upper Cretaceous) is described. *Viavenator* is characterized by a series of autapomorphies, including: transversely compressed parietal depressions on both

sides of the supraoccipital crest; ventral edges of the paraoccipital processes located above the level of the dorsal edge of the occipital condyle; basioccipital-opisthotic complex about two and a half times the width and almost twice the height of the occipital condyle, in posterior view; well-developed crest below the occipital condyle, diverging ventrally and defining the subcondylar recess; deeply excavated and sub-circular basisphenoidal recess, with its major axis transversely oriented; basipterygoid processes horizontally placed with respect to the cranial roof and located slightly dorsally to the basal tubera; mid and posterior cervical centra with slightly convex lateral and ventral surfaces; hyposphene-hypanthrum articular complex present from dorsal 2 onward; presence of an interspinous accessory articular system in middle and posterior dorsal vertebrae; presence of a pair of pneumatic foramina within the prespinal fossa in anterior caudal vertebrae; distal end of the scapular blade posteriorly curved. Particularly, *Viavenator* shows plesiomorphic cranial characters, i.e. flat frontals lacking domes or horns, combined with derived postcranial characters, e.g. the interspinous accessory joint system of dorsal vertebrae. This combination between plesiomorphic and derived traits suggests that *Viavenator* is a transitional form, which is an idea supported by its intermediate stratigraphic and phylogenetic placement between the basal and older (e.g. *Skorpiovenator*, *Ilokelesia*) and derived and younger members of the clade (e.g. *Aucasaurus*, *Carnotaurus*).

**Keywords:** *Abelisauridae*, *Furileusauria*, *Bajo de la Carpa Formation*, *Late Cretaceous*, *Neuquén Basin*.

## 1. Introduction

*Abelisauridae* represents the most abundant and best known group of Cretaceous theropod dinosaurs from Gondwana, and apparently also Europe. Several taxa have been definitely referred to *Abelisauridae* since its recognition as a monophyletic, mainly in South America (Bonaparte and Novas, 1985; Bonaparte, 1985; Coria and Salgado 1998; Coria, 2001; Coria et al., 2002; Kellner and Campos, 2002; Calvo et al., 2004; Canale et al., 2009), Africa (Depéret, 1896; Sereno et al., 2004; Sereno and Brusatte, 2008), the Indian subcontinent (Wilson et al., 2003; Novas et al., 2010,) and Europe (Le Loeuff and Buffetaut, 1991;

Tortosa et al., 2013). The taxonomic diversity of Abelisauridae notably increases the possibilities to interpret and discuss intragroup phylogenetic relationships. This lead to the recognition of new sublineages, such as the “western Gondwanan” South American brachyrostrans, and the “eastern Gondwanan” majungasaurines, which certainly can be considered as a result of both vicariant and dispersal events (Canale et al., 2009; Novas et al., 2013; Tortosa et al., 2013). A new abelisaurid, *Viavenator exxoni*, was described recently based on a incomplete, partially articulated skeleton comprising the posterior area of the skull, most of the axial sequence and some appendicular elements (Filippi et al., 2016). This abelisaurid comes from the Santonian deposits of the Bajo de la Carpa Formation, Upper Cretaceous, Río Colorado Subgroup, Neuquén Group (Filippi et al., 2016) and it exhibits characters suggesting that it represents a transitional form between the “middle” Cretaceous basal brachyrostrans and the highly-derived latest Cretaceous forms. *Viavenator* has primitive cranial characters combined with some derived features of the postcranial skeleton. This condition has enabled the polarization between cranial and postcranial transitional elements, which lead to a more precise phylogenetic placement of others taxa, as for example *Abelisaurus comahuensis*.

In the present work we provide a detailed and comparative anatomical description of the skeletal elements of *Viavenator exxoni*. The information supplied is essential for a better comprehension of the anatomical features of this taxon and abelisaurids as a whole, and will be a valuable data source for future studies about this clade of theropod dinosaurs.

## 2. Materials and methods

### 2.1. Anatomical abbreviations

**a**, acromion; **ape**, anterior projection of epiphysis; **aptp**, anterior projection of transverse process; **ati**, atlantal intercentrum; **bit**, biceps tubercle; **Bo**, basioccipital; **Bs**, basisphenoid; **bpt**, basipterygoid process; **bt**, basal tuber; **caaf**, caudal articular facet of chevron; **cdl**, centrodiapophyseal lamina; **cf**, coracoid foramen; **craf**, cranial articular facet of



chevron; **crpr**, cranial process of chevron; **cup**, cultriform process; **dex**, distal expansion of  
chevron; **dp**, diapophysis; **Eo**, exoccipital; **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; **na**, neural arch; **nc**, neural canal; **nct**, nuchal crest; **ns**, neural spine; **oa**,  
odontoid articulation; **oc**, occipital condyle; **oca**, occipital condyle articulation; **Op**,  
opisthotic; **Os**, orbitosphenoid; **P**, parietal; **pcdl**, posterior centrodiapophyseal lamina; **pcr**,  
paracondylar recess; **pe**, parietal eminence; **pf**, pneumatic foramen; **Po**, postorbital; **po**,  
postzygapophysis; **pop**, paraoccipital process; **posf**, postspinal fossa; **Pro**, prootic; **pp**,  
parapophysis; **pr**, prezygapophysis; **prel**, prezygoepipophyseal lamina; **pvp**, posteroventral  
process; **rbs**, basisphenoid recess; **rtl**, lateral tympanic recess; **sag**, sagittal bar; **scr**,  
subcondilar recess; **spgf**, supraglenoid fossa; **Sph**, sphenethmoid; **Sq**, squamosal; **So**,  
supraoccipital; **sot**, supraoccipital tuberosity; **stf**, supratemporal fenestra; **stfo**, supratemporal  
fossa; **ssr**, subselar recess; **tbs**, scar for *triceps brachii scapularis*; **tp**, transverse process;  
**vcd**, foramen vena capitis dorsalis; **vp**, ventral processes.

## 2.2. Institutional abbreviations

**MAU-Pv-LI**, Museo Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén  
province, Argentina; **MUCPv**, Museo de la Universidad del Comahue, Neuquén province,  
Argentina; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos  
Aires; Argentina; **MCF**, Museo “Carmen Funes”, Plaza Huincul, Neuquén province,  
Argentina; **MPM**, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; **MPCA**, Museo  
Carlos Ameghino, Cipolletti, Río Negro province, Argentina; **FMNH**, Field Museum of Natural  
History, Chicago, USA.

### 3. Systematic Paleontology

Theropoda Marsh, 1881

Ceratosauria Marsh 1884

Abelisauridae Bonaparte & Novas, 1985

Brachyrostra Canale et al., 2009

Furileosauria Filippi et al., 2016

*Viavenator exxoni* Filippi et al., 2016

**Holotype. MAU-Pv-LI-530** See Filippi et al. (2016) (Fig 1 – 16). A new material found in the same excavation, proximal end of the fibula is incorporated into the holotype.

**Diagnosis.** See Filippi et al. (2016).

### 4. Description

#### 4.1. Neurocranium

The holotype of *Viavenator* has preserved the complete neurocranium, which is considered as the set of bony elements that surrounds the brain and whose function is the protection of the brain and the sensory organs (Currie, 1997). The neurocranium of *Viavenator* includes: frontals, parietals, sphenethmoid, orbitosphenoids, laterosphenoids, prootics, opisthotics, supraoccipital, exoccipitals, basioccipital, parasphenoids, basisphenoid and also the interorbital septum (Fig. 1). Other cranial bones interconnected with the neurocranium are both postorbitals and squamosals. Clear sutures between most of the preserved cranial bones are not visible, although there are well-defined limits between the postorbitals, squamosals, laterosphenoids and sphenethmoids.

##### 4.1.1. Frontal

The frontal contacts the parietal posteriorly, the postorbital laterally and the laterosphenoids, orbitosphenoids and sphenethmoids ventrally (Fig.1A). The fronto-nasal contact is located anteriorly to the highest point of the orbit, as in some abelisaurids (e.g. *Carnotaurus*,

131 *Indosuchus* and *Rugops*), although differing from the condition of *Abelisaurus*, *Indosaurus*  
132 and *Majungasaurus*, in which the contact is located just on the highest point of orbit  
133 (Carrano and Sampson, 2008). The fronto-nasal articular surface is irregular and formed by  
134 small depressions or pits, differing from the immobile articulation observed in *Majungasaurus*  
135 in which it is formed by longitudinal grooves with foramina, flanked laterally a socket-like  
136 surface for a peg of the nasal (Sampson and Witmer, 2007). As in other abelisaurids, such as  
137 *Carnotaurus* (Bonaparte et al., 1990; Paulina Carabajal, 2011b), the frontals have a square-  
138 shape contour in dorsal view, being almost as wide as long. On the dorsal surface of the  
139 frontals is observed the presence of an ornamentation that consists of pits and sinuous  
140 furrows and ridges, although it is not well-preserved. This type of ornamentation is similar to  
141 that seen in *Carnotaurus*, *Abelisaurus*, *Aucasaurus*, and is common in derived abelisaurids  
142 (Sampson and Witmer, 2007). The suture between the frontals is not discernible, at least  
143 externally, although possibly it is developed internally as occurs in *Majungasaurus* (Sampson  
144 and Witmer, 2007). In *Aucasaurus* the frontals are not fused, but the interfrontal contact is  
145 obscured by the ornamented superficial bony layer (Paulina Carabajal, 2011a). The frontals  
146 are almost flat in *Viavenator*, unlike those of *Aucasaurus* (MCF-PVPH 236) in which the  
147 lateral margins are elevated in the orbital region so the cranial roof has a slightly concave  
148 shape in anterior or posterior view. They also differ from the frontals of *Abelisaurus* (MPCA  
149 11.098), which present conspicuous lateral prominences as "domes" frontals of *Carnotaurus*  
150 (Bonaparte et al., 1990; Paulina Carabajal, 2011b), which have remarkable lateral horn-  
151 shaped projections, and those from *Majungasaurus* and *Rajasaurus narmandensis*, which  
152 present a central projection (Wilson et al., 2003; Sampson and Witmer, 2007). Although the  
153 lacrimals are not preserved, it is possible to see that the frontals, are excluded from the  
154 dorsal margin of the orbit (Fig. 1A), due to the proximity between the postorbital and the  
155 lacrimal (Paulina Carabajal, 2011a, b), a common feature among abelisaurids (e.g.  
156 *Majungasaurus*, *Carnotaurus*, *Abelisaurus* and *Aucasaurus*). As in *Carnotaurus*, the  
157 supratemporal fossae are well excavated and markedly differ from the rest of the surface of  
158 the frontals by lack of ornamentation. The supratemporal fossae are anteriorly separated by

a triangular flat bony plate, which posteriorly narrows and is continuous with a thin sagittal crest that separates the posteromedial borders of the fossae as is also observed in *Carnotaurus*, *Abelisaurus*, *Aucasaurus*, *Majungasaurus* and *Ekrixinatosaurus* (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Paulina Carabajal, 2011a, b; Sampson and Witmer, 2007; Juárez Valieri et al., 2011). This triangular-shape surface in *Viavenator* has very well-defined sides, similarly to that present in *Carnotaurus* and *Abelisaurus*, while it differs from that observed in *Aucasaurus*, in which it has less defined and laterally concave edges. The supratemporal fossae are more anteroposteriorly than transversely developed in *Carnotaurus* and *Abelisaurus*, while in *Viavenator* they are more slightly transversely developed, as in *Majungasaurus*. On the other hand, they significantly differ from the fossae of *Ekrixinatosaurus* (MUCPv-294), which are markedly transversely developed.

#### 4.1.2. Parietals

The parietals contact anteriorly with the frontals, laterally with the squamosals, posteriorly with the supraoccipital, posterolaterally with the opisthotic and ventrally with the prootic and probably part of laterosphenoids (Fig. 1A,C). As in most theropods, it is difficult to recognize sutures between the parietals. A dorsomedial, caudally projected diamond-shape parietal eminence is observed in dorsal view, a common feature among abelisaurids. This eminence rises 20 mm about the cranial roof, similarly to the condition of *Abelisaurus* (Paulina Carabajal, 2011a) although differing from the higher process present in *Carnotaurus* and the lower one present in *Ekrixinatosaurus* and *Aucasaurus* (Juárez Valieri et al., 2011; Paulina Carabajal, 2011a, b). Moreover, the eminence has a posterior tongue-shaped structure as in other abelisaurids (Paulina Carabajal, 2011a, b), which overlaps the supraoccipital (Fig. 1 A-C). The posterior margin of the supratemporal fossa is relatively straight and perpendicularly located respect to the longitudinal axis. The nuchal crest is well-developed, formed by a thin and vertical plate which is more than twice the height of the foramen magnum and dorsally exceeding the level of the cranial roof (Fig. 1B). This crest is relatively less developed than in *Carnotaurus*, in which it has around three times the height of the foramen magnum (Bonaparte et al., 1990; Paulina Carabajal, 2011b). The posterior surface of the nuchal crest

of *Carnotaurus* and *Abelisaurus* presents two large oval-shaped depressions, on both sides of the supraoccipital crest, a more clearly defined in *Abelisaurus*, which were proposed as attachment areas of muscles related with the vertical movements of the head (Snively and Russell, 2007; Paulina Carabajal, 2011a, b). *Viavenator* also presents similar depressions on the posterior surface of the nuchal crest, although they are less developed than in the mentioned taxa (Fig. 1B).

#### 4.1.3. Supraoccipital

The supraoccipital is located dorsally to the foramen magnum; it contacts the parietals anteriorly, and the exoccipitals ventrolaterally (Fig 1B). Because the poor preservation of this sector, no sutures are distinguished between elements, so it is not possible to determine the participation of the supraoccipital in the dorsal edge of the foramen magnum. In *Majungasaurus* the contribution of the supraoccipital in the foramen magnum has been confirmed through CT scans (Sampson and Witmer, 2007), although in most abelisaurids this feature is unclear due the sutures are indistinguishable (Wilson et al., 2003; Paulina Carabajal, 2011a, b; Filippi et al., 2016). The supraoccipital crest is well-developed and originates in a zone located about 20 mm above the dorsal edge of the foramen magnum, extending vertically in dorsal direction until contacting the parietal eminence. On both sides of the supraoccipital crest, near the midline, are observed the foramina of the caudal middle cerebral veins, as in *Majungasaurus* (Sampson and Witmer, 2007), *Aucasaurus* (Coria et al., 2002; Paulina Carabajal, 2011) and *Arcovenator* (Tortosa et al., 2013).

#### 4.1.4. Exoccipital-opisthotic

The opisthotic and the exoccipital seem to be fused, because are not observed sutures between these elements. The exoccipitals contact dorsally with the supraoccipital and ventrally with the basioccipital, whereas the opisthotic contacts dorsolaterally with the parietals, posteroventrally with the basioccipital and anteriorly with the prootic and the

basisphenoid (Fig. 1B). Although no sutures are distinguished the exoccipitals form the lateral and possibly the laterodorsal margins of the foramen magnum, as apparently occurs in *Carnotaurus* (Paulina Carabajal, 2011b). The foramen magnum has a circular shape and is slightly smaller than the occipital condyle. The exoccipitals probably participate in the formation of the occipital condyle, as in *Carnotaurus* and *Aucasaurus* (Paulina Carabajal, 2011a, b), although there are no sutures that allow to confirm this. A single nerve XII foramen is observed laterally to the occipital condyle, within the deep ovoid paracondilar recess, similar to that of *Aucasaurus*, although in this taxon the poor preservation does not allow to identify the presence of one or two foramina for the exit of the nerve (Paulina Carabajal, 2011a). While *Abelisaurus* has two foramina for exit of the nerve XII (Paulina Carabajal, 2011a), *Majungasaurus* presents only one (Sampson and Witmer, 2007). In *Carnotaurus* it appears to be the same situation as in *Abelisaurus*, although the poor preservation in this zone does not allow confirmation. In *Viavenator* the height of the paraoccipital processes slightly exceeds the height of the foramen magnum. The proximal portion of the processes is vertically oriented while distally they are inclined posteroventrally, as in *Carnotaurus*, although differing from the processes of *Abelisaurus* which are completely in a vertical plane. This distal inclination would probably relate to how the muscles of the neck supported the head, thus allowing the transverse increasing of the muscle insertion surface (Paulina Carabajal, 2011b). In *Viavenator* the ventral edge of the paraoccipital processes is above the level of the dorsal edge of the occipital condyle, in posterior view, differently to the condition in other abelisaurids. This feature is related to the more lateral projection of the processes, in comparison to other abelisaurids such as *Carnotaurus* and *Majungasaurus* (Bonaparte et al., 1990; Sampson and Witmer, 2007; Paulina Carabajal, 2011b), in which the processes are more lateroventrally inclined.

#### 4.1.5. Basioccipital

Due the sutures between the elements are not clearly recognizable, it is not possible to determine if the basioccipital is the main component of the occipital condyle, as in *Carnotaurus*, *Aucasaurus* and *Ilokelesia* (Paulina Carabajal, 2011a). The occipital condyle is

spherical and similar to that of *Carnotaurus*, *Abelisaurus* and *Aucasaurus* (Fig. 1B, C). In posterior view it is wider than high. The constriction forming the neck of the occipital condyle is slightly developed, particularly in the transverse plane, mainly when it is compared with that of *Carnotaurus*, *Aucasaurus* and *Abelisaurus*. The dorsal surface of the neck has a well marked depression, different from the shallow depression observed in *Carnotaurus* (Paulina Carabajal, 2011b). Ventrally, the neck lacks a small keel or longitudinal medial ridge, as in *Aucasaurus* and *Ilokelesia* (Paulina Carabajal, 2011a), which conversely is present in *Carnotaurus*, *Abelisaurus* and *Majungasaurus* (Sampson and Witmer, 2007). *Viavenator* differs from other abelisaurids in that it presents a well-defined depression on the ventral surface of the condyle neck. The basal tubera are large and separated medially by a wide subcondylar recess (Fig. 1B), a different condition to that observed in *Carnotaurus*, *Majungasaurus* and *Abelisaurus*, in which the tubera are completely fused together forming a vertical bony plate that projects ventrally below the occipital condyle. A bony plate ventral to the occipital condyle is present in *Viavenator*, formed by part of the basioccipital and opisthotic, which is transversely wider and dorsoventrally higher than that in other abelisaurids. It is approximately two and a half times the width and almost twice the height of the occipital condyle. On the other hand, in *Carnotaurus* and *Abelisaurus* it is only twice the width and equals the height of the occipital condyle. The plate has a high and a well-developed central crest that diverges laterally toward the basal tubera, defining the ventral subcondylar recess, a condition much different from the slightly developed medial crest present in *Carnotaurus* and *Abelisaurus*. The basal tubera in *Viavenator* are bulbous structures posterolaterally projected, while in *Majungasaurus* they are laterally projected. In posterior view, *Viavenator* presents large oval depressions over the basal tubera at both sides of the midline, which are less developed in *Abelisaurus* and absent in *Carnotaurus* (Paulina Carabajal, 2011a, b).

#### 4.1.6. Basisphenoid

As occurs with the remaining elements of the braincase, it is not possible to determine the contact between the basisphenoid and the surrounding bones because sutures are not



clearly identifiable. A basisphenoidal recess (Fig. 1D) is anteriorly located with respect to the vertical bony plate formed by the basal tubera. This recess, is well-developed, ventrally oriented, with a sub-circular contour and it has well-defined edges constituted by thick lateral walls. The basisphenoidal recess is similar to that present in *Ceratosaurus* (Madsen and Welles, 2000), although slightly greater in transverse diameter. On the other hand, the recess differs from that of *Carnotaurus* (MACN-CH 894) where it has a square contour, and from that of *Majungasaurus* (FMNH PR 2100) where it presents a drop-shaped form with the widened portion anteriorly located. It is not possible to observe pneumatic openings within the recess. The basiptyergoid processes (Fig. 1B-D) are short and project posteroventrally, and more laterally than the basal tubera. As in *Ceratosaurus*, *Carnotaurus* and *Abelisaurus*, the basiptyergoid processes of *Viavenator* are finger-like projections, laterally compressed, whose distal ends are not expanded, reaching a lower level than the occipital condyle. In *Viavenator*, the basiptyergoid processes are horizontally disposed with respect to the cranial roof and in a slightly upper level than the basal tubera (Fig. 1C). By contrast, in *Abelisaurus*, *Carnotaurus*, *Ceratosaurus* and other derived theropods these processes are located ventrally to the level of the basal tubera (Paulina Carabajal, 2011a, b). The lateral sides of the basiptyergoid processes lack a basiptyergoid recess, as in other abelisaurids (Paulina Carabajal, 2011a, b). The enclosed area between the basal tubera and the basiptyergoid processes is more transversely than longitudinally longer, as in *Carnotaurus*, *Abelisaurus* and *Majungasaurus*. Medially to the basiptyergoid processes is a subsellar recess (Fig. 1D), similar to that of *Majungasaurus* (Sampson and Witmer, 2007), although anteriorly deeper and wider than in the latter taxon and developed until the end of the cultriform process of the presphenoid. In *Carnotaurus* the subsellar recess is hidden by sediment that fills the cavity (Paulina Carabajal, 2011b), whereas in *Abelisaurus* it is well-developed (Paulina Carabajal, 2011a). On the lateral surface of the basisphenoid a well-developed lateral tympanic recess is observed, which is partially covered by a preotic pendant anterodorsally located. This feature is also observed in *Carnotaurus* and *Abelisaurus*. In *Viavenator*, the presence of sediment that fills the recess precludes the recognition of its internal morphology, as well as



to distinguish the presence of foramina, as for example that corresponding to the internal carotid artery, which enters the braincase through the lateral tympanic recess. In *Abelisaurus*, the lateral tympanic recess is well-developed and subdivided into two smaller cavities, the most anterior of them presenting the input for the internal carotid artery, which flows into the pituitary fossa separately from its counterpart (Paulina Carabajal, 2011a). The preotic pendant in *Viavenator* is a laminar, wing-like structure, separated from the lateral wall of the braincase, and posteroventrally projected covering the anterodorsal sector of the lateral tympanic recess, a condition similar to that of *Carnotaurus* (Paulina Carabajal, 2011b). In *Viavenator*, a large ellipsoidal fenestra or "interorbital window" is not observed, which in other abelisaurids is located anteroventrally to the preotic crest and laterodorsally to the base of the cultriform process. This fenestra ("interorbital window") is present in *Carnotaurus*, *Abelisaurus* and *Majungasaurus*, which is delimited posteriorly by the basisphenoid, anteroventrally by the parasphenoid and anterodorsally by the ossified interorbital septum (Sampson and Witmer, 2007; Paulina Carabajal, 2011a, b). It connects to the orbital slots on both sides of the interorbital septum and with the pituitary fossa. The cultriform process in *Viavenator* is completely preserved, which is developed dorsally to the basipterygoid processes and anterodorsally projected, as in *Carnotaurus*, although in *Viavenator* the process becomes more horizontal and parallel to the cranial roof and distally it is more anterodorsally projected. Dorsally, the cultriform process is fused to the ossified interorbital septum, as occurs in *Carnotaurus* (Paulina Carabajal, 2011b).

#### 4.1.7. Prootic

The sutures between this bone and the surroundings of the braincase are also obscured by fusion of the elements, as is observed in *Carnotaurus*. The prootic-opisthotic contact is indicated by the columellar recess, whose opening is posteriorly oriented. As in *Carnotaurus*, the prootic partially covers the upper edge of the columellar recess, so the triangular shape of this opening is seen only in lateroventral view. The foramen for the trigeminal nerve (V2,3)

is circular in shape and is located dorsally to the preotic crest (see Paulina Carabajal and Filippi present issue). The ophthalmic branch of the trigeminal nerve is separated from the mandibular and maxillary branches, and goes outside through a foramen (V1) located dorsally and very close to the foramen V2,3, on a well-defined channel. The presence of an ophthalmic branch running through a channel (V1) and separated from the mandibular and maxillary branches (V2,3) is a condition also present in *Carnotaurus*, *Majungasaurus* and *Abelisaurus*, so this would be a characteristic feature of abelisaurids (Paulina Carabajal 2011a, b). As in *Carnotaurus*, posteriorly to the foramen V2,3 is observed a bony flange which is continuous with the dorsal edge of the preotic pendant. The foramen for cranial nerve VII possibly is located posteriorly or posteroventral to the foramen for V2,3, since is a condition present in most theropods (Paulina Carabajal, 2011b).

#### 4.1.8. Laterosphenoid

The laterosphenoid-frontal-postorbital contact is clearly observed. The postorbital process of the laterosphenoid projects laterally and below the laterosphenoid-frontal contact, without exceeding the lateral margin of the frontal (Fig. 1D) as in *Carnotaurus*. Also, the postorbital process is dorsoventrally expanded at its distal end, providing laterally a transverse contact surface with the postorbital. The foramen for V1 is circular and the opening is anteriorly oriented (see Paulina-Carabajal and Filippi present issue), similarly to that of *Carnotaurus*. A small foramen opens in the laterosphenoid, located dorsally to the foramen for V1 and near the contact with the frontal, which corresponds to the exit of the medial cerebral vein (Sampson and Witmer, 2007), as is also observed in *Carnotaurus*, *Abelisaurus* and *Majungasaurus*. The contact between the orbitosphenoid and the laterosphenoid is determined from the location of the foramina of the cranial nerves III + IV, whose posterior margins are formed by the laterosphenoid in most dinosaurs (Currie, 1997a). The foramen of the CN III + IV is oval and located posteroventrally to that of the CN II (see Paulina-Carabajal and Filippi present issue).

#### 4.1.9. Orbitosphenoid

Although there are no visible sutures, the orbitosphenoid-laterosphenoid contact is indicated indirectly from the location of the foramina of the CN III + IV, since the orbitosphenoid forms the anterior margins of them (Paulina Carabajal, 2011b). The foramen of the CN II is included in the orbitosphenoid and, as in other abelisaurids, it is not confluent with the opposite foramen of the CN II. As in *Carnotaurus* and *Abelisaurus*, in *Viavenator* the foramen of the CN II is circular, large in diameter and is anterodorsally located to the foramina of the CN III + IV (see Paulina-Carabajal and Filippi present issue).

#### 4.1.10. Ossified ethmoidal complex (sphenethmoid+mesethmoid)

As in other abelisaurids, such as *Carnotaurus*, *Abelisaurus*, *Ekrixinatosaurus* and *Majungasaurus*, the lateral and ventral walls of the cavities of the olfactory tract and olfactory bulbs are ossified (Sampson and Witmer, 2007; Paulina Carabajal, 2011a, b; Paulina Carabajal and Currie, 2012). In *Viavenator* the ethmoidal complex (Fig. 1C) is composed by the dorsally located sphenethmoid, which encloses the cavities of the olfactory bulbs and the olfactory tract, and the median internasal septum formed by mesethmoid (see Ali et al., 2008), as also occurs in *Carnotaurus* (Paulina Carabajal, 2011b). As in *Carnotaurus*, the sphenethmoid contacts dorsally with the frontal, posteriorly with the orbitosphenoid and ventrally with the ossified interorbital septum. In *Viavenator* no sutures are observed indicating the contact of the orbitosphenoid with the remaining elements. In *Viavenator* it is possible to differentiate the contact between the sphenethmoid and the frontal, because the elements are not entirely fused, as occurs in *Carnotaurus*. The sphenethmoid encloses the cavity of the olfactory bulbs dorsally, forming a ring-shaped structure, and thus excluding the cranial roof from the dorsal margin of the bulbs, as in *Abelisaurus* (Paulina Carabajal, 2011a). The foramen of the CN I (olfactory) (Fig. 1C,D) has a semicircular contour, a dorsally oriented opening and is separated from its counterpart by the medial septum formed by the mesethmoid, similarly to the condition of *Carnotaurus* (Paulina Carabajal, 2011b). The medial septum in *Viavenator* is anteriorly projected about 25 mm with respect to the foramen of the CN I and the sphenethmoid (only 2 mm more than in *Carnotaurus*), and it is attached dorsally to the frontal and reaching the fronto-nasal suture. This condition differs from that

observed in *Carnotaurus* in which the septum is shorter and it not reaches the fronto-nasal suture (Paulina Carabajal, 2011b). The sphenethmoid is ventrally firmly fused to the interorbital septum, as in *Carnotaurus*. A small foramen is located on the lateral aspect of the sphenethmoid, anterodorsally to the foramen of CN II and near the contact between the sphenethmoid and the frontal, which probably corresponds to an element of vascularization of the olfactory tract, as is observed in *Carnotaurus* and *Abelisaurus* and also in *Giganotosaurus* (Paulina Carabajal, 2011a, b).

#### 4.1.11. Ossified interorbital septum

As in other ceratosaurs (e.g. *Ceratosaurs*, *Eoabelisaurus*, *Carnotaurus*, *Abelisaurus* and *Majungasaurus*; Madsen and Welles, 2000; Sampson and Witmer, 2007; Paulina Carabajal, 2011a, b; Pol and Rauhut, 2012) the inteorbital septum in *Viavenator* is ossified. The septum is strongly ventrally fused to the cultriform process and dorsally with the ethmoid complex and a medial laminar bony plate (Fig. 1C), as is also observed in *Carnotaurus*. In contrast to *Abelisaurus* and *Carnotaurus*, in which the limit between the interorbital septum and the cultriform process is indicated by a textural change of the surface of the septum that consists of fine parallel grooves (Paulina Carabajal, 2011a, b), in *Viavenator* this limit is not clearly distinguishable. *Viavenator* shares with *Carnotaurus* the absence of an interorbital window, which conversely can be observed in *Majungasaurus* and *Abelisaurus*.

#### 4.2. Other skull elements

##### 4.2.1. Postorbital.

Both postorbitals are preserved, the right one complete (Fig. 1A, C). The postorbital has a derived "L" form (Tortosa et al., 2013), present in other abelisaurids such as *Carnotaurus* (Bonaparte et al., 1990), *Majungasaurus* (Krause et al., 2007) and *Skorpiovenator* (Canale et al., 2009). As in *Carnotaurus*, the postorbital is proportionally long, with an anteroventral process that approaches to the lacrimal and tends to close the orbit ventrally. The postorbital of *Viavenator* presents an anteriorly curved ventral process, with concave and convex anterior and posterior edges respectively, differing from the postorbital of *Ilokelesia*, which is T-shaped with a straight ventral process (Coria and Salgado, 2000), a morphology

considered as plesiomorphic for Abelisauridae (Tortosa et al., 2013). However, the morphology of the ventral process in *Ilokelesia* is doubtful because in referred specimens it is similar to that of other abelisaurids (Carrano and Sampson, 2008). *Viavenator* lacks a supraorbital ossification, as in *Ilokelesia* and *Abelisaurus* (Bonaparte and Novas, 1985; Coria and Salgado, 2000). The postorbital has an ornamented dorsal border, which is a common feature of most abelisaurids, but it differs from the strongly raised border present in *Skorpiovenator*, *Ekrixinatosaurus* and *Arcovenator* (Calvo et al., 2004; Canale et al., 2009; Tortosa et al., 2013). The ventral process of the postorbital in *Viavenator* is anteroposteriorly narrow, differing from the more robust and anteroposteriorly wider process of *Carnotaurus*, *Skorpiovenator* and *Majungasaurus*.

#### 4.2.2. Squamosal.

The squamosal (Fig.1 A, C) of *Viavenator* is tri-radiate, divided into an anterodorsal or parietal process, a ventral or quadratojugal process and a posteroventral or postquadrate process, as in other Abelisauridae such as *Carnotaurus*, *Abelisaurus*, *Majungasaurus*, *Skorpiovenator* and *Ekrixinatosaurus* (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson and Witmer, 2007; Canale et al., 2009; Juárez Valieri et al., 2011; Paulina Carabajal, 2011a ,b). As in *Carnotaurus*, the squamosal is relatively small, with only a small participation in the formation of the supratemporal fenestra. The ventral projection is slightly lateromedially compressed and relatively long with respect to the anterodorsal and posteroventral projections, as in *Skorpiovenator* (Canale et al., 2009), whereas in *Majungasaurus*, *Carnotaurus* and *Abelisaurus* is shorter (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson and Witmer, 2007). The squamosal contacts the postorbital dorsally and the parietal and the paraoccipital process laterally. An ellipsoidal foramen is located ventrally to the parietal-squamosal contact and below the paraoccipital process, which represents a remnant of the posttemporal fenestra present in other sauropsids. In *Viavenator* this fenestra is being reduced to a foramen, as also occurs in

other theropods (Witmer and Sampson, 2007). The articular cavity for the head of the quadrate is relatively deep in comparison with that present in *Carnotaurus*.

#### 4.2.3. Hyoid.

During the preparation it was found, close to the neurocranium, a delicate bone about 12.5 cm long, laterally compressed, which thins and curves distally (Fig. 2A). This delicate piece is interpreted as one of the ceratobranchial, very similar to that of the hyoid apparatus in *Carnotaurus* (Bonaparte et al., 1990)

#### 4.2.4. Teeth.

Associated to the *Viavenator* bones were found an incomplete tooth crown and a fragment of another tooth (Fig. 2 B). The crown lacks its distal apex and has well-developed mesial and distal carina with denticles that are inclined towards the apex of the crown. The mesial border is recognized because it curves slightly towards the apex. The distal border seems to have no inclination, i.e. seems to be straight. The denticles are chisel-like and were counted 11/5 mm, in the central sector of the mesial and distal carina. The denticles have proportionally the same size on both carinae, and were not observed cellae, interdenticular slits or blood grooves (Hendrickx et al., 2015, and references therein) between the denticles. Despite these teeth are fragmentary, the association with the skeleton and the presence of some characters considered as diagnostic for abelisaurid teeth (i.e., a convex mesial border and a straight distal one with serrated carinae extended from the base and chisel-shaped denticles, Smith, 2007; Hendrickx and Mateus, 2014), allow assigning them to *Viavenator*. Both the labial and the lingual side of the crown are mesiodistally convex, whereas the entire crown has a slight curvature to the labial side. The cross-section of the crown is sub-circular at the base, and it turns elliptical at the upper third of the crown. Due to the morphology of the crown, it is interpreted that the tooth would be located in an anterior position in the skull, probably either on the maxilla or on the dentary.

#### 4.3. Postcranial skeleton

The postcranial skeleton of *Viavenator* is represented by: eight cervical vertebrae, including the atlas; seven dorsal vertebrae, four of them articulated; twelve caudal vertebrae, including five proximals, five from the middle zone of the tail and two distals; ribs; gastralia; one chevron; scapulocoracoid; ischium foot; and fibulae; Except the atlas, other recovered cervical vertebrae were tentatively located in the position they occupied originally in the neck, according to comparisons made with *Carnotaurus* and *Majungasaurus*, which have preserved complete cervical sequences composed of ten elements.

#### 4.3.1. Cervical vertebrae

##### 4.3.1.1. Atlas.

The atlas (Fig. 3 A-C) is composed by the intercentrum fused to both distally incomplete neurapophyses, between which is the atlantal arch. Ventrally to this arch is located the neural canal, which is transversely elongated. The articular facet for the occipital condyle is concave and sub-circular in contour, whereas the articular surface for the axis is flat and with a dorsally marked notch corresponding to the facet joint for the odontoid process of the axis. In general terms, the atlas of *Viavenator* is similar to that of *Carnotaurus* (Bonaparte et al., 1990), though less robust and anteroposteriorly shorter. As in *Carnotaurus*, the ventral intercentrum has two small lateral processes separated by a large furrow. There are not observed prezygapophyseal facets in the neurapophyses, so it is inferred that the proatlas was absent, as also occurs in *Carnotaurus* and *Majungasaurus* (Bonaparte et al., 1990; O'Connor, 2007). The neurapophyses are posteriorly elongated, similar to the L-shaped neurapophyses observed in *Majungasaurus* and *Ceratosaurus*, and they are inclined posteriorly at 45°, an angle that falls in the same range as in other abelisaurids, e.g. *Carnotaurus* (40°) and *Majungasaurus* (35°). The postzygapophyses are small, as in *Carnotaurus* and *Majungasaurus*, and their facets are anteroposteriorly elongated and lateroventrally oriented.

##### 4.3.1.2. Third cervical.



488 The third cervical vertebra (Fig. 3D-G) lacks the posteroventral portion of the centrum. The  
489 centrum is dorsoventrally compressed. The anterior articular facet is slightly convex, as in  
490 *Carnotaurus*, *Majungasaurus* and *Rahiolisaurus*. In anterior view, the centrum is transversely  
491 wider than high, with a concavity in the dorsal surface that corresponds to the neural canal,  
492 and thus differing from the trapezoidal and ovoid aspects observed in *Carnotaurus* (Méndez,  
493 2014) and *Majungasaurus* (O'Connor, 2007) respectively. The inclination of the anterior  
494 articular facet appears to be slightly higher than in *Carnotaurus* and *Majungasaurus* and  
495 much higher than in *Rahiolisaurus* (Novas et al., 2010). A small pneumatic foramen appears  
496 to be present in the anterior half of the lateral surface of the centrum, but the preservation of  
497 this vertebra precludes to confirm the presence of another foramen posteriorly located, as  
498 observed in *Carnotaurus* and *Ilokelesia* (Bonaparte et al., 1990; Coria and Salgado, 1998;  
499 Méndez, 2014). The parapophyses are ventrolaterally directed, as in *Majungasaurus*, while  
500 in *Carnotaurus* the orientation of these structures is lateral (Méndez, 2010, 2014). The  
501 diapophyses are ventrolaterally directed, as in *Carnotaurus*, but are longer in *Viavenator*.  
502 They are anteriorly located, as occurs in *Majungasaurus* (O'Connor, 2007) and  
503 *Rahiolisaurus* (Novas et al., 2010) while in *Carnotaurus* are located along the midline of the  
504 centrum dorsally to the parapophyses (Méndez, 2014). The neural arch is almost complete,  
505 lacking the prezygapophyses and the end of the epiphysis on the right side. In anterior  
506 view, are present two laminopeduncular foramina at the sides of the neural canal, which are  
507 larger than those exhibited in *Carnotaurus* (Bonaparte et al., 1990) and *Majungasaurus*  
508 (O'Connor, 2007). The infrapostzygapophyseal fossae are very wide, as in *Carnotaurus* and  
509 *Rahiolisaurus*. Large pre- and postspinal fossae are present, similarly to other abelisaurids,  
510 such as *Carnotaurus*. The prezygapophyses have a sub-triangular contour and are  
511 dorsomedially oriented, a similar shape and inclination to those observed in *Carnotaurus*,  
512 although differing from the prezygapophyses of *Majungasaurus* and *Rahiolisaurus* which are  
513 sub-circular in contour and anterodorsally oriented. They exceed the anterior border of the  
514 centrum, as in *Majungasaurus*, *Carnotaurus* and *Ilokelesia* (Bonaparte et al., 1990; Coria



and Salgado, 1998; O'Connor, 2007). The prezygapophyses are attached to the epipophyses by prezygoepipophyseal laminae, which are relatively straight and different to the markedly convex laminae present in *Dahalokely tokana* (Farke and Sertich, 2013). These laminae in *Viavenator* are well-developed and slightly concave in dorsal and side view, with a smaller inclination than that observed in *Carnotaurus* and greater than that exhibited in *Majungasaurus*. The epipophyses are robust, especially at their distal ends, which are posteriorly projected, as in *Carnotaurus* and other abelisauroids. The postzygapophyses are lateroventrally inclined, as in *Carnotaurus*. They are reduced as in *Carnotaurus* although located in a more posterior position, as in *Majungasaurus* and *Ilokelesia*. The prespinal fossa is deep, bounded by well-developed spinoprezygapophyseal laminae, which are anteriorly projected almost to the medial borders of the prezygapophyses. A deep postspinal fossa is observed, bounded by robust laterodorsally located spinopostzygapophyseal laminae, by the ventral third of the postzygapophyses and ventrally by the intrapostzygapophyseal laminae

#### 4.3.1.3. Fourth cervical.

The fourth cervical vertebra (Fig. 4A-D) presents a dorsoventrally depressed centrum, even more than cervical 4 of *Carnotaurus* and *Majungasaurus* and differently to the cervical 4 of *Ilokelesia* and the anterior cervical of *Ekrixinatosaurus* in which the centrum is rounded in cranial view. The centrum has an almost flat anterior articular facet with a slight concavity in the ventral border, while the posterior articular facet is strongly concave. This condition is also observed in the fourth cervical of *Majungasaurus* (O'Connor, 2007), although in the fourth cervical of *Carnotaurus* and the cervical of *Ilokelesia* tentatively assigned as the fourth, the anterior articular surface is convex and the posterior one is concave (Coria and Salgado, 1998; Méndez, 2014). The anterior and posterior articular surfaces are strongly inclined (40°), a feature related to the dorsoventral flexion of the neck. Laterally the centrum exhibits one pleurocoel, which is located near the posterior border of the centra, as in *Majungasaurus*, and differing from the pair of pleurocoels located on the lateral side of the

centra in *Carnotaurus* and *Ilokelesia*. The ventral surface of the centrum is slightly transversely convex and presents a medial keel on the posterior portion, as in *Carnotaurus*, whereas in *Ilokelesia* this keel is well-developed. On the other hand, in *Majungasaurus* this keel is poorly developed and it can only be seen in the third cervical. The parapophyses are lateroventrally projected as in *Majungasaurus*, although differing from the laterally projected parapophyses of *Carnotaurus*. They have oval articular surfaces, with the major axis dorsoventrally located. The diapophyses are smaller than the parapophyses, they are lateroventrally inclined and are anteriorly joined to the neural arch by prezygodiapophyseal laminae, posteriorly by postzygodiapophyseal laminae, and ventroposteriorly by posterior centrodiapophyseal laminae. The diapophyses are located above the parapophyses, as in *Majungasaurus*, differing from the posterodorsal location of the parapophyses of *Carnotaurus*, which is related with the greater distance between the capitulum and tuberculum of the ribs (Mendez, 2014). The prezygapophysis has a large articular facet that is slightly inclined dorsomedially and anterodorsally exceeds the anterior border of the centrum, as also occurs in *Majungasaurus*, *Carnotaurus* and *Ilokelesia*. Below the prezygapophyses, between the junction of the centroprezygapophyseal and the prezygodiapophyseal laminae, a small pneumatic cavity is located, while another, deeper and larger, is located between the postzygodiapophyseal and the posteriorcentrodiapophyseal laminae. The prezygapophyses are connected with the epipophyses by prezygoepipophyseal laminae. These laminae are shorter and slightly concave in relation to those observed in *Carnotaurus*, *Majungasaurus* and *Ilokelesia*, in which they are longer and straight. In *Dahalokely tokana* (Farke and Sertich, 2013) these laminae are markedly convex. The postzygapophyses have large articular facet slightly lateromedially and posteroventrally inclined, as in *Majungasaurus*, whereas in *Carnotaurus* the lateral inclination is more marked (Méndez, 2014). The neural spine is very low and transversely compressed, similar to that of *Majungasaurus* and *Ilokelesia* although lower than that of *Carnotaurus*. On the other hand, it differs from the spine of the third cervical vertebra of *Majungasaurus* because in *Viavenator* it is very low, located at the posterior half

of the neural arch, it does not exceed the level of epipophyses and it is not inclined posteriorly surpassing the posterior border of the centrum. The prespinal fossa is deep, bounded by well-developed spinoprezygapophyseal laminae, which are anteriorly projected almost to the medial border of the prezygapophyses, whereas in *Ilokelesia* they are projected to the lateral border of the prezygapophyses. The epipophyses have a great development of the posterior projection and a lower development of the anterior projection. This morphology of epipophyses is similar to that observed in *Carnotaurus*, while it differs from that of *Majungasaurus*, *Skorpiovenator* and *Ilokelesia* because in the latter three taxa the epipophyses have developed only a caudal projection. A pronounced development of the anterior projection of the epipophyses in *Viavenator* would provide a larger muscle attachment area, possibly for to the *M. cervicalis ascendens* (Vanden Berge and Zweers, 1993) present in current birds and whose function is linked to dorsiflexion of the neck (Méndez, 2010).

#### 4.3.1.4. Fifth cervical.

The fifth cervical vertebra (Fig. 4E-H) is in general similar to the fourth one, but presents some differences. First, it is slightly larger, especially the neural arch. Furthermore, while the centrum of the C4 has an anterior articular facet almost flat with a slight concavity on the ventral border, the articular facet of the C5 is slightly convex. Also, the prezygapophyses are more anteriorly projected than in the preceding vertebra, conversely to the condition observed in *Carnotaurus* and *Majungasaurus* where the prezygapophyses are less anteriorly projected. The prezygoepipophyseal lamina is short and almost straight, with a much smaller inclination than that observed in *Carnotaurus*. The shape of this lamina differs from the slight convex lamina of *Majungasaurus* and from the sharply convex one of *Dahalokely* (O'Connor, 2007; Farke and Sertich, 2013). The epipophyses have a markedly developed anterior projection and the dorsal margin is straight, differing from the convex margin of the preceding vertebrae. The epipophyses are much more developed than that present in the fifth cervical of *Carnotaurus*. The neural spine is laterally compressed and reduced in

relation to the epiphyses, with marked anterior and posterior bulbous prominences, being different from the spine of *Majungasaurus* which lacks prominences (O'Connor 2007). These surfaces, delimited by the spinoprezygapophyseal and spinopostzygapophyseal laminae, are interpreted as insertion surfaces of interspinous ligaments, which are also present in the cervical 3 and 5 of *Majungasaurus*. As in the fourth cervical vertebra, the neural spine is located posteriorly to the middle zone of the centrum, differing from *Majungasaurus* in which the spine is located on the posterior border and from *Carnotaurus* in which the spine is located above the middle zone of the centrum.

#### 4.3.1.5. Seventh cervical.

As in the previous cervical, the seventh cervical vertebra (Fig. 5A-D) has a centrum longer than high, compressed in the middle zone, and with a slight transverse convexity in the middle of the ventral surface. The centrum has an anterior articular surface with a contour similar to that of cervical 3, although with a slight convexity in the upper third and a small concavity on the lower border, while the posterior articular surface is strongly concave. This condition is evidence of an incipient opisthocoely, which is different from the well-developed opisthocoelic condition exhibited in other abelisaurids as *Carnotaurus*, and *Ekrixinatosaurus*. The articular facets show the inclination related with the S-shape of the neck, although this trait is not as marked as in the preceding cervicals. These facets have a sub-circular contour, with a slight concavity in the dorsal border product of the remarkable size of the neural canal. Laterally the centrum exhibits one pleurocoel, located posteriorly near the posterior border of the centrum, and differing from the pair of pleurocoels on the lateral side of the centrum of *Carnotaurus* (Bonaparte et al., 1990). The parapophyses are lateroventrally projected, but in a less angle than in the fifth cervical. The diapophyses are more laterally projected with respect to the precedent vertebrae, dorsally located with respect to the parapophyses and are attached to the neural arch through prezygodiapophyseal, postzygodiapophyseal and posterior centrodiapophyseal laminae. The pneumatic cavities are markedly developed, and some of them are located around the

diapophyses. Anteriorly to the latter, and below to the prezygapophyses, is observed a relatively small pneumatic cavity with a sub-circular contour, which corresponds to the infraprezygapophyseal fossa. Below the postzygapophysis a larger pneumatic cavity with subcircular contour is located, corresponding to the infrapostzygapophyseal fossa. Finally, a pneumatic infradiapophyseal fossa is observed ventrally to the diapophyses. On the anterior and posterior sides of the neural arch are located laminopeduncular foramina, the anterior one being larger and deeper. The pre- and postzygapophyses have wide articular facets, with a great dorsomedial tilt and the major axis transversely located, as in *Majungasaurus*. The neural spine is compressed both anteroposteriorly and transversely, being relatively higher than the neural spines of the preceding cervical, although its dorsal end is below the level of epipophyses as in *Carnotaurus* and *Majungasaurus* (Bonaparte et al., 1990; Sampson and Witmer, 2007). The spine is located above the posterior half of the centrum, as in the fifth cervical vertebra. In dorsal view, it is observed that the anterior surface of the spine is slightly convex, the lateral sides are concave and the posterior side is flat. The prespinal fossa is deep and wide, bounded by intraprezygapophyseal and spinoprezygapophyseal laminae. The postspinal fossa also is deep and wide and is bounded by the spinopostzygapophyseal laminae, the medioventral edge of the postzygapophyses and the intrapostzygapophyseal laminae. The prezygoepipophyseal lamina is markedly concave in lateral view and strongly dorsally inclined, similar to the condition observed in the seventh cervical of *Carnotaurus* (Bonaparte et al., 1990) and different from that observed in the same vertebra of *Majungasaurus* (O'Connor, 2007), in which this lamina is straight and with a moderate dorsal tilt. The epipophyses have significantly developed anterior and posterior projections, as also occurs in *Carnotaurus* although differing from *Majungasaurus*, *Skorpiovenator* and *Ilokelesia* (Coria and Salgado, 1998; O'Connor, 2007; Canale et al., 2009), in which only the posterior projection is developed.

#### 4.3.1.6. Eighth cervical.

The eighth cervical vertebra (Fig. 5E-H) is badly preserved. It lacks the posteroventral portion of the centrum, the prezygapophyses, the ends of the diapophyses and the epipophyses, and the neural spine. The general morphology is much similar to the eighth cervical of *Carnotaurus*. The most remarkable difference is that the diapophyses in *Viavenator* are projected just behind the parapophyses, as in *Majungasaurus*, while in *Carnotaurus* the diapophyses are more posteriorly located and thus indicating a greater distance between the tuberculum and the capitulum of the corresponding cervical rib.

#### 4.3.1.7. Ninth cervical.

The ninth cervical vertebra (Fig. 6A-D) is nearly complete, lacking only both epipophyses and the left prezygapophysis. The centrum has anterior and posterior articular surfaces parallel each other and perpendicular to the floor of the neural canal. The ventral surface of the centrum is concave in lateral view. . The anterior articular surface is almost flat and with a sub-circular contour, while the posterior articular surface is circular and remarkably concave, similar to that observed in *Carnotaurus* (Méndez, 2014). Two pneumatic foramina are observed on the lateral side of the centrum, one located anteriorly with respect to the other. Prominent parapophyses are anteroventrally located in the centrum. There is no evidence of a ventral keel, as in *Majungasaurus*, which is present in *Carnotaurus* (Méndez, 2014). The diapophyses are more laterally than ventrally projected, while in *Carnotaurus* these structures reach a more ventral and posterior position. The prezygapophyses are subtriangular and mediodorsally oriented, as in *Carnotaurus*. The anterior ends of the prezygapophyses barely surpass the anterior border of the centrum, as in *Carnotaurus*, while in *Majungasaurus* the anterior projection is much more marked (Méndez, 2014). The prezygoepipophyseal lamina is almost straight and strongly tilted dorsally, as in *Carnotaurus*. The distal end of the epipophyses shows an anterior and a posterior projection, similarly to *Carnotaurus*, but less developed than in the two preceding vertebrae already described. The pre- and postspinal fossae are very wide and present rough surfaces, as those seen in *Carnotaurus* (Méndez, 2014).

## 677 4.3.1.8. Tenth cervical.

678 The tenth cervical vertebra (Fig. 6E-H) has a cylindrical centrum with parallel articular  
679 surfaces which are perpendicular to the floor of the neural canal, as in the ninth and tenth  
680 cervical vertebrae of *Carnotaurus*, *Majungasaurus* and *Ekrixinatosaurus*. In ventral view a  
681 marked constriction is observed in the middle part of the centrum, as in *Carnotaurus*,  
682 *Majungasaurus*, the abelisaurid MPM-99 (Martínez et al., 2004) and, although less marked,  
683 in *Ekrixinatosaurus*. However, as in the preceding cervical, in lateral and ventral sides the  
684 centrum exhibits a slight but visible convexity (Fig. 6H), which is not recorded in any other  
685 abelisaurid. On the ventral surface, the centrum does not show a ventral keel, as in  
686 *Majungasaurus* (O'Connor, 2007), or a modest keel, as that present in *Carnotaurus*  
687 (Méndez, 2014). The centrum has a slightly concave anterior articular facet, as in  
688 *Majungasaurus*, and a strongly concave posterior facet. The anterior articular surface has a  
689 flat and a concave dorsal and ventral border, respectively, while the posterior articular facet  
690 presents a sub-circular contour with slightly concave dorsal border, as also is observed in  
691 the preceding vertebra. The centrum exhibits two pleurocoels in its lateral surface, as in  
692 *Carnotaurus*, *Ekrixinatosaurus* and MPM-99, one located posterodorsally to the  
693 parapophysis and the other posteriorly located, near the posterior border of the centrum.  
694 *Majungasaurus* differs from this condition because it has one pleurocoel dorsally located and  
695 anteriorly to the parapophyses (O'Connor, 2007)). The parapophyses are located on the  
696 anterior border of the centrum, they are lateroventrally projected, they have oval articular  
697 surfaces with the major axis in dorsoventral direction and they are slightly inclined ventrally.  
698 The diapophyses are well-developed and are lateroventrally projected over the neural arch.  
699 They are attached to the centrum by the anterior and posterior centrodiaophyseal laminae  
700 and by prezigodiapophyseal and postzigodiapophyseal laminae. In lateral view, the height of  
701 the diapophyses greatly precludes observation of the position of the parapophyses, as in  
702 *Carnotaurus*, whereas in *Majungasaurus* and *Dahalokely* the diapophyses are more dorsally  
703 located (O'Connor, 2007; Farke and Sertich, 2013). The laminopeduncular foramina are less



conspicuous than in anterior cervicals. In *Carnotaurus*, *Ekrixinatosaurus*, *Majungasaurus* and MMP-99, these foramina are only present in the anterior neural arches (Méndez, 2010). As in the anterior cervicals, the infraprezygapophyseal fossae are at the junction between the centroprezygapophyseal and prezygodiapophyseal laminae, although it is more developed in the remaining cervical vertebrae. The posterior infrapostzygapophyseal fossa is delimited by the postzygodiapophyseal and centrodiapophyseal laminae. This fossa is deep and large, as that of the anterior cervicals. The prezygapophyses have extensive articular facets, subtriangular in shape, with the major axis lateromedially located and strongly dorsomedially inclined. They are anteriorly projected and exceed the anterior border of the centrum, as in *Carnotaurus*, while in *Majungasaurus* this projection is more pronounced (Méndez, 2014). The postzygapophyses have extensive articular facets, which are subtriangular and strongly lateroventrally inclined. The neural spine is transversely wide and anteroposteriorly compressed, it is located at approximately above the middle zone of the centrum, and it surpasses in height the epipophyses, as in *Majungasaurus*, although conversely to that observed in *Carnotaurus* in which the epipophyses are higher (Méndez, 2014). The prespinal fossa is less extensive than in the anterior cervicals, whereas the postspinal fossa is wide and deep. On the anterior surface of the neural spine is observed a rough, irregular zone, which extends from the middle of the prespinal fossa and is delimited by two lateral grooves. This roughened surface is similar to that present in *Carnotaurus* and is interpreted as an insertion area for interspinous ligaments. For its part, the postspinal fossa presents a cavity bounded by spinoepipophyseal and interpostzygapophyseal laminae. The epipophyses are smaller than those of the anterior cervicals, they are similar to those observed in *Majungasaurus* and MPM-99 although they differ from the epipophyses of *Carnotaurus* and *Ekrixinatosaurus*, which are well-developed even on the last cervical vertebrae.

#### 4.3.2. Dorsal vertebrae

##### 4.3.2.1. Second dorsal.



The second dorsal vertebra (Fig. 7A-D) has an amphicoelus spool-shaped centrum, characteristic of the anterior dorsals of the abelisaurids (e.g., *Carnotaurus*, *Majungasaurus*, and *Rajasaurus*; Bonaparte et al., 1990; Wilson et al., 2003; O'Connor, 2007). The ventral surface has a longitudinal shallow groove, more developed in the anterior half of the centrum, thus differing from the incipient keel present in *Majungasaurus* (O'Connor, 2007) or the marked keel observed in *Rajasaurus* (Wilson et al., 2003). The anterior articular surface is slightly concave and has an elliptical contour, with the major axis transversely located, as in *Carnotaurus* and *Rajasaurus*, while the posterior articular surface is strongly concave, with a sub-circular contour and with a concave dorsal border. The parapophyses have elliptical articular facets with the major axis in dorsoventral direction, as in *Carnotaurus*, *Majungasaurus*, *Rajasaurus* and *Dahalokely*, and are located in a more dorsal position with respect to those of the posterior cervicals. In *Carnotaurus*, the parapophyses in the second dorsal vertebra are located more ventrally. The articular surface of the parapophyses is oriented laterally as in *Carnotaurus*, *Majungasaurus*, *Rajasaurus* and *Dahalokely*. The parapophyses have a short and strong bony edge, located just below to the pleurocoel. The centrum laterally shows an infradiapophyseal fossa, delimited by the anterior and posterior centrodiapophyseal laminae. An isolated pneumatic foramen is posteriorly located at the parapophyses, as in *Majungasaurus*, *Rajasaurus* and *Xenotarsosaurus* (Martínez et al., 1986; Wilson et al., 2003; O'Connor, 2007), which is not present in the second dorsal of *Carnotaurus* (Bonaparte et al., 1990). The prezygapophyses have transversely elliptical articular surfaces, slightly inclined dorsomedially and whose anterior end exceeds the anterior border of the centrum. Below the prezygapophyses are observed infraprezygapophyseal fossae, which are bounded by the prezygapophyses, and the prezygodiapophyseal, the centroprezygapophyseal and the anterior centrodiapophyseal laminae. The laminopeduncular foramina are present at the sides of the neural canal, as in the posterior cervical vertebrae. The diapophyses project dorsolaterally in an approximately 30° angle, resembling the condition of *Carnotaurus* although differing from the diapophyses of *Majungasaurus* which project laterally in a right angle with respect to the transverse plane.

From the diapophyses extend four laminae: the prezygodiapophyseal, a thin anterior centrodiapophyseal, a robust posterior centrodiapophyseal and the postzygodiapophyseal. On the distal third of the dorsal face of the diapophyses is observed a notable crest, which proximally turns back over the posterior border. This structure can be interpreted as a muscle anchorage, probably for the insertion of the *M. tendinoarticularis* in Crocodylia or its homologous *M. ascendens thoracicus* in Neornithes (Organ, 2006), or also as insertion scars of intervertebral ligaments. The distal end of the diapophyses has a subtriangular contour, with a strong concave surface with an edge anterodorsally more marked. The postzygapophyses have subtriangular articular facets which are ventrally inclined and which not exceed the posterior border of the centrum. A well-developed hyposphene is observed, differently from *Majungasaurus* and *Carnotaurus* in which the hyposphenes are incipiently present from the third thoracic vertebra (Bonaparte et al., 1990; O'Connor, 2007). The neural spine has a square aspect in lateral view and is posteriorly inclined exceeding the distal end of the diapophyses. A small prespinal fossa is located on the base of the neural spine, whereas the postspinal fossa is larger and deeper and is bounded by the spinopostzygapophyseal and the interpostzygapophyseal laminae. The neural spine has a wide and triangular anterior surface that presents a bulbous structure on the distal portion. Posteriorly, a similar thickened bulbous structure is observed on the posterolateral border of the spine. Both the anterior and posterior protuberances are dorsally developed and exceed the dorsal end of the neural spine.

#### 4.3.2.2. Fourth dorsal.

The fourth dorsal vertebra (Fig. 7E-H) differs from the previously described dorsals because the anterior articular surface presents a sub-circular contour. On the ventral surface of the centrum is extended a groove, which is more conspicuous than that present in the second dorsal. The parapophyses are more laterally projected and their articular surfaces are

smaller in diameter and located on the neural arch, similarly to those observed in dorsal 4 of *Majungasaurus* although differing to those of dorsal 4 of *Carnotaurus* in which they are still located on the centrum. Lamination of this vertebra is more complex than that of the preceding dorsals, and is composed by a centroparapophyseal lamina, and a prezygoparapophyseal and a centrodiaepophyseal lamina connected to the anterior and posterior parts of the parapophyses, respectively. Dorsally to the parapophyses is extended a prezygoparapophyseal lamina, which joins dorsally to the prezygodiaepophyseal lamina, generating two pneumatic cavities, one anterior and other posteriorly located to the lamina, being the lateral the most developed. This lamina and the cavities are more conspicuous on the left side of the vertebra. The prezygapophyses are smaller than in the dorsal 2 and they have nearly horizontal facets with a hypantrum between them. Posteriorly, the hyposphene exhibits inverted cone morphology, as in *Carnotaurus* (Bonaparte et al., 1990). The neural spine is rectangular in lateral view and slightly reclined, similar to that observed in dorsal 4 of *Majungasaurus* (O'Connor, 2007). This spine lacks the large bulbous structures present in the preceding dorsal, but exhibits a brief longitudinal ridge. The side bulbous structures are close to the anterior border of the spine and have anteriorly projected thorny extensions, which are interpreted as part of an accessory interspinous articular system, being this a feature not reported in other theropods.

#### 4.3.2.3. Fifth dorsal.

The fifth dorsal vertebra (Fig. 8A-D) has a spool-shaped and slightly amphicoelus centrum. On the ventral surface is not observed a marked groove as in the preceding dorsals or a keel such as that present in dorsal 5 of *Carnotaurus* (Méndez, 2010). Both articular facets have a subcircular contour with a straight dorsal border. The centrum exhibits a pair of pneumatic foramina, one of them anteriorly located above the parapophyses and a larger one posteriorly located. The parapophyses are located on the neural arch, below the level of the prezygapophyses. Their articular facets are concave, subcircular in contour, smaller than in the anterior dorsals, and slightly projected in dorsoventral direction. The parapophyses are

reinforced by several laminae, including an anterior centroparapophyseal that joins to the anterior border of the centra, one posteriorly joined to the anterior centrodiapophyseal lamina, a short prezygoparapophyseal, and a prezygoparapophyseal that joins to the prezygodiapophyseal. The prezygapophyses are small and with a sub-circular contour, they are inclined anterodorsally surpassing the anterior border of the centra, and show the same inverted cone morphology observed in *Carnotaurus* (Bonaparte et al., 1990; Méndez, 2010). The hyposphene and the hypantrum are more developed than in the preceding dorsals. The diapophyses have a wing-shaped contour in dorsal view and are lateroposteriorly projected, with a convex anterior margin and a concave posterior one. This morphology is similar to that illustrated for dorsal 5 of *Carnotaurus* (Bonaparte et al., 1990), whereas it differs from dorsal 5 of *Majungasaurus* because in this taxon the anterior margin of the diapophyses is less curved and the posterior margin is almost straight (Méndez, 2010). The diapophyses are reinforced by a series of laminae, including a thin prezygodiapophyseal, a robust centrodiapophyseal, a parapodiapophyseal and a postzygodiapophyseal. The dorsal surface of the diapophyses exhibits a crest located on the distal third, similar to that observed in dorsal 2. The postzygapophyses have articular facets with a subcircular contour, placed horizontally with respect to the centrum, and they do not exceed the posterior border of the centrum. The hyposphene is strongly developed. The neural spine is square-shaped in lateral view and it is anteroposteriorly longer than the neural spine of the anterior dorsals. It is slightly posteriorly inclined, exceeding the level of the diapophyses. Despite the spine is damaged at its distal end, it is possible to observe the same projected structures like those present in the preceding dorsal, although much more robust. The pre- and postspinal fossae are proportionally equal in size; they are deep and located at the base of the spine.

#### 4.3.2.4. Seventh to tenth dorsal.

These groups of dorsal vertebrae were recovered articulated between them and they have particular characteristics (Fig. 9A-C). The centra are typically spool-shaped, with strongly concave lateral surfaces in ventral view. The articular surfaces of the centra are subcircular

with straight dorsal borders. The centra exhibit laterally a pair of pneumatic foramina, one anteriorly located and the other in the middle part of the centra, being the latter larger. Conversely, the dorsal 7, 8 and 10 of *Carnotaurus* (Bonaparte et al., 1990) show only one pneumatic foramen in a more anterior position, and only the dorsal 9 has two foramina. Other abelisaurids such as *Majungasaurus* (O'Connor 2007) do not present pneumatic foramina in the centra. The parapophyses have a subcircular outline, they are smaller than in the anterior dorsals and they are located just above the prezygapophyses in dorsal 7-9 and slightly dorsally located in dorsal 10. The parapophyses are laterally projected. Anteroventrally they are reinforced by the anterior centroparapophyseal lamina, dorsally by the paradiapophyseal lamina, which in turn is attached medially to the prezygodiapophyseal lamina, and posteriorly by a posterior paradiapophyseal lamina, which in turn is attached to the centrodiaophyseal lamina. The prezygapophyses of the first articulated vertebra have subcircular and small articular facets, horizontally oriented and anteriorly projected so they exceed the anterior border of the centrum. The hypantrum of dorsal 7 is well-developed, while the hyposphene of dorsal 10 is damaged and its morphology it is not observable. The transverse processes are wing-shaped in dorsal view, lateroposteriorly projected and with a dorsal inclination of approximately 40°. The diapophyses are reinforced anteriorly by a thin prezygodiapophyseal lamina much more developed in dorsal 7 and 8, ventrally by a robust centrodiaophyseal lamina and posteriorly by a postzygodiapophyseal lamina. The articular surface of the diapophyses is subtriangular in dorsal 7 and changes to a sub-circular shape in dorsal 10. The postzygapophyses are not easily observable, due to contact between vertebrae and the severely damaged posterior part of dorsal 10. The neural spines are transversely compressed and anteroposteriorly wide, with parallel anterior and posterior borders and are slightly posteriorly reclined. On the distal end of the neural spines there are cylindrical structures anteriorly and posteriorly projected, which contact with the same structures present on the spines of the adjacent vertebrae and thus connecting successive neural spines (Fig. 1A, D). These structures form part of an accessory intervertebral system, located at the distal end of the neural spines in the presacral vertebrae, which seems to

emerge on the anterior dorsals and acquires its greatest development in the posterior dorsals. These types of structures that form a strongly developed accessory articular interspinous system in *Viavenator* was not documented in any other abelisaurid to date. The Malagasy abelisauroid *Dahalokely* has slightly developed anterior and posterior projections on the distal end of the neural spines on the posterior dorsals (Farke and Sertich, 2013), but they differ significantly from the structures here described for *Viavenator*. Pre- and postspinal fossae are proportionally equal in size; they are deep and located at the base of the spines.

#### 4.3.3. Costal elements

##### 4.3.3.1 Cervical ribs.

Seven cervical ribs of *Viavenator* are preserved. They are tentatively identified as cervical ribs 3?, 8? and 10, on the right side, and the pairs of cervical ribs 5? and 7, articulated to the corresponding vertebrae (Fig.13A-E). *Viavenator* shows important pneumatic foramina in the anterior and posteromedial side of the cervical ribs, except in cervical rib10, as also occurs in *Majungasaurus* (O'Connor, 2007). The shaft in cervical rib10 is proximally bifurcated, as is observed in some cervical ribs of *Masiakasaurus*, *Carnotaurus* and *Majungasaurus*. The shaft of the cervical ribs is laterally convex, as in *Majungasaurus* and *Carnotaurus*. According to O'Connor (2007) this form allows the overlapping of adjacent ribs, which would be related to an interlocking osseoligamentous cervical complex. None of the styliform processes have been preserved in the cervical ribs. Cervical rib 3? of *Viavenator* is incomplete, although presents a tuberculum and a capitulum well-defined. The lateral surface of the tuberculum is concave. The anterior process of the rib is broken and only the proximal portion of the shaft has been preserved. With the exception of cervical rib 10, in all the other preserved cervical ribs the capitulum and the tuberculum project perpendicularly to the proximal region of the shaft, whereas in *Majungasaurus* they project in a more marked anterior angle. In *Viavenator*, the inclination of the capitulum and the tuberculum in cervical rib 10 is less than in *Majungasaurus*. In all the preserved cervical ribs these articular processes are connected through a short capitulotubercular web (O'Connor, 2007), a condition also observed in *Majungasaurus*. The tuberculum presents a quadrangular

articular surface, whereas the capitulum presents a subcircular and smaller articular surface. Towards the cervical rib10, the capitulum increases in length, becoming longer than the tuberculum. The lateral borders of the shafts of cervical rib5 and cervical rib 7 are convex, while in cervical ribs 8? and 10 they are straight, as in *Majungasaurus*.

#### 4.3.3.2. Dorsal ribs.

Six left and eight right dorsal ribs have been preserved (Fig. 14A-E). The general morphology of these is similar to the dorsal ribs of *Majungasaurus* and *Carnotaurus* (Bonaparte et al., 1990; O'Connor, 2007). The proximal region of the ribs of *Viavenator* and *Carnotaurus* differs from that of *Majungasaurus* in the presence of pneumatic cavities in the posterior side close to the tuberculum. The anterior dorsal ribs are longer and thicker and present a large capitulum and a robust tuberculum, as in *Carnotaurus*. The size and length of each rib decreases posteriorly, and the shaft of the capitulum becomes shorter, while the parapophyses migrate dorsally.

#### 4.3.3.3. Gastralialia.

Many slender fragments of bone were found in the quarry, which were assigned to gastralialia (Fig. 14F). One of these fragments is V-shaped, and is interpreted as a caudal acutely angled gastralium (Claessens, 2004), located near the pubis. The available gastralium has a subcircular diameter in cross-section and is fused in the ventral midline, where it is anteroposteriorly compressed.

#### 4.3.4. Caudals

##### 4.3.4.1. Anterior caudals.

The most anterior of the preserved caudal vertebrae (probably caudal8) has a damaged neural arch (Fig. 10A-D), although it is still possible to recognize the most typical features of these vertebrae in abelisaurids. This caudal vertebra is very similar to the caudal 9 of *Carnotaurus* (Bonaparte et al., 1990) and caudal 8 of *Aucasaurus* (Coria et al., 2002). The centrum is slightly amphicoelus, without distinctive pneumatic features. The articular surfaces of the centrum are slightly higher than wide, and in lateral view the anterior surface has a concave border whereas the posterior one has a convex one. The ventral surface has



a shallow groove. The preserved part of the neural arch presents a well-defined hyposphene and hypanthrum, and a narrow neural spine with a prespinal fossa showing cavities separated by a bony septum (Fig. 10C, D). Only the proximal part of the transverse processes is present. These seem to be slightly inclined upward and backward, and centrodiapophyseal laminae are distinguished covering the ventral surface of the processes. The following two caudal vertebrae (Fig. 10E-J) are morphologically similar to caudals 9 and 10 of *Aucasaurus*, with spool-shaped centra and a neural arch dominated by the presence of hypertrophied transverse processes. In these vertebrae the presence of a hyposphene-hypanthrum accessory articulation, a well-developed character in *Carnotaurus* and *Aucasaurus* and incipient in *Majungasaurus*, is barely observable due to poor the preservation of the pre- and postzygapophyses. The transverse processes are inclined dorsally in an angle of 40°, which is somewhat lower than that observed in *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus* (Bonaparte et al., 1990; Coria et al., 2002; Calvo et al., 2004) and MACN-RN-1012 (Ezcurra and Méndez, 2009) but higher than in *Pycnonemosaurus* (Kellner and Campos, 2002), *Skorpiovenator* (Canale et al., 2009), MPEFV-1699 (Rauhut et al., 2003), MPM-99 (Martínez et al., 2004), *Majungasaurus* (O'Connor, 2007) and *Rahiolisaurus* (Novas et al., 2010; Méndez, 2014). The distal ends of the transverse processes show a marked distal expansion with a tapered process anteriorly directed, as in *Carnotaurus* and *Aucasaurus*. Ventrally, the transverse processes present a well-developed centrodiapophyseal lamina, as is also observed in some abelisauroids (e.g., *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Ekrixinatosaurus*, *Skorpiovenator*, *Rahiolisaurus*, MPM-99-V-1699 MEFP and MACN-RN-1012; Méndez, 2014), and also it has a ventral keel, similarly to other abelisaurids as *Carnotaurus*, *Aucasaurus*, *Ekrixinatosaurus* and MACN-RN 1012 (Ezcurra and Méndez, 2009; Méndez, 2014). The neural spine is transversely narrow and is located on the posterior portion of the neural arch.

#### 4.3.4.2. Middle caudals.



Four middle caudal vertebrae were recovered (Fig.10K-M and Fig. 11A-B). One of them is considered as the most anterior and is the better preserved, while the remaining correspond to an incomplete caudal and two incomplete centra. All the centra are amphiplatyan, elongated and with the typical spool-shaped morphology. On the ventral surface, they exhibit a medial longitudinal shallow groove, unlike the keel present in *Ilokelesia* (Méndez, 2010) and *Rahiolisaurus* (Novas et al., 2010). The articular surfaces of the centra are concave and circular in contour, as in *Ceratosaurus*, *Ilokelesia*, *Ekrixinatosaurus* and *Rahiolisaurus*. The articular surfaces for the haemal arches are still observable. The middle caudals lack hyposphene-hypanthrum, as in *Ilokelesia*. The best preserved middle caudal, considered as the most anterior one, has laterodorsally projected and distally expanded transverse processes (Fig.10K-M). As in proximal caudals, the distal ends of the transverse processes have an anterior and a posterior projection, the posterior one being larger. In dorsal view (Fig. 10M), the transverse processes have anterior and posterior concave borders, as in the anterior caudals. The neural arch presents a neural spine anteroposteriorly shorter and located in a more posterior position, with respect to the anterior caudals. The pre- and postzygapophyses are elongated structures which project beyond the border of the centrum. The postzygapophyses are laterally separated from the neural spine, and they do not form a postspinal fossa between them. The following caudal vertebra differs by having less developed transverse processes, which are visible despite they are eroded (Fig. 11A-B). This caudal presents a low neural arch which has almost the same length of the vertebral centrum. In dorsal view the neural arch is wide and almost flat, medially delimited by a shallow ridge that is well-developed anteriorly close to the base of the prezygapophyses, and also is well-developed posteriorly where it becomes part of the neural spine. The pre- and postzygapophyses are not preserved, although it is inferred that they were well-developed and surpassing the border of the centrum, as in *Majungasaurus*. On the lateral surfaces of the neural arch is observed part of the transverse processes, which are less developed than those of the most anterior caudals.

#### 4.3.4.3. Distal caudals.

Two distal caudal vertebrae were recovered (Fig. 11C-F). One of them (Fig. 11C, D) has only preserved the centrum, the anterior half of the neural arch and the left prezygapophysis. The centrum is elongated and shows a marked polygonal shape due the presence of longitudinal ridges separating the lateral surfaces, as occurs in *Rahiolisaurus* (Novas et al., 2010). As in the middle caudals, the lateral and ventral sides are concave in anteroposterior direction. A ventral groove is absent. The neural arch is very low and almost equals the centrum in length. The prezygapophysis is slender and curved, with a convex dorsal and a concave ventral border, in lateral view. It is anterodorsally projected, exceeding the anterior border of the centrum by about one third of the length of the centrum, as in *Majungasaurus*. The articular facet of the prezygapophysis is medially inclined. Finally, the most distal caudal vertebra (Fig. 11E, F) has only preserved the centrum and part of the neural arch. As in the other distal vertebra preserved, the centrum has concave lateral and ventral surfaces. The only preserved parts of the neural arch are the lateral walls of the neural canal.

#### 4.3.4.4 Haemal arch.

Only one posterior haemal arch has been recovered (Fig.15A-C). It is relatively short, with a dorsally enclosed canal, as in *Carnotaurus*, *Ilokelesia* and *Majungasaurus* (Bonaparte et al., 1990; Coria and Salgado, 1998; O'Connor, 2007), and differing from the open condition present in *Aucasaurus* (Coria et al., 2002). It is transversely compressed, especially on the distal end, where it is also posteriorly projected. It has two different facet joints, one anterodorsal and another posterodorsal, the first being relatively longer, as in *Majungasaurus*. *Majungasaurus* has anterior and posterior haemal arches with a dorsally enclosed canal, so it is possible to infer this condition for the anterior arches of *Viavenator*.

#### 4.3.5. Scapulocoracoid

A complete left scapulocoracoid (Fig. 12 A-E) has been recovered. The scapulocoracoid suture is internally scarcely observed, which would indicate an adult ontogenetic state. The

scapular blade is proximodistally shorter and anteroposteriorly narrower (Table 1) than in *Majungasaurus* (Burch and Carrano, 2012). It presents a marked posteroventral widening, which confers a recurved appearance to the blade. Conversely, the distal end of the scapular blade slightly widens in *Ceratosaurus* (Madsen and Welles, 2000) and *Majungasaurus*, while in *Carnotaurus* it lacks any widening (Burch and Carrano, 2012). In cross section, the scapular blade is lateromedially compressed, in a similar way to *Majungasaurus* and *Carnotaurus*. The three proximal quarters have a form of teardrop becoming totally narrow in the distal end whereas in *Majungasaurus* the form of teardrops present only in the proximal part. The anterodorsal margin of the scapula is gradually expanded, the acromion is not observable because this sector has not been preserved. In lateral view, below the dorsal border of the scapula, just behind the acromion, there is a marked osseous ridge, which does not appear to be present in *Majungasaurus* or *Carnotaurus*. Posterodorsally to the glenoid cavity a deep fossa is observed, as in *Majungasaurus*. Posteroventrally to this fossa, on the posteroventral edge of the scapular blade, is located an elongated tubercle which probably is for the insertion of the *M. triceps brachii caput scapulare* (Jasinoski et al., 2006). The glenoid cavity has well-defined edges and is slightly laterally oriented, as also occurs in *Majungasaurus*. The scapular lip of the glenoid has a marked development as in *Carnotaurus* and more than in *Majungasaurus*. The development of these two structures makes the notch between them much more noticeable. The coracoid is long, with a rounded anteromedial margin and a posteroventral process which, although incomplete, it is inferred that it is prominent, all these conditions also observed in *Majungasaurus*. Anteriorly to the glenoid cavity, a roughness is observed, also present in *Majungasaurus*. Anteroventrally to this roughness is present the coracoid foramen, which passes through the bone obliquely. Anteroventral to the scapulocoracoid suture a subcircular contour depression is observed (subacromial depression sensu Bonaparte et al 1990), different from that present in *Carnotaurus* and *Majungasaurus*. Anteroventrally to the glenoid cavity is located the biceps tubercle for insertion of the *M. biceps brachii* (Jasinoski et al., 2006). Posteriorly to the subglenoid crest, is located the

subglenoid fossa, which presents a relatively triangular form and where the *M. brevis coracobrachialis* (Jasinoski et al., 2006) was probably inserted.

#### 4.3.6. Fibula

The proximal end of the right fibula is preserved (Fig. 12D-F). The bone is 13.5 cm in proximal width, and 6 cm in transverse length. The bone fragment has a marked anteroposterior expansion. In proximal view, it shows a rounded anterior margin and a more angular posterior one. This is also observed in the abelisauroids *Xenotarsosaurus* (Martínez et al., 1986), *Majungasaurus* (Carrano, 2007) and *Masiakasaurus* (Carrano et al., 2002, 2011) as well as in *Ceratosaurus* (Madsen and Welles, 2000), *Neovenator* (Brusatte et al., 2008) and *Tyrannosaurus* (Brochu, 2003). The fragmentary nature of the fibular shaft precludes the observation of the iliofibularis tubercle. In medial view, the most posterior sector is occupied by the fibular fossa, which, despite being incomplete, it can be observed that it is ellipsoidal. Thus this fossa has a shape and a location which resemble those observed in the abelisaurids *Majungasaurus* (Carrano, 2007) and *Rahiolisaurus* (Novas et al., 2010), and the abelisauroids K27/620 (Novas et al., 2004) and MPMA 08-0069-13 (Méndez et al., 2014). In *Ceratosaurus* and *Berberosaurus* (Allain et al., 2007) the fibular fossa is less developed. On the other hand, this fossa has a great development in the noasaurid *Masiakasaurus*. In lateral view, it is possible to observe on the upper margin, a conspicuous convex bulge. This structure, anteroposteriorly positioned, has not been observed in other taxa, and it could be an autapomorphy of *Viavenator* or maybe a bone pathology of this specimen.

#### 4.3.7. Ischial boot

Only the distal ends of both ischia (Fig. 12G-I) have been preserved. They are fused distally forming an ischial "boot", as in the noasaurid *Masiakasaurus* (Carrano et al., 2011), and the abelisaurids *Carnotaurus* (Bonaparte et al., 1990) and *Majungasaurus* (Carrano, 2007). The ischial "boot" of *Viavenator* is posteroventrally expanded and with a triangular form in proximal view, as in *Carnotaurus* and *Majungasaurus*, although it differs markedly from

the condition observed in *Eoabelisaurus* (Pol and Rauhut, 2012), in which this expansion is poorly developed.

## 5. Discussion and Conclusion

In the preliminary description of *Viavenator* (Filippi et al., 2016) were discussed the implications of the phylogenetic position of this taxon. The phylogenetic analysis performed in that work found *Viavenator* in an intermediate placement between Cenomanian-Turonian brachyrostran abelisaurids (e.g., *Skorpiovenator* and *Ekrixinatosaurus*) and Campanian-Maastrichtian brachyrostran abelisaurids (e.g. *Carnotaurus* and *Aucasaurus*). Related to this was commented that *Viavenator* presents highly-derived postcranial characters, which are shared with *Carnotaurus* and *Aucasaurus*, and a relatively plesiomorphic skull in comparison with these two taxa (Filippi et al., 2016). This interesting combination of features can be characterized in detail, based on the exhaustive osteological description made here. The plesiomorphic traits of the skull of *Viavenator* are mainly related with the anatomy of frontals. The frontals in this taxon lack osseous prominences such as domes or horns, which conversely are present in *Carnotaurus* and *Aucasaurus*. On the other hand, the vertebral features are considered derived and shared with the younger members of this group (i.e. *Carnotaurus*, *Aucasaurus*). Thus, the shape of the epipophyses of the cervical region, which are characterized by anterior and posterior projections, is shared by *Viavenator* and *Carnotaurus*, whereas it is not present in pre-Santonian forms such as *Ilokelesia* and *Skorpiovenator* or in non-brachyrostran abelisaurids. The marked development of the hyposphene-hypanthrum complex in the anterior caudal vertebrae observed in *Viavenator* is shared with *Aucasaurus* and *Carnotaurus*, whereas is only incipient in *Majungasaurus*. Further, the transverse processes of the caudal vertebrae of *Viavenator*, *Aucasaurus* and *Carnotaurus* have distal ends only anteriorly projected, in contrast with non-furileusaurian brachyrostrans, such as *Ilokelesia* and *Ekrixinatosaurus*, in which the distal end is projected both in anterior and posterior direction.

The derived vertebral characters mentioned, which are shared between *Viavenator*, *Aucasaurus* and *Carnotaurus*, are considered together as a specialization of the members of Furileusaria, which is linked with an increase in the structural rigidity of the vertebral column (Filippi et al., 2016, Méndez, 2010, Méndez, 2014a, b) and a particular disposition of the epaxial and hypaxial musculature (Méndez, 2010, Persons and Currie, 2011). Moreover, *Viavenator* exhibits a greater development of the vertebral accessory joint structures, since the hyposphene-hypanthrum complex is present from dorsal 2 onward, whereas in *Carnotaurus* and *Majungasaurus* this complex is well-developed from dorsal 4 onward. Further, is remarkable the presence of the accessory joints in the neural spines from dorsal 7 to 10 in *Viavenator*, which is a character not previously documented for any other known abelisaurid.

Another character shared with *Carnotaurus* and *Aucasaurus* is the presence of pneumatic openings along the entire dorsal series. This is a condition not observed in the most basal abelisaurids and neither in the majungasaurines (the clade including *Genusaurus*, *Arcovenator*, *Rajasaurus*, *Indosaurus* and *Majungasaurus*, sensu Filippi et al., 2016).

The transverse processes of the caudal vertebrae also show interesting changes, not only in their morphology but also in their position with respect to the corresponding vertebra. The elevation above the horizontal plane is checked in the anterior caudal vertebrae of all abelisaurids although among members of Brachyrostra there is a trend to increase the dorsal elevation of the transverse processes, which culminates with the strongly dorsally oriented processes of more derived taxa of this clade (e.g. *Aucasaurus*, *Carnotaurus*) (see Persons and Currie, 2011). *Viavenator* has transverse processes more dorsally oriented than basal brachyrostrans, such as *Ilokelesia* and *Ekrixinatosaurus*, although the angle of inclination is similar to that present in the caudals of *Skorpiovenator* (see Persons and Currie, 2011) and *Pycnomemosaurus* (Kellner and Campos, 2002). On the other hand, this angle is less than that observed in the caudals of *Aucasaurus* and *Carnotaurus*. In this way,

the inclination of the transverse processes of caudals of *Viavenator* also seems to represent a transitional condition between basal brachyrostrans and derived ones.

## 6. Concluding Remarks

As was explained above, in *Viavenator* coexists plesiomorphic characters in the skull with derived postcranial traits together, being this a particular anatomy which suggests that this taxon is a transitional form between basal brachyrostrans (e.g. *Skorpiovenator*, *Ilokelesia*) and more derived ones (i.e., *Carnotaurus* and *Aucasaurus*). This idea is supported by the intermediate phylogenetic position of *Viavenator* (sensu the phylogenetic analysis of Filippi et al., 2016), between basal and derived members of Brachyrostra. Moreover, this phylogenetic position is consistent with the stratigraphic provenance of these abelisaurids, since *Viavenator* occupies the time gap between the brachyrostrans of the lower Upper Cretaceous and those of the end of the Cretaceous (Filippi et al. 2016).

The radiation of the brachyrostran abelisaurids during the Upper Cretaceous in South America probably was favored by the extinction of the Carcharodontosauridae in the Turonian-Coniacian boundary (Apesteguía, 2002; Leanza et al., 2004; Novas et al., 2013). Also, the isolation of South America was a determinant factor. This placed brachyrostrans between the largest predators of this continent in the Santonian–Maastrichtian time span. Probably, one of the consequences of this radiation and the new ecological placement of these theropods was the specialization of some regions of the skeleton. Thus, the characteristic intervertebral articular joins of Abelisauridae was enhanced in the Upper Cretaceous South American brachyrostrans, i.e. the Furileosauria, which possibly was linked with an increase in the cursorial abilities (Persons and Currie, 2011) and this in turn markedly influenced the predatory habits of these abelisaurids.

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**Figure captions.**

**Figure 1.** Skull of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A) in dorsal, (B), posterior, (C), right lateral and (D) ventral views. Scale bar: 5 cm.

**Figure 2.** Probable Hyoid of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530 (A), and Tooth in lateral view, with detail of denticle carinae (B). Scale bar: (A) 5 cm and (B) 1 cm.

**Figure 3.** Anterior cervical vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Atlas (A), in anterior, (B), left lateral, (C), and posterior views. Third cervical vertebrae (D), in anterior, (E), dorsal, (F), posterior, (G) and left lateral views. Scale bar: 5 cm.

**Figure 4.** Anterior cervical vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A-D), fourth, (E-H) fifth, in anterior, dorsal, posterior and left lateral views, respectively. Scale bar: 5 cm.

**Figure 5.** Posterior cervical vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A-D), seventh, (E-H) eighth, in anterior, dorsal, posterior and left lateral views, respectively. Scale bar: 5 cm.

**Figure 6.** Posterior cervical vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A-D), ninth, (E-H) tenth, in anterior, dorsal, posterior and left lateral views, respectively. (D), in right lateral view. Scale bar: 5 cm.

**Figure 7.** Anterior dorsal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A-D), second, (E-H) fourth, in anterior, posterior, left lateral and dorsal views, respectively. Scale bar: 5 cm.

**Figure 8.** Five dorsal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), in anterior, (B), posterior, (C), left lateral, (D), and dorsal views. Scale bar: 5 cm.

**Figure 9.** Seven to ten dorsal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), in left lateral, (B), anterior, (C), dorsal views. (D), Detail and interpretation of interspinous accessory articulation system in dorsal view. Scale bar: 5 cm.

**Figure 10.** Anterior and anterior-middle caudal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Anteriormost caudal, (A, B, C), in anterior, right lateral, and dorsal views, respectively. (D), foramens detail in dorsal view. Anterior caudal vertebrae (E, F, G) and (H, I, J), in anterior, left lateral and dorsal views, respectively. Anterior-middle caudal vertebrae (K, L, M) in anterior, left lateral and dorsal views, respectively. Scale bar: 5 cm.

**Figure 11.** Middle and posterior caudal vertebrae of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Middle caudal, (A, B), in dorsal and right lateral views, respectively. Posterior caudal, (C, D), in dorsal and left lateral views, respectively. Distalmost caudal, (E, F), in dorsal and left lateral views, respectively. Scale bar: 5 cm.

**Figure 12.** Cervical ribs of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), third?, (B), five?, (C) seven, (D) eighth?, (E), ten, in laterodorsal views. Scale bar: 5 cm.

**Figure 13.** Dorsal ribs and gastralia of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A-E), anterior to posterior dorsal ribs in posterior views, respectively. (F), gastralia in ventral view. Scale bar: 5 cm.

**Figure 14.** Haemal arch of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. (A), in left lateral, (B), proximal, and (C), in anterior views. Scale bar: 5 cm.

**Figure 15.** Appendicular skeleton of *Viavenator exxoni* gen. et sp. nov. MAU-Pv-LI-530. Left scapulocoracoid, (A), in dorsal, (B), medial, and (C), left lateral views. Fibulae (D), in lateral, (E), proximal, and (F), medial views. Ischium foot, (G), anterior, (H) dorsal, and (I) posterior views. Scale bar: (A-C): 10 cm, (D-F) and (G-I): 5 cm.

**Table 1.** Measurements (cm) of *Viavenator exxoni* (MAU-Pv-LI-530) vertebrae and scapulocoracoid elements.

Vertebra	CL	CW	CH	NSH	IDPW	IPPW	EPL	TVH
Atlas	2.82	4.71	3.94	-	-	-	-	7.52
C3	6.20*	3.52	2.24	**	9.50*	5.00*	3.93	8.23
C4	8.51	4.51	2.53	1.73	12.20	6.40	4.00	11.49
C5	8.20	5.10	3.40	2.18	15.30	7.30	4.18	11.53
C7	7.40	6.20	4.40	3.20	13.50*	8.53	3.52	13.80
C8	6.52*	5.53*	4.20	**	**	8.80*	**	**
C9	7.80	6.12	5.40	3.51	20.52	7.80	3.12	18.54
C10	7.20	5.59	5.50	4.32	20.70	7.92	1.98	18.40
D2	7.10	4.62	5.90	5.38	22.00	9.00	-	18.20
D4	7.80	3.64	5.70	5.31	22.30	13.40	-	17.80
D5	8.70	3.72	6.20	6.23	20.50	18.00*	-	18.90
D7	8.42	3.62	6.17	7.00	20.90	19.20*	-	19.40
D8	-	-	-	-	-	-	-	-
D9	-	-	-	-	-	-	-	-
D10	8.33*	3.58	6.38	7.47	**	**	-	20.30*
Caudal vertebra	CL	CW	CH	NSH	TPW	TVH		
Anteriormost	8.92	4.26	7.12	**	**	**		
Anterior	8.35	2.80	6.10	**	26.30	**		
Anterior	8.23	2.67	4.67	6.31	**	14.50		
Anterior - middle	7.85	2.43	3.76	**	19.40	**		
Middle	7.59*	2.41	3.55	**	**	**		
Posterior	5.98	1.98	3.17	**	-	**		
Distalmost	3.17	1.10	1.15*	**	-	**		
Element	TL	SL	SAW	SMW	GW	GH		
Scapulocoracoid	49.50	35.30	6.28	2.13	4.37*	5.25*		

**Abbreviations:** **CL**, centrum length; **CW**, centrum width; **CH**, centrum height; **GH**, glenoid height; **GW**, glenoid width; **NSH**, neural spine height; **IDPW**, interdiapophyseal width – distance between lateral limit of diapophyses; **IPPW**, interparapophyseal width – distance between lateral limit of parapophyses; **EPL**, epipophyseal length – distance from caudal margin of postzygapophyseal facet to caudalmost extent of epipophysis; **SAW**, scapular anteroposterior width (measured at mid-scapular length); **SL**, scapular length; **SMW**, scapular mediolateral width; **TL**, total length **TPW**, transverse process width – distance between lateral limit of transverse process; **TVH**, total vertebra height. \*, estimative measurement due to missing bone. \*\*, unable to measure due to damaged/missing/fused bone. – , measurement not applicable for given vertebra.



































