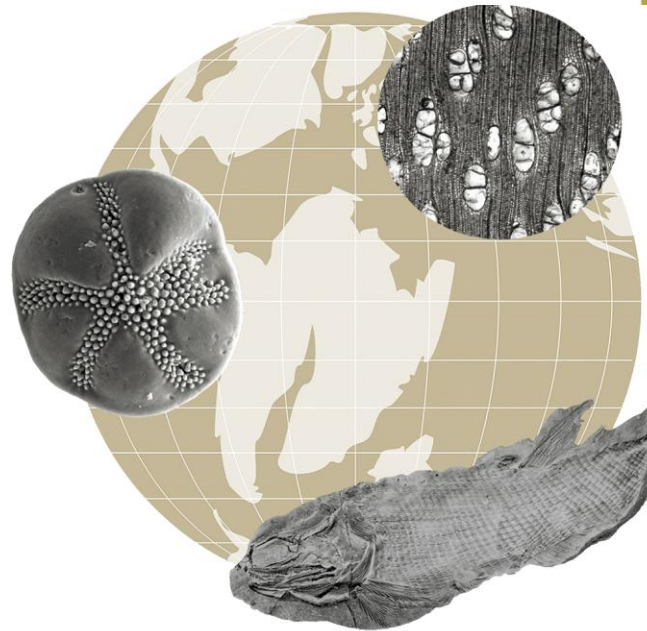




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PNEUMATIC STRUCTURES IN A CERVICAL VERTEBRA OF *VIAVENATOR EXXONI* (DINOSAURIA: THEROPODA)

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RUNNING HEADER: VALDÉZ, FERNÁNDEZ, ZURRIAGUZ, GIANECHINI,
FILIPPI and MÉNDEZ. PNEUMATICITY IN *VIAVENATOR EXXONI*

Short description: Analysis of the pneumaticity in a cervical vertebra of *Viavenator exxoni*

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Abstract. Abelisaurids are a group of mostly Gondwanan theropod dinosaurs, whose anatomy and phylogenetics relationships are well known. However, this is not the case for some paleobiological aspects such as postcranial pneumaticity. In this work, the pneumaticity of the fifth cervical vertebra of *Viavenator exxoni* was analyzed. This was done using CT scans and comparing their results with other abelisauroids. Furthermore, in order to obtain a more precise result regarding pneumaticity, an analysis was performed of air space proportion (ASP) of the fifth cervical vertebra of *Viavenator exxoni*. *Viavenator* has a polycamerate internal structure, similar to that of some noasaurids from Brazil and *Majungasaurus crenatissimus*. However, in *Viavenator*, unlike other analyzed taxa, a ventral pneumatic foramen was found, a unique characteristic among abelisaurids and even theropods. Regarding the ASP, it was found that the vertebra is more pneumatized in the anterior portion than in the posterior portion. This is the first ASP study on an abelisaurid vertebra, making it extremely important to expand this type of analysis in the future across this fascinating group of theropods.

Keywords. Abelisaurids, Pneumaticity, Air Space Proportion, Paleobiology, Polycamerate structure.

Resumen. ESTRUCTURAS NEUMÁTICAS EN UNA VÉRTEBRA CERVICAL DE *VIAVENATOR EXXONI* (DINOSAURIA: THEROPODA). Los abelisáuridos son un grupo de dinosaurios terópodos, principalmente gondwánicos, cuya anatomía y

relaciones filogenéticas son bien conocidas. Sin embargo, éste no es el caso de algunos aspectos paleobiológicos como la neumaticidad postcraneal. En este trabajo se analizó la neumaticidad de la quinta vértebra cervical de *Viavenator exxoni*. Esto se realizó mediante tomografías computadas, comparando los resultados con otros abelisáuridos. Además, para obtener un resultado más preciso con respecto a la neumaticidad, se realizó un análisis de la proporción del espacio aéreo (ASP) de la quinta vértebra cervical de *Viavenator exxoni*. *Viavenator* tiene una estructura interna policamerada, similar a la de algunos noasaurios de Brasil y a *Majungasaurus crenatissimus*. Sin embargo, en *Viavenator*, a diferencia de otros taxones analizados, se encontró un foramen neumático de posición ventral, lo que ofrece una característica única dentro de los abelisaurios e incluso los terópodos. Con respecto a los resultados de ASP, se encontró que la vértebra está más neumatizada en la porción anterior que en la porción posterior. Este es el primer estudio ASP sobre una vértebra de abelisáurido, por lo que es extremadamente importante ampliar este tipo de análisis en el futuro dentro de este fascinante grupo de terópodos.

Palabras clave. Abelisáuridos, Neumaticidad, Proporción de Espacio Aéreo, Paleobiología, Estructura policamerada

INTRODUCTION

ABELISAURIDS ARE A GROUP of non-avian theropods that mostly inhabited Gondwana during the Cretaceous (Bonaparte, 1991; Carrano & Sampson, 2008; Novas, 2009; Novas *et al.*, 2013; Zaher *et al.*, 2020). Abelisaurids are characterized by a medium to large body size, highly ornamented skulls, and extremely reduced forelimbs (Bonaparte & Novas, 1985; Bonaparte 1991; Novas 1997; Coria *et al.*, 2002; Carrano &

Sampson, 2008; Pol & Rauhut 2012; Novas *et al.*, 2013; Canale *et al.*, 2016). Their anatomical and phylogenetic aspects of this group of theropods are widely known (Bonaparte 1985; Sampson *et al.*, 1998; Coria *et al.*, 2002; Canale *et al.*, 2009; Farke & Sertich 2013; Filippi *et al.*, 2016; Aranciaga Rolando *et al.*, 2020; Gianechini *et al.*, 2020; Zaher *et al.*, 2020; Agnolin *et al.*, 2021; Baiano *et al.*, 2022, 2023; Pol *et al.*, 2024), but not their paleobiological aspects, especially those related to postcranial pneumaticity (PSP).

Currently, PSP is only present in birds, but in the past, it was distributed throughout almost the entire Saurischiaclade (Duncker, 1971; Britt, 1993; O'Connor, 2006; Wedel, 2009; Benson *et al.*, 2011). The PSP is the invasion of epithelial extensions called pneumatic diverticula within bones, whose origin from the air sacs connected to the lungs (King, 1966; Duncker, 1971). This invasion occurs through foramina that connect to internal cavities of the bones, which can be called camerae or camellae (Britt, 1993; Wedel, 2003a,b; O'Connor, 2006).

Despite its wide distribution, the PSP has been much more studied in sauropodomorphs than in theropods, with some exceptions (Britt, 1993; O'Connor, 2007; Sereno *et al.*, 2008; Benson *et al.*, 2011; Watanabe *et al.*, 2015; Aranciaga-Rolando *et al.*, 2020; Gianechini & Zurriaguz, 2021; Aureliano *et al.*, 2024; Windholz *et al.*, 2025).

The aim of this study is to analyze the external and internal pneumaticity of a single cervical vertebra of the abelisaurid *Viavenator exxoni* (Filippi *et al.*, 2016), which is an abelisaurid from the Bajo de la Carpia Formation (Santonian), whose remains were found in La Inveranda locality, near to Rincón de los Sauces, in the north of the province of Neuquén, Argentina and compare its pneumaticity with related taxa.

Institutional Abbreviations. **FMNH** Field Museum of Natural History, Chicago; United States of America; **MAU**, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **NMV**, National Museum of Victoria, Melbourne, Australia; **PIN**, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

MATERIALS AND METHODS

Materials

The material analyzed firsthand corresponds to the 5th cervical vertebra of the holotype specimen of *Viavenator exxoni* (MAU-Pv- LI-530). This vertebra is complete and presents a good state of preservation, with minimal deformation.

Methods

Naked-eye observations of the vertebra were performed to identify external pneumatic features, and, in addition, a CT scan of the vertebra was performed on a tomograph GE® BrightSpeed in Policlínico de Neuquén, Neuquén City, Argentina. The scan was made with 120 kV and the slices presented 0.625 mm of separation between them. The digital work of the tomographies was carried out with the following software: 3D Slicer v5.8 (Fedorov *et al.*, 2012).

To complement the CT scans, an ASP (Air Space Proportion) calculation was performed, in order to obtain a numerical value that allows quantifying the degree of pneumaticity of this vertebral element. This methodology was proposed by Wedel (2005) and consists to measure the area of a pneumatized bone that is occupied by pneumatic spaces. After performing the CT scans, the cross-section is taken and the

corresponding calculation is performed using the software Image J (Rasband, 2003). All images were obtained using Adobe PS 2018.

To identify the regions of the vertebra, the Romerian nomenclature was used (Romer, 1956) for the nomenclature of the fossae, the classification proposed by Wilson (2012) was followed, while the terminology of pneumatic spaces followed that proposed by Britt (1993) and Wedel (2003 a, b)

RESULTS

External and internal pneumaticity

The vertebral centrum is elongated and low, with one small lateral pneumatic foramina on each lateral surfaces, while the neural arch has three pairs of well-developed and deep fossae: the centroprezygapophyseal fossa (cprf), the centrodiapophyseal fossa (cdf), and the parapophyseal-centrodiapophyseal fossa (pacdf), all of which are visible in anterior view (Fig 1.A).

However, the most striking feature of this material is found on its ventral side, a circular foramen of considerable size (0.5 cm length x 0.9 cm width), which penetrates the interior of the vertebral centrum (Fig 1.B). It is important to consider that this ventrally positioned foramen is the only one present in the cervical vertebrae of *Viavenator*; even in other vertebral regions of the same species.

Both the foramen on the ventral face and the fossae that contains it, are of a pneumatic nature. This can be corroborated because a, mostly, polycamerate structure can be observed inside this vertebra (Fig 2).

Regarding the internal structure provided by the CT scans (Fig 2.A), it is observed that the entire length of all these spaces coincide with small camerae, presenting a polycamerate structure. The vertebral centrum, small, mostly irregularly shaped

pneumatic spaces can be observed. In the anterior portion of the centrum, these spaces are irregular in shape and small in size at the base of the centrum and near the parapophyses, and as they approach the neural canal, they progressively increase in size (Fig 2.B). The connection of the foramen present on the ventral surface with the interior of the vertebral center can also be clearly seen (Fig 2.B). In the mid-section of the vertebral centrum, the pneumatic spaces increase in size compared to those observed in the anterior portion. Their shape remains mostly irregular, but with a tendency towards a quadrangular shape (Fig 2.C). In the posterior portion, the pneumatic spaces again become small, and spaces containing bone become more prominent. The pneumatic spaces are mostly quadrangular in shape (Fig 2.D).

In contrast, the neural arch exhibits large pneumatic spaces corresponding to a polycamerate structure. These camerae range in shape from subtriangular to quadrangular, including irregular forms and are distributed throughout all anatomical structures, varying in size and shape depending on whether the anterior, middle, or posterior portion of the vertebra is analyzed (Fig 2). Both the anterior and middle sections show large, mostly quadrangular camerae, with a greater tendency towards a quadrangular shape in the anterior portion and a more rectangular shape in the middle (Fig 2.B.C). Conversely, in the posterior section, the camerae decrease in size and become mostly irregular in shape (Fig 2.D).

ASP

The ASP was calculated in three different vertebral cross sections—anterior, mid-centrum, and posterior—by taking the transverse planes from each region (Fig 2.A).

The results obtained were follows: 0.73 (73%), 0.69 (69%) and 0.56 (56%) in the anterior, mid-centrum, and posterior sections respectively, showing a decrease in the degree of pneumaticity along the element.

DISCUSSION

Comparison with other abelisaurids, noosaurids and *Ceratosaurus*:

Although *Viavenator* exhibits a polycamerate pneumaticity pattern, this may not be the case in other abelisaurids or related taxa such as noosaurids and *Ceratosaurus*.

Therefore, comparisons were made with the available material, showing a preference for taxa where the internal structure is visible.

In the case of abelisaurids, pneumaticity in cervical vertebrae has only been recorded in *Majungasaurus crenatissimus* (Déperet, 1896) Lavocat 1955, where O'Connor (2007) describes foramina and a camerate internal structure within the vertebral centra, consistent with that recorded in *Viavenator*.

With respect to other related taxa, Britt (1993) describes few foramina in an axis of *Ceratosaurus* Marsh 1884, (Britt, 1993, fig 15) although there is no record of CT scans or breakage of the material. These foramina are present on the lateral faces of the centrum (lpf) and on the neural arch (Britt, 1993, fig.15.1). However, there is no record of them on the ventral face of the centrum of the axis or on any other described cervical vertebra.

Within noosaurids, postcranial pneumaticity has been more thoroughly documented. For example, pneumatic foramina in cervical vertebrae are described in *Berthasaura leopoldinae* de Souza *et al.*, 2021 and *Masiakasaurus knopfleri* Sampson *et al.*, 2001, although there are no descriptions of the internal structure in either of these two taxa.

Regarding the description of the internal structure, there are cases such as those of Brum *et al.*, 2018, Poropat *et al.*, 2020 and Averianov *et al.*, 2024. A cervical vertebra of the Bauru Group (Brazil) described by Brum *et al.* (2018) presents, like *Viavenator*, a polycamerate structure (Brum *et al.* 2018, fig 2), while some noosaurids (Poropat *et al.*, 2020, fig.4) from Victoria (Australia) and *Kiyacursor longipes* (Averianov *et al.*, 2024, fig.S2), present camellated tissue . These results show that the internal structure is variable among abelisauroids which invites further exploration of what kind of structure other abelisauroids and noosaurids may have. Despite the existence of CT scans of the mentioned taxa above, no ASP calculation was performed on them, so this is the first time this proportion has been calculated in an abelisauroid, obtaining a result greater than 50%, which indicates that the cervical vertebrae were highly pneumatized.

Furthermore, despite unambiguous evidence of pneumaticity, a ventral foramen like that of *Viavenator* is not recorded in any abelisauroid to date, although its presence in was documented in some sauropods (Wedel, 2003). The causes of the presence of this ventral foramen in *Viavenator* are unclear, although it appears to be related to the irregular distribution of pneumatic features. In this case, pneumatic diverticula originating from the cervical air sac penetrated through the ventral surface, generating this foramen. This suggests that it is important to conduct studies of this nature, not only on abelisauroids, but on theropods in general, in order to establish whether it is possible to define distribution patterns of pneumatic foramina, expanding the paleobiological knowledge of past species.

CONCLUSION

Postcranial pneumaticity (PSP) is a poorly understood aspect of theropods, especially abelisauroids, a group in which anatomical and phylogenetic aspects are well known.

Using a cervical vertebra from *Viavenator exxoni* as an example, an analysis of this feature was performed.

Viavenator showed a polycamerate internal structure and an Air Space Proportion (ASP) between 56% in the posterior region and 73% in the anterior region of the vertebra, which shows an advanced degree of pneumaticity.

Viavenator also showed the same cervical polycamerate structure as *Majungasaurus crenatissimus* and the cervical vertebra of a noosaurid from Brazil.

This interesting and little-known aspect of this fascinating group of theropods deserves greater attention in the future, and new and promising analysis will be carried out accordingly.

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Appendices

Figure captions.

Figure 1. Fifth cervical vertebrae of *Viavenator exxoni* (MAU-Pv-LI-530). **A.** Diagram and photograph in anterior view of the 5th cervical vertebra showing various anatomical structures; **B.** Diagram and ventral view of the 5th cervical vertebra, showing anatomical structures and the ventral pneumatic foramen. Abbreviations: **cdf**, centrodiapophyseal fossa; **cprf**, centroprezygapophyseal fossa; **d**, diapophysis; **ep**, epipophysis; **nc**, neural canal; **ns**, neural spine; **pa**, parapophysis; **pacdf**, parapphyseal-centrodiapophyseal fossa; **pf**, pneumatic foramen; **podcf**, postzygapophyseal centrodiapophyseal fossa; **pr**, prezygapophysis; **sprf**, spinoprezygapofiseal fossa. Scale bar equals 5 cm.

Figure 2. CT scans of the fifth cervical vertebra of *Viavenator exxoni* (MAU-Pv-LI-530). **A.** Sections from where the CT scans were taken. **B, C** and **D.** Anterior, middle, and posterior cross sections, respectively, showing the pneumatic structures and its progression along the vertebra. Abbreviations: **cam**, camera; **d**, diapophysis; **ep**,

epipophysis; **nc**, neural canal; **ns**, neural spine; **pa**, parapophysis; **pf**, pneumatic foramen. Scale bars equals 5 cm

