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

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GONDWANAN PERSPECTIVES

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

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Abstract. Abelisaurids are a group of mostly Gondwanan theropod dinosaurs, whose anatomy and phylogenetic 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 the 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.

Key words. 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 noasauridos 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, 2021; Gianechini *et al.*, 2020; Zaher *et al.*, 2020; Agnolin *et al.*, 2022; 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 Saurischia clade (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 is 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).

This study aims 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 Carpa Formation (Santonian), whose remains were found in La Inveranda locality, near 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 the medical institution Policlínico de Neuquén, in Neuquén City, Argentina. The scan was made with 120 kV and the slices presented 0.625 mm of separation between them. The digital reconstruction and visualization of CT scan slices was carried out with the software: 3D Slicer v5.8 (Fedorov *et al.*, 2012).

In order to obtain a numerical value that allows quantifying the degree of pneumaticity of this vertebral element, to complement the CT scans, an Air Space Proportion (ASP) calculation was performed. This methodology was proposed by Wedel (2005) and consists of measuring the area of a pneumatized bone that is occupied by pneumatic spaces. This calculation was performed using the software Image J (Rasband, 2003). All images were obtained using Adobe PS 2018.

The identification of vertebral regions follows the Romerian nomenclature (Romer, 1956); the classification and nomenclature of fossae follows that of Wilson (2011); and the terminology of pneumatic spaces follows 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 foramen on each lateral surface, 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. 1A).

However, the most striking feature of this material is found on its ventral surface, where a circular foramen of considerable size (0.5 cm length x 0.9 cm width), penetrates the interior of the vertebral centrum (Fig. 1B). 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 surface 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).

The CT scans show an insight into the internal pneumatic system of the vertebra (Fig. 2A), represented by a polycamerate structure where the entire size of each of the identified spaces allows identifying them as small camerae. Each of the pneumatic spaces in the vertebral centrum is small and mostly irregular in shape. In the anterior portion of the centrum, at the base of the centrum

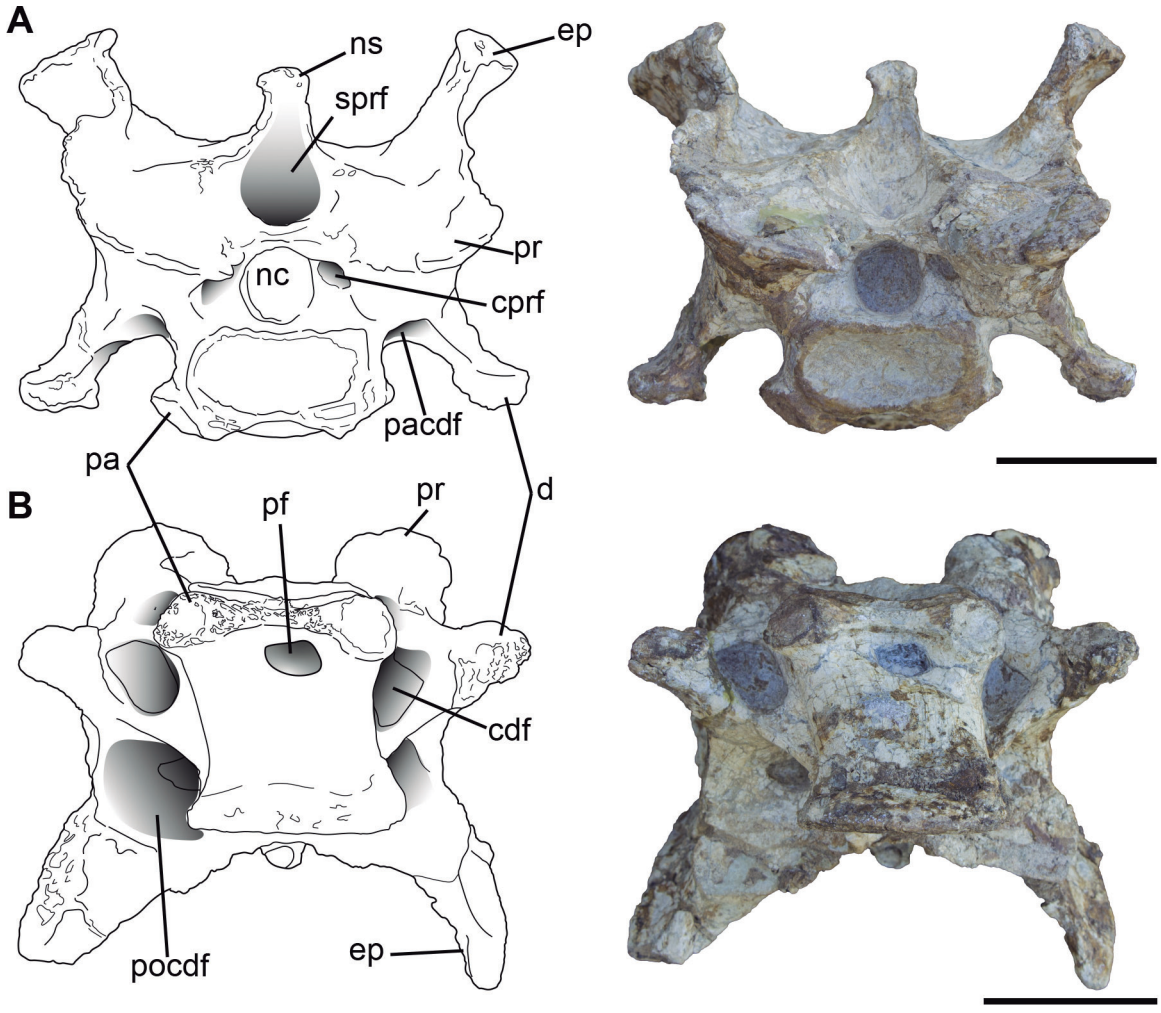


Figure 1. Fifth cervical vertebrae of ***Viavenator exxoni*** (**MAU-Pv-LI-530**). **A,** diagram and photograph in anterior view of the 5th cervical vertebra showing various anatomical structures; **B,** diagram and ventral view of the 5th cervical vertebra, showing anatomical structures and the ventral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

and at the level of the parapophyses, these spaces are irregular in shape and small in size, and as they approach the neural canal, they progressively increase in size (Fig. 2B). At this level in cross-section the connection of the ventral foramen with internal pneumatic camerae is evident (Fig. 2B). The pneumatic spaces observed in cross-section at the level of the mid-portion of the centrum show a size increase compared to those in the anterior portion. Their shape remains predominantly irregular, but shows a tendency towards a quadrangular outline (Fig. 2C). In the posterior portion of the vertebral centrum, at the level of the postzygapophyses, the pneumatic spaces reduce in size, and trabeculae limiting the spaces become thicker. The pneumatic spaces are mostly quadrangular in shape (Fig. 2D). Externally, the cortical bone shows additional thickening in some regions, such as the posterior narrowing of the neural pedicels, the base of the neural spine, and the articular facets of the parapophyses.

The neural arch similarly 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. 2B–2C). Conversely, in the posterior section, the camerae decrease in size and become mostly irregular in shape (Fig. 2D).

ASP

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

The resulting values were: 0.73 (73%), 0.69 (69%), and 0.56 (56%) for the anterior, mid-centrum, and posterior sections, respectively, indicating a decrease in pneumaticity along the element.

DISCUSSION

Although *Viavenator* exhibits a polycamerate pneumaticity pattern, this may not be the case in other abelisaurids or related taxa such as noasaurids and *Ceratosaurus*. Therefore, comparisons were made with the available material, showing a preference for taxa where the internal structure is visible.

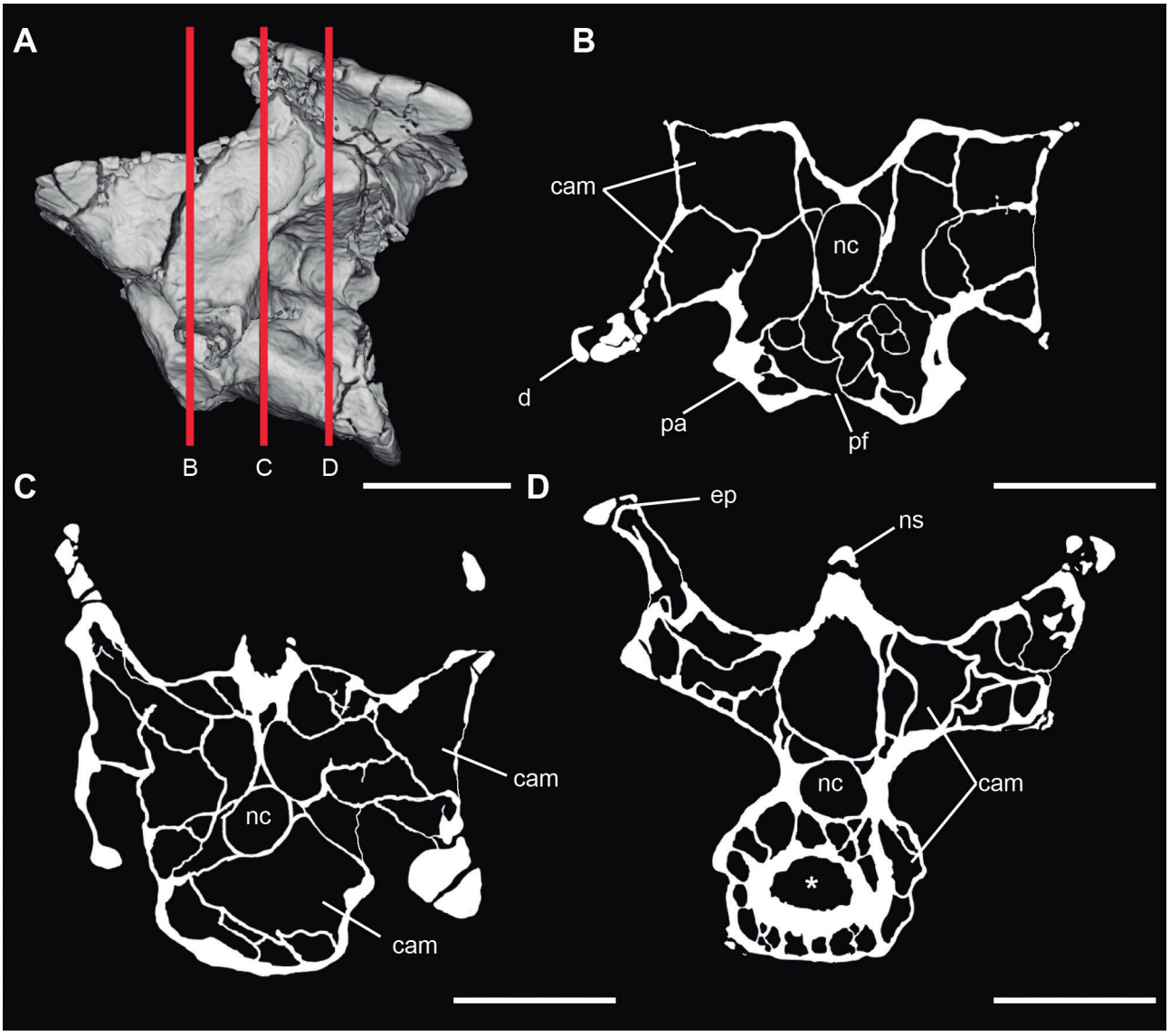


Figure 2. CT scans of the fifth cervical vertebra of ***Viavenator exxoni*** (**MAU-Pv-LI-530**). **A,** sections from where the CT scans were taken. **B, C** and **D,** anterior, middle, and posterior cross sections, respectively, showing the pneumatic structures and its progression along the vertebra**.** The asterisk in D corresponds to an external portion of the articular surface, not an internal space of 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.

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 noasaurids, 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 noasaurids (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 abelisaurids and noasaurids 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 skeletal pneumaticity (PSP) remains a poorly understood aspect of theropods anatomy, particularly in abelisaurids, despite of the relatively well-established anatomical and phylogenetic framework of the group. Using a cervical vertebra of *Viavenator exxoni* as a study case, we analyzed patterns of vertebral pneumaticity in this taxon.

Viavenator exhibits a polycamerate internal structure and an Air Space Proportion (ASP) ranging from 56% in the posterior region to 73% in the anterior region of the vertebra, indicating an advanced degree of pneumaticity.

Additionally, *Viavenator* shares this cervical polycamerate structure with *Majungasaurus crenatissimus* and a noasaurid cervical vertebra from Brazil, but not with noasaurid material from Australia and *Kiyacursor longipes*.

This interesting and little-known aspect of this fascinating group of theropods highlights the need of further studies of PSP in abelisauroids and other theropods to better understand the evolutionary and paleobiological significance of pneumatic variation, using comparative imaging tools and ASP estimates.

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