

Pneumatic structures in *Murusraptor barrosaensis* (Theropoda: Megaraptora), a large-bodied predator theropod from the Upper Cretaceous of Patagonia

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PNEUMATIC STRUCTURES IN *MURUSRAPTOR BARROSAENSIS* (THEROPODA: MEGARAPTORA), A LARGE-BODIED PREDATOR THEROPOD FROM THE UPPER CRETACEOUS OF PATAGONIA

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Abstract. Megaraptora is a clade of tetanuran theropod dinosaurs of uncertain phylogenetic affinity. Members of the constituent family Megaraptoridae are notable for their extreme skeletal pneumaticity. This is exemplified in *Murusraptor barrosaensis* from the Sierra Barrosa Formation of Patagonia, Argentina. We describe the postcranial pneumaticity of *Murusraptor* providing naked eye observations and CT scans of internal structures, comparing them with other megaraptorids and other theropod taxa, including birds. *Murusraptor*, as with other megaraptorids, exhibits pneumaticity patterns that are repeated along the vertebral sequence (e.g., centrum with a central camara surrounded by camellate tissue). However, *Murusraptor* is unique, given the presence of exposed camellate tissue in the neural spines and two pneumatic foramina in the pubis connected to the iliac peduncle in the ilium. Compared with other related taxa, *Murusraptor* possesses a pneumaticity pattern intermediate between tyrannosauroids (camellate tissue) and allosauroids (camerae). The exposed camellate tissue in the neural spine may correspond to a "multiple foramina" pattern present only in avian theropods; however, in birds, this feature is found in the neural canal. Further studies of this kind are needed to unravel the paleobiology of this enigmatic group of theropods.

Key words. Theropoda. Megaraptoridae. *Murusraptor*. Postcranial pneumaticity. CT scans. Patagonia.

Resumen. ESTRUCTURAS NEUMÁTICAS EN *MURUSRAPTOR BARROSAENSIS* (THEROPODA: MEGARAPTORA), UN TERÓPODO DE GRAN TAMAÑO DEL CRETÁCICO SUPERIOR DE PATAGONIA. Megaraptora es un grupo de terópodos tetanuros de afinidad filogenética incierta. Los miembros que constituyen la familia Megaraptoridae son notables por su esqueleto hiperneumatizado. Esto se ejemplifica en *Murusraptor barrosaensis*, procedente de la Formación Sierra Barrosa de Patagonia, Argentina. Aquí describimos la neumaticidad postcraneal de *Murusraptor* mediante observaciones a ojo desnudo y tomografías computadas de estructuras internas, comparándolas con otros megaraptóridos y otros taxones de terópodos, incluidas las aves. *Murusraptor*, al igual que otros megaraptóridos, exhibe patrones de neumatización que se repiten a lo largo de la secuencia vertebral (p. ej., centro vertebral con una cámara central rodeada de tejido camelado). Sin embargo, *Murusraptor* es único, dada la presencia de tejido camelado expuesto en las espinas neurales y dos forámenes neumáticos en el pubis, conectados al pedúnculo ilíaco en el ilion. En comparación con otros taxones relacionados, *Murusraptor* posee un patrón de neumatización intermedio entre los tiranosauroides (tejido camelado) y los alosauroides (cámaras). El tejido camelado expuesto en la espina neural podría corresponder a un patrón de "múltiples forámenes" presente únicamente en terópodos avianos; sin embargo, en las aves, esta característica se encuentra en el canal neural. Se necesitan más estudios de este tipo para desentrañar la paleobiología de este enigmático grupo de terópodos.

Palabras clave. Theropoda. Megaraptoridae. *Murusraptor*. Neumaticidad postcranial. Tomografías computadas. Patagonia.

INTRODUCTION

Megaraptorans constitute a group of dominant Gondwanan theropods, with some remains recorded in Laurasian landmasses (e.g., Novas, 1998; Azuma & Currie, 2000; Lamanna et al., 2004; Currie & Azuma, 2006; Sereno et al., 2008; Benson et al., 2010; Martinelli et al., 2013; White et al., 2013; Bell et al., 2016; Coria & Currie, 2016; Samathi et al., 2019; Aranciaga Rolando et al., 2020;

Lamanna et al., 2020; Aranciaga Rolando et al., 2021; Samathi et al., 2021; Kotevski et al., 2022; 2024; Ibiricu et al., 2025; Kotevski et al., 2025). Within the Megaraptora clade, the Megaraptoridae family stands out, comprising the vast majority of species. This family is of Gondwanan origin, specifically from Australia, where their oldest representatives were found (Bell et al., 2015; Kotevski et al., 2024). Although the megaraptoran (and megaraptorids) record has expanded

over the last 10 years, providing new information about the anatomy of these dinosaurs, their phylogenetic position within Theropoda is still debated. This group of bizarre theropods has variously been recovered within Allosauroidae (e.g., Benson et al., 2010), within Coelurosauria (Novas et al., 2013; Porfiri et al., 2018), within Tyrannosauroidae (Lamanna et al., 2020; Cau, 2024). Despite their unresolved phylogenetic position within Theropoda, megaraptorans are consistently characterized by having a medium to large body size (Holtz, 2021), a notable development of the manual ungual phalanges I and II (Porfiri et al., 2014), and a hyperpneumatized postcranial skeleton (Serenó et al., 2008; Aranciaga Rolando et al., 2020).

Postcranial pneumaticity is widely distributed within ornithomorphs (avian and non-avian saurischian dinosaurs and pterosaurs) (Seeley, 1870; Janensch, 1947; Britt 1993, 1997; Butler et al., 2009; Wedel, 2003a, b, 2005, 2006, 2007, 2009; Yates et al., 2012). Among extant tetrapods, only birds have developed a comparable postcranial pneumaticity (Duncker, 1971; Britt, 1993; Wedel, 2003a, b; O'Connor, 2006). Birds have a respiratory system that enables a unidirectional air flow through the presence of nine air sacs connected to the lungs, which in turn have finger-like structures called pneumatic diverticula that penetrate the bone through pneumatic foramina (King, 1966; Romer & Parsons, 1977; Britt, 1997; O'Connor, 2006).

Although postcranial pneumaticity occurs in sauropodomorph and theropod dinosaurs, this feature has been more extensively explored in the former (e.g., Wedel, 2003a, b, 2005, 2006, 2007, 2009; Schwarz et al., 2007; Cerda et al., 2012). Interestingly, this trend seems to have shifted in recent years, with several contributions focused on theropod pneumaticity (Serenó et al., 2008; Benson et al., 2012; Watanabe et al., 2015; Brum et al., 2016, 2018; Aranciaga Rolando et al., 2020; Gianechini & Zurriaguz, 2021; Aureliano et al., 2024; Windholz et al., 2025). In light of these more recent studies, megaraptorids seem to show an extreme pneumaticity along the axial skeleton and in some appendicular elements (e.g., ilium) (Serenó et al., 2008; Coria & Currie, 2016; Aranciaga Rolando et al., 2020). The goal of this work is to contribute to our understanding of the postcranial pneumaticity (external and internal) in megaraptorids by analyzing the remains of *Murusraptor*

barrosaensis, one of the best-preserved representatives of this clade, with a view to further exploration of this feature not only in megaraptorids but in theropods as a whole.

MATERIALS AND METHODS

Materials

Murusraptor barrosaensis Coria and Currie 2016, is a megaraptorid from the Sierra Barrosa locality, 30 km northeast of the city of Plaza Huincul (Neuquén Province, Argentina), and found in deposits of the Sierra Barrosa Formation (Coniacian, Upper Cretaceous).

The elements analyzed of the holotype specimen of *Murusraptor barrosaensis* (MCF-PVPH-411) include a centrum of a posterior dorsal vertebra, six neural arches of dorsal vertebrae, two sacral vertebrae (a neural arch and an almost complete vertebra), two neural arches of caudal vertebrae, and pelvic elements (ilium, ischium, and pubis).

Methods

Pneumaticity and CT scans. The characterization of external pneumaticity was carried out following the terminology of Britt (1993) and O'Connor (2006), while for the neural laminae and fossae, we used the terminology of Wilson (1999) and Wilson et al. (2011). Regarding the internal pneumaticity, we followed the terminology proposed by Britt (1993), Wedel et al. (2000), Wedel (2003a) and Brum et al., (2018). The internal arrangement was observed by using computed tomography, a reliable and non-destructive methodology to explore the internal portion of fossil bones (e.g., Racicot, 2017). The CT scans were performed at Sanatorio Plaza Huincul, Plaza Huincul, Neuquén Province, using a Toshiba Lightning Aquilion TSX-035 A scanner. The DICOM files were analyzed and processed with a programmed 3D Slicer. The DICOM files were converted to TIFF and then were digitally processed using Photoshop (Adobe, 2024), modifying the exposure and contrast to highlight black and white zones (white corresponding to bone and black to air spaces).

Comparison with other taxa. The external morphology and the internal arrangement of the skeletal elements of *Murusraptor* were compared with other theropods, especially megaraptorids. Some species were observed first-hand, such as *Aoniraptor libertatem* (MPCA-Pv 804/1-25), *Maip*

macrothorax (MPM 21.545), the juvenile specimen of *Megaraptor* (MUCPv 595), and the avians *Rhea americana* (CFA-Or 1648), *Cygnus olor* (MACN-Or 68033) and *Chauna torquata* (CFA-Or 1645), whereas others were observed through photography and/or previous works, such as *Aerosteon riocoloradensis* (MCNA-PV-3137), *Megaraptoridae* indet. (CPPLIP 1324), *Allosaurus fragilis* (AMNH 5767), *Sinraptor dongi* (IVPP 10600), *Albertosaurus sarcophagus* (RTMP 68.3.1, 85.98.1, 85.62.1) and *Struthio camelus* (MVZ 190732).

Institutional acronyms. **AMNH**, American Museum of Natural History, New York, USA; **CFA-Or**, Colección ornitológica de la Fundación de Historia Natural "Félix de Azara", Ciudad Autónoma de Buenos Aires, Argentina; **CPPLIP**, Centro de Pesquisas Paleontológicas "L. I. Price", Uberaba, Minas Gerais, Brazil; **KUVP**, Vertebrate Paleontology Division, University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, USA; **MACN-Or**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, colección de ornitología, Ciudad Autónoma de Buenos Aires, Argentina; **MCF-PVPH**, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huinul, Neuquén, Argentina; **MCNAM**, Museo de Ciencias Naturales y Antropológicas "J. C. Moyano", Mendoza, Mendoza, Argentina; **MPCA**, Museo Provincial "Carlos Ameghino", Cipolletti, Río Negro, Argentina; **MPM**, Museo Regional Provincial "Padre Jesús Molina", Río Gallegos, Santa Cruz, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **MVZ**, Museum of Vertebrate Zoology, University of California, Berkeley, USA; **NHMM**, Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands; **RTMP**, Royal Tyrrell Museum, Alberta, Canada.

RESULTS

The axial skeleton of the holotype specimen MCF-PVPH-411 of *Murusraptor barrosaensis* was described in detail when the species was originally published (Coria & Currie, 2016). Here we will focus on features related to the pneumaticity patterns.

External Pneumaticity of Dorsal Vertebrae

Dorsal Centrum (MCF-PVPH-411). This centrum is amphiplatyan, with a deep anteroposterior ventral concavity.

Small vascular foramina are observed on the ventral surface. The anterior and posterior surfaces are rugose, with a circular outline and visible camellate tissue (Fig. 1A, B). The lateral surfaces have one elliptical lateral pneumatic foramen (Fig. 1C, D), which are different in size. The left lateral pneumatic foramen (Fig. 1C) is very deep (3.3 cm long and 1.2 cm high), including a shallow, almost blind anterior portion, and a deep posterior portion. The right lateral pneumatic foramen (Fig. 1D) is shallower and has a length of 2.4 cm, a height of 1 cm, and a lamina that divides it dorsoventrally into two halves.

Dorsal Neural Arches (MCF-PVPH-411). All dorsal neural arches of *Murusraptor* exhibit camellate tissue at the level of the neural spine, on both anterior and posterior surfaces. All neural arches present the camellate tissue exposed in the same places. Thus, disappearance of cortical tissue due to erosion can be ruled out. This camellate tissue is composed of medium and large camellae, most of which are elongated (Fig. 2A). Due to the loss of cortical tissue in some areas, it is possible to observe that the diapophyses, prezygapophyses and postzygapophyses are pneumatic. As for the neural laminae and fossae, these structures are similar in all the neural arches analyzed throughout the dorsal series. The spinoprezygapophyseal lamina (sprl) is present in most neural arches and originates from the prezygodiapophyseal lamina (prdl). Anterior and posterior centrodiaepophyseal laminae (acdl and pcdl) are present in all dorsal neural arches, the former being thinner than the latter. These two laminae delimit a triangular centrodiaepophyseal fossa (cdf) (Fig. 3A, B). In some elements, the acdl is pierced by pneumatic foramina. A triangular centroprezygapophyseal fossa (cprf) is also present. There is a small and shallow spinoprezygapophyseal fossa (sprf) located at the base of the neural spine (Fig. 2A–C). The intrapostzygapophyseal lamina (tpol) is present in most elements and is V-shaped. The spinopostzygapophyseal (spol) and postzygodiapophyseal (podl) laminae are well-developed in almost all preserved elements. The spinopostzygapophyseal (spof) fossa is well-developed and very deep, with a conspicuous postspinal lamina (posl) and, in some cases, this fossa is perforated by pneumatic foramina. The postzygapophyseal centrodiaepophyseal fossa (pocdf) is deep, with slight size variations between the right and left sides.

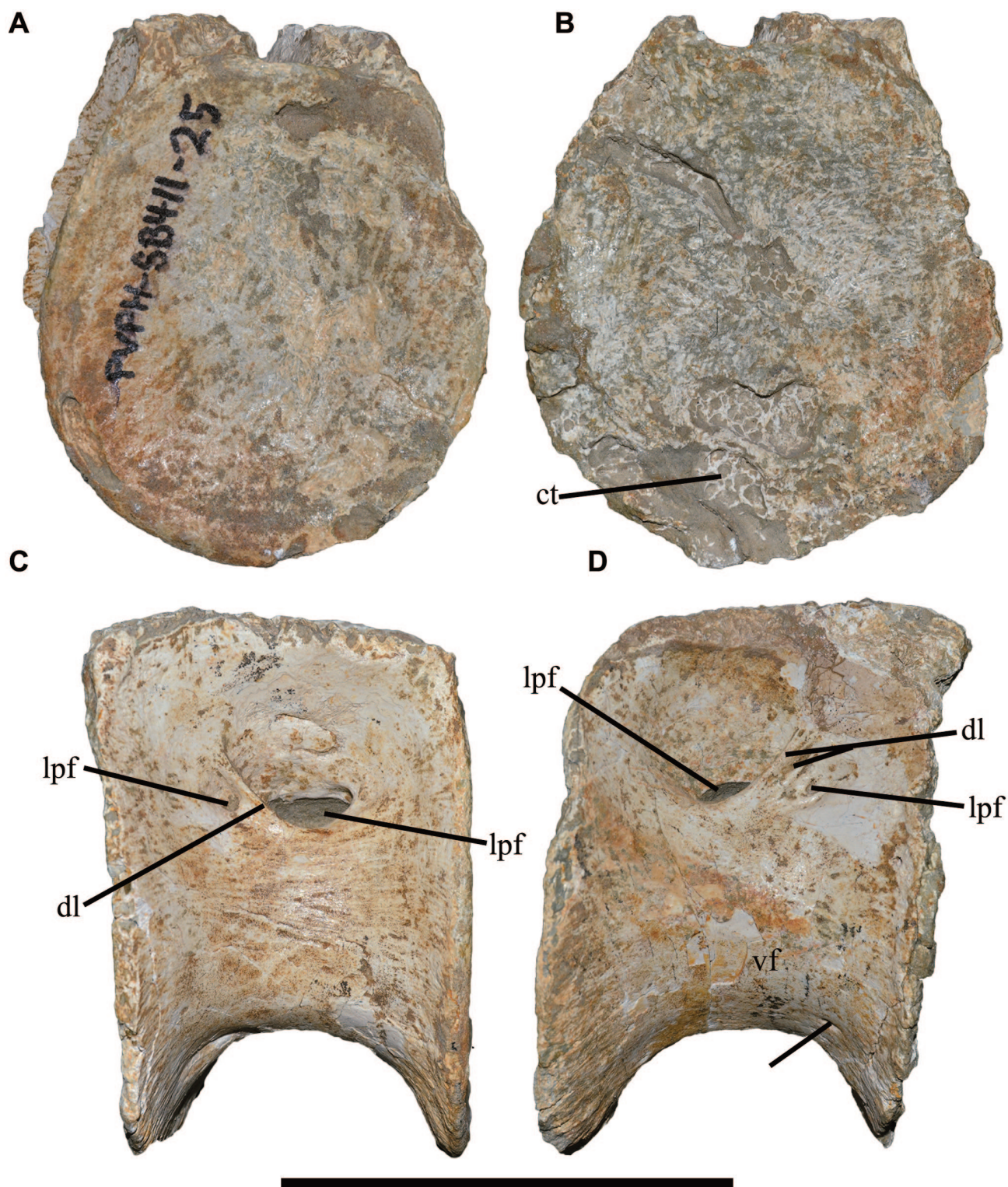


Figure 1. A–D, Dorsal vertebral centrum of *Murusraptor barrosaensis* (MCF-PVPH-411). A, anterior view; B posterior view; C left lateral view; D, right lateral view. Abbreviations: ct, camellate tissue; dl, dividing lamina; lpcf, lateral pneumatic foramen; vf, ventral foramen. Scale = 10 cm.

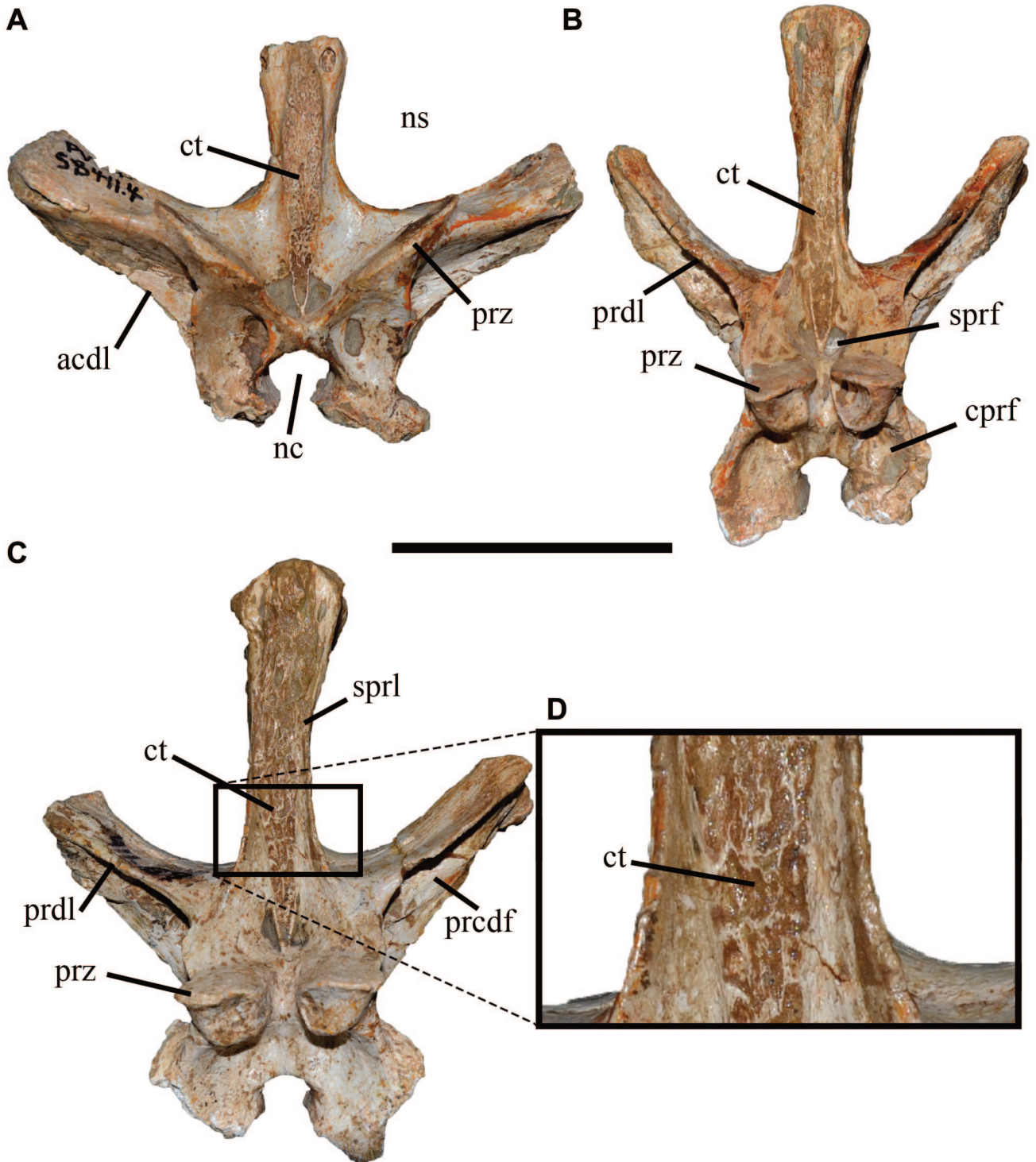


Figure 2. *Murusraptor barrosaensis* (MCF-PVPH-411). A, Anterior dorsal neural arch in anterior view; B, posterior dorsal neural arch in anterior view; C, posterior dorsal neural arch in anterior view; D, detail of the exposed camellate tissue. Abbreviations: *acd*, anterior centrodiapophyseal lamina; *cprf*, centro prezygapophyseal fossa; *ct*, camellate tissue; *nc*, neural canal; *ns*, neural spine; *prcdf*, prezygo-centrodiapophyseal fossa; *prdl*, prezygodiapophyseal lamina; *prz*, prezygapophyses; *sprf*, spinoprezygapophyseal fossa; *sprl*, spinoprezygapophyseal lamina. Scale = 10 cm.

External Pneumaticity of Sacral Vertebrae (MCF-PVPH-411). The sacral vertebrae include a complete vertebra fused to a fragment of the centrum of the following vertebra and a complete neural arch, which, like the dorsal vertebrae, shows camellate tissue exposed in the neural spine (Fig. 4).

The complete vertebra has an elongated opisthocoelic

centrum with a deep pneumatic foramen on each side, the right one 3.33 cm long x 0.6 cm high and the left one 4 cm long x 0.8 cm high. Although this vertebra preserves both centrum and neural arch, the latter has a complete anterior surface but a highly weathered posterior one (Fig. 4A).

The prezygapophyses have pneumatic foramina. The centroprezygapophyseal fossa (cprf) has a triangular

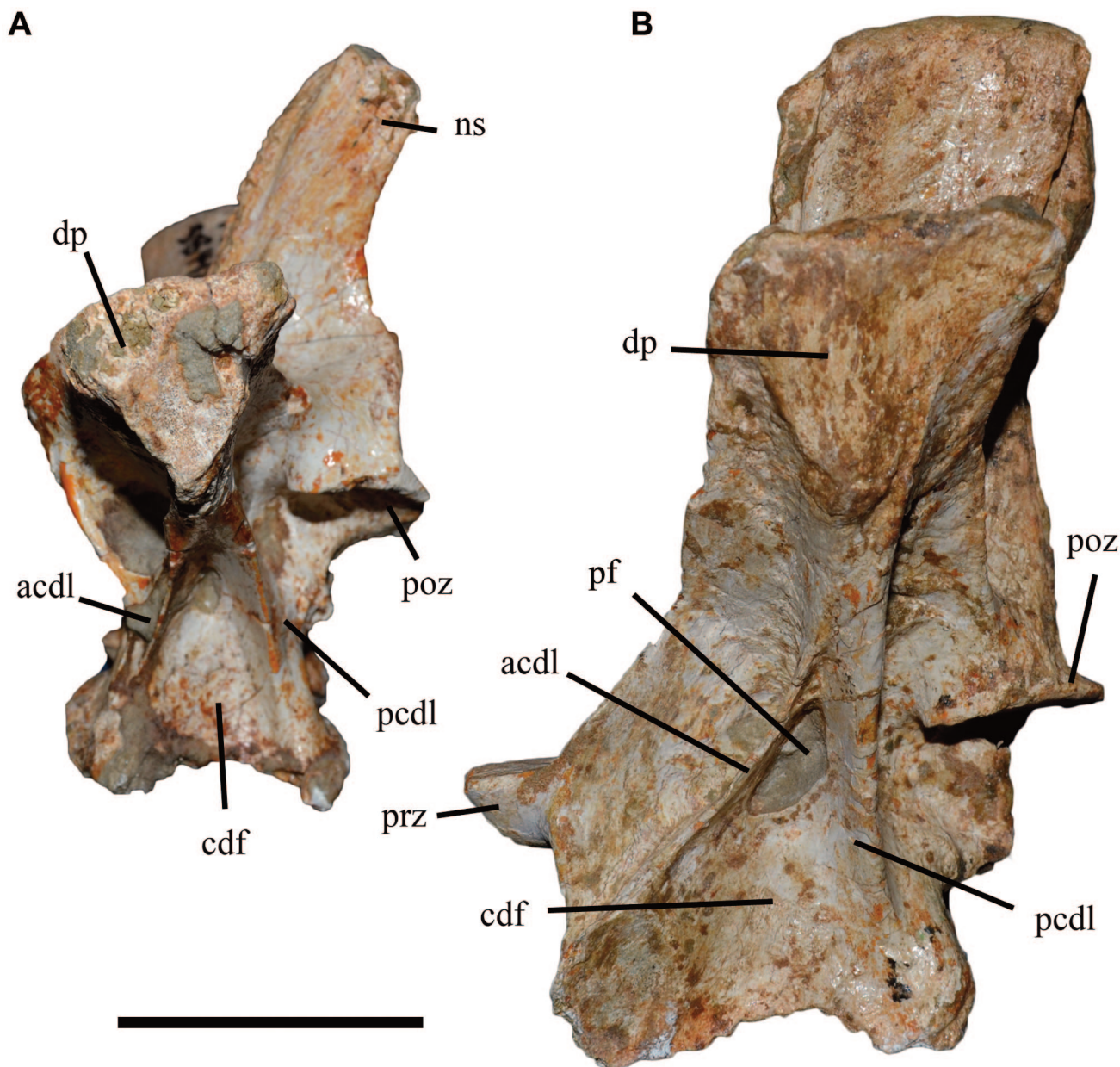


Figure 3. A–B, *Murusraptor barrosaensis* (MCF-PVPH-411). A, Anterior dorsal neural arch in left lateral view; B, posterior dorsal neural arch in left lateral view. Abbreviations: acdl, anterior centrodiapophyseal lamina; cdf, centrodiapophyseal fossa; dp, diapophyses; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pf, pneumatic foramen; poz, postzygapophyses; prz, prezygapophyses. Scale = 5 cm.

outline and is shallow, whereas the prezygapophyseal centrodiapophyseal fossa (prcdf) is triangular and deep, presenting with a foramen limited by two small horizontal laminae on the left side (Fig. 4A, B).

The posterior neural arch is complete. The centroprezygapophyseal lamina (cpri) is thin ventrally, although it thickens dorsally. This lamina laterally frames an oval centroprezygapophyseal fossa (cprf), which is shallow and dorsoventrally large. The spinoprezygapophyseal fossa (sprf) is shallow and delimited by the spinoprezygapophyseal laminae (sprl), which are thin and dorsoventrally elongated (Fig. 4C). The lateral surface presents a robust anterior centrodiapophyseal lamina (acdli) with a foramen in its middle part. This lamina and the posterior centrodiapophyseal lamina delimit a deep centrodiapophyseal fossa (cdf) (Fig. 4D). On the left side, in addition to the cdf, there is a large fossa delimited by the anterior centrodiapophyseal (acdli), centroprezygapophyseal (cpri), prezygodiapophyseal (prdi) and spinoprezygapophyseal (sprl) laminae, which is probably the prezygapophyseal spinodiapophyseal fossa (prsd) (Fig. 4C). The postzygodiapophyseal lamina (podli) is almost straight and thicker. The intrapostzygapophyseal lamina (tpol) is V-shaped and there is a deep and triangular spinopostzygapophyseal fossa (spof), delimited by two thin spinopostzygapophyseal laminae (spol) (Fig. 4E). The transverse processes have dorsoventrally expanded distal ends, which are deeply excavated by large fossae, anteriorly located, and framed by both acdli and pccli.

External Pneumaticity of Anterior Caudal Neural Arches (MCF-PVPH-411). As in the dorsal and sacral vertebrae, the caudal vertebrae have a neural spine with exposed camellate tissue (Fig. 5A). The intraprezygapophyseal lamina (tpri) is vestigial, while the spinoprezygapophyseal lamina (sprl) is thin. The centroprezygapophyseal lamina (cpri) is robust, while the prezygodiapophyseal lamina (prdi) is almost horizontal (Fig. 5A). The anterior centrodiapophyseal (acdli) and posterior centrodiapophyseal (pccli) laminae are well-developed and continue to delimit the centrodiapophyseal fossa as in the dorsal and sacral vertebrae (Fig. 5B, C). The spinopostzygapophyseal fossa (spof) is shallow, framed by almost vestigial spinopostzygapophyseal laminae (spol). The most complete neural arch has a deep and triangular postzygodiapophyseal centrodiapophyseal

fossa (pccli) with three foramina on the right side and two foramina with dividing laminae (Fig. 5D).

External Pneumaticity of Appendicular Skeleton Elements

Ilium (MCF-PVPH-411). The ilium is highly pneumatized, with the presence of numerous pneumatic foramina located in different portions of the element (Fig. 6A). The exposed camellae are large, in some cases, have small dividing laminae. In the area where the ilium contacts the sacrum, there are three large and deep foramina, although the greatest concentration of foramina is visible in the middle portion of the iliac blade. (Fig. 6B detail). Additionally, camellate tissue can be seen on the contact surface for the pubis (Fig. 6C in detail).

Pubis (MCF-PVPH-411) and Ischium (MCF-PVPH). The preserved part of the pubis is almost entirely apneumatic (Fig. 6D), except for the iliac peduncle where two foramina are present at the contact surface with the ilium (Fig. 6E). As for the ischium, only the distal half of the ischial shaft is preserved, which is completely apneumatic.

Internal Pneumaticity and CT Scans

CT scans were performed in order to examine the internal arrangement of the only preserved dorsal centrum and two dorsal neural arches (Fig. 7). On the central portion of the centrum there is a large camera, surrounded by camellate tissue both ventrally and dorsally. This camera is reduced at the anterior and posterior ends, where it is completely invaded by camellate tissue. (Fig. 7A, B). At the anterior and posterior ends of the vertebra, the camellate tissue appears irregular and without a specific shape, while in the presence of the central camera, the camellate tissue around it has a mostly quadrangular shape (Fig. 7C, D).

The neural arches consist entirely of camellate tissue with camellae of different sizes and shapes. The largest camellae occur in the neural spine and in the diapophyses of the anterior dorsal neural arch (12th presacral vertebra in Coria & Currie, 2016) (Fig. 7E, F). In the posterior neural arch, the camellate tissue reveals large camellae, which range from oval to subtriangular in the diapophyses (16th presacral vertebra in Coria & Currie, 2016) (Fig. 7G, H).

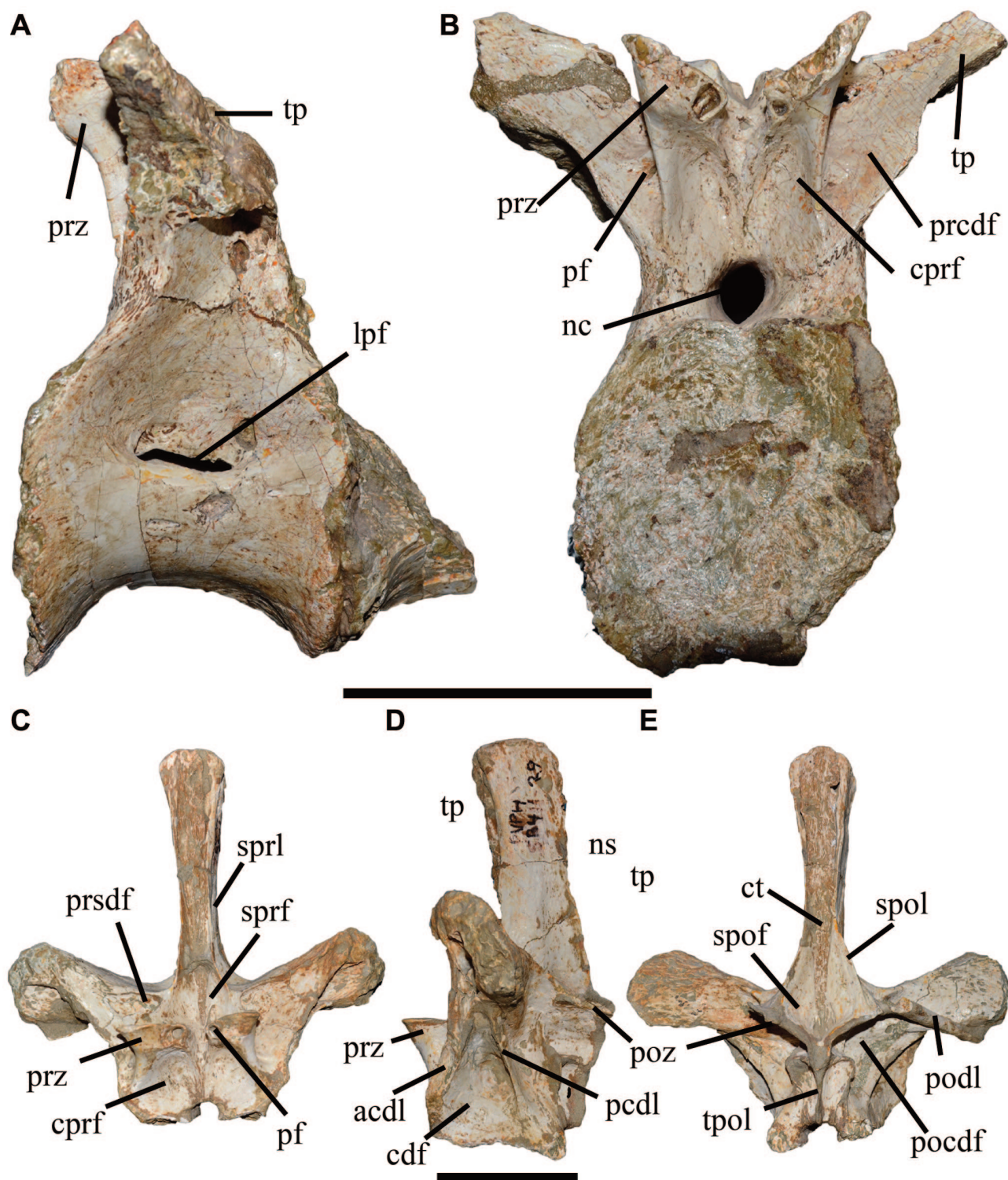


Figure 4. A–E, *Murusraptor barrosaensis* (MCF-PVPH-411). A–B, Anterior sacral vertebra; A, left lateral view; B, anterior view. C–E, Neural arch of posterior sacral vertebra; C, anterior view; D, left lateral view; E, posterior view. Abbreviations: acdl, anterior centrodiapophyseal lamina; cdf, centrodiapophyseal fossa; cprf, centroprezygapophyseal fossa; ct, camellate tissue; lpf, lateral pneumatic foramen; nc, neural canal; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygo-centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophyses; prcdf, prezygo-centrodiapophyseal fossa; prsdf, prezygo- spino diapophyseal fossa; prz, prezygapophyses; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tp, transverse process; tpol, intrapostzygapophyseal lamina. Scale = 10 cm.

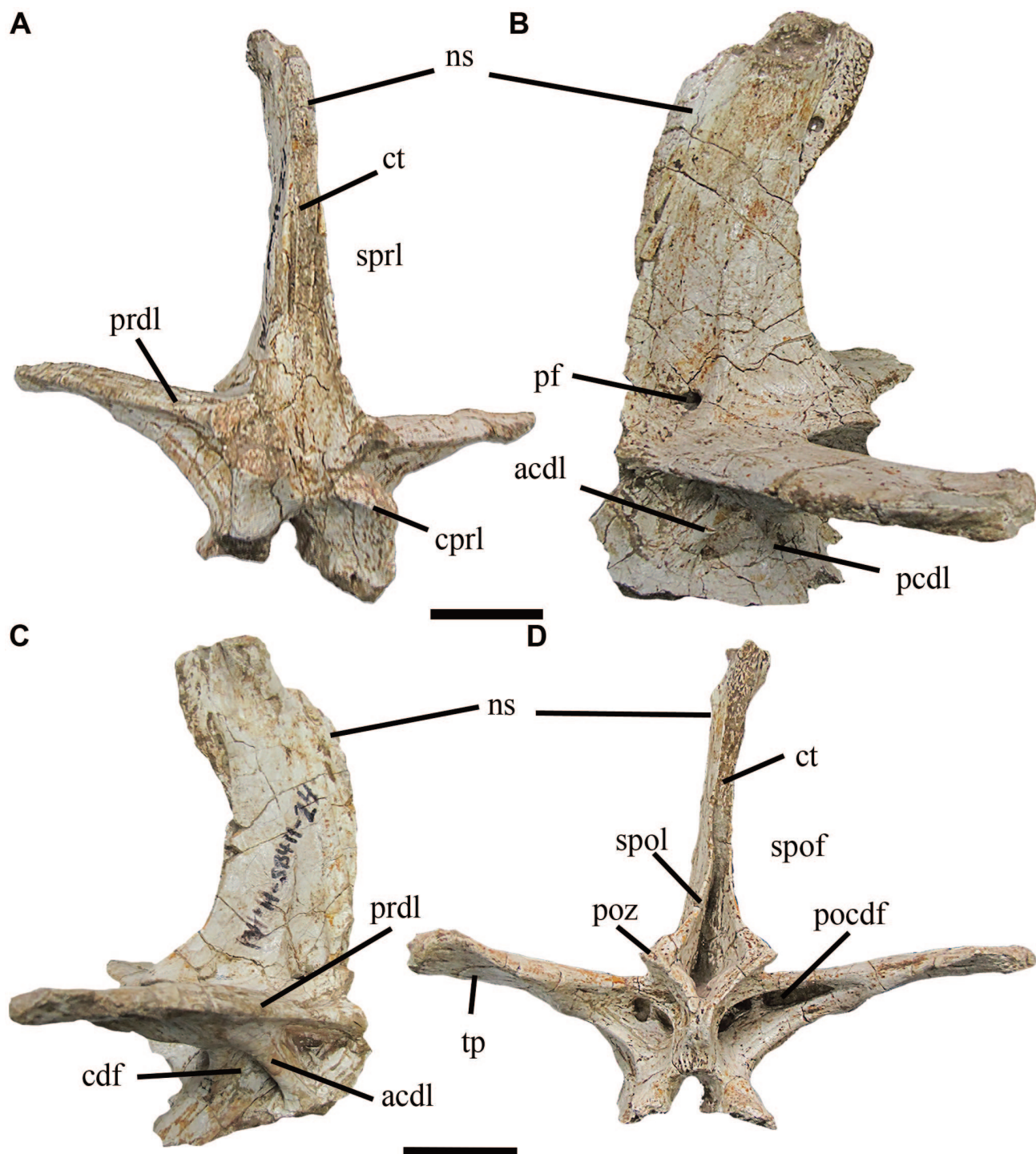


Figure 5. A–D, Caudal neural arches of *Murusraptor barrosaensis* (MCF-PVPH-411). A, anterior view; B, left lateral view; C, right lateral view; D, posterior view. Abbreviations: acdl, anterior centrodiapophyseal lamina; cdf, centrodiapophyseal fossa; cprl, centroprezygapophyseal lamina; ct, camellate tissue; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pf, pneumatic foramen; pocdf, postzygo-centrodiapophyseal fossa; poz, postzygapophyses; prdl, prezygodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tp, transverse process. Scale = 5 cm.

DISCUSSION

Pneumaticity patterns in *Murusraptor barrosaensis*

In almost all the studied vertebral material, which mostly consists of neural arches, there are practically no variations in pneumaticity patterns (Figs. 2–5). Of the preserved appendicular material is concerned, only the ischium is apneumatic. The ilium is highly pneumatized and

the pubis has two pneumatic foramina located at the iliac peduncle. Thus, it can be assumed that there was some sort of pneumatic communication between ilium and pubis (Fig. 6). Surprisingly, the pneumatic system of the ilium would also have communicated with the interior of the sacral vertebrae, as suggested by the highly pneumatic transverse processes of the sacral vertebra that contacted

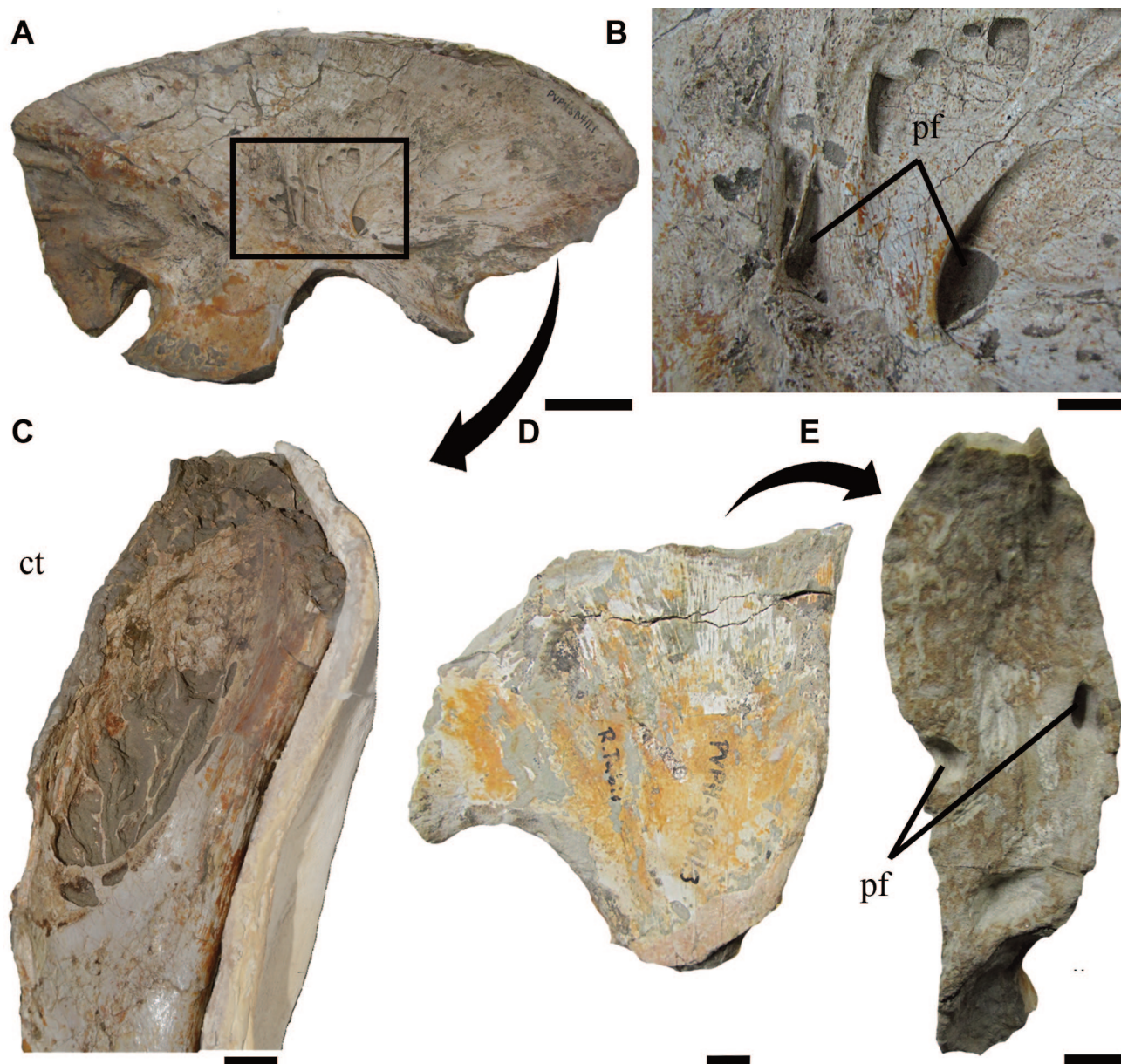


Figure 6. A–C, Ilium of *Murusraptor barrosaensis* (MCF-PVPH-411). A, medial view; B, detail showing the density of pneumatic foramina and camellate tissue in the medial region; C, joint area with the pubis. D–E, Pubis of *Murusraptor barrosaensis* (MCF-PVPH-411). D, lateral view; E, proximal view showing the two pneumatic foramina in connection with the ilium. Abbreviations: ct, camellate tissue; pf, pneumatic foramen. Scale = 10 cm (A) and 2 cm (B–E).

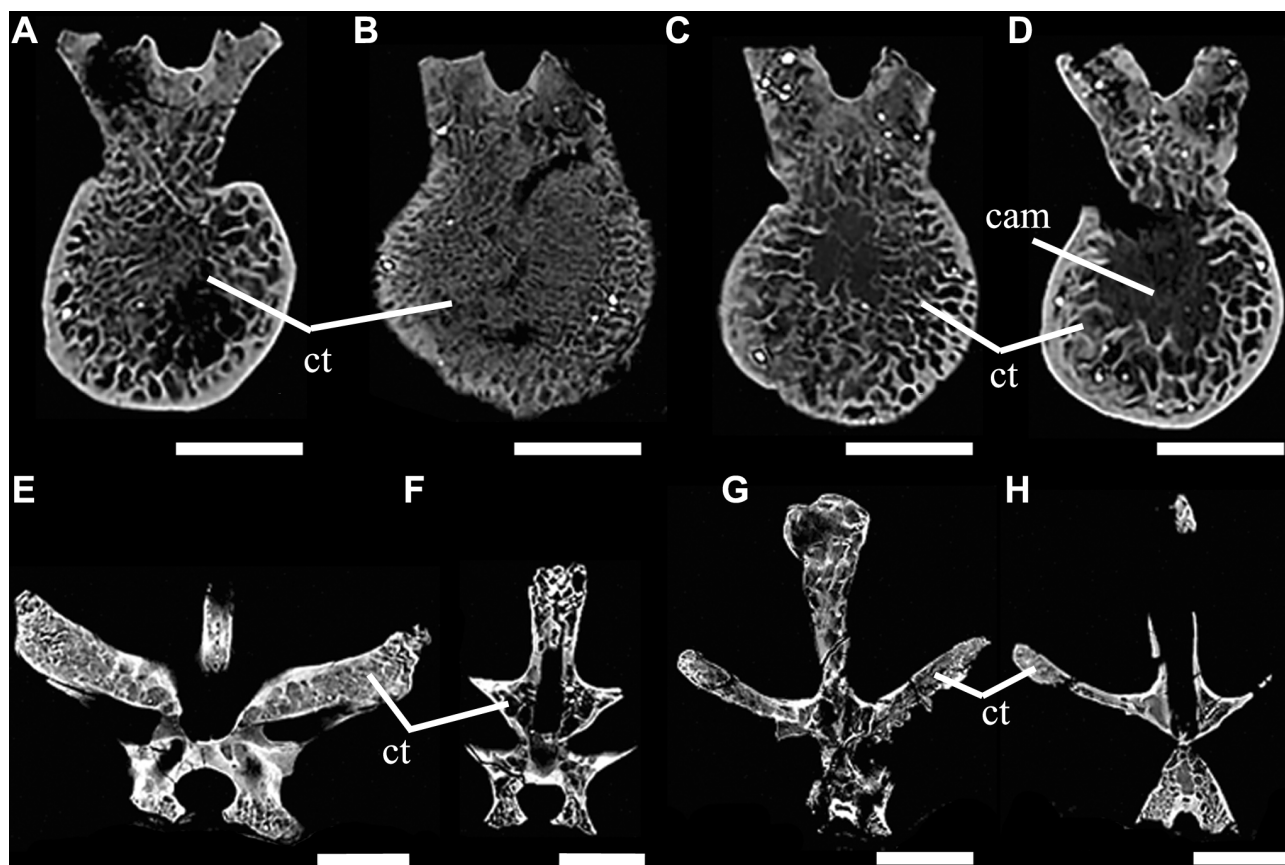


Figure 7. A–D, CT scans of a dorsal vertebral centrum of *Murusraptor barrosaensis* (MCF-PVPH-411). A, B, showing camellate tissue with reduction of the central camera; C, D, central camera with surrounding camellate tissue. E–H, CT scans of dorsal neural arches of *Murusraptor barrosaensis*, showing camellate tissue. Abbreviations: cam, camara; ct, camellate tissue. Scale = 5 cm.

with corresponding pneumatic foramina on the internal side of the ilium.

Comparisons with other megaraptorids

In order to determine whether the pneumaticity patterns of *Murusraptor* are unique for this species or instead are more widely distributed within Megaraptorida, a comparison was made with the following megaraptorid species: *Aoniraptor libertatem* (Aranciaga Rolando et al., 2020); *Maip macrothorax*, *Aerosteon riocoloradensis* (Aranciaga Rolando et al., 2022); *Megaraptor namunhauquii* (Porfiri et al., 2014); *Tratayenia rosalesi*; and *Orkoraptor burkei*.

External pneumaticity

Dorsal vertebrae. The centrum of *Murusraptor* has two lateral pneumatic foramina divided by septa. These structures are elliptical and well-excavated, as seen in *Maip*,

Tratayenia, *Aerosteon* and *Megaraptor*. Dividing septa are visible in other taxa such as *Tratayenia* (Porfiri et al., 2018), *Aerosteon* (Sereno et al., 2008; Aranciaga Rolando et al., 2021) and *Maip* (Fig. 8A).

The neural arches of *Murusraptor* exhibit diapophysis, parapophysis, prezygapophysis and postzygapophysis with camellate tissue and some foramina; this can also be seen in *Maip* (Fig. 8B), *Aerosteon* (Sereno et al., 2008, fig. 7B, 8A; Aranciaga Rolando et al., 2021, figs. 21, 23, 25, 27 and 29), *Megaraptor* (Porfiri et al., 2014, fig. 8E) and *Tratayenia* (Porfiri et al., 2018, fig. 4C, D) which, like *Murusraptor*, lost part of the cortical tissue that covered these structures, exposing the camellate tissue. Only *Murusraptor* exhibits exposed camellate tissue on the neural spines.

All megaraptorids examined herein exhibit a broadly similar pattern of dorsal laminae and fossae. This is especially evidenced by the presence of the centrodiaepophyseal

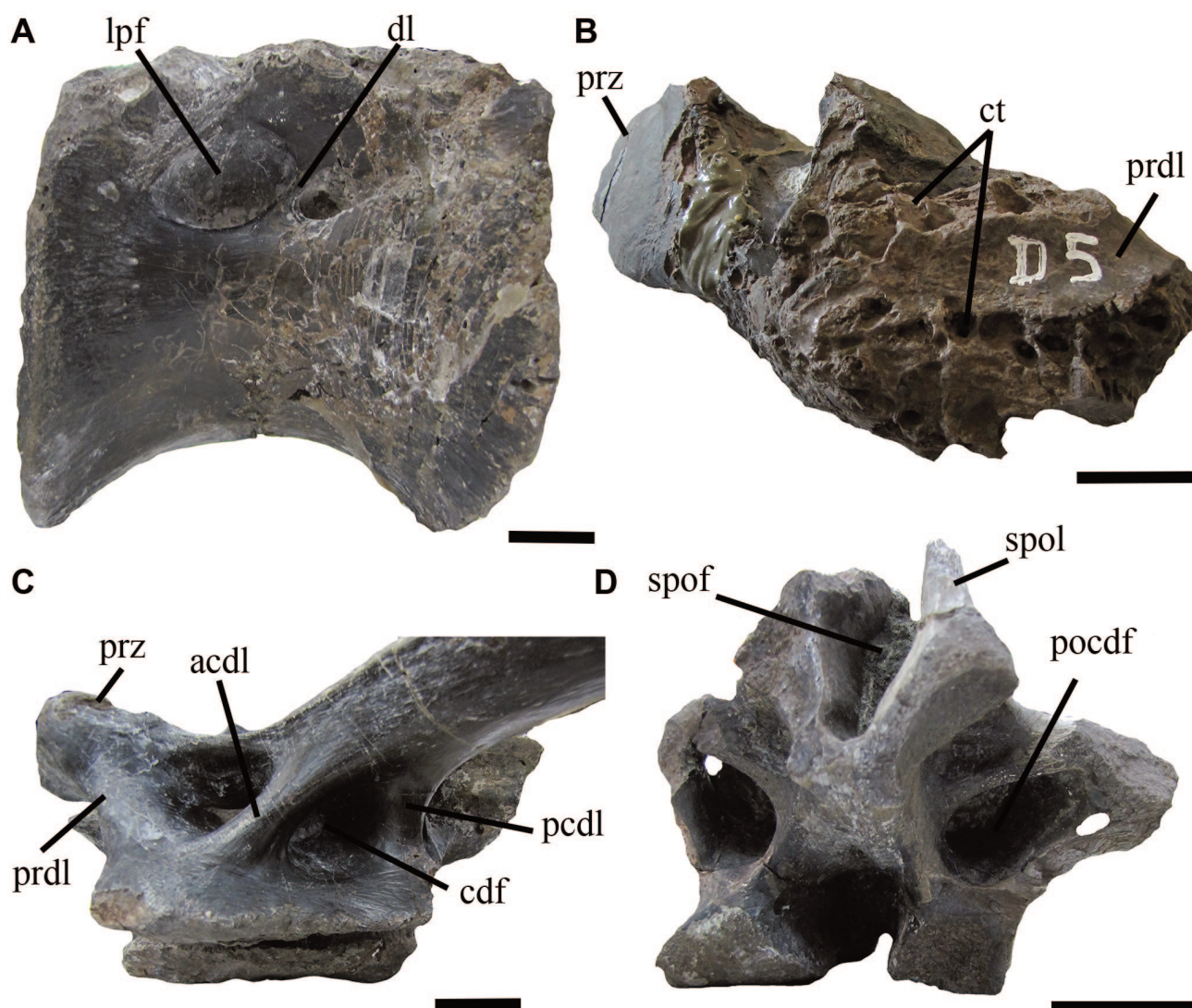


Figure 8. A–D, Dorsal vertebrae of *Maip macrothorax* (MPM–PV 21.,545). A, tenth or eleventh centrum in lateral view; B, diapophyses and prezygapophyses of fifth dorsal vertebra in lateral view; C, second dorsal neural arch in left ventrolateral view; D, second dorsal neural arch in posterior view. Abbreviations: acdl, anterior centrodiapophyseal lamina; cdf, centrodiapophyseal fossa; ct, camellate tissue; dl, dividing lamina; lpf, lateral pneumatic foramen; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygo-centrodiapophyseal fossa; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina. Scale = 2 cm.

fossa (cdf), which is delimited by the anterior and posterior centrodiapophyseal laminae (acdl and pcdl, respectively). Other neural laminae and fossae present in *Murusraptor* and the other taxa are the prezygodiapophyseal lamina (prdl), postzygodiapophyseal lamina (podl), spinopostzygapophyseal lamina (spol), spinopostzygapophyseal fossa (spof) and postzygo-centrodiapophyseal fossa (pocdf). These neural lamina and fossae are present in *Aerosteon*, (Serenó et al., 2008, figs. 7, 8; Aranciaga Rolando et al., 2021, figs. 19–30),

Maip (Fig. 8C, D), *Megaraptor* (Fig. 9), and *Tratayenia* (Porfiri et al., 2018, figs. 3, 4).

Sacral vertebrae. The sole preserved sacral vertebral centrum of *Murusraptor* *Murusraptor*, which is elongated with an eye-shaped lateral pneumatic foramen, as in *Tratayenia* (Porfiri et al., 2018, figs. 3B, 5A) and *Aoniraptor* (Aranciaga Rolando et al., 2020, fig. 2A, D, G).

As in the dorsal vertebrae, the anterior centrodiapophyseal lamina (acdl) and posterior centrodiapophyseal lamina (pcdl)

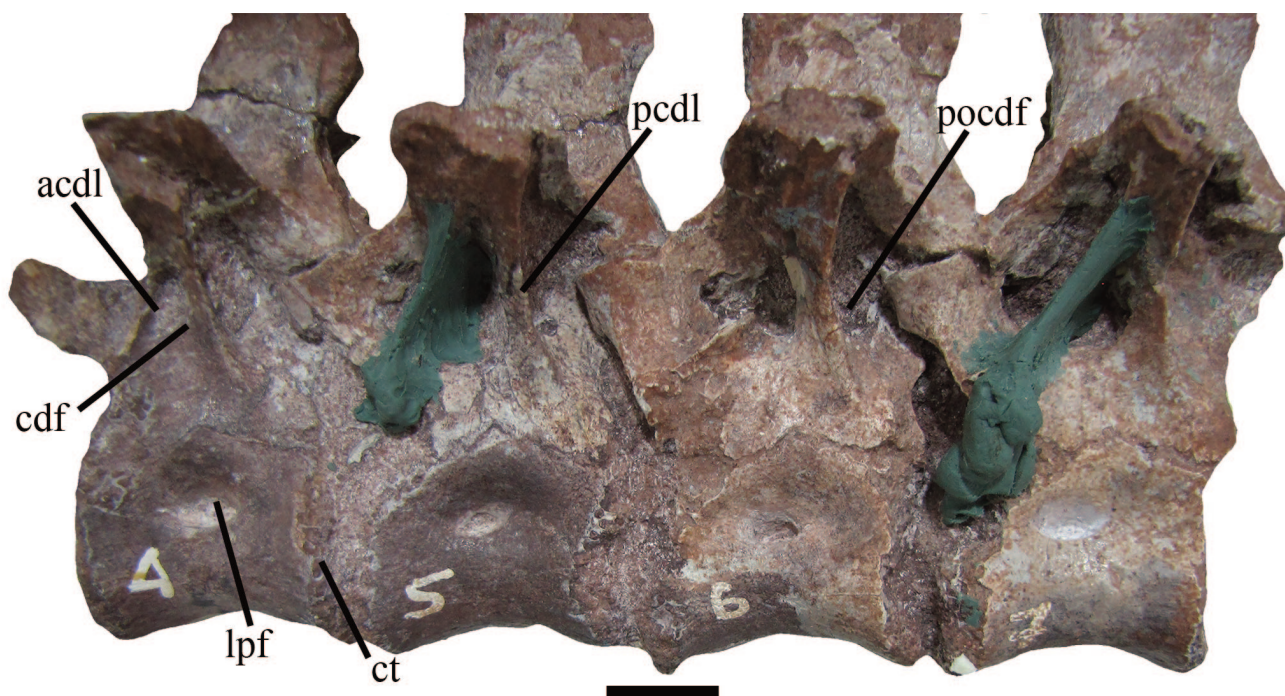


Figure 9. Fourth to seventh dorsal vertebrae of *Megaraptor namunhuaiquii* (MUCPv 595) in left lateral view. Abbreviations: acdl, anterior centrodiapophyseal lamina; cdf, centrodiapophyseal fossa; ct, camellate tissue; lpf, lateral pneumatic foramen; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygo-centrodiapophyseal fossa. Scale = 2 cm.

that delimit centrodiapophyseal fossa (cdf) are present in both *Aoniraptor* (Aranciaga Rolando et al., 2020, fig. 2K) and *Tratayenia* (Porfiri et al., 2018, fig. 5A). Other laminae and fossae present in the sacral vertebrae of these two taxa are not visible due to deterioration of the material in *Aoniraptor* or due to their articulation with each other and with the ilium in *Tratayenia*. Therefore, it is not possible to establish whether the patterns of laminae and fossae observed in *Murusraptor* are present in the sacral vertebrae of other megaraptorids or if they are exclusive to this taxon. None of the taxa analyzed has exposed camellate tissue in their neural spines.

Caudal vertebrae. Like other vertebrae, only the caudal vertebrae of *Murusraptor* present exposed camellate tissue. This feature was not observed in the caudal vertebrae of the other taxa analyzed.

Regarding neural laminae and fossae, as in the rest of the vertebral sequence, the centrodiapophyseal fossa (cdf) (delimited by anterior centrodiapophyseal lamina (acd1) and posterior centrodiapophyseal lamina (pcdl) respectively) has remained present in all the taxa analyzed, being reduced in

Orkoraptor (Novas et al., 2008, fig. 6B). Other laminae and fossae present in both *Murusraptor* and the other taxa are spinoprezygapophyseal lamina (sprl) (*Aerosteon*, Aranciaga Rolando et al., 2021, figs. 31, 32), postzygodiapophyseal lamina (podl) (*Maip*, Aranciaga Rolando et al., 2022, fig. 9), centroprezygapophyseal lamina (cprl), prezygodiapophyseal lamina (prdl), spinopostzygapophyseal lamina (spol), centroprezygapophyseal fossa (cprf), spinopostzygapophyseal fossa (spof) (*Aerosteon*, Aranciaga Rolando et al., 2021, figs. 31, 32; *Maip*, Aranciaga Rolando et al., 2022, fig. 9), and postzygo-centrodiapophyseal fossa (pocdf) (*Aerosteon*, Aranciaga Rolando et al., 2022, figs. 31, 32; *Maip*, Aranciaga Rolando et al., 2022, fig. 9; and *Aoniraptor*, Aranciaga Rolando et al., 2020, fig. 6B). The prezygapophyseal centrodiapophyseal fossa (prcdf) is present in all three taxa used for comparison, but absent in *Murusraptor*.

Illia and pubis. The ilium of *Murusraptor* has a high degree of pneumaticity which is evidenced by the presence of a high number of pneumatic foramina. The same condition is present in *Aerosteon* (Sereno et al., 2008, figs. 13, 14; Aranciaga Rolando et al., 2021, fig. 39B) and *Tratayenia*

(Porfiri et al., 2018, figs. 3B, 5A). However, in all cases, the highest density of foramina is found in contact with the sacral vertebrae, possibly as a result of a joint pneumatization of both elements through the abdominal air sac (O'Connor & Claessens, 2005; O'Connor, 2006; Wedel, 2009). The pubis of *Murusraptor* exhibits incipient pneumatization, possibly via the ilium, unlike *Megaraptor*, *Aerosteon* and *Tratayenia*, whose pubis is apneumatic.

Internal Pneumaticity

CT scans performed on the dorsal vertebral centrum and the two dorsal neural arches of *Murusraptor* revealed the presence of camellate tissue in the neural arches and at the edges and ends of the centrum, which, in the central portion, surround a camera. CT scans are available only for *Aoniraptor* (Fig. 10) and material of Megaraptora indet from Brazil (Martinelli et al., 2013, fig. 2E–H). The sacral (Fig. 10A, B) and caudal (Fig. 10C, D) vertebrae of *Aoniraptor* and CPPLIP 1324, a caudal vertebra of an indeterminate megaraptoran from Uberaba Formation from Brazil, show the same pattern of pneumaticity as in *Murusraptor* with neural arches with camellate tissue, and centra with a central camera surrounded by camellate tissue. It is possible that, such a pattern of camera surrounded by camellate tissue represents a synapomorphy of at least South American megaraptorids.

Considerations on pneumaticity in megaraptorids. External and internal pneumatic characters, pneumaticity patterns are conservative among megaraptorids. *Murusraptor* and the other taxa analyzed show similarity in the neural laminae and the fossae, especially in the centrodiapophyseal fossa (cdf) and the two laminae that surround it, anterior and posterior centrodiapophyseal laminae (acdl and pcldl). The same condition occurs with the internal pneumaticity: neural arches with camellate tissue and vertebral centra with a central camera surrounded by camellate tissue.

Comparisons with other relative taxa. *Albertosaurus sarcophagus*, *Allosaurus fragilis*, *Sinraptor dongi* and avian theropods (*Ichthyornis*, *Janavis*, *Struthio camelus*, *Rhea americana*, *Cygnus olor* and *Chauna torquata*). Currently, the phylogenetic affinities of megaraptorids are controversial, being considered either tyrannosauroids or allosauroids, thus particular taxa from both major clades were chosen for comparison.

Murusraptor possesses extreme pneumaticity, as this feature extends into the caudal vertebrae and the ilium. It has neural arches with camellate tissue, in which the neural spines have exposed camellate tissue and vertebral centra with a central camera surrounded by camellate tissue. This seems to be a pattern in the vast majority of megaraptorids. In related taxa (including birds) some similarities and differences can be seen. In the case of tyrannosauroids,

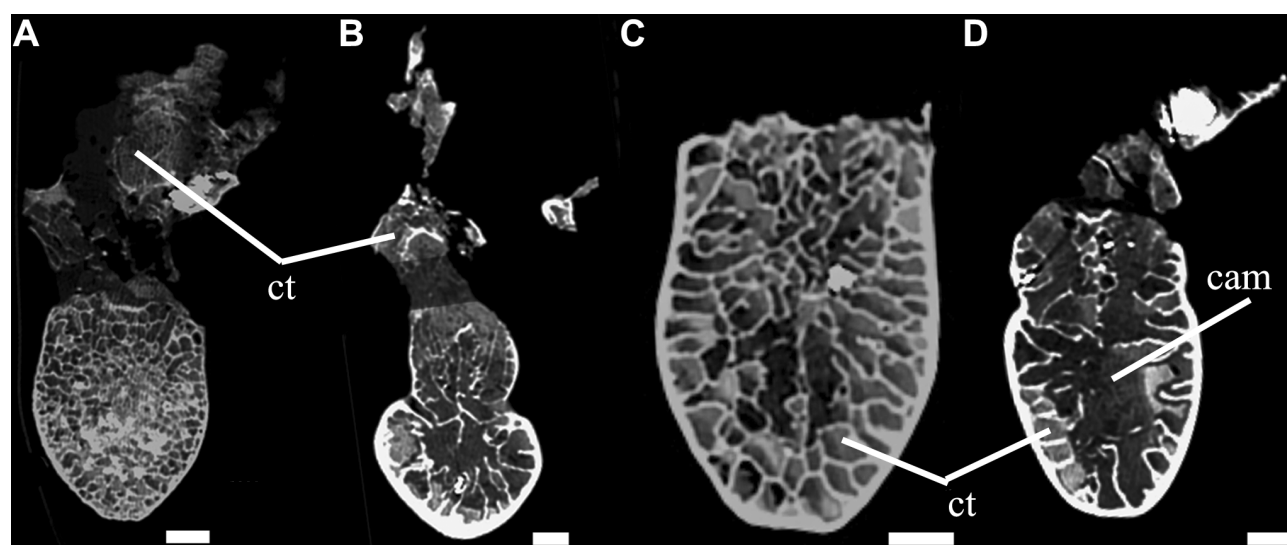


Figure 10. A–D, CT scans of *Aoniraptor libertatem* (MPCA-Pv 804/1–25). A, B, sacral vertebra; C, D, middle to posterior caudal vertebra. Abbreviations: cam, camera; ct, camellate tissue. (CT scans courtesy of Dr. Mauro Aranciaga Rolando). Scale = 1 cm.

such as *Albertosaurus sarcophagus*, there is camellate tissue in the centra and in the dorsal neural arches, which reach the apophyses (Britt, 1993, figs. 25, 26.1–4, 27.1, 27.3, 27.4). The sacral vertebrae have foramina, as do the caudal vertebrae, although pneumaticity is not recorded. The same morphology is observed in the ilium (Britt, 1993; Brochu, 2003). Conversely, among allosauroids, such as *Allosaurus fragilis*, there is pneumatization at least up to the second dorsal vertebra (although this pneumatization may possibly extend further). *Allosaurus* exhibits with apneumatic neural arches and vertebral centra with camerae divided by parasagittal septa (Fig. 11). In *Sinraptor dongi*, there are camerae in both neural arches and centra. In the latter, they are connected to the outside through lateral pneumatic foramina (Britt, 1993, figs. 21.4–6, 22). This condition corresponds to a pattern of pneumaticity present in basal saurischian taxa but not in *Murusraptor* (and possibly in other megaraptorids). It is possible that *Murusraptor* and other megaraptorids present with a condition of pneumaticity intermediate between basal tetanurans such as *Allosaurus*, with neural arches with camellate tissue and a vertebral centra that shares camellate tissue and a camera, and tyrannosauroids such as *Albertosaurus*, which has camellate tissue in both the neural arches and vertebral centra.

The presence of exposed camellate tissue in the neural spines of the entire vertebral sequence of *Murusraptor* does not seem to be a common feature within megaraptorids, and was not found in taxa such as *Albertosaurus*, *Allosaurus* and *Sinraptor*. Although it is also uncommon in other groups, some birds (e.g., *Struthio camelus* and *Emeus* sp.) might have it in the roof and floor of the neural canal. This pattern of multiple foramina is associated with paramedullary diverticula (Atterholt & Wedel, 2022, fig. 7C, D). In the common swan, *Cygnus olor*, this pattern of foramina is observed in the upper portion of the neural canal of the posterior cervical vertebrae (Fig. 12A), while in rhea *Rhea americana* this is mostly seen in the cervical and some dorsal vertebrae (Fig. 12B). The Southern screamer *Chauna torquata* shows this pattern only in dorsal vertebrae, although the foramina are small. In this species, the highest concentration of foramina is found in the posterior portion of the neural spine, exhibiting a fenestrated pattern (Fig.

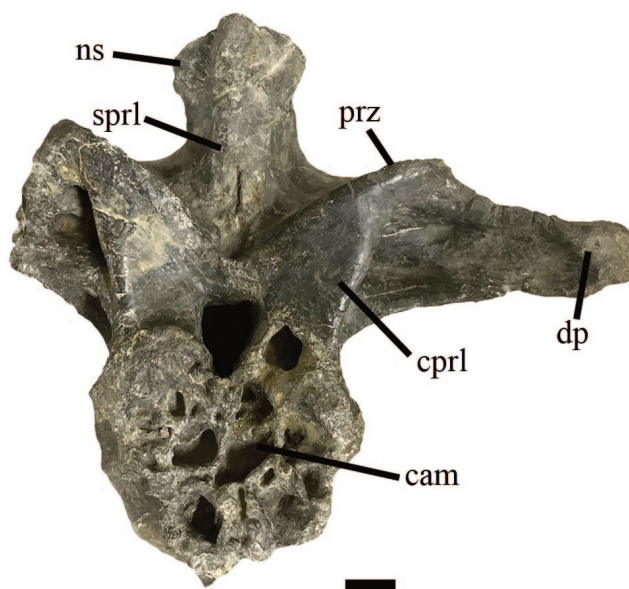


Figure 11. Second dorsal vertebra of *Allosaurus fragilis* (AMNH 5767) in anterior view. Abbreviations: cam, camara; cprl, centroprezygapophyseal lamina; dp, diapophyses; ns, neural spine; prz, prezygapophyses; sprl, spinoprezygapophyseal lamina. (Picture courtesy of Dr. Matthew Wedel). Scale = 2 cm.

12C). There is a record of osteological correlates for this type of diverticula in Mesozoic birds like *Ichthyornis* (KUV 119673) and *Janavis* (NHMM RD 271) (Atterholt et al., 2025, fig. 2). Conversely, in the fossil record of non-avian theropods, there is currently no evidence based on osteological correlates of the presence of these diverticula, with *Murusraptor* being the only record of possible paramedullary diverticula similar to the multiple foramina present in its neural spine.

Further analyses are necessary, by expanding the taxonomic sampling as well as by the inclusion of better and more complete specimens, in order to improve our knowledge about the evolution of the skeletal pneumatization among archosaurs, both extinct and extant.

CONCLUSIONS

Murusraptor barrosaensis exhibits extreme pneumaticity, characterized by the presence of camellate tissue in the neural arches and a pattern of central camara surrounded by camellate tissue in the centrum. Throughout the vertebral sequence, the fossae and neural laminae are retained, together with the exposed camellate tissue in the neural spine.

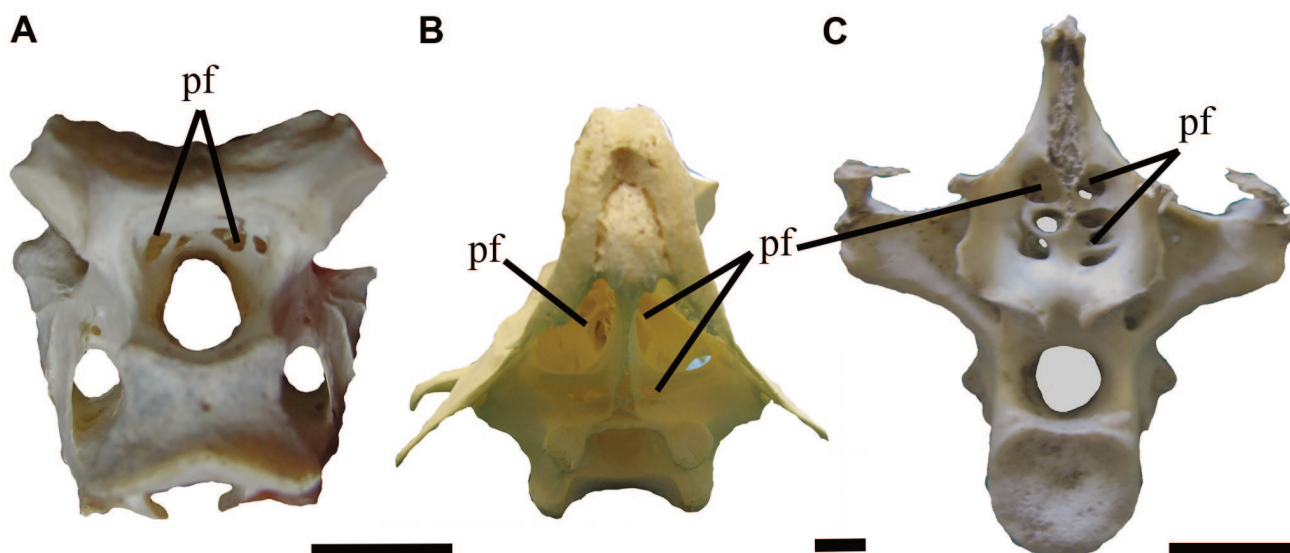


Figure 12. Multiple foramina in neural canal of vertebrae A, posterior cervical vertebra in posterior view of *Cygnus olor* (MACN-Or 68033); B, anterior dorsal vertebra in posterior view of *Rhea americana* (CFA-Or 1648); C, anterior dorsal vertebra in posterior view of *Chauna torquata* (CFA-Or 1645). Abbreviations: pf, pneumatic foramina. Scale = 1 cm.

In general, both *Murusraptor* and other megaraptorids present the same pneumatic patterns: 1) in the centra of dorsal vertebrae, the lateral pneumatic foramina are usually asymmetrical; 2) camellate tissue has been seen throughout the neural arch; and 3) the neural laminae and fossae are similar. The same occurs in sacral and caudal vertebrae, in which the pattern of asymmetry of the lateral pneumatic foramen is identical (e.g., *Aoniraptor*). A similar feature is observed in the neural laminae and fossae in neural arches. The only distinctive pneumatic feature of *Murusraptor* compared to other taxa is the presence of exposed camellate tissue in the neural spines. Regarding the appendicular skeleton, both *Murusraptor* and other megaraptorids with preserved ilia have shown the same pattern of pneumatic foramina in the region that contacts the sacral vertebrae (e.g., *Aerosteon*). The only difference between *Murusraptor* and other megaraptorids is the presence of two pneumatic foramina in the pubis, linked to the region of contact with the ilium. It is therefore possible that this connection was responsible for the pneumatization of the pubis.

Regarding internal structure, all neural arches scanned with CT scans have shown the presence of camellate tissue, while the centra exhibit a pattern of a central camara

surrounded by camellate tissue, regardless of the vertebrae analyzed. *Murusraptor* presents this pattern in the dorsal vertebrae. This feature is also present in sacral vertebrae (e.g., *Aoniraptor*) and caudal vertebrae (e.g., *Aoniraptor* and *Megaraptora* indet from Brazil). These are probably the features that characterize the pneumatic pattern present in megaraptorids.

With respect to comparisons with other related theropods, it is observed that the pneumaticity pattern of *Murusraptor* (and possibly of megaraptorids in general) is intermediate between that observed in tyrannosauroids (e.g., *Albertosaurus* with vertebrae with camellate tissue in the centra and neural arches) and allosauroids (e.g., *Allosaurus* with camerae in the centrum and apneumatic neural arch).

No comparable feature related to the presence of exposed camellate tissue has been described in any megaraptorid or related group. The only known exception is birds, (e.g., *Struthio camelus*), where a pattern known as "multiple foramina" exists, with these foramina present in the neural canal. This feature has also been observed in fossil birds (e.g., *Ichthyornis*). Although this feature is not present in the neural canal of *Murusraptor*, it is possible that its neural spine exhibits something similar.

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