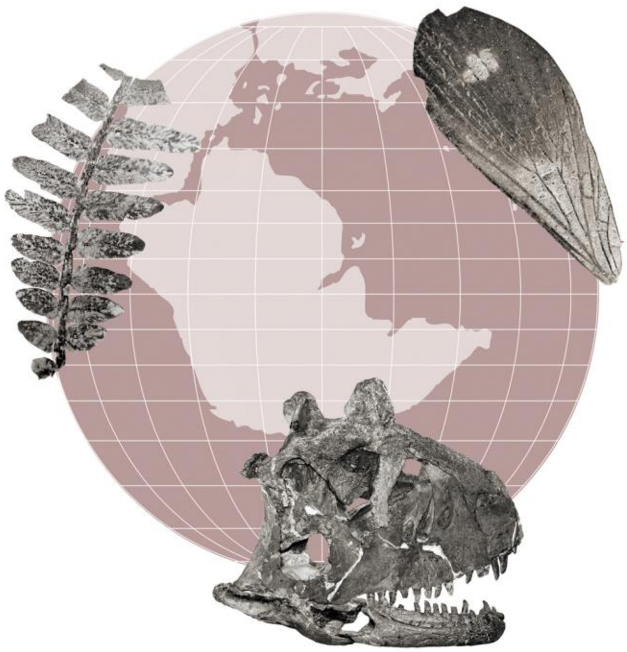
AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL



Submitted: 2 July 2025 - **Accepted**: 18 December 2025 - **Posted online**: 19 December 2025

To link and cite this article:

doi: 10.5710/AMGH.18.12.2025.3656

POSTCRANIAL PNEUMATICITY IN ABELISAURIDS (DINOSAURIA: THEROPODA): THE CASES OF *TRALKASAURUS CUYI*, *SKORPIOVENATOR BUSTINGORRYI* AND *CARNOTAURUS SASTREI*

VIRGINIA, ZURRIAGUZ[1] AND MAURICIO A. CERRONI[2]

1-Instituto de Paleobiología y Geología (UNRN-CONICET). Avenida Roca 1242, R8332, General Roca, Provincia de Río Negro, Argentina. vlzurriaguz@unrn.edu.ar

2- Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-CONICET) Ángel Gallardo 470, C1405DJR, CABA, Argentina. mauricio.cerroni@gmail.com

Running Header: ZURRIAGUZ AND CERRONI. POSTCRANIAL PNEUMATICITY IN ABELISAURIDS

Short description: Analysis of the postcranial pneumaticity of abelisaurids, in which a certain degree of variation was found in the caudal vertebrae

Corresponding author: Virginia Zurriaguz. E-mail: vlzurriaguz@unrn.edu.ar

Abstract. Abelisaurids were a group of mostly Gondwanan theropod dinosaurs, whose anatomy and phylogeny are well known. However, this is not the case for some paleobiological aspects such as postcranial pneumaticity. In this work, postcranial pneumaticity patterns were analyzed in three abelisaurids: *Tralkasaurus cuyi, Skorpiovenator bustingorryi*, and *Carnotaurus sastrei*, which were compared with other abelisaurids and closely related groups (*e.g.*, noasaurids). For this purpose, both naked-eye observations and CT scans of vertebral material (dorsal and caudal), as well as cervical and dorsal ribs were considered. The results obtained show that *Tralkasaurus* and *Skorpiovenator* have pneumatized dorsal vertebrae, like almost all the analyzed taxa (*e.g.*, *Majungasaurus crenatissimus*). The same occurs with the ribs of both *Skorpiovenator* and *Carnotaurus* and other taxa (*e.g.*, *Niebla antiqua*). In the case of *Carnotaurus*, only the cervical ribs were scanned, which showed camerae, while the dorsal ribs of *Skorpiovenator* showed a possible pneumatic space. The greatest variation is found in the caudal vertebrae, where *Skorpiovenator* presents pneumatization in the neural arches, while most abelisaurids have apneumatic caudal vertebrae, with the exception of *Aucasaurus garridoi* and an undetermined abelisaurid from Chubut. These results are unexpected, since the caudal vertebrae of abelisaurids were historically considered apneumatic, and highlight the need to delve deeper into this type of studies within this fascinating group of theropods.

Keywords. Ceratosauria, camellated tissue, ribs, presacral vertebrae, caudal vertebrae, CT scans, Cretaceous, Patagonia

Resumen. NEUMATICIDAD POSTCRANEANA EN ABELISÁURIDOS (DINOSAURIA: THEROPODA): LOS CASOS DE *TRALKASAURUS CUYI, SKORPIOVENATOR BUSTINGORRYI* Y *CARNOTAURUS SASTREI*. Los abelisáuridos fueron un grupo de terópodos, principalmente gondwánicos, cuya anatomía y filogenia son bien conocidas. Sin embargo, este no es el caso de algunos aspectos paleobiológicos, como la neumaticidad postcraneana. En este trabajo se analizaron los patrones de neumaticidad postcraneal en tres abelisáuridos: *Tralkasaurus cuyi, Skorpiovenator bustingorryi* y *Carnotaurus sastrei*, los cuales fueron comparados con otros abelisáuridos y grupos relacionados (p. ej., noasáuridos). Para este propósito, se consideraron tanto observaciones a ojo desnudo como tomografías computadas de material vertebral (dorsal y caudal) así como de costillas cervicales y dorsales. Los resultados obtenidos muestran que *Tralkasaurus* y *Skorpiovenator* presentan vértebras dorsales neumatizadas, como casi todos los taxones analizados (p. ej., *Majungasaurus crenatissimus*) y lo mismo ocurre con las costillas de *Skorpiovenator*, *Carnotaurus* y otros taxones (p. ej., *Niebla antiqua*). La mayor variación fue hallada en las vértebras caudales, donde *Skorpiovenator* presenta arcos neurales neumatizados, mientras que la

mayoría de los abelisáuridos presentan vértebras caudales aneumáticas, con la excepción de *Aucasaurus garridoi* y un abelisáurido indeterminado de Chubut. Estos resultados son inesperados, dado que las vértebras caudales de los abelisáuridos se consideraban históricamente aneumáticas, por lo cual resalta la necesidad de profundizar en este tipo de estudios dentro de este fascinante grupo de terópodos.

Palabras clave. Ceratosauria, tejido camelado, costillas, vértebras presacras, vértebras caudales, tomografías computadas, Cretácico, Patagonia

INTRODUCTION

Abelisaurids are a group of non-avian theropods, which inhabited mostly Gondwanan landscapes and whose records date back from the Valanginian (lower Cretaceous) until the Maastrichtian (upper Cretaceous), with the most abundant record of Argentinean Patagonia (Bonaparte 1991; Carrano and Sampson 2008; Novas 2009; Novas et al. 2013; Zaher et al. 2020). Abelisaurids present various sizes (from about 4 meters to about 8-9 meters) (Novas et al. 2013; Canale et al. 2016) and have some particular characteristics such as highly sculptured skulls with high snouts and extremely small forelimbs (Bonaparte and Novas 1985; Bonaparte 1991; Novas 1997; Coria et al. 2002; Canale et al. 2009, 2016; Carrano and Sampson 2008; Pol and Rauhut 2012). To this day, both anatomy and phylogenetic relationships of abelisaurids are well known and have been widely discussed (Bonaparte 1985; Sampson et al. 1998; Coria et al. 2002; Canale et al. 2009; Farke and Sertich 2013; Filippi et al. 2016; Zaher et al. 2020; Baiano et al. 2023; Pol et al. 2024), little is known about some of their paleobiological aspects, particularly those related to postcranial pneumaticity (PSP).

Postcranial pneumaticity is currently present only in birds (Duncker 1971, O’Connor 2006), but has spread within the clade Ornithodira, being found in both pterosaurs and saurischian dinosaurs (Britt 1993; Wedel 2009; Benson et al. 2011). PSP is the invasion of epithelial extensions called pneumatic diverticula within bones, whose origin came from the air sacs connected to the lungs (King 1966; Duncker 1971). This invasion occurs through foramina that connect to internal cavities called camerae or camellae (Britt 1993; Wedel 2003a,b; O'Connor 2006).

Although PSP is widely distributed within Saurischia, it has been studied much more in sauropods than in non-avian theropods (Britt 1993; O'Connor 2007; Sereno et al. 2008; Benson et al. 2011; Watanabe et al. 2015; Aranciaga-Rolando et al. 2020; Gianechini and Zurriaguz 2021; Aureliano et al. 2024; Windholz et al. 2025).

This study aims to describe the postcranial pneumaticity (PSP) of three distinct abelisaurid theropods (*Tralkasaurus cuyi* Cerroni et al. 2020*, Skorpiovenator bustingorryi* Canale et al. 2009 and *Carnotaurus sastrei* Bonaparte 1985). These results will expand not only the knowledge about PSP in theropods generally, and particularly the Abelisauridae, a group for which the distribution of this characteristic remains barely documented.

Institutional Abreviations. CPP, Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price," Peirópolis, Brazil**; DGM,** Departamento Nacional da Produçao Mineral, Museu de Cencias da Terra, Rio de Janeiro, Brazil; **FMNH** Field Museum of Natural History, Chicago; United States of America; **FSAC,** Faculté des Sciences Aïn Chock, Université Hassan II, Casablanca, Morocco**; MACN-Pv-CH**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Chubut, Ciudad Autónoma de Buenos Aires, Argentina; **MCF**, Museo "Carmen Funes", Plaza Huincul, Argentina; **MCT**, Museo de Ciencias da Terra, Rio de Janeiro, Brazil; **MEB (MMCH)**, Museo "Ernesto Bachmann", El Chocón, Argentina; **MEF**, Museo Egidio Feruglio, Trelew, Argentina;

MHNA, Muséum d'Histoire Naturelle d'Aix-en-Provence, France; **MHNH**, Muséum d'histoire naturelle du Havre, Havre, France; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MPCA**, Museo Provincial "Carlos Ameghino", Cipolletti, Argentina; **MPCN**, Museo Patagónico de Ciencias Naturales, General Roca, Argentina; **MPM**, Museo Padre Manuel Molina, Río Gallegos, Santa Cruz, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto, Sao Paulo, Brazil; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **NMV**, National Museum of Victoria, Melbourne, Australia; **PIN**, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscov, Russia; **UA**, University of Antananarivo, Antananarivo, Madagascar; **UNPSJBPV**, Universidad Nacional de la Patagonia San Juan Bosco, Colección Paleovertebrados, Chubut, Argentina

MATERIALS AND METHODS

Materials

The materials examined in this study include one posterior dorsal vertebra and three dorsal transverse process of *Tralkasaurus cuyi* (MPCA Pv-815; see Cerroni et al., 2020), two posterior dorsal vertebrae (10th and 11th), two anterior caudal vertebrae (1st and 3rd), four dorsal ribs of *Skorpiovenator bustingorryi* (MMCH-PV 48; see Canale et al., 2008) and three cervical (5th, 8th and 10th) and seven dorsal ribs of *Carnotaurus sastrei* (MACN-Pv-CH 894; see Bonaparte et al. 1990).

Methods

Pneumatic characters were described first-hand encompassing both external observations and internal morphology. The internal structure was described according to the terminologies of Britt (1993) and Wedel (2003a,b). Two of the three taxa were tomographed in Neuquén city: *Skorpiovenator* and *Tralkasaurus.* The CT scans were performed in Policlínico de Neuquén, using a tomograph GE® BrightSpeed. In both cases, the slices presented 0.625 mm of separation and 120 kV. In the case of *Carnotaurus*, the CT scans were performed at Maimonides University, with a slice thickness of 0.8 mm and 130 kV. The digital work of the CT scans was carried out with the following software: 3D Slicer v5.8 (Fedorov et al. 2012) to obtain improved and visualize three-dimensional models (exported as .stl files) and Adobe PS 2018 for image creation.

Also, comparisons were made with other abelisaurids by analyzing its dorsal and caudal vertebrae, as well ascervical and dorsal ribs in order to compare it with the three taxa studied here. Within these taxa used for comparative purposes, those in which there was unambiguous evidence of postcranial pneumaticity were selected.

DESCRIPTION

Dorsal vertebrae of *Tralkasaurus cuyi*

In these vertebrae, only small portions of the vertebral centra and neural arches have been preserved, which present a high degree of pneumatization (Fig 1). Due to the extreme deterioration of the material, external pneumatic features cannot be observed (e.g., foramina with visible connection to the interior of the vertebra), while the internal structure present is of camellated type and extends throughout all preserved parts of the neural arch reaching the distal ends of the diapophyses and parapophyses. As for the structure of the camellated tissue, the camellae are of considerable size and can be seen only in the parasagittal axis, in which the camellae exhibit an arrangement that is sometimes quadrangular (*i.e.*, base of the arch) and sometimes triangular or subtriangular (*i.e.*, diapophysis and parapophysis, especially on their ends) (Fig. 1.4; 1.5; 1.6; 1.7).

Dorsal vertebrae of *Skorpiovenator bustingorryi*

Because most dorsal vertebrae are articulated, only the 10th and 11th dorsal vertebrae could be CT scanned (Fig 2.1, 2.2, 2.3 and 2.4). In this case, and possibly due to the poor preservation of the material, it was not possible to appreciate any pneumatic feature, beyond some structures that could have formed part of the small chambers, called camellated tissue. In this case, it can be observed that the camellated tissue has collapsed, preventing the recognition of camellae (Fig 2.1, 2.2, 2.3 and 2.4).

Caudal Vertebrae of *Skorpiovenator bustingorryi*

These caudal vertebrae show, in general terms, apneumatic centra and pneumatized neural arches (Fig 2.5; 2.6; 2.7 and 2.8). The neural arches are completely pneumatized, especially in the transverse processes (Fig 2.5; 2.7 and 2.8). The pneumatization of the neural arches is composed of small chambers that correspond to a camellated tissue pattern. Due to wind erosion and root invasion, the material has been deteriorated, which affected the material, preventing the identification of the precise shape of this tissue. For the same reason, it was also not possible to observe pneumatic foramina that would serve as a connection to the internal camellated tissue.

Cervical and dorsal ribs of *Carnotaurus sastrei*

Both cervical and dorsal ribs, whether anterior, middle, or posterior, have a foramen located between the tubercle and the capitulum. In this taxon, this foramen is oval and of considerable size (approximately 3 cm), especially in the cervical ribs, where the separation between tubercle and capitulum is higher. These foramina are usually, placed deep inside the rib, and pneumatic camerae have been observed. (Fig 3.1; 3.2; 3,3; 3.4 and 3.5)

External and internal structure of dorsal ribs of *Skorpiovenator bustingorryi*

All the ribs analyzed have a small foramen, varying in size and shape from circular to oval, located between the tubercle and the capitulum (Fig 3.6; 3.7; 3.8 and 3.9)

In the CT scans it can be observed that there is camellated tissue possibly collapsed due to poor preservation, similar to the situation of the dorsal vertebra. This camellated tissue is observed near the foramen present near the tubercle and the capitulum and its extension covers the most proximal portion of the rib, disappearing as the shaft becomes distally laminar (Fig 3.6; 3.7; 3.8 and 3.9).

DISCUSSION

Analyzed specimens: *Tralkasaurus, Skorpiovenator* and *Carnotaurus*

In all of them it was possible to trace pneumatic characters distributed in the different portions of the analyzed body, which coincide, in part, with what was expected for this group (O'Connor 2007; Benson et al. 2012; Méndez 2014). PSP was recorded unambiguously in the dorsal vertebrae of *Tralkasaurus cuyi*. For *Skorpiovenator bustingorryi* it was recorded ambiguously in the dorsal vertebrae, unambiguously in the neural arches of the caudal vertebrae and unambiguously in the proximal end of the dorsal ribs, while *Carnotaurus sastrei* showed internal (cervical ribs) and external (dorsal ribs) pneumatic features. The most striking result is the presence of pneumaticity in the caudal vertebrae of *Skorpiovenator*, since for abelisaurids the tail region is usually considered as apneumatic (Benson et al. 2011; Méndez 2014)

Comparison with other abelisaurids, noasaurids and *Ceratosaurus*

Analyzing the presence of pneumaticity in the dorsal vertebrae, we have recorded its unambiguous presence in *Tralkasaurus* and, doubtfully, in *Skorpiovenator*. Previously reported taxa showing pneumaticity in their dorsal vertebrae were *Niebla antiqua* where camellated tissue can be seen on an isolated dorsal vertebra (Aranciaga-Rolando et al. 2021; Fig 4.1), *Dahalokely tokana* (UA 9855), *Xenotarsosaurus bonapartei* (UNPSJB PV 184) and *Ekrixinatosaurus novasi* (Martínez et al. 1987; Ibiricu et al. 2021; Farke and Sertich 2013; Calvo et al. 2004, MUCPv-294, Fig 4.2). In the last three taxa, the internal pneumatic structure of the camellate type can be seen at first hand observation and there are mentions to possible osteological correlates of pneumaticity, such as deep fossae, which are apparently connected to the interior of the vertebrae. This was also observed for various indeterminate abelisaurid remains [CPP 893, Novas et al. 2008; MPCN-Pv 69, Gianechini et al. 2015 (Fig 4.3)]. The first unambiguous evidence of pneumaticity comes from *Majungasaurus crenatissimus* Déperet 1896 (UA 8678; FMNH PR 2100), where, due to natural fragmentation of the material, it is possible to see its internal structure, which results in the presence of camellated tissue up to the last dorsal vertebrae except for the last one (O' Connor 2007). This article was recently supplemented by CT scans of the dorsal vertebrae of *Majungasaurus* (Aureliano et al. 2024), but unfortunately it is not possible to clearly see the structure and extent of pneumaticity within the vertebrae due to the technique used to colorize the images by such authors.

Regarding caudal vertebrae, those from *Skorpiovenator* showed apneumatic centra and pneumatized neural arches. According to comparisons made with other abelisaurid taxa, the situation of *Skorpiovenator* it is uncommon, and in fact, it does not match with any of the analyzed taxa. The most common pattern found in several abelisaurids is the occurrence of apneumatic caudal vertebrae, which is present in *Majungasaurus* (O' Connor 2007), *Kurupi itaata* (Iori et al. 2021) (MPMA 27-0001/02), *Pycnonemosaurus nevesi* Kellner and Campos 2002 (see in Delcourt 2017) (DGM 859-R), *Arcovenator escotae* (Tortosa et al. 2013) (MHNA.PV.2011.12.5; MHNA.PV.2011.12.198 and .213) and some remains of an undetermined abelisaurid from Cerro Barcino Formation (Rauhut et al. 2003). The only abelisaurid material showing pneumatic features in a mid-caudal vertebra, corresponds to an indeterminate abelisaurid from Bajo Barreal

Formation in the northern of Santa Cruz Province (MPM-99) (Martínez et al. 2004, see Baiano et al. 2023), where camellated tissue is observed in the vertebral centrum due to fragmentation of the material. Further, *Aucasaurus garridoi* Coria et al. 2002 (MCF-PVPH-236) shows caudal pneumaticity, which affected vertebral centra and neural arches, extending at least up to the 13th caudal vertebra (Baiano et al. 2023). Although *Skorpiovenator* also presents pneumaticity on its caudal vertebrae, this only affects the neural arches and this pattern was not recorded in the sample of analyzed abelisaurids. Finally, considering both the cervical and dorsal ribs, it is possible to see that in both *Carnotaurus* and *Skorpiovenator*, there are foramina closely placed to the proximal rib area, mostly over the lamina between the tubercle and the capitulum. Unfortunately, the poor preservation of *Skorpiovenator* prevented the pneumatic pattern from being properly recognized. A similar situation exists for *Carnotaurus* whose current preservation prevents tomography. Of all taxa analyzed, only *Niebla* preserves dorsal ribs where it is possible to visualize a pattern of large spaces within the tubercle and capitulum area (fig 8 in Aranciaga-Rolando et al. 2021), with a camerate structure. *Dahalokely* was also analyzed, but its dorsal ribs are apparently apneumatic (Farke and Sertich 2013).

Regarding the related taxa analyzed, only *Masiakasaurus knopfleri* Sampson et al. 2001 (FMNH PR 2837, FMNH PR 2481, FMNH PR 2485, *Berthasaura leopoldinae* de Souza et al. 2021 (MN 7821-V) and *Ceratosaurus* Marsh 1884 provide comparable material, including dorsal and caudal vertebrae, as well as ribs. Of these, internal pneumatic structures are known only for *Ceratosaurus*.Its dorsal vertebrae exhibit an internal pneumatization pattern intermediate between camellate and camerate structures, with non-pneumatized patches (*e.g.*, neural spine) (see fig 16 in Britt 1993). This does not match to that observed in *Tralkasaurus* and, possibly, in *Skorpiovenator*.

Both *Masiakasaurus* and *Berthasaura* have deep foramina of possible pneumatic origin in their presacral vertebrae; however, because their internal structure remains unknown, we do not deem it necessary to discuss this in further detail.

Unlike that observed in the caudal vertebrae of *Skorpiovenator*, the caudal elements of *Ceratosaurus* are apneumatic, although a single camera is strikingly present in the central portion of the vertebral centra, which was described as apneumatic because it lacks connection to the exterior through foramina (Britt 1993).

Regarding the ribs, as in *Carnotaurus, Masiakasaurus* has a foramen (see fig 17 in Carrano et al. 2011) and, as in *Carnotaurus* and *Skorpiovenator*, the dorsal ribs of *Ceratosaurus* have a large foramen (fig 15.3 in Britt 1993) in the same position as the taxa analyzed here. Furthermore, as to the internal structure, the dorsal ribs are pneumatized with a camerae structure (see fig 74 and 75 in Reid 1996).

Along with *Ceratosaurus*, noasaurids remains were also compared, although it was not possible to obtain overlapping material for comparison. These materials show that pneumatic tissue is already present in cervical vertebrae (Brum et al. 2018; Smyth et al. 2019; Poropat et al. 2020 in NMV P252004; Averianov et al. 2024 in *Kiyacursor longipes* (PIN 329/16), consistent with a symmetrical camerae pattern (Brum et al. 2018; Smyth et al. 2019) or camellated tissue (Poropat et al. 2020; Averianov et al. 2024).

Some considerations on the pneumaticity of abelisaurids

Abelisaurids form a diverse clade for which anatomical studies are the most common (Carrano and Sampson, 2008; Novas et al., 2013, and references therein), but even though certain aspects of their biology have been addressed (*e.g.*, neuroanatomy, Paulina-Carabajal et al., 2023, and references therein) some other aspects of their paleobiology have not been studied very frequently, an example of this is the case of the PSP (*e.g.*, O' Connor 2007). The analysis carried out here show the variations present in different species of abelisaurids and other theropods phylogenetically linked to them. According to the sample analyzed, we can affirm that the cervical vertebrae of abelisaurids are pneumatized and the same occurs for indeterminate noasaurids from Adamantina Formation, Brazil (Brum et al. 2016, 2018) and Ifezouane Formation, Morocco (Smyth et al. 2019) and *Ceratosaurus* (Britt, 1993). However, the pnemautic pattern varies among these taxa, with abelisaurids typically showing a camellated tissue characteristic of late-branching forms, whereas noasaurids and early branching taxa such as *Ceratosaurus*, tend to display a camerate condition . All these species show the "common pattern" of pneumatization, since their presacral vertebrae are generally pneumatized (Benson et al. 2011; this work).

The greatest variation in pneumaticity occurs in the caudal vertebrae. Depending on the species examined, caudal pneumaticity may be absent (as in most abelisaurids), restricted to the neural arch (e.g., *Skorpiovenator*), or developed in both the centra and neural arch (e.g., *Aucasaurus*), although the latter condition is comparatively rare. Moreover, taxa that are generally considered apneumatic can exhibit apparently pneumatic structures, such as the presence of camerae in *Ceratosaurus*.

Moving away from the analysis of the diversity of pneumatization in caudal vertebrae, it is interesting to highlight the case of an ilium of an indeterminate abelisaurid from Adamantina Formation, Brazil (DGM 927-R) (Brum et al. 2016) that was CT-scanned and showed pneumaticity with a camellate structure, and the transverse processes of sacral vertebrae in the French abelisaurid *Caletodraco cottardi* (Buffetaut et al. 2024) (MHNH 2024.1.1). In *Majungasaurus* (O' Connor 2007), external pneumatic features were also reported on its sacral vertebrae. The most striking feature about this taxon is that the last dorsal vertebra and all caudal vertebrae are apneumatic, which could indicate that it is possible within this theropod group the presence of "hiatuses", described as an erratic pattern of pneumatization recorded only in sauropods (Wedel and Taylor 2013). Given the high disparity in pneumaticity patterns, it is important to emphasize the need to deepen this type of studies in order to better understand the variation and distribution of postcranial PSP this diverse group of theropods. However, these results only apply for late Cretaceous abelisaurids, and it will be interesting in the near future to compare its PSP pattern with that of early branching abelisaurids from Jurassic period (*e.g.*, *Eoabelisaurus*; Pol and Rauhut, 2012) or those from the lower Cretaceous (*e.g.*, *Spectrovenator*; Zaher et al., 2020).

CONCLUSIONS

Postcranial pneumaticity (PSP) is a little-studied aspect within abelisaurids, so a comparative analysis of these features was carried out in several members of the clade, using *Tralkasaurus cuyi*, *Skorpiovenator bustingorryi* and *Carnotaurus sastrei* as the main case studies .

The dorsal vertebrae of *Tralkasaurus* shows unambiguous pneumaticity, consistent with all other taxa included in our comparison, namely abelisaurids, noasaurids, and *Ceratosaurus*. In *Skorpiovenator*, however, the internal structure of its dorsal vertebrae is too distorted to confidently confirm pneumaticity.. Regarding the caudal vertebrae, *Skorpiovenator* showed pneumatized neural arches, a condition that does not coincide with any of the compared taxa, since most of them have apneumatic caudal vertebrae, except for *Aucasaurus garridoi* and an undetermined abelisaurid from Chubut province.

Ribs across the sampled taxa usually show both external and internal pneumatic features, with the exception of Dahalokely, which lacks such traits. Abelisaurids display their greatest variation in the pneumaticity of the caudal series, a region traditionally regarded as apneumatic. This variability underscores the importance of expanding PSP studies to better understand in depth this aspect and the functional implications of pneumaticity in this remarkable group of theropods.

ACKNOWLEDGMENTS

We thank to Ignacio Cerda (MPCA), Martín Ezcurra (MACN), Agustin Martinelli (MACN), Belén Von Baczko (MACN), Jorge Calvo (UNComa) and Pablo Chafrat (MPCN) for their willingness to allow us to view the materials presented here. We also thanks to Santiago Reuil (MACN) for his useful comments about the rib cage anatomy of *Carnotaurus*. Further, we are deeply Juan Canale (MEB) not only for the willingness to allow access to materials, but also for sharing photos, comments on the original manuscript and giving an invaluable help in the CT scanning of *Skorpiovenator*. We also extend our gratitude to the staff of the Policlínico de Neuquén for allowing us to perform the CT scans presented here, especially to Dra. Graciela Bianchi, Dr. Gustavo Cuevas, Leonela Paredes, Ángeles Antiao and Maira Mella for performing the CT scans and to Eliana Guareschi for allowing us access to the CT scanner. We would also like to thank the CT scan staff at Universidad Maimónides.

We would like to extend our gratitude to the reviewers (Federico Gianechini and Matias Motta) for their valuable recommendations to improve this work.

REFERENCES

Aranciaga-Rolando, A. M., Garcia-Marsá, J.A., & Novas, F.E. (2020). Histology and pneumaticity of *Aoniraptor libertatem* (Dinosauria, Theropoda), an enigmatic mid-sized megaraptoran from Patagonia. *Journal of Anatomy 237*, 741–756.

Aranciaga-Rolando, A. M., Cerroni, M.A., Garcia-Marsà, J.A., Motta, M.J., Rozadilla, S., Brissón-Egli. F, & Novas, F.E. (2021). A new medium-sized abelisaurid (Theropoda, Dinosauria) from the late cretaceous (Maastrichtian) Allen Formation of Northern Patagonia. Argentina. *Journal of South American Earth Sciences 105*, 1-18

Aureliano, T., Almeida, W., Rasaona, M., & Ghilardi, A. (2024). The evolution of the air sac system in theropod dinosaurs: Evidence from the Upper Cretaceous of Madagascar. *Journal of Anatomy*. DOI: 10.1111/joa.14113

Averianov, A.O., Skutschas, P.P., Atuchin, A.A., Slobodin, D.A., Feofanova, O.A., &Vladimirova, O.N. (2024). The last ceratosaur of Asia: a new noasaurid from the Early Cretaceous Great Siberian Refugium. *Proceedings of the Royal Society Biological Sciences 291* (2023) https://doi.org/10.1098/rspb.2024.0537

Baiano, M.A., Coria, R., Chiappe, L.M., Zurriaguz, V., & Coria, L. (2023). Osteology of the axial skeleton of *Aucasaurus garridoi*: phylogenetic and paleobiological inferences. *PeerJ 11*:e16236 DOI 10.7717/peerj.16236

Benson, R. B. J., Butler, R. J., Carrano, M. T., & O’Connor, P. M. (2011). Air-filled postcranial bones in theropod dinosaurs: physiological implications and the “reptile”–bird transition. *Biological Reviews 87*(1): 168-193

Bonaparte, J. F., & Novas, F. E. (1985). *Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Cretácico Tardío de Patagonia. *Ameghiniana, 29* 259–265

Bonaparte, J. F., Novas, F. E., & Coria, R. A. (1990). *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the middle Cretaceous of Patagonia. *Contributions in Science. Natural History Museum of Los Angeles County 416*, 1-42.

Bonaparte, J. F. (1991). The Gondwanan theropod families Abelisauridae and Noasauridae. *Historical Biology 5*, 1–25.

Britt, B. B. (1993). *Pneumatic postcranial bones in dinosaurs and other archosaurs*. PhD. Thesis, University of Calgary.

Brum, A. S., Machado, E. B., D Almeida Campos, D., & Kellner, A. W. A. (2016). Morphology and internal structure of two new abelisaurid remains (Theropoda, Dinosauria) from the Adamantina Formation (Turonian–Maastrichtian), Bauru Group, Paraná Basin, Brazil. *Cretaceous Research 60*, 287-296.

Brum A. S., Machado, E. B., De Almeida Campos, D., & Kellner, A. W. A. (2018). Description of uncommon pneumatic structures of a noasaurid (Theropoda, Dinosauria) cervical vertebra from the Bauru Group (Upper Cretaceous), Brazil. *Cretaceous Research 85*, 193-206.

Buffetaut, E., Tong, H., Girard, J., Hoyez, B., & Párraga, J. (2024). *Caletodraco cottardi*: A New Furileusaurian Abelisaurid (Dinosauria: Theropoda) from the Cenomanian Chalk of Normandy (North-Western France). *Fossil Studies 2*, 177–195.

Calvo, J. O., Rubilar-Rogers, D., & Moreno, K. (2004). A new abelisauridae (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana 41*, 555–563.

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

Canale, J. I., Cerda I. A., Novas, F. E., & Haluza, A. (2016). Small-sized abelisaurid (Theropoda: Ceratosauria) remains from the Upper Cretaceous of northwest Patagonia, Argentina. *Cretaceous Research 62*, 18-28.

Carrano, M. T., & Sampson, S. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology 6*, 183-236.

Carrano, M. T., Loewen, M. A., & Sertich, J. J. W. (2011). New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). *Smithsonian Contributions to Paleobiology, 95:* 1-64. https://doi.org/10.5479/si.00810266.95.1

Cerroni, M. A., Motta, M. J., Agnolín, F. L., Aranciaga-Rolando, A. M., Brissón-Egli, F., & Novas, F. E. (2020). A new abelisaurid from the Huincul formation (Cenomanian-Turonian; upper cretaceous) of Río Negro province, Argentina. *Journal of South Americane Earth Sciences 98*, 102–445.

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

de Souza, G.A., Soares, M.B., Weinschütz, L.C., Wilner, E., Lopes, R.T., de Araújo, O.M., & Kellner, A.W. (2021). The first edentulous ceratosaur from South America. *Scientific Reports 11* (1): doi:10.1038/s41598-021-01312-4

Delcourt, R. (2017). Revised morphology of *Pycnonemosaurus nevesi* Kellner & Campos, 2002 (Theropoda: Abelisauridae) and its phylogenetic relationships. *Zootaxa 4276*(1), 1-45.

Depéret, C. (1896). Sur l’existence de dinosauriens sauropodes et théropodes dans le Crétacé supérieur de Madagascar. *Comptes Rendus de l’Academie des Sciences 122*, 483–485.

Duncker, H., (1971). Structure of avian lungs. *Respiration Physiology 14*, 44-63

Farke, A. A., & Sertich, J. J. W. (2013). An abelisauroid theropod dinosaur from the Turonian of Madagascar. *PLoS One 8* (4). https://doi.org/10.1371/journal.pone.0062047

Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet J., Fillion-Robin, J. C., Pujol, S., & Buatti, J. (2012). 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging 30*,1323–1341

Filippi, L.S., Méndez, A.H., Juárez Valieri, R.D., & Garrido, A.C. (2016). A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisaurids. *Cretaceous Research 61*, 209–219

Gianechini, F.A., Apesteguía, S., Landini, W., Finotti, F., Juárez Valieri, R.D., & Zandonai, F. (2015). New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia. Argentina. *Cretaceous Research 54*, 1–16

Gianechini, F.A., & Zurriaguz, V.L. (2021). Vertebral pneumaticity of the paravian theropod *Unenlagia comahuensis*, from the Upper Cretaceous of Patagonia. Argentina. *Cretaceous Research 127*, 1–14

Ibiricu, L.M., Baiano, M.A., Martínez, R.D., Alvarez, B.N., Lamanna, M.C., & Casal G.A. (2021). A detailed osteological description of *Xenotarsosaurus bonapartei* (Theropoda: Abelisauridae): implications for abelisauroid phylogeny. *Cretaceous Research 124*, 1-21

Iori, F.V., de Araújo-Júnior, H.I., Tavares, S.A.S., da Silva Marinho, T., & Martinelli, A.G. (2021). New theropod dinosaur from the Late Cretaceous of Brazil improves abelisaurid diversity. *Journal of South American Earth Sciences 112*, 1–15

Kellner, A. W., & Campos, D. D. A. (2002). On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. *Arquivos do Museu Nacional 60*(3), 163-170.

King, A.S. (1966). Structural and functional aspects of the aviang lungs and air sacs. *International Review of General and Experimental Zoology 2*, 171–267.

Marsh, O.C. (1884). On the united metatarsal bones of *Ceratosaurus*. *American Journal of Science 28* (164), 161–162.

Martínez R., Giménez, O., Rodríguez, J., & Bochatey, G. (1987). *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina. *IV Congreso Argentino de Paleontología y Bioestratigrafía* (pp.23-31). Buenos Aires.

Martínez, R.D., Novas, F., & Ambrosio, A. (2004). Abelisaurid remains (Theropoda, Ceratosauria) from southern Patagonia. *Ameghiniana 41*, 577–585.

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

Novas, F. E. (1997). South American dinosaurs. In Currie, P.J., Currie, P.J. (Eds.). *Encyclopedia of dinosaurs* (pp. 678–689). Academic Press.

Novas, F. E., Souza Carvalho, I. De, Ribeiro, L. C. B., & Méndez, A. H. (2008). First abelisaurid bone remains from the Maastrichtian Marilia Formation, Bauru basin, Brazil. *Cretaceous Research 29*(4), 625–635.

Novas, F. E. (2009). *The age of dinosaurs in South America*. Indiana University Press, Bloomington. Pp. 452.

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

O'Connor, P. M. (2006). Postcranial pneumaticity: an evaluation of soft tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology 267*(10), 1199-1226.

O'Connor, P. M. (2007). The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology 27*(8), 127–162.

Paulina-Carabajal, A., Bronzati, M., Cruzado-Caballero, P. (2023). Paleoneurology of Non-avian Dinosaurs: An Overview. In: Dozo, M.T., Paulina-Carabajal, A., Macrini, T.E., Walsh, S. (eds) Paleoneurology of Amniotes. Springer, Cham. https://doi.org/10.1007/978-3-031-13983-3_8

Pol, D., & Rauhut, O. W. M. (2012). A Middle Jurassic abelisaurid from Patagonia and the Early diversification of theropod dinosaurs. *Proceedings of the Royal Society Biological Sciences 279*, 3170-3175.

Pol, D., Baiano, M., Cerný, D., Novas, F., Cerda, I., & Pittman, M. (2024). A new abelisaurid dinosaur from the end Cretaceous of Patagonia and evolutionary rates among the Ceratosauria. *Cladistics 40(3),* 307-356

Poropat, S. F., Pentland, A. H., Duncan, R. J., Bevitt, J. J., Vickers-Rich, P., & Rich, T. H. (2020). First elaphrosaurine theropod dinosaur (Ceratosauria: Noasauridae) from Australia, a cervical vertebra from the Early Cretaceous of Victoria. *Gondwana Research 84*, 284-295.

Rauhut, O., Cladera, G., Vickers-Rich, P., & Rich, T. (2003). Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. *Cretaceous Research 24*, 487-497

Reid, R. E. H. (1996). Bone histology of the Cleveland-Lloyd dinosaurs and of dinosaurs in general. Part I: introduction to bone tissues. *Brigham Young University Geology Studies 41*, 25-72.

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

Sereno, P. C., Martínez, R. N., Wilson, J. A., Varricchio, D. J., Alcober, O. A., & Larsson, H.C.E. (2008). Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE 3* https://doi.org/10.1371/journal.pone.0003303

Smyth, R. S., Ibrahim, N., Kao, A., & Martill, D. M. (2020). Abelisauroid cervical vertebrae from the Cretaceous Kem Kem beds of Southern Morocco and a review of Kem Kem abelisauroids. *Cretaceous Research 108*, 104330.

Tortosa, T., Buffetaut, E., Vialle, N., Dutour, Y., Turini, E., & Cheylan, G. (2013). A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. *Annales de Paléontologie 100*, 63–86.

Watanabe, A., Leone Gold, M. E., Brusatte, S. L., Benson, R. B. J., Choiniere J., Davidson, A., Norell, & M. A. (2015). Vertebral pneumaticity in the ornithomimosaur *Archaeornithomimus* (Dinosauria: Theropoda) revealed by computed tomography imaging and reappraisal of axial pneumaticity in Ornithomimosauria. *PLoS ONE 10*(12) https://doi.org/10.1371/journal.pone.0145168

Wedel, M.J., (2003). The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology 23*, 344–357.

Wedel, M. J. (2003). Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology 29*, 243–255.

Wedel, M. J. (2009). Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of Experimental Zoology 311*A, 611-628.

Wedel, M.J., &Taylor, M.P. (2013) Caudal Pneumaticity and Pneumatic Hiatuses in the Sauropod Dinosaurs *Giraffatitan* and *Apatosaurus*. PLoS ONE 8(10): e78213. doi:10.1371/journal.pone.0078213

Windholz, G.J., Meso, J.G., Wedel, M.J., & Pittman, M. (2025) First unambiguous record of pneumaticity in the axial skeleton of alvarezsaurians (Theropoda: Coelurosauria). *PLoS ONE 20(4)*: e0320121.https://doi. org/10.1371/journal.pone.0320121

Zaher, H., Pol, D., Navarro, B. A., Delcourt, R., & Carvalho, A. B. (2020). An Early Cretaceous theropod dinosaur from Brazil sheds light on the cranial evolution of the Abelisauridae. *Comptes Rendus Palevol 19* (6): 101-115.

Appendices

Figure captions.

Figure 1. Dorsal vertebra and three transverse processes of ***Tralkasaurus cuyi*** (**MPCA Pv-815**). In **1**, lateral view; **2**, reconstruction of the vertebrae in lateral view, the dotted line represents how the vertebrae looked; **3**, dorsal view with reconstruction of the material (dot line and gray color), the straight line represents the level of the section at which the CT scans were made in the following figures: 4, 5, 6 and 7; **4, 5, 6** and **7**, CT scans at the level of the solid line indicated at **3** showing the camellated tissue present within the vertebra and the transverse processes. Abbreviations: **tp,** transverse process. Blue arrows: camellated tissue. Scale bar equals: 10 cm.

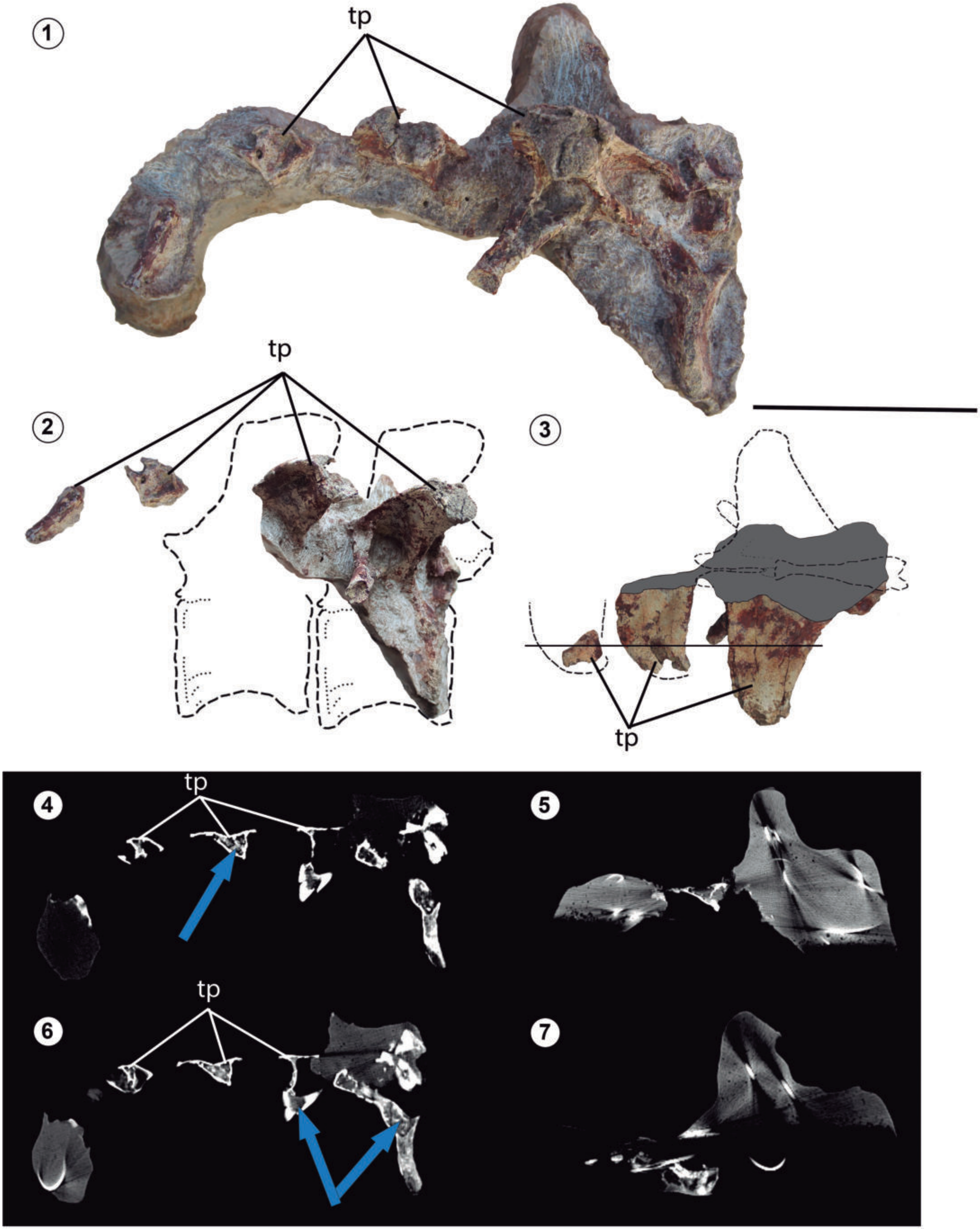
Figure 2. Dorsal and caudal vertebrae of ***Skorpiovenator bustingorryi*** (**MMCH-PV 48**) and their respective CT scans. In **1**, right lateral view of 10th dorsal vertebra; **2**, anterior view of 10th dorsal vertebra and its respective CT scan (below), showing the collapsed internal structure; **3** and **4**, right lateral and anterior views (above) of 11th dorsal vertebra and its respective CT scan (below), showing the collapsed internal structure; **5, 6, 7** and **8** 1st and 3rd caudal vertebrae in right lateral and anterior views (above) and their respective CT scans (below) showing the apneumatic vertebral centra and the pneumatized neural arches. Abbreviations: **nc,** neural canal. Blue arrows: camellated tissue. Scale bar equals: 5 cm.

Figure 3. Cervical ribs and their CT scans in dorsomedial views (**1-3**) and dorsal ribs in dorsomedial views (**4** and **5**) of ***Carnotaurus sastrei*** (**MACN-CH-894**) and dorsal ribs

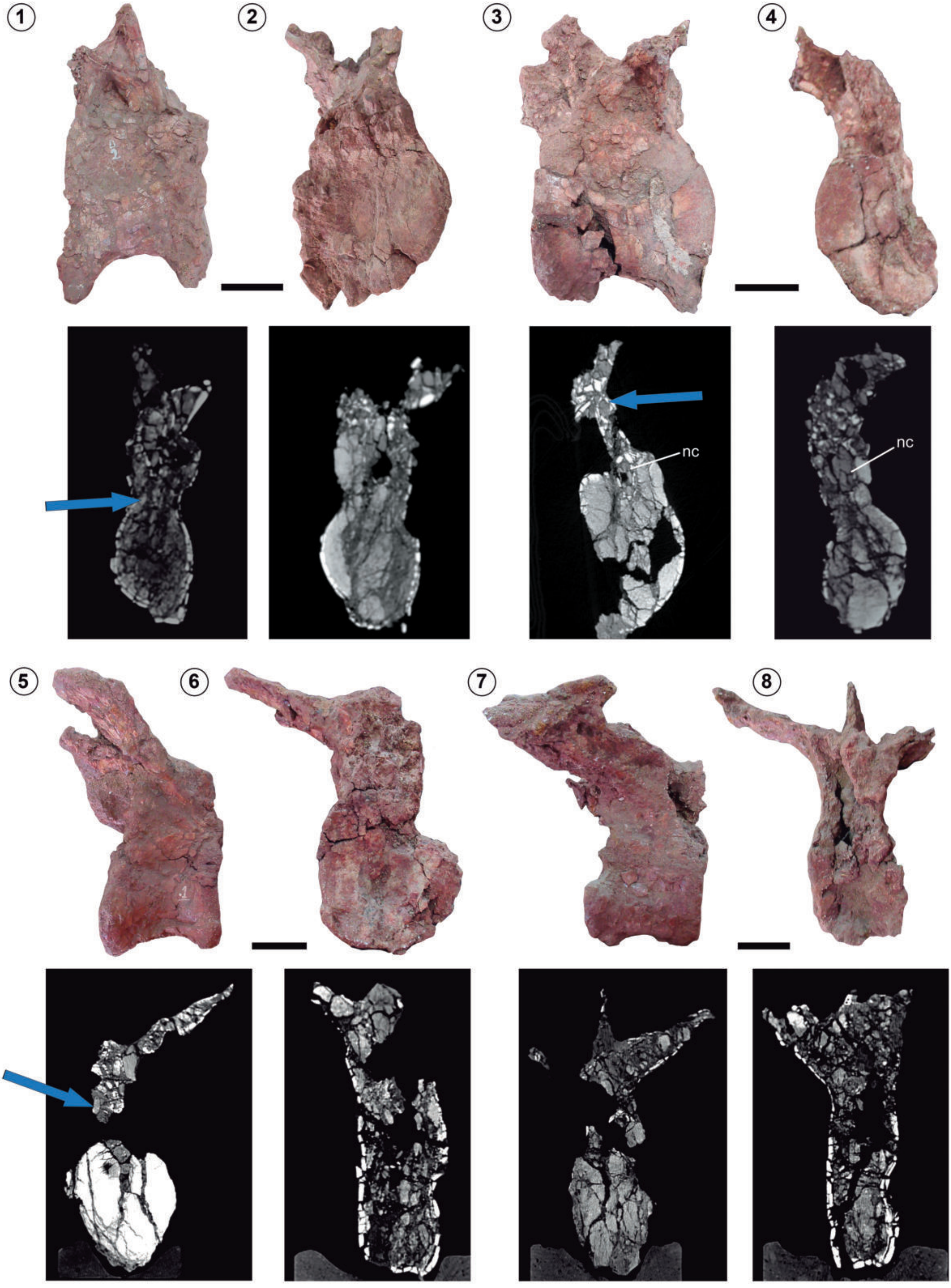
in medial view (**6-9**) of ***Skorpiovenator bustingorryi*** (**MMCH-PV 48**). In **1, 2** and **3** 5th, 8th and 10th cervical ribs respectively showing a large foramen in the medial area of the tubercle and capitulum; 1st and 2nd dorsal ribs showing a large foramen in the medial area of the tubercle and capitulum. Blue arrows: camellated tissue. Scale bar equals: 5 cm.

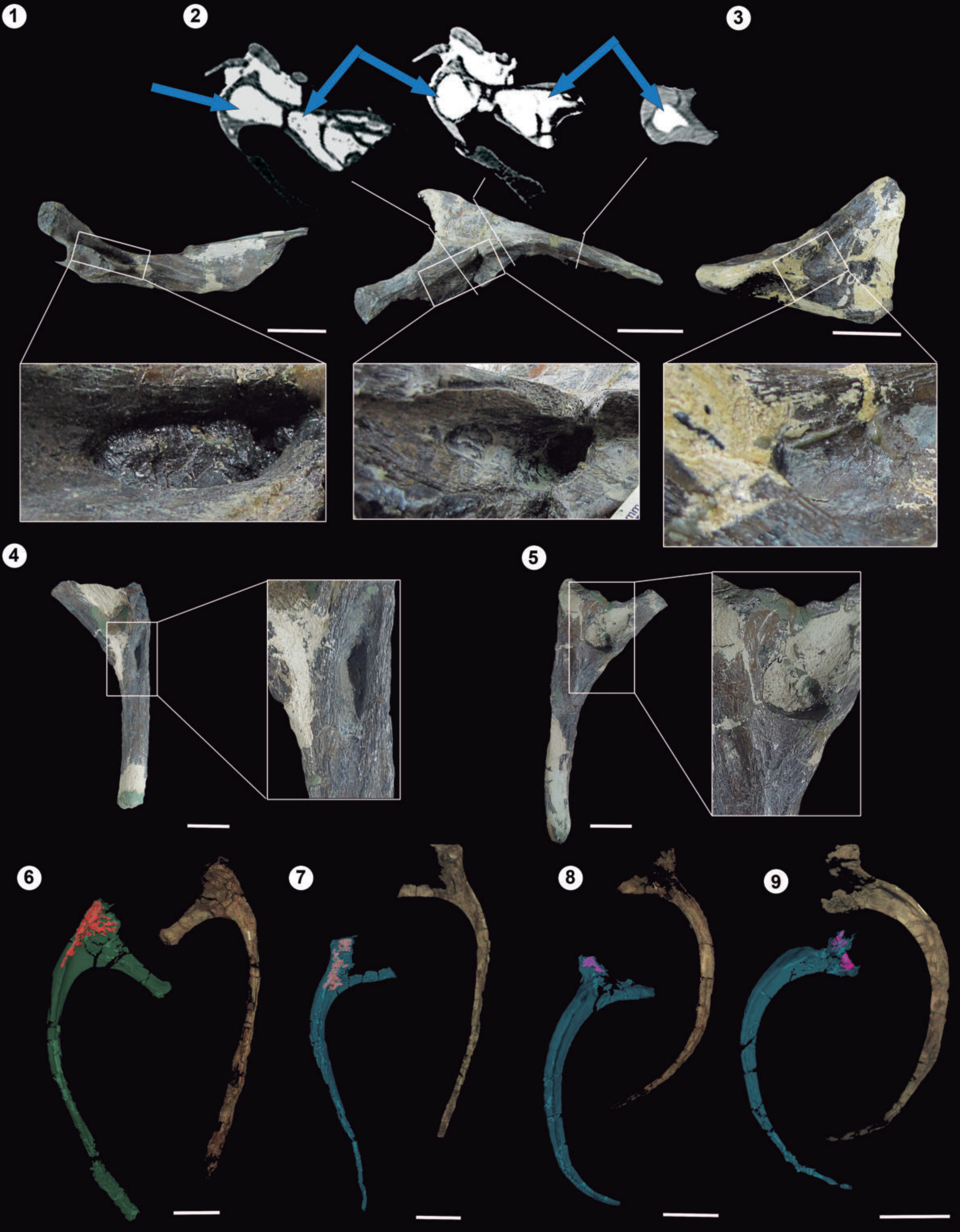
In **6, 7, 8** and **9**, 2^{nd}, 8^{th}, 9^{th} and 10^{th} dorsal ribs showing their CT scans, where the colored area represents the pneumatic space coinciding with the region where the foramen is located. Scale bar equals; 10 cm.

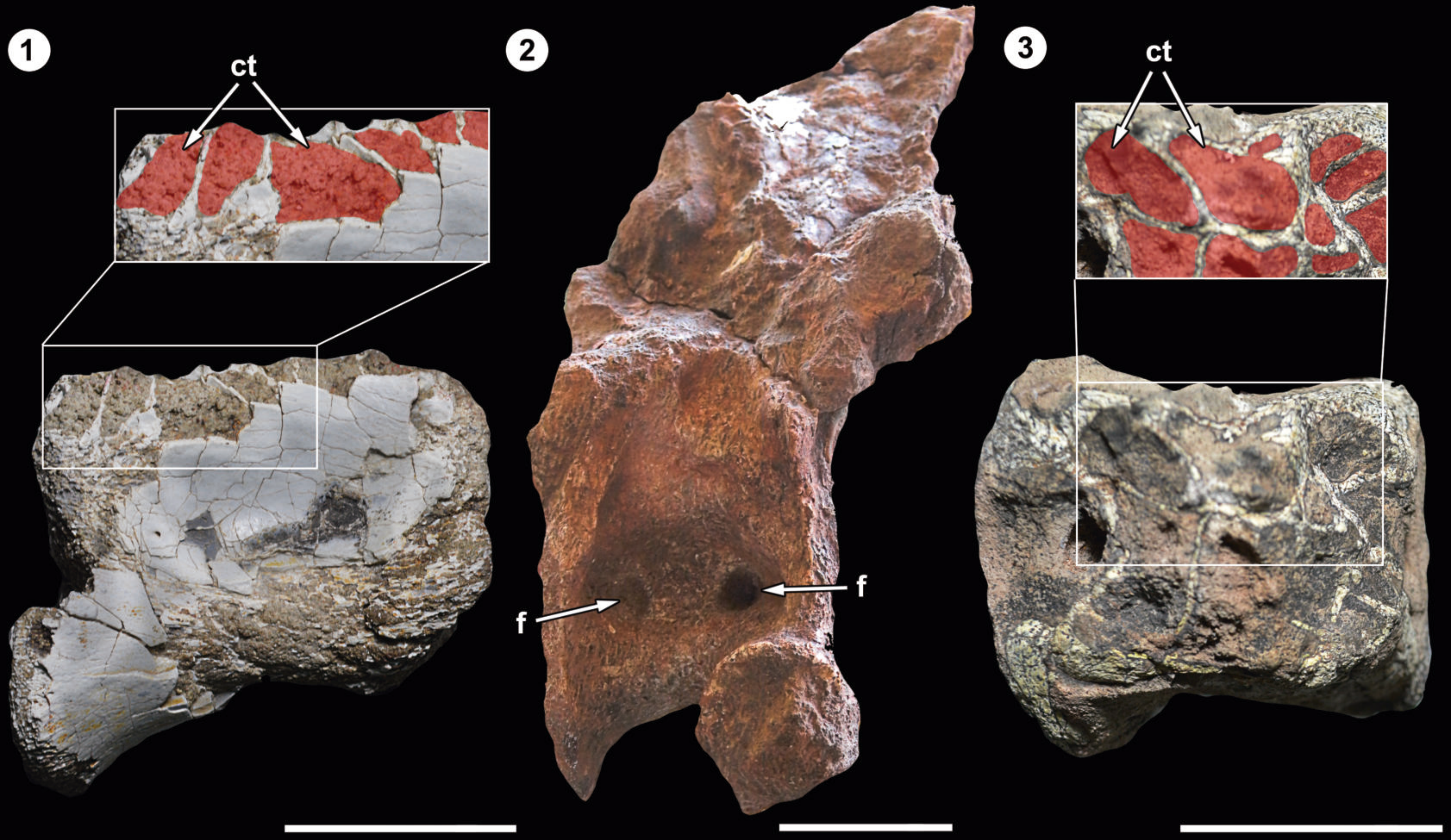
Figure 4. Dorsal vertebrae of ***Niebla antiqua*** (**MPCN-Pv-796**), ***Ekrixinatosaurus novasi*** (**MUC-Pv-294**) and Abelisauridae indet. of Anacleto Formation (**MPCN-Pv-69**) in Gianechini et al. 2015. In **1**, lateral view of dorsal vertebral centrum of *Niebla antiqua* showing camellated tissue; **2**, lateral view of 1st dorsal vertebra of *Ekrixinatosaurus novasi* showing two lateral foramina; **3,** Dorsal view of dorsal vertebral centrum of Abelisauridae indet. showing camellated tissue. In **1** and 3 the sediment in the camellate tissue has been digitally modified to enhance contrast. Abbreviations: **ct**, camellated tissue; **f**, foramen. Scale bar equals: 5 cm



tp
1
tp
2
3
tp
4
tp
5
tp
6
7


1
2
3
4
nc
nc
5
6
7
8


1
2
3
4
5
6
7
8
9


1
ct
2
f
f
3
ct