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Original Article

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Unique internal anatomy of vertebrae as a key factor for neck elongation in Triassic archosauromorphs

Adam Rytel[1,2,*], Dawid Surmik[3,*], Tomasz Szczygielski[1], Stephan N.F. Spiekman[4], Thomas van de Kamp[5,6], Marcus Zuber[5], Torsten M. Scheyer[2]

[1]Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland
[2]Department of Paleontology, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland
[3]Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Bedzinska 60, 41-200 Sosnowiec, Poland
[4]Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
[5]Institute for Photon Science and Synchrotron Radiation (IPS), Karlsruhe Institute of Technology (KIT), Hermann-von-Helmholtz-Platz 1, 76344 Eggenstein-Leopoldshafen, Germany
[6]Laboratory for Applications of Synchrotron Radiation (LAS), Karlsruhe Institute of Technology (KIT), Kaiserstraße 12, 76131 Karlsruhe, Germany

[*]Corresponding author. Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland. E-mail: adam.rytel@twarda.pan.pl; Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Bedzinska 60, 41-200 Sosnowiec, Poland. E-mail: dawid.surmik@us.edu.pl

ABSTRACT

The Triassic was a key period in the evolution of vertebrates, and reptiles in particular, giving rise to a plethora of successful lineages, some of which are still extant. One of the groups that flourished during the early Mesozoic were the tanysaurians (Archosauromorpha: Tanysauria). They had elongate neck vertebrae that in some genera reached extreme proportions. Here, we provide the first comprehensive description of the internal structure of these extraordinary elements, focusing on the famously bizarre *Tanystropheus*. Through computed tomography and sectioning, we were able to reveal some intriguing features comparable to those seen in pterosaurs and birds. However, contrary to what we see in pneumatic bones, cervicals of tanysaurians contain a singular voluminous cavity. This results in a cylindrical structure in these vertebrae, which likely provided durability, while contributing less to the weight of the neck. These insights are relevant for better understanding of a unique and extreme anatomy among tetrapods, which evolved as a result of very strict selection for some particular function. Importantly, our findings demonstrate that major modifications of the internal anatomy of vertebrae were not unique to derived avemetatarsalians (pterosaurs and dinosaurs), but more widespread among reptiles.

Keywords: Archosauromorpha; Tanysauria; Tanystropheidae; *Tanystropheus*; cervical vertebrae; pneumaticity; biomechanics

INTRODUCTION

The period following the End-Permian Mass Extinction saw the appearance, diversification, and radiation of several vertebrate lineages that became major components of later faunas (e.g. Foth *et al.* 2016, Ezcurra and Butler 2018, Simões *et al.* 2018, Benton and Wu 2022, Laboury *et al.* 2023, Sues and Schoch 2023). Among the Mesozoic tetrapods, diapsids achieved the most extensive evolutionary success, giving rise to the lineages that dominated terrestrial (non-avian dinosaurs, pseudosuchians, non-mosasaur squamates), aquatic (sauropterygians, ichthyosaurs, mosasaurs), and aerial (pterosaurs, birds) environments. Members of these groups evolved derived adaptations to the niches they occupied and adopted new, unique Bauplans. In the Triassic, one the most ecologically diverse clades of vertebrates were the tanysaurians (Tanysauria), a group of early-diverging archosauromorphs (Spiekman *et al.* 2024a). The Tanysauria contained terrestrial (e.g. Rieppel 1989, Renesto 1994), aquatic (e.g. Spiekman *et al.* 2024a, b), and possibly gliding (Dzik and Sulej 2016) forms. Members of this group exhibited substantial neck elongation, achieved through either cervical vertebrae count increase (trachelosaurids, see Spiekman *et al.* 2024a, b) or the hyperelongation of the cervicals (tanystropheids, see Wild 1973, Nosotti 2007, Dzik and Sulej 2016, Spiekman and Scheyer 2019, Spiekman *et al.* 2021). The first described and widely known tanysaurian *Tanystropheus* demonstrated an extreme extent of the latter condition, with its cervicals being over 10 times longer than tall (Fig. 1A–B; Spiekman and Scheyer 2019, Spiekman *et al.* 2021) and its neck constituting about half of the total body

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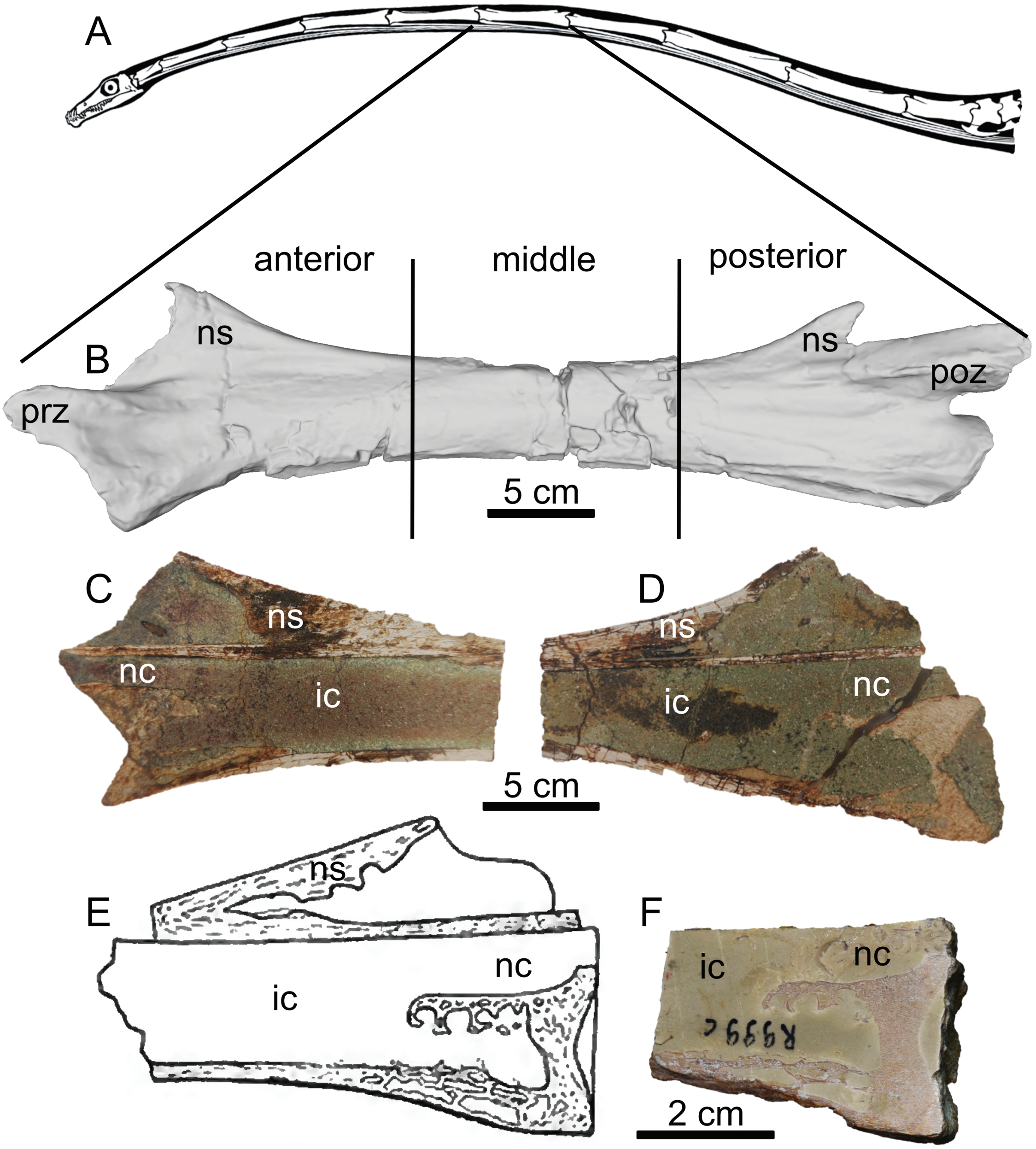

Figure 1. Reconstruction of the neck of *T. hydroides* (A), after Spiekman *et al.* (2020a, changed; Author: Beat Scheffold) and some of the sampled middle cervicals of *Tanystropheus* sp. from Miedary (B–D) and *T.* '*conspicuus*' (E, F): (B) ZPAL V. 36/101, surface model in left lateral view; (C) ZPAL V. 36/1016/1, polished longitudinal cross section of an anterior portion of a vertebra; (D) ZPAL V. 36/1016/2, polished longitudinal section of a posterior portion of a vertebra; (E) SMF R 999c, a longitudinal cross section through a posterior portion of a vertebra as originally illustrated by von Huene (1907–1908: fig. 251) and (F) as currently preserved. Anatomical abbreviations: ic—internal cavity; nc—neural canal; ns—neural spine; poz—postzygapophysis; prz—prezygapophysis.

length in large individuals (A. Rytel, personal observations; Wild 1973, Tschanz 1988). The lifestyle of *Tanystropheus* spp. remains not fully resolved, with recent developments in the subject pointing towards it being a shallow marine ambush predator (Nosotti 2007, Beardmore and Furrer 2017, Renesto and Saller 2018, Spiekman *et al.* 2020a, b). Currently, the main skeletal feature not in keeping with the inferred aquatic habitat is the internal structure of the cervical vertebrae, which are preserved as hollow inside, potentially implying a more terrestrial lifestyle (Broili 1915, Edinger 1924, Renesto 2005, Jaquier and Scheyer 2017).

Despite the internal anatomy of tanysaurian cervicals being widely known and acknowledged as unique (von Meyer 1847–1855, von Huene 1907–1908, Broili 1915, Edinger 1924, Wild 1973, Dalla Vecchia 2000, Rieppel 2001, Renesto 2005, Nosotti 2007, Dzik and Sulej 2016, Jaquier and Scheyer 2017, Formoso *et al.* 2019, Spiekman and Scheyer 2019, Miedema *et al.* 2020, Spiekman *et al.* 2020a), its function and evolution have never been investigated in detail. The distinct internal anatomy of the vertebrae was noted already in the original description of *Tanystropheus* '*conspicuus*' von Meyer, 1852. von Meyer (1847–1855) hypothesized that the internal cavity was filled with vascularized soft tissue, whereas the spinal cord developed as a series of intervertebral ganglia, located in the anterior and posterior concavities of the neural arch (see Edinger 1924). von Huene (1907–1908) corrected this interpretation, reporting on the neural canal being located more conservatively, between the centrum and the neural arch, and being ventrally floored by bone in its anteroposteriorly terminal sections, with only a hypothetical 'delicate periosteum' in the middle. Broili (1915) described the internal vertebral anatomy in more detail, noting the presence of some bony trabeculae inside of one of the vertebrae, and hypothesizing that the other specimens are devoid of them due to post-mortem alterations. Research on the subject was summarized by Edinger (1924), who stated that the spinal cord ran within the vertebral centra of *T.* '*conspicuus*', a feature unique among vertebrates. All of these authors considered the vertebrae of *Tanystropheus* spp. to be 'dinosaur' caudals. It was not until the articulated specimens from Monte San Giorgio were described (Peyer 1931) that the true nature of these bones was revealed. Wild (1973) provided a comprehensive summary of previous studies on the biology of *Tanystropheus* spp., as well as many additional insights on this subject. According to Wild (1973), the spinal cord in the cervicals of *Tanystropheus* spp. ran within the centra, and its course changed ventrodorsally along the anteroposterior axis of the neck (like a 'garland'), reaching the ventral surface of the internal cavity shortly after entering the vertebra. Jaquier and Scheyer (2017) were the first to comparatively investigate tanysaurian histology by sampling, among others, cervicals of *Macrocnemus bassanii* Nopcsa, 1930 and *Tanystropheus* spp., and revealing the generally homogenous, compact structure of the bone walls of these vertebrae. Recent studies employing phase-contrast synchrotron computed tomography provide insights into the internal morphology of the axes of *Macrocnemus bassanii* and *Tanystropheus hydroides* Spiekman, Neenan, Fraser, Fernandez, Rieppel, Nosotti, & Scheyer, 2020, which revealed the tubular structure of the anteriormost postatlantal cervicals (Miedema *et al.* 2020, Spiekman *et al.* 2020a). Similar anatomy can also be observed in the elongate cervicals of other tanysaurians—*Augustaburiania vatagini* Sennikov, 2011 from the late Olenekian of Russia (A. Rytel, personal observations; Sennikov 2011), *Czatkowiella harae* Borsuk-Białynicka & Evans, 2009 from the late Olenekian of Poland (T. Szczygielski, personal observations; Borsuk-Białynicka and Evans 2009), a putative tanysaurian *Microcnemus efremovi* von Huene, 1940 from the Early Triassic of Russia (von Huene 1940), the Moenkopi Formation tanystropheid from the early Anisian of the USA (Formoso *et al.* 2019), *Ozimek volans* Dzik & Sulej, 2016 from the late Carnian of Poland (Dzik and Sulej 2016), and *Tanytrachelos ahynis* Olsen, 1979 from the late Carnian of the USA (Spiekman *et al.* 2021), as well as the Homestead tanystropheids from the early-mid Norian of the USA (Heidenfelder *et al.* 2023). Thus, the observed 'hollowness' of the cervicals is potentially a characteristic feature of all tanystropheids and possibly non-tanystropheid tanysaurians, despite their disparate lifestyles, as well as the wide temporal (Early to Late Triassic) and spatial (North America to China) range of occurrence of the mentioned taxa. Therefore, it can be hypothesized that this unique vertebral anatomy was an important adaptation correlated with substantial neck elongation—a feature shared by all tanysaurians to at least some extent. Due to their elongation, the presence of the 'shaft' and internal cavity, the cervical vertebrae of some tanystropheids (e.g *Tanystropheus* spp., *Ozimek volans*) are similar in their general structure to long bones of avemetatarsalians, not only in their superficial anatomy, but potentially also the internal structure and biomechanical properties. This resemblance allows for intriguing comparisons with extant and extinct animals, but to further explore this phenomenon and its origin, broader and more detailed sampling was needed. Previous studies have been constrained by the scarcity of available three-dimensionally (3D) preserved material (Broili 1915, Wild 1973, Jaquier and Scheyer 2017), but the newly identified material from Silesia in southern Poland (Surmik *et al.* 2016, Czepiński *et al.* 2023) allows for a more extensive and holistic approach. Herein, we describe the internal anatomy of the cervical vertebrae of *Tanystropheus* spp. and '*Protanystropheus*' *antiquus*, employing both traditional sectioning and computed tomography (CT) scanning, to trace the evolution and function of the extensive modifications of the vertebral anatomy in tanysaurians.

MATERIAL AND METHODS

Institutional abbreviations

GIUS—Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia, Sosnowiec, Poland; **GPIH**—Geological-Palaeontological Institute and Museum of the University of Hamburg, Hamburg, Germany; **MGUWr**—Henryk Teisseyre Museum of Geology, University of Wrocław, Wrocław, Poland; **MHI**—Muschelkalk Museum Hagdorn, Ingelfingen, Germany; **PIMUZ**—Department of Paleontology of the University of Zurich, Zurich, Switzerland; **SMNS**—State Museum of Natural History, Stuttgart, Germany; **SMF**—Senckenberg Museum Frankfurt, Frankfurt a. M., Germany; **SUT-MG**—Czesław Poborski Museum of Mineral Deposit Geology, Faculty of Mining and Geology, Silesian University of Technology, Gliwice, Poland; **U-MO**—Urwelt Museum Oberfranken, Bayreuth, Germany; **WNoZ**—Earth Science Museum, Faculty of Natural Sciences, University of Silesia, Sosnowiec, Poland; **ZPAL**—Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Samples

Tanystropheus '*conspicuus*' von Meyer, 1852 was erected on the basis of elongate vertebrae found in Germany and Poland. No articulated remains of this animal have ever been described, but it shares its general anatomy with the more completely known *Tanystropheus hydroides* and *Tanystropheus longobardicus* (Bassani, 1886). These constitute all of the currently valid species of *Tanystropheus*. Taxonomic revisions of this taxon, combined with an extensive summary of referred material and its history, were provided by Wild (1973) and Spiekman and Scheyer (2019). Due to the lack of informative remains that would allow for a detailed comparison with the other *Tanystropheus* spp., Spiekman and Scheyer (2019) and Spiekman *et al.* (2021) considered *T.* '*conspicuus*' a nomen dubium. The newly uncovered locality of Miedary (southern Poland) has yielded abundant and diverse material of *Tanystropheus* sp., which is nearly indistinguishable from the known isolated specimens of *T.* '*conspicuus*'

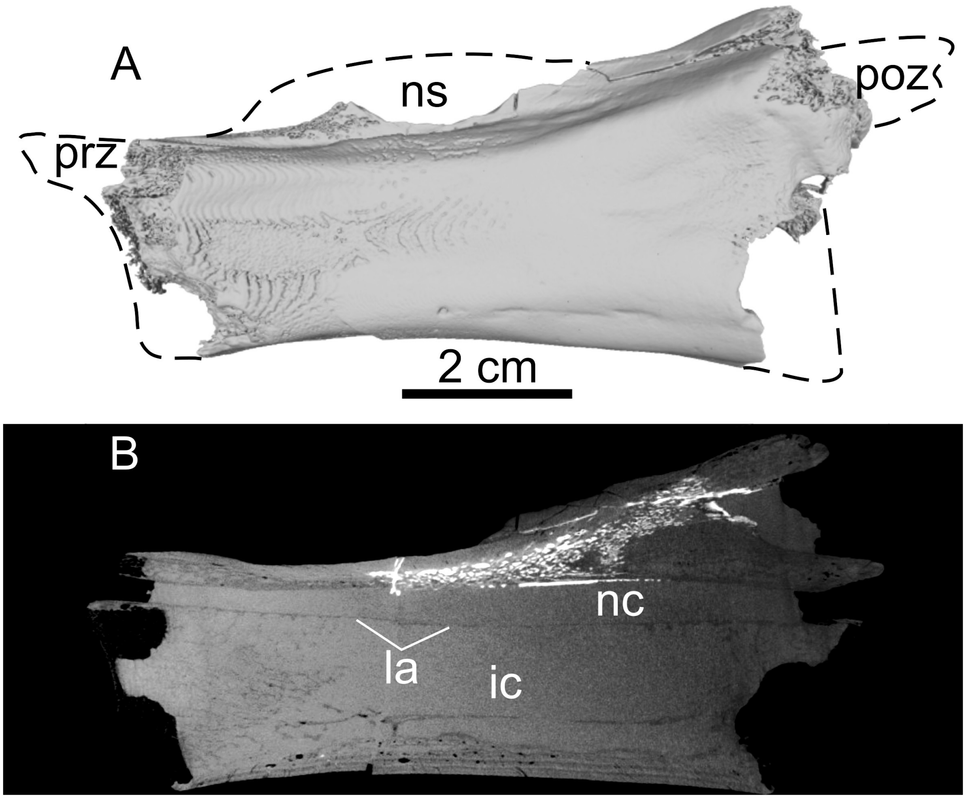

Figure 2. GIUS-7-3674, cervical of '*P*'. *antiquus*, surface model in left lateral view (A) and a longitudinal CT cross section (B). Notice the thin, but generally continuous neural canal floor. Anatomical abbreviations: ic—internal cavity; la—lamella that separates the neural canal from the internal cavity; nc—neural canal; ns—neural spine; poz—postzygapophysis; prz—prezygapophysis.

(see Czepiński *et al.* 2023). The osteological description of these remains, including an extensive analysis of validity of *T.* '*conspicuus*', will be carried out in the near future.

The majority of the studied specimens of *Tanystropheus* spp. (22 out of 30 cervicals, see Supporting information, Table S1) were recently excavated from the Miedary site (Czepiński *et al.* 2023). Similar to the typical preservational characteristics of this locality (Czepiński *et al.* 2023), these cervicals were found isolated and fully 3D preserved, but they quite often exhibited some degree of diagenetic alteration of their original morphology. Additionally, a well preserved 11th vertebra, SMNS 84821, described by Wild (1973, fig. 49), was CT scanned. Unfortunately, the postaxial cervicals of *Tanystropheus* spp. exhibit a strikingly similar morphology from the 3rd to the 9th vertebra (Rytel *et al.* 2024), and thus are extremely difficult to assign to their exact original position in the vertebral column (contra Wild 1973, see also Spiekman and Scheyer 2019). Therefore, only the posterior cervicals (vertebrae 10–13) could be confidently identified, and the postaxial vertebrae preceding them are referred to as 'middle' throughout the text. The sampled specimens varied in size, with the largest centra reaching over 35 cm in length (e.g. ZPAL V. 36/101—Fig. 1B) and the shortest being only 5 cm long (ZPAL V. 36/181). To better evaluate morphological change of the neck-torso transition, two well-preserved dorsal vertebrae of *Tanystropheus* were also CT-scanned: SMNS 54628 (*T.* '*conspicuus*') and ZPAL V. 36/112 (*Tanystropheus* sp. from Miedary).

Moreover, specimens published by previous authors were reanalysed. These included a polished longitudinal section of a posterior portion of a middle cervical of *T.* '*conspicuus*' SMF R 999 (von Huene 1907–1908: fig. 251), polished transverse sections of an 11th cervical of *T.* '*conspicuus*' U-MO BT 738.00 (Broili 1915: plates 2 and 3), and thin sections of four cervical vertebrae of *Tanystropheus* spp.: PIMUZ T 2784, PIMUZ T 2799, MHI 1104, and an uncatalogued 10th cervical from SMNS (Jaquier and Scheyer 2017). Additionally, synchrotron CT scans of the holotype of *T. hydroides* PIMUZ T 2790 (see Spiekman *et al.* 2020a, b), as well as a thin section of a cervical from the same specimen, were used to evaluate the internal morphology of the anteriormost postatlantal vertebrae.

Protanystropheus was introduced as a generic name by Sennikov (2011) to encompass the original material of '*Tanystropheus*' *antiquus* von Huene's (1907–1908), which included isolated cervical vertebrae originating from several Lower Muschelkalk localities in Silesia (southern Poland). Additional specimens were reported from the roughly contemporaneous strata of Germany and the Netherlands (Huene 1931, Wild and Oosterink 1984, Spiekman and Scheyer 2019, Spiekman *et al.* 2019), thus extending the biogeographic range of occurrence of the genus. To this day, the material referable to this taxon is constrained to scarce isolated cervicals, making any detailed interpretations of the biology of '*P*'. *antiquus* unattainable. These vertebrae are elongate, but proportionally much shorter than those of *Tanystropheus* spp. (Fig. 2). Morphologically, they are more reminiscent of those of other tanysaurians, e.g. *Amotosaurus rotfeldensis* Fraser and Rieppel 2006, *Augustaburiania vatagini*, or *Gracilicollum latens* Wang, Spiekman, Zhao, Rieppel, Scheyer, Fraser & Li, 2023 (A. Rytel, personal observations; Fraser and Rieppel 2006, Sennikov 2011, Spiekman *et al.* 2021, Wang *et al.* 2023b). This disparity between the cervicals of '*P*'. *antiquus* and all other vertebrae referred to the genus *Tanystropheus* has been noted by previous authors, before Sennikov (2011) introduced the new combination, with some suggesting the non-congenerity of these taxa (Wild 1973, 1987, Evans 1988, Fraser and Rieppel 2006). Sennikov (2011) was unaware that the syntypes housed in MGUWr had survived World War II (see Skawiński *et al.* 2017). The most recent study of this material was performed by Spiekman and Scheyer (2019) and Spiekman *et al.* (2021), who summarized the available data and research on this taxon. '*Protanystropheus*' *antiquus* was included in one of the phylogenetic analyses of Spiekman *et al.* (2021), where it was recovered among 'dinocephalosaurids' (= trachelosaurids). '*Protanystropheus*' *antiquus* requires a taxonomical redescription including the syntype material, which will be addressed in a separate publication. Herein, we confidently consider it an early diverging tanysaurian.

Seven cervicals of '*P*'. *antiquus* were analysed (see Supporting information, Table S1)—these included the syntypes of von Huene (1907–1908): MGUWr 3889s, MGUWr 3895s, MGUWr 3902s) as well as three other vertebrae identified recently by the authors—GIUS-7-3674, SUT-MG/F/Tvert/2, and WNoZ/s/7-39. The specimens studied herein originated from both historic (Gogolin, Nakło Śląskie) and novel (Sosnowiec, Żyglin) sites located in south-western Poland. These localities represent a short time interval (early Anisian). Most, if not all, of the studied '*P*'. *antiquus* specimens were found in marine carbonates of the Gogolin Formation—the lowermost part of the Lower Muschelkalk (see Kowal-Linka 2008, Skawiński *et al.* 2017), although the exact stratigraphic provenience of GPIH 5194c and WNoZ/s/7-39 is not certain. All of the '*P*'. *antiquus* vertebrae identified so far were found isolated, which, together with their scarcity and lack of research on their morphological disparity, precludes us from referring any of them to their exact original position in the vertebral column. Sampled specimens varied in size, with the largest centra reaching over 9 cm in length (WNoZ/s/7-39) and the shortest being only around 4 cm long (MGUWr 3889s). Even though these specimens are not fully complete, they are 3D preserved and virtually unaltered diagenetically, thus constituting material well suited for CT studies. The six mentioned vertebrae have been scanned, and subsequently GIUS-7-3674 and SUT-MG/F/Tvert/2 were thin sectioned transversely at the midpoint of their anteroposterior length. Two additional historical thin sections of a '*P*'. *antiquus* cervical vertebra were found in the collection of GPIH. The source specimen GPIH 5194c lost its original label, but additional notes on the sections indicate that it was collected by G. Gürich in Silesia, possibly in Gogolin.

Thus, the analysed dataset includes all of the published material (including historical specimens) in which the internal anatomy of tanysaurian cervicals was well visible. New specimens sampled for this study were investigated to complement and expand the available data, allowing for a comprehensive description of the internal morphology of these vertebrae. The full list of the studied specimens, including the sampling methods used for each of them, is provided in Supporting information, Table S1.

CT scans of the majority of the specimens studied herein were acquired using a GE Phoenix v|tome|x s CT scanner (GE Sensing and Inspection Technologies Phoenix|x-ray, Wunstorf, Germany), installed in the Faculty Laboratory of Computed Microtomography, Faculty of Science and Technology, University of Silesia in Katowice, Poland. Due to the elongation, fragility, and size of some of the vertebrae, several cervicals were scanned in parts, to preserve sufficient imaging resolution for their anterior and posterior portions. Reconstructed cross sections were used to generate 3D views of the whole specimens based on volume rendering. VG Studio Max 2.0 (Volume Graphics, Germany) and ImageJ (National Institutes of Health, USA) software was applied to visualize the internal structure of the samples. Finally, Mimics 14.11 (Materialise, Belgium) was used to model the surface of the internal cavities of '*P*'. *antiquus*.

The smallest *Tanystropheus* spp. cervical (ZPAL V. 36/181) was analysed using μCT. These data were collected with a Zeiss XRadia MicroXCT-200 system equipped with a 90 kV/8 W tungsten X-ray, located in the Laboratory of Microtomography, Institute of Paleobiology, Polish Academy of Sciences, Warsaw. Radial projections were reconstructed with XMReconstructor (Zeiss) software and viewed with XM3DViewer (Zeiss) software. Avizo Lite 2020.3.1 (Thermo Fisher Scientific, USA) was used to model the surface of the internal cavity of ZPAL V. 36/181.

The vertebrae of *T*. '*conspicuus*' SMNS 54628 and SMNS 84821 were scanned in the laboratory of the Institute for Photon Science and Synchrotron Radiation at KIT. A microfocus X-ray tube (XWT-225, X-RAY WorX, Garbsen, Germany) with an acceleration voltage of 200 kV and a flat panel detector (XRD 1621 CN14 ES, PerkinElmer, Waltham, USA) with a physical pixel size of 200 μm and a DRZ + scintillator were employed. The spectrum was hardened with an additional copper filter. For both samples, the field of view, magnification, tube power, and exposure time were optimized, resulting in an effective pixel size of 63.9 μm for SMNS 54628 with an exposure time of 2 s and a tube power of 60 W, and 62.7 μm for SMNS 84821 with an exposure time of 3 s and a tube power of 50 W. Three full CT scans were acquired for both samples and then stitched together. Each scan consisted of 2048 projections acquired over an angular range of 360°. CT reconstruction was performed using Octopus 8.6 (Inside Matters, Ghent, Belgium).

The new thin sections presented in this study (see Supporting information, Table S1) were created in the laboratories of the Institute of Paleobiology, Polish Academy of Sciences, University of Silesia in Katowice, and the Laboratory of Electron Microscopy, Microanalysis and X-Ray Diffraction, Faculty of Geology, University of Warsaw, Warsaw. The specimens selected for sectioning were sampled transversely. To allow for a more extensive comparison with the CT scan data, the vertebrae were cut at different points along their antero-posterior length (predominantly near the midpoint) and the thin sections thickness varied from 40 to 80 μm, to underline different aspects of their histology.

Additionally, two partially preserved, but diagenetically unaltered, middle cervical vertebrae of *Tanystropheus* sp. from Miedary, ZPAL V. 36/1016/1 (anterior part) and ZPAL V. 36/1016/2 (posterior part), were cut along their sagittal plane (Fig. 1C–D). Subsequently, the longitudinal cross sections were polished, to allow for a detailed comparison with the CT scan data.

Thin sections were examined using a Nikon Eclipse 80i transmitted light microscope fitted with a DS-5Mc cooled camera head (ZPAL), an Olympus BX51 polarized microscope equipped with an Olympus SC30 camera and a halogen light source (GIUS), as well as two Keyence VHX-7000 digital microscopes with a VHX-7100 fully integrated head with two lens systems (20–100×; 100–500×) and a polarization adapter, located at the University of Zurich and the University of Warsaw.

RESULTS

Bone histology and internal structure of vertebrae of '*P*.' *antiquus*

The CT examination of vertebrae was performed to nondestructively investigate the internal structure of each specimen and to assess the thickness of compact and cancellous bone in the different regions of the vertebrae. Within the anteroposteriorly terminal portions of all scanned '*P*.' *antiquus* centra, the core was filled with dense cancellous bone (identified in CT images so of uncertain tissue composition) and the cortex was relatively thin (Figs 2–4), whereas in the middle portion, where the internal cavity was revealed, the cortical bone was distinctly thicker. The transverse sections revealed the changes of the cortical bone thickness and the shape of internal cavities, with the mid-centrum being roughly cylindrical. The cortex was thinner near the anteroposteriorly terminal portions of the vertebrae and its thickness gradually increased up to approximately four times the original thickness (about 10% of bone diameter), near the midpoint (Fig. 3). The density of the cancellous bone of the anteroposteriorly terminal portions of the centrum decreased medially, with larger cavities being present closer to the midpoint. The transition to the empty internal cavity was relatively sharp. The anterior and posterior ends of the internal cavity were roughly hemispherical and surrounded circumferentially by marginalized trabeculae (Fig. 3). Long intermittent trabeculae composed of parallel-fibred bone moderately remodelled with endosteal secondary lamellar bone (Fig. 4D) crossed the internal cavity in varied directions, mainly diagonally. In some vertebrae they divided the internal cavity into several smaller terminus-like pockets (Figs 2B, 3). The neural canal was separated ventrally from the internal cavity by a horizontal, plate-like lamella consisting of endosteal lamellar bone (Figs 2B, 3, 4A–C), which was generally thinner than the internal trabeculae composed of the same tissue. This separation was not continuous, the neural canal floor was perforated by large openings in some specimens (Figs 2B and 3C–G) and seemed to disappear completely in others. For example, in MGUWr 3889s at least two large openings were present in the lamella separating the neural canal from the internal cavity. In MGUWr 3902 and GPIH 5194c there appeared to be no bony separation between the neural canal and the internal cavity for most of the length of the centrum. Because no fragments of broken bone were present anywhere inside of the neural canal or the internal cavity of the centrum, and this condition was present in several specimens approximately in the same area, it appears not to be an artifact of preservation. The cortex was predominately composed of parallel-fibred matrix (Fig. 4), with locally (especially in the dorsolateral part) highly organized arrays of mineralized collagen fibres. No rest lines were present. The vascularization was moderate, and its pattern was radial, which was especially evident in the ventral part of the vertebrae (Fig. 4A–C, H–I). Inside the neural arch, mostly dorsally to the neural canal (inside of the base of the neural spine) and in some specimens laterally to the neural canal there was a region of occurrence of secondary trabecular bone (Fig. 4J). Both the cavity and the neural canal were clear cut and lined with a thin layer of endosteal lamellar bone (Fig. 4E–J). Sharpey's fibres could be seen extending throughout the cortex, especially in the dorsolateral and ventrolateral regions of the centrum (Fig. 4C, G–I).

Bone histology and internal structure of vertebrae of *Tanystropheus* spp.

Anatomy of the middle cervicals

Within all of the studied vertebrae, a large cavity could be identified, surrounded by relatively thick cortex composed of alternating layers of well-organized parallel-fibred to lamellar bone (Figs 5–8). In the anterior and posterior terminal portions of the cervicals, discs of secondary cancellous bone of endosteal origin formed the articular regions of the centrum (Fig. 5B–D). Above them, the openings of the neural canal were present. In some of the middle cervicals the neural canal floor extended only slightly from the openings towards the middle of the vertebra, forming a shelf that partially separated the internal cavity from the neural canal (Figs 5B–E, 6C, F), although in some other of these vertebrae the neural canal transitioned smoothly into the internal cavity (compare Fig. 6B to Fig. 5B; Fig. 7B). In the transverse cross section, the inner surface of the bone wall of the internal cavity was generally parallel to the circumferential outline of the vertebra (Fig. 8A–E). In most of the studied specimens, the dorsal part of the internal cavity seemed to preserve a semicircular shape in the transverse cross section, whereas tissue layout of its ventrolateral portion was usually much less uniform, with an irregular resorption front cutting through multiple annuli (Fig. 8A, C, E). This was especially evident in larger specimens, whereas in the smallest cervical, the regions of resorption were much less developed, and the outline of the internal cavity in the transverse cross section was more regularly oval (Fig. 8B). The neural spine extended over two deep fossae, located on both of its anteroposteriorly terminal portions. They were triangular in longitudinal cross section and ventrally delimited by thin bone trabeculae, that also constituted the roof of the neural canal. The posterior cavity was larger, forming the 'postzygapophyseal trough' (Rieppel 2001). Contrary to what was observed for '*P*.' *antiquus*, in none of the studied sections of the *Tanystropheus* spp. middle cervicals did the internal cavity contain bony trabeculae extending internally from the surface of the bone wall. Some semi-symmetrical, slanted trabeculae of endosteal origin were present only incidentally in the anteroposteriorly terminal sections of the vertebrae (see Broili 1915: plate 3, fig. 4c). The roof of the neural canal was generally straight and parallel to the longitudinal axis of the vertebra. The ventral delimitation of the neural canal was seemingly absent for most of its length within a vertebra. Intriguingly, in one of the transverse polished sections from the anterior part of U-MO BT 738.00 (Fig. 8F), minute bony projections appeared symmetrically on each lateral side of

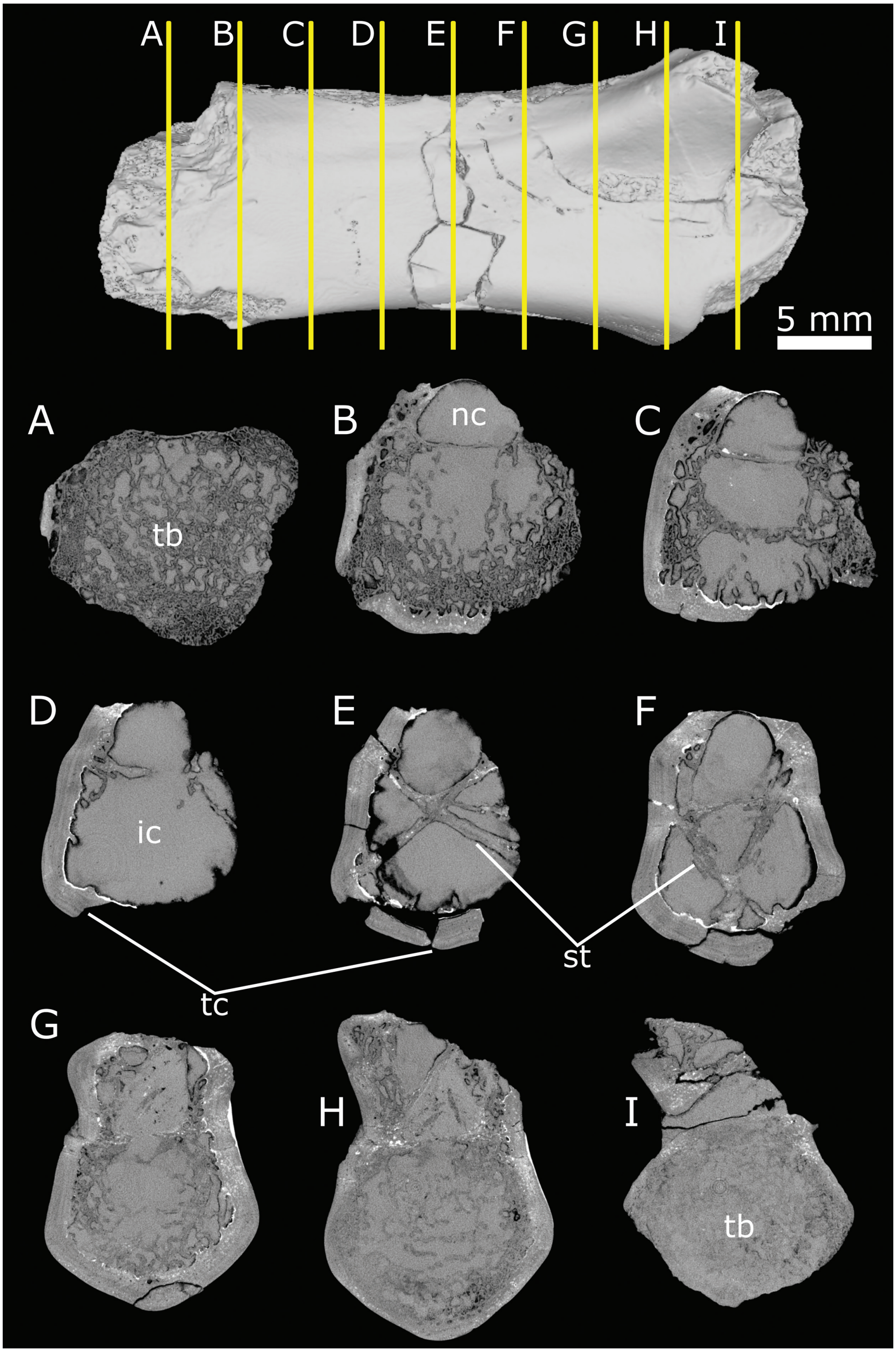

Figure 3. CT transverse cross sections (from anterior to posterior) of '*P*.' *antiquus* cervical MGUWr 3889s (surface model in left lateral view) showing internal structure of the vertebra. Sectioning planes are marked with lines. Note the presence of a large internal cavity (ic), thicker cortex layer (tc), and slanted trabeculae (st) spanning across the internal chamber. Trabecular bone (tb) is present in the anteroposteriorly terminal portions of the centrum.

the internal cavity. The colour of the limestone infill of the vertebra changed drastically at the same horizontal level, at which these projections were situated. Similar characteristics could be noted for the transverse thin section of ZPAL V. 36/166 (Fig. 8E), in which corresponding projections composed of periosteal bone were also present in the dorsolateral regions of the internal cavity. Between them, there was a sharp transition in sediment fraction, with the more coarse-grained infill occupying the ventral-more space. Presence of this feature possibly shows the differences in taphonomical microenvironments of the ventral

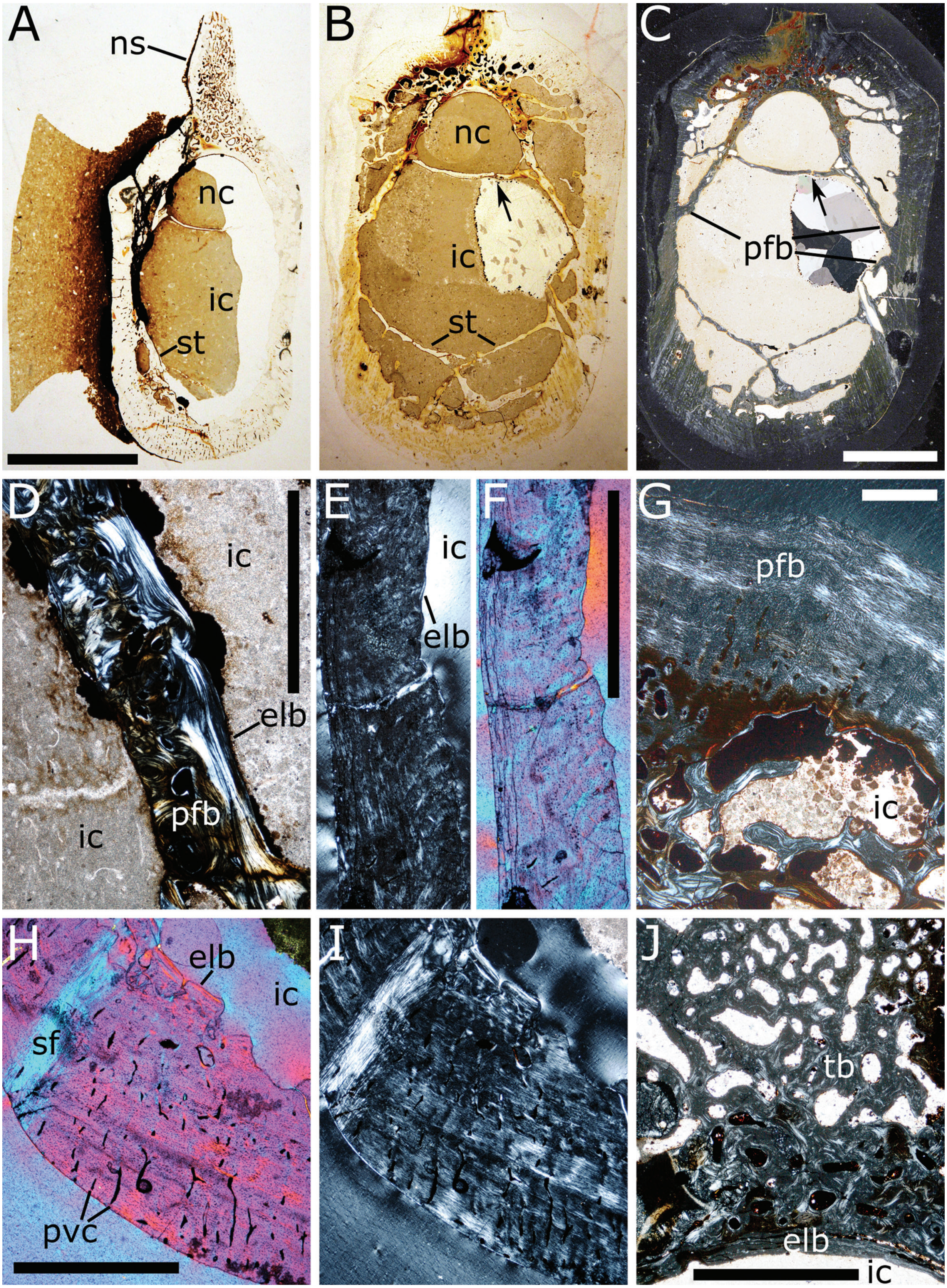

Figure 4. Thin sections of '*P*.' *antiquus* cervical vertebrae SUT-MG/F/Tvert/2 (A, E, F, H, I) and GIUS-7-3674 (B–D, G, J). A–C, thin sections in normal transmitted light (A, B) and in polarized light (C). The slight lateral asymmetry results from minor antero-posterior skewing of the plane of sectioning. D, close-up of the internal supporting trabeculae in polarized light, presenting heavy remodelling. E–F, the lateral cortex of the centrum in polarized light (E) and polarized light with lambda compensator (F) showing lack of distinctive zonation and loosely ordered bone structure. G, cortex of the dorsolateral region of the centrum displaying more pronounced zonation and dorsal internal slanted

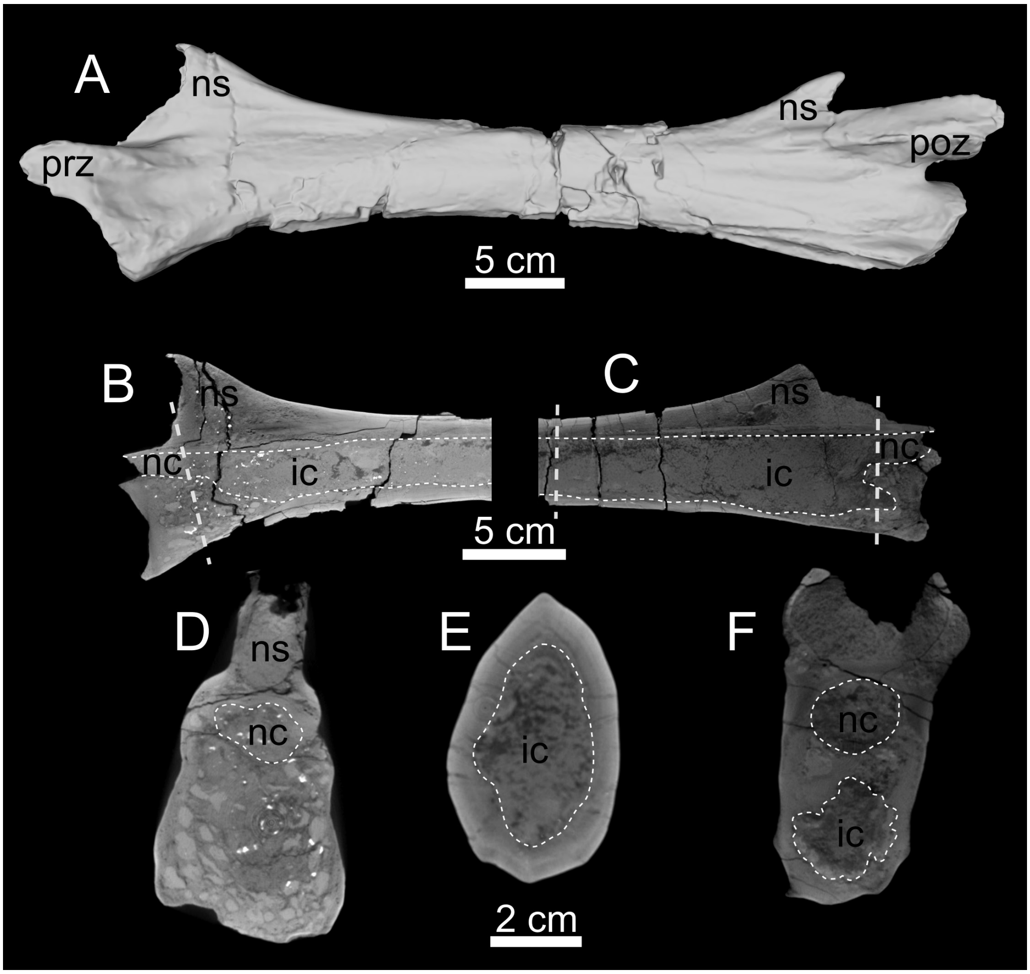

Figure 5. Middle cervicals of *Tanystropheus* sp. from Miedary: A, B, D—ZPAL V. 36/101; C, E, F—ZPAL V. 36/102; A is a surface model in left lateral view. B, C, longitudinal CT cross sections of an anterior (B) and a posterior portion (C) of the vertebra. D, E, F, transverse CT cross sections. Sectioning planes and walls of the neural canal and internal cavity have been outlined with white dashed lines, with the lines signifing the sectioning planes being thicker than the internal cavity outline. Anatomical abbreviations: ic—internal cavity; nc—neural canal; ns—neural spine; poz—postzygapophysis; prz—prezygapophysis.

and dorsal portions of the internal cavity, which may have been caused by the original existence of a no longer preserved barrier between them. Near the anteroposterior midpoint of the middle cervicals, two symmetrically placed foramina were located on the ventral side of the centrum. They entered the internal cavity as straight canals (Fig. 8B, E), perforating the dense cortex.

While in '*P*.' *antiquus* the neural spine was easily identifiable, it was much less recognizable in the middle cervicals of *Tanystropheus* spp. It was impossible to demarcate the border between the neural arch and the vertebral centrum—they were completely fused, with no preserved remnants of the suture between them, even in the smallest specimens, and little to no trabeculae within the neural arch. Continuous layers of dense parallel-fibred tissue sheathed the internal cavity. In the middle section of the larger middle cervicals of *Tanystropheus* spp. the outermost of these zones formed complete rings, whereas the ones located innermost were discontinued only due to resorption of the region ventral into the internal cavity, as well as the presence of the neural spine (Fig. 8A, C, Fig. 9B). In some of the studied transverse thin sections, including the smallest specimens, the spinous process was developed only as a thin, vertically oriented plate. It was located directly above the internal cavity and emerged from the parallel-fibred tissue of the bone walls in the dorsalmost portion of the vertebra, projecting slightly from the smooth outline of the transverse cross section. In the smallest specimen from Miedary, ZPAL V. 36/181, the neural spine was never overlain by parallel-fibred bone (Fig. 8B). In all of the larger specimens from Miedary, the anteroposteriorly

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trabeculae in polarized light. H–I, cortex of the ventrolateral region of centrum showing radial vascularization and a well-developed bundle of Sharpey's fibres in polarized light (H) and polarized light with lambda compensator (I). J, the trabecular bone of the neural arch in polarized light. Arrows indicate a perforation of the neural canal floor. Anatomical abbreviations: elb—endosteal lamellar bone; ic—internal cavity; nc—neural canal; ns—neural spine; pfb—parallel-fibred bone; pvc—primary vascular canals; sf—Sharpey's fibres; st—slanted trabeculae; tb—trabecular bone. Scale bars for panels A–C equal 5 mm and 0.5 mm for D–J.

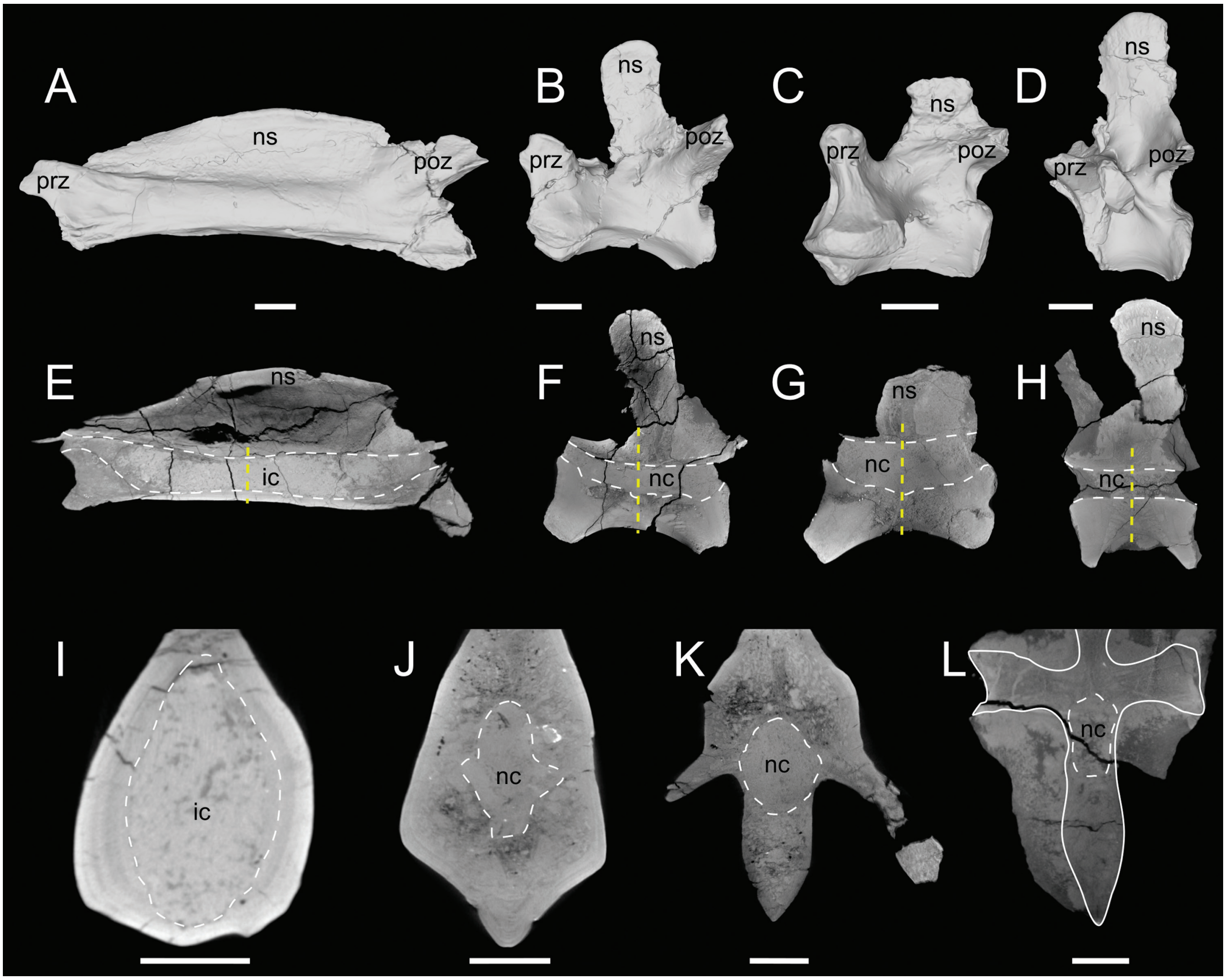

Figure 6. Vertebrae of *Tanystropheus* sp. from Miedary: A, E, I—ZPAL V. 36/106, 11th cervical; B, F, J—ZPAL V. 36/108, 12th cervical; C, G, K—ZPAL V. 36/110, 13th (last) cervical; D—ZPAL V. 36/1036, dorsal; H, L—ZPAL V. 36/112, dorsal. A–D, surface models in left lateral view. E–H, longitudinal CT cross sections. I–L, transverse CT cross sections. White dashed lines mark the sectioning planes (yellow) and walls of the neural canal and internal cavity (white). Anatomical abbreviations: ic—internal cavity; nc—neural canal; ns—neural spine; poz—postzygapophysis; prz—prezygapophysis. Scale bars equal 2 cm for A–H, and 1 cm for the other panels.

middle part of the spinous process was obscured by thick layers of tissue that formed the walls of the internal cavity. Compared to what was noted for '*P*'. *antiquus*, the dorsolateral regions of the *Tanystropheus* spp. cervicals were thickened (see Fig. 9). The neural spine was, thus, not relatively reduced in the latter, but rather embedded within the walls of the tubularly structured vertebra. As a result, the neural canal was located close to the middle of the height of the vertebra, as in '*P*'. *antiquus*. However, in *Tanystropheus* spp. there was more tissue dorsolaterally (see Fig. 9), due to the neural spine being hypertrophied along the middle section of its anteroposterior length.

Anatomy of the posterior cervicals

In *Tanystropheus* sp. from Miedary, the external morphology of the cervicals changed near the posterior subregion of the neck. The 10th and 11th vertebrae were still elongate, but, contrary to the middle cervicals, exhibited a well exposed, relatively tall and continuous neural spine (Fig. 6). The two last cervicals were relatively much shorter (Fig. 6B, C), and more similar in proportions to the dorsals (Rieppel *et al.* 2010, Rytel *et al.* 2024). This transition was paired with the modifications in the internal structure of these elements. The relative volume occupied by the trabeculae within the centra increased caudally, especially along the neck-torso transition. In the middle cervicals the centrum was nearly devoid of trabecular bone, but this changed within the more posterior vertebrae, with the last two cervicals and the dorsals exhibiting sparse trabeculae occupying the space between the articular discs. The 10th and 11th vertebrae were generally similar in their anatomy to the middle cervicals, with their internal cavities being surrounded by a dense cortex, forming a tube-like structure (Fig. 6I). However, in the succeeding vertebrae the internal cavity was greatly reduced and exhibited much thicker walls, composed of two regions: a relatively thin cortex and porous, cancellous bone encompassed by it. Especially in the middle portion of the centrum of the last two cervicals, there were several large chambers, similar to those present in the anteroposteriorly terminal portions of the more anteriorly located vertebrae (Fig. 8D). Some of them connected to the

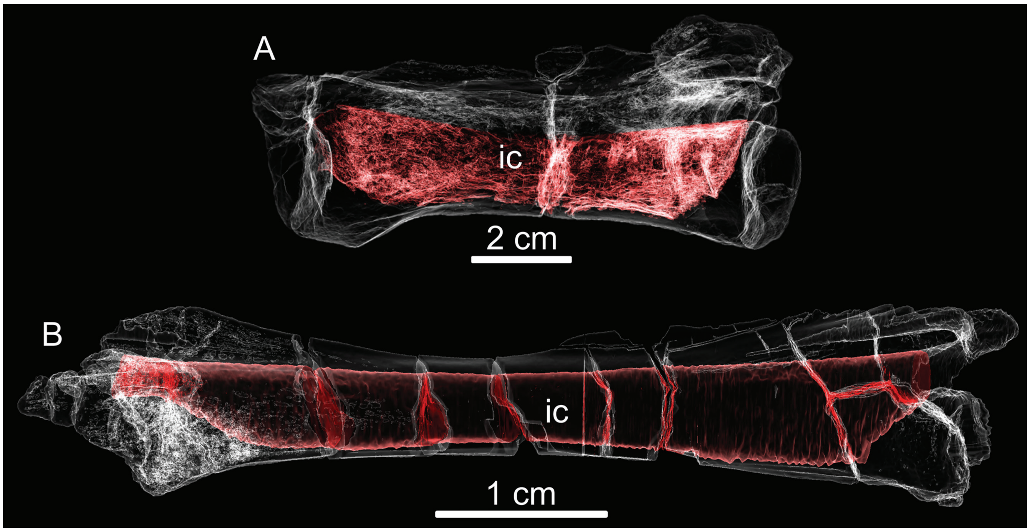

Figure 7. Internal cavity volume in the cervical vertebrae of '*P*.' *antiquus* MGUWr 3895s (A) and *Tanystropheus* sp. from Miedary ZPAL V. 36/181 (B). Anatomical abbreviation: ic—internal cavity. Images obtained using 'xray' shader in MeshLab v.2020.12 (Cignoni *et al.* 2008).

neural canal through its floor (Fig. 6E, F, H, I). The transverse cross sections of the posteriormost cervicals were less oval than in the preceding vertebrae, with the centrum being much more ventrally expanded, forming a distinct keel (Fig. 6J, K). The diameter of the neural canal was relatively constant along the length of each of the two last vertebrae. In the longitudinal cross section, it had a sagging appearance, with its middle portion being located more ventrally. In the transverse cross section, it was oval, with its dorsolateral regions being roughly semicircular and symmetrical in outline (Fig. 6J, K). A similar shape could be noted in the anteroposteriorly terminal sections of the rest of the postaxial cervicals, in which the neural canal floor was still present (e.g. Fig. 8D), and also in the dorsal vertebrae (Fig. 6L). In each of the two posteriormost neck vertebrae of *Tanystropheus* sp. from Miedary, up to two small subcentral foramina could be traced, with some specimens exhibiting only one subcentral foramen or none at all. In the studied posteriormost cervical ZPAL V. 36/110, a straight, non-branching canal connected the one present foramen with the neural canal (Fig. 10).

The dorsal vertebrae were generally similar to the posteriormost cervicals in their internal anatomy. They differed in a complete lack of subcentral foramina. Moreover, the neural canal of the dorsals extended anteroposteriorly straight, with its roof and floor remaining on a relatively constant horizontal level (Fig. 6H). Its transverse cross section was similar in shape to the posteriormost cervicals, but more regular. Congruently to what could be observed in the 12th and 13th cervical vertebrae, the internal portion of the centrum was composed of sparsely distributed trabeculae containing a large number of cavities, some of which opened to the neural canal through its floor.

Vertebral histology

The histological characteristics of the studied vertebrae of *Tanystropheus* spp. were congruent with the results of the study performed by Jaquier and Scheyer (2017 and the supplemental data provided therein). New data presented herein expand our knowledge on the anteroposterior and ontogenetic variation of their structure. The walls of the internal cavity were built of primary compact lamellar to parallel-fibred matrix of periosteal origin. Some intervals with decreased vascularization could be traced within these bone walls—they formed ellipsoidal annuli that alternated with more vascularized zones in parallel to the circumference of the vertebra (see Jaquier and Scheyer 2017). Closer to the terminal portions of the anteroposterior length of the cervicals, the tissue composition changed, with the internal cavity being dorsolaterally lined with secondary endosteal lamellar bone (Fig. 8H) and the ventrolateral portions of the bone centrum not exhibiting the regular annuli, but rather being nearly completely composed of endosteal lamellar bone scattered with secondary osteons and erosion cavities of varying size, forming a net of sparse trabeculae (Figs 5B–D, 8D, G). The core of the neural spine in larger specimens was highly remodelled with longitudinally oriented secondary osteons. Simple primary vascular canals extended radially in the middle part of the vertebrae, but became more longitudinally oriented, larger, and less organized in the anteroposteriorly terminal portions. The number of vascular canals was also smaller in the more compact sections of the cortex within a single cross section.

DISCUSSION

Ontogenetic age of the studied specimens

Microanatomical characteristics of ZPAL V. 36/181, the smallest vertebra in the analysed *Tanystropheus* spp. sample, advocate for a young ontogenetic age of this individual. Even though some evident zonation can be identified throughout the transverse cross sections, the annuli are mostly preserved as nearly complete ellipsoids that extend parallel to the external outline of the bone. A much smaller extent of resorption of both the walls of the internal cavity and the highly vascularized tissue of the neural spine can be observed (compare Fig. 8B to the larger individuals in the same figure). Notably, ZPAL V. 36/181 is the only analysed representative of the genus *Tanystropheus* in which the vestigial neural spine is not overlain by the continuous parallel-fibred tissue layers at any point along its anteroposterior length. These characteristics are congruent with the interpretation of

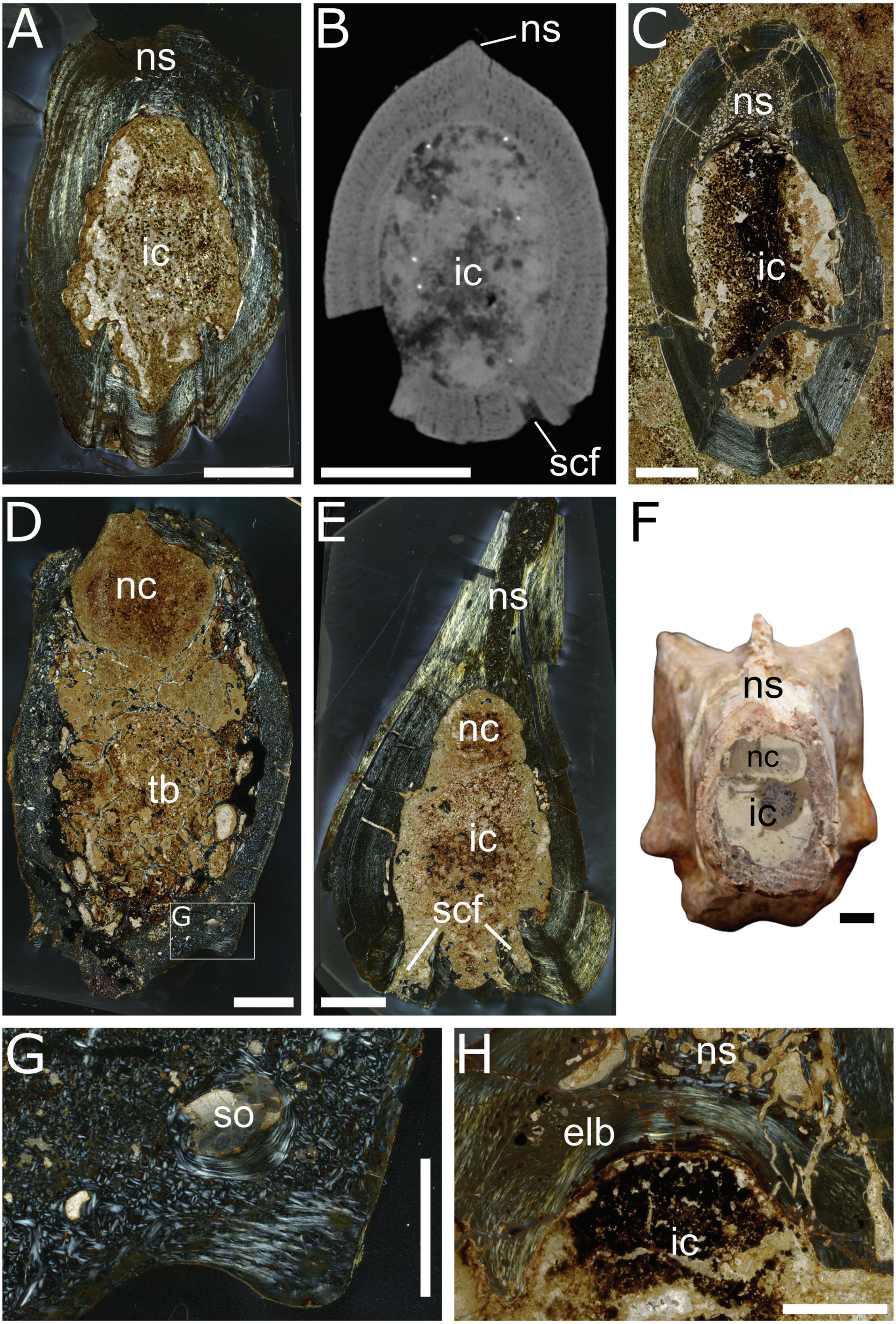

Figure 8. Transverse cross sections through the cervicals of *Tanystropheus* '*conspicuus*' (F) and *Tanystropheus* sp. from Miedary (all other panels). A, ZPAL V. 36/150, middle cervical, middle portion; (B) ZPAL V. 36/181, middle cervical, middle portion; (C) ZPAL V. 36/193, middle cervical, middle portion; (D) ZPAL V. 36/1099, 10th cervical, posterior portion; (E) ZPAL V. 36/166, 10th cervical, middle portion; (F) UMO BT 738.00, 11th cervical, anterior portion; (G) ZPAL V. 36/1099, 10th cervical, posterior portion, close-up on the right ventrolateral portion of the vertebra with bundles of longitudinally oriented secondary osteons; (H) ZPAL V. 36/156, middle cervical, middle

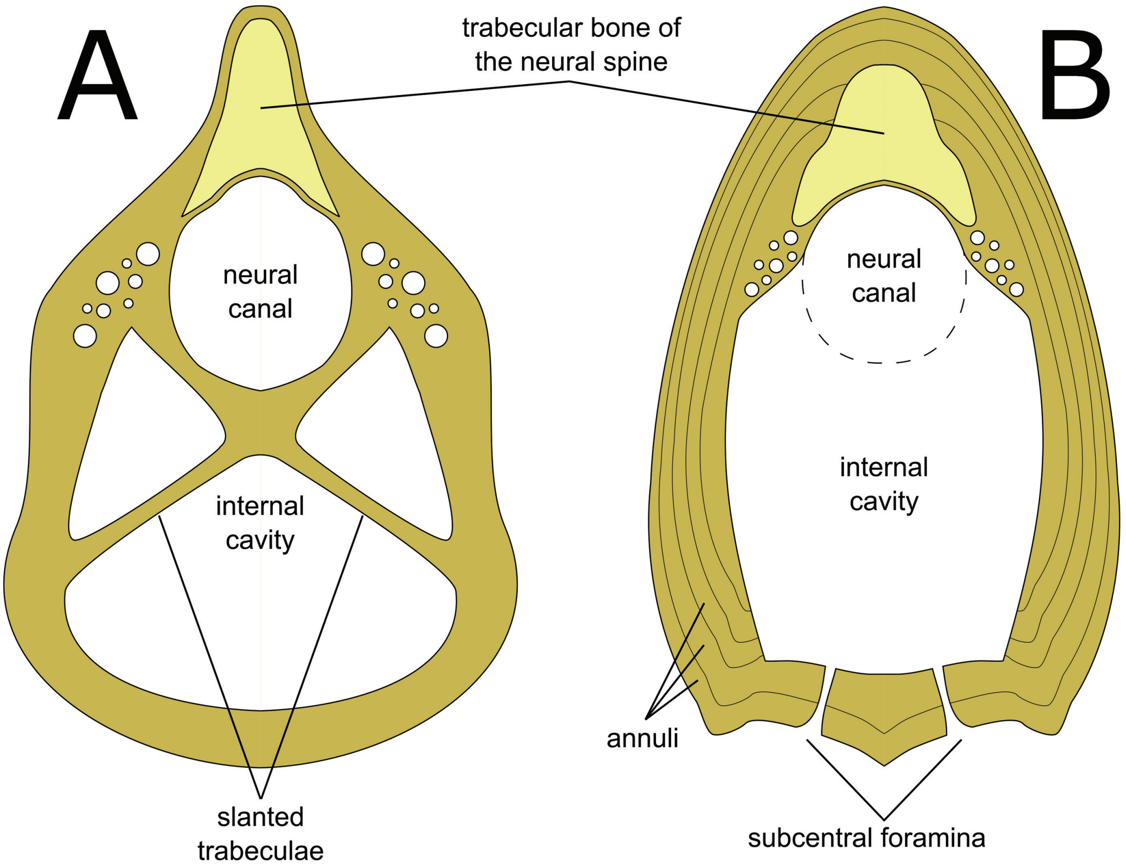

Figure 9. Interpretative drawings of the internal anatomy of a cervical vertebra of '*P*'. *antiquus* (A) and a middle cervical of an adult individual of *Tanystropheus* spp. (B) shown in the transverse cross section near the midpoint of their anteroposterior length.

Jaquier and Scheyer (2017), who suggested that in the middle section of the vertebrae of older individuals the spinous process grew relatively slower than the rest of the vertebrae, and was overlain by additional periosteal bone, as we see in the larger vertebrae studied herein. Thus, it can be assumed that the size variation of the analysed cervicals is a result of presence of individuals at different ontogenetic stages, additionally broadening the scale of insights obtained from the sampled specimens. Detailed studies on microanatomical and histological changes throughout ontogeny, including skeletochronology, require more detailed sampling along the anteroposterior axis of the vertebrae and between each vertebra in a sequence.

Interpreting the internal anatomy of the tanysaurian cervicals

In accord with previous works (von Meyer 1847–1855, von Huene 1907–1908, Edinger 1924, Wild 1973, Spiekman *et al.* 2020a), our observations confirm the presence of a large, open cavity that occupies most of the volume of the centrum (see Fig. 7) within the cervical vertebrae of *Tanystropheus* spp. and '*P*'. *antiquus*. The presence of the cavity in all of the cervicals studied herein, together with the structure of the cortex and the state of preservation of continuous, undamaged slanted trabeculae spanning across the cavity (in '*P*'. *antiquus*) indicate that this empty space did not originate from the post mortem dissolution or destruction of the trabecular bone (contra Broili 1915). In *Tanystropheus* spp., the middle portion of the vertebral centra was not filled with spongiosa *in vivo*, as there are no signs of abrasion on the inner walls of the internal cavity, regardless of specimen size. In U-MO BT 738.00, previously described by Broili (1915), the trabeculae are present due to the sampling location—in the anteroposteriorly terminal portions of the posterior cervicals they occur much more commonly (e.g. Fig. 8D).

The neural canal floor seems to be non-continuous in some of the specimens studied herein. Many birds and some non-avian saurischian dinosaurs have foramina in the neural canal that connect to pneumatic chambers in the vertebrae (Wedel *et al.* 2014). They tend to be located in the lateral or dorsal walls of the canal, although small foramina in the ventral floor of the canal are occasionally present in pelicans (*Pelecanus*) and large ratites (*Struthio*, *Dromaius*, *Rhea*). Those foramina are proportionally smaller than the gaps in the floor of the neural canal in '*P*'. *antiquus*, and in the dorsals and posteriormost cervicals of *Tanystropheus* spp. We are unaware of large gaps in the walls of the neural canal in apneumatic vertebrae. This may be a feature

section, close-up on the base of neural spine with the endosteal bone lining. A, C, D, E, G, H, thin sections viewed in polarized light. B, μCT image. F, polished section. Anatomical abbreviations: elb—endosteal lamellar bone; ic—internal cavity; nc—neural canal; ns—neural spine; scf—subcentral foramen; so—secondary osteons; tb—trabecular bone. Scale bar equals 2 mm for B, G, H, and 5 mm for the other panels.

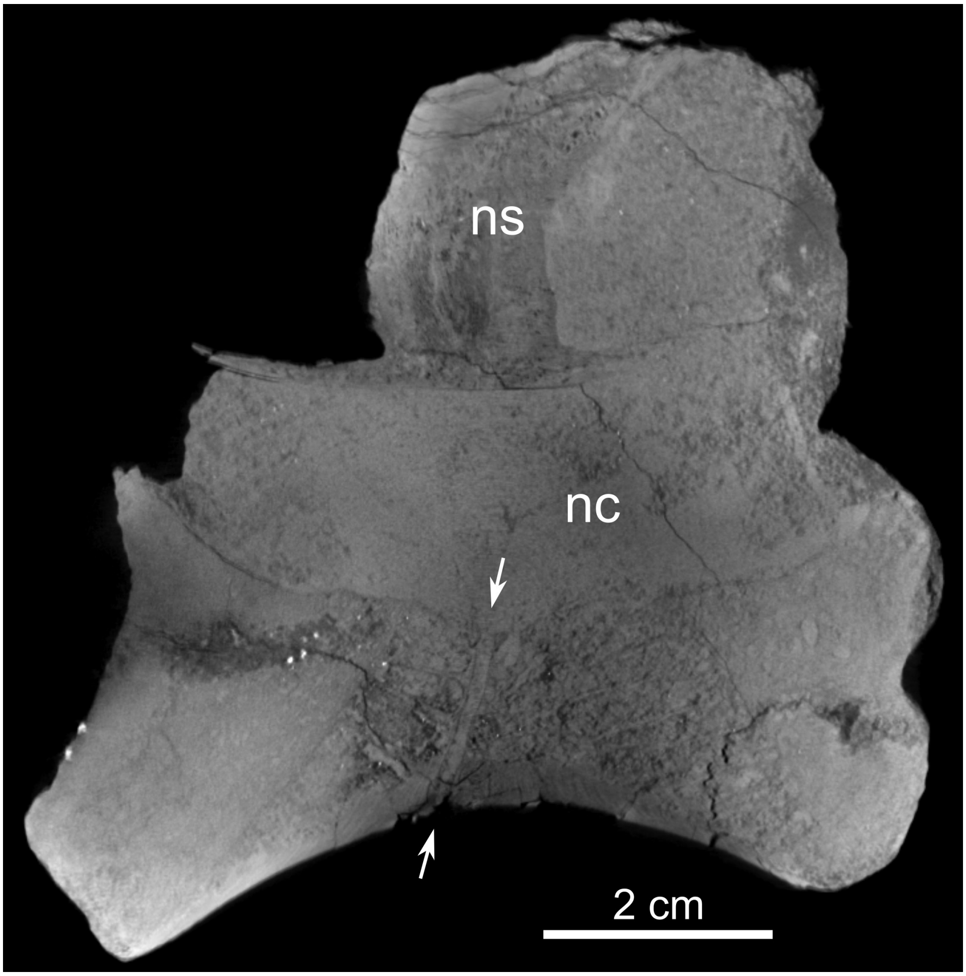

Figure 10. Longitudinal cross section of ZPAL V. 36/110, 13th (last) cervical vertebra of *Tanystropheus* sp. from Miedary, showing the course of the arterial canal (locations of its end sections are indicated with arrows). The anterior end of the vertebra points towards the left. Anatomical abbreviations: nc—neural canal; ns—neural spine.

unique to tanysaurians, although more work on the internal structure of vertebrae in other archosauromorphs will be required to adequately assess that possibility. None of the studied middle cervicals of *Tanystropheus* spp. exhibit any traces of the bony neural canal floor being present within their anteroposteriorly middle portion. Some support for the neural canal being ventrally delimited from the internal cavity with soft tissue can be observed in two of the studied specimens—U-MO BT 738.00 and ZPAL V. 36/166. Despite different sedimentation characteristics of the two source localities (calcareous vs. argillaceous), their rock infill was preserved as if two taphonomic microenvironments were present in the internal cavity, indicating that it might have been horizontally partitioned by a barrier that diversified the rock infill. In both specimens the outline of the more dorsally located portion is ellipsoidal and resembles the shape and proportions that would be expected for a neural canal cross section. Thus, through parsimony and some taphonomic evidence, we hypothesize that the neural canal in *Tanystropheus* spp. was ventrally delimited from the internal cavity not with bony trabeculae, but rather by a functionally analogous non-mineralized tissue barrier. Even in the two posteriormost cervicals, the neural canal seems to have been underlain with a layer of soft tissue, as can be determined by its ventrally varying outline. The neural canal anatomy of '*P*.' *antiquus* might approach morphology intermediate between the plesiomorphic condition of diapsids (fully ossified neural canal floor) and the condition observed in *Tanystropheus* spp. The cervicals of '*P*.' *antiquus* exhibit different degrees of ossification of the neural canal floor, from mostly absent (e.g. MGUWr 3902s) to nearly fully ossified, but with some gaps (e.g. MGUWr 3889s). This reflects the presence of an already highly modified vertebral anatomy among the early branching tanysaurians, and even more derived features occurring in later forms (*Tanystropheus* spp.).

Comparison of the studied vertebrae with the cavernous bone of other animals

Cavernous bone tissue is widespread among different vertebrate groups. In avemetatarsalians, this type of bone contains pneumatic diverticula, which are extensions of the lungs and air-sac system (King 1966, Duncker 1971, O'Connor 2004, 2006, 2009, O'Connor and Claessens 2005, Butler *et al.* 2012). Cavernous bones occur also in the skulls of mammals and archosaurs (pneumatic spaces; e.g. paranasal and paratympanic sinuses), as well as in various postcranial skeletal elements in theropods, sauropods, and pterosaurs, especially in the vertebrae (Wedel 2003a, b, 2005, Cerdae *et al.* 2012, Williams *et al.* 2021, Fronimos 2023, Aureliano *et al.* 2024). The vertebrae of the studied tanysaurians are distinct from the typical cavernous bone of tetrapods, and, despite sharing the presence of very considerable cavities, there are also several important differences between the internal anatomy of the cervicals of tanysaurians and avemetatarsalians. The chambers in the vertebrae studied herein grade evenly from the large central cavity that occupies virtually the entire centrum at its midpoint, through a complex network of trabeculae toward the anteroposteriorly terminal portions of the vertebrae. That level of heterogeneity in chamber size is not seen in pterosaurs (see Buchmann *et al.* 2021, Williams *et al.* 2021), nor in extant birds—the closest analogue among pneumatic vertebrae would be the polycamerate and semicamellate vertebrae of some sauropod dinosaurs, which have large open chambers at the mid-centrum (camerae) that grade into smaller, thin-walled chambers near the extremities of the centrum (camellae; Wedel *et al.* 2000, Wedel 2003a). In these sauropod vertebrae, the smallest pneumatic chambers are still much larger than the trabecular spaces of apneumatic vertebrae from the same taxa (e.g. Wedel 2005: fig. 7.7). The smallest pneumatic spaces in the vertebrae of birds and pterosaurs approach the size of trabecular spaces in apneumatic, marrow-filled bone, but the size of the pneumatic spaces tends to be consistent throughout the internal structure, giving the vertebrae a honeycombed appearance—the fully camellate condition described by Britt (1993), Wedel *et al.* (2000), and Wedel (2003a). Criteria for diagnosing pneumaticity in fossil vertebrates have been reviewed by many authors (Janensch 1947, Britt 1993, Witmer 1997, Wedel 2003a, b, 2005, 2007, O'Connor 2006, Butler, Barrett and Gower 2012, Yates *et al.* 2012). Most of the uncertainty in diagnosing pneumaticity is in regard to external fossae, which are pneumatic in some cases, but may also be associated with other soft tissues, including muscle, adipose deposits, and cartilage (O'Connor 2006). All of the cited authors agree that the least ambiguous evidence of pneumaticity is the presence of large internal chambers connected to large external foramina. Even here there is some uncertainty due to the considerable overlap in size between the largest neurovascular foramina and the smallest pneumatic foramina—see in particular the different views of Britt *et al.* (1998) and O'Connor (2006) on vertebral pneumaticity in *Archaeopteryx lithographica*. Butler *et al.* (2012) provided some clarification, noting that neurovascular foramina typically maintain the same diameter along their course (length exceeds diameter), whereas most pneumatic foramina open into chambers that are larger than the foramina (diameter exceeds length).

Foramina with possibly pneumatic affinities were not reported in any tanysaurians, nor in non-avemetatarsalian archosauromorphs as such (Spiekman *et al.* 2021 and the references cited therein). Numerous straight, narrow, not anastomosing canals, mostly located in the antero-ventral region of the centrum, cross the cortical bone of the vertebrae of the studied tanysaurians and open into the internal trabecular spaces. In size, number, spacing, and geometry, they are more consistent with neurovascular foramina than with pneumatic foramina. On the ventral side of most of the postaxial cervicals of *Tanystropheus* spp., near their anteroposterior midpoint, one or two anteroposteriorly elongate foramina are present, occupying both lateral sides of the ventral keel (see Figs 8B, D, 9–11). In ZPAL V. 36/110, a posteriormost cervical of *Tanystropheus* sp. from Miedary, a canal that forms from one of these foramina perforates the ventral surface of the centrum and the floor of the neural canal, with no visible branching along its tract. Thus, the mentioned foramen and, as an extension, all other similar openings in the cervicals of *Tanystropheus* spp. are not associated with pneumatization. Moreover, the geometry of internal cavities in the taxa studied herein also suggests that they were not filled with air. Therefore, we recognize no evidence for the presence of pneumaticity in tanysaurians. Apneumatic vertebrae with

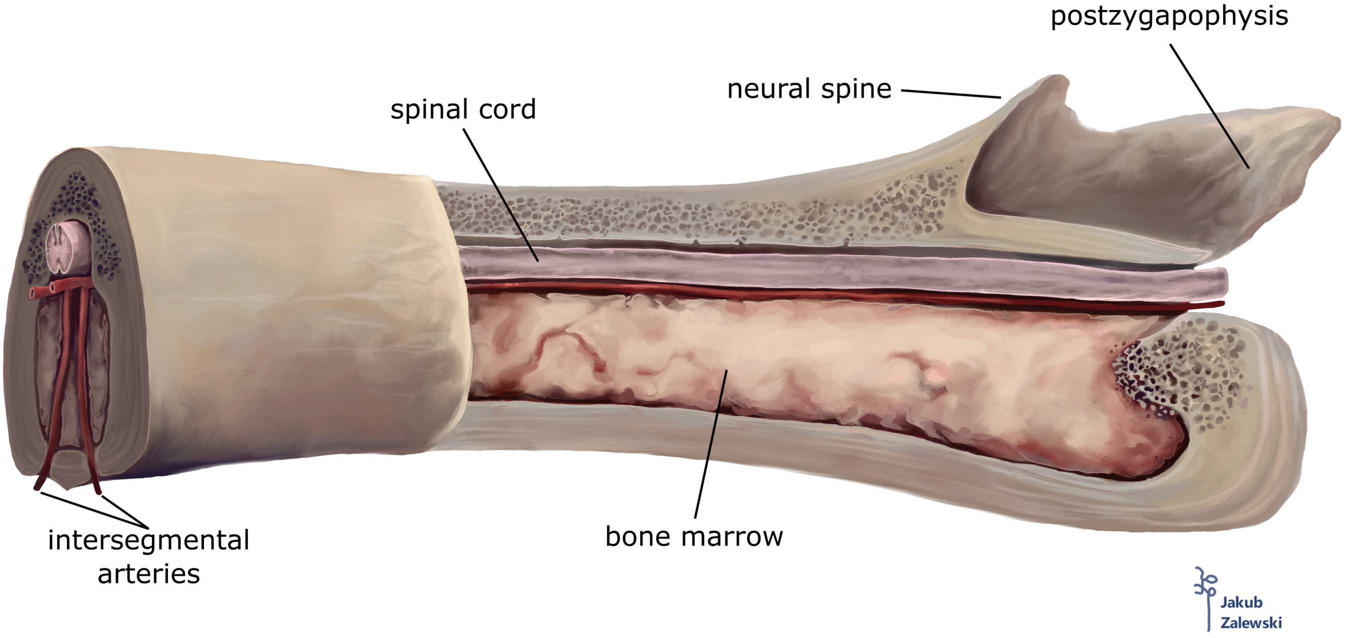

Figure 11. Artistic reconstruction of a cross section through the posterior portion of a middle cervical vertebra of *Tanystropheus* sp. from Miedary with hypothetical soft tissue layout included. Artwork by Jakub Zalewski.

a heterogeneous internal structure like that of the tanysaurian vertebrae are known in other animals. In particular, Butler *et al.* (2012) documented very similar internal structures in the vertebrae of *Varanus komodoensis*, *Chelonoidis nigra*, and *Alligator mississippiensis*. Their description of the internal structure of the alligator vertebrae is strikingly similar to that of '*P*.' *antiquus*, as well as the posterior cervicals and dorsals of *Tanystropheus* spp. (see Butler *et al.* 2012: 4–6). Furthermore, the CT cross sections of vertebrae of *Varanus komodoensis* and *Chelonoidis nigra* show large cavities similar to those reported herein, which are apneumatic and filled with marrow in life. Thus, the internal cavities of tanysaurians were most likely filled with soft tissue, probably with bone marrow (Fig. 11), following the hypothesis of Dzik and Sulej (2016), who suggested that the vertebrae were filled with fat. In many animals (including humans), the hematopoietic (blood-forming) 'red marrow' in the trabecular spaces of long bones grades into the 'yellow marrow' (with a high content of adipose tissue) in the shafts (Maniatis *et al.* 1971, Gurevitch *et al.* 2007). The composition (e.g., fat content) and volume of the soft tissue contained within the skeletal internal cavities might be dependent on lifestyle of an animal and changes through its ontogeny (see Krahl *et al.* 2013). Thus, with the currently available data, we cannot confidently identify the exact tissue that occupied the large vertebral internal cavities in tanysaurians.

Importantly, Butler *et al.* (2012) have also demonstrated that at least in some other early non-tanysaurian, non-archosauriform archosauromorphs (e.g. the rhynchosaur *Stenaulorhynchus*) the interior of the vertebrae was composed of densely packed trabecular bone with no large empty spaces. Studies on the skeletal internal morphology of other non-archosauriform archosauromorphs are thus needed to further investigate the phylogenetic distribution, evolution, and function of the intervertebral cavities, as well as their connection with the origin of pneumatization. Recent analyses have shown that vertebral pneumaticity has evolved independently in pterosaurs, theropods, and sauropods (Aureliano *et al.* 2022, 2024). It is perhaps possible that the large marrow-filled cavities observed in tanysaurians were more widespread in early archosauromorphs and only later, in certain lineages, were invaded by the diverticula of the air-sacs, thus potentially being a feature that was exapted for vertebral pneumaticity by some avemetatarsalians. A similar developmental process of bone marrow substitution by invading diverticula occurs postnatally in birds (Schepelmann 1990).

Role of the subcentral foramina in *Tanystropheus* spp.

The foramina present on the ventral side of most of the postaxial cervicals of *T.* '*conspicuus*' were already noticed by von Meyer (1847–1855). Wild (1973) described them in more detail, interpreting them as subcentral foramina. The 11th cervical is the last vertebra in which they are well outlined. In the much less elongate 12th and 13th cervicals, their size declines greatly, and in some specimens one or both of the foramina are absent (A. Rytel, personal observations). They are not present in the dorsals (A. Rytel, personal observations). Therefore, some correlation can be noted between the elongation of a vertebra and the presence and size of the aforementioned foramina. Interestingly, paired foramina of vascular origin, located on the ventral side of cervical vertebrae are also characteristic of another group of long-necked aquatic reptiles—the pistosauroids, especially plesiosaurs (Wintrich *et al.* 2017). In plesiosaurs, these foramina are a result of the persistence of the intersegmental arteries (Wintrich *et al.* 2017), yet it would be difficult to confirm a similar interpretation in the middle cervicals of *Tanystropheus* spp. due to the course of the presumed arteries not being preserved in the hollow vertebrae. However, as previously mentioned, the CT-scan of the posteriormost cervical ZPAL V. 36/110 reveals that the canal originating from the foramen is straight and directly connects the ventral surface of the centrum with the neural canal. This demonstrates the existence of intersegmental arteries within the described specimen, and, as an extension, in all postaxial cervicals of *Tanystropheus* spp. in which the subcentral foramina are present. Similar interpretation of the genesis of these subcentral foramina was formulated by Wild (1973). It can also be hypothesised that the size and occurrence rate decrease of the subcentral foramina in the anteroposteriorly terminal cervicals of *Tanystropheus* spp. is connected with their relatively shorter length. It seems that there was a much stronger selective pressure towards consistent persistence of intersegmental arteries in the longest vertebrae.

Convergent evolution of this feature in *Tanystropheus* spp. and pistosauroids, two taxa of long-necked aquatic reptiles employing extremely disparate strategies of achieving neck elongation (see Rytel *et al.* 2024) is intriguing. Its adaptive role remains enigmatic, but could be connected with providing sufficient cerebral blood supply (see Wintrich *et al.* 2017). If the voluminous internal cavity of tanysaurian vertebrae was filled with soft tissue, an adequate vascularization must have also been present there. This could additionally explain the size and occurrence rate decrease of the subcentral foramina in the shortest anterior- and posteriormost cervicals of *Tanystropheus* spp.—soft tissue volume was (relatively) much lower there than in the vertebrae from the middle section of the neck. Thus, the existence of large foramina on these elongate cervicals might be analogous to what can be observed in some appendicular bones (humeri, ulnae, femora, etc.) that also tend to have one or several larger nutrient foramina allowing access for the nutrient arteries and veins into the bone. Although no branching can be noted for the fully preserved arterial canal (Fig. 10), it cannot be ruled out that in the middle cervicals the vasculature entering the centrum though the subcentral foramina diverged into the tissue of the internal cavity.

Phylogenetic distribution and function of the unique cervical anatomy

Presence of a large internal cavity within the cervical vertebrae can be confirmed in all of the tanysaurian taxa in which the 3D preserved material was available for study—*Tanystropheus* spp., '*P*.' *antiquus*, *Augustaburiania vatagini*, *Macrocnemus bassanii*, *Ozimek volans*, *Tanytrachelos ahynis*, and the Moenkopi Formation and Homestead tanystropheids, as well as the putative tanysaurians *Czatkowiella harae* and *Microcnemus efremovi* (A. Rytel, personal observations; von Huene 1940, Dzik and Sulej 2016, Formoso *et al.* 2019, Miedema *et al.* 2020, Spiekman *et al.* 2021, Heidenfelder *et al.* 2023). The tubular structure of the elongated cervical centra can therefore be regarded as a possible synapomorphy of Tanystropheidae. Absence of the internal cavity has been confirmed only in one known tanysaurian—*Dinocephalosaurus orientalis*, in which there seems to be no indication for hollow centra (Spiekman *et al.* 2024b). Thus, for now, the tubular structure of the cervicals cannot be unanimously regarded as ancestral for Tanysauria. Notably, *Dinocephalosaurus orientalis* exhibits the highest degree of adaptation to life in open water among the known non-archosauriform archosauromorphs—the internal anatomy of its vertebrae might therefore have also been secondarily modified, as in other aquatic amniotes (see Houssaye *et al.* 2016). Interestingly, the presence of the large internal cavity in the vertebrae of tanystropheids does not seem to be affected by the disparity of their lifestyles, habitats, or spatial and temporal ranges of occurrence.

Although, as exemplified herein, some variation in its relative size and anatomy should be noted, it would seem that the tubular structure of the cervicals is related to a character shared by all of the aforementioned taxa—neck elongation. A similar condition can be observed in another extinct clade of Mesozoic reptiles, the pterosaurs. Cervicals of tanystropheids, and especially *Tanystropheus* spp., resemble those of azhdarchid pterosaurs in their general external morphology (Renesto 2005), despite the obvious differences between the members of these groups. Shared features include the extent of vertebral elongation and the low neural spine. The internal vertebral cavities of '*P*'. *antiquus* are also structurally similar to the pneumatic bone chambers of pterosaurs in the presence of intermittent trabeculae spanning across the cavity (Fastnacht 2005, Williams *et al.* 2021) and marginal trabeculae surrounding the ends of the cavity, but disappearing towards the mid-shaft (Martin and Palmer 2014). A recent study using CT scanning has revealed that at least in some azhdarchids the cervicals were structured as a 'tube within a tube' (Williams *et al.* 2021). Due to their superficial similarity, comparison of the internal anatomy of the neck vertebrae of tanystropheids and pterosaurs is particularly intriguing, and available for the first time in detail through the data presented herein. Our results demonstrate that azhdarchids converged on tanystropheids in the tubular structure of their cervicals, but detailed study reveals major differences between these elements. In the analysed vertebrae, the neural canal is wide and voluminous, the centrum is mostly hollow, with no (*Tanystropheus* spp.) or crossed ('*P*'. *antiquus*) trabeculae, a mostly thick and relatively compact cortex, and (in *Tanystropheus* spp.) an even thicker supraneural region. In azhdarchids the neural canal is relatively narrow and centrally located within an essentially hollow vertebra with helically arranged trabeculae roughly radiating away from the neural canal, a very thin cortex with no apparent differentiation between the centrum and neural arch, and no evidence of the neural spine (Williams *et al.* 2021). Thus, although some analogies exist between these two vertebral morphologies, it can be assumed that they mostly resulted from biomechanical limitations and plesiomorphic archosauromorph vertebral and muscular anatomy (general shape of the vertebra). The cervicals of both taxa evolved under conditions favouring neck elongation, which was achieved not by the adding to the cervical vertebrae count, but rather by increasing their relative length (Müller *et al.* 2010, Rytel *et al.* 2024). The resulting morphologies are a response to a similar biomechanical problem and using similar resources but resulting in a very different solution. In tanysaurians, and especially in *Tanystropheus* spp., the tubular structure of the vertebrae was achieved by replacement of the bony trabeculae of the centrum with soft tissue, which resulted in the appearance of a large internal cavity, sheathed with a dense bone layer.

The redistribution of bone mass towards the periphery of the vertebra most likely had a mechanical function, congruent with what was observed in pterosaurs (Fastnacht 2005, Williams *et al.* 2021). Hollow, cylindrical bones have increased bending and torsional strength, relative to their volume (Fastnacht 2005, Cuff and Rayfield 2013, Williams *et al.* 2021, Toyama *et al.* 2024). A heavy, compact cortex is also present in the long bones of birds, partially compromising their lightness but increasing their strength-to-weight and stiffness-to-weight ratios (Dumont 2010). In '*P*'. *antiquus* the relatively thick internal slanted trabeculae spanning across the internal cavity most likely increased the resistance to buckling (see Williams *et al.* 2021). Taking into consideration the ordered layout and heavy remodelling of these trabeculae, their biomechanical importance is evident. Thus, it can be hypothesized that with the increasing relative neck length of early archosauromorphs, their vertebrae were adapted to withstand more and more considerable tensions resulting from bending and torsion on the cervical column. An extreme result of this trend is well exemplified in *Tanystropheus* spp., which among known tanystropheids possessed the (absolutely and relatively) longest neck and vertebrae. The cervicals of this animal demonstrate a higher degree of modification than its stratigraphically older or contemporaneous relatives (e.g. '*P*'. *antiquus*; compare Figs 1 and 2), exhibiting a centrum structured as a cylinder of dense parallel-fibred bone, devoid of trabeculae, and with a triangularly-ellipsoidal transverse cross section. The decrease of the amount of bony trabeculae in the middle section of the vertebra was not an apomorphy of *Tanystropheus* spp., but rather a character that was widespread among tanystropheids, which *Tanystropheus* spp. only expanded on. Although the cervicals of *Tanystropheus* spp. are substantially longer than in other tanysaurians, their internal anatomy does not seem to correlate with further bone mass reduction, but rather achieving a more resistant cylindrical outline of the centrum. Overall, it should be noted that if the tanysaurian vertebrae were adapted for minimizing mass, the adaptation was probably in the material properties (especially the densities) of its compact bone and marrow, and not in the overall construction of the vertebrae, in contrast to the very light, pneumatic vertebrae of pterosaurs and saurischian dinosaurs.

Relationship of cervical anatomy to lifestyle in *Tanystropheus* spp.

Recent studies have nearly unequivocally supported a (semi) aquatic lifestyle for *Tanystropheus* spp. (Nosotti 2007, Renesto and Saller 2018, Spiekman *et al.* 2020a, b, Spiekman and Mujal 2023), but the lightly built cervicals of those animals could seem, at least at first glance, to contradict this hypothesis. The vertebrae of secondarily aquatic tetrapods such as cetaceans, ichthyosaurs, plesiosaurids, and mosasaurids are filled with dense trabecular bone and lack large open chambers (Dumont *et al.* 2013, Houssaye *et al.* 2016, 2018, Sander and Wintrich 2021). The cervicals of *Tanystropheus* spp. do not show internal vertebral microanatomy similar to fully aquatic tetrapods, and they also seem to lack the skeletal osteosclerosis, pachyostosis, or increased bone porosity in cortical bone that are present in numerous aquatic taxa, depending on the animal's lifestyle and habitat (Houssaye 2009, Houssaye *et al.* 2016). However, in most semi-aquatic taxa (e.g. crocodylians), the internal vertebral organization is more similar to that in terrestrial animals (see Butler *et al.* 2012, Houssaye *et al.* 2016), so the lack of microanatomical characters traditionally associated with a (semi)aquatic lifestyle does not preclude it. Trachelosaurids, which are a sister group of tanystropheids (Spiekman *et al.* 2021, 2024a, b), exhibit a roughly similar (although considerably less elongate) cervical shape, and yet several taxa from this group are clearly extensively adapted to an aquatic lifestyle (Liu *et al.* 2017, Li *et al.* 2017b, Wang *et al.* 2023a, b, Spiekman *et al.* 2024a, b). Interestingly, a large internal cavity is present in the core of some of the vertebral centra of Triassic eosauropterygians, especially in nothosaurids (Broili 1915, Klein *et al.* 2019; A. Rytel, personal observations). This cavity is relatively smaller and less regular than the clear-cut internal cavities of tanystropheids, but, being ventrolaterally encompassed only by dense cortex, it follows similar patterns of reorganization and redistribution of the mass of the vertebra to its periphery (Klein *et al.* 2019). Some eosauropterygian vertebrae are similar to those of '*P*.' *antiquus* in their internal anatomy and layout of the cavities (compare Fig. 9A with Klein *et al.* 2019: fig. 1C). Eosauropterygians exhibited extensive adaptations to an aquatic lifestyle (Klein *et al.* 2016). Therefore, it is evident that the presence of a large internal cavity in the vertebrae does not necessarily indicate a terrestrial lifestyle for an animal; contrastingly, Klein *et al.* (2019) interpreted it as a potential paedomorphic adaptation to life in an aquatic habitat. This constitutes another example of anatomical characters shared by *Tanystropheus* spp. and sauropterygians, the others including the hyperelongation of the neck, teeth layout, and morphology, as well as the here-proven retainment of the intersegmental arteries in adult individuals. Notably, remains of *Tanystropheus* spp. are virtually always accompanied by remains of nothosaurids (A. Rytel, personal observations). Thus, convergent evolution of the mentioned features in tanysaurians and early sauropterygians might have been related to them adapting to similar, or even overlapping, habitats.

Extensive 'cervicalization' of the dorsal vertebrae throughout the evolution of *Tanystropheus* spp. resulted in only 12 dorsals being present in the vertebral column of this animal (Rieppel *et al.* 2010, Rytel *et al.* 2024). This number is very low for a non-avian archosauromorph (see supporting information in Müller *et al.* 2010, Rytel *et al.* 2024), possibly the lowest among non-archosauriform members of the Archosauromorpha, matched solely by *Pectodens zhenyuensis* Li, Fraser, Rieppel, Zhao & Wang, 2017 (Li *et al.* 2017a). Therefore, the trunk of *Tanystropheus* spp. was not only short when compared to its neck, but generally composed of relatively few vertebrae. With the decrease of the number of dorsals and the shoulder girdle shifting its location along the body axis, the position of the centre of body mass was almost certainly also affected. The elongate cervicals, together with the bundles of nearly completely avascular cervical ribs (Jaquier and Scheyer 2017), might have contributed to the weight of the anterior portion of the body in a major way. Some researchers have suggested that the neck of *Tanystropheus* spp. was lightly built, due to the 'hollowness' of the cervicals, and thus allowed for locomotion on land (Renesto 2005, Renesto and Saller 2018). However, the tubular anatomy of these vertebrae does not have to equate to their light weight, taking into consideration their relatively high compactness. Correspondingly, extant birds and bats exhibit relatively heavy skeletons (compared to volume) that are resistant to stress, despite their delicate, slender appearance, and hollow, thin walled long bones (Dumont 2010). Tanysaurians may serve as another, well-fitting example of this phenomenon. Importantly, anterior displacement of the centre of mass relative to its position in terrestrial ancestors is one of the key adaptations to an aquatic lifestyle in non-avian tetrapods (Motani and Vermeij 2021). Thus, the increase of cervical vertebrae count and length, when compared to other tanystropheids (Rytel *et al.* 2024), could be interpreted as an adaptation correlated with the transition to an aquatic environment. However, further studies taking into account the physical properties of the cervicals of the early diverging archosauromorphs are needed to fully explore this hypothesis.

CONCLUSION

In his original description of *Tanystropheus* '*conspicuus*' von Meyer (1847–1855) summarized his hypothesis on the neurology of its vertebral column as follows: 'It is hardly conceivable that a contraption like the one to which the fossil vertebrae [of *Tanystropheus conspicuus*] point should stand alone and have only existed in a prehistoric animal' [translated from German]. Contrastingly, research presented herein demonstrates that the cervicals of some tanysaurians, especially *Tanystropheus* spp., are characterized by anatomical features that are unparalleled in any other animals known. Morphology (both external and internal) of these vertebrae is unique among vertebrates, with some extinct groups (e.g. azhdarchid pterosaurs, sauropods, sauropterygians) being the most comparable. Strikingly, evolution of an anatomical modification of such a considerable extent and intensity proceeded quickly—in the time shortly after (< 10 Mya) the End-Permian Extinction, underlining the fast pace of morphological diversification of archosauromorphs during this period (Foth *et al.* 2016, Ezcurra and Butler 2018). The unique Bauplan of *Tanystropheus* spp. is a result of extreme evolutionary trade-offs between cervical length, weight, and durability, induced by a selective pressure towards the transition to an aquatic lifestyle, but constrained by developmental and structural limitations. Interestingly, the hyperelongation of the neck vertebrae was not shared by all tanysaurians—in trachelosaurids, the sister group of tanystropheids, an entirely different strategy of neck elongation is exhibited. This is well exemplified in *Dinocephalosaurus orientalis*, a taxon much more extensively adapted to the aquatic lifestyle, which possessed over 60 presacral vertebrae (with only 25 in *Tanystropheus* spp.). Our findings provide further insights into the remarkable disparity of evolutionary innovations connected with neck elongation in early archosauromorphs.

While in '*P*.' *antiquus* some trabecular support structures are present within the cervical centra, they are absent in the middle neck vertebrae of *Tanystropheus* spp.—with the latter being nearly perfectly cylindrical in transverse cross section. This tubular architecture, together with the high compactness of the bone walls in the cervicals of both studied taxa, provided durability and forced rigidity of the vertebral column. The large internal cavities present in these vertebrae were filled with soft tissue, most probably bone marrow. Some tanysaurians were similar to long-necked avemetatarsalians in lightening of their elongate cervicals. Interestingly, they did so not through vertebral pneumatization, but rather by evolving a large internal cavity in the centrum, resulting in hollow, cylindrical vertebrae, morphologically unique among vertebrates. *Tanystropheus* serves as an extreme example of this feature, exhibiting major modifications of not only general vertebrae morphology, but also their histology and associated soft tissue layout. Especially noteworthy is the persistence of the intersegmental arteries in the cervicals of adult individuals of *Tanystropheus* spp., a unique feature among archosauromorphs. This character, together with the presence of the large internal cavity within vertebrae, is shared with sauropterygians, revealing some potential parallels in their evolution and convergent adaptation to an aquatic lifestyle in these groups.

The internal morphology of the cervicals of non-tanysaurian early archosauromorphs should be further explored to trace the evolution and development of the internal chambers within them, as well as their potential connection with the origin of bone pneumaticity in avemetatarsalians.

SUPPORTING INFORMATION

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

Table S1. List of the studied specimens, including the sampling methods.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY

CT data, specimen models, and photographs used in this study are available on MorphoSource: https://www.morphosource.org/projects/000661974

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