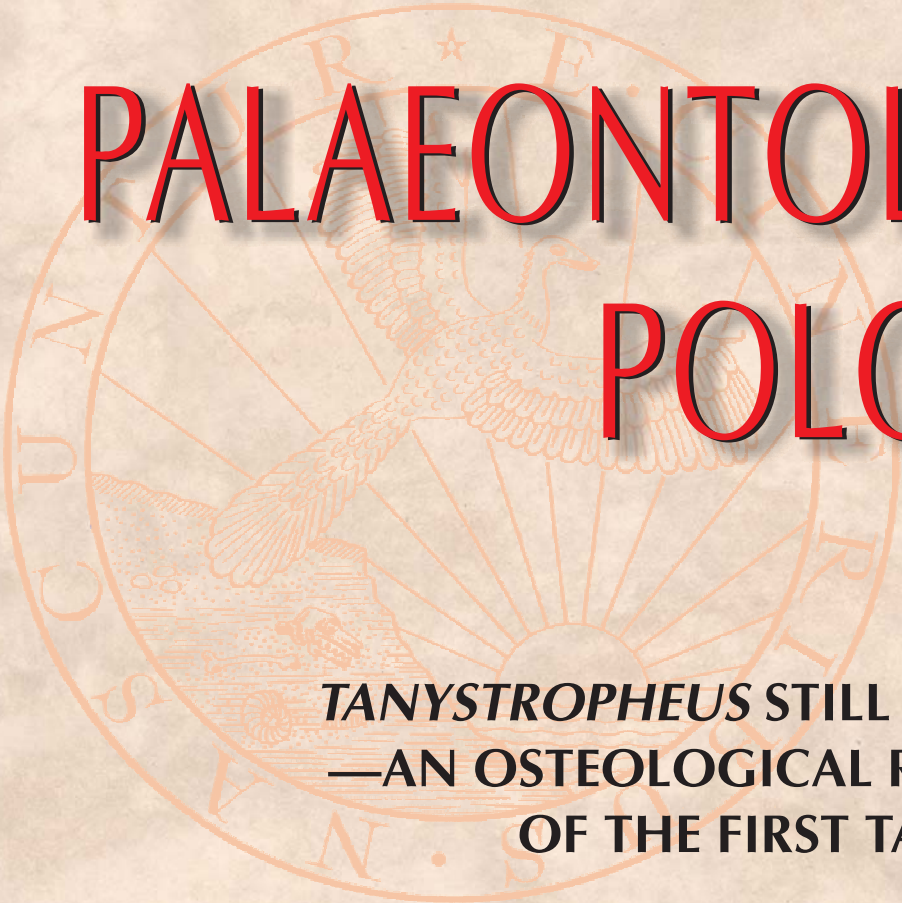


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Adam Rytel

***TANYSTROPHEUS* STILL CONSPICUOUS
—AN OSTEOLOGICAL REDESCRIPTION
OF THE FIRST TANYSTROPHEID**

Edited by Daniel E. Barta

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Tanystropheus still conspicuous—an osteological redescription of the first tanystropheid

ADAM RYTEL



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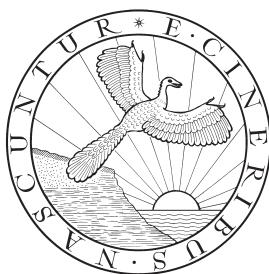
Archosauromorphs were the dominant clade of terrestrial vertebrates during the Mesozoic. Extant birds and crocodilians represent only a small remnant of the diversity of this lineage preserved within the fossil record. Especially in the Triassic, following the end-Permian mass extinction, archosauromorphs rapidly diversified into various forms with striking anatomical characteristics and disparate modes of life. Among these are the long-necked tanysaurians, which include the remarkable *Tanystropheus*, characterised by its extreme body proportions. Unlike other long-necked reptiles, it has relatively few cervical vertebrae, which are, however, extraordinarily elongated instead, resulting in morphology unseen in any other vertebrate. These elements, together with rod-like cervical ribs, form a bauplan that puzzled researchers for over a century. Its habitat, hunting strategy, and lifestyle have long remained enigmatic, due to the best preserved specimens being diagenetically flattened and spatially limited to the Monte San Giorgio area (Italy/Switzerland) and China. Despite its long history of research, functional anatomy and ecology of *Tanystropheus* remained poorly understood. The recent discovery of a diverse Ladinian vertebrate assemblage site in Miedary, Poland, has transformed this situation. The new material includes the remains of at least twenty individuals of *Tanystropheus*, both three-dimensionally isolated elements and articulated portions of several skeletons that together comprise most of the skeleton. These discoveries offer a unique opportunity to reassess the anatomy, taxonomy, and environmental preferences of *Tanystropheus*. Herein, the osteology of *Tanystropheus conspicuus* is described in detail, including the first unambiguous cranial remains referred to this species, providing valuable insights into its biology. Due to taphonomical and depositional characteristics of the material, Miedary serves as a good proxy for reconstructing the habitat of this animal. *Tanystropheus* is confirmed to have been an aquatic ambush predator that hunted in shallow nearshore settings.

Key words: Archosauromorpha, Tanystropheidae, Central European Basin, Middle Triassic, Anisian, Ladinian, Poland.

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Introduction

Archosauromorphs were the dominant clade of terrestrial vertebrates during the Mesozoic. They had a diverse size range, evolved into a plethora of lineages with disparate ecological characteristics, and gained a virtually global spatial range of occurrence (Foth et al. 2016; Ezcurra and Butler 2018; Ezcurra et al. 2020). Extant archosauromorphs, birds and crocodylians, despite being evolutionarily successful and diverse, represent only a fraction of the previous diversity of the clade. These forms are members of Archosauriformes, which was the only clade of archosauromorphs surviving to the Jurassic. Although in the Triassic the archosauriforms were already the dominant archosauromorph group, non-archosauriform archosauromorphs also spread quickly and diversified into several distinct lineages, each characterised by the presence of highly derived anatomical traits (Foth et al. 2016; Ezcurra and Butler 2018; Ezcurra et al. 2020). These included the allokotosaurians, mostly herbivorous, stoutly built land dwellers; the rhynchosaurians, a group of relatively small, stocky, herbivorous reptiles; and lastly, the tanysaurians, which were long-necked and ecologically extremely diverse (Ezcurra 2016; Foth et al. 2016; Ezcurra and Butler 2018; Ezcurra et al. 2020; Spiekman et al. 2021, 2024b). Tanysauria comprises two families, Tanystropheidae Gervais, 1859, and Trachelosauridae Abel, 1919. Whereas extensive adaptations to an aquatic lifestyle are extremely rare among archosauromorphs throughout their entire history, intriguingly in the Middle Triassic such adaptations appear separately in both groups of the Tanysauria—in the tanystropheid *Tanystropheus* von Meyer, 1849, and convergently in the trachelosaurids *Dinocephalosaurus* Li, 2003, and *Trachelosaurus* Broili & Fischer, 1918 (Wild 1973; Li et al. 2004; Nosotti 2007; Rieppel et al. 2008; Spiekman et al. 2020a, b, 2024b, c). This further underlines the fast pace of diversification and acquisition of specialised anatomical traits in the early-branching archosauromorphs during the Early and Middle Triassic (Foth et al. 2016). *Tanystropheus* and its relatives are, therefore, important taxa, which can help us understand the dynamic evolutionary changes taking place during this period.

Tanystropheus is an animal that in the past has been the subject of special interest for the scientific community (see bibliography in the synonymy section below), due to its peculiar bauplan. The elongate neck constitutes nearly half of the total body length of some individuals (Wild 1973; AR personal observation). Whereas similar proportions have appeared convergently in several other reptile groups (sauropterygians, choristoderans, trachelosaurids), in all of them the presacral vertebrae count increased (Rytel et al. 2024a). In tanystropheids this number seems to have been constrained to 25, and hence in *Tanystropheus* the neck elongation proceeded mostly via the elongation of the cervical vertebrae and the “cervicalisation” of some of the dorsal vertebrae (Wild 1973; Rytel et al. 2024a). The cervical vertebrae of *Tanystropheus* reached proportions un-

seen in any other animal, being superficially similar to limb bones. They were associated with straight, rod-like cervical ribs, which extended posteriorly across several succeeding intervertebral articulations. This cervical anatomy is unparalleled among known vertebrates, including both terrestrial and aquatic long-necked reptiles (Rytel et al. 2024a). This resulted in difficulties in deciphering the lifestyle of *Tanystropheus*. Moreover, the studies on *Tanystropheus* have been severely constrained due to the nature of its preservation—isolated three-dimensionally preserved bones were scarce, usually fragmentary, and of limited element diversity, whereas the relatively complete and articulated skeletons were compressed and often essentially two-dimensional. This contributed to the difficulties in understanding its unique bauplan and resulted in *Tanystropheus* being considered “enigmatic”, despite a very long history of research.

The first species of *Tanystropheus*, *Tanystropheus conspicuus* von Meyer, 1852, was described based on isolated cervical vertebrae from present-day Germany and Poland, which were then considered to likely be caudal vertebrae (von Meyer 1847–1855). It was not until the 1930s that the true identity of these elements was revealed by the articulated specimens of *Tanystropheus hydroides* Spiekman et al., 2020a, and *Tanystropheus longobardicus* (Bassani, 1886), recovered from the Besano Formation of Monte San Giorgio (Italy/Switzerland; Peyer 1930, 1931). Later studies predominantly focused on this material, culminating in the monograph of Wild (1973), which served as the basis for most of the studies on *Tanystropheus* for over half a century. Whereas the contribution of Wild (1973) to understanding and illustrating the osteology of *Tanystropheus* is indisputable, the comparative part of this work has become largely outdated. Wild (1973) considered tanystropheids as squamates, but they are now unequivocally regarded as archosauromorphs, with many new forms closely related to *Tanystropheus* being described in the interim (Evans 1988; Ezcurra 2016; Spiekman et al. 2021). The discovery of aquatic trachelosaurids, a sister group to tanystropheids, is especially worthy of notice in that context (Li 2003; Spiekman et al. 2021, 2024b, c). The bauplan of these animals demonstrates that some archosauromorphs were able to adapt well to life in Middle Triassic marine environments, evolving flipper-like limbs, viviparity and serpentine vertebral columns (Li 2003; Li et al. 2017; Liu et al. 2017; Spiekman et al. 2024b, c).

Since the publication of Wild (1973) further studies have brought to light new details on the postcranial anatomy of *Tanystropheus*, but they were all hampered by the relatively two-dimensional preservation of the novel specimens which are diagenetically flattened or still partially embedded in matrix (Wild 1980a; Renesto 2005; Li 2007; Nosotti 2007; Rieppel et al. 2010). The isolated bones of *Tanystropheus* sp. found in Canada (Sues and Olsen 2015), Hungary (Ősi et al. 2020), Israel (Peyer 1955; Rieppel 2001), Italy (Dalla Vecchia 2000, 2006, 2008;

Dalla Vecchia and Avanzini 2002; Dalla Vecchia and Simonetto 2018), Romania (Jurcsak 1973, 1975, 1978), and Saudi Arabia (Vickers-Rich et al. 1999) have provided additional insight into the spatiotemporal distribution of the genus, as well as some ontogenetic and morphological aspects, but this material was not found to be diagnostic because these parts of the postcranium were considered to exhibit a lot of intraspecific variation (Spiekman and Scheyer 2019). Previously there were also no cranial elements of *Tanystropheus* known from outside of the Monte San Giorgio region (Peyer 1931; Wild 1973, 1980a; Nosotti 2007; Spiekman et al. 2020b). Wild (1973) stated that *T. conspicuus* might be conspecific with *T. longobardicus* (and *T. hydroides*), but this can only be confirmed or refuted after more of the material of the former species is reported. With virtually no diagnostic remains of *T. conspicuus* having been reported in the subsequent period, Spiekman and Scheyer (2019) considered it a nomen dubium.

The discovery and description of the new site in Miedary (Upper Silesia, southern Poland) provided an unprecedented opportunity for the further meaningful studies of *Tanystropheus*, in particular *T. conspicuus* (see Czepiński et al. 2023). At this locality, remains of at least 20, predominantly large (i.e., ontogenetically mature) individuals of *Tanystropheus* were excavated, together with some scarce remains of juveniles and subadults. The abundant and diverse remains from Miedary permit for a broad analysis of three-dimensionally preserved specimens of *Tanystropheus*. Previously the majority of postcranial elements of *Tanystropheus* could have not been studied from this perspective. Of particular interest are the bones comprising the transitional cervico-dorsal region of the skeleton, as this region of the body was not well preserved in accessible specimens, and it is key to understanding the role and mobility of the neck. Moreover, cranial remains of *T. conspicuus* have been identified for the first time. Due to the presence of articulated and three-dimensionally preserved remains, the material from Miedary allows us not only to examine the osteology of most of the skeleton of *T. conspicuus*, but also combines the preservation characteristics of isolated finds from around the world and the diagenetically flattened individuals of *Tanystropheus* from Monte San Giorgio and China, constituting a key to their future comparisons, and further analyses.

The aim of this study is to: (i) analyse the currently accessible material of *Tanystropheus*, with an emphasis on the Miedary material, and carry out an osteological redescription of *T. conspicuus*; (ii) compare the material of *T. conspicuus* to other species of *Tanystropheus* and establish the taxonomic status of the former; (iii) interpret the functional anatomy of *Tanystropheus* based on the new three-dimensional material, and elucidate some enigmatic aspects of its biology, including its mode of life, its habitat and the role of the extremely elongated neck; (iv) explain the unexpected abundance of remains of *T. conspicuus* in the Miedary site.

Institutional abbreviations.—BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany; FG, Geowissenschaftliche Sammlungen, Technische Universität Bergakademie Freiberg, Germany; GG, Institut für Geographie und Geologie der Universität Greifswald, Germany; GMPKU, Geological Museum of Peking University, Beijing, China; GPIH, Geologisch-Paläontologischen Sammlungen, Leibniz-Institut zur Analyse des Biodiversitätswandels, Hamburg, Germany; GPIT, Geologisch-Paläontologisches Institut, Universität Tübingen, Germany; GPUL, Geologisch-Paläontologische Sammlung, Universität Leipzig, Germany; GZG, Geowissenschaftlichen Zentrum, Georg-August-Universität Göttingen, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MFSN, Museo Friulano di Scienze Naturali, Udine, Italy; MCSN, Museo Cantonale di Scienze Naturali, Lugano, Switzerland; MAN, Muséum-Aquarium de Nancy, France; MB, Museum für Naturkunde Berlin, Germany; MHI, Muschelkalk Museum Hagdorn, Ingelfingen, Germany; MLU, Geologisch-Paläontologischen Sammlungen, Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany; MNG, Museum der Natur Gotha, Germany; MNM, Museum für Naturkunde Magdeburg, Germany; MSBO, Museum am Schöler Berg für Natur und Umwelt, Osnabrück, Germany; MSNM, Museo di Storia Naturale, Milan, Italy; Muz. PGI-NRI, Polish Geological Institute Geological Institute-National Research Institute, Warsaw, Poland; NHMS, Naturhistorisches Museum Schleusingen, Germany; NHMUK, Natural History Museum, London, UK; NHMW, Naturhistorisches Museum Wien, Austria; NME, Naturkundemuseum Erfurt, Germany; NMK, Naturkundemuseum Kassel, Germany; PIMUZ, Paläontologisches Institut der Universität Zürich, Switzerland; PMJ, Phyletisches Museum Jena, Germany; PMU, Museum of Evolution, Uppsala University, Sweden; RE, Ruhr Museum Essen, Essen, Germany; SMF, Senckenberg Naturmuseum Frankfurt, Frankfurt a. M., Germany; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; SNSD, Senckenberg Naturhistorische Sammlungen Dresden, 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; WMNM, LWL-Museum für Naturkunde, Münster, Germany; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—CEB, Central European Basin; CT, computed tomography; ICZN, International Commission on Zoological Nomenclature; SEM, scanning electron microscope.

Historical background

Several elongate vertebrae were collected from the Upper Muschelkalk of the area around Bayreuth (Upper Franconia, Germany) in the first half of the 19th century (Fig. 1). Originally some were stored in the collection of Count Georg zu Münster, whereas others were repositied in the local state-owned collection in Bayreuth. Although some of the latter specimens were already illustrated by Braun (1840), their first description was incorporated within the voluminous monograph of von Meyer (1847–1855). While working on this publication, Hermann von Meyer had access to several other collections, including the specimens collected by Carl Mentzel from the Muschelkalk localities in Upper Silesia (present-day Poland), which were partially published in a separate work (von Meyer 1849). The material from Silesia contained an elongate vertebra (MB.S. 11, Fig. 1E) that, together with eight specimens from Franconia, served as a basis for a description of the genus *Tanystropheus* von Meyer, 1849, and its type species *Tanystropheus conspicuus* von Meyer, 1852. U-MO BT 3079, a humerus from Bayreuth was also illustrated by Braun (1840) and von Meyer (1847–1855), but first referred to *T. conspicuus* by Diedrich (2012); hence only the nine elongate cervical vertebrae constitute the type series of *T. conspicuus* (see SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Rytel_SOM.pdf). Another cervical vertebra from the Silesian Upper Muschelkalk of Laryszów (formerly Larischhof) was reported by Langenhan (1903, 1911). Skawiński et al. (2017) suggested that more than one syntype of *T. conspicuus* originated from Silesia, and that MB.S. 11 might have been gathered from the Lettenkeuper strata of Miedary instead, but Czepiński et al. (2023) saw no clear evidence for these claims and considered Miedary a newly discovered locality.

Some additional individual vertebrae of *T. conspicuus* (see SOM: table 1) were reported by Broili (1915), Edinger (1924), Peyer (1931), Lang and von Huene (1952), Adam (1953), Spiekman and Scheyer (2019), and Schwermann et al. (2025). The overwhelming majority of the historic specimens referred to *T. conspicuus* were described in various publications authored by Friedrich von Huene. Von Huene (1902) erected several new reptile taxa based on the isolated remains from the Upper Muschelkalk–Lower Keuper strata of Germany. These included: *Procerosaurus cruralis*, based on a large isolated femur GPIT-PV-60009; *Pectenosauros strunzi*, represented by a partial vertebra (GPIT-PV-60014); and a new testudine genus *Chelyzoon*, encompassing two species, *Chelyzoon blezingeri* and *Chelyzoon latum*, both based on singular isolated vertebrae (with SMNS 8728 being the holotype of *Chelyzoon blezingeri*). The type specimens of *Procerosaurus cruralis*, *Chelyzoon blezingeri*, *Chelyzoon latum*, and a “sauropterygian” sacral vertebra of von Huene (1902: 45; GPIT-PV-60011) were regarded as belonging to *T. conspicuus* by Wild (1973). The vertebra of *Pectenosauros strunzi* was referred to *Tanystropheus* by Kuhn (1963) and

to *T. conspicuus* by Spiekman and Scheyer (2019). Thus, four of the taxa erected by von Huene (1902) were at some point considered subjective junior synonyms of *T. conspicuus*, although Spiekman and Scheyer (2019) mentioned that the type specimens of both species of *Chelyzoon* appear to be morphologically disparate from the known vertebrae of *Tanystropheus*. Von Huene (1907–1908) described some previously unpublished vertebrae of *T. conspicuus*, including a cervical vertebra originating from present-day France (see SOM: table 1), and erected several new taxa of what he considered dinosaurs. These included a second species of *Tanystropheus*, *Tanystropheus antiquus* (herein not considered a species of *Tanystropheus*; see Rytel et al. 2024b for the most recent comment on the status of this taxon), and *Thecodontosaurus latespinatus*, with the type series for both consisting solely of isolated vertebrae. The temporal and spatial ranges of occurrence for the latter species have largely overlapped with *T. conspicuus*.

After the articulated skeletons from Monte San Giorgio were described by Peyer (1931), von Huene (1931) reevaluated the previous interpretations of the material from the Central European Basin (CEB; also known as the Germanic Basin), stating that the vertebrae of *Zanclodon laevis*, the holotype of *Procerosaurus cruralis* and the entirety of the material assigned to *Thecodontosaurus latespinatus* should likely be referred to *Tanystropheus*. *Zanclodon laevis* Plieninger, 1846a, was described on the basis of several isolated elements, of which only the lectotype jaw fragment (not belonging to *Tanystropheus*) survives to this day (see Plieninger 1846a, b; Wild 1973; Schoch 2011). Wild (1973) concurred with von Huene (1931), synonymising *Procerosaurus cruralis* and *Thecodontosaurus latespinatus* with *T. conspicuus*, referring all the described material to the latter species, together with three other vertebrae from the Upper Muschelkalk/Lettenkeuper (see SOM: table 1) illustrated by von Huene (1931). Moreover, Wild (1973) provided a discussion on the status of *Zanclodon laevis* and deemed a part of its type series, the two lost vertebrae, to likely belong to *T. conspicuus*. Von Huene (1920b) described a humerus, SMF R 4034, found near Bayreuth, and interpreted it as belonging to a “parasuchian”. Wild (1973) also referred this specimen to *T. conspicuus*. A specimen of similar morphology served as the basis for the description of *Megacnemus grandis* von Huene, 1954. Von Huene (1954) interpreted the relatively large (216 mm in length) limb bone as a femur of a new “protorosaurian”. Skawiński et al. (2015) pointed out that the specimen represents a humerus, rather than a femur, and that its morphology is nearly identical to the humeri of tanystropheids. Unfortunately, the specimen lost its original label during the Second World War, making its taxonomic interpretation difficult, due to the lack of stratigraphic and topographic data.

Corroy (1928) described a partial articulated hindlimb, originating from the Upper Muschelkalk of Mont-sur-Meurthe (France), that he referred to *Thecodontosaurus latespinatus*. Following the original interpretation, the spec-

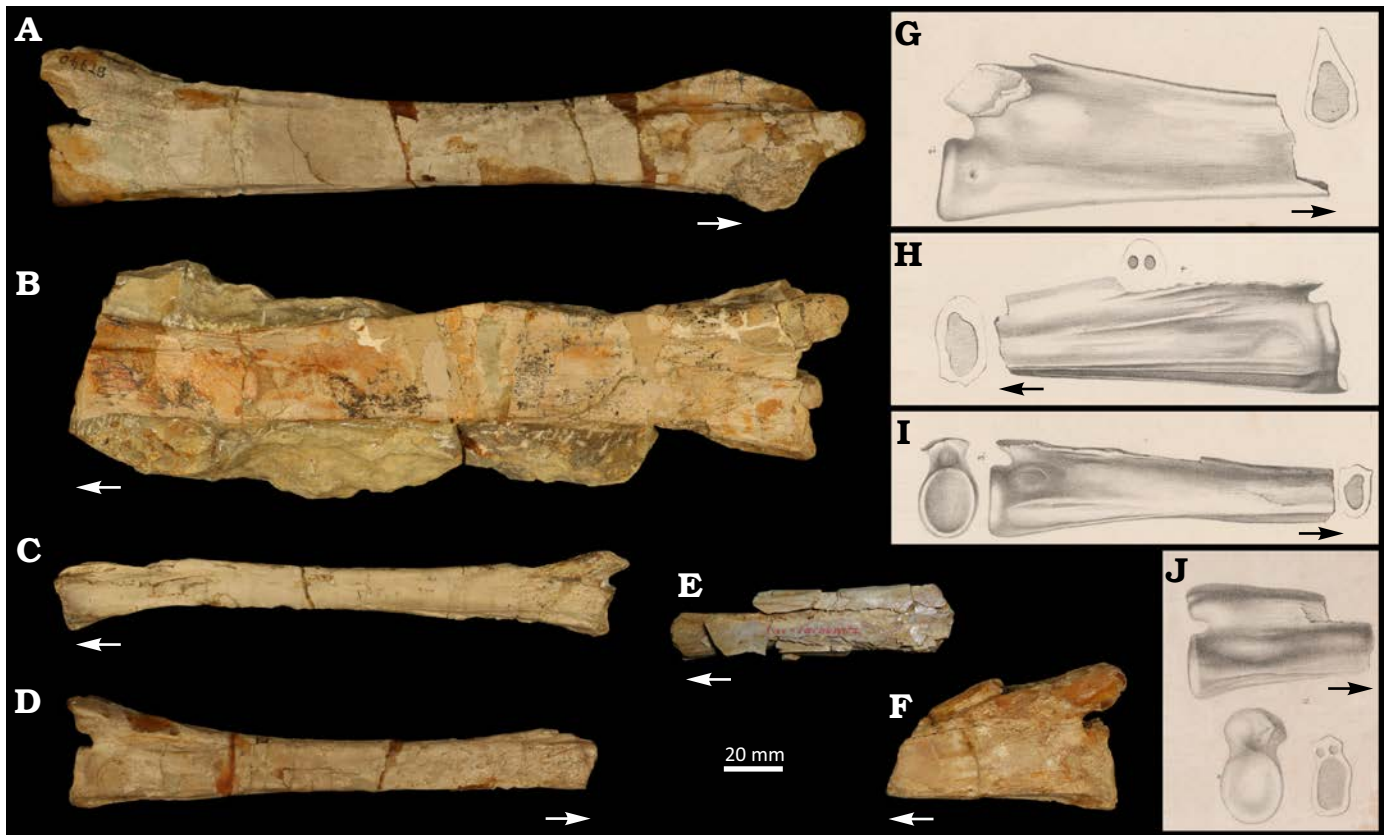


Fig. 1. The type series of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Upper Muschelkalk (upper Anisian, Middle Triassic) of Bayreuth, Germany (A–D, F–J) and Laryszów, Poland (E). Photographs (A–F), lithographs (G–J). Ten middle cervical vertebrae in right (A, D, G, I, J) and left (B, C, E, F, H) lateral views. A. U-MO BT 740, the lectotype. B. U-MO BT 737. C. U-MO BT 732. D. U-MO BT 733. E. MB.S.11. F. U-MO BT 734. G–J. The four lost specimens illustrated in von Meyer 1847–1855 (G–I, pl. 46: 2–4; J, pl. 30: 6). Arrows indicate anterior direction.

imen preserved a distal end of a femur, a fibula, and a potential tibia. It was stored at the University of Strasbourg, and later at the Museum and Aquarium Nancy under the number MAN 2016.0.213, but its current location is unknown (Thibaut Keinerknecht, personal communication 2023). Wild (1973) and Spiekman and Scheyer (2019) considered the partial limb bone to belong to *T. conspicuus*, but this hypothesis cannot be fully corroborated for as long as the specimen remains missing.

Teeth of *Tanystropheus* were described for the first time by Fraas (1896), who erected a new species of *Nothosaurus*, *Nothosaurus blezingeri*, on the basis of several isolated teeth (currently under a joint specimen number SMNS 52478) collected from the Grenzbonebed near Crailsheim (Germany) by Richard Blezinger. Fraas (1896) noted the similarity between the tooth morphology of the new species and that of *Pistosaurus grandaevus* von Meyer, 1855, a junior synonym of *P. longaevus* von Meyer, 1839 (see Sues 1987). Additional isolated teeth (MAN 2016.0.201 and MAN 2016.0.202) were described from the Muschelkalk localities of Lorraine (France) by Corroy (1928), who regarded *N. blezingeri* as a junior synonym of *P. grandaevus*. Finally, the teeth of *N. blezingeri* were considered to belong to *Tanystropheus* by Rieppel and Wild (1996) and Rieppel (2000). Schoch et al. (2018) were the first to delineate the morphological differ-

ences between the teeth of *Tanystropheus* and *Nothosaurus*, describing both morphotypes in more detail.

Wild (1973) summarised the state of knowledge on the genus *Tanystropheus* in an extensive monograph, providing a description of both historic and novel material, synonymy lists, diagnoses and establishing the types for each of the species of *Tanystropheus*. U-MO BT 740, one of the original specimens of von Meyer (1847–1855) was designated as the lectotype of *T. conspicuus*. More recently, several unpublished isolated bones and teeth of *T. conspicuus* from Germany (see SOM: table 1) were mentioned or illustrated in the studies of Diedrich (2009: fig. 12, 2015: fig. 10C.2), Ezcurra et al. (2014: figs. 16D, 18C), Ezcurra (2016: figs. 14a, b, 33b), Jaquier and Scheyer (2017), Spiekman and Scheyer (2019: supp. tab. 1), and Schwermann et al. (2025) but were not described osteologically. Spiekman and Scheyer (2019) expanded the work of Wild (1973), providing the most up-to-date list of known specimens referred to this species, including their historic background and the current location of individual elements.

Sites in Germany remained the main source of material of *T. conspicuus* for the last century, until the Miedary fauna was reported by Czepiński et al. (2023), which provided a description of a vertebra referred therein to *Tanystropheus* sp. Several more isolated cervical vertebrae from this site were analysed in the studies of Rytel et al. (2024a, b). Until now,

however, only a fraction of the total *Tanystropheus* material excavated in Miedary had been published. Consequently, the hypodigm of *T. conspicuus* was restricted to postcranial remains (vertebrae, humeri, femora) and some tentatively referred teeth, in sum a little over 100 individual elements, of which roughly only one half has been described.

Material and methods

To assess the presence of specimens referable to *Tanystropheus conspicuus* based on personal observations, I visited collections in Austria, Germany, Poland, Switzerland, and the United Kingdom. Therein, I have collected topographic and stratigraphic data for each element, the literature sources referring to it, as well as some morphometric measurements. These data are contained within the SOM: table 1, which also includes a list of specimens that are currently lost or no longer considered to belong to *T. conspicuus*. Three-dimensional models of all specimens of *T. conspicuus* from Miedary illustrated herein have been uploaded to MorphoSource, where they can be accessed: <https://www.morphosource.org/projects/000774422>.

The novel specimens from Miedary were collected during annual excavations coordinated by the Institute of Paleobiology, Polish Academy of Sciences, and the Institute of Evolutionary Biology, University of Warsaw, during the 2014–2024 field seasons. The material originated mostly from the M2, but also the M1 and M4 layers of Unit 1 of Czepiński et al. (2023). No fossils from the M3 layer, or the strata overlaying Unit 1 in the Miedary site, can currently be referred to *Tanystropheus*. The excavated remains were treated with cyanoacrylate adhesive and secured with plaster jackets to ensure the structural stability of the fossils during transport. Their preparation was carried out mainly with pneumatic needles.

Due to the lack of in situ association, an overwhelming majority of the analysed specimens could not be confidently regarded as originating from the same individual. Only a few articulated finds preserve larger portions of a skeleton. Isolated elements of *T. conspicuus* that were not a part of these associations, nor directly comparable with them, were identified based on morphological similarity with the largely complete individuals of *T. hydroides* and *T. longobardicus*. Only specimens presenting the original morphology most closely (i.e., the most complete and/or least distorted examples of each respective element) were illustrated, but the descriptions of individual skeletal elements are based on all accessible material.

Simple measurements were taken from all bones referred to *T. conspicuus* preserving at least one of the measured characteristics. For the anterior postaxial cervical vertebrae these included: maximum total length (the distance between the distal tips of corresponding zygapophysis and epipophysis), centrum length, height at mid-point, and maximum height (see further below). The same

measurements were taken for other postaxial vertebrae, except for height at mid-point, as it is roughly equal to their maximum height. For non-vertebral elements only two characters were measured: maximum length and maximum height. All measurements were recorded using digital callipers with an original resolution of 0.1 mm, rounded to the nearest half millimetre up. Photographs of ZPAL V. 36/584 were taken with a NIKON D5 camera, whereas all other photographs presented here were taken with a NIKON D5300 camera by the author.

Computed tomographic (CT) scans were generated for the maxilla ZPAL V. 36/1213 and the skull roof ZPAL V. 36/1244. To obtain the serial images of these specimens, a GE phoenix v|tomex|m device (GE Sensing and Inspection Technologies Phoenix|x-ray, Wunstorf, Germany) located in the Laboratory of X-ray Computed Tomography, Department of Geomechanics, Civil Engineering and Geotechnics, AGH University of Kraków, Poland, was used. For ZPAL V. 36/1213 it was operating at a voltage of 200 kV and a tube current of 240 μ A, acquiring 3000 projections. For ZPAL V. 36/1244 voltage was set to 190 kV and tube current to 190 μ A, and 2600 projections were generated. The spectrum was hardened with an additional copper filter. Isometric voxel size for both specimens equalled 0.07499975 mm. Avizo Lite 2020.3.1 (Thermo Fisher Scientific, USA) was used to create the models of individual bones. The surface of the ZPAL V. 36/1213 model was smoothed and simplified in MeshLab v.2023.12 (Cignoni et al. 2008), using Scale Dependant Laplacian Smooth tool with default settings and Simplification: Quadric Edge Collapse Decimation tool, reducing the model surface to 200 000 faces.

Surface scans of the analysed specimens were obtained using a Shining 3D EinScan Pro 2X 3D scanner fixed on a tripod, located in ZPAL, with an EinTurntable and EXScan Pro 3.7.4.0 software. The morphological data was acquired by either using the Ein-Turntable (alignment based on features) or without a turntable, by scanning the specimen manually. The number of turntable steps was varied, chosen dependent upon the specimen. The models were meshed using the Watertight Model and Medium Detail presets. Due to the large size of the semiarticulated cervical series ZPAL V. 36/100, its model was acquired through photogrammetry.

Snapshots of the models of specimens illustrated in the figures were captured in MeshLab v.2023.12 using the Save snapshot tool in orthographic view, with the “xray”, Lit Sphere Radiance Scaling or Lambertian Radiance Scaling shader enabled.

Scanning electron microscope (SEM) imaging was used to compare selected, well-preserved teeth of *T. conspicuus* (ZPAL V. 36/163, ZPAL V. 36/1204), *Nothosaurus* sp. (ZPAL V. 36/233, ZPAL V. 36/254), both from Miedary, and of *Pistosaurus* sp. (ZPAL V. 84/LA/001) from the Upper Muschelkalk of Laryszów (Poland). The non-sputtered samples were analysed in Low Vacuum mode and the water pressure in the SEM chamber was maintained at 50 Pa. The used Field Emission SEM was a Thermo Fisher Quattro

S Environmental Electron Microscope (ESEM located in ZPAL). The samples were mounted using conductive carbon tape adhesive and aluminium foil casing directly attached to a standard SEM stub. Large-area mapping was conducted using MAPS 3 software, which automates the acquisition of large overviews by stitching multiple images.

Following Rytel et al. (2024a, b) in the differentiation of the morphological subregions in the neck of *Tanystropheus*, I refer to the three last cervical vertebrae as “posterior”, and to the rest of the postaxial cervical vertebrae (three to ten) as “middle”. For the anatomical description I followed the terminology used by Ezcurra (2016) and Spiekman et al. (2021), with some minor differences. For example, when considering the vertebral elongation in archosauromorphs Ezcurra (2016) and Spiekman et al. (2021) used the ratio of centrum length to its anterior articular surface dorso-ventral height. However, in the articulated specimens the dorsal part of the anterior end of the centrum is usually obscured by the prezygapophysis and centroprezygapophyseal lamina (see Wild 1973, 1980a; Renesto 2005; Li 2007; Nosotti 2007; Rieppel et al. 2010). Instead, vertebral elongation is here defined as a ratio of centrum length to the height at the anteroposterior midpoint of the vertebra. This measurement can be taken consistently from virtually all complete *Tanystropheus* cervical vertebrae in lateral view. In the middle cervical vertebrae of *Tanystropheus* the maximal vertebral height is not reached near the midpoint of anteroposterior length due to the strong reduction of the neural spine here. Instead, the middle cervical vertebrae are taller near the anterior and posterior ends of the neural spine instead. To be able to quantitatively analyse this characteristic morphology, I recorded maximal height of complete vertebral specimens, and this was defined as the largest distance between the dorsal extent of the neural spine and the ventralmost point located on the ventral keel at same section of anteroposterior length of the vertebra (see SOM: table 1).

Systematic palaeontology

Class Reptilia Laurenti, 1768

Clade Archosauromorpha von Huene, 1946

Order Protorosauria Huxley, 1871

Clade Tanysauria Spiekman et al., 2024b

Family Tanystropheidae Gervais, 1859

Genus *Tanystropheus* von Meyer, 1849

Type species: *Tanystropheus conspicuus* von Meyer, 1852; Bindlacher Berg, Germany; Upper Muschelkalk, Upper Anisian.

Species included: *Tanystropheus hydroides* Spiekman et al., 2020a; *Tanystropheus longobardicus* (Bassani, 1886)

Former diagnosis.—The most recent former diagnosis was provided by Spiekman and Scheyer (2019): “Long-necked tanystropheid archosauromorphs distinguished from other genera by the following combination of characters (auta-

pomorphy among non-archosauriform archosauromorphs marked with an asterisk): (1) the absence of shagreen-like teeth on the vomers and palatines; (2) mid-cervical vertebrae with a vertebral centrum length more than 2.5 times their minimum height; (3) a low neural spine of the cervical vertebrae; (4) very long and extremely thin cervical ribs, being approximately three times the length of their corresponding vertebra in the mid-cervical region, bearing short free ending anterior processes; (5) ribs of second sacral vertebrae not bifurcated; (6) curved anterior margin of scapular blade, which is consequently directed posteriorly; (7) the absence of hyperphalangy; (8) only two ossified distal carpals*; and (9) a thyroid fenestra present between the pubis and ischium.”

Additionally, the phylogenetic analysis of Spiekman et al. (2021) found the following synapomorphies present within *Tanystropheus*: postaxial anterior or mid-cervical neural spines are only present at the anterior and posterior ends of the vertebrae but are completely or virtually lost at their anteroposterior midpoints; lengths of the fourth or fifth cervical centra versus the heights of their anterior articular surfaces between 14.58 and 15.58 or between 17.08 and 18.67; total length of the humerus versus the total length of the femur between 0.84 and 0.91.

Emended diagnosis.—Long-necked tanystropheid archosauromorph distinguished from other genera by the following combination of characters (autapomorphy among non-archosauriform archosauromorphs marked with an asterisk): (i) the absence of shagreen-like teeth on the vomers and palatines; (ii) ratio of centrum length of middle cervical vertebrae to height at midpoint of their anteroposterior length equal to or more than four, and in some specimens reaching more than 15*; (iii) neural spines of the third to ninth cervical vertebrae well outlined only in their anterior and posterior portions, and virtually completely reduced in the middle section of their anteroposterior length; (iv) one or two large subcentral foramina present on the ventral surface of the postaxial cervical vertebrae, near the mid-point of their anteroposterior length*; (v) very long and extremely thin cervical ribs, being approximately three to four times the length of their corresponding vertebra in the mid-cervical region, and bearing a distinct anterior free ending processes; (vi) curved anterior margin of scapular blade, which is directed posteriorly; (vii) absence of an ossified interclavicle; (viii) deltopectoral crest extremely reduced; (ix) presence of only two ossified distal carpals*; (x) a thyroid fenestra present between the pubis and ischium; and (xi) sexual dimorphism indicated by the presence of two pairs of elongate ossifications in the postcloacal region in individuals of one of the sexes.

Remarks.—The available generic name *Tanystropheus* was first mentioned in 1849 by von Meyer (1849), who attributed elongate vertebrae from Laryszów and Bayreuth to this animal. Following Article 11.4.1 of the International Commission on Zoological Nomenclature (ICZN 1999), this usage was valid, despite not being associated with any nominal species. Some of the soon-to-become syntypes from

Bayreuth were illustrated even earlier, by Braun (1840), but not named. The first comprehensive description encompassing the remains from both Franconia and Silesia was included in von Meyer (1847–1855), who introduced *T. conspicuus*, the type species of the genus. The investigation of Quenstedt (1963) has shown that this combination seems to have appeared in print in 1852, even though some of the plates including the lithographs of the type material could have been delivered as early as 1847 (contents of this publication were printed gradually, in instalments). According to Article 21.6 of the ICZN, 1852 is adopted as the year of publication containing the first valid usage of the specific name. Some authors (Broili 1915; Kuhn 1934) have argued that the genus name *Macroscelosaurus* Münster, 1834, has precedence over *Tanystropheus* von Meyer, 1852 (see Nosotti 2007). As a result of the requests of Wild (1975b, 1976b), the ICZN suppressed *Macroscelosaurus* Münster, 1834, and conserved the generic name *Tanystropheus* von Meyer, 1849 (Melville 1981). *Tanystropheus conspicuus* von Meyer, 1852 was designated as the type species by monotypy. Spiekman and Scheyer (2019) considered this species a nomen dubium, arguing that it is represented by material that is diagnostic on the genus level, but insufficient to distinguish it convincingly from other *Tanystropheus* species. The taxonomic status of *T. conspicuus* is further explored in this work, on the basis of the newly identified remains.

The authorship of family-group name Tanystropheidae was historically nearly unequivocally attributed to Gervais (1858) or Gervais (1859). Recently Spiekman et al. (2020a: supplemental information, methods S1) argued that this name does not appear in either of the two sources, but instead is mentioned for the first time in Camp (1945), with an incorrect spelling, as Tanystrophaeidae. According to ICZN Article 35.4.1, the emended name would be Tanystropheidae Camp, 1945. There are, however, at least two cases of older family-group names based upon synonyms of *Tanystropheus*, *Tribelesodontidae* von Nopcsa, 1923, and *Macroscelosauridae* Kuhn, 1934. As the type genus of the latter taxon has been suppressed (Melville 1981), this name is no longer valid, according to ICZN Article 39. *Tribelesodon* Bassani, 1886, was considered a junior synonym of *Tanystropheus* von Meyer, 1849 by Peyer (1930), and *Tribelesodontidae* von Nopcsa, 1923, has been in disuse since then. According to ICZN Article 40, Tanystropheidae Camp, 1945, should be maintained instead, due to its overwhelming prevailing usage, with *Tribelesodontidae* von Nopcsa, 1923, as its senior synonym. According to ICZN Recommendation 40A, the family-group name should be cited with its original author and date followed by the date of its priority, Tanystropheidae Camp, 1945 (1923). That is, if we consider the name used by Gervais (1859) as not valid. Gervais (1859: 485) mentions “*Les Tanystrophes*” as one of the extinct “reptile” families not yet observed in France (the list also included taxonomic names of relatively higher ranks: dicynodonts, rhynchosaurs, thecodontosaurs etc.), clearly using it as a scientific name to denote a supra-

generic taxon. Even though only the vernacular form of the taxon was mentioned, it is available as a family-group name with its original author and date, according to ICZN Article 11.7 (more explicitly, Article 11.7.2), as it has been latinised by later authors and has been generally accepted as valid by researchers interested in the group (e.g., Wild 1973; Rieppel 2001; Renesto 2005; Fraser and Rieppel 2006; Nosotti 2007; Sennikov 2011; Skawiński et al. 2017; Formoso et al. 2019; Dalla Vecchia 2020; Ösi et al. 2020; Sues and Schoch 2025). Before the publication of Spiekman et al. (2020a), virtually all authors attributed the authorship of Tanystropheidae to Paul Gervais, with some citing Gervais (1858) instead of Gervais (1859), albeit mistakenly, as there is no mention of *Tanystropheus* or “*Les Tanystrophes*” in Gervais (1858). For the sake of taxonomic stability, in accordance with the rules of ICZN, I propose to conserve the uniform usage of Tanystropheidae Gervais, 1859, as the name of the family with *Tanystropheus* as its type genus.

Protorosauria Huxley, 1871, has been widely used as a suprafamiliar group name that encompasses Tanystropheidae, usually at the rank of an order. The monophyly and composition of Protorosauria has been extensively studied and discussed (e.g., Dilkes 1998; Rieppel et al. 2003; Gottmann-Quesada and Sander 2009; Ezcurra et al. 2014; Pritchard et al. 2015; Ezcurra 2016; but see Spiekman et al. 2021 for a summary). Most recently, Spiekman et al. (2021) conducted a detailed phylogenetic analysis focusing on the group, and argued against its usage, due to its possible polyphyly. Yet, if defined as an order encompassing all non-crocopodan archosauromorphs, it is a grade (see Ezcurra et al. 2025 and Schoch et al. 2025 for the latest iterations of the phylogenetic analyses focusing on early archosauromorphs). Paraphyletic groups are an important and still widely used part of biological classification, and they can convey useful phylogenetic and evolutionary information (see Hörandl 2006; Hörandl and Stuessy 2010; Carter et al. 2015). It is beyond the scope of this work, however, to formally draw the boundaries of what is a protosaur. In the absence of a non-obscure alternative, Protorosauria is regarded as the order-rank taxon including *Tanystropheus*.

Stratigraphic and geographic range.—Aupa Turbidites Formation (Italy), Upper Anisian; Besano Formation (Italy/Switzerland), Upper Anisian to Lower Ladinian; „Calcare del Roen” (Italy), Late Ladinian; Cassina Beds (Switzerland), Lower Ladinian; Cava Inferiore Beds (Switzerland), Lower Ladinian; Gevanim and Saharonim Formations (Israel), Anisian to Ladinian; Jihl Formation (Saudi Arabia), Middle Triassic; Lugaşu de Sus and Peştiş localities (Romania), Middle Triassic; S-charl Formation (Switzerland), Late Anisian; Templomhegy Dolomite Member of the Csukma Dolomite Formation (Hungary), Ladinian; Upper Muschelkalk and Lower Keuper (France, Germany, Poland), Upper Anisian to Upper Ladinian; Val Degano Formation (Italy), Lower Carnian; Zhuganpo Member of the Falang Formation (China), Ladinian; and possibly also the Economy Formation (Canada), Middle Triassic.

Tanytropheus conspicuus von Meyer, 1852

- 1840 “Saurus” (partim); Braun 1840: 81–83, pl. 9: 5; pl. 11: 1, 6; pl. 12: post-cloacal bone, lowermost figure on the left; pl. 20: 3; pl. 21: 6.
- 1846 *Smilodon laevis* (partim) gen. nov. sp. nov.; Plieninger 1846a: 152, pl. 3: 4.
- 1846 *Zanclodon [laevis]* (partim); Plieninger 1846b: 247–248, 254.
- 1849 *Tanytropheus* gen. nov.; von Meyer 1849: 219.
- 1847–1855 [1852] *Tanytropheus conspicuus* sp. nov.; von Meyer 1847–1855 [1852]: throughout text, pl. 27: 19–20, pls. 30, 46, pl. 49: 3.
- 1854 *Tanytropheus*; von Meyer 1854: 52.
- 1860 *Tanytropheus*; von Meyer 1860: 17, 48.
- 1860 *Tanytropphaeus conspicuus*; Owen 1860: 220–222.
- 1862 *Tanytropheus*; Braun 1862: 11.
- 1864 *Tanytropheus conspicuus*; von Alberti 1864: 234.
- 1865 *Tanytropheus conspicuus*; Eck 1865: 122, 126.
- 1870 *Tanytropheus conspicuus*; Roemer 1870: 147.
- 1884 *Tanytropheus*; Gürich 1884: 141.
- 1887 *Tanytropphaeus conspicuus*; Cope 1887: 221.
- 1887–1890 *Tanytropphaeus conspicuus*; Zittel 1887–1890: 567, 733, 767, fig. 514.
- 1894 *Tanytropheus*; Fritsch 1894: 277.
- 1896 *Nothosaurus blezingeri* sp. nov. (partim); Fraas 1896: 11, fig. 4.
- 1896 *Tanytropheus conspicuus*; Fraas 1896: 5, 14–15.
- 1901 *Tanytropheus conspicuus*; Nopcsa 1901: 256.
- 1902 *Chelyzoon blezingeri* gen. nov. sp. nov.; von Huene 1902: 51, pl. 7: 1.
- 1902 *Chelyzoon latum* gen. nov. sp. nov.; von Huene 1902: 50–51, pl. 7: 2.
- 1902 *Procerosaurus cruralis* gen. nov. sp. nov.; von Huene 1902: 64–65, pl. 9: 1.
- 1902 *Tanytropphaeus* (partim); von Huene 1902: throughout text, text-fig. 50, pl. 6: 6.
- 1903 *Tanytropphaeus conspicuus*; Langenhan 1903: 19, pl. 15: 8.
- 1905 *Thecodontosaurus latespinatus* sp. nov. (nomen nudum); von Huene 1905: 349.
- 1905 *Tanytropphaeus conspicuus*; von Huene 1905: 349.
- 1906 *Tanytropphaeus conspicuus*; von Huene 1906: 118.
- 1907–1908 *Thecodontosaurus latespinatus* sp. nov.; von Huene 1907–1908: throughout text, text-figs. 237–243, pls. 91, 92.
- 1907–1908 *Tanytropphaeus conspicuus*; von Huene 1907–1908: throughout text, text-figs. 250–251, 351, pl. 94: 6–9, pls. 95, 96.
- 1907–1908 *Zanclodon laevis* (partim); von Huene 1907–1908: 187–190, text-figs. 201–202.
- 1910 *Procerosaurus cruralis*; von Huene 1910: 321.
- 1911 *Tanytropphaeus conspicuus*; Langenhan 1911: pl. 20: 30.
- 1913 *Tanytropheus conspicuus*; Assmann 1913: 337.
- 1914 *Procerosaurus*; von Huene 1914b: 157.
- 1914 *Procerosaurus cruralis*; von Huene 1914a: 672.
- 1914 *Procerosaurus cruralis*; von Huene 1914c: 12.
- 1914 *Tanytropphaeus conspicuus*; von Huene 1914c: 12.
- 1914 *Thecodontosaurus latespinatus*; von Huene 1914c: 12.
- 1915 *Tanytropphaeus conspicuus*; Broili 1915: throughout text, pl. 2, pl. 3: 4, 5.
- 1915 *Thecodontosaurus primus*; Broili 1915: 57–58, pl. 3: 3.
- 1915 *Chelyzoon blezingeri*; Drevermann 1915: 404.
- 1915 *Chelyzoon latum*; Drevermann 1915: 404.
- 1915 *Tanytropphaeus conspicuus*; Drevermann 1915: 404.
- 1916 *Chelyzoon blezingeri*; Jaekel 1916: 89.
- 1916 *Chelyzoon latum*; Jaekel 1916: 89.
- 1919 *Tanytropphaeus conspicuus*; Abel 1919: 580.
- 1920 “Parasuchier aus dem oberen Muschelkalk von Bayreuth”; von Huene 1920a: throughout text, fig. 1.
- 1920 *Procerosaurus*; von Huene 1920b: 162.
- 1921 *Nothosaurus blezingeri* (partim); Edinger 1921: 17–19.
- 1923 *Tanytropphaeus conspicuus*; Edinger 1923: 143.
- 1924 *Tanytropphaeus conspicuus*; Edinger 1924: throughout text, figs. 1–4.
- 1928 *Pistosaurus grandaevus* (partim); Corroy 1928: 121, pl. 3: 2, 7.
- 1928 *Chelyzoon blezingeri*; Schmidt 1928: 414, fig. 1161.
- 1928 *Chelyzoon latum*; Schmidt 1928: 413–414, fig. 1160.
- 1928 *Nothosaurus blezingeri*; Schmidt 1928: 398, fig. 1115.
- 1928 *Procerosaurus cruralis*; Schmidt 1928: 425, fig. 1190.
- 1928 *Tanytropphaeus conspicuus* (partim); Schmidt 1928: 424–425, fig. 1188a–c.
- 1928 *Thecodontosaurus latespinatus*; Schmidt 1928: 434, fig. 1213.
- 1931 *Tanytropheus conspicuus*; Edinger 1931: 846–847.
- 1931 “*Procerosaurus cruralis*”; von Huene 1931: 66, 69.
- 1931 “*Thecodontosaurus latespinatus*”; von Huene 1931: throughout text.
- 1931 *Tanytropheus conspicuus*; von Huene 1931: throughout text, figs. 1–3, 6.
- 1931 *Zanclodon laevis* (partim); von Huene 1931: throughout text.
- 1931 *Tanytropheus conspicuus*; Peyer 1931: throughout text, text-figs. 1–2, 24–25.
- 1932 *Chelyzoon blezingeri*; Case 1932: 88.
- 1932 *Chelyzoon latum*; Case 1932: 88.
- 1932 *Procerosaurus cruralis*; von Huene 1932: 33.
- 1932 *Tanytropheus conspicuus*; von Huene 1932: throughout text.
- 1932 *Tanytropheus conspicuus*; von Zittel 1932: 270.
- 1934 *Macroscelosaurus conspicuus*; Kuhn 1934: 118–119.
- 1934 *Nothosaurus blezingeri*; Kuhn 1934: 37.
- 1937 *Tanytropheus conspicuus*; Peyer 1937: 84, fig. 1.
- 1938 *Tanytropheus conspicuus*; Schmidt 1938: 75–76, fig. 1188a.
- 1938 *Tanytropheus* sp.; Schmidt 1938: 76, fig. 1188b.
- 1939 *Chelyzoon*; Kuhn 1939b: throughout text.
- 1939 *Procerosaurus cruralis*; Kuhn 1939a: 35.
- 1939 *Thecodontosaurus latespinatus*; Kuhn 1939b: 12.
- 1941 *Chelyzoon*; Kuhn 1941: 10.
- 1944 *Tanytropphaeus conspicuus*; Assmann 1944: 84–85.
- 1944 *Tanytropheus conspicuus*; von Huene 1944: 127.
- 1944 *Tanytropheus conspicuus*; Peyer 1944: 65, fig. 49.
- 1952 *Tanytropphaeus conspicuus*; Lang and von Huene 1952: 27.
- 1953 *Tanytropheus conspicuus*; Adam 1953: throughout text, fig. 1.
- 1954 *Megacnemus grandis* gen. nov. sp. nov.; von Huene 1954: throughout text, fig. 1.
- 1955 *Chelyzoon*; Bergounioux 1955: 521.
- 1955 *Thecodontosaurus latespinatus*; Lapparent and Lavocat 1955: 933.
- 1955 *Tanytropheus conspicuus*; Peyer 1955: 489.
- 1955 *Macroscelerosaurus*; Peyer and Kuhn-Schneider 1955: 578.
- 1955 *Tanytropheus conspicuus*; Peyer and Kuhn-Schneider 1955: 578, figs. 1, 21.
- 1956 *Megacnemus*; von Huene 1956: 648.
- 1956 *Tanytropheus* (partim); von Huene 1956: fig. 657e.
- 1956 *Tanytropheus* (partim); Romer 1956: fig. 122M.
- 1958 “Parasuchier” (partim); von Huene 1958a: 66, fig. 4.
- 1961 *Megacnemus*; Kuhn 1961b: 5.
- 1961 *Chelyzoon*; Kuhn 1961a: 32.
- 1963 *Megacnemus grandis*; Kuhn 1963: 9.
- 1963 *Tanytropheus conspicuus*; Kuhn 1963: 6.
- 1965 *Tanytropheus conspicuus*; Kuhn 1965: 45.
- 1965 “*Thecodontosaurus*” *latespinatus*; Kuhn 1965: 45.
- 1969 *Megacnemus grandis*; Kuhn 1969: 70, pl. 24: 3.
- 1969 *Tanytropheus conspicuus*; Kuhn 1969: 71.
- 1969 *Tanytropheus* (partim); Kuhn 1969: pl. 19: 18.
- 1969 *Thecodontosaurus* (partim); Kuhn 1969: pl. 21: 21.

- 1970 *Thecodontosaurus latespinatus*; Colbert 1970: 31–33.
 1971 *Chelyzoon blezingeri*; Kuhn 1971: 10.
 1971 *Chelyzoon latum*; Kuhn 1971: 10, pl. 17: 1.
 1971 *Megacnemus grandis*; Kuhn 1971: 12.
 1971 *Tanystropheus conspicuus*; Kuhn 1971: 11, pl. 21a: 1a–c, pl. 41b: 11, 12.
 1971 *Tanystropheus longobardicus* (partim); Kuhn 1971: pl. 21: 11.
 1971 *Thecodontosaurus latespinatus*; Kuhn 1971: 17, pl. 21: 26.
 1972 *Tanystropheus conspicuus*; Emmert and von Horstig 1972: pl. 2: 4.
 1973 *Tanystropheus conspicuus*; Wild 1973: throughout text, figs. 38–62, 67, 73, 97b, c.
 1973 *Megacnemus grandis*; Wild 1973: 119, pl. 21: 1.
 1974 *Tanystropheus conspicuus*; Kuhn-Schnyder 1974: 55–56.
 1975 *Tanystropheus conspicuus*; Juresak 1975: 46–48.
 1975 *Tanystropheus* sp.; Kuhn 1975: 9–10.
 1975 *Tanystropheus conspicuus*; Wild 1975a: 153, fig. 1.
 1975 *Tanystropheus conspicuus*; Wild 1975b: throughout text.
 1976 *Tanystropheus latespinatus*; Galton and Cluver 1976: 153.
 1976 *Tanystropheus conspicuus*; Wild 1976b: 125.
 1976 *Tanystropheus conspicuus*; Wild 1976a: 15, 20, fig. 3.
 1977 *Tanystropheus conspicuus*; Wild 1977: 675, fig. 1.
 1980 *Tanystropheus conspicuus*; Wild 1980a: throughout text.
 1980 *Tanystropheus conspicuus*; Wild 1980b: 201, 204–205.
 1981 *Tanystropheus conspicuus*; Melville 1981: 188.
 1986 *Tanystropheus conspicuus*; Benton 1986: 296–297.
 1986 *Tanystropheus conspicuus*; Chatterjee 1986: 311.
 1986 *Tanystropheus conspicuus*; Tschanz 1986: throughout text.
 1987 *Tanystropheus conspicuus*; Wild 1987: 37, 39, 42.
 1988 *Megacnemus*; Carroll 1988: 619.
 1988 *Tanystropheus conspicuus*; Hagdorn and Reif 1988: 130.
 1988 *Tanystropheus conspicuus*; Tschanz 1988: 997–998, 1002.
 1988 *Tanystropheus conspicuus*; Evans 1988: 227.
 1989 *Tanystropheus conspicuus*; Wild 1989: 40.
 1990 *Tanystropheus conspicuus*; Hagdorn 1990: 86.
 1991 *Tanystropheus conspicuus*; Olshevsky 1991: 106, 181–182.
 1995 *Tanystropheus conspicuus*; Lucas 1995: 94.
 1996 *Tanystropheus*; Rieppel and Wild 1996: 61.
 1997 *Tanystropheus conspicuus*; Benton and Allen 1997: 945, 947.
 1999 *Tanystropheus conspicuus*; Hagdorn and Rieppel 1999: 662, 664, 667.
 1999 *Tanystropheus conspicuus*; Hauschke and Wilde 1999: 332, 340, 590.
 1999 *Tanystropheus conspicuus*; Rieppel et al. 1999: 75.
 1999 *Tanystropheus conspicuus*; Schoch 1999: 14.
 2000 *Tanystropheus conspicuus*; Dalla Vecchia 2000: 136, 138–139.
 2001 *Tanystropheus conspicuus*; Rieppel 2001: throughout text.
 2003 *Tanystropheus conspicuus*; Oosterink et al. 2003: 42.
 2005 *Tanystropheus conspicuus*; Renesto 2005: 386.
 2005 *Megacnemus*; Sennikov 2005: 200, 206.
 2005 *Tanystropheus conspicuus*; Sennikov 2005: 207.
 2006 *Tanystropheus conspicuus*; Dalla Vecchia 2006: 40–42.
 2006 *Tanystropheus conspicuus*; Fraser and Rieppel 2006: 866, 870.
 2007 *Tanystropheus conspicuus*; Nosotti 2007: throughout text.
 2008 “*Tanystropheus conspicuus*”; Dalla Vecchia 2008: 81.
 2009 *Tanystropheus conspicuus*; Spielmann et al. 2009: 307, fig. 13.
 2009 *Tanystropheus longobardicus* (partim); Diedrich 2009: 1, 6, 12.
 2011 *Tanystropheus conspicuus*; Sennikov 2011: 100.
 2012 *Tanystropheus conspicuus*; Diedrich 2012: throughout text, fig. 14: 2–15.
 2014 *Tanystropheus longobardicus* (partim); Ezcurra et al. 2014: throughout text, figs. 16D, 18C.
 2014 *Tanystropheus conspicuus*; Ezcurra et al. 2014: 25.
 2015 *Tanystropheus conspicuus/Tanystropheus conspicuus*; Diedrich 2015: throughout text, fig. 10C2.
 2015 *Tanystropheus conspicuus*; Pritchard et al. 2015: 4, 9, 15.
 2015 *Tanystropheus conspicuus*; Nesbitt et al. 2015: throughout text.
 2015 *Tanystropheus conspicuus*; Schoch 2015: 243, fig. 10.7a, b.
 2015 *Tanystropheus* sp.; Schoch 2015: 243, fig. 10.131.
 2015 *Tanystropheus*; Hagdorn et al. 2015b: 336, 350, 354, 356.
 2016 *Tanystropheus longobardicus* (partim); Ezcurra 2016: throughout text, figs. 14A, B, 31B, 33B, 35A, 43A, B.
 2017 *Tanystropheus conspicuus*; Beardmore and Furrer 2017: 2.
 2017 *Tanystropheus* sp. (partim); Jaquier and Scheyer 2017: figs. 1B, C, 2A, E–H.
 2017 *Tanystropheus conspicuus*; Jaquier and Scheyer 2017: figs. 1E, 2D.
 2017 *Tanystropheus conspicuus*; Skawiński et al. 2017: 4, 14–15, fig. 5O–P.
 2017 *Tanystropheus conspicuus*; Sues 2017: 129–130.
 2018 *Tanystropheus conspicuus*; Renesto and Saller 2018: 23.
 2018 *Tanystropheus* (partim); Schoch et al. 2018: 630, fig. 4q.
 2019 *Tanystropheus conspicuus*; Rieppel 2019: throughout text.
 2019 *Tanystropheus conspicuus*; Spiekman and Scheyer 2019: throughout text.
 2019 *Tanystropheus conspicuus*; Spiekman et al. 2019: throughout text.
 2020 *Tanystropheus conspicuus*; Dalla Vecchia 2020: throughout text.
 2020 *Tanystropheus longobardicus* (partim); Ezcurra et al. 2020: fig. 1D.
 2020 *Tanystropheus conspicuus*; Ösi et al. 2020: 266.
 2020 *Tanystropheus “conspicuus”*; Spiekman et al. 2020b: 7, 59, 63.
 2021 *Tanystropheus conspicuus*; Brignon 2021b: 33.
 2021 *Tanystropheus* sp.; Brignon 2021a: throughout text, fig. 34B.
 2021 *Tanystropheus conspicuus*; Hauschke et al. 2021: 334.
 2021 *Megacnemus grandis*; Spiekman et al. 2021: 11.
 2021 *Tanystropheus “conspicuus”*; Spiekman et al. 2021: throughout text.
 2022 *Tanystropheus conspicuus*; Klein et al. 2022: 9–10.
 2022 *Tanystropheus conspicuus*; Sues et al. 2022: 7.
 2023 *Tanystropheus “conspicuus”*; Czepiński et al. 2023: 6.
 2024 *Tanystropheus “conspicuus”*; Rytel et al. 2024a: throughout text.
 2024 *Tanystropheus “conspicuus”*; Rytel et al. 2024b: throughout text.
 2024 *Tanystropheus “conspicuus”*; Spiekman et al. 2024b: 14, 28.
 2024 *Tanystropheus conspicuus*; Sues 2024: 4.
 2025 *Tanystropheus conspicuus*; Dalle-Laste et al. 2025: 46212.
 2025 *Tanystropheus conspicuus*; Schubul et al. 2025: 106, 114.
 2025 *Tanystropheus*; Schwermann et al. 2025: fig. 1.
 2025 *Tanystropheus conspicuus*; Sues and Schoch 2025: 441, fig. 8C.
 2025 “*Chelyzoon*”; Szczygielski et al. 2025: 23.
 2026 *Tanystropheus* sp.; Tałanda et al. in press: throughout text, fig. 2.
Type material: Lectotype: U-MO BT 740, isolated middle cervical vertebra. Paralectotypes: MB.S.11, U-MO BT 732, U-MO BT 733, U-MO BT 734, U-MO BT 737, five middle cervical vertebrae. The remaining paralectotypes (four middle cervical vertebrae) are ostensibly lost.
Type locality: Bindlach Berg near Bayreuth (after Wild 1973), Upper Franconia, Germany.
Type horizon: Upper Muschelkalk, upper Trochitenkalk Formation or lower Meißner Formation, upper Anisian, Middle Triassic (see Klein et al. 2022).
Material.—Hundreds of isolated bones and teeth, as well as several incomplete articulated individuals, altogether comprising a majority of the skeleton (lacking some of the cranial and autopodial elements). All from the Upper Muschelkalk to Lower Keuper (Upper Anisian to Upper Ladinian) of France, Germany, and Poland. For the full list of referred specimens see SOM: table 1.
Former diagnosis.—The most recent diagnosis for *T. conspicuus* was provided in Wild (1973: 149; translated from

German after Spiekman and Scheyer 2019): “Up to six(?) meters long species, that can be distinguished from *T. longobardicus* by the wider attachment sites of the cervical ribs and the split anterior end of the neural spine for the attachment of the dorsal ligament.” Note that Wild (1973) considered both the small and large sized individuals of *Tanytropheus* from the Monte San Giorgio to be conspecific (and belong to *T. longobardicus*), which was disproven by Spiekman et al. (2020a).

Emended diagnosis.—*Tanytropheus conspicuus* is distinguished from all other *Tanytropheus* species by the following combination of characters: (i) premaxilla lacking distinct prenarial and postnarial processes (shared with *T. hydroides*); (ii) single-cusped marginal teeth (shared with *T. hydroides*); (iii) no dentary tooth piercing through a foramen in the maxilla (shared with *T. longobardicus*); (iv) number of dentary teeth reaching up to 26 or more in some specimens; (v) dentary bearing a distinct ventral keel at its anterior end (shared with *T. hydroides*); (vi) frontal semi-trapezoidal in outline in dorsal view, with its transverse width notably greater than its anteroposterior length; (vii) lack of a shelf-like ridge on the dorsolateral surface of the 13th cervical rib; (viii) dorsal and sacral vertebrae at least two times taller than long; (ix) distal region of the neural spine laterodistally expanded and bulbous in appearance along the vertebral column from the 10th cervical to the anterior caudal vertebrae; (x) scapula with a distinct dorsoventral constriction located at its anteroposterior midpoint and a significantly posteriorly expanded scapular blade; and (xi) dorsolateral surface of the first three dorsal ribs anteroposteriorly expanded, forming a plate-like extension radiating distally from the tuberculum-capitulum conjunction.

Description.—Cranial elements of *T. conspicuus* are described only on a preliminary basis, as the Miedary site is still yielding new skull bones. A detailed comparative description of the cranial material of *T. conspicuus*, including a reconstruction of the skull, will be carried out in the future. Herein I describe the cranial features due to their usefulness in the species differentiation within *Tanytropheus*.

Skull: Premaxilla: The premaxilla of *T. conspicuus* is an elongate, flat, element (Fig. 2). Similar to the other species of *Tanytropheus*, it bears six circular alveoli, from which the anterior five are subequal in size (Fig. 2B; Wild 1973; Nosotti 2007; Spiekman and Scheyer 2019, Spiekman et al. 2020b). As in *T. hydroides*, the posteriormost alveolus is slightly smaller (Spiekman et al. 2020b). The alveoli are aligned in a single row, with the openings of the anterior three being more laterally oriented than the posterior three, which are predominantly ventral-facing (Fig. 2B₁). They are evenly spaced along the anterolateral margin of the premaxilla, and clearly outlined in dorsal view (Fig. 2A₂), being marked by a labial expansion of the dorsal alveolar wall, as in *T. hydroides* but unlike *T. longobardicus* (Fig. 2B; Nosotti 2007; Spiekman et al. 2020b). Tooth implantation was anisothecodont (= “subthecodont”, see Dentition sec-

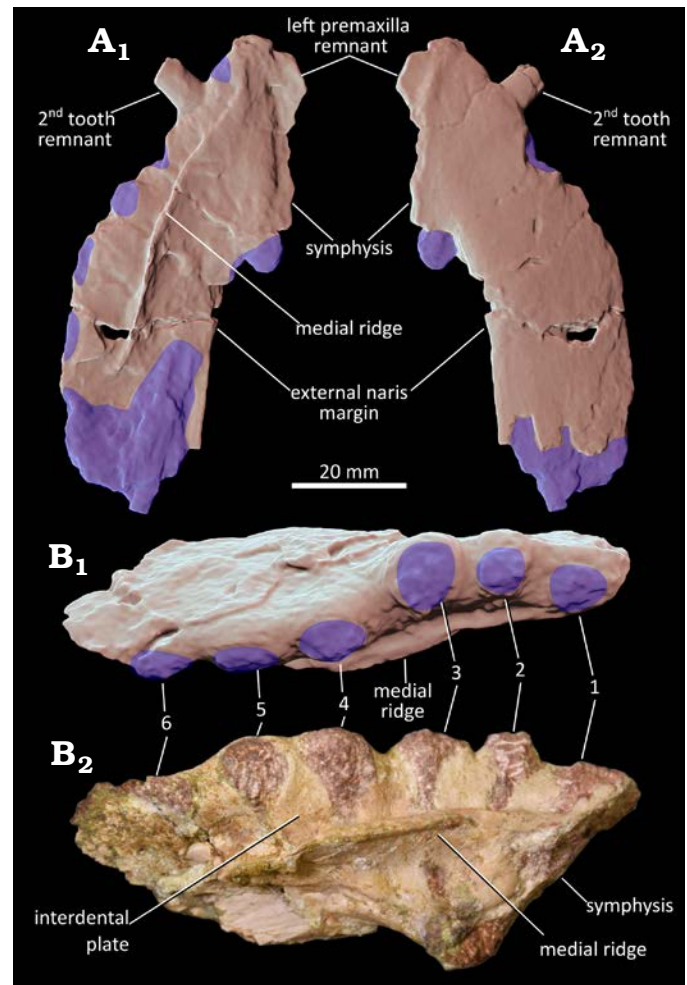


Fig. 2. Right premaxillae of the tanystropheid archosauromorph *Tanytropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photograph (B₂), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (A, B₁). ZPAL V. 36/179 (A) and ZPAL V. 36/2487 (B) in ventral (A₁, B₂), dorsal (A₂), and anterolateral (B₁) views. Numerals indicate the alveoli. Areas covered with sediment marked with blue hue.

tion below). Lingually, the premaxillary teeth were separated by triangular interdentary plates (Fig. 2B₂). This represents the first known occurrence of interdentary plates outside of Archosauriformes (Nesbitt 2011; Ezcurra 2016), in which this character occurs broadly, suggesting a considerably earlier origin of this trait than previously considered among Archosauromorpha. Between the interdentary plates, the lingual margin of each alveolus is distomesially constricted, but widens gradually towards its rounded lingual margin in ventral view, forming a deep, droplet shaped notch (Fig. 2B₂).

At the base of the lingual side of the alveoli, there is a distinct, sharp, medial ridge, which projects ventrally, roughly at the mid-point of the premaxilla. The symphyseal contact of the premaxilla with its antimeric (i.e., corresponding, symmetrical element) was along a straight line. Posterior to it, an incipient prenarial process was identified by Spiekman et al. (2020b) in *T. hydroides*. A similar, ventromedially ori-

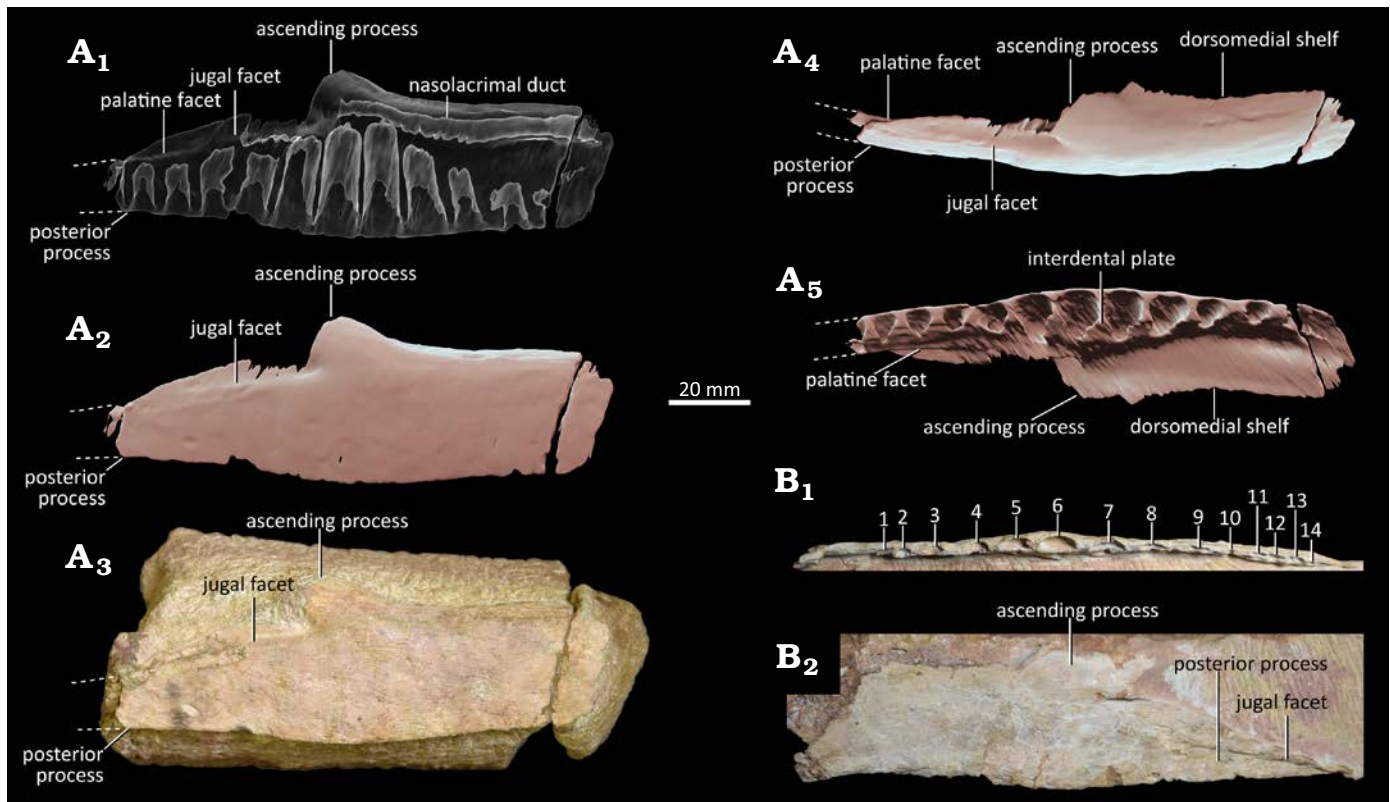


Fig. 3. Maxillae of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photographs (A₃, B), three-dimensional segmented model snapshots with X-ray (A₁), and Lit Sphere Radiance Scaling (A₂, A₄, A₅) shaders enabled. Right (ZPAL V. 36/1213, A) and left (ZPAL V. 36/2474, B) maxillae in lateral (A₁–A₃, B₂), dorsal (A₄), and ventral (A₅, B₁) views. Numerals indicate the alveoli.

ented ridge is present in the premaxillae of *T. conspicuus*, but it does not extend posteriorly nor does it possess a nasal facet. Therefore, as in *T. hydroides*, it is here interpreted as the posterior extension of the symphyseal margin instead. The dorsal surface of the premaxilla is rugose and bears no foramina, as in *T. hydroides*, but not in *T. longobardicus* (Nosotti 2007; Spiekman et al 2020b). Compared to the symphyseal margin, the posterior premaxillary edge, which articulated with the maxilla, retains a similar transverse width, but it is more inclined. The postnasal process is absent, similar to *T. hydroides* but unlike *T. longobardicus* (Nosotti 2007; Spiekman et al 2020b). As in *T. hydroides*, the dorsomedial edges of the premaxillae constituted the anterior margin of a single, dorsally oriented external naris (Fig. 2A). Overall, the maxilla of *T. conspicuus* closely resembles the maxilla of *T. hydroides*, but appears to be relatively more dorsoventrally flattened and anteroposteriorly elongate.

Maxilla: The maxilla of *T. conspicuus* is a relatively flat and slender element (Fig. 3). Thirteen or fourteen alveoli are present in the complete maxilla ZPAL V. 36/2474 (Fig. 3B). Although some intraspecific variation seems to exist, presence of a similar number of maxillary teeth has been reported for *T. longobardicus* (11–15; Wild 1973; Nosotti 2007) and *T. hydroides* (12–15; see Wild 1973; Spiekman et al. 2020b). Characteristics of the alveoli are similar to

those described for the premaxilla. In ventral view they are all circular, and densely packed along a single, straight line (Fig. 3A₅, B₁). Lingually, the maxillary teeth were separated by triangular interdental plates. Between the interdental plates, the lingual margin of each alveolus is formed as a deep, droplet-shaped notch. Unlike on the premaxilla, there is a considerable alveolus (tooth) size difference. The middle (sixth-seventh) maxillary teeth were likely comparable in size to the premaxillary teeth, but the maxillary teeth size gradually decreased both anteriorly and posteriorly to these teeth (Fig. 3A₁, B₁). In *T. hydroides* this configuration is identical (Spiekman et al. 2020b).

The anterior edge of the maxilla is straight in lateral view (Fig. 3A₂–A₃, B₂), and its articulation with the premaxilla seems to have been relatively simple. The dorsal surface of the anterior portion of the maxilla is flat and medially expanded, forming a distinct, ventromedially projecting dorsomedial shelf. Around the mid-length of the maxilla, the dorsal margin extends dorsomedially, forming the ascending process. It is triangular in lateral view, short, and composed of a thin bony plate that forms a rounded distal end.

A prominent longitudinal canal is present within the anterior portion of the maxilla, directly ventral to the dorsally rounded dorsal apex (Fig. 3A₁). Its diameter is constant and there are no branchings. Anteriorly, this canal continues at least to the articulation surface of the premaxilla.

Posteriorly, it terminates as a foramen on the medial side of the ascending process. In *T. hydroides* a canal of nearly identical morphology is present in the same relative location, posteriorly terminating at the articulation surface of the lacrimal (AR personal observation). Its occurrence was not mentioned by Spiekman et al. (2020b), but it was segmented within the left maxilla of PIMUZ T 2790. The lacrimal in this specimen is pierced by a large foramen for the nasolacrimal duct (Spiekman et al. 2020b), which corresponds with its size and location to the canal present in the maxilla. The canal present in the maxillae of both *T. conspicuus* and *T. hydroides* was likely a part of the nasolacrimal duct. Alternatively, it could be interpreted as the maxillary canal. However, this is less likely, as in other Permo-Triassic diapsids the maxillary canal is located ventral to the nasolacrimal duct, ventrally along the edge of the dental margin, and has branchings (Ford and Benson 2018; Benoit et al. 2021). The tube-like canal in the maxilla of *T. conspicuus* and *T. hydroides* is located parallel to the dorsal margin of the bone, but its dorsoventral distance from the alveoli changes significantly along its length (Fig. 3A₁).

The ventral maxillary edge is relatively straight in lateral view, being only slightly convex at mid-length (Fig. 3A₂, A₃, B₂). Its posterior portion forms a triangular process, which tapers to a point (Fig. 3B₂). On the dorsolateral surface of the posterior process of the maxilla, an elongate groove is present, marking the location of the jugal facet. Along the same section of the posterior process, but on its medial surface, a slightly medially extended shelf is present, which formed the articular facet for the palatine. Between the jugal and the palatine facets, an anteroposteriorly oriented ridge is located. It is lateromedially thin and extends dorsally. The lacrimal articulated between the posterior edge of the ascending process, and the anterior portion of the posterior process. The lateral surface of the maxilla is generally smooth, but with a slightly rugose texture. No large foramina are present.

The morphology of the maxilla of *T. conspicuus* is generally congruent with that of *T. hydroides*. Both species are different in similar respects to *T. longobardicus*. The latter has a proportionally much taller maxilla bearing tricuspid teeth that are homodont in size and a much more dorsally expanded ascending process (Nosotti 2007; Spiekman et al. 2020b). The overall configuration of the alveoli makes it likely that *T. hydroides* also possessed interdental plates, although the nature of the reconstructed CT data makes it difficult to identify these structures unambiguously (see Spiekman et al. 2020b: fig. 7). The maxilla of *T. conspicuus* is nevertheless distinct from that of *T. hydroides* in several features. Importantly, the maxilla of *T. conspicuus* lacks the foramen for a dentary tooth, the presence of which was considered an autapomorphy of *T. hydroides* by Spiekman et al. (2020b). In addition, the main character serving as a basis for differentiating the maxillae of *T. conspicuus* and *T. hydroides* is the relative height of the posterior process. In the former species it is much taller, being anteriorly nearly as tall as the portion of the maxilla anterior to the ascending process.

Skull roof: The skull roof of *T. conspicuus* is known only from one specimen, ZPAL V. 36/1244, which preserves the frontals, fused parietals, and partial postorbitals (Fig. 4). The postfrontals are seemingly absent, as in *T. hydroides* (see Spiekman et al. 2020b), but this is equivocal as the posterolateral portions of the preserved skull roof are damaged. The preserved elements are in tight articulation and therefore did not disassociate during postmortem transport, contrary to the great majority of vertebrate fossils from Miedary.

Frontal: The frontals are flat, dorsoventrally thin, and transversely wide elements. They are trapezoidal in dorsal view, with their posterior portions more expanded laterally than the anterior portions, and their transverse width notably greater than anteroposterior length (Fig. 4A₁–A₆). The anterior frontal margin is concave in dorsal view and bears a short, rounded anterior process on its medial side (Fig. 4A₁–A₇). Posterior to it, there is a distinct ridge on the dorsal surface of the frontal, which parallels the anterior edge in its curvature, with a crescent-shaped, flat, and relatively smooth surface formed between them (Fig. 4A₅). This is the facet for the nasal, which would have dorsally overlapped the frontal. In anterior view, the portion of the anterior margin of the frontal adjacent to the midline suture is slightly concave (Fig. 4A₇). As in *T. hydroides*, this concavity marks the anterior edge of the broad, obliquely oriented medial depression of the frontal, which extends towards the posteromedial corner of the bone (Fig. 4A₅; Spiekman et al. 2020b). Further laterally, the anterior margin is convex in dorsal view, forming the anterolateral corner of the frontal and the attachment area for the prefrontal. Posterior to it, the lateral margin of the frontal is dorsoventrally thickened and slightly convex in lateral view (Fig. 4A₉–A₁₀).

The posterior frontal margin is relatively straight in dorsal view and somewhat ventrally expanded, constituting the articulation surface for the medial process of the postorbital along its entire length. The posteromedial corner of the frontal tapers posteriorly to a point, forming the ventral portion of the anterior edge of the parietal foramen. The anterolateral process of the parietal articulated on top of the posteromedial region of the frontal, overlapping the distal portion of the medial process of the postorbital dorsally (Fig. 4A₂). The midline suture between the frontals is relatively straight, but interdigitating over part of its length, with several transversely extending laminae overlapping similar structures projecting from the antimeres (Fig. 4A₂–A₆). The dorsal surface of the frontals displays longitudinal grooves radiating from the centre of growth, with the orbital rim being especially rugose. On the ventral surface of the frontal, a poorly defined ridge, crista cranii, extends from the posteromedial corner of the bone, parallel to the midline suture (Fig. 4A₆). It tapers anteriorly, terminating approximately at mid-length of the element. Spiekman et al. (2020b) interpreted this feature as the posterior portion of the margin of the olfactory tract. As for *T. hydroides* but unlike *T. longobardicus*, there is no depression accommodating the olfactory bulb (Nosotti 2007; Spiekman et al. 2020b).

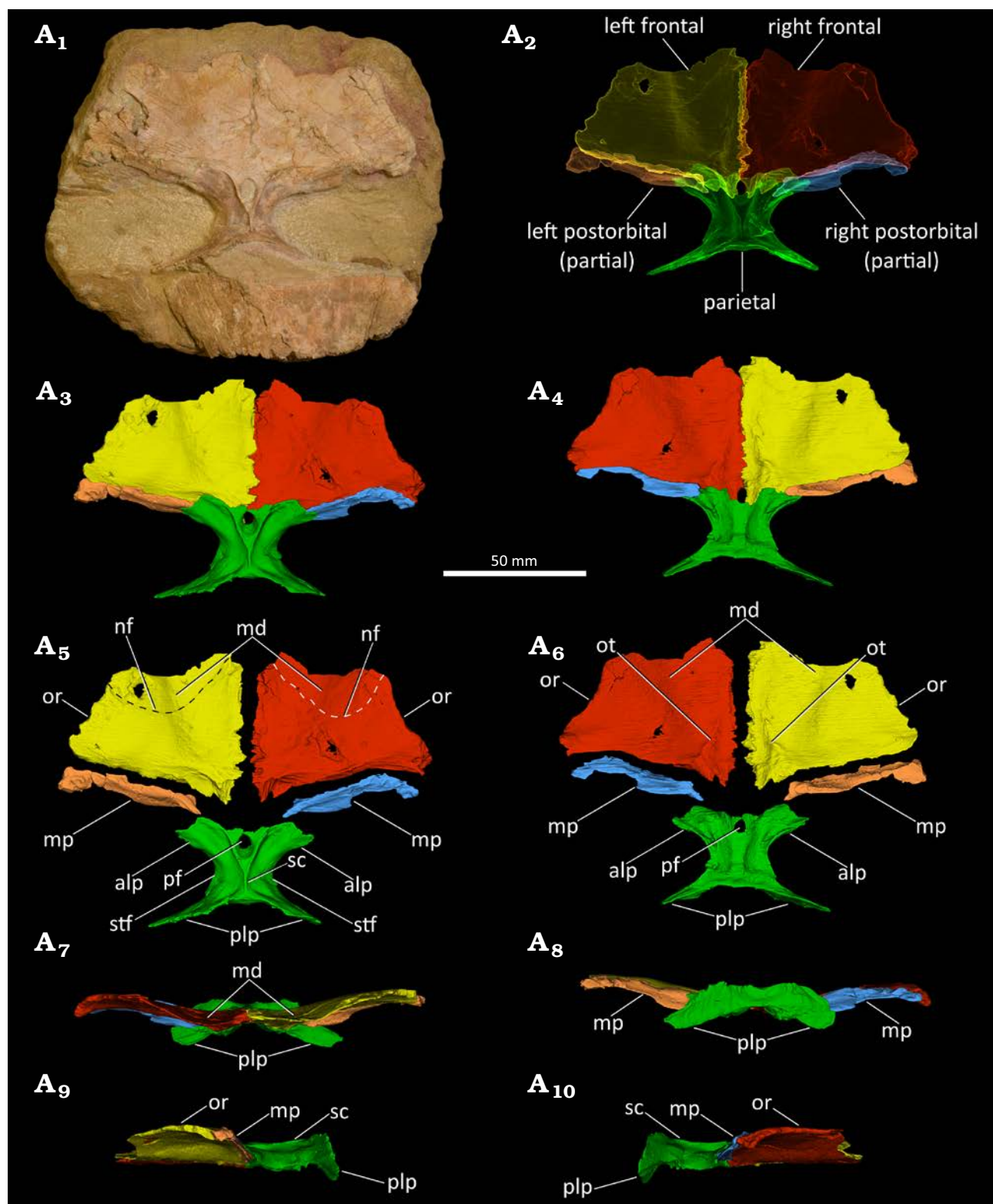


Fig. 4. Skull roof of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photograph (A₁), three-dimensional segmented model snapshots with X-ray (A₂), Lambertian Radiance Scaling (A₃–A₁₀) shaders enabled, specimen in natural articulation (A₁–A₄, A₇–A₁₀), manually disarticulated (A₅, A₆). ZPAL V. 36/1244 in dorsal (A₁–A₃, A₅), ventral (A₄, A₆), anterior (A₇), posterior (A₈), left (A₉) and right (A₁₀) lateral views. The lateral margin of the left dorsal was slightly damaged post-CT scanning, hence the difference in its morphology between the photograph (A₁) and the segmented model snapshots (A₂–A₁₀). Different colours demark different bones (see A₂). Dashed lines outline the posterior margin of the nasal facet. Abbreviations: alp, anterolateral process; md, medial depression; mp, medial process of a postorbital; nf, nasal facet (posterior extent); ot, olfactory tract margin (crista cranii); or, orbital rim; pf, parietal foramen; plp, posterolateral process; sc, sagittal crest; stf, supratemporal fossa.

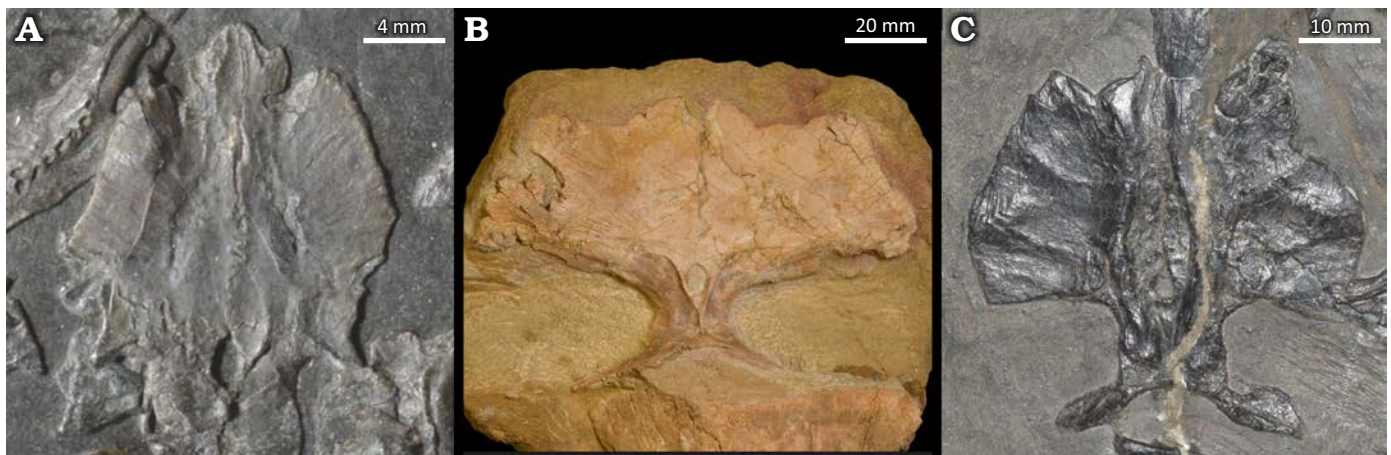


Fig. 5. Comparison of the skull roof (frontals) morphology in three species of the tanystropeid archosauromorph *Tanystropheus*. A. *Tanystropheus longobardicus* (Bassani, 1886) from the Besano Formation (upper Anisian to lower Ladinian) of Monte San Giorgio, Switzerland; PIMUZ T 2484 in dorsal view. B. *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland; ZPAL V. 36/1244 in dorsal view. C. *Tanystropheus hydroides* Spiekman et al., 2020a, from the Besano Formation (upper Anisian to lower Ladinian) of Monte San Giorgio, Switzerland; PIMUZ T 2787 in ventral view.

The overall anatomy of the skull roof is very reminiscent to the description for *T. hydroides* by Spiekman et al. (2020a, b), and the comparisons to other archosauromorph taxa (including *T. longobardicus*) made therein are valid for *T. conspicuus* as well. There are, however, several significant differences in the proportions of the frontals between the three known specimens of *T. hydroides* preserving them (PIMUZ T 2787, PIMUZ T 2790, PIMUZ T 2819) and *T. conspicuus* (Fig. 5). In the former the elements taper anteriorly, and their transverse width increases posteriorly at a relatively constant rate. Thus, in dorsal view they are roughly triangular (Fig. 5C). By contrast in *T. conspicuus* they are trapezoidal, with their anterior margin being slightly concave along the articulation with the nasals. Furthermore, because their anterior margin is more latero-medially oriented, the frontals of *T. conspicuus* are relatively shorter anteroposteriorly than in *T. hydroides* (Fig. 5B, C). *Tanystropheus conspicuus* exhibits an even more transversely wide interorbital region of the skull roof than the already remarkably expanded interorbital region of *T. hydroides* (see Spiekman et al. 2020b). Whereas in the latter the transverse width of the frontal is roughly equal to its anteroposterior length, in the former it is about 1.2–1.3 wider than long. The articulation facets for the nasals, well-marked in *T. conspicuus*, are not visible in the currently known specimens of *T. hydroides* (see Wild 1973; Spiekman et al. 2020b). The midline suture in *T. hydroides* is straight in all specimens in which it can be observed (PIMUZ T 2787, PIMUZ T 2790, PIMUZ T 2819; Spiekman et al. 2020a, b), and in contrast to the condition of *T. longobardicus* (Fig. 5; Nosotti 2007; Spiekman and Scheyer 2019; Spiekman et al. 2020b). As for *T. longobardicus*, in *T. conspicuus* the midline suture is interdigitating, especially along its posterior portion (Fig. 5A, C). Although this specific feature might change during ontogeny, the remaining aspects of the cranial morphology of *T. conspicuus* allow for its clear differentiation from other species of *Tanystropheus*.

Postorbital: The morphology of the postorbital in *T. conspicuus* is only partially known, as ZPAL V. 36/1244 only preserves the medial processes of both postorbitals. They are in tight articulation with the corresponding frontals and parietals (Fig. 4A₂). The medial process of the postorbital in *T. conspicuus* partially dorsally overlaps the posterior margin of the frontal and is more ventrally expanded, forming a vertically oriented, flat, plate-like projection, which tapers distally to a point. The base of the process is thickened and has a rugose dorsal surface. The medial process constituted the anterior margin of the supratemporal fenestra, separating it completely from the frontals. Whereas the morphology of the medial process of the postorbital in *T. hydroides* cannot be fully discerned from the holotype (Spiekman et al. 2020b), the referred specimen PIMUZ T 2819 exhibits both nearly identical proportions and an identical position for this process as in *T. conspicuus*.

Parietal: The parietals are seamlessly fused, forming a single element that is X-shaped in dorsal view. The anterior end of the parietal is composed of a complex set of pits, ridges, and grooves, which are bilaterally symmetrical, forming an intricate, tight articulation with the postorbitals and the frontals anteriorly (Fig. 4A₆). The anterolateral process of the parietal dorsally overlaps the posteromedial corner of the corresponding frontal and the distal portion of the medial process of the postorbital, which is enclosed by them. The parietal foramen is relatively large, subcircular, and well outlined. The frontals contributed only to the ventral portion of its anterior margin, with the parietals fully enclosing it along its dorsal rim (Fig. 4A₃, A₄).

The foramen is posterolaterally flanked by ridges that merge posteriorly to it, forming a low but well defined sagittal crest, which runs along the midline of the parietals (Fig. 4A₅). The surface of the parietals is bilaterally concave, forming the supratemporal fossae, which constituted the entire medial margin of the supratemporal fenestrae. The portion of

the fenestra enclosed by the parietal is semicircular, with the anterolateral parietal process contributing to its anteromedial edge and the posterolateral process contributing to its posteromedial edge (Fig. 4A₂–A₄). The posterolateral process is longer than the anterolateral process, forming an anteroposteriorly thin projection with a distal portion that is seemingly rounded in posterior view (Fig. 4A₈; the distal tip itself is not preserved in ZPAL V. 36/1244). As for *Tanystropheus hydroides*, it is dorsoventrally tall and almost entirely transversely oriented (Spiekman et al. 2020b). In fact, the parietal of *T. conspicuus* does not seem to differ from *T. hydroides* in any major feature (see Wild 1973; Nosotti 2007; Spiekman and Scheyer 2019; Spiekman et al. 2020b).

Quadrate: The quadrate of *T. conspicuus* strongly resembles the quadrate of *T. hydroides* (compare Fig. 6 herein and Spiekman et al. 2020b: fig. 14). The shaft is formed as a longitudinal, vertical thickening located along the transverse mid-width of the bone (Fig. 6). Its dorsal portion is nearly vertical (Fig. 6A₁). More ventrally it slopes gently posteriorly, with the middle portion of the shaft being slightly concave in lateral view and the ventral portion ventromedially directed (Fig. 6A₁, A₃, A₆). The dorsal margin of the quadrate is convex in posterior view, with the thickened dorsal portion of the shaft projecting posterodorsally from it (Fig. 6A₅, A₆, B).

The dorsolateral tip of the shaft has a rough surface, forming a distinct, slightly laterally expanded tuberosity. In *T. hydroides* this tuberosity forms a dorsal hook, which was considered to be one of the autapomorphic features of this taxon by Spiekman et al. (2020a, b). All known quadrates of *T. conspicuus* (ZPAL V. 36/574, 1350, 1764) are relatively well preserved, but the dorsal tuberosity in all of them is eroded and likely missing its tip, which was originally more laterally extended, possibly forming the conspicuous hook, as in *T. hydroides*.

Two thin plates of bone project from the shaft, anterolaterally and anteromedially, respectively, with a right angle formed between them (Fig. 6A₃). The anteromedial extension is the pterygoid ramus. It is roughly semicircular in medial view, although it is not fully preserved in any of the known specimens (Fig. 6A, B). On the posterior surface of the quadrate, near the pterygoid ramus, a faint elliptical concavity is present. On the opposite side of the ramus, a corresponding convexity is present (Fig. 6B). The anterolateral edge of the quadrate is constricted laterally at mid-height, with the two resulting triangular projections being separated by the posterior margin of the quadrate foramen (Fig. 6A₅, A₆, B). The one located dorsally to the notch bears the tympanic crest.

The lateral condyle is present ventrally to the tympanic crest and projects more strongly from the shaft (Fig. 6A₅, A₆, B). As in *T. hydroides*, its dorsolateral surface is occupied by an elliptical facet which receives the ventral portion of the quadratojugal (Fig. 6A₆; Spiekman et al. 2020b). Posterior to the lateral condyle, the ventral surface of the quadrate is concave in posterior view, forming a groove, which demarcates the boundary between the lateral and medial condyles of the ventral quadrate end (Fig. 6A₅, A₆, B). In ventral view, their

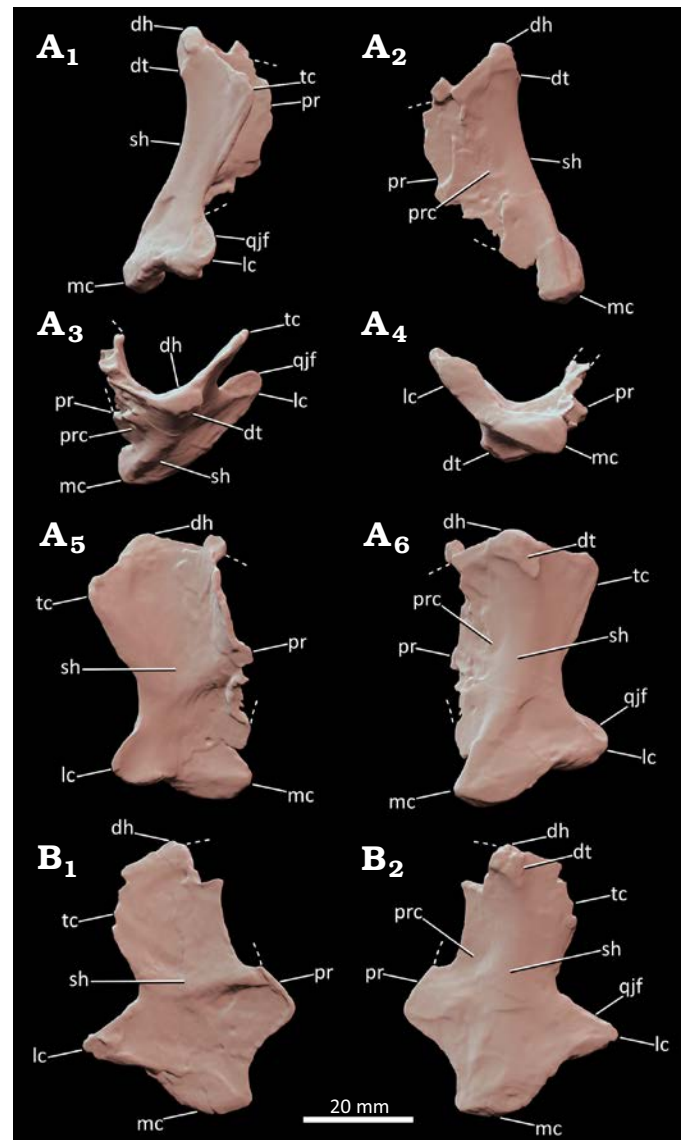


Fig. 6. Right quadrates of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/574 (A) and ZPAL V. 36/1764 (B) in lateral (A₁), medial (A₂), dorsal (A₃), ventral (A₄), anterior (A₅, B₁), and posterior (A₆, B₂) views. Abbreviations: dh, dorsal head; dt, dorsal tuberosity; lc, lateral condyle; mc, medial condyle; pr, pterygoid ramus; prc, pterygoid ramus concavity; qjf, quadratojugal facet; sh, shaft; tc, tympanic crest.

distal margins are thickened anteromedially, with an antero-posterior constriction of the ventral margin of the quadrate separating them (Fig. 6A₄). The medial condyle is more robust than the lateral condyle, and projects posteroventrally. Its posterior margin is confluent with the ventral portion of the shaft. The anterolateral edge of the quadrate and the posterior edge of the quadratojugal most likely formed a slit-like quadrate foramen, as in *T. hydroides* and *T. longobardicus* (Wild 1973: 12; Spiekman et al. 2020b: fig. 16).

Pterygoid: The pterygoid of *T. conspicuus* is known only from the incomplete specimen ZPAL V. 36/2541, which is

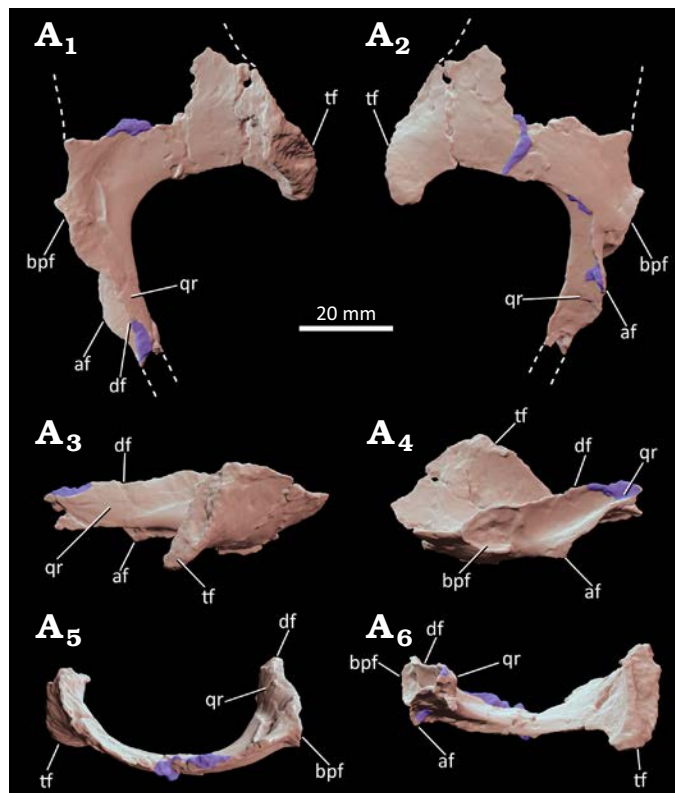


Fig. 7. Posterior portion of the right pterygoid of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/2541 in dorsal (A₁), ventral (A₂), lateral (A₃), medial (A₄), anterior (A₅), and posterior (A₆) views. Areas covered with sediment marked with blue hue. Abbreviations: af, arcuate flange; bpf, basipterygoid facet; df, dorsal flange; qr, quadrate ramus; tf, transverse flange.

missing the entire palatal ramus, but preserves most of the details of its posterior portion (Fig. 7). As most of the other cranial elements of *T. conspicuus*, the pterygoid is nearly indistinguishable from the pterygoid of *T. hydroides* as described by Spiekman et al. (2020b). The main difference is the more transversely concave dorsal surface of the pterygoid body in *T. conspicuus*, but this might be due to diagenetic changes. The bone is dorsoventrally thin and lateromedially slender, with the exception of the laterally extending transverse flange, which thickens considerably towards its distal end (Fig. 7A₆). As in *T. hydroides*, the articular surface of the transverse flange is rugose, flat, and spindle shaped in dorsolateral view (Fig. 7; Spiekman et al. 2020b).

The quadrate ramus projects strongly posteriorly, as a morphologically complex process. Between it and the transverse flange the posterior edge of the pterygoid is strongly concave in dorsal view, forming a wide, semi-circular embayment (Fig. 7A₁, A₂). The medial portion of the quadrate ramus is strongly concave in anterior or posterior view, with a deep groove flanked by two ridges—dorsally by an extremely thin dorsal flange, and ventrally by the ventromedially projecting arcuate flange (Fig. 7A₄). Both ridges are similar in height. The anterior portion of the groove, a cir-

cular basipterygoid facet, is distinctly outlined, with a dorsoventrally oriented ridge constituting its posterior margin.

Dentary: The elements constituting the posterior portion of the mandibular rami of *T. conspicuus* have still to be identified. Most of the length of the lower jaw is, however, preserved in several dentaries (e.g., ZPAL V. 36/2428). The dentary of *T. conspicuus* is a slender, elongate, and labiolingually thin element (Fig. 8). It bears at least 26 tooth alveoli (Fig. 8A₃), although no complete specimen has been found so far. As in the maxilla, the alveoli are all circular in dorsal view and densely packed in a single, continuous row along the entire preserved length of the dentary (Fig. 8A₃). As in the other jaw elements described here, the dentary teeth were lingually separated by triangular interdental plates (Fig. 8A₁, A₂). Between the interdental plates, the lingual margin of the anteriormost alveoli is formed as a deep, droplet-shaped notch (Fig. 8A₁, A₂). Similar to the maxilla, there are size differences in the alveoli (Fig. 8A₂). The anterior three alveoli are especially large, bearing teeth similar in size to the premaxillary teeth. Posterior to them, there is a series of about seven teeth which are much smaller. Continuing further posteriorly, the size of the alveoli changes in a manner similar to the maxilla, with some larger ones around the mid-length of the dentary and then

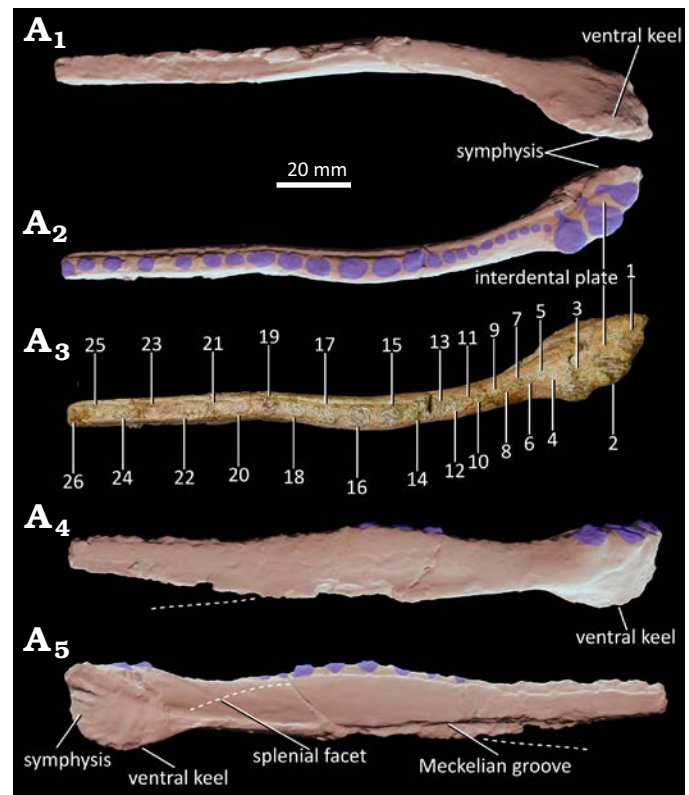


Fig. 8. Partial right dentary of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photograph (A₃), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (A₁, A₂, A₄, A₅). ZPAL V. 36/2428 in ventral (A₁), dorsal (A₂, A₃), lateral (A₄), and medial (A₅) views. Numerals indicate the alveoli. Areas covered with sediment marked with blue hue.

decreasing in size towards its posterior end. Although the alveoli are distributed in a single row, they are not located in a straight line in lateral view. Instead, their position changes labiolingually and dorsoventrally, undulating in two dimensions (Fig. 8A₂, A₄). The large anteriormost and middle teeth are located on the convexities of the dorsal margin of the dentary, thus being placed more labially and dorsally. All dentary teeth projected dorsally, with only the three anterior “fangs” being more anterodorsally oriented. In dorsal view, most of the length of the dentary is relatively straight, with only the middle section, which bore the larger teeth, being slightly labially expanded.

At the level of the maxilla-premaxilla contact, the anterior thickened portion of the dentary bends towards the contact with its antimere, following the curvature present in the premaxilla. The symphyseal surface is ventrally expanded, forming a ventral keel (Fig. 8A₄). The suture between the mandibular rami is interdigitating, with multiple longitudinal grooves and ridges being present (Fig. 8A₅). On the lingual surface of the dentary a plate-like portion of the bone is ventrally and dorsally limited by grooves that extend along the whole length of the dentary (Fig. 8A₅). The splenial articulated with this area. In medial view the anteriormost extent of the splenial facet is marked by a faint ridge, which extends obliquely (anteroventrally-posterodorsally) to the longitudinal axis of the bone, as in *T. hydroides* (Fig. 8A₅; Spiekman et al. 2020b). The preserved posterior portion of the dentary tapers in lateral view. Its posteroventral margin is formed as a lateromedially thin ridge (incompletely preserved in ZPAL V. 36/2428 see Fig. 8) which constituted the ventrolateral surface of the Meckelian groove (Fig. 8A₅). The middle section of the dentary, which bore the larger teeth, is dorsoventrally expanded and convex in lateral view. Between the middle expansion and the anterior portion, along the section that bears the smallest teeth, the dentary is dorsoventrally constricted. The lateral surface of the dentary is relatively smooth, with a slightly rugose texture. There are some foramina present along its anterior portion.

As with the maxilla, the anterior portion of the mandibular ramus of *T. conspicuus* is more similar in its morphology to *T. hydroides* than to *T. longobardicus*, but with some distinct differences. The ventral keel, which was considered a unique feature of *T. hydroides* by Spiekman et al. (2020b), and later described also for *Dinocephalosaurus orientalis* Li, 2003, by Spiekman et al. (2024c), is also present in *T. conspicuus*. Both *T. hydroides* and *T. longobardicus* have less than 20 dentary teeth, with the exact number being difficult to ascertain (Wild 1973; Nosotti 2007; Spiekman et al. 2020a, b). Even though the teeth positions and their size changes along the dentary are similar to what has been reported for *T. hydroides* (see Spiekman et al. 2020b), the incomplete dentary of *T. conspicuus* bears 26 alveoli, with some additional ones likely being present in its missing posterior portion. Thus, *T. conspicuus* probably had a considerably higher number of dentary teeth than other species of *Tanystropheus*.

Despite the general morphological similarity, the dentaries of *T. conspicuus* and *T. hydroides* differ in proportions. In the former the dentary is relatively lower and more dorsoventrally constricted along its anterior portion than the latter (Wild 1973; Spiekman et al. 2020b). In both species the dorsal surface of the dentary is undulating in lateral view, with a convexity mid-way along its length (Fig. 8A₂; Wild 1973; Spiekman et al. 2020b). There seems to be some variation in the relative differences of height changes of the dentary along its length in various *T. hydroides* individuals (undulating, Wild 1973: fig. 17 and relatively straight, Spiekman et al. 2020b: fig. 28), but in *T. conspicuus* the dorsal surface of the dentary is even more undulating.

Dentition: Although teeth referred here to *T. conspicuus* are only found isolated (excluding a fragment still preserved in an alveolus within the ZPAL V. 36/179 premaxilla), they are extremely similar to the teeth preserved in the jaws of *T. hydroides* and can be easily distinguished from the teeth of the other contemporaneous aquatic reptiles. Moreover, their relatively high frequency in Miedary corresponds to the large number of *T. conspicuus* bones found at that site. Due to the previous absence of cranial material of *T. conspicuus*, the published descriptions of its dentition were limited. Fraas (1896) mentioned that the teeth of *N. blezingeri* (junior synonym of *T. conspicuus*) are slender, slightly curved, and originated from the premaxilla. The apical half of their tooth crown was smooth, and the basal half had only a few shallow grooves, in contrast to other species of *Nothosaurus* in which the grooves are very close together and deep. Corroy (1928) mentioned that the “anterior” part of the crown of these teeth possess ridges, whereas the “posterior” side is smooth. The first extensive description of these teeth was provided by Schoch et al. (2018). It closely corresponds to the observations provided here.

The teeth of *T. conspicuus* are slender, tall, conical, and lingually curved (Fig. 9A, C). The longest known specimens reach about seven cm in total preserved length, of which less than a half can be considered the crown (not including the worn apex). The long root has a smooth surface and transitions into the crown without a change of tooth diameter. Although it is difficult to assign an exact position of an isolated tooth within a jaw ramus exclusively based on its morphology, the largest and most curved teeth of *T. conspicuus* (“fangs”) likely originated from the premaxillae and the anterior part of the dentary, as in *T. hydroides* (Wild 1973; Spiekman et al. 2020b). More posteriorly originating teeth are usually relatively shorter and straighter. All teeth referred to *T. conspicuus* herein share the same crown surface characteristics and general morphology (homodonty) with those of *T. hydroides*, but contrast to the heterodont dentition in *T. longobardicus* (Wild 1973; Spiekman et al. 2020a, b). The crown is lingually curved, with its apex frequently lingually worn. Low apicobasal ridges (see McCurry et al. 2019) are present on all surfaces of the crown. They are not strictly parallel to each other, with some ridges merging or bifurcating along their apicobasal length. On the labial side

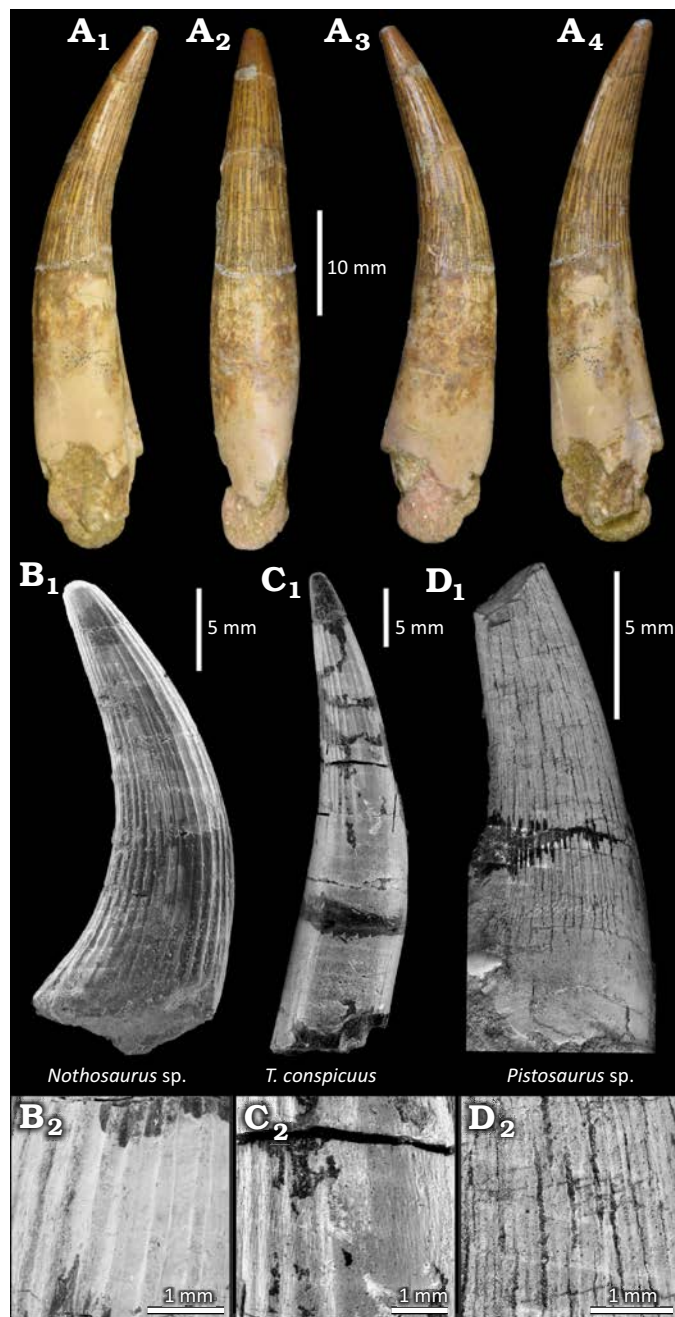


Fig. 9. Photographs (A) and stitched SEM images (B–D) of teeth of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland (ZPAL V. 36/1204, A; ZPAL V. 36/163, C), the nothosaurid sauropterygian *Nothosaurus* sp. from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland (ZPAL V. 36/254, B), and the pistosaurid sauropterygian *Pistosaurus* sp. from the Upper Muschelkalk (upper Anisian to lower Ladinian, Middle Triassic) of Laryszów, Poland (ZPAL V. 84/LA/001, D), in mesial/distal (A₁, A₃, B₁, C₁, D₁), labial (A₂), and lingual (A₄) views, and their surface under higher magnification (B₂, C₂, D₂).

of the crown they are much more sparsely and unevenly distributed, with finer secondary ridges being present between the main ones (pattern similar to *Tanystropheus* teeth reported by Dalla Vecchia 2006). The ridges are relatively taller, much better defined and organised. There are no ca-

rinae or serrations. SEM imaging reveals that the crown surface is covered with a network of microscopic ridges and grooves that are oriented semi-parallel to the apicobasal axis of the tooth (Fig. 9C₂). The implantation of all premaxillary, maxillary and dentary teeth in *T. conspicuus* was subthecodont (sensu Bertin et al. 2018) or anisothecodont (sensu Mestriner et al. 2025), in the sense that the tooth sockets are asymmetric and cover much more of the length of the tooth labially than lingually. The almost complete absence of teeth preserved in the jaws of *T. conspicuus* indicates that the teeth were not ankylosed to the jaw.

Teeth of *T. conspicuus* have long been confused with the teeth of sauropterygians, especially with species of *Nothosaurus* and *Pistosaurus*, with several works providing a brief comparison between them (Fraas 1896; Corroy 1928; Dalla Vecchia and Avanzini 2002; Dalla Vecchia 2006; Schoch et al. 2018). Results from a SEM analysis provide more definitive criteria to distinguish them from each other. By comparison with *T. conspicuus*, the apicobasal ridges are much more evenly distributed and regularly arranged in the teeth of *Nothosaurus* sp. from Miedary (compare Fig. 9B₁ and C₁). The SEM results show that at micro-scale the crown surface in *Nothosaurus* sp. is smooth and lacks any secondary ridges (Fig. 9B₂). Moreover, the teeth of *T. conspicuus* are much more frequently preserved with a root. These characteristics demonstrate that the teeth of *T. conspicuus* and *Nothosaurus* sp. can be readily distinguished, despite being somewhat similar at first glance.

As previously noted by Fraas (1896) and Corroy (1928), the teeth of *T. conspicuus* closely correspond in their morphology to those of *P. longaevus*. Even recently, Diedrich (2012: fig. 14.1) described a specimen U-MO BT 3078 as belonging to *T. conspicuus*, whereas in fact it is indistinguishable from the teeth of *P. longaevus*. A specimen referred to “*Tanystropheus longibardicus*” (sic) by Diedrich (2009: MSB No. Pal 327–534) is likely of the same affinities. Although the tooth crowns of both reptiles share the convergently acquired tall, slender, conical shape, those of *Pistosaurus* sp. are devoid of large, well-defined ridges, instead being covered with densely distributed, irregular, shallow grooves (compare Fig. 9C and D). On the microscopic scale their crown surface is also relatively smooth, similar to *Nothosaurus* sp. (Fig. 9B and D). The miniscule grooves and ridges scattered across the tooth crown surface in *T. conspicuus* do not seem to be present in Middle Triassic sauropterygians, but instead are likely characteristic of some Triassic archosauromorphs. The surface of the teeth of *T. conspicuus* is reminiscent in its morphology to that illustrated by Dorka (2002) for the specimens originating from the Ladinian deposits of Schöningen (Germany). The morphotypes 12 and 13, and some of the teeth referred to morphotype 1 (Dorka 2002: fig. 2C) bear a striking resemblance to the Miedary material despite the size difference. A similar morphology was also described by Ősi et al. (2020: morphotype 2) for the teeth from the Ladinian Templomhegy Dolomite in Hungary, which has yielded ma-

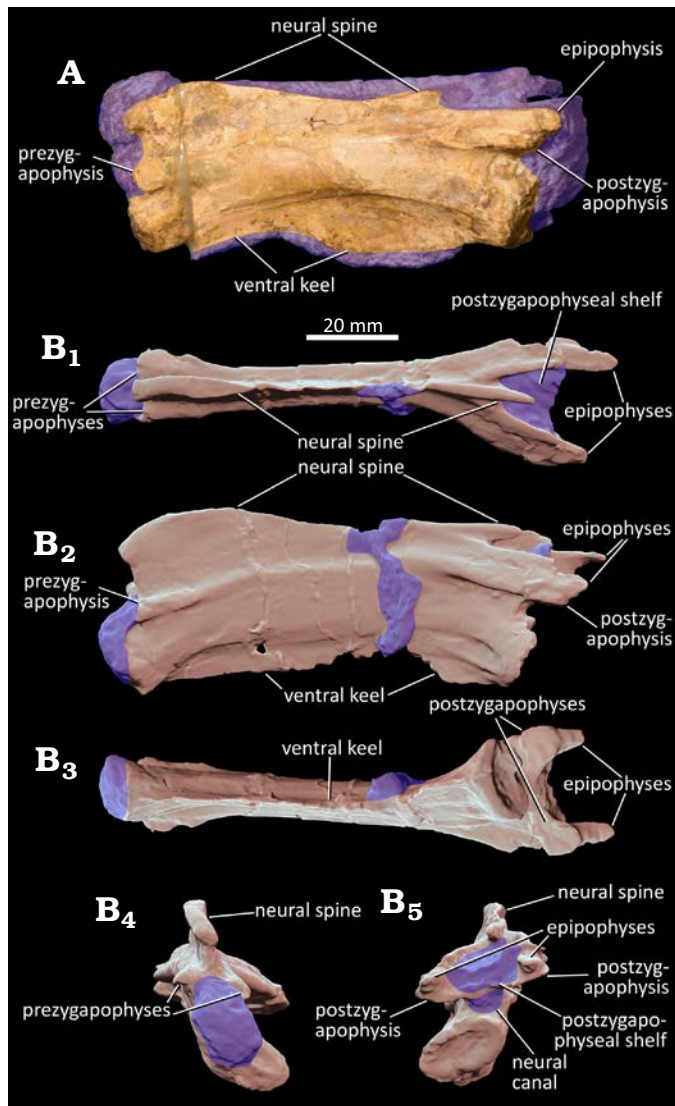


Fig. 10. Axes of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photograph (A), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (B). ZPAL V. 36/1170 (A) and ZPAL V. 36/847 (B) in left lateral (A, B₂), dorsal (B₁), ventral (B₃), anterior (B₄), and posterior (B₅) views. Areas covered with sediment marked with blue hue.

terial of *Tanystropheus* sp. More microscopic scale analyses are needed to better understand the morphological disparity of the teeth in early archosauromorphs and possibly permit their confident identification.

Postcranium: Axis: The axis of *T. conspicuus* is an elongate, slender element (Fig. 10). As in all the succeeding vertebrae, its centrum is amphicoelous but not notochordal and its articular surfaces are roughly circular in anterior and posterior views. The centrum is roughly two to three times longer than the vertebra is tall at its anteroposterior midpoint. Its ventral margin is formed as an extremely thin lamina, the ventral keel, which, compared to the other cervical vertebrae, is especially strongly developed in the axis (Fig. 10A). The anterior portion of the ventral keel is deeply concave in lateral

view, but the curvature of its distal margin changes around the mid-length of the centrum, becoming convex in its posterior portion (Fig. 10A). A pair of longitudinal laminae runs roughly parallel to the ventral margin of the axis on either side of the keel. There are no subcentral foramina on the ventral surface of the centrum. The articular surface for the rib occupies the anteroventral corner of the centrum, but it is not delimited in any way other than a change in bone texture.

The openings of the neural canal are rhomboidal. The prezygapophyses are strongly reduced, their distal margin does not extend beyond the anterior edge of the centrum (Fig. 10B₁, B₂). They are formed as slight anterolateral projections of the longitudinal laminae that mark the base of the neural spine (Fig. 10B₂). Their articular surfaces are small, elliptical in dorsal view and dorsolaterally oriented. The postzygapophyses are long and relatively slender. They extend far beyond the posterior edge of the centrum (Fig. 10B₂). Their elliptical articular surfaces are roughly ventral-facing (Fig. 10B₃). A thin plate-like lamina (= transpostzygapophyseal lamina, = Horizontallamelle sensu Wild 1973) spans the area between the postzygapophyses, constituting the posteriormost portion of the neural canal roof, and forming a triangular shelf in dorsal view (Fig. 10B₁). In posterior view this shelf extends anteriorly below the posterior overhang of the neural spine (postzygapophyseal trough sensu Rieppel 2001). The dorsal portion of both postzygapophyses is formed as a distinct ridge, which projects posteriorly as a process (epipophysis). The neural spine is low, especially in its posterior portion, and tapers posterodorsally to form a long, conical process, which is similar in its orientation and size to the distal tips of the epipophyses (Fig. 10B₁, B₂). The anterior portion of the neural spine is strongly convex in lateral view (Fig. 10A, B₂). Its anterior margin is nearly vertical and merges with its dorsal margin dorsal to the prezygapophyses, forming an anterior overhang. The antero-distal portion of the neural spine is distinctly transversely expanded and rugose (Fig. 10B₁).

The axis of *T. conspicuus* is similar in its proportions to the axes known for *T. hydroides* (e.g., PIMUZ T 2790, PIMUZ T 2819, see Wild 1973; Spiekman et al. 2020b) but it is relatively more elongate than the same element in *T. longobardicus* (e.g., MSNM BES SC 265, PIMUZ T 2791, PIMUZ T 3901, see Wild 1973, 1980a; Nosotti 2007). The high dorsal extent of the distal expansion of the anterior portion of the neural spine is, however, a feature shared by *T. conspicuus* and *T. longobardicus*, but in contrast with *T. hydroides*, in which the anterodistal margin of the neural spine is only slightly convex (Wild 1973; Spiekman et al. 2020b). Moreover, the axis of *T. conspicuus* is distinct from other species of *Tanystropheus* in the presence of a ventral keel with a convex distal margin (which is relatively straight and less well developed in both *T. hydroides* and *T. longobardicus*, compare Wild 1973, 1980a; Nosotti 2007; Spiekman et al. 2020b).

Middle cervical vertebrae: Due to their elongation, the middle cervical vertebrae are the most striking element of

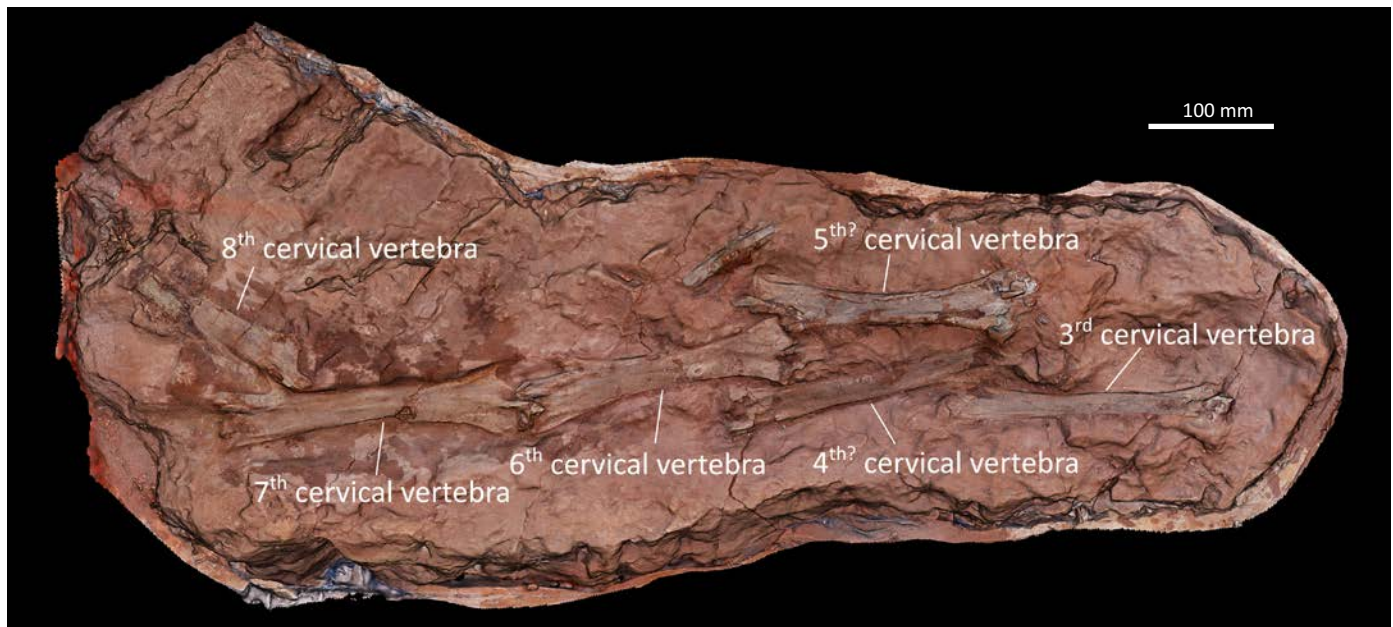


Fig. 11. A plaster jacket of ZPAL V. 36/100 preserving a semiarticulated series of middle cervical vertebrae of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Snapshot of a photogrammetric model with Lambertian Radiance Scaling shader enabled. Cervical vertebrae four and five are in left lateral view, and the rest in right lateral view. Model courtesy of Tomasz Szczygielski (ZPAL).

the osteology of *Tanystropheus*. They are the most elongate vertebrae among all known animals, with only azhdarchid pterosaurs reaching similar proportions (Renesto 2005; Rytel et al. 2024b). In all middle cervical vertebrae of *Tanystropheus* the elongation ratio (centrum length versus height at midpoint) exceeds four (AR personal observation, but see Wild 1973; Spiekman et al. 2021). This ratio varies highly between individuals, reaching up to about 20 in PIMUZ T 2790, the holotype of *Tanystropheus hydroides* (personal observation AR). In cervical vertebrae three to eight in *T. longobardicus* and *T. hydroides* it usually remains relatively constant, with an average value of around 13 (AR personal observation). In comparison, the same vertebrae in *T. conspicuus* are usually taller and more robust, with their average elongation ratio of around nine (see measurements in SOM: table 1). Whereas Wild (1973) was very specific in attributing each particular isolated cervical vertebra described by him to its original location in the vertebral column, the morphometric study of Rytel et al. (2024a) showed that the differences in shape within cervical vertebrae three to eight are marginal. Their morphology changes gradually along the vertebral column, and consequently, attributing any isolated cervical from this section to its exact place in the sequence is highly equivocal, as knowledge on the ontogenetic and intraspecific variation of skeletal morphology in *T. conspicuus* is limited. By contrast, the posterior-most cervical vertebrae nine to thirteen can be easily differentiated due to their markedly changing proportions and neural spine shape and are described separately.

Nevertheless, although it is difficult to refer isolated middle cervical vertebrae to their original position, some distinct differences between them are present. The anteri-

or-most middle cervical vertebrae are generally more slender and elongate than the succeeding vertebrae, as can be determined from the only known semi-articulated series of cervical vertebrae from the same individual of *T. conspicuus*, ZPAL V. 36/100 (see Fig. 11). However, the neural spine height varies substantially among the isolated middle cervical vertebrae referred to *T. conspicuus* (see measurements in SOM: table 1), and to a much larger extent than present in ZPAL V. 36/100 (see Fig. 11). This is likely due to a complex combination of several factors, and therefore the neural spine shape represents a poor proxy for identifying the position of isolated vertebrae. Importantly, the length changes of succeeding cervical vertebrae of *T. conspicuus* follow the pattern recorded for other species of *Tanystropheus* by Peyer (1931: fig. 27), Wild (1973: fig. 29), and Nosotti (2007: fig. 54). In ZPAL V. 36/100 (see Fig. 11), vertebrae three to six have a relatively constant centrum length, with the seventh cervical vertebra being only slightly longer (SOM: table 1). The ninth and tenth cervical vertebrae are the longest vertebrae of *T. conspicuus*, whereas the cervical vertebrae posterior to these are much shorter. This corresponds to the configuration in *T. hydroides* and *T. longobardicus* (Peyer 1931; Wild 1973; Nosotti 2007; AR personal observation).

The description of the cervical vertebrae three to eight is based on the lectotype specimen of *T. conspicuus*, U-MO BT 740 (Fig. 12), with some additional complementary data gathered from the newly referred specimens from Miedary (Fig. 13), including the semi-articulated cervical series ZPAL V. 36/100 (Fig. 11).

As in all other vertebrae, the centrum in the cervical vertebrae of *T. conspicuus* is deeply amphicoelous but not noto-

elliptical, but differ slightly in shape and location, even within the same pair. Posterior to the foramina, on the ventral surface of the centrum, two pairs of laminae are present, the ventromedial and posteroventral laminae (Figs. 12A₃, A₅, 13A₃, A₅). The ventromedial laminae extend obliquely between the ventral keel and the ventrolateral laminae. The posteroventral laminae are located posteriorly to them, along the midline between the posterior portion of the ventral keel and the ventrolateral laminae. Both anteroventral and posteroventral laminae are present in all middle cervical vertebrae of *T. conspicuus* in which this character can be assessed, as well as in the three-dimensionally preserved specimens from Romania and north-eastern Italy (Jurcsak 1975; Dalla Vecchia 2006; AR personal observation). They are seemingly absent in the specimens from Monte San Giorgio and China, but this might be due to the differences in preservation (i.e., diagenetic compression, AR personal observation).

The lateral surface of the centrum is smooth with no noticeable foramina. The parapophysis and diapophysis are extremely reduced and essentially confluent with each other, forming triangular rib attachment sites on the anterolateral corners of the centrum (Figs. 12A₃, 13A₃). They barely project from the centrum surface, with the associated ribs being located very close to the vertebra when compared to other archosauromorphs. The rib attachment site is partially located on a lamina, which connects the anteroventral corner of the centrum with the base of the prezygapophysis, extending beyond the anterior edge of the centrum.

The neural canal openings differ in shape, with the anterior one being triangular and the posterior one roughly circular (Figs. 12A₂, A₄). The prezygapophyses project strongly anteriorly and are triangular in transverse cross-section (Fig. 13A₂). Their distal end is formed as a rounded, non-tapering expansion in lateral view, which extends anteriorly from the lamina that connects the centrum and the prezygapophyseal articular surface. The dorsal surface of the prezygapophyses is confluent with the base of the neural spine (Figs. 12A₃, 13A₃). The prezygapophyseal articular surfaces are almost dorsally facing, with only a slight medial tilting (Figs. 12A₂, 13A₂). The postzygapophyses extend far beyond the posterior edge of the centrum and in lateral view are separated from it by a deep notch (Figs. 12A₃, 13A₃). Massive, tall epipophyses project posterodorsally from them. Contrasting with the morphology of the epipophyses of the axis, their distal tips are rounded and non-tapering in lateral view (Figs. 12A₃, 13A₃). Between the epipophyses, a broad shelf is located. It covers the entire surface between the neural spine and the posterior ends of the postzygapophyses (Figs. 12A₁, A₄, 13A₁, A₄). The postzygapophyseal articular surfaces are well outlined, elliptical, and oriented corresponding to the prezygapophyseal articular surfaces—nearly parallel to the horizontal plane, but with their lateral surface only slightly raised (Figs. 12A₄, 13A₄).

The neural spine is extremely low, being barely discernible in its middle section, with only its anterodistal and

posterodistal portions projecting from the dorsal surface of the vertebra (Figs. 12A₃, 13A₃). In some of the middle cervical vertebrae (e.g., U-MO BT 740) the neural spine is a distinct keel, running along most of the length of the vertebra, but histological studies indicate that neural spine height might, to some extent, change during ontogeny (Jaquier and Scheyer 2017; Rytel et al. 2024b). The shape of the anterior portion of the neural spine varies highly between different specimens, mostly because only a few cervical vertebrae preserving its distal tip due to their fragility (e.g., ZPAL V. 36/101, see Czepeński et al. 2023). In those most completely preserved specimens, the anterior portion of the neural spine is roughly triangular in lateral view. Its anterior edge is split, with two laminae running from its base merging distally, thus forming a deep, triangular concavity (Figs. 12A₂, 13A₂), which was interpreted as an attachment for the dorsal ligament by Wild (1973). The anterodorsal tip of the neural spine is anteriorly oriented. The posterior portion of the neural spine exhibits a similar morphology, but it is usually lower, and projects posteriorly as a tapering, conical process overhanging the postzygapophyseal shelf (Fig. 13A₃).

All known cervical vertebrae three to eight of *Tanystropheus* species share the neural spine morphology (von Meyer 1847–1855; von Huene 1907–1908; Peyer 1931; Wild 1973, 1980a; Jurcsak 1975; Renesto 2005; Dalla Vecchia 2006; Li 2007; Nosotti 2007; Rieppel et al. 2010) and hence they are not diagnostic at the species level, being differentiated mostly on the basis of size and provenance. The ninth cervical vertebra is the anteriormost postaxial vertebra of *T. conspicuus* in which the neural spine shape changes distinctly (Fig. 14), marking the beginning of the cervico-dorsal transition. Whereas in the preceding middle cervical vertebrae the neural spine is nearly completely reduced in its middle section, in the ninth cervical vertebra it forms a low, narrow, but continuous ridge (Fig. 14A₃). Its height changes along its length, forming a slight but distinct crest near the middle of the vertebral length.

The succeeding tenth cervical vertebra shares this morphology but with the neural spine height increased by a magnitude in its anteroposterior middle portion (Fig. 15). Whereas in the more anterior postaxial vertebrae the neural spine is concave (e.g., Fig. 13A₃), in the tenth cervical vertebra it is formed predominantly as a convex ridge in lateral view (Fig. 15A, B₃). Anterior to the mid-length of the vertebra, its neural spine becomes concave in lateral view, reaching the point of its minimum height, and then rises again to form the anterior extension found also in the preceding elements (Fig. 15A, B₃). The dorsal margin of the neural spine of the tenth cervical vertebra of *T. conspicuus* is, therefore, undulating in lateral view (Fig. 15A, B₃). The tenth cervical vertebra in other species of *Tanystropheus* has a much lower neural spine with a straight distal margin (see Wild 1973; Renesto 2005; Li 2007; Nosotti 2007; Rieppel et al. 2010). Moreover, in *T. conspicuus* the distal margin is distinctly transversely expanded, forming a distal thickening

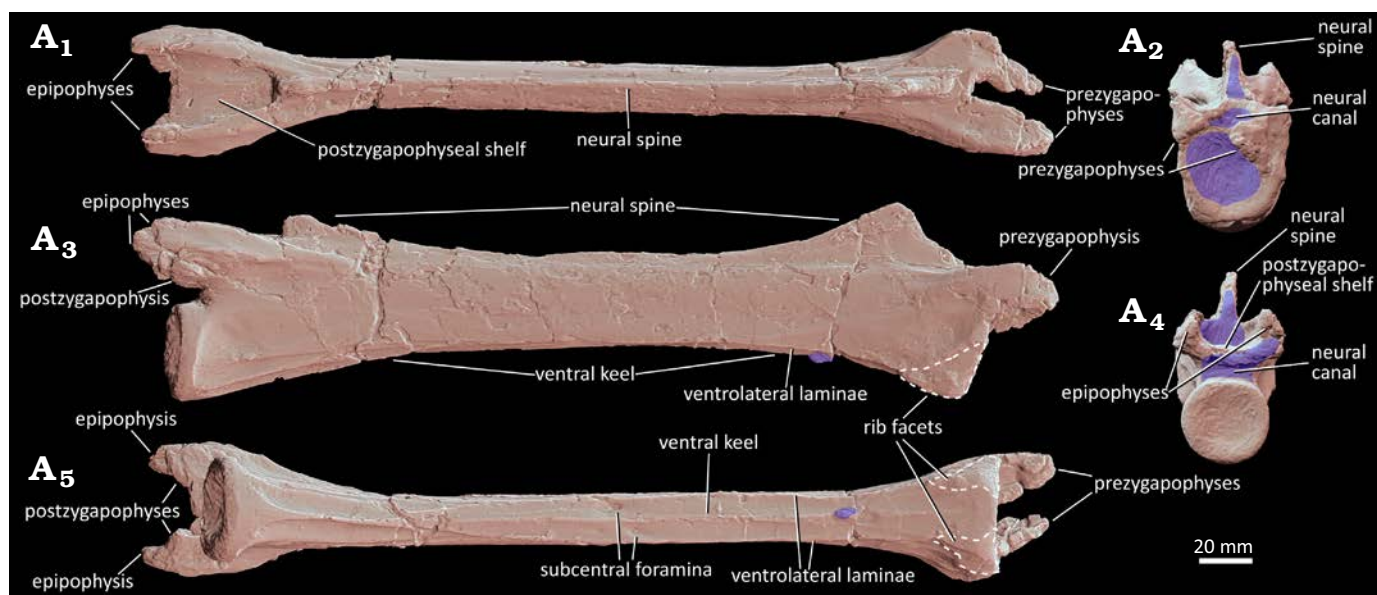


Fig. 14. Ninth cervical vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1202 in dorsal (A₁), anterior (A₂), right lateral (A₃), posterior (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

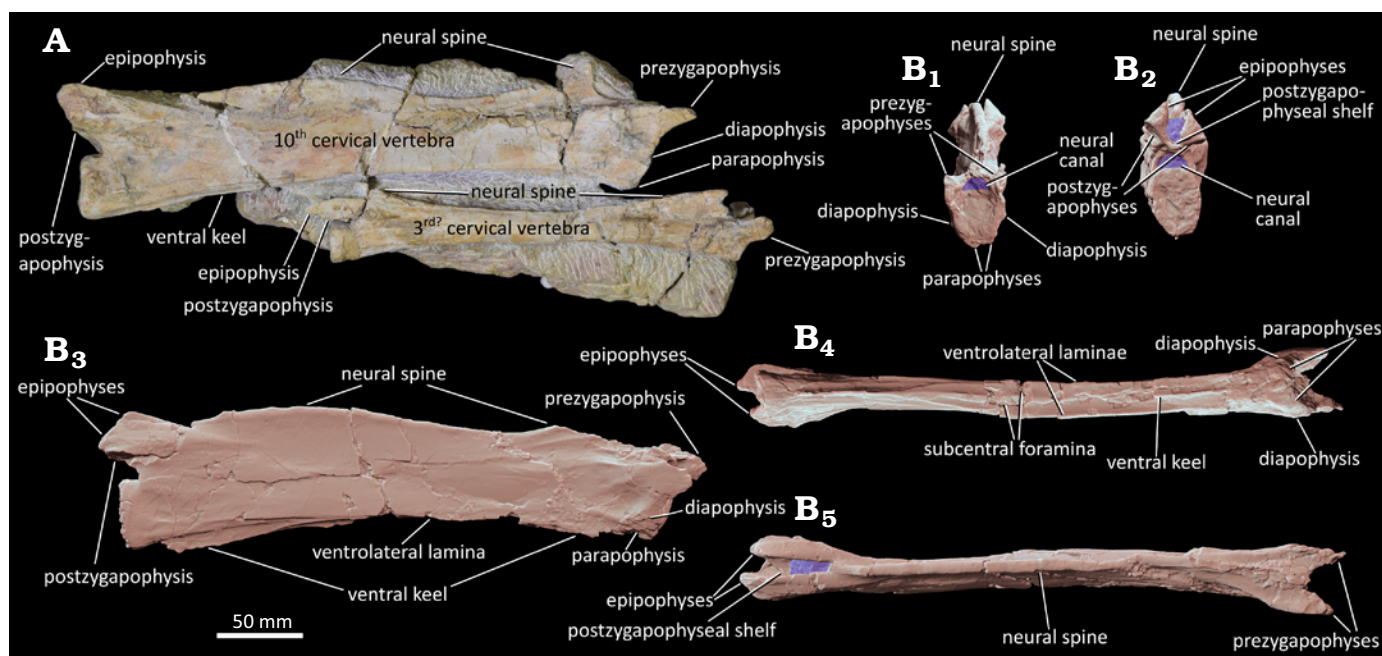


Fig. 15. Tenth cervical vertebrae of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photograph (A), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (B). ZPAL V. 36/186 (A) and ZPAL V. 36/105 (B) in right lateral (A, B₃), anterior (B₁), posterior (B₂), ventral (B₄), and dorsal (B₅) views. Areas covered with sediment marked with blue hue.

(Fig. 15B₅), which is also present in all succeeding vertebrae up to the anterior caudal vertebrae. A lamina is present on the anterior part of the lateral surface of the neural spine of the 10th vertebra. It runs parallel to its distal margin. Only present in this cervical, it can serve as a basis for the identification of partially preserved, isolated vertebrae. In the ninth and tenth cervical vertebrae the rib articulation surface is more prominent ventrally, but it is not until the eleventh cer-

vical vertebra that the parapophysis and diapophysis can be unequivocally regarded as functionally separate, with the capitulum and tuberculum of the corresponding rib also being distinctly separated (contra Wild 1973, who differentiated them in the two preceding cervical vertebrae as well).

Posterior cervical vertebrae: Between the tenth and eleventh cervical vertebrae of *Tanystropheus* there is considerable morphological disparity, probably caused by the

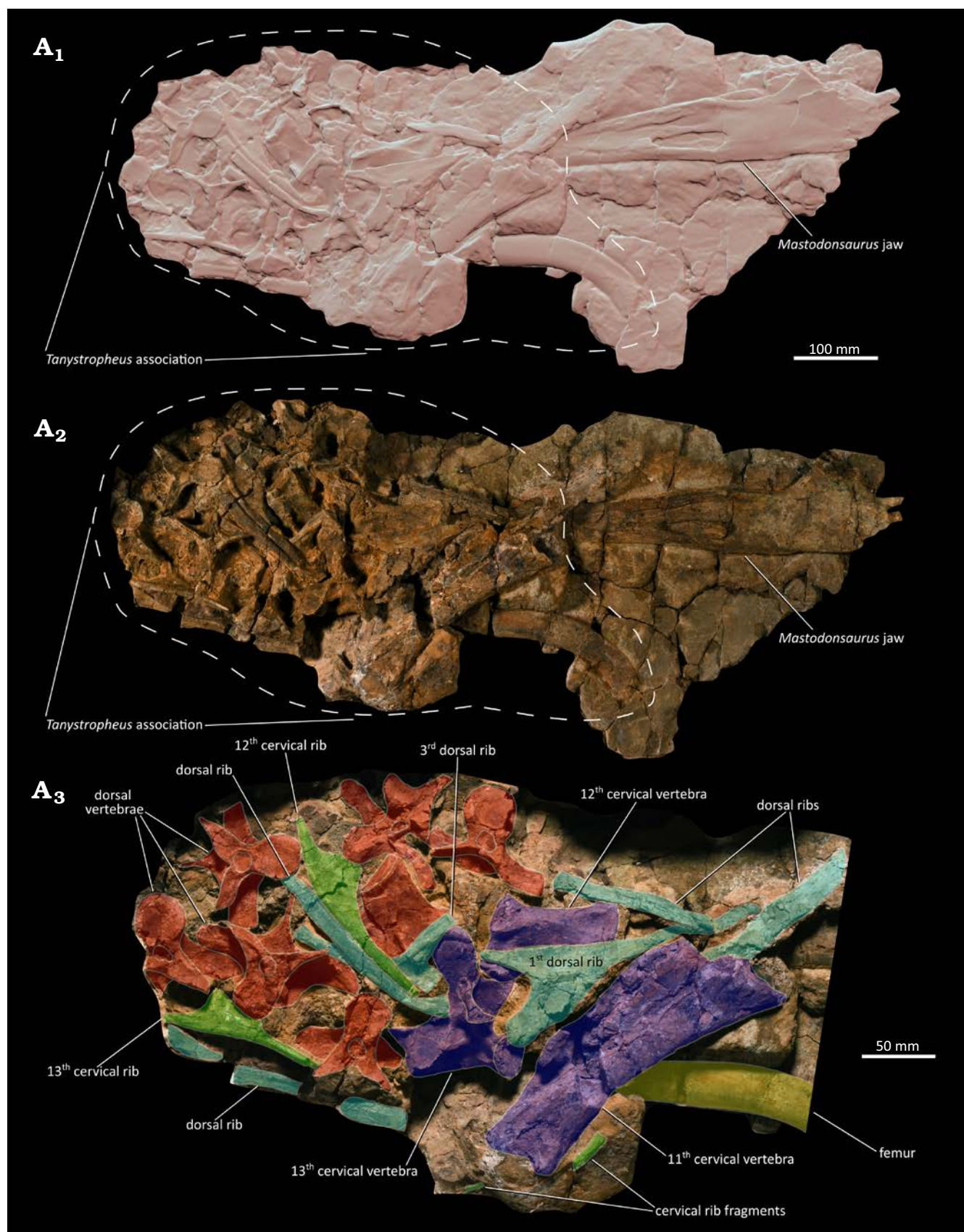


Fig. 16. Association of elements from the cervico-dorsal transition of a single individual (ZPAL V. 36/584) of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. A three-dimensional model snapshot with Lit Sphere Radiance Scaling shader enabled (A₁), and photograph (A₂), photograph with individual elements marked with different colours (A₃).

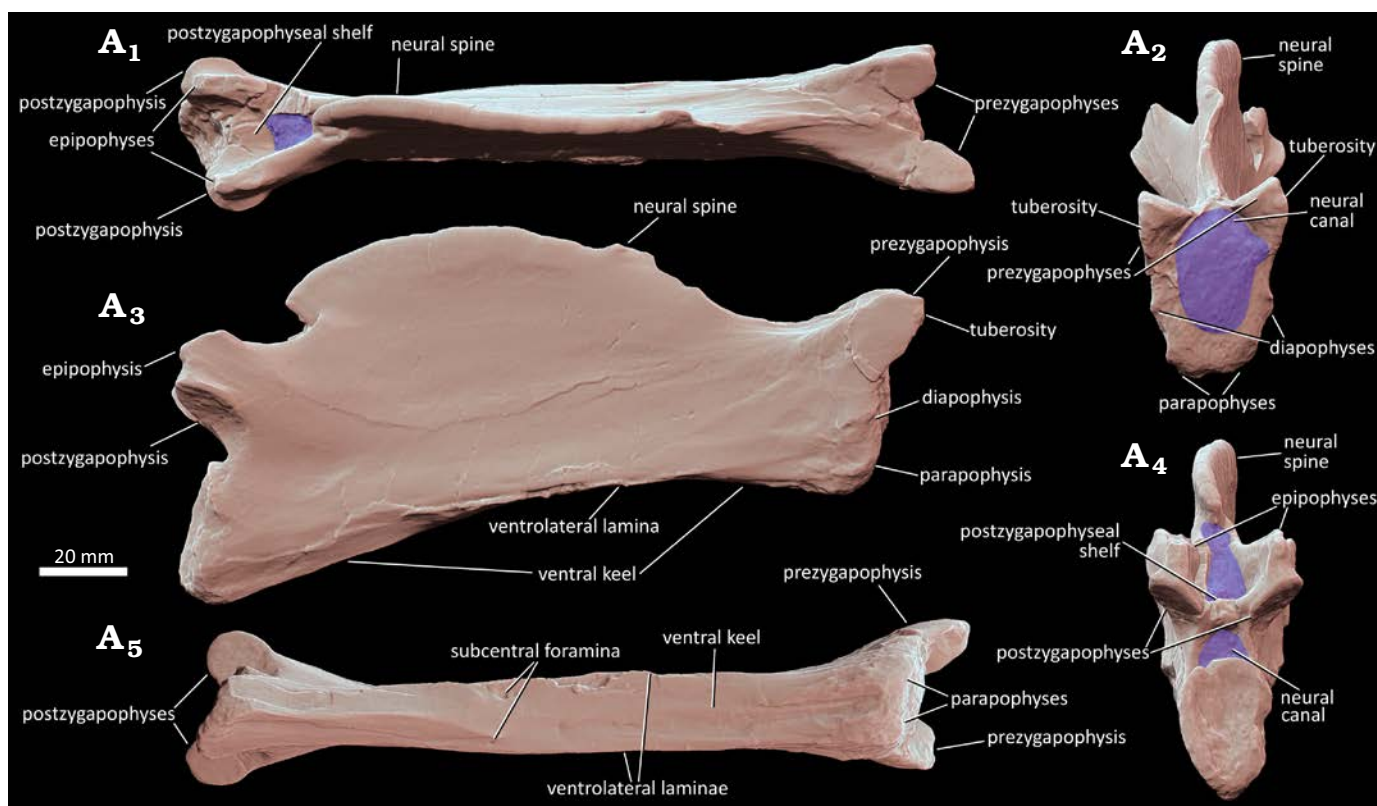


Fig. 17. Eleventh cervical vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1171 in dorsal (A₁), anterior (A₂), right lateral (A₃), posterior (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

expression of different sets of hox-genes (Rytel et al. 2024a). As a result, each of the three cervical vertebrae succeeding the tenth is less elongate than its predecessor. One of the newly referred specimens of *T. conspicuus*, ZPAL V. 36/584, preserves all three elements in close association, confirming their correct identification (Fig. 16).

The eleventh cervical vertebra, described in detail by Wild (1973), is still relatively elongate (Fig. 17). The characteristics of its centrum, other than the relative length, are generally similar to the middle cervical vertebrae. The subcentral foramina are located posterior to the mid-length of the vertebra (Fig. 17A₅). The ventral keel as well as the ventrolateral and posteroventral laminae are present (Fig. 17A₅). Importantly, although the articular surfaces of the centrum are vertical oriented and lie on parallel planes, the anterior articular surface is located much more dorsally than the posterior one (Fig. 17A₃). The ventral surface of the centrum is, therefore, inclined, as was also reported for the twelfth cervical vertebra of *T. longobardicus* by Renesto (2005). In *T. conspicuus* this features is much more pronounced than in other species of *Tanystropheus* (see Wild 1973; Renesto 2005; Li 2007; Nosotti 2007; Rieppel et al. 2010). The articular surfaces of the centrum are elliptical, being taller than wide (Fig. 17A₂, A₄). The diapophyses and parapophyses are separate and formed as robust, but weakly projecting tuberosities in the anteroventral portion of the centrum (Fig. 17A₂, A₃).

The openings of the neural canal are semicircular, with a flattened ventral margin (Fig. 17A₄). The pre- and postzygapophyses are relatively much shorter than in the preceding vertebrae, but they still extend beyond the corresponding end of the centrum (Fig. 17A₃). The anteroventral margin of the prezygapophysis is more dorsally located than in the middle cervical vertebrae, thus only covering the dorsalmost portion of the anterior articular surface of the centrum in lateral view (Fig. 17A₃). The anterodorsal margin of this lamina is convex, forming a mound-like tuberosity, which projects further anteriorly than the prezygapophyseal facet. All zygapophyseal articular surfaces are elliptical and sub-vertical, with their lateral margins slightly raised (Fig. 17A₂, A₄). The epipophyses are much more robust and taller, but anteroposteriorly shorter, than in the middle cervical vertebrae (Fig. 17A₃, A₄). They delimit the postzygapophyseal shelf bilaterally as tall, thick ridges and do not extend posteriorly beyond the postzygapophyses (Fig. 17A₁, A₃).

The concavity formed at the base of the posterior portion of the neural spine is deep. The neural spine is continuous and convex in lateral view. By contrast with the undulating distal margin observed in the neural spine of the tenth cervical vertebra, in the eleventh cervical vertebra the distal margin is expressed as a gradually sloping, crescent-shaped curve (Fig. 17A₃). It reaches its maximum height posterior to the mid-length of the vertebra. The anterodorsal margin of the neural spine is not bifurcated, and thus, the anterior

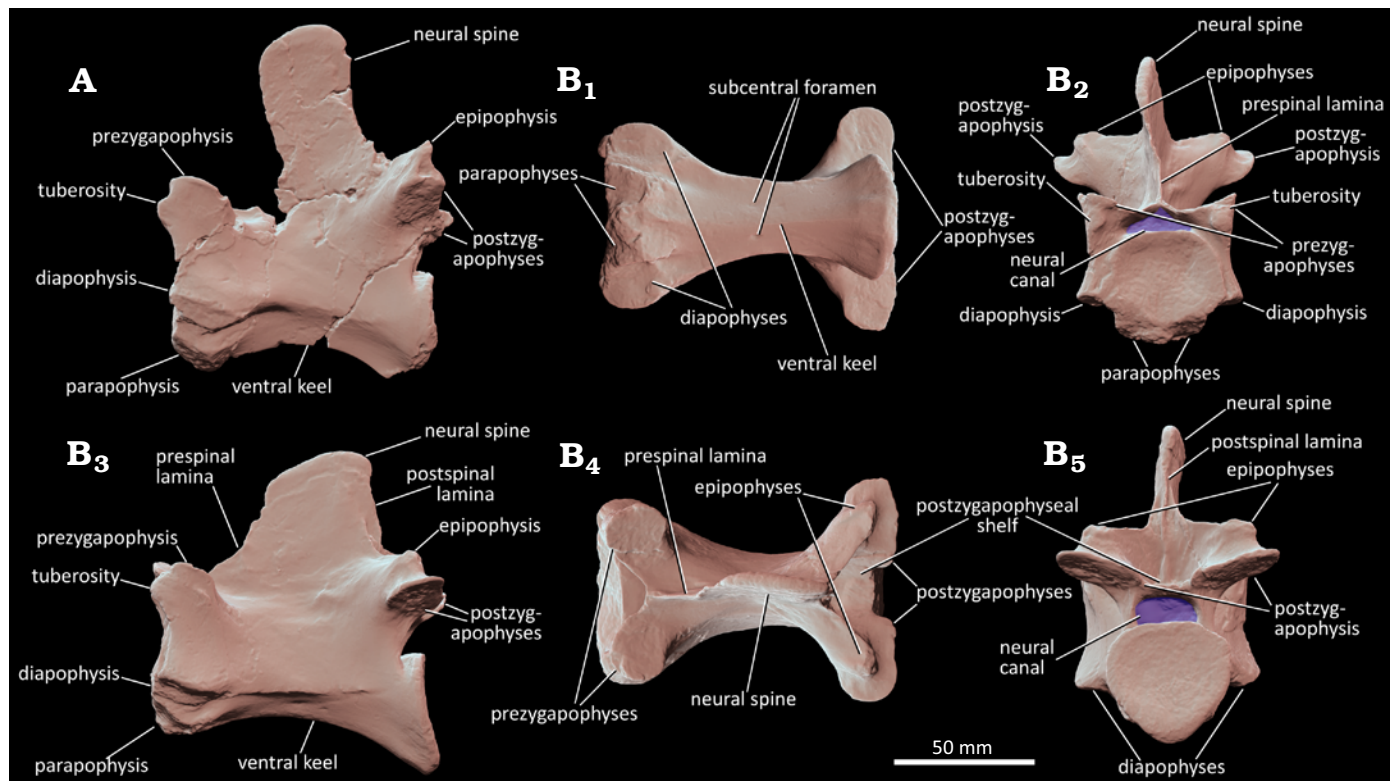


Fig. 18. Twelfth cervical vertebrae of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/108 (A) and ZPAL V. 36/1209 (B) in left lateral (A, B₃), ventral (B₁), anterior (B₂), dorsal (B₄), and posterior (B₅) views. Areas covered with sediment marked with blue hue.

concavity observed in the preceding vertebrae is absent (Fig. 17A₂). The distal margin of the neural spine is transversely expanded and thickened, especially in its tallest part (Fig. 17A₁). In some specimens the anterior portion of this expansion is marked by the presence of an anterodorsally projecting tuberosity (Fig. 17A₁–A₃). The posterior portion of the neural spine forms as a posteriorly projecting tapering process that overhangs the postzygapophyseal shelf (Fig. 17A₃). In the eleventh cervical vertebra of other species of *Tanystropheus* the neural spine is much lower, and its distal margin is straight, or even slightly concave, in lateral view (see Wild 1973; Renesto 2005; Li 2007; Nosotti 2007; Rieppel et al. 2010). Additionally, in *T. conspicuus* the height of the neural spine increases gradually along its anterior portion, whereas in other species of *Tanystropheus* it rises sharply and remains relatively constant along its entire length.

The twelfth cervical vertebra of *T. conspicuus* is a relatively robust element compared to the preceding cervical vertebrae (Fig. 18). Its height at mid-length is subequal to the length of the centrum (Fig. 18A, B₃). As for the eleventh cervical vertebra, the ventral surface of the twelfth cervical vertebra is inclined (Fig. 18A, B₃), corresponding to the condition reported for *T. longobardicus* by Renesto (2005). The centrum itself is parallelogram-shaped in lateral view, with its ventral surface being distinctly concave and marked by the presence of a weakly outlined keel (Fig. 18A, B₃). At

least one of the pair of subcentral foramina is usually present, situated lateral to the keel, but they are much smaller than in the preceding vertebrae (Fig. 18B₁). The anterior articular surface of the centrum is circular in anterior view (Fig. 18B₂). The posterior surface is ventrally expanded, appearing sub-triangular in posterior view (Fig. 18B₅). The centrum is spool-shaped in ventral view (Fig. 18B₁), with its middle section being laterally constricted, and its anterior portion being considerably expanded transversely due to the presence of robust, stout diapophyses and parapophyses. Their articular surfaces are elliptical and predominantly ventrally oriented (Fig. 18A, B₁, B₃). The parapophyses lie directly adjacent to each other, being separated only by the anterior portion of the ventral keel (Fig. 18B₁, B₂).

The anterior neural canal opening is triangular and the posterior one is subrectangular (Fig. 18B₂, B₅). The prezygapophyses are stocky, barely extending beyond the anterior articular surface of the centrum (Fig. 18A, B₃). Similar to the condition observed in the eleventh cervical vertebra, they bear distinct mound-like anteriorly projecting tuberosities (Fig. 18A, B₂, B₃), which are shorter but more robust than in the middle cervical vertebrae. The prezygapophyseal articular surfaces are positioned dorsal to the mound-like tuberosities, with an obtuse angle between them in anterior view (Fig. 18B₂). In contrast to the preceding vertebrae, they are transversely broad and anteroposteriorly short. The anteromedial surface of each prezygapophysis is

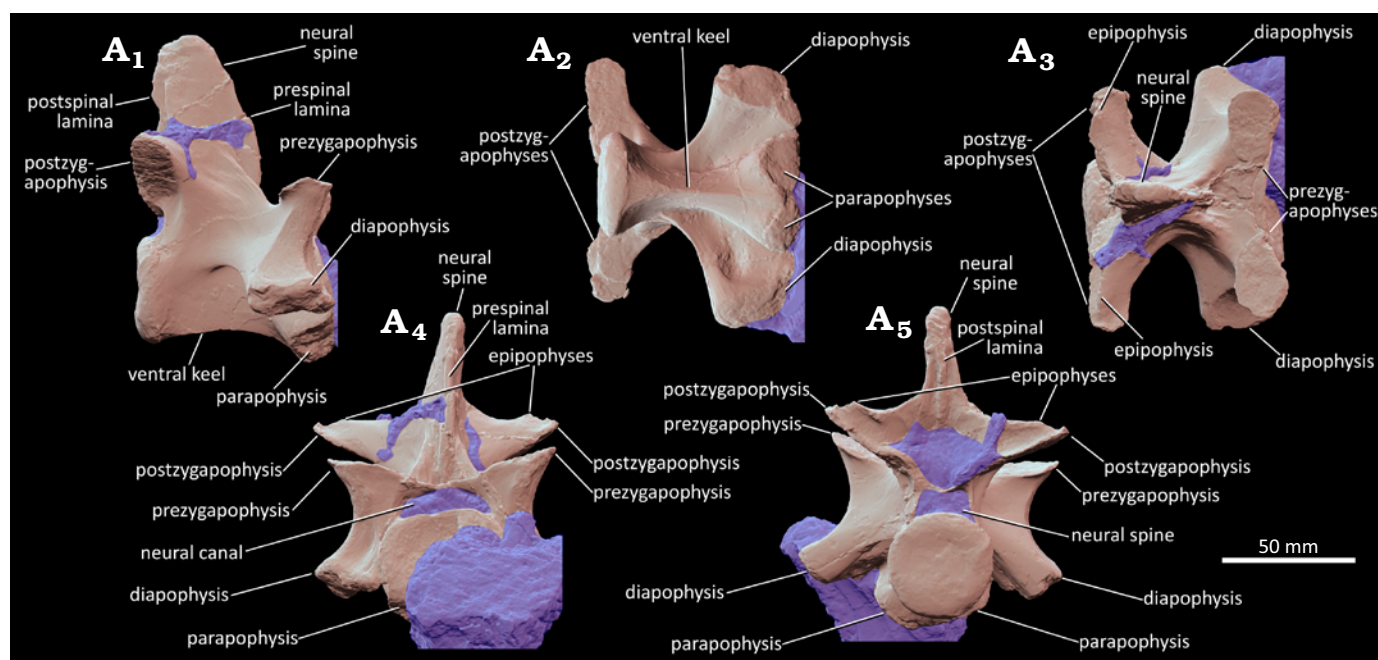


Fig. 19. Thirteenth cervical vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/2485 in right lateral (A₁), ventral (A₂), dorsal (A₃), anterior (A₄), and posterior (A₅) views. Areas covered with sediment marked with blue hue. The vertebra could not be fully prepared due to its association with a delicate skull bone.

formed as a thin lamina, which joins the prespinal lamina in a triradiate connection above the anterior neural canal opening (Fig. 18B₂). The postzygapophyses are similar in their characteristics to the prezygapophyses. They are robust and extend slightly beyond the posterior articular surface of the centrum (Fig. 18A, B₃). Their articular surfaces are broad and transversely wide. The angle formed between them is slightly obtuse (Fig. 18B₅). They are aligned with the floor of the postzygapophyseal shelf (Fig. 18B₅). The weakly posterodorsally projecting epipophyses are much smaller than in the preceding vertebrae and do not extend posteriorly beyond the postzygapophyses (Fig. 18A, B₃). The concavity formed at the base of the posterior portion of the neural spine is deep and flanked bilaterally by the postzygapophyses (Fig. 18B₅). A distinct postspinal lamina runs along the midline of its dorsal surface, becoming confluent with the neural spine near its posterodorsal corner (Fig. 18B₃, B₅).

The morphology of the neural spine itself can vary considerably between specimens (compare Fig. 18A and B₃). In some individuals the height of the thin prespinal lamina increases gradually before reaching the distal surface of the neural spine (Fig. 18B), whereas in others the anterior margin of the neural spine is deeply concave in lateral view and nearly vertical, with the neural spine being relatively taller but much shorter anteroposteriorly (Fig. 18A). All known vertebrae 12 of *T. conspicuus* share the characteristics of the distal surface of the neural spine, which is rounded, slightly transversely expanded, and with a more dorsally raised posterior portion, so that in lateral view it is anteroventrally inclined (Fig. 18A, B₃, B₄). Moreover, all known twelfth cervical vertebrae of *T. conspicuus* have a neural spine that

is considerably taller than in the corresponding vertebrae of other species of *Tanystropheus* (Wild 1973; Renesto 2005; Nosotti 2007; Rieppel et al. 2010; AR personal observation).

The thirteenth cervical vertebra is proportionally more similar to the succeeding dorsal vertebrae than the preceding cervical vertebrae (Fig. 19). The length of its centrum is always shorter than the height of the vertebra (Fig. 19A₁). The centrum is considerably constricted bilaterally and ventrally, being slightly concave in lateral view and hour-glass-shaped in ventral view (Fig. 19A₁, A₂). The midline of the ventral surface is marked by the presence of a weakly developed ventral keel (Fig. 19A₂). On its sides, near the anteroposterior midpoint are up to two subcentral foramina. In some instances there may only be one, or none at all, and they are always much smaller than the corresponding foramina in the preceding cervical vertebrae.

The neural canal openings are semicircular, with the anterior one being much lower but transversely broader than the posterior one (Fig. 19A₄, A₅). The articular surfaces of the centrum are circular and very weakly amphicoelous. The anterior one is larger and more ventrally located (Fig. 19A₄, A₅). The parapophyses are directly adjacent to each other, being separated only by the anterior portion of the ventral keel (Fig. 19A₂). The diapophyses are intermediate in length between those of the cervical vertebrae and the dorsal vertebrae. They are especially massive, projecting lateroventrally from the anterolateral portion of the centrum as stout processes, with a deep, broad concavity between them and the parapophyses (Fig. 19A₁, A₂). The rib articular surfaces of the parapophyses are flat, subcircular, and more anteriorly oriented than the elliptical, rounded, lateroventrally oriented

articular surfaces of the diapophyses (Fig. 19A₂). The lateral surface of the vertebra is concave between the diapophysis and the distal tip of the prezygapophysis, with its margin being semicircular in anterior view (Fig. 19A₄, A₅).

The prezygapophyses are relatively long, broad, and laterally projecting. They do not extend anteriorly beyond the articular surface of the centrum (Fig. 19A₁). The mound-like anterior tuberosities, present in the preceding cervical vertebrae, are absent, but the corresponding anteroventral surface of the prezygapophyses is rugose (Fig. 19A₄). The prezygapophyseal articular surfaces are elliptical. Their longer axis is sub-transversely oriented (Fig. 19A₃). The angle formed between them is obtuse (Fig. 19A₄). The postzygapophyses are longer than the prezygapophyses, with their articular surfaces also being transversely wider (Fig. 19A₃). They project dorsolaterally but do not extend posteriorly beyond the articular surface of the centrum (Fig. 19A₁). The angle formed between them is obtuse but to a lesser extent than between the prezygapophyses (Fig. 19A₅). The epipophyses are nearly completely reduced, being developed as minute projections on the dorsal surface of the postzygapophyses (Fig. 19A₅).

The base of the neural spine is anteriorly and posteriorly constricted by concavities in lateral view, with the posterior one being larger and deeper (Fig. 19A₄, A₅). These concavities are flanked by the laminae that connect the zygapophyses to the neural spine and ventrally floored by the laminae that constitute the roof of the neural canal. As for the twelfth vertebra, there is some disparity in the neural spine morphology in the last cervical of *T. conspicuus*, with its relative length varying considerably. In most specimens the neural spine is anteroposteriorly short but dorsoventrally tall and relatively straight, with distinct prespinal and postspinal laminae extending along its anterior and posterior margins (Fig. 19A₁). The distal surface of the neural spine is rounded in lateral view and slightly transversely expanded. As for most other vertebrae, the neural spine morphology is the main feature distinguishing *T. conspicuus* from *T. hydroides* and *T. longobardicus*, with the two latter exhibiting considerably shorter neural spines with a flat, straight distal surface (see Wild 1973; Renesto 2005; Nosotti 2007; Rieppel et al. 2010). However, all species of *Tanytropheus* share the characteristic robust diapophyses (see Wild 1980a; Rieppel et al. 2010).

Dorsal vertebrae: Similar to other species of *Tanytropheus*, twelve dorsal vertebrae are present in *T. conspicuus*, although no specimen preserves a full series (see Discussion). ZPAL V. 36/125 includes eleven dorsal vertebrae still in articulation, as well as the two sacral vertebrae, several caudal vertebrae, the left scapula, the left pubis, and the left ilium, as well as many ribs and gastralia (Fig. 20). All dorsal vertebrae of *T. conspicuus* are amphicoelous and lack any trace of the neurocentral suture.

The anterior dorsal vertebrae are similar in their morphology to the last cervical vertebra (compare Fig. 19 and Fig. 21). In *Tanytropheus* the dorsal vertebrae differ, how-

ever, from the cervical vertebrae in the complete absence of two major features, the subcentral foramina and the epipophyses. Moreover, in the anterior dorsal vertebrae the diapophyses are longer and laterally oriented, the postzygapophyses are shorter and more posteriorly projecting, and the anterior articular surface of the centrum is relatively smaller compared to the posterior cervical vertebrae. In the anteriormost dorsal vertebrae the centrum is parallelogram-shaped in lateral view and relatively longer than in the succeeding vertebrae (Fig. 21A₃). Its circular articular surfaces are roughly on the same dorsoventral level, with the anterior one being relatively larger. In ventral view the centrum is hourglass-shaped, with a median keel forming its ventral edge (Fig. 21A₅). The parapophyses are located in the ventrolateral corner of the anterior articular surface. Their bases nearly touch, being separated only by the ventral keel (Fig. 21A₅). They are short and sturdy, weakly ventrally expanded, and ventrolaterally oriented (Fig. 21A₃, A₅). The diapophyses originate from the lateral surface of the vertebra, roughly at the boundary between the centrum and the neural arch (Fig. 21A₃). They are relatively long and robust, extending laterally far beyond the zygapophyses. Their distal ends are elliptical in lateral view and thickened (Fig. 21A₃). Three distinct laminae are present along most of the length of the diapophysis (Fig. 21A₁, A₃, A₅), a lamina extending to the corresponding prezygapophysis (prezygodiapophyseal lamina), a lamina extending towards the corresponding parapophysis (anterior centrodia-epiphyseal/paradia-epiphyseal lamina), and finally a lamina extending towards the posteroventral corner of the centrum (posterior centrodia-epiphyseal lamina). Moreover, the posterolateral portion of the base of the diapophysis is connected to the base of the corresponding postzygapophysis by a weakly developed postzygodia-epiphyseal lamina (Fig. 21A₃). Between the diapophyseal laminae, there are deep, triangular pits (fossae), of which the fossa located anteriorly to the diapophysis (the prezygocentrodia-epiphyseal fossa) is the deepest (Fig. 21A₁).

The prezygapophyses are relatively large and transversely wide (Fig. 21A₁, A₄). Their distal margin is rounded and confluent with the edge of the corresponding articular surface (Fig. 21A₁). The prezygapophyseal articular surfaces are elliptical in dorsal view and have their lateral edges slightly raised, with an obtuse angle of around 150° being formed between the prezygapophyses (Fig. 21A₁, A₄). They connect to the centrum through centroprezygapophyseal laminae, which laterally flank the elliptical opening for the neural canal (Fig. 21A₁). Between the prezygapophysis and the neural spine there is a shelf (transprezygapophyseal lamina), which also constitutes the roof of the neural canal (Fig. 21A₁, A₄). This shelf is posteriorly delimited by the neural spine and the spinoprezygapophyseal laminae. The postzygapophyses are shorter than the prezygapophyses, and posterolaterally oriented (Fig. 21A₄). As in the prezygapophyses, they meet in an obtuse angle (Fig. 21A₂). Their articular surfaces are elliptical. The postzygapophyses connect to the centrum through the vertical centropostzyga-

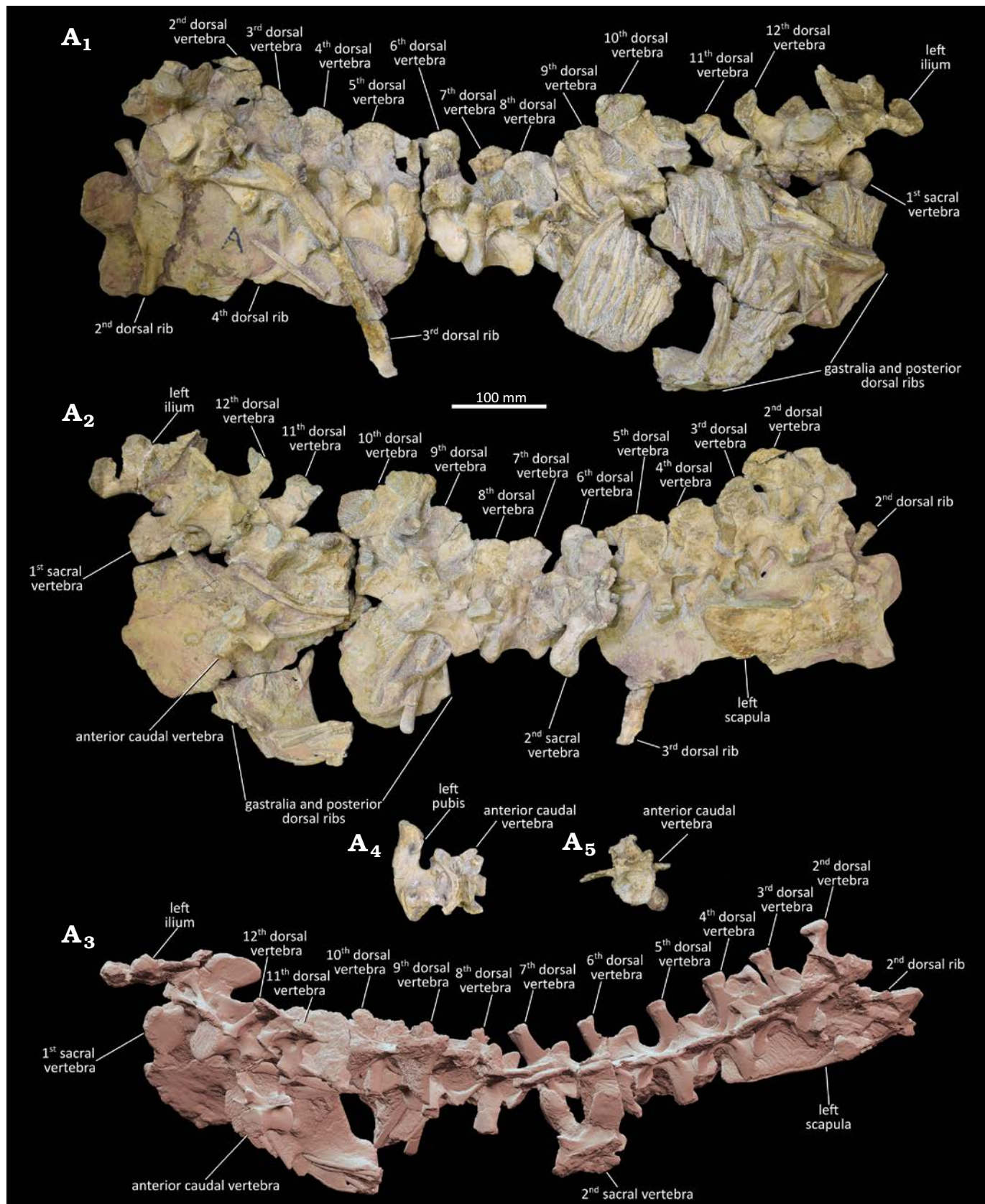


Fig. 20. Partial skeleton of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photographs (A₁, A₂, B, C), three-dimensional model snapshot with Lit Sphere Radiance Scaling shader enabled (A₃). ZPAL V. 36/125, including most of the torso of one individual (A) and some associated elements (B, C) in left (A₁) and right (A₂) lateral, dorsal (A₃, B), and anterior (C) views.

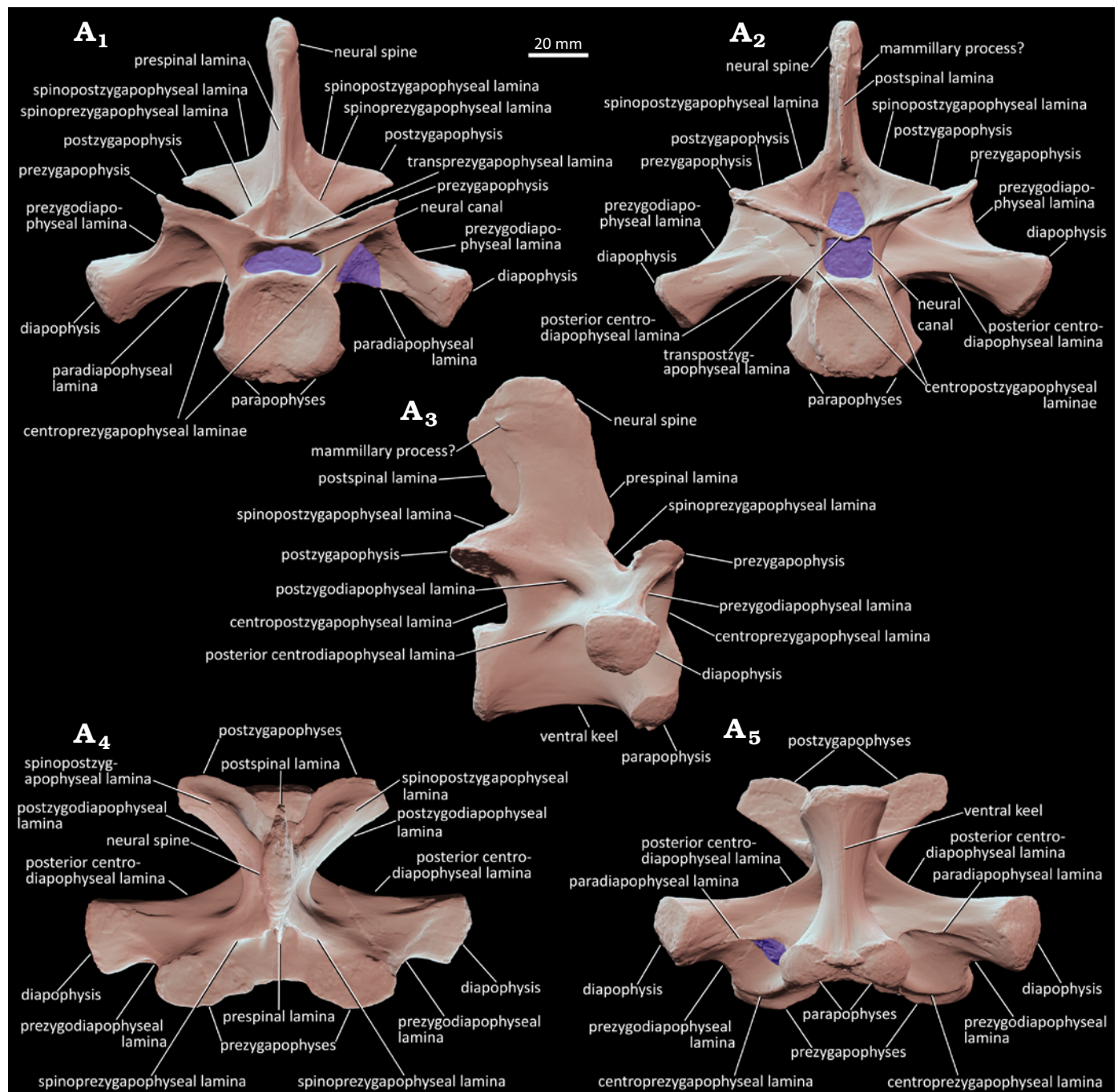


Fig. 21. Anterior dorsal vertebra of the tanystropheid archosauriform *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1249 in anterior (A₁), posterior (A₂), right lateral (A₃), dorsal (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

pophyseal laminae, which flank the posterior, rectangular, opening for the neural canal (Fig. 21A₂). The posterior portion of the neural canal is roofed by the transpostzygapophyseal lamina, which extends between the postzygapophyses and the base of the neural spine, forming a shelf that is anteriorly delimited by the spinopostzygapophyseal laminae (Fig. 21A₂, A₄).

The neural spine is tall. Its base is anteroposteriorly constricted through the presence of deep pits formed between the zygapophyses (Fig. 21A₁–A₃). From those pits, two laminae

extend towards the distal end of the neural spine, the anterior, prespinal lamina, and the posterior, postspinal lamina (Fig. 21A₁–A₃). They expand the anteroposterior width of the neural spine in lateral view, forming well outlined attachment sites for ligaments. The distal portion of the neural spine is posteriorly displaced relative to its base and the neural spine is consequently posteriorly curved (Fig. 21A₃). On its laterodistal surface, a tuberosity is present bilaterally, possibly forming a weakly laterally projecting mammillary process on both sides (Fig. 21A₂, A₃). The distal portion of the neural

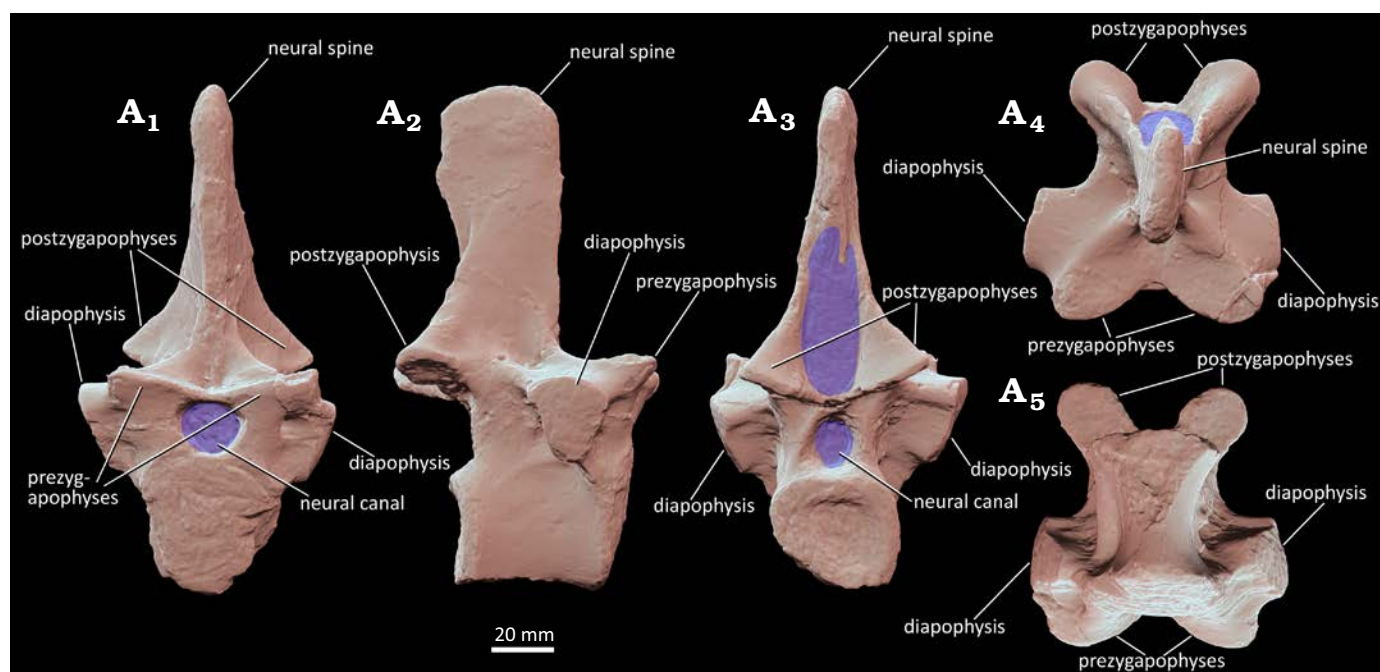


Fig. 22. Posterior (eleventh?) dorsal vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1033 in anterior (A₁), right lateral (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

spines is convex in lateral view, transversely expanded, and bulbous. Its surface is distinctly rugose and covered with a dense network of grooves, pits, and ridges (Fig. 21A₃, A₄).

The morphology of the succeeding dorsal vertebrae corresponds closely with that of the anterior ones, although several features change gradually along the length of the vertebral column (see Fig. 20). The centrum length remains relatively constant, with only the last three dorsal vertebrae being considerably shorter (Fig. 20A₂). Parapophyses are present up to the fourth dorsal vertebra, and in each succeeding vertebrae after the first one, they are slightly more distant from each other and the ventral keel (Fig. 20A₁). The transverse processes retain their length and anteroposterior width up to the tenth dorsal (Fig. 20A₃). In dorsal vertebrae three to ten, the transverse processes are situated near the anteroposterior mid-point of the centrum, with the prezygodiapophyseal lamina not extending towards the anterior edge of the prezygapophyses, and this lamina being nearly completely reduced in the last two dorsal vertebrae (Fig. 20A₁–A₃). From the third dorsal vertebra onwards, the shape of the diapophyseal articular surface for the rib attachment changes from elliptical to triangular, becoming dorsoventrally taller in lateral view (Fig. 20A₁, A₂). The zygapophyses become successively shorter and more anteroposteriorly projecting in each consecutive vertebra. The angle between their articular surfaces remains relatively constant and similar to that observed in the anterior dorsal vertebrae. Their articular surfaces are elliptical and transversely wide. The neural spine is posteriorly curved only in the first two dorsal vertebrae (Fig. 20A₁, A₂). In all succeeding elements it is relatively straight in lateral view.

Dorsal to the ridge extending between the prespinal and postspinal laminae in dorsal vertebrae five to ten the distal margin of the neural spine is anteroposteriorly expanded (Fig. 20A₁, A₂). As a result, the distal portion of their neural spines is rhomboidal in lateral view. All dorsal vertebrae share the presence of a rugose distal surface of the neural spine, although the exact morphology and the extent of this distal expansion are highly variable, sometimes differing between vertebrae from the same position in the vertebral column. The last two dorsal vertebrae differ from the preceding ones in several features, as previously documented in *Tanystropheus* by Wild (1973) and Nosotti (2007) who considered them as “lumbar” vertebrae. Their centra are relatively much shorter and lack the ventral keel, their neural spines are relatively taller, anteroposteriorly short, and distally less expanded (Fig. 22). Moreover, their diapophyses are more anteriorly located, occupying the space directly between the prezygapophyses and the centrum.

There are several morphological differences present between the dorsal vertebrae of *T. conspicuus* and other *Tanystropheus* species. For example, the diapophyses being much longer and more robust in the former (compare Figs. 20, 21 with the vertebrae illustrated by Wild 1973, 1980a; Renesto 2005; Nosotti 2007). Only a few of the vertebrae of *T. conspicuus* that Wild (1973) had access to preserved the distal portion of the neural spine, and with it, the distal rugose expansion and convex outline in lateral view. It is only evident now, through the discovery of further, complete, elements that *T. conspicuus* differs in neural spine morphology from the other *Tanystropheus* species. Among non-crocopodan archosauromorphs, this condition

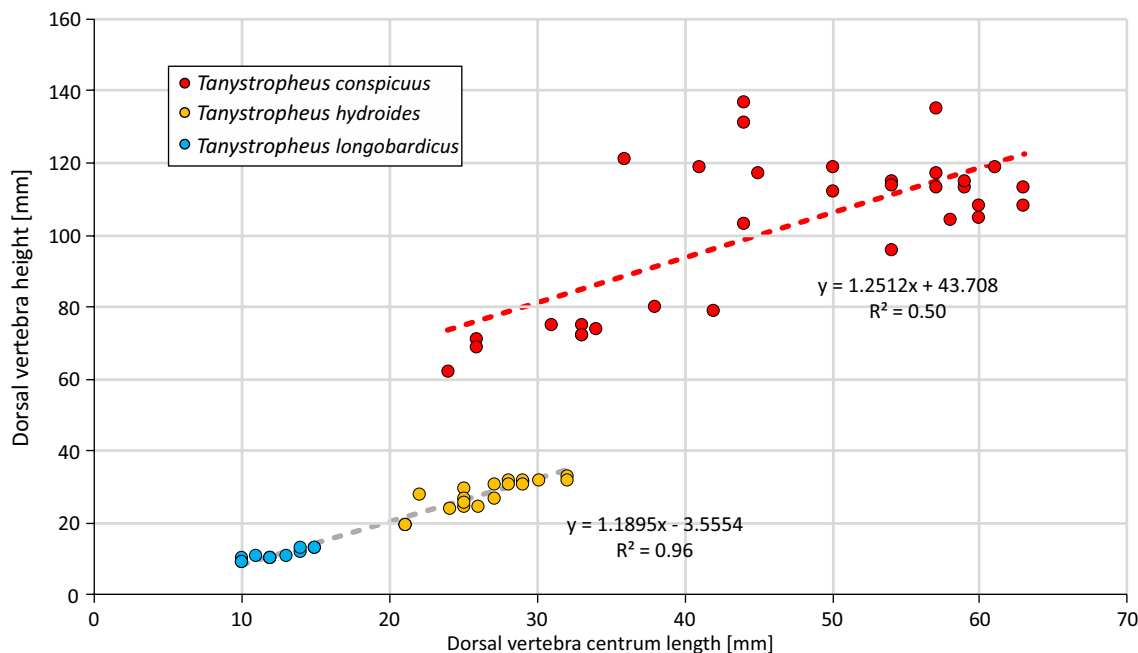


Fig. 23. Comparison of length to height ratio in the dorsal vertebrae of three species of *Tanystropheus*. See SOM: table 2 for the list of specimens used and the respective measured values. Dashed lines represent the linear regression fitted lines, one for *Tanystropheus conspicuus* and one treating *Tanystropheus hydroides* and *Tanystropheus longobardicus* as one population, with respective regression equation and coefficient of determination value provided next to them.

is present to a similar extent in only one other tanysaurian, *Trachelosaurus fischeri*. This taxon is also characterised by the presence of the rugose, convex thickening of the distal portion of the neural spine in most of its precaudal vertebrae, and with well-developed transverse striations marking its surface (Spiekman et al. 2024b). By contrast with the vertebrae known from the CEB referred to *T. conspicuus*, all other published dorsal vertebrae of *Tanystropheus* have a shorter neural spine, with a distal expansion formed as a straight, flat spine table (AR personal observation; Wild 1973; Wild 1980a; Renesto 2005; Dalla Vecchia 2006, 2008; Nosotti 2007; Rieppel et al. 2010; Ezcurra 2016; Dalla Vecchia and Simonetto 2018; Renesto and Saller 2018; Spiekman et al. 2021). In the dorsal vertebrae of these forms the vertebral height at the midpoint is usually subequal, or slightly larger than the length of the corresponding centrum (AR personal observation, Fig. 23, see also Wild 1973 and Nosotti 2007). In *T. conspicuus* the dorsal vertebrae are always about two to three times taller than long. There is some overlap of the centrum length between the largest known dorsal vertebrae of *T. hydroides* and the smallest measured dorsal vertebrae of *T. conspicuus*, but the neural spines of the latter are much taller (Fig. 23).

Sacral vertebrae: As in other species of *Tanystropheus*, there are two unfused sacral vertebrae present in *T. conspicuus* (Wild 1973; Nosotti 2007). Aside from the presence of the sacral ribs, they are morphologically similar to the posteriormost dorsal vertebra, and are of nearly identical size (Fig. 20). The centrum of the first sacral vertebra is relatively short, slightly amphicoelous, and does not have a ventral constriction nor a ventral keel (Fig. 24A₅). Its articular surfaces are round, with the posterior one being rela-

tively smaller (Fig. 24A₁, A₃). The sacral ribs are fully fused to the transverse processes without a discernible suture line. The ribs extend laterally from the anterodorsal corner of the lateral surfaces of the centrum (Fig. 24A₂). They anteroposteriorly widen distally, with their anterior portion being further laterally extended (Fig. 24A₄). Their distal margin is oriented obliquely to the longitudinal axis of the vertebra, with the articular surface for the ilium being ventrolaterally and slightly posteriorly facing. In lateral view the articular surface of the rib is elliptical (Fig. 24A₂). In anterior view, the sacral ribs have a straight dorsal and convex ventral margin (Fig. 24A₁). The neural canal openings are relatively small and circular (Fig. 24A₁, A₃). The prezygapophyses project dorsolaterally, with their articular surfaces being elliptical and transversely broad (Fig. 24A₄). The angle between them is obtuse in anterior view (Fig. 24A₁) and does not differ from the condition noted in the dorsal vertebrae. The postzygapophyses are relatively short and posterolaterally projecting (Fig. 24A₄). Their articular surfaces share the characteristics of the prezygapophyseal articular surfaces. The neural spine is tall and slightly anteroposteriorly expanded towards its distal end (Fig. 24A₂).

The second sacral vertebra differs from the first one mainly in the characteristics of the ribs. The second pair of dorsal ribs is ventrolaterally and somewhat anteriorly oriented, shorter, and they widen distally to a lesser extent than the first pair (Fig. 25). The anterior margin of the second sacral rib is flat in lateral view (Fig. 25A₂), forming an articulation surface for the posterolateral tip of the first sacral rib. On the posterodorsal margin of each of the second sacral ribs, at the level of the most dorsal extent of the posterior articular surface of the centrum, a posteriorly

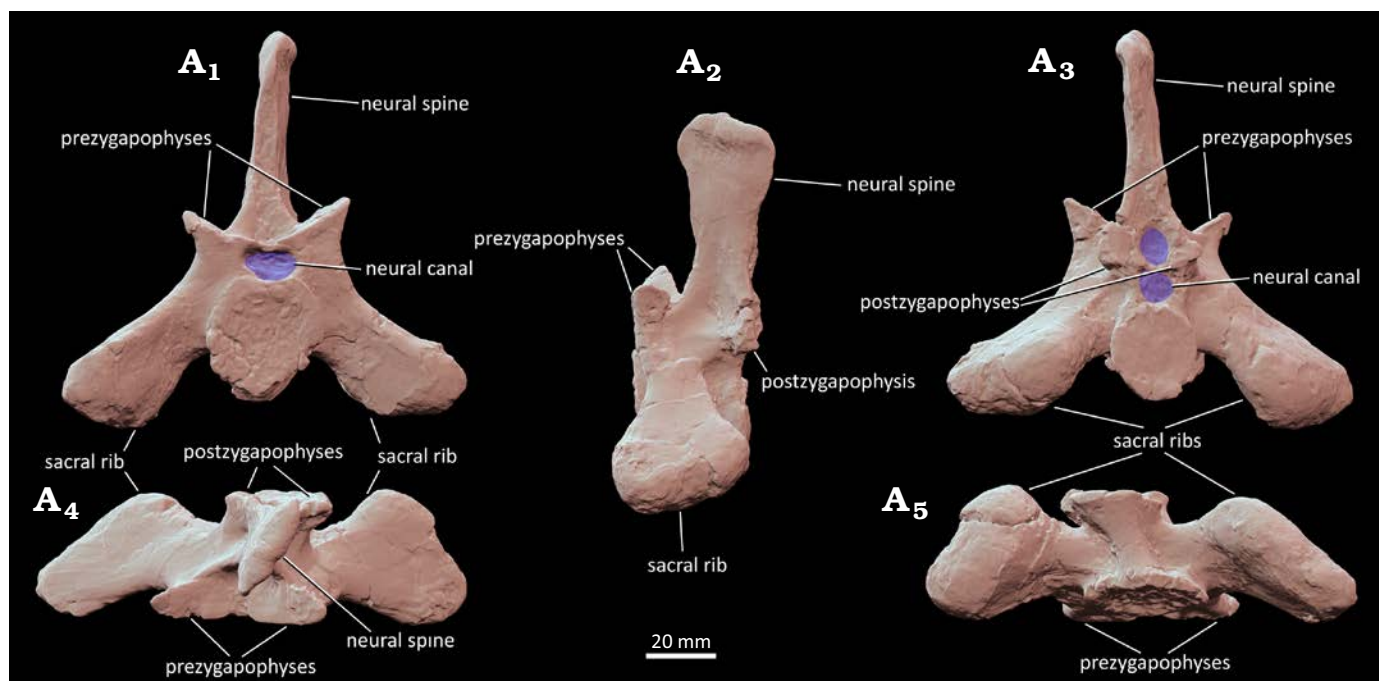


Fig. 24. First sacral vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1187 in anterior (A₁), left lateral (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

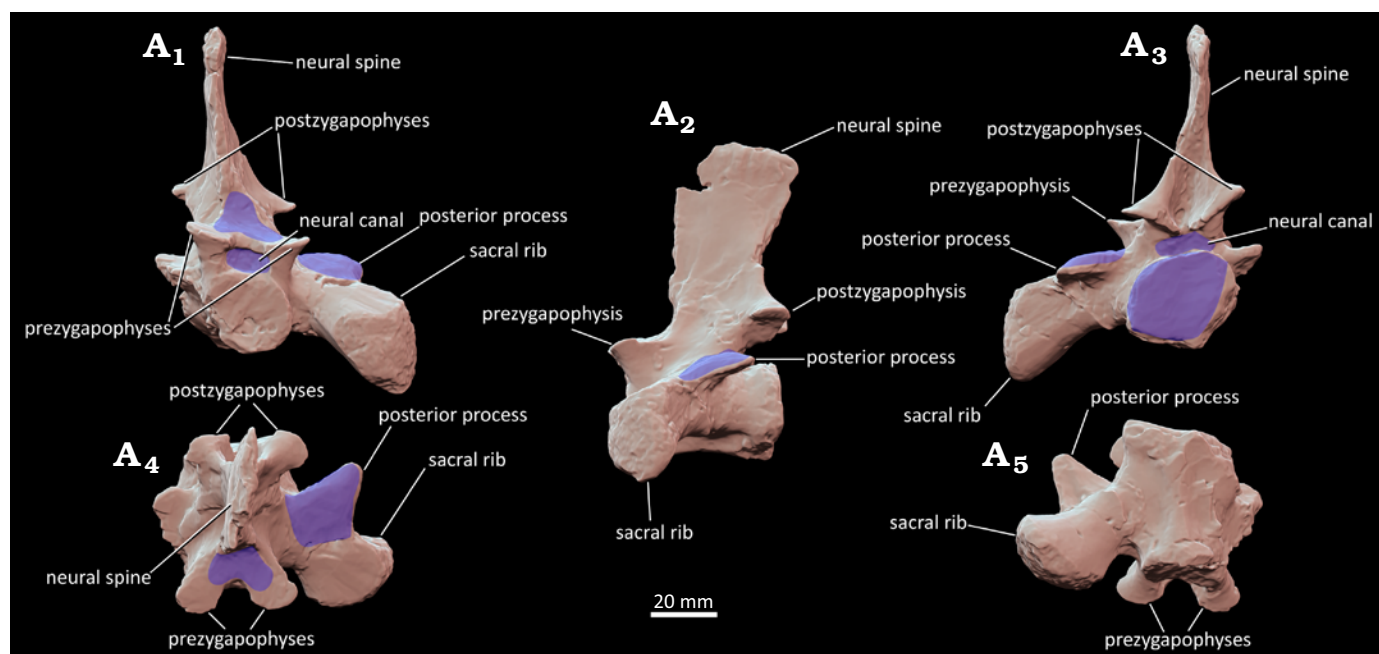


Fig. 25. Second sacral vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1037 in anterior (A₁), left lateral (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

projecting, anteroposteriorly flattened process is present. It is triangular in dorsal view and tapers to a point (Fig. 25A₄). Further differences between the first and the second sacral vertebrae of *T. conspicuus* include the presence of a weakly pronounced ventral keel on the centrum (Fig. 25A₅) and a more anteroposteriorly expanded neural spine in the latter (Fig. 25A₂). Moreover, the prezygapophyses in the second

sacral vertebra are positioned more ventrally than the postzygapophyses, conversely to the first sacral vertebra (compare Fig. 24 and Fig. 25).

Caudal vertebrae: In all known caudal vertebrae of *T. conspicuus* the transverse processes are seamlessly fused with ribs. In the text I refer to the whole fused element as a transverse process. They are present in approximately the

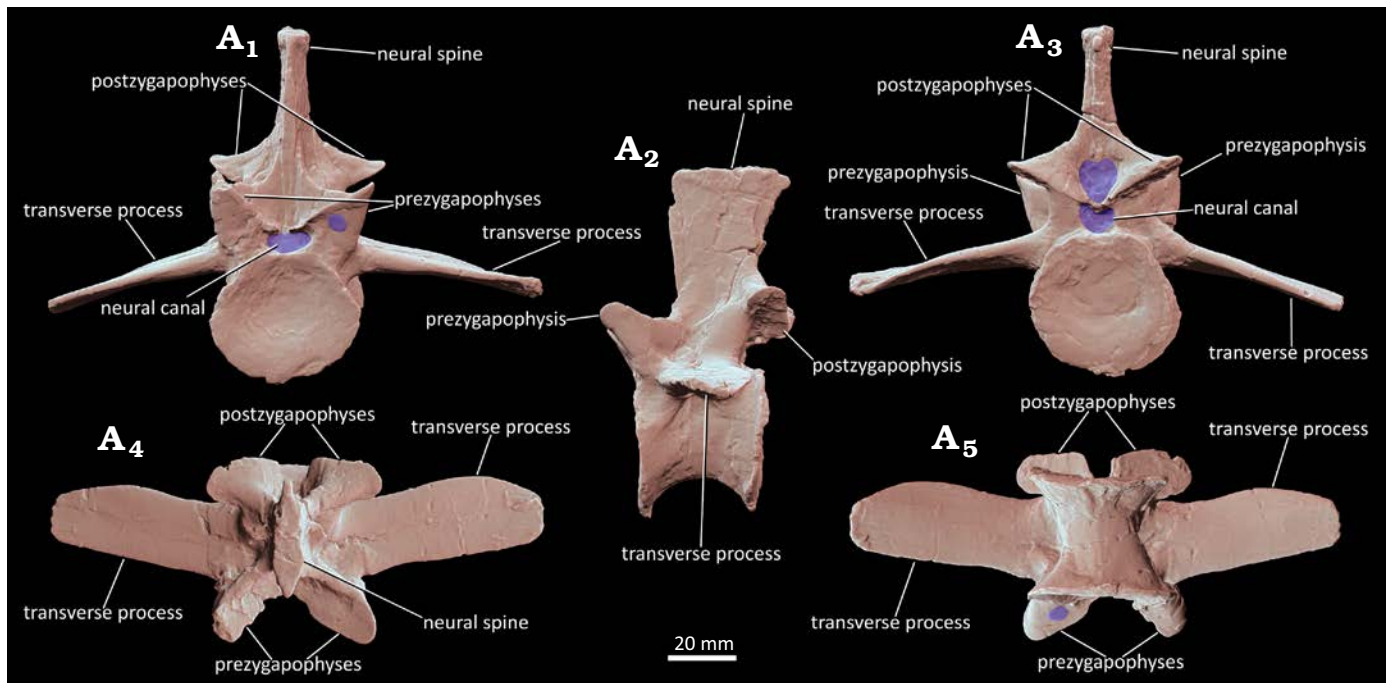


Fig. 26. Anterior caudal vertebra of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/114 in a anterior (A₁), left lateral (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. Areas covered with sediment marked with blue hue.

first fourteen caudal vertebrae in *T. hydroides* (Wild 1973), these can be considered the proximal caudal vertebrae. The inferred distal caudal vertebrae therefore lack a transverse process. The first caudal vertebra in *T. hydroides* and *T. longobardicus* can be distinguished by the presence of postero-laterally oriented, distally tapering, wing-like transverse processes (Wild 1973, 1980a). Further posteriorly, the proximal caudal vertebrae possess a non-tapering transverse processes with a relatively constant anteroposterior width, and hence when dealing with isolated vertebrae, it is only the first caudal vertebra that can be assigned to its original position in the vertebral column with any certainty in these two species. However, no caudal with such posterolaterally oriented and distally tapering transverse processes is known from Miedary. Wild (1973) identified a fragmentary vertebra as the first caudal of *T. conspicuus*, but due to the missing transverse processes, this identification is equivocal. The only specimen that can be regarded as a likely first caudal vertebra of *T. conspicuus* is MHI 2199/2, in which the transverse processes are reminiscent of butterfly wings, they are relatively short, triangular in dorsal view, and possess two extensions, one projecting posterolaterally and the other anteriorly. The former extension tapers slightly. This anteriorly projecting extension is present, but much less pronounced, in the first caudal vertebra of other *Tanystropheus* species (e.g., PIMUZ T 1270, PIMUZ T 2483, MCSN 4451). MHI 2199/2 does not possess a median groove, associated with the presence of the chevron, both of which are absent in the anteriormost caudal vertebrae of *Tanystropheus* (see Fig. 26A₅), but present along most of the length of the tail (see Wild 1973; Renesto and Saller 2018).

The proximal caudal vertebrae of *T. conspicuus* possess a relatively short, ventrally and laterally constricted centrum, corresponding to the preceding sacral and posterior dorsal vertebrae (Fig. 26A₂, A₅). Its articular surfaces are moderately amphicoelous and circular (Fig. 26A₂, A₃). The openings of the neural canal are heart-shaped, with a bilobed dorsal margin (Fig. 26A₁, A₃). The transverse processes project laterally from the boundary between the centrum and the neural arch at mid-length (Fig. 26B). They are dorsoventrally thin and flat, and anteroposteriorly wide. In the proximal caudal vertebrae, apart from the first, the transverse processes have a blunt end, with a rounded distal margin (Fig. 26A₄, A₅). Their anterior and posterior margins curve slightly posteriorly relative to their base in dorsal view (Fig. 26A₄, A₅).

The prezygapophyses in the proximal caudal vertebrae are longer, more slender, and further dorsally projecting than in the sacral vertebrae (Fig. 26A₂, A₄). Their articular surfaces are elliptical in dorsal view. In anterior view the angle between them is considerably smaller than in all the preceding dorsal and sacral vertebrae, but still obtuse (Fig. 26A₁). Unlike in nearly all the preceding vertebrae, the transprezygapophyseal and transpostzygapophyseal laminae are absent, with the corresponding zygapophyses separated by a notch in dorsal view (Fig. 26A₁, A₃, A₄). The postzygapophyses project further laterally than the prezygapophyses, with the longitudinal axes of their articular surfaces being nearly parallel to each other and perpendicular to the sagittal plane of the vertebra (Fig. 26A₄).

As for the preceding elements, the base of the neural spine is anteroposteriorly constrained by deep, triangular grooves located between the zygapophyses (Fig. 26A₁, A₃).

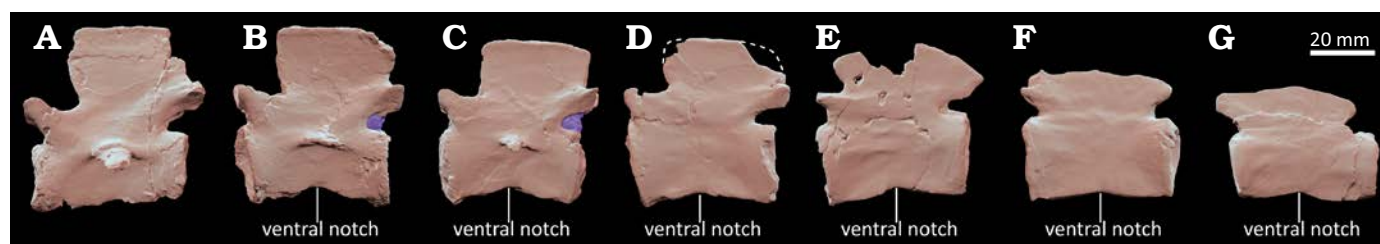


Fig. 27. A sequence of isolated middle-distal caudal vertebrae of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/2489 (A), ZPAL V. 36/2490 (B), ZPAL V. 36/2491 (C), ZPAL V. 36/139 (D), ZPAL V. 36/116 (E), ZPAL V. 36/115 (F), and ZPAL V. 36/1070 (G); in left (A, C, E, G) and right (mirrored; B, D, F) lateral views.

The neural spine is positioned relatively further posteriorly than in the preceding vertebrae (Fig. 26A₂). It is relatively shorter than in the dorsal and sacral vertebrae but still considerably taller in relative terms than in the corresponding elements of other *Tanystropheus* species (compare to Wild 1973; Dalla Vecchia 2000; Nosotti 2007). In lateral view its anterior and dorsal margins are straight, and the posterior edge is concave (Fig. 26A₂). The distal edge is spindle-shaped in dorsal view (Fig. 26A₄). It lacks the anteroposteriorly convex expansion present in the preceding elements but is formed as a rugose, flat “spine table” (see Ezcurra 2016; Renesto and Saller 2018; Spiekman et al. 2021), with the laterodistal surfaces of the neural spine also having a rough texture.

Posteriorly along the caudal column, the characters described above change gradually. The centrum retains its length or becomes slightly longer in the more posterior proximal vertebrae (Fig. 27). Distal to the first caudal vertebra, the centrum becomes more hourglass-shaped in ventral view, with its articular surfaces becoming less transversely expanded, but more concave. The most distal caudal vertebrae have an approximately constant centrum height along their length (Fig. 27F, G). A median groove is present, along with the hemal arches, in one of the first proximal caudal vertebrae, and also occurs on the ventral surface of most, if not all, succeeding caudal centra. The groove is flanked by well-defined lateral ridges, which decrease in height near the anteroposterior midpoint of the centrum. At the midpoint, a deep notch of the ventral centrum margin is visible in lateral view (Fig. 27B–G). This ventral notch is absent in the caudal vertebrae of *T. hydroides* and *T. longobardicus* (AR personal observation; see also Wild 1973, 1980a). The articulation surfaces for the hemal arches are poorly defined. The transverse processes decrease in length and anteroposterior width posteriorly along the caudal column to become a cone-shaped, tapering, laterally oriented projection in the posteriormost proximal caudal vertebrae (Fig. 27B, C). They are always located at the mid-length of the vertebra on the boundary between the centrum and the neural arch.

As in all other vertebrae of *Tanystropheus*, the fusion of the neural arch and the centrum is seamless in all caudal vertebrae. In all proximal caudal vertebrae of *T. conspicuus* the pre- and postzygapophyses extend slightly beyond the

centrum (Fig. 27A–C). Distally along the caudal series, the zygapophyses become relatively smaller, and increasingly slender, dorsally projecting, and tapering (Fig. 27E, F). In the posterior proximal and anterior distal caudal vertebrae, the angle between the zygapophyseal articular surfaces changes from obtuse to acute. In the distal-most caudal vertebrae the postzygapophyses become confluent with the posterior margin of the neural spine (Fig. 27F, G). The prezygapophyses, which decrease in size along the caudal series less than the postzygapophyses, change from anteriorly oriented, minute projections, to slight thickenings on the anterolateral surfaces of the neural spine (Fig. 27F, G).

Although the neural spine height decreases distally in the tail of *T. conspicuus*, all caudal vertebrae of this species seem to be distinctly taller than the corresponding vertebrae of *T. hydroides* and *T. longobardicus*. The distal margin of the neural spine in the latter two species is relatively straight in lateral view (see Wild 1973, 1980a; Nosotti 2007) or slightly concave in the distal caudal vertebrae of *T. hydroides* (PIMUZ T 2817, AR personal observation). In the distal caudal vertebrae of *T. conspicuus* the neural spine is distinctly convex, with its distalmost expansion point being located around the mid-length (Fig. 27D, G). The neural spine in the distal caudal vertebrae of both *T. conspicuus* and *T. hydroides* is positioned relatively much further anteriorly (see Peyer 1931: pl. 11, PIMUZ T 2793; Fig. 27) than in *T. longobardicus* (including the neotype PIMUZ T 2791, “Exemplar a” of Wild 1973). In the distal-most vertebrae of *T. conspicuus*, in which only remnants of the zygapophyses can be identified, the anterodistal and posterodistal margins of the low neural spine are rounded in lateral view (Fig. 27). The anterior portion of the neural spine in *T. conspicuus* extends beyond the centrum anteriorly, overhanging it (Fig. 27G).

Hemal arches similar to those known from the articulated specimens of *T. hydroides* and *T. longobardicus* (see Wild 1973; Nosotti 2007) have been found in Miedary, but they are not diagnostic enough to unequivocally refer them to *Tanystropheus*.

Cervical ribs: Only the two posteriormost, shortest, cervical ribs of *T. conspicuus* have been found as complete specimens. The longest preserved fragments of cervical ribs found in Miedary measure around 250 mm in length, but almost certainly reached over 100 cm when complete. All

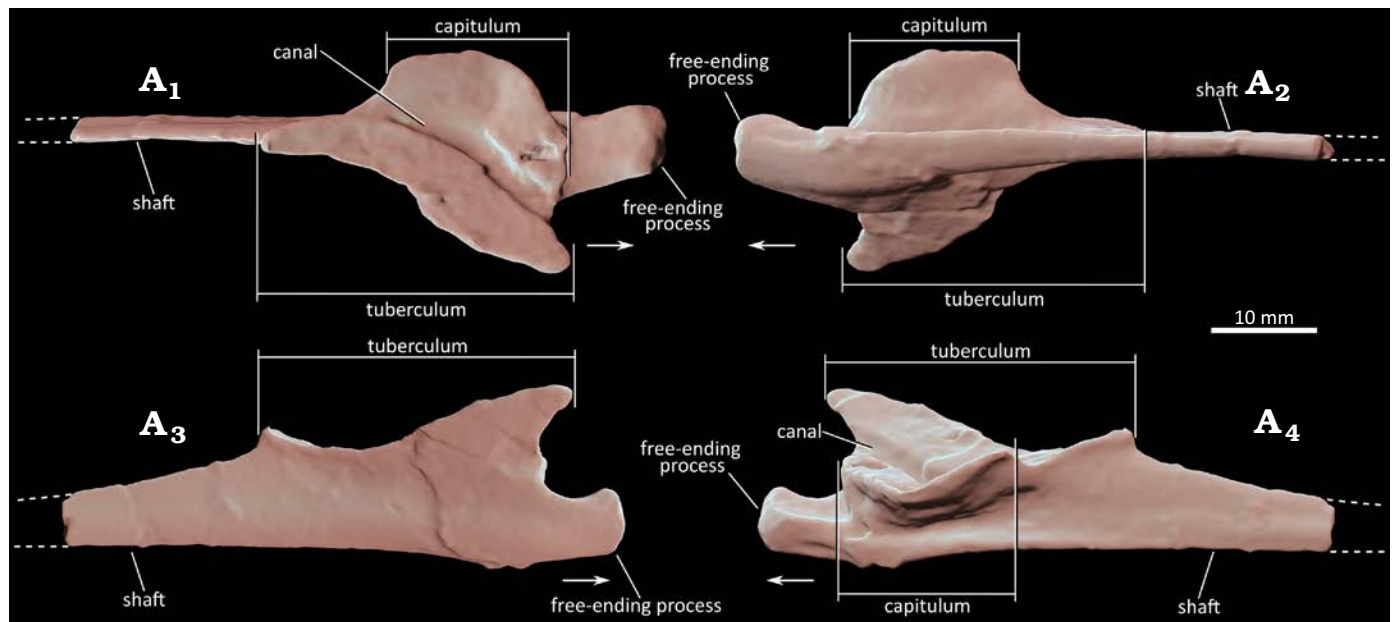


Fig. 28. Anterior portion of a right middle cervical rib head of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/2433 in dorsal (A₁), ventral (A₂), lateral (A₃), and medial (A₄) views. Arrows indicate anterior direction.

cervical ribs found in Miedary so far are dicephalous, with a narrow canal partitioning the articular head of the rib into capitulum and tuberculum (Fig. 28). Thus, in all species of *Tanystropheus* the cervical ribs were only functionally single-headed (contra Wild 1973 and following Nosotti 2007).

As in other species of *Tanystropheus*, the articular portion (anterior to the shaft) in all anterior and middle cervical ribs is exceedingly small when compared to the total length of the element. In contrast to the posterior cervical ribs, the anteromedially oriented free ending process is blunt, short, and does not taper (Fig. 28). Tuberculum and capitulum are dorsoventrally very short but well defined. The tuberculum is anteroposteriorly longer, with its articular surface being narrow, elongate, and oriented obliquely to the shaft (Fig. 28A₁). The dorsal edge of the tuberculum is concave in lateral view, with its anterior and posterior portions located more dorsally than the middle section, thereby forming a gentle curve in outline (Fig. 28A₃). The capitulum extends medially as a short, rounded, process (Fig. 28A₁, A₂, A₄). It is more robust, wider, and shorter than the tuberculum but its longitudinal axis is also oblique to the shaft (Fig. 28A₁). The articular surface of the capitulum is concave in medial view, forming a V-shaped depression (Fig. 28A₁). The space between the articular heads is restricted to a narrow and shallow canal (Fig. 28A₁). The shaft is formed as an extremely elongate, thin, tapering rod, with a semicircular cross section.

The cervical rib morphology changes markedly near the base of the neck, with the pair of ribs articulating with the eleventh cervical vertebra being shorter and more massive (Fig. 29A). Its anterior free-ending process tapers to a point and is dorsomedially oriented (Fig. 29A₃). Both articular heads are stocky but taller than in the preceding ribs (Fig. 29A₄). Their articular surfaces are semicircular and

flat (Fig. 29A₁). The dorsally oriented tuberculum is slightly larger and more elongate than the dorsomedially oriented capitulum (Fig. 29A₁). Between them, there is relatively much more space than in the more anterior ribs. Low, thin, laminae extend posteriorly from the articular heads, along the shaft, expanding its edge dorsally (Fig. 29A₃, A₄).

The twelfth cervical vertebra bears the first pair of relatively short ribs (Fig. 29B). They are also characterised by the presence of a long, tapering, dorsomedially oriented free-ending anterior process, and a highly curved, convex, ventral surface (Fig. 29B₃). Compared to the preceding ribs, the pair of ribs associated with the twelfth cervical vertebra has a more posteriorly located tuberculum, which is also taller and possesses a larger articular surface. The ventrally curved lamina that extends from the posterodorsal edge of the tuberculum reaches nearly to the end of the shaft (Fig. 29B₁, B₃). In contrast to the preceding ribs, the posterior end of the shaft is blunt, and does not taper (Fig. 29B₃).

The last pair of cervical ribs, associated with the thirteenth vertebra, differs from the preceding elements with its relatively straight ventral surface, and the presence of a shorter, relatively posteriorly recurved anterior free-ending process (Fig. 29C₃). Cervical ribs from the posteriormost pair are also relatively the shortest and the tallest (Fig. 29, compare C to A and B). Their articular heads are also much longer, and oriented anterodorsally, with acute angles formed between them and the anterior free-ending process (Fig. 29C₃). Similar to the preceding rib pairs, there are thin laminae extending between the articular heads and the posterior portion of the shaft (Fig. 29C₁, C₃, C₄). The one associated with the tuberculum is much taller (Fig. 29C₄). Radial striations are present on its lateral surface. They are more pronounced near the relatively straight dorsal

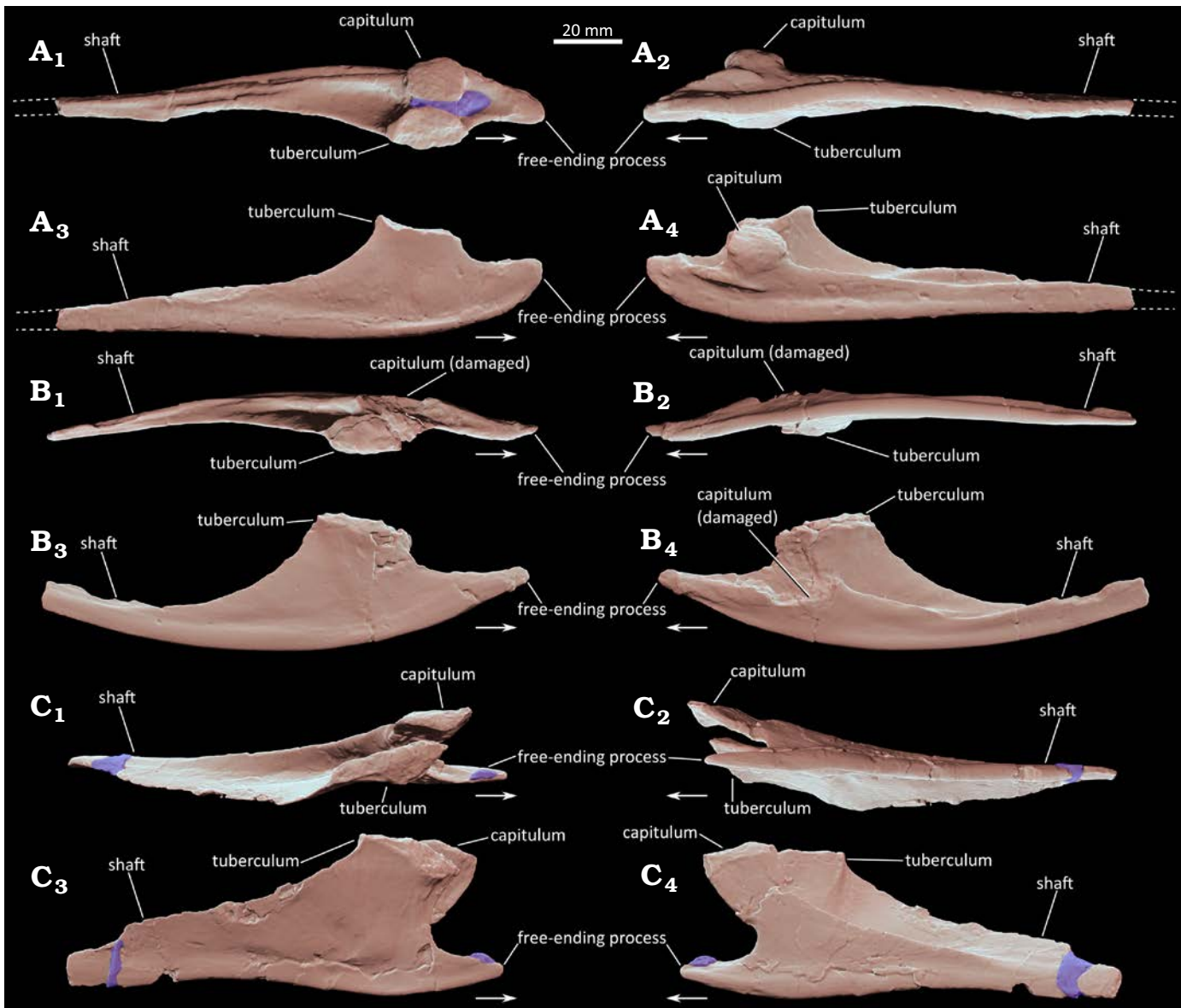


Fig. 29. Posterior cervical ribs of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. Anterior portion of the left eleventh cervical rib (ZPAL V. 36/1019, mirrored, **A**), left twelfth cervical rib (ZPAL V. 36/1000, mirrored, **B**), and right thirteenth cervical rib ZPAL V. 36/1251 (**C**), in ventral (**A**₁–**C**₁), dorsal (**A**₂–**C**₂), lateral (**A**₃–**C**₃), and medial (**A**₄–**C**₄) views. Arrows indicate anterior direction. Areas covered with sediment marked with blue hue. Note that the capitulum in ZPAL V. 36/1000 is largely missing and the tuberculum and capitulum in ZPAL V. 36/1251 are nearly touching due to diagenetic deformation.

edge of this lamina (Fig. 29C₃). The general morphology of the last cervical rib is shared between *T. conspicuus* and *T. hydroides* but not *T. longobardicus* (see Wild 1973; Nosotti 2007; Rieppel et al. 2010). In the latter, the lamina projecting from the tuberculum is not posterodorsally expanded. Intriguingly, there is a feature that is present in both *T. hydroides* (PIMUZ T 2787) from Monte San Giorgio and a *Tanystropheus* specimen (GMPKU P 1527) from China but not in any of the ribs of *T. conspicuus*: on the dorsolateral surface of the lamina connecting the tuberculum and the shaft in the last cervical rib of the two latter forms there is a horizontal shelf-like ridge parallel to the shaft. In *T. conspicuus* this surface is flat.

Dorsal ribs: As in many other archosauromorphs, the dorsal ribs of *T. conspicuus* are long, slender, and lateromedially curved elements (Fig. 30). Their morphology is clearly visible in the partial skeletons ZPAL V. 36/125 (Figs. 20, 30) and ZPAL V. 36/584 (Fig. 16). Whereas I generally consider most isolated dorsal ribs from Miedary as non-diagnostic for *Tanystropheus*, the dicephalous anterior dorsal ribs are distinct in their shape (see below) and can be referred to *T. conspicuus* with high confidence.

Among the dorsal ribs of other species of *Tanystropheus*, the first two or three pairs were identified as dicephalous (Wild 1973; Renesto 2005; Nosotti 2007), whereas the rest are holocephalous. Three dicephalous dorsal ribs are associ-

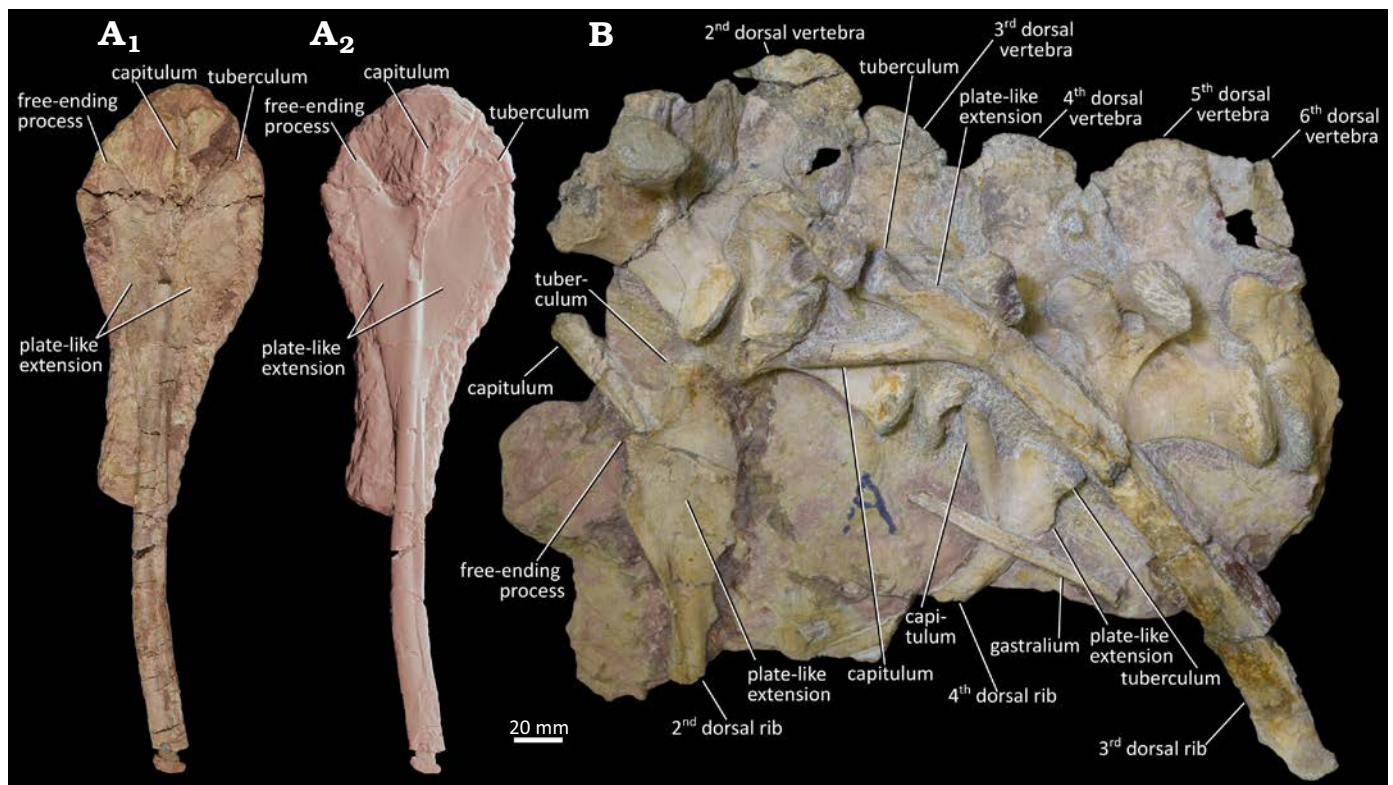


Fig. 30. Anterior dorsal ribs of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Photographs (A₁, B), three-dimensional model snapshot with Lit Sphere Radiance Scaling shader enabled (A₂). First right dorsal rib (ZPAL V. 36/123, A) and left anterior dorsal ribs associated within an anterior portion of a partial skeleton (ZPAL V. 36/125, B), in medial (A) and left lateral (B) views.

ated with their corresponding consecutive vertebrae within ZPAL V. 36/125 (Fig. 30). They were likely preceded by an unpreserved first dorsal vertebra (see Discussion), which implies that the four anteriormost pairs of dorsal ribs were dicephalous in *T. conspicuus*. They bear a well-separated, relatively long and slender capitulum and a stubby tuberculum, which becomes more massive in the more posterior elements. Dorsal ribs from the first pair, of which an example is preserved in isolation but identified based on its morphology, are similar in the morphology of their proximal portion to the posteriormost cervical ribs, and possess a large, triangular anterior free-ending process (Fig. 30A). It is nevertheless identified as a dorsal rib based on its shaft morphology. In the second dorsal rib pair the anterior free-ending process is very much reduced, and in the succeeding ribs it is completely absent (Fig. 30A).

The dicephalous anterior dorsal ribs of *T. conspicuus* bear a distinct feature—their dorsolateral surface is anteroposteriorly expanded along the shaft distal to the tuberculum-capitulum conjunction, forming a very thin plate-like extension (Fig. 30). Its lateral surface is relatively smooth but covered with radial striations. A similar structure is present in the posteriormost cervical ribs, but in the first dorsal ribs it is more distally expanded (compare Fig. 29C and Fig. 30A). In the first two dorsal rib pairs this extension is roughly triangular in lateral view, with laminae extending from the tuberculum and the free-ending process. Their anteroposte-

rior width diminishes distally, as they terminate around the middle of the length of the shaft (Fig. 30). The third dorsal rib preserves only a slightly expanded anterolateral ridge, a remnant of the plate-like extension found in the preceding elements (Fig. 30B). In the fourth dorsal rib, in which the capitulum and the tuberculum become nearly confluent, this ridge is reduced to a weakly projecting tuberosity on the posterolateral edge of the rib (Fig. 30B). A similar morphology can be noted for the ribs associated with the first dorsal vertebra of *T. hydroides* (e.g., PIMUZ T 2787, PIMUZ T 2793, PIMUZ T 2817, PIMUZ T 2818), *T. cf. T. longobardicus* (e.g., MCSN 4451) and *Tanystropheus* sp. (e.g., IVPP V 14472), all bearing the plate-like extension in at least the first pair of dorsal ribs, which also possess the free ending anterior process (PIMUZ T 2787, MCSN 4451). Wild (1973: fig. 35, “fourth” dorsal rib) misidentified this process as a rudimentary capitulum in the first pair of dorsal ribs of PIMUZ T 2787. The plate-like extension is relatively much less expanded in the other species of *Tanystropheus* than in *T. conspicuus*, and in the latter it is present also on the third pair of dorsal ribs, albeit in a much reduced form (Fig. 30B). This structure has not been reported in any other tanysaurian.

Posterior to the fourth dorsal vertebra the vertebrae bear holocephalous ribs, with each succeeding rib being shorter and less lateromedially curved. Wild (1973) interpreted the ribs of the last two dorsal vertebrae in *Tanystropheus* as pleurapophyses tightly fused with their corresponding ver-

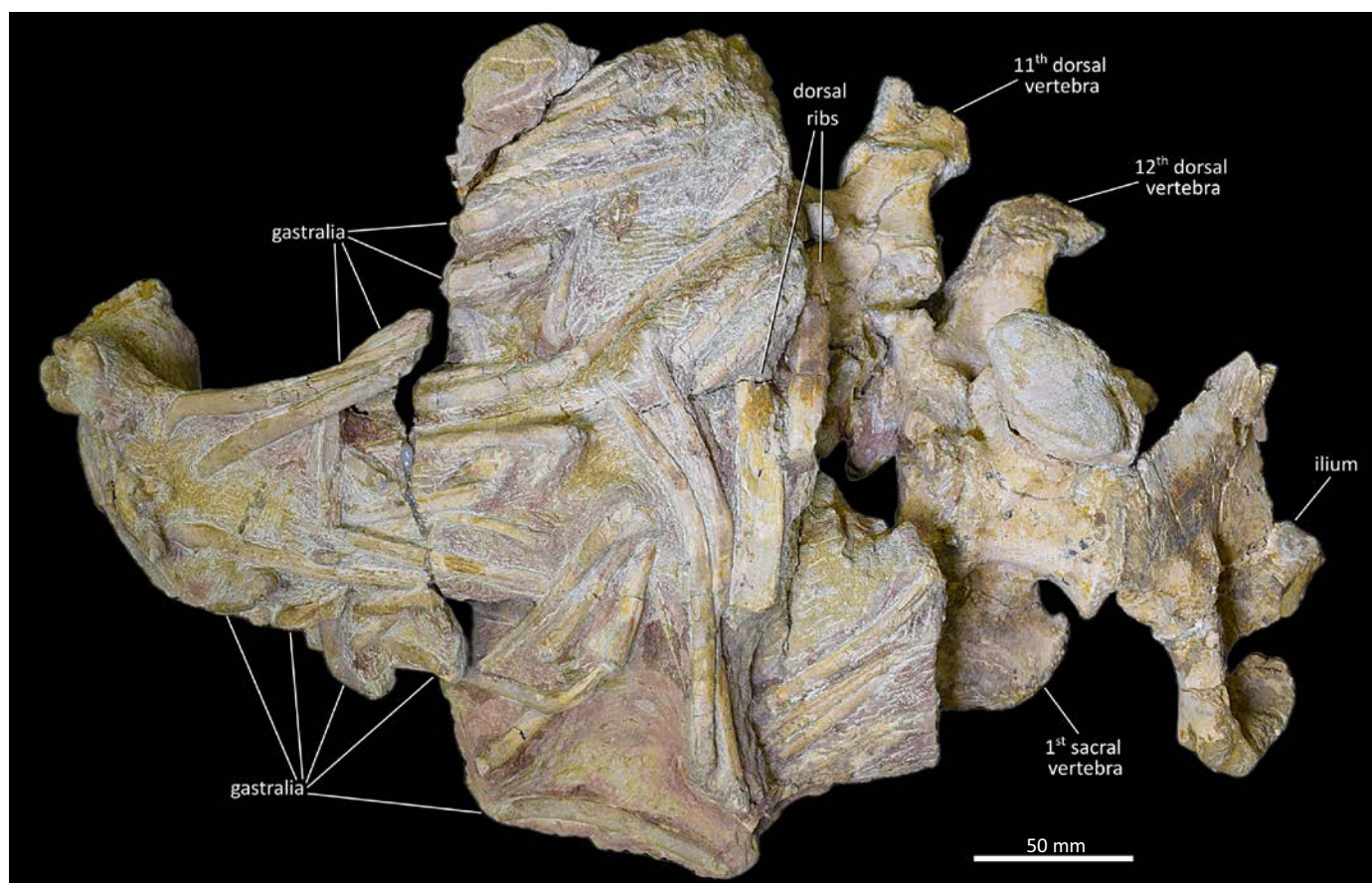


Fig. 31. Gastralia of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Association within the posterior portion of the partial skeleton (ZPAL V. 36/125) in left ventrolateral view.

tebrae. ZPAL V. 36/125 demonstrates that this was not the case in *T. conspicuus*. Diapophyses in this specimen are clearly separate in even the last pair of dorsal ribs, which are individual short elements.

Gastralia: Some isolated slender, elongate, roughly V-shaped elements similar to those known from the articulated specimens of *T. hydroides* and *T. longobardicus* have been found in Miedary, but they are not diagnostic enough to unequivocally identify them as gastralia of *Tanystropheus*. The only unequivocal gastralia of *T. conspicuus* are associated with the articulated partial skeleton ZPAL V. 36/125, which preserves a considerable number of intermingled, closely packed, relatively thin elements (Fig. 31) which in life would have formed an extensive gastral basket.

Consistent with descriptions for the other species of *Tanystropheus*, there are two morphotypes of gastralia, which intertwined with each other (Wild 1973). The more laterodorsally located ones were gently bent to form an obtuse angle, thus being bow-like in their shape. The elements forming the medioventral part of the gastral basket were generally straight, with only their ventralmost portion mediadorsally curved roughly at a right angle. These gastralia met along the midline of the ventralmost part of the torso, with the hook-like ending interlocking with corresponding element originating from the contra-lateral side. Together they formed

a transversely V-shaped structure, a condition widely distributed in other diapsids including tanysaurians (see Olsen 1979; Jaquier et al. 2017; Spiekman et al. 2024b, c).

Clavicle: Prior to this study, no elements from the pectoral girdle of *T. conspicuus* were known. Only a few non-archosaurian archosauromorphs have three-dimensionally preserved and complete clavicles. Comparative material is therefore limited and as a consequence the identification of isolated clavicles is often problematic. Wild (1973) interpreted the more widened blunt portion of the clavicle of *Tanystropheus* as articulating with the interclavicle, but this interpretation was challenged by Jaquier et al. (2017) who argued that it articulated with the scapula instead. Here I follow the latter study.

As in many other diapsids, the clavicle of *T. conspicuus* is an elongate sickle-shaped element (Fig. 32). The antero-medial portion of the element is rod-like, with its tapering end pointing ventromedially. Two well-defined parallel grooves extend for most of the length of the clavicle along its anteroventral surface, giving it a T-shaped transverse cross section (Fig. 32B₄). They are separated by an anteroventrally oriented ridge, which is especially expanded near the anteroposterior midpoint of the bone (Fig. 32B₃). As there is no evidence for the presence of an ossified interclavicle in *Tanystropheus* (see Discussion), the anteromedial portion of

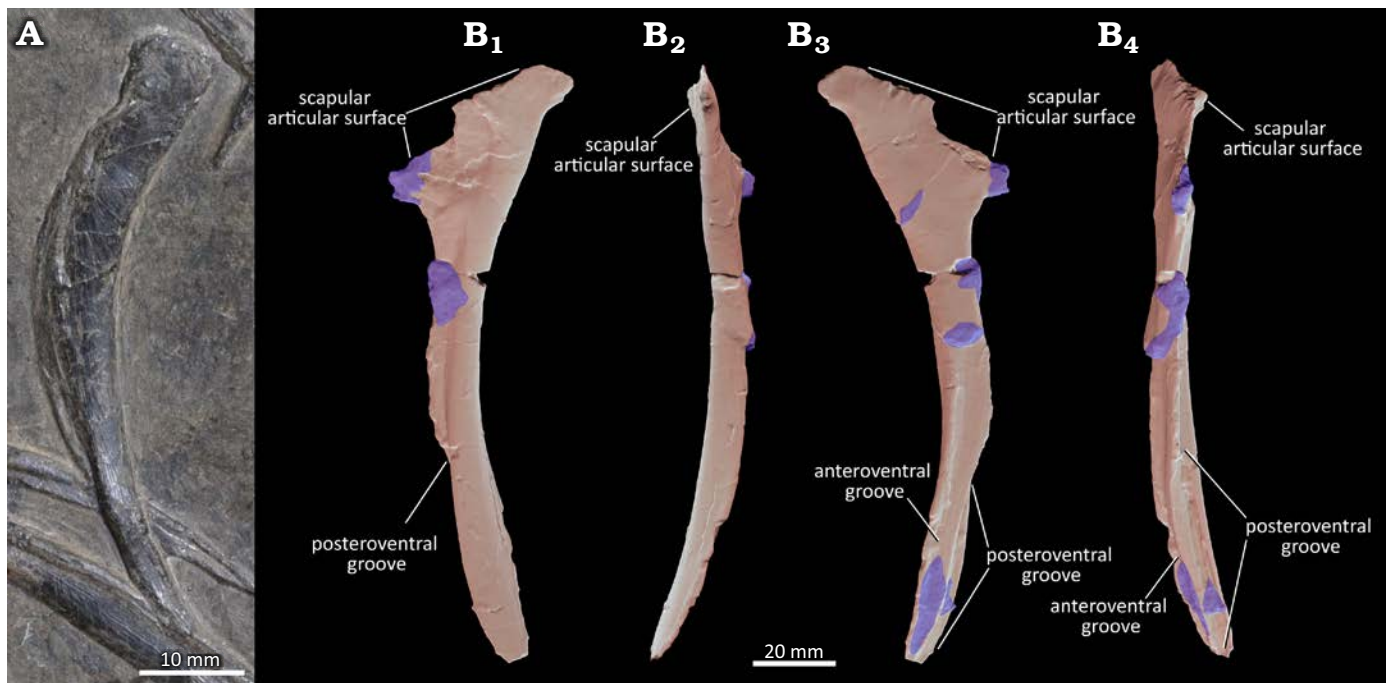


Fig. 32. Clavicles of the tanystropheid archosauromorph *Tanystropheus*. Photograph (A), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (B). **A.** *Tanystropheus hydroides* Spiekman et al., 2020a, from the Besano Formation (upper Anisian to lower Ladinian) of Monte San Giorgio, Switzerland, PIMUZ T 2787, left clavicle in dorsomedial view. **B.** *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland, ZPAL V. 36/2449 left clavicle in dorsomedial (B₁), anterodorsal (B₂), ventrolateral (B₃), and posteroventral (B₄) views. Areas covered with sediment marked with blue hue.

the clavicle was likely embedded in chondral tissue instead. The posterolateral end of the clavicle, which articulated with the scapula, is dorsoventrally widened, forming a triangular expansion deflected posterodorsally from the relatively straight anteromedial portion of the bone (Fig. 32B₁, B₃). Its surface is rugose and covered with striations that run perpendicular to the bone edge. Morphology of the posterior margin of the posterolateral portion of the clavicle varies between the two known specimens (ZPAL V. 36/1308 and 2449) and might be a subject of high intraspecific variation. In ZPAL V. 36/1308 it is formed as a lateromedially thin ridge that is straight in lateral view, whereas in ZPAL V. 36/2449 this margin has an irregular profile (Fig. 32B₁, B₃).

Elements from Miedary, interpreted as clavicles of *T. conspicuus*, are morphologically nearly identical to those of *T. hydroides* (see Fig. 32A). At the same time, the clavicular morphology of both *T. conspicuus* and *T. hydroides* differs from MFSN 31553, a *Tanystropheus* sp. clavicle described by Dalla Vecchia (2006: fig. 15). This specimen is relatively more robust and straight. Its posterolateral portion is not transversely expanded, contrary to what we see in *T. conspicuus*, but similar to what can be observed in *T. hydroides* and *T. longobardicus* (Wild 1973; Nosotti 2007). With the currently accessible sample size it is difficult to assess to what extent some of these differences might be attributable to preservation characteristics or individual size difference.

Scapula: The scapula in *T. conspicuus* is an extremely lateromedially thin, anteroposteriorly broad and dorsoventrally elongate bone (Fig. 33A). Its lateral surface is smooth,

with fine, straight striations radiating distally from the glenoid region (Fig. 33A). The glenoid peduncle is formed as a short but distinct process, with the glenoid fossa being located mainly ventrolaterally, and slightly posteriorly. Anterior to the glenoid, the anteroventral scapular edge is smoothly convex, forming a semicircular acromion process in lateral view (Fig. 33A). Posterodorsal to the acromion process and dorsal to the glenoid the anterodorsal edge of the scapula was slightly concave, forming a constriction near the middle of the anteroposterior length of the scapula in lateral view. Posterodorsal to the constriction, the scapula reached its dorsalmost extent, from which the dorsal scapular edge descended posteroventrally, forming the dorsal outline of the scapular blade in lateral view (Fig. 33A). Posterior to the glenoid, the edge of the scapula curved abruptly, at an angle close to 90°, and extended in a straight line posterodorsally, constituting the posteroventral outline of the scapular blade in lateral view. The scapular blade is similar to other species of *Tanystropheus* in being subtriangular in lateral view (Fig. 33A). Whereas Wild (1973, 1987) interpreted the scapula and coracoid of *Tanystropheus* as being fused anteriorly and/or posteriorly, for *T. conspicuus* there is no indication for any contact between them other than at the glenoid region, similar to what was noted for *T. hydroides* and *T. longobardicus* by Spiekman et al. (2021).

One scapula of *T. conspicuus* from Miedary ZPAL V. 36/2426 has been found in situ in a vertical position, with the dorsal edge of the scapular blade pointing upwards. The scapular blade in this specimen is as thin as in the other scapulae

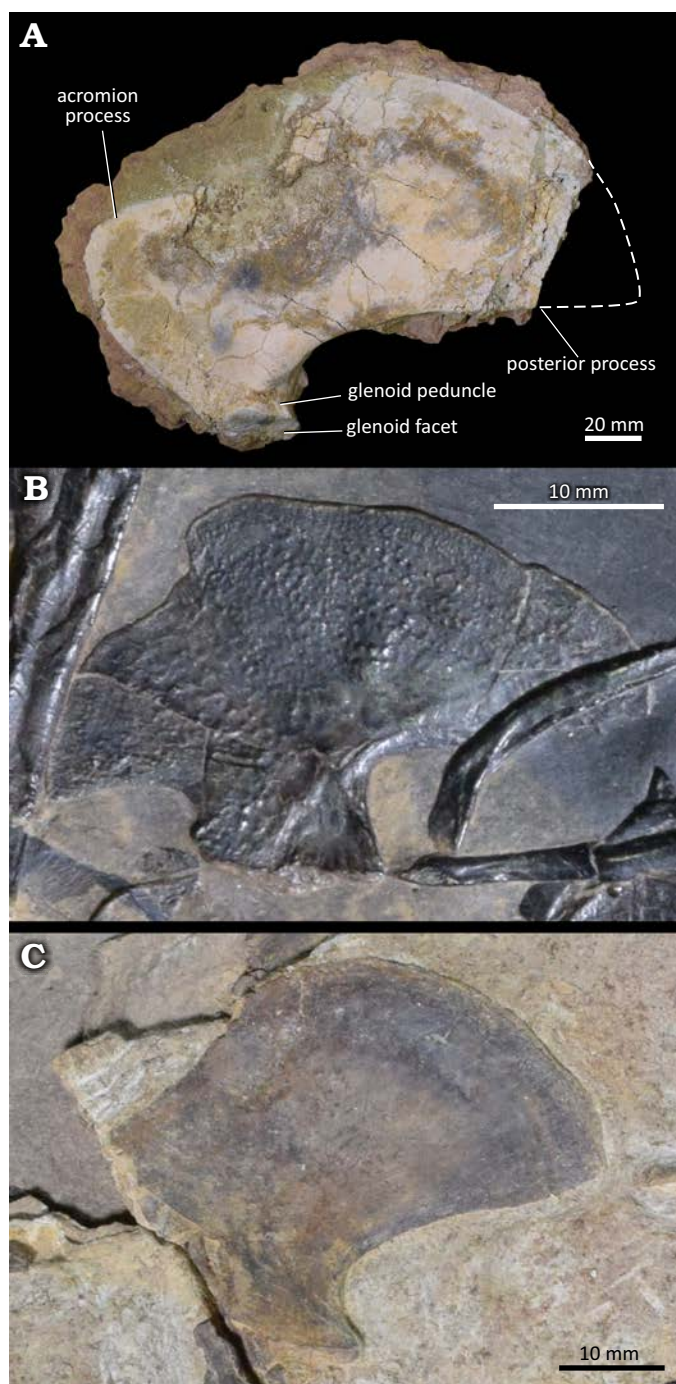


Fig. 33. Left scapulae of three species of the tanystropheid archosauromorph *Tanystropheus* in left lateral view. A. *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland, ZPAL V. 36/811, the posterior tip is missing. B. *Tanystropheus longobardicus* (Bassani, 1886), from the Besano Formation (upper Anisian to lower Ladinian) of Monte San Giorgio, Italy, MSNM BES SC 1018. C. *Tanystropheus hydroides* Spiekman et al., 2020a, from the Besano Formation (upper Anisian to lower Ladinian) of Monte San Giorgio, Switzerland, PIMUZ T 1270.

of *T. conspicuus*, indicating that the extremely limited thickness of these elements is not diagenetically-induced.

The scapula of *T. conspicuus* differs from other species of *Tanystropheus* in several features (see Fig. 33). In

T. longobardicus, and possibly in *T. hydroides*, the acromion process is triangular in lateral view, tapering anteroventrally to a point (Fig. 33B, C). The ventral edge of this process is roughly parallel to the ventral edge of the scapular blade. This is unlike *T. conspicuus*, where they are close to being perpendicular (Fig. 33A) as a result of the acromion process being semicircular and more dorsally directed. The anteroposterior constriction of the scapular blade is deeper and more posteriorly located in *T. conspicuus* than in other species of *Tanystropheus* (Fig. 33). At the same time, the most dorsally extended point of the scapular edge is also relatively more posteriorly located. When compared to other species of *Tanystropheus* the posterior part of the scapula in *T. conspicuus* was much more elongate and occupied a much larger area than its anterior portion (Fig. 33A–C). A similar morphology is present in other tanystropheids (e.g., PIMUZ T 1559, a referred specimen of *Macrocnemus fuyuanensis* Li et al., 2007), which share the constriction at the mid-length, semicircular acromion process and a long, triangular scapular blade (Jaquier et al. 2017). The scapula in *T. conspicuus* is, however, relatively more elongate and taller than in other tanysaurians, thus being distinct in its morphology. Moreover, the concavity present between the glenoid peduncle and the scapular blade in lateral view is much shallower than in its relatives (Fig. 33). These proportions are somewhat reminiscent to the scapular morphology of other early archosauromorphs, in which a fused scapulocoracoid is present (e.g., *Prolacerta broomi* Parrington, 1935, *Protorosaurus speneri* von Meyer, 1832; Gow 1975; Gottmann-Quesada and Sander 2009).

Coracoid: The coracoid in *T. conspicuus* is a flat plate-like and dorsoventrally thin bone (Fig. 34). There are no osteological correlates for any other contact with the scapula other than a relatively reduced surface medial to the glenoid. When in articulation, the coracoid and scapula of *T. conspicuus* were seemingly not firmly fused and joined only at the glenoid, with their anterior and posterior portions being separated and forming a scapulocoracoidal fenestra (sensu Spiekman et al. 2021). The glenoid is located near the middle of the dorsolateral edge of the coracoid and is dorsolaterally oriented (Fig. 34). Anteromedial to it, a coracoid foramen is present. The portion of the coracoid anterior to the glenoid is more expanded than the postglenoid process, but both are similarly rounded and semicircular in shape in dorsal view. The ventromedial edge, which might have articulated with the unossified interclavicle, is anteroposteriorly straight in dorsal view and dorsoventrally thickened (Fig. 34). Both the dorsal and ventral surfaces of the coracoid are covered with radial striations. These are perpendicular to the concentric thickenings that mark the growth of the animal (Fig. 34).

Humerus: All limb bones of *T. conspicuus* are morphologically nearly identical to the corresponding elements of *T. hydroides*, although direct comparisons are difficult due to the differences in preservation and the resulting lack of three-dimensional information for the latter. As for other species of *Tanystropheus* (see Wild 1973; Nosotti 2007), the

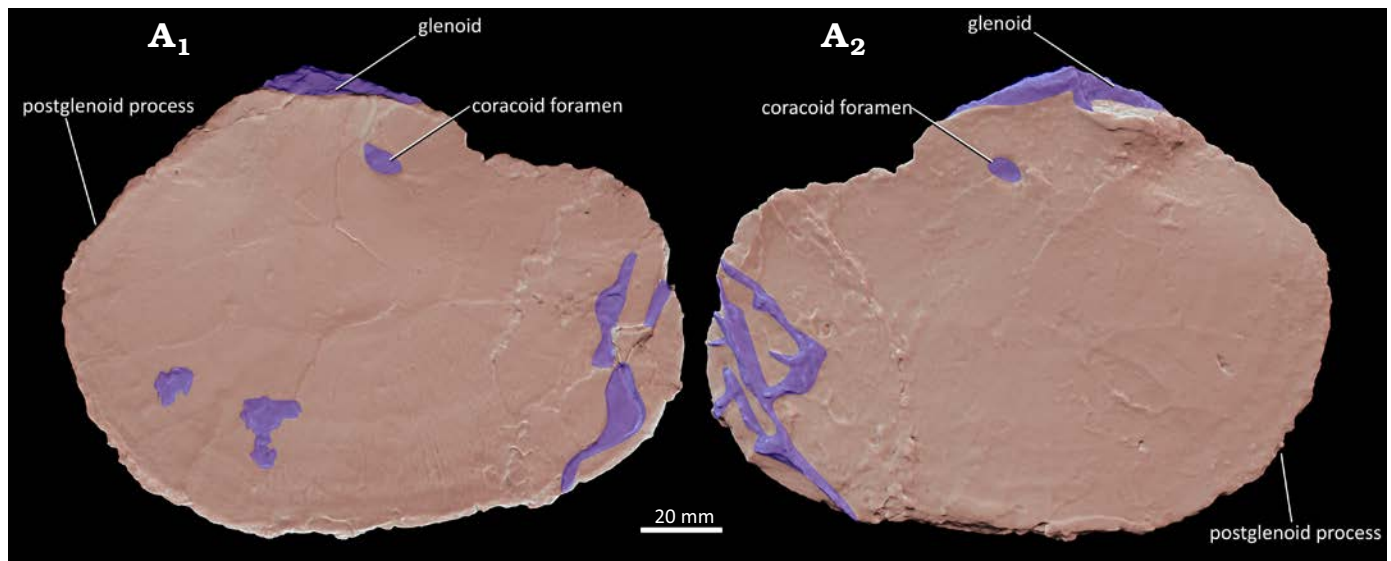


Fig. 34. Left coracoid of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1177 in dorsal (A₁) and ventral (A₂) views. Areas covered with sediment marked with blue hue.

humerus of *T. conspicuus* is less elongate than the femur. Its lateral and anterior (dorsal) margins are relatively straight, and its medial and posterior (ventral) margins are concave (Fig. 35). Significant torsion, reaching more than 45°, can be observed between the well-ossified proximal and distal ends of the humerus (Fig. 35A₃, A₄).

The proximal portion of the humerus is posteromedially expanded when compared to the thickness of the shaft (Fig. 35A). Its articular surface is elliptical in proximal view (Fig. 35A₅). In anterior view it is convex, and slightly more proximally expanded on its lateral side (Fig. 35A₃, A₄). No clear tubers can be distinguished, with the outline of the articular surface being oval in proximal view (Fig. 35A₅). Adjacent to the proximal articular surface, distal to its anterolateral corner, a very poorly defined deltopectoral crest is present (Fig. 35A₂–A₅).

The shaft has a nearly constant thickness along its length. The distal portion of the humerus is medially and slightly laterally expanded and larger than the proximal one. On its anterolateral margin, the supinator process is present (Fig. 35A₁, A₆). It is formed as a longitudinal ridge parallel to the shaft, confluent with the anterior surface of the distal end of the humerus but distinctly separated from its posterior surface by a proximodistally oriented groove.

The distal end of the humerus is composed of two condyles (Fig. 35A₆), the ectepicondyle (radial condyle) and the entepicondyle (ulnar condyle). They lie on two sides of a poorly outlined anteroposterior constriction of the distal portion of the humerus (Fig. 35A₆). The entepicondyle projects strongly medially from the shaft. Its medial and distal surfaces are roughly perpendicular, meeting in an obtuse angle. In distal view, the articular surface of entepicondyle is rounded and elliptical; it is separate from the ectepicondyle by an anteroposterior constriction and a poorly marked distal groove (Fig. 35A₆). Both condyles are distally ex-

panded to a similar extent, forming a relatively straight distal margin of the humerus (Fig. 35A₂). The ectepicondyle is larger and more broadly rounded in proximal view than the entepicondyle. It lies along the longitudinal axis of the shaft whereas the entepicondyle is distinctly offset from it and mediolaterally oriented (Fig. 35A₂).

Ulna: The ulna of *T. conspicuus* is a relatively straight element (Fig. 36). Its medial surface is slightly concave in anterior/dorsal view as a result of the lateromedial expansion of the proximal and distal ulnar ends (Fig. 36A₁, A₃). The ulna is virtually straight in medial view (Fig. 36A₂). In ZPAL V. 36/829, the only ulna referred to *T. conspicuus*, the articular surfaces are damaged but their margins are well outlined in anterior/dorsal view. The proximal portion of the ulna is more massive, with its articular surface being oriented obliquely to the longitudinal axis of the shaft in anterior/dorsal view (Fig. 36A₁, A₃). The olecranon process is absent. The lateral corner of the proximal end of the ulna is more proximally expanded than its medial corner (Fig. 36A₁, A₃). Distal to the proximal end of the ulna, a narrow, sharp ridge extends along the anteroposterior mid-width of the medial surface of bone (Fig. 36A₂). The distal end of the ulna in *T. conspicuus* is only slightly lateromedially expanded (Fig. 36A₁, A₃). It has a straight, nearly flat articular surface in anterior/dorsal view.

Radius: The radius is similar in its proportions to the ulna but is considerably more curved, with its posterior margin being strongly concave in anterior/dorsal view (Fig. 37). It is virtually straight in lateral view (Fig. 37A₂). The known radii referred to *T. conspicuus* do not have well preserved articular surfaces. The proximal articular surface is seemingly semi-triangular in proximal view, but this might be due to diagenetic alteration of its original morphology.

A fine ridge extends distal to the proximal portion along the posterolateral margin of the radius, parallel to the shaft

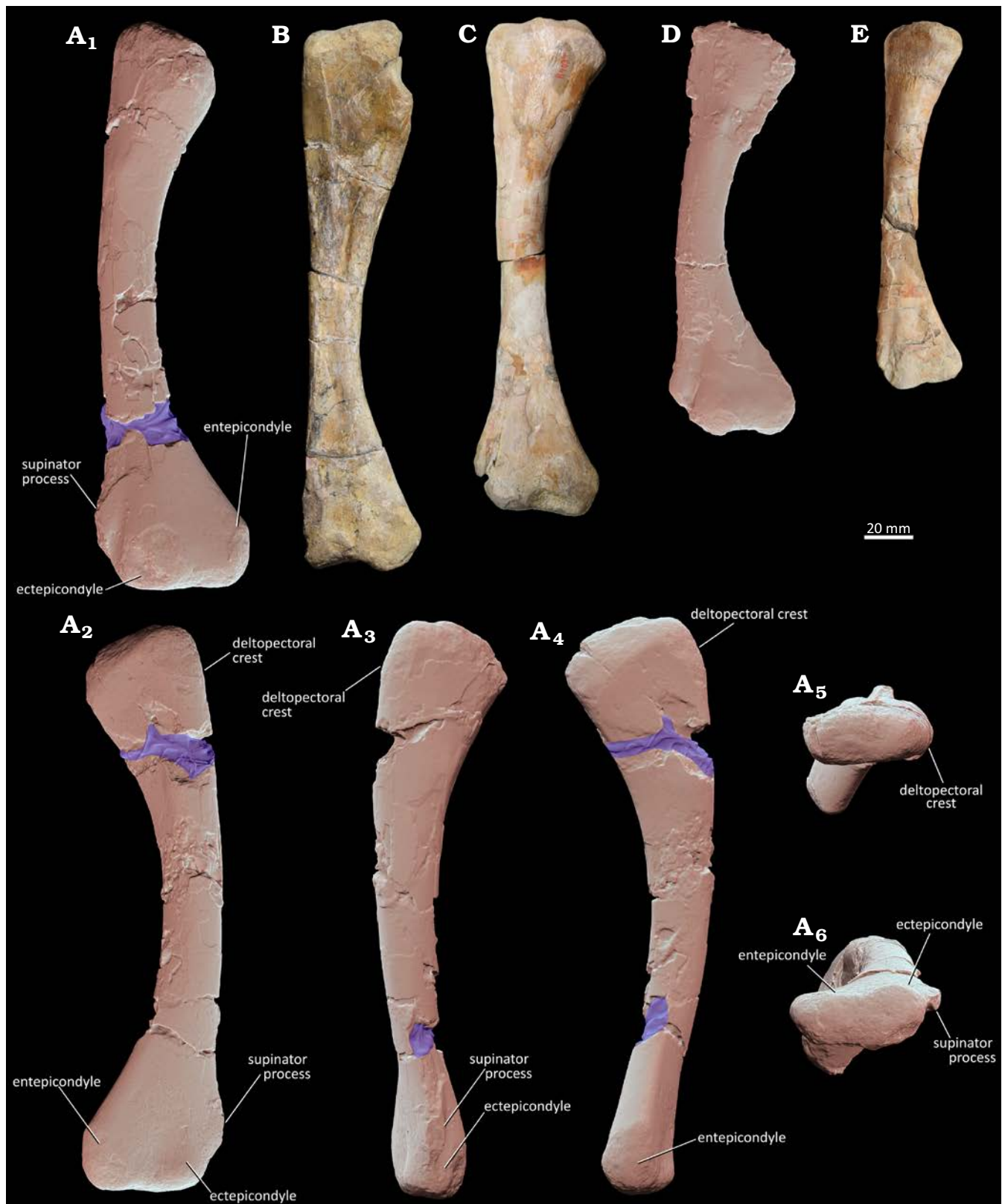


Fig. 35. Left humeri of the tanystropheid archosauriform *Tanystropheus conspicuus* von Meyer, 1852. Photographs (B–C, E), three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled (A, D). ZPAL V. 36/881 from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland (A), GPIH 253, the holotype of *Megacnemus grandis* von Huene, 1954, origin uncertain (B), ZPAL V. 36/882 from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland (C), SMF R 4034 from the Upper Muschelkalk (Upper Anisian, Middle Triassic) of Bindlach, Germany (D), and U-MO BT 3079 from the Upper Muschelkalk (Upper Anisian, Middle Triassic) of Bayreuth, Germany (E), in posterior/ventral (A₁, B–E), anterior/dorsal (A₂), lateral (A₃), medial (A₄), proximal (A₅), and distal (A₆) views. Areas covered with sediment marked with blue hue.

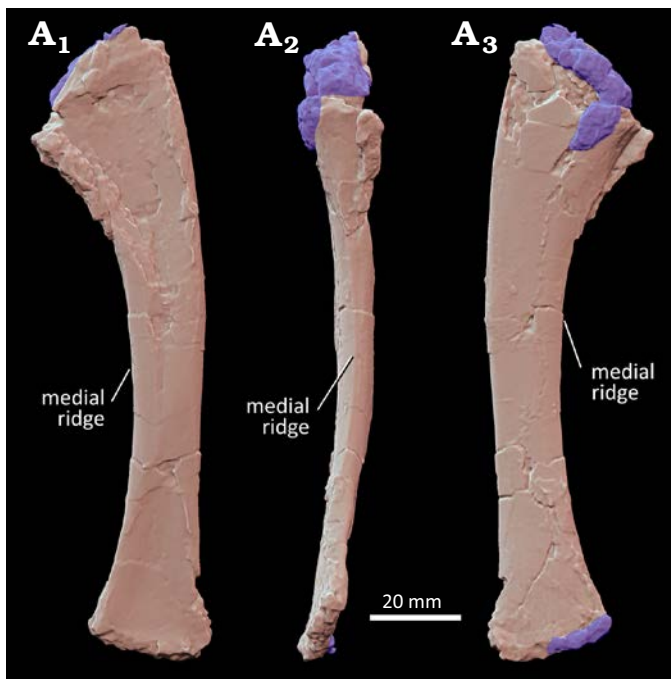


Fig. 36. Left? ulna of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/829 in anterior/dorsal (A₁), medial (A₂), and posterior/ventral (A₃) views. Areas covered with sediment marked with blue hue.

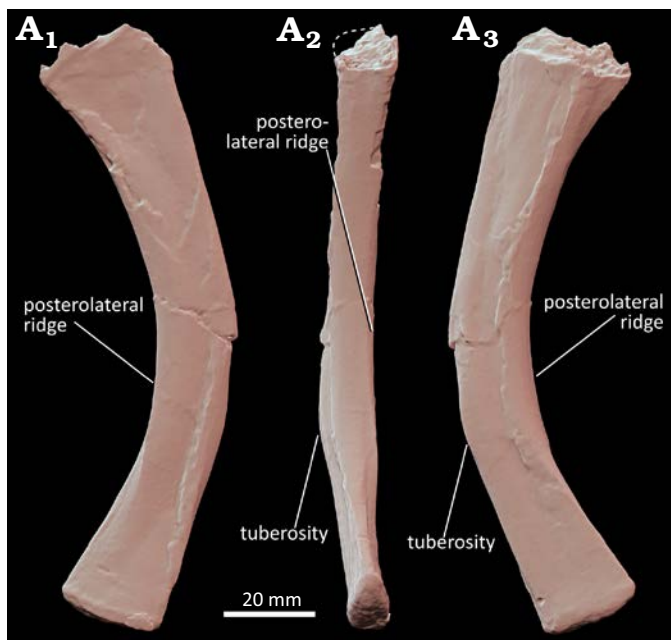


Fig. 37. Left? radius of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/830 in posterior/ventral (A₁), lateral (A₂), and anterior/dorsal (A₃) views.

(Fig. 37A₁, A₂). It becomes better defined and sharper in the middle section of the bone. An interosseous ligament likely stretched between this ridge, and the corresponding feature

present on the ulna. Closer to the distal end of the radius, the ridge becomes wider but lower and more confluent with the shaft surface. On the opposite side of the shaft, a poorly outlined tuberosity is located (Fig. 37A₂, A₃). It might correspond to a similar feature present in other early archosauromorphs (e.g., *Malerisaurus robinsonae* Chatterjee, 1980, see Sengupta et al. 2024: fig. 13). The distal end of the radius is only slightly less expanded than the proximal one, being marginally wider than the shaft (Fig. 37A₁, A₃). Its articular surface is elliptical in distal view and nearly straight in anterior/dorsal view.

Both the ulna and the radius of *T. conspicuus* are identical in their proportions to the corresponding elements of *T. hydroides*, being much more robust and thicker than the slender antibrachial bones of *T. longobardicus* (compare the “large” and “small” morphotypes of Wild 1973 and Nosotti 2007)

Autopodial elements: As for other Muschelkalk and Lettenkeuper sites, autopodial elements are scarce in Miedary. Several elongate bones from the site have been identified as reptile metatarsals and metacarpals, and it is highly likely that they belong to *T. conspicuus* but they are not diagnostic enough for this referral, at least not before articulated manus or pedes are found in Miedary.

Ilium: The ilium of *T. conspicuus* is relatively delicate for an animal of its size. It is composed of the acetabular region and the iliac blade, which are located on the opposite sides of the anteroposterior constriction of the ilium (Fig. 38). The majority of the acetabulum is located on the lateral surface of the ilium and the ischium, with only its anteroventral margin present on the lateroproximal portions of the pubis (Fig. 39). The pubic and ischial peduncles are similarly expanded anteroposteriorly, converging at an obtuse angle (Fig. 38A₁, A₂). The articular surface for the pubis is relatively straight and has a nearly uniform transverse width (Fig. 38A₂, A₃). The articular surface for the ischium is laterally concave, forming a lateroventrally oriented rhomboidal pit (Fig. 38A₂, A₃). Its triangular dorsal margin reaches deep within the acetabulum, pointing towards the posterior end of the supraacetabular crest (Fig. 38A₂). The posterolateral corner of the ischial peduncle is laterally expanded, forming a cone-shaped projection (Fig. 38A₂–A₄). The morphology and location of this feature are reminiscent of the antitrochanter (raised surface at the posterior portion of the acetabulum, see Nesbitt 2011) seen in more crownward archosaurs, including some Triassic forms (Nesbitt 2011; Ezcurra 2016; Spiekman et al. 2024a). The acetabulum is anterodorsally framed by the supraacetabular crest, which extends from the anteriormost portion of the pubic peduncle, constituting the ventral part of the anterior edge of the ilium (Fig. 38A₂). More posterodorsally, the supraacetabular crest is formed as a distinct, laterally projecting, rugose tuberosity, which terminates dorsal to the acetabulum (Fig. 38A₂).

The iliac blade constitutes the dorsal region of the ilium in *T. conspicuus*, with the preacetabular process and the postacetabular process extending off of it. The anterior edge of the preacetabular process is relatively straight in

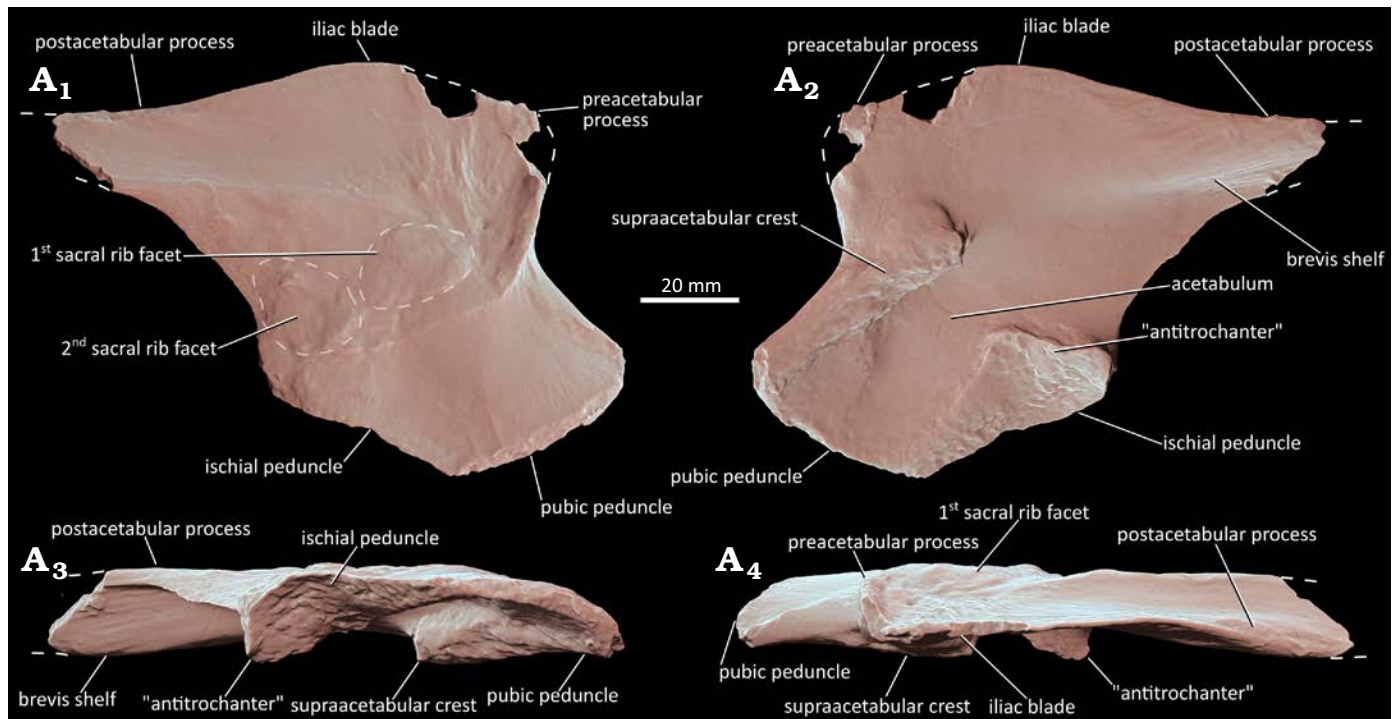


Fig. 38. Left ilium of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/813 in dorsomedial (A₁), ventrolateral (A₂), ventromedial (A₃), and dorsolateral (A₄) views.

lateral view, diverging anterodorsally from the supraacetabular crest near its mid-length (Fig. 38A₁, A₂). More dorsally, the edge of the preacetabular process is convex, curving to become confluent with the dorsal margin of the iliac blade (Fig. 38A₁, A₂). As can be observed in *T. hydroides* (see Wild 1973: fig. 93) and *Tanystropheus* sp. from north-eastern Italy (see Dalla Vecchia 2006: fig. 16), the minute anteriorly projecting extension of the preacetabular process described for *T. longobardicus* by Nosotti (2007) is absent in *T. conspicuus* (Fig. 38A₁, A₂). This character is, however, intraspecifically variable in *Tanystropheus* (see Spiekman et al. 2021). The iliac blade is composed of a lateromedially thin but ventrally thickened, plate of bone (Fig. 38A₄). The dorsal margin of the iliac blade is strongly convex in lateral view in its anterior portion, and its posterior portion is slightly concave (Fig. 38A₁, A₂). The postacetabular process is posterodorsally oriented and tapering (Fig. 38A₁, A₂). Its base is formed by a thin, concave, lamina extending from the ischial peduncle to the ventromedial edge of the postacetabular process in lateral view (Fig. 38A₁–A₃). Dorsolateral to it, the postacetabular process is slightly laterally expanded, forming a horizontal shelf on its dorsomedial side (Fig. 38A₁, A₂, A₄). This feature was interpreted by Ezcurra (2016) as homologous to the brevis shelf of Novas (1996), the origin of the musculus caudifemoralis brevis.

The medial side of the ilium is characterised by the presence of attachment sites for the sacral ribs (Fig. 38A₁). These are positioned posterodorsal to a curved ridge that extends posteroventrally from the notch in the anterior margin of the ilium (Fig. 38A₁). Both attachment sites for the sacral ribs

are similar in size and elliptical in medial view. They are located at the neck of the ilium, which formed by its antero-posterior constriction. The first sacral rib facet is more centrally located, with the second one being positioned closer to the posterior margin of the ischial peduncle.

Prior to this study, no elements from the pelvic girdle of *T. conspicuus* were known. Von Huene (1958b) interpreted a specimen as an ilium of *Tanystropheus* sp. but this element is a nothosaurian scapula (Wild 1973: 114; AR personal observation). The ilium of *T. conspicuus* is very similar in its morphology to the ilia of other species of *Tanystropheus* (AR personal observation, but see Wild 1973; Dalla Vecchia 2006; Nosotti 2007), with the elements herein referred to *T. conspicuus* being relatively slightly taller. Moreover in *T. conspicuus* the postacetabular process is relatively more slender (dorsoventrally narrower) in lateral view and its ventral surface is less concave (compare Fig. 38 herein and Wild 1973: fig. 93). The projection observed on the lateral surface of the ilium, posterior to the acetabulum (Fig. 38A₂–A₄), might also be present in *T. hydroides* and *T. longobardicus* (e.g., MSNM BES SC 1018, PIMUZ T 2483), but differences in preservation do not allow for a confident assessment. If this projection is interpreted as the antitrochanter, it would be its earliest occurrence (evolutionarily) within Archosauromorpha (Nesbitt 2011; Ezcurra 2016, Spiekman et al. 2021).

Pubis: The pubis of *T. conspicuus* is plate-like, but with a distinct lateral process (Fig. 40). Its dorsal region is the sturdiest portion of the bone and it is especially lateromedially thick near the acetabular contact with the ilium (Fig. 40).

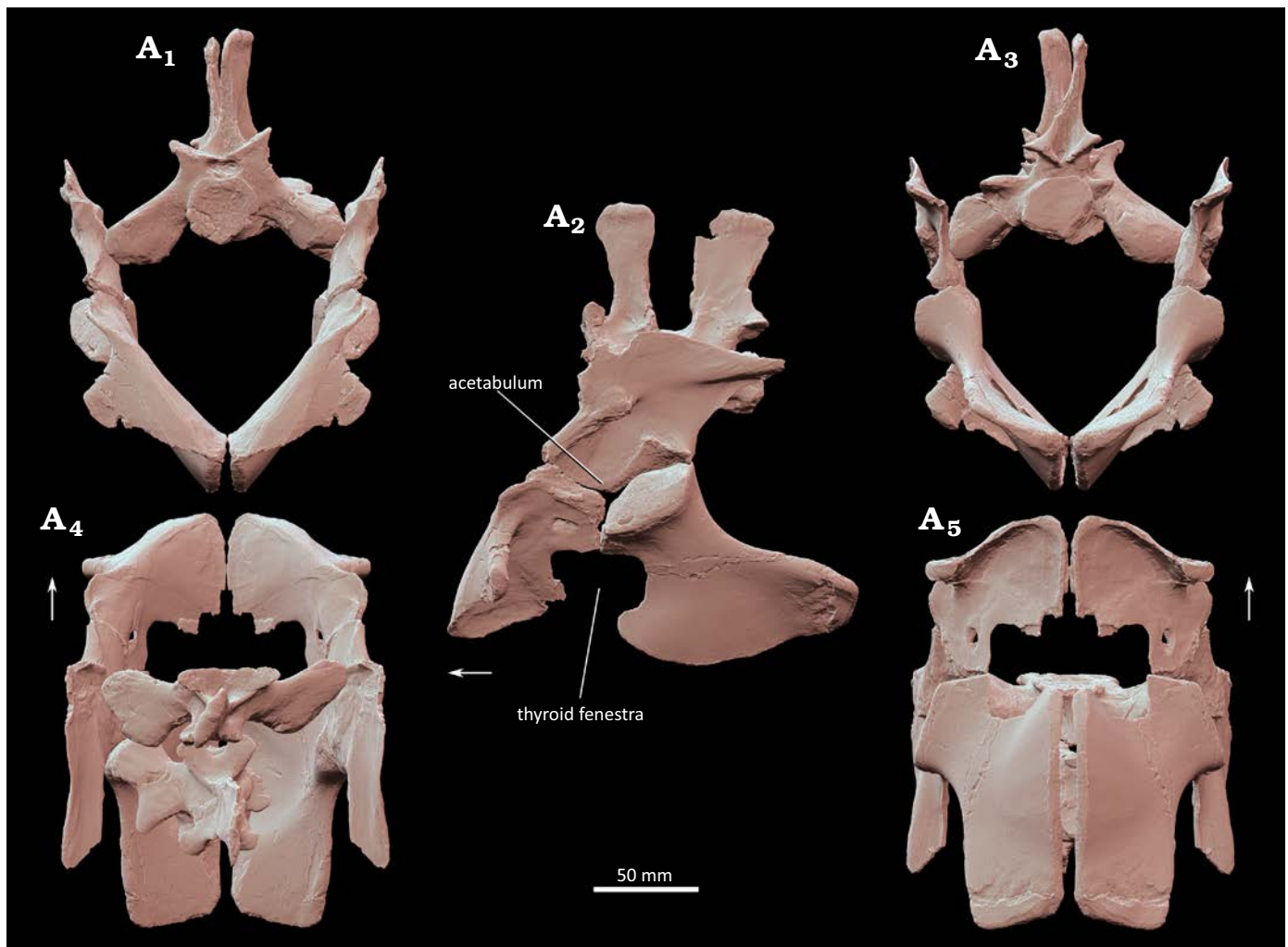


Fig. 39. The pelvis of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. The reconstructed model of pelvis in anterior (A_1), left lateral (A_2), posterior (A_3), dorsal (A_4), and ventral (A_5) views; composed of isolated specimens ZPAL V. 36/813, ZPAL V. 36/1006, ZPAL V. 36/1008, ZPAL V. 36/1037, ZPAL V. 36/1187, and their mirrored versions. The ZPAL V. 36/1006 ischium has been scaled down to about 80% of its original size. Note that none of the elements has been retrodeformed and some of their fragments are missing (e.g., right rib of the second sacral vertebra). Arrow indicates anterior direction.

The straight posterodorsal margin of the pubis is equally divided between the articular surface for the pubic peduncle of the ilium, and, more laterally, the ventral portion of the acetabulum (Fig. 40A₁, A₃). The articular surface for the ischium occupies a much smaller area, positioned ventral to the posterior edge of the articular surface for the ilium, with an obtuse angle formed between them (Fig. 40A₁, A₃). Anteroventral to this junction, the pubis is pierced by an obturator foramen (Fig. 40A₁, A₃). An anteriorly projecting, semi-circular ridge is present anterolateral to the ventral acetabulum margin (Fig. 40A₁–A₃). It forms the insertion point for the musculus ambiens (see Ezcurra 2016). Longitudinal striations covered the rugose surface of the pubis ventral to this process (Fig. 40A₂, A₃).

Distal to the articular portion of the bone, the pubis of *T. conspicuus* is composed of two plates of thin bone, the medial and the lateral plates, which meet roughly at a right angle along the edge of the pubic shaft (Fig. 40A₁). The lateral plate

is triangular in anterior view and ventrolaterally oriented (Fig. 40A₁, A₂). Its dorsal edge is straight and projects from the pubic shaft at an obtuse angle (Fig. 40A₂). Similar to some other reptiles (Wild 1973; Ezcurra 2016), it is distally thickened, forming a distinct lateral process, which terminates sharply with an elliptical, laterally oriented muscle attachment surface (Fig. 40A₁). From the ventral edge of this surface the ventrolateral margin of the lateral plate descends to converge with the medial pubic margin, decreasing ventrally in its transverse width (Fig. 40A₂). The anteroposteriorly extending medial plate has a broad, almost completely flat surface (Fig. 40A₁–A₃). Its posterodorsal margin forms a semicircular notch in lateral view (Fig. 40A₁, A₃). A constriction perpendicular to the pubic shaft is formed between this notch and the dorsal surface of the base of the lateral process (Fig. 40A₁, A₃). The posterior edge of the medial plate is straight and converges with the ventromedial pubic margin at an acute angle (Fig. 40A₁, A₃). It contributes to the anterior

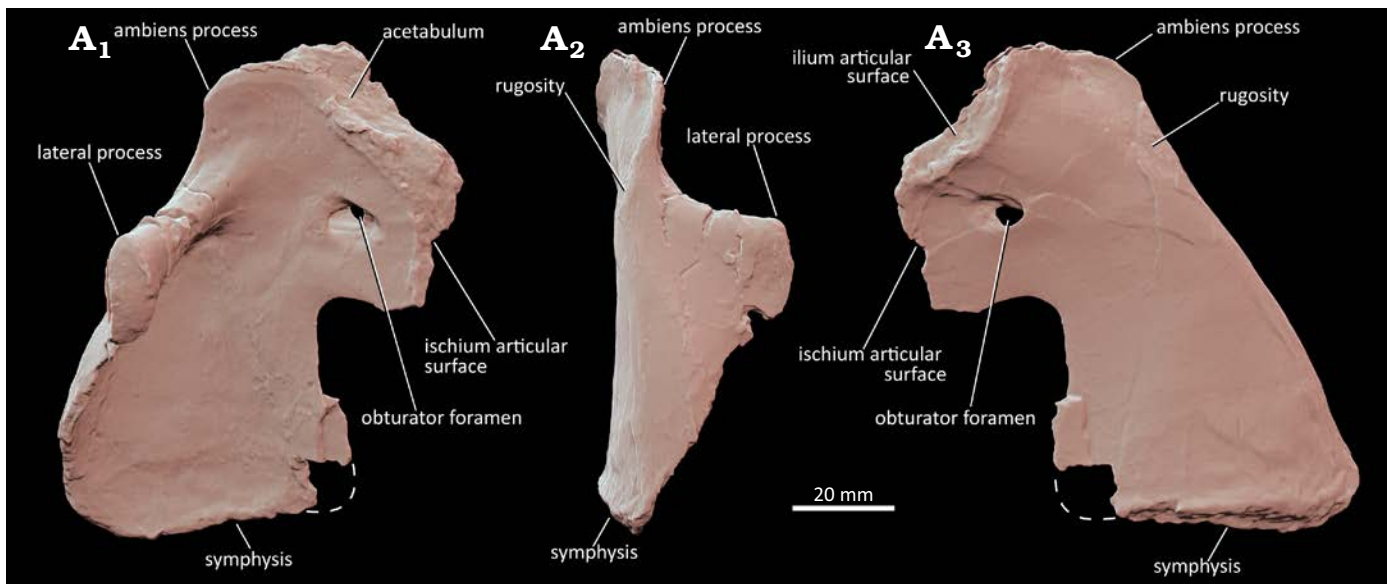


Fig. 40. Left pubis of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1008 in ventrolateral (A₁), anterior (A₂), and dorsomedial (A₃) views.

margin of the thyroid fenestra between the pubis and the ischium. The pubes of *T. conspicuus* articulated along their straight symphyseal margin, on the thickened ventral edge, and forming the pubic apron (Figs. 39, 40A₁, A₃).

Of the three bone pairs that formed the pelvic girdle of *Tanystropheus*, the pubes have the most three-dimensional features, due to the presence of the lateral process, and previously their original morphology could only be extrapolated from the diagenetically flattened individuals (Fig. 39; Wild 1973). Nevertheless, all three valid species of *Tanystropheus* seem to share the same pubis morphology (AR personal observation).

Ischium: The ischium of *T. conspicuus* is composed of the robust articular region and the lateromedially flat, fan-shaped distal portion (Fig. 41). The proximal portion of the ischium is separated into the iliac and the pubic articular surfaces as well as the posteroventral margin of the acetabulum (Figs. 39, 41A₁–A₃). The more dorsally located surface, which articulated with the ischial peduncle of the ilium, is nearly confluent with the acetabulum, forming a virtually flat dorsoproximal portion of the ischium (Fig. 41A₃). This region is elliptical in dorsal view, with the acetabulum being more laterally located, and the articular surface for the ilium being posteromedially expanded, far beyond the plane of the plate-like distal portion of the ischium (Fig. 41A₂). The articular surface for the pubis constitutes the anteroproximal portion of the articular region, converging at an obtuse angle with the iliac articular surface (Fig. 41A₁, A₃). It is triangular in lateral view, projecting anteroventrally and tapering to a point. The posterodorsal portion of the articular surface of the ischium might have contributed to the “anitrochanter” present on the ischium (Figs. 39, 41).

Ventrodorsal to the articular surface for the pubis, the anterior margin of the ischium forms the posterior edge

of the thyroid fenestra, developed as a deep, rectangular notch in ventrolateral view (Figs. 39, 41A₁, A₃). The anterior process of the ischial fan is present ventral to it. The lateromedially thin edge of the anterior process does not taper to a point, by contrast with some other archosauromorphs, including *T. hydroides* and *T. longobardicus* (Wild 1973; Ezcurra 2016). Instead, it is rounded in lateromedial view (Fig. 41A₁, A₃), and anteriorly expanded to a similar extent as the anteroventral corner of the pubic articular surface. The thyroid fenestra was ventrally open between the ischium and the pubis, albeit only with a narrow gap being present between the posterior process of the ischium, and the posteroventral edge of the pubis (Fig. 39). Ventral to the anterior process, the distal edge of the ischium is straight in lateral view, but concave in ventral view, due to its posteroventral corner being medially displaced (Fig. 41A₁, A₃, A₄). On the medial side of the ischial fan the distal edge of the ischium is convex, forming a distinct triangular and rugose thickening on which its antimeric articulated along the ischial symphysis (Fig. 41A₁). The posterior process of the ischium is located posterodorsal to the symphysis. It is triangular in lateral view and does not taper to a point (Fig. 41A₁, A₃). Anterodorsal to this process, the posterodorsal edge of the ischium is concave in lateral view, and ascends towards the posterior corner of the articular region (Fig. 41A₁, A₃), expanding transversely in thickness.

The ischia of *T. conspicuus* and *T. hydroides* are nearly identical in shape, with the main difference being the slight difference in curvature of the posterior margin of the thyroid fenestra, which is rectangular in *T. conspicuus* and heart-shaped in *T. hydroides* (Fig. 39; Wild 1973). In *T. longobardicus* the ischium is relatively less expanded posteriorly and its anterior and posterior edges taper to a point (compare Fig. 41 herein and Wild 1973: fig. 92). The ischial morphology de-

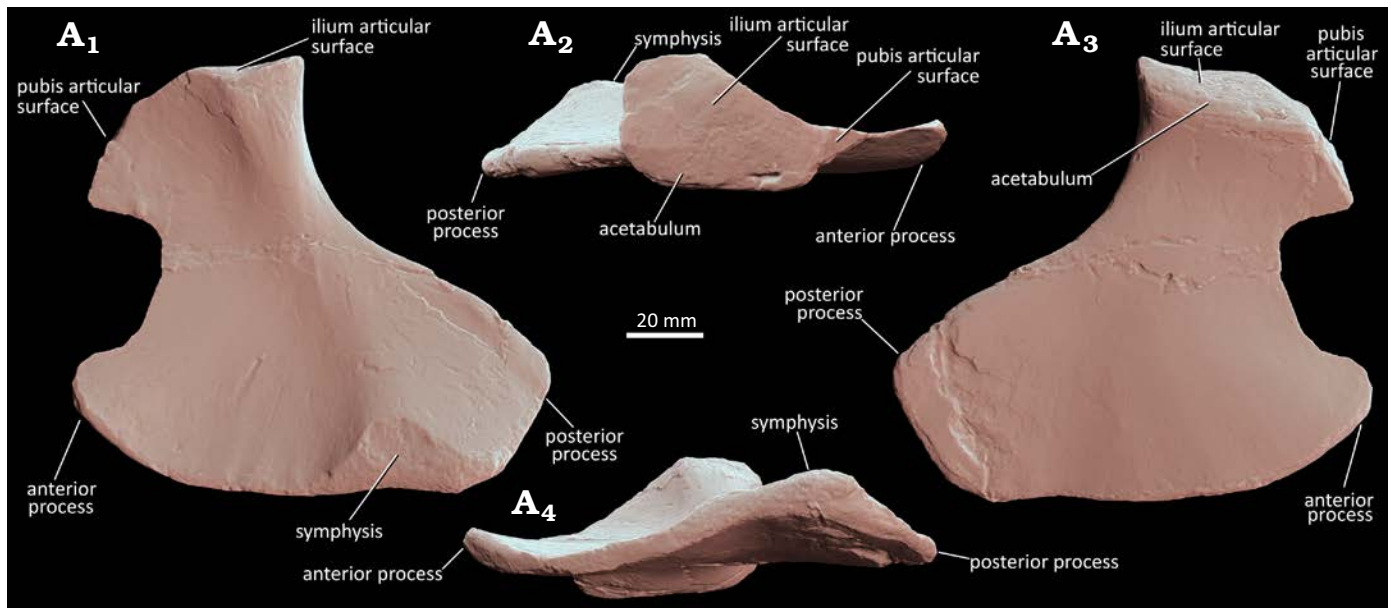


Fig. 41. Right ischium of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1006 in dorso-medial (A₁), dorsolateral (A₂), ventrolateral (A₃), and ventromedial (A₄) views.

scribed here is also reminiscent of the ischia reported by Dalla Vecchia (2006: fig. 4A, B) from the Aupa Valley, which were interpreted as belonging to a eusauropterygian. These can now be referred to *Tanystropheus* sp. as well. Isolated eusauropterygian ischia, with the ones referred to *Nothosaurus* being the most common, have a more constricted “neck” distal to the articular region and their fan-shaped distal end is more symmetrical (see Klein et al. 2022: fig. 17). Moreover, in both taxa there are some striations perpendicular to the distal edge of the ischium on its lateral and medial surfaces, but they are much more prominent in *Nothosaurus*.

Femur: The femur of *T. conspicuus* is relatively much more elongate than the humerus. It is a slender, sigmoidally curved element that retains a constant width along most of its length (Fig. 42). The proximal half of its anterior margin is concave in lateral view, whereas the distal half is convex; the posterior margin mirrors this curvature (Fig. 42A₁, A₃). The femur is relatively straight in anterior (dorsal) and posterior (ventral) views, with the proximal end being medially expanded to a similar degree as the distal end (Fig. 42A₂, A₄). Its proximal and distal ends are well-ossified among the collected specimens. The shaft is elliptical in transverse cross-section, with the longer axis being anteroposteriorly oriented.

The proximal femoral head is marked by the presence of a well-defined, posteromedially oriented internal trochanter (=greater/major trochanter). It is formed as a thick, straight, ridge, which extends from the mid-length of the shaft to the proximal edge of the bone where it reaches its greatest height (Fig. 42A₁, A₃, A₅). The proximal edge of the internal trochanter projects perpendicularly from the proximal articular surface of the femur and meets the posterior edge of the internal trochanter at an obtuse angle (Fig. 42A₁, A₃). On both

sides of the trochanteric ridge, there are deep and wide fossae (Fig. 42A₁, A₃, A₅). The medial one can be interpreted as the fossa intertrochanterica (sensu Novas 1996, but see Ezcurra 2016) as there is a slight depression anteroproximal to it, adjacent to the posterior margin of the proximal articular surface (Fig. 42A₃, A₅). The fossa located on the lateral side of the internal trochanter is broader, more clearly defined (Fig. 42A₁, A₅), and anterolaterally flanked by the anterior trochanter (= lesser/minor trochanter). The anterior trochanter is formed as a narrow but proximally widening ridge on the proximal one-third of the bone (Fig. 42A₁, A₂, A₅). As for the internal trochanter, its distal edge reaches the proximal articular surface of the femur, but in contrast to it, it is confluent with the margin of the proximal surface, forming the anterolateral portion of the anterior tuber (Fig. 42A₁, A₂, A₄, A₅). The proximal articular surface is slightly convex in lateral view, rounded, and dorsomedially oriented. In proximal view it is rhomboidal in outline (Fig. 42A₅). Opposite the anterior tuber, anteromedial to the fossa intertrochanterica, a posterior tuber is present (Fig. 42A₅). On the anteromedial surface of the shaft, slightly proximal to its mid-length, a distinct, large nutrient foramen is present (Fig. 42A₃, A₄).

The distal femoral end is distinctly constricted anteroposteriorly, with grooves separating the lateral (fibular) and medial (tibial) tubers in distal view (Fig. 42A₆). These tubers are rounded, semi-circular in distal view, and subequally expanded in their respective direction, forming a relatively straight distal articular surface (Fig. 42A₂, A₄). There is a slight concavity between the condyles (Fig. 42A₂, A₆). Lateral to the posterior groove between the tubers, and posterior to the lateral tuber, the crista tibiofibularis (Nesbitt 2011) is located, forming a mound-like posterior extension (Fig. 42A₁–A₃, A₆).



Fig. 42. Right femur of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/838 in lateral (A₁), posterior/ventral (A₂), medial (A₃), anterior/dorsal (A₄), proximal (A₅), and distal (A₆) views.

The femur of *T. conspicuus* does not differ from the femora of *T. hydroides* and *T. longobardicus* in its morphology.

Tibia: The tibia of *T. conspicuus* is a relatively straight and elongate element (Fig. 43). There is significant torsion between the proximal and distal ends although to some degree it might be partially due to diagenetic alteration. The proximal end of the tibia is transversely expanded and its articular surface is slightly convex and rounded in lateral view and elliptical in proximal view (Fig. 43A₂, A₄). Distal to the anterior edge of the proximal articular surface, a weakly

outlined crest is present (Fig. 43A₂, A₄). On the lateral surface of the proximal end of the tibia, a faintly outlined fibular condyle is visible, forming a tuberosity (Fig. 43A₂, A₄). Distal to it, a distinct nutrient foramen is present (Fig. 43A₂).

The distal end of the tibia is anteroposteriorly expanded. Its articular surface is smaller and more oval in distal view than that of the proximal portion (Fig. 43A₅). The lateral edge of the shaft is slightly concave in posterior view, and its posterolateral section is marked by the presence of a subtle ridge (Fig. 43A₁). Aside from these features, the surface of

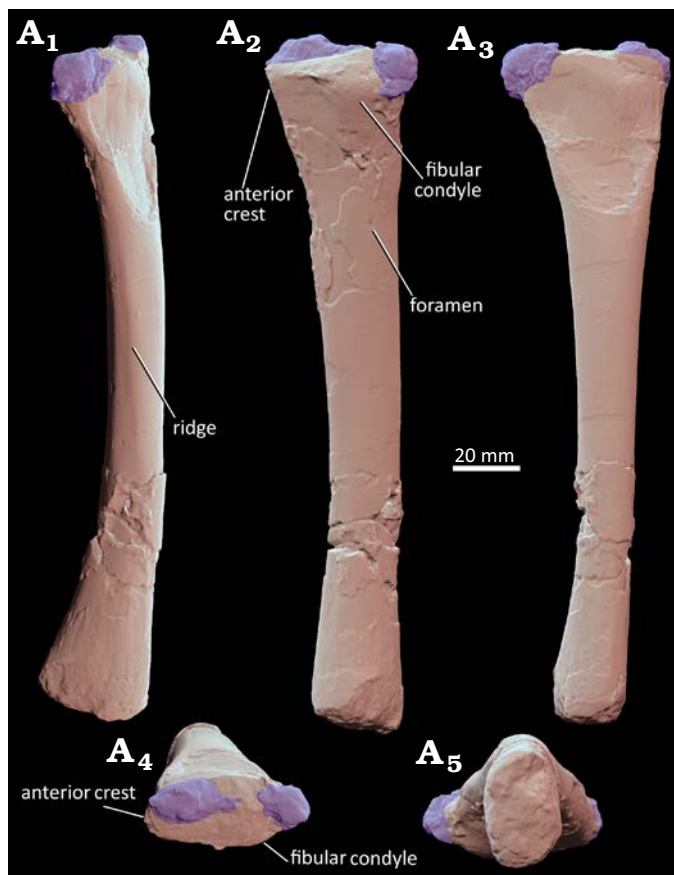


Fig. 43. Left tibia of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1200 in posterior (A₁), lateral (A₂), medial (A₃), proximal (A₄), and distal (A₅) views. Areas covered with sediment marked with blue hue.

the shaft is smooth and seemingly devoid of any other notable characters. The tibia of *T. conspicuus* is relatively more massive and thicker than the same element in other species of *Tanystropheus* (compare Wild 1973; Nosotti 2007). This characteristic might be partially due to individual size difference, as a large *T. hydroides* individual (PIMUZ T 2818) also exhibits a relatively robust tibia comparable in its proportions to those of *T. conspicuus*.

A limb bone described by von Huene (1958a) as a “parasuchian” radius from the Upper Muschelkalk of Wesseln (Germany) bears a strong morphological resemblance to the tibiae referred to *T. conspicuus* and falls within the size range of the elements from Miedary. Unfortunately, the original specimen could not be located (Ralf Kosma personal communication, 2024).

Fibula: As in most other diapsids, the fibula of *T. conspicuus* is much more slender and narrow at mid-length than tibia. It is also relatively straighter in anterior view, with both of its articular surfaces lying along the same axis (Fig. 44). In lateral view it is sigmoidally curved (Fig. 44A₁, A₂). The proximal articular surface is elliptical in proximal view and convex in lateral view, with rounded anterior and posterior

margins (Fig. 44A₁, A₂, A₄). At a point approximately one third down the length of the shaft, lies the insertion of the musculus iliofibularis (Fig. 44A₁, A₃). It forms an anteroposteriorly thick, low ridge, which separates an oval concavity on the lateral surface of the shaft from the anterior fibular margin (Fig. 44A₁). More distally, the anterolateral portion of the shaft is occupied by a deep groove, which is flanked anteriorly and posteriorly by distinct ridges (Fig. 44A₁, A₃). The anterior ridge extends parallel to the shaft, forming a thin lamina between the distal portion of the fibula and the insertion of musculus iliofibularis (Fig. 44A₁, A₃). Ezcurra (2016) stated that the shafts of the fibula and tibia in *Tanystropheus* are of approximately the same transverse width at about mid-length, but this is only due to the anterior fibular ridge appearing to increase the shaft thickness in lateral view (Fig. 44A₁). In all species of *Tanystropheus* the tibia is always the more robust of the two elements.

The distal portion of the illustrated fibula (Fig. 44) is thickened due to a pathological overgrowth (Fig. 44A₅). Compared

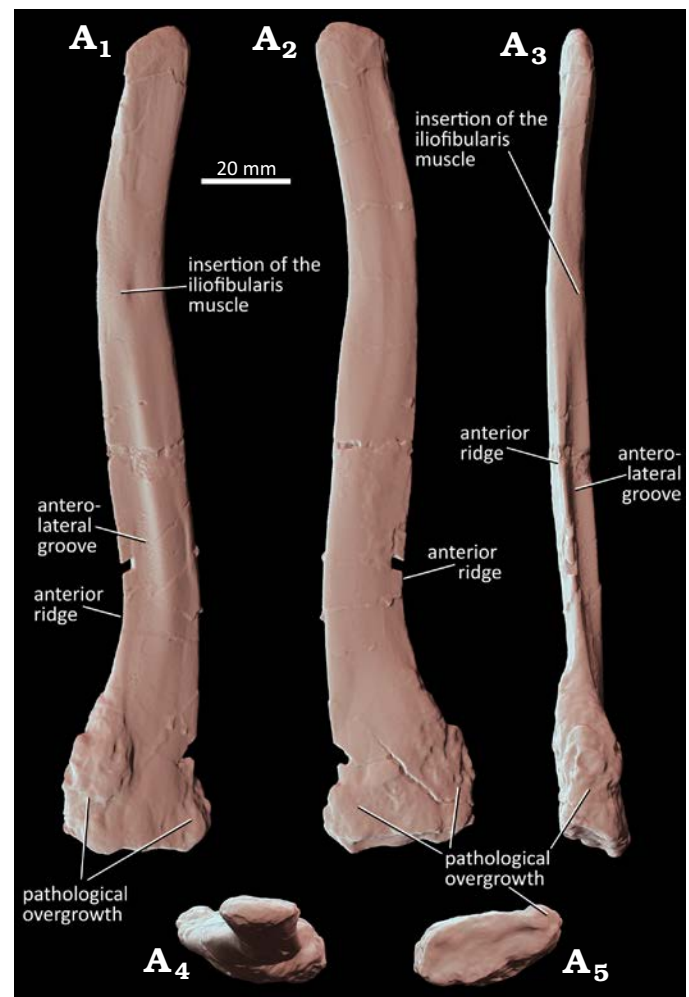


Fig. 44. Left fibula of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. ZPAL V. 36/1176 in lateral (A₁), medial (A₂), anterior (A₃), proximal (A₄), and distal (A₅) views.

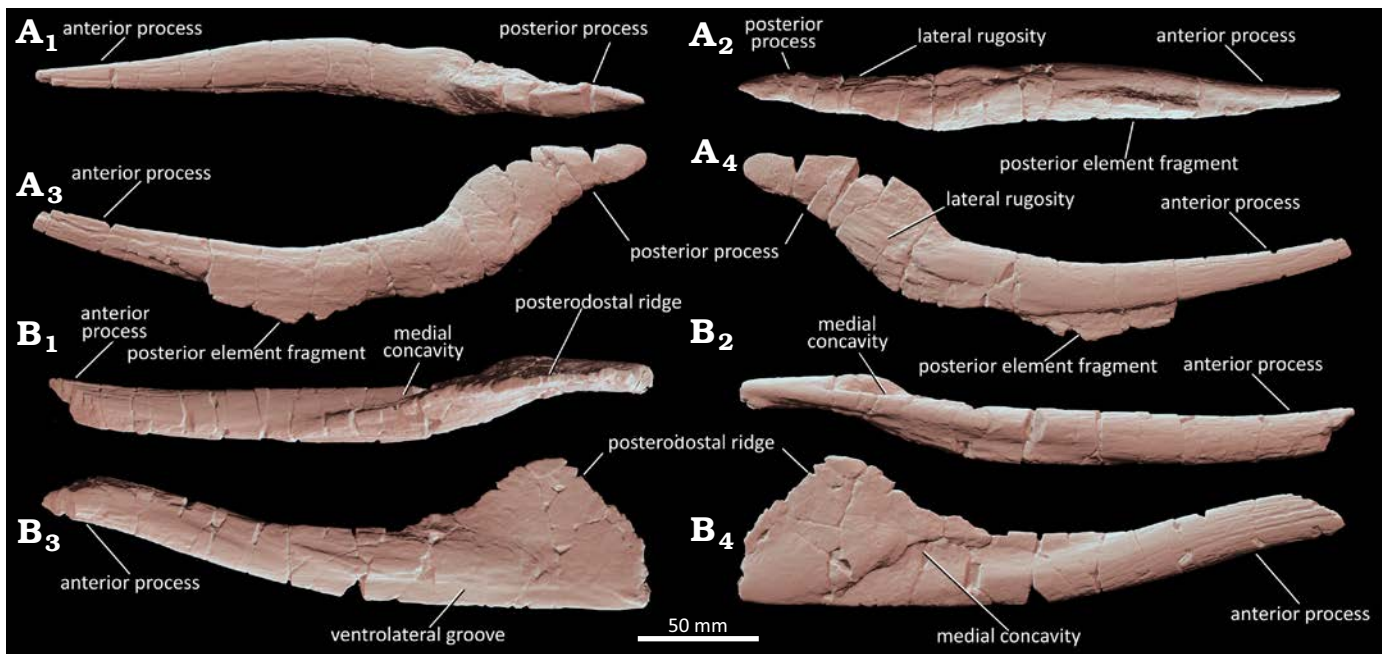


Fig. 45. Postcloacal bones of the tanystropheid archosauromorph *Tanystropheus conspicuus* von Meyer, 1852, from the Lower Keuper (lower Ladinian, Middle Triassic) of Miedary, Poland. Three-dimensional model snapshots with Lit Sphere Radiance Scaling shader enabled. Left anterior element (ZPAL V. 36/1147, A) and right posterior element (ZPAL V. 36/1148, B), in dorsal (A₁, B₁), ventral (A₂, B₂), lateral (A₄, B₃), and medial (A₃, B₄) views.

to unaltered specimens, it is more anteroposteriorly expanded and distally concave. Another specimen, ZPAL V. 36/834, shows that the distal fibular end is rounded and convex in lateral view and elliptical in distal view (Fig. 44A₅). Its articular surface is only slightly larger than that of the proximal end. Whereas most of the surface of the fibula shaft in *T. conspicuus* is smooth, small pits and longitudinal striations appear near the articular ends, especially on the lateral side.

Postcloacal bones: Isolated postcloacal bones identical to those present in *T. hydroides* and *T. longobardicus* (see Discussion) have been identified at Miedary (Fig. 45). As can be discerned from articulated skeletons the postcloacal apparatus in *Tanystropheus* is composed of four elements, two anterior and two posterior bones. In vivo they were located posterior to the pelvis (around the cloaca as interpreted by Wild 1973, 1980a). The anterior portion of the posterior element articulated along the ventral surface of the corresponding anterior element, near the anteroposterior midpoint of its length. Both articulated pairs are always preserved in separation from each other, and from any other bones. They ran parallel to the main body axis.

Both elements are elongate, straight, with a rough, highly rugose surface (Fig. 45). Their internal structure is distinct, with the bone tissue forming them being highly cavernous and poorly organised (in agreement with the observations of Wild 1973). The anterior elements can be easily distinguished from the posterior ones based on their shape. The largest of these elements is over 300 mm long, so that in large individuals the whole apparatus might have reached approximately half a meter in length.

The anterior element has two processes. The anterior process is rod-like, tapers anteriorly, and its surface is covered

with deep, longitudinal, striations (Fig. 45A). Near the ventrolateral portion of its base, the posterior element articulated in a deep groove. Isolated anterior postcloacal bones are often preserved with a broken anteriormost portion of the corresponding posterior postcloacal bone still attached (Fig. 45A). The posterior process of the anterior element is shorter than the anterior process. Its base ascends sharply posterodorsally, but its distal tapering end is posterolaterally oriented with the dorsal surfaces of the anterior and posterior processes being nearly parallel (Fig. 45A₃, A₄). On the lateral surface of the base of the posterior process, the anterior postcloacal bone is especially rugose, being covered by a set of roughly longitudinal, deep grooves and distinct ridges (Fig. 45A₄).

The posterior element is similar to the anterior postcloacal bone. It has a rod-like, tapering anterior process, with its surface covered by deep, longitudinal, striations (Fig. 45B). The process is relatively more massive in the posterior element. The ventrolateral portion of its base is occupied by a deep groove, which is dorsally demarcated by a distinct broad ridge (Fig. 45B₃). The posterior portion of the posterior element is dorsally expanded, with a tall and straight ridge forming the posterodorsal edge of the bone (Fig. 45B₃, B₄). Ventromedial to it, a deep medial concavity is present, with its longitudinal axis extending obliquely to the anteroposterior axis of the whole element (Fig. 45B₄). When in articulation, the tip of the posterior process of the anterior element nearly reached the posterodorsal edge of the posterior element, thus creating an open embayment between the bones, as in other species of *Tanystropheus* (Wild 1973).

Stratigraphic and geographic range.—Lower Upper Muschelkalk (lower Trochitenkalk Formation) to uppermost

Lower Keuper (Grenzdolomit, uppermost Erfurt Formation); upper Anisian to upper Ladinian. France (Alsace, Lorraine); Germany (Baden-Württemberg, Bavaria, ?Hesse, Lower Saxony, North Rhine-Westphalia, Thuringia); Poland (?Lesser Poland, Upper Silesia).

Discussion

Anatomy of the cervicodorsal region.—The anatomy of the cervico-dorsal transition in *Tanystropheus* was poorly understood, because vertebrae from known specimens were either missing, damaged, or only partially visible (see Wild 1973; Renesto 2005; Nosotti 2007). However, based on a new specimen, Rieppel et al. (2010) were able to identify the transitional thirteenth presacral vertebra as the last cervical vertebra. From the newly described *Tanystropheus conspicuus* material, three specimens preserve articulated sections of the vertebral column but none of them includes a complete cervical and dorsal series. The number of presacral vertebrae in this species can, therefore, only be inferred indirectly.

Nine dorsal vertebrae and the first sacral vertebra are preserved in an unpublished vertebral series SMNS 13337. ZPAL V. 36/125 contains 11 dorsal vertebrae, two sacral vertebrae and several associated caudal vertebrae. Finally, ZPAL V. 36/100 includes six cervical vertebrae. In the latter specimen, the preserved section most likely represents the anteriormost postaxial cervical vertebrae (vertebrae three to eight). This interpretation is based on the presence of an axis consistent in size found in close proximity to the anterior end of the specimen, indicating that it likely derived from the same individual but was slightly disarticulated from the rest of the preserved series. Furthermore, the changes in centrum length between the consecutive elements in the articulated series follow the pattern observed by Wild (1973) for the first five postaxial cervical vertebrae of *Tanystropheus*, where the size of the first four elements is relatively constant and then increasing in the seventh cervical vertebra (see SOM: table 1). Morphotypes identified as the five posteriormost cervical vertebrae (cervical vertebrae nine to thirteen) can be distinguished from the other isolated remains of *T. conspicuus* as they strictly correspond in their morphology to the elements found in other species of *Tanystropheus* (see Wild 1973; Rytel et al. 2024a) and are partially preserved in the disarticulated but close association of bones of ZPAL V. 36/584 (Fig. 16). Moreover, this specimen preserves a characteristic dorsal rib with a broad plate-like expansion and two posteriormost cervical ribs in close proximity. This dorsal rib is virtually identical to that of ZPAL V. 36/123 (Fig. 30A) and morphologically distinct from the rib that articulated with the anteriormost preserved dorsal vertebra in ZPAL V. 36/125 (Fig. 30B). Moreover, the morphotype represented by ZPAL V. 36/123 is closer in shape to the last cervical rib than the anteriormost dorsal rib preserved in ZPAL V. 36/125. This clearly implies that in the latter specimen at least one more dorsal vertebra was pres-

ent, with which the “transitional” first dorsal rib articulated. Thus, the combined morphological data gathered from both isolated and articulated specimens demonstrates that the presacral count in *T. conspicuus* is at least 13 cervical and at least 12 dorsal vertebrae, respectively. Importantly, the number of presacral vertebrae in tanystropheids seems to have been developmentally constrained to 25 (Rytel et al. 2024a), implying that these 25 vertebrae identified for *T. conspicuus* likely constituted the whole presacral section of the vertebral column. Based on several morphological characters and a similarity to closely related taxa, it can be assumed with high degree of confidence that *T. conspicuus* possessed 13 cervical and 12 dorsal vertebrae (see Rieppel et al. 2010; Spiekman et al. 2020a). The thirteenth cervical vertebra is more similar in its proportions to the succeeding dorsal vertebrae than the preceding cervical vertebrae. However, considering the morphology of the associated rib, which is tall, anteroposteriorly short, and horizontally oriented, together with the presence of subcentral foramina (see Rytel et al. 2024b) and epiphyses (features absent in the dorsal vertebrae) on the vertebra, I concur with Rieppel et al. (2010) in identifying the thirteenth vertebra as the last cervical vertebra in all species of *Tanystropheus*.

The posture of the neck of *Tanystropheus* has long been a subject of debate, with previous studies suggesting various hypotheses—from fully horizontal and stiff to “swan-like” flexible S-shaped (Peyer 1931; Wild 1973; Kummer 1975; Tschanz 1986; Nosotti 2007; see Tschanz 1988 and Renesto 2005 for detailed summaries). The flexibility of the neck was undoubtedly highly dependent on the elasticity of the extremely elongate cervical ribs, assessment of which is outside the scope of this work, and should be addressed by biomechanical studies. Concerning the posture, Renesto (2005: 389) pointed out that the morphology of the twelfth cervical vertebra, in which the posterior articular surface of the centrum was “forward slanting”, indicates that the base of the neck of this animal was dorsally inclined. This is reminiscent of the posture reconstructed by Wild (1973: pl. 1). Nosotti (2007) argued against this interpretation, maintaining that the presence of an asymmetrical intervertebral disc or a slightly dorsally curved vertebral column in the trunk could have counteracted the inclination, and the neck was likely held horizontally, as demonstrated by Tschanz (1986). The specimens of *T. conspicuus* described here provide new insights into the anatomy of the cervico-dorsal transition in *Tanystropheus* and the posture of the neck. In the thirteenth cervical vertebra the articular surfaces of the centrum are not parallel to each other, with the anterior one being slanted and facing slightly anterodorsally (Fig. 19). In the preceding twelfth vertebra, the dorsal inclination of the ventral surface of the centrum is evident (Fig. 18B₃), in agreement with the observation of Renesto (2005) for *T. longobardicus* and also corresponding to MFSN 34727, a *Tanystropheus* sp. specimen from the Aupa Valley reported by Dalla Vecchia (2008: figs. 61C, 64A). In the eleventh cervical vertebra the articular surfaces of the centrum are, however, even more

conspicuously located on different dorsoventral levels, with the anterior one being more dorsally positioned. In *T. conspicuus* this characteristic is much more pronounced than in other species of *Tanystropheus*, in which this vertebra is less inclined. This is possibly a function of the larger size of the former. In all middle cervical vertebrae of *T. conspicuus*, both articular surfaces of the centrum are either sub-parallel, or slightly downturned (Figs. 13–15).

Studies on the cervical anatomy of long necked animals, including sauropods, have shown that using purely osteological characters to reconstruct the neutral position of the neck can be error-prone, but also that the inclusion of the intervertebral tissue usually “raises” the neutral position (Taylor and Wedel 2013; Taylor 2014). Morphology of the cervical vertebrae of *T. conspicuus* indicates that in the neutral position the posteriormost portion of its neck was likely dorsally inclined and the portion anterior to the eleventh cervical vertebra was held relatively horizontally, but with slight ventral bowing. Consequently, the skull and the base of the neck were positioned lower than the middle section of the neck (Fig. 46). This hypothesis combines the observations presented in previous studies (Wild 1973; Tschanz 1986; Renesto 2005; Nosotti 2007) and is further supported by cervical rib morphology. Whereas the ribs associated with the middle cervical vertebrae (Fig. 28) and the last cervical vertebra (Fig. 29C) have a relatively straight ventral margin and an anteriorly projecting anterior free-ending process, the ribs associated with the eleventh and twelfth vertebrae differ in this respect. The latter two have distinctly upturned anterior free-ending processes (Fig. 29A, B) and moreover, the twelfth rib is crescent-shaped. These morphological features imply the presence of some curvature in this section of the neck and support the hypothesised dorsal inclination (Renesto 2005).

Based on the reduced muscle attachment sites on the cervical vertebrae *Tanystropheus* Wild (1973) noted that

the entire anterior and middle portions of neck of this animal were practically devoid of lateral musculature, but in turn the dorsal ligaments and ventral musculature were expanded. Tschanz (1986, 1988) hypothesised that the musculature was likely too weak to lift the neck beyond the horizontal level. Renesto (2005) argued that in conjunction with the inclined base of the neck, the cervical muscle/ligament system would be capable of raising the relatively light neck of *Tanystropheus*. Rieppel et al. (2010) reached similar conclusions concerning the vertical movements of the neck.

Although both a detailed range of motion analysis and a reconstruction of the myology of *T. conspicuus* are outside the scope of this work, the three-dimensional preservation of the new Miedary material allows for a preliminary re-assessment of this topic. Musculature on the lateral sides of the middle cervical vertebrae of *T. conspicuus* was apparently greatly reduced, with the cervical ribs located extremely close to the ventrolateral margin of the centrum and the zygapophyses projecting strongly anteroposteriorly. Attachment points for epaxial muscles and ligaments are especially well developed on the anterodorsal and posterodorsal portions of the middle cervical vertebrae. The free-ending processes of the ribs, expanded epipophyses, prominent anterior and posterior grooves at the base of the neural spine, together with the portions of the neural spine overhanging them, presumably supported an intricate muscle/ligament system.

In the four posteriormost cervical vertebrae these characteristics change—the centrum is shorter, the neural spine taller, and the vertebrae are more transversely expanded. In these vertebrae the epipophyses are less prominent, but distinct anteriorly projecting mound-like tuberosities on the prezygapophyses are more robust, forming additional attachment sites for the soft tissues of the more anterior portion of the neck. Posteriorly, the diapophyses and cervical ribs become much more massive and are located further from the

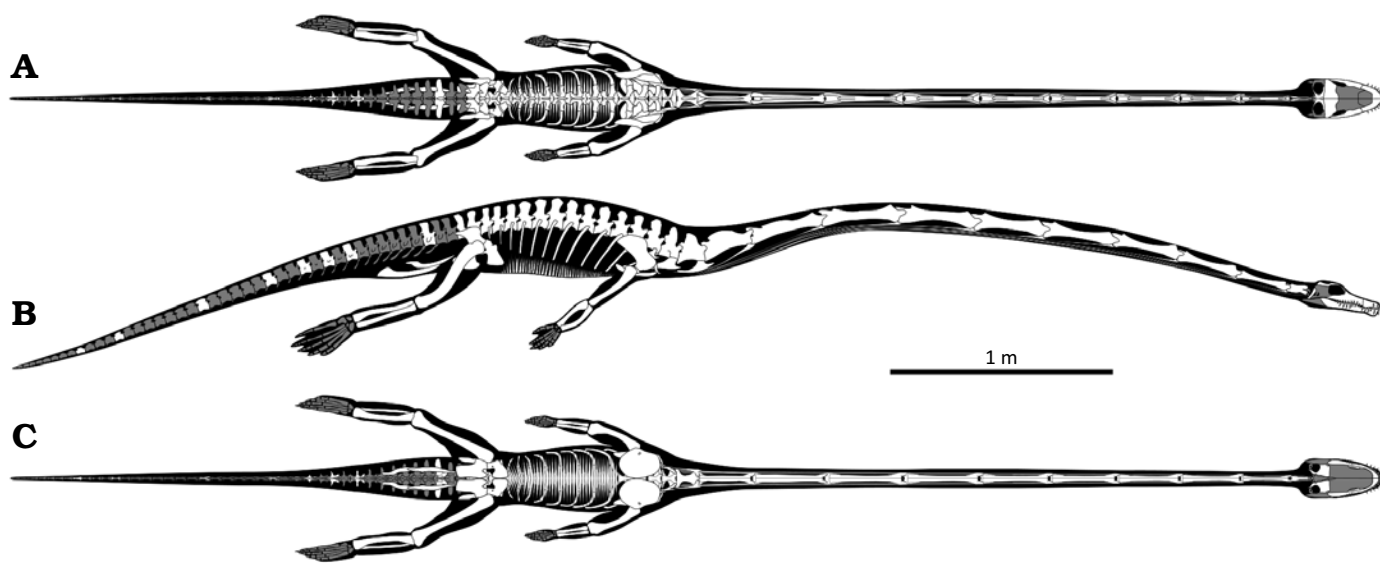


Fig. 46. An osteological reconstruction of a large individual of *Tanystropheus conspicuus* von Meyer, 1852, in dorsal (A), right lateral (B), and ventral (C) views. Bone outlines based on the specimens illustrated here (coloured in white), and the articulated specimens of *T. hydroides* (coloured in grey; for the skull see Spiekman et al. 2020b). Body proportions taken from the most complete known specimen of *T. hydroides* (PIMUZ T 2818).

centrum, implying the existence of expanded lateral musculature. The most striking feature of the posterior cervical vertebrae is the significant expansion of the distal end of the neural spine, which is developed as a bulbous thickening along its entire length. These would have served as attachment sites for the dorsal ligaments and muscles, providing stability for the neck, and allowing for the inclined posture.

Generally, the transitional cervicodorsal region in *T. conspicuus* is characterised by the presence of several broad, flat, plate-like bones (ribs associated with the transitional vertebrae, scapulae, coracoids). At least some of them could have served as large attachment sites for neck muscles and ligaments together with the distally expanded neural spines and possibly also the mammillary processes of the dorsal vertebrae. In *Tanytropheus*, the distal ends of most (up to seven pairs) cervical ribs reach to the section of the vertebral column between the eleventh cervical vertebra and the first dorsal vertebra, where they terminate essentially at the same point (Fig. 46; see PIMUZ T 2818). Their elongation served the purpose of not only stiffening the neck but also transmitting the attached muscles to the back of the neck (Tschanz 1986). Following Wild (1973), I hypothesise that the cervical muscle mass was relatively reduced in the middle portion of the neck of *Tanytropheus* but significantly expanded near the base of the neck. This would also explain the function of the anteroposteriorly projecting extensions of the anterior dorsal ribs. Regardless of the flexibility of the neck, but especially if it was as stiff as proposed by some (Tschanz 1986, 1988; Nosotti 2007), its movements would be mostly induced by the muscles and ligaments originating from the transitional cervicodorsal region.

Additional insights are provided by the change in the nature of the neural spine morphology. In the middle cervical vertebrae, the neural spine is well-developed in its posterior and anterior portions, but almost completely reduced in the middle. Moving the attachment points towards the peripheries of the extremely elongate vertebra could allow for finer control of the movement of the neck by providing a shorter lever. The middle section of the vertebra was reduced to a durable (but relatively light) tube-like structure described in detail by Rytel et al. (2024b). In the more posterior cervical vertebrae (10 to 13) the relative height of the middle section of the neural spine, as well as the height of the neural spine itself, increased markedly (these elements were held inclined in vivo), allowing for larger attachment areas for the muscles and ligaments originating from the torso. The proposed dorsally inclined posterior portion of the neck would allow for enhanced control of the movements of the neck (and the head) and thereby play a pivotal role in hunting (e.g., retraction during “kinetic inertial feeding” proposed by Tschanz 1986).

Miedary as a habitat of *Tanytropheus*.—Insights concerning the environment of deposition for an animal carcass can be gained by assessing the frequency of occurrence of specific isolated skeletal elements as they have different

hydrodynamic dispersal rates (Blob et al. 2022). To investigate this phenomenon, three sets of three-dimensionally preserved and isolated *Tanytropheus* bones can be compared, the material of *T. conspicuus*, divided into Miedary (n = 722) and the western part of the CEB (n = 185), as well as the *Tanytropheus* sp. remains reported by Dalla Vecchia (2000, 2006, 2008), and Dalla Vecchia and Simonetto (2018) from the Aupa Valley in north-eastern Italy (n = 204). All three collections have here been studied first-hand to minimise the possible effect of identification bias. Considerably fewer three-dimensionally preserved specimens have been published from sites in Canada (Sues and Olsen 2015), Hungary (Ősi et al. 2020), Israel (Rieppel 2001), Romania (Jurcsak 1975) and Saudi Arabia (Vickers-Rich et al. 1999). See Dalla Vecchia and Simonetto (2018) and SOM: table 1 for a full list of analysed specimens.

In the western part of the CEB a taphonomic bias towards the preservation of large long bones (middle cervical vertebrae and stylopodial elements) seems to have existed when compared to the relative occurrence of other elements. This group of sites is nearly completely devoid of the elements from the pectoral and pelvic girdles. The Aupa Valley sites exhibit a much higher diversity of elements, with flat bones and short vertebrae being relatively much more common. This corresponds to the pattern from Miedary, which has the highest element diversity among these three sets, and is the least dominated by long bones (which are, however, still the most common).

Quantitative characteristics of the analysed material indicate that the remains of *T. conspicuus* from the western part of the CEB underwent significant sorting. Transport of the *Tanytropheus* bones in the Aupa Valley sites, and especially in Miedary, seems to have been over much shorter distances as the element diversity is much higher. Similar to the Upper Muschelkalk localities, autopodial elements and distal-most caudal vertebrae are scarce in Miedary, suggesting that the assemblage has undergone some hydraulic sorting, although, uniquely, some delicate cranial elements are also preserved from this site (although this could also be the result of a larger total number of bones having been found in Miedary), indicating the presence of specific conditions leading to their preservation in this depositional environment. The inferral of variable transport distances is supported by the results of a study by Blob et al. (2022), which implied that the presence of vertebrae with a wide diversity of other skeletal elements is indicative of short transport distances whereas the presence of vertebrae as the primary preserved elements in an assemblage suggests a high likelihood of longer transport distances. It is, therefore, likely that *T. conspicuus* in Miedary lived, or at least died, in close proximity to the reservoir in which its remains were deposited.

The occurrences of the teeth of *T. conspicuus* are stratigraphically and spatially concentrated. Among the accessioned collections in Germany, I have been able to identify over 100 teeth of *T. conspicuus* (see SOM: table 1). Roughly half of the known specimens have originated from the

Grenzbonebed of the area around Crailsheim (Germany)—material collected mostly by Richard Blezinger (1847–1928). The majority of the teeth of *T. conspicuus* are stored in SMNS and GPIT collections. The Grenzbonebed outcrops of the area around Crailsheim (Germany) are characterised by a high frequency of occurrence of vertebrate fossils, especially teeth (see Hagdorn and Reif 1988). It can be safely assumed that the high number of teeth of *T. conspicuus* originating from this stratum (compared to bone fragments) is due to pre-diagenetic sorting.

The reasons for the high relative (compared to other tetrapods) and absolute frequency of occurrence of *T. conspicuus* in the Miedary site (see Czepiński et al. 2023) can be understood by comparing the characteristics of the assemblage and the locality itself to other outcrops within the local area and the broader region. In the western part of the CEB, where the remains of *T. conspicuus* are rare, its fossils appear to be even more scarce in the Keuper strata above the Grenzbonebed, which marks the transition from marine to more terrestrial settings. In marked contrast, in the outcrops around Miedary a considerable fluctuation in the abundance of remains of *T. conspicuus* is recorded in the local rock sequence. Three stratigraphic units with significant vertebrate fossil content can be distinguished here: (i) the marine Upper Muschelkalk, (ii) the Lettenkeuper glauconite beds deposited in shallow marine settings but with significant terrestrial influence, and (iii) the marine Lettenkeuper dolomite beds (see Sulej et al. 2011; Pawlak et al. 2022; Czepiński et al. 2023). Only two vertebrae of *T. conspicuus* were reported from the Upper Muschelkalk, compared to hundreds of sauropterygian remains (von Meyer 1847–1855; Langenhan 1903; AR personal observation). The slightly younger Lettenkeuper strata of Miedary (Unit 1, see Czepiński et al. 2023 for stratigraphy) have yielded the massive vertebrate fossil accumulation, in which elements of *T. conspicuus* were the most numerous throughout most of the layers (M1–M2 and M4, but not M3). The outcropping sediment sequence ends with the strata directly overlying Unit 1, clays and dolomites, which so far seem to be completely devoid of remains of *T. conspicuus*.

Tanystropheus conspicuus fossils have been found in the upper Anisian to upper Ladinian strata. The remains from Miedary originate roughly from the middle of this interval, lower Ladinian (Czepiński et al. 2023). Therefore, the extreme fluctuation of abundance of remains of *T. conspicuus* in the outcrops around Miedary is unlikely to be due to the emergence or extinction of the species in the region. The ages of the source strata fall well within the temporal range of occurrence for this animal in the western part of the basin. Instead, the absolute and relative frequency of occurrences of *T. conspicuus* seems to be tightly controlled by environmental factors, a correlation can be observed between the presence of remains of *T. conspicuus* and differences in depositional settings. Sedimentation of the Upper Muschelkalk strata proceeded in a shallow, restricted, epicontinental basin with euryhaline to polyhaline salinity and

limited terrestrial influence (see Korte et al. 2003; Franz et al. 2015; Pawlak et al. 2022). Similar conditions were present during the deposition of the dolomite beds in Miedary (Pawlak et al. 2022). Layers M1–M2 and M4 of Miedary were deposited in a very shallow, brackish, restricted reservoir with significant terrestrial input, and the M3 layer in (sub)terrestrial settings (Pawlak et al. 2022; Czepiński et al. 2023).

Combining the aforementioned factors concerning the occurrence of remains of *T. conspicuus* in Miedary—high variability within the local stratigraphic column and the relatively high element diversity and short transport in the layers in which *T. conspicuus* is prevalent—it becomes clear that this taxon had relatively strict environmental preferences. The data reported here imply that *T. conspicuus* was rare or absent in both marine (depositional settings of the Upper Muschelkalk and the dolomite beds from Miedary) and terrestrial (depositional settings of most of the Lettenkeuper above Grenzbonebed and the M3 layer from Miedary) environments and flourished in the transitional zones between them, which are recorded in the glauconite beds of Miedary (layers M1–M2, and to some extent M4). This hypothesis is consistent with the general environmental conditions (shallow marine with a significant terrestrial input) present in the localities from the Aupa Valley, described by Dalla Vecchia (2006, 2010) and Dalla Vecchia and Simonetto (2018), which is the only other known site in which *Tanystropheus* is also quantitatively dominant among the tetrapod finds. Regarding the other sites that have yielded abundant material of *Tanystropheus*, the Besano Formation of Monte San Giorgio, from which most of the articulated skeletons of *Tanystropheus* are known, was deposited in a euryhaline marine intraplatform basin with water depths between 30 and 130 m (Bernasconi and Riva 1993; Bernasconi 1994; Röhl et al. 2001; Beardmore and Furrer 2017). At first glance these characteristics could be viewed as inconsistent with the preferred habitat of *T. conspicuus* as reported here but the results of the taphonomic analysis of Beardmore and Furrer (2017) indicated that tanystropheid remains found in the Besano Formation have originated from nearshore settings, which has previously also been suggested by Renesto (2005) for specimens from other stratigraphic units of Monte San Giorgio. In China, the *Tanystropheus* cf. *T. hydroides* specimen GMPKU P 1527 described by Rieppel et al. (2010) originated from the Lower Assemblage of the Zhuganpo Member of the Falang Formation (Lu et al. 2018; Jiang et al. 2025). The general environmental and faunistic characteristics of this unit are similar to the Besano Formation. Washed-in articulated skeletons of the terrestrial tanystropheid *Macrocnemus* are present in both units as well (Lu et al. 2018; Jiang et al. 2025), indicating a similar taphonomical history of *Tanystropheus* remains (Beardmore and Furrer 2017). In general, all known remains that can currently be confidently referred to *Tanystropheus* have been found in strata that were deposited in shallow aquatic environments, or slightly deeper basins with significant ter-

restrial material influx. The Miedary site is unique among them in recording the setting that was likely the closest to the original habitat of *Tanystropheus*, at least in some of its aspects. This hypothesis is supported by multiple lines of taphonomic evidence as well as the presence of individuals of different sizes, from early juveniles to old, including very large individuals affected by various skeletal pathologies (AR personal observation). Environmental preferences of *T. conspicuus* can, to some extent, be extrapolated to other species of *Tanystropheus* and are congruent with virtually all the data reported. Even though the sedimentary sequence accessible at Miedary is relatively short, it showcases which environments were preferred by this animal—not terrestrial, but not fully marine either, and in the very shallow nearshore ecosystems. Such conditions were present during the deposition of the glauconite beds from Miedary (M1–M2, see Czepeński et al. 2023), which serve as a good proxy for reconstructing the habitat of *Tanystropheus*.

Mode of life.—The discussion on the mode of life of *Tanystropheus*, predominantly understood as its preferred habitat, hunting strategy and mode of locomotion, is as old as the “modern” understanding of the bauplan of this animal (Peyer 1930, 1931; but see Wild 1973 and Nosotti 2007 for a summary on the subject). Due to the lack of extant analogues for the unique anatomical features of this animal (see Rytel et al. 2024a), deciphering its biology has always been problematic.

Throughout the history of research on *Tanystropheus*, the views on its mode of life have changed markedly. Peyer (1931) did not find any adaptations for an aquatic lifestyle in the skeleton of this reptile, interpreting it as a fully terrestrial animal. Kuhn-Schnyder (1959) regarded the elongated fifth pedal digit of *Tanystropheus* as an indicator of aquatic locomotion. Wild (1973, 1980a) considered this animal to change its habitat preferences during ontogeny—from more terrestrial smaller forms to predominantly aquatic larger individuals, which used their long hindlimbs as the main source of propulsion. Tschanz (1986, 1988) argued that the anatomy of the elongate neck would be much more advantageous in an aquatic environment, which was therefore inferred to be the primary habitat of *Tanystropheus* regardless of ontogenetic stage. Contradicting with this view, based mostly on its lack of morphological adaptations towards an aquatic lifestyle, Renesto (2005) considered this animal to have mainly lived on land, as a shoreline dweller, similar to what Peyer (1931) suggested. Nosotti (2007) concurred with Tschanz (1986, 1988) in interpreting the functional anatomy of *Tanystropheus* as being unsuitable for terrestrial locomotion pointing towards an aquatic mode of life. Rieppel et al. (2010: 1088) stated that *Tanystropheus* “might have only come on land to lay eggs, or perhaps not at all”. The study of Jaquier and Scheyer (2017) showed that the histological characteristics of the bones of *Tanystropheus* indicate an amphibious lifestyle. Renesto and Saller (2018) revised the previous interpretations of Renesto (2005), and, based

on a re-interpretation of its caudal musculature, considered *Tanystropheus* a semi-aquatic animal that lived in a shoreline and/or shallow-water environment. A description of the cranial anatomy of *T. hydroides* by Spiekman et al. (2020a, b) revealed several adaptations to hunting in water, but the morphology of the inner ear suggests this animal likely did not spend much time in open-marine environments.

In general, all recent findings are congruent with the interpretation of *Tanystropheus* as an animal strictly connected with a shallow marine habitat rather than open pelagic or terrestrial environments. From among the known specimens of *Tanystropheus*, only the isolated cervical vertebra YPM VPPU.022000 (Sues and Olsen 2015: fig. 10; Sues et al. 2022: fig. 6A, B), referred to *Tanystropheus* sp. by Spiekman and Scheyer (2019) and Sues et al. (2022) has not originated from a marine-influenced environment but rather from a freshwater, fully terrestrial depositional setting of the Economy Member of the Wolfville Formation in Canada (Sues and Olsen 2015). This specimen, which is Middle Triassic in age, is currently the only record of *Tanystropheus* in North America (Spiekman and Scheyer 2019; Sues et al. 2022). Whereas this vertebra is similar to the neck vertebrae of *Tanystropheus* in its overall proportions, it seems to lack the subcentral foramina, and its rib articulation facets are much more prominent than in other representatives of this genus. It might, therefore, represent a separate taxon. If so, it would additionally strengthen the connection of *Tanystropheus* with marine environments or brackish reservoirs with some marine influence (e.g., Miedary, Vellberg, see Pawlak et al. 2022). The recent contributions to the discussion on the mode of life of *Tanystropheus*, together with the data concerning the occurrence of its remains presented herein, support the (semi-)aquatic hypothesis. The novel anatomical data on *T. conspicuus* give additional insight into this subject:

(i) The large size of the nasolacrimal duct in *T. conspicuus* and *T. hydroides* and its presence within the maxilla contrasts with the configuration documented their Triassic relatives (Sookias et al. 2020; Sobral 2023; Forster et al. 2024). In archosauromorphs the nasolacrimal duct is narrow and usually enclosed by the lacrimal and sometimes by the prefrontal bones, but in some taxa it can pass along the medial surface of the maxilla (e.g., in crocodilians, see Witmer 1997; Rehorek et al. 2005). Placement of the canal in the maxilla of *T. hydroides* in a continuum with the foramen piercing the lacrimal strongly supports its interpretation as the nasolacrimal duct, although its passage through the maxilla itself is a highly unusual feature. The disparity between the characteristics of the nasolacrimal duct in *Tanystropheus* and other archosauromorphs might result from differences in their lifestyles. Adaptation to osmoregulation in haline environments is one of the most important aspects of transition from terrestrial to marine habitats, and several aquatic lineages of reptiles have convergently modified their lacrimal apparatus to accustom their physiology to this factor (Fernández and Gasparini 2008; Babonis and

Brischoux 2012; Motani and Vermeij 2021; Cowgill et al. 2023). The diet of *Tanystropheus* consisted of food collected directly in sea (e.g., cephalopods, fish, Wild 1973), and recently Spiekman et al. (2020b) suggested that the large space of confluent external nares in *T. hydroides* could have facilitated a salt gland, although no skeletal correlates were identified for it. The modifications of the nasolacrimal duct morphology might serve as another example of adaptation of the osmoregulatory system of *Tanystropheus* to life in a marine environment. Further comparative data on the nasolacrimal duct morphology in archosauriforms are, however, needed to evaluate this hypothesis in more detail;

(ii) Importantly, all non-tricuspid teeth of *Tanystropheus* are characterised by the presence of apicobasal dental ridges. The role of this trait is not clear, but it has evolved independently numerous times, almost exclusively in taxa that feed within the aquatic environment (McCurry et al. 2019; Mackenzie et al. 2024). Among non-archosauriform archosauriforms, clearly outlined apicobasal ridges are present only in the fully aquatic trachelosaurid *Dinocephalosaurus orientalis* (Li 2003; Spiekman et al. 2024c);

(iii) If *Tanystropheus* could move on land, it would likely do so with a sprawling gait (Wild 1973; Nosotti 2007), which is further indicated by the three-dimensional morphology of the pelvic girdle, femur, tibia, and fibula of *T. conspicuus* presented here. This mode of locomotion is, however, not supported by the forelimb morphology in *Tanystropheus*. The neck of *Tanystropheus*, together with the expanded musculature at its base, would contribute significantly to the mass of the anterior part of the body of the animal, and yet the humerus is very simplified, with a barely discernible deltopectoral crest (Fig. 35), suggesting a decreased role of the musculus pectoralis and musculus deltoideus clavicularis. These muscles are generally expanded in Triassic reptiles for which a sprawling gait has been proposed (see Piechowski and Tałanda 2020). In *Macrocnemus*, a close relative of *Tanystropheus* that is widely considered a terrestrial reptile, the deltopectoral crest is noticeably more expanded and formed as a thin, long ridge (see Jaquier et al. 2017). This suggests a more prominent forelimb musculature in *Macrocnemus*, even though its neck was relatively much shorter than in *Tanystropheus* and therefore contributed significantly less to the relative weight of the anterior portion of the body. Moreover, the girdle elements of *Tanystropheus* are relatively delicate and transversely thin, with the thickness of the iliac and scapular blades decreasing distally and never exceeding 5 mm, and usually being much narrower. Furthermore, the girdle bones are generally relatively small, compared to the size of the animal (cf. Nosotti 2007), as in aquatic trachelosaurids (Spiekman et al. 2024b, c). These characteristics, together with the lack of well-developed muscle attachment sites on the humerus, are contra indicators of terrestrial locomotion. It is unlikely that the appendicular skeleton could support the body of *Tanystropheus* on land, at least for prolonged periods of time, especially considering the large size of some individuals of *T. conspicuus* and *T. hydroides*.

The centre of body mass of *Tanystropheus* represents a further concern regarding the relatively increased mass of the anterior part of the body, when compared to other tanystropheids. In aquatic tetrapods the centre of body mass is located closer to the centre of buoyancy (usually located near the lungs), which allows for finer control of their body trim in water (Motani and Vermeij 2021). The mass of their forelimbs and the pectoral girdle are consequently increased, with the forelimb and the pelvic girdle being reduced simultaneously, to achieve the anterior displacement of the centre of body mass (see Motani and Vermeij 2021). In *Tanystropheus*, however, the hindlimb, and not the forelimb, was larger and better adapted for propulsion in water (Kuhn-Schnyder 1959; Wild 1973; Tschanz 1986; Nosotti 2007; Renesto and Saller 2018). Although this disagrees with the pattern outlined above, this configuration corresponds with some other long-lived marine reptile lineages that have transitioned into aquatic habitats from terrestrial ones. An excellent example is found within the Thalattosuchia, in which the early diverging forms still possessed relatively gracile limbs and a hindlimb much longer than the forelimb (as in *Tanystropheus*), and their adaptation to life in an (shallow) aquatic environment is undisputed (see Pierce and Benton 2006; Cowgill et al. 2023; Young et al. 2024; Johnson et al. 2025). Moreover, in some fully aquatic trachelosaurids, which are the closest relatives of tanystropheids, the pectoral girdle and forelimbs were not hypertrophied (Liu et al. 2017; Spiekman et al. 2024b, c). Instead, the anterior displacement of the centre of body mass might have been achieved predominantly through the elongation of the neck, and the resulting mass increase of the anterior portion of the body, as in *Tanystropheus* (see Rytel et al. 2024b). There are further similarities between *Dinocephalosaurus orientalis*, *T. conspicuus*, and *T. hydroides*, which all had a transversely wide skull with long, conical or recurved teeth, undulating toothrows, an extremely long neck, and lacked an interclavicle (Spiekman et al. 2020b, 2024c; AR personal observation). A study by Gutarra et al. (2022) looked at the body dimensions of long-necked sauropterygians and shown that if trunk dimensions are kept constant while the neck is elongated up to double its length, drag does not significantly increase, although an even more elongate neck, with fixed trunk size, would incur some additional drag. In *Dinocephalosaurus orientalis*, *T. hydroides*, and *T. longobardicus* the neck is around two to three times longer than the torso (AR personal observation; Wild 1973; Spiekman et al. 2024c) but their trunk volume also increased during their evolution, in *Dinocephalosaurus orientalis* due to the increase in the count of dorsal vertebra, in *Tanystropheus* due to the expanded musculature of the cervicodorsal transitional region, and possibly the pelvic region (see Renesto and Saller 2018). Both genera are, therefore, mirroring the body proportions obtained for similarly built aquatic sauropterygians, which would suggest convergence directly related to an aquatic lifestyle.

It is clear that *Tanystropheus* hunted aquatic prey as fish and cephalopod remains have been found in the stomach

region of some individuals (Wild 1973). Wild (1973) stated that *Tanystropheus* was likely an extraordinarily efficient swimmer that could pursue even some fast-moving animals. Tschanz (1986) proposed “kinetic inertial feeding” (see Gans 1961, 1969), as seen in extant reptiles, to be the main mode of prey capture and manipulation in *Tanystropheus*. He considered the animal as an aquatic, slow moving ambush predator that caught its prey by suddenly lunging its head forward. Taylor (1989) emphasised that the ambush-strategy of prey capture would suit *Tanystropheus* best if it were not for the long, stiffened neck. Renesto (2005, following Peyer 1931) suggested that *Tanystropheus* hunted from land (“fishing rod hypothesis”), but the later study of Renesto and Saller (2018) concluded that the animal caught its prey in water. Due to the length of the neck, the main bulk of the body, which caused most of the water disturbance, would have been positioned some distance from the small head, allowing the animal to approach its prey by stealth (Renesto and Saller 2018). Spiekman et al. (2020a, b) and de Souza and Klein (2022) supported this interpretation, stating the active pursuit-predation was very unlikely employed by *Tanystropheus*. Suction feeding was also not considered a plausible mechanism for catching prey because of the presence of highly procumbent and elongate, fang-like teeth, which would interfere rather than aid during suction feeding (Spiekman et al. 2020a, b). Instead, based on the insights gained from the recently reconstructed skull of *T. hydroides*, Spiekman et al. (2020a, b) hypothesised that this taxon was an ambush predator which hunted using laterally directed snapping bites. The same strategy is also supported herein for *T. conspicuus*, which is characterised by a similar morphology of the jaws and teeth. Importantly, this hypothesis is not mutually exclusive with the “kinetic inertial feeding” proposed by Tschanz (1986). Nosotti (2007) found the latter strategy to be most plausible for *Tanystropheus*, but wondered whether the neck of the animal might have been too stiff to employ it. More recent studies refute the latter suggestion, as currently we know that there were 13, not 12, cervical vertebrae (Rieppel et al. 2010), and that the base of the neck was inclined and held by strong musculature at its base (see the Discussion herein). The anatomy of the transitional cervicodorsal region would allow some flexion and a capacity for storage of considerable amounts of elastic energy, which could be then released with a protraction of the neck during an attack on prey. It is, therefore, clear that the results of all recent studies on the subject, together with all the aforementioned correlates of an amphibious lifestyle, are congruent with the data provided. They point towards *Tanystropheus* being an ambush predator that caught its prey while fully submerged, employing either lateral snapping or forward lunges of the head.

Concerning the aquatic locomotion mode of *Tanystropheus*, there is currently no consensus on the main propulsion source of this animal. Various studies presented different hypotheses on the subject at various times. Kuhn-Schnyder (1959) was first to point out that the hindlimb was adapted to propelling the animal when it was submerged. Wild (1973)

supported this view and suggested that the tail of the animal was only for steering. Tschanz (1986, 1988) considered *Tanystropheus* an axial-subundulational swimmer, in which undulations of the trunk and tail were responsible for most of the propelling force, and were only supported by paddling of the hindlimbs. Renesto (2005) concluded that neither the tail nor the hindlimbs were adapted for efficient swimming. Nosotti (2007) provided an elaborate discussion on the subject, and after analysing the functional morphology of the hindlimb, concurred with Tschanz (1986, 1988) in interpreting lateral undulations of the body as the main propulsion source in *Tanystropheus*. Renesto and Saller (2018) opposed this view, as their reconstruction of the caudal musculature provided arguments (primarily the dorsoventral flattening) against the tail being an efficient propulsion source during lateral undulation. Instead, Renesto and Saller (2018) suggested symmetrical rowing of the hindlimbs as the more likely mode of locomotion. Spiekman et al. (2020b) found this hypothesis unlikely, stating that strokes of the hind limbs alone would have not provided sufficient underwater propulsion, and undulatory movements of the posterior portion of the body of *Tanystropheus* must have also contributed to its locomotion. Sennikov (2023: 441) noted that tanystropheids had “an anteriorly wide and flat tail”, which could have made its vertical movements a probable source of propulsion in water.

The findings provided herein contribute further insights on the subaqueous propulsion of *Tanystropheus*. The most striking and distinct feature for *T. conspicuus* is the presence of a relatively tall, distally expanded neural spine in many of its vertebrae. This indicates that the tail skeleton of *Tanystropheus* was not dorsoventrally flattened, with the transverse processes and the neural spine in the proximal caudal vertebrae of at *T. conspicuus* being of subequal length (Fig. 26), and the neural spine in the distal tail vertebrae being relatively tall (Fig. 27). Whereas the tail almost certainly contributed to some extent to the movement of the animal in water, in the absence of a biomechanical analysis its role should not be overstated. The suggestion of Sennikov (2023) concerning the possibility of the tail propelling the animal through vertical movements seems implausible for *Tanystropheus*, considering that in *T. conspicuus* the skeleton of the tail is more expanded dorsally than laterally. As already pointed out by Spiekman et al. (2020b), anterior caudal vertebrae with long transverse processes are common in (semi) aquatic reptiles, including those using lateral undulation of the tail, and reflect the presence of well-developed axial muscles. There is, thus, no evidence supporting the hypothesis of Sennikov (2023), especially when also considering that the ancestors of tanystropheids were terrestrial and relied on a sprawling gait for locomotion, which requires axial musculature capable of lateral, not vertical, undulation. Moreover, as mentioned by Renesto and Saller (2018), the complex of long postcloacal bones present in all species of *Tanystropheus* could have considerably impaired the vertical movements of the anterior portion of the tail, which also bears the longest transverse processes. Considering the shared bauplan,

it is unlikely that *T. conspicuus* differed significantly from *T. hydroides* and *T. longobardicus* in its mode of underwater propulsion. This makes interpreting the adaptive role of the distal expansion of the neural spine more difficult. It seems likely that the increased height of the vertebral column aided the lateral undulation of the body, supporting the hypotheses of Tschanz (1986, 1988), Nosotti (2007), and Spiekman et al. (2020b). The distal expansion of the neural spine is interpreted as a support structure for cingulate ligaments (Pritchard et al. 2015). The dorsal margin of the neural spine is transversely expanded, flat, and straight in lateral view in virtually all currently accessible dorsal, sacral, and anterior caudal vertebrae of *Tanystropheus*, excluding *T. conspicuus* (Wild 1973, 1980a; Dalla Vecchia 2000, 2006; Nosotti 2007; Renesto and Saller 2018). The anterior caudal vertebrae of *T. conspicuus* share this characteristic, but the dorsal margin in all its dorsal and sacral vertebrae is conspicuously dorsally expanded, rounded and strongly convex in lateral view (Figs. 20, 21, 24–26). This trait likely arose from the modified neural spine table, which is a feature widely present among archosauromorphs, including many other tanysaurians (e.g., *Dinocephalosaurus orientalis*, *Macrocnemus* spp., *Trachelosaurus fischeri*; see Ezcurra 2016; Pritchard et al. 2015; Renesto and Saller 2018; Scheyer et al. 2020; Spiekman et al. 2021, 2024b, c; AR personal observation). Renesto and Saller (2018) hypothesised that the expanded dorsal region of the neural spines of *Tanystropheus* supported a supraspinous ligament system that would have stiffened the trunk, and possibly limited the lateral undulation of the body. Spiekman et al. (2020b, 2024b) opposed this interpretation, stating that the spine table might have indeed contributed to the ligament system, but the novel data concerning the aquatic trachelosaurids suggest that the stiffening might have stabilised the vertebral column, but likely did not severely affect the efficiency of lateral undulation for propulsion. In the morphology of the distal portion of the neural spine, *T. conspicuus* resembles the trachelosaurid *Trachelosaurus fischeri* more than other *Tanystropheus* species, with the first two tanysaurians sharing the general shape, extent of dorsal expansion, and the presence of distinct transverse rugosities, although the neural spines in *T. conspicuus* are relatively much taller. Whereas lateral undulation was speculated to be the main propulsive source for aquatic trachelosaurids (Spiekman et al. 2024b, c), these forms have a serpentine vertebral column, which is composed of a far greater number of vertebrae and in its post-cervical section is relatively much longer than in tanystropheids. The distinct neural spine morphology of *T. conspicuus* might, therefore, represent an adaptation to an aquatic lifestyle that is only partially shared by other species of *Tanystropheus*. Alternatively, the evolution of this feature might have been related to the size increase of the animal, as *T. conspicuus* is the largest known tanystropheid. With increasing size, the mass of an animal increases exponentially, and further ligament support might have been needed to propel the animal in water and preserve finer control over the vertebral column, and especially the long neck, with the

anterior dorsal vertebrae contributing to its movements. This would explain the greater extent of the distal expansion of the neural spine in *T. conspicuus*, but not the other, smaller, species of *Tanystropheus*.

Interestingly, in *T. hydroides* and *T. longobardicus* there is a strong positive correlation between vertebral height and length in the dorsal vertebrae (Fig. 23), similar to the observations of Wild (1973) and Tschanz (1986, 1988). In contrast, within *T. conspicuus* this correlation seems to be much weaker, with the neural spines reaching variable heights for the vertebrae of roughly identical length (Fig. 23). This might be due to larger height differences within a series, or due to more prominent intraspecific variation. Nevertheless, the relatively tall dorsal, sacral, and caudal vertebrae of *T. conspicuus* likely contributed to the more efficient lateral undulation of the body. Corresponding to Tschanz (1986, 1988), Nosotti (2007), and Spiekman et al. (2020b), I interpret *Tanystropheus* as an animal that propelled itself underwater mainly by the movements of its trunk and tail. The role of the hindlimbs in locomotion is difficult to assess, and in the future should be analysed through dedicated myological and biomechanical studies, which are feasible with the Miedary material. It can be stated with confidence that *Tanystropheus* led an aquatic lifestyle within a shallow near-shore habitat, rather than a fully pelagic mode of life. Its skeletal adaptations to underwater propulsion are relatively subtle and do not support pelagic diving (Beardmore and Furrer 2017; Jaquier and Scheyer 2017; Nosotti 2007; Renesto and Saller 2018; Spiekman et al. 2020a; Spiekman and Mujal 2023).

Hypodigm of *Tanystropheus conspicuus*.—The majority of tanystropheid remains from Miedary are isolated, yet they can all be confidently referred to *Tanystropheus conspicuus* due to their highly diagnostic morphology. The axis ZPAL V. 36/550 from Miedary, originally reported by Czepeński et al. (2023), was not referred to *Tanystropheus* due to several morphological differences compared with the known axes of *Tanystropheus*. With new, more complete, specimens from the same site having been prepared (Fig. 10), this morphological disparity can be attributed to the incomplete preservation of ZPAL V. 36/550, as the specimen falls within the range of intraspecific variation of *T. conspicuus*. Currently there is no evidence for the presence of more than one taxon within the association of tanystropheid remains from the M1, M2 and M4 layers of Miedary. The only non-tanystropheid archosauromorph fossils from these strata include rare isolated ziphodont teeth and an osteoderm of the doswellid *Jaxtasuchus* sp. (see Czepeński et al. 2023). The presence of skeletal elements of a new archosauromorph taxon mentioned by Czepeński et al. (2023) seems to be constrained to the M3 layer, which has not yielded any tanystropheid remains. Whereas the Miedary strata preserve a multitaxic assemblage of archosauromorphs, the remains of *T. conspicuus* are quantitatively dominant. Bones and teeth of this animal can be identified with high confidence due to the morphological similarity to the elements known from articulated individuals of other species of

Tanystropheus (especially *T. hydroides*). Additionally, several specimens of *T. conspicuus* (Figs. 16, 20; SMNS 13337) preserve partially overlapping portions of the axial and appendicular skeletons between them, which together facilitate the identification of isolated remains based on shared diagnostic features (e.g., rugose distal portion of the neural spine). I refrain from detailed taxonomic identification of some less diagnostic bones (e.g., holocephalous ribs, gastralia, hemal arches, distal caudal vertebrae, autopodial elements) from the CEB, including Miedary, even though at least some likely belong to tanystropheids, as among early archosauromorphs many skeletal elements are morphologically similar and therefore hard to taxonomically identify in isolation. Thus, the hypodigm of *T. conspicuus* currently comprises most of the vertebral column, complete pelvic and pectoral girdles, stylopodium, zeugopodium, postcloacal bones, ribs, gastralia, several cranial elements and teeth.

Some intraspecific variation is present in the Miedary assemblage, but it does not exceed what might be expected within individuals from one population. For example, some vertebrae of *T. conspicuus* from the same position in the vertebral column differ considerably in the height and curvature of their neural spine (compare Fig. 18A and B; Fig. 23), but they nevertheless share most other morphological characteristics, including the diagnostic distal expansion of the neural spine. No further major morphological deviations can be identified within the material of *T. conspicuus*, including the remains from outside Miedary, which predominantly comprise highly diagnostic elements, vertebrae, teeth, femora and humeri. Importantly, the material referred to this species that originated from Germany and France (including the type series) falls within the size range and the spectrum of morphological disparity seen in the specimens from Miedary. Therefore, specimens from the western part of the CEB, which have been gathered from a multitude of outcrops that record several millions years, do not seem to differ in any taxonomically distinct way from the remains of *T. conspicuus* from Miedary. Moreover, the only paralectotype of *T. conspicuus* known from the eastern part of the CEB, a partial vertebra MB.S.11, originated from Laryszów, a village directly adjacent to the Miedary site. The specimen was found in the Boruszowice Beds, which underlay the strata outcropping in Miedary (von Meyer 1847–1855; Czepiński et al. 2023). Thus, through parsimony and lack of any contrary evidence, all large-sized *Tanystropheus* remains known from the Muschelkalk and Lower Keuper of the CEB, together with all the tanystropheid material from Miedary, can be considered as belonging to one species, and are all referred to *T. conspicuus* herein (see SOM: table 1).

Re-identification of historic specimens.—Through the long and convoluted research history on *T. conspicuus* many isolated specimens have been referred to this species, or its junior synonyms. Through comparisons with the novel material described herein, their status is reevaluated, providing an updated and better defined hypodigm of *T. conspicuus*.

Wild (1973) and Spiekman and Scheyer (2019) considered *Chelyzoon blezingeri*, *Chelyzoon latum*, *Procerosaurus cruralis*, and *Thecodontosaurus latespinatus* subjective junior synonyms of *T. conspicuus*, and these assessments are upheld here as there are no clear morphological differences between the type material of these taxa and the specimens referred to *T. conspicuus*. I consider two additional taxa as junior synonyms of *T. conspicuus*, *Nothosaurus blezingeri*, and *Megacnemus grandis*. The former was erected on the basis of teeth and some postcranial remains, of which only one tooth was illustrated (Fraas 1896: fig. 4), making it the only specimen of the type series that can be reliably identified. I was able to recover this specimen, together with several other teeth labelled as originals of Fraas (1896), selected by Rupert Wild and registered under the number SMNS 52478. They all exhibited a long root and sparse, uneven, ridges on the crown, clearly belonging to *T. conspicuus* and not to any species of *Nothosaurus*, corresponding with the previous suggestion of Rieppel and Wild (1996) and Rieppel (2000).

Concerning *Megacnemus grandis*, new data on the three-dimensional morphology of tanystropheid limb-bones allow a re-assessment of the affinities of the holotype and the only known specimen, the GPIH 253 humerus (von Huene 1954; Fig. 35B). This element falls within the known size range of humeri of *T. conspicuus*, being close in length to the largest specimens from Miedary (see Fig. 35). Moreover, despite some deformation, GPIH 253 preserves overall proportions and curvature congruent with the humeri of *T. conspicuus* and is also similar in the shape of the proximal and distal articular surfaces and the absence of a developed deltopectoral crest. The main feature which might differentiate *M. grandis* from *T. conspicuus* is the possible absence of the supinator process in the former (Fig. 35B). This characteristic might, however, be artificial and caused by the preservation of the specimen, with its proximal and distal ends being damaged and missing the portion that included the supinator process. Based on its preservation, von Huene (1954) hypothesised that GPIH 253 likely originated from the Triassic outcrops of Silesia. I agree with this interpretation as the preservation of the specimen is similar to those found in the Muschelkalk. Moreover, the few remaining labelled Triassic vertebrate specimens housed at GPIH, excluding the holotype of *Velocipes guerichi* (see Czepiński et al. 2021), all come from Muschelkalk localities of modern-day Poland and Germany. These include specimens from the collections of Max Grunday (1856–1946) and Georg Gürich (1859–1938), who both gathered thousands of fossils from the Triassic localities of Silesia. Some of those GPIH specimens originated from the Upper Muschelkalk of Tarnowskie Góry (“Tarnowitz”), strata which were the subject of research for Gürich (1884, 1887) who worked at the University of Hamburg for many years, after moving there from Silesia. Outcrops of this unit in the area (Laryszów/Larischhof) have yielded cervical vertebrae of *T. conspicuus* including one of the paralectotypes (von Meyer 1847–1855; Langenhan 1903). Taking into account the morphology, size and preservation of GPIH 253 as well as the historic back-

ground of the other Triassic vertebrae specimens housed at GPIH, it is very likely that the humerus belongs to *T. conspicuus* and originated from the Upper Muschelkalk of Upper Silesia (“Rybnaer Kalk”), and not from the Lower Muschelkalk of Gogolin as suggested by von Huene (1954). *Megacnemus grandis* is here regarded as a subjective junior synonym of *T. conspicuus*.

Whereas most of the type material of the junior synonyms of *T. conspicuus* is still accessible, the holotype of *Chelyzoon latum* was most likely destroyed during the Second World War while deposited in Munich (Wild 1973; AR personal observation). However, I identified two casts of that specimen in the GPIT collection (GPIT-PV-60024 and GPIT-PV-60025). Spiekman and Scheyer (2019) mentioned that the type specimens of both species of *Chelyzoon* appear to be morphologically disparate from the known vertebrae of *Tanystropheus*, yet I concur with Wild (1973) in designating both *Chelyzoon blezingeri* and *Chelyzoon latum* as junior synonyms of *T. conspicuus*. Their type specimens are indistinguishable from the two posteriormost neck vertebrae of *T. conspicuus*, with SMNS 8728 (the holotype of *Chelyzoon blezingeri*) being a twelfth cervical vertebra and the lost holotype of *Chelyzoon latum* a thirteenth cervical vertebra. ZPAL V. 36/584 (Fig. 16) preserves both corresponding vertebrae from these positions in a tight association with some other remains of a single individual of *T. conspicuus*, which further strengthens the referral of the type material of both species of *Chelyzoon* to this species.

Concerning the partial vertebra GPIT-PV-60014, the holotype of *Pectenosauros strunzi* von Huene, 1902, I concur with Rupert Wild’s note written on the specimen label in reidentifying it as belonging to a sauropterygian, not to *Tanystropheus* (contra Kuhn 1963, 1971; Spiekman and Scheyer 2019). The vertebra presents no clear archosauromorph features. *Pectenosauros strunzi* is deemed a nomen dubium and not a synonym of *T. conspicuus*.

Von Huene (1902: pl. 5: 6) described a long bone of uncertain affinities, found near Bayreuth, which he later (von Huene 1931) considered likely to be a humerus of *Tanystropheus*. Wild (1973) rejected this hypothesis but stated that the bone could not be located. I was able to rediscover the specimen in question in the U-MO collection as an uncatalogued and unlabelled bone. I can confirm confidently that the specimen described by von Huene (1902: pl. 5: 6) is not an archosauromorph humerus but rather a partially preserved sauropterygian clavicle articulated with an interclavicle.

An unpublished fragmentary right hemimandible SMNS 56289, originally identified as belonging to *T. conspicuus*, served as one of the sources of scoring for *Tanystropheus* in the phylogenetic analysis of Ezcurra (2016). The long, straight bone is indistinguishable from sauropterygian dentaries in its general morphology and proportions. Although the anteriormost part of the dentary is missing, the specimen preserves three large, laterally projecting alveoli and a row of smaller teeth of relatively homogenous size posterior to them. The same pattern is present in *Nothosaurus*

(Rieppel and Wild 1996: fig. 63). Considering how closely the *T. conspicuus* dentaries from Miedary resemble those of the *T. hydroides* holotype, SMNS 56289, which differs from both of them significantly, can confidently be stated not to be referable to *Tanystropheus*. Together with several unpublished ischia (see SOM: table 1) stored at SMNS and originally labelled as *T. conspicuus*, SMNS 56289 is regarded as belonging to an indeterminate sauropterygian.

Wild (1973) considered the lectotype specimen U-MO BT 740 to be a tenth cervical vertebra. As illustrated herein (Fig. 15), the main feature that differentiates the tenth cervical vertebra from the other neck vertebrae of *T. conspicuus* is the continuous and relatively tall neural spine characterised by its undulating, thickened, distal edge. U-MO BT 740 lacks this feature, with its neural spine being well-preserved as a low, narrow ridge that increases in height only in its anterior portion (Wild 1973: compare figs. 46 and 47). The neural spine height in the tenth vertebra of *T. conspicuus* seems to be affected by ontogeny, with the smallest known specimen SMF R 285 (erroneously identified as an eleventh cervical vertebra by Wild 1973) exhibiting a relatively straight distal edge. The morphology observed in U-MO BT 740 is, however, outside of this spectrum, and the specimen is regarded as a middle cervical vertebra instead. Whereas I find this particular minor reinterpretation worthy of mention due to the lectotype status of this vertebra, the full list of specimens, their status, and current identification, can be found within the SOM: table 1.

Remarks on the characters included in the diagnosis of the genus *Tanystropheus*.

Presence of bifurcated ribs in the sacral vertebrae: The absence of bifurcated ribs of the second sacral vertebra was regarded as one of the diagnostic features of *Tanystropheus* by Spiekman and Scheyer (2019), following Ezcurra (2016) and concurring with Rieppel (1989). There is no clear indication for the presence of this character in *Tanystropheus* species other than *T. conspicuus*, although in PIMUZ T 2817, one of the specimens referred to *T. hydroides* by Spiekman et al. (2020b), a miniscule hook-like posterior expansion of the left partially preserved second sacral rib can be observed (AR personal observation). The second sacral vertebra of *T. conspicuus* unequivocally possesses a distinct triangular projection, extending posteriorly from the sacral ribs at the same vertical level as the dorsal margin of the posterior articular surface of the centrum. Thus, the absence of bifurcated ribs of the second sacral vertebra is not shared by all species of *Tanystropheus* and is not a diagnostic feature of the genus. The previous diagnosis was based on a misidentification of the sacral vertebra of *T. conspicuus* SMNS 54631 as a second sacral vertebra (Ezcurra 2016: fig. 35A), which is actually a first sacral vertebra (in accord with Wild 1973: fig. 55), and which does indeed lack the bifurcating sacral ribs.

Presence of an interclavicle: An ossified interclavicle is present in the majority of early-diverging archosauromorphs (see Spiekman et al. 2021). In *Tanystropheus*, however, no articulated specimen preserves an element that can

be unequivocally identified as an interclavicle. Haas (1970) described an isolated interclavicle from Israel that he considered to likely be from *Tanystropheus*. The specimen was later found to belong to *Simosaurus* sp. (Rieppel et al. 1999). Wild (1973) noted the presence of an incomplete elongate bone in a partial skeleton PIMUZ T 2793 and interpreted it as an interclavicle, morphologically disparate from the one published in Haas (1970). This element (Wild 1973; fig. 64) is rod-like for most of its length, but widens to form a thin plate close to the edge of the rock slab. It overlays a proximal part of the third dorsal rib. Nosotti (2007) recognised a fragment of a tentative interclavicle in the *T. longobardicus* specimen MSNM BES SC 1018.

New morphological information provided herein allows for a reinterpretation of the “interclavicle” from PIMUZ T 2793 as one of the first dorsal ribs, which would explain its slight asymmetry as well. The element mentioned by Nosotti (2007) is likely of the same origin. Several partially preserved, isolated bones stored at SMNS, originally identified as *Tanystropheus* interclavicles, are disparate in their morphology and their taxonomic affinities are highly uncertain. Therefore, with the multiple articulated and complete skeletons not preserving an interclavicle, and no archosauromorph interclavicle being found in Miedary so far, it can be unequivocally confirmed that the interclavicle in *Tanystropheus*, if it was present in any form, was not ossified. This corroborates the scorings of the phylogenetic analyses of Spiekman et al. (2021, 2024c). Among tanysaurians in which this character can be assessed, only *Dinocephalosaurus orientalis* and *Ozimek volans* Dzik & Sulej, 2016, lack an ossified interclavicle (Dzik and Sulej 2016; Spiekman et al. 2024c).

Presence of subcentral foramina: Spiekman et al. (2021) stated that among all archosauromorph taxa analysed therein for which this character could be assessed, conspicuous foramina on the ventral side of the cervical vertebrae are present only in *T. conspicuus*, but their absence in other species of *Tanystropheus* cannot be confirmed either. These subcentral foramina were recently shown to be associated with intersegmental arteries that ran within the vertebrae (see Rytel et al. 2024b). The presence of this character can be unequivocally confirmed in the three-dimensionally preserved material referred to *Tanystropheus* sp., from the sites in Hungary (Ősi et al. 2020), NE Italy (Dalla Vecchia 2006; AR personal observation), Romania (Jurcsak 1975; AR personal observation) and small-sized vertebrae from the Lower Keuper of Germany (Schoch 2015: fig. 10.7C; Spiekman and Scheyer 2019: supplementary table 1 therein; AR personal observation). In the articulated specimens from Monte San Giorgio and China the existence of the subcentral foramina is difficult to assess due to the ventral side of the vertebrae rarely being visible. Interestingly, Wild (1980a) described PIMUZ T 3901 as having foramina on the lateral side of the cervical vertebrae, near the midpoints of their anteroposterior length. It is very likely that these foramina are homologous to subcentral foramina of other *Tanystropheus* species, and it is only

due to diagenetic alteration of the original morphology that they appear as if located on the lateral side of the centrum. Similarly, PIMUZ T 2819 preserves some three-dimensional information and was prepared in such a way that deep pits are visible on the ventral side of the centra, at an identical relative location as the subcentral foramina in other species of *Tanystropheus*. PIMUZ T 3901 was referred to *T. longobardicus* by Spiekman and Scheyer (2019) and PIMUZ T 2819 was referred to *T. hydroides* by Spiekman et al. (2020a). Therefore, the existence of subcentral foramina on the ventral surface of postaxial cervical vertebrae can be confirmed for all three valid species of *Tanystropheus* as well as in most other specimens in which the presence of this character could be assessed.

Reduction of the neural spine in the cervical vertebrae: An extreme elongation of a vertebra is usually accompanied by a reduction in neural spine height, resulting in convergently similar morphologies. This is evident when comparing the cervical vertebrae of tanysaurians and azhdarchoid pterosaurs, which, despite being comparable in general vertebral shape, exhibit clear differences in their internal anatomy, thereby indicating different biomechanical means for accommodating their extreme proportions (see Rytel et al. 2024b). Whereas the neural spine in the middle section of the middle cervical vertebrae of *Tanystropheus* is extremely low, histological and microanatomical studies prove that it was not lost, but rather embedded in a thick cortex (Rytel et al. 2024b). Thus, it cannot be regarded as “completely reduced” but rather only “virtually completely reduced”, as interpreted in some studies (e.g., Pritchard et al. 2015). The neural spine is present along the entire length of the middle cervical vertebrae of *Tanystropheus*, despite not being outlined in the middle sections of some of them.

Femur/humerus length ratio: Whereas Spiekman et al. (2021) found the ratio of the total length of the humerus versus the total length of the femur between 0.84 and 0.91 to be one of the synapomorphies present in *Tanystropheus*, this character is not included in the emended diagnosis herein. The articulated specimens from Monte San Giorgio area display a different state for this character, with the mentioned ratio reaching values from around 0.63 to around 0.76 (AR personal observation). These values are generally congruent with the measurements of Spiekman et al. (2021: supplementary material) and are similar to those present in other early-diverging archosauromorphs studied therein, thus not constituting a diagnostic character for *Tanystropheus*.

Presence of the postcloacal bones: In some articulated and largely complete individuals of *Tanystropheus* of various size (GMPKU P 1527, PIMUZ T 1270, PIMUZ T 1277, PIMUZ T 1307, PIMUZ T 2817) four elongate elements arranged in two pairs are present posterior to the pelvic girdle. These ossifications are absent in several other similarly sized individuals with a well preserved pelvic region (e.g., MSNM BES SC 265, PIMUZ T 2483, PIMUZ T 2791, PIMUZ T 2818). Wild (1973: 123) already noted that the presence of this feature is due to sexual dimorphism, inter-

preting these “calcified cartilage rods” as “penile elements”. Rieppel (1976) suggested that they are likely post-cloacal bones, a hypothesis that Wild (1980a) later supported.

Post-cloacal elements, as defined by Russell et al. (2016), are subcutaneous, mineralised (or at least radio-opaque) structures located in the base of the tail of some squamates (geckos, xantusiids) and lissamphibians (caecilians). In extant animals only the males bear them. The postcloacal bones are used during copulation but their specific function remains relatively poorly understood (Rieppel 1976; Russell 1977; Russell et al. 2016). The study of Jaquier and Scheyer (2017) has shown that the postcloacal bones in *Tanystropheus* have no cartilaginous precursor, and are bony elements, similar to structures that have been reported for the postcloacal bones of geckos, but unlike caecilians (Russell et al. 2016).

Among all archosauromorphs, only one other tanystropheid, *Tanytrachelos ahynis* Olsen, 1979, shares the presence of postcloacal bones with *Tanystropheus* (Olsen 1979; Casey et al. 2007). In both taxa there are two pairs of elongate, anteroposteriorly oriented elements. Whereas the complex postcloacal apparatus in Tanystropheidae has likely evolved only once, as *Tanystropheus* and *Tanytrachelos* seem to be closely related (see Spiekman et al. 2021), the later development of a similar anatomical feature in squamates appears to be convergent (contra Wild 1973). When compared to geckos, in which the postcloacal bones are relatively well-studied, the elements present in tanystropheids are relatively much larger, less mediolaterally expanded, and of more constant length within the whole apparatus (Wild 1973, 1980a; Rieppel 1976; Russell 1977; Olsen 1979; Kluge 1982; Russell et al. 2016). The homology between the postcloacal bones in squamates and tanystropheids is likely purely functional, although further finds of early reptiles with associated postcloacal bones could change this interpretation.

Olsen (1979) suggested that the ossifications in *Tanytrachelos ahynis* were characteristic to females and might have served a role of an egg pouch support, but it seems more parsimonious to concur with Wild (1973, 1980a) in attributing them to males, as observed in the extant squamates. In an animal of such extraordinary proportions as *Tanystropheus*, copulation might have demanded an additional structure that would serve as an attachment point for tissues associated with the copulatory organ of the male. Regardless of their function and distribution between the sexes, the postcloacal bones documented in all three species of *Tanystropheus* and *Tanytrachelos ahynis* give additional insights into the dimorphic features found among the early members of Archosauromorpha. Further indications for sexual dimorphism have also been reported from all other major clades of non-archosauriform archosauromorphs, some rhynchosaurians (different body proportions, see Chatterjee 1974; Benton 1983), the allokotosaurian *Shringasaurus* Sengupta et al., 2017 (presence of horns in some specimens), and possibly in the trachelosaurid *Dinocephalosaurus* (size difference between mature individuals; Liu et al. 2017; Spiekman et al. 2024c). Therefore, it seems that sexual dimorphism

in Triassic archosauromorphs was not uncommon and was expressed in diverse osteological forms. In combination with the already described articulated specimens of *Tanystropheus* with the postcloacal apparatus preserved in situ, the newly reported isolated postcloacal bones from Miedary (Fig. 45) will allow for a more comprehensive analysis of the function of these elements in the future.

Biogeographic distribution of *Tanystropheus conspicuus*.

—The earliest described specimens of *Tanystropheus* originated from Europe, specifically France, Germany, Poland (von Meyer 1847–1855; von Huene 1907–1908), Italy, and Switzerland (Bassani 1886; Peyer 1931). Outside of the CEB and the sites of Monte San Giorgio, remains of *Tanystropheus* have so far been reported from Canada (Sues and Olsen 2015), China (Li 2007; Rieppel et al. 2010), Hungary (Ősi et al. 2020), Israel (Peyer 1955; Rieppel 2001), several further localities in Italy (Dalla Vecchia 2000, 2006, 2008; Dalla Vecchia and Avanzini 2002; Dalla Vecchia and Simonetto 2018), Romania (Jurcsak 1973, 1975, 1978) and Saudi Arabia (Vickers-Rich et al. 1999), giving the genus a wide spatial range of occurrence (Spiekman and Scheyer 2019). The Polish sites constitute the northernmost confirmed occurrence of *Tanystropheus*, being located on higher palaeolatitudes than the sites from the western side of the CEB, due to the counterclockwise rotation of the tectonic plates that formed this portion of Pangaea relative to the modern day (see Nawrocki and Szulc 2000; Scotese 2014).

Whereas material of *T. hydroides* might potentially be present both in Europe and in China (Spiekman et al. 2020a), the finds of *T. conspicuus* are palaeobiogeographically constrained to the CEB (Fig. 47). Remains of the latter species are widespread in the upper Anisian–upper Ladinian outcrops of the basin. The first appearance of *T. conspicuus* is near the base of the Upper Muschelkalk (lower Trochitenkalk Formation of Bad Sulza in Germany), and its last record can be found in the uppermost stratum of the Lower Keuper (Grenz dolomit, uppermost Erfurt Formation of Molsdorf and Hoheneck in Germany). Overall, the taxon is known from around 70 localities (see SOM: table 1). The prevailing majority of these sites are located in Germany, forming three clusters (Fig. 47), one north of Stuttgart, one in Bavaria (Upper Franconia, Bayreuth area), and the third in Thuringia (around Erfurt). From among other localities, an ilium and a vertebra have been found in north-western Germany (Horn-Bad Meinberg and near Göttingen), several specimens have been described from four sites in Alsace and Lorraine (France), and the material from Laryszów and Miedary in Upper Silesia (Poland) is reported herein. An additional vertebra potentially belonging to *T. conspicuus* has been found in an Upper Muschelkalk quarry in Lamerden in Hesse, near the border with North Rhine-Westphalia (Germany, see Diedrich 2015) and a Lettenkeuper outcrop in Kościelec (nowadays a part of Chrzanów, Lesser Poland) has yielded a large postzyga-

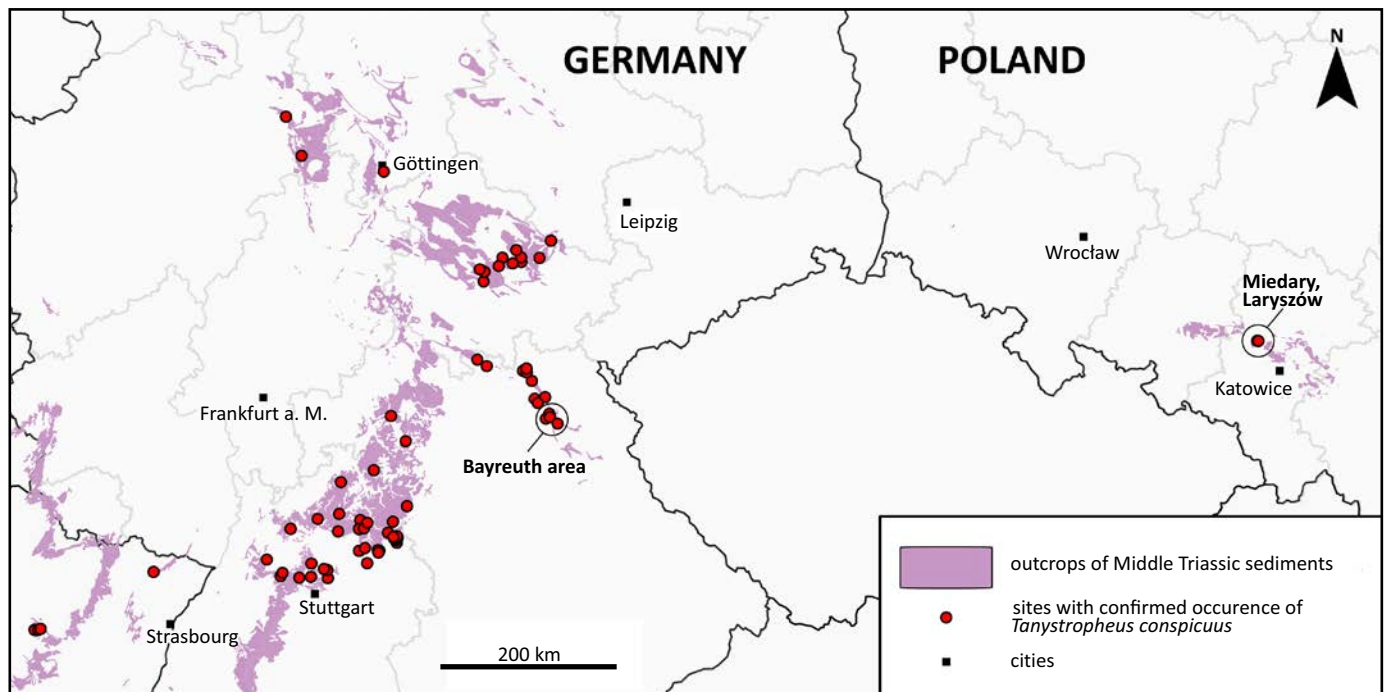


Fig. 47. Map of Central Europe with the outcrops of Middle Triassic (upper Anisian to upper Ladinian) sediments in the Central European Basin and the occurrences of *Tanystropheus conspicuus* von Meyer, 1852, marked. Outcrops in Poland based on Marks et al. (2022), and the rest on the Geologische Karte der Bundesrepublik Deutschland 1:1 000 000, created by the BGR (version 2024-04-23). For Poland the Middle Triassic outcrops are visible, and the rest of the marked area signifies the presence of the following strata, with the stratigraphy assigned by the BGR: Muschelkalk undivided, Upper Muschelkalk, Muschelkalk and Keuper undivided, Lower Keuper. Labelled localities represent the sites from which the type material derives (Bayreuth area, Laryszów) and the site with the largest amount of specimens (Miedary). For the full list of included localities refer to the SOM: table 1.

pophysis with a prominent epiphysis ZPAL P. 8 (partim), reminiscent of that of *Tanystropheus*.

The remains of *T. conspicuus* are, therefore, relatively evenly spatially spread within the accessible Upper Muschelkalk-Lettenkeuper sites of the CEB. They seem to be much less common in the northern part of Germany, possibly due to sampling bias, as some additional privately-held specimens (AR personal observation) suggest the occurrence of *T. conspicuus* is more common and widespread than documented by the material from public collections. Thus, throughout the existence of this taxon its range of occurrence likely covered most of the CEB. Among all the aforementioned material reported from outside of the CEB, no specimen is morphologically more similar to *T. conspicuus* than to *T. hydroides* or *T. longobardicus*, and none of them reached the size range of the larger individuals of *T. conspicuus*. This implies that the latter species might have been endemic to the CEB. Largely due to the sedimentary record in the region in the Middle Triassic, *T. conspicuus* is currently the species of *Tanystropheus* with the longest and most continuous unambiguous fossil record, encompassing several million years from the late Anisian to the late Ladinian. This suggests that *Tanystropheus* was well adapted to living in the environments of the CEB (contra Wild 1980b).

Co-occurrence of small and large sized individuals of *Tanystropheus* in the Central European Basin.—To estimate the total body size of an animal, we have to consider

the allometric growth of some of its body parts. Whereas in *T. hydroides* and *T. longobardicus* allometric growth can be noted for the cervical vertebrae (Tschanz 1986, 1988), humeral and femoral length seems to increase roughly isometrically to the total body length of the animal (AR personal observation). The largest limb bones of *T. conspicuus* are around 1.5 times longer than those of the largest known complete and articulated individual of *T. hydroides*, PIMUZ T 2818, which measured slightly over 4 m in length. Thus, the known maximal total body length for *Tanystropheus* is estimated at over 6 m. This is also supported by the size of the vertebrae from Miedary, the largest of which (ZPAL V. 36/182) has a nearly 400 mm long centrum. The relatively smallest element referred to *T. conspicuus*, a cervical vertebra ZPAL V. 36/181, is around eight times smaller, with its centrum measuring 49 mm. It is likely a ninth or tenth cervical vertebra as its neural spine is relatively tall in its mid-posterior portion (see Rytel et al. 2024b: fig. 7). Cervical vertebrae nine and ten of nearly the exact same size are present in the neotype of *T. longobardicus* (PIMUZ T 2791), a largely complete and articulated individual with an estimated total body length of around 0.85 m (AR personal observation; Wild 1973). As the body proportions of all *Tanystropheus* species are generally similar, the individual to which the ZPAL V. 36/181 vertebra belonged was likely similar in size to PIMUZ T 2791. Hence, the estimated value of total body length ratio between the largest and the smallest known individuals of *T. conspicuus* equals around seven.

In *T. hydroides* and *T. longobardicus* this value equals less than three, PIMUZ T 2792 (around 1.9 m) versus PIMUZ T 2793 (around 5 m) for the former and PIMUZ T 2481 (around 0.55 m) versus PIMUZ T 1277 (around 1.45 m) for the latter, based on estimates of Wild (1973) and complemented by the measurements made by the author. Most diagnostic features for *Tanystropheus* species from Monte San Giorgio refer to their cranium, and thus specimens not preserving the skull can only be referred to a species based on size (Spiekman and Scheyer 2019; Spiekman et al. 2020b). Hence, some size-overlap might exist but cannot be confirmed due to the preservation characteristics of this material.

The size range of *T. conspicuus* ranges from the equivalent of medium sized individuals of *T. longobardicus* (total body length under 1 m) to individuals larger than the largest known specimens referred to *T. hydroides* (total body length over 6 m). Some potential lines of arrested growth are already present in ZPAL V. 36/181 (Rytel et al. 2024b: fig. 8B), implying that this juvenile might have already gone through several cycles of growth, and the neonates were certainly even smaller. It is therefore possible that some of the specimens previously considered referable to *T. longobardicus* based on size, and lacking any associated cranial material, are in fact juveniles of *T. hydroides*. Further research on the ontogenetic variation of postcranial remains of all three species of *Tanystropheus* is needed to evaluate this hypothesis but should be preceded by broader studies on intra- and interspecific variation of these forms.

The Ladinian sediments of Germany have yielded small teeth, characterised by their tricuspid morphology, with one centrally located large central cusp flanked both distally and mesially by a small accessory cusp. Some of these specimens have been previously referred to ?Cynodontia, *T. cf. meridensis* (= *Tanystropheus* cf. *T. longobardicus*), or *Tanystropheus* sp. (Wild 1980a; Dorka 2002; Löffler et al. 2007; Schoch 2015; Schoch et al. 2018; Spiekman and Scheyer 2019). This tooth morphotype appears throughout the entire Lettenkeuper sequence, from its lowermost (Grenzbened) to its uppermost (Grenz dolomit) strata, but it is currently not known from the underlying Muschelkalk sediments (AR personal observation). Most of these specimens documented to date originated from the Vellberg-Eschenau locality in Baden-Württemberg, with Layer 6 of the Untere Graue Mergel being their most productive source. The same stratum at this site has yielded small *Tanystropheus* sp. vertebrae mentioned by Schoch (2015), Schoch et al. (2018) and Spiekman and Scheyer (2019). Importantly, a postloacal bone and several teeth here referred to *T. conspicuus* also originate from the Untere Graue Mergel of Vellberg-Eschenau. Another tooth morphotype represented by several specimens (e.g., SNSB-BSPG 1973 VII 85) found only in the western part of the CEB, is seemingly intermediate between the previously mentioned tricuspid teeth and the specimens referred to *T. conspicuus* herein. Most of the crown in this morphotype is indistinguishable from those of *T. conspicuus*, but min-

iscule mesial and distal cusps are present. The taxonomic affinities of these teeth might be revealed in future, if they are found preserved in jaw fragments.

Both the small cervical vertebrae of *Tanystropheus* sp. and the tricuspid teeth from the Lettenkeuper of Germany are reminiscent in size and morphology to those of *T. longobardicus*, as mentioned in previous studies (Wild 1980a; Dorka 2002; Schoch 2015; Schoch et al. 2018). Whereas the cervical vertebrae are not diagnostic to the species level in *Tanystropheus* (excluding *T. conspicuus*), the presence of tricuspid teeth is a clear autapomorphy of *T. longobardicus*. Although dentitions of similar morphology were present in basal pterosaurs and some cynodont synapsids (Hahn et al. 1984; Dorka 2002; Schoch 2015; Schoch et al. 2018), only Hahn et al. (1984) compared teeth of these three groups directly. The chronostratigraphically youngest specimen referred to *T. longobardicus* originated from the Cassina beds of the Meride Limestone, on the Swiss side of Monte San Giorgio (Wild 1980a; Spiekman et al. 2021). The $^{206}\text{Pb}/^{238}\text{U}$ age of 240.63 ± 0.13 Ma was assigned to Cassina beds by Stockar et al. (2012), making this interval contemporaneous with the lower Lettenkeuper strata of the CEB (Hagdorn et al. 2015a; Hagdorn and Simon 2020). Thus, it would seem most parsimonious to assume that the association of the small-sized *Tanystropheus* sp. vertebrae and the tricuspid teeth is due to the presence of a form very similar to *T. longobardicus*, or this species itself, in the Ladinian of Germany. This animal would co-occur with *T. conspicuus* in the western part of the CEB, demonstrating that the presence of two different-sized forms of *Tanystropheus* in one environment was characteristic not only to Monte San Giorgio (Spiekman et al. 2020a). Other possible cases of this phenomenon include the *Tanystropheus* material from Makhtesh Ramon in Israel (Rieppel 2001) and the Falang Formation in China (Li 2007; Rieppel et al. 2010).

In Miedary some small cervical vertebrae have been found but they represent juveniles of *T. conspicuus*, as evidenced by their microanatomy (see Rytel et al. 2024b). No tricuspid teeth have been identified despite intensive research on the vertebrate microremains from the site (Pawlak et al. 2022). Miedary is, however, older than the Lettenkeuper sites in the western part of the CEB (see Czepiński et al. 2023) and more distant from the sites from which *T. longobardicus* is known. It is possible that migration of the smaller *Tanystropheus* form occurred later during the Ladinian. Its appearance might have been connected to the environmental turnover of the CEB during the Muschelkalk/Keuper sedimentation transition, during which terrestrial habitats became increasingly more prevalent (see Franz et al. 2013).

To verify the likely presence of a second, small, species of *Tanystropheus* in the CEB, future research should be carried out to determine the ontogenetic age of the small cervical vertebrae from Vellberg-Eschenau as well as the comparative analysis of the tricuspid teeth and dentary morphologies in the Middle Triassic taxa. If in future remains of the small-sized *Tanystropheus* from the Lettenkeuper of

Germany are referred to *T. longobardicus*, and the Chinese specimen GMPKU P 1527 *Tanytropheus* cf. *T. hydroides* (see Rieppel et al. 2010; Spiekman et al. 2020b) can be referred to *T. hydroides*, then both of these species, together with *T. conspicuus*, would have a very similar temporal ranges, late Anisian to late Ladinian. For now, I refrain from reassessing the original taxonomic identification of the aforementioned specimens.

Conclusions

The novel lower Ladinian site in Miedary (southern Poland) has yielded a diverse assemblage of bones and teeth, including hundreds of elements referred here to *Tanytropheus conspicuus*. Based on these remains, combined with all the previously published specimens of *T. conspicuus*, this species is here no longer regarded as a *nomen dubium*. It differs distinctly from other species of *Tanytropheus* in several important characters, including the expansion of the distal portion of the neural spines in the torso, the posterodorsal extension of the scapular blade, and its large size, with the longest individuals likely reaching over six meters in total body length. The newly reported cranial elements constitute the first record of skull bones of *Tanytropheus* from outside of Monte San Giorgio, and provide important insights into the interrelationships of *Tanytropheus conspicuus*, *Tanytropheus hydroides*, and *Tanytropheus longobardicus*. Whereas *T. conspicuus* appears to be closely related to *T. hydroides* if we only take into account the cranial features, *T. longobardicus* and *T. hydroides* are more similar to each other, and disparate from *T. conspicuus*, in many aspects of their postcranial morphology (Figs. 23, 34). This provides valuable insights into the interrelationships of these taxa, and demonstrates a mosaic of features present among the three valid species of *Tanytropheus*. Future studies should focus on studying their inter- and intraspecific variation, assessing which morphological characters result from ontogenetic or size differences, and which might be phylogenetically significant.

This work will facilitate the identification of archosauromorph remains from a broader range of geographical areas. The first comprehensive evaluation of the three-dimensional morphology of *Tanytropheus* remains from the CEB allows for a better assessment of similar material from other regions (e.g., Jurcsak 1973; Vickers-Rich et al. 1999; Rieppel 2001; Dalla Vecchia 2000, 2006, 2008; Sues and Olsen 2015; Ősi et al. 2020). For now, *T. conspicuus* seems to be endemic to the CEB, but further detailed study on the aforementioned material might bring additional insights into the evolution and spread of *Tanytropheus* throughout the marine realm of the Tethys. Moreover, the material described here is also suitable for future research on myology, histology, pathologies, sexual dimorphism, biomechanics, propulsion style and other aspects of the biology of *Tanytropheus*,

which were previously mostly constrained by the preservation characteristics of known remains.

The environmental characteristics recorded at the Miedary site (specifically within layers M1, M2, and M4, see Czepeński et al. 2023) are a good proxy for inferring the preferred habitat of *Tanytropheus*. The number of elements of this animal recovered at Miedary, their diversity, and state of preservation, all point towards over 20 individuals of *T. conspicuus* dying, and likely living, in close proximity to the current excavation site. Previously known localities from which the remains of *Tanytropheus* were reported seem to be positioned further away from the actual habitat of the animal (Renesto 2005; Beardmore and Furrer 2017). Studying the fossil assemblage of Miedary, and the faunistic components contained within it, will bring us closer to understanding the trophic connections between *Tanytropheus* and the other taxa coinhabiting this environment. It is still an open question how constrained the niches occupied by various Middle Triassic aquatic long-necked piscivorous reptiles (nothosaurids, pistosaurids, *Tanytropheus*, trachelosaurids) were, and how their convergent evolution affected their emergence, success, and later disappearance.

Thanks to the material from Miedary the status of *T. conspicuus* changes from an obscure and dubious taxon based on fragmentary, isolated bones to one of the better documented Triassic archosauromorphs. It is known from over a thousand specimens. These are mostly isolated elements, but they include some articulated remains. *Tanytropheus conspicuus* is the largest tanytropheid known to date, and one of the longest Middle Triassic reptiles. There are multiple lines of evidence for its aquatic lifestyle (e.g., depositional environment, dental morphology, reduced deltopectoral crest, etc.), and no clear indication for terrestrial locomotion. This is congruent with hypotheses from previous studies on *Tanytropheus* (Tschanz 1986; Nosotti 2007; Rieppel et al. 2010; Beardmore and Furrer 2017; Jaquier and Scheyer 2017; Renesto and Saller 2018; Spiekman et al. 2020a, b; Spiekman and Mújal 2023; Rytel et al. 2024b). Virtually all our current knowledge on this genus points towards it being a (semi)aquatic ambush predator that lived and hunted in shallow marine or brackish waters. Its ability to walk on land is difficult to assess, it might have reproduced on land but the evolution of viviparity in the slightly older, closely related taxon, *Dinocephalosaurus* (Li et al. 2017; Liu et al. 2017), makes even this inference uncertain.

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