

Hips do not lie... histology of the pelvic girdle elements of *Metoposaurus* from the Late Triassic of Poland

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Abstract

The pelvic elements are among the least histologically studied skeletal elements of Temnospondyli, despite the fact that their histological framework can provide a lot of information about skeletochronology and function. One of the best histologically known taxon is *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów. To complete the histological studies of that taxon and obtain information about the intraskeletal variability, three ilia representing different ontogenetical stages and one ischium were sectioned. Microanatomically, all pelvic elements are porous, with a thin cortex, except for the midpart of the dorsal blade of the ilium. The dominating matrix type is coarse parallel-fibred bone, and growth marks are represented by thick zones and unusually thick annuli, always hosting few rest lines. Lines of Arrested Growth (LAGs) are not present. Sharpey's fibers are dense, especially laterally in the ilia. Typical for the ischium is a preservation of calcified cartilage. The histological framework is comparable to that known from long bones of the same taxon from the same size class representing similar growth patterns. The extended presence of calcified cartilage has already been described for intercentra indicating the slow ossification of the endochondral domain. Low compactness of all pelvic elements may suggest the reduced function of the pelvic girdle and hind limbs in locomotion of *Metoposaurus*.

Key Words

Growth marks, growth pattern, ilium, ischium, Krasiejów, palaeohistology

Introduction

The morphological change of the pelvic girdle was one of the key modifications crucial for the evolution of tetrapods, which relied more heavily on their hindlimbs for locomotion. In sarcopterygians, the pelvic girdle is a crescent-shaped bone (pelvis) attached to the body wall musculature and not to the vertebral column (Cole et al. 2011 and references therein), whereas in tetrapods the pelvic girdle (build from paired ilia, ischia and pubes) is connected via the sacral ribs to the vertebral column.

The tetrapod-type pelvis already appeared in *Tiktaalik rosae*, where the transitional fish-tetrapod

stage of the pelvis structure was recently described (Steward et al. 2024). While the construction of vertebrae in *Tiktaalik* is similar to fishes, its sacral rib processes are expanded and ventrally curved, likely indicating an attachment to the expanded iliac blade of the pelvis by ligamentous connection (Steward et al. 2024). The fully developed pelvis is present already in one of the earliest limbed tetrapodomorphs, *Ichthyostega* (Ahlberg et al. 2005; Pierce et al. 2012).

Among temnospondyls, the pelvis is composed of three bones: the paired ilia, ischia and when ossified, two pubes (Fig. 1A). The ilium is usually the first bone to ossify and in larval temnospondyls the only bone of the pelvic

girdle that is visible (Boy 1972, 1974, 1995; Schoch 1992, 2003; Witzmann and Pfretzschner 2003; Schoch and Witzmann 2024). Typically, the ilium has a posteriorly expanded dorsal blade which articulates medially with a single sacral rib and a ventral portion which bears the dorsal part of the acetabulum facet. The dorsal blade varies in the degree of its expansion not only between families but also within them; this is often evident in the ontogenetic stages of some temnospondyls (Bystrow and Efremov 1940; Schoch 1999; Sulej 2007; Rinehart and Lucas 2016). In most capitosaurids the dorsal iliac blade is rather short and stout, with the apex expanded anteroposteriorly, such as in *Paracyclotosaurus davidi* (Watson 1958) and *Parotosuchus pronus* (Howie 1970), whereas in *Eocyclotosaurus appetolatus* the dorsal blade is rather elongated and slim (Rinehart and Lucas 2016). In *Mastodonsaurus giganteus* the shaft bifurcates posteriorly (Schoch, 1999), which appears to be the plesiomorphic condition in tetrapods (Romer 1957; Jarvik 1996). In the small branchiosaurid *Tungussogyrinus bergi*, the dorsal blade is unusually extended anteriorly (Werneburg 2009), a character not known from any other temnospondyl (Werneburg 2009). Among Metoposauridae, the dorsal blade is unexpanded anteroposteriorly, similar to *Eocyclotosaurus*, but more massive in cross section (Dutuit 1976; Warren and Snell 1991; Sulej 2007). Ventrally, the ilium forms the wide, triangular shaped base, with a distinct edge of the acetabulum visible on the lateral side. Posteriorly, the ilium contacts the ischium. The ischia of temnospondyls are all roughly semicircular bones, with unfinished margins, except the dorsolateral edge. The variations in shape are not consistent within any of the Triassic families of temnospondyls (Warren and Snell 1991). During ontogeny, the ischium along with the scapula are the last elements to ossify in the pelvic and pectoral girdles respectively in eryopiforms, whereas in amphibamiform dissorophoids, the scapula and ischium ossify much earlier, at a similar time as the ilium and the interclavicle (Schoch 1992; Clack and Milner 2010; Schoch and Witzmann 2024). The pubis is the last element to ossify and indicates morphogenetic maturity of the pelvis. It is known only for the largest specimens of *Balanerpeton woodi* (Milner and Sequeira 1994), *Doleserpeton annectens* (Sigurdson and Bolt 2010), *Eryops megacephalus* (Pawley and Warren 2006), *Mastodonsaurus giganteus* (Schoch 1999), *Sclerocephalus haeuseri* (Schoch 2003; Schoch et al. 2007) and *Micropholis stowi* (Schoch and Rubidge 2005).

Among Eryopidae the pelvic girdle is massively built (Pawley and Warren 2006), whereas among Late Triassic Stereospondyli the simplification of the pelvis with size reduction of ilia and ischia is very distinct (Fig. 1A), especially when compared to their massive pectoral girdle (Schoch and Milner 2000; Mujal and Schoch 2020; Kalita et al. 2022).

Despite the importance of the pelvic girdle in the evolution of tetrapods with large changes in its size and morphology, it is one of the least studied elements of the

skeleton among early tetrapods. The main line of studies involving the pelvic characters focuses usually around the fin-limb transition stage, including sarcopterygian fishes and early Tetrapodomorpha (e.g. Ahlberg et al. 2005; Bosivert 2009; Don et al. 2013; Shubin et al. 2014; Esteve-Altava et al. 2019; Steward et al. 2024). Apart from the evolutionary significance of the pelvic girdle, there is very little research that goes beyond the actual morphology and links the shape to the function of the pelvis in early tetrapods. For example, Pierce et al. (2012) discussed the mobility of the hip joint of *Ichthyostega*, Molnar et al. (2020) investigated the hindlimb muscle anatomy across early tetrapods, and the dynamic simulation provided by Nyakatura et al. (2019) indicated that the stem amniote *Orobates* may have walked more like a *Caiman* (i.e., more erect) than a salamander. Among temnospondyls, Herbst et al. (2022) presented a novel method that enables the examination of full limb configurations rather than isolated joint poses and concludes that *E. megacephalus* may indeed have been capable of salamander-like hindlimb kinematics.

Equally rare are histological studies of the pelvic elements and any existing studies are limited only to temnospondyls. The histological study of ilium of the basal stereospondyl *Rhinesuchus* shows that this element preserved the greatest amount of Lines of Arrested Growth (LAGs) among all sectioned skeletal elements with the dorsal process of the ilium being the best approximation of minimum individual age (McHugh 2014). Contrarily, the ilium of *Panthasaurus maleriensis* studied by Teschner et al. (2020) does not show any growth marks, although the humerus exhibits clear growth marks. According to Teschner et al. (2020) this is a result of the high remodeling of the tissue due to the increased individual age of the bone. So far, no study has investigated the histology of the ischium among early tetrapods.

One of the best histologically studied taxa of Temnospondyli is *Metoposaurus krasiejowensis* from the Late Triassic of Poland (Sulej 2007). Almost all skeletal elements of *M. krasiejowensis* have been studied for their bone histology and microanatomy (Konietzko-Meier et al. 2012, 2014, 2018; Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Gruntmeier et al. 2016, 2019, 2021; Teschner et al. 2018, 2023; Kalita et al. 2022, 2025; Surmik et al. 2022), except for the pelvic bones.

Articulated skeletons of Metoposauridae, including pelvic elements, are known for *Dutuitosaurus ouazouli* from the Late Triassic of Morocco (Dutuit 1976), however, even then, it is challenging to determine accurately the orientation of the pelvic bones and position of the acetabulum because these elements are never found fully articulated. According to Dutuit (1976) the pelvis consists of two paired bones, ilium and ischium, which never co-ossified, and the acetabulum is located more anteriorly, whereas the pubis has been considered as cartilaginous. The numerous finds of *Metoposaurus* bones from Krasiejów also represent variably sized ilia and ischia but an ossified pubis has never been found. Thus, the pelvic girdle was

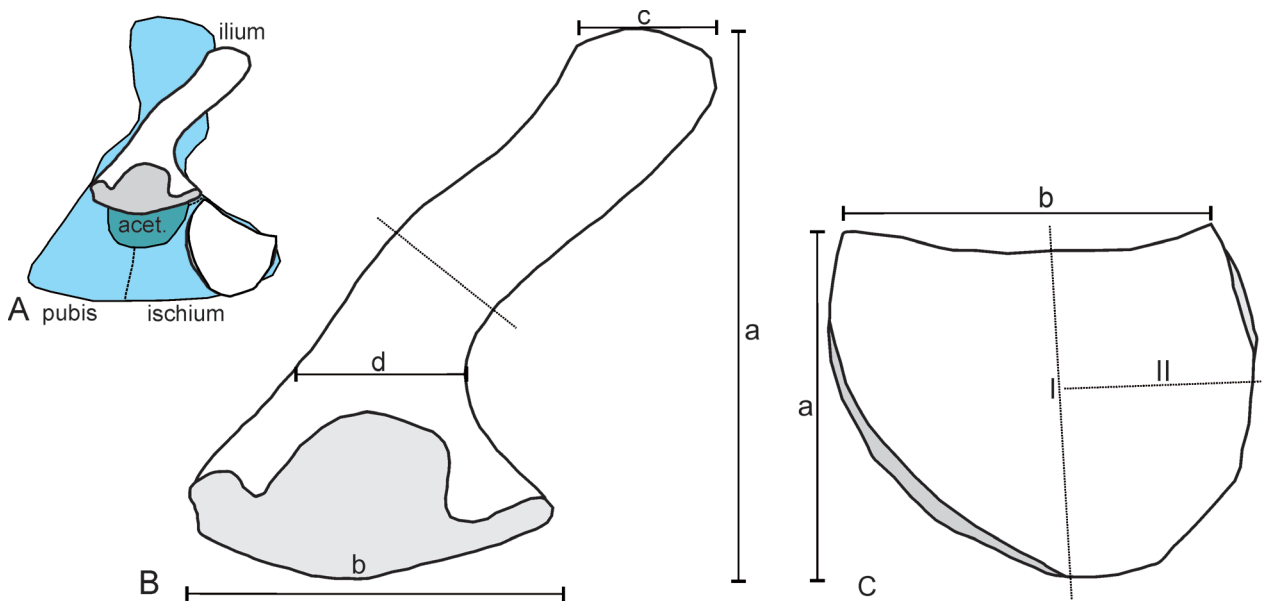


Figure 1. Schematic drawings of pelvic elements. **A.** The idealized reconstruction of the left pelvis of the Lower Permian *Eryops* sp. (based on Pawley and Warren 2006) in background (blue) and in the foreground the ilium and ischium of *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów; note the size and shape simplification of the pelvis among Stereospondyli when compared to *Eryops*; **B-C.** Pelvic elements of *Metoposaurus* as in A with marked measurements (see Table 1) and sectioning planes. **B.** Ilium; **C.** Ischium. Dropped lines and Roman numbers indicate the sectioning planes. Both bones are not to scale. **Abbreviation:** acet. – acetabulum.

reconstructed in a similar manner as for *Dutuitosaurus*, with only two bony elements (Sulej 2007).

In the light of the highly limited access to temnospondyl postcrania, it is worth testing pelvic bones for their relevance to skeletochronological analyses and for its environmental signal as a good substitution for long bones. Thus, the main goals of this study are to investigate the histology of the ilium and the ischium in order to evaluate the preservation of the growth marks in both pelvic elements relatively to other skeletal elements.

Material and methods

Three ilia (UOPB 00055, UOBS 02917 and UOBS 02916) and one ischium (UOPB 00037) from the Late Triassic of Krasiejów were sectioned (Table 1). The bones were assigned to *Metoposaurus krasiejowensis*, the most common temnospondyl taxon from this locality, based on the characters described by Sulej (2007; for morphological description see the results part). In Krasiejów the majority of metoposaurid bones are disarticulated, with the exception of very few elements like a fragment of the tail (Sulej 2007) or the pectoral girdle with articulated forelimb (Konietzko-Meier et al. 2020). The disarticulated state of preservation is a challenging issue when it comes to the reconstruction of the entire skeleton and the calculation of the proportions between body parts. The common method used in paleontology which helps to solve the problem of proportions is an estimation of missing dimensions based on measurements of known articulated fragments, if they are available, from given species and/or multiple articulated skeletons of closely related taxa to get the ratio between

elements (Sulej 2007; Bishop et al. 2020; Kalita et al. 2022; ElSafie 2024; Sullivan et al. 2024; and references therein).

The individual age of pelvic elements was calculated based on the amount of visible growth marks and the retrocalculation of the missing cycles (de Buffrénil et al. 2021a). To evaluate the intraskeletal variability, the calculated age of pelvic bones was compared to the age of femora belonging to the same class-size (Konietzko-Meier and Klein 2013).

The proportion between pelvic elements and between ilium and femur were estimated based on the numerous articulated skeletons of the closely related metoposaurid *Dutuitosaurus ouazzoui* from the Late Triassic of Morocco, (Dutuit, 1976; pers. obs. DKM). In *Dutuitosaurus* the length of the dorsolateral edge of the ischium is about 0.6 times of the total length of the ilium. The length of the ilium when compared to the femur is between 95% to 100% of the length of the femur. For this research the length of the ilium was taken as equal to the femur.

The ilia were sampled in the middle part of the dorsal iliac processes (Fig. 1B), where, according to McHugh (2014), the best record of growth marks is preserved. The ischium UOPB 00837 was sectioned perpendicularly to the dorsolateral edge (coronal plane – section I) and the remaining anterior part was sectioned parallel to the dorsolateral edge (transversal plane – section II) (Fig. 1C). Additionally, the ilium UOPB 00055 was micro-CT scanned in order to achieve information about the overall inner structure of the bone. The bone was scanned with a v|tome|x s scanner manufactured by GE phoenix|X-ray (Wunstorf, Germany), operated by the Bonn Institute of Organismic Biology, Section Paleontology, at the University of Bonn (Bonn, Germany).

Table 1. Measurements and age estimation of *Metoposaurus krasiejowensis* pelvic bones from the Late Triassic of Poland.

Col. Num.	Skeletal element	a (mm)	b (mm)	c (mm)	d (mm)	Estimated length of the femur ¹	Estimated age in years of the femur ²	Sequence of growth marks preserved in pelvic elements ³	Estimated age in years of the pelvic elements
UOBS 02916	ilium (right)	89,5	47,4	21,5	21	89,9 mm	4-5	-rem -1st a (rl)	4-5
UOPB 00055	ilium (right)	63	32	15,6	12,3	63 mm	2-3	-rem -1st z -1st a (rl) -2nd z -2nd a (rl)	3
UOBS 02917	ilium (right)	55,2	22,8/23*	17,2	11,0	55,2 mm	1	-rem -1st z -1st a	1-2
UOPB 00037	ischium (left)	34	37,5	–	–	62,5 mm	2	-rem -1st a -1st z -2nd a (rl)	2-3

The measured distances are marked on the Fig. 1. * – the apex of the basis is slightly broken, thus measured /reconstructed distance, ¹ – the proportions between ilium and ischium and the length of the femur were estimated based on the measurements taken by the first author on an articulated skeleton of *Dutuitosaurus ouazzoini* – housed at the MNHN Paris as well as from data published by Dutuit, 1976, ² – based on estimations from paper of Konietzko-Meier and Klein (2013), ³ – counted from the medullary region toward surface of the bone. Abbreviations: a – annulus, rem – remodeled region, rl – rest lines, z – zone.

The thin-sections were prepared according to the procedure described by Lamm (2013) with one exception: instead of silicon carbide paper to grind the thin section, a slush of silicon carbide grinding powder was used with grit sizes of 400 and 600. Furthermore, the sections were polished with a grit size of 800 and then covered with a coverslip. The microscope used for the observations of the sections was a LEICA DM LP polarizing light microscope with attached Canon EOS 2000D camera. The nomenclature used in the histological descriptions follows de Buffrénil et al. (2021b) and the morphological terminology is used after Sulej (2007).

Results

Morphological description

Ilium – The overall morphology of the three specimens is very similar, with a narrow dorsal iliac blade and a wide triangular base (Fig. 2A–F). The dorsal iliac blade is posteriorly inclined, especially in two smaller specimens (Fig. 2A–D) whereas in the largest specimen (UOBS 02916) the process is more straight with a slightly sinuoidal shape (Fig. 2E–F). In two specimens (UOBS 02917 and UOPB 00055) the shaft has a circular shape near its base, whereas in the largest one (UOBS 0216) it is more oval. In all specimens it gets elliptical and laterally flattened toward the dorsal apex. On the medial side, the process bears the internal oblique crest (*linea obliqua* sensu Sulej 2007) which is clearly visible in the largest specimen (Fig. 2E). This crest continues on the lateral side as an external oblique crest (Fig. 2D, F). The base of the ilia resembles an elongated triangle in ventral view with the posterior apex being the facet for ischium, and three edges, the lateral one bearing the acetabulum,

the short anterior one and a long, concave medial edge (Fig. 2A–F). The acetabulum is triangular and relatively high in the smallest specimen (Fig. 2B), while in the medium-sized individual it is still triangular but becomes proportionally wider at the bottom edge (Fig. 2D) and in the largest specimen the articulation facet is semicircular and much more horizontally elongated (Fig. 2F).

Ischium – The ischium (UOBS 00837) has a semicircular shape with the round edge facing ventromedially and the straight thin edge dorsolaterally (Fig. 2G, H). The bone is flattened along the mediodorsal-lateroventral axis, with its thickness gradually decreasing from the anterior part to the posterior one. The dorsolateral side is the thinnest part of the bone with a sharp and slightly concave edge which widens anteriorly. The remaining edges form a semicircular curve with roughened surface (Fig. 2G, H). The dorsomedial surface is roughened (Fig. 2G), possibly due to the presence of the vascular foramina, especially in the ventral part of the surface. The posterior part of this surface also has a clear albeit shallow depression, the *fossa externa* (Sulej 2007), while the anterior part is slightly more convex (Fig. 2G). The ventrolateral surface (Fig. 2H) is smoother than the dorsomedial one and along the dorsal part it possesses anterior and posterior depressions.

Histological description

Ilium – The smallest ilium UOBS 02917 has a nearly rounded cross-sectional shape with a very gentle rugosity visible on the lateral side of the section (Fig. 3A). The medullary cavity hosts large erosion cavities surrounded by a highly remodeled perimedullary region (Fig. 3A). That region gradually transforms into a mostly low vascularized primary cortex (Fig. 3B–F). The vascularization

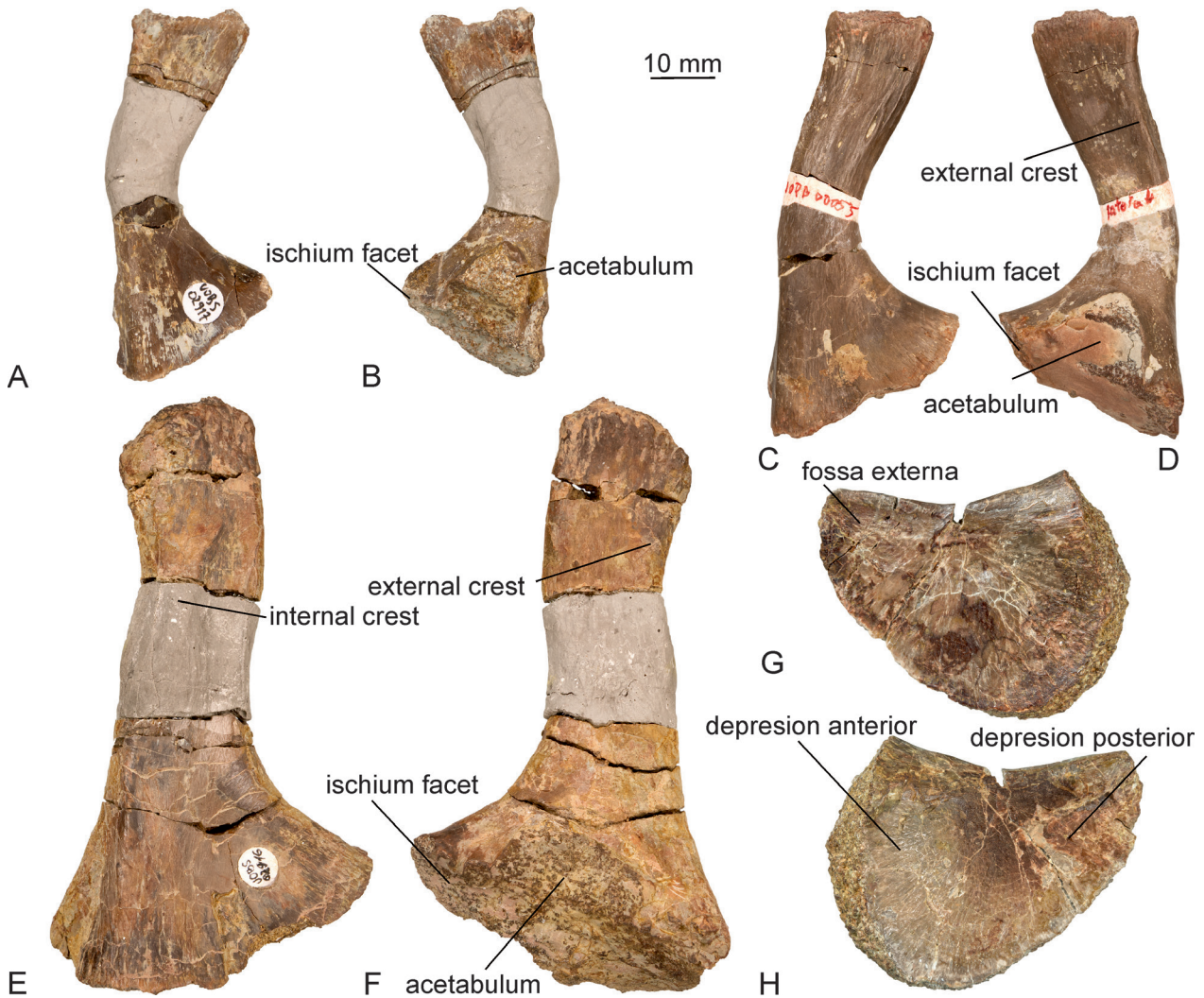


Figure 2. Ilium and ischium of *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów. **A, B.** Ilium UOBS 02917; **C, D.** Ilium UOPB 00055; **E, F.** Ilium UOBS 02916. **A, C, E.** In medial view; **B, D, F.** In lateral view; **G–H.** Ischium UOPB 00037; **G.** In dorsomedial view; **H.** In ventrolateral view.

is predominantly longitudinal, with secondary osteons dominating in the perimedullary domain, especially in the lateral part of the section (Fig. 3B). Rare, simple vascular canals are present in the primary region (Fig. 3B, D). Anteriorly, the vascular canals are irregularly scattered, whereas posteriorly and medially they are arranged in three rows, each separated by a thick avascular cortex (Fig. 3E). The remaining part of the cortex preserved deeper in the bone is the only fragment showing a moderate vascularization and low organized parallel-fibred bone with fine structure of collagen fibers (later named fine parallel-fibred type of the matrix) (Fig. 3E, F). The overall majority of the matrix is a high organized parallel-fibred bone, with thick collagen fibers (later described as a coarse parallel-fibred bone) and great inclusion of Sharpey's fibers, particularly developed on the lateral side (Fig. 3C, E, F). The change of the matrix type and vascularization density is the only expression of the growth cyclicity and could represent the zone and annulus (Fig. 3E). The minimum age of the specimen can be thus calculated as one year.

The micro-CT-scan of the ilium UOPB 00055 shows that the most compact part of the entire bone is the middle segment of the blade, whereas the base and the top of the blade are highly porous (Fig. 3G). The shape of the cross section of the middle-sized ilium UOPB 00055 is also roundish (Fig. 3H). The medullary region hosts few large secondary cavities surrounded by the perimedullary region moderately eroded with remains of primary matrix still visible between the secondary osteons and cavities (Fig. 3H–L). The overall size of the cavities is larger compared to the specimen UOBS 02917 (Fig. 3A). On the lateral side the matrix is fibrous through the entire thickness of the cortex, with only slight differences between zone and annuli (Fig. 3I–J). The perimedullary region transitions gradually into a strongly remodeled zone, then thick, avascular annulus which is followed by a second vascular zone and a second annulus (Fig. 3K, L). The matrix type varies between coarse parallel-fibred, which is typical for annuli and fine parallel-fibred bone typical for zones (Fig. 3M). The vascularization type changes from primarily secondary osteons present in the deeper

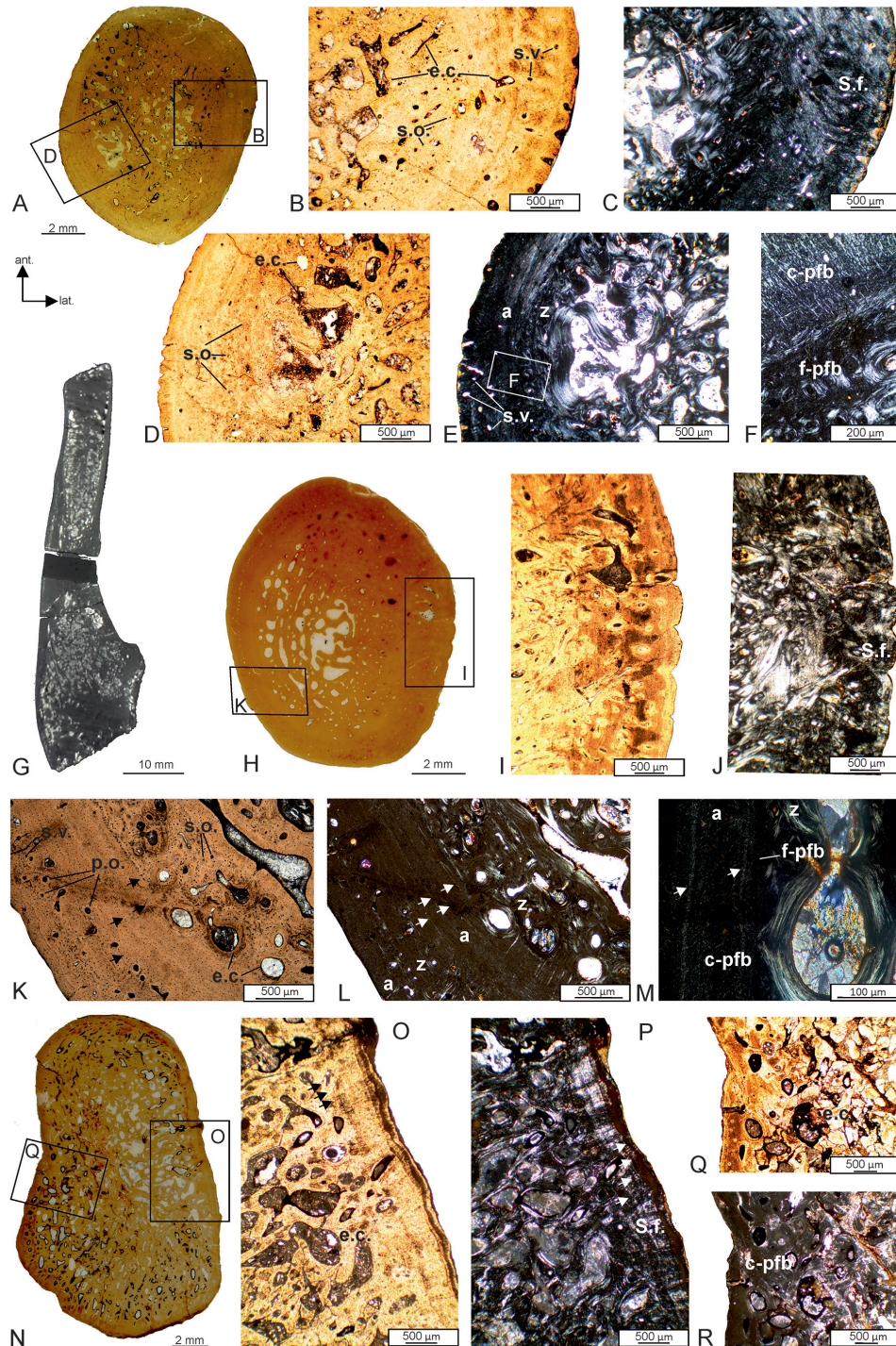


Figure 3. The histology of the midshaft of the ilia of *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów. **A-F.** Ilium UOBS 02917; **G-M.** Ilium UOPB 00055; **N-R.** Ilium UOBS 02916. **A.** Cross section of the iliac dorsal blade; **B.** Close-up of the lateral side of the section in A, image in plane polarized light; **C.** The same image as B, in cross-polarized light; **D.** Close-up of the medial edge of the section in A, in plane polarized light; **E.** Same image as D, in cross polarized light; **F.** Details of the matrix showing two types of collagen fibers organization, close up from E, in cross polarized light; **G.** Virtual longitudinal section of the ilium UOPB 00055 in posterior view; **H.** Cross section of the iliac dorsal blade; **I.** Close-up of the lateral side of the section in H, image in plane polarized light; **J.** The same image as I, in cross-polarized light; **K.** Close-up of the medial edge of the section in H, in plane polarized light; **L.** Same image as K, in cross polarized light; **M.** Details of the matrix showing two types of organization and rest lines; **N.** Cross section of the iliac dorsal blade; **O.** Close-up of the lateral side of the section in N, image in plane polarized light; **P.** The same image as O, in cross-polarized light; **Q.** Close-up of the medial edge of the section in N, in plane polarized light; **R.** same image as P, in cross polarized light. **Abbreviations:** a – annulus, ant. – anterior, c-pfb – coarse parallel-fibred bone, e.c. – erosion cavity, f-pfb – fine parallel-fibred bone, lat. – lateral, p.o. – primary osteons, s.o. – secondary osteons, S.f. – Sharpey's fibers, s.v. – simple vascular canals, z – zone, arrows indicate rest lines.

part of the cortex to simple, longitudinal vascular canals or primary osteons in the zone toward the outer periphery (Fig. 3K). Around the entire section numerous Sharpey's fibers are visible, with extreme representation on the lateral side (Fig. 3J). Growth marks are visible as two thick avascular annuli with few resting lines in each, separated by a vascular zone, and remains of the first zone preserved in the remodeled perimedullary region (Fig. 3L, M). The minimum age of the bone can be estimated as two years.

The largest ilium (UOBS 02916) is almost twice as large as the smallest one (UOBS 02917) (Table 1; Fig. 2). The cross section is distinctively larger compared to both smaller bones and elliptical in shape, with a well visible rugosity of the lateral surface (Fig. 3N). The entire bone shows an intensive remodeling, the primary coarse parallel-fibred cortex is limited only to the most external, thin, almost avascular layer, with only few secondary osteons visible in the posterior area (Fig. 3O–R). The remains of the primary cortex represent an annulus hosting few resting lines and numerous Sharpey's fibers (Fig. 3O, P).

Ischium - The cross section along the coronal plane has a shape of an elongated triangle with the top representing the dorsolateral edge and the wider bottom corresponding to the ventromedial edge (Fig. 4A). Most of the surface of the sections are occupied by trabecular bone, the cortex being limited to the top part of the section where it is the most prominent and gradually decreases in thickness towards the bottom (Fig. 4A–E). On the bottom edge of the section the trabecular bone is exposed, covered by calcified cartilage (Fig. 4F). Small islands of cartilage are also visible between the trabeculae in the bottom most part of the section (Fig. 4G). The trabeculae are clearly separated from the cortex (Fig. 4A, D, E). The erosion process is more distinct in the top region of the section, where there are fewer cavities located in the primary domain (Fig. 4A), whereas towards the bottom the erosion mostly occurs on the edge of the medullary cavity.

The primary matrix, similar to the ilia, varies between coarse, typical for a zone, and fine parallel-fibred bone, present in the annuli, with the fibers aligned dorsolaterally-medioventrally (Fig. 4E). Vascular canals in the form of longitudinal and plexiform primary and secondary osteons are present in the apex part of the section, whereas elongated simple canals are dominating close to the bottom of the section (Fig. 4A–E). Growth marks are the best expressed in the apex region as one zone and two annuli with resting lines, whereas the bottom cortex host only one annulus which continues from the top (Fig. 4E). Distinct, long Sharpey's fibers are present only next to the dorsolateral edge; the rest of the section exhibits short and gentle to nearly no Sharpey's fibers (Fig. 4C).

The transverse section of the ischium represents only the anterior part of the section with the widest edge corresponding to the anterior surface (Fig. 4H). Overall, the cortex is very thin and the section consists mostly of trabecular bone (Fig. 4H–J). The matrix is parallel-fibred with changing properties of fiber organization, from coarse

in the zones to fine in the annuli (Fig. 4J, L). Vascular canals are preserved mostly in the form of primary osteons or simple vascular canals (Fig. 4I, K). The vascularization pattern close to the cutting plane is more longitudinal (in coronal plane visible as elongated simple vascular canals) and elongated towards the anterior edge. The cortex of the lateroventral surface is relatively more vascular compared to the mediodorsal one, where the matrix is a highly organized parallel-fibred bone (Fig. 4I–L). Growth marks are best expressed as two annuli separated by one zone next to the central axis of the bone in the lateroventral wall. Towards the anterior edge the inner annulus and zone disappear gradually, and anteriorly only the external annulus is visible (Fig. 4J, L). The anterior surface is covered by calcified cartilage, and in addition, remains of that tissue are preserved between trabeculae (Fig. 4M, N).

Discussion

Morphological variability of pelvic elements

In general, the shape of the ilium is diverse within temnospondyls, and not only between families, but also within them, showing a great degree of intraspecific variation (Bystrow and Efremov 1940; Warren and Snell 1991; Schoch 1999; Sulej 2007; Rinehart and Lucas 2016, 2023). The problem is, however, the lack of systematic studies quantitatively evaluating the range and potential meaning of high intraspecific variation (Bystrow and Efremov 1940; Warren and Snell 1991; Schoch 1999; Sulej 2007; Rinehart and Lucas 2016, 2023). The only study quantitatively dealing with the skeletal variability is known for *Eocyclotosaurus appetolatus*, indicating a large individual variation of ilium metric characters (Rinehart and Lucas 2016). On the other hand, Rinehart and Lucas (2023) observed that the values of the distal angle of the dorsal processes in the ilia of *Koskinonodon* from the Lamy amphibian quarry aggregates in two clusters and thus this difference is rather a likely result of sexual dimorphism and not a random variability in the population.

Ontogenetically, the best studied variability of the ilia is known from that of *Benthosuchus sushkini* (Bystrow and Efremov 1940). Large forms have a marked anterior process in most specimens, but some smaller individuals may have an ilium which is almost identical to that of *Mastodonsaurus* with a posteriorly bifurcating shaft (Bystrow and Efremov 1940; Schoch 1999). In *Eryops* the three pelvic bones become fused as the animal ages with no discernible sutures separating the ilium, ischium, and pubis, and in very large specimens even the right and left elements seem to have co-ossified (Pawley and Warren 2006). The variability of *Metoposaurus krasiejowensis* pelvic elements has already been described by Sulej (2007) based on the numerous samples of ilia and ischia (2007). Sulej (2007) observed an overall high intraspecific variation of morphological characters, with few trends clearly representing ontogenetic changes,

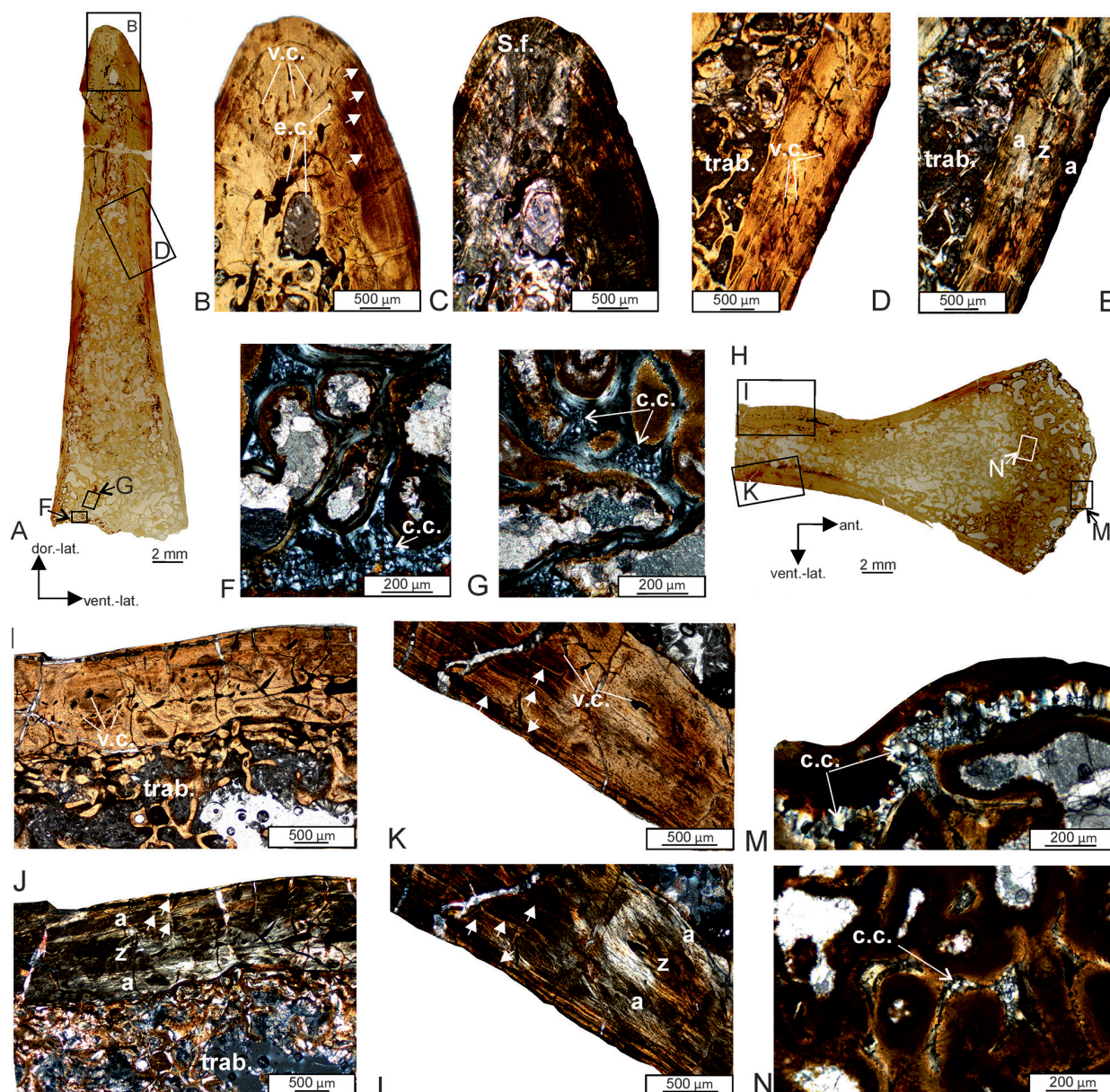


Figure 4. The histology of the ischium UOBS 00837 of *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów. **A–G.** Histological framework in coronal section (see Fig. 1, sectioning plane I); **H–N.** Histological framework in transverse section (see Fig. 1, sectioning plane II). **A.** Coronal section of the ischium; **B.** Close-up of the dorsolateral edge of the ischium in plane polarized light; **C.** The same image as B, in cross polarized light; **D.** Close-up of the cortical fragment from the lateroventral wall of the ischium, in plane polarized light; **E.** The same image as D, in cross polarized light; **F.** Fragment of the calcified cartilage layers on the ventromedial edge of the ischium; **G.** Islands of the calcified cartilage preserved between trabeculae; **H.** Fragmentary transverse section of the ischium showing the anterior half of the bone; **I.** Close-up of the dorsomedial side of the section in plane polarized light; **J.** The same image as I, in cross polarized light; **K.** Fragment of cortex from ventrolateral side, in plane polarized light; **L.** The same image as K, in cross polarized light; **M.** Fragment of calcified cartilage covering the anterior edge of the bone; **N.** Calcified cartilage located between trabeculae. **Abbreviations:** a – annulus, ant. – anterior, c.c. – calcified cartilage, dor-lat. – dorsolateral, e.c. – erosion cavity, S.f. – Sharpey's fibers, trab. – trabeculae, v.c. – vascular canals, vent.-lat. – ventrolateral, z – zone, arrows indicate rest lines.

like the ilium blade tending to be straighter in larger specimens with a wider dorsal end and the acetabulum varying from oval in small specimens to rectangular in the largest. Among ischia with the size increasing the fossa externa and an insertion for the interischial ligament become more indistinct in contrast to the small specimens (Sulej 2007).

The three ilia tested here fit well into the ontogenetic pattern proposed by Sulej (2007). The largest bone (UOBS 02916) has a more massive and straighter dorsal blade and a vertically elongated acetabulum when compared to the two smaller bones (Fig. 2). However, some other morphological differences can also be observed, especially between the smallest ilium (UOBS 02917) and the medium-sized

one (UOPB 00055) which exceeds the proposed range of ontogeny. The smaller bone (UOBS 02917) is slender with a relatively narrow base, the ratio between the height of the entire bone and the width of the base (Table 1) is about 2.4, whereas for the other two it remains under two. Moreover, the acetabulum in UOBS 02917 is very prominent with its height extending the length of its ventral margin as well as the width of the dorsal blade increasing dorsally more distinctively than in the other bones (Fig. 2, Table 1).

The overall intraspecific morphological variability can be triggered by many factors, like among others, ontogeny, environmental constraints, ecological adaptations, plasticity due to functional needs, sexual dimorphism or pathologies. For localities with at least two temnospondyl species co-occurring, as it is in Krasiejów with *Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius* (Sulej and Majer 2005; Dzik and Sulej 2007), the range of intraspecific variation can be additionally biased by taxonomical misassignment (Teschner et al. 2018, 2023). As long as the dermal elements of both taxa, independent of anatomical variation exhibit a diverse ornamentation pattern, the taxonomic assignment is mostly possible even for small bone fragments (Antczak and Bodzioch 2018; Prino et al. 2024), albeit the long bones can be difficult to differentiate (Teschner et al. 2023). The problem was already discussed by Teschner et al. (2023) indicating that, among others, the size is not a good proxy for taxonomical identification of disarticulated skeletal elements in bonebeds (Teschner et al. 2018, 2023). Teschner et al. (2018) studied a series of humeri of metoposaurs and recognized that the bones represented two different histotypes, the first showing the typical growth pattern of metoposaurs which includes thick annuli and rest lines and the second exhibiting a higher degree of vascularization and the absence of thick annuli. The proposed reasons for the variability were the separation of the populations in time and/or space and therefore being exposed to different environmental conditions which influenced the growth pattern. Later, after sampling the two equally large humeri belonging to a metoposaurus and a cyclotosaur, respectively represented two different growth models (Teschner et al. 2023), it was noted that some of the small humeri (showing the fast growing histotype) published earlier as *Metoposaurus* bones could indeed belong to *Cyclotosaurus*. The fact that some of the small ilia can indeed represent the juvenile forms of *Cyclotosaurus* was not considered by Sulej (2007). Thus, the possibility that the ilium UOBS 02917 belongs to a young cyclotosaur cannot be excluded, considering slightly different proportions and the shape of the dorsal process with an anterior-posterior expansion typical for capitosaurs rather than metoposaurids (Warren and Snell 1991). However, based only on the morphology, it is extremely speculative to conclude how important the observed morphological variations are on a taxonomic level, especially if the three described ilia herein represent a too small sample size and any other ilium of a certain *Cyclotosaurus* specimen is not known.

Histological variability of the pelvic elements

Whereas the assignment of disarticulated bones to a specific genus or species can be problematic due to morphological similarities, paleohistology holds the potential to come to the rescue (Hurum et al. 2006; Garilli et al. 2009; Redelstorff et al. 2014; Lomax et al. 2019; Nikolov et al. 2020; Perillo and Sander 2023; Teschner et al. 2023; Prino et al. 2024). The histology of temnospondyl bones is mostly known for aquatic forms and represents a whole range of histological patterns, from very compact, lamellar bone visible in the small *Apateon* (Sanchez et al. 2010a, b), moderately vascularized parallel-fibred in giant *Mastodonsaurus* (Sanchez et al. 2010c) to the highly porous tissue typical for the femur of *Plagiosuchus* (Konietzko-Meier and Schmitt 2014). It is interesting that within a particular group of temnospondyls of which the histology is known for multiple skeletal elements, the basic histological framework (tissue types, vascularization, extent of remodeling, growth marks pattern, etc.) seems to exhibit a common pattern across the entire skeleton, regardless of the type of bone (Witzmann and Soler-Gijón 2010; Konietzko-Meier et al. 2012, 2014; Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Sanchez and Schoch 2013; Konietzko-Meier and Schmitt 2014; Teschner et al. 2018, 2023). Thus, as it was presented by Teschner et al. (2023), the growth pattern can be, in specific cases, used as a supporting method to differentiate taxa on the genus level. The histology of *M. krasiejowensis* is well-known for different elements and in general is represented by a coarse parallel-fibred matrix with numerous Sharpey's fibers, moderate vascularization and unusually thick annuli with several rest lines alternating with thick zones and lack of Lines of Arrested Growth (LAGs) (Konietzko-Meier et al. 2012, 2014; Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Gruntmeier et al. 2016, 2021; Teschner et al. 2018, 2023; Kalita et al. 2022, 2025; Surmik et al. 2022). Especially, the thick annuli with the rest lines seem to be unique and are deposited as an answer to the local climate characterized by a relatively long unfavorable season, but not harsh enough to arrest the growth completely and create LAGs, as it is known from *Dutuitosaurus* (Steyer et al. 2004; Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Teschner et al. 2018). Interestingly, the phytosaurs and aetosaurs from Krasiejów also show a very similar growth pattern characterized by annuli with rest lines and lack of LAGs (Teschner et al. 2022).

Cyclotosaurus histology is known only from two large humeri originating from two localities, Bonenburg (Konietzko-Meier et al. 2019; Prino et al. 2024) and Krasiejów (Teschner et al. 2023). Moreover, two intercentra (Konietzko-Meier et al. 2014; Danto et al. 2016) and a fragmentary dermal bone (Kalita et al. 2022) are sampled from *Cyclotosaurus* from Krasiejów. Despite the low sample record and limitation mostly to large specimens, some basic differences on the histological level between these two taxa can be observed. Contrary to *Metoposaurus*, *Cyclotosaurus* from Krasiejów seems to have higher vascularized bones

(Konietzko-Meier et al. 2019; Kalita et al. 2022) with zones separated by thin annuli without rest lines (Teschner et al. 2023; Prino et al. 2024), fewer Sharpey's fibers and high organized parallel-fibred matrix (Teschner et al. 2023). Furthermore, Konietzko-Meier and Klein (2013) histologically tested numerous long bones from *Metoposaurus* and observed that one femur (UOBS 00643) did not fit into the growth series as its growth started with an annulus and showed a distinct Line of Arrested Growth (LAG) or a very thin annulus separating the cycles – a character not known for *Metoposaurus* – and concluded that despite the morphological similarity of all of the described femora, it most probably belongs to a different temnospondyl, likely to juvenile *Cyclotosaurus*. Considering the crucial differences between these two temnospondyl taxa on the histological level, the confirmation of the taxonomic affiliation based on histology should be possible.

Among bones tested here the growth pattern typical for *Metoposaurus* is present only by a middle-sized ilium (UOPB 00055) where growth marks are visible as two thick avascular annuli with few resting lines in each and two zones (Fig. 3L). The largest specimen (UOBS 02916) has a primary cortex preserved only rudimentarily as a thin layer with few rest lines (Fig. 3O–R). The structure of the primary tissue can be interpreted as a remnant of one annulus with rest lines and indicates that the bone belongs to an adult *Metoposaurus*. However, considering that the bone is very highly remodeled, the accumulation of lines in this case could be a signal of an external fundamental system (EFS) – in tetrapods the sign of achieving skeletal maturity (Cormack 1987). The morphology and advanced age of the bone rather support the *Metoposaurus* affinity of the ilium than *Cyclotosaurus*. The known humeri of cyclotosaurs with a total length of approximately 15 centimeters are showing still fast deposition of the cortex and low remodeling (Konietzko-Meier et al. 2019; Teschner et al. 2023; Prino et al. 2024), thus an ilium still small for *Cyclotosaurus* should rather not show indications for an advanced age. It is interesting that in the femur of a metoposaur similar in size to large ilium, the last two growth cycles are still well visible (Konietzko-Meier and Klein 2013), which indicates a more intensive remodeling rate of the pelvic elements.

The taxonomic affinity of the smallest ilium (UOBS 02917) is even more uncertain. Despite the surface of the cross-section being similarly large to the middle-sized bone, no clear growth marks are preserved, and no rest lines can be observed. The only fragment where a form of cyclical growth can be observed shows a change of matrix type from a fine organized parallel-fibred and moderately vascularized zone to a coarse parallel-fibred, almost avascular layer (Fig. 3B–F). Most probably this represents a remarkably thick annulus, interrupted only by few vascular canals. Konietzko-Meier and Klein (2013) observed a comparable growth pattern in a juvenile femur of *Metoposaurus* (UOPB 00052) and interpreted this as one zone with remains of incipient fibro-lamellar bone (FLB) and one annulus. In the femora, the remodeling is, however, less advanced and the FLB as an early juvenile tissue type in the smallest bone is still preserved, whereas in the ilium, due to remodeling the

first zone is only fragmentarily visible and the reconstruction of the FLB is not possible.

Considering all histological characters, like the lack of LAGs, high amount of Sharpey's fibers and coarse matrix, all three ilia sectioned here most probably represent an ontogenetic series of *Metoposaurus*. However, it shows as well that more intensive studies of the pelvic bones are necessary to distinguish between juvenile forms of *Cyclotosaurus* and adult metoposaurids.

Interestingly, the ilium of *Panthasaurus maleriensis* comparable in size (51 mm) to the described herein small bone UOBS 02917, shows a similar growth pattern (Teschner et al. 2020) – the central part of the bone is highly remodeled, and the primary cortex does not show any growth marks. Based on the relatively high degree of remodeling typical for advanced age and the lack of growth marks, normally present in long bones, the authors (Teschner et al. 2020) designated the bone as belonging to an old individual. Considering the observation of the growth of metoposaurid ilia from Krasiejów, it is highly probable that both bones, the small ilium described herein and the Indian specimen, indeed belong to juvenile metoposaurids and the growth marks are not well expressed not because of an advanced age and remodeling, but due to the juvenile age and the too short life span to deposit typical zones and annuli.

In our study, only one ischium was histologically sectioned, and its histological framework confirms that the bone belongs to *Metoposaurus*. Even if the annulus is much thinner than in the ilia, it is still massive when compared to the zone and it preserves rest lines. Interestingly the ischium shows preservation of calcified cartilage, which is present not only as a cover on the external surfaces, but also between the trabeculae (Fig. 4F, G, M, N). The thicker, secondary trabeculae are mostly present in the dorsolateral edge, and toward the edges the amount of calcified cartilage increases together with the thinning of the trabeculae. The remains of calcified cartilage preserved between the thin trabeculae suggest that these structures are endochondral trabeculae. The extended presence of the calcified cartilage late into ontogeny has been already observed within Stereospondyli intercentra (Konietzko-Meier et al. 2014) and in exoccipitals of *M. krasiejowensis* (Gruntmeier et al. 2016).

Intraskkeletal scaling of growth marks

Most of the skeletochronology studies are usually based on the long bones, especially femora, as they usually preserve the best record of growth marks due to easy morphology and early ossification. Among Temnospondyli the femora are rare and not always accessible for histological studies, thus it is important to test if other skeletal elements are informative enough for microanatomy and skeletochronology. McHugh (2014) proposed that the ilium is one of the bones which preserved the highest number of LAGs among all bones from one skeleton in the Permian temnospondyl *Rhinesuchus*.

Based on the presence of preserved growth marks in the form of zones and annuli and the estimated number of the growth marks lost through bone remodeling, the individual age of the smallest ilium (UOBS 02917) can be calculated up to two years (one cycle visible, one lost) and the middle-sized ilium (UOPB 00055) as three years (two cycles visible, one lost) (Table 1). The largest ilium (UOBS 02916?) preserved only a thin layer of the primary cortex with one annulus; however, the retrocalculation of the number of the missing cycles indicates that the total age could reach more than five years (Table 1). In the ischium the growth marks are not so distinct and due to the lack of comparative material it is impossible to estimate the amount of resorbed cycles. However, the scaling of the ischium size to that of the ilium based on the proportion of the *Dutuitosaurus* skeletons (Dutuit, 1976) indicates that the herein studied ischium fits well to the medium-sized ilium (UOPB 00055) and thus, its age can be counted as three years, with two cycles preserved and one estimated (Table 1).

In *Metoposaurus* the estimated number of cycles in the pelvic elements is very close to the age calculated for the correspondingly long femora (Table 1; Konietzko-Meier and Klein 2013). This stands in contrast to *Rhinesuchus*, where the number of cycles in the ilium far exceeds the number of cycles in the femur. McHugh (2014) explains this by the intense resorption in the femur and the relatively low intensity of this process in the ilia. It is as well not excluded that the amount of growth marks varies between taxa due to the different ontogenetic history of the skeleton, ossification sequence or function. It is important, as well to note, that calculations carried out here are based on unarticulated material, thus, further research is needed to calibrate the age estimation based on other elements like femora. However, the samples of *Metoposaurus* confirm the fact that the ilium is a bone with a well-expressed growth pattern.

Implication for function

The bone microstructure is not only a useful tool to interpret the mode of life of extinct taxa (Canoville et al. 2021), but indirectly it can be used to reconstruct the biomechanical loading of the bone, as bone loses strength and stiffness with increased porosity (Martin 1991; Currey 2012; Konietzko-Meier et al. 2018, and references therein). Additionally, an important source of information are Sharpey's fibres. Sharpey's fibres are considered the anatomical structures integrated into the muscles and their presence and distribution can be used as evidence of muscle attachment in extinct and extant forms (Pereyra et al. 2019).

The entire ischium shows osteoporotic conditions (Fig. 4A, H). The cortex is present only as a thin layer, and the entire bone is filled by thin trabeculae. The high porosity of the bone and the Sharpey's fibers limited only to the dorsolateral edge indicate the low biomechanical load on the ischium. Typical for the ischium is also the presence of calcified cartilage (Fig. 4F, G, M, N), which covers the rough surfaces suggesting the cartilage

expansion of the bone and connection to the unossified pubis as suggested by Dutuit (1976).

Based on micro-CT data the ilium of *Metoposaurus* also shows osteoporotic conditions with the most compact bone restricted to the middle part of the blade (Fig. 3G). It is different from *Rhinesuchus*, in which the entire bone has a low porosity with the most porous part in the middle of the process (McHugh 2014). The fibrous lateral side of the ilium with numerous Sharpey's fibers indicates a strong attachment of muscles (Molnar et al. 2018). Apart from that, the ilium similar to the ischium seems not to be adapted to a high stress.

The histological framework of the pelvic elements supports the results of the trackway analyses suggesting that among metoposaurids the hind limbs were less involved in underwater locomotion than the forelimbs (Mujal et al. 2020, 2023) or the tail (Konietzko-Meier et al. 2012).

Conclusions

The histological characters of pelvic elements of *Metoposaurus krasiejowensis* from the Late Triassic of Krasiejów are similar to those known from its long bones (Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Teschner et al. 2018, 2023). The dominating type of matrix is a coarse parallel-fibred bone with a large amount of Sharpey's fibers. Vascularization is moderate in zones to low in annuli. Characteristic for annuli are rest lines, known also from other skeletal elements. It is important that the number of estimated growth marks in ilia, ischia and femora from the same size-class are very similar. It makes them useful elements for skeletochronological studies, especially ilia. On a functional level, the high amount of Sharpey's fibers indicate a strong muscle connection on the lateral side of the ilia, but less developed on the medial side and in the ischium. The low density of all of the bones may suggest low biomechanical loading of the pelvis and thus allows indirectly to draw conclusions about the less significant function of the hind limbs in locomotion. However, it is important to note that the bones studied here were not articulated and thus future analyses including more specimens and/or articulated skeletons should be carried out.

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