


Variability of growth pattern observed in *Metoposaurus krasiejowensis* humeri and its biological meaning

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Abstract

Purpose Histological studies on temnospondyl amphibian bones remain rare. A systematic revision of the histology was applied for the purpose of testing the histovariability in the humeri and becoming new information about the growth pattern.

Methods The present study includes 12 humeri of *Metoposaurus krasiejowensis*, which originate from the Late Triassic clay pit near Krasiejów, southwestern Poland. The specimens were scanned with a microCT and the histological thin-sections have been obtained with the standard petrographic method.

Results The evaluation of the studied bones shows a uniform growth series resulting in one morphotype. Strikingly, the histological analysis reveals a greater diversity with two different histotypes: Histotype I shows a distinct differentiation between alternating zones and annuli with poor to moderate vascularization and increase of bone remodeling during growth. Histotype II does not show any distinct zones and annuli but is characterized by a high vascularization and fast growth coexisting with an extensive bone remodeling.

Conclusions Based on these two different growth patterns, several hypotheses can be established: The specimens do not show any pattern of histological variation; humeri

represent a taxonomic diversity; the analyzed *Metoposaurus* bones stem from two different populations separated by space and; or time or sexual dimorphism.

Keywords *Metoposaurus krasiejowensis* · Temnospondyli · Krasiejów · Bone histology · Humeri · Micro-CT

Resumen

Objetivo Los estudios histológicos sobre anfibios temnospondilos siguen siendo poco frecuentes. Se ha aplicado una revisión sistemática de la histología con el fin de probar la histovariabilidad en los húmeros y así conseguir nuevas informaciones sobre el patrón de crecimiento.

Métodos El presente estudio incluye 12 húmeros de *Metoposaurus krasiejowensis*, procedentes del arcillar del Triásico Superior próximo a Krasiejów, al suroeste de Polonia. Las muestras se escanearon con un microCT y las secciones finas histológicas se obtuvieron mediante el método petrográfico estándar.

Resultados La evaluación de los huesos estudiados muestra una serie de crecimiento uniforme que da como resultado un único morfotipo. Sorprendentemente, el análisis histológico revela una mayor diversidad con dos histotipos diferentes: el Histotipo I muestra una diferenciación clara entre las zonas alternas y los annuli con una vascularización pobre a moderada y un aumento de la remodelación ósea durante el crecimiento. El Histotipo II no muestra zonas y annuli distintivos, pero se caracteriza por una alta vascularización y un rápido crecimiento que coexisten con una extensa remodelación ósea.

Conclusiones Sobre la base de estos dos patrones de crecimiento diferentes, se pueden establecer varias hipótesis: los especímenes no muestran ningún patrón de variación histológica; los húmeros representan una diversidad

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taxonómica; los huesos de *Metoposaurus* analizados se derivan de dos poblaciones diferentes separadas por el espacio y/o tiempo o dimorfismo sexual.

Palabras clave *Metoposaurus krasiejowensis* · Temnospondyli · Krasiejów · Histología ósea · Húmeros · Micro-CT

1 Introduction

Temnospondyli Zittel, 1888 is a large and diverse clade of amphibians which range from the Early Carboniferous (e.g. Holmes and Carroll 1977) to the Early Cretaceous (Warren et al. 1997). They occupied various ecological niches, including aquatic, semi-aquatic and terrestrial habitats (Lindeman 1991; Schoch 2014). Their fossilized remains have been found all over the world, and show a high diversity in size and morphology.

Metoposaurids, included in Trematosauria (Fortuny et al. 2017; Schoch 2013), are limited to the Late Triassic but are known from several continents (Schoch 2014; Steyer et al. 2011). In Europe, metoposaurid remains are preserved in Southern Germany (Fraas 1913; von Meyer 1842), Poland (Dzik and Sulej 2007; Dzik et al. 2000) and Portugal (Brusatte et al. 2015; Witzmann and Gassner 2008). According to Brusatte et al. (2015), two genera and five species can be distinguished within Metoposauridae: *Metoposaurus diagnosticus* (von Meyer 1842), *Metoposaurus maleriensis* (Chowdhury 1965), *Dutuitosaurus ouazzoui* (Dutuit 1976), *Metoposaurus krasiejowensis* (Sulej 2002) and *Metoposaurus algarvensis* Brusatte et al. 2015. Brusatte et al. (2015) argue that the Polish *M. diagnosticus krasiejowensis* and the German *M. diagnosticus diagnosticus* (sensu Sulej 2002) should not be regarded as subspecies but as separate species (*M. diagnosticus* and *M. krasiejowensis*), a taxonomy which is followed here.

Histological analyses of the postcranial skeleton of Temnospondyli are usually based on long bones, vertebrae or dermal bones (de Buffrénil et al. 2016; Canoville and Chinsamy 2015; Damiani 2000; Gee et al. 2017; Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; Konietzko-Meier and Schmitt 2013; Konietzko-Meier et al. 2012, 2014, 2016; McHugh 2014; Mukherjee et al. 2010; Ray et al. 2009; de Ricqlès 1979; Sanchez and Schoch 2013; Sanchez et al. 2010a, b; Steyer et al. 2004; Witzmann 2009; Witzmann and Soler-Gijon 2010). However, only two histological studies are applied on humeri (Konietzko-Meier and Sander 2013; Mukherjee et al. 2010).

Mukherjee et al. (2010) described four humerus fragments (belonging to an indeterminate temnospondyl,

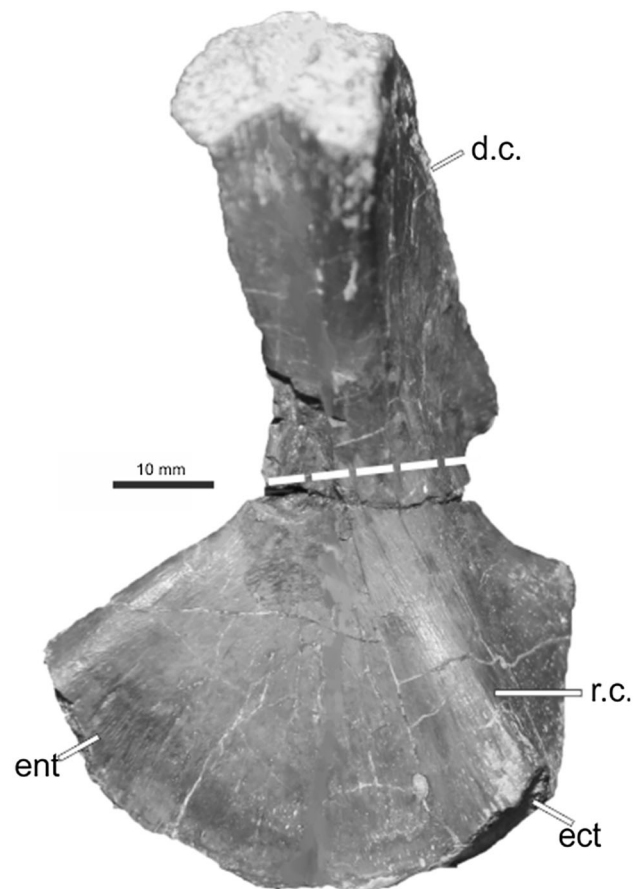


Fig. 1 Morphology of *Metoposaurus krasiejowensis* humerus (UOPB 00109) in dorsal view. The white dashed line indicated the approximately plane of section. *d.c.* deltopectoral crest, *ect* ectepicondyl, *ent* entepicondyl, *r.c.* radial crest

Trematosauridae, Paracyclotosauridae and Chigutisauridae) and suggested that the separate histological frameworks represent taxon-specific environmental adaptations and growth patterns. Konietzko-Meier and Sander (2013) analyzed postcranial fossil material including three humeri of *Metoposaurus krasiejowensis* and pointed out a high histological variability and the lack of clear growth pattern in the forelimb in contrast to the more uniform pattern typical for femora. Contrary to the simply-shaped femur, the anatomy of the humerus is more complicated. It is a short tetrahedron showing a clear torsion between the proximal and distal epiphyses with a short shaft and markedly widened at both ends (Fig. 1). The complex shape requires the intensive modeling process during growth and this may limit the preservation of the skeletochronological information. So far, it is not clear if and how the morphogenesis influences the histological framework and thus if the observed variability has a methodological reason (different sectioning planes) or if the humeri do not preserve a growth pattern due to their complicated shape and short bone shafts. These two

Table 1 Exact measurements of the humeri, including histotypes and the amount of visible and estimated cycles

Specimen	Bone length (mm)	Proximal width (mm)	Distal width (mm)	Midshaft width (mm)	Percentage of longest preserved bone (%)	Histotype	Amount of cycles	
							Visible	Estimated
UOBP 00033, R	59.7	23.3	–	21.8	56	I	2	3
UOBP 00034, L	67.1	24.7	43.5	16.2	62	I	1	1
UOBP 00109, L	69.2	26.5	43.4	22.1	64	I	2.5	3.5
UOBS 00777, L	71.4	24.3	42.9	21.9	66	I	2	3
UOBP 00036, R	76.3	26.9	49.5	27.4	71	I	3	4
UOBS 01418, L	80.3	29.1	48.2	23.3	75	I	3	4
UOBS 00494, L	82	28.8	–	22.2	76	I	2	4
UOBP 00113, L	64.9	25.5	–	20.8	60	II	1.5	1.5
UOBS 00574, L	65.4	24	36.1	20.5	61	II	1.5	1.5
UOBP 00108, R	67.2	27.4	44.1	22.3	63	II	1	2
UOBS 00126, R	82.6	30.7	53.4	24.2	77	II	2	2
UOBP 00110, R	–	31	52.4	–	77.2	II	2	3

Specimens are ordered by bone length for Histotype I and Histotype II. All measurements were taken with a sliding caliper. The bones are sorted by length; *R* right humerus, *L* left humerus. Percentage of longest preserves bone refers to ZPAL III 830 (107.5 mm, Barycka 2007)

characters require intensive bone modeling during ontogeny and caused adaptive process for changing a bones' size, shape, and position of midshaft during growth, thus the earliest deposited tissue could be destroyed because of intensity of this process (bone resorption and deposition) necessary to change the shape of bone.

In the light of the highly limited access to temnospondyl postcrania, it is important to test metoposaurid humeri for their relevance to skeletochronological analyses, i.e., assessing if the humeri show any observable growth pattern and environmental signal.

2 Materials and methods

2.1 Geological setting and locality

The clay pit in the vicinity of the village Krasiejów in southwestern Poland (50°39'54"N, 18°16'33"E) preserves two main bone-bearing horizons with both aquatic and terrestrial faunal elements (Bodzioch and Kowal-Linka 2012; Dzik et al. 2000). The sediments have been dated to the lower Norian (Racki and Szulc 2015). Krasiejów mainly preserves disarticulated vertebrate fossils which were sorted during mass catastrophic events caused by off-running rain water (Bodzioch and Kowal-Linka 2012; Szulc 2005, 2007).

Metoposaurus krasiejowensis is the most abundant taxon; less numerous is the second temnospondyl amphibian, *Cyclotosaurus intermedius* Sulej and Majer 2005. Apart from amphibians, several reptiles have also been excavated in the Krasiejów pit; In addition the quarry preserves also invertebrate material and plant remains (Brusatte et al. 2009; Dzik 2001, 2003; Dzik and Sulej 2007; Dzik et al. 2000; Sulej 2005, 2010).

2.2 Material

All here studied specimens have been collected exclusively from the lower bone-bearing horizon and are part of the collections of the Department of Biosystematics, Opole University (UOPB—new catalog system; UOBS—old catalog system). For this study, 12 humeri of *Metoposaurus krasiejowensis* were analyzed (Table 1). Specimens UOBS 00574, UOPB 00034, UOPB 00108, UOPB 00109, UOPB 00036, UOBS 01418 and UOBS 00126 were completely preserved. Specimens UOPB 00033, UOPB 00113, UOBS 00777 and UOBS 00494 had destroyed distal ends, whereas specimen UOPB 00110 had both ends well-preserved but was broken into two halves (Table 1). Nevertheless, based on the proximal ends width, it is possible to determine that specimen UOPB

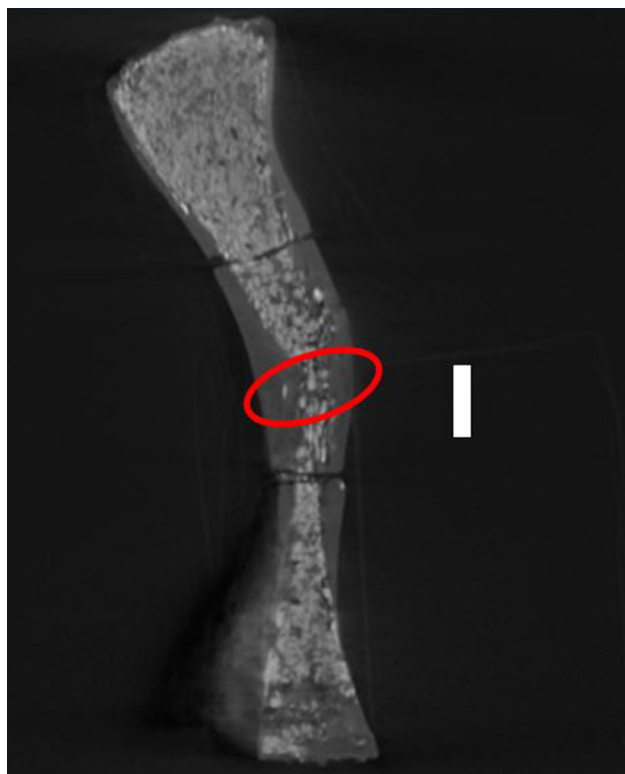


Fig. 2 Histological midshaft of the *Metoposaurus krasiejowensis* humerus (UOPB 00113) visible in the micro-CT-scanned specimen; the circle indicates the position of the histological midshaft which represents the most complete bone growth record. Image taken with the program VG Studio MAX. Scale bar equals 1 cm

00033 is the smallest one in the series, while specimen UOBS 00494 with its massive proximal end is the largest.

2.3 Measurements

After mechanical preparation, the bone length, the width of proximal and distal ends, and the midshaft width were measured (Table 1). The here used series of humeri range from 56 to 82.6 mm in length. Percentage of the length of the largest known *Metoposaurus krasiejowensis* humerus (ZPAL AbIII830; 107.5 mm—Barycka 2007), was calculated for each bone of this study (Table 1). The smallest specimen used in this study is also the smallest known preserved humerus of *M. krasiejowensis*. Specimen UOBS 00126 is the largest completely preserved bone in the present series with a length of 82.6 mm, which represents only 77% of the largest described *Metoposaurus* humerus (Table 1).

2.4 Micro-CT-scanning

To determine the exact sectioning plane the specimens were scanned with a high-resolution micro-computed

tomography scanner (μ CT) with a vltomelx s system by GE phoenixIX-ray at the Steinmann Institute in Bonn. Objects were scanned using a 240 kV X-ray tube. The data was processed and bundled into image stacks with VG Studio MAX 2.0 software by VOLUME Graphics GmbH. Finally, the data were transformed into a volumetric representation of the structure (Konietzko-Meier and Schmitt 2013). Using these generated three-dimensional models, the exact position of the histological midshaft was determined (Fig. 2), which varies for each single specimen and therefore has not been estimated as the halfway point between two epiphyses. The midshaft region has been chosen as it preserves bones' most complete growth record (Klein and Sander 2007, 2008).

2.5 Thin-sectioning

Thin-sections were done at the Steinmann Institute laboratory in Bonn, Germany according to the standard petrographic method (Lamm 2013—modified and Stein and Sander 2009—modified).

All bones listed in Table 1 were cross-sectioned at the plane of the micro-CT-determined midshaft. For the evaluation of the sections, a LEICA DM EP light microscope with normal transmitted and polarized light was used. Pictures were taken using a LEICA DFC420 digital camera attached to the microscope.

2.6 Estimating the number of eroded cycles

For the estimation of the number of missing growth marks the method of retrocalculation, which is based on the superimposition method (Bybee et al. 2006; Castanet et al. 2003; Leclair and Castanet 1987; Sanchez et al. 2010b) was performed. First, the number of growth marks in the morphologically smallest specimens was calculated for each Histotype separately (for Histotype I based on UOPB 00033 and for Histotype II based on UOPB 00113) and then fitted into the medullary cavity of the larger individuals. Based on this interpolation the number of eroded growth cycles was determined.

2.7 Terminology

Morphological terminology follows Barycka (2007) and Sulej (2007); the histological description is based on the definitions used by Francillon-Vieillot et al. (1990), except for the annuli that follow the definition used by Konietzko-Meier and Sander (2013). According to Francillon-Vieillot et al. (1990), an annual growth cycle consists of a zone and an annulus and ends in a line of arrested growth (LAG). In the current study, the term zone is used as in its traditional meaning for the highly vascularized layer, with a lower

organization of collagen fibers. The term annulus refers to the poorly vascularized layer and a higher organization of collagen fibers, but usually with a similar thickness as a zone. In the studied material, no annual LAGs occur, instead of adjacent to the annuli, numerous lines are present, which are referred to in this paper as rest lines. In some specimens, very thin lines occupy the space between rest lines, these are named additional lines.

3 Results

3.1 Micro-CT-imaging

All 12 humeri scans show that the histological midshaft (Konietzko-Meier and Klein 2013), a region with the most complete growth record (Klein and Sander 2007), is not in the arithmetical half of the bone length. It is interesting to mention that the sectioning plane is not perpendicular to the bones' longitudinal axis but always at a tilted angle (Fig. 2). The position of the nutrient canal of the humeri is not visible in the scanned bones. The midshaft region is very short and the amount of spongy bone in the whole bone is predominant over the compact bone.

3.2 General histological description

The cross-section of the humeral diaphysis is triangular in shape, with the apex of this triangle oriented dorsally and representing the radial crest. The flanks are more elongated and the shorter side is pointing out posteriorly (Fig. 3a).

In the cross-sections, the medullary region is filled with a network of secondary trabecular bone and is surrounded by the primary and secondary cortex. The cortex is the thickest on the dorsal side and the transitional region between the cortex and trabecula is difficult to trace (Fig. 3a). Parallel-fibred bone is the predominant bone tissue type in the cortex, higher organized in annuli and less organized in zones (Fig. 3c, f). Lamellar bone is preserved only as an infilling of the osteons (Fig. 3c, f). Two types of layers with different histological framework are visible. The layers with less organized collagen fibers and highly vascularized represent faster growing zones. Additionally, they are almost always wider than the annuli (Fig. 3b, c). In the innermost zone longitudinal vascular canals are predominant (Fig. 3d), whereas, in the outermost zone, the canals are more plexiform-shaped (Fig. 3e). Only in the anterior tip of each section, in the outermost zone the vascular canals are small and longitudinal in form whereas, in the innermost zone, the vascular canals are more plexiform shaped. On the dorso-anterior side in all zones, the second type of canals, which is radially oriented, is often preserved. In the outermost zone, primary osteons

predominate over secondary ones (Fig. 3d, e). Annuli are almost avascular or preserve a single row of vascular canals (Fig. 3a–c).

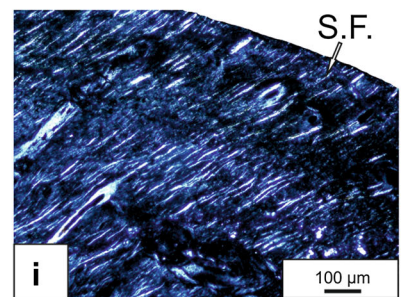
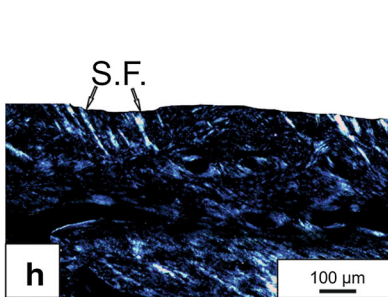
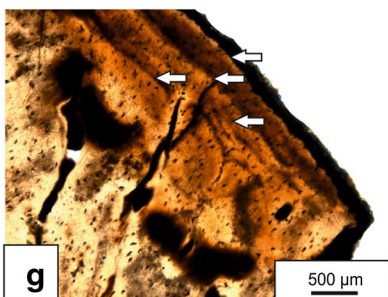
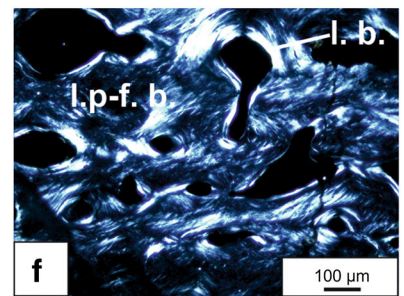
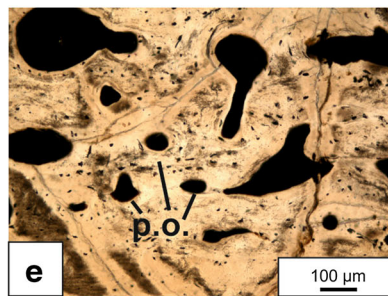
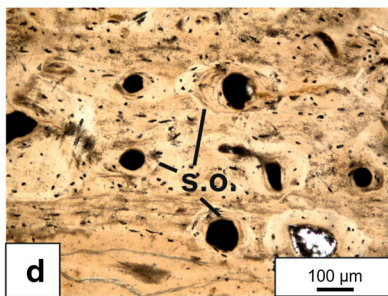
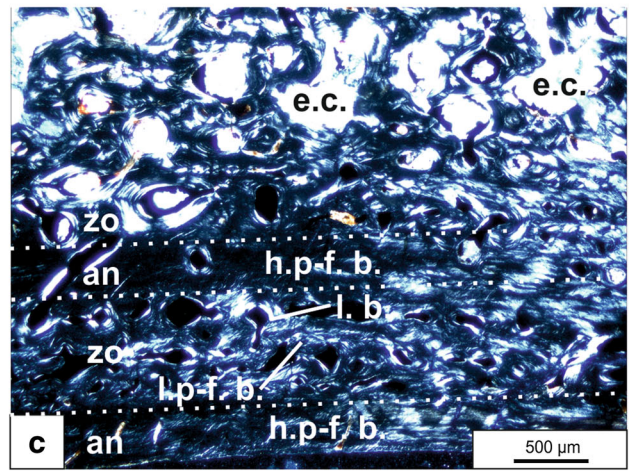
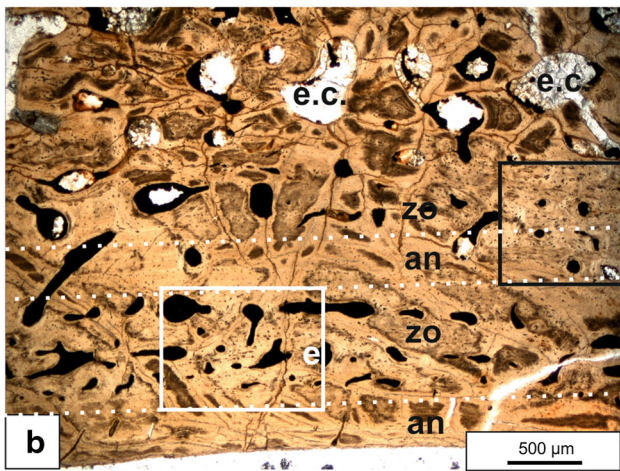
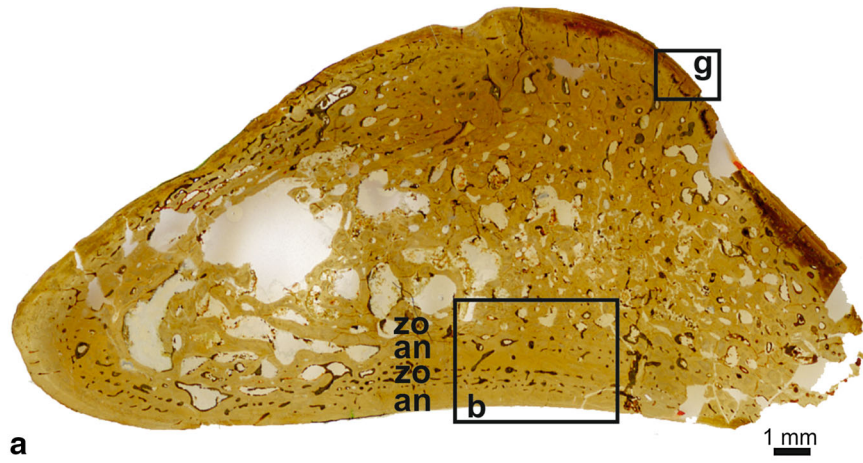
Numerous thin resting lines are visible in the outermost annulus (Fig. 3g), but their amount varies in each bone. They are the most distinctive in specimens UOPB 00033 and UOBS 00777 occurring within an annulus close to the bones' surface but in this specimen also in the inner annulus. In specimen UOPB 00036 they are not visible. Additionally very common in the sections are Sharpey's fibers. Two types of them can be observed there: shorter, fringed ones that occur only in the bones' outer margin (Fig. 3h), and elongated and slender ones which reach deep into the cortex (Fig. 3i).

In all bones, the remodeling degree increases with the bones' length. In some specimens (UOPB 00108, UOBS 00126 and UOPB 00110) the cortex is highly remodeled showing secondary osteons and erosion cavities reaching close to bones' surface.

3.3 Histotypes

Evaluation of histological structures seen in the growth series and the bone remodeling indicate that the humeri represent two different growth patterns (histotypes). Histotype I (Fig. 3), representing by specimens UOPB 00033, UOPB 00034, UOPB 00109, UOBS 00777, UOPB 00036, UOBS 01418 and UOBS 00494, shows a distinct alternation of zones and annuli; the vascularization in the zones is moderate and there is an increasing degree of remodeling visible in the bone series from the smallest to the largest specimen. In the inner zone, the vascularization degree is poor to moderate; the vascular canals are more disorganized and plexiform or reticular in orientation, whereas the outer zone possesses longitudinal canals. Bone erosion occurs only in the perimedullary region.

In Histotype II visible in specimens UOPB 00113, UOBS 00574, UOPB 00108, UOBS 00126 and UOPB 00110, the most characteristic feature is the high vascularization of the cortex (Fig. 4). The clear alternation of zones and annuli is not visible; instead, there is a wide zone divided into two sublayers with a variation in the organization of vascular canals (Fig. 4a). There is a change of the shape of the vascular canals observed in the zone: the canals are circular oriented in the inner part and more longitudinal and reticular towards to the outer cortex (Fig. 4b, c). In the layer with more longitudinal canals the matrix is higher organized, whereas the layer with plexiform canals represents lower organization of collagen fibers (Fig. 4b, c). The primary and secondary osteons are present in both layers (Fig. 4d, e). Additionally, the erosion occurs as large erosion cavities not only in the perimedullary region but also throughout the rest of the cortex



◀**Fig. 3** The microstructural (a) and histological (b–i) details of *Metoposaurus krasiejowensis* humeri UOBS 00494 representing Histotype I; **a** microstructure of the midshaft; **b** close-up of fragment of cortex from image **a** with alternation of zones and annuli, image in normal light; white, dropped lines mark the border between zones and annuli; **c** the same as **b** but in polarized light, note the different organization of parallel-fibred bone in zones and annuli; **d** details of inner zone with the longitudinal arrangement of vascular canals with domination of secondary canals, image in normal light; **e** details of external zone with plexiform canals, note the domination of primary osteons, image in normal light; **f** same like **e** but in polarized light showing details of lamellar and parallel-fibred bone; **g** numerous resting lines visible in outermost part of the cortex (white arrows), image in normal light; **h** white arrows indicate the exemplary short, finger-like Sharpey's fibers; **i** long Sharpey's fibers (indicated by white arrow). *an* annulus, *e.c.* erosion cavity, *h. p-f.* high organized parallel-fibred bone, *l. b.* lamellar bone, *l. p-f. b.* low organized parallel-fibred bone, *p.o.* primary osteons, *S.F.* Sharpey's Fibers, *s.o.* secondary osteons, *zo* zone

(Fig. 4a, b). The outermost cortex preserves an extremely thin annulus that cannot always be trailed in the entire section (Fig. 4a–c). On the ventral side the accumulation of numerous resting lines is visible (Fig. 4f). In specimen UOPB 00110 in the deeper part of cortex a second, extremely thin and avascular annulus is preserved, which separates a thick zone.

3.4 Estimation of the number of growth cycles

The count of visible growth cycles gives an individual age between 1 and 2 up to 3 years for humeri of both histotypes (Table 1, Fig. 5).

Applying the retrocalculation method, however, it was possible to estimate the number of remodeled cycles for each specimen (Table 1). Specimens UOPB 00033, UOBS 777 and UOPB 00110 show two preserved growth marks, with one additionally estimated cycle. In specimens UOPB 00036 and UOPB 01418, which preserve three growth cycles, one additional cycle can be estimated. Consequently, the individual age is estimated—to be between 1 and 4 years in specimens from Histotype I and 1.5 and 3 years in specimens from Histotype II (Table 1). However, the clear difference is visible between two histotypes; the bones representing Histotype II reach the given length 1 year earlier (Fig. 5).

4 Discussion

The *Metoposaurus krasiejowensis* humeri analyzed here represent a uniform morphotype, which was already described earlier by Sulej (2007) and Barycka (2007). Based only on morphological features all bones studied here belong to the same growth series showing a robust, thick proximal and a rather thin, fan-shaped distal head as well as a very prominent radial crest (Fig. 1).

The morphological stability of humeri contrasts with the morphology of the femora from the same locality, where two different morphotypes have been distinguished: one robust, X-shaped type, and one slender type with a longer shaft and a prominent distortion (Konietzko-Meier and Klein 2013). Despite the lack of morphological variability among humeri, different growth pattern can be observed at a histological level, contrary to an almost uniform histological framework in the hind limb bones (Konietzko-Meier and Klein 2013). Konietzko-Meier and Sander (2013) analyzed three humeri (UOPB 00123, UOPB 00031 and UOPB 00032) and concluded that any growth pattern cannot be observed. As the opposite is shown here, under the restricted sectioning conditions humeri show two clear growth patterns, thus the misinterpretation by Konietzko-Meier and Sander (2013) had a methodological origin.

4.1 Individual age estimation

Despite the various histological frameworks in both histotypes, the cyclicity of growth allows estimating the individual age of separate specimens. The direct estimation of the individual age of ectothermic animals relies on the amount of preserved growth marks (Castanet 1994). The thin annuli consist mostly of highly organized, lamellar bone and indicate a phase of slow growth in the animals' life, whereas the thick zones are usually highly vascularized with the tissue consisting of less organized bone (Francillon-Vieillot et al. 1990). A zone and an annulus together correspond to one annual growth cycle (Castanet and Smirina 1990; Castanet et al. 1993). Moreover sometimes, in fully grown animals the accumulation of the distinct lines visible in the superficial cortex, known as the External Fundamental System (EFS), may be observed (Chinsamy-Turan 2005; Erickson 2005; Sander 2000; Sander et al. 2011; Turvey et al. 2005).

The femora of *Metoposaurus krasiejowensis* show a unique organization of the growth marks (Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013). The fast-growing vascular zone seems to be structurally typical with less organized matrix and relatively high vascularization compared to annuli. Zone originated most likely during a favorable wet season (Konietzko-Meier and Sander 2013). More interesting are annuli with an accumulation of the distinctive lines, resembling an EFS. In femora, these structures are visible not only in the outermost part of the cortex but also in the annulus in the inner cortex (Konietzko-Meier and Sander 2013). Thus, those lines do not represent the EFS but originate from a period of prolonged slow growth, with multiple occasional cessation of growth during long seasons with unfavorable environmental conditions. Also, the thickness of the annuli is

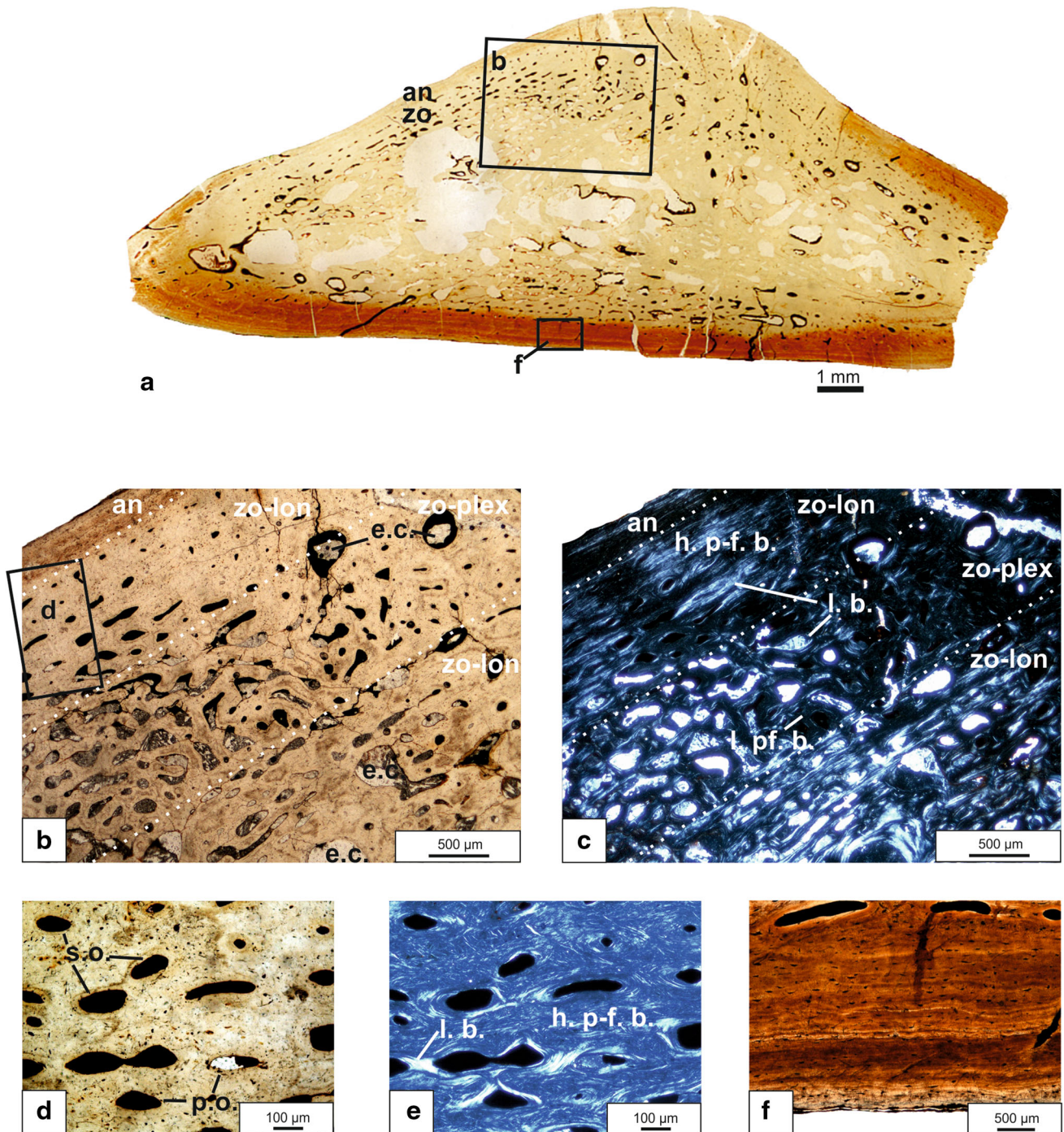


Fig. 4 The microstructural (a) and histological (b–i) details of *Metoposaurus krasiejowensis* humeri UOPB 00113 representing histotype II; **a** microstructure of the midshaft; **b** close-up of fragment of cortex from image **a** with a thick zone and thin annulus, image in normal light; **c** the same as **b** but in polarized light, note the different organization of parallel-fibred bone in two types of zones and in annulus; white, dropped lines indicate the borders between two types of zones with different orientation of vascular canals, and the outermost the border between zone and thin annulus; **d** details of

external part of zone with secondary and primary osteons, image in normal light; **e** same like **d** but in polarized light showing details of lamellar and parallel-fibred bone; **f** numerous resting lines visible in outermost part of the cortex, image in normal light. *an* annulus, *e.c.* erosion cavity, *h. p-f. b.* high organized parallel-fibred bone, *l. b.* lamellar bone, *l. pf. b.* low organized parallel-fibred bone, *p.o.* primary osteons, *s.o.* secondary osteons, *zo-lon* zone with longitudinal arrangement of vascular canals, *zo-plex* zone with plexiform arrangement of vascular canals

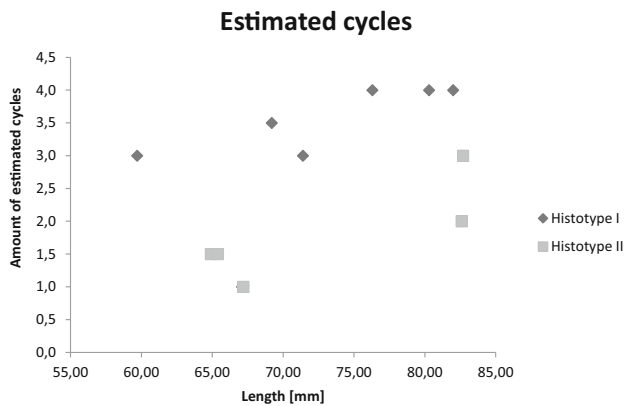


Fig. 5 The diagram illustrates the correlation between the *Metoposaurus krasiejowensis* humerus length versus the amount of total estimated cycles for Histotype I (H1) and Histotype II (H2). Here a faster growth rate can be observed for H1

unusual compared to other groups (Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013).

A similar pattern is represented in the humeri, especially in specimens UOPB 00033 and UOBS 00777, very prominent and distinctive multiple resting lines can be observed; they occur always close to the surface within an annulus.

The minimal number of estimated growth cycles varies between one and four which results in an individual age of 1 up to 4 years. Based on the studies done on *Duttonosaurus* femora (Steyer et al. 2004) the change in growth pattern which may indicate the achieving of adulthood is about 8 years. Thus the overall ontogenetic stage of all tested here bones is thus determined as a juvenile to a late juvenile.

4.2 Intraspecific variability

A possible cause of the two histotypes could be the affiliation of the bones to more than one taxon, despite their morphological similarities. Konietzko-Meier and Klein (2013) described for femora one consistent histotype, which is disturbed by one aberrant femur (UOBS 00643). That femur shows an empty medullary region and an entirely highly vascularized cortex. However, it is the only femur in which the growth record starts with a phase of slow growth (annulus) expressed mainly through the highly organized bone matrix, contrary to the less organized matrix present within the zone. Further on, the phase of slow growth (= annulus) and the phase of fast growth (= zone) are separated by a distinct LAG. On the basis of the small medullary region, which is surrounded by lamellar bone, and the lack of remodeling, an inner phase of fast growth was never deposited. Based on a sample size of 16 femora, the single bone (UOBS00643), which did not fit into the growth series of *Metoposaurus*, has been

suggested to belong to a different temnospondyl, such as *Cyclotosaurus* (Konietzko-Meier and Klein 2013). However, the observed variability among humeri rather indicates that this single femur does not represent a different species but represents the Histotype II (here established for humeri). The smallest humerus within Histotype II resembles very much the histological pattern described for femur UOBS 00643 (Konietzko-Meier and Klein 2013), excepting the presence of distinct LAG between two layers and the start of periosteal growth from a slower phase in the femur. Thus, based on the presented analysis of the histological variability of humeri, also two different histotypes can be assumed for femora.

Moreover, in the clay pit in Krasiejów only two temnospondyl species (*Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius*) have been discovered based on numerous excavated skulls, which are the most diagnostic skeletal elements. The femora of both taxa are so far morphologically not distinguishable, in contrast with humeri which are clearly distinguishable (Sulej and Majer 2005). Therefore, it would be highly unlikely to find postcranial material belonging to a third species, with a *Metoposaurus*-like humerus, without accompanying skulls or other bones.

Most probably the observed histological variability of humeri represents an intraspecific variability with several possible reasons.

4.3 Population separation

The high histological variability may be reasonably explained by intraspecific variability caused by the different environmental conditions. Konietzko-Meier and Klein (2013) speculated, based on the limited age range and common growth patterns that all femora from Krasiejów represent a single population, which died during the same catastrophic event. However, two histotypes may indicate the occurrence of two separated populations living in various environmental conditions. The climate in the Late Triassic is characterized by an alternation of dry periods and heavy rainfalls (Bodzioch and Kowal-Linka 2012). The seasonal alternation of dry–wet climate can be correlated with the pattern observed in Histotype I. In this case, the dry season, during which the growth rate decreased. This pattern has been also observed in the femora (Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013). Histotype II, however, does not show the alternation of zones and annuli but preserves broad zones, implying long favorable (nutrient-rich, optimal temperature, low predatory stress, etc.) life conditions. Opposite to Histotype I with wide annuli, the annuli here are very thin. This could be a result of the extremely dry season, thus the animal had to aestivate, and prolonged slow growth was not possible

like in Histotype I. Second possibility is, that dry season was very short and thus the annulus is thin. Such variability can occur due to a separation of two populations in space and/or time. The time separation would imply that the hypothetic two populations lived in different time accompanied by different life conditions, however, the duration of the time gap remains unknown. The space separation suggests the parallel existence of two separate populations living in two various local environments.

The studies of the bone diagenesis suggest that after the animals died, their carcasses have been transported by a catastrophic flood event caused by a heavy rainfall and after mass sorting, deposited together (Bodzioch and Kowal-Linka 2012). This confirms the observation based on histology that in the Krasiejów locality skulls of medium to larger sized animals are associated with juvenile postcranial elements (Konietzko-Meier and Klein 2013; Konietzko-Meier and Sander 2013; this study). The observed tendency is very likely a result of segregation of the material during the depositional process, which strongly supports the hypothesis of the space-separation of populations (see below).

However, the bones are almost perfectly preserved and show no round offs caused by a long transportation way. Furthermore, the taphonomy of the site suggests that all bones were buried in a single catastrophic event (Bodzioch and Kowal-Linka 2012); additionally the mineral infill in the bones is the same, a close catchment area (short transportation distance) is most likely supporting the lack of long transport and time separation of populations. Moreover, a separation in time would imply a different stage of diagenetic changes in the bones, which is not observed.

4.4 Sexual dimorphism

Another possible explanation would be that the two different histotypes represent different sexes. However, this hypothesis is difficult to prove and highly speculative as there is not much known about sexual features and mating behavior among Temnospondyli. An exceptional case of preservation of three body impressions of Mississippian temnospondyl from the Mississippian (Visean) of eastern Pennsylvania, USA suggest some sort of gregarious behavior and may indicate that internal fertilization occurred in temnospondyls (Lucas et al. 2010). In another study carried out on branchiosaurids, an observation on different fossilization of the chorda dorsalis has been made (Werneburg 2008) resulting as a very distinctive dimorphism. There in one fossil-rich slab coming, 110 well preserved skeletons of *Apateton dracyiensis* have been examined. A fossilized chorda

dorsalis has been preserved in 68 specimen and in 42 well-preserved skeletons the chorda dorsalis has missing. The conclusion of the author was that the fossilized chorda dorsalis represents male specimens.

In this case, the different growth pattern visible in two histotypes does not represent two different populations, but a different development for males and females inside one population. The growth rate was faster for one sex during a favorably season; however for some reasons this sex was not able to continue growth during the dry season.

Here we could assume that the more secondary remodeled and more porous bones of Histotype II are growing faster and thus in similar age, the forelimbs are longer. In modern salamanders, approximately 61% of 79 species show females being larger than males (Shine 1979); this may indicate that longer humeri here belong to females. Different microstructural framework indicates different usage of the forelimbs between sexes. Longer and more porous bones seem to be well adapted to more active swimming modes, and thus would be an obvious advantage for females which have to lay spawn in water. On the other hand the humeri with Histotype II are very porous and thus their biomechanical resistance is low, moreover, metoposaurids limbs are short compared to the body length and thus not useful as body propulsion. So far two growth patterns for *Metoposaurus* are known only for long bones and it is difficult to charge if the acceleration of growth applies only to limbs or the overall size was larger. The intercentra studied histologically do not show any clear variation in growth pattern (Konietzko-Meier et al. 2012). The dermal bones were studied only based on one skull and thus it is impossible to conclude about differentiation in the growth rate (Gruntmejer et al. 2016).

The discrepancy between the morphological and microstructural characters in temnospondyls was first observed for *Eryops* (Konietzko-Meier et al. 2016). Among other bones from the Early Permian Briar Creek Bonebed (Texas), three ulnae were studied. Based on the morphology all three ulnae were determined as *Eryops*. The similar length and ossification through the olecranon process for two of them indicated the same ontogenetic stage. However, in one bone the increase of bone mass was observed through secondary deposition and cortex compactness increase; in second bone the opposite process was observed—the cortex was highly eroded. It was not possible to determine if this variation has interspecific or intraspecific origin (Konietzko-Meier et al. 2016). In the light of the results obtained here based on the *Metoposaurus* humeri, it is possible that the bimodal growth pattern of long bones is a character typical for Temnospondyli and represent the sexual dimorphism.

5 Conclusions

Metoposaurid humeri are relevant for histological analysis; however, it has to be taken into consideration that a very precise methodology needs to be applied. Complying with this requirement, the bones were sectioned at the exact midshaft plane, which is short and obliquely oriented and exhibits the most complete growth record. Consistent sectioning at this plane allows for meaningful comparisons of separate specimens.

Bone morphology indicates a uniform bone growth represented by only one morphotype. In contrast to that, the femora showed a bimodal morphological distribution. However, the histological analysis indicates a histovariability resulting as two different patterns of growth: the first is characterized by fast growth and fast remodeling, while the second shows alternating phases of slowed growth.

Based on histology, two histotypes can be established: In Histotype I (UOPB 00033, UOPB 00034, UOPB 00109, UOBS 00777, UOPB 00036, UOBS 001418 and UOBS 0494) high remodeling is present in most samples and the vascularization ranges from poor to moderate. Vascular canals are disorganized and plexiform or reticular oriented in the inner zone and more longitudinally in the outer zone. The alternation of zones and annuli is well visible; the count of growth cycles corresponds to an individual age of between 1 and up to 3 years. These growth marks correspond to fast and slow growth and can be correlated with favorable and unfavorable seasons.

Histotype II (UOPB 00113, UOBS 00574, UOPB 00108, UOBS 00126, and UOPB 00110) is characterized by its vascularization and fast growth corresponding with favorable living conditions. The sections contain only a single zone and end with an annulus which is not completely traceable throughout the cortex. Individual age was estimated at 1 to 2 years.

The causes of the different growth patterns are unclear. Possible explanations may include taxonomic diversification, a separation of populations by time and/or space along with subsequent, postmortem redeposition, sexual dimorphism, and simple random variation. However, to clearly state what the growth patterns are indicating, more investigations have to be applied on the specimens e.g. geochemical analysis. Classical chemical analyses or more complex analyses as stable isotopes and rare earth elements could be helpful for reconstruction of the palaeoenvironment (Clementz 2012; Kowal-Linka and Bodzioch 2017; Tütken et al. 2006, 2008; Zigaite et al. 2015). By applying a precise sampling and measurement of chemical elements to each Histotype, or even single zone and annulus, the identification of different environmental settings would be

possible, which cannot be observed by petrographic analyses (Bodzioch and Kowal-Linka 2012). Therefore, the geochemical data will support (or not) the population separation hypothesis.

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