Title: Ornamentation of dermal bones of *Metoposaurus krasiejowensis* and its ecological implications.

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Abstract:

Background. Amphibians are animals strongly dependent on environmental conditions, like temperature, water accessibility, and reservoir trophy. Thus, they can be used in modern palaeoenvironmental analysis, reflecting ecological condition of the biotope.

Methods. To analyse the observed diversity of the temnospondyl *Metoposaurus krasiejowensis* from the Late Triassic deposits in Krasiejów (Opole Voivodeship, Poland), the ornamentation pattern (e.g., groove, ridge, and tubercule distribution) of 25 clavicles and 13 skulls were observed on macro- and microscales, including the use of a scanning electron microscope for high magnification. The characteristic ornamentation of these bones served for taxonomical and ecological analysis of inter- vs intraspecific variation.

Results. Two distinct types of ornamentation (fine, regular and sparse, or coarse, irregular and dense) were found, indicating either taxonomical, ecological, individual, or ontogenetic variation or sexual dimorphism.

Discussion. Analogies with modern Anura and Urodela, along to previous studies on temnospondyls and the geology of the Krasiejów site as well suggest that the differences found are rather intraspecific and respond to individual variation. Sexual dimorphism and ontogeny cannot be undoubtedly excluded, but ecological variation between populations of different environments or facultative neoteny (paedomorphism) of part of the population (with types of ornamentations being adaptations to a more aquatic or a more terrestrial lifestyle) are the most plausible explanations.

Introduction

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The fossil assemblage from the Late Triassic deposits in Krasiejów (SW Poland, near the city of Opole) is a unique discovery. Excavations carried out since 2000 have revealed new data concerning the evolution of continental Triassic faunas. In Krasiejów, although the remains of several groups of fish and archosaurs were also found (e.g. Dzik et al., 2000; Dzik & Sulej, 2007, 2016; Brussate et al., 2009; Piechowski & Dzik, 2010; Sulej, 2010; Skrzycki, 2015; Antczak, 2016), along to fossils of large temnospondyls described as *Metoposaurus krasiejowensis* (Sulej, 2002; species name revised by Brusatte et al., 2015) were the most abundant.

Despite many years of study, new data are still being collected and some aspects of the anatomy and ecology of extinct animals are being reinterpreted (e. g. Konietzko-Meier, Bodzioch & Sander, 2012; Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013), along with the age of bone accumulations in Krasiejów (Racki & Szulc, 2015; Lucas, 2015; Szulc, Racki & Jewuła, 2015) and their origin (Bodzioch & Kowal-Linka, 2012). One aspect not described in detail is the morphology of metoposaurid dermal bone ornamentation, which was assumed to be randomly variable (Sulej, 2007) or similar in all representatives of the species, as suggested by Witzmann et al. (2010). The aim of this paper is to describe in detail, on macro- and microscales, the ornamentation of metoposaurid clavicles and skull bones, in order to examine its variation and to test whether or not it is the same in all specimens. A thorough probe of skeletal elements from one site shows that differences between specimens are not random.

Material and methods

The size, number, shape, placement, and characteristics of ornamentation of the metoposaurid clavicles (and also of the skull bones) from the 'Trias' site at Krasiejów (SW Poland; Fig. 1), were analysed. The fine-grained Late Triassic (Carnian, according to Dzik & Sulej, 2007; Lucas, 2015; Norian, according to Szulc, 2005; 2007; Szulc, Racki & Jewuła, 2015;) mudstone and claystone deposits can be divided into three units (e.g. Gruszka & Zieliński, 2008), in which two bone-bearing horizons occur. The lower horizon, the product of a mudflow deposition that probably occurred during a heavy rainy season, is especially abundant in fossils, including *Metoposaurus krasiejowensis* remains. The upper horizon was described as massive claystones covering palaeochannels of low-energy meandering river. Within the upper horizon remains of the archosaurs *Silesaurus opolensis* and *Polonosuchus silesiacus* were found (Dzik & Sulej, 2007).

To test the diversity of dermal bone ornamentation in metoposaurids from Krasiejów, 25 clavicles (UOPB1152–1176) and 13 skulls (working numbers counting from the excavation site : UO/PP01–20)

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were analysed in detail (Tables 1–3). Morphometric measurements for 21 skulls were also made (Table 4). The clavicles were removed during the excavation and are held in the Opole University collection, while the skulls were preserved *in situ* in the palaeontological pavilion (also part of Opole University) at the digging site in Krasiejów; one of them is housed in the Faculty of Geographical and Geological Sciences Museum of Earth at the Adam Mickiewicz University in Poznań (uam/mz/586). As an outgroup, the skull and clavicle of *Cyclotosaurus* (ZPAL/AbIII/397) from Museum of evolution in Warsaw, were examined.

All described specimens were found in the lower bone-bearing horizon.

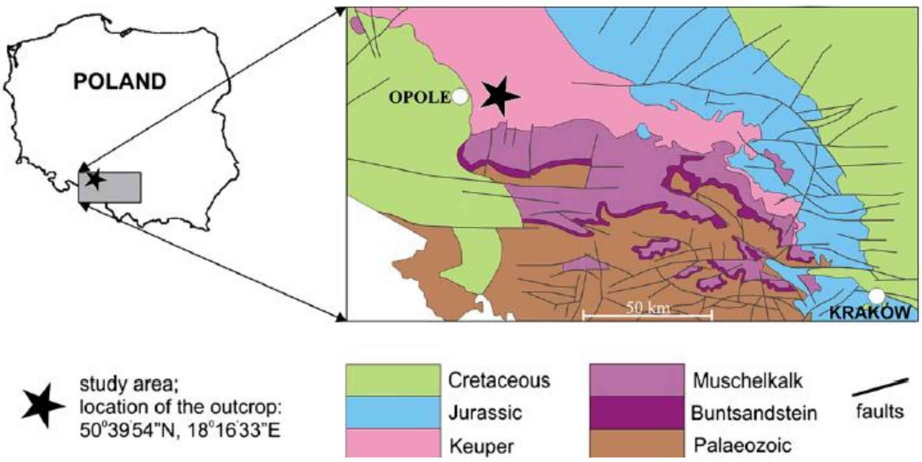

Fig. 1. Localization and geological map of Krasiejów (after Bodzioch & Kowal-Linka, 2012).

The characteristics of the polygonal and radial structure of clavicles were described, using over 20 features, including some of the 12 used by Witzmann et al. (2010). Observations are shown in Table 1, which groups similar features and assigns them numerical values.

Observations were made macroscopically and microscopically using an Olympus SZ61 binocular microscope, a Zeiss SteREO microscope, and a DIGEYE digital microscope.

Fragments of 10 clavicles were analysed using a Hitachi S-3000N Scanning Electron Microscope. Samples were taken from the same parts of the clavicles: radial ornamentation in the posterior part of the bone, several centimetres away from the ossification centre. Samples were sprayed with gold and palladium and observed under a high vacuum at the Institute of Plant Protection – National Research Institute in Poznań. One sample was observed using a Hitachi S-3700N at the SEM-EDS Laboratory of Faculty of Geographical and Geological Science of Adam Mickiewicz University in Poznań.

Selected macroscopic features of skull bones were described only as a result of the fact that the presentation of bones *in situ* makes it impossible to describe micro- or sub-microscopic features. Not

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all such features were described. Dermal bone ornamentation can be divided into radial ornamentation, composed of parallel or radial ridges without transverse ridges, and polygonal ornamentation, composed of short ridges connected to form polygons. The vertices of the polygons are called nodal points. The polygonal sculpture area is the ossification centre, the part of the bone that ossifies first. Near the ossification centre is an anterior appendix. Polygons may be hexagonal, pentagonal, rectangular, or irregular in shape. Polygons joined by means of a missing ridge are called multipolygons (Fig. 2). All measured features are listed in Table 1. SEM observations included features of the surface of the ridges, such as the number of foramina and degree of ridge roughness (Fig. 3). The possible relative individual ages of the clavicle specimens were determined using the method based on ornament development, presented by Witzmann et al. (2010) and improved by Zalecka (2012). The youngest specimens possessed no partition walls between radial ridges. An intermediate stage was represented by specimens with developing partition walls within radial ornaments, and the oldest specimens possessed many well-developed partition walls between radial ridges. Additionally, specimens described as the oldest, are the largest ones (UOPB1152 ~19,5cm x 9,7cm, UOPB1164 ~20cm x 9cm), while the youngest are usually of small size (UOPB1166 ~12cm x 6cm, UOPB1171 ~ 10cm x 5cm).

For testing the significance of described variation statistical test were used. At first Shapiro-Wilk test for testing normality of the data, then respectively test F, test T and test U. Test F was used if both compared samples had normal distribution. Test F was used for testing the variance. If the difference between variances were not significant, test T was used. If the variances were significantly different, or samples not had normal distribution, test U was used. If the final test gave the p-value (probability value) less than 0,05 it means that samples are significantly different.

Observations

Diagnosis: Clavicles

Clavicles of metoposaurids from Krasiejów showed diversity in ornamentation, having fine, regular and sparse, or coarse, irregular and dense sculpture. After this observation, the clavicles ornamentation was examined in greater detail.

Some of the analysed features show random variation or none; however, most are distributed bimodally. Therefore, in every specimen one or the other set of characteristics occur, and two types of ornamentation can be distinguished (Tc1 and Tc2).

Specimens classified as type 1 (Tc1) are characterised by more regular ornamentation of the clavicles: the borders of the ossification centre (polygonal sculpture) are easily recognised, the

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polygonal sculpture field has a square shape, and the ornamentation is fine and sparse, moreover, nodal points are more pronounced, being broader and higher than the ridges that connect them, ridges are usually narrow, hexagons with a low level of size diversity dominate, multipolygons are rare, clavicles, even when large, are relatively thin; the anterior process of the clavicle is usually flat and small (Fig. 2); while specimens classified as t**ype 2 (Tc2)** posses less regular ornamentation: the borders of the ossification centre (polygonal sculpture) are difficult to recognise, the polygonal sculpture field is characterised by a rectangular shape (elongated posteriorly), and the ornamentation is thicker and denser, moreover, nodal points are only slightly broader and higher than the ridges that connect them, ridges are wide or narrow, often rounded, polygons are more often pentagonal or irregular, multipolygons are frequent, clavicles are relatively thick, independently of their size or age, and the anterior process is usually round in cross section and expanded (Fig. 2).

Both types of *Metoposaurus* dermal bones ornamentation are however distinct from *Cyclotosaurus* sculpture (Sulej & Majer, 2005). *Cyclotosaurus* can be characterised by relatively large and rhomboidal polygons (sometimes elongated pentagons). Radial ornament is very sparse (spaces between ridges are wide). Ossification centre is large and posses distinct borders, but the polygon number is low (25). Clavicle is thick. Ridges are round and thick (ZPAL/AbIII/397, pers. observ).

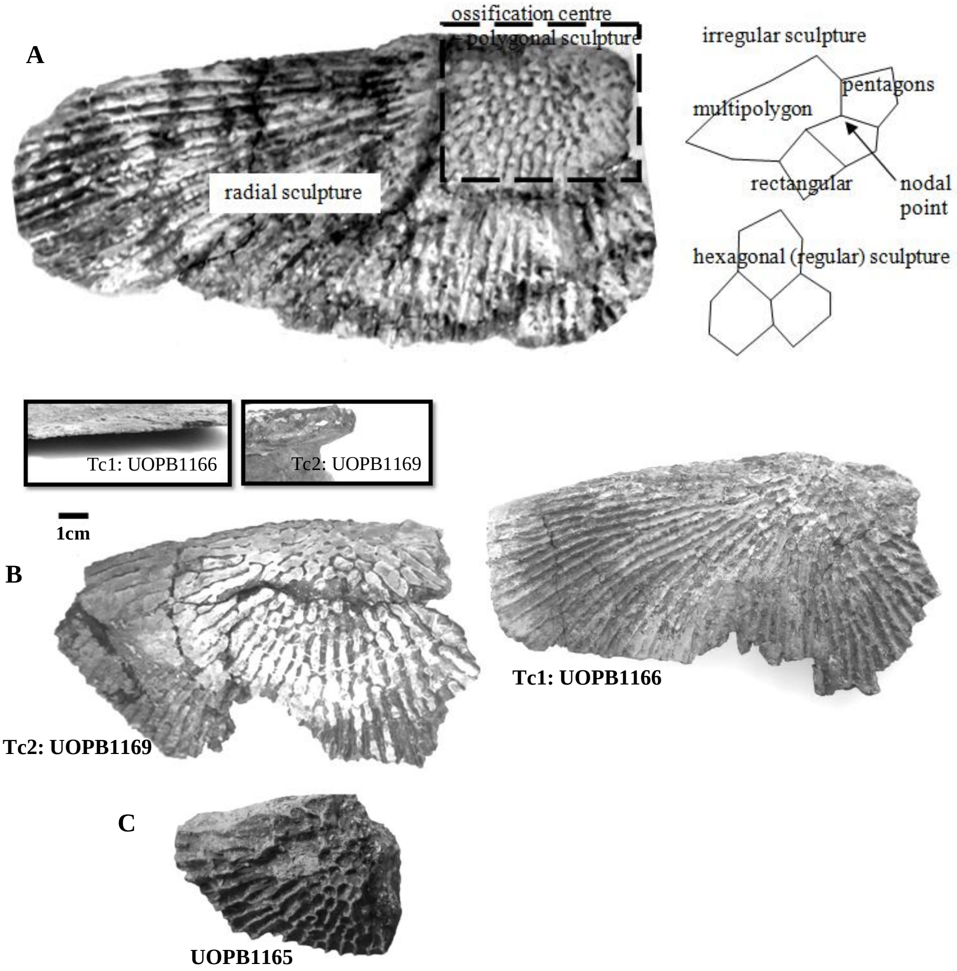

Fig. 2. Basic ornamentation features explanation (A). Clavicles assigned to two types of ornamentation (B). UOBP1165, partially incomplete specimen, not fitting to described types (C, Figs. 4-6).

The distribution of certain characteristics according to relative individual age or type assignment is presented on figures 3–7. All plots show bimodal distribution of the parameters, which are independent of estimated relative individual age of specimens. UOPB1165 (Fig. 2) specimen not fitting any of this types might be the representative of a different taxon, although it was the specimen with the largest part missing which may affect the result of its description. Some features were not described for this specimen i. e. borders and shape of the ossification centre or radial ridges character (Table 1). Estimated size of the complete specimen is small, but the ossification degree is

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high. Its assignment to a species other than *M. krasiejowensis* would be difficult without other findings.

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In table 5 results of conducted statistical test are presented – F and T or U, dependent on the data distribution. Considering described types as different groups, quantitative and qualitative data shows that they differ significantly (α = 0,05).

Explanations to figs 3-7:

- Tc1
- Tc2
- Youngest
- Intermediate
- Oldest
- Other species

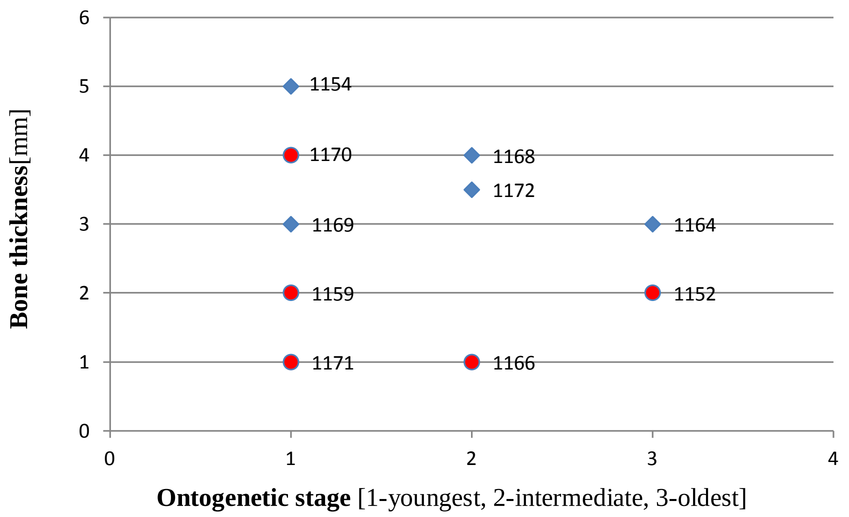

Fig. 3. Thickness of the bone in particular types and ontogenetic stages. Measurements made at the border of polygonal and radial ornamentation areas.

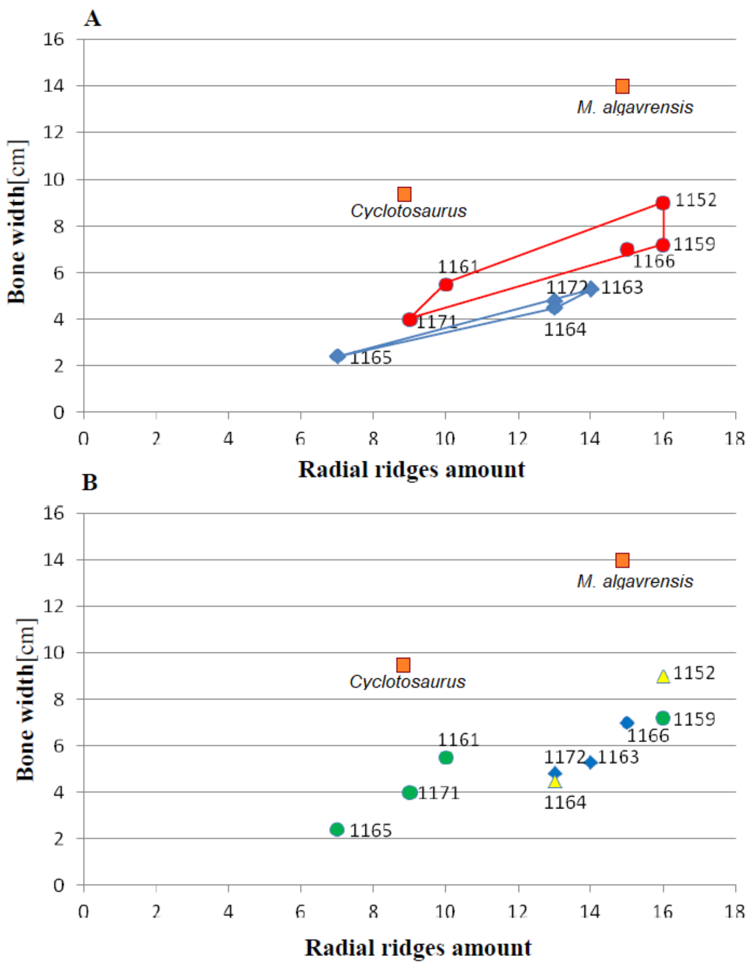

Fig. 4. Ratio of the bone width and amount of radial ridges (measurement taken 2,5 cm from ossification centre).

A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

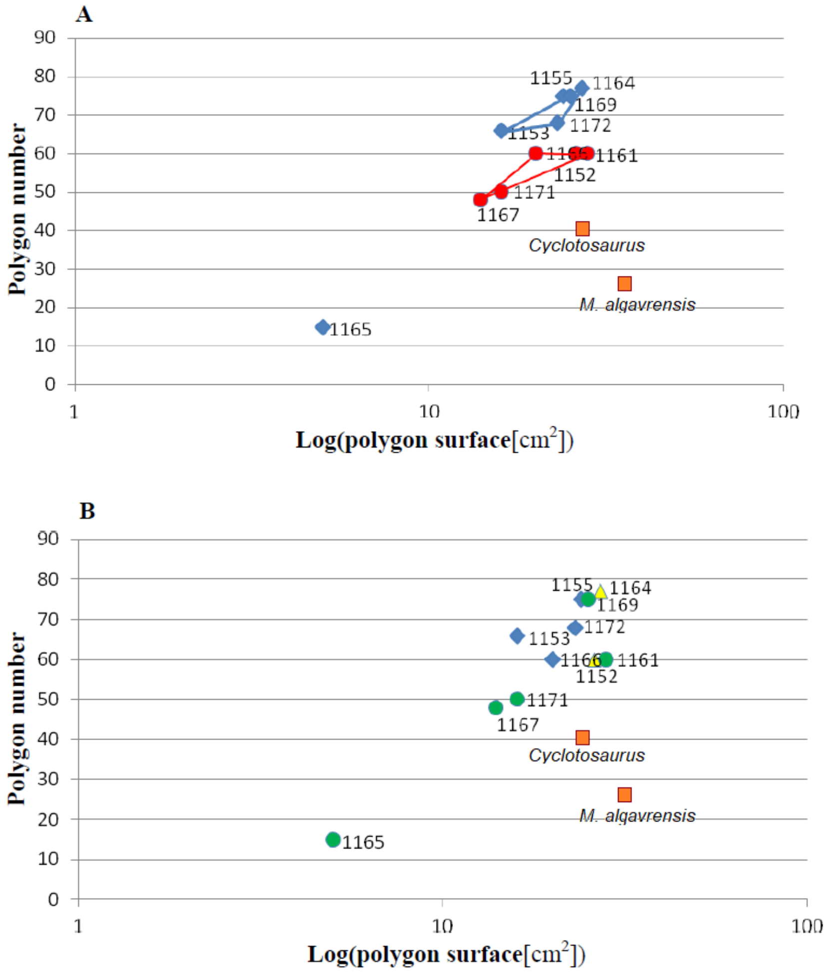

Fig. 5. Ratio of polygon number and surface.

A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

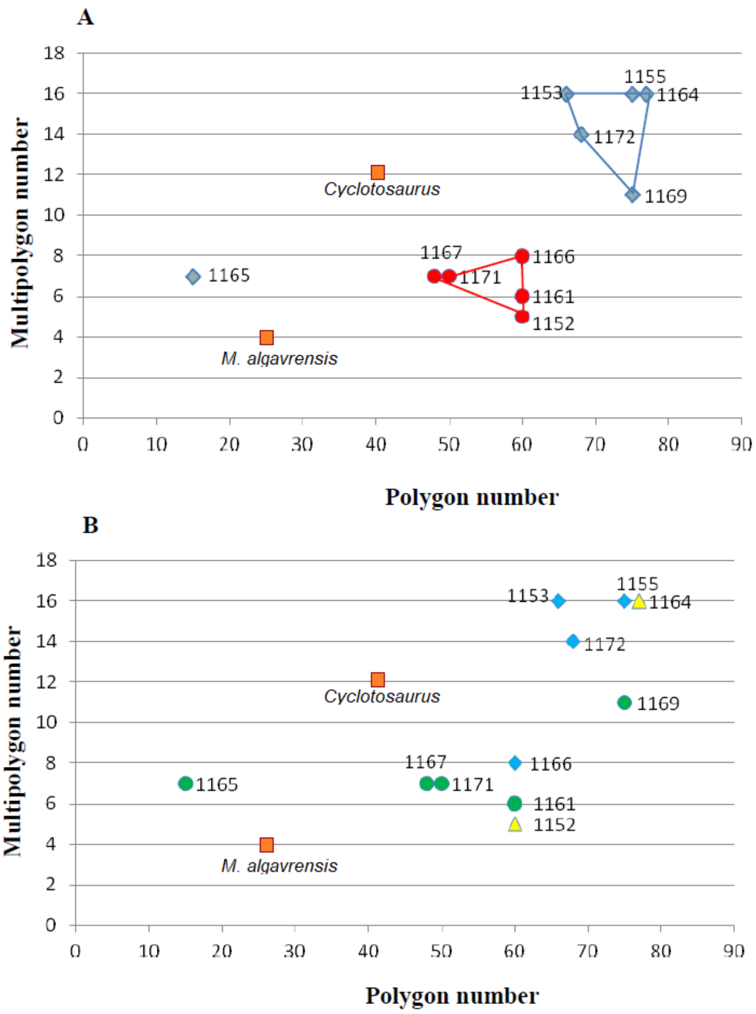

Fig. 6. Ratio of multipolygon and all polygons number.

A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

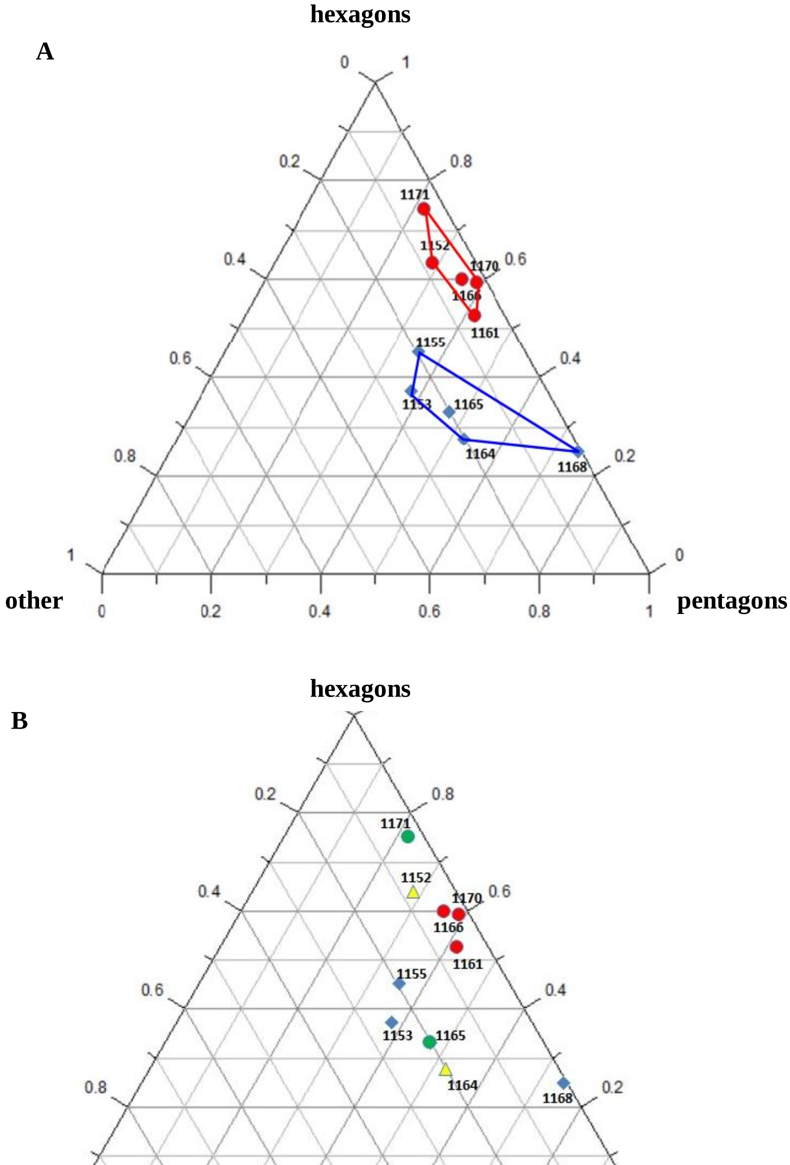

Fig. 7. Percentage of hexagonal, pentagonal and other polygons.

A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

Micro/nanoscale

Two types can also be distinguished according to the micromorphology of the ornamentation ridges and bone structure in cross-section. Clavicles assigned to type 1 do not possess striations (or striations, if present, are barely visible and sparse) and possess a low number of small capillary foramina at the slopes of the ridges (less than 7 per 100 μm^2). Usually they also have less than one foramen per 1 mm of ridge length and no distinct bumps or roughness at the top of the ridge (Figs. 8-9, Table 2). In cross-section they possess growth marks in close proximity within poorly vascularised upper cortex (Fig. 8).

Clavicles assigned to type 2 possess striations on the ridges and a greater number of small foramina (more than 7 per 100 μm^2). Usually they also have more than one foramen per 1 mm of ridge length and distinct bumps and roughness at the top of the ridge (Figs. 8-9, Table 2). In cross-section they possess growth marks separated by well-vascularised zones (Fig. 9). This difference in histological patterns is analogous to different growth strategies described for examples of long bones (Teschner, Sander & Konietzko-Meier, 2017).

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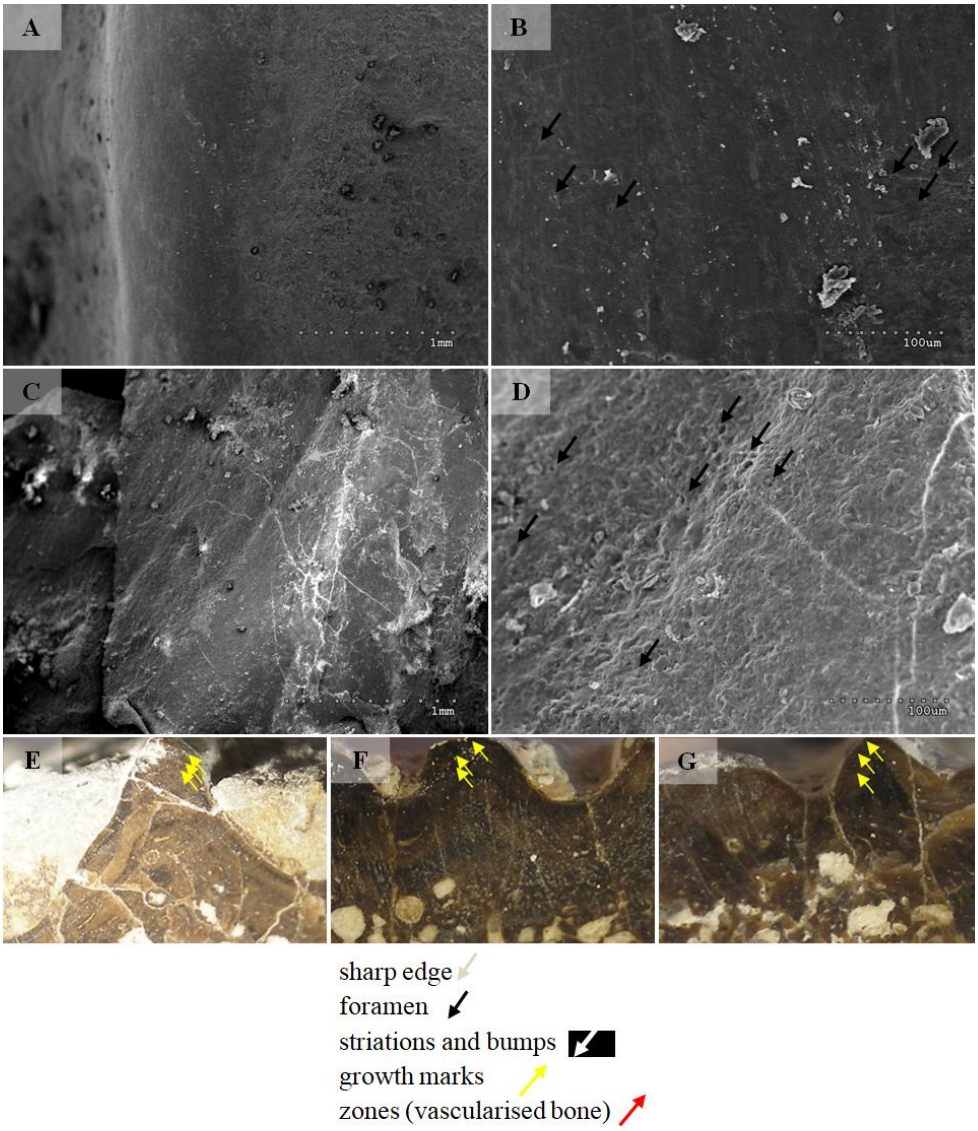

Fig. 8. SEM (SE) and histological observations of clavicle radial ridges for Tc1. A-B: UOPB1152; C-D: UOPB1161; E: UOPB1160; F: UOPB1167; G: UOPB1170.

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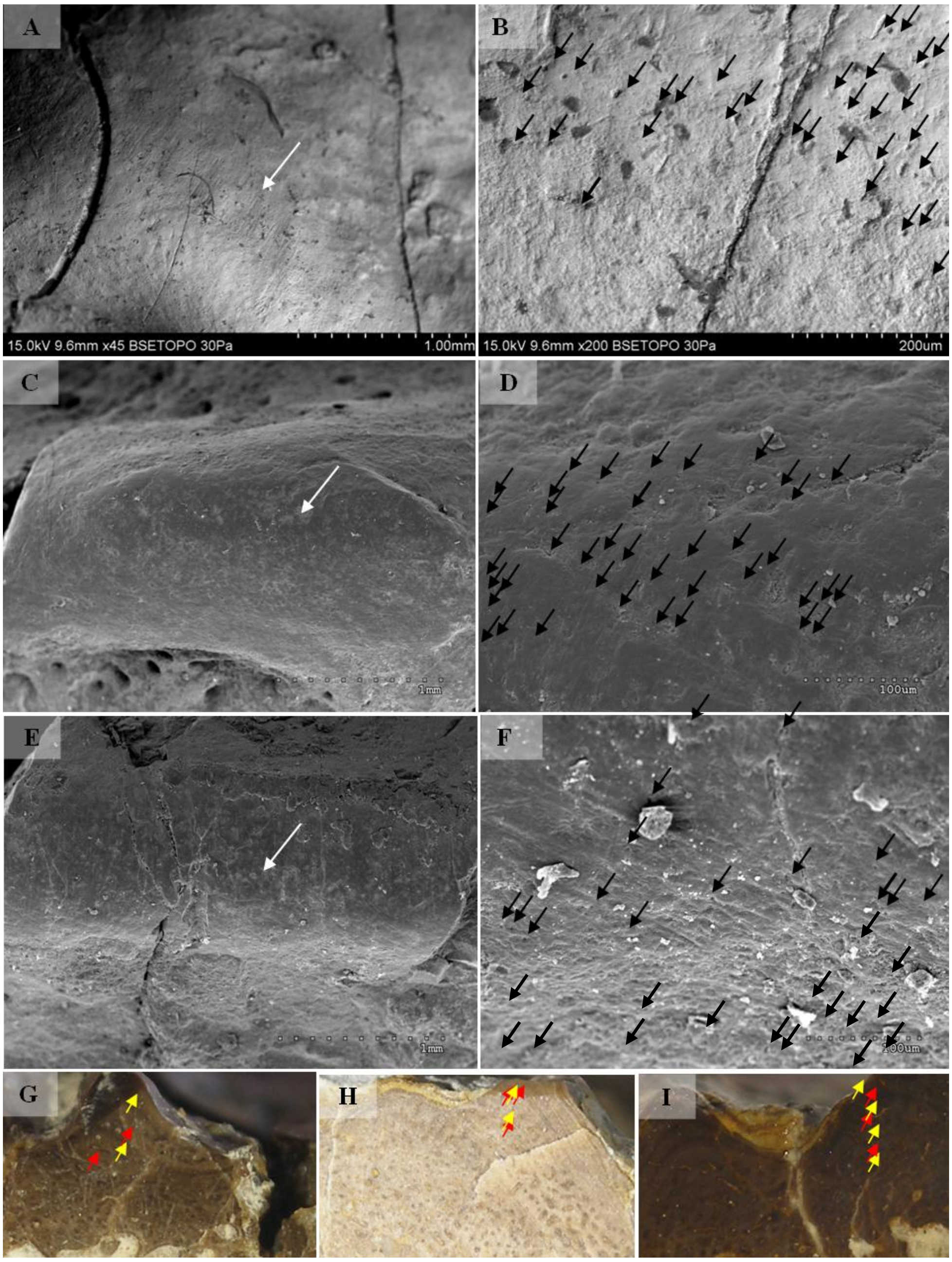

Fig. 9. SEM (SE) and histological observations of clavicle radial ridges for Tc2. A-B: uam/kng/02; C-D: UOBP1157; E-F: UOPB1163; G: UOPB1172; H: UOPB1158; I: UOPB1163.

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Remarks on other dermal bones

Skulls

Bimodal differences were found also in skulls (Table 3), which have been divided in the Ts1 and Ts2 types. The main characteristic of ornamentation of ossifying centers resembles either Tc1 (large, hexagonal, sparse polygons, almost no multipolygons; 6 specimens; Ts1) or Tc2 (small, irregular and dense polygons with common multipolygons; 7 specimens; Ts2). There is also a visible difference in the spatial distribution of polygonal and radial ornamentations between Ts1 and Ts2 (Fig. 10). In the first type, radial pattern covers large areas of the skulls roof in their both preorbital and postorbital (postfrontal, postorbital, supratemporal bones) parts, while in the second it occupies much smaller areas.

Comentario [GP11]: And this is not enough evidence to consider the presence of two ontogenetic stages?

An important fact is that the skulls classified as Ts2 are relatively small (averaging 28 cm in length) in contrast to Ts1 skulls (averaging 35 cm in length). However, this was not a rule. Among analysed skulls were two 35 cm in length (UO/PP04, 35 cm; UO/PP18, 35.4 cm) with different ornamentation types (Fig. 10, Tables 3, 4).

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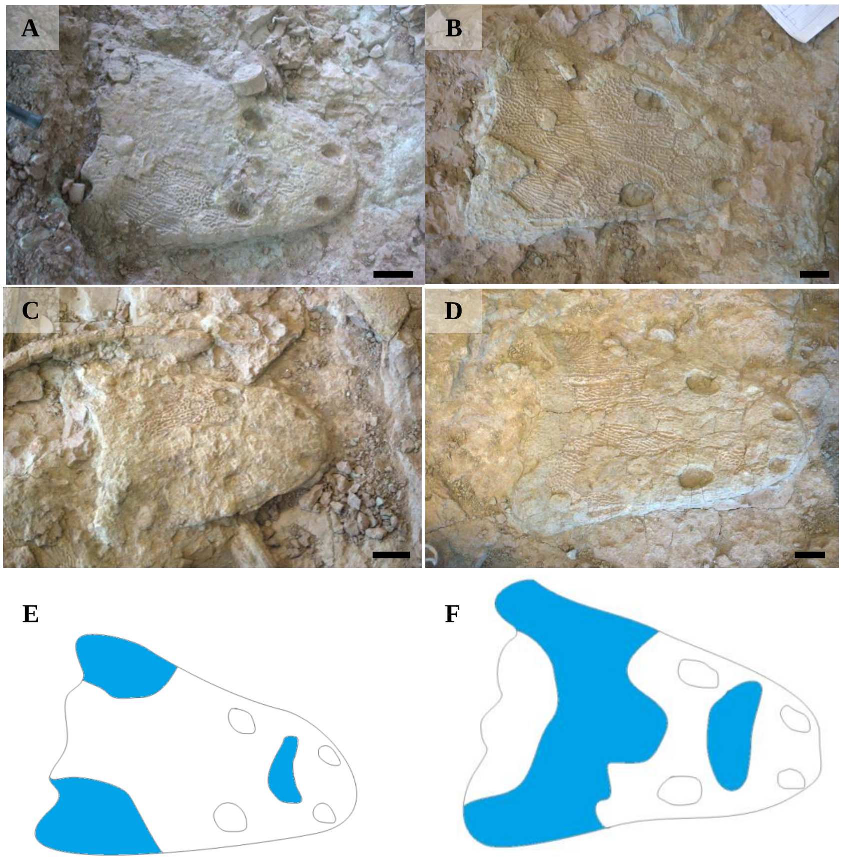

Fig. 10. Types of skulls ornamentation of metoposaurids from Krasiejów (*M. krasiejowensis*, as explained at Fig. 11). Blue area represents surface covered with radial ornamentation. A: UO/PP20; B: UO/PP13; C: UO/PP08; D: UO/PP09; E: Ts2 skull; F: Ts1 skull. Scale bar 5 cm.

Discussion

Reasons for the observed variation in dermal bone ornamentation

The presented diversity in the dermal bone ornamentation of *M. krasiejowensis* may be the result of species diversity, ontogenetic diversity, sexual dimorphism, individual variation, different habitats of two populations or facultative neoteny.

1. **Species diversity.** Given that no differences were found in axial and appendicular skeleton characteristics – all analyses described metoposaurid material as belonging to one species, *M. krasiejowensis* (i. e. Gądek; Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander,

Comentario [GP13]: Thus, you are suggesting that dermal ornamentation cannot be used as the only character to differentiate species diversity or sexual dimorphism, or ontogenetic stages.

Comentario [GP14]: This is not clear enough. You mean that previous studies on cranial and postcranial material from Krasiejów found that all them belong to M. Krasiejowensis? Please, reword.

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2013; 2012; Teschner, Konietzko-Meier & Sander, 2017) or in dermal bone measurements, it is also unlikely that the described differences in the analysed material represent differences between two species. Shape and ornamentation pattern of the clavicles (both described types) is strongly distinct from *M. algavrensis or Cyclotosaurus intermedius* (Figs. 4-6) (Sulej & Majer, 2005; , Brusatte et al., 2015). Only the distinct character of the UOPB1165 specimen observed on the bivariate plots of countable features might suggests that this specimen does not belong to the same species. The occurrence of some other taxon is possible because of the redeposited character of the fossils. Moreover, in skulls (both types – Ts1 and Ts2), the prepineal part of the parietals is short and the expansion angle of the sutures separating the parietal from the supratemporal vary between 19 and 26^{o} which is characteristic of *M. krasiejowensis* instead of *M. diagnosticus* (longer prepineal part and parietal expansion angle being around 13^{o}) (Sulej, 2002) (Fig. 11). Also relatively narrow shape of the skulls and shape of the sutures (i. e. between frontals and narials or parietals) is typical of *M. krasiejowensis*, being distinct from *M. diagnosticus*, *M. algavrensis* (Brusatte et al., 2015) (Fig. 11) or *Cyclotosaurus* (ZPAL/AbIII/397). According to this, all skull specimens belong to *Metoposaurus krasiejowensis*. As only one species (*M. krasiejowensis*) can be described considering skulls, and only this species was described in Krasiejów during over 15 years of studying metoposaurid material, it seems justified to consider all of the clavicles as belonging to *M. Krasiejowensis*, with possibly one exception – UOPB1165.

2. **Ontogenetic diversity.** According to Witzmann et al. (2010), all described specimens belongs to adult individuals, as they all can be assigned to the last stage of sculpture development (Witzmann et al., 2010: fig. 6E). Although singular features may be connected with the age of the specimen, the method of determination of relative age (youngest, intermediate, and oldest stages) based on the number of partition walls within the radial ornament shows that most of the analysed features, along with bone thickness, are not connected in this way. Unfortunately the histology of dermal bones cannot be used to determine the exact individual age, as different cross sections of the same bone reveals different stage of remodelling and counting the growth marks is unreliable (Gruntmejer, pers. comm.; Konietzko-Meier et al., 2018; Figs. 8-9). The diversity of skull sizes assigned to different types also argues against ontogenetic diversity. Relatively small skulls possess more polygonal (adult; Witzmann et al., 2010) ornament than the largest skulls. In addition, there are no differences in the ratio of skull portions according to size, whereas in the metoposaurids, in the younger specimens, the orbits are placed further back on the skull relative to its length (Davidow-Henry, 1989), i.e. the area between orbits grew faster in temnospondyls than the orbits themselves. Polygon characteristics also indicate the adult stage in all skull specimens.

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Comentario [GP17]: This is not in the reference list

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Comentario [GP19]: Yes, but you can have young and older adults, and maybe also you can have represented subadult individuals.

Rinehart et al. (2008) and Heckert et al. (2010) also suggest that all individuals are adults. Sulej (2002) suggests that size of the clavicle depends on the age and considered several clavicles of different size as ontogenetic sequence. Considering this ontogeny cannot be used to explain ornamentation variety, as the two types of sculpture occur in smaller and the larger specimens. The differentiation is also not the same as in the Rotten Hill, where age differences were proposed (Lucas et al., 2016). There are no size classes that can be correlated with sculpture variety in clavicles. In skulls, specimens assigned to type 2 are usually smaller, with exception of UO/PP18 (Table 4, Fig. 12).

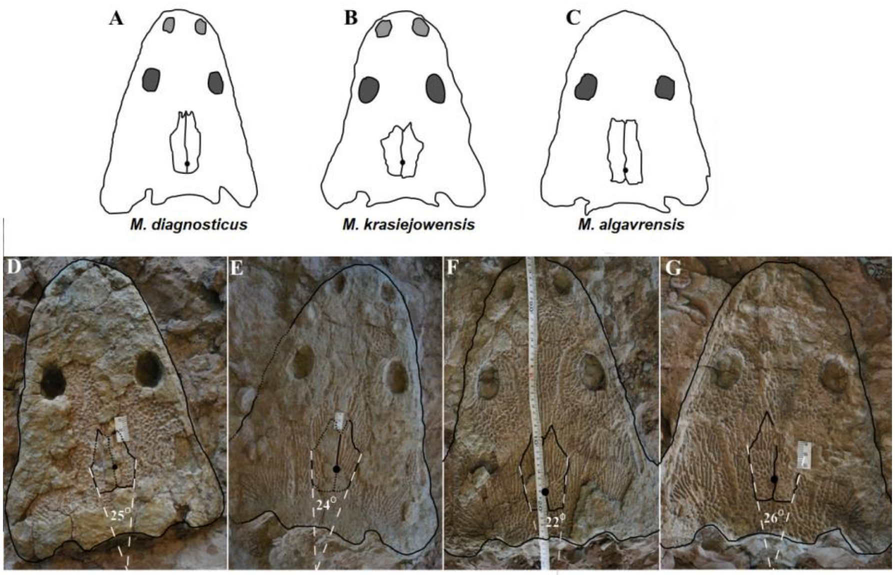

Fig. 11.Comparison of some of the analyzed skull materials with reconstructions of skulls of *Metoposaurus diagnosticus, M. krasiejowensis and M. algavrensis.*

A: *M. diagnosticus*; B: *M. krasiejowensis*; C: *M. algavrensis*; D: UO/PP02 (Ts2); E: UO/PP09 (Ts1); F: UO/PP13 (Ts1); G: UO/PP04 (Ts1). A-C after Brusatte et al., 2015.

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Comentario [GP20]: Could you show this in a figure? Can be better if you provide the photography and a schematic drawing of each clavicle, indicating the patterns that you interpreted to each.

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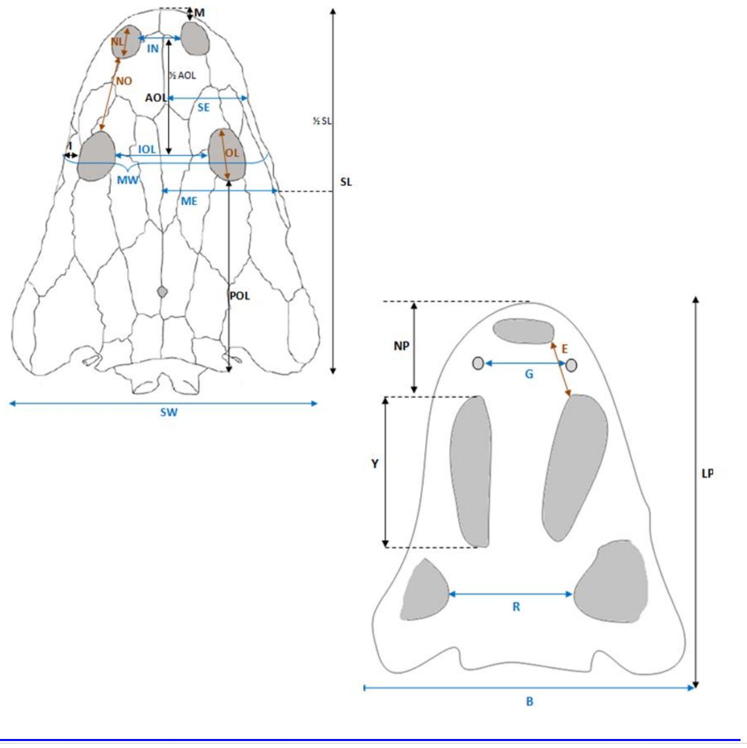

Fig. 12. Skull measurements.

3. **Sexual dimorphism.** In the described material there is lack of dimorphism in the shape of the skulls (Urban & Berman, 2007), clavicles or dentition (Kupfer, 2007). The location of clavicles (under the skin and on the ventral side of the body) and discussed function of the ornamentation excludes its role as 'display structures' in mating rituals (Kupfer, 2007) in contrast to i. e. *Zatrachys serratus* were spinescence and shape of the skull (rostrum) were considered as sexual dimorphism (Urban & Berman, 2007). Different growth strategy seen in clavicles (Figs. 8-9), skulls (Gruntmejer, pers. comm.) and long bones (Teschner, Sander & Konietzko-Meier, 2017) ("seasonal" growth marks separated by vascularised zones or slower growth with growth marks in close proximity within poorly vascularised bone) rather do not indicate different sexes, which could have been ecologically controlled.
4. **Individual variation.** The existence of two distinct types with no intermediate forms (Fig. 3-7) contradicts the possibility of individual variation; therefore there is low probability that individual variation is the main cause of the described variety.
5. **Different habitats**. Morphology of the dermal sculpture and vascularisation are not separable. Regularity of the ornamentation reflects the mode of life of temnospondyls to a certain degree. The coarser ornament, more pronounced ridges and irregularity is

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characteristic of rather terrestrial taxa (i. e. *Seymouria, Eryops*, see: Witzmann et al., 2010) – T2, while irregular sculpture represents rather aquatic animals (Witzmann et al., 2010) – T1. The variety seen within *M. krasiejowensis* allows expanding this conclusion, showing that the ecological difference (listed features) can be observed within one species.

Metamorphosis is a hormonally induced and controlled process; thus, its results might be morphologically unequal even in closely-related taxa (Fritzsch, 1990; Norris, 1999) or within taxa (Rafiński & Babik, 2000; Pogodziński, 2015). Because of this and the fact that amphibians, as animals very closely connected with the environment, are phenotypically plastic (examples below), the morphological diversity of the analysed material may be a result of differences between ecologically separated populations (geographic separation). Ecological separation of animals the remains of which are deposited in one bone-bed is possible, because of the bone-bed character (material partially redeposited, possibly from a large area, and partially local). Redeposition from different environments is suggested by the variant infill succession in the pore system and trace elements contents in the individual remains (Bodzioch & Kowal-Linka, 2012; Bodzioch, 2015). The more aquatic population might have lived at a different site – fossils are redeposited and material might be transported even from Variscian Upland according to isotopic analysis of Konieczna, Belka and Dopieralska (2015). Thus, geographical separation is probable explanation, because different ecological characters of specimens mean that two populations did not interbreed with each other. Time separation is also plausible as all material is redeposited. Some clavicles can be also reworked more than once, being removed from older levels than those which provided the skulls, which often seem to have a better preservation.

The more terrestrial population probably lived at the site, where environment resembles modern Gilgai relief of Texas or Australia (Szulc et al., 2015) while more aquatic populations lived at some distance from the shore, in larger reservoir(s).

Although the presence of some large skulls with no abrasion or weathering does not support transport from a distant area, a brief transport however is plausible as the teeth in the mandibles and upper jaws are usually lost (Heckert et al., 2010).

Other possibility is temporal diversity – gradually changing conditions of environment and amphibian morphology/behaviour, however some intermediate forms should have been noticed in this case – see 'individual variation'.

6. **Facultative neoteny (paedomorphism).** Explanation assuming the same environmental setting for the described morphotypes, but within a single population.

   The Late Triassic Krasiejów environmental conditions (dry and rainy season with possible periodic lack of food) may have even contributed to the formation of a neotenic population

Eliminado: to expand

Comentario [GP23]: I am no so sure, because you find them within a very small area. It is improbably, but not impossible, that you have fossils from populations that lived 30 or 40 km apart. If so, you have to demonstrate that, for instance, you may have more fragmentary specimens that display one of the found patterns. You may also have different types of sediment associated to one or another types (not always easy to demonstrate). You may have two populations separated by time (timeaveraging)

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Eliminado: population

Comentario [GP24]: Which are these different ecological characters?

Comentario [GP25]: Good point!

Comentario [GP26]: Spell complete names

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(Duellman & Trueb, 1986; Safi et al., 2004; Frobisch & Schoch, 2009). However, evidence of larval structures (i.e. branchial ossicles) in adult metoposaurids from Krasiejów is lacking. Nevertheless, facultative neoteny is possible (Motyl, 2008), as shown by the more radial (juvenile) sculpture on the large skulls of Ts1 (Witzmann et al. 2010). Facultative neoteny can be observed in several extant taxa, i. e. *Ambystoma talpoideum* with aquatic paedomorphic adults and terrestrial metamorphic adults (Whiteman, Krenz & Semlitsch, 2005). Breeding between such morphs is less common than within morphs, because paedomorphic adults begin to breed earlier (Krenz & Sever, 1995; Whiteman and Semlitsch, 2005). In this case, *M. Krasiejowensis* Type 2 (Tc2, Ts2) reflects metamorphic adults that transform into somewhat terrestrial, while Type 1 (Tc1, Ts1) reflects (partially) paedomorphic aquatic adults. This is possible because larval development is dependent on the environmental conditions. In Late Triassic Krasiejów dry and rainy seasons occurred which is known thanks to versicolor nature of claystone and faunal composition, including dipnoans (Szulc, 2005; 2007). Associated with these changes in water-level, food availability, living space and competition (Ghioca-Robrecht, Smith & Densmore, 2009) may influence the preferred lifestyle. Metamorphosis into terrestrial or paedomorphic aquatic form is in this case the response to the individual expected success in the environment (Wilbur & Collins, 1973; Whiteman, 1994; Michimae & Wakahara, 2002) controlled by endocrine signals (Pfennig, 1992). Facultative neoteny in metoposaurids may occur in a single population (no geographical separation is needed) – spatial separation of morphs may occur instead, with the paedomorphic concentrating in deeper habitats (Whiteman & Semlitsch, 2005).

Comentario [GP27]: It is 2004 or 2014?

Con formato: Resaltar

Eliminado:

Comentario [GP28]: This is not at the reference list

Con formato: Resaltar

Comentario [GP29]: And where are such terrestrial forms?

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Eliminado: ,

Ornamentation and lifestyle

The environmental differentiation is the most likely explanation regardless of whether caused by facultative neoteny or existence of two ecological types. Thus, described ornamentation types reflect more aquatic (Type 1) and more terrestrial (Type 2) morph of *Metoposaurus krasiejowensis*. In modern limbless serpentine amphibians (Gymnophonia: Apoda) and lizard-like salamanders (Caudata: Urodela), larvae resemble miniature adult specimens. Metamorphosis is gradual and there is little reorganisation of body plan (Zug, 1993). In fossil amphibians, body plan reorganisation was also minimal and rather gradual (Boy, 1974, 1988, 1990; Schoch, 2002, 2004), although its rate (trajectory: Schoch 2010) might differ between taxa depending on their habitat (Schoch, 2009). This is also the cause that there are no other features suggesting more aquatic or more terrestrial lifestyle. Such changes, like differences in lateral line morphology, requires more 'evolutionary effort', while changes in ornamentation are probably fast, reversible and do not require genetic changes (Rafiński & Babik, 2000; Babik & Rafiński, 2000).

Typically aquatic taxa are characterised by slow changes (low trajectory), sometimes with incomplete ossification of the pelvic region and limbs (last stages of ontogenetic trajectory). Terrestrial taxa are characterised by faster metamorphosis (high trajectory, with particular phases condensed within a short period of time), including final phases (limb ossification) enabling locomotion on land. The trajectory of semi-aquatic taxa lies between the two above-mentioned types.

This is an example of heterochrony. The length and composition of the ontogenetic trajectory of temnospondyls is ecologically controlled (Schoch, 2010). Metamorphosis in this case might be described as extreme heterochrony, because many phases are condensed within a short time span (Alberch, 1989).

Ontogenetic trajectory and the morphology of adult specimens and their sizes may differ between various environments inhabited by representatives of the same taxon (Schoch, 2010). There are several examples of such diversity, such as differences observed in the length of the hind limbs of modern frogs (Rafiński & Babik, 2000; Emerson, 1986; Emerson, Travis & Blouin, 1988; Dubois, 1982; Eiselt & Schmidtler, 1971; Schmidt, 1938; Emerson, 1986; Emerson, Travis & Blouin, 1988) and the morphology of extinct temnospondyls: the ontogenetic rate and dentition of *Apaeton* (Schoch, 1995); the size of *Micromelerpeton* (Boy, 2005; Boy & Suess, 2000; Schoch, 2010); the morphology of *Sclerocephalus* (Schoch, 2010); branchiosaurids (Werneburg, 1991, 2002; Werneburg, Ronchi & Schneider, 2007); and the plasticity of the plagiosaurid *Gerrothorax* (Schoch & Witzmann, 2012; Sanchez & Schoch, 2013). Polyphenism (environmentally controlled polymorphism) exists in a wide range of extant taxa (Roff, 1996) in adults (Whiteman, Krenz & Semlitsch, 2005) and tadpoles (Collins & Cheek, 1983; Pfennig, 1990; 1992; Walls, Belanger & Blaustein, 1993; Nyman, Wilinson & Hutcherson, 1993; Michimae & Wakahara, 2002; Pfennig & McGee, 2010).

Dimorphism in bone characteristics of metoposaurids from Krasiejów can be seen in dermal bones as well as non-dermal skeletal elements from Krasiejów. Two types connected with growth trajectory were seen in histological observations of metoposaur skulls (Gruntmejer, personal communication), humeri (Teschner, Sander & Konietzko-Meier, 2017), and the morphology of femora (Konietzko-Meier & Klein, 2013

New facts about metoposaurids from Krasiejów show that they were not fully aquatic animals. 3D computational biomechanics analysis of the skull of *Metoposaurus* show that it was capable of biting prey in the same manner as semi-aquatic and terrestrial animals like *Cyclotosaurus* or modern crocodiles (Gruntmejer, Konietzko-Meier & Bodzioch, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017; Konietzko-Meier et al., 2018).

Comentario [GP30]: So, you may have heterochronic different ontogenetic stages represented in your sample!

Comentario [GP31]: Is not on the reference list

Con formato: Resaltar

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The described diversity is consistent with the experiment of Schoch (1995) and the results of Werneburg (2002) and Schoch (2010). One of the *Metoposaurus* ornamentation types from Krasiejów (T2) thus represents a more terrestrial form (associated with the more variable and unstable environment of a river or a small lake or the metamorphic adult form of facultative neotenic population), while the other represents forms more closely related to water (a large lake habitat or partially paedomorphic aquatic adults) (T1) (ecological populations – as stated by Witzmann et al., 2010; but described as species-specific; neoteny as described by Whiteman, Krenz & Semlitsch, 2005).

The adaptations in T2 favouring a more terrestrial lifestyle are:

a) The increased mechanical strength of the bones (Rinehart & Lucas, 2013) (coarser, denser, irregular sculpture, thicker clavicles);
b) Protection for a greater number of blood vessels, improving thermoregulation (Gądek, 2012) (denser sculpture, more numerous polygons and radial rows, more numerous microforamina);
c) Stronger integration of bone and skin, which is thicker in terrestrial amphibians and exfoliates (Zug, 1993; Schoch, 2001) (coarser, denser sculpture, microstriations);
d) Stronger connection of the pectoral girdle elements and, potentially, limbs (expanded anterior projection of the clavicle);
e) Faster growth revealed by histological structure (growth marks separated by zones of highly vascularised bone).

The more terrestrial character of one of the population may also be proved by:

f) Faster (at younger age) metamorphosis revealed by smaller skulls;
g) The length of limb bones not correlated with individual age (Teschner, Sander & Konietzko-Meier, 2017) or a slender or robust femur (Konietzko-Meier & Klein, 2013); 10% elongation of limbs in Anura distinctly increases migration capabilities (Pogodziński, 2015; personal communication).

The dimorphic character of clavicles described herein and the two growth patterns of dermal and long bones (humeri) (Teschner, Sander & Konietzko-Meier, 2017) suggest that the ontogeny of specimens assigned to *Metoposaurus krasiejowensis* could have proceeded via a different growth rate and time span of metamorphosis, caused by different environmental conditions. The similar number of specimens from both populations (Tc1/Tc2 – 44%/56% and Ts1/Ts2 – 53%/47%) suggests stable populations.

Apart from dermal bone ornamentation, the degree of ossification and variation in skull sizes divides metoposaurids into two groups. Smaller skulls occur in the more terrestrial type, as in *Micromelerpeton* from Germany, where smaller specimens represent an unstable lake environment

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Comentario [GP32]: Which can be also related to normal growth

Comentario [GP33]: Not in the list

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(Boy & Sues, 2000). The described type T2 reflects a more terrestrial or riparian habitat, where environmental conditions are variable and amphibians are forced to change their dwellings more often (migration between watercourses or 'stream-type' small, drying lakes; Werneburg, Ronchi & Schneider, 2007). It does not mean that 'more terrestrial/stream' metoposaurids moved efficiently on land. Modern salamanders can migrate between rivers and lakes by 'pond-hopping' (Zug, 1993). The first type reflects a more stable habitat, possibly a large lake, where animals are not forced to migrate ('pond-type'; Werneburg, 2007).

Geological, sedimentological, and other analysis of the Krasiejów site shows that both of these habitats – episodic rivers and ponds at the excavation site and a large reservoir in close proximity – may have occurred there (redeposited charophytes and Unionidae bivalves; Szulc 2005, 2007), and that conditions changed over time (Dzik & Sulej, 2007; Gruszka & Zieliński, 2008; Bodzioch & Kowal-Linka, 2012). Differences in dermal bone ornamentation constitute an adaptative answer to changes in the environment (temperature, water level, food availability) over time or to geographical differentiation of habitats, i. e. faster metamorphosis (at smaller size) as an answer to higher temperatures; or metamorphosis into terrestrial adult vs. transformation into aquatic paedomorphic individuals.

Rapid changes in the ornamentation morphology in one population (or part of the population, when weather conditions favour such solution) are possible because they are the effects of hormonally induced metamorphosis. The water temperature in which larvae live strongly affects ectothermic animals. The growth of amphibians and larval development both depend on external environmental factors. At higher temperatures, not only metabolic rate but also development rate increases (Motyl, 2008). Low temperatures reduce development rates to a greater extent than they reduce growth rate, as a result of which amphibians metamorphose after achieving larger size (Wilbur & Collins, 1973) (Ts1 skulls are usually larger than Ts2 skulls). Prey abundance might exert some influence as well (Motyl, 2008), but probably not as much (Blouin & Loeb, 1990).

The Krasiejów ecosystem changed over time. The Late Triassic climate favoured evolution of freshwater environments. In Krasiejów, small periodic reservoirs, probably also inhabited (as in the environments of the Saar-Nahe Basin), occurred along with larger more stable ones (Szulc, 2005; 2007; Gruszka & Zieliński, 2008; Szulc, Racki & Jewuła, 2015). Small reservoirs (and potentially with higher temperature) or periodic rivers forced earlier metamorphosis, dwelling on land, or migration between lakes and watercourses. On the other hand, larger lakes or the proximity of a large reservoir enabled the development of a fully aquatic (Szulc, 2005), possible neotenic population.

Large reservoirs, stable over long periods of time, enable the development of a fully aquatic (neotenic?) ecotype T1 (Tc1, Ts1), reducing the need to dwell on land by virtue of providing:

- enough room for numerous large specimens;

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- shelter from mainland carnivores;
- stable, invariable conditions;
- potentially lower temperatures.

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The ontogenetic trajectories of the two metoposaurid ecotypes from Krasiejów cannot differ on a large scale, because they are assigned to the same semi-aquatic species. However, between types there was clearly some deflection into a more aquatic or more terrestrial form. In the case of a more terrestrial (stream-type) ecomorph, the trajectory would be more condensed (Schoch, 2001).

According to the described observations, it is possible to introduce an argument about the function of temnospondyl ornamentation into the discussion. There are several hypotheses as to the function of the ornamentation, which may have been:

1. mechanical strengthening of the bone (Coldiron, 1974; Rinehart & Lucas, 2013);
2. water-loss reduction (Seibert et al., 1974);
3. integration of the bone and skin (Romer, 1947; Bossy & Milner, 1998);
4. improvement of dermal respiration (Bystrow, 1974);
5. thermoregulation (Seidel, 1979; Grigg & Seebacher, 2001);
6. acting as a metamorphosis marker (Boy & Suess, 2000);
7. buffering of acidosis and lactic acid build-up in tissues due to anaerobic activity (Janis et al., 2012).

The microstructural observations described in this manuscript support two hypotheses. Ornamentation increases the surface area of the bone (Rinehart & Lucas, 2013) and thus improves its thermoregulatory abilities and probably its integration with the skin, as histological thin sections show many Sharpey's fibres residing deep in the ridges (Gądek, 2012). Moreover SEM photographs presented herein show more or less numerous striations (skin and bone contact) and vascular foramina.

The hypothesis put forward by Janis et al. (2012) of dermal bone ornamentation developed in primitive tetrapods for the purpose of buffering acidosis and lactic acid build-up in their tissues due to anaerobic activity is also plausible. This would enable the amphibians to spend longer times on land and thus better exploit the terrestrial environment. This statement is in agreement with a study by Witzmann et al. (2010), who stated that terrestrial forms (according to species or population) show more pronounced sculpture than aquatic forms.

Summary

The diversity of metoposaurid material from the 'Trias' site at Krasiejów (SW Poland) includes the ornamentation of clavicles and remarks of the ornamentation of skulls (although histological character suggests that all types of bones possess two types of bone growth). Similar differences in dermal bone ornamentation in Temnospondyli were cited as ecologically dependent by Witzmann et al. (2010); however, these differences were assigned to particular taxa. Detailed analysis of large probes from one species shows that ecologically induced ornamentation differences can be observed within one species (from a single site).

Except for UOPB1165 specimen, the taxonomical variety of the material was excluded. Observed differences in polygon shape, area, sculpture density, regularity and others (Table 1, Table 6) could be the result of individual, ontogenetic, sexual or ecological variation. Although some sort of sexual dimorphism or ontogenetic changes cannot be excluded, the most probable explanation for the described variation is ecological difference between two populations as stated by Witzmann et al. (2010); or existence of facultatively neotenic populations. Described ornamentation types within one semi-aquatic species possess characteristic of either more-terrestrial or more-aquatic taxa.

Assuming that the more-terrestrial or 'stream-type' form can be distinguished by its smaller size (earlier metamorphosis), coarser and more complicated sculpture, more numerous ridges for protection of more numerous blood vessels, and a stronger connection between bones and skin for increasing mechanical strength for land-dwelling the more-aquatic or 'pond-type' form is characterised by greater size (later metamorphosis) and sparser, more regular ornamentation. Comparable differences in ontogenetic trajectories were described in *Sclerocephalus* by Schoch (2010).

This ecological diversity corresponds with the geological description of Triassic Krasiejów, which includes redeposited material after flash floods, an environment with periodic rivers and ponds, and a large, more stable reservoir in close proximity, as described by Szulc (2005, 2007), Gruszka & Zieliński (2008), Bodzioch & Kowal-Linka (2012), and Szulc, Racki, & Jewuła (2015). The palaeoenvironment of the site, similar to modern Gilgai relief (Szulc, 2005; 2007; Szulc, Racki & Jewuła, 2015) could be the habitat of more terrestrial population, while the more aquatic one could have lived at some distance (closer – Heckert et al., 2010; or further – Konieczna, Belka & Dopieralska, 2015). One population with aquatic (paedomorphic) and terrestrial (metamorphic) individuals is also possible. In this case all metoposaurids could have lived in the same area with the paedomorphic concentrating in deeper habitats (Whiteman & Semlitsch, 2005) and metamorphic being more terrestrial (moving between shallow ponds and streams). Time difference between population is also plausible.

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Comentario [MA34]: We meant here growth patterns different between populations. More aquatic – more slope ontogenetic trajectory; more terrestrial – more steep trajectory. This is why specimens of the same age from different populations are different. Which is not the same as differences between specimens of various age in one population.

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The isotopic (or REE) analysis in the future may confirm the most probable explanation for metoposaurid ornamentation diversity and may provide valuable insight into the mechanism between it. More information about possible ornamentation character diversity can be obtained in the future considering distribution of shape (geometric morphometrics), possibly in all of the Metoposauridae.

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Eliminado:

Literature

Alberch, P. 1989. Development and the evolution of amphibian metamorphosis. *Fortschritte der Zoologie*, **35**: 163-173.

Antczak, M. 2016. Late Triassic aetosaur (Archosauria) from Krasiejów (SW Poland): new species or an example of individual variation? Geological Journal, **51**: 779-788.

Babik, W., Rafiński, J. 2000. Morphometric differentiation of the moor frog (*Rana arvalis* Nilss.) in Central Europe. *Journal of Zoological Systematics and Evolutionary Research*, **38:** 239-247.

Blouin, M. S., Loeb M. L. G. 1990. Effects of environmentally induced development-rate variation of the head and limb morphology in the green tree frog, *Hyla cinerea*. *The American Naturalists,***138 (3)**: 717–728.

Bodzioch, A., Kowal-Linka, M. 2012. Unraveling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **346-347**: 25–36.

Bodzioch, A. 2015. Idealized model of mineral infillings in bones of fossil freshwater animals, on the example of Late Triassic metoposaurs from Krasiejów (Poland). *Austin Journal of Earth Science*, **2:** 1–6.

Bossy, K. A., Milner, A. C. 1998. Order Nectridea Miall 1875. W: Wellnhofer, P. (red.). Handbuch der pala¨oherpetologie, 1. Mu¨nchen: Verlag Dr. Friedrich Pfeil: 73–131.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon-Trias). – *Paläontologische Zeitschrift*, **48**: 236–268.

Boy, J. A. 1988. Über einige Vertrteter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (? höchstes Karbon-Perm). 1. *Sclerocephalus*. – *Paläontologische Zeitschrift*, **62**: 107–132.

Boy, J. A. 1990. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstesKarbon – Perm). 3. *Onchiodon*. *Paläontologische Zeitschrift*, **64**:287–312.

Boy, J. A., Sues, H. D. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. In: Heatwole, H., Carroll, R. L. (red.). Amphibian Biology 4. Palaeontology. Chipping Norton: Surrey Beatty: 1150–1197.

Brusatte, S. L, Butler R. J., Mateus O., Steyer J. S. 2015. A new species of *Metoposaurus* from the Late Triassic of Portugal and comments on the systematics and biogeography of metoposaurid temnospondyls. *Journal of Vertebrate Paleontology*, **DOI**: 10.1080/02724634.2014.912988.

Bystrow, A. P. 1947. Hydrophilous and xerophilous labyrinthodonts. Acta Zoologica (Stockholm), **28**: 137190–274164.

Comentario [GP35]: Which isw the correct? 1974 or 1947?

Chaterjee, S. 1986. The Late Triassic Dockum vertebrates: their stratigraphic and paleobiologic significance. In: Padian, K. ed. The beginning of the age of dinosaurs: 140–150. New York, Cambridge University Press.

Comentario [GP36]: Not cited

Coldiron, R. W. 1974. Possible functions of ornament in labyrinthodont amphibians. Occasional Papers of the Museum of Natural History of Lawrence, 33: 1–19.

Collins, J. P., Cheek, J. E. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. *American Zoologist*, **23**: 77–84.

Davidow-Henry, B. R. 1989. Small metoposaurid amphibians from the Triassic of western North America and their significance. In: Lucas, S. G., Hunt, A. P. (eds). Dawn of the age of dinosaurs in the American southwest: 278-292. New Mexico Museum of Natural History, Albuquerque.

Dubois, A., 1982. Notes sur les grenouilles brunes (groupe de Ranatemporaria) I. Introduction. *Alytes*, **1**: 56–70.

Duellman, W., Trueb, L. 1986. Biology of Amphibians. Mc Graw-Hill Book Comp. New York, St. Louis, San Francisco, pp. 1–670.

Dzik, J., Sulej, T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologia Polonica*, **64**: 3–27.

Dzik, J., Sulej, T. 2016. An early Late Triassic long-necked reptile with a bony pectoral shield and gracile appendages. Acta Palaeontologica Polonica, 61(4), **DOI**: 10.4202/app.00276.2016

Con formato: Portugués (Brasil)

Emerson, S. B. 1986. Heterochrony and frogs: the relationship of a life history trait to morphological form. *American Naturalist*, **127**: 67–183.

Emerson, S. B., Travis, J., Blouin, M. 1988. Evaluating a hypothesis about heterochrony: larval life history traits and juvenile hind-limb morphology in *Hyla crucifer*. *Evolution*, **42**: 68–78.

Fortuny, J., Marcé-Nogué, J., Konietzko-Meier, D. 2017. Feeding biomechanics of Late Triassic metoposaurids (Amphibia: Temnospondyli): a 3D finite analysis approach. *Journal of anatomy*, **DOI**: 10.1111/joa.12605

Fritzsch, B. 1990. The evolution of metamorphosis in amphibians. *Journal of Neurobiology*, **21**: 1011–1021.

Frobisch, N. B., Schoch, R. R. 2009. The largest specimen of *Apateon* and the life history path way of neoteny in the Paleozoic temnospondyl family Branchiosauridae. *Fossil Record*, **12(1)**: 83–90.

Gądek, K. 2012. Palaeohistology of ribs and clavicle of *Metoposaurus diagnosticus* from Krasiejów (Upper Silesia, Poland). *Opole Scientific Society Natural Journal*, **45**: 39–42.

Ghioca-Robrecht, D. M., Smith, L. M., Densmore, L. D. 2009. Ecological correlates of trophic polyphenism in spadefoot tadpoles inhabiting playas. *Canadian Journal of Zoology*, **87**: 229–238.

Comentario [GP37]: Not cited

Grigg, G., Seebacher, F. 2001. Crocodilian thermal relations. W: Grigg, G. C., Seebacher, F., Franklin, C.E., (red.). Crocodilian biology and evolution, Chipping Norton: Surrey Beatty: 297–309.

Gruntmejer, K., Konietzko-Meier, D., Bodzioch, A. 2016. Cranial bone histology of *Metoposaurus krasiejowensis* (Amphibia, Temnospondyli) from the Late Triassic of Poland. PeerJ 4:e2685 https://doi.org/10.7717/peerj.2685.

Gruszka, B., Zieliński, T.2008. Evidence for a very low-energy fluvial system: a case study from the dinosaur-bearing Upper Triassic rocks of Southern Poland. *Geological Quarterly*, **52**: 139–252.

Janis, C.M., Devlin, K., Warren, D.E. and Witzmann, F., 2012, Dermal bone in early tetrapods: A paleophysiological hypothesis of adaptation for terrestrial acidosis. *Proceedings of the Royal Society B – Biological Sciences*, **279**: 3035–3040.

Konieczna, N., Belka, Z., Dopieralska, J., 2015. Nd and Sr isotopic evidence for provenance of clastic material of the Upper Triassic rocks of Silesia, Poland. Annales Societatis Geologorum Poloniae, **85**: 675–684.

Konietzko-Meier, D., Klein, N. 2013. Unique growth pattern of *Metoposaurus diagnosticus krasiejowensis* (Amphibia, Temnospondyli) from the Upper Triassic of Krasiejów, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **370**: 145-157.

Konietzko-Meier, D., Sander, P. M. 2013. Long bone histology of *Metoposaurus diagnosticus* (Temnospondyli) from the Late Triassic of Krasiejów (Poland) and its palaeobiological implicatios. *Journal of Palaeontology*, **33**: 1003–1018.Konietzko-Meier, D, Gruntmejer, K., Marcé-Nogué, J., Bodzioch, A., Fortuny, J. 2018. Merging cranial histology and 3D-computational biomechanics: a review of the feeding ecology of a Late Triassic temnospondyl amphibian. *PeerJ*, 6:e4426; **DOI**: 10.7717/peerj.4426

Krenz, J. D, Sever, D. M. 1995. Mating and oviposition in paedomorphic *Ambystoma talpoideum* precedes the arrival of terrestrial males. *Journal of Herpetology*, **51**: 387–393.

Kupfer, A. 2007. Sexual size dimorphism in amphibians: an overview. Chapter 5. In: Fairbairn, D. J., Blanckenhorn, In. U., Szekely, T. (eds.). Sex, size and gender roles: evolutionary studies of sexual size dimorphism: 50–59, Oxford University Press.

Lucas, S. G. 2015. Age and correlation of Late Triassic tetrapods from southern Poland. *Annales Societatis Geologorum Poloniae*, **85**: 627–635.

Lucas, S. G., Rinehart, L. F., Heckert, A. B., Hunt, A. P., Spielmann, J. 2016. Rotten Hill: a Late Triassic bone-bed in the Texas Panhandle, USA. New Mexico Museum of Natural History and Science Bulletin, **72**: 1–97.

Michimae, H., Wakahara, M. 2002. A tadpole-induced polyphenism in the salamander *Hynobius retardatus*. *Evolution*, **56**: 2029–2038.

Motyl, M. 2008. Od czego zależy metamorfoza [What determines the metamorphosis]. [amphibia.org.pl].

Norris, D. 1999. Thyroid hormones, in subavian vertebrates. In: Encyclopedia of Reproduction (Knobil, E., Neill J. D. eds), 4: 807–812. Academic Press, New York.

Con formato: Portugués (Brasil)

Comentario [GP38]: There are other **Konietzko-Meier in the text that were not included in the reference list- Please check!**

Con formato: Portugués (Brasil)

Eliminado: ,

Nyman, S., Wilinson, R. F., Hutcherson, J. E. 1993. Cannibalism and size relations in a cohort of larval ringed salamanders (*Ambystoma annulatum*). *Journal of Herpetology*, **27**: 78–84.

Piechowski, R., Dzik, J. 2010. The axial skeleton of Silesaurus opolensis. *Journal of Vertebrate Palaeontology*, **30**: 1127-1141.

Pfennig, D.W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia*, **85**: 101–107.

Pfennig, D. W. 1992. Polyphenism in spadefoot toad tadpoles as a locally-adjusted evolutionarily stable strategy. *Evolution*, **46**: 1408–1420.

Pfennig, D. W., McGee, M. 2010. Resource polyphenism increases species richness: a test of the hypothesis. *Philosophical Transactions of the Royal Society B*, **365**: 577–591.

Rafiński, J., Babik, W. 2000. Genetic differentiation among northern and southern populations of the moor frog *Rana arvalis* Nilsson in Central Europe. *Heredity*,**84**: 610–618.

Rinehart, L. F., Lucas, S. G., Heckert, A. B., Hunt, A. P. 2008. Preliminary analysis of growth and age structure of *Buettneria* (Amphibia: Metoposauridae) assemblages from the Upper Triassic of West Texas and New Mexico. *New Mexico Geology,* **30**: 56.

Rinehart, L. F., Lucas, G. L. 2013. The functional morphology of dermal bone ornamentation in temnospondyl amphibians. In: Tanner, L.H., Spielmann, J.A., Lucas, S.G., eds., 2013, The Triassic System. *New Mexico Museum of Natural History and Science, Bulletin*, **61.**

Roff, D. E. 1996. The evolution of threshold traits in animals. *Quarterly Review of Biology*, **71**: 3–35

Romer, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology at Harvard*, **99**: 1–368.

Safi, R., Bertrands, S., Marchand, O., Duffraisse, M., Luze, A., Vanacker, J., Maraninchi, M., Margotat, A., Demeneix, B., Laudet, V. 2014. The axolotl (*Ambystoma mexicanum*), a Neotenic Amphibian, Express Functional Thyroid Hormone Receptors. *Endochrynology*, **154**: 760–722.

Sanchez, S., Schoch, R. R. 2013.Bone Histology Reveals a High Environmental and Metabolic Plasticity as a Successful Evolutionary Strategy in a Long-Lived Homeostatic Triassic Temnospondyl. *Evolutionary Biology*, **DOI**: 10.1007/s11692-013-9238-3.

Schmidt, K. P. 1938. A geographic variation gradient in frogs. *Field Museum of Natural History. Zoological series*, Chicago **20**: 377–382.

Schoch, R. R. 1995. Heterochrony in the evolution of the amphibian head: 107–124. In: McNamara K., ed. Evolutionary change and heterochrony. Wiley, Chichester, U.K

Schoch, R. R. 2001. Can metamorphosis be recognized in Paleozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **220(3**): 335–367.

Schoch, R. R. 2002. The evolution of metamorphosis in temnospondyls. *Lethaia*,**35**: 309–327.

Schoch, R. R. 2004. Skeleton formation in the Branchiosauridae: a case study in comparing ontogenetic trajectories. *Journal of Vertebrate Paleontology*,**24:** 309–319.

Schoch, R. R. 2009. Life-cycle evolution as response to diverse lake habitats in Paleozoic amphibians. *Evolution*, **63**: 2738–2749.

Schoch, R. R. 2010. Heterochrony: the interplay between development and ecology exemplified by a Paleozoic amphibian clade. *Paleobiology*, **36(2)**: 318–334

Schoch, R. R., Witzmann, F. 2012. Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. *Lethaia*, **45**: 371–385.

Seidel, M. R. 1979. The osteoderms of the American Alligator and their functional significance. *Herpetologica*, **35**: 375–380.

Seibert, E. A., Lillywhite, H. B., Wassersug, R. J. 1974. Cranial co-ossification in frogs: relation483 ship to rate of evaporite water loss. *Physiological Zoology*, **47**: 261–265.

Skrzycki, P., 2015. New species of lungfish (Sarcopterygii, Dipnoi) from the Late Triassic Krasiejów site in Poland, with remarks on the ontogeny of Triassic dipnoan tooth plates. *Journal of Vertebrate Palaeontology*, **35 (5), DOI**: 10.1080/02724634.2015.964357

Sulej, T. 2002. Species discrimination of the Late Triassic temnospondyli amphibian *Metoposaurus diagnosticus. Acta Palaeontologica Polonica*,**47**: 535–546.

Szulc, J. 2007. Stop I.4. Krasiejów—inactive clay pit and tetrapod exposition. In: Szulc, J., Becker, A. eds.. *International Workshop on the Triassic of Southern Poland*. Polish Geological Institute and Institute of Geological Sciences, Jagiellonian University,Cracow, 53–55.

Szulc, J., Racki, G., Jewuła, K. 2015. Key aspects of the stratigraphy of the Upper Silesian middle Keuper, southern Poland. *Annales Societatis Geologorum Poloniae*, **85**: 557–586.

Teschner, E. M., Sander, P., Konietzko-Meier, D. 2017. Variability of growth pattern observed in Metoposaurus Krasiejowensis humeri and its biological meaning. *Journal of Iberian Geology*, **DOI**: 10.1007/s41513-017-0038-y.

Walls, S. C., Belanger, S. S., Blaustein, A. R. 1993. Morphological variation in a larval salamander: dietary induction of plasticity in head shape. *Oecologia*, **96**: 162–168.

Werneburg, R., 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. Veröff. *Naturhistorisches Museum Schloss Bertholdsburg Schleusingen*, **6**: 75–99.

Werneburg, R., 2002. *Apateon dracyiensis* - eine frühe Pionierform der Branchiosaurier aus dem Europäischen Rotliegend, Teil 2: Paläoökologie. Veröff. *Naturhistorisches Museum Schloss Bertholdsburg Schleusingen*,**17**: 17–32.

Werneburg, R., Ronchi, A., Schneider, J. W. 2007. The Early Permian Branchiosaurids (Amphibia) of Sardinia (Italy): Systematic Palaeontology, Palaeoecology, Biostratigraphy and Palaeobiogeographic Problems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**: 383-404.

Comentario [GP39]: Sulej, 2005, 2010, Sulej & Majer, 2005 were cited but not included in the list

Comentario [GP40]: Szulc, 2005 is cited but not included in the list

Wilbur, H. M., Collins, J. P. 1973. Ecological Aspects of Amphibian Metamorphosis: Nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. *Science*, **182(4119)**: 1305–1314.

Witzmann, F., Henning, S., Muller, J., Kardjilov N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. *Zoological Journal of Linnean Society*, **160**: 302–340.

Whiteman, H. H. 1994. Evolution of facultative paedomorphosis in salamanders. *Quarterly Review of Biology*, **69**: 205–221.

Whiteman, H. H., Krenz, J. D., Semlitsch, R. D. 2005. Intermorph breeding and the potential for reproductive isolation in polymorphic mole salamanders (*Ambystoma talpoideum*). *Behavioral Ecology and Sociobiology*, DOI 10.1007/s00265-005-0139-z.

Whiteman, H. H., Semlitsch, R. D. 2005. Asymmetric reproductive isolation among polymorphic salamanders. *Biological Journal of the Linnean Society*, **86**: 265–28.

Zalecka K. 2012. Międzyobojczyk Metoposaurus diagnosticus krasiejowensis (Amphibia, Temnospondyli) ze stanowiska dokumentacyjnego „Trias" w Krasiejowie. Unpublished Master Thesis. Opole University, pp. 81.

Zug, G. R. 1993. Herpetology. An introductory biology of amphibians and reptiles. Academic Press Limited, London. ISBN 0-12-782620-3.

Figure captions

Fig. 1. Localization and geological map of Krasiejów (Bodzioch & Kowal-Linka, 2012).

Fig. 2. Basic ornamentation features explanation (A). Clavicles assigned to two types of ornamentation (B).

Fig. 3. Thickness of the bone in particular types and ontogenetic stages. Measurements made at the border of polygonal and radial ornamentation areas.

Fig. 4. Ratio of the bone width and amount of radial ridges (measurement taken 2,5 cm from ossification centre). A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

Fig. 5. Ratio of polygon number and surface. A: Considering appointed types, showing two subsets within metoposaurid data; B: Considering individual age, showing no subsets within metoposaurid data.

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Fig. 6. Ratio of multipolygon and all polygons number. A: Considering appointed types, showing two subsets within metoposaurid data;B: Considering individual age, showing no subsets within metoposaurid data.

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Fig. 7. Percentage of hexagonal, pentagonal and other polygons. A: Considering appointed types, showing two subsets within metoposaurid data ;B: Considering individual age, showing no subsets within metoposaurid data.

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Fig. 8. SEM (SE) and histological observations of clavicle radial ridges for Tc1.

Fig. 9. SEM (SE) and histological observations of clavicle radial ridges for Tc2.

Fig. 10. Types of skulls ornamentation of metoposaurids from Krasiejów. Blue area represents surface covered with radial ornamentation. Size of the skulls in Table 4.

Fig. 11.Comparison of analyzed skull material (examples) with reconstructions of skulls of *Metoposaurus diagnosticus, M. krasiejowensis and M. algavrensis.*

A: *M. diagnosticus*; B: *M. krasiejowensis*; C: *M. algavrensis*; D: UO/PP02 (Ts2); E: UO/PP09 (Ts1); F: UO/PP13 (Ts1); G: UO/PP04 (Ts1). A-C after Brusatte et al., 2015.

Fig. 12. Skull measurements.

Tables

Types numerical codes:

Metoposaurus 1(aquatic, pond-type): 1 1 1 2 1 1 3 1 1 1 1 1 1 1 1 1 2 1 1 1 ?
Metoposaurus 2(terrestrial, stream-type): 2 2 2 1 3 2 2 2 1 2 2 2 2 2 2 1 2 2 1 1 ?

Table 1. Clavicles ornamentation.	ZPAL AbIII 397	UOPB 1152	**UOPB 1153**	**UOPB 1154**	**UOPB 1155**	**UOPB 1156**	**UOPB 1157**	UOPB 1158	UOPB 1159	UOPB 1160	UOPB 1161	UOPB 1162	**UOPB 1163**	**UOPB 1164**	**UOPB 1165**	UOPB 1166	UOPB 1167	**UOPB 1168**	**UOPB 1169**	UOPB 1170	UOPB 1171	**UOPB 1172**	UOPB 1173	UOPB 1174	**UOPB 1175**	UOPB 1176
	Cyclo.	T1	**T2**	**T2**	**T2**	**T2**	**T2**	T1	T1	T1	T1	T1	**T2**	**T2**	**T2**	T1	T1	**T2**	**T2**	T1	T1	**T2**	T1	T1	**T2**	T1
Age (Zalecka 2012): juvenile (J), intermediate (I), adult (A)		A	I	J	J				J	J/I				A	J/I	I	J	I	J	J	**I**	I	I	I	A	J
Regular (1), irregular (2)	1	1	2	2	2	2	2	1		1	1	1		2	2	1	1	2	2	1	1	2	1	1	2	1
Very fine (0), fine (1), coarse (2), very coarse (3)	3	1	1	2	2	2	2	1	1	1	2	2		1	2	1	0	2	2	0	1	2	1	1	2	1
Very sparse (0), sparse (1), dense (2)	0	1	2	2	2	1	2	1	1	1	1	1		2	2	1	2	2	2	2	1	1	2	1	2	1
Av. polygon diameter/av. ridge width **[<4 (1), >4 (2), >6 (3)]**	3	2	1		1	1	1	2		2	2	2		1	1	2	1		1	1	1	1				
Distinct borders of polygonal field (1), borders partially hard to recognize (2), hard to recognize (3)	3	1	2		3					1	1	1		3		1	1		2	1	1	3	1		3	1
Ridge quantity/bone width [measurement 2,5cm from polygon border]: **>2,3 (2), <2,3 (1), <2 (0)**	0	1	2	2					1		1	1		2	2	1		2	2	1	1					
Nodal points slightly wider than ridges (1); some nodal points distinctly wider than ridges (2); nodal points distinctly wider than ridges (3) **[Witzmann et al. 2010]**	3	3	2	1	1	1	1	3		3	3	2		2	2	3	3	1	1	3	3	1	1	3	1	3
Ridges edged (1); round or edged (2); round (3) **[Witzmann et al. 2010]**	3	1	2	3	3	3	2	1	2	2	2	2	3	2		1	1	3	3	2	2	2	2			
Deep polygons (1),deep or shallow polygons (2); shallow polygons (3)	1	1	1	3	3	3	3	1		1	1	2		2	1	1	1	2			1	2				
Polygon shape:**>50% hexagons (1), <50% hexagons (2), >50% quadrangle (3)**	3	1	2	2	2	2	2	1		1	1	1		2	2	1	1	2	2	1	2	2	1	1	2	1
Polygon size: usually small (1), usually large (2), very large (3) **[large: >0,4mm diameter].**	3	1	2	2	2	2	2	1		1	1	1		2	1	1	1	2	2	2	1	2	1	1	2	1
Multipolygons: several or none (1), numerous(2) **[more than 11]**	1	1	2	2	2	1	2	1		1	1	1		2	2	1	1	2	2	1	1	2	1	1	2	1
Polygon field shape: square (1), rectangular (2), elongated (3)	3	1	2		2			1			1			2		1	1		2		1	2	1			1
Ridge height: lower than nodal points (1), almost equal to nodal points (2)		1	2	2	2	2	2	1		1	1	2	2	2	1	1	2	1	2	1	1	2	1		2	
Ossification degree: low (1), high (thick bones) (2)	2	1	2	2	2	2			1	1	2	1		2	2	1	2	2	2	2	1	2		2	2	1
Anterior clavicle projection: small and flat (1), round and expanded (2), more than 45 deg. (3)	3	1	2	2	2	2				1	1			2	2		1	2	2	2	1	2	2			

More ramificatios: opening (1), closing (2)		1	1	1	1			2						1								
Shape of the radial ridges: undulated (1), straight (2)	2	2	2	2	2				2			2	2	2	2							
Ridge surface (macroscale): bumps (1), large cuts (2), small cuts (3)		1	2	2	3		2	3	3	3	3			1								
Ridge width<half of the polygon diameter: yes (1), no (2) (Witzmann et al. 2010)		1	1		2	1	1	1			1	1		1	1							
Radial ridges constrictions and height differences: distinct (1), not distinct (2)		1	1	2	2	2			1	1	1	2	1	1	1	1	2	2	2		2	1
Shape of the clavicle (angle) > **100^o (1), < 100^o (2)**	2	1		2	2						1			2		1		1			2	

Table 3. Skulls ornamentation characteristcs.

		UO/PP01	**UO/PP02**	UO/PP04	UO/PP06	**UO/PP08**	UO/PP09	**UO/PP12**	UO/PP13	UO/PP14	**UO/PP16**	UO/PP17	**UO/PP18**	**UO/PP20**	uam/mz/586
Parietal-supratemporal ornament	Mostly: polygons (2), radial ridges (1)		2	1	1	2	1	2	1	1	2	1	2	2	1
Postfrontal-postorbital ornament	Mostly: polygons (3), Polygons and radial ridges (2), radial ridges (1)		3	2	1	3	2	3	2		2	2	3	3	2
Squamosal ornament	Mostly: polygons (2), radial ridges (1)	1	1	1			1	1	1		1	1			1
Multipolygons	Occurs (2), not occur (1)		2	1				2	1		2	2			1
Polygon shape	Irregular (2), mostly hexagonal (1)	2	2	1		2	1	2	1	1	2	1	2	2	1
Polygon size	Small (2), large (1)		2	2		2	1	2	1	2	2	1	2	2	2
Polygon den sity	Sparse (1), dense (2)		2	1		2	1	2	1	x	2	x	2	2	1

Table 2. SEM observations of the clavicles.

	UOPB 1152	**UOPB 1153**	**UOPB 1155**	**UOPB 1157**	UOPB 1160	UOPB 1161	**UOPB 1163**	**UOPB 1164**	UOPB 1167	**UOPB 1168**	**UOPB 1169**
	x	v	V	v	v	v	v	v	x	v	v
Striations [v – distinct, numerous x - few]	x	v	v	v	x	x	v		x	v	v
Small foramina [v –more than 7/100um^2 x – less than 7/100um^2]	x	v	v	v	x	x	v	v	x	v	v
Large foramina [v - more than1/1 mm of length x – less than 1/1mm of length]	x	x	v	v	x	v	v	v	x	v	x

Table 4. Skull measurements [in cm].

	UO/PP01	UO/PP02	UO/PP03	UO/PP04	UO/PP05	UO/PP06	UO/PP07	UO/PP08	UO/PP09	UO/PP10	UO/PP11	UO/PP12	UO/PP13	UO/PP14	UO/PP15	UO/PP16	UO/PP17	UO/PP18	UO/PP19	UO/PP20
Skull roof																				
SL	25,2	28,4		35		34		28,8	43,1			28	42,7	28,5		30,3	34,1	35,4	32,7	33
SW	21	24,5		28,6		31		~23	36,8			~25,8	37	26,7		26,5	~26	27,2	28,6	~29
IN						5		4,7	6			~4,5	6	~4				4,4	4,1	5
IOL	7,5	7,6		9,1		8,4		8,5	12			7,8	12,1	8		9	9	8,8	9	9
AOL	10					14,2		13	13,5			9,4	13,7	8,9		10	10,3	11,1	10,1	10,5
POL	16,8	16		18,3		14,9		15,9	25,8			16,4	21,4	13,8		18,4	19,2	17,9	17,4	18
SE	5	7,2				6,8		6,2	10			6,4	10,7	8,1		8,2	8,5	8,8	7,5	8,3
ME	7	8,5		9,6		8,8		9	11,5				13,8	9,8		11	11,6	11	9,7	11,5
NL						2,6		2,1	3,6				3,9			3,1	3,2	3,4	~2,8	2,2
I (L)	2	2		1,7		1,6		1,8	2,5			1,8	2,3	1,9		2	1,9	2,3	2,3	2
I (P)	2	2		2,2		2,2		2,2	3			2	3	1,9		1,9	2,3	2	2	2,7
M		4,3				3,9		3	4				3	3,1			4	3,8	3,4	4,2
NO	6,1	6,3		7,9		7,4			9,8			6,5	9	6,7		6,4	7,2	7,5	7,4	7,5
LO	2,8	4		4,6		4		3,7	5,6			3,9	5,6	36		4	4	4,6	4,3	3,4
MW		16		19,4		18,6		18	24			15,7	23,5	17,2		19	19,1	19	18,5	19
Palate																				
LP			30		30,3					32,1	33,4				30					
NP.			9,9		10										7,9					
Y			15,4		15,1		14			14	16				14,7					
R			10,6		11,2		11,4			14,1	13,2				11,6					
B			23,5		~27		20,4			26,7	29				~24					
O															4,4					
E			6												4,4					
G			4,6																	

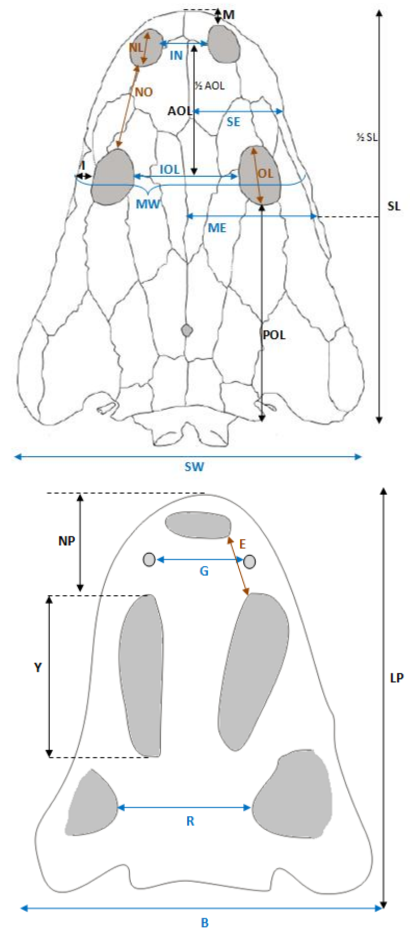

Table 5. Statistical tests.		p-value	
		T1	T2
av. polygon diameter/av. ridge width	Shapiro-Wilk Test	0,55655	0,24746
	Test F	0,321792	
	Test T	**0,00106**	
multipolygon number	Shapiro-Wilk Test	0,146977	0,04937
	Test U	**0,001676**	
ridge number/bone width	Shapiro-Wilk Test	0,0703221	0,010253
	Test U	**0,035556232**	
qualitative data	Shapiro-Wilk Test	2,587E-07	0,541135
	Test U	**0,000194**	

Table 6. Diagnosis and remarks on two populations of *M. krasiejowensis*.

	Type 1	Type 2
Diagnosis – clavicle ornamentation	Less numerous radial ridges	More numerous radial ridges
	Smaller ossification degree	Higher ossification degree
	Regular and fine ornamentation	Irregular and coarse ornamentation
	Sparse ornamentation	Gęsta ornamentacja kości skórnych
	Mostly hexagonal polygons	Mostly pentagonal (and other) polygons
	Few multipolygons	Numerous multipolygons
	Distinct border of ossification centre, square ossification centre	Border of ossification centre difficult to distinct, elongated ossification centre
	Polygonal ornamentation covering smaller area	Polygonal ornamentation covering larger area
	Less numerous microforamina and striations on the radial ridges	More numerous microforamina and striations on the radial Bridges
	Growth Marks in close proximity within almost avascular upper cortex	Growth Marks separated by vascularised zones
Remarks	Mostly radial ornamentation in the postorbital part of the skull	Mostly polygonal ornamentation in the postorbital part of the skull
	Larger skulls	Smaller skulls
	Two growth patterns seen in femora and humeri (Konietzko-Meier and Klein, 2013; Teschner, Sander & Konietzko-Meier, 2017)	

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