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

Mateusz Antczak[1], Adam Biodzioch[2]

[1] Institute of Geology, Adam Mickiewicz University of Poznan, Poznan, Poland

[2] Department of Biosystematics, University of Opole, Opole, Poland

Abstract:

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

Methods. To analyse the observed diversity of *Metoposaurus krasiejowensis* temnospondyli amphibians from the Late Triassic deposits in Krasiejów (Opole Voivodeship, Poland), the characteristics of the ornamentation of 25 clavicles and 21 skulls (such as grooves, ridges, tubercules) were observed on macro- and microscales, including the use of a scanning electron microscope for high magnification. The characteristics of the ornamentation of these bones served for taxonomical and ecological analysis (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, previous studies on temnospondyl amphibians and the geology of the Krasiejów site suggest that the most probable explanation for differences in ornamentation within *Metoposaurus* individuals is the ecological variation between populations of different environments, with types of ornamentations being adaptations to more aquatic or more terrestrial lifestyle.

Introduction

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 terrestrial 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), fossils of large temnospondyl amphibians 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; 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 and the same 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 the ornamentation elements of metoposaurid clavicles (and as a remark: skull bones) were analysed. The material derived from the 'Trias' site at Krasiejów (SW Poland; Fig. 1), where a very rich accumulation of fossils was found. The fine-grained (mudstones and claystones) Late Triassic (Carnian, according to Dzik & Sulej, 2007; Lucas, 2015; Norian, according to Szulc, 2005; 2007; Szulc, Racki & Jewuła, 2015;) 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 which probably occurred during a heavy rainy season (Bodzioch & Kowal-Linka, 2012), is especially abundant in fossils, including *Metoposaurus krasiejowensis*. 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 side: UO/PP01–20) were analysed in detail (Tables 1–3). Morphometric measurements for 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 presented *in situ* in a palaeontological pavilion 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).

The characteristics of the polygonal and radial structure of clavicles were described, using over 20 features, including some of the 12 described 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 behind 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 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, were the largest ones (UOPB1152 ~19,5cm x 9,7cm, UOPB1164 ~20cm x 9cm), while the youngest were usually of small size (UOPB1166 ~12cm x 6cm, UOPB1171 ~ 10cm x 5cm).

Observations

Diagnosis: Clavicles

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 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 **type 2 (Tc2)** possesses 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, the anterior process is usually round and expanded (Fig. 2).

The distribution of certain characteristics according to relative individual age or type assignment is presented on figures 3–7. All plots show very interesting and important bimodal distribution of the parameters, which are independent of estimated relative individual age of specimens. UOPB1165 specimen not fitting any of this types might be the representative of different taxon.
In table 5 results of conducted statistical test are presented – F and T or U, dependently on the data distribution. Considering described types as different groups, quantitative and qualitative data shows that they differ significantly ($\alpha = 0{,}05$).

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 (Figs. 9). This difference in histological patterns are analogous to different growth strategies described in the ground of long bones (Teschner, Sander & Konietzko-Meier, 2017).

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 centres 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 well 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.

An important fact is that the skulls classified as Ts2 were 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).

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 or in dermal bone measurements, it is 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 typical for *Metoposaurus,* being strongly distinct from *Cyclotosaurus intermedius* (ZPAL/AbIII/397: *Cyclotosaurus* possess distinctly larger, rhomboidal and elongated polygons, large ossification centre but with few polygons, thick and rounded radial ridges). 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 *M. Krasiejowensis.* The occurrence of some other taxon is possible because of redeposited character of the fossils. However, in skulls, the expansion angle of the sutures separating the parietal from the supratemporal vary between 19 and 26° which is characteristic of *M. krasiejowensis* instead of *M. diagnosticus* (around 13°) (Sulej, 2002). According to parietal character all skull specimens belong to *Metoposaurus krasiejowensis* species.
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 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., in prep; 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) ornaments 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 . 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 once again cannot be used to explain ornamentation variety, as two types of sculpture occur in smaller and larger specimen. 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, but there are exceptions.

3. **Sexual dimorphism.** Although it cannot be undoubtedly denied the lack of differences in the morphometry and shape of the skulls (Urban & Berman, 2007) or clavicles as well as a lack of differences in dentition and postcranial material contradicts this hypothesis (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 of '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 evidence (Urban & Berman, 2007). Different growth strategy seen in clavicles (Figs. 10-11), 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 indicates different sexes, but was 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 this interpretation can be rejected.
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 characteristic of rather terrestrial taxa (i. e. *Seymouria, Eryops*, see: Witzmann et al., 2010). The variety seen within *M. krasiejowensis* allow to expand 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 which remains are deposited in one bone-bed is possible, because of the bone-bed character (material partially redeposited, possibly from large area, and partially local) (Bodzioch & Kowal-Linka, 2012; Bodzioch, 2015).

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

The Late Triassic Krasiejów environmental conditions may have even contributed to the formation of a neotenic population (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 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 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 rainy and dry seasons occurred. Associated with this changes in water-level, food availability, living space, 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 single population (no geographical separation is needed) – spatial separation of morphs may occur instead, with the paedomorphic concentrating in deeper habitats (Whiteman & Semlitsch, 2005).

Ornamentation and lifestyle

The environmental differentiation is the most likely explanation regardless of whether caused by facultative neoteny or geographical separation. Thus, described ornamentation types reflects 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).

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); the gills and tails of (Wernerburg, 1991, 2002; Wernerburg, Ronchi & Schneider, 2007);

and the plasticity of plagiosaurid *Gerrothorax* (Schoch & Witzmann, 2012; Sanchez & Schoch, 2013). Polyphenism (environmentally controlled polymorphism) exist 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) morphology of femora (Konietzko-Meier & Klein, 2013

New facts about metoposaurids from Krasiejów show that they were not fully aquatic animals. Sutures in the skull of *Metoposaurus* show that it was capable to bite prey (Gruntmejer, Konietzko-Meier & Bodzioch, 2016), which suggests semi-aquatic lifestyle.

The described diversity is consistent with the experiment of Schoch (1995) and the results of Wernerburg (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) suggests that the ontogeny of specimens assign to *Metoposaurus krasiejowensis* could have proceeded via a different growth rate and time span of metamorphosis, caused by differing 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, like in *Micromelerpeton* from Germany, where smaller specimens represent an unstable lake environment (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; Wernerburg, 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'; Wernerburg, 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 morphology of ornamentation in one population (or part of the population, when weather conditions favours 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 large stable ones (Szulc, 2005; 2007; Gruszka & Zieliński, 2008; Szulc, Racki & Jewuła, 2015). Small reservoirs (and potentially higher temperature) or periodic rivers forced earlier metamorphosis, dwelling on land, or migration between lakes and watercourses. On the other hand, large lakes or the proximity of a large reservoir enabled the development of a fully aquatic population (Szulc, 2005).

More aquatic population would have lived at 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 character of specimens means that two population not interbreed with each other. More terrestrial population probably live at the site, where environment resembles modern Gilgai relief of Texas or Australia (Szulc et al., 2015) while more aquatic populations live in some distance in larger reservoir(s) (Szulc, 2005; Konieczna, Bełka & Dopieralska, 2015). The other possibility is partially neotenic population, where remains of aquatic (paedomorphic) and terrestrial (metamorphic) individuals were transported to the site.

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

- enough room for numerous large specimens;
- shelter from mainland carnivores;
- stable, invariable conditions;
- potentially lower temperatures.

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. Distinguishing more-aquatic and more-terrestrial ecotypes does not mean that the metoposaurids assigned to T2 (Tc2, Ts2) were animals that moved efficiently on land. (Modern salamanders described as belonging to a 'stream' ecotype may migrate between watercourses on a large scale by pond-hopping.) 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 presented herein SEM photographs 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 character of 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 cannot be excluded, the most probable explanation for described variation is ecological difference between two populations separated geographically as stated by Witzmann et al. (2010); expanded herein or the ecological difference between two morphs of facultatively neotenic population. Described ornamentation types within one semi-aquatic species possess characteristic of either more-terrestrial or more-aquatic taxa .

Assuming this the more-terrestrial or 'stream-type' form can be distinguished by 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 increased 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 live even at the Variscan Upland (according to Konieczna, Belka & Dopieralska, 2015 isotope analysis). One population with aquatic (paedomorphic) and terrestrial (metamorphic) individuals is also possible.

The isotopic (or REE) analysis in the future may confirm the most probable explanation for metoposaurid ornamentation diversity and 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 (geometrics morphometrics), possibly in all Metoposauridae family.

Acknowledgements