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, and can thus be used in modern and fossil environmental analysis.
Methods. To analyse the 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 (grooves, ridges, tubercules, etc.) 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 were found, indicating either taxonomical, ecological, individual, or ontogenetic variation or sexual dimorphism.
Discussion. Analogies with modern Anura and Urodela and previous studies on Temnospondyli amphibians and the geology of the Krasiejów site suggest that the most probable explanation for differences in ornamentation between Metoposaurus individuals is the ecological variation between populations of different environments.

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 and Sulej, 2007, 2016; Brussate et al., 2009; Piechowski and 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 (Bodzioch and Kowal-Linka, 2012), along with the age of bone accumulations in Krasiejów (Racki and Szulc, 2015; Szulc, Racki and Jewuła, 2015), are being reinterpreted. 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, interclavicles, and skull bones, in order to examine its variation statistically and to test whether or not it is the same in all specimens. A thorough probe of skeletal elements from one site shows that diversification is not random.

MATERIAL AND METHODS

The size, number, shape, placement, and characteristics of the ornamentation elements of metoposaurid dermal bones – clavicles, interclavicles, and 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 and Sulej; 2007; Norian, according to Szulc, 2005; 2007; Szulc, Racki and Jewuła, 2015) deposits can be divided into three units (e.g. Gruszka and 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 and Kowal-Linka, 2012), is especially abundant in fossils, including *Metoposaurus krasiejowensis*. To test the predicted diversity of the ornamentation of dermal bones of metoposaurids from Krasiejów, 25 clavicles (UOPB1152–1176), 16 skulls (working numbers counting from the excavation site side: UO/JP01–20), and several interclavicles (UOBS00656, 02488, 02452, 02480, 02465) were analysed in detail (Tables 1–3). Morphometric measurments for skulls were also made (Table 4). The clavicles and interclavicles were excavated during excavation procedures at the site 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).

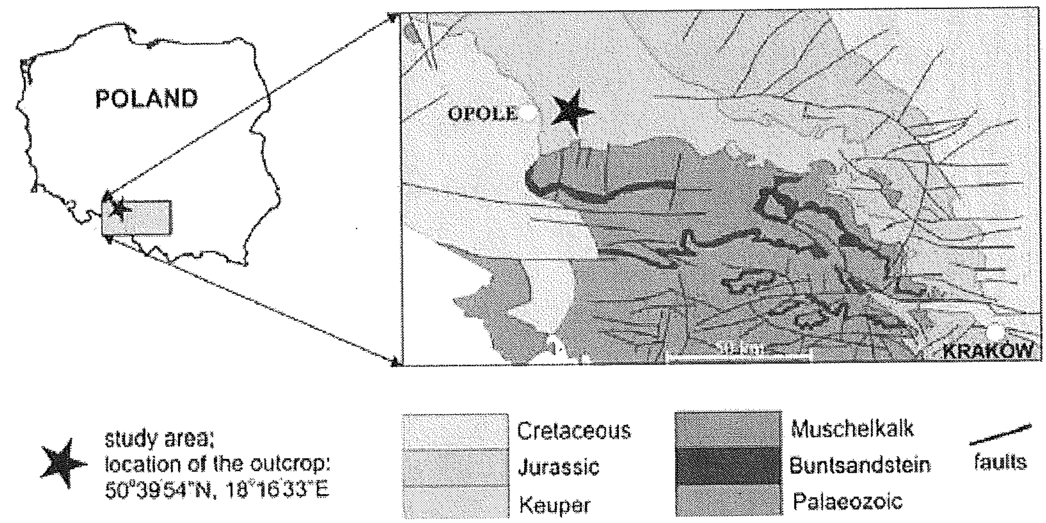

Figure 1. Localization and geology of Krasiejów (Bodzioch and Kowal-Linka, 2012).

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 as well in interclavicles, which were analysed at the Opole University where they are held. 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. The possible relative individual ages of the clavicle specimens were determined using the method presented 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. The oldest specimens possessed many well-developed partition walls between radial ridges (Fig. 2). Principal Components Analysis (PCA) was conducted using PAST. PCA, one of several statistical methods for factor analysis, can be used for nominal and countable data. A set of data consisting of N observations, where each observation includes K variables, can be interpreted as a cloud of N points in a K-dimensional space. PCA is often used to reduce the size of a statistical data set because it enables comparison of large data sets with multiple variables, such as the data obtained in the description of temnospondyli dermal bone ornamentation. Similar results (points in the diagram) are connected via convex hulls into subsets. In the presented analysis, PCA enables the comparison of the general characteristics of ornamentation of many skeletal elements as described by many variables on a single plot in order to distinguish some subsets within metoposaurids from Krasiejów or to establish a lack of variation (Krzanowski, 2000).

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 (T1 and T2). **Type 1** is characterised by more regular ornamentation of 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). **Type 2** 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, independent of their size or age; the anterior process is usually round and expanded (Fig. 2).

The distribution of certain characteristics according to age (ontogenetic stage, Zalecka, 2012) or type assignment is presented on figures 3–7. The charts show that the described morphological types are distinguishable, but independent of supposed individual age (ontogeny).

The Principal Component Analysis Charts presented below were created for a correlation matrix following transformation of the data using the equation B = (A – mean)/standard deviation, where B is the final value used for plotting the chart and A is the value before transformation. Untransformed data gave slightly different results, but points could be grouped in a similar way. For nominal data, PC1 represents 49.41percent and PC2 19.91percent of the variation. Eigenvalues are 7.91 and 3.19. For countable data (number of polygons, ridges, polygon area surface, ratio of pentagons to hexagons), PC1 represents 40.18percent PC2 25.92percent, and PC3 21.89percent of the variation. These values are presented below in the form of scree plots, illustrating the importance of eigenvalues of particular components. PC1 and PC2, for nominal data, and PC1, PC2, and PC3, for countable data, represent a majority of the variation (Fig. 8).

Principal component analysis, as presented in the charts of several countable features (Figs. 3–7), shows that the division of clavicles into two types is appropriate (Fig. 9). Negative values of PC1 can be linked with the regular, sparse sculpture of T1, while high values represent the irregular, coarse sculpture of T2. *Cyclotosaurus intermedius* and *Metoposaurus algarvensis* show further separation from both *Metoposaurus krasiejowensis* types. Points that were not included in convex hulls in the PCA charts represent clavicles with a great deal of data missing (UOPB1166–72) (Fig. 9).

Micro/nanoscale Two types can also be distinguished according to the micromorphology of the ornamentation ridges. Clavicles assigned to type 1 do not possess striations (or striations, if present, are barely visible and sparse) and possess a small number of small capillary foramina at the slopes of the ridges (less than 7 per 100 um2). 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 (Fig. 10, Table 5). Clavicles assigned to type

(2)

2 possess striations on the ridges and a greater number of small foramina (more than 7 per 100 um2). 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 (Fig. 10, Table 5).

Remarks on the dermal bones

Interclavicles Interclavicles were analysed at the Opole University warehouses where they are stored, and thus were not analysed in detail; nevertheless the two ornamentation patterns previously described in clavicles were also visible, i.e. in differentiation of polygon shape, occurrence of multipolygons, sculpture density, and polygon area borders (Table 3, Fig. 11). In addition, Dróżdżel (2009) described diversity in the general shape of the posterior edge of the clavicles, specifying a basic shape, a bell shape, and a protruding lobe shape.

Skulls Comparable differences were found in the ornamentation of *Metoposaurus krasiejowensis* skulls. Of 16 skulls (Fig. 12, Table 2):

- seven (7) possessed thick, irregular, usually small polygons, covering a large part of the surface of the skull; the radial ornamentation of these skulls was sparse in the postorbital part of the skull; multipolygons were frequent. These are features of T2 described in the clavicles.
- six (6) possessed larger, regular polygons, which covered a smaller part of the surface of the skull; radial ornamentation was common in the postorbital part of the skull (parietals, supratemporals, postfrontals, postorbitals). These are features of T1 described in the clavicles.
- three (3) skulls were largely covered with sediment, and thus cannot be attributed to either of the above types.

An important fact is that the skulls classified as T2 were relatively small (averaging 28 cm in length) in contrast to T1 skulls (averaging 35 cm in length). However, this was not a rule. Among analysed skulls were two 35 cm in length (UO/JP04, 35 cm; UO/JP18, 35.4 cm) with different ornamentation types (Fig. 12, Table 2, 4).

DISCUSSION

Possible solutions

The presented diversity in the dermal bone ornamentation of *M. krasiejowensis* may be the result of:

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 (Opole University Collection, Sulej, 2002). 3
2. **Ontogenetic diversity.** Although singular features, such as the number of offshoot radial ridges, may be connected with the age of the specimen, the method of determination of relative age (youngest, intermediate, and oldest stages) based on the ornamentation described by Zalecka (2012) shows that most of the analysed features, along with bone size, are not connected in this way. Moreover, Dróżdżel (2009) proved that the ossification centre does not change during ontogeny and that interclavicles grow proportionally (linearly). The diversity of skull sizes assigned to different types also argues against ontogenetic diversity. Relatively small skulls possess more polygonal (adult) 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 (Zalecka 2012). Polygon characteristics also indicate the adult stage in all skull specimens (Witzmann et al. 2010 – development of ornamentation).
3. **Sexual dimorphism.** The lack of differences in the morphometry of the skulls as well as a lack of differences in dentition and postcranial material contradicts this hypothesis (Kupfer, 2007). The location (under the skin and on the pectoral girdle on the ventral side of the body) and role of the ornamentation excludes the role of 'display structures' in mating rituals (Kupfer, 2007).
4. **Individual variation.** The existence of two distinct types with no intermediate forms contradicts the possibility of individual variation. This can also be seen in the PCA results.
5. **The differentiation between populations.** Caused by the different environmental and metamorphic conditions resulting from the different habitats of the population.

Metamorphosis is a hormonally induced and controlled process; thus, its results might be morphologically unequal even in closely-related taxa (Fritzsch, 1990; Norris, 1999). 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 is most likely a result of differences between ecologically separated populations (whether due to stratigraphic or geographic separation). Similar diversity was described in Temnospondyli by Witzmann et al. (2010), but stated as species-specific.

Heterochrony of Lissamphibia and Temnospondyli

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 and Babik, 2000; Emerson, 1986; Emerson, Travis and Blouin, 1988; Dubois, 1982; Eiselt and Schmidtler, 1971; Schmidt, 1938; Emerson, 1986; Emerson, Travis and Blouin, 1988) and the morphology of extinct temnospondyls: the ontogenetic rate and dentition of Apaeton (Schoch, 1995); the size of Micromelerpeton (Boy, 2005; Boy and Suess, 2000; Schoch, 2010); the morphology of Sclerocephalus (Schoch, 2010); the gills and tails of (Wernerburg, 1991, 2002; Wernerburg, Ronchi and Schneider, 2007); and the plasticity of branchiosaurids Gerrothorax (Schoch and Witzmann, 2012; Sanchez and Schoch, 2013). Dimorphism in bone characteristics can be seen also in non-dermal skeletal elements from Krasiejów. Two types connected with growth trajectory were seen in histological observations of metoposaur humeri (Teschner and Konietzko-Meier, 2015), morphology of femora (Konietzko-Meier and Klein, 2013), and fossilisation characteristics, e.g. mineral infillings in bones (Bodzioch and Kowal-Linka, 2012; Bodzioch, 2015) (Fig. 13). New facts about metoposauroids from Krasiejów show that they were not fully aquatic animals. Sutures in the skull of *Metoposaurus* show that it was capable of hunting on land (Gruntmejer, 2016).

Ornamentation and lifestyle

Material diversity is consistent with the experiment of Schoch (1995) and the results of Wernerburg (2002) and Schoch (2010). One of the metoposaurus types from Krasiejów thus represents a more terrestrial form (or one associated with the more variable and unstable environment of a river or a small lake), while the other represents forms more closely related to water (e.g. a large lake habitat). The adaptations in T2 favouring a more terrestrial lifestyle are:

1. The increased mechanical strength of the bones (Rinehart and Lucas, 2013) (coarser, denser, irregular sculpture, thicker clavicles);
2. Protection for a greater number of blood vessels, improving thermoregulation (Gadek, 2012) (denser sculpture, more numerous polygons and radial rows, more numerous microforamina);
3. Stronger integration of bone and skin, which is thicker in terrestrial amphibians and exfoliates (Zug, 1993; Schoch, 2001) (coarser, denser sculpture, microstriations);
4. Stronger connection of the pectoral girdle elements and, potentially, limbs (expanded anterior projection of the clavicle). More terrestrial character of one of the population can be proved also by:
5. The length of limb bones not correlated with individual age (Teschner and Konietzko-Meier, 2015) or a slender or robust femur (Konietzko-Meier and Klein, 2013); 10percent elongation of limbs in Anura distinctly increases migration capabilities (Pogodziński, 2015; personal communication);
6. Barite in the pores (Bodzioch and Kowal-Linka, 2012).

7. Histological structure –improved vascularization of the upper cortex.

The dimorphic character of the dermal bones described herein and the two growth patterns of long bones (humeri) discovered by Teschner and Konietzko-Meier (2015) 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 (M1/M2 – 44percent/56percent for clavicles and 53percent/47percent for skulls) suggests stable populations. Apart from dermal bone ornamentation, the degree of ossification and variation in skull sizes divides metoposaurids into two groups. Smaller skulls in the more terrestrial type, as in Micromelerpeton from Germany, represent an unstable lake environment (Boy and Suess, 2000). The second type 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 and 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 and Sulej, 2007; Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012). Differences in dermal bone ornamentation constitute an adaptative answer to changes in the environment over time or to geographical differentiation of habitats. Rapid changes in the morphology of ornamentation in one population 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 and Collins, 1973) (T1 skulls are usually larger than T2 skulls). Prey abundance might exert some influence as well (Motyl, 2008), but probably not as much (Blouin and 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 and Zieliński, 2008; Szulc, Racki and 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). As already mentioned, ecomorphs may also reflect changes over time. A primary large reservoir in which an aquatic population lives (Dzik and Sulej, 2007) dries out slowly, inducing gradual changes in the amphibian population from aquatic ecomorphs to more terrestrial ones. Metoposaurids adapted to unstable conditions; however, they still needed water for reproduction and to prevent hyperthermia. When a reservoir finally dried out (barite, carbonate concretes; Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012) amphibians hibernated in the sediment to survive the drought period (Konietzko-Meier and Sander, 2013). 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). Large reservoirs, stable over long periods of time, enable the development of a fully aquatic ecotype (T1), reducing the need to dwell on land by virtue of providing:

- Enough room for numerous large specimens;;
- Shelter the mainland carnivores;
- Stable, invariable conditions;
- Potentially lower temperature.

These conditions may have even contributed to the formation of a neotenic population (Duellman and Trueb, 1986; Safi et al., 2004; Frobisch and 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 ecotype

1. 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 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). One argument for the differentiation of types into a stream ecotype and a pond ecotype might be the ornamentation of a small metoposaurid skull from north America: TTUP 9216 (76 mm in length) from mudstone deposits (described as flash-flood by Chatterjee, 1986) in Garza County in Texas, which possesses some radial ornaments in the posterior part of the skull. Another skull, UCMP 82/39/37 (80 mm in length) from the river deposits of Lacey Point in Petrified Forest National Park, probably does not possess these ornaments (partially destroyed specimen). The ornamentation of clavicles and the degree of ossification enables us to plot hypothetical ontogentic curves for the described eco(morpho)types (Fig. 14).

Ornament function

According to the described observations, it is possible to introduce an argument about the function of temnospondyl ornamentation into the discussion. Blood vessels leave marks on the bone surface; the vascular surface appears first in the ontogeny, and thus participates in the shape of the bone. Blood vessels are bypassed or built over; canals, cavities, and foramina appear (Krysiak et al., 2011). Ornamentation is strongly connected to vascularity. The orientation of sculptural elements is the same as the orientation of blood vessels inside the bone and on its surface. There are several hypotheses as to the function of the ornamentation, which may have been:

1. Mechanical strenghtening of the bone (Coldiron, 1974);
2. Water-loss reduction (Seibert et al., 1974);
3. Integration of the bone and skin (Romer, 1947; Bossy and Milner, 1998);
4. Improvement of dermal respiration (Bystrow, 1974);
5. Thermoregulation (Seidel, 1979; Grigg and Seebacher, 2001);
6. Acting as a metamorphosis marker (Boy and Sues, 2000);
7. Buffering of acidosis and lactic acid build-up in tissues due to anaerobic activity (Janis et al., 2012).

The least plausible are the hypotheses connected with water-loss reduction (especially in highly aquatic species) and improvement in dermal respiration (vessels and foramina are numerous, but the volume-to-surface ratio of the animal's body contradicts this hypothesis; Rinehart and Lucas, 2013). Ornamentation without doubt strengthens the bone mechanically (calculations of Rinehart and Lucas, 2013, but the orientation of the sculptural elements is correlated not with the direction of stress, but with blood vessel orientation) and can be considered as the metamorphosis marker (appearance of polygonal structure); however, these are probably not the most important factors. Ornamentation increases the surface area of the bone (Rinehart and 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 (Gadek, 2012). The microstructural observations presented herein support these two hypotheses. 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.

CONCLUSIONS

The diversity of metoposaurid material from the 'Trias' site at Krasiejów (SW Poland) includes the character of ornamentation of the pectoral girdle (clavicles) and skulls of metoposaurs. Similar (but more general) 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). Differentiated types possess ornamentation characteristic of either more-terrestrial or more-aquatic taxa, but within one semi-aquatic species. 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). Populations could have been separated geographically (different sedimentary traces) or, less probably, stratigraphically, with gradual changes (singular deflections from the typical character of T2) over time along with changes of environment. Rapid changes in ecology and morphology were possible because they were induced by hormonally controlled metamorphosis. 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 and Zieliński (2008), Bodzioch and Kowal-Linka (2012), and Szulc, Racki and Jewuła (2015). The palaeoenvironment of the site (Szulc, 2005; 2007; Szulc, Racki and 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 and Dopieralska, 2015 isotope analysis). The characteristics of ornamentation and microstructure also enable us to suggest that the main functions of the sculpture were thermoregulation and integration of skin and bone.

REFERENCES

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 paläoherpetologie, 1. München: 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 (?hochstes Karbon-Perm). 1. *Sclerocephalus*. – Paläontologische Zeitschrift, 62: 107–132.

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

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